Phytotaxa 162 (4): 181–197
www.mapress.com/phytotaxa/

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

http://dx.doi.org/10.11646/phytotaxa.162.4.1

First record of the critically endangered *Hydrangea steyermarkii* Standl. (Hydrangeaceae) in Mexico, and description of a new widespread *Hydrangea* species of Mesoamerica

MARIE-STÉPHANIE SAMAIN[1,2], FRANCISCO HERNÁNDEZ NAJARRO[3] & ESTEBAN MANUEL MARTÍNEZ SALAS[4]

[1] *Instituto de Ecología, A.C., Centro Regional del Bajío, Avenida Lázaro Cárdenas 253, 61600 Pátzcuaro, Michoacán, Mexico; e-mail: MarieStephanie.Samain@gmail.com*

[2] *Ghent University, Department of Biology, Research Group Spermatophytes, 9000 Gent, Belgium*

[3] *Herbario CHIP, Dirección de Botánica Dr. Faustino Miranda, Secretaria de Medio Ambiente e Historia Natural, Apartado Postal 6, 29000 Tuxtla Gutiérrez, Chiapas, Mexico*

[4] *Herbario Nacional de México, Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México, 04510 Mexico City, Distrito Federal, Mexico*

Abstract

Based on our detailed observations in the field, completed with herbarium material of representatives of *Hydrangea* section *Cornidia* in southeastern Mexico and Central America, we found that *Hydrangea steyermarkii* Standley, in contrast to what has been assumed up to now, is restricted to the Tacaná Volcano on the border of Mexico and Guatemala. The majority of the specimens with reddish or whitish indument on their branches in South East Mexico and Central America, belonging to this nearly exclusively Neotropical *Hydrangea* clade, had been identified as such, but the characters of these collections do not coincide with the single type specimen of *H. steyermarkii*, neither with other individuals of this species growing in the type locality area. In fact, nearly all specimens of Mesoamerica that had been identified as this species belong to a new species with a relatively wide distribution, which we describe here. This new species is illustrated and compared with *H. steyermarkii*, of which we also provide an amended description and illustrations. Finally, on the basis of these two species we document previously suggested dioecism in this plant group, which not only has consequences for systematics and nomenclature in this clade, but also for conservation.

Key words: Hortensia, taxonomy, Neotropics, functional dioecism, conservation

Introduction

The genus *Hydrangea* Linnaeus (1753a: 397) (Hydrangeaceae) is with more than 1,000 cultivars and hybrids already since centuries a very popular ornamental plant group. These ornamentals with inflorescences with attractive marginal flowers are commonly known as hortensias, and descend from Asian shrubby species such as *H. macrophylla* (Thunb.) Ser. in de Candolle (1830: 15) and *H. aspera* D. Don (1825: 211). The Asian representatives of *Hydrangea* have been relatively well studied although the species boundaries and relationships continue to be disputed (Wei & Bartholomew 2001). Contrarily, the nearly exclusively American section *Cornidia* Ruiz & Pavón (1794: 53) is very poorly known from any point of view, be it taxonomical, biological or ecological, mainly because the available taxonomical and floristic studies are entirely based on the observation of fragmentary herbarium material. All representatives are evergreen root climbers growing up to 30–40 meter high in the canopy of mostly primary forests, with coriaceous leaves and hortensia-like whitish, greenish, yellowish or purplish inflorescences, with our without marginal so-called "sterile" flowers. Their distribution area extends from northern Mexico to southern Chile and Argentina with one species, *Hydrangea integrifolia* Hayata in Matsumura & Hayata (1906: 131), in China, Taiwan and the Philippines.

Accepted by Federico Luebert: 19 Feb 2014; published: 17 Mar. 2014

According to several recent molecular studies, *Hydrangea* section *Cornidia* (hereafter shortened as *Cornidia*) is monophyletic, including the single Asian species (Samain *et al.* 2010, Granados Mendoza *et al.* 2013a, b). However, it is currently unknown how many species belong to this section as our recent field work across the Neotropics has yielded new morphospecies which cannot be assigned to any known taxon (ongoing unpublished studies). Since the description of *Cornidia* as a genus by Ruiz & Pavón (1794: 53) – later included as a section in *Hydrangea* by Engler (1891: 76) – more than 40 taxa have been described in this group. The monograph of the genus *Hydrangea s.s.* by McClintock (1957), which is entirely based on the study of herbarium specimens, is the only available recent revision of this section and includes 12 accepted species, classified in two subsections, *Monosegia* Briquet (1919: 396) and *Polysegia* Briquet (1919: 396). Although McClintock (1957) revised many collections from the whole distribution area, it is obvious that this work oversimplifies the rather astonishing diversity of climbing Hydrangeas in the Neotropics. Subsequent publications have largely taken over the viewpoints of McClintock (1957) and also have been mainly or entirely based on herbarium material. Currently, 11 species and one variety are accepted in section *Cornidia*.

According to Christenhusz (2009) in the Flora Mesoamericana, the most widespread species in southeastern Mexico and Central America is *Hydrangea steyermarkii* Standley (1940: 233), based on a single collection from Julian Steyermark on the Guatemalan side of the Volcano Tacaná near the border with Mexico. However, our recent field observations demonstrated that the collections made in Chiapas by Dennis Breedlove and his collaborators in the framework of the project "Flora of Chiapas" (Breedlove, 1986) do not belong to *Hydrangea steyermarkii*, but to a yet undescribed relatively widespread species instead. After detailed comparison with the type specimen, we conclude that only our collections on the Mexican side of the Volcano Tacaná near the type locality of *H. steyermarkii* effectively belong to this species.

Throughout its distribution area, *Cornidia* not only seems to be undercollected but also highly endangered because of its occurrence in hyper-conserved primary forests, which are becoming rarer every day. For instance in Mexico, our intensive exploring field work since 2009 revealed the presence of new populations which had never been noticed before and which are already at risk. Moreover, the fact that these remarkable plants remained undiscovered up to now is especially striking because of their growth form and size. As a consequence of their exceptional dimensions, sufficient material for further study generally can only be collected using mountaineering equipment, a technique which is rarely applied in botanical field work (Fig. 1A). Previous collections often seem to be fallen branches where some floral parts have been shed already. As a result, the diversity in this clade has been underestimated. To date, the last new species in *Cornidia* has been described 45 years ago by Nevling and Gómez-Pompa (1968).

The aims of this paper are twofold: 1) presenting a description of the new *Hydrangea* species which has been confused with *H. steyermarkii* and had not been recognized before, and 2) providing an amended description of *H. steyermarkii*. Additionally, we discuss shortly the consequences for taxonomy and conservation of the functional dioecism observed in this *Hydrangea* clade.

Material and Methods

Extensive field work has been carried out in the state of Chiapas in southeastern Mexico and in Costa Rica during summer and winter seasons of 2011, 2012 and 2013, coinciding with the flowering seasons of both species. Individuals were carefully observed and herbarium material and flowers and fruits were collected for further study. Additionally, herbarium material of *Hydrangea* section *Cornidia* of the herbaria CAS, DUKE, F, INB, MEXU, MICH, MO and US has been studied and compared with our own collections (deposited in CHIP, GENT and MEXU, with the exception of the types which are deposited in more herbaria).

Material for Scanning Electron Microscopy (SEM) was taken from herbarium material and fixed to aluminium stubs (especially made for the Instituto de Biología, UNAM) using standard carbon adhesive tapes (Electron Microscopy Sciences), sputter-coated with carbon (20 nm) and gold (20 nm) under argon atmosphere using a Quorum Q150R ES sputter-coater. Images were obtained with a Hitachi SU1510 scanning electron microscope at acceleration voltage of 10 kV.

Hydrangea albostellata Samain, Najarro & E.Martínez, _spec. nov._, Figs. 1, 2, 3, 4

Mesoamerican functionally dioecious species which has been confused with *Hydrangea steyermarkii* Standl., from which it can be distinguished by the following characters: leaves with slightly undulate, spoon-shaped lamina with apiculate apex, abaxially densely white pubescent, especially in young stage, inflorescence axis densely pubescent with adnate, whitish, stellate hairs, calyx lobes of reduced flowers triangular, very small, sometimes nearly invisible, petals membranous, margin revolute.

TYPE:—MEXICO. Chiapas: Pueblo Nuevo Solistahuacan, along the road Pueblo Nuevo Solistahuacan–Rayón, 17°12'41.52"N, 92°57'50.61"W, 1827 m, 19 January 2012, *M.S. Samain et al. 2012-023* (holotype: MEXU!, isotypes: CHIP!, GENT!, IEB!, K!, MEXU!, MO!, US!) [functionally female].

