PhytoKeys 171: 1–24 (2021)
doi: 10.3897/phytokeys.171.61926
https://phytokeys.pensoft.net

RESEARCH ARTICLE

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Rediscovery of *Mazus lanceifolius* reveals a new genus and a new species in Mazaceae

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Academic editor: A. Paton | Received 11 December 2020 | Accepted 15 December 2020 | Published 6 January 2021

Citation: Xiang C-L, Pan H-L, Min D-Z, Zhang D-G, Zhao F, Liu B, Li B (2021) Rediscovery of *Mazus lanceifolius* reveals a new genus and a new species in Mazaceae. PhytoKeys 171: 1–24. https://doi.org/10.3897/phytokeys.171.61926

Abstract

Mazus lanceifolius (Mazaceae) is a perennial herb with opposite leaves and endemic to central China that has not been collected for 130 years. Rediscovery of this enigmatic species in the wild allows for determination of its phylogenetic position within Mazaceae. Phylogenetic reconstruction of Mazaceae based on DNA sequences from four plastid markers (*matK*, *rbcL*, *rps16* and *trnL-trnF*) and nuclear ribosome ITS consistently showed that *Mazus* was not monophyletic. *Mazus lanceifolius* is in the most basal clade within Mazaceae, as sister to the remaining species of three recognized genera *Dodartia*, *Lancea* and *Mazus*. These results support the separation of *M. lanceifolius* from *Mazus* as a new genus, which was established here as *Puchiumazus* Bo Li, D.G. Zhang & C.L. Xiang. Meanwhile, a collection from Shennongjia Forestry District of Hubei Province, China, misidentified as "*M. lanceifolius*" in previous molecular study, is here revealed to represent an undescribed species of *Mazus*, i.e., *M. fruticosus* Bo Li, D.G. Zhang & C.L. Xiang, **sp. nov.** Morphologically, *Puchiumazus* is clearly distinct from the other three genera by having quadrangular to somewhat ribbed stems, and obviously opposite leaves. In addition, we provide a taxonomic key to the four genera of Mazaceae.

Keywords

Dodartia, Lamiales, *Lancea*, new genus, *Puchiumazus*

* These authors contributed equally to this work.

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Introduction

Mazaceae (Reveal 2011) is a small herbaceous family in Lamiales currently containing three genera: *Dodartia* L., *Lancea* Hook.f. & Thomson and *Mazus* Lour. (APG IV 2016; Olmstead 2016; Christenhusz et al. 2017). The monotypic genus *Dodartia* based on *D. orientalis* L., occurs mainly in southern Russia and western to central Asia (Fischer 2004) and is characterized by having scale-like leaves and much-branched stems. The genus *Lancea* is found only in the Qinghai-Tibetan Plateau (QTP) where it includes two species, *L. tibetica* Hook.f. & Thomson and *L. hirsuta* Bonati (Chi et al. 2018, 2019), of which the former species is widely used in traditional Tibetan medicine. Morphologically, *Lancea* is characterized by leaves in a rosette and a lower corolla lip with a distinct palate. *Mazus* is the largest genus in Mazaceae, including approximately 30 species of annual or perennial herbs (Hong et al. 1998; Deng et al. 2016) distributed in Asia, Australia and New Zealand (Li 1954; Barker 1991; Fischer 2004). China is considered to be the center of distribution and differentiation of the genus (Yang 1979; Hsieh 2000), with ca. 26 species and three varieties currently recorded (Hong et al. 1998; Deng et al. 2016). Species delimitation in *Mazus* has been problematic because of relatively high levels of morphological variation (Li 1954; Hong et al. 1998). In general, *Mazus* can be distinguished from the other two genera by a combination of morphological characters: a strongly two-lipped corolla (3/2-bilabiatae), a palate with two longitudinal plaits and a capsule enveloped in a persistent calyx (Fischer 2004; Deng et al. 2019).

Dodartia, *Lancea* and *Mazus* were once placed in the traditionally circumscribed Scrophulariaceae (e.g. Von Wettstein 1891) but variably affiliated with tribe Gratioleae (Von Wettstein 1891; Thieret 1954, 1967) or Mimuleae (Dumortier 1829; Burtt 1965; Argue 1984; Fischer 2004). However, Scrophulariaceae were found to be polyphyletic and some genera were subsequently transferred to existing families like Orobanchaceae, Plantaginaceae, Phrymaceae and Stilbaceae, and some genera were separated as small monophyletic families, including Calceolariaceae, Linderniaceae, Mazaceae, Paulowniaceae, Schlegeliaceae, and Wightiaceae (Olmstead and Reeves 1995; Oxelman et al. 1999, 2005; Olmstead et al. 2001; Beardsley and Olmstead 2002; Albach et al. 2005; Rahmanzadeh et al. 2005; Tank et al. 2006; Schäferhoff et al. 2010; Liu et al. 2020), then leaving a much reduced Scrophulariaceae s.s. To date, a number of genera have not yet been sequenced and are still unplaced.

When redefining Phrymaceae based on molecular phylogenetics, Beardsley and Olmstead (2002) had first shown that *Mazus* and *Lancea* formed a well-supported group that was weakly supported as sister to the rest of Phrymaceae. Consequently, they tentatively included the two genera in the redefined Phrymaceae and assigned them to a provisional subfamily "Mazoideae" (Beardsley and Olmstead 2002). However, subsequent studies did not recover the sister relationship between "Mazoideae" and the rest of Phrymaceae, and *Mazus* and *Lancea* were found to be sister to the Or obanchaceae+Paulowniaceae+Phrymaceae clade (Oxelman et al. 2005; Albach et al. 2009; Schäferhoff et al. 2010). Thus, a new family Mazaceae Reveal (2011) was estab-

lished to accommodate this. When *Dodartia* was first included in a molecular analysis, Xia et al. (2012) found that this genus was closely related to *Lancea* and they together formed the sister clade of *Mazus*. Currently, Mazaceae Reveal (2011) with the inclusion of all these three genera has been widely accepted (Refulio-Rodriguez and Olmstead 2014; APG IV 2016; Olmstead 2016; Christenhusz et al. 2017). It was found to be a member of the clade comprising Lamiaceae, Mazaceae, Wightiaceae, Phrymaceae, Paulowniaceae and Orobanchaceae (Liu et al. 2020).

Within the genus *Mazus*, *M. lanceifolius* Hemsl. is a distinctive species through its quadrangular stems and narrowly lanceolate, mostly cauline, opposite leaves (Fig. 1). By contrast, the other species of *Mazus* have terete stems and leaves often in basal rosettes (Yang 1979; Hong et al. 1998). Therefore, *M. lanceifolius* was assigned to a monotypic section: sect. *Lanceifoliae* Bonati (1908), which was followed by Yang (1979). Since its description by Forbes and Hemsley (1890), *M. lanceifolius* has never been recorded by any specimens until two populations of the rare species were rediscovered in Sichuan Province of China in 2020. The rediscovery of *M. lanceifolius* after more than one century offers us a precious opportunity to test its phylogenetic position based on morphological and molecular data.

Since the establishment of the family Mazaceae (Reveal 2011), only one molecular phylogenetic study exclusively focused on its phylogeny (Deng et al. 2019), including one species from each *Lancea* and *Dodartia*, and 23 out of 30 species of *Mazus*. In that study, Deng et al. (2019) notably included two samples named as "*Mazus lanceifolius*", and stated that "*M. lanceifolius*" can be easily distinguished from other *Mazus* species by having lanceolate leaves and a robust stem. After consulting the vouchers of "*Mazus lanceifolius*" (*D.G. Zhang zdg6673*, Fig. 2) sampled by Deng et al. (2019) as well as the type specimens (*Henry 7250*, K001079356!; *Henry 5837*, K001079356!) and the original description of *M. lanceifolius*, we found that the plants of "*Mazus lanceifolius*" used by Deng et al. (2019) have opposite to subopposite leaves, which may have led the authors to identify the plant as *M. lanceifolius* because this species is the only known *Mazus* species with opposite leaves. However, except for these opposite leaves, their "*Mazus lanceifolius*" is remarkably different from the type specimen of *M. lanceifolius* in many aspects. For example, the plants sampled by Deng et al. (2019) are robust shrubs having numerous and much branched stems, leathery leaves that are acutely serrate on the apical half and multiflowered inflorescences (Fig. 2; see also fig. 2C in Deng et al. 2019), while the type material of *M. lanceifolius* is a slender herb having several unbranched stems, submembranaceous and almost entire leaves and remarkably sparse inflorescences with no more than six flowers (Fig. 1). We therefore have to conclude that the specimen sampled as "*M. lanceifolius*" by Deng et al. (2019) was misidentified, with the identity of that sample needing to be confirmed.

In the present study, we carried out an updated phylogeny of Mazaceae, in order to (1) investigate the phylogenetic placement of the distinct and enigmatic species *M. lanceifolius* based on its rediscovered populations; (2) confirm the identity of the misidentified *M. lanceifolius* by Deng et al. (2019); and (3) further contribute to a comprehensive phylogenetic framework for Mazaceae.

Material and methods

Field work, taxon sampling and data collection

Two populations of *Mazus lanceifolius* were rediscovered in June 2020 in Sichuan Province, China. One is located in the Qingchengshan Mountain near Dujiangyan City, and another was found in Qianfoshan Mountain near Mianyang City. Morphological observations were conducted based on wild individuals as well as the type specimens. Fresh leaves were collected in the field and dried with silica-gel for DNA extraction (Chase and Hills 1991). Voucher specimens are deposited in the herbarium of Shanghai Chenshan Botanical Garden (**CSH**).

In the present study, most DNA sequences are based on previous phylogenetic analyses (Deng et al. 2019), but some problematic sequences were excluded for analyses. For example, the *trnL-trnF* sequences of *Mazus japonicus* (Thunb.) Kuntze 3 (KX807207) in the study of (Deng et al. 2019) were actually under the name of *M. pumilus* (Burm. f.) Steenis in GenBank. Similarly, *trnL-trnF* sequences of two different species (i.e. *Mazus* sp., MK266435 and *Mazus japonicus* var. *delavayi* (Bonati) P.C. Tsoong, KX783521) are completely identical. Such kinds of sequences were excluded for analyses. In addition, two individuals of *Dodartia orientalis* and three individuals of *Lancea tibetica* were included for analyses. Thus, all genera (*Mazus*, *Lancea* and *Dodartia*) of the newly established family Mazaceae (Reveal 2011) were represented. Voucher information and GenBank accession numbers for taxa used in this study are provided in Appendix 1.

Based on previous studies (Schäferhoff et al. 2010; Refulio-Rodriguez and Olmstead 2014; Luna et al. 2019; Xia et al. 2019; Liu et al. 2020), 14 taxa representing 12 genera in five families (*Pedicularis* L., *Rehmannia* Libosch. ex Fisch. & C.A. Mey. and *Striga* Lour. [Orobanchaceae], *Paulownia* Siebold & Zucc. [Paulowniaceae], *Erythranthe* Spach, *Mimulus* L. and *Phryma* L. [Phrymaceae], *Wightia* Wall. [Wightiaceae], *Callicarpa* L., *Lamium* L., *Premna* L. and *Vitex* L. [Lamiaceae]) were selected as outgroups for the cpDNA dataset. While, because of the high divergence of nrITS sequences, only eight species from the above-mentioned families were selected as outgroups.

DNA extraction, amplification and sequencing

Total genomic DNA was obtained from silica-dried leaves using the CTAB procedure of Doyle and Doyle (1987). After extraction, the DNA was re-suspended in double-distilled water and kept at -40 °C for polymerase chain reaction (PCR) amplifications.

The DNA amplifications were performed in a thermocycler (Eppendorf Scientific, Inc., Westbury, NY, USA). Based on Deng et al. (2019), four cpDNA regions (*matK*, *rbcL*, *rps16* and *trnL-trnF*) and nrITS were selected for phylogenetic reconstruction. Primers, protocols for PCR, sequencing followed those in Deng et al. (2019) and references therein.

Phylogenetic analysis

Sequences were initially assembled and edited with Geneious v.7.1.7 (Kearse et al. 2012) and aligned using MUSCLE (Edgar 2004) as implemented in Geneious v.7.1.7 (Kearse et al. 2012). The final alignments were manually adjusted in PhyDe v.0.9971 (Müller et al. 2010). The four chloroplast DNA regions were combined directly because the plastid genome is mostly uniparentally inherited (Soltis and Soltis 1998) and supposedly safe to be combined in phylogenetic analyses (Olmstead and Sweere 1994). Nuclear (ITS) and the combined plastid data set were analyzed separately using maximum likelihood (ML) and Bayesian inference (BI) methods.

ML analyses were performed using RAxML-HPC2 v.8.2.9 (Stamatakis 2014) as implemented on the CIPRES Science Gateway (http://www.phylo.org/) (Miller et al. 2010) under the GTRGAMMA model. The partitioned model (-q) was used for the concatenated plastid data, bootstrap iterations (-# | -N) set to 1000, and other parameters followed default settings.

BI analyses using Markov chain Monte Carlo (MCMC) methods (Yang and Rannala 1997) were performed with MrBayes v3.2.2 (Ronquist et al. 2012) and implemented on the CIPRES Science Gateway (http://www.phylo.org/) (Miller et al. 2010). The optimal substitution models were selected using Model Finder (Kalyaanamoorthy et al. 2017) plugin in PhyloSuite (Zhang et al. 2018). Model parameters were estimated directly during the runs. For each Bayesian analysis, four MCMC chains were run simultaneously for 20 million generations. Each run began with one random tree and sampled one tree every 1000 generations. At the end of the run, chain convergence and estimated sample size (ESS) parameters were assessed with Tracer v.1.6.0 (Rambaut et al. 2014). A 50% majority-rule consensus tree was calculated for each dataset after discarding the first 25% of the trees as burn-in. In the resulting summary tree, posterior probability values (PP) ≥ 0.95 were considered to be strongly supported (Suzuki et al. 2002).

Results

Sequence and alignment characterization

Ten sequences were newly generated for this study (Appendix 1). The resulting combined and aligned cpDNA dataset contained 4514 positions (including gaps), of which 1287 positions belong to *matK*, 1266 to *rbcL*, 963 to the *rps16* partition and 998 to the *trnL-trnF* spacer. Of these 1259 (27.89%) nucleotides were variable in the dataset (Table 1). The aligned nrITS dataset includes 641 nucleotides, of which 300 (46.80%) were variable (Table 1).

Table 1. Properties and best-fitting models of data partitions used in this study.

Data matrix	Aligned positions	Variable characters	GC content (%)	AIC selected model
matK	1287	431	33.4%	GTR+F+G4
rbcL	1266	172	43.8%	GTR+F+I+G4
rps16	963	333	33.4%	GTR+F+G4
trnL-trnF	998	323	35.4%	GTR+F+G4
Combined cpDNA matrix	4514	1259	37.2%	GTR+F+I+G4
nrITS	641	300	60.1%	GTR+F+I+G4

Phylogenetic analysis of Mazaceae

In all analyses, the monophyly of Mazaceae was strongly supported (Figs 3, 4; ML BS: 100%, BI PP: 1.00; all values reported in this order below). Because the taxon sampling is different in the datasets of cpDNA and nrITS, we did not combine them for analyses.

Three subclades can be identified in the cpDNA (Fig. 3) as well as nrITS trees (Fig. 4). The two individuals of *M. lanceifolius* consistently form a clade sister to the rest of Mazaceae. Within the rest of the family, *Dodartia-Lancea* clade is sister to *Mazus* (Figs 3, 4). In both ML and BI analyses, a sister relationship between *Lancea* and *Dodartia* is well supported (87%, 1.00 in cpDNA tree; 92%, 1.00 in nrITS tree). Monophyly of *Mazus* is also strongly supported (97%, 1.00) based on cpDNA dataset while moderately supported in nrITS analyses (62%, 0.93). Relationships within the genus *Mazus* are not fully resolved (Figs 3, 4). The "*M. lanceifolius*" misidentified in Deng et al. (2019) was found to be grouped with *M. sunhangii* based on cpDNA analyses with low support values (Fig. 3), while emerging as an isolated lineage in nrITS analyses when ITS sequence of *M. sunhangii* was not available (Fig. 4).

Taxonomic treatment

***Puchiumazus* Bo Li, D.G. Zhang & C.L. Xiang, gen. nov.**
urn:lsid:ipni.org:names:77213610-1
Fig. 1

Type. *Puchiumazus lanceifolius* (Hemsl.) Bo Li, D.G. Zhang & C.L. Xiang ≡ *Mazus lanceifolius* Hemsl., in: *J. Linn. Soc.*, *Bot.* 26 (174): 181. 1890.

Diagnosis. The new genus is characterized by having quadrangular to somewhat ribbed stems and opposite, narrowly lanceolate leaves (Figs 1, 5A1–A3). *Puchiumazus* is sister to a clade composed of *Dodartia*, *Lancea* and *Mazus*. Morphologically, it is most similar to *Mazus*, but it differs in having quadrangular stems, lanceolate leaves (vs. terete stems and usually obovate-oblong leaves).

Description. Perennial herbs. Rhizomes fleshy, white, horizontal. Root thin, fibrous. Stems erect, unbranched, glabrous, up to 30 cm tall, old stems quadrangular, glabrous, young stems inconspicuously quadrangular to obtusely ribbed, minutely puberulent. Leaves opposite, petiole inconspicuous to nearly absent; leaf blade narrowly

lanceolate, 5.5–8.5 × 0.8–1.1 cm, submembranaceous to papery, adaxially green, pubescent, abaxially pale green, (sub)glabrous, base cuneate, margin basally entire and apically sparsely serrate, apex acute to long acuminate; lateral veins 3–5 pairs, abaxially raised and adaxially slightly depressed. Racemes terminal, 3–6 cm, flowers remarkably sparse, less than 6; pedicels 4–7 mm, sparsely puberulent; bracts tiny, narrowly lanceolate to linear. Calyx funnelform, 4–6 mm, sparsely pubescent outside, subglabrous inside, 5-lobed; lobes narrowly triangular to lanceolate, as long as tube in length, midrib conspicuous, apex acute. Corolla creamy yellow, 1.8–2.2 cm long, densely puberulent outside; tube straight, cylindric, long exserted from calyx, gradually dilated; limb 2-lipped, reddish in throat, posterior lip bilobed, lobes orbicular, anterior lip trilobed, lobes subequal, rounded. Stamens 4, didynamous, inserted on corolla tube, included, anterior pair longer; anthers bithecal, locules divergent, apically connivent; filaments filiform, glabrous. Styles included, glabrous, persistent; stigma 2-lamellate. Capsule ovoid, ca. 2 × 3 mm, glabrous.

Etymology. The generic name is derived from "*Puchiu*" (in honor of Prof. Pu Chiu Tsoong (1906–1981), who was a prominent Chinese taxonomist specializing in the taxonomy of Scrophulariaceae in the traditional sense) and "*mazus*", indicating that the new genus was separated from *Mazus* and is morphologically similar to it.

Common name (assigned here). Bu Qiu Cao Shu (补求草属; Chinese name).

Distribution. According to our data, this genus is endemic to Central China. It is known only from Hubei (Jianshi), Sichuan (Dayi and Dujiangyan) and Chongqing (Wushan) and can be found under evergreen broad-leaf forest at elevations of 600–1250 m.

Puchiumazus lanceifolius **(Hemsl.) Bo Li, D.G. Zhang & C.L. Xiang, comb. nov.**
urn:lsid:ipni.org:names:77213611-1
Fig. 1

Mazus lanceifolius Hemsl., in: *J. Linn. Soc.*, *Bot.* 26(174): 181. 1890. Lectotype (**designated here**): China. Hubei province (Hupeh): Jianshi (Chienchih), March 1889, *A. Henry 5837* (K barcode K001079356 [photo!]). Basionym.

Phenology. Flowering and fruiting from March to July.

Common name (assigned here). Bu Qiu Cao (补求草; Chinese name).

Additional specimens examined. China. Sichuan Province (Szechuen): South Wushan, March 1889, *A. Henry 7250* (K barcode K001079357 [photo!]); Duajiangyan City, Qingchengshan Mountain, under evergreen broad-leaf forest, 1200 m elev., 3 June 2020, *X.X. Zhou et al. LB1067*; Mianyang City, Dayi County, Qianfoshan Mountain, 850 m elev., 8 June 2020, *X.X. Zhou et al. LB1067-2.*

Note. In the protologue of *Mazus lanceifolius*, two collections from Sichuan (*A. Henry 7250*) and Hubei (*A. Henry 5837*), China, respectively, were simultaneously listed without exact type designation because that was not the practice in the 19th

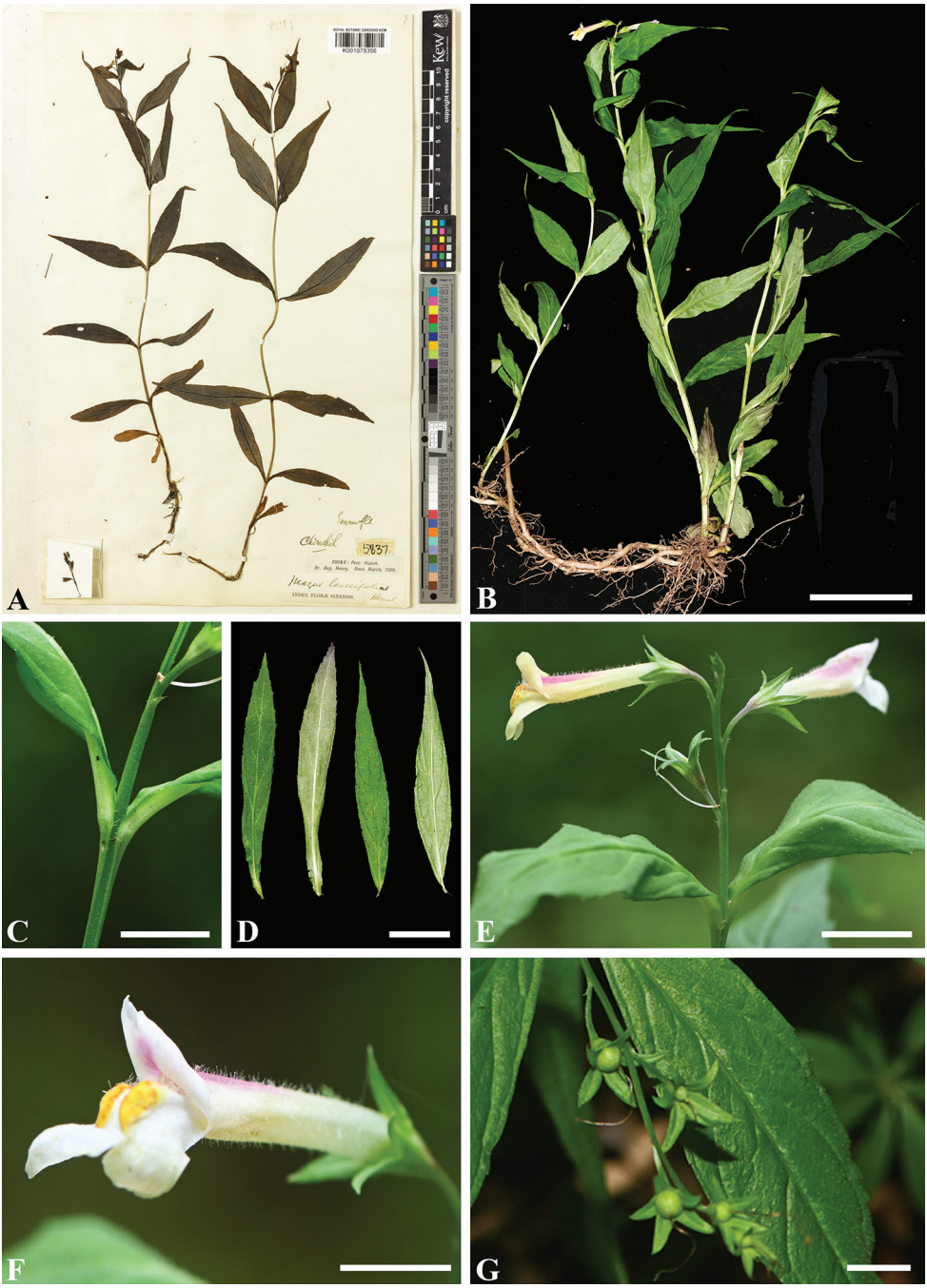

Figure 1. *Puchiumazus lanceifolius* (≡ *Mazus lanceifolius*) **A** lectotype deposited at K (*A. Henry 5837*, barcode K001079356) **B** habit **C** stem, showing the obtuse ribs **D** leaves **E** inflorescence **F** flower in lateral review **G** young fruits. Scale bars: 5 cm (**B**); 0.5 cm (**C, F, G**); 2 cm (**D**); 1 cm (**E**).

century. After checking all floras and literature dealing with *Mazus* in China, we are certain that *M. lanceifolius* has not been lectotypified before. Thus, we here propose the specimen *A. Henry 5837* (Kew barcode: K001079356) as lectotype of *M. lanceifolius* (Fig. 1A) in accordance with article 9.3 of the *International Code of Nomenclature for Algae*, *Fungi*, and *Plants* (*Shenzhen Code*) (Turland et al. 2018).

Mazus fruticosus **Bo Li, D.G. Zhang & C.L. Xiang, sp. nov.**
urn:lsid:ipni.org:names:77213612-1
Fig. 2

Type. China. Hubei Province: Shennongjia Forestry District, Laoyaya to Luoboxi, on rocky cliffs, 110°29'07.98"N, 31°19'23.92"E, 1282 m elev., 6 June 2012, *D.G. Zhang zdg6673* (Holotype: JIU!).

Diagnosis. *Mazus fruticosus* differs from all other conspecific taxa by being a shrub with numerous and much branched stems and having opposite to subopposite leathery leaves that are acutely serrate on apical half.

Description. Shrubs, 25–55 cm tall. Stems woody, numerous branched, old stems greyish brown, terete, leafless, glabrous, young stems and branchlets brown, densely puberulent. Leaves nearly fascicled on the top of branchlet, opposite to subopposite, subsessile; lamina lanceolate, leathery, 3.5–5.5 × 0.7–1.1 cm, adaxially green, subglabrous to sparsely puberulent, abaxially light green, subglabrous, puberulent on veins, apex acute to acuminate, base cuneate, margin acutely serrate on apical half; midrib conspicuous abaxially, lateral veins inconspicuous; petioles nearly absent, densely puberulent. Racemes terminal, ascending to 7.5 cm long, lax, multiflowered; pedicels slender, 1–1.5 cm long, puberulent; bracts narrowly lanceolate, 3–4 mm long, puberulent. Calyces broadly campanulate, ca. 5 mm long, slightly enlarged in fruit, 5-veined, pubescent outside, pubescent to subglabrous inside; lobes 5, broadly triangular, as long as tube, apex acute, midrib conspicuous, lateral veins inconspicuous. Corolla purple, dotted yellow on palate, 1.6–1.9 cm long, puberulent to subglabrous outside, tube cylindric, 1.1–1.3 cm long, exserted from calyx; limb 2-lipped, upper lip bilobed, erect, lobes triangular ovate; lower lip trilobed, middle lobe narrowly ovate, ca. 3 mm long, smaller than lateral lobes, lateral lobes spreading away from middle lobe, broadly ovate to rectangular; palate comprising 2 longitudinal elevations extending from point of filament fusion to base of lower lobes, with sparse erect hairs. Stamens 4, didynamous, glabrous, inserted at the same level in distal part of tube, included; anterior pair longer, curved, appressed to corolla tube, posterior pair spreading; anthers bithecal, positioned adjacent to corolla tube on upper lip; filaments filiform, glabrous. Styles 1.4–1.7 cm long, included, exserted beyond anthers, stigma 2-lamellate. Capsule globose, ca. 4 mm in diam, apex rounded, included by persistent calyx.

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

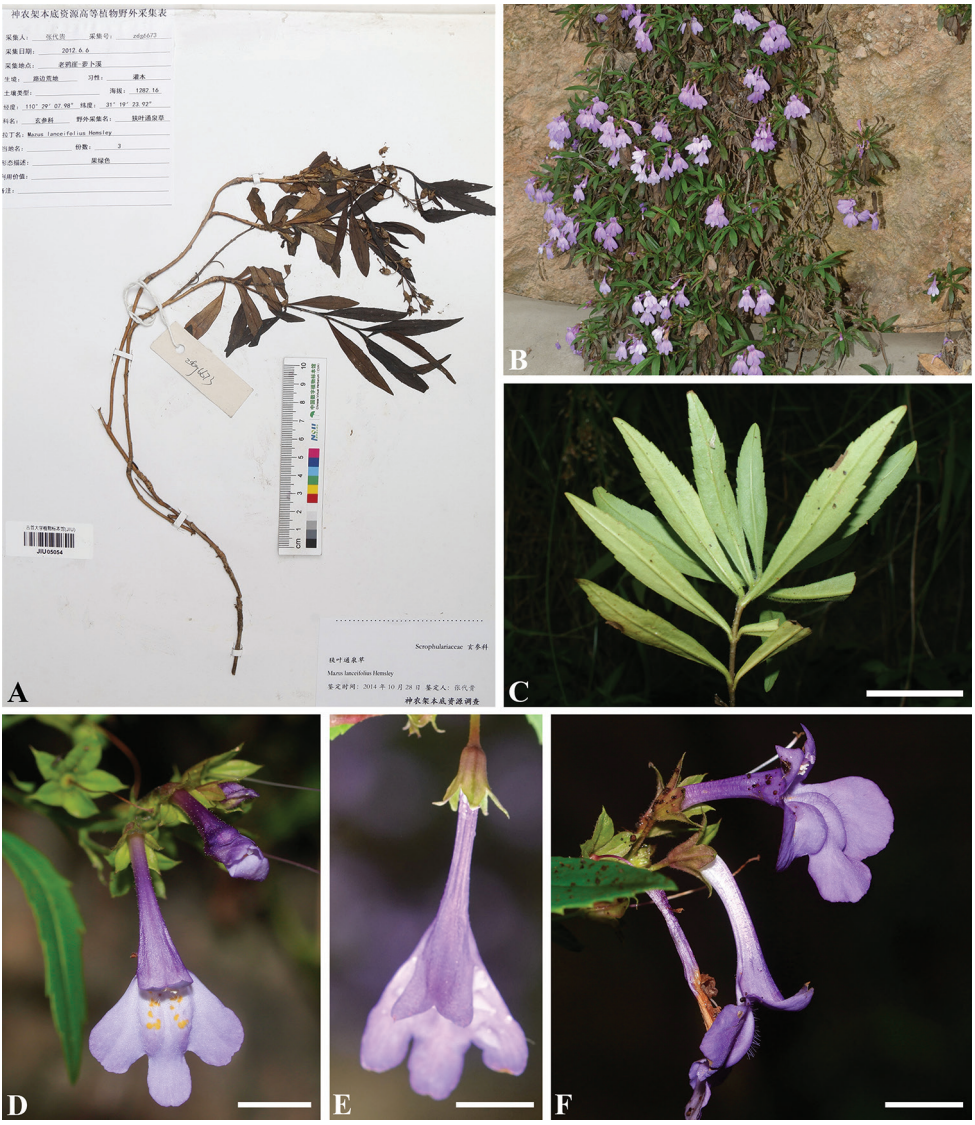

Figure 2. *Mazus fruticosus* **A** voucher of "*Mazus lanceifolius*" sampled in Deng et al. (2019), deposited at JIU (the herbarium of Jishou University, Hu'nan, China) **B** habit and habitat **C** leaves **D** flower in frontal view, showing morphology of its lower lips **E** flower in frontal view, showing morphology of its upper lips **F** flowers in lateral view. Scale bars: 2 cm (**C**); 0.5 cm (**D, E, F**).

Common name (assigned here). Guan Zhuang Tong Quan Cao (灌状通泉草; Chinese name).

Distribution and habitat. *Mazus fruticosus* is currently known only from Shenlongjia Forest District in Hubei Province, central China. It frequently occurs on rocky cliffs or near evergreen mixed forests at an elevation of 1100–1250 m.

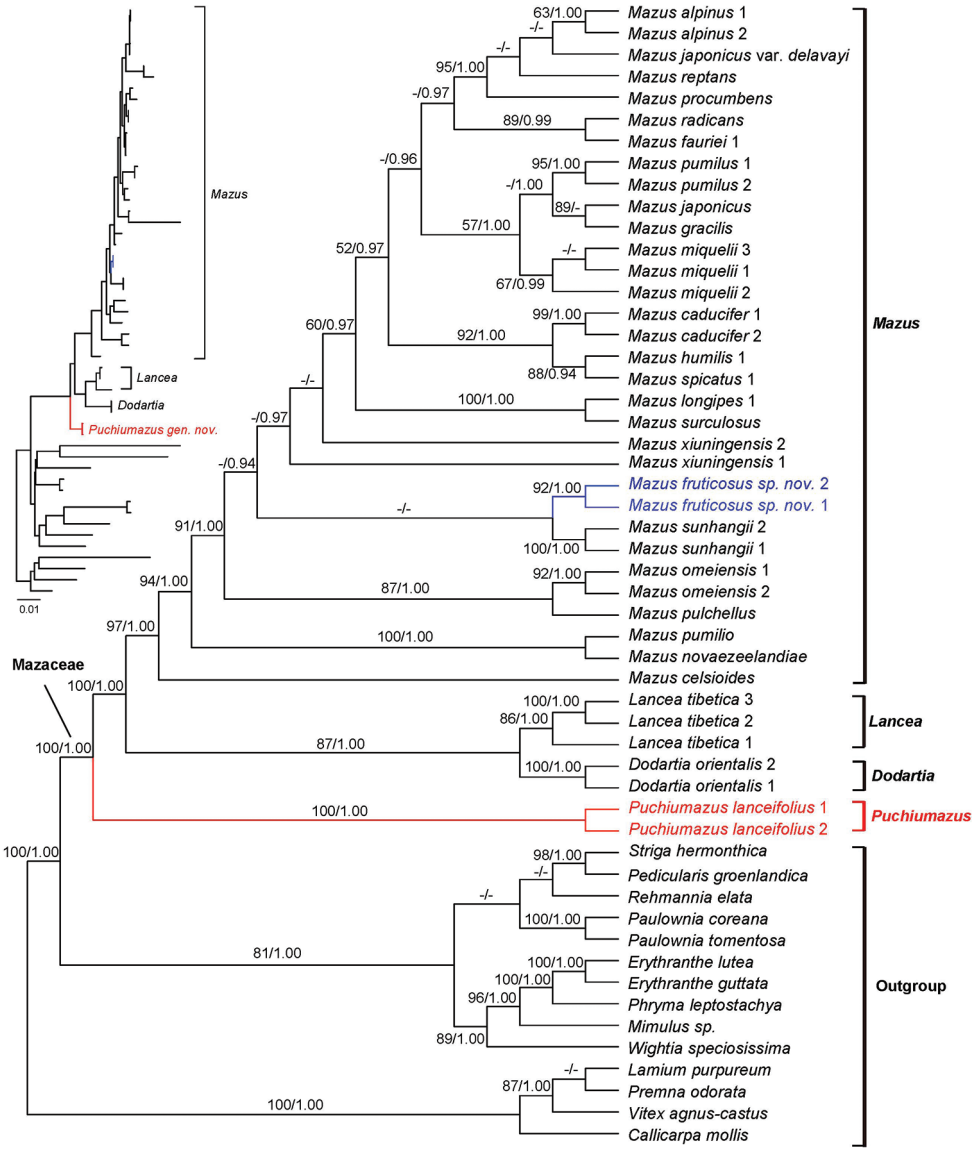

Figure 3. Maximum Likelihood phylogram of Mazaceae as inferred from analysis of combined dataset of *matK*, *rbcL*, *rps16* and *trnL-trnF*. Support values ≥ 50% BS or 0.90 PP are displayed near the branches following the order ML-BS/BI-PP.

Additional specimens examined. China. Hubei Province: Shennongjia Forestry District, 29 March 2012, *D.G. Zhang y1071* (JIU!); 11 May 2012, *D.G. Zhang zdg00023* (JIU!); 17 August 2012, *D.G. Zhang 00006* (JIU!); 21 May 2013, *D.G. Zhang 130521012* (JIU!); 23 April 2015, *D.G. Zhang 0423007* (JIU!).

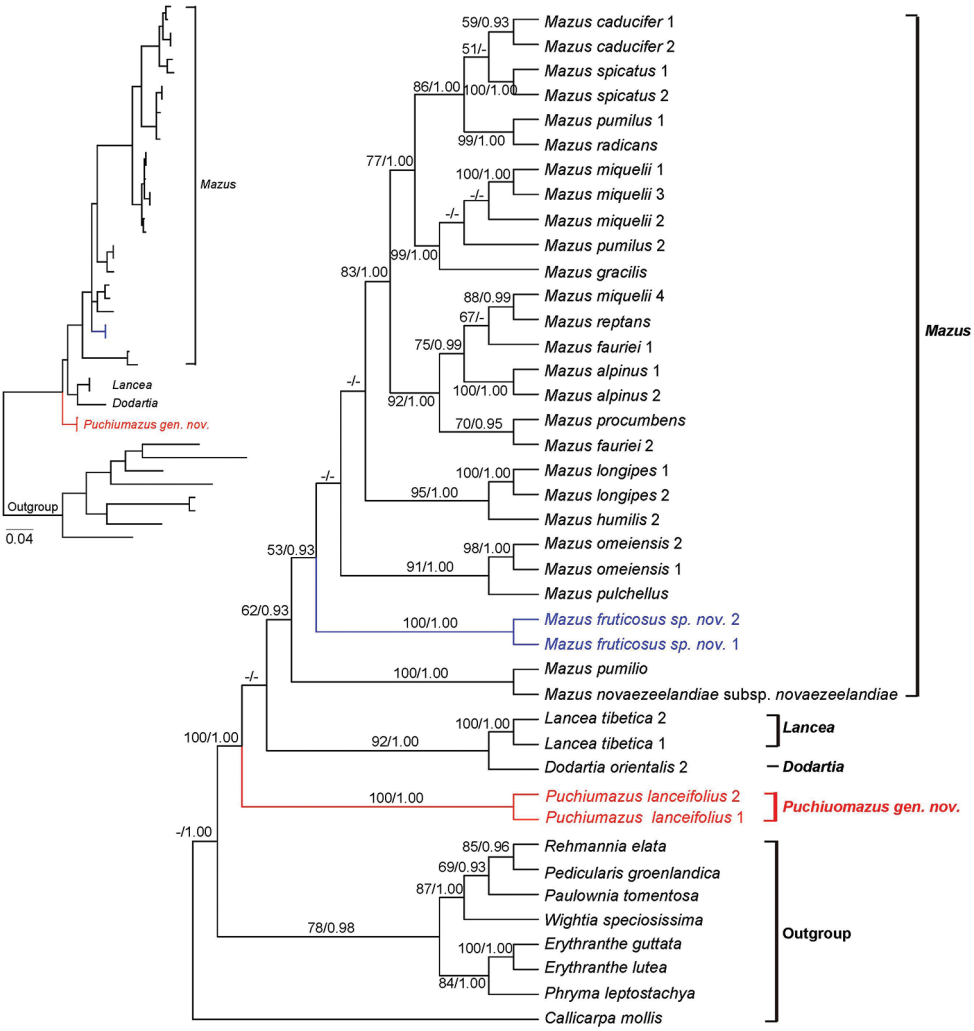

Figure 4. Maximum Likelihood phylogram of Mazaceae as inferred from analysis of nrITS. Support values ≥ 50% BS or 0.90 PP are displayed near the branches following the order ML-BS/BI-PP.

Key to the four genera of Mazaceae

1 Stems quadrangular or somewhat ribbed; leaves opposite..... ***Puchiumazus***

– Stems not quadrangular; leaves rosette, alternate or rarely opposite to subopposite.....**2**

2 Stems much branched; leaves reduced, scale-like; lower corolla lip without palate.....***Dodartia***

– Stems inconspicuous or unbranched, rarely much branched in *Mazus*; Leaves not reduced; lower lip with distinct palate.....**3**

3 Fruit usually completely enclosed in calyx when mature ..... ***Mazus***

– Fruit half enclosed by calyx when mature..... ***Lancea***

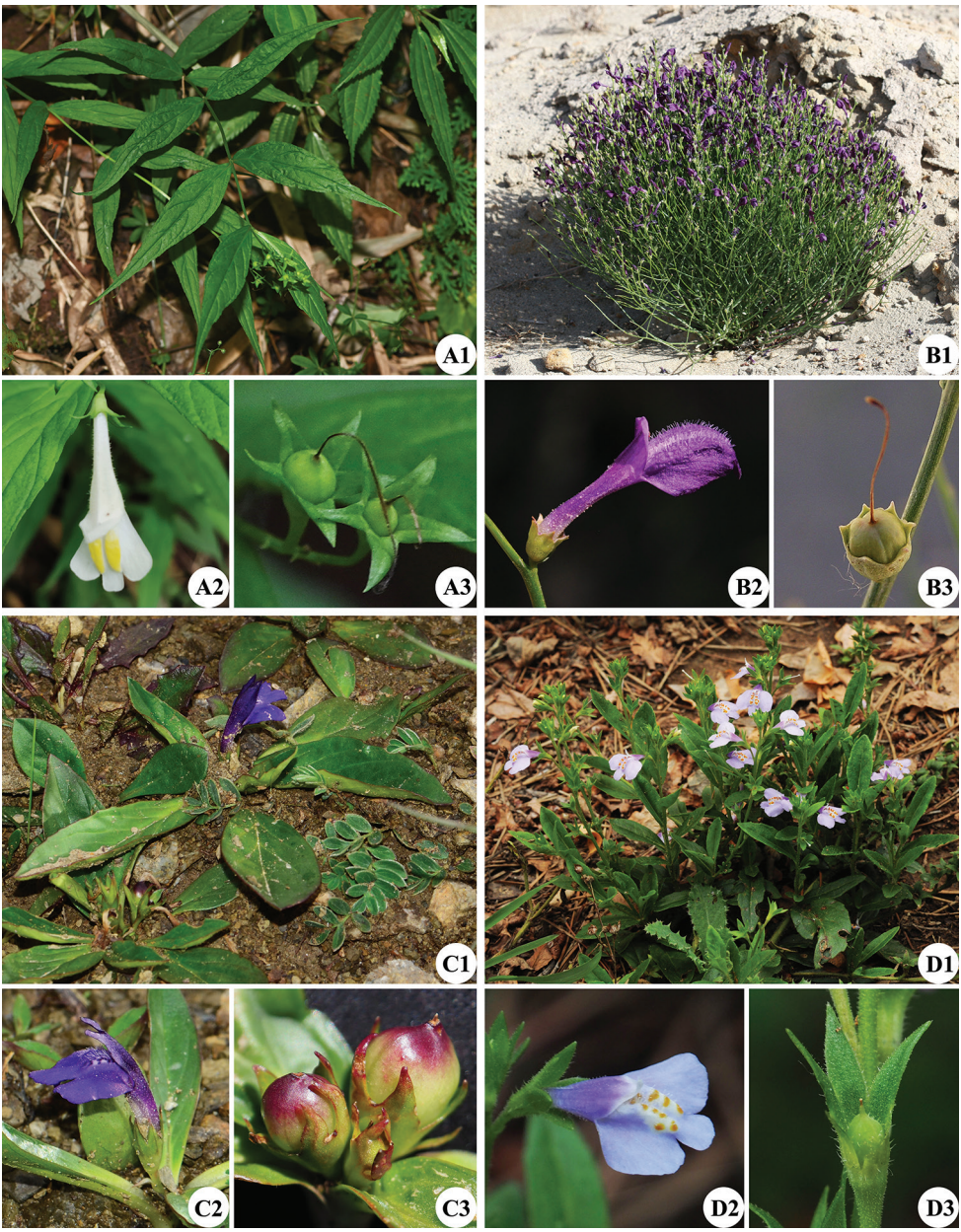

Figure 5. Morphological comparisons of the four genera of Mazaceae **A** *Puchiumazus lanceifolius* **B** *Dodartia orientalis* **C** *Lancea tibetica* **D** *Mazus stachydifolius* **A1, B1, C1, D1** habits **A2, B2, C2, D2** flowers **A3, B3, C3, D3** fruits.

Discussion

We here reconstruct the phylogeny of Mazaceae based on a combined cpDNA dataset of four markers (*matK*, *rbcL*, *rps16* and *trnL-trnF*), and nrDNA ITS dataset, which

have been used previously to infer relationships within Mazaceae (Deng et al. 2019; Yamamoto 2020) and among Lamiales (Refulio-Rodriguez and Olmstead 2014; Liu et al. 2020). The monophyly of Mazaceae is recovered as reported in previous work (Deng et al. 2019) relying on the same molecular markers. The major difference is that the third clade identified in the present study was not sampled by Deng et al. (2019).

Based on our analyses (Figs 3, 4), Mazaceae is composed of four genera (Fig. 5), including the new genus *Puchiumazus* described here. Three major clades can be identified for a re-circumscribed Mazaceae, and the cladogram is accompanied by some general morphological characters and geographical distribution patterns. The first clade is composed of two individuals of the new monotypic genus *Puchiumazus* (Figs 1, 5A1–A3), which is currently only known from three provinces in central China. Morphologically, the new genus can be distinguished clearly from other genera by having quadrangular to somewhat ribbed stems and opposite, narrowly lanceolate leaves.

The second clade consists of *Dodartia* (Fig. 5B1–B3) and *Lancea* (Fig. 5C1–C3). Both genera have broader distribution area than *Puchiumazus*, with *Lancea* always found at high elevations in QTP and *Dodartia* distributed in southern Russia and western to central Asia; it is cultivated as medical herb which has increased its distribution. Morphologically, both genera have small scale-like leaves (with a basal rosette of larger leaves in *Lancea*). Another important character is that ca. half of the capsule is enclosed by fruiting calyx and that calyx-teeth are much shorter than the fruit (Fig. 5B3, C3). In *Puchiumazus*, the style is persistent and ca. 2/3 of the fruit is enclosed in the fruiting calyx with calyx-teeth being much longer than the fruit. Calyx of *Mazus* is usually at least 1–2 times longer than capsule (e.g., Fig. 5D3).

Species of *Mazus* comprise the third clade, which is well supported in the cpDNA tree (94%, 1.00; Fig. 3), but moderately supported in the nrITS phylogeny (62%, 0.93; Fig. 4). *Mazus* is the largest genus of Mazaceae and it is widely distributed in East Asia and Australia. It can be distinguished from the other three genera by the more or less secund inflorescences and a corolla with a palate on the lower lip. Using the same DNA markers, Deng et al. (2019) produced a fully resolved phylogeny of *Mazus* in which five clades of the genus were highly supported (see Fig. 4 of their study). The interesting finding is that we cannot recover a similar topology, although the data of most species come from their dataset. Part of the reason for this may be that some sequences generated for their study were wrongly submitted to GenBank (see samples in Material and methods). Another possible reason is that they did not consider the topology incongruence between cpDNA and nrITS sequences, but concatenated the data for their analyses.

Phylogenetic analyses in our study did not support the sectional classification (i.e. *Lanceifoliae*, *Mazus* and *Trichogymus*) of *Mazus* proposed by Hong et al. (1998). At that time, *Mazus lanceifolius* was placed within *Mazus*, which we here recognize as a new genus. In addition, monophyly of the remaining two sections was also not supported, which was also the case in the study of Deng et al. (2019). Accordingly, they proposed a new infrageneric classification of *Mazus*, with two subgenera, *Mazus* and *Notomazus* T. Deng, N. Lin & H. Sun. Subgenus *Mazus* comprises most of the spe-

cies and is native to Asia, while subgenus *Notomazus* comprises all species native to Australia and New Zealand. However, the monophyly of the two subgenera were not supported in our study. In both cpDNA and nrITS trees, *Mazus radicans* (Hook.f.) Cheeseman from subgenus *Notomazus* is deeply nested in subgenus *Mazus*, indicating it is necessary to redefine subgenus *Notomazus*. Given the discordance between the trees presented here and the one presented in Deng et al. (2019), on the basis of the same sequence data, we think some additional checking of the data, perhaps even resampling of *M. radicans*, is needed before any revision is made to the subgeneric classification of *Mazus*. In addition, a future study including more individuals of each species and more DNA markers (especially single and/or low copy nuclear genes) is necessary to clarify internal relationships within *Mazus*.

Previously, all species of *Mazus* are described as herbs (Yang 1979; Hong et al. 1998; Fischer 2004), but five species (*M. caducifer* Hance, *M. celsioides* Hand.-Mazz., *M. spicatus* Vaniot, "*M. lanceifolius*" [described as *M. fruticosus* in the present study], and *M. sp.*) were recorded as having "no herbaceous stem" in Deng et al.'s (2019) study. Actually, *M. caducifer*, *M. spicatus*, *M. celsioides* have rigid stems that look woody, but are not actually forming wood, thus these should be recognized as having a herbaceous habit. The new species described in the present study is probably the only species with a shrubby habit in the genus *Mazus*. This interesting find will help us to better understand the character evolution of *Mazus*. If *Mazus sp*. in Deng et al.'s (2019) also has a shrubby habit, we can speculate this character originated independently at least twice within the genus.

The abovementioned findings mean that more intensive field collections are necessary even in the post-Flora time. Yang (1979) have noticed the morphological difference between *Puchiumazus lanceifolius* (≡ *Mazus lanceifolius*) and other *Mazus* species. He pointed out that the quadrangular stem is only found in this species, and the nearly entire lanceolate leaves are also rare in *Mazus*, thus he suggested that this species probably is generically distinct. At the same time, he also emphasized that, because no fully developed flowers could be investigated based on specimens, he placed this species within *Mazus*. In this study, the rediscovery of this species offers an opportunity to investigate morphological characters of *P. lanceifolius* and provide a chance to extract DNA for molecular phylogenetic analyses, which led to the establishment of the new genus in the present study.

In recent years, many plants of Lamiales were rediscovered from biodiversity hotspots of China, including *Aeschynanthus monetaria* Dunn (Gesneriaceae; Hu et al. 2020), *Ombrocharis dulcis* Hand.-Mazz. (Lamiaceae; Chen et al. 2016), *Wenchengia alternifolia* C.Y. Wu & S. Chow (Lamiaceae; Li et al. 2012) and *Pedicularis humilis* Bonati (Orobanchaceae; Li et al. 2016). Most of these species had only been collected once before. The new genus described in the present study was also only known from the type collections (*A. Henry 5837*, *7250*) before it was rediscovered. The type specimens of this were, until recently, the only known collections, and as a result, studies on the species since the original 1890 publication have been wanting. The re-investigation of this species is not only providing a chance to amend its

description, but also a chance for a recognition of a new genus and redefinition of the family. The study highlights the important roles of field collections for systematic and biodiversity studies, which are often neglected in this age of biodiversity informatics (Wen et al. 2015).

