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Taxonomic studies of *Glochidion* (Phyllanthaceae) from the Indo-China Peninsula (II): The identities of *G. anamiticum* and *G. annamense*

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Abstract

The names *Glochidion anamiticum* (Kuntze) Kuntze ex Merrill and *G. annamense* Beille were previously reduced to synonyms of *G. eriocarpum* Champ. ex Benth. However, literature examination and morphological comparison suggest that *G. annamense* is conspecific with *G. anamiticum* and the species can be readily distinguished from *G. eriocarpum* by its styles connate into a long cylindric column and up to 3 mm long, ovaries usually 3-locular, stigma usually 3-lobed, capsules pubescent and usually 6-grooved, persistent styles 3–4 mm long. Thus, the specific status of *G. anamiticum* is here reinstated and G. *annamense* is treated as its synonym.

Keywords

Glochidion, Phyllanthaceae, Taxonomy, Vietnam

Introduction

Glochidion J. R. Forster & G. Forster is a large genus within the tribe Phyllantheae Dumortier, family Phyllanthaceae Martinov (Webster 2014, APG 2016). It consists of over 300 species mainly distributed in the Indo-Pacific region, east to southeast Polynesia and south into Australia (Webster 2014, Yao and Zhang 2016). The genus can be distinguished from all the other genera in the tribe by its usually unlobed styles, apiculate anthers and usually fleshy seed coat (Webster 2014).

Molecular phylogenetic studies revealed that *Glochidion*, together with *Breynia* J. R. Forster & G. Forster, *Phyllanthodendron* Hemsl. and *Sauropus* Blume, were all deeply embedded within *Phyllanthus* L. s. str. (Hoffmann et al. 2006, Kathriarachchi et al. 2006). So, some authors suggested the merger of these genera with *Phyllanthus* and accepted the broad concept of *Phyllanthus* s. l. (including *Breynia*, *Glochidion*, *Phyllanthodendron* and *Sauropus*) as a super-genus that includes over 1,200 species (Hoffmann et al. 2006). However, Pruesapan et al. (2012) suggested that the reinstatement of *Breynia*, *Glochidion*, *Phyllanthodendron* and *Sauropus*, as well as the disintegration of the paraphyletic *Phyllanthus* s. str. (over 800 species) into smaller genera, seems to be more reasonable, because these groups can be distinguished easily from each other in morphology and *Phyllanthus* s. str. is actually a large and morphologically heterogeneous genus with wide distribution areas. The latter suggestion is further supported by morphological (van Welzen et al. 2014), palynological (Yao and Zhang 2016) and wood anatomical (Jangid and Gupta 2016) studies. Thus, the acceptance of the generic status of *Glochidion* is widely adopted in most recent literature (e.g. van Welzen et al. 2014, Webster 2014, Duocet Group 2016 onwards, Kato and Kawakita 2017).

The species *Glochidion anamiticum* (Kuntze) Kuntze ex Merrill was originally described by Kuntze (1891) in the genus *Diasperus* L. ex Kuntze based on one collection (*O. Kuntze 3798*) from Vietnam and *Glochidion annamense* Beill was described by Beille (1927) based on five collections (*F. Evrard 233*, *C. Gaudichaud 161*, *M. Krempf 1567*, *E. Poilane 7838* and *E. Poilane 10022*) from Vietnam, too. The latter was soon reduced to the synonymy of *G. anamiticum* (Merrill 1936). In the taxonomic study of the Thai Euphorbiaceae, Airy Shaw (1972) provisionally placed both names under *G. eriocarpum* Champ. ex Benth., expressing uncertainty by question marks and this questionable treatment was directly followed by van Welzen (2007) in Flora of Thailand. Subsequent taxonomists accepted Airy Shaw's proposal to treat G. anamiticum and G. *annamense* as synonyms of *G. eriocarpum* (Govaerts et al. 2000, Li and Gilbert 2008, The Plant List 2013 onwards, Govaerts et al. 2018). However, *G. annamense* was recognised as a separate species by Nguyen (2007) when treating the Vietnamese Euphorbiaceae, but *G. anamiticum* was not considered. In our comprehensive taxonomic studies of *Glochidion*, we found that *G. anamiticum* and *G. annamense* represent the same species, but this species is clearly different from *G. eriocarpum* in morphology. We therefore propose to reinstate the specific status of *G. anamiticum* and treat *G. annamense* as a synonym of *G. anamiticum*.

Material and methods

Specimens of *Glochidion* deposited in the herbaria HN, IBSC, K, KUN, NY, P and PE were studied carefully in the present study and field investigations of *G. anamiticum* and *G. eriocarpum* were carried out in recent years. Morphological characters of relevant species were also photographed and some of them were measured. Herbarium abbreviations cited here follow the Index Herbariorum (Thiers 2018 onwards).

Results and discussions

Glochidion anamiticum (Figures 1A and D) and *G. annamense* (Figure 1B) represent the same species, which is similar to *G. eriocarpum* (Figures 1C and E) in habit to some extent. However, the Vietnamese endemic species *G. anamiticum* is morphologically distinct and can be readily distinguished from *G. eriocarpum* (Table 1) by its stipules triangular to narrowly triangular and ca. 1−1.5 mm long (Figure 2A) (vs. narrowly triangular to linear, 1−4 mm long), sepals of female flowers ovate-triangular to narrowly triangular and pubescent outside (Figures 2A and C) (vs. oblong and villous outside; Figures 2B and D), styles connate into a long cylindrical column up to 3 mm long (Figures 2A and C) (vs. a cylindrical column 1−1.5 mm long; Figure 2B), ovaries usually 3-locular (vs. usually 4−5-locular), stigma usually 3-lobed (Figure 2A) (vs. usually 4−5-lobed; Figure 2B), capsules pubescent and usually 6-grooved (Figures 2E and F) (vs. villous and usually 8−10-grooved; Figure 2G), persistent style cylindrical column 3−4 mm long (Figures 2E and F) (vs. shortly column-shaped to subconical, less than 1 mm long; Figure 2G). Thus, our results suggest that it may be best to treat *G. anamiticum* and *G. eriocarpum* as separate species. The following taxonomic treatment is therefore necessary.

Taxonomic treatment

***Glochidion anamiticum* (Kuntze) Kuntze ex Merrill, Brittonia 2: 195. 1936**
Figures 1A, B, D, 2A, C, E, F

Basionym. *Diasperus anamiticus* Kuntze, Revis. Gen. Pl. 2: 601. 1891.

Type. Vietnam. Annam, Turong, March 1875, *O. Kuntze 3798* (lectotype designated by Merrill (1936: 195): NY-00263420, photo!; isolectotype: K-001081193, photo!).

Glochidion annamense Beille (1927, p. 627). Type: Vietnam. Annam, Lien-chien, 25 August 1923, *E. Poilane 7838* (lectotype designated by Nguyen (2007): HM; isolectotypes: K-001081192, P-00379159, P-00379160, photos!). Remaining syntypes: Vietnam. Annam, Trai-ca, province, Phanrang, 9 March 1924, *E. Poilane 10022* (P-00379161, photo!); Tourane, January 1837, *C. Gaudichaud 161* (P-00379151, photo!); Nha-trang, *M. Krempf 1567* (P-00379152, photo!); Dalat réserve du Calmy, 24 October 1920, *F. Evrard 233* (P-00379150, photo!).

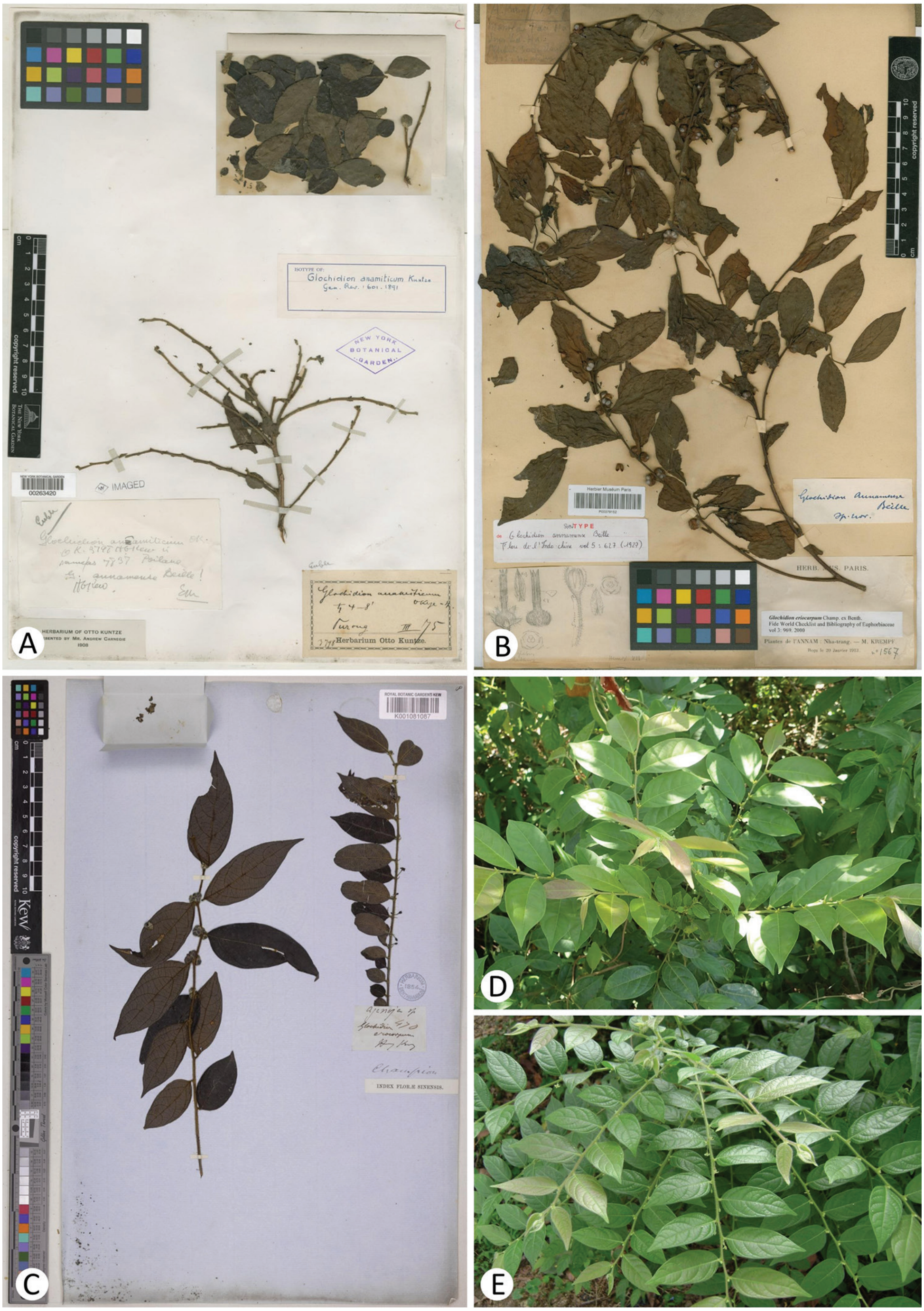

Figure 1. Type (**A–C**) and field images (**D–E**) of *Glochidion* species. **A** Lectotype of *G. anamiticum* (Kuntze) Kuntze ex Merrill (*O. Kuntze 3798*, NY-00263420) **B** Syntype of *G. annamense* Beille (*M. Krempf 1567*, P-00379152) **C** Type of *G. eriocarpum* Champ. ex Benth. (*J.G. Champion 470*, K-001081087) **D** *G. anamiticum*; E, *G. eriocarpum*.

Shrubs, 1–3 m tall, monoecious; branchlets usually pubescent; leaf blade membranous, 6–8 × 2.5–3 cm, lanceolate, oblong to ovate, sometimes asymmetrical, base acute to round, apex acuminate, adaxially dark brown or blackish, pubescent on the median rib, abaxially light brown, pubescent; lateral veins 6–8 pairs, elevated abaxially; petiole ca. 2–3 mm long, pubescent; stipules triangular to narrowly triangular, 1–1.5 mm long. Male flowers: pedicels ca. 10 mm long, pubescent; sepals 6, oblong to ovate, hairy outside, glabrous inside; stamens 3, connate, surmounted by a conical prolongation. Female flowers: in axillary clusters, subsessile; sepals 6, ca. 1.2 mm long, ovate-triangular or narrowly triangular, hairy outside, glabrous inside; ovary depressed globose, 3 (rarely 4)-locular, pubescent; style cylindrical column, long exceeding the sepals, 2–3 mm long, hairy in the lower quarter, glabrous in the upper part, 3 (rarely 4)-lobed at the top. Capsule depressed globose, 6 (rarely 8)-grooved, 7–9 mm in diameter, ca. 5 mm high, very briefly hairy; persistent style a long cylindrical column up 3–4 mm long; fruit pedicels stout, 3–4 mm long, pubescent.

Distribution and habitat. *Glochidion anamiticum* is endemic to Vietnam, mostly from Da Nang to Ninh Thuan (Nguyen 2007).

Notes. In the monograph *Revisio Generum Plantarum*, Kuntze (1891) transferred hundreds of *Glochidion* and *Phyllanthus* species into the genus *Diasperus* L. ex Kuntze and he also described many new species, including *Diasperus anamiticus* Kuntze which was based on one of Kuntze's collections (*O. Kuntze 3798*) from Vietnam. At the same time, however, a specific name (*Glochidion anamiticum*), under the generic name *Glochidion,* was also suggested for *D. anamiticus*, but it was listed as a synonym of the new species. According to Art. 34.1 of the ICN (McNeill et al. 2012), the name *G. anamiticum* Kuntze is invalid because it was not accepted by the author and just cited as a synonym of *Diasperus anamiticus*. On the other hand, many of the new species described by Kuntze (1891) were overlooked for a long time, until they were re-evaluated by Merrill (1936) and then the species *Glochidion anamiticum* was accepted formally as a member of *Glochidion* for the first time. So, the author's attribution of the species should be *Glochidion anamiticum* (Kuntze) Kuntze ex Merrill.

In his commentary on Loureiro's (1790) new species described from southern Vietnam, Merrill (1935) transferred the species *Nymphanthus pilosus* Lour. into *Glochidion* and reduced *Glochidion annamense* to a synonym of his new combination *Glochidion pilosum* (Lour.) Merr., although the type of *G. pilosum* was not examined in his study. Merrill's (1935) taxonomic treatment of *Glochidion annamense* was followed by Ho (2003) in An Illustrated Flora of Vietnam. However, as noted by Loureiro (1790) in the protologue of *Nymphanthus pilosus*, the species was characterised by pinnate leaves and bacciformis fruits, which are much different from those of the genus *Glochidion* (characterised by alternate and distichous leaves, fruits capsule), but consistent with those of *Emblica* Gaertn. or *Phyllanthus* sect. *Emblica*, thus the species also had been transferred into these two genera and named as *Emblica pilosa* (Lour.) Spreng. or *Phyllanthus pilosus* (Lour.) Müll. Arg., respectively. In the following year, however, Merrill (1936) treated the name *Glochidion annamense* as a synonym of *G. anamiticum,* based on the study of type specimens, but the name *G. pilosum* was not considered.

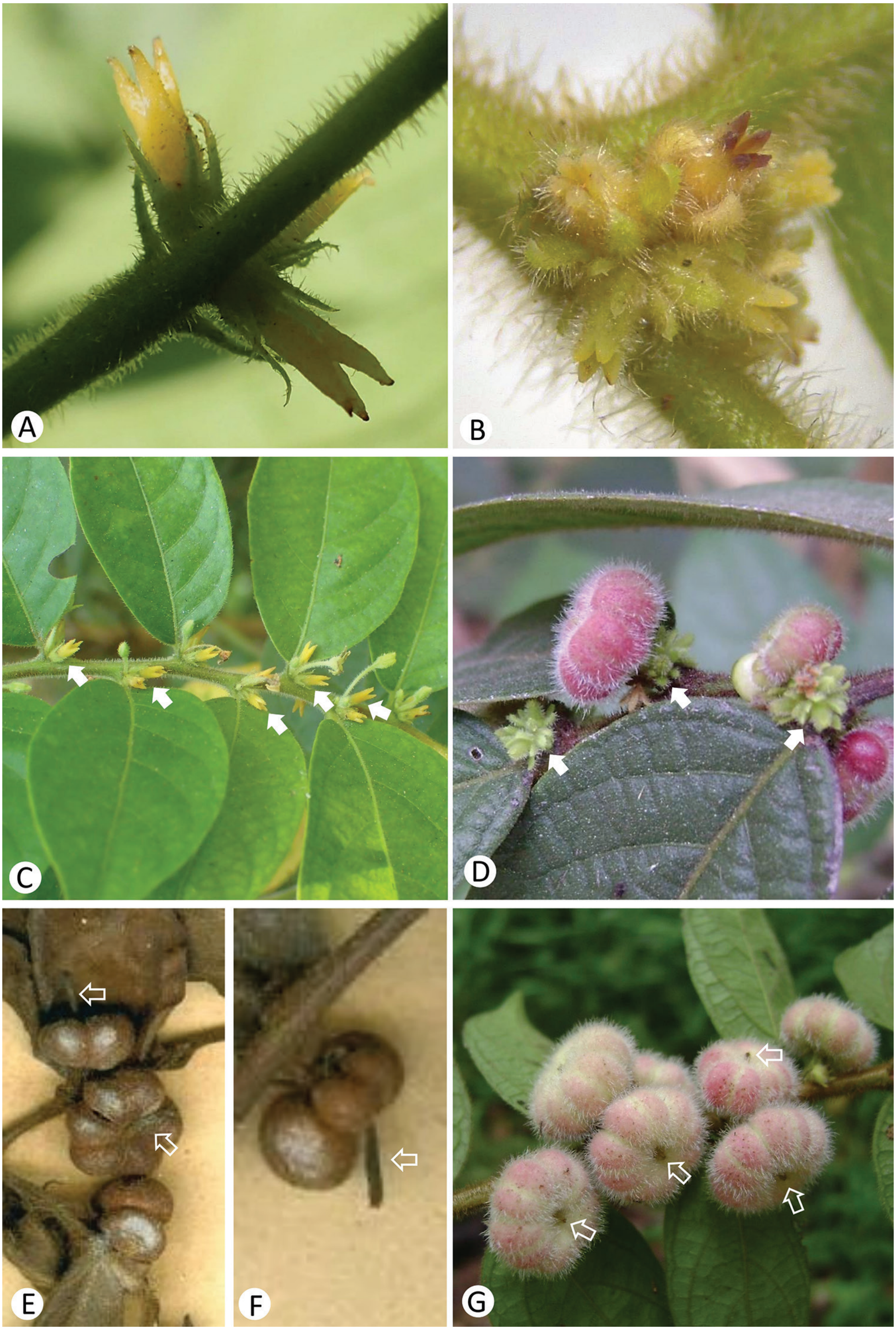

Figure 2. Morphological comparisons between *Glochidion anamiticum* (Kuntze) Kuntze ex Merrill (**A, C, E, F**) and *G. eriocarpum* Champ. ex Benth. (**B, D, G**). **A–D** Female flower **D–G** Fruit. The female flowers and persistent styles in the fruits are shown by the solid arrowhead and hollow arrowhead, respectively.

Table 1. Morphological comparisons between *Glochidion anamiticum* (Kuntze) Kuntze ex Merrill and *G. eriocarpum* Champ. ex Benth.

Traits/Species	*Glochidion anamiticum*	*G. eriocarpum*
Stipule	Triangular to narrowly triangular; ca. 1–1.5 mm long;	Narrowly triangular to linear; 1–4 mm long;
Sepals of female flower	Ovate-triangular to narrowly triangular; pubescent outside;	Oblong; villous outside;
Style	Cylindrical column, long exceeding the sepals, 2–3 mm long;	Cylindrical column, slightly exceeding the sepals, 1–1.5 mm long;
Stigma	Deeply 3(4)-lobed;	Deeply 4–5-lobed;
Ovary	Pubescent; 3(4)-locular;	Villous; 4–5-locular;
Capsule	Pubescent; 7–9 mm in diameter; deeply 6(8)-grooved;	Villous; 8–10 mm in diameter; deeply 8–10-grooved;
Persistent style	Cylindrical column; up to 4 mm long;	Shortly column-shaped to subconical; less than 1 mm long.

Morphological comparisons between *Glochidion anamiticum* and *G. eriocarpum* can be seen in Table 1 and Figures 1, 2. The most noticeable traits of *G. anamiticum* are its long style (up to 3 mm long) in the female flowers and long persistent style (up to 4 mm long) in the fruits.

Additional specimens examined. *Glochidion anamiticum:* VIETNAM. Detailed locality unknown, 7 April 1978, *Nhan 294* (HN); Annam, Hué, Flower pale yellow; Near river, 11 March 1927, *R.W. Squires 178* (P-00379167); Arbre Broyé (Tuyen Duc), altitude 1500 m, 29 March 1953, *M. Schmid s.n.* (P-00509785); Dalat, ravin au S. du Langbian Palace, 17 May 1924, *F. Evrard 910* (P-00379154); Dalat, lac des Soupirs, altitude 1500 m, 12 January 1964, *M. Schmid s.n.* (P-00509783); Dalat, ravin derrière la gendarmerie, 2 October 1924, *F. Evrard 1293* (P-00379155); Dalat, ravin au Sud du Langbian Palace, 14 November 1924, F. Evrard 1788 (P-00379156); Région de Dalat, September 1952, *M. Schmid 1288* (P-00509784); Cochinchine, prov. de Bienhoa, 11 October 1931, *E. Poilane 19574* (P-00379164); Env. de Huê, prov. Thua Thiên-Huê, 23 December 1943, *J.E. Vidal 917a* (P-00476551). Hue, Bach Ma National Park, 3 August 2018, *Y.H. Wu 17126* (IBSC). ***Glochidion eriocarpum:*** CHINA. Guangdong Province, Jiangmen, 21 October 2013, *L.X. Zhou 11542* (KUN); Guangdong Province, Yangchun, Ehuangzhang Nature Reserve, 14 November 2008, *G. Yao 018* (IBSC); Guangdong Province, Zhaoqing, Dinghushan Nature Reserve, 17 December 2008, *G. Yao 058* (IBSC); Guangxi Province, Rongshui, 24 October 2008, *G. Yao 08-008* (IBSC); Hainan Province, Xinglong, 6 March 2009, *G. Yao 101* (IBSC); Hongkong, J.G. Champion 470 (K); Yunan Province, Puer, 1 April 2003, *Y. Chen s.n.* (KUN); Yunan Province, Xishuangbanna, 29 July 1977, *G.D. Tao 15679* (KUN); VIETNAM. Annam, Environs du poste forestier de Bang Trê Lat sur sông Con, prov. de Vinh, 24 July 1929, *E. Poilane 16419* (P-00379163); Hanh Hoa Province, Thach Thanh District, Cuc Phuong NP, Thanh Yenh Commune, Sanh Village, altitude 150 m, 27 February 2001, *N.M. Cuong 1320* (P-00520940); Tonkin, Binh Lei, 43 km à l'ouest de Chapa, altitude 1000–1200 m, 12 August 1926, *E. Poilane 12899* (P-00379162); Tonkin, Taai Wong Mo Shan and vicinity, Ton fa market, Ha-coi, September 1939, *W.T. Tsang 29570* (P-00379168).

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Radiation of members of the *Soroseris hookeriana* complex (Asteraceae) on the Qinghai-Tibetan Plateau and their proposed taxonomic treatment

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Abstract

The existence of intermediate types is a major obstacle that can hinder the circumscription of species. Elucidating the mechanism responsible for intermediate types is essential for achieving a reasonable taxonomical treatment. In this study, we explored the evolutionary history and taxonomic treatment of the *Soroseris hookeriana* (C.B.Clarke) Stebbins complex, which comprises six named taxa that may be taxonomically distinct and are all native to the Qingha-Tibetan Plateau (QTP). We made an investigation across the distribution range of *Soroseris* Stebbins and sampled 27 populations, mostly from the complex. Internal transcribed spacer (ITS) and two chloroplast loci were sequenced and analysed using the neighbour-joining and Bayesian inference methods. The resulting phylogenies show no well supported inconsistence in topologies, in line with the lack of incongruence detected by the length difference test. However, all the trees were largely unresolved within *S. hookeriana* complex, irrespective of the optimality criterion employed. We interpret these results as an experience of radiation, which is a common process for native genera on the QTP. Thus, we suggest that all of the morphotypes might be different forms, generated by incipient speciation due to recent explosive differentiation, possibly triggered by the drastic environmental changes of the QTP. Given their evolutionary history, we propose a pragmatic method for treating all of these species as subspecies with a total of four new combinations.

Keywords

Radiation, *Soroseris hookeriana* complex, taxonomic treatment, Asteraceae

Introduction

The description and delimitation of species in an evolutionary framework is essential for understanding patterns of biodiversity and distribution, as well as when assessing conservation strategies for natural resources (Liu 2016; Yang 2016). However, species complexes, comprising a few distinct morphotypes with a series of intermediates at the species level, are a difficult problem for taxonomists (Liu 2016). These intermediates might be derived via various mechanisms such as intraspecies variation, interspecies hybridisation, convergent evolution or radiation (Wang et al. 2004; Liu et al. 2006). Increasing studies suggest that DNA sequences can be employed to elucidate the mechanisms responsible for intermediate types (Su et al. 2015; Zheng et al. 2017).

Soroseris is a genus comprising seven species and all are endemic to the Qingha-Tibetan Plateau (QTP) according to the latest comprehensive revision (Shi and Kilian 2011). Despite its restricted distribution and the paucity of species, this genus contains two species complexes. The first referred to as the *Soroseris glomerata* (Decne.) Stebbins complex comprises *S. glomerata* and five possibly distinct species, all of which have been treated as *S. glomerata* in some studies (Stebbins 1940; Shih 1997; Shi and Kilian 2011). Two were recognised as independent species in the latest revision, i.e. *S. pumila* Stebbins and *S. depressa* (Hook. f. & Thomson) J. W. Zhang, N. Kilian & H. Sun, whereas three, i.e. *S. bellidifolia* (Hand.-Mazz.) Stebbins, *S. deasyi* Stebbins, and *S. rosularis* (Diels) Stebbins, were accepted as synonyms with a comment that it is appropriate to recognise them as subspecies, awaiting more studies on variation and distribution (Shi and Kilian 2011). Phylogenetic studies, based on either nuclear the internal transcribed spacer (ITS) or plastid regions, showed that *S. glomerata* could be resolved into at least two distantly related clades (Zhang et al. 2011), thereby implying that it may not be monophyletic.

The second species complex, referred to as the *S. hookeriana* (C.B.Clarke) Stebbins complex, comprises *S. hookeriana* and five possibly independent species, where one was accepted as *S. erysimoides* (Hand.-Mazz.) C. Shih in the latest revision, whereas the other four, i.e. *S. occidentalis* (Stebbins) Tzvelev, *S. hirsuta* (J. Anthony) C. Shih, *S. gillii* (S. Moore) Stebbins and *S. gillii* subsp. *handelii* Stebbins, were treated as synonyms of *S. hookeriana* (Shi and Kilian 2011). Several other treatments have been proposed and we listed four of them in Table 1 (Stebbins 1940; Shih 1993, 1997; Shi and Kilian 2011). These taxa have all been treated at species rank except for *S. gillii* subs. *handelii*, yet in other treatments have been treated as synonyms or subspecies, notably, under different species (Stebbins 1940; Shih 1993; Tzvelev 2007; Shi and Kilian 2011). This complicated taxonomical controversy undoubtedly reflects the difficulty in delimitating taxa within *Soroseris* in terms of their morphology.

In addition to the controversial treatments mentioned above, the circumscription of *Soroseris* is also disputed. For example, two species of *Syncalathium* Lipschitz are included in *Soroseris* in some systems (Shih 1993). Recently, a number of studies based on pollen, achene morphology, karyotypes and multiple DNA loci (Zhang et al. 2007,

Table 1. Different taxonomical treatments of the possible members of the *Soroseris hookeriana* complex. FRPS: Flora Reipublicae Popularis Sinicae; FOC: Flora of China.

Stebbins (1940)	Shih C (1993)	FRPS (1997)	FOC (2011)
S. gillii subsp. *typica*	*S. trichocarpa*	*S. gillii*	*S. hookeriana*
S. gillii subsp. *occidentalis*	*S. hirsuta*	*S. hirsuta*	*S. hookeriana*
S. gillii subsp. *hirsuta*	*S. hirsuta*	*S. hirsuta*	*S. hookeriana*
S. gillii subsp. *handelii*	*S. hirsuta*	*S. hirsuta*	*S. hookeriana*
S. hookeriana subsp. *typica*	*S. hookeriana*	*S. hookeriana*	*S. hookeriana*
S. hookeriana subsp. *erysimoides*	*S. erysimoides*	*S. erysimoides*	*S. erysimoides*
S. bellidifolia	*S. hirsuta*	*S. hirsuta*	*S. glomerata*

2013; Zhang and Sun 2011; Peng et al. 2013) have supported the circumscription of the latest revision of *Soroseris* (Shi and Kilian 2011), but there are some slight differences compared with the first revision (Stebbins1940). In morphological terms, the genus is circumscribed mainly based on a densely crowded capitula on a thick and hollow stem, with two layers of phyllaries, where the outer layer are much smaller (Stebbins 1940). Molecular phylogenetic analyses indicate that *Syncalathium* might be the sister group of *Soroseris*, in line with their similarity in morphology, such as densely crowded capitula (Zhang et al. 2011), the chromosome number and the preferred habitat in high altitude (Zhang et al. 2007; Ying and Yang 2011; Yang et al. 2017).

Previous studies have resolved the circumscription and sister (*Syncalathium*) of *Soroseris*, but the delimitation within the two species complexes remains unresolved (Zhang and Sun 2011). A major problem is the lack of samples of multiple individuals and comparisons of intra-/interspecies genetic diversity (Zhang and Sun 2011). In this study, we focused on the *S. hookeriana* complex. We sampled multiple individuals and sequenced several loci in order: (1) to clarify the mechanisms responsible for the complicated relationships in terms of morphology in this species complex; and (2) to revise the taxonomy of the *S. hookeriana* complex. We supposed that, if hybridisation was documented, the parental species and the possible cases of hybridisation could be recognised or, if radiation was indicated, the number of species within the complex could be greatly reduced.

Materials and methods

Taxon sampling

In total, from the QTP, we collected 35 individuals from 27 populations belonging to *Soroseris* and two individuals from *Syncalathium* as an outgroup, according to a previous study (Zhang et al. 2011) and all the voucher specimens were deposited in the herbarium of Lanzhou University. The samples from *Soroseris* were identified as belonging to six species, with five from the latest revision (Shi and Kilian 2011)

Table 2. Taxa, collection localities, vouchers (or the references for those downloaded from NCBI) and their GenBank accession numbers.

Taxon (FOC, 2011)	Collection locality	Latitude (°N)	Longitude (°E)	Altitude (m)	Voucher	Genbank number (ITS, *matK*, *psbA-trnH*)
S. erysimoides	Cuona, Tibet, China	27.9269	91.8789	4519	Y.-J. Wang, CN30 (LZU)	MG932859; MG946722; MG932893
	Cuona, Tibet, China	27.9269	91.8789	4519	Y.-J. Wang, CN47 (LZU)	MG932861; MG946724; MG932895
	Cuona, Tibet, China	27.9269	91.8789	4519	Y.-J. Wang, CN48 (LZU)	MG932862; MG946725; MG932896
	Cuona, Tibet, China	27.9269	91.8789	4519	Y.-J. Wang, CN49 (LZU)	MG932863; MG946726; MG932897
	Cuona, Tibet, China	27.9269	91.8789	4519	Y.-J. Wang, CN50 (LZU)	MG932864; MG946727; MG932898
	Cuona, Tibet, China	27.9269	91.8789	4519	Y.-J. Wang, CN51 (LZU)	MG932865; MG946728; MG932899
	Geermu, Qinghai, China	35.4158	96.3409	4665	Y.-J. Wang, GEM3 (LZU)	MG932858; MG946721; MG932892
	Yadong, Tibet, China	27.5518	88.9306	3059	Y.-J. Wang, YD46 (LZU)	MG932860; MG946723; MG932894
	Xingu, Sichuan, China	–	–	–	Zhang et al. 2011	HQ436213; JF956518; HQ436180
	Tibet, China	–	–	–	Zhang et al. 2011	JF978800; JF956516; JN047244
	Deqin, Yunnan, China	–	–	–	Zhang et al. 2011	HQ436212; JF956517; HQ436179
	Sichuan, China	–	–	–	Zhang et al. 2011	JF978799; JF956515; JN047243
S. hookeriana	Chayu, Tibet, China	29.3252	97.0390	4705	Y.-J. Wang, CY39 (LZU)	MG932868; MG946742; MG932910
	Chayu, Tibet, China	29.3252	97.0390	4705	Y.-J. Wang, CY53 (LZU)	MG932869; MG946743; MG932917
	Daocheng, Sichuan, China	29.2953	100.1466	4404	Y.-J. Wang, DC9 (LZU)	MG932871; MG932921; MG932921
	Kangding, Sichuan, China	29.4446	101.4339	4657	Y.-J. Wang, KD11 (LZU)	--; MG946729; MG932900
	Kangding, Sichuan, China	30.0411	101.9532	2861	J.-Q. Liu, KD54 (LZU)	MG932870; MG946732; MG932918
	Kangding, Sichuan, China	30.0411	101.9532	2861	Y.-J. Wang, KD7 (LZU)	MG932877; MG946750; MG932914
	Xiangcheng, Sichuan, China	28.9312	99.7835	2927	Y.-J. Wang, XC10 (LZU)	MG932876; MG946747; MG932915
	Xiaojin, Sichuan, China	30.5473	102.5373	4519	Y.-J. Wang, XJ4 (LZU)	MG932873; MG946739; MG932911
	Xiaojin, Sichuan, China	30.5473	102.5373	4519	Y.-J. Wang, XJ5 (LZU)	MG932874; MG946740; MG932914
	Xiaojin, Sichuan, China	30.5473	102.5373	4519	Y.-J. Wang, XJ6 (LZU)	MG932875; MG946741; MG932920
	Zhiduo, Qinghai, China	33.5845	96.3409	4689	Y.-J. Wang, ZD2 (LZU)	MG932866; MG932902; MG932902
	Sichuan, China	–	–	–	Zhang et al. 2011	HQ446097; JF956522; JN047246
	Sichuan, China	–	–	–	Zhang et al. 2011	HQ436227; JF956521; JN047245
	Kangding, Sichuan, China	–	–	–	Zhang et al. 2011	HQ436214; JF956520; HQ436181
	Cuomei, Tibet, China	28.7853	91.7549	5048	Y.-J. Wang, CN25 (LZU)	MG932883; MG946734; MG932905
	Dingri, Tibet, China	28.5755	87.1136	4305	Y.-J. Wang, DR55 (LZU)	MG932886; MG946737; MG932919

Taxon (FOC, 2011)	**Collection locality**	**Latitude (°N)**	**Longitude (°E)**	**Altitude (m)**	**Voucher**	**Genbank number (ITS, *matK*, *psbA-trnH*)**
S. hookeriana	Dangxiong, Tibet, China	29.9018	90.1370	5400	Y.-J. Wang, DX17 (LZU)	MG932882; MG946733; MG932901
	Dangxiong, Tibet, China	29.9018	90.1370	5400	Y.-J. Wang, DX43 (LZU)	MG932885; MG946736; MG932912
	Longzi, Tibet, China	28.6027	92.2142	4906	Y.-J. Wang, LZ27 (LZU)	MG932884; MG946735; MG932906
	Longzi, Tibet, China	28.6371	92.2175	5106	Y.-J. Wang, LZ52 (LZU)	MG932878; MG946749; MG932916
	Yadong, Tibet, China	27.5527	88.9315	3059	Y.-J. Wang, YD21 (LZU)	MG932867; MG946731; MG932904
	Hongshan, Yunnan, China	–	–	–	Zhang et al. 2011	HQ436218; JF956532; HQ436185
	Tibet, China	–	–	–	Zhang et al. 2011)	JF978806; JF956530; JN047250
	Longzi, Tibet, China	28.6371	92.2175	5106	Y.-J. Wang, LZ33 (LZU)	MG932872; MG946738; MG932909
	Cuona, Tibet, China	27.9269	91.8788	4519	Y.-J. Wang, CN29 (LZU)	MG932880; MG946745; MG932907
	Cuona, Tibet, China	27.8476	91.8929	4732	Y.-J. Wang, CN32 (LZU)	MG932881; MG946746; MG932908
S. glomerata	Angren, Tibet, China	29.5021	86.2770	4753	Y.-J. Wang, AR18 (LZU)	MG932887; MG946744; MG932922
	Tibet, China	–	–	–	Zhang et al. 2011	JF978802; JF956523; JN047247
	Daxueshan, Yunnan, China	–	–	–	Zhang et al. 2011	HQ436217; JF956527; HQ436184
	Deqin, Yunnan, China	–	–	–	Zhang et al. 2011	HQ436216; JF956528; HQ436183
	Tibet, China	–	–	–	Zhang et al. 2011	JF978804; JF956525; JN047248
S. teres	Yadong, Tibet, China	27.5503	88.9316	3059	Y.-J. Wang, YD44 (LZU)	MG932888; MG946752; MG932924
	Yadong, Tibet, China	27.5503	88.9316	3059	Y.-J. Wang, YD45 (LZU)	MG932889; MG946753; MG932925
S. umbrella	Zhonggashan, Yunnan, China	–	–	–	Zhang et al. 2011	HQ436197; HQ436164; HQ436131
	Hongshan, Yunnan, China	–	–	–	Zhang et al. 2011	HQ436198; HQ436165; HQ436132
Soroseris sp.	Chayu, Tibet, China	29.3252	97.0390	4705	Y.-J. Wang, CY40 (LZU)	MG932879; MG946748; MG932923
Syncalathium disciforme	Heishui, Sichuan, China	32.1326	102.3633	4016	Y.-J. Wang, HS12 (LZU)	MG932890; MG946754; MG932926
Syncalathium kawaguchii	Luozha, Tibet, China	28.2504	91.0481	4112	Y.-J. Wang, LZ24 (LZU)	MG932891; MG946755; MG932927

and one that differed from all the known species (Voucher: CY40). The members of *S. hookeriana* complex, *S. hookeriana* and *S. erysimoides*, total up to thirty individuals and they could be further sorted into at least eight morphotypes. Six of them are largely comparable to six subspecies recognised by Stebbins (Stebbins 1940), although more or less variations exist. Two of them seem to intermediate amongst different subspecies and here we named them Intermediate A and B, tentatively. A morphological comparison amongst these specimens, together with several related ones, is listed in Suppl. material 1. In addition, sequences from 17 individuals belonging to three species, including nine from the *S. hookeriana* complex and one we failed to collect, i.e. *S. umbrella* (Franch.) Stebbins, were downloaded from GenBank, which were all obtained in the study by Zhang et al. (Zhang et al. 2011). All of the samples, voucher locations and GenBank numbers used in the analysis are listed in Table 2.

DNA extraction, PCR amplification, and sequencing

Genomic DNA was extracted from dried leaves in silica gel using the CTAB method (Doyle and Dickson 1987). Three regions (*psbA-trnH*, *matK* and ITS) were amplified and sequenced with the primers from published literature (White et al. 1990; Sang et al. 1997; Ford et al. 2009). The PCR reaction mixture comprising 25 µl was prepared and amplified according to the procedure described by Wang et al. (Wang et al. 2009). The PCR products were sent to the Beijing Genomics Institute for commercial sequencing. Sequences were aligned using CLUSTALX v.2.1 (Thompson et al. 1997) with the default settings and adjusted manually with Bioedit v.7.0.5 (Hall 1999). All of the sequences were registered in GenBank (Table 2).

Data analysis

Three datasets were constructed for the ITS sequences, the combination of *psbA–trnH* and *matK* and the combination of all the three fragments. For the first two datasets, genetic distance was calculated with Mega (Tamura et al. 2013) under Kimura's two-parameter (K-2P) model (Kimura 1980). For the last one, the congruence between ITS and the other two fragments was evaluated using the incongruence length difference (ILD) test in PAUP* 4.0b10. For all the three data sets, neighbour-joining (NJ) and Bayesian inference (BI) methods were employed to reconstruct the phylogenetic relationships. The NJ trees were built using PAUP version 4b10 with K-2P model (Swofford 2003). Node support was assessed based on bootstrap percentages (BP) of 100000 replicates. BI was implemented using MrBayes on XSEDE (v3.2.6) (Ronquist et al. 2012) and the optimal models for each marker were determined according to Akaike's information criterion (Akaike 1974) using jModelTest2 on XSEDE (v2.1.6) (Darriba et al. 2012).

Results

ITS sequences

The aligned ITS dataset comprised 607 base pairs (bp) with 58 variable sites, where 36 sites were potentially parsimony informative. A total of 12 mosaic sites are detected from eight individuals, mostly with one or two. The K-2P distance, ranged from 0 to 2.4%, is 0.6% on average within the ingroup, while 0.3% on average or 1% maxi-

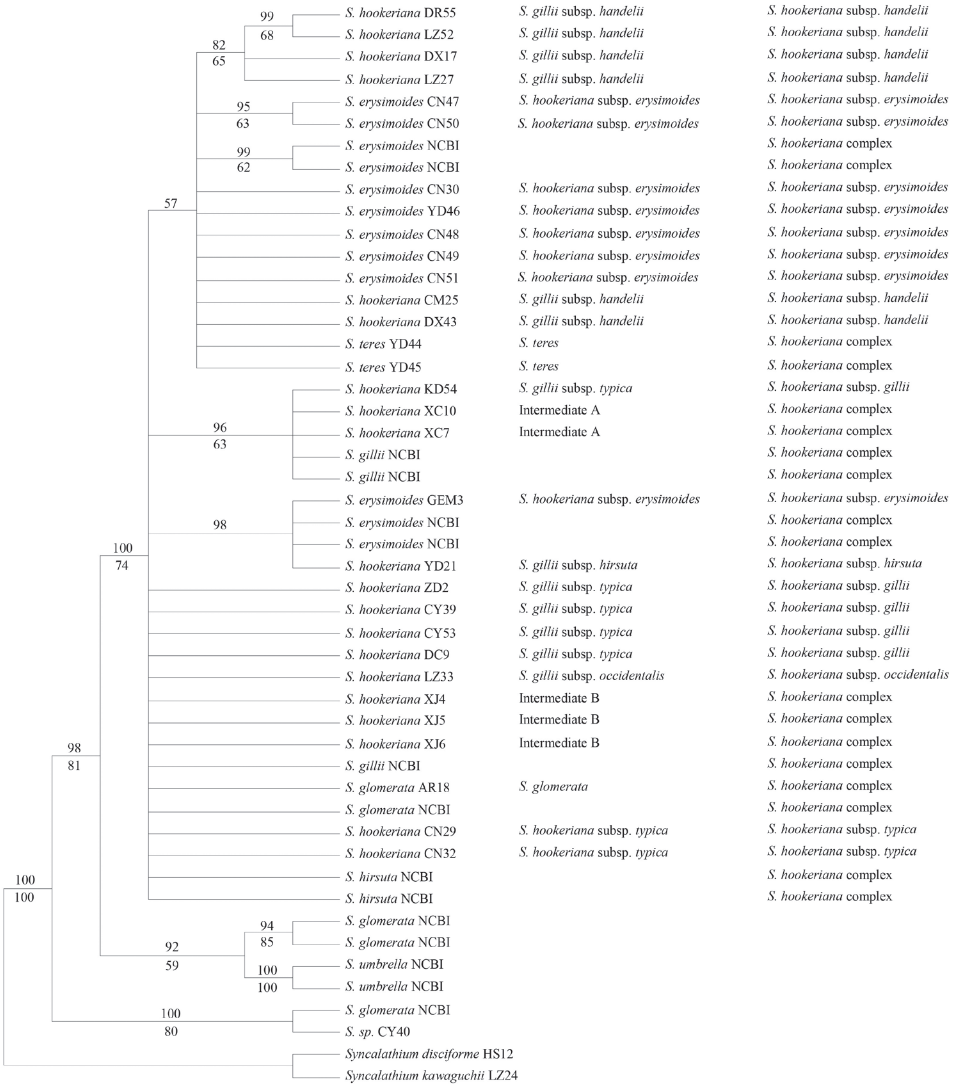

Figure 1. The 50% majority rule consensus tree derived from Bayesian inference of the nuclear internal transcribed spacer. Posterior probabilities and bootstrap percentages are indicated above and below the branches, respectively. The samples named according to FOC (2011) or NCBI, Stebbins (1940) and the present study are listed from left to right.

mally within the complex. The NJ tree was mostly congruent in terms of its topology with the 50% majority rule consensus tree derived from Bayesian analysis and the latter is shown in Fig. 1. The in-group samples were resolved into three clades. The first clade, which was a sister to the other two, comprised part of *S. glomerata* and a species that we failed to identify (BI = 100%, BP = 80%). The second clade contained two *S. glomerata* and *S. umbrella* sequences (BI = 92%, BP = 59%). The third clade

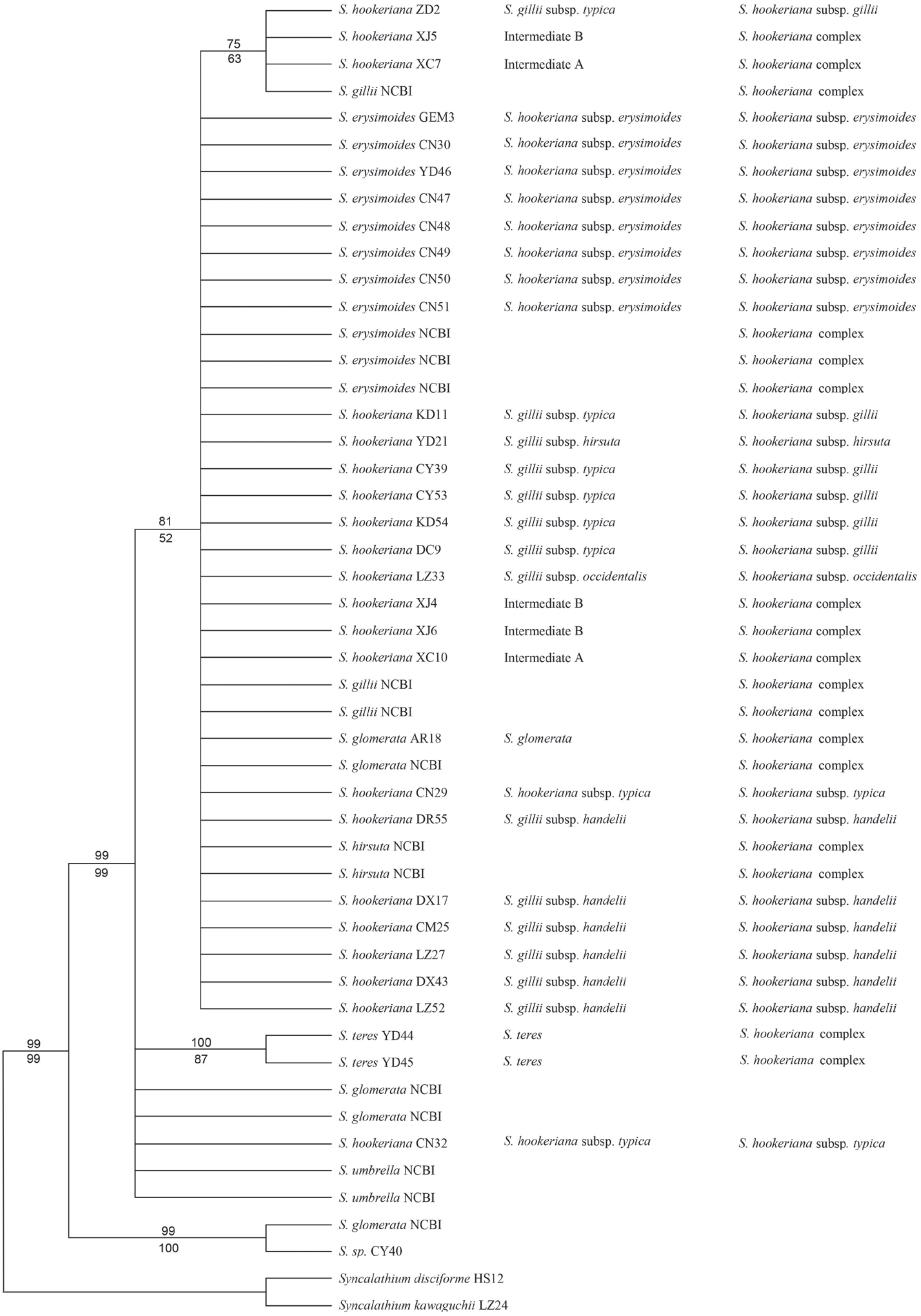

Figure 2. The 50% majority rule consensus tree derived from Bayesian inference of the combined sequences of *psbA-trnH* and *matK*. Posterior probabilities and bootstrap percentages are indicated above and below the branches, respectively. The samples named according to FOC (2011) or NCBI, Stebbins (1940) and the present study are listed from left to right.

comprised all of the others, including two *S. glomerata* individuals, two *S. teres* C. Shih individuals and all 37 from the *S. hookeriana* complex (BI = 100%, BP = 74%) but there was little resolution within this clade. Excluding *S. umbrella*, none of the species with multiple individual samples was recovered as monophyletic and *S. glomerata* samples were present in all three clades.

Combined psbA–trnH and matK sequences

The combined *psbA–trnH* and *matK* sequences measured 870 bp, where 54 nucleotide sites were variable and 23 were phylogenetically informative. The K-2P distance is estimated to be 0.2% on average and ranged from 0 to 1.8% within the ingroup, while 0.1% on average or 0.6% maximally within the complex. The NJ tree was congruent with the 50% major consensus tree obtained by BI and the latter is presented in Fig. 2. The topology recovered was very similar to that for ITS on the phylogenetic context of *S. hookeriana* complex, but two, one containing *S. umbrella* and the one containing *S. hookeriana* complex, of the three clades based on the ITS sequences, were combined as one.

Combined ITS, psbA-trnH and matK sequences

ILD test (P = 0.289000) detected no strong evidence of incongruence between the data partitions. Thus, the three fragments are combined and the resulting topologies from NJ and BI (Suppl. material 2) are concordant. Being highly similar to that from ITS, three major clades within *Soroseris* were recovered and the relationship within *S. hookeriana* complex remains largely unresolved.

Discussion

Aside from *S. umbrella*, no species were recovered in a monophyletic clade. In particular, *S. glomerata* was revealed to be present in all the three major clades (Figs 1, 2, Suppl. material 2), indicating that the circumscription of this species needed to be revised. All the members of the *S. hookeriana* complex formed a clade together with *S. teres* and part of *S. glomerata* (Figs 1, 2, Suppl. material 2), without subclades corresponded to the circumscription in the Flora of China or any other systems (Stebbins 1940; Shih 1993). Thus, the complex needs to be expanded to include all these members. However, the poor resolution was not sufficient to aid our selection from the proposed systems, although our results are helpful for understanding the processes or mechanisms responsible for the high variation within the complex.

In most cases, hybridisation is considered to explain the occurrence of intermediates. It is not possible to exclude this mechanism in the *S. hookeriana* complex, but it appears to conflict with the status of *Soroseris* because of the following reasons. First, hybridisation often results in different topologies when phylogenetic trees are reconstructed based on ITS and chloroplast sequences, which was not the case for *Soroseris*. Second, hybridisation might only affect the tree obtained based on a nuclear marker, but the grouping of the chloroplast sequences was also not species-specific for *Soroseris*. Third, the occurrence of hybridisation might be determined by the distribution of the parent species, where it usually occurs in areas where the ranges of the two species meet and thus the diversity of these populations might be higher than that of others. We found no evidence of hybridisation based on these three reasons in *Soroseris*. In addition, mosaic sites in nuclear ITS sequences, which are characteristic of many taxa generated by hybridisation, are rare in *Soroseris*.

Alternatively, we suggest that radiation might be the main mechanism responsible for the various forms of intermediates in *Soroseris*. Radiation involves the rapid differentiation of a lineage within a short time interval, which is mostly triggered by environmental change or morphological innovation (Liu et al. 2006). The rapid uplift of the QTP generated a large number of heterogeneous environments and promoted the rapid differentiation of genera such as *Rhododendron* L. (Milne 2004), *Ligularia* Cass (Liu et al. 2006) and *Saussurea* DC (Wang et al. 2009). The main typical characteristic of these genera is a poorly resolved phylogeny with a large number of parallel branches, as well as complicated but subtle morphological variation amongst populations or species (Wang et al. 2009). However, only a few variations might exist within a population or certain region, whereas hybridisation is characterised by high variation within a population (Meeus et al. 2016). In the present study, few morphological variations were detected in each *Soroseris* population, whereas many were found between populations, particularly in terms of the leaf shape, indumentum in the phyllary and the plant height. Two or more states were present for all three of these characters and various combinations were present in different populations. We consider that all the populations of the *S. hookeriana* complex might have been derived from the same widespread ancestor on the QTP, but various environmental changes following the uplift of the QTP reduced the gene flow amongst most of the populations to yield a number of parallel branches, while adaptation to the local environment also resulted in an array of morphotypes, which were treated as subspecies, possibly under different species, by different systems (Stebbins 1940; Shih 1997; Shi and Kilian 2011).

According to the phylogenetic context and little genetic differentiation (ITS: 0.3% on average while 1% maximally; concatenated cp: 0.1% on average while 0.6% maximally), all members of the *S. hookeriana* complex (include *S. teres* and part of *S. glomerate*) could be treated as single species. However, this revision will make it difficult to describe an assemblage. In addition, this treatment might fail to reflect the evolutionary history discussed above and the biodiversity may be underestimated. However, the alternative treatment is also not perfect because separating all of the species will make identification difficult, especially when encountering intermediates, which is common in the field. In order to address these issues, we propose to treat all of the morphotypes, especially those with the typical morphology and widespread distribution, as subspecies of *S. hookeriana* because this is the earliest name of a species reported within the complex. However, we abandoned, for the time being, assigning new names to *S. teres* and *S. glomerate* due to insufficient sampling as well as distinct morphology. In addition, the name *S. hookeriana* subsp. *erysimoides* (Hand.-Mazz.) Stebbins has been published previously and we suggest that it is restored. Thus, a total of eight taxa, including four new combinations, are proposed and a key is provided in the following.

Key to the possible members of the *S. hookeriana* complex

1a Cataphylls numerous on the lower part of the stem; leaf blades elliptic or spatulate; ligule of corollas mostly equal to or shorter than the tube............. ... ***S. glomerata*** **(only those closely related to the *S. hookeriana* complex)**
1b Cataphylls few or none; leaf blades lanceolate or oblanceolate; ligules distinctly exceeding the tube of the corolla...**2**
2a Synflorescence elongate and cylindric ....***S. teres***
2b Synflorescence hemispheric..**3**
3a Leaves entire or denticulate, obtuse at the apex; upper leaves, bracts of the inflorescence and peduncles glabrous or sparingly hirsute .... ***S. hookeriana*** **subsp.** ***erysimoides***
3b Leaves pinnatifid, acute at the apex; upper leaves, bracts of the inflorescence and peduncles strongly hirsute4a. Involucral bracts sparsely to strongly hirsute...**4**
4a Involucral bracts sparsely to strongly hirsute **5**
5a Leaves sinuate-pinnatifid, sinuate-dentate or merely denticulate; inner bracts sparsely to moderately hirsute ....***S. hookeriana*** **subsp.** ***occidentalis*** **(new combination)**
5b Leaves runcinate-pinnatifid; inner bracts densely hirsute............................**6**
6a Stem tall, 4–20 cm; leaf blade pinnately lobed, lobes narrowly triangular .... ***S. hookeriana*** **subsp.** ***typica***
6b Stem short, less than 6 cm tall; leaf blade pinnately lobed, lobes irregular .... ***S. hookeriana*** **subsp.** ***hirsuta*** **(new combination)**
4b Involucral bracts glabrous **7**
7a Leaf blade 3–8cm long, 0.7–1.8 cm wide... .... ***S. hookeriana*** **subsp.** ***gillii*** **(new combination)**
7b Leaf blade 2–4cm long, 0.5–1.3 cm wide.. .... ***S. hookeriana*** **subsp.** ***handelii*** **(new combination)**

Soroseris hookeriana **subsp.** ***gillii*** **(S.Moore) Yu.J. Wang & L.M. Heng, comb. et stat. nov.**
urn:lsid:ipni.org:names:60477690-2

≡*Crepis gillii* S. Moore in Journ. Bot. 37: 170. 1899 (Syntype: K000250191); ≡*Soroseris gillii* (S. Moore) Stebbins in Mem. Torrey Bot. Club 19 (3): 41. 1940; S. Y. Hu in Quart. Journ. Taiwan Mus. 21 (3–4): 166. 1968; Higher Plants of China

4: 686, figure 6786. 1975; Flora Reipublicae Popularis Sinicae. 80 (1): 199. 1997; ≡*Soroseris gillii* (S. Moore) Stebbins subsp. *typica* Stebbins in Mem. Torrey Bot. Club. 19 (3): 42. 1940; S. Y. Hu in Quart. Journ. Taiwan Mus. 21 (3–4): 166. 1968; ≡*Soroseris trichocarpa* (Franch.) Shih in Act. Phytotax. Sin 31: 446. 1993; Flora Reipublicae Popularis Sinicae. 80 (1): 199. 1997.

***Soroseris hookeriana* subsp. *hirsuta* (J.Anthony) Yu.J. Wang & L.M. Heng, comb. et stat. nov.**
urn:lsid:ipni.org:names:77192776-1

≡*Crepis gillii* S. Moore var. *hirsuta* J. Anthony in Notes Royal Bot. Gard. Edinb. 18: 193. 1934 (Syntype: E00383690); ≡*Soroseris gillii* (S. Moore) Stebbins subsp. *hirsuta* (J. Anthony) Stebbins in Mem. Torrey Bot. Club 19 (3): 44. 1940 (Syntype: E00383690); S. Y. Hu in Quart. Journ. Taiwan Mus. 21 (3–4): 166. 1968; ≡*Soroseris hirsuta* (J. Anthony) C. Shih in Act. Phytotax. Sin 31: 446.1993; Flora Reipublicae Popularis Sinicae. 80 (1): 201. 1997.

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***Soroseris hookeriana* subsp. *handelii* (Stebbins) Yu.J. Wang & L.M. Heng, comb. nov.**
urn:lsid:ipni.org:names:77192779-1

≡*Soroseris gillii* subsp. *handelii* Stebbins in Mem. Torrey Bot. Club. 19 (3): 42. 1940 (Isotype: E00383689); S. Y. Hu in Quart. Journ. Taiwan Mus. 21 (3–4): 166. 1968.

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Suppl. material 1

The main morphological difference amongst members of the *Soroseris hookeriana* complex and the closely related species

Authors: La-Mei Heng, Yu-Lin Zheng, Yong-Bao Zhao, Yu-Jin Wang

Data type: measurement

Link: https://doi.org/10.3897/phytokeys.114.29914.suppl1

Suppl. material 2

The 50% majority rule consensus tree derived from Bayesian inference of the combined sequences of nuclear internal transcribed spacer, psbA-trnH and matK

Authors: La-Mei Heng, Yu-Lin Zheng, Yong-Bao Zhao, Yu-Jin Wang

Data type: molecular data

Explanation note: Posterior probabilities and bootstrap percentages are indicated above and below the branches, respectively. The samples named according to FOC (2011) or NCBI, Stebbins (1940) and the present study are listed from left to right.

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Rediscovery of Chamisso's type specimens of Hawaiian *Psychotria* (Rubiaceae, Psychotrieae) in the herbarium of the Natural History Museum, Vienna

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Abstract

Between 1815 and 1818, Count Nikolai Romanzoff funded an expedition of the Russian brig *Rurik*. Besides their primary goal to discover the Northeast Passage, their aim was to collect scientific specimens, for which the botanist Adelbert von Chamisso and the entomologist Johann Friedrich von Eschscholtz were commissioned. On the Hawaiian Islands, they collected two unknown endemic species that Chamisso and Diederich Franz Leonhard von Schlechtendal later described as *Coffea kaduana* and *C. mariniana*, both now assigned to the large and complex genus *Psychotria* (Rubiaceae, Psychotrieae). The private herbarium of Chamisso is now preserved at the Komarov Botanical Institute, St. Petersburg (LE). In the late 1930s, their type collections of *Psychotria kaduana* and *P. mariniana* were sent out on loan for study, but got lost in transit during the aftermath of the Second World War. No extant original material was found during a subsequent revision of Hawaiian *Psychotria* and both species were consequently neotypified. These neotypes are superseded by the here-reported rediscovery of original material in the herbarium of Stephan Ladislaus Endlicher preserved at the Natural History Museum, Vienna (W) and these specimens are here designated as lectotypes. As both are rather fragmentary, the former neotypes are additionally designated as epitypes. In addition, some peculiarities and details of the expedition and its collections are noted.

Keywords

Lectotypification, *Psychotria*, Hawaii, Chamisso, herbarium history

Introduction

The Romanzoffian expedition, Chamisso and his collections

Between August 1815 and August 1818, Count Nikolai Romanzoff (1754–1826), Chancellor of the Russian Empire and a patron of science, commissioned an expedition around the world on the Russian brig *Rurik* under the command of captain and cartographer Otto von Kotzebue (1787–1846). Besides their primary goal to find the Northeast Passage from the Bering Strait to the Atlantic Ocean, their aim was to collect scientific specimens of all kinds, for which the botanist and famous poet Ludolf Karl Adelbert von Chamisso (1781–1838) and the zoologist Johann Friedrich von Eschscholtz (1793–1831), as well as the artist Louis Choris (1795–1828), were hired. A detailed description of Chamisso's life, works and the Romanzoffian Expedition was given by Bździach (2004) and Maaß (2016).

Whilst the expedition was not able to realise their nautical goal, they brought together ample collections of plants, animals and other objects, largely from the Pacific region. In his first report to Romanzoff, Chamisso (1818: 206) estimated that they had collected around 2,500 species of plants with a third of them being undescribed. To date, the total extent of their collections, including duplicates, remains unknown. After returning to Europe, Chamisso was allowed to take his botanical collections to Berlin for study and publication and the bulk of them remained there until his death (Hiepko 2004; Maaß 2016: 134; see also Chamisso 1818: 208).

In June 1819, Chamisso became an adjunct ("Zweiter Kustos") in the Berlin Botanical Garden, at that time located in Schöneberg. Amongst other tasks, he was commissioned with creating a garden herbarium, a duty he increasingly neglected in favour of working on his collections from the Romanzoffian expedition (Urban 1917: 16, 19; Schmid 1942; Hiepko 2004). In 1833 Chamisso succeeded his friend Diederich Franz Leonhard von Schlechtendal (1794–1866) as curator of the Royal Herbarium Berlin (B), a position he kept until his death (Schlechtendal 1839; Urban 1917: 20). Together they published ten volumes of the "De plantis in expeditione speculatoria Romanzoffiana observatis" (e.g. Chamisso and Schlechtendal 1826a, 1826b, 1827, 1829a, 1829b).

In that series, they described ca. 60 new genera and 1,150 species (http://www.ipni.org; retrieved June 2018). A large portion (ca. 50 gen. and 700 spp.) of these names was based on material collected during the expedition, but other specimens such as Brazilian collections by Friedrich Sellow were also included (Imchanitzkaja 2004: 124; Maaß 2016: 139). Chamisso and Schlechtendal worked on the bulk of the collections themselves. However, certain families were assigned to specialists such as Georg Friedrich Kaulfuß (ferns), Christian Friedrich Lessing (Asteraceae) and Carl Bernhard Trinius (Poaceae), in part explaining the dissemination of many of Chamisso's specimens (e.g. Schlechtendal 1839; Lasègue 1845; Schmid 1942: 10; Maaß 2016: 171–172).

Chamisso presented a complete set of specimens from the expedition to the Berlin Herbarium. Unfortunately, these specimens were destroyed during a bomb raid that hit the herbarium during the Second World War (Hiepko 1987). As specified in his will, an additional set of "1,800 plant species" was presented to his successor at B, Johann Friedrich Klotzsch, who generously donated them to the herbarium (Schlechtendal 1839: 104; Urban 1917: 19, 22, 336) and these were likewise destroyed. His colleague Schlechtendal, professor of botany and director of the Botanical Garden of the University Halle (HAL), also received duplicates for his extensive private herbarium, which was later purchased by HAL and is still extant (Werner 1988; Braun and Wittig 2003: 14).

In 1840, two years after Chamisso's death, his private herbarium containing 10,000 to 12,000 species (Ruprecht 1864: 4) and ca. 60,000 specimens, was purchased by the Botanical Museum of the St. Petersburg Academy of Sciences. This collection with the specimens from the Romanzoffian expedition and other regions, as well as collections from ca. 60 other botanists, is now at the Komarov Botanical Institute in St. Petersburg (LE), where it is kept separately. Several additional duplicates of some of Chamisso's collections came to LE via the purchase of other private herbaria. Likewise, LE acquired the herbarium of his fellow member of the Romanzoffian expedition, Eschscholtz, in 1825 (Urban 1917: 336; Imchanitzkaja 2004; Maaß 2016: 145, 171).

Taxonomic history of Hawaiian *Psychotria* L.

The genus *Psychotria* (Rubiaceae, Psychotrieae) is a speciose pantropical group, comprising mainly understorey shrubs from wet forests. Due to the large number of morphologically similar species and long-unclear generic boundaries with respect to related genera, *Psychotria* was long perceived as a taxonomic nightmare (e.g. Sohmer 1977: 103). However, DNA-phylogenetic studies and a re-interpretation of morphological characters have recently improved our understanding of the group (e.g. Nepokroeff et al. 1999; Razafimandimbison et al. 2014, 2017). These studies have led to a narrower circumscription of the tribe Psychotrieae now including the single genus *Psychotria* and the transfer of all related genera such as *Palicourea* Aubl. to a separate tribe, Palicoureeae. In addition, many species of *Psychotria* have been transferred to *Palicourea*, once thought to contain only species with conspicuous flowers adapted to hummingbird-pollination (e.g. Taylor et al. 2010; Taylor 2015a, 2015b, 2017, 2018; Taylor and Hollowell 2016; Berger 2017, 2018).

As currently circumscribed, the genus *Psychotria*, as well as the tribe Psychotrieae, has its centre of diversity in the Paleotropics and harbours at least 1,600 species. Within the Rubiaceae, the group is largely diagnosed by the presence of raphides, valvate corolla aestivation and the frequent occurrence of heterostyly (subfamily Rubioideae), as well as by a predominantly woody habit, mostly terminal inflorescences, single ovules per locule and predominantly fleshy and drupaceous fruits (Psychotrieae alliance). Within the alliance, a grey or reddish-brown drying colour, caducous stipules, inconspicuous whitish flowers, pyrenes without preformed germination slits and seeds with an alcohol-soluble red seed-coat pigment generally characterise the Psychotrieae and the genus *Psychotria*. The opposite character states are variously found in *Palicourea,* as well as in other Palicoureeae (e.g. Taylor 1996; Razafimandimbison et al. 2014).

In addition, species of the Palicoureeae are phytochemically differentiated from the Psychotrieae by largely accumulating alkaloids (e.g. Berger et al. 2012, 2015, 2016, 2017; Schinnerl et al. 2012), cyclotides (Koehbach et al. 2013) and different groups of flavonoids (e.g. Berger et al. 2016).

Psychotria is the only genus of the Psychotrieae and Palicoureeae that reached the Hawaiian Islands, where it forms a characteristic component of the native mesic to wet rain forests (Sohmer 1977, 1978; Wagner et al. 1999; Nepokroeff et al. 2003). The *Rurik* visited the islands in 1816 as well as in 1817. Whilst they did not stay on the island of Hawaii ("Big Island") for more than a "quick touch on the beach"(Chamisso 1826: 7, 1836a: 207, 210–211), they dropped anchor at Honolulu, at that time the largest port on the Hawaiian Islands and stayed there for a total of roughly four weeks. According to Chamisso's itinerary, they largely collected in the valleys around Honolulu. During two excursions that lasted several days, they also explored the two major mountain ranges and reached elevations of up to 730 m (Chamisso 1826: 7–8, 1836a).

Based on the specimens collected on Oahu, Chamisso and Schlechtendal described the first two Hawaiian species of *Psychotria* under the names *Coffea kaduana* Cham. & Schltdl. and *C. mariniana* Cham. & Schltdl. (Chamisso and Schlechtendal 1829a). Asa Gray (1858) subsequently transferred both to the newly established genus *Straussia* (DC) A.Gray and also added a new species (*S. hawaiiensis* A.Gray). Subsequently, numerous authors published new species and intraspecific taxa for both *Psychotria* and *Straussia*, thus considerably raising the number of Hawaiian taxa. Later, Francis Raymond Fosberg (1964) synonymised *Straussia* with *Psychotria* and provided the necessary combinations such as for the two above-mentioned species currently known as *P. kaduana* (Cham. & Schltdl.) Fosberg and *P. mariniana* (Cham. & Schltdl.) Fosberg.

More recently, Seymour Sohmer (1977) published an extensive review of Hawaiian *Psychotria*, reduced many names to synonymy and recognized 11 endemic species with 8 varieties within two endemic sections. As currently understood, these species form a monophyletic group and are the result of a single introduction to the Hawaiian Islands, with subsequent colonisation from the oldest to the youngest islands followed by radiation and speciation events partly accompanied by polyploidisation (Kiehn 1996; Nepokroeff et al. 2003; Kiehn and Lorence in review).

Chamisso's collections of Hawaiian *Psychotria*

The Romanzoffian Expedition was amongst the first scientific expeditions that touched the Hawaiian Islands and studied their native flora. As mentioned above, they collected the first specimens of the species currently known as *Psychotria kaduana* and *P. mariniana*. Type specimens of both should be expected at LE and several other herbaria (see above). However, no such specimens were catalogued in the LE digital herbarium (https://www.binran.ru/collections; retrieved June 2018) or the JSTOR Global Plants database (http://plants.jstor.org; retrieved June 2018). Likewise, no specimens are extant in the Berlin Herbarium and none has been found in the private herbarium of Schlechtendal at HAL (Braun and Wittig 2003). This appears to confirm the opinion of Sohmer (1977), who could not trace any original material in his extensive revision of Hawaiian *Psychotria*.

As part of his studies on various groups of Pacific Rubiaceae, Fosberg was the last taxonomist to see Chamisso's type collections of *P. kaduana* and *P. mariniana* at LE (Fosberg 1964). He received these specimens on loan shortly before the outbreak of the Second World War. After the war, he returned them to the Russian Embassy for return to LE. Unfortunately, though, the specimens never arrived or resurfaced elsewhere and were probably lost in the aftermath of the war. As no other original material could be located, Sohmer (1977) designated a neotype for each of these names (ICN, Melbourne Code, McNeill et al. 2012, Art. 9.7) and expressed his hope that they "will be supplanted eventually by the recovery of the holotype".

Although the present study cannot satisfy Sohmer's hopes for a rediscovery of the lost types from LE, the discovery of duplicates of these in the collection of the herbarium of the Natural History Museum (W) is reported here. These specimens are original material, so they supersede the neotypes (ICN, Art. 9.19) and are designated here as lectotypes. In order to maintain nomenclatural stability, the neotypes of Sohmer (1977) are additionally designated as epitypes to support these rather fragmentary lectotypes (ICN, Art. 9.8).

Taxonomic treatment

Psychotria kaduana (Cham. & Schltdl.) Fosberg, Occas. Pap. Bernice Pauahi Bishop Mus. 23(2): 43, 1962.

Coffea kaduana Cham. & Schltdl., Linnaea 4(1): 33–35, 1829a. ≡ *Straussia kaduana* (Cham. & Schltdl.) A.Gray, Proc. Amer. Acad. Arts 4: 43, 1860. **Type.** USA. Hawaii: Oahu, Southern Waianae Range, < 730 m alt., 7–10 Oct 1817, or, Southern Koolau Range, < 730 m alt., 12 Oct 1817, *L.K.A. von Chamisso s.n.* (lectotype, designated here: W-Endl. 0065914!); Oahu, Kahuauli Ridge, 500–750 m alt., 17 Dec 1931, *E. Christophersen & E. Hume 1426* (epitype, designated here: BISH barcode 1010994!, Sohmer 1977: fig. 52!).

General remarks. *Psychotria kaduana* (sect. *Straussia* (DC.) Fosberg) is the most widely distributed species of Hawaiian *Psychotria*. It is found on the islands of Kauai, Oahu, Molokai, Lanai and Maui. It possesses a wide ecological amplitude resulting in considerable morphological variation and many local forms, some of which have received taxonomic recognition. However, it was shown that these all intergrade and are best treated as a single polymorphic species. A detailed synonymy and description of *P. kaduana* including lists of specimens, distribution maps, drawings and photos illustrating morphological variations are found in Sohmer (1977: 148–159) and Wagner et al. (1999). According to molecular phylogenetic data, this species belongs to the "*greenwelliae*" clade, which also comprises *P. fauriei* (H.Lév.) Fosberg, *P. greenwelliae* Fosberg, *P. hathewayi* Fosberg, *P. hawaiiensis* var. *hillebrandii* (Rock) Fosberg and *P. mauiensis* Fosberg (Nepokroeff et al. 2003).

Etymology. The protologue of *Psychotria kaduana* lacks information about the etymology of the name, but a person called "Kadu" is frequently mentioned in Chamisso's publications. While visiting the Aur Atoll (Ratak Chain, Marshall Islands) in February 1817, the *Rurik* was approached by Kadu, a native of Woleai ("Ulea"), an atoll in the eastern Caroline Islands, Federated States of Micronesia. Four years before, a storm bore Kadu's boat far to the east and, after months at sea, he finally reached the Ratak Chain. With curiosity and the intention of being dropped off closer to home, he joined the expedition and became a close friend of Chamisso and his prime source of ethnographic information on Micronesia. After visiting distant places such as Alaska and Hawaii, the expedition returned to the Ratak Chain in November 1817, where Kadu finally settled in the Wotje Atoll (Chamisso 1818: 203, 1836a: 278–280; Kotzebue 1821: 86–93; Maaß 2016; Igler 2017).

