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EDITORIAL

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PhytoKeys at 100: progress in sustainability, innovation, and speed to enhance publication in plant systematics

W. John Kress[1], Sandra Knapp[2], Pavel Stoev[3,4], Lyubomir Penev[4,5]

1 *National Museum of Natural History, Smithsonian Institution, Washington DC, USA* **2** *Department of Life Sciences, The Natural History Museum, London, United Kingdom* **3** *National Museum of Natural History, Bulgarian Academy of Sciences, Sofia, Bulgaria* **4** *Pensoft Publishers, Sofia, Bulgaria* **5** *Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Sofia, Bulgaria*

Corresponding author: *Lyubomir Penev* (info@pensoft.net)

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Eight years have passed since the launch of PhytoKeys (Penev et al. 2010) – Pensoft's flagship journal in plant systematics – and six years from our last editorial commemorating the second year of its existence (Kress et al. 2012). Today we are publishing the journal's 100th issue! There is no better occasion to look back and consider the development and most significant achievements of PhytoKeys.

In a very short time period after its inception, PhytoKeys became one of the most popular and appreciated Open Access journals in botany. The journal started with only 48 submissions in 2011; by 2017 that number quadrupled to 187 manuscripts submitted annually (Table 1, Fig. 1). The number of published articles has grown as well, from 39 in 2011 to 112 in 2016, while the number of published pages increased from 75 in 2010 to 3141 in 2016. To date the journal has received in total 759 submissions and published 532 articles, of which 21 are full monographs. The average acceptance rate for the period 2011–2017 was 70%, which we believe is optimal and sustainable for a taxonomic journal.

The journal indexes all nomenclatural changes and additions in the International Plant Names Index (IPNI) (Penev et al. 2010, 2016). In all, one new tribe, 26 new genera or subgenera, and 439 new species or infraspecies have been de-

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Table 1. Total number of submitted manuscripts, published articles, and printed pages since 2010.

Year	Submitted manuscripts	Published articles	Published pages
2010	9	5	75
2011	48	39	397
2012	56	54	1042
2013	57	52	1494
2014	66	46	1342
2015	113	72	2035
2016	153	112	3141
2017	187	98	1973
2018*	70	54	1097
Total	**759**	**532**	**12569**

* Until 1.6.2018.

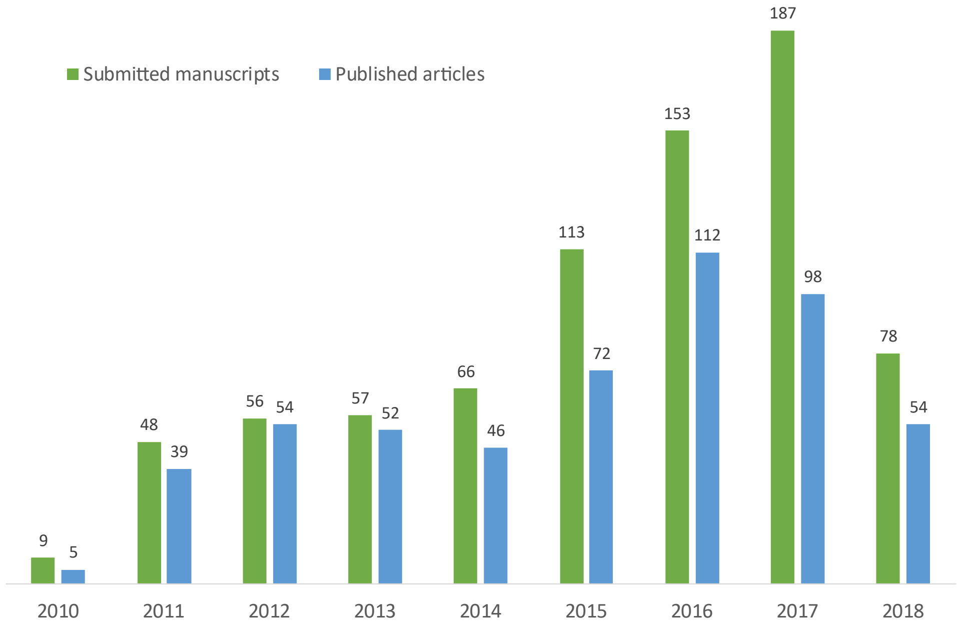

Figure 1. Growth of submitted manuscripts and published articles in PhytoKeys from 2010 to 2018 (until 1.6.2018).

scribed in the journal since its launch; this equates to 466 new taxa in total. In addition to new taxa, more than 400 new combinations, replacement names, new status designations, and other nomenclatural acts have been proposed in the journal since we began.

Over the years PhytoKeys has attracted a diverse range of botanical researchers from all parts of the world, with the highest numbers coming from the United States of America (193), Brazil (93), China (80), United Kingdom (53) and Germany (49).

Table 2. Total number of PhytoKeys authors per country.

Country	N	Country	N	Country	N
United States of America	193	Philippines	8	Taiwan	2
Brazil	93	Austria	7	Tanzania	2
China	80	Peru	7	Ireland	2
United Kingdom	53	Slovakia	6	Norway	2
Germany	49	Portugal	6	Mauritius	2
Belgium	39	Czech Republic	6	French Polynesia	2
Turkey	33	Ecuador	5	Hong Kong	1
Australia	27	Denmark	5	French Guyana	1
India	25	Sweden	5	Gabon	1
Netherlands	24	Poland	5	Ukraine	1
Spain	23	Korea, South	5	Uganda	1
France	22	Colombia	4	Cuba	1
Japan	19	Switzerland	4	Uruguay	1
New Zealand	17	Panama	4	Nepal	1
Vietnam	17	Paraguay	3	Lao PDR	1
South Africa	16	Cameroon	3	Uzbekistan	1
Thailand	14	Finland	3	Cambodia	1
Argentina	13	Myanmar	3	Kyrgyzstan	1
Canada	12	Papua New Guinea	3	Kenya	1
Mexico	12	Bulgaria	3	Hungary	1
Russia	10	Singapore	3	Costa Rica	1
Italy	10	Venezuela	3		
Malaysia	8	Chile	2		

Altogether 939 scientists from 67 countries have published in the journal from its launch until 1 June 2018 (Table 2).

In 2015 PhytoKeys was granted its first impact factor of 0.68, and it has gradually increased in the subsequent two years and reached 1.11 in 2017. The increase can be best explained by the stringent peer review of content, improved quality control, and manuscript management. In 2014 the journal was also accepted for coverage by Scopus. In December 2016 Scopus announced the introduction of CiteScore – a new journal level metrics. Currently for 2017, the Cite Score value of PhytoKeys is 1.08.

Along with our overall editorial improvements and advancements, a number of new technological solutions and features have been implemented in PhytoKeys in order to facilitate the efforts of editors, reviewers and authors (see Table 3).

PhytoKeys content is integrated with a significant number of global indexers and archives, such as PubMedCentral, CLOCKSS, Google Scholar, CAB Abstracts, DOAJ, Vifabio, BHL Citebank, to name just a few. In the two years from 2015 to 2017 Pensoft journals have been integrated with a number of global archives and data repositories that significantly increase visibility and searchability of published content. All journals operating on Pensoft's innovative platform ARPHA, including PhytoKeys,

Table 3. New technological solutions implemented in the journal.

Feature	For the benefit of	Link	Use
Automatic registrations of reviews at Publons	Reviewers and Editors	https://publons.com	Publons helps reviewers and editors get recognition of every review they make for the journal.
Dimensions	Authors, editors, administrators, publisher	https://www.dimensions.ai	Powerful tracker of citations; provides ranking of given research in a given field
Scopus CiteScore Metrics	Authors, editors, administrators, publisher	https://www.scopus.com/sourceid/19700201507	Interactive tool providing information on journal's performance
Export of published figures & supplementary materials to Biodiversity Literature Repository at ZENODO	Authors, data scientists, community in general	https://zenodo.org/communities/biosyslit/?page=1&size=20	Increases visibility and traceability of article and sub-article elements
Hypothes.is	Authors, readers	http://hypothes.is	Annotations on selected texts from the published article

have benefited from these developments. The list of the online libraries and databases which harvest and manage PhytoKeys content includes:

- Library of Congress (USA)
- CNKI (China)
- CINIPIEC (China)
- eLibrary (Russia)
- ORCID (International)
- Dryad Data Repository (International)
- Open Citations Corpus (International)

Since 2016 PhytoKeys has been using Altmetric – a technology providing article level metrics which enables authors to track the online shares and discussions of their published articles. Figure 2 demonstrates the combined results of the social media presence of PhytoKeys articles on Altmetric. The graph clearly shows an increase in the presence and visibility of the published content in social media and popular outlets since September 2016.

Pensoft continues to invest in the popularization of PhytoKeys via media campaigns. Some examples of press releases on articles published in the journal that grasped the attention of journalists and received large media coverage are listed in Table 4. Altogether the top ten articles with the highest number of unique views on PhytoKeys site have received 147,865 views. Four species described in PhytoKeys – the flowering tree named as a new genus *Sirdavidia solannona,* the dragon tree *Dracaena kaweesakii*, the orchid *Telipogon diabolicus* and the bush tomato from northwestern Australia, *Solanum ossicruentum* made it to the top 10 new species nominated by the State Univer-

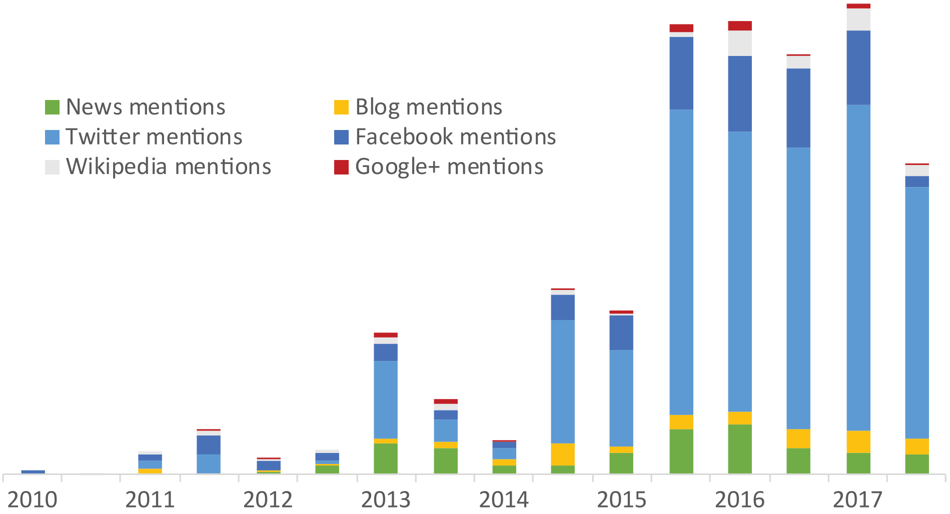

Figure 2. Total number of PhytoKeys mentions in social media and popular magazines.

sity of New York College of Environmental Science's International Institute for Species Exploration (IISE) (Deutsche Welle, Daily Mail, Publico, CoolEarth, EurekAlert!).

Over the eight years of the existence of PhytoKeys, the journal has positioned itself among the world's leading journals in systematic botany. Started by the editors primarily as a taxonomically-oriented journal, the journal has since extended its scope to enable publications across other botanical disciplines, such as plant ecology, genomics, evolutionary biology, paleontology, bioinformatics, ethnobotany, etc.

As the chief editors of PhytoKeys we have worked hard to expand the journal's editorial board, which has grown significantly and today is comprised of more than 80 experts from various scientific disciplines and geographical areas. The journal has achieved an international reputation by publishing milestone works that will affect all botanists, such as the changes to publication requirements made at the XVIII International Botanical Congress in Melbourne (Knapp et al. 2011a, b), the report on the nomenclature section of the 2005 XVII International Botanical Congress, Vienna (Flann et al. 2015) and the Shenzhen Declaration on Plant Sciences endorsed by 7,000 plant scientists from 77 countries at the XIX International Botanical Congress held in Shenzhen, China (Kress and Knapp 2017).

With its continuous technological innovation and support from subject editors and reviewers, PhytoKeys continues to receive recognition by the international community of plant researchers. This success would not have been possible without our authors, reviewers, subject editors, production staff, readers, and supporters, to which we express our sincerest gratitude and thanks! We cannot wait to see what the 200th issue will look like!

Table 4. The top ten PhytoKeys papers that attracted largest media interest.

Article	Press release	Media coverage
Schuette et al. (2018) The hidden *Heuchera*: How science Twitter uncovered a globally imperiled species in Pennsylvania, USA.	Science and Twitter join forces to uncover a globally imperiled plant species	Sverige Radio, Earth.com, PLOS Ecology, IFLScience
Caraballo-Ortiz and Trejo-Torres (2017) Two new endemic tree species from Puerto Rico: *Pisonia horneae* and *Pisonia roqueae* (Nyctaginaceae).	Two Caribbean bird-catcher trees named after 2 women with overlooked botanical works	Der Standard, Mongabay
Diazgranados and Sánchez (2017) *Espeletia praesidentis*, a new species of Espeletiinae (Millerieae, Asteraceae) from northeastern Colombia.	New Colombian plant discovered by Kew scientist honors Colombian president	Express, El Tiempo, La Nacion
Kolanowska et al. (2016) *Telipogon diabolicus* (Orchidaceae, Oncidiinae), a new species from southern Colombia.	Orchid or demon: Flower of a new species of orchid looks like a devil's head	The Washington Post, FOX news, РИА Новости, El Mundo
Martine et al. (2016) New functionally dioecious bush tomato from northwestern Australia, *Solanum ossicruentum*, may utilize "trample burr" dispersal.	Curious new bush species growing 'bleeding' fruits named by a US class of 150 7th graders	Science News, AOL, ABC
Martine et al. (2016) *Solanum watneyi*, a new bush tomato species from the Northern Territory, Australia named for Mark Watney of the book and film "The Martian".	New bush tomato species is the link between botany and an Oscar-nominated Hollywood movie	Live Science, New York Daily News, Huffington Post
Leopardi-Verde et al. (2016) *Encyclia inopinata* (Orchidaceae, Laeliinae) a new species from Mexico.	Serendipitous orchid: An unexpected species discovered in Mexican deciduous forests	Scientific American, National Geographic Indonesia, Газета.ru
Suetsugu and Fukunaga (2016) *Lecanorchis tabugawaensis* (Orchidaceae, Vanilloideae), a new mycoheterotrophic plant from Yakushima Island, Japan.	Plants cheat too: A new species of fungus-parasitizing orchid	Asian Scientist, Nature World News, La Vanguardia
Couvreur TLP, Niangadouma R, Sonké B, Sauquet H (2015) Sirdavidia, an extraordinary new genus of Annonaceae from Gabon. PhytoKeys 46: 1-19.	A rare new plant inspires the first plant genus named after Sir David Attenborough	The Guardian, Los Angeles Times, Discover Magazine
Fernando E, Quimado M, Doronila A (2014) Rinorea niccolifera (Violaceae), a new, nickel-hyperaccumulating species from Luzon Island, Philippines. PhytoKeys 37: 1-13.	New species of metal-eating plant discovered in the Philippines	International Business Times, Russia Today, Asian Scientist

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A taxonomic revision of *Curarea* Barneby & Krukoff (Menispermaceae)

Rosa del C. Ortiz[1]

1 *Missouri Botanical Garden, 4344 Shaw Blvd., St. Louis, Missouri 63110, USA*

Corresponding author: *Rosa del C. Ortiz* (rosa.ortiz-gentry@mobot.org)

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Abstract

A monograph of *Curarea*, a neotropical genus in the plant family Menispermaceae, is presented. *Curarea* is distinguished from related genera by the combination of staminate flowers with sepals in two whorls and pistillate flowers with three petals, three carpels and usually elongated carpophores bearing three sessile drupelets. Nine species are recognised, amongst them two new to science, *C. gentryana* from Ecuador and *C. barnebyana*, from Ecuador and Peru. Additionally, two new combinations, *C. iquitana* and *C. tomentocarpa*, are proposed for distinct taxa recovered in a multivariate analysis of quantitative characters of the broadly distributed and morphologically variable *C. toxicofera*. The anatomy and morphology of species in the genus is documented, identification key, species descriptions, distribution maps and a preliminary conservation assessment for all accepted species are also provided. Of the nine species recognised here, *C. barnebyana* is assigned a preliminary status of Vulnerable, *C. crassa* (known only from the coastal Atlantic Forest in Brazil) and *C. gentryana* (endemic to western Ecuador) are both assigned a preliminary status of Endangered.

Keywords

Arrow poison, curare, dioecious liana, neotropical clade, Ranunculales

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Introduction

Curarea Barneby & Krukoff of the plant family Menispermaceae, tribe Tiliacoreae, is a genus of understory or canopy dioecious lianas that are widely distributed in the humid forests of tropical America, mostly at low elevation from eastern Brazil to Costa Rica in Central America. Within Tiliacoreae, *Curarea* shares with remaining members of the tribe endocarps ornamented by longitudinal ribs, seeds hippocrepiform and without endosperm and fleshy cotyledons (Ortiz et al. 2016). *Curarea* was segregated from *Chondrodendron* Ruiz & Pav. to include species that differed in several floral and carpological features (Barneby and Krukoff 1971). In *Curarea*, the calyx of staminate flowers is composed of two whorls of three, scarcely fleshy and greenish sepals, these being variously described as sepaloid scales (Barneby and Krukoff 1971: 7) or as sepals (Barneby 1996). In *Chondrodendron*, the calyx is formed by four or more whorls of three, membranous sepals that are cream coloured and, hence, described as petaloid sepals (Barneby and Krukoff 1971: 7). Staminate flowers of both genera have 6 petals that are membranous and much shorter than the innermost sepals (Table 1). Pistillate flowers of *Curarea* have only 3 petals and 3 carpels, whilst those of *Chondrodendron* have 6 petals and 6 carpels. The drupelets of both genera have narrow supportive structures, but in *Curarea*, these are elongate carpophores that bear atop sessile fruits, while in *Chondrodendron* the fruits are conspicuously stipitate (Table 1). The distinct nature of *Curarea* is also supported in a family-wide phylogenetic analysis of chloroplast markers (Ortiz et al. 2016), where it is recovered as monophyletic and sister to *Sciadotenia* Miers, in a neotropical clade that also includes *Chondrodendron* (Fig. 1A; Ortiz et al. 2016). Within this neotropical clade, *Curarea* shares with *Sciadotenia* sessile drupelets borne on narrow elongated carpophores bearing six carpels in *Sciadotenia* and only three in *Curarea*. The two whorls of sepals in the staminate flowers distinguish *Curarea* from *Chondrodendron* and *Sciadotenia*, both of which have 3–7 whorls of sepals.

When first described, *Curarea* included four species: *C. candicans*, *C. cuatrecasasii*, *C. tecunarum* and *C. toxicofera*, with *C. toxicofera* designated as the type species of the genus (Barneby and Krukoff 1971). While *C. cuatrecasasii* and *C. tecunarum* were newly described, both *C. candicans* and *C. toxicofera* were transferred from *Chondrodendron*. Another species was later added to the original four with the recognition of *C. crassa*, an endemic new species from the Brazilian Atlantic Forest (Barneby 1996). Although the etymology of the generic epithet was never provided, the name *Curarea* doubtlessly refers to curare, the South American arrow-poison for which species of *Curarea* provide one of the ingredients.

In this first treatment of *Curarea* (Barneby and Krukoff 1971), which was also the most comprehensive one at that time, *C. toxicofera* was broadly interpreted and included entities formerly described as various taxa, rendering it a large complex with unclear patterns of morphological variation. However, subsequent works generally followed that of Barneby and Krukoff (1971) and used the five species they recognised in treatment of local, regional and national floras, e.g. Flora of Surinam (Jansen-Jacobs 1976); Flórula de Las Reservas Biológicas de Iquitos, Perú (Ortiz 1997); Flora of Ecuador (Ott 1997); Flora de Nicaragua (Ortiz 2001), amongst others. Seven species were later recognised in the most recent, taxonomic account of the genus (Ortiz-Gentry 2000) but *Curarea toxicofera* remained broadly circumscribed.

On the basis of shared macro- and micromorphology, Ortiz-Gentry (2000) suggested that there were two species groups in *Curarea*. These were not recovered in a later family-wide molecular study (Ortiz et al. 2016) where it was found that *C. candicans*

Table 1. Main features of *Curarea* and *Chondrodendron*.

Genus	♂ Flowers			♀ Flowers		Drupelets	Carpophore
	Whorls of sepals	Sepal texture	Sepal colour	Petal whorls	Carpel #		
Curarea	2	fleshy	greenish	1	3	sessile	present
Chondrodendron	≥ 4	membranous	yellowish	2	6	stipitate	absent

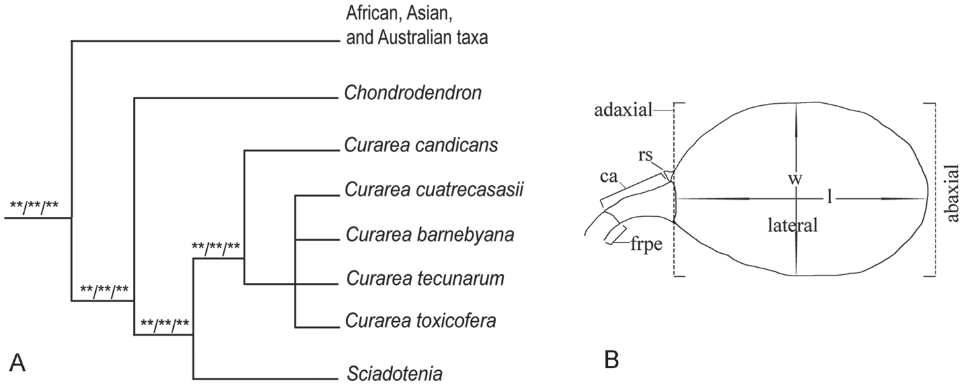

Figure 1. Schematic representation of affinities and drupelet: **A** phylogenetic affinities of *Curarea* and related taxa, modified from Ortiz et al. 2016, three asterisks (***) indicate 100% support in all analyses in the referred study **B** schematic illustration of a *Curarea* drupelet showing the length and width planes measured, ca = carpophore, frpe = fruiting pedicel, rs = remnant of style.

– an outlier in the study of Ortiz-Gentry (2000) – was sister to the remaining species of the genus. Species boundaries in most *Curarea* are relatively well defined with the exception of *C. toxicofera*, which, as mentioned above, has always been broadly defined. For instance, Barneby and Krukoff (1971) treated the three former *Chondrodendron* species [i.e. *Chondrodendron iquitanum* Diels, *C. polyanthum* (Diels) Diels and *C. tomentocarpum* (Rusby) Moldenke] as conspecific with *Curarea toxicofera*. Moreover, the type of *Cocculus toxicoferus* Wedd. is a sterile specimen and, hence, lacks diagnostic features to readily distinguish the species, further complicating the application of this name and circumscription of the taxon, which like most Menispermaceae is also dioecious. To evaluate patterns of morphological variation across the entire range of *Curarea toxicofera*, 200 collections of the taxon were sorted into five groups based on selected features such as relative size of petioles and leaves, lamina shape and indumentum type on its abaxial surface and general features of staminate inflorescence (i.e. slender *vs.* coarser, pedicels and staminate flowers conspicuously larger). These groups of specimens were further evaluated using selected quantitative morphological variables. Based on the outcome of the analyses, three entities are recognised within *C. toxicofera s.l.*, namely *C. toxicofera s.s.*, *C. iquitana* and *C. tomentocarpa*. Two of the five initial groups within *C. toxicofera*, although distinguished by qualitative features, were however not recovered in the multivariate analyses. Future studies that include other lines of evidence, in addition to morphology, might provide insights about their status and specimens associated with these groups are here tentatively placed under the species to which they are morphologically most similar, preceded by the "*aff.*" qualifier.

The present revision furthers that of Ortiz-Gentry (2000) which sought to evaluate the circumscription of species within the genus *Curarea*, using morphological and anatomical characters. In this study, I provide the taxonomic revision of the species recognised in that work and formally describe the new species treated by Ortiz-Gentry (2000), but were not effectively published there (viz. Melbourne Code Article 30.8). Additionally, in this study, I evaluate the taxonomic boundaries of the *C. toxicofera* complex based on multivariate analyses of the morphological variation across its distribution. Nine species are recognised in *Curarea*, of which two are newly described and two new combinations are proposed. Populations, tentatively identified here as *C.* aff. *iquitana* or *C.* aff. *Tomentocarpa,* exhibit complex variations that require additional field work in combination with molecular studies to better clarify their taxonomic boundaries. Of the newly described taxa, *C. barnebyana* occurs in Ecuador and Peru, while *C. gentryana* is endemic to western Ecuador and, in a preliminary assessment, is evaluated as endangered.

Materials and methods

The taxonomic treatment is based upon the examination of 429 herbarium collections from: A, B, BM, BR, ECON, F, G, GH, IAN, INB, K, MG, MO, NY, P, QCNE, R, RB, U, US and USM (acronyms follow Thiers continuously updated). The virtual herbaria of MG (http://marte.museu-goeldi.br/herbario), NY (http://sciweb.nybg.org/VirtualHerbarium.asp), US (http://collections.nmnh.si.edu/search/botany) and JSTOR Global Plants (http://plants.jstor.org) were also consulted. Additional specimens were collected during field trips to Ecuador and Peru. Label information of all specimens studied are available via TROPICOS, the Missouri Botanical Garden (MO) database, as are the images of all specimens housed at MO. Distribution maps were generated using ArcGIS Desktop Release 10 (ESRI Inc., Redlands, CA), a few specimens whose labels did not indicate coordinates, but had detailed locality information were georeferenced *post facto* using gazetteers, these being found within brackets in the selected specimens examined section under their respective species. A complete list of all specimens examined is presented in the Supplementary material that accompanies this article.

Species boundaries in *Curarea* were inferred based on qualitative and quantitative morphological data (available from the author upon request). Measurements were made from dried herbarium material for leaves, inflorescences and fruits. In *Curarea*, as in all Menispermaceae, development of the fruit is unequal, with the abaxial side developing more than the adaxial side such that the style scar ends up near the adaxial base of the fruit (Fig. 1B). Hence, it should be noted that, although measurements of the fruit length and width seem conventional, i.e. the length referring to the distance between the apex and base of the fruit, the actual apex of the fruit is near the base (Fig. 1B) because of the extreme curvature of the fruit in the Menispermoideae. Similar criteria are followed when measuring endocarps; however, the hippocrepiform embryos are measured from one end to the other, along the outer curvature.

The flowers were rehydrated before measurement. A ruler was used to measure leaves and inflorescences, a digital caliper (Digimatic CD-6” CX, Mitutoyo, Japan) was used to measure fruits and endocarps and a dissecting stereoscope (Nikon, Japan) with a micrometric ocular was used to measure flowers. Inflorescence length includes the short peduncle. The two whorls of sepals in both the staminate and pistillate flowers are always conspicuously different in size and sometimes also in shape, hence measurements of both whorls are reported. However, a single measurement is reported for the two whorls of petals and stamens in the staminate flowers, except when noticeable variation in size and shape is present. For each character, two to three measurements per specimen were taken, the ranges of the averages being used when describing the species.

Most *Curarea* species are morphologically distinct, except for the geographically and ecologically widespread *C. toxicofera s.l.* For the latter, I carried out multivariate analyses to evaluate patterns of morphological variation across its entire range. A total of 200 collections were examined and placed in five groups based mostly on variation in general features such as leaf shape and relative size, indumentum type on abaxial leaf surface, the general structure of the staminate inflorescence (i.e. lax or compact), relative staminate flower size and staminate flowers conspicuously pedicellate or subsessile. These five groups, called: **al** = allpahuayo, **iq** = iquitana, **to** = toxicofera, **tm** = tomentocarpa and **uc** = ucayali, below, were further tested by means of a linear discriminant analyses (lda) of selected quantitative data (Table 2) in order to assess the relative importance of the morphological traits in separating the groups (*cf.* Henderson 2005). Of the 200 collections, 73 specimens were staminate, 100 were pistillate and 29 specimens were sterile. To include most of the specimens, only leaves were scored for 197 specimens (Dataset 1), a total of 53 specimens were scored for all characters of leaves + staminate inflorescences + flowers (Dataset 2), 55 for staminate inflorescences + flowers (Dataset 3) and 21 specimens for leaves + fruit characters (Dataset 4). Further, a subset from Dataset 2 was extracted and analysed after removing the toxicofera group, this subset consisted of 27 specimens. All morphological measurements were recorded on an Excel 2010 spreadsheet and log-transformed prior to the analyses. Data analyses were carried out using the package MASS in R ver. 3.1.0 (The R Foundation for Statistical Computing; <http://www.R-project.org>).

A preliminary conservation status assessment for all taxa was carried out according to the IUCN (2012) criteria. Data were analysed using the Geospatial Conservation Assessment Tool, GeoCat (http://geocat.kew.org/) with the default 2 km grid cell.

Features such as wood anatomy, foliar anatomy and leaf venation patterns were also examined. While the few samples per species available for the examination of the characters precluded their inclusion in quantitative analyses, these observations further document interspecific variation in the genus and may provide another line of evidence to distinguish species in *Curarea* when more samples are included.

Table 2. Morphological characters included in multivariate analyses of *Curarea toxicofera* complex.

Organ	Characters (unit)
Leaf	Petiole length (cm)
	Lamina length (cm)
	Lamina width (cm)
Staminate inflorescence	Bract length (mm)
	Main axis length (cm)
	Secondary axis length (cm)
Staminate flowers	Pedicel length (mm)
	Flower length (mm)
	Bracteole length (mm)
	Outer sepal length (mm)
	Outer sepal width (mm)
	Inner sepal length (mm)
	Inner sepal width (mm)
	Outer petal length (mm)
	Outer petal width (mm)
	Inner petal length (mm)
	Inner petal width (mm)
	Outer filament length (mm)
	Outer anther length (mm)
	Inner filament length (mm)
	Inner anther length (mm)
Infructescences and fruits	Infructescence length (cm)
	Infructescence diameter (cm)
	Carpophore length (cm)
	Carpophore diameter (cm)
	Fruit length (cm)
	Fruit width (cm)

For wood anatomy studies, stem samples ca. 1.5 cm diameter were available for *Curarea* aff. *iquitana* (Diels) R. Ortiz [*Ortiz 181* & *186* (MO)], *C. aff. tomentocarpa* (Rusby) R. Ortiz [*Ortiz & Vargas 197* & *199* (MO)] and of about 5–15 cm wide for *C. tecunarum* [*Ortiz* & *Vásquez 214*, *Ortiz et al. 220* (MO), *van der Werff* & *Vásquez 13909* (MO)], whereas only small twigs of about 1 cm in diameter were available for *C. candicans* [*Lanjouw & Lindeman 2779* (U)], *C. cuatrecasasii* [*Aguilar 682*, *Gentry & Hamilton 41126* (MO)] and for *C. barnebyana* R.Ortiz [*Ortiz & Vargas 200* (MO)]. Permanent slides were prepared following standard techniques in wood anatomy studies. Terms are defined and features are described in accordance with the IAWA committee (1989) guidelines. Table 3 show averages based on 10 measurements of randomly selected cells of the individuals examined.

Sample preparations for foliar anatomy and leaf venation patterns followed Keating (2014). Transverse sections of petiole and mid-lamina, including midrib and lamina margin, were taken. For the petiole, both the apical and basal pulvini as well as the

Table 3. Wood anatomy, general features in *Curarea*. * = cambium production unit, *sensu* Jacques & de Franceschi (2007); diam = diameter; rc = ray cells; *crassa*, *gentryana*, *toxicofera* – not studied for wood anatomy.

	barnebyana	***candicans***	***tecunarum***	***cuatrecasasii***	***iquitana***	***tomentocarpa***
	Average (range)	Average (range)	Average (range)	Average (range)	Average (range)	Average (range)
Number of samples	1	1	3	2	2	2
pith diameter (mm)	3.2	3	3.4	2.4	2.2	1.2
fiber cap in pith	strong	moderate	strong	weak	weak	weak
Features of xylem bundles & rays in the first CPU*						
# of xylem bundles	39	51	37	25	28	16
xylem bundle shape	nearly terete	nearly terete	nearly terete	nearly terete	terete to wedged	terete to wedged
xylem bundle width adaxial	220(125–275)	160(75–200)	228(150–325)	242(175–350)	194(100–300)	202(125-275)
xylem bundle width abaxial	323(275–400)	233(175–350)	349(275–450)	442(300–575)	259(150–400)	374(175–525)
ray width adaxial	85(50–100)	105(75–125)	81(50–100)	125(75–175)	114(50–125)	12(50–250)
ray width abaxial	150(100–200)	275(225–325)	136(75–250)	210(100–275)	263(150–400)	619(425–1200)
Vessels						
# of vessels in xylem bundles in first CPU*	13(9–15)	17(11–25)	21(12–34)	31(22–48)	17(10–30)	32(20-49)
tangential diam. of vessel (µm)	118(50–200)	45(25–75)	107(50–200)	99(50–150)	45(25–75)	68(25-125)
element length (µm)	411(330-410)	359(310-400)	373(300-470)	357(260-470)	277(200–380)	301(100-410)
Rays						
height	>1 mm	>1 mm	>1 mm	>1 mm	>1 mm	>1 mm
cellular composition	procumbent & square	procumbent & square	procumbent	procumbent & square	procumbent & square	procumbent & square
Mineral inclusions						
prismatic crystals in pith	abundant	moderate	absent	sparse	abundant	abundant
prismatic crystals in ray cells	abundant	abundant	absent	abundant	abundant	moderate to abundant
druses in pith	sparse	sparse	absent	sparse	absent	moderate to abundant
druses in ray cells	absent	absent	absent	absent	absent	absent
stone cells in pith	sparse	sparse	abundant	sparse	absent	absent
stone cells in ray	sparse	absent	absent	sparse	absent	absent
Other cell inclusions						
tannins	abundant in rc	sparse in pith & rc	moderate in pith & rc	abundant in pith & rc	absent	sparse in pith cells
tyloses	abundant in pith & rc	abundant in pith & rc	abundant in pith & rc	abundant in pith & rc	abundant in pith & rc	abundant in pith & rc

mid-region of the petiole were sectioned. Both fresh and dried leaf samples were used. Fresh field collections were stored in 70% ethanol; dried leaves were first rehydrated in an aqueous solution of Kodak Photo-Flo 200 and stored in 70% ethanol before preparing samples. Observations were made through an Olympus BX40 light microscope at different magnifications. Table 4 summarises the leaf anatomical features and venation patterns observed in *Curarea*.

Table 4. Leaf anatomy general features in *Curarea*. av = average; diam = diameter; TS = transverse section; vb = vascular bundles.

	barnebyana	***candicans***	***crassa***	***tecunarum***	***cuatrecasasii***	***gentryana***	***iquitana***	***tomentocarpa***	***toxicofera***
Number of samples	2	2	1	2	3	1	3	2	2
average diam. of apical pulvinus (mm)	2	2.5	ca. 1	2.8	1.8	1.6	3	1.9	2.3
number of vb. in apical pulvinus	11–12	10	9	11–12	8–9	12	10–13	9–11	11–12
av. diam. in petiole mid-region (mm)	1.5	1.3	0.9	1.8	1.2	1.1	2.1	1.4	1.6
av. blade thickness (μm)	94	116	ca. 110	86	82	ca. 79	74	80	85
av. cuticle + adaxial periclinal cell wall size (μm)	23	24	ca. 21.5	19	14	ca. 16	17	17	19
adaxial epidermis cell shape	squarish, rectangular or irregular	squarish or rectangular	squarish or irregular	squarish or irregular	squarish, rectangular or irregular	squarish, rectangular or irregular	squarish, rectangular or irregular	squarish, rectangular or irregular	squarish or rectangular
tannins	abundant	moderate	moderate	moderate	scarce or absent	scarce or absent	scarce or absent	scarce or absent	absent to moderate
range of stomata number/crypt	17–102	15–32	15–46	36–34	16–27	10–17	12–34	7–30	27–37
mean stomata guard cell size (μm)	ca. 26 × 23	36 × 35	30 × 30	27 × 31	ca. 27 × 27	33 × 31	31 × 33	31 × 31	28 × 28
mesophyll palisade cell arrangement	rather compact	rather compact	rather compact	rather compact	loose	loose	rather compact	rather compact	rather compact
outer mesophyll palisade cell size (μm)	26 × 4	23 × 5	24 × 2.8	23 × 5	17 × 5	18 × 7	16 × 6	14 × 5	19 × 5
shape of mid-vein in TS:									
adaxially	concave	flattened or weakly concave	weakly concave	concave	flattened or weakly convex	flattened or weakly convex	weakly convex	flattened	flattened or weakly convex
abaxially	triangular or trapezoid	triangular or trapezoid	triangular or trapezoid	triangular, trapezoid or suborbicular	transversally ellipsoid	triangular	triangular or trapezoid	triangular or trapezoid	rectangular or transversally ellipsoid
trichomes on mid-vein abaxially	abundant	a few basal cells or glabrate	sparse to abundant	abundant	sparse to absent	sparse basal cells to glabrate	sparse basal cells to glabrate	sparse basal cells to glabrate	sparse basal cells to glabrate
number of vb. in mid-vein	3–6	3	6	3–5	3–5	3	3–7	4–6	5–9
number of vb. in petiole main axis	10–12	8–10	10–12	11–12	8–9	12	10–14	9–11	11–12
venation type of acrodromous	perfect	perfect	perfect	perfect	imperfect	imperfect	imperfect	imperfect	imperfect
veinlets	relatively thick	relatively thick	relatively thick	relatively thick	relatively thin	relatively thin	relatively thin	relatively thin	relatively thin

Cuticle preparations were obtained following methods cited in Christophel et al. (1996). Pieces of leaf of 1 cm^2 were taken from near the base of the lamina, placed in test tubes and soaked in 70-95% ethanol for about 24 hours. The ethanol was then decanted and 10 drops of 40% hydrogen peroxide and 5 drops of 90% ethanol were added to the tube and then gently boiled in a water bath until the sample turned light yellow. At this point, cuticles were peeled off and cellular material brushed away. Cleaned cuticles were then stained in 0.1% Crystal Violet, wet mounted in $CaCl_2$ and observed under the light microscope. Vouchers for leaf anatomy including cuticle and stomata are as follow: *C. barnebyana* [*Ortiz* & *Vargas 194* & *200* (MO)], *C. candicans* [*Jansen-Jacobs et al. 1995* (U)], *Pipoly* & *Boyan 8982* (NY), *C. crassa* [*Jardim et al. 609* (NY)], *C. cuatrecasasii* [*Kernan* & *Phillips 1147* (F), *Callejas 1183* (NY)], *C. gentryana* R.Ortiz [*Rubio* & *Quelal 1503* (MO)], *C. iquitana* [*Vásquez et al. 18715* (MO)], *C. aff. iquitana* [*Ortiz 185* (MO)], *C. tecunarum* [*van der Werff & Vásquez 13909* (MO), *Ortiz et al. 143* (MO)], *C. tomentocarpa* [*Reynel* & *Menezes 5025* (MO)], *C. aff. tomentocarpa* [*Ortiz & Vargas 199* (MO)], *C. toxicofera* [*Encarnación 1094* (MO) and *van der Werff & Vásquez 13990* (MO)].

Scanning electron microscope (SEM) observations of leaf trichomes and stomata were made on the adaxial surface of the samples. Samples of 5 mm^2 were removed from mid-lamina of apparently adult leaves of herbarium specimens and mounted on SEM stubs with double-sided carbon conductive tabs and coated with gold using a SEM coating unit E5000. Stomatal classification followed Wilkinson (1979) and trichome description and classification followed Theobald et al. (1979). Observations and photographs were made with a Hitachi S-450 SEM @ 20KV using Polaroid panchromatic film.

The difficulty in matching collections of male and female individuals in Menispermaceae has frequently been stressed in the past (Sandwith 1930, Barneby and Krukoff 1971) and the latter authors' observations regarding the few pistillate flowers in herbarium collections is still relevant at present. In addition to being dioecious, Menispermaceae are also, for the most part, canopy lianas and so difficult to reach, hence they are usually overlooked in biological inventories. It is noteworthy that, although in herbarium collections, there are frequently more pistillate than staminate plants, these pistillate plants are mostly in fruit of different degrees of maturity and therefore are not always readily comparable across species. This is also true for *Curarea*, therefore species are distinguished mostly by characters of the staminate inflorescences and staminate flowers. These latter features are supplemented by characters of the fruits, when available.

In this study, species are regarded as segments of separately evolving lineages of populations, as in the general lineage species concept (de Queiroz 1998, 2007). The criterion used to infer species boundaries is morphological discontinuity, species being diagnosed by unique combinations of qualitative and quantitative morphological features. These morphological features are, as indicated above, mostly based on characters of staminate plants and, for the most part, collections of pistillate plants are assigned to the recognised species if they occur in the same localities where staminate plants have been collected. This approach is rather arbitrary and could be viewed as questionable, especially when the species co-occur as is the case of *C. toxicofera s.s.* and the newly resurrected taxa; however, at present doing it in this manner is unavoidable in a dioecious group that is very poorly represented in herbaria collections.

General morphology

Habit and stem

Species of *Curarea* are all canopy or understory lianas, the canopy species attaining a height of ca. 30 m, the understory species usually only reaching about 10 m high. In understory species, stems are more or less terete (flattened in *C. toxicofera* and ca. 3 cm wide, *Grassl 10076*), with rings or partial rings centric to weakly eccentric, rarely strongly eccentric, in transverse section and 1.5–4 cm in diameter/width (Fig. 2A), while in canopy species, stems are consistently strongly flattened, the partial rings strongly eccentric in transverse section and up to ca. 40 cm in width (Fig. 2B). In both, bark of older stems is usually relatively thin, brittle and smooth, but it can be rugose with irregular shallow lengthwise fissures. Conspicuous tuberculate lenticels are frequent in *C. cuatrecasasii* and in *C. gentryana* and, to some extent, in *C. iquitana*.

Wood anatomy

Wood anatomy of *C. crassa*, *C. gentryana* and *C. toxicofera s.s.* was not investigated. For the remaining species, mostly one sample per species was examined. Transverse sections of the stem of *Curarea*, as of several other Menispermaceae, show an irregular pattern of secondary growth consisting of successive, complete or partial rings of vascular bundles, which are separated radially by wide interfascicular rays and tangentially by pericyclic fibres and tangential cortical parenchyma. This type of growth is typical of Menispermaceae and has been termed “anomalous secondary growth” (Solereder 1908); “included (interxylary) phloem” (Chalk and Chataway 1937; Metcalfe and Chalk 1950), “xylem and phloem concentrically alternating” (Metcalfe and Chalk 1983) or “successive cambia” (Carlquist 1988, 1996; Jacques and de Franceschi 2007).

Within *Curarea*, species differ moderately in their pith diameter, distribution patterns of vascular bundles and rays, occurrence of medullary sclerenchyma (e.g. fibre caps) and number and mean tangential diameter of vessels. Variation in these and other features are summarised in Table 3.

Successive and centric to weakly eccentric patterns of few (3–7) complete or partial rings are found in *C. aff. tomentocarpa* (Fig. 2A) and *C. cuatrecasasii* and several (ca. 45) strongly eccentric arches are observed in *C. tecunarum* (Fig. 2B), *C. candicans* and *C. barnebyana*. Wide rays (275–340 µm) in combination with more or less straight tangential margins and vascular bundles with smaller vessel diameter are observed in *C. aff. tomentocarpa* (Fig. 3A), *C. candicans* and, to some extent, in *C. cuatrecasasii*. There are tangential wedge-like layers of sclereids intruding into the rays in *C. tecunarum* (Fig. 3B) and *C. barnebyana* but, in all other species examined, the rays are tangentially uniform. Relatively narrow rays (150–136 µm) with conspicuous irregularly angulate radial margins combined with relatively wide (220–228 µm) vascular bundles with large tangential diameter of vessels and strongly developed medul-

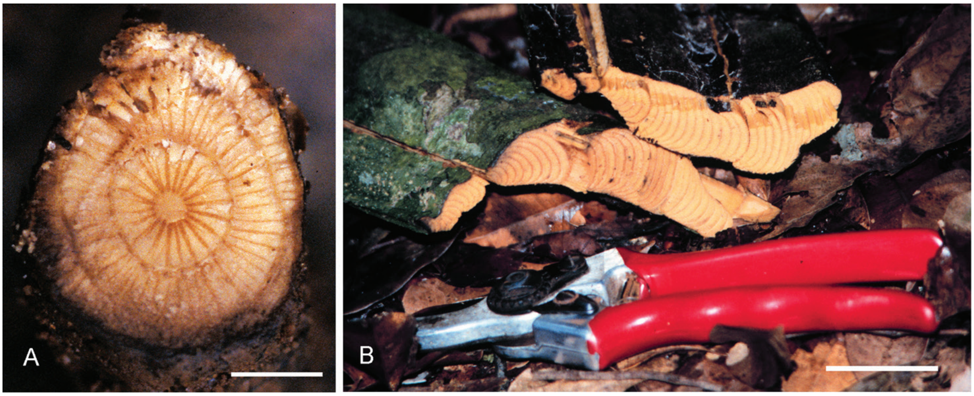

Figure 2. Transversal sections of stem of *Curarea*: **A** relatively round stem of *C. aff. tomentocarpa* (*Ortiz 197*), showing wide rays **B** flattened stem of *C. tecunarum* (*Ortiz & Vásquez 214*) showing successive partial rings. Scale bar: 0.5 cm (**A**); 1.7 cm (**B**).

lary sclerenchyma in the pith are characteristic of *C. tecunarum* (Fig. 3B) – this alone lacks crystalline inclusions– and *C. barnebyana*.

Relatively narrow rays with conspicuous irregularly angulate radial margins in combination with vascular bundles with large tangential diameters are also observed in *C. cuatrecasasii*. No representative of *C. toxicofera s.s.* was available in this study and sterile specimens provisionally identified as *C. toxicofera* show moderate to strongly eccentric arches of successive growth, although the width reaches only up to 3 cm.

Leaves

Within an individual, the shape and size of the lamina varies with age, position along the stem and exposure to sunlight. Thus, large blades with caudate apices are usually either juvenile and/or found in parts of the plant that are in shaded areas, while smaller blades with acute or acuminate apices are found in mature leaves that are usually exposed to direct sunlight. The latter are more conspicuous in species that reach the canopy. The type collection of *C. tecunarum* –i.e., *Krukoff 8713* and a sterile specimen of *Curarea* (*Cerón 2717*), which remains as *Curarea* sp., show a few leaves with cleft apices. The margins of blades are entire, but on rare occasions, they are scarcely lobed to apically trilobed in sterile specimens of *C. tecunarum* (*Vásquez et al. 15101*, *Lewis et al. 11759*) and the sterile specimen *L.C. Richard s.n.*, the type of *C. candicans*, also has an apically trilobed leaf blade. Leaf blades are chartaceous or subcoriaceous, sometimes thinly fleshy when young, surfaces are usually conspicuously discolorous (Fig. 4A–B) resulting from the dense silvery indumentum covering the adaxial surface (Fig. 4B), especially in juvenile leaves. Petioles are shorter in leaves of the canopy and longer in leaves of the understory and/or shaded areas, pulvinate at both ends, with the apical one more conspicuous.

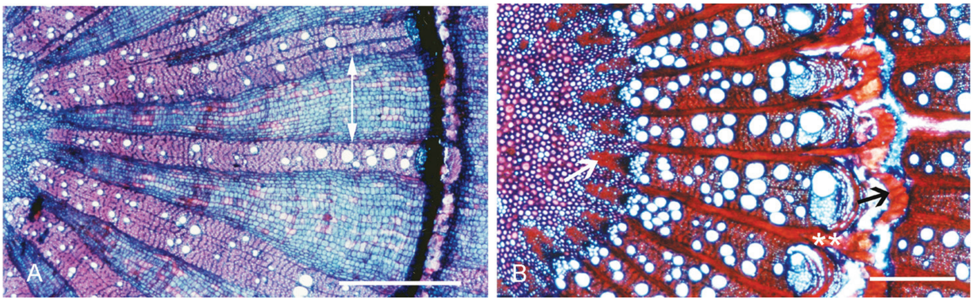

Figure 3. LM photographs of transverse sections of wood of *Curarea*: **A** small vessels, and broad rays (double arrow), *C. aff. tomentocarpa* (*Ortiz & Vargas 197*) **B** moderately large vessels, sclerotic pericyclic fibres (black arrow), strongly developed medullary sclerenchyma (white arrow) and sclerenchyma strongly intruding into the rays (two white asterisks), *C. tecunarum* (*van der Werff & Vásquez 13909*). Scale bar: 0.8 mm (**A, B**).

Indumentum

The indumentum in *Curarea* consists of two-celled unbranched trichomes with a short basal cell and an elongate terminal cell (Fig. 4C–D). Trichomes occur singly or in pairs.

Several-lobed trichomes have been reported for *C. toxicofera* by Wilkinson (1989), but could not be confirmed here. It is likely that the tendency for the terminal cells to collapse in an irregular fashion in dried and/or aged samples gives the impression of trichomes being lobed. Indumentum density varies with age in some species, frequently disappearing along the stems. This variation is of taxonomic use in *Curarea*. Thus, uniformly dense indumentum concealing the lower leaf surface is common in *C. crassa*,

C. barnebyana and *C. tecunarum* (Fig. 4E), whereas the indumentum mainly localised in the areole spaces, is common in *C. candicans* (Fig. 4F), *C. cuatrecasasii* and less frequently also in *C. toxicofera s.s.*

Venation pattern

The venation in *Curarea* conforms to the acrodromous type (*sensu* Hickey 1973, 1979) as observed in mature leaves. Primary veins vary from 3–5(–7), (Fig. 5A–B), however in one group of species (i.e. *C. candicans*, *C. crassa*, *C. barnebyana* and *C. tecunarum*, Fig. 5B), the innermost pair runs almost the whole length of the lamina and arches towards the apex, with only one pair of loosely brochidodromous secondary veins (this pair sometimes absent) and thick and coarse veinlets (higher-order veins), (Fig. 5C). In the other group of species which includes *C. cuatrecasasii*, *C. gentryana*, *C. iquitana*, *C. tomentocarpa* and *C. toxicofera*, although the innermost pair runs more than half the length of the lamina, frequently there are 2–3 pairs of strongly brochidodromous secondary veins and moderately thin and loose veinlets (Fig. 5B, D).

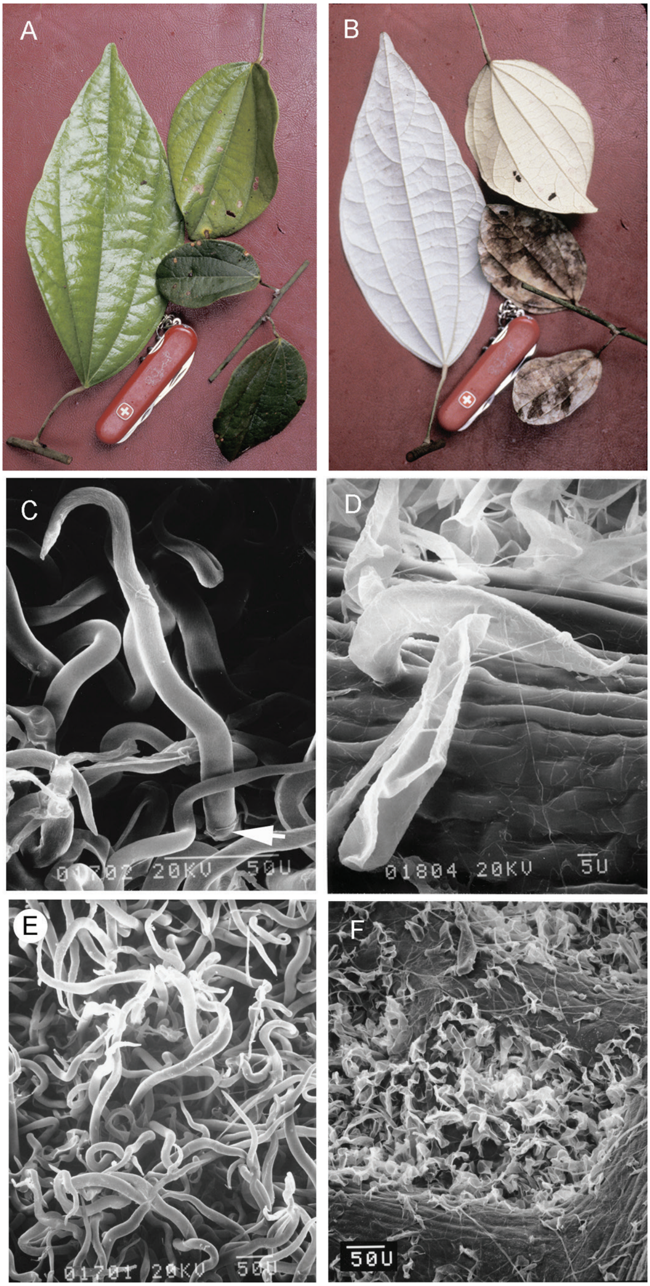

Figure 4. Leaf blade surfaces and SEM micrographs of trichomes of *Curarea*: **A** glabrous adaxial leaf blade surface of juvenile and adult leaves, *C. barnebyana* (*Ortiz & Vargas 194*) **B** densely pubescent adaxial leaf blade surface of juvenile and adult leaves showing whitish covering more conspicuously in juvenile leaves, *C. barnebyana* (*Ortiz & Vargas 194*) **C** elongate trichome with a short basal cell (white arrow) and a cylindrical terminal cell, *C. crassa* (*Jardim et al. 609*) **D** trichome with a moderately short terminal cell, *C. cuatrecasasii* (*Kernan & Phillips 1147*) **E** matted, elongate trichomes, *C. gentryana* (*Rubio & Quelal 1503*) **F** collapsed trichomes, *C. candicans* (*Jansen-Jacobs et al. 1995*).

Leaf anatomy: adaxial cuticle, transverse sections of petiole, lamina and mid-vein

Most of these features were studied by Wilkinson (1989) for *C. candicans* and *C. toxicofera s.l.* when describing characters common to Tiliacoreae as a whole.

Here, I add observations of the remaining species, the main variations being summarised in Table 4. Adaxial epidermal cells in all species are squarish, rectangular or irregularly shaped. In *C. candicans* (Fig. 6A), *C. crassa*, *C. barnebyana* and *C. tecunarum* these have abundant tanniferous cells, but there is little or no tanniferous cells in *C. cuatrecasasii* (Fig. 6B), *C. gentryana*, *C. iquitana*, *C. tomentocarpa* and *C. toxicofera*.

Curarea species are exclusively hypostomatic, as noted by Wilkinson (1989). The stomata, between the strongly projecting veins (Fig. 6C), are concealed by a dense indumentum. They occur typically in groups of 7–102 per areole, with the lowest number observed in *C. tomentocarpa* and the highest in *C. barnebyana* (Table 4). Stomata are elliptic in outline and immediately surrounding the aperture is a distinct peristomatal rim (Fig. 6D–E), the cell guards range in size from 26–36 × 23–35 µm. In all species, stomata are raised on a short column of ca. 4 cells (5–6 cells *fide* Wilkinson 1989).

Wilkinson (1989) described this arrangement of the epidermal cells under the guard cells as cyclocytic. Such projecting stomata with thick peristomatal rims are frequently associated with ecological factors such as high humidity and poor soils (Solereder 1908; Wilkinson 1979), conditions typical of the habitats occupied by species of *Curarea*.

The apical pulvinus of the petiole is more or less circular to weakly triangular in transverse section and weakly adaxially flattened in *C. candicans*, *C. crassa* and *C. tecunarum*. There are no trichomes or only a few persistent basal cells in *C. candicans*, *C. cuatrecasasii*, *C. gentryana*, *C. iquitana*, *C. tomentocarpa* and *C. toxicofera*; usually there are abundant trichomes in the remaining three species. The vascular tissue is a ring of 8–13 vascular bundles. Sclerenchyma cells surround the vascular tissue, externally forming an interrupted or continuous ring of several layers. There are a few small groupings of sclereids (stone cells) in the inner parenchyma of the cortex and, in the pith, a starch sheath (i.e. endodermis) is found around the vascular tissue in all species. A pulvinus at both ends of the petiole is a common feature in Menispermaceae and they are thought to bring the lamina into the optimum position to receive light (Wilkinson 1989). Pulvini have a large volume of parenchyma; therefore, they are always swollen compared to the rest of the petiole (Esau 1967). The mid-region of the petiole is circular, from about 1 mm diameter in *C. crassa* and *C. cuatrecasasii*, to about 2.1 mm in diameter in *C. iquitana*. Trichomes are few to rather abundant, frequently only the basal cells are present. There are 8–14 vascular bundles surrounded by a continuous ring of thick-walled sclerenchyma cells, the layers of parenchyma cells are much reduced and frequently thick-celled parenchyma is found in the pith (Fig. 7A).

Transverse section of the lamina shows mesophyll palisade cells that are somewhat short and loosely arranged especially the inner layer in *C. cuatrecasasii*, *C. iquitana*, *C. gentryana*, *C. tomentocarpa* and *C. toxicofera*. Palisade cells are moderately long and more or less compactly arranged in *C. barnebyana*, *C. candicans*, *C. crassa* and *C. tecunarum*.