Acknowledgements

We are grateful to Dr. Hong-Bo Ding (Xishuangbanna Tropical Botanical Garden, CAS) for sharing photos of *Mazus fruticosus*, to Dr. Maarten J. M. Christenhusz (Curtin University) and Dr. Su Liu (Shanghai Chenshan Botanical Garden) for their comments on nomenclature and improving the manuscript, and to Dr. Alan Paton for his comments on lectotypification of *Mazus lanceifolius*. We thank three peer reviewers and academic editors for their input in helping to improve the manuscript. The research was supported by the National Natural Science Foundation of China (31900181) granted to Bo Li, the Sino-Africa Joint Research Center, Chinese Academy of Sciences, CAS International Research and Education Development Program (SAJC201613) granted to Bing Liu, the CAS "Light of West China" program, Yunnan Fundamental Research Projects (2019FI009) and the "Ten Thousand Talents Program of Yunnan" (YNWR-QNBJ-2018-279) granted to Chun-Lei Xiang, the Major Program on Technology Innovation of Hubei Province (2018ACA132) and the Hubei Key Laboratory of Shennongjia Snub-nosed Monkey Conservation Fund (2018SNJ0009) granted to Dai-Gui Zhang, and Postdoctoral Directional Training Foundation of Yunnan Province granted to Fei Zhao.

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Appendix 1

Source publications and GenBank accession numbers of DNA sequences used in this study. If papers were not published, then indicated using superscript, references were listed below the table. GenBank accession numbers of the newly sequenced are marked in bold face. An n-dash (–) refers to a missing sequence.

Taxon	References	GenBank No.				
		matK	*rbcL*	*rps16*	*trnL–trnF*	ITS
Ingroups						
Dodartiao rientalis 1	Schäferhoff et al. (2010)	FN773539	–	FN794091	FN794057	–
Dodartiao rientalis 2	Deng et al. (2019)	MK392230	JQ342984	JQ342982	JQ342981	JQ342980
Lancea tibetica 1	Deng et al. (2019)	MK266276	KX783467	KX807200	KX807205	MK192678
Lancea tibetica 2	Xia et al. (2009); Zuniga et al. (2017)[a]	MF786907[a]	MF786661[a]	FJ172699	FJ172685	FJ172736
Lancea tibetica 3	Chi et al. (2018)	MF593117	MF593117	MF593117	MF593117	–
Mazus reptans	Refulio-Rodriguez and Olmstead (2014); Beardsley and Olmstead (2002)	HQ384502	HQ384872	HQ385147	AF479004	AF478940
Mazus alpinus 1	Deng et al. (2019)	MK266256	KX783481	KX783501	KX783520	MK192641
Mazus alpinus 2	Deng et al. (2019)	–	KX783480	KX783500	KX783519	MK192642
Mazus caducifer 1	Deng et al. (2019)	MK266277	KX783477	KX783497	KX783516	MK192664
Mazus caducifer 2	Deng et al. (2019)	–	KX783487	KX783506	KX783526	MK192659
Mazus celsioides	Deng et al. (2019)	–	KX783486	MK266366	KX783525	–
Mazus fauriei 1	Deng et al. (2019)	MK266255	–	KX783499	MK266420	MK192640
Mazus fauriei 2	Deng et al. (2019)	–	–	–	–	LC034207
Mazus gracilis	Xia et al. (2009)	–	FJ172729	FJ172701	FJ172687	FJ172738
Mazus humilis 1	Deng et al. (2019)	–	–	MK266367	MK266421	–
Mazus humilis 2	Deng et al. (2019)	–		–	–	MK192667
Mazus japonicus var. *delavayi*	Deng et al. (2019)	MK266257	KX783482	KX783502	KX783521	–
Mazus japonicas	Xia et al. (2009); Deng et al. (2019)	MK266259	FJ172728	FJ172700	FJ172686	–
Mazus fruticosus 1	Deng et al. (2019)	MK266261	KX783470	KX783490	KX783509	MK192660

Taxon	References	GenBank No.				
		matK	*rbcL*	*rps16*	*trnL–trnF*	ITS
Appendix 1 Continued						
Mazus fruticosus 2	Deng et al. (2019)	MK266254	KX783471	KX783491	KX783510	MK192649
Mazus longipes 1	Deng et al. (2019)	MK266267	KX783474	KX783494	KX783513	MK192652
Mazus longipes 2	Deng et al. (2019)	–	–	–	–	MK192654
Mazus miquelii 1	Deng et al. (2019)	–	KX783475	KX783495	KX783514	MK192637
Mazus miquelii 2	Deng et al. (2019)	MK266271	KX783476	KX783496	KX783515	MK192655
Mazus miquelii 3	Deng et al. (2019)	MK266272	KX783483	KX783503	KX783522	MK192656
Mazus miquelii 4	Umemoto et al. (2015)	–	–	–	–	LC027734
Mazus novaezeelandiae	Deng et al. (2019)	MK266278	KX783469	KX783489	KX783508	MK192676
Mazus omeiensis 1	Deng et al. (2019)	MK266252	KX807209	KX807203	KX807208	MK192636
Mazus omeiensis 2	Xia et al. (2009); Deng et al. (2019)	–	FJ172731	FJ172702	FJ172688	MK192663
Mazus pulchellus	Deng et al. (2019)	–	KX783472	KX783492	KX783511	MK192638
Mazus pumilus 1	Deng et al. (2019); Jiang et al. (2018)[b]; Xu et al. (2018)[c]	MH265198[b]	MK266346	KX807201	KX807206	MH711724[c]
Mazus pumilus 2	Xia et al. (2009); Schaefer et al. (2011); Deng et al. (2016)	HM850959	HM850162	KX807202	KX807207	FJ172737
Mazus pumilio	Deng et al. (2019)	MK266277	KX783468	KX783488	KX783507	MK192671
Mazus radicans	Deng et al. (2019); Smissen et al. (2015)[d]	–	KT626738[d]	MK266381	–	MK192635
Mazus spicatus 1	Xia et al. (2009)	MK266251	FJ172730	FJ172703	FJ172689	FJ172740
Mazus spicatus 2	Deng et al. (2019)	–	–	–	–	MK192681
Mazus surculosus	Deng et al. (2019)	–	KX783473	KX783493	KX783512	–
Mazus sunhangii 1	Deng et al. (2016)	–	KX783485	KX783505	KX783524	–
Mazus sunhangii 2	Deng et al. (2016)	–	KX783484	KX783504	KX783523	–
Mazus xiuningensis 1	Deng et al. (2019)	–	MK266348	MK266383	–	–
Mazus xiuningensis 2	Deng et al. (2019)	–	MK266349	MK266384	MK266430	–
Mazus procumbens	Deng et al. (2019)	MK266261	KX783478	KX783498	KX783517	MK192647
Puchiumazus lanceifolius 1	This study	**MW373735**	**MW373737**	**MW373739**	**MW373741**	**MW364623**
Puchiumazus lanceifolius 2	This study	**MW373736**	**MW373738**	**MW373740**	**MW373742**	**MW364624**
outgroups						
Paulownia tomentosa	Xu et al. (2018)[c]; Deng et al. (2019)	MK392226	KX783466	KX807199	KX807204	MH711291[c]
Paulownia coreana	Yi and Kim (2016)	NC_031435	NC_031435	NC_031435	NC_031435	–
Lamium purpureum	Wink and Kaufmann (1996); Oxelman et al. (2005); Refulio-Rodriguez and Olmstead (2014)	HQ384493	Z37403	HQ385141	AJ608588	–
Callicarpa mollis	Tsukaya et al. (2003); Refulio-Rodriguez and Olmstead (2014)	HQ384498	HQ384868	HQ385145	HQ412928	AB099648
Vitex agnus–castus	Refulio-Rodriguez and Olmstead (2014); Wagstaff and Olmstead (1997)	HQ384496	U78716	HQ385143	HQ412926	–
Premna odorata	Refulio-Rodriguez and Olmstead (2014)	HQ384494	HQ384866	HQ385142	HQ412925	–
Wightia speciosissima	Xia et al. (2019); Zhou et al. (2014)[e]	MK381318	MK381318	MK381318	MK381318	KJ563189[e]
Mimulus sp.	Zhao et al. (2021)	MT473772	MT473772	MT473772	MT473772	–
Phryma leptostachya	Wagstaff and Olmstead (1997); Bremer et al. (2002); Xu et al. (2018)[c]	AJ429341	U28881	AJ609150	AJ430928	MH711667[c]
Erythranthe lutea	Vallejo-Marín et al. (2016); Arroyo et al. (2019)	NC_030212	NC_030212	NC_030212	NC_030212	MH781192
Erythranthe guttata	Refulio-Rodriguez and Olmstead (2014); Kuzmina et al. (2017)	KJ161979	KJ161981	KJ161978	KJ161975	MG219646
Striga hermonthica	Wicke et al. (2016)	KU212372	KU212372	KU212372	KU212372	–

Taxon	References	GenBank No.				
		matK	*rbcL*	*rps16*	*trnL–trnF*	ITS
Appendix 1 Continued						
Rehmannia elata	Oxelman et al. (2005); Albach et al. (2006); Refulio-Rodriguez and Olmstead (2014)	HQ384505	HQ384874	DQ856490	AJ608572	DQ069315
Pedicularis groenlandica	Refulio-Rodriguez and Olmstead (2014); Tkach et al. (2014)	HQ384503	HQ384873	HQ385148	HQ412930	HG424130

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Supplementary material 1

Figures S1, S2

Authors: Chun-Lei Xiang, Hong-Li Pan, Dao-Zhang Min, Dai-Gui Zhang, Fei Zhao, Bing Liu, Bo Li

Data type: Phylogenetic tree

Explanation note: **Figure S1.** Bayesian Inference (BI) phylogram of Mazaceae based on the combined cpDNA dataset (*matK*, *rbcL*, *rps16*, and *trnL-F*). Bayesian posterior probabilities are shown near the branches. **Figure S2.** Bayesian Inference (BI) phylogram of Mazaceae based on the nrITS dataset. Bayesian posterior probabilities are shown near the branches.

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Link: https://doi.org/10.3897/phytokeys.171.61926.suppl1

PhytoKeys 171: 25–35 (2021)
doi: 10.3897/phytokeys.171.57277
https://phytokeys.pensoft.net

RESEARCH ARTICLE

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Morphology and molecules support the new monotypic genus *Fenghwaia* (Rhamnaceae) from south China

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Academic editor: H. Schaefer | Received 5 August 2020 | Accepted 14 December 2020 | Published 6 January 2021

Citation: Wang G-T, Shu J-P, Jiang G-B, Chen Y-Q, Wang R-J (2021) Morphology and molecules support the new monotypic genus *Fenghwaia* (Rhamnaceae) from south China. PhytoKeys 171: 25–35. https://doi.org/10.3897/phytokeys.171.57277

Abstract

Fenghwaia, a new monotypic genus, along with the new species *Fenghwaia gardeniicarpa*, is described from Guangdong Province, China. The combined features of inferior ovary, cylindrical drupaceous fruits and orbicular and dorsiventrally-compressed seeds with an elongate and pronounced basal appendage make the new genus significantly different from other genera of the family. In addition, its pollen morphology also showed great similarity to other species of this stenopalynous family. The molecular phylogenetic analysis, based on nuclear ribosomal internal transcribed spacer (ITS) and plastid *trnL-F* intron spacer (*trnL-F*) DNA sequence data from the new genus and the other 375 species representing 58 genera of Rhamnaceae, indicates that *Fenghwaia* is nested within the 'rhamnoid' group and sister to the tribe Rhamneae and then both sister to the tribe Maesopsideae. A taxonomic classification key to the 'rhamnoid' group is provided, based on morphological characters. A global conservation assessment is also performed and classifies *Fenghwaia gardeniicarpa* as Near Threatened (NT).

Keywords

Fenghwaia, IUCN, palynology, Rhamnoid, taxonomy

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Introduction

The buckthorns (Rhamnaceae Juss.) are a cosmopolitan family of small trees, shrubs, climbers and, occasionally, herbs and are well represented both in tropical and temperate regions (Raven and Axelrod 1974). This family includes approximately 900 species belonging to about 60 genera and 11 tribes. China hosts 13 genera and 137 species, distributed throughout the whole country, but mostly in south and southwest China (Chen and Schirarend 2007). The species of the family are mainly characterised by having basically cymose inflorescence mostly in the axillary position, usually 4–5-merous flowers, superior to inferior 2–4-loculed ovary with one ovule in each locule and indehiscent schizocarpic or capsular fruits (Medan and Schirarend 2004).

Rhamnaceae was recently revealed to be a monophyletic family and a member of the order Rosales with other eight families, viz. Rosaceae, Barbeyaceae, Dirachmaceae, Elaeagnaceae, Ulmaceae, Cannabaceae, Moraceae and Urticaceae on the basis of molecular evidence (APG IV 2016). The systematic treatment of Rhamnaceae, based on molecular data, morphological, anatomical and geographical information, indicated that Rhamnaceae should divided into three groups, viz. the 'rhamnoid' group, 'ziziphoid' group and the 'ampelozizyphoid' group (Richardson et al. 2000a, 2004; Hauenschild et al. 2016b).

During our field investigation in 2018, a treelet of Rhamnaceae, morphologically similar to *Sageretia* species, but bearing cylindrical and more or less fleshy drupaceous fruits with an inferior ovary and persistent calyxes, somewhat similar to the capsules of *Gardenia*, was found along the riverside of a secondary broad-leaf forest adjacent to a reservoir in Taishan, Jiangmen City, Guangdong Province. This plant is very different from any known species and evoked great interest for clarifying the taxonomic name and its phylogenetic relationship. Several field expeditions from March to August 2019 were subsequently undertaken to clarify its inflorescence and flower characters. Phylogenetic analysis, based on ITS and *trnL-F*, along with morphological comparisons, suggested that this species is best treated as a new taxon belonging to a new genus of Rhamnaceae.

Material and methods

All morphological data of the new species were collected by Light Microscope and Stereomicroscope. Palynological observations followed Guo and Wang (2011). The voucher specimens have been deposited at South China Botanical Garden, Chinese Academy of Sciences (IBSC).

Since nuclear ribosomal internal transcribed spacer region (ITS) and plastid *trnL-F* intron spacer region (*trnL-F*) were already shown to include sufficient information to reconstruct well-supported topologies in Rhamnaceae (Hauenschild et al. 2016a, b), hence a total of five genomic DNAs were extracted from five different individuals, using a modified cetyltrimethylammonium bromide (CTAB) method (Allen et al. 2006).

The primers and PCR protocols were outlined by Hauenschild et al. (2016a, b). The PCR products were sent to Sangon Biotech (Shanghai, China) and sequencing

was conducted using an ABI 3730xl DNA Analyzer (Applied Biosystems, Invitrogen, Foster City, CA, USA).

Multiple locus alignment of 590 operational taxonomic units (OTUs) was performed by Mafft v 7.453 (Katoh et al. 2002) with default parameters and ambiguous positions in the alignment were removed by GBlocks v 0.91b with the parameters (-b4 = 5, -b5 = h) (Castresana 2000). After filtering, the best-fit model (TIM+F+R4) was selected on the basis of the Bayesian Information Criterion (BIC) using Modelfinder (Kalyaanamoorthy et al. 2017) and the phylogenetic tree with the Maximum Likelihood (ML) method was performed by IQ-TREE v1.6.12 (Nguyen et al. 2015). Ultrafast bootstrap values were calculated with 1000 random replicates (Hoang et al. 2018). For Bayesian Inference (BI), we used the GTR+G+I model and performed four independent Markov Chain Monte Carlo (MCMC) reactions in MrBayes v3.2.6 (Ronquist and Huelsenbeck 2003), running five million generations every Markov Chain, sampling one tree every 1,000 generations, rejecting 25% of the trees as burn-in after the value of average standard deviation of split frequencies was lower than 0.01.

Results

All DNA data of 585 OTUs, representing 375 species of 58 genera and 11 Rhamnaceae tribes, released by Hauenschild et al. (2016a), were downloaded from GenBank and merged into our present analysis. The GenBank numbers of the newly-sequenced *Fenghwaia gardeniicarpa* are: *Y.Q.Chen & G.T. Wang* 1223-1, ITS: MN795061, *trnL-F*: MN793985; *Y.Q. Chen & G.T. Wang* 1223-2, ITS: MN795062, *trnL-F*: MN793986; *Y.Q. Chen & G.T. Wang* 1224-1, ITS: MN795063, *trnL-F*: MN793987; *Y.Q. Chen & G.T. Wang* 1224-2, ITS: MN795064, *trnL-F*: MN793988; *Y.Q. Chen & G.T. Wang* 1225, ITS: MN795065, *trnL-F*: MN793989.

The topology of our phylogenetic tree is similar to that of Hauenschild et al. (2016b), but the tribe Paliureae, defined by Hauenschild et al. (2016b) with very weak support, collapsed in our analysis, because of the exclusion of *Hovenia* and *Sarcomphalus*. The new genus *Fenghwaia* is nested into the 'rhamnoid' group and sister to the tribe Rhamneae with weak bootstrap support (BS/PP = 75/0.55), but then both sister to the tribe Maesopsideae with strong support (BS/PP = 100/1) (Fig. 1).

Taxonomic description

***Fenghwaia* G.T. Wang & R.J. Wang, gen. nov.**
urn:lsid:ipni.org:names:77213613-1

Type species. *Fenghwaia gardeniicarpa* G.T. Wang & R.J. Wang.

Diagnosis. *Fenghwaia* is distinctly different from other genera by a character combination of its cucullate flowering petals, inferior ovary with 3-locular and one ovule in each locule, elongate capsular fruit with five longitudinal ridges and verrucose seeds.

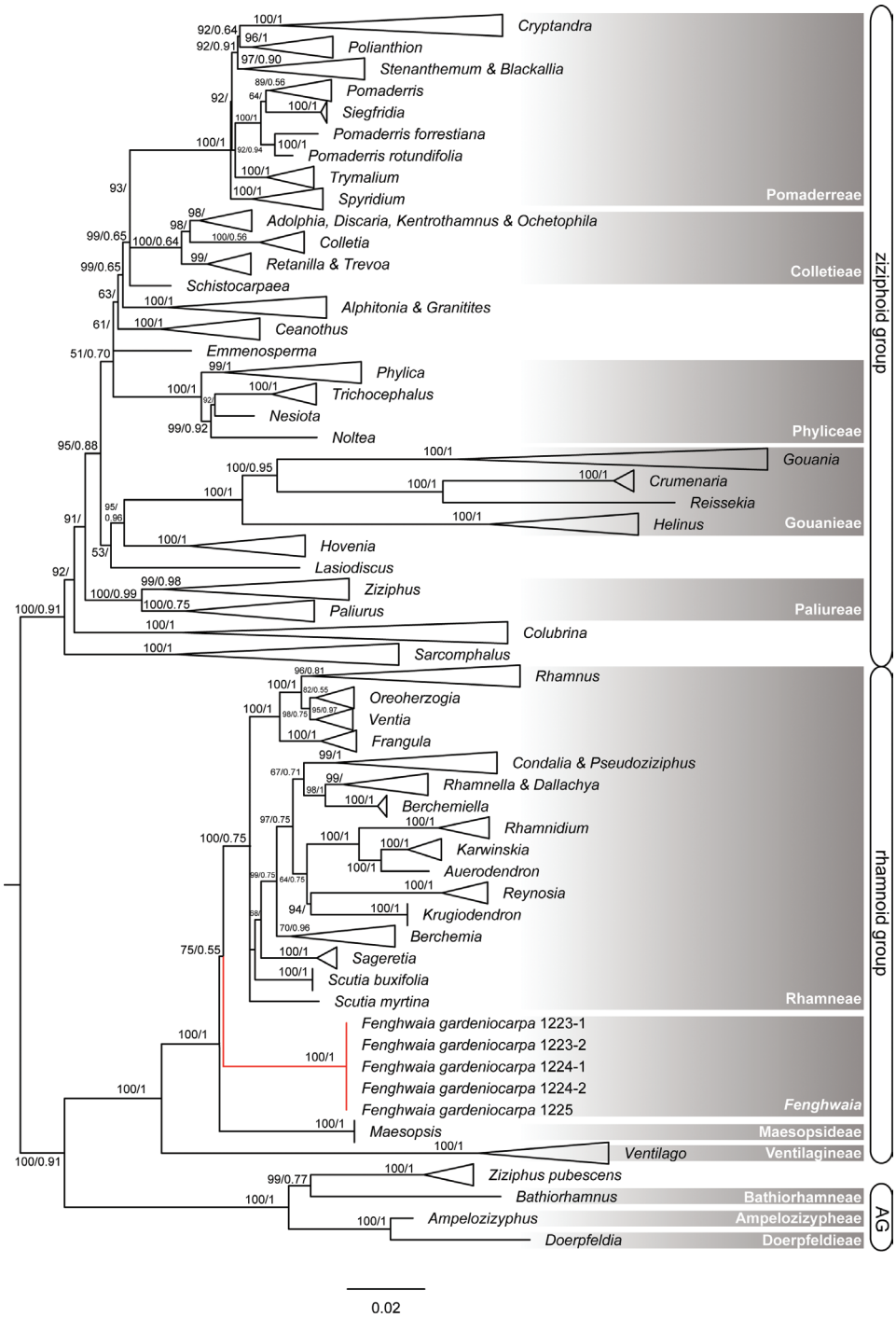

Figure 1. The phylogenetic consensus tree of Rhamnaceae with ML and BI methods, on the basis of ITS and *trnL-F* sequences. AG: 'ampelozizyphoid' group. The numbers above the branches are Maximum Likelihood support values (left) and MrBayes posterior probability (right).

A single species is only known from China.

Etymology. We dedicate this new genus to Professor Chen Fenghwai, a Chinese plant taxonomist, in honour of his great contribution to the botanical gardens in China.

***Fenghwaia gardeniicarpa* G.T. Wang & R.J. Wang, sp. nov.**
urn:lsid:ipni.org:names:77213614-1
Fig. 2

Type. China. Guangdong Province, Jiangmen City, Taishan, Mt. Nanfengshan, under secondary mixed forests, 22°11'N, 112°56'E, elev. ca. 410 m, 6 July 2019, *R.J. Wang, G.T. Wang & G.B. Jiang 1228* (***holotype*:** IBSC0849961; ***isotypes*:** CSH0171170; IBK00421260; IBSC0849962; IBSC0849963; KUN1347949; PE02251842).

Description. Treelet, evergreen, 0.5–2 m tall, slender, much branched at top; main stems dark or brown, slender, glabrous; young branches rusty strigose at surface. Leaves alternate, anisophyllous, often clustering at the top of branches; petiole 2–5 mm long, pubescent; leaf blade 5.5–10.1 × 1.9–4.0 cm, elliptic, oblanceolate-elliptic or ovate, thinly leathery, glabrous both sides, acuminate to caudate at apex, cuneate at base; secondary veins 3–5 each side, mid-rib and secondary veins smooth adaxially and prominent abaxially; margin entire at base and then serrate to apex. Inflorescence in sessile or shortly peduncled, axillary cymes or small thyrses, 3–5-flowered; bracts ca. 0.5–1.0 mm long, lanceolate to broadly triangular, yellow to rusty. Flowers bisexual, actinomorphic, yellowish-green, ca. 4–5 mm in diameter; pedicels very short to 4–6 mm long, glabrous; calyx lobes five, 2.0–3.0 × ca. 1.5 mm, ovate triangular, depressed longitudinally at middle; hypanthium 2–3 mm long, slightly campanulate; petals five, ca. 1.5 mm long, cucullate, each partly covering the pollen-presenting surface of the anthers, shortly clawed at base, concaved at apex; stamens five, antepetalous, ca. 1.3 mm long, enclosed by petals; anthers ca. 0.3 mm long, ovoid, 4-locular, dorsifixed, filaments ca. 1.0 mm long; disc inconspicuous, adnate to the lower part of hypanthium; styles ca. 1.5 mm long, stigma 3-lobed; ovary inferior, 3-1ocular, with one ovule in each locule, ovules anatropous, basal, erect. Fruit drupaceous, more or less fleshy, cylindrical, ca. 1.5 cm long, 0.4–0.6 cm in diam., with five longitudinal ridges on surface, slowly dehiscent at top and then septicidally, glabrous; calyx lobes persistent. Seeds ca. 4 × 3 mm, orbicular, dorsiventrally compressed, brown, verrucose at surface, with an elongate and pronounced basal appendage.

Phenology. Flowering from June to October; fruiting from August to December.

Palynology. The pollen grains of the new species are monads, isopolar, suboblate, radially symmetrical, angulaperturate, 3-zono-colporate apertures and psilate to perforate tectum. The pollen size is 14.9 (13.3–17.1) × 21.5 (16.1–21.1) μm and P/E value is 0.86 (Fig. 3).

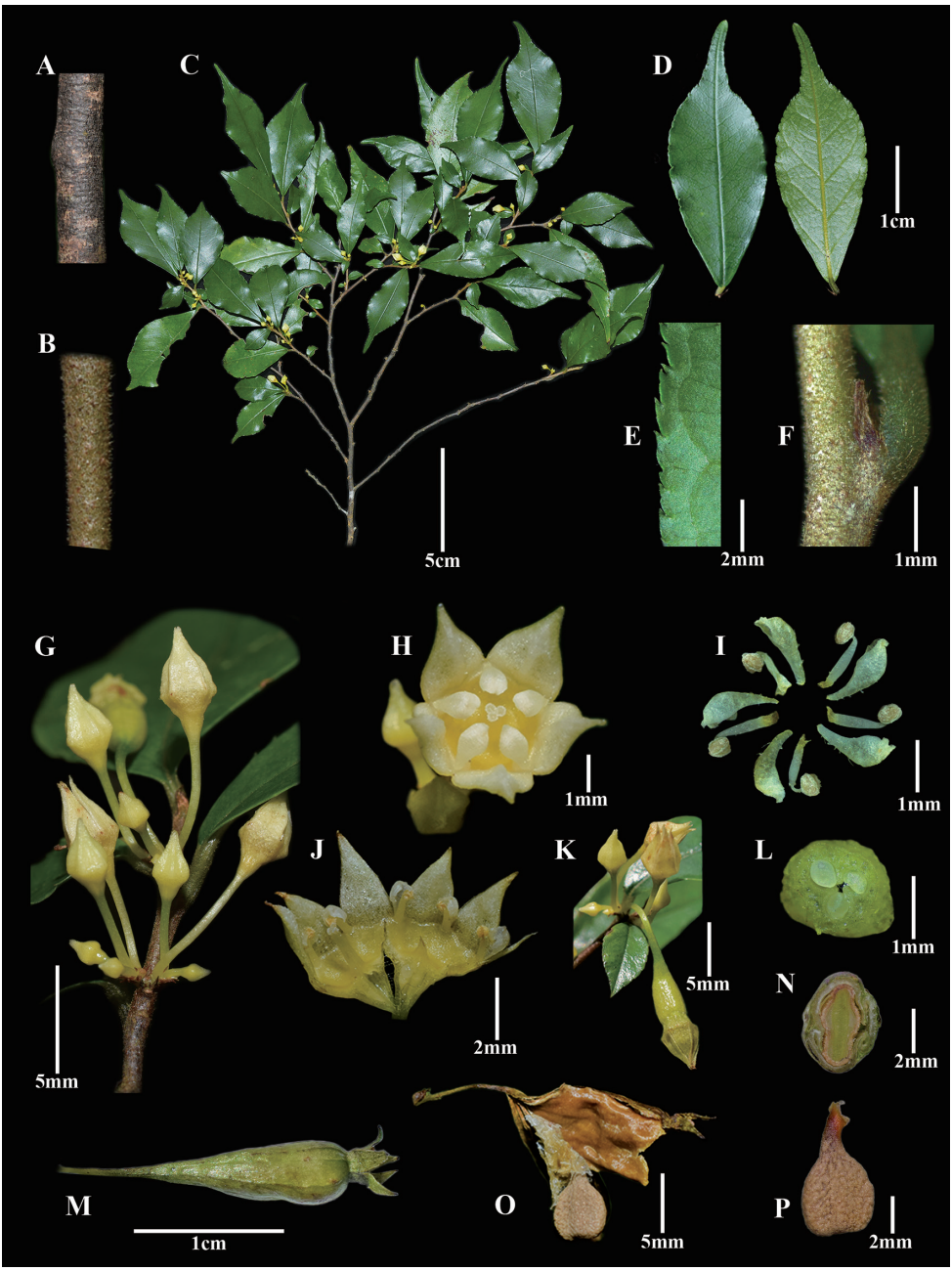

Figure 2. *Fenghwaia gardeniicarpa*: **A** main stem with glabrous surface **B** young stem with pubescent surface **C** fertile branches **D** adaxial (left) and abaxial (right) side of leaf blade, respectively **E** serrated leaf margin **F** stipule **G** inflorescence **H** flower in anthesis **I** morphology of petals and stamens **J** longitudinal section of a flower, showing the stamens enclosed by cucullate petals **K** young fruit **L** transection section of an ovary, showing three ovules **M** mature fruit **N** transection section of mature fruit with only one well-developed seed **O** dehiscent capsule **P** seed, with an elongate and pronounced basal appendage. Photos: G.T. Wang, G.B. Jiang.

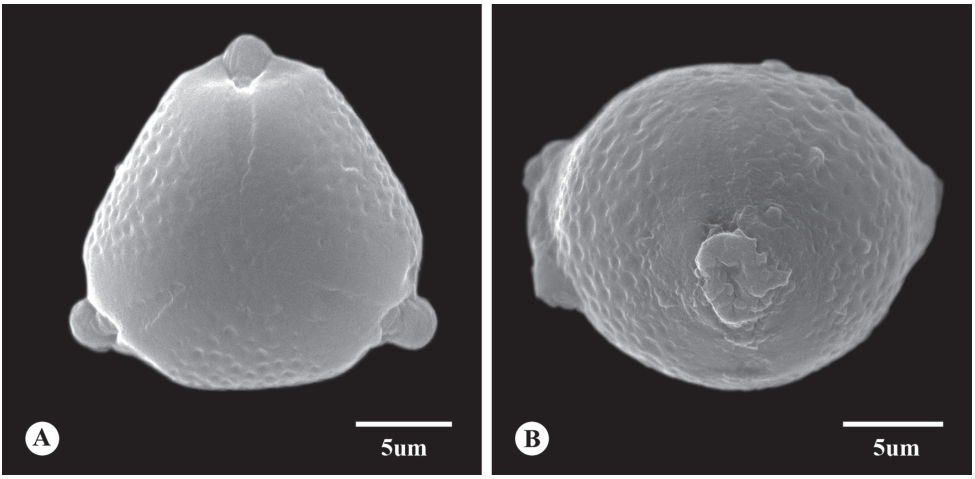

Figure 3. Pollen grains of *Fenghwaia gardeniicarpa*: **A** polar view **B** equatorial view.

Distribution and habitat. *Fenghwaia gardeniicarpa* is endemic to mountains in Jiangmen District, Guangdong Province, China. It grows under secondary mixed forests at altitudes of 230–450 m, mountain slopes with 60–70% canopy density, accompanying herbal *Gahnia tristis* Nees (Cyperaceae) and *Adiantum flabellulatum* L. (Adiantaceae) and woody *Barthea barthei* (Hance ex Benth.) Krasser (Melastomataceae), *Dunnia sinensis* Tutcher (Rubiaceae) and *Illicium dunnianum* Tutcher (Schisandraceae).

Preliminary conservation assessment. About 2000 mature *Fenghwaia gardeniicarpa* individuals from four localities have been found in less than 800 km^2 up to now. This area can be classified as the extent of occurrence. The plants have no any ornamental or medicinal uses. They are well protected in a Nature Reserve and the population is not severely fragmented. In addition, no population decline and no extreme fluctuations caused by natural events have been observed in their habitats. According to the International Union for Conservation of Nature (2012) and IUCN Standards and Petitions Committee (2019), a category of Near Threatened (NT) is recommended for *Fenghwaia gardeniicarpa* for the present.

Etymology. The species name highlights the striking resemblance with fruits of *Gardenia jasminoides* Ellis (Rubiaceae), an unusual and new feature for a fruit of Rhamnaceae.

Vernacular name. Feng Huai Mu (Chinese pronunciation); 封怀木 (Chinese name).

Paratypes. China: Guangdong Province, Jiangmen City, Taishan, Chixi Town, Tonggu Village, 21°55'N, 112°56'E, elev. 440 m, 2 June 2019, *Y.Q. Chen & G.T. Wang 1223, 1224, 1225, 1226* (IBSC!); Guangdong Province, Jiangmen City, Taishan, Chixi Town, Luobo Village, 21°55'N, 112°55'E, elev. 107 m, 20 June 2020, *R.J. Wang & Y.Y. Liu 5928* (IBSC!); Guangdong Province, Jiangmen City, Xinhui, Gudoushan Nature Reserve, 22°9'N, 112°55'E, elev. 231 m, 3 October 2019, *H.G. Ye et al. GDS-00849* (IBSC!).

Discussion

Palynology of *Fenghwaia gardeniicarpa*

Rhamnaceae is a stenopalynous family (Erdtman 1952). The pollen morphology of the Rhamnaceae usually has suboblate to oblate spheroidal or subprolate, a distinct triangular shape in polar view, oblate shape in equatorial view and 3-zonocolporate features. It does not show any special features and the descriptions usually concur with each other (Punt et al. 2003). The tectum of Rhamnaceae can be microreticulate, striate or rugulate to reticulate, baculate, verrucate, psilate, with more or less densely-spaced perforations and this variation of exine ornamentation has usually been used for classifying the pollen type (Schirarend and Köhler 1993; Medan and Schirarend 2004; Perveen and Qaiser 2005). In general, the main features of pollen grains of *Fenghwaia gardeniicarpa* are consistent with those of most other Rhamnaceae species with respect to the shape, polarity, symmetry, aperture number and position, size and tectum ornamentation (Medan and Schirarend 2004). However, the exine ornamentation of *Fenghwaia gardeniicarpa* is more similar to that of the tribe Rhamneae, as observed in *Berchemia* (reticulate), *Frangula*, *Rhamnus* (suprareticulate-rugulate, psilate), *Sageratia* (fossulate-perforate) than to that of the *Maesopsis*-type (baculate) (Punt et al. 2003; Perveen and Qaiser 2005; Naimat et al. 2012).

Phylogenetic relationship of *Fenghwaia*

Based on a phylogenetic analysis of *rbcL* and *trnL-F* sequences of the plastid genome, Richardson et al. (2000b) outlined a new tribal classification of Rhamnaceae, recognising 11 tribes encompassing the informally-named groups of 'rhamnoid', 'ampelozziphoid' and 'ziziphoid'. Our phylogenetic analysis showed that *Fenghwaia* is nested within the 'rhamnoid' group. Thus, the 'rhamnoid' group consists of the tribes of Rhamneae, Maesopsideae and Ventilagineae and the genus *Fenghwaia*. The weak support (ML = 75/BI = 0.55) of the clade Rhamneae/*Fenghwaia* was probably caused by lack of adequate informative sites in the applied fragments. For example, only *trnL-F* sequences of *Maesopsis eminii* were applied in the present analysis. Morphologically, Rhamneae can be easily recognised by its fleshy fruit and 2- or 4-locular ovary. Maesopsideae and Ventilagineae have superior or half inferior ovaries, 1–2-locular, drupe (tribe Maesopsideae), samara or rostrate capsules (tribe Ventilagineae). Moreover, *Maesopsis* differs from all other genera in Rhamnaceae in its single-celled ovary and a style laterally attached to the fruit, rather than apically. Ventilagineae is unique in its fruits with a pronounced apical appendage (Richardson et al. 2000b).

Fenghwaia has an inferior and 3-loculed ovary, orbicular and dorsiventrally compressed seeds with an elongate and pronounced basal appendage, but its morphological characters are obviously different from those of other taxa in the 'rhamnoid' group. In addition, the genera that have an inferior ovary and 3-locular in Rhamnaceae are all in the ziziphoid group, viz. *Phylica*, *Trichocephalus* and *Nesiota* of the tribe Phyliceae,

all genera of the tribe Gouanieae, *Siegfriedia*, *Spyridium* and *Cryptandra* of the tribe Pomaderreae, and *Alphitonia* and *Granitites* of the undefined tribe.

A taxonomic classification key of the 'rhamnoid' group

1 Ovary inferior, 3-locular; fruits dry, cylindrical, with ridges on the surface.... ..... ***Fenghwaia***
– Ovary superior, half-inferior or rarely inferior 1, 2-or 4-locular; fruits with wings, dry membranous rings or fleshy **2**
2 Fruit an apically-winged samara or a rostrate capsule ..... **Ventilagineae**
– Fruit a 1–4-locular drupe, not samara or a rostrate capsule **3**
3 Ovary superior or half-inferior, 2- or 4-locular..... **Rhamneae**
– Ovary superior, 1-locular ..... **Maesopsideae**

Acknowledgements

We are grateful to Professor HU Chi-Ming and Professor XIA Nian-He for their valuable nomenclature recommendation, Mr. YANG Yi for his constructive suggestions during the draft preparation.

The work was supported by the Guangdong Provincial Science & Technology Program (No. 2018B030320004) and the National Wild Plant Germplasm Resource Center for South China Botanical Garden, Chinese Academy of Sciences (ZWGX1905).

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PhytoKeys 171: 37–45 (2021)
doi: 10.3897/phytokeys.171.59562
https://phytokeys.pensoft.net

RESEARCH ARTICLE

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Gigantochloa glabrata (Poaceae, Bambusoideae), a new bamboo species from Yunnan, China

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Academic editor: E. Ruiz-Sanchez | Received 14 October 2020 | Accepted 1 December 2020 | Published 7 January 2021

Citation: Xu Z-C, Liu J-X, Li D-Z (2021) *Gigantochloa glabrata* (Poaceae, Bambusoideae), a new bamboo species from Yunnan, China. PhytoKeys 171: 37–45. https://doi.org/10.3897/phytokeys.171.59562

Abstract

Gigantochloa glabrata N. H. Xia & Y. Zeng ex D. Z. Li & Z. C. Xu, **sp. nov.**, a new species of paleotropical woody bamboo has been described and illustrated from Yunnan, China. The new species is morphologically similar to *G. albociliata* and *G. levis*, but differs from them by having erect culm sheath blades; culm sheath ligules 4–6 mm high, truncate, denticulate; and with a ring of white tomentum on the intranode and below the node. The new species was mistakenly identified as *Gigantochloa albociliata* in the *Flora of China* and was recognised with description of the vegetative characters in 2014, but it was not effectively published. Here, we designate a complete specimen with inflorescence as the type and describe it in accordance with the Code.

Keywords

Gigantochloa, new species, paleotropical woody bamboos

Introduction

Gigantochloa Kurz ex Munro was published as a new genus by Kurz (1864) without any detailed description. Munro described the morphological characters of this genus and validated the publication (Munro 1868). Currently, there are more than 60 species recognised in *Gigantochloa* from all over the world, which are distributed in the tropical lowlands of Southeast Asia (Holttum 1958; Widjaja 1987; Vorontsova et al. 2016), with seven species recorded in China (Li et al. 2006; Zeng et al. 2014). Species

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of *Gigantochloa* are characterised by their pseudospikelets clustered at each flowering branch node, oblong or linear, each with 2–4 florets and one terminal imperfect floret consisting only of an empty lemma, rhachilla internodes obscure, paleas 2-keeled, the keels and the inflexed margins long-ciliate above; lodicules often absent; stamens six, the filaments connated into a hyaline tube which can elongate and become membranous, with anthers apiculate with minutely hispidulous tips (Munro 1868). Since its eastablishment, many bamboo taxonomists have considered it as a "good genus", based on morphological characteristics (Kurz 1875, 1876; Holttum 1958; Clayton and Renvoize 1986; Widjaja 1987).

As a genus of paleotropical woody bamboo, *Gigantochloa* belongs to the subtribe Bambusinae Presl (BPG 2012). It was included in the *Bambusa-Dendrocalamus-Gigantochloa* (BDG) complex, together with *Bambusa* Schreber, *Dendrocalamus* Nees and closely-related small genera (Goh et al. 2010; Goh et al. 2013; Zhou et al. 2017). Morphologically, *Bambusa* can be distinguished from *Gigantochloa* by its conspicuous auricles and florets falling separately. *Dendrocalamus* can be recognised by its free filaments. In our recent molecular phylogenetic study, *Gigantochloa* was well resolved as a monophyletic group (Liu et al. 2020).

By studying the species of *Gigantochloa* from the Yunnan-Myanmar-Thailand floristic region, we found that *G. albociliata*, recorded in *Flora Reipublicae Popularis Sinicae* (Keng and Wang 1996) and *Flora of China* (Li et al. 2006) is not truly *G. albociliata* (Munro) Kurz. Accordingly, a new species needs to be described to clarify this long-existing taxonomic problem.

Materials and methods

All measurements and observation of morphological characters were conducted, based on the specimens at the Herbarium of the Kunming Institute of Botany (**KUN**), Herbarium of the Xishuangbanna Tropical Botanical Garden (**HITBC**) and the Herbarium of the South China Botanical Garden (**IBSC**), as well as the photos of living individuals taken from living collections of the Xishuangbanna Tropical Botanical Garden in the summer of 2019. Pseudospikelets were dissected under an OLYMPUS DP80 digital microscope at Germplasm Bank of Wild Species of the Kunming Institute of Botany. Morphological comparisons with closely-related species (*G. albociliata* and *G. levis* (Blanco) Merr. (Blanco 1837; Merrill 1916)) were based on characters recorded in literature and on the type specimens. The morphological terminology follows McClure (McClure 1966).

Taxonomy

Gigantochloa albociliata (Munro) Kurz was first recorded in Yunnan, southwest China by Sun (1984) and it was included in *Flora Reipublicae Popularis Sinicae* (Keng and Wang 1996), *Flora of China* (Li et al. 2006) and the *Flora of China Illustrations* (Zhang

2007). However, the description and illustrations of the *Flora of China* and the protologues of *G. albociliata* did not match. When we checked the specimens of *Gigantochloa* at the HITBC in 2019, we noticed that the inflorescence specimen, collected by *K. H. He* (no. *C130051*) in 2007, was identical with "*G. albociliata*" in the sense of *Flora of China*. We collected inflorescence material in the living collection of the Xishuangbanna Tropical Botanical Garden again in August 2019. After comparison with specimens of *G. albociliata* and other closely-related *Gigantochloa* species, we could not place it within any described species of *Gigantochloa*. In the meantime, we noticed that this species was recognised by Zeng (2014) as a new species with description of the vegetative characters. Zeng's new name is available via the International Plant Names Index (IPNI 2020); however, according to the Code (Turland et al. 2018), it was not effectively published, because it appeared only in a thesis submitted to a university for the purpose of obtaining a degree, with neither an ISBN number nor statement of the name of the printer, publisher or distributor in the original printed version (Art. 30.9). Here, we added reproductive characters and a detailed morphological comparison to validate the new species as *G. glabrata* N. H. Xia & Y. Zeng. We designate a complete specimen with an inflorescence as the type and describe it in accordance with the Code.

After checking the type specimens and protologue of *Gigantochloa albociliata*, it is confirmed that the true *G. albociliata* is naturally distributed in southern Yunnan, China, as well as northern Myanmar and northern Thailand. In Yunnan, it often grows in mixed forest or roadside.

***Gigantochloa glabrata* N. H. Xia & Y. Zeng ex D. Z. Li & Z. C. Xu, sp. nov.**
urn:lsid:ipni.org:names:77213497-1
"少毛巨竹"(Shao Mao Ju Zhu)
Figures 1, 2

Gigantochloa glabrata N. H. Xia & Y. Zeng in Y. Zeng Taxonomic Studies of *Gigantochloa* in China 36. 2014. *nom. nud.*. 'Type': CHINA. Yunnan: Xishuangbanna Tropical Botanical Garden (XTBG), Menglun, cultivated, 31 Aug 2012, *Y Zeng 17* ('holotype', IBSC).

= *Gigantochloa albociliata* auct. non (Munro) Kurz: C. J. Hsueh & J. L. Sun in Keng f. & Z. P. Wang, Fl. Reippubl. Poppularis. Sin. 9(1): 198. pl. 50, 1–11. 1996; D. Z. Li & Stapleton in Z. Y. Wu, P. H. Raven & D. Y. Hong, Fl. China 22: 47. 2006; L. B. Zhang in C. Y. Wu, P. H. Raven & D. Y. Hong, Fl. China Illustr. 22: 46. fig. 46:1–11, 2007.

Diagnosis. *Gigantochloa glabrata* has erect culm sheath blade and the culm sheath covered with sparsely deciduous setae, with truncate apex. It is morphologically similar to *G. albociliata* and *G. levis*, but can be easily distinguished from them by having erect blades; culm sheath ligule 4–6 mm high, truncate, denticulate; a ring of white tomentum on the intranode and below the node (Table 1).

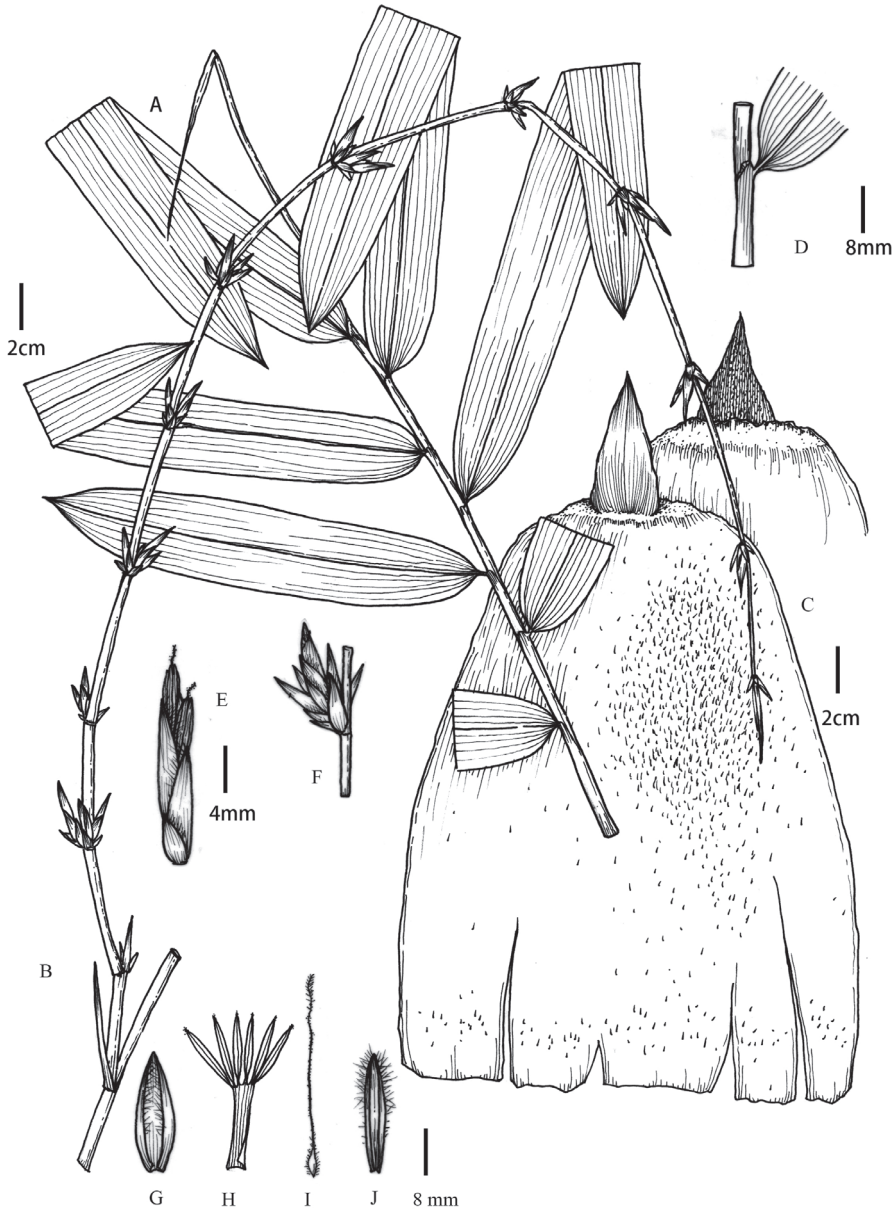

Figure 1. *Gigantochloa glabrata* N. H. Xia & Y. Zeng ex D. Z. Li & Z. C. Xu **A** leaf branch **B** flowering branch **C** culm sheath **D** leaf ligule **E** pseudospikelet **F** inflorescence **G** lemma **H** anthers **I** pistil **J** palea. Drawn from the type specimen and pictures by Yi-Fan Li. Scale bars: 2 cm (**A–C**); 8 mm (**G–J**); 4 mm (**D–F**).

Type. China. Yunnan: Xishuangbanna Tropical Botanical Garden (XTBG), Menglun, Mengla, 101.2522°E, 21.9303°N, 514 m alt., introduction no. 00.1978.0594, 22 August 2019, *Xuzc2019041* (holotype, KUN!).

Description. Sympodial bamboo, loosely tufted. Rhizomes pachymorph. Culms erect, lower nodes with verticillate aerial roots, apically pendulous, 9–14 m tall,

Table 1. Morphological differences between *Gigantochloa glabrata*, *G. albociliata* and *G. levis*.

Characters	*G. glabrata*	*G. albociliata*	*G. levis*
Diameter of culm	5–9 cm	1–5 cm	7–12 cm
Internode	yellow striped	white striped	not striped
Hairy ring	with a white hairy ring and below the node	without hairy ring	one brown hairy ring below the node
Culm sheath blade	erect	reflexed	reflexed
Culm sheath ligule	4–6 mm, truncate, denticulate	10–17 mm, convex in the middle, denticulate	9–14 mm, deep lacerations, bristle
Pseudospikelet	12–18 × 2–3 mm, lanceolate, straight	13–20 × 2–2.5 mm, slender, curved	11–12 × 3–4 mm, ovate, straight

5–9 cm in diameter; internodes terete, greyish-green, yellow striped, 20–40 cm long, wall 7–12 mm thick, culm surface initially densely covered with white to brown hairs when young and glabrous or patchy smudge later; nodes inconspicuous, internode 7–10 mm tall, with a ring of white tomentum at the intranode and below the node. Culm sheaths deciduous, leathery, adaxially glabrous, abaxially sparsely hispidous with brown to black deciduous hairs, strigose, 20–28 cm long, hay colour, with truncate apex; auricles narrowly falcate, 7–10 mm wide, 1–2 mm tall; ligules 4–6 mm tall, denticulate; blades triangular, erect, 4–7 cm long, 1/2 as wide as the apex of culm sheaths. Bud ovate, branching high, from 3–4 m above ground, branches several, one dominant. Foliage leaves 8–12 per ultimate branchlet, usually 10; sheaths initially sparsely white hairy and later glabrous, keeled; auricles inconspicuous; ligules ca. 2 mm tall, entire or split; collar with external ligule; blades lanceolate, 10–28 (-40) cm × 2–4 cm, base cuneate, glabrous, margins serrulate, secondary veins 7–11 pairs, pseudopetioles 2–4 mm long.

Inflorescence iterauctant; flowering branches pendulous, leafless, with clusters of 4–8 (-20) large fertile pseudospikelets mixed with a few small sterile ones at each node, subtended by glumaceous bracts; internodes 2–10 cm long, covered with white deciduous hairs. Pseudospikelets narrowly ovate, light green, 12–18 mm long, 2–3 mm wide; fertile ones sessile, perfect fertile florets 2–4, with diminished florets at the apex; disarticulated above glumes, but not between florets; rhachilla internodes compressed between florets. Glumes 2–3, broadly ovate, persistent, veined, 5–9 mm long, 4–6 mm wide, margins ciliated at upper half. Fertile lemma lanceolate, 14–16 mm long, chartaceous, apex mucronate, glabrous abaxially, margins ciliated; palea oblanceolate, 2-keeled, equal length to lemma, keels and margins long ciliated; lodicules absent; anthers 6, 8–10 mm long, yellow, with a finely-toothed gradual apical tip 0.5–1 mm long, filaments united into a firm tube, 6–10 mm long; stigmas one, purple, plumose, ovary umbonate, pubescent apically. Caryopsis unknown.

