

A NEW SPECIES OF CERATUZAMIA (ZAMIACEAE) FROM VERACRUZ, MEXICO WITH COMMENTS ON SPECIES RELATIONSHIPS, HABITATS, AND VEGETATIVE MORPHOLOGY IN CERATUZAMIA

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Stevenson, Dennis Wm. (Department of Biological Sciences, Barnard College, Columbia University, New York, NY 10027 and New York Botanical Garden, Bronx, NY 10458-5126), Sergio Sabato (Dipartimento di Biología Vegetale Università di Napoli, via Foria 223, 80139 Napoli, Italy), and Mario Vázquez Torres (Facultad de Ciencias Biológicas, Universidad Veracruzana, Xalapa, Veracruz, Mexico). A new species of *Ceratozamia* (Zamiaceae) from Veracruz, Mexico with comments on species relationships, habitats, and vegetative morphology in *Ceratozamia*. Brittonia 38: 17-26. 1986.—*Ceratozamia euryphyllidia* from Veracruz is described and illustrated. This species differs from all others in the genus in its very large, broad leaflets (9-16 cm wide) which have undulate margins, prominent veins, and a membranous to translucent texture at maturity. It is apparently related to a group of species which all have relatively small strobili and leaflets that are attenuate basally, oblanceolate to obovate, inequilateral, abruptly acuminate apically, and generally papyraceous to membranaceous. The allopatric species of this group inhabit moist to very wet areas. The wetter the habitat, the larger and thinner the leaflets. Thus, for example, *C. latifolia* which has the smallest leaflets grows in the driest habitat whereas *C. euryphyllidia* which grows in the wettest habitat has the largest leaflets in the genus.

Ceratozamia euryphyllidia Vázquez Torres, Sabato & Stevenson (Figs. 1-5)

Truncus semihypogaeus, humilis, ad 20 cm altus; cataphylla lanata, triangularia, 5 cm longa, basi 3.5 cm lata; folia pauca, usque 10, glabra; petiolus subteres teresve, 60-90 cm longus, parte infima dilatatus, validis spinis armatus; rachis semiteres, in dimidio inferiore paucis spinis armata, supra fere inermis vel inermis, in cuspidem 2-7 cm longam excurrens; foliola subopposita vel alterna, 6—13-juga, remota, oblanceolata vel late obovata, 18-31 cm longa, 9-16 cm lata, translucida, tenuia, basi cuneata, apicem versus subito asymmetricice caudato-acuminata, acumine fere 4 cm longo, margine integerrima, prope apicem repanda vel undulata, 40-66 nervis praedita; strobilus lineari-cylindricus, 28 cm longus, 3 cm latus; pedunculus tomentosus, 6-8 cm longus, 1.5-2 cm latus; strobilus cylindricus, 20 cm longus, 5 cm latus; pedunculus tomentosus, 12 cm longus, 1.4 cm latus; semina 2.3-2.7 cm longa, 2 cm lata.

Stem semihypogeous, short (less than 20 cm), cylindrical, covered by persistent leaf and cataphyll bases; *cataphylls* pubescent, stipulate, triangular, 5 cm long, 3.5 cm wide, winged at the margins; *leaves* 2-3.2 m long, stipulate, few (less than 10), sparsely pubescent when young, glabrous when fully expanded; *petiole* 60-90 cm long, subterete to terete with an expanded base, armed with robust prickles; *rachis* straight, semiterete, sparsely armed with prickles in the lower half and nearly smooth to smooth above, ending in a conical-linear apex 2-7 cm long; *leaflets* subopposite to alternate, 6-13 on each side, pairs widely spaced, oblanceolate to widely obovate, inequilateral, 18-31 cm long, 9-16 cm wide, membranaceous to translucent, thin, 0.3-0.4 mm thick, sessile, attenuate at base (5-10 mm wide) and abruptly acuminate at the strongly asymmetric apex (2-4 cm long), the veins 40-70, dichotomous, prominent and rigid, especially when dry, margins entire, undulate in the distal portion, dark cupric when young, dark green when fully expanded, glaucous on the adaxial surface; *microsporangiate strobilus* greenish-red when young, light gray when mature, usually solitary, long-cylindric to elongate-conical, 28 cm long just prior to shedding pollen, 3 cm in diam; *peduncle* tomentose to woolly, 6-8 cm long, 1.5-2 cm in diam, unarmed; *microsporophylls* deltoid to cuneate, 7-10 mm long, 6-9 mm wide, basally stalked,