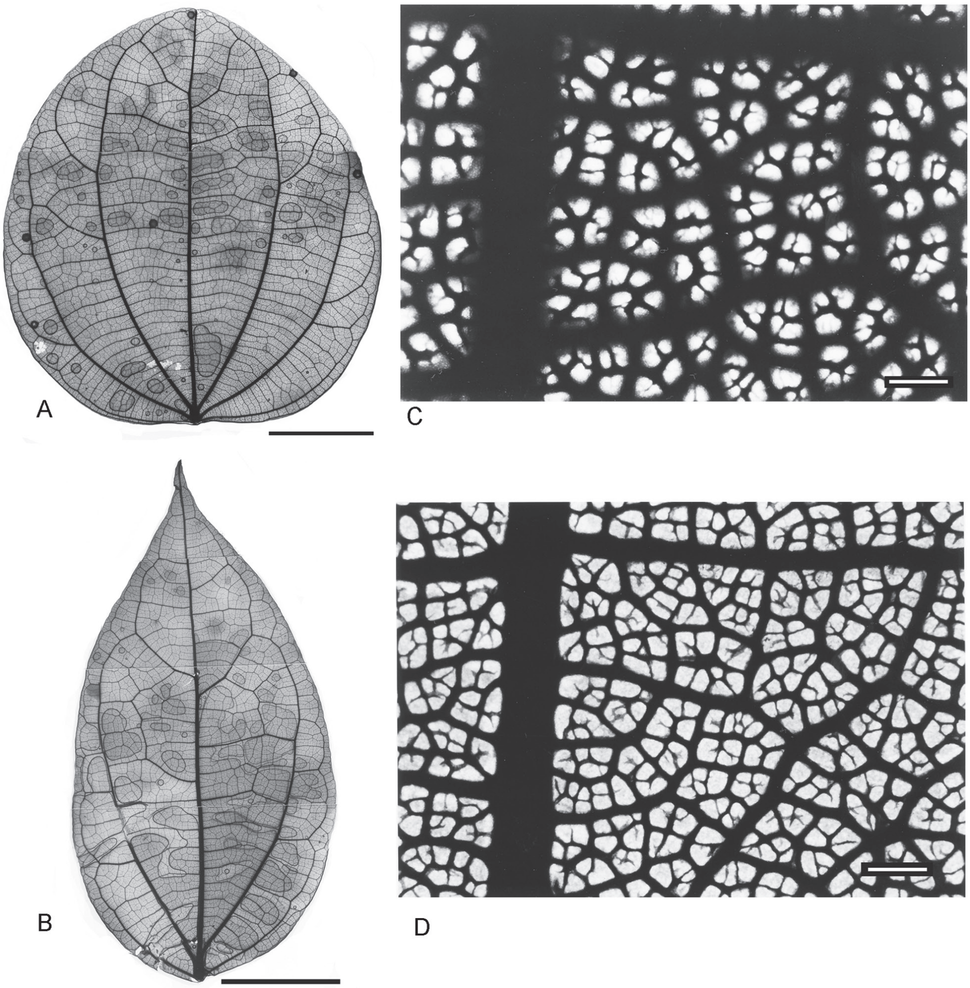

Figure 5. Venation types of *Curarea*: **A** innermost pair of main veins acrodromous perfect, 7 main veins from the base, the basal-most pair weakest, *C. tecunarum* (*van de Werff & Vásquez 13909*) **B** innermost pair acrodromous imperfect, 3 conspicuous main veins from the base, *C. toxicofera* (*van der Werff & Vásquez 13990*) **C** well-developed areolae and ultimate veinlets often thin, free vein endings uncommon, *C. candicans* (*Jansen-Jacobs et al. 1995*) **D** well-developed areolae and ultimate veinlets thin, once or twice branched, endings often free *C. cuatrecasasii* (*Morales et al. 3243*). Scale bar: 3.1 cm (**A**); 0.7 mm (**B**); 3.0 cm (**C**); 1.1 mm (**D**).

The midrib is adaxially concave and abaxially strongly raised and trapezoid or sub orbicular but always with abundant trichomes in *C. barnebyana*, *C. crassa* and *C. tecunarum* (Fig. 7B). In *C. cuatrecasasii*, *C. gentryana*, *C. iquitana*, *C. tomentocarpa* and *C. toxicofera*, the midrib is adaxially flat to weakly convex and abaxially strongly raised, triangular or trapeziform with few or no trichomes (Fig. 7C). The midrib in *C. candicans*

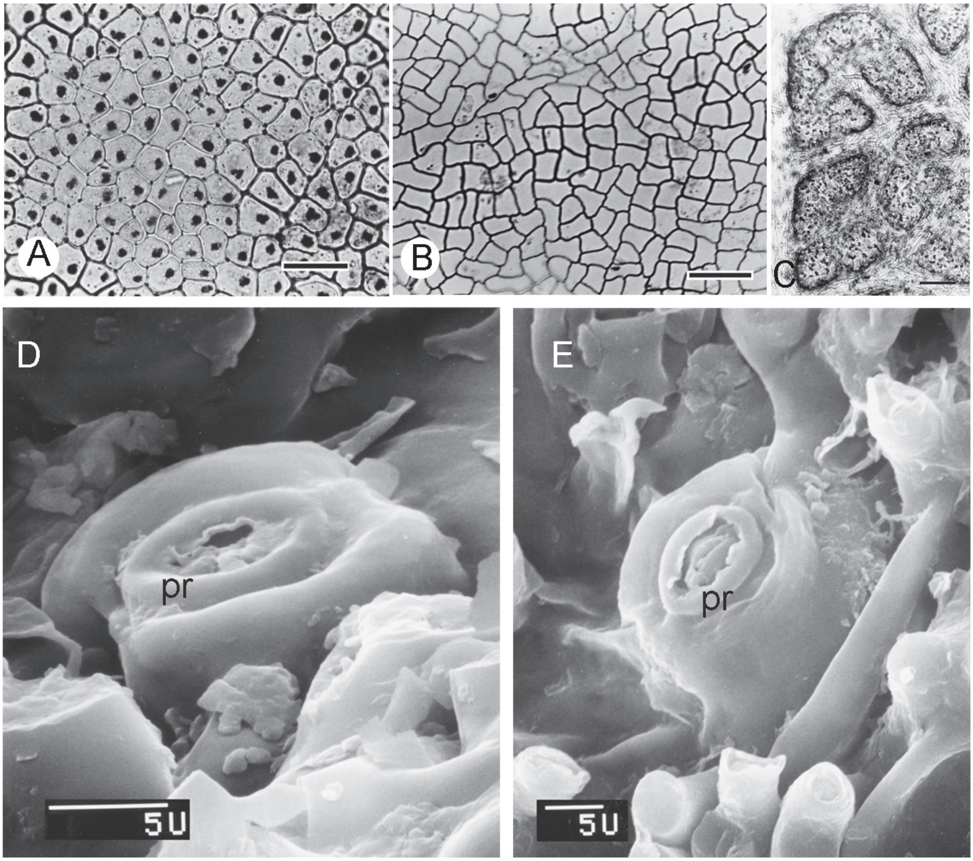

Figure 6. LM photograph and SEM micrographs of leaf adaxial, abaxial surface and stomata in *Curarea*: **A** isodiametric epidermal cells, *C. candicans* (*Jansen-Jacobs et al. nr-1995*) **B** triangular to hexagonal epidermal cells, *C. cuatrecasasii* (*Kernan & Phillips* 1147) **C** abaxial surface showing areoles (black dotted) in *C. toxicofera* (*van der Werff & Vásquez 13990*) **D, E** SEM micrographs of projecting stomata with distinct peristomatal rim **D** *C. tecunarum* (*Ortiz et al. 143*) **E** *C. tomentocarpa* (*Reynel & Meneses 5025*). Scale bar: 50 µm (**A**); 100 µm (**B**), 0.4 mm (**C**), **pr** = peristomatal rim.

adaxially is somewhat flat to weakly concave while abaxially, it is strongly raised and somewhat trapeziform with sparse trichomes or glabrate. As noted by

Wilkinson (1989), the vascular system in *Curarea* is frequently collateral. There are 3–9 vascular bundles distributed in an arc (Fig. 7B–C), the three central ones being largest. The vascular bundles are surrounded by several layers of sclerenchymatous cells. Adaxial to the vascular bundles there is a continuous (e.g. *C. barnebyana*, *C. candicans*, *C. crassa* and *C. tecunarum*) or sometimes interrupted (e.g. *C. cuatrecasasii*, *C. gentryana*, *C. iquitana*, *C. tomentocarpa* and *C. toxicofera*) layer of chlorenchyma cells and one or several layers of sclerenchymatous cells immediately below the epidermis.

Abaxially, parenchyma cells are abundant, with few to numerous stone cells scattered throughout and below the abaxial epidermis are sclerenchymatous cells.

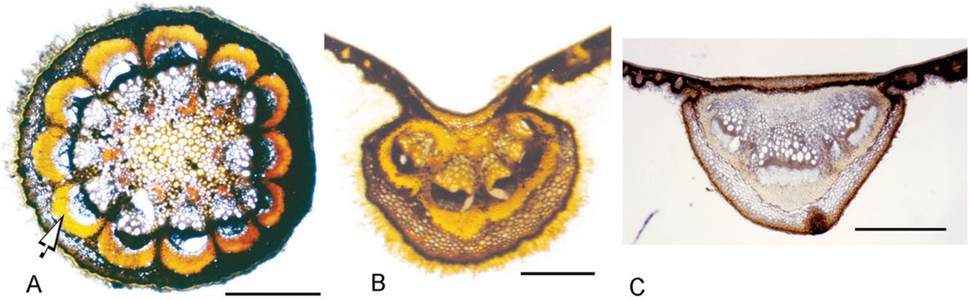

Figure 7. LM photographs of transverse sections of petiole and mid-veins of *Curarea*: **A** petiole mid-section of *C. tecunarum*, note the vascular bundles surrounded by sclerotic fibres on the outer part (arrow) **B** adaxially concave, abaxially strongly raised, rounded and tomentose mid-vein, *C. tecunarum* (A, B from *Ortiz et al. 143*); **C** adaxially flat, abaxially strongly raised, triangular and glabrescent mid-vein, *C. toxicofera* (*van der Werff & Vásquez 13990*). Scale bar: 0.6 mm (**A, C**), 1 mm (**B**).

Inflorescences

As all Menispermaceae, *Curarea* is also dioecious, with staminate and pistillate inflorescences in different plants. Staminate and pistillate inflorescences are solitary or more frequently fascicled, cauliflorous and arising from old leafless stems, axillary, supra axillary or terminal on young shoots. Inflorescences are basically thyrsi (*sensu* Weberling 1992), however, in pistillate inflorescences, the primary branches are sometimes reduced to solitary flowers, thus appearing racemiform; inflorescence axes are slender or moderately stout, sometimes conspicuously ridged, variously densely pubescent, with trichomes adpressed or ascending. The inflorescence bracts subtending the primary branches are ovate to lanceolate, markedly concave and usually fleshy, the adaxial side glabrous, the abaxial side variously pubescent, the indumentum appressed or spreading.

Staminate inflorescences usually multiflorous (Fig. 8A); lax primary branches with (2–)4–6 branching orders are characteristic of *C. cuatrecasasii*, *C. gentryana*, *C. iquitana*, *C. tomentocarpa*, *C. toxicofera* (Fig. 8A) and *C. tecunarum*. Rather condensed/compacted primary branches with 0–2 branching orders appearing umbelliform or irregularly cymose occur in *C. crassa*, *C. barnebyana* and *C. candicans*; occasionally, *C. candicans* may have 3 orders of branching. In *C. tecunarum*, higher branching orders frequently are reduced (i.e. they are not fully dichotomous and flowers are sessile or subsessile), occasionally in *C. gentryana* and *C. aff. iquitana*, reduced branching occurring on alternating sides along the length of the primary branches, appearing racemiform. In most species, the primary branches are moderately thick, but they are rather thin and filiform in *C. cuatrecasasii* and *C. gentryana*.

Pistillate inflorescences are usually pauciflorous (Fig. 8B), with the primary branches mostly simple dichasia subtended by an inflorescence bract. Some or all of the primary branches may be reduced to single flowers, thus resembling a raceme and these flowers are subtended by bracts. In branched inflorescences of both staminate and pistillate there may no be obvious floral bracts.

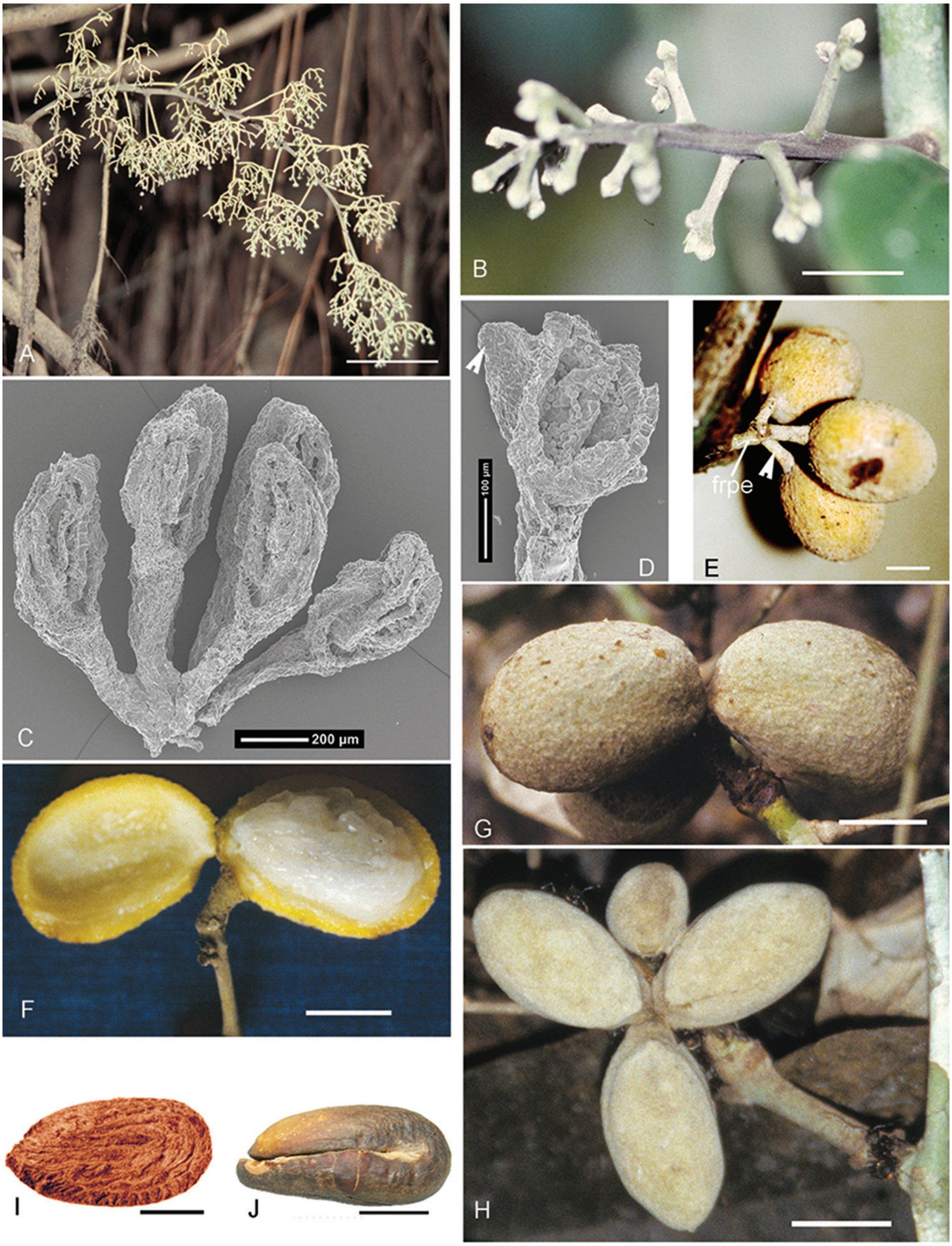

Figure 8. General morphology in *Curarea*: **A.** staminate inflorescence of *C. toxicofera* (*Ortiz et al. 157*) **B** pistillate inflorescence of *C. aff. iquitana* (*Ortiz 184*) **C** stamens of *C. toxicofera* (*Encarnación 1094*) **D** anther of *C. iquitana* showing the horn-like (arrow) adaxial protrusion of the connective (*Vásquez et al. 18994*) **E** ripe fruits of *C. aff. iquitana* showing the fruiting pedicel (frpe) and three elongate carpophores (white arrow) (*Ortiz & Ruiz 191*) **F** ripe fruit of *C. aff. iquitana*, exocarp of drupelet on right pulled away showing whitish mesocarp (*Ortiz & Pezo 208*) **G–H** immature fruits of *C. barnebyana* **G** lateral view **H** view from the top (**G–H** from *Ortiz & Vargas 194*) **I** weakly ornamented endocarp of *C. toxicofera* (*Lewis & Vásquez 4017*) **J** hippocrepiform embryo of *C. barnebyana* (*Ortiz & Vargas 194*). Scale bars: 5.2 cm (**A**), 1.1 cm (**B**), 1 cm (**E**), 1.25 cm (**F**), 1.5 cm (**G–H**), 0.5 cm (**I**), 1 cm (**J**).

Flowers

Flowers are unisexual, actinomorphic and trimerous; usually pedicellate, less frequently sessile. The pedicels are usually terete, moderately slender and sometimes ridged. At the apex of the pedicels there are 1–3(4) minute, more or less deciduous structures, usually alternating with the outer whorl of sepals. Although their morphological nature is often unclear, to facilitate description, here I am referring to them as bracteoles. These structures are most commonly ovate-lanceolate, narrowly ovate to ovate or oblong, fleshy, glabrous adaxially, variously pubescent abaxially. They are most often absent in staminate flowers and, hence, frequently not mentioned in earlier descriptions (i.e. Barneby and Krukoff 1971).

Staminate flowers are usually light coloured, frequently described as cream, whitish, greenish, yellowish, orangish, greyish or brownish; although flowers are usually pedicellate, they can be occasionally sessile in *C. toxicofera* and *C. barnebyana* and more often so in *C. tecunarum*. Sepals are commonly 6(–9), free, in 2(–3) unequal whorls (sometimes spirally arranged in *C. candicans*), mostly ovate, narrowly ovate to obovate, oblong, rhombic, elliptic or suborbicular, usually weakly concave and scarcely fleshy, glabrous adaxially, variously pubescent abaxially, the outermost whorl being smaller than the innermost whorl. The inner sepals have valvate aestivation and, after anthesis, their tips are usually reflexed (rarely erect). Petals are (5–)6(–9 in *C. tomentocarpa*), free, arranged in 2(–3) usually similar whorls, they are conspicuously smaller than the inner sepals, usually obovate-trilobed to rhombic or spatulate members, weakly concave, membranous, glabrous adaxially, glabrous or tomentellous abaxially, the lateral margins strongly inflexed and clasping the filaments of the stamens immediately opposite to them. In *C. gentryana*, the lateral margins of the inner whorl are adaxially connate or coherent. The stamens are (3–5)6, (Fig. 8C), arranged in two, more or less similar whorls (often one in *C. gentryana*); the filaments are free or variously connate (connate half their length in *C. aff. iquitana* to fully connate in *C. gentryana*) and clavate, clavate-sigmoid to almost terete, glabrous (abaxially tomentellous in *C. toxicofera*). The anthers are tetrasporangiate and dithecous, basifixed, ellipsoid or subglobose in shape, erect or slightly incurved and dehiscing by latrorse longitudinal slits. They are yellow in colour when fresh and light brown or cream when dried. Frequently, the sporangia appear half-immersed in the dilated connective. In all species, the connective is conspicuous on both sides, however, it is frequently thicker adaxially and variously protruding and it sometimes grows beyond the thecae to form a horn-like structure, as in *C. iquitana* (Fig. 8D). The connective is sometimes thinner abaxially and, at the apex in *C. tomentocarpa* and here, each theca may separate at the apex. Pistillode absent.

Pistillate flowers are greenish, yellowish or brownish coloured; pubescent abaxially. Sepals 6–9, free, in two, or more commonly three unequal whorls, mostly ovate-lanceolate to obovate, oblong, elliptic to rhombic or spatulate, usually weakly concave and scarcely fleshy to fleshy, glabrous adaxially, variously pubescent abaxially, the outermost whorl being smaller than the innermost whorl. The inner sepals have valvate aestivation and, after anthesis, their tips are usually reflexed (erect). Petals are usually in a single whorl of three, less frequently 4–6 petals are found in *Curarea aff. iquitana*, *C. tecunarum* and *C. tomentocarpa*, they are spatulate and weakly concave, membranous, glabrous adaxially, glabrous to scarcely pubescent abaxially. The petals are always smaller than the innermost whorl of sepals and are usually opposite the carpels. There are three (seldom four in *C. tomentocarpa*), free carpels, the ovaries are usually coherent when young, strongly gibbous and densely tomentose; the styles are glabrous and usually terete, weakly tapering distally, often reflexed, weakly grooved adaxially in transverse section and commonly subpersistent and located near the base of the fruit; the stigma is inconspicuous. Frequently only one carpel reaches maturity.

Infructescences and drupelets

Infructescences are similar to inflorescences, but are sometimes lenticellate or have exfoliating bark. Fruiting pedicels are clavate or terete, at times inconspicuous, slender or rather thick. As the carpel develops in *C. iquitana*, *C. tomentocarpa*, *C. toxicofera*, *C. cuatrecasasii* and *C. gentryana* (i.e. all understory species in which the fruits are close to the ground), the trilobed gynophore enlarges into three relatively short to moderately long stalks (Fig. 8E). This enlargement of the gynophore produces structures known as carpophores, which support the drupelets of each carpel (Forman 1975, 1986). They are weakly terete or clavate, straight or distally weakly incurved and reach 2.7–11.3 mm in length, the longest being observed in *C. toxicofera*. Carpophores are also found in other genera in the tribe Tiliacoreae (i.e. the neotropical *Sciadotenia* and some African and Indomalesian species of *Tiliacora*; Forman 1975), as well as other genera outside Tiliacoreae (viz. *Elephantomene* of Anomospermeae, see Krukoff and Barneby 1974; and *Anamirta* of Coscinieae, see Forman 1975). However, in *C. barnebyana*, *C. crassa* and *C. tecunarum*, this enlargement does not occur and only a subglobose, weakly trilobed structure is observed at the distal end of the peduncle and, in *C. candicans*, this is somewhat drum-like; these four species bear fruits in the canopy.

Drupelets are oblongoid, ellipsoid, obovate or subglobose (Fig. 8E–H) and are weakly laterally compressed when dried. They are obliquely attached to the summit of the carpophore, sessile or less frequently gradually attenuate toward the base, forming a short stipe ca. 3 mm long in some specimens of *C. cuatrecasasii*. The exocarp may be thin or thick, mealy-coriaceous in *C. toxicofera* (*sensu* Barneby and Krukoff 1971), the surface is smooth, rugulose or muriculate, pilosulous or velutinous-hispidulous, the trichomes being erect. The fruits are pale orange to yellow when ripe and frequently leathery outside and granular inside when dried. Although, in a strict sense, the single-layered outer epidermis of the pericarp is referred to as the exocarp, here I am following earlier characterisations of *Curarea* fruit by Barneby and Krukoff (1971), who described the several-layered outermost zone of the pericarp (including the epidermis) as the exocarp. It is worth noting, however, that it appears that Barneby (1996) interpreted the exocarp as the epidermis only and the remaining layers following the epidermis as the mesocarp when describing the fruit in *C. crassa* from dried herbarium material (e.g. Barneby 1996: 22). The mesocarp is white, fleshy and mucilaginous when fresh (Fig. 8F) and, when dried, turns into filamentous plates that adhere to the endocarp (Barneby and Krukoff 1971). Due to the eccentric development of the carpel, the scar of the style is found near the base of the developed fruit. The endocarp is oblong-ellipsoid or obovoid, hippocrepiform (i.e. horseshoe-shaped) (Fig. 8I), a shape produced by the unequal development of the abaxial side compared to the adaxial side (Botha 1980; Forman 1986); although the hippocrepiform shape is more noticeable from within rather than from the external surface. The texture is typically papyraceous (crustaceous in some specimens of *C. toxicofera*). Commonly the surface is fairly smooth, but muriculate or weakly reticulate in *C. toxicofera* (Fig. 8I). Seeds, like the endocarps, are hippocrepiform (Fig. 8J), semicircular in transverse section and brownish when dried. Seeds in *Curarea*, as in most members in the tribe Tiliacoreae, lack endosperm, the cotyledons are thick, fleshy and accumbent, both are usually of equal size, but in *C. barnebyana* one of them may be smaller and somewhat J-shaped. The seed (embryo) is hippocrepiform (i.e. curved around the condyle). The latter has not been studied in developing carpels in *Curarea*, however, features of the mature endocarp suggest that it conforms to a bilaterally compressed septiform condyle as described by Ortiz (2012); the condyle corresponds with a shallow groove on the lateral sides of the external surface of the endocarp.

Pollen morphology

Pollen morphology of *Curarea* represented by *C. toxicofera s.l.* was examined by Thanikaimoni (1968), Ferguson (1975) and Thanikaimoni et al. (1984); the latter authors included also *C. tecunarum*. Pollen is described as spheroidal, tricolporate, with circular equatorial outline, muri distinctly papillose, papillae in one or two rows.

Phytochemistry

Several members of Menispermaceae are known to contain toxic compounds and bisbenzyltetrahydroisoquinoline alkaloids are very common in the family (Bruneton 1995, Barbosa-Filho et al. 2000). Amongst the best known is (+)–tubocurarine, a muscle relaxant produced by *Chondrodendron tomentosum*, a close relative of *Curarea* and the basis for subsequently developed synthetic forms (Bruneton 1995, Tuba et al. 2002). *Curarea toxicofera* produce alkaloids with curare-like activities such as (-)-curine and (+)-chondrocurine, (+)-isochondrodendrine; the latter has also been reported in *C. tecunarum* (Barbosa-Filho et al. 2000).

Ethnobotany

Menispermaceae are rich in medicinal and toxic compounds and many species are used to cure a variety of illnesses across their global distribution. Amongst the best-known products is curare, the South American arrow and dart poison of which an overall introduction is given by Krukoff and Moldenke (1938). Curare is a general name for a large group of poisons with muscle paralysis activities (Neuvinger 1998) and several species of *Curarea* are a source of this type of poison. *Curarea candicans* [= *Chondrodendron candicans* (Rich. *ex* DC.) Sandwith)] was reported by Sandwith (1930), based on the label information of *Jenman 5199* to be used by the Warrou Indians of Guyana as a source of the "other kind of poison", a statement that was interpreted by Krukoff and Moldenke (1938) to refer to a different substance from the curare used by the Macusi Indians, also from Guyana.

Curarea tecunarum, variously identified as *Chondrodendron polyanthum* (Diels) Diels or as *Chondrodendron limaciifolium* (Diels) Moldenke, was reported as one of the main sources of curare for the Tecuna Indians from Brazil (Krukoff and Smith 1937; Krukoff and Moldenke 1938; Krukoff and Barneby 1970). The early report of Krukoff and Smith (1937) was later mentioned by Macbride (1938) in the Flora of Peru, under the name of *Chondrodendron polyanthum*. An extract from *C. tecunarum* is used as a long-term oral contraceptive for both men and women of the Denís tribe of Brazil (Barneby and Krukoff 1971; Prance 1972).

Curarea toxicofera (as *Cocculus toxicoferus* Wedd.) has long been known as an important source of curare for the Yaguas and Orijones of Amazonian Peru (de Castelnau 1851). Similar uses in this region have since been reported (Krukoff and Barneby 1970, Ayala Flores 1984), also for Brazil (Prance 1972), Colombia (García-Barriga 1992) and Ecuador (Cerón 1995). *Chondrodendron bioccai* G.Lusina (at present provisionally included in the synonym of *Curarea toxicofera*), was stated to be used as a principal source in the preparation of curare by the Maku Indians from Alto Rio Negro (Lusina 1954). Similarly, the sterile specimen (*Mexia 6321a*), previously identified as *Chondrodendron iquitanum* (Krukoff and Moldenke 1938) and later as *Curarea toxicofera* (Barneby and Krukoff 1971), was reported to be used as a source of dart poison by Indians in the Rio Santiago area. However, as the specimen in question was not available in this study, it is unclear to which of the two species it belongs.

Geographical distribution and habitat

Curarea is relatively widespread within tropical America, ranging from Costa Rica through Panama, to Bolivia, French Guiana, western Brazil and the Atlantic Forest of South-eastern Brazil (Figs 9, 21 and 25).

Species of *Curarea* are typically found in lowland tropical moist forests and lower montane forest (up to 1300 m elevation). They grow in periodically flooded forest (either *varzea* or *igapó*) to upland non-flooded forest, typically in primary forest, but are also occasionally present in secondary growth. The species are apparently locally rare and mainly allopatric, however, *Curarea aff. iquitana*, *C. toxicofera* and *C. tecunarum* were observed growing sympatrically in Peru.

Phylogenetic affinities

In phylogenetic analyses of the family using plastid markers, *Curarea* was recovered as sister to *Sciadotenia*, in a clade that also includes *Chondrodendron* (Ortiz et al. 2016).

These affinities are congruent with earlier suggestions (Barneby and Krukoff 1971: Triclisieae *sensu* Diels 1910; Tiliacoreae *sensu* Forman 1982, Ortiz et al. 2016). With *Sciadotenia*, *Curarea* shares palmatinerved or plinerved venation and more or less sessile drupelets borne on elongate carpophores. With *Chondrodendron*, *Curarea* shares stomata aggregated in areolar depressions and raised above the epidermal cells on a short column of cells and a thyrsoid staminate inflorescence. In the study of Ortiz et al. (2016), *C. candicans* is recovered as sister to a clade in which *C. cuatrecasasii*, *C. barnebyana*, *C. tecunarum* and *C. toxicofera s.l.* are all unresolved (Fig. 1B).

Morphological characters suggest two species groups within *Curarea* (Table 5), although these are not congruent with the results from analysis of molecular data. In the group including *C. barnebyana*, *C. candicans*, *C. crassa* and *C. tecunarum*, the innermost pair of primary veins of mature leaves, which are in the canopy, conforms to an acrodromous perfect venation, with all but *C. tecunarum* also sharing staminate inflorescences with compact primary branches that have few branching orders. All the above listed species, except for *C. candicans*, share villous indumentum on their abaxial leaf surface and short subglobose carpophores. Wood and leaf anatomy features shared amongst these species are summarised in Table 5. *Curarea candicans* differs from the other species in the first group by its web-like indumentum and its unique drum-like carpophores, its narrow vessel elements being more similar to species of the second group. In the latter group, which includes *C. cuatrecasasii*, *C. gentryana*, *C. iquitana*, *C. tomentocarpa* and *C. toxicofera* (Table 5), the innermost pair of primary veins on mature leaves are acrodromous imperfect, the species have a strigillose-tomentellous indumentum on their abaxial leaf surface (web-like/tomentellous in *C. gentryana*), staminate inflorescences with lax primary branches, these with 4–6 branch orders, elongate carpophores and a few other anatomical features (Table 5). However, *C. cuatrecasasii* shares wide vessels with species in the first group.

Multivariate analyses of *Curarea toxicofera s.l.*

The principal component analyses (PCA) of the datasets indicates no clear pattern in the morphological variation of the *C. toxicofera* complex (not shown). Of the five datasets, the linear discriminant analyses (lda) of dataset 2, is presented here. The analysis of this latter dataset, which corresponds to a combination of leaves + staminate inflorescences + staminate flowers, was significant (Wilk's lambda = 0.0043335, $P < 0.001$) and correctly assigned all individuals to their previously defined groups. The first two canonical discriminant functions recovered three clusters, namely groups **to**, **tm** + **uc** and **al** + **iq** (Fig. 10A). Moreover, the toxicofera (**to**) group is recovered as an independent cluster by the first canonical discriminant function, whereas **al**, **tm**, **iq** and **uc**, show various levels of overlap (Fig. 10B). The first

Table 5. Morphological features of the two species groups within *Curarea*. * = species not studied for wood anatomy.

	Group I				**Group II**				
Macro- and micro-morphological Characters	***barnebyana***	***candicans***	***crassa****	***tecunarum***	***cuatrecasasii***	***Gentryana****	***iquitana***	***tomentocarpa***	***toxicofera****
Wood									
rays in stem	relatively narrow	relatively narrow	n/a	relatively narrow	relatively narrow	n/a	wide	wide	n/a
average # of vascular bundles around pith	39	51	n/a	37	25	n/a	28	16	n/a
medullary sclerenchyma in pith	strong	strong	n/a	strong	weak	n/a	weak	weak	n/a
Leaf									
indumentum type on abaxial leaf blade surface	villous	web-like to tomentellous	villous	villous	strigillose-tomentellous	web-liketomentellous	tomentellous	tomentellous	strigillose-tomentellous
type of acrodromous venation	perfect	perfect	perfect	perfect	imperfect	imperfect	imperfect	imperfect	imperfect
veinlets	thick	thick	thick	thick	thin	thin	thin	thin	thin
mesophyll palisade cell arrangement	compact	compact	compact	compact	loose	loose	compact	loose	loose
mesophyll palisade size (mm)	23 × 5	24 × 6	28 × 3	23 × 6	14 × 7	14 × 7	15 × 6	14 × 5	19 × 5
Reproductive									
staminate inflorescence type of higher branching order	condensed	condensed	condensed	loose	loose	loose	loose	loose	loose
staminate inflorescence branching order	few	few	few	several	several	several	several	several	several
carpophore	subglobose	discoid	subglobose	subglobose	elongate	elongate	elongate	elongate	elongate

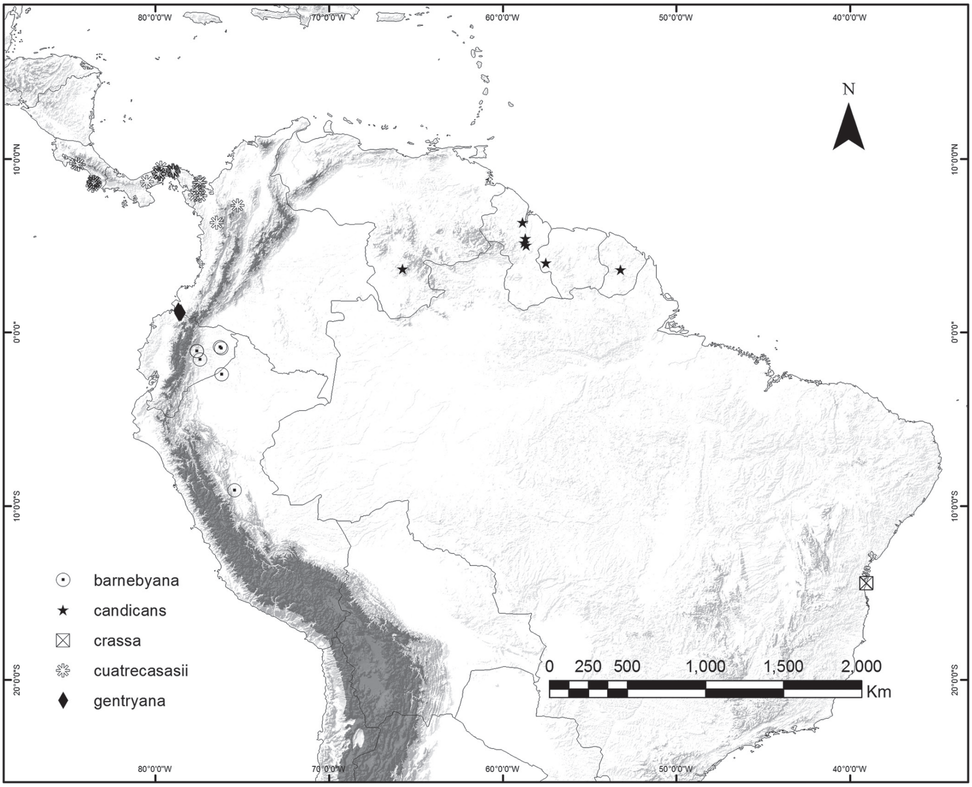

Figure 9. Geographic distribution of *Curarea barnebyana*, *C. candicans*, *C. crassa*, *C. cuatrecasasii* and *C. gentryana*.

two discriminant functions explained 68% and 16% of the variation respectively. Traits strongly correlated with the first discriminant function are inner whorl anther length, outer whorl anther length and inner whorl petal length. On the other hand, leaf width, leaf length and bract length are only weakly correlated with the second function. A cross validation (leave-one-out) classification showed that, overall, 70% of the specimens were correctly classified and individuals of the **tm** and **to** groups were 79% and 92% correctly classified, respectively.

Analysis of the subset of dataset 2, which excluded the toxicofera group, recovered three clusters, **al**, **iq** and **tm** + **uc**, however the Wilk's test was not significant (Wilk's lambda = 0.000022, p = 0.2368). Similarly, a cross validation analysis indicated that, overall, only 37% of the specimens were correctly classified (not shown).

Hence based on the results of the lda analysis of the quantitative traits in dataset 2, a conservative approach is to recognise: the toxicofera (**to**) group, the tomentocarpa (**tm**) group (including the ucayali [**uc**] group) and the iquitana (**iq**) group (including the allpahuayo [**al**] group) as separate entities (i.e. as three distinct species).

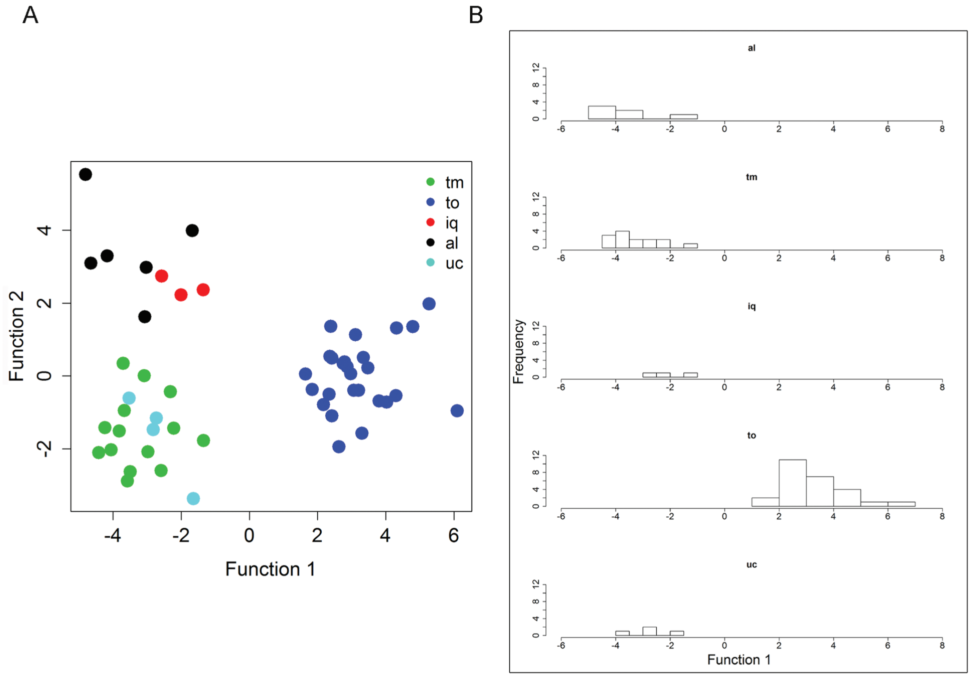

Figure 10. Linear discriminant analysis of characters from leaves, staminate inflorescences and staminate flowers of the five *a priori* groups of the *Curarea toxicofera* complex: **A** plot of scores of function 1 and function 2 **B** histograms of the first discriminant function values showing the positions of the five *a priori* defined groups, **al** = allpahuayo, **iq** = iquitana, **tm** = tomentocarpa, **to** = toxicofera and **uc** = ucayali, respectively.

The groups, here evaluated, appear to vary across an ecological gradient and the **al** and **uc** groups may represent separate entities that could be recognised when more material becomes available. Of the groups here recognised, one corresponds to *C. toxicofera s.s.*, the other two (**iq** and **tm**) were also previously described and two new combinations are here proposed.

Taxonomic treatment

Curarea Barneby & Krukoff

Curarea Barneby & Krukoff, Mem. New York Bot. Gard. 22(2): 7. 1971.

Type. *Curarea toxicofera* (Wedd.) Barneby & Krukoff.

Description. *Lianas*, dioecious, growing in canopies or understory; branchlets villous, strigose or strigillose-tomentellous to glabrate, conspicuously ridged. *Leaves* simple, spirally arranged; blade narrowly to broadly ovate or elliptic, oblong, broadly elliptic, suborbicular, less frequently obovate; attached to the petiole at the base or scarcely subpeltate, chartaceous to coriaceous, base truncate or obtuse to rounded or slightly cordate, margin entire (or very rarely minutely undulate, weakly lobed or apically bilobed in *C. candicans*), apex retuse (cleft), acute or acuminate, rarely mucronulate, often cuspidate in young shoots, surfaces usually discolorous, especially when juvenile, lustrous and glabrous adaxially, but midrib sometimes sparsely tomentose, abaxially with finely silvery tomentellous, strigillose-tomentellous or web-like indumentum or the latter coarse and cream or dark brown villous, sometimes restricted to the areolae with age; palmati- to plinerved, (3–)5–7 main veins, the innermost pair perfect or imperfect acrodromous, secondary veins 0–2(–3) pairs or rarely absent, departing from midrib above the middle of the blade; petiole terete, tomentose to glabrate, pulvinate at both ends, apical pulvinus usually more conspicuous, the surface weakly rugulose, sometimes adaxially flattened. *Inflorescences* are solitary or fascicled, cauliflorous, axillary, supra-axillary or terminal on young shoots, basically thyrsi or simple dichasia; bracts subtending the primary branches lanceolate, narrowly ovate or ovate, markedly concave, fleshy, glabrous adaxially, variously pubescent abaxially, indument appressed or spreading. *Staminate inflorescence* with the axes sometimes conspicuously ridged; primary branches either lax, with several branching orders or compact and with few branching orders, pauci or multiflowered, variously pubescent. *Pistillate inflorescences*, with primary branches consisting of simple dichasia or these reduced to single flowers, mostly pauciflorous. *Flowers* are unisexual, actinomorphic and trimerous; pedicels conspicuous (absent in staminate flowers), terete, moderately slender, sometimes ridged, pubescent; bracteoles 1–2(4), usually early caducous, especially in staminate flowers. *Staminate flowers* are cream, whitish, greenish, yellowish, orangish, greyish or brownish; sepals 6(–9), in 2(–3) unequal whorls (spirally arranged), free, mostly ovate, narrowly ovate to obovate, oblong, rhombic, elliptic or suborbicular, inner whorl larger than outer one, both whorls weakly concave, scarce fleshy, glabrous adaxially and variously densely pubescent abaxially, tip of inner sepals erect or reflexed past anthesis; petals (5–)6 in 2, more or less similar whorls, smaller than the inner sepals, free narrow or broadly obovate-trilobed, obovate-rhombic or spatulate, weakly concave, membranous, glabrous adaxially, glabrous to densely tomentellous abaxially, base cuneate to distinctly clawed, lateral margins weakly to strongly inflexed and partially clasping the filaments, rarely those of the inner whorl adaxially connate, apex acute, obtuse, truncate or retuse; stamens (3–)6 in (1–)2 similar whorls, filaments free or variously connate, clavate, clavate-sigmoid or weakly terete, glabrous adaxially, glabrous or tomentellous abaxially, anthers basifixed, erect or weakly incurved, the connective is frequently thicker adaxially and forms a keel or a hump at the base or at the apex of the anther, less frequently forming a horn-like structure beyond the anthers; thecae latrorsely opening by longitudinal slits, sometimes anthers splitting into two halves (i.e. abaxial and adaxial) due to the reduction of the connective; pistillode 0. *Pistillate flowers* are green, yellowish or brownish coloured; sepals 6–9 in 2–3 unequal whorls, free, ovate-lanceolate, elliptic, ovate, broadly ovate, oblong or rhombic, glabrous adaxially, pubescent abaxially, tips of inner sepals usually reflexed after anthesis; petals 3(–6), free, spatulate, weakly concave, membranous, glabrous adaxially, glabrous to sparsely tomentellous abaxially; staminodes

0; carpels 3(–4), tomentose, free, sometimes proximal half coherent when young, style slightly tapering distally, stigma inconspicuous. *Infructescences* sometimes lenticellate or with the bark exfoliating; fruiting pedicels weakly clavate or terete, at times inconspicuous; carpophores are elongated and terete in understory species or short and subglobose in canopy species (drum-like in *C. candicans*). *Drupelets* oblongoid, ellipsoid, broadly obovoid or subglobose, sometimes weakly flattened laterally, sessile or rarely gradually narrowing toward the base, thus rarely forming a short stipe; stylar scar basal and frequently conspicuous; exocarp thin to thick (including the several layers immediately beneath the epidermal layer), coriaceous when dried, smooth, rugulose or muriculate, densely pilosulose, velutinous to glabrate, dull orange to yellow when ripe; mesocarp mucilaginous; endocarp thin and papyraceous or crustaceous, surface smooth or weakly ribbed along its long axis, less frequently there are also transversal ribs. *Seed* with endosperm absent, embryo hippocrepiform, cotyledons thick, accumbent, sometimes unequal.

Key to the species of *Curarea*

1 Abaxial surface of leaf blades covered with coarse, golden, cream, dark brown or greyish tomentellous indumentum **2**

– Abaxial surface of leaf blades covered with finely silvery-tomentellous, strigillose-tomentellous or web-like indumentum **4**

2 Staminate inflorescences with primary branches lax, these with (2–)4 or more branching orders .... ***6. C. tecunarum***

– Staminate inflorescences with primary branches compact, these with 0–2 branching orders **3**

3 Staminate inflorescences with golden indumentum; drupelets broadly obovoid, weakly laterally compressed, centric or only weakly eccentrically attached; mature leaves broadly ovate to suborbicular; Atlantic Forest in Southeastern Brazil .... ***3. C. crassa***

– Staminate inflorescences with dark brown indumentum; drupelets narrowly obovoid to ellipsoid, laterally compressed, strongly eccentrically attached; mature leaves narrowly ovate to elliptic; foothill forests in Ecuadorian Amazon and eastern Peru .... ***1. C. barnebyana***

4 Staminate inflorescences with condensed primary branches; carpophores discoid-shaped .... ***2. C. candicans***

– Staminate inflorescences with lax primary branches; carpophores inconspicuous or elongated **5**

5 Staminate flowers with lateral margins of inner petals incurved and connate; stamens frequently 3; drupelets obovoid, ca. 4 × 2.8 cm, on inconspicuous carpophores .... ***5. C. gentryana***

– Staminate flowers with lateral margins of inner petals incurved but free; stamens frequently 6; drupelets ellipsoid or oblongoid, 1.3–3.2 × 0.8–1.8 cm, on conspicuously elongated carpophores **6**

6 Staminate inflorescence with filiform primary branches ...**4. *C. cuatrecasasii***

– Staminate inflorescences with moderately stout primary branches...............7

7 Staminate inflorescences with rufescent or silvery hispidulous indumentum; drupelets frequently with strongly muriculate surface ....**8. *C. tomentocarpa***

– Staminate inflorescences with greyish or brownish strigillose indumentum; drupelets with relatively smooth surface **8**

8 Staminate flowers up to 1.8 mm long, anthers up to 0.3 mm long with connective strongly protruding apically either conically or as a horn, less frequently humped; endocarps 1.7–2.4 cm long ....**7. *C. iquitana***

– Staminate flowers up to 2.4 mm long, anthers up to 0.6 mm long with connective usually not apically protruding or overgrowing as a hump when older; endocarps 0.7–0.9 cm long..**9. *C. toxicofera***

1. *Curarea barnebyana* R.Ortiz, sp. nov.

urn:lsid:ipni.org:names:77185798-1

Figs 11, 12

Diagnosis. The species is distinguished by its coriaceous leaves that are narrowly ovate or elliptic, with dense brown villous indumentum, primary branches of the staminate inflorescence contracted/condensed and drupelets broadly obovoid or ellipsoid.

Type. Ecuador. Pastaza: Pastaza Canton, pozo petrolero “Moretecocha” de ARCO 75 km al este de Puyo, bosque húmedo tropical, 01°34'S; 77°25'W, 580 m, 4–21 Oct 1990, (♂ fl), *Gudiño, Quelal & Caiga 952* (holotype: MO!; isotypes: QCNE!, NY!, US!).

Note. Ortiz-Gentry (2000; unpublished MS thesis) provisionally used the epithet *phaeofusca* for this taxon.

Description. Large canopy *lianas* about 20–30 m tall; older stem 6–20 cm wide, strongly flattened, with shallow lengthwise fissures; bark dark brown; branchlets densely coarsely dark brown villous tomentose. *Leaves*: blades 9–15 × 6–11 cm, ovate to elliptic, subcoriaceous to coriaceous when mature or when exposed to direct sunlight in the canopy; surfaces discolorous, lustrous and glabrous adaxially, coarsely dark brown or cream villous abaxially, trichomes concealing the epidermis at all stages, base obtuse to rounded, apex acuminate or retuse, cuspidate when juvenile, 5(7) palmati- or plinerved, innermost pair of main veins acrodromous perfect on mature leaves, acrodromous imperfect on juvenile ones, midrib and secondary veins slightly impressed adaxially, conspicuously raised abaxially, secondary veins 1–2 pairs, arising above the middle of the blade, veinlets immersed on the adaxial surface, raised abaxially; petioles 2.5–8.5(–15) cm long, terete, densely dark brown villous, apical pulvinus terete, rugulose. *Staminate inflorescences* solitary, axillary or slightly supra-axillary, thyrsi (Fig. 11A–B), densely dark brown villous; axes 7.4–9 cm long; primary branches, 1.2–1.9 cm long, with compact and reduced (0–1) branching orders; bracts 0.9–1.1 mm long, narrowly ovate, concave, fleshy, glabrous adaxially, dense dark brown villous abaxially. *Pistillate inflorescences*, solitary or fascicled, axillary, few-flowered thyrsi, the primary branches reduced to single flowers (Fig. 12A), indumentum as on staminate inflorescences; axes 4.8–5.3 cm long, terete or angular; bracts 0.7–1.1 mm long, ovate, concave, fleshy, glabrous adaxially, brown villous abaxially. *Staminate flowers* 1.4–1.7 mm long, cream to brownish; pedicels ca. 0.9–1.9 mm long, terete, indumentum as on the axis; bracteoles 1–2, 0.3 × 0.1–0.2 mm, ovate to oblong, fleshy, glabrous adaxially, brown tomentose abaxially; sepals 6, glabrous adaxially, brown tomentose abaxially; outer sepals 0.6–0.7 × 0.3–0.5 mm, ovate or oblong, base truncate, apex acute; inner sepals 1.3–1.5 × 1–1.3 mm, obovate or obovate-rhombic, base obtuse, apex obtuse or rounded, tip of inner sepals erect but not reflexed past anthesis; petals 6, 0.6–0.7 × 0.3–0.5 mm, inner ones a little narrower, obovate-rhombic, weakly concave, glabrous adaxially and abaxially, base obtuse to cuneate-truncate (shortly clawed), lateral margins inflexed, partially clasping the filaments, apex obtuse, acute or weakly retuse; stamens 6; filaments 0.4–0.5 mm long, clavate, moderately thick, free or shortly connivent, glabrous; anthers 0.2–0.3 mm long, erect, connective forming a conical-shaped protrusion adaxially, (Fig. 11G), not protruding beyond thecae apically. *Pistillate flowers* 1.6 mm long, brownish; pedicels 3.2–3.6 mm long, terete; bracteoles 2, 0.4–0.5 × 0.3 mm, ovate, fleshy, glabrous adaxially, brown tomentose abaxially; sepals 6–9, in 2–3 whorls, weakly concave, slightly fleshy to fleshy, glabrous adaxially, brown tomentose abaxially; outer sepals, 0.6–0.9 × 0.3–0.6 mm, ovate or oblong, base truncate, apex obtuse; middle sepals ca. 0.9 × 0.8 mm, obovate, base and apex obtuse; inner sepals 1.1–1.6 × 1–1.5 mm, weakly obovate or elliptic, base and apex obtuse, tips erect to reflexed past anthesis; petals 3, 0.8–1.3 × 0.6–1.4 mm, spatulate, weakly concave, glabrous adaxially, glabrous or sparsely tomentose abaxially, base clawed, apex retuse; carpels 3, 0.4–0.9 × 0.3–0.7 mm, dark brown villous tomentose, indumentum appressed-ascending; style 0.4–0.5 mm long. *Infructescences* axes 2–6.7 × 0.3–0.5 cm, indumentum as on pistillate inflorescences; fruiting pedicel 0.3–0.6 cm, clavate; carpophores triangular or subglobose, ca. 3.6 mm long, convex at apex, dark brown villous. *Drupelets* 2.9–4.5 × 2.3 3.1 cm, yellow or orange when ripe, narrowly obovoid to ellipsoid (Fig. 12F), weakly laterally flattened, at times gradually attenuate toward the base; base obtuse, strongly eccentrically attached; stylar scar not apparent; exocarp 4–6 mm thick, surface rugose, dark brown villous tomentose, granular when dried; mesocarp thin, mucilaginous; endocarp 2.5–3.5 × 1.5–1.9 cm, chartaceous, surface smooth. *Seeds* with embryo 5.8–6.9 cm long, cotyledons slightly unequal.

Distribution and ecology. Andean foothills of eastern Ecuador and eastern Peru (Fig. 9), at elevations of 200–450 m in tropical wet forest. Staminate flowering specimens were collected in January, June and October; fruiting and old pistillate flowering specimens were collected in January and June.

Common names and uses. Ecuador. "jondomebo" (Huaorani) (*Gudiño et al. 952*, ♂ fl).

Eponymy. The specific epithet honours the late Dr. Rupert C. Barneby whose work has laid the foundations for all subsequent taxonomic studies of neotropical Menispermaceae.

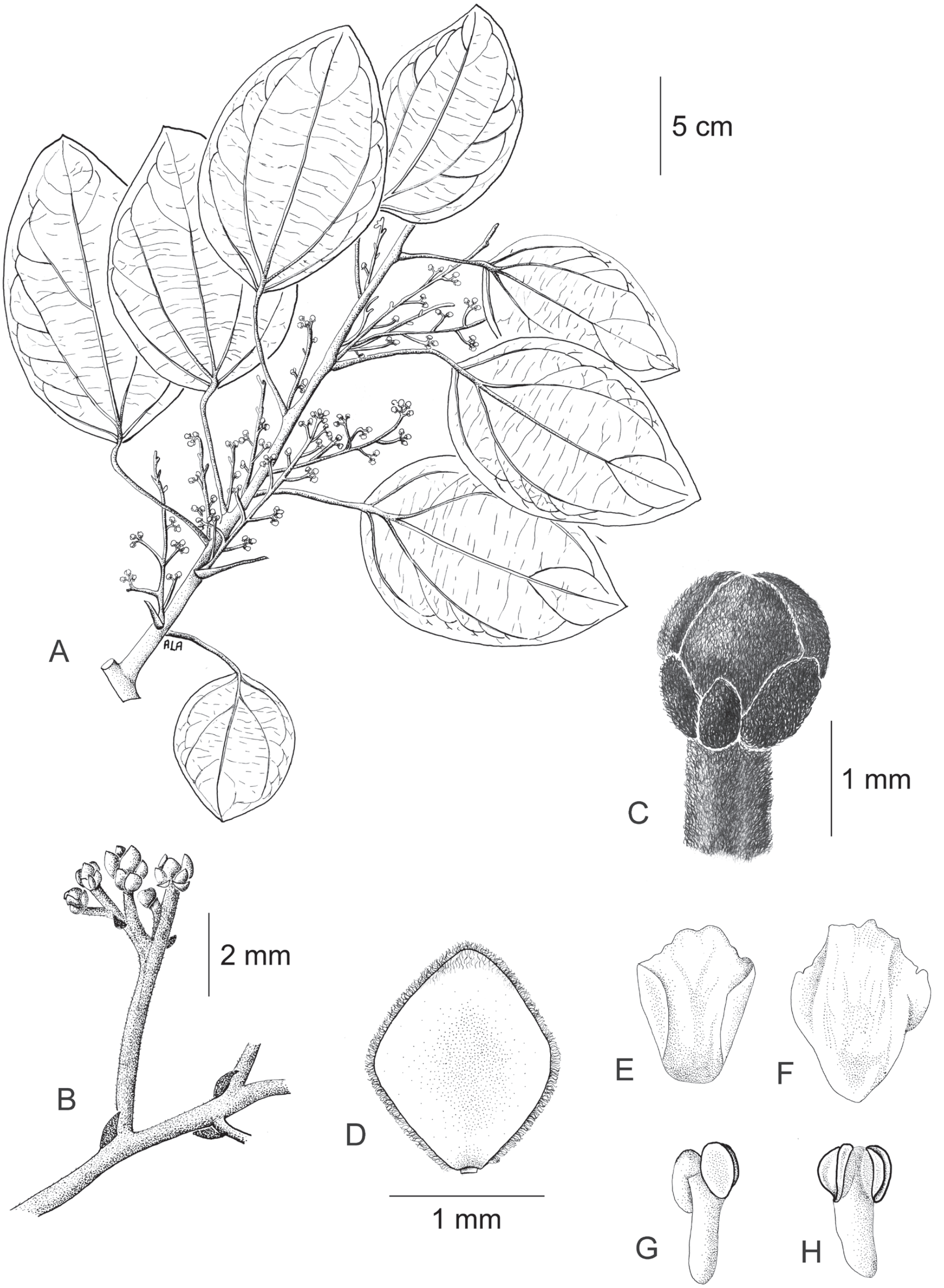

Figure 11. *Curarea barnebyana* staminate plant: **A** flowering branch **B** detail of inflorescence **C** flower bud **D** inner sepal, adaxial surface **E–F** outer and inner petals, adaxial and abaxial surfaces **G–H** outer stamens, latero-adaxial and abaxial surfaces (based on *Gudiño et al. 952*).