Phenology. New shoots May to August.

Distribution and habitat. *Gigantochloa glabrata* is cultivated at the Bamboo Garden, XTBG, introduced from Mengyang Town, Jinghong City, Yunnan, China in 1978 with XTBG accession no. 00.1978.0594. However, we could not find it over a field survey in Mengyang area in 2019.

Etymology. The specific epithet refers to the culm sheath covered with sparsely deciduous hairs.

Figure 2. *Gigantochloa glabrata* N. H. Xia & Y. Zeng ex D. Z. Li & Z. C. Xu **A–C** culm **D, F** culm sheath **E, I** leaf **G** flower branches **H, J** pseudospikelet **K, L** glume **M** lemma(l), palea(p), ovary(o), stamens(st). Scale bars: 1 m (**A**); 3 cm (**C**); 1 cm (**E, H**).

Additional specimens examined. China. Yunnan: Menghai Country, Daluo Town, Manka, 22 October 1978, *J. L. Sun 18070* (HITBC!); China. Yunnan: Mengla Country, Menglun Town, Bamboo Garden, XTBG, cultivated, 31 August 2012, *Y.*

Zeng 17 (IBSC!, with no flowering branches); ibid., 1 August 2007, *K. H. He* (何开红) *C130051* (HITBC!, HITBC0024167, flowering branches); ibid., 30 May 2020, *Xuzc2020001* (KUN!). All collections cited here (with the exception of *J. L. Sun 18070*) come from the same bamboo clump that was introduced to XTBG with the accession no. 00.1978.0594 in 1978 from Mengyang.

***Gigantochloa albociliata* (Munro) Kurz, Prelim. Rep. Forest Pegu, App. A:136 1875 ('*albo-ciliata*')**

≡ *Oxytenanthera albociliata* Munro, Trans. Linn. Soc. London, 26: 129. 1868 ('*albo-ciliata*'). –Type: Myanmar, Pegu, *Brandis 19* (syntype: K, K000710255!); Myanmar, Moulmein, *Falconer 27* (syntype: K, K000710256!).

Diagnosis. *Gigantochloa albociliata* has reflexed culm sheath blades, culm sheath ligules 14–18 mm high, erose-toothed; culms have white hispid; dominant branches conspicuous.

Specimen examined. China. Yunnan: Menghai Country, Daluo Town, 22 April 2016, *Liujx16024*, *Liujx16027* (KUN!); ibid., 10, December, 2016, *Liujx16056* (KUN!); ibid., Manka, 22 October 1978, *J. L. Sun 18069* (HITBC!); THAILAND. Sakon Nakhon, near Phu Pha National Park, 12 August 2018, *Liujx18009* (KUN!).

Discussion

Xishuangbanna is a hotspot of biodiversity in the world and it is also the northern edge of the distribution of *Gigantochloa*. Our discovery not only increases the bamboo species diversity of this area, but also solves the problem of erroneous identifications and citations of *G. albociliata* in Chinese botanical literature for two decades, including the authoritative *Flora Reipublicae Popularis Sinicae* and *Flora of China*, as well as provincial and regional Floras.

Acknowledgements

This study was supported by the National Natural Science Foundation of China (Grant No. 31670396) and the Strategic Priority Research Program of Chinese Academy of Sciences (Grant No. XDB31000000) to De-Zhu Li. We thank Mr. Yi-Fan Li for the illustration. We thank Ms. Yin Zhao and Mr. Yun-Xue Xiao of Xishuangbanna Tropical Botanical Garden, CAS for the assistance in obtaining the specimens. We thank Dr Maria S. Vorontsova of Royal Botanic Gardens Kew, Dr Cen Guo of Kunming Institute of Botany, CAS and Dr Yu-Xiao Zhang of Southwest Forestry University for their critical reading of the manuscript.

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PhytoKeys 171: 47–59 (2021)
doi: 10.3897/phytokeys.171.58900
https://phytokeys.pensoft.net

DATA PAPER

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Vascular plants dataset of the herbarium (HSS) of Agrarian Research Institute Finca "La Orden-Valdesequera" (CICYTEX), Extremadura, Spain

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Academic editor: M. Luján | Received 23 September 2020 | Accepted 18 November 2020 | Published 7 January 2021

Citation: Márquez-García F, García-Alonso D, Guerra-Barrena MJ, Vázquez-Pardo FM (2021) Vascular plants dataset of the herbarium (HSS) of Agrarian Research Institute Finca "La Orden-Valdesequera" (CICYTEX), Extremadura, Spain. PhytoKeys 171: 47–59. https://doi.org/10.3897/phytokeys.171.58900

Abstract

The HSS herbarium database includes 69,397 records of vascular plant taxa, representing 91.1% of the herbarium's specimens as for December, 2019, which are available through the Global Biodiversity Information Facility (GBIF) website (accessible at https://doi.org/10.15468/siye1z). The database represents 4,343 species and 787 infraspecific taxa (530 subspecies, 130 varieties and 127 notho-species or hybrids) of 196 families and 1,164 genera, and 105 type sheets. So far, 97.7% of the databased records are georeferenced (geographic coordinates or MRGS coordinates) and the geographic area with the largest number of specimens is the southwest quadrant of the Iberian Peninsula (Spain and Portugal).

Keywords

Herbarium collection, HSS, Portugal, Southwest Iberian Peninsula, Spain, vascular plants

The HSS herbarium

Forest biodiversity research (Vázquez et al. 1993) in the early 1990s by the Forest Production Department of the Agricultural Research Service (SIA) led to the creation of the HSS herbarium, which was initially located in the *Finca Santa Engracia* facilities

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(Badajoz, Extremadura, Spain). Later, 1995, the HSS herbarium was transferred to its current location, in the *Finca La Orden* (Guadajira, Badajoz), Institute of Agricultural Research *Finca La Orden-Valdesequera* of the Centre for Scientific and Technological Research of Extremadura (CICYTEX, Junta de Extremadura).

The HSS herbarium has five collections: fungi (HSS-F, 447 specimens), seeds (HSS-C, 727 entries), pollen (HSS-P, 402 entries), wood (HSS-X, 89 entries), and vascular plants (HSS, 76,136 specimens). Of the 76,136 total specimens, 91.1% (69,397 specimens) of the general vascular plant collection database is accessible on the GBIF platform (https://doi.org/10.15468/siye1z).

The vascular plant collection of the HSS herbarium is the result of research carried out over the last 25 years by the Department of Forest Production and Biodiversity. This research included studies on plant diversity (Vázquez et al. 2010; Vila-Viçosa et al. 2014) in the predominant forest systems of the southwest Iberian Peninsula, taxonomy, plants of ethnobotanical interest and their potential use as new crops, and ecosystem conservation centered on the study of endemic, rare or threatened species and the impact of potentially invasive species (Pinto-Gomes et al. 2006; Blanco and Vázquez 2014; Vázquez et al. 2015).

The main aim of this paper is to provide a vision about the specimens conserved in the HSS herbarium (diversity, distribution and types), and its potential uses in taxonomical, chorological and ecological studies.

Taxonomic coverage

The HSS herbarium collection database contains 69,397 records belonging to 196 families, 1,164 genera, 4,343 species and 787 infraspecific taxa (530 subspecies, 130 varieties, and 127 notho-species or hybrids). Of the specimens in the collection 98.5% are identified at species level.

97.4% of the specimens housed in the HSS herbarium database are angiosperms (Magnoliophyta Cronquist, Takht. & Zimmerm. *ex* Reveal) with thirteen groups/clade based in APGIII (2009), APGIV (2016), Chase and Reveal (2009), and Reveal and Chase (2011). 2.0% of the specimens are ferns (Pteridophyta Haeckel) with four subclasses based in Christenhusz et al. (2011a): Equisetidae Warm., Lycopodiidae Bek., Ophioglossidae Klinge, Polypodiidae Cronquist, Takht. & Zimmerm. Finally, 0.6% are gymnosperms (Coniferophyta W.Zimm.) distributed in three subclasses based in Christenhusz et al. (2011b): Ginkgoidae Engl., Pinidae Cronquist, Takht. & Zemmerm, and Gnetidae Pax (Table 1) (See Suppl. material 1: Taxonomic coverage of the HSS Herbarium).

The ten families with the highest number of specimens are: Poaceae Barnhart (7,728 specimens), Asteraceae Bercht. & J.Presl (6,945 specimens), Fagaceae Dumort. (6,541 specimens), Fabaceae Lindl. (5,277 specimens), Lamiaceae Martinov (3,763 specimens), Caryophyllaceae Juss. (2,528 specimens), Orchidaceae Juss. (2,117 specimens) Brassicaceae Burnett (2,031 specimens), Amaryllidaceae J.St.-Hil. (1,444 specimens), and

Table 1. Taxonomic coverage of the HSS Herbarium.

	Clade					Subclass	Specimens number	% value
Ferns	Ferns					Equisetidae	73	0.1
						Ophioglossidae	23	0.03
						Polypodiidae	1,168	1.7
	Lycophytes					Lycopodiidae	148	0.2
Gymnosperms						Ginkgoidae	1	0
						Gnetidae	12	0.02
						Pinidade	415	0.6
Angiosperms	Basal angiosperms						37	0.05
	Mesangiospermae	Magnoliids					280	0.4
		Monocots					16,994	24.5
		Eudicots					1,767	2.6
			Superasterids				4,159	6.0
				Asterids			946	1.4
					Campanulids		10,021	14.4
					Lamiids		10,169	14.6
			Superrosids				706	1.0
				Rosids			737	1.1
					Fabids		15,984	23.0
					Malvids		5,753	8.3
		Probable sister of Eudicots					4	0.01

Liliaceae Juss. (1,372 specimens). Ten genera with the largest number of specimens are: *Quercus* L. (6,454 specimens), *Gagea* Salisb.(1,261 specimens), *Trifolium* L. (1,071 specimens), *Narcissus* L. (978 specimens), *Bromus* L. (918 specimens), *Silene* L. (781 specimens), *Centaurea* L. (731 specimens), *Vitis* L. (730 specimens), *Ranunculus* L. (725 specimens), and *Thymus* L. (703 specimens) (Fig. 1).

Regarding the genera, those with the greatest number of species and infraespecific taxa (subspecies and varieties) represented are *Quercus* (81 species, 13 subspecies and 45 hybrids), *Centaurea* (47 species and 13 subspecies), *Euphorbia* L. (47 species and 5 subspecies), and *Trifolium* (47 species and 5 subspecies) (Fig. 2).

Geographical coverage

The geographical data are structured in the specimens on three levels: geographical coordinates (longitude, latitude, WGS84 datum), MGRS (Military Grid Reference System) coordinates with an accuracy of 10,000 or 1,000 meters (ETRS89 datum) and locality assignment indicating the continent, country, province, municipality and town.

The HSS herbarium database only includes 60 records without continent or country data, 244 records without province data and 466 records without municipality or town data. 40% of the records are georeferenced with geographic coordinates and MRGS coordinates with precision of 1,000 meters, 57.7% of the records are georeferenced with MRGS coordinate assignment with precision of 10.000 meters, and only 2.3% of the records lack coordinates.

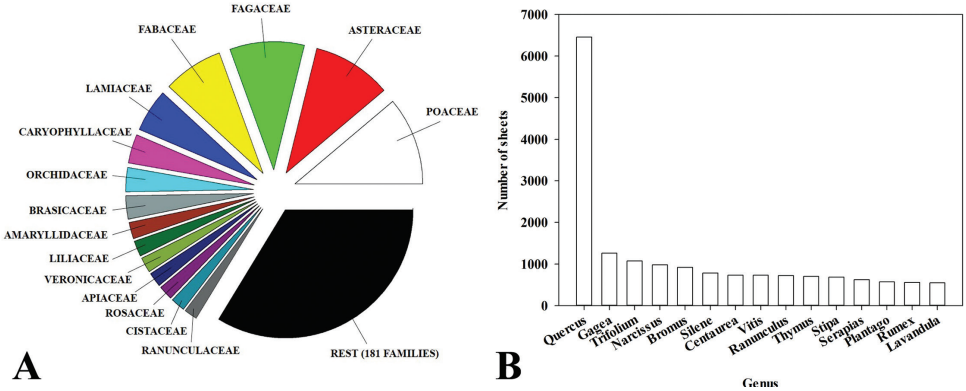

Figure 1. Families with greatest number of specimens in the HSS Herbarium (**A**) Genera represented by the highest number of specimens in the HSS Herbarium (**B**).

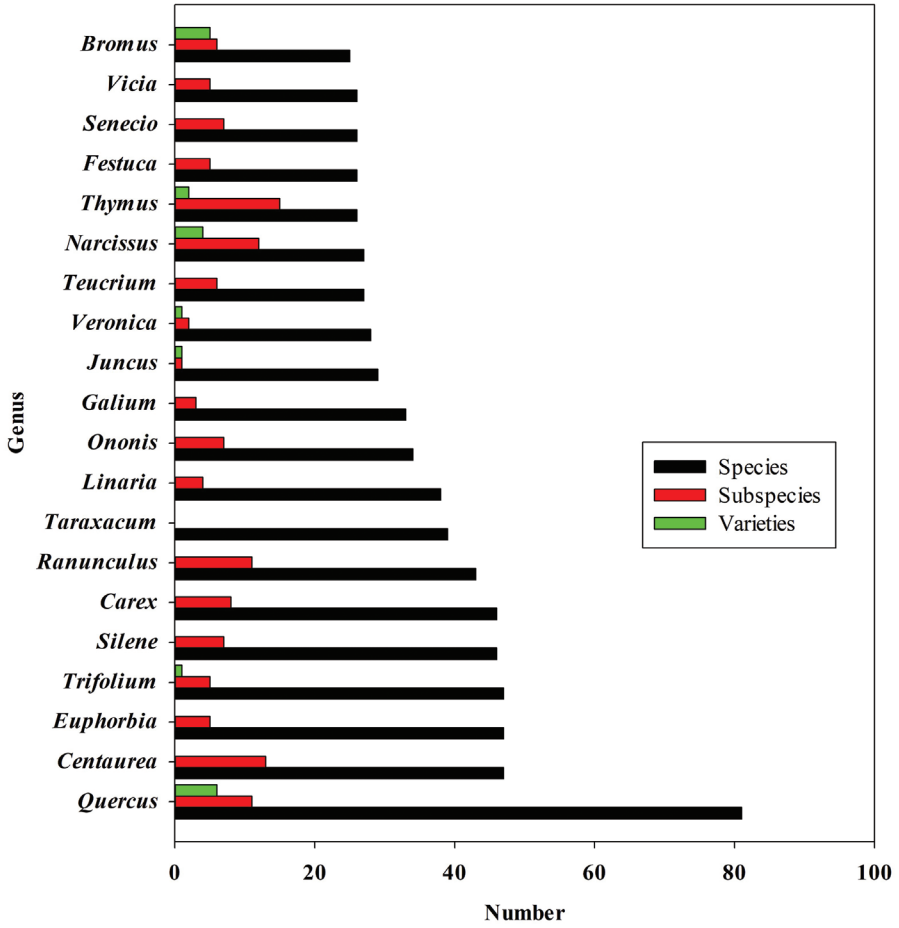

Figure 2. Genera with greatest number of species and infraespecific taxa (subspecies and varieties) in the HSS Herbarium.

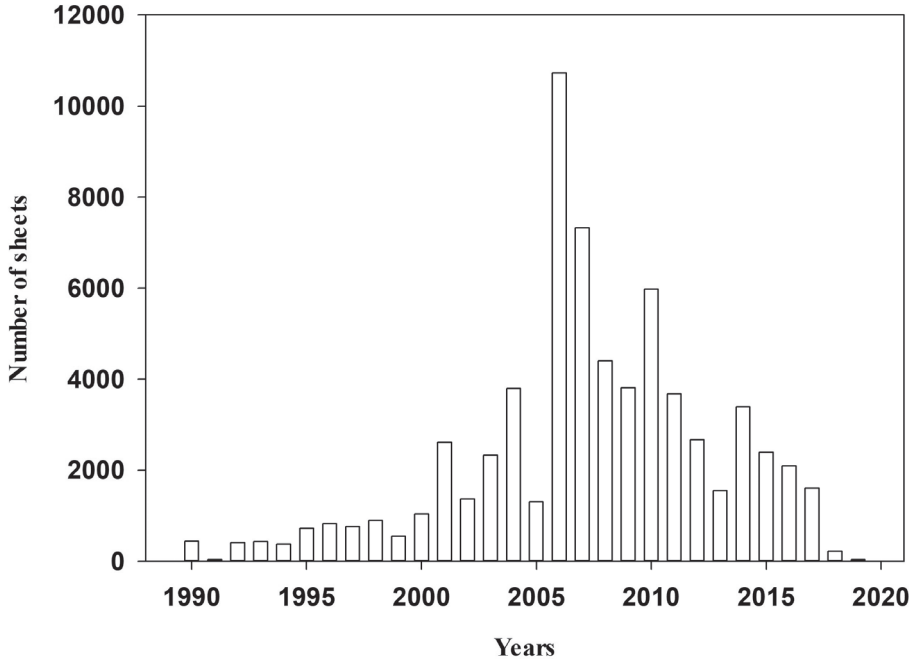

Figure 3. Geographical distribution of specimens of the HSS Herbarium in the Iberian Peninsula.

The geographical distribution of the materials preserved in the HSS herbarium is concentrated in the European continent (67,914 specimens, 97.8%), with small collections from other continents: Africa (959 specimens, 1.3%), North America (432 specimens, 0.6%), South America (47 specimens, 0.07%), Asia (25 specimens, 0.04%), and Oceania (20 specimens, 0.03%).

The geographical area with the highest number of specimens in the HSS Herbarium is the southwest quadrant of the Iberian Peninsula, which includes the Spanish provinces of Badajoz (27,542 records), Cáceres (20,727 records), Ávila (1,165 records), Salamanca (942 records), Huelva (966 records) and Seville (310 records), and the Portuguese provinces of High Alentejo (2,339 records), Low Alentejo (2,225 records), Algarve (1,112 records), and Estremadura (615 records) (Fig. 3).

In addition, there is notable representation from North Africa [Morocco (748 records) and Tunisia (209 records)], linked to collection trips for the study of the flora of the Atlas Mountains, being important in the description of new species and subspecies (Vázquez and Devesa 1997; Vázquez and Ramos 2007; Vázquez et al. 2012).

Temporal coverage

The HSS herbarium database includes specimens from 1906 to 2019, distributed in two periods: before 1990 the collection was growing from exchanges and donations

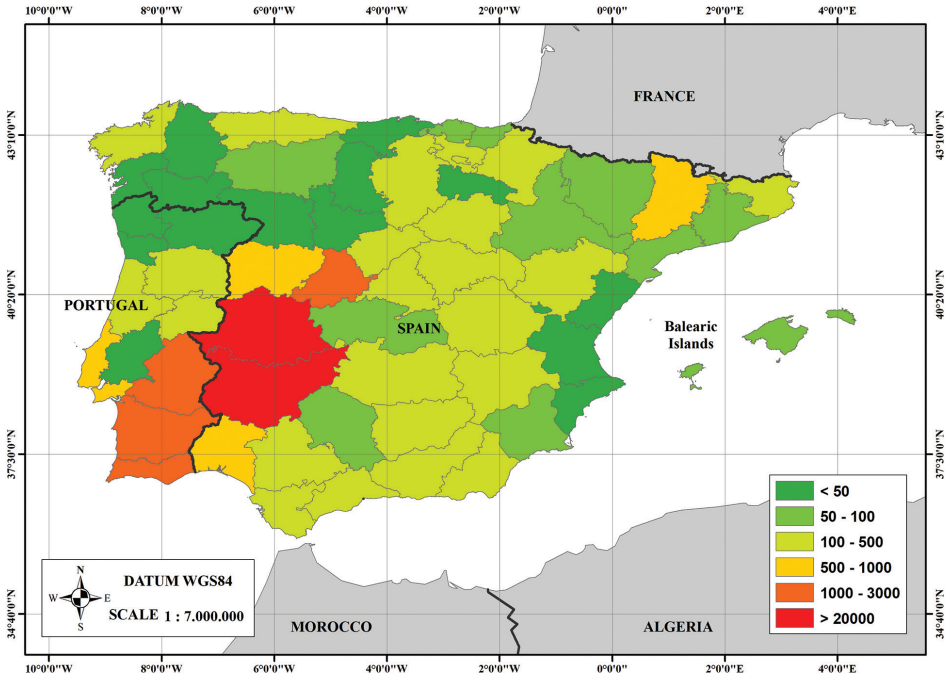

Figure 4. Number of specimens collected between 1990 and 2020.

from private herbaria (1,353 specimens), and after 1990 it was growing due to floristics and research activities (67,813 specimens). Finally, there are 231 specimens without collection data.

Between 1990 and 2019, the period of greatest activity and growth in the collection are the five-year period 2006–2010, with collections of more than 3,500 specimens per year, linked to the study of the unique and threatened flora and the state of conservation of the predominant habitats in Extremadura (Palacios et al. 2010) (Fig. 4).

The monthly distribution of the specimens preserved in the HSS herbarium shows that the months with the highest collection activity are March, April, May and June corresponding to spring in the northern hemisphere.

Plant processing procedures

The methodology used at the HSS herbarium for preserving specimens involves pressing and drying the fresh materials. To do this, the fresh material is placed between sheets of blotting paper and thick cardboard, including a sheet of corrugated aluminum foil for every 10–15 specimens, to facilitate drying (Singh and Subramaniam 2008). Drying is done at room temperature, with hot air used in exceptional cases.

After pressing and drying, the material is subjected to freezing (-40 °C) for 48 hours to facilitate the conservation of the material, thus avoiding insect or fungal attack. This process (adapted from Forman and Bridson 1998) is repeated every 8–12 months until the specimens are accessioned.

Quality control

1. Classification and identification phase. For the inclusion of plant material in the HSS herbarium, taxonomic identification is required, including assignment to genus, species, or to an infraspecific level where necessary. Works used in the identification process are referenced. For peninsular flora, the works of Amaral (1971–2003), Castroviejo (1986–2019), Devesa (1995), Tutin et al. (1964–1980), Valdés et al. (1987) are used. In addition, the determination of synonyms and taxonomic authors are consulted in the databases of The Plant List (http://www.theplantlist.org/), IPNI (The International Plant Names Index, http://www.ipni.org/), World Checklist of Selected Plant Families (WSSP) (https://wcsp.science.kew.org/), and the Euro+Med PlantBase (the information resource for Euro-Mediterranean plant diversity, http://ww2.bgbm.org/EuroPlusMed/). Finally, the organization of materials is done following the latest research on phylogeny of the plant kingdom: APGIII (2009), APGIV (2016), Chase and Reveal (2009), and Reveal and Chase (2011) in angiosperms; Christenhusz et al. (2011a); Pryer et al. (2004), and Smith et al. (2006) in ferns; and Christenhusz et al. (2011b) in conifers.

2. Georeferencing process. Approximately 98% of the specimens preserved in the HSS herbarium contain information regarding coordinates (UTM or geographic), with different levels of accuracy. There are 40% (27,761 specimens) with geographic coordinates and a level of uncertainty lower than 100 m. The working methodology followed for the georeferencing of the new data has been based on the collection of geographical coordinates (WGS84) with GPS in the field of sampling and collection points. Subsequently, at the laboratory, using web geoportals (https://www.ign.es/iberpix2/visor/, for Spain and http://geoportal.lneg.pt/geoportal/mapas/index.html for Portugal), province, municipality, town and altitude are assigned to each new record. For older specimens which did not have coordinates recorded in the field, the GEOLocate application (Rios and Bart 2010), and web geoportals, previously indicated, are used to assign geographic coordinates. Finally, with the help of geographic information systems such as QGIS (https://qgis.org/en/site/) and shapefile layers of MGRS coordinates (precise to 1 km^2) obtained from the National Geospatial-Intelligence Agency (USA) (https://earth-info.nga.mil/), the UTM1x1 coordinates of the collection point are assigned.

3. Computerization and web publication (GBIF). The database has Access support following Darwin Core standards (https://dwc.tdwg.org/) on biological biodiversity, and the data are periodically reviewed using OpenRefine (https://openrefine.org/).

For the publication of the HSS database in the GBIF portal, the Integrated Publishing Toolkit (IPT) portal of the Spanish GBIF network (https://ipt.gbif.es/resource?r=hss) is used.

Storage

The herbarium storage room is equipped with humidity and temperature control (30% humidity and 10 °C temperature), hermetically sealed mobile shelves and cardboard boxes. The specimens are organized into four groups (ferns, conifers, angiosperms-monocots and other angiosperms). Within each group specimens are ordered alphabetically following the sequence: families, genera, species, subspecies, varieties, and forms.

Interest in and use of the collection

The HSS herbarium includes 4560 taxa collected in the Iberian Peninsula, excluding hybrids, which represents around 40% of the 11,500 estimated taxa known from the Iberian flora, according to Flora Iberica (Castroviejo 1986–2019) and the web portals GBIF (https://www.gbif.org/), The Plant List (http://www.theplantlist.org/), and Euro + Med PlantBase (https://www.emplantbase.org/).

Regarding the flora of Extremadura, the herbarium holds specimens of 2986 taxa and 113 hybrids, approximately 98% of the taxa known from Extremadura (Castroviejo 1986–2019; Devesa 1995). In addition, the areas with the densest plant collections are located in protected areas with the highest plant diversity and best preserved in the region. These areas include the southern slope of the Gredos Mountain range, Gata Mountain range, Villuercas Mountain range, Badajoz Mountain range, the foothills of Sierra Morena, and Guadiana River valley (Fig. 5).

The HSS collection of vascular plants has served as the basis for various scientific works on the flora and vegetation of Extremadura and the bordering territories of Spain and Portugal. Among them are: the reviews and studies of the family Orchidaceae (Vázquez and Ramos 2005; Vázquez 2007, 2008a, 2008b, 2009; Vázquez et al. 2012), the genus *Quercus* (Vázquez et al. 1993, 2004; Vázquez 1995; Vázquez and Coombes 2016), *Stipa* L. (Vázquez and Devesa 1997; Vázquez and Ramos 2007), *Narcissus* (Vázquez et al. 2009; Vázquez 2013), *Bromus* (Vázquez and Scholz 2008), *Thymus* (Blanco et al. 2007), *Thymbra* L. (Blanco et al. 2007), *Scolymus* Tourn *ex* L. (Vázquez 2000), *Typha* Tourn *ex* L. (Vázquez 2012), *Taraxacum* F.H.Wigg (Vázquez 2014), *Festuca* L. (Vázquez and García 2016), *Vitis* L. (Vázquez and García 2017), and *Callitriche* L. (Márquez et al. 2017)

In addition, the HSS herbarium actively participates in the "Flora Iberica" project by providing material for the study of various genera of the Iberian Peninsula and Balearic Islands. The work carried out in the HSS herbarium allowed for the creation, in 2007, of the scientific journal "Folia Botanica Extremadurensis" a journal dedicated to scientific works and studies on the flora and vegetation of the southwest Iberian Peninsula.

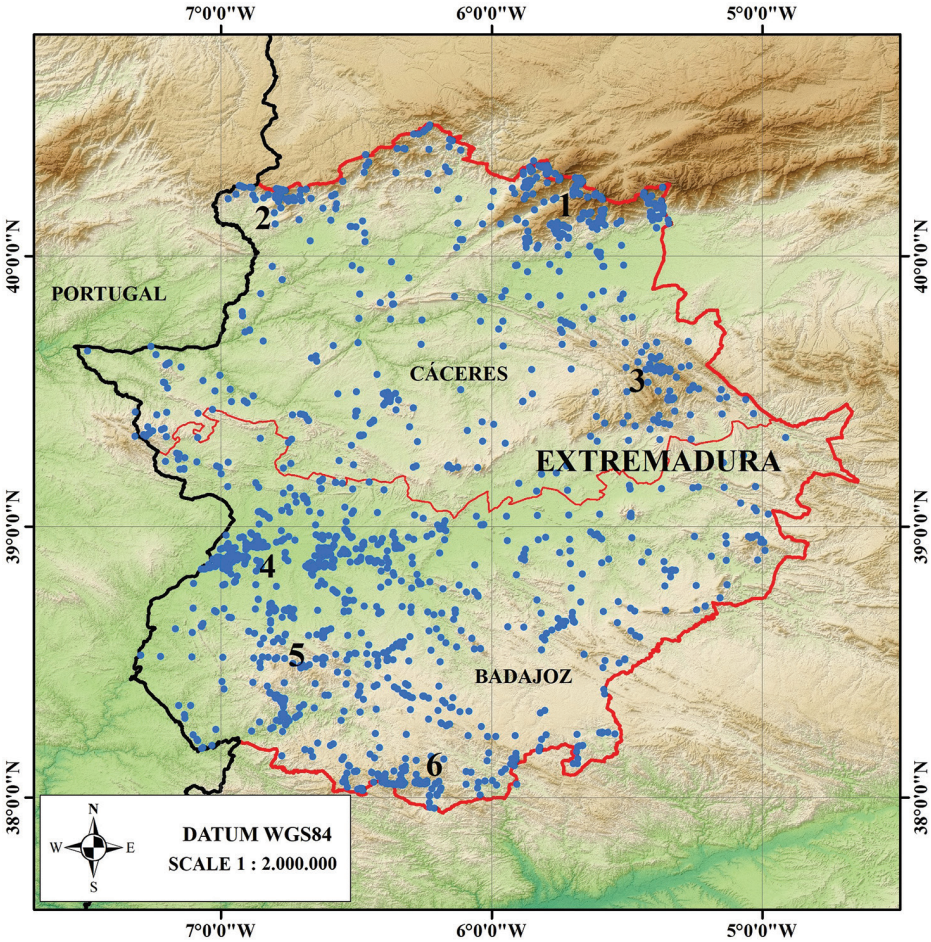

Figure 5. Collection points of the HSS Herbarium in Extremadura (Note: **1** southern slope of the Gredos Mountain range **2** Gata Mountain range **3** Villuercas Mountain range **4** Guadiana River valley **5** Badajoz Mountain range **6** foothills of Sierra Morena).

Finally, the HSS herbarium contains 105 type sheets (82 holotypes, 12 isotypes, 9 paratypes, 1 isoparatype, and 1 neotype) (See Suppl. material 2: Types of the HSS Herbarium). The families with largest number of type sheets are Orchidaceae [45 type sheets, of seven genera: *Ophrys* L. (19), *Orchis* Tourn. *ex* L. (10), *Neotinea* Rchb.f. (4), *Anacamptis* Rich. (5), *Serapias* L. (5), *Dactylorhiza* Neck. *ex* Nevski (1), and ×*Cephalorchis* F.M.Vázquez (1)], Poaceae [19 type sheets, of seven genera: *Celtica* F.M.Vázquez & Barkworth (5), *Stipa* (5), *Bromus* (3), *Poa* L. (3), *Alopecurus* L. (1), *Festuca* (1), and *Helictochloa* Romero Zarco (1)], Fagaceae (15 type sheets, genus *Quercus*), and Amaryllidaceae (10 type sheets, genus *Narcissus*). All type sheets in the HSS herbarium are from Spain (89 type sheets, 77 of them from Extremadura), Portugal (10 type sheets), Morocco (5 type sheets), and Tunisia (1 type sheets).

Maintenance and future work

Currently, the HSS herbarium has more than 6,000 sheets, corresponding to the collection trips of 2018–2019, which are not included in the database. The most immediate work is focused updating the database to include these records, and its subsequent updating in the GBIF network. Digitisation of the collection is currently prioritized as well.

Finally, the maintenance of the collection represents processing between 2,000–3,000 specimens annually.

Dataset description

Object name: Darwin Core Archive (DwC-A) Herbario HSS Finca La Orden-Valdesequera (CICYTEX). Gobierno de Extremadura
Collection Identifier: 837acfc2-f762-11e1-a439-00145eb45e9a
Character encoding: UTF-8
Format name: Darwin Core Archive format
Format version: 1.7
Distribution: https://doi:10.15468/siye1z
Publication date of data: 2020-06-25
Language: Spanish
Licences of use: Creative Commons Attribution Non-Commercial (CC-BY-NC) 4.0 License
Metadata language: Spanish
Date of metadata creation: 2015-03-16
Hierarchy level: Dataset

Acknowledgements

Acknowledgements to all those who have contributed to the development of the HSS herbarium. To Katia Cezón of the National Biodiversity Information Node (GBIF) for her help in publishing the data and Fergus Crystal for the review and comments of the original English. This work has been made possible thanks to the financing of the call for tenders for Technical Support Personnel (PTA) 2016 (Ministry of Science and Innovation, Government of Spain).

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Supplementary material 1

Taxonomic coverage of the HSS Herbarium

Authors: Francisco Márquez-García, David García-Alonso, María Josefa Guerra-Barrena, Francisco María Vázquez-Pardo

Data type: Taxonomic rank

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Supplementary material 2

Types HSS Herbarium

Authors: Francisco Márquez-García, David García-Alonso, María Josefa Guerra-Barrena, Francisco María Vázquez-Pardo

Data type: occurrence

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PhytoKeys 171: 61–73 (2021)
doi: 10.3897/phytokeys.171.60389
https://phytokeys.pensoft.net

RESEARCH ARTICLE

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Rediscovery of *Pogostemon dielsianus* (Lamiaceae, Lamioideae), a rare endemic species from southwestern China, after one century

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Academic editor: A. Paton | Received 4 November 2020 | Accepted 21 December 2020 | Published 12 January 2021

Citation: Hu G-X, Su T, An M-T, Wang X-Y (2021) Rediscovery of *Pogostemon dielsianus* (Lamiaceae, Lamioideae), a rare endemic species from southwestern China, after one century. PhytoKeys 171: 61–73. https://doi.org/10.3897/phytokeys.171.60389

Abstract

Pogostemon dielsianus (Lamiaceae) was described in 1913 based on a single gathering from northwestern Yunnan of China collected in 1905, and thereafter no further collections were observed until 2019. We rediscovered the rare endemic species in Lushui County, Yunnan. Molecular phylogenetic analyses based on four cpDNA markers (*rbcL*, *rps16*, *psbA-trnH*, and *trnL-trnF*) and the nuclear ribosomal internal transcribed spacer (ITS) region confirmed its infrageneric placement within subg. *Pogostemon*. Based on observations of the rediscovered population of *P. dielsianus*, we updated its morphological description, provided an illustration, and discussed its distribution. Under IUCN criteria, the species was categorized as "Critically Endangered (CR)".

Keywords

Critically endangered, Nujiang Canyon, *Pogostemon elsholtzioides*, *Pogostemon griffithii*, subg. *Pogostemon*, Yunnan

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Introduction

Pogostemon Desf. is the largest genus of tribe Pogostemoneae of subfamily Lamioideae in Lamiaceae (Bendiksby et al. 2011; Li et al. 2016). After combining with *Dysophylla* Blume based on the molecular phylogenetic analyses (Bendiksby et al. 2011; Yao et al. 2015, 2016), *Pogostemon*, as currently circumscribed in a broad sense, contains approximately 80 species. On the basis of molecular and morphological evidence, *Pogostemon* was divided into two subgenera: subg. *Pogostemon* and subg. *Dysophyllus* (Bl.) Bhatti & Ingr. ex G. Yao, Y.F. Deng & X.J. Ge (Yao et al. 2016). The genus can be easily distinguished from other Lamiaceae genera by possessing moniliform hairs at the middle of the staminal filaments. *Pogostemon* is distributed mainly in tropical and subtropical regions of Asia with a few species in tropical Africa, Northern Australia, Japan and the Korea Peninsula (Bhatti and Ingrouille 1997; Harley et al. 2004; Yao et al. 2015).

In China, 27 species and two varieties were recorded, of which 10 species and one variety are endemic (Yao et al. 2015; Yao and Ge 2018). *Pogostemon dielsianus* was described in 1913 based on a gathering (*G. Forrest 875*) with two specimens deposited at E and K respectively from Fugong County, northwest Yunnan, China and was not collected again since over the following 100 years. When conducting a taxonomic revision of Chinese *Pogostemon*, Yao et al. (2015) noted that only the type specimens of *P. dielsianus* were examined, and the species was unable to be included in the subsequent molecular phylogenetic analysis (Yao et al. 2016).

During a scientific field trip in Nujiang Canyon, northwestern Yunnan of China in November 2019, a population of *Pogostemon* was discovered in thickets near a tributary of Nujiang River (also known as Salween River). After scrutiny of the data available (Wu and Huang 1977; Li and Hedge 1994; Bhatti and Ingrouille 1997; Yao et al. 2015), we rediscovered *Pogostemon dielsianus* after 106 years. This finding allowed us to update its morphological description, discuss its geographic distribution, assess its conservation status, and infer its phylogenetic position within *Pogostemon*.

Materials and methods

Taxon sampling, DNA extraction, amplification and sequencing

Following the latest phylogenetic study (Yao et al. 2016), a total of 28 species (including *Pogostemon dielsianus*) were sampled from both subgenera of *Pogostemon* to explore the phylogenetic position of *P. dielsianus* (Table 1). In addition, three species of its sister genus *Anisomeles* R. Brown were selected as outgroups based on previous studies (Li et al. 2016; Yao et al. 2016). Except for the newly generated sequences of *P. dielsianus*, all other data were downloaded from GenBank.

Total genomic DNA of *Pogostemon dielsianus* was extracted from silica gel-dried leaf material following the modified CTAB method of Doyle and Doyle (1987). The nuclear ribosomal internal transcribed spacer (ITS) region was amplified using primers

Table 1. Voucher information and GenBank accession numbers for taxa used in this study. *indicates the new sequences, and "–" indicates missing data.

Taxa	Voucher	GenBank accession numbers				
		nrITS	*rbcL*	*rps16*	*trnH-psbA*	*trnL-F*
Anisomeles. heyneana Benth.		–	–	HQ911589	–	HQ911659
A. indica (L.) Kuntze	G. Yao 369 (IBSC)	KR608726	KR608471	KR608595	KR608530	KR608658
A. malabarica (L.) R. Br. ex Sims	Fagerlind & Klackenberg 343 (S)	MH456886	–	FJ854013	–	FJ854260
Pogostemon benghalensis (Burm. f.) Kuntze	R. G. Troth 677 (US)	–	–	HQ911592	KR608568	HQ911663
P. amaranthoides Benth.	J. Chen 668 (KUN)	KR608745	KR608490	KR608614	KR608549	KR608677
P. aquaticus (C.H. Wright) Press	Bidgood et al. 3387 (K)	KR608767	KR608527	KR608655	KR608592	KR608717
P. auricularius (L.) Hassk.	G. Yao 362 (IBSC)	KR608761	KR608513	KR608638	KR608575	KR608700
P. barbatus Bhatti & Ingr.	G. Yao 274 (IBSC)	KR608762	KR608514	KR608639	KR608576	KR608701
P. brachystachyus Benth.	G. Yao 358 (IBSC)	KR608775	KR608517	KR608642	KR608579	KR608704
P. cablin (Blanco) Benth.	G. Yao 291 (IBSC)	KR608757	KR608503	KR608627	KR608562	KR608690
P. chinensis C.Y. Wu & Y.C. Huang	G. Yao 445 (IBSC)	KR608742	KR608512	KR608637	KR608573	KR608699
P. dielsianus Dunn	Hu et al 636 (GACP)	MW194872*	MW194874*	MW194875*	MW194873*	MW194876*
P. elsholtzioides Benth.	Syn. s.n. (US sheet no. 262106)	–	–	KR608633	KR608569	KR608720
P. formosanus Oliver	R. Q. Gao & S. H. Lai 710 (PE)	KR608779	KR608500	KR608624	KR608559	KR608687
P. fraternus Miq.	Syn. 7655 (KUN)	KR608781	–	KR608648	KR608585	KR608710
P. glaber Benth.	G. Yao 364 (IBSC)	KR608740	KR608496	KR608620	KR608555	KR608683
P. heyneanus Benth.	G. Yao 297 (IBSC)	KR608751	KR608492	KR608616	KR608551	KR608679
P. hispidocalyx C.Y. Wu & Y.C. Huang	Expedition to QTP 9446 (KUN)	KR608780	–	KR608644	KR608581	KR608706
P. linearis (Benth.) Kuntze	G. Yao 348 (IBSC)	KR608764	KR608521	KR608649	KR608586	KR608711
P. litigiosus Doan ex Suddee & A. J. Paton	V. D. Nong 31712077 (IBSC)	KR608776	KR608519	KR608645	KR608582	KR608707
P. macgregorii W. W. Sm.	K.Iwatsuki et al. 9659 (A)	KR608778	–	–	–	–
P. paniculatus (Willd.) Benth.	Middleton et al. 1532 (K)	–	–	–	KR608574	KR608721
P. paniculatus (Willd.) Benth.	J. Klackenberg & R. Lundin 565 (S)	–	–	FJ854071	–	
P. parviflorus Benth.	G. Yao 365 (IBSC)	KR608749	KR608501	KR608625	KR608560	KR608688
P. petelotii Doan ex G. Yao, Y.F. Deng & X.J. Ge	T. Sorensen et al. 6313 (KUN)	KR608772	KR608529	KR608657	KR608594	KR608719
P. plectranthoides Desf.	G. Yao 449 (IBSC)	KR608758	KR608510	KR608635	KR608571	KR608697
P. quadrifolius (Benth.) F. Muell.	F. G. Dickason 8194(A)	KR608773	KR608518	KR608643	KR608580	KR608705
P. rogersii N E. Br.	Phillips 3855 (K)	KR608782	–	KR608647	KR608584	KR608709
P. sampsonii (Hance) Press	G. Yao 273 (IBSC)	KR608769	KR608524	KR608652	KR608589	KR608714
P. septentrionalis C.Y. Wu & Y.C. Huang	G. Yao 264 (IBSC)	KR608747	KR608497	KR608621	KR608556	KR608684
P. stellatus (Lour.) Kuntze	B. Z. Xiao 4826 (K)	KR608768	KR608523	KR608651	KR608588	KR608713
P. xanthiifolius C.Y. Wu & Y.C. Huang	H. T. Tsai 59-10586 (KUN)	KR608746	KR608493	KR608617	KR608552	KR608680
P. yatabeanus (Makino) Press	G. Yao 285 (IBSC)	KR608766	KR608526	KR608654	KR608591	KR608716

ITS5 and ITS4 (White et al. 1990). Four chloroplast DNA markers were employed to make phylogenetic analyses and the *rbcL* was amplified with primers of Z1F and 51R (Soltis et al. 1992), the *rps16* with rps-LamF and rps-LamR (Bendiksby et al. 2011), the *psbA-trnH* with psbAF and trnHR (Sang et al. 1997), and the *trnL-trnF* with trn-c and trn-f (Taberlet et al. 1991). All makers were amplified and sequenced with the same conditions following Hu et al. (2020).

Sequence alignment and phylogenetic analyses

Sequences were checked and assembled employing Sequencher v.4.1.4 (Gene Codes, Ann Arbor, Michigan, USA) and then aligned Mafft-win v7.221 (Katoh and Standley 2013) by default. The final alignments were manually adjusted in PhyDE v.0.9971 (Müller et al. 2010). Nuclear dataset (ITS) and plastid matrix (consisting of *rbcL*, *rps16*, *psbA-trnH*, and *trnL-trnF*) were analyzed separately using maximum likelihood (ML) and Bayesian inference (BI). ML analyses were performed using RAxML-HPC2 on XSEDE v.8.2.12 (Stamatakis 2014) under the GTRCAT model on the CIPRES science gateway portal (http://www.phylo.org/) (Miller et al. 2010). Except for setting the bootstrap iterations (-# | -N) to 1000, other parameters followed default. BI analysis was performed in MrBayes v3.2.6 (Ronquist et al. 2012) as implemented in PhyloSuite (Zhang et al. 2020) with the ModelFinder used to select the best model (Kalyaanamoorthy et al. 2017). Under the Akaike information criterion (AIC), the GTR+F+G4 model was selected for nrDNA dataset and the GTR+F+I+G4 for cpDNA matrix. In each analysis, four Markov chain Monte Carlo (MCMC) chains were run simultaneously for 20 million generations, starting with one random tree and sampling one tree every 1000th generation. Convergence of runs was reached when the average standard deviation of split frequencies (ASDSF) fell below 0.01. After discarding the first 25% of the resulting trees as burn-in, the remaining trees were used to assess posterior probabilities (PP) in a majority-rule consensus tree.

Results and discussion

Phylogenetic position of *Pogostemon dielsianus*

Both nrDNA and cpDNA analyses supported the monophylies of *Pogostemon* and its two subgenera (subg. *Pogostemon* and subg. *Dysophyllus*). Although *Pogostemon dielsianus* fell into the subg. *Pogostemon* in both trees, its phylogenetic position was not entirely consistent (Figs 1, 2). In nrDNA topology, *P. dielsianus* seemed to be sister to *P. glaber* Benth., then together sister to the clade consisting of *P. chinensis* C.Y. Wu & Y.C. Huang + *P. septentrionalis* C.Y. Wu & Y.C. Huang + *P. amaranthoides* Benth. (Fig. 1). However, in cpDNA tree, *P. dielsianus*, instead of grouping with *P. glaber*, was sister to *P. amaranthoides*, then together sister to *P. chinensis* (Fig. 2).

Morphologically, *Pogostemon dielsianus* is similar to *P. elsholtzioides* Benth. and *P. griffithii* Prain in having lanceolate leaves (Yao et al. 2015). For the two similar species, only four cpDNA sequences of *P. elsholtzioides* are available in GenBank. In the cpDNA topology, instead of grouping with the morphologically similar species (*P. dielsianus*), *P. elsholtzioides* was sister to the clade consisting of *P. glaber* and *P. xanthiiphyllus* C.Y. Wu & Y.C. Huang. However, due to the unavailability of nrDNA sequences of *P. elsholtzioides*, the conclusion that *P. dielsianus* is not closely related to *P. elsholtzioides* solely on the basis of cpDNA result, cannot be drawn at present.

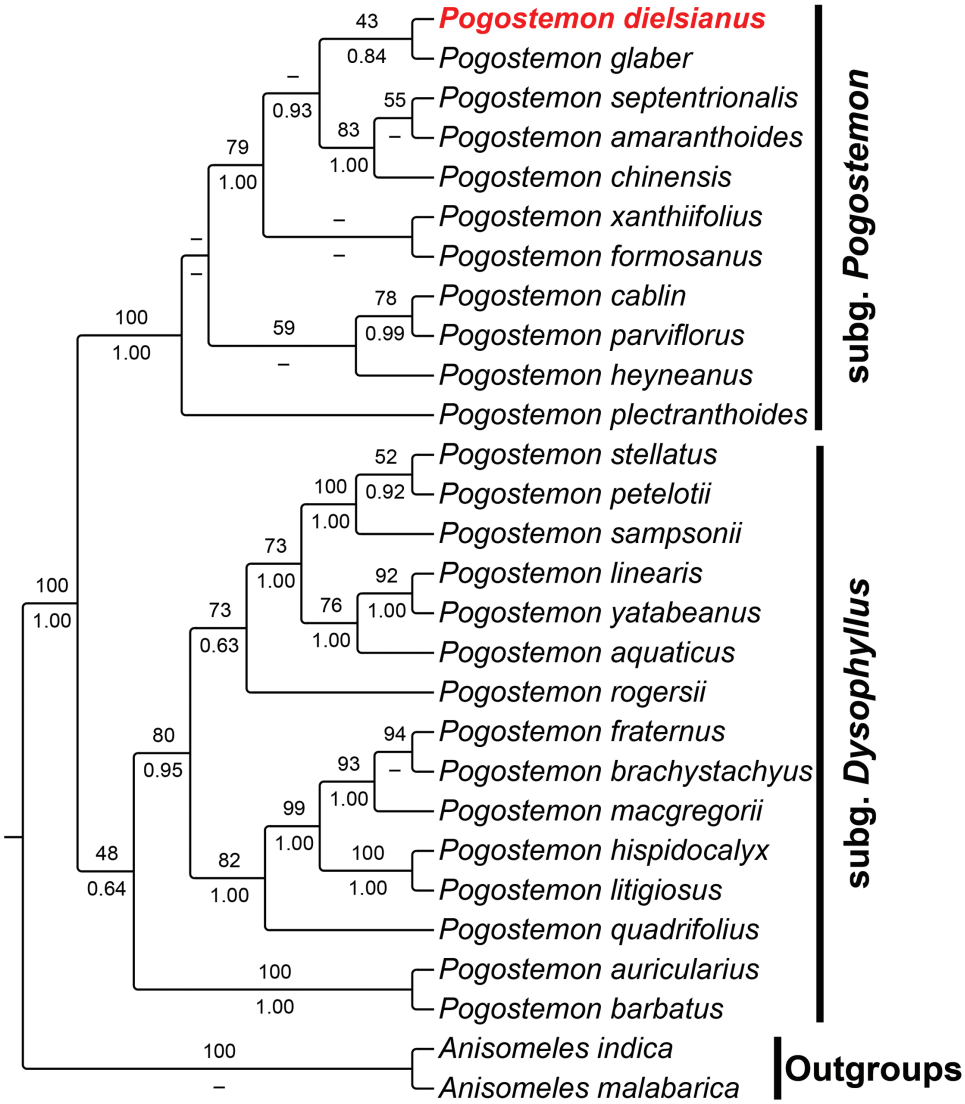

Figure 1. Cladogram of *Pogostemon* based on ML analysis of internal transcribed spacers (ITS) matrix. *Pogostemon dielsianus* is highlighted in red. Bootstrap values of ML are given above the branches with posterior probabilities (PP) of BI below. Bootstrap values <40% and PP< 0.6 are indicated by a dash.

In fact, discordances stemming from nuclear and plastid genomes are common in Lamiaceae, which may be attributed to ancient hybridization with chloroplast capture (Drew and Sytsma 2013; Xiang et al. 2013; Drew et al. 2014; Deng et al. 2015; Hu et al. 2018). Therefore, further studies, especially including nrDNA sequences of *P. elsholtzioides* and *P. griffithii*, are needed to clarify the true phylogenetic position of *P. dielsianus* within subg. *Pogostemon*.