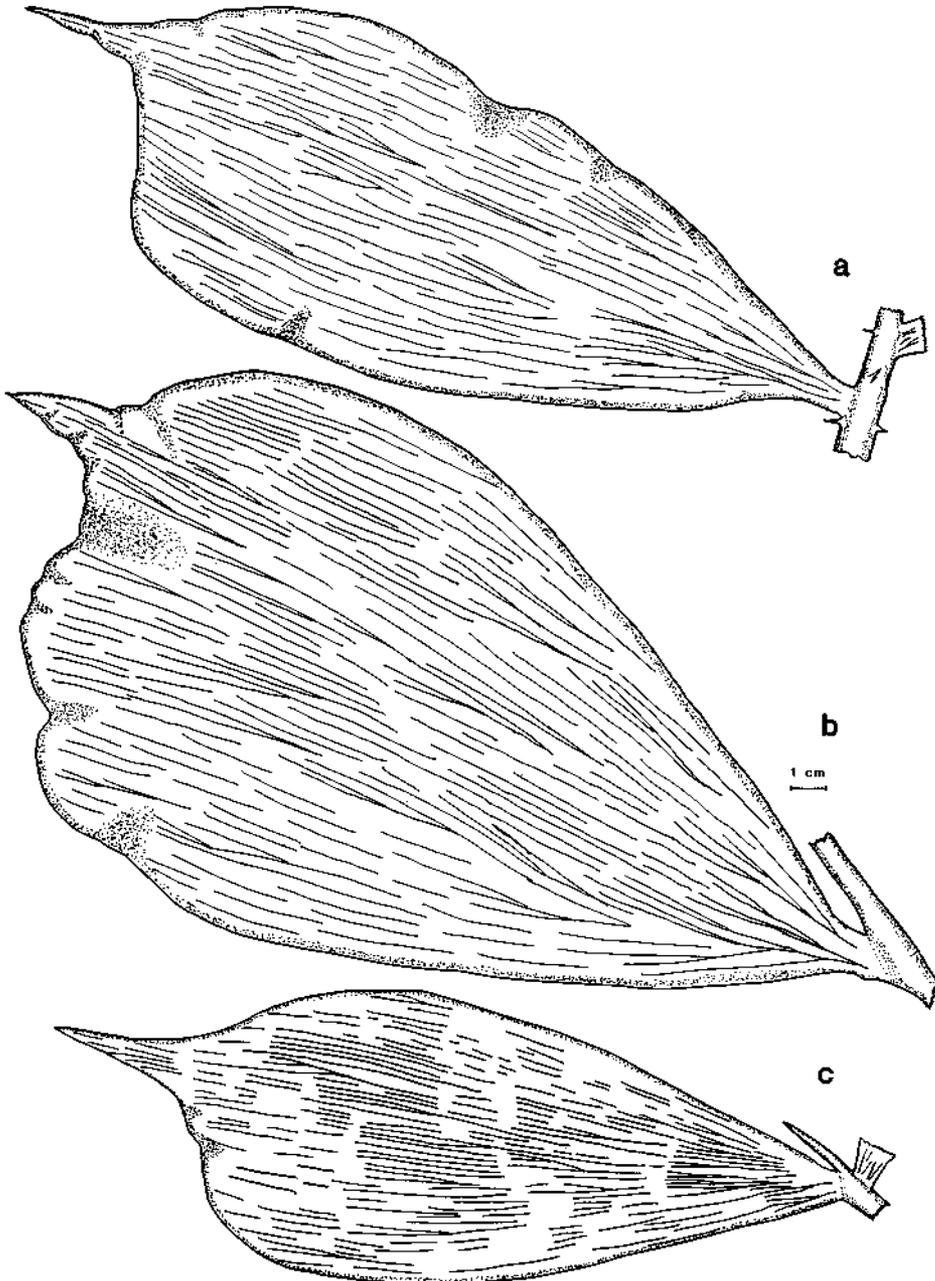


FIG. 1. Leaflets of *Ceratozamia euryphyllidia*. Based on the holotype (Vázquez Torres 2842, NY). A. Basal leaflet. B. Leaflet from median region of the rachis. C. Leaflet from terminal pair.

apex slightly peltate with 2 horns 1-2 mm long; *microsporangia* covering the unexposed abaxial surface (from $\frac{2}{3}$ - $\frac{3}{4}$ the total length), in clusters of (2) 3 (4-5), dehiscing longitudinally; *megasporangiate strobilus* wine red when young, brown to dark brown when mature, usually solitary, cylindric or slightly conical, 20 cm long including the peduncle, 5 cm in diam, the apex mucronate; *peduncle* to-