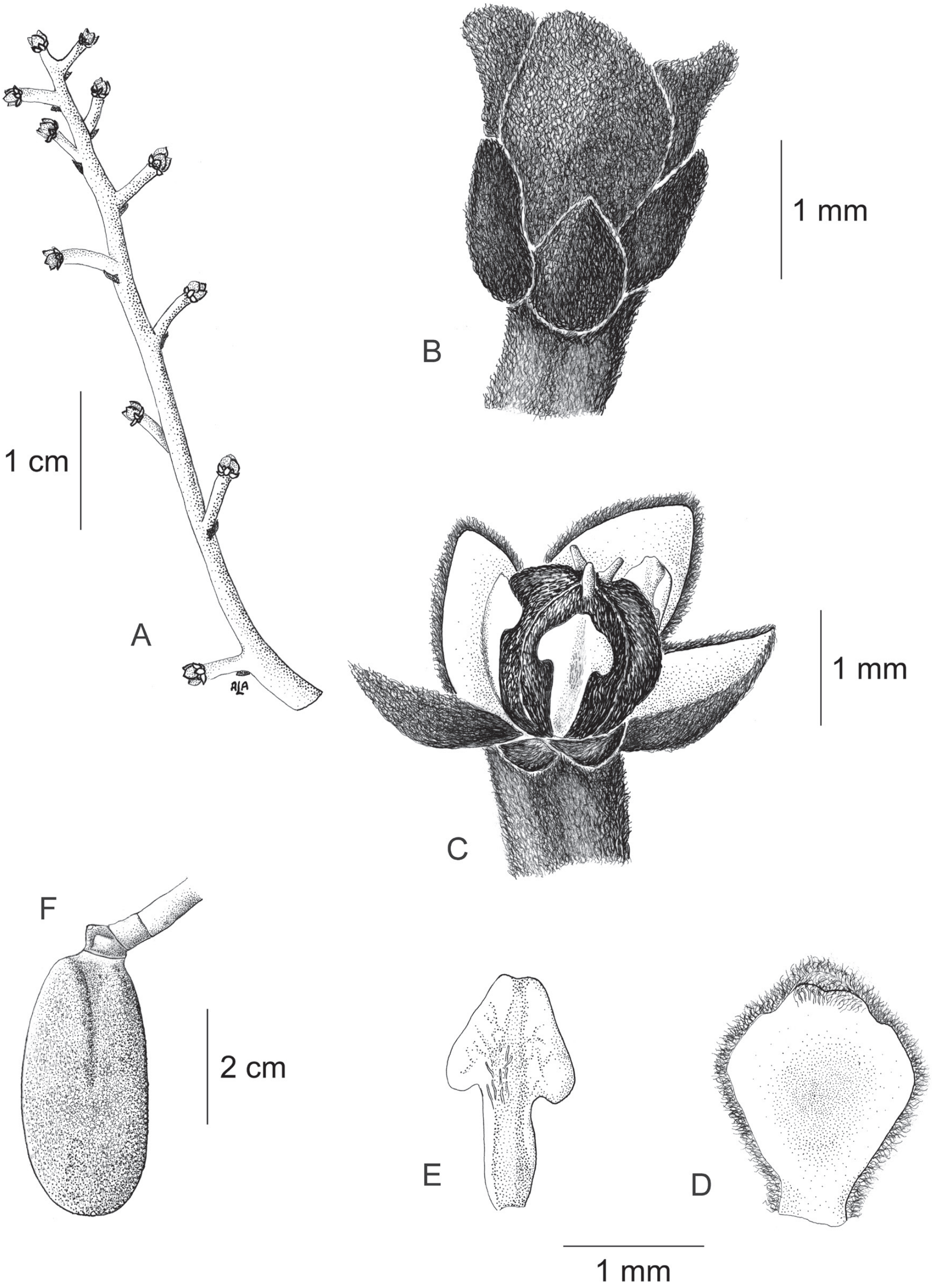

Figure 12. *Curarea barnebyana* pistillate plant: **A** inflorescence **B** flower **C** opened flower showing the petals and carpels **D** innermost sepal, adaxial surface **E** petal, abaxial surface **F** fruit, lateral surface. (**A–E** based on *Ortiz & Vargas 200* **F** based on *Dik 1213*).

Conservation status. The calculated Extent of Occurrence (EOO) based on ten collections representing six localities of *C. barnebyana* resulted in 72,674 km^2, whereas the Area of Occupancy (AOO) was estimated as 24 km^2. Of the six sub populations representing four locations, two of the latter are found nearby private or national protected areas in eastern Ecuador and is very likely that more individuals will be found within these areas. Of the two other locations found across the border, in Peru, one of them is in a rather continuous tract of forests, whereas the other is found in a nearby area where there is increasing deforestation, which may result not only in a decline in habitat quality, but also likely reduction of the geographic range of the species in the future. Based on these considerations, *C. barnebyana* is assigned a preliminary status of “Vulnerable ” [VU, A3c + B1b(i,ii,iii,iv) + B2b(i,ii,iii,iv)].

Discussion. *C. barnebyana* is recognised by its large obovoid or ellipsoid and weakly laterally flattened drupelets covered with a dark brown villous tomentose indumentum and borne on claviform fruiting pedicels. Similar indumentum is found in *C. tecunarum*, but the primary branches of the staminate inflorescences of the latter are laxly branched, while the primary branches of the inflorescences of *C. barnebyana* are condensed similar to those of *C. crassa* and *C. candicans* (see discussion under *C. crassa*). Shared anatomical features amongst these species, which make up group 1, are summarised in Table 5. In the fruiting condition, *C. barnebyana* loosely resembles *C. crassa*, but it is readily distinguished by its relatively long (ca. 8 cm in length) infructescence axis, clavate fruiting pedicels and narrowly obovoid to ellipsoid drupelets that are weakly laterally flattened and have a dark brown indumentum. *Curarea crassa*, on the other hand, has a short (ca. 0.5–2 mm long) infructescence axis, terete fruiting peduncles and broadly obovoid drupelets with a dense, golden villous indumentum.

Paratypes. ECUADOR. **Napo:** Parque Nacional Yasuní, Pozo Petrolero Daimi 2, 00°55'S; 076°11'W, 200 m, 26 May–8 Jun 1988, (fl bud), *Cerón & Hurtado 4094* (MO!, QCNE!); Canton Tena Estación Biológica Jatun Sacha, 8 km al este de Misahuallí, bosque muy húmedo tropical, 01°04'S; 077°36'W, 400 m, 23–31 Jan 1989, (imm fr), *Cerón 6008* (G!, MO!, NY!, QCNE!); Reserva Etnica Huaorani, Carretera y oleoducto de Maxus en construcción, km 86–89, 00°51'S; 76°15'W, 260 m, 25–30 Mar 1994, (mat fr), *Dik 1213* (MO!, QCNE n.v.); Canton Tena Estación Biológica Jatun Sacha, 450 m, 7 Jan 1989, (imm fr), *Neill 8705* (G!, NY!, QCNE!); ibid., (♀ fl & imm fr), *Neill 8712* (G! [2], MO!); Estación Biológica Jatún Sacha, 28 Jun 1996, (♀ fl & imm fr), *Ortiz & Vargas 194* (MO! [2]); ibid., 29 Jun 1996, (♀ fl & imm fr), *Ortiz & Vargas 195* (MO!); ibid., 3 Jul 1996, (♀ fl & imm fr), *Ortiz & Vargas 200* (MO!).

PERU. **Loreto:** Campamento Forestal, 16 km from the Ecuador border near Río Conventes, overgrown road cut margins, [02°25'S; 076°10'W], 12 Apr 1979, (old fr), *Aronson & Rodrigues 859* (MO!). **Ucayali:** Prov. de Padre Abad, distrito de Padre Abad, carretera al caserío San Miguel y Mapuya, 12–17 km de Aguaytía, bosque primario con abundante luz solar, 09°05'S; 075°26'W, 350 m, 8 Oct 2004, (♂ fl), *Schunke & Graham 16307* (F n.v., MO!).

2. ***Curarea candicans*** **(Rich. *ex* DC.) Barneby & Krukoff**

Figs 13A, 14

Curarea candicans (Rich. *ex* DC.) Barneby & Krukoff, Mem. New York Bot. Gard. 22(2): 12. 1971.

Abuta candicans Rich. *ex* DC., Syst. 1: 543. 1818.

Type: French Guiana. Cayenne: "Cayensibus dicitur, genus affine *Cissampelos*", no date [1781–1789], (sterile), *L.C. Richard s.n.* (lectotype, designated here [or perhaps holotype]): P–Jussieu Herbarium 10832, photocopy of microfiche P!, IDC microfiche 6206. 803.I). Guyana. Demerara: Mabura Hill Concession, ridgetop ecotone between Wallaba and Purpleheart forest, 05°25'N; 058°40'W, 50 m, 20 Nov 1986, (♂ fl), *Pipoly & Boyan 8982* (epitype, designated here: MO!; isoepitypes: NY!, US!). Note: Following Art. 9.8 of the Melbourne Code (MacNeill et al. 2012), I am here designating an epitype to serve as an interpretative type of *Abuta candicans*, whose sterile condition makes it ambiguous for identification purposes.

Sciadotenia candicans (Rich. *ex* DC.) Diels, in Engl. Pflanzenr. 4(94): 87. 1910.

Type: Based on *Abuta candicans* Rich. *ex* DC.

Chondrodendron candicans (Rich. *ex* DC.) Sandwith, Bull. Misc. Informat. Kew. 1930: 342.

Type: Based on *Abuta candicans* Rich. *ex* DC.

Cocculus dichroa Mart., Flora 24, Beibl. II: 46. 1841.

Type: Brazil. Para: Habitat in silvis, no date, (sterile), *Martius s.n.* (lectotype, designated here: M! [image seen]; isolectotype: B! frag., likely of M).

Sciadotenia leucophylla Miers, Contr. Bot. 3: 344. 1871.

Type: In Guiana [Guyana]. Guiana Batavana: no date, (sterile), *Anderson s.n.* (holotype: BM! [BM000071492]).

Abuta limaciifolia Diels, in Engler, Pflanzenr. IV.94(Heft 46): 194. 1910.

Type: Brazil. Para: Peixe Boi, [25] July 1907, (♂ fl bud), *Rodr. Sigueira s.n.* [Herbário Amazônico Museu Paraênsis (Museu Goeldi) MG-8266], (lectotype designation effected by Krukoff and Moldenke 1938: 20: B!, F neg. 4993; isolectotypes: BM! [BM000071503], MG! [image seen]). Note: The F negative of B specimen has two annotations, one at the bottom right that reads: *Abuta limaciifolia* Diels and a second one to the bottom left that reads: "*Anomospermum limaciifolium* Diels sp. nov.", a non-published name, this later annotation is missing in the B specimen available in this study, which may suggest that this second annotation label was not glued-down or the existence of another specimen at B. However, the B specimen I studied appears in every other feature to be the source of the F photograph. Additionally, the measurements included in the original description of the species, suggest that Diels did not examine the duplicates at BM and MG, hence the lectotype designated is the B specimen examined here. The citation by Diels of "Herbário Amazônico Museu Paraênsis" is in reference to the label of the material in B, not to a sheet in MG.

Chondrodendron limaciifolium (Diels) Moldenke, in Krukoff & Moldenke, Brittonia 3: 20. 1938.

Type: Based on *Abuta limaciifolia* Diels.

Abuta (?) *pullei* Diels, Rec. Trav. Bot. Neerl. 22: 348. 1925.

Type: Suriname. Without locality, 4 Sep 1920, (sterile), *Pulle 408* (lectotype designation effected by Krukoff and Moldenke 1938: 18: U! [U-30956, photographs at F!, G!, GH!, MO!; isolectotypes: B!, frag., U! [U-30955]). Note: the original material of *Abuta*? *pullei* comprises juvenile leaves and is mounted on two sheets at U. Both appear to have Diels' handwriting and the sheet U-30956 has one, more or less, complete leaf and two fragmentary leaves. The second sheet, labelled as U-30955, is a much younger leaf and it appears that its measurements were not included in the description of the species. Hence the U-30956 specimen has been considered the holotype and annotated as such by previous authors, a designation that is followed in this study.

Description. Large canopy *lianas* ca. 25 m tall; older stem flattened (width unknown); bark dark brown, with shallow lengthwise fissures; branchlets densely brownish to silvery strigose. *Leaves:* blades 9–23 × 5–12 cm, elliptic, oblong or narrowly ovate, subcoriaceous to coriaceous when mature and up in the canopy; surfaces conspicuously discolorous when juvenile, lustrous and glabrate to glabrous when mature adaxially, silvery web-like indumentum concealing the abaxial epidermis when juvenile, with few brownish trichomes on main veins, densely tomentellous with age, indumentum usually confined to the areolae, base obtuse, rounded or cuneate, margin entire, (minutely undulate –"*crispatulo subdentato*"– (de Candolle 1818: 543), apex acuminate (bilobulate), cuspidate when juvenile, usually 3–5(7) palmatinerved, less frequently plinerved, innermost pair of main veins acrodromous perfect on mature leaves, usually acrodromous imperfect on leaves from young shoots, midrib immersed or raised adaxially, raised abaxially, secondary veins 0–3 pairs, usually arising above the middle of the blade, veinlets weakly prominent adaxially in juvenile leaves, immersed on mature ones, always raised abaxially, sparsely silvery-tomentose adaxially when juvenile; petioles 2.5–16 cm long, the smaller sizes are frequently associated with canopy leaves and thus fertile plants, silvery, greyish or rufous strigillose-tomentellous, the trichomes appressed or ascending, glabrate with age, apical pulvinus conspicuous, rugulose, shallowly grooved adaxially. *Staminate inflorescences* solitary or fascicled, slightly supra-axillary or axillary, narrowly branched thyrsi (Fig. 13A–B), densely silvery to greyish or rufescent strigillose tomentellous, conspicuously ridged; axes (1.2–)6.5–10.6 cm; primary branches 0.6–2.1 cm long, compact and 1–2(–3) branching orders (Fig. 13B); bracts 0.5–0.9 mm long, ovate, concave, fleshy, glabrous adaxially, abaxially indumentum as on inflorescence. *Pistillate inflorescences* unknown. *Staminate flowers* 1.2–1.3 mm long, greenish, yellowish or brownish; pedicels 0.9–5.6 mm long, conspicuously ridged, indumentum as on staminate inflorescence; bracteoles 1–3, 0.3–0.5 × 0.2–0.3 mm, ovate, ovate-lanceolate or oblong, fleshy, glabrous adaxially, silvery tomentellous abaxially; sepals 6, usually 2-whorled (spirally arranged (?) and 8 in number, *Steyermark et al. 125686*), glabrous adaxially, silvery tomentellous abaxially; outer sepals 0.7–1.2 × 0.2–0.6 mm, narrowly ovate or ovate-lanceolate, base obtuse or truncate, apex acute (middle sepals ca.1–1.2 × 0.7 mm, obovate, base obtuse, apex rounded); inner sepals 0.9–1.6 × 0.8–1 mm, obovate to suborbicular, base obtuse, apex acute or obtuse (weakly retuse), tip of inner sepals erect to reflexed past anthesis; petals 6, 0.4–0.8 × 0.2–0.6 mm, inner ones slightly shorter and narrower, obovate to obovate-trilobed, weakly concave, membranous, glabrous adaxially, glabrous to sparsely tomentellous abaxially, base cuneate, lateral margins inflexed, partially clasping the filaments, apex obtuse or truncate; stamens 6, filaments 0.2–0.6, mm long, inner ones slightly longer, clavate-terete, moderately thick, free or connivent, glabrous; anthers 0.1–0.3 mm long, erect, connective slightly protruding apically, thicker adaxially and forming a protruding keel at the base of the anthers or shortly overgrowing thecae when older (Fig. 13G–H). *Pistillate flowers* unknown. *Infructescences* axes 2.5–2.7 × 0.3 cm, thyrsi (Fig. 14A–B), velutinous; fruiting pedicel 0.5–1.1 cm long, terete; carpophore drum-like, ca. 1.3 mm long, apically weakly concave, velutinous. *Drupelets* ca. 2.5 × 1.7 cm, (colour when ripe unknown), broadly ellipsoid to subglobose (Fig. 14B), slightly eccentrically attached, base obtuse; stylar scar weakly protruding; exocarp 2 mm thick, surface rugulose or weakly muriculate, velutinous, granular when dried; mesocarp not seen; endocarp papyraceous, surface smooth. *Seeds* and embryo not seen.

Distribution and ecology. North-eastern South America, from southern Venezuela, Guyana, Suriname, French Guiana and northern Para in Brazil (Fig. 9), in Terra Firme forest from near sea level to 710 m in Lely Mt., Suriname. Staminate flowering specimens were collected in January, July, October and November; the single fruiting specimen was collected in February.

Common names and uses. Guyana: “teteabo (Arawak), “granny’s backbone” (Creole), (Sandwith 1930, *Sandwith 561*, ♂ fl); used in the preparation of “warrou’s other kind of poison” (*Jenman 5199*, ♂ fl). **Suriname**: “dobroedoea” (*Vreden 11706*, st). **Venezuela:** “shiña-ten” (*Steyermark et al. 125686*, ♂ fl bud).

Etymology. The epithet “candicans” doubtlessly stems from the silvery indumentum on the abaxial surface of leaves, which is dense and matted in young individuals.

Conservation status. Analysis of the seven collections representing seven localities resulted in an Extent of Occurrence (EOO) of 209,650 km^2 and an Area of Occupancy (AOO) of 28 km^2. Of the seven subpopulations, the most recent collection –a sterile specimen– was made in 2004. While the species has not been collected during the past decade, which may be suggestive of population decline, it is also likely that, due to its climbing habit, the species might have been overlooked by collectors. Additionally, one of the seven individuals occurred in a nature reserve in Venezuela and the locality where one collection was made in French Guiana in the early 1990s, has also become a nature reserve. Based on these observations and the results of the assessment, *C. candicans* is assigned a preliminary status of “Least Concern” (LC).

Discussion. The drum-like carpophores of *C. candicans* (Fig. 14B) are unique in the genus. In all other species, these are elongated or subglobose. Vegetatively, *C. candicans* is also distinctive on account of the sparse appressed or ascending brownish trichomes on main veins and dense silvery web-like indumentum on the abaxial surface of leaves from young shoots. This indumentum later changes to a tomentellous

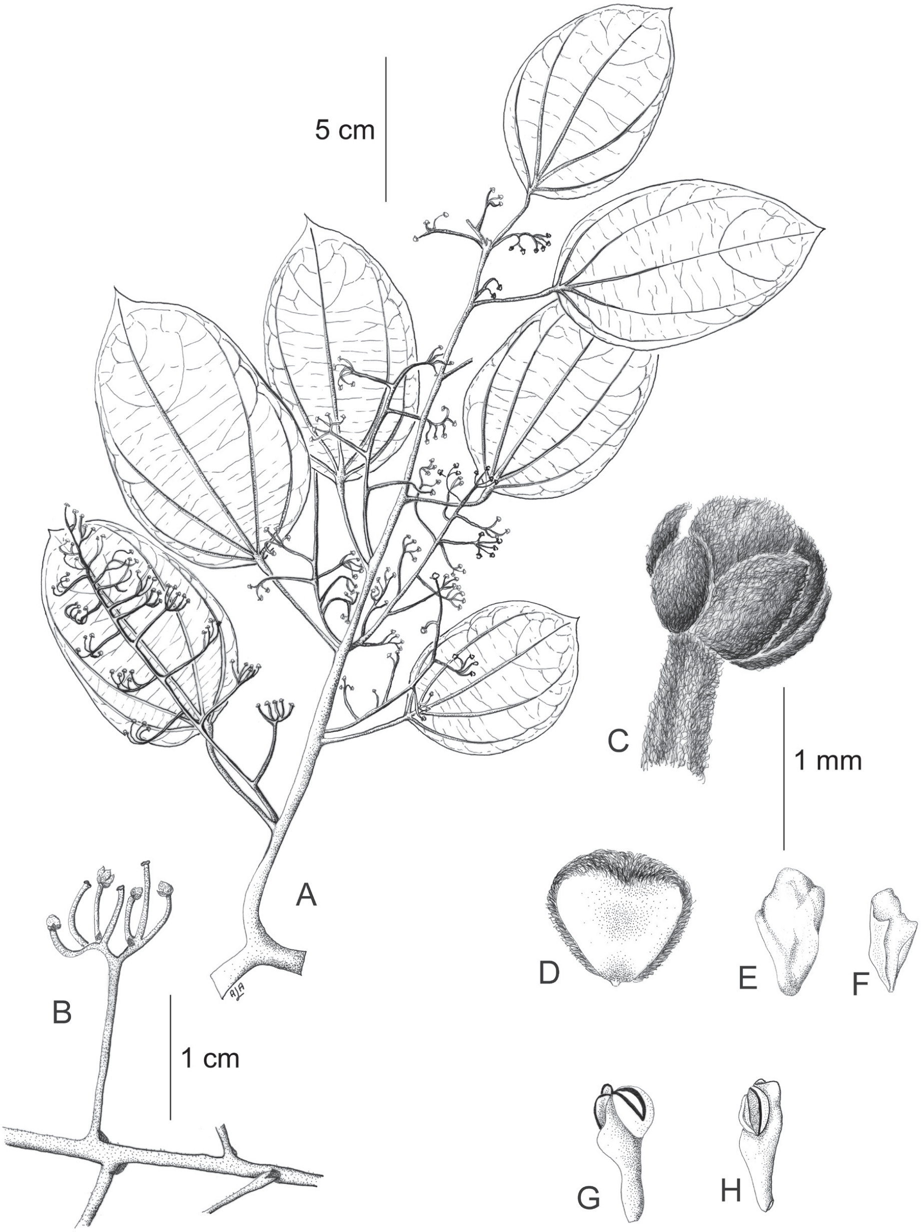

Figure 13. *Curarea candicans* staminate plant: **A** flowering branch **B** detail of inflorescence **C** flower bud **D** inner sepal, adaxial surface **E–F** outer and inner petals **G–H** outer stamens, latero-adaxial and lateral surfaces (based on *Pipoly & Boyan 8982*).

cover that usually becomes restricted to the areoles with age. The only other species with similar web-like indumentum is *C. gentryana*, described below, but this lacks the brownish appressed trichomes on the main veins of *C. candicans* and, moreover, its

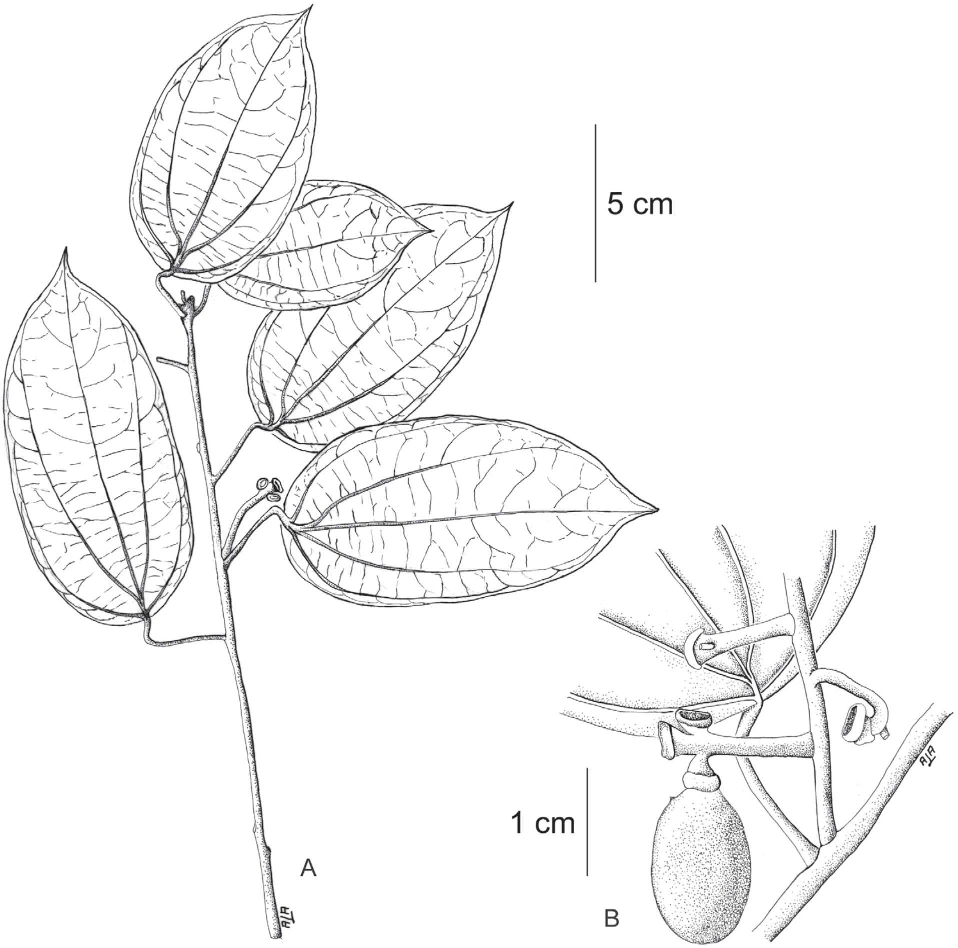

Figure 14. *Curarea candicans* pistillate plant: **A** branch showing fruiting peduncle with no fruits **B** fruiting branch (based on [*Jardim Botanico do Rio RB-19508*]).

web-like indumentum persists on old leaves. When leaves of *C. candicans* are tomentellous and this indumentum is not yet restricted to the areoles, they are indistinguishable from those of *C. toxicofera* and *C. cuatrecasasii*. However, neither of the two occurs in the Guianas and both have laxly branching rather than compact primary branches of the inflorescences of *C. candicans*.

In a family-wide phylogenetic analysis, *C. candicans* is recovered as sister to the remaining sampled species and support for this placement is high (Ortiz et al. 2016). It shares similar narrowly branched secondary axes in the staminate inflorescences with *C. crassa* and *C. barnebyana*.

The type of *Abuta candicans*, the basionym of *Curarea candicans* (Rich. *ex* DC.) Barneby & Krukoff, is a sterile and unnumbered Richard collection from French Guiana (deposited in the P herbarium). Although the specimen in question shows features usually not associated with the remaining specimens referred to *C. candicans*, such as leaves with bilobulate apex, minutely undulate margins and penninerved venation, these features have sporadically been observed in a few sterile specimens of other *Curarea* species, although not in the same combination on the same specimen. I follow earlier workers in accepting this sterile specimen as the type of the basionym of *Curarea candicans*; as described by de Candolle (1818), the leaves are abaxially "*glabris candicantibus*", hence the specific epithet, which highlights a distinctive feature of this species. However, in order to unequivocally fix the application of the name, an epitype is being designated is this study.

On another unnumbered collection of Richard, also at P, one of the four labels has the annotation "Type coll. 2" made by Krukoff in 1968. This specimen is rather dissimilar from the type material: its leaf blades are elliptic, the apices are not bilobed and the secondary veins arise beyond the middle of the leaf, towards the apex; however, the abaxial surface is whitish. A comparison of this second specimen with other collections from the region suggests that it is conspecific with the fertile representatives of the species. However, there is no indication in de Candolle's original description of the existence of another specimen and he described the lamina as having a bilobed apex; thus this second specimen should not be considered part of the original material.

In the protologue, von Martius (1841) contrasted *Cocculus dichroa* with *Abuta candicans*. Eichler (1864) considered the two conspecific and placed *Cocculus dichroa* as a synonym. Similarly, Miers (1871: 392) in listing *Abuta*? *candicans* as a presumed species, imperfectly known species in current terminology, he also listed *Cocculus dichroa* as synonym of *A. candicans*. Miers also noted that, due to its lack of inflorescences, it was uncertain whether the specimen in question belonged in *Abuta* or in *Chondrodendron*. Subsequently, *Cocculus dichroa* Mart., has been considered a synonym of *Sciadotenia candicans* (Rich. *ex* DC.) Diels (Diels 1910), *Chondrodendron candicans* (Rich.) Sandwith (Sandwith 1930) and, more recently, *Curarea candicans* (Rich. *ex* DC.) Barneby & Krukoff (Barneby and Krukoff 1971).

The sterile type material of *Cocculus dichroa* at M, image from JStore, has the leaf blades ovate, with a long-acuminate apex and the adaxial surface somewhat bullate. While ovate and long-acuminate leaves are characteristic of juvenile leaves of all species of *Curarea*, however a somewhat bullate adaxial surface has not been observed in *C. candicans*. This vegetative feature might turn out to be a distinguishing character when studied in more specimens and the extent of morphological variation *C. candicans* is better understood. At this time however, *C. candicans* is the only other species known to occur in Para and, in this study, I hesitantly follow earlier workers in the family in including *C. dichroa* as a synonym of *C. candicans*.

Specimens examined. BRAZIL. Pará: Santa Isabel. Ea. de F. [Estrada de Ferro] de Bragança, 15 Feb 1909, (detached old fr), *collector unknown*, (RB n°. 19508!).

FRENCH GUIANA. Cayenne: *Richard s.n.*, no date, (st), (P!). **Saül:** Vicinity of Eaux Claires, Sentier Botanique, between Crique Tortue and Split in trail, 03°37'N, 053°12'W, 200-400 m, 1 Nov 1992, (♂ fl), *Mori et al. 22743* (NY!).

GUYANA. Demerara: Mabura Hill, Ekuk compartment, mixed forest on loamy sand, 05°10'N; 058°45'W, 12 Oct 1989, (♂ buds & fl) *Jansen-Jacobs et al. 1995*, (NY!, U!); Upper Demerara-Berbice, Pibiri Research Site, 53 km S of Mabura Hill, 05°01'N; 058°37'W, 2 Feb 2004, (st), *Torke et al. 310* (MO!). **Cuyuni-Mazaruni Region:** Kartabo, Willems Timber Concession, Wallaba (Eperua) forest on white sand, 06°21'N; 58°50'W, 100 m, 22 Jan 1989, (old ♂ fl), *Hahn & Tiwari 5136* (US!). **Essequibo:** Basin of Issororo River, 1888, (♂ fl), *Jenman 5199* (K!); Essequibo River, Moraballi Creek, near Bartica, near sea level, 6 Nov 1929, (♂ fl), *Sandwith 561* (K! [3], NY n.v.).

SURINAME. Without locality, Nov 1941, (st), *Krukoff 12305* (GH!, NY n.v.); Railroad Paramaribo-Dam, Nov 1941, (st), *Krukoff 12335* (GH! [2], NY n.v., US n.v.); In hellingbos tussen, km 11.0 en 11.1, montibus, qui dicuntur Nassau, 17 Mar 1949, (st), *Lanjou & Lindeman 2775a* (NY n.v., U!); ibid., (st), *Lanjouw & Lindeman 2779* (NY n.v., U!); Nickerie, area of Kabalebo Dam Project, 30–130 m, Boegroemaka forest on gentle slope towards creek, west of road, km 80, 04°00'N; 57°30'W, 22 Sep 1980, (st), *Lindeman et al. 539* (U!); Lely Mts., SW plateaus covered by ferrobauxite, forest on plateau S of camp 4, 550–710 m, 5 Oct 1975, (st), *Lindeman et al. 805* (MO!, NY n.v.);

Open spot from fallen tree near 7100 m in line from road, km 80 eastward, area of Kabalebo Dam Project, 30–130 m, 11 Nov 1981, (st), *Lindeman & de Roon 808* (U!); Mapane Creek area, along Sarwa road, plot in succession, no date, (st), *Vreden 11663* (U!); Mapane Creek area, 29 Apr 1967, (st), *Vreden 11706* (U!); Without locality, (st), no date, *collector unknown* (U-32454-B!).

VENEZUELA. Amazonas: Atabapo, Rio Cunucunuma, entre las comunidades La Culebra y Huachamacari, entre El Cerro Duida y Huachamacari, 03°40'N; 065°45'W, 180-210 m, 28 Jan–8 Feb 1982, (♂ fl bud), *Steyermark et al. 125686* (MO!, NY!, US!).

3. *Curarea crassa* Barneby

Figs 15, 16

Curarea crassa Barneby, Brittonia 48: 20. 1996.

Type: Brazil. Bahia: Uruçuca, 14°25'S; 39°01'W [39°03'W], 2 Dec 1994 (old fr), *Jardim et al. 351* (holotype: CEPEC n.v.; isotypes: K!, NY! [image seen].

Description. Large canopy *lianas* ca. 24 m tall; older stems with the lower part strongly flattened (width unknown); bark greyish to dark brown; branchlets dense and coarsely golden to silvery villose. *Leaves*: blades 8–10 × 6–9 cm, broadly elliptic to suborbicular, (narrowly ovate), coriaceous when mature or when directly exposed to sunlight in the canopy; surfaces discolorous, lustrous and glabrous adaxially, but sometimes sparsely tomentellous on main veins, golden or cream villous abaxially, the indumentum concealing the epidermis at all stages, base truncate to widely obtuse, margin entire, apex acuminate (especially when juvenile or not directly exposed to sunlight) to acute or retuse when mature or exposed to direct sunlight up in the canopy, 5–7 palmati- or plinerved, innermost pair of main veins acrodromous perfect on mature leaves, acrodromous imperfect on juvenile ones, secondary veins 0–2 pairs, arising almost at the apex of the blade, all veins slightly immersed adaxially, raised abaxially, but concealed by the indumentum; petioles 2.7–4.5 cm long, ridged, sparsely to densely golden or silvery villous, apical pulvinus conspicuous, rugulose, slightly flat to shallowly grooved or rounded adaxially. *Staminate inflorescences* solitary or fascicled, axillary or supra-axillary, thyrsi (Fig. 15A–B), golden villous tomentose; axes 9.8 cm long; primary branches compact and up to 1.1 cm long, with reduced (0–1) branching orders; bracts ca. 0.8 mm long, ovate, concave, fleshy, glabrous adaxially, golden villose abaxially.

Pistillate inflorescences (old) solitary or fascicled, axillary, few-flowered thyrsi, indumentum as on staminate inflorescences; axes ca. 3.8 cm long; bracts not seen, primary branches 0.6 cm long, indumentum as on the axis. *Staminate flowers* ca. 1.4 mm long, pale cream; pedicels ca. 1.3 mm long, terete, indumentum as on the axis; bracteoles 2, ca. 0.5 × 0.3 mm, narrowly ovate, fleshy, glabrous adaxially, light golden tomentose abaxially; sepals 6, indumentum as on bracteoles; outer sepals ca. 0.8 × 0.5 mm, ovate-lanceolate to ovate, base truncate, apex acute to obtuse; inner sepals ca. 1.4 × 1.3 mm, obovate or rhombic, base and apex obtuse, tip of inner sepals erect to hardly inflexed past anthesis; petals 6, ca. 0.7–0.8 × 0.6 mm, obovate, weakly concave, membranous, glabrous adaxially and abaxially, base cuneate, lateral margins inflexed, partially clasping the filaments, apex truncate or weakly retuse; stamens 6; filaments ca. 0.5 mm long, clavate, thick, free, glabrous adaxially and abaxially; anthers ca. 0.3 mm long, erect, connective thicker adaxially and forming a protruding keel at the base of the anthers (Fig. 15H), not overgrowing the thecae when older. *Pistillate flowers* ca. 2.1 mm long, greenish; pedicels ca. 0.5 mm long, appearing ridged, indumentum as on staminate inflorescences; bracteoles 2, 0.7 × 0.4 mm, ovate-lanceolate, fleshy, glabrous adaxially, light golden tomentose abaxially; sepals 9, in three whorls, glabrous adaxially, light golden tomentose abaxially; outer sepals ca. 0.9 × 0.5 mm, ovate-lanceolate; middle sepals ca. 1.6 × 0.7 mm, lanceolate to ovate-lanceolate; inner sepals 2.1 × 1.2 mm, elliptic or rhombic, their tips erect or weakly reflexed past anthesis; petals 3, ca. 1.3 × 1 mm, spatulate, weakly concave, membranous, glabrous adaxially, sparsely to densely silvery tomentellous abaxially, base clawed, apex truncate to slightly retuse; carpels 3, 1.1 × 0.7 mm, villous; style 0.4 mm long. *Infructescences* axes ca. 0.5–1.2 × 0.4–0.6 cm, indumentum moderate greyish-silvery tomentose; fruiting pedicels 5.8–6.1 mm long, terete; carpophores subglobose, ca. 2.4 mm long, convex at apex, golden villous. *Drupelets* 3.5 × 2.9 cm, (colour when ripe unknown), broadly obovoid (Fig. 16A), centrically or only weakly eccentrically attached, base oblique, stylar scar inconspicuous, surface golden villous; exocarp 6.7 mm thick, outer surface rugose, granular when dried; mesocarp not seen, but likely thin and mucilaginous; endocarp ca. 2.6 × 2.2 cm, papyraceous to chartaceous, surface smooth. *Seeds* and embryo not seen, (horny, ca. 23 × 18 mm, Barneby 1996).

Distribution and ecology. *Curarea crassa* is known only from the coastal Atlantic Forest of Bahia in Brazil (Fig. 9), at ca. 76 m in elevation. Staminate flowering specimens were collected in May, whereas a pistillate flowering specimen was collected in February and immature fruiting specimens were collected in July and December.

Common names and uses. Brazil: “buta” (*Fróes 12701/67*, st).

Etymology. Not explained in protologue, but likely the name is in reference to its thick exocarp (mesocarp in original description).

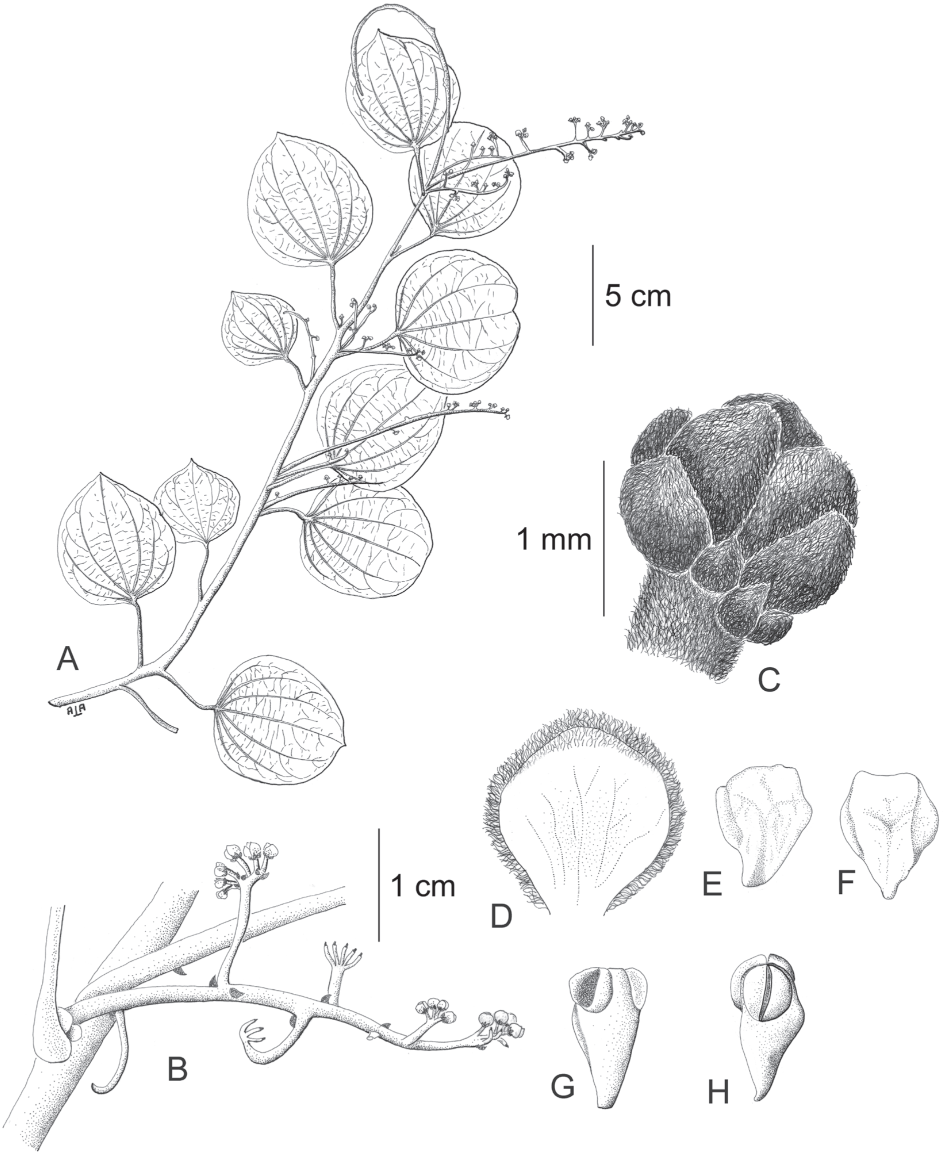

Figure15. *Curarea crassa* staminate plant: **A** flowering branch **B** detail of inflorescence **C** flower bud **D** inner sepal, adaxial surface **E–F** outer and inner petals, abaxial views **G–H** outer stamens, abaxial-lateral surfaces (based on *Thomas et al. 10900*).

Conservation status. The five collections representing three localities resulted in an estimated EOO of 45 km^2 and an AOO of 12 km^2. The three localities correspond to two subpopulations and two locations, of which one is found within a protected area.

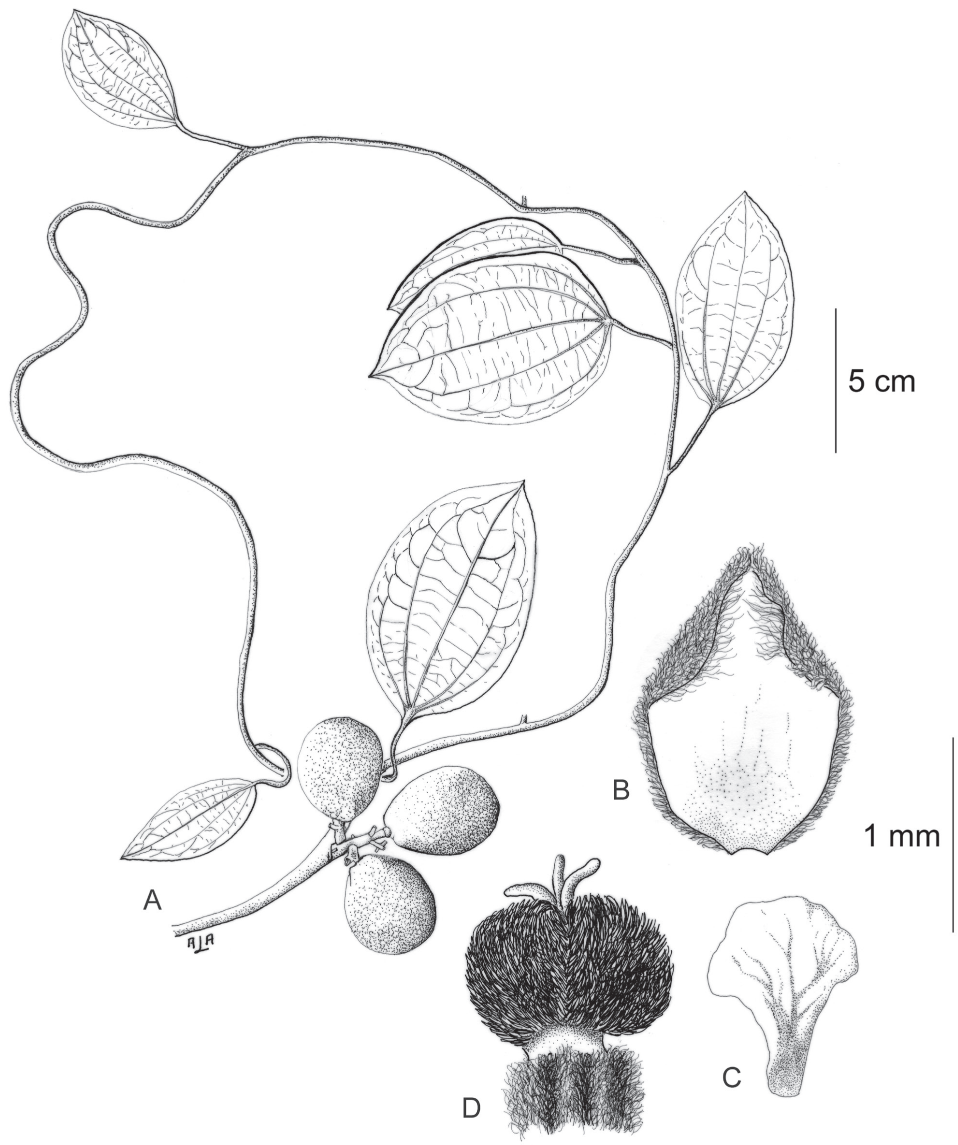

Figure 16. *Curarea crassa* pistillate plant: **A** fruiting branch **B** innermost sepal, adaxial surface **C** petal, abaxial surface **D** carpels (based on *Jardim et al. 609*).

However, ongoing deforestation in the largely degraded Brazilian Atlantic forest may negatively affect the already localised subpopulations of *C. crassa*, further reducing suitable habitat. Based on these considerations, *C. crassa* is here assigned a preliminary status of "Endangered" [EN B1ab(i,ii,ii,iv,v) + B2ab(i,ii,ii,iv,v)].

Discussion. *Curarea crassa* is vegetatively conspicuous because of its broadly elliptic or suborbicular leaves covered with a dense golden or creamy villous indumentum on the abaxial leaf blade surface. Similar indumentum may sometimes also be observed on the abaxial leaf blade surfaces of *C. barnebyana* and *C. tecunarum*; from *C. barnebyana*, it differs by its woolly, greyish-golden indumentum in the staminate inflorescences (*vs.* dark-brown). From *C. tecunarum*, *C. crassa* differs by its primary branches with few branching orders in the staminate inflorescence (*vs.* primary branches with several branching orders in *C. tecunarum*). Also, the large and broadly obovoid drupelets are unique to *C. crassa*.

The thick layer, from which the specific epithet is likely derived, was described as the mesocarp (Barneby 1996), however it is likely that the mesocarp in *C. crassa*, as in *C. barnebyana*, *C. tecunarum* and *C. aff. iquitana*, is mucilaginous and no longer noticeable in dried fruits, as was the case reported for *C. tecunarum* (Barneby and Krukoff 1971).

On morphological grounds, *C. crassa* is placed with the species of Group I. Micro-morphological characters shared amongst species in Group I are summarised in Table 5. *Curarea crassa* shares its staminate inflorescences with condensed branch orders with species of that group. They differ in the inflorescence indumentum colour, this being cream or golden in *C. crassa vs.* dark brown or greyish in *C. barnebyana*. The primary branches of the staminate inflorescences are also condensed in *C. candicans*, but there, trichomes are strigillose-tomentellous and not villous as in *C. crassa*.

In the protologue of *C. crassa*, Barneby (1996) described staminate flowers as having 9 sepals, but only 6 sepals were found in the only staminate plant available in this study (*Thomas et al. 10900*). This discrepancy is likely due to infraspecific variation as was also occasionally observed in *C. candicans* and in *C. aff. iquitana*.

Specimens examined. BRAZIL. Bahia: Uruçuca, Serra Grande, 7.3 km na Estrada Serra Grande/Itacaré, Fazenda Lagoa do Conjunto Fazenda Santa Cruz, 14°25'S; 39°01'W [39°03'W], 19 Jul 1994, (♂ fl), *Carvalho et al. 4563* (CEPEC n.v., NY! [image seen]; Região da Mata Atlântica, 14 Jul 1995, (imm fr), *Carvalho et al. 6031* (NY!); Una, Reserva Biológica do Mico-Leão (IBAMA), entrada no km 46 da rod, BA-001, Ilhéus/Una, Região da Mata Higrófila Sul Bahiana, 8–10 km na Estrada que margeia ao Rio Maruim, 15°09'S; 39°05W, 6 Jun 1996, (imm fr), *Carvalho et al. 6222* (CEPEC n.v., NY! [image seen]); Ilhéus, basin of Rio Santa Ana, high forest, near Bom Gosto, 8 Dec 1942 (st), *Fróes 12701/67* (A!, NY n.v.); Uruçuca, Serra Grande, 7 .3 km na estrada Serra Grande/Itacaré, Fazenda Lagoa do Conjunto Fazenda Santa Cruz, 14°25'S; 39°01'W [39°03'W], 9 Feb 1995, (♀ fl), *Jardim et al. 609* (NY!); 7.4 km north of Serra Grande on road to Itacaré, 14°25'24"S; 039°03'38"W, 12 May 1995, (♂ fl), *Thomas et al. 10900* (MO!, NY!).

4. *Curarea cuatrecasasii* Barneby & Krukoff

Figs 17, 18

Curarea cuatrecasasii Barneby & Krukoff, Mem. New York Bot. Gard. 22(2): 14. 1971.

Type: Colombia. Antioquia: Rain forest of Villa Agraria, Las Caucheras, basin of Río León o Bacubá, 95 m, 2 Oct 1961, ([imm?] fr), *Cuatrecasas & Willard 26168* (holotype: COL!, NY neg. 8433; isotypes: NY! [NY00008325, frag.], US! [US00104020]).

Description. Medium-sized understory *lianas* about 5–10 m tall; older stem more or less terete to weakly irregularly flattened, 0.5–1.5 cm wide; bark dark brown, with shallow lengthwise fissures and conspicuously tuberculate-lenticellate; branchlets densely brownish to silvery strigillose-tomentellous to glabrate. *Leaves:* blades 9–26 × 4.3–13.5 cm, ovate to elliptic, chartaceous at all stages, base obtuse to rounded, apex acuminate, cuspidate when juvenile; surfaces discolorous, lustrous and glabrous adaxially, indumentum finely silvery strigillose-tomentellous abaxially, rarely confined to the areoles with age; 3(5) palmati- or plinerved, innermost pair of main veins acrodromous imperfect at all stages, midrib and lateral nerves slightly raised above, conspicuously raised abaxially, secondary veins 2(3) pairs, veinlets slightly prominent adaxially in both juvenile and mature leaves, raised abaxially; petioles (2.9–)6.2–18 cm long, ridged, rugulose, brownish or silvey strigillose-tomentellous to glabrate, distal pulvinus rugulose. *Staminate inflorescences* fascicled, cauliflorous, lax thyrsi (Fig. 17B–C), densely silvery or brownish strigillose-tomentellous; axes 2.2–8 cm long; primary branches 1.8–6.2 cm long, filiform, with several (2–)4–5 branching orders; bracts 0.4–1.1 mm long, lanceolate to narrow ovate, concave, fleshy, indumentum as on inflorescence.

Pistillate inflorescences unknown. *Staminate flowers* 1.2–1.6 mm long, green, greenish or brownish; pedicels 0.4–2.8 mm long, terete, sometimes ridged, indumentum as on the axis; bracteoles 2–3, 0.2–0.6 × 0.1–0.4 mm, ovate-lanceolate, oblong or ovate-rhombic, fleshy, glabrous adaxially, light brown tomentellous abaxially; sepals 6, glabrous adaxially, light brown to silvery tomentellous abaxially; outer sepals 0.8–1 × 0.5–0.8 mm, ovate-lanceolate, ovate or obovate, base and apex obtuse; inner sepals 1.2–1.7 × 0.6–1.1 mm, obovate or elliptic, sometimes oblong or ovate-rhombic, base cuneate, apex acute to obtuse, tip of inner sepals erect to strongly reflexed past anthesis; petals (5)6, 0.5–0.9 × 0.2–0.5 mm, inner ones slightly longer, narrowly obovate-trilobed or spatulate, weakly concave, membranous, glabrous adaxially, glabrous to sparsely silvery tomentellous abaxially, weakly to strongly recurved above the cuneate base, lateral margins inflexed, partially clasping the filaments, apex acute, sometimes obtuse; stamens (3–)6; filaments 0.3–0.7 mm long, inner ones slightly longer clavate to clavate-sigmoid, moderately thick, free or connate at base, glabrous; anthers 0.2–0.3 mm long, erect, connective thicker adaxially and forming (or not) a protruding keel at the base of the anther, sometimes apically overgrowing thecae and forming a hump adaxially when older (Fig. 17H–I). *Pistillate flowers* unknown. *Infructescences* axes 1.3–4 × 0.2–0.7 cm, bark exfoliating, cauliflorous, lax thyrsi, with simple dichasia as primary branches, brownish strigillose-tomentellous; fruiting pedicels (1.2–)6.5 mm long, terete to weakly clavate; carpophores 2.4–4.5 mm long, elongate, weakly terete to claviform, truncate or convex at apex, velutinous. *Drupelets* 1.9–3.2 × 1.2–1.8 cm, yellow or pale orange when ripe, oblongoid or ellipsoid (Fig. 18B), (weakly reniform), weakly

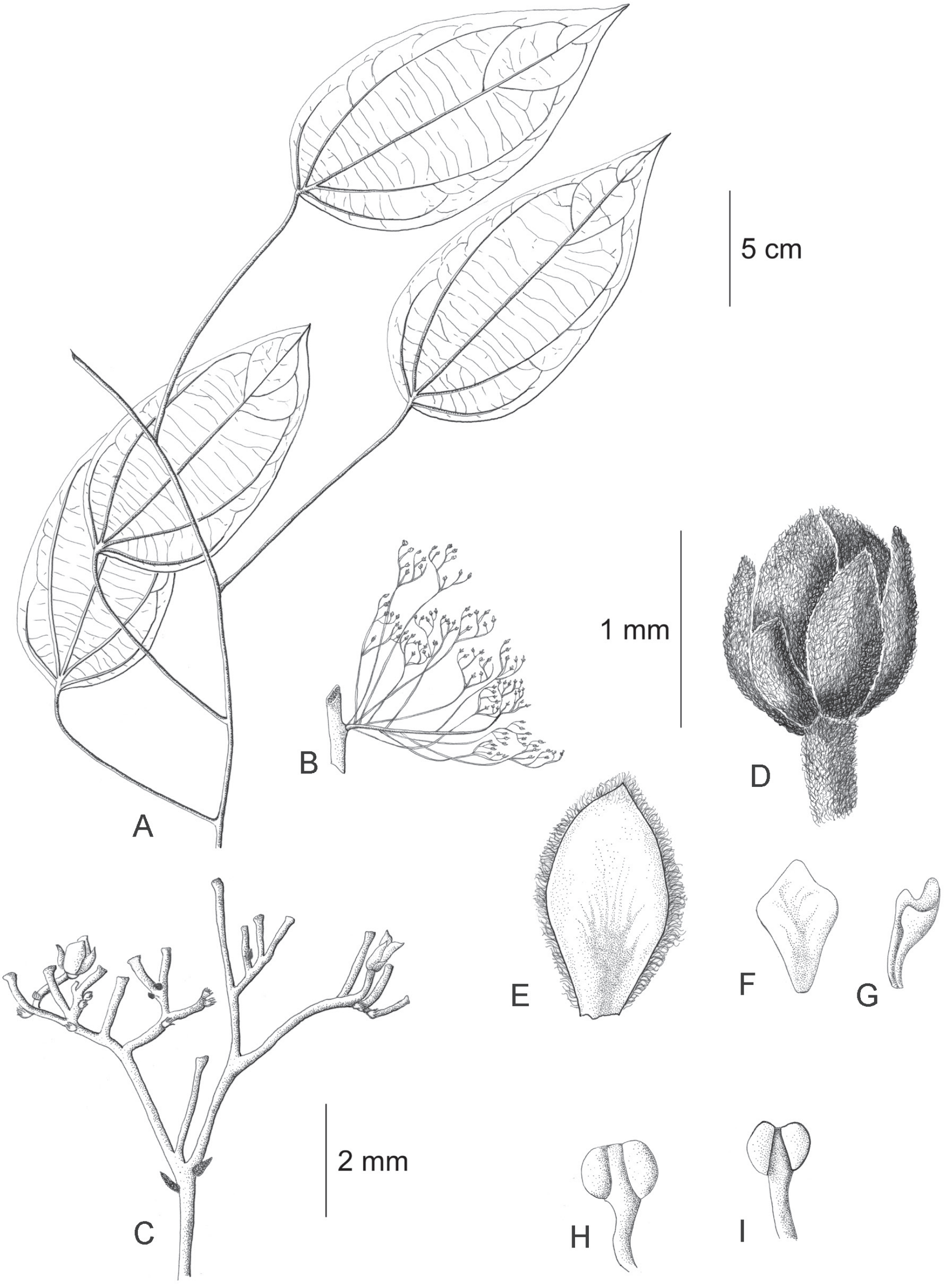

Figure 17. *Curarea cuatrecasasii* staminate plant: **A** habit **B** inflorescence **C** inflorescence detail **D** flower bud **E** inner sepal, adaxial surface **F–G** outer and inner petals, abaxial and lateral surfaces **H–I** outer stamens, adaxial and abaxial surfaces (based on *Aguilar 3303*).

