A New Species of *Ceratozamia* (Cycadales, Zamiaceae) from Veracruz, Mexico

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Abstract. *Ceratozamia decumbens* (Zamiaceae, Cycadales) is newly described and illustrated. This species, endemic to Veracruz, has affinity with *C. morettii* Vázquez Torres & Vovides, but differs in leaf morphology and leaflet habit as well as in the microsporangiate and megasporangiate strobili and trunk. *Ceratozamia decumbens* is considered part of the *C. latifolia* species complex, which includes *C. latifolia* Miquel, *C. microstrobila* Vovides & J. D. Rees, *C. huastecorum* Avendaño, Vovides & Castillo-Campos, and *C. morettii*.

Key words: *Ceratozamia* species complex, Cycad, floristic refuges, IUCN Red List, Mesoamerica, Pleistocene, Zamiaceae.

During botanical explorations (1982) in the mountainous region of central Veracruz, Mexico, we discovered and collected an interesting *Ceratozamia* Brongniart in tropical subdeciduous rainforest, which we identified as belonging to the *C. latifolia* Miquel species complex (Vovides et al., 2004). The habitat of the new species lies within the Córdoba Pleistocene floristic refugium (Toledo, 1982) on the lower slopes of the Sierra Madre. This Pleistocene refuge, along with two others—the Los Tuxtlas refugium in southern Veracruz and the Sierra de Juárez in Oaxaca, form three secondary refugia where biota were protected from decreasing temperatures or precipitation (Toledo, 1982). Other cycad species have been reported from these three regions or their vicinities: *C. robusta* Miquel, *C. miqueliana* H. Wendland, *Dioon purpusii* Rose, *D. caputoi* De Luca, Sabato & Vázquez Torres, and *D. califanoi* De Luca & Sabato. In the nearby but more humid Cenozoic "Arc Refugium" of Wendt (1987), at its western extreme neighboring the Córdoba and Sierra de Juárez refugia, *D. spinulosum* Dyer, *D. rzedowskii* De Luca, A. Moretti, Sabato & Vázquez Torres, and *Zamia loddigesii* Miquel are found. This refugium spans the high rainfall areas of southern Veracruz, southern Tabasco, northern Oaxaca, and northern Chiapas and includes the cycads *C. becerrae* Pérez-Farrera, Vovides & Schutzman, *C. zoquorum* Pérez-Farrera, Vovides & Iglesias, another population of *C. miqueliana* and *Z. purpurea* Vovides, J. D. Rees & Vázquez Torres, and *Z. cremnophila* Vovides, Schutzman & Dehgan. There is a general consensus of opinion on the existence of areas with floristic and faunistic affinities of great age (refugia) in southern Mexico (Brown, 1976; Toledo, 1982; Wendt, 1987). During the past 40,000 years, tropical forests in Mexico have been disrupted and displaced due to climatic changes, with cycles of cold-dry, cold-wet, and warm-dry climates. It appears that *Ceratozamia* (*Cycadopodites*) was present in the Miocene flora of the southern Mexican region of Pichucalco, Chiapas (Palacios & Rzedowski, 1993), and in Cenozoic *Engelhardtia* Leschenault ex Blume forests in Oaxaca, which have a fossil pollen spectrum that is remarkably similar to the modern pollen spectrum (Rzedowski & Palacios, 1977).

Several individuals of the new species have been under cultivation at the Francisco Javier Clavijero Botanic Garden (JBC) since 1982. Further collections were made during 1993 by Terrence Walters (Montgomery Botanical Center) and collaborators and during 2002 by the second author. After closely

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examining living plants in the field and at the JBC, herbarium material, and reproductive structures and comparing these with its congeners and descriptions by Miquel (1848), especially of *Ceratozamia longifolia* Miquel and microsporophyll illustrations of forma *fuscoviridis* (Miquel) J. Schuster of *C. mexicana* var. *longifolia* J. Schuster (Schuster, 1932), we conclude that this species is new to science. The new species has affinities with *C. morettii* Vázquez Torres & Vovides. *Ceratozamia morettii* is found in a cloud forest habitat on steep slopes with humus-rich, grayish yellow, clay soil of volcanic origin on the transverse Mexican Neovolcanic mountain range or the "Eje Neovolcánico Transversal" (Toledo, 1982).

Ceratozamia decumbens Vovides, Avendaño, Pérez-Farrera & González-Astorga, sp. nov. TYPE: Mexico. Veracruz: 8 Apr. 2005, *S. Avendaño & G. Alducin 5706* (holotype, XAL; isotypes, HEM, MO). Figure 1.