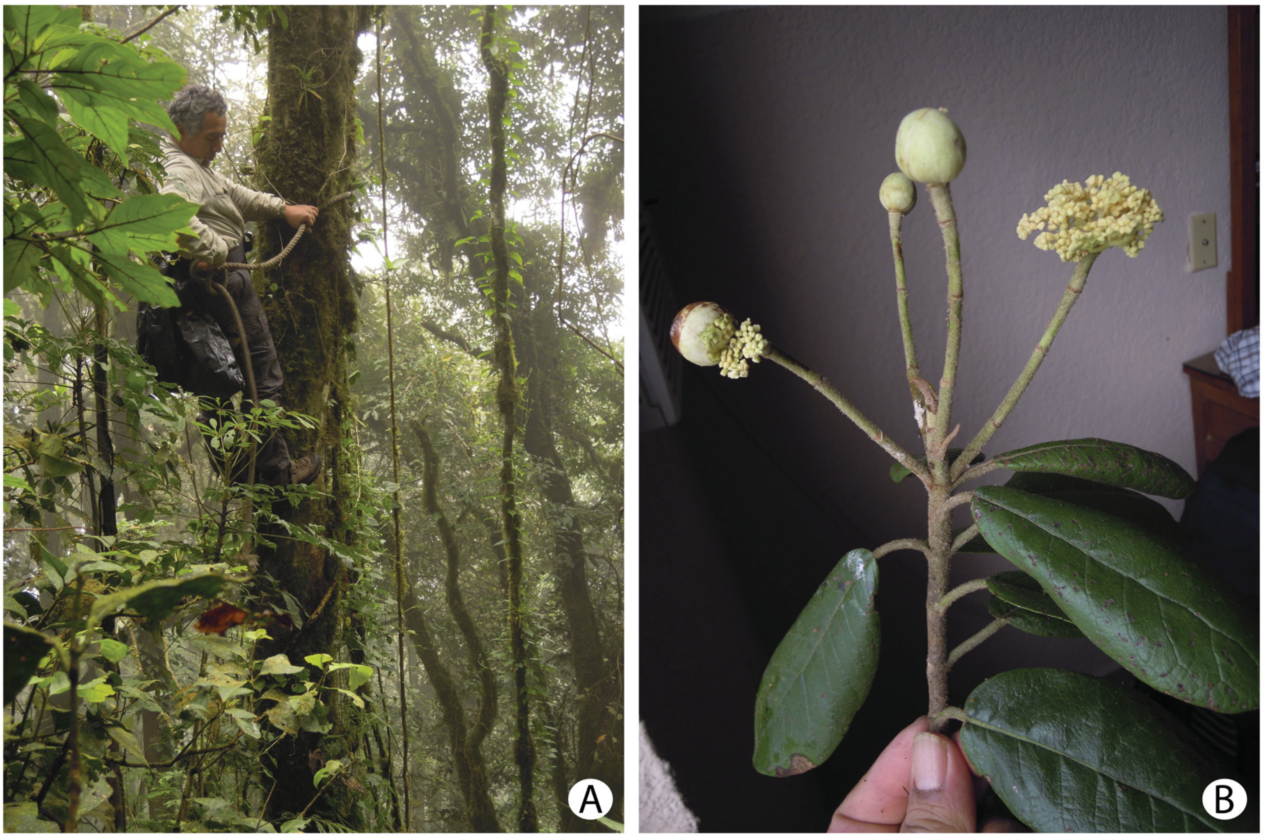

FIGURE 1. Field pictures. A. Climbing a *Hydrangea* host tree with specific equipment (Tapalapa, Chiapas, Mexico). B. Branch of *Hydrangea albostellata* with four inflorescences, all inflorescence bracts already shed in lower right one where the flower buds are visible, lower left inflorescence partially opened, apical inflorescences still covered by all inflorescence bracts (*M.S. Samain & E. Martínez S. 2012-090*).

Root-climbing liana of up to 35 m high, funtionally dioecious. Main stem clinging to the host tree with many adventitious roots, up to 20 cm diameter, bark dark brown, with lenticels. Runner shoots (stolons) reddish, with adventitious roots and stellate hairs, with small kataphylls. Branches many-ribbed, slightly angular, with many kataphyll scars, branches attached to host tree with adventitious roots, these roots fibrous, slightly flattened, with caducous stellate indument, free-growing branches terete, slightly fissured and exfoliant. Petiole sulcate adaxially, terete and corchy abaxially, this corchy line sometimes continuing in the abaxial midvein for approximately 1 cm, cortex fragmenting in mature ones, colour brownish grey, when young with whitish penicellate hairs, when mature (nearly) glabrous, 1–3 cm long, leaving a triangular scar on the branch when leaves fall (scar sometimes with slightly rounded borders). Leaves decussate, lanceolate-obovate to elliptic, lamina slightly undulated/spoon-shaped, 9–14 cm long, 4–8 cm broad, base cuneate, apex apiculate, leaf margin smooth, venation brochidodromous, veins 6–9, adaxial leaf side with only slightly visible midvein, secondary and tertiary veins very lightly marked, secondary veins join to form submarginal or intramarginal vein, glabrous with few simple, short, white hairs along the basal half of the midvein, abaxially with protruding veins, sparsely pubescent in mature leaves (caducous) and even less hairy on primary and secondary veins, opaque whitish-green, young leaves densely pubescent, slightly reddish, indument caducous except on the midvein, acarodomatia absent, but much indument present in vein axils. Inflorescence axis densely pubescent with adnate, whitish, stellate hairs, 4–15–(25) cm long, robust in functionally female plants, delicate in functionally male plants, with 2–5 opposite or decussate leaf pairs below the inflorescence, the upper two pairs inserted at the base of the inflorescence below the inflorescence bracts, caducous, petiole 2–4 mm long, 3 mm broad, petioles of upper leaf pairs nearly sessile, lamina 0.8–3.5 cm long, 0.7–1.1cm broad, starting from the base of the floral axis, each leaf pair with gradually diminishing size towards the inflorescence, apex of the floral axis woody, cone-shaped, elongated bract scars visible, thickening at the top, 6–8 mm broad, 3–4 mm high in functionally female plants, 5 mm broad, 2 mm high in functionally male plants, inflorescence bracts cucullate, reddish, coriaceous, border membranous, adaxially slightly pubescent, abaxially densely pubescent with whitish stellate hairs, veins nearly invisible because of pubescence, bracts increasing in size, lowermost bract 1.5 cm large, 2 cm broad, higher bracts up to 3.5 cm large, 3 cm broad, consecutively and rapidly caducous during inflorescence development, bracts of partial inflorescences linear, reddish, 8 mm long, 1 mm broad at the base, gradually tapering towards a pointed apex, caducous, inflorescences lateral, opposite, 1–3 pairs of inflorescences per flowering branch, sometimes only 1 inflorescence developing, flowering branch only continues growing vegetatively very slowly during inflorescence development, with maximum two leaf pairs above the inflorescences, or kataphylls only, up to eight pairs, linear, with whitish stellate hairs and a corchy abaxial line, inflorescence axes with basal lignified parts of inflorescences of previous years visible in robust well-collected specimens, allowing to observe growth and flower periodicity, these rests 9–22 cm apart (but relatively constant within one specimen), with 4–9 decussate leaf pairs (or the scars of these leaves, this number constant within one specimen), medulla central in the branch, disappearing in older branches, leaving a hole only, leaves at the base of the inflorescence absent, inflorescence umbellate, buds up to 3.5 cm broad and 3 cm high before opening (Figs. 1B, 4A), in flowering stage 5–14 cm diameter, 4–8 cm high, with 3–4 main axes in functionally male plants, 6–9 main axes in functionally female plants, partial inflorescences cymes (when enlarged marginal flowers are present, these terminally placed in each cyme), secondary and tertiary inflorescence axes with whitish stellate hairs, pubescence gradually decreasing towards flower insertion where there are some scarce hairs only. Enlarged marginal flowers sometimes present (Figs. 3A, 4A, B), flower pedicel 0.8–1(–1.8) cm long, receptacle rectangular, with 4 lateral ribs, 1.5 mm high, 2.5–3 mm broad, 2 mm diameter, ovary inferior, sepals 4, yellowish to greenish, coriaceous with marked veins, quadrangular with rounded margins to orbicular, sometimes spoon-shaped, margin inwards revolute, (2.5–)4–8 mm long, (2.5–)4–7(–9) mm broad, petals reduced and caducous, stamens (3–)6, filaments reduced and flattened, 0.3 mm long, 0.2 mm broad, anthers 0.3 mm long, pistils 2, style 1–2 mm long, stigma spathulate to rounded, very shortly penicillate, sometimes with seeds. Flower pedicel of reduced flowers 1.5–2 mm long in functionally male flowers, (2–)3–4(–5) mm long in functionally female flowers, receptacle broadly campanulate in functionally male flowers (Figs. 3B, 4C), semiglobose in functionally female flowers (Figs. 3C, 4D), ovary inferior, calyx lobes 4, triangular, in some specimens nearly invisible, 0.1–0.3 mm long, seemingly pushing downwards the border of the receptable, petals 4, valvate, cucullate, margin revolute, membranous, 1.8–2.5 mm long, 1.5 mm broad, white; functionally male flowers (Fig. 3D): hypanthium 1.5–2 mm diameter to completely round or even quadrangular, stamens up to 9, well-developed, filaments 2.5–4 mm long, anthers 0.7–1 mm long, 0.3–0.5 mm broad, pistils 2, reduced, 0.5–0.6 mm long, stigmas not penicellate; functionally female flowers: stamens 7–9 (if 9: 7 reduced and 2 rudimentary), reduced, filaments 0.1–0.5 mm long, anthers 0.2–0.7 mm long, 0.3 mm broad, pistils 2, 1.2–1.5 mm long, enlarging up to 3 mm during fruit maturation, stigmas apically clavate and shortly penicellate, fruit a semiglobose capsule with 8 lateral ribs (Figs. 3C, 4D), apically with a conspicuous border, brownish, (2–)3(–4) mm high, 3.5 mm broad above, 2–3 mm diameter, opening between the two pistils to release seeds, seeds reddish, elongated, with pointed apices, 0.7–1 mm long, 0.2 mm thick.

Habitat:—This species is restricted to cloud forest ("selva mediana perennifolia" according to Miranda & Hernández X. (1963), "bosque mesófilo de montaña" according to Rzedowski (1978)) with permanent high humidity, up to 5000 mm rainfall, and high nubosity, on strong to moderate slopes of different geological substrates, metamorphic and sedimentary rocks. It occurs mainly on northeast-facing slopes, where the trade winds strike, in conserved places or on disturbed localities near water streams.

Distribution:—*Hydrangea albostellata* is characterized by a wide geographical and altitudinal distribution. In Mexico it occurs in the north and northeast of the state of Chiapas, wherever the required habitat is present, between 1200 and 2300 m above sea level. Interestingly, all recent collections are located between 1800 and 1900 m altitude. Furthermore, this species has been collected in Honduras, El Salvador, Nicaragua and Costa Rica. It is not known from South America.

