

Monograph of *Ceratozamia* (Zamiaceae, Cycadales): an endangered genus

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Abstract

Ceratozamia (Zamiaceae, Cycadales), is a member one of the most endangered seed plant groups. Species of *Ceratozamia* grow from near sea level up to 2,100 meters in Mexico and Mesoamerica. We present a modern taxonomic treatment of *Ceratozamia*, based on fieldwork combined with detailed study of herbarium specimens in and from Mexico and Central America. This new revision is based on incorporation of morphological, molecular and biogeographic data that have been previously published in circumscriptions of species complexes by our group. Detailed morphological descriptions of the 36 species of *Ceratozamia* are provided and relevant characters for the genus are discussed and described. A majority are endemic to Mexico and are concentrated at high elevations in mountainous areas. Synonymies, lectotypifications, etymologies, taxonomic notes, distribution maps, illustrations and detailed species-level comparisons are included, as well as a dichotomous key for identification of all species. Data on distributional ranges and habitats of all species are summarized. *Ceratozamia osbornei* D.W.Stev., Mart.-Domínguez & Nic.-Mor., **sp. nov.** is described from evergreen tropical forests of Belize and we highlight new populations and distributional ranges for *C. subroseophylla* Mart.-Domínguez & Nic.-Mor. and *C. vovidesii* Pérez-Farr. & Iglesias in the Mesoamerican region.

Keywords

Circumscription, cryptic species, cycads, lectotypification, Mesoamerica, Mexico

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Introduction

Ceratozamia Brongn. (Zamiaceae, Cycadales) is characterized by being dioecious with both megasporophylls and microsporophylls having two distinct apical horns. The 36 species of *Ceratozamia* occur in the tropical region of Mega-Mexico II *sensu* Rzedowski (1991), which was established using floristic criteria and includes Mexico, Guatemala, Belize and northern Nicaragua. This genus inhabits in all these countries except Nicaragua and the greatest diversity and endemism in *Ceratozamia* are concentrated in the Sierra Madre Oriental and Southwest regions of Mexico (Nicolalde-Morejón et al. 2014; Martínez-Domínguez et al. 2018a). Species described as *Ceratozamia* from outside this region are properly recognized as other cycad genera (see Excluded names). The genus primarily occurs in oak forest, cloud forest and tropical rain forest on karstic rocks, at an elevational range of 19–2,050 m. *Ceratozamia* is morphologically distinguished from other genera of Zamiaceae by its two parallel adaxial canals along the rachis, entire leaflet margins, and two horns on the distal end of sporophylls in ovulate and pollen strobili.

Ceratozamia is monophyletic with a fossil record dating to the lower Oligocene (Kvaček 2014). Recent phylogenetic analyses of molecular data have supported *Stangeria* (Kunze) Baill. as sister to *Ceratozamia* (Nagalingum et al. 2011) while others have placed *Stangeria* as sister to *Microcycas* (Miq.) A.DC. + *Zamia* L. (Salas-Leiva et al. 2013; Condamine et al. 2015; Liu et al. 2022). The phylogenetic relationships within *Ceratozamia* have been explored using different molecular data sets. González and Vovides (2012) sampled half of the known species and used three genes (*nrITS*, *trnL-F*, *D-SCAR*). More recently, a phylogenetic analysis of this genus that included 28 species and a molecular data set composed of six genes (*nrITS*, *rpoC1*, *matK*, *rbcL*, *psbKII*, *atpF/H*) produced a topology resolved with low support values (Medina-Villarreal et al. 2019); in turn, Martínez-Domínguez et al. (2020) sampled 32 species and only

two genes (*nrITS* and *matK*) but produced a poorly resolved topology. Studies of diversification ages of Cycadales using phylogenomic analyses have included between 70 and 83% of currently accepted *Ceratozamia* species, which recovered better node support (Nagalingum et al. 2011; Condamine et al. 2015; Liu et al. 2022). As a result, species relationships within *Ceratozamia* are becoming clearer and more work will be needed with continued exploration that will undoubtedly lead to new discoveries.

Since the description of the genus by Brongniart (1846), there has been an explosion of interest in this group. Miquel (1848) described five new species using only vegetative characters. *Ceratozamia* poses a taxonomic challenge, however, due to its significant vegetative morphological variation, which was a fact realized by Miquel (1868, 1869a) when he lumped all of his previously described species into *C. mexicana* Brongn. These early taxonomic treatments varied greatly in the number of species recognized within the genus with contrasting findings in each treatment (Regel 1857a, b; Miquel 1861, 1868, 1869a, b; Regel 1876a, b; Thiselton-Dyer 1884; Schuster 1932). Particularly, the ‘Miquel taxonomic names’ have undergone a series of rearrangements in synonymy and recognition of infraspecific categories. Many of these names were clarified by Stevenson and Sabato (1986) when they focused on the typification of all described species in the genus at that time, but did not include a list of invalid names. More recently, a regional taxonomic review focused on the Mexican Sierra Madre Oriental provided new observations that have allowed detailed reassessment and designation of nomenclatural types for some of these names (Martínez-Domínguez et al. 2018a).

Explorations in Mexico during the past three decades have uncovered new species of *Ceratozamia*, thereby, rapidly increasing its known diversity. Nevertheless, the taxonomy of *Ceratozamia* has been mainly characterized by rearrangements of infrageneric taxa, treatments in floristic works and species-level treatments of species complexes (Vovides et al. 1983; Stevenson et al. 1986; Pérez-Farrera et al. 1999; Avendaño et al. 2003; Pérez-Farrera et al. 2009; Vovides et al. 2012; Martínez-Domínguez et al. 2016, 2017c). Recent taxonomic efforts based on analyses of quantitative and qualitative morphological variation, phenology as well as DNA sequences of nuclear, plastid and mitochondrial genomes have produced new insights on the circumscription of species complexes and the most comprehensive taxonomic reviews of *Ceratozamia* to date (Martínez-Domínguez et al. 2016, 2017a, b, 2018a, 2022a). In addition, work focusing on the morphometric variation of vegetative characters and anatomical features have contributed to the clarification of some species (Pérez-Farrera et al. 2014; Vovides et al. 2016; Medina-Villarreal et al. 2019; Gutiérrez-Ortega et al. 2021). These studies have greatly enhanced our understanding of morphological variation, particularly in vegetative characters. Recently, genomic data from 100 nuclear single-copy genes have provided evidence for future directions in the study of the ontogeny of reproductive structures and associated evolutionary processes (Liu et al. 2022).

Currently, quantitative vegetative morphological characters are considered as the most taxonomically informative characters within *Ceratozamia* (Vovides et al. 2004; Pérez-Farrera et al. 2009). Because these types of characters exhibit high intra- and interspecific variation, renewed morphological exploration into reproductive structures

has contributed additional information. This is particularly the case for ovulate strobilus characters, such as the angle between the horns of the megasporophylls, the strobilus apex and the shape of the distal face of megasporophylls (Martínez-Domínguez et al. 2018a). Additional characters are also present in pollen strobili such as the shape of the microsporophylls, the size of the horns, and shape of the fertile and infertile part. However, the use of reproductive characters has been limited by the difficulty of collecting reproductive structures in the field and the lack of these in herbaria. Also, usually ovulate and/or pollen strobili are fragmented as a result of incorrect processing of these structures and damage during handling.

The reproductive phenology of *Ceratozamia* is annual (Stevenson 1981). To date, our knowledge of the phenological phases for ovulate and pollen strobili indicates four phases in each (Martínez-Domínguez et al. 2022a). In both pollen and ovulate strobili the cycle starts with emergence, which is characterized by emergence from among the cataphylls. In pollen strobili, the sequence goes from a closed strobilus, followed by an open strobilus with dehiscence of the sporangia and, finally, senescence. In ovulate strobili, opening cracks develop between sporophylls (indicating receptivity), then a late ovulate strobilus with seeds if pollinated and, finally, disintegration (Martínez-Domínguez et al. 2018b). The receptivity and open pollen phases are critical for pollination and subsequent fertilization of ovules because this genus is pollinated by “pleasing fungus beetles” of family Erotylidae (Norstog and Nicholls 1997).

In this paper, as part of our comprehensive systematic review of the genus, we describe in detail ovulate and pollen strobili, including internal structures and their character states. This was possible by broad sampling in wild populations. We also examine overlooked morphological characters, conduct a nomenclatural review of species, and offer a comprehensive identification key for the genus. Here, we synthesize biogeographic information to account for their distributional range. By default, *Ceratozamia* and all of its species are listed and covered by CITES Appendix 1, but only 21 of the 36 species have had assessments (Calonje et al. 2013–2022; IUCN 2021). Those data are included in species treatments when available. Thus, this monograph is particularly timely and valuable in this era of habitat destruction and illegal collecting. Having a complete taxonomic treatment will allow for appropriate identifications that will lead to informed conservation assessments and actions (Stevenson et al. 2003; Rutherford et al. 2013; Martínez-Domínguez et al. 2021).

Materials and methods

The species circumscriptions for *Ceratozamia* presented here are based on extensive fieldwork, as well as review of specimens from a substantial number of herbaria, including BIGU, BM, BRH, CAS, CH, CHAPA, CHIP, CIB, EAP, ENCB, F, FCME, FTG, GH, HEM, HNT, IBUG, IEB, K, L, LE, LSU, MICH, MEXU, MO, NAP, NY, P, SERO, SLPM, TEFH, U, US, XAL, XALU, UAT, USCG (acronyms according to Thiers 2022), either by examining the specimens physically or electronically through

the Global Plants web portal (<http://plants.jstor.org/>). Because most cycad specimens are sterile, we have taken the opportunity to record the presence of cones when they are present in a collection. We also examined the protologues of all species described and exhaustively searched for type specimens in the registered herbaria. It should be noted, however, that the type specimens for *C. chimalapensis* Pérez-Farr. & Vovides, *C. dominguezii* Pérez-Farr. & Gut.Ortega, *C. sancheziae* Pérez-Farr., Gut.Ortega & Vovides, and *C. zoquorum* Pérez-Farr., Vovides & Iglesias could not be found. Decisions on lectotypes were taken only when we confirmed that there was no evidence of the holotype's existence at the herbaria cited in the protologue. The specimens collected by us were under scientific collection permit SGPA/DGVS/5506 from SEMARNAT (Mexico) and MP-0209-2021 from ICF (Honduras). The geographical coordinates of each specimen were compiled in a database in ArcMap 10.2 (Esri, Redlands, USA) to determine the distribution of *Ceratozamia* using the biogeographic regionalization of the Neotropical region scheme of Morrone et al. (2022). Because species are all CITES listed, the specimens examined only indicate Municipality and elevation.

Criteria to delimit species. The taxonomic treatment presented here is partly based on our previously published work on species complexes, considered from an integrative taxonomy perspective for corroboration or refutation of taxonomic hypotheses and employing the “taxonomic circle” *sensu* DeSalle et al. (2005), in which multiple data sources are analyzed independently for hypotheses testing (Martínez-Domínguez et al. 2016; 2017a, b, 2018a, 2020, 2022a, b). For taxa we have not treated previously, species were recognized by a unique combination of morphological characters evaluated at the population level, considering their biogeographic distribution patterns as an additional source of evidence. We have recognized neither subspecies nor varieties, but have rather described the variability when it was present.

Specialized characters and terminology. The morphological terminology used in the descriptions was standardized according to Moreno (1984) and Harris and Harris (2000). Most *Ceratozamia* reproductive structures and characters have been recently described (Martínez-Domínguez et al. 2020). We evaluated 20 qualitative and 23 quantitative reproductive characters in pollen and ovulate strobili (Figs 1, 2; Table 1; Suppl. material 1). Generally, the terminology for the orientation of ovulate strobilus is given using the terms “decumbent” or “erect”. However, the fertile portion of a strobilus could be inclined at an angle of 180° or prostrate, but not curved. Usually, this condition is derived from weight at maturity. Only the peduncle is curved or erect; the definition for decumbent is reclined with tip ascending, but the peduncle in this genus is not ascending. Here, we have used “pendulous”, which is a more appropriate term and is defined as drooping downward, rather than “decumbent”, as often appears in previous literature.

In microsporophylls, seven qualitative characters have been described: 1) microsporophyll shape, 2) distal face of the microsporophyll, 3) microsporophyll horn type, 4) infertile apical portion shape, 5) fertile portion shape, 6) direction of microsporophyll horns, and 7) angle between the horns of the microsporophylls. The direction of horns was coded in relation to the base of the infertile portion in the microsporophyll.

In addition, six quantitative characters have been evaluated: 1) length of microsporophylls, 2) width of microsporophylls, 3) number of microsporangia per microsporophyll, 4) horn length of microsporophylls, 5) distance between the horns of a microsporophyll, and 6) length of the infertile apical portion of a microsporophyll (Figs 2, 3; see Suppl. material 1 for details).

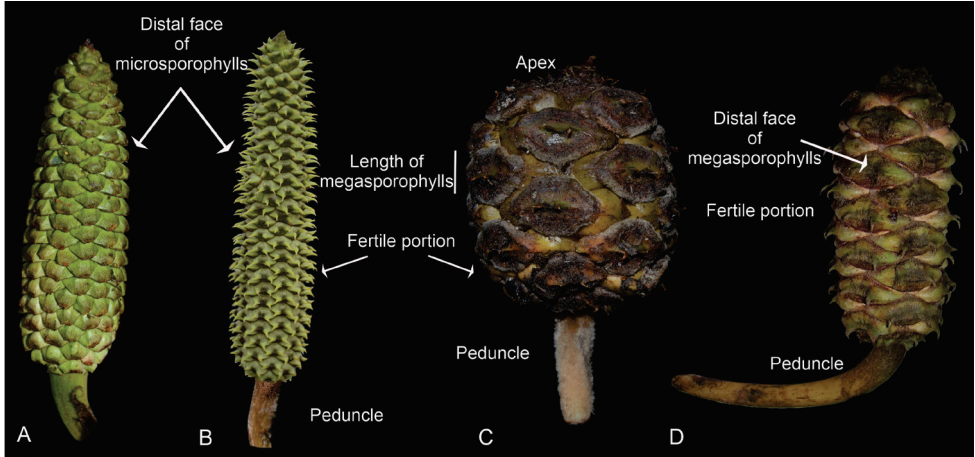


Figure 1. Characters evaluated in reproductive structures **A** pollen strobilus of *Ceratozamia sabatoi* **B** pollen strobilus of *C. santillanii* **C** ovulate strobilus of *C. aurantiaca* **D** ovulate strobilus of *C. zoquorum*.

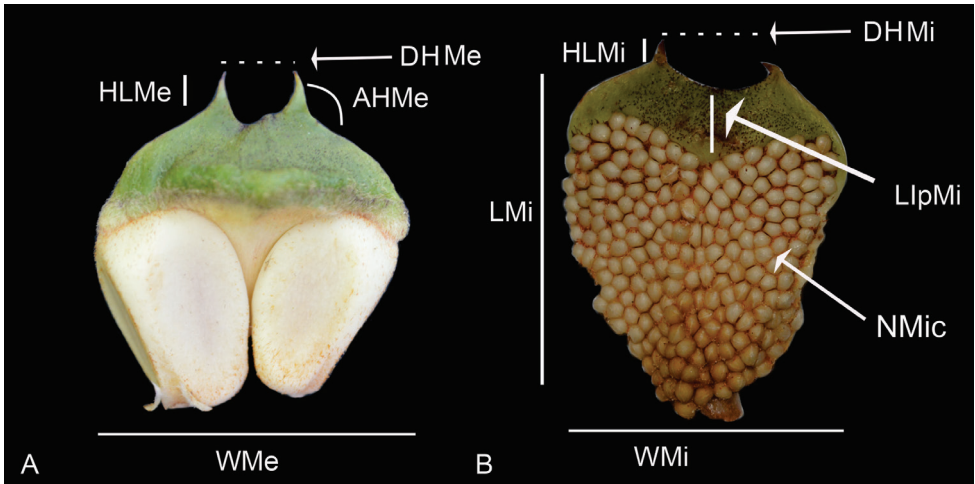


Figure 2. Characters evaluated in sporophylls **A** megasporophylls of *Ceratozamia delucana* **B** microsporophylls of *C. delucana*. HLMe = Horn length of megasporophylls; DHMe = Distance between horn of megasporophylls; AHMe = Angle between horns of megasporophylls; WMe = Width of megasporophylls; LMi = Length of microsporophylls; WMi = Width of microsporophylls; NMic = Number of microsporangia; LlpMi = Length infertile portion of microsporophylls; DHMi = Distance between horn of microsporophylls; HLMi = Horn length of microsporophylls.

Table 1. Qualitative and quantitative morphological characters evaluated in *Ceratozamia* reproductive structures.

Character	Character state
Pollen strobilus position	(0) erect; (1) pendulous
Pollen strobilus shape	(0) angulate; (1) cylindrical
Pollen strobilus color	(0) greenish yellow; (1) greenish brown (2) reddish brown; (3) yellowish brown
Distal face of microsporophylls	(0) non-recurved; (1) recurved
Microsporophylls shape	(0) discoid; (1) obconic; (2) elliptic
Microsporophylls horns type	(0) thin; (1) robust
Infertile portion shape	(0) orbicular; (1) rounded; (2) linear
Fertile portion shape	(0) lobate; (1) deeply lobate
Orientation of horns microsporophylls	(0) straight; (1) curved
Angle between horns of microsporophylls	(0) acute; (1) obtuse; (2) right
Ovulate strobilus position	(0) erect; (1) pendulous
Ovulate strobilus color (trichomes)	(0) light brown; (1) blackish to dark; (2) brown; (3) reddish brown; (4) greyish; (5) wine
Ovulate strobilus apex	(0) acuminate; (1) acute; (2) mucronate; (3) apiculate
Ovulate strobilus shape	(0) cylindrical; (1) globose
Angle between horns of megasporophylls	(0) acute; (1) right; (2) obtuse
Megasporophylls horns type	(0) thin; (1) robust
Direction of horns megasporophylls	(0) non-recurved; (1) recurved
Orientation of horn horns megasporophylls	(0) straight; (1) curved
Distal face of megasporophylls shape	(0) truncate; (1) prominent
Sarcotesta color	(0) whitish yellow; (1) whitish red
Seed shape	(0) ovate; (1) globose; (2) spherical

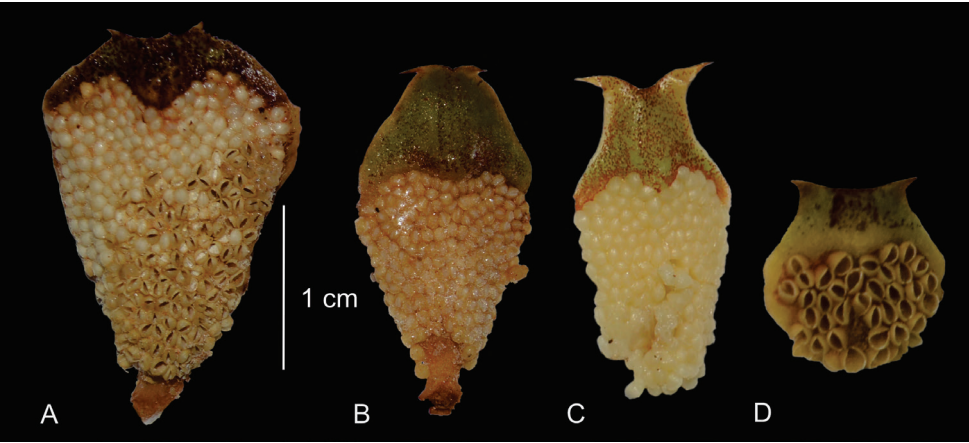


Figure 3. Comparison of qualitative characters of microsporophylls **A** *Ceratozamia fuscoviridis* **B** *C. brevifrons* **C** *C. chamberlainii* **D** *C. kuesteriana*.

The position of leaves is a character that refers to the arrangement of the leaves in relation to the stem apex. The leaves are ascending when they are oriented obliquely upward or with the upper half of the leaf curved apically. The prickles on the petioles of leaves can be robust when the prickle is abruptly tapered from the base to the apex or thin when the shape is homogenous or is gradually tapering. In several species, the prickles are grouped and can bifurcate. The number of prickles

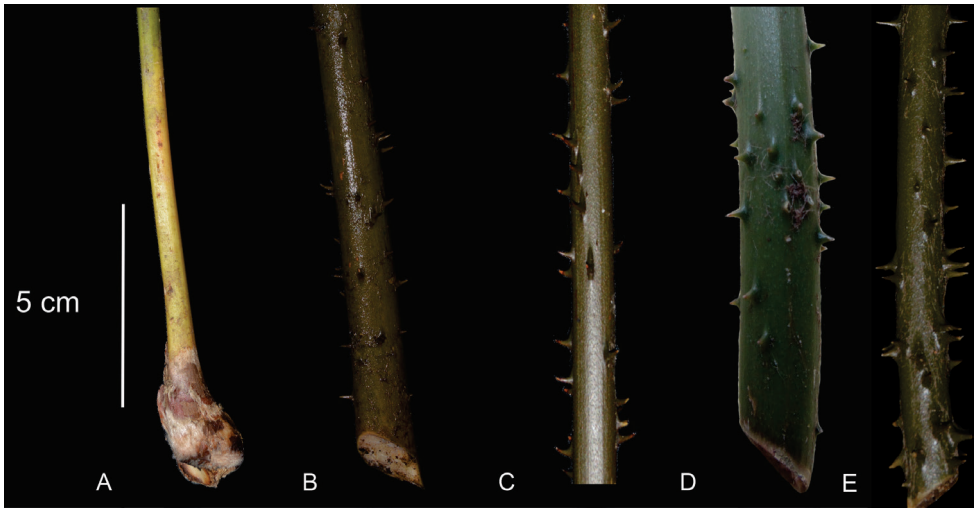


Figure 4. Type and number of prickles on the petiole **A** unarmed **B** thin prickles **C** robust and long prickles **D** robust and short prickles **E** bifurcate.

differs among species; this character is most conspicuous at the base of the petiole. Here, the prickles were counted along 10 cm from the base to distal end on the petiole (Fig. 4).

Results

Circumscription

We recognize 36 species in *Ceratozamia*, including one new species from Belize, characterized by megasporophylls covered by abundant purple to wine-colored trichomes present throughout the ontogeny of the strobilus, the acuminate apex of its ovulate strobili, and pollen strobili with a long infertile portion from 0.65 to 0.80 cm long (Figs 5, 6).

Habit

The species are terrestrial or rupicolous. *Ceratozamia brevifrons* Miq., *C. morettii* Vázq. Torres & Vovides and *C. tenuis* (Dyer) D.W.Stev. & Vovides are terrestrial, but all three species can occasionally be found as epiphytes (Fig. 7J). We found ovuliferous plants of *C. morettii* growing as epiphytes in Veracruz, Mexico. Adult individuals have been recorded growing up to 8 meters in height from the base of a host tree. All *Ceratozamia* species have a pachycaulous stem and are epigeous or semi-epigeous. Most of the species have erect stems, which may branch dichotomously with age. Only four species have an arborescent appearance, with stems of up to 2.5 meters long (*C. aurantiaca* Pérez-

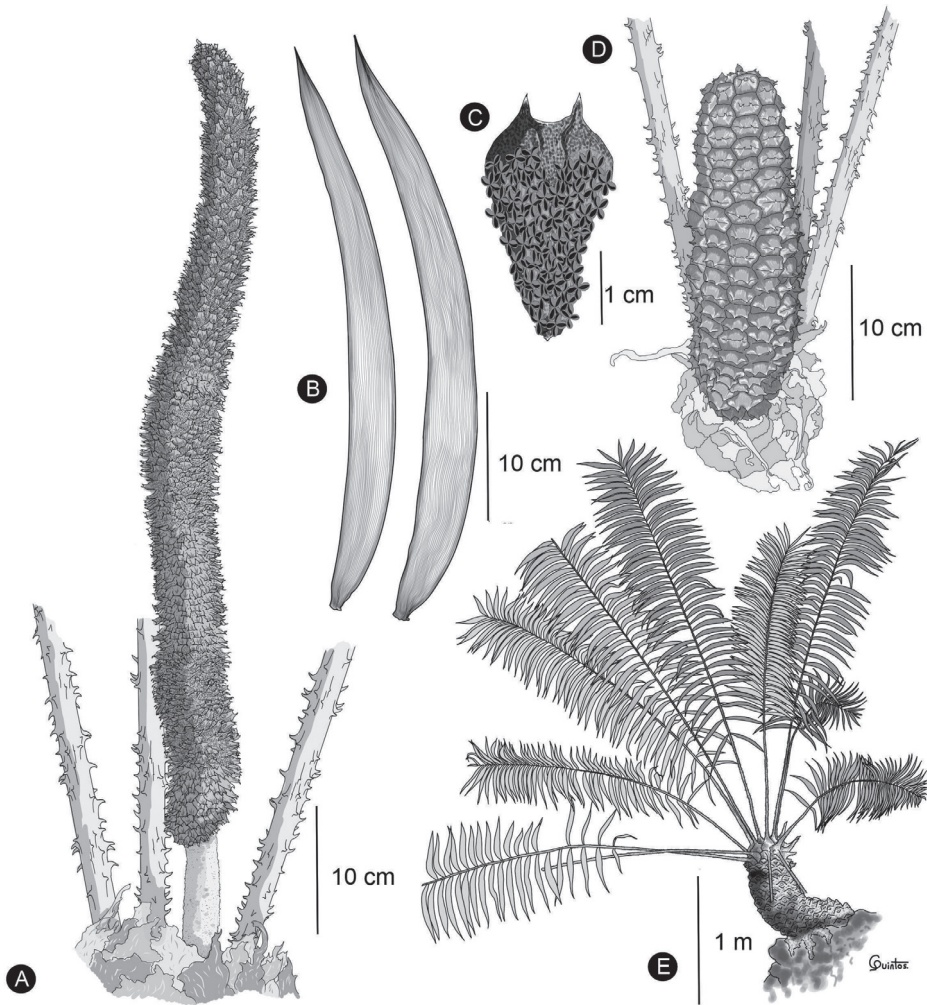


Figure 5. Illustration of *Ceratozamia osbornei* **A** pollen strobilus at maturity **B** variation of leaflets **C** microsporophyll **D** ovulate strobilus at maturity **E** adult plant **A–C** based on *B. K. Holst 4105* and **D, E** based on cultivated plant in Fairchild Tropical Botanic Garden.

Farr., Gut.Ortega, J.L.Haynes & Vovides, *C. osbornei* sp. nov., *C. robusta* Miq., and *C. subroseophylla* Mart.-Domínguez & Nic.-Mor.). Some plants of *C. subroseophylla* have a stem up to 5 meters long but decumbent.

Vegetative morphology

The ptyxis of leaves can be inflexed as in *C. matudae* Lundell or circinate as in *C. miqueliana* H.Wendl. (Fig. 8). The petiole of leaves elongates during leaf growth while the leaflets are progressively expanded. In the early stages of elongation, the apical end of the leaf becomes reflexed and subsequently straightens. During their



Figure 6. Ovulate strobilus of *Ceratozamia osbornei* **A** immature ovulate strobilus **B** mature ovulate strobilus. These photos were taken in Fairchild Tropical Botanic Garden.

development, the leaves have trichomes that are unbranched and brown or white in color. The trichomes are shed during elongation of the leaf. The color of new leaves can be green to yellowish or brown to reddish brown (Fig. 9). This leaf coloration disappears at maturity, except for a few species such as *C. chamberlainii* Mart.-Domínguez, Nic.-Mor. & D.W.Stev., in which the color remains at the base of the leaflets, margin and rachis. The emerging leaf color is generally homogeneous among individuals in a population and within a species. However, this character is polymorphic in *C. fuscoviridis* W.Bull. and *C. sancheziae* Pérez-Farr., Gut.Ortega & Vovides where different individual plants may have brown or green leaves at emergence.

Ceratozamia has cataphylls and well-developed stipules (Stevenson 1981, 1992). The stipules are positioned on the base of petioles as a winglike structure with each stipule having two free tips. These stipules, which encircle shoot apex, have a linear shape and are covered by light brown trichomes (Figs 10C, D, 11) and are usually between 1.5 to 5 cm long and 0.4 to 2 cm wide. Cataphylls are foliar organs that emerge from apex of stem associated with reproductive events. Their development occurs in a series of two or more cataphylls. These are brown to reddish brown and triangular to narrowly triangular and covered by scarce or abundant brown or dark brown trichomes (Figs 10A, B, 11). They become glabrous or partially glabrous at maturity (Fig. 10A).



Figure 7. Plants of *Ceratozamia* in habitat **A** *C. kuesteriana*. **B** *C. latifolia* **C** *C. leptoceras* **D** *C. matudae* **E** *C. mexicana* **F** *C. miqueliana* **G** *C. mirandae* **H** *C. mixeorum* **I** *C. moretii* **J** Epiphytic *C. moretii*.

Reproductive morphology

Pollen grains are sulcate, and exine surface and sexine nearly identical (Dehgan and Dehgan 1988). Some slight differences in measurements of grains have been found; however, the ornamentation and shape of pollen are similar in all species (Vovides et al. 2021).

The ovulate and pollen strobili have two horns at the distal end of each sporophyll. The ovulate strobili show minimal variation at the species level. In most species, the

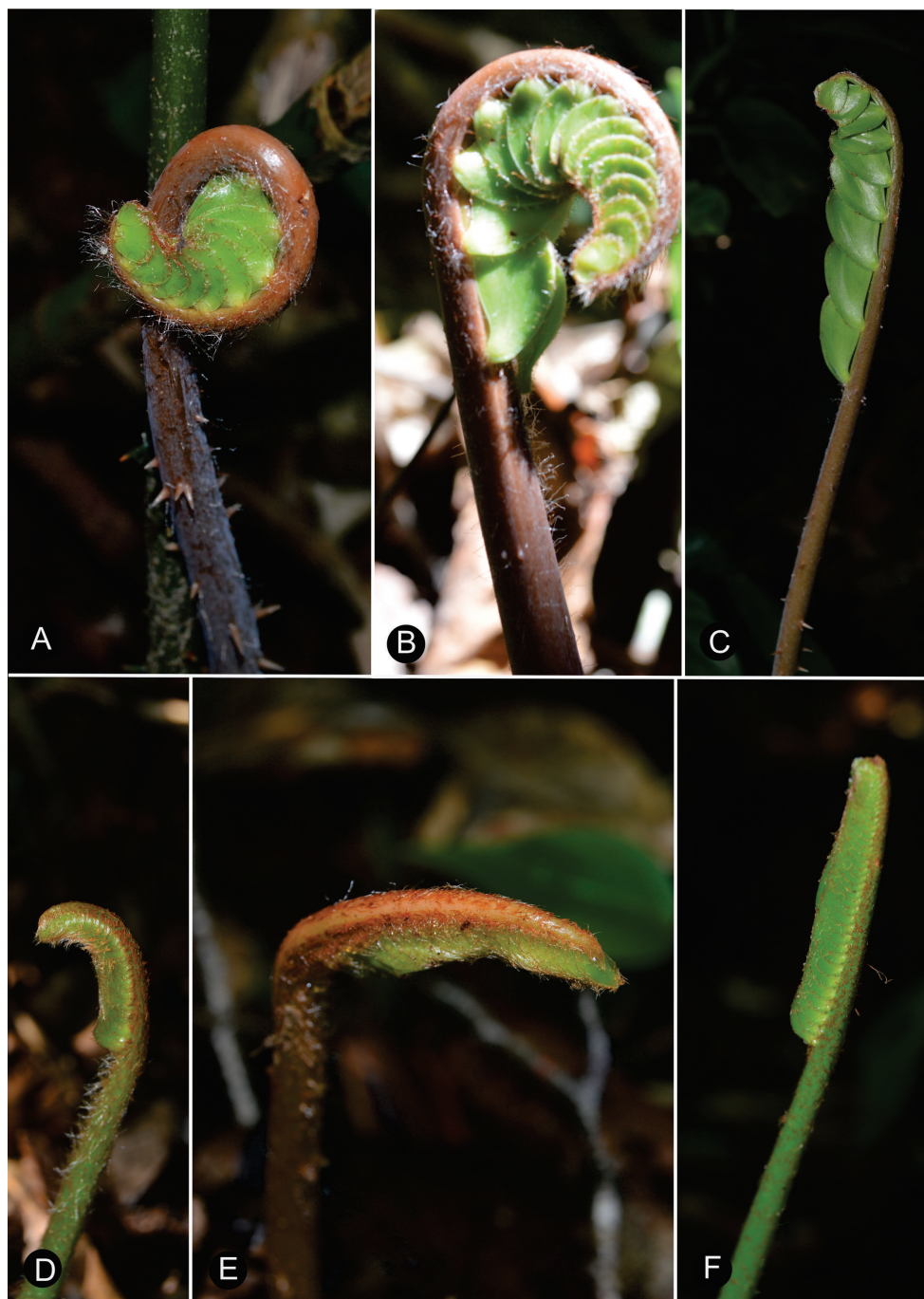


Figure 8. Ptyxis in *Ceratozamia* **A–C** *Ceratozamia miqueliana* **D–F** *C. matudae*.



Figure 9. Color of leaves at emergence **A** *Ceratozamia sancheziae* **B** *C. kuesteriana* **C** *C. fuscoviridis* **D** *C. miqueliana*.

ovulate strobilus shape is cylindrical, whereas in *Ceratozamia morettii* and *C. matudae* it is globose. However, the color of trichomes, apex shape, angle between horns and the distal face of megasporophylls are useful for discriminating between species (Table 1). In contrast, the pollen strobili possess distinctive characters for identifying several species including closely related taxa (Table 1). The microsporophyll horns can be thin or robust, and show different orientations (i.e., straight or recurved). *C. sabatoi* Vovides & Vázq.Torres is the only species with recurved microsporophylls with a downward distal face (Fig. 1A).

Generally, the characters of reproductive structures exhibit little variation within populations. However, these characters are polymorphic in some species such as *Ceratozamia delucana* Vázq.Torres, A.Moretti & Carv.-Hern., in which the infertile apical portion shape of microsporophylls can be orbicular or discoid in the same

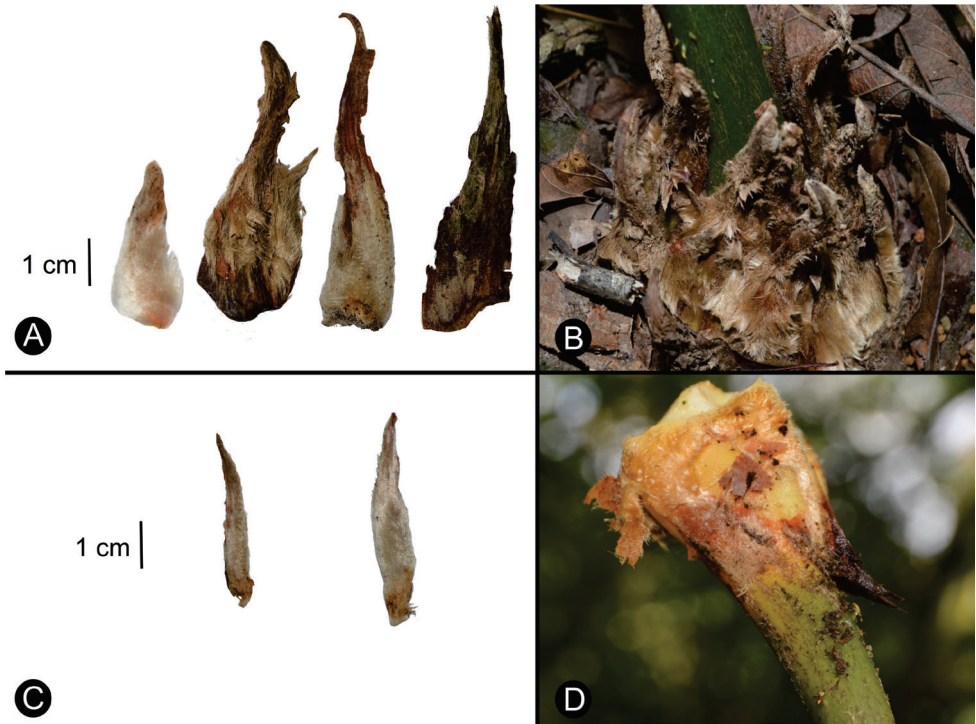


Figure 10. Shapes and pubescence of cataphylls and stipules **A** from left to right: *Ceratozamia latifolia*, *C. delucana*, *C. morettii* at emergence and *C. morettii* at maturity **B** cataphylls of *C. delucana* **C** stipules of *C. morettii* **D** stipules of *C. matudae*.

population. Other species with a similar variation pattern are *C. alvarezii* Pérez-Farr., Vovides & Iglesias and *C. mirandae* Vovides, Pérez-Farr. & Iglesias. Both of these species have an angle between the horns of microsporophylls that is either obtuse or acute.

The seeds are very similar in all species. The most common shape is ovate that can be somewhat irregular, whereas some species such as *Ceratozamia alvarezii* and *C. mirandae* have spherical seeds, and *C. matudae* and *C. sancheziae* have globose seeds (Fig. 12). Seeds are brown to light brown and are between 1.5 and 2.5 cm long, although some species have seeds up to 3.8 cm long (e.g., *C. subroseophylla*).

Phenology

Plants produce a new flush of leaves annually or biannually in a low spiral. The leaves emerge in flushes of from 2, as *C. latifolia* Miq., to 20 as in adult plants of *C. osbornei* and *C. subroseophylla*. However, the plants of most species produce between six and 12 leaves. Generally, the leaves emerge during January to March. Some plants at population level may produce leaves during August to September.

The ovulate and pollen strobili emerge from among the cataphylls. Polliniferous plants produce between 1 to 2 strobili per apex, whereas ovulate plants produce only 1 strobilus per apex and very rarely two in vigorous large plants such as

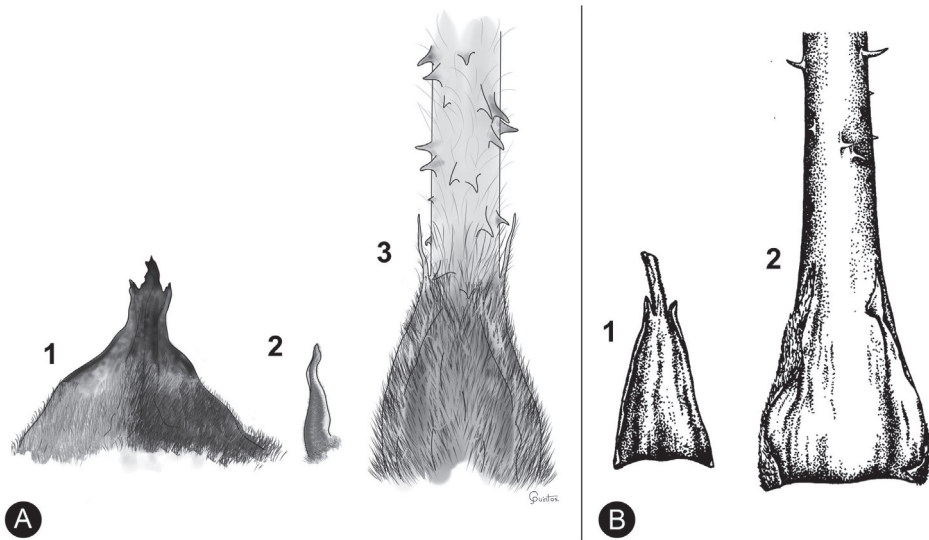


Figure 11. Shape and position of cataphylls and stipules of *Ceratozamia* **A** *C. miqueliana* (1) Cataphylls (2–3) Stipules **B** *C. mexicana* from Stevenson (1981). (1) Cataphylls. (2) Stipules.

Ceratozamia osbornei and *C. mexicana*, particularly in cultivation. We found up to 5 pollen strobili in the same plant during a reproductive season; generally, these pollen strobili emerge within 1 to 2 months of each other. We have recorded very few ovulate plants with more than one strobilus. The phenology shows a slightly different pattern between species. Generally, the strobili emerge between July and September. However, in some species the emergence can occur two months later (e.g., *C. miqueliana*).

Distribution, endemism and habitat

Ceratozamia occurs from Mexico to Guatemala, Belize and Honduras in Central America. According to the biogeographic regionalization of the Neotropical region (Morrone et al. 2022) *Ceratozamia* occurs in Mexican Transition Zone and Mesoamerican dominion of Brazilian subregion (Fig. 13). In the first, there are 69% (25 of 36 species) of the species, which are distributed in Sierra Madre Oriental (SMO), Sierra Madre del Sur (SMS), Transmexican Volcanic Belt Province (TVBP), and Chiapas Highlands (CH). The SMO and CH are the provinces with the highest concentration of species richness in the genus (8 species in each province). The SMS and TVBP have 5 (*C. aurantiaca*, *C. leptoceras* Mart.-Domínguez, Nic.-Mor., D.W.Stev. & Lorea-Hern., *C. mixeorum* Chemnick, T.J.Greg. & Salas-Mor., *C. oliversacksii* D.W.Stev., Mart.-Domínguez & Nic.-Mor., and *C. whitelockiana* Chemnick & T.J.Greg.) and 4 species, respectively (*C. delucana*, *C. mexicana*, *C. morettii* and *C. tenuis*).

In the Mesoamerican dominion of the Brazilian subregion, species occur in two provinces: Veracruz province and Mosquito province. In Veracruz province 14 species are present (*C. becerrae* Pérez-Farr., Vovides & Schutzman, *C. brevifrons*, *C. chimalapensis*, *C. decumbens* Vovides, Avendaño, Pérez-Farr. & Gonz.-Astorga,



Figure 12. Seeds of *Ceratozamia* **A** *C. sancheziae* **B** *C. alvarezii* **C** *C. brevifrons*. **D** *C. subroseophylla*.

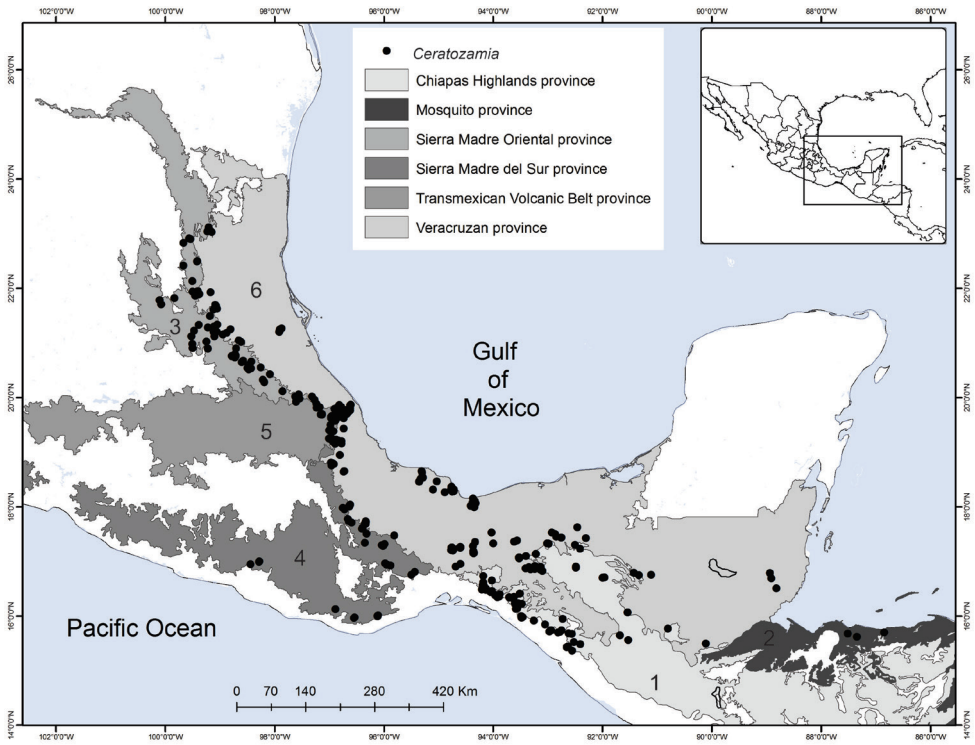


Figure 13. Distribution of *Ceratozamia* genus. Biogeographic regionalization of the Neotropical region according to Morrone et al. (2022).

C. delucana, *C. euryphyllidia* Vázq.Torres, Sabato & D.W.Stev., *C. huastecorum* Avendaño, Vovides & Cast.-Campos, *C. mexicana*, *C. miqueliana*, *C. robusta*, *C. santillanii* Pérez-Farr. & Vovides, *C. subroseophylla*, *C. osbornei*, and *C. zoquorum* Pérez-Farr., Vovides & Iglesias), whereas in Mosquito province only a single species (*C. hondurensis* J.L.Haynes, Whitelock, Schutzman & R.S.Adams) occurs. In particular,

C. mexicana and *C. delucana* also occur in TVBP and *C. robusta* in CH and Veracruz provinces. *Ceratozamia* has not been reported from the Yucatán Peninsula province (Fig. 13); we believe this is due to lack of collections in the southwest of Yucatán (Mexico). The apparent disjunct pattern from El Petén Department (Guatemala) may be explained by this collection deficiency.

With 32 endemic species of *Ceratozamia*, Mexico is the center of endemism of the genus. Only four species occur in Central American countries: *C. hondurensis* from Honduras; *C. osbornei* from Belize; and *C. robusta* and *C. vovidesii* Pérez-Farr. & Iglesias from Guatemala. Some species have a broad geographic range, while others occur in a very limited area. Most of the species that have narrower distributions can be considered micro-endemics, such as *C. alvarezii* and *C. morettii* in Chiapas States and Central Veracruz from Mexico, respectively. In contrast, *C. robusta* has a broad distribution, with a range from northwest Chiapas (Mexico) to Guatemala. Other species of the genus with broad distributions are *C. miqueliana* and *C. subroseophylla*. The latter species has been considered endemic to the montane region of Los Tuxtlas (State of Veracruz, Mexico). However, we found populations at southwest of Veracruz in the Uxpanapa region and Tabasco State, which represent an extension of its geographical range. In particular, the population of *C. subroseophylla* from Tabasco represents a new record for this Mexican state.

Montane regions show the highest diversity of *Ceratozamia* species. The distributional pattern is congruent with the existence of the main mountain systems of Mexico. The mean elevation for *Ceratozamia* species is 1,100 m (range 19–2,000 m), with the majority of the species occurring between 800 to 1,200 m. *Ceratozamia miqueliana*, occurs at 19 meters of elevation in lowland vegetation of Veracruz, while *C. mixeorum* and *C. zaragozae* Medellín are the species that occur at higher elevations above 1,200 m of Oaxaca and San Luis Potosí, respectively.

Species richness in *Ceratozamia* tends to be correlated with moister habitats, principally in limestone rock areas. The genus is found in four vegetation types: cloud forest, evergreen tropical forest, oak forest and oak-pine forest. Most species inhabit cloud forest, whereas in oak-pine forest there are only a few species. No species is known from dry forest. Some species do grow near to rivers or lagoons, e.g., *C. aurantiaca* and *C. miqueliana* near the Santo Domingo River and Majahual lagoons, respectively.

Discussion

The cycad genus *Ceratozamia* as here circumscribed includes 36 species, 34 of which are found in Mexico with 32 of those endemic to Mexico. *C. robusta* is the species with the widest distribution in the genus, occurring continuously from the central region of Chiapas State in Mexico to Guatemala. Unfortunately, herbarium specimens from Guatemala are infertile and there are few sterile specimens in herbaria in general, which has led to ambiguous and/or conflicting taxonomic identifications. Comparative vegetative morphology with these specimens suggests that *C. robusta* also has a wide

elevational range between 400 meters and up to 1,300 meters of elevation. However, recently collected reproductive material has been observed for plants from Belize, which have revealed features that demonstrate that the Belize plants can be distinguished from those in Mexico and Guatemala resulting in our description of *C. osbornei*. Further population level studies of this species are needed to evaluate genetic differentiation and gene flow throughout the entire ranges of both *C. osbornei* and *C. robusta*. *C. matudae* was reported for Guatemala from the Sierra de Cuchumatanes in the 1940s, but no past or recently collected specimens have been located. Considering this paucity of information and the exceptionally rapid loss of forest cover in the region, a thorough exploration and study of these localities is essential.

Recently, Vovides et al. (2020) recircumscribed the *Ceratozamia miqueliana* complex using leaflet anatomy and other macromorphological characters. As a result, *C. zoquorum* was recircumscribed with a much narrower taxonomic concept. They considered the presence or absence of girder sclerenchyma and a lignified hypodermis to be a significant trait to distinguish between *C. zoquorum* and *C. becerrae*, and the latter was removed from synonymy under *C. zoquorum*. However, we found that the corresponding taxonomic key failed to properly identify these closely related species with anatomical characters that are contradictory to the descriptions. Thus, there is a lack of correspondence between the key entries and homologous character states in both supposed species (Vovides et al. 2020; p. 11).

Therefore, the only two remaining anatomical characters relevant in this case are: 1) girder sclerenchyma present in *Ceratozamia zoquorum* and mostly absent in *C. becerrae*, and 2) a lignified adaxial hypodermis in *C. zoquorum* that is also absent in *C. becerrae*. According to the descriptions provided by the authors, the hypodermis in *C. becerrae* is absent only in the revolute leaflet margin with up to three layers of fibres, whereas in *C. zoquorum* such margin is discontinuous with 1–7 lignified isodiametric fibres.

In their anatomical evaluation, Vovides et al. (2020: 2) studied two cultivated individuals for evaluating phenotypic variation. The anatomical characters should therefore be characterized and reassessed under a broader approach by testing the morphological variation through different populations at the intra- and inter-population level: most leaflet macromorphological characters—including qualitative ones—often exhibit polymorphisms, as well as wide variation at the population level. Generally, leaflets exhibit high variation mainly in quantitative characters (Pérez-Farrera et al. 2009; Martínez-Domínguez et al. 2017a, c). Considering then that leaflets in *Ceratozamia* species show contrasting shapes between geographically close species, but similar shapes even when the biogeographic pattern is disjunct, we suggest that the leaflet anatomy should be re-assessed through broader sampling.

Based on our research, the taxonomic value of some traditional morphological characters—such as leaflet size—should only be secondarily important, and the focus should be put on defining qualitative characters in both leaves and leaflets, and characters derived from reproductive structures as proposed in Table 1. Regarding the latter, we observed that the position of ovulate strobilus was not consistent throughout the different ontogenetic states. Ovulate strobili can recline due to the weight of the fertile

portion of ovulate strobilus and because of the position of the plant growing on a rocky wall. This is mainly because the ovulate strobilus position is correlated with the length of the peduncle of strobili and the fact that the peduncle curves at maturity. Our data support that other characters such as those of the microsporophylls and the shape of their horns can be coded into discrete character states and, therefore, provide more taxonomic utility than previously understood.

This modern taxonomic treatment is drawn from wide sampling, thorough review of specimens in collections and molecular data (Martínez-Domínguez et al. 2016, 2017c, 2020), thus establishing a framework for future research and providing a resource for disentangling confusing species. Ultimately, this work contributes to the conservation of this threatened genus. Despite advances in the taxonomy and systematics of this genus, taxon-level data are required for a complete systematic evaluation. We suggest that the use of phenological information as well as a more nuanced understanding of phenotypic evolution—including, for example, instances of plasticity and other ontogenetic development-related phenomena—that might impact diversification in species complexes or other groups of closest related species in this gymnosperm genus, will be increasingly relevant for the task.

Taxonomic treatment

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

Type species. *Ceratozamia mexicana* Brongn.

Description. *Stem* 10–250 cm long, 8–40 cm in diameter, epigeous or semi-hypogeous, erect or decumbent. *Cataphylls* persistent, triangular to narrowly triangular, reddish brown, tomentose to densely tomentose at emergence, partially tomentose at maturity, apex acuminate. *Leaves* stipulate, ascending to descending, light green or reddish brown at emergence with whitish gray or brown trichomes, generally glabrous at maturity; stipulate 2–6 cm long, linear, tomentose at maturity. *Petiole* straight or twisted, sometimes brown in mature leaves, without prickles or heavily to lightly armed with prickles; prickles can be bifurcate. *Rachis* straight or twisted, without prickles or armed with prickles up to half the length of the leaves. *Leaflets* articulate, sessile, membranaceous to coriaceous, linear to obovate, opposite to subopposite or clustered, not imbricate, generally acuminate at apex, attenuate at base, margins entire; articulations green to brown. *Pollen strobili* 1–2, with sterile tip, erect, cylindrical, green to cream with blackish to reddish brown trichomes at maturity; pollen sporangiophores deltoid to cuneate, basally stalked, distal face bicornate, fertile abaxial surface with 24–280 sporangia in clusters of (2)3(4–5), dehiscent by longitudinal slit; peduncle pubescent to tomentose. *Ovulate strobili* usually solitary, globose to cylindrical; green with pale pink to blackish trichomes at maturity, acute to apiculate apex; ovulate sporangiophores peltate with a narrow basal stalk and transversely hexagonal tips, bicornate at distal end; peduncle pubescent to tomentose, erect to pendulous. *Seeds* (ovules) 2 per megasporophyll projecting inward toward the strobilus axis, spherical, sarcotesta pink to yellowish when immature, light brown at maturity, sclerotesta smooth with several furrows longitudinal from micropylar end.

Distribution and habitats. The 36 species of *Ceratozamia* are only found from Mexico to Central America, usually in montane habitats on limestone soils at elevations from 19 to 2,000 m. Most of the species are narrowly endemic, and all are on CITES Appendix I.

Artificial key for *Ceratozamia*

- 1 Petiole and rachis twisted 2
- Petiole and rachis straight 3
- 2 Petiole and rachis with prickles *C. norstogii*
- Petiole and rachis unarmed *C. zaragozae*
- 3 Leaflets fasciculate *C. hildae*
- Leaflets opposite to subopposite 4
- 4 Leaflets obovate; veins prominent 5
- Leaflets oblong to linear; veins not prominent 6
- 5 Leaflets with sinuate margin at the distal end and an asymmetrical apex
..... *C. euryphyllidia*
- Leaflets with entire margin at the distal end and a symmetrical apex
..... *C. hondurensis*
- 6 Leaflets oblong to oblanceolate 7
- Leaflets linear to lanceolate 19
- 7 Leaflets papyraceous 8
- Leaflets coriaceous 12
- 8 Petiole and rachis unarmed *C. latifolia*
- Petiole and rachis with prickles 9
- 9 Leaflets with a symmetric apex *C. totonacorum*
- Leaflets with an asymmetric or abruptly symmetrical apex 10
- 10 New leaves reddish brown at emergence; ovulate strobilus green with brown
trichomes at maturity; microsporophylls with the infertile apical portion par-
tially covered with trichomes *C. aurantiaca*
- New leaves green at emergence; ovulate strobilus green with black trichomes
at maturity; microsporophylls with the infertile apical portion completely
covered with trichomes 11
- 11 Petiole armed with robust prickles; microsporophylls rounded; ovulate stro-
bilus with an acuminate apex *C. miqueliana*
- Petiole armed with thin prickles; microsporophylls orbicular; ovulate strobi-
lus with an acute apex *C. delucana*
- 12 New leaves reddish brown at emergence; ovulate strobilus with abundant
wine-colored to reddish brown trichomes 13
- New leaves green at emergence; ovulate strobilus with blackish brown tri-
chomes 14
- 13 Petiole armed with robust prickles; rachis armed with prickles; ovulate strobi-
lus more than 20 cm long with an acuminate apex *C. chamberlainii*
- Petiole armed with thin prickles; rachis unarmed to armed with few prickles;
ovulate strobilus up to 15 cm long with an acute apex *C. decumbens*

14	Petiole prickles less than or equal to 0.20 cm long	15
–	Petiole prickles more than 0.20 cm long	18
15	Apical leaflets less than or equal to 3.5 cm wide; brown trichomes of leaves at emergence; ovulate strobilus with an apiculate apex	<i>C. morettii</i>
–	Apical leaflets more than 3.5 cm wide; whitish gray trichomes of leaves at emergence; ovulate strobilus with an acute apex	16
16	Peduncle of ovulate strobilus 3 cm long or shorter	<i>C. santillanii</i>
–	Peduncle of ovulate strobilus more than 3 cm long	17
17	Plants from Sierra Madrigal at the border of Tabasco and Chiapas States (Mexico)	<i>C. becerrae</i>
–	Plants from northern mountains of Chiapas State (Mexico)	<i>C. zoquorum</i>
18	Leaves with 20–43 pairs of leaflets; microsporophylls 1.3 cm long or longer, 1.3 cm wide or wider; trichomes of leaves at emergence brown; 10 or more leaves per leaf crown	<i>C. delucana</i>
–	Leaves with 8–18 pairs of leaflets; microsporophylls less than 1.3 cm long, less than 1.3 cm wide; trichomes of leaves at emergence whitish gray; less than 10 leaves per leaf crown	<i>C. huastecorum</i>
19	Leaflets coriaceous	20
–	Leaflets papyraceous to membranaceous	22
20	Leaflets keeled; petiole armed with robust prickles	<i>C. brevifrons</i>
–	Leaflets plane; petiole armed with thin prickles	21
21	Petiole sparsely prickly (30 prickles or fewer); microsporophylls with infertile apical portion more than 0.45 cm long, horns more than 0.25 cm long	<i>C. mexicana</i>
–	Petiole abundantly prickly (more than 35 prickles); microsporophylls with infertile apical portion less than 0.45 cm, horns less than or equal to 0.25 cm .	<i>C. delucana</i>
22	Leaflets involute to lightly involute or canaliculate	23
–	Leaflets flat	26
23	New leaves at emergence dark green with brown trichomes; basal leaflet more than or equal to 1 cm wide	<i>C. tenuis</i>
–	New leaves at emergence brown to reddish brown with whitish gray trichomes; basal leaflet less than 1 cm wide	24
24	Petiole sparsely prickly (less than or equal to 10 prickles); prickles short (less than or equal to 0.15 cm); microsporophylls discoid, up to 1.1 cm long	<i>C. kuesteriana</i>
–	Petiole abundant prickly (more than 10 prickles); prickles long (more than 0.15 cm); microsporophylls elliptic, more than 1.2 cm long	25
25	Leaves with rachis the same length or shorter than the petiole; plants from Cintalapa and Juquipilas municipalities in Chiapas State (Mexico)	<i>C. alvarezii</i>
–	Leaves with rachis longer than petiole; plants from Sierra Morena and Tres Picos in Chiapas State (Mexico)	<i>C. mirandae</i>

26	Petiole armed with robust prickles	27
–	Petiole armed with thin prickles.....	29
27	Leaflets abaxially curved in both median and apical portions; ovulate strobilus dark green with scarce blackish trichomes or glabrous at maturity; microsporophylls with curved horns	<i>C. robusta</i>
–	Leaflets abaxially curved in the median and mostly planar in the apical portion; ovulate strobilus green with abundant trichomes reddish brown to purple at maturity; microsporophylls with straight horns	28
28	Ovulate strobilus with base pale pink megasporophylls and dark brown to reddish brown trichomes at maturity; microsporophylls with a lobate fertile portion and infertile portion up to 0.65 cm long	<i>C. subroseophylla</i>
–	Ovulate strobilus with green megasporophylls base and dark purple to wine trichomes at maturity; microsporophylls with a deeply lobate fertile portion and infertile portion more than 0.65 cm long.....	<i>C. osbornei</i>
29	Leaflets linear.....	30
–	Leaflets lanceolate	31
30	Leaflets membranaceous	<i>C. leptoceras</i>
–	Leaflets papyraceous.....	32
31	Base of leaflets and articulations yellow	<i>C. matudae</i>
–	Base of leaflets and articulations green to brown	34
32	Prickles on the petiole more than or equal to 0.50 cm long; horns of microsporophylls thin	<i>C. oliversacksii</i>
–	Prickles on the petiole less than or equal 0.34 cm long; horns of microsporophylls robust	33
33	Leaflets less than or equal 1.5 cm wide; recurved downward distal face of microsporophylls	<i>C. sabatoi</i>
–	Leaflets more than 1.5 cm wide; non-recurved distal face of microsporophylls.....	<i>C. sancheziae</i>
34	New leaves green to yellowish green.....	35
–	New leaves brown to reddish brown.....	36
35	Rachis unarmed.....	<i>C. whitelockiana</i>
–	Rachis with prickles.....	37
36	Microsporophylls with an orbicular infertile portion; megasporophylls with a truncate distal face	<i>C. fuscoviridis</i>
–	Microsporophylls with a rounded to linear infertile portion; megasporophylls with a prominent distal face.....	39
37	Leaves descending.....	<i>C. mixeorum</i>
–	Leaves ascending.....	38
38	Leaflets more than or equal 2.3 cm wide.....	<i>C. delucana</i>
–	Leaflets less than 2.3 cm wide	<i>C. fuscoviridis</i>
39	Microsporophylls elliptic with curved horns	<i>C. chimalapensis</i>
–	Microsporophylls obconic with straight horns	<i>C. vovidesii</i>

1. *Ceratozamia alvarezii* Pérez-Farr., Vovides & Iglesias, Novon 9: 410. 1999

Figs 12B, 15A

Type. MEXICO. Chiapas: Mun. Cintalapa, Rancho El Cafetal, 950 m, 4 Mar 1996, *M.A. Pérez-Farrera* 889 (holotype: CHIP! [acc. # 14306]; isotypes: F! [acc. # 2193633], HEM! [acc. # HEM004830], MEXU! [MEXU00827362], MO! [acc. # 04882667]).

Description. *Stem* 20–60 cm long, 15–30 cm in diameter, epigeous, erect and decumbent. *Cataphylls* 2.0–5.0 × 1.5–3.0 cm wide at the base, persistent, triangular, reddish brown, densely brownish tomentose at emergence, partially tomentose at maturity, apex acuminate. *Leaves* 2–30 (40), 36–125 cm long, ascending, brown at emergence with whitish gray trichomes, glabrous at maturity. *Petiole* 10–60 cm long, terete, linear, brown in mature leaves; with 11–40 thin prickles, 0.19–0.37 cm long. *Rachis* 25–87 cm long, terete, linear, brown to greenish brown in mature leaves, with prickles. *Leaflets* 25–68 pairs, opposite to subopposite, insertion in one plane, linear to lanceolate, generally longitudinally planar, not basally falcate, papyraceous, slightly involute, green with adaxial and abaxial sides glabrous, distal end with entire margins, acuminate and symmetric at the apex, attenuate at base, with conspicuous and light-green veins; median leaflets 12–38 × 0.3–0.9 cm, 0.14–1.30 cm between leaflets; articulations 0.14–0.75 cm wide, brown. *Pollen strobili* 15–40 cm long, 3.5–5.1 cm in diameter, solitary, cylindrical, erect, yellowish green with brown trichomes at emergence, yellowish cream with blackish brown trichomes at maturity; peduncle 4–10 cm long, 1.5–2.1 cm in diameter, reddish brown to brown pubescent; microsporophylls 1.24–1.56 × 0.59–0.83 cm, elliptic with a non-recurved distal face and a lobate fertile portion, infertile portion 0.50–0.81 cm long and linear with straight horns 0.14–0.30 cm long, 0.45–0.90 cm and an obtuse to acute angle between the horns. *Ovulate strobili* 17–27 cm long, 7.2–12.3 cm in diameter, solitary, cylindrical, erect, yellowish green with abundant blackish trichomes at emergence, glaucous green with reddish brown to blackish trichomes at maturity, acuminate apex; peduncle 4.0–10 cm long, 1.1–2.2 cm in diameter, erect, with scarce brownish tan trichomes; megasporophylls 20–80, 4–8 orthostichies with 5–10 sporophylls per orthostichy, 2.15–2.80 × 3.90–6.30 cm, with a prominent distal face, horns straight and thin and 0.32–0.51 cm long, 0.69–1.80 cm between horns with an obtuse angle between the horns. *Seeds* 2.5–3.0 cm long, 2.3–2.9 cm in diameter, spherical, sarcotesta whitish pink when immature, light brown at maturity.

Distribution and habitat. *Ceratozamia alvarezii* is endemic to Mexico and only known from Cintalapa and Jiquipilas municipalities in Chiapas State, at the transition zone between pine and oak forest and oak forest; plants occur on karstic rocks between 900 and 1,450 m elevation (Fig. 14A).

Etymology. The specific epithet honors Miguel Álvarez del Toro in recognition of its outstanding contributions for conservation in Chiapas and the establishment of its first reserves (Pérez-Farrera et al. 1999).

Common names. Mexico. Chiapas: Espadaña cimarrona (*L. Martínez-Domínguez et al.* 1370); palma, palmita (*M.A. Pérez-Farrera* 889).

Uses. The seeds are used as food (*M.A. Pérez-Farrera* 889).

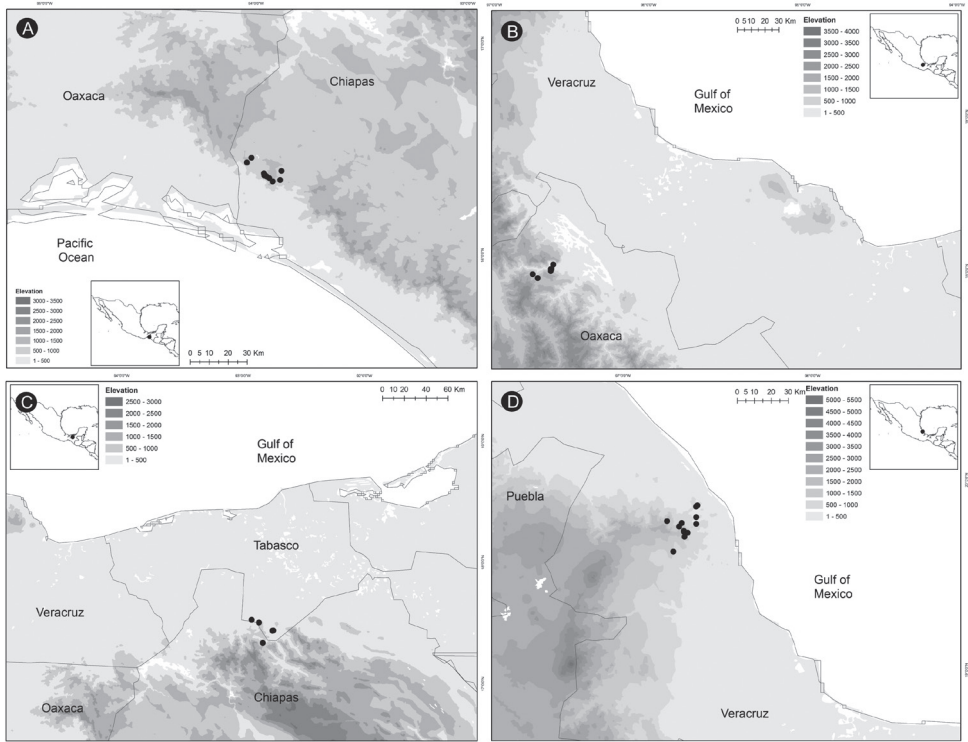


Figure 14. Distribution of *Ceratozamia* species **A** *C. alvarezii* **B** *C. aurantiaca* **C** *C. becerrae* **D** *C. brevifrons*.

Conservation status. (IUCN 2021). Endangered; A2ac; B1ab(I,iii)+2ab(i,iii); C1.

Discussion. The morphology of *Ceratozamia alvarezii* is not very different from *C. mirandae*. At population level, this species differs from *C. mirandae* by having generally shorter leaves, smaller ovulate strobilus (up to 27 cm long and 5 to 10 sporophylls per orthostichy), and longer seeds.

Specimens examined. MEXICO. **Chiapas:** Mun. Cintalapa, 1,100 m, 10 Mar 1993, A.P. Vovides 1234 (XAL); 920 m, 21 Jun 2018, F. Nicolalde-Morejón et al. 2791–2799 (CIB); 980 m, 22 Jun 2018, F. Nicolalde-Morejón et al. 2830 (CIB); 1,107 m, 18 Jun 2019, F. Nicolalde-Morejón & L. Martínez-Domínguez 3177–3183 (CIB); 1,350 m, 18 Jun 2019, F. Nicolalde-Morejón & L. Martínez-Domínguez 3186–3196 (CIB); 1,450 m, 11 Oct 1994, J. Castillo et al. 445 (CHIP); 920 m, 21 Jun 2018, L. Martínez-Domínguez et al. 1359–1369 (CIB), 1370 (CIB, MEXU); 980 m, 22 Jun 2018, L. Martínez-Domínguez et al. 1402 (CIB, MEXU); 925 m, 18 Jun 2019, L. Martínez-Domínguez & F. Nicolalde-Morejón 1770 (CIB); 1,107 m, 18 Jun 2019, L. Martínez-Domínguez & F. Nicolalde-Morejón 1771, 1772 (CIB, MEXU), 1773 (CIB), 1774 (CIB, MEXU), 1775–1777 (CIB); 1,350 m, 18 Jun 2019, L. Martínez-Domínguez & F. Nicolalde-Morejón 1784–1794 (CIB); 900 m, 10 Jul 1994, M.A. Pérez-Farrera 71 (CIB, CHIP, MEXU); 950 m, 5 Sep 1995, M.A. Pérez-Farrera 776 (CIB, XAL);



Figure 15. Plants of *Ceratozamia* in habitat **A** *C. alvarezii* **B** *C. aurantiaca* **C** *C. becerrae* **D** *C. brevifrons* **E** *C. chamberlainii* **F** *C. chimalapensis* **G** *C. decumbens* **H** *C. delucana* **I** *C. euryphyllidia* **J** *C. fuscoviridis* **K** *C. hondurensis* **L** *C. huastecorum*.

1,000 m, 27 Mar 2000, *O. Farrera* S. 2068 (CHIP). **Mun. Jiquipilas**, 1,200 m, 6 Jun 2002, *A. Reyes-García* 5017 (MEXU); 1,380 m, 17 Feb 2000, *E. Palacios* E. 2469 (CHIP); 1,170 m, 7 Jul 1994, *M.A. Pérez-Farrera* 68 (CIB).

2. *Ceratozamia aurantiaca* Pérez-Farr., Gut.Ortega, J.L.Haynes & Vovides, Taxonomy 1: 249. 2021

Figs 1C, 15B

Ceratozamia martinezii Mart.-Domínguez, Nic.-Mor. & D.W.Stev., Nordic J. Bot. 1: 2. 2021 [2022]. Type. MEXICO. Oaxaca: Mun. San Pedro Teutila, El Faro, 615 m, 28 Sep 2020, *L. Martínez-Domínguez et al.* 2049 ♀ (holotype: CIB! [acc. # 22845UV]; isotypes: MEXU!, NY!).

Type. MEXICO. Oaxaca: Mun. San Pedro Teutila, Sierra Norte, 30 May 2021, *M.A. Pérez-Farrera & P. Díaz-Jiménez* 4014 (holotype: HEM [n.v.]; isotype: XAL [n.v.]).

Description. *Stem* 30–250 cm long, 10–15 cm in diameter, epigeous, erect or sometimes decumbent. *Cataphylls* 3.6–6.5 × 2–3.3 cm wide at the base, persistent, triangular, reddish brown, densely brown tomentose at emergence, glabrous at maturity, apex acuminate. *Leaves* 7–30 (50), 117–240 cm long, ascending, reddish brown at emergence, with whitish gray trichomes, glabrous at maturity. *Petiole* 45–85 cm long, terete, linear, reddish brown or greenish brown at emergence, dark green in mature leaves; with 16–47 thin prickles, 0.30–0.66 cm long. *Rachis* 70–160 cm long, terete, linear, dark green in mature leaves, with prickles in lower third. *Leaflets* 12–38 pairs, opposite to subopposite, insertion in one plane, oblong, generally longitudinally planar, not basally falcate, papyraceous, flat, green with adaxial and abaxial sides glabrous, distal end with entire margins, abruptly acuminate and symmetrical at the apex, attenuate at base, veins conspicuous and light-green; median leaflets 21–42.5 × 3.3–4.8 cm, 3.2–6.0 cm between leaflets; articulations 0.9–1.5 cm wide, green. *Pollen strobili* 20–35 cm long, 3.1–4.6 cm in diameter, solitary, cylindrical, erect, greenish with reddish trichomes at emergence, greenish yellow with reddish brown trichomes at maturity; peduncle 7.0–15 cm long, 1.5–2.1 cm in diameter, pubescent, reddish brown; microsporophylls 1.50–2.2 × 0.98–1.30 cm, obconic with a non-recurved distal face and a lobate fertile portion, infertile portion rounded and 0.47–0.84 cm long with horns straight and 0.16–0.38 cm long, 0.50–0.80 cm between horns with an acute angle between the horns. *Ovulate strobili* 11–36 cm long, 9.4–12.5 cm in diameter, solitary, cylindrical, erect, greenish yellow with an abundant reddish trichomes at emergence, green with brown trichomes at maturity, with an acute apex; peduncle 5.0–19.5 cm long, 1.3–2.3 cm in diameter, erect, light brown pubescent; megasporophylls 20–200, 5–11 orthostichies with 4–19 sporophylls per orthostichy, 2.25–2.72 × 3.6–4.3 cm, with a truncate distal face, horns curved and 0.54–0.90 cm long, 1.05–1.77 cm between horns with an acute angle between the horns. *Seeds* 2.4–3.0 cm long, 1.4–1.7 cm in diameter, ovate, sarcotesta whitish yellow to yellow when immature, light brown at maturity.

Distribution and habitat. *Ceratozamia aurantiaca* occurs in highlands south of Río Santo Domingo and north of Sierra Norte in Oaxaca State, Mexico (Fig. 14B), where it occurs in the evergreen tropical forest on karstic rocks at 458–800 m.

Etymology. The specific epithet alludes to the leaf color at emergence. This is derived from Latin word *aurantiacus* for the orange color of emerging leaves.

Common names. None recorded.

Uses. People use the leaves of *Ceratozamia aurantiaca* to make flower arrangements in wreaths (Martínez-Domínguez et al. 2022a).

Preliminary conservation status. We visited three populations for *Ceratozamia aurantiaca* in which we recorded between 100 to 300 adult plants. We observed seedlings, juveniles and reproductive individuals. However, one of these populations is in a risk area due to anthropogenic land-use changes and was affected by fire in 2018. In addition, it is not found within protected areas. Based upon this information, *C. aurantiaca* should be considered “Endangered (EN)” in accordance with IUCN criteria.

Discussion. *Ceratozamia aurantiaca* is most similar to *C. whitelockiana*, however, differs from it in its oblong leaflets abruptly acuminate with a symmetric apex, its petiole with abundant (16–24) and long prickles (0.32–0.55 cm), and its rachis that has prickles in the proximal third of the leaf. In addition, the ovulate strobili have an acute apex, and the pollen strobili have obconic microsporophylls with a rounded infertile portion. The leaves are reddish brown at emergence, whereas in *C. whitelockiana* they are green.

Specimens examined. MEXICO. **Oaxaca:** **Mun. Chiquihuitlán de Benito Juárez**, 861 m, 26 Nov 2004, *C.A. Cruz-Espinosa & G. Juárez-García* 1945 (MEXU). **Mun. San Felipe Jalapa de Díaz**, 500 m, 28 Jun 2008, *J.A. Pérez de la Rosa et al.* 1966 (IBUG). **Mun. San Pedro Teutila**, 458 m, 23 Sep 2020, *F. Nicolalde-Morejón et al.* 3323–3333 (CIB); 500 m, 23 Sep 2020, *F. Nicolalde-Morejón et al.* 3334–3337 (CIB); 615 m, 28 Sep 2020, *F. Nicolalde-Morejón et al.* 3415–3419 (CIB); 708 m, 10 Jun 2004, *G. Juárez-García* 425 (MEXU); 458 m, 23 Sep 2020, *L. Martínez-Domínguez et al.* 1946–1950 (CIB), 1951 (CIB, MEXU), 1952–1957 (CIB); 500 m, 23 Sep 2020, *L. Martínez-Domínguez et al.* 1958–1960 (CIB, MEXU), 1961 (CIB); 615 m, 28 Sep 2020, *L. Martínez-Domínguez et al.* 2050, 2052 (CIB, MEXU), 2051, 2053 (CIB); 539 m, 6 Apr 2021, *L. Martínez-Domínguez et al.* 2141, 2142, 2144 (CIB), 2143 (CIB, MEXU, NY). **Mun. Santa María Tlalixtac**, 675 m, 25 Nov 2004, *G. Juárez-García & C.A. Cruz-Espinosa* 868 (MEXU).

3. *Ceratozamia becerrae* Pérez-Farr., Vovides & Schutzman, Bot. J. Linn. Soc. 146: 124. 2004

Fig. 15C

Type. MEXICO. Tabasco: Mun. Teapa, hill Madrigal, Aug 2003, *A.P. Vovides* 1458 (holotype: XAL [XAL0148355]).

Description. **Stem** 13–38 cm long, 9–15 cm in diameter, epigeous, semi-hypogeous, erect. **Cataphylls** 2.6–5.7 × 1.3–4.5 cm wide at the base, persistent, triangular, reddish brown, densely brownish tomentose at emergence, glabrous at apex when mature, apex acuminate. **Leaves** 2–12 (17), 49–210 cm long, descending, light green, glaucous at emergence with whitish gray trichomes, glabrous at maturity. **Petiole** 35–111.5 cm long, terete, linear, pink at emergence, yellowish green when

mature; unarmed to armed with 3–27 thin prickles, 0.02–0.13 cm long. **Rachis** 30–105 cm long, terete, linear, pink at emergence, yellowish green at mature leaves, generally unarmed. **Leaflets** 6–15 pairs, opposite to subopposite, insertion in one plane, oblong to oblanceolate, longitudinally curved abaxially to planar, generally basally falcate, coriaceous, flat, green with adaxial and abaxial sides glaucous or glabrous, distal end with entire margins, acuminate to acute, and asymmetrical (rarely symmetrical in apical leaflets) at the apex, attenuate at base, with conspicuous and light-green veins; median leaflets 16–30 × 4.5–8.8 cm, 5.5–11.1 cm between the leaflets; articulations 0.5–1.5 cm wide, green and yellowish. **Pollen strobili** solitary, 10.8–20 cm long, 2.8–4.0 cm in diameter, cylindrical, erect, green with blackish trichomes at emergence, yellow-cream with blackish trichomes at maturity; peduncle 5–10 cm long, 1.5–2.0 cm in diameter, tomentose, light brown; microsporophylls 0.9–1.37 × 0.7–0.9 cm, discoid with a non-recurved distal face and a deeply lobate fertile portion, infertile portion 0.35–0.39 cm long and linear with straight horns and 0.30–0.45 cm long, 0.70–0.80 cm and an acute angle between the horns. **Ovulate strobili** 15–23 cm long, 7.5–8.5 cm in diameter, solitary, cylindrical, erect, green with reddish brown trichomes at emergence, green with brown to blackish trichomes at maturity, acute apex; peduncle 5–12 cm long, 1.6–2 cm in diameter, pendulous and erect, tomentose, light brown; megasporophylls 43–56, 6–8 orthostichies with 5–7 sporophylls per orthostichy, 1.7–2.0 × 3.5–4.0 cm, with a prominent distal face, horns straight and 0.70–0.87 cm long, 0.92–1.50 cm between horns with a right angle between the horns. **Seeds** 1.5–2.4 cm long, 1.2–2.0 cm in diameter, ovate, sarcotesta whitish pink at emergence, light brown at maturity.

Distribution and habitat. *Ceratozamia becerrae* is endemic to the mountains of Sierra Madrigal in southern Tabasco and Chiapas States, Mexico (Fig. 14C), where it occurs on karstic outcrops in evergreen tropical forest and oak forest from 100–800 m.

Etymology. The specific epithet was established in honor of Professor Marco E. Becerra for his relevant contributions in ethnology, archaeology and floristic research in Tabasco (Vovides et al. 2004).

Common names. None recorded.

Uses. None recorded.

Conservation status. (IUCN 2021). Endangered; A2ac+4ac; B2ab(i,ii,iv); C1.

Discussion. *Ceratozamia becerrae* has oblong and coriaceous leaflets and leaves that have a few thin and short prickles. This species belongs to a cryptic taxonomic group with *C. zoquorum* and *C. santillanii* (c.f. Martínez-Domínguez et al. 2017c; Vovides et al. 2020) and is morphologically similar in both vegetative and reproductive characters to *C. zoquorum*. This species differs from *C. santillanii* by its peduncle of ovulate strobili more than 3 cm long, but lacks morphological diagnoses with *C. zoquorum*.