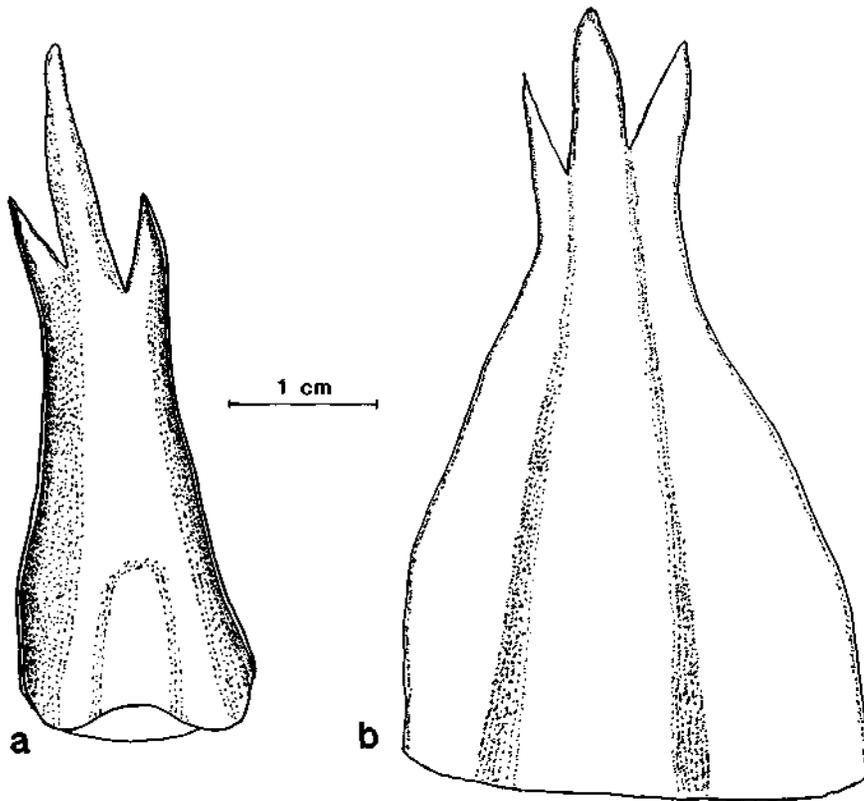


FIG. 2. Cataphylls of *Ceratozamia euryphyllidia*. Based on the holotype (*Vázquez Torres 2842*, NY). A. Adaxial view. B. Abaxial view.

mentose, grayish, elongate, 12 cm long, 1.4 cm in diam, unarmed; *megasporophylls* peltate with a narrow basal stalk and transversely hexagonal tips bearing 2 stout horns with many fine ridges between them, 1.5-3 cm long including the stalk, 1.5-2 cm wide; *ovules* 2 per megasporophyll, projecting inward toward the strobilus axis, red-pubescent when young, a prominent white-pubescent collar at the base of each ovule through maturity; *seeds* smooth, 2.3-2.7 cm long, 2 cm in diam.