FIGURE 2. Field pictures. A–B, *Hydrangea albostellata*, C–D, *Hydrangea steyermarkii* (*M.S. Samain et al. 2012-010*). A. Branch with one mature green inflorescence with old male flowers and inflorescence axes with the basal lignified parts of inflorescences of previous years (*M.S. Samain et al. 2012-005*). B. Abaxial leaf side with dense pubescence consisting of whitish stellate hairs, note the typical spoon-shape and broadly revolute margin (*M.S. Samain & E. Martínez S. 2012-090*). C. Young branch, many-ribbed, with typical brownish-reddish cortex which contracts and forms corchy patches. D. Abaxial side of young leaf with whitish stellate indument, the leaf surface typically red-brown, the margin crenate with the marked bright green glandular teeth.

Phenology:—In Mexico, this species has been observed flowering from September to January and fruiting in January only. In Central America, plants seems to flower and fruit throughout the year.

Etymology:—This species can be easily distinguished from all other Mexican and Central American species because of the stellate white pubescence on leaves and inflorescence branches (Figs. 2B, 4E). These stellate hairs are partially caducous, which sometimes results in less notoriously pubescent leaves in dried specimens.

Observations:—*Hydrangea albostellata* has a larger distribution area than the majority of other species of section *Cornidia*. This is the only species of southeastern Mexico which had been collected by Dennis Breedlove and his collaborators from the California Academy of Sciences in the framework of the project Flora of Chiapas (Breedlove, 1986). Nearly all Mexican and Central American collections listed among the additional specimens here studied had been identified on the specimen labels as *H. steyermarkii*. Three of the five specimens mentioned as *H. steyermarkii* in the Flora Mesoamericana (Christenhusz 2009) in fact belong to *H. albostellata*. See Table 1 for a summary of differentiating characters between both species.

The different duplicates of *Breedlove 29829* (see additional specimens examined for details) are functionally female or male, with one specimen (CAS) being mixed. It is highly doubtful that they belong to one and the same individual; leaves of functionally male branches of this collection are narrower and smaller than those of functionally female branches.This is congruent with the 1994 notes on the CAS specimen of Elizabeth McClintock, who worked in the same institute as Breedlove.

As can be seen from the description, the enlarged marginal flowers are not sterile as has been generally assumed, but which we already questioned earlier (Samain *et al.* 2010). The description of the marginal flower in this case is from a functionally female plant. The functionally male plants we observed did not have enlarged marginal flowers, showing the intraspecific variability of the presence or absence of this structure in this species, in contrast to e.g. *H. seemannii* from northern Mexico and *H. asterolasia* in Costa Rica and northern South America, which always have whitish marginal flowers. Interestingly, we have also observed one enlarged marginal flower in a functionally female plant of *H. nebulicola* in the Mexican state of Veracruz (*M.S. Samain & E. Martinez S. 2011-215*), whereas this was not documented for the functionally male plants in the original description by Nevling & Gómez-Pompa (1968).

TABLE 1. Comparison of differentiating characters of *H. albostellata* and *H. steyermarkii*.

	H. albostellata	*H. steyermarkii*
Bark main stem	dark brown, with lenticels	dark brown to black, with reddish lenticels
Runner shoots	reddish, with small kataphylls	dark brown, fibrous, with small leaves
Lamina	lanceolate-obovate to elliptic, slightly undulate, spoon-shaped	lanceolate-obovate
Leaf margin	smooth	crenate with marked glandular teeth, especially notorious in leaves of young branches and of stolons
Leaf base	cuneate	cuneate to slightly rounded, sometimes slightly asymmetric
Leaf apex	apiculate	acute to acuminate
Number of leaf veins	6 to 9	8 to 9
Venation adaxial leaf side	only slightly visible midvein	secondary veins end in the glandular teeth, tertiary veins protruding, forming areole
Venation abaxial leaf side	veins protruding	primary and secondary veins protruding in young leaves, sunken in mature leaves, tertiary veins well defined in young leaves, invisible in mature leaves
Indument adaxial leaf side	glabrous with few simple, short, white hairs along the basal half of the midvein; young leaves densely pubescent	glabrous
Indument abaxial leaf side	abaxially densely white pubescent, especially in young stage	sparsely whitish pubescent on midvein to pubescent allover; densely pubescent in young leaves
Leaf colour	opaque whitish-green; young leaves slightly reddish	shiny dark green; young leaves red-brown, but glands green
Acarodomatia abaxial leaf side	absent	present
Number of leaf pairs above the node where the uppermost inflorescences originate	maximum 2 leaf pairs (or kataphylls only)	up to four
Indument inflorescence axis	densely pubescent with adnate, whitish, stellate hairs	reddish stellate hairs
Number of leaf pairs on the inflorescence axis below the inflorescence	2–5	2
Inflorescence type	umbellate	corymbous
Enlarged marginal fertile flowers	sometimes present	always absent
Calyx reduced flowers	triangular, very small, sometimes nearly invisible	triangular with rounded apex
Corolla reduced flowers	membranous, margin revolute	coriaceous, smooth adaxially and abaxially
Distribution	relatively widespread, known from SE Mexico to Costa Rica	currently known only from the Volcano Tacaná on the border of Mexico and Guatemala

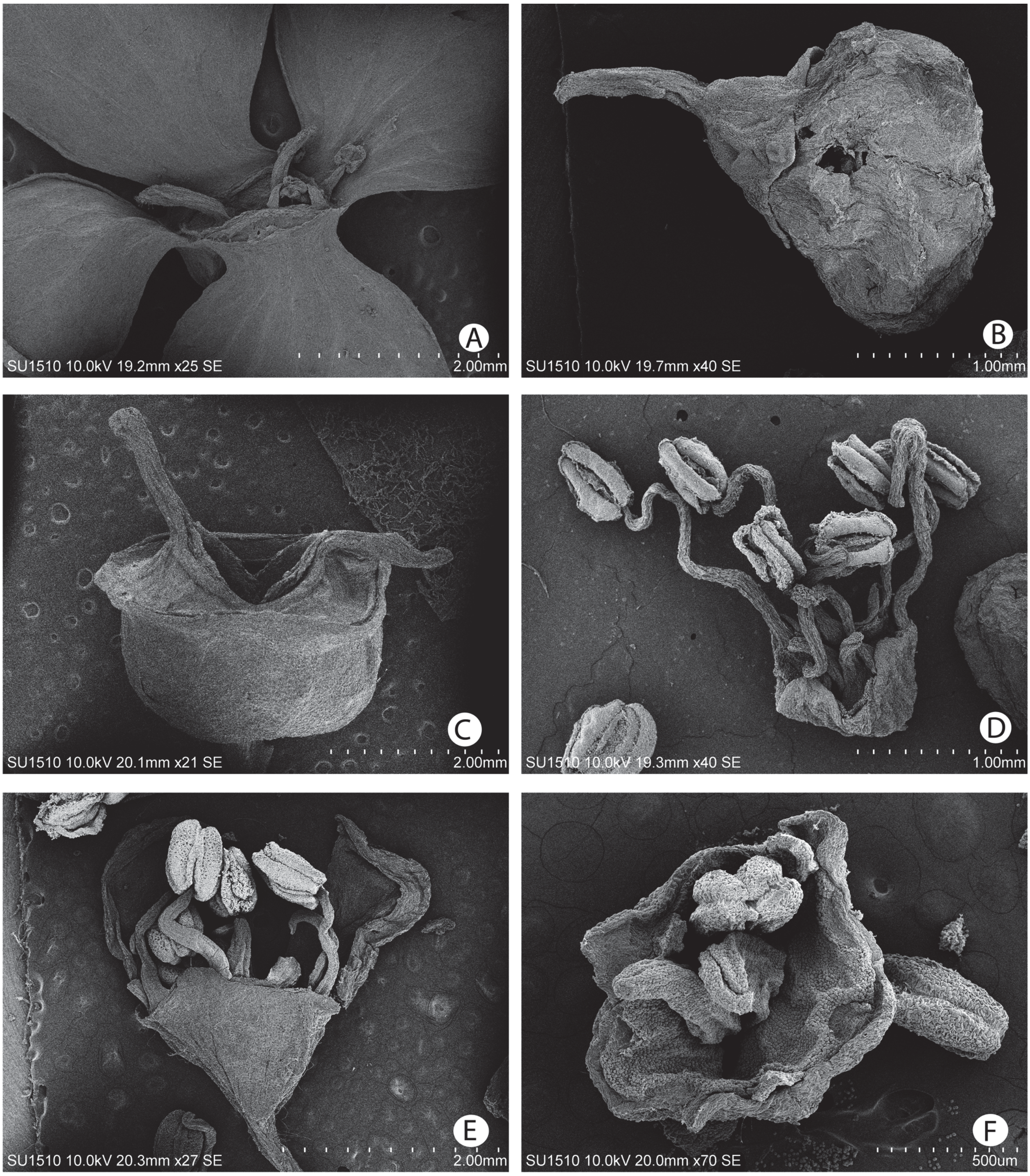

FIGURE 3. SEM pictures of flowers of *Hydrangea albostellata* (A–D; A, C, *M.S. Samain et al. 2012-023*. B, D–E: *M.S. Samain & E. Martínez S. 2012-088*) and *Hydrangea steyermarkii* (E–F, *M.S. Samain et al. 2012-078*). A. Central parts of marginal female flower, with two large pistils and 3 small stamens visible. B. Flower bud of male flower; note the campanulate hypanthium and the valvate petals. C. Mature fruit opened between the pistils to release the seeds. D. Male flower; note the extreme difference in size between the long stamens and the diminute pistils. E. Lateral view of male flower. F. Apical view of male flower.