Specimens examined. MEXICO. **Chiapas: Mun. Amatán**, 300 m, J.M. Lázaro Z. 376 (CHIP). **Tabasco: Mun. Tacotalpa**, 260 m, 12 Apr 2014, F. Nicolalde-Morejón et al. 1999, 2000 (CIB); 260 m, 12 Apr 2014, L. Martínez-Domínguez et al. 108–127 (CIB); 19 Jan 2001, S. Avendaño R. 5214b (XAL). **Mun. Teapa**, 100 m, 29 Jan 1985, B.M. Schutzman 645, 648–650 (XAL); 204 m, 22 Feb 2014, F. Nicolalde-Morejón et

al. 1968, 1969 (CIB); 800 m, 11 Jun 1989, *J.A. Alejandre Rosas 494* (CIB); 204 m, 22 Feb 2014, *L. Martínez-Domínguez et al. 35–40* (CIB); 400 m, 16 Apr 1996, *M.A. Pérez-Farrera 901* (CHIP, HEM, MEXU); 800 m, 7 Apr 1914, *M.E. Becerra s/n* (MEXU).

4. *Ceratozamia brevifrons* Miq., Tijdschr. Wis-en natuurk Wet. 1: 41. 1847

Figs 3B, 12C, 14D, 15D

Type. MEXICO. Veracruz: Mun. Alto Lucero de Gutiérrez Barrios, Apr 2005, *S. Avendaño R. 5699* (neotype, designated by Vovides et al. 2012, pg. 38: XAL! [XAL0132508]).

Description. *Stem* 20–70 cm long, 15–40 cm in diameter, epigeous, erect. *Cataphylls* 2–5 × 1.5–4 cm wide at the base, persistent, triangular, reddish brown, densely brownish tomentose at emergence, glabrous at maturity with an acuminate apex. *Leaves* 6–36, 58–173.5 cm long, descending, yellowish green at emergence with brown trichomes, glabrous at maturity. *Petiole* 20–56 cm long, terete, linear, green in mature leaves; with 40–90 robust prickles, 0.24–50 cm long. *Rachis* 35–125.5 cm long, terete, linear, green in mature leaves, with prickles. *Leaflets* 13–38 pairs, opposite to subopposite, insertion keeled, sometimes imbricate, lanceolate, abaxially curved, basally falcate, coriaceous, flat, light green with adaxial and abaxial sides glabrous, distal end with entire margins, acuminate and symmetrical to asymmetrical at the apex, attenuate at base, with conspicuous and green-light veins; median leaflets 15.5–41 × 2–4.1 cm, 0.5–3.2 cm between leaflets; articulations 0.6–1.7 cm wide, yellow. *Pollen strobili* 18–31 cm long, 4–7 cm in diameter, solitary, cylindrical, erect, greenish yellow at emergence, greenish yellow with brown to blackish trichomes at maturity; peduncle 4–10.3 cm long, 1.7–2.2 cm in diameter, reddish brown to light-brown pubescent; microsporophylls 1.55–2.3 × 0.80–1.5 cm, obconic with a non-recurved distal and a lobate fertile portion, infertile portion 0.50–0.70 cm long and rounded with straight horns 0.24–0.40 cm long, 0.50–1.02 cm and an acute angle between the horns. *Ovulate strobili* 25–33 cm long, 9.8–12.5 cm in diameter, solitary, cylindrical, erect, green with blackish trichomes at emergence, greenish yellow with brown to blackish trichomes at maturity and with an acuminate and apiculate apex; peduncle 6–14 cm long, 2.0–2.4 cm in diameter, pendulous and erect, brown to reddish brown pubescent; megasporophylls 80–224, 8–16 orthostichies with 10–15 sporophylls per orthostichy, 1.5–2.8 × 2.5–3.2 cm, with a prominent distal face, horns straight and robust and 0.75–0.95 cm long, 1.15–1.70 cm between horns with an acute angle between the horns. *Seeds* 2.0–3.0 cm long, 1.3–2.0 cm in diameter, ovate, sarcotesta whitish yellow to yellow when immature, light brown at maturity.

Distribution and habitat. *Ceratozamia brevifrons* is known only from Sierra de Chiconquiaco in Veracruz State, Mexico (Fig. 14D) where it occurs in the transition zone between cloud forest and oak forest at 450 to 1,370 m.

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

Common names. Mexico. Veracruz: Palma (J. Rees 1636); palmilla (A.P. Vovides et al. 682).

Uses. None recorded.

Conservation status. The area of distribution of *Ceratozamia brevifrons* is small and populations are close. Martínez-Domínguez et al. (2021) using ecological niche model estimated approximately 817 km² of potential distribution with 558 km² of transformed habitat. In addition, this species is not in a protected area. All data suggest that *C. brevifrons* could be assigned as “Endangered (EN)”.

Discussion. *Ceratozamia brevifrons* is easily distinguished from its congeners by having adaxially keeled and coriaceous leaflets, petioles armed with abundant short and robust prickles and greenish yellow ovulate strobili with brown to blackish brown trichomes at maturity.

Specimens examined. MEXICO. Veracruz: **Mun. Alto Lucero de Gutiérrez Barrios**, 24 Aug 1976, *A.P. Vovides* 119 (XAL); 8 Jan 2009, *D. Jimeno-Sevilla* 694 (XAL); 1,052 m, 12 Jan 2013, *F. Nicolalde-Morejón et al.* 1711–1731 (CIB); 1,052 m, 22 Aug 2014, *F. Nicolalde-Morejón & L. Martínez-Domínguez* 2027–2046 (CIB); 1,250 m, 6 Apr 1981, *G. Castillo-Campos* 1297 (XAL); 700 m, 3 Dec 1974, *J. Rees* 1636 (MO, XAL), 1641, 1642, 850 m, 21 Sep 1976, 1675 (XAL); 1,052 m, 21 Jun 2014, *L. Martínez-Domínguez & F. Nicolalde-Morejón* 130–133 (CIB); 842 m, 6 Feb 2015, *L. Martínez-Domínguez & F. Nicolalde-Morejón* 216–226 (CIB); 1,052 m, 22 Mar 2015, *L. Martínez-Domínguez & F. Nicolalde-Morejón* 298–309 (CIB); 450 m, 14 Jul 1995, *M. Vázquez-Torres* 4790 (CIB); 24 Jun 2010, *M. Vázquez-Torres et al.* 9186 (CIB); 850 m, 10 Jan 2001, *T.W. Walters* 2001-02-A, B (XAL). **Mun. Chiconquiaco**, 1,268 m, 10 April. 2015, *F. Nicolalde-Morejón & L. Martínez-Domínguez* 2237–2241 (CIB); 1,340 m, 2 May 2019, *F. Nicolalde-Morejón et al.* 3138–3147 (CIB); 1,268 m, 10 Apr 2015, *L. Martínez-Domínguez & F. Nicolalde-Morejón* 556–560 (CIB); 1,340 m, 2 May 2019, *L. Martínez-Domínguez et al.* 1729–1738 (CIB). **Mun. Colipa**, *Marts* 1841 (MO). **Mun. Juchique de Ferrer**, 850 m, 30 Aug 1981, *A.P. Vovides* 682 (XAL); 1,250 m, 6 May 1981, *G. Castillo-Campos* 1710, 1763, 1768 (XAL); 1,300 m, 7 May 1981, *G. Castillo-Campos* 1815, 1824, 1981 (XAL); 1,370 m, 24 Jul 2008, *M. Vázquez-Torres* 8633 (CIB). **Mun. Vega de Alatorre**, 650 m, 21 Jul 1981, *B. Guerrero & J.I. Calzada* 1826 (XAL); 550 m, 21 Jul 1981, *G. Castillo-Campos* 2033 (XAL).

5. *Ceratozamia chamberlainii* Mart.-Domínguez, Nic.-Mor. & D.W.Stev., *Phytotaxa* 317(1): 22. 2017

Figs 3C, 15E

Type. MEXICO. San Luis Potosí: Mun. Xilitla, 1,044 m, 20 Mar 2016, *L. Martínez-Domínguez et al.* 933 ♀ (holotype: CIB! [acc. # 17766UV]; isotypes: MEXU! [MEXU1492226, MEXU1492227, MEXU14922278], NY!).

Description. *Stem* 20–60 cm long, 15–30 cm in diameter, epigeous, erect and decumbent. *Cataphylls* 2.5–5.5 × 1.5–3.5 cm wide at the base, persistent, narrowly triangular, reddish brown, densely brownish tomentose at emergence, glabrous at maturity, apex acuminate. *Leaves* (5)10–40, 100–207 cm long, descending, reddish brown at emergence with whitish gray trichomes, glabrous at maturity. *Petiole* 30–69 cm long, terete, linear, blackish brown in mature leaves; with 9–30 robust prickles, 0.03–0.30 cm long. *Rachis* 65–144 cm long, terete, linear, reddish brown in mature leaves, with prickles. *Leaflets* 20–42 pairs, opposite to subopposite, insertion in one plane, oblong, longitudinally curved abaxially to planar, not basally falcate, coriaceous, flat, dark green with adaxial and abaxial sides glabrous, distal end with entire margins, acuminate and asymmetric at the 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 0.5–1.3 cm wide, generally reddish brown. *Pollen strobili* 20–31 cm long, 4.5–6 cm in diameter, generally solitary (1–2), cylindrical, erect, greenish brown at emergence with reddish trichomes becoming greenish with reddish brown trichomes at maturity; peduncle 5.2–8.1 cm long, 1.6–2.3 cm in diameter, reddish brown pubescent; microsporophylls 1.6–2.3 × 0.9–1.5 cm, obconic with a non-recurved distal face and a deeply lobate fertile portion, infertile portion 0.44–0.55 cm long and linear with curved horns 0.25–0.40 cm long, 0.40–0.80 cm and an acute angle between the horns. *Ovulate strobili* 25.5–30 cm long, 7.5–10.5 cm in diameter, cylindrical, erect, greyish green with reddish brown trichomes at emergence and becoming light grayish brown with reddish brown trichomes at maturity with an acuminate apex; peduncle 4.5–11.5 cm long, 1.3–2.5 cm in diameter, erect, tomentose, brown to reddish brown; megasporophylls 49–180, 7–12 orthostichies with 7–15 sporophylls per orthostichy, 2.0–3.0 × 2.3–4.0 cm, with a prominent distal face, horns straight and 0.40–0.80 cm long, 2.0–2.70 cm between horns with an acute angle between the horns. *Seeds* 2.2–3.5 (4) cm long, 0.6–1.7 cm in diameter, ovate, sarcotesta whitish red to pink when immature, light brown at maturity.

Distribution and habitat. *Ceratozamia chamberlainii* is distributed in the northern montane region of Carso Huasteco in San Luis Potosí, Querétaro and Hidalgo States, Mexico (Fig. 16A), where it occurs in cloud forest and pine-oak forest on rocky outcrops between 900–1,200 m.

Etymology. The specific epithet is in honor of Charles Joseph Chamberlain in recognition of his remarkable contributions to knowledge of the biology of the cycads and his fieldwork on Mexican Cycads (Martínez-Domínguez et al. 2017a).

Common names. Mexico. San Luis Potosí: Chamal (A.P. Vovides 1288), chamalillo (H. Puig 3979); Hidalgo: teocintle (A. Vite-Reyes et al. 23).

Uses. None recorded.

Preliminary conservation status. According to the IUCN criteria, the data suggest “Endangered (EN)”. *Ceratozamia chamberlainii* is included in Biosphere Reserve Sierra Gorda and have 9 populations recorded by us with several adult plants, juveniles and seedlings.

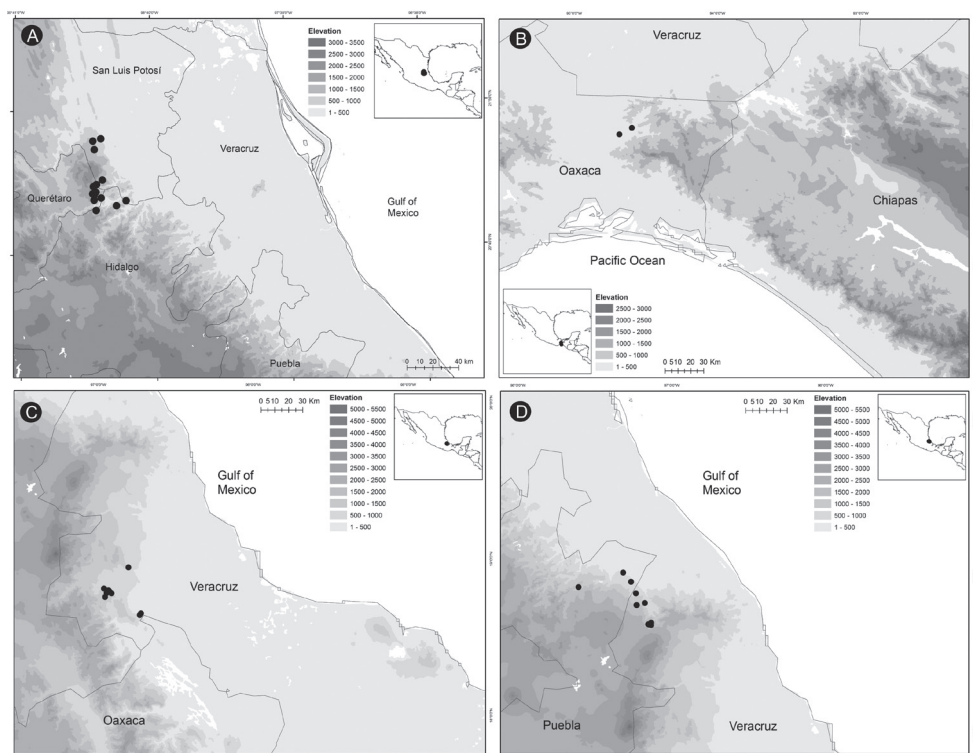


Figure 16. Distribution of *Ceratozamia* species **A** *C. chamberlainii* **B** *C. chimalapensis* **C** *C. decumbens* **D** *C. delucana*.

Discussion. *Ceratozamia chamberlainii* is close geographically and morphologically to *C. fuscoviridis* and *C. latifolia*; however, it differs by its petioles and rachis bearing abundant and short prickles, and its oblong and coriaceous leaflets with conspicuous, reddish brown veins. In addition, the leaves are reddish brown at emergence and at maturity have this color in the leaflet articulations and at the base of leaflets in contrast to the yellowish to greenish articulations in *C. fuscoviridis* and *C. latifolia*.

Specimens examined. MEXICO. **Hidalgo:** **Mun. Chapulhuacán**, 1,500 m, 21 Feb 1998, *Alcántara-Ayala* 3650 (FCME); 8 Jan 2009, *A. Vite-Reyes et al.* 23 (XAL); 1,157 m, 30 Mar 2015, *F. Nicolalde-Morejón et al.* 2200–2203 (CIB); 20 Sep 1964, *L. González-Quintero* 4634 (ENCB); 1,157 m, 30 Mar 2015, *L. Martínez-Domínguez et al.* 429–454 (CIB). **Mun. La Misión**, 1,120 a 1,400 m, 5 Oct 2007, *A. Castro-Castro et al.* 1017 (IBUG, XAL); 7 Jan 2009, *A. Vite-Reyes et al.* 20 (XAL). **Querétaro:** **Mun. Landa de Matamoros**, 1,050 m, 28 May 1999, *A.P. Vovides* 1288, 1289, 1290, 2000 (XAL), 1291 (XAL, MEXU); 2 Apr 1991, *E. Carranza* 6333 (IEB); 940 m, 2 Apr 1991, 3119 (MEXU); 1,335 m, 30 Mar 2015, *F. Nicolalde-Morejón et al.* 2192–2197 (CIB); 1,145 m, 30 Mar 2015, *F. Nicolalde-Morejón et al.* 2198, 2199 (CIB); 1,335

m, 30 Mar 2015, *L. Martínez-Domínguez et al.* 379 (CIB, MEXU), 380–407 (CIB); 1,145 m, 30 Mar 2015, *L. Martínez-Domínguez et al.* 408–428 (CIB); 1,070 m, 9 May 1989, *R. Hiram* 647 (XAL). **San Luis Potosí: Mun. Aquismón**, 600 m, 10 Feb 1969, *H. Puig* 3979 (ENCB, P); 27 May 1979, *J.A. Alcorn* 3093 (MEXU); 1,125 m, 9 Jun 2015, *T. Diego-Vargas & M. Bonta* 35 (XAL). **Mun. Tamazunchale**, Jul 1952, *A. Wilson* 273, 274 (US); Jul 1937, *C.L. Lundell & A.A. Lundell* 7235 (CIB, IEB); 600–900 m, 29 Jun 1959, *J. Rzedowski* 11087 (ENCB). **Mun. Xilitla**, 1,044 m, 20 Mar 2016, *F. Nicolalde-Morejón et al.* 2407–2420 (CIB); 1,044 m, 20 Mar 2016, *L. Martínez-Domínguez et al.* 924–932, 934–937 (CIB), 938 (CIB, MEXU), 939 (CIB); 1,948 m, 12 Jan 2001, *T.W. Walters*, TW-2001-04-A,B (XAL), TW-2001-04-C (MEXU).

6. *Ceratozamia chimalapensis* Pérez-Farr. & Vovides, Bot. J. Linn. Soc. 157: 169. 2008

Fig. 15F

Type. MEXICO. Oaxaca: Chimalapa, 21 Jan 2002, *M.A. Pérez-Farrera* 2622 ♀ (holotype: HEM [n.v.]; isotypes: XAL [XAL0146074], MEXU [n.v.], MO [n.v.]).

Description. **Stem** 20–60 cm long, 15–30 cm in diameter, epigeous, erect and decumbent. **Cataphylls** 4–7.5 × 2.5–4.3 cm wide at the base, persistent, triangular, reddish brown, scarce brown tomentose at emergence, glabrous at maturity, apex acuminate. **Leaves** 7–24, 66–250 cm long, ascending, brown at emergence, glabrous at maturity. **Petiole** 40–70 cm long, terete, linear, green in mature leaves; with 20–30 thin prickles, 0.05–0.30 cm long. **Rachis** 60–150 cm long, terete, linear, green in mature leaves, with prickles. **Leaflets** 36–70 pairs, opposite to subopposite, insertion in one plane, lanceolate, longitudinally curved abaxially to planar, not basally falcate, papyraceous, flat, light green with adaxial and abaxial sides glabrous, distal end with entire margins, acuminate and symmetrical at the apex, attenuate at base, with conspicuous and green-light veins; median leaflets 27–46 × 1.2–1.8 cm, 0.8–1.3 cm between leaflets; articulations 0.5–0.9 cm wide, brown to yellowish brown. **Pollen strobili** 25–40 cm long, 3–5 cm in diameter, solitary, cylindrical, erect, greenish yellow at emergence with few brown trichomes, greenish to cream at maturity; peduncle 5–11 cm long, 1.5–3 cm in diameter, reddish brown pubescent; microsporophylls 1.3–2 × 0.6–1 cm, elliptic with a non-recurved distal face and a lobate to slightly lobate fertile portion, infertile portion 0.7–1.1 cm long and linear with curved horns 0.30–0.43 cm long, 0.8–1.1 cm and an acute angle between the horns. **Ovulate strobili** 35–40 cm long, 7.3–10.6 cm in diameter, solitary, cylindrical, erect, green with blackish trichomes at emergence, green with blackish trichomes at maturity, acuminate apex; peduncle 7–11 cm long, 1.7–2 cm in diameter, erect, brown to reddish brown pubescent; megasporophylls 99–192, 11–12 orthostichies with 9–16 sporophylls per orthostichy, 4–5.9 × 1.8–2.5 cm, with a prominent distal face, horns straight and thin and 0.78–0.98 cm long, 0.98–2.0 cm between horns with an acute angle between the horns. **Seeds** 2.0–3.0 cm long, 1.4–

1.9 cm in diameter, ovate, sarcotesta whitish yellow to yellow when immature, light brown at maturity.

Distribution and habitat. *Ceratozamia chimalapensis* is endemic to Oaxaca State (Mexico) in the Sierra Atravesada mountain range at 290–1,000 m (Fig. 16B) in oak forest on clay soils.

Etymology. The specific epithet is in honor of the Chimalapa region renowned for its biological richness, particularly its floristic diversity.

Common names. Mexico. Oaxaca: Mazacopa (Vovides et al. 2008).

Uses. The sarcotesta of seeds is used as food; the ground seed is used as a rodenticide and with honey added, used as an insecticide (Vovides et al. 2008).

Preliminary conservation status. *Ceratozamia chimalapensis* is only known from a narrow area with several individuals. Data are insufficient to propose a conservation status at this time.

Discussion. *Ceratozamia chimalapensis* is similar to *C. mirandae* and *C. alvarezii* in leaf morphology; however, there are differences in reproductive structures; the ovulate strobilus of *C. chimalapensis* is longer than in these species. The ovulate strobili have between 11–12 orthostichies with 9–16 sporophylls per orthostichy, and more than 90 seeds per strobilus. The seeds are ovate, whereas in the other two species, they are spherical.

Specimens examined. MEXICO. Oaxaca: Mun. Santa María Chimalapa, 290 m, 11 Jun 1995, R. García S. 319 (SERO, XAL). Mun. Santiago Niltepec, 1000 m, 3 Apr 1946, E. Hernández Xolocotzi & A.J. Sharp 1277 (MEXU).

7. *Ceratozamia decumbens* Vovides, Avendaño, Pérez-Farr. & Gonz.-Astorga, Nov-on 18 (1): 110. 2008

Fig. 15G

Type. MEXICO. Veracruz: Naranja, Near Cueva de Los Muñecos, 700 m, 8 Apr 2005, S. Avendaño & G. Alducin 5706 (holotype: XAL! [XAL0005416, XAL0005418]; isotypes: HEM [n.v.], MO!).

Description. **Stem** 10–40 cm long, 10–25 cm in diameter, epigeous, erect and decumbent. **Cataphylls** 1.5–3 × 2–4.2 cm wide at the base, persistent, triangular, densely tomentose at emergence, reddish brown and partially tomentose at maturity, apex acuminate. **Leaves** 2–7, 80–190 cm long, descending, reddish brown at emergence with whitish gray trichomes, glabrous at maturity. **Petiole** 40–100 cm long, terete, linear, greenish brown in mature leaves; with 2–22 (28) thin prickles, 0.02–0.23 cm long. **Rachis** 40–123 cm long, terete, linear, brown and green in mature leaves, with prickles and occasionally unarmed. **Leaflets** 8–24 pairs, opposite to subopposite, insertion in one plane, oblong, in general longitudinally planar, not basally falcate, coriaceous, flat, green, adaxial and abaxial sides glabrous, distal end with entire margins, acuminate and symmetrical to asymmetrical at the 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; with articulations 0.7–1.2 cm wide, brown. **Pollen strobili** 20–23 cm long, 3.8–4.5 cm in diameter, solitary, cylindrical, erect, greenish yellow at emergence with reddish brown trichomes at maturity; peduncle 8–10.8 cm long, 1.2–1.6 cm in diameter, reddish brown to brown pubescent; microsporophylls $1\text{--}1.9 \times 1\text{--}1.4$ cm, obconic with a non-recurved distal face and lobate fertile portion, infertile portion 0.59–0.65 cm long and linear with straight horns 0.27–0.33 cm long, 0.67–0.80 cm and an acute angle between the horns. **Ovulate strobili** 9–11 cm long, 7–8 cm in diameter, solitary, cylindrical, erect, wine at emergence, wine with blackish brown trichomes at maturity, with an acute apex; peduncle 3–4 cm long, 1–1.2 cm in diameter, erect, brown pubescent; megasporophylls 18–49, 6–7 orthostichies with 3–7 sporophylls per orthostichy, $2.3\text{--}2.5 \times 2\text{--}3$ cm, with truncate distal face, horns straight and thin and 0.45–0.58 cm long, 0.99–1.48 cm between horns with a right angle between the horns. **Seeds** 1.2–2 cm long, 1.2–1.5 cm in diameter, ovate, sarcotesta whitish red when immature, light brown at maturity.

Distribution and habitat. *Ceratozamia decumbens* is endemic to a small central mountain range in Veracruz State, Mexico (Fig. 16C) growing on karstic rocks in mountain tropical forest and cloud forest at 450–1,100 m.

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

Common names. None recorded.

Uses. None recorded.

Preliminary conservation status. *Ceratozamia decumbens* has not been listed in the IUCN Red List of Threatened Species (<https://www.iucnredlist.org/>). Its distribution area has been severely affected by anthropogenic land-use changes (Martínez-Domínguez et al. 2021). However, known populations have between 100 to 150 adult plants with juvenile and seedlings. All data suggest that the conservation status should be “Endangered (EN)”.

Discussion. *Ceratozamia decumbens* is distinguished from its most similar species (*C. mexicana* and *C. moretti*) by the ovulate strobili which are wine red with blackish brown trichomes at maturity and an acute apex, whereas in *C. mexicana* they are green with blackish brown and gray trichomes with an acuminate apex, and *C. moretti* are green with blackish brown trichomes with an apiculate apex. In terms of vegetative morphology, it differs from these species by its reddish brown leaves with whitish gray trichomes at emergence.

Specimens examined. MEXICO. Veracruz: Mun. Atoyac, 900 m, 28 Jan 1986, R. Acevedo R. 728 (XAL). Mun. Coetzala, 650 m, 30 Nov 2001, A. Rincón G. 2798 (MEXU, XAL); 870 m, 15 Jul 2015, L. Martínez-Domínguez et al. 655–683 (CIB). Mun. Córdoba, 1,100 m, 10 Jun 1985, A. Espíritu & J.L. Martínez 94 (XAL). Mun. Ixtaczoquitlán, 1,090 m, 25 May 1985, A. Pérez P. 282 (XAL). Mun. Naranja, 11 Sep 1982, A.P. Vovides 751 (XAL); 10 Oct 1993, Brigada T. Walters s/n (XAL); 11 Sep 1982, J. Rees 1690 (XAL); 10 Oct 1993, T.W. Walters 41277, 41308, 41397 (XAL). Mun. Tequila, 445 m, 28 Oct 2007, J.E. Rivera Hdez. & A. Vergara

V. 4195 (MEXU, XAL); 959 m, 15 Jul 2015, *F. Nicolalde-Morejón et al.* 2259, 2260 (CIB); 959 m, 15 Jul 2015, *L. Martínez-Domínguez et al.* 684–703 (CIB). **Mun. Tezonapa**, 1 Dec 1995, *M.A. García B.* 980 (XAL); 475 m, 24 Jun 1986, *R. Robles G.* 882 (XAL). **Mun. Zongolica**, 11 Mar 2011, *L. Hermann Bojórquez G. et al.* 2337 (CIB).

8. *Ceratozamia delucana* Vázq. Torres, A. Moretti & Carv.-Hern., Delpinoa 50–51: 129. 2013 (“2008–2009”)

Figs 2A, B, 10A, B, 15H

Type. MEXICO. Veracruz: Mun. Atzalan, road Atzalan–Tlapacoyan, 3 km NE from Atzalan, 20 Jan 2012, *M. Vázquez-Torres & C. Carvajal-Hernández* 10200 ♀ (holotype: CIB! [acc. # 13915UV]; isotypes: XAL [n.v.], XALU!).

Description. **Stem** 20–90 cm long, 25–40 cm in diameter, epigeous, erect and decumbent. **Cataphylls** 2–5.5 × 2.5–4.5 cm wide at the base, persistent, narrowly triangular, reddish brown, densely tomentose at emergence, partially tomentose at maturity, apex acuminate. **Leaves** 10–100, 106–223 cm long, ascending, yellowish green at emergence with brown trichomes, glabrous at maturity. **Petiole** 30–87 cm long, terete, linear, light green at mature leaves; with 35–76 thin prickles, 0.21–0.76 cm long. **Rachis** 60–150 cm long, terete, linear, green in mature leaves, with prickles. **Leaflets** 20–43 pairs, opposite to subopposite, insertion in one plane, lanceolate and oblong, longitudinally curved abaxially to planar, basally falcate to non-basally falcate, papyraceous to coriaceous, flat, green, adaxial side glaucous and glabrous and abaxial side glaucous, distal end with entire margins, acuminate and symmetrical to asymmetrical at the 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 0.6–1.6 cm wide, green. **Pollen strobili** 24–32 cm long, 5.5–7.6 cm in diameter, solitary, cylindrical, erect, greenish yellow at emergence, greenish yellow with blackish trichomes at maturity; peduncle 3.5–12.5 cm long, 1.3–2 cm in diameter, tomentose, reddish brown to light-brown; microsporophylls 1.5–2.5 × 1.3–2 cm, discoid and obconic with a non-recurved distal face and a lobate fertile portion, infertile portion 0.30–0.45 cm long and orbicular with straight horns 0.15–0.25 cm long, 0.40–0.60 cm and a right angle between the horns. **Ovulate strobili** 17–40 cm long, 10–13.5 cm in diameter, solitary, cylindrical and globose, erect, dark green with blackish trichomes at emergence, green, generally glabrous at maturity, acute apex; peduncle 5.2–15 cm long, 1.8–2.2 cm in diameter, erect and pendulous, tomentose, brown to reddish brown; megasporophylls 48–266, 7–14 orthostichies with 6–19 sporophylls per orthostichy, 2.2–4.2 × 3.4–4.5 cm, with a truncate distal face, horns straight and 0.45–0.72 cm long, 1.05–1.67 cm between horns with a right angle between the horns. **Seeds** 2.0–3 cm long, 1.35–2.1 cm in diameter, ovate, sarcotesta whitish yellow to yellow when immature, light brown at maturity.

Distribution and habitat. *Ceratozamia delucana* occurs in Veracruz and Puebla States, Mexico (Fig. 16D) and grows on karstic rocks in evergreen tropical forest at 500–1,650 m.

Etymology. The epithet is in honor of Dr. Paolo De Luca, Professor at University of Naples Federico II and a researcher into the biology of Mexican cycads (Vázquez-Torres et al. 2013).

Common names. None recorded.

Uses. None recorded.

Conservation status. During the last 6 years, we have monitored the 6 populations for *Ceratozamia delucana*, in which no loss of individuals and regeneration has been observed. These populations are periodically producing ovulate and pollen strobili. The main problem is the loss of habitat in the central area of Veracruz, where there are no protected natural areas (Martínez-Domínguez et al. 2021). These data suggest the category “Endangered (EN)” under (B1ab(iii)) criteria.

Discussion. *Ceratozamia delucana* is highly variable and in vegetative morphology similar to *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 a larger plant than *C. morettii*, with *C. delucana* having leaves up to 223 cm long with up to 43 pairs of leaflets and ovulate strobili 17–40 cm long.

Specimens examined. MEXICO. **Puebla:** **Mun. Hueytamalco**, 520 m, 25 Feb 2008, G. Ibarra Manríquez et al. 5485 (MEXU, MO). **Mun. Xochitlán de Vicente Suárez**, 1,644 m, 9 Jun 2015, F. Nicolalde-Morejón & L. Martínez-Domínguez 2244, 2245 (CIB); 850 m, 25 Apr 1991, G. Villalobos & E. Guerrero C. 325 (MEXU); 1,644 m, 9 Jun 2015, L. Martínez-Domínguez & F. Nicolalde-Morejón 587–616 (CIB). **Veracruz:** **Mun. Atzacan**, 1,400 m, 20 Feb 2013, F. Nicolalde-Morejón et al. 1740–1742 (CIB); 1,400 m, 16 Aug 2014, F. Nicolalde-Morejón et al. 2125–2144 (CIB); 1,400 m, 13 Mar 2015, F. Nicolalde-Morejón et al. 2168 (CIB); 1,400 m, 27 Oct 2008, L. Lagunes-Galindo et al. 153 (CIB); 1396 m, 28 Oct 2008, L. Lagunes-Galindo et al. 155 (CIB); 1,400 m, 16 Aug 2014, L. Martínez-Domínguez et al. 163 (CIB); 863 m, 13 Mar 2015, L. Martínez-Domínguez et al. 228–238 (CIB); 1,400 m, 13 Mar 2015, L. Martínez-Domínguez et al. 239–248 (CIB). **Mun. Las Minas**, 2 Jun 1979, A.P. Vovides 427 (XAL); 1,500 m, 22 Sep 1988, C. Durán et al. 658 (XAL), 660 (MEXU, XAL); 1,500 m, 22 Sep 1988, C. Durán E. 659 (MEXU, XAL); 1,586 m, 20 Feb 2013, F. Nicolalde-Morejón et al. 1735–1739 (CIB); 1,621 m, 16 Aug 2014, F. Nicolalde-Morejón & L. Martínez-Domínguez 2107–2124 (CIB); 1,621 m, 16 Aug 2014, L. Martínez-Domínguez et al. 162 (CIB); 1,621 m, 18 Mar 2015, L. Martínez-Domínguez et al. 249–260 (CIB); 1 Mar 2005, 1,430 m, L.H. Bojórquez-Galván 1349 (CIB); 1,420 m, 16 Mar 2005, L.H. Bojórquez-Galván 1374 (CIB); 1,470 m, 28 Apr 2009, M. Vázquez-Torres et al. 8972 (CIB). **Mun. Tlapacoyan**, 900 m, 10 Jun 1970, Nevling & A. Gómez-Pompa 1083 (MEXU).

9. *Ceratozamia euryphyllidia* Vázq.Torres, Sabato & D.W.Stev., Brittonia 38(1): 17. 1986

Fig. 15I

Type. MEXICO. Veracruz: Mun. Minatitlán, 21 Jun 1984, *M. Vázquez-Torres* 2842 ♀ (holotype: NY! [acc. # 1157–1166]; isotypes: CHAPA [n.v.], NY! [♂ acc. # 00001167–00001173], XALU [n.v.]).

Description. *Stem* 25–50 cm long, 8–15.3 cm in diameter, semi-hypogeous, erect and decumbent. *Cataphylls* 4.5–7 × 4.2–7.5 cm wide at the base, persistent, triangular, reddish brown, densely tomentose at emergence, glabrous at maturity, apex acute. *Leaves* 2–22, 95–337.5 cm long, ascending, light green, glaucous at emergence, with whitish gray trichomes, glabrous at maturity. *Petiole* 40–193 cm long, terete, linear, green to yellowish (pink in new leaves); with 8–35 thin prickles, 0.13–0.50 cm long. *Rachis* 53–218.5 cm long, terete, linear, green to yellowish in mature leaves, with prickles. *Leaflets* 6–17 pairs, opposite to subopposite, insertion in one plane, broadly obovate, in general longitudinally planar, not basally falcate, membranaceous, flat, green with adaxial and abaxial sides glabrous, distal end with sinuate margins, acuminate and asymmetrical at the apex, attenuate at base, with prominent and light-green veins; median leaflets 19.9–35.7 × 8.5–17.6 cm, 9–22 cm between leaflets; articulations 0.9–1.4 cm wide, yellow and green. *Pollen strobili* 27–35 cm long, 3–4.3 cm in diameter, solitary, cylindrical, erect, greenish yellow with reddish trichomes at emergence, greenish with black trichomes at maturity; peduncle 6–12 cm long, 1.5–2 cm in diameter, tomentose, reddish brown to brown; microsporophylls 1.0–1.5 × 0.5–1.3 cm, discoid with a non-recurved distal face and a lobate fertile portion, infertile portion 0.37–0.45 cm long and orbicular and rounded with straight horns 0.35–0.50 cm long, 0.60–0.72 cm and an acute angle between the horns. *Ovulate strobili* 15–20 cm long, 5–6 cm in diameter, solitary, cylindrical, erect, yellowish green to green with abundant, deep red trichomes at emergence, greenish brown with abundant, dark reddish brown trichomes at maturity, acuminate apex; peduncle 5–11.5 cm long, 1–2.5 cm in diameter, erect, tomentose, light brown; megasporophylls 35–64, 1.5–3 × 1.2–1.8 cm, 7–8 orthostichies with 5–8 sporophylls per orthostichy, 2.0–4.0 × 2.8–3.4 cm wide, with a truncate distal face, horns straight and 0.60–0.80 cm long, 0.99–1.40 cm between horns with an acute angle between the horns. *Seeds* 2.3–2.5 cm long, 1.5–1.7 cm in diameter, ovate, sarcotesta whitish red when immature, light brown at maturity.

Distribution and habit. *Ceratozamia euryphyllidia* is endemic to the forest of Uxpanapa-Chimalapas in Oaxaca and Veracruz States, Mexico (Fig. 17A) where it inhabits evergreen tropical rain forest on clay soils at the top and sides of hills between 100 and 630 m elevation.

Etymology. The specific epithet represents the very wide, diagnostic leaflets of this species. It comes from the Greek *euryphyllos*, which means, “wide leaflet”.

Common names. None recorded.

Uses. None recorded.

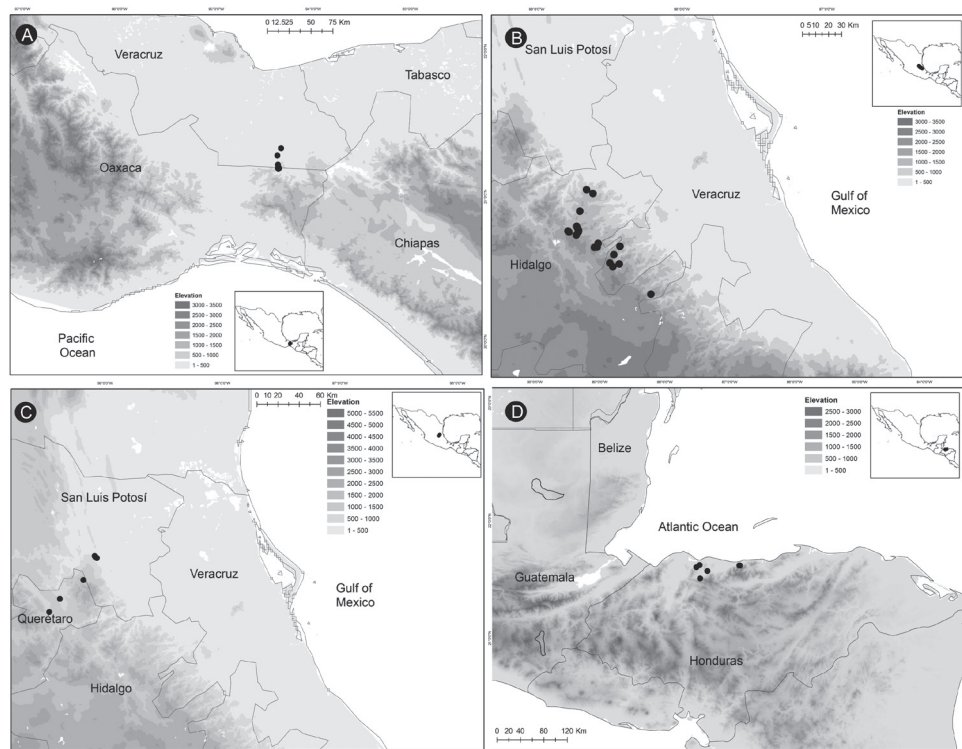


Figure 17. Distribution of *Ceratozamia* species **A** *C. euryphyllidia* **B** *C. fuscoviridis* **C** *C. hildae* **D** *C. hondurensis*.

Conservation status. (IUCN 2021). *Ceratozamia euryphyllidia* is listed as “Critically Endangered (CR)” under criteria B2ab(i,ii,iii,iv,v). We carried out a census in two populations for this species, in which we found between 20 to 60 adult plants. The population in Veracruz has reproductive plants, juvenile and seedlings; however, it is a small population and the surrounding area has been transformed to anthropogenic landscapes. We suggest that this status should be maintained.

Discussion. *Ceratozamia euryphyllidia* is easily diagnosable from its congeners in Mexico by its broadly obovate, lustrous and membranaceous leaflets asymmetrical apex of leaflets. Also, the ovulate strobili are greenish brown with an acuminate apex, and its megasporophylls are green with abundant dark brown trichomes. This species is most similar to *C. hondurensis*, but it can be distinguished by its sinuate margins at distal end of leaflets, whereas in *C. hondurensis* they are entire.

Specimens examined. MEXICO. **Veracruz:** **Mun. Minatitlán**, 100 m, 24 Jul 1986, A.P. Vovides & E.R. Acosta 1108 (MO, XAL); 21 Jun 1984, M. Vázquez-Torres 1157 (NY). **Mun. Jesús Carranza**, 24 May 1982, M. Vázquez-Torres 2532 (CIB, MEXU); 26 Mar 1982, M. Vázquez-Torres et al. 2374 (CHAPA, MEXU, NY); 100 m, 5 Jun 1989, M. Vázquez-Torres & J.P. Sclavo 4037 (CIB); 18 Apr 1982, M. Vázquez-Torres 2451 (CHAPA, MEXU, MO, NY); 120 m, 28 Jul 1983, M. Vázquez-Torres 2614

(CIB, NY); 21 Jun 1984, *M. Vázquez-Torres* 4126 (NY); 120 m, 28 Dec 1984, *T. Wenth et al.* 4732 (CHAPA). **Mun. Uxpanapa**, 398 m, 18 Mar 2014, *F. Nicolalde-Morejón & L. Martínez-Domínguez* 1984 (CIB); 19 Mar 2014, *L. Martínez-Domínguez & F. Nicolalde-Morejón* 71–77 (CIB). **Mun. Hidalgotitlán** (plant cultivated at JBC-INECOL), *V.E. Luna M.* 1520 (XAL). **Oaxaca: Mun. Santa María Chimalapa**, 232 m, 13 May 1995, *E. Torres B.* 687 (SERO, XAL); 398 m, 18 Mar 2014, *F. Nicolalde-Morejón & L. Martínez-Domínguez* 1982, 1983 (CIB); 335 m, 5 May 1996, *J.E. Rivera H. & S. Escobedo* 102 (XAL); 630 m, 16 May 1998, *J.E. Rivera H. et al.* 700 (MEXU); 475 m, 21 Mar 1999, *J.E. Rivera H. et al.* 1195 (SERO); 398 m, 18 Mar 2014, *L. Martínez-Domínguez & F. Nicolalde-Morejón* 51–70 (CIB).

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

Figs 3A, 9C, 15J

Ceratozamia mexicana Brongn. f. *fuscoviridis* (W.Bull.) J.Schust., Pflanzenr. (Engler) Heft 99, 4 fam 1: 132. 1932, as *C. mexicana* var. *longifolia* f. *fuscoviridis*. Type: Based on *Ceratozamia fuscoviridis* W.Bull.

Type. Cultivated at Glasnevin, Ireland “Hort. Bot. Glasnevin”, 21 Mar 1878 (accessioned 1881), *D. Moore s.n.* (neotype, designated by Calonje and Sennikov 2017, pg. 161: K! [K000501714, K000501712, K000501713]). Mexico. Hidalgo: Mun. Molango, km 3 carretera Molango-Xochicoatlán, 1,860 m, 31 Mar 2015, *L. Martínez-Domínguez et al.* 493 ♀ (epitype, designated by Martínez-Domínguez et al. 2018a: 105: CIB! [acc. # 17465UV]; isoeotype: MEXU! [acc. # 1520508, 1520282, 1520519]).

Description. *Stem* 20–90 cm long, 25–40 cm in diameter, epigeous, erect and decumbent. *Cataphylls* 2–4.5 × 2–3.5 cm wide at the base, persistent, narrowly triangular, reddish brown, densely brownish tomentose at emergence, tomentose at maturity, apex acuminate. *Leaves* 10–70, 92–215 cm long, ascending, light green and dark brown at emergence, with whitish gray trichomes, glabrous at maturity. *Petiole* 40–95 cm long, terete, linear, dark green in mature leaves; with 14–60 (66) thin prickles, 0.09–0.33 cm long. *Rachis* 65–150 cm long, terete, linear, green in mature leaves, with prickles. *Leaflets* 28–67 pairs, opposite to subopposite, insertion in one plane, lanceolate, abaxially curved longitudinally, basally falcate, papyraceous, flat, green, with adaxial and abaxial sides glabrous, distal end with entire margins, acuminate and symmetrical at the apex, attenuate at base, with conspicuous and green-light brown veins; median leaflets 16.6–42 × 1.3–2.1 cm, 0.6–2 cm between leaflets; articulations 0.6–1.3 cm wide, green and brown. *Pollen strobili* 22–30 cm long, 5–8 cm in diameter, solitary, cylindrical, erect, brownish yellow at emergence, greenish brown with reddish brown trichomes at maturity; peduncle 5–14.5 cm long, 1.6–2.3 cm in diameter, tomentose, reddish brown to brown; microsporophylls 1.6–2.4 × 1.2–1.6 cm, obconic with a non-recurved distal face and a deeply lobate fertile portion, infertile portion 0.45–0.56 cm long and orbicular with straight horns

0.16–0.29 cm long, 0.53–0.80 cm and a right angle between the horns. **Ovulate strobili** 24–35 cm long, 8.5–15 cm in diameter, solitary, cylindrical, erect, green with brown trichomes at emergence, brown-green with dark brown trichomes at maturity, acuminate apex; peduncle 4–15.5 cm long, 1.8–2.5 cm in diameter, erect or pendulous, tomentose, brown to reddish brown; megasporophylls 49–195, 7–15 orthostichies with 7–15 sporophylls per orthostichy, $2.3\text{--}3.5 \times 3.0\text{--}4.0$ cm, with a truncate distal face, horns straight and 0.70–0.99 cm long, 1.7–2.1 cm between horns and an obtuse angle between the horns. **Seeds** 2–2.6 cm long, 1.5–2 cm in diameter, ovate, sarcotesta whitish yellow to yellow when immature, light brown at maturity.

Distribution and habitat. *Ceratozamia fuscoviridis* is endemic to south to central Carso Huasteco in Mexico from Hidalgo to northwest of Veracruz States (Fig. 17B) in cloud forests between 1,300–1,900 m elevation.

Etymology. The epithet refers to the dark-brown color of the leaf at emergence.

Common names. Mexico. Veracruz: teocintle, teocintli and tepecintli (Bonta et al. 2019).

Uses. This species has decorative uses associated with religious ceremonies and national holidays. The leaves are commonly used to make arches in the entrances of some Roman Catholic churches or decorate the walls during national holidays.

Conservation status. (IUCN 2021). *Ceratozamia fuscoviridis* is listed as “Critically Endangered” under criteria B1ab(i,iii,iv,v). This species requires a reassessment of its conservation status because new populations have recently been recorded, including its current circumscription that includes populations from Veracruz State. Based on the number of populations, modelled potential geographical distribution from ecological niche and its occurrence in a Natural Protected Areas (Los Mármoles National Park), *C. fuscoviridis* could be listed as “Endangered (EN)” (Martínez-Domínguez et al. 2021).

Discussion. *Ceratozamia fuscoviridis* is polymorphic within populations because individual plants may have either a light green or dark-brown leaf color at emergence. Individuals with dark-brown leaf at emergence also have a brownish abaxial side. This species is most geographically proximate to *C. chamberlainii*, but it can be distinguished by lanceolate and papyraceous leaflets, a petiole armed with long and thin prickles; and ovulate strobili that are brownish green with dark trichomes at maturity.

Osborne et al. (2006) intended to validate *Ceratozamia fuscoviridis* D.Moore, which was invalidly published in 1878. However, in 2017, Calonje & Sennikov published the correction to this name using a brief description by William Bull in horticultural catalogues. This work is the valid publication for the specie and the name “*C. fuscoviridis* D.Moore” is an isonym with no nomenclatural status.

Specimens examined. MEXICO. **Hidalgo: Mun. Eloxochitlán**, 18 Mar 1995, *I. Luna-Vega* 54716 (FCME). **Mun. Metztlán**, 30 Dec 1992, *J.L. López-García* 449 (ENCB, IBUG, MEXU). **Mun. Molango de Escamilla**, 1,380 m, 29 May 1999, *A.P. Vovides* 1298 (XAL); 1,400 m, 29 May 1999, *A.P. Vovides* 1301 (XAL); 1,500 m, 24 Jul 2008, *A. Vite-Reyes et al.* 6 (XAL); 1,860 m, 31 Mar 2015, *F. Nicolalde-Morejón et al.* 2209–2211 (CIB); 1,860 m, 31 Mar 2015, *L. Martínez-Domínguez et al.* 485–492, 494–514 (CIB); *T.W. Walters* 2001-03-A (XAL). **Mun. Tenango de Doria**, 1,700 m, 12 Mar 1993, *I. Luna-*

Vega 914 (FCME). **Mun. Tlanchinol**, 1,450 m, 25 Aug 1992, *I. Luna-Vega s/n* (FCME); 1,420 m, 7 Oct 1992, *I. Luna-Vega 625* (FCME, XAL); 25 Aug 1992, *I. Luna-Vega 789* (XAL); 1,312 m, 31 Mar 2015, *F. Nicolalde-Morejón et al. 2204–2208* (CIB); 1,312 m, 31 Mar 2015, *L. Martínez-Domínguez et al. 455–484* (CIB). **Mun. Zacualtipán de Ángeles**, 23 Jan, 1983, *J. Rees 389* (CHAPA, FCME, MEXU); 1,360 m, 4 Dec 1974, *J. Rees 1611* (CHIP, XAL); 4 Dec 1974, *J. Rees 6339* (IEB). **Veracruz: Mun. Huayacocotla**, 1,913 m, 23 Feb 2005, *D. Saavedra Millán 64* (FCME); 1,850 m, 13 Mar 1980, *J. Palma G. 63* (XAL); 1,844 m, 1 Apr 2015, *F. Nicolalde-Morejón et al. 2212–2214* (CIB); 1,700 m, 24 Mar 1981, *L. Ballesteros & F. Ballesteros 460* (XAL); 1,550 m, 23 Apr 1981, *L.G. Juárez G. 47* (XAL); 1,844 m, 1 Apr 2015, *L. Martínez-Domínguez et al. 515–544* (CIB); 1,900 m, 11 Feb 1972, *R. Hernández M. 1507* (MEXU, XAL); 26 Feb 1975, *V. Sosa 59* (XAL).

11. *Ceratozamia hildae* G.P.Landry & M.C.Wilson, *Brittonia* 31(3): 422. 1979

Fig. 18

Type. Cultivated in Baton Rouge, Louisiana USA at 5988 South Pollard Parkway (plants originally from several km N of Xilitla, San Luis Potosí, Mexico), *G. Landry 76521*♂ (holotype: GH! [00003274]; isotypes: FTG!, LSU! [LSU00048484], MEXU! [MEXU00443083, MEXU00443084, MEXU00443085], MICH! [1050284A, 1050284B], NY! [00001153–00001156], US! [00011993]).

Description. *Stem* 10–20 cm long, 10–15 cm in diameter, semi-hypogeous, erect. *Cataphylls* 2.1–4.2 × 0.8–1.9 cm wide at the base, persistent, triangular, reddish brown, densely brown tomentose at emergence, partially tomentose at maturity, apex acuminate. *Leaves* 2–7, 95–202 cm long, ascending, reddish brown at emergence with whitish gray trichomes, glabrous at maturity. *Petiole* 43–89 cm long, terete, linear, greenish brown and green in adult leaves; with 2–12 thin prickles, 0.01–0.2 cm long. *Rachis* 60–130 cm long, terete, linear, greenish brown in mature leaves, with prickles and occasionally unarmed. *Leaflets* in 5–11 fascicles, 16–56 leaflets in total, clustered, insertion in one plane, oblong, in general longitudinally planar, basally falcate to non-basally falcate, membranaceous, flat, green with adaxial and abaxial sides glaucous, distal end with entire margins, acuminate and symmetrical to asymmetrical at the apex, attenuate at base, with conspicuous and green-light veins; median leaflets 14.5–24 × 2.4–5 cm, 6–15 cm between leaflets; articulations 0.2–0.5 cm wide, brown and green. *Pollen strobili* 8–12.5 cm long, 2–2.5 cm in diameter, solitary, cylindrical, erect, brown with reddish brown trichomes at emergence, reddish brown at maturity; peduncle 6–8 cm long, 0.8–1 cm in diameter, tomentose, reddish brown to brown; microsporophylls 0.8–1.2 × 0.6–1 cm, discoid with non-recurved distal face and a lobate fertile portion, infertile portion 0.23–0.29 cm long and rounded with curved horns, 0.20–0.25 cm long, 0.39–0.50 cm and an acute angle between the horns. *Ovulate strobili* 10–15 cm long, 6–9 cm in diameter, solitary, cylindrical, erect, green at emergence with brown trichomes, green with brown to blackish trichomes at maturity, acuminate apex; peduncle 7.5–16 cm long, 1.2–1.5 cm in diameter, erect, tomentose, brown; megasporophylls

20–56, 5–8 orthostichies with 4–7 sporophylls per orthostichy, $2\text{--}3.7 \times 2\text{--}4$ cm, with a prominent distal face, horns straight and $0.30\text{--}0.50$ cm long, $1.70\text{--}1.90$ cm between horns with a right angle between the horns. **Seeds** $1.3\text{--}2.3$ cm long, $1.2\text{--}1.5$ cm in diameter, ovate, sarcotesta whitish red when immature, light brown at maturity.

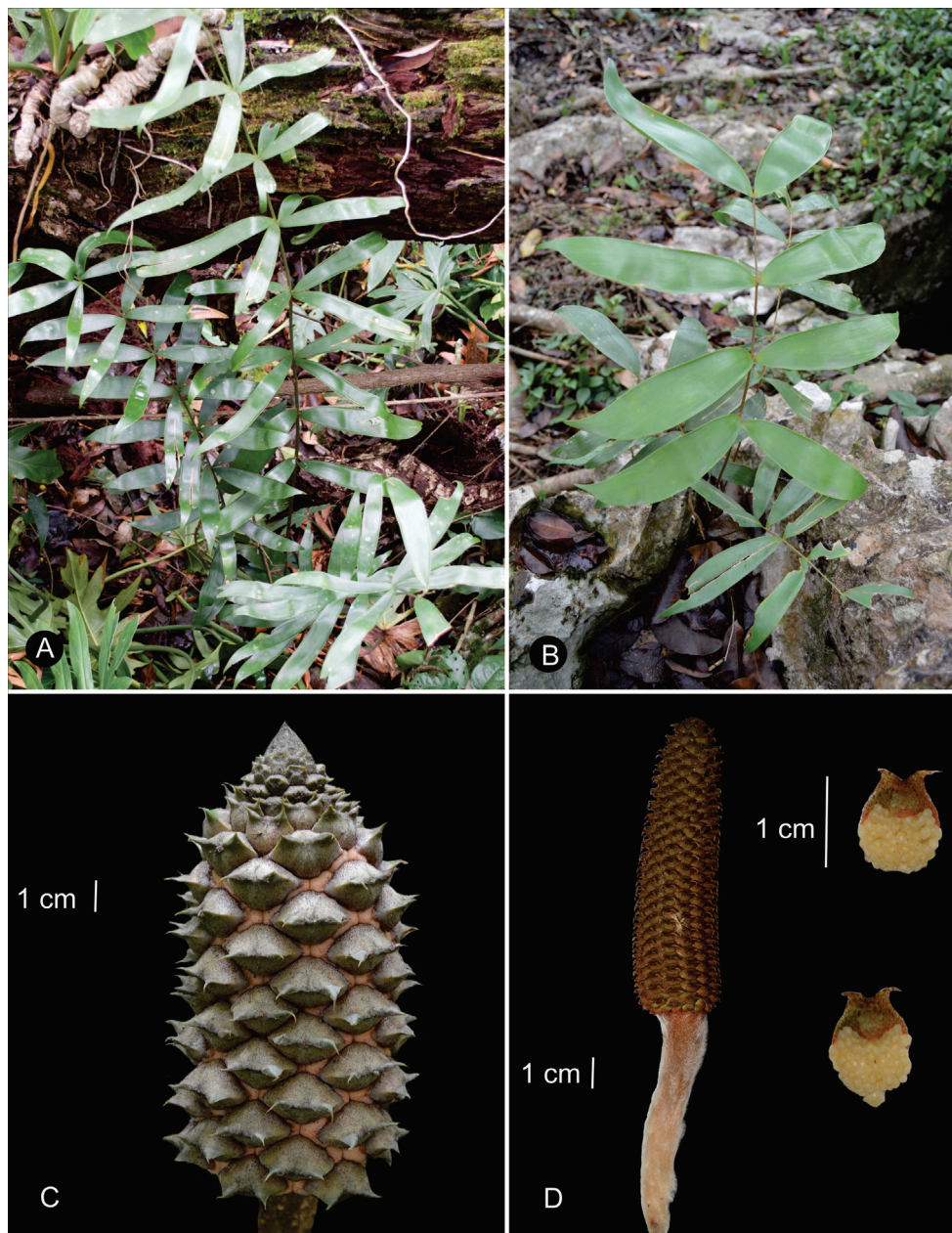


Figure 18. *Ceratozamia hildae* **A** leaves of an adult plant **B** leaves of a juvenile plant **C** mature ovulate strobilus **D** mature pollen strobilus and microsporophylls.

Distribution and habitat. *Ceratozamia hildae* is endemic to Sierra Gorda in Mexico, particularly in San Luis Potosí and Querétaro (Fig. 17C), where it occurs in the evergreen tropical forests on karstic rocks at 300–1,200 m.

Etymology. The epithet is in honor of Hilda Guerra Walker, daughter of the original collector (Luciano E. Guerra, plant collector from Mission Texas) (Landry and Wilson 1979).

Common names. Mexico. Querétaro: Chamalillo, pata de gallo (J. Rees 312).

Uses. None recorded.

Conservation status. (IUCN 2021). *Ceratozamia hildae* is listed as “Endangered” under criteria A2abcd; B1ab(ii,iii,iv).

Discussion. *Ceratozamia hildae* is easily distinguished from other members of the group by its clustered membranous oblong leaflets (Fig. 18A).

Specimens examined. MEXICO. **Querétaro: Mun. Arroyo Seco**, 1,181 m, 9 Nov 2003, J.A. Pérez de la Rosa & G. Vargas A. 1908 (IBUG). **Mun. Jalpan de Serra**, 850 m, 29 Dec 1977, A.P. Vovides 337 (XAL); 29 Dec 1977, A.P. Vovides s/n (IEB); 1,200 m, 8 Mar 1991, B. Servin 870 (MEXU); 1,200 m, 20 Mar 1991, B. Servin 986 (MEXU); 8 Mar 1991, B. Servin 6328 (IEB); 20 Apr 1991, B. Servin 6330 (IEB); Sep 1977, J. Rees s/n (IEB); 312 (XAL). **San Luis Potosí: Mun. Aquismón**, 300 m, 22 Sep 1977, A.P. Vovides & J. Rees 312 (MEXU, XAL); 357 m, 20 Mar 2016, F. Nicolalde-Morejón et al. 2391–2406 (CIB); 357 m, 20 Mar 2016, L. Martínez-Domínguez et al. 910–921, 923, 940 (CIB), 922 (CIB, MEXU); 26 Nov 1970, S. Longoria s/n (MEXU; US); 617 m, 15 Jan 2001, T.W. Walters TW-2001-14-A (MEXU, XAL), TW-2001-14-B (XAL), TW-2001-14-C (MEXU).

12. *Ceratozamia hondurensis* J.L.Haynes, Whitelock, Schutzman & R.S.Adams, *The Cycad Newsletter* 31 (2/3): 16. 2008

Fig. 15K

Type. HONDURAS. Atlántida: Mun. Esparta, 0.5 km SE of Jilamo Nuevo along the Río Jilamito, 13 Apr 1994, A.E. Brand & R. Zúñiga 2830, (lectotype, designated here: MO! [acc. # 5943287–5943289]; isoelectotype: MEXU! [MEXU01347996–MEXU01347999]).

Description. **Stems** 20–50 cm long, 20 cm in diameter, semi-hypogeous, erect and decumbent. **Cataphylls** 4.5–7 × 4.5–7.5 cm wide at the base, persistent, triangular, reddish brown, densely brown tomentose at emergence, glabrous at maturity, apex acuminate. **Leaves** 3–25, 120–322 cm long, ascending, light green at emergence with whitish gray trichomes, glabrous at maturity. **Petiole** 56–150 cm long, terete, linear, green in mature leaves; with 8–34 thin prickles, 0.26–0.50 cm long. **Rachis** 80–200 cm long, terete, linear, with prickles, green in mature leaves. **Leaflets** 10–18 pairs, opposite to subopposite, insertion in one plane, obovate to broadly oblanceolate, in general longitudinally planar, generally not basally falcate, membranaceous, flat, green with adaxial side glabrous and abaxial side glaucous, distal end with entire margins, acuminate and symmetrical at the apex, attenuate at base, with prominent and light-green veins; median leaflets 23–

34.5 × 8–12.8 cm, 8.5–16 cm between leaflets; articulations 0.5–1.6 cm wide, green and yellow. **Pollen strobili** 30–35 cm long, 4–5 cm in diameter, solitary, cylindrical, erect, yellowish green at emergence, yellowish cream with blackish trichomes at maturity; peduncle 2–4 cm long, 2–3 cm in diameter, tomentose, brown; microsporophylls 0.9–1.2 × 0.7–1.2 cm, discoid with a non-recurved distal face and lobate fertile portion, infertile portion 0.52–0.60 cm long, and orbicular and rounded with straight horns 0.18–0.23 cm long, 0.50–0.62 cm and an acute angle between the horns. **Ovulate strobili** 18–22 cm long, 8–10 cm in diameter, solitary, cylindrical, erect, yellowish green to green with abundant, deep red trichomes at emergence, greenish brown with abundant, blackish trichomes at maturity, mucronate apex; peduncle 5–15 cm long, 1.0–3.0 cm in diameter, erect, tomentose, brown; megasporophylls 72–120, 9–11 orthostichies with 8–11 sporophylls per orthostichy, 1.5–2.5 × 4–5.5 cm, with a prominent distal face, horns curved and 0.60–0.80 cm long, 0.99–1.40 cm between the horns with an acute angle between horns. **Seeds** 2.1–2.6 cm long, 1.46–1.89 cm in diameter, ovate, sarcotesta whitish yellow to yellow when immature, light brown at maturity.

Distribution and habitat. *Ceratozamia hondurensis* is endemic to Honduras in the Atlántida department (Fig. 17D), where it grows in evergreen tropical forest between 20–600 m elevation.

Etymology. The specific epithet alludes to the endemism of the species in Honduras.

Common names. Honduras. Atlántida: Camotillo (Haynes et al. 2008).

Uses. The stems are used to elaborate an infusion for poison animals or people. (L. Martínez-Domínguez et al. 2241). Also, the stems are processed for medicinal purposes (Bonta et al. 2019).

Preliminary conservation status. *Ceratozamia hondurensis* is not listed in The IUCN Red List of Threatened Species. There is insufficient data on the population's status of this species, however, it is known that populations have suffered illegal wildlife trade as shown by seizures made at Customs of Honduras.

Discussion. *Ceratozamia hondurensis* is similar in leaf morphology to *C. euryphyllidia*. It differs in its leaflets with a symmetric apex and an entire margin at distal end as compared to the asymmetric apex and sinuate margin at distal end of the leaflets in *C. euryphyllidia*. Additionally, *C. hondurensis* differs in reproductive structures; the ovulate strobilus has mucronate apex, whereas in *C. euryphyllidia* the ovulate strobilus has long (up to 5 cm) acuminate apex.

In protologue, two specimens from “A.E. Brand & R. Zúniga 2830” were cited as types: holotype in EAP and isotype in MO. The type specimen was not deposited in EAP (the herbarium has no record of this material nor was it found in unprocessed material). In addition, we consulted TEFH, the other herbarium in Honduras, with the same result. However, we found a duplicate specimen in MEXU. Thus, we are here designating the specimen in MO cited as isotype as the lectotype and the specimen at MEXU as the isoelectotype.

Specimens examined. HONDURAS. Atlántida: Mun. La Ceiba, 225 m, 14 Apr 1996, D.R. Hodel & Schleider 1485 (MO); 217 m, 29 Jul 2003, J. Haynes et al. 47

(TEFH); 151 m, 19 May 2022, *L. Martínez-Domínguez et al.* 2440, 2443, 2444, 2446–2448 (TEFH). **Mun. Tela**, 0–500 m, 10 Feb 1994, *C. Nelson et al.* 17586 (TEFH); 200–500 m, 9 Apr 1994, *D.L. Hazlett et al.* 8036 (MO); 615 m, 13 Jul 2008, *G. Sandoval et al.* 1312 (TEFH); 615 m, 31 Jul 2003, *J. Haynes et al.* 40 (TEFH); Cultivated, 615 m, 16 Mar 2017, *L. Ferrufino et al.* 777 (TEFH); 163 m, 17 May 2022, *L. Martínez-Domínguez et al.* 2421, 2423, 2425, 2428–2430 (TEFH).

13. *Ceratozamia huastecorum* Avendaño, Vovides & Cast.-Campos, Bot. J. Linn. Soc. 141(3): 395. 2003

Fig. 15L

Type. MEXICO. Veracruz: Mun. Tepetzintla, Sierra de San Juan Otontepec, 1,300 m, 16 Dec 1981, *G. Castillo-Campos et al.* 2567 ♀ (holotype: XAL! [XAL0016937]).

Description. *Stem* 20–50 cm long, 14–20 cm in diameter, semi-hypogeous, erect and decumbent. *Cataphylls* 3.0–4.0 × 2.5–3.0 cm wide at the base, persistent, triangular, reddish brown, densely brown tomentose at emergence, glabrous at maturity, apex acuminate. *Leaves* 4–7, 50–80 cm long, ascending, light green at emergence with whitish gray trichomes, glabrous at maturity. *Petiole* 20–40 cm long, terete, linear, green in mature leaves; with 10–30 thin prickles 0.21–0.35 cm long. *Rachis* 40–70 cm long, terete, linear, green in mature leaves, with prickles. *Leaflets* 8–18 pairs, opposite to subopposite, insertion in one plane, oblong, in general longitudinally planar, not basally falcate, coriaceous, flat, green with adaxial side glabrous and abaxial side glaucous, distal end with entire margins, acuminate and asymmetrical at the apex, attenuate at base, with prominent and light-green veins; median leaflets 12–22 × 2.5–6 cm, 1.6–5 cm between leaflets; articulations 0.4–1.1 cm wide, green. *Pollen strobili* 15–18 cm long, 2.5–3.2 cm in diameter, solitary, cylindrical, erect, yellowish green at emergence, yellowish cream with blackish trichomes at maturity; peduncle 6–23 cm long, 1.6–2.2 cm in diameter, tomentose, brown; microsporophylls 0.8–1.2 × 0.72–1.0 cm, discoid with a non-recurved distal face and a lobate fertile portion, infertile portion 0.28–0.35 cm long and orbicular with straight horns 0.11–0.18 cm long, 0.50–0.68 cm and an acute angle between the horns. *Ovulate strobili* 13.5–18 cm long, 6–10 cm in diameter, solitary, cylindrical, erect, green at emergence, dark green with abundant blackish trichomes at maturity, acuminate apex; peduncle 3–8 cm long, 1.0–2.2 cm in diameter, erect, tomentose, brown; megasporophylls 54–99, 9–10 orthostichies with 6–9 sporophylls per orthostichy, 1.4–1.8 × 1.8–2.0 cm, with a truncate distal face, horns straight and 0.40–0.56 cm long, 1.0–1.60 cm between the horns with an acute angle between the horns. *Seeds* 1.1–1.5 cm long, 1.0–1.2 cm in diameter, ovate, sarcotesta light brown at maturity.

Distribution and habitat. *Ceratozamia huastecorum* is endemic to the Sierra de Otontepec in the northwest of Veracruz State, Mexico (Fig. 19A) where it occurs in cloud forest on clay soils with rocky outcrops at 800 to 1,300 m.

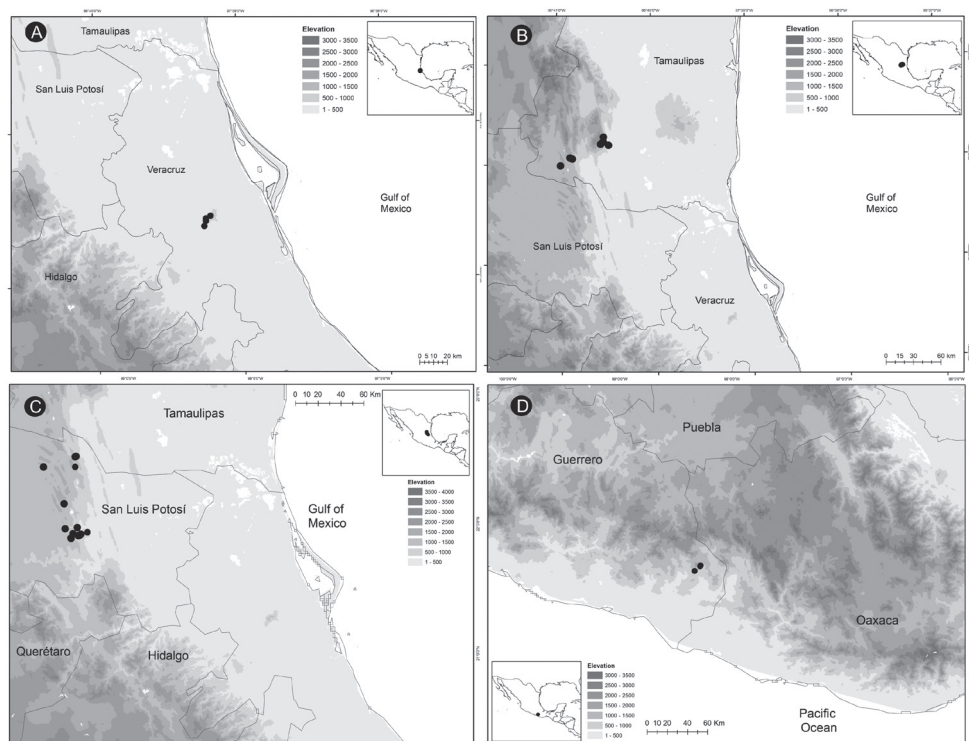


Figure 19. Distribution of *Ceratozamia* species **A** *C. huastecorum* **B** *C. kuesteriana* **C** *C. latifolia* **D** *C. leptoceras*.

Etymology. The specific epithet commemorates the Huasteca region, where this species is found; this region has cultural importance in Veracruz, Mexico.

Common names. Mexico. Veracruz: Palmilla (Bonta et al. 2019).

Uses. None recorded.

Conservation status. (IUCN 2021). *Ceratozamia huastecorum* is currently listed as “Critically Endangered” under criteria B2ab(iii,v).

Discussion. *Ceratozamia huastecorum* has a close morphological similarity to *C. latifolia*. However, *C. huastecorum* has light-green emergent leaves and coriaceous leaflets, whereas in *C. latifolia* the leaflets are reddish brown at emergence and papyraceous. In addition, the ovulate strobili are larger than *C. latifolia*, with 9 to 10 orthostichies as compared to *C. latifolia* with 4–7 orthostichies.

Specimens examined. MEXICO. **Veracruz:** **Mun. Tepetzintla**, 1,250 m, 26 Aug 1981, G. Castillo-Campos & A. Benavides M. 2215 (XAL); 1,200 m, 27 Aug 1981, G. Castillo-Campos & A. Benavides M. 2232, 2244 (XAL); 820 m, 14 Dec 1981, G. Castillo-Campos 2480, 2481, 2482 (XAL); 850 m, 10 Jan 1986, G. Castillo-Campos 4472 (XAL); 20 Sep 1989, P. Zamora C. et al. 1197 (CH, MEXU, XAL); 21 Sep 1989, P. Zamora et al. 1249 (MEXU, XAL).

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

Figs 3D, 7A, 9B

Type. Cultivated in St. Petersburg, Russia “Ex Horto Petropolitano”, 1856, *E. Regel s.n.* (holotype: LE! [LE00009046]; isotype: U! [U0007272]).

Description. *Stem* 10–30 cm long, 10–25 cm in diameter, semi-hypogeous, erect. *Cataphylls* 1.5–4 × 2–3.5 cm wide at the base, persistent, triangular, reddish brown, densely brown tomentose at emergence, partially tomentose at maturity, apex acuminate. *Leaves* 1–11, 80–133 cm long, ascending, reddish brown at emergence, with whitish gray trichomes, glabrous at maturity. *Petiole* 30–72 cm long, terete, linear, greenish brown in mature leaves; with 1–10 thin prickles, 0.01–0.15 cm long. *Rachis* 40–72 cm long, terete, linear, greenish brown in mature leaves, with prickles and rarely unarmed. *Leaflets* 22–50 pairs, opposite to subopposite, insertion in one plane, linear, adaxially curved, basally falcate, papyraceous, caniculate, green, adaxial and abaxial sides glabrous, distal end with entire margins, acuminate and symmetrical at the apex, attenuate at base, with conspicuous and light veins; median leaflets 17–32 × 0.6–1 cm, 0.3–2.5 cm between leaflets; articulations 0.2–0.8 cm wide, brown. *Pollen strobili* 11–15 cm long, 1.6–2.5 cm in diameter, solitary, cylindrical, erect, greenish yellow with brown trichomes at emergence, yellowish brown with reddish brown trichomes at maturity; peduncle 8–14 cm long, 0.7–1 cm in diameter, reddish brown to brown pubescent; microsporophylls 0.6–1.1 × 0.5–1 cm, discoid with a non-recurved distal face and a lobate fertile portion, infertile portion 0.28–0.32 cm long and linear with straight horns 0.05–0.25 cm long, 0.45–0.53 cm and an acute angle between the horns. *Ovulate strobili* 13–21 cm long, 7–9 cm in diameter, solitary, cylindrical, erect, green at emergence with brown trichomes, grayish light green with black trichomes at maturity, acuminate apex; peduncle 9–16 cm long, 1–2 cm in diameter, erect, tomentose, brown; megasporophylls 30–72, 6–8 orthostichies with 5–9 sporophylls per orthostichy, 2.5–4.0 × 2.3–3.5 cm, with a truncate distal face, horns straight and 0.30–0.52 cm long, 0.60–0.94 cm between horns with an obtuse angle between the horns. *Seeds* 1.5–2.3 cm long, 1.2–1.8 cm in diameter, ovate, sarcotesta whitish red when immature, light brown at maturity.

Distribution and habitat. *Ceratozamia kuesteriana* is endemic to Tamaulipas State, Mexico (Fig. 19B), where it occurs on karstic rocks in pine-oak and cloud forests at 1,100–1,500 m.

Etymology. The specific epithet is in honor of Baron K. von Kuester.

Common names. None recorded.

Uses. None recorded.

Conservation status. (IUCN 2021). The status for *Ceratozamia kuesteriana* “Critically Endangered” under criteria A2cd; B2ab(ii,iii,iv).

Discussion. *Ceratozamia kuesteriana* is similar to *C. sabatoi*, but it is easily distinguished by its canaliculate leaflets and ascending leaves.

Specimens examined: MEXICO. Tamaulipas: **Mun. Gómez Farías**, 1,260 m, 1 May 1967, *A. Gómez-Pompa* 2029 (MEXU); 1,150 m, 12 Aug 1983, *A.P. Vovides* 791, 800, 2056 (XAL); 13 Aug 1983, *A.P. Vovides* & *G. Pattison* 771, 772, 801 (XAL); 27 Jun 2017, *C.I. Carvajal-Hernández et al.* 1355 (CIB); 1,200–1400 m, 20 Nov 1970, *F. González-Medrano* & *E. Martínez* 3288 (MEXU); 1,100 m, 21 Jan 1970, *F. González-Medrano et al.* 3362 (MEXU, MO); 13 Aug 1985, *L. Trejo* s/n (UAT); 1,050 m, 30 Mar 1961, *P.S. Martin* & *C. Saravia* 1170 (ENCB). **Mun. Ocampo**, 1,255 m, 14 Jan 2001, *T.W. Walters* TW-201-11-A (XAL), TW-201-11-B (MEXU). **Mun. Tula**, 1,450 m, 21 Jul 1983, *D.W. Stevenson* 569H, 569G, 569K (MEXU); 1,296 m, 19 Mar 2016, *F. Nicolalde-Morejón et al.* 2357–2365 (CIB); 1,296 m, 19 Mar 2016, *L. Martínez-Domínguez et al.* 854–867, 869 (CIB), 868 (CIB, MEXU); 1,140 m, 19 Mar 2016, *L. Martínez-Domínguez et al.* 870–881 (CIB); 24 Apr 2001, *S. Avendaño* 5328 (MEXU).

15. *Ceratozamia latifolia* Miq., Tijdschr. Wis-Natuurk. Wetensch. Eerste Kl. Kon. Ned. Inst. Wetensch. 1(4): 206. 1848

Figs 7B, 10A

Ceratozamia mexicana Brongn. var. *latifolia* (Miq.) J.Schust., Pflanzenr. 99: 131. 1932.

Type: Based on *Ceratozamia latifolia* Miq.

Ceratozamia microstrobila Vovides & Rees, Madroño 30: 39. 1983. Type: MEXICO. San Luis Potosí: Mun. Ciudad del Maíz, Ejido Las Abritas, km 47 Ciudad Mante-Ciudad del Maíz, 850 m, 7 Nov 1974, *J. Rees* 1613 (holotype: XAL! [XAL0099666]; isotypes: FCME! [acc. # 132849], IBUG! [acc. # 155413], MO! [acc. # 5715707], XAL [n.v.]).

Type. MEXICO. San Luis Potosí: Route 70, 46 km West of Ciudad Valles, 650 m, 20 Jul 1983, *D.E. Stevenson* 565E (neotype, designated by Stevenson and Sabato 1986, pg. 579: NY! [00001117]; isoneotypes: MEXU! [MEXU00469173, MEXU00469148]).

Description. *Stem* 5–15 cm long, 10–25 cm in diameter, semi-hypogeous, erect. *Cataphylls* 1.5–3 × 2–4 cm wide at the base, persistent, triangular, reddish brown, densely brown tomentose at emergence, partially tomentose at maturity, apex acuminate. *Leaves* 1–8, 53–163.5 cm long, descending, reddish brown at emergence, with whitish gray trichomes, glabrous at maturity. *Petiole* 25–80 cm long, terete, linear, greenish brown in mature leaves, generally unarmed, rarely up to 3 prickles, 0.08–0.10 cm long. *Rachis* 25–110 cm long, terete, linear, greenish brown in mature leaves, unarmed. *Leaflets* 7–22 pairs, opposite to subopposite, insertion in one plane, oblong, in general longitudinally planar, basally falcate, papyraceous, flat, green with adaxial and abaxial sides glabrous, distal end with entire margins, acuminate and asymmetrical at the 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 0.4–1.1 cm wide, brown. *Pollen strobili* 10–20 cm long, 2.1–2.5 cm in diameter, solitary, cylindrical,

erect, greenish yellow with reddish brown trichomes at emergence, reddish brown at maturity; peduncle 5–15 cm long, 0.79–1.5 cm in diameter, reddish brown to brown pubescent; microsporophylls $0.5\text{--}1.3 \times 0.5\text{--}1.1$ cm, discoid with a non-recurved distal face and a lobate fertile portion, infertile portion 0.20–0.30 cm long and rounded with straight horns 0.1–0.20 cm long, 0.40–0.55 cm and a right angle between the horns.

Ovulate strobili 6.5–16 cm long, 5.5–8.0 cm in diameter, solitary, globose, erect, light green at emergence with brown trichomes, greyish light brown with brown trichomes at maturity, apiculate apex; peduncle 4–13.5 cm long, 1.3–1.8 cm in diameter, erect, brown pubescent; megasporophylls 24–63, 5–7 orthostichies with 4–9 sporophylls per orthostichy, $1.0\text{--}2.7 \times 1.6\text{--}2.9$ cm, with a prominent distal face, horns straight and 0.36–0.76 cm long, 0.54–0.63 cm between horns with an obtuse angle between the horns. **Seeds** 1.5–2.2 cm long, 1.2–1.6 cm in diameter, ovate, sarcotesta whitish red when immature, light brown at maturity.

Distribution and habitat. *Ceratozamia latifolia* is distributed widely in the mountainous region of San Luis Potosí State, Mexico (Fig. 19C), where it occurs in pine-oak, oak and cloud forests between 600–1,100 m.

Etymology. The specific epithet is derived from the Latin word “latus” (wide) and “folium” (leaves).