TYPE: MEXICO. VERACRUZ: selva alta perennifolia, elev. 120 m, 22 Jun 1984, *Vázquez Torres 2842* (HOLOTYPE: NY; ISOTYPES: CHAPA, NY, XALU).

Paratypes: MEXICO. VERACRUZ: selva alta perennifolia con *Guarea*, *Pouteria*, *Gutteria*, *Cyclanthaceae*, lomeríos con suelos profundos sombreados húmedos, con abundante materia orgánica, elev. 140 m, 26 Mar 1982, *Vázquez Torres, Wendt, Lorence & Navarrete 2374* (CHAPA, NY, XALU); bosque tropical perennifolio mezclado con jimales (comunidad densa del bambú *Olmeca recta*), elev. 150 m, 18 Apr 1982, *Vázquez Torres 2451* (CHAPA, NY, XALU); bosque tropical perennifolio, lomeríos suaves, suelo arcilloso, pocas rocas calizas aflorantes, elev. 120 m, 28 Jul 1983, *Vázquez Torres 2614* (CHAPA, NY, XALU).

We have purposely omitted precise locality data in an attempt to prevent the eradication of the populations by commercial collectors. We have seen only 30 plants in the wild, and are convinced that commercial collectors would, either intentionally or unintentionally, cause its eventual extinction.

Ceratozamia euryphyllidia is perhaps the most distinctive species in the genus. Its more pronounced morphological characters are the enormous leaves and trans-

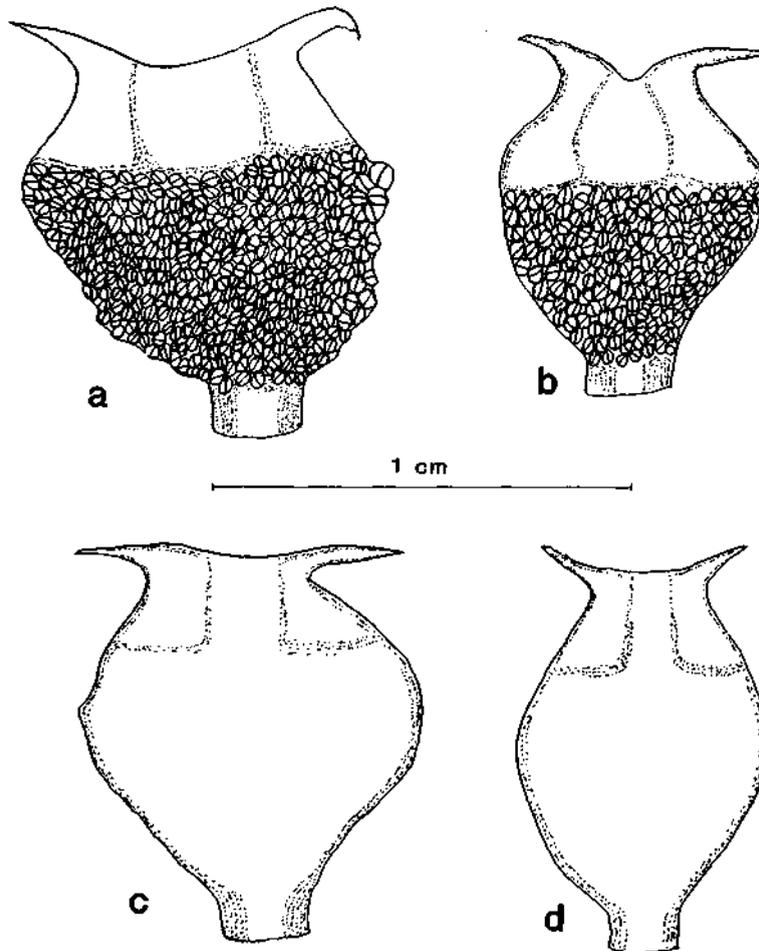


FIG. 3. Microsporophylls of *Ceratozamia euryphyllidia*. Based on the isotype (Vázquez Torres 2842. NY). A & B. Abaxial views. C & D. Adaxial views.