The specimen *Breedlove 24174* from Solosuchiapa, Chiapas (CAS) belongs to an unidentified species of the family Malpighiaceae, of which juvenile forms have been confused with *Hydrangea* also in other countries than Mexico, e.g. *Salick & Stijfhoorn 8265* (MO!) from Boca de Sábalo, Nicaragua. Nevertheless, even in very young stages, they can be easily distinguished from each other, as leaves of *Hydrangea* are coriaceous with a dentate to serrate margin, whereas leaves of Malpighiaceae are membranous with a smooth margin. In addition, the specimen from Nicaragua occurs at a very low altitude (± 45 m asl), whereas to our knowledge none of the *Hydrangea* species in Mesoamerica occurs below 900 m above sea level.

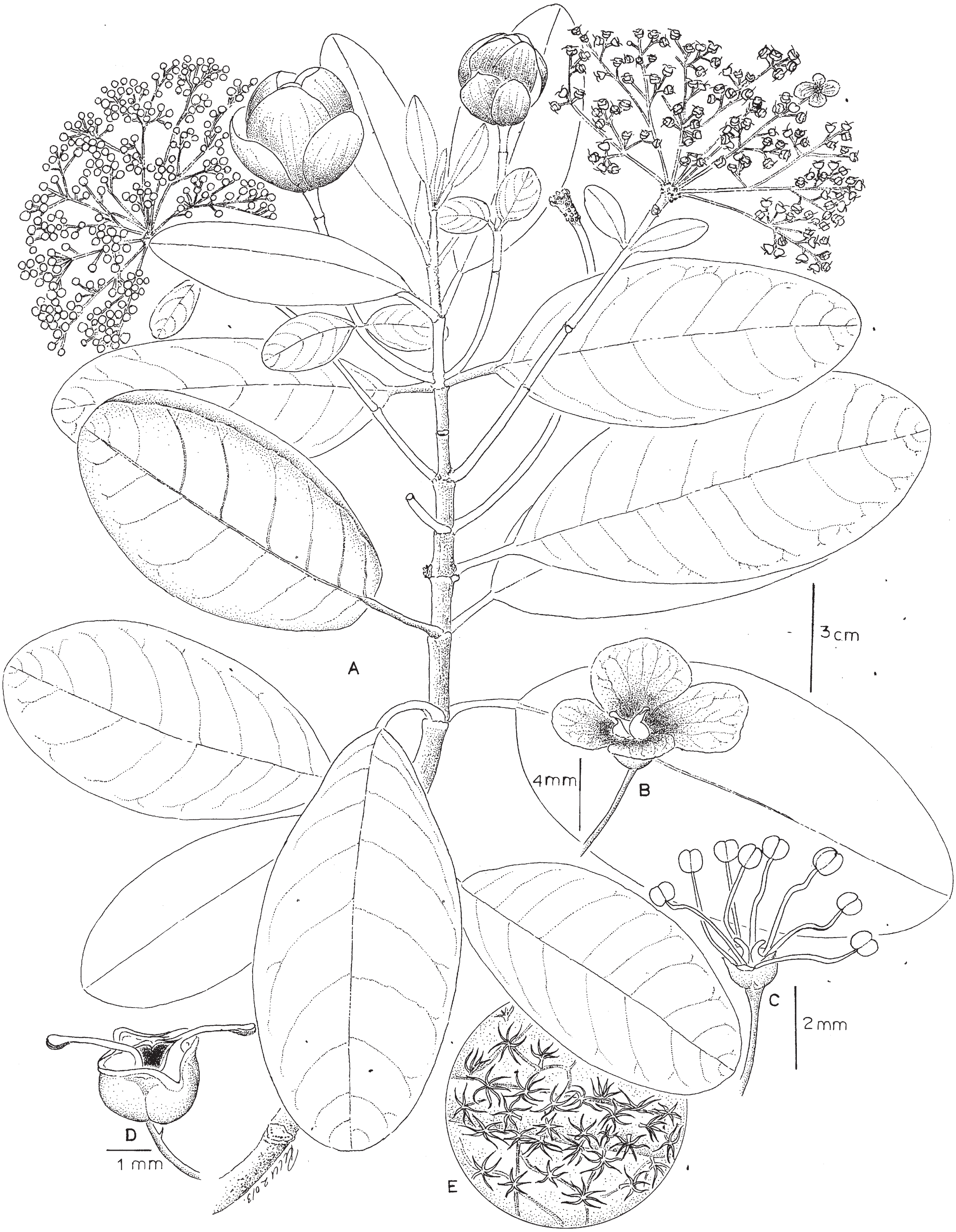

FIGURE 4. *Hydrangea albostellata*. A. Habitus of branch with inflorescences in different developmental stages (inflorescence buds, inflorescence with flower buds and infructescence). B. Enlarged marginal flower with two pistils with fertile stigmas. C. Functionally male flower with 8 fertile stamens and 2 reduced pistils. D. Maturing capsule, fertile stigmas still visible, seeds are released through the opening between the 2 pistils. E. Detail of abaxial leaf surface with stellate indument. Drawn by Ramiro Cruz Durán from the holotype *M.S. Samain et al. 2012-023* (MEXU; A, B), and from the specimens *M.S. Samain et al. 2012-021* (MEXU; A, D, E) and *M.S. Samain & E. Martínez S. 2012-088* (MEXU; C).

The basal lignified parts of inflorescences and the inflorescence axes of previous years are only visible in robust well-collected specimens, e.g. *M.S. Samain & E. Martínez S. 2012-088, 2012-090* (Fig. 2A).

Enlarged marginal flowers are sometimes present, e.g. *M.S. Samain et al. 2012-021, 2012-023*.

Additional specimens examined:—COSTA RICA. Alajuela: San Ramón, R. B. Monteverde, Cordillera de Tilarán, bosque primario en la Fila Cerros Centinela, 10°17'55"N, 84°47'23"W, 1600 m, 6 June 1994, *J.F. Morales 3366 & G. Carnevalli* (INB!) [functionally male]. Cartago: Cartago, al lado del camino Copatchi–San Rafaël Arriba, en la fila del cerro, 9°49'35.34"N, 84°2'3.93"W, 1890 m, 27 July 2012, *M.S. Samain & E. Martínez S. 2012-033* (CR!, GENT!, INB!, MEXU!) [dry inflorescences]; loc. cit., 1781 m, 9°49'34.81"N, 84°2'9.27"W, 16 January 2013, *M.S. Samain & E. Martínez S. 2013-002* (GENT!, INB!) [dry inflorescences]. Guanacaste: Tilarán, al lado del camino de Santa Elena al Mirador Lodge, 1.01 km desde la desviación hacia la Reserva Bosque Nuboso Santa Elena, 10°21'10.11"N, 84°48'6.81"W, 1592 m, 31 July 2012, *M.S. Samain & E. Martínez S. 2012-049* (CR!, GENT!, INB!, MEXU!) [inflorescence buds]; San Gerardo Abajo, Río Caño Negro, Fincas Quesada y Arce, 10°18'40"N, 84°50'2"W, 1100–1200 m, 05 December 1991, *E. Bello 4286 & E. Cruz* (CR!, INB!, MO!) [functionally female, fruits]. Puntarenas: Puntarenas, Ojo de Agua, Monteverde, Finca Méndez, Río Aranjuez, 10°17', 84°46', 1550 m, 14 November 1987, *W. Haber 7728 & E. Bello* (CR!) [functionally female, fruits]; Monteverde, Pacific slope above Quebrada Máquina, 10°18'N, 84°48'W, 1400 m, 26 September 1991, *W. Haber 10885* (CR!, INB!, MO!) [flower buds]; Monteverde, Quebrada Máquina upstream from Hotel Belmar, 10°18'N, 84°48'W, 1400 m, 17 December 1991, *W. Haber 10935 & W. Zuchowski* (CR!, MO!) [functionally female, fruits]; upper San Luis River Valley on Pacific slope below Monteverde, 10°20'N, 84°50'W, 1300–1400 m, 26 August 1986, *W.A. Haber ex E. Bello C., A. Clagget & M. Powell 5398* (INB!) [functionally male]; San Luis, Monteverde, camino a Veracruz, 10°16'35"N, 84°47'45"W, 1040–1060 m, 16 October 1992, *A. Fernández 438* (INB!) [flower buds]; R.B. Monteverde, Cordillera de Tilarán, San Luis, Finca Juan Ramón Fuentes, Buen Amigo, 10°16'33"N, 84°47'45"W, 1220 m, 10 December 1993, *Z. Fuentes 445 & E. Fuentes* (CR!, INB!) [functionally male]; R.B. Monteverde, Cordillera de Tilarán, San Luis de Monteverde, bosque en la cuenca de San Luis, 10°16'33"N, 84°47'45"W, 1100 m, 15 August 1993, *K. Taylor 112* (CR!, INB!, MO!) [inflorescence buds]; Monteverde Reserve, high peaks near TV towers, 10°20'N, 84°50'W, 1775 m, 11 October 1985, *W.A. Haber ex E. Bello 3070* (CR!, MO!; label on MO specimen only mentions *E. Bello 3070*) [functionally male]. San José, Escazú, ZP Cerros de Escazú, Cuenca del Tárcoles, San Antonio, Bebedero, Cercanías de las antenas, La Ventolera, a orilla del camino, 9°53'27"N, 84°9'22"W, 1784–1800 m, 10 September 2005, *D. Santamaria 3001 & R. Aguilar* (INB!) [inflorescence buds]. HONDURAS. Lempira: alrededor de el Río Naranjo y bajo el Campamento Don Tómas. Parque Nacional de Celaque, 14°33'N, 88°40'W, 2000 m, 27 May 1991, *P. House 996* (CAS!, EAP, HEH, MO!, TEFH) [functionally female, fruits]; loc. cit., 13 November 1991, *P. House 1105* (EAP, HEH, MEXU!, MO(2)!, TEFH) [functionally male]. Yoro: Río Pijol Valley, 7 km south east of Nueva Esperanza, along forested Quebrada that flows into Río Pijol, adjacent slopes, and coffee finca above, 15°12'N, 87°35'W, 1300–1500 m, 30 May 1993, *R.L. Liesner 26699* (MO) [functionally female, fruits]. EL SALVADOR. Volcán de San Salvador, 1000–1800 m, 7 April 1922, *P.C. Standley 22966* (US(2)!) [juvenile]. MEXICO. Chiapas: La Trinitaria, 4 km east of Laguna Tsiskaw [Tziscao] near Dos Lagos, 1300 m, 19 October 1974, *D.E. Breedlove 38792* (CAS!, DUKE!, MO!, NY!) [functionally male]; loc. cit., between Lago Tziscao and Dos Lagos, Lagos de Montebello National Park, 1372 m, 13 October 1981, *D.E. Breedlove 53460* (CAS!, MO!) [functionally male]; slopes east of Laguna Tzikaw [Tziscao], Monte Bello National Park, 1300 m, 23 January 1973, *D.E. Breedlove 32250 & A.R. Smith* (CAS!) [functionally female, mature fruits]; Rayón, steep slope in the Selva Negra 10 km above Rayón Mezcalapa along road to Jitotol, 1700 m, 25 November 1972, *D.E. Breedlove 29829 & R.L. Dressler* (CAS! Mixed functionally male and female) , DUKE! [294758-♂, 294765-♀], MEXU! ♀ (immature fruits), MICH! ♂, MO! [3884984-♂, 3884985-♀], US! ♀ (flowers (buds) + immature fruits) [different duplicates are functionally female or male]; loc. cit., 9 miles northwest of Pueblo Nuevo Solistahuacan along road between Rincon Chamula and Rayón, 5800 feet, September 1971, *R.F. Thorne & E. Lathrop 41591-A* (CAS!) [inflorescence buds]; Tenejapa, Paraje Shohleh, 8400 feet, 12 January 1966, *A. Shilom Ton 573* (MO!) [functionally female, immature fruits]; La Independencia, third ridge along road from Las Margaritas to Campo Alegre, 2300 m, 5 November 1984, *D.E. Breedlove 62118* (CAS!) [functionally male]; loc. cit., 5 November 1984, D.E. Breedlove 62117 (CAS!, MICH!) [functionally female, flowers + immature fruits]; Jitotol, about 12 km north of Jitotol along a side road to an oil well, 2000 m, 28 September 1971, *D.E. Breedlove 19944* (CAS!) [juvenile]; Pueblo Nuevo Solistahuacan, along the road Pueblo Nuevo Solistahuacan–Rayón, 17°12'40.88"N, 92°57'49.71"W, 1848 m, 19 January 2012, *M.S. Samain et al. 2012-*