Planta rupestris; caule hypogeo vel leviter epigeo, globoso vel cilíndrico, decumbens; folia (2)4(6), ascendentia vel descendentia, petiolo et rhachidi rectis vel arcuatis, foliolis 7- ad 19-jugatis, coriaceis, lanceolatis, subfalcatis, planis, apice symmetrico vel asymmetrico, articulis rubiginosis.

Rupicolous plants with globose to cylindrical trunks, partially or entirely subterranean, decumbent, branched, protected by reddish brown, persistent petiole bases and cataphylls, (9–)13.2(–20) cm long, (8–)10(–14) cm diam. (n = 5). *Leaf cataphylls* deltoid, stipulate, reddish brown, tomentose, 1.8–2.2 × 2.4–3.9 cm. *Leaves* (2 to)4(to 6), ascending to descending, pendulous in older mature plants, pinnate, vernation erect, reddish brown upon emergence, dark to olive green at maturity, forming an open crown, (70–)117(–150) × (39–)55.9(–78) cm (n = 7); *petiole and rachis* linear to arching, terete with 2 parallel adaxial channels at level of leaflet articulations, unarmed or with few, distantly spaced, short stout prickles, pubescent at emergence, glabrous at maturity, petiole (22–)39(–69) cm (n = 7), base swollen, covered with beige tomentum, 1–2.6 cm wide, rachis (30–)49.8(–93) cm (n = 6). *Leaflets* coriaceous, flat, 7 to 19 pairs, lanceolate, subfalcate, symmetrical or asymmetrical toward acuminate apex, leaflets wider and more asymmetrical in juvenile and young adult plants at times with a cleft toward apex, base attenuate, opposite to subopposite along apical and middle portion of leaf, alternate to subalternate along basal portion of leaf, margins subrevolute, entire, dark to olive green on adaxial surface, lighter green on abaxial surface, inserted flat, perpendicular to the rachis at proximal and middle portions of leaf, at slight angle toward distal portion, (21–)30.2(–38) × (2.4–)3.5(–4) cm (n = 11); *articulation* reddish brown becoming dark green at leaf senescence, (0.7–)0.79(–1.1) cm wide (n = 8), (16 to)24(to 34) veins visible on adaxial surface (n = 14), intervein distance (0.1–)0.15(–0.2) cm (n = 18), seedling eophylls 2, distance between leaflets (2.3–)3.8(–5) cm (n = 6). *Microstrobili* cylindrical, erect, green at emergence, dark green to light brown at maturity, (12–)15.5(–19) cm long, (2.3–)2.7(–3) cm diam. (n = 2); peduncle tomentose, light brown at emergence to brown at cone maturity, 2–14 cm long, 0.6–0.8 cm diam.; *microsporophylls* indeterminate, cuneiform, inserted spirally and perpendicular with respect to cone axis forming orthostichies, dark brown tomentulose, bicornate on distal surface, fertile portion covering 1/2 to 2/3 of abaxial surface excluding the horns, (0.9–)0.99(–1.2) × (0.6–)0.69(–0.8) cm (n = 8); horns straight to divergent, (0.2–)0.28(–0.4) cm, distance between horns (0.6–)0.67(–0.8) cm (n = 8); microsporangia numerous in sori of 2 to 3, dehiscence by longitudinal slit. *Megastrobilus* cylindrical or barrel-shaped, erect, olive green at emergence, dark green to brown at maturity, 11 cm long, 7.8 cm diam.; peduncle light beige tomentose, 3.8 cm long, 0.8 cm diam.; *cataphylls* long-triangular, stipulate, tomentose; *megasporophylls* indeterminate, peltate, spirally inserted along cone axis, (3.1–)3.3(–3.5) cm, including horns, distal face hexagonal to rhomboid, bicornate, dark metallic green with light beige tomentulum on margin, long axis (2.3–)2.5(–3.4) cm, short axis (1.1–)1.3(–1.5) cm (n = 6), horns diverging, (0.4–)0.6(–0.8) cm long, distance between horns (1.1–)1.2(–1.3) cm (n = 6). *Seeds* ovate-angulate, sarcotesta white when immature turning creamy beige to light brown at maturity, sclerotesta smooth, beige, with 8 to 12 visible rays radiating from the chalaza to the micropyle, (2.1–)2.4(–2.6) cm long, (1.6–)1.7(–1.8) cm diam. (n = 6). Chromosome number $2n$ = 16 (this study).