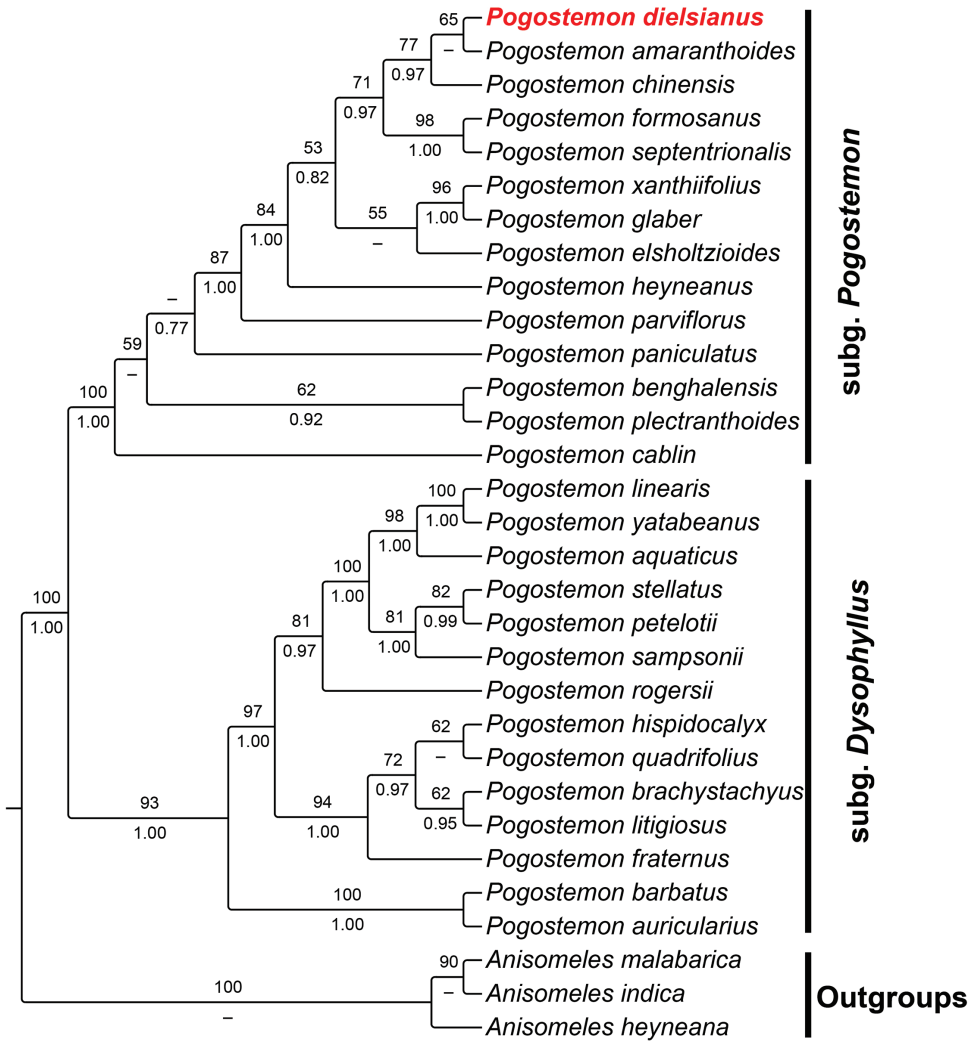

Figure 2. Cladogram of *Pogostemon* based on ML analysis of the combined cpDNA (*rbcL*, *rps16*, *psbA-trnH*, and *trnL-trnF*) dataset. *Pogostemon dielsianus* is highlighted in red. Bootstrap values of ML are given above the branches with posterior probabilities (PP) of BI below. Bootstrap values <40% and PP< 0.6 are indicated by a dash.

Taxonomic treatment

Pogostemon dielsianus **Dunn in Notes Bot. Gard. Edinburgh 8: 159. 1913.**
Figs 3, 4

Lectotype (designated by Bhatti and Ingrouille in Bull. Nat. Hist. Mus. Lond. (Bot.) 27: 99. 1997). China. Yunnan: Fugong, Valley of the Salween, between Shih-chi-ti and Shia-ku-ti, Salween-Irrawaddy Divide, 26°20'N, 1524–1829 m, November

Figure 3. *Pogostemon dielsianus* **A** floral branches **B** bract and bracteole **C** flower **D** dissected calyx **E** dissected corolla showing stamens **F** stamen **G** pistil. Drawn by Xiao-Yu Wang based on *Hu et al. 636* (GACP).

1905, G. Forrest 875 (E [barcode E00087126, image!]; isolectotype: K [barcode K000249619, image!]).

Revised description. Perennial shrubs, up to 3 m tall. Stems solid, gray, ground diameter to 3.5 cm, branches terete or angular, slightly dilated at nodes, the initial branches green, densely strigose-pubescent, 2–3-year-old branches yellow-brown, sub-

glabrous. Leaves opposite; petiole 0.5–2.5 cm long; blade linear-lanceolate to lanceolate, 8–14 × 2–4 cm, papery, both sides densely strigose-puberulent when young, the mature gradually subglabrous, base cuneate, margin serrate, apex acuminate, lateral veins 3–6 pairs. Spikes 3.5–7 cm long, 8–12 mm wide, terminal and axillary, subcontinuous, basally somewhat lax, with more than two lateral branches, densely appressed pubescent except for corolla, pedunculate, 0.5–2 cm long; cymes sessile, 8–14-flowered, flowers sessile. Bracts 4–6.5 mm, bracteoles 1.8–2.3 mm. Calyx tubular, 3.5–4.5 mm long, 5-veined; teeth 5, triangular, 1/5–1/4 as long as the calyx tube. Corolla rose, 2-liped, 7–9 mm long, glabrous outside; tube cylindric, dilated at throat, ca. 2× as long as calyx; upper lip 3-lobed, lobes triangular, subequal, 1.1–1.3 × 0.9–1.1 mm; lower lip entire, ca. 0.9 × 0.7 mm. Stamens 4, exserted from corolla; filaments 5.5–7 mm long, exserted portion ca. 3.5 mm. Style 6.3–8.5 mm long; stigma bifid, lobes subequal, 1.1–1.3 mm. Disc ca. 0.7 mm long. Nutlets 4, ca. 1.5 × 0.8 mm, lanceolate.

Distribution and habitat. The type locality of *Pogostemon dielsianus* was recorded in Fugong County, northwestern Yunnan of China, which is the only historical known site until our new discovery. As coordinate information of the collection is incomplete due to the lack of longitude data, the precise situation of type specimen is unclear. Based on the latitude provided in the original record, the type specimen is more likely to be collected in the north of Lushui County, a neighboring county of Fugong (Fig. 5). Although the recently collected population was also discovered in north Lushui County, distribution of the two populations does not overlap because they are located on different sides of Nujiang River (Fig. 5). In accordance with type specimen record, *P. dielsianus* grows amongst thickets on dry rocky hillsides with elevations ranging from 1524–1829 m. The finding that the newly recorded population grows on the riverside indicates that *P. dielsianus* is more likely to occur in humid areas of dry hillsides. Actually, a similar habitat can also be found elsewhere in Nujiang Canyon. Potential populations of this species, therefore, may be discovered through further field investigation in this region.

Phenology. Flowering and fruiting from November to December.

Conservation status and preliminary IUCN assessment. *Pogostemon dielsianus* is historically known from only two specimens collected from the type locality (Fugong, Yunnan, China) in 1905, and it has not been recollected for the past 114 years until our expedition to Nujiang Canyon in 2019. In the newly recorded locality (Lushui, Yunnan, China), only about 10 mature individuals have been discovered. Due to the lack of exact geographical information of the type locality, it is difficult to confirm the number of individuals there. Based on current investigations and historical records, we inferred that mature individuals of this species may be fewer than 250, and no subpopulation contains more than 50 mature individuals. Therefore, under the IUCN criteria C2a(i) (IUCN 2012), we propose that *P. dielsianus* should be classified as "Critically Endangered (CR)".

Additional specimens examined. China. Yunnan: Lushui County, Daxingdi Town, Tuanjie Village, Luchuluo, amongst a thicket near the Luchuluo River, elevation 1786 m, 26°7.14'N, 98°53.78'E, 24 November 2019, *Hu et al. 636* (GACP!, IBSC!, KUN!).

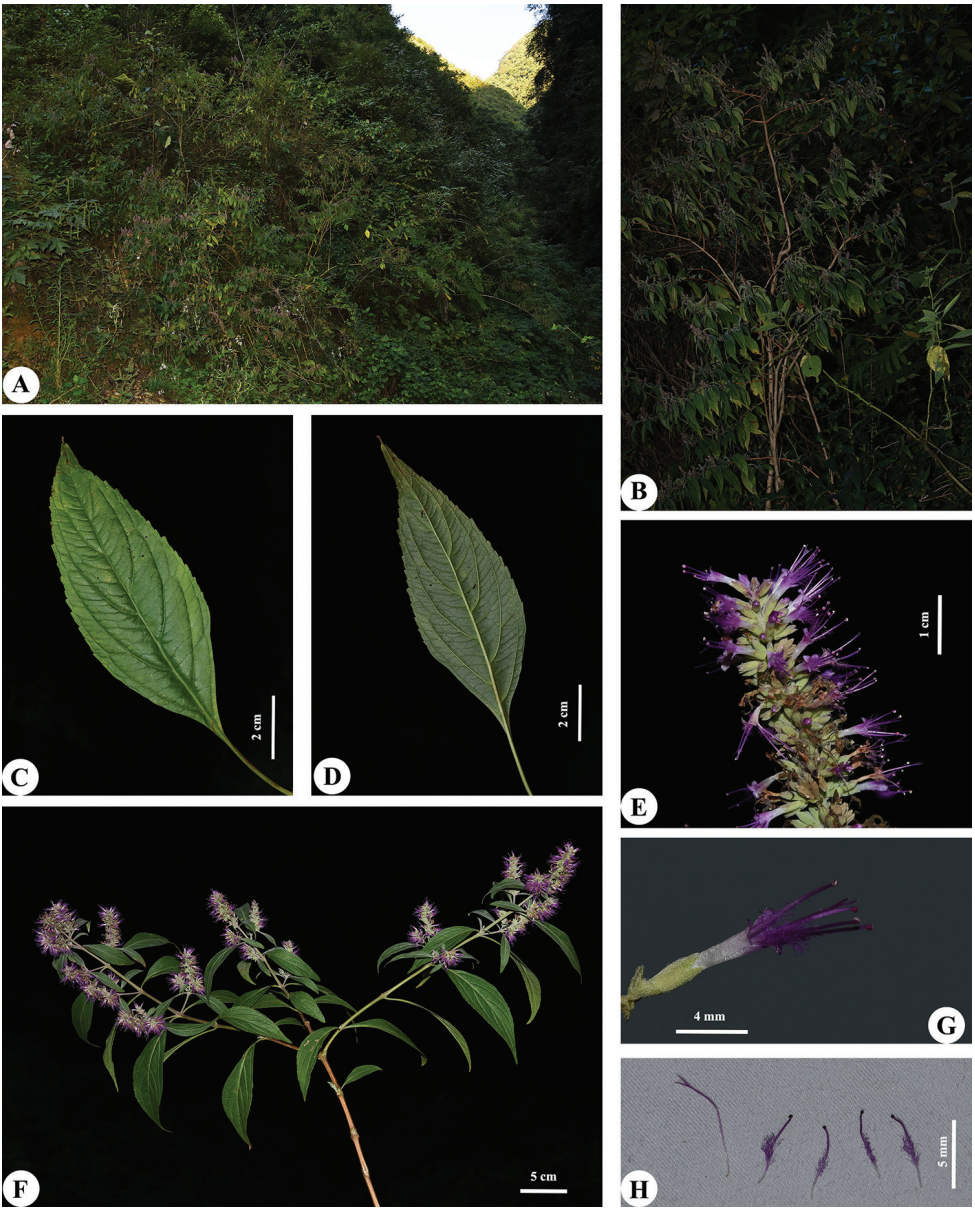

Figure 4. Habitat and morphology of *Pogostemon dielsianus* **A** habitat **B** habit **C** leaf, adaxial view **D** leaf, abaxial view **E** inflorescence **F** floral branches **G** flower **H** Stamens and style. Photographed by G.X. Hu.

Notes. *Pogostemon dielsianus* is morphologically similar to *P. elsholtzioides* and *P. griffithii* in having lanceolate leaves. However, *P. dielsianus* can be easily distinguished from *P. elsholtzioides* and *P. griffithii* by its longer and tubular calyx, smaller ratio of the length of calyx teeth and calyx tube and longer corolla, filament and style (Table 2). In addition, the geographical distribution of these three species is also different in that

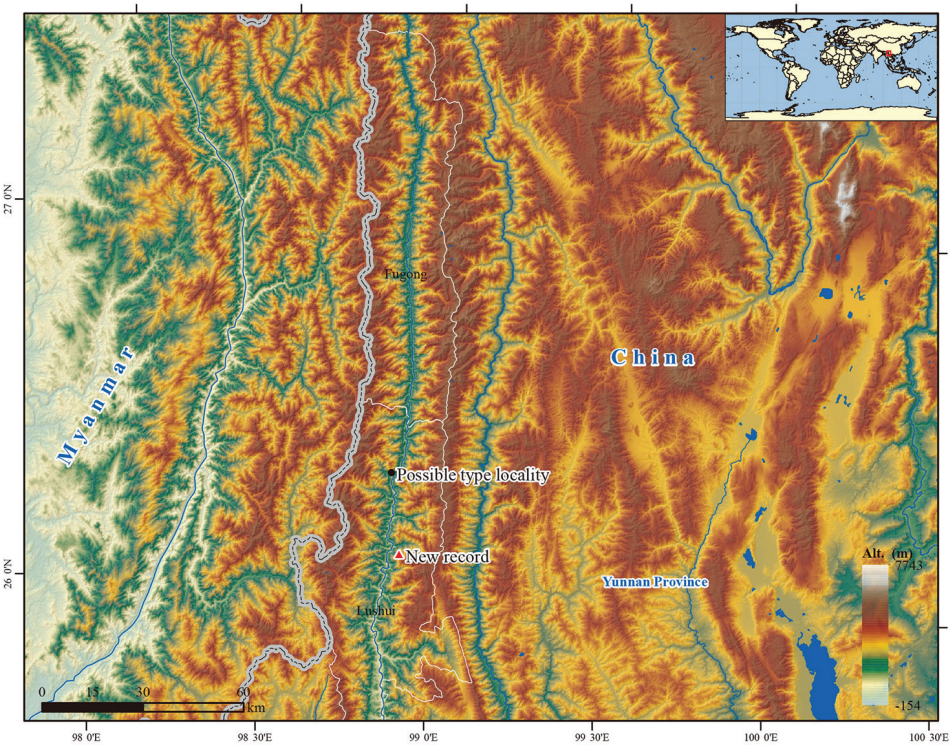

Figure 5. Current distribution of *Pogostemon dielsianus*.

Table 2. Morphological comparison between *Pogostemon dielsianus* and its morphologically similar species.

Character	*Pogostemon dielsianus*	*Pogostemon elsholtzioides*	*Pogostemon griffithii*
Calyx	tubular, 3.5–4.5 mm long	campanulate, 3–3.5 mm long	campanulate, ca. 3.5 mm long
Ratio of the length of calyx teeth and calyx tube	1/5–1/4	1/3–1/2	1/2–1
Corolla length	7–9 mm	ca. 4.5 mm	ca. 5 mm
Filament length	6.2–7 mm	4.5–5 mm	4.7–5.2 mm
Style length	6.3–8.8 mm	ca. 5.5 mm	ca. 5.5 mm
Nutlet	lanceolate	lanceolate	oblong
Distribution	China (NW Yunnan)	Bhutan, India, China (SE Xizang)	Myanmar

P. dielsianus is endemic to NW Yunnan, China, *P. elsholtzioides* is widely distributed in the Himalayan regions (Bhutan, India, and SE Xizang, China), and *P. griffithii* is endemic to Myanmar (Bhatti and Ingrouille 1997; Yao et al. 2015; Yao and Ge 2018).

In the protologue, Dunn (1913) did not designate a type for the name *Pogostemon dielsianus* Dunn. Bhatti and Ingrouille (1997) indicated the specimen deposited in E and K as holotype and isotype, respectively. In fact, they effectively chose the lectotype for the name and the term"holotype" and "isotype" can be corrected as "lectotype" and "isolectotype" according to Article 9.10 of the International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) (Turland et al. 2018).

Acknowledgements

We thank Wei Zhang, Yan-Bing Yang and Jin-Zhu Shi for help with field work, Ling-Bin Yan for drawing the geographic distribution map, and two reviewers and the academic editor for their helpful suggestions and comments on how to improve the manuscript. This work was supported by the National Natural Science Foundation of China (32060048 and 31600164).

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PhytoKeys 171: 75–90 (2021)
doi: 10.3897/phytokeys.171.55397
https://phytokeys.pensoft.net

RESEARCH ARTICLE

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Taxonomic updates in *Amphitecna* (Bignoniaceae): A new Mexican species and the re-establishment of the giant-leaved *A. megalophylla*

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Academic editor: L. Lohmann | Received 13 June 2020 | Accepted 22 December 2020 | Published 25 January 2021

Citation: Gómez-Domínguez H, Ortiz-Rodríguez AE, Velasco-Espino D, Hernández-Burguete R (2021) Taxonomic updates in *Amphitecna* (Bignoniaceae): A new Mexican species and the re-establishment of the giant-leaved *A. megalophylla*. PhytoKeys 171: 75–90. https://doi.org/10.3897/phytokeys.171.55397

Abstract

In this study, we analyzed the morphological affinities of the 24 species of *Amphitecna* based on detailed morphological studies and multivariate cluster analyses. Our results suggest that the genus *Amphitecna* includes six morphological groups that can be easily distinguished based on floral and fruits characteristics: *A. donnell-smithii* group, *A. macrophylla* group, *A. megalophylla* group, *A. molinae* group, *A. spathicalyx* group, and *A. steyermarkii* group. A new species from Mexico, *Amphitecna fonceti*, is described. This new species is clearly differentiated by the predominantly ramiflorous inflorescences bearing multiple flowers per shoot, buds rounded at the apex, large flowers with a transverse fold in the corolla throat, calyx surface pubescent and strongly costate, and fruits elliptic, apiculate at the apex. We discuss the characteristics of each morphological group and their geographical distribution, provide a detailed description of the new species including ethnobotany notes, and propose the re-establishment of the giant-leaved species *A. megalophylla*.

Keywords

Chiapas, conservation, Crescentieae, Neotropics, Mexico

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Introduction

Amphitecna Miers is a Neotropical genus of small to medium-size trees (Gentry 1980). The genus includes around 25 species, most restricted to tropical rainforests. Molecular phylogenetic and morphological data indicate that *Amphitecna* is closely related to the Neotropical genera *Crescentia* L. and *Parmentiera* DC., from which it differs by the combination of simple and alternate leaves, greenish corollas with petal lobes fused, and pepo-type fruits (Gentry 1980, Grose and Olmstead 2007).

The distribution range of *Amphitecna* encompasses two regions with high species diversity (Table 1). The first region includes 14 species and encompasses the rainforests from Mexico to Honduras. The second region contains eight endemic species that range from Northern Nicaragua to the North of Colombia (Table 1). The only widely distributed species is *A. latifolia* (Mill.) A.H. Gentry, that occurs in the coastal areas of Florida (USA), the Caribbean, the Pacific slope of Mexico, and coastal areas of Central America to Colombia, Ecuador, and Venezuela (Gentry 1980). The wide distribution of *A. latifolia* may be associated with its water-dispersed fruits, while most of the narrowly distributed species are mammal-dispersed (Gentry 1980).

Reproductive characteristics of species of *Amphitecna* are quite variable, with most species exhibiting clear differences in flower and fruit morphology (Gentry 1980; Gentry 1982a; Ortiz-Rodriguez et al. 2016). However, most species are similar vegetatively, often leading to taxonomic confusion and misidentifications. For example, the four giant-leaved species, with leaves 50–100 cm long × 10–15 cm wide, i.e., *Amphitecna costata*, *A. megalophylla*, *A. macrophylla*, and *A. regalis*, are frequently misidentified in herbaria. Despite the similarity in leaf traits, these four species are easily differentiated reproductively (Gentry 1980, Table 2). Among the most variable reproductive features of *Amphitecna* are the corolla shape, inflorescence position, number of flowers per shoot, pedicel length, and the number of calyx components (Gentry 1980; Gentry 1982a; Burger and Gentry 2000). Flower bud shape, fruit morphology, and calyx surface also represent important features for species identification (Ortiz-Rodriguez et al. 2016).

Here, we carried out a multivariate cluster analyses of all 24 species of *Amphitecna* currently recognized to infer the morphological affinities among species and establish the position of a newly described species of *Amphitecna* from the Sierra Madre de Chiapas, Mexico.

Materials and methods

To infer the morphological similarities among the 24 species of *Amphitecna*, we performed a hierarchical clustering analysis on a matrix that included 15 flower traits. The data were analyzed using the unweighted pair group method with arithmetic mean (UPGMA, Sokal and Michener 1958) and the Gower index (Gower 1971), allowing a simultaneous use of binary and continuous characters (Dunn and Everitt 1982; Yang et al. 2007; Zanella et al. 2011; Tuler et al. 2017; Svoboda and Ballard 2018; Wahlsteen

Table 1. Species currently recognized in *Amphitecna* (Bignoniaceae) and their respective geographical distribution. The species are ordered by the morphological groups recovered in the clustering analysis. *Amphitecna latifolia* (from the *A. molinae* group, cluster "A") was excluded because it is the only broadly distributed species. NM = Northern Mesoamerica; SM = Southern Mesoamerica.

Species	Group	Cluster	Distribution
Amphitecna costata A.H.Gentry	*Amphitecna megalophylla* group	A	NM: Guatemala
Amphitecna megalophylla (J.D.Sm.) A.H.Gentry	*Amphitecna megalophylla* group	A	NM: Guatemala
Amphitecna apiculata A.H.Gentry	*Amphitecna molinae* group	A	NM: Mexico, Guatemala, Belize
Amphitecna breedlovei A.H.Gentry	*Amphitecna molinae* group	A	NM: Mexico, Guatemala, Belize
Amphitecna fonceti Ortiz-Rodr. & Gómez-Domínguez	*Amphitecna molinae* group	A	NM: Mexico
Amphitecna gentryii W.C.Burger	*Amphitecna molinae* group	A	SM: Costa Rica
Amphitecna isthmica (A.H.Gentry) A.H.Gentry	*Amphitecna molinae* group	A	SM: Costa Rica, Panama, Colombia
Amphitecna kennedyae (A.H.Gentry) A.H.Gentry	*Amphitecna molinae* group	A	SM: Honduras, Costa Rica, Panama, Colombia
Amphitecna molinae L.O.Williams	*Amphitecna molinae* group	A	SM: Honduras, Nicaragua
Amphitecna sessilifolia (Donn.Sm.) L.O.Williams	*Amphitecna molinae* group	A	SM: Costa Rica
Amphitecna silvicola L.O.Williams	*Amphitecna molinae* group	A	NM: Mexico, Guatemala
Amphitecna spathicalyx (A.H.Gentry) A.H.Gentry	*Amphitecna spathicalyx* group	A	SM: Panama
Amphitecna donnell-smithii (Sprague) L.O.Williams	*Amphitecna donnell-smithii*group	B	NM: Guatemala
Amphitecna parviflora A.H.Gentry	*Amphitecna donnell-smithii*group	B	SM: Costa Rica
Amphitecna loreae Ortíz-Rodr. & Burelo	*Amphitecna macrophylla* group	B	NM: Mexico
Amphitecna macrophylla Miers ex Baill.	*Amphitecna macrophylla* group	B	NM: Mexico
Amphitecna montana L.O.Williams	*Amphitecna macrophylla* group	B	NM: Mexico, Guatemala
Amphitecna regalis (Linden) A.H.Gentry	*Amphitecna macrophylla* group	B	NM: Mexico
Amphitecna tuxtlensis A.H.Gentry	*Amphitecna macrophylla* group	B	NM: Mexico
Amphitecna haberi A.H.Gentry	*Amphitecna steyermarkii* group	C	SM: Costa Rica
Amphitecna lundellii A.H.Gentry	*Amphitecna steyermarkii* group	C	NM: Guatemala, Belize
Amphitecna steyermarkii (A.H.Gentry) A.H.Gentry	*Amphitecna steyermarkii* group	C	NM: Mexico, Guatemala

Table 2. Comparison of diagnostic morphological features among the giant-leaved species of *Amphitecna* (Bignoniaceae).

Morphological features	*Amphitecna costata*	*Amphitecna macrophylla*	*Amphitecna megalophylla*	*Amphitecna regalis*
Habit	Branched tree	Pachycaul tree	Pachycaul tree	Pachycaul tree
Leaf long	Less than 60 cm	Less than 60 cm	up to 100 cm	up to 100 cm
Flowers per shoot	1 or 2	1-to-several	3-to-several	1-to-several
Pedicel length	up to 25 mm	up to 25 mm	up to 60 mm	up to 10 mm
Calyx length	up to 15 mm	up to 35 mm	up to 18 mm	up to 28 mm
Transverse fold in the throat of corolla	Present	Absent	Present	Absent
Corolla length	up to 40 mm	up to 50 mm	up to 40 mm	up to 60 mm
Fruit surface	Costate	Smooth	Costate	Not seen

and Tyler 2019). All morphological characters were obtained from original species descriptions (Gentry 1980; Gentry 1982b; Burger and Gentry 2000; Ortiz-Rodriguez et al. 2016), herbarium specimens deposited at MEXU (www.ibdata.ib.unam.mx), and type specimens available online (https://www.gbif.org/ and https://plants.jstor.org/).

The UPGMA results were contrasted with those derived from other clustering algorithms, specifically Ward, single linkage, complete linkage, WPGMA, WPGMC, and UPGMC, implemented in the R-package *stats*, using the function *hclust* (R Core Team 2020: https://www.r-project.org/). We then determined the similarities and differences among the various clustering dendrograms by calculating the cophenetic correlation (a Pearson's measure) between each clustering result using the *cor.dendlist* and the *corrplot* functions from the *corrplot* R-package (Wei and Simko 2017). For each dendrogram,

the agglomerative coefficient was calculated using the *agnes* function from the *cluster* R-package (Maechler et al. 2019). The agglomerative coefficient measures the amount of clustering structure, with values closer to 1 suggesting stronger clustering structure. Also, the Fowlkes-Mallows Index (from the *dendextend* R-package, Galili 2015) was used to compare the species composition within clusters (k = 3–8) obtained from the UPGMA analysis and other algorithms. The optimal number of morphological clusters in *Amphitecna* was determined based on the greater similarity between clustering algorithms (values closer to 1). We further performed an internal clustering validation (a cluster stability test) by calculating the average silhouette width (*Si*) for each cluster (k = 3–8) resulting from each of the algorithms used. While *Si* values greater than 0.71 suggest strong structure and cluster stability, values between 0.51 and 0.70 are interpreted as reasonable, values between 0.26 and 0.50 indicate weak structure, and values lower than or equal to 0.25 are not worth further discussion (Kaufman and Rousseeuw 2005). The graphical representation of the UPGMA dendrogram was carried out in the R software, using the function *hclust* implemented in the R-packages *ape*, and *ggtree* (Yu et al. 2017; Paradis and Schliep 2018).

The new species described was recognized by a unique combination of features (Donoghue 1985) identified through comparisons with morphologically similar taxa and literature review (Gentry 1982a, b, Burger and Gentry 2000; Ortiz-Rodriguez et al. 2016). We assessed the conservation status by calculating the extent of occurrence (EOO) and the area of occupancy (AOO) using the GeoCAT tool (Bachman et al. 2011) and applying the IUCN Red List Categories and criteria (IUCN 2019).

Results

The UPGMA dendrogram is shown in Figure 1. The results of this analysis are very similar to those obtained using other clustering algorithms (correlation values between 0.78 and 0.98, Suppl. material 1: Figure S1). The agglomerative coefficient value for the UPGMA dendrogram was 0.67 (between 0.47 and 0.83 in analyses conducted with other approaches), suggesting a moderate to strong structure among species of *Amphitecna*. The Fowlkes-Mallows Index showed that six groups (k = 6) show significantly similar clusters when the UPGMA is compared to the other clustering algorithms (FM values between 0.71 and 1). Silhouette width values consistently showed the highest values (*Si* value 0.35 for all algorithms) when each dendrogram was divided into six clusters.

The UPGMA results indicate that the genus *Amphitecna* can be classified into six morphological groups (Figure 1A) and three main clusters (A–C). The *A. molinae*, *A. megalophylla*, and *A. spathicalyx* groups are characterized by corollas with a transverse fold in the throat (Figure 1B). In the UPGMA dendrogram, these species are nested within cluster "A" (Figure 1A). The *Amphitecna molinae* group consists of 10 species with sessile leaves, 15–40 cm long, flower buds rounded at apex, and smooth fruit surface, rarely warty. The *A. megalophylla* group includes two species with short-

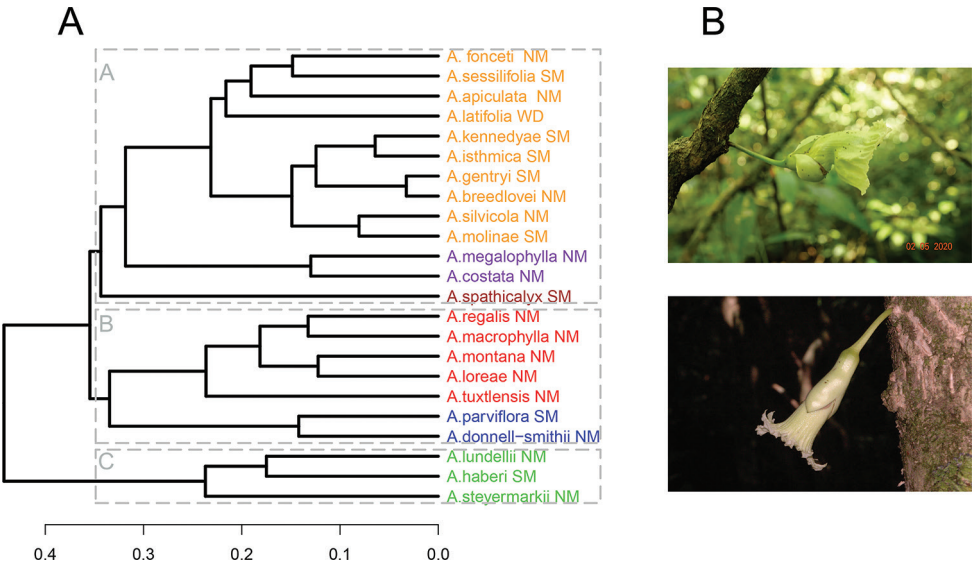

Figure 1. Morphological similarities among the 24 species of *Amphitecna* currently recognized **A** dendrogram based on the results from an UPGMA analysis **B** main flower types found in *Amphitecna*, flowers with a transverse fold in the corolla throat (*Amphitecna costata*, top right) and flowers radially symmetric, without a transverse fold in the throat (*Amphitecna tuxtlensis*, bottom right). Photographs by Hector Gómez Domínguez (*A. costata*) and Pablo Carrillo Reyes (*A. tuxtlensis*). NM = Northern Mesoamerica; SM = Southern Mesoamerica.

petiolate leaves, long leaf blades (50–100 cm long), flower buds rounded at the apex, and fruit surface costate. The new species, *Amphitecna fonceti*, is part of the *A. molinae* group and is morphologically most similar to the *A. latifolia* and *A. sessilifolia* groups (Table 3). *Amphitecna spathicalyx* is also placed within cluster "A" (i.e., the *A. spathicalyx* group) and is distinguished from other species by the pointed flower buds and spathaceous calyces.

Cluster "B" is composed of the *A. macrophylla* and *A.donnell-smithii* groups (Figure 1A). The species from these groups are best recognized by their short-petiolate leaves, inflorescences born along the main trunk or leafless branches, mostly composed of 1–2 flowers per shoot, flowers without a transverse fold in the corolla throat, and calyces bilabiate or trilabiate (Figure 1B). The *A. macrophylla* group contains five species with cauliflorous inflorescences and long and funnelform corollas (up to 70 mm long). The *A. donnell-smithii* group consists of two ramiflorous species with small flowers (less than 28 mm long) and broadly campanulate corollas. The only two species of *Amphitecna* with broadly campanulate flowers are included in the *A. donnell-smithii* group.

Cluster "C" consists of the *Amphitecna steyermarkii* group and is composed of three species that are characterized by their terminal inflorescences with several flowers per shoot, flower buds with a sharp acumen, flowers without a transverse fold in the corolla throat, and spathaceous calyces.

Key for the identification of species of *Amphitecna* (Bignoniaceae)

1 Corollas with a transverse fold in the throat **2**
– Corollas without a transverse fold in the throat **3**
2 Flowers buds with a sharp acumen and spathaceous calyx ..... ***A. spathicalyx* (Panama and Colombia)**
– Flowers buds obtuse to rounded at apex (rarely acute in *A. sessilifolia*); calyx bilabiate or trilabiate **4**
3 Inflorescences terminal; flowers buds with a sharp acumen (sometimes lacking in *A. haberi*) **5**
– Inflorescences on leafless portions of branches and throughout the main trunk; flower buds obtuse to rounded at apex (acute in *A. tuxtlensis*) **6**
4 Inflorescences terminal **7**
– Inflorescences axillary, on leafless portions of branches and throughout the main trunk **8**
5 Leaves shortly petiolate, up to 18 cm long, acute at the base; longer pedicels up to 75 mm long **9**
– Leaves sessile, often longer than 20 cm long, obtuse to rounded at base; longer pedicels up to 50 mm long ..... ***A. steyermarkii* (Mexico and Guatemala)**
6 Pedicels 60–100 mm long; fruits globose or nearly so, rounded at apex **10**
– Pedicels 10–40 mm long; fruits elliptic to narrowly elliptic, acute to apiculate at apex **11**
7 Inflorescences composed of 3-to-several flowers per shoot **12**
– Inflorescences composed of 1 or 2 flowers per shoot **13**
8 Pachycaul trees; leaves 50–100 cm long; fruit surface costate **14**
– Branched trees; leaves 15–40 cm long; fruit surface smooth or rough, rarely costate **15**
9 Inflorescences composed of 1 or 2 flowers per shoot; calyx spathaceous, up to 45 mm long ..... ***Amphitecna lundellii* (Guatemala and Belize)**
– Inflorescences composed of 3-to-several flowers per shoot; calyx bilabiate, up to 20 mm long ..... ***Amphitecna haberi* (Costa Rica)**
10 Mature leaves longer than 25 cm; inflorescences ramiflorous, composed of one or two flowers per shoot; pedicels more than 70 mm long ..... ***A. montana* (Mexico and Guatemala)**
– Mature leaves shorter than 25 cm long; inflorescences trunciflorous, composed of 3-to-several flowers per shoot; pedicels less than 70 mm long ..... ***A. loreae* (Mexico)**
11 Pachycaul trees; leaves 50–100 cm long **16**
– Branched trees; leaves 18–25 cm long **17**
12 Corolla tubular, up to 30 mm long; calyx almost as long as the corolla ..... ***A. apiculata* (Mexico, Guatemala, and Belize)**
– Corolla funnelform, up to 65 mm long; calyx much smaller than the corolla **18**

13 Leaves with 14 secondary veins or more; mature fruits longer than 10 cm long **19**

– Leaves with fewer than 14 secondary veins; mature fruits shorter than 10 cm long **20**

14 Inflorescences composed of 1 or 2 flowers per shoot; pedicels up to 25 mm long ..... ***A. costata*** **(Guatemala)**

– Inflorescences composed of 3-to-several flowers per shoot; pedicels up to 60 mm long ..... ***A. megalophylla*** **(Guatemala)**

15 Leaves shortly petiolate; inflorescences composed of 1 or 2 flowers per shoot; calyx smooth **21**

– Leaves sessile; inflorescences composed of 3-to-several flowers per shoot; calyx costate, with 6–10 longitudinal ridges per lobe, surface densely covered by lenticels-like white dots ..... ***A. fonceti*** **(Mexico)**

16. Longer leaves up to 100 cm long; pedicels ca. 10 mm long; corolla 52–65 mm long, 23–30 mm wide at mouth of tube ..... ***A. regalis*** **(Mexico)**

– Longer leaves up to 60 cm long; pedicels 15–40 mm long; corolla 37–50 mm long, 10–15 mm wide at mouth of tube ..... ***A. macrophylla*** **(Mexico)**

17 Flower bud rounded at apex; corolla campanulate, up to 30 mm long **22**

– Flower buds acute at apex; corolla funnelform, up to 60 mm long ..... ***A. tuxtlensis*** **(Mexico)**

18 Leaves elliptic or widely obovate, coriaceous; pedicels up to 40 mm long; fruits globose with rounded apex; restricted to coastal ecosystems ..... ***A. latifolia*** **(widely distributed)**

– Leaves narrowly obovate to oblanceolate, chartaceous; pedicels up to 80 mm long; fruits elliptic with elongated apex; restricted to montane ecosystems (1300–2000 m alt) ..... ***A. sessilifolia*** **(Costa Rica and Panama)**

19 Corolla 44–60 mm long ..... ***A. isthmica*** **(Costa Rica and Panama)**

– Corolla 35–45 mm long ..... ***A. molinae*** **(Honduras)**

20 Corolla tube 5 mm wide at base or larger ..... ***A. gentryi*** **(Costa Rica)**

– Corolla tube less than 5 mm wide at the base ..... ***A. breedlovei*** **(Mexico)**

21 Leaves 20–40 cm long × 5–15 cm wide; inflorescences on the main trunk and on the old branches; restricted to lowland forests (below 1000 m alt) ..... ***A. kennedyae*** **(Honduras, Costa Rica and Panama)**

– Leaves smaller 5–20 cm long × 1–5 cm wide, inflorescences on the old branches and among the foliage; growing in montane forests (between 900 m and 1500 m alt) ..... ***A. silvicola*** **(Mexico and Guatemala)**

22 Scandent shrub; leaves 20 cm long or larger; inflorescences on the main trunk ..... ***A. parviflora*** **(Panama)**

– Small trees; leaves up to 15 cm long; inflorescences on old branches and among the foliage ..... ***A. donnell-smithii*** **(Mexico and Guatemala)**

Discussion

Morphological groups and their distribution

The results presented here show that *Amphitecna* consists of several morphological groups (Figure 1). These groups do not necessarily represent lineages and, according to internal clustering validation (*Si* value), their stability should be tested with additional data. Nonetheless, the resulting morphological grouping recovered provides new insights into the understanding of relationships among species of *Amphitecna*.

Although little is known about the reproductive ecology of *Amphitecna*, the flower and fruits differences among groups are likely linked to their pollinators and seed dispersers. Most species have exposed inflorescences (terminal and cauliflorous), consisting of one-to several flowers with a transverse fold in the corolla throat fitting the *Crescentia*-type pollination syndrome, which includes bat-pollinated flowers (Gentry 1980, Fleming et al. 2009). However, hummingbirds and other birds also visit flowers of some *Amphitecna* species, such as *A. apiculata*, *A. latifolia*, and *A. sessilifolia* (Richardson 1984). On the other hand, the fleshy and indehiscent fruits (mostly mammalian-dispersed) are only found in *Amphitecna* and close relatives (Gentry 1980), showing considerable variation in fruit shape and surface.

The distribution of species within the various morphological groups seems to follow a geographical pattern. Cluster "A" (species with a transverse fold in the corolla throat) includes taxa that are distributed throughout Mesoamerica (from Mexico to Colombia) (Table 1). On the other hand, sub-groups within cluster "A" show variable distribution patterns. For example, the *A. molinae* group from cluster "A" has members in both regions of Mesoamerica (i.e., Northern Mesoamerica and Southern Mesoamerica; Table 1), with the *A. megalophylla* group endemic to the northern portions of Mesoamerica (from Mexico and Guatemala), and the *A. spathicalyx* group endemic to the southern portions of Mesoamerica (found in Panama exclusively). On the other hand, cluster "B" includes members of the *A. macrophylla* and *A. donnell-smithii* groups, occurring predominantly in northern Mesoamerica. Except from *A. parviflora* that is endemic to Costa Rica, the remaining six species of cluster "B" are found in Mexico and Guatemala exclusively. Finally, two species placed in the *Amphitecna steyermarkii* group occur in northern Mesoamerica (Mexico, Guatemala, and Belize), with a single species endemic to Costa Rica. Based on the above, northern Mesoamerica is not only the center of diversity of *Amphitecna*, but also the most diverse region morphologically (Table 1).

Taxonomic implications

Amphitecna megalophylla was first treated as a synonym of *A. macrophylla* by Seibert (1940), which was subsequently followed by Standley and Williams (1974), Nelson (2008), and the iPlants Project (http://powo.science.kew.org/taxon/11655-2). Although Gentry (1980) highlighted the morphological features that characterize *A. megalophylla*, the species has continued to be treated as a synonym.

Table 3. Comparison of diagnostic morphological features among *Amphitecna fonceti* (Bignoniaceae) and close relatives.

Morphological features	*Amphitecna fonceti*	*Amphitecna apiculata*	*Amphitecna latifolia*	*Amphitecna sessilifolia*
Leaf long	Up to 40 cm	Up to 40 cm	Up to 20 cm	Up to 30 cm
Leaf wide	Up to 13 cm	Up to 12 cm	Up to 11 cm	Up to 9 cm
Inflorescences	Mostly ramiflorous	Mostly terminal	Mostly terminal	Terminal
Pedicel length	Up to 60 mm	Up to 50 mm	Up to 40 mm	Up to 80 mm
Calyx length	up to 32 mm	up to 20 mm	up to 37 mm	up to 30 mm
Calyx surface	Strongly costate, pubescent and densely covered with lenticels-like white dots	Smooth and glabrous	Smooth and glabrous	Smooth and glabrous
Corolla shape	Funnelform	Tubular	Funnelform	Funnelform
Corolla length	up to 45 mm	up to 28 mm	up to 62 mm	up to 52 mm
Corolla mouth	23 mm diam.	10 mm diam.	24 mm diam.	16 mm diam.
Stamens	3, rarely 4	4	4	4
Stamen insertion	4–12 mm from base of the tube	10 mm from base of the tube	15–20 mm from base of the tube	13–18 mm from base of the tube
Style length	33–37 mm	?	45–50 mm	38–39 mm
Fruits shape	Elliptic	Elliptic	Globose	Elliptic
Fruits apex	Acute to short apiculate	Apiculate	Rounded	Apiculate
Habitat	Oak forest at c. 1500 m altitude	Lowland wet forest mostly below 500 m altitude	Restricted to coastal forest and mangrove	Montane wet forest mostly between 1300 and 2000 m alt

The results presented here show that *Amphitecna megalophylla* and *A. macrophylla* are clearly distinct and are best treated as separate taxa (Table 2). *Amphitecna megalophylla* is part of the *A. megalophylla* group together with *A. costata*, both of which are placed within cluster "A" based on its multi-flowered inflorescences, buds rounded at apex, and long pedicellate corollas with a transverse fold in the throat (Figure 1). In contrast, *A. macrophylla* is placed within the *A. macrophylla* group (cluster "B") along with two other giant-leaved species based on its inflorescences with 1 (rarely 2) short pedicellate flowers that lack a transverse fold in the corolla throat (radially symmetric). In addition, *A. macrophylla* is endemic to Veracruz (Mexico), while *A. megalophylla* is endemic to Guatemala (Gentry 1980).

Results from our cluster analyses suggest that *A. fonceti* is part of the *A. molinae* group (cluster "A") along with *A. apiculata*, *A. latifolia*, and *A. sessilifolia*. Species within cluster "A" share multi-flowered inflorescences and flowers with a transverse fold in the throat, while showing several differences in their flower and fruit morphology (Table 3). Hence, *A. fonceti* is best treated as a separate taxon, which is described below and compared to other morphologically similar taxa.

Taxonomic treatment

***Amphitecna fonceti* Ortiz-Rodr. & Gómez-Domínguez, sp. nov.**
urn:lsid:ipni.org:names:77214647-1
Figures 2, 3

Type. Mexico. Chiapas, Municipio de La Concordia, Área de Protección de Recursos Naturales La Fraylesca, Rancho "Pacayal" a 3 kilómetros del ejido Solo Dios,1441 m,

15°46'57.7"N, 92°59'04.6"W, 24 May 2020(fl, fr) *Gómez- Domínguez H. y Hernández-Burguete R. 3840* (holotype HEM; isotypes: MEXU, MO).

Diagnosis. *Amphitecna fonceti* is distinguishable from the other species of *Amphitecna* by its ramiflorous inflorescences that bear multiple flowers per shoot, buds rounded at apex, large flowers with a transverse fold in the corolla throat, calyx surface pubescent and strongly costate, and fruits elliptic, apiculate at the apex. *Amphitecna fonceti* is morphologically similar to *A. apiculata* and *A. latifolia*, both of which occur in Mexico. However, *A. apiculata* differs by the small and tubular corollas, and by the calyx with a smooth and glabrous surface. *Amphitecna latifolia*, on the other hand, differs by the smaller leaves, smooth and glabrous calyx surface, and globose fruits with a rounded apex. The three species show different climatic preferences (Table 3).

Description. Small to medium sized trees, 3–9 m alt., 6–25 cm DBH, the secondary branches terete. *Leaves* alternate-verticillate, clustered near the apex of branches, olive-green when dry, glabrous, coriaceous, 13–35 cm long × 6–13.2 cm wide, oblanceolate to obovate, short acuminate, acute to attenuate basis, midrib slightly raised on the upper surface, prominent on the lower surface; secondary veins 10–20 on each side, slightly raised above, prominent below; petiole shorter than 1 cm long, merging with attenuate leaf base, red wine *in vivo*. *Inflorescences* bearing three to six flowers (rarely with a single flower), borne on leafless portions of old branches, rarely terminal or along the main trunk (cauliflory), with a sour-odor; pedicels, outer side of buds, and calyces pubescent and densely covered with lenticel-like white dots. *Flowers* more or less erect, not pendant, pedicel 38–60 mm long; buds, rounded at apex; calyx campanulate, 25–32 mm long, coriaceous, evenly *2–3*-labiate, strongly costate, with 6–10 longitudinal ridges per lobe; corolla funnelform, with a transverse fold on throat between 22–27 mm from the base, pale green, 38–46 mm long × 20–23 mm wide at the tube mouth, the basal portion of the corolla funnel-shaped, 9–13 mm long, lobes more or less fused into a frilly-margined rim; androecium with stamens 3 or 4, included, inserted 4–12 mm from base of the tube, anther thecae divergent, 5–6 mm long, filaments 12–29 mm long, staminodes shorter than 20 mm long when present, inserted 3–6 mm from base of the tube; gynoecium with ovary ca. 8 mm long × ca. 4 mm wide, broadly elliptic, glandular-papillose, style 25–29 mm long, stigma bifurcate; disc annular-pulvinate, ca. 11 mm in diameter. *Fruits* elliptic, 110–180 mm long × 70–105 mm wide, acute to short acuminate at apex, rounded to short acuminate at the base.

Habitat and ecology. This species is known only from the type locality in Chiapas, Mexico. The species inhabits areas with sedimentary soils, mostly formed by sandstones with a thin layer of organic matter, mostly within altered remnants of oak and pine-oak forest. The species with which it coexists are *Quercus rugosa* Née, *Inga vera* Willd, *Damburneya coriacea* (Sw.) Trofimov & Rohwer, *Eugenia capuli* (Schltdl. & Cham.) Hook. & Arn., *Trema micrantha* (L.) Blume, *Cecropia obtusifolia* Bertol., and *Coffea arabica* L.

Phenology. Specimens were collected in full bloom or with ripe fruit in April and May. Flower buds were observed in March and ripe fruits in June.

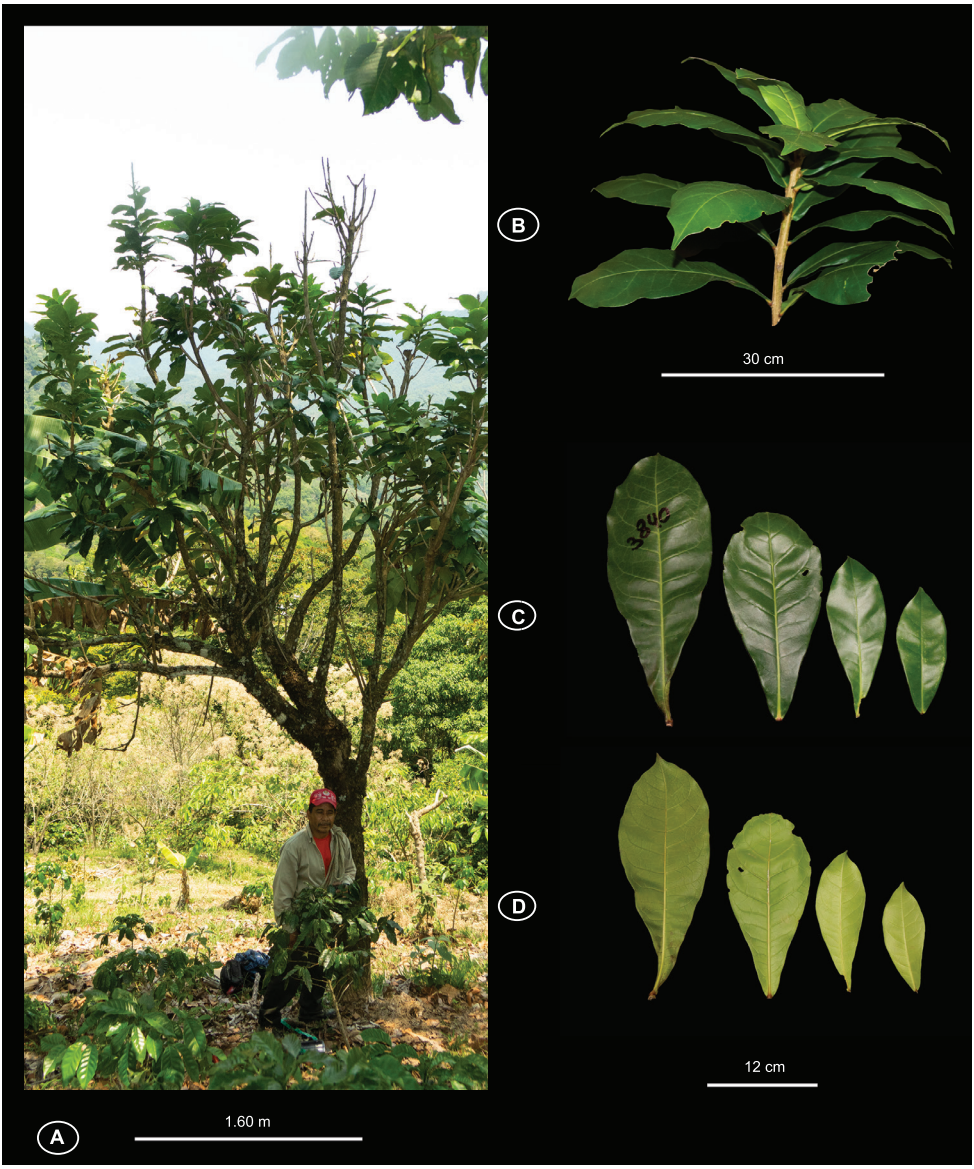

Figure 2. Vegetative features of *Amphitecna fonceti* sp. nov. **A** habit **B** phyllotaxy **C** adaxial side of leaf **D** abaxial side of leaf. Photographs by Hector Gómez Domínguez.

Etymology. The specific epithet honors FONCET (Fondo de Conservación El Triunfo, A.C.), in recognition of 18 years of funding dedicated to conservation projects in natural protected areas within the Sierra Madre de Chiapas, Mexico.