022 (CHIP!, GENT!, IEB!, MEXU!) [functionally female, young fruits]; loc. cit., 17°12'40.55"N, 92°57'48.53"W, 1850 m, 19 January 2012, *M.S. Samain et al. 2012-024* (CHIP!, GENT!, MEXU!) [fallen bracts only]; Arroyo Grande–Pueblo Nuevo Solistahuacan, 17°10'53.64"N, 92°52'34.94"W, 1878 m, 19 January 2012, *M.S. Samain et al. 2012-021* (CHIP!, GENT!, IEB!, MEXU!) [functionally female, immature fruits]; loc. cit., 9 September 2012, *M.S. Samain & E. Martínez S. 2012-089* (CHIP!, GENT!, IEB!, MEXU!) [functionally female]; Tapalapa, camino Coapilla–Ocotepec, near Río Quachi, 17°11'35.91"N, 93°7'51.81"W, 1862 m, 3 January 2012, *M.S. Samain et al. 2012-005* (CHIP!, CR!, GENT!, GUAT!, IEB!, MEXU!, MO!, UAMIZ!, US!) [functionally male]; loc. cit., 9 September 2012, *M.S. Samain & E. Martínez S. 2012-090* (CHIP!, GENT!, IEB!, MEXU!) [functionally male]; loc. cit., 17°11' 36.37"N, 93°7'56.74"W, 1736 m, 3 January 2012, *M.S. Samain et al. 2012-006* (CHIP!, GENT!, IEB!, MEXU!, QMEX!) [functionally female, mature fruits]; Yajalón, La Ventana, 17°9'59.17"N, 92°23'50.90"W, 1843 m, 6 September 2012, *M.S. Samain et al. 2012-085* (CHIP!, GENT!, MEXU!) [sterile depauperated individual]; loc. cit., 17°9'24.36"N, 92°22'42.01"W, 1823 m, 6 September 2012, *M.S. Samain et al. 2012-088* (CHIP!, GENT!, MEXU!) [functionally male]; Tapalapa, Cerro de la Bandera, 17°12'37.41"N, 93°5'49.94"W, 1937 m, 19 August 2011, *M.S. Samain et al. 2011-201* (CHIP!, GENT!, MEXU!) (juvenile). NICARAGUA: Matagalpa, Cordillera Central of Nicaragua between Aranjuez and Peor es Nada, 1500 m, 1 November 1968, *A. Molina R. 22965* (MO!) [functionally male]; Mountain El Arenal, road to Aranjuez, 1300 m, 7 January 1977, *A. Molina R. 31589* (MO!) [functionally male]. Jinotega, road between Jinotega and Matagalpa, La Galia, 1600 m, 6 December 1958, *J.G. Hawkes, J.P. Hjerting & R.N. Lester 2183* (K!) [juvenile].

Conservation:—According to the criteria and categories of IUCN (2012), *H. albostellata* should be considered as endangered, but the current intrinsic threats of its habitat will soon drive it to be critically endangered, especially as a consequence of habitat destruction. The population in the municipality of La Trinitaria is probably extinct as a consequence of fires during the El Niño in 1997 and 1998. It had not rained since October 1997 for 8 months, when in May 1998 fires allover the state of Chiapas destroyed 250,000 hectares of primary forest (Martínez, 2003). The annual precipitation in La Trinitaria then averaged 5000 mm, with daily rains, so it is even quite probable that all plants died before the fires, as was observed in the region of the Chimalapas in eastern Chiapas and in western Oaxaca (Silvia Salas, pers. comm.). The population in the municipality of La Independencia could not yet be found, but it is highly probably that some individuals still survive in the remaining patches of primary cloud forest. The population in the municipality of Pueblo Nuevo Solistahuacan has been detected and seems viable, despite the fact that many mature individuals grow in primary forest areas near the roads. During our exploring expeditions, new populations have been discovered in the municipalities of Tapalapa and Yajalón, both in local reserves, guaranteeing their survival for at least some time. Taking into consideration its current extensive but fragmented distribution area, it was probably once a relatively common species in humid cloud forest from southeastern Mexico to Costa Rica.

Hydrangea steyermarkii **Standl., amended description, Figs. 2, 3, 5**

TYPE:—GUATEMALA. San Marcos: Along Quebrada Canjulá, between Sibinal and Canjulá, Volcán de Tacaná, 2200–2500 m, 18 February 1940, *J.A. Steyermark 36044* (F!, GH! (photo)) [functionally female, immature fruits].

Root-climbing liana of up to 30 m high, functionally dioecious. Main stem clinging to the host tree with many large adventitious roots, up to 12 cm diameter, bark dark brown to black, with reddish lenticels. Runner shoots (stolons) dark brown, fibrous, with adventitious roots and stellate hairs, with small leaves. Branches many-ribbed, with reddish pubescence and adventitious roots, cortex brownish-reddish, contracting, forming corchy patches (Fig. 2C), notorious line between petioles of opposite leaves. Petiole sulcate adaxially, terete abaxially, reddish pubescent, sparsely pubescent with short hairs in young stage, glabrous in mature stage, 1.5–3 cm long, leaving a semicircular scar on the branch when leaves fall. Leaves decussate, lanceolate-obovate, base cuneate to slightly rounded, sometimes slightly asymmetric, 10–18 cm long, 4.5–6 cm broad, apex acute to acuminate, leaf margin crenate with marked glandular teeth, especially notorious in leaves of young branches and of stolons, venation brochidodromous, veins 8–9, adaxial leaf side with protruding tertiary veins forming areole, secondary veins end in the glandular teeth, abaxially with protruding primary and secondary veins in young leaves, sunken in mature leaves, tertiary veins well defined in young leaves, invisible in mature leaves, glabrous, abaxial leaf side sparsely whitish pubescent on midvein to pubescent allover the surface, with whitish stellate adnate hairs, shiny dark green, young leaves red-brown, but glands green, with whitish indument (Fig. 2D), all veins reddish-brownish, acarodomatia form cavities between midvein and primary veins, sometimes even in between primary and secondary veins. Inflorescence axis with reddish stellate hairs, 7 cm long, with two small decussate leaf pairs below the inflorescence, petiole 1 cm long, lamina 2–3.5 cm long, apex of the floral axis not visible, inflorescence bracts rapidly deciduous, decussate, about 8, of different sizes, consecutively and rapidly caducous during inflorescence development, with whitish to reddish, adnate, stellate hairs, including margin, inflorescences lateral, opposite, two per flowering branch which continues growing vegetatively during inflorescence development, with up to four leaf pairs above the node where the inflorescences originate in the axil of a leaf pair with reduced petiole (0.6–1.5 cm) and without lamina, these 'leaves' caducous, only present at the base of inflorescence buds, leaving a scar at the base of mature inflorescences, corymbous, 5 cm diameter, 2–3 cm high, with 5–6 partial inflorescences (corymbs) which on their turn again consist of several corymbs, secondary and tertiary inflorescence axes with reddish stellate hairs. Flower pedicel 0.8–2 mm long, receptacle campanulate in functionally male flowers, broadly semiglobose in functionally female flowers, 2 mm long, ovary inferior, calyx lobes 4, triangular with rounded apex, 1 mm long, petals 4, white, valvate, cucullate, coriaceous, smooth adaxially and abaxially, 1.2–2 mm long, 1,2 mm broad, functionally male flowers (Figs. 3 D, E, F, 5 B): hypanthium 2–2.5 mm diameter, stamens (6–)8(–9), well-developed, filaments 1.5–2 mm long, anthers 0.7–0.8 mm long, 0.5 mm broad, pistils 2, reduced, 1–1.2 mm long, remnants of ovules present, functionally female flowers (Fig. 5 C): stamens in the only available female specimen shriveled as this specimen has only nearly mature fruits, pistils 2, not seen in fertile stage, enlarging up to 3–4 mm in mature fruits, stigmas apically clavate and shortly penicellate, fruit a broadly semiglobose capsule, lateral ribs cannot be distinguished because of the shriveled state of the fruits, dark brown, 3–4 mm high, 4–5 mm broad above, 3–4 mm diameter, opening between the two pistils to release seeds, seeds not seen.