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

Distribution and habitat. *Ceratozamia decumbens* is endemic on karstic hills in central Veracruz, Mexico. It grows on karstic rocks in subdeciduous tropical rainforest or bosque tropical subperennifolia sensu Rzedowski (1978) at an altitude of 712 m on shallow tropical rendzina soils. The more common tree species in the upper stratum of the forest at the type locality are: *Brosimum alicastrum* Swartz, *Bursera simaruba* Sargent, *Cedrela odorata* L., and *Ficus obtusifolia* HBK. Associated species in the herbaceous layer are *Begonia* L., *Jacobinia spicigera* L. H. Bailey, and the undergrowth palms *Chamaedorea elatior* Martius, *Chamaedorea tepejilote* Liebmann, and *Chamaedorea elegans* Martius. The climate of this

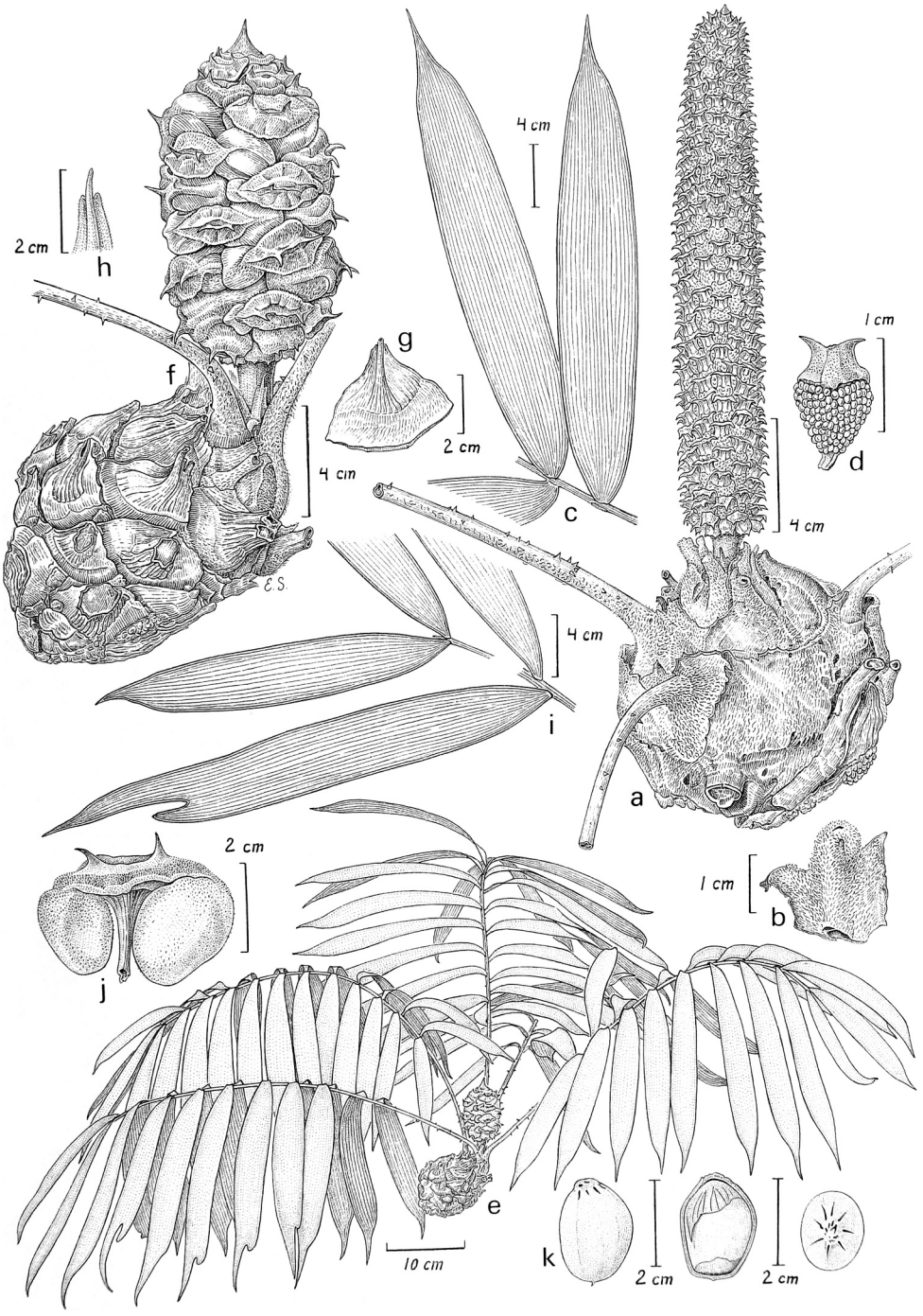

Figure 1. *Ceratozamia decumbens* Vovides, Avendaño, Pérez-Farrera & González-Astorga. —A. Mature microstrobilus attached to plant. —B. Detail of leaf cataphyll. —C. Midportion of leaf highlighting detail of articulation and leaflet veins. —D. Microsporophyll showing microsporangia. —E. Habit of female plant. —F. Detail of mature megastrobilus attached to plant. —G. Petiole base. —H. Detail of female cone cataphyll. —I. Distal portion of leaf highlighting leaflets and articulation. —J. Megasporophyll with two attached ovules. —K. Seed highlighting sclerotesta texture (left), split seed showing part of papery testa (center), and chalazal view (right). Drawn by Edmundo Saavedra from living collections at JBC (accession nos. 93-130.01 [female] and 82-439.02 [male]).

locality is semi-hot and subhumid with a total annual precipitation between 1000 and 1200 mm; it has a mean annual temperature of 21.5°C, a minimum extreme temperature of the coldest month ranging between 12°C and 13°C, and a maximum extreme temperature of the hottest month of more than 34°C. The climate cryptogram is (A)Cw_1 (Soto et al., 1996). Elements of evergreen rainforests that are tolerant of dry conditions such as *Cedrela odorata*, *Ceiba pentandra* (L.) Gaertner, *Cordia alliodora* (Ruiz & Pavón) Oken, *Dendropanax arboreus* (L.) Decaisne & Planchon, *Pithecellobium arboreum* (L.) Urban, and *Sapindus saponaria* L., which are present in this tropical subdeciduous forest, are indicative of a drier past that conforms to the secondary type refuge according to Toledo (1982).

Discussion. Miquel (1848) described a number of *Ceratozamia* species from Mexico, but specimens of the original material were not found and Stevenson and Sabato (1986) lectotypified Miquel's taxa by referring to the original descriptions. However, these descriptions are incomplete and do not include reproductive structures, nor are they supported by botanical illustrations. Upon examining Miquel's descriptions of *C. longifolia*, *C. intermedia* Miquel, and *C. latifolia*, we found that some leaflet measurements of Miquel's taxa coincided with our description, especially that of *C. longifolia*. The description of *C. longifolia* was based on plants cultivated at "Hort. Amstelaed" and the habitat is simply listed as "Hab Mexicum," and since no reproductive structures were included, we