Common names. Mexico. San Luis Potosí: Chamalillo, corosillo (S. Sabato et al. 2340); Konlif in the teenek/haasteco language (Bonta et al. 2019).

Uses. The seeds are used to obtain meal for tortillas (Bonta et al. 2019).

Conservation status. (IUCN 2021). The status listed for *Ceratozamia latifolia* is “Endangered” under criteria A2cd+4cd. However, the current circumscription and distribution data indicate that status should be changed to “Vulnerable (V)”.

Discussion. *Ceratozamia latifolia* differs from *C. chamberlainii* by its unarmed petiole or if armed with no more than 3 prickles, its papyraceous leaflets, and discoid microsporophylls with a rounded distal face and horns up to 0.20 cm long. Additionally, this species is characterized by reddish brown leaves at emergence and ovulate strobilus is greyish light brown with brown trichomes at maturity and an apiculate apex.

Specimens examined. MEXICO. **San Luis Potosí:** Cultivated, 24 Jan 1994, *F. García S. s/n* (SLPM); Dec 1977, *N.F. McCarten 2552* (ENCB). **Mun. Alaquines,** 1,428 m, 21 Dec 2008, *J. Fortanelli M. & H.A. Castillo 141* (SLPM). **Mun. Cárdenas,** 950 m, 12 to 15 Sep 1967, *J. Rzedowski 24746* (ENCB). **Mun. Ciudad del Maíz,** 750 m, 13 Oct 1968, *H. Puig 3420* (ENCB, P); 25 Apr 2001, *S. Avendaño 5320* (MEXU); 900–1,300 m, 5 Feb 1984, *S. Sabato et al. 2340* (ENCB, MEXU, MO). **Mun. El Naranjo,** 7 Nov 1951, *Clint 144* (US); 20 Jul 1997, *D.W. Stevenson 567* (XAL); 900 m, 19 Mar 2016, *F. Nicolalde-Morejón et al. 2375–2389* (CIB); 900 m, 19 Mar 2016, *L. Martínez-Domínguez et al. 894–909* (CIB); 895 m, 13 Jan 2001, *T.W. Walters TW-2001-08*; 895 M, 14 Jan 2001, *TW-2001-10A,B* (MEXU, XAL). **Mun. Rayón,** 812 m, 5 Aug 2003, *A.P. Vovides et al. 1466* (XAL); 20 Jul 1983, *D.W. Stevenson 1117* (NY); 650 m, 20 Jul 1983, *D.W. Stevenson 565A* (MEXU), *565B,C* (MEXU, XAL); 993 m, 18. Mar 2016, *F. Nicolalde-Morejón et al. 2320–2334* (CIB); 1,100 m, 30 Jun 1962, *F. Medellín L. 1330* (ENCB, MEXU, SLPM); 1,221 m, 6 Apr 2013,

H.A. Castillo-Gómez et al. 558 (SLPM); 600 m, 17 Jul 1988, *J.A. Pérez de la Rosa & L.M. González-Villarreal* 1564 (IBUG); 993 m, 18 Mar 2016, *L. Martínez-Domínguez et al.* 811–827 (CIB); 24 Apr 2001, *S. Avendaño* 5282 (MEXU). **Mun. Tamasopo**, 700 m, 15 Aug 2003, *A.P. Vovides et al.* 1465 (MEXU, XAL); 2 Jun 1968, *F. Medellín L.* 27241 (ENCB); 2 Jun 1968, *F. Medellín L.* s/n (ENCB, IBUG, MEXU, SLPM); 716 m, 18. Mar 2016, *F. Nicolalde-Morejón et al.* 2335–2348 (CIB); 716 m, 18 Mar 2016, *L. Martínez-Domínguez et al.* 828–844 (CIB); 750 m, 11 Sep 1967, *J. Rzedowski* 24571 (ENCB); 900 m, 24 May 1981, *P.A. Fryxell & W.R. Anderson* 3586 (NY; US); 856 m, 19 Jan 2013, *U. Pineda M.* 70 (SLPM).

16. *Ceratozamia leptoceras* Mart.-Domínguez, Nic.-Mor., D.W.Stev. & Lorea-Hern., PhytoKeys 156: 13. 2020

Fig. 7C

Type. MEXICO. Guerrero: Mun. Tlacoachistlahuaca, 3 km NW de San Pedro Cuitlapan, 1,400 m, 26 Jun 2019, *L. Martínez-Domínguez & F. Nicolalde-Morejón* 1867 ♀ (holotype: CIB! [acc. # 22405UV]; isotypes: MEXU!, NY!).

Description. *Stem* 30–150 cm long, 11–35 cm in diameter, epigeous, erect to decumbent. *Cataphylls* 9–11 × 2.5–3 cm wide at the base, persistent, triangular, reddish brown, densely brown tomentose abaxially at emergence, pubescent at maturity, apex acuminate. *Leaves* 7–37 (55), 93.5–281 cm long, descending, green at emergence with sparse reddish brown pubescent, glabrous at maturity. *Petiole* 45–85 cm long, terete, linear, copperish green in mature leaves; with 50–75 thin prickles, 0.48–0.68 cm long. *Rachis* 75–196 cm long, terete, linear, green in mature leaves, with prickles. *Leaflets* 22–61 pairs, opposite to subopposite, insertion in one plane, linear, abaxially curved, not basally falcate, membranaceous, flat, green with adaxial and abaxial sides glabrous, distal end with entire margins, acuminate and symmetrical at the apex, attenuate at base, with conspicuous and greenish veins; median leaflets 28–43.5 × 1.9–2.8 cm, 1.8–2.8 cm between leaflets; articulations 0.70–1.15 cm, generally copperish green. *Pollen strobili* 40–45 cm long 6.0–7.8 cm in diameter, generally solitary (rarely 2), cylindrical, erect, brownish yellow at emergence, yellowish green with brownish trichomes at maturity; peduncle 13–19 cm long, 1.5–2.0 cm in diameter tomentose, reddish brown to brown; microsporophylls 2.1–2.45 × 1.09–1.30 cm, obconic with a non-recurved distal face and a deeply lobate fertile portion, infertile portion 0.83–0.96 cm long and linear with straight and thin horns and 0.1–0.23 cm long, 0.44–0.56 cm and an acute angle between the horns. *Ovulate strobili* 23.5–28 cm long, 9.5–11 cm in diameter, solitary, cylindrical, erect, brownish green with greyish black trichomes at emergence, copperish green with greyish black pubescent at maturity with an acute apex; peduncle 11–16 cm long, 1.5–2.0 cm in diameter, erect, tomentose, brown; megasporophylls 56–81, 8–9 orthostichies with 7–9 sporophylls per orthostichy, 4.9–5.6 × 2.2–2.6 cm, with a prominent distal face, horns straight and robust and 0.63–0.81 cm long, 0.95–1.35 cm between horns and angle straight between the horns. *Seeds* 2.43–2.71 cm in

long, 1.4–1.8 cm in diameter, ovoid, sarcotesta whitish pink when immature, light brown at maturity.

Distribution and habitat. *Ceratozamia leptoceras* is endemic to the Sierra Madre del Sur in Guerrero State, Mexico (Fig. 19D), where it occurs on karstic rocks in cloud forest at 1,170–1,400 m.

Etymology. The specific epithet is derived from the Greek words that describe the shape of the horns on the sporophylls: “lepto” for thin or fine and “ceras” in reference to the horns.

Common names. Mexico. Guerrero: Shalukaá is the name used by the “Mixteco” ethnic group (Martínez-Domínguez et al. 2020).

Uses. None recorded.

Preliminary conservation status. Only three populations of *Ceratozamia leptoceras* are known. In particular, one of these populations has few adult plants (approximately 30 individuals). The cloud forests in this area are less affected by anthropogenic pressures; however, this vegetation type is one of the most threatened in Mexico (Williams-Linera 2002). Based upon this information, *C. leptoceras* should be considered “Endangered (EN)” in accordance with IUCN criteria.

Discussion. *Ceratozamia leptoceras* is distinguished from *C. oliversacksii* by its linear and membranaceous leaflets. The main differences are in reproductive structures, *C. leptoceras* has and linear infertile portion of microsporophylls and ovulate strobilus with abundant pubescence at the base of the megasporophylls.

Specimens examined. MEXICO. Guerrero: Mun. Cochoapa El Grande, 1,170 m, 4 Feb 1984, *F. Lorea-Hernández* 2928 (FCME). Mun. Tlacoachistlahuaca, 1,200 m, 29 May 2019, *F. Nicolalde-Morejón et al.* 3173 (XAL), 3174 (FCME), 3175 (CIB); 1,200 m, 29 May 2019, *L. Martínez-Domínguez et al.* 1756 (CIB), 1757 (CIB, MEXU), 1758 (XAL), 1759 (CIB, MEXU); 1,400 m, 26 Jun 2019, *F. Nicolalde-Morejón & L. Martínez-Domínguez* 3255–3261 (CIB); 1,400 m, 26 Jun 2019, *L. Martínez-Domínguez & F. Nicolalde-Morejón* 1860, 1861 (MEXU), 1862–1866 (CIB).

17. *Ceratozamia matudae* Lundell, *Lloydia* 2: 75. 1939

Figs 7D, 8D–F, 10D

Type. MEXICO. Chiapas: northern slope of Mt. Ovando, 1,000 m, Feb 1939, *E. Matuda* 2645 ♂ (holotype: MICH! [1002583]; isotypes: CAS! [0001920], MEXU! [acc. # 86830], US! [00620111]).

Description. **Stem** 30–50 cm long, 20–30 cm in diameter, epigeous, erect and decumbent. **Cataphylls** 4–6.0 × 2.5–4.5 cm wide at the base, persistent, triangular, reddish brown, densely brown tomentose at emergence, partially tomentose at maturity, apex acuminate. **Leaves** 3–14, 80–155 cm long, descending, green at emergence with brown trichomes, glabrous at maturity. **Petiole** 30–79 cm long, terete, linear, green in adult leaves; unarmed to armed with 18–36 thin prickles, 0.1–0.28 cm long. **Rachis** 45–76 cm long, terete, linear, green with abundant brown trichomes in young leaves,

yellow to yellowish green in mature leaves, unarmed to armed with prickles. **Leaflets** 23–53 pairs, opposite to subopposite, insertion in one plane, lanceolate, longitudinally curved abaxially to planar, not basally falcate, papyraceous, flat, green with base yellow and adaxial and abaxial sides glabrous, distal end with entire margins, acuminate and symmetrical at the apex, attenuate at base, with conspicuous and light-green veins; median leaflets 23–40 × 0.6–1.3 cm, 0.6–1.7 cm between leaflets; articulations 0.3–0.8 cm wide, yellow. **Pollen strobili** 9.5–16 cm long, 3.5–5 cm in diameter, solitary, cylindrical, erect, yellowish green with reddish brown trichomes at emergence, yellowish cream with reddish brown trichomes at maturity; peduncle 8–14 cm long, 1.8–2.2 cm in diameter, pubescent, reddish brown to brown; microsporophylls 0.78–1.4 × 0.77–1.1 cm, discoid with a non-recurved distal face and deeply lobate fertile portion, infertile portion 0.37–0.56 cm long and orbicular with straight horns 0.16–0.35 cm long, 0.50–0.81 cm and an acute angle between the horns. **Ovulate strobili** 8–15 cm long, 5–8 cm in diameter, solitary, globose, erect, yellowish green with abundant blackish trichomes at emergence, dark green with blackish trichomes at maturity, aristate apex; peduncle 11–17 cm long, 1–2 cm in diameter, pendulous, with trichomes scarce, blackish, pendulous and erect; megasporophylls 16–25, 4–5 orthostichies with 4–6 sporophylls per orthostichy, 2.5–3.4 × 4.5–5.3 cm, with a prominent distal face, horns recurved, straight and thin and 0.59–1.50 cm long, 0.92–1.56 cm between horns with an obtuse angle between the horns. **Seeds** 2.9–4.0 cm long, 1.9–4.0 cm in diameter, globose, sarcotesta whitish yellow to yellow when immature, light brown at maturity.

Distribution and habitat. *Ceratozamia matudae* is endemic to Chiapas in Mexico (Fig. 20A), where it occurs on karstic rocks in evergreen tropical forest at 1,000–1,500 m.

Etymology. The specific epithet is in honor of professor Eizi Matuda, for his contributions to botany in Mexico.

Common names. None recorded.

Uses. None recorded.

Conservation status. (IUCN 2021). Currently, *Ceratozamia matudae* is listed as “Endangered” under criteria B1ab(ii,iii,v); C1.

Discussion. *Ceratozamia matudae* differs from other *Ceratozamia* species by its yellow rachis and petiole and leaflets with yellow base and articulations. In addition, the length of the peduncle is the same or longer than the fertile portion of ovulate strobili. The ovulate strobili have an aristate apex, and the megasporophylls have long recurved horns.

Specimens examined. MEXICO. **Chiapas:** **Mun. Acacoyagua**, 1,400 m, *A.P. Vovides* 1069 (XAL); 1,300 m, 9 Jan 1987, *D.W. Stevenson et al.* 681 (FTG; MO; NY; US); 1,000 m, Feb 1939, *E. Matuda* 2646 (MEXU); 1,420 m, 24 Jun 2018, *F. Nicolalde-Morejón et al.* 2832–2840 (CIB); 1,420 m, 24 Jun 2018, *L. Martínez-Domínguez et al.* 1404–1409, 1412, 1415, 1416, 1418, 1419 (CIB), 1405, 1407 (CIB, MEXU); 1,480 m, 29 Dec 1993, *M.A. Pérez-Farrera* 27 (CIB, CH, CHIP, MEXU, USCG); 22 Feb 1995, *M.A. Pérez-Farrera* 142 (CHIP, FTG, MEXU). **Mun. Escuintla**, 8 Feb 2000, *O. Farrera S.* 1875 (CHIP). **Mun. Siltepec**, 1,500 m, 6 Nov 1945, *E.H. Xolocotzi & A.J. Sharp* 367 (MEXU); 1,500 m, Oct–Nov 1940, *E. Matuda* 4032 (MEXU; NY).

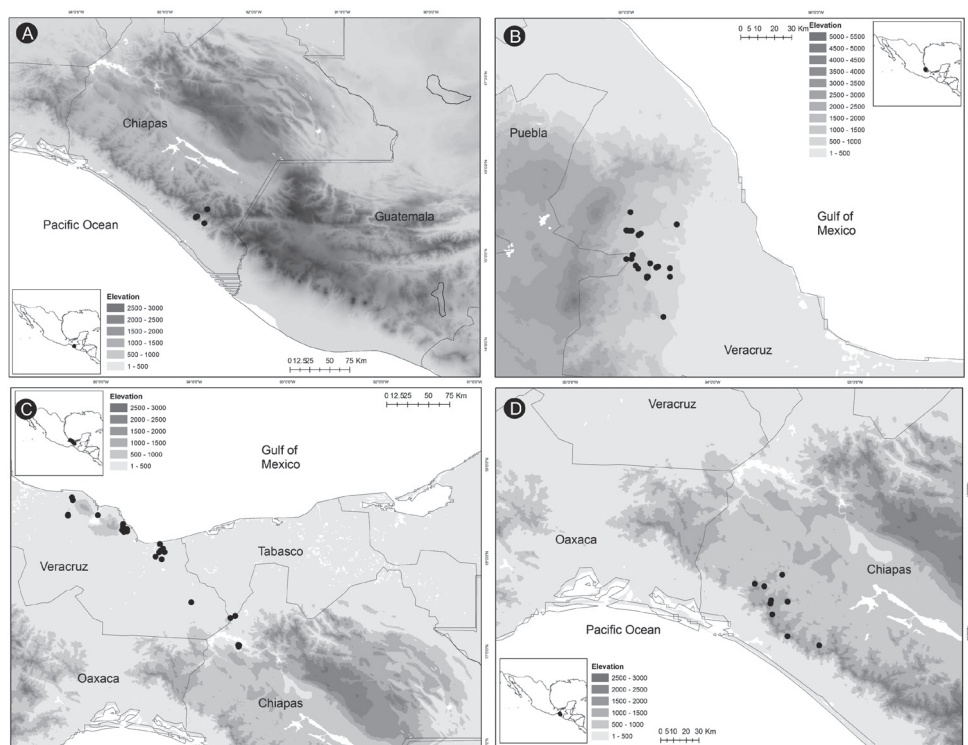


Figure 20. Distribution of *Ceratozamia* species **A** *C. matudae* **B** *C. mexicana* **C** *C. miqueliana* **D** *C. mirandae*.

18. *Ceratozamia mexicana* Brongn., Ann. Sci. Nat., Bot. sér. 3, 5: 8, t. 1. 1846.
Figs 7E, 11B

Ceratozamia intermedia Miq., Tijdschr. Wis-Natuurk. Wetensch. Eerste Kl. Kon. Ned. Inst. Wetensch. 1(4): 40. 1848. Type. MEXICO. Veracruz: Mun. Puente Nacional, 1 km S of Palmillas, 600 m, 13 Mar 1985, *G. Castillo-Campo & Medina* 4275 (neotype, designated by Martínez-Domínguez et al. 2018a, pg. 111: XAL! [acc. # 16924]).

Ceratozamia longifolia Miq., Tijdschr. Wis-Natuurk. Wetensch. Eerste Kl. Kon. Ned. Inst. Wetensch. 1(4): 40. 1848. Type. MEXICO. Veracruz: Mun. Zacuapam, Apr 1913, *C. Purpus s.n.* [6362]! (neotype, designated by Martínez-Domínguez et al. 2018a, pg. 111: MO! [acc. # 741393]).

Ceratozamia longifolia Miq. var. *minor* Miq., Tijdschr. Wis-Natuurk. Wetensch. Eerste Kl. Kon. Ned. Inst. Wetensch. 2(4): 290. 1849. Type. MEXICO. Veracruz: Mun. Teocelo, Barranca of Teocelo, 1,020 m, 23 Dec 1975, *M.G. Zola* 146 (neotype, designated by Martínez-Domínguez et al. 2018a, pg. 111: XAL! [acc. # 16957]).

Ceratozamia mexicana Brongn. var. *longifolia* (Miq.) Dyer, Biol. Cent.-Amer., Bot. 3: 193. 1884. Type: Based on *Ceratozamia longifolia* Miq.

Type. Cultivated in Paris “Hort. Bot. Parisiensis”, original material sent by A. Ghiesbrecht from Mexico, 1845, *Anon. s.n.* (holotype: P! [P02441737, P01637464–P01637466]). Mexico. Veracruz: Mun. Totutla, Barranca El Coyotito, 1 km road from El Mirador to Conejos, 900 m, 8 Sep 1982, *J. Rees & A.P. Vovides 1688* (epitype, designated by Vovides et al. 2016, pg. 427: XAL! [acc. # 17004]).

Description. *Stem* 20–80 cm long, 20–45 cm in diameter, epigeous, erect and decumbent. *Cataphylls* 2–6 × 2.5–6 cm wide at the base, persistent, triangular, reddish brown, densely brown tomentose at emergence, partially tomentose at maturity, apex acuminate. *Leaves* 5–55, 100–270 cm long, descending, green at emergence, with brown trichomes, glabrous at maturity. *Petiole* 30–93 cm long, terete, linear, dark green in mature leaves; with 8–30 thin prickles, 0.06–0.20 cm long. *Rachis* 56–154 cm long, terete, linear, green in mature leaves, with prickles and unarmed. *Leaflets* 25–42 pairs, opposite to subopposite, insertion in one plane, lanceolate, in general longitudinally planar, basally falcate, coriaceous, flat, green with adaxial and abaxial sides glabrous, distal end with entire margins, acuminate and symmetrical at the apex, attenuate at base, with conspicuous and green-light veins; median leaflets 29–51 × 2.3–3.7 cm, 1.8–4 cm between leaflets; articulations 0.6–1.5 cm wide, green. *Pollen strobili* 20–40 cm long, 4.5–7.6 cm in diameter, generally solitary (1–2), cylindrical, erect, greenish yellow at emergence, greenish yellow with blackish trichomes at maturity; peduncle 3.5–9 cm long, 1.5–2.3 cm in diameter, tomentose, reddish brown to light-brown; microsporophylls 1.5–2.7 × 0.9–2.1 cm, obconic with a non-recurved distal face and a lobate fertile portion, infertile portion 0.47–0.68 cm long and orbicular with straight horns 0.29–0.40 cm long, 0.51–1.05 cm and an acute angle between the horns. *Ovulate strobili* 23.5–40 cm long, 8–15 cm in diameter, generally solitary (1–2), cylindrical, erect, dark green with blackish trichomes at emergence, dark green with black and gray trichomes at maturity, acuminate apex; peduncle 7.6–11.5 cm long, 2.5–3 cm in diameter, tomentose, brown to reddish brown, erect or pendulous; megasporophylls 64–240, 8–16 orthostichies with 8–15 sporophylls per orthostichy, 2.0–2.7 × 3.2–5.3 cm, with a prominent distal face, horns straight and 0.53–1.2 cm long, 1–2.1 cm between horns and a right angle between the horns. *Seeds* 2.0–3.3 cm long, 1.4–2.5 cm in diameter, ovate, sarcotesta whitish yellow to yellow when immature, light brown at maturity.

Distribution and habitat. *Ceratozamia mexicana* is endemic to Veracruz State, Mexico from the River La Antigua drainage system to the southern end of the Sierra Madre Oriental (Fig. 20B). It occurs in cloud forest on karstic rocks at 500–1,100 m.

Etymology. The specific epithet is derived from the country of origin of the material used for the description of this species. *Ceratozamia mexicana* was the first species described in the genus.

Common names. None recorded.

Uses. None recorded.

Conservation status. (IUCN 2021). *Ceratozamia mexicana* is listed as “Vulnerable” under criteria A2acd+4cd. According to the current circumscription, this species

only occurs in a narrow area, which suffered dramatic decline in forest (Martínez-Domínguez et al. 2021). Besides, the populations visited by us have only between 30 and 50 adult plants. This data suggest *C. mexicana* should be listed as “Critically Endangered (CR)” under criteria B1ab(iiii, iv)

Discussion. *Ceratozamia mexicana* is similar to *C. tenuis*, *C. morettii* and *C. brevifrons*, but it can be easily distinguished from vegetative and reproductive characters. This species has lanceolate leaflets, whereas *C. tenuis* and *C. morettii* have linear and oblong leaflets, respectively. In addition, *C. mexicana* has insertion in one plane for leaflets and thin prickles on petiole, whereas *C. brevifrons* has keeled leaflets and petioles armed with robust prickles.

Specimens examined. MEXICO. **Veracruz: Mun. Coatepec**, 1,600 m, 26 Jun 1990, *P. Zamora C. 2450* (MEXU, XAL). **Mun. Comapa**, 1,003 m, 18 Feb 2013, *F. Nicolalde-Morejón et al. 1732–1734* (CIB); 1,003 m, 28 Sep 2014, *F. Nicolalde-Morejón et al. 2145–2156* (CIB); 970 m, 13 Nov 2015, *F. Nicolalde-Morejón et al. 2269–2272* (CIB); 1,003 m, 28 Sep 2014, *L. Martínez-Domínguez et al. 164* (CIB); 970 m, 13 Nov 2015, *L. Martínez-Domínguez & F. Nicolalde-Morejón 716–723, 725–730* (CIB), 724 (CIB, MEXU). **Mun. Puente Nacional**, 600 m, 13 Mar 1985, *G. Castillo-Campos & M. E. Medina 4299* (XAL). **Mun. Sochiapa**, 1,058 m, 9 Jul 2008, *M. Vázquez-Torres 8589* (CIB). **Mun. Teocelo**, 900 m, 16 Feb 1997, *L.H. Bojórquez-Galván et al. 531* (CIB); 1,070 m, 20 Nov 2015, *F. Nicolalde-Morejón et al. 2273–2278* (CIB); 1,065 m, 20 Nov 2015, *L. Martínez-Domínguez et al. 731* (CIB); 1,070 m, 20 Nov 2015, *L. Martínez-Domínguez et al. 732–733, 735–750* (CIB), 734 (CIB, MEXU); 1,070 m, 11 Mar 2016, *L. Martínez-Domínguez et al. 764, 765, 767–770* (CIB), 766 (CIB, MEXU); 740–800 m, 20 Jul 1995, *M. Vázquez-Torres 4865* (CIB). **Mun. Tlaltetela**, 1,196 m, 5 Jun 2015, *F. Nicolalde-Morejón & L. Martínez-Domínguez 2242* (CIB); 1,084 m, 5 Jun 2015, *F. Nicolalde-Morejón & L. Martínez-Domínguez 2243* (CIB); 1,196 m, 10 Jun 2015, *F. Nicolalde-Morejón & L. Martínez-Domínguez 2246* (CIB); 1,130 m, 21 Jun 2015, *F. Nicolalde-Morejón & L. Martínez-Domínguez 2253–2257* (CIB); 1,084 m, 5 Jun 2015, *L. Martínez-Domínguez & F. Nicolalde-Morejón 584–586* (CIB); 1,196 m, 10 Jun 2015, *L. Martínez-Domínguez & F. Nicolalde-Morejón 620* (CIB); 1,130 m, 21 Jun 2015, *L. Martínez-Domínguez & F. Nicolalde-Morejón 628–635* (CIB). **Mun. Totutla**, 900 m, 23 Feb 1982, *A.P. Vovides 730–733* (XAL); 900 m, 8 Sep 1982, *A.P. Vovides 748* (XAL); 900 m, 9 Oct 1993, *Brigada T. Walters s/n* (XAL); 875 m, 8 Aug 2015, *F. Nicolalde-Morejón et al. 2262* (CIB); 864 m, 27 Jan 2016, *F. Nicolalde-Morejón et al. 2279–2281* (CIB); *F. Vázquez B. 730* (XAL); 1,094 m, 21 Jun 2016, *J.M. Ramírez-Amezcuca & A. Paizanni Guillén 715* (MEXU); 8 Sep 1982, *J. Rees 6344* (IEB); 800 m, 30 Dec 1975, *J. Rees & A.P. Vovides 1660, 1672* (XAL); 900 m, 8 Sep 1982, *J. Rees & A.P. Vovides 1689* (XAL); 875 m, 8 Aug 2015, *L. Martínez-Domínguez et al. 704–707* (CIB); 864 m, 27 Jan 2016, *L. Martínez-Domínguez et al. 752, 754–757* (CIB, MEXU), 758 (CIB). **Mun. Xico**, 1,195 m, 10 Jul 2015, *L. Martínez-Domínguez & F. Nicolalde-Morejón 640–646* (CIB); 1,159 m, 10 Jul 2015, *L. Martínez-Domínguez & F. Nicolalde-Morejón 647, 648* (CIB); 900 m, 13 Nov 1981, *M. Nee 23035* (NY).

19. *Ceratozamia miqueliana* H.Wendl., Index Palm. 68. 1854

Figs 7F, 8A–C, 9D, 11A

Ceratozamia mexicana Brongn. var. *miqueliana* (H.Wendl.) J. Schust., Pflanzenr. (Engler) Heft 99, 4 fam 1: 131. 1932. Type: Based on *Ceratozamia miqueliana* H. Wendl.

Type. MEXICO. Veracruz: West of Santiago Tuxtla, Cerro el Vigía, 5 Jul 1983, *D.W. Stevenson 542 F* (neotype, designated by Stevenson and Sabato 1986, pg. 580: NY! [00001118]).

Description. *Stem* 45–75 cm long, 16–18 cm in diameter, epigeous, erect and decumbent. *Cataphylls* 3–7 × 1.5–4 cm wide at the base, persistent, triangular, reddish brown, densely brown tomentose at emergence, glabrous at maturity, apex acuminate. *Leaves* 12–37, 35–261 cm long, ascending, light green and glaucous at emergence with brown trichomes, glabrous at maturity. *Petiole* 31–97 cm long, terete, linear, pink at emergence, green in mature leaves; with 8–60 robust prickles, 0.22–0.59 cm long. *Rachis* 41–164 cm long, terete, linear, pink at emergence, yellowish green in mature leaves, with prickles. *Leaflets* 12–23 pairs, opposite to subopposite, insertion in one plane, oblong, in general longitudinally planar, not basally falcate, papyraceous, flat, green with abaxial and adaxial sides glabrous, acuminate and asymmetrical at the apex, distal end with entire margins, attenuate at base, with conspicuous and green-light veins; median leaflets 16–36 × 4.4–8.7 cm, 2.9–8.5 cm between leaflets; articulations 0.3–1.8 cm wide, greenish. *Pollen strobili* 15–30 cm long, 3.1–4.2 cm in diameter, usually solitary (1–2), cylindrical, erect, greenish yellow with red trichomes at emergence, greenish yellow to cream at maturity; peduncle 3.5–5.0 cm long, 1.9–2.2 cm in diameter, tomentose, light brown; microsporophylls 1–2 × 0.7–1.5 cm, obconical with a non-recurved distal face and deeply lobate fertile portion, infertile portion 0.35–0.50 cm long and rounded with straight horns 0.30–0.42 cm long, 0.52–0.70 cm and an acute angle between the horns. *Ovulate strobili* 22–30 cm long, 8.9–12 cm in diameter, solitary, cylindrical, erect, green with blackish trichomes, yellowish green with blackish trichomes at maturity, acuminate apex; peduncle 7–12 cm long, 2.7–3.3 cm in diameter, erect and pendulous, tomentose, light brown; megasporophylls 64–110, 8–11 orthostichies with 8–10 sporophylls per orthostichy, 2.0–3.0 × 3.5–4.2 cm, with a prominent distal face, horns straight and 0.35–0.43 cm long, 1.06–1.12 cm between horns with a right angle between the horns. *Seeds* 2.4–3 cm long, 1.3–1.8 cm in diameter, ovate, sarcotesta whitish yellow to yellow when immature, light brown at maturity.

Distribution and habitat. *Ceratozamia miqueliana* is endemic to southwest Mexico in Chiapas, Tabasco and Veracruz States (Fig. 20C), where it occurs on shallow soils in evergreen tropical rain forest at 19–1,000 m.

Etymology. The specific epithet was assigned in honor of Friedrich Anton Wilhelm Miquel.

Common names. Mexico. Veracruz: Palmita (J. Rees 1657).

Uses. The leaves are used for decorations during festivities in Santiago Tuxtla (Veracruz).

Conservation status. (IUCN 2021). *Ceratozamia miqueliana* is listed as “Critically Endangered” under criteria A2acd. This species has a wide distribution; however, the evergreen tropical rain forest in Veracruz has declined dramatically in recent years (Guevara et al. 2004). In addition, most of the populations occur in areas of interest for the oil industry.

Discussion. *Ceratozamia miqueliana* differs from its congeners by its robust and long prickles, and papyraceous, oblong and glabrous (lustrous) leaflets. In addition, ovulate strobili are yellowish yellowish green with blackish trichomes and have an acuminate apex at maturity. This species is closely related to *C. zoquorum*, however, that species has descending leaves with coriaceous leaflets.

Specimens examined. MEXICO. **Chiapas: Mun. Ocozocoautla de Espinosa**, 421 m, 23 Oct 1997, *R. Juárez-Galdamez* 4 (CHIP, MO, XAL); 800 m, 21 Jan 2001, *S. Avendaño* 5223 (MEXU); 765 m, 21 Jan 2001, *T.W. Walters* 2001–2036-A (MEXU); 2001–2036-C (XAL). **Tabasco: Mun. Huimanguillo**, 405 m, 10 Aug 2013, *F. Nicolalde-Morejón et al.* 1826–1846 (CIB); 23 Jun 1998, *G. Ortiz G.* 5291 (MEXU). **Veracruz: Mun. Ángel R. Cabada**, 231 m, 29 Oct 2013, *F. Nicolalde-Morejón et al.* 1868–1887 (CIB); 30 Oct 2013, *F. Nicolalde-Morejón et al.* 1888–1909 (CIB). **Mun. Catemaco**, 31 Oct 2013, *F. Nicolalde-Morejón et al.* 1910–1929 (CIB). **Mun. Coatzacoalcos**, 22 m, 2 Apr 2003, *C.H. Ramos* 2266 (MEXU); Jun 1960, *E. Hernández X. et al.* 162 (CHAPA); 26 Jun 1997, *G. Castillo C. & F. Morocini* 16267 (XAL); 30 m, 7 Sep 2005, 30 m, *L.H. Bojórquez-Galván* 1601 (CIB); 18 Jan 2001, *S. Avendaño R.* 5214 (MEXU); 31 m, 18 Jan 2001, *T.W. Walters* 2001–21-A, B (XAL); *T.W. Walters* 2001–21-D (MEXU). **Mun. Ixhuatlán del Sureste**, 45 m, 13 Sep 2011, *J. Calónico-Soto & B. Gómez C.* 27780 (MEXU). **Mun. Las Choapas**, 115 m, 26 Nov 2011, *A. Rincón G.* 2894 (XAL); 115 m, 30 Jun 2003, *E. López P.* 634 (XAL); 100 m, 25 Nov 2004, *F. Nicolalde-Morejón et al.* 1434 (XAL). **Mun. Mecayapan**, 13 Jul 1994, *G. Castillo-Campos et al.* 12,565 (ENCB, XAL); 9 Mar 1995, *G. Castillo-Campos et al.* 13470, 13489 (XAL); 5 Aug 1985, *J.I. Calzada* 11207 (CH, MEXU); 300 m, 16 Jul 1982, *M. Nee et al.* 25066 (XAL), 25118 (MO, NY, XAL); 950 m, 26 Jan 1992, *M. Vázquez-Torres* 4123 (CIB); 5 May 1995, *M. Vázquez-Torres* 5017 (CIB). **Mun. Moloacán**, 60 m, 19 Dec 1974, *J. Rees* 1657 (MEXU, XAL), 1658 (XAL), 6347, 6348 (IEB). **Mun. Nanchital**, 34 m, 12 Aug 2011, *J. Rivera H. et al.* 4530 (XAL). **Mun. Santiago Tuxtla**, 900–1,000 m, 5 Jul 1983, *D.W. Stevenson et al.* 541 A–C–F, I, K (NY), G, H, J, N (MEXU, NY); 5 Jul 1983, *D.W. Stevenson et al.* 542 A–E, H (NY); 650 m, 28 Mar 2014, *F. Nicolalde-Morejón & L. Martínez-Domínguez* 1988–1998 (CIB); 950 m, 24 Jan 1972, *J.H. Beaman* 5507 (XAL); 650 m, 28 Mar 2014, *L. Martínez-Domínguez & F. Nicolalde-Morejón* 88–106 (CIB), 107 (CIB, MEXU); 800 m, 28 May 1967, *L. Scheinvar* 673 (MEXU); 29 Aug 1967, *M. Sousa* 3201 (MEXU); 845 m, 17 Jan 2001, *S. Avendaño R.* 5207 (MEXU); 845 m, 17 Jan 2001, *T.W. Walters et al.* TW 2001–2019 (MEXU, XAL). **Mun. Pajapan**, 830–980 m, 15 Jul 1982, *M. Nee et al.* 25066 (XAL). **Mun. Soteapan**, 250 m, 13 May 1986, *M. Vázquez-Torres* 3360 (CIB, XAL). **Mun. Tatahuicapan de Juárez**, 849 m, *C.I. Carvajal & M.J. Fragoso* 797 (CIB); 15 Mar 2008, *L.H. Bojórquez-Galván et al.* 1939, 1946 (CIB).

20. *Ceratozamia mirandae* Vovides, Pérez-Farr. & Iglesias, Bot. J. Linn. Soc. 137: 81. 2001

Fig. 7G

Type. MEXICO. Chiapas: Mun. Villa Flores, Ejido La Sombra de la Selva, 880 m, 20 Sep 1997, *J. De La Cruz Rodríguez* 66 (lectotype, designated here: MEXU! [MEXU00934924, MEXU00934907, MEXU00934905]).

Description. *Stem* 20–60 cm long, 20–30 cm in diameter, epigeous, erect and decumbent. *Cataphylls* 3–8.0 × 1.5–4.0 cm wide at the base, persistent, triangular, reddish brown, densely brown tomentose at emergence, partially tomentose at maturity, apex acuminate. *Leaves* 2–50 (150), 46–242.5 cm long, ascending, brown at emergence with whitish gray trichomes, glabrous at maturity. *Petiole* 16–98 cm long, terete, linear, brown in mature leaves; with 11–46 thin prickles, 0.30–0.40 cm long. *Rachis* 26–144.5 cm long, terete, linear, brown to greenish brown in mature leaves, lower 2/3rds with prickles. *Leaflets* 28–94 pairs, opposite to subopposite, insertion in one plane, linear to lanceolate, in general longitudinally planar, not basally falcate, papyraceous, lightly involute, green with adaxial and abaxial sides glabrous, distal end with entire margins, acuminate and symmetrical at the apex, attenuate at base, with conspicuous and light-green veins; median leaflets 10–40 × 0.4–0.9 cm, 0.2–1.6 cm between leaflets; articulations 0.12–1.20 cm wide, brown. *Pollen strobili* 16–55 cm long, 4.0–7.7 cm in diameter, solitary, cylindrical, erect, yellowish green with brown trichomes at emergence, yellowish cream with blackish trichomes at maturity; peduncle 5–11 cm long, 0.8–1.4 cm in diameter, pubescent, reddish brown to brown; microsporophylls 1.23–1.80 × 0.62–0.86 cm, elliptic with a non-recurved distal face and a lobate fertile portion, infertile portion 0.62–0.81 cm long and linear with straight horns 0.17–0.39 cm long, 0.56–0.95 cm and an obtuse to acute angle between the horns. *Ovulate strobili* 13.5–35 cm long, 7–12.6 cm in diameter, solitary, cylindrical, erect, yellowish green with abundant blackish trichomes at emergence, glaucous green with reddish brown to blackish trichomes at maturity, acuminate apex; peduncle with trichomes scarce, brownish, 4.5–12 cm long, 1.0–2.2 cm in diameter, erect; megasporophylls 42–72, 6–8 orthostichies with 7–10 sporophylls per orthostichy, 2.0–3.0 × 2.8–6.1 cm, with a prominent distal face, horns straight and 0.29–1.47 cm long, 1.55–2.09 cm between horns with an obtuse angle between the horns. *Seeds* 1.9–2.9 cm long, 1.2–2.5 cm in diameter, spherical, sarcotesta whitish pink when immature, light brown at maturity.

Distribution and habitat. *Ceratozamia mirandae* is widely distributed in Chiapas State, Mexico from “Tres Picos” hill and Sierra Morena to a mountain range in Mun. Jiquipilas (Fig. 20D); it occurs on karstic rocks with abundant organic material in oak forest and transitional oak forest between pine oak forest and cloud forest between 850 and 1,500 m.

Etymology. This species was named in honor of Dr. Faustino Miranda for his untiring contributions to the flora of Chiapas (Vovides et al. 2001).

Common names. Mexico. Chiapas: Amenduai (L. Martínez-Domínguez et al. 1428; M.A. Pérez-Farrera 1261A), Espadaña de cochi (M.A. Pérez-Farrera 26A), Peinetilla (M.A. Pérez-Farrera 37).

Uses. The mature seeds are used as food (U. Bachem C. & R. Rojas 579).

Conservation status. (IUCN 2021). *Ceratozamia mirandae* is listed as “Endangered” under criteria C1.

Discussion. *Ceratozamia mirandae* is similar to *C. alvarezii*. However, in *C. mirandae*, the leaves and ovulate strobilus are larger at the population level than in *C. alvarezii*, which is a more diminutive species overall.

In the original publication of *C. mirandae*, there were no isotypes cited, only the holotype in CHIP. Because no holotype of *C. mirandae* has been found in CHIP, despite intensive searches, we designate the uncited isotype found in MEXU as the lectotype.

Specimens examined. MEXICO. **Chiapas: Mun. Jiquipilas**, 1,170 m, 19 Jun 2018, *F. Nicolalde-Morejón et al.* 2749–2759 (CIB); 1,015 m, 8 Mar 1995, *J.J. Castillo-Hernández* 548 (CHIP); 1,170 m, 19 Jun 2018, *L. Martínez-Domínguez et al.* 1312–1316, 1318, 1320, 1321 (CIB), 1317 (CIB, MEXU), 1319 (CIB, MEXU); 1,270 m, 25 May 1995, *M.A. Pérez-Farrera* 465 (CHIP). **Mun. Villa Corzo**, 1,320 m, 12 Jul 2004, *A. Reyes-García et al.* 7134 (MEXU); 1,500 m, 9 Feb 1972, *D.E. Breedlove* 23999 (MEXU, MO); 1,170 m, 16 Mar 1989, *U. Bachem & R. Rojas C.* 579 (CHIP, MEXU, SLPM). **Mun. Villaflores**, 960 m, 6 Apr 1995, *A.P. Vovides & M.A. Pérez-Farrera* 1261 (XAL); 1,157 m, 7 Jul 2004, *D. Álvarez* 9809 (MEXU); 1,277 m, 25 Jun 2018, *F. Nicolalde-Morejón et al.* 2854–2863 (CIB); 1,195 m, 20 Jun 2019, *F. Nicolalde-Morejón & L. Martínez-Domínguez* 3208–3213 (CIB); 1,350 m, 21 Jun 2019, *F. Nicolalde-Morejón & L. Martínez-Domínguez* 3215–3224 (CIB); 1,015 m, 5 Aug 1994, *J.J. Castillo-Hernández* 230 (CIB, MEXU, USCG); 1,250 m, 5 Apr 1995, *J.J. Castillo-Hernández* 595 (CHIP); 1,140 m, 6 Aug 2002, *L. Alvarado C. et al.* 368 (MEXU); 1,195 m, 20 Jun 2019, *L. Martínez-Domínguez & F. Nicolalde-Morejón* 1808–1813 (CIB); 1,350 m, 21 Jun 2019, *L. Martínez-Domínguez & F. Nicolalde-Morejón* 1814–1825 (CIB); 1,277 m, 25 Jun 2018, *L. Martínez-Domínguez et al.* 1428, 1429, 1431–1438 (CIB), 1430 (CIB, MEXU); 940 m, 22 Dec 1993, *M.A. Pérez-Farrera s/n* (XAL), 26 (CHIP, XAL); 910 m, 28 Apr 1994, *M.A. Pérez-Farrera* 37 (CHIP, XAL); 1,460 m, 16 Sep 1994, *M.A. Pérez-Farrera* 126 (CHIP); 950 m, 12 Apr 1996, *M.A. Pérez-Farrera* 1480 (CHIP).

21. *Ceratozamia mixeorum* Chemnick, T.J.Greg. & Salas-Mor., Phytologia 83(1): 47 1998 (“1997”)

Fig. 7H

Type. MEXICO. Oaxaca: Cercanía a Juquila Mixe, 1,737 m, 21 May 1997. *J. Chemnick & T. Gregory* 49 (lectotype, designated by Nicolalde-Morejón and Avendaño 2011, pg. 1033: XAL! [XAL0065870]).

Description. *Stem* 30–100 cm long, 18–25 cm in diameter, epigeous, decumbent. *Cataphylls* 1.8–4.6 × 1.9–4.3 cm wide at the base, persistent, triangular, reddish brown, densely brown tomentose at emergence, partially tomentose at maturity, apex acuminate. *Leaves* 3–17 (30), 85–246 cm long, descending, light green and glaucous at emergence with light brown trichomes, glabrous at maturity. *Petiole* 46–132 cm long,

terete, linear, green in mature leaves; with 30–50 thin prickles, 0.20–0.38 cm long. **Rachis** 58–118 cm long, terete, linear, green to greenish in mature leaves, with scarce prickles. **Leaflets** 19–35 pairs, opposite to subopposite insertion in one plane, lanceolate, abaxially curved, rarely planar, not basally falcate, papyraceous, flat, green with adaxial and abaxial sides glabrous, distal end with entire margins, acuminate and symmetrical at the apex, attenuate at base, with conspicuous and green-light veins; median leaflets $24\text{--}39 \times 1.9\text{--}2.9$ cm, $1.7\text{--}3.0$ cm between leaflets; articulations 0.6–1.0 cm wide, green. **Pollen strobili** 22–30 cm long, 4.5–7 cm in diameter, generally solitary (1–2), cylindrical, erect, greenish at emergence with reddish trichomes, greenish yellow with reddish brown trichomes at maturity; peduncle 10–15 cm long, 1.2–2.0 cm in diameter, glabrous or with trichomes scarce reddish brown to brown; microsporophylls $1.4\text{--}2.4 \times 0.7\text{--}1.3$ cm, obconic with a non-recurved distal face and lobate fertile portion, infertile portion 0.39–0.48 cm long and linear with straight horns 0.30–0.50 cm long, 0.50–0.93 cm and a right angle between the horns. **Ovulate strobili** 23–32 cm long, 12–16 cm in diameter, solitary, cylindrical, erect, yellowish green with abundant blackish trichomes at emergence, green with brown to blackish trichomes at maturity, apiculate apex; peduncle 12–23.5 cm long, 1.3–2.1 cm in diameter, pendulous, glabrous or with scarce reddish brown trichomes; megasporophylls 60–112, 6–9 orthostichies with 10–14 sporophylls per orthostichy, $2.4\text{--}2.8 \times 4.0\text{--}5.1$ cm, with a truncate distal face, horns straight and 0.90–1.1 cm long, 0.92–1.2 cm between horns and a right angle between the horns. **Seeds** 2.2–3.0 cm long, 1.6–2.0 cm in diameter, ovate, sarcotesta whitish yellow to yellow when immature, light brown at maturity.

Distribution and habitat. *Ceratozamia mixeorum* is endemic to the southern portion of Sierra Norte of Oaxaca State (Mexico), along the highlands in the Mixe area (Fig. 21A), where it occurs in karstic rocks of cloud and oak forests between 1,170 to 2,150 m.

Etymology. The specific epithet was named in honor of the Mixe people.

Common names. Mexico. Oaxaca: Carrete (Chemnick et al. 1998).

Uses. The pollen strobilus is used as a toy (Chemnick et al. 1998).

Conservation status. (IUCN 2021). *Ceratozamia mixeorum* is listed under criteria A2cd+4cd; B1ab(ii,iii,v) as “Endangered”.

Discussion. *Ceratozamia mixeorum* is similar to *C. whitelockiana*, but has prickles on the rachis of the leaf and a densely prickly petiole (up to 50 prickles), ovulate strobili with long and pendulous peduncle up to 23.5 cm long. The fertile portion of ovulate strobilus has 6–9 orthostichies and 10–14 sporophylls per orthostichy; in contrast to 4–5 orthostichies and 5–8 sporophylls per orthostichy in *C. whitelockiana*.

Specimens examined. MEXICO. **Oaxaca: Mun. Guevea de Humboldt**, 1,300 m, 30 Mar 1991, *A. Campos* 3614 (MEXU). **Mun. San Juan Juquila Mixes**, 1,605 m, 7 Apr 1995, *E. Torres* B. 563 (SERO, XAL); 1,595 m, 25 Sep 2020, *F. Nicolalde-Morejón et al.* 3368 (CIB); 1,681 m, 25 Sep 2020, *F. Nicolalde-Morejón et al.* 3369–3371 (CIB); 1,595 m, 25 Sep 2020, *L. Martínez-Domínguez et al.* 2001, 2002 (CIB); 1,681 m, 25 Sep 2020, *L. Martínez-Domínguez et al.* 2003 (CIB, MEXU), 2004–2006 (CIB). **Mun. San Pedro Ocotepec**, 8 Apr 1995, 1,600 m, *E. Torres* B. et al. 607 (XAL). **Mun. Santa**

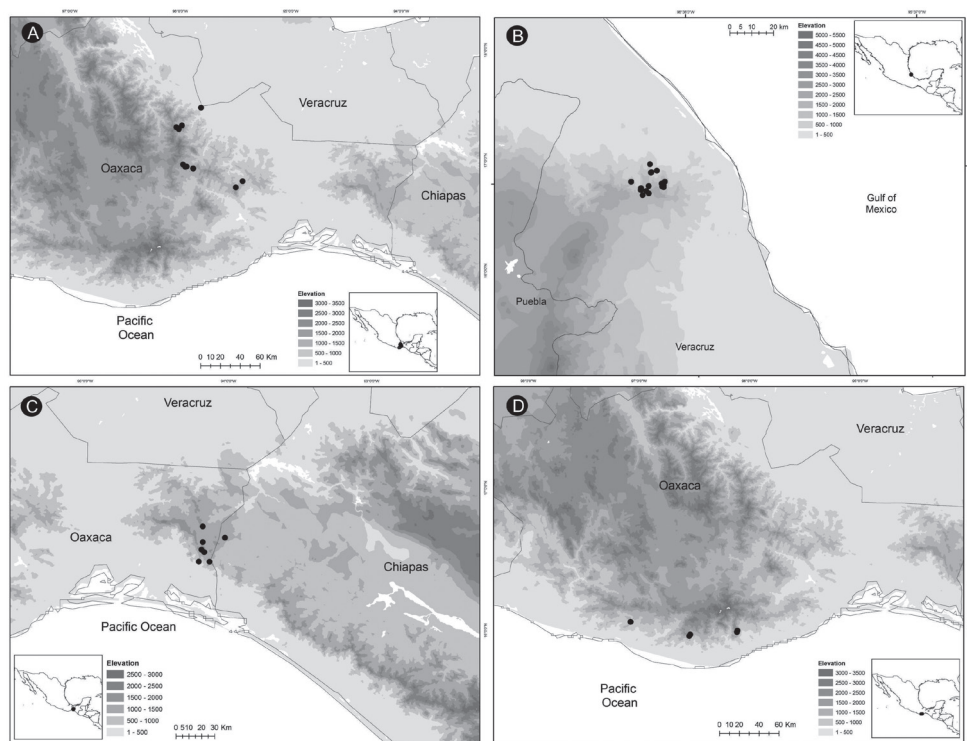


Figure 21. Distribution of *Ceratozamia* species **A** *C. mixeorum*. **B** *C. morettii*. **C** *C. norstogii*. **D** *C. oliversacksii*.

María Guienagati, 1,200 m, 25 Jan 1996, *M. Cerón C. et al.* 249 (MEXU, SERO, XAL). **Mun. Santa María Tepantlali**, 1,728 m, 25 Sep 2020, *F. Nicolalde-Morejón et al.* 3362–3367 (CIB); 2,147 m, 15 May 2011, *G. Juárez-García* 3871 (MEXU); 1,728 m, 25 Sep 2020, *L. Martínez-Domínguez et al.* 1994–1995 (CIB, MEXU), 1996–2000 (CIB). **Mun. Totontepec Villa de Morelos**, 1,300 m, 7 Dec 1989, *E. Vargas-Ruiz* 476 (MEXU); 1,900 m, 21 Apr 1986, *J. Rivera-Reyes & Gary J. Martin* 246 (MEXU); 1,700 m, 15 Jul 1987, *E. Velasco-López & G.J. Martin* 60 (MEXU); 1,900 m, 6 Jan 1988, *J. Rivera-Reyes & G.J. Martin* 920 (MEXU); 2,000 m, 16 Sep 1987, *W. Ruiz S.* 46 (MEXU).

22. *Ceratozamia morettii* Vázquez-Torres & Vovides, Novon 8 (1): 87. 1998
Figs 7I–J, 10A, C

Type. MEXICO. Veracruz: Mun. Landero y Coss, El Raicero, 4 km NE from Landero y Coss, 1,500 m, 7 Jan 1992, *M. Vázquez-Torres & H. Barney* 4097 (holotype: CIB! [acc. # 22297UV]; isotypes: CIB! [acc. # 24578UV], MEXU [n.v.], XAL! [XAL0001061, XAL0001064])

Description. *Stem* 20–23 (50) cm long, 20–35 cm in diameter, epigeous, erect and decumbent. *Cataphylls* 4–6.5 × 3–3.5 cm wide at the base, persistent, triangular, reddish brown, densely brown tomentose at emergence, partially tomentose at maturity, apex acuminate. *Leaves* 3–30, 82–200 cm long, descending, light green at emergence, with brown trichomes, glabrous at maturity. *Petiole* 30–90 cm long, terete, linear, green in mature leaves; with 8–60 thin prickles, 0.01–0.20 cm long. *Rachis* 50–116 cm long, terete, linear, green in mature leaves, with prickles. *Leaflets* 10–23 pairs, opposite to subopposite, oblong, longitudinally curved abaxially to planar, not basally falcate, coriaceous, green with adaxial side glabrous and abaxial side glaucous, distal end with entire margins, acuminate and asymmetrical at the apex, attenuate at base, and with conspicuous and green-light veins; median leaflets 17.5–41 × 2.6–4.3 cm wide, 2.1–6 cm between leaflets; articulations 0.5–1.6 cm wide, green and yellow. *Pollen strobili* 12–22 (35.5) cm long, 3.8–5.2 cm in diameter, solitary, cylindrical, erect, brownish yellow at emergence, greenish yellow with blackish pubescent at maturity; peduncle 3–7 (12.5) cm long, 1.1–1.6 cm in diameter, tomentose, reddish brown to brown; microsporophylls 1.0–2.0 × 0.9–1.15 cm, obconic with a non-recurved distal face and a lobate fertile portion, infertile portion 0.37–0.75 cm long and orbicular with straight horns 0.15–0.53 cm long, 0.47–0.92 cm and an acute angle between the horns. *Ovulate strobili* 14–20 cm long, 8–9.9 cm in diameter, solitary, globose, erect, yellowish green with brown trichomes at emergence, green with blackish trichomes at maturity and with apiculate apex; peduncle 4–7 cm long, 1.2–1.8 cm in diameter, erect, tomentose, brown; megasporophylls 35–81 (108), 7–10 orthostichies with 5–9 sporophylls per orthostichy, 1.7–2.6 × 3.0–4.5 cm, with a truncate distal face, horns straight and 0.32–0.69 cm long, 1.05–1.6 cm between horns and a right angle between the horns. *Seeds* 1.5–2.3 cm, 1–1.6 cm in diameter, ovate and globose, sarcotesta whitish yellow to yellow when immature, light brown at maturity.

Distribution and habitat. *Ceratozamia morettii* is endemic to the Sierra de Chic-onquiaco in Veracruz State, Mexico (Fig. 21B), here it occurs in cloud forest on karstic rocks and cliffs between 1,150–1,850 m.

Etymology. The specific epithet honors the Italian botanist Aldo Moretti from the Orto Botanico and Istituto di Biologia Vegetale at the University of Naples Federico II, in recognition of his scientific contributions to cycad biology (Vázquez-Torres et al. 1998).

Common names. Mexico. Veracruz: Palmita (J. Rees & A.P. Vovides 1663), palmilla (J. Rees & A.P. Vovides 1676).

Uses. Leaves are used in flower arrangements to decorate the homes during religious rites (Fig. 28A).

Conservation status. (IUCN 2021). *Ceratozamia morettii* has been listed as “Endangered” under criteria B1ab(i,iv,v)+2ab(i,iv,v).

Discussion. In leaf morphology, *Ceratozamia morettii* is morphologically similar to *C. delucana*; however, there are differences in the total size of the plant and in its reproductive structures. The microsporophyll horns of *C. morettii* form an acute angle, whereas those of *C. delucana* form a right angle. The ovulate strobilus in *C. morettii*

is green with blackish trichomes at maturity and an apiculate apex. In contrast, in *C. delucana*, the ovulate strobilus is green and glabrous at maturity with an acute apex.

Specimens examined. MEXICO. **Veracruz:** **Mun. Chiconquiaco**, 1,700 m, 5 Sep 1981, *A.P. Vovides* 687 (XAL); 1,850 m, 18 Dec 1981, *A.P. Vovides* 704 (XAL); Sep 1829, *C.J.W. Schiede* s/n (XAL); 1,598 m, 17 Sep 2020, *F. Nicolalde-Morejón et al.* 3318–3322 (CIB); 26 Nov 1974, *J. Rees* 6336 (IEB); 1,700 m, 5 Jun 2018, *L. Lagunes G.* 83, 84, 85, 86 (CIB); 1,600 m, 26 Apr 2018, *L. Martínez-Domínguez et al.* 1280–1290 (CIB); 1,700 m, 3 Dec 2018, *L. Martínez-Domínguez et al.* 1567, 1568 (CIB); 1,500 m, 15 Mar 2019, *L. Martínez-Domínguez et al.* 1660, 1661 (CIB); 1,550 m, 26 Mar 2019, *L. Martínez-Domínguez et al.* 1680, 1681 (CIB); 1,598 m, 17 Sep 2020, *L. Martínez-Domínguez et al.* 1931–1934, 1936 (CIB), 1935 (CIB, MEXU). **Mun. Landero y Coss**, 1,750 m, 1 Jan 1976, *J. Rees & A.P. Vovides* 1662–1664 (XAL); 1,750 m, 23 Sep 1976, *J. Rees & A.P. Vovides* 1676 (XAL); 1,830 m, 3 Mar 2011, *L.H. Bojórquez G. et al.* 23101–2316 (CIB); 1,472 m, 29 Jan 2015, *L. Martínez-Domínguez et al.* 185–214 (CIB); 1,765 M, 22 Apr 2008, *M. Vázquez-Torres et al.* 8349 (CIB); 3 Mar 2001, *S. Avendaño* 5378 (MEXU); 1,520 m, 10 Jan 2001, *T.W. Walters* 2001-01-E (XAL). **Mun. Tenochtitlán**, 1,500 m, 10 Apr 2002, *A. Rincón G. et al.* 2996, 2997 (XAL); 1,500 m, 12 Apr 2002, *A. Rincón G. et al.* 2998 (XAL). **Mun. Yecuatla**, 1,400 m, 26 May 1981, *C. Gutiérrez B. & A. Montoya L.* 134 (MO, XAL); 1,211 m, 28 Sep 2014, *F. Nicolalde-Morejón & L. Martínez-Domínguez* 2087–2106 (CIB); 1,200 m, 26 Sep 1976, *J. Rees* 1677 (XAL); 1,211 m, 9 Aug 2014, *L. Martínez-Domínguez et al.* 161 (CIB).

23. *Ceratozamia norstogii* D.W.Stev., *Brittonia* 34: 181. 1982

Fig. 27A

Type. MEXICO. Chiapas: Rancho Fenia, Mar–Apr 1925, *C. Purpus* 6 ♀ (holotype: NY! [00001116]; isotypes: F! [acc. # 1530231], MO!, US! [00620294]).

Description. **Stem** 30–60 cm long, 20–40 cm in diameter, epigeous, erect and decumbent. **Cataphylls** 4.5–6 × 2.5–6.4 cm wide at the base, persistent, long triangular, reddish brown, densely brown tomentose at emergence, tomentose at maturity, apex acuminate. **Leaves** 5–48, 50–126 cm long, ascending, copperish brown at emergence with whitish gray trichomes, glabrous at maturity. **Petiole** 10–49 cm long, terete, twisted, copperish with abundant greyish trichomes in young leaves, copperish and glabrous in mature leaves; with 30–60 robust prickles, 0.11–0.31 cm long. **Rachis** 40–88 cm long, terete, twisted, copperish with abundant greyish trichomes in young leaves, copperish and glabrous in mature leaves, with prickles. **Leaflets** 33–91 pairs, opposite to subopposite, insertion irregular to in one plane, linear, in general longitudinally planar, not basally falcate to basally falcate, coriaceous, strongly involute to caniculate, green with yellowish green base and with adaxial side glabrous and abaxial side glaucous, distal end with entire margins, acute and symmetric at the apex, attenuate at base, with conspicuous and light-green veins; median leaflets

14–48 × 0.21–0.46 cm, 0.2–1.3 cm between leaflets; articulations 0.08–0.66 cm wide, yellowish. **Pollen strobili** 13.2–25 cm long, 3.1–8 cm in diameter, solitary, cylindrical, erect, brown with reddish brown trichomes at emergence, yellowish green to cream at maturity; peduncle 2.0–5.5 cm long, 1.3–2.3 cm in diameter, tomentose, brown; microsporophylls 0.92–1.16 × 0.86–0.1.1 cm, discoid with a non-recurved distal face and a lobate fertile portion, infertile portion 0.36–0.45 cm long and orbicular with straight horns 0.07–0.13 cm long, 0.35–0.56 cm and an acute angle between the horns. **Ovulate strobili** 21–35 cm long, 8.5–10.5 cm in diameter, solitary, cylindrical, erect, green with abundant blackish trichomes at emergence, grayish green with abundant blackish trichomes at maturity, acuminate apex; peduncle 4.8–9 cm long, 1.8–2.2 cm in diameter, erect, tomentose, brown; megasporophylls 42–63, 6–7 orthostichies with 7–9 sporophylls per orthostichy, 2.6–3.0 × 3.6–4.0 cm, with a truncated distal face, horns straight and 0.37–0.58 cm long, 0.37–0.42 cm between horns with a right angle between the horns. **Seeds** 2.0–3.5 cm long, 1.1–1.9 cm in diameter ovate, sarcotesta whitish pink when immature, light brown at maturity.

Distribution and habitat. *Ceratozamia norstogii* is distributed in mountainous regions in Chiapas and Oaxaca States, Mexico (Fig. 21C), where it occurs on karstic rocks in pine-oak forest and the transition between pine forest and oak forest between 800–1,650 m.

Etymology. This species was named in honor of Knut Norstog, for his extensive and significant contributions to cycad biology (Stevenson 1982).

Common names. None recorded.

Uses. None recorded.

Conservation status. (IUCN 2021). The current category of threat to *Ceratozamia norstogii* is “Endangered” under criteria A2abd; B1ab(iii,iv,v); C1.

Discussion. *Ceratozamia norstogii* is easily diagnosable by its petiole and raquis twisted. The linear leaflets are coriaceous, strongly involute and appear caniculate and have an acute apex.

Specimens examined. MEXICO. **Chiapas: Mun. Cintalapa**, 1,100 m, 19 Mar 1993, *A.P. Vovides et al.* 1230, 1231, 1233, 1235 (XAL); 1,600 m, 3 Nov 1971, *D.E. Breedlove* 21813 (MEXU, MO); 1,600 m, 21 Apr 1972, *D.E. Breedlove* 24709 (MO); 1,600 m, 12 Oct 1979, *D.E. Breedlove* 44431 (MEXU); 800 m, 4 May 1988, *E. Palacios E.* 375 (CHIP, IBUG); 1,240 m, 6 Jun 1993, *E. Palacios E.* 2155 (CHIP); 1,280 m, 22 May 2001, *J.M. Lázaro-Zermeño* 251 (CHIP); 1,038 m, 20 Jun 2018, *F. Nicolalde-Morejón et al.* 2762–2770 (CIB); 1,325 m, 20 Jun 2018, *F. Nicolalde-Morejón et al.* 2771–2780 (CIB); 1,038 m, 20 Jun 2018, *L. Martínez-Domínguez et al.* 1326–1334 (CIB), 1335 (CIB, MEXU); 1,325 m, 20 Jun 2018, *L. Martínez-Domínguez et al.* 1337–1349 (CIB); 1,100 m, 5 Oct 1995, *M.A. Pérez-Farrera* 775 (CH, CIB, XAL); 5 Dec 1996, *M.A. Pérez-Farrera* 1483 (HEM). **Oaxaca: Mun. San Miguel Chimalapa**, 1,120 m, 1 Apr 1996, *S. Salas-Morales et al.* 1173 (SERO, XAL). **Mun. Santo Domingo Zanatepec**, 800 m, 22 Jun 2018, *F. Nicolalde-Morejón et al.* 2819–2828 (CIB); 800 m, 22 Jun 2018, *L. Martínez-Domínguez et al.* 1380, 1381, 1383, 1386, 1389–1391, 1394, 1396, 1399 (CIB).

24. *Ceratozamia oliversacksii* D.W.Stev., Mart.-Domínguez & Nic.-Mor., Kew Bull. 77: 212. 2022

Fig. 27B

Type. MEXICO. Oaxaca: Mun. Candelaria Loxicha, Cerro Perico, 1,616 m, 10 Jun 2021, *L. Martínez-Domínguez et al.* 2261 ♀ (holotype: CIB! [acc. # 23411UV]; isotypes: K!, MEXU!, NY!).

Description. *Stem* 30–80 cm long, 10–40 cm in diameter, epigeous, decumbent. *Cataphylls* 6.5–7.5 × 1.6–2.0 cm wide at the base, persistent, triangular, reddish brown, brown tomentose at emergence, glabrous at maturity, apex acuminate. *Leaves* 7–36 (50), 124–258 cm long, descending, green at emergence with brown trichomes, glabrous at maturity. *Petiole* 45–110 cm long, terete, linear, green at emergence, dark green in mature leaves; with 40–65 thin prickles, 0.50–0.70 cm long. *Rachis* 85–182 cm long, terete, linear, dark green in mature leaves with prickles. *Leaflets* 24–47 pairs, opposite to subopposite, insertion in one plane, linear, longitudinally curved abaxially to planar, not basally falcate, papyraceous, flat, green with adaxial and abaxial sides glabrous, distal end with entire margins, acuminate and symmetrical (rarely asymmetrical) at the apex, attenuate at base, with conspicuous and light-green veins; median leaflets 25–40 × 2.3–3.6 cm, 2.0–3.3 cm between leaflets; articulations 0.5–1.1 cm wide, green. *Pollen strobili* 20–35 cm long, 3.0–5.7 cm in diameter, solitary, cylindrical, erect, greenish with reddish trichomes at emergence, greenish yellow with reddish brown trichomes at maturity; peduncle 10–15 cm long, 1.2–1.8 cm in diameter, pubescent, reddish brown; microsporophylls 2.5–2.75 × 0.99–1.28 cm, obconic with a non-recurved distal face and a lobate fertile portion, infertile portion 0.60–0.80 cm long and a rounded with straight horns 0.08–0.18 cm long, 0.50–0.70 cm and an acute angle between the horns. *Ovulate strobili* 33–36 cm long, 11.5–14 cm in diameter, solitary, cylindrical, erect, greenish yellow with few reddish trichomes at emergence, green with brown to reddish brown trichomes or glabrous at maturity, acute apex; peduncle 8.0–10.0 cm long, 1.4–1.6 cm in diameter, erect, pubescent, light brown; megasporophylls 80–210, 9–10 orthostichies with 11–13 sporophylls per orthostichy, 2.3–2.9 × 3.9–5.0 cm, with a truncate distal face, horns straight and 0.31–0.53 cm long, 1.33–1.40 cm between horns with a right angle between the horns. *Seeds* 2.45–2.65 cm long, 1.4–1.6 cm in diameter, ovate, sarcotesta whitish yellow to yellow when immature, light brown at maturity.

Distribution and habitat. *Ceratozamia oliversacksii* occurs along the Eastern Sierra Madre del Sur in the Oaxacan Highlands, Mexico (Fig. 21D), it is found on karstic rocks with abundant organic matter in cloud forest and the transition zone between it and pine forest between 1,040 to 1,850 m.

Etymology. The specific epithet honors Oliver Sacks, who loved cycads and was a distinguished American neurologist and historian of science. Sacks published *Island of the Color Blind* and *Cycad Island* (Sacks 1997) and *Oaxaca Journal* (Sacks 2002) (Martínez-Domínguez et al. 2022b).

Common names. None recorded.

Uses. None recorded.

Preliminary conservation status. *Ceratozamia oliversacksii* should be listed as “Vulnerable (V)”. We visited four populations in Oaxaca in which each population size was between 50 to 300 adult plants. We observed different age classes from seedling to reproductive individuals.

Discussion. *Ceratozamia oliversacksii* is similar to *C. robusta* and *C. leptoceras* but is characterized by green leaves at emergence and the combination of linear and papyraceous leaflets. The ovulate strobili have 11 to 13 sporophylls per orthostichies and an acute apex, acute horns of megasporophylls up to 0.53 cm long, and microsporophylls with a rounded distal face and straight horns.

Specimens examined. MEXICO. **Oaxaca: Mun. Candelaria Loxicha**, 1,380 m, 3 May 2005, *A. Luna-José & B. Rendón-Aguilar* 1472, 1473 (XAL); 1,630 m, 23 Jun 2019, *F. Nicolalde-Morejón & L. Martínez-Domínguez* 3231–3243 (CIB); 1,630 m, 23 Jun 2019, *L. Martínez-Domínguez & F. Nicolalde-Morejón* 1832–1839 (CIB), 1840 (CIB, MEXU); 1,418 m, 20 April 2021, *L. Martínez-Domínguez et al.* 2160, 2161 (CIB); 1,616 m, 10 Jun 2021, *M. Rios-Méndez et al.* 105 (CIB). **Mun. San Agustín Loxicha**, 1,760 m, 12 Oct 2003, *A. Luna-José & B. Rendón-Aguilar* 518 (XAL); 1,400 m, 23 Jun 2019, *F. Nicolalde-Morejón & L. Martínez-Domínguez* 3229, 3230 (CIB); 1,400 m, 23 Jun 2019, *L. Martínez-Domínguez & F. Nicolalde-Morejón* 1829–1831 (CIB). **Mun. Santa Catarina Juquila**, 1,850 m, 13 Apr 1965, *J. Rzedowski* 19557 (ENCB); 1,450–1,700 m, 11 Feb 1965, *R. McVaugh* 22346 (ENCB; MICH). **Mun. San Miguel del Puerto**, 1,060 m, 25 Jun 2019, *F. Nicolalde-Morejón & L. Martínez-Domínguez* 3244–3249 (CIB); 1,430 m, 17 Apr 2000, *J. Rivera H. et al.* 2378 (FCME, SERO); 1,060 m, 25 Jun 2019, *L. Martínez-Domínguez & F. Nicolalde-Morejón* 1847–1849, 1851, 1852 (CIB), 1850 (CIB, MEXU); 1,040 m, 1 Apr 2003, *L. Schibli et al.* 152 (SERO).

25. *Ceratozamia osbornei* D.W.Stev., Mart.-Domínguez & Nic.-Mor., sp. nov.

urn:lsid:ipni.org:names:77305494-1

Figs 5, 6

Diagnosis. Similar to *Ceratozamia robusta* and *C. subroseophylla*, but distinguished by characters of reproductive structures. It has megasporophylls with abundant purple to wine-colored trichomes, ovulate strobili with an acuminate apex and up to 12 orthostichies with 31 sporophylls per orthostichy and pollen strobili with a long infertile portion from 0.65 to 0.80 cm long.

Type. BELIZE. Toledo: Southwestern Maya Mountains, Columbia River Forest Reserve, Union Camp. 6 Apr 1992, *B.K. Holst* 4105 (holotype: NY! [01340569]; isotype: MO! [acc. # 04661737, 04661738]).

Description. *Stem* 30–200 cm long, 20–40 cm in diameter, epigeous, generally decumbent. *Cataphylls* 5.5–8 × 2–3 cm wide at the base, persistent, triangular, reddish

brown, brown tomentose at emergence, glabrous at maturity, apex acuminate. **Leaves** 12–50, 90–300 cm long, ascending, brown at emergence, with whitish gray trichomes, glabrous at maturity. **Petiole** 75–100 cm long, terete, linear, greenish brown or dark brown at emergence, green in mature leaves; with 20–40 robust prickles, 0.20–0.45 cm long. **Rachis** 90–200 cm long, terete, linear, greenish brown or dark brown at emergence, green in mature leaves, with prickles. **Leaflets** 26–51 pairs, opposite to subopposite, insertion in one plane, lanceolate, longitudinally curved abaxially to planar, not basally falcate, papyraceous, flat, dark green, adaxial side glabrous, abaxial side glabrous, distal end with entire margins, acuminate and symmetric at the apex, attenuate at base, with conspicuous and light-green veins; median leaflets 30–45 × 2.5–4.0 cm, 1.7–5 cm between leaflets; articulations 0.9–1.6 cm wide, brown in young leaves and green in mature leaves. **Pollen strobili** 60–80 cm long, 7–9 cm in diameter, solitary, cylindrical, erect, green with wine trichomes at emergence, greenish yellow at maturity with wine to purple trichomes; peduncle 7–11 cm long, 2.5–3.5 cm in diameter, tomentose, brown; microsporophylls 2.0–3.3 × 1.1–1.85 cm, obconic with a non-recurved distal face and deeply lobate fertile portion, infertile portion 0.65–0.80 cm long and rounded with straight horns 0.20–0.29 cm long, 0.55–0.75 cm and a right angle between the horns. **Ovulate strobili** 30–50 cm long, 9–14 cm in diameter, solitary, cylindrical, erect, green with abundant wine to dark purple trichomes at emergence, green with abundant dark purple trichomes at maturity, acuminate apex; peduncle 12–20 cm long, 2.5–4.5 cm in diameter, erect, tomentose, reddish brown; megasporophylls 108–280, 9–12 orthostichies with 12–31 sporophylls per orthostichy, 1.8–2.3 × 2.3–4.1 cm, with a prominent distal face, horns straight and 0.36–0.50 cm long, 0.90–1.35 cm between horns with a right angle between the horns. **Seeds** 3.0–4.5 cm long, 2.0–3.0 cm in diameter, ovate, sarcotesta whitish pink when immature, light brown at maturity.

Distribution and habitat. *Ceratozamia osbornei* is endemic to Belize (Fig. 22A), where it occurs in evergreen tropical forest on karstic rocks with abundant organic matter between 200 and 750 m elevation.

Etymology. The specific epithet honors Roy Osborne in recognition of his remarkable contributions to the knowledge of the cycad diversity in the world. In particular, he has actively participated in the project “The World List of Cycads” since its inception (<https://www.cycadlist.org>).

Common names. None recorded.

Uses. None recorded.

Conservation status. There is insufficient data for evaluation, but it is known that some populations have more than 100 plants.

Paratypes. BELIZE. **Cayo:** 19 Aug 2008, *M. Calonje et al.* BZ08-042 (FTG); 20 Aug 2008, *M. Calonje et al.* BZ08-056 (FTG); 25 Feb 1992, *C. Hubbuck et al.* (FTG); 6 Apr 1971, *S. Kiem s.n.* [027932] (FTG); Spring, 1973, *S. Kiem s.n.* [027929] (FTG); 550 m, 4 Aug 1980, *Sutton et al.* 15 (MEXU, MO); 455 m, 12 Dec 1996, *T. Hawkins* 1186 (NY, MO). **Toledo:** 750 m, 15 May 1979, *C. Whiteford* 1764 (BM); 800–1,200 m, 23–27 Apr 1976, *G.R. Proctor* 35985 (BM, MO).

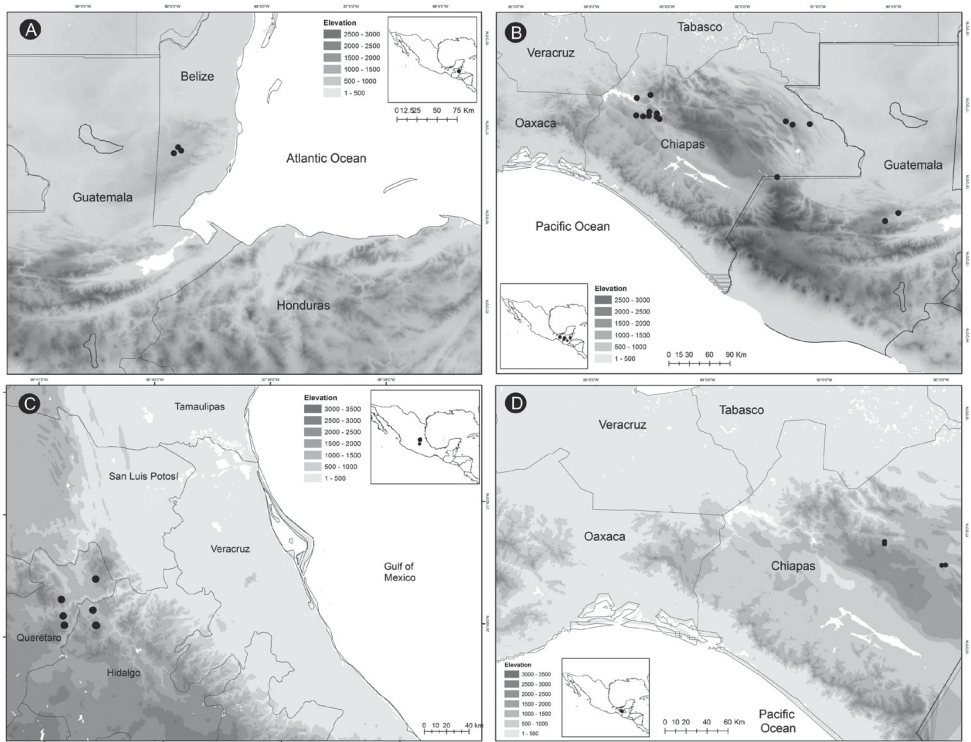


Figure 22. Distribution of *Ceratozamia* species. **A** *C. osbornei* **B** *C. robusta* **C** *C. sabatoi* **D** *C. sancheziae*.

26. *Ceratozamia robusta* Miq., Tijdschr. Wis-Natuurk. Wetensch. Eerste Kl. Kon. Ned. Inst. Wetensch. 1: 42. 1847

Fig. 27C

Ceratozamia mexicana Brongn. var. *robusta* (Miq.) Dyer, Biol. Cent.-Amer., Bot. 3: 193. 1884. Type. Based on: *Ceratozamia robusta* Miq.

Type. MEXICO. Chiapas: NW of Tuxtla Gutiérrez on road through San Fernando 23.5 km from route 190, 1,000 m, 9 Jul 1983, *D.W. Stevenson 549A* (neotype, designated by Stevenson and Sabato 1986, pg. 581: NY! [00001119]).

Description. *Stem* 30–100 cm long, 20–40 cm in diameter, epigeous, erect and decumbent. *Cataphylls* 5.0–9.0 × 3.5–7.5 cm wide at the base, persistent, long triangular, reddish brown, densely brown tomentose at emergence, partially tomentose at maturity, apex acuminate. *Leaves* 10–50, 138–266 cm long, ascending, dark brown at emergence, green and glabrous at maturity. *Petiole* 56–85 cm long, terete, linear, brown in young leaves, green in mature leaves; with 27–55 robust prickles, 0.48–0.70 cm long. *Rachis* 60–190 cm long, terete, linear, brown in young leaves, green in mature leaves, with prickles. *Leaflets* 20–45 pairs, opposite to subopposite,

insertion in one plane, lanceolate, in general longitudinally planar, not basally falcate, papyraceous, flat, green with adaxial side glabrous and abaxial side glaucous, distal end with entire margins, acuminate and asymmetrical at the apex, attenuate at base, with conspicuous and light-green veins; median leaflets $28\text{--}42 \times 2.5\text{--}4.0$ cm, $3.0\text{--}4.5$ cm between leaflets; articulations $0.2\text{--}0.8$ cm wide, green. **Pollen strobili** $50\text{--}70$ cm long, $7.0\text{--}8.5$ cm in diameter, solitary, cylindrical, erect, light green to yellowish green with blackish trichomes at emergence, yellowish cream with reddish brown trichomes at maturity; peduncle $10\text{--}15$ cm long, $2.5\text{--}3.2$ cm in diameter, tomentose, reddish brown to brown; microsporophylls $2.33\text{--}3.0 \times 1.14\text{--}1.90$ cm, obconic with a non-recurved distal face and deeply lobate fertile portion, infertile portion $0.45\text{--}0.65$ cm long and rounded with curved horns $0.26\text{--}0.40$ cm long, $0.55\text{--}0.75$ cm and a right angle between the horns. **Ovulate strobili** $26\text{--}40$ cm long, $11\text{--}14.5$ cm in diameter, solitary, cylindrical, erect, dark green at emergence, dark green with scarce blackish trichomes at maturity, acuminate apex; peduncle $5.0\text{--}11.0$ cm long, $2.5\text{--}4.0$ cm in diameter, erect, tomentose, reddish brown; megasporophylls $153\text{--}280$, $8\text{--}14$ orthostichies with $17\text{--}20$ sporophylls per orthostichy, $1.7\text{--}2.5 \times 2.3\text{--}3.5$ cm, with a prominent distal face, horns straight and $0.38\text{--}0.50$ cm long, $1.35\text{--}1.60$ cm between horns with a right angle between the horns. **Seeds** $2.5\text{--}3.5$ cm long, $1.9\text{--}2.5$ cm in diameter, ovate, sarcotesta whitish yellow to yellow when immature, light brown at maturity.

Distribution and habitat. *Ceratozamia robusta* is widely distributed in Chiapas State, Mexico and northern Guatemala (Fig. 22B). It occurs in evergreen tropical forest between 400 to 1,300 m on karstic rocks with humus soil.