Chamisso wrote with great admiration about his "companion, teacher and dearest friend" Kadu, and dedicated to him the genus *Kadua* Cham. & Schltdl., a group of Pacific Rubiaceae-Spermacoceae with its centre of diversity on the Hawaiian Islands (Chamisso and Schlechtendal 1829b: 157–158 "Nomen in honorem amicissimi Kadu ex Ulea, dulcissimi nobis in expecitione Romanzoffiana per aliquot menses sodalist atque magistri", Terrell et al. 2005). A naturalistic lithographed portrait of Kadu in his traditional dress is given by the expedition's artist Choris (1822: Iles Sandwich, pl. 17). The same portrait with European dress is found in the honorary frontispiece of Chamisso's expedition report (1836b), once more illustrating Chamisso's connection with Kadu. Ultimately, it may not be clarified if the epitheton "kaduana" refers to a superficial resemblance with the genus *Kadua*, the person Kadu or both.

Typification. The protologue of *Psychotria kaduana* gives the type information as "In nemorosis montium Insulae O-Wahu A. D. 1817 legimus" (Chamisso and Schlechtendal 1829a: 33–35). Information provided in the itinerary (Chamisso 1826: 7–8) allows dating of their second visit to Oahu and the period in which the type collection was made to the time between 2 and 14 October 1817. The diary of Chamisso (1836a: 344) provides additional information about their collecting activities and reports only two occasions where plants have been collected during that visit.

Between 7 and 10 October 1817, Chamisso explored the "western mountain range of the island" (Chamisso 1836a: 344), which he and his two guides climbed from around Pearl River. Likely, the information denotes the Waianae Range, the western of the two mountain ranges on the island of Oahu. During that time, Eschscholtz suffered from a sore leg, could not attend the expedition and was left in care of drying previous collections on board the *Rurik*. On the 12th of October 1817, Eschscholtz had recovered and both made a daytrip to "the mountains", this time denoting the Koolau Range behind Honolulu (Chamisso 1836a: 342, 344–347).

At the Herbarium of the National History Museum (W), a peculiar specimen of *P. kaduana* is preserved (Figure 1). The sheet contains a small sterile branchlet and a

Figure 1. Lectotype of *Psychotria kaduana* (Cham. & Schltdl.) Fosberg collected by L.K.A. von Chamisso during the Romanzoffian Expedition in 1817 (*L.K.A. von Chamisso s.n.*, W-Endl. 0065914). The sheet originates from the private herbarium of S.L. Endlicher, now preserved at the Herbarium of the Natural History Museum, Vienna. Photo: Courtesy of the Natural History Museum, Vienna.

capsule with some leaves, an inflorescence and an immature fruit. The label gives the names "*Coffea kaduana*" and "*Coffea kaduana* Cham." in two different hands as well as the island "O. Wahu", but no information about the collector. On the upper right corner, "Hb. Endl." in ink indicates that the specimen originated from the private herbarium of Stephan Ladislaus Endlicher (1804–1849) and which he presented to the Botanical Museum after he was appointed curator (Torrey 1836; Anonymous 1845). Sohmer (1977: 157) subsequently confirmed the identification of the specimen and cited it as "Oahu without specific locality, *Endlicher s.n.* (W)".

Endlicher, however, never visited the Hawaiian Islands, so the respective specimen was not collected by him. The age of the specimen, the name and the locality on the label indicate that it could be original material of *Psychotria kaduana*. Comparison with specimens at LE (e.g. Imchanitzkaja 2004; Popov 2014; Maaß 2016: 149–170) and HAL (international herbarium database JACQ, http://herbarium.univie.ac.at/database) shows that Chamisso's labels are characteristic in size, paper and handwriting and confirm that this specimen was indeed collected by Chamisso. Therefore, it constitutes type material for *P. kaduana*.

Concerning the history of the specimen, Endlicher was professor of botany, director of the Botanical Garden and the Botanical Museum of Vienna from 1839–1849 (Anonymous 1849). As one of the foremost systematicists, taxonomists and prolific writers of his time (e.g. Flora brasiliensis, Nova genera et species plantarum, Genera plantarum), he was in contact with many contemporary botanists. A letter preserved in the Berlin State Library (Endlicher 1833), shows that he was in correspondence with Chamisso and that they exchanged specimens. This could explain how Chamisso's specimens from the Romanzoffian Expedition came into the possession of Endlicher.

The rediscovery of a type specimen of *P. kaduana* at W supersedes the neotypification of Sohmer (1977; ICN, Art. 9.19). Although rather fragmentary, the respective specimen is the only original material known and is here designated as the lectotype of this name (ICN, Art. 9.11). In order to maintain nomenclatural stability, the former neotype *E. Christophersen & E. Hume 1426* (BISH) is additionally designated as an epitype to support the limited lectotype material (ICN, Art. 9.8).

Psychotria mariniana (Cham. & Schltdl.) Fosberg, Occas. Pap. Bernice Pauahi Bishop Mus. 23(2): 43, 1962.

Coffea mariniana Cham. & Schltdl., Linnaea 4(1): 35–36, 1829a. ≡ *Straussia mariniana* (Cham. & Schltdl.) A.Gray, Proc. Amer. Acad. Arts 4: 43, 1860. **Type.** USA. Hawaii: Oahu, Southern Koolau Range, < 730 m alt., 28 Nov to 14 Dec [probably 8–9 Dec] 1816, *L.K.A. von Chamisso s.n.* (lectotype, designated here: W-Endl. 0066414!); Kaeleku, west branch near trail, 1 Jun 1933, *G.W. Russ s.n.* (epitype, designated here: BISH barcode 1010995!, Sohmer 1977: fig. 36! under erroneous collection "*Russ*, 1. July, 1938").

General remarks. *Psychotria mariniana* (sect. *Straussia*) is widespread and found on the islands of Kauai, Oahu, Molokai, Lanai and Maui. The species is variable in morphology and habitat preferences and grows in both wet and dry forests (Sohmer 1977, 1978; Wagner et al. 1999). A detailed synonymy and description of the species including lists of specimens, distribution maps, drawings and photos illustrating morphological variations is found in Sohmer (1977: 141–148). According to molecular phylogenetic data, *Psychotria mariniana* belongs to the "*mariniana*" clade comprising also *Psychotria hawaiiensis* (A.Gray) Fosberg var. *hawaiiensis* and *Psychotria wawrae* Sohm. (Nepokroeff et al. 2003).

Etymology. The protologue of *Psychotria mariniana* lacks information about the etymology of the name, but the species appears to be named in honour of the Spanish Don Francisco de Paulo Marín (1774–1837), who is mentioned in Chamisso's expedition report (1836a: 218, 340ff). Initially an apprentice on a Spanish ship associated with the Malaspina Expedition, he deserted and jumped ship at Nootka Sound (Canada) in 1792. According to Marín's own account, he was then tricked aboard a ship in San Francisco and kidnapped to Hawaii (Chamisso 1836a: 218, but see Cutter 1980: 20 on the credibility of Marín's stories). According to archival sources, he joined the U.S. ship *Lady Washington* under the command of Captain John Kendrick and finally reached Oahu in 1793 or 1794 (Gast 1973; Cutter 1980).

Marín settled on the island of Oahu and soon became an influential advisor to the Hawaiian King Kamehameha I, a wealthy merchant, horticulturalist and introducer of many useful plants and animals such as pineapple (Nagata 1985). During both of Chamisso's visits to Oahu, Marín provided information, advice and logistic support for his collecting activities (Chamisso 1836a: 218, 340ff; Hillebrand 1888: 179).

Typification. The protologue gives the type information as "Legimus in nemorosis montium O-Wahu A. D. 1816" (Chamisso and Schlechtendal 1829a: 35–36). Using the information in the itinerary (Chamisso 1826: 7–8) and diary (Chamisso 1836a: 215–222, 230) allows dating the expedition's first visit to Oahu from 28 November to 14 December 1816. Details on their collecting activities during that time are found in the diary and point towards higher altitudes of the Koolau Range as the type locality, which is an area where *Psychotria mariniana* frequently occurs today (Sohmer 1977: fig. 37).

Chamisso made his first botanical collections on the island of Oahu on an "old crater behind Honolulu", which became known as Diamond Head. He subsequently focused his collecting efforts on the forested valleys around Honolulu. Once, he also collected at higher elevations, for which he made an excursion on 8–9 December 1816. He ascended a valley behind Honolulu, crossed the ridge of the Koolau Range and descended towards the coast. The next day, he returned through a much higher mountain pass to the west (Chamisso 1836a: 230). As the only high-elevation area where collections were made during that visit, the type locality "forested mountains" points towards the aforementioned crossing of the Koolau Range. This appears to be supported by a comparison of collecting localities of different species, in which Chamisso indicated lower-elevation sites such as near sea-level habitats, foothills or other special

Figure 2. Lectotype of *Psychotria mariniana* (Cham. & Schltdl.) Fosberg collected by L.K.A. von Chamisso during the Romanzoffian Expedition in 1817 (*L.K.A. von Chamisso s.n.*, W-Endl. 0066414). The sheet originates from the private herbarium of S.L. Endlicher, now preserved at the Herbarium of the Natural History Museum, Vienna. Photo: Courtesy of the Natural History Museum, Vienna.

habitat types in a different way (e.g. Chamisso and Schlechtendal 1826a: 167, 1826b: 539, 1827: 36; Chamisso 1830: 44).

In a similar case as described above, a type specimen of *Psychotria mariniana* is preserved in the private herbarium of Endlicher at W (Figure 2). As with the *P. kaduana* material, the form and details of its label agree with other of Chamisso's collections, although it lacks any inscriptions in his hand. Instead, it says only "Chamisso", "Oahu" and "6/31" in ink, as well as "200" in pencil, which was probably added at a later date. The meaning of the numbers is unclear, but the former could refer to the time of acquisition in the herbarium of Endlicher. In 1984, Sohmer confirmed the identification of this specimen as *P. mariniana*.

Typification. As for *Psychotria kaduana*, the rediscovered original material of *P. mariniana* supersedes the neotype designated by Sohmer (1977; ICN, Art. 9.19). This specimen is also incomplete, with two small sterile branchlets and a packet with loose leaves and a single fruit. This specimen is here designated as the lectotype of *P. mariniana* and, in order to maintain nomenclatural stability, the former neotype *G.W. Russ s.n.* (BISH) is here designated as an epitype (ICN, Art. 9.8).

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Taxonomic note of *Parnassia* (Celastraceae) in China: a reassessment of Subsect. *Xiphosandra*

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Abstract

P. brevistyla, *P. delavayi* and *P. leptophylla*. belong to Celastraceae, *Parnassia* L., Sect. *Nectarotrilobos* Drude, Subsect. *Xiphosandra* (Franch.) Ku. Due to lack of material, the reliability of their taxonomic characteristics remained unknown and all three species have been retained. Following extensive field investigations, population sampling and examination of specimens, we determined that the previously used characteristics to distinguish these three species, i.e. the shape of basal leaves and the depth of staminode lobes, vary continuously within populations and should not be used to distinguish separate species. Therefore, *P. brevistyla* and *P. leptophylla* are hereby designated as synonyms of *P. delavayi*.

Keywords

Subsect. *Xiphosandra*, Celastraceae, new synonym, taxonomy

Introduction

Parnassia L. (Linnaeus 1753) is a genus that is predominantly distributed in the arctic and temperate zones of the Northern Hemisphere; it is most speciose in China and the Himalayas (Simmons 2004). All species of *Parnassia* are perennial herbs, glabrous;

flowers solitary, borne on unbranched scape, actinomorphic, hermaphrodite; staminodes 5, inserted opposite to petals, terete and entire or flat and divided into lobes or filiform rays. The genus was traditionally placed in the family Saxifragaceae (Hooker and Thompson 1858, Engler 1930, Cronquist 1981, Ku 1995, Ku and Hultgård 2001); however, it was recently transferred to Celastraceae (APG IV 2016, Ball 2016) based on molecular evidence (Soltis et al. 1997, Soltis et al. 2000, Zhang and Simmons 2006, APG IV 2016). The latest updated checklist of the genus recognised 61 species, 2 subspecies, 11 varieties and 1 forma (Shu et al. 2017).

Subsect. *Xiphosandra* (Franch.) Ku (1987) has been recognised as consisting of those species in which the stamen connectives apically project as lanceolate appendages (Fig. 1g). It includes three species: *P. brevistyla*, *P. delavayi* and *P. leptophylla*. Based on unique morphological characteristics (i.e. the stamen connectives apically project as lanceolate appendages), the three species were placed in Sect. *Xiphosandra* Franch. (Franchet 1897) with the support of Wu et al. (2003). Alternatively, most researchers placed them into Subsect. *Xiphosandra* of Sect. *Nectarotrilobos* Drude (Ku 1987, Wu 2005) or directly into Sect. *Nectarotrilobos* due to their flat and 3-lobed staminodes (Nekrassova 1927, Engler 1930, Handel-Mazzetti 1941).

Parnassia delavayi Franch. was published based on three collections (*Delavay 217*, *Delavay s.n.* and *Delavay Parnassia n. 2*) (Franchet 1896). Then, *Parnassia delavayi* Franch. var. *brevistyla* Brieger was proposed in 1922 based on specimens collected from Tibet, China, 3750 m and Schenhsi, China, 2600 m, *s.n.* (Brieger 1922). Handel-Mazzetti (1931) promoted *Parnassia delavayi* var. *brevistyla* into the new species *Parnassia brevistyla* (Brieg.) Hand.-Mazz. Handel-Mazzetti (1941) published 10 new taxa, including *Parnassia leptophylla* Hand.-Mazz., on the basis of a specimen collected from Baoxing, Sichuan, China—*KL Chu 3231*. Since the authors did not specify the holotype of *Parnassia delavayi* or *P. leptophylla* in their publications, P00709352 (Fig. 2) was designated as the lectotype of *P. delavayi* and PE00866146 (Fig. 3) was designated as the lectotype of *P. leptophylla* by Shu et al. (2017). However, according to the information provided by the original description of *P. brevistyla*, these types of *P. brevistyla* were not found after reviewing the specimens and high-resolution images of specimens in major herbaria, which was also mentioned by Stafleu and Mennega (1995).

Based on the descriptions of *P. brevistyla*, *P. delavayi* and *P. leptophylla*, the differences amongst them mainly consist of two characteristics: the shape of leaf blades and the depth of staminode lobes (Ku 1995, Table 1). With regard to the shape of blades: *P. brevistyla* has ovate-cordate basal leaves, while the other two species have reniform

Table 1. Morphological characters of the specimens amongst *Parnassia brevistyla*, *P. delavayi* and *P. leptophylla*.

	P. brevistyla	***P. delavayi***	***P. leptophylla***
Leaves	Ovate-cordate	Reniform, occasionally suborbicular	Reniform, occasionally suborbicular
Staminodes	Shallowly 3-lobed,the length of lobes is 1/6 or less of their length	Shallowly 3-lobed or to half their length	3-lobed for ca. 3/4 of their length

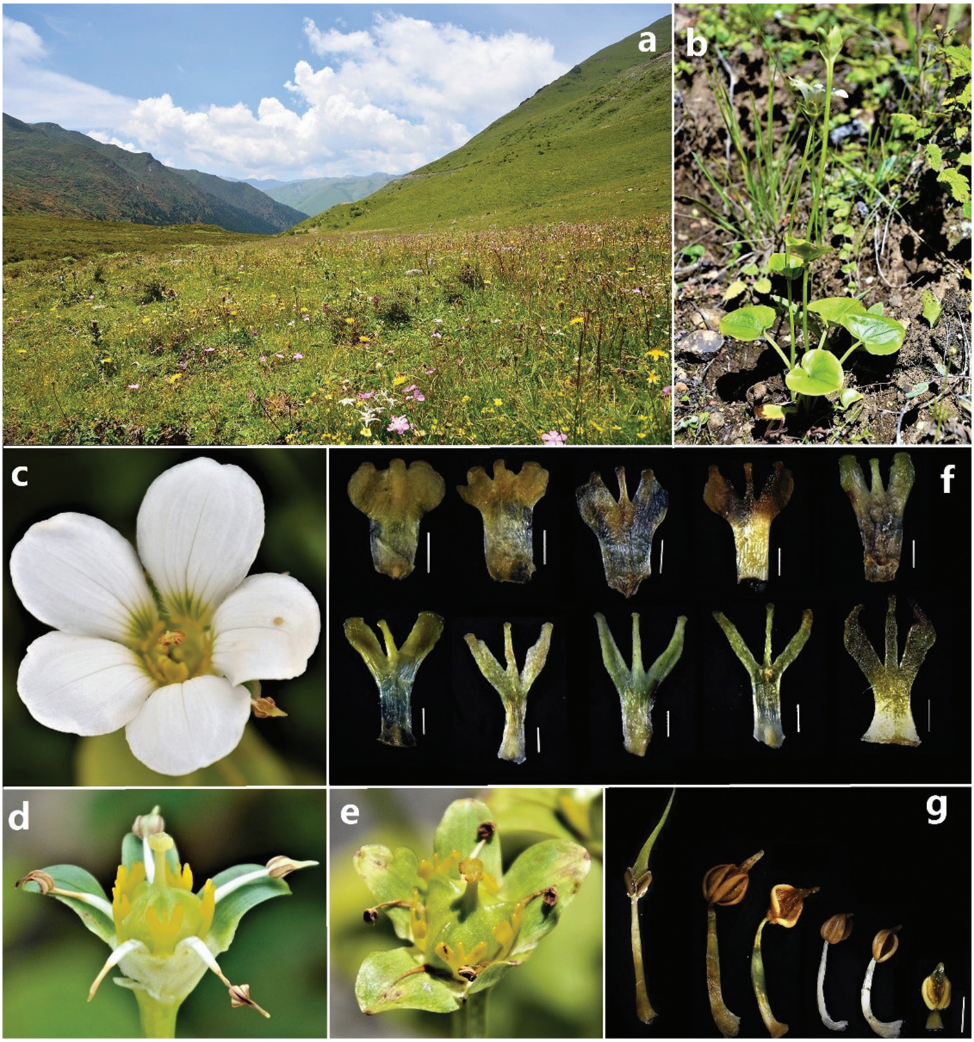

Figure 1. *Parnassia delavayi*: habitat (**a**), individual (**b**), flower (**c**), fruits (**d, e**), staminodes (**f**) and stamens (**g**). Scale bar: 1 mm.

or occasionally suborbicular basal leaves. With regard to the depth of staminode lobes: *P. brevistyla* staminodes are shallowly 3-lobed and the length of lobes is 1/6 or less of staminodes' length; *P. delavayi* staminodes are shallowly 3-lobed or to half their length; *P. leptophylla* staminodes are 3-lobed for ca. 3/4 of their length.

Through observation of herbarium specimens, we found that the three species of Subsect. *Xiphosandra* are extremely similar in morphology and there is obvious overlap amongst *P. brevistyla*, *P. delavayi* and *P. leptophylla* in the shape of leaf blades and the depth of staminode lobes. Moreover, during extensive field work, we found that the shape of basal leaves and the depth of staminode lobes varied significantly within pop-

Figure 2. *Parnassia delavayi*, lectotype (P05556394).

Figure 3. *Parnassia leptophylla*, lectotype (PE00866146).

ulations, even sometimes within individuals. Therefore, the aim of this study was to clarify the classification relationship amongst *P. brevistyla*, *P. delavayi* and *P. leptophylla* by re-evaluating their morphological characteristics, particularly the shape of blades and the depth of staminode lobes.

Material and methods

Specimens from **BJFC**, **CDBI**, **IMC**, **KUN**, **QFNU**, **P**, **PE**, **SM**, **SZ** and **WCNU** (Suppl. material 1) were examined during this study. High-resolution photographs were also captured. The measurements provided herein were mostly obtained from dried herbarium specimens. Since the shape of both the leaf base and the apex are basically identical, the leaf shape is defined by the aspect ratio of leaves in this study. The primary examined populations were in Chongqing, Gansu, Guizhou, Hebei, Henan, Hubei, Hunan, Shanxi, Sichuan, Tibet and Yunnan. These populations include the type localities of *P. brevistyla*, *P. delavayi* and *P. leptophylla* (Taibai, Shanxi; Baoxing, Sichuan; Heqing, Dali). To ensure the data are fully comprehensive, we have recorded all measurable traits, such as sepals and petals, in each population.

An Olympus SZX16 dissecting microscope was used for observations and an Olympus DP72 cooled digital colour camera was used to photograph leaves and staminodes. TpsDig software: Version 2.17 (http://life.bio.sunysb.edu/ee/rohlf/software.html) was used to measure the lengths and widths of leaves, thus improving the accuracy of experimental results.

Overlapping or non-overlapping standard deviations can be used to determine if there is continuous or discontinuous variation of a quantitative trait between two or more groups, thus providing evidence for species differentiation or merging. This approach was applied to the aspect ratio of leaves (the width of leaves / the length of leaves) and the depth of staminode lobes (the length of central lobes / the length of staminodes) (Fig. 4). A total of 100 populations from 11 provinces were studied. To ensure the universality and comprehensive nature of the data, we measured all available individuals.

Figure 4. Measurements of leaves and staminodes: W: the width of leaves; L: the length of leaves / staminodes; L1: the length of central lobes.

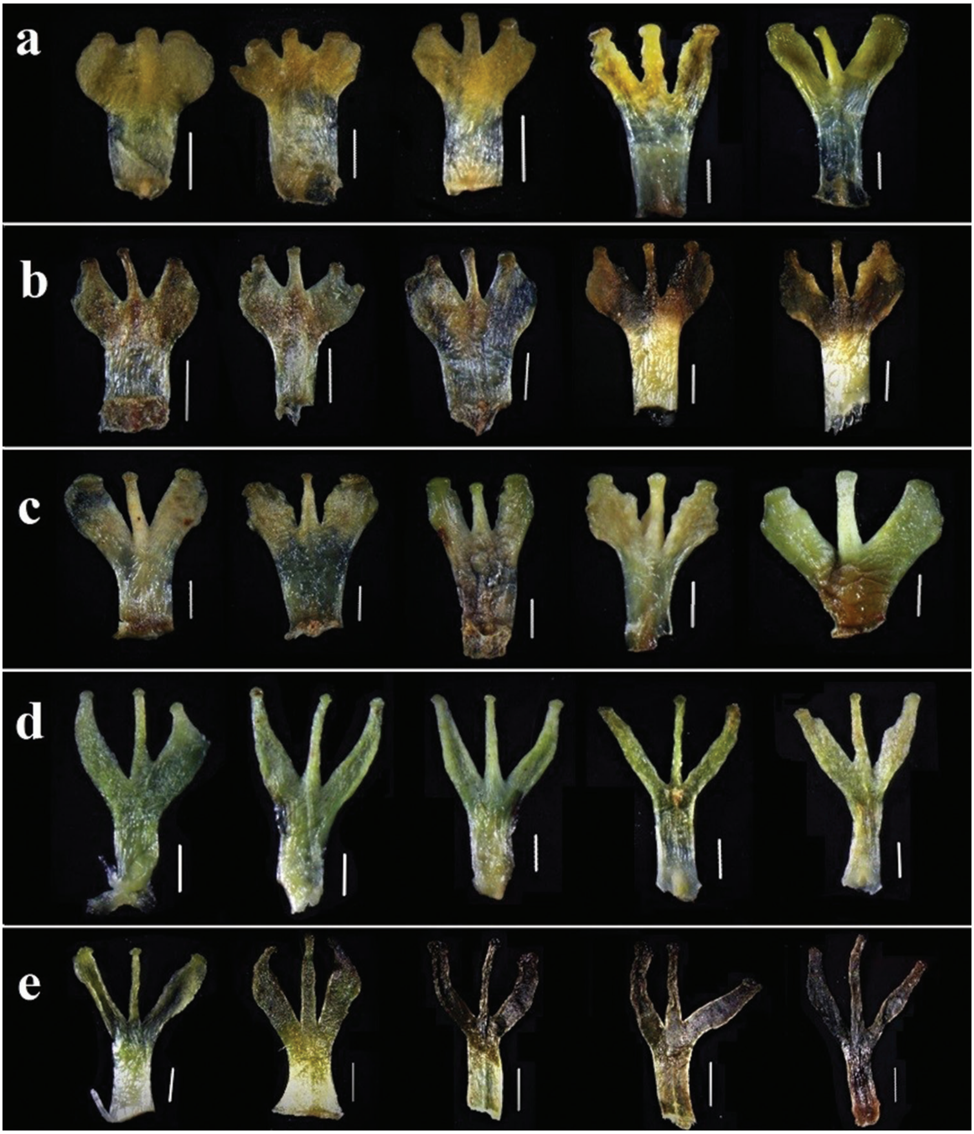

Figure 5. Variation of staminodes: **a, b** represent variation of the depth of staminode lobes in population of Kangding, Sichuan **c** represents variation of the depth of staminode lobes in population of Baoxing, Sichuan (the type locality of *Parnassia leptophylla*) **d** represents variation of the depth of staminode lobes in population of Cangshan, Dali (the type locality of *P. delavayi*) **e** represents variation of the depth of staminode lobes in population of Mabian, Sichuan. Scale bar: 1 mm.

Results

The morphological observations showed that the depth of staminode lobes varies considerably in the sampled populations, ranging from shallowly 3-lobed to 3-lobed for ca. 2/3 of their length (Fig. 5). Furthermore, the standard deviation analysis of the depth of staminode lobes also showed statistical continuity amongst populations of

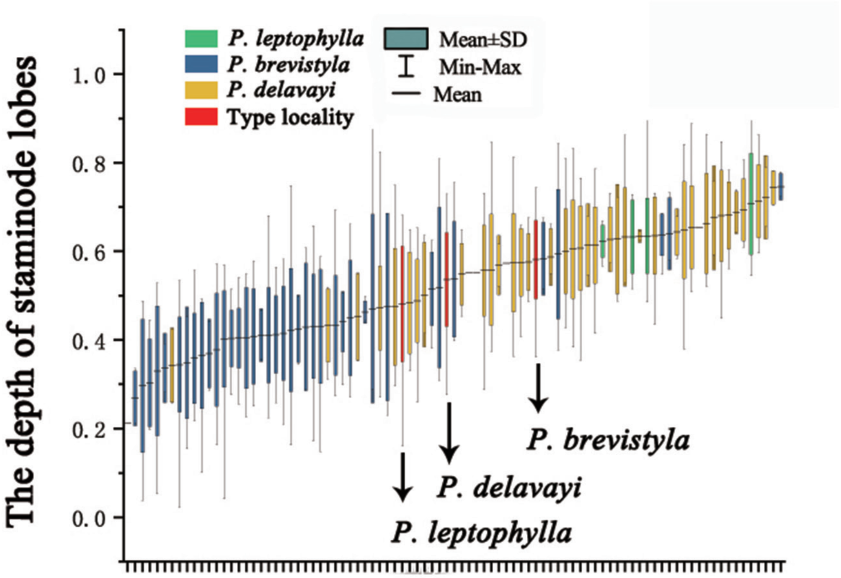

Figure 6. The standard deviation analysis of the depth of staminode lobes.

P. brevistyla, *P. delavayi* and *P. leptophylla*. As shown in Fig. 6, the variation of the depth of staminodes in the specimens collected from Baoji County, Heqing County and Baoxing County, where the types of *P. brevistyla*, *P. delavayi* and *P. leptophylla* were collected, is within the variation range of the population of *P. brevistyla*. There is also significant overlap of the depth of staminode lobes amongst the three species. Thus, *P. brevistyla*, *P. delavayi* and *P. leptophylla* show no differences in the depth of staminode lobes.

The shape of basal leaves has also been considered to be a distinguishing characteristic in previous treatments (Ku 1987, 1995). However, we found that the shape of basal leaves varies greatly within populations. Based on field experience, we found that their leaf shape varies dramatically, not only amongst different regions, but also in the same population. Shapes range from reniform, broadly cordate, to cordate and ovate-cordate. As shown in Fig. 7, the variation of the blade aspect ratio in the specimens collected from type localities of *P. brevistyla*, *P. delavayi* and *P. leptophylla* is within the variation range of *P. brevistyla* populations. Furthermore, a significant overlap was found for the blade aspect ratio amongst these three species with respect to the observed ranges as well as the standard deviations (Fig. 7). Based on this continuous variation, it is difficult to find a dividing line to distinguish different leaf shapes.

In summary, *P. brevistyla*, *P. delavayi* and *P. leptophylla* show no differences in the shape of blades and the depth of staminode lobes. Thus, we treated *P. brevistyla* and *P. leptophylla* as new synonyms of *P. delavayi*.

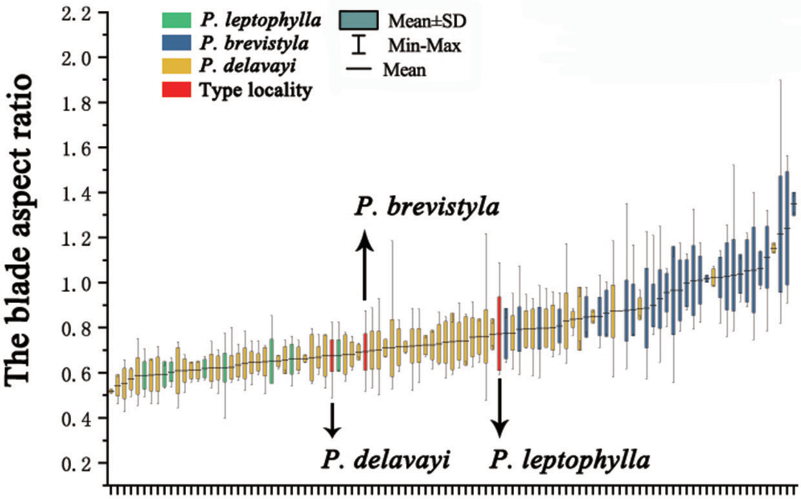

Figure 7. The standard deviation analysis of the blade aspect ratio.

Discussion

Hong (2016) proposed a new operational species concept called the morphological-biological species concept which emphasises that two or more qualitative traits or statistically discontinuous quantitative characters should exist between two species (Liu 2016). We applied this species concept in this study.

Taxonomically delimited species can be regarded as an assemblage of populations or individuals that have common morphological features and show distinct morphological discontinuity with other such assemblages in a number of characteristics (Singh 2004). That is, individuals of a given species show continuous variation in some characteristics. However, due to limitations of herbarium material, researchers can only observe a certain state of an individual within a population, rather than its variation within populations. Therefore, field investigation and random sampling within populations are important components of taxonomic studies (Xu et al. 2017). In this study, through both random sampling and statistical analysis within populations, the variability of morphological characteristics used in previous taxonomic treatments were analysed and reconsidered to avoid taxonomic artifacts that may be caused by undersampling.

We determined that both major characteristics that were previously used to distinguish *P. brevistyla*, *P. delavayi* and *P. leptophylla*, i.e. the shape of blades and the depth of staminode lobes, vary remarkably and continuously. Therefore, these characteristics should not be used to justify the recognition of three species. Furthermore, based on our examination of herbarium specimens as well as field observations, we found no other distinct characteristics to separate *P. brevistyla*, *P. delavayi* and *P. leptophylla* at the species level.

Furthermore, the distributions of these three species are continuous and overlap. Therefore, since these three species lack clear morphologic distinction and overlap in their distribution range, we hereby reduce *P. brevistyla* and *P. leptophylla* to synonyms of *P. delavayi*.

Taxonomic treatment

Parnassia delavayi Franchet, 1896: 267

Fig. 2

=*Parnassia brevistyla* (Brieg.) Hand.-Mazz., 1931: 434. Syn. nov.

≡*Parnassia delavayi* Franch. var. *brevistyla* Brieger, 1922: 400. Syn. nov. Type: China. Tibet, '*Beju-Batang, Nadelwalder bei Chieda am Anstieg zum Passe Mala*', 3500 m alt. (syntypes: not located); China. Schenhsi, Qingling, Taibaishan, Tempels Wanschuen-gou, 2600 m alt., *s.n. 2720* (syntypes: not located).

=*Parnassia leptophylla* Hand.-Mazz., 1941: 120. Syn. nov. (Fig. 3) Type: China. Sichuan, Baoxing, *KL Chu 3231* (lectotype designated by Shu et al. 2017: PE00866146!; isolectotypes: IBSC0145403!, PE00865960!, SZ00179815!). Fig. 3.

Type. CHINA. Yunnan, Eryuan (Lan-kong), Hee Chanmen, 2800 m alt., 16 August 1883, *Delavay 217* (lectotype designated by Shu et al. 2017: P05556394!; isolectotypes: P00709355!, P00709356!, P05556395!, P06392624!); CHINA. Yunnan, Eryuan, Lanho, Yanginchan, 7 August 1883, *Delavay 130* (syntypes: P00709357!, P00709358!, P06392623!)

Description. Stems 1–5, 10–40 cm, with 1 cauline leaf proximally or near middle. Basal leaves 3–7(10); petiole 2–16 cm; blade reniform, cordate or ovate-cordate, 1–4 × 1–4.5 cm, base deeply cordate to subcordate, apex rounded, apiculate. Flower 2–4.5 cm in diam.; hypanthium turbinate or campanulate. Sepals oblong, ovate to obovate, 4–13 × 2–8 mm, margin entire, apex rounded-obtuse. Petals white, sometimes green at base, obovate or oblong-obovate, 8–25 × 5–12 mm, base attenuate, margin erose in proximal 1/3, apex rounded or acute. Anthers ellipsoid, connective projected at apex into a lanceolate appendage, to 5 mm; filaments ca. 5.5 mm; staminodes 3–6 mm, shallowly 3-lobed or to half their length, rarely lateral ones 2-lobulate, lateral lobes usually wider than central one. Ovary superior, subglobose; stigma 3-lobed. Capsule obovoid with 3 thickened, longitudinal angles. Seeds brown, glossy, oblong. $2n = 14$.

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Supplementary material 1

A list of herbarium specimens examined

Authors: Huiying Yu, Feiyi Guo, Yumin Shu, Zhixiang Zhang

Data type: species data

Link: https://doi.org/10.3897/phytokeys.114.30551.suppl1

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RESEARCH ARTICLE

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Taxonomic revision of the African genus *Greenwayodendron* (Annonaceae)

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Abstract

Greenwayodendron (Annonaceae) is a tropical African genus of trees occurring mainly in rain forests. Until recently, *Greenwayodendron* contained only two species: *Greenwayodendron oliveri* from West Africa and *Greenwayodendron suaveolens* from Central and East Africa.

Genetic data, using chloroplast haplotypes and nuclear microsatellites as well as morphometric analyses, provided important information on the delineation of species. *Greenwayodendron* now contains six species, including two new species (*Greenwayodendron glabrum* Lissambou, Hardy & Couvreur, **sp. nov.** and *Greenwayodendron littorale* Lissambou, Dauby & Couvreur, **sp. nov.**). *Greenwayodendron suaveolens* var. *gabonica* and *Greenwayodendron suaveolens* subsp. *usambaricum* are recognised as distinct species: *Greenwayodendron gabonicum* **comb. nov.** and *Greenwayodendron usambaricum* **comb. nov.**, respectively. A key, detailed descriptions of morphology and geographic distributions, as well as notes on their ecology and uses are presented for all species. Preliminary conservation assessments following IUCN criteria are also provided. Two species are preliminarily identified as threatened, one as Endangered and one as Vulnerable.

Keywords

Annonaceae, *Greenwayodendron*, tree, rainforest, new species

Introduction

The family Annonaceae (Magnoliidae) comprises trees, shrubs and lianas (APG 2003; Chatrou et al. 2012; Couvreur et al. 2015) that play a key ecological role in tropical forests (Gentry 1993). In continental Africa (excluding Madagascar), 42 genera and around 400 species have been recorded to date (Couvreur et al. 2011; Couvreur et al. 2012; Ghogue et al. 2017). During the last decade, several revisions and monographs have significantly improved our understanding of African Annonaceae such as *Hexalobus* (Botermans et al. 2011), *Monodora* and *Isolona* (Couvreur 2009), *Uvariastrum* (Couvreur 2014), *Neostenanthera* (Fero et al. 2014), *Brieya* and *Piptostigma* (Ghogue et al. 2017), *Annickia* (Versteegh and Sosef 2007) and *Duguetia* (Maas et al. 2003).

The tribe Piptostigmateae (Malmeoideae) contains seven African genera: *Annickia* Setten & Maas, *Brieya* De Wild., *Greenwayodendron* Verdc., *Mwasumbia* Couvreur & Johnson, *Piptostigma* Oliv., *Polyceratocarpus* Engl. & Diels and *Sirdavidia* Couvreur & Sauquet (Couvreur et al. 2009; Chatrou et al. 2012; Couvreur et al. 2015; Ghogue et al. 2017). *Greenwayodendron* is inferred with strong support as sister to a clade containing the genera *Mwasumbia*, *Sirdavidia*, *Brieya*, *Polyceratocarpus* and *Piptostigma* (Couvreur et al. 2015; Ghogue et al. 2017).

Greenwayodendron contains two species (Table 1), namely *G. oliveri* (Engl) Verdc. in West Africa and *G. suaveolens* (Engl. & Diels) Verdc. in Central Africa (Le Thomas 1969; Verdcourt 1969). *Greenwayodendron suaveolens* was further divided into two subspecies (subsp. *usambaricum* Verdc. and subsp. *suaveolens* Verdc.), with the latter subspecies containing two varieties (var. *gabonica* and var. *suaveolens*). However, population genetic analyses of short plastid DNA sequences revealed that individuals of var. *gabonica* represent a genetically distinct lineage from var. *suaveolens* (Dauby et al. 2010). This genetic differentiation between the two varieties was further confirmed based on the analyses of nuclear microsatellites (Piñeiro et al. 2017; Lissambou et al. in prep.). A species delimitation study within *Greenwayodendron,* based on eight nuclear microsatellites (Piñeiro et al. 2016) coupled with a detailed morphometric dataset of 33 vegetative, floral and fruit traits, confirmed the existence of at least four potentially different species within the *G. suaveolens* complex (Lissambou et al. in prep.). Indeed, besides confirming the strong genetic differentiation between the *gabonica* and *suaveolens* varieties, the latter study identified two new taxa. The subspecies *usambaricum*, although geographically isolated from Central African species, is differentiated from *suaveolens* by vegetative characters, essentially determined by the number of lateral veins (≤ 12 veins in *suaveolens* and ≥ 14 in *usambaricum*. In addition, a molecular phylogeny of the genus based on numerous nuclear markers (unpublished data), confirmed that *G. suaveolens* subsp. *usambaricum* is phylogenetically distinct from *G. suaveolens* subsp. *suaveolens*. Most of these discriminant traits had already been recognised by several authors (Le Thomas 1969; Verdcourt 1969; Dauby et al. 2010; Piñeiro et al. 2016) and argue that the taxon *G. suaveolens* subsp. *suaveolens* var. *gabonica* and *G. suaveolens* subsp. *suaveolens* var. *suaveolens* can be elevated to the rank of species, as already proposed by Dauby et al. (2010).

Table 1. Past and currently proposed infrageneric species composition of *Greenwayodendron*.

Previous species delineation	Current species delineation
Greenwayodendron suaveolens subsp. *suaveolens* var. *suaveolens*	*Greenwayodendron suaveolens*
Greenwayodendron suaveolens subsp. *suaveolens* var. *gabonica*	*Greenwayodendron gabonicum*
Greenwayodendron suaveolens subsp. *usambaricum*	*Greenwayodendron usambaricum*
Greenwayodendron oliveri	*Greenwayodendron oliveri*
NA	*Greenwayodendron littorale*
NA	*Greenwayodendron glabrum*

These new insights into the genetic and morphological diversity of *Greenwayodendron* spp. warrant the need for a taxonomic revision of the genus. Here, we formally describe two new species and undertake two new combinations.

Taxonomical history

Oliver (1868) in Flora of Tropical Africa, described *Polyalthia*? *acuminata*. Oliver (1868), acknowledging clear morphological differences between the known *Polyalthia* spp. and this new African species, extended the generic diagnosis of *Polyalthia* to accommodate this new entity. However, the species epithet *acuminata* was already occupied by a South Asian species of *Polyalthia* named by Thwaites (1864). Engler and Prantl (1897) erected sect. *Afropolyalthia* within *Polyalthia*, to accommodate the species described by Oliver (1868) under the new replacement name *P. oliveri* Engl. A few years later, Engler and Diels (1901) published a new species, *P. suaveolens* Engl. & Diels, within the section *Afropolyalthia*. Subsequently, a number of species were described across Africa: *Polyalthia mortehanii* De Wild (De Wildeman 1914), *Maba gossweileri* Greves (Greves 1929) and *Xylopia otunga* Exell (Exell 1931) recognised as synonyms of *Greenwayodendron suaveolens* and *Polyalthia aubrevillei* Ghesq. ex Aubrév (Aubréville 1936) considered a synonym of *Greenwayodendron oliveri* (Aubréville 1936). Pellegrin (1949) named a new variety from Gabon as *Polyalthia oliveri* var. *gabonica* Pellegrin. This taxon had no Latin diagnosis rendering it as a *nomen nudum*. Le Thomas (1965) however, suggested that this new taxon is a variety of *Polyalthia suaveolens* (and not *P. oliveri*) and validly published the name *Polyalthia suaveolens* var. *gabonica* Le Thomas. A few years later, Verdcourt (1969) erected the genus *Greenwayodendron* to accommodate the species described within *Polyalthia* sect. *Afropolyalthia*. Indeed, he argued that there were sufficient morphological differences with the Southeast Asian *Polyalthia* species to warrant a new generic status. In addition, he also described *Greenwayodendron suaveolens* subsp. *usambaricum* Verdc. known from a very small isolated population in Tanzania. The same year, in the Flore du Gabon, Le Thomas (1969) did not accept the new generic name proposed by Verdcourt. Indeed, she postulated that the African species might be closely related to the Asian ones and argued in favour of a more variable *Polyalthia* s.l. circumscription with fewer generic names. However, subsequent morphological (Doyle and Le Thomas 1994; Doyle and Le Thomas 1996) and molecular phylogenetic studies (Chatrou et al. 2012) validated *Greenwayodendron* as a phylogenetically and morphologically distinct genus from *Polyalthia* s.l. Finally, *Polyalthia* s.l. is a mainly Southeast Asian genus (but see these articles for recent changes: Mols et al. 2004; Chatrou et al. 2012; Xue et al. 2014).

Material and methods

Around 500 specimens of *Greenwayodendron* present in the following herbaria BRLU, BM, BR, COI, K, LBV, P, WAG and YA (abbreviations follows Holmgren et al. (1990)) were examined for this study. The online resources JSTOR Global Plants (http://plants.jstor.org), IPNI (http://www.ipni.org), Tropicos (http://www.tropicos.org), the Museum of Natural History, Paris (http://www.mnhn.fr) and the Herbarium at the University of Coimbra (http://coicatalogue.uc.pt) were consulted for the study of type specimens. Species descriptions are based on living and herbarium specimens. The open source software QGis was used to generate the different taxon distribution maps. The Latin name *Greenwayodendron* is neutral (derived from the Greek word "*dendron*" meaning tree). New epithets names and combinations proposed here are thus concordant with the neutral gender.

Preliminary conservation assessments of each taxon were assessed using the IUCN Red List Categories and Criteria (IUCN 2012) using criterion B based on the distribution of each species inferred from georeferenced herbarium specimens (Schatz 2002). The extent of occurrence (EOO) and the area of occupancy (AOO) were estimated using the *ConR* R package (Dauby et al. 2017). The minimum AOO was estimated based on a user defined grid cell of 4 km^2, as recommended by IUCN (2017). Each collecting locality was regarded as a separate subpopulation. The number of 'locations' (as defined by IUCN 2017) was calculated with regard to the type of threats, such that a single 'location' may encompass more than one adjacent subpopulation. Vernacular names are mainly taken from herbarium specimen label information and from Raponda-Walker and Sillans (1961) and Aubréville (1936) for species found in Gabon.

Results and discussion

Morphology of *Greenwayodendron*

Habit. The different species of *Greenwayodendron* vary from large trees up to 45 metres tall (*G. suaveolens*) to small trees, no higher than 5 m (*G. littorale*). The trunks of *Greenwayodendron* are generally straight and cylindrical with a grey bark covered in large white/grey spots. The slash is bright orange with a distinct black ring under the bark. This black ring is also found in some other African species of Annonaceae such as *Anonidium mannii* Engl. & Diels. In terms of phylotaxis of the main axis, species in

Greenwayodendron follow the spiral pattern, which is common to all other members of the tribe Piptostigmateae (Johnson 2003).

Branches. In terms of pubescence, young branches vary from tomentose (i.e. dense brown pubescence) in *G. gabonicum* to sparsely pubescent to glabrous in the other four species. The pubescence tends to disappear with age and branches are generally sparsely pubescent to glabrous when older. However, in *G. gabonicum*, the pubescence persists even in old branches.

Leaves. The leaves of *Greenwayodendron* follow the typical Annonaceae characters: they are estipulate, simple, entire, distichous and alternate. The petiole of all species can be tomentose (*G. gabonicum*) to glabrous (*G. glabrum*). The leaf lamina varies from elliptic to narrowly elliptic in shape, while the base is rounded or cuneate. The apex of the leaves can be very variable even within species. For example, in *G. glabrum,* the apex varies from acuminate to emarginated (see for example Fig. 3D–G). Leaf size varies from 4.2–7.8 cm in *G. littorale* up to 10.0–26.3 cm long in *G. gabonicum*. In most species (*G. glabrum, G. littorale* and *G. oliveri*), the leaf lamina is glabrous on the upper side and sparsely pubescent on the lower side. Only *G. gabonicum* is characterised by a densely pubescent leaf upper side.

Midrib. As for most African genera (Couvreur 2009; Le Thomas 1969), the midrib is impressed on the upper side. The midrib varies from densely pubescent on both sides (*G. gabonicum*) to glabrous on both sides (*G. glabrum*). Secondary veins are brochidodromous or loop-forming (in contrast to other common Annonaceae venation type eucamptodromous) with prominent intermarginal veins and secondary veins that are straight then arcuate towards the margin (Klucking 1986; Scharaschkin and Doyle 2006). Tertiary veins are reticulate (forming a network) in all species, in contrast to other genera of the tribe (Couvreur et al. 2015) that are either percurrent (*Brieya*, *Piptostigma*, *Polycertocarpus*) (parallel) or intermediate between reticulate and percurrent (*Annickia* and *Mwasumbia*).

Inflorescence. The inflorescences in Annonaceae are characterised by a terminal flower with more lateral branched partial inflorescences (Weberling and Hoppe 1996). The inflorescence of the genus *Greenwayodendron* is terminal (leaf opposed) and generally extra-axillary on old branches. The majority of genera in Piptostigmateae, except *Annickia* Setten & Maas, have axillary inflorescences (Couvreur et al. 2009; Couvreur et al. 2015). Inflorescences are reduced to a compact rhipidium which contains 1–4 flowers. Very often, there is only one flower that develops. In general, the pedicels of all *Greenwayodendron* species are bibracteate, meaning they have two bracts. This conforms to the type 2 of Fries (1955) and is common to most Annonaceae species. The bract, just under the calyx, is referred to as the upper bract and the lower bract corresponds to the bract located in the lower half of the pedicel.

Flowers. Flowers in *Greenwayodendron* are actinomorphic, cyclic and trimerous, with 9 tepals. The external whorl of three tepals is typically referred to as sepals, whereas the two inner whorls of three petals each are termed outer and inner petals. *Greenwayodendron* species are androdioecious, with male and hermaphrodite individuals. Within Piptostigmateae, only two other genera, *Sirdavidia* Couvreur & Sauquet and *Polycerato-*

carpus Engl. & Diels are also androdiecious, the rest of the genera being bisexual (Couvreur et al. 2009; Couvreur et al. 2015). For *G. glabrum* and *G. littorale,* we did not observe staminate flowers whereas for *G. gabonicum* only male flowers have been seen to date. It is not excluded that the former two species are in fact truly bisexual, but more data needs to be gathered before we can conclude on their sexual systems. Indeed, some African genera of Annonaceae are generally androdioecious but also have functionally bisexual or even monoecious species (Verdcourt 1986; Couvreur and Luke 2010). In contrast to some other African genera such as *Uvariopsis* Engl. (Le Thomas 1969), there is no apparent sexual dimorphism between staminate and hermaphrodite flowers, both being similar in their general aspect such as pedicel length or tepal shape and size. The sepals are small, never longer than 5 mm. The two whorls of petals, are sub-equal in length and similar in shape. We thus did not differentiate them in the descriptions. In vivo, the petals spread out horizontally and recurve slightly downwards towards the apex. Petals range in size from 22–24 mm long in *G. gabonicum* to 11.5–12.5 mm long in *G. littorale*.

In staminate flowers, the stamens range from 16–33 and are packed into several whorls whereas in the bisexual flowers the stamens are fewer in number (4–15) and form a single whorl around the carpels. The connective shield, i.e. the apical extension of the connective between both thecae, is generally tongue shaped and also termed umbonate (Maas et al. 2003) but is flattened and discoid or lobulated in *G. oliveri*. Connective shape has also been shown to be an important taxonomic character in other genera such as *Duguetia* A.St.-Hil. (Maas et al. 2003) or *Uvariastrum* Engl. & Diels (Couvreur 2014). The carpels are free (apocarpic) as for most Annonaceae genera (van Heusden 1992) and vary from 8–20 in number.

Fruits. Fruits in *Greenwayodendron* are composed of several shortly stipitate monocarps. The stipes and the fruit pedicels are sparsely pubescent to glabrous and generally the same colour as the monocarp. The monocarps are broadly ellipsoid to globular, sparsely pubescent to glabrous and green to dark purple at maturity. ellipsoid to globular, sparsely pubescent to glabrous and green to dark purple at maturity.

Seeds. The seeds of *Greenwayodendron* range from 1–4 per monocarp. They are ellipsoid to globular, flattened when there is more than one seed per monocarp and surrounded by a furrow. The surface of the seed is covered with a rough white integument and the raphe is always impressed.

Key to the species of *Greenwayodendron*

For a key to the genera of Piptostigmateae, see Ghogue et al. (2017).

1	Upper side of leaf lamina clearly densely pubescent	***G. gabonicum***
–	Upper side of leaf lamina sparsely pubescent to glabrous	**2**
2	Upper side of midrib glabrous	***G. glabrum***
–	Upper side of midrib to sparsely pubescent	**3**

3 Connective of the stamens flattened or discoid in shape (West Africa) .... ***G. oliveri***

– Connective of the stamens tongue-shaped or lobulated (Central and East Africa).. **4**

4 Tree 2–5 m tall, stamens in hermaphrodite flowers 4–5; mature monocarps 2.5 × 4.2 cm in diameter (coastal Gabon and Republic of Congo)....... ***G. littorale***

– Tree up to 45 m lower limit of height, stamens in hermaphrodite flowers 5–10; mature fruits 7.2 × 16.4 cm in diameter **5**

5 Secondary veins ≤ 12 (Central Africa, widespread)................. ***G. suaveolens***

– Secondary veins ≥ 14 (Tanzania, Eastern Arc Mountains).....***G. usambaricum***

Greenwayodendron **Verdc., Adansonia, sér. 2, 9 1. (1969)**

Polyalthia sect. *Afropolyalthia* Engler & Prantl., Leipzig,W. Engelmann.160. (1897)

Type species. *Greenwayodendron oliveri* Engl.

Tree 2–45 m tall, d.b.h. 2–125 cm; stem cylindrical, bark smooth with large white stains, slice orange with a black ring, aromatic and rapidly turning brown. Young branches at first densely pubescent, later glabrous, trichomes 0.1–1.0 mm long; older branches sparsely pubescent to glabrous. Leaves entire, simple, alternate, astipulate; petiole 1.0–11.1 mm long, 0.8–3.3 mm in diameter, densely pubescent to glabrous, trichomes 0.1–1.2 mm long, indument brown; lamina 4.2–26.3 cm long, 2.0–9.6 cm wide, length: width ratio 1.5–4.0; elliptic to narrowly elliptic, base rounded or cuneate, apex acuminate, acute, apiculate, aristate or caudate, acumen 1–40 mm long, upper side sparsely pubescent to glabrous, lower side densely to sparsely pubescent; midrib upper side base densely pubescent to glabrous, lower side densely pubescent to glabrous, trichomes 0.1–1.2 mm long, indument tomentose; secondary veins 4–18 pairs, upper side sparsely pubescent to glabrous, lower side densely pubescent to glabrous, trichomes 0.1–1.0 mm long; tertiary veins upper side sparsely pubescent to glabrous, lower side sparsely pubescent to glabrous, irregularly prominent, slightly raised, distinct or indistinct above. Inflorescence axillary, 1–4 flowered rhipidium. Floral buds ellipsoid, 4–9 mm long, 2–5 mm in diameter, densely covered with short and long trichomes. Flowering pedicel 3.0–6.3 mm long, 0.5–2.2 mm in diameter, densely pubescent when young, becoming glabrous, trichomes 0.1–0.5 mm long; lower bract in lower half of pedicel, minute, sparsely pubescent; upper bract apical, just below the calyx, 0.9–5.2 mm in diameter, sparsely pubescent, trichomes 0.1–0.6 mm long. Sepals 1.3–5.0 mm long, 1.6–4.7 mm wide, length:width ratio 0.5–0.9 broadly ovate, imbricate, fused at the base, apex acuminate, base truncate, densely to sparsely pubescent outside, sparsely pubescent towards the centre inside, trichomes 0.1–0.5 mm long. Inner and outer petals subequal, 8.0–24.6 mm long, 1.3–3.5 mm wide, length:width ratio 0.5–0.9, narrowly ovate to elliptic, apex acuminate, base rounded, green maturing pale yellow, outside tomentose, trichomes 0.1–0.5 mm long, erect, inside sparsely pubescent to glabrous; glabrous part to 2–8 mm long. Male flowers: stamens 10–33, in several whorls, 1.2–4.2 mm long, 0.4–0.9 mm wide, tightly appressed; connective shield of stamens tongue-shaped, lobulated or flattened/discoid; hermaphrodite flowers: stamens 4–10 in a single whorl, appressed, 0.9–2.2 mm long and 0.3–0.8 mm wide, connective stamen tongue-shaped, lobulated or flattened; carpels 8–20, 0.7–2.1 mm long, 0.5–0.9 mm in diameter, length:width ratio 1.2–2.8 narrowly oblong, densely pubescent; ovules 1–2, oblong; stigmata ovoid, densely pubescent, trichomes 0.1–0.5 mm long. Fruiting pedicel 4.5–13.1 mm long, 1.0–3.5 mm in diameter, sparsely pubescent to glabrous, trichomes ca. 0.1–0.5 mm long; stipes 3.0–12 mm long and 1.0–3.2 mm in diameter, sparsely pubescent; monocarps 1–8, 2.5–21.1 mm in diameter, broadly ellipsoid to globose, sparsely pubescent to glabrous, green turning wine red at maturity; seeds 1–4 per monocarp, 3.0–15.4 mm in diameter, ellipsoid to globose, flattened on one side or hemi-ellipsoid when more than one seed per monocarp, surface covered by a white tegument; raphe impressed.

Greenwayodendron gabonicum **(Le Thomas) Lissambou & Couvreur, comb. nov.**

urn:lsid:ipni.org:names:77192855-1
Fig. 1

Polyalthia suaveolens (Engl. & Diels) var. *gabonica* Pellegr. ex Le Thomas., Muséum National d'Histoire Naturelle. Paris. Vol. 16. 206. (1969) ≡ *Greenwayodendron suaveolens* var. *gabonica* (Pellegr., ex Le Thomas) Verdc., Adansonia, sér. 2, 9 (1). (1969).

Type. GABON. Ogooué-Lolo: Région de Lastoursville, 25 Feb 1930, *G.M.P.C. Le Testu 7936* (lectotype, designated by Le Thomas 1965 p. 453, P![P00363322]; isotypes: BM web [BM000547163]; BR![BR880441]; P![P0036331]).

Tree 4–20 m tall, d.b.h. 4–40 cm in diameter. Young branches densely to sparsely pubescent, trichomes 0.5–1.0 mm long; old branches sparsely pubescent. Leaves: petiole 4.0–11.1 mm long, 1.0–3.3 mm in diameter, densely to sparsely pubescent, trichomes 0.4–1.2 mm long, indumenta brown; lamina 10.0–26.3 cm long, 4.0–9.6 cm wide, length:width ratio 1.9–3.6, elliptic to narrowly elliptic, base rounded cuneate, apex acuminate, acute, apiculate or emarginate, acumen 8–35 mm long, upper side densely pubescent, lower side densely pubescent; midrib upper and lower sides densely pubescent, trichomes 0.5–1.2 mm long, indumenta tomentose; secondary veins 6–11 pairs, upper side pubescent, lower side densely pubescent, trichomes 0.3–1.0 mm long; tertiary veins upper side sparsely pubescent, lower side densely pubescent, irregularly prominent or indistinct above. Inflorescence axillary, a 1–4 flowered rhipidium. Floral buds ellipsoid, 6–9 mm long, 2.0–3.2 mm in diameter, densely covered with long trichomes. Flowering pedicel 4.5–6.0 mm long, 2.0–2.2 mm in diameter, densely pubescent, trichomes ca. 0.5 mm long, lower bract in lower haft of pedicel, minute, upper bract apical, just below the calyx, 4.8–5.2 mm in diameter, densely pubescent,

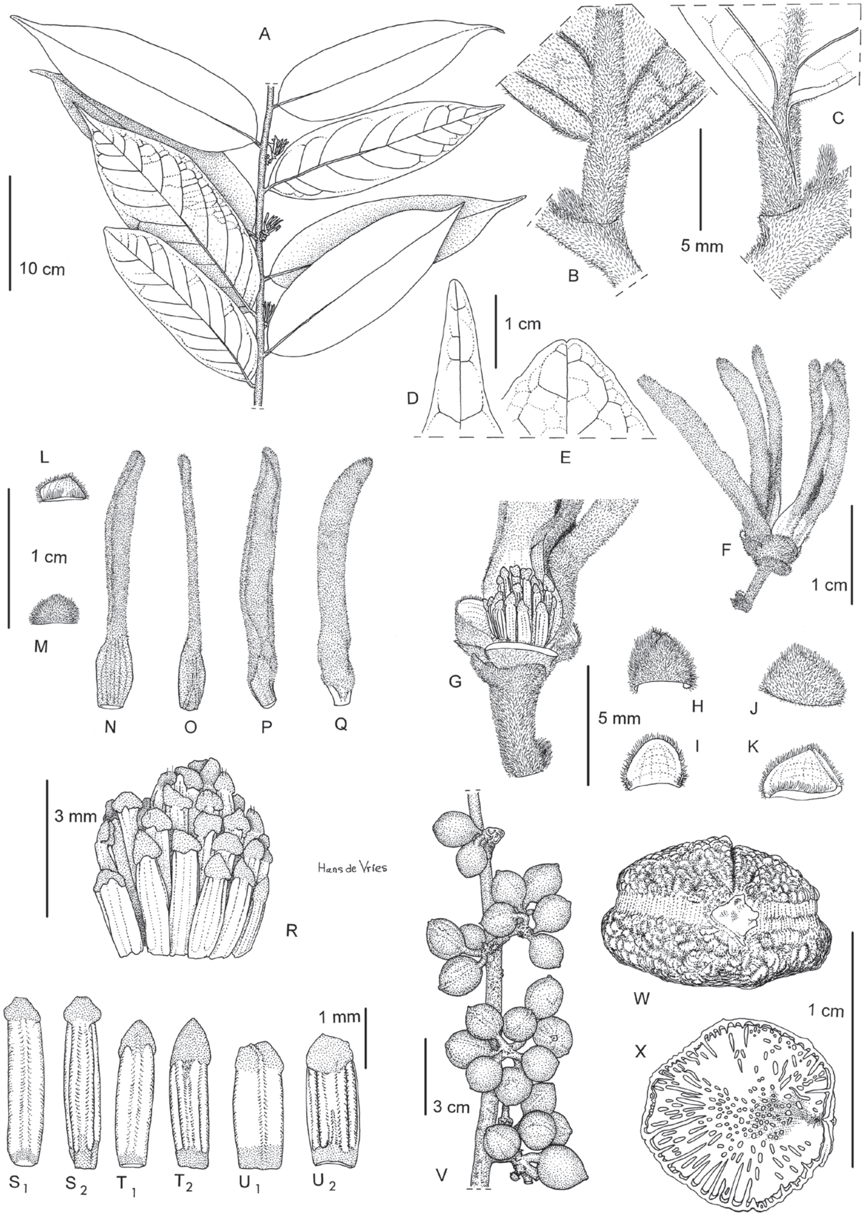

Figure 1. *Greenwayodendron gabonicum*. **A** Flowering branch **B** Detail of lower leaf surface **C** Detail of upper leaf surface **D-E** Detail of leaf apex **F** Flower **G** Detail of male receptacle, inner and outer petals removed **H** Outside view of basal bract **I** Inside view of basal bract **J** Outside view of upper bract **K** Inside view of upper bract **L** Inside view of sepal **M** Outside view of sepal **N** Inside view of outer petal **O** Outside view of outer petal **P** Outside view of inner petal **Q** Inside view of inner petal **R** Detail of androecium **S** Detail of inner row of anthers (**S1** Inside view, **S2** Outside view) **T** Detail of outer row of anthers (**T1** Inside view, **T2** Outside view) **U** Detail of outer row of anthers, different morphology (**U1** Inside view, **U2** Outside view) **V** Fruiting branch **W** Seed, latitudinal view **X** Longitudinal section of seed showing ruminations. **A** *Le Testu, G.M.P.C. 7936* **B–U2** *McPherson, G. 13736* **V–X** *McPherson, G. 15498*. Drawing by Hans de Vries.

trichomes ca. 0.6 mm long. Sepals 3.5–4.1 mm long, 4.5–4.7 mm wide, length:width ratio 0.8–0.9 broadly ovate, imbricate, fused at the base, apex acuminate, base truncate, outside pubescent, inside sparsely pubescent, trichomes 0.1–0.5 mm long. Inner and outer petals 22.7–24.6 mm long, 2.3–3.5 mm wide, length:width ratio 0.8–0.9, narrowly ovate to narrowly elliptic, apex acuminate, base rounded; outside tomentose, trichomes 0.5–0.6 mm long; inside sparsely pubescent to glabrous; glabrous part to 4.2–4.6 mm long from the base; petals green maturing pale yellow. Male flowers: stamens 24–33, in several whorls, 3.2–4.2 mm long, 0.4–0.6 mm wide, tightly appressed; connectives tongue-shaped or lobulated. Hermaphrodite flowers: not observed. Fruiting pedicel 7.0–13.1 mm long, 2.0–3.5 mm in diameter, sparsely pubescent, trichomes ca. 0.5 mm long; stipes 5.5–12.0 mm long, 1.5–3.1 mm in diameter, sparsely pubescent; monocarps 1–8, 11.0–19.5 mm in diameter, broadly ellipsoid to globose, sparsely pubescent to glabrous, green turning wine red at maturity; seeds 1–4 per monocarp, 7.8–15.4 mm in diameter, ellipsoid to globose, hemispherical or flattened, flattened on one side when more than one seed per monocarp, surface covered by a white tegument.

Distribution. Mainly occurring in Gabon and one collection from the Republic of Congo; 10–500 m (Fig 2).

Habitat and ecology. In primary and secondary forests, also occurring in forest-savannah mosaics (Lope and Wonga Wongué).

Phenology. In Gabon, *G. gabonicum* flowers from January to March, immature fruits May to October and mature fruits November to December (Amman Bush; Personal communication), also based on herbaria.

Vernacular names. Gabon: Mutunga (Aduma, Awadji, Nzebi), Otunga (Fang, Kota, Obamba).

Preliminary conservation status of IUCN. Least Concern [LC]. The extent of occurrence (EOO) of *Greenwayodendron gabonicum* is estimated to be over 106,375.19 km^2, whereas its area of occupancy (AOO) is estimated to be 128 km^2 (which falls within the limits for Vulnerable status under criterion B2). The species, recorded from Gabon and the Republic of Congo, is now known from at least 35 specimens representing 22 subpopulations. These 22 subpopulations represent 20 different locations (sensu IUCN 2012), many more than 10 locations, which are the upper limit for Vulnerable status under the subcriterion 'a'. *Greenwayodendron gabonicum* has been collected in 5 protected areas in Gabon (National Park: Moukalaba-Doudou, Lopé, Ivindo, Waka) and Wonga Wongue Reserve and from unprotected areas. This taxon is relatively low in abundance except in two localities (Wonga Wongue Reserve and Lopé Park) where the relative abundance is high. The main threat to *G. gabonicum* is its habitat destruction resulting from logging activities, especially in the coastal part of Gabon. Notwithstanding these human activities, with varying levels of impact, the species appears not as threatened as it is an abundant and quite widespread species. The available information suggests that the number of subpopulations and mature individuals of *G. gabonicum*, as well as its EOO and AOO, will not decrease noticeably in the near future.

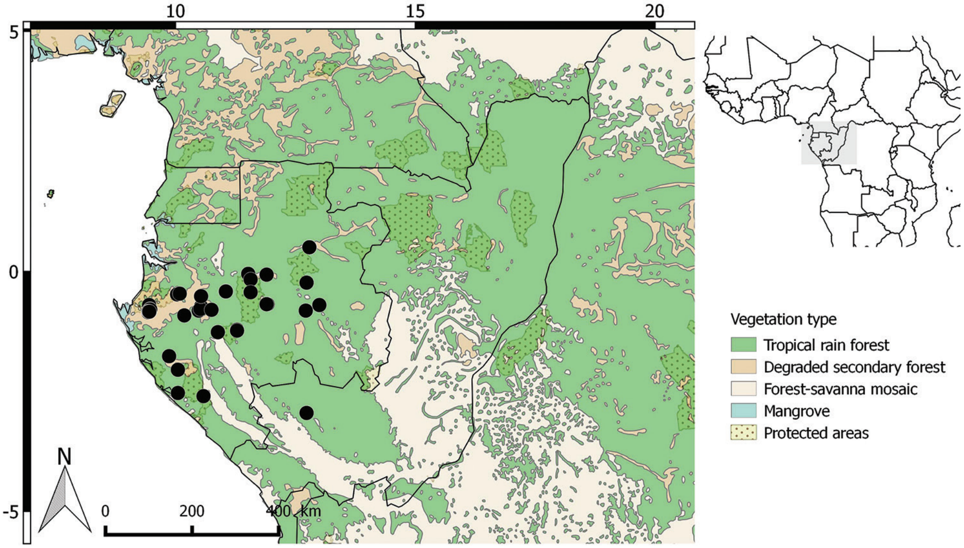

Figure 2. Distribution of *Greenwayodendron gabonicum*.

Uses. Unknown.

Notes. *Greenwayodendron gabonicum* is easily differentiated from all other species of the genus by its dense tomentose pubescence mainly along the petiole and midrib. In addition, *G. gabonicum* is the only species to have a densely pubescent or sparsely pubescent upper leaf lamina and has the longest leaves, petals and monocarps of the genus.

This species was initially described as a variety of *G. suaveolens*. However, phylogeographics (Dauby et al. 2010), genetic data (Piñeiro et al. 2017; Lissambou et al. in prep.) and morphological characters (leaf size, pubescent, flower and fruit size) clearly support the hypothesis that this entity represents a distinct species altogether leading us to make this new combination.

Since there were two specimens of *Le Testu 7936* in Paris, we chose the specimen barcoded P00363322 as the holotype of *G. gabonicum*. Specimen P0036331 is thus an isotype.

This species was, until recently, suggested as a strict endemic to Gabon, however it has also been collected in the Republic of Congo (*P. Sita 4045*) in the Niari region (Fig. 2).

Selected specimens examined. Gabon. Haut-Ogooué: Ossélé village, 45 km on road from Franceville to Kessala, 1°51.28'S, 13°50.80'E, 23 Mar 2015, *Couvreur, T.P.L. 746* (WAG, LBV, BRLU). **Moyen-Ogooué:** Zone de Mabounié, 45 km southwest of Lambaréné, north bank of the Ngounié River, 0°26.706'S, 10°19.458'E, 13 Dec 2012, *Bidault, E. 800* (BRLU, LBV, MO); Concession Rougier du Haut-Abanga, southeast of Mikongo, northern part of the Mekie Mountains, 0°24.135'N, 11°13.212'E, 13 Jun 2008 *Dauby, G. 909* (BRLU, LBV, MO); *ibid. loc.*, 0°46.3956'S, 10°28.3332'E, 10 May 2012, *Dauby, G. 2809* (BRLU, LBV, MO). **Ngounié:** *ibid. loc.*, 0°28.854'S, 10°18.846'E, 14 Nov 2013, *Bidault, E. 1297* (BRLU, LBV, MO); *ibid. loc.*, 0°47.729'S, 10°31.991'E, 8 May 2012, *IRD plot 91* (BRLU, LBV, MO). **Nyanga:** Chantier CEB, ca. 35 km SW of Doussala, 2°30'S, 10°30'E, 18 May 1985, *Reitsma, J.M. 1030* (LBV, WAG); Inventory, chantier CEB, ca. 50 km SW of Doussala, 2°36'S, 10°35'E, 19 Oct 1985, *Reitsma, J.M. 1679* (LBV). **Ogooué Ivindo:** Route chantier Doti 3 – Leroy Gabon. Forêt des abeilles, 0°41'S, 11°54'E, 5 Oct 1993, *Gesnot 8* (BRLU, LBV, MO); Forêt des abeilles, 0°41'S, 11°54'E, 15 Nov 1993, *Gesnot 165* (BRLU, LBV, MO); Station de Recherche de l'Institut de Recherche en Ecologie tropicale (IRET-Ipassa), 0°30.303'N, 12°47.748'E, 18 Dec 2014, *Lissambou, B.J. 300* (BRLU, LBV); *ibid. loc.,* 0°28.62'N, 12°46.71'E, 28 Apr 2015, *Lissambou, B.J. 1134* (BRLU, LBV); Réserve de la Lopé au sud d'Ayem, chantier Soforga, 0°25'S, 11°30'E, 5 Mar 1989, *McPherson, G.D. 13716* (LBV); South of Ayem, western border of Lopé-Okanda Reserve, 0°25'S, 11°30'E, 9 Nov 1991, *McPherson, G.D. 15498* (BR, LBV, P, WAG). **Ogooué Lolo:** Région de Lastoursville, 0°49'S, 12°43'E, 25 Feb 1930, *Le Testu, G.M.P.C. 7936* (BR, P). **Ogooué Maritime:** Région du lac Alombié, +/- 10 km to the north of Mpaga, 0°29.412'S, 9°16.3608'E, Oct 2014, *Lachenaud, O.L.S. 1926* (LBV, BRLU); Mpaga. Département de Bendjé, 0°50.005'S, 9°27.771'E, 11 Oct 2014, *Lissambou, B.J. 0001* (BR, BRLU, L, LBV, MO, P); *ibid. loc.*, 0°50.030'S, 9°26.175'E, 11 Oct 2014, *Lissambou, B.J. 0004* (BR, BRLU, L, LBV, MO, P); Mpaga. Département de Bendjé, SW of Lambaréné, near Lake Ezanga; Conoco drilling site; sandy soil, 1°0.345'S, 10°11.818'E, 13 Feb 1991, *McPherson, G.D. 15293* (LBV).

The Republic Congo. **Niari:** Chaillu, Région de Komono, about Mbaya Mossendjo road, 2°57'S, 12°43'E, 15 Nov 1976, *Sita, P. 4045* (BR).

Greenwayodendron glabrum Lissambou, Hardy & Couvreur, sp. nov.

urn:lsid:ipni.org:names:77192856-1

Fig. 3

Diagnosis. *Greenwayodendron glabrum* is morphologically similar to *G. suaveolens* but differs from it by the absence of trichomes on the petiole, midrib and lower and upper side of the leaf lamina.