lucent leaflets with undulate margins. In our opinion, its nearest relative is *C. miqueliana* H. A. Wendl., which, although similar in leaflet shape, differs significantly in the smaller size of its leaves and leaflets, which are also papyraceous and lack the undulate margins of *C. euryphyllidia*.

The discovery of this new species has led to the following conclusions concerning morphological trends in the genus that appear to be related to habitat and biogeography.

Morphology and Distribution

Recent field work on the genus *Ceratozamia* in Mexico (Landry & Wilson, 1979; Moretti et al., 1980, 1982; Vovides & Rees, 1980, 1983; Vovides et al., 1983; Stevenson, 1982) has provided a better understanding of the species and their distributions. As a result, there appear to be two groups of species within the genus. While these two groups are readily distinguishable from each other, we do not wish at this time to designate formal taxonomic ranks until we have been able to conclude our current studies on cytology, phytochemistry, anatomy,

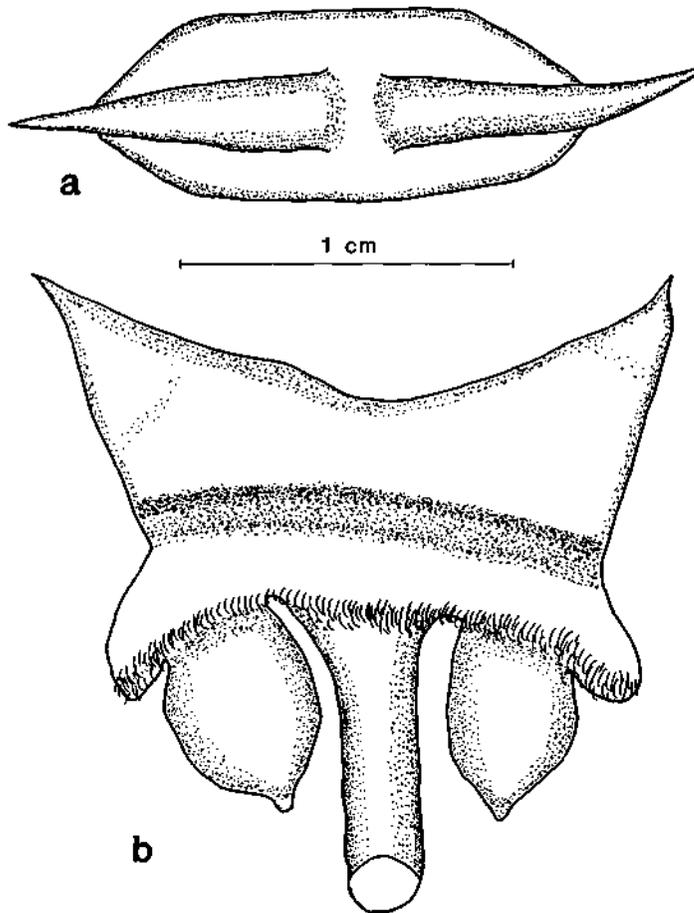


FIG. 4. Megasporephyll of *Ceratozamia euryphyllidia*. Based on the holotype (Vázquez Torres 2842, NY). A. End view. B. Adaxial view.

and controlled environmental experiments. Nomenclature and typification for *Ceratozamia* may be found in Stevenson and Sabato (In press).