Etymology. The epithet is derived from the robust appearance of the species.

Common names. Mexico. Chiapas: Amendu (M.A. Pérez-Farrera 30), piña del tlacoache (A.P. Vovides & J.I. Calzada 481).

Uses. The seeds are used as food, and the leaves to decorate altars.

Conservation status. (IUCN 2021). *Ceratozamia robusta* is listed as “Endangered” under criteria A2acd. This species has a wide distribution, but some populations previously considered to be part of this entity have been assigned to described species during the last ten years. Therefore, a reassessment of its conservation status is required.

Discussion. *Ceratozamia robusta* is similar to *C. subroseophylla* and distinguished by its dark green ovulate strobilus with sparse blackish trichomes on megasporophylls at maturity, prominent distal face, straight horns with a right angle between them, differentiating it easily from *C. subroseophylla*. The pollen strobilus of *C. robusta* is the largest in the genus (up to 70 cm long).

Specimens examined. GUATEMALA. **Alta Verapaz:** 200 m, 13 Jul 2002, S. Hernández 757 (MO); 1,800–2,000 m, 27 Feb 1939, C.L. Wilson 262 (F); 300–500 m, 17 Apr 1942, J.A. Steyermark 45734 (US); 879 m, 15 Mar 2008, M. Véliz et al. 19998 (BIGU). **Huehuetenango:** 2,000 m, 10 Sep 1942, J.A. Steyermark 52046 (NY, US); 1,150 m, 26 Jul 1943, J.A. Steyermark 49506 (F; MO; NY); 400 m, 27 Jul 1942, J.A. Steyermark 49682 (NY); 900–1,300 m, 3 Sep 1942, J.A. Steyermark

51818 (F; NY; US); 900–1,000 m, 6 Mar 2009, *M.J.M. Christenhusz et al.* 5600 (MO); 1,161 m, 21 Dec 2010, *L. Vélasquez et al.* 1566 (BIGU). MEXICO. **Chiapas:** **Mun. Berriozábal**, 1,129 m, 6 Mar 2014, *F. Nicolalde-Morejón et al.* 1970–1975 (CIB); 1,129 m, 6 Mar 2014, *L. Martínez-Domínguez et al.* 41–47, 49, 50 (CIB), 48 (CIB, MEXU). **Mun. Copainalá**, 1,100 m, *M. Gutiérrez & T. Acero* 240 (CHIP). **Mun. Ocosingo**, 900 m, 16 Mar 1981, *A.P. Vovides & J.I. Calzada* 481 (XAL); 14 Apr 1967, *D.E. Breedlove* 15687 (ENCB); 700 m, 18 Apr 1985, *E. Martínez S.* 12067 (MEXU); 860 m, 24 Feb 1984, *J. García F.* 720 (CH, CIB, XAL). **Mun. Ocozacoatl de Espinosa**, 818 m, 11 Nov 1997, *R. Álvarez G.* 6 (CHIP). **Mun. Osumacinta**, 692, 18 Jul 2008, *R. Gallegos Ramos* 211 (CHIP). **Mun. San Fernando**, 680 m, 29 Apr 1995, *A.P. Vovides & M.A. Pérez-Farrera* 1266^a (XAL); 22 Sep 1993, *Brigada T. Walters s/n* (XAL); 9 Jul 1983, *D.W. Stevenson et al.* 549 B–F (NY); 1,000 m, 9 Jul 1983, *D.W. Stevenson et al.* 550 A–C (NY), 24 Apr 1999, *M.A. Isidro V.* 388 (CHIP); 29 Apr 1995, *M.A. Pérez-Farrera* 293 (MEXU); 12 Jun 2009, *N. Martínez-Meléndez* 2692 (MEXU); 1,200 m, 5 Dec 2000, *R.A. Palestina & I. Acosta* 2707 (XAL). **Mun. Tuxtla Gutiérrez**, 1,235 m, 19 Mar 1994, *M.A. Pérez-Farrera* 30 (CH, MEXU, XAL); 1,200 m, 1 Nov 1995, *M.A. Pérez-Farrera* 820 (CHIP).

27. *Ceratozamia sabatoi* Vovides, Vázq.Torres, Schutzman & Iglesias, Novon 3 (4): 502. 1993

Figs 1A, 27D

Type. MEXICO. Querétaro: Mun. San Joaquín, La Mojonera, 2 km on road San Joaquín-El Aguacate, 1,850 m, 15 Apr 1991, *A.P. Vovides & P. Fawcett* 1205 ♀ (holotype: XAL! [XAL0005310]).

Description. **Stem** 8–30 cm long, 20–35 cm in diameter, epigeous, erect and decumbent. **Cataphylls** 3–4.5 × 2–3.5 cm wide at the base, persistent, triangular, reddish brown, densely brown tomentose at emergence, partially tomentose at maturity, apex acuminate. **Leaves** 3–40, 60–129 cm long, descending, dark brown at emergence with whitish gray trichomes, glabrous at maturity. **Petiole** 20–60 cm long, terete, linear, greenish brown in mature leaves; with 5–40 thin prickles, 0.02–0.19 cm long. **Rachis** 40–92 cm long, terete, linear, brown in mature leaves, with prickles. **Leaflets** 26–54 pairs, opposite to subopposite, insertion in one plane, linear, longitudinally curved abaxially to planar, basally falcate, papyraceous, flat, green with adaxial and abaxial sides glabrous, distal end with entire margins, acuminate and symmetrical at the apex, attenuate at base, with conspicuous and green-light veins; median leaflets 13–32 × 0.6–1.5 cm, 0.5–1.5 cm between leaflets; articulations 0.3–0.7 cm wide, brown. **Pollen strobili** 11–18 cm long, 3.5–4.8 cm in diameter, solitary, cylindrical, erect, greenish yellow at emergence, greenish yellow with blackish trichomes at maturity; peduncle 7–13 cm long, 1.1–1.9 cm in diameter,

tomentose, reddish brown to brown; microsporophylls $1.0\text{--}1.9 \times 0.85\text{--}1.90$ cm, discoid with a recurved downward distal face and lobate fertile portion, infertile portion $0.33\text{--}0.43$ cm long and rounded with straight horns $0.06\text{--}0.20$ cm long, $0.30\text{--}0.71$ cm and a right angle between the horns. **Ovulate strobili** $14\text{--}19.5$ cm long, $5.5\text{--}8.5$ cm in diameter, solitary, cylindrical, erect, yellowish green with brown trichomes at emergence, blue green with blackish trichomes at maturity, apiculate apex; peduncle $3.5\text{--}7$ cm long, $1.2\text{--}2.5$ cm in diameter, erect, tomentose, brown; megasporophylls $72\text{--}110$, $8\text{--}10$ orthostichies with $9\text{--}11$ sporophylls per orthostichy, $3.5\text{--}5 \times 3.8\text{--}4.5$ cm, with a truncate distal face, horns straight and $0.28\text{--}0.40$ cm long, $1.2\text{--}1.6$ cm between horns with a right angle between the horns. **Seeds** $1.2\text{--}2.0$ cm long, $1.2\text{--}1.5$ cm in diameter, ovate, sarcotesta whitish red when immature, light brown at maturity.

Distribution and habitat. *Ceratozamia sabatoi* is endemic to the Sierra Gorda mountain range in Mexico, particularly in Querétaro and Hidalgo States (Fig. 22C), where it occurs in the understory herbaceous layer of the transition zone between oak forest and cloud forest at $1,600\text{--}1,900$ m.

Etymology. The specific epithet honors Sergio Sabato, a distinguished professor at the University of Naples Federico II for his outstanding contributions to knowledge of the biology of Zamiaceae (Vovides et al. 1993).

Common names. None recorded.

Uses. None recorded.

Conservation status. (IUCN 2021). *Ceratozamia sabatoi* is listed as “Endangered” under criteria A2c; B1ab(i,ii,iv)+2ab(i,ii,iv); C1.

Discussion. *Ceratozamia sabatoi* differs from all *Ceratozamia* species by its microsporophylls with a recurved downward distal face. In addition, this species differs from *C. kuesteriana* by its flat leaflets and descending leaves.

Specimens examined. MEXICO. **Hidalgo: Mun. Jacala de Ledezma**, $1,725$ m, 16 Aug 2007, *A. Frias-Castro et al.* 578 (IBUG); $1,500$ m, 29 Oct 1946, *H.E. Moore, Jr.* 1788 (CHAPA). **Mun. Zimapán**, $2,000$ m, 2 Jun 1989, *M. Vázquez-Torres & J.P. Sclavo* 4035 (CIB); $1,235$ m, 22 May 2003, *R. Contreras-Medina* 55, 56 (XAL); $1,900$ m, 13 Sep 1981, *R. Fernandez-Nava* 6561 (MEXU, MO, XAL). **Querétaro: Mun. Cadereyta de Montes**, $1,850$ m, 15 Apr 1991, *A.P. Vovides & K. Norstog* 1193 (XAL); *A.P. Vovides et al.* 1196–1199 (XAL), 1203 (MEXU, XAL); $1,850$ m, 15 Apr 1991,); *A.P. Vovides* 1201, 1205 (XAL); $1,924$ m, 28 Mar 2015, *F. Nicolalde-Morejón et al.* 2169, 2170 (CIB); $1,924$ m, 28 Mar 2015, *L. Martínez-Domínguez et al.* 313–343 (CIB); 29 Mar 1995, *R. Fernández-Nava s/n* (MEXU); 7 Dec 1990, *R. Zirahuén-Ortega V.* 328 (MEXU). **Mun. Landa de Matamoros**, $1,439$ m, 12 Jan 2001, *T.W. Walters* 2001-05-A, B (XAL). **Mun. Pinal de Amoles**, $1,760$ m, 17 Sep 2001, *E. Carranza G. & I. Silva* 6254 (MO); $1,678$ m, 29 Mar 2015, *F. Nicolalde-Morejón et al.* 2171, 2172 (CIB); $1,678$ m, 29 Mar 2015, *L. Martínez-Domínguez et al.* 344–372 (CIB); $1,700$ m, 11 Dec 1988, *Rzedowski s/n* (XAL); $1,650$ m, 4 Apr 1987, *R. Fernández N.* 3819 (ENCB).

28. *Ceratozamia sancheziae* Pérez-Farr., Gut.Ortega & Vovides, Phytotaxa 500 (3): 209. 2021

Figs 9A, 12A, 23 D–F

Type. MEXICO. Chiapas: Mun. Tenejapa, 1,500 m, 16 May 2017, *M.A. Pérez Farrera* 3558 ♀ (holotype: HEM [n.v.]; isotypes: MEXU [n.v.], XAL [n.v.]).

Description. *Stem* 8–30 cm long, 10–20 cm in diameter, semi-hypogeous, erect. *Cataphylls* 2.5–5.8 × 1.3–5 cm wide at the base, persistent, triangular, reddish brown, densely brown tomentose at emergence, glabrous at maturity, apex acuminate. *Leaves* 4–12 (20), 100–232.5 cm long, descending, green or brown at emergence with whitish gray trichomes, glabrous at maturity. *Petiole* 40–134.5 cm long, terete, linear, greenish brown or green in mature leaves; unarmed or with prickles 2–28 thin, 0.05–0.34 cm long. *Rachis* 55–120 cm long, terete, linear, brown or green in mature leaves, unarmed or with scarce prickles. *Leaflets* 20–35 pairs, opposite to subopposite, insertion in one plane, linear, in general longitudinally planar, not basally falcate (sometimes basally falcate), papyraceous, flat, green with adaxial side glabrous and abaxial side glaucous, distal end with entire margins, acuminate and symmetrical at the apex, attenuate at base, with conspicuous and green-light veins; median leaflets 22–36 × 1.7–3.0 cm, 1.4–3.5 cm between leaflets; articulations 0.55–1.1 cm wide, green. *Pollen strobili* 15–20 cm long, 1.8–3.2 cm in diameter, solitary, cylindrical, erect, light green at emergence, green with blackish trichomes at maturity; peduncle 6–10 cm long, 0.7–1.5 cm in diameter, tomentose, reddish brown to brown; microsporophylls 0.88–1.2 × 0.65–0.80 cm, discoid with a non-recurved distal face and a lobate fertile portion, infertile portion 0.32–0.40 cm long and rounded with straight horns 0.10–0.20 cm long, 0.63–0.70 cm and an acute angle between the horns. *Ovulate strobili* 12–25 cm long, 7.0–8.5 cm in diameter, solitary, cylindrical, erect, yellowish green at emergence, green with scarce blackish trichomes at maturity, acuminate apex; peduncle 5.0–11 cm long, 0.9–1.1 cm in diameter, erect, tomentose, brown; megasporophylls 35–100, 7–10 orthostichies with 5–10 sporophylls per orthostichy, 0.9–1.2 × 3.5–4 cm, with a prominent distal face, horns curved to straight and 0.50–0.73 cm long, 1.2–1.4 cm between horns with a right angle between the horns. *Seeds* 1.9–2.3 cm long, 1.4–1.5 cm in diameter, globose, sarcotesta whitish yellow when immature, light brown at maturity.

Distribution and habitat. *Ceratozamia sancheziae* is endemic to Chiapas State, Mexico (Fig. 22D), where it occurs in oak forest and pine-oak forest between 1,000–1,536 m.

Etymology. This species was named in honor of María Ydelia Sánchez-Tinoco, for contributions to our knowledge of the anatomy of Mexican cycad seeds (Gutiérrez-Ortega et al. 2021).

Common names. None recorded.

Uses. The community in Tenejapa use the leaves of this species for ornaments in traditional community festivities.

Preliminary conservation status. *Ceratozamia sancheziae* could be included as “Endangered” (EN) in the IUCN Red List of Threatened Species based on the number of populations, which have between 70 to 250 adult plants.

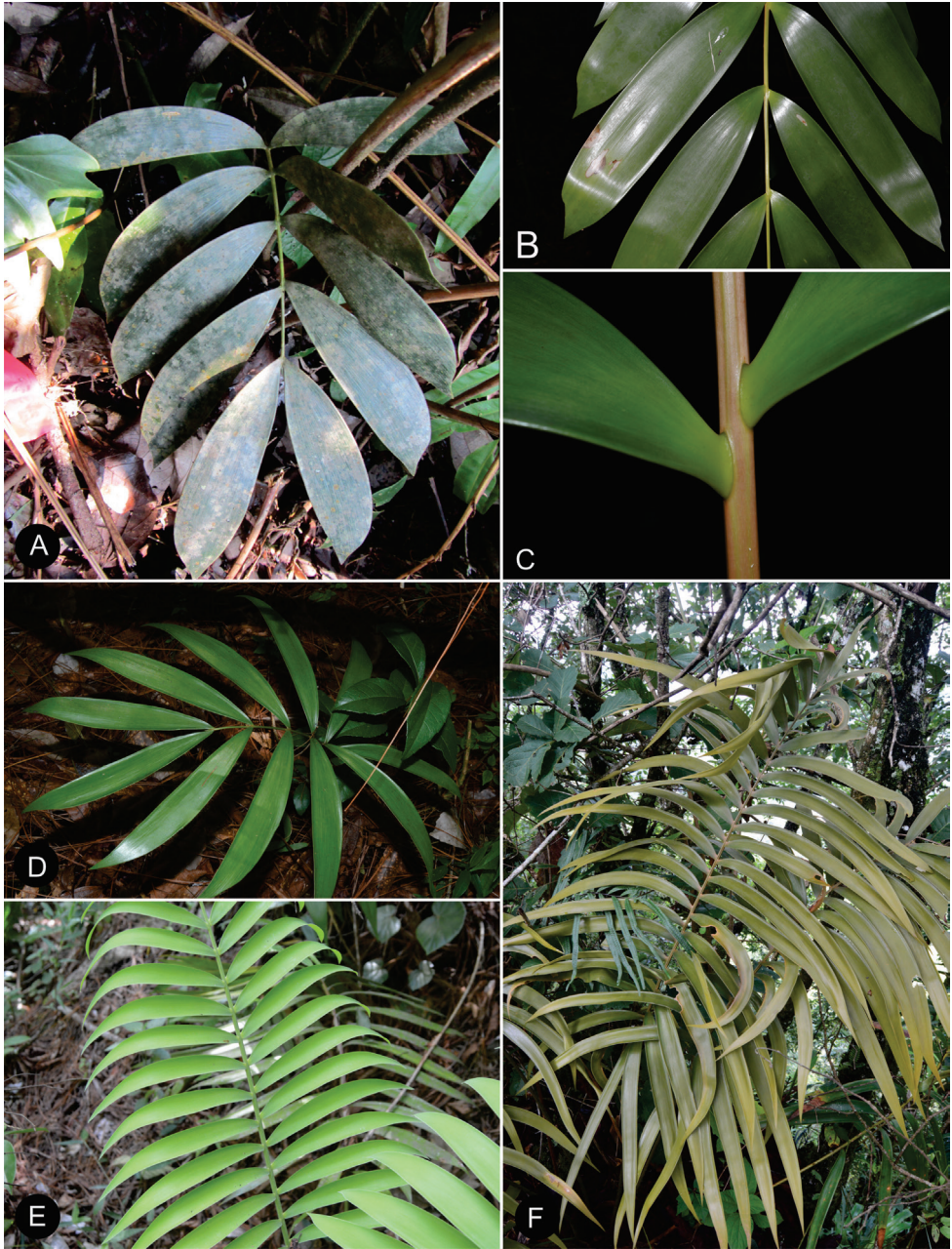


Figure 23. Vegetative comparison between *Ceratozamia zoquorum* (A–C) and *C. sancheziae* (D–F). **A** juvenile plant **B** mature leaf **C** detail of leaflets and rachis **D** juvenile plant **E**, **F** leaves at emergence of adult plants.

Discussion. *Ceratozamia sancheziae* is geographically close to *C. robusta*, but differs from it by its linear leaflets, leaves at emergence that are light green or reddish brown with a glaucous appearance, and ovulate strobili with curved to straight horns up to 0.73 cm long.

Here, we have recircumscribed and clarified the taxonomic identity of *Ceratozamia sancheziae*. In the description of this species, the authors mentioned Petalcingo as a municipality, but this is a locality that corresponds to Tila municipality in Chiapas (c.f. Gutiérrez-Ortega et al. 2021). The distribution range for this species was considered to extend from Tenajapa municipality in Chiapas to the mountain area close to the border with the State of Tabasco (Gutiérrez-Ortega et al. 2021). However, we found specimens from Yajalón of Chiapas (*M.A. Pérez Farrera* 1635 from XAL) that do not correspond to the species description (Suppl. material 2). We carried out fieldwork and collected botanical material at the population level in the surroundings of Yajalón, Tila, Altamirano and Tenejapa. Based on the revision of herbarium specimens and the botanical material collected by us, we recircumscribed the populations for *Ceratozamia* in this region into two species: *C. sancheziae* and *C. zoquorum*. One diagnostic character for *C. sancheziae* is oblanceolate leaflets when juvenile, but we found in the field juveniles with linear leaflets only (Gutiérrez-Ortega et al. 2021: 2009; Fig. 23D). Furthermore, we did not find populations near Yajalón or Tila that correspond to *C. sancheziae*. The paratypes cited from Yajalón (*Méndez Ton* 5498, 5722 both MEXU) have some vegetative characters that do not correspond with the species description; however, these could be part of the overall species variation of *C. sancheziae*. Considering that sympatry is possible in this genus and that there is broad variation in *C. zoquorum*, research at population level with reproductive structures and molecular variation could clarify what species is represented by these plants collected near Yajalón. In addition, we have extended the range for *C. sancheziae* to the south of Chiapas (i.e., populations from Altamirano municipality).

Specimens examined. MEXICO. Chiapas: Mun. Altamirano, 1,215 m, 16 Jul 2021, *F. Nicolalde-Morejón et al.* 3691–3697 (CIB); 1,215 m, 16 Jul 2021, *L. Martínez-Domínguez* 2318–2325 (CIB); 1,210 m, 28 Nov 1996, *M.A. Pérez-Farrera* 1468 (CHIP); 1,200 m, 18 May 1993, *M. González-Espinosa et al.*, 1973 (CH). Mun. Tenejapa, 1,000 m, 5 Jun 1972, *D.E. Breedlove* 25506 (MEXU); 1,536 m, 15 Jul 2021, *F. Nicolalde-Morejón et al.* 3683–3690 (CIB); 1,536 m, 15 Jul 2021, *L. Martínez-Domínguez et al.* 2310–2317 (CIB). Mun. Yajalón, 1,434 m, 26 Aug 2015, *F. Hernández-Najarro* 4382 (CHIP).

29. *Ceratozamia santillanii* Pérez-Farr. & Vovides, Syst. Biodivers. 7 (4): 435. 2009

Figs 1B, 27E

Type. MEXICO. Chiapas: Mun. Berriozábal, road Berriozábal-El Cairo, 15 Oct 2004, *M.A. Pérez Farrera* 3030 ♀ (holotype: HEM! [HEM020981]; isotypes: XAL! [XAL0005415], MEXU [n.v.]).

Description. *Stem* 10–50 cm long, 11–13 cm in diameter, semi-hypogeous, erect and decumbent. *Cataphylls* 2–4.5 × 1.7–4 cm wide at the base, persistent, triangular, reddish brown, densely brown tomentose at emergence, with apex partiality glabrous

at maturity, apex acuminate. **Leaves** 2–3, 50.5–79.3 cm long, descending, light green and glaucous at emergence, with whitish gray trichomes, green and glabrous at maturity. **Petiole** 23.5–45 cm long, terete, linear, yellowish green in mature leaves; with 4–15 thin prickles, 0.05–0.15 cm long or unarmed. **Rachis** 23–40 cm long, terete, linear, yellowish green at emergence, yellowish green in mature leaves, unarmed to armed with prickles. **Leaflets** 6–12 pairs, opposite to subopposite, insertion in one plane, oblong, longitudinally curved abaxially to planar, not basally falcate to basally falcate, coriaceous, flat, green with adaxial and abaxial sides glaucous, distal end with entire margins, acuminate and asymmetrical at the apex, attenuate at base, with conspicuous and green-light veins; median leaflets $17.4\text{--}30.6 \times 4.2\text{--}6.5$ cm, $3.5\text{--}7.1$ cm between leaflets; articulations 0.7–1.1 cm wide, yellow. **Pollen strobili** 15–20 cm long, 1.5–3.0 cm in diameter, solitary, cylindrical, erect, green with blackish trichomes at emergence, yellow-cream with blackish at maturity; peduncle 2–4 cm long, 1.0–1.3 cm in diameter, scarce pubescent, reddish brown to brown; microsporophylls $1.2\text{--}2 \times 0.5\text{--}1$ cm, discoid with a non-recurved distal face and a lobate fertile portion, infertile portion 0.34–0.37 cm long and linear with straight horns 0.20–0.25 cm long, 0.50–0.65 cm and an acute angle between the horns. **Ovulate strobili** 12–20 cm long, 7–9 cm in diameter, solitary, cylindrical, erect, green with blackish trichomes at emergence, green with scarce blackish trichomes at maturity, acute apex; peduncle 2–3 cm long, 0.9–1.3 cm in diameter, erect, tomentose, light brown; megasporophylls 21–56, 7–8 orthostichies with 3–7 sporophylls per orthostichy, $1.3\text{--}2.2 \times 1.5\text{--}2.2$ cm, with a prominent distal face, horns straight and 0.60–0.80 cm long, 1.65–1.90 cm between horns with an acute angle between the horns. **Seeds** 2.2–2.4 cm long, 1.8–2.0 cm in diameter, ovate, sarcotesta whitish pink when immature, light brown at maturity.

Distribution and habitat. *Ceratozamia santillanii* is endemic to the northern highlands of Chiapas State, Mexico and only known from the type locality in the municipality of Berriozábal (Fig. 24A), where it was collected in evergreen tropical rain forest on karstic rocks at 800–900 m.

Etymology. The specific epithet was assigned in honor of Professor Trinidad Alemán Santillán in recognition of his academic accomplishments in the training of young biologists in botany and ecology (Pérez-Farrera et al. 2009).

Common names. None recorded.

Uses. None recorded.

Preliminary conservation status. According to IUCN criteria *Ceratozamia santillanii* should be listed as “Critically Endangered” (CR).

Discussion. *Ceratozamia santillanii* belongs to a cryptic taxonomic group with *C. zoquorum* and *C. becerrae*, which is characterized by oblong and coriaceous leaflets with an acuminate and asymmetric apex. *C. santillanii* is easily distinguished from the other taxa in this complex with internal transcribed spacer region of nuclear ribosomal (nrITS) (Martínez-Domínguez et al. 2017c), and peduncle of ovulate strobilus 3 cm long or shorter.

Specimens examined. MEXICO. **Chiapas:** Known only from the type locality. 15 Oct 2004, M.A. Pérez-Farrera 2944 (HEM).

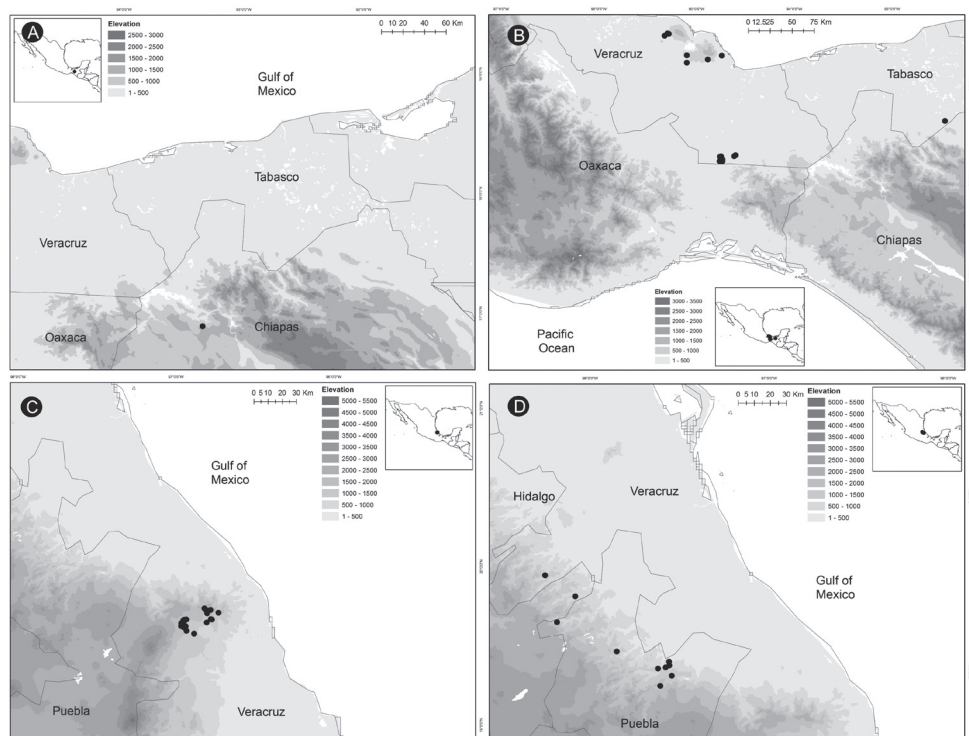


Figure 24. Distribution of *Ceratozamia* species. **A** *C. santillanii* **B** *C. subroseophylla* **C** *C. tenuis* **D** *C. totonacorum*.

30. *Ceratozamia subroseophylla* Mart.-Domínguez & Nic.-Mor., Phytotaxa 268(1): 35. 2016

Figs 12D, 25, 26

Ceratozamia dominguezii Pérez-Farr. & Gut.Ortega, Taxonomy 1: 353. 2021. Type: MEXICO. Veracruz: Mun. Uxpanapa, 130 m, 29 May 2021, *M.A. Pérez-Farrera 4013* (holotype: HEM [n.v]; isotypes: MEXU [n.v], XAL [n.v]).

Type. MEXICO. Veracruz: Mun. Santiago Tuxtla, hill in front Sinapán, 425 m, 15 Jul 2014, *L. Martínez-Domínguez 158* ♀ (holotype: CIB! [acc. # 16893UV]; isotypes: MEXU! [MEXU01446538–MEXU01446542], NY!).

Description. *Stem* 30–250 (500) cm long, 18–45 cm in diameter, epigeous, erect and decumbent. *Cataphylls* 5–7 × 2–2.5 cm wide at the base, persistent, triangular, reddish brown, densely brown tomentose at emergence, glabrous at maturity, apex acuminate. *Leaves* 10–83, 72–370 cm long, ascending, yellowish brown at emergence, with whitish gray trichomes, glabrous at maturity. *Petiole* 50–150 cm long, terete, linear, greenish brown or dark brown at emergence, green in mature leaves; with 25–55 robust prickles, 0.40–0.85 cm long. *Rachis* 80–255 cm long, terete, linear, greenish brown or dark brown at emergence, green in mature leaves, with prick-

les. **Leaflets** 23–48 pairs, opposite to subopposite, insertion in one plane, lanceolate, abaxially curved longitudinally along distal half, not basally falcate, papyraceous, flat, dark green with adaxial side glabrous and abaxial side glaucous, acuminate and symmetrical at the apex, attenuate at base, with conspicuous and light-green veins; median leaflets $18\text{--}45 \times 2.5\text{--}4$ cm, $1.7\text{--}6.5$ cm between leaflets; articulations $0.7\text{--}1.9$ cm wide, brown in young leaves and green in mature leaves. **Pollen strobili** $15\text{--}30$ cm long, $3.1\text{--}5.4$ cm in diameter, solitary, cylindrical, erect, green with reddish trichomes at emergence, greenish yellow at maturity with dark brown trichomes; peduncle $9.5\text{--}19$ cm long, $1.5\text{--}2.7$ cm in diameter, tomentose, reddish brown; microsporophylls $1.47\text{--}2.8 \times 1.01\text{--}1.4$ cm, obconic with a non-recurved distal face and lobate fertile portion, infertile portion $0.49\text{--}0.65$ cm long and rounded with straight horns $0.20\text{--}0.30$ cm long, $0.48\text{--}0.53$ cm and an acute angle between the horns. **Ovulate strobili** $15.5\text{--}40$ cm long, $7\text{--}11.6$ cm in diameter, solitary, cylindrical, erect, yellow with reddish to purple trichomes at emergence, green and megasporophylls with base pale pink and dark brown to reddish brown trichomes at maturity, mucronate apex; peduncle $9.8\text{--}17.5$ cm long, $1.8\text{--}2.3$ cm in diameter, erect, tomentose, light brown; megasporophylls $110\text{--}210$, $9\text{--}12$ orthostichies with $11\text{--}20$ sporophylls orthostichy, $1.8\text{--}2.5 \times 2.5\text{--}4.47$ cm, with a prominent distal face, horns straight $0.34\text{--}1.0$ cm long and $0.70\text{--}1.40$ cm between horns with a right angle between the horns. **Seeds** $2.9\text{--}3.8$ cm long, $0.80\text{--}1.75$ cm in diameter ovate, sarcotesta whitish pink when immature, light brown at maturity.

Distribution and habitat. *Ceratozamia subroseophylla* occurs from southeastern Veracruz State to Tabasco State, Mexico including the montane zone of the region Santiago Tuxtla and Uxpanapa (Fig. 24B). It occurs on soils of volcanic origin and karstic rocks in evergreen tropical rain forest between 111 and 1,050 m.

Etymology. The specific epithet refers to the rosaceous (i.e., pale pink) color at the base of megasporophylls.

Common names. Mexico. Veracruz: Hymniom pekmuk (Popoluca ethnic group) (Leonti 542).

Uses. The stem is boiled to make medicinal tea to treat kidney stones (Leonti 542).

Preliminary conservation status. *Ceratozamia subroseophylla* has several populations throughout its distribution range, but anthropogenic land-use changes affect the populations of Veracruz and Tabasco. According to the IUCN Red List criteria, we recommend “Endangered” (EN) for this species.

Discussion. *Ceratozamia subroseophylla* is distinguished from *C. leptoceras* and *C. oliversacksii* by its green-brownish petiole and rachis with abundant and robust prickles, and its lanceolate and papyraceous leaflets (Fig. 25). In addition, *C. subroseophylla* has affinity with *C. robusta*, but it is easily identified by the ovulate strobilus which has mucronate apex, rosaceous base of megasporophylls rosaceous with dark brown to reddish brown trichomes at maturity (Fig. 26).

Populations from Uxpanapa (Veracruz) were recently described as *Ceratozamia dominguezii*, however, these fall within the range of variation of *C. subroseophylla* as circumscribed here. Our circumscription is based on comparative morphology, both vegetative and reproductive structures, and phenology (Figs 25, 26).



Figure 25. Vegetative characters of *Ceratozamia subroseophylla* **A** adult plant (from Uxpanapa, Veracruz) **B** young leaf (from Santiago Tuxtla, Veracruz) **C** new leaves of adult plant (from Santiago Tuxtla, Veracruz) **D** prickles on rachis (from Uxpanapa, Veracruz).

Specimens examined. MEXICO. **Tabasco:** Mun. Macuspana, 185 m, 13 Jul 2021, *F. Nicolalde-Morejón et al.* 3674–3680 (CIB); 185 m, 13 Jul 2021, *L. Martínez-Domínguez et al.* 2295–2300 (CIB), 190 m, 13 Jul 2021, *L. Martínez-Domínguez et al.* 2301 (CIB, MEXU). **Veracruz:** Mun. Catemaco, 1953, *H. Bravo* 26 (MEXU); 18 May

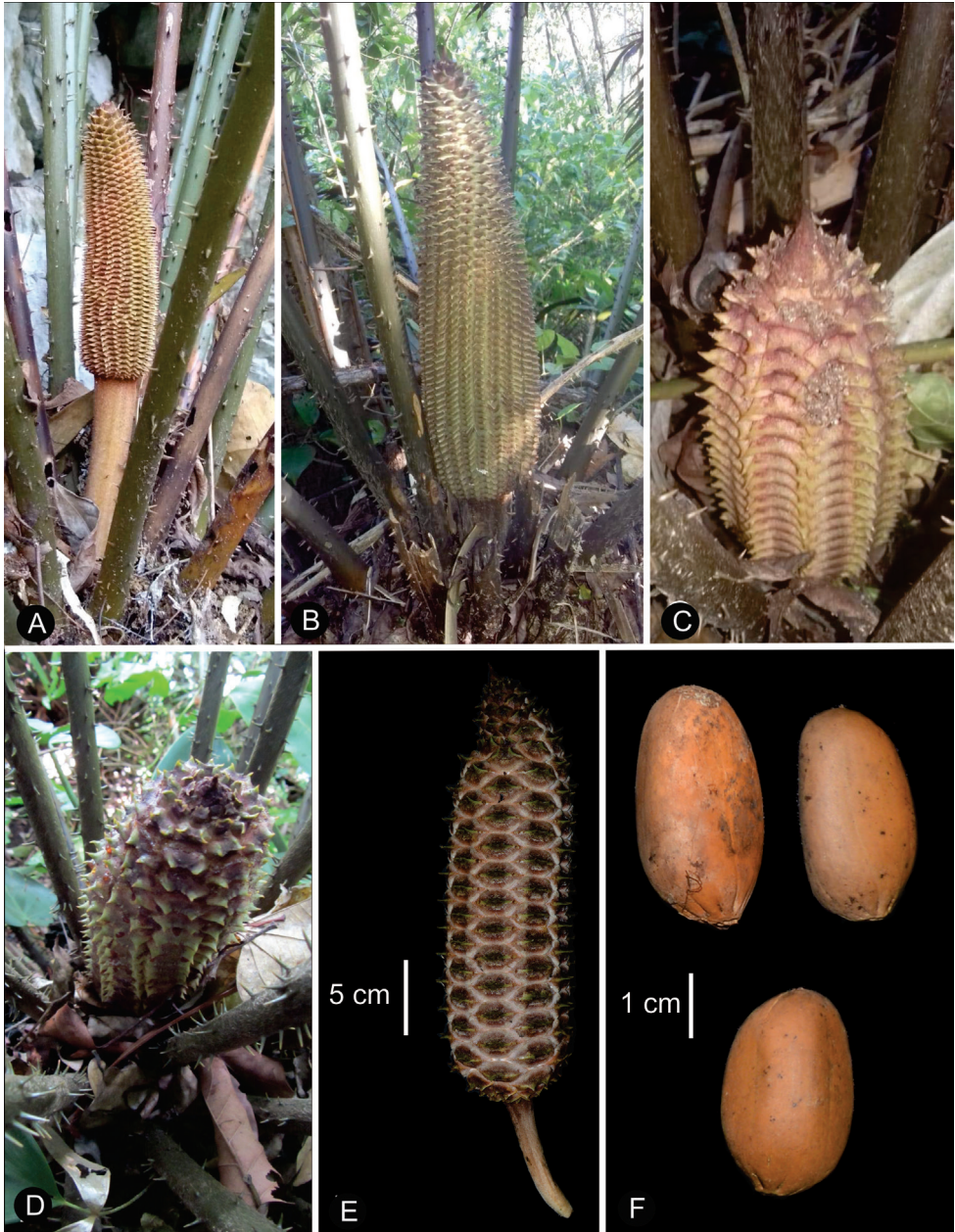


Figure 26. Reproductive characters of *Ceratozamia subroseophylla* **A** immature pollen strobilus (from Santiago Tuxtla, Veracruz) **B** pollen strobilus at maturity (from Santiago Tuxtla, Veracruz) **C** immature ovulate strobilus (from Uxpanapa, Veracruz) **D** immature ovulate strobilus (from Santiago Tuxtla, Veracruz) **E** ovulate strobilus at maturity (Uxpanapa, Veracruz) **F** seeds.

1995, *M.A. García B. et al.* 813 (XAL). **Mun. Hidalgotitlán**, 150 m, 16 Jan 1975, *Brigada Vázquez* 1760 (MO, XAL); 140 m, 16 Dec 1974, *J. Rees* 1655 (XAL); 16 Apr 1975, *M. Vázquez-Torres* 1760 (MEXU). **Mun. Hueyapan de Ocampo**, 400 m, 14

May 2000, *Leonti* 542 (MEXU). **Mun. Jesús Carranza**, 100 m, 19 Feb 2009, *D. Jimeno-Sevilla* 1045 (MEXU, MO, XAL); 131 m, 27 Sep 2020, *L. Martínez-Domínguez et al.* 2040 (CIB); *M. Vázquez-Torres* 2430 (CHAPA, ENCB, MEXU, NY, SLP, XAL). **Mun. Mecayapan**, 950 m, 26 Jan 1992, *M. Vázquez-Torres et al.* 4122 (CIB). **Mun. Santiago Tuxtla**, 500 m, 5 Jul 1983, *D.W. Stevenson et al.* 539 A–L (NY), 540 F–H (NY); 420 m, 28 Mar 2014, *F. Nicolalde-Morejón & L. Martínez-Domínguez* 1985–1987 (CIB); 250–500 m, 30 Sep 1983, *J.F. Ortega O. et al.* 358 (XAL); 420 m, 28 Mar 2014, *L. Martínez-Domínguez & F. Nicolalde-Morejón* 78, 79 (NY), 80, 81 (XAL), 82–87 (CIB); 420 m, 7 Jun 2014, *L. Martínez-Domínguez & F. Nicolalde-Morejón* 129 (CIB); 425 m, 15 Jul 2014, *L. Martínez-Domínguez* 136–157, 159 (CIB); 500 m, 12 May 1965, *M. Sousa* 2420 (MEXU); 23 Aug 1962, *R.F. Andrie* 64 (US); 497 m, 17 Jan 2001, *T.W. Walters* TW-2001-17 (MEXU, XAL). **Mun. Soteapan**, 21 Jun 1963, *G.N. Ross* 57 (US); 1,050 m, 17 Mar 1968, *M. Sousa* 3645 (MEXU); 500 m, 18 May 1986, *M. Vázquez-Torres et al.* 3579 (CIB). **Mun. Tatahuicapan de Juárez**, 849 m, *C.I. Carvajal-Hernández & M. Juárez* F. 796 (CIB). **Mun. Uxpanapa**, 131 m, 27 Sep 2020, *L. Martínez-Domínguez et al.* 2040 (CIB, MEXU); 111 m, 27 Sep 2020, *L. Martínez-Domínguez et al.* 2041 (CIB), 2042 (CIB, MEXU), 2043–2048 (CIB); 111 m, 11 Jun 2021, *L. Martínez-Domínguez et al.* 2273 (CIB).

31. *Ceratozamia tenuis* (Dyer) D.W.Stev. & Vovides, Bot. Sci. 94 (2): 425. 2016
Fig. 27F

Ceratozamia tenuis Type. Cultivated in England at the Royal Botanic Gardens Kew “Hort. Kew Palm House”, 1881, *Anon. s.n.* (lectotype, designated by Vovides et al. 2016, pg. 425: K! [K001092673, K001092674]). Mexico. Veracruz: Mun. Jilotepec, 19 Jan 1976, *A.P. Vovides* 18 ♂ (epitype, designated by Martínez-Domínguez et al. 2018a, 117: XAL! [acc. # 16980]; isoeotype: NY!).

Ceratozamia mexicana Brongn. var. *vulgaris* J.Schust., Pflanzenr. (Engler) Heft 99, 4 fam 1: 131. 1932. MEXICO. Veracruz: Mun. Xalapa, Chilttoyac, 1,270 m, 18 Oct 2016, *L. Martínez-Domínguez et al.* 984 (neotype, designated by Martínez-Domínguez et al. 2018a, pg. 117: CIB! [acc. # 17988UV]).

Ceratozamia mexicana f. *tenuis* (Dyer) J.Schust., Pflanzenr. (Engler) Heft 99, 4 fam 1: 132. 1932, as “*Ceratozamia mexicana* var. *longifolia* f. *tenuis*”. Type: Based on *Ceratozamia mexicana* Brongn. var. *tenuis* Dyer

Type. Based on *Ceratozamia mexicana* Brongn. var. *tenuis* Dyer, Biol. Cent.-Amer., Bot. 3: 193. 1884.

Description. *Stem* 20–100 cm long, 30–45 cm in diameter, epigeous, erect and decumbent. *Cataphylls* 2–6 × 2–5.5 cm wide at the base, persistent, triangular, reddish brown, densely brown tomentose at emergence, partially tomentose at maturity, apex acuminate. *Leaves* 6–56, 85–225 cm long, ascending, dark green at emergence with brown trichomes, glabrous at maturity. *Petiole* 30–93 cm long, terete, linear, green in

mature leaves; with 10–55 thin prickles, 0.20–0.49 cm long. **Rachis** 56–154 cm long, terete, linear, green in mature leaves, with prickles. **Leaflets** 30–56 pairs, opposite to subopposite, insertion in one plane, linear, longitudinally curved abaxially to planar, basally falcate, papyraceous, involute, green with adaxial and abaxial sides glabrous, distal end with entire margins, acuminate and symmetrical at 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 0.4–1.4 cm wide, green. **Pollen strobili** 25–50 cm long, 4–8 cm in diameter, solitary, cylindrical, erect, greenish yellow at emergence, greenish yellow with blackish trichomes at maturity; peduncle 3.7–22 cm long, 1.2–2.5 cm in diameter, tomentose, reddish brown to light-brown; microsporophylls 1.7–2.7 × 1.2–1.9 cm, obconic with a non-recurved distal face and a lobate fertile portion, infertile portion 0.50–0.65 cm long and orbicular with recurved horns 0.25–0.46 cm long, 0.35–0.65 cm between the horns and a right angle between the horns. **Ovulate strobili** 22–35 cm long, (7.6) 10–14 cm in diameter, solitary, cylindrical, erect, dark green with blackish trichomes at emergence, dark green with blackish trichomes at maturity, acuminate apex; peduncle 8–23 cm long, 1.5–2.4 cm in diameter, erect or pendulous, tomentose, brown to reddish brown; megasporophylls (48) 80–196, 7–16 orthostichies with 6–14 sporophylls per orthostichy, 2.1–3.1 × 3.0–5.0 cm, with a prominent distal face, horns curved and 0.32–0.80 cm long, 0.80–1.60 cm between horns with a right angle between the horns. **Seeds** 2.5–3 cm long, 1.3–1.8 cm in diameter, ovate, sarcotesta whitish yellow to yellow when immature, light brown at maturity.

Distribution and habitat. *Ceratozamia tenuis* is endemic to the central montane region in Veracruz State, Mexico (Fig. 24C), where it occurs in cloud forest at 1,200–1,920 m elevation on volcanic soils with basaltic rocks.

Etymology. The specific epithet is derived from its thin leaflets.

Common names. Mexico. Veracruz: Costilla de león (L. Martínez-Domínguez et al. 573); palma del monte (L. Martínez-Domínguez et al. 166).

Uses. Ovulate strobili are used as an insecticide; these are cut in half and mixed with milk or sugar to kill flies (L. Martínez-Domínguez et al. 980).

Conservation status. *Ceratozamia tenuis* has not been assessed for The IUCN Red List of Threatened Species. This species has populations with several adult plants (between 100 to 300); however, the total area of distribution is narrow and it is one of the areas that is highly affected by changes in land use in recent years. According to IUCN criteria this species should be considered as “Endangered” (EN) under A1acd; B1ab(iii).

Discussion. *Ceratozamia tenuis* is characterized by a petiole with thin prickles, and linear leaflets that are papyraceous and involute with a symmetric apex. The ovulate strobilus is dark green with blackish trichomes at maturity, a prominent distal face, and a right angle between the horns.

Specimens examined. MEXICO. Veracruz: **Mun. Banderilla**, 1,450 m, 21 Apr 2017, L. Martínez-Domínguez et al. 1000 (CIB). **Mun. Chiconquiaco**, 1,800 m, 26 Nov 1974, D. Jimeno-Sevilla 754 (XAL); 1,916 m, 27 Sep 2016, F. Nicolalde-Morejón et al. 2456–2464 (CIB); 1,800 m, 26 Nov 1974, J. Rees 1625 (XAL), 1626

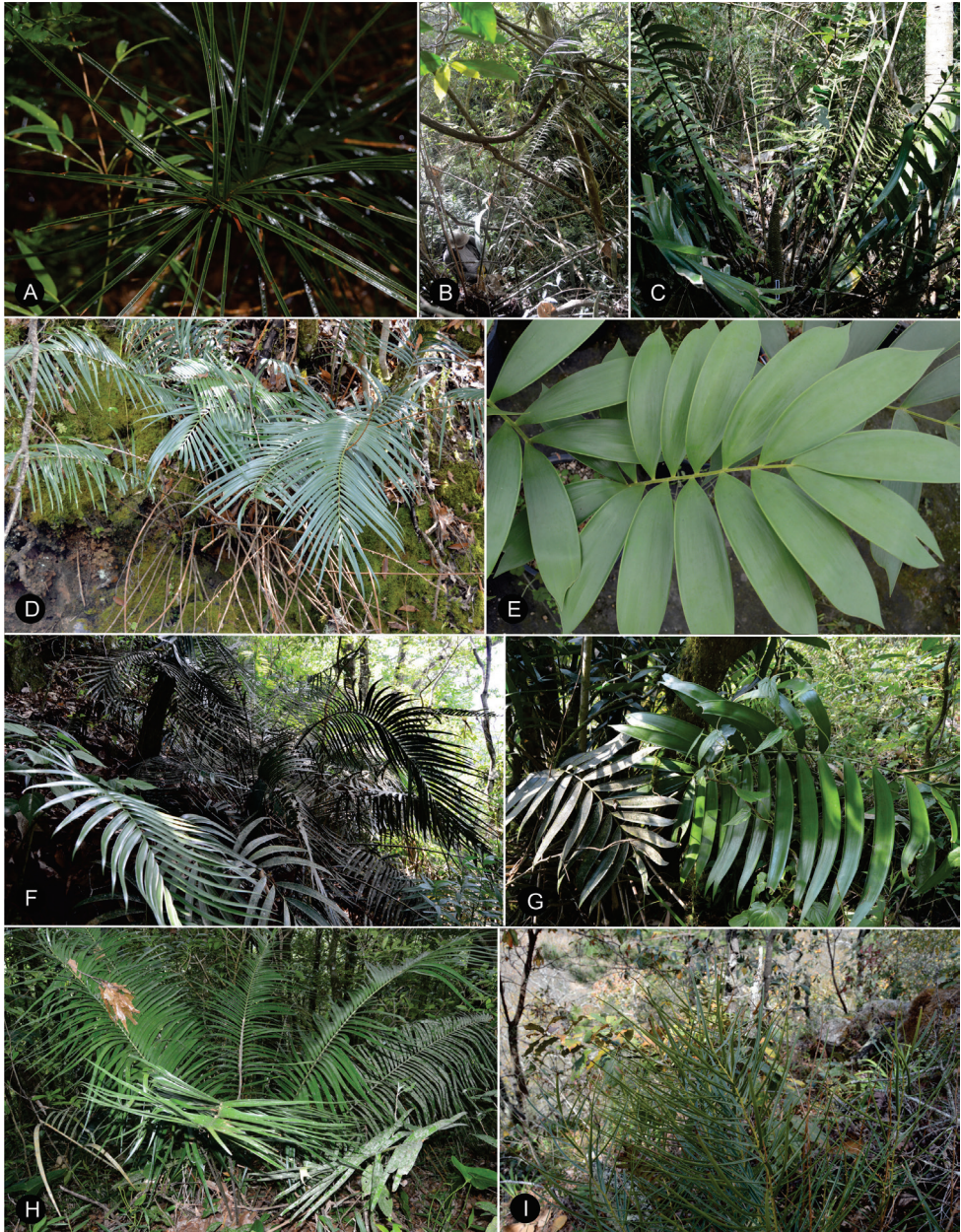


Figure 27. Plants of *Ceratozamia* in habitat. **A** *C. norstogii*. **B** *C. oliversacksii* **C** *C. robusta* **D** *C. sabatoi* **E** *C. santillanii* **F** *C. tenuis* **G** *C. totonacorum* **H** *C. vovidesii* **I** *C. zaragozae*.

(MEXU, XAL); 1,916 m, 27 Sep 2016, *L. Martínez-Domínguez et al.* 971, 973–981 (CIB), 972 (CIB, MEXU); 13 Apr 1967, *R. Fernández-Nava* 385A (MEXU). **Mun. Coacoatzintla**, 8 Mar 1985, *F. Vázquez* B. 2275 (XAL); 1,400 m, 7 Jan 1977, *G. Castillo-Campos* 118 (XAL); 1,550 m, 3 Jun 2005, *L.H. Bojórquez-Galván & A.M. Zapata-Aquino* 1484, 1485 (CIB); 1,435 m, 9 Jan 2015, *L. Martínez-Domínguez et*

al. 165–184 (CIB); 1, 435 m, 18 Mar 2015, *L. Martínez-Domínguez et al.* 273–282 (CIB); 1,540 m, 9 Feb 2016, *L. Martínez-Domínguez et al.* 759 (CIB). **Mun. Jilotepec**, 1,300 m, 29 Feb 1980, *A.P. Vovides* 470 (XAL), 471 (IBUG, MEXU, XAL); 1,300 m, 14 Apr 1982, 735 (XAL); 1,385 m, 15 Nov 1978, *E. Estrada et al.* 757 (MEXU); 1,316 m, 22 Aug 2014, *F. Nicolalde-Morejón & L. Martínez-Domínguez* 2067–2086 (CIB); 1,350 m, 7 Dec 1970, *F. Ventura A.* 2936 (ENCB); 1,300 m, 22 Jan 1971, *F. Ventura A.* 3014 (ENCB); 1,300 m, 18 Nov 1974, *J. Rees* 1620 (XAL); 1,363 m, 29 May 2015, *L. Martínez-Domínguez et al.* 573–583 (CIB); 1,250 m, 23 Aug 1973, *M.G. Zola* 657 (XAL), 667 (MEXU, XAL); 1,250 m, 23 Aug 1975, *R. Ortega J.* 525 (XAL); Mar 2001, *S. Avendaño* 5395 (MEXU). **Mun. Tepetlán**, 1,420 m, 12 Jan 2013, *F. Nicolalde-Morejón et al.* 1691–1710 (CIB); 1,418 m, 21 Jun 2014, *F. Nicolalde-Morejón & L. Martínez-Domínguez* 2001–2004 (CIB); 1,418 m, 22 Aug 2014, *F. Nicolalde-Morejón & L. Martínez-Domínguez* 2047–2066 (CIB); 1,662 m, 10 Apr 2015, *F. Nicolalde-Morejón & L. Martínez-Domínguez* 2217–2226 (CIB); 1,421 m, 26 Jul 2014, *L. Martínez-Domínguez et al.* 160 (CIB); 22 Mar 2015, *L. Martínez-Domínguez & F. Nicolalde-Morejón* 283–293 (CIB); 1,662 m, 10 Apr 2015, *L. Martínez-Domínguez & F. Nicolalde-Morejón* 545–555 (CIB); 2 Jul 2010, *M. Vázquez-Torres et al.* 9215 (CIB). **Mun. Tlacolulan**, 1,540 m, 16 Jun 2017, *F. Nicolalde-Morejón et al.* 2516 (CIB); 1,540 m, 16 Jun 2017, *L. Martínez-Domínguez et al.* 1041, 1042 (CIB). **Mun. Xalapa**, 1,270 m, 18 Oct 2016, *F. Nicolalde-Morejón et al.* 2466–2468 (CIB); 1,270 m, 18 Oct 2016, *L. Martínez-Domínguez et al.* 985, 987 (CIB), 986 (CIB, MEXU).

32. *Ceratozamia totonacorum* Mart.-Domínguez & Nic.-Mor., *Brittonia* 69 (4): 518. 2017

Figs 27G, 28B

Type. MEXICO. Puebla: Mun. Jonotla, 600 m, 9 Jun 2015, *L. Martínez-Domínguez & F. Nicolalde-Morejón* 618 ♀ (holotype: CIB! [acc. # 16735UV]).

Description. *Stem* 10–45 cm long, 10–25 cm in diameter, epigeous, erect and decumbent. *Cataphylls* 2–5 × 1.2–2.5 cm wide at the base, persistent, triangular, reddish brown, densely brown tomentose at emergence, glabrous at maturity, apex acuminate. *Leaves* 10–63, 100–265 cm long, descending, brown at emergence, with brown trichomes, glabrous at maturity. *Petiole* 30–80 cm long, terete, straight, green in mature leaves; with 10–40 thin prickles, 0.05–0.25 cm long. *Rachis* 85–185 cm long, terete, straight, green in adult leaves, with prickles. *Leaflets* 11–33 pairs, opposite to subopposite, insertion in one plane, oblong, longitudinally planar, not basally falcate to occasionally falcate, papyraceous, flat, green with adaxial side glabrous and abaxial side glaucous, distal end with entire margins, acuminate and symmetrical at the 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 0.5–1.3 cm wide, green. *Pollen strobili* 28–31 cm long, 5.0–6.0 cm in diameter, generally solitary (up to 2), cylindrical, erect, greenish yellow at emergence, yellow with brown trichomes at maturity; peduncle

9–12 cm long, 1.5–2 cm in diameter, tomentose, light brown; microsporophylls 1.5–2.7 × 0.9–2.0 cm, obconic with a non-recurved distal face and a lobate fertile portion, infertile portion 0.39–0.57 cm long and rounded with straight horns 0.19–0.25 cm long, 0.52–0.69 cm and a right angle between the horns. **Ovulate strobili** 20.5–28.7 cm long, 8.4–9.3 cm in diameter, solitary, cylindrical, erect, light green and glaucous, with orange to light brown trichomes at emergence, green with yellowish brown trichomes at maturity, acuminate apex; peduncle 10–11.2 cm long, 1.5–2.4 cm in diameter, erect or pendulous, tomentose, light brown; megasporophylls 64–120, 8–10 orthostichies with 8–13 sporophylls per orthostichy, 1.6–2.3 × 2.6–3.6 cm, with a prominent distal face, horns straight and 0.55–0.80 cm long, 1.45–1.80 cm between horns with a right angle between the horns. **Seeds** 2.5–3.5 (4) cm long, 0.88–1.6 cm in diameter, ovate, sarcotesta whitish red when immature, cream to light brown at maturity.

Distribution and habitat. *Ceratozamia totonacorum* occurs in the Sierra Norte de Puebla and the mountain region in Hidalgo and Veracruz States, Mexico (Fig. 24D). It occurs in cloud forest and the transition zone between evergreen tropical forest and cloud forest on rocky outcrops in exposed walls up to 80 m tall at 600–1,800 m.

Etymology. The specific epithet is in reference to the Totonaco ethnic group of Santiago Ecatlán in Sierra Norte of Puebla, Mexico.

Common names. Mexico. Puebla: Kun (Totonaco ethnic group) (Martínez-Domínguez et al. 2017b).

Uses. In Sierra Norte of Puebla, the residents use the leaves of this species in local rituals to make “arcos” and altars (Fig. 28B) (Martínez-Domínguez et al. 2017b).

Preliminary conservation status. Based on total populations and the potential distribution and reduction of vegetation in the area for *Ceratozamia totonacorum*, we recommend that it should be listed as “Vulnerable” in The IUCN Red List of Threatened Species.

Discussion. *Ceratozamia totonacorum* is distinguished from *C. delucana* by its brown leaves at emergence, but this color disappears in the mature leaves which become green; besides, the leaves are descending. The ovulate strobilus is yellowish green with brown trichomes.

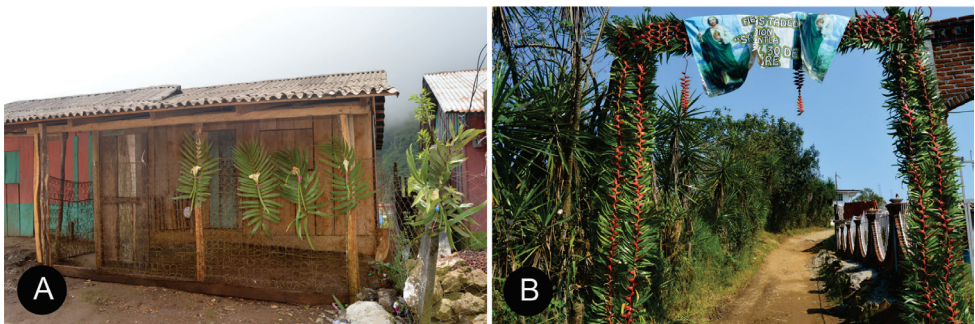


Figure 28. Leaves of *Ceratozamia* are used for religious ceremonies **A** *C. moretii* used during local celebrations in La Estrella (Chiconquiaco municipality, Veracruz, Mexico) **B** *C. totonacorum* used during “San Judas Tadeo” festivities in La Unión Atiayan (Nauzontla municipality, Puebla, Mexico).

Specimens examined. MEXICO. **Hidalgo:** Mun. Huehuetla, 1,150 m, 2 Jun 1976, *A.P. Vovides* 23 (XAL). **Puebla:** Mun. Atlequizayan, 1 Apr 2014, 867 m, *L. Caamaño Onofre & A.B. Cerón Carpio* 4995 (XAL). Mun. Cuetzalan del Progreso, 1,470 m, 1 Nov 2017, *L. Martínez-Domínguez et al.* 1180–1189 (CIB). Mun. Jonotla, 760 m, 13 Feb 2014, *F. Nicolalde-Morejón et al.* 1948 (CIB); 600 m, 13 Feb 2014, *F. Nicolalde-Morejón et al.* 1949–1955 (CIB), 1956 (MEXU), 1957 (NY), 1958–1965 (CIB); 1,006 m, 14 Feb 2014, *F. Nicolalde-Morejón et al.* 1966, 1967 (CIB); 600 m, 9 Jun 2015, *L. Martínez-Domínguez & F. Nicolalde-Morejón* 619 (CIB). Mun. Pahuatlán, 1,800 m, 12 Jan 1987, *G. Toriz et al.* 226 (MEXU). Mun. Tlapacoya, 1,010 m, 14 Feb 1985, *E. Meza P.* 14 (XAL). Mun. Zacapoaxtla, 1, 365 m, 30 May 2014, *L. Camaño-Onofre* 5329 (XAL). **Veracruz:** Mun. Tlachichilco, 1,300 m, 12 Sep 2001, *A. Rincón G. et al.* 2584 (XAL), 2585 (MEXU, XAL).

33. *Ceratozamia vovidesii* Pérez-Farr. & Iglesias, Bot. J. Linn. Soc. 153: 394. 2007
Fig. 27H

Type. MEXICO. Chiapas: Mun. La Concordia, Between Finca Santa Cruz and El Puente, Rancho Las Cabañas, 1,156 m, 19 Jul 2001, *M.A. Pérez-Farrera* 2620a ♀ (holotype: HEM!; isotypes: CHIP [n.v.], MEXU [n.v.], MO [n.v.], XAL [n.v.]).

Description. *Stem* 50–80 cm long, 20–30 cm in diameter, epigeous, erect and decumbent. *Cataphylls* 5–7.5 × 2.7–5 cm wide at the base, persistent, triangular, reddish brown, densely brown tomentose at emergence, partially tomentose at maturity, apex acuminate. *Leaves* 3–18, 97–238 cm long, ascending, reddish brown at emergence with whitish gray trichomes, glabrous at maturity. *Petiole* terete, linear, 40–164 cm long, green in adult leaves, with 15–55 thin prickles, 0.14–0.38 cm long. *Rachis* terete, linear, 54–153 cm long, green in mature leaves, with prickles. *Leaflets* 30–85, opposite to subopposite, insertion in one plane, lanceolate, mostly longitudinally planar, generally basally falcate, papyraceous, flat, green with adaxial side glabrous and abaxial side glaucous, distal end with entire margins, acuminate and symmetrical apex, attenuate at base, with conspicuous and light-green veins; median leaflets 20–45 × 0.7–1.4 cm, 0.3–2.4 cm between leaflets; articulations 0.2–0.8 cm wide, green. *Pollen strobili* 15–45 cm long, 3.5–5 cm in diameter, solitary, cylindrical, erect, yellowish green with reddish brown trichomes at emergence, yellowish cream with reddish brown trichomes at maturity; peduncle 6–9.5 cm long, 1.6–1.9 cm in diameter, tomentose, reddish brown to brown; microsporophylls 1.2–1.5 × 0.8–1.04 cm, obconic with a non-recurved distal face and lobate fertile portion, infertile portion 0.37–0.50 cm long and rounded with straight horns 0.30–0.42 cm long, 0.52–0.84 cm with a right angle between the horns. *Ovulate strobili* 26–40 cm long, 7.1–9.6 cm in diameter, solitary, cylindrical, erect, greyish green with abundant reddish brown trichomes at emergence, green with abundant blackish trichomes at maturity, acuminate apex; peduncle 7–15 cm long, 1.7–2.2 cm in diameter, erect or pendulous, pubescent, brown; megasporophylls 60–70, 6–8 orthostichies with 7–12 sporophylls per row, 3.8–4.5 × 4–5 cm, with a prominent distal face, horns straight and 0.60–0.80 cm long, 0.99–1.40 cm between horns with an

obtuse angle between the horns. **Seeds** 2.2–2.7 cm long, 1.3–1.7 cm in diameter, ovate, sarcotesta whitish yellow to yellow when immature, light brown at maturity.

Distribution and habitat. *Ceratozamia vovidesii* is distributed along the Sierra Madre of Chiapas State in Mexico to Guatemala. It occurs on karstic rocks in cloud forest between 800 and 1,850 m elevation (Fig. 29A).

Etymology. The specific epithet honors Andrew P. Vovides in recognition of his systematic and ecological studies and efforts in the conservation of Mexican cycads, including the creation of the Mexican National Cycad Collection at the Francisco Javier Clavijero Botanic Garden in Xalapa (Veracruz, Mexico) (Pérez-Farrera et al. 2007).

Common names. None recorded.

Uses. Decorative (M.A. Pérez-Farrera 2620a).

Conservation status. (IUCN 2021). *Ceratozamia vovidesii* is listed as “Vulnerable” (V) under criteria D2. Here, we extended the distribution range for this species to Guatemala. Based on number of populations and data obtained during fieldwork we recommend not changing the current status.

Discussion. *Ceratozamia vovidesii* shares several vegetative characteristics with *C. mirandae*. However, there are differences in their pollen strobili; *C. vovidesii* has obconic microsporophylls with rounded infertile portions, whereas those of *C. mirandae* are elliptic with a linear infertile portion.

There is some confusion concerning the holotype for *C. vovidesii*. In 2012 the gathering Pérez-Farrera 2620^a also was used as the holotype in the protologue of *Zamia grijalvensis* Perez-Farr., Vovides & Mart.-Camilo (Pérez-Farrera et al. 2012). The specimen, Pérez-Farrera 2620^a is clearly a *Ceratozamia* and not a *Zamia* and corresponds to the protologue of *C. vovidesii*. Another specimen, Pérez-Farrera 3026, is labelled as the holotype for *Z. grijalvensis* and it clearly matches the protologue of that taxon. We are treating this miscitation of Pérez-Farrera 2620^a in the protologue of *Z. grijalvensis* as a typographical error, which is now corrected.

Specimens examined. GUATEMALA. **Huehuetenango:** 900–1,300 m, 3 Sep 1942, J.A. Steyermark 51818 (NY; US); 1,630 m, 9 Jul 2006, M. Véliz & V. Davila 17042, 17043, 17044 (BIGU); 30 May 1906, O.F. Cook 51 (US); 1,629 m, 10 Jul 2006, V. Davila & M. Véliz 1050 (BIGU); 1,622 m, 10. Jul 2006, V. Davila & M. Véliz 1052, 1053 (BIGU). MEXICO. **Chiapas: Mun. Ángel Albino Corzo,** 730 m, 23 Jan 1968, Alush Shilom Ton 3554 (ENCB); 14 Dec 1980, 1,380 m, D.E. Breedlove 48678 (NY); 800–1,000 m, 8 Nov 1945, E.H. Xolocotzi & A.J. Sharp 402 (CHAPA, ENCB, MEXU); 1,000 m, 2 Jun 1987, E.M. Martínez S. et al. 21586 (MEXU); 1,819 m, 13 Aug 2009, H. Gómez-Domínguez 2316 (MEXU); 1,650 m, 18 May 1982, J.I. Calzada et al. 9131 (XAL); 5 Mar 1989, U. Bachem C. & R. Rojas 405 (CHIP). **Mun. Jaltenango de la Paz,** Jun 1995, E. Matuda s/n (MEXU); 1,500 m, 23 Jun 1990, M. Heath & A. Long 1287 (CHIP); 25 Feb 1995, Miranda 7042 (MEXU). **Mun. La Concordia,** 1,000 m, 5 Jun 1988, E. Palacios E. 1050 (CHIP); 1,840 m, 26 Jun 2018, F. Nicolalde-Morejón et al. 2864–2875 (CIB); 1,840 m, 26 Jun 2018, L. Martínez-Domínguez et al. 1439–1451 (CIB); 1,156 m, 19 Sep 2001, M.A. Pérez-Farrera 2621 (XAL); 1,600 m, M.A. Pérez-Farrera s/n (CHIP); 1,120 m, 17 Jun 2014, M.G. Díaz M. 961 (CHIP);

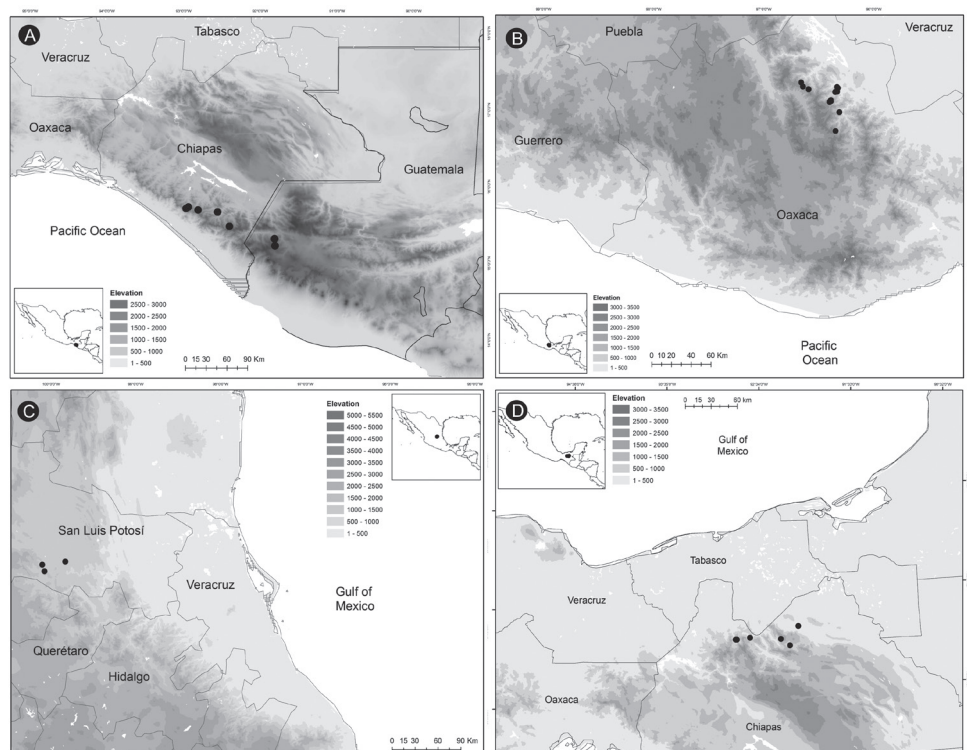


Figure 29. Distribution of *Ceratozamia* species. **A** *C. vovidesii* **B** *C. whitelockiana* **C** *C. zaragozae* **D** *C. zoquorum*.

24 Mar 2001, *R. Martínez-Camilo* 54 (CHIP); 1,100 m, 11 Jun 1988, *T.G. Cabrera-Cachón* 74 (CHIP); 1,700 m, 1 Jun 1989, *U. Bachem C. & R. Rojas* 795 (CHIP). **Mun. Mapastepec**, 1,750 m, 13 May 1982, *J.I. Calzada et al.* 8874 (IBUG, MEXU, MO, XAL). **Mun. Siltepec**, 28 Feb 2000, *O. Farrera S.* 1958 (CHIP).

34. *Ceratozamia whitelockiana* Chemnick & T.J.Greg., Phytologia 79(1): 51. 1996 ("1995")

Fig. 30

Type. MEXICO. Oaxaca: Vicinity of Metates, south of Valle Nacional, 628 m, 10 May 1995, *J. Chemnick & T. Gregory* 5 (holotype: HNT [n.v.]; isotypes: FTG!, XALU [n.v.]).

Description. **Stem** 20–80 cm long, 18–30 cm in diameter, epigeous, decumbent. **Cataphylls** 2–5 × 2–5 cm wide at the base, persistent, triangular, reddish brown, densely brown tomentose at emergence, partially tomentose at maturity, apex acuminate. **Leaves** 3–10, 129–250 cm long, descending, light green and glaucous at emergence with whitish gray trichomes, glabrous at maturity. **Petiole** 60–140 cm long, terete, linear, green in mature leaves; with 3–22 thin prickles, 0.06–0.39 cm long.

Rachis 70–160 cm long, terete, linear, greenish in mature leaves, unarmed. **Leaflets** 20–48 pairs, opposite to subopposite, insertion in one plane, lanceolate, generally longitudinally planar, not basally falcate, papyraceous, flat, green with adaxial and abaxial sides glabrous, distal end with entire margins, acuminate and symmetrical at the apex, attenuate at base, with conspicuous and green-light veins; median leaflets $25\text{--}38.5 \times 2.0\text{--}3.7$ cm, $1.6\text{--}3.1$ cm between leaflets; articulations $0.5\text{--}1.4$ cm wide, green. **Pollen strobili** 20–30 cm long, 3–5 cm in diameter, generally solitary (1–2), cylindrical, erect, greenish at emergence with reddish trichomes, greenish yellow with reddish brown trichomes at maturity; peduncle 15–25 cm long, $1.2\text{--}1.9$ cm in diameter, glabrous or with trichomes scarce reddish brown to brown; microsporophylls $1.5\text{--}3.0 \times 0.8\text{--}1.5$ cm, elliptic with a non-recurved distal face and a lobate fertile portion, infertile portion $0.40\text{--}0.50$ cm long and linear with straight horns $0.38\text{--}0.50$ cm long, $0.50\text{--}1.0$ cm and a right angle between the horns. **Ovulate strobili** 14–20 cm long, 7–10 cm in diameter, solitary, cylindrical, erect, yellowish green with abundant blackish trichomes at emergence, green with brown to blackish trichomes at maturity, apiculate apex; peduncle 1–4 cm long, $1.0\text{--}1.8$ cm in diameter, erect, glabrous or with trichomes scarce, reddish brown; megasporophylls 24–40, 4–5 orthostichies with 5–8 sporophylls per orthostichy, $1.7\text{--}2.2 \times 4.5\text{--}5.1$ cm, with a truncate distal face, horns straight and $0.98\text{--}1.4$ cm long, $0.95\text{--}1.3$ cm between horns and an acute angle between the horns. **Seeds** $2.1\text{--}2.7$ cm long, $1.4\text{--}1.8$ cm in diameter, ovate, sarcotesta whitish yellow to yellow when immature, light brown at maturity.

Distribution and habitat. *Ceratozamia whitelockiana* is endemic to the Sierra Norte of Oaxaca (Mexico), between 500 to 1,800 m in La Chinantla area (Fig. 29B). It occurs in the elevational gradient of evergreen tropical forest with *Quercus* sp. and cloud forest with *Oreomunnea mexicana* (Standl.) J.-F.Leroy on karstic rocks.

Etymology. This species was named in honor of Loran Whitelock for his contributions to cycad biology (Chemnick and Gregory 1996).

Common names. None recorded.

Uses. None recorded.

Conservation status. (IUCN 2021). *Ceratozamia whitelockiana* is listed as “Endangered (EN)” under criteria A2c; B1ab(i,ii,iii,v)+2ab(i,ii,iii,v); C1.

Discussion. *Ceratozamia whitelockiana* is similar to *C. mixeorum* in leaf morphology; the only difference is the sparse prickles in *C. whitelockiana* (between 3 to 22, in number), whereas *C. mixeorum* has more than 28 prickles. Additionally, the length of the petiole is very long in relation to the total size of the leaf in *C. whitelockiana*. In reproductive structures, the ovulate strobili in *C. whitelockiana* have a long peduncle 12–23 cm and the fertile portion has 4–5 orthostichies with 5–8 sporophylls per orthostichy and the pollen strobili have a long peduncle that is the same size as the fertile part or longer (Fig. 30 A, C). In contrast, *C. mixeorum* has ovulate strobili with a short peduncle from 1–4 cm long and pollen strobili with peduncles shorter than the fertile area.

Specimens examined. MEXICO. Oaxaca: 660 m, 29 Jun 1977, T.B. Croat 39751 (MO). Mun. Ixtlán de Juárez, 1,640 m, 29 Jan 1998, Y. Arellanes C. et al. 283

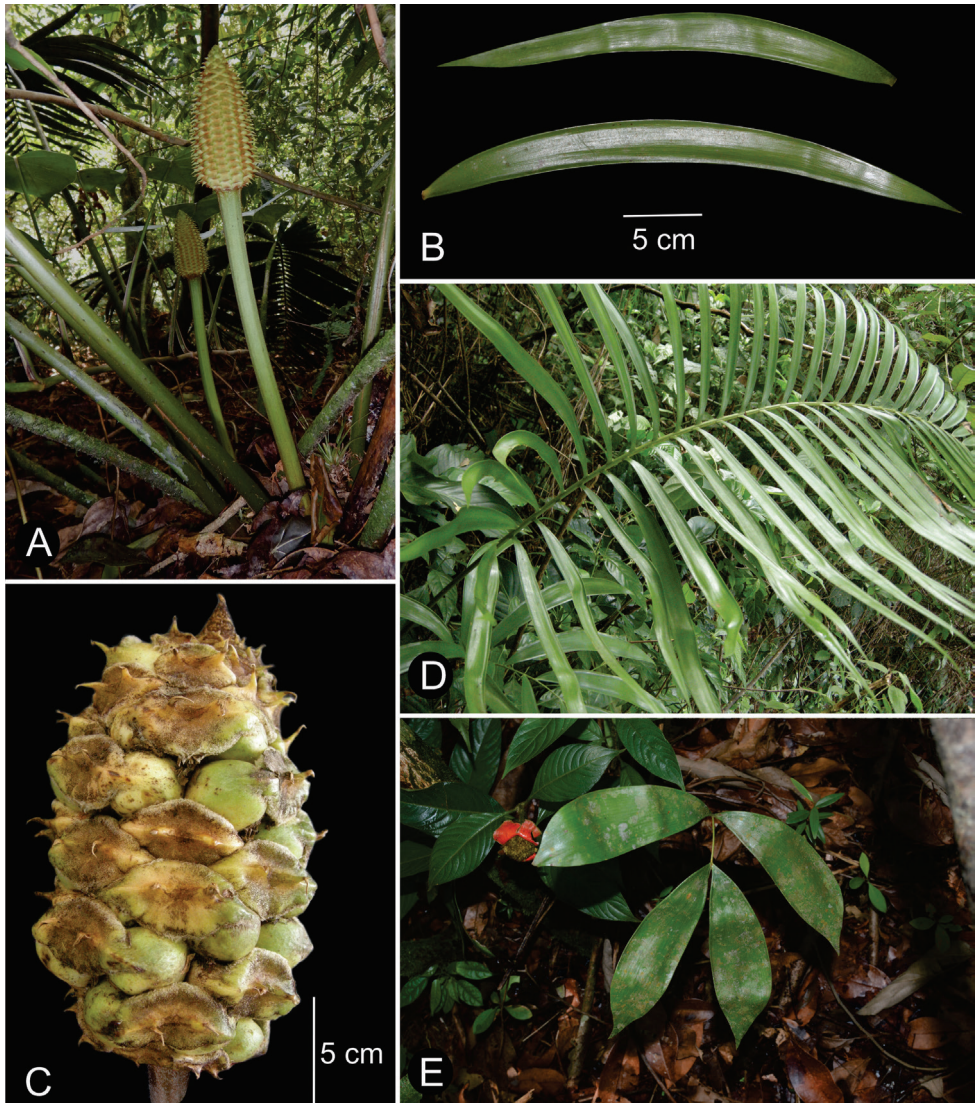


Figure 30. *Ceratozamia whitelockiana* **A** immature pollen strobili **B** leaflet variation **C** mature ovulate strobilus **D** leaves **E** seedling.

(SERO); 1,640 m, 21 Aug 1998, *Y. Arellanes C. et al.* 413 (MEXU, MO, SERO). **Mun. San Felipe Usila**, 24 Oct 1994, *P. Osorio H.* 312 (MEXU). **Mun. San Juan Bautista Valle Nacional**, 650 m, 24 Sep 2020, *F. Nicolalde-Morejón et al.* 3346 (CIB); 650 m, 24 Sep 2020, *L. Martínez-Domínguez et al.* 1968 (CIB, MEXU); 500 m, 22 Jan 2001, *S. Avendaño R.* 5375 (MEXU); 518 m, 22 Jan 2001, *T.W. Walters* 2001-39-D,E (XAL). **Mun. San Juquila Vijanos**, 1,900 m, 15 Nov 1996, *X. Munn et al.* 233 (XAL). **Mun. San Pedro Sochiapam**, 1,682 m, 2 Nov 2016, *M.B. Velasco-Pichardo et al.* 225 (MEXU). **Mun. San Juan Tepeuxila**, 1,538 m, 9 May 2008, *J.E. Rivera-*

Hernández 4289 (MEXU, XAL); 1,538 m, 30 Jul 2008, *J.E. Rivera-Hernández* 4380 (MEXU). **Mun. Santiago Comaltepec**, 1,750 m, 8. Jan 1995, *A. Rincón G. et al.* 516 (MEXU, MO, XAL); 560 m, 24 Sep 2020, *F. Nicolalde-Morejón et al.* 3348–3355 (CIB); 560 m, 24 Sep 2020, *L. Martínez-Domínguez et al.* 1973–1975, 1980 (CIB, MEXU), 1976, 1978, 1979, 1981 (CIB), 1977 (CIB, MEXU, NY); 1,600 m, 10 Jun 1988, *R. López-Luna & G.J. Martin* 285 (MEXU), 1,760 m, 26 Jan 1988, *R. Torres C. & E. Martínez S.* 11345 (MEXU).