Type. CAMEROON. South region: 40 km from Kribi, 5 km E of Edea road, tract of Fifinda-Bella road (SFIA), 6 Feb 1970, *J.J. Bos* 6267 (holotype WAG! [WAG1433854]; isotypes (WAG! [WAG1433855]; YA)

Tree 7–30 m tall, d.b.h. 3–20 cm. Young branches sparsely pubescent trichomes ca. 0.1 mm long; old branches glabrous. Leaves: petiole 2.5–6.2 mm long, 1.0–2.2 mm in diameter, glabrous; lamina 6.5–16.2 cm long, 2.1–5.8 cm wide, length: width ratio 2.2–3.6; elliptic to narrowly elliptic, base rounded or cuneate, apex acuminate, aristate, apiculate or caudate, acumen 4–40 mm long, upper side glabrous, lower side sparsely pubescent to glabrous; midrib glabrous on the upper and lower side; secondary veins 5–7 pairs, upper side glabrous, lower side sparsely pubescent to glabrous, trichomes ca. 0.1 mm long; tertiary veins irregularly and indistinct above. Inflorescence axillary, a 1–4 flowered rhipidium. Floral buds ellipsoid, 4.0–4.5 mm long, 3.5–4.0 mm in diameter,

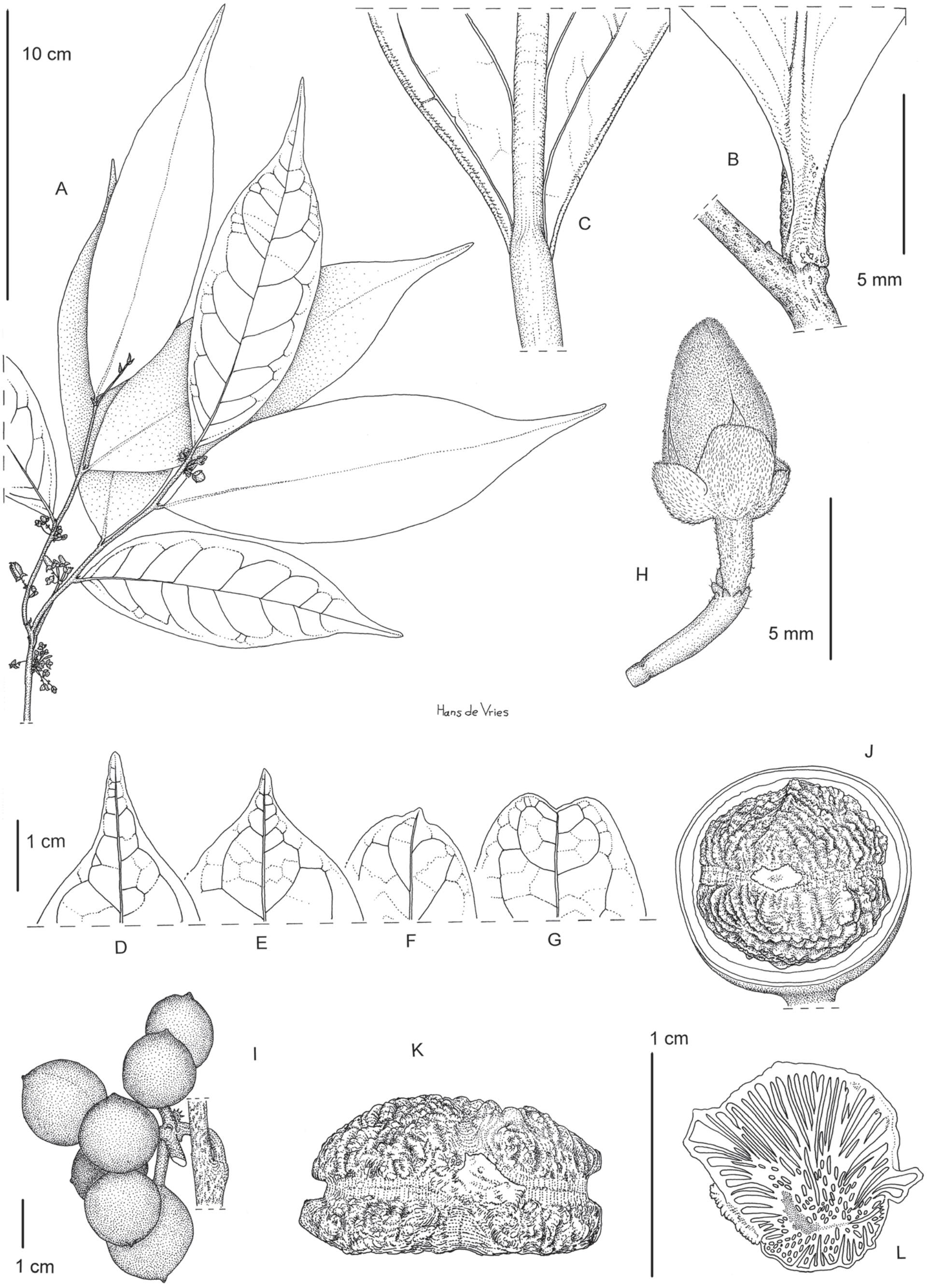

Figure 3. *Greenwayodendron glabrum*. **A** Flowering branch **B** Detail of lower leaf surface **C** Detail of upper leaf surface **D–G** Different types leaf apex **H** Flower bud **I** Infructescence **J** Longitudinal section of fruit revealing seed **K** Seed, latitudinal view **L** Longitudinal section of seed showing ruminations. **A–C, G–H** *Letouzey, R. 12869* **D–F, I–L** Bos, J.J. 6267. Drawing by Hans de Vries.

densely covered with short trichomes. Flowering pedicel 3.5–4.0 mm long, 0.5–1.1 mm in diameter, sparsely pubescent covered with short trichomes, becoming glabrous, trichomes 0.1 mm long, lower bract in lower haft of pedicel, minute, densely pubescent, upper bract apical, just below the calyx, 2.0–2.2 mm in diameter, densely pubescent, trichomes 0.2–0.3 mm long. Sepals 3.0–3.1 mm long, 3.2–3.5 mm wide, length:width ratio ca. 0.9, broadly ovate, imbricate, fused at the base, apex acuminate, base truncate, densely pubescent outside, sparsely pubescent inside, trichomes 0.1–0.2 mm long. Inner and outer petals 12–13 mm long, 2.0–2.5 mm wide, length:width ratio ca. 0.9, narrowly ovate to narrowly elliptic, apex acuminate, base rounded; outside tomentose, trichomes ca. 0.3 mm long; inside sparsely pubescent to glabrous; glabrous part to 4.2–4.6 mm long; green maturing pale yellow. Male flowers: not observed. Hermaphrodite flowers: stamens 10–15 in a single whorl, appressed, 1.2–1.5 mm long and 0.3–0.4 mm wide, stamens tongue-shaped or lobulated in shape; carpels 10–15, 1.1–1.2 mm long, 0.5–0.6 mm in diameter, length:width ratio 2.8, narrowly oblong, densely pubescent; ovules 1–2, oblong; stigmata ovoid, densely pubescent, trichomes ca. 0.1–0.2 mm long. Fruiting pedicel 6–13 mm long, 1.3–2.2 mm in diameter, sparsely pubescent, trichomes ca. 0.2 mm long; stipes 4.5–10.2 mm long and 1.1–3.2 mm in diameter, glabrous; monocarps 2–8, 11.0–21.1 mm in diameter, broadly ellipsoid to globose, sparsely pubescent to glabrous, green turning wine red at maturity; seeds 1–4 per monocarp, 7.0–12.6 mm in diameter, ellipsoid to globose, flattened on one side or hemi-ellipsoid when more than one seed per monocarp, surface covered by a white tegument.

Distribution. Distributed in south-western Cameroon and north-western and central Gabon; 20–750 m (Fig. 4).

Habitat and ecology. A sub-canopy tree, in dense moist evergreen mature and secondary forests.

Phenology. Flowering and fruiting are not well known. A flowering sample was collected in February and several fruiting samples were collected in November in Gabon and in February in Cameroon.

Vernacular names. Unknown.

Uses. Unknown.

Preliminary conservation status of IUCN. Least Concern [LC]. The extent of occurrence (EOO) of *Greenwayodendron glabrum* is estimated to be over 78,284.28 km^2, whereas its area of occupancy (AOO) is estimated to be 108 km^2 (which falls within the limits for Vulnerable status under criterion B2. The species, recorded from Gabon and Cameroon, is now known from at least 31 specimens representing 22 subpopulations. These 20 subpopulations represent 20 different locations (sensu IUCN 2012), many more than 10 locations, which are the upper limit for Vulnerable status under subcriterion ‘a’. *Greenwayodendron glabrum* has been collected in 3 protected areas in Cameroon (Campo-Ma’an National Park), Equatorial Guinea (Monte Alen Nation), Gabon (National Park of Crystal Mountains) and from unprotected areas. This taxon has a low relative abundance except in localities from the region going from the northwest of Gabon to the south of Cameroon where the relative abundance is high. The main threat to *G. glabrum* is its habitat destruction resulting from logging activities and intensive

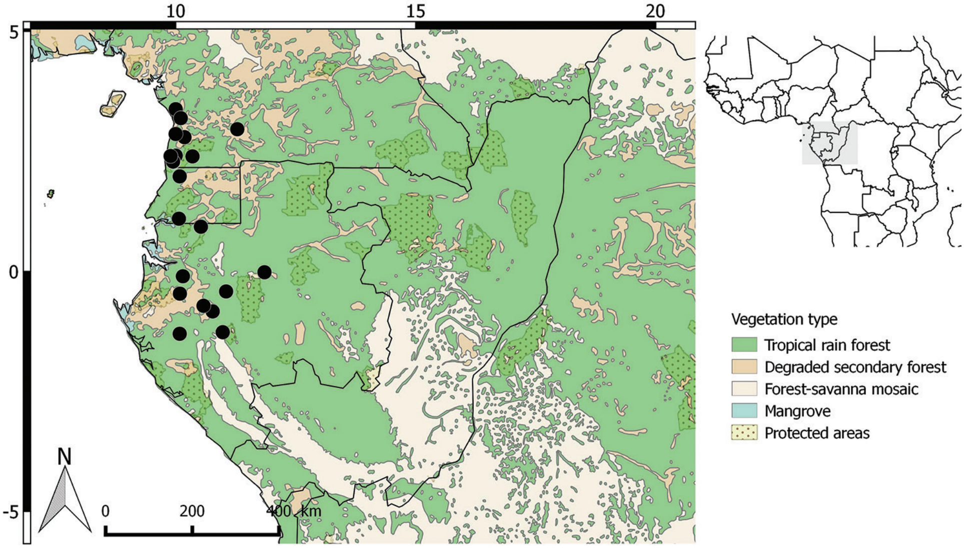

Figure 4. Distribution of *Greenwayodendron glabrum*.

agriculture in Cameroon. Notwithstanding these human activities, with varying levels of impact, the species appears not as threatened as it is abundant. The available information suggests that the number of subpopulations and mature individuals of *G. glabrum*, as well as its EOO and AOO, will not decrease noticeably in the next ten years.

Notes. This species was found growing in sympatry with *G. suaveolens* in southern Cameroon. However, *G. glabrum* differs from other species of the genus by the absence of trichomes on the petioles, midrib and lower and upper side of the leaf lamina. Nevertheless, some specimens do present small isolated tufts of trichomes on the lower side of the leaf lamina. This general lack of pubescence was observed both *in situ* on fresh specimens (adults and juveniles) but also on herbarium samples. This species is also genetically distinct from *G. suaveolens* and other species in the genus based on DNA microsatellite data (Lissambou et al. in prep.) and a nuclear gene phylogenetic analysis (Couvreur et al. in prep).

Selected specimens examined. Cameroon. South Province: 40 km from Kribi, 5 km E of Edea road, tract of Fifinda-Bella road (SFIA), 3°13'N, 10°04'E, 6 Feb 1970, *Bos, J.J. 6267* (BR, P, WAG, YA,); Mvindi 35 km E of Campo, 2°24'N, 10°21'E, 19 Dec 1983, *Kaji, M. 4* (YA, P); Left bank Nyong R., 30 km S of Edea, near [a/the] bridge on [a/the] road to Kribi, 3°33'N, 9°59'E, *Leeuwenberg, A.J.M. 5582* (BR); Parc Campo MA'AN, 2°17.11572'N, 9°57.006'E, 17 Jan 2016, *Lissambou, B.J. 1745* (BRLU); *ibid. loc.*, 2°17.110'N, 9°56.812'E, 17 Jan 2016, *Lissambou, B.J. 1755* (BRLU); *ibid. loc.*, 2°17.5189'N, 9°56.730'E, 18 Jan 2016, *Lissambou, B.J. 1807* (BRLU); Concession forestière Wishema, 2°24.446'N, 9°53.781'E, 19 Jan 2016, *Lissambou, B.J. 1828* (BRLU); *ibid. loc.,* 2°24.411'N, 9°53.698'E, 19 Jan 2016, *Lissambou, B.J. 1830* (BRLU). **Littoral:** Near Ndogtima Nyong (15 km NE from mouthpiece Nyong) Edea, 3°23'N, 10°00'E, 3 Feb 1974, *Letouzey, R. 12869* (BR, YA, P); Canton du Ntem, 16 km SW from Nyabessan, 2°48'N, 10°11'E, 30 Nov 1982, *Nkongmeneck, B.A. 400* (YA, P).

Gabon. Estuaire: Tchimbele, 0°37.07'N, 10°23.57'E, 14 Feb 2010, *Phillippe 83* (BRLU, LBV, MO). **Moyen Ogooué:** Lac Azingo. Grands lacs Moyen Ogooué, 0°28.66'S, 10°1.98'E, 16 Oct 2014, *Lissambou, B.J. 0013* (BR, BRLU, L, LBV, MO, P); *ibid. loc.*, 0°27.768'S, 10°5.2044'E, 17 Oct 2014, *Lissambou, B.J.0014* (BR, BRLU, L, LBV, MO, P); *ibid. loc.*, Lac Azingo. Grands lacs, 0°27.773'S, 10°5.238'E, 26 Oct 2014, *Lissambou, B.J. 0015* (BR, BRLU, L, LBV, MO, P). **Ngounié:** Mabounié, forest on the south side of the N'gounié River, 0°43.116'S, 10°35.933'E, 15 Oct 2012, *Bidault, E. 847* (BRLU, LBV, MO); Upper Waka area, ca.3 km road Mikanda Forestry Camp to Ekanga, 1°18'S, 10°50'E, 29 Mar 2004, *Wieringa, J.J. 5129* (WAG). **Ogooué Ivindo:** South of Ayem; western border of Lopé-Okanda Reserve, 0°25'S, 11°30'E, 19 May 1992, *McPherson, G.D. 15802* (BR, P).

Equatorial Guinea. Rio Muni, Centro-Sur: SW from Monte Alén National Park, on the Mosumo Ecofac transect at 500 m from the beginning of the ride, 1°30'N, 10°04'E, 10 Feb 2001, *Senterre, B. 171* (BRLU, LBV, MO); SW from Monte Alén National Park, 200 m S of Transcito Ecofac de Mosumo at 1620 m from the start of the trail, 1°35'N, 10°03'E, 7 Mar 2001, *Senterre, B. 697* (BRLU, LBV, MO).

Greenwayodendron littorale Lissambou, Dauby & Couvreur, sp. nov.

urn:lsid:ipni.org:names:77192857-1

Fig. 5

Diagnosis. *Greenwayodendron littorale* resembles *G. oliveri* by being small trees and from the shape and size of their leaves. *Greenwayodendron littorale* is however different, being smaller in size (2–5 m versus 5–10 m for *G. oliveri*) and the shape of the stamen connectives being tongue-shaped, obtuse or short versus flattened in *G. oliveri*.

Type. GABON. Ogooué-Maritime: Gamba, ca. 2 km on sand-track to Sete Cama, 15 Mar 1994, *J.J. Wieringa 2476* (holotype: WAG! [WAG0065156]; Isotypes (BM, BR![BR0000015305985], C, EA, FHO, IAGB, IEC, K![K001595], LBV!, LY, MA, MO, MPU, P![P06900984], PRE, UGDA, U![U0045159; U0045160], US, W, WAG! [WAG0065155; WAG0065154], YA, Z.)

Tree 2–5 m tall, d.b.h. 2–5 cm. Young branches at first sparsely pubescent, later glabrous, trichomes ca. 0.1 mm long; old branches glabrous. Leaves: petiole 1.0–3.1 mm long, 0.8–1.2 mm in diameter, sparsely pubescent, trichomes ca. 0.1 mm long; lamina 4.2–7.8 cm long, 2.0–3.8 cm wide, length: width ratio 1.5–2.3, elliptic, base rounded or cuneate, apex acuminate, aristate or caudate, acumen 5–12 mm long, upper and lower side sparsely pubescent; midrib upper side and lower side densely to sparsely pubescent, trichomes ca. 0.1 mm long; secondary veins 4–6 pairs, upper side glabrous, lower side sparsely pubescent, trichomes 0.1 mm long; tertiary veins irregular, indistinct above. Inflorescence axillary, a 1–4 flowered rhipidium. Floral buds ellipsoid, 5.0–5.5 mm long, 2.5–3.0 mm in diameter, densely pubescent; Flowering

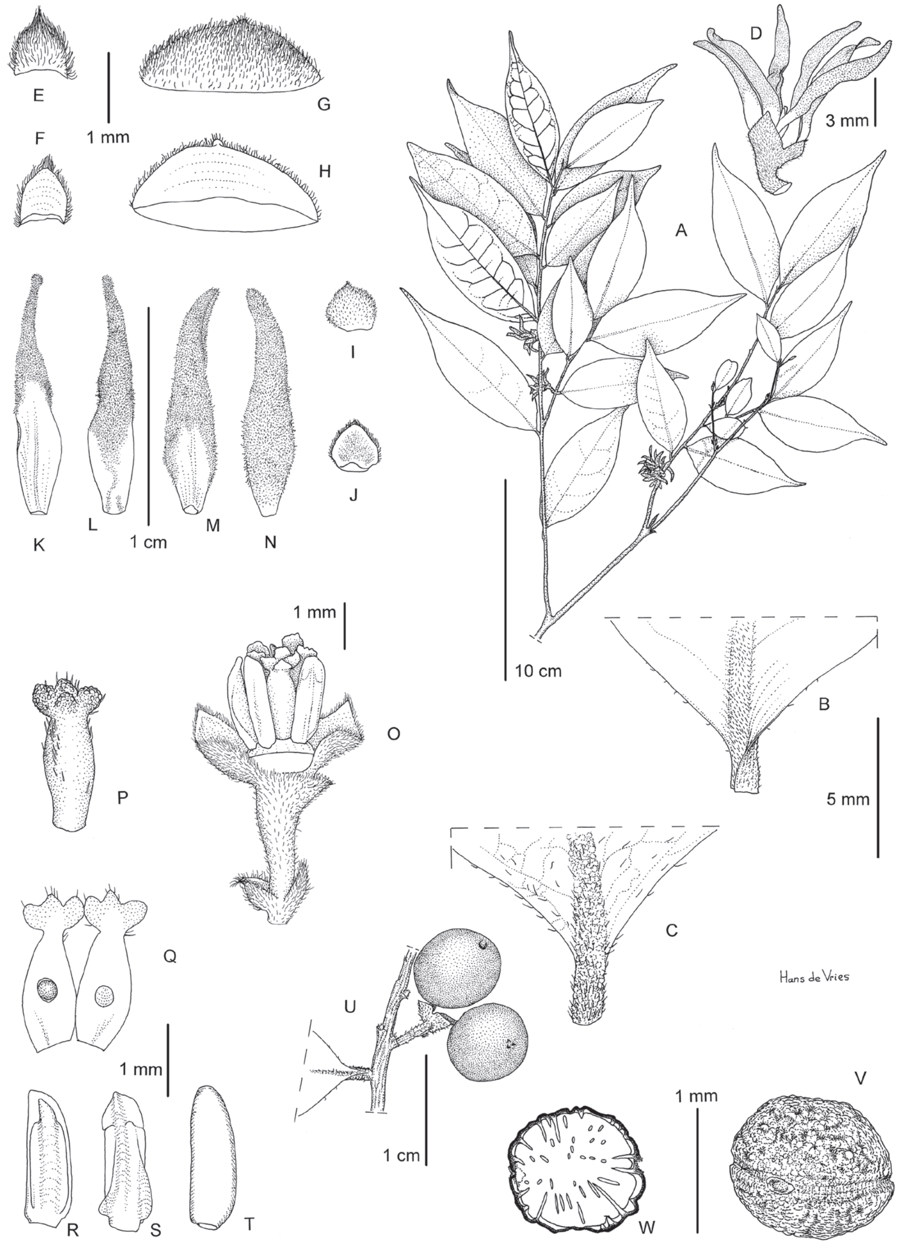

Figure 5. *Greenwayodendron littorale*. **A** Flowering branch **B** Detail of lower leaf surface **C** Detail of upper leaf surface **D** Flower **E** Outside view of basal bract **F** Inside view of basal bract **G** Outside view of upper bract **H** Inside view of upper bract **I** Inside view of sepal **J** Outside view of sepal **K** Inside view of outer petal **L** Outside view of outer petal **M** Outside view of inner petal **N** Inside view of inner petal **O** Detail of hermaphrodite receptacle showing stamens and carpels, all petals removed **P** Detail of one carpel **Q** Longitudinal section of two carpels, showing single ovule **R** Detail of stamen, outside view **S** Detail of stamen, inside view **T** Detail of stamen, inside view **U** Fruiting branch **V** Seed, latitudinal view **W** Longitudinal section of seed showing ruminations **A-T** *Wieringa, J.J. 2476* **U–W** *Breteler, F.J. 5649*. Drawing by Hans de Vries.

pedicel 3.0–3.1 mm long, 0.5–0.6 mm in diameter, densely pubescent when young, becoming pubescent to sparsely pubescent at anthesis, trichomes 0.1 mm long, lower bract in lower haft of pedicel, minute; upper bract apical, just below the calyx, 0.9–1.0 mm in diameter, sparsely pubescent, trichomes 0.2–0.3 mm long. Sepals 1.5–1.9 mm long, 1.9–2.2 mm wide, length: width ratio 0.9 broadly ovate, imbricate, fused at the base, apex acuminate, base truncate, outside densely pubescent, inside sparsely pubescent towards the centre inside, trichomes 0.1–0.2 mm long. Inner and outer petals 11.5–12.5 mm long, 1.6–1.8 mm wide, length: width ratio 0.9, narrowly ovate to narrowly elliptic, apex acuminate, base rounded, outside tomentose, trichomes 0.1–0.2 mm long, inside sparsely pubescent to glabrous, glabrous part to 0.5–1.2 mm long, green maturing pale yellow. Male flowers not observed. Hermaphrodite flowers: stamens 4–5 in a single whorl, appressed, 1.7–2.1 mm long, 0.6–0.9 mm wide, connective tongue-shaped, obtuse, short and little developed; carpels 8–10, 1.9–2.1 mm long, 0.6–0.8 mm wide, length:width ratio 2.8, oblong, densely pubescent; ovules 1, oblong; stigmata ovoid, densely pubescent, trichomes ca. 0.1 mm long. Fruiting pedicel 4.5–6.5 mm long, 1.5–2.0 mm in diameter, sparsely pubescent, trichomes ca. 0.1 mm long; stipes 3–4 mm long and 1–2 mm in diameter, sparsely pubescent; monocarps 1–4, 2.5–4.2 mm in diameter, broadly ellipsoid to globose, sparsely pubescent to glabrous, green turning wine red at maturity; seed 1 per monocarp, 1.5–4.0 mm in diameter, ellipsoid to globose, surface covered by a white tegument.

Phenology. Flowering and fruiting times are not well known. However, a flowering specimen was collected in March and a fruiting one in September.

Distribution. Restricted to the southern coastal part of Gabon and northern Republic of Congo, 5–50 m (Fig. 6).

Habitat and ecology. Growing on coastal and periodically inundated forests, on sandy soils.

Vernacular names. Unknown.

Use. Unknown.

Preliminary conservation status of IUCN. Endangered [EN]. The extent of occurrence (EOO) of *Greenwayodendron littorale* is estimated to be over 4,506 km^2 and its minimal area of occupancy (AOO) is estimated to be 24 km^2 (within the limits for Endangered status under criterion B2). *Greenwayodendron littorale* is endemic to western Gabon and the Republic of Congo and develops in the lowland coastal forest where it is a dominant species in the undergrowth. The species is found in protected areas (Loango National Park). It is also known from several unprotected forests subjected to logging and habitat destruction due to human activities. *Greenwayodendron littorale* is known from eight specimens representing five subpopulations. These 5 subpopulations represent a total of 5 "locations" (*sensu* IUCN 2012), falling within the limit for Endangered status. We project that the ongoing loss of its habitat will induce a continuous decline in the number of mature individuals. *Greenwayodendron littorale* is therefore assigned a preliminary status of EN B1 ab(iii,v)+2ab(iii,v).

Notes. *Greenwayodendron littorale* was previously confused with *G. oliveri* from West Africa. Besides their clear allopatric distribution (West versus Central Africa),

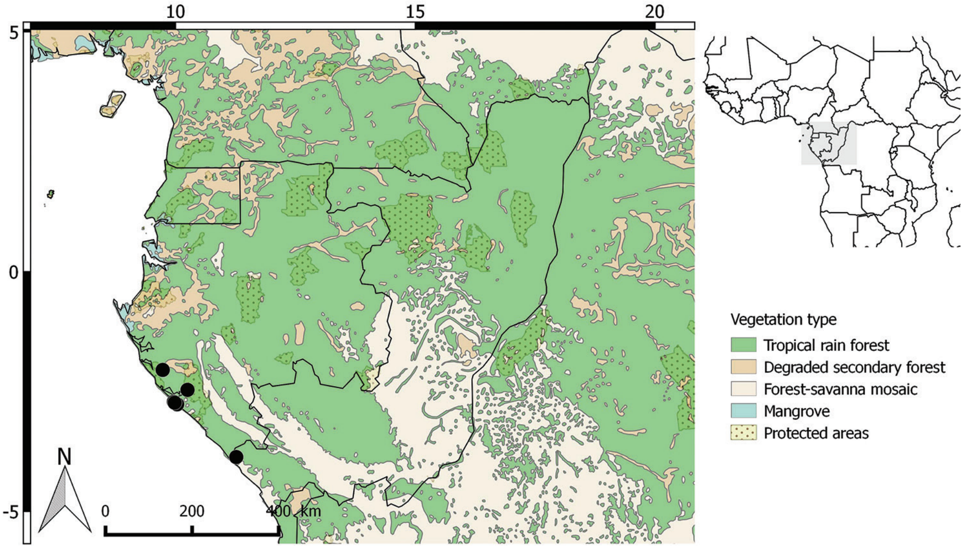

Figure 6. Distribution of *Greenwayodendron littorale*.

both species are distinct at the morphological level with *G. oliveri* being a taller tree (5–10 m versus 2–5 m) with usually longer leaves (up to 15 cm long versus up to 8 cm long). Both species also differ in the shape of the stamen connective, being flattened in *G. oliveri* and tongue-shaped, obtuse, short and little developed in *G. littorale*. Finally, genetic studies also confirm the distinct nature of both species (Lissambou et al. in prep.). To date, only hermaphrodite flowers were observed.

Selected specimens examined. Gabon. Nyanga: 6 km southeast of Mayumba, 3°28.21'S, 10°41.90'E, 20 Nov 2015, *Wieringa, J.J. 8490* (LBV, WAG). **Ogooué Maritime:** Gamba, 2°46'S, 10°20'E, 26 Sep 1968, *Breteler, F.J. 5649* (LBV, WAG); Near Nyanga river, S of Gamba, 2°28'S, 10°15'E, 25 Jul 1998, *Breteler, F.J. 14481* (WAG); Setté Cama, 2°32'S, 9°46'E, 23 Apr 1997, *McPherson, G.D. 16812* (LBV); Gamba. 9.1 km N of Gamba-airport along production road branching from road to Ndogo wharf, 2°44.70'S, 9°59.70'E, 28 Dec 1994, *Wild, J.J.F.E. de 11217* (LBV, BRLU).

Republic of Congo. Kouilou: P.C.A. NZAMBI, around N'tiétié, N'Gongo forest road 4 km from N'Tiété, 3°52'S, 11°16'E, 29 Apr 1974, *Sita, P. 3698* (P).

Greenwayodendron oliveri **(Engl) Verdc., Adansonia sér. 2, 9: 92. (1969).**

Fig. 7

Polyalthia oliveri Engl. & Prantl., Leipzig,W. Engelmann.160. (1897).

Type. IVORY COAST. Lagunes: Bagroo River, 1961, *G.O. Mann* 841 (lectotype, designated by Verdcourt 1969 p. 92, K![K000580895]; isolectotypes K![K000580894], P![P00363358]).

Tree 5–10 m tall, d.b.h. 3–25 cm. Young branches sparsely pubescent to glabrous, trichomes 0.1–0.2 mm long; old branches glabrous; Leaves: petiole 2.0–5.3 mm long, 1.0–2.3 mm in diameter, sparsely pubescent to glabrous, trichomes 0.1–0.2 mm long, indumenta brown; lamina 4.2–15.4 cm long, 2.0–6.1 cm wide, length: width ratio 1.5–3.4; elliptic to narrowly elliptic, base rounded or cuneate, apex acuminate, apiculate, aristate or caudate, acumen 1–33 mm long, upper and lower side sparsely pubescent; midrib pubescent to sparsely pubescent to glabrous on the upper side, pubescent to glabrous on the lower side, trichomes 0.1–0.4 mm long, brown; secondary veins 5–6 pairs, upper side glabrous, lower side pubescent to sparsely pubescent, trichomes ca. 0.1 mm long; tertiary veins irregular. Inflorescence axillary, a 1–4 flowered rhipidium. Floral buds ellipsoid, 5.8–7.5 mm long, 3.1–5.0 mm in diameter, densely pubescent; young pedicel densely pubescent. Flowering pedicel 3.8–6.2 mm long, 0.5–1.3 mm in diameter, densely to sparsely pubescent, trichomes 0.2–0.3 mm long, lower bract (on?) lower haft of pedicel, minute densely pubescent; upper bract apical, just below the calyx, 1.2–1.5 mm in diameter, densely pubescent, trichomes 0.2–0.3 mm long. Sepals 1.3–2.6 mm long, 1.6–3.2 mm wide, length:width ratio 0.5–0.9 broadly ovate, imbricate, fused at the base, apex acuminate, base truncate, outside pubescent, inside sparsely pubescent, trichomes 0.1–0.3 mm long. Inner and outer petals 8–18 mm long, 1.5–2.2 mm wide, length:width ratio 0.5–0.9, narrowly ovate, twisted or not, apex elliptic acuminate, base rounded; green maturing pale yellow, outside tomentose, trichomes 0.1–0.3 mm long, inside sparsely pubescent to glabrous; glabrous part to 4.5–8.0 mm long. Male flowers: stamens 10–25, in several whorls, 1.4–2.2 mm long, 0.4–0.9 mm wide; connectives of the flattened stamen; hermaphrodite flowers: stamens 5–10 in a single whorl, appressed, 1.4–1.8 mm long and 0.3–0.7 mm wide, connective of the stamens crushed-flattened in shape; carpels 10–15, 1.3–2.1 mm long, 0.6–0.9 mm in diameter, length:width ratio 1.2–2.0 narrowly oblong, densely pubescent; ovules 1–2, oblong; stigmata ovoid, densely pubescent, trichomes ca. 0.3 mm long. Fruiting pedicel 6–13 mm long, 1–2 mm in diameter, sparsely pubescent, trichomes ca. 0.4 mm long; stipes 7.5–8.3 mm long, 1.0–2.1 mm in diameter; monocarps 4–8, 3.0–8.2 mm in diameter, broadly ellipsoid to globose, sparsely pubescent, green turning wine red at maturity; seeds 1 per monocarp, 2.8–6.9 mm in diameter, ellipsoid to globose, flattened when more than one seed per monocarp, surface covered by a white tegument.

Distribution. Occurs in Ivory Coast, Guinea Conakry, Ghana, Liberia and Sierra Leone; 55–864 m (Fig. 8).

Habitat and ecology. In moist and semi-deciduous forests.

Phenology. In Ivory Coast and Ghana, flowering from February to April. Fruits are immature from May to September and fruits are mature from October to December.

Vernacular names. Ivory Coast: Mpahouéfon (Abé), Baouéfou, **Sierra Leone.** Gatema (Mendé).

Uses. Unknown.

Preliminary conservation status of IUCN. Least Concern [LC]. The extent of occurrence (EOO) of *Greenwayodendron oliveri* is estimated to be over 260,482,084 km^2, whereas its area of occupancy (AOO) is estimated to be 136 km^2 (which falls within

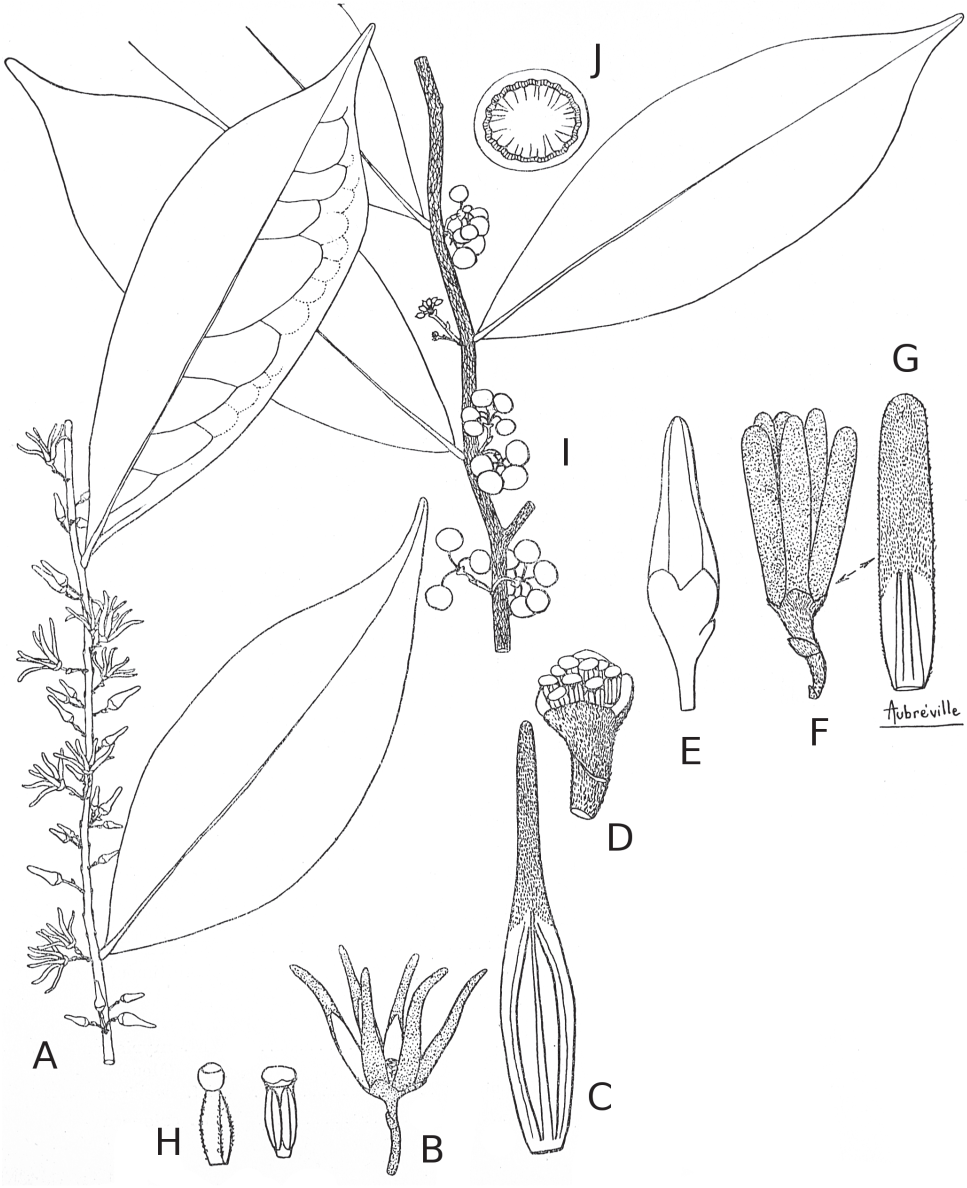

Figure 7. *Greenwayodendron oliveri*. **A** Leaves and inflorescence **B** Open flower **C** Inner petal **D** Androecium, male flower **E** Floral buds **F–G** Petals of a flower bud **H** Carpels and stamens **I** Leaves and fruits **J** Fruit section. Aubréville A (1936) *La flore forestière de la Côte d'Ivoire*, Volume 2. Larose, Paris, 296 p.

the limits for Endangered status under criterion B2). The species, recorded from five countries (Ivory Coast, Guinea Conakry, Ghana, Liberia and Sierra Leone), is now known from at least 34 specimens representing 26 subpopulations. These 26 subpopulations represent 22 different locations (sensu IUCN 2012), many more than 10 locations, which are the upper limit for Vulnerable status under subcriterion 'a'.

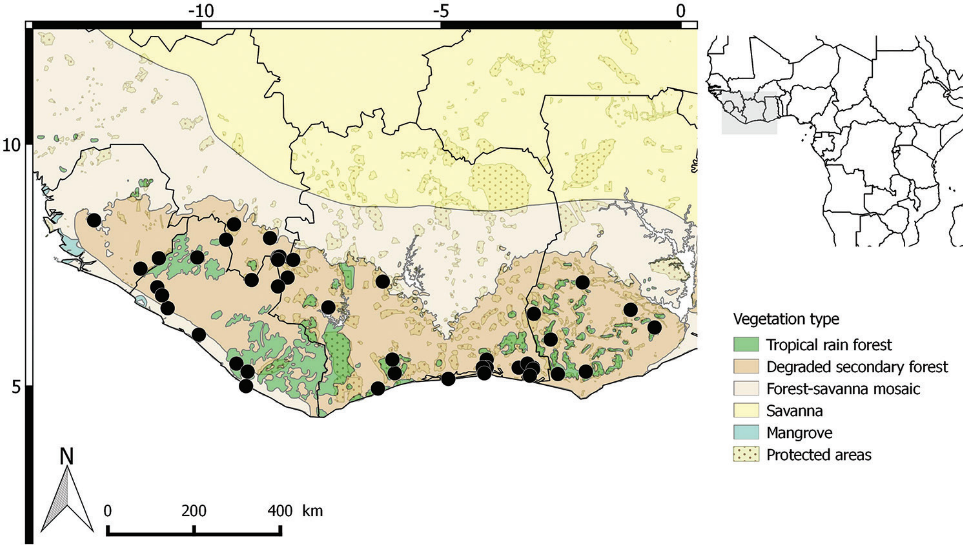

Figure 8. Distribution of *Greenwayodendron oliveri*.

Greenwayodendron oliveri has been collected in 10 protected areas in the following countries (Ivory Coast, Guinea Conakry, Ghana, Liberia and Sierra Leone). The main threat to *G. oliveri* is its habitat destruction resulting from logging activities and intensive agriculture in West Africa. Notwithstanding these human activities, with varying levels of impact, the species appears not as threatened as it is abundant. The available information suggests that the number of subpopulations and mature individuals of *G. oliveri*, as well as its EOO and AOO, will not decrease noticeably in the next ten years.

Notes. This species closely resembles *G. littorale*, see under that species for more details.

Selected specimens examined. Ghana. Eastern Region: Atewa Range Forest Reserve, along footpath going uphill from Apapam to the South, 6°4.8'N, 0°21.6'W, 20 Oct 1994, *Jongkind, C.C.H. 1795* (P); Atewa range Forest Reserve: ca. 2.0 km S of the town of Asiakwa, 6°8.142'N, 0°19.86'W, 15 Nov 1995, *Schmidt, H.H. 1706* (WAG). **Western Region:** Pra Suhien Forest Reserve, 5°15'N, 2°36'W, 10 Nov 1971, *Deaw, J. 371 (*WAG); Dunkwa Dist, Denyau Forest Reserve, 7°9'N, 2°30'W, 19 Feb 1963, *Enti, A.A. 7812* (WAG); Ankasa R.R, 5°35.30'N, 2°26.097'W, 22 Feb 2013, *Hawthorn, H.C. 339* (BRLU).

Guinea. Nzérékoré: Nimba Montains, SMFG iron ore mine concession, Gouan River valley, 7°41.32'N, 8°23.17'W, 14 Oct 2011, *Bilivogui, D. 116* (P); Nimba Mountains, Gouan Valley, 7°41.40'N, 8°22.90'W, 21 Aug 2008, *Jongkind, C.C.H. 8378* (WAG).

Ivory Coast. Bas-Sassadra: Tai – Grabe, forest at W Mono, 5°31'N, 7°19'W, 23 Mar 1969, *Bamps, P. 2225* (BR); 35 km SW of Guéyo, 5°33'N, 6°10'W, 27 Mar 1962, *Leeuwenberg, A.J.M. 3742* (BR, P). **Lagunes:** Abidjan, Banco Forest Reserve, south of Arboretum, 5°22'N, 4°30'W, 20 Jul 1973, *Koning, J. de 1953* (WAG); Baouéfou. Banco, 5°23.40'N, 4°3.07'W, 15 Jan 1931, *Martineau 318* (P); ca. 5 km SE of O.R.S.T.O.M. Ile Boulay beyond lagune Ebrié, 5°16'N, 4°60'W, 22 Jul 1963, sandy soil, *Wilde, W.J.J.O.*

de 510 (BR, P); Pinhou, Plantation planche, 6°38.16'N, 7°21.24'W, Mar 1970, *Bamps 2585* (MO, P). **Région Sud Comoé:** Ashanti, 6°35'N, 1°30'W, Jan 1951, *Andoh, J.E. 5458* (BR); Forêt d'Anguédédou, 5°23'N, 4°80'W, 5 Sep 1969, *Thijssen, M.T. 317* (P).

Liberia. Bomi: Gola Forest NE of Bomi Hills, forest just outside the National Forest, 6°53'N, 10°49'W, 29 Apr 1966, *Bos, J.J. 1953* (BR, P, WAG); Place, 32 km W of Bomi Hills, road to Mano, 6°53.21'N, 10°49.39'W, 12 Nov 1969, *Jansen, J.W.A. 1509* (U). **Grand Bassa:** 32 km N of Buchanan, near waterfalls in the Zoh River (Bassa dial.), 6°40'N, 10°30'W, 20 Nov 1970, *Jansen, J.W.A. 1890* (WAG). **Gbarpolu:** Kpelle National Forest, 93 km E of Bopolu, 7°40'N, 10°50'W, 18 Jan 1978, *Gier, A. de. 205* (WAG); South-west of Togba Ville, 5°28.6'N, 9°16.3'W, 2 Dec 2012, *Jongkind, C.C.H. 10018* (WAG). **Grand Gedeh:** Mim Timber Co (Fijnhout), 5°18'N, 9°2'W, 14 May 1970, *Koning, J. de 453* (WAG); Eastern Province, Putu District. Near the village of Kanweake, ca. 70 km S of Chiehn (Zwedru village), 7°37'N, 8°50'W, 1962, *Wilde, J.J.F.E. de 10083* (P). **Nimba:** Nimba Mountains, 7°12'N, 8°57'W, 10 Apr 1962, V*oorhoeve, A.G.O.1073* (BR, WAG).

Sierra Leone. Eastern Province: Gola National Park, central block. East of Malimbe Camp, 7°39'N, 10°53'W, 23 Oct 2013, *Burgt, X.M. van der. 1612* (P); **Southern Province:** Yoni bani, 8°26.37'N, 12°14.22'W, 11 Nov 1914, *Thomas, N.W. 5059* (BR).

Greenwayodendron suaveolens **(Engl. & Diels) Verdc. Adansonia, n.s. 9: 90. 1969;** Figs 9, 10

Polyalthia suaveolens Engl. & Diels, Monogr. Afr. Pfl. 6: 42. (**1901**).**Type. GABON. Estuaire**: Munda Sibange Farm, 20 Feb 1881, *H. Soyaux 218* (holotype material presumably destroyed at B†; lectotype, here designated: P![P00363356]; isolectotype K![K000580898]).

Polyalthia mortehanii De Wild., Bulletin Jardin Botanique. État Bruxelles, 4: 384. (1914). **Type. DEMOCRATIC REPUBLIC OF CONGO**. **Kasaï-Oriental:** Lekimi, Dec 1913, *S. De Giorgi 1576* (lectotype, here designated: BR![BR8804408]).

Polyalthia aubrevillei Ghesquière ex Aubréville, Fl. For. Côte d'Ivoire, i. 114 (1936). **Type. CAMEROON. South Region:** Bipindé, Urwaldgebiet, 1913, *G. Zenker,* 1306 (lectotype, here designated: P![P01985238]; isolectotypes: L web [L.1761577], MO web, P web [P01985239], WAG web [WAG.1379971].

Maba gossweileri Greves., J. Bot. 67 (Suppl. 2): 76. (1929). **Type. ANGOLA. Cabinda:** Buco Zau - Maiombe, 8 Jan 1917, *J. Gossweiler* 6923 (holotype BM web [BM000547162]; isotype COI! [COI00004858].

Xylopia otunga Exell., J. Bot. 69: 99 (1931). **Type. CAMEROON. Central:** Bitye Yaoundé, 1919, *G.L. Bates 1226* (holotype: BM web [000513697], isotype LISC web [LISC000385]).

Description. Tree 8–45 m tall, d.b.h. 10–125 cm. Young branches at first sparsely pubescent, later glabrous, trichomes 0.2–0.8 mm long, erect; old branches glabrous.

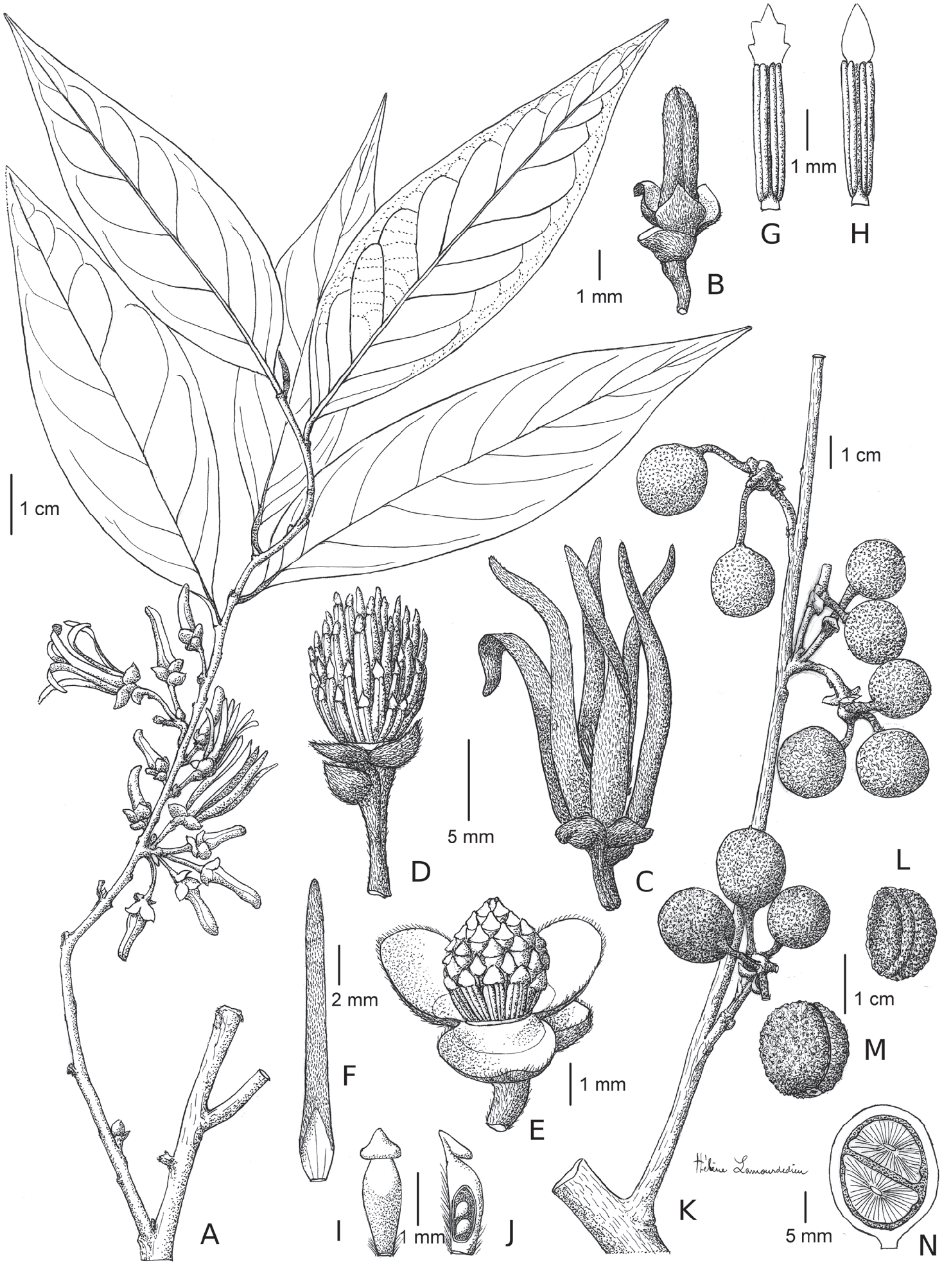

Figure 9. *Greenwayodendron suaveolens*. **A** Flowering branch **B** Flower bud **C** Flower at anthesis **D** Detail of male receptacle, petals removed **E** detail of hermaphrodite receptacle, petals removed **F** Inside view of outer petal **G** Stamen **H** Stamen **I** Carpel **J** Longitudinal section of carpel **K** Fruiting branch **L** Lateral view of seed **M** Seed **N** Longitudinal section of a single monocarp showing two seeds and their ruminations. Drawings Helène Lamourdedieu, © Publications Scientifiques du Muséum national d'Histoire naturelle, Paris; modified from Le Thomas (1969: 205, pl. 37). **A–D, F–H** *Le Testu 9408* **E, I, J** *Gilbert 936* **K–N** *Letouzey 5322*.

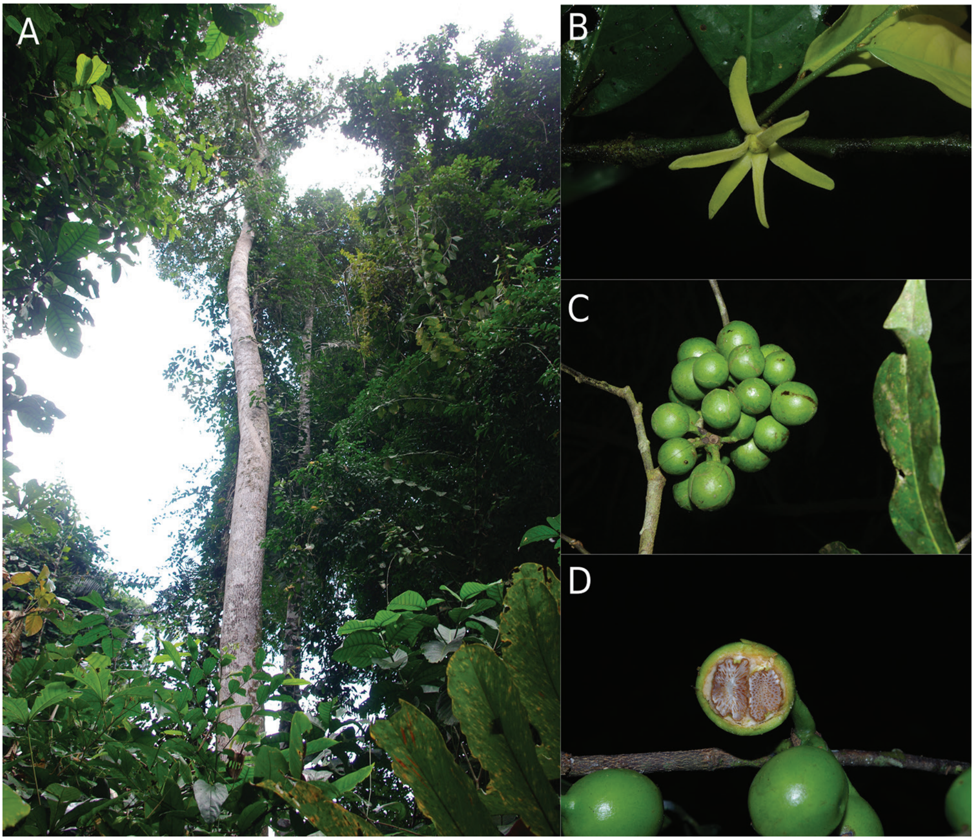

Figure 10. *Greenwayondendron suaveolens*. **A** Habit **B** Flower **C** Fruits and monocarps **D** Latitudinal section of one monocarp showing ruminate endosperm of seeds. Photos: TLP Couvreur.

Leaves: petiole 2–8 mm long, 1.0–2.5 mm in diameter, pubescent to glabrous, trichomes 0.3–0.8 mm long, indumenta brown; lamina 5.1–15.6 cm long, 2.0–6.7 cm wide; length:width ratio 1.5–4.0; elliptic to narrowly elliptic, base rounded or cuneate, apex acuminate, apiculate, aristate or caudate, acumen 6–14 mm long, upper side glabrous, lower side densely to sparsely pubescent; midrib upper side basely sparsely pubescent, lower side densely to sparsely pubescent, trichomes 0.4–0.8 mm long; secondary veins 5–12 pairs, upper side glabrous, lower side pubescent to sparsely pubescent, trichomes 0.3–0.8 mm long; tertiary veins irregularly prominent, slightly raised or indistinct above. Inflorescence 1–4 flowered per rhipidium. Floral buds ellipsoid, 4–8 mm long, 3.0–4.6 mm in diameter, densely pubescent. Flowers, flowering pedicel 3.0–6.3 mm long, 0.8–2.1 mm wide, trichomes ca. 0.5 mm long, bract 1.4–3.1 mm in diameter, pubescent, trichomes 0.4–0.5 mm long. Sepals 1.8–3.8 mm long, 2.1–3.9 mm wide, length:width ratio 0.5–0.9 broadly ovate, apex acuminate, base truncate, outside pubescent, inside sparsely pubescent towards the centre, trichomes 0.1–0.5 mm long. Inner and outer petals 8–18 mm long, 1.3–2.6 mm wide, length: width ratio 0.7–0.9, narrowly ovate, to narrowly elliptic, apex acuminate, base rounded, outside pubescent, trichomes 0.2–0.5 mm long tomentose, erect, inside sparsely pubescent to glabrous, glabrous part to 2.0–4.1 mm long green maturing pale yellow. Male flowers: stamens 16–25, in several whorls, 2–4 mm long, 0.4–0.8 mm wide, tightly appressed; connectives tongue-shaped; hermaphrodite flowers: stamens 5–10 in a single whorl, appressed, 0.9–2.2 mm long and 0.3–0.8 mm wide, connective tongue-shaped; carpels 12–20, 0.7–1.6 mm long, 0.5–0.8 mm wide, length:width ratio 2.3–2.7 oblong, densely pubescent; ovules 1–2, oblong; stigmata ovoid, densely pubescent, trichomes ca. 0.5 mm long. Fruiting pedicel 5.5–12.0 mm long, 1.5–2.5 mm wide, sparsely pubescent, trichomes ca. 0.5 mm long; stipes 4.5–10.0 mm long and 1.0–2.5 mm wide, sparsely pubescent; monocarps 2–8, 7.2–16.4 mm in diameter, broadly ellipsoid to globose, sparsely pubescent to glabrous, green turning wine red at maturity; seeds 1–4 per monocarp, 3.0–11.2 mm in diameter, ellipsoid to globose, flattened when more than one seed per monocarp, surface covered by a white tegument.

Distribution. Widespread across Central Africa, in Nigeria, Cameroon, Republic of Congo, Gabon, Equatorial Guinea (Rio Muni), Central African Republic, Uganda, São Tomé-and-Prìncipe, Democratic Republic of the Congo, Angola (Cabinda) (Fig. 11).

Habitat and ecology. Moist evergreen and semi-deciduous lowland and mid-altitude 30–1600 m in forests.

Phenology. In Gabon and southwest Cameroon, flowering from January to April. Fruits are mature from November to December.

Vernacular names. Cameroon: Moabé noir (Nzime), Otunga (Fang), Otungui (Ewondo) Ntoulen (bassa), Botounga (Baka). **Gabon:** Mutunga (Aduma, Awandji and Nzebi), Otunga (Fang, Kota and Obamba). **Democratic Republic of Congo:** Yako-Ledale, Babua Embaye, Bombai Bo Ilo (Turumbu), Mwamba (Kiumba), Moamba Ndombe, Bombaye, Djako-Ledale. **Central African Republic:** Modienge (Lissango), Motunga. **Nigeria:** Nchua (Bokyi), EDO Ewáé (Edo), Eleku (Isekiri) okeren (Kennedy) Atorewa (Urhobo), agudugbu (Yoruba).

Uses. The wood of *Greenwayodendron suaveolens* is used for carpentry and construction of habitats, but also for the manufacture of hunting and fishing spears (Le Thomas 1969). Bark decoctions are used as a laxative to facilitate childbirth and as a stimulant for women's fertility in the Republic of Congo (Boutique 1951). In Cameroon and Gabon, bark ash is rubbed in scarifications, on the forehead to treat psychosis and bark paste is applied externally to treat rheumatism, headache, epilepsy, toothache and malaria (Le Thomas 1965, Raponda-Walker and Silians 1961). In the Democratic Republic of Congo, decoctions of the bark are used to calm colic. In Nigeria, the leaf has been recorded as being taken internally for menorrhagia.

Preliminary IUCN conservation status. Least Concern [LC]. The extent of occurrence (EOO) of *Greenwayodendron suaveolens* is estimated to be over 2,316,419 km^2, whereas its area of occupancy (AOO) is estimated to be 476 km^2 (which falls within the limits for Vulnerable status under criterion B2). The species, recorded from 10 countries (Nigeria, Cameroon, Republic of Congo, Gabon, Equatorial Guinea (Rio Muni), Central African Republic, Uganda, Sao Tome and Principe, Democratic Republic of Congo and Angola (Cabinda)), is now known from at least 126 specimens

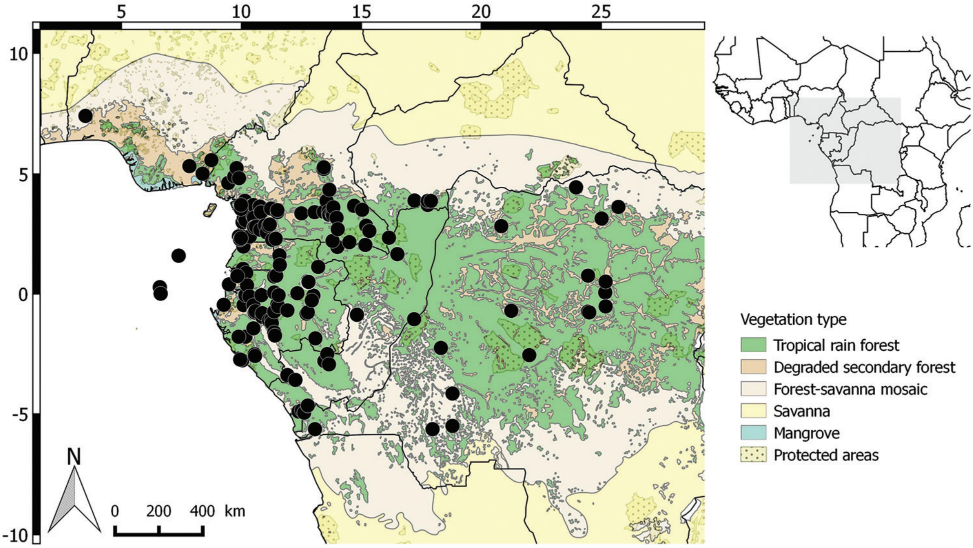

Figure 11. Distribution of *Greenwayodendron suaveolens*.

representing 88 subpopulations. These 88 subpopulations represent 93 different locations (sensu IUCN 2012), many more than 10 locations, which are the upper limit for Vulnerable status under subcriterion 'a'. *Greenwayodendron suaveolens* has been collected in 13 protected areas in the following countries: Nigeria, Cameroon, Republic of Congo, Gabon, Equatorial Guinea (Rio Muni), Central African Republic, Uganda, São Tomé-and-Prìncipe, Democratic Republic of the Congo, Angola (Cabinda). The main threat to *G. suaveolens* is its habitat destruction resulting from urbanisation in Central Africa as well as intensive agriculture and mining in the Democratic Republic of Congo. Notwithstanding these human activities, with varying levels of impact, the species appears not as threatened as it is abundant. The available information suggests that the number of subpopulations and mature individuals of *G. suaveolens*, as well as its EOO and AOO, will not decrease noticeably in the next ten years.

Notes. In Gabon, *G. suaveolens* and *G. gabonicum* occupy the same habitat (mature *tierra firme* forest) and can occur in sympatry. However, *G. gabonicum* has a clearly tomentose pubescence of the lower face of the lamina which is sparsely pubescent in *G. suaveolens*.

In the original description of *P.? acumianata*, Oliver cited two syntypes (*Mann 841* and *Thomson 109*). However, both represent different species (Verdcourt 1969). The former is the type species of *G. oliveri* and the latter a specimen of *G. suaveolens*.

We lectotypified the type specimen of *G. suaveolens*, as the specimen *H. Soyaux* 218 from Berlin is thought to have been destroyed. In describing *Polyalthia mortehani*, De Wildeman (De Wildeman, 1914) did not designate a type specimen. The observation of the two specimens present in BR (*Mortehan 362*; *De Giorgi 1576*), led us to select the sample *De Giorgio* 1576 as the lectotype because it contains the best flowers' information.

In their description of *Polyalthia oliveri*, Engler and Diels (1901) identified the Zenker G.A. specimens from Cameroon as *P. oliveri*. In the Flore Forestière de la Côte d'Ivoire (1936), Aubréville indicates that these Zenker specimens are not *P. oliveri* and introduces the name *P. aubrevillei* (now a synonym of *G. suaveolens*). He refers to the illustration of Engler and Diels (1901) of *P. oliveri* as being *Polyalthia aubrevillei*. He provided a key to separate both species (*P. oliveri* and *P. aubrevillei*) with "Etamines à connectif très allongé aigu" [Stamens with very long and acute connective] for *P. aubrévillei*. Following the code (Art. 38.13, McNeill et al. 2012), this description is valid because it contains a diagnose (the key) and was published prior to 1953 validating the direct reference of a previous description for the specimens belonging to this new name. Based on the specimens cited by Engler and Diels (1901) from Cameroon, we selected *Zenker 1306* as the lectotype because it contains numerous opened flowers.

Finally, it must be noted that analyses of morphology and genetic diversity (Lissambou et al. in press) identified a group of specimens collected in São Tomé and Prìncipe as possibly distinct. However, to date, the status of this group of specimens is inconclusive, partly related to the lack of fertile material.

Selected specimens examined. Angola. Luali – Buco Zan: Ponga Mungo-Subluali, 4°39.10'S, 12°46.10'E, 14 Feb 1916, *J. Gossweiler.* 6275 (COI); Maiombe – Subluali, 4°39.11'S, 12°46.15'E, 31 Sep 1916, *J. Gossweiler* 6229 (COI); Ponga Mungo – Subluali Maiombe, 14 Jan 1916, *J. Gossweiler* 6145 (COI).

Cameroon. Central: 2 km NW of Ossoéssam (Village among Rhaphia) about 40 km SSW Of Mbalmayo, 3°25'N, 11°30'E, 1 Apr 1965, *Leeuwenberg, A.J.M. 5755* (BR, P); 41 km from the LBC Eseka sawmill, 3°39'N, 10°46'E, 14 Feb 1953, *Mpom, B. 74* (P, YA); Forêt classée de Mbalmayo, 3°43'N, 9°59'E, 15 Nov 1970, *Mpom, B. 537* (P, YA); Riverine forest. Bank Nyong Rivers, near the new bridge, about 65 km SSW of Eséka, 3°39'N, 10°46'E, 17 Jul 1964, *Wilde, W.J.J.O. de. 2857* (BR; P). **East region:** Around the village of Mindourou I. UFA managed by Pallisco, 3°16.464'N, 13°23.01'E, 9 Nov 2012, *Droissart, V. 1420* (BRLU); 15 E of Dimako, 4°21'N, 13°40'E, 11 Dec 1965, *Leeuwenberg, A.J.M. 7322* (BR, P, WAG); Colline de l'ENE de Mbalam (140 km) of ESE Djoum, near Souanke-Congo, 2°13'N, 13°48'E, 20 Jan 1973, *Letouzey, R. 11866* (P, YA, WAG); UFA 10039B Palisco Mindourou, 3°26.0712'N, 13°26.081'E, 12 Mar 2016, *Lissambou, B.J. 2100* (BRLU). **Littoral:** 20 km from Kribi lumbering, 3°00'N, 10°03'E, 9 Jun 1970, *Bos, J.J. 4769* (BR, P, YA, WAG); EDEA/Village Pout-loloma, 3°53.041'N, 10°8.824'E, 15 Jan 2016, *Lissambou, B.J. 1725* (BRLU); EDEA/Village Pout-loloma, 16 Jan 2016, *Lissambou, B.J. 1726* (BRLU). **South Region:** La lobé, 0°32'N, 12°46'E, 2 Dec 1927, *Hedin 1943* (BR); Ebolowa-Ambam, 16 km on the road from Ebolowa to Minkok, 2°58'N, 11°17'E, 12 Sep 1975, *Wilde, J.J.F.E de. 8465* (BR, YA, P); 13 km along the road from Kribi to Ebolowa. Raphia swamp with small creek in the middle, 2°52'N, 10°00'E, 26 Nov 1975, *Wilde, J.J.F.E. de 8674* (P, YA, WAG); 10 km environ à l'ESE de Campo Kribi, 2°15'N, 9°60'E, 26 Mar 1968, *Letouzey, R. 9198* (YA, P); Parc Campo MA'AN. Mature primary forest, 2°17.424'N, 9°56.893'E, 18 Jan 2016, *Lissambou, B.J. 1795* (BRLU); Nkomekak, 2°46.990'N, 10°31.858'E, 5 Feb 2016, *Lissambou, B.J. 1900*

(BRLU); Bipendi. Urwaldgebiet, 3°40'N, 10°24'E, 1900, *Zenker, G.A. 2166* (YA, P, WAG); Bipendi. Urwaldgebiet, 3°40'N, 10°34'E, 1912, *Zenker, G.A. 4435* (P, WAG). **South West region:** Near Ngombombeng village, north of Nyasoso, 4°54'N, 9°42'E, 31 Apr 1986, *Etuge, M. 30* (P, U, YA); Mile 12 Mamfé road between Kumba and Baduma, 4°45'N, 9°29'E, 4 Oct 1986, *Nemba, J. 291* (P, WAG).

Central African Republic. Sangha-Mbaéré: Réserve de Dzanga-Sangha. Lowland forest, 2°22'N, 16°10'E, 14 Oct 1988, *David, J. 1414* (BR); Grima (Commun de Ngotto), 3°54'N, 17°13'E, 11 Mar 1999, *Yangakola, J.M. 153* (BRLU); Ngotto, 3°54'N, 17°13'E, 26 Jul 1994, *Yalibanda, Y. 94/36* (BRLU). **Lobaye:** Boukoko, forest, 3°43'N, 17°46'E, 7 Oct 1948, *Tisserant, C. 1172* (BR, P); Boukoko, 3°43'N, 17°46'E, 25 Aug 1953, *Tisserant, R.P.* 2573 (P).

Democratic Republic of the Congo. Kantanga: Kiobo, 5°38'S, 13°07'E, 2 Apr 1944, *Donis, C. 84* (BR). **Kasaï-Oriental:** South o Booke (Terre, Kolo), 2°33'S, 22°00'E, May 1958, *Robin, R. 90* (BR); Dundusana, Lekimi, 2°53'N, 22°23'E, Dec 1913, *Mortehan 362* (BR). **Orientale:** Luki, vallée N'tosi, 5°38'S, 13°04'E, 14 Jul 1948, *Donis, C. 1916* (BR); Yangambi, 0°46'N, 24°27'E, May 1937, *Gilbert 96* (BR, P); Yangambi, Réserve flore Isalowe, 0°44'S, 24°27'E, 19 Aug 1938, *Louis, J. 10916* (MO, P).

Equatorial Guinea. Rio Muni, Cento-Sur: Mont Alén, 1°30'N, 10°04'E, 16 Jun 1998, *Ngomo, D. 342* (BRLU, MO); SO National Monte Alen Park, 200 m S of transct Ecofac of Mosumo 1620 early layon, 1°35'N, 10°03'E, 10 Mar 2011, *Senterre, B. 784* (BRLU, MO).

Gabon. Estuaire: Brigade forestière d'Ekouk (nouvelles parcelles), 15 km north of Koulounga, 0°45'N, 9°50'E, 22 Sep 1983, *Floret, JJ. 1389* (LBV, WAG); S of Ekouk, 0°6'S, 10°20'E, 2 Nov 1983, *Louis, A.M. 308* (LBV, WAG); Forest exploitation Leroy, in road construction area, 0°57'S, 10°52'E, 19 Jan 1983, *Wilde, J.J.F.E. 73* (LBV, WAG, U); Crystal Mountains, 0°53'S, 10°12'E, 20 km NW of Asok, Closed high forest in hilly country, 20 Jan 1983, *Wilde, J.J.F.E. 101* (LBV, WAG, P). **Moyen-Ogooué:** Mabounié, 45 km southwest of Lambaréné, north bank of the Ngounié River, 0°28.854'S, 10°18.846'E, 13 Nov 2013, *Bidault, E. 1297* (BRLU, LBV, MO). **Ngounié:** *ibid. loc.,* 0°26.706'S, 10°19.458'E, 13 Oct 2012, *Bidault, E. 798* (BR, BRLU, LBV, MO); Parc National de Waka, 1°06'S, 11°09'E, 7 Oct 2007, *Boussiengui Nongo, J. 259* (LVB); Between Mouila to Yeno about 60 km from Mouila, 1°44'S, 11°24'E, 21 Sep 1986, *Breteler, F.J. 8086* (BR, LBV, WAG); Massif du Chaillu, northeast of Mouila, Leroy shipyard, 1°40'S, 11°15'E, 24 Apr 1989, *McPherson, G.D. 13907* (BR, P). **Nyanga:** Chantier CEB, ca. 45 km SW of Doussala, 2°35'S, 10°34'E, 22 Oct 1985, *Reitsma, J.M. 1737* (LBV); Kwassa. Fishing village next to Banio Lagune, 3°23'S, 11°55'E, 13 May 2001, *Walters, G.M. 656* (LBV). **Ogooué-Ivindo:** Makande surroundings, ca. 65 km SSW of Booué, 0°41'S, 11°55'E, 9 Feb 1999, *Breteler, F.J. 14970* (LBV); Station de Recherche de l'Institut de Recherche en Ecologie tropicale (IRET-Ipassa), 0°29.808'N, 12°46.961'E, 1 May 2015, *Lissambou, B.J. 1299* (BRLU, LBV, MO); Réserve de la Lopé, south of Ayem, site SOFORGA, 00°25'S, 11°30'E, 10 Mar 1989, *McPherson, G.D 13748* (LBV); 25 km NE of Booué, 0°00'S, 12°20'E, 19 May 1987, *Wilks 1544* (MO, P). **Ogooué-Lolo:** ca. 30 km E of Lastoursville, 0°40'S, 13°00'E, 20 Nov 1991, *Breteler, F.J. 10611* (LBV); Forêt des Abeilles; 9 km S of Confluence Gongue-Offoue, 0°48'S, 11°45'E, 28 Jun 1996, *Wilks, C.M. 2695* (WAG); Région de Lastoursville, 0°49'S, 12°43'E, 12 Mar 1931, *Le Testu M.G. 8698* (BR, P). **Ogooué-Maritime:** Mont Doudou, Campagne, 2°31'S, 10°33'E, 19 Sep 2000, *Bourobou, H.P. 323* (LBV); Toucan, edge road, 1°47'S, 9°53'E, 8 Jun 2002, *Bourobou H.P. 704* (WAG); Lac Azingo. Grands lacs Moyen, 0°28.638'S, 10°1.992'E, 15 Oct 2014, *Lissambou, B.J. 0011* (BR, BRLU, LBV, MO, P, WAG). **Woleu-Ntem:** ca. 25 km WSW of Mintsic, inventory Oveng, 0°44'N, 11°22'E, 9 Feb 1987, *Reitsma, J.M. 2957* (LBV, WAG); ca 25 km WSW of Mintsic, Chantier Oveng, 0°44'N, 11°22'E, 9 Nov 1986, *Reitsma, J.M. 2580* (LBV); Inselberg Milobo, 0°56'N, 10°30.9'E, 8 Jul 2001, Ngok Banak, L. 45 (LBV); Near Essong, ± 5 km NW of Mitzic, along exploitation road, 0°46'N, 11°27'E, 9 Nov 1991, *Louis, A.M. 550* (LBV, P, WAG).

Nigeria. South Eastern State: Boshi extension Forest Reserve, 13°20'N, 9°20'W, 25 May 1971, *Van Meer, P.P.C. 1795* (WAG); Forest Reserve of Enyong, 5°20'N, 7°50'W, 8 Apr 1971, *Van Meer, P.P.C. 1228* (WAG). **Western State:** Abeokuta, 3°30'N, 7°25'W, *Wit, P. 2111* (K).

São Tomé and Príncipe. Prìncipe: Alentours de Zona ecológica. Pico Papagaio (Zona ecológica), 1°36.75'N, 7°391'E, 26 Mar 1998, *Oliveira F. de. 588* (BRLU, MO). **São Tomé. Mé-Zochi:** Bom Sucesso to Lagoa Amelia (site S.P, km 0,6), 0°7.02'N, 6°35'E, 4 Jul 1987, *Lejoly, J. 97/362* (BRLU, MO); Base Pico Maria Fernandes, 0°10'N, 6°38'E, 27 Feb 2003, *Ogonovszky, M. 293* (BRLU, MO); Lago Amelia, south of Bom Sucesso Botanical Garden, 0°16'N, 6°35'E, 11 Feb 2009, *Dauby, G.1574* (BRLU, MO).

Republic of Congo. Kouilou: Forest site at 20 km N of Loundji Moyombe, 0°52'S, 14°49'E, 23 Mar 1969, *Attims, Y. 115* (P); Douakani, 2°56.038'N, 13°8.975'E, *Kamit, T 1015* (K); Road to Boungolo site, Kakamoeka (Point-Noir). **Niari:** Lepoutou, 2°47.895'S, 13°27.52'E, 25 Jun 2011, *Mpandzou, A.L. 1104* (K).

Greenwayodendron usambaricum **(Verdc.) Lissambou, Hardy & Couvreur, comb. nov.**

urn:lsid:ipni.org:names:77192859-1

Greenwayodendron suaveolens subsp. *usambaricum* Verdc., Adansonia, sér. 2, 91. (1969).

Type. TANZANIA. Tanga: Kwamkoro to Potwe. E. Usambaras, Dec 1936, *P.J. Greenway 4810* (lectotype, designated by Verdcourt 1969 p. 69, K![K000580892]; isotypes K![K000580893], EA).

Tree 12–30 m tall, d.b.h not observed. Young branches at first sparsely pubescent, later glabrous, trichomes 0.1–0.8 mm long, erect; old branches glabrous. Leaves: petiole 4.5–6.0 mm long, 1.5–2.1 mm in diameter, densely to sparsely pubescent, trichomes 0.1–0.8 mm long, indumenta brown; lamina 11.2–16.5 cm long, 4.1–6.4 cm wide; length:width ratio 2.3–3.0; elliptic to narrowly elliptic, base rounded or cuneate, apex acuminate, apiculate, acumen 10–25 mm long, upper side glabrous, lower side densely pubescent to sparsely pubescent; midrib upper side basely sparsely pubescent, lower side densely to sparsely pubescent, trichomes 0.3–0.7 mm long; secondary veins 14–18 pairs, upper side glabrous, lower side pubescent to sparsely pubescent, trichomes 0.3–0.8 mm long; tertiary veins irregularly prominent, slightly raised or indistinct above. Floral buds ellipsoid, 6–9 mm long, 2.0–3.2 mm in diameter, densely pubescent. Flowers not observed. Fruiting pedicel 12–13 mm long, 2.0–2.5 mm wide, sparsely pubescent, trichomes 0.4–0.5 mm long; stipes 5.5–6.5 mm long and 1.0–1.2 mm wide, sparsely pubescent; monocarps 2–4, 11.6–12.2 mm in diameter, broadly ellipsoid to globose, sparsely pubescent to glabrous, green turning wine red at maturity; seeds 1–2 per monocarp, 11.0–11.2 mm in diameter, ellipsoid to globose, flattened on one side when more than one seed per monocarp, surface covered by a white tegument.