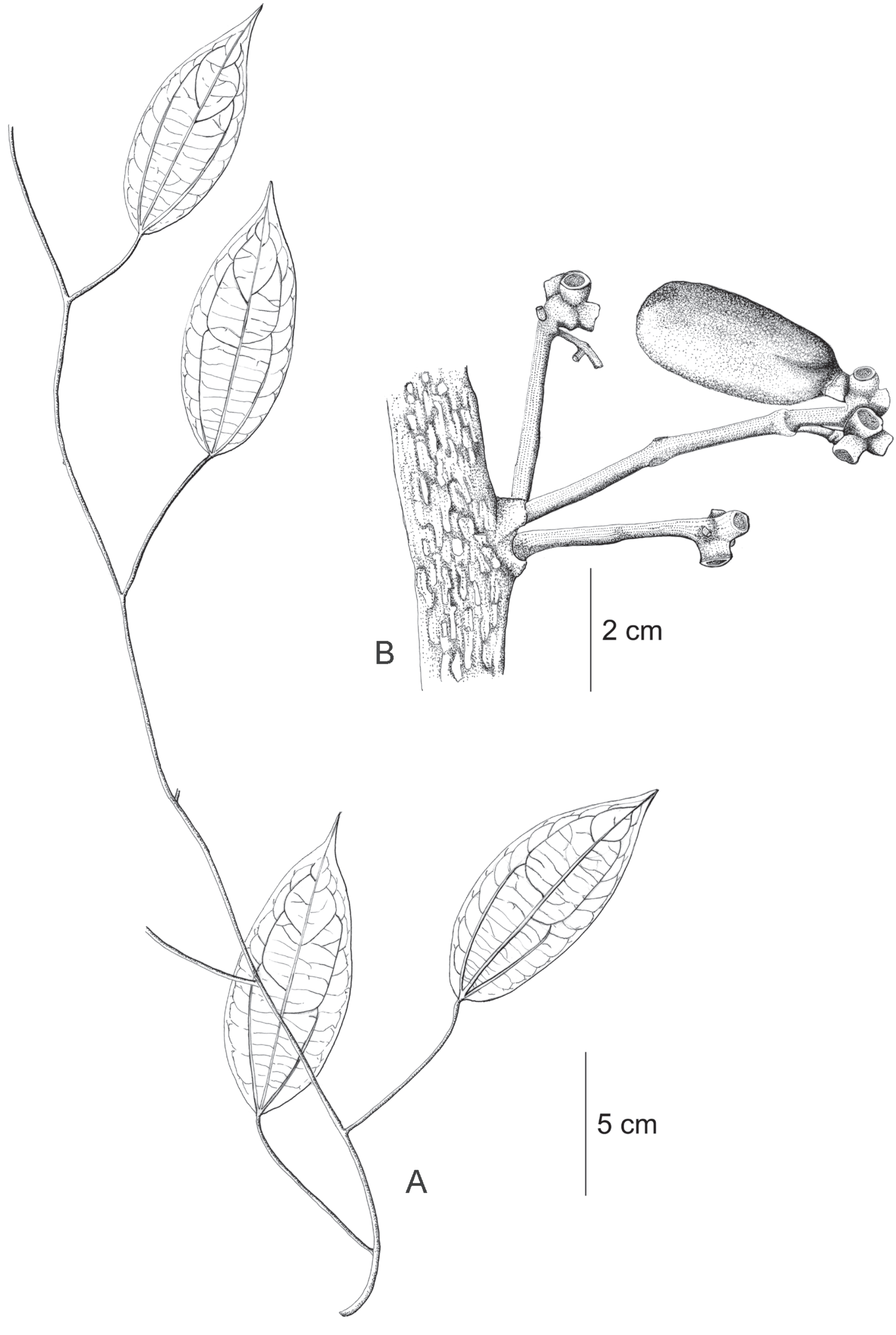

Figure 18. *Curarea cuatrecasasii* pistillate plant: **A** habit **B** infructescence (**A**, based on *Cuatrecasas & Willard 26168*; **B** based on *Marin 246*).

to strongly eccentrically attached, base truncate, obtuse to cuneate (gradually narrowed toward the base in a short (3–3.5 mm) stipe; stylar scar conspicuous; exocarp 1.2–1.9 mm thick, surface rugulose or muriculate, velutinous, granular when dried; mesocarp thin, mucilaginous; endocarp 1.5–2.4 × 0.9–1 cm, chartaceous, surface smooth. *Seeds* with embryo 3.8–4.8 cm long, crustaceous, cotyledons sometimes unequal.

Distribution and ecology. From Costa Rica throughout Panama to northwestern Colombia (Fig. 9), at elevations of 10–650(–1100) m. In wet tropical lowland to premontane forests. Staminate flowering specimens were collected in March, April, May, June and September; pistillate flowering specimens are unknown; fruiting specimens were collected in January, March and July–December.

Common names and uses. Costa Rica: edible fruits (*Morales et al. 3243*, mat fr). **Colombia:** used as magic plant by the Waunana (*Forero 666*, st).

Eponymy. As per Barneby and Krukoff (1971), "the specific epithet honors Dr. José Cuatrecasas, who contributed greatly to the knowledge of the Colombian Flora and was a co-collector of the holotype".

Conservation status. The calculated Extent of Occurrence (EOO) based on 26 collections representing 25 localities is 184,445 km^2, whereas the Area of Occupancy (AOO) is estimated as 100 km^2. Of the 23 subpopulations, 12 occurred in protected areas in Panama and Costa Rica and, although the species is not abundant where it occurs, it has a broad distribution. Hence, *C. cuatrecasasii* is assigned a preliminary category of "Least Concern" (LC).

Discussion. *Curarea cuatrecasasii* is distinguished from its congeners by the combination of slender staminate inflorescences bearing filiform primary branches, petals weakly to strongly recurved shortly above the base, connectives forming an adaxial hump at the apex of thecae when older and ovate or ovate-elliptic, 3–5-veined leaves with silvery strigillose-tomentellous indumentum on the abaxial surface. The staminate inflorescence of this species resembles those of *C. gentryana* and is discussed under the latter species.

In fruit, *C. cuatrecasasii* is indistinguishable from *C. iquitana*, *C. tomentocarpa* and *C. toxicofera* and they all share elongate carpophores, but they can be separated geographically: *C. cuatrecasasii* is restricted to the Pacific side of the Andes from North Eastern Colombia to Costa Rica and the other species are known only from the eastern side of the Andes in Colombia, Ecuador, Peru, Brazil and Bolivia.

The vessels width of *C. cuatrecasasii* is like that of *C. tecunarum* and *C. barnebyana* in being, on average, larger than the remaining species in group II (Table 5).

Selected specimens examined. COSTA RICA. Puntarenas: Reserva Forestal Golfo Dulce, Aguabuena, Sector Norte, [08°42'20"N; 083°28'30"W], 50–150 m, 21 Nov 1991, (imm fr), *Aguilar 682* (MO!); Parque Nacional Corcovado, Sirena, Corcovado basin trail, [08°29'N; 083°35'W], 50 m, 30 May 1989 (♂ fl), *Kernan & Phillips 1147* (CR!, F [2]!, INB!, MO!). **San José:** Puriscal, Z.P. La Cangreja, faja Costeña del Valle de Parrita, Mastatal de Puriscal, bosque primario en la cuenca del Río Negro, por La Ceiba, 09°41'24"N; 084°23'24"W, 300 m, 25 Nov 1994, (mat fr), *Morales et al. 3243* (CR!, MO!).

PANAMA. Canal Zone: Along Rio Mendoza and small tributary, 1/2-1 km upstream from Pipeline Road bridge, 8 km NW of Gamboa, Premontane wet forest, 100 m, 1 Nov 1973, (imm fr), *Nee 7731* (COL!, F n.v., MO-2035834, US!. **Coclé:** Along Llano Grande to Coclesito road above Cascajal, near divide, forest, 08°42'N; 080°28'W, 500 m, 11 Jan 1986, (imm fr), *McPherson 7956* (MO!). **Colón:** Rio Guanche, ca. 2.5 km upriver from bridge on road to Portobelo, [09°30'N; 079°39'W], 10–100 m, 14 Dec 1974, (imm fr), *Mori & Kallunki 3695* (MO!). **Darien:** Area from below the Rancho Frio to near ridgetop of Pirre Chain, [07°49'N; 077°43'W], 600–1100 m, 15 Nov 1977, (imm fr), *Folsom et al. 6357* (MO!, NY!). **Panama:** Pipeline road, premontane wet forest, [09°14'42N; 079°48'53"W–09°07'26"N; 079°42'33"W], 50–120 m, 11 Mar 1983, (♂ fl), *Gentry & Hamilton 41126* (MO!); Primary forest, along road between El Llano and Carti-Tupile road, from 12 miles above Pan American Hwy to continental Divide, [09°18'N; 078°56'W–09°19'N; 078°57'W], 200–500 m, 30 Mar 1973, (imm fr), *Liesner 1325* (MO-2035837); Pipeline Road, ca. 12 km NW of Gamboa, Tropical wet forest, [09°10'N; 079°45'W], 100 m, 26 Aug 1975, (imm fr), *Mori 7946* (MO!). **San Blas:** Quebrada E of town of Puerto Obaldia, upriver from the dam (represa), [08°40'N; 077°24'W], 0–50 m, 18 Apr 1982, (♂ fl), *Knapp & Mallet 4706* (MO!).

COLOMBIA. Antioquia: Mpio. Taraza, corregimiento "El Doce", Hacienda Las Mercedes, La Quebradona, 200 m NE de Medellin, 650 m, 3 Jul 1980, (imm fr), *Callejas 1183* (NY!); Mpio. Chigorodó, vereda Bohios, Finca La Cabaña, 30 m, 4 Apr 1985, (♂ fl.), *Renteria 3754* (JAUM n.v., MO!). **Bolivar:** Mpio. Achi, Inspección de La Raya, 100 m, 6 May 1987, (♂ fl), *Cuadros & Gentry 3606*, (JBGP n.v., MO!, NY!). **Chocó:** Mpio. de Riosucio, Zona de Urabá, Cerros del Cuchillo, Sector Cuchillo Negro, 10–30 m, 7 Sep 1987, (imm fr), *Cárdenas 374*, (JAUM n.v., MO!); Mpio. Bahia Solano, Corregimiento El Valle, trocha El Valle-Boro Boro, 06°21'N; 076°26'W, 17 Apr 1989, (♂ fl), *Espina et al. 2645* (MO!).

5. *Curarea gentryana* R.Ortiz, sp. nov.

urn:lsid:ipni.org:names:77185799-1

Fig. 19

Diagnosis. The species is distinguished from its congeners by its staminate flowers with the lateral margins of inner petals adaxially connate or connivent, also by its large broadly obovoid or ellipsoid drupelet that has a silvery tomentellous indumentum.

Type. Ecuador. Esmeraldas: San Lorenzo Canton, Reserva Indígena Awá, Parroquia Ricaurte, Comunidad Balsareño, Río Palabí, bosque muy húmedo tropical, bosque primario, disturbado, 01°09'N; 078°31'W, 100 m, 15–29 Apr 1991, (♂ fl), *Rubio & Quelal 1503* (holotype: MO!; isotypes: NY!, QCNE!).

Note. The earlier listing of the name in Ortiz-Gentry (2000) does not constitute effective publication as per article 30.8 of the Melbourne Code (MacNeill et al. 2012), and is therefore here being validated.

Description. Medium-sized understory *lianas* ca. 8 m tall, older stems more or less terete, 0.5–1 cm diameter, bark dark brown, with shallow lengthwise fissures and conspicuously tuberculate-lenticellate; branchlets brownish strigillose-tomentellous to glabrate. *Leaves*: blades 17–22 × 14–23 cm; broadly ovate, base truncate or weakly cordate, apex acuminate, cuspidate when juvenile; chartaceous when mature or when exposed to direct sunlight, otherwise membranous; surfaces discolorous, lustrous and glabrous adaxially, finely silvery web-like abaxially, indumentum concealing the surface, persistent at all stages; 5-palmatinerved, innermost pair of main veins acrodromous imperfect at all stages, midrib and lateral nerves slightly raised to weakly sunken adaxially, conspicuously raised abaxially, secondary veins 2(3) pairs, arising above the middle of the blade, veinlets raised on both surfaces; petioles 11.3–16.9 cm long, ridged, silvery or brownish strigillose-tomentellous to glabrate, weakly pulvinate at both ends, apical one conspicuous, rugulose. *Staminate inflorescences* fascicled, axillary or cauliflorous, lax thyrsi (Fig. 19A–B), silvery or brownish strigillose-tomentellous to glabrate; axes ca. 7.6 cm long; primary branches ca. 4 cm long, with several (2–5) orders of cymose branching, less frequently the higher branch orders are reduced on alternating sides, appearing racemiform; bracts ca. 1.1 mm long, lanceolate, concave, fleshy, indumentum as on inflorescence. *Pistillate inflorescences* unknown. *Staminate flowers* ca. 1.3 mm long, cream; pedicels ca. 0.7 mm long, terete, indumentum as on inflorescence; bracteoles 1–2, ca. 0.2 × 0.2 mm, ovate or oblong, fleshy, glabrous adaxially, silvery tomentellous abaxially; sepals 6, glabrous adaxially, silvery tomentellous abaxially; outer sepals ca. 1 × 0.6 mm, narrowly ovate or ovate-rhombic, base obtuse to truncate, apex acute or obtuse; inner sepals ca. 1.6 × 0.9 mm, obovate or weakly rhombic, base obtuse to cuneate, apex acute to obtuse, tip of inner sepals erect to strongly reflexed at anthesis; petals 6, ca.0.8– 0.9 × 0.4–0.5 mm, narrowly obovate-trilobed to strongly spatulate, the latter the more so when there are only three stamens, moderately concave, membranous, glabrous adaxially, glabrous or sparsely silvery tomentellous abaxially, base cuneate or strongly clawed, lateral margins strongly inflexed, partially clasping the filaments and sometimes the inner ones are adaxially connate or coherent, when 3 stamens are present, apex rounded to slightly retuse or truncate; stamens 3(–6), 1(2)-whorled, filaments ca. 0.6 mm long, clavate, free (or variously connate when 4–6), glabrous; anthers ca. 0.3 mm long, erect, connective adaxially thicker, sometimes forming a keel at the base of the anthers, apically overgrowing thecae and forming a hump when older (Fig. 19H). *Pistillate flowers* unknown. *Infructescences* axes ca. (1.3)3.5 × 0.3–0.4 cm, conspicuously lenticellate, strigillose-tomentellous or glabrate; fruiting pedicels (in immature fruits) 4.7–6.3 mm long, terete; carpophores 2.5–3.1 mm long, terete in immature fruits, not seen in mature fruits, truncate at apex, velutinous. *Drupelets* 3.6–4.6 × 2.1–2.8 cm, (colour when ripe unknown), weakly obovoid or ellipsoid (Fig. 19I), weakly eccentrically attached, base obtuse, stylar scar not apparent; exocarp ca. 2.6 mm thick, surface rugose, sparsely brownish velutinous tomentellous or glabrate, granular when dried; mesocarp thin and mucilaginous; endocarp ca. 3.7 × 2.2 cm, papyraceous, surface smooth. *Seeds* with embryo ca. 8 cm long, cotyledons unequal.

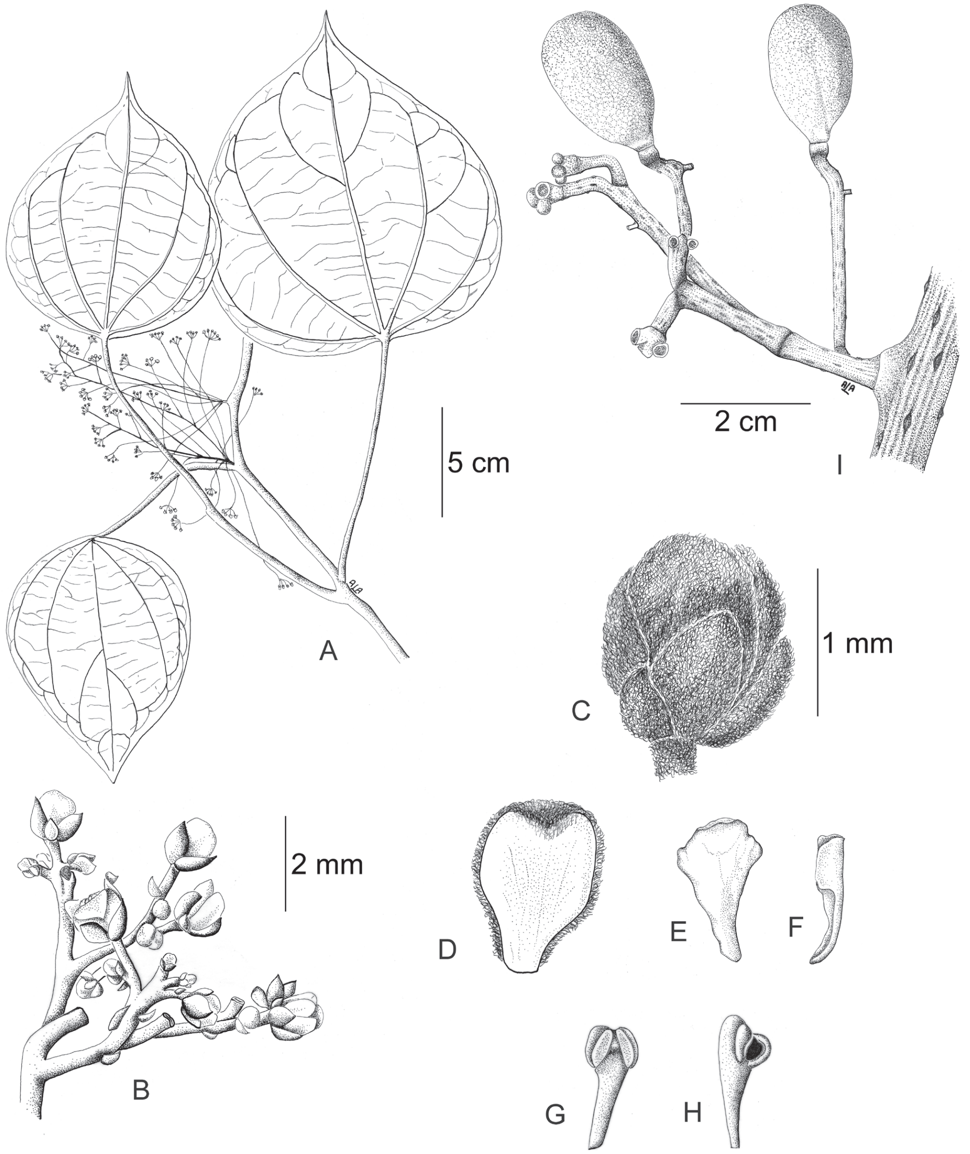

Figure 19. *Curarea gentryana* staminate plant: **A** flowering branch **B** detail of inflorescence **C** flower bud **D** inner sepal, adaxial surface **E–F** outer and inner petals, abaxial and latero-adaxial surfaces **G–H** outer stamens, abaxial and lateral views **I** pistillate plant, infructescence (**A–H** based on *Rubio & Quelal 1503* **I** based on *Aulestia et al. 9*).

Distribution and ecology. *Curarea gentryana* is known only from northwestern Ecuador (Fig. 9), at elevations of 80–225 m. It is found along creek margins in lowland tropical wet forest. Flowering specimens were collected in April and fruiting specimens were found in February, April and July.

Common names and uses. Ecuador. "granadilla" (*Rubio & Quelal 1434*, imm fr).

Eponymy. The specific epithet honours the late Dr. Alwyn H. Gentry, a dedicated and extraordinary botanist and inspiring mentor, who died tragically in a plane crash in August 1993 while surveying a dry forest reserve in western Ecuador.

Conservation status. The species is known only from four collections from three localities from northwestern Ecuador. Assessment based on these collections resulted in an Extent of Occurrence (EOO) of 92.6 km^2 and an Area of Occupancy (AOO) of 12 km^2. The three localities represent three subpopulations, each found in a small communal protected area (Reserva Etnica Awá), the surrounding area of which has been subject to increased land conversion. Therefore, it is expected that the species will in the future be negatively affected by loss of its habitat quality that may lead to reduction in the population and potentially threatening its survival. Thus, *C. gentryana* is assigned a preliminary status of Endangered [EN, B1ab(i,ii,iii,iv,v) + B2ab(ii,iii,iv,v)].

Discussion. The velutinous tomentellous indumentum covering the large obovoid or ellipsoid drupelets and the web-like indumentum on the abaxial surface of the broadly ovate leaves are unique to *Curarea gentryana*. The staminate inflorescences of *C. gentryana* somewhat resemble those of *C. cuatrecasasii*. However, *C. gentryana* has the spatulate inner petals with the lateral margins adaxially connate; spatulate inner petals may also be found in *C. cuatrecasasii*, but the lateral margins are not adaxially connate.

Paratypes. ECUADOR. Esmeraldas: San Lorenzo Canton, Reserva Indígena Awá, Parroquia Ricaurte, Centro Guadualito, 01°15'N; 078°40W, 80 m, 20–29 Apr 1992, (fr), *Aulestia et al. 9* (MO!, QCNE!); Creek on left side of Rio Palaví, going up river, 2 bends up from Awá encampment past first island, 01°07N; 078°37'W, 225 m, 14 Feb 1988, (imm fr), *Hoover et al. 4530* (MO!); Comunidad Balsareño, Río Palabí, 01°09'N; 078°31W, 100 m, 15–29 Apr 1991, (fr), *Rubio & Quelal 1434* (MO!, QCNE!).

6. *Curarea iquitana* (Diels) R.Ortiz, comb. nov.

urn:lsid:ipni.org:names:77185800-1
Fig. 20

Chondrodendron iquitanum Diels, in Mildbr., Notizbl. Bot. Gart. Berlin 9: 997. 1926. Type: Peru. "Oberes Marañon-Gebit. Mündung des Santiago", 160 m, [3] Oct 1924, (♂ fl), *Tessmann 4196* (lectotype designation effected by Krukoff and Moldenke 1938, pg. 24: B!, photographs at MO!, NY!; isolectotypes: G! [G (2), F neg. 27514], NY! [NY00008329, frag.]).

Description. Medium-sized understory *lianas*, (0.5–)2–7 m tall; older stems more or less terete, up to 1.5 cm diameter, bark dark brown, with shallow lengthwise fissures and scarcely tuberculate-lenticellate; branchlets glabrescent. *Leaves*: blades (11–)14–37 × (5–)14 –30 cm; ovate to broadly ovate; chartaceous when mature or when exposed to direct sunlight, base obtuse, truncate or weakly cordate, apex acute, acuminate, to cuspidate; surfaces discolorous, lustrous and glabrous adaxially, finely silvery tomentellous abaxially, indumentum concealing the surface at all stages, 3–5 palmati- to shortly plinerved, innermost pair of main veins acrodromous imperfect at all stages, midrib and lateral nerves slightly raised to weakly sunken adaxially, conspicuously raised abaxially, secondary veins 3(4) pairs, arising above the middle of the blade, veinlets raised above and below; petioles (3.9–)12–29.2 cm long, ridged, brownish-greyish strigillose to glabrate, apical pulvinus conspicuous, rugulose, scarcely flattened adaxially. *Staminate inflorescences* solitary or fascicled, axillary or cauliflorous, thyrsi, brownish to silvery strigillose, indumentum adpressed; axes (2.2–)7–14 cm long; primary branches 1–6 cm long, with (1)4–5 orders of branching; bracts (0.2–)0.7–1.2 mm long, ovate, concave, ascending, fleshy, glabrous adaxially, brown villous tomentellous abaxially. *Pistillate inflorescences* basically a thyrse, sometimes the primary branches reduced to single flowers, hence appearing racemose, brownish to silvery strigillose; axes 0.6–3.8 cm long; bracts 0.6–1 mm long, ovate, rather fleshy, glabrous adaxially, brownish villous abaxially. *Staminate flowers* 1.3–1.8 mm long, whitish, greenish, green-yellowish or orangish; pedicels (0.6–)1.3–3.1 mm long, terete, relatively thick, indumentum as on the axis, but somewhat spreading; bracteoles 2–3, 0.23–0.4 mm long, ovate or oblong, fleshy, glabrous adaxially greyish or silver villous-tomentellous abaxially; sepals 6, indumentum as on bracteoles; outer sepals 0.6–1.3 × 0.4–0.7 mm, ovate or ovate-elliptic, base truncate, apex acute; inner sepals 1.2–2.2 × 1–1.5 mm, narrowly ovate, ovate, elliptic or weakly obovate, base obtuse or cuneate, apex acute to rounded, tip of inner sepals erect, sometimes reflexed past anthesis; petals 6, 0.6–1.2 × 0.3–0.8 mm, inner ones slightly smaller and narrower, obovate, obovate-trilobed or flabelliform, weakly to moderately concave, membranous, glabrous adaxially, sparsely silvery tomentellous abaxially, base cuneate or slightly clawed, lateral margins inflexed, partially clasping the filaments, apex acute, sometimes obtuse in the inner ones; stamens 6, filaments 0.4–0.8 mm long, inner ones slightly longer, clavate, free or connivent, less frequently connate ca. half their length, glabrous; anthers 0.2–0.3 mm long, erect, connective protruding adaxially and forming a hump or a horn apically or not, protrusion more conspicuous when older. *Pistillate flowers* (mostly old) 1.7–2.2 mm long, greenish; pedicels 1.3–5.1 mm long, terete, indumentum as on the axis; bracteoles 1–3(4), 0.2–0.6 × 0.3–0.6 mm, ovate or oblong, rather fleshy, glabrous adaxially, greyish or silvery villous tomentellous abaxially; sepals 6–9(12), weakly concave, moderately fleshy, in 2–3 whorls, glabrous adaxially, greyish or silvery villous tomentellous abaxially; outer sepals ca. 0.5–1.3 × 0.4–0.8 mm, ovate, base truncate, apex acute; middle sepals 0.6–2.2 × 0.6–1.4 mm, broadly ovate to obovate, base obtuse or cuneate, apex acute; inner sepals 1.6–2.2 × 1.3–1.7 mm, ovate, obovate or elliptic, base cuneate or clawed, apex obtuse or rounded, tips erect to weakly reflexed past anthesis; petals 3(4), 1.3–1.7 × 0.6–0.8 mm, spatulate or obovate-trilobed, weakly concave, membranous, glabrous adaxially, glabrous or sparsely silvery tomentellous abaxially, base clawed, apex obtuse; carpels 3, 0.6–0.9 × 0.4–0.6 mm, dark to light brown villose, trichomes appressed-ascending; style 0.6–1.1 mm long. *Infructescences* axes 1–6 × 0.3–0.9 cm long, at times moderately stout, brown to silvery-strigillose-tomentose or glabrous; fruiting pedicels 2.3–4.6 mm long, terete, sometimes rather thick; carpophores 4–8 mm long, clavate in mature fruits, truncate at apex, cream or brownish velutinous. *Drupelets* 1.8–2.8 × 1.2–1.6 cm, yellow

Chondodendron iquitanum Diels

Verified by H. N. Moldenke
March, 1938

Station: Oberer Marañon Land. Regenwald v. Ostperu Nr. 4196
Wissensch. Name:
Einheim. Name: Name des Standorts: Mündung d. Santiago
Beschaffenheit des Standorts: Flutfreier Hochwald
Höhe ü. d. M.: 160 m
Wuchs, Größe, Blütenfarbe etc.: Stiel u. Sep. grün, ziemlich [illegible] behaart. Pet. [illegible] grün am Rand [illegible] behaart [illegible] Braun mit ockerigen Punkten. [illegible] 15 mm Durchm.; 3 m hoch kletternd
Gesammelt am 3 Oktober 24 Sammler: G. Tessmann

Curarea toxicofera (Weddell) Barneby & Krukoff
det. confirm. C. Ott, MJG, 1995

Museum botanicum Berolinense.
acc. 18 VI. 1925
Chondodendron iquitanum Diels n. sp.
Ost-Peru: Stromgebiet des Maranon von Iquitos aufwärts bis zur Santiago-Mündung am Pongo de Manseriche, ca. 77° 30 West.
1924 G. Tessmann. No. 4196

Figure 20. *Curarea iquitana* (photograph of the type of *Chondrodendron iquitanum*, *Tessmann 4196*, B).

when ripe, ellipsoid or weakly oblongoid, weakly eccentrically attached, base obtuse, stylar scar basal; exocarp 0.9–1.2 mm thick, surface rugulose, cream or silvery velutinous or glabrescent, granular when dried; mesocarp said to be “clear and slimy” (*Berlin 542*); endocarp 1.7–2.4 × 0.8–1.2 cm, chartaceous, surface reticulate by scarcely pronounced veins. *Seeds* with embryo 3.6–4.9 cm long, cotyledons unequal.

Distribution and ecology. Known from the lowlands to mid elevations in eastern to central Peru (Fig. 21), including the departments of Amazonas, Loreto and Pasco, from elevations of 106 m in Loreto up to 1380 m in Pasco. Staminate plants were collected in January-February, July-August and November. Pistillate flowers were found in February, October and December, whereas fruiting specimens were found all year round.

Common names and uses. Peru: “dabau” (*Ancuash 660*, ♂ fl, *Kayap 749*, imm fr, *1205*, mat fr); “dúpam” (*Berlin 542*, mat fr); “tsegásnum” (Aguaruna) (*Castro et al. 18929*, imm fr; *Lewis et al. 18475*, imm fr); “namaú” (*Kayap 156*, mat fr); “tseas daek” (*Kayap 1032*, imm fr); “tsegas” (*Kujikat 107*, imm fr); “tseusnum” (*Ancuash 1219*, ♂ fl); “ampihuasca amarilla” (*Schunke Vigo 2981*, mat fr); “ampihuasca delgadito” (*Schunke Vigo 6836*, ♂ fl); “ampihuasca negra” (*Schunke Vigo 7125*, ♂ fl).

Note. Krukoff and Moldenke (1938) cited *Chondrodendron iquitanum* (*Curarea iquitana* in this study) as a “source of poison for darts of Indians” based on the label of the sterile *Mexia 6321a*. This specimen was later identified as *Curarea toxicofera* (Barneby and Krukoff 1971). I have not examined the referred specimen and hence I have not been able to confirm its identity.

Etymology. Presumably in reference to Iquitos, the largest city in Peruvian Amazonia and in which general area the type specimen was surely collected.

Conservation status. The assessment was based on 37 collections corresponding to 18 localities that yielded an Extent of Occurrence (EOO) of 279,551 km^2 and an Area of Occupancy (AOO) of 72 km^2. The 18 localities represent 17 subpopulations of which four occur within protected areas (Allpahuayo-Mishana National Reserve in the Iquitos area) and three are found on private lands. Although *Curarea iquitana* is not abundant where it occurs, it is however broadly distributed and hence it is assigned a preliminary status of “Least Concern” (LC).

Discussion. *Curarea iquitana* is here resurrected from synonymy under *C. toxicofera*. *Curarea iquitana*, as defined here, encompasses a broad range of morphological variation and includes, at least provisionally, what is labelled the allpahuayo group (**al**) in the linear discriminant analysis. While the iquitana (**iq**) and allpahuayo (**al**) groups may represent different entities, at present it is premature to recognise them as different species, given that the morphological quantitative characters evaluated in this study partially or completely overlap between the two groups (Fig. 10B).

Additionally, features of pistillate flowers are still fragmentary or lacking, hence the extent of variation, if any, in these features, remains unknown. Collections from the foothills of central-eastern Peru in the Amazonas department from 200–800 m elevation closely resemble the type of *Chondrodendron iquitanum* Diels (*Tessmann 4196*), which was collected in the same general area – in the basin of the Marañon River, at

160 m in elevation – around which my concept of *Curarea iquitana* is centred. These collections tend to have conspicuously large, ovate or broadly ovate leaves with 5–7 main veins. The staminate inflorescences have a brownish to silvery strigillose indumentum and small flowers that range from 1.6 to 1.8 mm long, (mostly greyish villous and 1.3–1.8 mm long in the allpahuayo group). The adaxial horn-like protrusion of the connective at the apex of anthers, characteristic of *Curarea iquitana*, is variable amongst the studied collections, appearing as a horn (long and weakly incurved), as an apical-adaxial keel or as an adaxial hump, the latter more frequently being observed in the allpahuayo group; anthers are for the most part immersed in the connective. An old and fragmentary pistillate inflorescence of *C. iquitana s.s.* is a thyrse with brownish or silvery villous indumentum and the rugulose or muriculate drupelets have a golden-brownish velutinous-hispidulous indumentum. The only pistillate inflorescence known in the allpahuayo group has cymose primary branches proximally, distally these being reduced to single flowers giving the appearance of being racemose. The immature condition of the drupelets in most collections studied precludes their use in analyses of quantitative variation of the groups. Collections from non-flooded areas around Iquitos in eastern Peru, ca. 110–140 m in elevation and those from the Andean foothills in Pasco department, from 500–1380 m elevation, are here provisionally included in *C. iquitana*.

Selected specimens examined. PERU. Amazonas: [Prov.] Condorcanqui, Río Cenepa, Camino Etseketal, norte de Huampami, monte, 600–800 ft, 31 Jul 1974, (♂ fl), *Ancuash 660* (MO!, NY!); Prov. Bagua, Distrito Imaza, Región Nororiental del Marañon, Comunidad Aguaruna de Kusú-Listra, Cerro Apág, margen derecha Quebrada Kusú, 05°02'24"S; 078°19'12"W, 600–700 m, 17 Sep 1996, (imm fr), *Díaz et al. 8239* (MO!); Rio Cenepa región, monte, orilla de Quebrada Huampami, 18 Jan 1973, (mat fr), *Kayap 156* (MO!); Río Cenepa, vicinity of Huampami, ca. 5 km east of Chávez Valdivia, Que Quebrada Najamtai entsa, en bosque primario, 04° 30'S; 78° 30'W, 200–250 m, 3 Aug 1978 (♀ fl & imm fr), *Kujikat 107* (MO!); Comunidad de Yamayakat, Río Marañon, bosque primario, 04°55'S; 078°19'W, 320 m, 15 Jul 1994, (♂ fl), *Vásquez et al. 18715* (MO!). **Loreto:** Prov. Maynas, Distrito de Indiana, campamento turístico de Explorama, bosque, 03°30'S; 073°14'W, 110 m, 10 Feb 1996, (♂ fl), *Ortiz et al. 167* (MO!); ibid., 11 Feb 1996, (mat. fr.), *Ortiz et al. 172* (MO!); Distrito de Iquitos, Estación Experimental de Allpahuayo, IIAP, bosque, 04°10'S; 073°30'W, 120–140 m, 20 Feb 1996, (♂ fl), *Ortiz 176* (MO!); ibid., 22 Feb 1996 (♂ fl), *Ortiz 181* (MO!); ibid., 23 Feb 1996, (♀ fl), *Ortiz 184* (MO!); ibid., 23 Feb 1986, (♀ fl, imm & mat fr), *Ortiz 186* (MO!). **Pasco:** Dist. Palcazu, Comunidad Nativa Alto Lagarto (Reserva Comunal Yanesha), remanente de bosque primario, 10°08'04"S; 075°22'06"W, 500 m, 9 Feb 2011, (mat fr), *Rojas & Ortiz 7674* (HOXA n.v., MO!, USM!); Prov. Oxapampa, Parque Nacional Yanachaga-Chemillen, sector Alto Lagarto, remanente de bosque primario, 10°07'44"S; 075°26'41"W, 1380 m, 20 Aug 2011, (imm fr), *Rojas et al. 7909* (HOXA n.v., MO!, USM!); Prov. Oxapampa, Gran Pajonal, trail between Chequitavo and Shumahuani, primary forest, 1200–1300 m, 10°45'S; 074°23'W, 30 Mar 1984, (mat fr), *Smith 6584* (MO!).

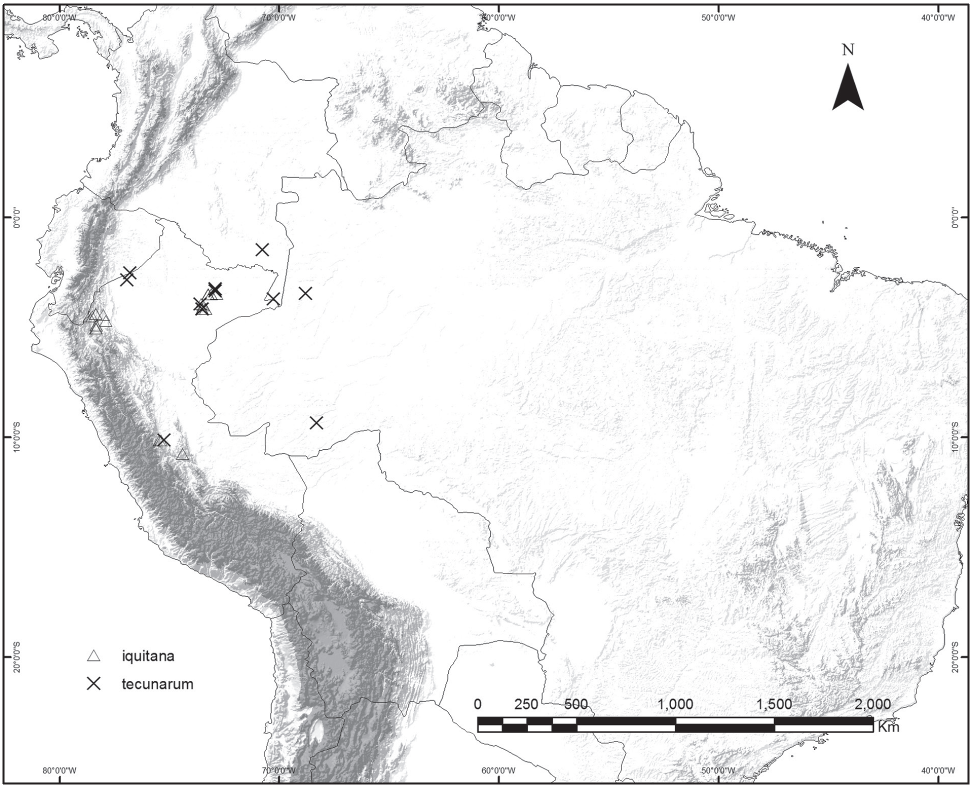

Figure 21. Geographic distribution of *Curarea iquitana* and *C. tecunarum*, for the latter selected specimens only, because most of the specimens are sterile.

7. *Curarea tecunarum* Barneby & Krukoff

Figs 22, 23

Curarea tecunarum Barneby & Krukoff, Mem. New York Bot. Gard. 22(2): 12. 1971. Type: Brazil. Amazonas: Basin of Rio Solimões, Municipality São Paulo de Olivença, basin of creek Belem, 26 Oct–11 Dec 1936, (♂ fl), *Krukoff 8713* (holotype: NY!; isotypes: BM!, BR!, F!, MO!, U!, US!).

Description. Large canopy *lianas* about 20–30 m tall; older stems, 5–15 cm wide, strongly flattened; bark dark brown, with shallow lengthwise fissures; branchlets brown to creamy villous. *Leaves:* blades 9–30 × 7–20 cm, ovate to broadly ovate; chartaceous to subcoriaceous when mature or when directly exposed to sunlight, base truncate, obtuse or shallowly cordate, margin entire, apex acuminate to retuse (cleft in *Krukoff 8713*), cuspidate when juvenile; surfaces conspicuously discolorous, lustrous and glabrous adaxially, coarsely cream to silvery tomentulose abaxially, matted when older, indumentum concealing the abaxial surface at all stages, (5–)7–9 palmati- or plinerved, innermost pair of main veins acrodromous perfect on mature leaves, acrodromous imperfect on juvenile ones, midrib and lateral nerves slightly impressed adaxially, conspicuously raised abaxially, secondary veins 1–2 pairs, arising above the middle of the blade, sometimes absent, veinlets immersed adaxially, raised abaxially; petioles 4.7–21 cm long, smooth, densely creamy or brownish villous to glabrate, apical pulvinus more conspicuous, rugose, weakly flattened adaxially. *Staminate inflorescences* solitary or fasciculate, axillary or slightly supra-axillary, thyrsi (Fig. 22A–B), densely brownish or greyish tomentellous; axes 5.7–19 cm long; primary branches 1.1–3.5 cm long, lax, with several (3–6) cymose orders of branching, higher order branching frequently reduced; flowers frequently sessile at the centre of the irregularly further dichotomous branchings; bracts 0.7–1.1 mm long, narrowly ovate, concave, fleshy, glabrous adaxially, brown tomentellous abaxially. *Pistillate inflorescences* solitary or fascicled, axillary stout thyrsi (Fig. 23B), with dichasial primary branches or these less frequently reduced to single flowers and hence appearing racemiform, densely light brown or greyish tomentellous; axes ca. 5 cm long; bracts ca. 2 mm long, ovate, concave, fleshy, indumentum as on inflorescence. *Staminate flowers*, 1.2–1.7 mm long, green; pedicels (0–)0.3–3.3 mm long, thick, terete, indumentum as on staminate inflorescence; bracteoles 1–2, 0.2–0.4 × 0.1–0.3 mm, narrowly ovate, fleshy, glabrous adaxially, light brown or creamy tomentellous abaxially; sepals 6; outer sepals 0.4–0.9 × 0.3–0.7 mm, ovate or oblong, indumentum as on bracteoles, base truncate, apex acute; inner sepals 1.1–1.9 × 1–1.7 mm, obovate or ovate-rhombic, mostly light brown or greyish tomentellous abaxially, obtuse at base, apex obtuse or rounded, tip of inner sepals erect or spreading, less frequently reflexed past anthesis; petals 6, 0.4–0.8 × 0.2–0.6 mm, inner ones slightly shorter and narrower, obovate-trilobed or rhombic, weakly concave, membranous, glabrous adaxially and abaxially, base cuneate-truncate, lateral margins inflexed, partially clasping the filaments, apex obtuse, truncate or retuse; stamens 6; filaments 0.2–0.5 mm long, clavate, thick, free or shortly connate at base, glabrous; anthers 0.2–0.3 mm long, erect, connective thicker adaxially forming a keel (Fig. 22 G–H), not overgrowing thecae apically. *Pistillate flowers* ca. 1.6 mm long, brownish; pedicels ca. (0–)1.7 mm long; terete, indumentum as on pistillate inflorescence; bracteoles 3, ca. 0.4 × 0.2 mm, oblong or ovate, fleshy, glabrous adaxially, brownish tomentellous abaxially; sepals 6, weakly concave, fleshy, indumentum as on bracteoles; outer sepals ca. 0.5 × 0.3 mm, ovate or oblong; inner sepals ca. 1.5 × 0.9 mm, obovate tips erect to reflexed past anthesis; petals 3(4), ca. 0.9 × 0.6 mm, opposed to and/or alternating with the carpels, spatulate, weakly concave, membranous, glabrous adaxially, glabrous to sparsely light brown tomentellous abaxially, clawed at base, apex acute to retuse; carpels 3(4), ca. 0.6 × 0.5 mm, brown tomentose; style ca. 0.4 mm long. *Infructescences* axes ca. 4 (–6) × 0.3–0.4 cm, indumentum as on inflorescences; fruiting pedicels inconspicuous; carpophores ca. 2.7 × 4.3 mm, subglobose (seen in immature fruits only), brownish to creamy villose. *Drupelets* ca. 2.9 × 2 cm, ellipsoid to oblongoid (Fig. 23G), conspicuously eccentrically attached, base obtuse, stylar scar not apparent; exocarp 1.8–1.9 mm thick, surface rugose, brownish villous, granular when dried; mesocarp thin and mucilaginous; endocarp 2–2.5 × 1.1–1.5 cm, papyraceous, surface smooth. *Seeds* with embryo 4–6 cm long, cotyledons slightly unequal.

Distribution and ecology. Lowland Amazonia in Brazil, Colombia, and Peru (Fig. 21 –fertile and only a few sterile ones are mapped), at elevations of 120–300 m (550 m in Bagua, based on *Vásquez et al. 19467*, a sterile collection from Bagua, in Peru, here identified tentatively) in tropical wet forest. It is also expected in the eastern lowlands of Ecuador (see below). Staminate flowering specimens were collected in February, July and September–November; the only pistillate flowering specimen was collected in November and fruiting specimens were collected in February and March.

Common names and uses (sterile specimens are indicated as st). **Brazil**: component of curare made by Tecuna Indians, "atinupa" (Krukoff and Smith 1937, Krukoff and Moldenke 1938, Macbride 1938), (*Krukoff 7535*, st; *Krukoff 7578*, ♂ fl buds); as ingredient of arrow and dart poison, "bicava" (*Prance et al. 13931*, st); as ingredient of Jamamadi Indian arrow poison "bicafo" (*Campbell et al. P21256*, st); as a contraceptive by the Deni Indians, "beku" (*Prance et al. 16453*, st). **Colombia**: "taufe-lleida" (Huitoto) (*Díaz 10*, st); "arrow poison" (*Naranjo & Wiederhold 16*, st); as curare (*Pinkley 392*, st); "awa puh", as ingredient of arrow poison (Bara maku), (*Silverwood-Cope 23*, st). **Ecuador**: "oonta", to make dart poison (*Davis & Yost 943*, st); "ontame", hunting, (Huaorani), (*Freire & Naranjo 685*, st); "oonta", used to make blowgun dart poison, (Huaorani), (*King et al. 972*, 977, st); "palahuasca", as ingredient of curare (Quichua) (*Lewis et al. 13848*, st); "largancho" (*Moya & Reyes 274*, st); "zapepa", employed in arrow poison (*Naranjo 7*, st); "ontame", hunting (Huaorani) *Naranjo & Freire 363*, st); "unta", hunting (Huaorani) (*Naranjo & Freire 635*, st); as curare (*Pinkley 285*, st). **Peru**: "abuta, abote", used as vermifugue (*Huamán et al. 417*, st); "tseás" as ingredient of curare (Mayna Jívaro) (*Lewis et al. 10224*, st); "macháp" (Mayna Jívaro) (*Lewis et al. 10425*, st); "machaap", as main ingredient of curare (Achual Jívaro) (*Lewis et al. 11759*, st); "macháp" (Achuar Jívaro), "nakaapur, papur" (Achuar Jívaro), medicinal, to treat leishmaniasis lesions, also as ingredient of curare (*Lewis et al. 14349*, st); "abuta", to prepare poison for hunting (*Martin & Lau-Cam 1204*, st); "abuta hembra" (*Martin & Lau-Cam 1273*, st); "abuta hembra (*Mathias & Taylor 3555*, st); "abuta" (*Mathias & Taylor 5004*, *5010*, st); "abuta amarilla" (*Rimachi 11394*, ♂ fl); "abuta ancho" (*Schunke 5848*, *5849*, *5850*, and *5851*, all st); "abuta amarilla" (*Tina & Oliveira* 2343, st); "medicinal, (*Vásquez 16803*, st); "abuta negra" (*Woytkowski 5336*, st); "ampi" (*Woytkowski 5354*, *5355*, st).

Etymology. In reference to the Tecuna Indians who used the plant as a source of curare (Barneby and Krukoff 1971),

Comments. Specimens from Brazil (*Prance et al. 13991* and *Campbell et al.* P21256) were previously identified as *C. toxicofera*. Likewise, the common name of "atinupa" attributed to *Chondrodendron polyanthum* or to *Chondrodendron toxicoferum* (= *Curarea toxicofera*) (Krukoff and Smith 1937, Krukoff and Moldenke 1938, Macbride 1938, Barneby and Krukoff 1971) are here confirmed to refer to *Curarea tecunarum*.

Conservation status. The 14 collections evaluated correspond to 11 localities and yielded an Extent of occurrence (EOO) of 712,212 km^2 and an Area of Occupancy (AOO) of 44 km^2. The 11 localities, represent 11 subpopulations and 9 locations, four are found within protected areas (one in Parque Nacional Natural Amacayacu

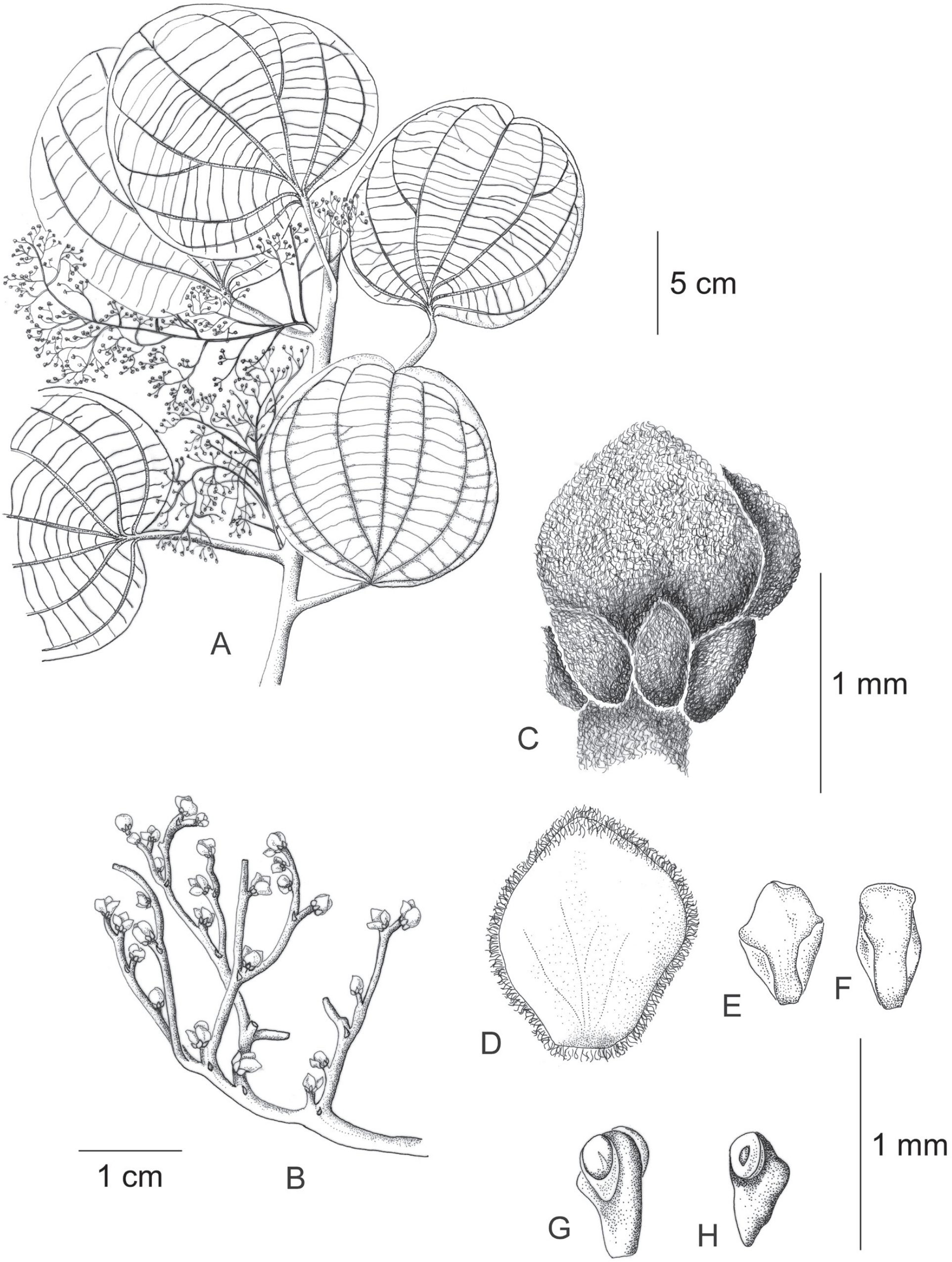

Figure 22. *Curarea tecunarum* staminate plant: **A** flowering branch **B** detail of inflorescence **C** flower bud **D** inner sepal, adaxial surface **E–F** outer and inner petals, adaxial surfaces **G–H** outer stamens, latero-abaxial and lateral surfaces (**A–B** based on *Krukoff 8713* **C–H** based on *Pipoly et al. 12846*).

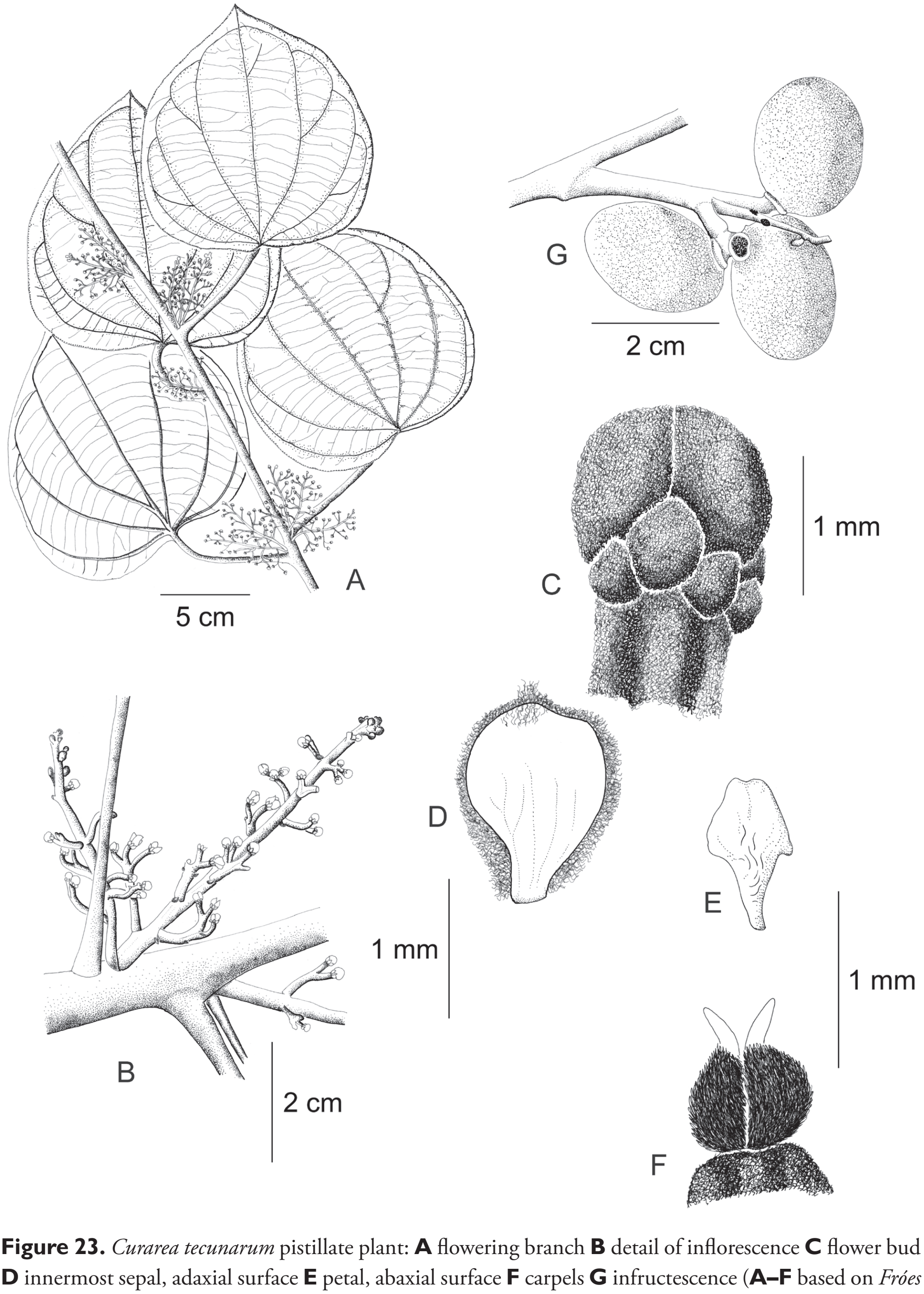

Figure 23. *Curarea tecunarum* pistillate plant: **A** flowering branch **B** detail of inflorescence **C** flower bud **D** innermost sepal, adaxial surface **E** petal, abaxial surface **F** carpels **G** infructescence (**A–F** based on *Fróes 21446* **G** based on *van der Werff & Vásquez 13909*).

and another in Parque Nacional Cahuinarí, both in Colombia and two in Allpahuayo-Mishana National Reserve in Peru). Additionally, one was found in private lands in Peru. Based on several sterile specimens that are here assigned tentatively (and were not mapped nor included in the conservation assessment), the species appears to be distributed across the Amazon basin, hence the estimated AOO may be greater than that reported here. Therefore *C. tecunarum* is assigned a preliminary status of "Least Concern" (LC).

Discussion. Laxly multi-branched staminate inflorescences covered with brownish or creamy tomentellous indumentum and flowers that are usually sessile on irregular higher order branches are unique to *C. tecunarum*. The species shares with *C. barnebyana* and *C. crassa* a tomentellous indumentum on the abaxial leaf surface as well as subglobose carpophores, but the latter two have staminate inflorescences with condensed/contracted primary branches. These species also share some anatomical features (Table 5; discussion of *C. crassa*).

Selected specimens examined. BRAZIL. Acre: Sena Madureira, Floresta Estadual do Antymari, ramal do Ouro, ca 30 km da sede Úirapuro (Servicio Florestal), 09°19'47"S; 68°18'12"W, 9 Mar 13, (mat fr), *Medeiros et al. 1091* (NY!). **Amazonas:** Igarapé Curucuhy, São Gabriel, 27 Nov 1945, (♀ fl), *Fróes 21446* (F!, IAN!, NY!); Munic. São Paulo de Olivença, ibid., near Palmares, 11 Sept 1936–26 Oct 1936, (♂ fl), *Krukoff 8370* (A!, BM!, BR!, F [2]!, G!, MO!, NY!, U!). **Rio de Janeiro:** Cultivated in Rio de Janeiro, no specific locality (st), *Glaziou 9610* (P [2]!–a duplicate at F! as "9610" instead = *C. toxicofera*. **Rondônia:** Rodovia, Alvorada-Costa Marques, km 90, colectado no transectum, mata de terra firme, solo areno-argiloso, 2 Jul 1983, (♂ fl), *Silva 6538* (IAN!, MG!, RB-2!); Margen direita do Río Pacáas Novos, entre a 1ra e 2da cachoeira, mata de várzea, 20 Mar 1978, (imm fr), *Ubiratan et al. 218* (GH!, MO!, NY!).

COLOMBIA. Amazonas: La Pedrera, Inspección de Santa Isabel, Parque Nacional Natural Cahuinarí, Estación Biológica Puerto Barbados; várzea (rebalse alta) sobre suelos lateríticos, dominada por *Astrocaryum*, 01°28'S; 070°46'W, 300 m, 29 Nov 1990, (♂ fl), *Pipoly et al. 12846* (MO!, NY!). **Comisaría del Putumayo:** Between Río San Miguel and Río Guamués, Aug 1963, (st), *Naranjo 7* (AMES!). **Vaupés:** Right tributary of Rio Macu-Parana, 1–8 Jun 1970, (st), *Silverwood-Cope 23* (AMES!).