35. *Ceratozamia zaragozae* Medellín-Leal, *Brittonia* 15: 175. 1963

Fig. 27I

Type. MEXICO. San Luis Potosí: Mun. Río Verde, 22 Jul 1962, *F. Medellín-Leal* 1452 ♀ (holotype: SLPM! [acc. # 003530]; isotypes: ENCB! [ENCB003716], GH! [00003279], MEXU! [MEXU00162859, MEXU0053418], MICH! [1192896], US! [00011997]).

Description. *Stem* 10–20 cm long, 10–15 cm in diameter, semi-hypogeous, erect. *Cataphylls* 1.8–2.5 × 1–2 cm wide at the base, persistent, triangular, reddish brown, densely brown tomentose at emergence, partially tomentose at maturity, apex acuminate. *Leaves* 3–27, 95–202 cm long, ascending, reddish brown at emergence with whitish gray trichomes, glabrous at maturity. *Petiole* 11–36 cm long, terete, twisted, green in mature leaves, unarmed. *Rachis* 40–77 cm long, terete, twisted, green in mature leaves, unarmed. *Leaflets* 25–46, opposite to subopposite, insertion in one plane, linear, generally longitudinally planar, basally falcate, membranaceous, strongly involute, green with adaxial and abaxial sides glabrous, distal end with entire margins, acute and symmetrical at the 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 0.2–0.3 cm wide, yellow. *Pollen strobili* 15–19 cm long, 2–3.5 cm in diameter, solitary, cylindrical, erect, greenish with reddish brown trichomes at emergence, reddish brown at maturity; peduncle 5–8 cm long, 1.5–1.8 cm in diameter, tomentose, reddish brown to brown; microsporophylls 0.8–1.2 × 0.3–0.6 cm, obconic with a non-recurved distal face and a lobate fertile portion, infertile portion 0.25–0.35 cm long and rounded with straight horns 0.20–0.30 cm long, 0.22–0.30 cm and an obtuse angle between the horns. *Ovulate strobili* 7–12 cm long, 5.5–7.3 cm in diameter, solitary, cylindrical, erect, green with scarce reddish brown trichomes at emergence, dark green at maturity, acute apex; peduncle 6–9 cm long, 0.9–1.2 cm in diameter, erect, tomentose, brown; megasporophylls 24–49, 5–7 orthostichies with 5–6 sporophylls per orthostichy, 2.0–2.6 × 2.2–3.7 cm, with a truncate distal face, horns straight and 0.33–0.45 cm long, 1.95–2.35 cm between horns with an obtuse angle between the horns. *Seeds* 2–2.8 cm long, 1.8–2 cm in diameter, ovate, sarcotesta light brown at maturity.

Distribution and habitat. *Ceratozamia zaragozae* is endemic to Mexico in a small mountain range in San Luis Potosí (Fig. 29C), where it occurs in pine-oak forest on karstic rocks at 1,500–1,950 m.

Etymology. The specific epithet refers to General Ignacio Zaragoza, who was a hero in the Battle of Puebla against the French Army in May of 1862.

Common names. None recorded.

Uses. None recorded.

Conservation status. (IUCN 2021). *Ceratozamia zaragozae* is listed as “Critically Endangered (CR)” under criteria A2acd; B1ab(iii,iv,v)+2ab(iii,iv,v); C1. Castillo-Lara et al. (2018) evaluated the population structure and spatial distribution for this species and found that the populations have several individuals with a density variable from four to 209 plants in an area of 2500 m², but low population growth. These authors suggest that the status for this species could be modified to “Endangered (EN)”.

Discussion. *Ceratozamia zaragozae* and *C. norstogii* are the only species in the genus with twisted petiole and rachis, but the first has an unarmed petiole, whereas *C. norstogii* has abundant and robust prickles on the petiole. Additionally, leaflets are membranaceous in *C. zaragozae*, whereas in *C. norstogii* they are coriaceous.

Specimens examined. MEXICO. **San Luis Potosí: Mun. Río Verde**, 1,700 m, 29 Mar 1984, *A.G. Mendoza & L. Vargas* 1389 (MEXU); 1,750 m, 20 Sep 1979, *A.P. Vovides* 435 (XAL); 22 Jul 1962, *E. Molseed* 34 (MEXU; MICH); 1,860 m, 24 Jan 1994, *F. García S. s/n* (SLPM); 1,800 m, 22 Jul 1962, *F. Medellín-Leal* 1451 (SLPM; US); 28 Oct 1965, *F. Medellín-Leal s/n* (SLPM); 1,900 m, Sep 1994, *F. Medellín-Leal s/n* (SLPM); 1,956 m, 18 Mar 2016, *F. Nicolalde-Morejón et al.* 2307–2319 (CIB); 1,750 m, 13 Apr 1968, *J. Rzedowski* 25658 (ENCB; MICH); 1,956 m, 18 Mar 2016, *L. Martínez-Domínguez et al.* 792, 794–796, 798–808 (CIB), 793, 797, 799 (CIB, MEXU); 2031 m, 31 Jul 2017, *P. Chávez C. et al.* 98 (SLPM); 1,532 m, 13 Jan 2001, *T. Walters et al.* TW-2001-07 (MEXU, XAL). **Mun. Zaragoza**, 1,869 m, 9 Nov 2012, *P. Castillo-Lara et al.* 593 (SLPM); 1,847 m, 14 Jul 2016, *P. Castillo-Lara et al.* 1073 (SLPM).

36. *Ceratozamia zoquorum* Pérez-Farr., Vovides & Iglesias. Bot. J. Linn. Soc. 137 (1): 77. 2001

Figs 1D, 23 A–C

Type. MEXICO. Chiapas: Northern mountain range, 18 Nov 1998, *M.A. Pérez-Farrera* 1732 ♂ (holotype: CHIP [n.v]).

Description. **Stem** 12–30 cm long, 8–15 cm in diameter, epigeous, semi-hypogeous, erect. **Cataphylls** 2.5–6.9 × 1.3–4.5 cm wide at the base, persistent, triangular, reddish brown, densely brown tomentose at emergence, glabrous at apex when mature, apex acuminate. **Leaves** 2–17, 46–216.5 cm long, descending, light green or brown, glaucous at emergence with whitish gray trichomes, glabrous at maturity. **Petiole** 23.3–111.5 cm long, terete, linear, pink at emergence, yellowish green at mature leaves; unarmed to armed with 3–27 thin prickles 0.08–0.15 cm long. **Rachis** 17.6–114.5 cm long, terete, linear, pink at emergence, yellowish green at mature leaves, generally unarmed. **Leaflets** 6–17 pairs, opposite to subopposite, insertion in one plane, oblong to

oblanceolate, longitudinally curved abaxially to planar, generally basally falcate, coriaceous, flat, green with adaxial and/or abaxial side glaucous, distal end with entire margins, acuminate (rarely acute) and asymmetrical (rarely symmetrical in apical leaflets) at the apex, attenuate at base, with conspicuous and light-green veins; median leaflets $22\text{--}37 \times 3.9\text{--}5.6$ (7) cm, $4.6\text{--}11.1$ cm between leaflets; articulations $0.5\text{--}1.5$ cm wide, green and yellowish. **Pollen strobili** solitary (up to 2), $10.8\text{--}25$ cm long, $2.8\text{--}4.3$ cm in diameter, cylindrical, erect, green with blackish trichomes at emergence, yellow-cream with blackish trichomes at maturity; peduncle $5\text{--}13$ cm long, $1.5\text{--}1.8$ cm in diameter, tomentose, light brown; microsporophylls $0.9\text{--}1.4 \times 0.7\text{--}0.9$ cm, discoid with a non-recurved distal face and a deeply lobate fertile portion, infertile portion $0.35\text{--}0.40$ cm long and linear with straight horns $0.30\text{--}0.45$ cm long, $0.73\text{--}0.80$ cm and an acute angle between the horns. **Ovulate strobili** $15\text{--}26$ cm long, $7.5\text{--}9.5$ cm in diameter, solitary, cylindrical, erect, green with reddish brown trichomes at emergence, green with brown to blackish trichomes at maturity, acute apex; peduncle $5\text{--}18.5$ cm long, $1.6\text{--}2$ cm in diameter, pendulous and erect, tomentose, light brown; megasporophylls $30\text{--}56$, $6\text{--}8$ orthostichies with $5\text{--}7$ sporophylls per orthostichy, $1.5\text{--}2.0 \times 3.5\text{--}4.0$ cm, with a prominent distal face, horns curved to straight and $0.70\text{--}0.90$ cm long, $0.92\text{--}1.56$ cm between horns with a right angle between the horns. **Seeds** $2\text{--}2.8$ cm long, $1.8\text{--}2$ cm in diameter, ovate, sarcotesta whitish pink at emergence, light brown at maturity.

Distribution and habitat. *Ceratozamia zoquorum* is endemic to the northern mountains of Chiapas, Mexico (Fig. 29D), where it occurs on karstic outcrops in evergreen tropical forest and oak forest between 500 and 1,150 m.

Etymology. The specific epithet was established in honor of the Zoque culture (Pérez-Farrera et al. 2001).

Common names. None recorded.

Uses. None recorded.

Conservation status. (IUCN 2021). *Ceratozamia zoquorum* is listed as “Critically Endangered” under criteria A2c+4c; B1ab(i,ii,iii,v).

Discussion. *Ceratozamia zoquorum* has oblong and coriaceous leaflets and leaves with scarce thin and short prickles. It belongs to a cryptic taxonomic group, and is geographically close to populations of *C. becerrae* and *C. santillanii*, the other two species in this group. The three taxa are distinguishable with the nrITS (Martínez-Domínguez et al. 2017c). Morphologically, *C. zoquorum* differs from *C. santillanii* by its peduncle of ovulate strobili more than 3 cm long.

Specimens examined. MEXICO. **Chiapas: Mun. Solosuchiapa**, 530 m, 23 Jan 2014, *F. Nicolalde-Morejón et al.* 1931, 1932 (CIB); 550 m, 23 Jan 2014, *F. Nicolalde-Morejón et al.* 1933–1935 (CIB); 682 m, 24 Jan 2014, *F. Nicolalde-Morejón et al.* 1936–1947 (CIB); 531 m, 23 Jan 2014, *L. Martínez-Domínguez et al.* 1–5 (CIB); 500 m, 23 Jan 2014, *L. Martínez-Domínguez et al.* 6–14 (CIB); 682 m, 23 Jan 2014, *L. Martínez-Domínguez et al.* 15–34 (CIB); 520 m, 17 Apr 1996, *M.A. Pérez-Farrera* 905 (CH, CHIP, HEM); 520 m, 16 Apr 1996, *M.A. Pérez-Farrera s/n* (HEM); 19 Jan 2001, *S. Avendaño* 5216 (MEXU); 531 m, 20 Jan 2001, *T.W. Walters* 2001–2028-A (XAL). **Mun. Tila**, 1,135 m, 16 Jul 2021, *F. Nicolalde-Morejón et al.* 3698–3702 (CIB); 1,135 m, 16 Jul 2021, *L. Martínez-Domínguez et al.* 2326–2330 (CIB).

“Names” (designations) not validly published

Ceratozamia angustifolia Linden, Illustr. Hort. 28: 32. 1881, nomen nudum, name in list, no description and diagnosis.

Ceratozamia ensiformis hort. ex J.Schust., Pflanzenr. 99: 130. 1932, pro syn.

Ceratozamia eriolepis hort. ex J.Schust., Pflanzenr. 99: 132. 1932, pro syn.

Ceratozamia fusca hort. ex J.Schust., Pflanzenr. 99: 132. 1932, pro syn.

Ceratozamia fuscata hort. ex J.Schust., Pflanzenr. 99: 132. 1932, pro syn.

Ceratozamia ghiesbreghtii Brongn., Compte Rendue 81: 303. 1875, nomen nudum, name in list, no description and diagnosis.

Ceratozamia × *hybrida* J.Schust., Pflanzenr. 99: 132. 1932, pro syn.

Ceratozamia karsteniana hort. ex Dyer, Biol. Cent.-Amer., Bot. 3: 192. 1884, pro syn.

Thiselton-Dyer cited this name as synonym of *C. latifolia*.

Ceratozamia longipinnata hort. ex J.Schust., Pflanzenr. 99: 130. 1932, pro syn.

Ceratozamia miquelii hort., Vilm. Blumengärtn., ed. 3. 1: 1246. 1895, pro syn.

Ceratozamia muricata Miq. ex Linden, Illustr. Hort. 32. 1881, nomen nudum.

Ceratozamia ottonis hort. ex J.Schust., Pflanzenr. 99: 130. pro syn. 1932, pro syn.

Ceratozamia purpurea Matte, Recherches Appareil Libéro-Lign. Cycad. 125. 1914, nomen nudum.

Dipsacozamia Lehm. ex Lindl., The Vegetable Kingdom, 225. 1846, nomen nudum, not validly published; no diagnosis and description (Art. 39).

Dipsacozamia mexicana Liebm. ex Dyer, Biol. Cent.-Amer., Bot. 3: 193. 1884, pro syn.

Thiselton-Dyer cited this name as synonym of *C. mexicana*.

Excluded names

Ceratozamia boliviana Brongn., Ann. Sci. Nat., Bot. ser. 3, 5: 9. 1846. Lectotype: P [P02441739]. Taxonomic Status: synonym of *Zamia boliviana* (Brongn.) A.DC.

Ceratozamia katzeriana Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 4(4): 298. 1876.

Lectotype: LE [LE00009045]. Taxonomic Status: synonym of *Zamia katzeriana* (Regel) E.Rettig.

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Torres, Damián Reyes, Manuel Hernández, Mario Guzmán, Javier Reyes, Artemio Reyes, Enok Martínez, Abelino Rodríguez, Sergio Pablo, Camilo Zarate, Tisoc Morgan, Librado Ventura, Sirilo Santiago, Don Urbano, Don Antonio, and local allies and collaborators in all communities visited. Also, we extend special thanks for assistance in the field to personnel of “Jardín Botánico Lancetilla”, in particular Wilson Zuniga and Jonathan Hernández, and from “CURLA-UNAH” to Kelvin Bodden, Carlos Rivera, Carlos Vindel, Adrian Zelaya and Gisela Hernández Girón. We are thankful to the curators of all herbaria cited in this paper, for access to their collections and/or loans, especially Mario Véliz and Carlos Durán. Special thanks to Jahzeel Mendoza Martínez, María del Rosario García Peña, Gilda Ortiz Calderón and Alberto Reyes García for the support with specimens in CIB and MEXU herbaria; Alvar González Christen and Ernesto Santelices for logistic support. Also, María Hilda Flores Olvera and Francisco Lorea Hernández, for helpful comments on morphology and taxonomy; Olvin Oyuela, Lilian Ferrufino and German Sandoval, for providing specimens and information from Honduras; Curan Bonham for providing information and photos from Guatemala, and María Biaanni Velasco, for the provision of photographs used in Fig. 30A. We thank Gerardo Quintos Andrade for the botanical illustration of the new species and Fig. 11A. Finally, we wish to thank the three reviewers for their diligence in providing thorough and constructive comments that vastly improved this publication and Sandra Knapp for her comments and extensive help in finalizing the text. This research was financed in part by an IAPT Research Grants to LMD, CONACyT grant 134960 to FNM, and NSF Grants BSR-8607049, EF-0629817 and DEB-2140319 to DWS. FNM received further support from the Instituto de Investigaciones Biológicas (UV), and LMD and FVS were also supported by Instituto de Biología, Universidad Nacional Autónoma de México (UNAM).

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Supplementary material 1

Glossary

Authors: L. Martínez-Domínguez, F. Nicolalde-Morejón, D. W. Stevenson

Data type: Text

Explanation note: Glossary for characters associated to reproductive structures.

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Link: <https://doi.org/10.3897/phytokeys.208.80382.suppl1>

Supplementary material 2

Herbarium specimens for *Ceratozamia sancheziae* and *C. zoquorum*

Author: L. Martínez-Domínguez

Data type: Images

Explanation note: Specimens: M.A. Pérez-Farrera 1635; D.E. Breedlove 25506.

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Revision of Ardissonaceae (Bacillariophyta, Mediophyceae) from Micronesian populations, with descriptions of two new genera, *Ardissonopsis* and *Grunowago*, and new species in *Ardissona*, *Synedrosphenia* and *Climacosphenia*

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Abstract

Ardissona was resurrected from *Synedra* in 1986 and was included as a genus by Round, Crawford and Mann (“The Diatoms”) in its own Family and Order. They commented that there might be several genera involved since the type species of the genus possesses a double-walled structure and other taxa placed in *Ardissona* have only a single-walled structure. Two other genera of “big sticks,” *Toxarium* and *Climacosphenia*, were placed in their own Families and Orders but share many characters with Ardissonaceae, especially growth from a bifacial annulus. Eighteen taxa (11 new species) from Micronesia were compared with the literature and remnant material from Grunow’s Honduras *Sargassum* sample to address the concepts of *Ardissona* and Ardissonaceae. Phylogenetic and morphological analyses showed three clades within *Ardissona* sensu lato: *Ardissona* emend. for the double-walled taxa, *Synedrosphenia* emend. and *Ardissonopsis* **gen. nov.** for single-walled taxa. New species include *Ardissona densistriata* **sp. nov.**; *Synedrosphenia bikarensis* **sp. nov.**, *S. licmophoropsis* **sp. nov.**, *S. parva* **sp. nov.**, and *S. recta* **sp. nov.**; *Ardissonopsis fulgicans* **sp. nov.**, *A. appressata* **sp. nov.**, and *A. gracilis* **sp. nov.** Transfers include *Synedrosphenia crystallina* **comb. nov.** and *S. fulgens* **comb. nov.** *Synedra undosa*, seen for the first time in SEM in Grunow’s material, is transferred to *Ardissonopsis undosa* **comb. nov.** Three more genera have similar structure: *Toxarium*, *Climacosphenia* and *Grunowago* **gen. nov.**, erected for *Synedra bacillaris* and

a lanceolate species, *G. pacifica* **sp. nov.** Morphological characters of *Toxarium* in our region support separation of *Toxarium hennedyanum* and *T. undulatum* and suggest additional species here and elsewhere. *Climacosphenia moniligera* was not found but we clarify its characters based on the literature and distinguish *C. soulonalis* **sp. nov.** from it. *Climacosphenia elongata* and a very long, slender *C. elegantissima* **sp. nov.**, previously identified as *C. elongata*, were present along with *C. scimiter*. Morphological and molecular phylogenetics strongly suggested that all these genera belong in one family and we propose to include them in the Ardissonaceae and to reinstate the Order Ardissonales Round.

Keywords

Ardissonales, biodiversity, coral reefs, Grunow, Mediophyceae, systematics, Toxariales, Western Pacific

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Introduction

Bilaterally symmetrical, stick-like diatoms, 300–1300 µm long, are common and sometimes abundant epiphytes on seaweeds of coral reefs. Some have bilateral growth of the valve (“pennate” diatoms) and are in the Class Fragilariophyceae, including *Stricosus* Sabir & E.C. Theriot, 2018 and longer species of *Hyalosynedra* D.M. Williams

& F.E. Round, 1986 (Sabir et al. 2018). However, several common genera have valve growth from a bifacial annulus, at or near the edge of the valve face, forming striae internally and externally (Mann 1984; Kaczmarek et al. 2020) and were moved to Class Mediophyceae (bi- to multipolar diatoms) (Medlin et al. 2008) and are presently placed in four families in the Order Toxariales (Cox 2015). All are non-pennate but emerge in 7-gene phylogenetic trees in a clade sister to the pennate diatoms (Kooistra et al. 2003; Medlin et al. 2008; Theriot et al. 2015; Medlin and Desdevises 2020). Previously Round et al. (1990) had placed four genera—*Ardissona* De Notaris, 1870 in De Notaris and Baglietto (1871), *Toxarium* J.W. Bailey, 1854, and *Climacosphenia* Ehrenberg, 1843, plus *Synedrosphenia* (H. Peragallo) Azpeitia, 1911—in three Families, each in a separate Order in Fragilariophyceae. The sexual reproduction of *A. crystallina* (Agardh) Grunow ex De Toni, 1892 has similarities to that of Fragilariophyceae in being isogamous (Davidovich et al. 2017) and in morphology of its auxospores (Kaczmarek et al. 2018), yet the valve morphogenesis reinforces its position among Mediophyceae (Kaczmarek et al. 2020). Gliding motility is present in these diatoms, even though they lack a raphe—the structure usually associated diatom motility—and even though they are habitually sessile on mucilage stalks. Gliding was demonstrated in *A. crystallina*, with mucilage secretion apparently occurring via a deep groove between the valve and valvocopula at each end of the cell (Pickett-Heaps et al. 1991), and in *Toxarium*, which has a similar apical structure (Kooistra et al. 2003).

Each genus in the Toxariales has a confused taxonomic history that has not yet been addressed with electron microscopy and several issues need to be resolved. The genus *Ardissona*, subsumed as a subgenus of *Synedra* Ehrenberg, 1830 and declared by Hustedt (1931–1959: 238) to be a “difficult group of ... *Synedra*,” was resurrected and emended by Poulin et al. (1986) based on SEM study, and the spelling of the name corrected (from *Ardissonia*) by Round et al. (1990). The generitype *Ardissona robusta* (Ralfs) De Notaris, 1871 was not among the species studied by Poulin et al. (1986) but apparently was the species Round et al. (1990) used to illustrate the structure of the genus. The structure of *A. formosa* (Hantzsch) Grunow ex De Toni, 1892, studied by Sullivan and Wear (1995), differs significantly from the taxa studied by Poulin et al. (1986, 1987) [*A. crystallina* and *A. fulgens* (Greville) Grunow ex De Toni, 1892] in having a double wall and unperforated girdle bands. On the other hand, the genus *Synedrosphenia*, as illustrated by Round et al. (1990), while having a structure very similar to *Ardissona* species shown by Poulin et al. (1986), has heteropolar valves and was classified by Round et al. (1990) with the heteropolar genus *Climacosphenia* in the Climacospheniaceae. Round et al. (1990: 420) commented about *Ardissona* that, “It may prove best to place the non-chambered species in yet another genus,” but this has not yet been done. The definition of the genus has become confused because while Poulin et al. (1986) based their emendation on *A. crystallina* and characterized the transapical costae in these single-walled taxa as providing “chambering,” Round et al. (1990) based their description on *A. robusta*, the generitype, and thus included the internal plate and complete chambering of the valve as a character. Kanjer et al. (2021) regarded *A. fulgens* as “differing only slightly” from the generitype in lacking the internal plate.

The genera *Toxarium* and *Climacosphenia* differ from the others in different ways. *Climacosphenia* was formerly classified alongside *Licmophora*, while *Toxarium* was in *Synedra* (Peragallo and Peragallo 1897–1908; Hustedt 1931–1959). *Toxarium* is defined by the presence of scattered areolae within the annulus and *Climacosphenia* by the presence of craticular bars on the valvocopula. Both have a history of debate over whether there are one or two species of each, distinguished only by cell shape. This led to an assumption that there are only two species in each to choose from, i.e., *Toxarium undulatum* J.W. Bailey, 1854 (generitype) and *T. hennedyanum* (Gregory) Pelletan, 1889; *Climacosphenia moniligera* Ehrenberg, 1843 (generitype) and *C. elongata* J.W. Bailey, 1854.

Finally, one seemingly less similar taxon that occurs among *Ardissonaea*, *Toxarium* and *Climacosphenia* spp. in our flora has been reported as *Synedra bacillaris* (Grunow) Hustedt, 1932 (= *Synedra crystallina* var. *bacillaris* Grunow, 1880) (Lobban et al. 2012); this species has a distinct central costa and apparently lacks an annulus. Even though many marine species formerly in *Synedra* have been removed to new genera (Williams and Round 1986), *S. bacillaris* has yet to be revised, despite Sullivan and Wear's (1995) observations.

The initial objective of this study was to describe several new species of *Ardissonaea*, but in our morphological study for taxonomy and floristics we were led to address the systematics of the whole group. We here present descriptions of the taxa in Micronesia, including new genera and new species, plus some related species from Grunow's (1867, 1877) Honduras materials. We analyze sequence data and morphological characters, make the case for including *Toxarium* and *Climacosphenia* in Ardissonaceae, within a reinstated Ardissonales Round, and, finally, make nomenclatural changes that reflect our conclusions. These include transfer of single-walled *Ardissonaea* species into *Synedrosphenia* and a new genus *Ardissonopsis*, amending the generic descriptions as needed, and a new genus for *Synedra bacillaris*.

Materials and methods

Sample collection and imaging

Samples from our extensive collection of benthic diatoms from Micronesian coral reef habitats, preserved and prepared using the protocols standard in the U. Guam diatoms laboratory (Lobban 2021b), were surveyed for taxa of interest. Origins of the samples used in this study are listed in Table 1. Some material was observed alive, and often then transferred as a whole mount onto a filter, dried, and mounted for SEM; this enabled us to study the girdle bands in situ. In addition, we were able to observe the rich material in Grunow's Honduras sample, collected by A. Lindig ca. 1860 and published in Grunow (1867, 1877). They were unmounted remnants of acid cleaned material he used for preparation of slides of other species; these were listed in Lobban et al. (2021a, table 1).

Table 1. Collection localities of specimens mentioned in this study.

Country	Entity (Island)	Municipality ("State")	Locality name	Locality code	GPS coordinates
United States of America	Guam	Yona Municipality	UOG Marine Laboratory	GU7	13.428°N, 144.799°E
United States of America	Guam	Inarajan Municipality	Saluglula Pools, Inarajan	GU21	13.271°N, 144.748°E
United States of America	Guam	Hagatna Municipality	Agana Boat Basin	GU26	13.478°N, 144.749°E
United States of America	Guam	Santa Rita Municipality	GabGab Reef	GU44	13.443°N, 144.643°E
United States of America	Guam	Piti Municipality	Scuba (Outhouse) Beach	GU52	13.464°N, 144.656°E
United States of America	Guam	Umatat Municipality	Nathan's Dent	GU54	13.336°N, 144.641°E
United States of America	Guam	Agat Municipality	"Pete's Reef"	GU55	13.347°N, 144.639°E
United States of America	Guam	Merizo Municipality	Achang mangroves	GU58	13.249°N, 144.697°E
United States of America	Guam	Merizo Municipality	Cocos West @ MDA buoy	GU56	13.252°N, 144.648°E
United States of America	Guam	Santa Rita Municipality	GabGab Reef II	GU66	13.444°N, 144.644°E
United States of America	Guam	Santa Rita Municipality	Western Shoals, Apra Harbor	GU68	13.451°N, 144.656°E
United States of America	Guam	Agat Municipality	Agat Reef nr Coral Gardens	GU75	13.357°N, 144.645°E
United States of America	Guam	Santa Rita Municipality	Vecky's Reef	GU76	13.449°N, 144.625°E
United States of America	CNMI	Saipan Municipality	American Memorial Park	SPN2022-1-4	15.218°N, 145.721°E
Federated States of Micronesia	Yap	Weloy Municipality	Nimpal MPA reef	Y36	9.542°N, 138.084°E
Federated States of Micronesia	Yap	Weloy Municipality	Nimpal MPA reef	Y37	9.542°N, 138.082°E
Federated States of Micronesia	Yap	Tomil Municipality	Tagireeng Channel	Y39	9.562°N, 138.145°E
Federated States of Micronesia	Yap	Tomil Municipality	Peelaek Corner	Y42	9.515°N, 138.179°E
Federated States of Micronesia	Chuuk	Weno Municipality	Eastern Passage, Moch Islet	TK4, TK28	7.514°N, 151.967°E
Republic of Marshall Islands	Majuro	Majuro Atoll Municipality	Mile 28 near Laura, outer reef	M1, M2	7.137°N, 171.038°E
Republic of Marshall Islands	Jaluit	Jaluit Atoll Municipality	Kabbenbock Islet	J5	5.930°N, 169.636°E
Republic of Marshall Islands	Bikar	none (uninhabited)	Within the lagoon	BA1 thru 11	12.223°N, 170.096°E

Light microscopy was done on Nikon 80i microscopes with differential interference contrast, imaging with the Nikon DS-Fi1 camera system. Some SEM images were taken with a PhenomWorld G2Pro desktop SEM as in previous work, but many final images, including those using a eucentric (tilting) stage and all those of *Toxarium* and *Climacosphenia*, were made on a Thermo-Fisher Phenom XL SEM (NanoScience Instruments, Phoenix, AZ) after recoating stubs with gold using a Luxor Gold sputter-coater (NanoScience Instruments, Phoenix, AZ). The materials observed were valves or frustules on strewn slides and SEM stubs in the diatom collection of the University of Guam Herbarium (GUAM), linked to collection data by the sample number and are referenced here by that sample number. Cataloguing of selected, imaged specimens of individual specimens has begun, using the Specify™ software, but is only in the earliest stages, so that catalog numbers have not yet been assigned to the specimens studied, but the developing website is accessible via the Guam Ecosystems Collaboratorium for Corals and Oceans (GECCO) Biorepository Specify Portal at <https://specifyportal.uog.edu>.

DNA isolation, amplification and sequencing

Culture conditions for the strains sequenced and photographed in this study were dependent on where the strains were isolated. Strains isolated from Guam and Saudi Arabia were maintained in a Percival model I-36LL incubation chamber (Percival, Boone, Iowa, USA) at 27 °C under a 12:12 hr light:dark period. Strains isolated from Florida

and North Carolina were maintained on a lab bench between 20–24 °C, illuminated by a north-facing window. DNA sequencing of these strains was conducted using the DNeasy Plant Minikit, adding a 45 s incubation in a Beadbeater (Biospec Products, Bartlesville, OK, USA) with 1.0 mm glass pellets for cell disruption. Three markers—the nuclear-encoded ribosomal SSU and chloroplast-encoded *rbcL* and *psbC*—were amplified by PCR, purified and sequenced following the protocols outlined in Lobban et al. (2021b).

Sequence data were added to a dataset of diatoms, with *Bolidomonas pacifica* Guillou & Chrétiennot-Dinet, 1999 used as an outgroup (see Suppl. material 1: Table S1 for GenBank accession numbers). Data were initially partitioned by gene, by paired and unpaired sites in SSU secondary structure (determined by the SSUalign program following Lobban et al. 2019) and codon position in *rbcL* and *psbC*. Model and partition testing were performed using PartitionFinder 2 with the best model chosen using the corrected Akaike information criterion (AICc). The dataset and partitioning scheme were analyzed under maximum likelihood using RAxML ver. 8.2.7 (Stamatakis 2014) compiled as the pthread-AVX version on an Intel i7 based processor in Linux Mint 18 and IQ-TREE version 1.6.12 for Linux. For RAxML, we ran 15 replicates with 400 rapid BS replicates each with ML optimizations and 4 replicates each with 1500 rapid BS replicates with ML optimization, with bootstrap support assessed by the BS replicates from the run which produced the optimal ML score. Bootstrap support for the IQ-TREE analysis was assessed from 1000 replicates. A Bayesian Inference based phylogeny was inferred by a multi-threaded MPI hybrid variant of ExaBayes version 1.5, using four independent runs with two coupled chains where branch lengths were linked. Convergence parameters monitored included the average deviation of split frequencies of less than or equal to 5% with a minimum of 10,000,000 generations. Bayesian nodal support was assessed using posterior probabilities, with the first 25% of the trees removed as “burn-in”.

Morphological analysis

Patterson (1982, 1988) proposed three tests of homology: similarity, conjunction, and congruence. He further proposed that similarity in some aspect of shape, form, or development was sufficient to postulate homology, with congruence as the decisive test, which we take to mean that similarity is the first test. Cracraft (1981) even more strongly argued that similarity was the first step in testing homology, writing that we are compelled to postulate homology for observed similarity. Following that philosophy, we coded multistate characters as additive where such nested similarity was apparent, an approach simultaneously and independently argued by Wilkinson (1992), Lipscomb (1992) and Theriot (1992). Such a treatment does not rely on assumptions about character evolution but instead relies on the principle of parsimony in the same way homology was initially postulated for binary characters (Sober 1983); that is, multistate characters represent nested sets of simi-

larity (and in fact, can be represented as a series of binary characters in a matrix for computer analysis.) The matrix (Suppl. material 2: Table S2) was analyzed under maximum parsimony using Winclada version 1.00.08, which serves as a tool for inputting data into a matrix, as a GUI for inputting commands into NONA version 2 for phylogenetic analysis, and as a tool for tree and character mapping visualization (Nixon 2002), with the following settings: Maximum trees to keep = 1001, Number of replications = 1000, Starting trees per hold = 1, Search strategy = Multiple TBR + TBR, and Search = unconstrained. Two characters were treated as additive: pseudoseptum (0 = absent, 1 = present, 2 = uniform rim all around valve) and valvocopula external poration (0 = absent, 1 = one row, 2 = multiple rows). Settings were heuristic search, 5000 replicates, mult*max*. *Toxarium hennedeyanum* was used as the outgroup.

Terminology

The frustules in the taxa treated here appear either heteropolar or isopolar, even though most are attached to the substrate at one pole by mucilage pads or stalks. Heteropolarity may be evident in the shape of the valve (cuneate or clavate), and/or in a cuneate girdle view caused by tapering girdle bands and narrower mantle toward the basal pole. We coded polar morphology as isopolar if the shapes were essentially similar at opposite poles. We avoid the term ‘apices’ because it can be ambiguous, and refer instead to ‘poles’; in heteropolar species we distinguish the ‘basal pole’, i.e., attachment end, from the ‘apical pole’. In some species the valve mantle, especially at the poles, is “recurved as a lip or poorly developed pseudoseptum” (Pickett-Heaps et al. 1991: 723); for this we use the term ‘pseudoseptum’ without qualification (see also Kanjer et al. 2021). In these species, the valvocopula and copula are shaped to fit around the pseudoseptum leaving a groove, the copula with very long fimbriae draped over the valvocopula, as clearly shown in Pickett-Heaps et al. (1991, fig. 18); we call this ‘complex polar architecture’. In some of these species, there is a broad notch in the valvocopula at the poles, producing a tunnel against the pseudoseptum (Round et al. 1990). In yet other species the rim of the valve is straight and the pars interior at the valvocopula pole is correspondingly simpler (fitting into the valve the way the sides of a cookie tin fit into the lid); we call this ‘simple polar architecture’. Most species have three girdle bands in the epicingulum and mature hypocingulum, which, following von Stosch (1975) and Sullivan and Wear (1995), are designated as valvocopula, copula and pleura; the pleura is usually very small and easily hidden or lost in preparation. In *Climacosphenia*, the septum of the valvocopula has a costa along each side with ingrowths forming the craticular bars, i.e., having the structure of a ladder, for which the genus is named. The ingrowths usually meet in the middle and form unions that may be seamless (Round 1982 called those “complete”) or complex; sometimes two outgrowths from one side will anastomose with one from the other side. Other terminology follows Anon (1975) and the revision by Ross et al. (1979).

Results

Morphology

We review the literature and present our observations on the taxa in the following groups, (1) those with **double walls + pseudosepta**, (2) those with **single walls + pseudosepta**, (3) those with **single walls but without pseudosepta**, (4) *Synedra bacillaris*, (5) *Toxarium*, and (6) *Climacosphenia*.

Group 1: Double-walled taxa with pseudosepta

Table 2

Table 2. Comparison of species of *Ardissonea* sensu stricto.

	Length μm	Width μm	Shape	Stria density in 10 μm	Valvocopula exterior pores	Copula exterior pores	Pleura
<i>A. robusta</i>	200–520	30–40	Broadly linear-lanceolate	7	Unknown	Unknown	Unknown
<i>A. formosa</i>	200–700	15–25	Linear	9–10	Absent	± irregular abvalvar row	Narrow, continuous, porate
<i>A. pulcherrima</i>	240–750	18–28	Linear, the cuneate poles somewhat inflated	9	Unknown	Unknown	Unknown
<i>A. densistriata</i> sp. nov.	46–103	7–10	Lanceolate	16–17	Absent	Single abvalvar row	Continuous, porate

Ardissonea formosa (Hantzsch) De Toni, 1892

Fig. 1

References. Peragallo and Peragallo 1897–1908, p. 310, pl. 78, fig. 6; Hustedt 1931–1959, p. 233, fig. 720; Sullivan and Wear 1995, p. 181, figs 1–8; Navarro 1982, p. 260, figs 61–63; Navarro and Lobban 2009, p. 136; Lobban et al. 2012, p. 259, pl. 15, figs 4, 5, pl. 16, figs 1, 2; Park et al. 2018, p. 105, fig. 5.

Description from literature. Hustedt (1931–1959) described this species as linear with ends somewhat narrowed, 200–700 μm long, 15–25 μm wide, 9–10 transapical costae in 10 μm, two rows of areolae between each costa; two or three longitudinal costae and an inner layer, dividing the wall into a series of chambers, each with a single foramen in the inner wall, resulting in three or four chambers. The series of foramina have been described as rows of “pearls,” parallel to the longitudinal lines of the annulus with its underlying costae and sometimes a central costa. Hustedt (1931–1959) specifically referred to a (3rd) longitudinal costa down the middle sometimes, and his fig. 720b shows two rows of foramina between the annular lines, suggesting a costa between them, as the chambers were supposed to have only a single opening. A similar situation is seen in Sullivan and Wear (1995: fig. 4). Hustedt (1931–1959) showed two rows of areolae between the transapical costae, but Sullivan and Wear (1995) reported only one and noted the discrepancy. With SEM they showed that the valvocopula had a prominent notch in the advalvar side and a fimbriate edge to the pars interior. They

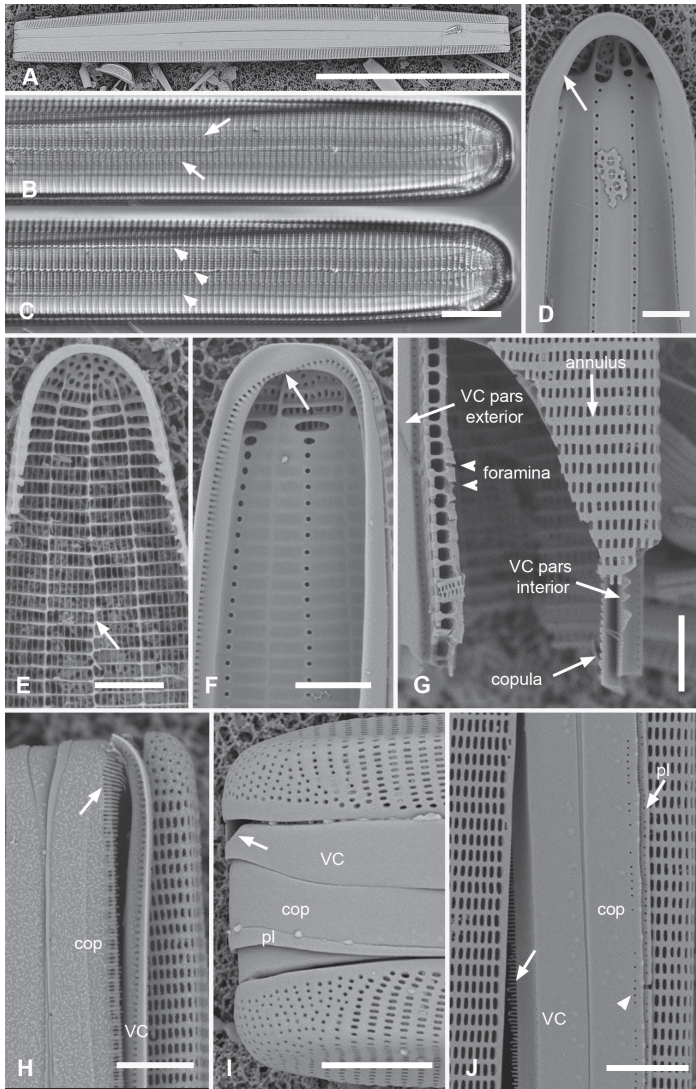


Figure 1. Micrographs of *Ardissonaea formosa* **A** whole frustule, length 380 μm , girdle view in SEM, showing isopolarity (Guam: GU44BH-5) **B, C** light micrographs at two focal planes, apical part of valve showing internal foramina (**B** arrows), annulus and central costa (**C** arrowheads) (Jaluit: J5) **D** SEM of internal aspect showing inner wall with foramina and narrow apical pseudoseptum (arrow) (GU44BJ-2) **E** internal aspect of valve pole with inner wall missing, showing a central longitudinal costa (arrow) (Yap: Y42-1) **F** internal view of pole of valve with valvocopula, showing double wall with one central line of foramina, transverse and longitudinal costae showing through the interior wall, and the pores of the valvocopula asymmetrically deflected around the notch (arrow) (Y42-1) **G** broken frustule showing details of wall structure—inner and outer layers separated by costae, inner layer with foramina—in relation to valvocopula and copula (GU44BJ-4) **H** pole of frustule showing long fimbriae at tip of copula (arrow) (GU75A-4) **I** detail of frustule pole in girdle view, showing the three girdle bands with no pores in the external surfaces and the groove in the valvocopula apex (arrow) (GU44BH-5) **J** details of mid portion of frustule in girdle view, showing a line of pores on the edge of the copula (arrowhead) and on the pleura, and the fimbriate inner edge of the valvocopula (arrow) (GU52R-2). Abbreviations used on figures: VC = valvocopula; cop = copula; pl = pleura. Scale bars: 100 μm (**A**); 10 μm (**B–C, I**); 5 μm (**D–H, J**).

noted that the areolae at the poles were smaller, circular, less dense and more loosely organized but not an apical pore field.

Materials examined. GUAM: GU44BH-5!, GU26A!, GU52R-2!. FEDERATED STATES OF MICRONESIA: Yap: Y39A!, Y42-1!. MARSHALL ISLANDS: Jaluit Atoll: J5!; Bakir Atoll: BA2!.

Observations. Valves linear with broadly rounded poles, 201–300 μm long, 22–24 μm wide, striae 8–10 in 10 μm , isopolar in both valve and girdle view (Fig. 1A). Plastids numerous, lenticular, displaying peristrophy and karyostrophy depending on light intensity (Suppl. material 3: Fig. S1). Three or five longitudinal lines seen in two focal planes (Fig. 1B, C): if five, the annulus, subtending a longitudinal costa, on the valve face (not hidden at the valve margin), a central line where the offset striae meet; between these, on the inner wall, two rows of foramina (Fig. 1B–D). If three lines, one central row of foramina with no longitudinal costa (Fig. 1F). Two additional rows of foramina along the angle of the valve–mantle junction seen in SEM but obscured in LM (Fig. 1D, F). The pattern of costae underlying the inner wall can be traced in Fig. 1D and seen directly in Fig. 1E. We have also seen specimens with one row of foramina along the midline (Fig. 1F). Commonly one or two longitudinal depressions in valve surface, giving a shallow *v* (Fig. 1I) or *w* profile. Striae comprising single row of oval areolae between each transapical costa (Fig. 1C, E, G); loose rows of smaller, circular areolae at the poles, especially noticeable on mantle (Fig. 1I). Narrow pseudoseptum around poles (Fig. 1D, E), elsewhere the double wall forms a thick rim (Fig. 1G). Three girdle bands as follows (Fig. 1F–J). Valvocopula with line of small pores along edge of pars interior, usually obscured in girdle view, deflecting asymmetrically inwards at pole (Fig. 1F), corresponding to location of the notch on advalvar side, which however, is nearly central (Fig. 1I). Interior edge of valvocopula with short fimbriae (Fig. 1G, J). Copula with long fringe of fimbriae at pole, overlapping the valvocopula (Fig. 1H), as described by Sullivan and Wear (1995); an irregular line of pores along abvalvar margin of copula in some specimens (Fig. 1J, arrowhead). Narrow pleura (Fig. 1I, J) with a row of small pores on pars interior.

Taxonomic comments. The biseriata striae described by Hustedt (1931–1959) and the uniseriate striae in Sullivan and Wear's (1995) materials suggest that they were observing different species. Sullivan and Wear (1995) observed only two bands on the epicingulum and none on the hypocingulum but we observed the pleura. *Ardissonea* s.s. superficially resembles *Synedra* in the current restricted sense (= *Catacombas*) in shape and double wall but differs in lacking rimoportulae and polar pore fields.

Ardissonea densistriata Lobban, sp. nov.

Fig. 2

Diagnosis. Differing from *A. formosa* in small, lanceolate valves with 16–17 striae in 10 μm and externally porate copula.

Description. Valves lanceolate, weakly rostrate, 46–103 μm long, 7–10 μm wide, striae parallel, 16–17 in 10 μm (Fig. 2A–C), meeting in an irregular sternum (Fig. 2B, C). Isopolar in both valve and girdle views (Fig. 2A–E). Areolae oval, apically elongate.

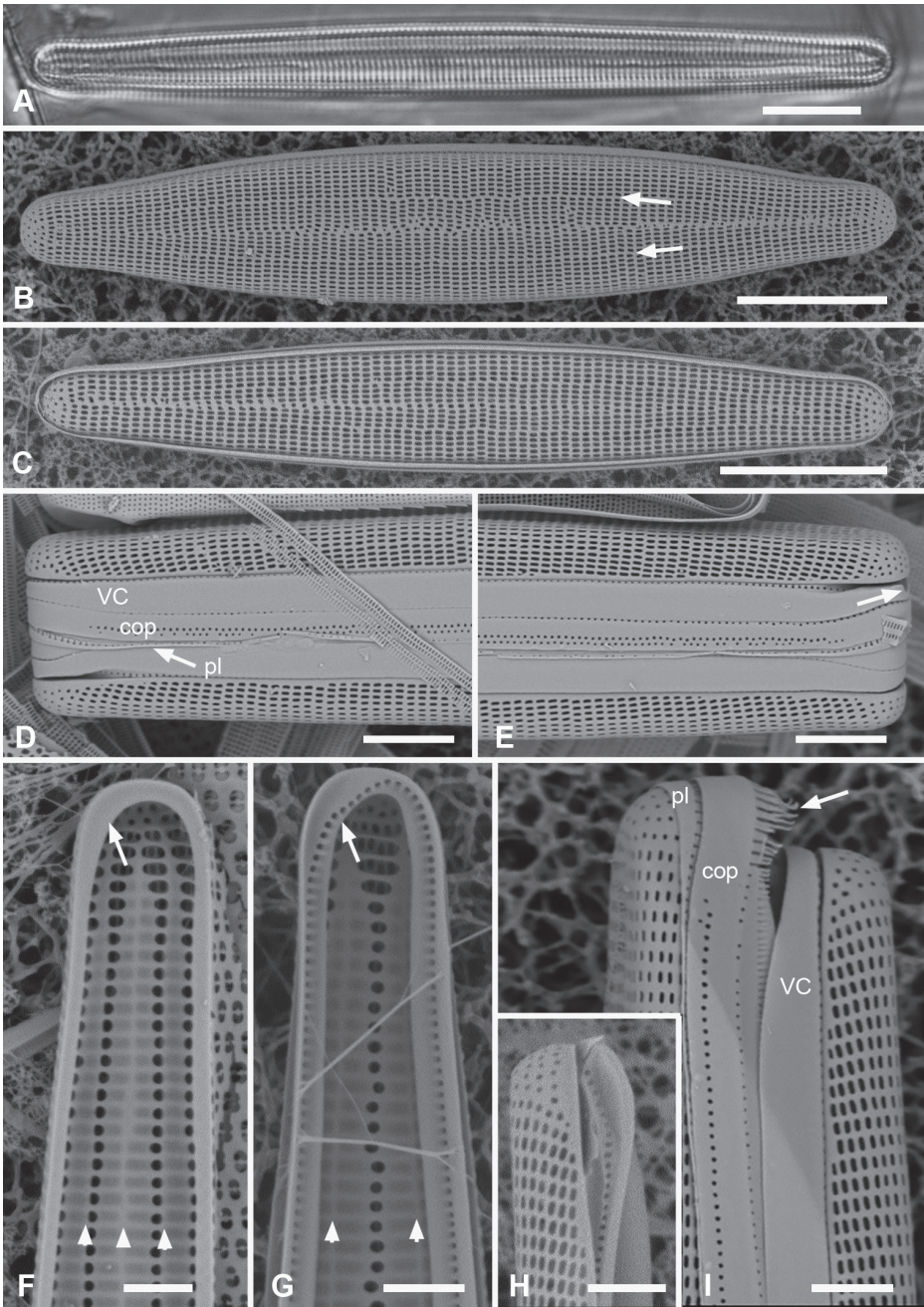


Figure 2. *Ardissonaea densistriata* sp. nov. **A** holotype from Bikar Atoll, BA1 (LM) **B, C** external views of valves in SEM; arrows on **B** point to location of annulus (**B** Y42-1, **C** BA-1) **D, E** external view of two ends of same frustule showing isopolarity; arrow on **E** points to apical notch in VC (J5) **F, G** internal views of valves with one and two middle lines of foramina, arrows showing asymmetrical pseudoseptum on valve in **F** and asymmetrical pole of the valvocopula in **G**; arrowheads point to longitudinal costae (BA1) **H, I** external views of frustules from Bikar and Jaluit, respectively, showing profile of pole of valvocopula in **H** and apical comb of fimbriae on copula in **I** (arrow). Scale bars: 10 µm (**A–C**); 5 µm (**D, E**); 2.5 µm (**F–I**).

Two or three longitudinal costae appearing through internal plate (Fig. 2F, G); correspondingly three or four rows of foramina are present. Fig. 2F suggests a costa under sternum. Valve with rim expanded into asymmetric pseudoseptum at poles (Fig. 2F). Girdle bands: Valvocopula pars interior at pole developed asymmetrically, matching the pseudoseptum and with deep notch in advalvar surface (Fig. 2G, arrow, 2H). One line of pores on pars interior, exterior plain (Fig. 2D, I). Copula (Fig. 2D, I) with 1–3 irregular rows of pores on the exterior, pars interior with a row of small pores partially exposed to exterior and a fimbriate inner edge, particularly well developed at poles (Fig. 2I). Pleura narrow with single row of pores, continuous along the cell length (Fig. 2D, E).

Holotype (designated here). Specimen at 16.6 mm E and 11.5 mm S of the mark on slide 2911, deposited at ANSP accession # ANSP-GC20089. Fig. 2A.

Registration. Phycobank <http://phycobank.org/103235>.

Type locality. MARSHALL ISLANDS: Bikar Atoll, 12.223°N, 170.096°E. Filamentous seaweed sample from shallow subtidal farmer fish territory in the lagoon, precise location not recorded. Collection number BA1, October 2019. Andrew McInnis leg.

Additional materials examined. FEDERATED STATES OF MICRONESIA: Yap: Y42-1!, Y42-3!.

Etymology. *Densus + striatus* (Latin) = densely striated, in comparison to congeners.

Taxonomic comments. Given the small number of double-walled *Ardissonea* species, this species is easily distinguished by the small size, lanceolate shape and relatively high stria density. It is more readily confused in our flora with *Grunowago pacifica* sp. nov. (see below), but in LM the latter can be distinguished by the lack of an inner wall (indicated by absence of foramina) and presence of a longitudinal costa along the midline, in SEM by the extensive poration on the copula. To date this species has not been observed in Guam samples. A different lanceolate, double-walled *Ardissonea* was observed in samples from Chuuk and Jaluit, with stria density 9–12 μm , length 116–211 μm , but we do not have complete information from either population. These samples are similar in shape and stria density to a Red Sea species '*Ardissonea AdnU041*' observed by Sabir et al. (unpublished: http://www.protistcentral.org/Taxa/get/taxa_id/586376 and Ashworth, personal communication). This unnamed species is 83–125 μm long and has no external poration on the girdle bands (as in *A. formosa*). The sequence data have been published as UTKSA0041, shown in our Fig. 33, sister to *A. formosa*.

Group 2: Single-walled taxa with pseudosepta

Table 3

Ardissonea crystallina (C. Agardh) Grunow, 1880

Fig. 3

References. Peragallo and Peragallo 1897–1908, p. 310, pl. 79, fig. 1; Hustedt 1931–1959, p. 232, fig. 719; Navarro 1982, p. 260, figs 59, 60; Poulin et al. 1986, figs 28–30; Poulin et al. 1987, p. 2689, figs 1–11; Pickett-Heaps et al. 1991, figs 9–19; Lobban et al. 2012, p. 259, pl. 15, figs 1–3; Davidovich et al. 2017, figs 1, 2.

Table 3. Comparison of species of *Synedrosphenia*†.

	Length µm	Greatest width µm	Shape	Stria density in 10 µm	Valvocopula exterior pores	Copula exterior pores	Pleura
<i>S. baculus</i>	200–1000	13–27	Linear	10.5	Unknown	Unknown	Unknown
<i>S. bikarensis</i> sp. nov.	214–277	12–14	Spathulate	21	3 rows reducing to 1; very coarse fimbriae	Irregular lines of slits (rimae)	Separate porate polar caps, apical larger
<i>S. crystallina</i>	200–700 [220–350]	8–20 [11–16]	Linear	11 [16–19]	2–3 rows [3–4 rows]	Ca. 5 rows [10 rows]	Probably continuous
<i>S. giennensis</i>	195	35	Clavate, widest ¼ from apical pole	12	Unknown	Unknown	Unknown
<i>S. gomphonema</i>	250–475	27–36	Clavate, substrate apical pole	12 basal / 14 apical [13–14/14– 16] †	4 rows decreasing to 2 near basal pole	Decussate striae, forming fimbriae on abvalvar margin	Apical cap
<i>S. fulgens</i> ‡	330–346	9.5–11.5	Linear, center slightly inflated	15–16	Numerous rows	Unknown	Unknown
<i>S. licmophoropsis</i> sp. nov.	600–735	27	Cuneate	19	5 rows reducing to 2	10 rows decreasing to 5	Narrow, continuous
<i>S. parva</i> sp. nov.	196–250	18	Clavate	16 basal, 18–20 apical	3 rows decreasing to 1	7 rows decreasing to 3	Polar caps porate; apical cap large, fimbriate
<i>S. recta</i> sp. nov.	406–430	13–16	Linear	16–18	None	Slits	Small polar caps joined by narrow perforated band, not fimbriate?

† Data for known species are from literature cited in text, data for Micronesian specimens given in brackets where different.

‡ data for type material from Kanjer et al. (2021).

Description from literature. Valves 200–700 µm long, 8–20 µm wide, linear but slightly wider at the middle and poles; 11 striae in 10 µm but much closer in “transitional forms such as var. *dalmatica*” (Hustedt 1931–1959). Internally with prominent costae developed on every virga except at poles, and with two longitudinal costae corresponding to location of annular ring; spines completely absent. Edge of valve recurved into a pseudoseptum; an interpretive diagram in Pickett-Heaps et al. (1991) shows the relationship between the valve, valvocopula, copula and a small, plain pleura at the pole. Valvocopula and copula have interior comb-like fringe, exterior part with four or more rows of pores arranged decussately; an apical groove between the pseudoseptum and a fold in the valvocopula provides an exit for attachment mucilage (Poulin et al. 1987; Pickett Heaps et al. 1991) but Pickett-Heaps et al. (1991) argued that this groove was a very different structure from the apical pore in *A. formosa* as shown by Round et al. (1990). Shorenko et al. (2016) obtained auxospores of this species and determined a maximum length of 678 µm.

Materials examined. GUAM: GU44Y-13!, GU44AV-8!, GU44BJ-4!, GU56A-2!. FEDERATED STATES OF MICRONESIA: Chuuk: TK4, TK28. MARSHALL ISLANDS: M1!

Observations. Specimens from Guam and Chuuk 220–350 µm long, 11–16 µm wide, isopolar in both valve and girdle views, striae 16–19 in 10 µm, slightly offset on internal and external sides of annulus (Fig. 3A, B). Annulus well separated from valve-margin junction and clearly visible in LM and SEM, including around the poles (Fig. 3A, B).

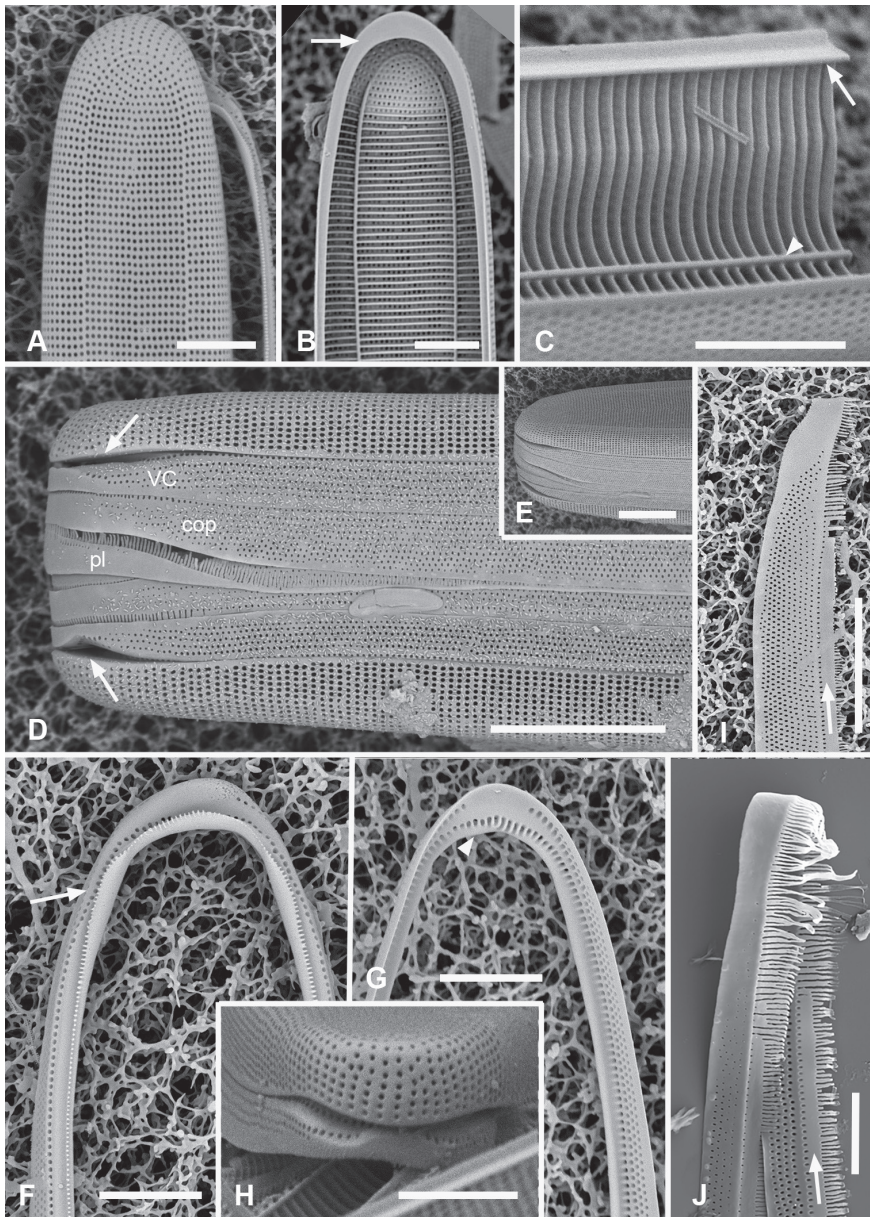


Figure 3. *Ardisonea crystallina* **A, B** external and internal views of valve poles from, respectively Majuro (M1) and Guam (GU44J-4), showing pseudoseptum (**B** arrow) **C** internal SEM view (60° tilt) of broken valve showing internal costae including longitudinal costa subtending the annulus (arrowhead) and continuous rim on valve (arrow) (Chuuk: TK4) **D, E** pole of frustule in girdle view and tilted to 45° to confirm identity; showing the asymmetrical gaps between the pseudoseptum and valvocupula (arrows) (GU75A-4) **F, G** polar portions of valvocupulae from advalvar side and abvalvar sides, respectively, arrow on **F** showing where pores along edge of pars interior move to the back of the gap, arrowhead on **G** showing that slits do not form an open comb (Chuuk: TK4) **H** polar view of pole with valvocupula showing the asymmetrical gaps (TK4) **I, J** poles of copulae from wild material (TK4) and culture (GU44AV-8), respectively, arrows indicating fused bases of fimbriae away from the pole. Scale bars: 10 μm (**D, E, I**); 5 μm (**A–C, F–H, J**).

Pseudoseptum at poles (Fig. 3B) and rim along entire valve (Fig. 3C), facing pars interior of the valvocopula. Apical spines not observed (Fig. 3A, D, H). Costae well developed (Fig. 3B, C). Three girdle bands present (Fig. 3D): valvocopula fimbriate (Fig. 3D, F–H), forming a slot on one side of the pole and a sharper notch on the other (Fig. 3D arrows, Fig. 3H); pores on pars interior passing across back of flange, elongated into slits at pole, clearly closed at inner margin (Fig. 3G arrow) and pars interior expanded and recurved at pole (Fig. 3F). Pores on pars exterior discontinuous around pole in front of the groove (Fig. 3F–H). Copula (Fig. 3D, I, J) broader and flat, even at pole, with up to 10 rows of circular pores in a decussate pattern; pars interior fimbriate with free fimbriae highly developed at pole, where they overlap the valvocopula, elsewhere shorter fimbriae arising from fused base (arrows, Fig. 3I, J). Small difference in shape, number of rows of pores and length of fimbriae between Fig. 3I and J may be due to origin of material (Fig. 3D and 3I are from Chuuk wild samples, Fig. 3J from Guam culture) but copulae from wild material from Guam (not shown) also had >6 rows of pores. Pleura (Fig. 3D) fimbriate, an apical cap extending along the valve as a very narrow ribbon.

Taxonomic comments. *Ardissonaea crystallina* cannot remain in *Ardissonaea* sensu stricto and will be transferred in the Taxonomic Revisions section at the end of the paper. Álvarez-Blanco and Blanco (2014) show Mediterranean specimens of *Ardissonaea dalmatica* (Kützinger) De Toni, restored to species status without comment, but the length ranges only up to 151 µm. There was a row of papillae/spines around the pole, not present in our material and the length range in the literature is 100–151 µm, but the stria density matches our specimens more closely. We leave our identification at *A. crystallina* pending broader study. Although Hustedt (1931–1959) noted *A. crystallina* as distributed on coasts of warmer waters, Poulin et al. (1987) reported it as the only *Ardissonaea* on the coast of Québec, an area that is far from tropical. Likewise, Shorenko et al. (2016) and Davidovich et al. (2017) collected it from the Black Sea. We do not agree with Pickett-Heaps et al. (1991) that there is a fundamental difference in the architecture at the pole of the valvocopulae of *A. formosa* and *A. crystallina* as both involve irregularities in the surface of the flange of the valvocopula where it lies below the pseudoseptum.

***Synedrosphenia gomphonema* (Janisch & Rabenhorst) Hustedt, 1932 in Hustedt, 1931–1959**

Figs 4, 5

References. Janisch and Rabenhorst 1863, p. 13, pl. 2, fig. 6; Grunow 1877, p. 169, pl. 194, fig. 3a, b, c, d; Peragallo and Peragallo 1897–1908, p. 313, pl. 78, figs 1, 2 (as *S. cuneata* Grunow); Hustedt 1914 in Schmidt et al. (1874–1959), pl. 305, figs 32, 33; Hustedt 1931–1959, p. 231, fig. 723; Cheng and Gao 2011, figs 147, 148; Hein et al. 2008, pl. 14, fig. 3, pl. 15, fig. 1; Hernández-Almeida et al. 2013, figs 39–42 (as *Synedrosphenia cuneata*).

Description from literature. The valve shape as shown by both Grunow (1877) and Hustedt (1914, 1931–1959) has a basal part with nearly parallel sides that then tapers wider, flaring more abruptly near the apical pole. Hustedt gave length as 250–475 µm, maximum width 27–36 µm, basal and apical stria densities 12 and 14 in

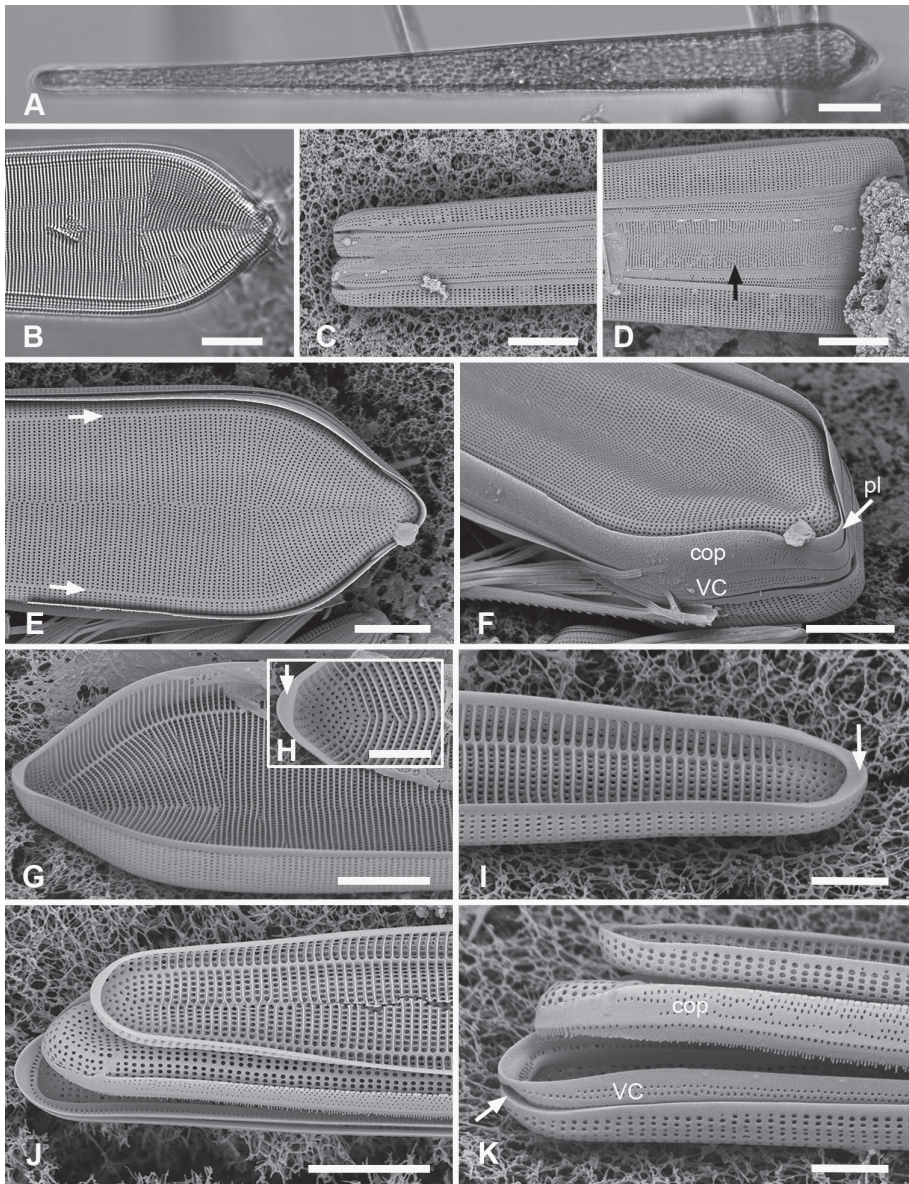


Figure 4. *Synedrosphenia gomphonema* **A** live specimen in valve view showing heteropolar cell shape and plastids (GU44BJ-4) **B** apical portion of cleaned valve in LM showing change in stria orientation where cell narrows (GU44BD-4) **C, D** recently divided frustule in girdle view with details of basal and apical poles, respectively, showing heteropolarity; black arrow indicates slit formation on the copula (GU44BJ-4) **E, F** valvar view of frustule at 0° and 60° tilt, respectively, arrows on **E** showing location of annulus, labels on **F** naming the girdle bands (abbreviations as before) **G–I** apical and basal portions of valve, internal view tilted 60°, showing pseudosepta at poles (**H, I** arrows) and transverse and longitudinal costae (TK4); inset (**H**) shows tip of same valve at 0° tilt with lack of costae between the last few striae but continuation of annulus **J, K** basal portions of a broken, recently divided frustule from Chuuk, viewed at 0° and 60° tilt, respectively, valves and girdle bands of one daughter cell with one valve of other daughter on top; arrow shows the notch between valve and valvocopula (TK4). Scale bars: 25 μm (**A**); 10 μm (**B–G, I**); 5 μm (**H, J**).

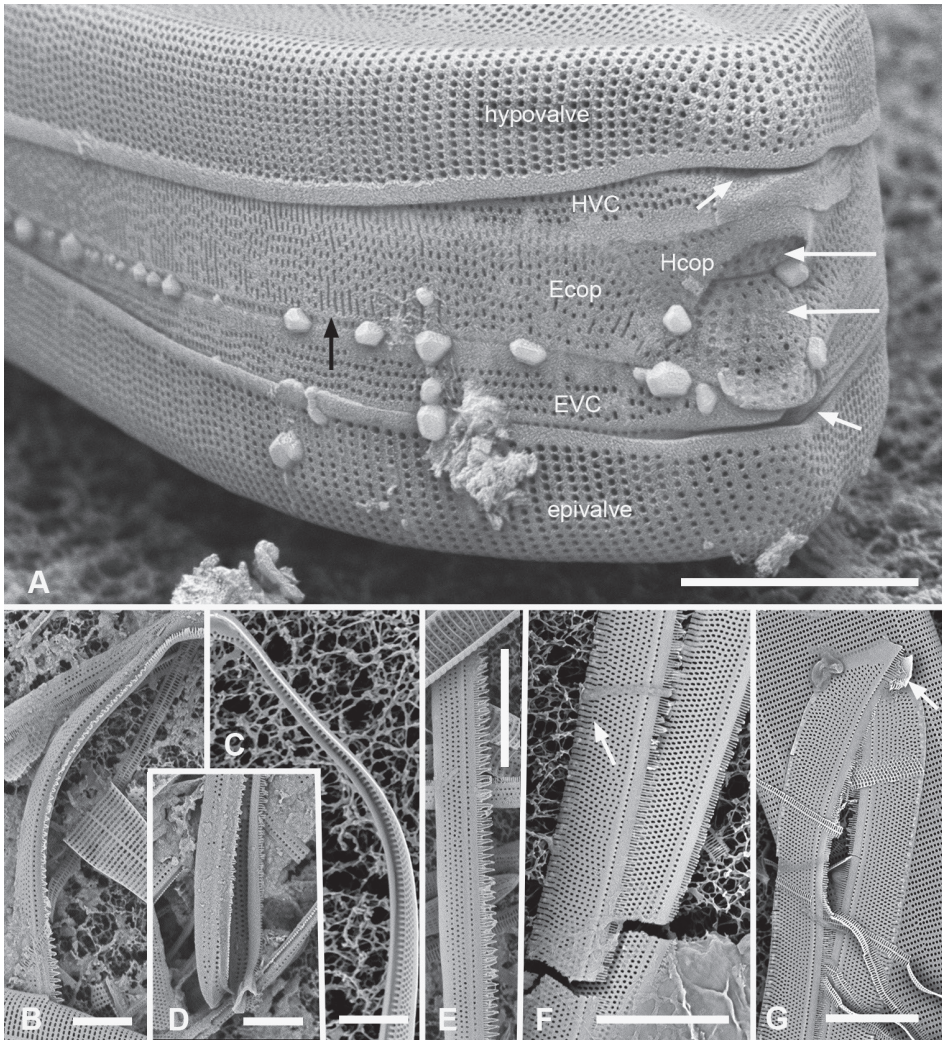


Figure 5. *Synedrosphenia gomphonema* cont. **A** apical pole of frustule in polar view tilted 60°, showing the valvocopula and copula of the hypocingulum (HVC and Hcop) largely hidden under the epicingulum bands (EVC and Ecop); the pleurae are missing and in the space where they were the tips of the newly formed valves are visible (long arrows). Short white arrows point to the apical notches slightly off-center in opposite directions; black arrow shows some slit formation in the copula (GU44BJ-4) **B–E** valvocopula with apical pole in advalvar view (**B**) showing recurved pars interior at the tip, abvalvar view (**C**), basal pole (**D**) and middle (**E**), all showing fimbriae (**B, D, E** from same specimen in GU44BI-4, **C** from TK4) **F, G** copula middle and apical pole, respectively, external view, showing fimbriae developing on the abvalvar edge of the pars exterior (arrow) (TK4). Scale bars: 10 μm (**A, E, F, G**); 5 μm (**B–D**).

10 μm , respectively. Striae change abruptly from parallel to radiate where the apical pole narrows. Transapical costae on the virgae often continuous across the valve and obscuring the midline; a longitudinal rib near each margin. Round et al. (1990: 444) noted that in *Synedrosphenia* stria density is higher on the girdle bands than on the

valve (Fig. 10A), whereas in *Climacosphenia* it is lower on the girdle bands (Fig. 28A). This holds true for all our species.

Materials examined. GUAM GU44Y-13!, GU44BD-4!, GU44BH-5!, GU 44BJ-2!, GU44BJ-4!. FEDERATED STATES OF MICRONESIA: Chuuk: TK28!; Yap: Y42-1!. MARSHALL ISLANDS: Jaluit, J5!.

Observations. Frustules heteropolar, cuneate in both valve and girdle view, numerous small, oblong plastids (Fig. 4A–D). Valve margins parallel near basal pole, then gradually widening with slight flare below subrostrate apical pole (Fig. 4E, F). Length 255–>414 μm , greatest width 27–29 μm , stria densities in 10 μm 13–14 basal, 14–16 apical. Striae parallel except changing abruptly to radial at apical pole with several interpolated short striae (Fig. 4B, E, G); areolae circular. Annulus near valve–mantle junction but clearly visible in both LM and SEM (Fig. 4B, E–I), continuous around the poles (Fig. 4E, H, J). Internal costae underlie annulus and virgae, except at the poles. Three girdle bands present (Figs 4F, 5A). Valvocopula (Figs 4J, K, 5B–E) with about 4 longitudinal rows of pores on pars exterior, decreasing to two near basal pole, pars interior with a fimbriate margin comprising a shelf with a single row of pores and a groove; poles with asymmetrical notch (Figs 4C, K, 5A). Copula (Figs 4J, K, 5A, F, G) pars interior with longitudinal line of pores along edge, the rest of pars interior plain with fringe of fimbriae, longer around apical and basal poles (Figs 4K, 5G). Copula pars exterior abruptly narrowed at apical pole, pores arranged in \pm decussate striae across the band reaching abvalvar margin and forming fimbriae; no pores around poles. Copulae in Guam specimens tending to form slits (Fig. 4D and Fig. 5A black arrows), not observed in Chuuk specimens (Fig. 5F, G). Pleura visible as apical cap (Fig. 4F), seemingly lost during cell division (Fig. 5A; compare Fig. 12E, F).

A frustule of *Sceptroneis cuneata* in remnants of Grunow 639 (Fig. 6), showed the valve and copula. Valve stria densities were lower than in our material: basal 12, apical 13 in 10 μm . The copula differed in having a hyaline abvalvar border with no tendency to form fimbriae (Fig. 6D, E) and a longer hyaline area at the basal pole (Fig. 6E vs Fig. 4F). The apical cap of the pleura may be smaller than in our specimens. A valve apical pole with part of the valvocopula (Fig. 6F, G) had 11 striae in 10 μm and there were no pores in the exterior, in contrast to Guam specimens.

Taxonomic comments. There are too many differences from Grunow's specimens to identify our species as *Sceptroneis cuneata*. We also cannot confirm whether our specimens match *Synedrosphenia gomphonema* without SEM of authentic specimens. The taxonomy of *Synedrosphenia* is convoluted. As explained by Fourtanier and Kociolek (1999):

“Originally described (and validly published) as a subgenus of Synedra: Synedra subgenus Synedrosphenia H. Peragallo in H. and M. Peragallo 1900 [Peragallo and Peragallo 1897–1908], p. 308, 312. Three species were included, Sceptroneis [Synedra] cuneata Grun., S. clavata Grev. and S. dubia Grun. and no type was designated. Although Azpeitia 1911, p. 220 introduces the name as “El genero ó subgenero Synedrosphenia” (the genus or subgenus Synedrosphenia), he treats it as a genus when describing his new species Synedrosphenia giennensis. Although S. giennensis Azpeitia is the only species formed as binomial with Synedrosphenia in Azpeitia 1911, Azpeitia, in his treatment of Synedrosphenia also clearly included the 3 species that constituted Peragallo's subgenus

(but did not make transfers to genus *Synedrosphenia*). No type was designated by Azpeitia. The generic name cannot be attributed directly to Azpeitia because he did not provide a generic description. The authorship of *Synedrosphenia* is therefore "(H. Peragallo in H. Perag. and M. Perag.) Azpeitia," and the type has to be chosen among the species originally included in the subgenus by Peragallo. The choice of *S. giennensis* as the type species by Round, Crawford and Mann (1990) p. 444 and 704 is therefore untenable."

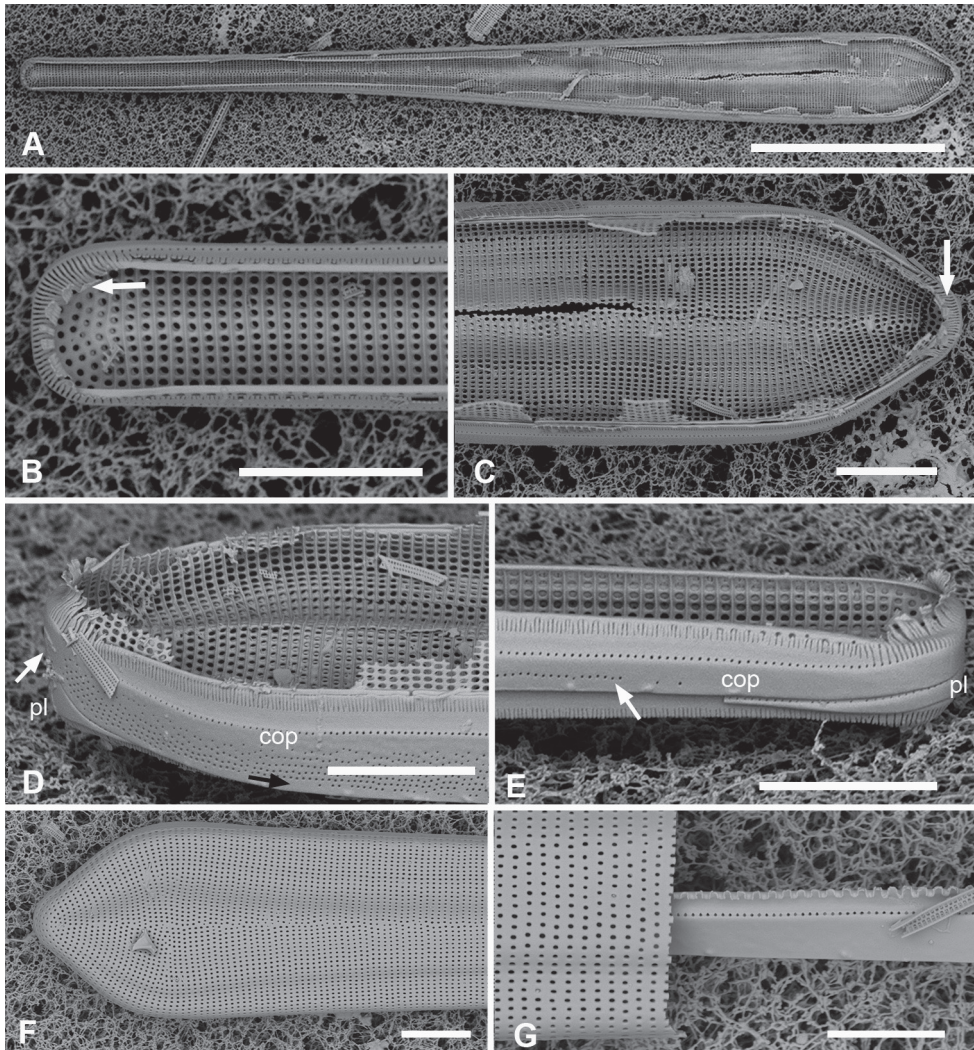


Figure 6. Specimens of *Sceptraoneis cuneata* from Grunow's Honduras sample **A–C** whole frustule at 0° tilt and details of basal pole and apical poles, respectively, showing internal costae and the copula; arrows point to long fimbriae overlapping valvocopula at both poles **D, E** same specimen, tilt = 60°, details of apical and basal poles, respectively, showing copula, including shallow cut-away matching smaller pleura (arrow on **D**), hyaline abvalvar margin of copula (black arrow on **D**), and reduced poration near basal pole (arrow on **E**) **F** apical part of valve in external view **G** valvocopula associated with same specimen. Scale bars: 50 μ m (**A**); 10 μ m (**B–F**); 5 μ m (**G**).