Conservation status. According to the IUCN (2019), this species is considered as Critically Endangered [CR B1ab (iii)]. Its area of occupancy (AOO) is 8.0 km^2 and the extent of occurrence (EOO) is 0.154 km^2, showing a restricted distribution. Although

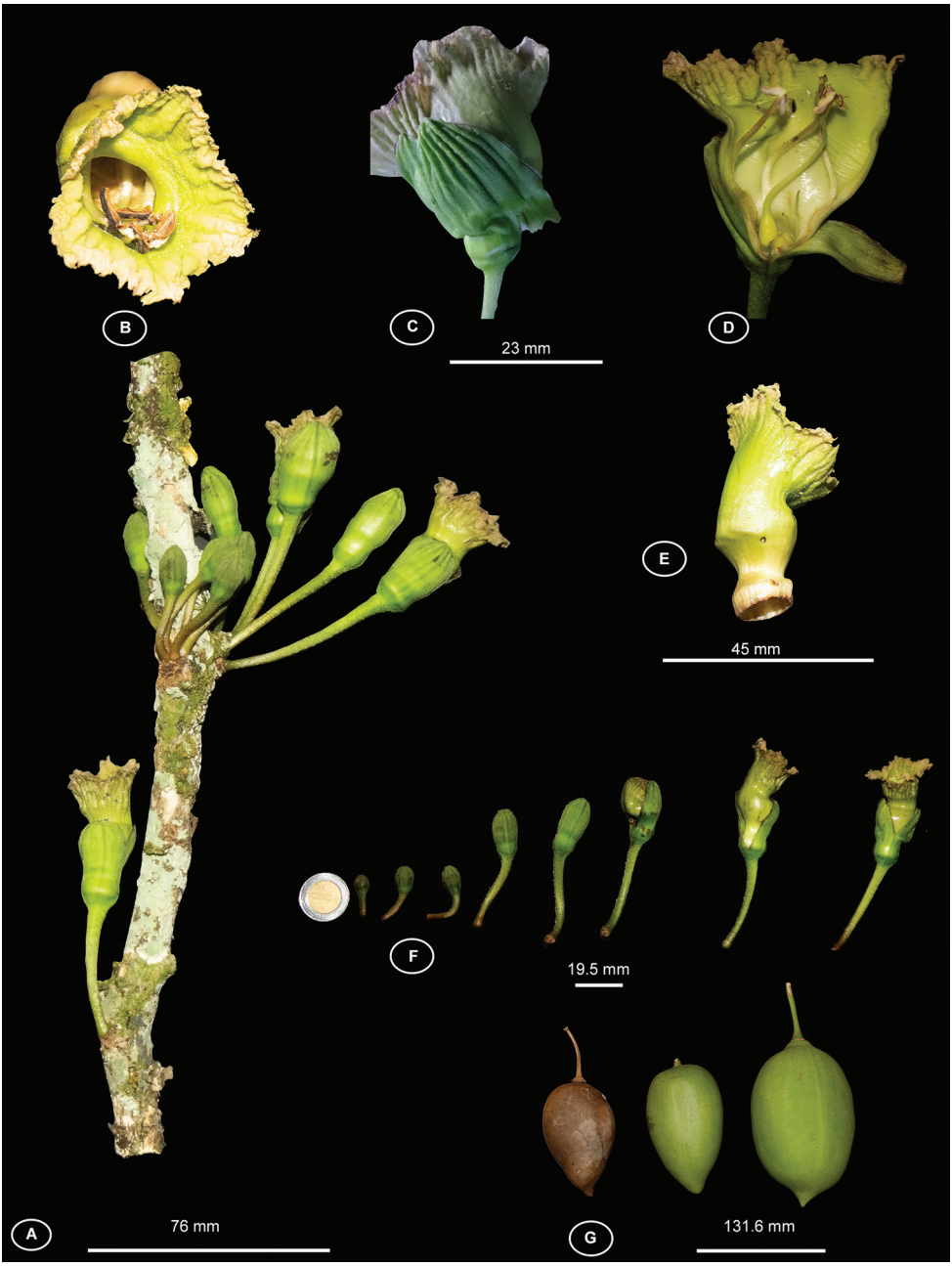

Figure 3. Reproductive features of *Amphitecna fonceti* sp. nov. **A** ramiflorous inflorescences with several flowers per shoot **B** corolla mouth **C** strongly costate calyx **D** corolla showing three stamens **E** corolla showing the transverse fold in the throat **F** flower developmental stages, from bud to anthesis **G** fruit shape variation. Photographs by Hector Gómez Domínguez.

the new species is distributed within a protected natural area, the oak, pine-oak forest at the type locality is seriously fragmented, with only small remnants persisting. *Amphitecna fonceti* is rare, with only 12 individuals being known to date.

Uses. The indigenous community where *A. fonceti* is found uses the fruits to treat respiratory diseases. The seeds of ripe fruits are extracted and soaked in a bottle of tequila for a week, after which a small glass is drunk in the morning to treat asthma. For whooping cough, two tablespoons of honey and almond oil are poured into the fruit after the removal of the fruit tip. The fruit is then cooked in water bath and its interior used as syrup. Its medicinal use likely helps the maintenance of this species within local coffee plantations.

Additional specimens examined. Mexico. Chiapas, La Concordia: Área de Protección de Recursos Naturales, La Fraylesca; Rancho Pacayal a 3 kilómetros del ejido Solo Dios, 15°46'54.9"N, 92°59'04.8"W, 1359 m., 24 de Mayo de 2020., *Gómez-Domínguez, H.* and *Hernández-Burguete, R. 3841* (HEM); same locality, *Gómez-Domínguez, H.* and *Hernández-Burguete, R. 3842* (HEM); *Gómez- Domínguez, H., Velazco Espino, D.* and *Hernández-Burguete, R. 3841* (XAL).

Notes. In addition to *A. apiculata* and *A. latifolia*, *A. fonceti* can also be confused with *A. sessilifolia*, another species from the *A. molinae* group. However, *A. sessilifolia* (endemic to Costa Rica) shows terminal flowers, larger corollas, stamens inserted 13–18 mm from base of the corolla tube, larger pistils, smooth and glabrous calyces (Gentry 1980, Table 3). *Amphitecna sessilifolia* has been incorrectly reported to Mexico (Martínez-Meléndez et al. 2017) based on misidentified specimens of *A. breedlovei* (e.g., Faustino Miranda 6916, MEXU-67682), *A. latifolia* (e.g., G. Martínez C. 2294, MEXU-733205), and *A. tuxtlensis* (e.g., J.I. Calzada 1457, MEXU-309621).

Amphitecna megalophylla resurrected

Our results indicate that *A. megalophylla* is best treated as a separate taxon that can be identified by the following features: pachycaul trees, with leaves up to 1 m long, multiflowered inflorescences, cauliflorous and long-pedicellate flowers with a transverse fold in the corolla throat, and fruits with costate/angulate surfaces. The following species is thus treated as an accepted taxon here:

Amphitecna megalophylla (Donn. Sm.) A.H. Gentry

Neotuerckheimia megalophylla Donn. Sm., Bot. Gaz. (Crawfordsville) 47: 258, f.l. 1909. Basionym.

Distribution. Guatemala (endemic).

Specimens examined. Guatemala. Alta Verapaz, Coban: 1350 m, *Türckheim H. von II 2278* (isosyntype, M).

Acknowledgements

We are grateful to Yuyini Licona Vera, Ivett Reynoso, Juan Francisco Ornelas, José Luis Villaseñor, Lulu Rico Arce, Alan Paton, and an anonymous reviewer for providing many useful comments on the manuscript. We also thank Christopher Davidson and Sharon Davidson for their support during field work.

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Supplementary material 1

Figure S1. Cophenetic correlation between clustering results from eight different linkage algorithms and Gower similarity index.

Authors: Héctor Gómez-Domínguez, Andrés Ernesto Ortiz-Rodríguez, Delfilia Velasco-Espino, Rene Hernández-Burguete

Data type: graphical data type

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Link: https://doi.org/10.3897/phytokeys.171.55397.suppl1

Supplementary material 2

Morphological dataset

Authors: Héctor Gómez-Domínguez, Andrés Ernesto Ortiz-Rodríguez, Delfilia Velasco-Espino, Rene Hernández-Burguete

Data type: morphological

Explanation note: Flower and leaves characteristics of 24 species of *Amphitecna*.

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Link: https://doi.org/10.3897/phytokeys.171.55397.suppl2

PhytoKeys 171: 91–153 (2021)
doi: 10.3897/phytokeys.171.56351
https://phytokeys.pensoft.net

RESEARCH ARTICLE

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On *Hydrangea peruviana*, an endangered species from Ecuador, and *Hydrangea oerstedii*, very common in Costa Rica and Panama, and seven threatened Central and South American Hydrangeas, which have been confounded with these

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Academic editor: S. Knapp | Received 9 July 2020 | Accepted 8 January 2021 | Published 26 January 2021

Citation: Samain M-S, Granados Mendoza C, Martínez Salas EM (2021) On *Hydrangea peruviana*, an endangered species from Ecuador, and *Hydrangea oerstedii*, very common in Costa Rica and Panama, and seven threatened Central and South American Hydrangeas, which have been confounded with these. PhytoKeys 171: 91–153. https://doi.org/10.3897/phytokeys.171.56351

Abstract

Hydrangea section *Cornidia*, currently consisting of 19 accepted taxa, occurs from Mexico to Chile and Argentina, with one species in southeast Asia. Its representatives are root-climbing lianas which may grow up to 60 m high in the tree canopy of temperate to (sub)tropical forests. Our extensive field work throughout its distribution area, study of herbarium specimens and ongoing molecular studies have resulted in the discovery of species new to science, as well as new insights into the circumscription of many taxa. We here present amended descriptions for seven *Hydrangea* species of Central and South America and discuss the taxonomical situation of two Colombian Hydrangeas, including an identification key, illustrations, and distribution maps. Field work was carried out in Costa Rica, Panama, Ecuador and Peru, including exploration in areas where the genus had not been collected before. These specimens and observations were complemented with the study of specimens of 41 herbaria of North, Central and South America, as well as Europe. Detailed morphological studies of all species were carried out, based on living plants in their natural habitat, as well as on dried specimens from our own collections and all available

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herbarium material. Type material was studied in detail for all species concerned. Based on an extensive number of morphological characters, combined with distribution patterns, phenological differences and ecological preferences, including molecular data in most cases, *Hydrangea peruviana* and *H. oerstedii* are clearly distinct taxa, as well as the other seven species mentioned here, which had been synonymized with either of these two species. The present study results in the recognition of 26 species in section *Cornidia* and exemplifies the urgent need for profound taxonomic studies in plants, as in many families we do not dispose of well-circumscribed units for conservation to mitigate the already occurring unprecedented loss of biodiversity.

Resumen

Hydrangea sección *Cornidia*, que actualmente consiste en 19 taxones aceptados, se distribuye desde México hasta Chile y Argentina, con una especie en el sureste asiático. Sus representantes son lianas trepadoras que pueden crecer hasta 60 m de altura en la copa de los árboles de los bosques templados a (sub) tropicales. Nuestro extenso trabajo de campo en toda su área de distribución, la revisión de especímenes de herbario y los estudios moleculares en curso han dado como resultado el descubrimiento de especies nuevas para la ciencia, así como conocimiento nuevo sobre la circunscripción de muchos taxones. Aquí presentamos descripciones enmendadas para siete especies de *Hydrangea* de Centro y Suramérica y discutimos la situación taxonómica de dos Hydrangeas colombianas, incluyendo una clave de identificación, ilustraciones y mapas de distribución. El trabajo de campo se llevó a cabo en Costa Rica, Panamá, Ecuador y Perú, incluída la exploración en áreas donde el género no había sido recolectado antes. Estos especímenes y observaciones se complementaron con el estudio de especímenes de 41 herbarios de Norte, Centro y Suramérica, así como de Europa. Se llevaron a cabo estudios morfológicos detallados de todas las especies, basados en plantas vivas en su hábitat natural, así como en muestras secas de nuestras propias colecciones y todo el material de herbario disponible. El material tipo se estudió en detalle para todas las especies en cuestión. En base a una gran cantidad de caracteres morfológicos, combinados con patrones de distribución, diferencias fenológicas y preferencias ecológicas, incluyendo datos moleculares en la mayoría de los casos, *Hydrangea peruviana* y *H. oerstedii* son taxones claramente distintos, así como las otras siete especies mencionadas aquí, que habían sido sinonimizadas con cualquiera de estas dos especies. El presente estudio resulta en el reconocimiento de 26 especies en la sección *Cornidia* y ejemplifica la necesidad urgente de estudios taxonómicos profundos en plantas, ya que en muchas familias no disponemos de unidades de conservación bien circunscritas para mitigar la pérdida de biodiversidad sin precedentes.

Keywords

Conservation, Ecuador, functional dioecism, hortensia, lianas, Neotropics, Peru, taxonomy

Introduction

The relatively poorly known *Hydrangea* L. section *Cornidia* Ruiz & Pav. consists of 19 currently accepted taxa (18 species and one variety) and a yet undefined number of species new to science and taxa that have been erroneously synonymized. The representatives of this section occur from northern Mexico to southern Chile and Argentina with one species, *Hydrangea integrifolia* Hayata, in southeastern Asia (Samain et al. 2014; Samain and Martínez Salas 2015; Samain et al. 2019). All taxa are evergreen root climbers growing up to 60 m high in the canopy of mostly primary forests, or rarely on boulders and rock walls (Granados Mendoza et al. 2014), generally

functionally dioecious, rarely monoecious, with coriaceous leaves and hortensia-like whitish-, greenish-, yellowish-, reddish- or purplish-tinged inflorescences, with or without enlarged marginal flowers.

Hydrangea section *Cornidia* (hereafter shortened as *Cornidia*) is monophyletic, including the single Asian species (Samain et al. 2010; Granados Mendoza et al. 2013a, b, 2015; De Smet et al. 2015), and is sister to the section *Calyptranthe* Maxim., consisting of Asian climbing species (De Smet et al. 2015). Both clades together are sister to the section *Asperae* (Rehder) Y.De Smet & Samain, encompassing Asian shrubby species (De Smet et al. 2015). As already noted by Samain et al. (2019), we do not follow the nomenclatural changes proposed by Ohba and Akiyama (2016), who suggest recognition of *Cornidia* as a segregate genus within tribe Hydrangeeae, together with most of the other sections published by De Smet et al. (2015), as they do not take into account the evolutionary context in which the new classification of the tribe Hydrangeeae was presented.

The monography of the genus *Hydrangea s.s.* by McClintock (1957), which is entirely based on herbarium specimens, is the only available recent complete revision of this section and includes 12 accepted species, classified in two subsections, *Monosegia* Briq. and *Polysegia* Briq. As mentioned by Samain et al. (2014), the revision by McClintock (1957) oversimplifies the high morphological variation within *Cornidia* in the Neotropics, due to inappropriate synonymization of taxa (since the description of *Cornidia* as a genus by Ruiz and Pavón (1794), more than 40 taxa have been described within this group), and to the fact that many diagnostic morphological characters were not taken into account (Samain et al. 2010, 2019). Following the revision of the genus *Hydrangea* by Freire-Fierro (2004) for the Flora of Ecuador, who considered *Hydrangea oerstedii* Briq. as a variety of *Hydrangea peruviana* Moric. ex Ser., only eleven species were recognized before the start of our revision of the genus (Samain et al. 2014).

We have carried out extensive field work throughout the distribution area of *Cornidia* since 2009, and as a consequence, we realized that its representatives are much more common than previously known (albeit most of them are severely threatened, mainly because of habitat destruction) and that its incredible morphological variation definitely did not fit into the then eleven accepted species. However, contrary to Mexico where we have recently described seven new *Hydrangea* species and registered one new record of a species until then only known from Guatemala (Samain et al. 2014, 2019), an important portion of the morpho-species in Central and South America do coincide with earlier described species which are currently considered to be synonyms.

Apart from the considerable confusion over names, an additional challenge in this group is the functional dioecism, which we have observed in most individuals during our extensive field work throughout the Neotropics, and which is reflected by a notoriously different size and shape of flower receptacle, anthers and pistils between functionally female and male flowers (Samain et al. 2014, 2019; Samain and Martínez Salas 2015). Interestingly, some species do not show this functional dioecism at all (e.g., *H. seemannii* L.Riley which has bisexual flowers, Samain et al. 2019), whereas some others may show functionally dioecious or perfect flowers depending on the individual.

The above-mentioned issues emphasize the need for a complete and urgent revision of *Cornidia*, especially in the light of conservation of these species. Their pristine habitat with very specific conditions (near water, often flat topography near the plants, efficient drainage) makes them not only promising bio-indicators, but also poses an additional threat as these habitats are being destroyed because they are highly appreciated by local people for agriculture (Samain et al. 2019). Our recent publications on *Cornidia* focused on the Mexican species were based on 186 herbarium collections, of which 50% were collected by ourselves (Samain et al. 2014, 2019).

The present work aims at resolving the complex of nine species from Central and South American species that had been formally synonymized under *Hydrangea peruviana* (*H. schlimii* Briq., *H. caucana* Engl., *H. durifolia* Briq., *H. goudotii* Briq., *H. oerstedii* Briq., *H. panamensis* Standl., *H. peruviana* Moric. ex. Ser., *H. trianae* Briq. and *H. weberbaueri* Engl.). The main objective of the present study is to show that we are dealing with nine different species, primarily based on morphological characters, and strengthened by preliminary molecular data. The identification key which is presented here thus has no other aim than showing that these species can be distinguished with relative ease based on morphological characters that are straightforward to observe. Based on meticulous observations in the field and of herbarium specimens, we here present amended descriptions for seven *Hydrangea* species of Central and South America and discuss the taxonomic situation of two more species of this group, including an identification key of species as recognized here, illustrations, and distribution maps, as well as information about their diversity, their global conservation status, and their affinities with other *Cornidia* species.

Material and methods

Field work focused on *Hydrangea* has been carried out by the authors during dry and rainy seasons in Costa Rica (2012, 2013), Ecuador (2012), Panama (2019) and Peru (2011, 2012, 2013), coinciding with the flowering and fruiting seasons, based on herbarium material of most of the species included. Exploring field work was not only carried out in the areas where previous collections had been made, but also in zones where Hydrangeas had not yet been recorded and where we suspected they would be present, based on our knowledge of their habitat preferences. Branches with inflorescences, flowers and fruits of all stages were collected and preserved. Moreover, in several individuals where architectural traits seemed to be important, whole branches were collected, of course without affecting the viability of the individual plants, cut and subsequently numbered in order to maintain the architecture available for further study. All specimens were deposited in local herbaria in the respective countries where we collected (CR (including INB), HOXA, PMA, QCNE and USM) with duplicates in the herbaria of the Instituto de Ecología, A.C. (IEB) in Pátzcuaro, Michoacán, Mexico, the Ghent University (GENT), in Ghent, Belgium and the National Herbarium of Mexico (MEXU) in Mexico City, Mexico.

Our field observations were complemented with a detailed study of relevant herbarium specimens of 41 herbaria in Europe, North, Central and South America (A, AAU, AMAZ, B, BM, BR, C, CAS, COL, CR, DUKE, E, F, G, GENT, GB, GH, HOXA, HUA, IEB, INB (now CR), K, LOJA, MA, MEXU, MICH, MO, MOL, MPU, NY, P, PMA, QCA, QCNE, QPLS, UC, UCH, UPS, US, USM, and WU; acronyms according to Thiers, continuously updated), most of them loaned, few (mainly type specimens) in high resolution on JSTOR Global Plants (https://plants.jstor.org/). A few herbaria, where loans were not allowed or logistically not possible, were visited in person to study the material in detail and take high quality photographs for later reference. A total number of 407 collections are included in this study, of which 75 have been collected by the authors of this paper. Both numbers may seem relatively low for a taxonomic revision; however, given that most of the species are rare to very rare on the one hand, and that hiking to primary vegetation followed by climbing of the host tree is required to reach inflorescences in most individuals on the other hand, these are highly representative. Indeed, as can be seen from the list of herbaria, most herbaria in the study area, as well as foreign herbaria with important collections (both recent and historical), have been consulted. Countries in the Specimens Examined section are listed alphabetically. For each specimen with reproductive structures studied, we mention whether it is functionally female (♀) or functionally male (♂), as well as which structures are present. Measurements were taken from dry herbarium specimens and three or more measurements per structure were taken when possible. Floral organ measurements were based on dry flowers. Colors were based on photographs of living plants and notes on herbarium labels. With respect to the leaf vein morphology, we use the standard terms we have used since our first treatment of this genus (Samain et al. 2014) in order to provide consistency: midvein for the central vein of the leaf, primary veins for the first order veins, secondary veins for the second order veins, and tertiary veins for the third order veins. The leaf characters in the identification key refer to the large, mature leaves on the stems and not to the leaves on the inflorescence axes.

Red List categories were obtained according to the IUCN Red List criteria (IUCN 2012). All known localities, including those of herbarium specimens without coordinates, were geo-referenced using Google Earth (2020). Extent of Occurrence (EOO) and Area of Occupancy (AOO) of all species were calculated with GeoCAT (Bachmann et al. 2011). Distribution maps were obtained with the same set of coordinates using ArcGIS v.10 software by Esri (www.esri.com).

Results

Taxonomy

The present treatment includes the *Cornidia* species *Hydrangea oerstedii* and *H. peruviana*, plus seven other species which had been erroneously synonymized with the former two. Amended morphological descriptions for seven of these and an identification key

to the taxa treated here are provided. We do not repeat here the morphological description of the section as this has been published in an Open Access paper by Samain et al. (2019). All species included here are characterized by lateral and umbellate inflorescences with reddish to purplish marginal and reduced flowers, except for *H. panamensis*, which has been reported with pink, yellow or white marginal flowers; hence, the earlier confusion of all these species, although in fact they are easily distinguishable. There are other taxa with similar colors in this section, but these have never been synonymized with the two abovementioned species, although South American herbarium specimens of these taxa may also be identified as *H. peruviana*. These taxa will be treated in an upcoming manuscript with species surrounding *Hydrangea preslii* Briq.

It should be mentioned that our ongoing molecular studies in the *Cornidia* clade show that most of the species studied here are even not closely related, with the exception of *Hydrangea panamensis* and *H. peruviana* on the one hand, and *H. goudotii* and *H. trianae* on the other hand (Granados Mendoza 2013; Granados Mendoza et al. unpublished data). Hence, we are not treating a monophyletic group of species here. Nevertheless, given that the focus of the present paper is morphological-taxonomical, and as all nine species since the 1950s are continuously considered as *H. peruviana*/*H. oerstedii* on herbarium specimens, in revisions and treatments (McClintock 1957; Freire-Fierro 2004; Christenhusz 2009), as well as in local floristic lists and catalogues such as those of Costa Rica (Morales Quirós 2007), Ecuador (Jørgensen and León-Yánez 1999), Panama (Correa et al. 2004), and Peru (Brako and Zarucchi 1993), we consider it appropriate to show in a single treatment that we are dealing with clearly distinct taxa which deserve recognition at species level based on an extensive range of morphological characters.

Of the nine taxa treated below, we have observed six in the field throughout their distribution area. *Hydrangea caucana* Engl., *H. durifolia* Briq. and *H. schlimii* Briq. have not been collected recently and are known with certainty from nine herbarium specimens, the type collection and a putative additional herbarium specimen, or the type collection only, respectively. The three of them are endemic to Colombia, where we have not yet been able to collect Hydrangeas due to collection permit and export regulations.

Key to the species of *Hydrangea* section *Cornidia* which have been confused with *Hydrangea oerstedii* and *Hydrangea peruviana*, including these two species

(Note: as mentioned above, this is a partial key that shows that these species are easy to distinguish. It cannot be used to identify all red-flowered Hydrangeas of Central and South America)

1 Inflorescences mainly consisting of flowers with enlarged sepals; currently only known from the type locality in Colombia.....**7. *H. schlimii* Briq.**

– Inflorescences with only the marginal flowers with enlarged sepals, these flowers placed terminally on cymes or racemes, one per partial inflorescence, or rarely absent; occurring in Costa Rica, Panama, Colombia, Ecuador or Peru.....**2**

2 Leaves up to 13 cm long and 6 cm wide.....**3**

– Leaves longer than 13 cm and wider than 6 cm.....**6**

3 Leaf apex rounded with a very small acumen; acarodomatia on the abaxial side 0–2 per leaf; Costa Rica and Panama ..... **5. *H. panamensis* Standl.**
– Leaf apex acute to acuminate, rarely mucronate; acarodomatia more numerous; occurring in Central and South America **4**
4 Lamina very slightly spoon-shaped, elliptic to slightly obovate; leaf margin serrate to slightly dentate; endemic to Ecuador ..... **6. *H. peruviana* Moric. ex Ser.**
– Lamina flat, ovate to lanceolate-elliptic; leaf margin glandular dentate; Costa Rica, Panama and Colombia **5**
5 Free-growing branches and inflorescence axes pubescent with persistent reddish brown stellate hairs; endemic to Colombia..... **1. *H. caucana* Engl.**
– Free-growing branches glabrous, and inflorescence axes pubescent with caducous, appressed, white stellate hairs; Costa Rica and Panama ..... **4. *H. oerstedii* Briq.**
6 Leaves with primary veins and secondary veins parallel to each other and forming a distinct regular pattern with all veins arching towards the apex; Colombia, Ecuador and Peru..... **9. *H. weberbaueri* Engl.**
– Leaves with a pinnate leaf vein pattern **7**
7 Free-growing branches and inflorescence axes glabrous..... **8**
– Free-growing branches with appressed white caducous stellate pubescence..... **9**
8 Abaxial leaf side with a granulate texture due to remaining basal stalks of stellate pubescence; inflorescence axis terete; inflorescence 5–9.5 cm wide; cymes compact; currently known from Colombia only ..... **2. *H. durifolia* Briq.**
– Abaxial leaf side pubescent with caducous, appressed, white, stellate hairs; inflorescence axis angled; inflorescence 6–28 cm wide; cymes lax; widely distributed in Costa Rica and Panama ..... **4. *H. oerstedii* Briq.**
9 Leaves markedly coriaceous; secondary and tertiary veins on the abaxial leaf side forming a reticulate network, connecting the primary veins; apical portion of flowering branch including leaves and buds densely pubescent with erect hairs; Colombia, Ecuador and Peru ..... **8. *H. trianae* Briq.**
– Leaves papyraceous; secondary and tertiary veins on the abaxial leaf side not forming a reticulate network; apical portion of flowering branch including leaves and buds scarcely to densely pubescent with appressed hairs; Colombia and Ecuador ..... **9. *H. goudotii* Briq.**

1. *Hydrangea caucana* Engl., Nat. Pflanzenfam. (ed. 2) 18a: 206. 1930.
Figures 1, 2

Type. Colombia. Cauca: Caldas, Las Pavas Cimarronas, 1200–1600 m, ♀, flowers, *F.C. Lehmann 5106* (lectotype, designated by McClintock 1957, pg. 240 [as "isotype"], second-step designated here: K! [K000486133], isolectotypes: F! [F0066623F], K! [K000486134].

Description. Root-climbing liana of probably not more than 15–20 m high; functionally dioecious; ***free-growing branches*** slightly quadrangular, densely pubescent with reddish brown stellate hairs; ***leaves*** decussate, petiole sulcate adaxially, terete

abaxially, color reddish brown, densely pubescent with caducous, reddish-brown, stellate hairs, 0.6–1.5 cm long, leaving a semicircular scar on the branch when leaves shed; lamina flat, ovate to lanceolate-elliptic, 6–12 cm long, 2.6–5.5 cm broad, base rounded to decurrent, sometimes asymmetric, apex acuminate, leaf margin glandular dentate, teeth generally small, larger in only a few leaves, venation brochidodromous, veins 5–7 pairs, adaxial leaf side with marked midvein, primary and secondary veins lightly marked, primary veins join to form submarginal vein, sparsely pubescent with appressed, white stellate hairs, in young leaves more dense and reddish hairs, abaxially with protruding veins, primary veins sometimes alternating protruding and marked in the same leaf, dark brown green, densely pubescent with appressed stellate reddish hairs near the midvein, rest of the lamina more sparsely pubescent, acarodomatia present, numerous, consisting of a simple cavity, but often not very conspicuous as they lay hidden under the midvein pubescence, in axils of midvein and primary veins; ***inflorescence axis*** densely pubescent with persistent reddish brown, stellate hairs, more dense towards the apex, 8–21 cm long, many-ribbed, with up to 3 opposite or decussate leaf pairs and up to 3 scars of possibly kataphyll pairs below the inflorescence, deciduous, petiole 5–15 mm long, lamina 6–12.5 cm long, 2.5–5.5 cm broad, kataphylls not seen, ***apex of the floral axis*** woody, basally quadrangular, apically triangular, elongated bract scars visible, 3–4 mm broad, 1.5–2 mm high in functionally female plants, 3.5–5 mm broad, 2–2.5 mm high in functionally male plants, ***inflorescence bracts*** cucullate densely pubescent, hairs reddish-brown, stellate, increasing in size, lowermost bract 1.5 cm large, 1.2 cm broad, other bracts not visible, ***inflorescences*** lateral (Fig. 1), decussate, 1–3 pairs of inflorescences per flowering branch, flowering branch only continues growing vegetatively rapidly during inflorescence development, with up to 6 leaf and kataphyll pairs above the inflorescences, inflorescence axes with basal lignified parts of inflorescences of previous years not seen, kataphylls at the base of the inflorescence present, orbicular, inflorescence umbellate, buds not seen, in flowering stage 4–12 cm diameter, 2.5–7 cm high, with 6–9 main axes in functionally male plants, 6–8 main axes in functionally female plants, partial inflorescences cymes, secondary and tertiary inflorescence axes densely pubescent with reddish, stellate hairs, pubescence gradually decreasing towards flower insertion; ***enlarged marginal flowers*** always present, terminally placed in a cyme, sepals 4, separate, with marked veins, pistils 2, fertile or reduced, some flowers with mature fruit, in these cases only 1 sepal visible, 1.5–2.3 cm diameter, pedicel 1–2 cm long, reddish-purple; ***flower pedicel of reduced flowers***, 0.2–1.5 mm long in functionally male flowers, 0.5–2(–3) mm long in functionally female flowers, ***receptacle*** triangular in functionally male flowers, semiglobose in functionally female flowers, ***ovary*** inferior, ***calyx lobes*** 4, triangular in male flowers, nearly reduced to zero in female flowers, enlarging during fruit maturation, reduced, ***petals*** 4, bright red to purple, cucullate, 1.2 mm long; ***functionally male flowers***: hypanthium 1–1.2 mm broad, 0.8–1 mm high, stamens 8, well-developed, pink, filaments 0.5–1.5 mm long, anthers 0.5 mm long, 0.2 mm broad, pistils 2, reduced, 0.2 mm long, stigmas not penicellate; ***functionally female flowers***: hypanthium 1 mm diameter, 0.5 mm high, stamens 8, reduced, filaments and anthers together 0.2 mm long,

Figure 1. *Hydrangea caucana*. Branch with infructescences with mature fruits and enlarged marginal flowers. Image of specimen *A. Cogollo et al. 2669* (MO).

pistils 2, 0.5–0.8 mm long, enlarging up to 2 mm during fruit maturation, stigmas slightly apically clavate and shortly penicellate; ***fruit*** a semiglobose capsule, apically with a thickened border, dark reddish brown, 0.8–1.2 mm high, 1.5 mm broad above, 1.5 mm diameter, opening between the two pistils to release seeds, seeds not seen.

Distribution. This species is endemic to Colombia and currently only known from the departments of Antioquia, Nariño and Valle de Cauca (Fig. 2).

Habitat. *Hydrangea caucana* is known from mountain cloud forest at elevations between 750–1365 m.

Phenology. *Hydrangea caucana* has been collected with flowers and fruits between November and March.

Notes. McClintock (1957) cited the K material as lectotype albeit without designating a specific sheet, which was copied by Freire-Fierro (2004). The holotype in B was destroyed; a photo of this specimen is available in F. We here select the better of the two sheets at K in a second-step lectotypification.

Hydrangea caucana should not be considered a synonym of *H. peruviana* and can be distinguished from the latter species by the flat, ovate to lanceolate-elliptic leaves with a glandular dentate margin. In contrast, *H. peruviana* is characterized by very slightly spoon-shaped, elliptic to slightly obovate leaves with a serrate to slightly dentate margin. Moreover, *H. caucana* is currently only known from Colombia, whereas *H. peruviana* is restricted to Ecuador.

We have not observed this species in the field, and herbarium labels of the known specimens of *H. caucana* do not record the size of the plants.

The phylogenetic relationships of *Hydrangea caucana* are yet unknown as there was no fresh material available for our molecular study (Granados Mendoza et al. unpublished results).

Preliminary conservation status. Based on the available herbarium collections, this species is Endangered according to the IUCN categories and criteria (IUCN 2012), with an AAO of 32 km^2, fewer than five locations and an extensive reduction in both EOO and AOO due to habitat destruction and fragmentation. The most recent collection of this species we have seen is from 1992, so further exploration is needed to know the current distribution and conservation status of this species.

Additional specimens examined. Colombia. Antioquia: Urrao, Aguadas, 1300 m, 8 Dec 1992, sterile, *Pipoly et al. 16776* (MO); Frontino, Vereda Venados, Parque Nacional Natural Las Orquídeas, margen izq. Río Venados (Garrucha y Alto Bonito), 6°32'N, 76°19'W, 800–850 m, 30 Jan 1995, ♂, flowers, *Pipoly et al. 18117* (MO, NY); same data as preceding, Parque Nacional Natural las Orquídeas, sector Calles, margen derecha del Río Calles, 1310–1365 m, ♀, fruits, 27 Mar 1988, *Cogollo et al. 2669* (COL, MO); same data as preceding, 1360 m, ♂, flowers, 19 Feb 1989, *Cogollo et al. 4091* (MO); **Nariño:** Mpio. de Ricaurte, Resguardo Indígena Nulpe Medio, camino a la quebrada La Conga, 1°6'N, 78°13'W, 750 m, 8 Jan 1996, ♂, flowers, *González & Ramírez 1636* (QCA); municipio Barbacoas, corregimiento Altaquer, Vías Las Vegas, al borde del río Veza, 870 m, flower buds, Mar 1995, *Fernández et al. 12459* (COL); **Valle de Cauca:** Cordillera Occidental, vertiente occidental, Hoya del Río Di-

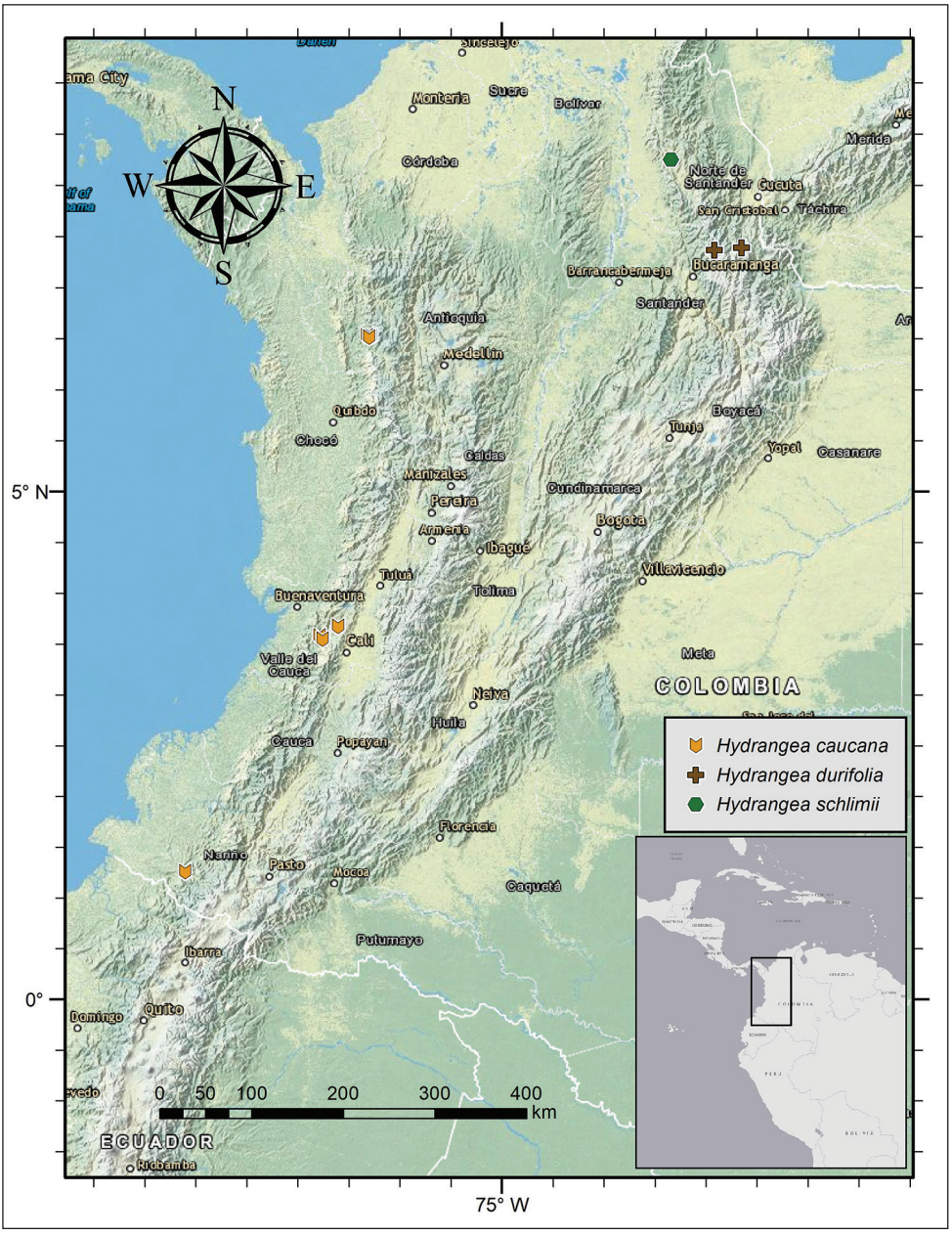

Figure 2. Distribution of *Hydrangea caucana*, *Hydrangea durifolia* and *Hydrangea schlimii*.

gua, lado derecho, La Elsa, 1000–1200 m, 9 Nov 1943, ♀, flowers, fruits, *Cuatrecasas 15326* (F, P, US); Cordillera Occidental, vertiente occidental, Hoya del Río Digua, lado derecho, entre Queremal y La Elsa, 1200–1160 m, ♀, 27, 29 Mar 1947, ♀, flowers, *Cuatrecasas 23994* (F, US).

2. *Hydrangea durifolia* Briq., Annuaire Conserv. Jard. Bot. Genève 20: 406. 1919.
Figures 2–4

Type. Colombia. Norte de Santander: Pamplona, ♂, flowers, *N. Funck & L.J. Schlim 1393* (lectotype, designated by McClintock 1957, pg. 238 [as "holotype"], second-step designated here: G! [G00223926]; isolectotypes: BR (photo in COL!), G! [G00301423], MPU! [MPU22860]).

Description. The most complete description to date can be found in the treatment by Briquet (1919), pages 406–407.

Distribution. *Hydrangea durifolia* is known from the type and an additional collection in northern Colombia (Fig. 2).

Notes. McClintock (1957) cited the type collection at G as "holotype", but there are two specimens, as in the case of *H. caucana*, so we here designate a second-step lectotype with the better of the G sheets. She also mentioned the existence of a fragment and photo in F, but we have not seen these, despite a visit to this herbarium. Apart from the original syntype (*Holton 661*, G, with locality in the "regione neogranadino-bogotana"), there is only one other specimen (see details below) that with certainty belongs to this species amongst the material we have studied for this revision. The leaves of the type specimen and of the *Holton 661* specimen are part of the inflorescence, which complicates the recognition of this species, as "vegetative" leaves are important for a correct identification at species level. However, these leaves are present in the only additional specimen we could assign with certainty to this species (Fig. 3). We have noticed that we are only able to identify collections with mere inflorescences of *Cornidia* up to species level, after having studied many samples of a specific taxon, as the leaves on the inflorescence axis do not have easily definable species-specific characteristics in comparison with the "regular" leaves.

The herbaria COL and F each house a black and white photo of a specimen of the *Linden 1393* collection, presumably taken in the BR and G herbaria, respectively.

Because of the lack of material and therefore, the uncertainty about this species´ circumscription, it is currently not possible to present an amended description. However, we also have no elements to consider this species as a synonym of one of the other species treated here, although it is morphologically close to *H. oerstedii* Briq. Briquet (1919) distinguished *H. oerstedii* by the much less coriaceous leaves, the inflorescence which has twice the width, the lax cymes as opposed to the more compact ones in *H. durifolia*, the sepals of the marginal flowers being two or three times larger, more papyraceous, with more abundant joined and protruding veins, which we can confirm based on the type specimens of both taxa. The few specimens of *H. durifolia* are known from the Colombian departments of Norte de Santander and Santander, whereas *H. oerstedii* is distributed in Costa Rica and Panama. Exploring field work in forests at elevations of around 2000–3000 m in the departments of Norte de Santander and Santander in the area of Pamplona might lead to the rediscovery of this species and the material will be helpful to define its taxonomic status.

Figure 3. *Hydrangea durifolia*. Branch with distinct "vegetative" leaves, floral axes with leaves and inflorescence buds. Image of specimen *E.P. Killip & A.C. Smith 18366* (GH).

Figure 4. *Hydrangea durifolia*. Branch with inflorescence buds and inflorescences. Image of specimen *E.P. Killip & A.C. Smith 18366* (US).

The phylogenetic relationships of *Hydrangea durifolia* are yet unknown as there was no fresh material available for our molecular study (Granados Mendoza et al. unpublished results).

Preliminary conservation status. It is possible this species is Critically Endangered according to the IUCN categories and criteria (IUCN 2012), given its AAO of 8 km^2, the existence of less than five locations and an extensive reduction in both EOO and AOO because of habitat destruction and fragmentation. However, we currently propose this species as Data Deficient, as its actual status is not well-known.

Additional specimen examined. Colombia. Santander: Vicinity of La Baja, 3000 m, 14–31 Jan 1927, ♂, inflorescence buds, flower buds, flowers, *Killip & Smith 18366* (GH (2), NY, US) (Figs 3–4).

3. *Hydrangea goudotii* Briq., Annuaire Conserv. Jard. Bot. Genève 20: 404. 1919. Figures 5, 6

Type. Colombia. Tolima: massif du Quindío á Portiohuelo, ♀, flower buds, flowers, *J. Goudot s.n.* (lectotype, designated by McClintock 1957, pg. 238 [as "holotype"]): G! [G00418961]; isolectotype: F! [F0066624F]).

Description. Root-climbing liana of up to 10 m high; functionally dioecious; ***free-growing branches*** many-ribbed, slightly angular to quadrangular, apically with dense appressed white caducous stellate hairs; ***leaves*** papyraceous, decussate, petiole terete, rarely slightly quadrangular or sulcate adaxially, basally with broadly sulcate adaxially, color dark green, scarcely pubescent with small, white stellate hairs, 1.5–2.7 cm long, leaving a triangular scar on the branch when leaves shed; lamina elliptic to obovate, 14–25 cm long, 7–14 cm broad, base cuneate, slightly decurrent, sometimes asymmetric, apex mucronate to acuminate, leaf margin (widely) serrate, venation brochidodromous, veins 8–9 pairs, adaxial leaf side with midvein protruding along its whole length, primary and secondary veins also protruding, angle primary veins up to 50 degrees, secondary veins reticulate and connecting the primary veins resulting in a network with parallel secondary veins nearly perpendicular with respect to the primary veins, white stellate pubescence scarce, only near the leaf base, abaxially with protruding veins, opaque olive green, scarcely to densely pubescent with appressed stellate white hairs, the latter depending on the specimen, nearly sessile to shortly stalked, acarodomatia numerous, present in axils of midvein and primary veins in the lower 2/3 of the lamina, consisting of a simple cavity, glabrous or sometimes with stellate hairs in the entrance; ***inflorescence axis*** densely pubescent with appressed, white, stellate hairs (Fig. 5B), 6–15 cm long, gradually broadening towards the apex, with 2 opposite leaf pairs along the axis and one opposite kataphyll pair immediately below the inflorescence, deciduous, petiole 1 cm long, lamina 3.5–9.3 cm long, 2.5–6 cm broad, abaxially densely pubescent with white stellate hairs, ***apex of the floral axis*** woody, cone-shaped, elongated bract scars visible, thickening at the top, 8–9 mm broad, 5–6 mm high in functionally female plants, 6–7 mm broad, 2–2.5 mm high

Figure 5. *Hydrangea goudotii* **A** branch with leaves seen abaxially, old inflorescence axes and the vegetative portion of the flowering branch **B** inflorescence bud with cucullate inflorescence bracts and densely pubescent inflorescence axis **C** inflorescence of functionally male plant, with enlarged marginal flowers and a few flowers that still show stamens **A** field image of collection *Granados Mendoza et al. 2012-105* **B, C** field images of collection *Granados Mendoza et al. 2012-43*.

in functionally male plants, ***inflorescence bracts*** cucullate, dark green to light pink (Fig. 5B), coriaceous, abaxially densely pubescent with whitish stellate hairs, margin membranous and glabrous, veins not visible as a consequence of the pubescence, bracts increasing in size distally, consecutively and rapidly deciduous during inflorescence development, ***inflorescences*** lateral (Fig. 5C), opposite, 1–4 pairs of inflorescences per flowering branch, up to 3 decussate small leaf pairs (or their scars) between the two inflorescence pairs, flowering branch continues growing vegetatively very rapidly during inflorescence development, with already up to 4 decussate leaf pairs above the inflorescences when the upper inflorescences are still in bud, linear, with dense white stellate hairs, inflorescence umbellate, buds up to 3.4 cm broad and 3 cm high before opening, in flowering stage 5–12 cm diameter, 2.5–8 cm high, with 5–10 main axes in functionally male plants, 5–6 main axes in functionally female plants, partial inflorescences umbels, secondary and tertiary inflorescence axes with reddish-white, appressed, stellate hairs; ***enlarged marginal flowers*** always present (Fig. 5C), terminally placed in a cyme, up to 3.6 cm diameter in female plants, up to 1 cm in male plants, sepals with marked veins, pistils 2 or sometimes not at all developed, reduced stigma not developed, receptacle rudimentary, globose, nearly the same size as that of reduced flowers, further characters not observed in detail, pedicel in male plants up to 1.5 cm; ***flower pedicel of reduced flowers*** 0.1–2.2 mm long in functionally male flowers, 1 mm long in functionally female flowers, enlarging during fruit development, 1.5 mm long in mature fruits, ***receptacle*** broadly campanulate in functionally male flowers, semiglobose in functionally female flowers, ***ovary*** inferior, ***calyx lobes*** 4, triangular, 0.3–0.5 mm long, ***petals*** 4, pinkish to wine red, imbricate, cucullate, membranous, 2 mm long, 1 mm broad; ***functionally male flowers*** (Fig. 5C): hypanthium 1 mm diameter, 1.5 mm high, stamens 8, well-developed, filaments 1–1.5 mm long, anthers 1 mm long, 0.2 mm broad, pistils 2, reduced, 0.1 mm long, stigmas not penicellate; ***functionally female flowers***: hypanthium 1.5 mm diameter, 1–1.5 mm high, stamens extremely reduced, as such their number could not be determined and their filaments and anthers have not been measured, pistils 2, 1 mm long, enlarging up to 1.5 mm during fruit maturation, stigmas apically clavate and shortly penicellate, 0.2 mm long; ***fruit*** a semiglobose capsule, apically with a conspicuous border, dark reddish brown, 2 mm high, 2.5 mm broad above, 3 mm long, opening between the two pistils to release seeds, seeds not seen.

Distribution. *Hydrangea goudotii* is endemic to Colombia and Ecuador. Further exploration for this species throughout both countries is required, as its currently known distribution pattern is fragmentary.

Habitat. This species occurs in mountain cloud forest, sometimes on heavy slopes at elevations between 1000–2500 m.

Phenology. This species has been collected in flower and fruit in January, March, June, July, August, and December. Although further studies on its biology are needed, it is likely that *H. goudotii* is characterized by two distinct flowering and fruiting periods: December–March and June–August. However, it remains to be investigated whether these two periods take place each year.

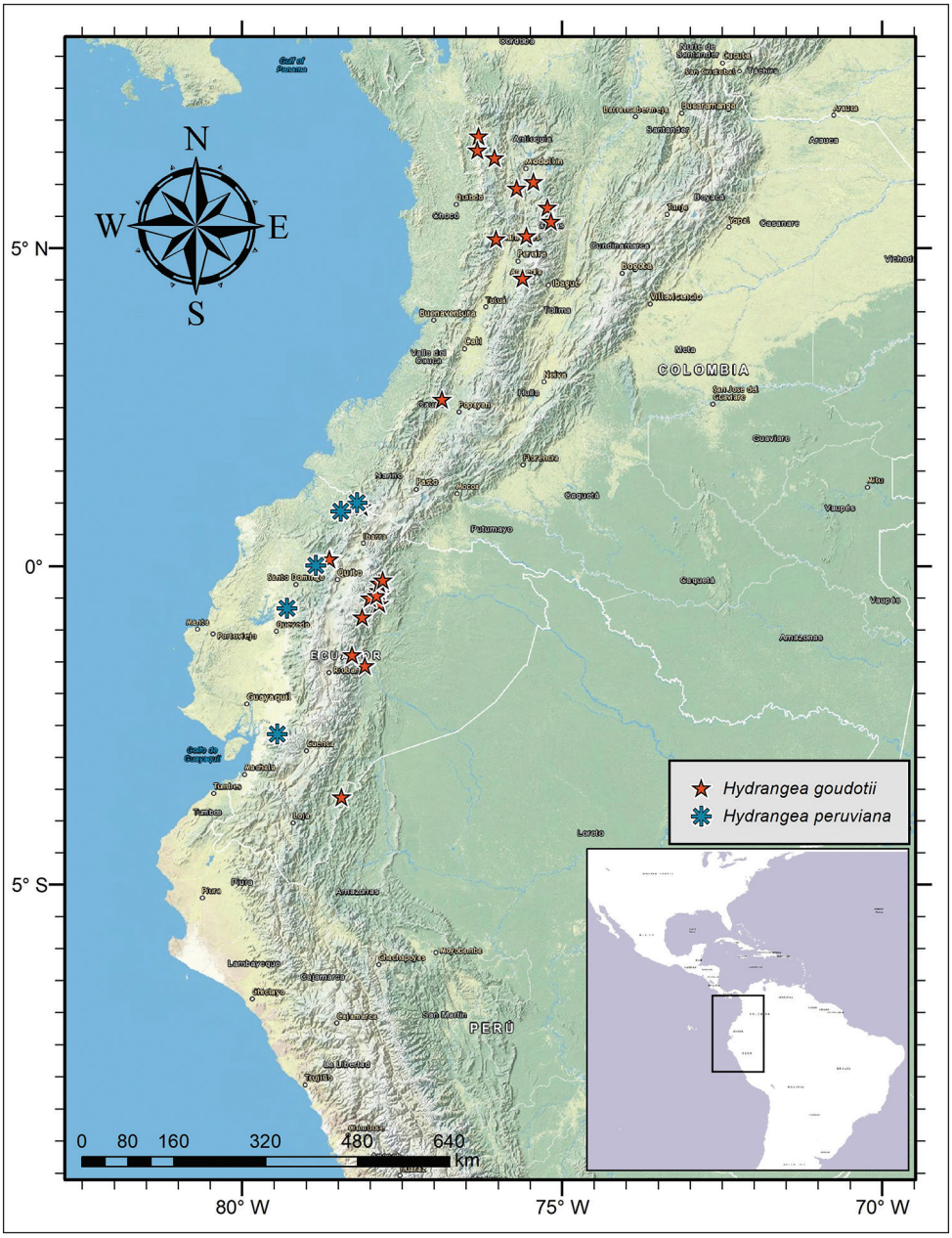

Figure 6. Distribution of *Hydrangea goudotii* and *Hydrangea peruviana*.