ECUADOR. Napo: Confluence of Quiwado and Tiwaeno Rivers, 13 Apr 1981, (st), *Davis & Yost 943* (AMES!). **Orellana:** Loreto, Reserva Étnica Huaorani, Comunidad Miwaguno a 140 km al sur del Coca, vía al Pindo, bloque 14 (ENCAN), Río Shiripuno, 00°43'32S; 076°43'36"W, 250 m, 9 May 2004, (st), *Freire & Naranjo 685* (MO!, QCNE n.v.). **Pastaza:** Kapawí (Amuntai), Río Pastaza, village area, secondary and primary forests and pastures, 02°31'S; 076°48'W, 235 m, 25–29 July 1989, (st), *Lewis et al. 13848* (MO!).

PERU. Amazonas: Bagua, Distrito Imaza, Región del Marañon, Comunidad de Yamayakat, Quebrada Kusu-Chapi, Río Marañon, 04°55'S; 078°19'W, 550 m, Feb 1995, (st), *Vásquez et al. 19467* (MO!). **Loreto:** Maynas, Distrito Las Amazonas, Quebrada Sucusari, bosque maduro en tierra firme, 03°15'S; 072°55'W, 140 m, 1 Feb 1996, (imm fr), *Ortiz et al. 143* (MO!); ibid., (♂ fl), *Ortiz et al. 144* (MO!); Distrito de Iquitos, Estación Experimental de Allpahuayo, IIAP, 04°10'S; 073°30'W, 120 m, 24 Feb 1996, (old ♂ fl), *Ortiz & Ruiz 188* (MO!); Carretera Iquitos-Nauta, km 21, trocha de penetración del fundo Pichiri, en terreno alto y arenoso, 150 m, 18 Oct 1995, (♂ fl), *Rimachi 11394* (MO!). **Pasco:** Oxapampa, vivero, Proyecto Pichis Palcazu, Puerto Bermudez, transect 2, 10°12'S; 074°57'W, 200 m, 16 Jun 1983, (st), *Gentry et al. 42061* (MO!). **San Martin–Ucayali:** Vicinity of Aguaytía, high ground in forest, east of Aguaytía, between Pucallpa road and Río Aguaytía, 28 Jun 1960, (st), *Mathias & Taylor 5004* (F!). **Ucayali:** Aguaytía, Fundo Vista Alegre, 29 Mar 1962, (st), *Schunke 5848* (F! [2]).

VENEZUELA. Amazonas: Cerro Neblina base camp on Rio Mawarinuma, mature forest on sandy "ultisol", 140 m, 23 Apr 1984, (st), *Gentry & Stein 46878* (MO!).

8. *Curarea tomentocarpa* (Rusby) R.Ortiz, comb. nov.

urn:lsid:ipni.org:names:77185802-1
Fig. 24

Cissampelos tomentocarpa Rusby, Descr. So. Amer. Pl. 17. 1920.
Type: Bolivia. San Buena Ventura, 1400 feet, 22 Nov 1901, (imm fr), *Williams 616* (lectotype, designated by Dorr 1991, pg. 230: NY! [NY320534]; isolectotype: NY! [NY320535]).
Chondrodendron tomentocarpum (Rusby) Moldenke in Krukoff & Moldenke, Brittonia 3: 21. 1938.
Type: based on *Cissampelos tomentocarpa* Rusby
Abuta boliviana Rusby, Mem. New York Bot. Gard. 7: 241. 1927.
Type: Bolivia. Rurrenabaque, [Beni: Gral. Jose Ballivian], 1000 ft, 25 Nov 1921, (♂ fl), *White 1812* (holotype: NY! [NY320439]; isotypes: BKL! [2] [image seen], the inflorescence on the left of the BKL00004029 sheet only, leaves do not belong to Menispermaceae, GH! [GH00038884), K!, MICH! [image seen], US! (US-1232429).

Description. Small to medium-sized understory *lianas* about (0.5–)3–10 tall; older stems more or less terete ca. 0.5–1.5 cm diameter; bark greyish to dark brown, with shallow lengthwise fissures and scarcely tuberculate-lenticellate; branchlets greyish to brownish hispidulous. *Leaves:* blades 7–22 × 5–14 cm, ovate, narrowly ovate or elliptic; membranous when juvenile, chartaceous when mature or when directly exposed to sunlight; surfaces conspicuously discolorous, lustrous and glabrous adaxially, finely silvery tomentellous abaxially, intermixed with some coarser hairs, concealing the surface at all stages, base truncate, obtuse, rounded or shallowly cordate, apex acute, long-acuminate when juvenile, 3(5) palmati- or plinerved, innermost pair of main veins acrodromous imperfect at all stages, midrib shallowly impressed to flat adaxially, conspicuously raised abaxially, secondary veins 2–4 pairs, arising above the middle of the blade, impressed adaxially, raised abaxially, veinlets slightly prominent adaxially,

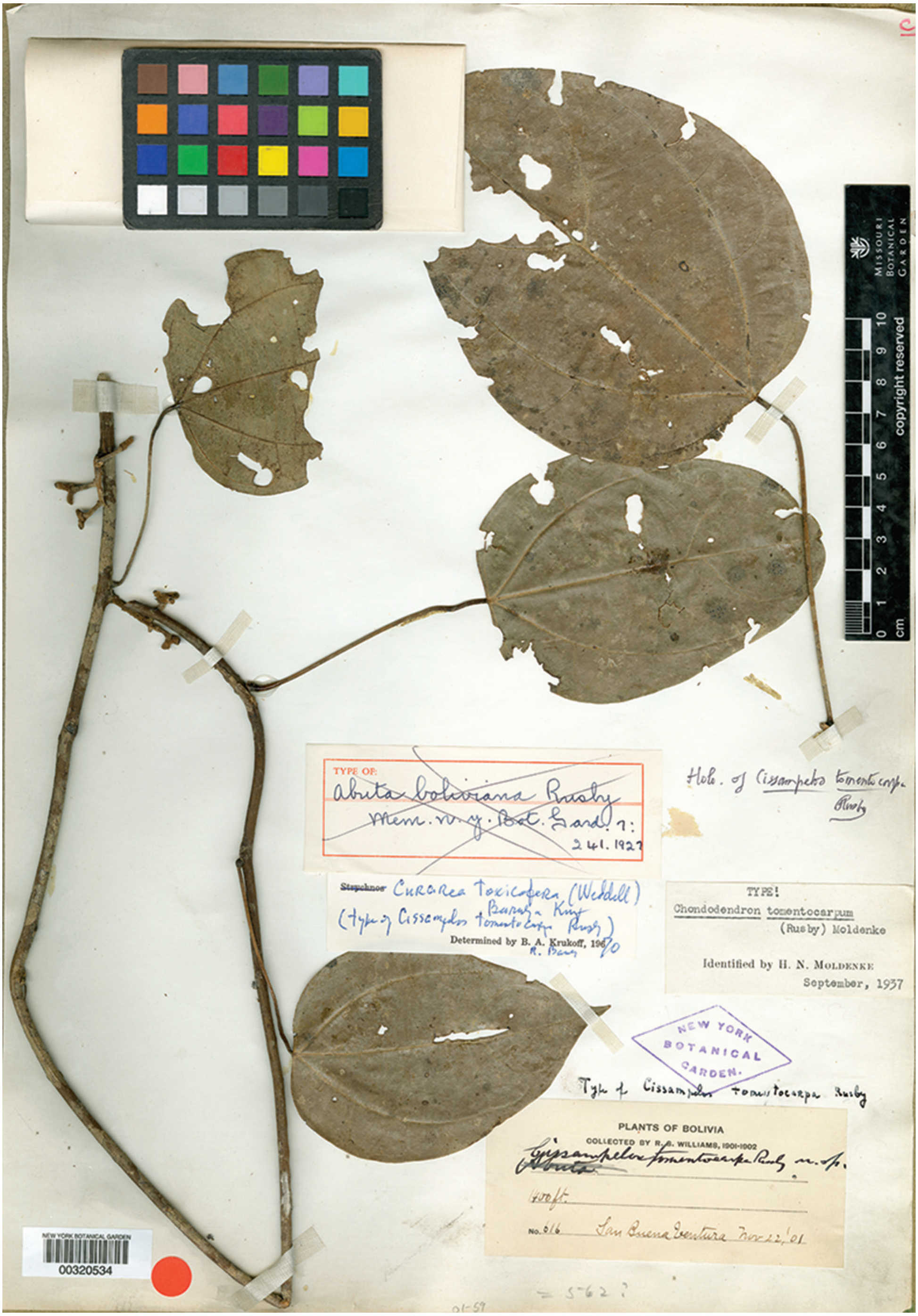

Figure 24. *Curarea tomentocarpa* (photograph of the type of *Cissampelos tomentocarpa*, *Williams 616*, NY).

conspicuously raised abaxially, but then concealed by the indumentum; petioles 3–11 cm long, ridged, rufescent or greyish strigillose to glabrate, distal pulvinus moderately conspicuous, rugulose, sometimes weakly flat adaxially. *Staminate inflorescences* solitary or fascicled, cauliflorous or axillary, thyrsi, densely brownish rufescent or silvery hispidulous, trichomes moderately long; axes 6–15(–25) cm long; primary branches slender, 1.7–3.7(–7.5) cm long, with 2–3(–5) branching orders laxly arranged; bracts 0.7–1.3 mm long, narrow ovate to ovate, concave, ascending, moderately fleshy, glabrous adaxially, brownish, rufescent or silvery villose abaxially, trichomes moderately spreading. *Pistillate inflorescences* fascicled, cauliflorous, moderately slender, few-flowered thyrsi, these with the primary branches reduced to single flowers, light brown or rufescent hispidulous; axes 4.2(–8.6) cm long; bracts 0.8(–1.2) mm long, ovate, concave, scarcely fleshy, glabrous adaxially, brown tomentellous abaxially. *Staminate flowers*, 1.2–2 mm long, brownish, greyish, yellowish or greenish; pedicels 0.8–2.8 mm long, terete, thick, indumentum as on the staminate inflorescence; bracteoles 1–4, 0.2–0.4 × 0.2–0.4 mm, ovate, moderately fleshy, glabrous adaxially, rufescent or light golden villose abaxially, trichomes moderately spreading; sepals 6(9), 2(3)–whorled, glabrous adaxially, abaxially with a rufescent to silvery or greyish indumentum, trichomes moderately spreading; outer sepals 0.5–1.1 × 0.4–0.8 mm, ovate or elliptic, base truncate, apex obtuse; (middle sepals 1.2–1.6 x 0.8–0.9 mm, narrow ovate to ovate, base and apex obtuse, moderately fleshy); inner sepals 1.1–2.2 × 1.1–1.7 mm, ovate or elliptic, base obtuse or cuneate, apex acute or obtuse, tip of inner sepals mostly erect past anthesis; petals 6(9), 0.6–1.3 × 0.4–0.9 mm, the inner one slightly smaller and narrower, obovate-trilobed (spatuliform-trilobed), strongly concave, membranous, glabrous adaxially, glabrous to sparsely silvery tomentellous abaxially, base cuneate or distinctly clawed, lateral margin inflexed, partially clasping the filaments, apex obtuse or truncate; stamens 6, filaments 0.4–0.9 mm long, clavate, rarely weakly terete, free (shortly connate at base), glabrous; anthers 0.2–0.3 mm long, erect, connective frequently thinner apically, thecae splitting into two halves, connective thicker adaxially (protruding as a hump at the base or at the apex of thecae). *Pistillate flowers* ca. 1.8 mm long, yellowish to brownish; pedicels ca. 6.4 mm long, terete, indumentum as on the pistillate inflorescence; bracteoles 2, ca. 0.4 × 0.3 mm, ovate, weakly concave, fleshy, glabrous adaxially, brownish, silvery or rufescent villous abaxially, trichomes moderately spreading; sepals 6–9, weakly concave and scarcely fleshy, in 2–3 whorls, indumentum as on bracteoles; outer sepals ca. 0.5 × 0.4 mm, ovate, base truncate, apex acute or obtuse; (middle sepals, ca. 0.9 × 0.8 mm, ovate to broadly ovate, base and apex obtuse); inner sepals ca. 1.5 × 1.4 mm, elliptic, apex and base obtuse, tips erect to weakly reflexed past anthesis; petals 3(6), ca. 1.2 × 0.7 mm, spatulate, weakly concave, membranous, glabrous adaxially and abaxially, base cuneate or clawed, apex obtuse, (when six petals, the inner ones usually narrower); carpels 3(4), ca. 0.6 × 0.3 mm, pilose; style ca. 0.6 mm long. *Infructescences* moderately slender, rufescent, brownish or silvery villous, indumentum spreading; axes 1.7–6 × 0.2–0.5 cm; fruiting pedicels (of mature fruits only) 0.4–1.6 cm long, terete; carpophores 4.1–10.6 mm long, free, clavate or terete, brownish-silvery velutinous. *Drupelets* 1.3–2.4 × 0.8–1.5 cm, dull orange to yellow when ripe, oblongoid or ellipsoid, eccentrically attached, shortly stipitate, base attenuate or truncate, stylar scar usually conspicuous; exocarp 0.7–1.5 mm thick, surface usually strongly muriculate, brownish to greyish hispidulous; mesocarp mucilaginous; endocarp 1.3–2.5 x 0.7–1.2 cm, papyraceous, surface weakly reticulate by slightly prominent fibers throughout. *Seeds* with embryo 2.6–4.4 cm long, cotyledons equal.

Distribution and ecology. The species ranges from eastern Ecuador (Napo Prov.) through central-southern Peru (Huánuco, Madre de Dios, Puno, San Martín and Ucayali departments), northern Bolivia (Beni, La Paz, and Pando) to western Brazil (Acre and Rondônia) (Fig. 25). It occurs mostly on non-flooded forest, from about 71 m in Acre (Brazil) up to 1550 m elevation in Franz Calabatea (Bolivia).

Common names and uses. Bolivia: "betchusajaja" (Tacana name), and "huevo de mono" (Spanish name), fruits edible when ripe (*DeWalt et al. 865*, imm fr); "chocolatillo" (*Perry et al. 654*, st); "uvilla", fruit edible, but astringent (*Smith et al. 12882*, mat fr). **Brazil:** "cipó cacau" (Portuguese) (*Daly et al. 9172*, ♂ fl); "cipó cacauí" (*Daly et al. 9233*, imm fr; *11472*, imm fr). **Ecuador:** "curare" (*Palacios et al. 881*, ♂ fl); "chichico huasca" (Kichwa), fruits edible (*Reyes & Carrillo 827*, mat fr*; Carrillo & Reyes 695*, mat fr). **Peru:** "ampihuasca amarilla" (*Schunke 2981*, mat fr); "ampihuasca delgadito" (*Schunke 6836*, ♂ fl, MO sheet sterile); "ampihuasca negra" (*Schunke 7125*, ♂ fl).

Etymology. Possibly in reference of the hispidulous-muriculate surface of the drupelets which is frequently described as warty in herbarium specimens.

Conservation status. The Extent of Occurrence (EOO), calculated for the 67 collections corresponding to 45 localities of *C. tomentocarpa*, is 984,251 km^2 and its Area of Occupancy (AOO) is 176 km^2. Although the species is not abundant where it occurs and, of the 39 subpopulations, 10 are found within protected areas across its distribution in Bolivia, Ecuador and Peru. This suggests that its AOO may be larger than the one estimated here; therefore, *C. tomentocarpa* is assigned a preliminary category of "Least Concern" (LC).

Discussion. The species is distinguished by its staminate inflorescence with densely brownish, rufescent or silvery hispidulous, moderately long and spreading indumentum and by the anthers with thin connective that the former frequently split into two halves. The only pistillate inflorescence available in this study has the primary branches reduced to single flowers, thus appearing racemiform. However, fruiting specimens from the same areas, that are similar in other features, appear to be clearly thyrsoid. It is likely that the inflorescence becomes more differentiated during further development, but that has not been confirmed here. The drupelets are always strongly muriculate. However, a single fruiting collection from Huánuco in central Peru (*Schunke 2981*) has a smooth surface and velutinous indumentum, although no pistillate flowers from the area were available in this study. The quantitative characters evaluated here in a few staminate plants from San Martín (*Gentry 25720*; *Schunke 6836*, *7125*) and from Ucayali (*Schunke 2690*) that resemble, in leaf shape and indumentum, the fruiting specimen mentioned above, completely overlap with those of *tomentocarpa* (Fig. 11B). Hence, I am unable to match variation in the staminate specimens to that in the fruiting material. Therefore, all of these collections are here provisionally placed under *C. tomentocarpa*.

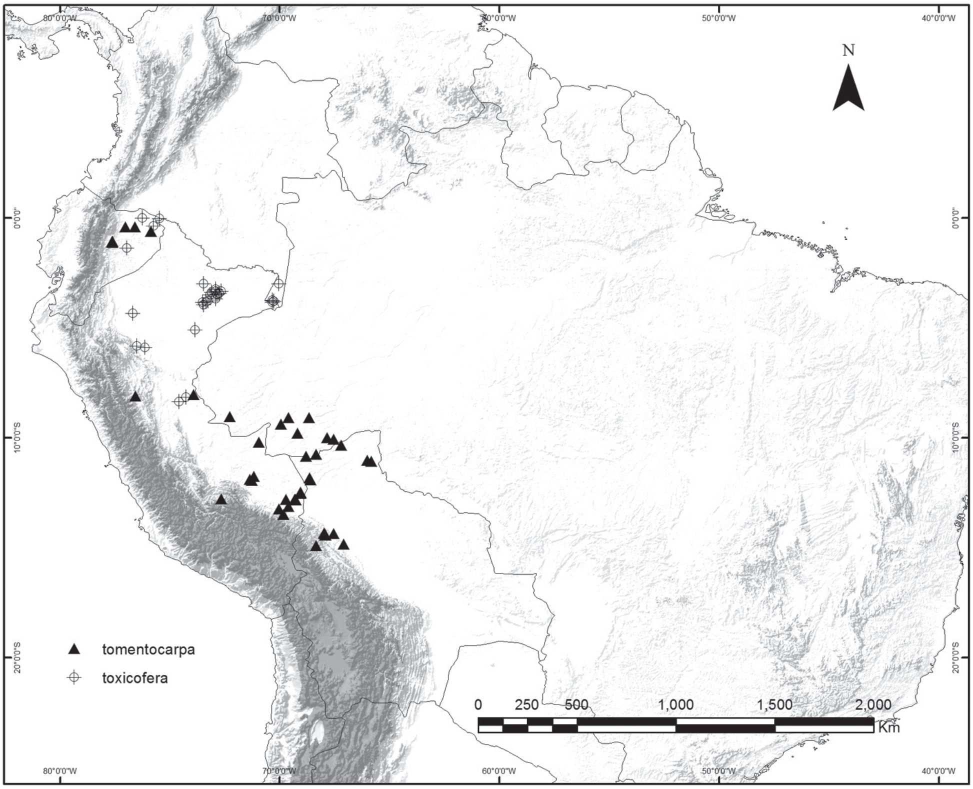

Figure 25. Geographic distribution of *Curarea tomentocarpa* and *C. toxicofera*.

Selected specimens examined. BOLIVIA. Beni: Vaca Diez, 9.2 km N from the road between Riberalta and Guayaramarín, on the old road to Cachuela Esperanza, primary forest, 11°05'S; 065°50'W, 230 m, 18 Sep 1981, (mat fr), *Solomon 6317* (MO!, NY!). **La Paz:** Franz Tamayo, Parque Nacional Madidi, laguna Chalalan, senda Jaguar, bosque amazonico preandino, 14°25'30S; 067°55'16"W, 300 m, 26 Sep 2006, (mat fr), *Araujo-M. et al. 3131* (LPB n.v., MO!, NY n.v.); Abel Iturralde, Comunidad de Buena Vista, parcela permamente de estudio etnobotánico, 3 km al NE de Buenavista, 14°22'S; 067°33'W, 180 m, 12 Apr 1995, (imm fr), *DeWalt et al. 865* (MO!); Parque Nacional y Area de Manejo Integrado Madidi, Laguna Chalalán, entrando 45 min., sobre orilla izquierda de Río Tuichí, vegetación borde de laguna, dominada por *Mauritia flexuosa* y helechos arbóreos, 14°26'S; 067°55'W, 450 m, 23 Apr 1997, (mat fr), *Paniagua & Beck 1171* (LPB n.v., MO!). **Pando:** Manuripi, Carretera entre Cobijá y Chicé km al S del Río Manuripi, 11°55'S; 068°36'W, 200 m, 1 Oct 1991, (mat fr), *Perry et al. 413* (LPB n.v., MO!).

BRAZIL. Acre: Mun. Sena Madureira, basin of Rio Purus, Rio Macauã, Colocacãa Apuí, river descending, 3 m below high water mark, terra firme forest on poorly drained soil, undulating terrain dissected by numerous streams, 09°48'S; 069°11'W, 29 Mar 1994, (imm fr), *Daly et al. 8073* (MO!, NY! [image seen]); Rio Acre, Antimary, Jul 1904, (fr), *Huber 4286* (B! frag., MG, n.v.); Km 16 from Rio Branco on Rio Branco-Brasiléia road, 20 Oct 1980, (♂ fl), *Lowrie et al. 595* (NY!, US [2]!); Estrada Rio Branco-Brasiléia, km 42, mata primaria de terra firme, 10°00'S; 067°50'W, 16 Oct 1980, (mat fr), *Nelson 716* (NY!).

ECUADOR. Napo: Tena, Estación Biológica Jatun Sacha, bosque muy húmedo tropical, suelo principalmente compuesto por arcilla roja, 01°04'S; 077°36'W, 450 m, 29 Jun 1996, (imm fr), *Ortiz & Vargas 197* (MO!); ibid., 3 Jul 1996, (♂ fl), *Ortiz & Vargas 199* (MO!); Río Arajuno, Sola Cocha, bosque muy húmedo tropical, suelo rojo arcilloso (ultisol), colinas pendientes, 01°07'S; 077°36'W, 500 m, 23–27 Oct 1985, (♂ fl), *Palacios et al. 881* (AAU n.v., MO-2!, NY!, QCA n.v., QCNE n.v.); Estación Biológica Jatun Sacha, bosque muy húmedo tropical, bosque primario sobre suelos rojos de colinas, 01°04'S; 077°37'W, 450 m, 06–14 Oct 1988, (♂ fl), *Palacios 3106* (MO!, NY!).

Orellana: Reserva Florística El Chuncho, 5 Km al norte de Coca, bosque húmedo tropical, suelos rojos sobre colinas disectadas, parcela permanente, 00°25'S; 077°01'W, 250 m, 23 May 1993, (mat fr), *Palacios 10725* (MO!, QCNE n.v.); Aguarico, Parroquia Capitán Agusto Rivadeneira, comunidad Chiro Isla (Kichwa), bosque de matorrales, 00°37'28S; 075°51'31"W, 200 m, 22 Feb 2005, (mat fr), *Reyes & Carrillo 827* (MO!, QCNE n.v.).

PERU. Cusco: La Convención, Río Manguriari (Manguyari), Tropical Forests – Alto Urubamba; upstream to Río Manguriari, forest edge, 12°47'S; 072°40'W, 750 m, 2 Feb 1991, (st), *Núñez & Ortíz 12765* (MO!). **Huánuco:** Pachitea, Dtto. Puerto Inca, Bosque Nacional de Iparia, región de bosque seco tropical a lo largo del Río Pachitea, cerca del pueblo de Puerto Inca (unos 85 km en distancia lineal de la confluencia con el Río Ucayali), 12 Jan 1969, (mat fr), *Schunke 2981* (F!, G!, NY!, US!). **Madre de Dios:** Manu. Parque Nacional de Manu, in forest near Cocha Cashu Station, on an old ox-bow lake of the Rio Manu, 11 Aug 1973, (mat fr), *Foster 2543* (NY!); Vicinity of Cocha Cashu, 400 m, 4 Aug 1977, (mat fr), *Foster & Terborgh 6480* (F!, NY!); Trails 4, 5 and 9, Cashu Cocha Camp, Manu National Park, non-inundated forest on alluvial soil, 380 m, 21 Oct 1979, (♀ fl), *Gentry et al. 27080* (F!, MO!, NY!); Tambopata Reserve, Río Tambopata at mouth of Río D'Orbigny, non-transect, [12°50'S; 069°17'W], 200 m, 2 Mar 1981, (imm fr), *Gentry & Young 31927* (MO!, USM n.v.); Zona reservada de Tambopata, 12°49'S; 069°18'W, 280 m, 10 Aug 1990, (imm fr), *Reynel & Meneses 5025* (MO!); Dist. Puerto Maldonado, Cusco Amazónico, bosque Primario, 250–300 m, 13°08'S; 069°36'W, 22 Nov 2002, (♂ fl), *Valenzuela et al. 975* (CUZ, n.v., MO!, USM, n.v.). **Puno:** Carabaya, Cabeceras del Río Candamo, 550–600 m, 13°15'S; 070°02'W, 24 Oct 1996, (mat fr), *Cornejo 2650* (MO!, fruit not seen); Río Candamo, fila at mouth of Río Guacamayo, ridge top forest with cloud forest aspect, 13°30'S; 069°50'W, 800 m, 26 May 1992, (imm fr), *Gentry et al. 77256* (MO!). **San Martin:** Fundo Curareland near Tinanta, 20 km NW of Tocache, at N edge of palm plantation, mature forest and forest edge, on alluvial soil near Rio Huallaga, 08°06'31"S; 076°3314"W, 500 m, 14 Mar 1979, (♂ fl), *Gentry et al. 25720* (F!, MO!, NY!, USM!); Mariscal Caceres, Dtto. de Tocache Nuevo, Santa Rosa de Mishollo (margen derecha del Rio Mishollo), 500 m, 15 Aug 1976, (♂ fl), *Schunke 6836* (MO!, NY!); Quebrada de Huaquisha (margen derecha del Rio Huallaga), 450 m, 2 Jul 1974, (♂ fl), *Schunke 7125* (F!, MO!, USM!). **Ucayali:** Coronel Portillo, Vicinity of LSU base camp, Quebrada Shesha (tributary of Río Abujao), ca. 65 km NE of Pucallpa, 08°02'S; 073°55'W, 250 m, 25 Jun 1987, (imm fr), *Gentry & Díaz 58512* (F!, MO!); [Distrito de] Iparia, a lo largo del Río Ucayali, cerca del pueblo de Iparia (unos 80 km arriba de la confluencia con el Río Pachitea), 300 m, 26 Aug 1968, (♂ fl buds & fl), *Schunke 2690* (F!, G, NY!); Dtto. Purús, Rio la Novia, margen derecha del caserio de la comunidad nativa San José, bosque alto, terreno húmedo, 10°12'S; 070°57'W, 180 m, 13 Feb 2002, (mat fr), *Schunke & Graham 14779* (MO!).

9. *Curarea toxicofera* (Wedd.) Barneby & Krukoff

Figs 26A–H, 27A–F

Curarea toxicofera (Wedd.) Barneby & Krukoff, Mem. New York Bot. Gard. 22(2): 9. 1971. fig. 1.

Cocculus toxicoferus Wedd., in Castelnau, Expéd. Part. Cent. Amér. Sud. 5: 22. 1851. Type. Peru. "Vulg. Pani–base d'un poison pour les flèches utilisé chez les Indiens Pebas–Hte. Amazone", [1847], *Castelnau s.n.* (sterile) (lectotype designation effected by Krukoff and Moldenke 1939, pg. 338: P! [P00048602] which is annotated as *Cocculus toxicoferus* in the hand of Weddell and has the eight leaves mentioned by Krukoff and Moldenke. Moreover, this specimen was also annotated in 1939 by Moldenke as "Type", photograph at NY!; presumed isolectotypes: F! [F-893667, frag.], P!). Peru, Florida, Río Putumayo, at mouth of Río Zubineta, forest, 200 m, Mar 1931–Apr 1931, (♂ fl), *Klug 2042* (epitype, designated here: MO!; isoepitypes: BM!, F!, GH!, K!, NY!, US!). Note: Following Art. 9.8 of the Melbourne Code (MacNeill et al. 2012), I am here designating an epitype to serve as an interpretative type of *Cocculus toxicoferus*, whose sterile condition makes it ambiguous for identification purposes.

Chondrodendron toxicoferum (Wedd.) Moldenke & Krukoff, Brittonia 3(2): 338. 1938. Type: Based on *Cocculus toxicoferus* Wedd., in Castelnau Expéd. Part. Cent. Amér. Sud. 5: 22. 1851.

Hyperbaena polyantha Diels, Verh. Bot. Ver. Brand. 50: 73. 1908.
Type: Brazil. Amazonas: Juruá Miry, Lago de Esperança, Aug 1901, (♂ fl), *Ule 5631* (lectotype designation effected by Krukoff and Moldenke 1938, pg. 23: B!, F neg. 4985]; isolectotypes: CORD! [image seen], F! [F-1014713, frag.], G!; K! [image seen], MG!, [image seen], NY! [NY00320584, frag.]).

Chondrodendron polyanthum (Diels) Diels, in Engler, Pflanzenr. 4(94): 78. 1910.
Type: Based on *Hyperbaena polyantha* Diels.

?*Chondrodendron bioccai* G. Lusina, Revista Mus. Paul. Univ. São Paulo II. 8: 227, figs 1–2. 1954.
Type: Brazil? Locality unknown, collector unknown.

Description. Medium-sized understory *lianas* about 10–12 m tall; older stems more or less terete or less frequently flattened, then ca. 3 cm wide; bark greyish to dark brown, with shallow lengthwise fissures; branchlets brownish, greyish to silvery puberulent-strigillose. *Leaves:* blades 8–24 × 5–17 cm, narrowly to broadly ovate, chartaceous at all stages; surfaces discolorous, lustrous and glabrous adaxially, finely silvery tomentellous abaxially, sometimes creamish when older, indumentum mostly concealing the surface at all stages, base truncate, obtuse or shallowly cordate, apex acute or acuminate, long-acuminate when juvenile, 3–5(–7) palmati- or shortly plinerved, innermost pair of main veins acrodromous imperfect at all stages, midrib adaxially shallowly sunken at the base, becoming flat, conspicuously raised abaxially, secondary veins 2–3(–5) pairs, arising above the middle of the blade, raised on both surfaces, more conspicuous abaxially, veinlets slightly prominent adaxially, more conspicuous abaxially; petioles (2.7–)6–25 cm long, ridged, brownish to silvery strigillose-tomentellous or glabrate, distal pulvinus more conspicuous, rugulose, rounded, sometimes more or less flat adaxially. *Staminate inflorescences* solitary or fascicled, cauliflorous or axillary thyrsi, brownish, greyish or silvery strigillose-tomentellous, (trichomes spreading); axes, 10–42 cm long (less frequently simple dichasia arising in young terminal shoots, then the dichasia axes 2–4 cm long) (Fig. 26A), densely brown; primary branches 1.4–9.4 cm long, with several (2–4) branching orders, these laxly arranged; bracts 0.5–1.2 mm long, narrow ovate to ovate, concave, moderately fleshy, indumentum as on the inflorescence. *Pistillate inflorescences* solitary or fascicled, cauliflorous, moderately stout, few-flowered thyrsi (Fig. 27A), brownish strigillose- tomentellous; axes ca. 2.5 cm long; primary branches 0.7 cm long; bracts ca. 0.8 mm long, ovate, concave, moderately fleshy, glabrous adaxially, brown strigillose-tomentellous abaxially. *Staminate flowers* 1.6–2.4 mm long, greenish, green-yellowish or whitish; pedicels 1.6–6.0 mm long, mostly slender, ridged, indumentum as on staminate inflorescence; bracteoles 1–2, 0.2–0.6 × 0.1–0.4 mm, ovate, moderately fleshy, glabrous adaxially, greyish or silvery villous-tomentellous abaxially; sepals 6, glabrous adaxially, greyish or silvery villous-tomentellous abaxially; outer sepals 0.5–1.4 × 0.3–0.8 mm, narrowly ovate or elliptic, base truncate, apex obtuse; inner sepals 1.5–2.4 × 0.8–1.8 mm, elliptic, ovate, oblong or weakly obovate, base obtuse, cuneate or shortly clawed, apex acute or obtuse, tips mostly strongly reflexed past anthesis; petals 6, 0.7–1.6 × 0.6–1.1 mm, inner ones slightly smaller and narrower, obovate-trilobed or spatulate, weakly concave, membranous, glabrous adaxially, sparse silvery tomentellous abaxially, base cuneate or distinctly short- to long-clawed, lateral margins inflexed, partially clasping the filaments, apex obtuse or truncate; stamens (5)6, filaments 0.3–)0.7–1.4 mm long, clavate or clavate-sigmoid, free (shortly connate), glabrous adaxially, glabrous to mostly silvery tomentellous abaxially; anthers 0.3–0.6 mm long, erect or weakly incurved, especially when older, connective thicker adaxially and protruding as a hump (Fig. 26G) or as a keel at the base of thecae (also apically); thecae not separating apically and, for the most part, not immersed in the connective. *Pistillate flowers* ca. 2.1 mm long, green; pedicels ca. 1.1 mm long, ridged, brown strigillose-tomentellous; bracteoles 3, ca. 0.4 × 0.3 mm, ovate, fleshy, weakly concave, glabrous adaxially, brownish villose-tomentellous

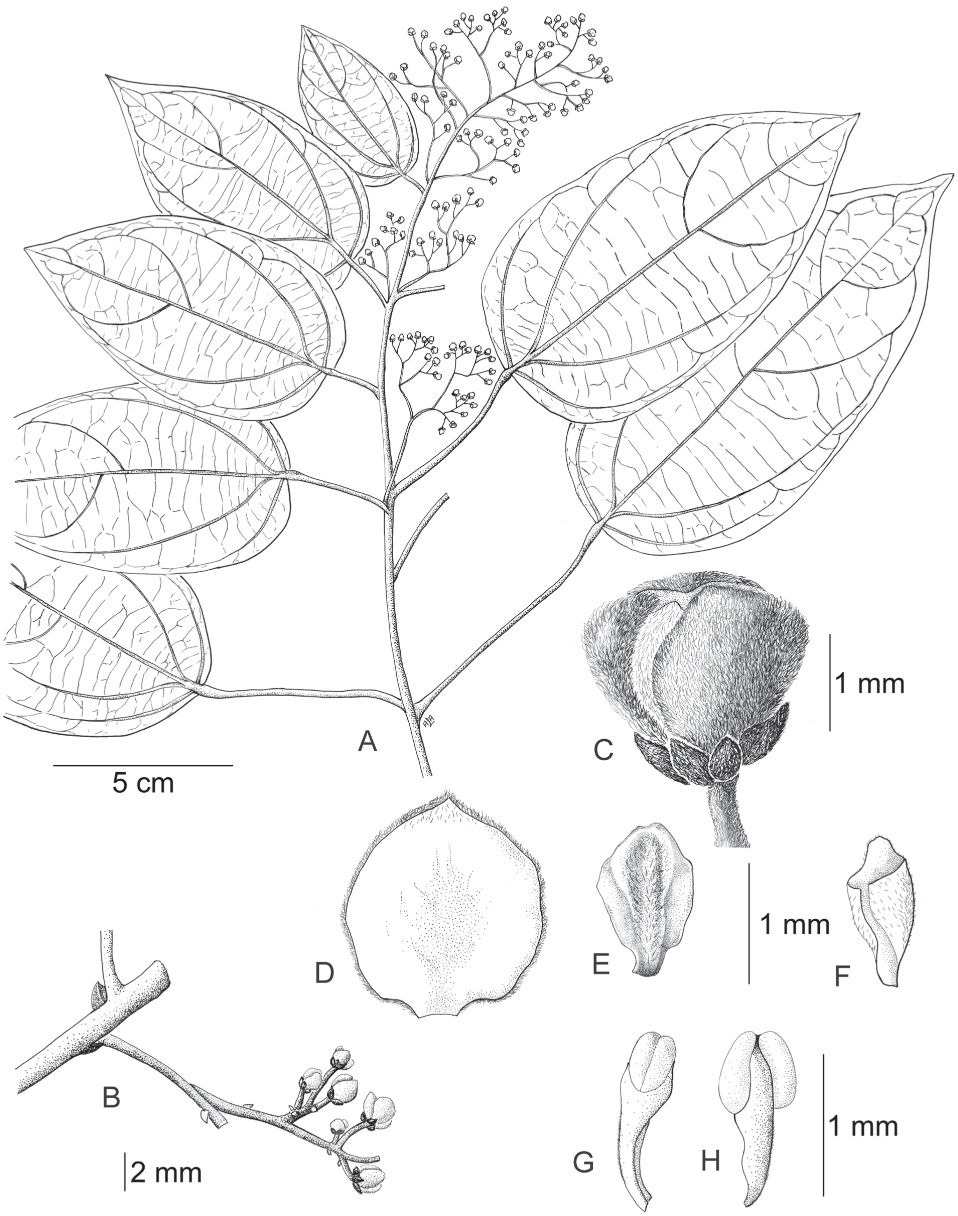

Figure 26. *Curarea toxicofera* staminate plant: **A** flowering branch **B** detail of inflorescence **C** flower bud **D** inner sepal, adaxial surface **E–F** outer and inner petals, abaxial and latero-adaxial surfaces **G–H** outer stamens, lateral and abaxial surfaces (**A–B** based on *Ule 5631* **C–H** based on *Encarnación 1094*).

abaxially; sepals 6–9, weakly concave and slightly fleshy to fleshy, glabrous adaxially, brownish, greyish to silvery villous-tomentellous abaxially; outer sepals ca. 0.7 × 0.6 mm, ovate, base truncate, apex acute; middle sepals ca. 1.6 × 1.8 mm, ovate to broadly

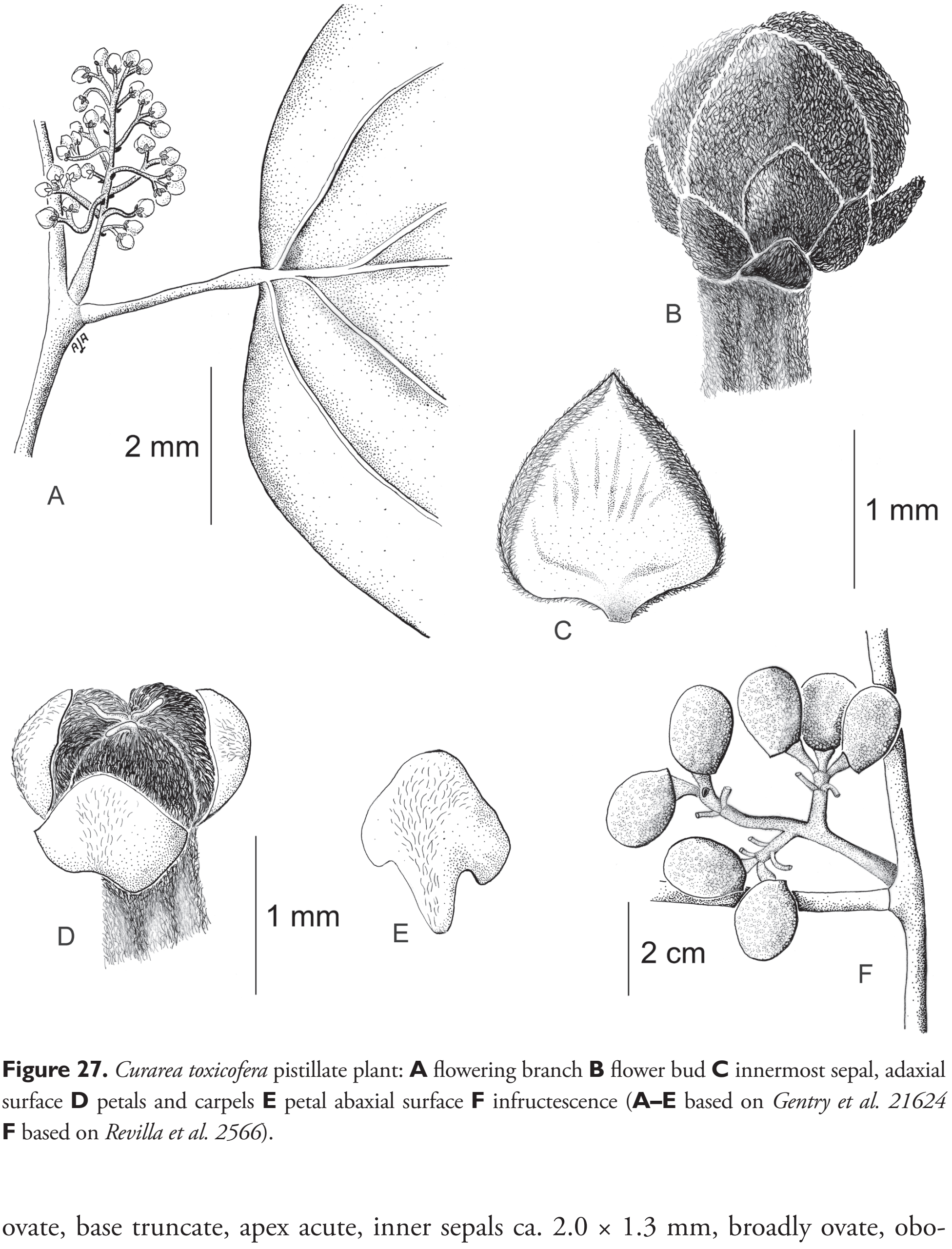

Figure 27. *Curarea toxicofera* pistillate plant: **A** flowering branch **B** flower bud **C** innermost sepal, adaxial surface **D** petals and carpels **E** petal abaxial surface **F** infructescence (**A–E** based on *Gentry et al. 21624* **F** based on *Revilla et al. 2566*).

ovate, base truncate, apex acute, inner sepals ca. 2.0 × 1.3 mm, broadly ovate, obovate, spatulate, elliptic or rhombic, base obtuse or truncate, apex acute or rounded, tips strongly reflexed past anthesis; petals 3, ca. 1.6 × 1.5 mm, spatulate, membranous, weakly concave, glabrous adaxially, moderate silvery tomentellous abaxially, clawed at base, apex obtuse or retuse; carpels 3, ca. 0.7 × 0.7 mm, brown villous tomentellous; style ca. 0.7 mm long. *Infructescences* axes (2–)8 × 0.3–0.7cm, indumentum as on pistillate inflorescences; fruiting pedicels 1.3–3.5 mm long, terete, slender to moderately stout;

carpophores 3.8–11.3 mm long, free or basally connate up to 1/3 of their lengths, claviform or terete, spreading or incurved distally, brown velutinous-hispidulous. *Drupelets* 1.8–2.1 × 0.9–1.3 cm, dull orange to yellowish when ripe, oblongoid, ellipsoid or subglobose (Fig. 27F), eccentrically attached, base attenuate or truncate, (shortly stipitate); stylar scar conspicuous; exocarp 0.6–0.8 mm thick, surface smooth, rugulose or weakly muriculate, silvery to greyish velutinous; mesocarp mucilaginous; endocarp 0.7–0.9 × 1.5–1.8 cm, papyraceous to chartaceous, smooth, with slightly prominent fibres or weakly rugulose throughout. *Seeds* with embryo 3.2–4 cm long, cotyledons equal.

Distribution and ecology. In north-western Amazonia, including the eastern slopes of the Andes in Peru (Fig. 25). The species commonly grows in periodically flooded forests, but also in non-flooded lowland forests and up to 350 (500) m in elevation. Flowering and fruiting material were collected all year round.

Common names and uses (sterile specimens are indicated as st). **Brazil**: fruits edible (*Fróes 26364*). **Colombia:** "taufe-lleida" (*Diaz 36*, st); "Ñamitá" (en Karijona) (*García-Barriga 14578*, st); cure for fevers, antimalarial (*Grassl 10076*, st); said to be "formerly used by Karijona Indians in arrow-poison" (Krukoff and Barneby 1970) (*Schultes 5526*, st). **Ecuador**: to hunt wild animals, "ambi-huasca" (Quichua) (*Cerón et al. 39668*, st). **Peru**: "pani' (*Castelnau s.n.*,1851); "abuta amarilla, "isaveño" (Huitoto) (*Martin & Lau-Cam 1266*, st); "ampihuasca" (*Mathias & Taylor 3900*, imm fr); "abuta amarilla" (*Rimachi 10636*, mat fr; *Tina & Tello 2066*, ♂ fl); "sarívana" (*Weiss 132*, st); "ampihuasca", medicinal (*Woytkowski 108*, st); "ampihuasca" (*Woytkowski 5108*, st); "abuta negra" (*Rimachi 10503*, st).

Note. Sterile collections such as *Fox 12* (K), from Peru and *Schultes 3522* from Colombia, had previously been identified as *Chondrodendron toxicoferum* (= *Curarea toxicofera*) (Krukoff and Barneby 1970), the first being reported as "poison used for blow pipe" and the second as a source of curare with the common name of "sa pe pa" (Kofán) (Krukoff and Barneby 1970). Both specimens cannot be determined with certainty and are here tentatively identified as *Curarea* sp.

Etymology. Presumably in reference to the toxic effects attributed to the plant, as the type specimen was collected in the Pevas region, amongst the Yaguas who use the plant in the preparation of arrow poison (de Castelnau 1851: 22).

Conservation status. The Extent of Occurrence (EOO), based on 34 collections corresponding to 28 localities of *C. toxicofera*, is calculated as 419,469 km^2 and an Area of Occupancy (AOO) of 108 km^2. The 28 localities correspond to 27 subpopulations, of which two are within protected areas in Ecuador and four subpopulations are found in private reserves near Iquitos, Peru. In addition the species is widespread across its distribution. Therefore, *C. toxicofera* is assigned a preliminary category of "Least Concern" (LC).

Discussion. The typical form of *C. toxicofera* as circumscribed here, ranges from the Amazonian lowlands of Ecuador, Colombia, Peru and Brazil (including the sterile type specimen of *Cocculus toxicoferus* Wedd., *Castelnau s.n.*, Peru and the type of *Hyperbaena polyantha* Diels, *Ule 5631*, Brazil).

Individuals are frequently found in periodically flooded forests, but can also be found in non-flooded forests up to 500 m in elevation. Most have ovate leaves with 5 main veins and staminate and pistillate inflorescences with very short, brownish to greyish, appressed indumentum, but slightly longer (up to 0.3 mm long) and silvery or cream indumentum is also observed in specimens from the lower Amazon basin in Brazil (e.g. *Prance 11272*, *Fróes 29639* and *Ducke 2134*).

In the staminate condition, *C. toxicofera* is readily distinguished from *C. tomentocarpa* by its brown strigillose-tomentellous indumentum (*vs.* a rufescent to silvery hispidulous) and its larger flowers –they are the largest in the genus– with greyish to silvery villous-tomentellous, adpressed indumentum (*vs.* rufescent or silvery spreading indumentum). However, separation from *C. iquitana* is more challenging and at present is distinguished by its slender pedicels in staminate flowers (vs. thicker in *C. iquitana*). However, more field and taxonomic work remains to be done in order to be able to confidently match the staminate and pistillate specimens of the taxa involved.

Chondrodendron bioccai is here included in the synonymy with hesitation. As discussed by Krukoff and Barneby (1970), the species appears to have been described from two collections (from the region of Rio Tiquiê and the region of Rio Uaupés by Biocca and Giacone, respectively). A holotype was not stated, two photographs (listed as Figs 15, 16, but published as Figs 1, 2) presumably of the original material were published in the protologue (Lusina 1954). Krukoff and Barneby (1970) hesitantly placed *Chondrodendron bioccai* as a synonym of *Chondrodendron toxicoferum* and later as a synonym of *Curarea toxicofera* (Barneby & Krukoff, 1971). The repository of the type collection remains uncertain at the present time and hence the taxonomic identity cannot be established firmly.

Selected specimens examined. BRAZIL. Acre. Proje. RADAM-Sub-base de Cruzeiro do Sul-Ponto 7-Sb-18-ZD, 23 Feb 1976, (imm fr), *Marinho 291* (NY!). **Amazonas:** Paraná do Careiro (Boca do Solimões), (varzea, igapó do Lago Capitari), 8 Jun 1948 (♂ fl), *Ducke 2134* (COL!, GH!, NY!, R!); Mun. Eirunepe, Lago Dois Unidus, Ituxy, restinga, 30 Nov 1946, (♂ fl), *Fróes 21802*A (NY!); Beira do lago de Badajós, igapó, 24 Ago 1950, (imm fr), *Fróes 26364* (IAN!); Vicinity of Manaus, Igarapé Ipixuna, Lower Rio Negro opposite Manaus, Igapó, 1 Apr 1971, (♂ fl), *Prance, et al. 11272* (F!, MG!, NY!, US!). **Rondônia:** Esperança (ad ostium fluminis Javari), silva loco alto, high forest, 27 Oct 1945, (♂ fl bud), *Ducke 1968* (NY!, R!); Rio Machado, curso inferior, igapó, Jan 1981, (♂ fl), *Goulding 1187* (MG!).

COLOMBIA. Amazonas: Quebrada El Mochilero, afluente del Yarí, márgenes y zona de rebalse aluvial, 150 m, 24 Apr 1986, (imm fr), *Galeano et al. 1135* (COL!); Río Caquetá, La Pedrera, 1–4 Oct 1952, (st.), *García-Barriga 14578* (COL!, MO!); Puerto Nariño, Trocha de Panduro a San Martin, bosque no inundable, 03°50'S; 070°20'W, 100 m, 24 Feb 1993, (♂ fl), *Madriñán 702* (MO!); Leticia, Parque Nacional Natural Amacayacu, Centro Administrativo Mata-matá (Inderena), a orillas de la quebrada Mata-matá en zona de várzea, 03°47'S; 070°15'W, 100 m, 11 Mar 1991, (imm fr), *Rudas et al. 1528* (MO!); Corregimiento de Tarapacá; Caño Pupuña (afluente del Río Cotuhé), a las orillas del caño, 02°59'S; 070°02'W, 100 m, 25 Jun 1991, (♂ fl), *Rudas et al. 2512* (MO!). **Vaupés:** Mayaca River, vicinity of Cachivera del Diablo and mouth of river, 300 m, 1 May 1943, (mat fr), *Schultes 5526* (AMES!).

ECUADOR. Napo: Rio Yasuni, periodically inundated forest, ca. 80 km upriver from Nuevo Rocafuerte, 225 m, 17 Sep 1977, (♂ fl bud & fl), *Foster 3722* (F!). **Orella-**

na: Cantón Nuevo Rocafuerte Isla aproximadamente 10 Ha. entre la Laguna de Jatun Cocha, cerca del Río Yasuní, Parque Nacional Yasuní, Igapó, 00°01'S; 075°28'W, 280 m, 17 Sep 1999, (st), *Cerón et al. 39668* (MO!). **Pastaza:** Curaray, SE of the airstrip, rain forest and *Mauritia* várzea, understorey dominated of Melastomataceae, Rubiaceae and palms, 01°22'S; 076°57'W, 250 m, 20 Mar 1980, (mat fr), *Holm–Nielsen et al. 22169* (AAU n.v., NY!). **Sucumbíos**: Lago Agrio, Reserva Cuyabeno, Río Cuyabeno, 2-3 km arriba de Laguna Grande, área inundada estacionalmente por aguas negras, 00°00'S; 076°14'W, 230 m, 16 Nov 1991, (♂ fl), *Palacios et al. 9032* (MO!); Río Zábalo, bosque húmedo tropical, bosque afectado por inundaciones de aguas negras, 00°22'S; 075°45'W, 230 m, 22 Nov 1991, (imm fr), *Palacios et al. 9493* (MO!, NY!).

PERU. Loreto: Yanamono, campamento Explorama Lodge, terreno de altura, 03°25'S; 072°45'W, 120 m, 31 May 1979, (mat fr), *Díaz et al. 1187* (MO!); Requena, Caño Yarina, a 300 m de la Base Yarina en la Zona Reservada del Río Pacaya, margen izquierda del Río Ucayali, bosque inundable, 6 Apr 1977, (♂ fl), *Encarnación 1094* (G!, MO!, NY!, US!); Rio Itaya, inundated tahuampa forest, [03°46'S; 073°15'W], 120 m, 20 Mar 1977, (♂ fl), *Gentry et al. 18505* (F!, MO!, NY!); Maynas, tahuampa near Río Amazonas between Punchana and Santa Clara de Nanay, outskirts of Iquitos, 120 m, 3 Feb 1978, (♀ fl & imm fr), *Gentry et al. 21624* (F!, MO!); Alto Amazonas, Balsapuerto (lower Rio Huallaga basin); dense forest, [05°49'S; 76°33'W], 150–350 m, 28–30 Aug 1929, (♂ fl), *Killip & Smith 28665* (F!, NY!); Alto Amazonas, Fortaleza, near Yurimaguas, [05°54'S; 76°07'W], 140 m, Nov 1932, (♂ fl), *Klug 2782* (BM!, F!, G!, GH!, K!, MO, NY!, US!); Distrito Las Amazonas, Quebrada Sucusari, bosque maduro en tierra firme, camino de ACEER hacia el Napo, 03°15'S; 072°55'W, 140 m, 4 Feb 1996, (♂ fl), *Ortiz et al. 157* (MO!); Distrito Iquitos, Rio Itaya, San Juan de Muniches, borde de purma, 16 Oct 1976, (mat fr), *Revilla & Carillo 1501* (F!, MO!, NY!); Indiana, Yanamono, Explorama Lodge, Bosque inundable estacional (aguas blancas), 106 m, 03°28'S; 072°50'W, 19 Feb 1989, (♂ fl), *Vásquez & Jaramillo 11714* (MO!); Explor Napo Camp at Río Sucusari, primary forest, flooded forest, collected from canoe along Río Sucusari, 03°20'S; 072°55'W, 120 m, 22 Mar 1996, (♂ fl buds & fl), *van der Werff & Vásquez 13990* (MO!). **Ucayali:** Prov. Coronel Portillo, Distrito Calleria, Quebrada Pumayacu, margen izquierda del Río Utiquinia, al borde de la quebrada, en bosque alto, 150–175 m, 08°09'S; 074°15'W, 13 Ma 2003, (♂ fl bud & fl), *Schunke 15323* (F n.v., MO!).

VENEZUELA. Amazonas: Embanchure du Guaviare, Plantes du Haut Orenoque, 1887, (♂ fl), *Gaillard 184* (P!); Forest immediately behind "El Tobogan de La Selva" camping area; 35 km south of Puerto Ayacucho, 85 m, 21 Feb 1979, (st), *Plowman 7712* (F!).

Tribute

This contribution is dedicated to the memory of Alwyn H. Gentry, an extraordinary field biologist, inspiring mentor, dear friend and colleague who was always eager to share his knowledge and who died tragically in a plane crash during the summer of 1993, while surveying a dry forest in western Ecuador.

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Several years in the making, this contribution is, for the most part, based on the study completed in partial fulfilment of requirements for the Masters of Science degree at the University of Missouri-St. Louis. Species boundaries in *Curarea* were reinterpreted in light of more data available that allowed for further analyses to be performed. I thank Peter F. Stevens and John F. Pruski for their critical reading of earlier versions of the manuscript. Gordon McPherson, Mike Grayum and Kanchi Gandhi kindly advised on nomenclatural issues. Guidance and support from Henk van der Werff, Mick Richardson, Robert Marquis, Charlotte M. Taylor and Roy Gereau, in early stages of the work is greatly appreciated. I thank Oyomoare Ozuwa-Peters, Dilys Vela Diaz and Cynthia Hong-Wa for their advice with data analyses. I am grateful to Cynthia for her assistance with the conservation status analyses. Alba L. Arbeláez made the fine illustrations for several of the species. The comments and suggestions provided by Marco Pellegrini, David Neill, Frédéric M.B. Jacques and the *Phytokeys* subject editor Cliff Morden, greatly contributed to improve this manuscript. Financial support was provided by the National Geographic Society Grant No. 5472-95 to Oliver Phillips and Rodolfo Vásquez, a posthumous grant to Alwyn H. Gentry from the National Tropical Botanical Garden and a grant from the Missouri Botanical Garden Alumni Fund. Mike Veith, formerly at Washington University in St. Louis, assisted with the SEM. Richard Keating at the Missouri Botanical Garden, kindly helped with the leaf anatomy and leaf clearing preparations. Gracielza Dos Santos and Regis Miller, formerly at the Forest Product Laboratory, USDA Forest Service, Madison, Wisconsin, provided assistance with wood anatomy sample preparations. I also thank the several people who in many ways contributed to my field work, especially to David Neill and Mercedes Asanza in Ecuador and Rodolfo Vásquez in Peru. Jim Solomon, curator of the herbarium at the Missouri Botanical Garden (MO) is thanked for requesting on loan the specimens on which most of this study is based. Similarly, thanks are also due to the curators of the aforementioned herbaria for loaning the *Curarea* specimens on which this study was based.

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Supplementary material 1

List of specimens examined

Authors: Rosa del C. Ortiz

Data type: Index of specimens examined

Explanation note: Index of collectors, collector numbers, and corresponding curarea species.