The first group of species includes *C. euryphyllidia*, *C. hildae* G. Landry & M. Wilson, *C. latifolia* Miq., *C. microstrobila* Vovides & J. Rees, and *C. miqueliana*. All of these species have seedling leaves with pinnae that are attenuate basally, obovate to oblanceolate in form, inequilateral, abruptly acuminate apically, and papyraceous to membranaceous in texture. As the plants become sexually mature, the leaflets become broader, the inequilateral shape becomes accentuated as does the acuminate apex, and the texture becomes thinner. The stems of these species are always hypogeous and the strobili are smaller than the smallest of the second group.

Pinna morphology of the various species exhibits a correlation with habitat. Those with the smallest and most papyraceous pinnae, *C. latifolia*, *C. hildae*, and *C. microstrobila*, occur in cloud forests dominated by oaks (*Quercus* spp.). In contrast to this *C. miqueliana*, which has wider and thinner leaflets, grows in semideciduous rain forest. *Ceratozamia euryphyllidia*, which has the largest and thinnest pinnae of the species in this group, grows in tropical evergreen rain forest.

None of these species are sympatric, with the exception of *C. latifolia* and *C.*

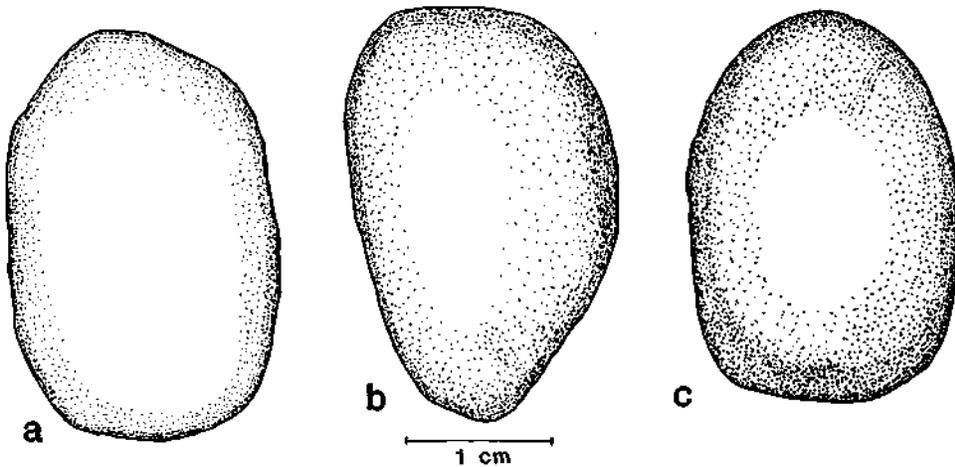
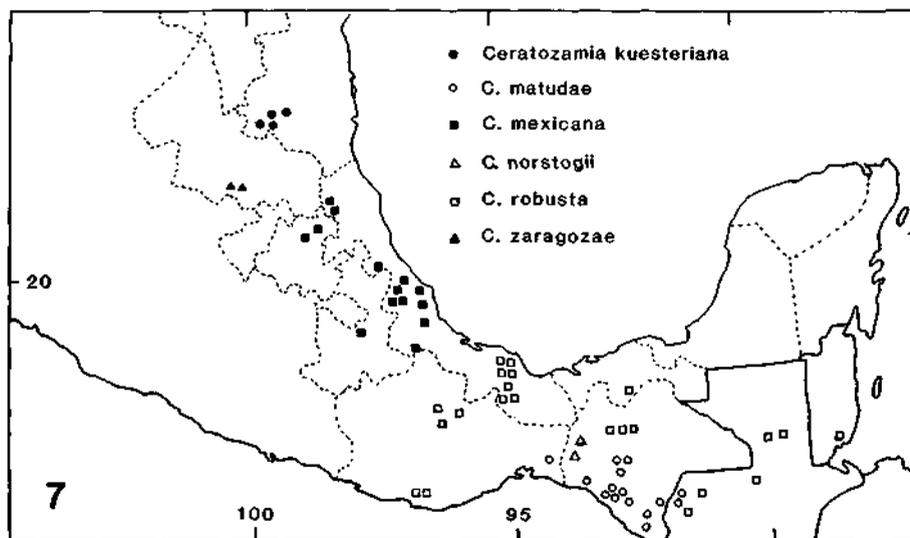
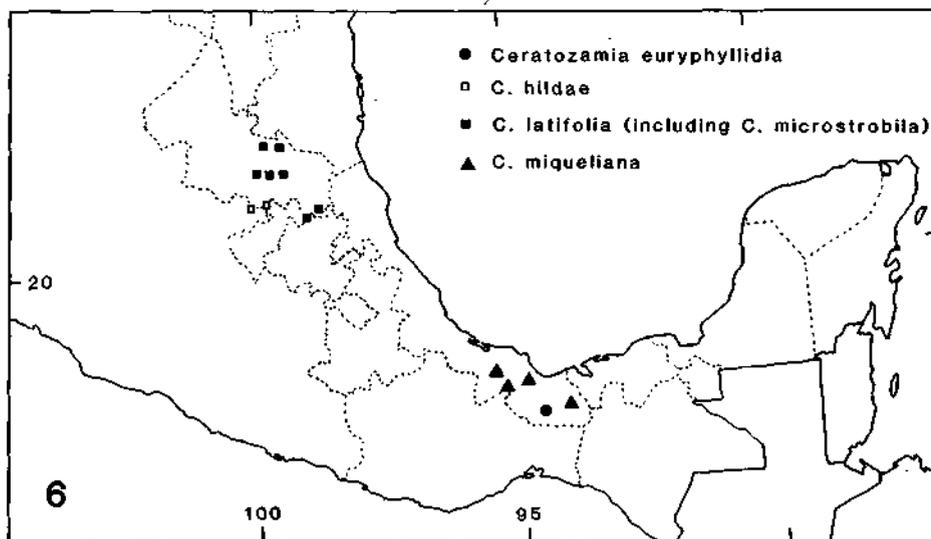