Habitat:—Very deep valleys in cloud forest ("selva mediana perennifolia" according to Miranda & Hernández X., 1963, "bosque mesófilo de montaña" according to Rzedowski, 1978) dominated by *Hedyosmum mexicanum*. This species gets easily established in primary forest on very steep slopes in ravines where there are recurrent disturbances as a consequence of very strong winds which cause treefall. This species occurs in conserved localities, as well as on disturbed places with very strong succession dynamics, protected from the humid winds from the south, on igneous rocks, with approximately 3000 mm rainfall.

Distribution:—South-facing slopes of the volcano Tacaná in México and Guatemala, between 2200 and 3000 m.

Phenology:—This species has been observed flowering in September and fruiting in February.

Observations:—The population on the Mexican side of the volcano Tacaná near the village of Chiquihuite, 5–6 km in straight line from the type locality, is the first record of this species in Mexico. Interestingly, the type specimen belongs to a functionally female individual, whereas our collection is a male specimen. Despite extensive explorations on the Mexican side of the volcano Tacaná, it has not been possible to encounter a female specimen. In contrast to the description, which mentions as habit a climbing epiphytic shrub ('*frutex scandens epiphyticus*'; Standley 1940: 233), this species is a root-climbing liana.

Standley (1940), in the description of *H. steyermarkii*, mentions a dense reddish pubescence for the branches ('*quoque pilis stellatis brunnescentibus laxe tomentosis*'). Nevertheless, this reddish 'indument' is a mixture of young adventitious roots and penicellate, stellate hairs. In contrast, the indument on the lamina is whitish on the type specimen and all other studied collections.

The marginal vein is closer to the leaf margin than in *H. albostellata*. The apex of the leaves on the terminal branch of *M.S. Samain et al. 2012-009* and *M.S. Samain et al. 2012-010*) is acuminate.

The majority of the available herbarium specimens of Guatemala, Honduras, El Salvador and Nicaragua as well as a few collections of Costa Rica bear the identification of *H. steyermarkii*. However, only the specimens mentioned below coincide with the type of this species and nearly all other specimens belong to *H. albostellata*.

The number of stamens in the observed functionally female flowers is variable although the average number is 8 with 6 large stamens and 2 smaller stamens. When there are only 6 stamens, they are all of the same size.

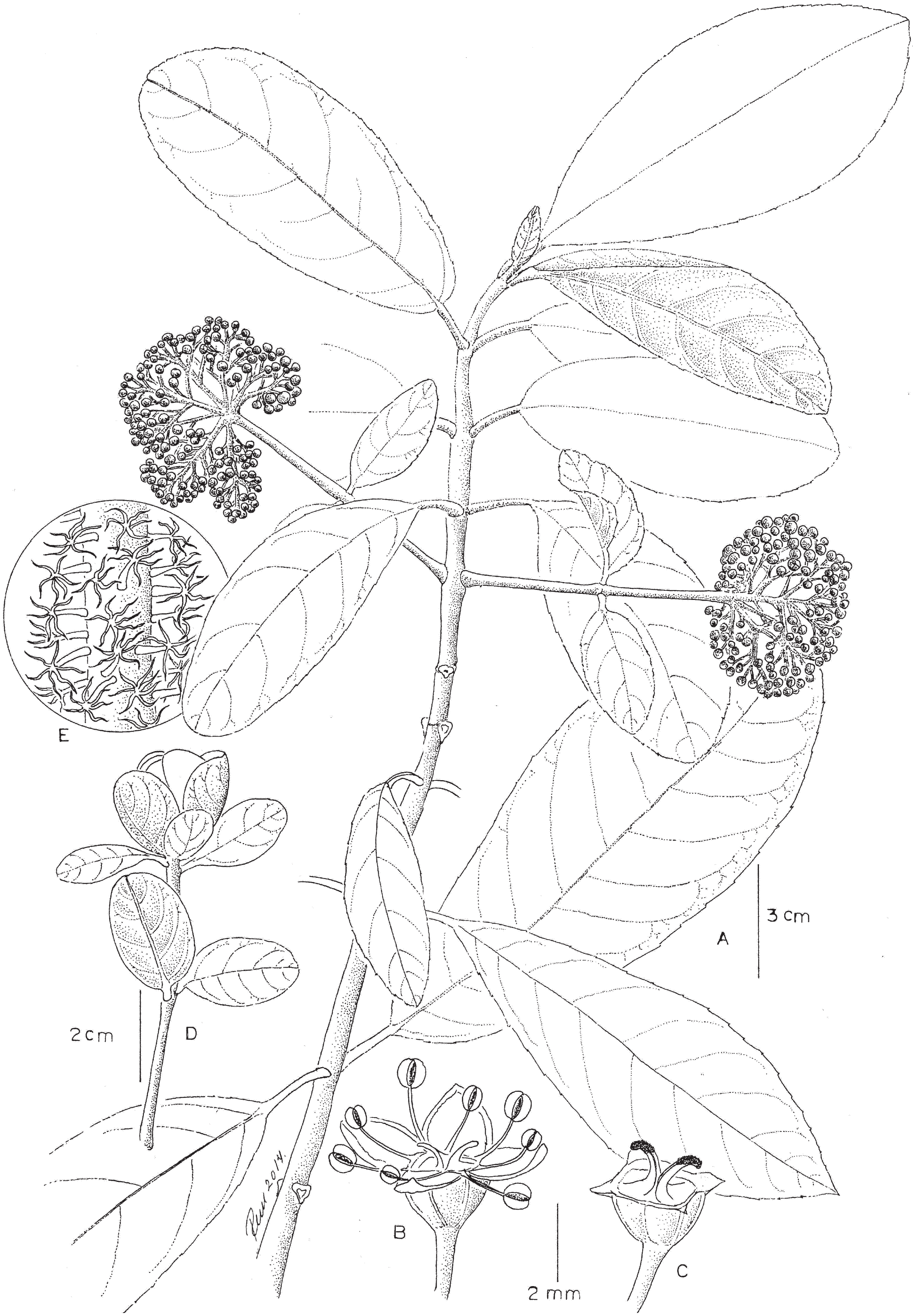

FIGURE 5. *Hydrangea steyermarkii*. A. Habitus of branch with inflorescences. B. Functionally male flower with 8 fertile stamens and 2 reduced pistils. C. Maturing capsule, fertile stigmas still visible, seeds are released through the opening between the 2 pistils. D. Inflorescence branch with inflorescence bud, inflorescence bracts and leaf pair visible. E. Detail of inflorescence branch with stellate indument. Drawn by Ramiro Cruz Durán from the specimen *M.S. Samain et al. 2012-078* (MEXU; A, B, D, E), and from the holotype *J.A. Steyermark 36044* (F; C).

Additional specimens examined:—GUATEMALA. San Marcos: Río Vega, near San Rafael and Guatemala-Mexico boundary, Volcán de Tacaná, 2500–3000 m, *J.A. Steyermark 36250* (F) [sterile]; between Canjulá and La Unión Juárez, near southeast portion of Volcán de Tacaná, 2000–3000 m, slopes of Río Tonaná, *J.A. Steyermark 36411* (F) [sterile]; El Progreso: between Finca Piamonte and top of Montaña Piamonte, along Joya Pacayal, 2500–3000 m, *J.A. Steyermark 43635* (US!); Quezaltenango: western slopes of Volcán Zunil, opposite Santa María de Jesús, 1500 m, 21 January 1940, *J.A. Steyermark 35109* (GH! (photo of F specimen)); Huehuetenango, Cerro Huitz, between Barillas and Mimanhuitz, Sierra de los Cuchumatanes, 1600–2600 m, 14 July 1942, *J.A. Steyermark 48536* (US!) [sterile]; wet cloud forest at Cruz de Limón, between San Mateo Ixtatán and Nucá, Sierra de los Cuchumatanes; 2600–3000 m, 31 July 1942, *J.A. Steyermark 49826* (US!) [sterile]. MEXICO. Chiapas: Cacahoatán, Volcan Tacaná, Chiquihuite, 15°6'23.07"N, 92°6'9.13"W, 2362 m, 3 September 2012, *M.S. Samain et al. 2012-078* (CHIP!, GENT!, MEXU!) [functionally male]; loc. cit., 15°6'24.83"N, 92°6'4.25"W, 2476 m, 4 January 2012, *M.S. Samain et al. 2012-008* (GENT!, MEXU!) [sterile]; loc. cit., 15°6'25.1"N, 92°6'4.11"W, 2481 m, 4 January 2012, *M.S. Samain et al. 2012-009* (GENT!, MEXU!) [sterile]; loc. cit., 15°6'23.23"N, 92°6'7.26"W, 2426 m, 4 January 2012, *M.S. Samain et al. 2012-010* (GENT!, MEXU!) [sterile]; loc. cit., 15°6'22.28"N, 92°6'11.11"W, 2423 m, 5 January 2012, *M.S. Samain et al. 2012-011* (GENT!, MEXU!) [sterile], *M.S. Samain et al. 2012-012* (GENT!, MEXU!) [sterile].