Notes. Briquet (1919) based his description of *H. goudotii* on three collections, all by Goudot (without number): "Columbia: Ibaque (Ibagué), Cahi (Cali) [G00223928, G00418963]; rives du Combayma (Combeima) [G00418962]; massif du Quindiu

(Quindio), a Portoihuelo (?) [G00418961]" (correct current locality names and G barcode numbers are placed between brackets). It seems all three collections are from the Central Cordillera between Ibagué and Armenia in the department of Tolima (R. Callejas, Universidad de Antioquia, Colombia, pers. comm.). McClintock (1957) selected the latter of the three syntypes mentioned in the original description by Briquet (1919) as lectotype, although she referred to it as holotype which is not correct according to the ICN (Art. 9, Turland et al. 2018). However, as in several other species for which McClintock (1957) realized lectotypifications and synonimizations, we doubt that she actually has had access to the involved specimens. In the case of *H. goudotii*, she considered the most representative specimen to be the collection which has been fragmented to take material to the herbarium F. Indeed, the specimen in F [F0066624F] consists, apart from the fragments of leaves and inflorescences, of a photo of the original Goudot collection. Careful examination of the latter shows that it consists of the branch which was designated as lectotype by McClintock (1957) [G00418961], which has been turned around 180 degrees, and an additional branch which was fragmented and is the F specimen. The latter is considered as isolectotype in that herbarium. However, because of the fragmentation of the original collection, the material that remained in G does lack fully developed enlarged marginal flowers.

Hydrangea goudotii should not be considered a synonym of *H. oerstedii* or *H. peruviana* var. *oerstedii* from which it can be distinguished by the appressed white caducous stellate pubescence on free-growing branches, these being glabrous in *H. oerstedii*. Moreover, *H. goudotii* is currently only known from Colombia and Ecuador, whereas *H. oerstedii* occurs in Costa Rica and Panama.

According to our molecular study, *Hydrangea goudotii* is closely related to *H. trianae* (Granados Mendoza et al. unpublished results).

Preliminary conservation status. Although this species has an EOO of about 154,700 km^2, it is Endangered according to the IUCN categories and criteria (IUCN 2012), with an AAO of 100 km^2, as well as an extensive reduction in both EOO and AOO due to habitat destruction and fragmentation.

Additional specimens examined. Colombia. Antioquia: Urrao, Vereda Calles, Parque Nacional Natural "Las Orquídeas', margen derecha del Río Calles, en el filo NW de la Cabaña de Calles, 1450 m, 6 Dec 1993, ♀, inflorescence buds, flower buds, *Cogollo et al. 7857* (MO); Zona limítrofe del Parque Nacional Natural Las Orquídeas, vereda Calles, Alto de Palmitas, ca 1 km de la Cabaña de Calles del INDERENA, 6°32'N, 76°19'W, 1300–1400 m, 1 Dec 1993, inflorescence bud, *Pipoly et al. 17468* (MO); municipio Urrao, carretera Urrao–Caicedo, 1 km antes del Alto de Caicedo, bosques a lo largo de Quebrada Villa Riaga, 6°28'N, 76°10'W, 2180 m, 5 Dec 1986, ♀, fruits, *Callejas et al. 3165* (F, HUA); Alto de Cuevas, 10 km W of Blanquita, 12 km W of Nutibara, transect B, 1720 m, 3 Mar 1992, ♂, flowers, *Gentry et al. 76116* (MO); municipio de Venecia, Vereda El Rincón, camino a Cerro Bravo, 5°56'19"N, 75°42'17"W, 1600–2300 m, 5 Jul 2007, flower buds, *David et al. 2192* (HUA); La Ceja, 2300 m, Sep 1964, ♀, fruits, *Espinal 1777* (COL). **Caldas:** Pueblo Rico, La Selva, 1400 m, 4 Jan

1946, ♀, flower buds, fruits, *von Sneidern 5265* (AAU, C, F, GH, MICH, US); Mcpio. Pensilvania, Vereda Líbano, al lado del camino del puente de Líbano, ca. 2400 m, 11 Jul 1982, ♀, flowers, *Albert de Escobar & Brand 2095* (HUA); **Cauca:** municipio El Tambo, Correg. La Romelia, km 75 vía a La Gallera, 1700–2000 m, 29 Jan 1995, ♂, flower buds, flowers, *Ruiz et al. 361* (COL); **Nariño:** en la quebradita de El Osa, 1900 m, 8 Jan 1949, ♂, flowers, *Uribe 1913* (COL); **Risaralda:** municipio de Santuario, estribación Oriental de la Cordillera Occidental, transecto de las Colonias, hacia Alto del Tigre, 2500 m, 31 Jan 1983, ♀, fruits, *Torres et al. 1359* (COL).

Ecuador. Carchi: near Maldonado, 1400 m, 30 Jul 1989, ♂, flowers, *van der Werff & Gudiño 10778* (QCNE); **Napo:** San Francisco de Borja, small forest high above banks of river beyond meadow at S. E. of town, hotel and square, 6 Jul 1980, ♂, flowers, *Sobel 2392* (NY); vicinity of Baeza, 1900 m, 27 Mar 1972, ♀, flowers, fruits, *Dwyer & McBryde 9601* (QCA); carretera El Chaco–Oyacachi, cerca del Río San Juan Grande, 0°16'S, 77°51'W, 1730 m, 15 Dec 1993, ♀, fruits, *Freire-Fierro & Yánez 2694* (QCA); El Chaco, fincas en la parte Este del pueblo, 0°13'S, 77°48'W, 1700–2000 m, 15 Mar 1991, ♂, flowers, *Gavilanes & Quezada 470* (AAU, QCA); Cerro Antisana, montane forest 2 mi. S. E. Borja, 5700 ft, 3 Aug 1960, ♀, flowers, *Grubb 1216* (K, NY); Mera, surroundings of Sevilla de Oro, 6.9 airline km S [of] Shell, 1°33'40.5"S, 78°4'29.3"W, 1080 m, 15 Jun 2012, inflorescence bud, *Granados Mendoza et al. 2012-43* (GENT, HOXA, IEB, MEXU, QCNE); El Chaco, ca. 2.1 airline km W of Sardinas, 0°23'2.7"S, 77°51'23.9"W, 1996 m, 10 Jul 2012, inflorescence bud, *Granados Mendoza et al. 2012-105* (GENT, HOXA, IEB, MEXU, QCNE); same data as preceding, ca. 2 airline km W of Sardinas, 0°23'1.3"S, 77°51'22.4"W, 1987 m, 10 Jul 2012, sterile, old inflorescences axes of previous year visible, *Granados Mendoza et al. 2012-107* (GENT, HOXA, IEB, MEXU, QCNE); Tena, Cordillera de los Huacamayos, localidad Pigui Yacu (Verde Yacu) Río Cushillo Yacu (Río Grande se origina en la cabecera de Sisahua), 1620 m, 30 Dec 1995, ♀, flowers, *Jaramillo & Tapia 18583* (QCA); Quijos, Cosanga. Cerca de la población de Cosanga, a 500 m del Río Cosanga, 2000 m, 11 May 1990, ♂, flowers, *Palacios 4895* (MO, QCNE); **Pichincha:** Nanegal, Sendero de la Unión de los Ríos, secondary lower montane rain forest along Río Umachaca, 00°07.5'N, 78°37.5'W, 1450 m, 24 Jun 1996, ♂, flowers, *Kelch et al. 31803* (QCNE); Quito, Parroquia Nanegal, montane rain forest along trail from Río Umachaca to Loma Sta. Lucía, c. 6 km airline SE of Nanegal, near top ridge, 00°07.5'N, 78°37'W, 1635 m, 6 Sep 1993, inflorescence buds, *Webster et al. 30392* (QCNE); Quito, Nanegal, Reserva Biológica Maquipucuna, 1200–1700 m, 20 May 1991, ♀, flowers, *Tipaz & Quelal 207* (AAU, MO, NY, QCNE); Quito, Maquipucuna Reserve, trail to Hacienda Esparragos, 00°07'N, 78°38'W, c. 1400 m, 27 Aug 1989, ♂, flowers, *Webster et al. 27062* (QCA); **Tungurahua:** Baños, ca. 2 km E of Río Verde on touristic path before tunnel on road to Baños–Mera, 1°23'25.1"S, 78°16'51.2"W, 1721 m, 16 Jun 2012, sterile, *Granados Mendoza et al. 2012-45* (GENT, HOXA, IEB, MEXU, QCNE); **Zamore-Chinchipe:** in the vicinity of the mining camp, at the Río Tundaime, along road to military base El Condor, 3°37'31"S, 78°26'26"W, 1000 m, 5 Nov 2004, ♀, fruits, *van der Werff et al. 19315* (LOJA, QCNE).

4. *Hydrangea oerstedii* Briq., Annuaire Conserv. Jard. Bot. Genève 20: 407–408. 1919. Figures 7, 8

Cornidia radiata Oerst., Vidensk. Meddel. Naturhist. Foren. Kjobenhaven 1856: 42. 1856. Type. Costa Rica. Cartago: in monte Candelaria, 6000–7000 ft, Feb 1847, ♂, flowers, *A.S. Oersted 1782* (lectotype, designated by McClintock 1957, pg. 238 [as "holotype"]: C!, isolectotypes: F! [V0066575F], US! [00097007]).

Hydrangea peruviana var. *oerstedii* (Briq.) Freire Fierro, Fl. Ecuador 73: 34. 2004. Type. Based on *Hydrangea oerstedii* Briq.

Type. Based on (replacement name for) *Cornidia radiata* Oerst.

Description. Root-climbing liana of up to 60 m high, often bending downwards, functionally dioecious; ***free-growing branches*** quadrangular, glabrous (Fig. 7A); ***leaves*** decussate, petiole flattened or sulcate adaxially, terete abaxially, color dark green, pubescent with caducous, appressed, white stellate hairs, 1.5–3 cm long, leaving a rhomboid scar on the branch when leaves fall; lamina flat, ovate to lanceolate-elliptic, 8–25 cm long, 4–14 cm broad, base cuneate, apex acuminate, leaf margin glandular-dentate, venation brochidodromous, veins 6–9 pairs, adaxial leaf side with midvein and primary veins sunken, secondary veins slightly visible, primary veins joining to form a submarginal or intramarginal vein, pubescent with caducous, appressed, white, stellate hairs, older leaves glabrous, abaxially with protruding veins, secondary veins connecting the primary veins, opaque olive green, densely pubescent with caducous, appressed, white, stellate hairs, acarodomatia numerous, consisting of simple cavities, in axils of midvein and primary veins; ***inflorescence axis*** angular, pubescent with caducous, appressed, white, stellate hairs, 8–42 cm long, with 3–6 decussate leaf below the inflorescence, persistent, petiole 1–1.5 cm long, lamina 6–13 cm long, 2.5–8 cm broad, ***apex of the floral axis*** woody, cone-shaped, elongated bract scars visible, thickening at the top, 6–11 mm broad, 3–7 mm high in functionally female plants, 10 mm broad, 5 mm high in functionally male plants, ***inflorescence bracts*** cucullate, cream-colored, coriaceous, abaxial surface tubercled, margin pubescent, adaxially white pubescent, margin membranous, veins slightly marked, bracts increasing in size, lowermost bract 3 cm large, 4 cm broad, higher bracts up to 5 cm large, 5.5 cm broad, consecutively and rapidly deciduous during inflorescence development, ***inflorescences*** lateral, decussate, 1–4 pairs of inflorescences per flowering branch (Fig. 7B), sometimes only one inflorescence developing, flowering branch continues growing vegetatively with the same vigor and periodicity above the inflorescences as below these, inflorescence axes with basal lignified parts of inflorescences of previous years visible in well-collected specimens, allowing to observe growth and flower periodicity, these rests 18–51 cm apart, with 5–11 decussate leaf pairs, but constant within one specimen (*Samain et al. 2012-047*, *Samain et al. 2012-072*), medulla central in the branch, disappearing in older branches, leaving a hole only, inflorescence umbellate, buds up to 4–5 cm broad and 3.5–4 cm high before opening, in flowering stage 6–28 cm diameter, 4–17 cm high, with 8 main axes in functionally male plants (Fig. 7C, D), 5–14 main axes in function-

Figure 7. *Hydrangea oerstedii* **A** branch with leaves seen abaxially **B** flowering branch of functionally male plant with three inflorescences with enlarged marginal flowers and many flowers with large stamens **C** inflorescence of functionally male plant with enlarged marginal flowers, most flowers in bud with petals visible, and a few open flowers with long stamens **D** close-up of functionally male inflorescence **E** close-up of functionally male flowers with reduced pistils **F** close-up of functionally female flowers with reduced stamens and large pistils. **A** field image of collection *Samain & Martínez 2012-044* **B** field image of collection *Samain & Martínez 2013-025* **C** field image of collection *Samain & Martínez 2012-044* **D** field image of collection *Samain et al. 2019-003* **E** field image of collection *Samain & Martínez 2013-025* **F** field image of collection *Samain & Martínez 2013-021*.

ally female plants (Fig. 7F), partial inflorescences cymes, lax, secondary and tertiary inflorescence axes towards the exterior glabrous, towards its center densely pubescent with whitish stellate hairs; ***enlarged marginal flowers*** generally present (Fig. 7B–D),

rarely absent (e.g. *Haber 1511*), terminally placed in a cyme, sepals 4, pinkish red to wine red, whitish in old inflorescence and infructescences, separate at their base, with marked veins, palmate, pistils 2 or reduced, central part of the flower often amorph, 1–1.5 cm diameter, growing up to 4 cm diameter during flower development, further characters not observed in detail, pedicel 1–4 cm long; ***flower pedicel of reduced flowers*** (0.2–)0.5–2(–4) mm long in functionally male flowers, 2–0.5(–2) mm long in functionally female flowers, ***receptacle*** broadly triangular in functionally male flowers, semiglobose to semirectangular in functionally female flowers, ***ovary*** inferior, ***calyx lobes*** 4, triangular, 0.2–0.3 mm long, 0.8 mm broad, ***petals*** 4, pinkish red to purple, valvate, cucullate, papyraceous, 1–2 mm long, 0.6–1.0 mm broad; ***functionally male flowers*** (Fig. 7E): hypanthium 1.5–2.0 mm diameter, stamens 8, well-developed, filaments 1.5–3 mm long, anthers 0.8–1.2 mm long, 0.5–0.8 mm broad, pistils 2, reduced, 0.5 mm long, transparent, stigmas not penicellate; ***functionally female flowers*** (Fig. 7F): hypanthium 1.2–2 mm diameter, 1 mm high, stamens 8, reduced, filaments 0.5 mm long, anthers 0.5 mm long, 0.2 mm broad, pistils 2, 1.2–1.5 mm long, rarely enlarging up to 2 mm during fruit maturation, stigmas apically clavate and shortly penicellate; ***fruit*** a semiglobose to semirectangular capsule, apically with a conspicuous, thickened border, ribs 4–6, dark brown with dark reddish brown margin, 1.8–3 mm high, 1.8–3 mm broad above, 1.5–2.5 mm diameter, opening between the two pistils to release seeds, seeds not seen.

Distribution. *Hydrangea oerstedii* is very abundant in Costa Rica and Panama. It is the most common species of this study (Fig. 8).

Habitat. This species occurs in mountain cloud forest at elevations between 1100 and 2500 m. In contrast to most of the other *Hydrangea* species, it is common to find this species in disturbed habitats, even when there is no primary forest left and only the very humid microhabitat and protection against direct sunlight remain.

Phenology. This species has been collected with flowers and fruits throughout the year.

Notes. Not to be considered as a variety of *H. peruviana*, from which it can be distinguished by the flat, ovate to lanceolate-elliptic leaves with white pubescence abaxially and a glandular dentate margin. In contrast, *H. peruviana* is characterized by very slightly spoon-shaped, elliptic to slightly obovate leaves with reddish pubescence adaxially and a serrate to slightly dentate margin. Moreover, *H. oerstedii* is a relatively common species in Costa Rica and Panama, whereas *H. peruviana* is a very rare species from Ecuador.

Freire Fierro (2004) also mentioned the presence of an isotype in K, but although this specimen bears the same locality data on its label as the type, it cannot be confirmed that it concerns the same collection, given that no number is mentioned.

According to our molecular study, *Hydrangea oerstedii* is not related to any of the species included in this study (Granados Mendoza et al. unpublished results).

Preliminary conservation status. With an EOO of slightly more than 20,760 km^2 and an AAO of 428 km^2, this species is Near Threatened according to the IUCN categories and criteria (IUCN 2012). Although its habitat is continuously being destroyed and fragmented, this species is robust, and basically only needs

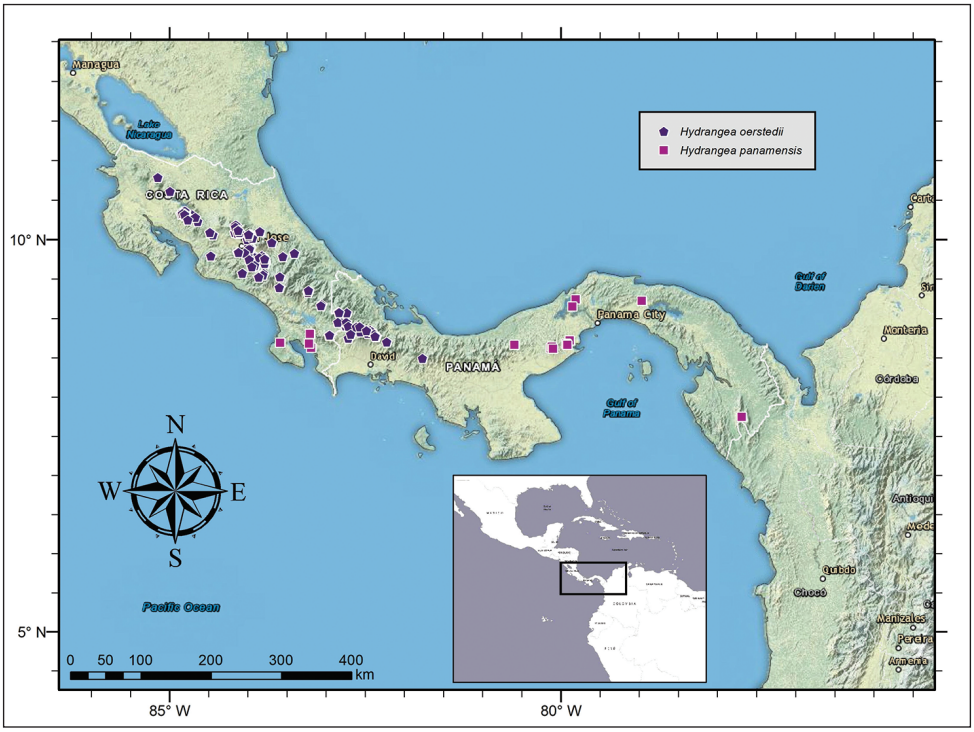

Figure 8. Distribution of *Hydrangea oerstedii* and *Hydrangea panamensis*.

a host tree that remains of the primary forest. As the older plants bend downwards and often have their eye-catching inflorescences just a few meters above ground level, it is even possible that this species is favored when trees are being logged. Nevertheless, should large areas of forest be destroyed, this species may well enter into a threatened category.

Additional specimens examined. Costa Rica. Alajuela: Alajuela, Distrito 3° Carrizal, 13.1 km N of Heredia via Rte. 114 (10.9 km. N of Barva), 20 ft. from rd., 10°5'26.4"N, 84°9'56.71"W, 1500–2000 m, 15 May 1990, ♀, fruits, *Grantham 90.0433 & Parsons* (CAS); San Ramón, Distrito 1° San Ramón, Vicinity of San Ramón, La Palma de San Ramón, 14 Dec 1926, ♀, fruits, *Brenes 5221* (CR, NY); R.B. Monteverde, Cordillera de Tilarán, Sendero Rancho Alegre, 10°17'40"N, 84°45'W, 1000 m, 4 Apr 1995, ♀, fruits, *Martínez 379* (CR, MO); La Palma, Picada San Antonio, 1 Dec 1922, ♀, fruits, *Brenes 3807* (CR, F, GH); Reserva Biológica Bosque Nuboso de Monteverde, al lado del Sendero Chomogo, 1.15 km al NE de la caseta de entrada, 10°18'22.23"N, 84°47'11.12"W, 1710 m, 2 Aug 2012, ♀, fruits, *Samain & Martínez 2012-045bis* (CR, GENT, IEB, MEXU); Peñas Blancas, R.B. Monteverde, Peñas Blancas River Valley, Atlantic slope, 10°20'N, 84°50'W, 1250 m, 12 Oct 1985, ♂, flowers, *Haber 3102* (CR); Reserva Biológica Bosque Nuboso de Monteverde, al lado del Sendero Camino, 10°17'59.87"N, 84°46'58.35"W, 21 Jan 2013, 1519 m, ♂, flowers,

Samain & Martínez 2013-025 (CR, GENT, IEB, MEXU); cerca de División continental (Ventana), 1550–1580 m, 14 Dec 1976, ♀, flower buds, fruits, *Dryer 1080* (CR, F, MO); Monteverde Reserve, Atlantic Slope, Río Peñas Blancas valley, ridge trail above Quebrada Leona, 1050–1300 m, 17 Jan 1985, ♀, flowers, fruits, *Haber 1304* (MO); Monteverde Reserve, Atlantic Slope, Río Peñas Blancas valley, 960 m, 19 Nov 1984, ♀, fruits, *Haber 1035* (MO); same data as preceding, 1300 m, 20 Mar 1985, ♀, flower buds, *Haber 1511* (MO); Reserva Biológica Monteverde, Río Peñas Blancas, Parcela de Rockwell, 10°19'N, 84°43'W, 820 m, 21 Dec 1988, ♂, flowers, *Bello 632* (CR, MO); Alajuela, no protegida, Cuenca del Sarapiquí, Hotel Posada Volcán Poás, Viento fresco, 10°10'27.81"N, 84°10'10.072"W, 1800 m, *13 Mar 2003*, ♀, old fruits, *Kriebel 2911* (CR); San Ramón, Cerros de la Palma, 1500 m, 24 Jan 1984, ♀, fruits, *Gómez-Laurito 9802* (CR, F); San Ramón, La Palma, 13 Mar 1929, ♀, fruits, *Brenes 19368* (CR); La Palma, Picada de San Antonio, Dec 1922, ♀, old fruits, *Brenes 19366* (CR); La Palma de San Ramón, 22 Dec 1922, ♀, old fruits, *Brenes 19367* (CR); Bosque Húmedo en San Pedro de San Ramón, 11 Jan 1924, ♀, old fruits, *Brenes 19370* (CR); La Palma, Picada de San Antonio, Dec 1922, ♀, old fruits, *Brenes 19371* (CR); San Ramón, Bosque húmedo de las colonias de San Pedro, 1200 m, 11 Jan 1924, ♀, fruits, *Brenes 3984* (F); **Cartago:** Cartago, Distrito 5° San Francisco, 0.5 km N. of Tapantí, 9°47'56.64"N, 83°55'37.57"W, 1300 m, 7 Nov 1971, ♀, young fruits, *Lent 2210* (F, GB, US); El Guarco, Distrito 2° San Isidro, dry wooded slopes about 13 km south of the Taras Intersection along the Interamerican Highway or about 18 km north of El Empalme, 9°47'52.05"N, 83°56'49.10"W, 4 Jul 1976, ♂, old flowers, *Wilbur 19852* (DUKE); Empalme, Cartago, 9°43'5.91"N, 83°56'50.32"W, 2300 m, 1 Dec 1983, ♂, flower buds, flowers, *Gómez 22176* (CR, F, MO, UC); Cartago, slopes in the vicinity of Palo Verde and the Quebrada Cangreja on the road to Estrella, 9°47'0.07"N, 83°57'11.48"W, 1600 m, 19 Dec 1974, ♀, fruits, *Wilbur 18437 & Luteyn* (CAS, DUKE, F); Turrialba, Distrito 8° Tayutic, Turrialba, Jicotea, por la fila al lado oeste del Río Jicotea, Finca del señor Israel Martínez, 9°47'5"N, 83°33'15"W, 1100–1200 m, 7 Dec 1994, ♀, fruits, *Sánchez et al. 424* (CR, F, K); Cartago, hills above Platanillo, 9°49'31.24"N, 83°24'16.91"W, 915 m, 7 Nov 1967, ♂, old flowers, *Stone 2324* (DUKE); Paraíso, Distrito 3° Orosi, about 15 km south of Tapantí along the new road, on the east slope above the Río Grande de Orosi near the concrete bridge, 9°46'44.28"N, 83°47'46.78"W, 1500 m, 30 Dec 1970, ♀, fruits, *Burger 7525 & Liesner* (F, GB); Cartago, Distrito 5° San Francisco, about 3–5 km S of Muñeco along the Río Sombrero, 9°45'38.34"N, 83°54'21.62"W, 1400–1500 m, 25 Feb 1978, ♀, fruits, *Wilbur 24976* (DUKE); Cartago, ca. 2.5 km S of Muñeco, 9°46'15.95"N, 83°54'17.34"W, 1500 m, 25 Feb 1978, ♀, fruits, *Almeda & Nakai 3937* (CAS, CR); El Guarco, Distrito 2° San Isidro, Alto de La Estrella, 26–27 Mar 1924, ♀, fruits, *Standley 39080* (US); Cartago, al lado del camino Copatchi–San Rafaël Arriba, 9°49'47.52"N, 84°2'22.83"W, 1838 m, 27 Jul 2012, sterile, *Samain & Martínez 2012-034* (CR, GENT, IEB, MEXU); al lado del camino Copatchi–Quebradilla, 9°49'54.96"N, 84°1'38.37"W, 1931 m, 27 Jul 2012, sterile, *Samain & Martínez 2012–035* (CR, GENT, IEB, MEXU); El Guarco, Cuenca del Reventazón, San Isidro, Ruta al Cerro de la Muerte, entrada a Palo

Verde, 1 km después de la entrada, 9°47'56"N, 83°56'51"W, 1800 m, 26 Nov 1998, inflorescence buds, *Rodríguez et al. 4208* (CR, MO); camino San Isidro de El General–Cartago, 9°41'23.46"N, 83°54'12.64"W, 2532 m, 11 Aug 2012, ♀, fruits, *Samain & Martínez 2012-072* (CR, GENT, IEB, MEXU); camino Cartago–San Isidro de El General, 9°46'16.46"N, 83°59'1.03"W, 1770 m, 23 Jan 2013, ♂, flowers, *Samain & Martínez 2013-030* (CR, GENT, IEB, MEXU); same data as preceding, 9°46'16.46"N, 83°59'1.03"W, 1769 m, 23 Jan 2013, ♀, fruits, *Samain & Martínez 2013-031* (CR, GENT, IEB, MEXU); same data as preceding, 9°41'23.72"N, 83°54'12.58"W, 2489 m, 23 Jan 2013, ♀, fruits, *Samain & Martínez 2013-032* (CR, GENT, IEB, MEXU); Paraíso, P.N. Tapantí, Valle del Reventazón, Río Grande de Orosi, fila innominada al sur del cruce de la toma del Río Humo, 9°43'5"N, 83°46'50"W, 1500–1600 m, 21 Jun 1996, floral buds, *Morales 5394 et al.* (CR, MO); Cartago, Paraíso, Cordillera de Talamanca, Río Grande de Orosí, Tapantí, bosque alterado por crecientes del Río Villegas, cerca de la toma de agua, 9°41'50"N, 83°46'50"W, 1500 m, 22 Jul 1994, ♂, old flowers, *Morales 3059* (CR, F); Cartago, El Guarco, No protegida, Cuenca del Pirrís–Damas, Cerros de la Muerte, 9°47'47.6085"N, 83°59'54.3782"W, 2100 m, 18 Feb 2002, ♂, young flowers, *González 1528* (CR); Cartago, Paraíso, P.N. Tapantí, Valle del Reventazón, Estación Tapantí, Sendero La Heliconia, 9°45'20"N, 83°47'W, 1300 m,10 Jun 1995, ♂, old flowers, *Mora 661* (CR); Cartago, Paraíso, P.N. Tapantí–Macizo de la Muerte, Cuenca del Reventazón, P.N. Tapantí, Sendero Árboles Caídos, 9°45'4"N, 83°47"W, 1300–1413 m, 18 Jun 2005, ♂, old flowers, *Morales 13225* (CR); Cartago, Paraíso, No protegida, Cuenca del Reventazón, entrada a Monte Sky, 9°44'53.9065"N, 83°50'4.8525"W, 1537 m, 5 Dec 2000, ♀, fruits, *González 1225* (CR); Cartago, Paraíso, P.N. Tapantí, Valle del Reventazón, Sector Dos Amigos, Sendero Rancho Negro, 9°45'20"N, 83°47'W, 1300 m, 20 Jul 1994, floral buds, *Morales 289* (CR); Cartago, La Unión, San Rafael, Cerros de La Carpintera, Campo Iztarú de los Scouts, Alrededores del área administrativa, 9°53'24.8"N, 83°58'6.8"W, 1730 m, 13 Oct 2010, ♂, old flowers, *Cascante 2250* (CR); Prov. de Cartago, La Unión, Tres Ríos, 1350 m, 12 Apr 1953, ♀, fruits, *Córdoba 327* (CR): Cartago, San Nicolás, Cerros de la Carpintera, Campo Escuela Iztarú, propiedad de la Asociación Scouts de Costa Rica, sendero hacia la cima de los cerros, 9°52'55.8"N, 83°58'40.3"W, 1854 m, 11 Jun 2007, ♀, fruits, *Estrada 3977* (CR); Cartago, Paraíso, Orosí, Camino del pueblo de Río Macho al Embalse, área de cafetales y pequeños bosques alterados, 9°46'15"N, 83°51'15"W, 1500 m, 26 Jan 2010, ♀, fruits, *Cascante 2179* (CR); Tapantí, 1300 m, 15 Jul 1937, floral buds, *Valerio 1658* (F); Cartago, very steep slopes with open forest and many epiphytes about 10 km south of Tapantí along the new road on the east slope above th Río Grande de Orosí, 9°42'N, 83°47'W, 1400–1600 m, 10–24 Jun 1968, ♀, fruits, *Burger & Stolze 6108* (F); Turrialba, Las Cortinas 1 km al norte del Monumento Guayabo, Manglares del Río Guayabo, 9°57'50"N, 83°41'30"W, 1100 m, 13 Oct 1992, ♀, fruits, *Rivera 2007* (CR, F, MO); Refugio Nacional de Vida Silvestre Tapantí, about 7–15 km beyond the main entrance to the reserve; roadsides and trails through wet montane rainforest, 1500–1650 m, 3 Mar 1991, ♀, fruits, *Almeda et al. 6912* (CR, MO); **Guanacaste:** Tilarán, Área no protegida, Cordillera de Tilarán, Reserva Biológica

del Colegio de Monteverde, 10°21'20"N, 84°49'50"W, 1600–1700 m, 10 Jan 1992, ♀, fruits, *Bello 4328* (CR, MO); Z.P. Tenorio, Cordillera V Tilarán, Tierras Morenas, Río San Lorenzo, 1050 m, 10°36'40"N, 84°59'45"W, 10 May 1994, ♂, old flowers, *Rodríguez 13* (CR, MO); Santa Elena, cerca de la entrada del Parque Selvatura, 10°20'31.23"N, 84°47'56.94"W, 1618 m, 1 Aug 2012, ♂, *Samain & Martínez 2012-044* (CR, GENT, IEB, MEXU); Santa Elena, en el límite de la Reserva Bosque Nuboso Santa Elena, 10°20'35.12"N, 84°47'50.53"W, 1659 m, 31 Jul 2012, ♀, fruits, *Samain & Martínez 2012-045* (CR, GENT, IEB, MEXU); Reserva Bosque Nuboso Santa Elena, al lado del camino a la Laguna de Arenal, 827 m al NE de la caseta de entrada, 10°20'58.70"N, 84°47'33.56"W, 1582 m, 31 Jul 2012, ♀, fruits, *Samain & Martínez 2012-046* (CR, GENT, IEB, MEXU); Reserva Bosque Nuboso Santa Elena, al lado del camino a la Laguna de Arenal, 1.27 km al NE de la caseta de entrada, 10°21'14.67"N, 84°47'34.77"W, 1555 m, 31 Jul 2012, ♀, old inflorescence axes, fruits, *Samain & Martínez 2012-047* (CR, GENT, IEB, MEXU); Reserva Bosque Nuboso Santa Elena, al lado del camino a la Laguna de Arenal, 415 m al NE de la caseta de entrada, 10°20'48.66"N, 84°47'40.36"W, 1643 m, 31 Jul 2012, ♀, fruits, *Samain & Martínez 2012-048* (CR, GENT, IEB, MEXU); al lado del camino de Santa Elena al Mirador Lodge, 1.01 km desde la desviación hacia la Reserva Bosque Nuboso Santa Elena, 10°21'9.35"N, 84°48'6.97"W, 1545 m, 20 Jan 2013, inflorescence buds, floral buds, *Samain & Martínez 2013-019* (CR, GENT, IEB, MEXU); al lado del camino de Santa Elena al Mirador Lodge, 1.74 km desde la desviación hacia la Reserva Bosque Nuboso Santa Elena, 10°21'32.08"N, 84°48'9.79"W, 1495 m, 20 Jan 2013, ♀, inflorescence buds, flowers, *Samain & Martínez 2013-021* (CR, GENT, IEB, MEXU); al lado del camino de Santa Elena al Mirador Lodge, 2,069 m desde la desviación hacia la Reserva Bosque Nuboso Santa Elena, 10°21'43.64"N, 84°48'16.32"W, 1509 m, 20 Jan 2013, ♀, fruits, *Samain & Martínez 2013-022* (CR, GENT, IEB, MEXU); Heredia, Heredia, Distrito 6° San José de la Montaña, Cantón de Barva. Cerca de Porrosatí, 10°6'N, 84°7'W, 2000 m, 6 Jan 1991, ♂, flowers, *Hammel 18228* (CR, K, MO); **Heredia:** Distrito Varablanca, Vara Blanca de Sarapiquí, north slope of Central Cordillera, between Poás and Barba volcanoes, 10°11'2.85"N, 84°9'12"W, 1680 m, 1 Jan 1938, ♀, flowers, fruits, *Skutch 3393* (K, MO, US); Region between San Rafaél and the Río San Rafaél about 3 km east of Vara Blanca, 1800 m, 10°10'17.96"N, 84°8'21.84"W, 23 Feb 1976, ♀, flower buds, flowers, fruits, *Utley & Utley 4166* (DUKE, MO); Barva, No protegida, Cuenca del Tárcoles, entre Porrosatí y Sacramento, faldas del Volcán Barva, 10°5'22"N, 84°6'22"W, 1950 m, 24 Apr 2002, ♀, young fruits, *Hammel 22523* (CR); Barva, P.N. Braulio Carrillo, S slope of west forest, 1950 m, 16 Jan 1965, ♀, flower buds, flowers, *Hatheway 1275* (CR); Barva, Montaña, La Isla, Sacramento, 2500 m, ♂, old flowers, 13 Jan 1987, *Gómez-Laurito 11304* (CR, F); Barva, Cordillera Central, entre Porrosatí y Sacramento, faldas del Volcán Barva, 10°5'22"N, 84°6'22"W, 2000 m, 24 Jan 1996, ♂, flowers, *Hammel 20131* (CR, MO); cord. V. Central, faldas de V. Barva, Porrosatí, camino al volcán Barva, 10°5'45"N, 84°7'10"W, 2000 m, 12 Nov 1993, ♂, flowers, *Jiménez 1406* (CR, MO); faldas del Volcán Barva, entre Porrosatí y Sacramento, 2047 m, 10°5'38.20"N, 84°6'12.75"W,

6 Aug 2012, ♀, fruits, *Samain & Martínez 2012-041* (CR, GENT, IEB, MEXU); same data as preceding, 10°5'38.28"N, 84°6'15.92"W, 2035 m, 28 Jul 2012, inflorescence buds, *Samain & Martínez 2012-042* (CR, GENT, IEB, MEXU); Vara Blanca, terreno del restaurante Vara Blanca, 10°9'32.40"N, 84°9'20.28"W, 1842 m, 15 Jan 2013, ♂, inflorescence buds, flowers, *Samain & Martínez 2013-001* (CR, GENT, IEB, MEXU); faldas del Volcán Barva, entre Porrosatí y la entrada al parque, 10°7'17.65"N, 84°7'23.48"W, 2447 m, 18 Jan 2013, ♀, flowers, *Samain & Martínez 2013-012* (CR, GENT, IEB, MEXU); Heredia, 13.1 km N of Heredia via Rte. 114 (10.9 km N of Barva), 20 ft from road, 1500–2000 m, 15 May 1990, *Grantham & Parsons 0013-90* (CAS); **Limón:** Talamanca, Cordillera de Talamanca, Quebrada Kuisa, al paso del Sendero entre Ujarrás y San José Cabécar, 9°20'N, 83°13'55"W, 2100 m, 13 Mar 1993, ♀, fruits, *Fernández 653* (CR, MO); P.N. La Amistad, cuenca del Sixaola, sobre transecto 5, 9°21'18.1080"N, 83°13'29.9820"W, 1848 m, ♀, fruits, 25 Feb 2007, *Solano 4048* (PMA); Parque Internacional La Amistad, sendero Transtalamancana, entre Ujarras y San José Cabécar, alrededores del Río Lori, 9°21'18.6080"N, 83°13'19.2000"W, 1850–1900 m, 25 Feb 2007, ♀, fruits, *Rodríguez et al. 10829* (CR, PMA); Talamanca, P.N. La Amistad, Cuenca del Sixaola, transecto 5, 9°21'18.108"N, 83°13'29.892"W, 1848 m, 25 Feb 2007, ♀, fruits, *Solano 4046* (CR); Guápiles, Los Angeles, San Miguel, siguiendo el camino que lleva a San Gerardo de Oreamuno, volcán Irazú, 10°6'10"N, 83°50'45"W, 1300 m, 23 Feb 1990, ♂, flowers, *Herrera 3789 & Schik* (CR, MO); Cordillera de Talamanca, headwaters of the unnamed western branch of the Río Teribe, between the Río Sini and the continental divide at Cerro Bekom, 9°10'45"N, 83°3'30"W, 2500–2600 m, 21&27 Mar 1984, inflorescence bud, floral buds, *Davidse et al. 26158* (CR, MO); **Puntarenas:** Distrito Monteverde, Z. P. Arenal-Monteverde, Cuencas del Lagarto y Guacimal, Reserva Biológica Monteverde, a 1 km del inicio del Sendero principal, 10°19'17"N, 84°48'35"W, 1540 m, 1 Jun 1999, ♀, flower buds, flowers, *Hurtado 156* (CR, NY); on and near Continental Divide about 2 to 5 km. east and southeast of Monteverde, 10°18'9.94"N, 84°47'44.07"W, 1580–1700 m, 17–20 Mar 1973, ♀, fruits, *Burger 8613 & Gentry, Jr.* (DUKE, F, MO); Buenos Aires, P.N. La Amistad, Cuenca Térraba-Sierpe, sendero de Bekon a Tres Colinas, 9°9'42.965"N, 83°4'1.44"W, 2400–2500 m, 18 Apr 2002, ♂, flowers, *Alfaro 3978 et al.* (CR, MO); Z.P. Las Tablas, Cuenca Térraba-Sierpe, Zona Protectora Las Tablas, Surá, 7 km NO de Progreso, 8°54'17"N, 82°45'3"W, 2050 m, 18 Jan 1987, ♂, old flowers, *Navarro 579* (CR, MO); Puntarenas, Reserva Biológica Monteverde, Ojo de Agua, Finca de Leonel Hernández, lado pacífico de la reserva, 10°15'N, 84°46'W, 1600 m,18 Nov 1987, ♀, flower buds, flowers, *Haber 7811 & Bello* (CR, MO); Monteverde Community, Pacific slope, 1450 m, 10°20'N, 84°50'W, 13 Aug 1986, ♂, old flowers, *Haber ex Bello 5295* (MO); Reserva Biológica Monteverde, Pacific slope and continental divide, 10°18'N, 84°48'W, 1600 m, 17 Jun 1992, ♀, fruits, *Haber & Zuchowski 11210* (CR, MO); R.B. Monteverde, Cordilla de Tilarán, Monteverde, camino hacia Alto Cebadilla, 10°19'30"N, 84°51'W, 1300 m, 9 Feb 1994, ♀, fruits, *Ramírez 242 & Poveda* (CR, MO); Monteverde Cloud Forest Reserve, Cordillera de Tilarán, pacific slope of continental divide, Pantanoso trail, 1500–1620 m, 29 Dic 1984, ♀, fruits, *Pounds 379*

(MO); Forest along trail between Las Alturas and Cotonsito, along the Río Cotón, 8°56'30"N, 82°48'W, 1400 m, 31 Aug 1983, ♂, flowers, *Davidse 24651* (CR, F, MO, MEXU); Foothills of the Cordillera de Talamanca, lower montane forest along the Río Bella Vista, NW of Las Alturas, 8°57'N, 82°51'W, 1450–1600 m, 30 Aug 1983, ♂, inflorescence buds, flowers, *Davidse 24300* (CR, MO); Monteverde Cloud forest Reserve, continental divide near La Ventana and elfin forest, 10°20'N, 84°50'W, 1600 m, 14 Dec 1985, ♂, inflorescence buds, flowers, *Haber ex Bello 3959* (CR, MO); same data as preceding, ♂, flowers, *Haber ex Bello 3969* (CR, MO); forest and forest edges on and around Wilson's finca, 6 km south of San Vito de Java, about 4000 ft, 16 Aug 1967, floral buds, *Raven 21806* (F, MO); Puntarenas, Coto Brus, Z.P. Las Tablas, Cuenca Terraba-Sierpe, Sendero Sura, Zonas Protectora Las Tablas, 8°56'57"N, 82°44'37"W, 1920 m, 20 Dec 1997, ♂, old flowers, *Navarro 827* (CR, MO); Puntarenas, Puntarenas, Reserva Biológica Monteverde, Ojo de Agua, Finca de Leonel Hernández, lado pacífico de la reserva, 10°15'N, 84°46'W, 1600 m, 18 Nov 1987, floral buds, *Haber 7811* & Bello (CR, MO); Puntarenas, Bob Wilson´s Forest, San Vito de Java, near the Panamanian border, 22 Aug 1965, ♂, old flowers, *Walker 164* (F); Puntarenas, near Bob Wilson's finca at San Vito Vine, 20 Aug 1965, ♂, old flowers, *Croat 1067* (MO); Foothills of the Cordillera de Talamanca, lower montane forest along the Río Bella Vista, NW of Las Alturas, 8°57'N, 82°51'W, 1450–1600 m, 30 Aug 1983, floral buds, *Davidse 24281* (MO); Monte Verde, 1500 m, 27 Dec 1984, ♂, inflorescence buds, flower buds, flowers, *de Nevers & Charnley 4427* (MO, PMA); **San José:** Desamparados, Distrito 2° San Miguel, Altos de Tablazo, about 5 km SE of Higuito on Calle Tablazo or about 12 km SE of Desamperados, 9°49'54.82"N, 84°2'28.28"W, 1800–1900 m, 30 Jan 1976, ♂, inflorescence bud, flowers, *Utley & Utley 3838* (DUKE, F); Distrito 8° San Cristobal, Cordillera de Talamanca. 4 km. north of El Empalme, 9°44'45.61"N, 83°58'36.99"W, 2070 m, 3 Mar 1986 ♂, flowers, *Almeda & Anderson 5298* (CAS); Distrito 9° Rosario, about 12 km. S of Higuito on the slopes of Altos Tablazo, 9°49'53.39"N, 84°2'26.69"W, 1800 m, 20 Feb 1978, ♂, flower buds, flowers, *Almeda 3757 & Nakai* (CR, CAS); Dota, Distrito 3° Copey, near Finca La Cima, above Los Lotes, North of El Copey, 9°40'15.4"N, 83°54'48.85"W, 2100–2400 m, 21–22 Dec 1925, ♀, flower buds, flowers, *Standley 42569* (US); Pérez Zeledón, Distrito 1° San Isidro de El General, roads above San Isidro de Coronado, 10°0'6.90"N, 84°0'21.38"W, 1400–1600 m, 1 Dec 1937–1 Jan 1938, ♀, flowers, *Allen 534* (F, GH); Vasquez de Coronado, Distrito 3° Jesús, La Hondura, 10°3'44.72"N, 83°58'55.21"W, 1300–1700 m, 16 Mar 1924, ♀, fruits, *Standley 37781* (US); Lisière des forets a L´Alto de la Palma, 10°2'55.35"N, 83°59'22.02"W, 1542 m, 30 Aug 1898, ♀, fruits, *Tonduz 12507* (US); La Palma, 10°2'55.71"N, 83°59'18.93"W, 1600 m, 3 Feb 1924, ♀, fruits, *Standley 33163* (US); Río Claro valley (Río La Hondura drainage) below La Palma northeast of San Jerónimo, 10°3'N, 83°58'W, 19 Nov 1969, 1000–1200 m, inflorescence buds, *Burger 6290 & Liesner* (CR, F, GB, NY); Woods above Río Hondura, 10°3'30"N, 83°58'28.86"W, 1150 m, 5 Dec 1971, ♀, fruits, *Lent 2272* (COL, CR, F, MEXU); heavily wooded slope leading from Alto La Palma to Bajo la Hondura about 12 km NNE of San Vicente de Moravia in Route 220 in the saddle

between Irazú and Barba, 10°3'19.33"N, 83°59'10.46"W, 1200 m, 19 May 1971, ♀, fruits, *Wilbur 14687* (DUKE); Desamparados, Distrito 2° San Miguel, Altos de Tablazo, about 5 km SE of Higuito on Calle Tablazo or about 12 km SE of Desamparados, 9°49'54.82"N, 84°2'28.28"W, 1800–1900 m, 30 Jan 1976, ♀, fruits, *Utley & Utley 3844* (DUKE, F, MO); Perez Zeledon, Distrito, 4° Rivas, P. I. La Amistad, Cordillera de Talamanca, Entre las Nacientes de las quebradas Barranca y Río Blanco, Finca San Carlos, 9°31'47"N, 83°35'30"W, 05 Apr 1995, 2350 m, ♀, fruits, *Aguilar 3816 & Garrote* (CR, F, K, NY); Dota, San Gerardo de Dota, 2291 m, 9°34'18.56"N, 83°48'4.46"W, 24 Jan 2013, ♂, old flowers, *Samain & Martínez 2013-035* (CR, GENT, IEB, MEXU); Escazú, San Antonio, Z.P. Cerros de Escazú, falda SE del Alto Hierbabuena, 9°50'30"N, 84°7'35"W, 2100 m, 15 Oct 1992, ♀, flowers, fruits, *Morales 767* (CR, F, MO); Perez Zeledon, al lado del camino a San Gerardo de Dota, 4.22 km al SO del crucero con la Carretera Interamericana San Isidro de El General–Cartago, 9°33'27.20"N, 83°48'14.31"W, 2299 m, 11 Aug 2012, sterile, *Samain & Martínez 2012-068bis* (CR, GENT, IEB, MEXU); Turrubares, San Luis, Z.P. Cerros Turrubares, faldas del Cerro Bares, 9°47'30"N, 84°28'30"W, 1600 m, 6 Nov 1990, ♀, fruits, *Jiménez 919 et al.* (CR, F, MO); Bajo de Hondura, P.N. Braulio Carrillo, 10°4'N, 83°58'W, 1100–1200 m, 23 Jan 1983, ♂, old flowers, *Davidse 23195* (CR, MO); along Ca-2 on western ascent of Cerro de la Muerte, north of turnoff for road 222, 2000 m, 27 Feb 1976, ♂, inflorescence buds, flowers, *Croat 32829* (MO); San José, Sendero del camino viejo, hacia el Río La Hondura, P.N. Braulio Carrillo, 1250 m, 6–9 Dec 1983, ♂, old flowers, *Zamora & Carlson 418* (MO); San José, Aserrí, Cerros de Escazú, Tarbaca, bosque secundario en las cabeceras de la quebrada Saurez, 9°50'15"N, 84°7'10"W, 1900–2000 m, 6 Nov 1993, ♀, young fruits, *Morales 1979* (CR); San José, Vasquez de Coronado, R.F. Cordillera Volcánica Central, Cuenca del Sarapiquí, Cascajal de Coronado, calle Monserrat, 10°1'4"N, 83°56'31"W, 1700–1800 m, 6 Jul 2000, ♂, old flowers, *Vargas 459* (CR); San José, Moravia, No protegida, cuenca del Sarapiquí, paso de la Palma, de las Lecherías, 10°2'50"N, 83°59'20"W, 1500 m, 8 Nov 2003, floral buds, *Morales 10053* (CR); San José, Pérez Zeledón, Cordillera de Talamanca, Las Nubes de Santa Elena, tajo a orilla de la carretera, 9°23'30"N, 83°35'50"W, 1210 m, 7 Aug 1995, ♀, fruits, *Mora 245* (CR); San José, Parque Nal. Braulio Carrillo, camino entre El Bajo de la Hondura y La Montura, ca. 1200 m, 1 May 1982, ♂, old flowers, *Gómez-Laurito 8408* (CR, F); San José, Terrazú, San Lorenzo, R.F. Los Santos, fila San Isidro, 9°34'20"N, 84°4'10"W, 1350 m, 5 Nov 1997, ♂, flowers, *Valverde 384* (CR); San José, Dota, Santa María, Cerca de Palmitera de Dota, 1700 m, 20 Dec 1963, ♂, flowers, *Jiménez 1466* (CR, F); San José, Dota, Copey, R.F. Los Santos, San Gerardo de Dota, orillas del río Savegre, 2200 m, 26 Nov 1985, ♂, old flowers, *Soto s.n.* (CR); San José, Pérez Zeledón, Páramo, R.F. Los Santos, Lira, Estribaciones Noroeste de Cerro Lira, 9°31'30"N, 83°51'40"W, 1800 m, 8 Dec 1994, ♂, old flowers, *Martén 673 & Herrera* (CR, F); San José, P.N. Braulio Carrillo, Sendero del Camino Viejo, hacia El Río La Hondura, 1250 m, 9 Dec 1983, ♂, old flowers, *Zamora 417* (CR); without locality, ♂, old flowers, *Warcewicz 27368* (MO, photo from Delessert Herbarium).