FIG. 5. Seeds of *Ceratozamia euryphyllidia*. Based on the holotype (Vázquez Torres 2842, NY). A. Ventral view. B. Lateral view. C. Dorsal view.

microstrobila discussed below. Besides the habitat preference, species of this group show a north-south distribution (Fig. 6). That is, *C. euryphyllidia*, which grows in the wettest habitat, is found only near the Oaxaca-Veracruz border. *Ceratozamia miqueliana*, which grows in cooler, less wet habitats, occurs in only three localities in southern Veracruz and one near the Tabasco-Chiapas border, some 300 km from *C. euryphyllidia*. The most northerly taxa in this group, *C. latifolia*, *C. hildae*, and *C. microstrobila*, occur in the driest habitats and have the most papyraceous pinnae. These three taxa are limited to San Luis Potosí and neighboring Hidalgo and Querétaro. Of these three taxa, *C. hildae* is distinguished by leaflets borne in clusters along the rachis. It is not sympatric with any other of the species and is known from only two localities in the wild where it has been essentially eradicated by recent commercial collecting. We would like to note that an occasional leaf with clustered leaflets does appear in *C. latifolia*, but this is rare. Also rare is the occurrence in *C. hildae* of individual leaves with non-clustered leaflets, most frequently observed in seedlings and young plants. Plants assignable to the recently described *C. microstrobila* are present in each of the eight populations of *C. latifolia* that we have observed in the field. In fact, all plants at the type locality (the only locality mentioned in the protologue) of *C. microstrobila* are attributable to *C. latifolia*. Presumably, *C. microstrobila* can only be distinguished from *C. latifolia* by smaller leaves and leaflets that are thicker (sometimes being subcoriaceous). The strobili of both are essentially identical. The forms described as *C. microstrobila* appear to grow in the more dry sunny areas of these populations. When cultivated in conditions of high moisture and deep shade, plants assignable to *C. microstrobila* "turn into" *C. latifolia*. Conversely, when plants assignable to *C. latifolia* are exposed to conditions that are dry with high light intensity, they "turn into" plants of *C. microstrobila*. Thus, it appears that this is not a unique case of sympatry in *Ceratozamia*, but rather that these two taxa are one and the same entity. In our opinion, the plants that have been referred to *C. microstrobila* are nothing more than forms of *C. latifolia* that are phenotypical expressions of environmental conditions. Therefore, we recognize only *C. latifolia* and consider *C. microstrobila* to be a synonym.