Distribution. Only known from northern Tanzania, in the East Usambara Mountains, 320–1124 m (Fig. 12).

Habitat and ecology. Mature forest in mid-altitude mountain.

Phenology. Flowering and fruiting are not well known. Nevertheless, floral buds samples were collected in November and December. Fruit specimens were collected from August to November.

Vernacular names. Unknown.

Uses. Unknown.

Preliminary IUCN conservation status. Vulnerable [VU]. The extent of occurrence (EOO) of *Greenwayodendron usambaricum* is estimated to be over 2 km^2 (within the 20,000 km^2 upper limit for Endangered status under criterion B1) whereas its minimal area of occupancy (AOO) is estimated to be 36 km^2 which falls within the limits for Endangered status under criterion B2. *Greenwayodendron usambaricum* is endemic to the Usambara Mountains in Tanzania where it is dominated under canopy. It has been collected in one protected area (Mount Usambara). This species is known from 9 specimens representing 7 subpopulations. These 7 subpopulations represent a total of 7 "locations" (*sensu* IUCN 2012), exceeding the upper limit for Endangered status, but falling within the limit for Vulnerable status. The main *G. usambaricum* threat is habitat destruction resulting from logging and intensive agriculture in Tanzania. We project that the ongoing loss of its habitat will induce a strong continuous decline in the number of subpopulations and mature individuals in the next ten years as well as an important decline of its EOO and AOO. *Greenwayodendron usambaricum* is therefore assigned a preliminary status of VU B1ab(i,ii,iii,iv,v) + B2ab(i,ii,iii,iv,v).

Notes. Initially, individuals from the Usambara Mountains in Tanzania were considered part of *G. oliveri*. Indeed, Engler and Diels (1901) cited the specimen *Scheffler 74* (Usambaras) under *Polylathia oliveri*. Verdcourt (1969) then described the Usambara specimens as a subspecies of *G. suaveolens*, recognising little morphological differentiation with *G. suaveolens*. Here, we consider these individuals as representing a separate species from *G. suaveolens*. Indeed, besides its disjunct and isolated distribution, *G. usambaricum* can be distinguished from *G. suaveolens* by the higher number

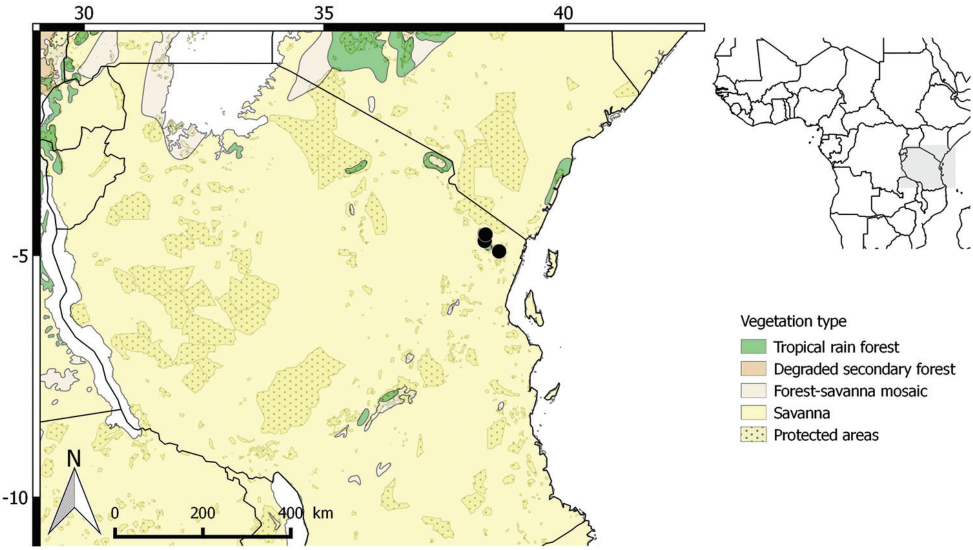

Figure 12. Distribution of *Greenwayodendron usambaricum*.

of secondary veins (≥ 14 versus ≤ 12 for *G. suaveolens*). Nevertheless, more flowering material is needed to better understand the morphological differences between these two species. These observations are corroborated to a certain extent by population genetic data such as microsatellites (Lissambou et al. in prep.) and especially nuclear phylogenetic analyses of the genus (Couvreur et al. in prep.). In the latter case, *G. usambaricum* was reconstructed as sister with maximum support to a clade containing *G. gabonicum, G. glabrum, G. litorale* and *G. suaveolens*.

Specimens examined. Tanzania. **Tanga:** Bomole, Amani, hill trail ca. halfway to summit in area of natural forest, 5°02'S, 39°10'E, 4 Jun 1996, *Johnson, D.M. 1943*. Bomole, Amani Nature Reserve. East Usambara Mountains. Mature forest, 4°55'S, 38°36'E, 10 Oct 2007, *Marshall, A.R. 1260* (K); Bomole, Amani Nature Reserve. East Usambara Mountains, 4°55'S, 38°36'E, 8 Aug 2007, *Marshall, A.R. 1094* (K). Usambara, Afrika, Landsaft, 4°42'S, 38°21'E, 29 Aug 1916, *Peter, A.* 17595 (K, WAG); Usambara, Afrika, Landsaft, 4°42'S, 38°21'E, 29 Aug 1916, *Peter, A.* 18130 (K, WAG); Tanga. Kwamkoro, 4°42'S, 38°21'E, 11 Jun 1986, *Ruffo, A.* 2195 (K); Tanga. Kwamkoro F.R, 4°42'S, 38°21'E, 4 Aug 1961, *Sensé, SR. 3238* (BR).

Excluded names

Polyalthia? acuminata Oliver (Oliver 1868): This name is not validly published as the name was already taken (*Polylathia acuminata* Thwaites, a species from South East Asia)

Polyalthia oliveri (Engl.) var. *gabonica* Pellegrin, Bull. Sco. Bot. Fr., Mém. 31: 67. 1949: *nomen nudum*, no Latin diagnosis.

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Attims, Y. 115 (*suaveolens*)
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Bamps, C. 2240, 2150 (*oliveri*)
Bamps, P.R.J. 2225, 2267, 2394, 2585 (*oliveri*)
Bastin 81, 89, 189 (*suaveolens*)
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Yangakola, J-M. 111, 153 (*suaveolens*)
Zenker, G.A. 328, 1278, 1284, 1306, 1633, 2062, 2166, 2841, 3872, 3872a, 4435, 4739, 4841, 4896 (*suaveolens*)

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New species of *Paullinia* (Sapindaceae) from continental tropical America

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Abstract

Six new species are described in the large Neotropical genus *Paullinia* (Sapindaceae), *P. cidii*, *P. decorticans*, *P. fruticosa*, *P. hondurensis*; *P. martinellii* and *P. wurdackii*. In addition, they are illustrated and contrasted to the morphologically most similar species currently known. The new species were discovered while working on a forthcoming revision of the genus.

Resumo

Ao trabalhar na revisão do grande gênero neotropical *Paullinia*, descobrimos várias espécies novas para a ciência, dentre estas, seis são descritas *P. cidii*, *P. decorticans*, *P. fruticosa*, *P. hondurensis*, *P. martinellii* e *P. wurdackii*. Além disso, estas são ilustradas e contrastadas com outras espécies conhecidas atualmente mais morfologicamente semelhantes.

Keywords

Neotropics, Sapindales, Paullinieae, lianas, climbing shrubs, Amazonia, Brazil, Ecuador, Guatemala, Honduras, Peru

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Introduction

While working on a revision of the Neotropical genus *Paullinia*, we discovered several species new to science. *Paullinia* is one of the largest genera of Sapindaceae with more than 200 species. A recent taxonomic paper establishes *Paullinia* as monophyletic and related to other genera of the Neotropical tribe Paullinieae (Acevedo-Rodríguez et al. 2017). These species although not yet placed in a phylogenetic system, are sufficiently distinct as to be considered new to science. These are here described and contrasted to species considered their closest relatives due to their overall morphological similarities.

Materials and methods

The descriptions of the new species are based on herbarium collections, field notes and photographs taken by the senior author. The recognition of the new species is based on comparative morphological studies that have shown consistent morphological uniqueness (two or more characters) correlated with a particular geographical area and or habitat. Descriptions of the new species follow the format used for the family in our previous publications, ongoing floristic treatments and monographic studies of the genus (Acevedo-Rodríguez and Somner in prep.). Herbarium acronyms given for the studied collections follow Index Herbariorum (Thiers continuously updated). Preliminary conservation status of the new species was assessed by using IUCN guidelines (2001).

Taxonomic treatment

Paullinia cidii Somner & Acev.-Rodr., sp. nov.

urn:lsid:ipni.org:names:77192860-1
Fig. 1

Diagnosis. *Paullinia cidii* differs from *P. bipinnata* Poir., *P. filicifolia* Cuatrec. and *P. hondurensis* Acev.-Rodr. & Somner, the only three congeners with partially tripinnate leaves with triangular outline, by its globose, long-stipitate, unwinged capsules (vs. shortly stipitate, and winged). It is unique within *Paullinia* by having the referred combination of characters.

Type. BRAZIL. Amazonas; Mun. Borba, [Rio Madeira], 30 km along road from Borba to Rio Mapuri; disturbed terra firme forest on clayish soil, 24 Jun 1983 (fr), *C.A. Cid Ferreira 3912* (holotype: NY!; isotypes: INPA, RB-410311!, US-00842969!)

Description. Liana or climbing shrub. Stems terete, striate, minutely ferruginous-pubescent, glabrescent, becoming dark brown to blackish with lines of reddish-brown lenticels when mature; cross section simple. Stipules subulate, 1–1.5 mm long, pu-

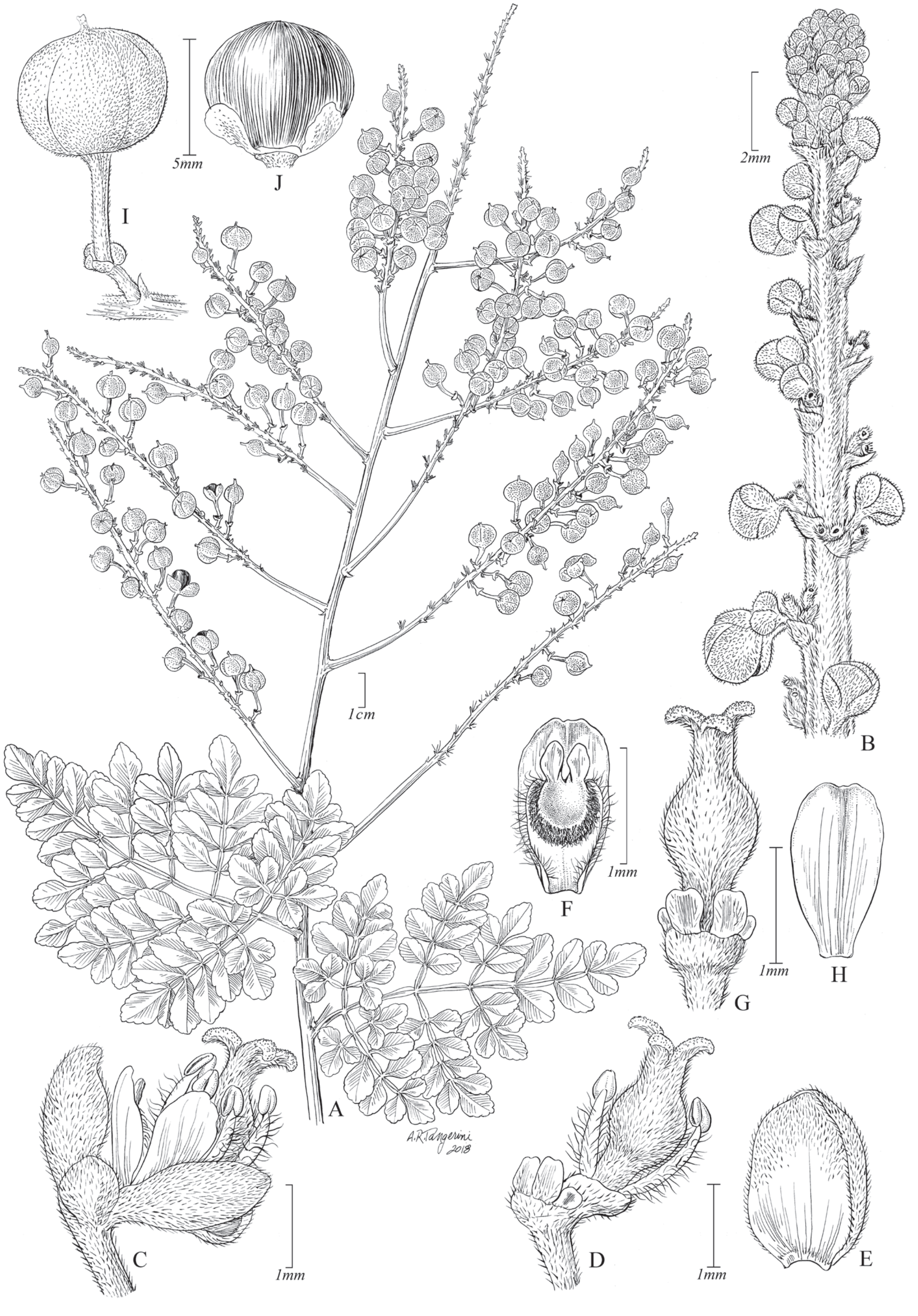

Figure 1. *Paullinia cidii*. **A** Fruiting branch **B** Detail of inflorescence with flower buds **C** Pistillate flower, lateral view **D** Pistillate flower with removed perianth, showing nectary glands and torus **E** Posterior sepal, frontal view **F** Posterior petal with appendix, frontal view **G** Gynoecium and nectary glands at base, posterior view **H** Posterior petal dorsal view **I** Mature capsule **J** Seed, dorsal view. **A, I, J** from *J.E.L.S. Ribeiro et al 2660* (US) **B–H** from *Zartman 7124* (US).

berulent. Leaves partially tripinnate, with triangular outline; petiole narrowly winged or marginate, 1.6–2.5 cm long; rachis winged, 3.8–5 cm long, central ridge ciliate or glabrous, wings 1–2.5 mm wide; leaflets 6–15 × 4–8 mm, chartaceous, discolorous (abaxially lighter), glabrous or puberulent on both surfaces, sometimes abaxially glandular punctate, sessile and attenuate at base, obtuse, rounded, or truncate at apex, with dentate margins; distal leaflets rhomboid, with symmetrical base, lateral leaflets elliptic or obovate, with slightly asymmetrical base; venation craspedodromous, tertiary venation inconspicuous. Thyrses distal and paniculate or axillary and racemose, 15–32 cm long; peduncle 1.8–4 cm long; rachis 3.5–8.8 cm long, minutely appressed pubescent; bracts ca. 0.5 mm long, triangular, puberulent; cincinni 6- to 10-flowered, sessile; bracteoles ca. 0.2 mm long, similar to bracts; pedicels 0.5–0.7 mm long, articulate in lower third. Sepals 5, flavo-sericeous, concave, sub-coriaceous, ciliate, the outer sepals ovate, ca. 0.5 mm long; inner sepals obovate, 1–2 mm long; petals obovate, ca. 1.5 mm long; appendages hood-shaped, ca. 1 mm long, crest fleshy, yellow, bicorniculate in posterior appendages; nectary 4-lobed, pilose, the posterior lobes oblong-ovoid, truncate at apex, anterior lobes minute, torus pilose; sterile stamens with pilose filaments; gynoecium ca. 2 mm long, the ovary ellipsoid, sericeous-tomentose, style 0.1–0.5 mm long. Capsule depressed globose, unwinged, reddish, 5–10 × 7–12 mm, faintly 6-costate, crustaceous, flavo-puberulent, with slightly prominent vein network and a stipe 3–6 mm long; mesocarp 0.1–0.2 mm thick; endocarp glabrous. Seeds 1 or 2 per capsule, depressed globose, 5–7 × 7–9 mm, dark brown, pilose, with white, bilobed arillode in lower third; embryo depressed ovoid, cotyledons sub-straight.

Distribution and ecology. Known only from the state of Amazonas, Brazil in non-flooded (*terra firme*) forest < 100 m elevation.

Phenology. Collected in flower from May to July and in fruit in June.

Etymology. The specific epithet honours Cid [Carlos A. Cid Ferreira], a functionary of INPA and prolific collector of Amazonian plants, who made the type collection.

Conservation status. Known from five collections from lowland, non-flooded, moist forests NE and SE of Manaus, Amazonas, Brazil. Its known distribution has an extent of occurrence (EOO) of 22,000 km^2. Since only a few collections are known of *P. cidii,* it is here treated as data deficient (DD) within IUCN guidelines.

Additional specimens examined. BRAZIL. Amazonas, Rio Abacaxis, Terra Preta, terra firme forest, clayish soil, 4°22'S, 58°40'W, 5 Jul 1983 (fl), *Todzia et al. 2317* (INPA, MO, NY, RB, US); Município Presidente Figueiredo, Rebio Uatumã Grade do PPBio, 22 May 2007 (fl), *Zartman, et al. 7124* (INPA, US), Balbina, Rebio Uatumã, 1°00'S, 59°00'W, 15 Jul 2006 (fr), *Ribeiro et al. 2660* (INPA, US), Vila da Balbina, próximo a Ilha do Jacaré, 20 Jun 2006 (fr), *da Silva et al. 1207* (INPA, US).

Discussion. *Paullinia cidii* is vegetatively similar to *P. bipinnata, P. filicifolia* and *P. hondurensis* by the characters mentioned in the diagnosis. Other species with similar fruits as those found in *P. cidii* include *P. carpopoda* Cambess. and *P. olivacea* Radlk. However, the leaves in *P. carpopoda* are 3-jugate (partially bipinnate), much larger and have entire margins (vs. smaller and serrate in *P. cidii*) while, in *P. olivacea*, they are 5-pinnate and the leaflets are much larger.

Paullinia decorticans Somner & Acev.-Rodr., sp. nov.

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Fig. 2

Diagnosis. *Paullinia decorticans* shares with *P. martinellii* Acev.-Rodr. & Somner the presence of bulbous axillary buds with large cataphylls and large overlapping bracts. However, *P. decorticans* differs from *P. martinellii* by the sericeous-lanate, glabrescent stems with defoliating bark (vs. tomentulose, glabrescent, without defoliating bark), the subulate 3–4 cm long stipules (vs. ovate to cordiform and clasping the stem, 3–5 cm long) and the depressed globose, sessile, puberulous fruits (vs. ellipsoid, long attenuate at the base and hirtellous).

Type. ECUADOR. Napo; Yasuní National Park, 44–45 km along Maxus Petroleum Road, growing on trees along roadside, terra firme forest, 00°40'S, 76°23'W, 200–300 m elev., 18 Jan 1998 (fl, fr), *Burnham 1551* (holotype: US!; isotype: F!, QCA!)

Description. Liana climbing on trees. Young stems sericeous-lanate, with beige, straight, trichomes, 5–8 mm long; mature stems to 3.3 cm diam., sub-terete, furrowed, glabrous, light brown, with lines of lenticels, producing abundant milky latex; bark thin, defoliating in small, rectangular plates; cross section simple, with solid medulla and lobed xylem. Axillary buds bulbous, ovoid, 8–25 mm long; cataphylls numerous, overlapping, acrescent, 5–10 × 1–3 cm, oblong, membranaceous, furfuraceous and sericeous. Stipules subulate 3–4 cm long, abaxially sparsely sericeous, early deciduous. Leaves pinnately 5- or 7-foliolate; petioles and rachis naked, sericeous when young, becoming glabrous and striate, with defoliating, thin epidermal layer; petioles 3–16(24.5) cm long; rachis 3–7.5(17) cm long; distal petiolules 5–15 mm long, lateral and basal petiolules 5–10 mm long; leaflets 9–14 (20) × 3–5 cm, chartaceous, elliptic, oblong or less often lanceolate or oblanceolate, adaxially glabrous, abaxially sparsely sericeous along primary and secondary veins, attenuate at base on distal leaflet, obtuse or rounded and asymmetrical on lateral leaflets, caudate at apex, with entire or undulate margins, venation brochidodromous, tertiary venation percurrent between secondary veins. Thyrses axillary, spicate, 5–14 cm long, axis robust, shortly flavo-tomentose, without tendrils; bracts 7–10 mm long, deltate-ovate, coriaceous, abaxially shortly flavo-tomentose, overlapping; cincinni 4- to 6-flowered, sessile; bracteoles 3–5 mm long, deltate-lanceolate, coriaceous, abaxially shortly flavo-tomentose; pedicels ca. 3 mm long, shortly flavo-tomentose, articulate in upper third. Sepals 5, shortly flavo-tomentose, concave, coriaceous, the outer sepals ovate, ca. 5.5 mm long, inner sepals suborbicular, 7–7.5 mm long, the two anterior sepals connate ca. ½ of their length; petals elliptic, ca. 12 mm long, atrolineate, acuminate at apex; appendages ca. 8 mm long, crest fleshy, bifurcate; nectary 2- or 4-lobed, glabrous, posterior lobes rectangular, brownish, ca. 2 mm long, anterior lobes deltate, ca. 1 mm long, or obsolete; torus flavo-tomentose; filaments densely lanate; gynoecium ca. 5.5 mm long, ovary trilobed-ellipsoid, densely ferruginous-tomentose. Capsule ellipsoid to globose-trilobed, unwinged, reddish, 3–4 × 2.2–3 cm, woody, puberulent or glabrous, sessile, apiculate at apex; pericarp ca. 8 mm thick. Seeds 1 to 3 per capsule, trigono-ellipsoid (with 2 flat sides), ca. 2.5 cm long, testa dark brown, dull, without arillode.

Figure 2. *Paullinia decorticans*. **A** Fruiting branch **B** Detail of abaxial surface of leaflet **C** Insertion of two basal leaflets showing defoliating rachis and petiole **D** Axillary shoot with overlapping cataphylls **E** Bulbous, young axillary shoot covered by cataphylls **F** Stipule **G** Staminate flower, lateral view **H** Posterior petal, dorsal view **I** Posterior petal with appendage, frontal view **J** Staminate flower with removed perianth showing nectary lobes and stamens, posterior view **K** Axillary infructescence with a fruit **L** Seed, ventral view. **A, B, E, G–J** from *Burnham 1551* (US) **C** from *Cerón & Hurtado 4167* (US) **D** from *Vásquez & Jaramillo 17138* (MO) **F** from *Hurtado 2819* (MO) **K, L** from *Vásquez & Criollo 1804* (US).

Distribution and ecology. Known from NW Amazonia, in Ecuador and Peru in non-flooded, dense forest 140–400 m elevation.

Phenology. Collected in flower in May, December and January and in fruit from December to January.

Etymology. The specific epithet refers to the defoliating bark and epidermis of leaf axes present in the new species.

Conservation status. Although *Paullinia decorticans* is known from few collections, they come within an EOO of ca. 80,000 km^2, which include the Yasuní National Park and densely forested areas within Loreto, Peru. Given the low level of threats associated with this vast region, this species is here treated as least concern (LC) within IUCN guidelines.

Additional specimens examined. ECUADOR: Napo. Parque Nacional Yasuní, Pozo petrolero Daimi 2, primary humid, partly flooded forest along river, 00°55'S, 76°11'W, 200 m elev., 26 May–8 Jun 1988 (fl), *Cerón & Hurtado 4167* (US). Pastaza. Petroleum well Villano 2 de Arco, primary, humid forest, 01°25'S, 77°20'W, 400 m 1–18 Dec 1991 (fl), *Hurtado 2819* (MO), Mun. Puyo; Los Vencedores, Experimental Station ESPOCH, ca. 30 minutes by car, S of Puyo, premontane rainforest, 1°30'S, 77°56'W, 13 Dec 1995 (fl, fr), *Soerjato et al. 9392* (F). Orellana. Parque Nacional Yasuní, Parcela permanente de 50 ha del Proyecto "Dinamica del Bosque Yasuní a 1 km de la estación Científica del Yasuní, bosque muy húmedo, 0°41'00"S, 76°24'10"W, 230 m elev., 31 May 2006 (st), *Romero-Saltos et al., 2583* (QCA). PERU. Loreto. Quebrada Sucursari, (N side tributary of Río Napo), mature terra firme forest, 3°15'S, 72°55'W, 140 m elev., 14 Jun 1986 (st), *Gentry et al. 54367* (MO); Maynas. Explorama Lodge ½ way between Indiana and mouth of Napo river, mature forest on lateritic soil, 3°28'S, 72°50'W, 140 m elev., 5 Jan 1991 (st), *Gentry el al 72124* (MO); vicinity of Aguaytía, woods, 1 Jul 1967 (st), *Mathias & Taylor 5076* (F), Pto Alianza, Tamshiyacu creek, primary forest, 04°08'S, 72°55'W, 160 m elev., 28 May 1981 (fr), *Vásquez & Criollo 1804* (US), Explorama Inn, ca. 2 km W of Indiana on Rio Amazonas, well-drained forest on good soil, 3°30'S, 73°02'W, 130 m elev., 14 Feb 1987 (st), *Gentry et al. 55862* (F, MO), Iquitos, seasonally flooded, primary forest, 04°10'S, 73°30'W, 150–180 m elev., 6 Jul 1991 (st), *Vásquez & Jaramillo17138* (MO).

Vernacular name. Equador. Pastaza: *Chunda* (fide *Hurtado 2819*), *Macote* (fide *Mathias 5076*).

Discussion. *Paullinia decorticans* differs from *P. martinellii,* the only other species of Paullinia with bulbous axillary buds with large cataphylls and large overlapping bracts by the features discussed in the diagnosis. *Paullinia decorticans* is the only species within the genus recorded as having defoliating bark and defoliating leaf rachis epidermis.

***Paullinia fruticosa* Somner & Acev.-Rodr., sp. nov.**

urn:lsid:ipni.org:names:77192862-1

Fig. 3

Diagnosis. *Paullinia fruticosa* differs from *P. gigantea* Poepp. & Endl. and *P. killipii* Macbr., the only two other species of *Paullinia* with a combination of simple stems, 5-foliolate pinnate leaves, large foliaceous stipules and cauliflorous inflorescences, by its glabrous, bi-canaliculate, petioles 10.5–25 cm long, rachis 4.2–6.5 cm long; shrubby habit and the presence of unwinged fruits; these two congeners are lianas and their fruits are winged.

Type. PERU. Madre de Dios; Manú National Park, Río Sotileja, low floodplain forest, 400 m elev., 8 Oct 1986 (fr), *Foster et al. 11693* (holotype: US!; isotype: F!)

Description. Erect shrub 1–2 m tall. Stems sulcate, glabrous, light green, sometimes fistulose, with white latex; cross-section simple. Stipules falcate-elliptic to rhombate, 2–3.1 × 1.5–2.2 cm, chartaceous, stramineous, glabrous, with numerous parallel, prominent veins. Leaves pinnately 5-foliolate; petiole and rachis naked, distal petiolules 1–1.5 cm long, lateral petiolules 0.3–0.7 cm long; leaflets 15–26 × 4.5–9.3 cm, chartaceous, glabrous, oblanceolate, elliptic, obovate or ovate, cuneate at base on distal leaflet, obtuse or acute and asymmetrical on lateral ones, obtusely acuminate or acuminate at apex, margins nearly entire or remote crenate-dentate, teeth with a submarginal gland, venation brochidodromous or mixed craspedodromous, abaxially prominent, especially the midvein, tertiary venation reticulate. Thyrses axillary, glomerate, axes glabrous, ca. 2 cm long; bracts ca. 1 mm long, deltate, glabrous; cincinni 5- to 7-flowered; peduncle 4–8 mm long; bracteoles ca. 0.5 mm long, triangular, ciliate; pedicels 5–6.5 mm long, articulate near the base. Sepals 5, glabrous, yellowish, membranaceous, ciliate, the outer sepals ovate, 2–2.5 mm long, inner sepals obovate, 3–3.5 mm long; petals white, elliptic, ca. 3.5 mm long; appendage ca. 3mm long, crest of posterior appendage with 2 corniform projections; nectary 4-lobed, posterior lobes ovate, obtuse or truncate at apex, anterior lobes smaller, pilose; torus glabrous; filaments pubescent, 2–4 mm long, flat, anthers glabrous; gynoecium ca. 2 mm long, the ovary ovoid, ca. 1 mm long, sparsely villose. Capsule ellipsoid, unwinged, 1–1.8 × ca. 0.7 cm, coriaceous, glabrous, densely parallel-veined, sessile, apiculate at apex; mesocarp ca. 0.5 mm thick; endocarp lanose. Seed one per capsule, ellipsoid, 0.9–1.5 cm long, pubescent, with bilobed sarcotesta on lower ½; embryo, elliptic, ca. 0.8 × 0.5 cm, abaxial cotyledon curve, adaxial cotyledon biplicate.

Distribution and ecology. Known from SW Amazonia, in Peru and the state of Acre in Brazil, in non-flooded, dense forest 100–500 m elevation.

Phenology. Collected in flower from August to November and in fruit from October to December and June.

Etymology. The specific epithet refers to the shrubby habit of the new species.

Conservation status. Known from ten collections within an EOO of 150,000 km^2, in moist forest understorey in the south-western Amazon region. Although this species is known only from few collections, its conservation status is here treated as least concern (LC) due to its occurrence within Manú National Park in Peru.

Additional specimens examined. BRAZIL. Acre. Mun. Mâncio Lima; Upper Rio Moa, base of Serra Azul, ca. 07°29'S, 73°39'W, 12 Oct 1986 (fr), *Campbell et al. 8947* (NY). PERU: Loreto; Puerto Arturo, lower Rio Huallaga, below Yurimaguas, ca. 135 m elev., dense forest, 24–25 Aug 1929 (fl), *Killip & A.C. Smith 27876* (US), Santa Rosa, ca. 135 m elev., dense forest, 1–5 Sep 1929 (fl), *Killip & A.C. Smith 28741* (US), *28876* (F, US). Madre de Dios; Manú, Manú settlement in forest, 4 Aug 1973 (fl), *Foster 2469* (F), Parque Nacional Manú, Rio Sotileja, steep forested hills along stream,

Figure 3. *Paullinia fruticosa*. **A** Fruiting branch **B** Detail of stems with stipules and axillary inflorescence **C** Posterior petal, dorsal view **D** Detail of inflorescence **E** Pistillate flower, lateral view **F** Outer sepal, frontal view **G** Posterior sepal, frontal view **H** Posterior petal with appendage, frontal view **I** Pistillate flower with removed perianth showing nectary lobes and staminodes, posterior view **J** Pistillate flower with removed perianth and some staminodes, showing nectary lobes and ovary, posterior view **K** Fruit **L** Seed, ventral view. **A** from *Foster et al 11693* (US) **B, D–L** from *Killip & Smith 27876* (US) **C** from *Klug 4200* (US).

11°40'S, 71°55'W, 400–500 m elev., 2 Oct 1986 (fl), *Foster et al. 11579* (F). San Martín, Juanjui, upper Río Huallaga, 400–800 m elev., forest, Dec 1935 (fr), *Klug 4200* (F, US). Ucayali, Trail from Quebrada Shesha (tributary of Río Abujao) to base of Cerro las Cachoeiras, ca. 70 km NE of Tucallpa, 08°02'S, 73°55'W, 300–400 m elev., 24 Jun 1987 (fr), *Gentry & Diaz 58491* (MO, QCA); Coronel Portillo, Callería, Cuenca del Río Utiquinia, Quebrada Espjoyacu, afluente de la Quebrada Manuela, primary forest, 07°56.67'S, 73°53.61'W, 300 m elev., 8 Nov 2003 (fl, fr), *Graham 2636* (US).

Discussion. *Paullinia fruticosa* is the only species in the genus that is consistently described in collection labels as a shrub. Other species of *Paullinia* (e.g. *P. cuneata Radlk.* and *P. dasystachya*) may present a shrubby habit but only during early stages but later developing into lianas. In addition, *Paullinia killipii.* was originally described as a shrub, based on mixed collections including *Killip & A.C. Smith 27876* and *28876,* which are referable to *P. fruticosa*. As seen in several collections, *P. killipii* develops as a liana that grows into the forest's canopy. These three species also differ from *P. fruticosa* by the presence of winged fruits.

Paullinia hondurensis **Acev.-Rodr. & Somner, sp. nov.**

urn:lsid:ipni.org:names:77192863-1
Fig. 4

Diagnosis. *Paullinia hondurensis* has partially tripinnate leaves, a character that is shared only with *P. bipinnata* Poir., *P. cidii* Somner & Acev.-Rodr. and *P. filicifolia* Cuatrec. *Paullinia hondurensis* can be distinguished from *P. bipinnata* by the glabrous stems, inflorescence axes and calyx (vs. tomentose), as well as by the glabrous and 2–2.8 cm long capsules (vs. pubescent, 1 cm long). *Paullinia hondurensis* can be distinguished from *P. cidii* by its deltate, 2–3 mm long stipules, the nearly terete petioles and the 3-winged, trilobed-turbinate capsules (vs. subulate, 1–1.5 mm long stipules, winged or marginate petioles and unwinged depressed globose capsules). *Paullinia hondurensis* differs from *P. filicifolia* by the glabrescent stems and foliage (vs. pubescent), by the distal leaflets with obtuse apex (vs. acuminate) and by the coriaceous, obtriangular, glabrous capsules with straight wings (vs. chartaceous, ellipsoid, pubescent capsules with revolute wings).

Type. HONDURAS. Dept. F. Morazán; [National Park La Tigra], humid and cloud forests, Rancho Quemado, Montaña La Tigra, 2000 m elev., 10 Dec 1958 (fr), *A. Molina R. 8767* (holotype: US!; isotypes: EAP, MO).

Description. Vine 4–6 m long. Stems nearly terete, striate, reddish-brown, minutely pubescent when young, glabrescent and with lines of minute lenticels when mature; cross section simple. Stipules deltate, 2–3 mm long. Leaves partially tripinnate, with triangular outline; petioles 2.2–4.5 cm long, nearly terete, adaxially bi-canaliculate, with a central pubescent ridge; rachis 6–10 cm long, marginate or with wings 1–2.5 mm wide, revolute, pubescent along central ridge; leaflets 1.6–2 × 0.6–1.3 cm, subcoriaceous, discolorous, glabrous, attenuate at base, acute or obtuse and sometimes mucronate at apex,

Figure 4. *Paullinia hondurensis*. **A** Fruiting branch **B** Detail of cross section of stem **C** Seed, lateral view **D** Seed, frontal view **E** Fruit. All from *Thomas et al. 139* (TEFH).

margins serrate near the apex, distal leaflets rhomboid, lateral and basal leaflet elliptic, obovate or ovate, slightly asymmetrical at base; venation mixed craspedodromous, adaxially with prominent pubescent midvein, abaxially with midvein and secondary veins prominent and hair domatia on lower secondary axils; tertiary venation reticulate. Thyrses axillary, racemose, 4–9 cm long, with pubescent axes; bracts ca. 2 mm long subulate; cincinni shortly stipitate, 3- or 4-flowered; pedicels 2–3 mm long, articulate at middle. Sepals 5, concave, chartaceous, ciliate, the outer sepals ovate 2.5–2.7 × 1.8–1.9 mm, inner sepals sub-orbicular or obovate, 3.4–3.5 × 2.6–3.2 mm; petals oblong, unguiculate, ca. 4 × 2 mm, with glandular trichomes on adaxial surface; appendages ca. 3 mm long, crest emarginate; nectary 4-lobed, puberulent, the posterior lobes ca. 1 mm long, ovate, anterior lobes ca. 0.6 mm, elliptic; stamens unequal, free to base, 2–2.7 mm long, filament pubescent; ovary glabrous. Capsule trilobed-turbinate, 3-winged, red, 2–2.8 × 1.5–2.3 cm, coriaceous, prominently veined, with subglobose coccus, glabrous, truncate and apiculate at apex, wings dorsal-apical (on upper half portion of capsule), 4–7 mm wide, cuneate at base and with stipe 2.5–5 mm long; mesocarp ca. 0.5 mm thick; endocarp yellowish-brown tomentose. Seeds 1–3 per capsule, trigonous-obovoid, ca. 1 × 0.8 cm long, dark brown, glabrous, shiny, with bilobed arillode in lower half; embryo ellipsoid; abaxial cotyledon curve, adaxial cotyledon biplicate.

Distribution and ecology. In moist or cloud forest between 1900–2000 m elevation.

Phenology. Known to flower in July and to fruit in December and January.

Etymology. The specific epithet refers to the country where the species was first collected.

Conservation status. Known only from four localities from montane cloud forests (1990–2000 m elevation) in Guatemala and Honduras, with an approximate EOO of 11,000 km^2. The type collection indicates that the species was frequent in the area, however, due to the small area of occurrence and the lack of recent collections, the species is here treated as vulnerable (VU) within IUCN guidelines.

Additional specimens examined. GUATEMALA. Prov. Alta Verapaz. Mun. San Juan Chamelco. Montaña Caquipec, from Caquipec to Chicacnab I, 15°22'49"N, 90°10'59"W, ca. 1900 m, secondary forest and primary cloud forest, 9 Sep 1999 (st), *Förther 10489* (US). HONDURAS. Dept. Lempira. Dense, mixed cloud forest on the east slopes of Quebrada Naranja, 10 km SE of Gracias, Celaque National Park, 14°33'N, 88°40'W, 1950 m, 29 Jan 1992 (fr), *Thomas et al. 139* (EAP, HEH, MO, TEFH). Dept. F. Morazán, National Park La Tigra, SW of San Juancito, dense, cloud, montane forest, 2000 m, 14 Jul 1961 (fl), *A. Molina R. 10120* (US).

Discussion. We have not been able to infer the phylogenetic relationship of the new species with any other species in the genus due to the lack of adequate quality genome material. The suggested relationships with *P. bipinnata, P. cidii* and *P. filicifolia* are based on the overall morphological similarity discussed in the diagnosis. The current infrageneric classification of *Paullinia* based on fruit morphology (Radlkofer 1895, 1934) would place the new species in the proximity of *P. tricornis* Radlk., as both species have winged, trilobed-turbinate, prominent veined capsules with subglobose cocci. However, *P. hondurensis* clearly differs from *P. tricornis* by the partially tripinnate leaves (vs. 5-pinnate).

Paullinia hondurensis is easily confused with sterile collections of *Serjania rhachitera* Radlk., which has tripinnate leaves with winged rachis and an overlapping distribution. However, sterile *S. rachiptera* can be distinguished *from P. hondurensis* by the sulcate stems that lack lenticels and leaflets that lack hair domatia.

Paullinia martinellii **Acev.-Rodr. & Somner, sp. nov.**

urn:lsid:ipni.org:names:77192864-1
Fig. 5

Diagnosis. *Paullinia martinellii* is unique within the genus by its large (3–5 cm long), membranaceous, clasping stipules and overlapping cataphylls and by the large (ca. 1 cm long), overlapping, boat-shaped bracts, resembling no other species of *Paullinia*.

Type. BRAZIL. Pará; Mun. Oriximiná, Rio Caxipacoró, km 72 on the road north of Cachoeira Porteira, along disturbed roadside, 30 Jun 1980 (fl, fr), *Davidson & Martinelli 10661* (holotype US!; isotypes INPA!, NY!).

Description. Liana. Stems furrowed and tomentulose when young, becoming glabrous, terete and lenticellate with age; cross-section simple; xylem with wide rays and phloem wedges. Tendrils similar to those in other *Paullinia* but not associated with inflorescences. Cataphylls overlapping, similar to stipules in size and texture, produced at base of lateral branches. Stipules foliaceous, membranaceous, ovate to cordiform, clasping the stem, 3–5 × 2–4 cm, puberulous, conspicuously veined, with undulate margins. Leaves pinnately 5-foliolate; petiole and rachis nearly terete, adaxially furrowed, tomentose or tomentulose; petiole 14.5–16.5 cm long, pulvinate at base; rachis 6–8.5 cm long; petiolules pulvinate, tomentulose, distal petiolule ca. 1 cm long, lateral petiolules 2–5 mm long; leaflets membranaceous with linear punctations, glabrous except veins tomentulose on adaxial surface and puberulent on abaxial surface, acuminate at apex, margins dentate or subentire, with secondary veins projecting as glandular teeth; venation craspedodromous, abaxially prominent; tertiary venation reticulate-percurrent between the secondary veins; distal leaflet 24–25 × 12–15.5 cm, broadly elliptic to obovate, attenuate at base; lateral leaflets 15–18 × 9–11 cm, oblong to ovate, rounded or sub-cordate at base. Thyrses cauliflorous, lacking tendrils, in fascicles of 5–7; axes robust, woody, 20–34 cm long, ferruginous-tomentose; bracts ovate concave, crustose, 8–10 × 6–8 mm, minutely sericeous; cincinni 2- or 3-flowered, sessile; bracteoles broadly elliptic, concave, tomentulose, ca. 5 mm long, covering the cincinnus; pedicels articulate at base. Sepals 4, sericeous tomentose, crustose, the outer sepals ovate, ca. 5 mm long, inner sepals broadly elliptic, concave, 5.5–6 mm long, anterior sepal emarginate; petals obovate, ca. 6.5 mm long, abaxially covered with glandular trichomes; appendages hood-shaped, ca. 5 mm long, with fleshy, yellow, corniform crests, two in posterior appendages, one in anterior appendages; nectary 4-lobed, posterior lobes rectangular with emarginate or truncate apex, anterior lobes triangular; torus villose; filaments connate at base, lanate throughout, 2–3 mm long; anthers glabrous. Capsule (immature) ellipsoid, unwinged, orange, ferruginous-hirtellous, long-attenuate at base, and obtuse and apiculate at apex.

Figure 5. *Paullinia martinellii*. **A** Branch fragment with leaf, stipules and tendrils **B** Branch with cataphylls **C** Flower bud covered by bracts and bracteoles **D** Immature flower **E** Inflorescence **F** Posterior sepal, frontal view **G** Branch showing stipules **H** Immature fruit **I** Immature cincinnus with overlapping bracts and bracteoles. **A–D, F, H** from *Davidson & Martinelli 10661* (US) **E, G** from *Martinelli & Davidson 7158* (RB) **I** from *Cid et al. 1223* (INPA).

Distribution and ecology. Terra firme forest at elevations below 100 m.

Phenology. Old flowers and young fruits known from June–July.

Etymology. The specific epithet honours Dr. Gustavo Martinelli, eminent Brazilian botanist at Rio de Janeiro Botanical Garden, who made the first collection of this species.

Conservation status. Known from three collections from two localities with an EOO of ca. 3,000 km^2 in the Municipality of Oriximiná in the state of Pará, Brazil. The new species seems to be rare and, because of its small known EOO, it is here treated as vulnerable (VU) within IUCN guidelines.

Additional specimens examined. BRAZIL. Pará; Mun. Oriximiná, Estrada da Cachoeira Porteira km 72, próximo ao igarapé Caxicoporó, margem esquerda, mata firme, solo argiloso, 1 Jul 1980 (fl), *Cid Ferreira et al. 1223* (INPA), Rio Cachorro, Cachoeira de Varador, terra firme forest, 90 m elev., 22 Jun 1980 (fl, fr), *Martinelli & Davidson 7158* (MG, NY, RB).

Discussion. *Paullinia martinellii* is the only species within the genus known to have large (3–5 cm long), membranaceous, clasping stipules and large (ca. 1 cm long), overlapping, boat-shaped bracts. Its position within the genus has not been ascertained as no adequate material is available for carpological or molecular analyses.

Paullinia wurdackii Acev.-Rodr. & Somner, sp. nov.

urn:lsid:ipni.org:names:77192865-1
Figs 6, 7

Diagnosis. *Paullinia wurdackii* differs from *P. ingifolia* Juss. by the lanate or lanate-tomentose stems and inflorescence axes (vs. tomentose or tomentulose), the oblong-lanceolate, ovate or deltate bracts 9–15 mm long that enclose the cincinni (vs. deltate, 1–2.5 mm long, not enclosing the cincinni), the ovate-lanceolate bracteoles 4–5 mm long (vs. deltate, ca. 1 mm long) and the sessile, depressed-globose capsules (vs. long stipitate, globose or trigonous-globose).

Type. ECUADOR. Orellana; Yasuní Forest Reserve, 1 km W of PUCE Scientific Station, moist forest along road, 0°41.956'S, 76°28.075'W, 250–300 m elev., 5 Jul 1995 (fl♀), *Acevedo-Rodríguez & J.A. Cedeño 7654* (holotype US!, isotype QCA).

Description. Liana 20–25 m long. Stem terete, ferruginous lanate or lanate-tomentose, becoming glabrous and lenticellate with age, producing abundant milky sap; cross section simple, up to 10 cm diam. Stipules early deciduous, leaving a scar 7–10 mm wide. Leaves imparipinnate with 1 basal pair of trifoliolate pinnae and 2 or 3 pairs of simple lateral leaflets (thus with 11 or 13 ultimate leaflets); petiole and rachis winged; petiole 10.5–23.5 cm long, wings 0.4–0.8 cm wide; rachis 7–14 cm long, wings 0.4–0.7 cm wide, puberulent; lower pair of trifoliolate pinnae with winged petiolules 1.4–1.8 cm long; leaflets 13.5–16 × 3.8–4.5 cm, coriaceous, oblong, oblong-elliptic or less often oblanceolate, discolorous, abaxially papillate; cuneate at base on distal leaflet, acute, obtuse, attenuate or sometimes asymmetrical on lateral leaflets, obtusely acuminate to caudate at apex with margins remotely serrate on distal third to half of the

Figure 6. *Paullinia wurdackii*. **A** Leaf with stem fragment **B** Inflorescence **C** Bulbous, axillary bud **D** Cross section of stem **E** Pistillate flower, lateral view **F** Posterior petal with appendage, frontal view **G** Fruit **H** Flower with removed perianth showing nectary lobes, staminodes, and gynoecium **I** Seed, ventral view. **A** from *Croat 58698* (MO) **B–F, H** from *Acevedo-Rodríguez & Cedeño 7654* (US) **G, I** from *Pitman 602* (US).

blade, teeth with a sub-marginal gland-like callosity; venation craspedodromous, abaxially prominent with scattered setose trichomes, without domatia, tertiary venation reticulate-percurrent between secondary veins. Thyrses terminal, paniculate, 24.5–27 cm long; axes robust, ferruginous lanate or lanate-tomentose; branches 8–16 cm long, with axillary bulbous buds; cataphylls oblong, concave, 13–37 × 8–17 mm, ferruginous sericeous-lanate, deciduous, leaving a scar 5–12 mm wide; bracts 9–15 mm long, oblong-lanceolate, ovate or deltate, flavo sericeous, enclosing the cincinni, which are clothed by overlapping bracteoles, similar in shape, texture and indument to the bracts, but smaller (4–5 mm long), both bracts and bracteoles early deciduous; cincinni 5- to 7-flowered, sessile or sub-sessile; pedicels 2–3 mm long, articulate at middle. Calyx light green when fresh, albo-tomentose when dry, sepals 4, concave, coriaceous, outer sepals ovate, 4–5.5 mm long, inner sepals oblong-ovate, 4.5–7 mm long, the anterior sepal emarginate; petals white to cream, oblong, 4.5–7 mm long, papillate, appendages hood-shaped, 4–5 mm long, crest of posterior appendages emarginate; nectary 4-lobed, the posterior lobes ca. 1.5 mm long, oblong, emarginate at apex, anterior lobes oblong, smaller than the posterior; filaments lanate, 4.5–7 mm long, connate at the very base; gynoecium 3–3.5 mm long; ovary trilobed-ovoid, flavo sericeous-tomentose. Capsule depressed-globose, unwinged, 2–2.3 × 1.8–2 cm, 3-costate, woody, ferruginous sericeous-tomentose, sessile, apiculate at apex; mesocarp 2.5–3 mm thick; endocarp sericeous-tomentose. Seeds oblong-obovate, trigonous in transverse section, entirely sarcotestal, ca. 1.5 cm long.

Distribution and ecology. Western Amazonia, in moist forests between 250–375 m elevation.

Phenology. Flowering from October to April and known to fruit in July.

Etymology. The specific epithet honours the late Dr. John J. Wurdack from the Smithsonian Institution, Curator of Melastomataceae and assiduous collector of South American plants, who made one of the first collections of this species.

Conservation status. Known from an EOO of ca. 150,000 km^2 in western Amazonia on Ecuadorian and Peruvian territories. The new species is known only from 5 collections from this vast area, which seems to indicate that the new species is extremely rare. However, because the species occurs in a National Park in Ecuador and in vastly forested areas of Peru with no immediate threats to the ecosystem, the new species is here treated as least concern (LC) within IUCN guidelines.

Additional specimens examined. ECUADOR. Orellana. Aguarico, Reserva Etnica Huaorani, maxus road and pipeline construction Project, km 100–102, moist primary forest on red soils & undulating hills, 0°56'S, 76°13'W, 250 m elev., 18 Jul 1994 (fr), *Pitman 602* (MO, QCNE, US); Sucumbíos, 9.3 km E of Lumbaqui, ca. 0°06'N, 77°16'W, 375 m elev., 29 Apr 1984 (fl), *Croat 58698* (MO, NY, QCA, US). PERU. Amazonas. Pongo de Manseriche, on high land, without date (fl), *Tessmann 3889* (NY); Provincia Bagua, forested ridge on right bank of Río Santiago, 3–4 km above mouth, 300–350 m elev., 29 Oct 1962 (fl ♂, ♀, fr), *J.J. Wurdack 2476* (US).

Discussion. *Paullinia wurdackii* is vegetatively similar to *P. ingifolia*. as both species are robust lianas with imparipinnate leaves with trifoliolate lower pinnae and winged rachides and petioles; oblong, elliptic or oblanceolate leaflets with caudate apices; large

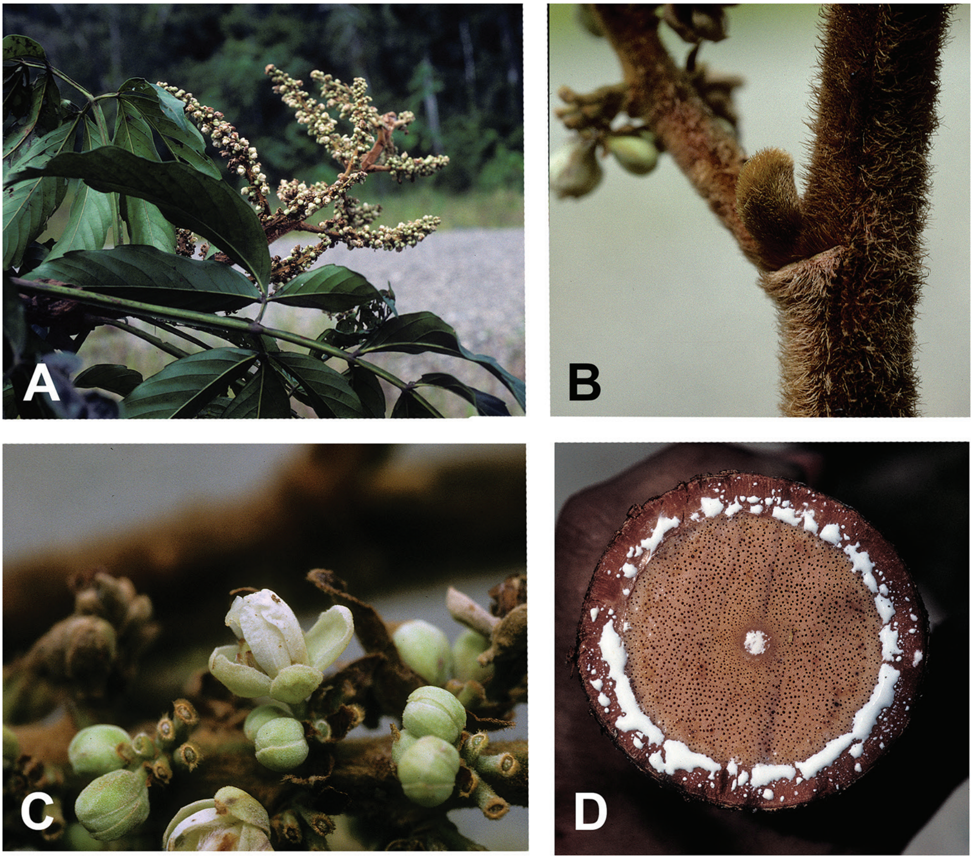

Figure 7. *Paullinia wurdackii*. **A** Flowering branch **B** Inflorescence axis with lanate indument and bulbous axillary bud covered by cataphylls **C** Detail of inflorescence showing sessile cincinni and few remnant bracts **D** Cross section of stem showing regular anatomy and abundant milky latex emanating from the phloem and medulla. Photos by P. Acevedo, based on *Acevedo-Rodríguez & Cedeño 7654*.

deciduous stipules; and unwinged, woody fruits. *Paullinia wurdackii* however, is easily recognised by its lanate or lanate-tomentose stems and inflorescence axes, the large bracts and overlapping bracteoles that enclose the cincinni and the sessile fruits. While *P. ingifolia* has a wide distribution that ranges from Costa Rica south to Bolivia, *P. wurdackii* is restricted to the NW region of the Amazon basin.

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RESEARCH ARTICLE

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Tacca khanhhoaensis V.S. Dang & Vuong (Taccaceae), a new species from southern Vietnam

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Abstract

Tacca khanhhoaensis V.S. Dang & Vuong (Taccaceae) is described as a new species from Hon Ba Nature Reserve in southern Vietnam. This species is morphologically similar to *T. chantrieri* and *T. ampliplacenta* but differs from its allies by several salient characters: size of leaves and petioles, inflorescent much shorter leaves, number of flowers, stigma lobes, buds colour. A description, conservation assessment, together with photographs and a key to the species of *Tacca* in Vietnam are presented.

Keywords

Hon Ba Nature Reserve, Khanh Hoa, Taccaceae, Taxonomy, Vietnam

Introduction

The family Taccaceae is composed of only one genus, *Tacca* J.R. Forster & G. Forster and its 11 species (Ding et al. 2000). Its species are distributed mainly in tropical regions of Asia and Oceania, except for *T. parkeri* Seem. known only in South America (Ding and Larsen 2000, Drenth 1972, 1976). Currently, six species of the genus *Tacca* have been recorded in Vietnam: *T. chantrieri* André, *T. integrifolia* Ker Gawl., *T. leontopetaloides* (L.) Kuntze, *T. palmate* Blume, *T. plantaginea* (Hance) Drenth and *T. subflabellata* P.P. Ling & C.Ting (Pham 2000, Vo 2007).

During botanical field surveys in Hon Ba Nature Reserve, Khanh Hoa Province, southern Vietnam in 2017, a species of *Tacca* was collected. After thorough examination of the *Tacca* species in Drenth (1972, 1976), Ding and Larsen (2000), Pham (2000), Vo (2007) and Zhang et al. (2005, 2006), re-examination of specimens deposited in the Vietnamese herbaria VNM, HN and VNMN, as well as specimen images on the website of JSTOR Global Plants, P and K, we concluded that our sample belongs to a new species, which we describe in this study.

Materials and methods

The description of the new species was based on material collected in Hon Ba Nature Reserve (over 19,000 ha), Khanh Hoa Province, southern Vietnam (Figure 1). The measurements and description were prepared from living plants with a ruler accurate to 0.5 mm. Herbarium material was dried and preserved in 70% ethanol and stored at the Institute of Tropical Biology (VNM). All the photos were taken with a Canon 600D fitted with a EF–S 60 mm f/2.8 Macro USM lens.

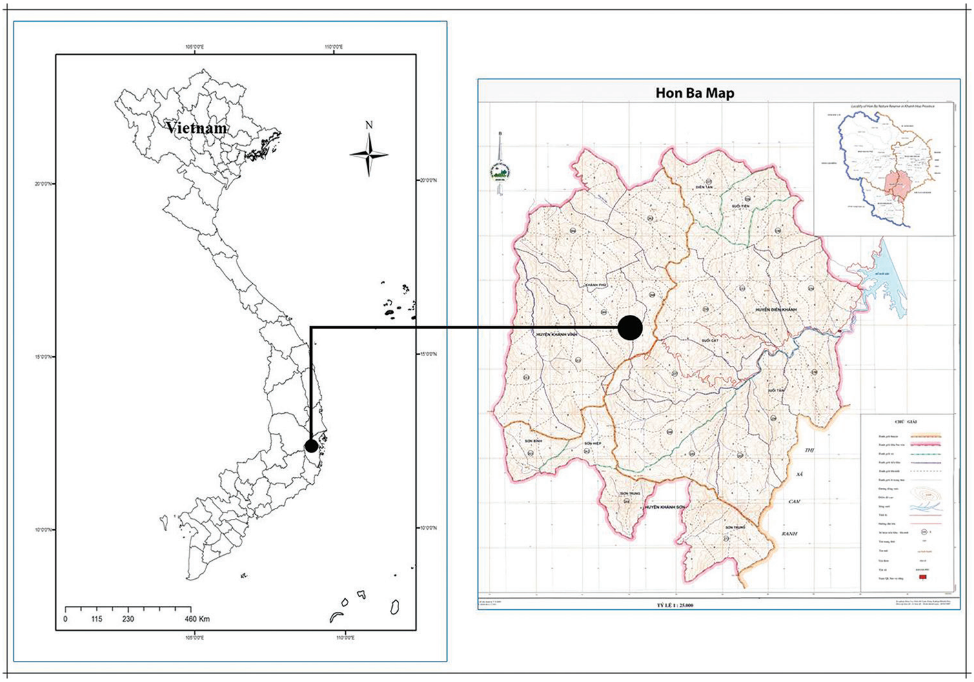

Figure 1. Type locality of *Tacca khanhhoaensis* V.S. Dang & Vuong.

Taxonomy

Tacca khanhhoaensis V.S. Dang & Vuong, sp. nov.

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Figures 2, 3

Diagnosis. *Tacca khanhhoaensis* is similar to *Tacca chantrieri* André in leaf shape and bracts, but differs from it in having shorter leaves (up to 45 cm vs. 60 cm long) and petioles (up to 22 cm vs. 43 cm long), inflorescences with fewer flowers (5 to 10 vs. 15 to 25), 2-lobed stigma vs. 3-lobed stigma and dark red buds vs. green buds. The new species is also somewhat similar to *T. ampliplacenta* L. Zhang & Q.-J. Li of China, but differs from it by having smaller leaves (30–45 × 10–14 cm vs. 55 cm long) and fruits (3–4 × 1.5–2 cm vs. 4–6 × 2–2.5 cm) and very short petioles (22 cm vs. 50 cm long), inflorescent much shorter leaves (vs. longer), number of flowers (5 to 10 vs. 25) and dark red buds vs. black-purple.

Type. VIETNAM. Khanh Hoa Province, Hon Ba Nature Reserve, terrestrial under the shade of the canopy on dry soil or close to the stream, alt. 353 m, 12°06.36'N, 108°59.46'E, 16 April 2017, *Truong Ba Vuong, Mang Van Lam, Dang Van Son, BV256* (holotype VNM!; isotype VNM!, the herbarium of Hon Ba Nature Reserve!).

Description. Perennial herbs. *Rhizome* cylindric, fleshy, with many stout roots. *Leaves* radical, 5 to 8 leaves; laminae oblong to obovate or oblong-elliptic, 30–45 × 10–14 cm, apex acute, base attenuate, margin slightly undulate; main veins pinnate; petiole erect, 14–22 × 0.5–1 cm, green to purplish-green, sheathing at base. *Inflorescence* umbel, 5–10-flowered; scape erect, 20–38 cm long, nodding, pale green-purple at base, more dark purple above. *Involucral bracts* 4, decussate, sessile; two outer bracts vertical arrangement, unequally, ovate-lanceolate, 4.5–5.5 × 2–2.5 cm, black-purple, apex acuminate, base obtuse; two inner bracts horizontal arrangement, broadly ovate, 6–6.5 × 4–5 cm, deep purple red with dark purple at margin, apex acuminate, base rounded, margin undulate, slightly erose at base, possessing numerous veins. *Filiform bracts* 8–15, up to 32 cm long, dark purple. *Flowers* narrowly triangular, buds dark red flowers greenish-purple when young, when older black-purple; perianth tube 5–6 mm long, white and purple inside. *Perianth lobes* 6, three outer lobes narrowly ovate or triangular, 10 × 3–5 mm, apex acute; three inner lobes broadly ovate to ovate-triangular, 8–10 × 4–6 mm, apex acuminate, recurved when flower fully opening. *Stamens* 6, attached to the base of perianth tube, beset with stigma lobes, dark purple to dark red, filament short, anther and connective forming a hood-like structure, individual stamens with 2 thecae, each theca 2 mm long. *Stigma* 3, ca. 5 mm in diameter, fleshy, apex 2-lobed with finely white pubescence, lobes slightly curved down; style 8–9 mm in diameter, sub-orbicular to round-triangular in outline, surface with minute black hairs. *Ovaries* inferior, obtriangular, 5–6 × 8–9 mm, dark red. *Fruit* berry, 3–4 × 1.5–2 cm, black to dark purple, triangular in transverse section; stalk 1.5–2 cm long. *Seeds* reniform to nearly half orbicular, 1.5–5 × 1–1.5 mm, slightly brown, 4–7-ribbed.

Figure 2. *Tacca khanhhoaensis* V.S. Dang & Vuong. **A** Habit **B** Inflorescent much shorter leaves **C** Habitat.

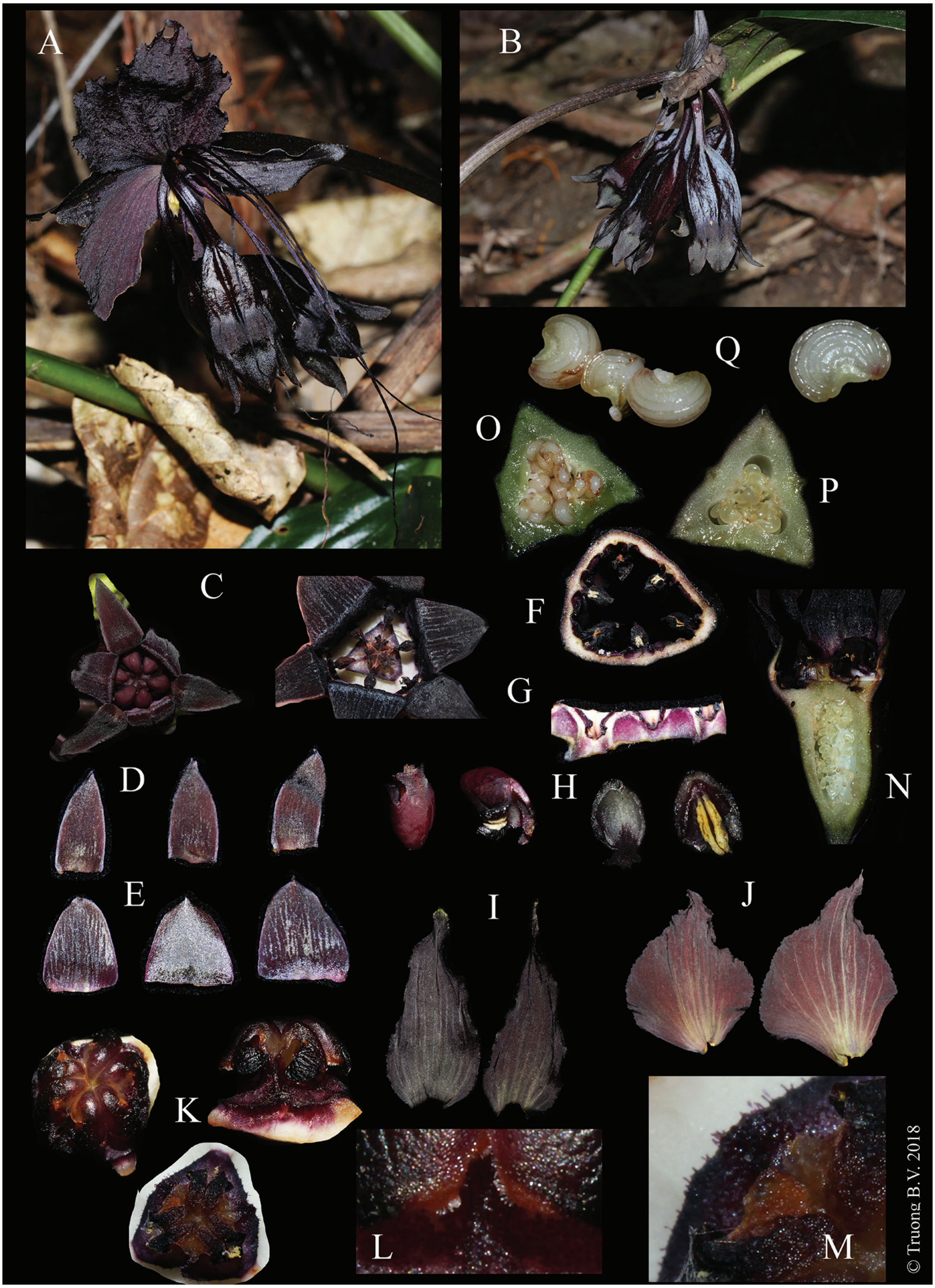

Figure 3. *Tacca khanhhoaensis* V.S. Dang & Vuong. **A** Inflorescence **B** Fruits **C** Flowers, top view showing perianth lobes, stamens and stigma **D** Outer perianth lobes **E** Inner perianth lobes **F** Inner surface of perianth tube **G** Anther and connective **H** Longitudinal section of Anther with a pair of theca **I** Outer involucral bracts **J** Inner involucral bracts **K** Stigmas **L** Finely pubescent hairs at apex of stigma lobes **M** Black hairs on style **N** Longitudinal section of flower **O** Transverse section of fruit **P** Transverse section of ovary **Q** Seeds.

Other specimen examined. VIETNAM. Khanh Hoa Province, Hon Ba Nature Reserve, growing under forest canopy, uncommonly along the riparian forest, alt. 400 m, 12°06.37'N, 108°59.44'E, 16 November 2017, *Truong Ba Vuong, Mang Van Lam, BV256a* (VNM!, the herbarium of Hon Ba Nature Reserve!).

Phenology. Flowers were observed in April and May. Immature and mature fruits were observed in May and June.

Distribution and habitat. *Tacca khanhhoaensis* is only known from Hon Ba Nature Reserve, Khanh Hoa Province, southern Vietnam. It was growing under the shade of the canopy on dry soil or close to the stream, where *Aporosa tetragona* Tagane & V.S. Dang, *Bambusa* sp., *Barringtonia macrostachya* (Jack) Kurz, *Calamus* sp., *Croton* sp., *Desmos* sp., *Goniothalamus flagellistylus* Tagane & V.S. Dang, *Ixora* sp., *Microcos tomentosa* Sm., *Phyllanthus reticulatus* Poir. and *Streblus indicus* (Bureau) Corner are dominant.

Etymology. The name of this species is derived from the name of the province Khanh Hoa, where the species was discovered.

Conservation status. *Tacca khanhhoaensis* was collected from a small population under forest canopy in Hon Ba Nature Reserve at 300–400 m altitude. The forest habitat where we found this new species was frequently logged and disturbed. Therefore, *Tacca khanhhoaensis* is assessed as Critically Endangered (CR) based on the IUCN Red List Categories (IUCN 2012), although some individuals might be found by more thorough surveys.

Note. *Tacca khanhhoaensis* is morphologically similar to *T. chantrieri* and *T. ampliplacenta*. The comparisons of morphological characters amongst these three species are summarised in Table 1.

Key to the species of *Tacca* in Vietnam

1	Leaves lobed	**2**
–	Leaves entire	**3**
2	Leaves 3-lobed, each lobe pinnately. Filiform bracts present	***T. leontopetaloides***
–	Leaves 3–13-lobed, each lobe simple. Filiform bracts absent	***T. palmata***
3	Leaf-base attenuate and decurrent. Fruit dehiscent	***T. plantaginea***
–	Leaf-base attenuate but not decurrent. Fruit indehiscent	**4**
4	Inner two involucral bracts long petiolate	***T. integrifolia***
–	Inner two involucral bracts sessile	**5**
5	Inner involucral bracts suborbicular-fan-shaped	***T. subflabellata***
–	Inner involucral bracts broadly ovate	**6**
6	Inflorescence with 15–25-flowered. Apex of stigma lobes 3-lobed. Seeds reniform, brown, 9–14-ribbed	***T. chantrieri***
–	Inflorescence with 5–10-flowered. Apex of stigma lobes emarginated or 2-lobed. Seeds reniform, slightly brown, 4–7-ribbed	***T. khanhhoaensis***

Table 1. Morphological comparison of *Tacca khanhhoaensis* with its closest congeners (modified from Drenth 1972; Phengklai 1993; Ding and Larsen 2000; Pham 2000; Zhang et al. 2008; Baruah et al. 2015).

Characters	*T. khanhhoaensis*	*T. chantrieri*	*T. ampliplacenta*
Leaves			
– number	5 to 8	3 to 12	5 to 10
– shape of leaf lamina	oblong to obovate or oblong-elliptic	oblong to oblong-elliptic	oblong-obovate
– length of leaf lamina	30–45 cm	20–50(–60) cm	55 cm
– length of petiole	14–22 × 0.5–1 cm	11–43 × 0.2–0.5 cm	30–50 × 0.7–1.2 cm
Inflorescence			
– number of flowers	5 to 10	15 to 25	25
– length of scape	20–38 cm	6–63 cm	40–70 cm
– outer involucral bracts	ovate-lanceolate,	ovate-lanceolate,	lanceolate to oblong-ovate,
	4.5–5.5 × 2–2.5 cm	2–9 × 0.8–4 cm	6–8 × 3–4 cm
– inner involucral bracts	broadly ovate,	broadly ovate,	broad-triangular,
	6–6.5 × 4–5 cm	2.5–10 × 1.5–9 cm	10–16 × 8–10 cm
Flowers			
– colour of buds	dark red	green	black-purple
– outer perianth lobes	narrowly ovate or triangular,	oblong-ovate or narrowly triangular,	oblong,
	10 × 3–5 mm	5–12 × 3–8 mm	12 × 8 mm
– inner perianth lobes	broadly ovate,	broadly ovate or triangular,	broad-ovate,
	8–10 × 4–6 mm	4–11 × 4–12 mm	12 × 10 mm
Apex of stigma lobes	2-lobed	3-lobed	2-lobed
Ovaries	5–6 × 8–9 mm	2–7 × 3–5 mm	5–8 × 10 mm
Fruits	3–4 × 1.5–2 cm	2–4 × 1–2 cm	4–6 × 2–2.5 cm
Seeds	1.5–5 × 1–1.5 mm, slightly brown, 4–7-ribbed	2–4 × 1–2 mm, brown, 9–14-ribbed	2–3 × 1.5–2 mm, brownish-red, many ribbed

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RESEARCH ARTICLE

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Revision of *Muhlenbergia* (Poaceae, Chloridoideae, Cynodonteae, Muhlenbergiinae) in Peru: classification, phylogeny, and a new species, *M. romaschenkoi*

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Abstract

A taxonomic treatment, phylogeny based on analysis of six DNA sequence markers (ITS, *ndhA* intron, *rpl32-trnL*, *rps3*, *rps16* intron and *rps16-trnK*) and classification of *Muhlenbergia* for Peru is given. Seventeen species and one presumed hybrid are recognised. *Muhlenbergia romaschenkoi* **sp. nov.** is newly described from the Río Huallaga Valley, northeast of Huánuco. The type of *Podosemum angustatum* [≡ *Muhlenbergia angustata*] clearly aligns with what we had been referring to as the hybrid between this species and *M. rigida*. Therefore, we adopt the next available heterotypic name, *Muhlenbergia coerulea,* for what we had been calling *M. angustata* and change the hybrid designation to *M. coerulea* × *M. rigida*. Lectotypes are designated for *Epicampes coerulea* Griseb., *Muhlenbergia affinis* Trin., *Muhlenbergia berlandieri* Trin., *Muhlenbergia beyrichiana* Kunth, *Muhlenbergia elegans* var. *atroviolacea* Kuntze, *Muhlenbergia elegans* var. *subviridis* Kuntze and *Muhlenbergia phragmitoides* Griseb.

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† Deceased

Resumen

Brindamos un tratamiento taxonómico, una filogenia basado en el análisis de seis marcadores de secuencia de ADN (ITS, *intrón ndhA*, *rpl32-trnL, rps3, intrón rps16, rps16-trnK*) y la clasificación de *Muhlenbergia* para Perú. Se reconocen diecisiete especies y un supuesto híbrido. *Muhlenbergia romaschenkoi* **sp. nov.** es descrita como especie nueva procedente del valle de Huallaga, al noreste de Huánuco. El tipo de *Podosemum angustatum* [≡ *Muhlenbergia angustata*] se alinea claramente con lo que nosotros habíamos referido como el híbrido entre esta especie y *M. rigida*. Por lo tanto, adoptamos el siguiente nombre heterotípico disponible, *Muhlenbergia coerulea* para lo que habíamos estado llamando *M. angustata*, y cambiamos la designación híbrida a *M. coerulea* × *M. rigida*. Los lectotipos son designados para *Epicampes coerulea* Griseb., *Muhlenbergia affinis* Trin., *Muhlenbergia berlandieri* Trin., *Muhlenbergia beyrichiana* Kunth, *Muhlenbergia elegans* var. *atroviolacea* Kuntze, *Muhlenbergia elegans* var. *subviridis* Kuntze y *Muhlenbergia phragmitoides* Griseb.

Keywords

classification, ITS, lectotypification, *Muhlenbergia*, Peru, phylogeny, plastid DNA sequences, Poaceae, systematics, taxonomy

Introduction

Peru is located in the central and western part of South America between 0° and 18° south latitude. The central Andes or backbone divides Peru into three great regions: coast, mountain, and forest (Weberbauer 1936). The coastal region next to the Pacific Ocean is an extremely xeric, narrow, sandy plain that rises abruptly to the east. This region is occasionally transected by river valleys and the climate is very mild and warm. The mountain region or "cordillera de Andes" consists of high peaks and extensive high plains (altiplano) that are sometimes dissected by deep, narrow valleys. The climate in this region can be very cold and it is not uncommon to have snow above 3800 m. The tropical forest region, east of the cordillera, extends into the Amazonian river basin where there are high levels of biodiversity associated with many different habitats. The climate here is very warm and humid with high levels of precipitation and there are large rivers including the Río Marañon and the Río Ucayali that feed into the Río Amazonas.