Hustedt (1931–1959) very clearly synonymized *Sceptroneis cuneata* into *Synedrosphenia gomphonema* (1931–1959, fig. 723, pp. 220–221 in Jensen's (1985) translation, pp. 241–242 in orig.). The drawing in Janisch and Rabenhorst (1863) is, as Hustedt (1931–1959) said, “very schematic and erroneous to be sure,” showing a prominent sternum, but Hustedt based his synonymy on examination of many specimens from both Janisch and Grunow, both of whom worked on collections from Honduras. The other two species, *S. clavata* and *S. dubia*, are poorly known, perhaps not seen since their original descriptions, both characterized as very rare, and perhaps not even attributable to this genus. We thus propose *Sceptroneis cuneata* Grunow as the lectotype, below, recognizing the synonymy with *S. gomphonema* as the current name for the Honduras species, but pending evidence from Janisch and Rabenhorst's materials to test whether our species is the same. *Synedrosphenia giennensis* Azpeitia (1911, p. 219, pl. 6, figs 1, 2) was based on LM of a single clavate valve, maximum width $\frac{1}{4}$ of the way from one end, costae between striae not always continuous across the valve. Azpeitia made no mention of longitudinal costae. The dimensions were $195 \times 35 \mu\text{m}$, 12 striae in $10 \mu\text{m}$, areolae 19–20 in $10 \mu\text{m}$. This does appear to belong in *Synedrosphenia* but certainly needs further study.

***Synedrosphenia bikarensis* Lobban, sp. nov.**

Figs 7, 8

Diagnosis. Valve spatulate, heteropolar, differing from *S. parva* and *S. gomphonema* in valve shape and in the fimbriate pars exterior of the copula.

Description. Cells heteropolar, probably attached by basal pole to seaweeds. Valves spatulate, $214\text{--}277 \mu\text{m}$ long with linear, wider apical portion $12\text{--}14 \mu\text{m}$ wide, narrowing abruptly about halfway down the valve and then more gradually to $6 \mu\text{m}$ near the basal pole, which is weakly inflated to $7 \mu\text{m}$ (Fig. 7A–C). Both poles bluntly rounded. Striae parallel except weakly radiating at apical pole, 21 in $10 \mu\text{m}$; areolae circular, 25 in $10 \mu\text{m}$ (Fig. 7D–F). Internally costae on all virgae except at poles (Figs 7G, 8D, E). Bifacial annulus indicated only by an offset between striae on valve face and mantle (Fig. 7D, oval). There was a junction down the midline of the valve where the inward-growing striae met but no sternum (Fig. 7B–E).

Girdle bands: Cingulum comprising two large, closed bands and a large apical cap (pleura) (Figs 7I, J, 8). Valvocopula porate (Figs 7I, J, 8A–E); the pars interior forming a sturdy comb (Fig. 8A–C) that matched up with the internal costae of the valve (Fig. 8D), though it was not clear whether they aligned or interdigitated with the costae. This was followed by an internal ridge and an adjacent series of pores, often hidden under the valve (Figs 7I, J, 8B, C). The pars interior was modified asymmetrically at each pole (Fig. 8D, E), with a shelf supporting a prominent asymmetrical notch (Fig. 7I, J and Fig. 8A, C). Apical and basal asymmetries were on opposite sides of the valvocopula (Fig. 8D, E, arrows) and the symmetry on the hypotheca was the mirror image of the epitheca (Fig. 7I, J, arrows). Pars exterior with three irregular rows of pores, 30 in $10 \mu\text{m}$, reducing to two and then one at the basal pole. The copula also

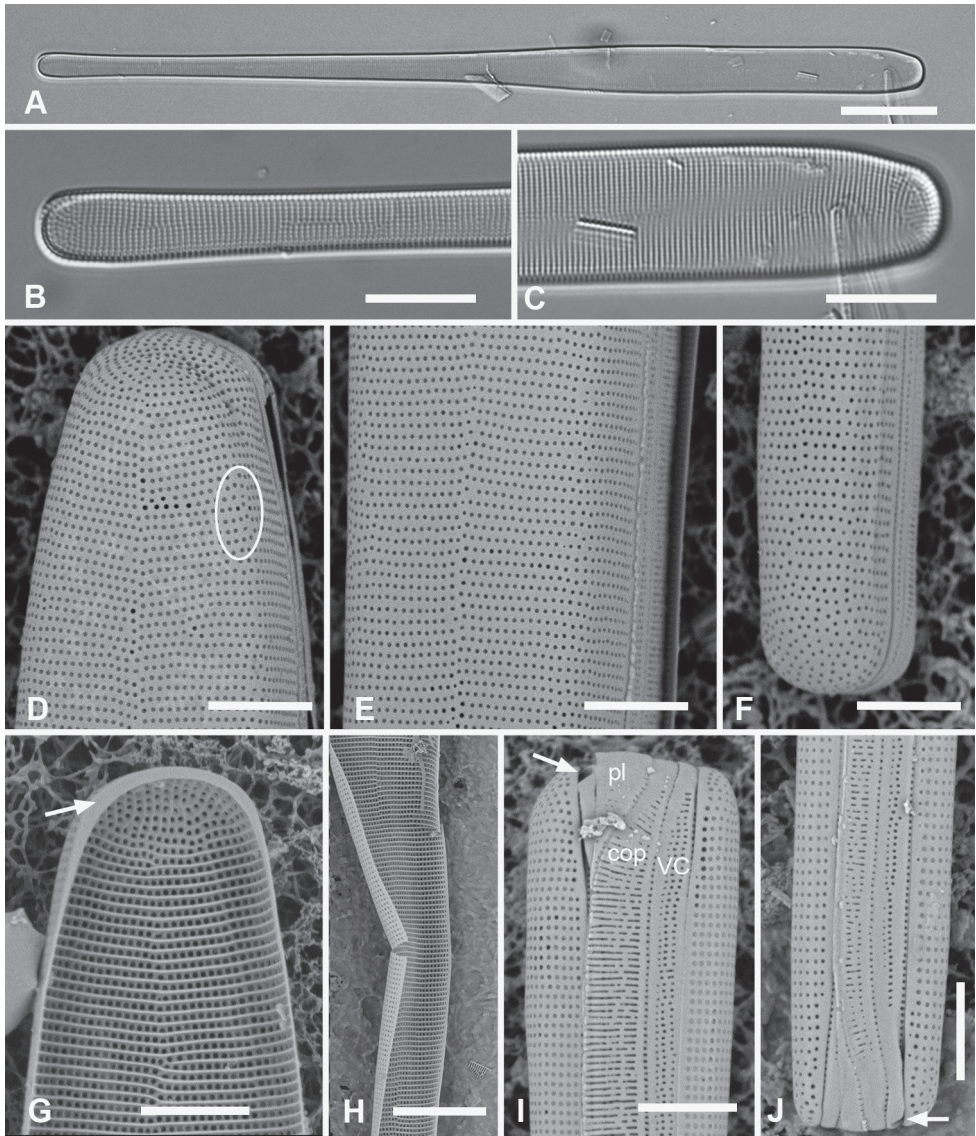


Figure 7. *Synedrosphenia bikarensis* sp. nov. (all from Bikar sample BA5) **A–C** holotype whole valve, basal and apical portions, respectively (LM) **D–F** external SEM views of apical, middle and basal portions, respectively, of a frustule, showing valve structure. Oval in **D** highlights area where break in striae across the annulus can be seen, even though the annulus is not readily visible **G, H** internal views of apical pole with pseudoseptum (arrow) and middle portion (**H**) showing transverse costae and the lack of a longitudinal costa under the annulus **I, J** frustule in girdle view, apical and basal portions, respectively, showing heteropolarity and girdle bands of the epicingulum. Arrows mark the notches visible on the hypovalvocopula at the apical pole and epivalvocopula at the basal pole, indicating the asymmetry. Scale bars: 25 µm (**A**); 10 µm (**B, C, H**); 5 µm (**D–G, I, J**).

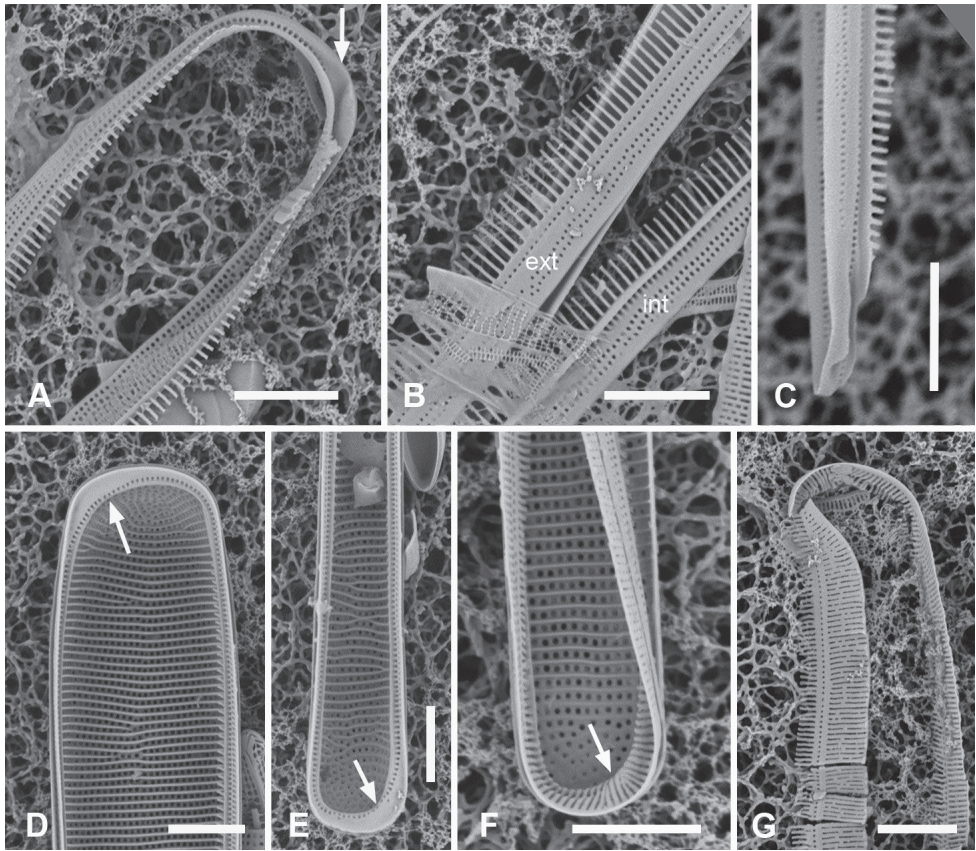


Figure 8. *Synedrosphenia bikarensis*, cont. **A–C** valvocopula: apical portion in advalvar view (**A**) with asymmetrical notch at apical pole (arrow), middle portion (**B**) with long sturdy fimbriae (ext = external surface, int = internal surface), and basal portion in girdle view (**C**) **D, E** internal views of apical and basal poles, respectively, of same valve with valvocopula, showing opposite asymmetry of the notches (arrows) **F** basal portion of valve with attached girdle bands, showing how the copula fimbriae fit over the valvocopula at poles (arrow) **G** apical portion of copula showing poration. Scale bars: 5 µm.

had a comb along inner edge of pars interior and a row of pores just under the overlapping valvocopula (Fig. 8F, G). Copula internal comb continued around the apical pole; pars exterior dominated by a series of long slits (rimae) that often extended to abvalvar margin (Figs 7I, J, 8G), resulting in a fringe along the edge of the cingulum except at poles. Both valvocopula and copula narrowed at the poles, leaving a space filled by the pleura, which is possibly a continuous band (Fig. 7I, J). We did not see the pars interior of the pleura but it is likely to be fimbriate (see *S. parva* below).

Holotype (designated here). Specimen at 14.9 mm E and 9.6 mm S of the mark on slide 2920, deposited at ANSP, accession # ANSP-GC20090. Fig. 7A–C.

Registration. Phycobank <http://phycobank.org/103236>.

Type locality. Bikar Atoll, Marshall Islands, 12.223°N, 170.096°E, on seaweed filaments attached to coral from a farmer fish territory in the lagoon. Collection number BA-5, October 2019. Andrew McInnis leg.

Etymology. Named for Bikar Atoll, Republic of the Marshall Islands, where it was collected.

Taxonomic comments. The apparent absence of a bifacial annulus is unique among the *Synedrosphenia* species described here, where there is usually at least a hyaline line visible on the valve face or at the face-mantle margin. There is, however, a misalignment of striae evident in places along the valve–mantle junction (Fig. 7D, E), as observed in the other bifacial-annulus taxa described here, and hence no reason to suppose the growth of the valve proceeds differently. We hypothesize that there is an effective annulus present.

***Synedrosphenia licmophoropsis* Lobban, sp. nov.**

Figs 9, 10

Diagnosis. Extremely long heteropolar cells, differing from other species in the cuneate shape in valve and girdle views.

Description. Frustules heteropolar, tapering uniformly in both valve and girdle view (Figs 9D, 10A, B), attached to seaweed substrata by mucilage stalks; plastids numerous, lenticular to oval (Fig. 9A, B). Valve margins parallel near basal pole, 14 μm wide, widening evenly to 27 μm wide just before the cuneate obtuse or slightly rostrate apical pole, length 600–735 μm (Fig. 9A–D). Striae parallel except radiate near apical pole, 19 in 10 μm near the apical pole, 16–17 near the basal pole (Fig. 9E–H). Annulus, evident even in living specimens (Fig. 9A), nearly halfway between centerline and valve margin (Fig. 9B–H), underlain by a longitudinal costa except at apical pole (Fig. 9G, H). Valve border with a rim along its length and shallow pseudosepta at each pole (Fig. 9G, H), the latter matched by extensive development of the valvocopula. In girdle view, three bands evident, all fimbriate (Fig. 10A–C, F). Valvocopula bearing a row of pores at the edge of the pars interior and five rows of pores on the exterior near the apical pole, reduced to two near the basal pole, the pores in a decussate pattern, 27 in 10 μm , the edge of the pars interior bearing short fimbriae near the apical pole, longer elsewhere (Fig. 10D–F). The pars interior of the valvocopula at the poles formed a deep shelf with an irregular surface (Fig. 10D, E), creating a notch on one side and a shallower, longer gap on the other (Fig. 10A, B); notches were on opposite sides of both the valvocopula itself and when comparing epitheca and hypotheca (Fig. 10A, B arrows). The line of pores along the edge of pars exterior moved to inner edge of the gap and became slitlike (Fig. 10G, arrow). Copula (Fig. 10A, B, F, H) wider, again with pores in a decussate pattern, about 10 rows near apical pole diminishing to five at the basal pole, a wide delicate fringe along the edge of the pars interior. The relationship between the first two girdle bands at the poles is shown in Fig. 10I. The pleura (Fig. 10A–C) had a broad apical cap, quickly tapering to a narrow external line with fimbriate pars interior, broadening again somewhat at the basal pole; this band lacked pores.

Holotype (designated here). Specimen at 13.0 mm E and 5.0 mm S of the mark on slide 455, deposited at ANSP accession # ANSP-GC20086. Fig. 9B–D.

Registration. Phycobank <http://phycobank.org/103237>.

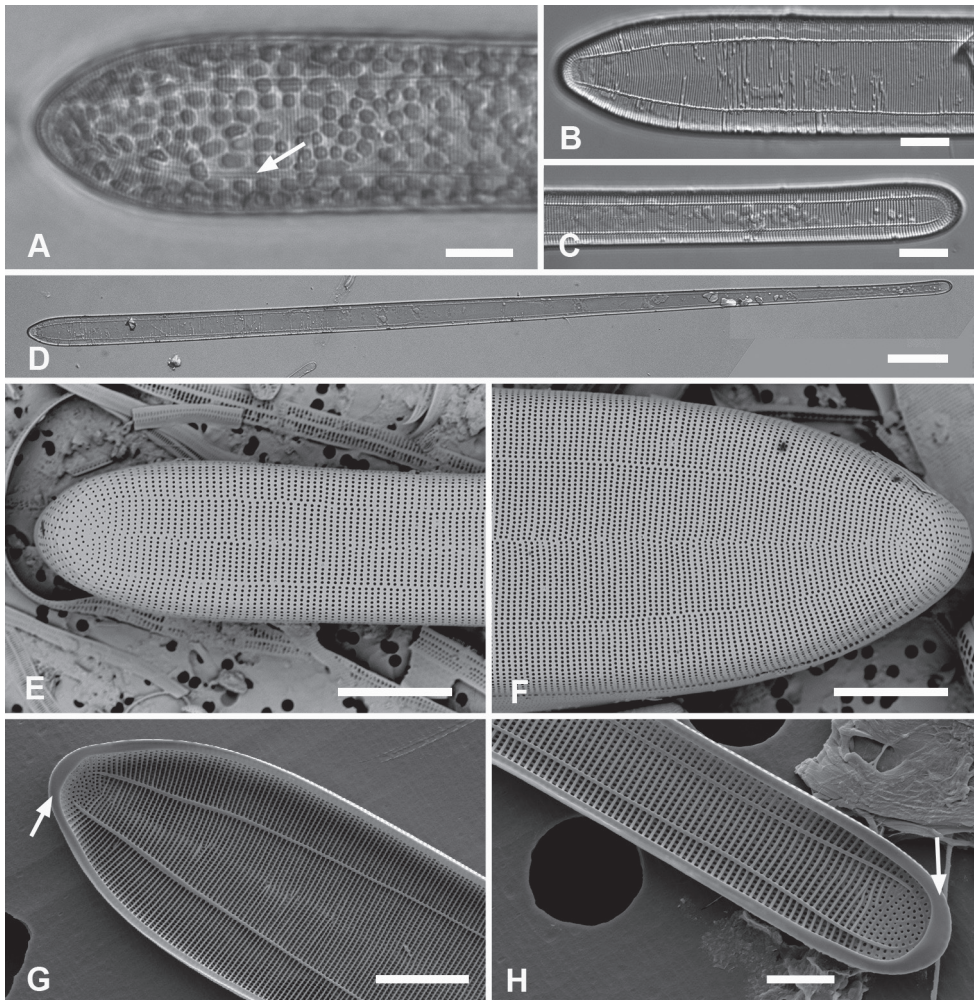


Figure 9. *Synedrosphenia licmophoropsis* sp. nov. **A** apical pole of living cell showing plastids and annulus (arrow) (GU44AV-8) **B–D** holotype valve from GU55B-4 in LM: apical and basal portions showing annulus and entire valve **E, F** external view of valve, SEM: basal and apical poles, respectively, same scale (GU44Y-13) **G, H** apical and basal poles, respectively, valve in internal view, SEM, showing longitudinal and transverse costae and pseudosepta (arrows) (GU56A-2). Scale bars: 50 µm (**D**); 10 µm (**A–C, E–G**); 5 µm (**H**).

Type locality. “Pete’s Reef” (commercial dive site), Agat Bay, 13.347°N, 144.639°E. Epiphytic on *Halimeda* at 10 m, collection number GU55B-4, 13 Dec. 2008. C. Lobban and M. Schefter, leg.

Additional materials examined. GUAM: GU44Y-13!, GU44AV-8!, GU54A-B!, GU56A-2!, GU66B-6!, GU76B-2. FEDERATED STATES OF MICRONESIA: Yap: Y-37-8!; MARSHALL ISLANDS: Bikar Atoll BA-5!.

Etymology. Named for its resemblance to certain large *Licmophora* spp., especially *L. attenuata* Lobban, Tharngan and Ashworth.

Taxonomic comments. Longer and more evenly tapered, apical pole broadly rounded, striae denser compared to *S. gomphonema*; valves appearing narrower than *S. gomphonema* because of the greater length, but the apical poles are equally wide.

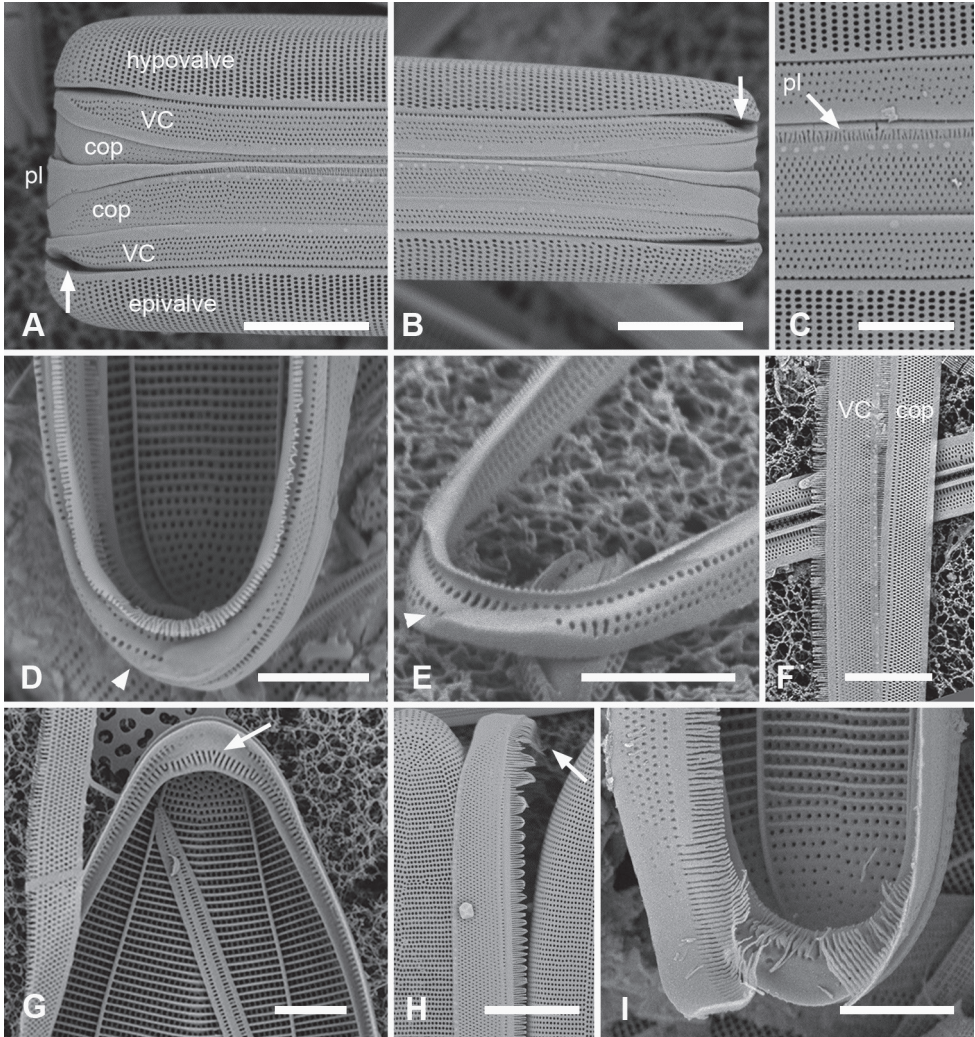


Figure 10. *Synedrosphenia licmophoropsis* sp. nov., girdle bands **A, B** frustule in girdle view with thecal elements labeled, respectively on the apical part and the basal pole of the same cell also showing the asymmetrical apical notches in the valvocupula (arrows) (GU55D-3) **C** small portion near middle of frustule where pleura (pl) is exposed (GU76B-2) **D, E** basal pole of valvocupulae at 0° tilt with opposite valve in the background and tilted to show complex shape of the pars interior, arrowhead pointing toward notch (GU76B-2 and TK4, respectively) **F** portions of valvocupula and copula showing fimbriate inner edges (GU55D-3) **G** valvocupula, apical pole in abvalvar aspect with attached valve, showing elongated pores on inner edge (arrow) (GU44BJ-2) **H** apical portion of copula showing very long fimbriae at the tip (arrow) (GU55D-3) **I** relationship between first two girdle bands at basal pole, the long fimbriae of the copula overlapping the valvocupula (GU76B-2). Scale bars: 10 µm (**A, B, F, H**); 5 µm (**C-E, G, I**).

***Synedrosphenia parva* Lobban, sp. nov.**

Figs 11, 12

Diagnosis. Shorter and narrower than *S. gomphonema* and more finely striated. Girdle bands distinctive: copula with very long internal fimbriae at poles, pleura a large apical cap.

Description. Frustules heteropolar in valve and girdle views (Fig. 11A, F, G) with numerous small plastids (not shown). Valves 196–250 μm long, 18 μm wide near the apical pole, clavate with acutely rounded to weakly rostrate apical poles (Fig. 11A–E). The annulus evident in LM but close to edge of valve face (Fig. 11A, C). Valve surface with weak longitudinal furrows, mantle deeper toward apical pole (ca. 11 vs. 5 areolae

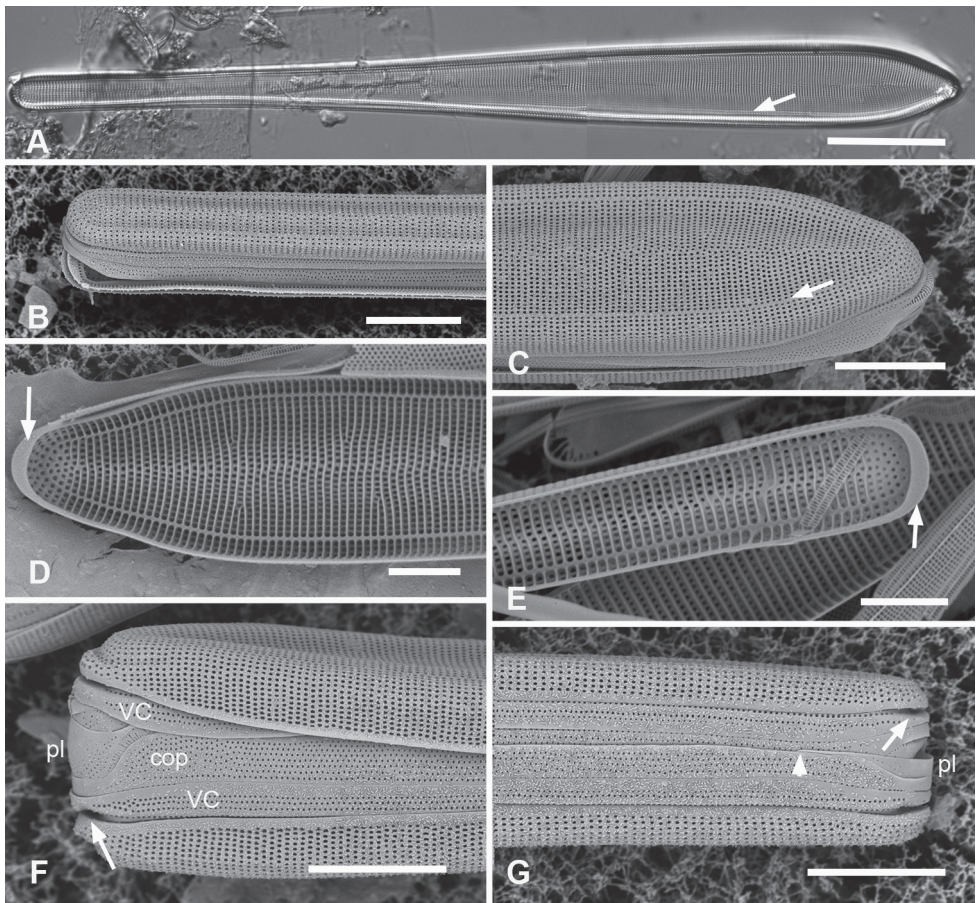


Figure 11. *Synedrosphenia parva* sp. nov. **A** holotype from Guam in LM, arrow indicates annulus near valve face–mantle junction (GU75A-4) **B, C** valve in external view (SEM), basal and apical poles, respectively, arrow indicates annulus (GU75A-4) **D, E** internal views of apical and basal poles, respectively, arrows indicate pseudoseptum (J5) **F, G** frustule in girdle view, apical and basal portions, respectively, showing the girdle bands including the large apical cap of the pleura, smaller at the basal pole and perhaps not connected (arrowhead in **G** indicates the apparent end of the pleura); arrows on **F, G** point to polar notches (GU75A-4). Scale bars: 25 μm (**A**); 10 μm (**B, C, F, G**); 5 μm (**D, E**).

deep) (Fig. 11 B, C, F, G). Striae 16 in 10 μm near basal pole, 18–20 in 10 μm near apical pole, parallel except radiate at apical pole (Fig. 11A–E). Pseudosepta present at both poles (Fig. 11D, E); longitudinal costae subtending annulus and transverse costae on vimenes except at apical pole (Fig. 11D, E). Three girdle bands are present (Figs 11F, G, 12E–G). Valvocopula with a row of pores along outer edge of pars interior plus three rows decreasing to one on pars exterior; pars interior with a notched flange at each pole and a fimbriate edge (Fig. 12B). Copula with up to nine rows of pores at apical pole in decussate pattern, decreasing to three near basal pole (Figs 11F, G, 12C, D). Pleurae a pair of polar caps (connecting band not seen), the apical cap relatively massive with small pores and fimbriate (Figs 11F, 12E–G), basal cap smaller, with fewer pores (Fig. 11G arrowhead).

Holotype (designated here). Specimen at 15.3 mm E and 12.7 mm S of the mark on slide 2326, deposited at ANSP accession # ANSP-GC20088. Fig. 11A.

Registration. Phycobank <http://phycobank.org/103238>.

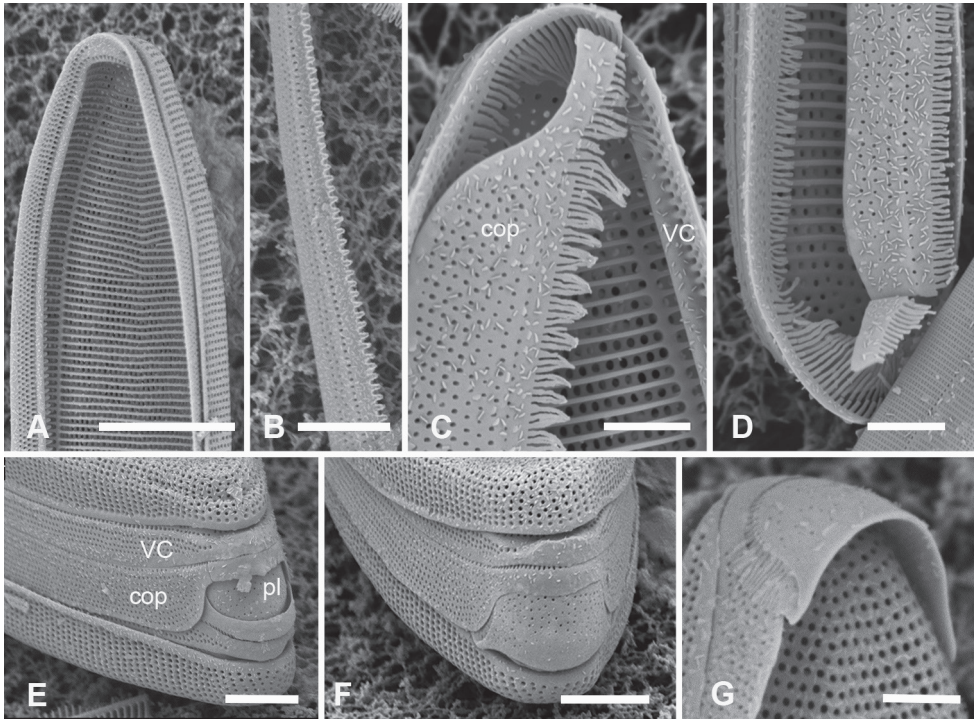


Figure 12. *Syndrosphenia parva* sp. nov., cont. All GU75A-4 **A, B** valvocopula showing apical internal side from abvalvar position, and portion of middle from advalvar side, respectively, showing row of pores along base of pars interior and fimbriae **C** internal view of apical pole with valvocopula in situ and the copula, broken in the middle, covering the valvocopula around the apical pole and left side **D** basal pole of same specimen, again showing the long fimbriae overlapping the valvocopula **E, F** frustules tilted to show polar (apical) architecture of, respectively a recently divided cell, where the pleura is in place between the copulae of the two cingula, and a non-dividing cell **G** detail of a pleura loosened from its position and showing some of the fimbriae (still tucked under the copula at top of image). Scale bars: 10 μm (**A**); 5 μm (**B, D–F**); 2.5 μm (**C, D, G**).

Type locality. Agat Reef behind Anae I., Agat Bay, 13.357°N, 144.645°E. Epiphytic on seaweed at low tide line, collection number GU75A-4, 6 May 2017. C. Lobban and M. Schefter leg.

Additional materials examined. F.S.M.: Chuuk, TK4!; MARSHALL ISLANDS: Jaluit Atoll, J5!.

Etymology. Named for its small size within the genus.

***Synedrosphenia recta* Lobban, sp. nov.**

Fig. 13

Diagnosis. Long, straight valves with isopolar, bluntly rounded poles, differing from *Synedrosphenia* (*Ardissonea*) *crystallina* in the marginal annulus, shape of pole, and poration on girdle bands, and from *Synedrosphenia* (*Ardissonea*) *fulgens* in the notch and poration of the valvocopula.

Description. Valves linear, slightly wider in the middle, isopolar with bluntly rounded poles, length 406–430 µm, width 13–16 µm, striae parallel except at pole, 16–18 in 10 µm, areolae slightly elongated in apical axis (Fig. 13A–D). Valve face longitudinally depressed along midline (Fig. 13F, I, K). Annulus detectable externally as a narrow space between areolae around pole and along edge of valve face (Fig. 13D arrows); internally, the end is seen between the areolae at the pole and can be traced around the same as externally (Fig. 13H, L arrows). There are no longitudinal costae (Fig. 13E, J arrow) and transverse costae underlie the vimines as continuous costae from one marginal rim to the other (Fig. 13J). Valvocopula (Fig. 13E–J) lacking external areolae, pores along edge of pars interior have costae between them on the pars interior, appearing to be slits (compare Fig. 13H, J) and the line deflects around the asymmetric sculpting at pole (Fig. 13H). A discrete notch at pole of valvocopula (Fig. 13F, G, I); fimbriae not observed. Copula (Fig. 13E, F) broader with a line along interior–exterior boundary dividing internal bifurcated fimbriae from external part perforated by long slits (rimae) that sometimes continued to the abvalvar edge; perforations discontinued around pole. Pleura glimpsed in Fig. 13K, apparently apical caps joined by very narrow perforated band lacking fimbriae.

Holotype (designated here). Specimen at 14.3 mm E and 5.7 mm S of the larger mark on slide 154, deposited at ANSP accession # ANSP-GC20113. Fig. 13A, C.

Registration. Phycobank <http://phycobank.org/103239>.

Type locality. FEDERATED STATES OF MICRONESIA: Chuuk: Moch Islet at Eastern Passage of the barrier reef (7°30'50.7"N, 151°57'59.8"E), epiphytic on filamentous seaweeds in farmer fish territory, collection number TK28, 30 May 1991. C.S. Lobban and M. Schefter leg.

Additional materials examined. GUAM: GU76B-2!. MARSHALL ISLANDS: Jaluit, J5!.

Etymology. *L. rectus*, straight. Named for its parallel sides and isopolarity.

Taxonomic comments. This species resembles two former *Ardissonea* species which we are separating into different genera. The complex polar architecture places it in *Synedrosphenia*, within which it is differentiated from *S. (Ardissonea) crystallina* by

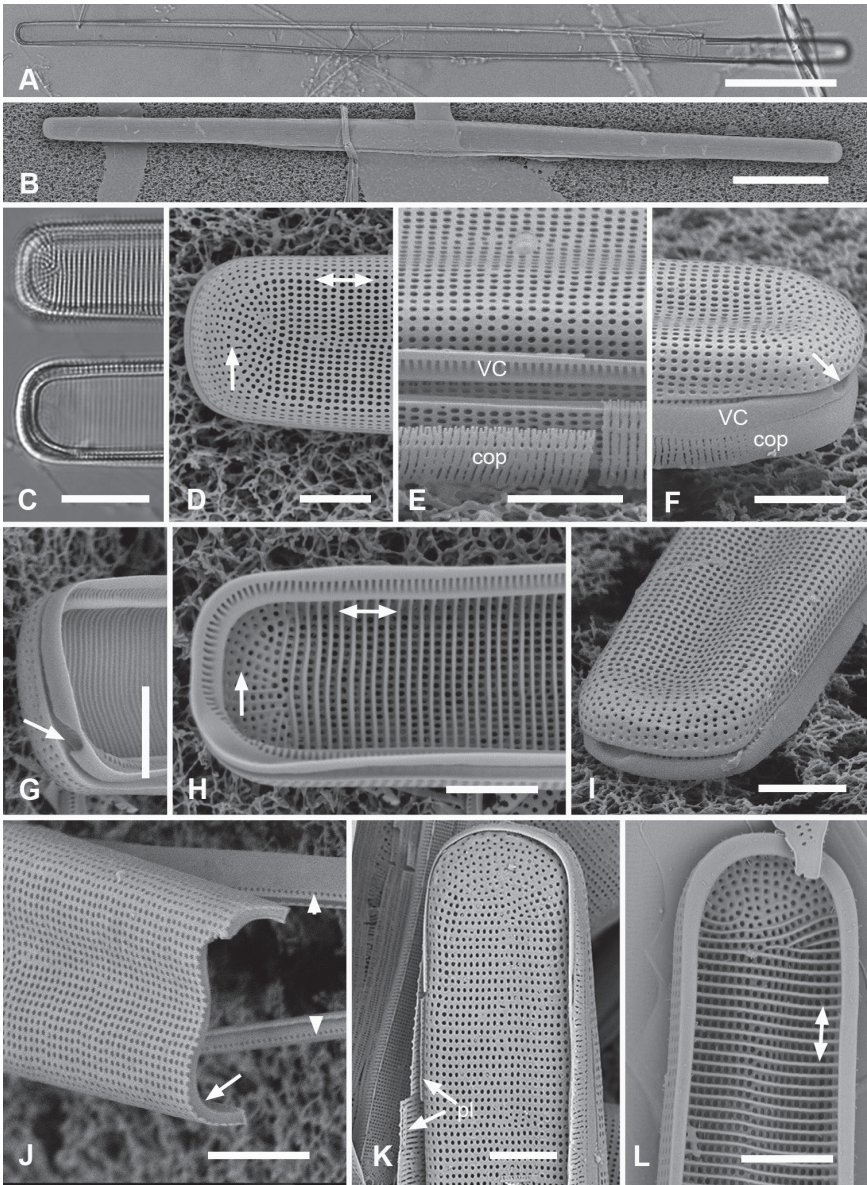


Figure 13. *Synedrosphenia recta* sp. nov. Chuuk TK28 except as noted **A, C** holotype and details of pole at two focal planes, showing valve face and valvocopula **B, D–F** specimen in SEM with details of pole at 0° tilt (**D**), arrows showing position of annulus, and 60° tilted views of central portion (**E**) showing copula and opposite pole (**F**) showing copula and valvocopula with apical notch (arrow) **G, H** internal view of a pole with valve and valvocopula at 60° tilt, showing apical notch (arrow), and at 0° tilt, showing apical area without transapical costae; arrows show inferred position of annulus as in **D** and absence of longitudinal costae **I** polar view of valve with valvocopula, showing apical notch **J** broken valve showing continuous transverse costae (arrow) and pores on pars interior of valvocopula (arrowheads) **K** specimen from Guam (GU76B-4), showing fragments of very narrow pleura (pl, arrows) **L** specimen from Jaluit (J5), pole of valve without valvocopula, showing continuous rim and absence of longitudinal costae; two-way arrow marks position of annulus, as in **D, H**. Scale bars: 50 μm (**A, B**); 10 μm (**C**); 5 μm (**D–L**).

the marginal annulus, bluntly rounded poles, plain valvocopula and slits on the copula. The shape of the poles and the marginal annulus resemble *Ardissoneopsis fulgicans*, and in LM of Chuuk samples *S. recta* was distinguishable only by length, the *A. fulgicans* specimens being only 300 µm long. We first noticed it when we found a specimen, apparently of *A. fulgicans*, with a valvocopula pole evidently of the *Synedrosphenia* type (Fig. 13H). It was necessary to tilt specimens to see girdle band characters.

Specimens from Bikar Atoll (not illustrated) with longer (to 583 µm) but narrower (7 µm) valves, weakly inflated at the poles and in the middle, were structurally indistinguishable from the Chuuk specimens on which the species is defined, including the lack of longitudinal costae. Without further evidence, we cannot decide whether to assign this to a formal varietal status, describe it as a separate species, or leave it within the scope of *S. recta*. We mention it here to underline the point that the present study does not exhaust the biodiversity of these genera in Micronesia.

Ardissonea fulgens (Greville) Grunow ex De Toni, 1892

Table 3

References. Peragallo and Peragallo 1897–1908, p. 311, pl. 79, fig. 5; Hustedt 1931–1959, p. 228, fig. 717a; Navarro 1982, p. 260, figs 64, 65; Poulin et al. 1986, figs 31, 32; Witkowski et al. 2000, p. 44, pl. 31, figs 9–11; Hein et al. 2008, p. 23, pl. 8: 1, 2).

Description from literature. Kanjer et al. (2021) reported the ultrastructure of Greville's type material of this species, collected at Mull, Scotland, and clearly showed a pseudoseptum and sculpted apices on the valvocopula; no apical notch was observed. That architecture is not visible in LM and so we can only assume that collections reported from Atlantic and Mediterranean Europe are the same until they can be examined. The species as traditionally understood is described as follows: Valves narrow, linear except slightly wider in the middle, 170–450 µm long, 10–15 µm wide, striae 12–14 in 10 µm, offset slightly where they meet such that a central line (“pseudoraphe”) is distinct but very narrow; longitudinal costae very near to the valve edge and normally difficult to see (Hustedt 1931–1959). Kanjer et al. (2021) show an undulation in the annulus near the middle of the valves in holotype material, a feature not reported elsewhere; they reported a stria density of 15–16 in 10 µm. Poulin et al. (1986, figs 31, 32) showed a valve without pseudoseptum, i.e., of the *Ardissoneopsis* type, with transapical costae on the virgae except at the poles, and the annulus near the valve-mantle junction marked externally by a gap in the areolae and internally by a longitudinal costa on each side. SEMs of var. *mediterranea*, with 17 striae in 10 µm, in Güttinger (1989), include an oblique view suggesting that the annulus is not internally thickened. Navarro (1982) gave dimensions of 554 µm long by 13.5 µm wide, 14–15 striae in 10 µm. Hein et al. (2008) showed “*Ardissonea* cf. *fulgens*” with dimensions of 123–186 µm long by 6.5 µm wide, striae 20 in 10 µm—i.e., smaller and more finely striated than classical descriptions, and they noted that their counts of striae from images in Witkowski et al. (2000) showed stria densities of 19–22 in 10 µm.

Taxonomic comments. For the reasons given below for separating single-walled *Ardissonea* taxa, it cannot remain in *Ardissonea* sensu stricto. If this species is confirmed to lack the apical notch, its pseudoseptum and sculpted valvocopula are sufficiently strong characters to place it in *Synedrosphenia*; it certainly does not belong in *Ardissoneopsis*, proposed below, which lacks those characters, and we therefore must describe our *fulgens*-like taxa as new species and propose a new combination of *Synedrosphenia fulgens* for Greville's species.

Group 3: Single-walled taxa without pseudosepta

Table 4

Table 4. Comparison of species of *Ardissoneopsis*†.

	Length µm	Width µm	Shape	Stria density in 10 µm	Valvocopula exterior pores	Copula exterior pores	Pleura
<i>A. appressata</i> sp. nov.	400–1000 [560–900]	10–15 [9–12]	Linear, center and poles inflated	13–14 [18–19]	2 rows, decreasing to 1	6 rows, decreasing to 4	Very narrow; apical caps?
<i>A. fulgicans</i> sp. nov.	205–320	9–15	Linear, center slightly inflated	17–19	4 rows, decreasing to 2	4–5 rows	Very narrow; apical caps?
<i>A. gracilis</i> sp. nov.	217–431	5–7	Linear, undulate, center ± inflated	10–12	4 rows, decreasing to 1 near basal pole, but increasing at both poles	Ca. 8 rows decreasing to 2	Narrow; continuous?
<i>A. undosa</i>	To 850	10–11	Linear, undulate, center and poles inflated	19–22	Unknown	Unknown	Unknown

† data for known species are from literature cited in text, data for Micronesian specimens of given in brackets where different.

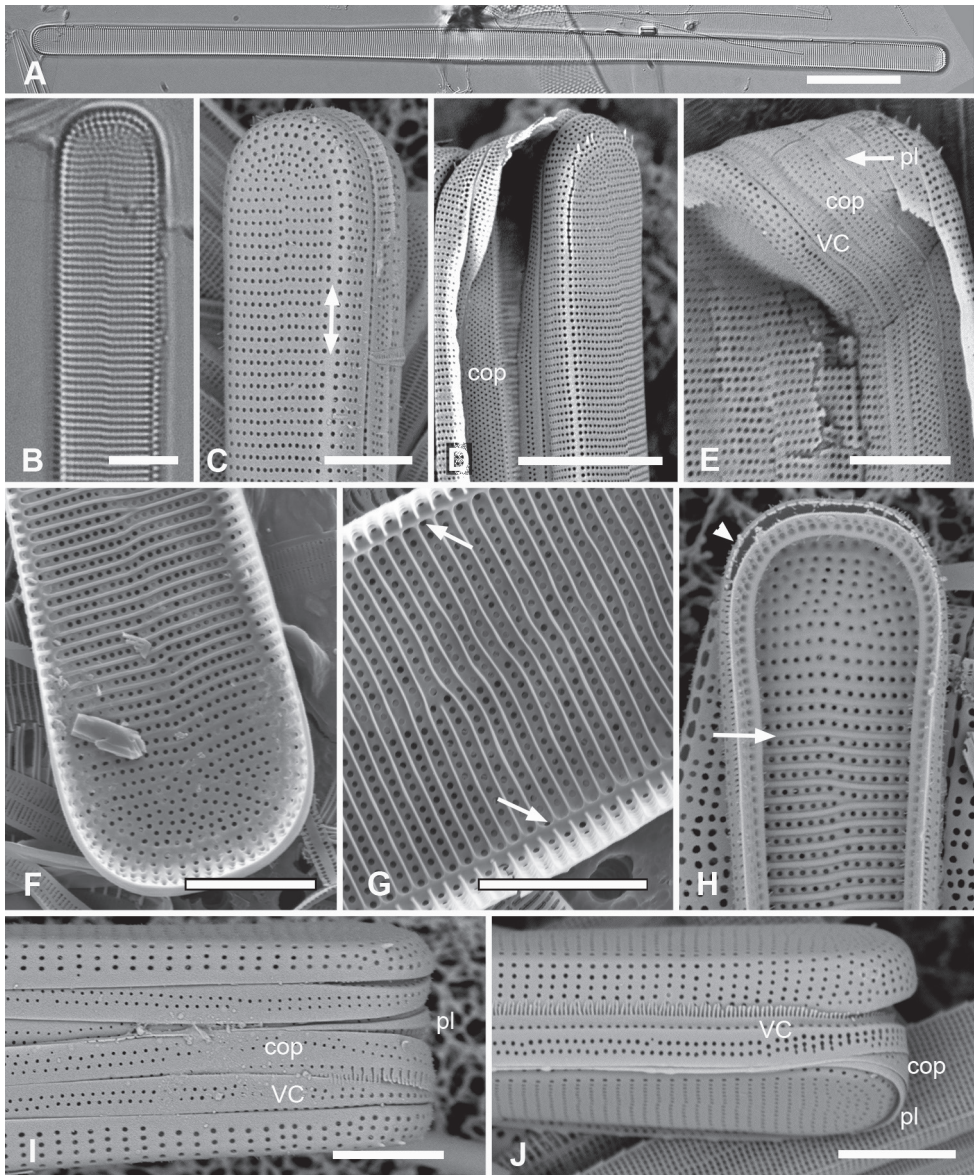
Ardissoneopsis fulgicans Lobban & Ashworth, sp. nov.

Fig. 14

Ardissonea fulgens (Greville) Grunow sensu Lobban et al. 2012, p. 259, pl. 16, figs 3–5.
Synonym.

Diagnosis. Differing from congeners in the straight outline, only weakly inflated at the center.

Description. Valves 205–320 µm long, 9–15 µm wide, usually slightly widened in the middle and bluntly rounded at poles (Fig. 14A–F); 17–19 parallel striae in 10 µm. Cells attached by one pole to sturdy mucilage stalks (not shown). Annulus along valve–margin junction and not visible in LM, underlain by longitudinal costae (Fig. 14C, D, F, G); sternum absent but striae often out of alignment at the midline (Fig. 14B, H); often spines on poles (Fig. 14D, I). Valve rims straight (i.e., lacking a pseudoseptum) and valvocopula simple, therefore no apical groove (Fig. 14E, F); transverse costae on the mantle thinning toward the margin (Fig. 14G; contrast Fig. 13J). Transverse costae on most vimenes but absent from a relatively large area at the poles (compared to *Synedrosphenia recta*, Fig. 13H) (Fig. 14F, H). Three girdle bands were present (Fig. 14E, I, J). Valvocopula (Fig. 14E, H, J) with generally two rows of pores on pars exterior; pars interior with a single row along outer edge and a fimbriate



Figures 14. *Ardissonopsis fulgicans* sp. nov. **A, B** valve in LM showing shape and striation (TK28) **C** pole of frustule from acid cleaned material in SEM, showing annulus (double-headed arrow) (J5) **D, E** poles of frustules in whole mounts, attached at opposite ends, showing girdle bands and apical spines (GU7R) **F, G** internal views of valve pole and central portion, showing the absence of pseudoseptum at pole and presence of longitudinal costae (arrows) (GU44N-A) **H** pole of valve with valvocopula, showing start of transverse costae (arrow) (contrast with pole of *Synedrosphenia recta* Fig. 13H); arrowhead indicates edge of fimbriate copula (J5) **I, J** poles of frustules showing fimbriae on copula and valvocopula, respectively (J5). Scale bars: 25 μ m (**A**); 10 μ m (**D**); 5 μ m (**B, C, E–J**).

inner edge. Copula (Fig. 14D, E, I) with multiple rows of pores forming a decussate pattern, and a fimbriate advalvar margin. Pleura barely visible as a narrow cap at each end, possibly connected, apparently fimbriate at the poles (Fig. 14E, I).

Holotype (designated here). Slide 449, multiple specimens present. Slide deposited at ANSP, accession # ANSP-GC20111. Representative specimen published in Lobban et al. 2012, *Micronesica* 43: pl. 16, figs 4, 5.

Registration. Phycobank <http://phycobank.org/103241>.

Type locality. GUAM: Apra Harbor, GabGab reef. 13.443°N, 144.643°E, sparse filamentous algal turf in farmer fish territory (*Plectroglyphidodon lacrymans*), depth ca. 5 m., collection number GU44Y-13, 10 May 2009. C. Lobban, M. Schefter leg.

Additional materials examined. GUAM: GU7R!, GU44Z-15!, GU44L!, GU44N-A!, GU44AC-3!, GU44BJ-4! (inter alia); FEDERATED STATES OF MICRONESIA: Chuuk: TK28!; MARSHALL ISLANDS: Jaluit J5!.

Etymology. Adjective (Latin), *fulgens* (shiny) + *-icans* (“indicates... resemblance sometimes so close as to be almost identical” – Stearn 1973: 309).

Taxonomic comments. In our region, this species is hard to positively identify in LM from the new species *Synedrosphenia recta* described above, and some other species so far only glimpsed but differs in (1) having simple apical structure unlike *Synedrosphenia* spp.; (2) the presence of two or more rows of pores on the valvocopula exterior. Lobban et al. (2012) previously identified this species as *Ardissonaea fulgens* on the basis of literature but Kanjer et al.’s (2021) surprising finding about the type material (see above) forced the reevaluation.

***Ardissonopsis appressata* Lobban & Ashworth, sp. nov.**

Figs 15, 16

Ardissonaea fulgens var. *gigantea* (Lobarzewsky) Rabenhorst sensu Lobban et al. 2012, p. 260, pl. 1, figs 1, 2, pl. 16, figs 6–8. Synonym.

Diagnosis. Differentiated from congeners in the straight valve with inflated center and apices, and valve-appressed colony formation.

Description. Cells valve-appressed to form flat colonies from sturdy mucilage pads, cells toward the outside increasingly curved in the apical axis (Fig. 15A–D). Nucleus in widest part of the cell and appressed to one side, numerous lenticular plastids (Fig. 15B). Valves very long and narrow, inflated at the middle and poles (Fig. 15E–G); frustule also inflated in the middle in girdle view because of deeper mantle and wider girdle bands (Fig. 15C vs D). Length 560–900 µm, width at center 9–12 µm, poles 7–10 µm, 5 µm in between; striae 18 in 10 µm (Figs 15F, G, 16A–C). Annulus along junction of valve face and mantle except at poles, where it is further back (Fig. 16B, C); some thickening under annulus but not as thick as transverse costae (Fig. 16E). Striae parallel except radiate at poles (Fig. 16B, C). Internally, costae on most virgae

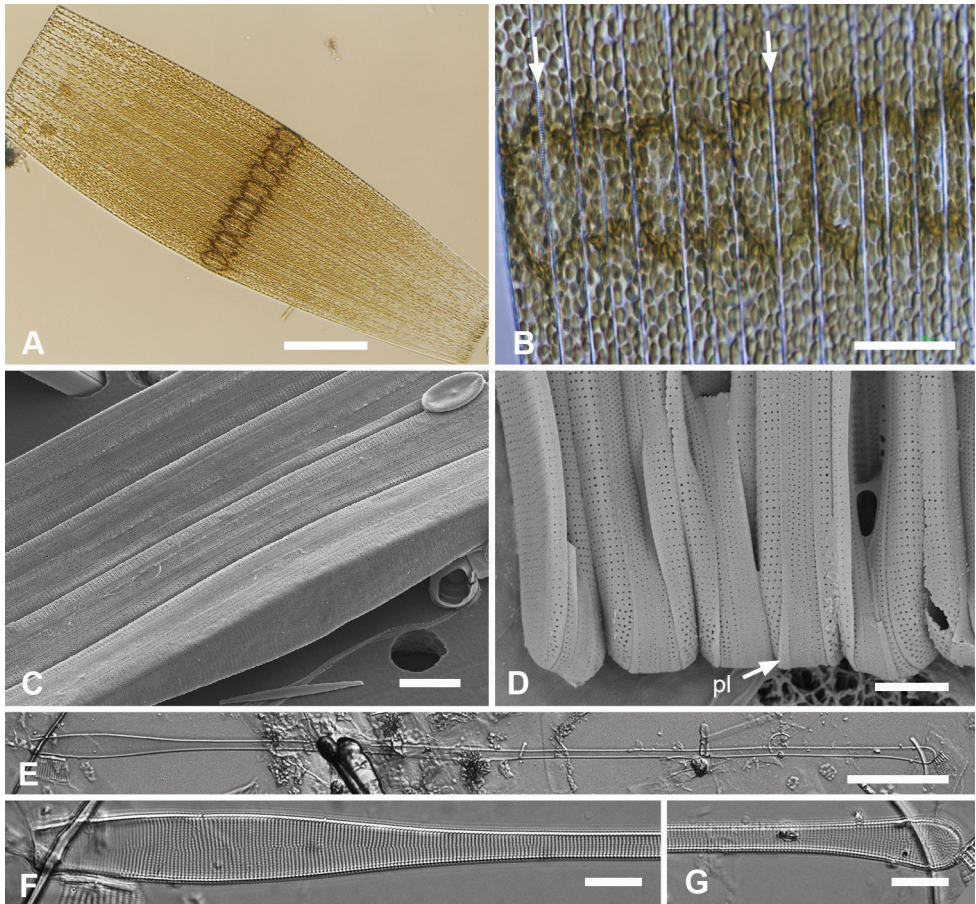


Figure 15. *Ardissonopsis appressata* sp. nov. **A, B** flabellate colony and detail showing hemispherical nuclei surrounded by plastids and appressed to girdle faces; arrows on **B** show two of the many walls between cells (GU68H-1) **C** middle of colony in oblique view, showing inflation where nuclei are located **D** base of colony, showing parts of six frustules including pleura (pl, arrow) (GU44AP-2) **E–G** half valve from Yap, acid cleaned, with details of central and polar portions showing shape and stria density (Y42-1). Scale bars: 100 µm (**A**); 50 µm (**E**); 25 µm (**B**); 10 µm (**C, F, G**).

except near poles (Fig. 16C, E, F). Spines absent. No pseudosepta (Fig. 16C); transverse costae on the mantle diminishing toward margin (Fig. 16E arrowhead; contrast Fig. 13J). Three girdle bands present (Figs 15D, 16A); fimbriate valvocopula (Fig. 16A, F) with two rows of pores around the poles, decreasing to one toward the basal pole, along with one row along bottom edge of pars interior; fimbriate copula (Fig. 16A, D) with six rows of pores in a decussate pattern, decreasing to four near basal pole; pleura (Fig. 15D) very narrow, pars interior not observed.

Holotype (designated here). Slide 449, multiple specimens present. Slide deposited at ANSP accession # ANSP-GC20111. Representative specimen published in Lobban et al. 2012, *Micronesica* 43: pl. 16, figs 6, 7.

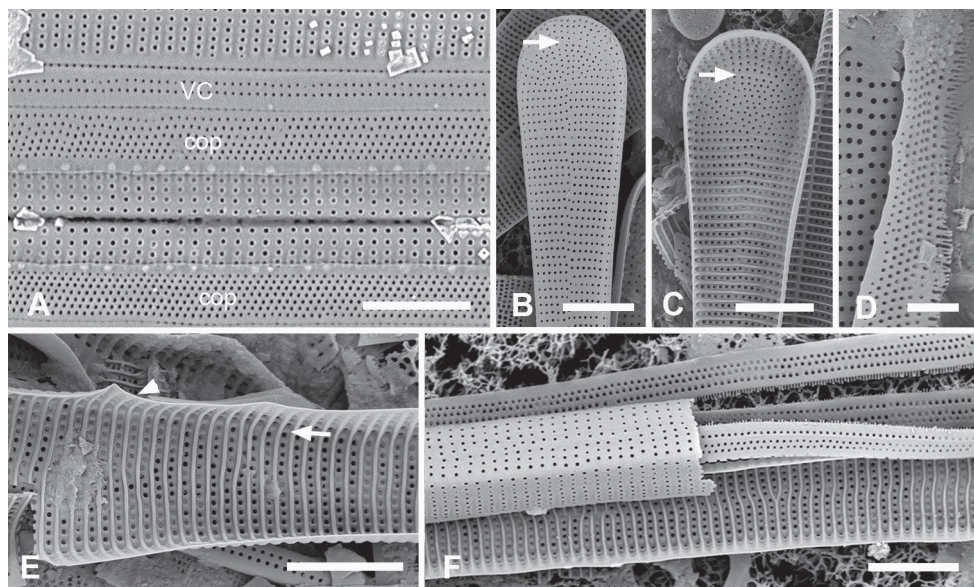


Figure 16. *Ardissonopsis appressata* sp. nov., cont. GU44BJ-4 except as noted **A** girdle view of part of colony showing cells joined valve to valve, and the pattern of pores in valvocopula (VC) and copula (cop) (GU44AE-2) **B, C** valve pole in external and internal view, respectively showing tip of annulus (arrows) **D** portion of copula showing fimbriae **E** portion of valve near center: arrow points along longitudinal thickening below annulus and arrowhead indicates narrowing of transverse costae at margin **F** portion of frustule in narrow part, showing internal and external aspects and portions of the fimbriate valvocopulae (GU44T-1). Scale bars: 5 μ m (**A–C, E, F**); 2 μ m (**D**).

Registration. Phycobank <http://phycobank.org/103242>.

Type locality. GUAM: Apra Harbor, GabGab reef. 13.443°N, 144.643°E, sparse filamentous algal turf in farmer fish territory (*Plectroglyphidodon lacrymans*), depth ca. 5 m., collection number GU44Y-13, 10 May 2009. C. Lobban and M. Schefter leg.

Additional materials examined. GUAM: GU68H-1!, GU44Z-15!, GU44T-1!, GU44BJ-4!, inter alia. FEDERATED STATES OF MICRONESIA: Yap: Y42-1!; Chuuk: TK28!.

Etymology. Adjective (L.) *appressus*, appressed, with reference to the colony formation.

Taxonomic comments. We previously (Lobban et al. 2012) identified this species as *Ardissona fulgens* var. *gigantea* (Lobarzewsky) Rabenhorst, based on literature. Starting from Peragallo and Peragallo (1897–1908), that taxon has been described as extremely long (400 μ m to 1 mm), with a broad central portion joined to capitate poles by very narrow linear portions, the striae 13–14 in 10 μ m, but not forming distinctive colonies. Cells from Guam matched this description, except for somewhat higher stria density, but adhered valve to valve while still attached to massive mucilaginous stalks, giving colonies a unique form, a characteristic not mentioned in the literature. The variety is distinctive enough by the shape and colony formation to differentiate it from the nominate variety but has been even less studied than *A. fulgens*.

However, drawings of *Synedra gigantea* Lobarzewsky (1840, p. 276, pl. 6, fig. a–c) show a highly elongated diatom occurring in valve-appressed clusters, somewhat similar to those seen in Guam, but not showing any bulge in the middle and being apparently very flexible; as far as one can tell, the frustule is uniformly linear in both views, but he stated that the side (i.e., valve) view is 3–4 times narrower and with a *wavy outline*. This does not well accord with valve views of *Ardissonaea fulgens* var. *gigantea*, which has never been depicted as wavy but has been shown with a strong central inflation. Lobarzewsky's drawings look more like *Licmophora flucticulata* Lobban, Schefter and Ruck (2011), which is wavy and very narrow and occurs in valve-appressed clusters, except that the clusters of that species in girdle view are very obviously tapered. The descriptions of this taxon were carried forward into Rabenhorst (1864: 140) and De Toni (1892: 674) but there is no mention of the valve outline. The comparison of its shape to *Toxarium hennedyanum* (W. Gregory) Pelletan seems to have begun with Peragallo and Peragallo (1897–1908), who clearly describe the valve shape and stria density for the first time, but show a smooth valve outline. This taxon was said to be frequent in the Mediterranean (Peragallo and Peragallo 1897–1908), yet neither they nor Hustedt (1931–1959) refer to valves sticking together in distinctive fan-shaped clusters. The extreme length is the sole character that could link the acid cleaned frustules so accurately described by the Peragalloes to the taxon drawn by Lobarzewski (1840), and that is insufficient, so that the identity of *Synedra gigantea* is a mystery, while the lack of colony information and the lower stria density leave doubt about how the Guam population is related to any European taxa. Given findings of Kanjer et al. (2021) on the nominate variety, we reject our earlier identification and propose a new species for our material.

Synedra undosa Grunow, 1867

Fig. 17

Reference. Grunow 1867, p. 4; Grunow 1877, p. 167, pl. 193, fig. 8a–c.

Description from literature. Very long, to 850 μm , slender, inflated at the center and poles, undulate in between, striae 19 in 10 μm (20–22 according to De Toni 1892). *Synedra undosa* has the outline of *Toxarium undulatum*, but linear striae as in *Ardissonoeopsis appressata*.

Materials examined. Remnant material of Grunow 839-4611 [W catalog # W0127010, Acquisition # W-1901-0004611]. Not found in Micronesian samples.

Observations. We have not encountered this in the Guam flora but found several fragments in Grunow's Honduras gathering that showed internal and external structure, confirming the similarity of structure to the two aforementioned *Ardissonoeopsis* spp. A fragment including the central inflation and one pole suggests a total length of ca. 690 μm (Fig. 17A). Widths were 10–11 μm across the center, 9 μm across the poles and 4–5 μm between; stria density 19–21 in 10 μm . The annulus along valve face–mantle junction at least partially subtended by longitudinal costae (Fig. 17B–E).

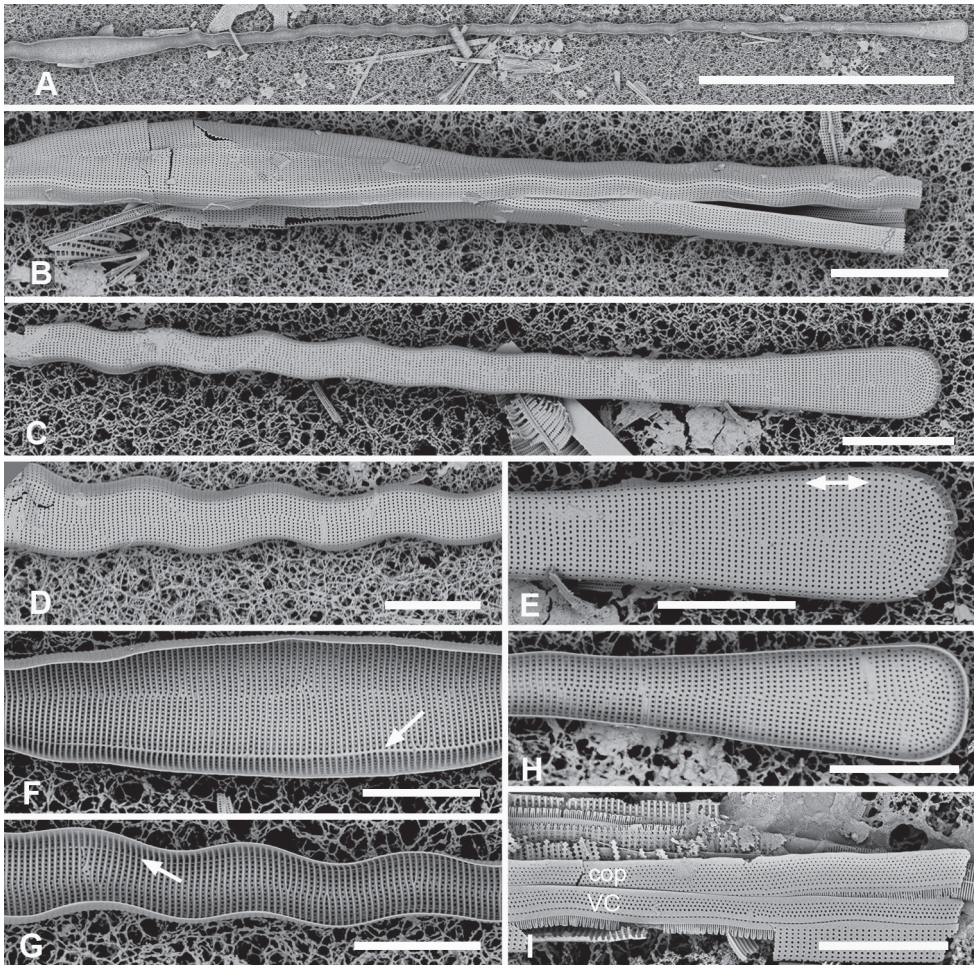


Figure 17. *Synedra undosa* from Grunow's Honduras material **A** internal view of half valve, total length would have been ca. 690 μm **B** external view of fragment of frustule including the central inflation **C** external view of valve fragment with pole **D** external view of valve fragment near central area showing the strong undulation **E** detail of external pole showing annulus (double-headed arrow) and spines **F–H** internal views of central, near central (cf. **D**), and polar portions of valve, respectively, showing longitudinal costae (arrows) and transverse costae; transverse costae developing gradually toward left in **H**. **I** girdle bands, showing fimbriate valvocopula and copula with glimpses of interior costate surface of valve. Scale bars: 100 μm (**A**); 15 μm (**B**, **C**); 10 μm (**D–I**).

Transverse costae also evident throughout except near poles (Fig. 17F–H). No pseudoseptum. Valvocopula and copula both with multiple rows of pores in decussate pattern on exterior, one row of interior pores, fimbriate inner margin and lacking sculpted apices (Fig. 17I). Copula wider, with fimbriae commonly bifurcated.

Taxonomic comments. According to AlgaeBase (Miranda in Guiry and Guiry 2020), *S. undosa* is currently referred to as *Toxarium undosum* (Grunow) De Toni,

1892, which De Toni recognized as distinct from *T. undulatum*. We have not found more recent mention of this species, but it clearly cannot remain in *Toxarium*. Hustedt (1931–1959, pp 224–225) stated that, while Grunow had made clear the abundance of *Synedra undosa* in his Honduras material, “one must assume he also included *S. (Toxarium) undulata*,” because Hustedt had not observed specimens matching Grunow’s drawings in Honduras material he examined. Hustedt concluded that this species requires further examination. Grunow, however, was clear that *S. undosa* was different from *S. undulata* and the SEM images here clearly prove him right. On the evidence that it is a species in its own right, we propose below its transfer to *Ardissoneopsis*.

***Ardissoneopsis gracilis* Lobban, sp. nov.**

Fig. 18

Diagnosis. Differing from *A. fulgicans* in valves being more slender, slightly wavy outline, lower stria density, and markedly heteropolar frustule in girdle view and from *A. undosa* by lack of central inflation.

Description. Frustules cuneate in girdle view (Fig. 18C, D, N, O), both valve mantle and width of girdle bands decreasing from apical pole to basal pole; hypothesized to be attached to mucilage pads at the basal pole, but not observed in live or raw material. Valves slender, weakly undulating, slightly inflated in the middle and at poles, slightly heteropolar but poles not consistently distinguishable except for mantle depth (Fig. 18A, B, G, E). Dimensions: 206–431 μm long, 5 μm wide except 7 μm across the middle and poles (Fig. 18A–G). Striae parallel, 10–12 in 10 μm , except radiating at poles, areolae small, circular. The annulus near valve–mantle junction, indicated only in places where striae on mantle are offset from those on valve face (oval on Fig. 18I). There is often also an offset across the midline but no sternum. Several spines occur on both poles. (Fig. 18H, K, N, O). Internally, interstriae are barely thickened, not forming costae, and there are no longitudinal costae on the annulus (Fig. 18L, M). Three girdle bands were present (Fig. 18N–R): valvocopula with a row of pores along the edge of the pars interior and a fimbriate internal margin (Fig. 18Q); two rows of pores occur around basal pole, but become one within 10 μm from base, further out becoming two and then three or more rows (Fig. 18N, O). In the copula, also bearing a fimbriate flange (Fig. 18P, R), pars exterior has numerous pores arranged in a generally decussate pattern but becoming looser near basal pole (Fig. 18N, O). The pleura is very narrow even at the poles (Fig. 18N, O, P).

Holotype (designated here). Specimen at 11.0 mm E, 2.5 mm S of the mark on slide 1831, deposited at ANSP accession # ANSP-GC20087. Fig. 18E, F.

Registration. Phycobank <http://phycobank.org/103243>.

Type locality. GUAM: Apra Harbor: GabGab reef, 13.443°N, 144.643°E, sparse filamentous algal turf on farmer fish territory (*Plectroglyphidodon lacrymans*), associated with *A. gigantea* and *Toxarium undulatum*, depth ca. 8 m., collection number GU44BJ-4, 8 Feb. 2015. C.S. Lobban and M. Scheffer leg.

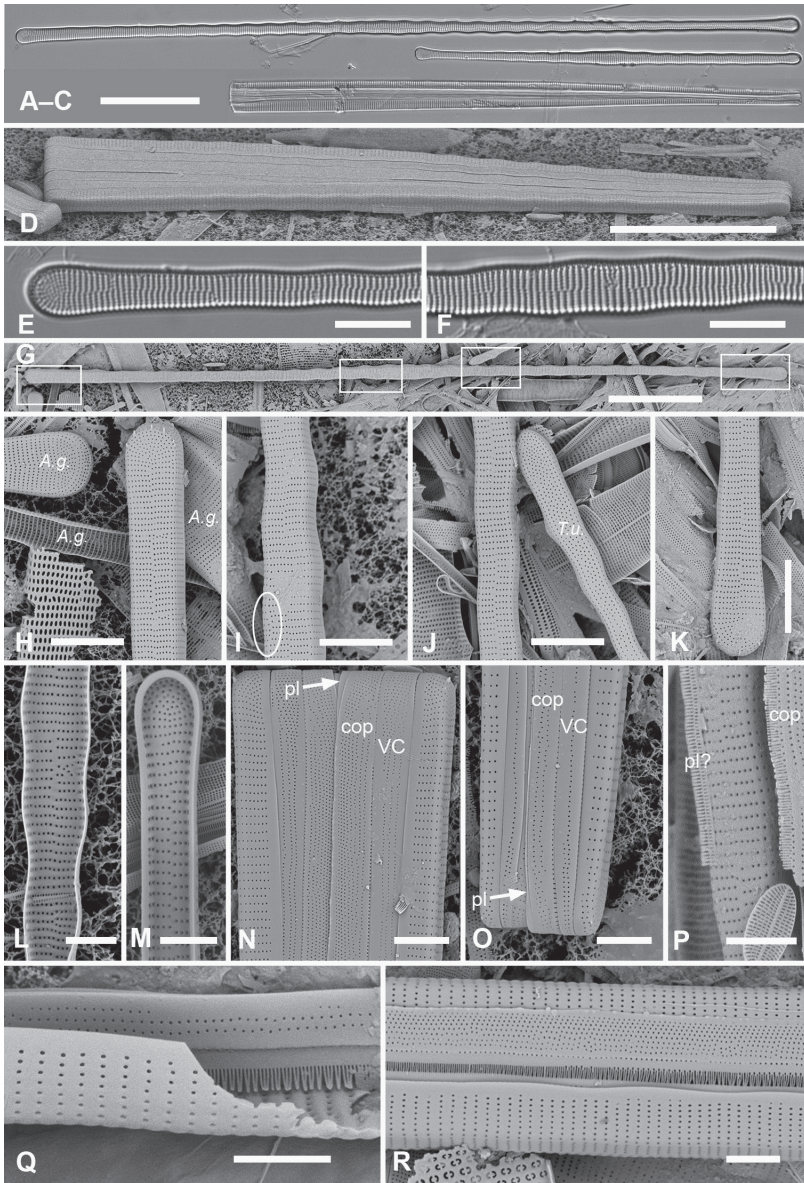


Figure 18. *Ardissonopsis gracilis* sp. nov. (GU44BJ-4, except **B** TK28) **A–C** three specimens to scale in LM to show size range: valves from Guam (**A**) and Chuuk (**B**), frustule from Guam in girdle view (**C**) showing heteropolarity **D** frustule in SEM tilted 60°, showing both valve and girdle faces **E, F** pole and mid-section of holotype **G–K** external views of valve in SEM with other species adjacent for comparison (GU44BJ-4): index image (**G**) with locations of details marked, apical pole (**H**) (shown by depth of mantle), compare stria density with *Ardissonopsis appressata* (*A.g.*); top half of center (**I**), offset areolae in striae within the oval suggest location of annulus; narrow portion below center (**J**), compare with scattered areolae in adjacent *Toxarium undulatum* (*T.u.*); basal pole (**K**), note spines on both poles **L, M** internal aspect near middle and at the apical pole, showing lack of costae **N, O** girdle view of frustule apical and basal poles, showing taper in mantle and girdle bands **P** possible piece of pleura (pl?) with fimbriae **Q, R** fimbriate edges of valvocopula and copula, respectively. Scale bars: 50 μ m (**A–D, G**); 10 μ m (**E, F, H–K**); 5 μ m (**L–R**).

Other materials examined. GUAM: Apra Harbor: GU52P-7!, GU52AI-1!. FEDERATED STATES OF MICRONESIA: Chuuk: TK28!; Yap: Y36-2!. MARSHALL ISLANDS: Majuro: M1!, Jaluit, J1!.

Etymology. Adjective (Latin), slender.

Taxonomic comments. Most similar to *Ardissonopsis fulgicans* but differing in the wavy margin, width only half that of *A. fulgicans*, and in having only 10–12 striae vs. 19–20 in 10 μm . Its shape resembles some *Toxarium hennedeyanum*, which can sometimes be slightly wavy and only weakly inflated in the middle (e.g., Suppl. material 4: Fig. S2A–C) but always has a random pattern of areolae on the valve face. Much less inflated in the middle, much less strongly undulate, and more coarsely striated than *Synedra undosa*.

Group 4: *Synedra bacillaris* complex

Synedra bacillaris (Grunow) Hustedt, 1932

Fig. 19

References. Grunow 1877, p. 167, pl. 193, fig. 12a–c; Hustedt 1931–1959, p. 230, fig. 718; Sullivan and Wear 1995, p. 182, figs 9–12.

Description from literature. As described from LM (Hustedt 1931–1959), this taxon is easily distinguished from *Ardissonaea* spp. by the prominent longitudinal costa on the midline and the absence of lateral longitudinal costae (i.e., no observable annulus). There is only one wall layer. Valves linear, usually slightly wider in the middle, 320–700 μm long, 16–20 μm wide, 8–9 striae in 10 μm . Robust transapical costae on each of the virgae. As seen in SEM (Sullivan and Wear 1995), the valve has a single wall, areolae are circular, those at the poles slightly smaller and not organized into striae, elsewhere the striae are framed by the transapical costae. Sullivan and Wear stated that the costae extend from the margin to the median costa, but their fig. 12 shows some costae extending from the median costa and the costae are not consistently thick. Sullivan and Wear reported an absence of spines, polar pore fields and rimoportulae. Girdle bands closed, not more than five (three on the epicingulum): the valvocopula broad with a single row of small, circular pores near the advalvar edge of the pars exterior and a large flange that fits inside the valve mantle; there was said to be short fimbriae along its inner edge but they are not evident in the micrographs. There are additional rows of pores on the valvocopula just around the poles. The valvocopula has a flange that fits around the valve mantle but there is no apical notch. The copula is also broad but with several rows of pores (their fig. 11 shows these loosely organized in straight striae of at least three pores), and there is a narrow pleura (Sullivan and Wear 1995); none of their images show the inner edge of the girdle bands. Although not specifically stated in these descriptions, the frustules are implicitly isopolar. Sullivan and Wear (1995) particularly noted the circular areolae, in contrast to the large oval areolae they saw in *Ardissonaea formosa*. Grunow's (1877) published drawings (as *Synedra crystallina* var. *bacillaris*) do not include details of areolae but unpublished drawings archived in

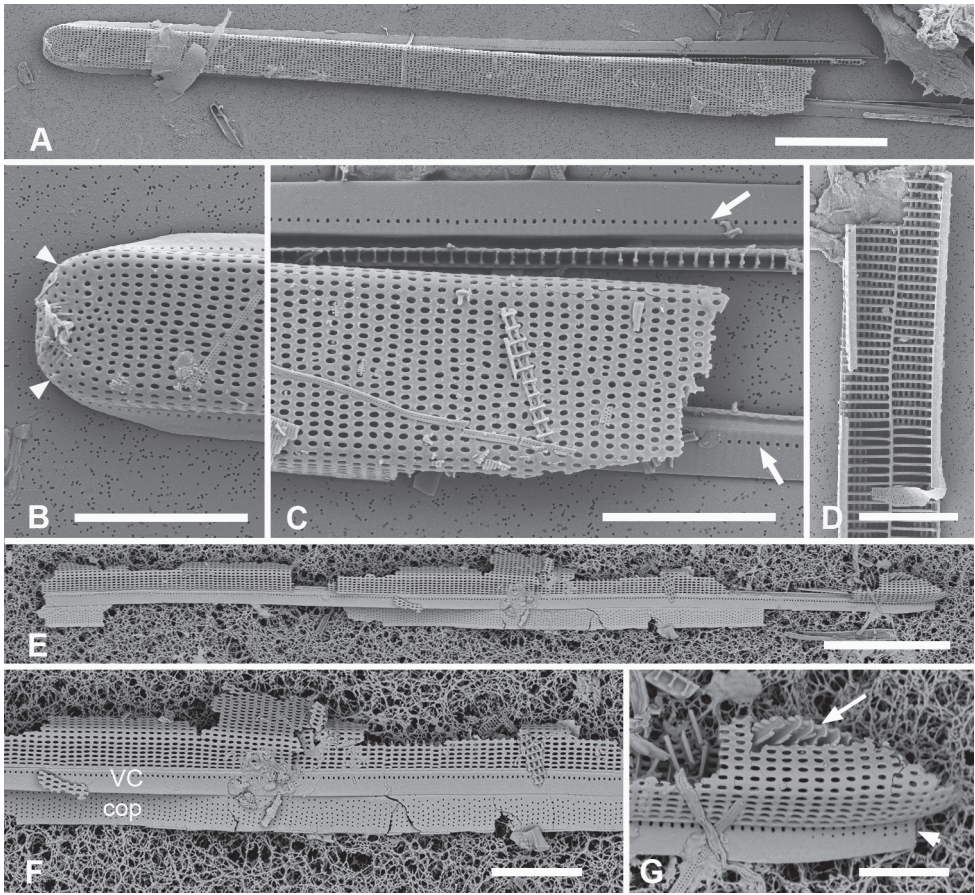


Figure 19. Putative *Synedra crystallina* var. *bacillaris* from Grunow's Honduras material **A–C** specimen in external view with valvocopula, identified by the length, the straight sides and blunt pole, stria density (11 in 10 μm), and row of pores in the exterior of the valvocopula (arrows); small spines on apex (arrowheads on **B**) **D** fragment of valve, interior view, showing central longitudinal costa and transverse costae **E–G** fragment of frustule showing valvocopula and copula **G** showing transverse costae (arrow) and absence of inner wall, arrowhead shows additional pores on valvocopula pole. Scale bars: 25 μm (**A**, **E**); 10 μm (**B–D**, **F**); 5 μm (**G**).

the Grunow drawing collection at W (W1901-5465) include several sketches where the areolae appear to be oval. Grunow's drawings, like those of later authors, show this species as linear and isopolar, with bluntly rounded poles, but his unpublished girdle view shows a slightly tapered frustule.