regard this description (Miquel, 1848, vol. 1, p. 40) as ambiguous. However, Schuster (1932) in his monograph (pp. 131–132) treated *C. longifolia* as *C. mexicana* var. *longifolia* (Miquel) J. Schuster and illustrated microsporophylls of forma *fuscoviridis* (Schuster, 1932: fig. 19Q–T). Upon comparing Schuster's microsporophyll illustrations with those of *C. decumbens*, we find differences in the shape of the sterile portion, the shape of the horns, and the extent of the fertile portion, which is greater in *C. decumbens*.

In view of our current knowledge of cycad biology and the general tendency of cycad species to be either endemic or restricted in distribution, we decided to treat this taxon as new based on the recommendations of Walters et al. (2004), where cycad descriptions should be based on population criteria taking into account ecological, edaphic, and topographical data as well as plant associations; ex situ cultivation in order to assess plasticity of discriminatory characters; and geographical and climatic data, distribution range, and profile, but withholding precise locality information that may jeopardize the species survival.

Relationships. *Ceratozamia decumbens* has affinity with *C. morettii*, but differs in leaflet shape and articulation, leaflet width and color, and megasporophyll color. There are also differences in the leaf crown that cannot be appreciated in herbarium vouchers. *Ceratozamia decumbens* typically has four and rarely to six leaves per crown with erect vernation, which are ascending to descending and pendulous in older plants, and is found in subdeciduous tropical forest on karstic soils. *Ceratozamia morettii* has up to 10 leaves, which are decurrent to prostrate with circinate vernation, and grows on volcanic soils in cloud forest habitat with frequent mists (Vázquez-Torres & Vovides, 1998). Comparing *C. decumbens* with the other dwarf, broad-leaflet ceratozamias, several basic differences are found. Both *C. zoquorum* Pérez-Farrera, Vovides & Iglesias and *C. becerrae* are found in distinct oreographic regions of Mexico and have oblong to oblanceolate leaflets with brown and olive green tomentulum, respectively, associated with the megasporophylls, whereas *C. decumbens* has lanceolate leaflets and light beige tomentulum associated with the megasporophylls, *C. huastecorum* Avendaño, Vovides & Castillo-Campos has ascending leaves with oblanceolate leaflets, armed petioles, and scarce grisaceous indument associated with the megasporophylls, and *C. microstrobila* Vovides & J. D. Rees has ascending leaves, unarmed petioles, lanceolate to long-elliptic leaflets, and greenish brown megastrobili with glabrous to scarce light brown tomentulum associated with the megasporophylls. The leaflets in *C. decumbens* and *C. microstrobila* are opaque, while those of *C. morettii* and *C. huastecorum* are translucent, enabling the veins to be visible when the leaflets are held up to a light source. The petiole in *C. decumbens* is unarmed or with few stout prickles, while in both *C. morettii* and *C. huastecorum* the petiole is heavily armed and that of *C. microstrobila* is unarmed (see Table 1).