The Poaceae is a diverse family occupying a myriad of terrestrial habitats in Peru, with the exception of the permanent snow fields. The taxonomic knowledge of this family in Peru is incomplete and it is still possible to encounter novel species.

Hitchcock (1927), in his treatment of the grasses of Ecuador, Peru and Bolivia, recognised 12 species of *Muhlenbergia* Schreb., 10 of these being reported in Peru. Standley (1936), in his Flora of Peru, recorded 10 species. More recently, Tovar (1993) produced an integral study of the Peruvian grasses, including 14 species of *Muhlenbergia*. Brako and Zarucchi (1993) list 13 species as being present in Peru. All of these treatments are out of date and, subsequently, there have been new reports of grasses from Peru. As *Muhlenbergia* is a relatively large genus in North and Central America and is easily dispersed, a modern investigation was undertaken to more clearly understand its systematics and biogeography. In Peru, we report 17 species of *Muhlenbergia* (one of these is new) and one proposed hybrid.

The subtribe Muhlenbergiinae Pilg. (tribe Cynodonteae Dumort.) is a diverse assemblage of 182 species represented by a single, monophyletic genus, *Muhlenbergia* (Peterson et al. 2010a, b; 2016; Soreng et al. 2017; Peterson et al. 2018). Species within *Muhlenbergia* are morphologically highly variable and are characterised in having membranous ligules (rarely a line of hairs); paniculate inflorescences that are rebranched or composed only of primary branches; spikelets that are usually solitary but sometimes in pairs or triads, with cleistogenes (self-pollinated flowers that do not open at maturity) occasionally present in the leaf sheaths; one floret (rarely more) per spikelet that is perfect, staminate or sterile; glumes that are awned or unawned; lemmas 3-nerved, apex awned or unawned; and a base chromosome number of x = 8–10 (Peterson et al. 1995, 1997, 2007a, b; Peterson 2000, 2003). Two subtypes of C_4 photosynthesis based on nicotinamide adenine dinucleotide cofactor malic enzyme (NAD-ME) and phosphoenolpyruvate carboxykinase (PCK) have been found in *Muhlenbergia*; subtypes in most species have been verified by anatomy and in a few species by biochemical assay (Gutierrez et al. 1974; Brown 1977; Hattersley and Watson 1992).

Based on seven molecular markers (nuclear ITS and plastid *ndhA* intron, *ndhF, rps16-trnK, rps16* intron, *rps3* and *rpl32-trnL*), Peterson et al. (2010b) provided a phylogeny and classification for 124 species (68%) of the Muhlenbergiinae. They recognised five subgenera within *Muhlenbergia*: *M.* subg. *Bealia* (Scribn.) P.M. Peterson, *M.* subg. *Clomena* (P. Beauv.) Hack., *M.* subg. *Muhlenbergia*, *M.* subg. *Pseudosporobolus* (Parodi) P.M. Peterson and *M.* subg. *Trichochloa* (P. Beauv.) A. Gray. Here we present an updated phylogeny of 146 species (80%) of *Muhlenbergia* with 13 new species based on six molecular markers (nuclear ITS and plastid *ndhA* intron, *rpl32-trnL*, *rps3, rps16* intron and *rps16-trnK*), classification and a taxonomic revision of the genus for Peru.

Material and methods

Phylogenetic analyses

Detailed methods for DNA extraction, amplification, sequencing and phylogenetic analysis are given in Peterson et al. (2010a, b, 2014a, 2015a, b, 2016). In brief, the phylogeny was estimated among members of *Muhlenbergia* based on the analysis of six molecular markers (nuclear ITS 1&2, and plastid *ndhA* intron, *rpl32-trnL*, *rps3, rps16* intron, *rps16-trnK*). We sampled most species within subtribe Muhlenbergiinae and included outgroups: *Distichlis scoparia* (Nees ex Kunth) Arechav. (Monanthochloinae Pilg. ex Potztal), *Willkommia sarmentosa* Hack. (Traginae P.M. Peterson & Columbus) and *Sporobolus indicus* L. (Zoysieae Benth., Sporobolinae Benth.) [Peterson et al. 2010a, 2015a, 2014b, 2016; Soreng et al. 2017]. Voucher information and GenBank numbers for all samples (including the new ones) are given in Table 1.

The resulting plastid and ITS topologies were inspected for conflicting nodes with posterior probabilities (PP) ≥ 0.95. If no supported conflict was found, plastid and

ITS sequences were combined (Figure 1). When conflicting topologies were present, the datasets for inconsistently placed taxa were duplicated in the matrix. One set of the taxon was represented by only the corresponding plastid sequences, the other taxon set by only ITS sequences. The remaining positions for the duplicated datasets were then coded as missing data. We use this “taxon duplication” approach (Pirie et al. 2008; Pelser et al. 2010; Peterson et al. 2015b, 2016) to resolve our phylogenetic tree, minimising the diffusing effects of taxa with strongly supported incongruence between the plastid and ITS data and to represent their alternative placements in relation to the remaining phylogenetic groups, among which relationships are congruent.

Taxonomy

Specimens of *Muhlenbergia* from Peru were reviewed in the following herbaria: AAU, COL, CPUN, CUZ, F, HAO, K, LIL, LPB, MO, MOL, NY, US and USM. The first author (PMP) travelled and collected 3042 numbers (primarily grasses) while on seven expeditions to Peru between 1997 and 2008. Of these, 258 are collections of *Muhlenbergia* and all are accounted for here. Synonymy is mainly limited to names of taxa described from South America. Additional synonyms accepted by us can be found in the Catalogue of New World Grasses, vol. II (Peterson et al. 2001) and on the Catalogue of New World Grasses web site (http://www.tropicos.org/Project/CNWG) that is continually updated within TROPICOS (http://www.tropicos.org). When counting culm nodes, it is best to start counting 1 cm above the base. Blade width is measured from margin to margin on a flat blade but not when the blade is tightly involute. Glabrous refers to without pubescence. Smooth indicates no prickle-hairs with broad bases and/or hooked or pointed apices (i.e. pubescence can occur on a smooth surface and a scabrous surface can be glabrous). Excluded species and an infrageneric classification of the accepted species of *Muhlenbergia* in Peru are presented at the end of the taxonomic treatment.

Results and discussion

Phylogeny

A total of 226 new sequences from 146 species of *Muhlenbergia* are newly reported in GenBank (Table 1). The following 13 species are new in the phylogeny of *Muhlenbergia*: *M. capillipes* (M.E. Jones) P.M. Peterson & Annable, *M. ligularis* (Hack.) Hitchc., *M. flabellata* Mez, *M. bushii* R.W. Pohl, *M. diversiglumis* Trin., *M. frondosa* (Poir.) Fernald, *M. glabrifloris* Scribn., *M. romaschenkoi* P.M. Peterson, *M. setaroides* E. Fourn., *M. sylvatica* (Torr.) Torr. ex A Gray, *M. breviligula* Hitchc., *M. lehmanniana* Henrard and *M. venezuelae* Luces (Peterson et al. 2010b; 2018). Total aligned characters for individual regions and other parameters are noted in Table 2. The plastid–ITS sequences were combined in the analysis except where incongruence between datasets was detected (Fig. 1).

The Bayesian tree from the combined analysis of ITS and five plastid regions (*ndhA* intron, *rpl32-trnL, rps3, rps16* intron and *rps16-trnK*) is well resolved with strong support for the monophyly of *Muhlenbergia*, including *M. ramulosa* (Kunth) Swallen, sister to *M.* subg. *Bealia*–*M.* subg. *Trichochloa*, these all being in one clade that is sister to *M.* subg. *Clomena*–*M.* subg. *Pseudosporobolus* and sister to *M.* subg. *Muhlenbergia*. (Fig. 1; posterior probability, PP = 0.95–1, shown with thick branches). Each of the five major clades, corresponding to the five subgeneric divisions that have been recognised previously (Peterson et al. 2010b), include species that occur in Peru and/or South America (red) or as wide ranging species from the Americas. The species in each of these five subgenera share salient morphological characteristics or trends.

Species of *M.* subg. *Bealia* are strongly caespitose, never rhizomatous, annuals or perennials with pubescent margins or midnerves at least on the lower ½ of the lemma (only *M. ligularis* is without pubescence) and round, equal primary, secondary and tertiary vascular bundles without well-developed schlerenchyma (Peterson and Herrera Arrieta 2001; Peterson 2003; Peterson et al. 2010b). The Peruvian endemic, *M. caxamarcensis* Lægaard & Sánchez Vega and the wide-ranging, *M. ligularis* (Central and South America), are members of this subgenus.

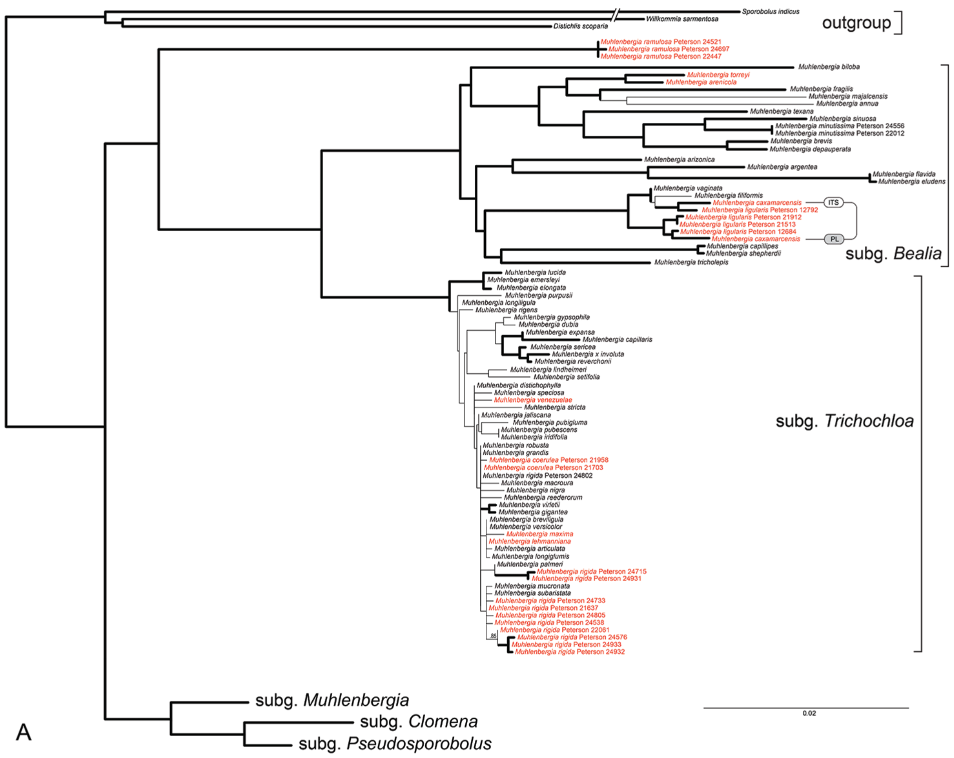

Figure 1. A, B Maximum-likelihood tree inferred from combined plastid (*ndhA* intron, *rps16-trnK, rps16* intron, *rps3*, and *rpl32-trnL*) and ITS sequences. Thick branches indicate posterior probabilities of 0.95–1; species in red occur in South America; scale bar = 2%.

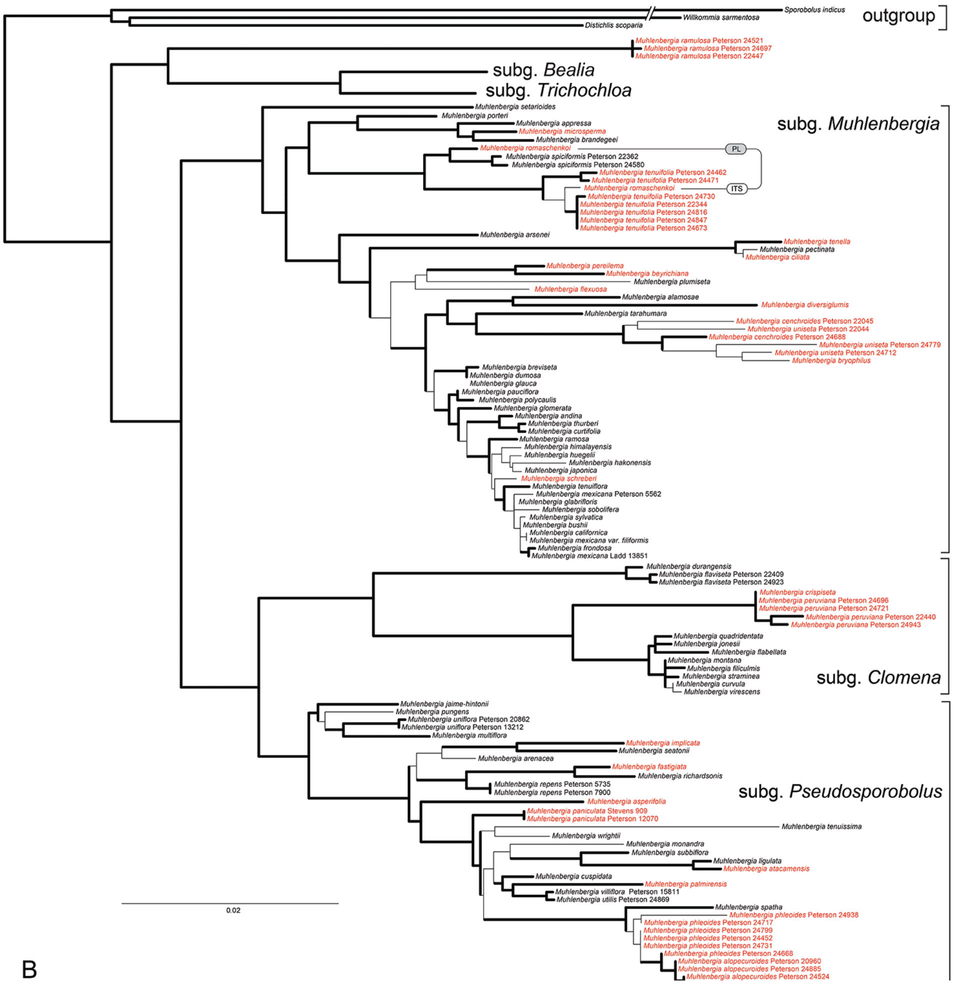

Figure 1. Continued.

Although the clade of species representing the *M.* subg. *Trichochloa* is strongly supported in our analyses (Fig. 1), there is little resolution among members, suggesting very low levels of genetic divergence among the species in this subgenus. The low level of divergence may be a consequence of rapid speciation events. Within *Muhlenbergia*, this group is by far the most difficult to determine because there are very few morphological differences among the taxa and discrete (nonplastic) characteristics are few. The species of *M.* subg. *Trichochloa* consist of robust perennials up to 3 metres tall with compressed-keeled or rounded basal sheaths, 1-veined glumes and unequal rectangular or obovate/elliptic secondary and tertiary vascular bundles with well-developed sclerenchyma girders, these usually with sclerosed phloem (Peterson and Herrera Arrieta 2001; Herrera Arrieta and Peterson 2007, 2017, 2018; Peterson et al. 2010b). In Peru, *M. coerulea* (Griseb.) Mez, *M. coerulea*×*M. rigida, M. maxima* Lægaard & Sánchez Vega (endemic) and *M. rigida* (Kunth) Kunth are placed in *M.* subg. *Trichochloa*.

Table 1. Taxon voucher (collector, number, and where the specimen is housed), country of origin, and GenBank accession for DNA sequences of *rps3, rps16-trnK, rps16* intron, *ndhA* intron, *rpl32-trnL*, and ITS regions (**bold** indicates new accession); a dash (–) indicates missing data; an asterisk (*) indicates sequences not generated in our lab.

N	Taxon	Voucher	Country	rps3	rps16-trnK	rps16 intron	ndhA intron	rpl32-trnL	ITS
Outgroup									
1	*Distichlis scoparia* var. *erinacea* (Nees ex Kunth) Arechav.	Peterson 17475, Soreng & Refulio-Rodriguez (US)	Argentina, Neuquen	GU360034	GU360501	GU360477	GU359480	GU359803	GU359334
2	*Sporobolus indicus* (L.) R. Br.	Peterson 22025 & Saarela (US)	Mexico, Chihuahua	GU360161	GU360630	GU360355	GU359504	GU359913	GU359209
3	*Willkommia sarmentosa* Hack.	Schweickerdt 2181 (US)	South Africa	GU360252	GU360645	GU360343	GU359545	GU359924	GU359194
Muhlenbergia									
4	*Muhlenbergia ramulosa* (Kunth) Swallen	Peterson 22447 & Saarela (US)	Mexico, Durango	GU360254	GU360717	GU360406	GU359444	GU359953	GU359115
5	*Muhlenbergia ramulosa* (Kunth) Swallen	Peterson 24521 & Romaschenko (US)	Mexico, Coahuila	**MK090816**	**MK090876**	**MK090848**	**MK090728**	**MK090773**	**MK090686**
6	*Muhlenbergia ramulosa* (Kunth) Swallen	Peterson 24697, Romaschenko & Zamudio Ruíz (US)	Mexico, Queretaro	**MK090817**	**MK090877**	**MK090849**	**MK090729**	**MK090774**	**MK090687**
subg. *Bealia*									
7	*Muhlenbergia annua* (Vasey) Swallen	Peterson 22022 & Saarela (US)	Mexico, Chihuahua	HM143247	HM143629	HM143534	HM143351	HM143144	HM143043
8	*Muhlenbergia arenicola* Buckley	Peterson 19947 & Lara-Contreras (US)	Mexico, Coahuila	GU360209	GU360674	GU360413	GU359462	GU359960	GU359166
9	*Muhlenbergia argentea* Vasey	Peterson 22095 & Saarela (US)	Mexico, Chihuahua	HM143248	HM143630	HM143535	HM143352	HM143145	HM143044
10	*Muhlenbergia arizonica* Scribn.	Peterson 22173 & Saarela (US)	Mexico, Chihuahua	HM143249	HM143631	HM143536	HM143353	HM143146	HM143045
11	*Muhlenbergia biloba* Hitchc.	Peterson 7946, Annable & Herrera (US)	Mexico, Chihuahua	GU360098	GU360550	GU360309	–	GU359859	GU359258
12	*Muhlenbergia brevis* C.O. Goodd.	Peterson 22023 & Saarela (US)	Mexico, Chihuahua	HM143253	HM143635	HM143540	HM143357	HM143150	HM143049
13	*Muhlenbergia capillipes* (M.E. Jones) P.M. Peterson & Annable	Peterson 20013 & Sánchez Alvarado (US)	Mexico, Durango	**MK090802**	**MK090862**	**MK090835**	**MK090714**	**MK090751**	**MK090664**
14	*Muhlenbergia caxamarcensis* Lægaard & Sánchez Vega	Peterson 21965, Soreng & Montoya Quino (US)	Peru, La Libertad	HM143256	HM143639	HM143543	HM143360	HM143153	HM143052

N	Taxon	Voucher	Country	rps3	rps16-trnK	rps16 intron	ndhA intron	rpl32-trnL	ITS
15	*Muhlenbergia depauperata* Scribn.	Peterson 21293, Saarela & Flores Villegas (US)	Mexico, Zacatecas	HM143261	HM143642	HM143547	HM143363	HM143157	HM143056
16	*Muhlenbergia eludens* C. Reeder	Peterson 22188 & Saarela (US)	Mexico, Sinaloa	HM143268	HM143649	HM143554	HM143370	HM143164	HM143062
17	*Muhlenbergia filiformis* (Thurb. ex S. Watson) Rydb.	Peterson 10433, Annable & Weinpahl (US)	USA, California	HM143272	HM143653	HM143558	HM143374	HM143168	HM143066
18	*Muhlenbergia flavida* Vasey	Peterson 22237 & Saarela (US)	Mexico, Sinaloa	HM143273	HM143654	HM143559	HM143375	HM143169	HM143067
19	*Muhlenbergia fragilis* Swallen	Peterson 22194 & Saarela (US)	Mexico, Sinaloa	HM143275	HM143656	HM143561	HM143377	HM143171	HM143069
20	*Muhlenbergia ligularis* (Hack.) Hitchc.	Peterson 12684, Annable, Lægaard & Soreng (US)	Bolivia, La Paz	**MK090808**	**MK090868**	**MK090842**	**MK090720**	**MK090760**	**MK090674**
21	*Muhlenbergia ligularis* (Hack.) Hitchc.	Peterson 12792, Annable, Lægaard & Soreng (US)	Bolivia, Oruro	**MK090809**	**MK090869**	**MK090843**	**MK090721**	**MK090761**	**MK090675**
22	*Muhlenbergia ligularis* (Hack.) Hitchc.	Peterson 21513, Soreng, Torre & Rojas Fox (US)	Peru, Ancash	**MK090810**	**MK090870**	**MK090844**	**MK090722**	**MK090762**	**MK090676**
23	*Muhlenbergia ligularis* (Hack.) Hitchc.	Peterson 21912, Soreng & Montoya Quino (US)	Peru, Cajamarca	**MK090811**	**MK090871**	**MK090845**	**MK090723**	**MK090763**	**MK090677**
24	*Muhlenbergia majalcensis* P.M. Peterson	Peterson 4519 & Annable (US)	Mexico, Chihuahua	HM143295	HM143675	HM143577	HM143394	HM143190	HM143088
25	*Muhlenbergia minutissima* (Steud.) Swallen	Peterson 22012 & Saarela (US)	Mexico, Chihuahua	HM143300	HM143680	–	–	HM143195	HM143093
26	*Muhlenbergia minutissima* (Steud.) Swallen	Peterson 24556 & Romaschenko (US)	Mexico, Coahuila	**MK090813**	**MK090873**	–	–	**MK090765**	**MK090679**
27	*Muhlenbergia shepherdii* (Vasey) Swallen	Peterson 22452 & Saarela (US)	Mexico, Durango	GU360102	GU360560	GU360320	GU359419	GU359854	GU359277
28	*Muhlenbergia sinuosa* Swallen	Peterson 7976, Annable & Herrera Arrieta (US)	Mexico, Chihuahua	HM143323	HM143704	HM143603	HM143419	HM143219	HM143117
29	*Muhlenbergia texana* Buckley	Peterson 22016 & Saarela (US)	Mexico, Chihuahua	HM143334	HM143714	HM143614	–	HM143230	HM143128
30	*Muhlenbergia torreyi* (Kunth) Hitchc. ex Bush	Peterson 19429, Soreng, Salariato & Panizza (US)	Argentina, Catamarca	GU360266	GU360720	GU360267	**MK090744**	GU359992	GU359118
31	*Muhlenbergia tricholepis* (Torr.) Columbus	Peterson 22099 & Saarela (US)	Mexico, Chihuahua	GU360103	GU360559	GU360305	GU359418	GU359853	GU359278
32	*Muhlenbergia vaginata* Swallen	Peterson 22417 & Saarela (US)	Mexico, Durango	–	HM143718	HM143618	**MK090745**	HM143234	**MK090708**

N	Taxon	Voucher	Country	rps3	rps16-trnK	rps16 intron	ndhA intron	rpl32-trnL	ITS
subg. *Clomena*									
33	*Muhlenbergia crispiseta* Hitchc.	Peterson 10768, Annable & Valdes Reyna (US)		HM143258	–	–	–	–	–
34	*Muhlenbergia curvula* Swallen	Peterson 24830, Romaschenko, Rodriguez Avalos, Herrera-Simoni & Garcia Rodriguez (US)	Mexico, Aguascalientes	–	–	–	–	**MK090754**	**MK090667**
35	*Muhlenbergia flaviseta* Scribn.	Peterson 22409 & Saarela (US)	Mexico, Durango	GU360250	GU360685	GU360410	GU359448	GU359957	GU359127
36	*Muhlenbergia flaviseta* Scribn.	Peterson 24923, Romaschenko & González-Elizondo (US)	Mexico, Durango	–	–	**MK090839**	–	**MK090757**	**MK090670**
37	*Muhlenbergia filiculmis* Vasey	Peterson 11954 & Annable (US)	USA, Wyoming	HM143271	HM143652	HM143557	HM143373	HM143167	HM143065
38	*Muhlenbergia flabellata* Mez	Senalobo 1985 (MO)	Costa Rica,	**MK090805**	**MK090865**	**MK090838**	**MK090717**	**MK090756**	**MK090669**
39	*Muhlenbergia jonesii* (Vasey) Hitchc.	Peterson 4861 & Annable (US)	USA, California	HM143289	HM143669	–	HM143390	HM143185	HM143083
40	*Muhlenbergia montana* (Nutt.) Hitchc.	Peterson 22046 & Saarela (US)	Mexico, Chihuahua	HM143301	HM143681	HM143582	HM143398	HM143196	HM143094
41	*Muhlenbergia peruviana* (P. Beauv.) Steud.	Peterson 22440 & Saarela (US)	Mexico, Durango	GU360221	GU360713	GU360408	GU359446	GU359955	GU359154
42	*Muhlenbergia peruviana* (P. Beauv.) Steud.	Peterson 24696, Romaschenko & Zamudio Ruíz (US)	Mexico, Querétaro	–	–	–	–	**MK090767**	**MK090680**
43	*Muhlenbergia peruviana* (P. Beauv.) Steud.	Peterson 24721, Romaschenko & Zamudio Ruíz (US)	Mexico, Querétaro	–	–	–	–	**MK090768**	**MK090681**
44	*Muhlenbergia peruviana* (P. Beauv.) Steud.	Peterson 24943, Romaschenko & Zamudio Ruíz (US)	Mexico, Querétaro	–	–	–	–	**MK090769**	**MK090682**
45	*Muhlenbergia quadridentata* (Kunth) Trin.	Peterson 16103 & Rosales (US)	Mexico, Jalisco	HM143313	HM143694	–	HM143410	HM143209	HM143107
46	*Muhlenbergia straminea* Hitchc.	Peterson 15238 & Cayouette (US)	USA, Arizona	HM143327	HM143707	HM143607	**MK090737**	HM143223	HM143121
47	*Muhlenbergia virescens* (Kunth) Trin.	Peterson 22412 & Saarela (US)	Mexico, Durango	HM143342	HM143722	HM143621	HM143432	HM143238	HM143134

N	Taxon	Voucher	Country	rps3	rps16-trnK	rps16 intron	ndhA intron	rpl32-trnL	ITS
subg. *Muhlenbergia*									
48	*Muhlenbergia alamosae* Vasey	Peterson 22104 & Saarela (US)	Mexico, Chihuahua	HM143243	HM143626	HM143530	HM143347	HM143140	HM143039
49	*Muhlenbergia andina* (Nutt.) Hitchc.	Peterson 10432, Annable & Weinpahl (US)	USA, California	HM143244	–	HM143531	HM143348	HM143141	HM143040
50	*Muhlenbergia appressa* C.O. Goodd.	Peterson 4183 & Annable (US)	USA, Arizona	GU360211	GU360676	GU360415	GU359443	GU359962	GU359164
51	*Muhlenbergia arsenei* Hitchc.	Peterson 15208 & Cayouette (US)	Mexico, Baja California Norte	HM143250	HM143632	HM143537	HM143354	HM143147	HM143046
52	*Muhlenbergia beyrichiana* Kunth	Peterson 20366, Soreng & Romaschenko (US)	Peru, Huánuco	GU360247	GU360712	GU360280	GU359493	GU359995	GU359129
53	*Muhlenbergia brandegeei* C. Reeder	Peterson 4760 & Annable (US)	Mexico, Baja California Sur	GU360208	GU360711	GU360412	GU359450	GU359959	GU359167
54	*Muhlenbergia breviseta* Griseb. ex E. Fourn.	McVaugh 22930 (US)	Mexico	–	HM143636	–	–	–	–
55	*Muhlenbergia bryophilus* (Döll) P.M. Peterson	Columbus 3565 (RSA)	Peru, Cusco	–	–	–	–	–	GQ397862*
56	*Muhlenbergia bushii* R.W. Pohl	Brant 4542 & O'Donnell (MO)	USA, Missouri	**MK090801**	**MK090861**	**MK090834**	**MK090713**	**MK090750**	**MK090663**
57	*Muhlenbergia californica* Vasey	Peterson 5013 & Barron (US)	USA, California	HM143254	HM143637	HM143541	HM143358	HM143151	HM143050
58	*Muhlenbergia cenchroides* (Humb. & Bonpl. ex Willd.) P.M. Peterson	Peterson 22045 & Saarela (US)	Mexico, Chihuahua	GU360143	GU360578	GU360274	GU359403	GU360011	GU359259
59	*Muhlenbergia cenchroides* (Humb. & Bonpl. ex Willd.) P.M. Peterson	Peterson 24688, Romaschenko & Zamudio Ruíz (US)	Mexico, Querétaro	–	–	–	–	**MK090752**	**MK090665**
60	*Muhlenbergia ciliata* (Kunth) Trin.	Peterson 22193 & Saarela (US)	Mexico, Sinaloa	HM143257	HM143640	HM143544	HM143361	HM143154	HM143053
61	*Muhlenbergia curtifolia* Scribn.	Peterson 5631 & Annable (US)	USA, Arizona	HM143259	HM143641	HM143545	HM143362	HM143155	HM143054
62	*Muhlenbergia diversiglumis* Trin.	Peterson 4611 & Annable (US)	Mexico, Chihuahua	**MK090804**	**MK090864**	**MK090837**	**MK090716**	**MK090755**	**MK090668**
63	*Muhlenbergia dumosa* Scribn. ex Vasey	Peterson 13438, Knowles, Dietrich & Braxton (US)	Mexico, Durango	HM143265	HM143646	HM143551	HM143367	HM143161	HM143059

N	Taxon	Voucher	Country	rps3	rps16-trnK	rps16 intron	ndhA intron	rpl32-trnL	ITS
64	*Muhlenbergia flexuosa* Hitchc.	Peterson 20373, Soreng & Romaschenko (US)	Peru, Huánuco	HM143274	HM143655	HM143560	HM143376	HM143170	HM143068
65	*Muhlenbergia frondosa* (Poir.) Fernald	Yatskievych 04-224, Smith, McKenzie & Nagel (MO)	USA, Missouri	**MK090806**	**MK090866**	**MK090840**	**MK090718**	**MK090758**	**MK090671**
66	*Muhlenbergia glabrifloris* Scribn.	Brant 2659 (MO)	USA, Missouri	**MK090807**	**MK090867**	**MK090841**	**MK090719**	**MK090759**	**MK090672**
67	*Muhlenbergia glauca* (Nees) B.D. Jacks.	Peterson 21180, Saarela, Gonzalez Elizondo, Rosen & Reid (US)	Mexico, Durango	HM143277	HM143659	HM143564	HM143380	HM143174	HM143071
68	*Muhlenbergia glomerata* (Willd.) Trin.	Peterson 20924, Saarela & Howard (US)	USA, New York	GU360253	GU360716	GU360407	GU359445	GU359954	GU359114
69	*Muhlenbergia hakonensis* (Hack. ex Matsum.) Makino	Kim 2009858	Korea (South)	–	–	–	–	–	HQ600507*
70	*Muhlenbergia himalayensis* Hack. ex Hook. f.	Soreng 5666, Peterson & Sun Hang (US)	China, Xizang	HM143281	HM143662	HM143566	HM143383	HM143177	HM143075
71	*Muhlenbergia huegelii* Trin.	Soreng 5344, Peterson & Sun Hang (US)	China, Sichuan	HM143282	HM143663	HM143567	HM143384	HM143178	HM143076
72	*Muhlenbergia japonica* Steud.	Soreng 5240, Peterson & Sun Hang (US)	China, Yunnan	HM143287	HM143667	HM143571	HM143388	HM143183	HM143081
73	*Muhlenbergia mexicana* (L.) Trin.	Ladd 13851 (US)	USA, Missouri	**MK090812**	**MK090872**	**MK090846**	–	**MK090764**	**MK090678**
74	*Muhlenbergia mexicana* (L.) Trin.	Peterson 5562 & Annable (US)	USA, New Mexico	HM143297	HM143677	HM143580	HM143396	HM143193	HM143090
75	*Muhlenbergia mexicana* var. *filiformis* (Torr.) Scribn.	Peterson 20861 & Saarela (US)	USA, New York.	HM143298	HM143678	HM143579	HM143395	HM143192	HM143091
76	*Muhlenbergia microsperma* (DC.) Kunth	Peterson 21855 & Soreng (US)	Peru, Cajamarca	HM143299	HM143679	HM143581	HM143397	HM143194	HM143092
77	*Muhlenbergia pauciflora* Buckley	Peterson 22048 & Saarela (US)	Mexico, Chihuahua	–	HM143686	HM143587	HM143403	HM143201	HM143099
78	*Muhlenbergia pectinata* C.O. Goodd.	Peterson 22108 & Saarela (US)	Mexico, Sonora	HM143306	HM143687	HM143588	HM143404	HM143202	HM143100
79	*Muhlenbergia pereilema* P.M. Peterson	Peterson 22191 & Saarela (US)	Mexico, Sinaloa	GU360245	GU360710	GU360282	GU359519	GU359993	GU359131
80	*Muhlenbergia plumiseta* Columbus	Peterson 20106, Hall, Alvarez Marvan & Alvarez Jimenez (US)	Mexico, Guerrero	GU360246	GU360719	GU360281	GU359516	GU359979	GU359130

N	Taxon	Voucher	Country	rps3	rps16-trnK	rps16 intron	ndhA intron	rpl32-trnL	ITS
81	*Muhlenbergia polycaulis* Scribn.	Peterson 22092 & Saarela (US)	Mexico, Chihuahua	HM143307	HM143688	HM143589	**MK090727**	HM143203	HM143101
82	*Muhlenbergia porteri* Scribn. ex Beal	Peterson 19846 & Lara Contreras (US)	Mexico, Coahuila	HM143308	HM143689	HM143590	HM143405	HM143204	HM143102
83	*Muhlenbergia ramosa* (Hack. ex Matsum.) Makino	Soreng 5302, Peterson & Sun Hang (US)	China, Yunnan	HM143314	HM143695	HM143595	HM143411	HM143210	HM143108
84	*Muhlenbergia romaschenkoi* P.M. Peterson	Peterson 20331, Soreng & Romashchenko (US)	Peru, Huánuco	–	–	–	–	**MK090784**	**MK096270**
85	*Muhlenbergia schreberi* J.F. Gmel.	Peterson 19443, Soreng, Salariato & Panizza (US)	Argentina, Tucuman	GU360214	GU360679	GU360404	GU359456	GU359950	GU359161
86	*Muhlenbergia setarioides* E. Fourn.	Peterson 9897 & Annable (US)	Mexico, Oaxaca	**MK090823**	**MK090883**	**MK090853**	**MK090736**	**MK090785**	**MK090697**
87	*Muhlenbergia sobolifera* (Muhl. ex Willd.) Trin.	Peterson 20834 & Saarela (US)	USA, Virginia	HM143324	**MK090884**	HM143604	HM143420	HM143220	HM143118
88	*Muhlenbergia spiciformis* Trin.	Peterson 22362 & Saarela (US)	Mexico, Oaxaca	HM143326	HM143706	HM143606	HM143422	HM143222	HM143120
89	*Muhlenbergia spiciformis* Trin.	Peterson 24580, Romaschenko & Valdés-Reyna (US)	Mexico, Coahuila	–	–	–	–	**MK090786**	**MK090698**
90	*Muhlenbergia sylvatica* (Torr.) Torr. ex A. Gray	Brant 4783 (MO)	USA, Missouri	**MK090824**	**MK090885**	**MK090854**	**MK090738**	**MK090787**	**MK090699**
91	*Muhlenbergia tarahumara* P.M. Peterson & Columbus	Peterson 22053 & Saarela (US)	Mexico, Chihuahua	HM143330	HM143710	HM143610	HM143425	HM143226	HM143124
92	*Muhlenbergia tenella* (Kunth) Trin.	Peterson 22141 & Saarela (US)	Mexico, Chihuahua	HM143331	HM143711	HM143611	–	HM143227	HM143125
93	*Muhlenbergia tenuiflora* (Willd.) Britton, Sterns & Poggenb.	Peterson 15778 & Saarela (US)	USA, Virginia.	HM143332	HM143712	HM143612	HM143426	HM143228	HM143126
94	*Muhlenbergia tenuifolia* (Kunth) Kunth	Peterson 22344 & Saarela (US)	Mexico, Oaxaca	HM143333	HM143713	HM143613	HM143427	HM143229	HM143127
95	*Muhlenbergia tenuifolia* (Kunth) Kunth	Peterson 24462, Romaschenko & Valdés-Reyna (US)	Mexico, Coahuila	–	–	–	–	**MK090788**	**MK090700**
96	*Muhlenbergia tenuifolia* (Kunth) Kunth	Peterson 24471 & Romaschenko (US)	Mexico, Coahuila	–	–	–	–	**MK090789**	**MK090701**
97	*Muhlenbergia tenuifolia* (Kunth) Kunth	Peterson 24673 & Romaschenko (US)	Mexico, San Luis Potosí	**MK090825**	**MK090886**	–	**MK090739**	**MK090790**	**MK090702**
98	*Muhlenbergia tenuifolia* (Kunth) Kunth	Peterson 24730, Romaschenko & Zamudio Ruíz (US)	Mexico, Queretaro	**MK090826**	**MK090887**	–	**MK090740**	**MK090791**	**MK090703**

N	Taxon	Voucher	Country	rps3	rps16-trnK	rps16 intron	ndhA intron	rpl32-trnL	ITS
99	*Muhlenbergia tenuifolia* (Kunth) Kunth	Peterson 24816, Romaschenko, Rodriguez Avalos, Herrera-Simoni & Garcia Rodriguez (US)	Mexico, Aguascalientes	**MK090827**	**MK090888**	–	**MK090741**	**MK090792**	**MK090704**
100	*Muhlenbergia tenuifolia* (Kunth) Kunth	Peterson 24847 & Romaschenko (US)	Mexico, Zacatecas	**MK090828**	**MK090889**	**MK090855**	**MK090742**	**MK090793**	**MK090705**
101	*Muhlenbergia thurberi* (Scribn.) Rydb.	Peterson 5619 & Annable (US)	USA, Arizona	HM143335	HM143715	HM143615	HM143428	HM143231	HM143129
102	*Muhlenbergia uniseta* (Lag.) Columbus	Peterson 22044 & Saarela (US)	Mexico, Chihuahua	GU360128	GU360577	GU360278	GU359392	GU360012	GU359260
103	*Muhlenbergia uniseta* (Lag.) Columbus	Peterson 24712, Romaschenko & Zamudio Ruíz (US)	Mexico, Queretaro	–	–	–	–	**MK090794**	**MK090706**
104	*Muhlenbergia uniseta* (Lag.) Columbus	Peterson 24779, Romaschenko & Zamudio Ruíz (US)	Mexico, Queretaro	–	–	–	–	**MK090795**	**MK090707**
subg. *Pseudosporobolus*									
105	*Muhlenbergia alopecuroides* (Griseb.) P.M. Peterson & Columbus	Peterson 20960, Saarela, Lara Contreras & Reyna Alvarez (US)	Mexico, Coahuila	GU360224	GU360688	GU360426	GU359425	GU359976	GU359152
106	*Muhlenbergia alopecuroides* (Griseb.) P.M. Peterson & Columbus	Peterson 22008 & Saarela (US)	Mexico, Chihuahua	GU360223	GU360687	GU360425	GU359451	GU359975	GU359153
107	*Muhlenbergia alopecuroides* (Griseb.) P.M. Peterson & Columbus	Peterson 24524 & Romaschenko (US)	Mexico, Coahuila	**MK090798**	**MK090858**	**MK090831**	**MK090711**	**MK090747**	**MK090660**
108	*Muhlenbergia alopecuroides* (Griseb.) P.M. Peterson & Columbus	Peterson 24885 & Romaschenko (US)	Mexico, San Luis Potosí	**MK090799**	**MK090859**	**MK090832**	**MK090712**	**MK090748**	**MK090661**
109	*Muhlenbergia arenacea* (Buckley) Hitchc.	Peterson 10624 & Annable (US)	Mexico, Coahuila	GU360210	GU360675	GU360414	GU359452	GU359961	GU359165
110	*Muhlenbergia asperifolia* (Nees & Meyen ex Trin.) Parodi	Peterson 15452, Soreng, Finot & Judziewicz (US)	Chile, Region III (Atacama)	HM143252	HM143634	HM143539	HM143356	HM143149	HM143048
111	*Muhlenbergia atacamensis* Parodi	Peterson 19626, Soreng, Salariato, & Panizza, (US)	Argentina, Jujuy	GU360115	GU360595	GU360489	GU359382	GU359879	GU359344
112	*Muhlenbergia cuspidata* (Torr. ex Hook.) Rydb.	Hill 35331 (US)	USA	HM143260	–	HM143546	–	HM143156	HM143055

N	Taxon	Voucher	Country	rps3	rps16-trnK	rps16 intron	ndhA intron	rpl32-trnL	ITS
113	*Muhlenbergia fastigiata* (J. Presl) Henrard	Peterson 21512, Soreng, LaTorre & Rojas Fox (US)	Peru, Ancash	HM143270	HM143651	HM143556	HM143372	HM143166	HM143064
114	*Muhlenbergia implicata* (Kunth) Trin.	Peterson 22266, Saarela (US)	Mexico, Oaxaca	HM143283	HM143664	HM143568	HM143385	HM143179	HM143077
115	*Muhlenbergia jaime-hintonii* P.M. Peterson & Valdés-Reyna	Peterson 15841 & Valdes Reyna (US)	Mexico, Nuevo León	HM143285	HM143665	HM143569	HM143386	HM143181	HM143079
116	*Muhlenbergia ligulata* (E. Fourn.) Scribn. & Merr.	Peterson 22416 & Saarela (US)	Mexico, Durango	GU360069	GU360551	GU360440	GU359381	GU359863	GU359273
117	*Muhlenbergia monandra* Alegría & Rúgolo	Peterson 17990 & Refulio Rodriguez (US)	Peru, Lima	–	–	–	–	–	GQ397891*
118	*Muhlenbergia multiflora* Columbus	Peterson 7845 & Annable (US)	USA, Colorado	GU360191	GU360702	GU360289	GU359525	GU359985	GU359138
119	*Muhlenbergia palmirensis* Grignon & Lægaard	Peterson 9317 & Judziewicz (US)	Ecuador, Chimborazo	HM143305	HM143685	HM143586	HM143402	HM143200	HM143098
120	*Muhlenbergia paniculata* (Nutt.) Columbus	Peterson 12070 & Annable (US)	USA, Colorado	GU360170	GU360673	GU360375	GU359529	GU359936	GU359201
121	*Muhlenbergia paniculata* (Nutt.) Columbus	Stevens 909 (US)	USA	**MK090814**	**MK090874**	**MK090847**	**MK090726**	**MK090766**	–
122	*Muhlenbergia phleoides* (Kunth) Columbus	Peterson 24452, Romaschenko & Valdés-Reyna (US)	Mexico, Nuevo León	–	–	–	–	MH400231	MH400228
123	*Muhlenbergia phleoides* (Kunth) Columbus	Peterson 24668 & Romaschenko (US)	Mexico, San Luis Potosí	–	–	–	–	**MK090770**	**MK090683**
124	*Muhlenbergia phleoides* (Kunth) Columbus	Peterson 24717, Romaschenko & Zamudio Ruíz (US)	Mexico, Querétaro	–	–	–	–	**MK090771**	**MK090684**
125	*Muhlenbergia phleoides* (Kunth) Columbus	Peterson 24731, Romaschenko & Zamudio Ruíz (US)	Mexico, Querétaro	–	–	–	–	**MK090772**	**MK090685**
126	*Muhlenbergia phleoides* (Kunth) Columbus	Peterson 24799, Romaschenko, Rodriguez Avalos, Herrera-Simoni, & Garcia Rodriguez (US)	Mexico, Aguascalientes	–	–	–	–	MH400232	MH400229
127	*Muhlenbergia phleoides* (Kunth) Columbus	Peterson 24938, Romaschenko & González-Elizondo (US)	Mexico, Durango	–	–	–	–	KX582659	KX582383
128	*Muhlenbergia pungens* Thurb. ex A. Gray	Ricketson 4642 (MO)	USA, Arizona	**MK090815**	**MK090875**	MH508106	–	MH508102	MH508098

N	Taxon	Voucher	Country	rps3	rps16-trnK	rps16 intron	ndhA intron	rpl32-trnL	ITS
129	*Muhlenbergia repens* (J. Presl) Hitchc.	Peterson 7900 & Annable (US)	USA, New Mexico	HM143316	HM143697	HM143596	HM143413	HM143212	HM143110
130	*Muhlenbergia repens* (J. Presl) Hitchc.	Peterson 5735 & Annable (US)	USA, Texas	HM143338	HM143717	HM143617	HM143430	HM143233	HM143131
131	*Muhlenbergia richardsonis* (Trin.) Rydb.	Peterson 19817, Saarela & Sears (US)	USA, California	GU360212	GU360677	GU360431	GU359454	GU359978	GU359163
132	*Muhlenbergia seatonii* Scribn.	Peterson 9946 & Annable (US)	Mexico, Puebla	**MK090822**	**MK090882**	MH508107	**MK090735**	MH508103	MH508099
133	*Muhlenbergia spatha* Columbus	Schaffner 134 (US)	Mexico	–	–	–	–	GU359981	MH400230
134	*Muhlenbergia subbiflora* Hitchc.	Peterson 21158, Saarela, Rosen & Reid (US)	Mexico, Durango	GU360036	GU360518	GU360439	GU359428	GU359877	GU359318
135	*Muhlenbergia tenuissima* (J. Presl) Kunth	Peterson 4751 & Annable (US)	Mexico, Jalisco	**MK090829**	**MK090890**	MH508108	**MK090743**	MH508104	MH508100
136	*Muhlenbergia uniflora* (Muhl.) Fernald	Peterson 13212, Annable, Pizzolato, Gordon, Frett, Frick, Morrone & Griner (US)	USA, New Jersey	HM143337	HM143716	HM143616	HM143429	HM143232	HM143130
137	*Muhlenbergia uniflora* (Muhl.) Fernald	Peterson 20862 & Saarela (US)	USA, New York	GU360258	GU360715	GU360275	GU359463	GU359994	GU359119
138	*Muhlenbergia utilis* (Torr.) Hitchc.	Peterson 24869 & Romaschenko (US)	Mexico, San Luis Potosí	–	–	–	–	MH508105	MH508101
139	*Muhlenbergia villiflora* Hitchc.	Peterson 15811 & Valdes Reyna (US)	Mexico, Nuevo León	HM143340	HM143720	HM143620	HM143431	HM143236	HM143133
140	*Muhlenbergia wrightii* Vasey ex J.M. Coult.	Peterson 20964, Saarela, Lara Contreras & Reyna Alvarez (US)	Mexico, Coahuila	HM143344	HM143723	HM143623	HM143434	HM143240	HM143137
subg. *Trichochloa*									
141	*Muhlenbergia articulata* Scribn.	Peterson 13386 & Knowles (US)	Mexico, San Luis Potosi	HM143251	HM143633	HM143538	HM143355	HM143148	HM143047
142	*Muhlenbergia breviligula* Hitchc.	Pohl 13392 & Gabel (MO)	Honduras, Santa Bárbara	**MK090800**	**MK090860**	**MK090833**	–	**MK090749**	**MK090662**
143	*Muhlenbergia capillaris* (Lam.) Trin.	Peterson 14236, Weakley & LeBlond (US)	USA, North Carolina	HM143255	HM143638	HM143542	HM143359	HM143152	HM143051
144	*Muhlenbergia distichophylla* (J. Presl) Kunth	Peterson 15913 & Valdes Reyna (US)	Mexico, Tamaulipas	HM143262	HM143643	HM143548	HM143364	HM143158	–
145	*Muhlenbergia coerulea* (Griseb.) Mez	Peterson 21703, Soreng, LaTorre & Rojas Fox (US)	Peru, Ancash	HM143245	HM143627	HM143532	HM143349	HM143142	HM143041

N	Taxon	Voucher	Country	rps3	rps16-trnK	rps16 intron	ndhA intron	rpl32-trnL	ITS
146	*Muhlenbergia coerulea* (Griseb.) Mez	Peterson 21958, Soreng & Montoya Quino (US)	Peru, La Libertad	HM143246	HM143628	HM143533	HM143350	HM143143	HM143042
147	*Muhlenbergia dubia* E. Fourn.	Peterson 21105 & Saarela (US)	Mexico, Nuevo León	HM143263	HM143644	HM143550	HM143365	HM143160	HM143057
148	*Muhlenbergia durangensis* Y. Herrera	Peterson 13644, Knowles, Dietrich, Braxton & Gonzalez-Elizondo (US)	Mexico, Durango	HM143266	HM143647	HM143552	HM143368	HM143162	HM143060
149	*Muhlenbergia elongata* Scribn. ex Beal	Peterson 22164 & Saarela (US)	Mexico, Chihuahua	HM143267	HM143648	HM143553	HM143369	HM143163	HM143061
150	*Muhlenbergia emersleyi* Vasey	Peterson 22096 & Saarela (US)	Mexico, Chihuahua	GU360207	GU360672	GU360411	GU359449	GU359958	GU359168
151	*Muhlenbergia expansa* (Poir.) Trin.	Peterson 14234, Weakley & LeBlond (US)	USA, North Carolina	HM143269	HM143650	HM143555	HM143371	HM143165	HM143063
152	*Muhlenbergia gigantea* (E. Fourn.) Hitchc.	Peterson 22260 & Saarela (US)	Mexico, Oaxaca	GU360215	GU360680	GU360419	GU359457	GU359966	GU359160
153	*Muhlenbergia grandis* Vasey	Peterson 13413, Knowles, Dietrich & Braxton (US)	Mexico, Sinaloa	HM143279	HM143660	HM143565	HM143381	HM143175	HM143073
154	*Muhlenbergia gypsophila* Reeder & C. Reeder	Peterson 15840 & Valdes Reyna (US)	Mexico, Nuevo León	HM143280	HM143661	–	HM143382	HM143176	HM143074
155	*Muhlenbergia iridifolia* Soderstr.	Peterson 6133 & Annable (US)	Mexico, Jalisco	HM143284	–	–	–	HM143180	HM143078
156	*Muhlenbergia jaliscana* Swallen	Peterson 6149 & Annable (US)	Mexico, Jalisco	HM143286	HM143666	HM143570	HM143387	HM143182	HM143080
157	*Muhlenbergia lehmanniana* Henrard	Santamaria 3760 (MO)	Colombia	–	–	–	–	–	**MK090673**
158	*Muhlenbergia lindheimeri* Hitchc.	Peterson 6280 & Annable (US)	USA, Texas	HM143290	HM143670	HM143573	HM143391	HM143186	HM143084
159	*Muhlenbergia longiglumis* Vasey	Peterson 13666, Knowles, Dietrich, Braxton & Gonzalez Elizondo (US)	Mexico, Durango	HM143291	HM143671	–	–	–	–
160	*Muhlenbergia longiligula* Hitchc.	Peterson 15224 & Cayouette (US)	USA, Arizona	HM143292	HM143672	HM143574	**MK090724**	HM143187	HM143085
161	*Muhlenbergia lucida* Swallen	Peterson 22134 & Saarela (US)	Mexico, Chihuahua	HM143294	HM143674	HM143575	HM143392	HM143188	HM143086
162	*Muhlenbergia macroura* (Kunth) Hitchc.	Peterson 22062 & Saarela (US)	Mexico, Chihuahua	GU360265	GU360683	GU360409	GU359447	GU359956	GU359125
163	*Muhlenbergia maxima* Lægaard & Sánchez Vega	Peterson 21884, Soreng & Sanchez Vega (US)	Peru, Cajamarca	HM143296	HM143676	HM143578	**MK090725**	HM143191	HM143089

N	Taxon	Voucher	Country	rps3	rps16-trnK	rps16 intron	ndhA intron	rpl32-trnL	ITS
164	*Muhlenbergia mucronata* (Kunth) Trin.	Peterson 22038 & Saarela (US)	Mexico, Chihuahua	HM143302	HM143682	HM143583	HM143399	HM143197	HM143095
165	*Muhlenbergia nigra* Hitchc.	Peterson 16097 & Rosales (US)	Mexico, Jalisco	HM143303	HM143683	HM143584	HM143400	HM143198	HM143096
166	*Muhlenbergia palmeri* Vasey	Peterson 5478 & Annable (US)	USA, Arizona	HM143304	HM143684	HM143585	HM143401	HM143199	HM143097
167	*Muhlenbergia pubescens* (Kunth) Hitchc.	Peterson 21250 & Saarela (US)	Mexico, Durango	HM143310	HM143691	HM143592	HM143406	HM143205	HM143103
168	*Muhlenbergia pubigluma* Swallen	Peterson 15838 & Valdes Reyna (US)	Mexico, Nuevo León	HM143311	HM143692	HM143593	HM143408	HM143207	HM143105
169	*Muhlenbergia purpusii* Mez	Peterson 6227 & Annable (US)	Mexico, San Luis Potosi	HM143312	HM143693	HM143594	HM143409	HM143208	HM143106
170	*Muhlenbergia reederorum* Soderstr.	Peterson 21262 & Saarela (US)	Mexico, Durango	HM143315	HM143696	–	HM143412	HM143211	HM143109
171	*Muhlenbergia reverchonii* Vasey & Scribn.	Peterson 6285 & Annable (US)	USA, Texas	HM143317	HM143698	HM143597	HM143414	HM143213	HM143111
172	*Muhlenbergia rigens* (Benth.) Hitchc.	Peterson 22129 & Saarela (US)	Mexico, Chihuahua	GU360256	GU360729	GU360357	GU359481	GU359951	GU359117
173	*Muhlenbergia rigida* (Kunth) Kunth	Peterson 21637, Soreng, LaTorre & Rojas Fox (US)	Peru, Ancash	GU360255	GU360718	GU360405	GU359380	GU359952	GU359116
174	*Muhlenbergia rigida* (Kunth) Kunth	Peterson 22061 & Saarela (US)	Mexico, Chihuahua	HM143319	HM143700	HM143599	HM143416	HM143215	HM143113
175	*Muhlenbergia rigida* (Kunth) Kunth	Peterson 24538 & Romaschenko (US)	Mexico, Coahuila	**MK090818**	**MK090878**	**MK090850**	**MK090730**	**MK090775**	**MK090688**
176	*Muhlenbergia rigida* (Kunth) Kunth	Peterson 24576, Romaschenko & Valdés-Reyna (US)	Mexico, Coahuila	**MK090819**	**MK090879**	**MK090851**	**MK090731**	**MK090776**	**MK090689**
177	*Muhlenbergia rigida* (Kunth) Kunth	Peterson 24715, Romaschenko & Zamudio Ruíz (US)	Mexico, Queretaro	–	–	–	–	**MK090777**	**MK090690**
178	*Muhlenbergia rigida* (Kunth) Kunth	Peterson 24733, Romaschenko & Zamudio Ruíz (US)	Mexico, Queretaro	–	–	–	–	**MK090778**	**MK090691**
179	*Muhlenbergia rigida* (Kunth) Kunth	Peterson 24802, Romaschenko, Rodriguez Avalos, Herrera-Simoni & Garcia Rodriguez (US)	Mexico, Aguascalientes	**MK090820**	**MK090880**	**MK090852**	**MK090732**	**MK090779**	**MK090692**

N	Taxon	Voucher	Country	rps3	rps16-trnK	rps16 intron	ndhA intron	rpl32-trnL	ITS
180	*Muhlenbergia rigida* (Kunth) Kunth	Peterson 24805, Romaschenko, Rodriguez Avalos, Herrera-Simoni & Garcia Rodriguez (US)	Mexico, Aguascalientes	–	–	–	–	**MK090780**	**MK090693**
181	*Muhlenbergia rigida* (Kunth) Kunth	Peterson 24931, Romaschenko & González-Elizondo (US)	Mexico, Durango	–	–	–	–	**MK090781**	**MK090694**
182	*Muhlenbergia rigida* (Kunth) Kunth	Peterson 24932, Romaschenko & González-Elizondo (US)	Mexico, Durango	–	–	–	–	**MK090782**	**MK090695**
183	*Muhlenbergia rigida* (Kunth) Kunth	Peterson 24933, Romaschenko & González-Elizondo (US)	Mexico, Durango	**MK090821**	**MK090881**	–	**MK090733**	**MK090783**	**MK090696**
184	*Muhlenbergia robusta* (E. Fourn.) Hitchc.	Peterson 15928 & Valdes Reyna (US)	Mexico, Nuevo Leon	HM143320	HM143701	HM143600	**MK090734**	HM143216	HM143114
185	*Muhlenbergia sericea* (Michx.) P.M. Peterson	Peterson 14843, Blackburn & Peterson (US)	USA, South Carolina	HM143321	HM143702	HM143601	HM143417	HM143217	HM143115
186	*Muhlenbergia setifolia* Vasey	Peterson 20942, Saarela, Lara Contreras & Reyna Alvarez (US)	Mexico, Coahuila	HM143322	HM143703	HM143602	HM143418	HM143218	HM143116
187	*Muhlenbergia speciosa* Vasey	Peterson 13616, Knowles, Dietrich, Braxton, & Gonzalez Elizondo (US)	Mexico, Durango	HM143325	HM143705	HM143605	HM143421	HM143221	HM143119
188	*Muhlenbergia stricta* (J. Presl) Kunth	Peterson 13709 (US)	Mexico, Jalisco	HM143328	HM143708	HM143608	HM143423	HM143224	HM143122
189	*Muhlenbergia subaristata* Swallen	Peterson 21243 & Saarela (US)	Mexico, Durango	HM143329	HM143709	HM143609	HM143424	HM143225	HM143123
190	*Muhlenbergia venezuelae* Luces	Briceño 266 & Adamo (MO)	Venezuela, Merida	**MK090830**	**MK090891**	**MK090856**	**MK090746**	**MK090796**	**MK090709**
191	*Muhlenbergia versicolor* Swallen	Peterson 9913 & Annable (US)	Mexico, Oaxaca	HM143339	HM143719	HM143619	–	HM143235	HM143132
192	*Muhlenbergia virletii* (E. Fourn.) Soderstr.	Peterson 9724 & Campos Villanueva (US)	Mexico, Oaxaca	HM143343	**MK090892**	**MK090857**	–	HM143239	HM143136
193	*Muhlenbergia x involuta* Swallen	Peterson 6284 & Annable (US)	USA, Texas	HM143345	HM143724	HM143624	HM143435	HM143241	HM143138

Table 2. Characteristics of the six regions, *rps3*, *rps16-trnK*, *rps16 intron*, *ndhA intron*, *rpl32-trnL*, *and ITS*, and parameters used in Bayesian analyses indicated by Akaike Information Criterion (AIC).

	rps3	***rps16-trnK***	***rps16 intron***	***ndhA intron***	***rpl32-trnL***	***ITS***	**Overall**
Total aligned characters	615	1000	1088	1189	996	761	5649
Number of new sequences	31 (19.5%)	33 (20.8%)	26 (17.2%)	34 (23%)	48 (25.9%)	50 (26.7%)	222 (22.4%)
Likelihood score (-lnL)	2342.85	3659.76	3429.94	5167.05	4762.52	9632.65	
Number of substitution types	6	6	6	6	6	6	–
Model for among-site rate variation	gamma	gamma	gamma	gamma	gamma	gamma	–
Substitution rates							
rAC	0.90029	1.07678	1.23238	0.75118	1.09619	1.43396	–
rAG	1.92233	3.01634	1.29662	2.20104	1.87400	2.69229	
rAT	0.56014	0.53859	0.46844	0.62199	0.45930	1.81818	
rCG	1.67415	1.17251	1.02428	1.66881	1.25539	0.71134	
rCT	3.50831	2.22649	2.45667	2.58721	1.47927	5.08729	
rGT	1.00000	1.00000	1.00000	1.00000	1.00000	1.00000	
Character state frequencies							
fA	0.43511	0.31626	0.38612	0.38183	0.38425	0.26145	–
fC	0.14841	0.12963	0.11052	0.11648	0.11939	0.19766	
fG	0.16534	0.13166	0.17725	0.13533	0.12321	0.24978	
fT	0.25114	0.42244	0.32611	0.36637	0.37315	0.29111	
Proportion of invariable sites	0.19372	0.10382	0.38367	0.07818	0.1631	0.38392	–
Gamma shape parameter (α)	0.74961	1.26136	0.92705	0.96285	0.93242	0.80871	–

Species of *M*. subg. *Clomena* have 3-veined upper glumes that are often 3-toothed, densely caespitose non-rhizomatous culms with lower leaf sheaths that are often flat and somewhat papery at maturity and lemmas with flexuous awns [only *M. jonesii* (Vasey) Hitchc. lacks an awn, apex is mucronate] (Reeder and Reeder 1995; Herrera Arrieta 1998; Peterson 2003; Peterson et al. 2010b). The wide-ranging *M. peruviana* (P. Beauv.) Steud. is the only species of this subgenus that reaches South America, including Peru.

Members of *M*. subg. *Pseudosporobolus* usually have plumbeous spikelets, well-developed adaxial and abaxial sclerenchyma in their primary vascular bundles, narrow to loosely open panicles, unawned, mucronate or short-awned lemmas [long-awned in *M. implicata* (Kunth) Trin. and *M. seatonii* Scribn.] and the plants are rhizomatous when perennial (Peterson and Herrera Arrieta 2001; Peterson 2003; Peterson et al. 2010b). In Peru, *M. fastigiata* (J. Presl) Henrard, *M. monandra* Alegría & Rúgolo (endemic) and *M. phalaroides* (Kunth) P.M. Peterson are placed in *M*. subg. *Pseudosporobolus*.

Morphologically, species of the *M*. subg. *Muhlenbergia* clade have broad, flat leaf blades, most have well-developed, scaly and creeping rhizomes and panicles that are usually narrow at maturity (Peterson et al. 2010b). This is the only subgenus where the PCK subtype of C_4 photosynthesis has been found. PCK species contain chlorenchyma composed of tabular cells that are indistinctly radiate and continuous between bundles [PCK type, defined as centrifugal/evenly distributed photosynthetic carbon reduction (PCRD) cell chloroplasts (with grana). The major veins are surrounded by two bundle sheaths, an inner mestome sheath of elongate non-chlorenchymatous cells and an outer chlorenchymatous sheath of shorter PCRD cells (designated XyMS+structural type; Hattersley and Watson 1976, 1992; Dengler et al. 1986). In addition, the leaf blades of these species contain fan- to shield-shaped bulliform cells that do not form a column of colourless cells from the adaxial to the abaxial surface and they generally have four or more secondary and/or tertiary vascular bundles between consecutive primary vascular bundles (Gutierrez et al. 1974; Brown 1977; Peterson and Herrera Arrieta 2001). Anatomically, *Muhlenbergia tarahumara* P.M. Peterson & Columbus is an exception to the standard PKC-type leaf structure in having non-contiguous chlorenchyma separated by columns of colourless cells between adjacent vascular bundles (Peterson and Columbus 2009; Peterson et al. 2010b). In Peru, *M. beyrichiana* Kunth, *M. bryophilus* (Döll) P.M. Peterson, *M. cenchroides* (Humb. & Bonpl. ex Willd.) P.M. Peterson, *M. ciliata* (Kunth) Trin., *M. diversiglumis, M. flexuosa* Hitchc. (endemic), *M. microsperma* (DC.) Kunth and *M. romaschenkoi* (endemic) are placed in *M.* subg. *Muhlenbergia*.

Taxonomic treatment

Muhlenbergia **Schreb., Gen. Pl. 1: 44. 1789.**

Dilepyrum Michx., Fl. Bor.-Amer. 1: 40. 1803. Type: *Dilepyrum minutiflorum* Michx. (= *Muhlenbergia schreberi* J. F. Gmel.).

Aegopogon Humb. & Bonpl. ex Willd., Sp. Pl. 4 (2): 899. 1805 [1806] Type: *Aegopogon cenchroides* Humb. & Bonpl. ex Willd. [≡ *Muhlenbergia cenchroides* (Humb. & Bonpl. ex Willd.) P.M. Peterson].

Podosemum Desv., Nouv. Bull. Sci. Soc. Philom. Paris 2: 188. 1810. Type: *Podosemum capillare* (Lam.) Desv. [= *Muhlenbergia capillaris* (Lam.) Trin.].

Clomena P. Beauv., Ess. Agrostogr. 28. 1812. Type: *Clomena peruviana* P. Beauv. [≡ *Muhlenbergia peruviana* (P. Beauv.) Steud.].

Tosagris P. Beauv., Ess. Agrostogr. 29. 1812. Type: *Tosagris agrostidea* P. Beauv. [= *Muhlenbergia capillaris* (Lam.) Trin.].

Trichochloa P. Beauv., Ess. Agrostogr. 29. 1812. Type: *Trichochloa purpurea* P. Beauv. [= *Muhlenbergia expansa* (Poir.) Trin.].

Podosaemum Kunth, Mem. Mus. Hist. Nat. 2: 72. 1815; orth. var. *Podosemum*.

Hymenothecium Lag., Gen. Sp. Pl. 4. 1816. Lectotype: *Cynosurus tenellus* Cav. ex DC., designated by Hitchcock 1920: 169 [≡ *Lamarckia tenella* DC. ≡ *Hymenothecium tenellum* (Cav. ex DC.) Lag. = *Muhlenbergia uniseta* (Lag.) Columbus].

Lycurus Kunth, Nov. Gen. Sp. 1: 141. 1815 [1816]. Lectotype: *Lycurus phleoides* Kunth, designated by Hitchcock 1920: 139 [≡ *Muhlenbergia phleoides* (Kunth) Columbus].

Anthipsimus Raf., J. Phys. Chim. Hist. Nat. Arts 89: 105. 1819. Type: *Anthipsimus gonopodus* Raf. (= *Muhlenbergia schreberi* J.F. Gmel.).

Sericrostis Raf., Neogenyton 4. 1825. Lectotype: *Stipa sericea* Michx, designated by Pfeiffer 1874: 1142 [≡ *Muhlenbergia sericea* (Michx.) P.M. Peterson].

Pereilema J. Presl, Reliq. Haenk. 1 (4–5): 233.1830. Type: *Pereilema crinitum* J. Presl (≡ *Muhlenbergia pereilema* P.M.Peterson).

Epicampes J. Presl, Reliq. Haenk. 1 (4–5): 235. 1830. Type: *Epicampes stricta* J. Presl [= *Muhlenbergia robusta* (E. Fourn.) Hitchc.].

Dactylogramma Link, Hort. Berol. 2: 248. 1833. Type: *Dactylogramma cinnoides* Link [= *Muhlenbergia glomerata* (Willd.) Trin.].

Calycodon Nutt., Proc. Acad. Nat. Sci. Philadelphia 4: 23. 1848. Type: *Calycodon montanum* Nutt. [≡ *Muhlenbergia montana* (Nutt.) Hitchc.].

Pleopogon Nutt., Proc. Acad. Nat. Sci. Philadelphia 4: 25. 1848. Type: *Pleopogon setosum* Nutt. [≡ *Lycurus setosus* (Nutt.) C.G. Reeder = *Muhlenbergia alopecuroides* (Griseb.) P.M. Peterson & Columbus].

Schedonnardus Steud., Syn. Pl. Glumac. 1: 146. 1854. Type: *Schedonnardus texanus* Steud. [*Spirochloe paniculata* Nutt. = *Schedonnardus paniculatus* (Nutt.) Branner & Coville = *Muhlenbergia paniculata* (Nutt.) Columbus].

Vaseya Thurb., Proc. Acad. Nat. Sci. Philadelphia 15: 79. 1863. Type: *Vaseya comata* Thurb. [= *Muhlenbergia andina* (Nutt.) Hitchc.].

Chaboissaea E. Fourn., Mexic. Pl. 2: 112. 1886. Type: *Chaboissaea ligulata* E. Fourn. [≡ *Muhlenbergia ligulata* (E. Fourn.) Scribn. & Merr.].

Crypsinna E. Fourn., Mexic. Pl. 2: 90. 1886. Lectotype: *Crypsis macroura* Kunth, designated by Hitchcock 1920: 144. [≡ *Crypsinna macroura* (Kunth) E. Fourn.≡ *Muhlenbergia macroura* (Kunth) Hitchc.].

Redfieldia Vasey, Bull. Torrey Bot. Club 14: 133. 1887. Type: *Graphephorum flexuosum* Thurb. ex A. Gray [≡ *Redfieldia flexuosa* (Thurb. ex A. Gray) Vasey ≡ *Muhlenbergia multiflora* Columbus].

Bealia Scribn., True Grasses 104, f. 45a. 1890. Type: *Bealia mexicana* Scribn. (≡ *Muhlenbergia biloba* Hitchc.).

Blepharoneuron Nash, Bull. Torrey Bot. Club 25(2): 88. 1898. Lectotype: *Vilfa tricholepis* Torr., designated by Peterson and Annable 1990: 522 [≡ *Blepharoneuron tricholepis* (Torr.) Nash ≡ *Muhlenbergia tricholepis* (Torr.) Columbus].

Schaffnerella Nash, N. Amer. Fl. 17(2): 141. 1912. Type: *Schaffnera gracilis* Benth. [≡ *Schaffnerella gracilis* (Benth.) Nash ≡ *Muhlenbergia spatha* Columbus].

Description. Plants *annual* or *perennial*; synoecious sometimes andromonoecious; sometimes rhizomatous, often cespitose, sometimes mat-forming, rarely stoloniferous. *Culms* 2–300 cm, erect, geniculate or decumbent, usually herbaceous, sometimes becoming woody. *Sheaths* open, overlapping below; *ligules* membranous or hyaline (rarely firm or coriaceous), acuminate to truncate, sometimes minutely ciliolate, sometimes with lateral lobes longer than the central portion; *blades* narrow, flat, folded, or involute, sometimes arcuate. *Inflorescences* terminal, sometimes also axillary, open to contracted, raceme-like or spike-like panicles; *cleistogamous panicles* sometimes present in the axils of the lower cauline leaves, enclosed by a tightly rolled, somewhat indurate sheath; *disarticulation* usually above the glumes, occasionally below the pedicels. *Spikelets* mostly perfect with 1 (2–6) florets, sometimes staminate or sterile, occasionally paired or in groups of threes then the central spikelet perfect and the lateral ones staminate or sterile; chasmogamous, rarely cleistogamous; *glumes* usually (0)1(2–3)-veined, apices entire, erose or toothed, truncate to acuminate, sometimes mucronate or awned from the midvein, occasionally awned from the lateral veins; *lower glumes* sometimes rudimentary or absent, occasionally bifid; *upper glumes* shorter than to longer than the florets; *calluses* poorly developed, glabrous or with a few hairs; *lemmas* glabrous, scabrous or with short hairs, 3-veined (rarely appearing 5-veined), apices awned from the midvein, mucronate or unawned; *awns*, if present, straight, flexuous, sinuous or curled, sometimes borne between 2 minute teeth, lateral veins occasionally extended into awns; *paleas* shorter than or equal to the lemmas, 2-veined, apices; *anthers* (1–2)3, purple, orange, yellow, olivaceous or whitish; *ovary* with 2 styles, stigmas plumose. *Caryopses* elongate, fusiform or elliptic, slightly dorsally compressed, rarely laterally compressed, glabrous; *hilum* short; *pericarp* fused.

Chromosome base number is × = (8 or 9) 10 and these are relatively small in size.

Distribution. The genus is primarily distributed in the Western Hemisphere in North Central and South America. There are also seven species known to occur in south-eastern Asia, six of these are found in China (Wu and Peterson 2006).

Ecology. The species occur in open habitats in deserts, grasslands, sclerophllous scrubland and margins of forests often in xeric to meso-xeric habitats from near sea level to more than 4000 m.

Etymology. Named for Gotthilf Heinrich Ernst Muhlenberg (1753–1815), a Lutheran minister and pioneering botanist of Pennsylvania, USA.