Observations. We were able to find a few fragments of *Synedra crystallina* var. *bacillaris* Grunow in an SEM preparation from Grunow's Honduras gathering (Fig. 19). The external view (Fig. 19A–C), of a fragment 172 μm long that appeared to reach the slightly inflated middle, was distinguished from *Ardissonea formosa*, also present on the stub, by the row of pores on the exterior of the valvocopula. The pole was blunt,

with small spines (Fig. 19B, arrowheads), and the valve linear, although a little wider in the middle. Both valves had 11 striae in 10 μm , comprising oval areolae, and the small fragment, width 10 μm , showing the interior had the characteristic central longitudinal costa and prominent transapical costae (Fig. 19D). A second frustule fragment (Fig. 19E–G), 174 μm long, showed the single line of pores on the valvocopula were 19 in 10 μm , striae on the copula 18 in 10 μm . The broken tip of this valve showed the transverse costae (Fig. 19G).

Taxonomic comments. Specimens provisionally identified as *S. bacillaris* were found in samples from across Micronesia but there was a range of stria densities and dimensions. All had oval areolae and many had spines. However, there were few fitting the literature description, even overlooking the shape of the areolae, i.e., those with linear valves, blunt poles and 8–9 striae in 10 μm . Those in Guam were mostly among populations of lanceolate specimens and probably part of them (see next taxon). The small, circular areolae shown by Sullivan and Wear (1995) are certainly different from the oval areolae in our specimens but determining the identities of these specimens relative to one another and to the literature will require much further study.

***Grunowago pacifica* Lobban & Ashworth, sp. nov.**

Figs 20, 21

References. Lobban et al. 2012, pp. 256–257, pl. 13, figs 1, 2 [as *Synedra bacillaris* (Grunow) Hustedt].

Diagnosis. Differing from *Grunowago* (*Synedra*) *bacillaris* in width and lanceolate outline of valve.

Description. Valves lanceolate, often slightly rostrate, 194–341 μm long, 11–16 μm wide, striae 9–10 in 10 μm (Fig. 20A–D), the striae comprising large oval pores; poles with smaller, circular pores, but not organized into polar pore fields (Figs 20E, 21A). Isopolar but wider in the middle in girdle view (Fig. 18F–H). Two small spines usually present on each pole (Figs 20G–I, 21B). Rim present on the valve border but not extended into a pseudoseptum (Fig. 21A). Valve single-walled (Figs 20J, 21A), internally costate with a distinctive central costa the entire length of valve and thickened vimes (Figs 20J, 21A), no annulus detected either as a break in the striae, or any other longitudinal costae (Fig. 21A). Three girdle bands were present (Fig. 20F–H). Valvocopula (Figs 20I, J, 21A, C) without extended lip but having groove on pars interior that fits rim of valve. A single row of pores on advalvar side of pars exterior, circular except elongated near poles (Figs 20G, H, 21A, C), a short line of pores around poles on pars interior (Figs 20I, 21C). Copula has a row of pores on outer edge of pars interior (Fig. 21A, B, D), often hidden under valvocopula and a well-developed fringe on the pars interior; up to 5 rows of pores on pars exterior (Figs 20G, H, 21B, D). Pleura a very thin fimbriate band, continuous along cell length (Figs 20G, H, 21B, D).

Holotype (designated here). Specimen at 18.3 mm E and 6.4 mm S of the mark on slide 146, deposited at ANSP accession # ANSP-GC20085. Fig. 20D, E.

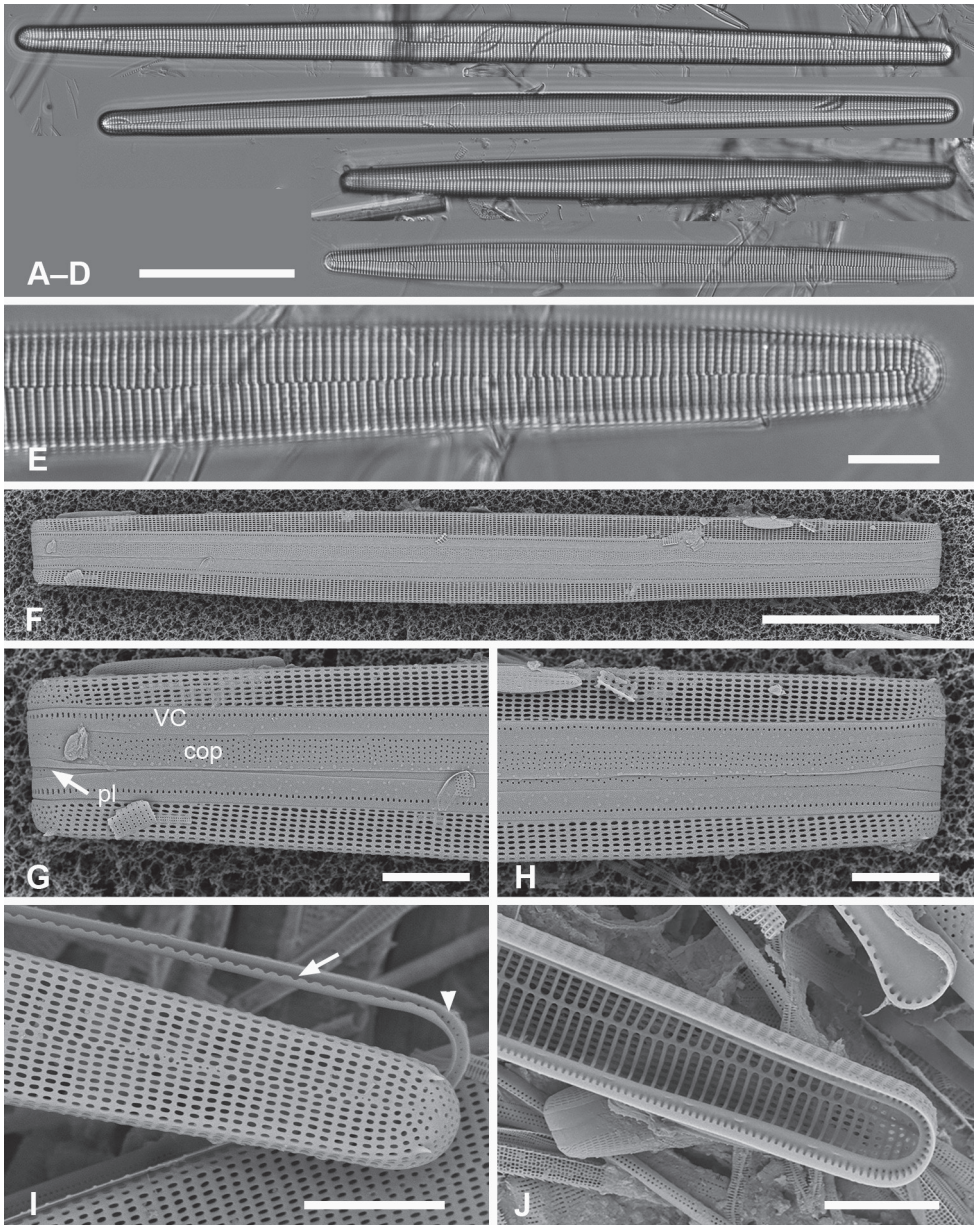


Figure 20. *Grunowago pacifica* sp. nov. **A–D** LM of specimens from GU44BJ-4 (**A–C**) and GU44Z-15 (**D**). **D, E** holotype specimen **F–H** frustule in girdle view, showing isopolar frustule wider in the middle and three girdle bands (GU44BJ-4) **I** external view of pole and advalvar surface of valvocopula, the latter showing a short row of small pores on the apical part of the pars interior (arrowhead) and the crenulated edge of the pars interior (arrow) **J** internal view of pole and abvalvar surface of valvocopula. Scale bars: 50 µm (**A–D, F**); 10 µm (**E, G–J**).

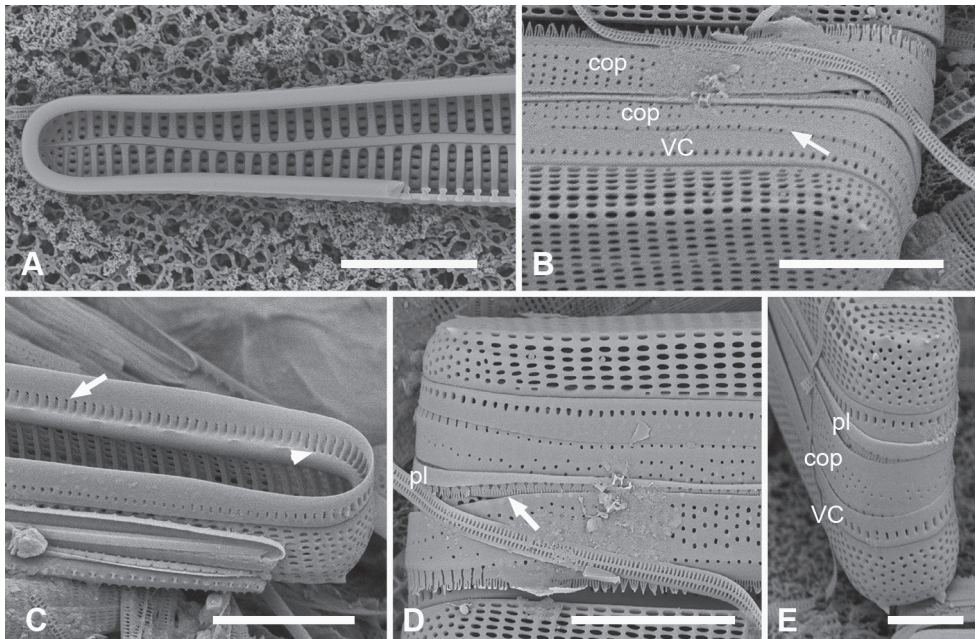


Figure 21. *Grunowago pacifica* sp. nov., cont., all GU44BJ-4, except **A** = SPN2022-1-4 **A** valve apex showing continuous rim, broken away at lower right, not expanded into a pseudoseptum **B** frustule at 40° tilt, showing fimbriate inner margin of copula on the hypotheca (top) and line of pores on pars interior (arrow) **C** valvocopula, showing internal and external aspects, the pars exterior pores (arrow) separated by ridges on the pars interior, and the presence of pores on the pars interior at the pole (arrowhead) **D** frustule in girdle view with fimbriate pars interior of pleura exposed (arrow) **E** frustule in polar view tilted 60°, showing girdle bands. Scale bars: 10 μm (**A–D**); 5 μm (**E**).

Registration. Phycobank <http://phycobank.org/103245>.

Type locality. GabGab reef, Apra Harbor, GUAM, 13.443°N, 144.643°E, ca. 1 m depth, collection number GU44Z-15, 20 June 2009. C.S. Lobban and M. Schefter leg. Additional slides from this sample have previously been deposited at California Academy of Sciences (CAS) for other species holotypes, but specimens of *G. pacifica* are not marked. Slides include CAS accession/slide numbers: 627386/223007 (*Periderrailon* spp.), 627383/223005 (*Gato hyalinus*); 627409/223023 (*Astrosyne radiata*); and 627396/223010 (*Hanicella moenia*).

Additional materials examined. GUAM: GU44L-C!, GU44AI-5! (in culture), GU44AP-8!, GU44BH-5!.

Etymology. Adjective (Latin) with reference to its presence in the Western Pacific Ocean.

Taxonomic comments. Specimens that we (Lobban et al. 2012) referred to *Synedra bacillaris* were 180–400 μm long, 14 μm wide, with 9–14 striae in 10 μm . This range of stria density is suspiciously large for Ardissonaceae and suggests that two or more species are being confounded. Some specimens in GU44BJ-4 population

were nearly linear but most likely represent an extreme within *G. pacifica* rather than an occasional *G. bacillaris*. Both Hustedt (1931–1959) and Sullivan and Wear (1995) remarked on the ease of identifying this species by the strong central costa, compared to other *Ardissona* spp., but as with other taxa where a strong identifying character has masked species diversity (e.g., *Cyclophora tenuis* – Ashworth et al. 2012, *Bleakeleya notata* – Lobban and Perez 2016), we suspect that there is hidden diversity within “*Synedra bacillaris*”. The genetic branches are long between lanceolate samples from Guam (GU44AI-5) and Florida (HK291) (see, below, Fig. 33). For now, we can only describe *Grunowago pacifica* and deal with the generic placement of that species cluster.

Group 5: Genus *Toxarium*

Toxarium hennedyanum (Gregory) Pelletan, 1889

Fig. 22

References. Hustedt 1931–1959, p. 222, 224, fig. 713 (as *Synedra hennedyana*); Round et al. 1990, p. 422–423; Lobban et al. 2012, p. 260, pl. 17, figs 1–5; Kooistra et al. 2003, fig. 1A–R (as *T. undulatum*); Hein et al. 2008, p.33, pl. 15, fig. 3; Álvarez-Blanco and Blanco 2014, p. 128, pl. 63, figs 4–6.

Description from literature. Colonial on stout mucilage stalks. Long, narrow valves, usually straight, inflated at the poles and the middle, valve lengths ranging from 300 to >1000 μm (Álvarez-Blanco and Blanco 2014); widths 6–8 μm in the middle, 5–6 μm at poles, and about 2 μm elsewhere; transapical striae very short, 9–11 in 10 μm , with scattered areolae in wider central and polar areas (Hustedt 1931–1959). Lobban et al. (2012, pl. 17, figs 4, 5) illustrated variants with few/no pores in the central part of the valve face. Girdle bands are all closed (Kooistra et al. 2003). The valvocopula has a single row of pores along junction between the pars interior and pars exterior and an asymmetrical, notched shelf that fits against the pseudoseptum. The copula has striae that are either porate or become slit-like with broadly fimbriate margins of the pars interior (compare their fig. 1I, L with our Figs 22J, 23J). The narrow pleura has a single row of pores along the junction between the pars interior and pars exterior.

Materials examined. GUAM: GU21AK-11!, GU44AK-4!, GU44BJ-4!. FEDERATED STATES OF MICRONESIA: Chuuk, TK28!. MARSHALL ISLANDS: Majuro: M1!; Jaluit: J5!; Bikar: BA2!; inter alia.

Observations. Valves 156–334 μm long, usually straight but sometimes curved, 7 μm wide at middle, 4–5 μm at poles, with a single row of areolae on the shallow mantle (Fig. 22H, J, asterisk) and two rows before the scattered areolae (Fig. 22B, D, I), making the short transverse striae 3 areolae long; stria density 10–14 in 10 μm (Fig. 22A, B, D, I, J). In the context of the present analysis, we confirm the presence of an asymmetrical pseudoseptum (Fig. 22E), asymmetrical valvocopula poles with apical notch (Fig. 22F–H), valvocopula finely fimbriate (Fig. 22I), and the copula structure tending toward slits, the striae 28 in 10 μm at the poles (Fig. 22G) increasing to 36 in

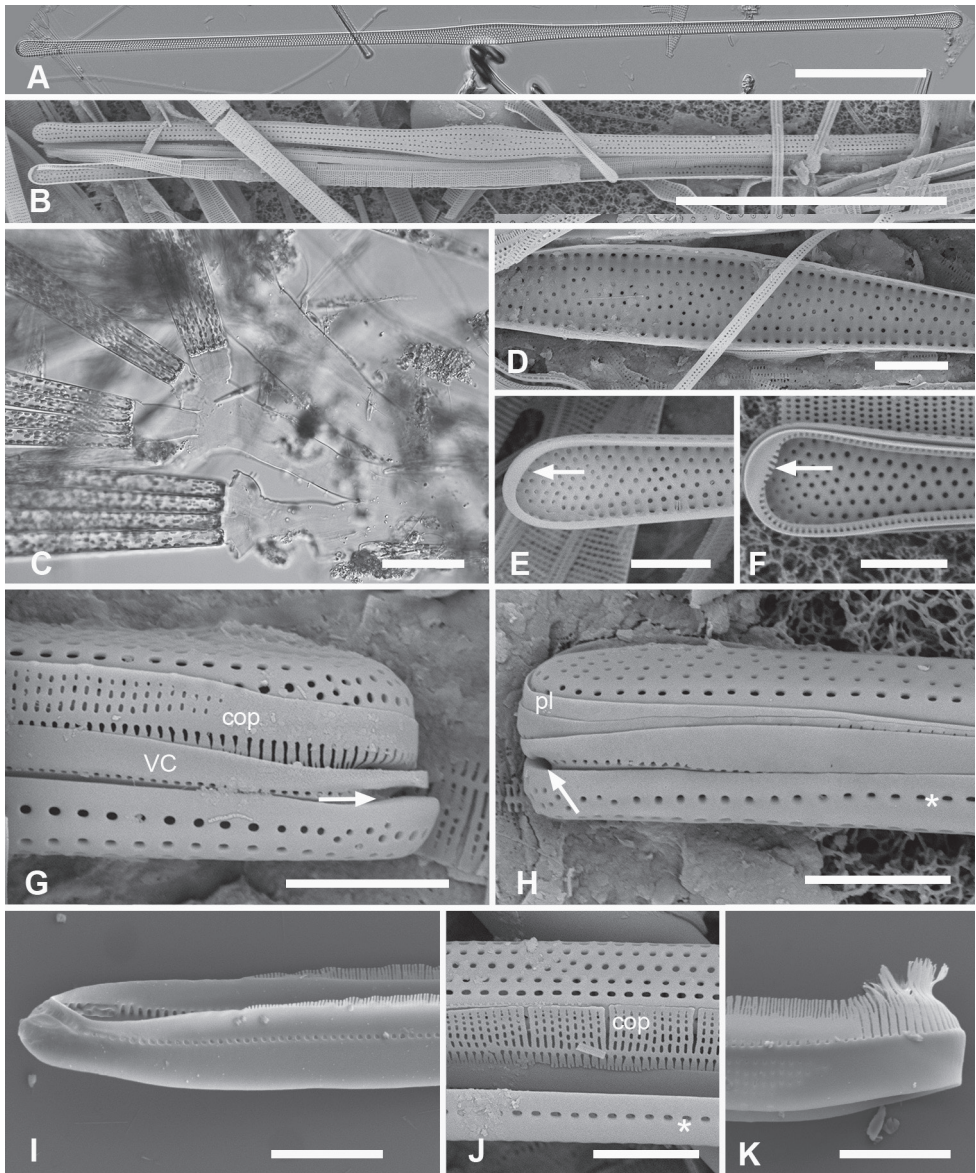


Figure 22. *Toxarium hennedyanum*, all from GU44BJ-4 except **C** GU21AK-11, and **I**, **K** culture from GU44AK-4 **A** LM of valve with typical pattern in central area; 9 striae in 10 µm **B** SEM of a valve from same sample, 12 striae in 10 µm, with reduced central area **C** mucilaginous stalks with clusters of cells **D** internal central area, showing lack of costae **E**, **F** internal pole of valve showing asymmetrical pseudoseptum (arrow) and valve with valvocopula showing similar asymmetry (arrow) **G** pole of frustule in girdle view showing apical groove (arrow) on valvocopula and fimbriae partially exposed on copula **H** pole of frustule in girdle view showing apical notch (arrow) and the pleura (pl); note single row of areolae on mantle (*) **I** pole of valvocopula in girdle view, fimbriae absent from the tip **J** narrow portion of valve showing structure of copula (compare with Fig. 23J) and single row of pores on mantle (*) **K** pole of copula in girdle view showing long fimbriae. Scale bars: 50 µm (**A–C**); 10 µm (**I**); 5 µm (**D–K**).

10 μm with broadly fimbriate pars interior (Fig. 22J). There is a knuckle-like series of arched slits on the valvocopula pars interior (Fig. 22F), different from the structure in *Synedrosphenia* (compare with Fig. 8B and Fig. 10D, E, G). Spines absent. We note that the pars exterior of the copula is hyaline around the poles. However, the fine fimbriae on the pars interior of the valvocopula (Fig. 22I) are absent from the specimens in Kooistra et al. (2003 fig. 1J, K). A pleura was present (Fig. 22H), the pars interior also fimbriate (not shown).

Taxonomic comments. Kooistra et al. (2003) show a single row of pores on the mantle and a copula that matches those shown here for *T. hennedyanum*. They do not state a stria density, but we count 11 in 10 μm , measured from their fig. 1E. There has been a tendency to ignore stria density, reflecting the marginal striae and the domination of the valve face by scattered areolae. Kooistra et al. (2003) had monoclonal cultures in which both *hennedyanum*-like and *undulatum*-like cells were present, and they proposed a merger of the two species. The specimens they show had a rippled edge, but not a strongly wavy outline (contrast Poulin et al. 1986; Hein et al. 2008, and our Fig. 23); i.e., a midline along the apical axis is straight, whereas that in *T. undulatum* is sinusoidal. If the Micronesian specimens shown here are indeed *T. hennedyanum* and *T. undulatum* (by no means certain), our results would suggest that the rippled edge seen in the cultures of Kooistra et al. (2003) was a phenotypic expression of *T. hennedyanum* and was not *T. undulatum*. We previously noted (Lobban et al. 2012) the significant genetic variation in Guam isolates of *T. hennedyanum* and *T. undulatum* reported by Theriot et al. (2010, 2011) and this is even more evident now; however, in reviewing the vouchers, we find no data from specimens attributable to *T. undulatum*; all the variation shown in Fig. 33 appears to be part of a *T. hennedyanum* complex.

Toxarium undulatum J.W. Bailey, 1854

Figs 23, 24

References. Bailey 1854, p. 15, plate (1), figs 24, 25; Peragallo and Peragallo 1897–1908, p. 314, pl. 78, fig. 7; Hustedt 1931–1959, p. 222, 224, fig. 714; Güttinger 1991 (both as *Synedra undulata*); Poulin et al. 1986, figs 33–36; Hein et al. 2008, p. 33, pl. 15, fig. 3; Lobban et al. 2012, p. 260, pl. 17, figs 6–8; Álvarez-Blanco and Blanco 2014, p. 128, pl. 63, figs 4–6.

Description from literature. *Toxarium undulatum*, the generitype, was said to differ only in the wavy outline of the valve (Hustedt 1931–1959), stria density rarely reported but Peragallo and Peragallo (1897–1908) state 12 in 10 μm . The outline in Bailey's (1854) plate is shown as undulating with a long wavelength, in Peragallo and Peragallo (1897–1908), with a shorter wavelength, and in Hustedt (1931–1959) the center clearly has a wavy edge but the “horns” are scarcely undulate. Micrographs in recent works (Witkowski et al. 2000; Hein et al. 2008) show distinctly undulate outlines. In the SEMs shown by Poulin et al. (1986) we count 19–21 striae in 10 μm , whereas Güttinger (1991: 2.01.30–10) shows specimens with lengths of 485 and 580 μm , widths 8

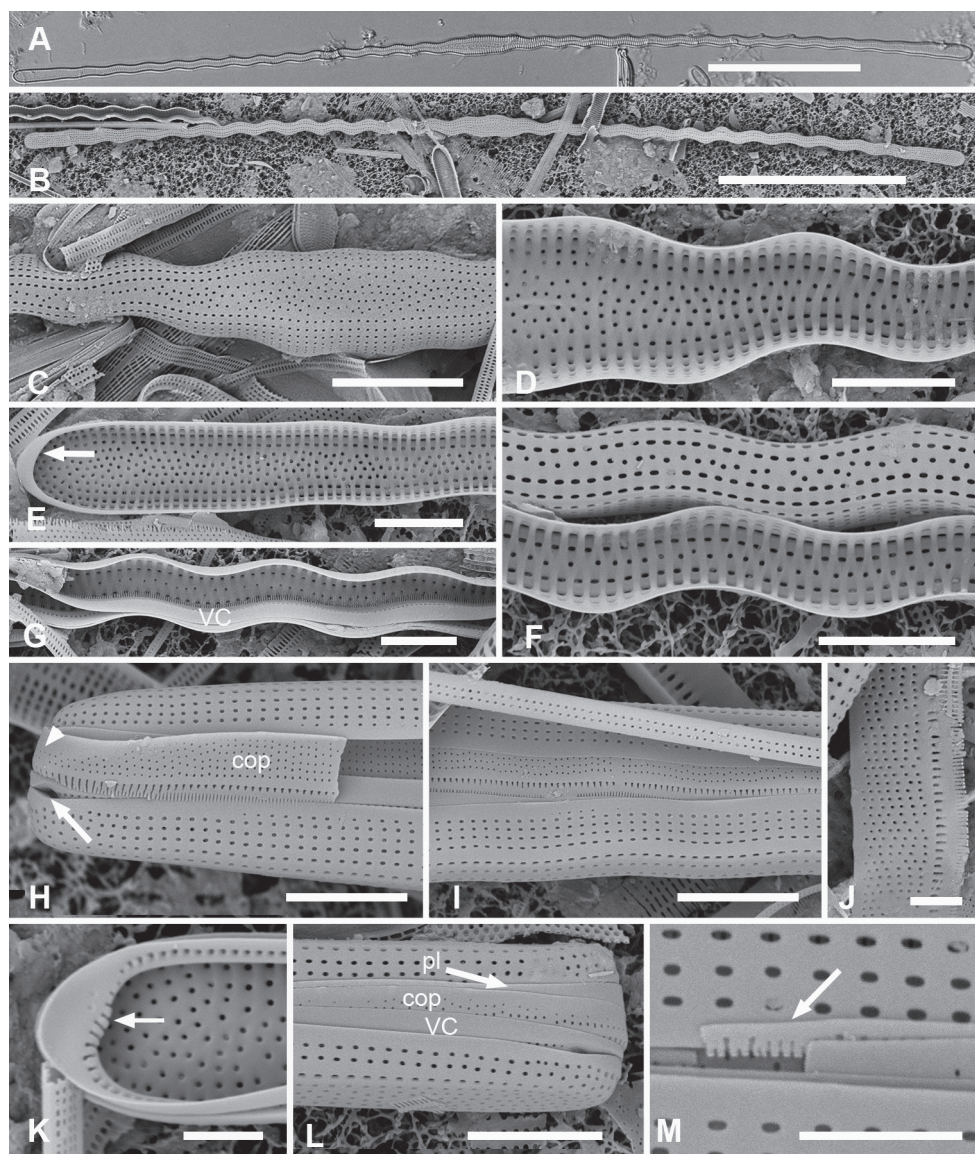


Figure 23. *Toxarium undulatum* (all from Guam, GU44BJ-4) **A, B** entire valves in LM and SEM, respectively, showing prominent undulation **C, D** central expanded portion external and internal views, respectively, the latter showing costae **E** pole, internal view showing asymmetrical pseudoseptum (arrow) **F** internal and external aspects of valve in the narrow part **G** valvocopula lying inside narrow part of valve **H, I** portion of frustules in girdle view, showing multiple rows of pores on mantle, valvocopula with apical notch (arrow), and copula with pores continuing around the pole (arrowhead) **J** detail of copula, for comparison with Fig. 22J **K** pole of valvocopula showing arched slits **L** frustule in girdle view showing pleura **M** fragment of the pleura, showing fimbriae. Scale bars: 50 μm (**A, B**); 10 μm (**C**); 5 μm (**D–I, K**); 2 μm (**J, K, M**).

μm at center, $5\ \mu\text{m}$ at poles, but with 12 striae in $10\ \mu\text{m}$. Lobban et al. (2012) reported lengths of $270\text{--}400\ \mu\text{m}$, widths $5\text{--}9$ at the center, $6\ \mu\text{m}$ at poles, $4\ \mu\text{m}$ in between, with some specimens having virtually no central inflation; no stria density stated but their fig. 7 shows 12–13 striae in $10\ \mu\text{m}$. *T. undulatum* has usually been illustrated as straight but curved specimens are shown by Hein et al. (2008) and Lobban et al. (2012). The genus was emended by Poulin et al. (1986), whose SEM images of *T. undulatum* show an asymmetrical polar pseudoseptum and internal transverse costae “in parts of the valve between the poles and the center and sometimes anastomosing” (also shown in Güttinger 1991). The *T. undulatum* from Guam (GU44S / HK210 / ECT 3802) used by Ruck et al. (2016) showed very shallow undulations, at least after culture, and additional images of the voucher stub show that it has a single row of areolae on the mantle (Suppl. material 4: Fig. S2A–C), so we would therefore identify it as *T. hennedyanum*. A similar specimen from wild material is also shown in the Suppl. material 4: Fig. S2D–F.

Materials examined. GUAM: GU44X-2!, GU44Z-15!, GU44BJ-4!, inter alia; FEDERATED STATES OF MICRONESIA: Chuuk, TK28!; Yap, Y36-2!, Y42-3!. MARSHALL ISLANDS: Majuro, M1!, Jaluit, J5!

Observations. Valves straight or commonly curved overall, strongly sinusoidal along the narrow part, the oval central portion with a wavy outline, apical portions straight sided (Fig. 23A, B, F), length $255\text{--}326\ \mu\text{m}$, width $5\ \mu\text{m}$ at poles, $7\ \mu\text{m}$ at the center, $3\ \mu\text{m}$ in between, stria densities $14\text{--}17$ in $10\ \mu\text{m}$ (Fig. 23C–I). Mantles deep with typically 3–4 areolae in the stria there (Fig. 23H, I, K). Spines absent. Valvocopula plain except for single row of pores along the base of the pars interior, fimbriate edge to pars interior (Fig. 23G), knuckle-like structure at poles, as in *T. hennedyanum* (Fig. 23K, compare with Fig. 22F). Copula with a regular pattern of small areolae on the pars exterior, forming striae consistently 34 in $10\ \mu\text{m}$ (Fig. 23H–J, L), in which the pars interior, while similar to that of *T. hennedyanum* near the poles, quickly becomes a fringe of short, narrow fimbriae with a line of triangular pores along the junction with the pars exterior (Fig. 23H). The narrow pleura was largely or entirely obscured (Fig. 23L) (this pole identified as *T. undulata* by 2+ rows of areolae on the mantle, and pores on the poles of the copula; contrast Fig. 22H); a small exposed portion showed a fimbriate edge (Fig. 23M).

We also documented *T. undulatum* in Grunow’s Honduras sample (Fig. 24). A whole valve was $700\ \mu\text{m}$ long (Fig. 24A) with long-wavelength undulations. The deep mantle sometimes exhibited longitudinal waves in the areolae (not solely an artefact of the wave in the valve, shown by short additional longitudinal lines of areolae—Fig. 24D, arrows). The striae on the valve face were two areolae long on each side bordering scattered areolae in the inflated center and poles (Fig. 24C, E), internally, the virgae were thickened into costae (Fig. 24C). Valvocopula (Fig. 24C, E–G) with a single line of areolae on the exterior, short fimbriae along the interior margin except at the sculpted poles, and a series of arched slits (Fig. 24F, G; compare Fig. 23K). Copula (Fig. 24C–E, H) wide with coarse fimbriae on the pars interior, forked at the tips, exterior with striae of pores tending to merge into slits, especially on the advalvar side. Fimbriate pleura clearly seen in Fig. 24H.

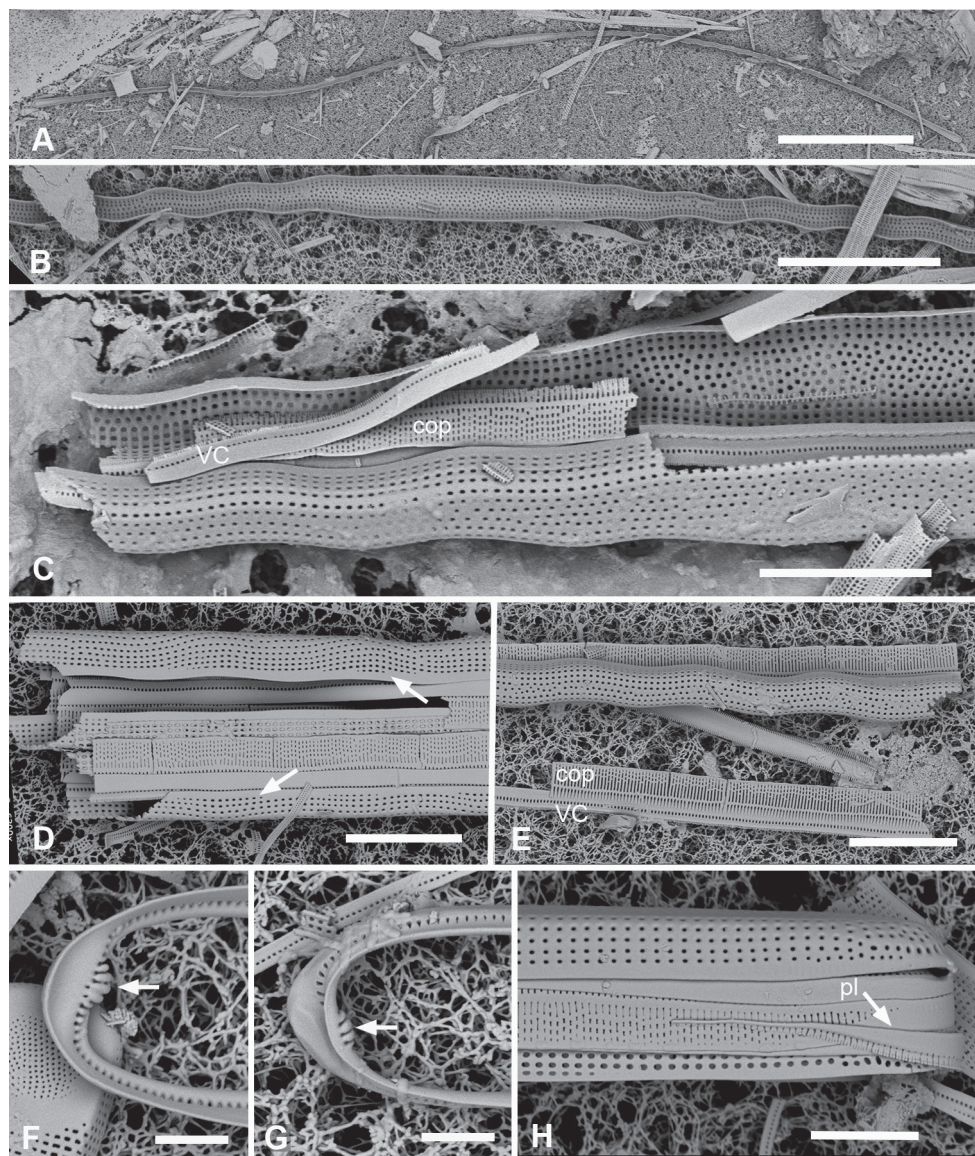


Figure 24. *Toxarium undulatum* from Grunow's Honduras material **A**, **B** entire valve, 700 µm long, and detail of central portion, showing long-wavelength undulations **C** portion with the central inflation, showing mantle depth, internal costae, valvocupula and copula (stria density 14 in 10 µm) **D** frustule in girdle view, showing vertical wave in rows of areolae with inserted arcs (arrows); notice also the different depths of the two mantles (stria density 17 in 10 µm) **E** portion of valve with copula and valvocupula **F**, **G** valvocupula pole, abvalvar and advalvar surfaces, respectively, showing series of arched slits (compare with Fig. 22F) **H** pole of frustule showing fimbriate pleura and notch in valvocupula. Scale bars: 100 µm (**A**); 25 µm (**B**); 10 µm (**C–E**); 5 µm (**F–H**).

Taxonomic comments. The specimens from Grunow's Honduras material are near the length ("about 35m" = 890 μm ; see Itaki and Bjørklund 2006) and shape described by Bailey (1854) for specimens from *Sargassum* in Narragansett Bay. As noted by Hustedt (1931–1959), Grunow (1877) did not mention this species (in the context of presenting new species), but Hustedt says he observed it on Grunow's slides.

In the Micronesian samples, depths of the mantle, and structure of the copula were different in the two species, so we can assert that the specimens shown here for *T. hennedyanum* and *T. undulatum* are different species. The large genetic variation in *Toxarium* materials we have sequenced (Fig. 33) casts doubt on whether either of them might be identified to authentic Atlantic types, a question highlighted by the Grunow specimens. It similarly raises questions about the number of species there might be in Micronesia. Both questions require much more work to define the range of character states and their combinations, but the oft-repeated claim that the two species differ only in outline is already not supported by morphological evidence. The more important point for the present study is to establish generic characters for comparison to those of the genera in Ardissonaceae and Climacospheeniaceae.

The *Toxarium* spp. specimens shown here from sample GU44BJ-4 were in a community with the new species *Ardissonopsis gracilis* (see above), which has a slightly undulate outline but is distinguished from *T. undulatum* by the cuneate girdle view, regular striae across the valve face, apical spines, and the decussate pattern of pores on the girdle bands (Fig. 18). Also present were *Synedrosphenia gomphonema*, *S. crystallina*, *Ardissonopsis fulgicans*, *A. appressata*, and *Grunowago pacifica*.

Group 6: Genus *Climacospheenia*

Table 5

Climacospheenia elongata J.W. Bailey, 1854

Fig. 25

References. Bailey 1854, p. 353, pl. 1, figs 10, 11; Peragallo and Peragallo 1897–1908, p. 352, pl. 86, figs 2–4; Hustedt 1914, pl. 307, figs 1–4; Ricard 1977, figs 669–677; Montgomery 1978, pl. 114, fig. E–H; Round 1982, figs 1–38 (in part); Round et al. 1990, p. 442.

Description from literature. *C. elongata* has been described (e.g., by Peragallo and Peragallo 1897–1908 and Hustedt 1931–1959) as identical to *C. moniligera* Ehrenberg, 1843 except for the valve tapering more abruptly to a stem with parallel sides. Yet Bailey (1854) had specifically distinguished his species from *C. moniligera* by the finer stria density (without giving numbers) and described a species 330 μm long, with very wide craticular bars (as shown also in Peragallo and Peragallo 1897–1908, pl. 86, fig. 5; Hustedt 1914, pl. 307, figs 1–4; and Round 1982, fig. 3) (Table 5). Peragallo and Peragallo (1897–1908) gave stria densities of 18–21 near the basal pole, 27–>30 near the apical pole for *C. elongata* versus 16–17 in 10 μm basal and 19–20 in 10 μm apical for *C. moniligera* but expressed the opinion that there was intergradation between the

Table 5. Comparison of *Climacosphenia* species from literature and present observations.

	Valve length, μm	Width near basal pole, μm	Shape	Valvocopula width near apical pole†, μm	Annulus width near apical pole†, μm	Stria density in 10 μm	Craticular bars
<i>C. elegantissima</i>	700–1305	10	Spathulate	22–24	8	18–21 basal, 27–28 apical	Narrow throughout, complex unions in stem often double
<i>C. elongata</i> ‡ (literature)	325–525	–	Clavate	–	–	18–21 basal, 27–30 apical	± Narrow throughout, complex unions in stem
<i>C. elongata</i> (this study)	278–516	8–9	Clavate	30–31	14–18	22 basal, 28 apical	± Narrow throughout, complex unions in lower stem
<i>C. moniligera</i> ‡ (literature)	200–700	10	Gradual taper	15–40	–	16–17 basal, 19–20 apical	Wide throughout; complex unions ?throughout
<i>C. scimiter</i>	390–612	9	Curved	25–26	7–10	21 basal, 29 apical	Narrow throughout, complex unions absent
<i>C. soulonalis</i>	390–530	10–12	Gradual taper	29–35	15	18–20 basal, 28–29 apical	Narrow throughout, complex unions only in basal 1–3 bars

† We have tried to standardize width measurements for comparison with annulus width by measuring width across the valvocopula rather than the valve because the mantles are deep and tend to spread out, but width data for *C. moniligera* are from the literature.
‡ Confusion between *moniligera* and *elongata* in the literature (see text) has led to a wide range of morphometrics; here we have summarized dimensions from Bailey (1854) and Peragallo and Peragallo (1897–1908) for these species, and craticular bars from drawings in Ehrenberg (1853, pl. 2, part 6, fig. 1a, b), Peragallo and Peragallo (1897–1908, plate 86, fig. 5), Hustedt (1914, pl. 307, figs 1–4), and Round (1982, fig. 3). Navarro et al. (1989, fig. 11) and Witkowski et al. (2000, pl. 18, fig. 1) also show recognizable *C. moniligera* in LM.

two species. Hustedt (1931–1959) said that Peragallo and Peragallo had confused their European specimens of *C. elongata* with *C. moniligera* and he attempted to resolve the confusion with an original drawing of a cell with a very long, very narrow stem. The drawing (his fig. 626) was based on Samoan specimens he had published in “Schmidt’s Atlas” (Hustedt 1914). Round (1982) attempted to clarify the difference between the two species, not considering the variation within *C. elongata*, but his drawings of *C. elongata* show specimens no more than 320 μm long. In recent literature, Álvarez Blanco and Blanco (2014), show short cells similar those in Peragallo and Peragallo (1897–1908), while Navarro and Lobban (2009) reported cells 750–1200 μm long from a Guam sample, similar in shape to those in Hustedt (1931–1959), a range that otherwise occurs only in Hustedt’s report (table in Álvarez Blanco and Blanco 2014: 103). Ultrastructural characters: Apical spines present; costae generally present; frustules have only two girdle bands, both with fimbriate inner margins (Ricard 1987, fig. 677; Montgomery 1978, pl. 114, fig. G; Round 1982).

Materials examined. GUAM: GU44Y-13!, GU44U-1B!, GU44BM-4!, GU44BM-7!, GU52X-1!. FEDERATED STATES OF MICRONESIA: Chuuk, TK4!

Observations. Valve clavate, apical part gradually tapering to a narrow stem nearly half the total length of 278–516 μm (Fig. 25A, B); maximum width 30–33 at apical pole, 7–8 μm across stem and expanding slightly to 9 μm across basal pole (Table 5); annulus closed at both poles, gradually tapering from maximum width of 16–17 μm near apical pole (Fig. 25B arrows, D, E). Stria densities 28 in 10 μm near apical pole (Fig. 25E), 22 in 10 μm near basal pole outside the annulus; sparser and more loosely organized inside annulus at basal pole (Fig. 25D, G). Apical spines present (Fig. 25E),

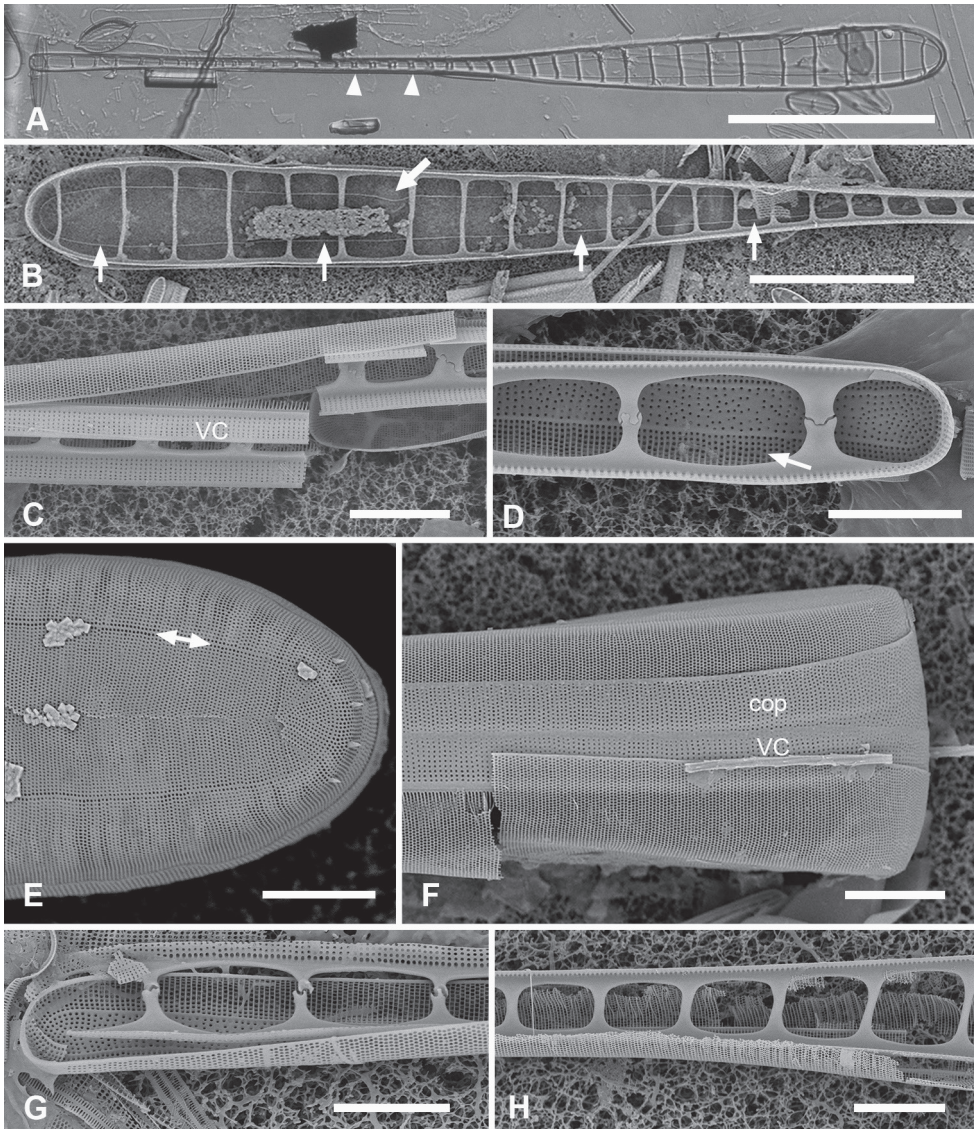


Figure 25. *Climacosphenia elongata*, GU44BM-7, except as noted **A** valve with valvocopula in LM, showing consistently narrow craticular bars, some double (arrowheads) (GU44X-2) **B** apical part of a valve with valvocopula in SEM, showing the progressive narrowing of the annular ring (series of small arrows) and the wider space between craticular bars where the nucleus resides (thick arrow) **C** narrow portion of valve with valvocopula showing the fibmbriae **D** basal pole of valve with valvocopula, showing the scattered pattern of areolae inside the annulus gradually becoming regular striae, development of costae (arrow), and complex unions in the craticular bars **E** external view of apical pole showing annulus (double-headed arrow) and spines **F** frustule in girdle view showing the two girdle bands **G**, **H** valvocopula near basal pole and in tapering part at top of “stem,” respectively, showing complex versus simple unions in the craticular bars (TK4). Scale bars: 100 μm (**A**); 50 μm (**B**); 10 μm (**C–H**).

pseudoseptum absent (Fig. 25G). Costae present except at basal pole, where they start at margin and extend centripetally, eventually thickening the virgae inside the annulus (Fig. 25G). Valvocopula stria density 19 in 10 μm (Fig. 25E, F), pars interior with comb of long, unbranched fimbriae (Fig. 25C). Craticular bars consistently narrow (1 μm) (Fig. 25B, D, G, H), though sometimes doubled (Fig. 25A), the spaces between them rectangular with rounded corners; connections complex in most of the stem, becoming simple where the valve widened (Fig. 25C, D, G vs Fig. 25B, H). There was a wider space between two of the bars in the middle of the wide part (Fig. 25B, thick arrow); based on our observations on *C. elegantissima* (below), this is probably the location of the nucleus. Copula with 24 striae in 10 μm (Fig. 25F), pars interior not observed.

Taxonomic comments. The shape and morphometrics accord adequately with the literature on *C. elongata*, the narrow craticular bars, especially in the stem, differing from the sturdy bars and oval spaces of *C. moniligera*, and from the very long-stemmed specimens depicted by Hustedt (1931–1959, p. 89, fig. 626). Based on the available evidence, we accept the hypothesis that the specimens shown in Fig. 25 are Bailey's species.

Climacospheonia elegantissima Lobban & Ashworth, sp. nov.

Figs 26–28

References. ?Hustedt 1914 in Schmidt et al. 1874–1959, pl. 308, figs 5–10; ?Hustedt 1931–1959, fig. 626; Navarro and Lobban 2009, p. 136, figs 64, 65 (all as *C. elongata* Bailey).

Diagnosis. Differing from *C. elongata* in the greater length, especially in the stem, and narrower, linear apical portion, and from *C. truncata* Hustedt ex Simonsen in the shape of the wide part of the valve.

Description. Cells attached in small groups to stout, branched mucilage stalks (Fig. 26A, E), at least 110 μm wide at the base and up to 2 mm long. Frustule generally deeper than wide, especially where stem first narrows below the apical pole, ratio there about 15 μm deep to 5 μm wide (Fig. 27A). Nucleus situated between two more-widely spaced craticular bars about 120 μm from apical pole (Fig. 26A, D); plastids lenticular. Valves 750–1305 μm long, linear toward apical pole, 22–24 μm wide, then tapering to a long linear stem, 5 μm wide, expanding to 10 μm at the pole (Figs 26A–C, 27A). Stria density 27–28 in 10 μm through most of the valve but 18–21 in 10 μm near basal pole, sparser and more scattered inside annulus near basal pole (Fig. 27D, E, G). There was a crescent of scattered areolae at top of mantle at apical pole (Figs 27D, G, 28A) (noticed in *Climacospheonia* spp. by Round 1982: figs 15, 16, 25). Annulus apparently open at basal pole, sides \pm parallel in the wide area, 8.3 μm apart, in the stem 2.3 μm apart, expanded to 5 μm at the basal pole (Fig. 27C–G). Two or more stout spines on external apical pole (Figs 27D, 28A), shallow transapical costae throughout except near basal pole (Fig. 27E, G). Pseudoseptum absent (Fig. 27F, G). Two girdle bands (Fig. 28A): valvocopula (Figs 26B, F, 27B, C, F, I, 28A–C) with fimbriate inner edge

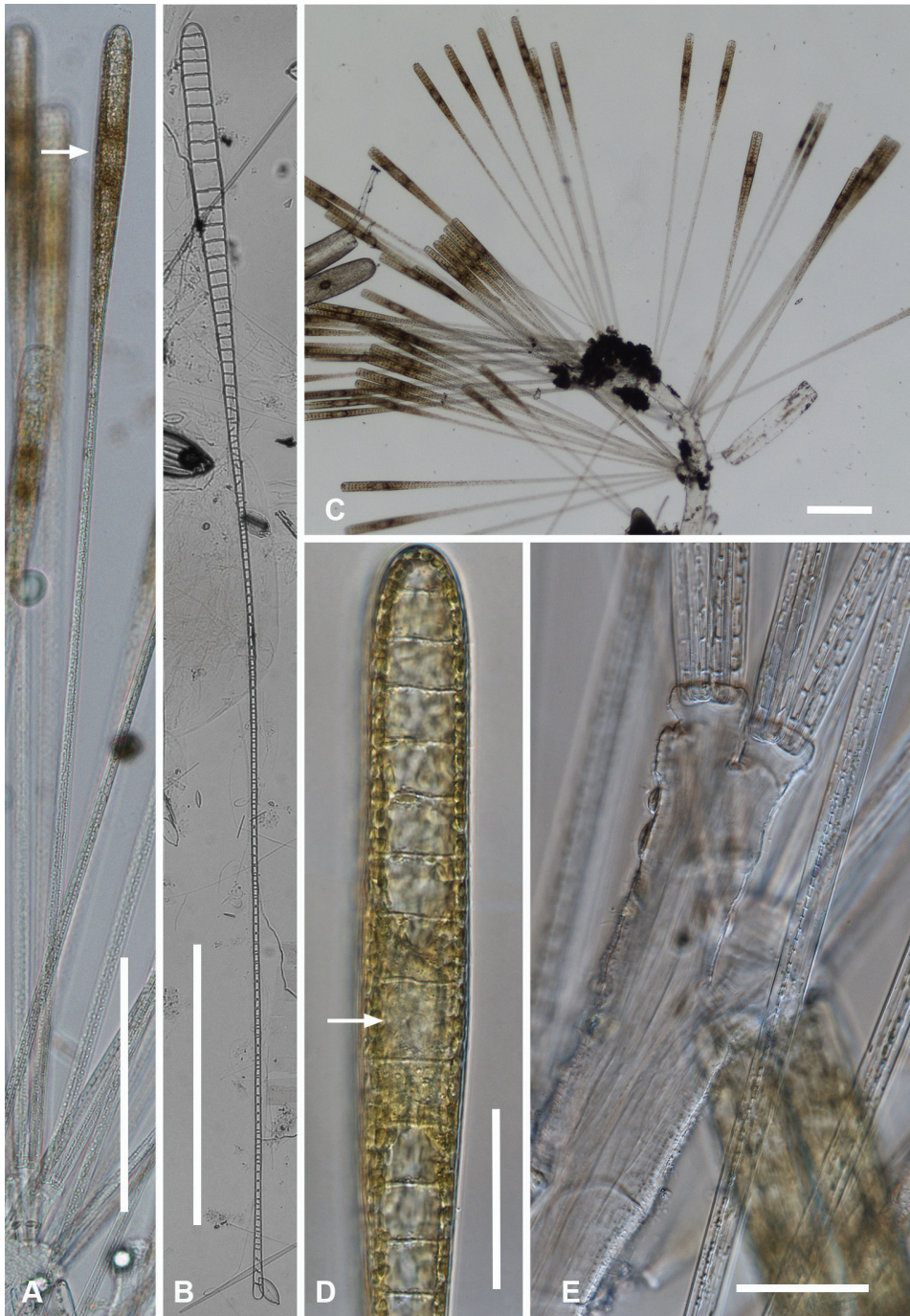


Figure 26. *Climacosphenia elegantissima* sp. nov., (GU52AI-1 except **B** from GU52U-2) **A, D** living cell, showing extreme length and location of nucleus (arrow) **B** acid-cleaned complete valvocopula, emphasizing the very long, narrow stem **C** portion of colony, showing cells attached to mucilage stalk; the two cells to right of middle are 1300 μm long **E** detail of mucilage stalk with bases of attached cells. Scale bars: 250 μm (**A–C**); 50 μm (**D, E**).

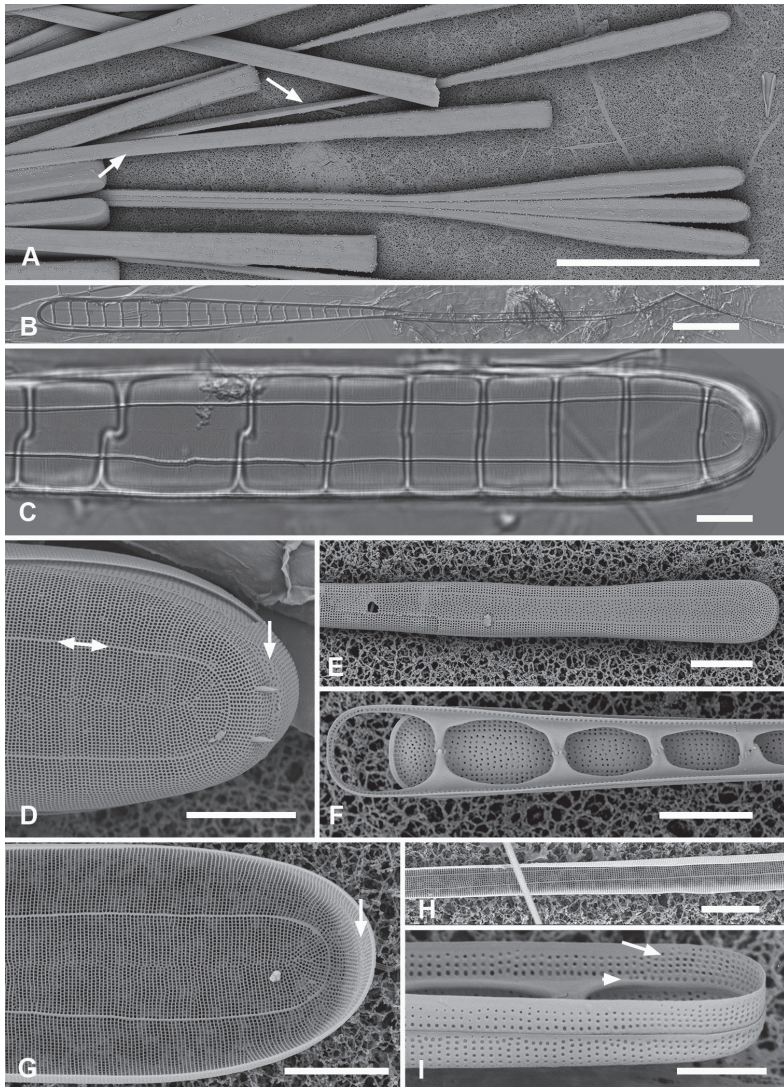


Figure 27. *Climacosphenia elegantissima* sp. nov., cont. GU52AI-1, except GU52U-2 (**B**) and GU52X-1 (**G, H**) **A** whole mount of colony in SEM, showing contrasting width versus depth of frustule in the stem (arrows at approximately same distance from apical poles) **B** portion of holotype in LM; although specimen is broken in two places, the basal pole of the valvocopula is also present, total length ca. 835 µm **C** apical pole of valve and valvocopula in LM, showing parallel sides of annulus and some misaligned unions in the craticular bars **D** SEM of external valve surface at apical pole, showing annulus (double-headed arrow) continuing around apical pole, two spines, and crescent of scattered areolae at top of mantle (arrow) **E** external valve surface at basal pole, showing variation in areola density and alignment within the annulus, apparent discontinuity of annulus at pole, and width of basal pole relative to stem (cf. **H** at same scale) **F** internal aspect of basal pole of valve and valvocopula, showing absence of pseudoseptum (arrow) and associated structure in valvocopula **G, H** internal aspect of valve at apical pole, showing crescent of scattered areolae (arrow) and in the narrow stem, respectively **I** oblique view of basal pole with valve and valvocopula, showing increase in areola density on the valvocopula around the pole (arrow) and short row of pores on pars interior (arrowhead). Scale bars: 200 µm (**A**); 50 µm (**B**); 10 µm (**C–H**); 5 µm (**I**).

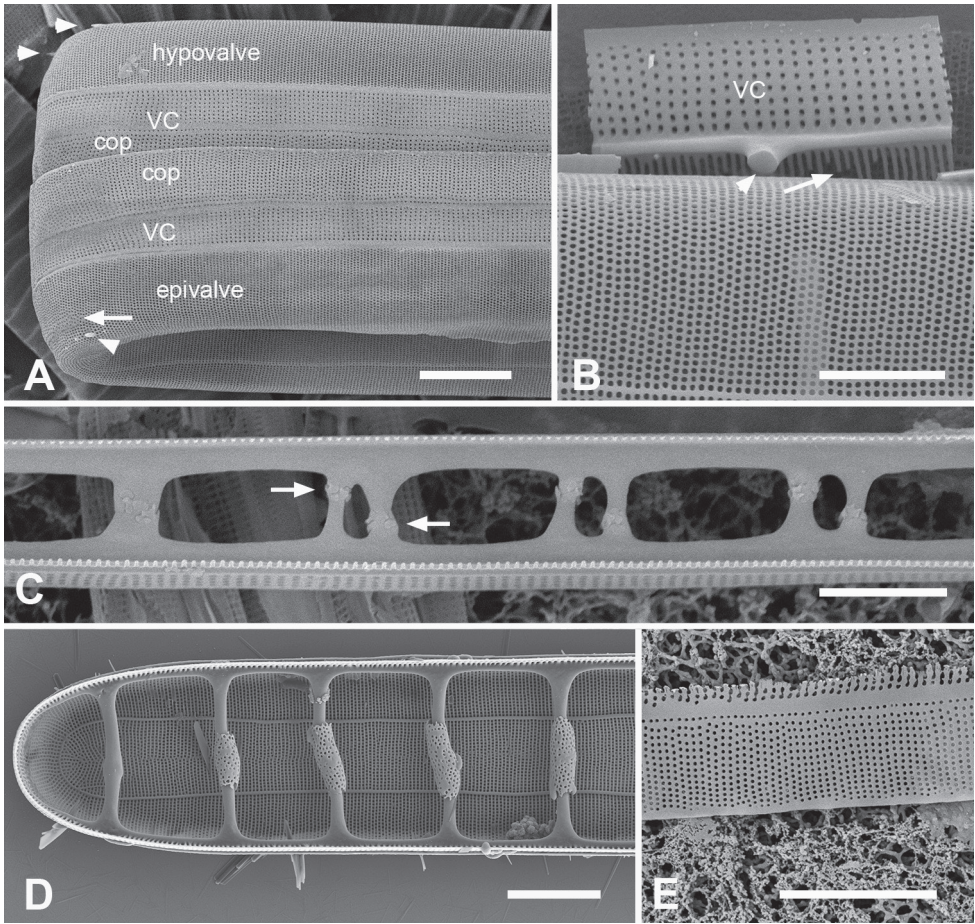


Figure 28. *Climacosphenia elegantissima* sp. nov., cont. GU52U-2 (**A**), GU52X-1 (**B**, **C**), GU44AI-5 culture (**D**), GU52AI-1 (**E**) **A** whole mount of frustule apical pole in girdle view, showing two girdle bands, patch of irregular areolae on the valve mantle (arrow), spines (arrowheads) **B** part of valvocopula broken away and showing a solid circular cross-section of the craticular bar (arrowhead) and well-developed fimbriae (arrow) **C** portion of valvocopula from stem, showing double craticular bars, ingrowths from opposite sides **D** apical pole with valvocopula showing porous bands of silica around several craticular bars **E** detail of copula showing stria density and fimbriate margin on pars interior. Scale bars: 10 μm (**A**, **D**, **E**); 5 μm (**B**, **C**).

(Fig. 28B), stria density 19 in 10 μm (Fig. 28A, B) but increasing around foot pole, where there was also a row of pores on pars interior (Fig. 27I). Craticular bars widely spaced in wide part of the cell, with widest space corresponding to the location of the nucleus (Figs 26B, 27B); in the stem becoming much closer together (Figs 26B, 28C), often paired with the two bars apparently growing from opposite sides (Fig. 28C). In one specimen from culture, we observed porous bands of silica around several craticular bars near the apical pole (Fig. 28D). Copula fimbriate, more densely striated than the valvocopula but less than the valve, 22 in 10 μm (Fig. 28A, E). A search of abundant girdle views in whole mounts showed no sign of a pleura.

Holotype (designated here). Specimen at 16.1 mm E, 12.8 mm S of the mark on slide 1861; deposited at Academy of Natural Sciences, Drexel University, Philadelphia, accession number ANSP GC20108. Fig. 27B.

Registration. Phycobank <http://phycobank.org/103246>.

Type locality. GUAM: Apra Harbor, Scuba Beach, 13.464°N, 144.656°E, epiphytic on filamentous red algae in farmer fish territory, collection number GU52U-2, 10 May 2015. C.S. Lobban and M. Scheffter leg.

Additional materials examined. GU44AI-5! (culture), GU44BM-7!, GU52G-B!, GU52X-1!, GU52Y-3B!, GU52AI-1!.

Etymology. Superlative of *elegans*, with reference to the slender appearance of the extremely long cells.

Taxonomic comments. The width of the apical pole and especially the distance between the annular lines are narrower than in *C. elongata* (Table 5) and the stem is also narrower, though the basal pole is inflated and slightly wider than *C. elongata*. Hustedt's (1914) drawings of *C. elongata* have the greatly extended stems that are present in our new species, but the apical portions of his cells are generally elliptical rather than linear. However, the valvocopula (Hustedt 1914, pl. 308, fig. 6) is notable in having parallel sides as far as the large space (i.e., where the nucleus would have been), so it is possible they represent *C. elegantissima*. *Climacosphenia truncata* from Borneo is also illustrated there (pl. 308, figs 1–4); it also has a very long stem but possesses an essentially triangular blade with a bluntly rounded apical pole. *C. elegantissima* is common as an epiphyte on filamentous seaweeds in Guam farmer fish territories and such habitats around the western Pacific/ IndoPacific may yield new material of *C. truncata* and other *Climacosphenia* spp.

Round (1982) showed porous bands of silica on craticular bars near the basal pole of both species only found in Hawaiian material. We saw them only once on apical bars in *C. elegantissima*. Their distribution and function are unknown.

Climacosphenia scimitar A. Mann, 1925

Figs 29, 30

Reference. Mann 1925, p. 59, pl. 12, fig. 4.

Description from literature. Cells tapering uniformly and strongly curved, the septa “delicate,” very narrow, “and showing at the middle either obscurely or not at all the break or sutural division common to specimens of this genus.” Length 414 µm, width at apical pole 28 µm, stria density not specified.

Materials examined. GUAM: GU52U-2!, GU52AH!, GU44Z-15!. F.S.M.: Chuuk: TK28!.

Observations. Specimens fitting this description have been found in Guam and Chuuk, often together with *C. elegantissima*. Colonies on branched mucilaginous stalks, the nucleus near the apical pole between two of the widely spaced craticular bars (Fig. 29A). Length 390–612 µm, maximum width 25–26 µm near apical pole, 8–10 µm across basal pole (Fig. 29A, B). Stria densities outside the annulus 21 in 10 µm in lower

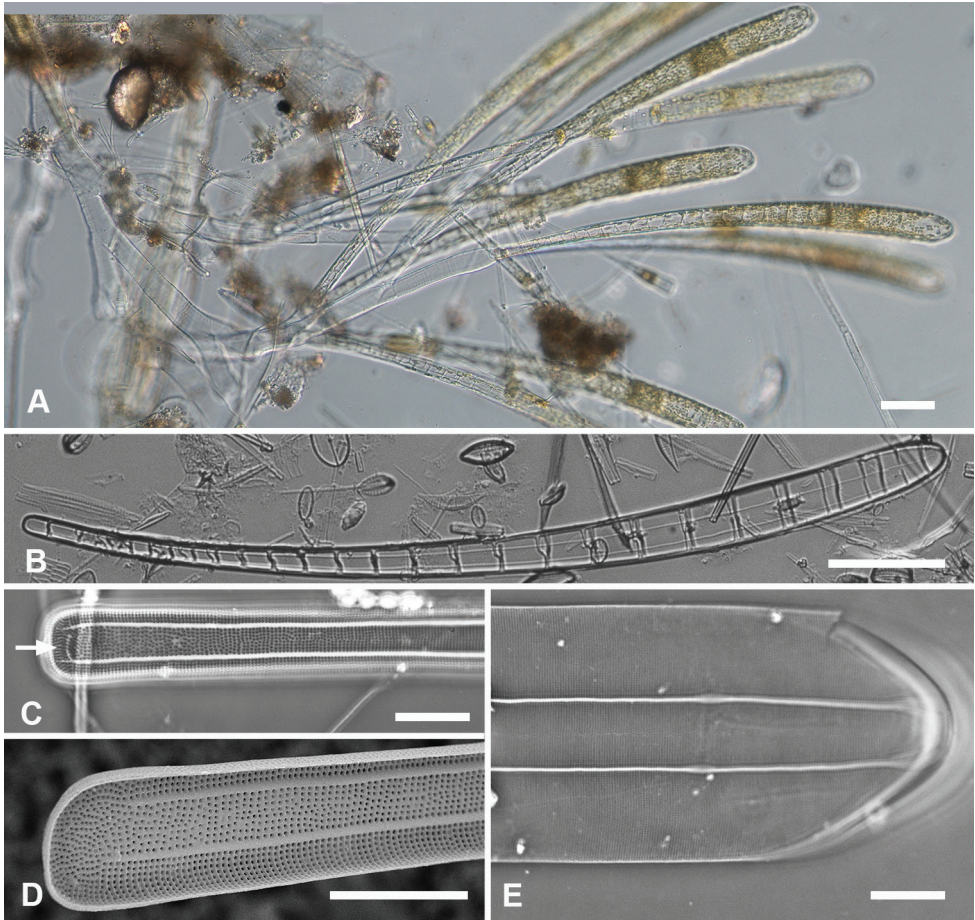


Figure 29. *Climacosphenia scimitar*, all from GU52X-1 **A** colony of living cells on branched mucilage stalk **B** valve and valvocopula of cleaned material, LM-DIC, showing consistently narrow craticular bars **C**, **E** valve in phase contrast LM, showing more strongly silicified basal pole in **C** and weakly silicified apical portion in **E**, along with difference in stria density; note appearance of annulus at basal pole (arrow, **C**) **D** basal pole in SEM, oblique view, showing shallow mantle and very weak costae and apparently discontinuous annulus. Scale bars: 50 μm (**A**, **B**); 10 μm (**C**–**E**).

part, 29 in 10 μm at apical pole; striae within annulus at basal pole about 16 in 10 μm , areolae more, or less aligned (Fig. 29C–E vs Fig. 30A). Maximum distance across annulus 10 μm (Figs 29B, D, 30A). While annulus appears discontinuous in SEM, phase contrast suggests continuity (Fig. 29C). Valves delicate except at basal pole, apical striae hard to resolve in LM even with phase contrast (Fig. 29C, E), costae not developed on either vimines or annulus, except near basal pole (Fig. 29D). Two spines on apical pole of valve (Fig. 30A, D). Two girdle bands present, both broad and with regular striae, but at different densities, valvocopula 20 in 10 μm , copula 24 in 10 μm (Fig. 30D). Valvocopulae fimbriate with narrow, widely spaced craticular bars, unions all seamless (Fig. 30E–G).

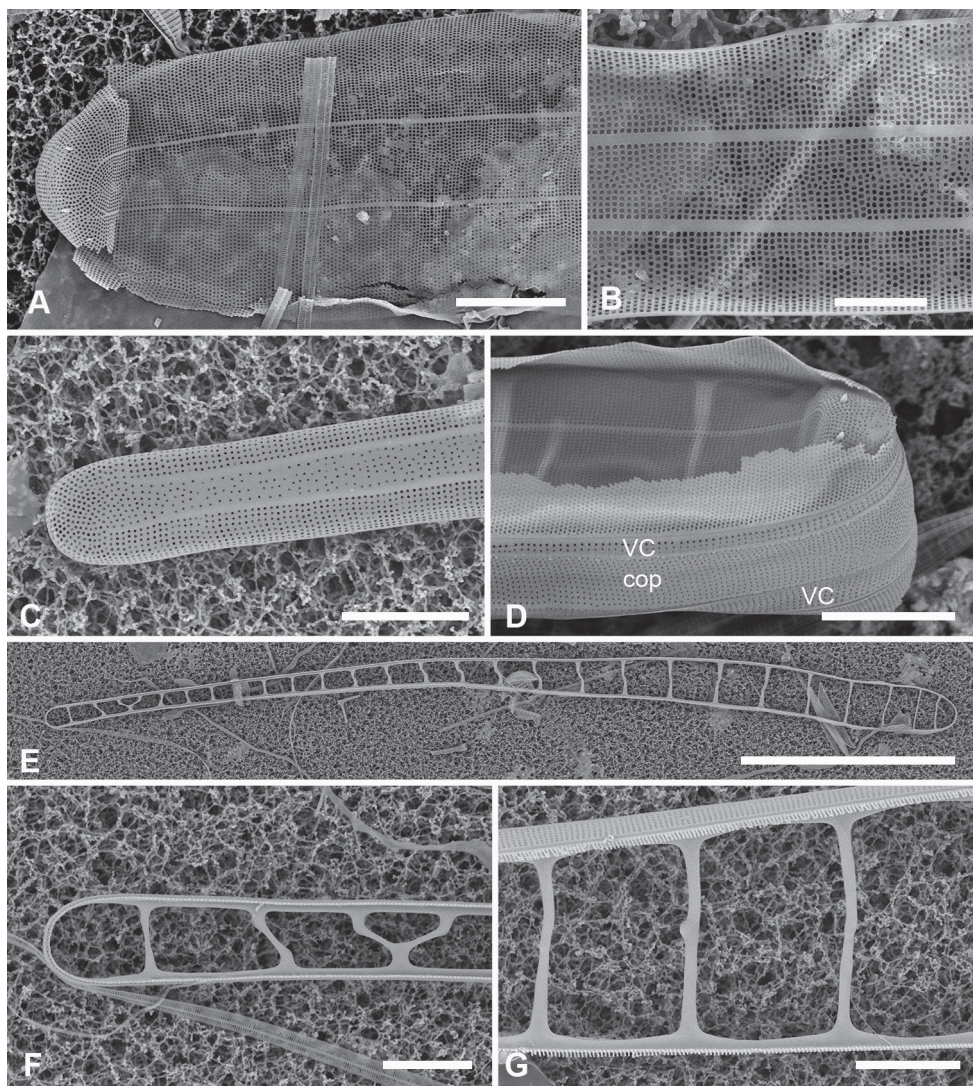


Figure 30. *Climacosphenia scimiter*, cont. All GU52X-1 except **D**, GU52U-2 **A** apical pole of valve, exterior view, showing stria density and spines **B** detail of valve internal aspect, showing absence of costae **C** detail of external valve face at basal pole, showing more scattered areolae inside annulus **D** whole mount of frustule, apical pole, showing spines and girdle bands **E–G** valvocopulae showing consistently seamless craticular bars. Scale bars: 100 μm (**E**); 10 μm (**A**, **C**, **D**, **F**, **G**); 5 μm (**B**).

Taxonomic comments. Observations are completely in accord with Mann’s (1925) description of specimens from the Philippines (Mann noted that data on the locations of the dredge samples were lost). Given also that this species was discovered not far from Micronesia, we are confident in the identification. We cannot accept that this is merely a curved *C. moniligera*, as suggested by Round (1982), because of the great difference in septum characters and differences in stria densities. Whether there exist straight versions of this species, or curved *C. moniligera* populations, remain open questions.

Climacosphenia soulonalis Lobban & Joon S. Park, sp. nov.

Fig. 31

Diagnosis. Differing from *C. moniligera* in apical stria density and delicate craticular bars throughout, seamless except for complex unions in the most basal 1–4 bars and from *C. scimiter* in straight outline, presence of complex unions, and cell width.

Description. Valves straight, gradually tapering from apical pole almost to basal pole (Fig. 31A–C), only a short basal part with parallel sides. Length 390–530 μm , width 29–35 μm across apical pole (measured on valvocopula; total valve width including mantles 50 μm), 10–12 μm across basal pole at last craticular bar (Fig. 31A–

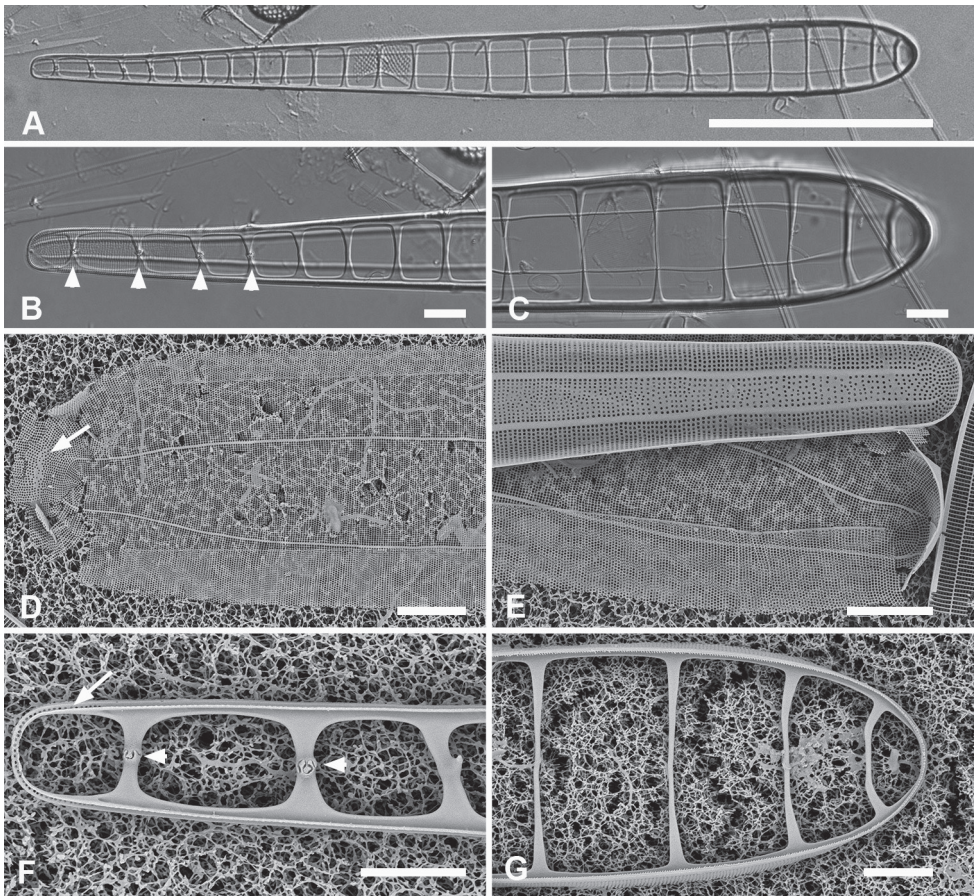


Figure 31. *Climacosphenia soulonalis* sp. nov. All TK4 **A–C** holotype valve with valvocopula, entire, basal pole and apical pole, respectively, showing seamless craticular bars except near basal pole; arrow-heads on **B** show complex unions **D** external valve apical pole showing irregular patch of areolae (arrow), spines, and narrowing of the annulus at apical pole **E** internal aspects of basal and apical poles, showing lack of costae (contrast costae in the piece of *Synedrosphenia crystallina* to the right) **F, G** valvocopula with two complex unions at the basal pole (arrowheads, **F**) and showing the row of pores on the pars interior around the basal pole (arrow). Scale bars: 100 μm (**A**); 10 μm (**B–G**).

G). Annulus narrower at apical pole (Fig. 31C–E), widest 15 μm , steadily tapering to 4 μm , apparently open at basal pole (Fig. 31E). Stria densities 18–20 in 10 μm in lower part of the periphery, 28–29 in 10 μm in periphery at apical pole, about 16 in 10 μm in middle part above basal pole (Fig. 31E). Spines present on apical pole and a small patch of irregular areolae (Fig. 31D). Costae apparently poorly developed. Valvocopula fimbriate with narrow, widely spaced craticular bars that have seamless unions except for the most basal 1–4 (Fig. 31B, F); a row of pores on pars interior just around basal pole (Fig. 31F). Copula not positively identified.

Holotype (designated here). Specimen at 17.8 E, 10.9 mm S of the mark on slide 153; deposited at ANSP, accession number GC20109. Fig. 31A–C.

Registration. Phycobank <http://phycobank.org/103247>.

Type locality. FEDERATED STATES OF MICRONESIA: Chuuk: Northeast Pass into Chuuk Lagoon, 7.514°N, 151.967°E, on algal turf from farmer fish territory, lee side of Moch I., collection number TK4!, 30 May 1991. C.S. Lobban and M. Schefter leg.

Additional materials examined. Chuuk: TK28!, exposed reef, ca. 6 m deep, southeast corner of Northeast Passage.

Etymology. Belonging to Sou-lon, “the Chuukese god of ocean depths and storms, equivalent, perhaps to Neptune” (W.M. Peck 1992, Chuukese Testament. Storyboard: A Journal of Pacific Imagery 2: 44).