Conservation:—Critically Endangered; known from one population with adult flowering and juvenile runner shoots on the Volcano Tacaná on the border of Mexico and Guatemala, and five sterile, mostly juvenile collections by Julian Steyermark from Guatemala, none of them recent. Monitoring of remaining populations in Guatemala would be important for evaluation of the conservation status of *H. steyermarkii* in that country. On the Mexican side of the volcano ascending from the village of Chiquihuite, several flowering individuals have been observed, although only one functionally male individual could be sampled up to now, as a consequence of the quite inaccessible extremely steep slopes. There are many runner shoots on this locality, showing that this population most probably reproduces vegetatively. This area is located at approximately 5–6 km in straight line from the type locality on the Guatemalan side which could not yet be visited. The Mexican (sub)population is suffering as a consequence of habitat destruction and land use change, such as floriculture of *Zantedeschia aethiopica* ('alcatraz') and *Hydrangea macrophylla* cultivars.

Discussion

Hydrangea *section* Cornidia *in Mexico*

Two endemic species of *Hydrangea* section *Cornidia* were known up to now for Mexico, not taking into account the erroneous identifications mentioned above: *Hydrangea seemannii* L. Riley (1924: 207) from temperate coniferous forests in the northern states of Chihuahua, Durango, Nayarit, Sinaloa and Sonora, and *Hydrangea nebulicola* Nevling & Gómez Pompa (1968: 231) from cloud forests and oak-*Liquidambar* Linnaeus (1753b: 999) forests in the states of Querétaro and Veracruz, central and eastern Mexico respectively (Nevling & Gómez-Pompa 1968, Durán-Espinosa 1999, Pérez-Calix 2004). The current contribution doubles the number of *Cornidia* species for Mexico, although it does not alter the number of endemic species. *Hydrangea steyermarkii* Standl. is a new record for the country. The majority of the specimens of *H. albostellata* have been collected in Mexico. In contrast to Central and South American *Cornidia* species (south of Nicaragua) where both species with whitish-greenish-yellowish or reddish-purple flowers occur, all currently known Mexican species have whitish flowers.

Up to now, only one Mexican *Hydrangea* species, *H. nebulicola*, has been considered as threatened or endangered since more than 35 years in one of the first ever contributions on plant extinction (Vovides & Gómez-Pompa, 1976). Later on, the species was listed by the Mexican authorities as endangered in 1994 (NORMA Oficial Mexicana NOM-059-ECOL-1994) and as threatened with extinction since 2001 (NOM-059-SEMARNAT-2001 (SEMARNAT, 2002) and NOM-059-SEMARNAT-2010 (SEMARNAT, 2010). A Red List of *Hydrangea sensu stricto* (see Samain *et al.* 2010) worldwide is in preparation in cooperation with Botanic Gardens Conservation International, based on our field observations throughout their distribution area.

Circumscription of Hydrangea steyermarkii *and growth form of* Cornidia *species*

Hydrangea steyermarkii has been confused with *Hydrangea albostellata* and even with a repent Malpighiaceae species from tropical rainforest. From our ongoing revision in *Cornidia*, it is obvious that the confusion around species circumscriptions especially originated as a consequence of the annotations of McClintock on most herbarium specimens, which have been used as the basis for the majority of subsequent floristic contributions (e.g. Christenhusz 2009). Two additional factors that have led to this confusion are the fragmentary Latin description of *H. steyermarkii* and the availability of only one (functionally female) flowering type specimen.

During our field work focussed on *Hydrangea* throughout the Neotropics, it has become clear that observation of living plants throughout the distribution area of each species is essential to understand the full range of intra- and interspecific variation in this clade. Obviously, a herbarium specimen can only grasp a fraction of the characters of plants measuring up to 40 m high, generally flowering just below or above the host tree canopy. This size hampers not only the collection of complete flowering structures, but also correct observation of growth form.

Indeed, previous studies and notes on herbarium specimen labels of the Neotropical Hydrangeas often mention a shrubby or epiphytic form (e.g. Standley 1940, Christenhusz 2009). However, our field observations without any exception show root climbing and lianous individuals rooting near the base of its host tree. Nevertheless, in some cases the apical portion of the plant, protruding above the canopy of its host tree, or rarely above the rock wall on which the plant grows, does show affinities to a "shrubby" growth form (Granados Mendoza *et al.*, unpublished data). We consider the root climbing growth form as potential synapomorphy for *Hydrangea* section *Cornidia*. However, taking into account this character within the whole genus *Hydrangea* sensu lato (see Samain *et al.* 2010), it is potentially apomorphic considering that several Asian species of *Hydrangea* section *Hydrangea* (e.g. *H. anomala* D. Don (1825: 211)) and of the satellite genera of the tribe Hydrangeeae (e.g. *Pileostegia* J.D. Hooker & Thomson (1858: 57) also are root climbers (see also Nevling 1964).

Sexual dimorphism in Hydrangea *section* Cornidia

McClintock (1957) proposed the hypothesis that *Cornidia* species might be dimorphic, showing specimens either with undeveloped anthers or undeveloped styles. This hypothesis has been taken over by Nevling & Gómez-Pompa (1968) who suggest such specimens to be respectively female and male plants, as in their description of *Hydrangea nebulicola* Nevl. & Gómez-Pompa from the state of Veracruz, Mexico. Freire-Fierro (2004) in the Flora of Ecuador also mentions functional dioecism for *Cornidia* species *H. peruviana* Moric. ex A.P. de Candolle (1830: 14) , *H. preslii* Briquet (1919: 409), *H. jelskii* Szyszyłowicz (1895: 218) and *H. tarapotensis* Briquet (1919: 415). In the early nineties of the twentieth century, McClintock also has made new annotations on a large amount of specimens of this group, not only changing identifications (without any further explanation), but also with more detailed observation on this dimorphism. To our knowledge, these new insights have not been published anywhere. During our extensive field work throughout the Neotropics, we have observed sexual dimorphism, although never as extreme as suggested by McClintock (1957), because both anthers and styles are always present, but either androecium or gynoecium is less developed and smaller than the other structure. In some species the stamens of functionally female flowers are shed relatively rapidly; this might lead to the erroneous observation that stamens are absent. Hence, our observations rather suggest functional dimorphism as observed by Freire-Fierro (2004), although further studies to investigate this in detail are needed. As can be seen from figures 3 C, 4 D and 5 C, and the descriptions above, functionally female flowers have a semiglobose receptacle which often enlarges during seed development, large pistils with a penicillate stigma and anthers with short filaments with very small, rudimentary anthers without pollen. The pistils also increase in size during seed development. In contrast, functionally male flowers are characterized by a campanulate hypanthium, stamens with remarkably long filaments and globose tetrasporangiate anthers full of pollen, and small pistils without receptive surface (see figures 3 F, 4 C and 5 B). We have observed a few intermediate examples, although not in the species discussed above.

Consequences of sexual dimorphism for taxonomy and conservation

The often remarkable different size in receptacle between functionally female and male flowers has caused some authors to consider both forms as representatives of different species and other authors to synonymize species or to rank them as subspecies or varieties. In contrast, Nevling & Gómez-Pompa (1968) in their publication of *H. nebulicola* describe the existence of functional unisexual flowers, although they merely encountered functionally male plants. They mention a similar case for *H. oerstedii* Briquet (1919: 407) and *H. peruviana* based on McClintock's (1957) identification key. *Hydrangea oerstedii* has been considered as a variety of *H. peruviana* by Freire-Fierro (2004: 34), and more recently has been synonymized with *H. peruviana* by Christenhusz (2009). However, like McClintock's (1957) revision, these contributions oversimplify the enormous morphological variation in *Hydrangea* s.s. and it seems that the two taxa mentioned above belong to a group with many different morphospecies distributed in Central and South America.

The presence of this sexual dimorphism, the lack of insight in its ecology and evolution and the overall gap in knowledge about the biology of this group challenge our ongoing conservation work of these species in Mexico and other Latin American countries. In their recent review of sexual dimorphism in flowering plants, Barret & Hough (2013) discuss niche differences and spatial segregation of female and male plants, which we also have observed in *Cornidia*. Additionally, Vamosi & Vamosi (2005) mention that tropical dioecious woody plants might be more prone to extinction. Nevertheless, vegetative reproduction seems to be the rule in the majority of the *Cornidia* localities, and despite the massive seed production, we rarely observe juvenile plants, even not in large populations. In contrast, it is quite common to observe stolons, or runner shoots according to Nevling & Gómez-Pompa (1968), on the forest floor between several host trees. It is generally impossible to follow these runner shoots, but as already noted by these authors for *H. nebulicola* in the Mexican state of Veracruz, one individual might climb several trees. As a consequence, it is not evident to define individual plants versus populations.

Although the two species described above as well other species we are studying might be locally relatively abundant, they are restricted to the higher or even highest elevations in their respective distribution areas in cloud forest. The pristine habitat with very specific topographical conditions and the mycorrhiza (own observations) they require make them not only promising bio-indicators for this kind of habitat, but also highly endangered as these forests become rarer by the day, because they are highly appreciated by local people for agriculture and cattle. Additionally, logging for appreciated woods is also frequent in these habitats. However, the most dramatic cause that might bring several of these long-lived species to extinction in the near future is the current and future predicted climate change which is driving cloud forest species in eastern and southern Mexico towards upward migration to higher elevation (Rojas-Soto *et al.* 2012).

To conclude, although in recent years our knowledge of the morphology, biology and evolution of this group based on wild-collected plants has increased, much additional research in various disciplines is needed to build the basis for saving some of these botanical “Lonesome Georges” from extinction.