Key to the species of *Muhlenbergia* in Peru

1 Spikelets grouped in fascicles of 2–4 spikelets **2**

– Spikelets not grouped in fascicles **5**

2 Each fascicle subtended by 10–15 bristles, the bristles 1–5 mm long; ligules auriculate, the auricles 1–2 mm long, ciliate, sometimes cauducous at maturity, the cilia about 1 mm long .... **1. *M. beyrichiana***

– Fascicles never subtended by bristles; ligules not auriculate and not ciliate or hairy **3**

3 Anthers 0.5–0.7 mm long; sprawling, slender annuals (4–) 6–30 cm long; sessile or inconspicuously pedicelled perfect spikelet associated with one (rarely two) staminate or sterile pedicelled spikelets .... **2. *M. bryophilus***

– Anthers 1.6–2 mm long; sprawling perennials, 10–55 cm long; sessile or inconspicuously pedicelled spikelet perfect and associated with two staminate or sterile pedicelled spikelets or the lower short-pedicelled spikelet perfect, staminate or sterile and the upper longer-pedicelled spikelet perfect, staminate or sterile **4**

4 Apex of lemmas 3-awned, the central awns 5–13 mm long, lateral awns 2–3 mm long; lemmas 2.5–3 mm long with glabrous margins; lower glumes 1-veined, apex deeply notched with triangular lobes .... **4. *M. cenchroides***

– Apex of lemmas 1-awned, sometimes mucronate or unawned, the awns 1–3 mm long; lemmas 3–4 mm long with hirsute to lanate margins, the hairs 0.1–0.3 mm long; lower glumes commonly 2 or 3-veined, usually 2-awned (from lateral veins), apex not deeply notched and without triangular lobes .... **16. *M. phalaroides***

5 Plants annual **6**

– Plants perennial **13**

6 Upper glumes 3-veined, the apex broad and truncate, usually 2- or 3-toothed .... **15. *M. peruviana***

– Upper glumes 1-veined, the apex acute, acuminate, or subulate, not 2- or 3-toothed 7

7 Lemmas mucronate, the mucro usually less than 1 mm long or occasionally short-awned with the awn up to 1.5 mm long **8**

– Lemmas awned, the awns 1.2–30 mm long, at least some of the spikelets with awns much longer than 1.2 mm **9**

8 Lemmas sericeous, lower ½–¾ with scattered hairs, the hairs 0.3–0.5 mm long; paleas hairy between the nerves .... **3. *M. caxamarcensis***

– Lemmas glabrous; paleas glabrous between the nerves .... **11. *M. ligularis***

9 Florets with a single stamen; panicles 2–9 mm wide, tightly spiciform; lemma awns 1.2–5 mm long; both glumes as long or longer than the floret .... **14. *M. monandra***

– Florets with 3 stamens; panicles 1.8–13.5 cm wide, sometimes narrow or contracted when immature but with spreading or reflexed branches at maturity; lemma awns 5–30 mm long; both glumes not longer than the floret (lower glume longer in *M. diversiglumis*) **10**

10 Cleistogamous panicles with 1–3 spikelets present in the axils of the lower sheaths; glume apices obtuse, unawned .... **13. *M. microsperma***

– Cleistogamous panicles not present in the axils of the lower sheaths; glume apices acute to acuminate and usually awned **11**

11 Panicles secund; primary branches with 2–5 spikelets; secondary branches not developed; spikelets dimorphic with respect to the glumes, the glumes of the proximal spikelet on each branch subequal, to 0.7 mm long, orbicular and unawned, those of the distal spikelets evidently unequal, the lower glumes to 8 mm long and usually awned, the upper glumes orbicular, sometimes awned .... **8. *M. diversiglumis***

– Panicles not secund; primary branches always with more than 2 spikelets, usually with more than 5; secondary branches well-developed; spikelets monomorphic with respect to the glumes **12**

12 Ligules 0.2–0.8 mm long, apex truncate, entire; paleas glabrous between the nerves on the proximal ½; 6–13 nodes along the panicle; panicles 4–12 cm long .... **5. *M. ciliata***

– Ligules 1.2–3.0 (–5.0) mm long, acute to obtuse, lacerate; paleas sparsely appressed pubescent between the nerves on the proximal ½; 15–23 nodes along the panicle axis; panicles 7–15 cm long.......... **18. *M. romaschenkoi***

13 Culms 40–140 cm tall; leaf blades 12–45 cm long.......... **14**

– Culms 2–40 cm tall; leaf blades 0.3–12 cm long.......... **15**

14 Panicles contracted and spike-like, 0.6–2 cm wide, usually plumbeous to reddish-purple; panicle branches tightly ascending from the rachises at maturity.......... **6**

– Panicles loosely contracted to loosely spreading, (2–) 3–6 (–15) cm wide; panicle branches ascending and/or spreading up to 80° from the rachises.......... **17**

16 Glumes (4–) 5–7 (–8) mm long, usually as long or longer than the floret; lemmas unawned, mucronate or short-awned, the awns 1–3(–4) mm long... .... **6. *M. coerulea***

– Glumes 2.5–3.5 (–4) mm long, 1/2–3/4 as long as the floret; lemmas awned, the awns generally 3–8(–10) mm long.......... **7. *M. coerulea* × *M. rigida***

17 Lemmas 2.5–2.8 mm long with scattered sericeous hairs along the veins above the hairy callus; caryopses 1.4–1.7 mm long.......... **12. *M. maxima***

– Lemmas 3.5–6 mm long, glabrous along the veins above the hairy callus; glumes caryopses 2–3.5 mm long.......... **18**

18 Lemmatal awns 3–8 (–10) mm long; glumes ½–¾ as long as the floret, 2.5–3.5 (–4) mm long; lemmas 4–6 mm long; spikelets plumbeous to reddish-purple.......... **7. *M. coerulea* × *M. rigida***

– Lemmatal awns (8–) 10–22 mm long; glumes less than ½ as long as the floret, 1–1.7 (–2) mm long; lemmas 3.5–5 mm long; spikelets reddish-purple.. .... **17. *M. rigida***

15 Lemmas awned, the awns 14–30 mm long.......... **19**

– Lemmas unawned, mucronate, the mucro usually less than 1 mm long or occasionally short-awned with an awn up to 3 mm long.......... **20**

19 Lower glumes 2.8–4 mm long including the mucro or short-awn if present; ligules 0.3–0.5 mm long, apex truncate; anthers 1.3–1.6 mm long.......... **10. *M. flexuosa***

– Lower glumes 1–2.5 mm long including the mucro if present; ligules 1.2–3 (–5.0) mm long, apex acute; anthers 0.3–0.4 mm long.......... **18. *M. romaschenkoi***

20 Lower glumes commonly 2 or 3-veined and awned from the lateral veins, the 2 awns 1–3 mm long; spikelets paired on a branch, the lower spikelet staminate or sterile and the upper perfect.......... **16. *M. phalaroides***

– Lower glumes 1-veined and unawned; spikelets borne singly on a branch or, if in pairs, the upper and lower both perfect.......... **21**

21 Plants rhizomatous, the main root or rhizome 1–2 (–2.5) mm wide; leaf blades tightly involute, arcuate, apex often pungent, the blades 2–8.5 mm long long .... **9. *M. fastigiata***

– Plants not rhizomatous, the roots less than 0.8 mm wide; leaf blades usually flat, straight, not pungent, the blades 3–22 mm long................................ **22**

22 Lemmas sericeous, lower ½–¾ with scattered hairs, the hairs 0.3–0.5 mm long; paleas hairy between the veins............................. **3. *M. caxamarcensis***

– Lemmas glabrous; paleas glabrous between the veins........... **11. *M. ligularis***

1. *Muhlenbergia beyrichiana* Kunth, Enum. Pl. 1: 200. 1833.

Fig. 2A–F

Pereilema beyrichianum (Kunth) Hitchc., Contr. U.S. Natl. Herb. 24(8): 385. 1927. Type: Brazil, Province de Saint-Paul, Voyage d'Auguste de Saint-Hilaire de 1816 a 1821, *Saint-Hilare Cat. B #1028* (lectotype, designated here: P-00751689!; isolectotype: US-1645654! ex P).

Description. Caespitose *annuals. Culms* 30–80 cm tall, slender, terete, glabrous, often branching from the aereal nodes below, usually with stilt-roots from lower nodes. *Leaf sheaths* usually shorter than the internodes, furrowed, scabrous; *ligules* 0.5–0.7 mm long, membranous; *auricles* 1–2 mm long, ciliate, sometimes cauducous at maturity, the cilia about 1 mm long; *blades* 8–20 cm long, 3–6 (–8) mm wide, flat, scabrous, apex attenuate. *Panicles* 5–16 (–20) cm long, 1–2.5 cm wide, contracted, spike-like, interrupted, the branches widely spaced along the rachis; *primary branches* 1–3 cm long, appressed, ascending or divergent and spreading. *Spikelets* in dense clusters of 2–4 subtended by 10–15 bristles, the bristles 1–5 mm long; *glumes* 0.7–1 mm long, ovate, membranous, 1-veined, apex awned, bidentate, the awns 3.5–5 mm long; *lemmas* (1.2–) 2–2.2 mm long, lanceolate, 3-veined, cartilaginous, scaberulous, awned, the awns 10–16 (–20) mm long, straight; *callus* short, the hairs 0.2–0.4 mm long; *paleas* as long as the lemmas, 2-veined, these often extending into mucros 0.1–0.3 mm long; *stamens* 3, *anthers* 0.7–1 mm long, purplish. *Caryopses* 1–1.3 mm long, ellipsoid.

Distribution. *Muhlenbergia beyrichiana* is known to occur in Brazil, Ecuador and Peru. Earlier, it was reported in Mexico and Central America but these are probably an error for *Muhlenbergia diandra* (R.W. Pohl) Columbus, a more recently described species that superficially resembles *M. beyrichiana* (Espejo Serna et al. 2000; Lægaard and Peterson 2001; Peterson et al. 2001).

Ecology. This species occurs in xerophilic savannahs with Cactaceae, roadsides and along moist ravines; 150–2000 m (Lægaard and Peterson 2001).

Comments. *Muhlenbergia beyrichiana* is morphologically similar to *M. pereilema* P.M. Peterson, which does not occur in Peru, but can be separated from the latter in having interrupted panicles with divergent primary branches (versus uninterruped

Figure 2. A–E *Muhlenbergia beyrichiana* Kunth **A** habit **B** ligule with auricles **C** glumes **D** floret **E** stamens and pistil **F–H** *Muhlenbergia maxima* Lægaard & Sánchez Vega **F** habit **G** end of panicle branch **H** floret. **A–E** drawn from *A.S. Hitchcock 20635* (US) **F–H** drawings from Lægaard & Sánchez Vega (1990) drawn from the holotype collection *Sánchez Vega & Ruíz Vigo 3561*.

panicles with tightly appressed primary branches in *M. pereilema*), straight lemma awns (versus flexuous or wavy), wide leaf blades 3–6 (–8) mm (versus 2–3 mm) and ciliate auricles (versus not ciliate) [Lægaard and Peterson 2001].

Muhlenbergia beyrichiana is in a clade with *M. pereilema* and *M. plumiseta* and is sister to *M. flexuosa* Hitchc. in *M.* subg. *Muhlenbergia* (Fig. 1B; Peterson et al. 2010b).

Specimens examined. Peru. **Junín:** Huancayo, abajo de Pariahuanca, 2000 m, 5 May 1979, Tovar 7880 (US, USM), Tovar 7901 (USM).

2. *Muhlenbergia bryophilus* (Döll) P.M. Peterson, Caldasia 31(2): 279, f. 2 A–B, 2009.

Fig. 3A, B

Aegopogon bryophilus Döll, Fl. Bras. 2(3):239. 1880. Type: BRAZIL, Minas Gerais, 10 Apr 1879, *A.F.M. Glaziou 11661* (holotype: P-01863266 [image!]; isotypes: C-10016716 [image!], K-000309079 [image!], US-1280026!).

Aegopogon geminiflorus var. *muticus* Pilg., Bot. Jahrb. Syst. 27(1–2):25. 1899. Type: Bolivia, La Paz, near Sorata, 1 May 1892, *M. Bang 1307* (holotype: unknown; isotypes: CM-0179 [image!], K-000309080 [image!], NDG-07662 [image!], PUL-00000320 [image!], US-2473254!; W-18930005256 [image!]).

Aegopogon argentinus Mez, Repert. Spec. Nov. Regni Veg. 17(8–12):145. 1921. Type: ARGENTINA. Salta: Sierra Nevada del Castillo, *P.G. Lorentz & G. Hieronymus 182* (holotype: B?; isotypes: BAA-00001256 [image!], US-75037 fragm. ex B!).

Aegopogon fiebrigii Mez, Repert. Spec. Nov. Regni Veg. 17(8–12):145. 1921. Type: BOLIVIA. Camacho, *K. Fiebrig 2865* (holotype: B?; isotypes: MVFA-0000127 [image!], US-75308 fragm. ex B!).

Description. Slender often sprawling, caespitose *annuals*. *Culms* (4–) 6–30 cm long, glabrous below the nodes; *internodes* 0.6–6 cm long, glabrous to pilose. *Leaf sheaths* mostly 0.5–4.8 cm long, shorter than the internodes, glabrous to sparingly pilose; *ligules* 0.6–1.5 mm long, glabrous, apex mostly truncate, lacerate, auricles absent; *blades* 1.5–6 cm long, 0.5–1.5(–1.7) mm wide, flat, scaberulent and pubescent above, mostly smooth beneath. *Panicles* 2–6 cm long, 0.5–1.2 cm wide, open, loosely-flowered; *primary branches* 0.2–0.6 mm long, excluding the awns, one per node, racemosely inserted. *Fertile spikelets* 2.4–3 mm long, in fascicles of two, rarely three per branch, often greenish or purplish, the clusters with one short-pedicelled spikelet (bisexual); *pedicels* (0.0–) 0.2–0.5 mm long (fertile spikelets) and the other two spikelets (sterile or staminate) longer pedicelled; *pedicels* about 0.7–1 mm long (sterile or staminate); *glumes* 1–1.3 mm long, narrowly acuminate, apex prolonged, aristate; *lemmas* 2.4–3 mm long, 3-awned, the central awns (3–) 5–8 (–12) mm long, lateral awns usually 0.8–1.4 mm long; *paleas* 2.2–2.8 mm long, puberulent, apex aristate, the awns usually 1–1.2 mm long; *anthers* 0.5–0.7 mm long, yellowish. *Caryopses* about 1 mm long, obovoid, light brownish.

Distribution. *Muhlenbergia bryophilus* is found in South America, occuring in Argentina, Bolivia, Brazil, Chile, Colombia, Ecuador and Peru.

Ecology. This species occurs on moist slopes, cliffs, barrancas, canyons, roadsides and along or near springs usually in shaded areas associated with *Cenchrus clandestinus*

Figure 3. A, B *Muhlenbergia bryophilus* (Döll) P. M. Peterson **A** habit **B** spikelet **C, D** *Muhlenbergia cenchroides* (Humb. & Bonpl. ex Willd.) P. M. Peterson **C** habit **D** spikelet. Drawings from Giraldo-Cañas and Peterson (2009) **A, B** drawn from *S.G. Beck 818* (LPB) **C, D** drawn from *S.G. Beck 7464* (LPB).

(Hochst. ex Chiov.) Morrone, *Bouteloua simplex* Lag., *Festuca myruos* L., *Urochloa*, *Veronica*, *Eragrostis*, *Baccharis*, *Salvia*, *Agave* and *Erodium*; 1500–3700 m. Flowering December through May.

Comments. *Muhlenbergia bryophilus* is morphologically similar to *M. cenchroides* and can be separated from the latter in having anthers 0.5–0.7 mm long, the annual habit with culms (4–) 6–30 cm tall and sessile or inconspicuously pedicelled perfect spikelet associated with one (rarely two) staminate or sterile pedicelled spikelet (Tovar 1993; Giraldo-Cañas and Peterson 2009). The central lemmatal awn length of the sessile or inconspicuously pedicelled spikelet was used by Beetle (1948) to differentiate between these two species but we found this measure to be completely overlapping. *Muhlenbergia bryophilus* is sister to a single entry of *M. uniseta* (Peterson 24712) in our new analysis (Fig. 1B). We have only a single marker (ITS) for *M. bryophilus*, so its alignment may change with additional plastid markers.

Specimens examined. Peru. **Cusco**: Prov. Anta, Mollepata–Takawana, C. Vargas C. 19050 (USM); Prov. Urubamba, SW facing slope of Machu Picchu Mountain, V. Ugent 5324 (USM); **Junín**: Prov. Huancayo, Abajo de Pariahuanca, O. Tovar 7895, 7904 (USM); Cerro E of Huancayo, O. Tovar 2137 (USM); **La Libertad**: Prov. Bolivar, W of Longotea, 0.5 km towards San Vicente, 7°2'35.6"S, 77°52'39.8"W, 3202 m, 31 Mar 2008, P.M. Peterson 21966, R.J. Soreng & J. Montoya Quino (US, USM); **Lima**: Prov. Canta, 8 km SW of San Jose Canta towards Huamantango, 11°31'10"S, 76°42'16.3"W, 2770 m, 28 Mar 2004, P.M. Peterson & N. Refulio Rodríguez 17995 (US, USM); **Piura**: Prov. Huancabamba, La Beatita, S. Llatas Quiroz 1850, 1851 (CPUN); **Puno**: Prov. Sandia, Debajo de Cuyocuyo, R. Ferreyra & A. Vera Beuner 16636 (USM).

3. *Muhlenbergia caxamarcensis* Lægaard & Sánchez Vega, Nordic J. Bot. 10:437. 1990.

Fig. 4A–C

Type. Peru, Cajamarca, Micuypampa, 62 km from Cajamarca towards Celendín, 3600 m, 26 Mar 1988, *S.A. Renvoize & S. Lægaard 4962* (holotype: CPUN!; isotypes: AAU!, K!, MO-3712393!, US-3185350!).

Description. Loosely caespitose *perennials*. *Culms* 8–12 cm tall, 0.2–0.4 mm diameter just below the panicle, erect to decumbent near base, slender, scaberulous to glabrous, profusely branched below; *lower internodes* 5–10 mm long with repeated intravaginal branching. *Leaf sheaths* 4–27 mm long, glabrous, generally longer than the internodes, rounded near base; *ligules* (1.5–) 1.8–2.5 mm long, hyaline, often lacerate, margins decurrent, apex obtuse; *blades* 0.5–1.5 cm long, 0.6–1.2 mm wide, flat or folded, prominently veined, sometimes conspicuously crystalline or spiculate on both surfaces, otherwise glabrous below, sparsely scaberulous above and along margins, tapering to a boat shaped tip. *Panicles* (1.0–)1.5–4.0 cm long, 1–3 mm wide, exserted or included in the uppermost sheath, loosely contracted, narrow; *primary branches* 0.5–2 cm long, appressed to the culm axis, one per node.*pedicels* 1–5 mm long, stiff, densely scabrous,

Figure 4. A–C *Muhlenbergia caxamarcensis* Lægaard & Sánchez Vega **A** habit **B** panicle branch **C** floret **D–G** *Muhlenbergia ciliata* (Kunth) Trin **D** habit **E** ligule **F** glumes **G** floret. Drawings **A–C** from Lægaard and Sánchez Vega (1990) from holotype collection (*S.A. Renvoize & S. Lægaard 4962*) **D–G** from Peterson and Annable (1991) drawn from *P.M. Peterson & C.R. Annable 4541* (WS).

spiculate, erect; *nodes* 4–6 per inflorescence. *Spikelets* 2.4–2.8 mm long (excluding the mucro or awn), plumbeous to reddish-purple; *glumes* 1.2–1.6 mm long, shorter than the floret, subequal to equal, 1-nerved, glabrous, often reddish-purple near apex and greenish-grey below, apex obtuse; *lemmas* 2.4–2.8 mm long, lanceolate, keeled, prominently 3-nerved, dark reddish-purple to plumbeous above greenish-grey below, sericeous, lower ½ to ¾ with scattered appressed hairs, the hairs 0.3–0.5 mm long, apex acuminate, mucronate or short-awned, the awn up to 1.5 mm long, scabrous; *paleas* 2.4–2.6 mm long, as long as the lemma, lanceolate, hairy between the nerves; *anthers* 1–1.3 mm long, purple or yellow. *Caryopses* 0.9–1.1 mm long, elliptic to fusiform, terete, yellowish-brown.

Distribution. This species is endemic to Peru, known only from Cajamarca and La Libertad departments.

Ecology. *Muhlenbergia caxamarcensis* occurs on shallow soils on rock shelves and rocky outcrops often of calcareous origins, mud flats, open grassy meadows and slopes associated with *Festuca, Carex, Calamagrostis* (probably better treated as *Cinnagrostis* Griseb. but combinations are not yet made; Saarela et al. 2017, Soreng et al. 2017), *Polylepis*, *Muhlenbergia ligularis*, *M. peruviana* and *M. cenchroides*; 3000–3600 m. Flowering March through May.

Comments. *Muhlenbergia caxamarcensis* is morphologically similar to *M. ligularis* and *M. fastigiata* and can be separated from both of these species in possessing sericeous florets (lemma and palea) with hairs readily visible under 10× magnification.

Muhlenbergia caxamarcensis is a member of *M.* subg. *Bealia* and is sister to the North American *M. filiformis* (Thurb. ex S. Watson) Rydb.– *M. vaginata* Swallen pair (Peterson et al. 2010b). In our new analysis, *M. caxamarcensis* appears to have evolved within *M. ligularis* (Fig. 1A, plastid only). However, the ITS marker clearly aligns *M. caxamarcensis* with a single accession of *M. ligularis* (Fig. 1A). This pair is sister to *M. filiformis* and all three accessions are sister to *M. vaginata*. These results suggest multiple origins for *M. caxamarcensis* from North and South American progenitors.

Specimens examined. PERU. **Cajamarca**: Prov. Cajamarca, 16 km W of Cajamarca up road (Avenida Peru) towards Cumbemayo, 3440 m, 31 Mar 1997, P.M. Peterson & N. Refulio Rodriguez 14010 (US, USM); 18 km W of Cajamarca up road (Avenida Peru) towards Cumbe Mayo, 3600 m, 31 Mar 1997, P.M. Peterson & N. Refulio Rodriguez 14013 (US, USM); 29 km from Cajamarca on road to Celendín, S.A. Renvoize & S. Lægaard 4974 (AAU, CPUN, K, US); Cumbe Mayo, I. Sánchez Vega & W. Ruiz Vigo 598 (CPUN), I. Sánchez Vega 4690 (CPUN); Cumbe Mayo, W of Cajamarca, S.A. Renvoize 5000, 5004 & 5005 S. Lægaard & I. Sánchez Vega (AAU, CPUN, K, US); Micuypampa, 62 km from Cajamarca towards Celendín, S.A. Renvoize & S. Lægaard 4961 (AAU, CPUN, K, US); Prov. San Miguel, 61 km N of Cajamarca on hwy 3N towards Bambamarca, 3640 m, 16 Mar 2000, P.M. Peterson & N. Refulio Rodriguez 14916 (CPUN, US, USM); Cajamarca to Celendín, 3 km NE of Encañada, I. Sánchez Vega 2777, V. Torrel & E. Medina (CPUN); S.A. Renvoize & S. Lægaard 4849 (CPUN). **La Libertad**: Prov. Bolivar, 3 air km ESE of Longotea on road to Bolivar, 3202 m, 31 Mar 2008, P.M. Peterson 21965, R.J. Soreng & J. Montoyo Quino (US, USM); Nevado Cajamarquilla, 3500 m, 9 Sep 1946, J. Infantes Vera 937 (MOL).

4. ***Muhlenbergia cenchroides*** **(Humb. & Bonpl. ex Willd.) P.M. Peterson, Caldasia 31(2): 280, f. 2 C–D. 2009.**

Fig. 3C, D

Aegopogon cenchroides Humb. & Bonpl. ex Willd., Sp. Pl. 4(2):899. 1806. Type: Venezuela, Sucre, Cumaná, *F.W.H.A. Humboldt & A.J.A. Bonpland s.n.* (holotype: B-W-01637-020 [image!]; isotypes: P!, US-75957 fragm. ex P!).

Aegopogon geminiflorus Kunth, Nov. Gen. Sp. (quarto ed.) 1:133, t. 43. 1815 (1816). *Aegopogon cenchroides* var. *geminiflorus* (Kunth) Griseb., Abh. Königl. Ges. Wiss. Göttingen 24:301. 1879. Type: Venezuela, Amazonas, inter Cerro Duida et Rio Tamatama, juxta Esmeralda, May, F.W.H.A. *Humboldt & A.J.A. Bonpland s.n.* (holotype: P; isotype: US-75956 fragm. ex P!).

Hymenothecium quinquesetum Lag., Gen. Sp. Pl. 4. 1816. *Aegopogon quinquesetus* (Lag.) Roem. & Schult., Syst. Veg. 1:805. 1817. Type: Mexico, México Iperio, *Ludovicus Nee* (holotype: MA; isotype: BAA-00002156 [image!]).

Hymenothecium trisetum Lag., Gen. Sp. Pl. 4. 1816. *Aegopogon trisetus* (Lag.) Roem. & Schult., Syst. Veg. 2:805. 1817. *Aegopogon cenchroides* var. *trisetus* (Lag.) E. Fourn., Mexic. Pl. 2:72. 1886. Type: Mexico, México Imperio (holotype: MA; isotype: BAA-00002158 [image!]).

Aegopogon setifer Nees, Linnaea 19(6):691. 1847. Type: Mexico, *A. Aschenborn 132* (holotype: B; isotypes: FR-0036375 [image!], FR-0036376 [image!], US-75953 fragm. ex B!).

Aegopogon cenchroides var. *multisetus* E. Fourn., Mexic. Pl. 2: 72. 1886. Type: Mexico, Moran. in rupibus, 1840, *H. Galeotti 5808* (lectotoype: BR, designated by P.M. Peterson, Contr. U.S. Natl. Herb. 41: 10. 2001; isolectotypes: P!, US-75958 fragm. ex P!).

Description. Caespitose *perennials* often sprawling, occasionally with stolons. *Culms* (10–) 25–55 cm long, glabrous below the nodes; *internodes* glabrous. Leaf sheaths mostly 0.8–8 cm long, shorter than the internodes, glabrous; *ligules* 1–2 mm long, apex acute, lacerate; *blades* 1.5–6 cm long, 0.5–2 mm wide, flat, scaberulous above, smooth beneath. *Panicles* 2–8 cm long, 0.5–1.2 cm wide, open, loosely-flowered with recemosely arranged branches; *primary branches* 2–4 mm long, excluding the awns, one per node, often purplish. *Spikelet* fascicles of three with one sessile or subsessile perfect spikelet and two short-pedicelled lateral spikelets staminate or sterile, the *pedicels* less than 0.2–0.5 mm long and the other two spikelets short-pedicelled, the *pedicels* about 0.7–1.2 mm long; *glumes* (1–)1.5–2.8 mm long, oblong and wider distally, 1-veined, apex deeply notched, awned, the awns 2–4 mm long, lobes triangular, acute; *lemmas* 2.5–3 mm long, fusiform, 3-awned, the central awns 5–13 mm long, lateral awns 2–3 mm long; *paleas* 2.5–3 mm long, puberulent, apex awned, the awns 1–2 mm long; *anthers* 1.6–1.8 mm long, yellowish to purplish. *Caryopses* 1–1.4 mm long, fusiform. $2n$ = 40, 60, 80.

Distribution. *Muhlenbergia cenchroides* ranges from throughout México, Central America to South America in Bolivia, Brazil, Colombia, Ecuador, Peru, Guyana and Venezuela.

Ecology. *Muhlenbergia cenchroides* occurs on rocky slopes, canyons, cliffs, roadcuts, arroyos, seeps and meadows associated *Baccharis* spp., *Festuca myuros*, *Alnus*, *Polylepis*, *Fucaria*, *Salvia* spp., *Urochloa, Salvia* spp., *Calceolaria* spp., *Eupatorium*, *Festuca*, *Puya*, *Rubus*, *Schizachyrium*, *Cenchrus clandestinus*, *Calamagrostis* spp., *Muhlenbergia* spp., *Hyptis*, *Oxalis*, *Aristida, Begonia*, *Adiantum, Bidens, Lepechinia, Oreocallis grandiflora* (Lam.) R. Br., *Desmodium*, *Cortaderia bifida* Pilg., *Cortaderia jubata* (Lemoine ex Carriere) Stapf, *Sporobolus*, *Monnina*, *Carex*, *Cheilanthes*, *Eragrostis*, *Lupinus*, *Lycopodium*, *Jarava*, *Nassella*, *Werneria*, *Agave*, *Eucalyptus*, *Thalictrum* and *Chusquea*; 1430–3850 m. Flowering December through September.

Comments. *Muhlenbergia cenchroides* can be separated from *M. bryophilus* in having anthers 1.6–1.8 mm long, the perennial habit with (10–) 25–55 cm tall culms and sessile or inconspicuously pedicelled perfect spikelets usually associated with two staminate or sterile pedicelled spikelets (Tovar 1993; Giraldo-Cañas and Peterson 2009).

Muhlenbergia cenchroides lies in a clade with *M. tarahumara, M. uniseta* and *M. bryophilus* in *M.* subg. *Muhlenbergia* (Fig. 1B; Peterson et al. 2010b). The multiple sampled individuals of *M. cenchroides* and *M. uniseta* in the current analyses do not resolve into reciprocally monophyletic lineages, but one sublineage, including accessions of each species, is strongly supported. This strongly suggests gene flow among individuals of these two species.

Specimens examined. Peru. **Ancash**: Prov. Bolognesi, Paramarca, cerros al E de Chiquián, 3680 m, 8 Apr 1952, E. Cerrate 1396 (MOL, USM); Prov. Carhuaz, Cordillera Negra, 22 km SW of Shupluy and Rio Santa, 9°17'19.7"S, 77°44'39.3"W, 3770 m, 13 Mar 2008, P.M. Peterson 21652, R.J. Soreng, M.I. La Torre & J.V. Rojas Fox (US, USM); Prov. Corongo, Cordillera Blanca, 3 km E of Yanac, 8°35'55.6"S, 77°50'4.8"W, 2849 m, 18 Mar 2008, P.M. Peterson & R.J. Soreng 21786 (US, USM); Prov. Corongo, Cordillera Blanca, E of Yungay, 3400 m, 5 Apr 1988, S.A. Renvoize & S. Lægaard 5055 (CPUN, K); Prov. Huaraz, W side of Cordillera Blanca, S of Quebrada Ishinca, 9°24'55.8"S, 77°32'45.8"W, 2885 m, 12 Mar 2008, P.M. Peterson 21614, R.J. Soreng, M.I. La Torre & J.V. Rojas Fox (US, USM); Prov. Huaraz–Recuay border, W side of Rio Santa Canyon, 19 km S of Huaraz, 9°40'58.1"S, 77°28'29.7"W, 3202 m, 11 Mar 2008, P.M. Peterson 21600, R.J. Soreng, M.I. La Torre & J.V. Rojas Fox (US, USM); Prov Huaylas, Cordillera Blanca, encima de Caraz, 3200 m, A Weberbauer 3234 (MOL); Prov. Huaylas, Huata, M.I. La Torre 2793 (USM); Prov. Pallasca, 17 km N of Huandoval and 6 km S of Pallasca, 3360 m, 27 Mar 1997, P.M. Peterson & N. Refulio Rodríguez 13927 (US, USM); 3.4 km N of Huandoval towards Huascaschuque, 8°18'59.5"S, 77°58'9.5"W, 2949 m, 21 Mar 2008, P.M. Peterson & R.J. Soreng 21817 (US, USM); Prov. Huari, near Laguna de Puruhay, M.I. La Torre 3692 (USM); San Marcos, A. Cano 13505 (USM); Huascarán National Park, Quebrada Rurichinchay, D. Smith 12659, A. Gonzales & D. Maldonado (USM); Prov. Recuay, Cordillera Blanca, 16 km E of Catac on road towards Chavin de Huantar, 3630 m, 21 Mar 1997, P.M. Peterson & N. Refulio Rodríguez 13833 (US, USM); Prov. Yungay, Cordillera Blanca, 20 km ENE of Yungay, 9°6'26.2"S, 77°41'8.2"W 3247 m, 15 Mar 2008, P.M. Peterson 21712, R.J. Soreng, M.I. La Torre & J.V. Rojas Fox (US, USM);

Quebrada Llauganuco, 24 km ENE of Yungay, 9°5'46.3"S, 77°40'19.3"W, 3309 m, 16 Mar 2008, P.M. Peterson 21739, R.J. Soreng, M.I. La Torre & J.V. Rojas Fox (US, USM); Prov. Yungay, Huascarán National Park, Llanganuco sector, María Josefa trail between Chinancocha and Pucayacu, 77°39'W, 9°05'S, 3700–3850 m, 7 May 1985, D.N. Smith 10512 (CPUN, MO). **Ayacucho**: Ayna, L. Aucasime 258 (USM); Seqseqa, L. Aucasime 81 (USM); Prov. Huanca Sancos, 27 km NW of Putajasa and 3 km S of Sacsamarca, 13°57'51.1"S, 74°18'41.5"W, 3650 m, 25 Feb 2002, P.M. Peterson 16278, A. Cano, M. I. La Torre, A. Ramirez & D. Susanibar Cruz (US, USM). **Cajamarca**: near Cajamarca, 2700 m, 11 Mar 1986, B, Becker & F.M. Terrones H. 601 (LPB); Cajamarca to Celendín, 95 km from Cajamarca, above Quillimbas, 3000 m, 22 Mar 1988, S.A. Renvoize & S. Lægaard 4868 (CPUN, K); Prov. Cajamarca, 16 km W of Central Plaza of Cajamarca up road towards Cumbemayo on Avenida Peru, 3440 m, 31 Mar 1997, P.M. Peterson & N. Refulio Rodríguez 14012 (US, USM); Prov. Cajamarca, Dist. Baños del Inca, Tres Tingos, margen Oeste del río Chonta, 2900 m, 2 Mar 2002, I. Sánchez Vega 11261 (CPUN); Prov. Cajamarca, Cerro Huairapongo–Baños del Inca, 19 Nov 1965, I. Sánchez Vega 126 & Julio Mercado (CPUN); Prov. Cajamarca, Fundo Aylambo, a 5 km antes de la ciudad, 8 May 1969, I. Sánchez Vega 385 & W. Ruiz Vigo (CPUN); Prov. Cajamarca, cerca al Paso El Gavilán, 3100 m, 19 Apr 1975, I. Sánchez Vega 1407, P. Brandelard & J. Sanabria (CPUN); Prov. Cajamarca, Laguna de Moyococha, 2550 m, 29 Aug 1965, I. Sánchez Vega 92 (CPUN); Prov. Cajamarca, Dist. San Juan, lugar Huacraruco, 2350 m, 19 Jun 1993, J. Cabanillas S. & J. Guevara B. 615 (CPUN); Chotén, en el Arboretum de CICAFOR, a 4 km de la carretera Pacasmayo–Cajamarca, 2990 m, 23 May 1981, I. Sánchez Vega 2562, V. Torrel & E. Medina (CPUN); Prov. Cajamarca, Dist. Cajamarca. Paso El Gavilán, 3100 m, 26 Jun 1966, I. Sánchez Vega 239 (CPUN); Prov. Cajamarca, ladera que converge al Valle Cajamarca, Lla Colpa, 2900 m, 22 Apr 1975, I. Sánchez Vega 1416, P. Brandelard, J, Sanabria & W. Ruiz Vigo (CPUN); Prov. Cajamarca, Sais Atahualpa de Porcón, en el Arboretum de CICAFOR, 3400 m, 16 May 1981, I. Sánchez Vega 2512, V. Torrel P. & E. Medina (CPUN); Prov. Cajamarca, Dist. Namora, Hacienda Polloquito, 3000 m, 6 May 1967, I. Sánchez Vega 321 (CPUN);12 km N of Cajamarca on road towards Bambamarca, 3020 m, 14 Mar 2000, P.M. Peterson & N. Refulio Rodríguez 14855 (CPUN, US, USM); S of Paso El Gavelan, 10 air km S of Cajamarca, 7°15'37.2"S, 78°30'34.5"W, 2544 m, 26 Mar 2008, P.M. Peterson 21875, R.J. Soreng & I. Sánchez Vega (US, USM); cumbre El Gavilán, R. Ferreyra 3255 (USM); Prov. Celendin, 4 air km W of Celendin, 6°54'13.5"S, 78°10'8.4"W, 2687 m, 29 Mar 2008, P.M. Peterson 21925, R. J. Soreng & J. Montoya Quino (US, USM); Prov. San Ignacio, 31 km E of Sondor on road towards Tabaconas, 2490 m, 31 Mar 2000, P.M. Peterson & N. Refulio Rodríguez 15128 (CPUN, US, USM); Prov. San Miguel, Niepos, 2200 m, 30 Oct 1985, S. Llatas 1503 (CPUN); Prov. San Pablo, Dist. San Pablo, lugar El Molino, 2200 m, 12 Jun 1993, J. Sánchez Vega 663 (CPUN). **Cusco**: Prov. Calca, Manto a Amparaes, 2650 m, 18 Apr 1966, C. Vargas C. 17393 (LPB); Prov. Cusco, Socorro–K'inka, C. Vargas C. 13161 (USM); Ruinas de Sacsahuamán, 3500 m, 6 May 1983, S.G. Beck 8365 (LPB); Mandor, abajo de Machupicchu, 2000 m, 13 Apr 1957, H. Ellenberg 988 (LPB);

Cusco–Huancaro hwy, P. Gutte & G. Muller 9425a (USM); Machupicchu, camino entre la ciudad inca de Machupicchu y el Puente del Inca, 2000 m, 18 Sep 2004, D. Giraldo-Cañas 3759 (COL). **Huancavelica**: Prov. Huancavelica, Huando, O. Tovar 1254 (USM). **Huánuco**: Prov. Huánuco, Carpish, cumbre entre Huánuco y Tingo María, 2700 m, 1 Oct 1950, R. Ferreyra 8070 (MOL); Prov. Huánuco, Carpish, cumbre entre Huánuco y Tingo María, R. Ferreyra 10022 (USM); 48.6 km NE of Huánuco towards Tingo María, T. Plowman & P.M. Rury s.n. (USM); Prov. Pachitea, 21 air km ENE of Huánuco, 9°51'53.1"S, 76°2'55.1"W, 2498 m, 6 Mar 2007, P.M. Peterson 20341, R.J. Soreng & K. Romaschenko (US, USM); Canyon of the Rio Grande, 44 air km E of Huánuco, P.M. Peterson 20363, R.J. Soreng & K. Romaschenko (US, USM). **Junín**: Prov. Huancayo, near Paián, O. Tovar 9311 (USM); Cerro al E de Huancayo, 3900 m, 2 May 1954, O. Tovar 2173 (US, USM); Prov. Tarma, entre Huancapistana, 2200 m, A. Weberbauer 2042 (MOL). **La Libertad**: Prov. Bolivar, entre el desvío a Uchumarca y Santa Luisa, 7°04'S, 77°49'W, 3700 m, 11 Nov 2001, I. Sánchez Vega 11194, M. Dillon & G. Iberico (CPUN); Prov. Bolivar, E side of Cerro Salumpuy, 8 air km NW of Bolivar, 7°7'39.2"S, 77°46'9.9"W, 3390 m, 30 Mar 2008, P.M. Peterson 21942, R. J. Soreng & J. Montoya Quino (US, USM); 3 air km ESE of Longotea on road to Bolivar, 7°3'27.9"S, 77°51'2.2"W, 3202 m, 31 Mar 2008, P.M. Peterson 21961, R. J. Soreng & J. Montoya Quino (US, USM). **Lambayeque**: Prov. Ferreñafe, Inkawasi, S. Llatas Quiroz 4122 (USM). **Pasco**: Prov. Oxapampa, Río Boqueria, 26 km from Oxapampa via Río Yamaquizu, D. Smith 1807, A. Pretel & L. Acosta (USM). **Piura:** Prov. Huancabamba, Porculla, 2200 m, 10 May 1992, S. Llatas Quiroz & H. De la Cruz S. 3098 (CPUN). **San Martín**: Prov. Mariscal Cáceres, puerto de Norte de Río Abiseo, A. Cano 7466, B. Young & J. Roque (USM).

5. *Muhlenbergia ciliata* (Kunth) Trin., Gram. Unifl. Sesquifl. 193. t.5, f.16. 1824.

Fig. 4D–G

Podosemum ciliatum Kunth, Nov. Gen. Sp. (quarto ed.) 1:128–129. 1816. *Trichochloa ciliata* (Kunth) Roem. & Schult., Syst. Veg. 2:386. 1817. *Polypogon ciliatus* (Kunth) Spreng., Syst. Veg. 1:243. 1825. Type: Mexico, Michoacán, Volcán de Jorullo, Sep, *F.W.H.A. Humboldt & A.J.A. Bonpland s.n.* (holotype: P-HBK!; isotypes: BAA-1619 ex P!, BM!, P-Bonpl!, US-91918 fragm. ex P!).

Muhlenbergia adspersa Trin., Mém. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 4(3–4):291. 1841. Type: Peru, Lima, *ex herb. C.H. Mertens s.n.* (holotype: LE?; isotypes: LE-TRIN-1486.01 fragm. ex LE herb. Mertens!, US-87236 fragm. ex LE herb. Mertens!).

Description. Sprawling, slender *annuals*. *Culms* 8–30 (–50) cm tall, glabrous, filiform, often tufted, freely branching at lower nodes; 0.2–0.5 mm diameter just below the inflorescence; *internodes* 6–42 mm long. *Leaf sheaths* (8–) 20–44 mm long, glabrous or sparsely pilose along the margins, shorter than the internodes; *ligules* 0.2–0.8 mm long, a ciliate membrane; apex truncate; margin with a tuft of hairs up to 1 mm long; *blades* 1–4 cm long, 0.6–1.4 mm wide, flat or loosely involute, often sparsely pilose above, glabrous below. *Panicles* 4–12 cm long, 1.8–5.0 cm wide, terminal, densely flowered; *primary branches* 1.5–3.7 cm long spreading and reflexed at maturity up to 90° from the rachises, one per node; *pedicels* 0.5–3 mm long, glabrous, appressed, erect; nodes 6–13 per panicle; *Spikelets* appressed to the branches, overlapping; *glumes* 0.7–1.7 mm long, subequal, glabrous, 1-nerved; apex acuminate, often mucronate; the mucro up to 0.5 mm long; *lower glumes* 0.7–1.5 mm long; *upper glumes* 0.8–1.7 mm long; *lemmas* 1.8–2.5 mm long, lanceolate, slender, awned, strongly 3-nerved but appearing five-nerved, the intermediate "nerves" actually rows of short barbs on top of folded epidermal ridges, sometimes with prominent short hairs (scabers) along the lateral nerves, often appearing glabrous without magnification, awns 5–11(–18) mm long, flexuous; *callus* minutely short pubescent; *paleas* 1.6–2.4 mm long, narrowly lanceolate, glabrous; *anthers* 0.3–0.5 mm long, yellowish. *Caryopses* 0.8–1.8 mm long, narrowly fusiform, brownish. 2*n* = 20.

Distribution. *Muhlenbergia ciliata* is found throughout México and Central America in Ecuador, Peru, Brazil, Bolivia, Brazil and Argentina.

Ecology. *Muhlenbergia ciliata* is found on moist to dry soils usually beneath taller vegetation, sandy drainages, steep rocky slopes, rock outcrops and disturbed roadsides in woodlands with *Acacia*, *Agave*, *Andropogon*, *Bidens*, *Baccharis* spp., *Bothriochloa*, *Eupatorium*, *Melinus minutiflora* P. Beauv., *Muhlenbergia bryophilus*, *M. flexuosa*, *M. rigida*, *Puya* and *Salvia*; 1000–2400 m.

Comments. *Muhlenbergia ciliata* is morphologically similar to *M. romaschenkoi* and can be differentiated from the latter in having short ligules 0.2–0.8 mm long [1.2–3.0 (–5.0) mm long in *M. romaschenkoi*], paleas that are glabrous between the veins on the proximal ½ (versus appressed pubescent), 6–13 nodes along the panicle (versus 15–23) and panicles that are 4–12 cm long (versus 7–15 cm long) [Peterson and Giraldo-Cañas 2011, 2012]. Some individuals of *M. ciliata* from Peru do not have prominent cilia along the lateral veins that are present in most individuals from North America.

Muhlenbergia ciliata is closely related to *M. pectinata* C.O. Goodd. (North America) and *M. tenella* (Kunth) Trin. (North America, Central America and Colombia) [Peterson and Annable 1991]. These three species form a clade in *Muhlenbergia* subg. *Muhlenbergia* (Peterson et al. 2010b; Fig. 1B).

Specimens examined. Peru. **Amazonas:** Piedra Grande, near Rio Santo Domingo, 5000 ft alt., 14–19 May 1923, J.F. Macbride 3684 (F, US). **Cusco:** Urubamba, Ruinas de Macchu Picchu, 2500 m, 27 May 1963, D. Ugent 5356 (US), 2300 m, 11 Apr 1963, C. Vargas C. 14354 (US), Mar 1987, I. Grignon 2306 (AAU, US); Quebrada Termas Macchu Picchu, 25 Mar 1966, C. Vargas C. 17145 (USM). **Huánuco:** 21 air km NE of Pachitea, 7 km E of Puerto Rancho junction, 9°49'45.9"S, 76°3'12.9"W, 2094 m, 6 Mar 2007, P.M. Peterson, R.J. Soreng & K. Romaschenko 20336 (US); Pachitea, canyon of the Rio Grande, along trail 1 air km NW of Estación Huacachay, 9°50'44.7"S, 75°50'5.2"W, 2323 m, 8 Mar 2007, P.M. Peterson, R.J. Soreng & K. Romaschenko 20378 (US); 2 air km ESE of Eastación Huacachay, 9°51'34.7"S, 75°50'48.1"W, 1867 m, 7 Mar 2007, P.M. Peterson, R.J. Soreng & K. Romaschenko 20359 (US). **Junín:** between Tarma and La Merced, 3000 m, 14 Oct 1923, A.S. Hitchcock 22154 (US); Mito, 9000 ft alt., 8–18 Apr 1923, J.F. Macbride 3376 (F, US); Province Huancayo, abajo de Pariabuena, 2000 m, 6 May 1969, O. Tovar 7936 (USM). **La Libertad:** Bolivar, W of Longotea ca. 0.5 km towards San Vicente on Balsas–Longotea road, 7°2'35.6"S, 77°52'39.8"W, 2487 m, 31 Mar 2008, P.M. Peterson, R.J. Soreng & J. Montoya Quino 21967 (US).

6. *Muhlenbergia coerulea* (Griseb.) Mez, Repert. Spec. Nov. Regni Veg. 17:213. 1921.

Figs 5A–D, 6A–C

Epicampes coerulea Griseb., Abh. Königl. Ges. Wiss. Göttingen 19:256. 1874. Type: Sierra de Tucumán, Den grossen isolierten Buescheln an der Cuesta de Juntas, 23 Mar 1872, *P.G. Lorentz 86* (lectotype, designated here: GOET-006633 [image!]; isolectotypes: CORD-00004624!, CORD-00004625!, US-865981!).

Crypsis phleoides Kunth, Nov. Gen. Sp. (quarto ed.) 1:140. 1816, non *Muhlenbergia phleoides* (Kunth) Columbus. *Cinna phleoides* (Kunth) Kunth, Révis. Gramin. 1:67. 1829. *Epicampes phleoides* (Kunth) Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 256. 1874. Type: Venezuela, Sucre, Sep, *F.W.H.A. von Humboldt & A.J.A. Bonpland s.n.* (holotype: P!; isotype: US-A865652 fragm. ex P!).

Crypsis stricta Kunth, Nov. Gen. Sp. (quarto ed.) 1:140. 1816, non *Muhlenbergia stricta* (J. Presl) Kunth. *Cinna stricta* (Kunth) Kunth, Révis. Gramin. 1:67. 1829. *Crypsinna stricta* (Kunth) E. Fourn., Mexic. Pl. 2:90. 1886. Type: Peru, Prov. de los Pastos, Dec, *F.W.H.A. von Humboldt & A.J.A. Bonpland s.n.* (holotype: B-W; isotype: US-A865653 fragm. ex B-W!).

Epicampes coerulea var. *submutica* Hack., Anales Mus. Nac. Buenos Aires 13:471. 1906. Type: Argentina, Tucumán, Dep. Tafí, Cuesta de Malamala, 2500 m, 4 Feb 1904, *Stuckert herb. Arg. 14900 ex Lillo 3402* (holotype: W-1916-0026677 [image!]; isotypes: CORD-00001624 [image!], LIL-000053 [image!], US3168604!).

Description. Densely caespitose *perennials. Culms* 50–100(–120) cm tall, erect, rigid, hirsute below the basal, terete nodes; usually 1 node per culm; *internodes* mostly glabrous and scabrous. *Leaf sheaths* mostly 5–18 cm long, glabrous to scaberulous above, rounded near base, lower sheaths often becoming fibrous with age; *ligules* 8–15 mm long, firm below, strongly decurrent, often lacerate, apex obtuse to acute; *blades* 15–35(–45) cm long, 2–5 mm wide, tightly involute, glabrous to scaberulous below mostly scaberulous near above. *Panicles* (6–)10–24(–30) cm long, 6–15 mm wide, narrow, spike-like, usually plumbeous; *primary branches* 0.2–2.5 cm long, erect and tightly ascending appressed, floriferous to base; *pedicels* 0.5–4 mm long, usually shorter than the spikelets, hispid. *Spikelets* 5–7(–8) mm long, plumbeous, rarely 2-flowered; *glumes* (4–)5–7(–8) mm long, usually as long or longer than the floret, sometimes a little shorter, lanceolate, about equal, 1-nerved, scabrous, apex acuminate, unawned, mu-

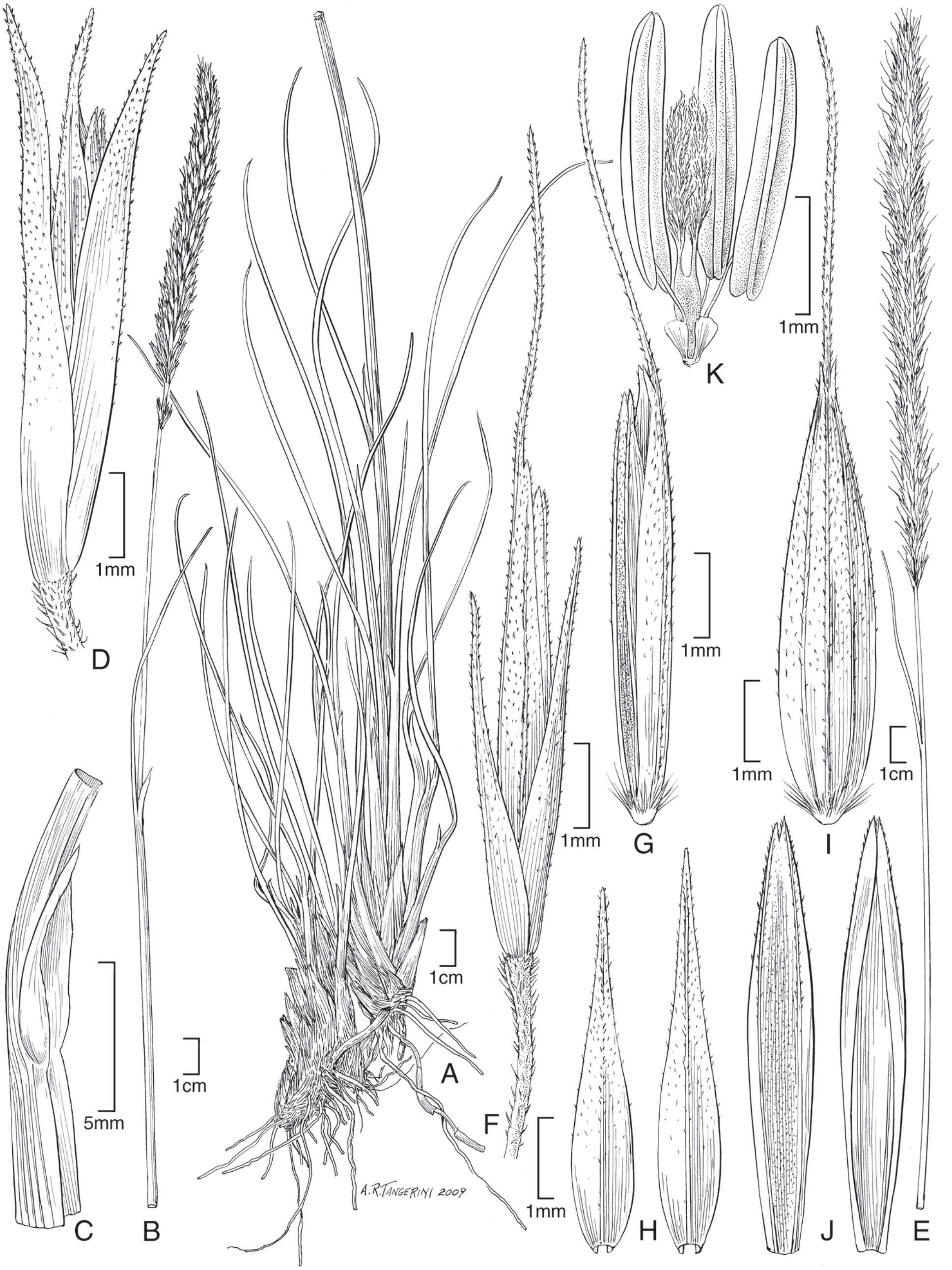

Figure 5. A–D *Muhlenbergia coerulea* (Griseb.) Mez **A** habit **B** culm and panicle **C** ligule **D** spikelet **E–K** *Muhlenbergia coerulea* (Griseb.) Mez × *Muhlenbergia rigida* (Kunth) Kunth **E** culm and panicle **F** spikelet **G** floret **H** glumes **I** lemma **J** paleas, dorsal and ventral view **K** lodicules, stamens, and pistil. **A–D** drawn from *P.M. Peterson, R.J. Soreng & J. Montoya Quino 21957* (US) **E–K** drawn *from P.M. Peterson & N. Refulio Rodriguez 14860* (US).

Figure 6. A–C *Muhlenbergia coerulea* (Griseb.) Mez **A** habit **B** panicle **C** spikelet **D–F** *Muhlenbergia rigida* (Kunth) Kunth **D** habit **E** panicle **F** spikelet. Drawings from Giraldo-Cañas and Peterson (2009), Peterson and Giraldo-Cañas (2011). **A–C** drawn from *S.G. Beck 7700* (LPB) **D** drawn from *P.M. Peterson 9659* (US) **E, F** drawn from *P.M. Peterson, C.R. Annable & J. Valdés-Reyna 10876* (US).

cronate, or short-awned; *lemmas* (4.6–)5–6.7(–7.1) mm long, lanceolate, plumbeous, scabrous, apex acuminate, unawned, mucronate or short-awned, the awn 1–3(–4) mm long, inserted just below the apex; *callus* sparsely short bearded, the hairs 0.1–0.2 mm long; *paleas* (4.6–)5–6.5 mm long, about as long as the lemma, narrowly lanceolate, scaberulous, apex acuminate; *anthers* 2–3 mm long, purplish or yellowish. *Caryopses* 2.5–3.5 mm long, fusiform, dark reddish-brown.

Distribution. *Muhlenbergia coerulea* ranges throughout the Andean Cordillera from Colombia, Venezuela, Ecuador to Argentina, Peru and Bolivia.

Ecology. *Muhlenbergia coerulea* grows on rocky, often sandy slopes, derived from volcanic origins usually near arroyos associated with of *Alnus*, *Anatherostipa obtusa* (Nees & Meyen) Peñail., *Aristida*, *Calamagrostis*, *Calceolaria*, *Festuca*, *Hypericum*, *Jarava ichu* Ruiz & Pav., *Lupinus*, *Monnina*, *Nassella*, *Oreocallis grandiflora* (Lam.) R. Br., *Polylepis*, *Puya*, *Rubus*, *Schizachyrium* and cultivated *Pinus*; 2450–4900 m. Flowering February through August.

Comments. In recent literature (Giraldo-Cañas and Peterson 2009; Peterson and Giraldo-Cañas 2011, 2012), this species was referred to as *Muhlenbergia angustata* (J. Presl) Kunth but the type [*Podosemum angustatum* J. Presl] clearly aligns with what we had been referring to as the hybrid between this species and *M. rigida*. Therefore, we adopt the next available name, *Muhlenbergia coerulea* and change the hybrid designation to *M. coerulea* × *M. rigida*. Many specimens studied are intermediate between *M. coerulea* and *M. rigida*. These are treated as hybrids [*M. coerulea* (Griseb.) Mez × *M. rigida* (Kunth) Kunth; Lægaard and Peterson 2001; Peterson and Giraldo-Cañas 2011, 2012] since the size, width and colour of the panicles and the surface structure and length of the glumes and lemmas, are intermediate between these two recognised species.

Muhlenbergia coerulea is deeply embedded in the *M.* subg. *Trichochloa* clade, a group of tall, rather robust perennials historically placed in *Podosemum* or *Epicampes* (Soderstrom 1967; Peterson et al. 2010b; Fig. 1A).

Specimens examined. Peru. **Ancash**: Prov. Huaylas, Pueblo Libre, Antircán, A. Cano 11714 (USM); Prov. Huari, Huascarán National Park, Quebrada Pachachaca, D.N. Smith 12619, A. Gonzalez & D. Maldonado (USM); Quebrada Los Cedros, D.N. Smith 9892, R. Valencia & L. Minaya (CPUN); Prov. Huari, Huascarán National Park, Alpamayo–Cashampampa trail, 3950 m, 13 Mar 1985, D.N. Smith 10054 & R. Valencia (MO, USM); Prov. Recuay, between Pequipalpa and Rachacoco, L.I. Masías 44 (USM); Huascarán National Park, Auqispuquipio, D.N. Smith 12115, R. Valencia & M. Buddensiek (MO, USM); Prov. Yungay, Cordillera Blanca, 20 km ENE of Yungay, 9°6'26.2"S, 77°41'8.2"W, 3247 m, 15 Mar 2008, P.M. Peterson 21703, R.J. Soreng, M. La Torre & J.V. Rojas Fox (US, USM); quebrada Llauganuco, 24 km ENE of Yungay, 9°5'46.3"S, 77°40'19.3"W, 3309 m, 16 Mar 2008, P.M. Peterson 21720, R.J. Soreng, M. La Torre & J.V. Rojas Fox (US, USM). **Arequipa:** Prov. Caraveli, Quicacha, 5 May 1955, A. Guevara s.n. (USM). **Ayacucho:** Prov. Huanca Sancos, 19 km NW of Putajasa on road towards Huanca Sancos, 14°00'2.6"S, 74°17'14.1"W, 3900 m, 25 Feb 2002, P.M. Peterson 16268, A. Cano, M. La Torre, A Ramirez & D. Susanibar (US, USM). **Cajamarca:** Prov. Cajabamba, ca. 20 km WSW of Cajabamba, 7°42'18.0"S, 78°14'1.5"W, 3263 m, 23 Mar 2008, P.M. Peterson & R.J. Soreng 21868 (US, USM); Prov. Cajamarca, La Encañada, Cerro Negro, M. Cabanillas Medina & M. Sánchez Montoya 1530 (CPUN); La Encañada, ruta Combayo–Yanacocha, I. Sánchez Vega 10574 (CPUN); N del canal Cumbe Mayo, I Sánchez –Vega U. Molau 3733 (CPUN); Cumbe Mayo, W of Cajamarca, S.A. Renvoize 4990, S. Lægaard & I. Sánchez Vega (CPUN, K, US); Pampas de Guanico, ruta a Guagal, I. Sánchez Vega 1141 (CPUN); Sais Atahualpa, de Porcón, I Sánchez Vega 2528, V. Torrel & E. Medina (CPUN); Quebrada de la Esperanza along road to Cumbe Mayo, I. Sánchez Vega & V. Torre 3289 (CPUN); Cerro Campanario, I. Sánchez Vega 6605 (CPUN); Prov. Celendin, Celendin, 3600 m, 24 Jun 1961, R. Ferreyra 15117 (USM); Prov. San Miguel, 64 km N of Cajamarca and 3 km SW of El Cobro, 3530 m, 16 Mar 2000, P.M. Peterson & N. Refulio Rodriguez 14926 (CPUN, US, USM); Prov. San Pablo, 32 km NW of Cajamarca towards San Pablo, 3470 m, 15 Mar 2000, P.M. Peterson & N. Refulio Rodriguez 14882 (US, USM); Cajamarca–Chota road, km 37–40 marker, A. Gentry 61575, C. Diaz & C. Blaney (MO, USM). **Huancavelica:** Prov. Huancavelica, Canyon of Rio Ichu, SW of Huancavelica, 12°48'48.2"S, 75°3'24.5"W, 4894 m, 14 Mar 2007, P.M. Peterson 20462, R.J. Soreng, K. Romaschenko & D. Susanibar (US, USM); Tayacaja, Hacienda Tocas, between Colcabamba and Paucarbamba, 3400 m, 20 Apr 1954, O. Tovar 1981 (US, USM). **Huánuco:** Prov. de Huánuco, Mitotambo, above Mito, R. Ferreyra 6895 (MOL, US, USM); above Mitotambo, R. Ferreyra 9434 (USM); 3–6 mi NW of Mito, J.F. Macbride and Featherstone 1929 (F, US), Mito, J.F. Macbride and Featherstone 1721 (F, US); Prov. Ambo, Huarmiragra, A. Granda 1676 (USM). **Junín:** Pachacaya–Huari, 3600 m, 25 Mar 1979, O. Tovar 7838 (USM); Prov. Huancayo, Cerros E of Huancayo, O. Tovar 3259 (US); above Ocopilla, near Huancayo, O. Tovar 4506 (US, USM); above Huancayo, O. Tovar 2795 (US, USM); Palián, O. Tovar 9339 (USM); Cerros E of Huancayo, O. Tovar 3259 (USM); Oroya, A.S. Hitchcock 22182 (US). **La Libertad:** Prov. Huancayo, Acopalca, 4000 m, 20 Jul 1945, J. Infantes Vera 406 (LIL); Prov. Bolivar, 3 km ESE of Longotea and 9 km W of Uchumarca, 7°3'27.9"S, 77°51'2.2"W, 3202 m, 31 Mar 2008, P.M. Peterson 21957, R.J. Soreng & J. Montoya Quino (US, USM); Prov. Otuzco, Trujillo–Huamachuco road, 10–15 km before Shorey, D.N. Smith & R. Vasquez 3289 (MO, USM); Larbimbambu, 2450 m, 5 Feb 1949, J. Infantes Vera 1654 (LIL); Cerro Sango, A. Sagástegui 14428 (HAO); Prov. Santiago de Chuco, Shoreyo–Truillo road, 5 km from Shoreyo, D. Smith 2339 (MO, US, USM). **Lambayeque:** Prov. Ferreñafe, Incahuasi, S. Llatas Q. 1934 (CPUN, HAO, USM). **Piura:** Prov. Huancabamba, 14 km E of Sondor on road towards Tabaconas, 2540 m, 31 Mar 2000, P.M. Peterson & N. Refulio Rodriguez 15153 (CPUN, US, USM). **Puno:** Chijnaya, Pueblo de Pucará, 3900 m, Mar 1964, A. Vera 107 (COL); Hacienda Caracara, entre Llave y Pucará, 3850 m, 4 Mar 1966, O. Tovar 5162 (US); Hacienda Sollocota, 3850 m, 7 Mar 1966, O. Tovar 5229 (USM); Camacani, 9 Mar 1966, 3850 m, O. Tovar 5263 (USM); Prov. Carabaya, 10 km S of Ollachea, J.D. Boeke & S. Boeke 2974 (NY, US); Prov. Chucuito, 3 km S of Pizacoma, 4050 m, 7 Mar 1999, P.M. Peterson & N. Refulio Rodriguez 14694 (US, USM).

7. ***Muhlenbergia coerulea*** **(Griseb.) Mez ×** ***M. rigida*** **(Kunth) Kunth.**
Fig. 5E–K

Podosemum angustatum J. Presl, Reliq. Haenk. 1(4–5):229. 1830. *Muhlenbergia angustata* (J. Presl) Kunth, Enum. Pl. 1: 202. 1833. Type: Peru, *Haenke s.n.* (holotype: PR-4657!; isotype: PRC-450958 [image!]).

Muhlenbergia phragmitoides Griseb. var. *breviaristata* Hack., Annuaire Conserv. Jard. Bot. Genève 17: 291. 1914. *Muhlenbergia breviaristata* (Hack.) Parodi, Physis (Buenos Aires) 9: 219. 1928. Type: Argentina, Tucumán, Lara, 3200 m s.m., 28 Mar 1912, *M. Lillo 11322, Herb. T. Stuckert 22470* (holotype: W-1916-0039607!; isotypes: LIL-40186!, US-3412353 fragm. ex W!).

Muhlenbergia holwayorum Hitchc., Contr. U.S. Natl. Herb. 24(8):389. 1927. Type: Bolivia, Sorata, 16 Apr *1920, E.W.D. Holway & M. M. Holway 530* (holotype: US-1108445!).

Description. *Panicles* (–0.6)1–4 cm wide, spike-like with lower branches slightly prolonged, erect, plumbeous to reddish-purple. *Spikelets* plumbeous to reddish-purple, scabrous; *glumes* 2.5–3.5(–4) mm long, ½ to ¾ as long as the floret; *lemmas* 4–6 mm long, awned, the awns generally 3–8(–10) mm long, straight.

Distribution. This presumed hybrid is known to occur in Argentina, Chile, Colombia, Ecuador, Peru and Venezuela.

Ecology. The hybrid occurs on gravelly slopes and near cultivated fields in many different plant communities between 2200–3800 m in association with *Alnus*, *Aristida adscensionis* L. *Baccharis*, *Berberis*, *Calceolaria*, *Cenchrus clandestinus*, *Eragrostis pastoensis* (Kunth) Trin., *Festuca*, *Jarava*, *Lantana*, *Lupinus*, *Muhlenbergia cenchroides*, *M. phalaroides*, *M. rigida*, *Oxalis*, *Polygala*, *Puya*, *Schinus molle* L., *Schizochyrium* and *Solanum*.

Comments. As expected, individuals of *M. coerulea* × *M. rigida* have an intermediate morphology, such as: lemma awn length [3–8 (–10) mm], glume length (1/2–3/4 as long as the lemma) and spikelet colouration (plumbeous to reddish-purple). In the Flora of Ecuador, Lægaard and Peterson (2001) recognised two intermediate forms (“intermediate” and “subangustata”) based on lemma awn length, glume length, colour of the spekelets and surface scabrosity of the glumes and lemmas.

There are no molecular studies investigating the population genetics of the hybrid with both presumed parents but we hope to persue this in the future. In our analysis, two samples of *M. coerulea* from Peru form a pair with little variation and two samples of *M. rigida*, one from Mexico and the other from Peru, form a pair with little variation in the analysis of seven DNA sequence markers (Peterson et al. 2010b). Each of these two clades of *M. coerulea* and *M. rigida* were not paired but were placed along a comb-like grade in the *M.* subg. *Trichochloa* clade. In our new analysis, there are more samples of *M. rigida* from Mexico and there is greater genetic variability among individuals of this species (Fig. 1). However, overall there appears to be low levels of divergence among species in *M.* subg. *Trichochloa*, hence the comb-like appearance suggesting rapid speciation (Peterson et al. 2010b).

Specimens examined. Peru. **Ancash:** 10 km towards Casma, S.A. Renvoize & S. Lægaard 5154 (CPUN); E of Yungay, S.A. Renvoize & S. Lægaard 5058 (CPUN); Prov. Asunción, Chacas, A. Cano 14572, M. La Torre & W. Mendoza (USM); Prov. Bolognesi, above Chiquián, E. Cerrate 1549 (US, USM); Prov. Corongo, Ocshmarca, S. Leiva 51 (USM); Prov. Huaylas, Huascarán National Park, Auquispuquio ruins, D.N. Smith 11960, R. Valencia & M. Buddensiek (CPUN, USM); Huascarán National Park, Pueblo Libre, A. Cano 11619 (USM); Pueblo Libre, Antircán, A. Cano 11714 (USM). **Apurimac**: Prov. Abancay, 48 km SW of Abamcay on road towards Andahuaylas, 13°42'23.6"S, 72°57'20.3"W, 3280 m, 21 Mar 2002, P.M. Peterson & N. Refulio Rodriguez 16650 (US, USM). **Ayacucho:** Prov. Huamanga, 23 km S of Ayacucho on hwy 3 towards Abancay, 13°16'21.5"S, 74°13'46.8"W, 3575 m, 15 Mar 2007, P.M. Peterson 20490, 20496, R.J. Soreng, K. Romaschenko & D. Susanibar Cruz (US, USM); 27 km S of Ayacucho on hwy 3 towards Abancay, 13°17'9.8"S, 74°13'41.9"W, 3684 m, 16 Mar 2007, P.M. Peterson 20502, R.J. Soreng, K. Romaschenko & D. Susanibar Cruz (US, USM); Prov. Huanca Sancos, 23 km NW of Putajasa on road towards Huanca Sancos, 13°58'11.1"S, 74°18'9.0W, 3800 m, 25 Feb 2002, P.M. Peterson 16272, A. Cano, M. La Torre, A Ramirez & D. Susanibar (US, USM); Prov. Huanca Sancos, 27 km NW of Putajasa and 3 km S of Sacsamarca, 13°57'51.1"S, 74°18'41.5"W, 3650 m, 25 Feb 2002, P.M. Peterson 16273B, A. Cano, M. La Torre, A Ramirez & D. Susanibar (US, USM); Prov. Lucanas, 13 km E of Puquio at km 172 marker, 14°41'18.5S, 74°4'26.8W, 3730 m, 8 Apr 2004, P.M. Peterson & N. Refulio Rodriguez 18207 (US, USM); Ancamarca, L. Vargas & G. Mora 337 (USM). **Cajamarca:** Prov. Cajamarca, 12 km N of Cajamarca on road toward Bambamarca, 3020 m, 14 Mar 2000, P.M. Peterson & N. Refulio Rodriguez 14860 (CPUN, US, USM); Cajamarca–Bambamarca, 13–18 km from Cajamarca, D.N. Smith & R. Vasquez M. 3441 (MO, US, USM); Chotén, 4 km de la carretera Pacasmayo, I. Sánchez Vega 2570, V. Torrel & E. Medina (CPUN); Porcón, I. Sánchez Vega 51 (CPUN, US); above La Encañada ruta a Celendín, I. Sánchez Vega & W. Ruiz Vigo 1730 (CPUN); Prov. Celendín, La Tranca, I. Sánchez Vega & W. Ruiz Vigo 1815 (CPUN); Prov. Celendín, 4 air km W of Celendín, 6°54'13.5"S, 78°10'8.4"W, 2687 m, 29 Mar 2008, P.M. Peterson 21921 & 21922, R.J. Soreng & J. Montoya Quino (US, USM); 10 km from Celendín towards Rio Marañon, S.A. Renvoize & S. Lægaard 4883 (CPUN); Celendín to Cajamarca, near Quillimbas, S.A. Renvoize & S. Lægaard 4871 (CPUN); Cerro Conturami 10 km from Celendín, S.A. Renvoize & S. Lægaard 4946 (CPUN); Prov. Contumaza, Tres Cruces, A. Sagástegui & M. Fukushima 5119 (US); Celendín–Balsas road, 3–10 km from Celendín, D.N. Smith & I. Sánchez Vega 4300 (MO, US). **Cusco:** Prov. Calca, 10 km N of Calca on road towards Lares, 13°16'2.9"S, 71°55'20.1W, 3490 m, 17 Mar 2002, P.M. Peterson & N. Refulio Rodriguez 16597 (US, USM); Prov. Santo Tomas, Chumbivilcas, Apr 1982, M.E. Tapia 208 (USM). **Huancavelica:** Motcca, cerca a Conaica, 3500 m, 1 Apr, 1967, O. Tovar 5889 (USM); Prov. Huancavelica, Pararpuquio, below Conaica, O. Tovar 169 (MOL, US, USM); Sachahuajta, 7 km to Conaica, O. Tovar 950 (US, USM); near Yauli, O. Tovar 2996 (US, USM); Yacu-huanay, O. Tovar 3695 (USM, US); Prov. Tayacaja, Andaimarca, between Colcabamba and Surcubamba, O. Tovar 1821 (US, USM). **Huánuco:** Prov. de Huánuco, Mitotambo above Mito, R. Ferreyra 9477 (US, USM); Mito, J.F. Macbride 3320 (F, US). **Junín:** Prov. Huancayo, Paccba, 20 km S of Huancayo, O. Tovar 3294 (US, USM); Cerro La Libertad, O. Verlarde Nuñez 2637 (MOL). **La Libertad:** Prov. Bolivar, above Longotea, ruta Bolivar, I. Sánchez Vega 5015 (CPUN); Prov. Otuzco, Agallpampa, A. López M. 1041 (US); Trujillo–Huamachuco road, D.N. Smith & R. Vasquez 3309 (MO, USM). **Lambayeque:** Prov. Ferreñafe, Inkawasi, S. Llatas Quiroz 4114 (USM). **Lima:** Prov. Canta, 2 km SE of San Jose Canta, 11°30'2.0"S, 76°40'23.4W, 2232 m, 27 Mar 2004, P.M. Peterson & N. Refulio Rodriguez 17984 (US, USM). **Piura:** 14 km E of Sondor on road towards Tabaconas, 2540 m, 31 Mar 2000, P.M. Peterson & N. Refulio Rodriguez 15160 (CPUN, US, USM).

8. ***Muhlenbergia diversiglumis*** **Trin., Mém. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 6,4(3–4):298. 1841.**

Fig. 7A–D

Type. Mexico, Porto Pedro, *Karwinsky 1393* (holotype: LE-TRIN-1497.01!; isotypes: US-84831! fragm. ex LE-TRIN-1497.02, W!).

Description. Sprawling *annuals*. *Culms* 16–50 cm tall, decumbent, rooting at the lower nodes; *nodes* retrorsely pilose; *internodes* smooth or scabridulous. *Leaf sheaths* 1.5–8.5 cm long, sparsely or densely pilose, hairs to 3 mm long, papillose-based; *ligules* 0.5–0.8 mm long, membranous, apex truncate, erose; *blades* 2–6 cm long, 1.5–4 mm wide, flat, bases distinctly narrowed to the junction with the sheath, surfaces scabridulous and sparsely pilose, hairs papillose-based. *Panicles* 6–10.5 cm long, 2.0–4.5 cm wide, secund, open; *primary branches* 0.8–3.5 cm long, secund, spreading at right angles or somewhat reflexed usually lying to one side with 2–5 spikelets; *secondary branches* not developed; *pedicels* 1–5 mm long, scabrous or shortly pilose, hairs papillose-based; *disarticulation* at the base of the primary branches where there is a weak and contorted stipe. *Spikelets* 4–8 mm long, dimorphic with respect to the glumes, proximal spikelets on each branch almost sessile; *glumes of proximal spikelets* on each branch subequal, 0.2–0.7 mm long, orbicular, truncate, often erose or irregularly toothed, unawned; *glumes of distal spikelets* on each branch markedly unequal; *lower* glumes to 8 mm long, 1-veined, acute, usually awned, awns 0.5–3 mm; *upper* glumes orbicular, acute, sometimes awn-tipped; *lemmas* 4.0–7.6 mm long, linear to broadly lanceolate, light greenish, smooth or scabrous, usually with greenish veins, apices acuminate, awned, awns 6–19 mm long, usually straight, scabrous; *paleas* 3.7–6.8 mm long, narrowly lanceolate, coarsely papillate or almost smooth, 2-keeled, the veins prominent, scabrous, greenish, sometimes extending as minute awns, acuminate; *anthers* 0.4–0.8 mm long, yellowish. *Caryopses* 1.8–3 mm long, oblong-ovoid, flattened, brownish. $2n = 20$.

Distribution. The species is native to North America, Central America, Colombia, Venezuela, Ecuador, Peru, and Argentina.