A preliminary phylogeny of the genus *Ceratozamia* using nuclear ribosomal DNA ITS and chloroplast DNA *trnL-F* noncoding region has generated a consensus tree showing our new species (not attributed to species earlier) to be sister to a large clade that includes *C. morettii* and *C. mexicana* Brongniart, which grow in cloud forests on the transverse Mexican Neovolcanic mountain range (González & Vovides, 2002: *Ceratozamia* (1), fig. 5). This clade also includes a group of unresolved *Ceratozamia* species that lie to the north and northeast of this mountain range, which was interpreted as being the result of recent speciation following the amelioration of climates after the Pleistocene (González & Vovides, 2002). The presence of *C. decumbens* at the southern base of the transverse Mexican Neovolcanic mountain

Table 1. Comparative table separating *Ceratozamia decumbens* from *C. morettii*, *C. huastecorum*, and *C. microstrobila*.

Character	*C. decumbens*	*C. morettii*	*C. huastecorum*	*C. microstrobila*
Leaf vernation	erect	circinate	erect	erect
Leaflets	lanceolate	linear-lanceolate	oblanceolate	lanceolate to elliptic
Leaflet articulation	reddish brown	green	green	green
Megasporophyll	dark green	reddish brown	olive green	greenish brown
Megasporophyll indument	abundant, light beige	scarce, reddish brown	scarce, grisaceous	scarce, light brown
Seed length (cm)	2.1–2.6	1.5–1.8	1.2	1.8–1.9
Trunk shape	globose to cylindrical	globose to cylindrical	globose	ovoid to subcylindric
Petiole	unarmed or with few prickles	armed with short prickles	armed with short prickles	unarmed
Vein visibility when leaflet is held up to the light	not visible	visible	visible	not visible

range is particularly interesting, since it is within the Córdoba Pleistocene floristic refugium of Toledo (1982) and is sister to the taxa situated at and north of the transverse Mexican Neovolcanic mountain range, which appear to have been the product of a recent vicariance event (González & Vovides, 2002).

The recent speciation in cycads as a result of historical biogeographical effects has been related to the Pleistocene glaciations and floristic refugia and has been discussed for *Ceratozamia* by González and Vovides (2002) and for *Dioon edule* Lindley and *D. angustifolium* Miquel by González-Astorga et al. (2003a, b, 2005). Also, similar trends have been observed in other taxa such as *Pinus flexilis* E. James (Jørgensen et al., 2002) and *Lophocereus schottii* (Engelmann) Britton & Rose (Nason et al., 2002).

IUCN Red List category. *Ceratozamia decumbens* is native only to one karstic sierra in central Veracruz, Mexico. Specific locality information has purposely been omitted in order to discourage illegal commercial collecting of this critically endangered species. The removal of the herbaceous layer and undergrowth for the expansion of coffee plantations over recent years has severely affected the three known populations, and we estimate a total of less than 1000 individuals for these populations in a collective area of less than 10 km^2. We recommend an IUCN Red List category of Critically Endangered with very small or restricted populations (CR B2) (IUCN, 2001).

Paratypes. MEXICO. **Veracruz:** 31 May 2002, S. *Avendaño & A. Vázquez 5389*, *5390*, *5391*, *5392*, *5393* (MEXU, NY, XAL); 11 Sep. 1982, *J. D. Rees & A. P. Vovides 1690*, *A. P. Vovides 751* (XAL); 31 Oct. 2001, *A. Rincón 2798* (XAL); 10 Oct. 1993, *T. Walters 3–1*, *3–5* (FTG, XAL).

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