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RESEARCH ARTICLE

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Taxonomic review of *Ceratozamia* (Zamiaceae) in the Sierra Madre Oriental, Mexico

Lilí Martínez-Domínguez[1,2], Fernando Nicolalde-Morejón[1],
Francisco Vergara-Silva[3], Dennis Wm. Stevenson[4]

1 *Laboratorio de Taxonomía Integrativa, Instituto de Investigaciones Biológicas, Universidad Veracruzana, Xalapa, 91190, Veracruz, México* **2** *Centro de Investigaciones Tropicales, Universidad Veracruzana, José María Morelos 44, Zona Centro, Xalapa, 91000, Veracruz, México* **3** *Laboratorio de Sistemática Molecular (Jardín Botánico), Instituto de Biología, Universidad Nacional Autónoma de México, 3er Circuito Exterior, Ciudad Universitaria, Coyoacán 04510, México, D. F., México* **4** *The New York Botanical Garden, Bronx, Nueva York, 10458-5120, USA*

Corresponding author: *Fernando Nicolalde-Morejón* (enicolalde@uv.mx)

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Abstract

The genus *Ceratozamia* is revised for the Sierra Madre Oriental in Mexico. This region is one of the biogeographic areas with the greatest diversity of species in this genus. These species are highly variable morphologically and this variability has led to a complex taxonomic history with many synonyms, particularly with reference to *C. mexicana*. We present a comprehensive taxonomic revision with history of nomenclature and the morphology, relationships, distribution and use of these species. We also introduce a key for their identification, descriptions, full synonymy, nomenclatural notes, etymologies and neotypes as well as taxonomic comments describing relevant taxonomic changes. We recognise fourteen species in this biogeographic province*:* *C. brevifrons*, *C. chamberlainii*, *C. decumbens*, *C. delucana*, *C. fuscoviridis*, *C. hildae*, *C. kuesteriana*, *C. latifolia*, *C. mexicana*, *C. morettii*, *C. sabatoi*, *C. tenuis*, *C. totonacorum* and *C. zaragozae*. This study provides a foundation for future taxonomic work in Neotropical species of *Ceratozamia*.

Keywords

Cycadales, Mexican cycads, Neotropical gymnosperms, taxonomic circumscription

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Introduction

Ceratozamia Brongn. is one of the eight genera in the most diverse cycad family, Zamiaceae (order Cycadales). This genus is endemic to Mega-Mexico (*sensu* Rzedowski 1991), ranging from Mexico to Honduras. Mexico is considered the centre of diversity for *Ceratozamia*, given that 30 out of 31 recognised species occur in its territory (Vovides et al. 2004a; Nicolalde-Morejón et al. 2014), 90 percent of which are endemic (Calonje et al. 2013-2018). Diversity for this genus is particularly prevalent along the Sierra Madre Oriental and Southwest Mexico, especially in the political states of Veracruz, Oaxaca, Chiapas and Tabasco. *Ceratozamia* plants mainly inhabit high-elevation cloud forests ("bosque mesófilo de montaña"), pine-oak forests and relatively elevated sectors of evergreen forest in a narrow but continuous distribution (Moretti et al. 1980; Vovides et al. 2004b).

Ecologically, *Ceratozamia* requires conditions of abundant humidity to ensure proper development of immature embryos because the seeds are usually released from ovulate strobili approximately one year before germination (Norstog and Nicholls 1997). Considering the deforestation rates in Mexico and historical patterns of botanical collection, *Ceratozamia* is amongst the most threatened plant groups in the country and the genus is placed in the IUCN Red List (IUCN 2016), listed on CITES Appendix 1 and listed in the 'Norma Oficial Mexicana NOM-059-SEMARNAT-2010' (SEMARNAT 2010; Donaldson 2003). The latter is an official document issued by Mexican authorities listing protection categories under which diverse taxonomic groups should be placed.

Species of *Ceratozamia* are similar in morphology, particularly with regards to vegetative characters' states, making taxonomic identification problematic. The most recent species-level taxonomic treatment of the genus is over eight decades old (Schuster 1932). Since then, researchers have focused on the study of the taxonomy of individual species and/or species complexes (Vovides et al. 2003; Osborne et al. 2006; Pérez-Farrera et al. 2009; Vovides et al. 2016).

In recent taxonomic works, quantitative morphological characters such as plant size and leaflet width have been commonly used as a basis for the identification and description of new species because they exhibit variability across the genus (Vovides et al. 2004a, c; Whitelock 2004). However, other contemporary studies have shown that these characters can be highly variable between and amongst populations, which limits species diagnosis (Martínez-Domínguez et al. 2016; 2017a, b, c). Other characters commonly used are the direction, form and texture of leaflets and the formation of prickles (Pérez-Farrera et al. 2001; Vovides et al. 2003). However, analysis of morphological patterns for these characters along the distribution range of *Ceratozamia* indicates that leaflet shape is highly similar in many species (Stevenson et al. 1986).

Ceratozamia was first described by Brongniart (1846) based on the sole species *C. mexicana*, which was described from wild specimens later cultivated at the Natural History Museum of Paris. Later, Miquel (1847, 1848) described five new species –namely, *C. brevifrons*, *C. intermedia*, *C. latifolia*, *C. longifolia* and *C. robusta*. In 1849, this Dutch botanist reduced *C. intermedia* as a variety of *C. longifolia* (var. *minor* Miq.). Later on, Regel (1857a, b) recognised only *C. mexicana* and *C. robusta*, along with a new species, *C. kuesteriana* Regel. All other Miquel names were placed in synonymy within *C. mexicana*.

Miquel (1861) recognised all species listed in his 1849 work plus *Ceratozamia kuesteriana* and subsequently synonymised all of these names with *C. mexicana* (Miquel 1868, 1869a, b). Regel (1876a, b) conserved his 1857 system, which recognised *C. robusta*. The two most recent taxonomic treatments of *Ceratozamia*, written by Thiselton-Dyer (1884) and Schuster (1932), are highly contrasting in the recognition of species and infraspecific categories. The first author recognises four species and the latter only two species, placing the rest of older names as varieties. Specimen scarcity and lack of nomenclatural types seem to have been largely responsible for the nomenclatural instability in *Ceratozamia*. This issue was clarified by Stevenson and Sabato (1986).

Given the considerable increase in activities dedicated to the exploration of cycad diversity in Mexico (the target of the main taxonomic interest for the last 40 years) and the unstable taxonomy and nomenclature in *Ceratozamia*, we present a taxonomic clarification of the *Ceratozamia* species found along the Sierra Madre Oriental (SMO) from North Tamaulipas to North Oaxaca, which represent areas of endemism for this biogeographic province.

Materials and methods

Species-level circumscription is based on results of a phylogenetic analyses performed for *Ceratozamia* species that included quantitative and qualitative morphological data, molecular evidence, as a well as analyses of herbarium specimens (Martínez-Domínguez 2018). We present the taxonomic treatment for a part of the genus, corresponding to a well-delimited biogeographic region (Fig. 1). We examined herbarium specimens deposited in the following herbaria: CHAPA, CIB, ENCB, FCME, FTG, GH, HEM, IEB, K, LE, LSU, MB, MICH, MEXU, MO, NY, P, SERO, SLPM, U, UAT, US, XAL and XALU. This information was complemented by a review of the original taxonomic accounts for the relevant *Ceratozamia* species and additional data collected during fieldwork to evaluate diagnostic characters. The corresponding populations were monitored during four years (2014-2017) to evaluate reproductive structure characters, as well as some ontogenetic stages in these characters. In all cases, nomenclatural types were reviewed by all authors or at least one of them.

Results

Vegetative morphology. Stems of the species here studied are epigeous and erect. They become decumbent with age and may develop two or more apices, with the exception of *Ceratozamia latifolia*, *C. hildae*, *C. kuesteriana* and *C. zaragozae*, which have semi-epigeous stems.

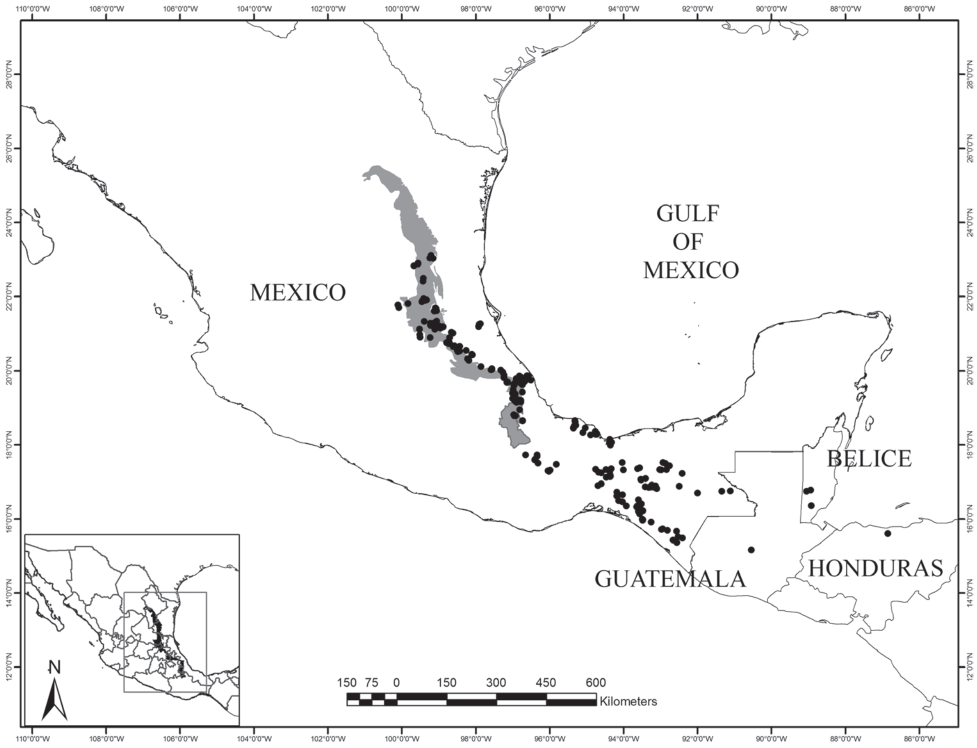

Figure 1. Map of the entire distribution of Ceratozamia in relation to the Sierra Madre Oriental (in grey).

Ceratozamia species can produce 4 to 15 leaves per year and each apex can carry up to 100 leaves. *C. hildae* and *C. latifolia* are exceptional in this respect because they only produce 1 to 3 leaves per year. Leaves of most species reach up to 2.80 m long. The longest leaves are present in *C. mexicana*, *C. hildae* and *C. tenuis*, whereas the shortest can be observed in *C. latifolia* and *C. zaragozae*. New leaf colour can vary from light green to yellowish, as in *C. brevifrons*, to dark green (blackish) as in *C. tenuis* or reddish-brown as in *C. chamberlainii*. Leaf colour can be persistent in some species and remain at the leaf base, margins, nerves and/or undersides of leaflets and the leaf rachis and/or petiole as in *C. latifolia*, *C. chamberlainii*, *C. kuesteriana* and *C. fuscoviridis*. In other species, leaf colouration can disappear at maturity as in *C. totonacorum*. At emergence, the leaf petiole and rachis have abundant trichomes of two types: brown for species distributed in Central or South Sierra Madre Oriental with the exception of *C. decumbens* and white for species distributed in North SMO (Fig. 2).

In most species, presence of prickles in the petiole and rachis is highly variable intraspecifically. Prickles can be long as in *C. tenuis* where they are up to 0.6 cm long or very short as in *C. sabatoi* of approximately 0.1 cm. However, the shape of prickles is a constant character within populations. Two forms have been identified: 1) thin and easily detached and 2) robust, wide and hard to separate from the plant.

Leaflet form can be lanceolate, oblong or linear. This character can be polymorphic within and between populations as in *Ceratozamia delucana* (Fig. 3). Leaflet width can

Figure 2. Trichome colour variation. **A** brown, *Ceratozamia tenuis* **B** white, *C. sabatoi*.

vary from narrow, 0.4–0.7 cm in *C. zaragozae* (Fig. 4), to broad, up to 5 cm as in *C. latifolia* and *C. decumbens*. Other characters with taxonomic value are leaflet symmetry and texture. However, these characters can be polymorphic as in *C. delucana*. Leaflet texture is generally papyraceous as in *C. latifolia* or coriaceous as in *C. brevifrons*. In contrast, leaflets in *C. hildae* and *C. zaragozae* are membranaceous. Leaflet symmetry can be curved as in *C. fuscoviridis* or straight from the base to the apex as in *C. latifolia*. In terms of leaflet lamina shape, some species are abaxially curved, while others are planar, as *C. fuscoviridis* and *C. decumbens*, respectively.

Reproductive morphology. All qualitative characters of both the pollen strobili and the ovulate strobili are not very polymorphic within and between populations, with the exception of strobilar apices in ovulate plants for certain species, e.g. *Ceratozamia brevifrons*, which can have acuminate and apiculate apex. Several reproductive characters contribute to diagnosable characters separating closely related taxa.

Ovuliferous strobili provide most of the diagnostic/differential in *Ceratozamia*. The most relevant of these characters are the colour of the strobilus, the shape of the fertile part of the entire strobilus, horn form in the distal end of sporophylls and colour of the sarcotesta (Fig. 5). The colour of ovuliferous strobili at maturity vary from dark green, as in *C. mexicana*, to wine red, as in *C. decumbens*. The shape of the strobilus is

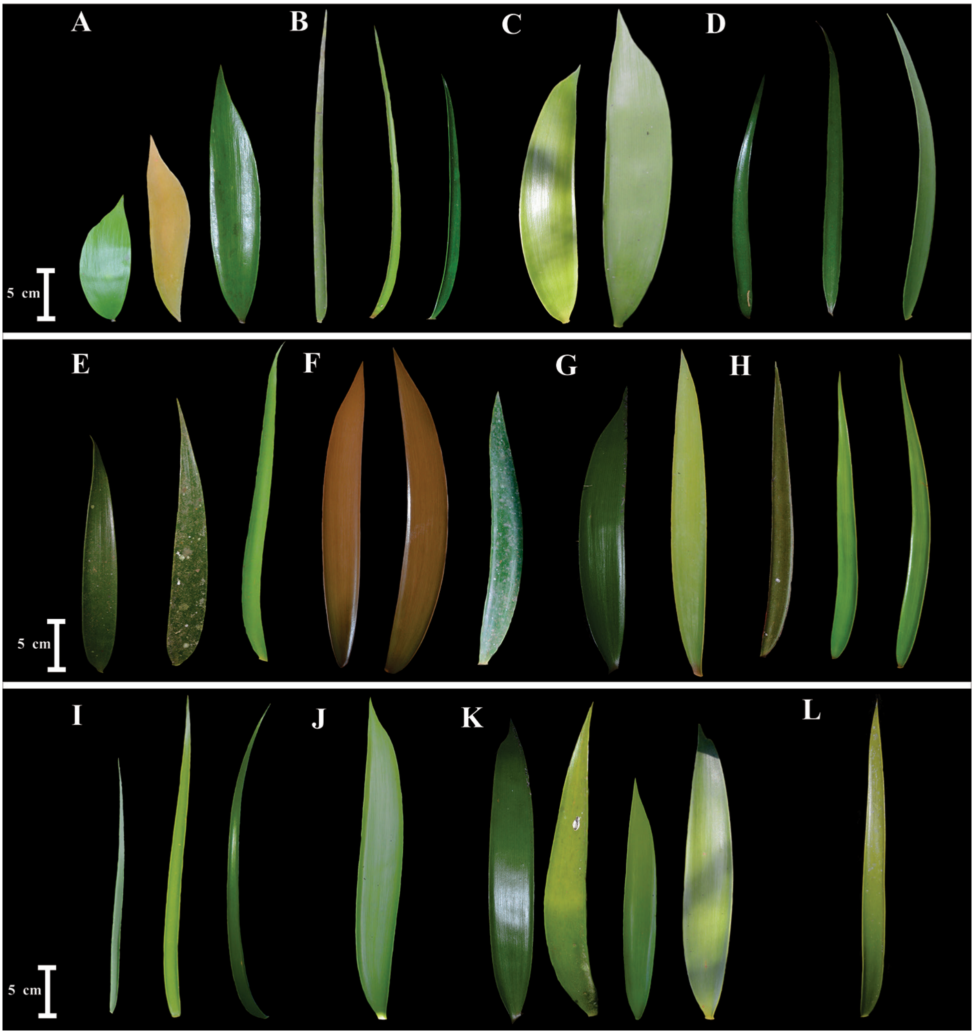

Figure 3. Shapes of leaflets. **A** *C. latifolia* **B** *C. kuesteriana* **C** *C. morettii* **D** *C. sabatoi* **E** *Ceratozamia brevifrons* **F** *C. chamberlainii* **G** *C. decumbens* **H** *C. fuscoviridis* **I** *C. tenuis* **J** *C. totonacorum* **K** *C. delucana* **L** *C. mexicana*.

cylindric in most species, with the exception of *C. morettii* and *C. latifolia* where it is globose. In *C. delucana*, this character is polymorphic as both shapes can occur.

Finally, polliniferous strobili provide two diagnostic characters. First, the distal end of sporophylls can be recurved upon itself or not curved (Fig. 6). Second, the colour may be greenish, yellowish with abundant brown or blackish trichomes or reddish-brown or yellowish-brown (Fig. 7). This character needs to be coded before the shedding of pollen. This is because mature pollen strobili turn yellow or cream-coloured and lose their characteristic colouration upon pollen shedding. The microsporangia cover the whole lower part of the sporophylls in such a crowded manner that they become angular, often irregular in shape and encroached upon one another. Therefore, the arrangements of microsporangia are not informative.

Figure 4. Types of leaves and leaflets. **A** Linear petiole and rachis with clustered leaflets **B** Twisted petioles and rachis, with opposite to subopposite leaflets.

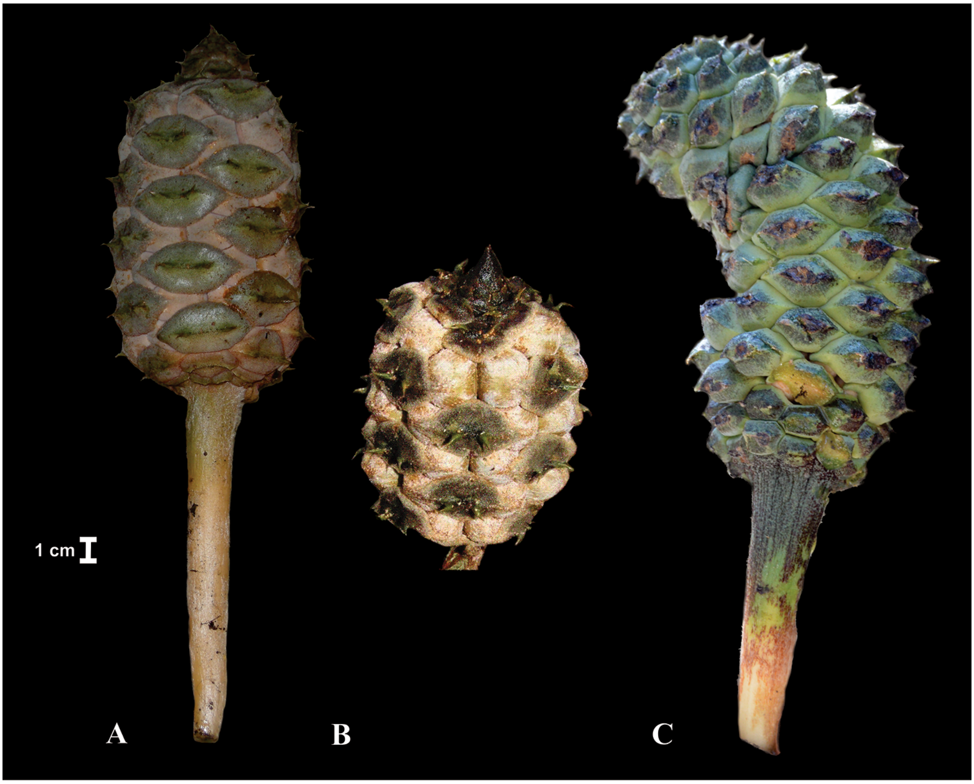

Figure 5. Shapes of ovuliferous strobili. **A** *Ceratozamia latifolia* **B** *C. decumbens* **C** *C. zaragozae*.

Key to the species of *Ceratozamia* for the Sierra Madre Oriental

1 Leaflets clustered ... ***C. hildae***

– Leaflets evenly spaced, opposite to subopposite ... **2**

2 Rachis and petiole twisted ... ***C. zaragozae***

– Rachis and petiole straight ... **3**

3 Leaflets linear to lanceolate, 0.4–2 cm wide ... **4**

– Leaflets lanceolate to oblong, >2 cm wide ... **5**

4 Leaflet lamina caniculate ... **6**

– Leaflet lamina flat ... **7**

5 Petiole with prickles, stem epigeous ... **8**

– Petiole unarmed, stem semi-epigeous ... ***C. latifolia***

6 Stem semi-hypogeous, new leaves reddish-brown, whitish pubescence, ovuliferous strobilus greyish-light green with black trichomes ... ***C. kuesteriana***

– Stem epigeous, new leaves dark-green, brown pubescence, ovuliferous strobilus dark green with blackish trichomes ... ***C. tenuis***

7 Leaves descending, leaflets linear, microsporophyll with distal end recurved, ovuliferous strobilus blue green with blackish trichomes ... ***C. sabatoi***

– Leaves ascending, leaflets lanceolate, microsporophyll with distal end straight, ovuliferous strobilus brown-green with dark brown trichomes at maturity ... ***C. fuscoviridis***

8 Leaves ascending ... ***C. delucana***

– Leaves descending ... **9**

9 Leaflets lanceolate ... **10**

– Leaflets oblong ... **11**

10 Leaflets keeled, petiole with long (0.3–0.6 cm), prickles robust and abundant (>50), ovuliferous strobilus greenish-yellow with brown to blackish trichomes ... ***C. brevifrons***

– Leaflets plane, petiole with short (0.1–0.2 cm), prickles thin and sparse (<40), ovuliferous strobilus dark green with black and grey trichomes ... ***C. mexicana***

11 New leaves light green, ovuliferous strobilus globose and green with blackish trichomes ... ***C. morettii***

– New leaves brown to reddish-brown, ovuliferous strobilus cylindric and brown to wine red ... **12**

12 New leaves light brown, petiole with long prickles ... ***C. totonacorum***

– New leaves dark-brown to reddish brown, petiole with short prickles ... **13**

13 Veins reddish-brown, ovuliferous strobilus light greyish-brown with abundant reddish-brown trichomes and acuminate apex ... ***C. chamberlainii***

– Veins light green, ovuliferous strobili wine with blackish trichomes and acute apex ... ***C. decumbens***

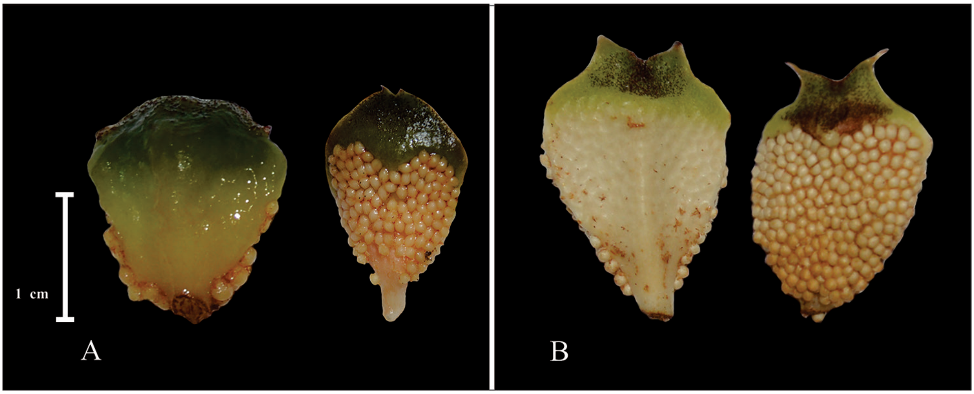

Figure 6. Microsporophylls. **A** *C. sabatoi* **B** *C. brevifrons*.

Figure 7. Shapes of polliniferous strobilus. **A** *Ceratozamia sabatoi* **B** *C. hildae* **C** *C. kuesteriana*.

Taxonomic treatment

1. *Ceratozamia brevifrons* Miq. Tijdschr. wis-en natuurk Wet. 1: 41–42. 1847.

Figures 3E, 6B

Type. MEXICO. Veracruz: Alto Lucero de Gutiérrez Barrios, Apr. 2005, *S. Avendaño R. 5699* (neotype, designated by Vovides et al. 2012, XAL)

Description. *Stem* epigeous, erect, 20–70 cm in length, 15–40 cm in diameter. *Cataphylls* persistent, densely tomentose at emergence, reddish-brown and glabrous at maturity, triangular, apex acuminate, 2–5 × 1.5–4 cm at base. *Leaves* 6–36, descending, 58–173.5 cm, yellowish-green at emergence with a brown pubescence, glabrous at maturity. *Petiole* terete, straight, 20–56 cm, armed with short and robust prickles, green in adult leaves. *Rachis* terete, straight, 35–125.5 cm, armed with prickles, green in adult leaves. *Leaflets* 13–38, lanceolate, abaxially curved and planar, basally falcate, coriaceous, flat, opposite to subopposite, keeled, light green, adaxial and abaxial surfaces glabrous, acuminate apex, symmetric to asymmetric apex, attenuate at base, with conspicuous and light green veins; median leaflets 15.5–41 × 2–4.1 cm, 0.5–3.2 cm between leaflets; articulations yellow, 0.6–1.7 cm wide. *Polliniferous strobilus* solitary, cylindrical, erect, 22–31 cm in length, 5–7 cm in diameter, greenish-yellow at emergence, greenish-yellow with brown to blackish pubescence at maturity; peduncle tomentose, reddish-brown to light-brown, 5.5–9.5 cm in length, 1.8–2.2 cm in diameter; microsporophylls 1.6–2.3 × 1.1–1.5 cm, distal face not recurved. *Ovuliferous strobilus* solitary, cylindrical, erect, 26.5–30 cm in length, 9.8–12 cm in diameter, green with blackish pubescence at emergence, greenish-yellow with brown to blackish trichomes at maturity, acuminate and apiculate apex; peduncle tomentose, brown to reddish-brown, 6–12 cm in length, 2.1–2.4 cm in diameter; megasporophylls 80–154, 1.5–2.5 × 2.3–3.0 cm, prominent distal face, right angle between horns. *Seeds* ovoid, sarcotesta whitish-yellow to yellow when immature, light brown at maturity, 2.5–3 cm in length, 1.7–2 cm in diameter.

Distribution and habitat. Endemic to Mexico and only known from the State of Veracruz, in the vicinity of the Sierra de Chiconquiaco, at the transition zone between cloud forest and oak forest, between 500 and 1,350 m of elevation (Fig. 8).

Etymology. The epithet is derived from referring to its relatively short leaves.

Distinguishing features. This species is easily distinguished from its congeners by having leaflets adaxially keeled, falcate, basally falcate and coriaceous, petioles armed with short, robust prickles, ovulate strobili greenish-yellow with brown to blackish trichomes at maturity and megasporophylls with a prominent distal face and right angle between horns.

Specimens examined. MEXICO. **Veracruz**: Alto Lucero de Gutiérrez Barrios, *A. P. Vovides 119* (XAL), *D. Jimeno-Sevilla 694* (XAL), *F. Nicolalde-Morejón & L. Martínez-Domínguez 2027-2046* (CIB), *G. Castillo-Campos 1297* (XAL), *J. Rees*

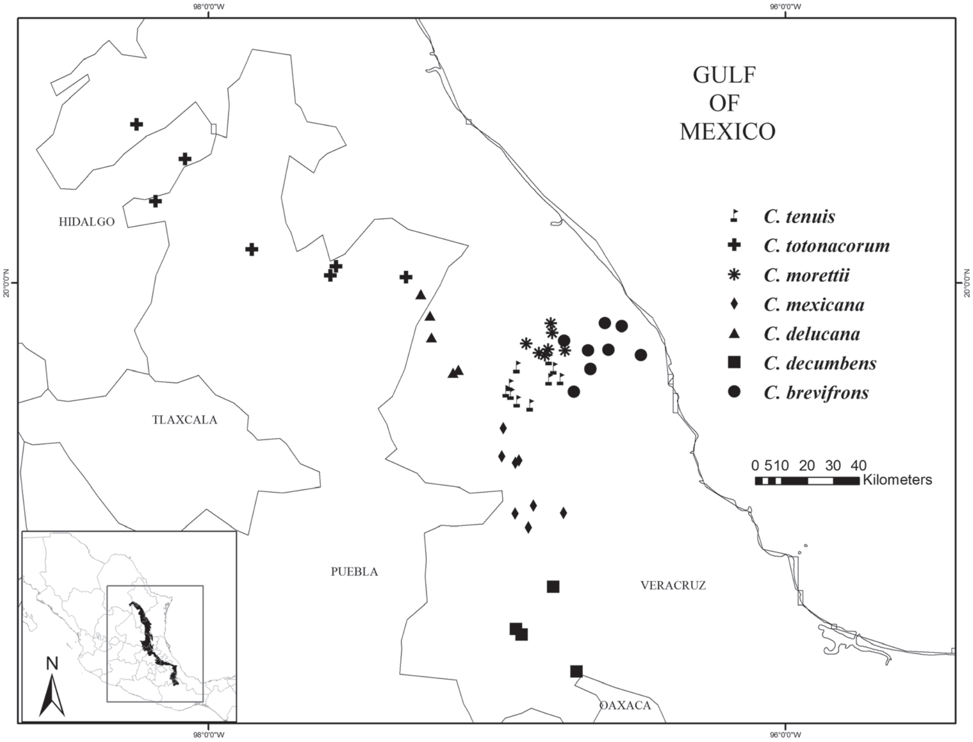

Figure 8. Distribution map of *Ceratozamia tenuis*, *C. totonacorum*, *C. morettii*, *C. mexicana*, *C. delucana*, *C. decumbens* and *C. brevifrons*.

1636 (MO, XAL), *1641, 1642, 1675* (XAL), *6345* (IEB), *L. Martínez-Domíguez & F. Nicolalde-Morejón 130-133, 216, 229-309* (CIB), *M. Vázquez-Torres 4790* (CIB), *T. W. Walters 2001-02-A, B* (XAL); Chiconquiaco, *F. Nicolalde-Morejón & L. Martínez-Domínguez 2237-2241* (CIB), *L. Martínez-Domíguez & F. Nicolalde-Morejón 556-560* (CIB); Juchique de Ferrer, *A. P Vovides 682* (XAL), *G. Castillo-Campos 1710, 1763, 1768, 1815, 1824, 1981* (XAL), *M. Vázquez-Torres 8633* (CIB); Vega de Alatorre, *B. Guerrero & J. I. Calzada 1826* (XAL), *G. Castillo-Campos 2033* (XAL).

Taxonomic comments. This species name implies a long history of synonymy, which describes a series of substantial taxonomic disagreements. In the pioneer taxonomic treatments for the genus, *C. brevifrons* was considered as a synonym to *C. mexicana* (Miquel 1861, 1868-1869; Regel 1876a; Thiselton-Dyer 1884; Schuster 1932), whereas in the most recent treatment it was placed as a synonym of *C. mexicana* var. *mexicana* (Vovides et al. 1983). In 2012, Vovides and collaborators removed the binomial from this synonymy after finding plants in the wild, which morphologically corresponded to its original description.

2. *Ceratozamia chamberlainii* Mart.-Domínguez, Nic-Mor. & D.W. Stev. Phytotaxa 317(1): 17–28. 2017.

Figure 3F

Type. MEXICO. San Luis Potosí: Xilitla, 20 Mar. 2016, *L. Martínez-Domínguez et al. 933* ♀ (holotype: CIB; isotypes: MEXU, NY).

Description. *Stem* epigeous, erect and decumbent, 20–60 cm in length, 15–30 cm in diameter. *Cataphylls* persistent, densely tomentose at emergence, reddish-brown and glabrous at maturity, triangular, apex acuminate, 2.5–5.5 × 1.5–3.5 cm at base. *Leaves* 5–40, descending, 100–207 cm, reddish-brown at emergence with whitish-grey pubescence, glabrous at maturity. *Petiole* terete, straight, 30–69 cm, armed with short and robust prickles, blackish-brown in adult leaves. *Rachis* terete, straight, 65–144 cm, armed with prickles, reddish-brown in mature leaves. *Leaflets* 20–42, oblong, planar and abaxially curved, not basally falcate, coriaceous, flat, opposite to subopposite, plane, dark green, adaxial and abaxial surfaces glabrous, acuminate and asymmetric apex, attenuate at base, with conspicuous and reddish-brown veins; median leaflets 20–37 × 2.3–4 cm, 1.6–3.5 cm between leaflets; articulations generally reddish-brown, 0.5–1.3 cm wide. *Polliniferous strobilus* generally solitary (1–2), cylindrical, erect, 26–31 cm in length, 4.8–6 cm in diameter, greenish-brown at emergence, greenish with reddish-brown pubescence at maturity; peduncle tomentose, reddish-brown, 6–10.3 cm in length, 1.6–2 cm in diameter; microsporophylls 1.6–2.3 × 1.1–1.5 cm, not recurved distal face. *Ovuliferous strobilus* cylindrical, erect, 28–30 cm in length, 9–10.5 cm in diameter, greyish-green with reddish-brown pubescence at emergence, light greyish-brown with reddish-brown trichomes at maturity, acuminate apex; peduncle tomentose, brown to reddish-brown, 4.5–11 cm in length, 1.3–2.5 cm in diameter; megasporophylls 72–190, 1.5–2.5 × 2.3–3.0 cm, prominent distal face, acute angle between horns. *Seeds* ovoid, sarcotesta whitish-red to pink when immature, light brown at maturity, 3.0–4.0 cm in length, 0.6–1.2 cm in diameter.

Distribution and habitat. Its range includes the states of San Luis Potosí, Querétaro and Hidalgo (Fig. 9). *Ceratozamia chamberlainii* occurs in the cloud forest on rocky outcrops at 900–1,200 m.

Etymology. The specific epithet honours Charles Joseph Chamberlain in recognition of his outstanding contributions to knowledge of the biology of the cycads and his fieldwork on Mexican cycads.

Distinguishing features. This species is distinguished by its petioles and rachis with abundant, short prickles; reddish-brown leaves at emergence with coloured articulations at the leaflet attachment to the rachis in adult leaves. Leaflets are oblong and coriaceous with conspicuous, reddish-brown veins.

Specimens examined. MEXICO. **Hidalgo**: Chapulhuacán, *Alcántara-Ayala 3650* (FCME), *F. Nicolalde-Morejón et al. 2200-2203* (CIB), *L. Martínez-Domínguez et al. 429–430* (CIB), *441–443* ♀ (CIB), *447* ♂ (CIB), *Vite-Reyes et al. 23* (XAL); La Misión, *Castro-Castro et al. 1017* (XAL), *Vite-Reyes et al. 20* (XAL). **Querétaro**: Landa de Matamoros, *A. P. Vovides 1291* (XAL, MEXU), *1288, 1290*, 2000 (XAL), *E. Carranza 633* (IEB),

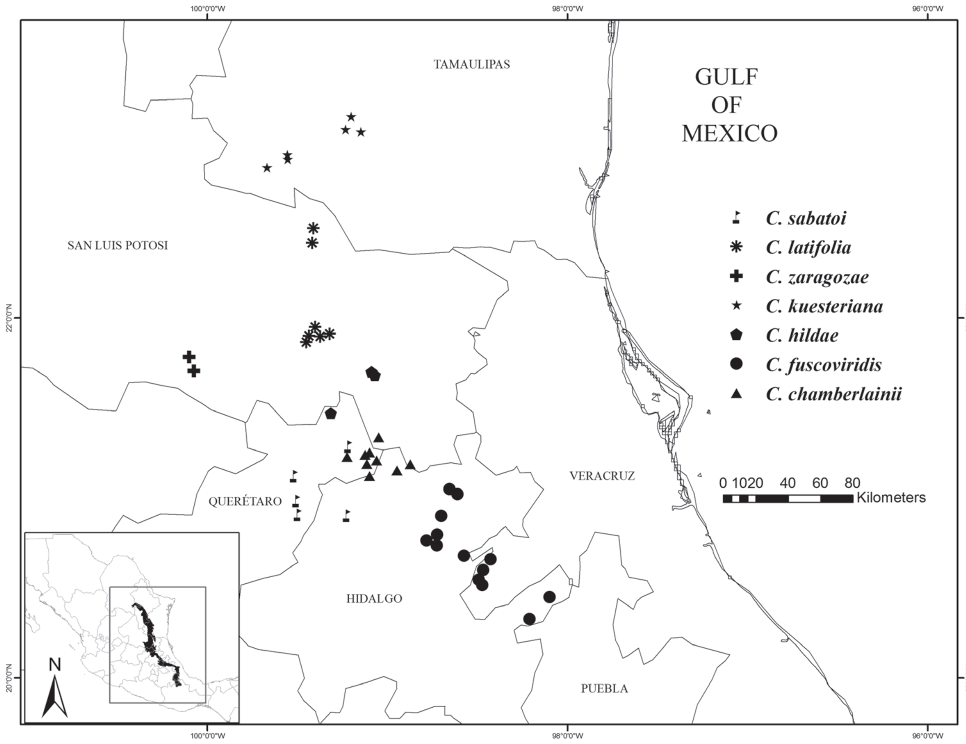

Figure 9. Distribution map of *Ceratozamia sabatoi*, *C. latifolia*, *C. zaragozae*, *C. kuesteriana*, *C. hildae*, *C. fuscoviridis* and *C. chamberlainii*.

3119 (MEXU), *F. Nicolalde-Morejón et al. 2192-2199* (CIB); *L. Martínez-Domínguez et al. 379, 405* ♂ (CIB), *380–404* (CIB); *L. Martínez-Domínguez et al. 408–426* (CIB), *427, 428* ♂ (CIB), *Rubio Hiram 6332*, *6334* (IEB), *647* (XAL). **San Luis Potosí**: Tamazunchale, *C. L. Lundell 7235* (IEB); Xilitla, *F. Nicolalde-Morejón et al. 2407-2420* (CIB), *L. Martínez-Domínguez et al. 924–932* (CIB); *T. W. Walters, TW-2001-04-A* (XAL).

3. *Ceratozamia decumbens* Vovides, Avendaño, Pérez-Farr. & Gonz.-Astorga. Novon 18 (1): 109–114. 2008.

Figure 3G

Type. MEXICO. Veracruz: Naranjal, 8 Apr. 2005, *S. Avendaño & G. Alducin 5706* (holotype: XAL; isotypes: HEM, MO).

Description. *Stem* epigeous, erect and decumbent, 10–40 cm in length, 10–25 cm in diameter. *Cataphylls* persistent, densely tomentose at emergence, reddish-brown and partially tomentose at maturity, triangular, apex acuminate, 1.5–3 × 2–4.2 cm at base. *Leaves* 2–7, descending, 80–190 cm, reddish-brown at emergence, whitish-grey pubescence, glabrous at maturity. *Petiole* terete, straight, 40–100 cm, armed with short and thin prickles, greenish-brown in adult leaves. *Rachis* terete, straight, 40–123 cm, armed with prickles and occasionally unarmed, brown and green in adult leaves. *Leaflets* 8–24, oblong, mostly planar, not basally falcate, coriaceous, flat, opposite to subopposite, plane, green, adaxial and abaxial side glabrous, acuminate apex, symmetric and asymmetric apex, attenuate at base, with conspicuous and light green veins; median leaflets 23–47.5 × 2.8–5 cm, 2.6–6.5 cm between leaflets; articulations brown, 0.7–1.2 cm wide. *Polliniferous strobilus* solitary, cylindrical, erect, 20–23 cm in length, 4–4.5 cm in diameter, greenish-yellow at emergence, greenish with reddish-brown pubescence at maturity; peduncle tomentose, reddish-brown to brown, 8–8.5 cm in length, 1.2–1.5 cm in diameter; microsporophylls 1–1.9 × 1–1.4 cm wide, non-recurved distal face. *Ovuliferous strobilus* solitary, cylindrical, erect, 9–11 cm in length, 7–8 cm in diameter, wine at emergence, wine with blackish trichomes at maturity, acute apex; peduncle tomentose, brown, 3–4 cm in length, 1–1.2 cm in diameter; megasporophylls 24–49, 2.3–2.5× 2–3 cm, truncate distal face, right angle between horns. *Seeds* ovoid, sarcotesta whitish-red when immature, light brown at maturity, 1.2–2 cm, 1.2–1.5 cm in diameter.

Distribution and habitat. Endemic to a small mountain range in central Veracruz, 450–1,000 m elevation (Fig. 8). The vegetation type of the habitat is mountain tropical forest and cloud forest on karstic rocks.

Etymology. The epithet alludes to the decumbent nature of trunks in older mature plants.

Distinguishing features. *Ceratozamia decumbens* is distinguished by its oblong coriaceous, mostly planar and basally falcate leaflets; ovulate strobilus wine red with blackish trichomes at maturity and acute apex.

Specimens examined. MEXICO. **Veracruz**: Atoyac, *R. Acevedo R. 728* (XAL); Coetzala, *A. Rincón G. 2798* (MEXU, XAL), *L. Martínez-Domínguez et al. 655-683* (CIB); Ixtaczoquitlán, *A. Pérez P. 282* (XAL); Naranjal, *A. P. Vovides 751* (XAL), *Brigada T. Walters s/n* (XAL), *J. Rees 1690* (XAL), *S. Avendaño R. & G. Alducin 5706* (XAL), *T. W. Walters 41277, 41308, 41397* (XAL); Tequila, *Jaime E. Rivera Hdez. & Antoevàn Vergara V. 4195* (MEXU, XAL), *F. Nicolalde-Morejón et al. 2259, 2260* (CIB), *L. Martínez-Domínguez et al. 684-703*; Tezonapa, *M. A. García B. 980* (XAL), *R. Robles G. 882* (XAL).

4. *Ceratozamia delucana* Vázq.-Torres, Moretti & Carvajal-Hernández. Delpinoa, 50–51, 129–133. 2013.

Figure 3K

Type. MEXICO. Veracruz: Atzalan, 20 Jan. 2012, *M. Vázquez-Torres & C. Carvajal-Hernández 10200* (holotype: CIB; isotypes: XAL, XALU).

Description. *Stem* epigeous, erect and decumbent, 20–90 cm in length, 25–40 cm in diameter. *Cataphylls* persistent, densely tomentose at emergence, reddish-brown and partially tomentose at maturity, triangular, apex acuminate, 2–5.5 × 2.5–4.5 cm at base. *Leaves* 10–100, ascending, 106–223 cm, yellowish-green at emergence, brown pubescence, glabrous at maturity. *Petiole* terete, straight, 30–87 cm, armed with short and thin prickles, green in adult leaves. *Rachis* terete, straight, 60–150 cm, armed with prickles, green in adult leaves. *Leaflets* 20–43, lanceolate and oblong, planar and abaxially curved, basally falcate to non-basally falcate, papyraceous to coriaceous, flat, opposite to subopposite, plane, green, adaxial side glaucous and glabrous and abaxial side glaucous, acuminate apex, symmetric to asymmetric apex, attenuate at base, with conspicuous and light green veins; median leaflets 22–45 × 2.3–4.6 cm, 1.5–5 cm between leaflets; articulations green, 0.6–1.6 cm wide. *Polliniferous strobilus* solitary, cylindrical, erect, 24–31 cm in length, 5.5–7.6 cm in diameter, greenish-yellow at emergence, greenish-yellow with blackish pubescence at maturity; peduncle tomentose, reddish-brown to light-brown, 3.5–12.5 cm in length, 1.3–2 cm in diameter; microsporophylls 1.5–2.5 × 1.3–2 cm, non-recurved distal face. *Ovuliferous strobilus* solitary, cylindrical and globose, erect, 18–40 cm in length, 10–12.5 cm in diameter, dark green with blackish pubescence at emergence, green generally glabrous at maturity, acute apex; peduncle tomentose, brown to reddish-brown, 5.2–15 cm in length, 1.8–2.2 cm in diameter; megasporophylls 72–182, 2.5–4.2 × 2.3–3.5 cm, truncate distal face, right angle between horns. *Seeds* ovoid, sarcotesta whitish-yellow to yellow when immature, light brown at maturity, 2.1–3 cm in length, 1.6–2.1 cm in diameter.

Distribution and habitat. This species is known from the states of Veracruz and Puebla at 200–700 m in evergreen tropical forest (Fig. 8).

Etymology. The epithet is in honour of Dr. Paolo De Luca, Professor at University of Naples Federico II and researcher in the biology of Mexican cycads.

Distinguishing features. *Ceratozamia delucana* is highly variable and shares a number of characteristics with *C. morettii*. However, there are clear differences in their ovulate strobili. In *C. delucana*, ovulate strobili are green and generally without trichomes at maturity and have an acute apex, whereas in *C. morettii* they are green with blackish trichomes at maturity and have an apiculate apex. Additionally, *C. delucana* is larger than *C. morettii*, with *C. delucana* having leaves up to 223 cm with up to 43 pairs of leaflets and ovulate strobili 18–40 cm long.

Specimens examined. MEXICO. **Puebla**: Xochitlán de Vicente Suárez, *G. Villalobos & E. Guerrero C. 325* (MEXU), *L. Martínez-Domínguez & F. Nicolalde-Morejón 587-616* (CIB). **Veracruz**: Atzalan, *F. Nicolalde-Morejón & L. Martínez-Domínguez 2125-2144* (CIB), *L. Martínez-Domínguez et al. 228-248* (CIB); Las Minas, *A. P. Vovides 427* (XAL), *C. Durán E. 6343* (IEB), *659* (MEXU, XAL), *C. Durán, P. Burgos, A. P. Vovides 658* (XAL), *660* (MEXU, XAL), *F. Nicolalde-Morejón & L. Martínez-Domínguez 2107-2124* (CIB), *L. Martínez-Domínguez et al. 168* (CIB), 249-260; Tlapacoyan, *Nevling & A. Gómez-Pompa 1083* (MEXU).

5. ***Ceratozamia fuscoviridis* W. Bull. Retail List 154: 4. 1879.**

Figure 3H

Type. Hort. Bot. Glasnevin, 21 Mar. 1878 (accessioned 1881), *D. Moore s.n.* (neotype, designated by Calonje and Sennikov 2017, K). **Epitype** (designated here). MEXICO.

Hidalgo: Molango, 31 Mar. 2015, *L. Martínez-Domínguez et al. 493* [♀strob.] (CIB). **Isoepitype** (designated here). *L. Martínez-Domínguez et al. 493* (MEXU).

Ceratozamia mexicana var. *longifolia* f. *fuscoviridis* (W. Bull) Schuster. Pflanzenr 99:132. 1932. Type: Based on *Ceratozamia fuscoviridis* W. Bull.

Description. *Stem* epigeous, erect and decumbent, 20–90 cm in length, 25–40 cm in diameter. *Cataphylls* persistent, densely tomentose at emergence, reddish-brown and partially tomentose at maturity, triangular, apex acuminate, 2–4.5 × 2–3.5 cm at base. *Leaves* 10–70, ascending, 92–215 cm, light green and dark brown at emergence, whitish- grey pubescence, glabrous at maturity. *Petiole* terete, straight, 40–95 cm, armed with long and thin prickles, dark green in adult leaves. *Rachis* terete, straight, 65–150 cm, armed with prickles, green in adult leaves. *Leaflets* 28–67, lanceolate, abaxially curved, basally falcate, papyraceous, flat, opposite to subopposite, plane, green, adaxial and abaxial side glabrous, acuminate and symmetric apex, attenuate at base, with conspicuous, and light green and brown veins; median leaflets 16.6–42 × 1.3–2.1 cm, 0.6–2 cm between leaflets; articulations green and brown, 0.6–1.3 cm wide. *Polliniferous strobilus* solitary, cylindrical, erect, 26.5–28 cm in length, 5–8 cm in diameter, brownish-yellow at emergence, greenish-brown with reddish-brown pubescence at maturity; peduncle tomentose, reddish-brown to brown, 5–14.5 cm in length, 1.6–2.3 cm in diameter; microsporophylls 1.9–2.3 × 1.3–1.5 cm, non-recurved distal face. *Ovuliferous strobilus* solitary, cylindrical, erect or pendulous, 24–35 cm in length, 8.5–10.5 cm in diameter, green with brown pubescence at emergence, brown-green with dark brown trichomes at maturity, acuminate apex; peduncle tomentose, brown to reddish-brown, 4–10 cm in length, 1.8–2.2 cm in diameter; megasporophylls 99–143, 2.5–3.8× 2.3–3.3 cm, truncate distal face, obtuse angle between horns. *Seeds* ovoid, sarcotesta whitish-yellow to yellow when immature, light brown at maturity, 2–2.6 cm in length, 1.5–2 cm in diameter.

Distribution and habitat. Endemic of south-central Carso Huasteco, from central Hidalgo mountain range, to southeast of Hidalgo, including the western portion of Veracruz at an elevation ranging between 1,800–1,900 m in cloud forest (Fig. 9).

Etymology. The epithet alludes to the dark-brown colour of the leaf at emergence.

Distinguishing features. This species is distinguished by lanceolate and papyraceous leaflets; petiole armed with long, thin prickles; ovulate strobilus brown-green with dark trichomes at maturity. This species is polymorphic within populations as it has light green or dark-brown leaf colour at emergence in all populations.

Specimens examined. MEXICO. **Hidalgo**: Eloxochitlán, *I. Luna Vega 54716* (FCME), *O. Alcántara Ayala 54805* (FCME); Metztitlán, *J. L. López-García 449* (MEXU); Molango de Escamilla, *A. Vite-Reyes et al. 6* (XAL), *A. P. Vovides 1298, 1301* (XAL), *F. Nicolalde-Morejón et al. 2209-2211* (CIB), *L. Martínez-Domínguez et al. 485-514* (CIB), *R. Mayorga-Saucedo & O. Alcántara-Ayala s/n* (FCME), *T. W. Walters 2001-03-A* (XAL); Tenango de Doria, *I. Luna Vega 794* (FCME); Tlanchinol, *I. Luna Vega s/n* (FCME), *625, 789* (XAL), *F. Nicolalde-Morejón et al. 2204-2208* (CIB), *L. Martínez-Domínguez et al. 455-484* (CIB); Zacualtipán de Ángeles, *J. Rees 389* (FCME, MEXU), *1611* (XAL), *6339* (IEB). **Veracruz**: Huayacocotla, *D. Saavedra Millán 64* (FCME), *J. Palma G. 63* (XAL), *F. Nicolalde-Morejón et al. 2212-2214* (CIB), *L. Ballesteros & F. Ballesteros 460* (XAL), *L. G. Juárez G. 47* (XAL), *L. Martínez-Domínguez et al. 515-544* (CIB), *R. Hernández M. 1507* (MEXU, XAL), *V. Sosa 59* (XAL).

Taxonomic comments. This binomial has experienced different reassignments and transferences since its informal publication as "*Ceratozamia fusca-viridis*" by Moore in 1878. This author considered it as a provisional name ("proviso nomen") and thus was not validly published. The changes that this name has undergone are the following: synonymy under *Ceratozamia mexicana* var. *longifolia* (Thiselton-Dyer 1884); transference from variety to form (Schuster 1932); and attempted validation of the name in accordance with current nomenclatural rules (Osborne et al. 2006). Recently, though, Calonje and Sennikov (2017) have attributed authorship of the binomial to Bull (1879) who presented a brief description of the taxon in a commercial catalogue of plants.

6. *Ceratozamia hildae* G. P. Landry & M. C. Wilson. Brittonia 31(3): 422–424. 1979.

Figures 4A, 7B

Type. Louisiana, Baton Rouge, cultivated at 5988 South Pollard Parkway (originally from several km N of Xilitla, San Luis Potosí, Mexico), *Landry G 76521* (holotype: GH; isotypes: FTG, LSU, MEXU, MICH, NY, US).

Description. *Stem* semi-epigeous, erect, 10–20 cm in length, 10–15 cm in diameter. *Cataphylls* persistent, densely tomentose at emergence, reddish-brown and partially tomentose at maturity, triangular, apex acuminate, 2.1–3 × 0.8–1.5 cm at base. *Leaves* 2–7, ascending, 95–202 cm, reddish-brown at emergence with whitish-grey pubescence, glabrous at maturity. *Petiole* terete, straight, 43–89 cm, armed with thin and short prickles, greenish-brown and green in adult leaves. *Rachis* terete, straight, 60–130 cm, armed with prickles and occasionally unarmed, greenish-brown in adult leaves. *Leaflets* with 5–11 fascicles, 16–56 leaflets in total, oblong, mostly planar, basally falcate to non-basally falcate, membranaceous, flat, clustered, plane, green, adaxial and abaxial side glaucous, acuminate apex, symmetric and asymmetric apex, attenuate at base, with conspicuous and light green veins; median leaflets 14.5–24 × 2.4–5 cm, 6–15 cm between leaflets; articulations brown and green, 0.2–0.5 cm wide. *Polliniferous strobilus* solitary, cylindrical, erect, 8–10 cm in length, 2–2.5 cm in diameter, brown with reddish-brown pubescence at emergence, reddish-brown at maturity; peduncle tomentose, reddish-brown to brown, 6–7.5 cm in length, 0.9–1 cm in diameter; microsporophylls 0.8–1.2 × 0.6–0.9 cm, non-recurved distal face. *Ovuliferous strobilus* solitary, cylindrical, erect, 10–14 cm in length, 6–9 cm in diameter, green at emergence with brown trichomes, green with brown to blackish trichomes at maturity, acuminate apex; peduncle tomentose, brown, 5–6 cm in length, 1.2–1.5 cm in diameter; megasporophylls 36–77, 2–3.7 × 2–4 cm, prominent distal face, right angle between horns. *Seeds* ovoid, sarcotesta whitish-red when immature, light brown at maturity, 1.3–2.3 cm in length, 1.2–1.5 cm in diameter.

Distribution and habitat. Endemic to Mexico in San Luis Potosí (Fig. 9), in the evergreen tropical forests.

Etymology. The epithet is in honour of Hilda Guerra Walker, daughter of the original collector.

Distinguishing features. *Ceratozamia hildae* differs from its congeners by its clustered leaflets. Besides, leaflets are membranaceous and oblong.

Specimens examined. MEXICO. **Querétaro**: Jalpan de Serra, *A. P. Vovides 337* (XAL), *A. P. Vovides s/n* (IEB), *B. Servin 870*, *986* (MEXU), *6328, 6330* (IEB), *J. Rees s/n* (IEB), *312* (XAL). **San Luis Potosí**: Aquismón, *A. P. Vovides & J. Rees 312* (MEXU, XAL), *F. Nicolalde-Morejón et al. 2391-2406* (CIB), *L. Martínez-Domínguez et al. 910-923* (CIB), *S. Longoria s/n* (XAL), *T. W. Walters TW-2001-14-A* (MEXU, XAL), *TW-2001-14-B* (XAL), *TW-2001-14-C* (MEXU).

7. *Ceratozamia kuesteriana* Regel. Bull. Soc. Imp. Naturalistes Moscou 30: 187–188, t. 3. 1857.

Figures 3B, 7C

Type. ex Horto Petropolitano, 1856, *Regel s.n.* (holotype, LE; isotypes: U).

Description. *Stem* semihypogeous, erect, 10–30 cm in length, 10–25 cm in diameter. *Cataphylls* persistent, densely tomentose at emergence, reddish-brown and partially tomentose at maturity, triangular, apex acuminate, 1.5–4 × 2–3.5 cm at base. *Leaves* 1–11, ascending, 80–133 cm, reddish-brown at emergence, whitish-grey pubescence, glabrous at maturity. *Petiole* terete, straight, 30–72 cm, armed with thin and short prickles, greenish-brown in adult leaves. *Rachis* terete, straight, 40–72 cm, armed with prickles and rarely unarmed, greenish-brown in adult leaves. *Leaflets* 22–50, linear, adaxially curved, basally falcate, papyraceous, caniculate, opposite to subopposite, plane, green, adaxial and abaxial side glabrous, acuminate apex, symmetric apex, attenuate at base, with conspicuous and light green veins; median leaflets 17–32 × 0.6–1 cm 0.3–2.5 cm between leaflets; articulations brown, 0.2–0.8 cm wide. *Polliniferous strobilus* solitary, cylindrical, erect, 11–15 cm in length, 2.2–3 cm in diameter, greenish-yellow with brown pubescence at emergence, yellowish-brown with reddish-brown pubescence at maturity; peduncle tomentose, reddish-brown to brown, 9–14 cm in length, 0.9–1 cm in diameter; microsporophylls 0.6–1.1 × 0.6–1 cm, not recurved distal face. *Ovuliferous strobilus* solitary, cylindrical, erect, 13–21 cm in length, 7–9 cm in diameter, green at emergence with brown trichomes, greyish-light green with black trichomes at maturity, acuminate apex; peduncle tomentose, brown, 11–15 cm in length, 1–2 cm in diameter; megasporophylls 52–90, 2.5–4 × 2.3–3.5 cm, truncate distal face, obtuse angle between horns. *Seeds* ovoid, sarcotesta whitish-red when immature, light brown at maturity, 1.5–2.2 cm in length, 1.2–1.8 cm in diameter.

Distribution and habitat. Endemic to Mexico in Tamaulipas at 1,100–1,500 m (Fig. 9), in pine-oak and cloud forests.

Etymology. The specific epithet is in honour of Baron K. von Kuester, 19th century plant collector.

Distinguishing features. This species is distinguished by leaflets linear, planar and abaxially curved, not basally falcate, papyraceous, flat and symmetric apex.

Specimens examined. MEXICO. **Tamaulipas**: Gómez Farías, *A. Gómez-Pompa 2029* (MEXU), *A. P. Vovides 771, 772, 791, 800, 801* (XAL), *F. González-Medrano et al. 3362* (MEXU, MO), *F. González-Medrano & E. Martínez 3288* (MEXU), *L. Trejo s/n* (UAT); Ocampo, *T. W. Walters TW-201-11-A* (XAL), *TW-201-11-B* (MEXU); Tula, *D. W. Stevenson 569H, 569G, 569K* (MEXU), *F. Nicolalde-Morejón et al. 2357-2365* (CIB), *L. Martínez-Domínguez et al. 854-881* (CIB), *S. Avendaño 5328* (MEXU).