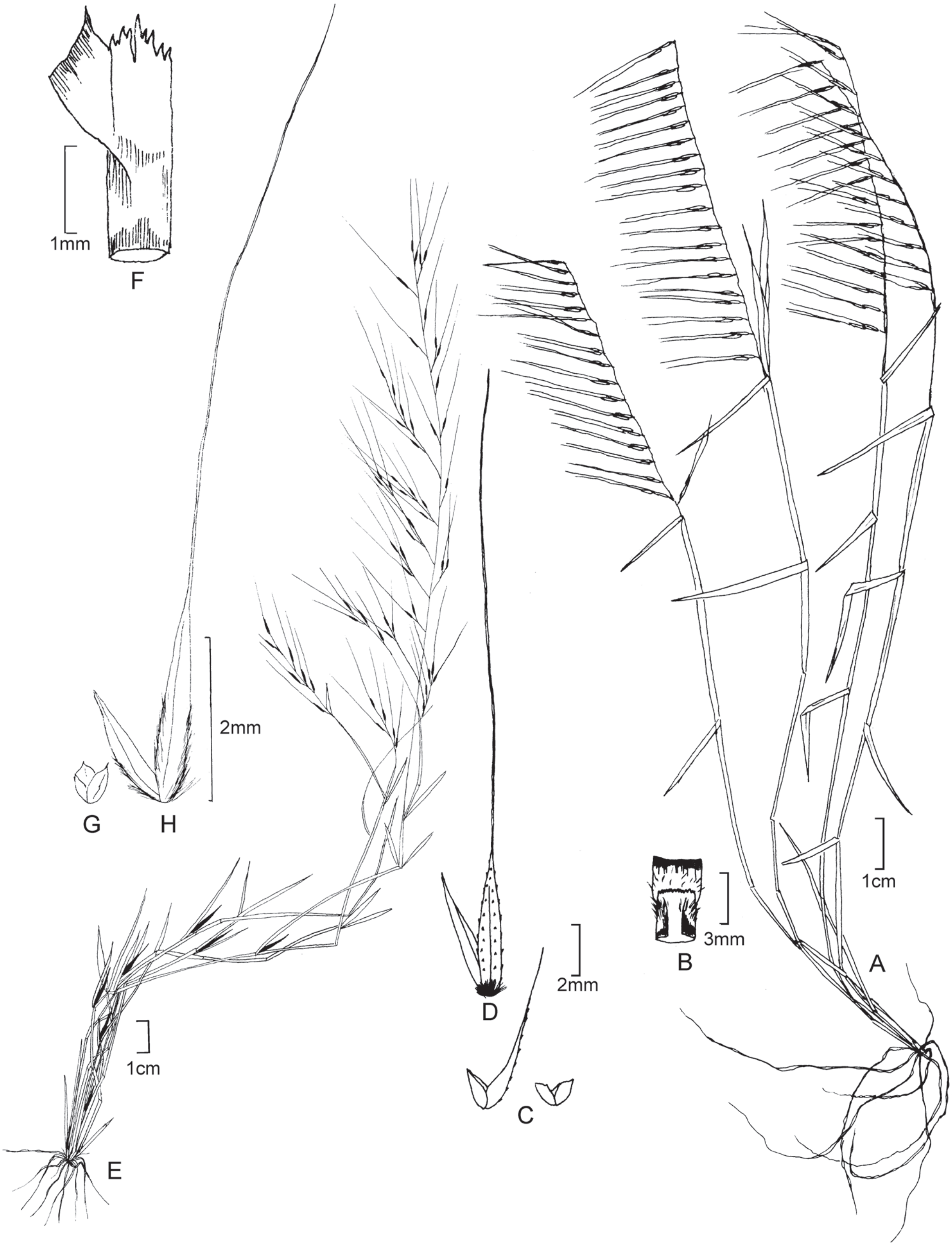

Figure 7. A–D *Muhlenbergia diversiglumis* Trin **A** habit **B** ligule **C** glumes **D** floret **E–H** *Muhlenbergia microsperma* (DC.) Kunth **E** habit **F** ligule **G** glumes **H** lemma. Drawings from Peterson and Annable (1991) **A–D** drawn from *P.M. Peterson & C.R. Annable 4158* (WS) **F–H** drawn from *P.M. Peterson & C.R. Annable 4185* (WS).

Ecology. *Muhlenbergia diversiglumis* grows on moist cliffs, along water courses, sandy slopes, and road cuts, primarily in moist shaded environments of broadleaf evergreen forests and pine-oak forests, at elevations of 600–2500 m.

Comments. *Muhlenbergia diversiglumis* can be differentiated from *M. ciliata*, *M. microsperma*, and *M. romaschenkoi* in having secund panicles (versus not secund in the latter three species) with each primary branch consisting of 2–5 dimorphic spikelets where the proximal spikelets have short orbicular glumes less than 1 mm long, and the distal spikelets have glumes up to 8 mm long (Peterson and Annable 1991; Giraldo-Cañas and Peterson 2009).

Muhlenbergia diversiglumis is a member of *M.* subg. *Muhlenbergia* and is sister to *M. alamosae* Vasey and together they are sister to the *M. tarahumara*–*M. cenchroides*–*M. bryophilus*–*M. uniseta* clade (Fig. 1B).

Specimens examined. Peru. **Amazonas:** Dist. Vista Alegre, Puente sobre el Río Salas, 1525 m, 30 Jun 1998, I.M. Sánchez Vega, M.O. Dillon & M. Zapata 9580 (HAO, MO). **Ayacucho:** Naranjayoc, entre Ayna y el Río Apurimac, 900 m, 16 May 1969, O. Tovar 6136 (USM); Ayna, cerca entre Tambo y San Francisco, Jan 1969, L. Aucasime 428 (USM); Province La Mar, Machente, entre Yanamonte y Ayna, 1200 m, 16 May 1969, O. Tovar 6126 (USM); Province La Mar, entre Ayna & Río Apurimac, 900 m, 16 May 1969, O. Tovar 6136 (USM); Ayna, between Huanta and Río Apurimac, 750 m, 7 May 1929, E.P. Killip & A.C. Smith 23127 (US). **Cusco:** Urubamba Valley, San Miguel, 1800 m, 28 May 1913, O.F. Cook & G.B. Gilbert 958 (US); Urubamba, Ciudadela Macchu Picchu, 2300 m, 11 Apr 1963, C. Vargas C. 2159 (US), 14355 (US, USM); Urubamba, Macchu Picchu, 2040 m, Mar 1949, F. Marin 1381 (US); Urubamba, 110 km de Cusco en el camino y atrás de las aguas termales con plantaciones de palta, Macchu Picchu, 2050 m, 21 May 1988; G. Valencia & R. Ochoa 9147 (MO, US). **Huánuco:** Province Leoncio Prado, La Divisoria, carretera a Pucallpa, 1600 m, 21 Apr 1989, J. Schunke Vigo 11349 (MO, US, USM). **Piura:** Huancabamba, Porculla, 1770 m, 6 Mar 1989, S. Llatas Quiroz 2431 (CPUN, HAO, MO).

9. *Muhlenbergia fastigiata* (J. Presl) Henrard, Meded. Rijks-Herb. 40: 59. 1921.

Fig. 8A–E

Sporobolus fastigiatus J. Presl, Reliq. Haenk. 1 (4–5): 241. 1830. Type: Peru, *Haenke s.n.* (holotype: PR, isotypes: PRC-450197 [image!], US-3048470! fragm. ex PR).

Muhlenbergia cleefii Lægaard, Caldasia 17 (82–85): 409–411. 1995. Type: Colombia, Boyacá, Sierra Nevada del Cocuy, Alto Valle de Lagunilla, páramo pantanoso al sur de la Laguna Cuadrada, 4060 m, 26 sep 1972, *A. Cleef & P.A. Florschutz 5578* (holotype: COL!; isotypes: U-0007997 [image!], US-2785756!).

Description. Dense mat-forming *perennials* with scaly rhizomes, the acute scales 4.5–8.1 (–10) mm long, the rhizomes 1–2 (–2.5) mm in diameter. *Culms* 2–8 (–11) cm long, mostly erect, 2–3 (4) mm diameter below; *internodes* 1–10 mm long, compressed.

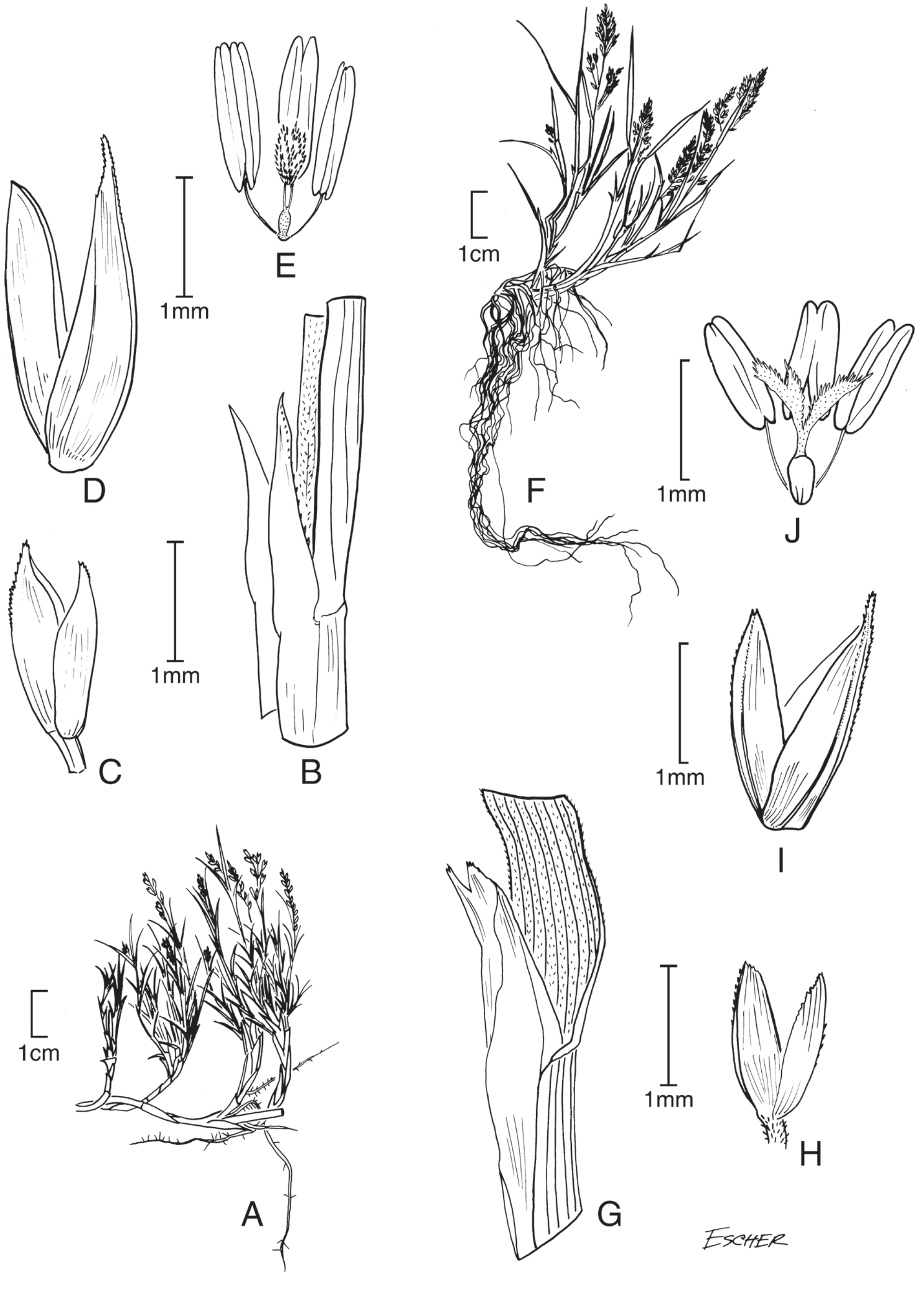

Figure 8. A–E *Muhlenbergia fastigiata* (J.Presl) Henrard **A** habit **B** ligule **C** glumes **D** floret **E** stamens and pistil **F–J** *Muhlenbergia ligularais* (Hack.) Hitchc **F** habit **G** ligule **H** glumes **I** floret **J** stamens and pistil. Drawings from Giraldo-Cañas and Peterson (2009), Peterson and Giraldo-Cañas (2011) **A–E** drawn from *P.M. Peterson, S. Lægaard, R.J. Soreng & C.R. Annable 12709* (US) **F–J** drawn from *P.M. Peterson, S. Lægaard, R.J. Soreng & C.R. Annable 12684* (US).

Leaf sheaths 3–6 (–10) mm long, distichous, overlapping, margins hyaline; *ligules* 6–1.4 mm long, membranous, decurrent, apex acute to obtuse; *blades* 2.5–8.5 mm long, 0.6–1.1 mm wide, involute, arcuate, glabrous to finely papillose, margins scabrous, apex navicular, often pungent. *Panicles* 1–2 cm long, 1–5 mm wide, contracted, narrow, usually exserted with 3–9 nodes; *primary branches* 0.4–1 cm long, ascending, solitary at a node; *rachis* papillose-roughened just below the spikelets. Spikelets (1.8--) 2–2.5 mm long, plumbeous; *glumes* (0.8–) 1–1.6 mm long,about ½ as long as the floret, subequal, 1-veined, rarely 2-veined, apex acute to obtuse; *lemmas* (1.7–) 1.9–2.4 mm long, 3-veined, glabrous, plumbeous, apex acute, mucronate, the mucros less than 0.3 mm long; *paleas* (1.6–) 1.8–2.4 mm long, 2-veined, glabrous; *anthers* 1–1.7 mm long, yellow or purple. *Caryopses* 1–1.3 mm long, about 0.4 mm wide, ellipsoid, dark brown.

Distribution. *Muhlenbergia fastigiata* is found in South America in the Andean highlands of Argentina, Bolivia, Chile, Colombia, and Peru (Morden 1985; Morden and Hatch 1996).

Ecology. *Muhlenbergia fastigiata* occurs on grassy flats, playas, slopes, rock outcrops, near gravelly creeks and lake margins in granitic and calcareous soils associated with *Baccharis*, *Berberis*, *Calamagrostis*, *Ephedra*, *Festuca*, *Jarava*, *Margyricarpus*, *Muhlenbergia*, *ligularis*, *M. peruviana*, and *Nassella*; 3000–4900 m.

Comments. Morphologically, *M. fastigiata* can sometimes be confused with the distantly related *M. ligularis* (*M.* subg. *Bealia*; Fig. 1B). However, the former has well developed rhizomes (absent in *M. ligularis*) and tightly involute, acuate leaf blades (versus flat and straight). *Muhlenbergia richardsonis* (Trin.) Rydb., a wide ranging North American species, is also morphologically similar to *M. fastigiata* in most characters, although *M. richardsonis* has a taller habit and differes in leaf anatomy (Morden 1985; Morden and Hatch 1996). *Aciachne acicularis* Lægaard and *A. pulvinata* Benth., two small, compact, mat-forming perennials, can also be mistaken for *M. fastigiata*. However, both species of *Aciachne* (Pooideae: Stipeae) have longer spikelets ranging from 3.8–6 mm long, glumes that are 3–5-veined, and tightly overlapping lemma margins (Renvoize 1998; Giraldo-Cañas and Peterson 2009).

Muhlenbergia fastigiata is sister to the North American, *M. richardsonis* in *M.* subg. *Pseudosporobolus* [Fig. 1; Peterson et al. 2010b].

Specimens examined. Peru. **Ancash:** Recuay, Cordillera Blanca, 39 km S of Catac on road towards Raquia, 3980 m, 21 Mar 1997, P.M. Peterson 13825 & N. Refulio Rodriguez (US, USM); Cordillera Negra, E slope of Cerro Pullicharca (Purac), ca. 1.5 km W of hwy 109 and then 3.6 km S of Tapacocha along Rio Santa, 9°55'39.4"S, 77°23'45.3"W, 3822 m, 9 Mar 2008, P.M. Peterson 21512, R.J. Soreng, M.I. La Torre & J.V. Rojas Fox (US, USM); between Santa Rosa and Araranca 12 Apr 1915, O.F. Cook & G.B. Gilbert 168 (US). **Arequipa:** Prov. Caylloma, Valle de Colca, Chiray–Tuti, 3900 m, 12 Jan 1999, S.G. Beck 26354 (LPB); Prov. Caylloma, Pampa Cañahuas, “Grama dulce”, 4200 m, 3 Jul 2001, M. Rodríguez Diaz 1130 (USM). **Cajamarca:** Prov. Hualgayoc, 8 km NE of Hualgayoc on hwy 3N towards Bambamarca, 3080 m, 17 Mar 2000, P.M. Peterson & N. Refulio Rodriguez 14950 (CPUN, US, USM). Kanzel, above Sunchubamba, 3680 m, 6 Aug 1957, H. Ellenberg 1852 (US).

Cusco: Chumbivilias, Rio de Velille, 3850 m, C. Vargas C. 14084 (US); Espinar, alrededores de Yauri, 3900 m, 26 Mar 1956, 26 Mar 1956, C. Vargas C. 11209 (US). **Huancavelica:** Huancavelica, Canyon of Rio Ichu, SW of Huancavelica ca. 5 km on Hwy 3 to Santa Ines and Ayacucho, 12°48'48.2"S, 75°3'24.5"W, 4894 m, 14 Mar 2007, P.M. Peterson 20463, R.J. Soreng, K. Romaschenko & D. Susanibar Cruz (US, USM); Tayacaja, Just above Chuquitambo, 4 km SW of Pazo, 3975 m, 9 Apr 1997, P.M. Peterson 14151 & O. Tovar (US, USM). **Junín:** Prov. Huancayo, Acopalca, 3900 m, 25 Jul 1945, J. Infantes Vera s.n. (LIL); Prov. Huancayo, Acopalca, 4000 m, 20 July 1947, J. Infantes Vera 446 (LIL); entre Tarma y La Oroya, 3700 m, A. Weberbauer 2525 (MOL); Hacienda Cachi-Cachi, 4000 m, 22 Oct 1950, O. Velarde Nuñez 2869 (MOL); Jauja, 34 km SE of La Oroya on road towards Jauja, 3600 m, 9 Apr 1997, P.M. Peterson 14125 & O. Tovar (US, USM); Jauja, Tarma–Jauja road, 28 km from Tarma, 11°35'S, 75°38'W, 3950 m, 10 Jan 1984, D.N. Smith 5694 (MO, US); Junín, SE shore of Lago Chinchay Cocha (Junin) and 8 km S of Huayre, 4110 m, 7 Apr 1997, P.M. Peterson 14096 & O. Tovar (US, USM); Yauli, 156 km W of Lima just above Yauli, 4120 m, 5 Apr 1997, P.M. Peterson 14040 & O. Tovar (US, USM); Yauli, La Oroya, 30 Nov 1924, F.L. Stevens 1 (US); Oroyo, 23 Oct 1923, A.S. Hitchcock 22135 (US), 21 Feb 1954, Hirsch s,n. (US), Stevens 1 (US); entre Tarma y Oroya, 3400 m, 29 Jun 1948, R. Ferreyra 3828 (MOL, US, USM); ca. 24 km W of Tarma, 4050 m, 6 May 1979, Teppner 79/387 (US). **La Libertad:** Prov. Huamachuco, Cangau Sartimbamba, 3200 m, 28 Jan 1952, J. Infantes Vera 4072 (LIL); Prov. Huamachuco, Cangau Sartimbamba, 4000 m, 29 Jan 1952, J. Infantes Vera 4045 (LIL); Prov. Huamachuco, Huailillas, 3800 m, 8 Aug 1951, J. Infantes Vera s.n. (LIL). **Lima:** Provincia Huarochiri, Chilca, Bella Vista, 3800 m, 5 Jun 1940, E. Asplund 11436 (NY, US); road from Lima to Huancayo, 3300 m, 20 May 1981, G. Sullivan, K. Young, S. Sánchez & D. Soejarto 1021 (MO, US). **Pasco:** Pasco, 8 km W of NW arm of Laguna de Junín, 10°55'51.9"S, 76°18'8.6"W, 4141 m, 5 Mar 2007, P.M. Peterson 20313, R.J. Soreng & K. Romashchenko (US, USM). **Puno:** Chucuito, 3 km NE of Zepita on road towards Copani, 3820 m, 5 Mar 1999, P.M. Peterson 14631, N. Refulio Rodriguez & F. Salvador Perez (US, USM); 20 km E of Huacullani on road towards Desaguadero, 3880 m, 5 Mar 1999, P.M. Peterson 14645, N. Refulio Rodriguez & F. Salvador Perez (US, USM); 5 km S of Kelluyo, 3860 m, 7 Mar 1999, P.M. Peterson 14686, N. Refulio Rodriguez & F. Salvador Perez (US, USM); El Collao, 11 km E of Santa Rosa and 5 km W of Mazo Cruz, 3880 m, 2 Mar 1999, P.M. Peterson 14598, N. Refulio Rodriguez & F. Salvador Perez (US, USM); 9 km N of Conduriri and 63 km S of Ilave along the Rio Huenque, 3820 m, 3 Mar 1999, P.M. Peterson 14600, N. Refulio Rodriguez & F. Salvador Perez (US, USM); Provincia Melgar, 7 km WNW of Santa. Rosa, 14°35'54.9"S, 70°51'34.7"W, 4002 m, 23 Mar 2007, P.M. Peterson 20605, R.J. Soreng & K. Romashchenko (US, USM); SW of Juliaca ca. 8 km on Hwy 30 to Arequipa, 15°32'37.2"S, 70°12'55.9"W, 3854 m, 31 Mar 2007, P.M. Peterson 20715, R.J. Soreng, K. Romaschenko & S. Gonzalez Elizondo (US, USM); Puno, 2 km N of Laraquerion road towards Puno, 16°6'59.1"S, 70°1'59.1"W, 3940 m, 18 Apr 2004, P.M. Peterson 18327 & N. Refulio Rodriguez (US, USM); San Roman, 4 km E of Santa Lucia, 15°41'4.2"S, 70°34'8.0"W, 4030 m, 19 Apr 2004, P.M. Peterson 18332 & N. Refulio Rodriguez (US, USM); 21 km W of Santa Lucia and 5 km E of Puente Cañuma (Laguna Lagunillas), 15°40'4.1"S, 70°47'4.4"W, 4260 m, 20 Apr 2004, P.M. Peterson 18344 & N. Refulio Rodriguez (US, USM); Camjata Hacienda, Capachica Peninsula, Lake Titicaca, Tutin 975 (NY); between Juliaca and Cusco, 3880 m, 27 Nov 1923, A.S. Hitchcock 22448 (US); Hacienda Pairumani, 20 mi SW of Llave, 3900 m, 21 Jul 1946, O.P. Pearson & A. Pearson 14 (US); between Puno and Laguna Umayo, N of Puno, 3970 m, 12 Sep 1959, H.G. Barclay 9265 (US). **Tacna:** Cordillera Volcan Tacora, Ancara, Werderman 1138 (NY, US); Tarata, 11 km NW of Yabroco on road towards Cano, 3680 m, 16 Mar 1999, P.M. Peterson 14814, N. Refulio Rodriguez & F. Salvador Perez (US, USM).

10. *Muhlenbergia flexuosa* Hitchc., Contr. U.S. Natl. Herb. 24(8): 388. 1927.

Fig. 9A–E

Type. Peru, Huacachi Estacion near Muna, summit of rocky crest, 2000 m, 20 May–1 Jun 1923, *J.F. Macbride 3874* (holotype: F-534937!; isotypes: BAA-1622!, BM-000938657 [image!], G-00099373 [image!], K!, LE!, US-1256339!).

Description. Caespitose *perennials*. *Culms* 15–40 cm tall, slender, 0.3–0.4 mm diameter just below the panicle with 6–8 nodes per culm; *internodes* 1–6 cm long near base, glabrous, shiny. *Leaf sheaths* about as long as the internodes below, glabrous; *ligules* 0.3–0.5 mm long, membranous, apex truncate, lacerate; *blades* 2–5 cm long, 1–2.2 mm wide, flat, scaberulous, apex acuminate. *Panicles* 3.5–6.5 (–7) cm long, 0.5–1.5 cm wide, narrow, spiciform, sometimes interrupted below; *primary branches* 0.5–2.5 cm long, tightly apressed to loosely ascending or spreading, not more than 45° from the culm axis. *Spikelets* 2.8–4.2 mm long, yellowish to light brown, erect or drooping; *glumes* 2.8–4 mm long, including mucos or awns, subequal, hyaline to membranous, glabrous, 1-veined, scabrous along the midvein, apex acute, unawned, mucronate or awned, the awns up to 1.3 mm long, straight or loosely flexuous; *lemmas* 2.8–4.2 mm long, hyaline to membranous, 3-veined, scaberulous, lower 1/3 sparsely hairy, apically awned, the awns 14–30 mm long, flexuous, callus hairy, the hairs up to 0.4 mm long; *paleas* about as long as the lemmas, 2-veined, glabrous, apex acuminate, often mucronate; *anthers* 1.3–1.6 mm long, purple. *Caryopses* 1.4–1.6 mm long fusiform, light brown.

Distribution. *Muhlenbergia flexuosa* endemic to Peru and is known from only a few collections from Huánuco, Pasco and San Martín departments (Hitchcock 1927; Tovar 1993).

Ecology. Steep talus slopes, rocky trail cuts and rock outcropts with *Andropogon*, *Acacia*, *Chusquea*, *Baccharis*, *Puya*, *Salvia*, *Rubus*, *Muhlenbergia ciliata*, *M. beyrichiana*, Acanthaceae and Melastomataceae; 1200–2530 m.

Comments. Hitchcock (1927) suggested *Muhlenbergia flexuosa* was allied with *M. flaviseta* Scribn. and *M. watsoniana* Hitchc. (≡ *M. scabra* S. Watson), since all have

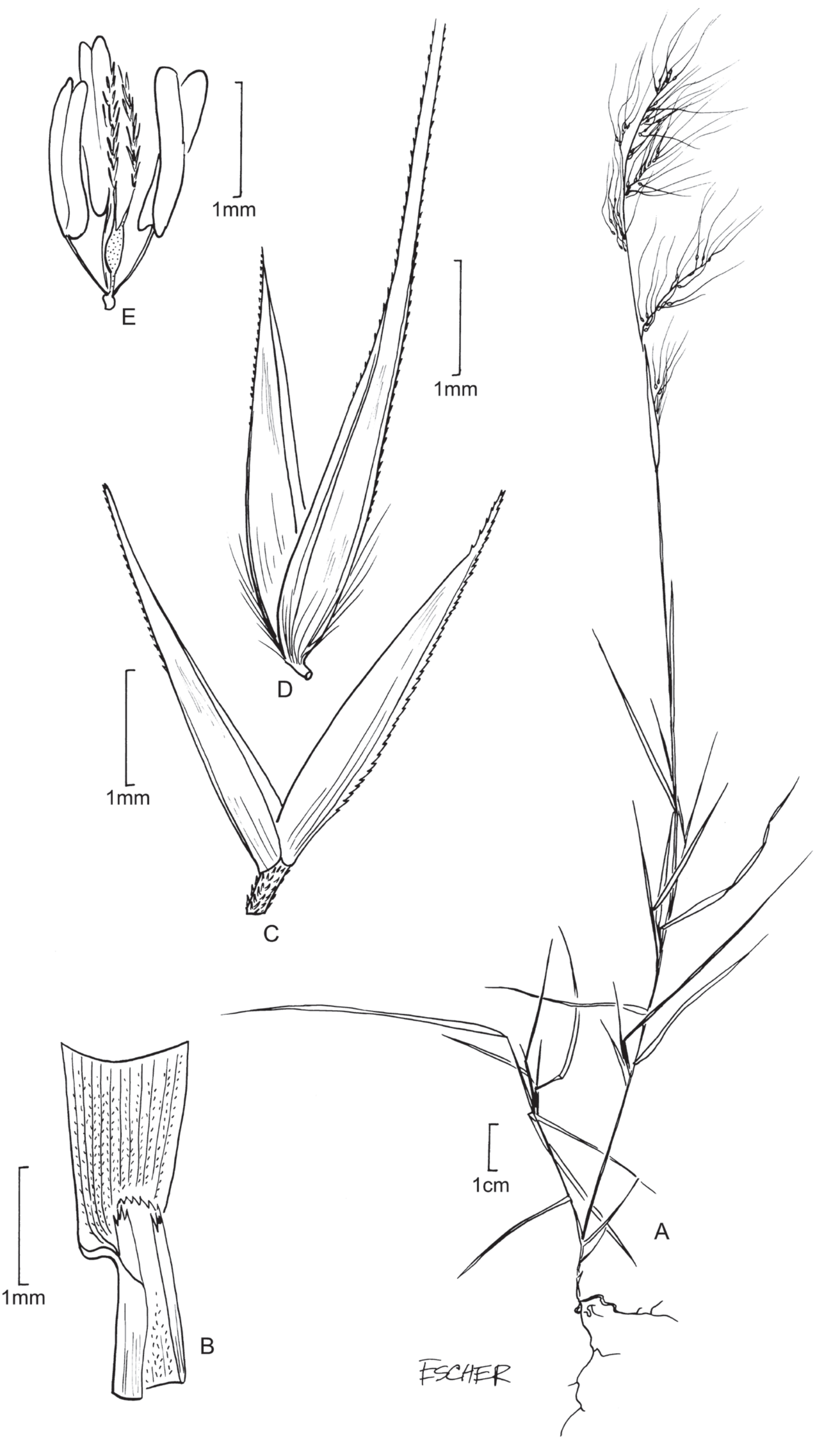

Figure 9. A–E *Muhlenbergia flexuosa* Hitchc. **A** habit **B** ligule **C** glumes **D** floret **E** stamens and pistil. Drawn from *H. Teppner 79-293* (US).

short flat blades, spike-like panicles and slender flexuous awns. However, *Muhlenbergia flaviseta* and *M. watsoniana* are members of the *M.* subg. *Clomena* clade while *M. flexuosa* is sister to *M. plumiseta* Columbus–*M. pereilema* P.M. Peterson–*M. beyrichiana* clade, all of which are included in *M.* subg. *Muhlenbergi*a (Fig. 1; Peterson et al. 2010b). Within *Muhlenbergia,* the derivation of a slender flexuous awn found in *M. flexuosa* has occurred in four of the five subgenera currently recognised within the genus and is only lacking in *M.* subg. *Pseudosporobolus* (Fig. 1B; Peterson et al. 2010b).

Specimens examined. Peru. **Huánuco:** Rio Huallaga Cañon, below Rio Santo Domingo, 1316 m, 3 Jun 1923, J.F. Macbride 4205 (US); Pachitea, Canyon of the Rio Grande, 44 air km E of Huánuco, 2 air km ESE of Estación Huacachay (Huacachi), 9°51'34.7"S, 75°50'48.1"W, 1867 m, 7 Mar 2007, P.M. Peterson, R.J. Soreng & K. Romaschenko 20358 (MO, US, USM); 1.5 air km SE of Estación Huacachay (Huacachi), 9°51'42.8"S, 75°50'23.4"W, 2383 m, 8 Mar 2007, P.M. Peterson, R.J. Soreng & K. Romaschenko 20365 (MO, US, USM); along trail 1/3 air km NW of Estación Huacachay (Huacachi), 9°51'1.4"S, 75°49'53.4"W, 2519 m, 8 Mar 2007, P.M. Peterson, R.J. Soreng & K. Romaschenko 20373 (US, USM). **Junin:** Cerro Taldes, Rio Huancabamba, 31 km S of Pozuzo and 3 km N of Llullitunqui, 1370 m, 1 Jun 1979, H. Teppner 79-293 (US). Pasco: Oxapampa, Pozuzo, 21 Jul 1978, Ellemberg 8934 (USM). **San Martín:** Mariscal Caceres, 2350 m, 13 Aug 1986, K. Young 4234 (MO).

11. *Muhlenbergia ligularis* (Hack.) Hitchc., Contr. U.S. Natl. Herb. 24(8):388. 1927.

Fig. 8F–J

Sporobolus ligularis Hack., Oesterr. Bot. Z. 52(2):57. 1902. Type: Ecuador, Pichincha, 23 Jan 1899, *Sodiro s.n.* (holotype: W; isotypes: BAA-2905! ex W, US-3274313! ex W, US-1163183!).

Muhlenbergia calcicola Swallen, Contr. U.S. Natl. Herb. 29(9):407. 1950. Type: Guatemala, Huehuetenango, Chemal, Sierra de los Chuchumatanes, 3300 m, 31 Dec 1940, *P.C. Standley 81703* (holotype: US-1910686!; isotypes: F-1200274 [image!], US-2236500US!).

Muhlenbergia breviculmis Swallen, Contr. U.S. Natl. Herb. 29(9):408. 1950. Type: Guatemala, Huehuetenango, Cerro Chemalito, Sierra de los Cuchumatanes, 3.5 mi W of Santa Eulalia, 3100–3150 m, 2 Aug 1942, *J.A. Steyermark 49905* (holotype: US-1935054!; isotypes: F, US-2208654!).

Muhlenbergia minuscula H. Scholz, Willdenowia 14:393. 1984. Type: Bolivia, Canton Ulla-Ulla, Pampa von Ulla-Ulla, Apolobamba Cordillera, 4450 m, 26 Feb 1983, *Menhofer 1974* (holotype: B!; isotype: LPB-0000293 [image!]).

Description. Loosely tufted *annuals* to short-lived *perennials*. *Culms* 2–12 cm tall, 0.2–0.4 mm diameter just below the panicle, erect or decumbent, slender, glabrous, sometimes flowering the first year, up to 15 cm broad, dying in the centre, profusely branched below, a short branchlet with fascicled leaves borne at each node, with 4–6 nodes; *internodes* 2–20 mm long. *Leaf sheaths* 2–20 mm long, generally shorter than the internodes, glabrous, ridged, flattened by the densely fascicled branches; *ligules* 0.6–2.5 mm long, membranous to hyaline, apex truncate to rounded; *blades* 0.3–2.2 cm long, 0.8–1.5 mm wide, flat or folded, prominently veined, thick, firm, usually with whitish-thickened midvein and margins, conspicuously crystalline or spiculate on both surfaces, otherwise glabrous below, sparsely scaberulous above and along margins, tapering to a boat shaped tip. *Panicles* 1.0–3.0 cm long, 0.3–1.4 cm wide, long exserted or included in the uppermost sheath, loosely contracted; *branches* 5–9 mm long, one per node, appressed or reflexed at maturity up to 70° from the culm axis; *pedicels* 1–3 mm long, stiff, densely scabrous, spiculate, erect. *Spikelets* 1.5–3.0 mm long, often plumbeous to reddish-purple; *glumes* 1.0–1.9 mm long, subequal, glabrous, apex acute to obtuse, often minutely erose, greenish-grey; *lower glumes* 1.0–1.7 mm long, 1-veined; *upper glumes* 1.1–1.9 mm long, 1-veined or occasionally 3-veined; *lemmas* 1.5–3.0 mm long, lanceolate, 3-veined, keeled, glabrous, mottled with greenish-black areas or dark greenish mottles on a pale background, apex minutely scaberulous, acuminate, entire or mucronate; mucro rarely more than 1 (–1.2) mm long; *paleas* 1.4–2.9 mm long, lanceolate, glabrous; *anthers* 0.8–1.1 mm long, purplish becoming pale. *Caryopses* 0.8–1.2 mm long, elliptic to fusiform, brownish.

Distribution. This species ranges from Guatemala and Costa Rica (Pohl 1980, at Chirripo Grande) to Colombia, Venezuela, Ecuador, Bolivia, Peru and Argentina.

Ecology. *Muhlenbergia ligularis* occurs in grassy flats, moist depressions, wet meadows, gravelly banks, ridgetops and gravelly roadsides often derived from calcarious subtrates associated with *Achnatherum*, *Aciachne*, *Agrostis*, *Alnus*, *Anatherostipa*, *Baccharis*, *Berberis*, *Bidens*, *Buddleya*, *Caiophora*, *Calamagrostis*, *Carex*, *Colletia spinosissima* J.F. Gmel., *Eleocharis*, *Festuca*, *Gaultheria*, *Hypericum*, *Jarava*, *Juncus*, *Lepidophyllum*, *Lupinus*, *Margyricarpus*, *Muhlenbergia* spp., *Nassella*, *Cenchrus clandestinus*, *Plantago*, *Poa*, *Puya*, *Rumex*, *Salvia* and *Senecio*; 2320–4650 m. Flowering September through January in Central America and February to July in Peru or when moisture is available.

Comments. *Muhlenbergia ligularis* is morphologically similar to *M. fastigiata* and can be separated from the latter by possessing flat leaf blades, 0.8–1.5 mm wide and a rather loosely tufted habit without wiry creeping rootstocks and scaly rhizomes. Morphologically, *M. ligularis* differs from *M. caxamarcensis* in having glabrous lemmas (sericious hairs on lower 1/2–3/4 in the latter).

Molecular DNA sequence analysis indicates *M. ligularis* falls within *M.* subg. *Bealia* and is polyphyletic (Fig. 1A). Perhaps, cryptic speciation followed by morphological convergence has occurred within *M. ligularis*, also suggested in *Ehrharta* Thund. and *Eriochrysis* P. Beauv. (Verboom et al. 2003; Welker et al. 2016).

Specimens examined. Peru. **Amazonas:** Chachapoyas, 1.5 km al SW of Chachapoyas, 2320 m, 24 May 1962, J.J. Wurdack 504 (US, USM); **Ancash:** Huaraz, Huascaran National Park, Quebrada Rajucolta, 77°22'W, 9°32'S, 4000 m, 17 Apr 1986, D.N. Smith, R. Valencia, M. Buddensiek 12192 (CPUN, MO); S of Huaraz, 28 km from Pachacoto towards La Union, 4500 m, 6 Apr 1988, S.A. Renvoize & S. Lægaard 5118 (CPUN, K); Huari, Cordillera Blanca, 24 km N of Huari on road towards San Luis, 3820 m, 22 Mar 1997, P.M. Peterson & N. Refulio Rodriguez 13871 (MO, US, USM); Huascarán. National Park, Quebrada Pachachaca, a lateral valley of Quebrada Rurichinchay, 77°16'W, 9°77'S, 3700 m, 12 Jun 1986, D.N. Smith, A. Gonzales & D. Maldonado 12562 (CPUN, MO); Prov. Pallasca, Hacienda Chalan, Mar 1949, A. Tito Ureña 7 (MOL); Recuay, Cordillera Blanca, 37 km E of Raquia on Route 02-014 on road towards Huarez, 3900 m, 20 Mar 1997, P.M. Peterson & N. Refulio Rodriguez 13816 (US, USM); 2 km SW of Conococha on Ruta 02-014. 10°8'18.2"S, 77°18'5.4"W, 4107 m, 21 Mar 2004, P.M. Peterson, N. Refulio Rodriguez, A. Cano, M. La Torre & I. Salinas 17902 (MO, US, USM); 3 km E of Conococha, 10°6'55.5"S, 77°16'20.2"W, 4050 m, 24 Mar 2004, P.M. Peterson & N. Refulio Rodriguez 17935 (MO, US, USM); Cordillera Negra, E slope of Cerro Pullicharca (Purac), ca. 1.5 km W of hwy 109 and then 3.6 km S of Tapacocha along Rio Santa, 9°55'39.4"S, 77°23'45.3"W, 3822 m, 9 Mar 2008, P.M. Peterson, R.J. Soreng, M. La Torre & J. Rojas Fox 21513 (US, USM); Cordillera Negra, 30 km from Huaraz towards Casma, Punta Callán, 4200 m, 7 Apr 1988, S.A. Renvoize & S. Lægaard 5162 (CPUN, K); Sihaus, 31 km N of Pomabamba on road towards Sihaus, 3780 m, 24 Mar 1997, P.M. Peterson & N. Refulio Rodriguez 13906 (MO, US, USM); Quebrada Huanca, 77°23'W, 9°55'S, 3950 m, 2 Jul 1985, D.N. Smith & M. Buddensiek 10970 (CPUN, MO); Yungay, W slope of Cordillera Blanca, Rio at E end of Lago Llanganuco, ca. 29 km ENE of new city of Yungay, Parque Nacional Huascaran, Sector Llanganuco, 9°4'8.9"S, 77°38'25.2"W, 3663 m, 16 Mar 2008, P.M. Peterson, R.J. Soreng, M. La Torre & J. Rojas Fox 21747 (US, USM); W slope of Cordillera Blanca on road to pass E of Lago Llanganuco and Yanama, ca. 37 km ENE of new city of Yungay, Parque Nacional Huascaran, Sector Llauganuco, 9°3'16.6"S, 77°35'57.6"W, 3931 m, 16 Mar 2008, P M. Peterson, R.J. Soreng, M. La Torre & J. Rojas Fox 21758 (US, USM); 37 km E of Yungay, 4200 m, 5 Apr 1988, S.A. Renvoize & S. Lægaard 5080 (CPUN, K). **Apurimac:** Aymaraes, 25 km NE of Chalhuanca on road towards Yanaca, at Paseo., 14°15'30.6"S, 73°12'6.9"W, 4300 m, 13 Mar 2002, P.M. Peterson & N. Refulio Rodriguez 16504 (US, USM). **Arequipa:** Caylloma, 15 km SE of Callalli on road towards Condoroma, 15°28'14"S, 71°22'26.9"W, 4610 m, 12 Apr 2004, P.M. Peterson & N. Refulio Rodriguez 18279 (MO, US, USM). **Ayacucho:** Huamanga, S of Ayacucho ca. 45 km on Hwy 3 toward Abancay, 13°20'27"S, 74°9'34.7"W, 4207 m, 16 Mar 2007, P.M. Peterson, R.J. Soreng, K. Romashchenko & D. Susanibar Cruz 20522 (US, USM); 68 km SW of Ayacucho on road towards Pisco, 13°20'5"S, 74°36'36.7"W, 4045 m, 22 Mar 2002, P.M. Peterson & N. Refulio Rodriguez 16659 (US, USM); Lucanas, 2 km SW of Putajasa, 14°8'15.9"S, 74°11'18.4"W, 3900 m, 24 Feb 2002, P.M. Peterson, A. Cano, M. La Torre, A. Ramírez & D. Susanibar Cruz 16225 (US, USM); 25 km E of Puquio on road towards Cusco, 14°37'40.3"S, 74°2'19.1"W, 4150 m, 12 Mar 2002, P.M. Peterson & N. Refulio Rodriguez 16454 (US, USM); 25 km NE of Villatambo on road towards Lucanas at Reserva "Pampa Galeras". 14°40'46.2"S, 74°23'59.2"W, 3805 m, 8 Apr 2004, P.M. Peterson & N. Refulio Rodriguez 18179 (US, USM); 13 km E of Puquio at km 172 mark, 14°41'18.5"S, 74°4'26.8"W, 3730 m, 8 Apr 2004, P.M. Peterson & N. Refulio Rodriguez 18214 (MO, US, USM); Parinacochas, along arroyo near small rio above (north) of Laguna Parinacochas, 15°14'41"S, 73°44'20.3"W, 3300 m, 1 Mar 2002, P.M. Peterson, M. La Torre, A. Ramírez & D. Susanibar Cruz 16326 (US, USM). **Cajamarca:** Cajamarca, 21 km W of Central Plaza of Cajamarca at Cumbemayo (take Avenida Peru), 3600 m, 31 Mar 1997, P.M. Peterson & N. Refulio Rodriguez 14014 (MO, US, USM); Cumbe Mayo, subiendo el curso del canal, 3500 m, 20 Mar 1988, I. Sánchez Vega 4692 (CPUN); Cumbe Mayo, west of Cajamarca. growing in seeping water, 3600 m, 27 Mar 1988, S.A. Renvoize, S. Lægaard & I. Sánchez Vega 4997 (CPUN, K).Cordillera Comullca, 57 km. from Cajamarca on road to Celendín,"Jalca" páramo, 3600 m, 26 Mar 1988, S.A. Renvoize & S. Lægaard 4964 (CPUN, K); Pampa de Guanico, ruta a Guagal, 17 May 1973, 3500 m, I. Sánchez Vega.1145 & J. Tejada Mayta (CPUN); desvío a Guagal, ruta a Celendín, 2700 m, 17 May 1977, I. Sánchez Vega 2027, W. Ruiz V. & J. Sánchez Vega.(CPUN); Dist. La Encañada. Cerro Negro, extremo SE de las pampas de Cerro Negro, 3480 m, 19 Jul 2003, M. Cabanillas Soriano 1548, M. Cabanillas Medina & M. Sánchez Montoya (CPUN); entre Cajamarca y La Encañada, 2700 m, 22 May 1974, I. Sánchez Vega 1302 & W. Ruiz Vigo (CPUN); Dist. La Encañada, Pampas de Cerro Negro, 3540 m, 12 Jul 2003, M. Cabanillas Soriano 1501, M. Cabanillas Medina & M. Sánchez Montoya (CPUN); Cajamarca to Bambamarca, on side road to Chugur, 88 km from Cajamarca, just below first mine, 3700 m, 20 Mar 1988, S.A. Renvoize, S. Lægaard & I. Sánchez Vega 4822 (CPUN, K); Las lagunas, 50 km from Cajamarca on road to Bambamarca, 4000 m, 29 Mar 1988, S.A. Renvoize & S. Lægaard 5030 (CPUN, K); Dist Cajamarca. Pampa Larga, al N de Yancocha, 3900 m, 14 May 1994, I. Sánchez Vega 7135, Homero Bazán & Alfonso Miranda (CPUN); Micuypampa, 62 km from Cajamarca towards Celendin, 2600 m, 26 Mar 1988, S.A. Renvoize & S. Lægaard 4963 (CPUN, K);Celendin, S of Cajamarca–Celendin Hwy, E of pass between provincia borders and ca. 11 km along road to Huagal, vic. La Honda, 7°5'15.6"S, 78°11'39.9"W, 3525 m, 28 Mar 2008, P.M. Peterson, R.J. Soreng & J. Montoya Quino 21912 (US, USM); San Miguel, 61 km N of Cajamarca on Hwy 3N towards Bambamarca, 3640 m, 16 Mar 2000, P.M. Peterson & N. Refulio Rodriguez 14915 (CPUN, MO, US, USM); San Pablo, 33 km NW of Cajamarca on road towards San Pablo via Porcon, 3510 m, 14 Mar 2000, P.M. Peterson & N. Refulio Rodriguez 14876 (CPUN, MO, US, USM). **Cusco:** Calca, 26 km E of Pisac on road to Colquepata, 13°23'2.1"S, 71°44'46.9"W, 4120 m, 18 Mar 2002, P.M. Peterson & N. Refulio Rodriguez 16602 (US, USM); Canchis, Dist. Marangani, Lay Raya, 14.46666S 71.016666W, 7 May 2003, L. Valenzuela, J. Farfán, I. Huamantupa, E. Suclli, & H. Coasaca 1970 (MO); Cusco, Sacsaihuamán, 3600 m, Apr 1944, C. Vargas C. 4167 (US); Espinar, alrededores de Yauri, 3900 m, 26 Mar 1956, C. Vargas C. 11213 (US); Espinar, Hda. C'achachi, 4200 m, 20 Mar 1956, C. Vargas C. 11160 (US); Paucartambo, 21 km NE of Paucartambo on road to Tres Cruces., 13°11'54.8"S, 71°38'40.5"W, 3460 m, 18 Mar 2002, P.M. Peterson & N. Refulio Rodriguez 16621 (US, USM); 1 km E of Mirador Tres Cruces and 35 km N of Paucartambo, 13°8'11.6"S, 71°37'40.3"W, 3625 m, 19 Mar 2002, P.M. Peterson & N. Refulio Rodriguez 16639 (US, USM); Quispicanchi, 23 km up new Hwy 28 from Urcos to Ccatcca (Catsa), ESE of Cusco ca. 45 air km, 13°39'39.5"S, 71°35'29.7"W, 4080 m, 19 Mar 2007, P.M. Peterson, R.J. Soreng & K. Romashchenko 20564 (US, USM); Vilacabamba, Paltaybamba, Ayangate, 13.0494444S 72.7208334W, 2300 m, 10 Jun 2002, L. Valenzuela, E. Suclli, I. Huamantupa & F. Carazas 225 (MO). **Huancavelica:** Castrovirreyna, 30 km SW of Huancavelica along Rio Pucapampa, 12°56'10"S, 75°5'57.2"W, 4510 m, 8 Mar 2002, P.M. Peterson & O. Tovar 16399 (US, USM); Castrovirreyna, Choclococha, 4500 m, 5 May 1958, O. Tovar 2907 (US, USM); Castrovirreyna, Choclococha, 4700 m, 3 May 1958, O. Tovar 2854 (US, USM); 3 km S of Astobamba on road towards Pucapampa, 12°58'47.7"S, 75°5'27.4"W, 4540 m, 4 Apr 2004, P.M. Peterson & N. Refulio Rodriguez 18118 (MO, US, USM); 4 km S of Choclococha and 8 km N of Santa Ines, 13°10'44"S, 75°5'15.3"W, 4615 m, 5 Apr 2004, P.M. Peterson & N. Refulio Rodriguez 18145 (MO, US, USM); Huancavelica, 56 km S of Izacuchaca on road towards Huancavelica, 4020 m, 10 Apr 1997, P.M. Peterson & O. Tovar 14157 (US, USM);15 km NE of Huancavelica above Sachapite, 4100 m, 10 Apr 1997, P.M. Peterson & O. Tovar 14171 (US, USM); 12 km S of Huancavelica on road towards Santa Barbara, 4120 m, 11 Apr 1997, P.M. Peterson & O. Tovar 14191 (MO, US, USM); 13 km N of Huancavelica on road towards Palca, 12°43'9"S, 74°59'11.9"W, 4470 m, 2 Apr 2004, P.M. Peterson & N. Refulio Rodriguez 18098 (MO, US, USM); Huaytara, Rio Pampas, along Hwy 3 (old 24) 12 km NW of jct. with new Hwy 24 and 18 km SE of Santa Ines, SE of Pilpichaca, 13°19'24.2"S, 75°00'56.6"W, 4164 m, 13 Mar 2007, P.M. Peterson, R.J. Soreng, K. Romashchenko & D. Susanibar Cruz 20432 (US, USM); Occoro, entre Conaica y Tansiri, 4200 m, 2 Apr 1953, O. Tovar 1195 (US, USM); Occoro, 4200 m, 3 Apr 1953, O. Tovar 1214 (US, USM); Tayacaja, Hda. Alalay entre Mariscal Caceres y Pampas, 3900 m, 13 Apr 1953, O. Tovar 1333 (MO, US, USM); Tayacaja, 2 km E of Acostambo on road towards Izcuchaca, 12°22'3.7"S, 75°2'33.3"W, 3350 m, 1 Apr 2004, P.M. Peterson & N. Refulio Rodriguez 18087 (US, USM); Tayacaja, Patacancha, Conaica, 4100 m, 8 Apr 1961, O. Tovar 3131 (US, USM); Chascca, cerca a Conaica, 3800 m, 13 May 1956, O. Tovar 2588 (US, USM); Tayacaja, arriba de Hda. Toca, entre Calcabamba y Paucarbamba, 3800 m, 20 Apr 1954, O. Tovar 2021 (US, USM); Urubamba, Piri, 2860 m, 15 May 1948, C. Vargas C. 7208 (US). **Junin:** Junin, SE shore of Lago Chinchay Cocha (Junin) and 8 km S of Huayre, 4110 m, 7 Apr 1997, P.M. Peterson & O. Tovar 14097 (MO, US, USM); Tarma, Hacienda Casa Blanca, 18 air km SSE of Tarma, 4000 m, 27 Nov 1962, H.H. Iltis, C.M. Iltis, D. Ugent & V. Ugent s.n. (US); Yanli, La Oroya, 11°32'S, 75°53'W, 3700 m, 7 Jan 1983, D.N. Smith 2974 (MO, US); Yanli, Marcapomacocha, 4800 m, O. Velarde 8751 (US, USM). **La Libertad:** Bolivar, E side of Cerro Salumpuy, between Laplat and Unamen, WSW of Unamen, ca. 8 air km NW of Bolivar, 7°7'39.2"S, 77°46'9.9"W, 3390 m, 30 Mar 2008, P.M. Peterson, R.J. Soreng & J. Montoya Quino 21946 (US, USM); Pataz, cueva de Manachaqui, Parque Nacional Río Abiceo, 3600 m, 28 Feb 1998, B. León & K. Young 1116. (MO, USM); Santiago de Chuco, 23 km SW of Huamachuco on road towards Alto de Tamboras and Pampas, 3540 m, 29 Mar 1997, P.M. Peterson & N. Refulio Refulio 13966 (MO, US, USM). **Lambayeque:** Ferrenafe, 3300 m, 12 Sep 1985, A. Sagástegui A., D. Skillman, J. Mostacero L. & L. Ramírez V. 12812 (MO); Laguna

Tembladera, Uyurpampa, 3320 m, 25 Aug 1993, S. Llatas Quiroz 3359 (MO). **Pasco:** Pasco, 4 km NE of Huayllay on road towards Canchacucho, 10°58'20.8"S, 76°19'18"W, 4160 m, 31 Mar 2004, P.M. Peterson & N. Refulio Rodriguez 18067 (MO, US, USM); plains ca. 8 km W of NW arm of Laguna de Junin, S side of Rio Colorado and E of new Hwy and railroad tracks, 12 km NE of Huayllay on Hwy 18, 10°55'51.9"S, 76°18'8.6"W, 4141 m, 5 Mar 2007, P.M. Peterson, R.J. Soreng & K. Romashchenko 20314 (US, USM). **Piura:** Ayabaca, Ruinas de Aypate, 2700 m, 21 May 1996, V. Quipuzcoa S. 544, O. Angulo Z. & R. Yahuana R. (HAO, MO); Huancabamba, 23 km E of Sondor on road towards Tabaconas, 2740 m, 31 Mar 2000, P.M. Peterson & N. Refulio Rodriguez 15133 (CPUN, MO, US, USM). **Puno:** Abra la Raya, along railroad between Santa Rosa and Marangani, 4300 m, 18 May 1985, J.C. Solomon 2920 (MO); Azangaro, Checayani, NE of Azangaro, 3900 m, 27 Mar 1957, H. Ellenberg 426 (US); Chuquibambilla, Florez 13 (WS); Granja Salcedo, Apr 1936, J. Sonkup 112 (US); Cerro Santa Barbara, 3700 m, 15 May 1958, O. Tovar 3071 (US, USM); Huerta, N of Puno, 3900 m, 22 Mar 1957, H. Ellenberg 242 (US); Pucará, Pampa, 3890 m, Apr 1964, A. Vera 105 (COL); alrededores de Puno, 3870 m, 16 Apr 1965, A. Vera 204 (COL); quebrada en los alrededores de Puno, 3850 m, 1 Oct 1965, A. Vera 340 (COL); Chucuito, 3 km NE of Zepita on road towards Copani, 3820 m, 5 Mar 1999, P.M. Peterson, N. Refulio Rodriguez & F. Salvador Perez 14633 (US, USM); 2 km S of Huacullani, 4000 m, 6 Mar 1999, P.M. Peterson, N. Refulio Rodriguez & F. Salvador Perez 14659 (MO, US, USM); Lampa, NW end of Laguna Lagunillas, 20 air km W of Santa Lucia, N and S sides of new Hwy 30 to Arequipa, 74 air km WSW of Juliaca, 15°41'1.7"S, 70°48'5.4"W, 4185 m, 31 Mar 2007, P.M. Peterson, R.J. Soreng, K. Romashchenko & M.S. Gonzalez Elizondo 20735 (US, USM); Melgar, ca. 7 km WNW of Santa Rosa on Hwy 3 and 1 km W toward Quishuara, along Rio Santa Rosa, 14°35'54.9"S, 70°51'34.7"W, 4002 m, 23 Mar 2007, P.M. Peterson, R.J. Soreng & K. Romashchenko 20606 (US, USM); Puno, 2 km N of Laraquerion road towards Puno, 16°6'59.1"S, 70°1'59.1"W, 3940 m, 18 Apr 2004, P.M. Peterson & N. Refulio Rodriguez 18328 (MO, US, USM); San Roman, 21 km W of Santa Lucia and 5 km E of Puente Cañuma (Laguna Lagunillas), 15°40'4.1"S, 70°47'4.4"W, 4260 m, 20 Apr 2004, P.M. Peterson & N. Refulio Rodriguez 18345 (MO, US, USM). **San Martín:** Mariscal Caceres, 7°00'01"S, 77°00'3"W, 3350 m, 18 Jul 1987, K. Young & B. León 4793 (MO, USM).

12. *Muhlenbergia maxima* Lægaard & Sánchez Vega, Nordic J. Bot. 10: 439. 1990.

Fig. 2F–H

Type. Peru, Prov. Cajamarca, Choten between Paso El Gavilán and San Juan at km 153 on the road to the coast, 2900 m, 29 May 1984, *I. Sánchez Vega & Ruiz Vigo 3561* (holotype: CPUN!; isotypes: AAU!, K!, US!, USM!).

Description. Loosely caespitose *perennials*. *Culms* 100–140 cm tall, erect, rigid, terete, ca. 2–3.2 mm diameter near base with 3 or 4 glabrous to pubescent nodes; internodes terete above. *Leaf sheaths* longer than the internodes, mostly basally inserted, compressed-keeled near base, becoming fibrous with age, scaberulous, finely striate; *ligules* 3–5 mm long, apex irregularly toothed to lacinate, margins entire and extended above to form auricles; *blades* 25–45 cm long, 2.8–4 mm wide, flat to folded, striate, scabrous, apex attenuate, midvein prominent. *Panicles* 30–46 cm long, 3–6 cm wide, narrow; *branches* 6–11 cm long, scabrous, ascending, appressed to loosely spreading, mostly floriferous to base, except on lowest branches; *pedicels* mostly shorter than the spikelets. *Spikelets* 2.5–2.8 mm long, 1-flowered, greenish with reddish-purple tinting; *glumes* 2.2–2.6 mm long, almost equal or shorter than the floret, hyaline to membranous, faintly 1-veined, subequal, the lower usually slightly shorter, glabrous to scattered pubescent, scaberulous; *lemmas* 2.5–2.8 mm long, ovate, 3-veined, awned, with scattered sericeous hairs more numerous along the veins, scaberulous, the callus pilose, the flexuous awn inserted just below the obtuse to acute apex, the awn 4–9 mm long; *paleas* about as long as the lemma, faintly 2-veined, sericeous between the veins below; *lodicules* about 0.1 mm long, truncate, glabrous; *stamens* 3; anthers 1.3–1.8 mm long, purple. *Caryopses* 1.4–1.7 mm long, fusiform, brownish.

Distribution. A Peruvian endemic known only from Amazonas and Cajamarca departments.

Ecology. Rocky slopes near rivers and grassy slopes in disturbed ground along roads associated with *Acacia*, *Begonia*, *Cortaderia bifida*, *C. jubata*, *Desmodium*, *Dodonaea viscosa* Jacq., *Hyptis*, *Lepechinia*, *Oxalis*, *Puya*, *Salvia* and *Schizachyrium*; 2100–2900 m.

Comments. *Muhlenbergia maxima* is a member of *M.* subg. *Trichochloa* (Peterson et al. 2010b). *Muhlenbergia inaequalis* Soderstr. endemic to Colombia and Venezuela and *M. lehmanniana* Henr. ranging from Costa Rica to Colombia (Lægaard and Sánchez Vega 1990; Giraldo-Cañas and Peterson 2009) are morphologically similar to *M. maxima*. *Muhlenbergia maxima* differs from *M. inaequalis* and *M. lehmanniana* in having shorter lemmatal awns and a longer ligule than *M. inaequalis* (0.5–1.5 mm long) and a shorter ligule than *M. lehmanniana* (1–2.5 cm long). There is not much genetic variation among all members of *M.* subg. *Trichochloa* in Peterson et al. (2010a) and a detailed population genetic study of these three South American species is needed to interpret their evolutionary history.

Specimens examined. Peru. **Amazonas:** 27 km from Balsas towards Leymabamba, 2250 m, 23 Mar 1988, S.A. Renvoize & S. Lægaard 4908 (CPUN, K); 66 km from Leymebamba towards Balsas, 2100 m, 25 Mar 1988, S.A. Renvoize & S. Lægaard 4935 (CPUN, K, MO, US). **Cajamarca:** Prov. Cajabamba, 14 air km WSW of Cajabamba and 2.5 km on road W of Araqueda, 7°39'9.1"S, 78°9'58.9"W, 2242 m, 23 Mar 2008, P.M. Peterson & R.J. Soreng 21853 (MO, US, USM); Prov. Cajamarca, S of Paso El Gavelán, ca. 10 air km S of Cajamarca, just above km post 150 on hwy 8 above San Juan, 7°15'37.2"S, 78°30'34.5"W, 2544 m, 26 Mar 2008, P.M. Peterson, R.J. Soreng & I Sánchez Vega 21884 (US, USM); Dist. San Juan, entre San Juan y Paso el Gavilán, 2650 m, 30 May 2003, I. Sánchez Vega 11965, M. Sánchez M. y R. Cueva R. (CPUN, HAO); Celendin, Marañón River Valley, Chachapoyas–Cajamarca road, 2100 m, 28 May 1984, D.N. Smith & J.M. Cabanillas S. 7271 (MO, US).

13. ***Muhlenbergia microsperma*** (DC.) Kunth, Révis. Gramin. 1:64. 1829.

Fig. 7E–H

Trichochloa microsperma DC., Cat. Pl. Horti Monsp. 151. 1813. *Muhlenbergia microsperma* (DC.) Trin., Gram. Unifl. Sesquifl. 193. 1824, *nom. inval.* Type: Mexico, cultivated at the botanical gardern at Montpellier from seeds collected in Mexico and distributed by the Botanical Garden of Madrid, *M. Sésse & J.M. Mociño s.n.* (holotype: MPU; isotypes: G-00099434 [image!], P!, US fragm. ex P!).

Agrostis microsperma Lag., Gen. Sp. Pl. 2. 1816. Type: Mexico, plants grown at H.R. Matritensis (= Herbario del Real Jardín Botánico de Madrid, see Sutherland 1997) from seeds collected by M. Sessé & J.M. Mociño in Nueva Espania, Oct, 1806, *M. Sessé & J.M. Mociño s.n.* (lectotype, here designated: SEL-H10620 [image!]).

Podosemum debile Kunth, Nov. Gen. Sp. (quarto ed.) 1: 128. 1816. *Trichochloa debilis* (Kunth) Roem. & Schult., Syst. Veg. 2:385. 1817. *Muhlenbergia debilis* (Kunth) Trin., Gram. Unifl. Sesquifl. 193, t. 5, f. 18. 1824. Type: Ecuador, Prov. Pichincha, Quito, *F.W.H.A. Humboldt & A.J.A. Bonpland s.n.* (holotype: P-Bonpl!; isotypes: B-W, P!, US-91924 fragm. ex P-Bonpl!).

Podosemum setosum Kunth, Nov. Gen. Sp. (quarto ed.) 1:129. 1816. *Trichochloa setosa* (Kunth) Roem. & Schult., Syst. Veg. 2:386. 1817. *Agrostis setosa* (Kunth) Spreng., Syst. Veg. 1:262. 1825. *Muhlenbergia setosa* (Kunth) Trin., Gram. Unifl. Sesquifl. 193, t. 5, f. 22. 1824. *Muhlenbergia setosa* (Kunth) Kunth, Révis. Gramin. 1:63. 1829, *isonym*. Type: Mexico, between Gueguetoque and Tula, Aug, *F.W.H.A. Humboldt & A.J.A. Bonpland 4174* (holotype: P-Bonpl!; isotypes: B-W, US-91917 fragm. ex P-Bonpl!).

Muhlenbergia purpurea Nutt., J. Acad. Nat. Sci. Philadelphia, ser. 2, 1:186. 1848. Type: U.S.A., California, Santa Barbara Co., Santa Barbara and Santa Catalina Island, *Gambel s.n.* (holotype: K!).

Muhlenbergia ramosissima Vasey, Bull. Torrey Bot. Club 13(12):231. 1886. Type: Mexico, Chihuahua, SW Chihuahua, Aug–Nov 1885, *E. Palmer 158* (lectotype: NY-00381467! designated by Hitchcock, N. Amer. Fl. 27:441. 1935, but without indicating the specific specimen; Peterson and Annable, Syst. Bot. Monogr. 31:61. 1991, indicated the specific specimen; isolectotypes: LE!, GH-00024043 [image!], MO-2974152!, NY-00381468 [image!], P-00644106!, PH-00018772 [image!], US-995580!, W-19160027660 [image!]).

Description. Caespitose *annuals*, sometimes appearing as short-lived perennials. *Culms* 10–80 cm tall, often geniculate at the base, slender, often striate, much branched near the base, scaberulous below the nodes; *internodes* 1.8–8.6 mm long, mostly scaberulous or smooth. *Leaf sheaths* 2.2–6.6 mm long, commonly shorter than the internodes, glabrous, smooth or scaberulous; *ligules* 1–2 mm long, membranous to hyaline, decurrent, margins often extended, apex truncate to obtuse; *blades* 3–8.5(–10) cm long, 1–2.5 mm wide, flat or loosely involute, scabrous below, strigulose above, often deciduous with age. *Panicles* 6.5–13.5 cm long, 1–6.5 cm wide, open and not densely flowered, often purplish; *primary branches* 1.6–4 cm long, ascending or diverging up to 80° from the rachises, spikelet-bearing to the base; *pedicels* 2–6 mm long, appressed to divaricate, antrorsely scabrous. *Cleistogamous panicles* with 1–3 spikelets present in the axils of the lower sheaths. *Spikelets* 2.5–5.5 mm long; *glumes* 0.4–1.3 mm long, exceeded by the florets, 1-nerved, obtuse, often minutely erose; *lower glumes* 0.4–1 mm long; *upper glumes* 0.6–1.3 mm long; *lemmas* 2.5–3.8(–5.3) mm long, narrowly lanceolate, mostly smooth, scaberulous distally, lower 1/2 of the margins and midveins, the hairs 0.2–0.5 mm long, the callus hairy, apices acuminate, often bidentate, awned, awns 10–30 mm long, straight to flexuous; *paleas* 2.2–4.8 mm long, narrowly lanceolate, acuminate; *anthers* 0.3–1.2 mm long, purplish. *Caryopses* 1.7–2.5 mm long, fusiform, reddish-brown. $2n = 20, 40, 60$.

Distribution. *Muhlenbergia microsperma* occurs in Hawaii, south-western U.S.A., Mexico, Guatemala, Colombia, Venezuela, Ecuador (including the Galapagos Islands), Peru and Bolivia (Peterson and Annable 1991).

Ecology. Rocky slopes, rock outcrops, sandy drainages, cliffs and disturbed roadsides usually in desert scrub vegetation with *Acacia, Aristida adcensionis* L., *Baccharis*, *Bothriochloa*, Bombacaceae, Cactaceae, *Dodonaea viscosa*, *Eragrostis nigricans*, *E. lugens* Nees, *Fucraea*, *Heliotropium*, *Heteropogon contortus* (L.) P. Beauv. ex Roem. & Schult., *Lantana*, *Muhlenbergia rigida*, *Pitcairnia*, *Prosopis*, *Puya*, *Salvia*, *Schinus molle* and *Schizachyrium*; 1150–3500 m.

Comments. *Muhlenbergia microsperma* can sometimes be confused with *M. romaschenkoi* and differs from it by having cleistogamous panicles in the axils of the lower sheaths and shorter, obtuse glumes, 0.4–1.3 mm long (glumes acute to acuminate, 2–2.8 mm long in *M. romaschenkoi*).

In a molecular DNA sequence study, *M. microsperma* forms a strongly supported clade with two other annuals, *M. appressa* C.O. Godding and *M. brandegei* C.G. Reeder, all members of *M.* subg. *Muhlenbergia* (Fig. 1B; Peterson et al. 2010b). These three species produce cleistogamous spikelets in the axils of the lower culm branches, enclosed by a sheath (Peterson and Annable 1991). Cleistogamous spikelets appear to have evolved twice within *Muhlenbergia*, once in *M.* subg. *Muhlenbergia* within the *M. appressa*–*M. brandegei*–*M. microsperma* clade and once in *M.* sect. *Pseudosporobolus* in *M. cuspidata* (Torr. ex Hook.) Rydb. (Morden and Hatch 1984; Peterson et al. 2010b).

Specimens examined. Peru. **Ancash:** at the Rio Yanamayo crossing, 57 km N of San Luis on road towards Pomabamba, 2540 m, 24 Mar 1997, P.M. Peterson & N. Refulio Rodriguez 13896 (US, USM); 68 km from Casma towards Huaraz, 1700 m, 4 Apr 1988, S.A. Renvoize & S. Lægaard 5047 (CPUN, K); Pallasca, divide between Rio Conchucos and Rio Plata, low end of road up to Pampas from Rio Conchucos, above Mollapata crossing of Rio Tablachaca, 8°12'9.1"S, 77°56'20.6"W, 2233 m, 21 Mar 2008, P.M. Peterson & R.J. Soreng 21833 (MO, US, USM). **Apurimac:** Aymaraes, 16 km NW of Chalhuanca, 14°10'16.4"S, 73°19'26.1"W, 2670 m, 14 Mar 2002, P.M. Peterson & N. Refulio Rodriguez 16511 (US, USM); Chincheros, canyon of Rio Pampas, between Ayacucho and Abancay on hwy 7, 7 km S of bridge over Rio Pampas, 13°28'42.1"S, 73°49'32"W, 2049 m, 17 Mar 2007, P.M. Peterson, R.J. Soreng, K. Romaschenko & D. Susanibar Cruz 20535 (MO, US, USM). **Ayacucho:** alrededores de Huanta, 2400 m, 30 Apr 1964, O. Tovar 4829 (US, USM). **Cajamarca:** Cajabamba, WSW of Cajabamba, 14 air km E of Araqueda, 7°39'9.1"S, 78°9'58.9"W, 2242 m, 23 Mar 2008, P.M. Peterson & R.J. Soreng 21855 (US, USM); Cajamarca, Cerro Huacaris, valle de Cajamarca, 1 Jun 1971, I. Sánchez Vega 726, W. Ruiz Vigo & J. Tejada (CPUN); Cajamarca, abajo de San Juan, siguiendo la carretera Cajamarca–Pacasmayo, 1900 m, 18 May 1986, I. Sánchez Vega 4072 (CPUN); Cajamarca, entre San Juan y Magdalena, 1800 m, 15 May 1971, I. Sánchez Vega 657 & W. Ruiz Vigo (CPUN); entre Chancay y Valle de Condebamba, 2600 m, 6 May 1972, I. Sánchez Vega 944, W. Ruiz Vigo & M. Malpica R. (CPUN); Dist. Ichocán, en el Arboretum Ichocán II de CICAFOR, entre la localidad de Chacay y Valle Condebamba, 2450 m, 29 Mar 1981, I. Sánchez Vega 2409, V. Torrel & E. Medina (CPUN); Celendin, Marañón River Valley, Chachapoyas–Cajamarca road, 1900 m, 28 May 1984, D.N. Smith & J. Cabanillas 7254 (MO, US); Chota, Dist. Cochabamba, a 1km sobre la carretera Cochabamba–Cutervo, 1720 m, 15 Jun 1980, I. Sánchez Vega 2288 (CPUN). **Cusco:** Anta, Sisal, Limatambo, 2300 m, 15 Mar 1963, C. Vargas C. 14327 (US, USM); Anta, Sisal–Cunyaee, 2100 m, 14 May 1965, C. Vargas C. 16316 (US, USM). **Huancavelica:** Salcabamba–Colcabamba, camino a Pampas, 2000 m, 22 Apr 1962, O. Tovar 3834 (US, USM); Tayacaja, alrededores de Mayoc, 2400 m, 9 Apr 1966, O. Tovar 5589 (US, USM). **Huánuco:** Huánuco, W side of canyon of Rio Huallaga, S of Ambo, 7 km on hwy 3 towards Cerro de Pasco, 10°11'49"S, 76°9'54"W, 2345 m, 6 Mar 2007, P.M. Peterson, R.J. Soreng & K. Romaschenko 20326 (US, USM); Huánuco, 2125 M, 25 Apr 1923, J.F. Macbride 3514 (F, US); 5 Apr 1923, J.F. Macbride 3217 (F, US). **La Libertad:** Bolivar, 4.6 air km NW of Longotea, SE of San Vicente on road from Balsas to Longotea, 7°0'38"S, 77°54'15.2"W, 2058 m, 31 Mar 2008, P.M. Peterson, R.J. Soreng & J. Montoya Quino 21970 (MO, US, USM); Otuzco, Quirrpe–Membrillar, 1150 m, 7 Dec 1952, A. López Miranda 927 (US); Santiago de Chuco, 22 km E of Huamachuco on road towards Sarin above Rio Chusgon, 2500 m, 29 Mar 1997, P.M. Peterson & N. Refulio Rodriguez 13973 (US, USM). **Lima:** Canta, 2 km SE of San Jose Canta, 11°30'2"S, 76°40'23.4"W, 2232 m, 27 Mar 2004, P.M. Peterson & N. Refulio Rodriguez 17985 (MO, US, USM); Huarochiri, Matucana, 2430 m, 12 Apr 1922, J.F. Macbride & Featherstone 392 (F, US); Huarochiri, km 70 carretera Lima–Oroya, 1800 m, 15 May 1963, R. Ferreyra 14892 (US, USM); km 68, cerca Surco, entre Chosica y Matucana, 1400 m, 27 Mar 1955, R. Ferreyra 10498 (US, USM); km 72 de la carretera Lima–Oroya, cerca de Surro, 1800 m, 14 May 1948, R. Ferreyra 3485 (MOL, US, USM); Prov. Lima, above Paya, E. Asplund 10825 (NY). **Piura:** Huancabamba, 10 km N of Sondor and 3 km S of Huancabamba, 1860 m, 1 Apr 2000, P.M. Peterson & N. Refulio Rodriguez 15167 (CPUN, MO, US, USM). **Tacna:** Zarata, Sitiqui, 3500 m, 7 Apr 1959, C. Vargas C. 12588 (US, USM).

14. *Muhlenbergia monandra* Alegría & Rúgolo, Darwiniana 39(1–2): 20, 22, f. 1–3.
Fig. 10A–M

Type. Peru, Depto. Lima, Prov. Canta, 5 km arriba de San José en camino a Huamantanga, frente a Apio, 2700 m, 21 May 1999, *A. Granda Paucar & J.J. Alegría Olivera 2230* (holotype: MOL; isotypes: BRIT-23827 [image!], SI! [SI-016006 image!], TEX, US-3376226! [US-00901642 image!], USM-000747 [image!]).