Acknowledgements

We are very grateful to the Mohammed Bin Zayed Species Conservation Fund (project number 11251854) and Rita Carron (Gent, Belgium) for financial support of our *Hydrangea* conservation work and research in Mexico. We thank the Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT; permit number SGPA/DGGFS/712/3804/10) for permission to collect material; Francisco Javier Jiménez González, Regional Director Frontera Sur, Istmo y Pacifico Sur of the Comisión Nacional de Áreas Naturales Protegidas (CONANP), for permission to collect within Natural Protected Areas as well as the local CONANP staff members for help with logistics and support in the field; the staff of the Herbario Nacional de México of the Universidad Nacional Autónoma de México and of the herbarium CHIP, Dirección de Botánica Dr. Faustino Miranda in Tuxtla Gutiérrez, Chiapas for support with field and herbarium work; the curators of the herbaria CAS, CR, DUKE, EAP, F, GENT, HEH, INB, MEXU, MICH, MO, NY, TEFH and US for permission to study material, the numerous local people in each area for assistance with field work and logistics; and Sara Oldfield, Secretary-General of Botanic Gardens Conservation International (Kew, UK) for her invaluable support. Ramiro Cruz Durán (Facultad de Ciencias, Universidad Nacional Autónoma de México), María Berenit Mendoza Garfias (Laboratorio de microscopía electrónica y fotografía de la biodiversidad (I), Instituto de Biología, Universidad Nacional Autónoma de México) and Edgar Aguilar are greatly acknowledged for the fast work on the splendid drawings, the SEM pictures, and the compilation of the figures, respectively.

References

Barret, S.C.H. & Hough, J. (2013) Sexual dimorphism in flowering plants. *Journal of Experimental Botany* 64: 67–82. http://dx.doi.org/10.1093/jxb/ers308

Breedlove, D.E. (1986) *Listados florísticos de México. IV Flora de Chiapas.* Instituto de Biología, Universidad Nacional Autónoma de México, Distrito Federal, Mexico, 246 pp.

Briquet, J.I. (1919) Saxifragaceae. *Annuaire Conservatoire et Jardin Botanique de Genève* 20: 393–421.

Christenhusz, M.J.M. (2009) Hydrangeaceae. *In*: Davidse, G., Sousa, M. & Knapp, S. (eds.). *Flora Mesoamericana* 3(2). Universidad Nacional Autónoma de México, Ciudad Universitaria, México D.F., pp. 1–9.

de Candolle, A.P. (1830) Saxifragaceae. *Prodromus systematis naturalis regni vegetabilis* 4. Treuttel & Würts, Paris, pp. 1–54. http://dx.doi.org/10.5962/bhl.title.286

Don, D. (1825) *Prodromus Florae Nepalensis*. J. Gale, London, xii + 256 pp. http://dx.doi.org/10.5962/bhl.title.86

Durán-Espinosa, C. (1999) Hydrangeaceae. In: Sosa, V. (ed.), *Flora de Veracruz* 109. Instituto de Ecología, A.C., Xalapa, Veracruz, Mexico & University of California, Riverside, CA, pp. 1–22.

Engler, A. (1891) Saxifragaceae. *In*: Engler, A. & Prantl, K. (eds.), *Die natürlichen Pflanzenfamilien* III(2a). W. Engelmann, Leipzig, pp. 41–93. http://dx.doi.org/10.5962/bhl.title.4635

Freire-Fierro, A. (2004) Hydrangeaceae. *In*: Harling, G. & Andersson, L. (eds) *Flora of Ecuador* 73. Botanical Institute, Göteborg University, Sweden, pp. 25–40.

Granados Mendoza, C., Wanke, S., Salomo, K., Goetghebeur, P. & Samain, M.S. (2013a) First application of the phylogenetic informativeness method to chloroplast markers: A test case of closely related species in tribe Hydrangeeae (Hydrangeaceae). *Molecular Phylogenetics and Evolution* 66: 233–242. http://dx.doi.org/10.1016/j.ympev.2012.09.029

Granados Mendoza, C., Wanke, S., Goetghebeur, P. & Samain, M.S. (2013b) Facilitating wide hybridization in Hortensia cultivars: a phylogenetic and marker-assisted approach. *Molecular Breeding* 32: 233–239. http://dx.doi.org/10.1007/s11032-012-9822-8

Hooker, J.D. & Thomson, T. (1858) Precursores ad Floram Indicam: being Sketches of the Natural Families of Indian Plants, with Remarks on their Distribution, Structure and Affinities. *Journal of the Linnean Society*, *Botany* 2: 1–29 and 57–103. http://dx.doi.org/10.1111/j.1095-8339.1857.tb02465.x

Instituto Nacional de Ecología (1994) *NORMA Oficial Mexicana NOM-059-ECOL-1994, que determina las especies y subespecies de flora y fauna silvestres terrestres y acuáticas en peligro de extinción, amenazadas, raras y las sujetas a protección especial, y que establece especificaciones para su protección*. Diario Oficial de la Federación. 28 April 1994. Segunda Sección. pp. 1–66.

IUCN (2012) *IUCN Red List Categories and Criteria*: Version 3.1. Second edition. Gland, Switzerland and Cambridge, UK: IUCN. iv + 32pp.

Linnaeus, C. (1753a) *Species Plantarum* 1. Imprensis Laurentii Salvii, Holmiae, Sweden, pp. 1–560. http://dx.doi.org/10.5962/bhl.title.669

Linnaeus, C. (1753b) *Species Plantarum* 2. Imprensis Laurentii Salvii, Holmiae, Sweden, pp. 561–1200. http://dx.doi.org/10.5962/bhl.title.669

Martínez, E. (2003) *Comunidad Lacandona. La Deforestación en 24 regiones PRODERS*. Comisión Nacional de Áreas Naturales Protegidas, SEMARNAT, México, pp. 52–61.

Matsumura, J. & Hayata, B. (1906) Enumeratio Plantarum in Insula Formosa sponte crescentium hucusque rite cognitarum adjectis descriptionibus et figuris Specierum pro regione novarum. *The Journal of the College of Science, Imperial University of Tokyo, Japan* 22: 1–702.

McClintock, E. (1957) A monograph of the genus *Hydrangea*. *Proceedings of the California Academy of Sciences* 29: 147–256.

Miranda, F. & Hernández X., E. (1963) Los tipos de vegetación de México y su clasificación. *Boletín de la Sociedad Botánica de México* 28:29–179.

Nevling, L.I. Jr. (1964) Climbing Hydrangeas and their relatives. *Arnoldia* 24: 17–39.

Nevling, L.I. Jr. & Gómez-Pompa, A. (1968) A new *Hydrangea* of Mexico. *Journal of the Arnold Arboretum* 49: 225–232.

Pérez-Calix, E. (2004) Hydrangeaceae. *In*: Rzedowski Rotter, J. & Calderón de Rzedowski, G. (eds.), *Flora del Bajío y de Regiones Adyacentes* 126. Instituto de Ecología A.C., Centro Regional del Bajío, Pátzcuaro, Michoacán, pp. 1–15.

Riley, L.A.M. (1924) Contributions to the flora of Sinaloa. *Bulletin of Miscellaneous Information Kew* 1924 5: 206–222. http://dx.doi.org/10.2307/4111748

Rojas-Soto, O.R., Sosa, V. & Ornelas J.F. (2012) Forecasting cloud forest in eastern and southern Mexico: conservation insights under future climate change scenarios. *Biodiversity and Conservation* 21: 2671–2690. http://dx.doi.org/10.1007/s10531-012-0327-x

Ruiz, H. & Pavón, J. (1794) *Florae Peruvianae et Chilensis Prodromus.* Sancha, Madrid, xxii + 154 pp. + xxxvi lam.

Rzedowski, J. (1978) *La vegetación de México*. Limusa, Distrito Federal, Mexico, 432 pp.

Samain, M.S., Wanke, S. & Goetghebeur, P. (2010) Unraveling extensive paraphyly in the genus *Hydrangea* s.l. with implications for the systematics of tribe Hydrangeeae. *Systematic Botany* 35: 593–600. http://dx.doi.org/10.1600/036364410792495827

SEMARNAT (2002) *Norma Oficial Mexicana NOM-059-SEMARNAT-2001, Protección ambiental-Especies nativas de México de flora y fauna silvestres-Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio-Lista de especies en riesgo*. Diario Oficial de la Federación. 6 March 2002. Segunda Sección, pp. 1–153.

SEMARNAT (2010) *Norma Oficial Mexicana NOM-059-SEMARNAT-2010, Protección ambiental-Especies nativas de México* *de flora y fauna silvestres-Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio-Lista de especies en riesgo*. Diario Oficial de la Federación. 30 December 2010. Segunda Sección, pp. 1–77.

Standley, P.C. (1940) Studies of Central American plants-I, Saxifragaceae. *Publications of the Field Museum of Natural History, Botanical Series* 22(4): 233–234.

Szyszyłowicz, I. von (1895) Diagnoses plantarum novarum a Cl. D. Const. Jelski in Peruvia lectarum. Pars prima. Rozprawy Akademii Umiejetnosci: Wydzial Matematyczno-Przyrodniczy 29: 215-239.

Vovides, A.P. & Gómez-Pompa, A. (1976) The problems of threatened and endangered plant species of Mexico. pp. 77–88. *In*: Prance, G.T. & Elias, T.S. (eds.). *Extinction is Forever: The Status of Threatened and Endangered Plants of the Americas.* The New York Botanical Garden, New York, 437 pp.

Vamosi, J.C. & Vamosi, S.M. (2005) Present day risk of extinction may exacerbate the lower species richness of dioecious clades. *Diversity and Distributions* 11: 25–32.
http://dx.doi.org/10.1111/j.1366-9516.2005.00119.x

Wei, W. & Bartholomew, B. (2001) *Hydrangea*. In: Zhengyi, W. & Raven, P.H. (eds.) *Flora of China* 8. Missouri Botanical Garden Press, St. Louis and Science Press, Beijing, pp. 411–422.