Panama. Bocas del Toro: Cordillera de Talamanca, headwaters of the Río Culubre, 6 airline km NW of the peak of Cerro Echandi on the Costa Rican–Panamian international border, 09°05'00"N, 82°50'30"W, 2450–2600 m, 2–3 Mar 1984, ♀, fruits, *Davidse et al. 25254* (CR, MEXU, MO, PMA); E branch, headwater of Colubre River, 2300–2500 m, 2 Mar 1984, inflorescence bud, *Gómez et al. 22303* (MO); La Pata del Cedro, ridgetop, 09°04.270'N, 82°44.174'W, 1750 m, 11 Mar 2004, ♀, fruits, *Monro & Alfaro 4315* (CR, MO, PMA); **Chiriquí:** 1.4 mi S of Cerro Punta, 1850 m, 28 Dec 1963, ♀, fruits, *Graham 297* (MICH); along road and in pasturelands and stream banks above Las Nubes, NW of Cerro Punta, 1900–2100 m, 26 May 1973, ♀, fruits, *Luteyn 3797* (DUKE, MICH); Parque Internacional La Amistad, 100 m al SSW de la oficina, 8°53'36.3"N, 82°36'58.1"W, 2207 m, 10 May 2019, ♂, inflorescence buds, flowers, *Samain et al. 2019-003* (IEB, MEXU, PMA); Parque Internacional La Amistad, sendero El Retoño, 190 m al WNW de la oficina, 8°53'39"N, 82°37'0.53"W, 2227 m, 10 May 2019, ♀, flowers, *Samain et al. 2019-006* (IEB, MEXU, PMA); along trail between N fork of Río Palo Alto and Cerro Pate Macho, ca 6 km NE of Boquete, 8°48'N, 82°23.5"W, 1600–1700 m, 6 Feb 1986, ♂, old flowers, *Grayum et al. 6370* (MO); Alto Pineda, end of road, right turn just before cooperativa entrance to Cerro Punta, 8400 ft, 11 Apr 1979, ♂, inflorescence axes, old flowers, *Hammel et al. 6976* (MO); District Boquete, Alto Quiel, Finca Lerida, 05 Nov 1994, *Quiroz 166 & Garrido* (F, NY, PMA) (old inflorescence axes, flower buds); District Boquete, Bajo Chorro, 6000 ft, 7 Jan 1938, ♀, fruits, *Davidson 74* (F, GH, MO, UC, US); edge of forested slope above Cerro Punta toward Bajo Grande in Quebrado Bajo Grande, about 6500 ft, 14 Jan 1970, ♀, flowers, fruits, *Wilbur 10923 et al.* (DUKE, F, MICH, MO); Jurutungo, de la Fca. Los Quetzales, luego hacia la der. para luego bajar por el Río, 8°54'N, 82°43'W, ca. 1900 m, 24 Sep 1996, ♀, fruits, *Aranda 3251 et al.* (DUKE, MO, NY, PMA); Las Nubes, 5 km NW of Cerro Punta, 6000–6500 ft, 19 Jul 1975, ♂, flowers, *Mori & Bolten 7248* (MO); Monte Azul, 1.4 mi N of Entre Ríos on E slopes of Cerro Punta, 3 mi by road from town to Cerro Punta, 2250 m, 22 Nov 1979, ♀, flower buds, *Antonio 2693* (MEXU, MO, PMA); pastured area and bordering woods NE of Cerro Punta about 2.5 km, about 7200 ft, 29 May 1972, ♀, fruits, *Wilbur et al. 17149* (DUKE, MICH); road to Cerro Punta National Park from Alto Quiel and Boquete, 8°51'N, 82°29'W, c. 1850 m, inflorescence buds, 16 Jan 1986, *McPherson 8031* (MEXU, MO, PMA); trail up Cerro Pate Macho, 08°50'N, 82°25'W, 1500–1900 m, 7 Jan 1983, ♀, fruits, *Stein et al. 1215* (MEXU, MO); Valley of the upper Río Chiriquí Viejo, 18 Jan 1938, ♀, fruits, *White & White 90a* (MO); Vicinity of "New Switzerland", central valley of Río Chiriquí Viejo, 1800–2000 m, 6–14 Jan 1939, ♂, flowers, *Allen 1400* (UC, US); 7 km northwest of Cerro Punta, Las Nubes region, 7200 ft, 11 Feb. 1978, floral buds, *Hammel 1428* (MO, PMA); vicinity of Fortuna, 8°45'N, 82°15'W, ca. 1250 m, 28 Apr 1986, ♀, fruits, *McPherson 9115* (MEXU, MO); Chiriquí, Boquete, Bajo Mono, 1600 m, Jan 1979, ♀, fruits, *Beliz 463* (PMA); Boquete, Sendero a Culebra, 1800 m, 18 Jan 2004, sex not visible because of insect damage, *Cáceres et al. 1836* (UCH); vicinity of Bajo Mona and Quebrada Chiquero, 1500 m, 18 Jul 1940, ♀, fruits, *Woodson & Schery 511* (GH, MO); distrito San Felix,

Comarca Gnöbe Buglé, km 0 al 10 entre Hato Chami y Hato Ratón, ± 27–37 km al N de la 8°29'41"N, 81°46'16"W, 1386–1576 m, 20 May 2001, ♀, fruits, *Galdames et al. 4691* (F, PMA); Reserva Forestal Fortuna, Sendero La Casa Rosada, bosque cercano al Río Hornito, 8°42'00"N, 82°13'26"W, 1147 m, 31 Jan 2013, ♂, old flowers, *Ortiz 1172 et al.* (PMA). Without locality, either in Costa Rica or Panama ("Costa Rica et Veragua "), without date, ♂, flowers, *Warszewicz 1* (G).

5. *Hydrangea panamensis* Standl., J. Wash. Acad. Sci. 17(1): 10. 1927.
Figures 8, 9

Type. Panama. Colón, along Río Fato, 10–100 m, floral buds, *H.F. Pittier 3919* (holotype: US! [00097000], isotypes: A!, BM! [BM000028808], C!, F! [V0066620F], GH! [00042780], K! [K000486137], NY! [00007170]) floral buds.

Description. Root-climbing liana of up to 20 m high, never reaching above the lower branches of its host tree canopy (Fig. 9A), sometimes bending downwards, functionally dioecious; ***leaves*** decussate, petiole sulcate adaxially, terete abaxially, color reddish brown, densely pubescent with caducous, appressed, reddish, stellate hairs, 1–2 cm long, leaving a nearly triangular scar on the branch when leaves fall; lamina obovate to slightly elliptic, 5–12 cm long, 3–6 cm broad, base cuneate to rounded, slightly asymmetric, apex rounded with a very small acumen, leaf margin very slightly glandular-dentate, slightly revolute, venation brochidodromous, veins 4–6 pairs, adaxial leaf side with midvein and primary veins marked, primary veins join to form submarginal vein, pubescent with caducous, appressed, stellate hairs, the basal stalk reddish, the rest whitish, opaque pale green, abaxially with protruding midvein, primary veins alternately protruding and marked, secondary veins marked, regularly with concave cleavages on the junction of primary and secondary veins, opaque pale reddish brown, densely pubescent with appressed, stellate hairs, the basal stalk reddish, the rest whitish, acarodomatia very rare, 0–2 per leaf, consisting of a simple cavity in the axil of the midvein and primary veins; ***inflorescence axis*** pubescent with appressed, small, yellow-reddish, stellate hairs, shedding in older specimens, 2–10 cm long, quadrangular, with 1 decussate leaf and 1 kataphyll pair below the inflorescence, rapidly deciduous, ***apex of the floral axis*** woody, quadrangular, elongated bract scars visible, thickening at the top, 2–3 mm broad, 1–1.5 mm high in functionally female plants, 2–3 mm broad, 1 mm high in functionally male plants, ***inflorescence bracts*** cucullate, membranous, densely pubescent with reddish stellate hairs, veins palmate, bracts increasing in size, lowermost bract 1.5 cm large, 1.1 cm broad, higher bracts up to 2 cm large, 1.6 cm broad, ***inflorescences*** lateral, decussate, 1–3 pairs of inflorescences per flowering branch, flowering branch only continues growing very rapidly during inflorescence development, with up to 7 leaf pairs above the inflorescences, giving a very homogeneous aspect, inflorescence axes with basal lignified parts of inflorescences of previous years not observed, leaves or kataphylls present at the base of the inflorescence, inflorescence umbellate (Fig. 9B), buds up to 2 cm broad and 1.5 cm high before opening, in flowering stage

Figure 9. *Hydrangea panamensis* **A** plant growing along the stem of a *Cecropia* **B** infructescence with young and mature fruits, and enlarged marginal flowers. *Hydrangea peruviana* **C** stolons with adventitious roots and decussate leaves. **A, B** field images of collection *Samain & Martínez 2012-063* **C** field image of collection *Granados Mendoza et al. 2012-112*.

3–10 cm diameter, 1.5–5 cm high, with 5–8 main axes in functionally male plants, 5–8 main axes in functionally female plants, partial inflorescences racemoid, secondary and tertiary inflorescence axes with yellowish white stellate hairs, pubescence slightly decreasing towards flower insertion; ***enlarged marginal flowers*** always present (Fig. 9B), terminally placed in a raceme, sepals white, yellow or pink, fertile or reduced, when fertile stamens 8, pistils 2, fruit developing, when reduced only sepals developed, central part of the flower amorph, 0.5–0.7 cm diameter when flowering, 1.5–2 cm diameter with mature fruits, pedicel 1.2 cm long when flowering, 1.5–2 cm long with pedicel 1.5–2 cm long with mature fruits; ***flower pedicel of reduced flowers*** 0.5–2 mm long in functionally male flowers, 0.5–2 mm long in functionally female flowers, ***receptacle*** broadly triangular in functionally male flowers, semiglobose in functionally female flowers, ***ovary*** inferior, ***calyx lobes*** 4, broadly triangular, 0.2–0.3 mm long, ***petals*** 4, white, valvate, cucullate, membranous, 1.5–2 mm long, 1.5–1.8 mm broad; ***functionally male flowers***: hypanthium 1.2–1.8 mm diameter, 0.8–1 mm high, stamens 8, well-developed, filaments 1 mm long, anthers 0.5 mm long, 0.2 mm broad, pistils 2, reduced, 0.1–0.2 mm long, stigmas not penicellate; ***functionally female flowers***: hypanthium 1.5–1.6 mm diameter, 1–1.5 mm high, stamens 8, reduced, filaments

0.5 mm long, anthers 0.1 mm long, 0.1 mm broad, translucent, pistils 2, 1 mm long, enlarging up to 1.8 mm during fruit maturation, stigmas apically clavate and shortly penicellate; ***fruit*** a semiglobose capsule, apically with a conspicuous, slightly revolute border, 6–8 well marked ribs, dark reddish brown, 1.5 mm high, 3–3.5 mm broad above, 2 mm diameter, opening between the two pistils to release seeds, seeds not seen.

Distribution. This species is known from Costa Rica and Panama (Fig. 8).

Habitat. *Hydrangea panamensis* grows in tropical rainforest between 200 and 1000 m elevation. It usually occurs near water streams at lower elevations. Of all the species of the present study, this is the one that grows at the lowest elevation.

Phenology. *Hydrangea panamensis* has been collected with flowers and fruits between June and September.

Notes. Not to be considered a synonym of *H. peruviana* from which it can be distinguished by the rounded leaf apex with a very small acumen and the very few acarodomatia (0–2/leaf) on the abaxial leaf side vs. the acute to acuminate, rarely mucronate leaf apex and the many acarodomatia (present in both axils of midvein and primary veins and those of primary and secondary veins) of *H. peruviana*. Moreover, their known distribution areas are far away from each other, with *H. panamensis* only growing in Central America and *H. peruviana* being endemic to Ecuador.

The label of the specimen *Gentry 5569B* mentions that the flowers are red, whereas the label of the specimen *Mori & Bolten 7674* says "summit of ovary of fertile flowers reddish-pink". It seems there is some color variation in this species in both the marginal and reduced flowers. Both flower types are generally white, and this is also the color we have observed in the field ourselves.

According to our molecular study, *Hydrangea panamensis* is closely related to *H. peruviana* (Granados Mendoza et al. unpublished results).

Preliminary conservation status. Although this species has an EOO of about 50,123 km^2, it is Endangered according to the IUCN categories and criteria (IUCN 2012), with an AAO of 60 km^2, as well as an extensive reduction in both EOO and AOO as a consequence of habitat destruction and fragmentation.

Additional specimens examined. Costa Rica. Puntarenas: Golfito, Playa Cacao, Cuenca Superior de Quebrada Nazareno, 8°37'50"N, 83°11'30"W, 200 m, 11 Jun 1994, ♂, flowers, *Herrera & Rivera 7152* (CR, F, K, MO); Golfito–La Gamba (km 37), gap by the waterfall – Sendero Ozelot near the Rainforest Lodge, 8°41'N, 83°13'W, 70–300 m, 20 Jun 1997, inflorescence buds, *Weissenhofer W105* (CR, WU); Golfito, Bosque de los Austriacos, Fila Gamba, Avilán woodcutter way, 8°41'N, 83°13'W, 250 m, 3 Jun 1997, ♂, old flowers, *Huber & Weissenhofer 747-3.6.97* (CR); Osa, al lado del camino Rincon–Bahía Drake, 2.23 km al ONO de Rancho Quemado, 8°41'35.39"N, 83°35'7.42"W, 237 m, 8 Aug 2012, ♀, fruits, *Samain & Martínez 2012-063* (CR, GENT, IEB, MEXU); Cerro Anguciana, cabeceras del Río Piedras Blancas, 4.96 km al NE de Piedras Blancas, 8°48'27.49"N, 83°12'18.05"W, 676 m, 9 Aug 2012, ♀, fruits, *Samain & Martínez 2012-064* (CR, GENT, IEB, MEXU).

Panama. Darién: Cana and vicinity, 2000–6500 ft, 7 Apr 1908–8 Jun 1908, old inflorescence branches, *Williams 775* (NY); **Coclé:** between Cerro Pilón and el Valle

de Antón, 700–900 m, 15 May 1967, ♀, flowers, *Duke & Dwyer 13952* (MO); region north of El Valle de Anton, 1000 m, 27 Sep 1946, ♀, fruits, *Allen 3712* (E, GH, F, MO, P, UPS); alrededores de El Valle de Antón, Altos de La Mesa, 1.3 km al N de la bifurcación hacia Río Indio, 8°38'38" N, 80°06'51"W, 735 m, ♂, flowers, 13 Aug 2014, *Galdames et al. 7676* (PMA); Distrito La Pintada, cerca de las cabañas de ANAM, 8°40'05"N, 80°35'34"W, 800–900 m, 14 Aug 2007, ♀, fruits, *Hernández et al. 528* (PMA); **Panama:** Canal Zone, Barro Colorado Island, E. Of Wheeler 13, 18 Aug 1970, ♀, flowers, *Foster 1797* (DUKE, F, PMA, UC); Barro Colorado Island, forest 200 m E of Wheeler Trail 1300, 18 Aug 1970, ♀, fruits, *Croat 11850* (AAU, DUKE, E, F, MO); pipeline road, 14 Sep 1971, ♀, fruits, *Gentry 1792* (DUKE, F, GH, MO); Panamá, North of El Llano, 500–800 m, 25 Jul 1972, ♀, flowers, *Gentry 5569B* (MO); Cerro Campana, 45 km SW of Panama City on Inter-American Hwy, 8 Aug 1975, ♀, fruits, *Mori & Bolten 7674* (AAU, MO); Distrito de Capira, Parque Nacional Altos de Campana, Sendero de Interpretación, 8°40'54"N, 79°55'40"W, ca. 750 m, 23 Aug 1990, ♀, fruits, *Galdames 880* (PMA); Parque Nacional Altos de Campana, Sendero de interpretación, 1 km al este del campamento de los guardaparques de INRENARE, parcela 10-8, 8°40'N, 79°55'W, 800–900 m, 19 Aug 1993, ♂, flowers, *Correa & Montenegro 9780* (PMA, UCH).

6. *Hydrangea peruviana* Moric. ex Ser., Prodr. [A.P. de Candolle] 4: 14. 1830.
Figures 6, 9–11

Cornidia peruviana (Moric. ex DC.) Small, North American Flora 22(2): 161. 1905.

Type. Ecuador. "In Peruvia prope Huyaquaquil", ♀, fruits, *J.A. Pavón s.n.* [*J.J. Tafalla s.n.*] (holotype: G! [G00301424], isotypes: F!, MA! [MA-811940])

Description. Root-climbing liana of up to 30 m high, up to 20 cm diameter, functionally dioecious; ***leaves*** decussate, coriaceous, petiole sulcate adaxially, clasping its branch, color reddish brown, densely pubescent with partially caducous, reddish simple and stellate hairs, 0.5–2 cm long, leaving a semicircular scar on the branch when leaves shed; lamina very slightly spoon-shaped (Figs 9C, 10A, B), elliptic to slightly obovate, 7.5–12.8 cm long, 4.2–5.4 cm broad, base rounded to decurrent, sometimes asymmetric or very slightly cordate, apex acute to acuminate, rarely mucronate, leaf margin serrate to slightly dentate, venation brochidodromous, veins 6–10 pairs, adaxial leaf side with midvein and primary veins slightly protruding secondary veins marked, primary veins join to form submarginal vein, pubescent with small, stellate whitish pubescence, abaxially with protruding midvein and primary veins, sometimes with a few smaller less visible primary veins between the clearly visible primary veins, marked secondary veins, secondary and tertiary veins forming a reticulate network, connecting the primary veins, reddish brown, pubescent with small, stellate reddish hairs, especially on the veins, young leaves densely pubescent, acarodomatia numerous, present in axils of midvein and primary veins as well as axils of secondary veins, veins broadening

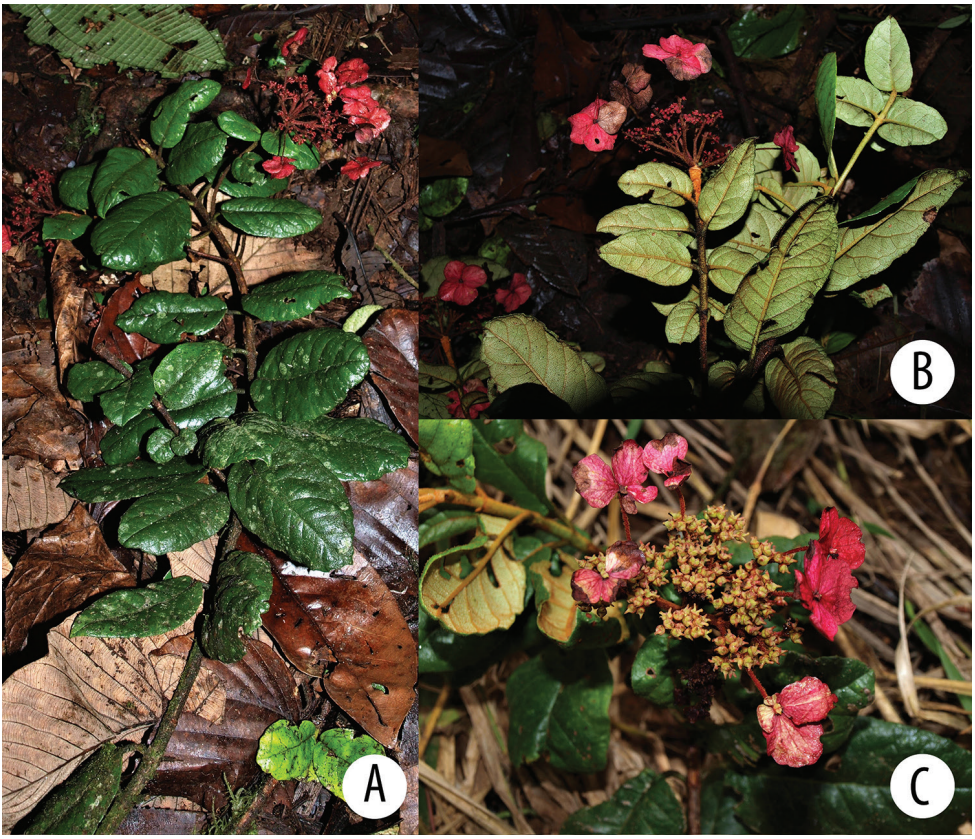

Figure 10. *Hydrangea peruviana* **A** branch with inflorescence **B** branch with leaves seen abaxially and inflorescence **C** close up of infructescence with maturing fruits and enlarged marginal flowers. **A, B** field images of collection *Granados Mendoza et al. 2012-111* **C** field image of collection *Granados Mendoza et al. 2012-112*.

the acarodomatia, consisting of a cavity, rarely with hairs; ***inflorescence axis*** densely pubescent with brownish stellate hairs (Fig. 11), 7–12 cm long, broadening towards the apex, with 3–4 opposite or decussate leaf or kataphyll pairs below the inflorescence, generally not deciduous, petiole 2–4 mm long, adaxially sulcate, lamina nearly orbicular to obovate, 1.3–4.2 cm long, 1.2–2.8 cm broad, densely pubescent, scars of 2 pairs of kataphylls present, ***apex of the inflorescence axis*** woody, cone-shaped, slightly quadrangular, elongated bract scars visible (Fig. 11), narrower at the top, 4–5 mm broad, 2–3 mm high in functionally female plants, male inflorescences not seen; ***inflorescence bracts*** not seen, ***inflorescences*** lateral, opposite, 1 pair of inflorescences per flowering branch, sometimes only one inflorescence developing (Fig. 10A,B), flowering branch continues growing vegetatively very rapidly during inflorescence development, including additional branching, with up to 5 leaf pairs above the inflorescences and below the first branch, with kataphylls opposite the branches, with dense reddish stellate hairs, inflorescence umbellate, buds not seen, in flowering stage 4.5–10 cm diameter, 4–7 cm

Figure 11. *Hydrangea peruviana*. Infructescence with young fruits and densely pubescent apex of the inflorescence axis. Field image of collection *Granados Mendoza et al. 2012-112*.

high, 3–7 main axes in functionally female plants, partial inflorescences cymes, secondary and tertiary inflorescence axes with dense reddish stellate hairs; ***enlarged marginal flowers*** always present (Figs 10–11), terminally placed in a cyme, 1.5–2 cm diameter, sepals 1–4, sepals with marked veins, remnants of 2 pistils visible, further characters not observed in detail, pedicel 1.2–2.4 cm long; male flowers not seen, (0–)1–1.5(–2) mm long in functionally female flowers, ***receptacle*** semiglobose in functionally female flowers, ***ovary*** inferior, ***calyx lobes*** 4, triangular, papyraceous, 0.25 mm long, 0.25 mm broad, ***petals*** not seen; ***functionally female flowers***: hypanthium 1.5 mm broad, 1 mm high, 8 well-marked ribs, stamen scars visible but too small to detect a number, pistils 2, 0.2–0.3 mm long, enlarging up to 2–2.5 mm during fruit maturation, stigmas apically clavate and shortly penicellate; ***fruit*** a semiglobose capsule (Figs 10, 11C), apically with a revolute border, dark reddish brown, 1.5 mm high, 2 mm broad above, 3 mm diameter, opening between the two pistils to release seeds, seeds not seen.

Distribution. *Hydrangea peruviana* is a rare species which is known from Ecuador only (Fig. 6). Apart from the type collection, it is only known of six collections since 1980, two of which were realized during the explorations in the framework of our revision of the Neotropical Hydrangeas. It was found in a primary mountain cloud forest flowering very high (about 30 m) in the tree canopy. The cloudy environment

in combination with the height at which the specimens were flowering made them very difficult to spot, potentially being the reason why this species has been so rarely collected by botanists.

Habitat. This species has been reported in rainforest and cloud forest at elevations between 682 and 1300 m.

Phenology. This species has been collected with flowers and fruits in March and July. Only female plants have been observed. There are no collections known of male individuals.

Notes. Since the revision by McClintock (1957), most of the species mentioned in this paper had been lumped in *H. peruviana*. Following the treatment of the genus *Hydrangea* for Ecuador by Freire-Fierro (2004), *H. oerstedii* was reduced to a variety of *H. peruviana*, consequently all species of the present study belonged to what was until recently considered as a species complex. However, based on our extensive study of herbarium specimens, including type material, and field observations, it became clear that *H. peruviana* is a very distinct taxon which can easily be recognized by the densely pubescent reddish brown leaves with an acute to acuminate, rarely mucronate, apex, a serrate to slightly dentate margin and many characteristically shaped acarodomatia.

In contrast to what might be expected because of its name, *H. peruviana* is not known from Peru, the type locality area of Guayaquil now being the second largest city of neighboring Ecuador, and this country´s main harbor. However, at the time of its collection in the late 18th century, modern-day Peru and most of Spanish-ruled South America belonged to the Viceroyalty of Peru.

As mentioned by Macbride (1938), it is generally accepted that their collections in the area that correspond with present-day Ecuador were not realized by Spanish botanists Ruiz and Pavón, but by their collaborator Juan José Tafalla.

According to our molecular study, *Hydrangea peruviana* is closely related to *H. panamensis*, the two of them unrelated to the other species of this study (Granados Mendoza et al. unpublished results).

Preliminary conservation status. Although this species has an EOO of about 13,515 km^2, it is Endangered according to the IUCN categories and criteria (IUCN 2012), with an AAO of 20 km^2, less than five locations, as well as an extensive reduction in both EOO and AOO because of habitat destruction and fragmentation.

Additional specimens examined. Ecuador. Carchi: Camino Chical–Peñas Blancas–Tobar Donoso, colec. a 5 horas de camino, 1°0'N, 78°12'W, 6 Dec 1993, 1200 m, sterile, *Freire-Fierro 2616* (AAU, QCA); **Esmeraldas:** environs of Lita, on the Ibarra–San Lorenzo R.R., 550–650 m, 11 Jun 1978, ♀, fruits, *Madison et al. 5251* (F, QCA); **Pichincha:** km 87–84 old road Quito–Santo Domingo, 1200–1300 m, 21 Mar 1980, ♀, fruits, *Dodson 9733* (MO); Los Ríos, Road Patricia Pilar–Montañas de Ila, km 18, N side of Torre de Bijagual, below antenas, 00°38'S, 79°17'W, 620–680 m, 28 Feb 1993, ♀, fruits, *Øllgaard & Borchsenius 100686* (QCA, QCNE); **Santo Domingo de los Tsáchilas:** 5.3 airline Km SW of Corina Parral, 0°39'20.8"S, 79°17'27.7"W, 693 m, 11 Jul 2012, ♀, fruits, *Granados Mendoza et al. 2012-111* (GENT, IEB, MEXU, QCNE); same data as preceding, 0°39'21.5"S, 79°17'29.2"W, 682 m, 11 Jul 2012, ♀, fruits, *Granados Mendoza et al. 2012-112* (GENT, HOXA, IEB, MEXU, QCNE).

7. *Hydrangea schlimii* Briq., Annuaire Conserv. Jard. Bot. Genève 20: 400. 1919.
Figures 2, 12

Type. Colombia. Norte de Santander, Ocaña, without date, ♂, old flowers, *J.J. Linden 1139* (lectotype, designated by McClintock 1957, pg. 238 [as "holotype"]: G; isotypes: BR! [BR0000005119318], US! [00097002]).

Description. The most complete description to date can be found in the treatment by Briquet (1919), pages 400–401.

Distribution. This species is currently known from the type locality in Colombia only (Fig. 2).

Notes. This species concerns a very distinct taxon with more enlarged "marginal" flowers than any other member of *Cornidia*. In fact, from the type specimen it seems that most flowers possess enlarged sepals. It is only known from its type collection made around 1850 and to our knowledge has not been collected since. It cannot be excluded that it concerns a local "mophead" mutation, but in the absence of recently collected material and as the leaf morphology of the type specimens cannot be matched with better-known species, we decide here to recognize this taxon as a distinct species, although we cannot present an amended description at this time, given that we only dispose of the type specimen, which already was given an excellent description by Briquet (1919).

As in the case of *H. durifolia*, exploring field work in forests around Ocaña in the Colombian department of Norte de Santander might lead to the rediscovery of this species, which will be helpful to define its taxonomic status.

McClintock (1957) cited as "holotype" the collection in G, which we have not been able to locate. Based on the many enlarged marginal flowers and the inflorescence leaf morphology, this species should not be considered a synonym of *H. oerstedii*.

The phylogenetic relationships of *Hydrangea schlimii* are yet unknown as there was no fresh material available for our molecular study (Granados Mendoza et al. unpublished results).

Preliminary conservation status. We currently propose this species as Data Deficient (DD), as its taxonomic status in unclear, it is only known from the type locality, and no recent collections are available.

8. *Hydrangea trianae* Briq., Annuaire Conserv. Jard. Bot. Genève 20: 403. 1919.
Figures 13, 14

H. lehmannii Engl., Nat. Pflanzenfam. (ed. 2) 18a: 207. 1930. Type. Colombia. Valle del Cauca: Cali, 4 Oct. 1900, ♀, fruits, *F.C. Lehmann 9074* (lectotype, designated by Freire-Fierro 2004, pg. 33, second-step designated here: K! [K000486136]; isolectotypes: B [destroyed, F neg. 4144], K! [K000486135])

Hydrangea platyphylla Briq., Annuaire Conserv. Jard. Bot. Genève 20: 401. 1919. Type. Colombia. Tolima: Mariquita, ♂, old flowers, *J.J. Linden 894* (lectotype, designated by McClintock 1957, pg. 238 [as "holotype"], second-step designated

Figure 12. *Hydrangea schlimii*. Branch with inflorescences with many enlarged flowers. Image of specimen *Linden 1139* (BR).

here: G! [G00439775, F neg. 27369]; isotypes: F [V0066625F]!, G! [G00439776, G00223929], GENT! [BR0000005119332, BR0000005119660] (photos of both on one sheet in COL!, GH!, K!, NY!), K! [K000486132]!

Type. Colombia. Tolima: Quindío, ♂, flowers, *J.J. Triana s.n.* (holotype: G-DC n.v. (photo in GENT!), isotypes: BM!, BR [BR0000005119011, BR0000005119974, BR0000005119646]!., COL [COL000369449] !, F! [V0066627F], MEXU! [acc. # 14858], MICH!)

Description. Root-climbing liana of up to 20 m high, functionally dioecious; ***free-growing branches*** many-ribbed, slightly angular, old branches quadrangular, with erect, white stellate hairs (Fig. 13A); ***leaves*** decussate, petiole terete, sometimes abaxially flattened, color dark green, sometimes drying black, pubescent with small, erect, whitish to yellowish stellate hairs, 1.5–4 cm long, leaving a semicircular scar on the branch when leaves shed; lamina spoon-shaped, obovate to elliptic, (slightly) asymmetric, coriaceous, 15–29 cm long, 8.5–18 cm broad, with varying length-width ratios, base cuneate, acute or decurrent, apex rounded to acuminate, leaf margin (slightly) dentate, venation brochidodromous, veins 8–9 pairs, adaxial leaf side with protruding midvein and primary veins, secondary veins slightly protruding, primary veins join to form submarginal vein, dark green, slightly pubescent with white stellate hairs, especially near the margin, abaxially with protruding veins, midvein notoriously protruding, opaque olive green, pubescent with stellate white hairs, primary veins branching towards the margin, ending in a submarginal vein very near the margin, secondary and tertiary veins forming a reticulate network, connecting the primary veins, acarodomatia numerous, consisting of an often small simple cavity in axils of midvein and primary veins, sometimes covered by a membrane; ***inflorescence axis*** in the axils of kataphylls of 1–1.4 cm long or fully grown leaves, pubescent with erect, white, stellate hairs (Fig. 13C), 6–25 cm long, many-ribbed, with 2 opposite rapidly shedding leaf or kataphyll pairs along the axis, petiole of the leaves 5–10 mm long, lamina obovate to lanceolate, (slightly) asymmetric, 2–7 cm long, 1.4–4.3 cm broad, margin glandular dentate, small, appressed, stellate, abaxially and adaxially with white hairs along the midveins, similar pubescence between the veins but not appressed and larger, veins 6 pairs, all protruding, in the case of kataphylls, these initially protecting the small inflorescence buds (Fig. 13A), followed by elongation of the axis occurring between the kataphylls and the inflorescence bud, ***apex of the inflorescence axis*** woody, quadrangular, elongated bract scars visible, thickening at the top, 7–8 mm broad, 2 mm high in functionally female plants, 6–7 mm broad, 2–3 mm high in functionally male plants, inflorescence bracts cucullate, dark green, coriaceous, abaxially (densely) pubescent with small, erect, whitish and yellowish stellate hairs, ***inflorescences*** lateral, opposite, 1–2 pairs of inflorescences per flowering branch, flowering branch continues growing rapidly during inflorescence development, with up to three decussate leaf pairs above the inflorescences, with appressed, whitish and yellowish stellate hairs, dense when young, rapidly shedding, inflorescence axes with basal lignified parts of inflorescences of previous years visible in well-collected specimens, allowing to observe growth and flower periodicity, these rests 2.5–5 cm apart, 7 cm when inflorescence originate in the axils of the regular leaves, with none or one decussate leaf pair (or the scars of these leaves) in between, inflorescence umbellate, buds up to 4 cm broad and 4.5 cm high before opening, in flowering stage 7–19 cm diameter, 4–12 cm high, with 5–9 main axes in functionally male plants, 4–8 main axes in functionally female plants, partial

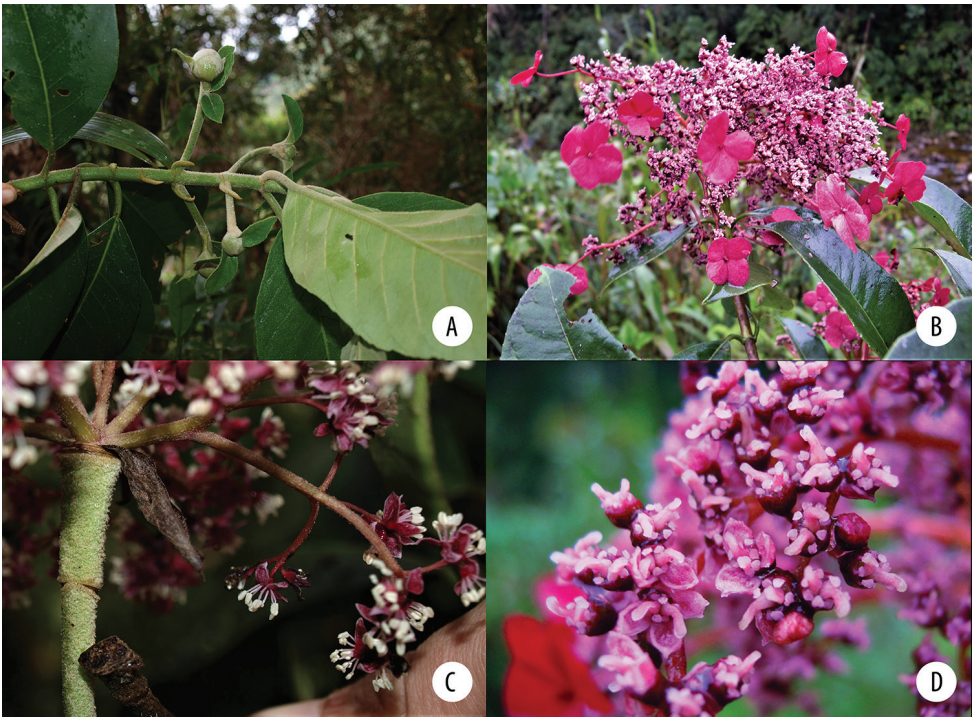

Figure 13. *Hydrangea trianae* **A** branch with leaves seen abaxially and inflorescence buds **B** functionally female inflorescence with enlarged marginal flowers **C** basal portion of functionally male inflorescence with densely pubescent apex of the inflorescence axis, and a few open male flowers with large stamens **D** close-up of functionally female flowers with petals, reduced stamens and large pistils. **A, C** field images of collection *Samain et al. 2011-064* **B, D** field images of collection *Samain et al. 2011-067*.

inflorescences dichasia, secondary and tertiary inflorescence axes with whitish and/or reddish stellate hairs; ***enlarged marginal flowers*** generally present (but e.g. absent in *Samain et al. 2011-064*) (Fig. 13B), terminally placed in a cyme, 1.8–4 cm diameter, sepals with marked palmate veins, fully separated or fused at the base, sometimes one or two reduced or even absent, pistils very rudimentary, pedicel 1–3.5 cm long; ***flower pedicel of reduced flowers*** 1–2 mm long in functionally male flowers, 1–5 mm long in functionally female flowers, ***receptacle*** semiglobose in functionally male flowers, broadly semiglobose in functionally female flowers, ***ovary*** inferior, ***calyx lobes*** 4, triangular, translucid, 0.2–0.5 mm long, 0.6–1 mm broad, ***petals*** 4, adaxially red, abaxially purple with white margin, valvate, cucullate with a small mucron at the apex, coriaceous, 1.5–3 mm long, 1–1.5 mm broad; ***functionally male flowers*** (Fig. 13C): hypanthium 1.5–2 mm diameter, 1.5 mm high, stamens 8, well-developed, filaments 1.2–2 mm long, anthers 1–1.5 mm long, 0.5–1 mm broad, purple, pistils 2, very reduced, 0.5 mm long, stigmas not penicellate; ***functionally female flowers*** (Fig. 13D): hypanthium 1.2–2.2 mm diameter, 1.5 mm high, stamens 8, very reduced, filaments

0.2–0.5 mm long, anthers 0.2–0.4 mm long, 0.1–0.2 mm broad, pistils 2(–3), 1.5–2 mm long, broad at the base, narrower in the middle and broadening towards the apex, enlarging up to 3.2 mm during fruit maturation, stigmas apically clavate and shortly penicellate, 0.5 mm long; ***fruit*** a semiglobose capsule, apically with a conspicuous border, dark reddish brown, 2.5 mm high, 4–4.5 mm broad above, 3–4 mm diameter, the part around the pistils thickening upwards up to 1 mm during fruit maturation, opening between the two pistils to release seeds, seeds not seen.

Distribution. *Hydrangea trianae* is a widespread species occurring in Colombia, Ecuador and Peru (Fig. 14).

Habitat. *Hydrangea trianae* is known from cloud forest and remnants of this vegetation type at elevation between 400–3680 m. Moreover, it has been noted to occur in disturbed or late secondary forests.

Phenology. This species has been collected with flowers and fruits throughout the year.

Notes. *Hydrangea trianae* should not be considered a synonym of *H. peruviana*, from which it can be distinguished by the notoriously coriaceous leaves, the abaxial reticulate network of secondary and tertiary veins connecting the primary ones, and the abaxial white pubescence.

Hydrangea lehmannii was synonymized with *H. peruviana* by McClintock (1957), whereas she considered *H. platyphylla* as a synonym of *H. oerstedii*.

With respect to the type material of *Hydrangea lehmannii*, McClintock (1957) cited the K material as an isotype, albeit without designating a specific sheet, and this was also cited by Freire-Fierro (2004).

With respect to the type material of *H. platyphylla*, McClintock (1957) cited G material as holotype, which effectively lectotypified the name. However, there are two specimens of this collection in G, therefore requiring second-step lectotypification, which is done here.

One of the F specimens (V0066626F), which supposedly is an isotype of *H. platyphylla*, does not belong to this species based on leaf venation, probably due to a labeling error; however, it is not possible to propose any other identification as the material is very limited.

Briquet (1919) distinguished *H. trianae* and *H. platyphylla* based on leaf shape and venation, as well as size of cymes, sepals of enlarged marginal flowers and styles, which can be contributed to the sex of the single collections of both species he used for his descriptions, the specimens of *H. trianae* being functionally female and the ones of *H. platyphylla* which are functionally male.

The specimen of *Triana 4668* in NY does not correspond with *H. trianae* or any of the other species treated here, in contrast with the specimen with the same number in COL. Triana's numbers do not correspond to field collection numbers as currently used, but instead are generic numbers based on the Endlicher system (Kirkbride 1982; Aymard 2017).

According to our molecular study, *Hydrangea trianae* is closely related to *H. goudotii* (Granados Mendoza et al. unpublished results).

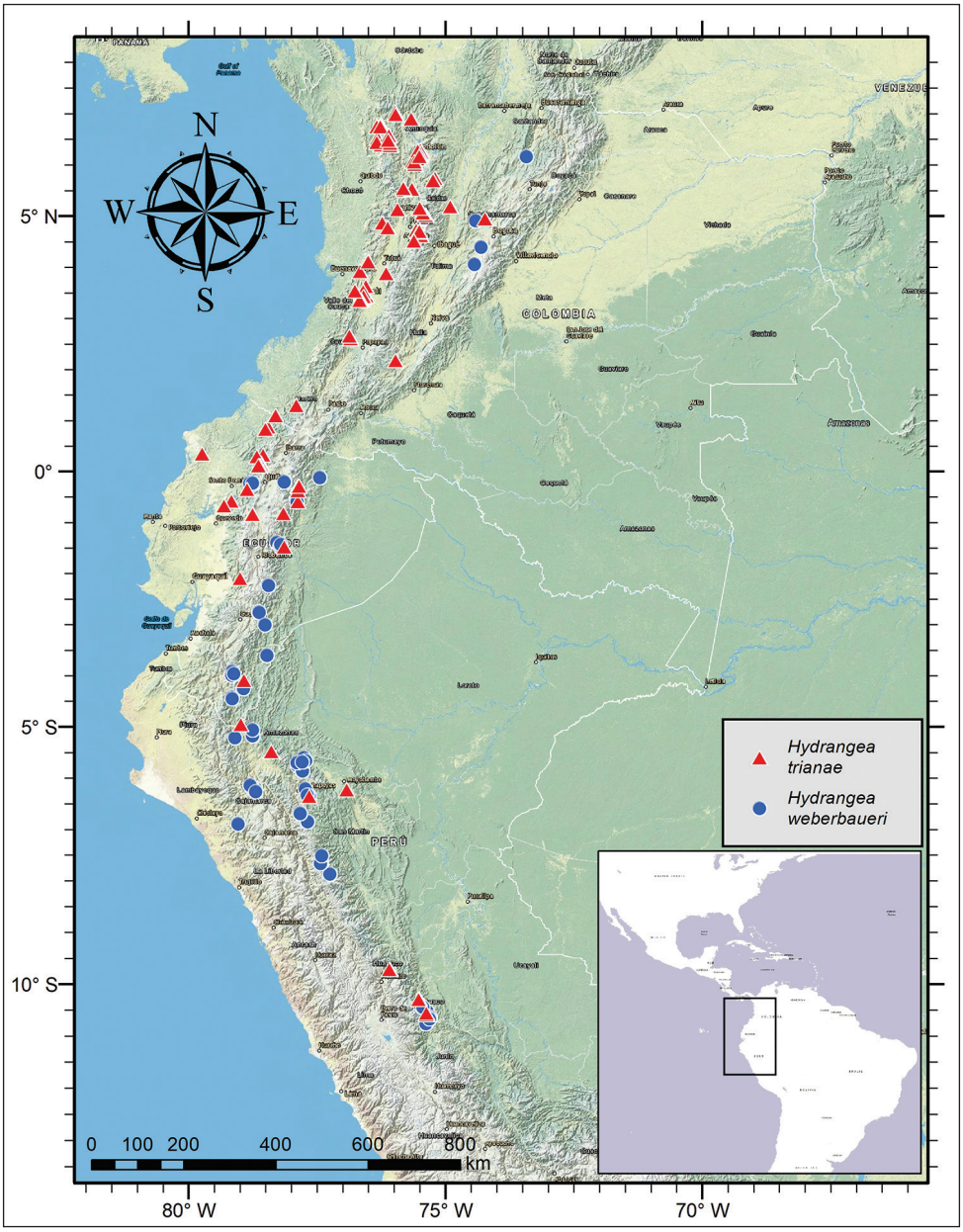

Figure 14. Distribution of *Hydrangea trianae* and *Hydrangea weberbaueri*.

Preliminary conservation status. Although this species has an EOO of nearly 726,300 km^2, it is Endangered (B2abiii) according to the IUCN categories and criteria (IUCN 2012), with an AOO of 372 km^2, as well as an extensive reduction in both EOO and AOO as a consequence of habitat destruction and fragmentation.

Additional specimens examined. Colombia. Antioquia: Argelia, km 17 of road Sonsón–Argelia (2 km past fork in road to Nariño), 2160 m, 3 Oct 1987, ♀, fruits, *Zarucchi et al. 6164* (HUA, MO); Frontino, Correg. Nutibara, Nutibara–La Blanquita road, region of Murrí, Alto de Cuevas, 6°45'N, 76°20'W, 1700–1800 m, 19 Apr 1988, ♂, old flowers, *Luteyn et al. 12047* (HUA, K, MO); Urrao, Parque Nacional Natural las Orquideas, vereda Calles, 06°32'N, 76°19'W, 1350–1450 m, 5 Dec 1993, ♀, inflorescence buds, flowers, *Pipoly et al. 17737* (MO); Jardín, km 20 of road Jardín–Riosucio (dpto. Caldas), ca 15 km SSE of Jardín, Alto de Ventanas, 29 Oct 1988, 2700–2790 m, ♂, flower buds, *Zarucchi et al. 6962* (HUA, MO); road between Jardín and Río Sucio, ca 9 km from Jardín, 2300–2400 m, 29 Jan 1989, ♂, flowers, *MacDougal & Roldán 3581* (HUA, MO); Frontino, region of Murrí, road between Nutibara and La Blanquita, 19.2 km from centro de Nutibara, 1560 m, 11 Feb 1989, ♂, old flowers, *MacDougal et al. 3929* (CR, HUA, MO); Frontino, Corregimiento Nutibara, Región Murí, márgen de río, 1500 m, 11 Jul 1986, ♀, old inflorescences, *Acevedo et al. 1260* (HUA, NY, US); along road between Caramanta and Supia (Risaralda), ca 4 mi S of Caramanta, 2030 m, 27 Jan 1990, ♀, flowers, *Croat 70038* (MO); Medellín y Guarne, Parque Ecológico Piedras Blancas, laguna de Guarne, 2350 m, 26 Aug 1995, ♂, old inflorescences, *Roldán & Medina 2385* (HUA, MO); Parque Ecológico Piedras Blancas, sector Lajas, 2350 m, 23 Sep 1995, ♂, flowers, *Fonnegra et al. 5643* (HUA, MO); Parque Nacional Natural "Las Orquideas", sector Calles, margen derecha del río Calles, 1250 m, 30 May 1988, ♀, fruits, *Cogollo et al. 3087* (COL, MO); Urrao, Corregimiento Encarnación, sitio El Río, 1 hora de camino del Páramo de Frontino, 3120 m, 7 Apr 1989, inflorescence buds, *Callejas et al. 7774* (HUA, NY); same data as preceding, 3000–3150 m, 8 Apr 1989, ♀, flower buds, flowers, *Callejas et al. 7835* (HUA, MO); Envigado, Vereda "El Escobero", Costa Occidental Cerro "San Luis", 2100–2250 m, 15 May 1996, ♂, inflorescence bud, flower buds, flowers, *Correa & Carona 1073* (COL, HUA, MO); cerca de San José de San Andrés, 1 May 1948, inflorescence buds, floral buds, *Correa & Velasquez 45* (US); bosque bajo de la cumbre cerca de Santa Elena, camino entre Medellín y Río Negro, 2300–2500 m, 3 Aug 1945, ♀, fruits, *Medina 239* (US); municipio de Caldas, Alto de San Miguel, 2200 m, 8 Jul 1996, ♂, flowers, *Monsalve 38* (F); municipio de Peque, 7°2'6.7"N, 75°58'27"W, 2500 m, 19 Nov 1995, ♀, fruits, *Benítez et al. 584* (COL); municipio de Peque, vereda Romeral, 6°59'18.4"N, 75°58'02.5"W, 2650 m, 16 Nov 1995, floral buds, *Benítez et al. 452* (COL); municipio Caldas, Reserva "Alto de San Miguel", cuenca alta del río Medellín, 6°5'N, 75°38'W, 2100 m, ♂, old flowers, *Roldán et al. 2516* (HUA); municipio de Caldas, vereda La Corrala, Finca "La Zarza", Alto del Gallinazo, ca. 2600 m, 4 Feb 1986, inflorescence buds, *Albert de Escobar y Stein 6238* (HUA); municipio de Urrao, Finca La Clara, cerca del río Mina y La Clara, 2340 m, 6 Dec 1984, ♀, fruits, *Orozco et al. 1782* (COL); camino de Urrao al páramo de Frontino, 2400 m, 19 May 1985, ♂, flower buds, flowers, *Cárdenas 128* (HUA); Argelia, vereda La Vibora, antiguo camino de Sonsón a Argelia, 2200–2700 m, 28 Aug 1989, ♂, flowers, *Hoyos y Avendaño 1300* (HUA); municipio Ríonegro, vereda Yarumales, 20–30 km SE

de Medellín en la vía a Rionegro, 6°15'N, 75°28'W, 2140–2410 m, 12 Nov 1990, ♀, fruits, *Callejas & Roldán 9628* (HUA); municipio de Urrao, Páramo de Frontino, El Río, 3020 m, 6 Jan 1985, ♀, fruits, *Londoño et al. 669* (HUA); Páramo de Frontino, Urrao – zona situada entre el 15 y la Esperanza, 2980–3680 m, 18 May 1985, ♀, fruits, *Rentería 4082* (HUA): Medellín, corregimiento de Santa Elena, Sector de Piedras Blancas, 6°17'N, 75°32'W, 2400 m, May 1998, ♂, flowers, *Cardona y Alzate 551* (HUA); Medellín, corregimiento de Santa Elena, Reserva Natural Montevivo, sector Casapalo, 6°12'48"N, 75°29'32.2"W, 2500 m, 30 Sep 2002, ♀, fruits, *David & Idarraga 291* (HUA); municipio de Caldas, vereda La Corrala, Finca "La Zarza", Camino La Zarza – Alto del Gallinazo, ca. 2440 m, 10 Nov 1987, ♂, old flowers, *Albert de Escobar et al. 8022* (HUA); municipio de Urrao, Páramo de Frontino, 6°29'N, 76°7'W, 2890–2250 m, 16 May 1987, ♂, old flowers, *Estrada et al. 108* (HUA); municipio de Medellín, corregimiento de Santa Elena, vereda El Llano y Perico, cabeceras y recorrido Q. San Pedro, 2550 m, 8 May 1996, ♀, fruits, *Giraldo et al. 785* (HUA); **Caldas:** Vereda la Corrala, Finca La Zarza, al lado del camino entre la cascada y el Alto del Gallinazo, 2550 m, 27 Apr 1987, floral buds, *Albert de Escobar 7576* (HUA, UC); **Chocó:** municipio San José del Palmar, hacia el galápago, 1380 m, 11 Nov 1985, ♀, fruits, *Lozano et al. 4920* (COL); **Cundinamarca:** San Francisco, hacienda "La Laja", 2880 m, 30 May 2004, ♂, flowers, *Parra et al. 465* (COL); **Huila:** municipio de la Argentina, Quebrada del pueblo, 1850 m, 25 Sep 1984, ♀, fruits, *Lozano et al. 3981* (COL); **Nariño:** Mpio. de Ricaurte, Reserva Indígena Gualcalá, Santa Fé, camino al Río Gualcalá, 1°18'N, 77°54'W, 1100–1200 m, 18 Dec 1995, inflorescence buds, floral buds, *Ramírez & González 9135* (QCA). **Quindío:** Parque Nacional de Cocora, Quebrada Santa Lucía, 3000 m, 08 May 1990, ♀, flowers, *Franco 3095* (NY); **Risaralda:** municipio de Pereira, corregimiento La Florida, SFF Otún Quimbaya, 4°44'17"N, 75°34'01"W, 1900 m, 22–28 Feb 2004, floral buds, *Alzate et al. 1962* (F); municipio de Pereira, orilla del camino entre Ceylan y el Cedral, 2150 m, 4 Dec 1989, ♀, fruits, *Franco et al. 2929* (COL); Mpio. Pereira, Parque Nat. Reg. UCUMARI, 2200–2450 m, ♀, fruits, *González 1635* (COL); municipio de Pereira, Parque Regional Ucumari, vereda la Pastora, camino de el Ceilán a El Cedral, borde de la quebrada Miraflores, 2340 m, 30 Jul 1989, floral buds, *Galeano 222* (COL); municipio de Apía, vereda "La Cumbre", 2285 m, 24 Feb 1983, ♀, fruits, *Torres et al. 2192* (COL); **Tolima**: Quindio, El Roble, old inflorescence axis, *Triana 358* (US); same data as preceding, ♂, flowers, *Triana 359* (US); same data as preceding, ♂, flowers, Triana 2805 (US); **Valle del Cauca:** San Antonio, about 25 km W of Cali, 1800 m, 25 Jan 1988, ♂, flowers, *van der Werff & Giraldo 9746* (MEXU, MO); same data as preceding, *van der Werff & J. Giraldo 9747* (CR, MO); Cordillera Occidental, vertiente occidental, Hoya del Río Digua, lado izquierdo, Piedra de Moler, 900–1180 m, 19–28 Aug 1943, ♀, fruits, *Cuatrecasas 14974* (F); Cali, forests of West Cordillera above Cali, 2000–2200 m, June 1900, ♀, young fruits, *B.T. 623* (NY); Finca Zingara, km 18 de la carretera Calia–Buenaventura, km 4 vía a Dapa, corregimiento de la Elvira, cordillera Occidental, 1900 m, 23 Jan 1994, ♀, flowers, *Giraldo-Gensini & Agredo 130* (MO); same data as preceding, 26 Feb 1995, ♀, fruits, *Giraldo-Gensini & Agredo 611*

(MO); same data as preceding, 25 Aug 1996, ♀, fruits, *Giraldo-Gensini & Corrales 765* (MO); Cuenca del Río Cali, cercanías de Peñas Blancas, 10 Jan 1963, sterile, *López Figueiras 8139* (US); Cordillera Occidental, vertiente oriental, Hoya del río Cali, río Pichindé, entre los Cárpatos y El Olivo, 2920–2025 m, 5 Aug 1946, inflorescence buds, *Cuatrecasas 21935* (F, P, US); Cordillera Occidental, Los Farallones, extremo N, vertiente oriental, Almorzadero, bosques, 2980 m, 13 Oct 1944, ♂, flowers, *Cuatrecasas 18113* (F, US); Yumbo, Finca La Samaria, NE of Darien, near Lago Calima (reservoir), 1700–1750 m, 14 Feb 1984, ♀, flowers, *Juncosa 2181* (MO); Peñas Blancas, los Cárpatos, 1600–1700 m, 9 Sep 1988, inflorescence buds, *Franco et al. 2509* (COL, MO); Bosque de San Antonio, W of Cali, near television tower, 2250 m, 15 Jul 1984, ♀, fruits, *Gentry 48079 et al.* (MO); Buga, Carretera a El Retiro, a 1 km de carretera Buga–El Placer (desvío a Retiro está a 12 km antes de El Placer), Cordillera Central, vertiente occidental, al lado de carretera, 2300 m, 15 Sep 1991, ♂, flowers, *Silverstone-Sopkin & Giraldo-Gensini 6400* (MO); Restrepo, Río Calima, Cusumbo, 680 m, 21 Feb 1989, ♀, fruits, *Devia & Prado 2581* (US); El Silencio, Hacienda Himalaya, Cordillera Occidental W of Yumbo, transect 1, 1860 m, 2 Jan 1989, ♂, flowers, *Gentry et al. 65414* (MO); Argelia, Vereda Las Brisas, 2050–2200 m, 21 Jan 1983, ♀, fruits, *Díaz P. 3854* (COL, MO); Manizales, vereda La Esperanza, Reserva Torre Cuatro, cerca de la quebrada La Siberia, 5°1'41"N, 75°23'10"W, 2650–2750 m, 28 Mar 1999, ♂, old flowers, *Alvear et al. 314* (COL); Manizales, 1851–1857, ♂, old flowers, *Triana s.n.* (K); Neira, Cementos Caldas, 5°9'45"N, 75°29'43.1"W, 2203 m, 29 Jul 2004, ♀, fruits, *Mancera 553* (COL); Manizales, Reserva Río Blanco, 2600 m, 28 Feb 2003, sterile, *Sanin 39* (HUA); Manizales, Río Blanco, El Paso nivel, 2500 m, 10 Jul 2003, sterile, *Sanin 958* (HUA). Cauca, Parque Nacional Munchique, El Tambo, vereda La Romelia, la Gallera, 1950 m, 25 Jul 1993, ♀, fruits, *Velayos et al. 6891* (COL); El Tambo, Parque Nacional Munchique, vereda La Romelia, la Gallera, 2385 m, 26 Jul 1993, ♂, old flowers, *Velayos et al. 6917* (COL). With three localities: Quindio: Mariquita, Roble, 2080 m; Antioquia, Manizales, 2140 m: Buenaventura, Cordillera Occidental, 2190 m, Jul 1833, ♂, old flowers, *Triana 4668* (COL); same data as preceding, floral buds, *Triana 1866* (photo in F of a specimen in G).