8. *Ceratozamia latifolia* Hort. Belg. ex Miq. Tijdschr. Wis-Natuurk. Wetensch. Eerste Kl. Kon. Ned. Inst. Wetensch. 1 (4): 206. 1848.

Figures 3A, 5A, 10

Type. MEXICO. San Luis Potosí: 20 Jul. 1983, (neotype, designated by Stevenson and Sabato 1986, *Stevenson 565 E* (NY); isoneotypes: MEXU).

Ceratozamia mexicana var. *latifolia* (Miquel) Schuster. Pflanzenr. 99:131. 1932. Type: Based on *Ceratozamia latifolia* Miq.

Ceratozamia microstrobila Vovides & Rees. Madroño, 30: 9–42. 1983. Type: MEXICO. San Luis Potosí, Ciudad del Maíz, 7 Nov. 1974, *J. Rees 1613* (holotype: XAL).

Description. *Stem* semihypogeous, erect, 5–15 cm in length, 10–25 cm in diameter. *Cataphylls* persistent, densely tomentose at emergence, reddish-brown and partially tomentose at maturity, triangular, apex acuminate, 1.5–3 × 2–4 cm at base. *Leaves* 1–8, descending, 53–163.5 cm, reddish-brown at emergence, whitish-grey pubescence, glabrous at maturity. *Petiole* terete, straight, 25–80 cm, generally unarmed, greenish-brown in adult leaves. *Rachis* terete, straight, 25–110 cm, unarmed, greenish-brown in adult leaves. *Leaflets* 7–22, oblong, mostly planar, basally falcate, papyraceous, flat, opposite to subopposite, plane, green, adaxial and abaxial side glabrous, acuminate apex, asymmetric apex, attenuate at base, with conspicuous and indistinct veins; median leaflets 12–28 × 2.3–5.1 cm, 1.7–12.5 cm between leaflets; articulations brown, 0.4–1.1 cm wide. *Polliniferous strobilus* solitary, cylindrical, erect, 10.5–20 cm in length, 2.1–2.5 cm in diameter, greenish-yellow with reddish-brown pubescence at emergence, reddish-brown at maturity; peduncle tomentose, reddish-brown to brown, 5–11 cm in length, 0.9–1.2 cm in diameter; microsporophylls 0.5–1 × 0.6–1.1 cm, non-recurved distal face. *Ovuliferous strobilus* solitary, globose, erect, 7.5–16 cm in length, 5.5–7 cm in diameter, light green at emergence with brown trichomes, greyish-light brown with brown trichomes at maturity, apiculate apex; peduncle tomentose, brown, 4–13.5 cm in length, 1.5–1.8 cm in diameter; megasporophylls 24–56, 1.2–2 × 1.7–2.5 cm, prominent distal face, obtuse angle between horns. *Seeds* ovoid, sarcotesta whitish-red when immature, light brown at maturity, 1.5–2 cm in length, 1.2–1.5 cm in diameter.

Distribution and habitat. This species is distributed widely in San Luis Potosí and southeast of Querétaro mountain region, between 600–1,100 m elevation (Fig. 9). The vegetation type of its habitat is pine-oak forest and cloud forest.

Etymology. The specific epithet is derived from the Latin word for wide leaf (latus=wide and folium=leaf).

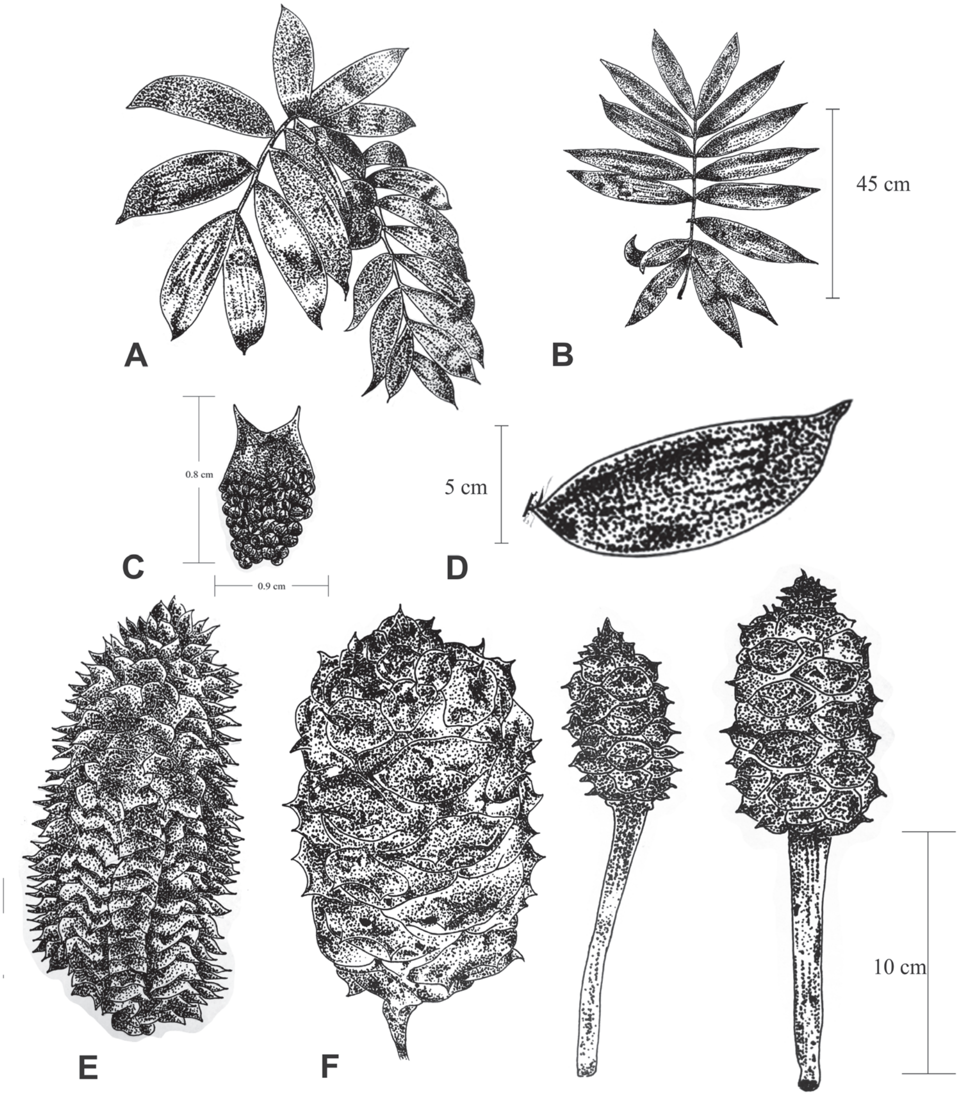

Figure 10. *Ceratozamia latifolia*.

Distinguishing features. Leaves reddish-brown at emergence, petiole generally unarmed, leaflets oblong, mostly planar, not basally falcate and papyraceous with asymmetric apex; ovulate strobilus greyish-light brown with brown trichomes at maturity, apiculate apex, prominent distal face and obtuse angle between horns (Fig. 5A).

Specimens examined. MEXICO. **San Luis Potosí**: Ciudad del Maíz, *H. Puig 3420* (P), *J. Rees 1613* (MO, XAL), *S. Avendaño 5320* (MEXU), *S. Sabato et al. 2340* (MEXU, MO); El Naranjo, *D. W. Stevenson 567* (XAL), *F. Nicolalde-Morejón et al. 2375-2389* (CIB), *L. Martínez-Domínguez et al. 894-909* (CIB), *T. W. Walters TW-2001-08*, *TW-2001-10* (MEXU, XAL); Rayón, *A. P. Vovides et al. 1466* (XAL), *D. W. Stevenson 1117* (NY), *565 A* (MEXU), *565 B,C,E* (MEXU, XAL), F. *Medellin L. 1330* (MEXU), *27252* (ENCB), *S. Avendaño 5282* (MEXU); Tamasopo, A. *P. Vovides et al. 1465* (MEXU, XAL), *F. Medellin L. 27241* (ENCB), *F. Medellin L. s/n* (MEXU), *F. Nicolalde-Morejón et al. 2320-2348* (CIB), *L. Martínez-Domínguez et al. 811-844* (CIB).

Taxonomic comments. As circumscribed here, *Ceratozamia latifolia* has been addressed in different ways, implying disagreements with the original Miquel (1848) description and, at the same time, bearing a relationship to the limits of *C. mexicana*. Several years after its original description, *C. latifolia* was considered doubtful (De Candolle 1864-1868); Miquel (1868-1869a, b) placed it in synonymy and as part of *C. mexicana*. On the other hand, Regel (1876a) considered it as a synonym of *C. miqueliana*, although ten years later Thiselton-Dyer (1884) recognised it as a species. However, Schuster (1983) transferred this binomial to the category of variety under the epithet *C. mexicana* var. *latifolia*, a status maintained until the work of Vovides et al. (1983). In our treatment, this binomial is recognised as a species, rendering it incongruent with *C. mexicana* var. *latifolia sensu* Vovides et al. (1983). This decision stems from the typification by Stevenson and Sabato (1986), where a neotype specimen geographically located in San Luis Potosí was designated to validate the binomial. In addition, we consider that *C. microstrobila* is part of *C. latifolia*, due to the absence of morphological and molecular evidence to recognise the former as a distinct species.

9. ***Ceratozamia mexicana* Brongn. Ann. Sci. Nat., Bot. ser. 3, 5: 7–8, t. 1. 1846.**

Figures 3L, 11

Type. MEXICO, from Ghiesbrecht, cult. in Hort. Bot. Parisiensis, 1845, *Brongniart s.n.* (holotype: P). Epitype (designated by Vovides et al. 2016). MEXICO. Veracruz: Totutla, 08 Sep. 1982, *J. Rees & A. P. Vovides 1688* (XAL).

Ceratozamia intermedia Miq. Tijdschr. Wis-Natuurk. Wetensch. Eerste Kl. Kon. Ned. Inst. Wetensch. 1 (4): 40–41. 1848. Neotype (designated here). MEXICO. Veracruz: Puente Nacional, 13 Mar. 1985, *G. Castillo-Campo & Medina 4275* (XAL).

This specimen represents part of the variation found in *Ceratozamia mexicana* and the locality is on the collection route that was followed by 19th century collectors to the centre of Veracruz.

Ceratozamia longifolia. Miq. Tijdschr. Wis-Natuurk. Wetensch. Eerste Kl. Kon. Ned. Inst. Wetensch. 1 (4): 40. 1848. Neotype (designated here). MEXICO. Veracruz: Zacuapam, Apr. 1913, *Purpus s/n* (MO [6362]).

This locality is a historic collection from the central region of Veracruz for *Ceratozamia mexicana*, which was one of the most collected cycads during the 19th century.

Ceratozamia mexicana Brongn. var. *mexicana*.

Ceratozamia longifolia var. *minor.* Miq. Tijdschr. Wis-Natuurk. Wetensch. Eerste Kl. Kon. Ned. Inst. Wetensch. 2 (4): 290. 1849. Neotype (designated here). MEXICO. Veracruz: Teocelo, 23 Dic. 1975, *M. G. Zola 146* (XAL).

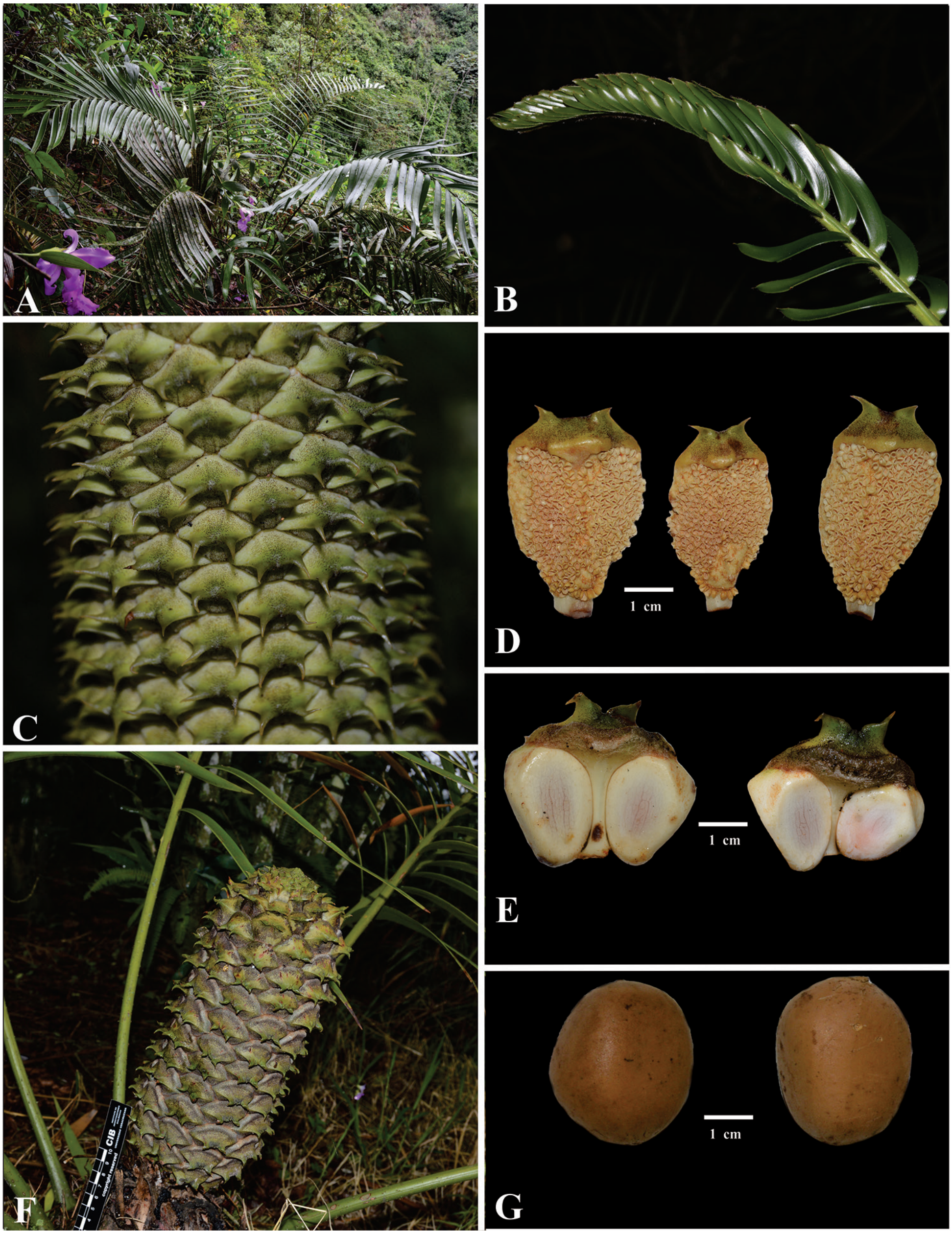

Figure 11. *Ceratozamia mexicana*. **A** Adult plant in habit **B** Leaf at emergence **C** Detail of pollen strobili **D** Microsporophyll **E** Megasporophyll **F** Detail of ovulate strobili **G** Seeds.

This locality is on the historic collection route for *Ceratozamia* and represents the northern end of the distribution for *Ceratozamia mexicana* where plants with lower leaflet widths have been recorded.

Ceratozamia mexicana var. *longifolia*. (Miquel) Dyer. Biol. cent.- amer., Bot. 3 (16): 193. 1884. Type: Based on *Ceratozamia longifolia*.

Description. *Stem* epigeous, erect and decumbent, 20–80 cm in length, 20–45 cm in diameter. *Cataphylls* persistent, densely tomentose at emergence, reddish-brown and partially tomentose at maturity, triangular, apex acuminate, 2–6 × 2.5–6 cm at base. *Leaves* 5–55, descending, 100–270 cm, light green at emergence, brown pubescence, glabrous at maturity. *Petiole* terete, straight, 30–93 cm, armed with short and thin prickles, dark green in adult leaves. *Rachis* terete, straight, 56–154 cm, armed with prickles and unarmed, green in adult leaves. *Leaflets* 25–42, lanceolate, mostly planar, basally falcate, coriaceous, flat, opposite to subopposite, plane, green, adaxial and abaxial side glabrous, acuminate and symmetric apex, attenuate at base, with conspicuous and light green veins; median leaflets 29–51 × 2.3–3.7 cm, 1.8–4 cm between leaflets; articulations green, 0.6–1.5 cm wide. *Polliniferous strobilus* generally solitary (1–2), cylindrical, erect, 24–40 cm in length, 5.5–7.6 cm in diameter, greenish-yellow at emergence, greenish-yellow with blackish pubescence at maturity; peduncle tomentose, reddish-brown to light brown, 3.5–5 cm in length, 1.8–2.3 cm in diameter; microsporophylls 1.6–2.7 × 0.9–2.1 cm, non-recurved distal face. *Ovuliferous strobilus* generally solitary (1–2), cylindrical, erect or pendular, 23.5–38 cm in length, 10.5–14.6 cm in diameter, dark green with blackish pubescence at emergence, dark green with black and grey trichomes at maturity, acuminate apex; peduncle tomentose, brown to reddish-brown, 8–11.5 cm in length, 2.5–3 cm in diameter; megasporophylls 55–224, 2–4 × 4.4–5.3 cm, prominent distal face, obtuse angle between horns. *Seeds* ovoid, sarcotesta whitish-yellow to yellow when immature, light brown at maturity, 2–3.3 cm in length, 1.5–2.5 cm in diameter.

Distribution and habitat. Endemic to Mexico from the River La Antigua drainage system within Xico, Teocelo and Coatepec municipalities to south end of Sierra Madre Oriental in Veracruz state, between 500–1,300 m in cloud forest (Figure 8).

Etymology. The epithet is derived from the country of origin of the material for the description of the genus.

Distinguishing features. *Ceratozamia mexicana* is distinguished by its lanceolate, coriaceous and flat leaflets with a symmetric apex, ovulate strobilus dark green with black and grey trichomes at maturity, and a prominent distal face with an obtuse angle between horns (Fig. 11).

Specimens examined. MEXICO. **Veracruz**: Coatepec, *P. Zamora C. 2450* (MEXU, XAL); Comapa, *F. Nicolalde-Morejón et al. 2146-2156* (CIB), *L. Martínez-Domínguez et al. 164, 716-730* (CIB); Puente Nacional, *G. Castillo-Campos & M. E. Medina 4299* (XAL); Sochiapa, *M. Vázquez-Torres 8589* (CIB); Teocelo, *F. Nicolalde-Morejón et al. 2273-2278* (CIB), *M. G. Zola 146* (XAL), *M. Vázquez-Torres* 4865 (CIB), *L. Martínez-Domínguez et al. 731-750, 764-770* (CIB); Tlaltetela, *F. Nicolalde-Morejón & L. Martínez-Domínguez 2246, 2253-2256* (CIB), *L. Martínez-Domínguez & F. Nicolalde-Morejón 584-586, 620, 628-635* (CIB); Totutla, *A. P. Vovides 730-733, 748* (XAL), *Brigada T. Walters s/n* (XAL), *F. Nicolalde-Morejón et al. 2279-2281* (CIB), *F. Vázquez B. 730* (XAL), *J. Rees 6344* (IEB), *J. Rees & A. P. Vovides 1660, 1672, 1689* (XAL), *L. Martínez-Domínguez et al. 704-707, L. Martínez-Domínguez et al. 752-758* (CIB); Xico, *L. Martínez-Domínguez & F. Nicolalde-Morejón 640-648* (CIB).

Taxonomic comments. The taxonomy of *Ceratozamia mexicana* has undergone constant changes since its original publication in 1846. The identity of this binomial was ambiguous for several decades. This taxonomic uncertainty was due to the complexity of relationships with some of the other names published by Miquel during the immediately succeeding years (1847, 1848 and 1849), following the original publication of the genus –namely, *C. brevifrons*, *C. robusta*, *C. intermedia*, *C. longifolia*, and *C. latifolia*. Later on, some names were placed in synonymy and others were characterised as *nomina nuda*; in particular, *C. brevifrons* was listed as a synonym of *C. mexicana* under the assumption that it was in fact a juvenile form of the latter (see Miquel 1848, 1861).

In further taxonomic treatments of *Ceratozamia* –specifically, in De Candolle (1864–1868) and including Miquel's *Nouveaux matériaux pour servir à la connaissance des Cycadées* (1868–1869a, b)– this nomenclatural status was maintained. In his mature work, Miquel considered the variation observed between juveniles and adults was due to the corresponding ontogenetic modifications and collapsed into synonymy with *C. mexicana* all five species previously described.

Half a century later, Schuster (1932) circumscribed the genus to include only two species: *Ceratozamia kuesteriana* and *C. mexicana*, with two varieties and two forms. However, in the first modern taxonomic treatment (Vovides et al. 1983) and continuing with the typification of names within the genus (Stevenson and Sabato 1986), the type species was circumscribed to the central region of Veracruz. In this context, Vovides et al. (1983) attributed a wide geographic distribution and high variation of morphological characters to *C. mexicana* while recognising three varieties: *C. mexicana* var. *mexicana*, *C. mexicana* var. *latifolia* (Miq.) Schuster and *C. mexicana* var. *robusta* (Miq.) Dyer.

The original *Ceratozamia mexicana* specimens were collected by the Belgian botanist and explorer A. B. Ghiesbreght, who probably did his fieldwork in the region of Huatusco, Veracruz. This location is recognised as part of his route for botanical collections between 1835 and 1838 (Barnhart 1965; Sartorius 1990; Rzedowski et al. 2009). Besides the "El Mirador" locality, mentioned by Thiselton-Dyer (1884) and Schuster (1932) as the main reference place, the species still exists in Huatusco. Due to coffee cultivation, the original vegetation has been replaced almost in its entirety. However, the species still occurs in the wild in relictual secondary vegetation within a property called "Hacienda Zacuapam". This property was part of a former "El Mirador" hacienda, early in the XIX century (Sartorius 1990).

10. *Ceratozamia morettii* Vázq. Torres & Vovides. Novon 8 (1): 87–90. 1998.

Figure 3C

Type. MEXICO. Veracruz: Landero y Coss, 7 Jan. 1992, *M. Vázquez-Torres & H. Barney 4097* (holotype: CIB; isotypes: CIB, MEXU, XAL).

Description. *Stem* epigeous, erect and decumbent, 20–50 cm in length, 20–35 cm in diameter. *Cataphylls* persistent, densely tomentose at emergence, reddish-brown and partially tomentose at maturity, triangular, apex acuminate, 4–6.5 × 3–3.5 cm at base. *Leaves* 3–30, descending, 82–200 cm, light green at emergence, brown pubescence, glabrous at maturity. *Petiole* terete, straight, 30–90 cm, armed with short and thin prickles, green in adult leaves. *Rachis* terete, straight, 50–116 cm, armed with prickles, green in adult leaves. *Leaflets* 10–23, oblong, planar and abaxially curved, not basally falcate, coriaceous, flat, opposite to subopposite, plane, green, adaxial side glabrous and abaxial side glaucous, acuminate apex, asymmetric apex, attenuate at base, with conspicuous and light green veins; median leaflets 17.5–41 × 2.6–4.3 cm, 2.1–6 cm between leaflets; articulations green and yellow, 0.5–1.6 cm wide. *Polliniferous strobilus* solitary, cylindrical, erect, 12–15 cm in length, 3.8–4.5 cm in diameter, brownish-yellow at emergence, greenish-yellow with brown pubescence at maturity; peduncle tomentose, reddish-brown to brown, 3–7 cm in length, 1.1–1.3 cm in diameter; microsporophylls 1.0–1.3 × 0.8–1 cm, non-recurved distal face. *Ovuliferous strobilus* solitary, globose, erect, 14–18 cm in length, 8–9.5 cm in diameter, yellowish-green with brown pubescence at emergence, green with blackish trichomes at maturity, apiculate apex; peduncle tomentose, brown, 4–7 cm in length, 1.2–1.8 cm in diameter; megasporophylls 40–108, 2.1–2.6× 3.2–3.6 cm, truncate distal face, right angle of horns. *Seeds* ovoid, sarcotesta whitish-yellow to yellow when immature, light brown at maturity, 1.5–2 cm in length, 1–1.2 cm in diameter.

Distribution and habitat. Endemic to Veracruz, on karstic rocks and cliffs of the Sierra de Chiconquiaco, between 1,200–1,850 m (Fig. 8). The vegetation type where this species grows is cloud forest.

Etymology. The specific epithet honours Aldo Moretti, in recognition of his scientific contributions in the field of cycad biology. He is a researcher in the Orto Botanico and Istituto di Biologia Vegetale at the University of Naples Federico II, Italia.

Distinguishing features. *Ceratozamia morettii* is similar to *C. delucana* in leaf morphology; however, there are differences in the total size of plant and in reproductive structures. This species has leaves with up to 23 pairs of leaflets and the ovulate strobilus is green with blackish trichomes at maturity, 14–18 cm long, 8–9.5 cm in diameter and an apiculate apex. Moreover, *C. morettii* has minimal variation at the population level.

Specimens examined. MEXICO. **Veracruz**: Chiconquiaco, *A. P. Vovides 687, 704* (XAL), *C. J. W. Schiede s/n* (XAL), *J. Rees 6336* (IEB), *L. Lagunes G. 83, 84* (CIB); Landero y Coss, *A. P. Vovides 1662* (XAL), *J. Rees 6342* (IEB), *J. Rees & A. P. Vovides 1663, 1664, 1676* (XAL), *L. Martínez-Domínguez et al. 185-214* (CIB), *M. Vázquez-Torres 4097* (XAL), *8349* (CIB), *S. Avendaño 5378* (XAL), *T. W. Walters 2001-01-E* (XAL); Tenochtitlán, *A. Rincón G. et al. 296-298* (XAL); Yecuatla, *C. Gutiérrez B. 134* (XAL), *J. Rees 1677* (XAL), *F. Nicolalde-Morejón & L. Martínez-Domínguez 2087-2106* (CIB), *L. Martínez-Domínguez et al. 161* (CIB).

11. *Ceratozamia sabatoi* Vovides & Vázq. Torres. Novon 3 (4): 502–504. 1993.
Figures 2B, 3D, 6A, 7A

Type. MEXICO. Querétaro: San Joaquín, 15 Apr. 1991, *A. P. Vovides 1205* (holotype: XAL).

Description. *Stem* epigeous, erect and decumbent, 8–30 cm in length, 20–35 cm in diameter. *Cataphylls* persistent, densely tomentose at emergence, reddish-brown and partially tomentose at maturity, triangular, apex acuminate, 3–4.5 × 2–3.5 cm at base. *Leaves* 3–40, descending, 60–129 cm, dark brown at emergence, whitish-grey pubescence, glabrous at maturity. *Petiole* terete, straight, 20–60 cm, armed with short and thin prickles, greenish-brown in adult leaves. *Rachis* terete, straight, 40–92 cm, armed with prickles, brown in adult leaves. *Leaflets* 26–54, linear, planar and abaxially curved, basally falcate, papyraceous, flat, opposite to subopposite, plane, green, adaxial and abaxial side glabrous, acuminate apex, symmetric apex, attenuate at base, with conspicuous and light green veins; median leaflets 13–32 × 0.6–1.5 cm, 0.5–1.5 cm between leaflets; articulations brown, 0.3–0.7 cm wide. *Polliniferous strobilus* solitary, cylindrical, erect, 11–18 cm in length, 3.5–4.8 cm in diameter, greenish-yellow at emergence, greenish-yellow with blackish pubescence at maturity; peduncle tomentose, reddish-brown to brown, 7–10.5 cm in length, 1.1–1.9 cm in diameter; microsporophylls 1–1.9 × 1–1.4 cm, recurved distal face. *Ovuliferous strobilus* solitary, cylindrical, erect, 15.5–18 cm in length, 6–8.5 cm in diameter, yellowish-green with brown pubescence at emergence, blue green with blackish trichomes at maturity, apiculate apex; peduncle tomentose, brown, 4–7 cm in length, 1.2–1.8 cm in diameter; megasporophylls 98–108, 2.3–2.5× 2–3 cm, truncate distal face, right angle between horns. *Seeds* ovoid, sarcotesta whitish-red when immature, light brown at maturity, 1.2–2 cm in length, 1.2–1.5 cm in diameter.

Distribution and habitat. Endemic to Mexico and known from the states of Querétaro and Hidalgo, at 1,600–1,900 m in the Sierra Gorda mountain range of Querétaro, along the mountain range northwest of Hidalgo (Fig. 9). It inhabits the understorey herbaceous layer of the transition zone between oak forest and cloud forest.

Etymology. The specific epithet honours the late Sergio Sabato, distinguished professor at the University of Naples Federico II, Italia, for his contributions to knowledge of the biology and systematics of cycads, particularly in the Neotropics.

Distinguishing features. Leaflets lanceolate, papyraceous, symmetric apex and with brown articulations; pollen strobilus greenish-yellow with blackish pubescence at maturity and microsporophylls with recurved distal face (Fig. 6A).

Specimens examined. MEXICO. **Hidalgo**: Zimapán, *R. Contreras-Medina 55, 56* (XAL), *R. Fernandez-Nava 6561* (MEXU, MO, XAL). **Querétaro**: Cadereyta de Montes, *A. P. Vovides 1193, 1196-1199, 1201, 1205* (XAL), *A. P. Vovides et al. 1203* (MEXU, XAL), *F. Nicolalde-Morejón et al. 2169, 2170* (CIB), *L. Martínez-Domínguez et al. 313-343* (CIB), *O. V. Zirahuen 128014* (IEB), *R. Fernandez-Nava s/n* (QMEX), *R. Zirahuén-Ortega V. 328* (MEXU); Landa de Matamoros, *T. W. Walters 2001-05-A, B* (XAL); Pinal de Amoles, *F. Nicolalde-Morejón et al. 2171, 2172* (CIB), *L. Martínez-Domínguez et al. 344-372* (CIB), *Rzedowski s/n* (XAL).

12. *Ceratozamia tenuis* (Dyer) D. W. Stev. & Vovides. Botanical Sciences 94 (2): 419–429. 2016.

Figures 2A, 3I

Type. Hort. Kew Palm House: *Thistleton-Dyer s.n. 1881* (lectotype: K). Epitype (designated here). MEXICO. Veracruz: Jilotepec, 19 Jan. 1976, *A. P. Vovides 18* (XAL). Type: Based on *Ceratozamia mexicana* var. *tenuis* Dyer Biol. Cent.-Amer., Bot. 3: 193. 1884. Isoepitype (designated here). *A. P. Vovides 18* (NY).

Ceratozamia mexicana var. *vulgaris*. Schuster. Pflanzener 99: 131. 1932. Neotype (designated here). MEXICO. Veracruz: Xalapa, Chiltoyac, 18 Oct. 2016, *Martínez-Domínguez et al. 984* (CIB).

Schuster mentioned "Jalapa" in his treatment and Chiltoyac (Xalapa, Veracruz), which is very near to Xalapa and thus seems appropriate because the plants match the description by Schuster.

Ceratozamia mexicana var. *longifolia* f. *tenuis* (Dyer) Schuster. Pflanzener 99: 132. 1932. Type: Based on *Ceratozamia mexicana* var. *tenuis*.

Description. *Stem* epigeous, erect and decumbent, 20–100 cm in length, 30–45 cm in diameter. *Cataphylls* persistent, densely tomentose at emergence, reddish-brown and partially tomentose at maturity, triangular, apex acuminate, 2–6 × 2–5.5 cm at base. *Leaves* 6–56, ascending, 85–225 cm, dark green at emergence, brown pubescence, glabrous at maturity. *Petiole* terete, straight, 30–93 cm, armed with short and thin prickles, green in adult leaves. *Rachis* terete, straight, 56–154 cm, armed with prickles, green in adult leaves. *Leaflets* 30–56, linear, planar and abaxially curved, basally falcate, papyraceous, caniculate, opposite to subopposite, plane, green, adaxial and abaxial side glabrous, acuminate and symmetric apex, attenuate at base, with conspicuous and light green veins; median leaflets 23–50.5 × 1–2.1 cm, 0.3–2.5 cm between leaflets; articulations green, 0.4–1.4 cm wide. *Polliniferous strobilus* solitary, cylindrical, erect, 26–50 cm in length, 5–7 cm in diameter, greenish-yellow at emergence, greenish-yellow with blackish pubescence at maturity; peduncle tomentose, reddish-brown to light-brown, 3.7–22 cm in length, 1.2–2.5 cm in diameter; microsporophylls 1.7–2.7 × 1.2–1.9 cm, non-recurved distal face. *Ovuliferous strobilus* solitary, cylindrical, erect or pendular, 22–35 cm in length, 7.6–13.3 cm in diameter, dark green with blackish pubescence at emergence, dark green with blackish trichomes at maturity, acuminate apex; peduncle tomentose, brown to reddish-brown, 8–16.5 cm in length, 1.5–2.4 cm in diameter; megasporophylls 48–195, 2.7–3.1 × 4.2–5 cm, prominent distal face, right angle between horns. *Seeds* ovoid, sarcotesta whitish-yellow to yellow when immature, light brown at maturity, 2.5–3 cm in length, 1.3–1.8 cm in diameter.

Distribution and habitat. Endemic to Mexico in the central Veracruz mountain region at 1,200–1,850 m elevation on volcanic soils with basaltic rocks (Fig. 8). The vegetation type of the habitat is cloud forest.

Etymology. The specific epithet alludes to thin leaflets.

Distinguishing features. Characterised by leaflets linear, papyraceous and caniculate with symmetric apex; petiole and rachis armed with thin prickles; new leaves are dark green at emergence; ovulate strobilus dark green with blackish trichomes at maturity, prominent distal face, and right angle between horns.

Specimens examined. MEXICO. **Veracruz:** Chiconquiaco, *D. Jimeno Sevilla 754* (XAL), *J. Rees 1625* (XAL), *1626* (MEXU, XAL), *L. Martínez-Domínguez et al. 971-981* (CIB), *R. Fernandez-Nava 385* (MEXU); Coacoatzintla, *F. Vazquez B.* (XAL), G. *Castillo-Campos 118* (XAL), *L. Martínez-Domínguez et al. 165-184,* 273-282, 759 (CIB); Jilotepec, *A. P. Vovides 470* (XAL), *471* (MEXU, XAL), *735* (XAL), *E. Estrada et al. 757* (MEXU), *J. Rees 1620* (XAL), *F. Nicolalde-Morejón* & *L. Martínez-Domínguez 2067-2086* (CIB), *L. Martínez-Domínguez et al. 573-583* (CIB), *M. G. Zola 667* (MEXU, XAL), *R. Ortega J. 525* (XAL), *S. Avendaño 5395* (MEXU); Tepetlán, *F. Nicolalde-Morejón & L. Martínez-Domínguez 2001-2004* (CIB), *2047-2066* (CIB), *2217-2226* (CIB), *L. Martínez-Domínguez et al. 160, 283-293, 545-555* (CIB); Xalapa, *L. Martínez-Domínguez et al. 985-987* (CIB).

Taxonomic comments. This name has been controversial due to a series of transferences and the lack of material. This species was initially described as *C. mexicana* var. *tenuis* (Thiselton-Dyer 1884) and Schuster (1932) transferred it to form status under the name *C. mexicana* var. *longifolia* f. *tenuis*. However, its identity has been questioned for decades due to the scarcity of type specimens. The discovery of a specimen collected and examined by Thiselton-Dyer for his protologue description and the subsequent lectotypification of this specimen, has allowed a clearer concept of this taxon (Vovides et al. 2016). Recently, this entity was transferred to the species level after the analysis of quantitative morphological and anatomical evidence which allowed the separation of populations previously associated with the *C. mexicana* and their assignment as a new entity (Vovides et al. 2016). Individuals in these populations bear correspondence to lectotype specimens in the Royal Botanic Gardens Kew herbarium, which correspond to *Ceratozamia mexicana* var. *tenuis* (Vovides et al. 2016). Two specimens were incorrectly designated by Vovides et al. (2016) as epitypes [A. Vovides 018 (XAL, NY)]. According to the International Code of Nomenclature (McNeil et al. 2012), we correct the designation of the epitype and designate an isoepitype (Section 2, Article 9, Recommendation 9C). Finally, we note that the historical *Ceratozamia* populations from Jilotepec and Coacoatzintla have been associated to the *C. mexicana* species since the morphological work of Chamberlain (1912).

13. *Ceratozamia totonacorum* Mart.-Domínguez & Nic.-Mor. Brittonia. 2017.
Figure 3J

Type. MEXICO. Puebla: Jonotla, 9 Jun. 2015, *L. Martínez-Domínguez* & *F. Nicolalde-Morejón 618* ♀ (holotype: CIB).

Description. *Stem* epigeous, erect and decumbent, 10–45 cm in length, 10–25 cm in diameter. *Cataphylls* persistent, densely tomentose at emergence, reddish-brown and glabrous at maturity, triangular, apex acuminate, 2–5 × 1.2–2.5 cm at base. *Leaves* 10–55, descending, 90–265 cm, brown at emergence, with brown pubescence, glabrous at maturity. *Petiole* terete, straight, 30–70 cm, armed with long and thin prickles, green in adult leaves. *Rachis* terete, straight, 85–181 cm, armed with prickles, green in adult leaves. *Leaflets* 11–33, oblong, mostly planar, not basally falcate and occasionally falcate, papyraceous, flat, opposite to subopposite, plane, green, adaxial side glabrous and glaucous, abaxial side glaucous, acuminate apex, symmetric apex, attenuate at base, with conspicuous and light green veins; median leaflets 17–40 × 2.7–4.2 cm, 2–5.6 cm between leaflets; articulations green, 0.5–1.3 cm wide. *Polliniferous strobilus* generally solitary (1–2), cylindrical, erect, 29–31 cm in length, 5.4–5.6 cm in diameter, greenish-yellow at emergence, yellow with brown pubescence at maturity; peduncle tomentose, light brown, 9–12 cm in length, 1.5–2 cm in diameter; microsporophylls 1.5–2.2 × 1.3–1.8 cm, non-recurved distal face. *Ovuliferous strobilus* solitary, cylindrical, erect or pendular, 20.5–26 cm in length, 8.5–9.3 cm in diameter, light green and glaucous, with orange to light brown pubescence at emergence, green with yellowish-brown trichomes at maturity, acuminate apex; peduncle tomentose, light brown, 10–11.2 cm in length, 1.3–1.5 cm in diameter; megasporophylls 74–92, 1.6–2.2 × 2.6–3.4 cm, prominent distal face, right angle between horns. *Seeds* ovoid, sarcotesta whitish-red when immature, cream to light brown at maturity; 3.3–4.0 cm in length, 0.8–1.2 cm in diameter.

Distribution and habitat. Endemic to Mexico in the Sierra Norte of Puebla mountain region on rocky outcrops in exposed walls up to 80 m at 600–1,050 m (Fig. 8). It inhabits the transition zone between cloud forest and evergreen tropical forest.

Etymology. The specific epithet makes reference to the Totonaco ethnic group of Santiago Ecatlán in Sierra Norte of Puebla, whose residents use and manage this species in local cultural contexts related to rituals.

Distinguishing features. This species is distinguished by its petioles with abundant and long, thin prickles, brown leaves at emergence, but the colour disappears in the adult leaves; leaflets are oblong and papyraceous with asymmetric apex. Ovulate strobilus yellowish-green with brown trichomes.

Specimens examined. MEXICO. **Hidalgo**: Huehuetla, *A. P. Vovides 23* (XAL). **Puebla**: Jonotla, *F. Nicolalde-Morejón et al. 1948* ♂ (CIB), *1956* (MEXU), *1957* (NY), *1949-1955* (CIB), *1958-1967* (CIB), *F. Nicolalde-Morejón et al. 1966* (CIB), *L. Martínez-Domínguez & F. Nicolalde-Morejón 619* ♀ (CIB); Pahuatlán, *G. Toriz et al. 226* (MEXU); Tlapacoyan, *E. Meza P. 14* (XAL). **Veracruz**: Tlachichilco, *A. Rincón G. et al. 2584* (XAL), *2585* (MEXU, XAL).

14. *Ceratozamia zaragozae* Medellín-Leal. Brittonia 15: 175–176. 1963.

Figures 4B, 5C

Type. MEXICO. San Luis Potosí: Río Verde, 22 Jul. 1962. *F. Medellín-Leal 1452* (holotype: SLPM; isotypes: ENCB, MICH, US).

Description. *Stem* semihypogeous, erect, 10–20 cm in length, 10–15 cm in diameter. *Cataphylls* persistent, densely tomentose at emergence, reddish-brown and partially tomentose at maturity, triangular, apex acuminate, 1.8–2.5 × 1–2 cm at base. *Leaves* 3–27, ascending, 95–202 cm, reddish-brown at emergence with whitish-grey pubescence, glabrous at maturity. *Petiole* terete, twisted, 11–36 cm, unarmed, green in adult leaves. *Rachis* terete, twisted, 40–77 cm, unarmed, green in adult leaves. *Leaflets* 25–46, linear, mostly planar, basally falcate, membranaceous, strongly caniculate, opposite to subopposite, plane, green, adaxial and abaxial side glabrous, acute apex, symmetric apex, attenuate at base, with conspicuous and light green veins; median leaflets 17–31.5 × 0.4–0.7 cm, 0.8–2.3 cm between leaflets; articulations yellow, 0.2–0.3 cm wide. *Polliniferous strobilus* solitary, cylindrical, erect, 15–19 cm in length, 2–3.5 cm in diameter, greenish with reddish-brown pubescence at emergence, reddish-brown at maturity; peduncle tomentose, reddish-brown to brown, 5–8 cm in length, 1.5–1.8 cm in diameter; microsporophylls 0.8–1.2 × 0.3–0.6 cm, non-recurved distal face. *Ovuliferous strobilus* solitary, cylindrical, erect, 8.2–12 cm in length, 5.8–7 cm in diameter, green with scarcely reddish-brown trichomes at emergence, dark green at maturity, acute apex; peduncle tomentose, brown, 6–9 cm in length, 0.9–1.2 cm in diameter; megasporophylls 24–49, 2.2–3.7 × 2–2.6 cm, truncate distal face, obtuse angle between horns. *Seeds* ovoid, sarcotesta light brown at maturity, 2–2.8 cm in length, 1.8–2 cm in diameter.

Distribution and habitat. Endemic to Mexico in a small mountain range in South Central San Luis Potosí at 1,500–1,800 m elevation (Fig. 9). The vegetation type of the habitat is pine-oak forest.

Etymology. The specific epithet is refers to General Ignacio Zaragoza, a hero of the Battle of Puebla (May 1862) against the French Army.

Distinguishing features. This species is distinguished by having petiole and rachis unarmed and twisted. Leaflets are lanceolate, mostly planar, not basally falcate, membranaceous and caniculate, with symmetric apex.

Specimens examined. MEXICO. **San Luis Potosí**: Río Verde, *A. G. Mendoza & L. Vargas 1389* (MEXU), *A. P. Vovides 435* (XAL), *E. Molseed 34* (MEXU), *F. Nicolalde-Morejón et al. 2307-2319* (CIB), *L. Martínez-Domínguez et al. 792-808* (CIB), T. *Walters et al. TW-2001-07* (MEXU, XAL).

Discussion

The taxonomic history of species names in the genus Ceratozamia, as presented here, allow us to conclude that infrageneric concepts in this gymnosperm taxon are increasingly stringent and that infraspecific ranks are no longer recognised (cf. Osborne and Walters 2004). Most of these changes elevate varieties through the inclusion of new species. In general, several taxonomic changes have taken place, including diverse transfers at the species level, and substantial taxonomic disagreements have occurred, such as those involving the synonymy of *C. microstrobila*. In particular, the case of *C. mexicana* has been controversial, as demonstrated by the series of relationships and taxonomic changes, which have been established around it. With respect to the recent publication of two independent works in which contrasting taxonomic scenarios were proposed with respect to *C. mexicana* (Medina-Villareal and González-Astorga 2016;

Vovides et al. 2016), the present morphological evaluation validates the proposal of Vovides et al. (2016).

Further support can be raised in connection with our position on recent taxonomic stances for *Ceratozamia mexicana*. On the basis of their phenetic analysis, Medina-Villarreal and González-Astorga (2016) suggested that the type species of the genus, *C. mexicana*, should be geographically anchored to the locality of the *C. brevifrons* neotype, given its morphometric similarity to the *C. mexicana* holotype. Under this assumption, these authors consider that *C. decumbens*, *C. morettii* and *C. brevifrons* should all be synonyms of *C. mexicana*. On the other hand, according to Medina-Villarreal and González-Astorga (2016), populations from the Naolinco Valley, Veracruz, should be described as a new species. Vovides et al. (2016) disagree on this point and suggest that those populations correspond in turn to *C. mexicana* var. *tenuis*, whose taxonomic treatment would then be recognised at the species level as *C. tenuis*. Under this perspective, *C. mexicana* would be recircumscribed to populations in the southern extreme of Veracruz. With our recircumscription proposal and review of historical documents, we consider that the locality of the *C. mexicana* holotype corresponds to the proposal of Vovides et al. (2016).

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RESEARCH ARTICLE

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New insights into the taxonomy of tribe Euclidieae (Brassicaceae), evidence from nrITS sequence data

Hongliang Chen[1,2], Ihsan A. Al-Shehbaz[3], Jipei Yue[1], Hang Sun[1]

1 *Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences, 132 Lanhei Road, Kunming, Yunnan 650201, China* **2** *University of Chinese Academy of Sciences, Beijing 100049, China* **3** *Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, USA*

Corresponding authors: *Hang Sun* (hsun@mail.kib.ac.cn); *Jipei Yue* (yuejipei@mail.kib.ac.cn)

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Abstract

As currently delimitated, the species-rich mustard tribe Euclidieae DC. (Brassicaceae) comprises 28 genera and 152 species distributed primarily in Asia. To date, no tribe-wide comprehensive phylogenetic analysis has been conducted. In this study, sequence data from the nuclear ribosomal internal transcribed spacer (nrITS) region of 82 species in all 28 genera of Euclidieae were used to test its monophyly and infer inter- and intra-generic relationships within. Phylogenetic analyses revealed that *Rhammatophyllum* and *Sisymbriopsis* are embedded within *Solms-laubachia* s.l., and *Solms-laubachia lanuginosa* (*Eurycarpus lanuginosus*) fell outside the tribe. Therefore, *Solms-laubachia* s.l. as currently recognized is not monophyletic and its generic delimitation needed further study. Besides, our results suggest that the genera *Lepidostemon*, *Neotorularia*, and *Tetracme* are polyphyletic.

Keywords

Euclidieae, Brassicaceae, Cruciferae, *Solms-laubachia*, Phylogeny, nrITS

Introduction

The Brassicaceae (Cruciferae) includes 52 tribes, 341 genera, and 3,997 species (BrassiBase: https://brassibase.cos.uni-heidelberg.de/, accessed 5 February 2018, Koch et al. 2012, Kiefer et al. 2014) distributed worldwide, primarily in the temperate regions

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(Al-Shehbaz 1984, Al-Shehbaz et al. 2006). The family is academically and economically important (Franzke et al. 2011, Al-Shehbaz 2012, Huang et al. 2016), as it contains the well-known model plant species *Arabidopsis thaliana* (L.) Heynh. and many crops (e.g., cabbage, cauliflower, turnip, rape, canola, radish, wasabi) and ornamentals (e.g., species of *Lobularia* Desv., *Iberis* L., *Hesperis* L., *Matthiola* W. T. Aiton). Although the family is easily recognized morphologically, it is often difficult to assign an individual plant to a given genus, and there are tremendous controversies on generic delimitations and tribal assignments (Al-Shehbaz et al. 2006, Al-Shehbaz 2012). The total number of tribes and genera they include varied among different systems. For example, Schulz (1936) and Janchen (1942) recognized 19 and 15 tribes, respectively. By contrast, others (e.g., Zhou et al. 2001, Appel and Al-Shehbaz 2003) adopted an alphabetical arrangement of genera. The use of molecular sequences to infer phylogenetic relationships during the past two decades have greatly improved our understanding of the evolution within the Brassicaceae. That led Al-Shehbaz et al. (2006) to propose the first phylogenetic tribal classification system based on prior molecular studies, especially the chloroplast *ndh*F sequences (Beilstein et al. 2006), and had since been expanded to include 52 tribes (Al-Shehbaz 2012, German and Friesen 2014, Chen et al. 2016). Generic boundaries had also been redefined, and studies on *Solms-laubachia* s.l. (Yue et al. 2006, 2008), *Eutrema* R. Br. (Al-Shehbaz and Warwick 2005), *Microthlaspi* F. K. Mey. (Ali et al. 2016), to name a few, demonstrate that trend.

The tribe Euclidieae DC. was established ca. 200 years ago (de Candolle 1821), and it has been accepted in subsequent tribal classifications, though the delimitation of its component genera remained controversial. Of the 14 genera recognized by Schulz (1936) in the tribe, only *Euclidium* W. T. Aiton and *Lachnoloma* Bunge were maintained by Al-Shehbaz (2012) (Table 1). As currently delimited (Warwick et al. 2007, Al-Shehbaz and German 2016, BrassiBase) (Table 1), the tribe comprises 28 genera and 152 species, including the species-rich *Solms-laubachia* Muschl. (33 spp.), *Strigosella* Boiss. (24 spp.), and *Braya* Sternb. & Hoppe (22 spp.), as well as 12 monospecific genera.

Because taxa sampling varied in previous studies, the interrelationships among genera of Euclidieae varied a great deal. In order to gain knowledge of phylogenetic relationship of the tribe, we conducted the first comprehensive study that included representatives of all genera.

Materials and methods

Plant materials and molecular data

This study comprised 33 genera and 88 species, including 28 genera and 82 species of Euclidieae. Forty-nine ITS sequences of 37 species were newly generated here, and all others were downloaded from GenBank (Table 2 and Appendix 1). Six species of Lineage III (sensu Beilstein et al. 2006), namely *Sterigmostemum sulphureum* (Banks & Sol.) Bornm. and *S. billardieri* (DC.) D. A. German (Anchonieae), *Bunias erucago*

Table 1. Three different taxonomic treatments and current delimitation of Euclidieae. Number of species included in the study and the total species number of the genus based on current delimitation (BrassiBase) are given in parentheses (sampled/total).

de Candolle (1821)	Schulz (1936)	Al-Shehbaz (2012)	Current delimitation (BrassiBase)
Euclidium W. T. Aiton	*Anastatica* L.	*Atelanthera* Hook. f. & Thomson	*Anzhengxia* Al-Shehbaz & D. A. German (1/1)
Ochthodium DC.	*Boreava* Jaub. & Spach	*Braya* Sternb. & Hoppe	*Atelanthera* Hook. f. & Thomson (1/1)
Pugionium Gaertn.	*Bunias* L.	*Catenulina* Soják	*Braya* Sternb. & Hoppe (13/22)
	Euclidium W. T. Aiton	*Christolea* Cambess.	*Catenulina* Soják (1/ 1)
	Hymenophysa C. A. Mey.	*Cryptospora* Kar. & Kir.	*Christolea* Cambess. (1 /2)
	Lachnoloma Bunge	*Cymatocarpus* O. E. Schulz	*Cryptospora* Kar. & Kir.(/3)
	Myagrum L.	*Dichasianthus* Ovcz. & Yunussov	*Cymatocarpus* O. E. Schulz (1/3)
	Neslia Desv.	*Dilophia* Thomson	*Dichasianthus* Ovcz. & Yunussov (1 /1)
	Ochthodium DC.	*Euclidium* W. T. Aiton	*Dilophia* Thomson (1/2)
	Octoceras Bunge	*Lachnoloma* Bunge	*Euclidium* W. T. Aiton (1/1)
	Schimpera Hochst. & Steud. ex Schimper	*Leiospora* (C.A.Mey.) Dvořák	*Lachnoloma* Bunge (1/1)
	Spirorhynchus Kar. & Kir.	*Lepidostemon* Hook. f. & Thomson	*Leiospora* (C.A.Mey.) Dvořák (5/8)
	Tauscheria Fisch. ex DC.	*Leptaleum* DC.	*Lepidostemon* Hook. f. & Thomson (2/6)
	Texiera Jaub. & Spach	*Neotorularia* Hedge & J. Léonard	*Leptaleum* DC. (1/2)
		Octoceras Bunge	*Metashangrilaia* Al-Shehbaz & D. A. German (1/1)
		Pycnoplinthopsis Jafri	*Neotorularia* Hedge & J. Léonard (4/6)
		Pycnoplinthus O. E. Schulz	*Octoceras* Bunge (1/1)
		Rhammatophyllum O. E. Schulz	*Pycnoplinthopsis* Jafri (1 /1)
		Shangrilaia Al-Shehbaz, J. P. Yue & H. Sun	*Pycnoplinthus* O. E. Schulz (1/1)
		Sisymbriopsis Botsch. & Tzvelev	*Rhammatophyllum* O. E. Schulz (5/7)
		Solms-laubachia Muschl.	*Rudolf-kamelinia* Al-Shehbaz & D. A. German (1/1)
		Spryginia Popov	*Shangrilaia* Al-Shehbaz, J. P. Yue & H. Sun (1/1)
		Streptoloma Bunge	*Sisymbriopsis* Botsch. & Tzvelev (3/4)
		Strigosella Boiss.	*Solms-laubachia* Muschl. (23/33)
		Tetracme Bunge	*Spryginia* Popov (2/7)
			Streptoloma Bunge (1/2)
			Strigosella Boiss. (3/24)
			Tetracme Bunge (3/9)

Table 2. List of studied taxa including voucher information and GenBank accession numbers.

Taxon	Geographical origin	Collection number (Herbarium: KUN)	GenBank accession No.
Anzhengxia yechengnica (Z. X. An) Al-Shehbaz & D. A. German	Pishan, Xinjiang	YC-XZ111	MH237681
	Yecheng, Xinjiang	YC-XZ115	MH237682
Braya parvia (Z. X. An) Al-Shehbaz & D. A. German	Aheqi, Xinjiang	YC-XZ090	MH237683
	Zhada, Xizang	YC-XZ150	MH237684
Braya rosea Bunge	Aketao, Xinjiang	YC-XZ105	MH237685
	Kunming, Yunnan	SCSY-042	MH237686
Braya scharnhorstii Regel & Schmalh.	Aketao, Xinjiang	YC-XZ101	MH237687
Christolea crassifolia Cambess.	Aketao, Xinjiang	YC-XZ103	MH237688
Dilophia salsa Thomson	Pishan, Xinjiang	YC-XZ128	MH237689
	Qumalai, Qinghai	ZH645	MH237690
Euclidium syriacum (L.) W. T. Aiton	Urumqi, Xinjiang	YC-XZ076	MH237691
Eurycarpus lanuginosus (Hook. f. & Thomson) Botsch.	Zhada, Xizang	YC-XZ152	MH237692
			MH237693
			MH237694
Leiospora eriocalyx (Regel & Schmalh.) F. Dvořák	Yecheng, Xinjiang	YC-XZ122	MH237695
	Pishan, Xinjiang	YC-XZ125	MH237696
Leiospora pamirica (Botsch. & Vved.) Botsch. & Pachom.	Aketao, Xinjiang	YC-XZ102	MH237697
	Aketao, Xinjiang	YC-XZ104	MH237698
Lepidostemon rosularis (K. C. Kuan & Z. X. An) Al-Shehbaz	Cuona, Xizang	ZJW3888	MH237699
Metashangrilaia forrestii (W. W. Sm.) Al-Shehbaz & D. A. German	Baqing, Xizang	YZC227	MH237700
Pycnoplinthus uniflora (Hook. f. & Thomson) O. E. Schulz	Ritu, Xizang	YC-XZ134	MH237701
Rudolf-kamelinia korolkowii (Regel & Schmalh.) Al-Shehbaz & D. A. German	Aheqi, Xinjiang	YC-XZ089	MH237702
	Aketao, Xinjiang	YC-XZ107	MH237703
Shangrilaia nana Al-Shehbaz, J. P. Yue & H. Sun	Shangrila, Yunnan	CHY008	MH237704
Sisymbriopsis mollipila (Maxim.) Botsch.	Yecheng, Xinjiang	YC-XZ119	MH237705
Sisymbriopsis pamirica (Y. C. Lan & Z. X. An) Al-Shehbaz, Z. X. An & G. Yang	Aketao, Xinjiang	YC-XZ100	MH237706
Sisymbriopsis schugnana Botsch. & Tzvelev	Aketao, Xinjiang	YC-XZ106	MH237707
Solms-laubachia angustifolia J. P. Yue, Al-Shehbaz & H. Sun	Daocheng, Sichuan	YZC252	MH237708
Solms-laubachia baiogoinensis (K. C. Kuan & Z. X. An) J. P. Yue, Al-Shehbaz & H. Sun	Gongbujiangda, Xizang	YZC195	MH237709
Solms-laubachia calcicola J. P. Yue, Al-Shehbaz & H. Sun	Leiwuqi, Xizang	YZC233	MH237710
Solms-laubachia eurycarpa (Maxim.) Botsch.	Basu, Xizang	YZC023	MH237711
Solms-laubachia himalayensis (Cambess.) J. P. Yue, Al-Shehbaz & H. Sun	Ritu, Xizang	YC-XZ130	MH237712
	Zhada, Xizang	YC-XZ151	MH237713
Solms-laubachia jafrii (Al-Shehbaz) J. P. Yue, Al-Shehbaz & H. Sun	Lhasa, Xizang	YZC214	MH237714
	Jilong, Xizang	NZ143	MH237715
Solms-laubachia kashgarica (Botsch.) J. P. Yue, Al-Shehbaz & H. Sun	Aheqi, Xinjiang	YC-XZ096	MH237716

Taxon	Geographical origin	Collection number (Herbarium: KUN)	GenBank accession No.
Solms-laubachia lanata Botsch.	Lhasa, Xizang	YZC215	MH237717
Solms-laubachia linearlifolia (W. W. Sm.) O. E. Schulz	Deqin, Yunnan	YZC001	MH237718
Solms-laubachia linearis (N. Busch) J. P. Yue, Al-Shehbaz & H. Sun	Pishan, Xinjiang	YC-XZ123	MH237719
Solms-laubachia mieheorum (Al-Shehbaz) J. P. Yue, Al-Shehbaz & H. Sun	Angren, Xizang	YC-XZ160	MH237720
Solms-laubachia platycarpa (Hook. f. & Thomson) Botsch.	Dangxiong, Xizang	YZC216	MH237721
Solms-laubachia prolifera (Maxim.) J. P. Yue, Al-Shehbaz & H. Sun	Mangkang, Xizang	YZC019	MH237722
Solms-laubachia pulcherrima Muschl.	Lijiang, Yunnan	ChenHongliang202	MH237723
Solms-laubachia retropilosa Botsch.	Xiangcheng, Sichuan	ChenHongliang209	MH237724
Solms-laubachia villosa (Maxim.) J. P. Yue, Al-Shehbaz & H. Sun	Yushu, Qinghai	YZC239	MH237725
Solms-laubachia xerophyte (W. W. Sm.) H. F .Comber	Shangrila, Yunnan	YZC277	MH237726
Solms-laubachia zhongdianensis J. P. Yue, Al-Shehbaz & H. Sun	Shangrila, Yunnan	CHY007	MH237727
Strigosella africana (L.) Botsch.	Altay, Xinjiang	YC-XZ031	MH237728
	Yecheng, Xinjiang	YC-XZ117	MH237729

L. (Buniadeae), *Clausia aprica* (Stephan ex Willd.) Korn.-Trotzky (Dontostemoneae), and *Hesperis sibirica* L. and *H. isatidea* (Boiss.) D. A. German & Al-Shehbaz (Hesperideae), were used as outgroups.