Description. Tufted *annuals*. *Culms* 4–25 cm tall, 0.3–0.7 mm in diameter near base, erect to decumbent, branching below, glabrous, 2 or 3 glabrous nodes, scaberulous below the nodes; *internodes* 0.5–9 cm long. *Leaf sheaths* 0.5–4.7 cm long, usually shorter than the internodes, compressed, mostly glabrous, scaberulous near the summit, margins scarious; *ligules* 1–3 mm long, hyaline, decurrent, apex truncate to obtuse, lacinate to irregularly dentate; *blades* (0.5–)1–8 cm long, 0.7–3.6 mm wide, flat or loosely folded, finely pilose above and scabrous below, margins scabrous, apex mostly acuminate, rarely acute. *Panicles* (0.5–)1–7 cm long, 2–9 mm wide, tightly spiciform, often interrupted below, elliptic to oblong, terminal and axillary, often partially included in the sheath below; *primary branches* 4–15 mm long, tightly ascending-appressed, verticillate below with 5–10 per node, scabrous; *pedicles* 0.1–1.2 mm long, shorter than the spikelets, scabrous. *Spikelets* 3.4–4.6 mm long, 1-flowered, tightly carinate, cleistogamous; *glumes* 3.5–4.7 mm long, longer than the floret, nearly equal in length, membranous, linear lanceolate, 1-veined, scaberulous along the midvein, apex acuminate, mucronate, the mucro 0.2–0.7 mm long; *lemmas* 1.5–2.1 mm long, hyaline to membranous, ovate, 3-veined, the lateral veins faint, mottled with irregular plumbeous areas, sparingly appressed pilose, the hairs 0.2–0.4 mm long, apex truncate to obtuse, subapically awned, the awns 1.2–5 mm long, straight; *callus* pilose; *paleas* 1.4–2 mm long, hyaline, ovate, sparingly pilose, apex truncate, the veins extending as mucros up to 0.2 mm long; *lodicules* 0.1–0.2 mm long, truncate; *stamen* 1, anthers 0.3–0.6 mm long, whitish to yellow. *Caryopses* 1–1.6 mm long, ovoid, laterally flattened, light brown.

Distribution. A Peruvian endemic known only from near San Jose de Canta, Peru.

Ecology. This species occurs on gravelly slopes among xerophytic scrub vegetation with *Bouteloua simplex*, *Eragrostis mexicana* subsp. *virescens* (J. Presl) S.D. Koch & Sánchez Vega, *Muhlenbergia bryophilus*, *Urochloa* sp., *Veronica* sp. and *Festuca myruos* between 2700 and 2800 m.

Comments. Molecular DNA sequence analysis indicates *Muhlenbergia monandra* is an unsupported sister to the *M. atacamensis*–*M. decumbens*–*M. ligulata*–*M. subbiflora* clade in *M.* subg. *Pseudosporobolus* (Fig. 1B).

Specimens examined. Peru. **Lima:** Prov. Canta, 8 km SW of San Jose Canta towards Huamantango, 11°31'10.0"S, 76°42'16.3"W, 2770 m, 28 Mar 2004, P.M. Peterson & N. Refulio Rodriguez 17990 (MO, US, USM); entre Huamantanga y Puruchuco, 2800 m, 1 May 1994, J.J. Alegría Olivera 739 (MOL, SI).

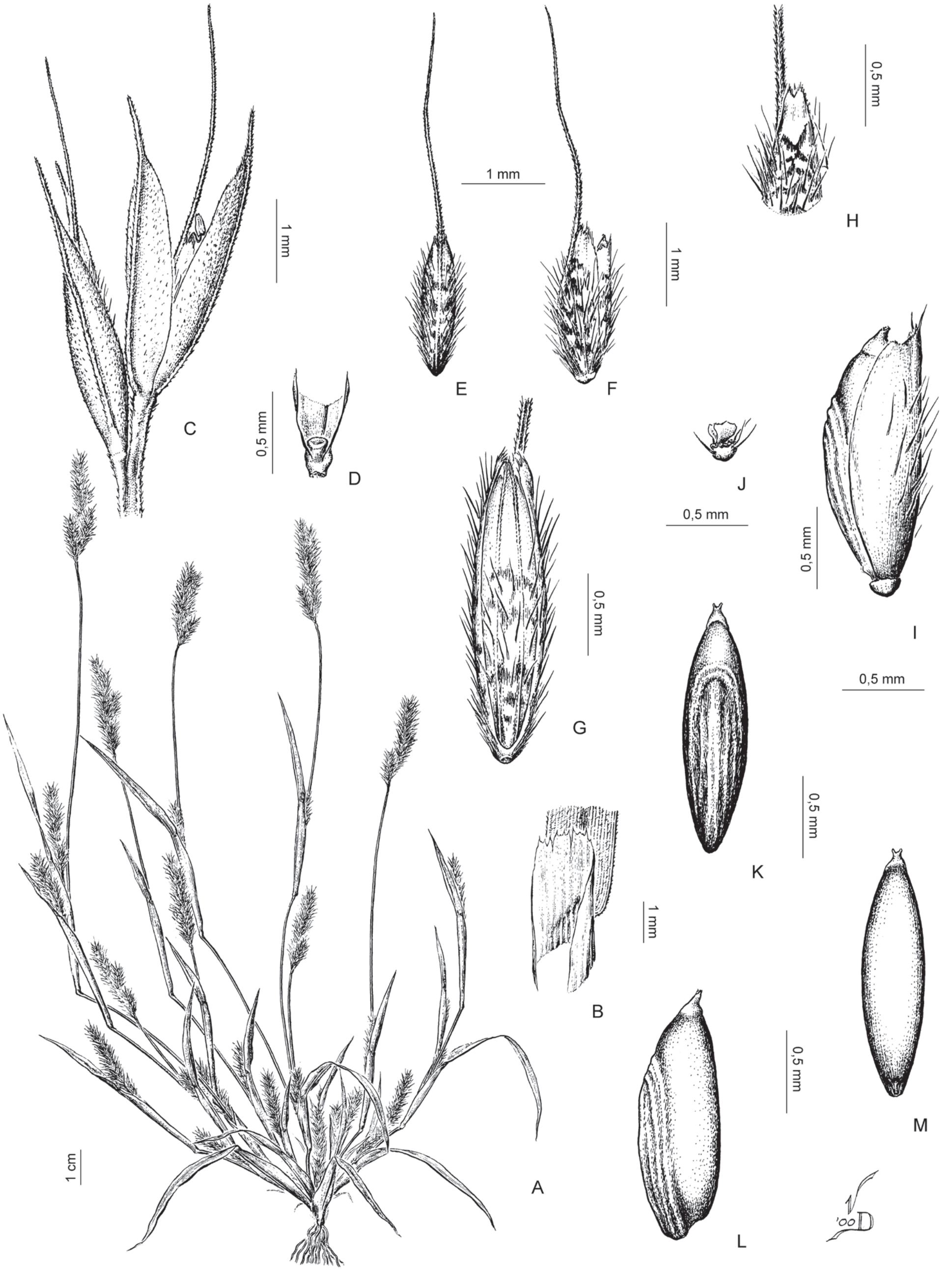

Figure 10. A–M *Muhlenbergia monandra* Alegría & Rúgolo **A** habit **B** ligule **C** two spikelets **D** glume base and rachilla **E** lemma, dorsal view **F** floret, side view **G** floret, ventral view **H** apex of lemma with two small teeth **I** palea and caryopsis, lateral view **J** lodícules **K** caryopsis, dorsal view **L** caryopsis, lateral view **M** caryopsis, ventral view. Drawings from the holotype collection *Granda Paucar & Alegría Olivera 2230.*

15. ***Muhlenbergia peruviana*** **(P. Beauv.) Steud., Nomencl. Bot. (ed. 2) 1:41. 1840.** Fig. 11A–D

Clomena peruviana P. Beauv., Ess. Agrostogr. 28, t. 7, f. 10; t. 3, f. 20. 1812. *Agrostis peruviana* (P. Beauv.) Spreng., Syst. Veg. 1:262. 1825. Type: Peru, *M. Thibaut s.n.* (holotype: P!; isotype: E-00373717 [image!]).

Clomena peruviana var. *pulvinata* Nees, Gramineae 12–13. 1841. *Muhlenbergia peruviana* var. *pulvinata* (Nees) Nees & E. Mey. ex Kuntze, Revis. Gen. Pl. 3(3):357. 1898. Type: Peru, Lago Titicaca, Apr, *J.F.J. Meyen s.n.* (holotype: B; isotype: US-3376134 fragm. ex B!).

Muhlenbergia nana Benth., Pl. Hartw. 262. 1846. Type: Ecuador, Mt. Cotopaxi, 1843, *Hartweg 1458* (holotype: K!; isotypes: BAA-1629!, K!, LE!, P!, US-91916 fragm. ex P!, US-995896 fragm. ex P-STEUD & fragm. ex BR!).

Muhlenbergia pusilla Steud., Syn. Pl. Glumac. 1:177. 1854. Type: Mexico, México, Valley of Toluca, Oct. 1827, J.*L. Berlandier 1141* (holotype: P!; isotypes: BAA-1635!, K!, MO-2974185!, P!, US-1084517!, US-2561239!, US-91910 fragm. ex P!).

Epicampes bourgeaei E. Fourn., Mexic. Pl. 2: 88. 1886. Type: Mexico, Veracruz, Escamala, Refrou D'Orizaba, 26 Aug 1866, *E. Bourgeau 2973* (holotype: P!; isotype: US-A0865984 fragm ex P!).

Muhlenbergia bourgeaei E. Fourn., Mexic. Pl. 2:86. 1886. *Epicampes bourgeaei* (E. Fourn.) M.E. Jones, Contr. W. Bot. 14:7. 1912, *nom. illeg. hom.*Type: Mexico, Valle de Mexico, Desierto Viejo, 3 Nov 1865, *M. Bourgeau 1309* (lectotype: P! designated by Peterson and Annable, Syst. Bot. Monogr. 31:73. 1991; isotype: US-87243 fragm. ex P!).

Muhlenbergia pulcherrima Scribn. ex Beal, Grass. N. Amer. 2:240. 1896. Type: Mexico, Chihuahua: Sierra Madres, dry ledges of porphyry, 30 Sep 1887, *C.G. Pringle 1416* (holotype: MSC!; isotypes MO-3727978!, NY!, US-995494!, VT!).

Muhlenbergia peruviana var. *elatior* Kuntze, Revis. Gen. Pl. 3(2): 357. 1898. Type: Bolivia, Tunarigebirge, 3000 m, May 1892, *Kuntze s.n.* (lectotype: NY! designated by Peterson and Annable, Syst. Bot. Monogr. 31:73. 1991: isotype: fragm. & photo US!).

Muhlenbergia peruviana var. *subcaespitosa* Kuntze, Revis. Gen. Pl. 3(3):357. 1898. Type: Bolivia, Tunari Mts., 4600 m, 4 May 1892, *Kuntze s.n.* (lectotype: NY! designated by Peterson and Annable, Syst. Bot. Monogr. 31:73. 1991).

Muhlenbergia peruviana fo. *versicolor* Kuntze, Revis. Gen. Pl. 3(3):357. 1898. Type: Bolivia, Tunarigebirge, 3000 m, May 1892, *Kuntze s.n.* (lectotype: NY! designated by Peterson and Annable, Syst. Bot. Monogr. 31:73. 1991; isotype: US fragm. ex NY!).

Muhlenbergia peruviana fo. *viridis* Kuntze, Revis. Gen. Pl. 3(3):357. 1898. Type: Bolivia, Puna, 4000 m, 11 Mar 1892, *Kuntze s.n.* (lectotype: NY! designated by Peterson and Annable, Syst. Bot. Monogr. 31:73. 1991).

Muhlenbergia herzogiana Henrard, Meded. Rijks-Herb. 40:58. 1921. Type: Bolivia, Cordillera de Santa Bonita, Jun 1911, *T. Herzog 2226* (holotype: L!; isotypes: US-87248 fragm. ex L!, US-1161342!, W-1926-23724!).

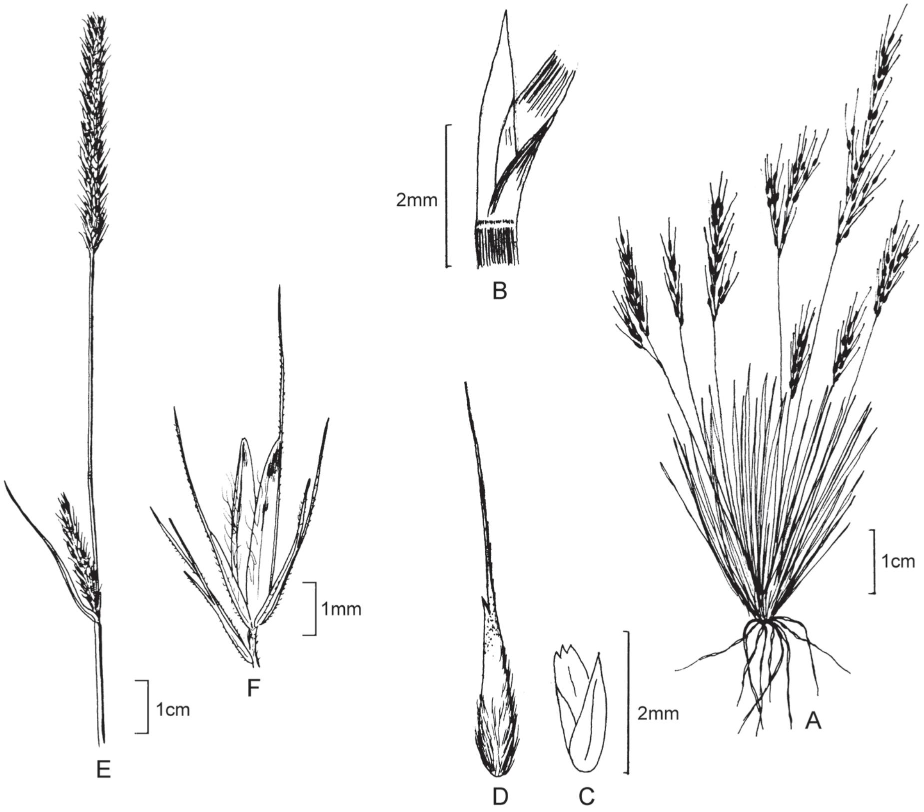

Figure 11. A–D *Muhlenbergia peruviana* (P. Beauv.) Steud **A** habit **B** ligule **C** glumes **D** floret **E, F** *Muhlenbergia phalaroides* (Kunth) P.M. Peterson **E** panicle **F** spikelet. Drawings **A–D** from Peterson and Annable (1991) drawn from *P.M. Peterson & C.R. Annable 4739* (WS) **E, F** from Giraldo-Cañas and Peterson (2009) drawn from *S. Lægaard 71419* (AAU).

Description. Tufted *annuals*. *Culms* 3–27 cm tall, erect, glabrous. *Leaf sheaths* usually longer than the internodes, smooth or scabridulous; *ligules* 1.5–3 mm long, membranous, acute; *blades* 1–5 cm long, 0.6–1.5 mm wide, flat to involute, smooth or scabridulous abaxially, sometimes shortly pubescent adaxially. *Panicles* 2–8 cm long, 0.3–3.4 cm wide, contracted or open; *primary* branches 1–5 cm long, diverging up to 80° from the rachises; *pedicels* 0.4–5 mm long, smooth or scabrous. *Spikelets* 1.4 4.2 mm long, 1-flowered; *glumes* smooth or scabridulous; *lower glumes* 0.8–2.8 mm long, narrow to broadly lanceolate, 1-veined, acute, often awn-tipped; *upper glumes* 0.9–3 mm long, wider than the lower glumes, lanceolate, 3 (2)-veined, truncate to acute, 2- or 3-toothed; *lemmas* 1.4–4.2 mm long, ovate, widest near the base, purplish mottled with dark green areas, hairy on the calluses and lower 2/3 of the lemma bodies, hairs to 0.5 mm long, apices acuminate, usually bifid and awned from between the teeth, teeth to 0.5 mm long, awns 3–10 mm long, flexuous, purplish; *paleas* 1.3–3.8 mm, narrowly lanceolate, acuminate to subacute; *anthers* 0.5–1 mm long, purplish to yellowish. *Caryopses* 1–1.6 mm long, fusiform, brownish. $2n = 30$.

Distribution. *Muhlenbergia peruviana* occurs in Arizona and New Mexico, U.S.A, throughout Mexico to Guatemala and then in Argentina, Bolivia, Chile, Ecuador and Peru (Peterson and Annable 1991).

Ecology. Grassy flats, open gravelly flats, rock outcrops, sandy washes, gravelly drainages, wet or dry meadows, canyons, gravelly or sandy slopes, valleys, shores along lakes, open ridgetops and disturbed road cuts associated with *Aciachne pulvinata* Benth., *Anatherostipa*, *Berberis*, *Calamagrostis* spp., *Colletia spinosissima*, *Ephedra*, *Festuca orthophylla* Pilg., *Festuca* spp., *Jarava*, *Juncus*, *Lepidophyllum*, *Luzula*, *Margyricarpus*, *Monnina*, *Muhlenbergia* spp., *Nassella*, *Plantago*, *Poa* spp., *Polylepis*, *Puya*, *Pycnophyllum*, *Salvia oppositiflora* Ruiz & Pav., *Stevia* and *Tagetes*; 3000–4900 m.

Comments. As treated here, *Muhlenbergia peruviana* includes (as synonyms) what was sometimes identified as *M. pulcherrima* Scribn. ex Beal (south-western U.S.A. and northern Mexico) and *M. pusilla* Steud. (central Mexico to Guatemala). There are many more morphological forms than just these and since the only chromosome count of this species suggests triploidy ($2n = 3\times = 30$), perhaps this species is apomictic (Reeder 1968). We believe apomixis is occurring in this species but it it not obligate and that gene flow takes place sporadically to form intermediates maintained by asexual seed formation (Peterson and Annable 1991).

In a molecular DNA sequence analysis, *Muhlenbergia peruviana* is sister to *M. crispiseta* Hitchc., another annual known only from Texas and north-central Mexico and this pair is embedded in the strongly supported *M.* subg. *Clomena* clade (Peterson et al. 2010b; Fig. 1B). Members of *M.* subg. *Clomena* possess spikelets with upper glumes that are 3-veined and often 3-toothed and individuals with a densely caespitose habit (Peterson et al. 2010b). *Muhlenbergia peruviana* can be separated from *M. crispiseta* in having irregularly flexuous, purplish awns (versus sinuous-wavy, crisped and curled, olive-green awns in *M. crispiseta*) and narrow, gradually acuminate lemmas (versus lemmas that are plump near middle) [Peterson and Annable 1991]. In our current DNA-derived phylogeny, *M. crispiseta* falls within the *M. peruviana* clade (Fig. 1B). However, *rps3*, the single marker we have for *M. crispiseta,* is not variable enough to distinguish these two species that are easily separated morphologically. In the future, we hope to clarify this with a full set of markers for *M. crispiseta*.

Specimens examined. Peru. **Amazonas:** Prov. Chachapoyas, Cerros Calla Calla, 3100 m, 19 Jun 1964, D.C. Hutchison & J.K. Wright 5756 (LIL, MO). **Ancash:** Cordillera Blanca, 4 km north of Recuay, 3400 m, 6 Apr 1988, S.A. Renvoize & S. Lægaard 5101 (CPUN, K); Cordillera Negra, 3 km N of Punta Callán, W of Huaraz, 4400 m, 7 Apr 1988, S.A. Renvoize & S. Lægaard 5171 (CPUN, K); Cordillera Negra, 30 km from Huaraz towards Casma, Punta Callán, 4200 m, 7 April 1988, S.A. Renvoize & S. Lægaard 5166 (CPUN, K); Pariarracra, Pampa de Lampas, 4160 m, 2 May 1952, E. Cerrate 1465 (MOL); Prov. Bolognesi, Capillapunta, 3350 m, 14 Apr 1949, R. Ferreyra 5716 (MOL, USM); Prov. Bolognesi, cerros al E de Chiquián, 3500 m, 10 May 1950, R. Ferreyra 7345 (US, USM); Prov. Bolognesi, Matarragra, cerro al NO de

Chiquián, 3560 m, 8 Apr 1949, R. Ferreyra 5633 (US, USM); Prov. Bolognesi, Shincush, arriba de Chiquián, 4000 m, 19 Apr 1949, R. Ferreyra 5624 (US, USM); Carhuaz, Cordillera Negra, E slope, ca. 22 km SW of Shupluy, 09°17'19.7"S, 77°44'39.3"W, 3770 m, 13 Mar 2008, P.M. Peterson, R.J. Soreng, M.I. La Torre & J.V. Rojas Fox 21655 (US, USM); Recuay, Cordillera Blanca, 37 km E of Raquia on Route 02-014 on road towards Huarez, 3900 m, 20 Mar 1997, P.M. Peterson & N. Refulio Rodriguez 13818 (MO, US, USM); Recuay, Cordillera Negra W slope N of Quebrada Parin, 23 km NE of Cotaparaco on road to pass above Lago Ututo and Utcuyacu, 09°55'10.7"S, 77°32'02.2"W, 4216 m, 10 Mar 2008, P.M. Peterson, R.J. Soreng, M.I La Torre & J.V. Rojas Fox 21564 (US, USM); Recuay, Cordillera Negra, en cima de Caraz, 4300 m, A. Weberbauer 3098 (MOL); Huaraz, Huascarán National Park, quebrada Llaca, north side of valley, 9°27'S, 77°27'W, 4350 m, 25 May 1986, D.N. Smith 12428 (CPUN, MO); Recuay, quebrada Huanca, 9°55'S, 77°23'W, 3950 m, 2 Jul 1985, D.N. Smith & M. Buddensiek 10959 (CPUN, LPB, MO); Recuay, Huascarán National Park, mouth of quebrada Quenua Ragra, 10°2'S, 77°15'W, 4200 m, 10 May 1985, D.N. Smith, R. Valencia & A. Gonzales 10624 (CPUN, MO); Huari, Huascarán National Park, south side of quebrada Carhuazcancha, 9°28'S, 77°15'W, 3790 m, 6 May 1986, D.N. Smith, R. Valencia, A. Gonzales & M. Buddensiek 12294 (CPUN, MO); Recuay, 2 km SW of Conococha on Ruta 02-014, 10°8'18.2"S, 77°18'5.4"W, 4107 m, 21 Mar 2004, P.M. Peterson, N. Refulio Rodriguez, A. Cano, M.I. La Torre & I. Salinas 17903 (US, USM); Recuay, 3 km E of Conococha, 10°6'55.5"S, 77°16'20.2"W, 4050 m, 24 Mar 2004, P.M. Peterson & N. Refulio Rodriguez 17939 (MO, US, USM); Recuay. Huascarán National Park, Sector Querococha, above guardstation, 9°44'S, 77°20'W, 3875 m, 5 Jul 1985, D.N. Smith & M. Buddensiek 11045 (CPUN, LPB, MO); Yungay, Huascarán National Park, Llanganuco sector, Maria Josefa trail between Chinancocha and Pucuyacu, 9°5'S, 77°39'W, 3700–3850 m, 7 May 1985, D.N. Smith 10548 (CPUN, MO). **Apurimac:** Aymaraes, 24 km NE of Chalhuanca on road towards Yanaca, 14°15'26.4"S, 73°12'18.8"W, 4260 m, 13 Mar 2002, P.M. Peterson & N. Refulio Rodriguez 16506 (US, USM). **Arequipa:** Arequipa,10 km W of Patahuasi on road towards Arequipa, 16°4'37.3"S, 71°29'49.8"W, 4100 m, 11 Apr 2004, P.M. Peterson & N. Refulio Rodriguez 18243 (MO, US, USM); Arequipa, Jesus–Chiqüata, 2900 m, Jun 1977, C. Vargas C. s.n. (LIL); Arequipa, cerca a Chiquata, 3100 m, 31 Mar 1949, C. Vargas C. 8092 (CUZ, US); Caylloma, 10 km SE of Callalli on road towards Condoroma, 15°29'26"S, 71°23'5.9"W, 4340 m, 12 Apr 2004, P.M. Peterson & N. Refulio Rodriguez 18270 (MO, US, USM); Prov. Caylloma, Pampa Cañahuas. "Llapa pasto", 4200 m, 30 May 2001, M. Rodríguez Diaz 1126 (USM). **Ayacucho:** Marcahrasi, arriba de Puquio, 3400 m, 24 Apr 1950, R. Ferreyra 7215 (MOL, US, 8USM); Huamanga, S of Ayacucho ca. 23 km on Hwy 3 toward Abancay, 13°16'21.5"S, 74°13'46.8"W, 3575 m, 15 Mar 2007, P.M. Peterson, R.J. Soreng, K. Romashchenko & D. Susanibar Cruz 20497 (US, USM); Huamanga, S of Ayacucho ca. 27 km on Hwy 3 toward Abancay, 13°17'9.8"S, 74°13'41.9"W, 3684 m, 16 Mar 2007, P.M. Peterson, R.J. Soreng, K. Romashchenko & D. Susanibar Cruz 20508 (US, USM); Huanca Sancos, 16 km NW of Putajasa on road towards Huanca Sancos, 14°1'42.5"S, 74°16'16.6"W, 3900 m, 25 Feb 2002, P.M. Peterson, A. Cano, M.I. La Torre, A. Ramirez & D. Susanibar Cruz 16254 (US, USM); Lucanas, 13 km E of Puquio at km 172 mark, 14°41'18.5"S, 74°4'26.8"W, 3730 m, 8 Apr 2004, P.M. Peterson & N. Refulio Rodriguez 18213 (MO, US, USM); Lucanas, 25 km NE of Villatambo on road towards Lucanas at Reserva "Pampa Galeras", 14°40'46.2"S, 74°23'59.2"W, 3805 m, 8 Apr 2004, P.M. Peterson & N. Refulio Rodriguez 18181 (MO, US, USM); Pampalca, between Huanta and Rio Apurimac, 3200 m, 4 May 1929, E.P. Killip & A.C. Smith 22216 (US). **Cajamarca:** Cajamarca, S of Cajamarca ca. 9 air km, 7°14'8.1"S, 78°19'17.9"W, 3270 m, 27 Mar 2008, P.M. Peterson, R.J. Soreng, I. Sánchez Vega & J. Montoya Quino 21885 (US, USM); Cajamarca, Cerro Piedras Gachas, entre Yanacocha y Llaucán, 3900 m, 23 Apr 1994, I. Sánchez Vega 6997 & M. Cabanillas S. (CPUN); Cajamarca, entre Cajamarca y Cumbe Mayo, Fundo de la Universidad, 3450 m, 22 May 1971, I. Sánchez Vega 685 & M. Vilhena (CPUN); Cajamarca, entre Cajamarca y Cumbe Mayo, km 14, en el Arboretum Cumbe Mayo CICAFOR, 3400 m, 18 Apr 1981, I. Sánchez Vega 2466, V. Torrel & E. Medina (CPUN); Cajamarca, Dist. Cajamarca. Sais Atahualpa de Porcón en el Arboretum de CICAFOR, 3400 m, 16 May 1981, I. Sánchez Vega 2524, V. Torrel & E. Medina (CPUN); Cajamarca, Dist. Cajamarca, Cerro Gavilán, 3100 m, 26 Jun 1966, I. Sánchez Vega 238 (CPUN); Cajamarca, Dist. Cajamarca, Hacienda Porcón, a 35 km de Cajamarca, 3400 m, 31 May 1969, I. Sánchez Vega 401 (CPUN); Cajamarca, Dist. Cajamarca, Cerro Minas, Granja Porcón, 35 km al N de Cajamarca, 3900 m, 22 Jun 1994, I. Sánchez Vega 7293 & G. Bazan H. (CPUN); Cajamarca. Dist. Cajamarca, Tamiacocha, Cerro Negro, Gavilán, distancia 5 km en línea recta, queda a la vertiente occidental, 7°15'S, 78°28'W, 3558 m, 26 May 2001, I. Sánchez Vega 10618 (CPUN); Cajamarca, ladera que coverge a la Colpa, 2900 m, 22 Apr 1975, I. Sánchez Vega 1419, P. Brandelard, J. Sanabria & W. Ruiz Vigo (CPUN); Cajamarca, Corisorgona, al Norte de la ciudad de Cajamarca, carretera a Chamis, 3050 m, 25 Apr 1991, I. Sánchez Vega 5585 & A. Briones (CPUN); San Miguel, 61 km N of Cajamarca on hwy 3N towards Bambamarca, 3640 m, 16 Mar 2000, P.M. Peterson & N. Refulio Rodriguez 14913 (CPUN, MO, US, USM). **Cusco:** Prov. Calea, Uchumuca–Pisae, Apr 1994, F. Marin 386 (LIL); Calca, 20 km N of Calca on road towards Lares, 13°13'52.9"S, 71°54'26.5"W, 4060 m, 16 Mar 2002, P.M. Peterson & N. Refulio Rodriguez 16546 (US, USM); Prov. Canchis, temple of Viracocha near Tinta, 3500 m, 15 Apr 1913, O.F. Cook & G.B. Gilbert 211 (US); Prov. Cusco, Ruinas Sacsahramán, 3500 m, 6 May 1983, S.G. Beck 8366 (LPB, MO); Prov. Cusco, Tambomachay, 3700 m, Apr 1949, F. Marin 1420 (US, LIL); Prov. Cusco, Cusco–Huancar, 3500 m, 18 Jun 1982, Gutte and Miller 9424 (USM); Prov. Espinar, alrrededores de Youri, 3900 m, 26 Mar 1956, C. Vargas C. 11210, 11211 (CUZ, US); Prov. Espinar, Hacienda C'uyo, 4200 m, 24 Mar 1956, C. Vargas C. 11180 (CUZ, US); Prov. Espinar, Hacienda C'achachi, 4200 m, 20 Mar 1956, C. Vargas C. 11151, 11163 (CUZ, US); Prov. Paucartambo, 1936, J. Soukup s.n. (US); Prov. Paucartambo, Acjanacu, 3600 m, 6 Jul 1948, C. Vargas C. 7299 (CUZ, US); Prov. Paucartambo, Yanamayo, 9 Jul 1946, C. Vargas C. 609 (CUZ, US); Quispicanchi, 23 km up new hwy 28 from Urcos to Ccatcca (Catsa), ESE of Cusco ca. 45 air km, 13°39'39"S, 71°35'29.7"W, 4080 m, 19 Mar 2007, P.M. Peterson, R.J. Soreng & K. Romashchenko 20563 (MO, US, USM); Prov. Urubamba, quebrada Pumahuanca, 3200 m, 31 Dec 1962, H.H. Iltis & C.M. Iltis 1014 (LIL). **Huancavelica:** Castrovirreyna, 4 km S of Choclococha and 8 km N of Santa Ines, 13°10'44"S, 75°5'15.3"W, 4615 m, 5 Apr 2004, P.M. Peterson & N. Refulio Rodriguez 18147 (MO, US, USM); Huancavelica, Huancavelica, 4000 m, 8 Apr 1961, O. Tovar 3171 (MO, USM); Huancavelica, 56 km S of Izacuchaca on road towards Huancavelica, 4020 m, 10 Apr 1997, P.M. Peterson & O. Tovar 14160 (MO, US, USM); Huancavelica, 12 km S of Huancavelica on road towards Santa Barbara, 4120 m, 11 Apr 1997, P.M. Peterson & O. Tovar 14189 (MO, US, USM); Huancavelica, Sachahuajta, a 6 km de Conaica, 3600 m, 3 Apr 1952, O. Tovar 944 (US, USM); Huancavelica, Huando, 3600 m, 6 Apr 1953, O. Tovar 1277 (US, USM); Huancavelica, Canyon of Rio Ichu, SW of Huancavelica ca. 5 km on hwy 3 to Santa Ines and Ayacucho, 12°48'48.2"S, 75°3'24.5"W, 4894 m, 14 Mar 2007, P.M. Peterson, R.J. Soreng, K. Romashchenko & D. Susanibar Cruz 20464 (MO, US, USM); Huaytara, along Rio Pampas, along hwy 3 (old 24), 12 km NW of jct with new hwy 24 and 18 km SE of Santa Ines, SE of Pilpichaca, 13°19'24.2"S, 75°0'56.6"W, 4164 m, 13 Mar 2007, P.M. Peterson, R.J. Soreng, K. Romashchenko & D. Susanibar Cruz 20438 (US, USM); Huaytara, 7 km W of Pilpichaca on road towards Huancavelica. 13°18'46.5"S, 75°2'7"W, 4250 m, 5 Apr 2004, P.M. Peterson & N. Refulio Rodriguez 18157 (MO, US, USM); Tayacaja, just above Chuquitambo, 4 km SW of Pazos, 3975 m, 9 Apr 1997, P.M. Peterson & O. Tovar 14150 (MO, US, USM); Tayacaja, arriba de Hacienda Tocos, entre Colcabamba y Paucarbamba, 3700 m, 20 Apr 1954, O. Tovar 1961, 2013 (US, USM); Tayacaja, Hacienda Huari, 3700 m, 10 Aug 1949, O. Velarde Nuñez 2038 (US, USM). **Huanuco:** 18 mi SE of Huanuco, 31 May 1922, J.F. Macbride & W. Featherstone 2114 (F, US); **Junín:** Prov. Cerro, Goyllarisquisca, 4100 m, 22 Jun 1940, E. Asplund (US); Prov. Huancayo, Acopalca, 3800 m, 20 Jul 1943, J. Infantes Vera 412 (LIL); Prov. Concepción, Cani, 7 mi NE of Mito, 2800 m, 16 Apr 1923, J.F. Macbride 3401 (F, US); Prov. Huancayo, Laive, 3600 m, 15 Mar 1947, J. Infantes Vera 920 (LIL); Prov. Jaupa, 6 km a Concepción, quebrada de Iscos, 3300 m, Mar 1947, C. Ochoa 81 (LIL, MOL, USM); Prov. Yauli, La Oroya, 3950 m, 27 May 1922, J.F. Macbride & W. Featherstone 984 (F, US); Prov. Yauli, Yauli, 4450 m, 25 May 1922, J.F. Macbride & W. Featherstone 916 (F, US). **La Libertad:** Prov. Otuzco, Purrupumpa, 3585 m, 15 May 1991, S. Leiva, P. Leiva & E. Zavaleta 273 (HAO); Prov. Stgo. Chuco, Cerro La Botica, arriba de Cachicadán, 3050 m, 10 Jun 2001, A. Sagastegui, S. Leiva & M. Zapata 16685 (HAO). **Lambayeque:** Ferrenafe, 3300 m, 29 Jun 1996, S. Llatas Quiroz 4121 (MO). **Lima:** arriba de Sucro, 3000 m, 1 May 1948, R. Ferreyra 3445 (MOL, US, USM); Prov. Huarochiri, Matucana, 13 Apr 1922, J.F. Macbride & W. Featherstone 450 (F, US). **Moquegua:** Carumas, 3200 m, 21 Feb 1925, A. Weberbauer 7295 (US); 1 km S of Puentes Vizcachas, 32 km NE of Humajalso and 18 km S of Titiri, 16°37'14.8"S, 70°24'50.2"W, 4310 m, 18 Apr 2004, P.M. Peterson & N. Refulio Rodriguez 18317 (MO, US, USM). **Pasco:** Pasco, 4 km NE of Huayllay on road towards Canchacucho at "Bosque de Piedras", 10°58'20.8"S, 76°19'18"W, 4160 m, 31 Mar 2004, P.M. Peterson & N. Refulio Rodriguez 18068 (MO, US, USM). **Piura:** Huancabamba, abajo del Tabo, 3 Jul 1961, C. Acleto 313 (USM). **Puno:** Araranca, 4100 m, 21 Apr 1925, F.W. Pennell 13466 (US); W of Llave, 3900 m, 21 Jul 1946, O.P. Pearson & A. Pearson 8 (US); Prov. Carabaya, Ockopuno, 4800 m, Apr 1949, C. Vargas C. 8142 (CUZ, MO, US); Cerro Orco Pata, 4000 m, 17 Jan 1964, R.A. Arevalo 27 (LIL); Prov. Carabaya, Fauchinta Allinccapac, 4600 m, 1 Apr 1948, C. Vargas C. 7157 (CUZ, US); Provincia Lampa, distrito Pucará, inmediaciones del pueblo de Chijnaya, en sustratos arenoso-rocosos en los bordes de la carretera, 4000 m, 14 Jul 2013, D. Giraldo-Cañas 5532 (COL); Pucará, lugar Chijnaya, 3990 m, Mar 1964, A. Vera 108 (COL); Hacienda Iriapata, estación Pucará, 3990 m, Oct 1963, A. Vera s.n. (COL); Chuquibambilla, 3900 m, 19 Apr 1925, F.W. Pennell 13375-1 (US); Chucuito, 2 km S of Huacullani, 4000 m, 6 Mar 1999, P.M. Peterson, N. Refulio Rodriguez & F. Salvador Perez 14660 (MO, US, USM); Chucuito, 5 km S of Huacullani on road towards Kelluyo, 4250 m, 6 Mar 1999, P.M. Peterson, N. Refulio Rodriguez & F. Salvador Perez 14679 (MO, US, USM); Chucuito, 27 km NW of San Jose Ancomarca, 4280 m, 8 Mar 1999, P.M. Peterson, N. Refulio Rodriguez & F. Salvador Perez 14702 (MO, US, USM); El Collao, 34 km E of El Cruce and 24 km W of Mazo Cruz, 4180 m, 2 Mar 1999, P.M. Peterson, N. Refulio Rodriguez & F. Salvador Perez 14595 (MO, US, USM); Lampa, NW end of Laguna Lagunillas, 20 air km W of Santa Lucia, 74 air km WSW of Juliaca, 15°41'1.7"S, 70°48'5.4"W, 4185 m, 31 Mar 2007, P.M. Peterson, R.J. Soreng, K. Romashchenko & M.S. Gonzalez Elizondo 20738 (US, USM); Prov. Lampa, Pucará, A. Weberbauer 415 (US); Melgar, ca. 7 km WNW of Santa Rosa on hwy 3 and 1 km W towards Quishuara, along Rio Santa Rosa, 14°35'54.9"S, 70°51'34.7"W, 4002 m, 23 Mar 2007, P.M. Peterson, R.J. Soreng & K. Romashchenko 20604 (MO, US, USM); Puno, 2 km N of Laraquerion on road towards Puno, 16°6'59.1"S, 70°1'59.1"W, 3940 m, 18 Apr 2004, P.M. Peterson & N. Refulio Rodriguez 18329 (MO, US, USM); San Roman, 4 km E of Santa Lucia, along Rio Cabanillas, 15°41'4.2"S, 70°34'8.8"W, 4030 m, 19 Apr 2004, P.M. Peterson & N. Refulio Rodriguez 18334 (MO, US, USM); San Roman, 21 km W of Santa Lucia and 5 km E of Puente Cañuma (Laguna Lagunillas), 15°40'4.1"S, 70°47'4.4"W, 4260 m, 20 Apr 2004, P.M. Peterson & N. Refulio Rodriguez 18341 (MO, US, USM).

16. *Muhlenbergia phalaroides* (Kunth) P.M. Peterson, Caldasia 31(2): 294–296, f. 7 A–B. 2009.

Fig. 11E, F

Lycurus phalaroides Kunth, Nov. Gen. Sp. (quarto ed.) 1: 142. 1815 (1816). Type: Mexico, Michoacán, near Valladolid, Alberca de Palangeo and Patzcuaro, Sep, *F.W.H.A. Humboldt & A.J.A. Bonpland s.n.* (holotype: P-00669405 [image!]; isotypes: B-W-1630, BM!, BAA-1530!, US-91988 fragm. ex P-BONPL!, US-610837 fragm. ex LE-TRIN!).

Muhlenbergia lycuroides Vasey ex Beal, Grass. N. Amer. 2: 239. 1896. Type: Mexico, Jalisco, Guadalajara, Jul–Oct 1886, *E. Palmer 489* (holotype: MSC; isotypes: GH-00023916 [image!], LE, MEXU, MO-2972929!, NDG-07247 [image!], NY, P-00644181 [image!], P-00644182 [image!], S14-29628 [image!], US-822925!, US-81642!, YU-000898 [image!]).

Lycurus phleoides var. *brevifolius* Scribn. ex Beal, Grass. N. Amer. 2: 271. 1896. Type: Mexico, Jalisco, plains of Guadalajara, 23 Oct 1889, *C.G. Pringle 2470* (lectotype: MSC, designated by C. Reeder, Phytologia 57(4): 288. 1985; isolectotypes: BAA!, GH, MEXU, MO-2972926!, NY!, P-00644183 [image!], P-00644184 [image!], US-996049!, W-18900000580 [image!], W-19160029092 [image!]).

Description. *Perennials*, intricately branched near base. *Culms* 10–30 cm tall, erect, mostly glabrous, usually decumbent and sprawling below, bent at the pubescent to short pilose nodes; *internodes* 0.4–10 (–15) cm long, pubescent to short pilose. *Leaf sheaths* much shorter than the internodes above, hyaline near the margins, pilose near summit; *ligules* 0.4–1 mm long, membranous, apex truncate to deltoid, often erose and lacerate; *blades* 0.5–6.5 cm long, 0.5–1.2 mm wide, shorter near the base of culms, flat, folded or loosely involute, lanate above and glabrous or with scattered, short appressed hairs below, margins whitish-thickened, apex navicular, occasionally with a short seta, seta usually less than 2 mm long. *Panicles* 1.5–6.5 cm long, 3–8 mm wide, spiciform and spike-like, densely flowered, often interrupted below with only a few spikelets, terminal or axillary; *rachis* lanate to hispid, the short hairs antrose or appressed; *branches* 1.5–7 mm long, very short, the spiklets usually in pairs, rarely 1 or 3 per terminal branch, when in pairs the lower short-pedicelled spikelet perfect, staminate or sterile and the upper longer-pedicelled spikelet usually perfect; *pedicels* 0.3–1.4 mm long; *disarticulation* usually at the base of the pedicel, each spikelet falling as a unit leaving a small cup-like tip. *Spikelets* 3–4 mm long, stramineous with plumbeous mottles, sometimes additionally with purplish mottles; *glumes* 1–2.1 mm long, shorter than the lemma, subequal, 1–3-veined; *lower glumes* commonly 2 or 3-veined, usually 2-awned, ocassionally 1 or 3 awned, the awns 1–3 mm long, equal or subequal, scabrous, recurved; *upper glumes* commonly 1-veined, usually 1-awned, the awns 1–2.5 mm long; *lemmas* 3–4 mm long, narrowly lanceolate, 3-veined, margins hirsute to lanate and occasionally the lower ½ sparsely hairy, the hairs 0.1–0.3 mm long, apex usually awned, occasionally unawned or mucronate, the awns 1–3 mm long; *paleas* 2.8–3.8 mm long, hairy between the veins, the veins occasionally extending as mucros; anthers 1.3–2 mm long, yellowish. *Caryopses* 1.7–2 mm long, fusiform, brownish.

Distribution. *Muhlenbergia phalaroides* ranges from Mexico to South America where it is found in Argentina, Bolivia, Columbia, Ecuador and Peru (Reeder 1985; Sánchez and Rúgolo de Agrasar 1986; Davidse and Pohl 1994).

Ecology. This species occurs in open grasslands and savannahs on steep rocky slopes flats and along disturbed irrigation canals in deep clayish-loam to sandy soils associated with *Baccharis*, *Berberis*, *Cheilanthes*, *Condalia*, *Dodonaea viscosa*, *Eragrostis*, *Jarava ichu Opuntia*, *Muhlenbergia cenchroides*, *M. rigida*, *Nassella*, *Plantago*, *Puya* and *Sporobolus indicus* (L.) R. Br.; 2800–3500 m.

Comments. *Muhlenbergia phalaroides* is morphologically similar to *M. phleoides* (Kunth) Columbus, known in south-western U.S.A. and Mexico and *M. alopecuroides* found in south-western U.S.A., Mexico and disjunct in Argentina and Bolivia (Davidse and Pohl 1994, Renvoize 1998, Reeder 2003; Peterson and Giraldo-Cañas 2012). *Muhlenbergia alopecuroides* differs from *M. phalaroides* in having leaf blades with terminal seta (3–)4–7(–12) mm long and ligules(2–)3–12 mm long whereas *M. phleoides* differs in having auriculate ligules 1–2 mm long (Reeder 1985, 2003). These morphological differences are perhaps better recognised at the subspecific level but there have been no population studies comparing these three species, other than Peterson and Morrone (1997) who investigated populations of only the amphitropical, *M. alocpecuroides* [as *Lycurus setosus*].

Muhlenbergia phalaroides lies within *M.* subg. *Pseudosporobolus*, aligning with *M. alopecuroides* and *M. phleoides* (Peterson and Romaschenko, in prep.). Many members of this subgenus have narrow panicles, plumbeous spikelets with unawned, mucronate or short-awned lemmas (Peterson et al. 2010b).

Specimens examined. Peru. **Ancash:** 15 Mar 1947, J. Infantes Vera 1170 (LIL). **Ayacucho:** Huanca Sancos, 27 km NW of Putajasa and 3 km S of Sacsamarca, 13°57'51.1"S, 74°18'41.5"W, 3650 m, 25 Feb 2002, P.M. Peterson 16277, A.A. Cano, M.I. LaTorre, A. Ramirez & D. Susanibar (US, USM). **Cusco:** Canchis, Hacienda Occobamba, 3450 m, 4 Apr 1950, C. Vargas C. 9410 (CUZ, US); Prov. Quispicanchis, Pikillacta, 3250 m, 28 Apr 1946, C. Vargas C. 6033 (CUZ, US). **Huancavelica:** near Huancayo, 3270 m, 1 Apr 1952, O. Tovar 344 (US, USM); Sacxhahuajta, a 6 km de Conaica, 3600 m, 3 Apr 1952, O. Tovar 939 (US, USM). **Junín:** Huancayo, 3317 m, Mar 1943, J. Soukup 1900 (COL, LIL, US); Prov. Huancayo, Agua de las Virgenes, 3270 m, 1 Apr 1951, O. Tovar 344 (MOL, USM); Tarma, between La Oroya and La Merced, 3000 m, 24 Oct 1923, A.S. Hitchcock 22169 (US).

17. *Muhlenbergia rigida* (Kunth) Kunth, Révis. Gramin. 1: 63. 1829.

Fig. 6D–F

Podosemum rigidum Kunth, Nov. Gen. Sp. (quarto ed.) 1: 129. 1816. *Trichochloa rigida* (Kunth) Roem. & Schult., Syst. Veg. 2: 386. 1817. *Agrostis rigida* (Kunth) Spreng., Syst. Veg. 1: 262. 1825. Type: Mexico, Guanajuato, near Guanajuato, Sep, *F.W.H.A. Humboldt & A.J.A. Bonpland s.n.* (holotype: P!; isotypes: BAA!, US-91920 fragm. ex P!).

Podosemum elegans Kunth, Nov. Gen. Sp. (quarto ed.) 1: 130. 1816. *Trichochloa elegans* (Kunth) Roem. & Schult., Syst. Veg. 2: 387. 1817. *Agrostis quitensis* Spreng., Syst. Veg. 1: 262. 1825. Type: Ecuador, Chimborazo, Paramo de las Puntas & Pomallacta, Jun, *F.W.H.A. Humboldt & A.J.A. Bonpland s.n.* (holotype: P!; isotype: BAA!).

Podosemum glabratum Kunth, Nov. Gen. Sp. (quarto ed.) 1: 130. 1816. *Trichochloa glabrata* (Kunth) Roem. & Schult., Syst. Veg. 2: 387. 1817. *Agrostis glabrata* (Kunth) Spreng., Syst. Veg. 1: 262. 1825. Type: Mexico, Santa Rosa de la Sierra and Cañada de Acabuca, Sep, *F.W.H.A. Humboldt & A.J.A. Bonpland s.n.* (holotype: P-Bonpl!; isotype: US-91921 fragm. ex P-Bonpl!).

Muhlenbergia berlandieri Trin., Mém. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 6,4(3–4): 299. 1841. Type: Mexico, Distrito Federal, Mountains near México, Aug 1827, *J.L. Berlandier 676, 684* (lectotype, designated here: LE-TRIN-1487.01!, both collection numbers appear on the label with a single specimen and figure); México, 26 Aug 1827, *J.L. Berlandier 676* (isolectotypes: COL-000006382 [image!]; P-00644117 [image!], P-00644119 [image!], US-2557457!, US-87241 fragm!, W-239604!, W-0029177 [image!]).

Muhlenbergia affinis Trin., Mém. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 6,4(3–4): 301. 1841. *Podosemum affine* (Trin.) Bush, Amer. Midl. Naturalist 7(2):40. 1921. Type: Mexico, México, Toluca, *J.L. Berlandier 1083* (lectotype, designated here: P-00644141 [image!]; isolectotypes: G-00099411 [image!], G-00099410 [image!], G-00099409 [image!], LE-TRIN-1485.01 fragm.!, P-00644142 [image!], US-87237 fragm.!).

Muhlenbergia phragmitoides Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 255. 1874. Type: Argentina, Tucumán: Cuesta de Anfama, Sierra de Tucumán, 23 Mar 1872, *P.G. Lorentz 79* (lectotype, designated here: GOET-006649 [image!]; isolectotypes: BAA-00002225 [image!], CORD-00004622 [image!], GOET-006648 [image!], SI-002780 [image!], US-91911 fragm. ex GOET!).

Muhlenbergia elegans var. *atroviolacea* Kuntze, Revis. Gen. Pl. 3(3): 357. 1898. Type: Bolivia, Cochabamba, 3000 m, 26 Mar 1892, *O. Kuntze s.n.* (lectotype, designated here: NY-00381485 [image!].

Muhlenbergia elegans var. *subviridis* Kuntze, Revis. Gen. Pl. 3(3): 357. 1898. Type: Bolivia, Tunari Mts, 1600 m, *O. Kuntze* (lectotype, designated here: NY-00381486 [image!]).

Muhlenbergia metcalfei M.E. Jones, Contr. W. Bot. 14: 12. 1912. Type: U.S.A. New Mexico: Grant Co., Santa Rita Mountains, in and around S end of the Black Range, 7000 ft alt., 9 Oct 1904, *O.B. Metcalf 1485* (holotype: POM-116640!; isotypes: GH-00023980 [image!], MO!, US!).

Muhlenbergia holwayorum Hitchc., Contr. U.S. Natl. Herb. 24(8): 389. 1927. Type: Bolivia, Sorata, 16 Apr 1920, *E.W.D. Holway & M.M. Holway 530* (holotype: US-1108445!).

Description. Densely caespitose *perennials*. *Culms* 40–100 cm tall, stiffly erect, glabrous to scaberulous below the basal, terete nodes, usually 1 node per culm; *internodes* mostly glabrous. *Leaf sheaths* 2–30 cm long, longer than the internodes, glabrous to scaberulous, rounded near base; *ligules* (1–)3–6(–8) mm long, often lacerate, firmer below, strongly decurrent, apex obtuse to acute; *blades* 12–35 cm long, 1–3 mm wide, flat or involute, glabrous to scaberulous below and scaberulous to hirsutulous above.

Panicles (4–)10–35 cm long, (2–)3–5(–15) cm wide, loosely contracted to open and lax, reddish-purple; *primary branches* 0.4–10 cm long, sometimes capillary, ascending and spreading up to 80° from the rachises; *pedicels* 1–10 mm long, mostly longer than the spikelets. *Spikelets* 3.5–5 mm long, reddish-purple; *glumes* 1–1.7(–2) mm long, much shorter than the floret, about equal, 1-nerved, unawned, apex obtuse to subacute, sometimes hirsutulous, rarely mucronate; *lemmas* 3.5–5 mm long, narrow lanceolate, scaberulous to scabrous, purple, awned, callus with hairs up to 0.5 mm long, apex acuminate, the awns (8–)10–22 mm long, flexuous; *paleas* 3.5–5 mm long, narrow lanceolate, purple, scaberulous, apex acuminate; *anthers* 1.7–2.3 mm long, reddish-purple. *Caryopses* 2–3.5 mm long, fusiform, brownish. 2*n* = 40, 44.

Distribution. *Muhlenbergia rigida* ranges from Arizona, New Mexico and southwestern Texas, throughout México and Central America to South America where it occurs along the Andes from Columbia, Venezuela, Ecuador, Bolivia, Peru and Argentina.

Ecology. This species occurs on rocky slopes, ravines and sandy, gravelly slopes derived from granitic and calcareous substrates associated with *Acacia*, *Agave*, *Aristida*, *A. adscensionis*, *Baccharis*, *Berberis*, *Bidens*, *Bouteloua curtipendula* (Michx.) Torr., *Caesalpinia*, *Calamagrostis*, *Colletia spinosissima*, *Cortaderia bifida*, *C. jubata*, *Desmodium*, *Dodonaea viscosa*, *Ephedra*, *Eragrostis*, *Eupatorium*, *Festuca*, *Fucaria*, *Hypericum*, *Jarava*, *Krameria*, *Lepechinia*, *Lupinus*, *Lycium*, *Melinus minutiflora*, *Mirabilis*, *Opuntia*, *Paspalum*, *Cenchrus clandestinus*, *Peperomia*, *Puya*, *Salvia*, *Schinus molle*, *Schizachyrium*, *Sporobolus*, *Tillandsia* and *Trichocereus*; 2000–3650 m.

Comments. This species is highly variable and is one of the most common upland bunchgrasses forming almost pure stands in northern México, less common in Peru and South America where it is usually found in smaller populations. *Muhlenbergia rigida* can be distinguished morphologically from *M. coerulea* and *M. coerulea* × *rigida* in having shorter lemmas 3.5–5 mm long with long flexuous awns (8–)10–22 mm long and shorter glumes 1–1.7(–2) mm long.

Molecular DNA sequence analysis indicates *M. rigida* lies within *Muhlenbergia* subg. *Trichochloa* and genetically is highly variable (Fig. 1A; Peterson et al. 2010b).

Specimens examined. Peru. **Amazonas:** 66 km from Leymebamba towards Balsas, S.A. Renvoize & S. Lægaard 4934 (CPUN); Prov. Chachapoyas, Cerro Puma Urco S of Chachapoyas, C.P. Cowen 4308, J. Canne & V. Torrel (USM). **Ancash:** E of Yungay, S.A. Renvoize & S. Lægaard 5053 (CPUN); 10 km from Huaraz towards Casma, S.A. Renvoize & S. Lægaard 5153 (CPUN); Prov. Bolognesi, Tanás, E. Cerrate 1381 (US, USM); Aynín, E. Cerrate 1341 (USM); Casca, below Chiquián, R. Ferreyra 7285 (US, USM); above Chiquián, E. Cerrate 372, 480 (US, USM); Shapash, near Chiquián, F. Ferreyra 5696 (US); Yungay, Prov. Huaraz, 23 Apr 1995, S. Llatas Quiroz 3630 & J. Campos de la Cruz (USM); Prov. Huaraz, W side of Cordillera Blanca, S of quebrada Ishinca, 9°24'55.8"S, 77°32'45.8"W, 2885 m, 12 Mar 2008, P.M. Peterson 21610, R.J. Soreng, M. La Torre & J.V. Rojas Fox (US, USM); Corongo, N end of Cordillera Blanca, 12 km W of Tarica towards Yuacmarca, 8°35'55.6"S, 77°50'4.8"W, 2849 m, 18 Mar 2008, P.M. Peterson 21782 & R.J. Soreng (US, USM); Cordillera Negra E slope, S side of quebrada W of Shupluy, 9°13'30.0"S, 77°42'6.6"W, 2476 m, 13 Mar 2008, P.M. Peterson 21628, R.J. Soreng, M. La Torre & J.V. Rojas Fox (US, USM); Prov. Huaraz-Recuay border, W side of Rio Santa Canyon, 9°40'58.1"S, 77°28'29.7"W, 3202 m, 11 Mar 2008, P.M. Peterson 21605, R.J. Soreng, M. La Torre & J.V. Rojas Fox (US, USM); Prov. Huari, Cordillera Blanca, 21 km S of Huari on road towards San Marcos, 2850 m, 22 Mar 1997, P.M. Peterson & N. Refulio Rodriguez 13862 (US, USM); Uco near Rio Puchca, A. Cano 14317, M.I. La Torre, W. Mendoza & C. Mendoza (USM); San Marcos, A. Cano 13395, W. Mendoza, I. Salinas & A. Ramirez (USM); Prov. Huaylas, below Huaylas, E. Carrillo 1297, W. Medina & P. Huamán (USM); Pueblo Libre, A. Cano 11616 (USM); Prov. Pallasca, 3.4 km N of Huandoval towards Huascaschuque and Pallasca, 8°18'59.2"S, 77°58'9.5"W, 2949 m, 21 Mar 2008, P.M. Peterson & R.J. Soreng 21818 (US, USM); divide between Rio Conchucos and Rio Plata, 8°12'9.1"S, 77°56'20.6"W, 2233 m, 21 Mar 2008, P.M. Peterson & R.J. Soreng 21834 (US, USM); Prov. Recuay, Catac, L.I. Masias 47 (USM); Prov. Yungay, Cordillera Negra, 18 km SW of Shuplay and Rio Santa, 9°14'52.7"S, 77°43'44.1"W, 2901 m, 13 Mar 2008, P.M. Peterson 21637, R.J. Soreng, M. La Torre & J.V. Rojas Fox (US, USM); Cordillera Blanca W slope, 5 km E of Yungay, below Shillcop, 9°9'11.7"S, 77°43'27.6"W, 2597 m, 15 Mar 2008, P.M. Peterson 21687, R.J. Soreng, M. La Torre & J.V. Rojas Fox (US, USM); Kuisho, M. La Torre 419 (USM); Shupluy, A. Cano 11354 (USM); Shilco, E. Cerrate 7753 (USM). **Apurimac:** Prov. Grau, Cotobambas–Cochapata, C. Vargas C. 5789 (US). **Ayacucho:** A. Weberbauer 5525 (US); Prov. Lucanas, Quebrada Chuela, 3 Apr 1942, R.D. Metcalf 30315 (LIL); Prov. Huamanga, Quellagocha, 4000 m, 5 Apr 1967, V. Palomino 242 (USM); Prov. Huamanga, 4 km S of Ayacucho on hwy 3 towards Abancay, 13°11'33.8"S, 74°12'2.1"W, 2952 m, 15 Mar 2007, P.M. Peterson 20475, R.J. Soreng, K. Romaschenko & D. Susanibar Cruz (US, USM); 21 km S of Ayacucho on hwy 3 towards Abancay, 13°16'21.5"S, 74°13'46.8"W, 3575 m, 15 Mar 2007, P.M. Peterson 20487, R.J. Soreng, K. Romaschenko & D. Susanibar Cruz (US, USM); Cerro Acuchimay above Ayacucho, O. Tovar 5399 (USM); Huatalás, V. Palomino 34 (USM); Prov. Huanca Sancos, 27 km NW of Putajasa and 3 km S of Sacsamarca, 13°57'51.1"S, 74°18'41.5"W, 3650 m, 25 Feb 2002, P.M. Peterson 16273A, A. Cano, M. La Torre, A Ramirez & D. Susanibar (US, USM); Prov. Huata, Rio Cachi below Huanta, O. Tovar 4946 (US, USM); Prov. Lucanas, near Puquio, R. Ferreyra 7187 (MOL,US, USM); vicinity of Puquio, O. Tovar 9 (USM). **Cajamarca:** near side road to Chugur, 95 km from Cajamarca, S.A. Renvoize 4847, S. Lægaard & I. Sánchez Vega (CPUN); above Celendín, S.A. Renvoize & S. Lægaard 4877 (CPUN); Prov. Cajabamba, 14 km WSW of Cajabamba, E of Araqueda, 7°39'9.1"S, 78°9'58.9"W, 2242 m, 23 Mar 2008, P.M. Peterson & R.J. Soreng 21854 (US, USM); Prov. Cajamarca, 6 km NW of San Marcos on road towards Cajamarca, 2570 m, 30 Mar 1997, P.M. Peterson & N. Refulio Rodriguez 14009 (US, USM); 1 km S of Huambocancha on road towards Cajamarca, 2770 m, 14 Mar 2000, P.M. Peterson & N. Refulio Rodriguez 14853 (CPUN, US, USM); Parque forestall Aylambo, 4 km de Cajamarca, I. Sánchez Vega 987 (CPUN); 4 km S of Jesús, I. Sánchez Vega 2376 (CPUN); Tres Molinos, T. Tejada 46 (CPUN); S of Paso El Gavelán, 10 air km S of Cajamarca, 7°15'37.2"S, 78°30'34.5"W, 2544 m, 26 Mar 2008, P.M. Peterson 21878, R.J. Soreng & I. Sánchez Vega (US, USM); near Gavilán and San Juan, I. Sánchez Vega & W. Ruiz Vigo 650 (CPUN); bajando Paso El Gavilán a San Juan, I. Sánchez Vega & W. Ruiz Vigo (CPUN); near Paso El Gavilán, I. Sánchez Vega 1400, P. Brandelard & J. Sanabria (CPUN); bajadas de Chancay a Valle de Condebamba, I. Sánchez Vega 1112 (CPUN); above San Pablo, I. Sánchez Vega 1495 (CPUN); near Jesús, I. Sánchez Vega 1066 (CPUN); S of Jesús Tabada, I. Sánchez Vega 2376 (CPUN, US); between Cajamarca and Celendín, R. Ferreyra 15004 (USM); 20 km from Celendín, P. Gutti & G. Müller s.n. (USM); Chotén, 4 km de la carretera Pacasmayo, I. Sánchez Vega 2569, V. Torrel & E. Medina (CPUN); Bellavista, I. Sánchez Vega 1842, W. Ruiz Vigo & J. Sánchez Vega (CPUN); Chotén Bajo, J. Cabanillas S. & J. Guevara B. 665 (CPUN); Cerro Rumicucho, km 11 de la carretera Cajamarca Cajabamba, I. Sánchez Vega 2492, V. Torrel & E. Medina (CPUN); near Chancay and Valle de Condebamba, I. Sánchez Vega 2412, V. Torrel & E. Medina (CPUN); Cerro Huacarís, Valle de Cajamarca, I. Sánchez Vega 444 (CPUN); Prov. Celendín, above Limon, 27 km E of Celendín, 6°53'15.2"S, 78°5'30.5"W, 2215 m, 29 Mar 2008, P.M. Peterson 21927, R.J. Soreng & J. Montoya Quino (US, USM); Marañón river Valley, Chachapoyas–Cajamarca road, D.N. Smith & J. Cabanillas 7272 (MO, US); Prov. Chota, 5 km de Cochabamba a Cutervo, I. Sánchez Vega 4845 (CPUN); 6 km de Cochabamba, I. Sánchez Vega 2334 (CPUN); Prov. Contumaza, Hacienda San Lorenzo, San Benito, A. Sagástegui 3784 (US), Cerro Campanillas, A. Sagástegui 2992 (US); Shamon, A. Sagástegui 14305 (HAO); Prov. Cutervo, 13 km W of Cutervo on road towards Socoto, 2160 m, 20 Mar 2000, P.M. Peterson & N. Refulio Rodriguez 15008 (CPUN, US, USM). **Cusco:** 2 km S of San Jeronimo and 10 km SE of Cusco, J.C. Soloman 2985 (USM); Prov. Anta, Mollepata, C. Vargas C. 19049 (USM); Prov. Calea, Pisai, F. Marin 512a (LIL); Prov. Cusco, Cusco–Huancar, P. Gutti & G. Müller 94269b (USM); Prov. Urubamba, Cerro Chicón, P. Nuñez V. 8895 (MO, US); Chincheros, just below Perga Kachun, S. King 316, E. Franquemont, C. Franquemont & C. Sperling (USM); lower end of quebrada Pumahuanca, H.H. Iltis 855, C.M. Iltis & C. Vargas C. (LIL, USM); Machu Pichu, I. Grignon 2305 (US); ESE of Cusco, H. Ellenberg 1018 (US); Prov. Yaurisque, Paruro, SW of Cusco, P. Nuñez 7383 (USM). **Huancavelica:** Prov. Huancavelica, Mariscal Cáceres, O. Tovar 1405 (US, USM); Prov. Tayacaja, near Huachocolpa, O. Tovar (US, USM); near Surcubamba, O. Tovar 4240 (US, USM); Mejorada, O. Tovar 2454 (US, USM); Mamacha-rumi, O. Tovar 2439 (US, USM); Prov. Taycaya, Valle del Rio Mantero, A. Weberbauer 6448 (MOL). **Huánuco:** Prov. Ambo, above Hacienda Quicacán, near Huánuco and Ambo, R. Ferreyra 9228 (US, USM); Huarmiragra, A. Granda Paucar 1791 (USM); Prov. Huánuco, 7 km S of Ambo on hwy 3 towards Cerro de Pasco, 10°11'49"S, 76°9'54"W, 2345 m, 6 Mar 2007, P.M. Peterson 20322, R.J. Soreng & K. Romaschenko (US, USM); Cerro San Cristobal, P. Aguilar 808 (USM); Prov. Pachitea, 21 air km NE of Huánuco, 7 km E of Puerto Rancho junction, 9°49'45.9"S, 76°3'12.9"W, 2094 m, 6 Mar 2007, P.M. Peterson 20334, R.J. Soreng & K. Romaschenko (US, USM). **Junín:** Chorrillos, B. Maass 487 (USM); Prov. Huancayo, near Huancayo, O. Tovar 2747 (US, USM); Prov. Huancayo, Acopalca, 20 Jan 1952, J. Infantes Vera 1586 (LIL); Huancayo, 3317 m, Mar 1943, J. Soukup 1899 (COL, US); Montaro Valley W of Huancayo, 3800 m, 14 Jul 1982, S.A. Renvoize 4328 (USM); below Pariahuana, O. Tovar 7899, 7944 (USM); Prov. Tarma, 1 km up road to Hacienda Maraynioc out of Palca, 2800 m, 6 Apr 1997, P.M. Peterson & O. Tovar 14055 (US, USM); Tarma, E.P. Killip & A.C. Smith 21802 (US); A.S. Hitchcock 22165 (US). **La Libertad:** Usquil, E. Anderson 1293 (US); Prov. Bolivar, 0.5 km W of Longotea towards San Vicente, 7°2'35.6"S, 77°52'39.8"W, 2487 m, 31 Mar 2008, P.M. Peterson 21968, R.J. Soreng & J. Montoya Quino (US, USM); 4.6 km NW of Longotea, SE of San Vicente, 7°00'38.0"S, 77°54'15.2"W, 2058 m, 31 Mar 2008, P.M. Peterson 21969, R.J. Soreng & J. Montoya Quino (US, USM); Prov. Huamachuco, Llautobamba, J. Infautes 5509 (US); Prov. Santiago de Chuco, 22 km E of Huamachuco on road towards Sarin, 2500 m, 29 Mar 1997, P.M. Peterson & N. Refulio Rodriguez 13984 (US, USM). **Lima:** Prov. Huarochiri, Tambo de Viso, J.F. Macbride & Featherstone 765 (F, US); Matucana, J.F. Macbride & Featherstone 358 (F, US). **Pasco**: 10 km unterhalb Tarma, Ellenberg 8787 (USM). **Piura:** Prov. Huancabamba, 7 km E of Sondor on road towards Tabaconas, 2200 m, 31 Mar 2000, P.M. Peterson & N. Refulio Rodriguez 15162 (CPUN, US, USM); Abra de Porculla, R. Ferreyra 13734 (US, USM); 11 km Huancabamba–Salalá, I. Sánchez Vega 5160 (CPUN).

18. *Muhlenbergia romaschenkoi* P.M. Peterson, sp. nov.

urn:lsid:ipni.org:names:77192895-1

Fig. 12A–L

Type. Peru. Depto. Huánuco, Pachitea, 21 air km NE of Huánuco, 7 km E of Puerto Rancho jtn on road to Panao, along Río Huallaga, 9°49'45.9"S, 76°3'12.9"W, 2094 m, 6 Mar 2007, *P.M. Peterson 20331, R.J. Soreng & K. Romaschenko* (holotype: US-3730646!; isotypes: MO!, USM!).

Description. Loosely caespitose to densely tufted, *annuals* to short-lived *perennials* with delicate bases, flowering the first year. *Culms* 20–40 cm tall, erect or decumbent at the base, branching at the lower and middle nodes, scaberulous below the terete nodes; *internodes* generally 2.0–9.5 cm long. *Leaf sheaths* 4.0–7.5 cm long, glabrous or scaberulous, commonly shorter than the internodes; *ligules* 1.2–3.0(–5.0) mm long, hyaline, apex acute to obtuse, often lacerate with age; *blades* 3–12 cm long, 1.2–2.5 mm wide, flat or loosely involute, scaberulous to glabrous below and scabrous above. *Panicles* 7–15 cm long, 0.6–2 cm wide, narrow and contracted to loosely spreading, interrupted below, terminal and axillary, 15–23 nodes per panicle; *primary branches* 3.5–7.5 cm long, usually one per node, when immature the branches mostly appressed and ascending, when mature the branches sometimes widely spreading up to 50° from the rachises; *pedicels* 1–3 mm long, usually shorter than the spikelets, antrorsely scabrous, stout, appressed. *Spikelets* 2–4 mm long, erect, stramineous to purplish; *glumes* 1–2.8 mm long, unequal, 1-nerved, scabrous along the nerves, apex acute to acuminate, often mucronate or erose,

Figure 12. *Muhlenbergia romaschenkoi* P.M. Peterson **A** habit **B** ligule **C** spikelet **D** lower glume **E** upper glume **F** lemma, lateral view **G** lemma, dorsal view **H** palea, dorsal view **I** palea, lateral view **J** palea, ventral view **K** lodicules, stamens, and pistil **L** caryopsis. Drawings from the holotype collection *P.M. Peterson, R.J. Soreng & K. Romaschenko 20331*.

the mucro up to 0.5 mm long; *lower glumes* 1–2.0 mm long; *upper glumes* 1.5–2.8 mm long, more than ½ as long as the lemma; *lemmas* 2.0–3.5(–4.0) mm long, lanceolate, widest near base, awned, scaberulous above and villous on proximal 1/2 along the margins and the midvein, the hairs 0.5–1.5 mm long, callus short-pubescent, the awn 10–30 mm long, scabrous, flexuous; *paleas* 1.8–3.4(–3.8) mm long, lanceolate, sparsely appressed pubescent between the nerves on the proximal ½; *anthers* 0.3–0.4 mm long, purplish, yellow with age. *Caryopses* 1.0–2.2 mm long, narrowly fusiform, terete, brownish.

Distribution. Endemic to Peru and known only from Huánuco.

Ecology. *Muhlenbergia romaschenkoi* grows on rocky slopes and limestone rock outcrops in grasslands with *Aristida adscensionis*, *Bidens*, *Bothriochloa*, *Eragrostis nigricans* (Kunth) Steud., *Eupatorium*, *Melinus minutiflora*, *Microchloa kunthii* Desv., *Muhlenbergia ciliata*, *M. rigida and Nassella*; 1800–2500 m.

Etymology. We honour Dr. Konstantin Romaschenko (born 1969) who accompanied PMP and Robert J. Soreng on the collecting trip in which material of the species was gathered.

Comments. *Muhlenbergia romaschenkoi* can be separated from *M. microsperma* in having longer acute to acuminate glumes (1–2.8 mm long) and by lacking cleistogamous panicles present in the axils of the lower sheaths. *Muhlenbergia tenuifolia* (Kunth) Kunth, a species ranging from southern Arizona, New Mexico and Texas, U.S.A., throughout México and then again in Venezuela, Bolivia and Argentina, is morphologically similar to *M. romaschenkoi* but differs in having yellowish anthers 0.9–1.5 mm long (Peterson and Annable 1991; Peterson 2003; Peterson et al. 2007b; Peterson and Giraldo-Cañas 2011, 2012). Initially we thought the new species was *M. tenuiofolia* with immature anthers 0.3–0.4 mm long. However, our collection of *M. romaschenkoi* includes well-developed florets with mature caryopses and anthers. Therefore, the observed small anthers in *M. romaschenkoi* are not a result of immaturity but represent a genetic difference, from *M. tenuifolia*, which is not known in Peru.

Muhlenbergia romaschenkoi, a member of *M.* subg. *Muhlenbergia,* is sister to *M. spiciformis* Trin. (plastid marker), a species known from south-western United States and throughout Mexico whereas ITS marker aligns it within the *M. tenuifolia* clade (Fig. 1B). *Muhlenbergia spiciformis* differs from the new species in having shorter glumes 0.3–1 mm long and larger anthers 0.9–1.6 mm long (Peterson 2003; Peterson et al. 2007b). These results suggest multiple origins for *M. romaschenkoi* from North and South American progenitors. Similar to *M. caxamarcenis*, this scenario appears to be a common pattern of speciation for South American species of *Muhlenbergia,* needing further study.

Specimen examined. Peru. **Huánuco**: between Huánuco and Tingo María, vereda Taruka, 17 km NE of Huánuco in valley of Río Huallaga, T. Croat 57781 (MO).

Infrageneric classification of the species of *Muhlenbergia* in Peru

Muhlenbergia subg. *Bealia* (Scribn.) P.M. Peterson: *M. caxamarcensis, M. ligularis.*
Muhlenbergia subg. *Clomena* (P. Beauv.) Hack.: *M. peruviana.*

Muhlenbergia subg. *Muhlenbergia*: *M. beyrichiana, M. bryophilus, M. cenchroides, M. ciliata, M. diversiglumis, M. flexuosa, M. microsperma, M. romaschenkoi*.

Muhlenbergia subg. *Pseudosporobolus* (Parodi) P.M. Peterson: *M. fastigiata, M. monandra, M. phalaroides.*

Muhlenbergia subg. *Trichochloa* (P. Beauv.) A. Gray: *M. coerulea, M. coerulea* × *M. rigida, M. maxima, M. rigida.*

Species excluded

Muhlenbergia tenuissima (Presl) Kunth, Enum. Pl. 1: 198. 1833.

Discussion. This taxon is a distinctive species which seems to be restricted to chalky limestone flats usually occurring as a dense carpet on clay-like soils in open savannahs; known from North America and Central America (Peterson and Annable 1991; Brako and Zarucchi 1993). Although previously included for Peru in Hitchcock (1927), Standley (1936) and Tovar (1993), the specimens cited are *M. ciliata* without prominent cilia along the lateral veins (see discussion of *M. ciliata*).

Muhlenbergia tenuifolia (Kunth) Kunth, Révis. Gramin. 1(4):63. 1829.

Discussion. This taxon was reported for Peru in Brako and Zarucchi (1993) who cited *Croat 57781* which we place in *M. romaschenkoi*.

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