Ecuador. Carchi: prominent hillcrest directly N of Lita, on N side of Río Mira and just to E of Río Baboso, on steep W-facing slope, 760 m, 7 Aug 1994, sterile, *Boyle 3476* (MO); along Chical–Pailon–San Marcos trail, 01°06'N, 78°18'W, 600–1200 m, 18–19 Nov 1983, ♂, flowers, *Kvist et al. 48670* (AAU, QCA, QCNE); El Pailon, ca. 45 km above Maldonado along a footpath to Tobar Donoso, 0°49'S, 78°9'W, 800 m, 1 Dec 1979, ♀, fruits, *Madison & Besse 7226* (QCA); **Esmeraldas:** Quininde, Bilsa Biological Station, Montañas de Mache, 35 km W of Quininde, 5 km W of Santa Isabel, slope between banana plantation and stream SE of Station, 400–600 m, 9 Dec 1994, ♀, fruits, *Bass & Pitman 320* (MEXU, MO, QCNE); same data as preceding, 31 Dec. 1994, ♀, flowers, *Pitman & Marsh 1133* (MO, QCNE); San Lorenzo, Alto Tambo, Frente Finca del Sr. Lalama, a 1.5 km del sector de El Cristal, 650 m, 13 May 1992, ♂, flowers, *Quelal & Luteyn 489* (MO, QCNE); **Imbabura:** Cordillera Occidental, La Union, lower Intag Valley, 4600 ft, 20 Sep 1944, ♀, flowers, *Drew*

E-684 (NY, US); **Los Ríos:** Quevedo, Centinela–La Pirámide, vía Santa Domingo de los Colorados–Quevedo entrando por Patricia Pilar km 41, 650 m, 25 Feb 1992, ♂, flowers, *Quelal & Tipaz 347* (MO, QCNE); Collections from path following ridge line at El Centinela at crest of Montañas de Ila on road from Patricia Pilar to 24 de Mayo at km 12, Patricia Pilar is at Km 45 on road from Sto. Domingo to Quevedo, 600 m, 4 Feb 1983, ♀, fruits, *Dodson 13654* (MO, QCNE); same data as preceding, 6 Apr 1980, inflorescence bud, *Dodson s.n.* (MO); **Napo:** Quijos, along road 1 km SE of Cosanga, 00°35'S, 77°52'W, 2000 m, 31 Jul 1990, floral buds, *Webster & Richerson 28512* (QCNE); El Chaco, San Juan Chico, camino hacia el Río Oyacachi, 00°17'S, 77°52'W, 2000 m, ♀, fruits, *Alvarez 97 et al.* (QCNE); Baeza–Sardinas Alto, col. en borde de carretero, al NO de Sardinas Alto, a 1.5 km, 00°22'S, 77°52'W, 1780 m, 15 Dec 1993, inflorescence buds, *Freire-Fierro & Yánez 2693* (QCA, QCNE); hills above R. San Juan, at confluence with R. Oyacachi, ca 10 km W of El Chaco, 00°17'S, 77°51'W, 1800–2000 m, ♀, fruits, *Ståhl et al. 2354* (QCA); Napo–Pastaza, Mera, 26 Mar 1940, ♀, fruits, *Lugo 126* (C, MO); **Pichincha:** along road and trail from Maquipucuna Lodge to Ecolodge Santa Lucia, 2 km N of Maquipucuna entrance, 1400 m, 15 Mar 2006, ♀, fruits, *Croat 95938* (MO); Maquipucuna, 5 km E of Nanegal, Transect # 5, 1550 m, 10 Feb 1991, ♀, flowers, *Gentry & Valencia 73174* (AAU, MO, QCNE); Quito, Nanegal, Bosque protector Maquipucuna, 5 km airline SE of Nanegal, disturbed rainforest above Río Tulambi, 00°07.5'N, 78°38.5'W, 1500 m, 31 Aug 1993, ♂, old flowers, Webster et al. 30003 (QCNE); Reserva Biológica Maquipucuna, Nanegal, colectada en primer lindero, camino del Inca, 1600 m, 9 Jan 1992, ♂, flowers, *Tipaz et al. 593* (AAU, MO, QCNE); Maquipucuna Tropical Reserve, western slopes of Andes, northern boundary of reserve, 10 km north of Nanegalito, 1200 m, 2 Dec 1988, inflorescences, floral buds, *Neill et al. 8643* (MO, QCNE); Reserva Biológica Maquipucuna, 1300 m, 31 Jan 1991, ♀, flowers, *Alvarado 406* (COL, MO, QCNE); along road and trail from Maquipucuna Lodge to Ecolodge Santa Lucia, 2 km N of Maquipucuna entrance, 00°07'19"N, 78°37'06"W, 1400 m, 15 Mar 2006, ♀, fruits, *Croat et al. 95939* (MO, QCNE); Mindo, on western slopes of Andes, 1200 m, 16 Apr 1994, ♂, flowers, *Neill & Asanza 10349* (MO, QCNE); 11 km W of Tandapi, trail along Chictoa River, tributary of Río Pilatón, 1350–1550 m, 26 Oct 1974, ♀, fruits, *Gentry et al. 12073* (MO, QCA); **Tungurahua:** Baños, 2.8 airline km SSW of Río Negro, near El Coral, 1481 m, 1°25'59.5"S, 78°12'1.5"W, 13 Jun 2012, sterile, *Granados Mendoza et al. 2012-38* (GENT, HOXA, IEB, MEXU, QCNE); ca. 2 km E of Río Verde on touristic path before tunnel on road to Baños–Mera, 1629 m, 1°23'41.5"S, 78°16'53.2"W, 16 Jun 2012, sterile, *Granados Mendoza et al. 2012-44* (GENT, HOXA, IEB, MEXU, QCNE); Zamora-Chinchipe, Zamora, Jamboe Bajo, Eastern border of Podocarpus National Park, 1100 m, 5 Nov 1996, sterile, *Clark 3283* (MO); Westkordillere, 1000 m, 28 Sep 1934, sterile, *Heinrichs 741* (NY).

Peru. Amazonas: Bagua, Aramango, 8.86 km SE of Aramango, 1.23 km SW of Nueva Esperanza, 1806 m, 5°28'28.9"S, 78°23'08.4"W, 3 Jul 2011, sterile, *Samain et al. 2011-110* (GENT, IEB, MEXU, USM); Chachapoyas, Soloco, Paraje las Tinas, 5.26 km SE of Quitachi, E of road to Pampa del Tío, 2108 m, 6°21'06.45"S,

77°38'52.95"W, 22 Jun 2011, ♂, flowers, *Samain et al. 2011-064* (IEB, GENT, MEXU, USM); **Cajamarca:** San Ignacio, San José de Lourdes, localidad Estrella del Oriente, 1630 m, 2 Sep 1997, ♀, fruits, *Campos 4326 & Rodriguez* (F, MO, NY); **Huánuco:** Chinchao, 0.86 km ESE of Carpish, 330 m SE of road Huánuco–Tingo María, 2681 m, 9°42'24.3"S, 76°05'11.2"W, 17 Jul 2011, sterile, *Samain et al. 2011-185* (GENT, IEB, MEXU, USM); Chinchao, Carpish, 2626 m, 9°42'21.29"S, 76°05'14.46"W, 29 Nov 2013, ♂, inflorescence buds, flowers, *Samain et al. 2013-109* (IEB, GENT, MEXU, USM); same data as preceding, 9°42'20.41"S, 76°05'15.79"W, 2610 m, 29 Nov 2013, ♀, fruits, *Samain et al. 2013-112* (IEB, GENT, MEXU, USM); 0.85 km ESE of Carpish, 330 m SE of road Huánuco–Tingo María, 2700 m, 9°42'24.5"S, 76°05'11.6"W, 17 Jul 2011, sterile, old inflorescence axes, *Samain et al. 2011-186* (GENT, IEB, MEXU, USM); **Pasco:** Oxapampa, Valle de San Alberto, east of Oxapampa, above hydroelectric plant, at base of Cordillera Yanachaga, 1900 m, 1 Jan 1984, ♂, flowers, *Foster 7703 et al.* (F, MEXU, NY, USM); Oxapampa, Huancabamba, Sector Tunqui, Parque Nacional Yanachaga Chemillén, camino al valle del Palcazú, 10°16'24"S, 75°30'37"W, 2006 m, 15 Sep 2009, floral buds, *Castillo et al. 1006* (HOXA); Oxapampa, Huancabamba, Parque Nacional Yanachaga Chemillen, parte media de la Quebrada Muchuy Mayo, sector Tunqui, 10°17'30"S, 75°31'05"W, 1800 m, 26 Oct 2007, functionally male, inflorescence buds, young flowers, *Monteagudo et al. 15627* (HOXA); Oxapampa, sector San Alberto, 10°32'58"S, 75°21'58"W, 2353 m, 23 Dec 2007, ♀, fruits, *Rojas et al. 5052* (HOXA); **San Martín:** Moyobamba, Jepelacio, Cascada Paccha, 1.15 km SW of San Miguel, road Jepelacio–Carrizal, 6°13'19.5"S, 76°55'14.9"W, 1229 m, 28 Jun 2011, ♀, fruits, *Samain et al. 2011-092* (IEB, GENT, MEXU, USM).

9. *Hydrangea weberbaueri* Engl., Nat. Pflanzenfam. (ed. 2) 18a: 207. 1930.
Figures 14–16

Type. Peru. Amazonas: Cheto, ♀, inflorescence bud, flower buds, flowers, *A. Weberbauer 4372* (holotype: B (destroyed), F neg. 4146); lectotype: F! (fragment)). Peru. Amazonas: Chachapoyas, Soloco, Paraje Olia, 1.44 km S of Quitachi, W of road to Pampa del Tío, 6°20'2.85"S, 77°41'2.91"W, 2304 m, 22 Jun. 2011, ♀, flowers, M.S. Samain et al. 2011-062 epitype, designated here: USM!; isoepitypes: GENT!, IEB!, MEXU!).

Description. Root-climbing liana of up to 20 m high, functionally dioecious; ***free-growing branches*** quadrangular, slightly fissured; ***leaves*** decussate, petiole flattened adaxially, sulcate in young leaves (Fig. 15B), terete abaxially, color dark brown to black, glabrous, leaving a semicircular to triangular scar on the branch when leaves fall, 1.0–2.6 cm long; lamina (ob)ovate to lanceolate, 13–21 cm long, 6–12 cm broad, base cuneate, sometimes asymmetric, apex rounded to acuminate, leaf margin slightly glandular-dentate, venation brochidodromous, veins 6–10 pairs, adaxial leaf side with midvein protruding, primary veins lightly marked, secondary veins barely visible, moderately pubescent with white, stellate hairs, caducous, abaxially with protruding

Figure 15. *Hydrangea weberbaueri* **A** apical portion of a branch with young leaves where the characteristic leaf venation and margin can be observed **B** adaxial leaf side showing the typical leaf venation of this species **C** glabrous apex of the inflorescence axis of a functionally female inflorescence. **A** field image of collection *Granados Mendoza et al. 2012-23* **B** field image of collection *Samain et al. 2011-056* **C** field image of collection *Samain et al. 2011-068*.

midvein and primary veins, secondary veins marked, opaque olive green, secondary veins in between the primary veins parallel to these and forming a distinctive regular pattern with veins arching towards the apex (Fig. 15A), sometimes, primary and secondary veins starting from nearly the same position on the midvein, densely pubescent with stellate reddish hairs, especially on the veins, caducous, sometimes nearly

glabrous, acarodomatia numerous, not very conspicuous as they are hidden under the pubescence, in axils of midvein and primary veins, sometimes forming a small membrane partially covering the cavity; ***inflorescence axis*** pubescent with simple white hairs to glabrous (Fig. 15C), 9–47 cm long, with 3–5 decussate leaf pairs below the inflorescence, persistent, petiole 0.5–1 cm long, lamina 2–11.5 cm long, 1.1–7.5 cm broad, adaxially glabrous, abaxially pubescent with small stellate hairs, ***apex of the inflorescence axis*** woody, cylindrical, elongated bract scars visible, thickening at the top, 6–10 mm broad, 4–7 mm high in functionally female plants, 5–7 mm broad, 4 mm high in functionally male plants, inflorescence bracts cucullate, cream-colored, coriaceous, margin membranous and glabrous to densely pubescent with yellowish stellate hairs, veins darker, parallel, bracts increasing in size, lowermost bract 2.5–3 cm large, 2.4–2.5 cm broad, ***inflorescences*** lateral, decussate, 1–3 pairs of inflorescences per flowering branch (Fig. 16A), sometimes only one inflorescence developing, flowering branch continues growing vegetatively with the same vigor and periodicity above the inflorescences as below these, inflorescence axes with basal lignified parts of inflorescences of previous years visible in well-collected specimens, allowing to observe growth and flower periodicity, these rests 53 cm apart (in between the main branch ramified and those branches also carried inflorescences that flowered at the same time as the last inflorescences, *Samain et al. 2013-130*), medulla central in the branch, disappearing in older branches, leaving a hole only, inflorescence umbellate, buds up to 4.1 cm broad and 3.6 cm high before opening, in flowering stage 8–22.5 cm diameter, 3.5–14 cm high, with 6–10 main axes in functionally male plants, 7–14 main axes in functionally female plants, partial inflorescences cymes, secondary and tertiary inflorescence axes with reddish stellate hairs, pubescence gradually increasing towards flower insertion; ***enlarged marginal flowers*** sometimes present (Fig. 16A–C), terminally placed in a cyme, sepals with marked veins, (2–)4, separate at the base, veins marked, palmate, reticulate, pistils 2, reduced, central part of the flower generally amorph, further characters not observed in detail, 1.5–3.7 cm diameter, pedicel 1–2.5 cm long; ***flower pedicel of reduced flowers*** 3–7 mm long in functionally male flowers, 3 mm long in functionally female flowers, ***receptacle*** triangular in functionally male flowers, rectangular in functionally female flowers, ***ovary*** inferior, ***calyx lobes*** 4, triangular, 0.2 mm long, ***petals*** 3–4, purple, valvate, cucullate, papyraceous, 2.2–2.5 mm long, 1.2–1.3 mm broad; ***functionally male flowers*** (Fig. 16D): hypanthium 1.1–1.8 mm diameter, stamens 8, well-developed, filaments 3 mm long, anthers 0.8–1.0 mm long, 0.6 mm broad, pistils 2, reduced, 0.5 mm long, stigmas not penicellate; ***functionally female flowers*** (Fig. 16E): hypanthium 1.0–1.8 mm diameter, stamens 8, reduced, filaments 0.1–0.4 mm long, anthers 0.1 mm long, 0.3–0.4 mm broad, pistils 2, 0.7 mm long, enlarging to 2–3 mm during fruit maturation, stigmas apically clavate and shortly penicellate; ***fruit*** a rectangular capsule, apically with a conspicuous border, ribs 4–6, pale reddish brown, 1.5 mm high, 2.5 mm broad above, 1.5 mm diameter, opening between the two pistils to release seeds, seeds not seen.

Distribution. *Hydrangea weberbaueri* is known from Colombia, Ecuador and Peru (Fig. 14).

Figure 16. *Hydrangea weberbaueri* **A** branch with inflorescences with enlarged marginal flowers **B** functionally male inflorescence with enlarged marginal flowers, and reduced flowers with large stamens **C** functionally female inflorescence with enlarged marginal flowers **D** close-up of functionally male flowers with large stamens and reduced pistils **E** close-up of functionally female flowers with reduced stamens and large pistils. **A, B** field images of collection *Granados Mendoza et al. 2012-16* **C** field image of collection *Granados Mendoza et al. 2012-21* **D** field image of collection *Samain et al. 2011-068*.

Habitat. This species grows in tropical rainforest and mountain cloud forest at elevations between 974–3500 m.

Phenology. This species has been collected with flowers and fruits throughout the year.

Vernacular names and use. The following vernacular names are indicated on the specimen *Ellemann 75381* (AAU, LOJA, MO, QCA): bejuco matapalo (Spanish), yura huanutic caspic (Quichua). Its use as fuel wood is also indicated on the label of these specimens. This is the only species of this study of which vernacular name and use have been recorded.

Notes. Not to be considered a synonym of *H. peruviana* from which it can be distinguished by the notorious regular venation pattern with primary veins and secondary veins parallel to each other, all of them arching towards the apex.

No duplicate material of the original type collection has been located in the herbarium MOL of the Universidad Nacional Agraria La Molina in Lima, Peru, nor any other herbarium where we have searched. The fragment held in F that is the obligate lectotype is fragmentary and does not have the diagnostic features of this taxon, therefore we designate an epitype here for diagnostic purposes. The epitype specimen was collected approximately 8.5 km south of the original type location, which at the time of our field work was the nearest location to Cheto with primary forest. Unfortunately, satellite images (Google Earth 2020) show that the forest where the epitype has been collected was destroyed for land use change less than five years after our visit.

A Weberbauer collection with the same number as the original type is present in the herbarium USM, but this is an entirely different species (with branched inflorescences) which does not belong to this group. The label on the USM specimen is not the original Weberbauer label, suggesting this represents a labeling error.

The leaf venation in the specimens from Colombia does slightly differ from that in the material from Ecuador and Peru, although it is still very recognizable. Therefore, we decided to include these in *H. weberbaueri*, although future studies on Colombian hydrangeas may well show it concerns a distinct and new species.

According to our molecular study, *Hydrangea weberbaueri* is not closely related to any of the species mentioned here, but it occurs in a clade which is sister to the one with *H. goudotii* and *H. trianae* (Granados Mendoza et al. unpublished results).

Preliminary conservation status. Although this species has an EOO of nearly 660,000 km^2, it is Endangered according to the IUCN categories and criteria (IUCN 2012), with an AAO of 224 km^2, as well as an extensive reduction in both EOO and AOO resulting from severe habitat destruction and fragmentation.

Additional specimens examined. Colombia. Cundinamarca: Quebrada la Aguadita, 2 km arriba de la carretera a Fusagasugá, 1800 m, 28 Nov 1960, ♀, fruits, *Idrobo 4186* (COL); Cordillera Oriental, municipio San Bernardo, Vereda de Venecia, margen izquierda del río Chorrera, afluente del Sumapáz, 2450 m, 21 Jul 1981, floral buds, *Jaramillo et al. 6844* (COL); Sasaima, vereda San Bernardo, quebrada La María y Río Dulce, 1800 m, sterile, Jan 1958, sterile, *García-Barriga 15757* (COL); **Santander:** municipio Suaita, corregimiento San José de Suaita, carretera a La Veterana, bosque al

lado de la carretera, vereda San Imidio, 6°9'44.5"N, 73°25'09.4"W, 1800–1910 m, 6 Apr 2003, ♀, fruits, *Betancur et al. 10122* (COL, HUA).

Ecuador. Azuay: the eastern Cordillera, 1–8 km, north of the village of Sevilla de Oro, 8000–9000 ft, 27 Jul–12 Aug 1945, inflorescence buds, *Camp E-4464* (AAU, F, MO); Sevilla de Oro, ca 1.7 airline km E of Osorancho (El Cisne), N Sevilla de Oro, 2°45'42"S, 78°37'38.1"W, 2804 m, 8 Jun 2012, sterile, *Granados Mendoza et al. 2012-22* (GENT, HOXA, IEB, MEXU, QCNE); same data as preceding, 2°45'42.1"S, 78°37'37.4"W, 2804 m, 8 Jun 2012, sterile, *Granados Mendoza et al. 2012-23* (GENT, HOXA, IEB, MEXU, QCNE); same data as preceding, 2°45'42"S, 78°37'37.3"W, 2805 m, 8 Jun 2012, sterile, *Granados Mendoza et al. 2012-24* (GENT, HOXA, IEB, MEXU, QCNE); ca 1.8 airline km E of Osorancho (El Cisne), N Sevilla de Oro, 2°45'43.3"S, 78°37'35.9"W, 2813 m, 8 Jun 2012, inflorescence buds, *Granados Mendoza et al. 2012-25* (GENT, HOXA, IEB, MEXU, QCNE); **Loja:** Río Jipiro near Hda. Jipiro, about 7 km northeast of Loja, 03°58'S, 79°07'W, 8000 ft, 14–16 Jun 1944, ♂, flower buds, flowers, *Prieto AP-27* (AAU, NY); between Nudo de Sabanillas and Río Cachiyacu at Tambo Cachiyacu, 3000–3500 m, 17 Oct 1943, ♂, flowers, *Steyermark 54551* (F, US); Loja–Zamora, 12 km from Loja, on the finca of Dr. David Espinosa, 03°55'S, 79°09'W, 2400–2600 m, 17 Nov 1988, ♀, fruits, *Ellemann 75381* (AAU, LOJA, MO, QCA); old road Loja-Zamora, El Tiro, 2600 m, 10 Oct 2004, ♂, flowers, *Homeier 1399* (LOJA, QCNE); Loja, 3.5 Km S of Nudo de Sabanillas on road Yangana–Valladolid, 4°26'54.2"S, 79°8'51.3"W, 2798 m, 2 Jun 2012, sterile, *Granados Mendoza et al. 2012-11* (GENT, HOXA, IEB, MEXU, QCNE); **Morona Santiago:** Parque Nacional Sangay-Tinguichaca, 2°13'559632"S, 78°26'364956"W, 2870 m, 29 Aug 2011, sterile, *Duchicela et al. 759* (QCA); Morona, ca. 4.5 airline km WNW of Plan de Milagro on road Plan de Milagro–Gualaceo, 3°0'14.6"S, 78°30'29.2"W, 2158 m, 7 Jun 2012, ♀, fruits, *Granados Mendoza et al. 2012-21* (GENT, HOXA, IEB, MEXU, QCNE); **Napo:** area of the Yanayacu biological station, 5 km SW of Cosanga, 00°36'S, 77°53'W, 2100 m, 27 Sep 2005, ♀, fruits, *Homeier 1680* (QCNE); **Pichincha:** Reserva Florística – Ecológica " Río Guajalito", km 59 de la carretera antigua Quito – Sto. Domingo de los Colorados, a 3.5 km al NE de la carretera, estribaciones occidentales del Volcán Pichincha, 0°13'53"S, 78°48'10"W, 1800–2200 m, 9 Aug 1985, ♂, flowers, *Jaramillo & Zak 7900* (NY, QCA, US); same data as preceding, 2200 m, 25 Apr 1987, sterile, *Grijalva 317* (QCA); road from Chiriboga to Santo Domingo, 1910 m, 3 May 1985, ♂, flowers, *Stein 2680* (AAU, NY, QCNE); Cordillera Oriental, Oya Cachi, 3200 m, 26 Oct 1945, ♂, old flowers, *Acosta 11144* (F); **Sucumbios:** Gonzalo Pizarro, near km 14 of Vía a casa de Máquinas of Bosque Protector los Cedros, 0°7'21.9"S, 77°26'42.1"W, 974 m, 9 Jul 2012, sterile, *Granados Mendoza et al. 2012-103* (GENT, HOXA, IEB, MEXU, QCNE); **Tungurahua:** Cordillera el Encanto, ca. 6 airline km SSW of Río Negro, 1°27'33.4"S, 78°13'7"W, 1815 m, 13 Jun 2012, floral buds, *Granados Mendoza et al. 2012-35* (GENT, HOXA, IEB, MEXU, QCNE); same data as preceding, 1°27'34.6"S, 78°12'53.7"W, 1810 m, 13 Jun 2012, inflorescence buds, *Granados Mendoza et al. 2012-36* (GENT, HOXA, IEB, MEXU, QCNE); same data as preceding, 1°27'42.5"S, 78°12'52"W, 1806 m, 13

Jun 2012, inflorescence buds, *Granados Mendoza et al. 2012-37* (GENT, HOXA, IEB, MEXU, QCNE); **Zamora-Chinchipe:** Carretera Loja–Zamora, km 15–18, falda oriental, 3°58'S, 79°7'W, 23 Sep 1982, floral buds, *Balslev 3181* (AAU, MO, NY, QCA); Zamora, 3.7 km on foot path S Romerillos Alto, 4°14'49.9"S, 78°56'9.1"W, 1681 m, 4 Jun 2012, ♂, inflorescence buds, flowers, *Granados Mendoza et al. 2012-16* (GENT, HOXA, IEB, MEXU, QCNE); ca. 4.8 km on foot path S Romerillos Alto, 4°15'0.6"S, 78°55'40.4"W, 1801 m, 4 Jun 2012, sterile, *Granados Mendoza et al. 2012-17* (GENT, HOXA, IEB, MEXU, QCNE); same data as preceding, 4°15'0"S, 78°55'39.9"W, 1795 m, 4 Jun 2012, sterile, *Granados Mendoza et al. 2012-18* (GENT, HOXA, IEB, MEXU, QCNE); same data as preceding, 4°15'0.2"S, 78°55'39.4"W, 1796 m, 4 Jun 2012, ♂, flowers, *Granados Mendoza et al. 2012-19* (GENT, HOXA, IEB, MEXU, QCNE); El Pangui, ca. 5.7 km SSE of Tundayme on dirt road to military base El Condor, 3°36'19.6"S, 78°28'21.1"W, 1092 m, 7 Jun 2012, sterile, dry inflorescences, *Granados Mendoza et al. 2012-20* (GENT, HOXA, IEB, MEXU, QCNE).

Peru. Amazonas: Bongará, Jumbilla, Bosque de Protección Alto Mayo, surroundings of Chichilac, 4.79 km NNE of Jumbilla, 5°51'51.33"S, 77°47'16.7"W, 2462 m, 10 Dec 2013, ♀, old fruits, *Samain et al. 2013-130* (GENT, IEB, MEXU, USM); same data as preceding, 4.65 km NNE of Jumbilla, 5°51'56.7"S, 77°46'55.6"W, 2649 m, 30 Jun 2011, ♂, flowers, *Samain et al. 2011-103* (GENT, IEB, MEXU, USM); same data as preceding, 4.57 km NNE of Jumbilla, 5°51'51.9"S, 77°47'16.7"W, 2397 m, 30 Jun 2011, ♀, flower buds, flowers, *Samain et al. 2011-097* (GENT, IEB, MEXU, USM); Bosque de Protección Alto Mayo, surroundings of Chichilac, 4.78 km NNE of Jumbilla, 5°51'52.51"S, 77°47'0.86"W, 2570 m, 10 Dec 2013, ♀, fruits, *Samain et al. 2013-133* (GENT, IEB, MEXU, USM); Bongará, Yambrasbamba, carretera Chiclayo–Tarapoto, km 370.2, antes de Puente Nieva, 5°41'6.1"S, 77°46'56.5"W, 2031 m, 9 Dec 2013, ♂, flower buds, flowers, *Samain et al. 2013-127* (GENT, IEB, MEXU, USM); margen del Río Nieva, km 381 de la Carretera Marginal, 5°41'S, 77°47'W, 1070 m, 11 Jul 1999, ♀, flower developing into fruits, *Sánchez Vega 10031* (F); Florida, 4–8 km E of Pomacocha on road to Rioja, 5°45'S, 77°53'W, 2100–2200 m, 9 Feb 1984, ♂, flowers, *Gentry 45191* (AMAZ, CAS, COL, MEXU, MO); Chachapoyas, Leymebamba, Hacienda San Cristobal del Yeso, 3.08 km NW of Leymebamba, 6°41'34.9"S, 77°49'36.3"W, 2766 m, 20 Jun 2011, ♂, flowers, *Samain et al. 2011-046* (GENT, IEB, MEXU, USM); same data as preceding, Hacienda San Cristobal del Yeso, 2.7 km NNW of Leymebamba, 6°41'39.33"S, 77°49'29.23"W, 2738 m, 8 Dec 2013, ♀, fruits, *Samain et al. 2013-124* (GENT, IEB, MEXU, USM); alrededor de la Laguna de Los Cóndores, parte sur, 6°51.20'S, 77°40.96'W, 2500–2700 m, 16 Aug 1998, ♀, fruits, *Quipuscoa 1218* (F, NY, QCNE); San Francisco de Daguas, 2.4 km NNE of Pipus, Chachapoyas–Molinopampa road, km 30, 6°12'32.3"S, 77°43'22.8"W, 2110 m, 21 Jun 2011, ♀, fruits, *Samain et al. 2011-056* (GENT, IEB, MEXU, USM); Pampa del Tio, camino entre Quitachi y (las) Tinas, 2000 m, 5 Jul 1991, ♂, flowers, *Díaz 4609* (USM); **Cajamarca:** Cutervo, San Andrés de Cutervo, 3.9 km SE of San Andres Cutervo, road Cutervo–Socota–Chiple, 6°16'05.6"S, 78°41'35.4"W, 2513 m, 8 Jul 2011, inflorescence buds, *Samain et al. 2011-141* (GENT, IEB, MEXU, USM); same

data as preceding, 3.92 km SE of San Andrés de Cutervo, road Cutervo–Socota–Chiple, 6°16'05.5"S, 78°41'34.5"W, 2518 m, 8 Jul 2011, ♀, inflorescence buds, *Samain et al. 2011-143* (GENT, IEB, MEXU, USM); La Pucarilla, entre Socota y San Andrés, 2500 m, 3 Nov 1991, ♂, flowers, *Sánchez 5947* (F, MO, UC); Bosque Cutervo, Parque Nacional de Cutervo, NW corner of Cordillera Tarros, Chorro Blanco sector, ca. 10 km WNW of San Andres de Cutervo, 6°12'S, 78°46'W, 2650 m, 4 Nov 1990, ♂, inflorescence buds, flowers, *Dillon 6152* (F, UC); Cutervo National Park, Chorro Blanco area, 15 km N of San Andres de Cutervo, 6°10'S, 78°40'W, 2400–2650 m, 13 Sep 1991, ♀, flower buds, flowers, *Gentry 74745* (F, USM); Parque Nacional Cutervo, arriba del Saucedal pasando por Chorro Blanco, 2250 m, 3 Aug 1988, ♂, inflorescence buds, flower buds, flowers, *Díaz 2943* (USM); Cutervo National Park, 12 km NE of San Andres Cutervo, transect 5, 6°10'S, 78°40'W, 2240 m, 11 Sep 1991, sterile, *Gentry 74670* (MO, USM); Madre Mia, entre el Suro y la Flor al NO del Parque, 2400 m, 25 Jun 1992, ♂, inflorescence buds, flower buds, flowers, *Sánchez Vega 6329* (F); Bosque Cutervo, Parque Nacional de Cutervo, NW corner of Cordillera Tarros, Chorro Blanco sector, ca. 10 km WNW of San Andres de Cutervo, 6°12'S, 78°46'W, 2600 m, 5 Nov 1990, ♂, flowers, *Dillon 6184* (F); Hualgayoc, 2 km. above Palmito. Hacienda Taulis, between the Casa Hacienda and Palmito, 2575 m, 31 Aug 1964, ♂, flowers, *Hutchinson 6395* (GH, F, US); San Ignacio, Huarango, poblado Selva Andina, 05°03'37"S, 078°45'13"W, 1798 m, 18 Apr 2007, ♀, fruits, *Perea & Mateo 2929* (MO, QCNE); San Ignacio, 12.83 km SW of San Ignacio, 3.05 km SSW of Alto Ihuamaca, 5°12'52.8"S, 79°05'47.9"W, 2129 m, 6 Jul 2011, ♀, fruits, *Samain et al. 2011-127* (GENT, IEB, MEXU, USM); Nuevo Mundo–Pisaguas, 5°10'S, 68°32'W (the correct coordinates are 78°32'W), 1550 m, ♀, fruits, 13 Nov 1997, *Campos 4632* (F, MEXU, MO, NY, USM); **Pasco:** Oxapampa, Parque Nacional Yanachaga Chemillén, parte alta del Refugio el Cedro, 10°32'S, 75°21'W, 2450–2680 m, 20 Mar 2003, inflorescence buds, *Monteagudo 4762* (F, HOXA, USM); Oxapampa, sector Chacos parte media, 10°38'42.9"S, 75°17'30"W, 2740 m, 4 Nov 2004, floral buds, *Monteagudo et al. 7534* (HOXA); Oxapampa, camino a Paucartambo (a la altura de Mesapata), < 1800 m, 21 Mar 2005, ♀, flower buds, fruits, *Arias et al. 261* (HOXA); Oxapampa, Huancabamba, camino hacia la Laguna San Daniel, Granapazú-Sector San Daniel, Parque Nacional Yanachaga-Chemillén, 10°26'15.6"S, 75°27'9.9"W, 2200 m, 12 Sep 2005, sterile, *Ortiz et al. 950* (HOXA); Oxapampa, Huancabamba, Parque Nacional Yanachaga-Chemillen, sector San Daniel, 10°26'35S, 75°26'16W, 2200–2500 m, 6 Mar 2006, ♂, flowers, *Vásquez et al.* 30989 (HOXA); Oxapampa, Huancabamba, sector Quebrada Yanachaga (paralela a la quebrada), 10°24'08"S, 75°29'18"W, 2097 m, 14 Sep 2004, sterile, *Perea & Mateo 1682* (HOXA); Oxapampa, El Abra, camino Oxapampa–Villa Rica, 10°40'30"S, 75°18'21"W, 2365 m, 24 Apr 2004, ♂, flowers, *Rojas et al. 2242* (HOXA); **San Martín:** Mariscal Cáceres, Huicungo, Río Abiseo National Park, 7°S, 77°W, 2700 m, 22 Jul 1985, ♀, flowers, *Young 1230* (F, NY); near La playa base camp, Río Abiseo National Park, 7°27'N, 77°2'W, 2650 m, 30 Aug 1985, ♂, inflorescence buds, flowers, *Young 1512* (MO); Río Abiseo National Park, ridge top on hill E of that with Gran Pajaten ruins, 2550 m, 14 Aug

1986, ♀, fruits, *Young 4141* (USM); trail between La Playa camp and Papayas camp, Rio Abiseo National Park, 7°S, 77°W, 2650–2750 m, 25 Jul 1987, ♀, flower buds, flowers, *Young 5014* (F, USM); Pardo Miguel, Caserío Jorge Chávez, km 398 de Carretera Marginal, 5°40'S, 77°43'W, 1400 m, 1 Jul 1999, ♀, fruits, *Sánchez Vega 9966* (F); **Rioja:** Pardo Miguel, 7.90 km E of El Progreso, Chiclayo–Tarapoto road, km 369.7, 5°41'18.8"S, 77°47'12.0"W, 2063 m, 23 Jun 2011, ♀, flower buds, flowers, *Samain et al. 2011-067* (GENT, IEB, MEXU, USM); same data as preceding, 7.94 km E of El Progreso, Chiclayo–Tarapoto road, km 369.7, 5°41'16.9"S, 77°47'11.9"W, 2132 m, 23 Jun 2011, ♀, inflorescence buds, flower buds, flowers, fruits, *Samain et al. 2011-068* (GENT, IEB, MEXU, USM); carretera Chiclayo–Tarapoto, km 377.5, 5°35'59.8"S, 77°45'18.7"W, 1867 m, 9 Dec 2013, ♀, fruits, *Samain et al. 2013-129* (GENT, IEB, MEXU, USM); Buenos Aires, along road Pedro Ruiz–Rioja, 5°42'9"S, 77°53'6"W, 2000 m, 21 Mar 1998, ♀, inflorescence buds, flower buds, flowers, *van der Werff 15329* (MEXU, USM).

Discussion

Unraveling taxonomic chaos in Central and South American *Hydrangeas*

The review of this morphological species complex surrounding *Hydrangea peruviana* and *H. oerstedii* of mostly red to purple flowered Central and South American climbing Hydrangeas attempts to unravel the taxonomic chaos in the group, based on the most complete sampling to date of herbarium specimens, as well as our own field collections and observations throughout their distribution area. Very importantly, type material was studied in all cases, generally the specimens themselves, rarely high-resolution scans on JSTOR Global Plants or shared by the curators of the respective herbaria. Many taxa had been synonymized, as important characters were, following their first descriptions in the 19th and early 20th centuries (especially by Briquet (1919), the most recent ones described in 1930), not considered of taxonomic value to distinguish species, except for the excellent treatment of the genus in the Flora of Peru (Macbride 1938). Additionally, in this particular group of Hydrangeas, we hypothesize that the authors who published on this group following Macbride (1938) did not have access to the type specimens, hence some misconceptions were merely copied from earlier sources, instead of critically reviewed with the support of the original material. Most of these nine species have been described based on the type specimen only (hence, the importance of studying type material) or on very few collections altogether, but after careful comparison of all currently known collections with type material, we can be certain that all abovementioned taxa deserve recognition as separate species, based on an extensive number of morphological characters, combined with distribution patterns, phenological differences and ecological preferences. Moreover, most of these species are also supported by our ongoing molecular studies (Granados Mendoza 2013; Granados Mendoza et al. unpublished results).

This study, as are those of other "species complexes" we are currently studying, e.g., *Hydrangea asterolasia* Diels, *Hydrangea preslii* Briq. and *Hydrangea* species with branched inflorescences, is extremely complicated, and the result of a decade of field and herbarium work, matching and re-matching specimens with type material and descriptions, comparisons with studies by McClintock (1957), Freire-Fierro (2004) and Christenhusz (2009), and adding many additional observations. These not only concern those related to functional dioecism, but also to plant branching, pubescence, leaf venation, presence or absence of acarodomatia, inflorescence architecture, and morphology of marginal flowers, amongst other characters.

As a result of our study, the number of accepted species in *Cornidia* currently totals 26. A complete key for morphological identification of all Neotropical species can currently not be provided as the species we have not yet treated (with the exception of this study, and those by Samain et al. 2014, 2019) are not yet well-defined at continental scale.

Classification of species in *Hydrangea* section *Cornidia*

In his otherwise excellent revision of the then known species of *Cornidia*, including the description of 11 new species in the section, all unusually elaborate for that time, Briquet (1919) classified all species in two subsections, each with their respective series: subsection *Monosegia* Briq, with series *Speciosae* Briq. and *Aphananthae* Briq., and subsection *Polysegia* Briq. subdivided in series *Synstyleae* Briq. and *Chorystyleae* Briq. Subsection *Monosegia*, according to Briquet (1919), is characterized by a single pseudo-umbellate cyme, and its series by the presence or absence of "sterile flowers", respectively (these flowers are not sterile, but have enlarged sepals; hence, we prefer the term "enlarged marginal flowers", see Samain et al. 2014). Subsection *Polysegia*, again according to Briquet (1919), can be recognized by the thyrsoid inflorescence consisting of several pseudo-umbellate cymes and its series amongst others by short stamens and pubescent leaves, and long stamens and glabrous leaves, respectively. Although the morphological classification in subsections at first sight may seem valid, several specimens of different species we have observed both in the field and in herbarium collections show both inflorescence types (single clusters in the axil of a leaf vs. several clusters on a branched inflorescence), indicating that these subsections are not natural, which is also reflected by our ongoing molecular work (Granados Mendoza 2013; Granados Mendoza et al. unpublished results). With respect to the series of subsection *Monosegia*, we have observed that, although the enlarged marginal flowers generally characterize specific species, they may also be absent in some individuals of those species (although this is not the case in the species studied here), or they may be present, reduced in size or parts, or not reduced, in species that generally do not possess them. With respect to the series of the subsection *Polysegia*, the first character is the stamen length, but this seems very artificial, as this distinguishes both sexes within a dioecious species: stamens in male individuals have long filaments, whereas these are short in female individuals. Hence, it may be hypothesized that this classification seemed workable based on the relatively few specimens Briquet (1919) had access to at the time, but current morphological

observations of an extensive number of specimens, as well as molecular data of a representative number of these, show that this is not the case. Based on our currently available data, we do not have sufficient elements to subdivide *Hydrangea* section *Cornidia* into subsections (Granados Mendoza et al. unpublished results).

Growth form controversies

A surprisingly high number of herbarium labels of the specimens studied here, as well as some references (e.g., Christenhusz 2009), mention growth forms such as hemiepiphytic shrubs, hemiepiphytic lianas, hemiepiphytic trees, epiphytes, shrubs, trees, climbing shrubs, parasitic shrubs or trees, etc. To our knowledge, and according to our observations in the field, all representatives of *Cornidia* are root-climbing lianas. When the base of their stem or their host tree is damaged or cut, they will die very soon because of lack of water and nutrients (personal observations), and lack of support, respectively. This stresses the importance of precise field observations for a correct interpretation of plant habits.

Distribution patterns

Of the nine species mentioned above, five are relatively widespread, whereas four have a relatively to very restricted distribution. On the one hand, the taxonomic and conservation statuses of two endemic Colombian species, *H. durifolia* and *H. schlimii*, are not completely clear in the absence of more and/or recent collections. A third species, *H. caucana*, endemic to Colombia as well, also does not have recent collections, but the existing ones do allow to understand its distribution pattern in the western cordillera. The fourth species with a restricted distribution is *H. peruviana* from Ecuador. On the other hand, *H. oerstedii* is the most widespread species studied here, known from more than 150 collections from Costa Rica and Panama. Despite the fact that this species grows in montane cloud forest, which is seriously being reduced throughout is whole distribution area (see Bruijnzeel et al. 2010), it seems to be very resilient against disturbance, as we have often observed it along roads and near villages, since it basically only needs its host tree to persist. As it is one of the few *Hydrangea* species that bends downwards with age and because of its conspicuous inflorescences, it may even be favored by local people. *Hydrangea panamensis*, which also is restricted to Costa Rica and Panama, is much less common than *H. oerstedii* (known from 17 collections only) and grows in tropical rainforest. *Hydrangea goudotii* and *H. trianae* are yet two other species described from Colombia. The present study confirms that both extend southwards into Ecuador, and the latter one also into Central Peru, being the most widespread species of this group in South America (known from 109 collections). Finally, *Hydrangea weberbaueri*, described from northern Peru, is shown here to have a continuous distribution from northern Ecuador to northern Peru, with a few collections from central Peru and from northeastern Colombia. The latter, as mentioned above, differ slightly from the southern ones, but can still be referred to this species based on the peculiar leaf vein patterns.

The overall distribution area of the species studied here is from northern Costa Rica to central Peru, which is the area with the highest diversity of Neotropical Hydrangeas, apart from Mexico (Samain et al. 2014, 2019). The few specimens of the countries north of Costa Rica and south of Mexico (Guatemala, Honduras, El Salvador and Nicaragua) belong to the widespread *Hydrangea albostellata* Samain, Najarro & Martínez (Samain et al. 2014) or remain unidentified because of a lack of fertile material, but definitely do not show affinity with the group studied here. Similarly, the few fertile specimens from Venezuela do have white flowers and belong to a group we will be treating in an upcoming study. The few specimens collected southwards of the Selva Central in Peru are generally also morphologically distinct. From both this study and ongoing morphological work in *Cornidia*, it becomes clear that especially Colombia needs to be further explored with respect to *Hydrangea*, as the record in this country seems very fragmentary and several species are known from very few collections or their type locality only.

Impact of taxonomic studies on conservation actions

Although a few populations of most of the species studied here do occur in protected areas, their long-term conservation is seriously compromised because of the significant threats from which their habitats suffer throughout their distribution area, related to fragmentation, land use change and climate change. Moreover, it is likely their dioecism makes these species even more prone to local extinction because of habitat destruction and fragmentation, as female and male individuals generally do not occur near each other, and their functional biology is not well-understood to date. During our field work, especially in Peru, where Hydrangeas often occur on private properties, in contrast with e.g. Costa Rica and Panama, where many collections were made in areas protected at national level, we have tried to sensitize the land-owners about the uniqueness of this group as a whole. Derived of the current contribution, we will also be able to do so at species level, which is especially important for the threatened taxa.

Finally, it is difficult to believe – though not surprising taking into account our recent discoveries of seven new species in Mexico (Samain et al. 2014, 2019) – that one species, of which we now know it is extremely rare (*H. peruviana*), was considered to encompass eight other taxa which can be recognized by distinctive and species-constant characters, either at the varietal level (*H. oerstedii*), or as synonyms of the typical variety or of var. *oerstedii*. Moreover, if we look at global biodiversity databases such as GBIF, the situation is even worse, as the majority of the known specimens of the white-flowered *H. seemannii*, endemic to northwestern Mexico, and several species of Central America, northern South America, Peru and Bolivia are also identified as *H. peruviana*, whereas this species is endemic to Ecuador. This latter situation calls for a more critical use of such database information, as e.g., when preparing a distribution map of *H. peruviana* with GBIF data in GeoCAT (Bachmann et al. 2011) for the purpose of an IUCN Red List assessment, one might come up with an Extent of Occurrence (EOO) of nearly 12 million km^2 based on 599 occurrence points reaching from Canada to Bo-

livia, whereas the correct EOO is 13,515.020 km^2 only, based on 7 verified occurrence points in Ecuador. Even the combined EOO of all species of this study does not total 2 million km^2. As a consequence, the present study exemplifies the urgent need for more interest for profound taxonomic studies in plants in general and funding to carry these out; though intrinsic costs are not high, these studies are very time-consuming, as in many plant families we do not dispose of well-circumscribed units for conservation to mitigate the currently occurring unprecedented loss of biodiversity.

Acknowledgements

We are grateful to the authorities of Costa Rica, Ecuador, Panama and Peru for issuing the collection permits 020-2012-SINAC, 041-2012-SINAC, 001-12-IC-FLO-DNB/MA, SE/P-11-19, 0124-2011-AG-DGFFS-DGEFFS and 0395-2013-MINAGRI-DGFFS/DGEFFS, respectively. We thank the curators of all abovementioned herbaria for loaning the material required for this study and Laurence Loze of the herbarium G of the Conservatoire et Jardin botaniques de la Ville de Genève, for kindly sharing photos of the original syntypes of *Hydrangea goudotii*. Thanks to Alina Freire-Fierro, Maarten Christenhusz for their valuable comments on this manuscript and to Sandy Knapp for the detailed review and suggestions that have greatly improved this study. In Colombia, we thank Ricardo Callejas and Favio González for permission to take pictures in the herbaria HUA and COL, respectively. In Costa Rica, we thank Frank González, Barry Hammel, Esteban Jiménez, Julio Morales, and Nelson Zamora for help with logistics and sharing their knowledge. In Ecuador, Diana Fernández, Efraín Freire, Edison Jiménez, and Juan C. Cerón Factos for their invaluable help obtaining the research and collection permits and/or performing field work. In Panama, María de Stapf, Vielka Murillo, and Jorge Valdés Sánchez for their support in obtaining the collection and export permits and field work logistics. In Peru, Joaquina Albán, Carlos Bambarén, Asunción Cano, Mercedes Flores, Víctor Morales, Guillermo Pino, Rigoberto Rivera (who also helped in Ecuador), Rocío Rojas, Merly Saavedra, Rodolfo Vázquez for their help with all herbarium, permit and field logistics. In Peru, we are especially grateful to the local guides, *los grandes conocedores*, the great connoisseurs, as we used to refer to them in the field, many of whom have Hydrangeas on their private properties. We dedicate this manuscript to these people from the Peruvian countryside, especially to Lino Rojas from Chichilac, Jumbilla, and the children of Nueva Esperanza, Aramango, both in the department of Amazonas.

Funding

Field work was funded by the Bijzonder Onderzoeksfonds of the Ghent University, Belgium, the Research Foundation Flanders, the Systematics Association and private funds of the first author and of Rita Carron, Gent, Belgium.

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