DNA extraction, PCR amplification, and sequencing

Total genomic DNA was extracted from silica gel-dried leaf materials using the Plant Genomic DNA Kit (Tiangen Biotech, Beijing, China) following the manufacturer's protocol. The ITS region was amplified with the primers ITS-18F as modified by Mummenhoff et al. (1997) and ITS4 (White et al. 1990). All polymerase chain reactions (PCR) were performed in a 25 µL volume consisting of 1–2µL sample DNA (approx. 1–10 ng), 12.5µL Premix Taq^{TM} (Takara Biomedical Technology, Beijing, China), 1µL of 10 µM stock of each primer, adjusted to 25 µL with ddH_2O. The PCR protocol of the ITS region involved a hot start with 4 min at 94 °C, and 30–32 cycles of amplification (1 min denaturing at 94 °C, 45–60 s annealing at 52–53 °C, 60–80 s extension at 72 °C), and a final elongation step for 10 min at 72 °C. The sequencing primers are the same as amplified primers.

Phylogenetic analyses

Original chromatograms were evaluated with Sequencher 4.1.4 (Gene Codes Corporation 2002) for base confirmation and contiguous sequences editing, and sequences were aligned with MAFFT v7.311 (Katoh et al. 2002, Katoh and Standley 2013) and were manually adjusted with MEGA 7.0.14 (Kumar et al. 2016). The aligned sequences were analyzed with maximum parsimony (MP) and Bayesian inference (BI).

Maximum parsimony analysis were performed by PAUP* 4.0a161 (Swofford 2018) with all characters unweighted. Heuristic parsimony searches were conducted with 100 replicates of random addition of sequences to search for multiple islands of most parsimonious trees (Maddison 1991). Bootstrap analyses (BS) (Felsenstein 1985) to assess the relative support for monophyletic groups were calculated from 1000 replicates using a heuristic search with ten random-addition subreplicates, TBR branch swapping and MULPARS in effect. For Bayesian inference analysis, jModeltest v2.1.7 (Darriba et al. 2012) was used to select the best-fitted model of nucleotide substitution based on the Akaike information criterion (AICc), and the SYM+I+G model was selected for the ITS dataset. Bayesian inference based on the Markov chain Monte Carlo methods (Yang and Rannala 1997) was performed using MrBayes v3.2.6 (Ronquist et al. 2012), four simultaneous Monte Carlo Markov chains (MCMCs) were run for five million generations, and one tree sampled every 1000 generations. The first 1250 trees (25% of total trees) were discarded as burn-in. The remaining trees were summarized in a 50% majority-rule consensus tree, and the posterior probabilities (PP) were calculated.

Results

The aligned ITS dataset comprised 88 species (100 accessions) with 609 characters, of which 256 were variable and 187 (30.7%) were parsimony-informative.

The resolution of MP analysis was relatively weaker than the outcome of BI analysis. Only the topologies of Bayesian phylogenetic analysis were shown (Figure 1). The result clearly showed that all 28 genera of Euclidieae formed a moderately to strongly supported clade (PP / BS = 0.99 / 61; Figure 1). *Dilophia* Thomson, *Lachnoloma*, and *Spryginia* Popov formed the early branching lineage of the tribe in BI analysis (Figure 1). Five species of *Rhammatophyllum*, three of *Sisymbriopsis*, and 23 of *Solms-laubachia* formed a well-supported subclade within Euclidieae (PP / BS = 0.95 / 68; Figure 1), and then clustered with *Anzhengxia* Al-Shehbaz & D.A.German and *Pycnoplinthus* O.E.Schulz (PP / BS = 0.99 / 55; Figure 1).

All *Braya* species formed a subclade (PP / BS = 1 / 89; Figure 1) sister to *Shangrilaia* Al-Shehbaz, J. P. Yue & H. Sun, *Metashangrilaia* Al-Shehbaz & D. A. German, *Lepidostemon* Hook. f. & Thomson, and *Pycnoplinthopsis* Jafri (Figure 1). Species of *Neotorularia* Hedge & J. Léonard, *Streptoloma* Bunge, *Octoceras* Bunge, *Tetracme* Bunge, *Cymatocarpus* O. E. Schulz, *Cryptospora* Kar. & Kir., *Atelanthera* Hook. f. & Thomson, and *Catenulina* Soják clustered into one clade in BI analysis (PP = 1; Figure 1), whereas both *Neotorularia* and *Tetracme* were found to be polyphyletic. As for the four species of *Neotorularia*, *N. contortuplicata* (Stephan ex Willd.) Hedge & J. Léonard and *N. torulosa* (Desf.) Hedge & J. Léonard formed one clade (PP / BS = 1 / 99; Figure 1),

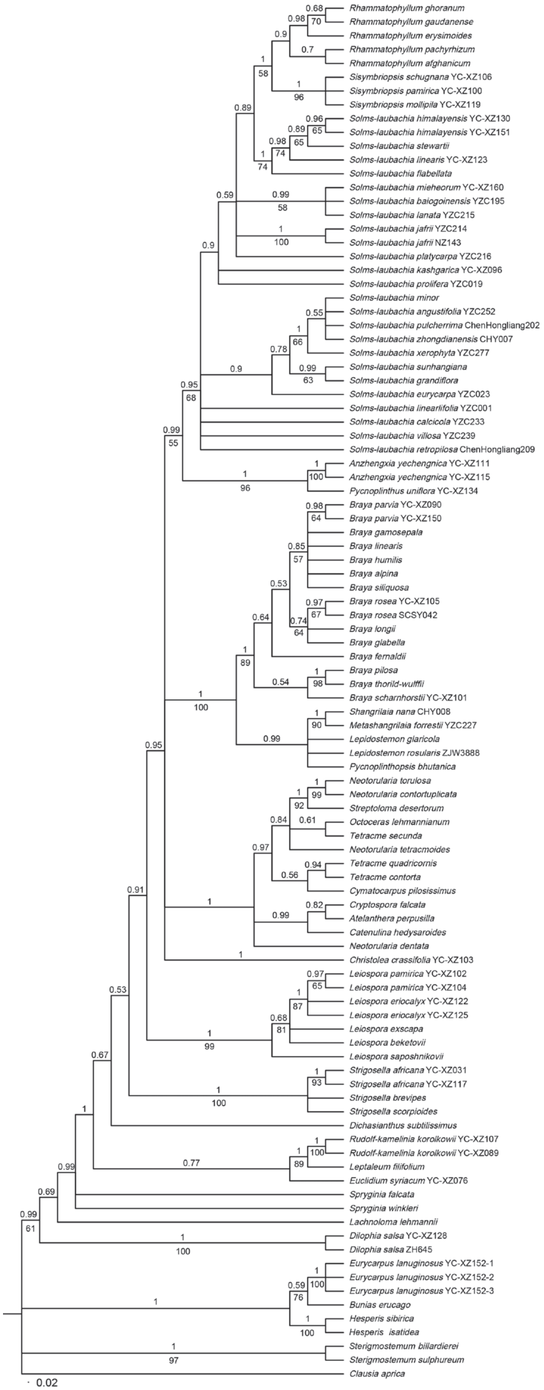

Figure 1. Phylogenetic tree resulting from Bayesian analysis of the ITS sequences of the 88 Brassicaceae species, of which 28 genera and 82 species in Euclidieae. Posterior probabilities are indicated above branches. Bootstrap support values (>50%) are noted below branches.

while *N. tetracmoides* (Boiss. & Hausskn.) Hedge & J. Léonard and *N. dentata* (Freyn & Sint.) Hedge & J. Léonard each formed a solitary branch. The three species of *Tetracme* formed two independent subclades in BI analysis, one of which comprised of *T. quadricornis* (Stephan ex Willd.) Bunge and *T. contorta* Boiss. (PP = 0.94; Figure 1), and the other consisted of *T. secunda* Boiss. and *Octoceras lehmannianum* Bunge (PP = 0.61; Figure 1).

In addition to the above clades, species of *Leiospora* (C. A. Mey.) Dvořák and *Strigosella* formed two well supported clades, suggesting that both are monophyletic. However, *Solms-laubachia lanuginosa* (Hook. f. & Thomson) D. A. German & Al-Shehbaz (formerly *Eurycarpus lanuginosus* (Hook. f. & Thomson) Botsch.) did not fall within the *Solms-laubachia-Rhammatophyllum-Sisymbriopsis* clade. Instead, three accessions of this species formed a clade with outgroup taxa *Bunias erucago* (PP / BS = 0.59 / 76; Figure 1), indicating that *S. lanuginosa* is neither a member of genus *Solms-laubachia* nor of the tribe Euclidieae.

Discussion

Our results suggested that *Solms-laubachia* s.l. is not monophyletic, within which both *Rhammatophyllum* and *Sisymbriopsis* are embedded. Besides, *S. lanuginosa* fell outside of the clade. The closeness of *Solms-laubachia*, *Rhammatophyllum*, and *Sisymbriopsis* was revealed in previous studies (e.g., Belstein et al. 2006, 2008, Warwick et al. 2007, German et al. 2009). However, these studies only sampled one or two representative species of each genus and therefore did not reach a convincible conclusion on their generic status. By contrast, this study sampled 23 of 33 species of *Solms-laubachia*, five of seven of *Rhammatophyllum*, and three of four of *Sisymbriopsis*, representing thus far the most complete taxa sampling on these three genera.

Solms-laubachia had recently been subjected to a series of studies, including taxonomy (Lan and Zhou 1981, Al-Shehbaz and Yang 2000), cytology (Yue et al. 2003, 2004), molecular phylogeny (Yue et al. 2006, 2008), and biogeography (Yue et al. 2009). As traditionally circumscribed, this genus contained nine to thirteen species distributed from Southwest China to East-Himalayan. However, molecular phylogenetic studies demonstrated that *Desideria* Pamp. and *Phaeonychium* O. E. Schulz should be included in it, and that led to greatly expanding of the morphological and geographic boundaries of *Solms-laubachia*. For example, previously delimited *Solms-laubachia* species have entire, pinnately veined leaves and latiseptate fruit, whereas the expanded *Solms-laubachia* also has palmately veined leaves, and terete fruit. The geographic distribution of *Solms-laubachia* s.l. is also expanded westward into Central Asia.

Rhammatophyllum consists of shrubs or subshrubs with soft malpighiaceous, submalpighiaceous, or rarely subdendritic trichomes, filiform to linear or lanceolate, entire cauline leaves, and dehiscent fruit with torulose valves. Its seven species are distributed from Turkmenistan and W Kazakhstan into W Mongolia (Botschantzev 1987, Al-Shehbaz and Appel 2002, Kamelin 2002, German et al. 2006, Moazzeni et al. 2014).

By contrast, *Sisymbriopsis* includes annual, biennial or perennial herbs primarily with stalked and 1- or 2-forked to dendritic trichomes, pinnately lobed to coarsely dentate or rarely subentire basal and cauline leaves, and linear, flattened and latiseptate fruit with torulose valves and complete septum. Its four species are distributed in Afghanistan, China (Qinghai, Xinjiang, and Xizang), Kyrgyzstan, and Tajikistan (Al-Shehbaz et al. 1999, Al-Shehbaz and German 2016).

Although our results suggest combining *Solms-laubachia*, *Rhammatophyllum*, and *Sisymbriopsis* into one monophyletic genus, merging these three genera into one will make it vastly heterogeneous morphologically (Table 3).The combined genus would be highly variable by encompassing nearly all habit types in the family, nearly all petals colors, and almost all inflorescence types, and would be almost impossible to delimit morphologically. Alternatively, one could keep both *Rhammatophyllum* and *Sisymbriopsis* as separate monophyletic genera (Figure 1), and split *Solms-laubachia* s.l. into several well-delimited smaller genera depending on how different the species cluster together. Because our phylogenetic analyses was based on single ITS sequence fragments, infra-generic relationships can be satisfactorily resolved only by further studies dealing with cpDNA and other single-copy nuclear markers.

As for the outlier *Solms-laubachia lanuginosa*, its three accessions formed a clade clustered with *Bunias erucago* (Buniadeae), *Hesperis sibirica*, and *H. isatidea* (Hesperideae). Because it fell out of *Solms-laubachia* and the remainder of Euclidieae, we suggest restoring its previous status in the genus *Eurycarpus* Botsch. The incongruence between taxonomic treatments based strictly on morphology call for the need to draw generic limits and relationships after conducting adequate molecular phylogenetic analyses. Identifying the tribal position of *Eurycarpus* is beyond the scope of this paper, and it will be conducted in the near future with nuclear and chloroplast sequences data.

The monospecific genus *Metashangrilaia* was established based on *M. forrestii* (W.W.Sm.) Al-Shehbaz & D.A.German, a species used to be put in *Braya*. Previous molecular analyses revealed that it had very distinct ITS sequences and formed a well-supported clade sister to the rest of *Braya* (Warwick et al. 2004). Besides, it showed great morphological divergences from other *Braya* species (Al-Shehbaz et al. 2004, Al-Shehbaz and German 2016). All these led Al-Shehbaz and German (2016) to separate it from *Braya* and accommodate it in the newly established *Metashangrilaia*. This study provides further evidence on a strong sister taxon relationship between *Metashangrilaia* and *Shangrilaia* (Figure 1), supporting the decision by Al-Shehbaz and German (2016).

Our results also suggest that *Neotorularia*, *Tetracme*, and *Lepidostemon* are not monophyletic. Of the four species sampled from *Neotorularia*, the generic type *N. torulosa* clustered with *N. contortuplicata,* and they were sister to *Streptoloma desertorum* Bunge, while *N. tetracmoides* and *N. dentata* each formed an independent clade (Figure 1). The three sampled *Tetracme* formed two separate clades, one of which was *T. contorta* and *T. quadricornis*, whereas the other was *T. secunda* and *Octoceras lehmannianum* (Figure 1). The non-monophyly of both genera is congruent with previous studies (Warwick et al. 2004, 2007).

Table 3. Comparsions on morphological characters of *Solms-laubachia*, *Sisymbriopsis*, *Rhammatophyllum,* and *Eurycarpus*.

	Sisymbriopsis	***Rhammatophyllum***	***Solms-laubachia***	***Eurycarpus***
Habit	annual, biennial, or perennial herbs	shrubs or subshrubs	perennial herbs	perennial herbs
Trichomes	simple and/or stalked forked or dendritic	softly malpighiaceous, submalpighiaceou, rarely subdendritic	absent or simple, rarely short-stalked, 2-rayed	simple mixed with stalked 1- to 3-forked ones
Basal leaves	rosulate or not	not rosulate	rosulate	rosulate
Leaf margin	dentate, rarely subentire	entire	entire or 3- to 9(to 11)-toothed	entire
Leaf venation	pinnate	pinnate	pinnate or palmate	pinnate
Cauline leaves	present	present	present or absent	absent
Flower	in racemes, ebracteate or bracteate corymbose	in racemes, ebracteate corymbose	solitary or in racemes, ebracteate or bracteate corymbose	in racemes, ebracteate corymbose
Sepals	equal, nonsaccate	subequal, nonsaccate	equal, nonsaccate	equal, nonsaccate
Petal colour	white or lavender	yellow, creamy white, or rarely purple	purple, blue, pink, or rarely white	purple
Anther apex	obtuse or apiculate	apiculate	obtuse	obtuse
Anther shape	ovate or oblong	oblong	oblong-linear to ovate	oblong
Median nectaries	present	absent or present	absent or present	present
Fruit shape	dehiscent silicles, linear, flattened and latiseptate	dehiscent siliques, linear, latiseptate	dehiscent silique or silicle, linear, oblong, ovate, lanceolate, or ellipsoid, latiseptate or terete	dehiscent silicles, oblong, elliptic, ovate-oblong, or ovate-lanceolate, strongly latiseptate
Fruit valve	valves papery, prominently veined, glabrous or pubescent, torulose	valves papery, prominently veined, pubescent, torulose	valves papery, reticulate veined, glabrous or pubescent, smooth or torulose	valves obscurely veined, glabrous, smooth
Septum	complete	complete	complete or rarely perforated or reduced to a rim	complete or reduced to a rim
Style	obsolete	obsolete or distinct	obsolete or distinct	obsolete
Stigma	capitate, entire or 2-lobed, lobes not decurrent	capitate, entire or 2-lobed, lobes not decurrent	capitate, entire or 2-lobed, lobes not decurrent	capitate, entire
Seed	uniseriate, wingless or rarely distally with a small wing	uniseriate, winged, margined, or wingless	uniseriate or biseriate, wingless, seed coat reticulate, rugose, or papillate, not mucilaginous when wetted	biseriate, wingless, seed coat minutely reticulate, not mucilaginous when wetted
Cotyledons	obliquely accumbent	accumbent or rarely incumbent	accumbent	incumbent or accumbent

Finally, *Lepidostemon* used to be a monospecific genus, the type species is *L. pedunculosus* Hook. f. & Thomson. It was expanded by Al-Shehbaz (2000, 2002), to include six species endemic to the Mid-western Himalaya (Al-Shehbaz 2015). The ITS sequence of *L. glaricola* (H. Hara) Al-Shehbaz (Couvreur et al. 2010) did not fall with our newly sequenced *L. rosularis* (K. C. Kuan & Z. X. An) Al-Shehbaz in one clade. However, due to limited data and low solution of ITS sequences, further studies with extensive sampling and more molecular markers are needed to clarify the taxonomic circumscription of the non-monophyletic genera – *Neotorularia*, *Tetracme*, and *Lepidostemon*.

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Appendix I

Taxa and accession numbers downloaded from GenBank for the ITS sequences used in the study.

Outgroups: Tribe Anchonieae: *Sterigmostemum billardierei* (DC.) D. A. German (DQ357513), *S. sulphureum* (Banks & Sol.) Bornm. (KJ663764). Tribe Buniadeae: *Bunias erucago* L. (GQ497885). Tribe Dontostemoneae: *Clausia aprica* (Stephan ex Willd.) Korn.-Trotzky (LK021257). Tribe Hesperideae: *Hesperis isatidea* (Boiss.) D. A. German & Al-Shehbaz (GQ497882); *Hesperis sibirica* L. (DQ357549). **Ingroups**: Tribe Euclidieae: *Atelanthera perpusilla* Hook. f. & Thomson (FM164518, FM164519); *Braya alpina* Sternb. & Hoppe (AY353096), *B. fernaldii* Abbe (AY353152), *B. gamosepala* (Hedge) Al-Shehbaz & S. I. Warwick (AF137565), *B. glabella* Richardson (AF137578), *B. humilis* (C. A. Mey.) B. L. Rob. (AY237325), *B. linearis* Rouy (AY353102), *B. longii* Fernald (AY237310), *B. pilosa* Hook. (KT727927), *B. siliquosa* Bunge (AY353105), *B. thorild-wulffii* Ostenf. (AY353098); *Catenulina hedysaroides* (Botsch.) Soják (GQ424607); *Cryptospora falcata* Kar. & Kir. (DQ357532); *Cymatocarpus pilosissimus* (Trautv.) O. E. Schulz (GQ497858); *Dichasianthus subtilissimus* (Popov) Ovcz. & Junussov (AY353169); *Lachnoloma lehmannii* Bunge (GQ497889); *Leiospora beketovii* (Krasn.) D.A. German & Al-Shehbaz (FN821579); *L. exscapa* (Ledeb.) F. Dvořák (FN821615), *L. saposhnikovii* (A.N. Vassiljeva) D.A. German & Al-Shehbaz (FN821554); *Lepidostemon glaricola* (H.Hara) Al-Shehbaz (GQ424542); *Leptaleum filifolium* (Willd.) DC. (KJ623485); *Neotorularia contortuplicata* (Stephan ex Willd.) Hedge & J. Léonard (AY353165), *N. dentata* (Freyn & Sint.) Hedge & J. Léonard (AY353160), *N. tetracmoides* (Boiss. & Hausskn.) Hedge & J. Léonard (AY353162), *N. torulosa* (Desf.) Hedge & J. Léonard (AY353167); *Octoceras lehmannianum* Bunge (GQ424609); *Pycnoplinthopsis bhutanica* (H. Hara) Jafri (GQ497878); *Rhammatophyllum afghanicum* (Rech. f.) Al-Shehbaz & O. Appel (DQ357583), *R. erysimoides* (Kar. & Kir.) Al-Shehbaz & O. Appel (DQ357587), *R. gaudanense* (Litv.) Al-Shehbaz & O. Appel (DQ357585), *R. ghoranum* (Rech. f.) Al-Shehbaz & O. Appel (DQ357586), *R. pachyrhizum* (Kar. & Kir.) O. E. Schulz (DQ357588); *Solms-laubachia flabellata* (Regel) J. P. Yue, Al-Shehbaz & H. Sun (GQ497886), *S. grandiflora* J.P. Yue, Al-Shehbaz & H. Sun (DQ523419), *S. minor* Hand.-Mazz. (DQ523418), *S. stewartii* (T.Anderson) J. P. Yue, Al-Shehbaz & H. Sun (FN821609), *S. sunhangiana* J.P. Yue & Al-Shehbaz (EU186027); *Sprygina falcata* Botsch (FN821518), *S. winkleri* (Regel) Popov (GQ424563); *Streptoloma desertorum* Bunge (FM164618, FM164619); *Strigosella brevipes* (Bunge) Botsch. (DQ357558), *S. scorpioides* (Bunge) Botsch. (KJ623536); *Tetracme contorta* Boiss. (DQ357600), *T. quadricornis* (Stephan ex Willd.) Bunge (DQ357602), *T. secunda* Boiss. (DQ357604).

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RESEARCH ARTICLE

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Poa laegaardiana, a new species from Ecuador (Poaceae, Pooideae, Poeae, Poinae)

Paul M. Peterson[1], Robert J. Soreng[1]

[1] *Department of Botany MRC-166, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013-7012, USA*

Corresponding author: *Paul M. Peterson* (peterson@si.edu)

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Abstract

Poa laegaardiana **sp. nov.**, is described and illustrated. The new species was found growing on sandy, volcanic soil in *Festuca*-*Calamagrostis* dominated grasslands southwest of Ambato and 2.2 km from Fecundo Vela in Provincia de Bolivar. The new species is morphologically similar to *Poa gigantea* but differs in having glumes 3/4 to 7/8 as long as the adjacent lemmas, a callus with a sparse, short, dorsal tuft of woolly hairs, culms 50–72 cm tall and spikelets 4.1–4.8 mm long. In addition, we include a key to the narrow-spikelike panicled species of *Poa* in Ecuador.

Resumen

Se describe e ilustra una nueva especie, *Poa laegaardiana* **sp. nov.** La especie se encontró creciendo en suelo arenoso y volcánico en pastizales dominados por *Festuca*-*Calamagrostis* al suroeste de Ambato y a 2.2 km de Fecundo Vela en la Provincia de Bolívar. La nueva especie es morfológicamente similar a *Poa gigantea*, pero se distinque por glumas ¾ a 7/8 tan larga como los lemmas adyacentes, un callo con un mechón escaso, corto, dorsal de pelos lanosos, culmos de 50–72 cm de altura, y espiguillas 4.1–4.8 mm de largo. Además, incluimos una clave para las especies de *Poa* con panículas espiciformes de Ecuador.

Keywords

Ecuador, *Poa*, Poaceae, taxonomy

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Introduction

Poa L., one of the two largest genera of grasses, is distributed in temperate regions of both hemispheres and in mountainous regions of the tropics (Soreng et al. 2017). Hitchcock (1927) in his treatment of the grasses of Ecuador, Peru and Bolivia reported eight species of *Poa* occurring in Ecuador. Hjorth (1991) prepared descriptions and a key to 11 species of *Poa* in Ecuador. Jørgensen and León-Yánez (1999) listed 14 species of *Poa* in Ecuador. Of names not in synonymy in the latter checklist, we consider *Poa kunthii* Lindm., nom. nov. for *Poa remota* Kunth, non Forselles, a synonym of *Lolium arundinaceum* (Schreb.) Darbysh.; *Poa pinchachensis* Hack., nom. nov. for *Poa trachyphylla* Hack., non Pilg., a synonym of *Poa trivialis* L. and; *Poa paramoensis* Laegaard a synonym of *Poa huancavelicae* Tovar (Sylvester et al. 2016). In addition, *Aphanelytrum procumbens* Hack. is now treated as *Poa hitchcockiana* Soreng & P.M. Peterson (Peterson and Soreng 2016). This brings the total to 16 known species of *Poa* in Ecuador including our new one.

The subtribe Poinae Dumort. is a large assemblage of 550 species represented by a single, monophyletic genus, *Poa* (Gillespie et al. 2007, 2008; Soreng 1990; Soreng et al. 2017). Species within *Poa* are morphologically highly variable and are characterised by having monoclinous or diclinous flowers, flag leaf sheath margins fused 1/15–3/4 (or more) from the base, leaf blades usually with an adaxial groove on each side of the midvein, ligules hyaline to sub-chartaceous, paniclulate inflorescences, spikelets that are usually laterally compressed with 2–6 (rarely 1 or more than 6) florets that disarticulate individually above the glumes, keeled glumes usually with 1–3 veins and usually shorter than the lowest lemma, callus glabrous or webbed with soft woolly hairs (rarely a crown of hairs), lemmas 3–5(–11)-veined, usually keeled (apex rarely with a brief awn), 2 lodicules, each with a lateral lobe, glabrous ovaries, caryopses elliptical to fusiform, short hilum, endosperm hard with lipid and a base chromosome number of $x = 7$ (Soreng 2007; Soreng and Peterson 2012; Zhu et al. 2006). Based on molecular phylogenetic studies, *Poa* has been divided into five subgenera: *Sylvestres* (V.L. Marsh ex Soreng) Soreng & L.J. Gillespie, *Ochlopoa* (Asch. & Graebn.) Hyl., *Pseudopoa* (K. Koch) Stapf, *Stenopoa* (Dumort.) Soreng & L.J. Gillespie and *Poa*, corresponding to the five major clades (Gillespie et al. 2007, 2008; Giussani et al. 2016; Soreng et al. 2010).

While reviewing Ecuadorian specimens of *Poa*, RJS found an interesting undetermined specimen collected in 1990 by PMP and Carol R. Annable (*Peterson 8997 & Annable*) from the Provincia de Bolivar southwest of Ambato and 2.2 km from Fecundo Vela. The specimen has unique morphological characters but superficially resembles *Poa gigantea* (Tovar) Refulio, known only from Peru and *P. subspicata* (J. Presl) Kunth, known from Columbia, Ecuador, Peru and Venezuela. We describe it as a new species of *Poa* and, to aid in identification, include a key to all narrow and spikelike-panicled species of *Poa* in Ecuador.

Taxonomy

Poa laegaardiana **Soreng & P.M. Peterson, sp. nov.**
urn:lsid:ipni.org:names:60476587-2
Fig. 1A–J

Type. Ecuador. Province de Bolivar, 66.5 km SW of Ambato on hwy to Guaranda and 2.2 km along road to Facundo Vela, [est. 1.516022 S, 79.007192 W], 4300 m a.s.l., growing on sandy, volcanic soil in *Festuca*-*Calamagrostis* [s.l.] grassland, 3 May 1990, *P.M. Peterson 8997 & C.R. Annable* (holotype: US-3244349!; isotypes: AAU!, MO-3853338!, QCA!).

Diagnosis. Differing from *Poa gigantea* (Tovar) Refulio in having glumes 3/4 to 7/8 as long as the adjacent lemmas (versus glumes about as long or longer than the adjacent lemma), a callus with a sparse, short, dorsal tuft of woolly hairs (versus no web), culms 50–72 cm tall (versus 22–58 cm tall) and spikelets 4.1–4.8 mm long (versus 5–5.5 mm long).

Description. Gynomonoecious. **Perennials**, densely tufted, without lateral tending shoots or with infrequent short lateral tending shoots, greyish-green, with anthocyanic tinges; tillers extravaginal, erect; **culms** 50–72 cm tall, erect, culm nodes and internodes, terete, smooth, glabrous, 0 nodes exposed, highest node in lower 1/10 of culm. **Leaves** concentrated at base; **sheaths** 14–30 cm long, laterally compressed, slightly keeled, smooth, glabrous, proximal sheaths chartaceous, strongly overlapping at base, butt sheaths papery, smooth, glabrous and inconspicuously shredding with age; **uppermost culm sheath** to 30 cm long, margins fused ca. 10% their length, ca. 3–4× longer than their blade; **throats and collars**, smooth, glabrous; **ligules** to 3.5–6.6 mm long, of sterile shoots to 3.5 mm long, membranous, abaxially scaberulous, margins decurrent, apicies acute, apex of distal-most sometimes fimbriate; **blades** to 22 cm long, 1.5--3 mm wide (expanded), uppermost to 8 cm long, firm, stiff, erect, tightly folded to involute, keeled, abaxially smooth or obscurely scaberulous along the veins, adaxially densely scabrous, mostly along the veins on a nearly level surface (aside from the single channels flanking the central vein), apex narrowly prow tipped, acuminate, stiff; **sterile shoot blades** like those of the culm, crowded, to 22 cm long above the initial cataphylls if any. **Panicles** 7.6–11.5 cm long, 0.6–1.2 cm wide, contracted, spiciform, erect, narrow, interrupted below with areas along the rachis with no branches, with 50–60 spikelets; **proximal internodes** 2.5–3.5 cm long, smooth, axis with mostly 2 branches at lower nodes; **branches** 2.5–3.5 cm long, with up to 12 spikelets crowded in the distal 2/3, appressed (ascending at anthesis), terete to slightly angled, short scabrous mainly along the angles; **lateral pedicels** mostly 0.5–1 mm long. **Spikelets** 4.1–4.8 mm long, 2–2.5× longer than wide, lanceolate, laterally compressed, not bulbiferous, violaceous in part at maturity, florets 2, the upper slightly reduced; **rachilla** internode above the proximal

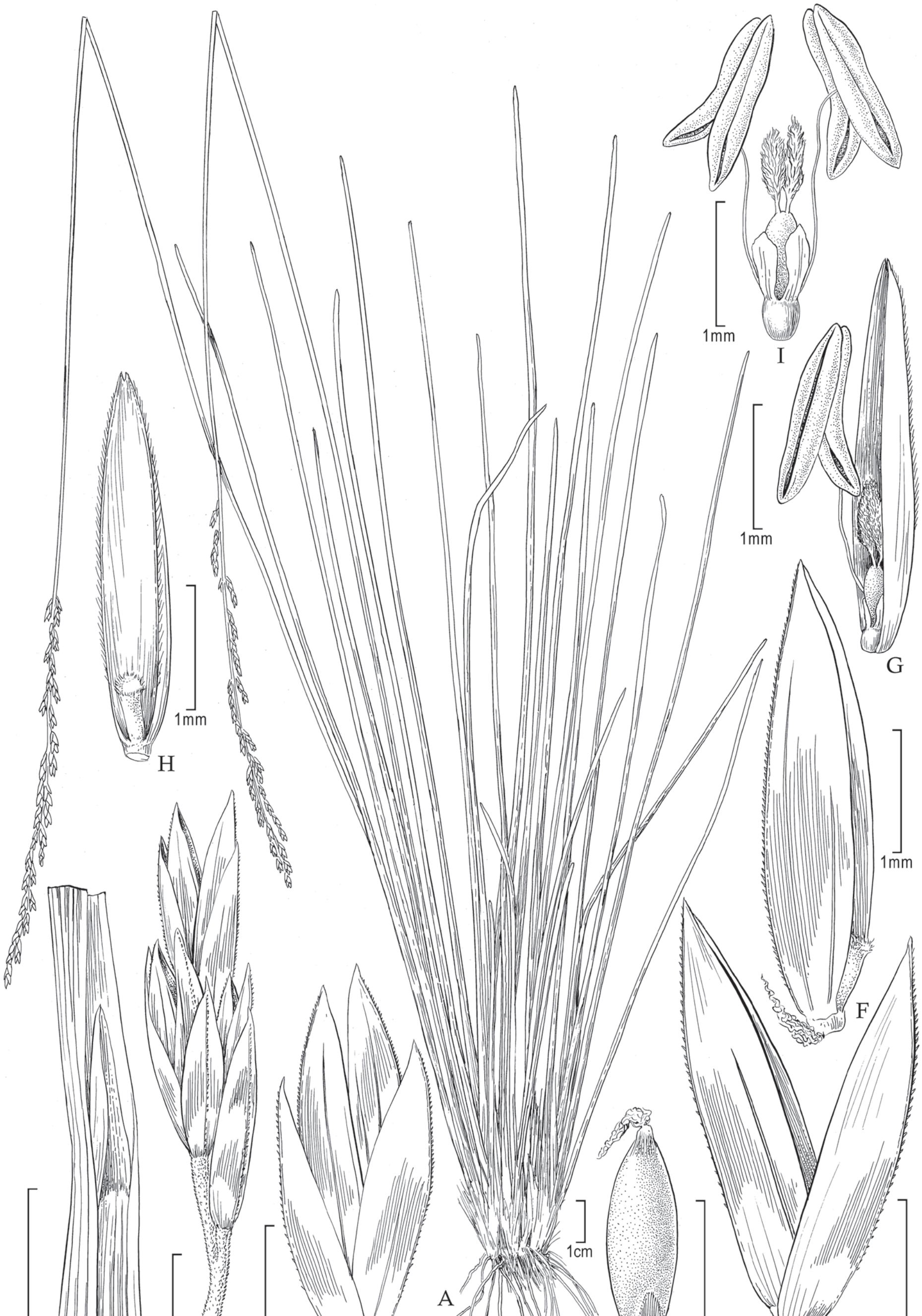

Figure 1. *Poa laegaardiana*: **A** Habit **B** Sheath, ligule and blade **C** Panicle branch **D** Spikelet **E** Glumes **F** Floret **G** Palea enclosing lodicules, ovary and stamen **H** Palea, ventral view **I** Lodicules, ovary and stamens **J** Caryopsis. Drawn from the holotype collection (*Peterson 8997 & Annable*).

floret 0.5 mm long, terete, scabrous to hirtellous; **glumes** 3/4 to 7/8 as long as the adjacent lemma, subequal, lanceolate to oblong, keels smooth or distally obscurely scaberulous, margins distally smooth, apex acute; **lower glumes** 3–3.5 mm long, 1 (3)-veined; **upper glumes** 3.4–3.8 mm long, 3-veined; **calluses** webbed, with a sparse, short, dorsal tuft of woolly hairs to about 1 mm long; **lemmas** 3.5–4.2 mm long, 5-veined, lanceolate in side-view, violaceous in part, strongly laterally compressed, distinctly keeled, glabrous throughout, keel distally scaberulous or nearly smooth, sides smooth (appearing densely granular due to abundant short-cells), intermediate veins obscure to distinct, margins inrolled below at maturity, narrowly scareous above, edges smooth, apicies acute; **paleas** 3.3–3.7 mm long, a little shorter than the lemma, texture like the lemma, 2-keeled, the keels distally scaberulous, glabrous between the keels. **Flowers** pistillate over perfect within the spikelets; **lodicules** 0.25 mm long, 2, lobed; **stamens** 3, **anthers** 1.4–1.6 mm long, light yellow, vestigial in upper floret less than 0.1 mm long; **ovary** glabrous; **caryopses** 1.6–2 mm long, elliptical in side-view, brown, translucent, sulcus broad and shallow, hilum ca. 0.15 mm long, round, grain loosely adherent to the palea.

Distribution. The species is known only from the type collection in Provincia Bolivar, Ecuador.

Conservation status. The species is apparently rare. Google Earth view [26 Mar 2018] of the pass location where the new species was collected in 1990 indicates the area is now covered by small farms.

Etymology. The specific epithet honors Simon Laegaard (1933–), a renowned Danish Botanist, who has made extensive collections in Ecuador, Greenland and South America.

Discussion. There are a number gynomonoecious species of *Poa* occurring in northern South America, Central America and central Mexico but all have loose, open panicles, except the new species and species of *Poa* sect. *Dissanthelium* (Trin.) Refulio (Refulio-Rodriguez et al. 2012). Most of these open-panicled species of *Poa* supersect. *Homalopoa* (Dumort.) Soreng & L.J. Gillespie and the new species have glabrous lemmas and a web on the callus with a perfect lower floret and a pistillate upper floret. The new species appears to belong within *Poa* subg. *Poa* supersect. *Homalopoa* (Giussani et al. 2016). *Poa* sect. *Homalopoa* s.str. may be restricted to Eurasia and North America while most species of the New World are placed in sect. *Homalopoa* s.l. (Giussani et al. 2016; Soreng et al. 2003).

Poa gigantea (*Poa* sect. *Dissanthelium*) is morphologically similar to our new species but differs in having glumes longer than or equalling the adjacent lemma, an unwebbed callus, shorter culms 22–58 cm tall and larger spikelets 5–5.5 mm long (Tovar Serpa 1985; Refulio-Rodriguez 2012). Other Ecuadorian species of *Poa* with narrow, spikelike panicles includes: *P. chamaeclinos* Pilg., *P. scaberula* Hook. f. and *P. subspicata*. We provide a key to separate these from the new species below (Hjorth 1991; Soreng and Peterson 2012).

Key to the narrow, spikelike-panicled species of *Poa* in Ecuador

1 Panicles 0.8–1.5 cm long; culms 1–3.5 (–5) cm tall; glumes obovate to subflabellate; callus glabrous .... ***P. chamaeclinos***

– Panicles 2.5–18(–20) cm long; culms (5–) 8–75 cm tall; glumes lanceolate to oblong; callus with a web of woolly hairs **2**

2 Spikelets (2.5–) 3–4 mm long; anthers 0.3–0.7 mm long; short-lived perennials .... ***P. scaberula***

– Spikelets (3.5–) 4–6.5 mm long; anthers 0.5–1.6 mm long; long-lived perennials **3**

3 Glumes 3/4 to 7/8 as long as the adjacent lemma; anthers 1.4–1.6 mm long; spikelets with 2 florets; lemma glabrous .... ***P. laegaardiana***

– Glumes 1/2 to 3/4 as long as the adjacent lemma; anthers 0.5–1.2 mm long; spikelets with 3, sometimes 4 florets; lemma keels and marginal veins sparely to densely sericeous to villous basally to near apex or infrequently glabrous throughout .... ***P. subspicata***

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RESEARCH ARTICLE

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Sindora stipitata (Detarioideae, Leguminosae), a new species from Thailand

Wilawan Promprom[1], Wannachai Chatan[1], Peerapol Saisaard[2]

1 *Department of Biology, Faculty of Science, Mahasarakham University, Kantharawichai District, Maha Sarakham Province, 44150, Thailand* **2** *Number 57, Village No. 3, Thung Kula Subdistrict, Tha Tum district, Surin Province, Thailand*

Corresponding author: *Wannachai Chatan* (wannachaichatan@gmail.com)

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Abstract

Sindora stipitata, a new species in the subfamily Detarioideae (Leguminosae), collected from Nakhon Phanom Province, Thailand, is described and illustrated. The new species is morphologically similar to *S. leiocarpa* but differs in its smaller stature (3–5 m high), 6-foliolate paripinnate leaves, falcate persistent stipules, presence of a petal auricle, absence of a petal claw, stipitate ovary and capitate stigma. A key to the Thailand and Malesia species of *Sindora* is provided.

Keywords

Sindora, Fabaceae, Nakhon Phanom Province, plant diversity, Thailand, taxonomy

Introduction

Sindora Miq. is a genus in the tribe Detarieae (Detarioideae: Leguminosae) (McKinder 2005). It consists of 18–20 species distributed in Southeast Asia, one in Africa (Larsen et al. 1984, Lock and Heald 1994, McKinder 2005), two species in the South Asia (Kumar and Sane 2003) and two species in China (Chen et al. 2010). Three species have been identified in Thailand. Of these, *S. siamensis* Teysmann ex Miq. is a very common species of dry deciduous dipterocarp forests and beach forests, especially the type variety (Larsen et al. 1984).

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During floristic surveys in the years 2009 to 2016 in the northeast of Thailand, a specimen of *Sindora* was collected from the Phulangka National Park in Nakhon Phanom Province which, on further investigation, was found to be clearly different from the previously reported species. It closely resembled *S. leiocarpa* Backer ex de Wit from Malesia. This was confirmed after comparing it against the type and description of *S. leiocarpa* and is here described as a new species.

Materials and methods

Morphological characters were studied based on living plants observed during a field trip in the northeast of Thailand in the years 2009 to 2016 and from dried herbarium specimens housed in BKF and K. The studies consulted all relevant taxonomic literature in Thailand and neighbouring countries. Measurements were made using a vernier caliper and were examined under a stereo dissecting microscope. The conservation status of the new species was evaluated based on the guidelines of the International Union for Conservation of Nature (IUCN 2017).

Taxonomy

Sindora stipitata **Chatan & Promprom, sp. nov.**
urn:lsid:ipni.org:names:60476588-2
Figs 1, 2

Diagnosis. *Sindora stipitata* is very similar to *S. leiocarpa* from Malesia, but it is easily distinguished by the following characters: a smaller stature (3-5 m high), 6-foliolate paripinnate leaves, falcate persistent stipules, presence of a petal auricle, absence of a petal claw, stipitate ovary and capitate stigma.

Type. THAILAND. Nakhon Phanom Province: Phu Langka National Park, elevation 250–350 m, 17°59'18.7"N 104°07'50.1"E (Fig. 3), 20 April 2012, *W. Chatan 1231* (Holotype: BKF!; Isotype: K!).

Description. Small tree, 3–5 m high. Stem diameter 3–5 cm. Stipules falcate, 23–25 × 1.0–1.3 mm, coriaceous, glabrous on both surfaces, persistent, venation distinctly reticulate. Leaves 6-foliolate, paripinnate, leaflets opposite; petioles 3.0–5.5 cm long, with sparse minute hairs or glabrescent; rachis 7–11 cm long, with sparse minute hairs or glabrescent. Leaflets rigidly coriaceous, elliptic or ovate or obovate or oblong, 7.5–11.5 × 3.5–5.3 cm; apex obtuse or sometime shallowly emarginate; base obtuse or cuneate, slightly asymmetric, glabrous on both surfaces, sometimes with a few minute hairs on the blade margin; abaxial side dull. Petiolules 3–6 mm long; glabrescent or with sparse minute hairs. Inflorescences paniculate, lax, up to 20 cm long, lateral branches up to 6 cm long, both rachises and lateral braches densely pubescent; bracts and bracteoles ca. 4.5 × 1.5 mm, puberulous; pedicels 11–12 mm long, densely puberulous. Buds

Figure 1. *Sindora stipitata*. **A** habit and habitat **B** branches and inflorescences **C** branch with leaves and stipules **D** branch with fruits. Photographs of the type specimen by W. Chatan.

ca. 15 × 10 mm, elliptic. Pedicel 10–11 mm long, densely puberulous. Hypanthium asymmetrically short and funnel-like, 0.5–1.0 mm long, brownish-yellow. Calyx lobes 4, thick, brownish-yellow, without any spiny outgrowth on the outer surface, densely puberulous outside, appressed hairs inside; the posterior lobe boat-shaped and obovate, 14–20 × 10–11 mm, apices acuminate; the other three lobes narrower, 15–20 × 4–6 mm, narrowly oblong or elliptic, apices narrowly acute. Corolla comprised of a solitary boat–shaped petal, lanceolate or narrowly obovate, thick, 15–17 × 5–6 mm, apices acute or acuminate, bases auriculate, puberulous outside, glabrous inside. Stamens 10, dorsifixed; upper stamen free, staminodal, 10–11 mm long, lower 2/3 of filament length densely puberulous, upper 1/3 of filament length sparsely hairy and glabrous near apex; remaining nine stamens, fertile, joined at the base into a sheath; sheath ca. 8–9 × 4.0–4.5 mm, densely puberulous on both surfaces; the two largest stamens are fertile, free parts of filament ca. 22–25 mm, lower half of the free parts of filament sparsely hairy and the upper half glabrous; anthers 5.5–6.0 × 1.5–1.6 mm, glabrous; other fertile stamens seven, free parts of filament 7–8 mm, lower 1/3 of the free parts densely puberulous, upper 2/3 of the free parts sparsely hairy and glabrous near apex; anthers, 2.5–3.0 × 1.0–1.2 mm, glabrous. Pistils with 5–6 mm stipe length; stipes densely puberulous; ovary asymmetrically elliptic; 7–8 × 4.5–5.0 mm, densely

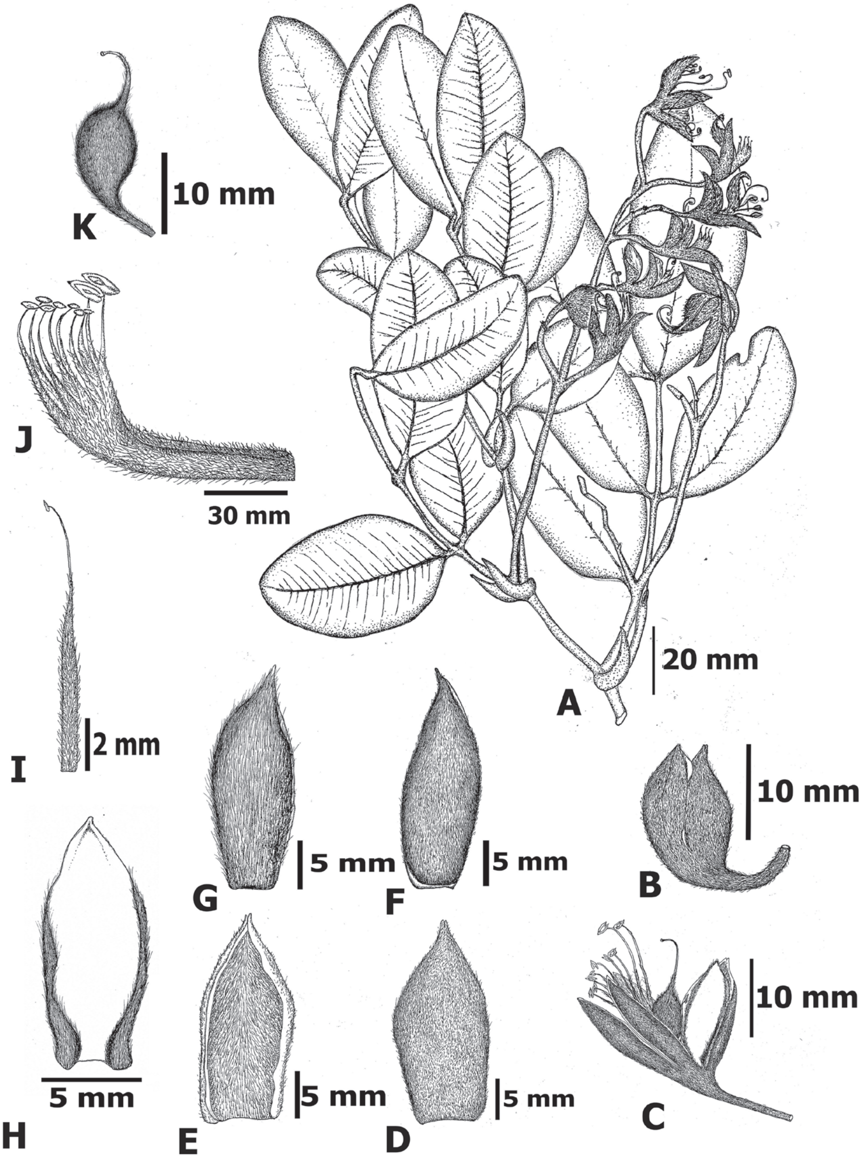

Figure 2. Line drawing of *Sindora stipitata* Chatan & Promprom, sp. nov. **A** a branch with leaves and inflorescence **B** floral bud **C** floret **D** posterior sepal (abaxial side) **E** posterior sepal (adaxial side) **F** one of the remaining narrower sepal (abaxial side) **G** one of the remaining narrower sepal (adaxial side) **H** petal (adaxial side) **I** free staminode **J** fused stamen **K** pistil. Illustration by W. Chatan (based on type specimen).

puberulous, no spiny outgrowth; style 9–11 mm long, densely puberulous on lower parts and sparsely hairy on the anterior side of upper parts; stigma capitate, glabrous. Pods circular or ellipsoid to obovate, 3.3–9.0 × 3.5–5.5 cm diameter, flattened, slightly smooth, unarmed, obscurely veined, with 1.5–5.0 mm long beaks, sparsely hairy on both surfaces, densely appressed hairs on the margin; seeds 1–4.

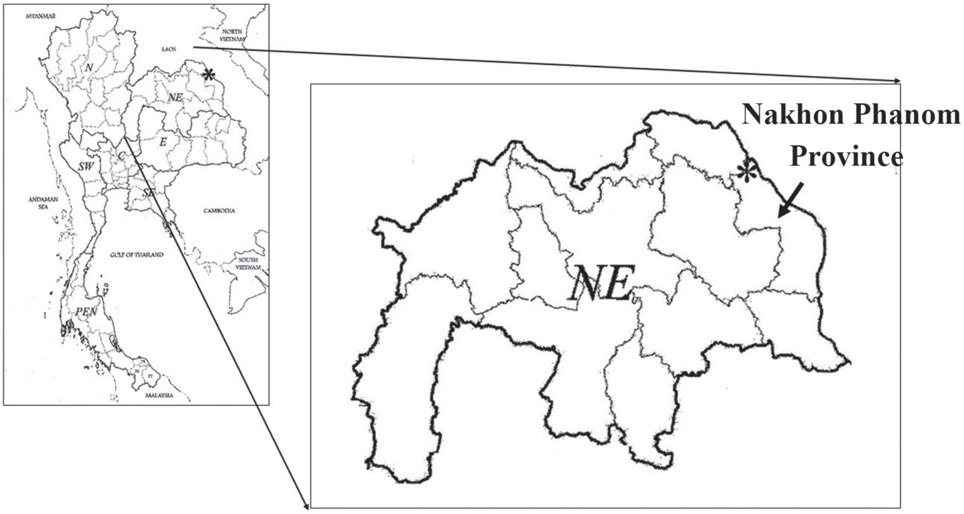

Figure 3. Distribution of *Sindora stipitata* Chatan & Promprom (*) in Phu Langka National Park, Nakhon Phanom Province, Thailand.

Other specimen examined. THAILAND. Nakhon Phanom Province: Phu Langka National Park, 29 June 2013, fruiting, *P. Saisaard 55* (BKF).

Flowering and fruiting. Flowering in March–May and fruiting April–June.

Distribution. The new species is a Thai endemic and is known from only the type locality in the Phulangka National Park, Ban Pheang District, Nakhon Phanom Province, North-eastern Thailand.

Ecology. This new species grows in open areas of dry deciduous forest at an elevation of 250–350 m.

Vernacular name. Ma Kha Tae Nakhon Phanom, Mak Tae.

Etymology. The specific epithet refers to its distinctly long ovary stipe. This character is one of many morphological characters that distinguishes the new species from its closely related species.

Preliminary conservation status. *Sindora stipitata* is known only from the type locality and its estimated extent of occurrence is less than 100 km^2. The number of mature individuals was less than 1,000 and the occupied area is continuing to decline slightly. Therefore, it should be considered as "Critically Endangered" according to the IUCN criteria B1 (IUCN 2017).

Discussion. *Sindora stipitata* is closely related to *S. leiocarpa*, a plant that grows in Sumatra (Jimbi, Palembang and Riau) and Borneo (Sarawak, Brunei, Sabah and Kalimantan) (Hou 2000), but is easily distinguished from the latter by several morphological characters. Details of the differences between *S. stipitata* and *S. leiocarpa* are presented in Table 1.

The new species is also related to *S. coriacea* (Baker) Prain. Both have unarmed sepals, but *S. stipitata* is clearly different from *S. coriacea* by its stature of a small tree (3–5 m high) (vs. a large tree up to 50 m high), its abaxial leaflet surface dull brown

Table 1. Distinguishing features between *S. stipitata* Chatan & Promprom and *S. leiocarpa* de Wit.

Characters	*S. stipitata* sp. nov.	*S. leiocarpa*
1. Habit	Small tree 3–5 m high, 3–5 cm diam.	Large tree, 25–45 m high, 45–80 cm diam.
2. Stipule	Falcate, 23–25 mm long	Lancelate, 3–5 mm long, caducous
3. Leaflet size	7.5–11.5 × 3.5-5.3 cm	2.5–9.5 × 2–5 cm
4. Pedicel length	10–11 mm	1–1.5 mm
5. Sepal size	14–20 × 4-11 mm	2–6 × 2–3.5 mm
6. Petal length	15–17 mm	5–6 mm
7. Petal claw	Absent	Present at about the lower half
8. Petal auricle	Present	Absent
9. Staminal sheath	8–9 mm long (high)	2–3 mm long (high)
10. Free filament part length of united stamens	7–25 mm	ca. 7 mm
11. Anther length of two largest stamens	22–25 mm	2–2.5 mm
12. Anther length of seven smallest fertile stamens	7–8 mm	Up to 0.75 mm
13. Ovary stipe length	5–6 mm	Subsessile or shortly stipitate (ca. 1 mm)
14. Ovary length	7–8 mm	ca. 4.5 mm
15. Stigma	Capitate	Obscure

(vs. shining), the two largest stamen 22–25 mm long (vs. ca. 10 mm long) and anthers 5.5–6 mm long (vs. 2–3 mm long). The new species also clearly differs from *S. laotica* Gagnep., a species that is distributed near the border of Thailand (in Vientiane, Phou Khao Khouay National Biodiversity Conservation Area, Lao) and Vietnam (Larsen, Larsen and Vidal 1980); the two species are different in that there is no spiny outgrowth on the outer surface of the calyx of the new species (vs. calyx spinescent). The following identification key for *Sindora* in Thailand and Malesia is constructed by modification of the key from the Flora Malesiana (Hou 2000).

Key to *Sindora* Species in Thailand and Malesia

1 Leaflets minutely puberulous or pubescent on both surfaces ...... ***S. siamensis***

– Leaflets glabrous on both surfaces or minutely puberulous or pubescent on the lower surface or rarely sparsely puberulous above **2**

2 Leaflets glabrous on both surfaces **3**

– Leaflets only minutely puberulous or pubescent on the lower surface or rarely sparsely puberulous above **8**

3 Apex of leaflet obtuse, rounded, retuse or emarginate **4**

– Apex of leaflets acute to acuminate **6**

4 Calyx lobes densely spinescent .... ***S. supa***

– Calyx lobes smooth, unarmed **5**

5 Petal auricle present, petal claw absent, ovary stipe 5-6 mm long..... ***S. stipitata***

– Petal auricle absent, petal claw present, ovary subsessile or shortly stipitate ... . ***S. leiocarpa***

6 Midrib on the lower surface of the leaflet without a gland near the tip .... ***S. inermis***
– Midrib on the lower surface of the leaflet with a gland near the tip **7**
7 Midrib narrow and shallowly grooved on the upper surface .... ***S. coriacea***
– Midrib slightly prominent on upper surface .... ***S. galedupa***
8 Fertile stamens 9, the uppermost staminode absent .... ***S. javanica***
– Fertile stamens and staminodes 10, the uppermost staminode present **9**
9 Calyx lobes with spinescent outgrowths or warts **10**
– Calyx lobes smooth, unarmed **13**
10 Leaves 3-jugate **11**
– Leaves 4- or 5-jugate **12**
11 Leaflets with apex acute or acuminate .... ***S. sumatrana***
– Leaflets with apex obtuse, the tip slightly notched .... ***S. echinocalyx***
12 Calyx with spiny outgrowth mostly at the upper half .... ***S. wallichii***
– Calyx with loosely, irregularly, minute, spiny outgrowth outside ..... ***S. affinis***
13 Leaflets 3- or 4-jugate. Petals hairy on the longitudinal, central part .... ***S. beccariana***
– Leaflets often 5- or 6-jugate. Petal glabous inside **14**
14 Ovary glabous in the longitudinal, central part .... ***S. bruggemanii***
– Ovary all densely woolly **15**
15 Abaxial side of leaflet usually densely hirsute .... ***S. velutina***
– Abaxial side of leaflet sparsely and minutely puberulous .... ***S. irpicina***

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