Taxonomic comments. Valves resemble *C. moniligera* in size and stria densities (Table 5) but differ in the valve shape and the narrow and mostly seamless craticular bars are unlike the massive septum with complex unions in the bars reported for *C. moniligera* (Peragallo and Peragallo 1897–1908; Hustedt 1931–1959; Round 1982).

Systematics

Morphological cladistics

The cladistic analysis of the character set (Suppl. material 2: Table S2) resolved 18 equally parsimonious trees, which we have summarized as a strict consensus tree (Fig. 32). The genera with striae perpendicular to the bifacial annulus across the entirety of the valve (*Ardissonea*, *Synedrosphenia*, *Ardissoneopsis*, *Climacosphenia* and *Grunowago*) formed a monophyletic group (*Toxarium hennedeyanum* was used as the outgroup). Three genera appear to have morphological synapomorphies: *Climacosphenia* (craticular bars on the valvocopula), *Ardissonea* (the internal wall) and *Grunowago* (the central longitudinal costa). Morphological synapomorphies for *Ardissoneopsis* and *Synedrosphenia* are less clear but each genus has a unique combination of the main characters (Table 6). The species of *Ardissoneopsis* form a polytomy with *Climacosphenia*, sharing the heteropolar shape of the frustule in girdle view (though this character is lost in *A. fulgicans*). The taxa in *Synedrosphenia* have a range of character states, and the only characters shared by all the species (internal transverse costae, pseudosepta, apical notch on the valvocopula and fimbriate girdle bands) are also shared by species in other genera.

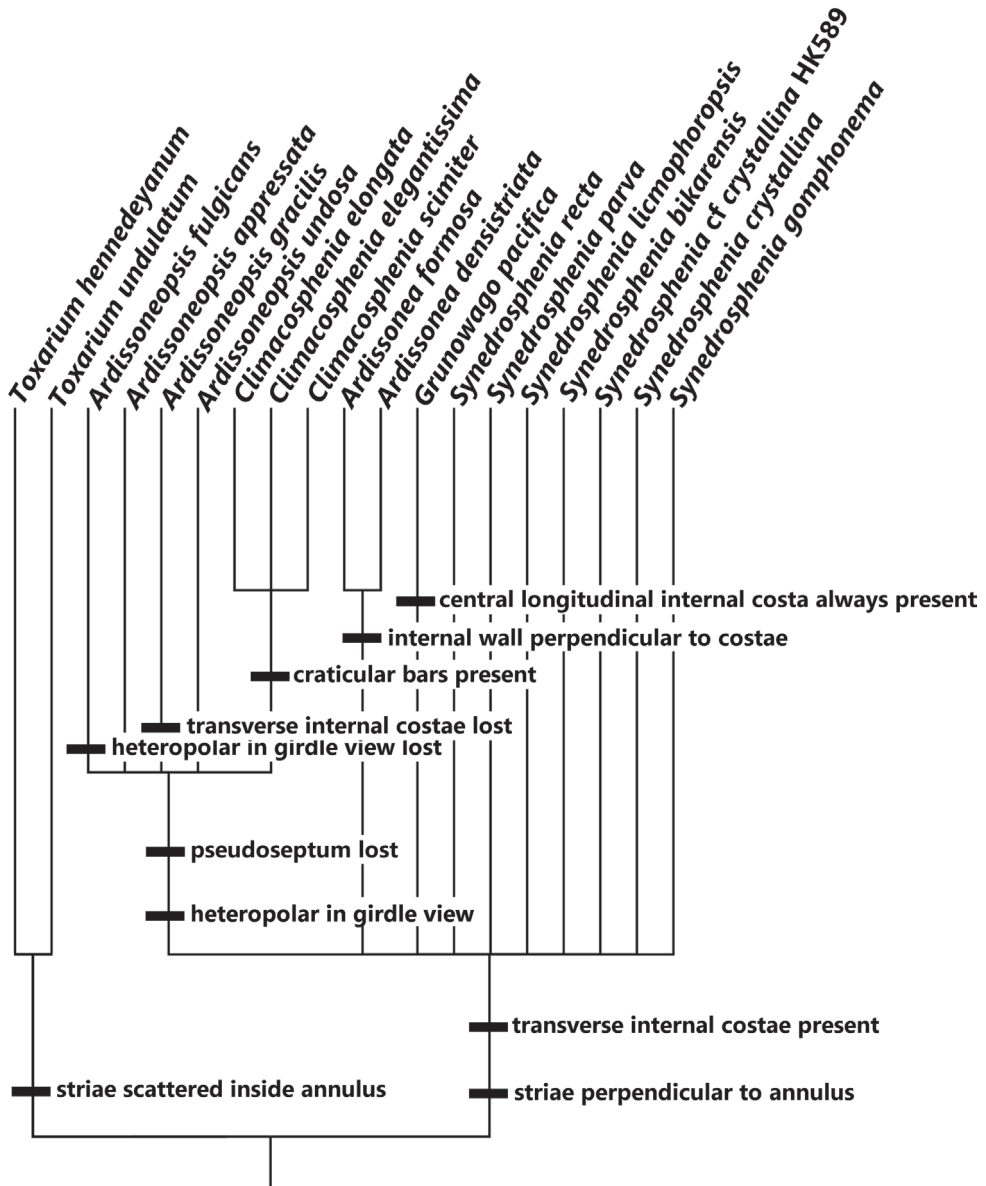


Figure 32. Strict consensus tree summarizing the 18 most-parsimonious trees resolved from the cladistic analysis of the morphological dataset in Suppl. material 2: Table S2. Several diagnostic character states shown on the diagram. Length = 34 steps; Consistency Index = 0.55; Retention Index = 0.75.

Phylogenetics

Under all three analytical programs, a well-supported clade (bootstrap support [bs] = 100%, posterior probability [pp] = 1.0) contained all the sequenced *Climacosphenia*, *Toxarium*, *Grunowago* and *Ardissonia* sensu lato strains (Fig. 33). The *Ardissonia*

Table 6. Summary of Ardissonaceae generic characters.

Genus	Valve wall	Polar architecture†	Striae on valve face	Central long costa	Craticular bars
<i>Ardissonaea</i>	Double	Complex	Linear	Absent	Absent
<i>Synedrosphenia</i>	Single	Complex	Linear	Absent	Absent
<i>Ardissonaeopsis</i>	Single	Simple	Linear	Absent	Absent
<i>Grunowago</i>	Single	Simple	Linear	Present	Absent
<i>Toxarium</i>	Single	Complex	Scattered	Absent	Absent
<i>Climacosphenia</i>	Single	Simple	Linear	Absent	Present

† Complex refers to the presence of a pseudoseptum on the valve poles + corresponding shelf on valvocopula poles + long fimbriae on the copula poles.

sensu lato strains sequenced here represent the *Ardissonaea* sensu stricto morphology (*Ardissonaea* sp. UTKSA0041 and *Ardissonaea formosa* HK209), *Ardissonaeopsis* morphology (*Ardissonaeopsis fulgicans* HK305 and *Ardissonaeopsis appressata* HK167), the *Synedrosphenia* morphology (*Ardissonaea* sp. HK589, *Ardissonaea baculus* WK76 and *Ardissonaea crystallina* ND3-0722-E) and the *Grunowago* morphology (*Synedra bacillaris* HK291 and HK697). All morphotypes were monophyletic (bs > 72%, pp > 0.98), though support was lowest under the RAxML analysis.

The genera *Climacosphenia* and *Toxarium* were also monophyletic in all three analyses (bs > 99%, pp = 1.0), though their position relative to other taxa changed between the analyses. The *Climacosphenia* sequences were sister to the rest of the clade in the ExaBayes analysis (pp = 1.0). In the Maximum Likelihood analyses, *Climacosphenia* was either sister to the *Ardissonaea* clades (IQTREE, bs = 63%) or sister to the *Ardissonaeopsis*-morphotype strains, but with extremely low support (RAxML, bs = 18%). Strains with the *Ardissonaea* sensu stricto morphology were either sister to the *Synedrosphenia* morph strains (IQTREE bs = 75%, ExaBayes pp = 0.73) or sister to a clade containing the *Grunowago* and *Synedrosphenia* morphs (RAxML bs = 77%). The *Ardissonaeopsis* morph clade was sister to the rest of the *Ardissonaea* sensu lato clades in the IQTREE and ExaBayes analyses (bs = 85%, pp = 0.98, respectively), but in a clade with *Climacosphenia* which was sister to *Toxarium* in the RAxML analysis (bs = 30%).

Discussion

The results support a conclusion that there is one monophyletic group containing six genera (Table 6), i.e., *Ardissonaea* sensu stricto with double walls and pseudosepta; (2) *Synedrosphenia*, including *Ardissonaea crystallina* and *A. fulgens*, with single walls and pseudosepta; (3) *Ardissonaeopsis* gen. nov., including *Synedra undosa* Grunow, with single walls but without pseudosepta; (4) *Grunowago* gen. nov. including *Synedra bacillaris*, with a central costa; (5) *Toxarium* with scattered areolae on the valve face; and (6) *Climacosphenia* with craticular bars on the valvocopula. The following paragraphs further discuss the new and emended genera, before considering the limitations of the study and what we can conclude about the Family/Ordinal level.

There is a clear distinction within *Ardissonaea* sensu lato, between species with a double wall and those with a single wall, as noted by Round et al. (1990), i.e. the

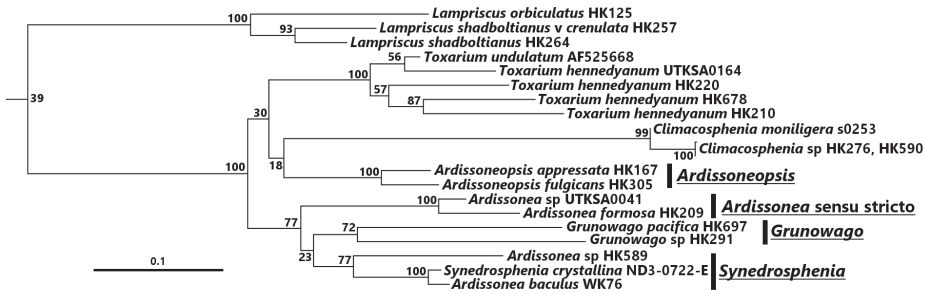
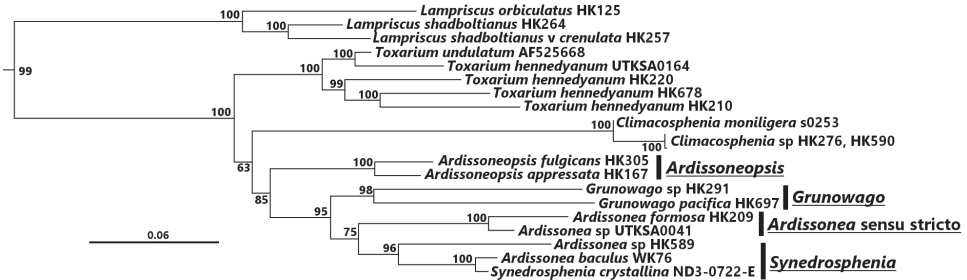
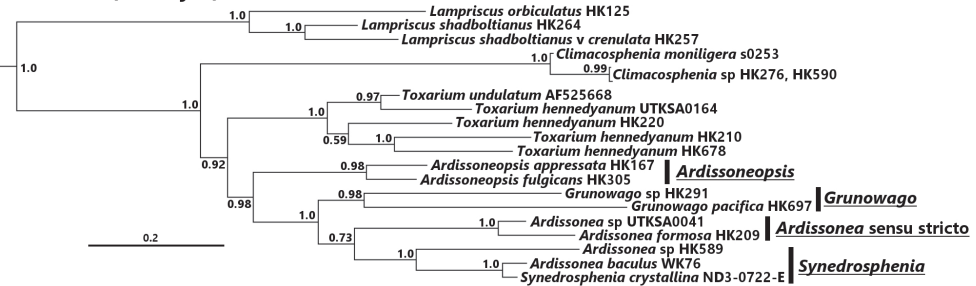
A: ML tree (RAxML)**B: ML tree (IQTREE)****C: BI tree (ExaBayes)**

Figure 33. Phylogenetic trees resulting from three analytical methods of the 3-gene DNA sequence dataset assembled for this manuscript. Only the Ardissonaceae and their sister group in the molecular phylogeny, *Lampriscus*, is shown here—the complete trees can be found in Suppl. materials 5–7: Figs S3–S5 **A** Maximum Likelihood phylogeny resolved by RAxML, where values at nodes are bootstrap support values **B** Maximum Likelihood phylogeny resolved by IQTREE, where values at nodes are bootstrap support values **C** Bayesian Inference phylogeny resolved by ExaBayes, where values at nodes are posterior probability values. Strain taxonomy (name followed by DNA voucher ID or strain ID) follows currently accepted classification, with proposed genera based on morphology shown to the right of strain ID.

double wall is a synapomorphy for *Ardissonaea* sensu stricto. Even without *Ardissonaea* s.s., single-walled taxa under the name *Ardissonaea* were not monophyletic and resolved into two clades. In Micronesia, several species differ subtly but perhaps significantly from the known taxa, and there are species sufficiently different to be recognized as undescribed even without sequencing. The two clades of single-walled *Ardissonaea* spp. can be separated on the structure of the poles, one group, including *Synedrosphenia gomphonema* and therefore taking that genus name, with complex polar architecture

(also seen in *Ardissonaea* s.s.) including a narrow, often asymmetrical extension (pseudoseptum) of the rim of the valve at the apical pole, a corresponding folding of the valvocopula to form a shelf with a groove or notch, often overlapped internally by very long fimbriae of the copula. The other group has simple polar architecture, commonly seen in diatoms, with a straight edge to the mantle and the pars interior of the valvocopula; we propose *Ardissonopsis* for this group, including three new species, and typified by Grunow's obscure species *Synedra undosa*. *Toxarium* is within a clade with the other genera discussed here in two of three molecular analyses and does not clearly separate in morphological cladistics, suggesting that all belong in one family.

Synedrosphenia was kept separate from *Synedra* by Hustedt (1931–1959), even though he rejected *Ardissonaea* as a genus. His argument was that, despite the many similarities, the heteropolar shape of the valve was more important, and he cited pairs of genera, e.g., *Gomphonema* and *Navicula*, in which heteropolar species were separated from isopolar. *Synedrosphenia* was said by Round et al. (1990) to be in “urgent need of re-investigation,” but, based on the ultrastructure and cell shape, they recognized a relationship with *Climacosphenia*. With more recent EM studies on single-walled *Ardissonaea* species (Poulin et al. 1987; Kaczmarek et al. 2020), especially the recognition of complex polar architecture in *Ardissonaea fulgens* type material (Kanjor et al. 2021), and our observations on *Synedrosphenia* from Micronesia and Grunow's historical material from Honduras, it is now clear that the ultrastructural similarities must outweigh the heteropolarity. (We reserve judgement on specimens identified in the literature as *A. fulgens* var. *gigantea* for reasons detailed in Results.) As seen in our new species, the shape presents more of a gradient and strongly suggests that all the single-wall *Ardissonaea* and new species with a pseudoseptum should be placed in *Synedrosphenia* rather than erecting a new genus. A dearth of sequenced taxa means that this conclusion is not yet supported by molecular data.

The new genus *Ardissonopsis* is necessary to accommodate *Ardissonaea*-like species with single walls but simple polar architecture. These include not only two species in Micronesia that we had previously identified with *Ardissonaea fulgens* and its var. *gigantea*, but also Grunow's *Synedra undosa*, which we were able to observe for the first time in SEM, and a new species. While it is better to have a positive synapomorphy for a genus, the complexity of the apical structure of valve and valvocopula in some other genera in this group is a strong character, comparable to the presence of an inner wall layer, and warrants separating those that have it from those that do not. This genus is presently small but we anticipate it will grow as Ardissonaceae are more fully explored in other regions.

The new genus *Grunowago* is required to accommodate a new species and *Synedra bacillaris*. The latter cannot remain in *Synedra*, which, although defined by Round et al. (1990) as a freshwater genus and now clarified as a small *marine* genus, with *Catacombas* as a junior synonym (Williams and Karthick 2021), has a double wall, rimoportulae, and polar pore fields. Valve structure in *Grunowago* has some important differences that seem to set it apart from the Ardissonaceae, including a strong central costa and lack of lateral costae that implies bilateral growth rather than annular

growth. Nevertheless, sequence results show that it is part of this Family. Not all the other Ardissonaceae have evident annular rings, however. As noted above, the ring is not visible in *Synedrosphenia bikarensis*; this species has not been sequenced yet. Our hypothesis to explain this is that there is annular growth in these species, since that is the defining character of the group. Regardless of its eventual systematic position, this genus helps resolve *Synedra*.

Our study was largely restricted to observations on materials from Western Pacific Islands, those from Guam usually examined fresh, others only after acid cleaning. Having stubs with remnants from Grunow's Honduras materials, we made use of them, but the large specimens were very broken up and we had much more success with species with distinctive shapes (*Synedra undosa*, *Toxarium undulatum*, Figs 17, 24) than with the linear species with several similar species that we could not identify. We managed to identify putative *Synedra crystallina* var. *bacillaris* (Fig. 19) but it was hard to be sure that the specimens did not have a double wall when *Ardissonaea* was also present. We restricted descriptions of new species to those that could be confidently differentiated from known species, leaving others, such as the two *Toxarium* spp. with the widely used names as working hypotheses. The other major limitation in this study is low taxon sampling for sequencing. Low taxon sampling may not change quickly, as Medlin et al. (2008) commented that *Ardissonaea* and *Climacosphenia* are difficult to culture, and that has been our experience as well. Many of the new species were found only after acid cleaning of samples that had been preserved in the herbarium and therefore could provide no information on organic components, including DNA. Low taxon sampling is also the cause of the apparently sister relationship with the centric diatom *Lampriscus* (Fig. 33); it is closest but not close.

Despite the limitations of the study, we can draw some conclusions about the Families and Order. Molecular and morphological evidence support a hypothesis that the six genera in our flora are in one monophyletic family but there is no known common ancestor, from which to derive a synapomorphy for the Family, which now appears to stand alone in an Order with no other Mediophyceae nearby. In the past they were placed in several Families and usually more than one Order; the most recent summary of diatom taxonomy has them in four families under one Order, Toxariales (Cox 2015). Round et al. (1990) described *Ardissonaea* based on the type species, *A. robusta*, without reference to the single walled forms that Poulin et al. (1986) had used as the basis for their emendation. However, they also defined a Family and an Order with one and the same paragraph, which, because it was based entirely on the characters of *A. robusta*, even excludes the single-walled species from these higher taxa. Cox (2015) partially resolved these issues by eliminating the Ardissonales and placing the family in Toxariales. However, her description of Ardissonaceae mirrors Round's and she lists only one genus—*Ardissonaea*, with only 2 species (presumably *A. robusta* and *A. formosa*), still leaving the single-walled taxa in limbo. Moreover, she also follows Round et al. (1990) in placing *Synedrosphenia* in Climacospheniaceae, which is defined as having valvocopulae with septa that meet in the middle, true

only for *Climacosphenia*. We therefore need to emend the description of Ardissonaceae. First, *Ardissonaea*, *Ardissonopsis* and *Synedrosphenia* (Groups 1–3 as defined above) clearly all belong in Ardissonaceae as presently conceived. Second, there seems to be little justification for maintaining separate Family+Order for each of *Toxarium* and *Climacosphenia*, given the similarities to the Ardissonaceae. *Toxarium* has characters of both *Ardissonopsis* (weakly developed costae) and *Synedrosphenia* (pseudoseptum + valvocopular notch) and is distinguished only by the scattered areolae in the wider areas (when there are any inside the annulus). While the craticular bars of *Climacosphenia* are its defining character, unique within the Order, we do not see this as warranting a separate family, especially considering the distribution of such valvocopulae within the biraphid genus *Climaconeis*, where craticular bars distinguish only 2 of 20 species (Lobban 2021a). We therefore propose to transfer *Toxarium* and *Climacosphenia* to the Ardissonaceae and to restore that family to the Ardissonales, emended.

Much work remains to be done even in our region to tease out the biodiversity of these genera, and that work depends on progress in other regions and especially on type materials. Some species, e.g., *Ardissonaea formosa* and *A. pulcherrima*, were described from the East Indies, others from Atlantic/Caribbean waters, e.g. *A. robusta* from Kattagat Strait, Europe, and several species from Honduras. In many cases precise type locations are unknown – Hantzsch received samples labeled only from the East Indies Archipelago; Lindig did not inform Grunow whether his Honduras samples were from its east or west coast. It is tempting but counterproductive to assume that everything is everywhere. Moreover, Williams (2011) and Williams and Kociolek (2017), among others, have found evidence of regional endemism in freshwater diatoms, and our studies of *Licmophora* (Lobban and Santos in review) indicate the same in that marine genus. Williams (2011) even proposed that we should start from the assumption that everything is endemic, rather than that everything is everywhere. At least we should not assume that everything is everywhere, nor that there is anywhere that the full biodiversity of Ardissonaceae has been discovered. Likely more species will be resolved with further study both in our region and in other places where these large but understudied species occur.

Taxonomic revisions

ARDISSONEALES Round 1990, emend. Lobban & Ashworth

Description. Highly elongate valves with development from a bifacial annulus (not always visible) and lacking rimoportulae and apical pore fields (ocelli/ocellulimbi). Frustules often morphologically heteropolar in valve view, girdle view, or both, attached to substrata by mucilage stalks. Valves with simple areolae in uniseriate striae, internal transapical costae more or less developed. Valvocopula and copula closed, fimbriate internal margins. Pleura (when present) narrow, fimbriate inner margin, with larger apical caps.

ARDISSONEACEAE Round 1990, emend. Lobban & Ashworth

Remark. With the characters of the Order.

Included genera.

Ardissonea De Notaris, sensu stricto

Ardissoneopsis Lobban & Ashworth, gen. nov.

Synedrosphenia (Peragallo) Azpeitia

Grunowago Lobban & Ashworth, gen. nov.

Toxarium J.W. Bailey

Climacosphenia Ehrenberg

ARDISSONEA De Notaris 1871, emend. Poulin et al. 1986, emend. Lobban & Ashworth

Description. Valves elongate, linear to lanceolate, alveolate except at the apical pole, owing to an internal silica plate and longitudinal costae under the annulus and sometimes under the midline. Inner plate opening through several large foramina at the poles and each alveolus opening by a small foramen into the cell interior.

Included species.

Ardissonea robusta (Ralfs) De Notaris (generitype).

Ardissonea densistriata Lobban sp. nov.

Ardissonea formosa (Hantzsch) Grunow ex De Toni.

Ardissonea pulcherrima (Hantzsch) Grunow ex De Toni.

SYNEDROSPHENIA (H. Peragallo in H. Peragallo and M. Peragallo 1897–1908) Azpeitia 1911, emend. Lobban & Ashworth

Synedrosphenia gomphonema (Janisch and Rabenhorst) Hustedt, 1932. Synonym.

≡ *Synedra gomphonema* Janisch & Rabenhorst, 1863 Beiträge zur näheren Kenntniss und Verbreitung der Algen. Heft I, p. 13, pl. 2: fig. 6. Synonym.

Lectotype species here designated. *Sceptroneis cuneata* Grunow, 1877, Monthly Microsc. J. 18: 169, pl. 194, fig. 3 ≡ *Synedra cuneata* Grunow, 1866, Hedwigia 1: 5.

Registration of lectotype. Phycobank <http://phycobank.org/103264>.

Description. Valves elongate, linear or tapered from a broader apical pole. Wall a single layer usually with internal costae on the virgae, and a pseudoseptum on the rim of the valve at each pole, forming a complex structure with the valvocopula. Midline absent or indistinct (not subtended by a longitudinal costa), annulus usually evident, though sometimes coinciding with the valve-mantle junction.

Included species.

Synedrosphenia gomphonema (Janisch and Rabenhorst) Hustedt (= *Sceptroneis cuneata* Grunow; type species).

Synedrosphenia baculum (Gregory) Lobban & Ashworth, comb. nov.

Synedrosphenia bikarensis sp. nov.

Synedrosphenia crystallina (C. Agardh) Lobban & Ashworth comb. nov.

Synedrosphenia fulgens (Greville) Lobban & Ashworth comb. nov.

Synedrosphenia licmophoropsis sp. nov.

Synedrosphenia parva sp. nov.

***Synedrosphenia crystallina* (C. Agardh) Lobban & Ashworth comb. nov.**

Diatoma crystallinum C. Agardh 1824, Systema Algarum, p. 3. Basionym.

Synedra crystallina (C. Agardh) Kützing, 1844, Die Kieselschaligen Bacillarien oder Diatomeen, p. 69, pl. 16: fig. 1. Synonym.

Ardissonaea crystallina (C. Agardh) Grunow ex De Toni 1892. Synonym.

Registration. Phycobank <http://phycobank.org/103250>.

***Synedrosphenia baculum* (Gregory) Lobban & Ashworth, comb. nov.**

Synedra baculus Gregory, Trans. Micr. Soc. London, 5: p. 83, pl. 1, fig. 54, 1857. Based on GenBank sequence wk76 (Wiebe Kooistra). Basionym.

Registration. Phycobank <http://phycobank.org/103252>.

Comment. Since *baculum* (baton, rod) is used as a noun in apposition, it should retain its neuter ending, even though Gregory (1857) wrote it *Baculus*. This is an orthographical change that does not require any formal action under ICN rules, Art. 61 (Turland et al. 2018).

In addition, *A. dalmatica* (Kützing) De Toni, 1892, shown by Álvarez-Blanco and Blanco (2014) to have a pseudoseptum and single wall, clearly belongs in *Synedrosphenia*. We have not made a new combination here, pending further investigation into its relationship to *A. crystallina*. Similarly, we do not have enough information to decide where to place *Ardissonaea brockmannii* ‘*brockmanni*’ Hustedt, 1932 (Hustedt 1931–1959, p. 228, fig. 716).

***Synedrosphenia fulgens* (Greville) Lobban & Ashworth comb. nov.**

Exilaria fulgens Greville, Scottish Cryptogamic Flora, Vol. 5: pl. 291, 1827. Basionym.

Synedra fulgens (Greville) W. Smith, A Synopsis of British Diatomaceae, vol. 1, p. 74, pl. 12, fig. 103, 1853. Synonym.

Ardissonaea fulgens (Greville) Grunow ex De Toni, Sylloge, p. 674, 1892. Synonym.

Ardissonaea fulgens (Greville) Kanjer, Kusber & Van de Vijver 2021, Notulae Algarum 215: 1–6, figs 1–16. Synonym.

Registration. Phycobank <http://phycobank.org/103259>.

Comment. We do not include *Ardissonaea fulgens* var. *gigantea* (Lobarzewsky) Rabenhorst in this transfer because of the uncertainty about its morphology.

***Ardissonopsis* Lobban & Ashworth, gen. nov.**

Description. Valves single walled, isopolar or weakly heteropolar, simple polar architecture on valve and valvocopula.

Type species. *Ardissonopsis undosa* (Grunow) Lobban & Ashworth comb. nov.

Etymology. *Ardissonaea* [named for Italian phycologist Francesco Ardissona (1837–1910)] + *-opsis*, L. similar to.

Included species.

Ardissonopsis fulgicans Lobban & Ashworth, sp. nov.

Ardissonopsis appressata Lobban & Ashworth, sp. nov.

Ardissonopsis gracilis Lobban sp. nov.

Ardissonopsis undosa (Grunow) Lobban & Ashworth comb. nov.

Registration. Phycobank <http://phycobank.org/103240>.

***Ardissonopsis undosa* (Grunow) Lobban & Ashworth comb. nov.**

Synedra undosa Grunow 1867 Hedwigia 6: 4; and 1877 Monthly Microscopical Journal 18: p. 167, pl. 193, fig. 8a–c. Basionym.

Toxarium undosum (Grunow) De Toni 1892, Sylloge, p. 677. Synonym.

Registration. Phycobank <http://phycobank.org/103260>.

***Grunowago* Lobban & Ashworth, gen. nov.**

Description. Valves linear to lanceolate, isopolar; uniseriate striae, virgae thickened internally and a prominent longitudinal costa under the midline. Annulus not apparent even on the valve–mantle junction. No pseudoseptum but continuous rim on valve border.

Type species. *Grunowago bacillaris* (Grunow) Lobban & Ashworth.

Etymology. Grunow + *-ago* (from *agere*, to move, perform, achieve, etc.; see Stearn 1973: 293) Named in recognition of the body of work of Albert Grunow (1826–1914), which included the original recognition of the type species in his study of a Honduras sample. The compound noun is feminine.

Included species.

Grunowago bacillaris (Grunow) Lobban & Ashworth, comb. nov.

Grunowago pacifica sp. nov.

Registration. Phycobank <http://phycobank.org/103244>.

***Grunowago bacillaris* (Grunow) Lobban & Ashworth, comb. nov.**

Synedra crystallina var. *bacillaris* Grunow 1877, Monthly Microscopical Journal 18: 167, pl. 193, fig. 12. [Grunow gives the authorship there as Grunow, rather than sp. nov., implying that he had already described it, but it is not in his original work on the Honduras material (Grunow 1867).]. Basionym.

Ardissonea crystallina var. *bacillaris* (Grunow) Grunow in Cleve and Grunow 1880, Kongliga Svenska Vetenskaps-Akademiens Handlingar 17(2): 108. Synonym.

Synedra superba Peragallo 1900, Diatomees Marine de France, pl. 79, fig. 7 (Peragallo and Peragallo 1897–1908). Synonym.

Synedra bacillaris (Grunow) Hustedt 1931–1959, Die Kieselalgen 2(2): 230, fig. 718. Synonym.

Registration. Phycobank <http://phycobank.org/103261>.

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Supplementary material 1

Table S1. Metadata for strains used in the molecular phylogenetic analysis, including strain extraction voucher ID and GenBank accession numbers

Authors: Matt P. Ashworth

Data type: Table of GenBank numbers (word file)

Explanation note: **Table S1.** Metadata for strains used in the molecular phylogenetic analysis, including strain extraction voucher ID and GenBank accession numbers. Collection site for the source of the original strain isolation is also included, where known. Extraction voucher ID corresponds to the culture material extracted for the DNA used here and references dried frustules left over from the DNA extraction as well as photomicrographs of the cells, available from authors MPA or ECT. Taxa are listed alphabetically.

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Link: <https://doi.org/10.3897/phytokeys.208.89913.suppl1>

Supplementary material 2

Table S2. Morphological characters and character states evaluated for the morphological cladistic analysis

Authors: Christopher S. Lobban, Matt P. Ashworth

Data type: Morphological character matrix (excel file)

Explanation note: **Table S2.** Morphological characters and character states evaluated for the morphological cladistic analysis. Taxa are arranged by the taxonomy proposed in this manuscript, but are labeled by their basionyms. Character state “U” indicates where the state is unknown for a taxon. Characters “pseudoseptum” and “valvocopula external poration” were treated as additive in the analysis.

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Supplementary material 3

Figure S1. Plastids in a living cell of *Ardissonea formosa* showing movement from dispersed (peristrophy) to concentrated around the nucleus (karyostrophy)

Authors: Christopher S. Lobban

Data type: Images (jpg, file)

Explanation note: **Figure S1.** Plastids in a living cell of *Ardissonea formosa* showing movement from dispersed (peristrophy) to concentrated around the nucleus (karyostrophy). Process already underway in Fig. S1A. Girdle views in A–C, F; valve views in D, E. Fig. **A** Entire living cell (length 456 μm) with plastids still mostly spread out. **B** Detail near pole showing shape of plastids. **C, D** Detail of central nucleus with surrounding plastids in girdle view (C) and 2:21 minutes later in valve view (D). **E** Pole of cell in valve view for identification. **F** Same living cell 9:00 minutes after images in A and B, showing almost all plastids around the nucleus. Scale bars: 50 μm (A, F); 10 μm (B–E).

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Link: <https://doi.org/10.3897/phytokeys.208.89913.suppl3>

Supplementary material 4

Figure S2. *Toxarium* sp. from Guam

Authors: Matt P. Ashworth, Christopher S. Lobban

Data type: SEM images (jpg, file)

Explanation note: **Figure S2.** *Toxarium* sp. from Guam. **A–C** SEM showing rippled margin and single row of mantle pores. **A–C** GU44S / HK210 / ECT 3802. **D–F** Wild specimen from GU44BK-1 showing undulate outline but single row of areolae on mantle (F, arrow). Scale bars: 50 μm (**A, D**), 10 μm (**E, F**), 5 μm (**B, C**).

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Supplementary material 5

Figure S3. Molecular phylogenetic tree illustrating the results of the RAxML Maximum Likelihood analysis of the 3-gene dataset

Authors: Matt P. Ashworth, Daryl W. Lam

Data type: Phylogenetic tree (pdf. file)

Explanation note: **Figure S3.** Molecular phylogenetic tree illustrating the results of the RAxML Maximum Likelihood analysis of the 3-gene dataset (nuclear-encoded small subunit rDNA, chloroplast-encoded *rbcL* and *psbC* markers). The taxon *Bolidomonas pacifica* was used as an outgroup and all taxa labels are followed by Extraction Voucher ID or Strain ID. Bootstrap support values are present at each corresponding node. This is the complete tree which corresponds to Fig. 33A.

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Link: <https://doi.org/10.3897/phytokeys.208.89913.suppl5>

Supplementary material 6

Figure S4. Molecular phylogenetic tree illustrating the results of the IQTREE Maximum Likelihood analysis of the 3-gene dataset

Authors: Matt P. Ashworth, Daryl W. Lam

Data type: Phylogenetic tree (pdf. file)

Explanation note: **Figure S4.** Molecular phylogenetic tree illustrating the results of the IQTREE Maximum Likelihood analysis of the 3-gene dataset (nuclear-encoded small subunit rDNA, chloroplast-encoded *rbcL* and *psbC* markers). The taxon *Bolidomonas pacifica* was used as an outgroup and all taxa labels are followed by Extraction Voucher ID or Strain ID. Bootstrap support values are present at each corresponding node. This is the complete tree which corresponds to Fig. 33B.

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Link: <https://doi.org/10.3897/phytokeys.208.89913.suppl6>

Supplementary material 7

Figure S5. Molecular phylogenetic tree illustrating the results of the ExaBayes Bayesian Inference analysis of the 3-gene dataset

Authors: Matt P. Ashworth, Daryl W. Lam

Data type: Phylogenetic tree (pdf. file)

Explanation note: **Figure S5.** Molecular phylogenetic tree illustrating the results of the ExaBayes Bayesian Inference analysis of the 3-gene dataset (nuclear-encoded small subunit rDNA, chloroplast-encoded *rbcL* and *psbC* markers). The taxon *Bolidomonas pacifica* was used as an outgroup and all taxa labels are followed by Extraction Voucher ID or Strain ID. Posterior probability values are present at each corresponding node. This is the complete tree which corresponds to Fig. 33C.

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Mosla dadoensis (Lamiaceae), a new species from the southern islands of South Korea

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Abstract

Mosla dadoensis (Lamiaceae), a new species from the southern islands of South Korea, is described and illustrated. The new species is morphologically similar to *M. chinensis*, but is distinguished from the latter by having two types of hairs on its stems, wider leaf blades, longer corolla length, and ellipsoid nutlets with a narrowly U-shaped extended area of abscission scar. *Mosla dadoensis* is also distinguished from the Chinese narrow endemic *M. hangchouensis* by having an included pistil to the corolla, smaller ellipsoid nutlets, and later flowering and fruiting season. Phylogenetic analyses, based on two nuclear ribosomal (ETS, ITS) and three chloroplast (*rbcl*, *matK*, *trnL-F*) DNA regions, confirmed that the new species was constructed as monophyletic, and that *M. dadoensis* and *M. hangchouensis* form a sister group with robust support. We hereby provide a detailed morphological description of *M. dadoensis* with its corresponding geographical distributions, and comparison tables of related taxa.

Keywords

Elsholtzieae, Korean endemic plant, morphology, phylogeny, taxonomy

Introduction

Mosla (Benth.) Buch.-Ham. ex Maxim. is a genus within the sixth largest family, Lamiaceae (the mint family). Although *Mosla* is a small genus of approximately 20 species, it is the second largest genus in the tribe Elsholtzieae (Wu and Li 1977a, b; Li and Hedge 1994; Harley et al. 2004). Elsholtzieae contains eight genera and roughly 70 species and is the smallest tribe within the most species-rich subfamily Nepetoideae (105 genera and about 3,400 spp.; Zhao et al. 2021). *Mosla* is mainly distributed in China, Japan, and Korea; however, *M. dianthera* (Buch.-Hamilt. ex Roxb.) Maxim. occurs in eastern Russia, the western Himalayas, and some Southeast Asian countries (Wu and Li 1977b; Li and Hedge 1994; Zhou et al. 1997; Govaerts et al. 2022). Phylogenetically, *Mosla* is nested within the eastern Asian *Mosla*-*Keiskea*-*Perilla* clade, and the monophyly of *Mosla* is strongly supported by previous morphological and taxonomic studies (Zhou 1995; Zhou et al. 1997; Li et al. 2017). Four fertile stamens are common in Elsholtzieae, and subequal or anterior pairs are normally longer, except in *Mosla*, which is characterized by two posterior fertile stamens (Harley et al. 2004; Kim 2018).

In Korea, four species of *Mosla* are recognized, namely *M. chinensis* Maxim., *M. dianthera*, *M. japonica* (Benth. ex Oliv.) Maxim., and *M. scabra* (Thunb.) C.W.Wu & H.W.Li (Seo and Park 2018; Korea National Arboretum 2020). The main diagnostic characteristics for species identification are the different leaf and calyx shapes. Leaves with a linear to linear-lanceolate shape are found only in *M. chinensis* and *M. japonica*, characterized by a subequal 5-toothed calyx. Although *M. scabra* and *M. dianthera* both have a 2-labiate calyx, the apex of the calyx lobe differs and is acute in *M. scabra* and obtuse in *M. dianthera* (Kim 2018).

During general floristic study in the southern part of Korea during October 2021, we found an unusual species which is restricted to the southern islands. This species is readily distinguished from previously known *Mosla* species in Korea by a considerably longer corolla. *M. chinensis* could be the closest ally, but the leaf shapes and flower features are significantly different. After a thorough literature survey and investigation of the relevant specimens, we designate *M. dadoensis* K.K.Jeong, M.J.Nam & H.J.Choi as a new species of *Mosla* from the southern islands of Korea. To clarify the systematic status of *M. dadoensis* we also conducted barcoding analysis based on nuclear ribosomal (nr) and chloroplast (cp) DNA regions, and observed detailed nutlet morphology, which is well known as a systematically important characteristic in Lamiaceae (Moon et al. 2009; Ryding 2010; Jeon et al. 2020). A detailed morphological description of *M. dadoensis* and its geographical distribution is also provided.

Materials and methods

Morphological characters

Morphological descriptions were based on specimens from the KB, KH (abbreviations are according to the Index Herbariorum [<http://sweetgum.nybg.org/science/ih/>]), and

the herbarium of Changwon National University. Field surveys were also conducted from October 2021 to February 2022. Materials preserved in 70% ethanol were used for observation and measurement of floral parts. For quantitative characters, measurements were based on at least 50 samples.

Microscopic analysis

For morphological observations and size measurements, the nutlets were first examined using a stereomicroscope (SM; Olympus SZX16, Olympus, Tokyo, Japan). Nutlet sizes were measured using at least 30 randomly chosen individuals from each species. Prior to scanning electron microscopic observations, all the dried nutlets were rehydrated overnight using the wetting agent Agepon (Agfa-Gevaert, Leverkusen, Germany) and distilled water (1:200) at 37–40 °C. The rehydrated materials were dehydrated through an ethanol series (50%, 70%, 90%, 95%, and 100%) at room temperature for 1 h each. The completely dehydrated materials were immersed in liquid carbon dioxide (CO₂) for critical point-drying (CPD; SPI-13200J-AB, SPI Supplies, West Chester, PA, USA). For the micromorphological observations, selected nutlets were mounted on aluminum stubs using a double-sided adhesive conductive carbon disk (05073-BA, SPI Supplies, West Chester, PA, USA). Specimens were coated with gold using an ion-sputtering device (208HR, Cressington Scientific Instruments Ltd., Watford, UK), and then observed using a low-voltage field emission scanning electron microscope (FE-SEM; JSM-7600F, JEOL, Tokyo, Japan) at an accelerating voltage of 10 kV and a working distance of 8–10 mm (Song and Hong 2020).

Phylogenetic analysis

To confirm the systematic placement of the putative new species within the genus *Mosla*, molecular phylogenetic analyses were conducted. The combined cpDNA dataset (*rbcL*, *matK*, and *trnL-trnF*) and nrDNA dataset (ITS, ETS) used in Li et al. (2017) were employed with the addition of three individuals (*H.J. Choi* 210923-001_1–3) of the putative new species (Table 1). *Keiskea japonica* Miq. was selected as the outgroup since it is a member of Elsholtzieae placed within the sister clade to *Mosla* (Li et al. 2017). Details of voucher information and GenBank accession numbers of the species used in this study are provided in Table 2.

Total genomic DNA of *M. dadoensis* was extracted from silica gel-dried leaf materials using a DNeasy Plant Mini Kit (Qiagen Ltd., Crawley, West Sussex, UK). We conducted PCR with a ProFlex 96-Well PCR System (Applied Biosystems, Foster City, CA, USA). Each reaction mixture contained AccuPower PCR PreMix (Bioneer, Daejeon, South Korea), ca. 10 ng (1 µL) of genomic DNA, and 100 pM of primers in a total volume of 20 µL. Conditions included an initial denaturation at 95 °C for 5 min, followed by 40 amplification cycles comprising 95 °C for 30 sec, 50 °C for 30 sec, and 72 °C for 1 min, with a final extension at 72 °C for 5 min. After the PCR products were visualized on 2% agarose gels, they were treated with a MG PCR Purification kit (MGmed), and sequenced with the ABI 3730xl Analyzer, using the ABI BigDye Terminator v3.1 Cycle Sequencing Kits (Applied Biosystems, Foster City, CA, USA).

Table 1. List of the primers used in phylogenetic analysis.

Fragment	Primer	Sequence 5' → 3'	Reference
ITS	ITS1	TCCGTAGGTGAACCTGCCG	White et al. (1990)
	ITS4	TCCTCCGCTTATTGATATGC	
ETS	ETS-B	ATAGAGCGCGTGAGTGTT	Baldwin and Markos (1998)
	18S-IGS	GAGACAAGCATATGACTACTG	Beardsley and Olmstead (2002)
<i>rbcL</i>	<i>rbcL</i> _1F	ATGTCACCACAAACAGAAAC	Fay et al. (1998)
	<i>rbcL</i> _724R	TCGCATGTACCTGCAGTAGC	
<i>matK</i>	3F_Kim_F	CGTACAGTACTTTTGTGTTTA	K.J.Kim, pers. comm.
	1R_Kim_R	ACCCAGTCCATCTGGAAATCT	
<i>trnL</i> -F	B49317	CGAAATCGGTAGACGCTACG	Taberlet et al. (1991)
	A50272	ATTTGAACTGGTGACACGAG	

Table 2. List of voucher information and GenBank accessions of species used in this study.

Species	Voucher	ETS	ITS	<i>matK</i>	<i>rbcL</i>	<i>trnL</i> -F
<i>Mosla dadoensis</i> 1	H.J.Choi_210923_001_1	ON619797	ON033689	ON619803	ON619806	ON619800
<i>Mosla dadoensis</i> 2	H.J.Choi_210923_001_2	ON619798	ON033690	ON619804	ON619807	ON619801
<i>Mosla dadoensis</i> 3	H.J.Choi_210923_001_3	ON619799	ON033691	ON619805	ON619808	ON619802
<i>Mosla cavaleriei</i>	PNLI20120445	KY552608	KY552540	KY624903	KY624972	KY625040
<i>Mosla chinensis</i>	PNLI20120245	KY552609	KY552541	KY624904	KY624973	KY625041
<i>Mosla dianthera</i>	PNLI20120248	KY552610	KY552542	KY624905	KY624974	KY625042
<i>Mosla hangchouensis</i>	PNLI20120424-1	KY552611	KY552543	KY624906	KY624975	KY625043
<i>Mosla japonica</i>	PNLI20120416	KY552612	KY552544	KY624907	KY624976	KY625044
<i>Mosla scabra</i>	PNLI20120427	KY552613	KY552545	KY624908	KY624977	KY625045
<i>Mosla soochouensis</i>	PNLI20120414	KY552614	KY552546	KY624909	KY624978	KY625046
<i>Mosla tamdaoensis</i>	C-K-393	KY552615	KY552547	KY624910	KY624979	KY625047
<i>Keiskea japonica</i>	PNLI20120049-1	KY552605	KY552537	KY624901	KY624969	KY625037

Phylogenetic analyses were conducted using maximum likelihood (ML). The obtained sequences were aligned using MAFFT with Geneious Prime 2019.2.3 (Biomatters Ltd., Auckland, NZ). To assess the confidence of the phylogenetic relationships, a bootstrap test was conducted with 1,000 replications for the ML analysis. Kimura’s three-parameter model (Kimura 1980) was selected as the substitution model.

Results and discussion

Taxonomic treatment

Mosla dadoensis K.K.Jeong, M.J.Nam & H.J.Choi, sp. nov.

urn:lsid:ipni.org:names:77305495-1

Figs 1, 2, 3A, C, E, G, 4A, C, E

Diagnosis. This new species is morphologically similar to *M. chinensis*, but is easily distinguished from the latter by having two types of hairs on its stems, wider leaf

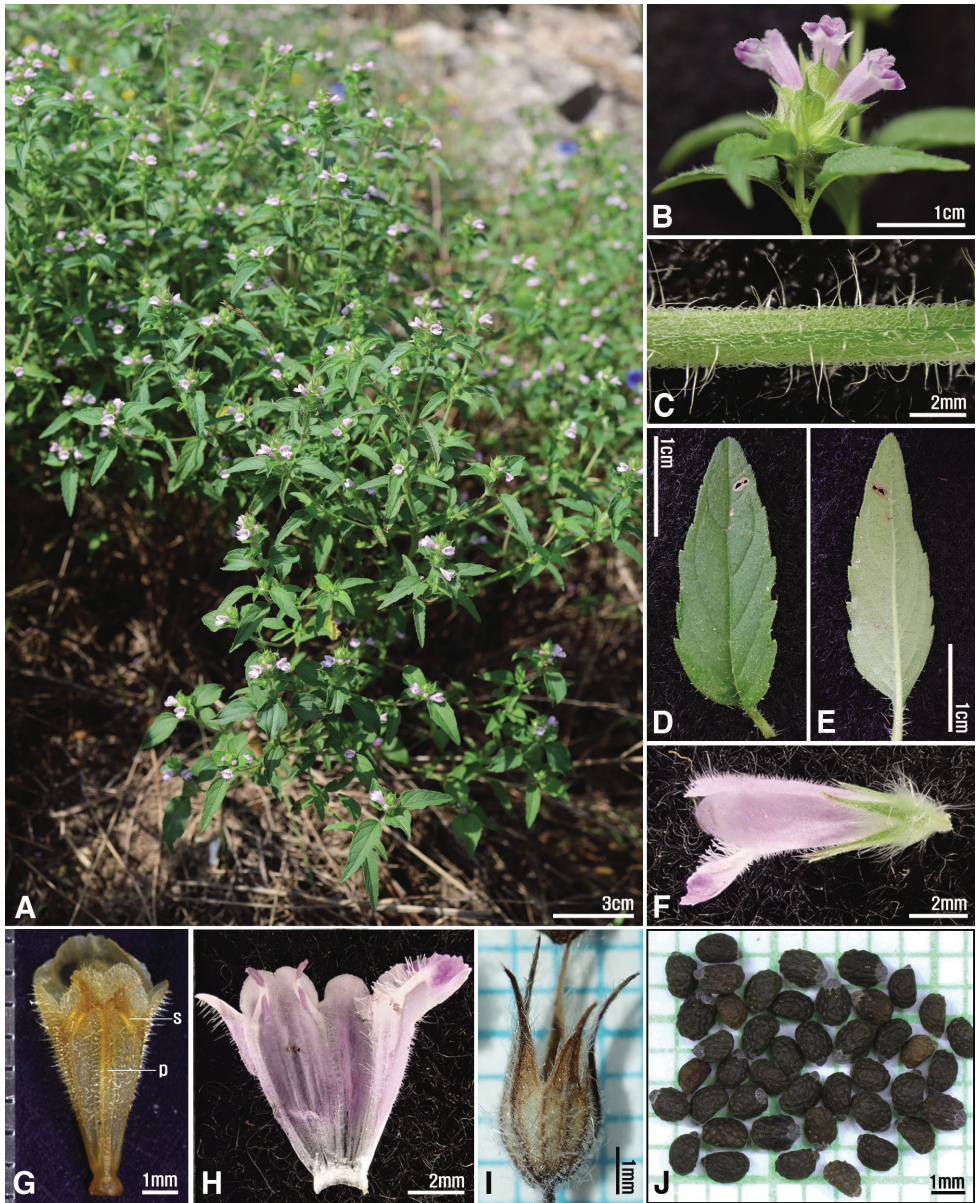


Figure 1. *Mosla dadoensis* **A** habit **B** raceme **C** stem **D, E** leaf (**D** adaxial **E** abaxial) **F** flower **G, H** corolla (**S** stamen **P** pistil) **I** calyx **J** seed. Photos from *H.J. Choi 210923-001* (**A–H**) and *H.J. Choi 211025-001* (**I, J**).

blades, longer corolla length, and ellipsoid nutlets with a narrowly U-shaped extended area of abscission scar.

Type. KOREA. Jeonnam: Yeosu-si, Geumo-do Isl., 34°30'11.1"N, 127°44'34.2"E, elev. 110 m, 22 Sep 2021 [H], *H.J. Choi 210923-001* [Holotype: KB (Fig. 2); Isotypes: CWNU, KB, KH, KIOM, KSM].



Figure 2. Photograph of the holotype of *Mosla dadoensis*.

Description. Herbs annual, aromatic. Stems 10–60 cm tall, many branched from base, densely pubescent with white recurved hairs and densely to moderately inter-mixed with white villous, with impressed glands. Leaves petiolate; petiole 2–5 mm

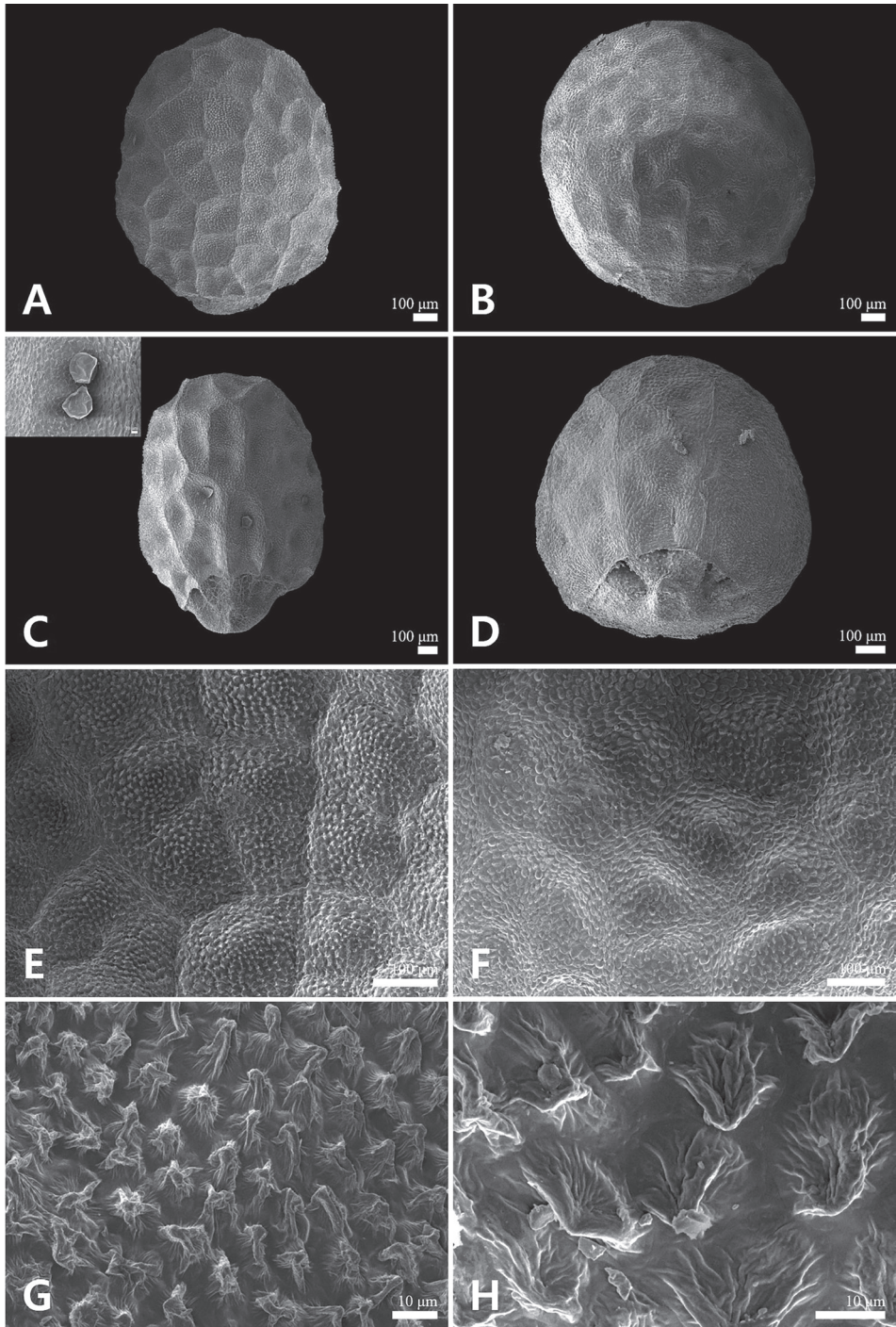


Figure 3. Scanning electron microscope micrographs of nutlets in *Mosla dadoensis* (A, C, E, G) and *M. chinensis* (B, D, F, H) A, B abaxial C, D adaxial (C small picture showing gland) E, F primary sculpture pattern G, H secondary sculpture pattern (micropapillate).

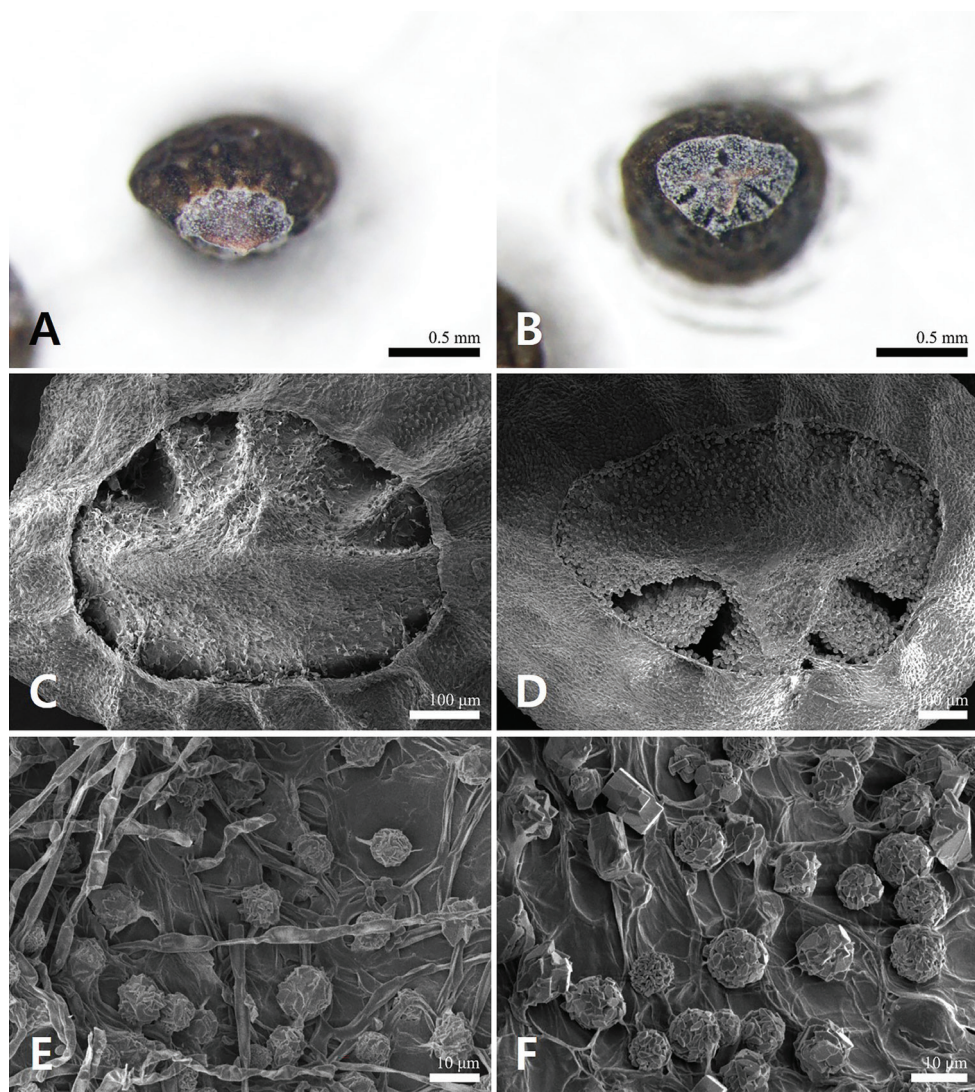


Figure 4. Stereo- and scanning electron microscope micrographs of abscission scar in *Mosla dadoensis* (A, C, E) and *M. chinensis* (B, D, F).

long, pubescent with white villous; blades narrowly lanceolate to lance-ovate, 1–3 cm × 4–10 mm, sparsely pubescent, dotted with impressed glands, adaxially olive green, abaxially gray, base cuneate, margin remotely serrate, apex acute. Racemes terminal, 1–2.5 cm, bracts overlapping, circular-obovate, 5–7 × 4–5 mm, margin ciliate, apex caudate. Pedicel pubescent. Calyx campanulate, ca. 5 × 3 mm, dilated after anthesis, subequally 5-toothed; teeth subulate, ca. 2/3 to 3/4 as long as calyx tube. Corolla slightly 2-labiate, pale purple, ca. 1.5 times longer than bracts, 8–9 mm long, pubescent outside, pubescent with long white villous on lower lip inside; upper lip

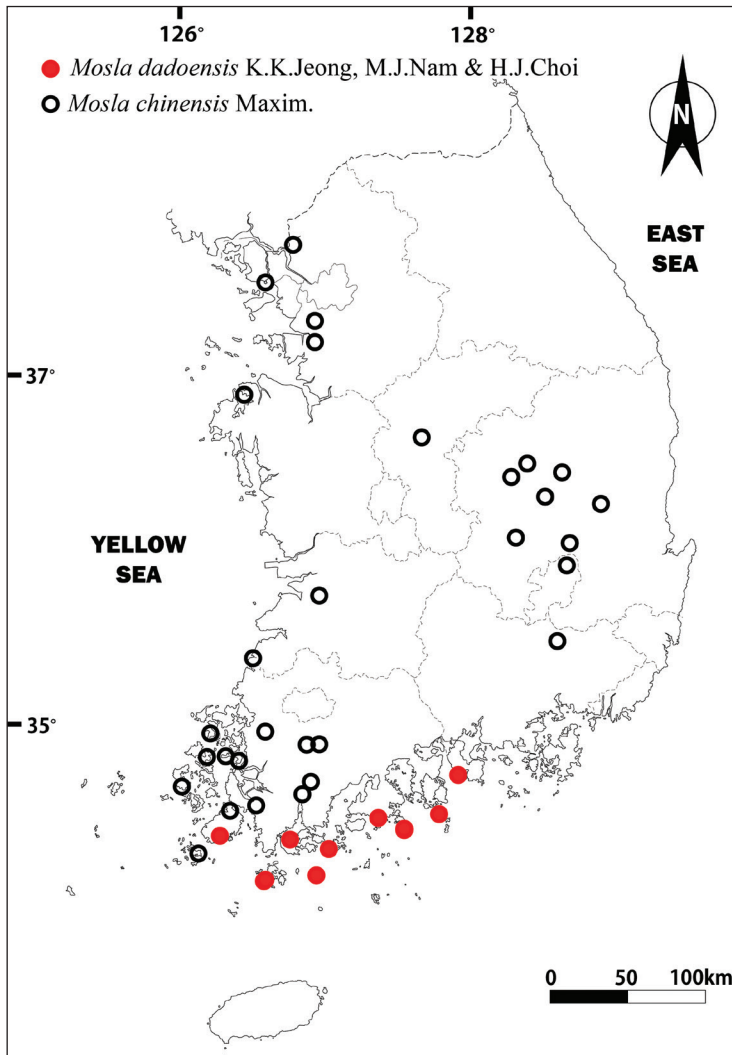


Figure 5. Distribution map of *Mosla dadoensis* and *M. chinensis* in Korea.

straight, emarginate; lower lip 3-lobed, middle lobe largest, slightly recurved. Stamens 4, included (non-exserted); filaments shorter than anthers; anthers linear, cells divergent, ca. 2 mm long, connectives distinct. Pistil included; sigma bifid. Nutlets brown to blackish-brown, ellipsoid, $1.2\text{--}1.6 \times 0.9\text{--}1.3$ mm, glabrous or sparsely pubescent with gland, pitted with deep depressions, abscission scar basal position, elliptic, extended, extended area narrowly U-shaped at the ventral side, ratio of abscission scar / nutlet diameter $0.51\text{--}0.53$, primary sculpture outline of cells isodiametric, tetragonal to hexagonal, anticlinal walls straight, raised, thin, periclinal walls concave, secondary sculpture micropapillate.

Phenology. Flowering and fruiting from August to November.

Distribution and habitat. Endemic to southern coastal regions of Korea (Fig. 5). Open rocky area near the coast; at altitudes of 8–500 m.

Etymology. The specific epithet, “*dadoensis*”, is based on the name of location, the Dadohae southern coastal region of Korea, where *Mosla dadoensis* was discovered.

Vernacular name. The Korean name of the new species is “Da-do-hae-san-deul-kkae (다도해산들깨)”.

Morphological assessment. *Mosla dadoensis* is morphologically similar to *M. chinensis*, from which it is clearly differentiated by the hairs on its stems [white recurved hairs and intermixed with white villous (Fig. 1B) vs. white recurved hairs only], shape and size of leaf blades [narrowly lanceolate to lance-ovate, 1–3 cm × 4–10 mm (Figs 1D, E) vs. linear to linear-lanceolate, 1–5 cm × 1.3–4 mm], length of corolla [8–9 mm (Figs 1G, H) vs. 5–6 mm], and shape of nutlets [ellipsoid with narrowly U-shaped extended area of abscission scar (Figs 1J, 3A, C, 4A, C) vs. globose to subglobose with widely U-shaped extended area of abscission scar (Figs 3B, D, 4B, D)]. *Mosla dadoensis* is also distinguished from *M. chinensis* by its distinctive tetragonal to hexagonal nutlet surface cells with straight and thin anticlinal walls (Table 3; Fig. 3). In addition, this new species is morphologically similar to Chinese narrow endemic *M. hangchouensis* Matsuda. However, it is easily distinguished by its length of corolla [8–9 mm and ca. twice as long as calyx (Fig. 1F) vs. ca. 10 mm and ca. three times longer than calyx], relative length of pistil to the corolla [included (Figs 1B, F, G) vs. clearly exserted], shape and size of nutlets [ellipsoid, 0.9–1.3 mm in diam. (Figs 1J, 3A, C) vs. globose to subglobose, ca. 2.1 mm in diam], and later flowering and fruiting season (August to November vs. June to September). The major characters of the new species are compared to those of the related *M. chinensis* and *M. hangchouensis* in Table 3.

Phylogenetic analysis. The combined dataset has 12 aligned sequences comprising 2,910 bp (609 bp for ITS, 371 bp for ETS, 439 bp for *rbcl*, 736 bp for *matK*, and 755 bp for *trnL-F*), of which 102 occupied variable positions (3.51%). Our phylogenetic tree (Fig. 6) revealed a similar topology to that obtained in the previous study (Li et al. 2017). *Mosla* species were constructed as monophyletic, and *M. dadoensis* was classified as a clade independent from other members of *Mosla* on the ML tree. *M. dadoensis* was distinguished from *M. chinensis*, a related species distributed in China and Korea. Instead, the tree is shown to form a clade closer to *M. dadoensis* in Korea and *M. hangchouensis* in China (Fig. 6).

Additional specimens examined. *Mosla dadoensis* (Paratypes): **KOREA: Jeonnam:** Yeosu-si, Geumo-do Isl., 34°30'11.1"N, 127°44'34.2"E, elev. 110 m, 25 Oct 2021 (fr), *H.J.Choi 211025-001* (CWNU); Goheung-gun (Naro-do Isl.), Bongrae-myeon, Jangpo-san, 34°25'25.46"N, 127°30'26.90"E, elev. 307 m, 26 Feb 2022, *K.K.Jeong s.n.* (CWNU); Goheung-gun (Naro-do Isl.), Bongrae-myeon, Bongrae-san, 34°25'45.51"N, 127°30'56.77"E, elev. 150 m, 26 Feb 2022, *K.K.Jeong s.n.* (CWNU); Jindo-gun, Yeogui-san, 34°23'41.91"N, 126°14'21.00"E, elev. 296 m, 27 Feb 2022, *K.K.Jeong s.n.* (CWNU); Jindo-gun, Imhoe-myeon, Namdong-ri, Hanbok-san, 34°22'18.1"N, 126°9'42.7"E, elev. 96 m, 9 Oct 2013 (fl, fr), *JJP7102* (KB); Goheung-gun, Dohwa-myeon, 34°29'14.01"N, 127°19'26.06"E, elev. 8 m, 3

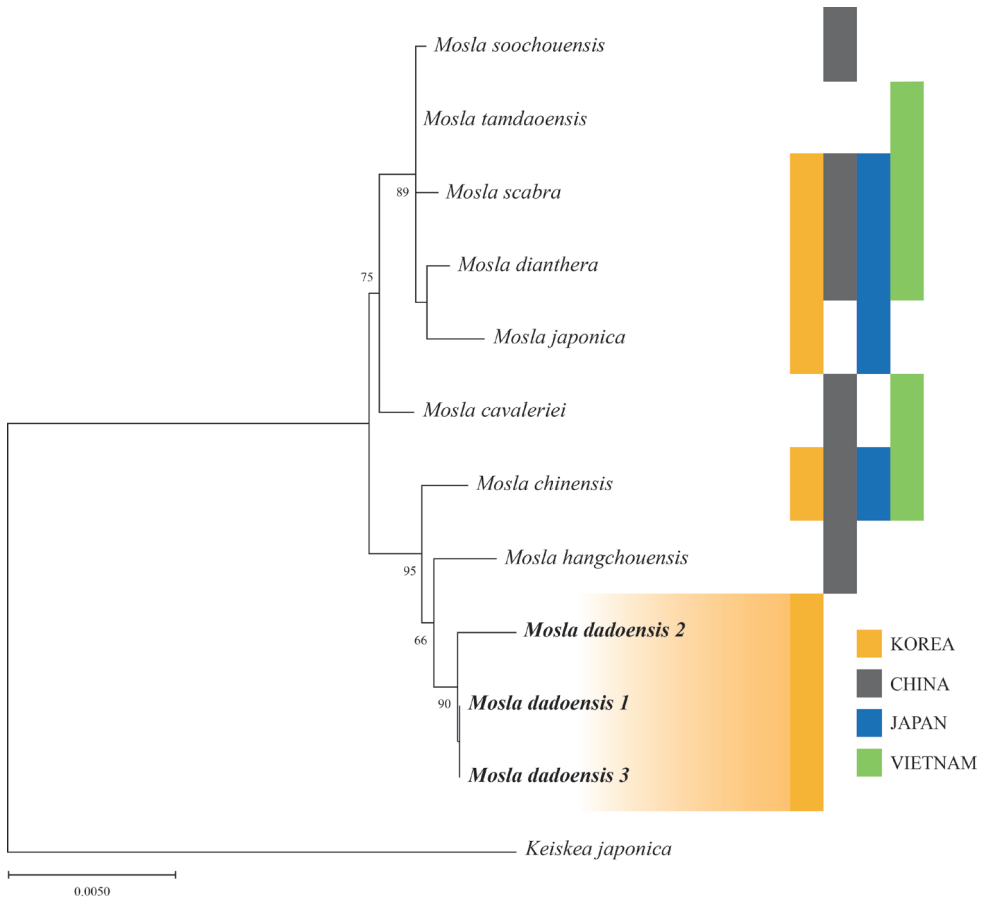


Figure 6. Phylogenetic tree of *Mosla dadoensis* and related taxa based on concatenated alignments of two nrDNA (ITS, ETS) and three cpDNA regions (*rbcL*, *matK*, *trnL-F*). The numbers above branches are bootstrap values (BS > 50%) used in the maximum likelihood method. Distribution information was obtained from Plants of the World Online (<https://powo.science.kew.org>).

Mar 2022, *K.K.Jeong s.n.* (CWNU); Goheung-gun, Dohwa-myeon, 34°26'42.11"N, 127°20'06.30"E, elev. 39 m, 3 Mar 2022, *K.K.Jeong s.n.* (CWNU); Wando-gun, Bogil-myeon, Jeokja-bong, 3 Oct 2003 (fr), *B.Y.Sun et al. s.n.* (KB); Wando-gun, Bogil-myeon, Yesong-ri, Geokja-bong, 34°32'38.88"N, 126°55'39.32"E, elev. 303 m, 24 Oct 2013 (fr), *kjs 130042* (KB); Wando-gun, Wando-eup, Daeya-ri, 34°22'12.22"N, 126°40'56.03"E, elev. 505 m, 11 Aug 2014, *Y.H.Cho & H.J.Na 140811107* (KB); Wando-gun, Bogil-myeon, Buhwang-ri, 34.128717N, 126.535047E, elev. 50 m, 7 Oct 2017, *WR-171007-075* (KH); Wando-gun, Bogil-myeon, Yesong-ri, Gyeokjabong, 34°08'15.50"N, 126°33'32.90"E, elev. 148 m, 7 Nov 2009 (fr), *HNHM-2010-0355* (KH); Wando-gun, Cheongsan-myeon, Cheonggye-ri, 34.159905N, 126.897922E, elev. 80 m, 8 Sep 2017 (fl, fr), *WR-170908-003* (KH); Wando-gun, Saengil-myeon, Bongseon-ri, 7 Sep 2003 (fl), *Lee.Y.H. 030062* (KH). **Gyeongnam:** Namhae-gun

Table 3. Comparison of major characters of *Mosla dadoensis*, *M. chinensis*, and *M. hangzhouensis* (*: data from Li and Hedge 1994; Zhou et al. 1997; Ge and Chang 2001).

Character		<i>M. dadoensis</i>	<i>M. chinensis</i>	<i>M. hangzhouensis</i> *
Habitat		open rocky area along the coast	grassy slope, forest edge, wet land	sunny side of hill peak, forest edge, and under forest along the coast
Plant	height (cm)	10–60	10–40	20–120
Stem	trichome	densely pubescent with white recurved hairs and moderately intermixed with white villous	densely pubescent with white recurved hairs	pubescent, brown glandular sometime intermixed with spreading pilose hairs
Leaf blade	shape	lanceolate to lance-ovate	linear to linear-lanceolate	lanceolate
	size	1–3 cm × 4–10 mm	1–5 cm × 1.3–4 mm	1.5–4.2 cm × 5–13 mm
Corolla	length (mm)	8–9	5–6	ca. 10
	length ratio of corolla/calyx	ca. 2.0	ca. 1.5	ca. 3.0
Pistil	relative length to corolla	included	included	clearly exerted
Nutlet	shape	ellipsoid	globose to subglobose	globose to subglobose
	diameter (mm)	0.9–1.3	1.0–1.2	ca. 2.1
	extended area of abscission scar	narrowly U-shaped at the ventral side	widely U-shaped at the ventral side	widely U-shaped at the ventral side
	ratio of abscission scar/nutlet diameter	0.51–0.53	0.61–0.69	NA
	outline of surface cell	tetragonal to hexagonal	rounded	tetragonal to hexagonal
	anticlinal walls of surface	straight, thin	curved, thick	straight, thin
Flowering and fruiting		August to November	June to October	June to September

(Namhae-do Isl.), Nam-myeon, Eungbong-san, 34°43'40.24"N, 127°53'15.65"E, elev. 268 m, 1 Mar 2022, *K.K.Jeong s.n.* (CWNNU).

Mosla chinensis: **KOREA: Gyeonggi:** Anyang-si, Dongan-gu, Bisan-dong, 37°25'23."N, 126°57'34.4"E, elev. 235 m, (fr), *PWK-133* (KH); Suwon-si, Gwon-seon-gu, Homaesil-dong, Chilbo-san, 37°15'40.39"N, 126°55'47.4"E, elev. 84 m, 24 Sep 2009 (fr), *NIBRVP0000209769* (KB); Incheon-si, Ganghwa-gun, Gilsang-myeon, Donggeom-ri, Donggeom-do Isl., 37°35'25.2"N, 126°31'2.7"E, elev. 63 m, 8 Sep 2012, *NIBRVP0000400499* (KB); Paju-si, Tanhyeon-myeon, Bupheung-ri, 37°46'02.4"N, 126°41'19.4"E, elev. 100 m, 30 Aug 2006, *VP-NAPI-376034-053* (KB). **Chungbuk:** Jeungpyeong-gun, Jeungpyeong-eup, Jwagu-san, 36°42'41.8"N, 127°39'39.2"E, elev. 500 m, 25 Aug 2011 (fl), *Geumbuk-203* (KH). **Chungnam:** Seosan-si, Daesan-eup, Ungdo-ri, 36°55'04.4"N, 126°22'24.8"E, elev. 0 m, 15 Aug 2012, *DJUIDC20120154* (KH). **Jeonbuk:** Gimje-si, Dojang-dong, Hwang-san, 35°46'35"N, 126°56'30.1"E, elev. 12 m, 27 Aug 2011, *357014-0420* (KB). **Jeonnam:** Haenam-gun, Hwangsan-myeon, Wonho-ri, Hakdong village, 34°34'15.14"N, 126°29'2.22"E, elev. 3 m, 17 Sep 2008 (fl), *ParkSH81875* (KH); Jindo-gun, Jodo-myeon, Sinyuk-ri, Hajo-do Isl., Sinjeon beach, 34°17'21.5"N, 126°01'88.1"E, elev. 39 m, 6 Sep 2011, *HS110899* (KH); Sinan-gun, Docho-myeon, Oryu-ri, Near Simok Sandbeach, 34.725447N,

125.908671E, elev. 30 m, 24 Oct 2007, *WR-071024-170* (KH); Sinan-gun, Docho-myeon, Oryu-ri, Near Simok Sandbeach, 34.725447N, 125.908671E, elev. 30 m, 24 Oct 2007, *NAM-071024-199* (KH); Yeonggwang-gun, Hongnong-eup, Gyema-ri, Gamami beach, 11 Sep 2012, *P126974* (KH); Hwasun-gun, Doam-myeon, Daecho-ri, Cheonbulsan, Unjusa, 34°55'27.3"N, 126°52'14.0"E, elev. 109 m, 6 Sep 2009, *SGU 0940* (KH); Gangjin-gun, Byeongyeong-myeon, Jiro-ri, Suin-san, 34°42'56.9"N, 126°50'18.5"E, elev. 174 m, 12 Aug 2014 (fl), *HNHM-D-140197* (KH); Sinan-gun, Aphae-myeon, Songgong-ri, Songgong-san wetland, 34.844604N, 126.252203E, elev. 25 m, 19 Sep 2007 (fl), *WR-070919-255* (KH); Jindo-gun, Gunnae-myeon, Geumseong-ri, 34°32'54.1"N, 126°17'38.6"E, elev. 30 m, 14 Sep 2005 (fr), *ESJeon 52851* (KH); Naju-si, Dado-myeon, Masan-ri, Bulhoe-sa Temple, 34°55'15.7"N, 126°53'35.8", elev. 126 m, 14 Sep 2005, *ESJeon 52829* (KH); Hampyeong-gun, Hakgyo-myeon, Gokchang-ri, 35.026751°N, 126.570272°E, elev. 100 m, 9 Sep 2012 (fl), *WR-20120909-044* (KH); Sinan-gun, Amtae-myeon, Songgok-ri, Amtae-do Isl., 34°50'20.5"N, 126°8'35.9"E, elev. 13 m, 10 Oct 2019, *YLJLVP0000006165* (KB); Gangjin-gun, Gundong-myeon, Pungdong-ri, Seongjak-gol, 34°30'48.45"N, 126°40'49.90"E, elev. 294 m, 23 Sep 2010, *C201009-0117* (KB); Sinan-gun, Aphae-myeon, Janggam-ri, 34°49'3.9"N, 126°20'58.1"E, elev. 14 m, 4 Oct 2012 (fl), *KO-SPVP0000256241* (KB); Jindo-gun, Gunnae-myeon, Dunjeon-ri, Geumgol-san, 34°32'24.8"N, 126°17'39.2"E, elev. 81 m, 27 Oct 2013 (fl), *KOSPVP0000291190* (KB); Sinan-gun, Jeungdo-myeon, Jeungdong-ri, Gubunpo, Gwakdae-bong to Bunpo reservoir, 28 Sep 1997 (fl), *EN97CUB404* (KB). **Gyeongbuk:** Sangju-si, Jungdong-myeon, Hoesang-ri, Hwanggeum-san, 36°27'55.3"N, 128°16'34.2"E, elev. 210 m, 9 Sep 2012 (fl), *KTPSA-2012076* (KH); Daegu-si, Dong-gu, Jimyo-dong, 35°56'25.09"N, 128°39'49.04"E, elev. 202 m, 21 Aug 2013 (fl), *DJUIDC2013-212* (KH); Yecheon-gun, Jibo-myeon, Amcheon-ri, 36°33'06.00"N, 128°27'11.09"E, elev. 11 m, 7 Sep 2011 (fl), *Nakdong-1632* (KH); Gyeongbuk, Sangju-si, Jungdong-myeon, Hoesang-ri, 36°27'54.9"N, 128°16'37.0"E, elev. 236 m, 8 Sep 2012, *NAPI2012-0153* (KH); Cheongsong-gun, Hyeonseo-myeon, Hwamok-ri, 36°16'24.4"N, 128°52'22.1"E, elev. 387 m, 3 Aug 2018, *NIBRVP0000703391* (KB); Gunwi-gun, Bugye-myeon, Changpyeong-ri, San 100, 36°4'56.36"N, 128°41'34.59"E, elev. 225 m, 27 Sep 2019 (fr), *NIBRVP0000756907* (KB); Andong-si, Iljik-myeon, Wonho-ri, Jaam-san, 36°29'54.08"N, 128°40'37.14"E, elev. 302 m, 21 Aug 2017 (fl), *NIBRVP0000632258* (KB); Gunwi-gun, Bugye-myeon, Changpyeong-ri, 36°4'59.04"N, 128°41'35.97"E, elev. 220m, 29 Aug 2019, *NIBRVP0000754852* (KB); Uiseong-gun, Bian-myeon, Jarak-ri, Haemang-san, 36°22'52.31"N, 128°31'3.79"E, elev. 202 m, 3 Oct 2017 (fr), *NI-BRVP0000643724* (KB); Gimcheon-si, Nam-myeon, Busang-ri, Geumo-san, San 168-7, 36°3'58.8"N, 128°16'34.1"E, elev. 220 m, 20 Sep 2015 (fl), *NIBRVP0000585241* (KB); Gumi-si, Namtong-dong, Geumo-san, Peak to Beopseong temple, 36°5'52.5"N, 128°19'46"E, elev. 250 m, 5 Oct 2015 (fr), *NIBRVP0000586707* (KB). **Gyeongnam:** Milyang-si, Muan-myeon, Garye-ri, Yeongchwi-san, 35°29'57.40"N, 128°35'02.20", elev. 201 m, 14 Sep 2009 (fr), *HNHM-2009-0392* (KH).

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