The second group contains *C. mexicana* Brongn., *C. robusta* Miq., *C. kuesteriana* Regel, *C. zaragozæ* F. Medellin, *C. matudae* [*matudai*] Lundell, and *C. norstogii* Stevenson. These taxa are characterized by leaflets that are linear-lan-



FIGS. 6 and 7. Maps of Mexico, Belize, and Guatemala. 6. Distribution of the broad-pinnae species of *Ceratozamia*. 7. Distribution of the narrow-pinnae species of *Ceratozamia*.

ceolate to lanceolate, often subfalcate to falcate, and equilateral to slightly inequilateral. The leaflet apices are, in adult plants, long-attenuate or acute. Leaflets, in mature plants, are less than three cm wide, although they may be as wide as five cm in juveniles. It is interesting to note that all of these species have seedling leaves that conform to the description given for adult plants of the first group. As the plants become older, the leaflets become narrower and more coriaceous.

Ovulate strobili are, in general, much larger than in the first group, being greater than 12 cm in length and often reaching lengths of 50 cm or more in *C. robusta*. On the other hand, they may be as small as eight cm in young plants of *C. zaragozae*. The stems of these taxa are generally epigeous and vary from very

well defined trunks up to two m tall in *C. robusta* to short trunks less than one m in *C. mexicana* and less than 30 cm in *C. kuesteriana*, *C. matudae*, and *C. norstogii* to semi-epigeous in *C. zaragozae*.

Although leaflet shape shows little variability, leaf length and leaflet width and texture do vary. The latter features, in particular, are associated with habitat. *Ceratozamia zaragozae* and *C. norstogii* have the most coriaceous leaflets in the genus. The leaflets are rolled adaxially and less than one cm wide and the rachis is twisted. These two species grow in pine-oak forest that is the driest habitat for species of *Ceratozamia*. Their distribution illustrates a common pattern in the group, namely north-south disjunctions between pairs of quite similar species (Fig. 7). Thus, *C. zaragozae* is found only in a small area of southern San Luis Potosí near Río Verde, whereas *C. norstogii* is found only some 900 kilometers to the south in the Sierra Madre de Chiapas in western Chiapas.

In more moist pine-oak habitats that are basically cloud forest one finds *C. kuesteriana* and *C. matudae*, which have leaflets one to two cm wide, not adaxially rolled, and subcoriaceous. The former has generally unarmed petioles (an occasional prickle may be present) and microsporophylls fertile for less than half their length, whereas that latter has heavily armed petioles and microsporophylls fertile for three-fourths of their length. These two species also have a north-south vicariant distribution (Fig. 7). Thus, *C. kuesteriana* is only found in the Sierra Madre Oriental in southern Tamaulipas and *C. matudae* is centered some 1200 km to the south in south western Chiapas and eastern Guatemala with one disjunct locality in Oaxaca near the Chiapas border.

In even wetter habitats of tropical semideciduous rain forest are found *C. mexicana* and *C. robusta*, with the widest and thinnest textured leaves in this group. Leaflet width is three to five cm and leaflet texture is generally papyraceous, especially in *C. robusta*. Whereas *C. robusta* has trunks up to two m tall, leaves to three m long, and leaflets subfalcate to falcate with acute apices, *C. mexicana* is of smaller stature (trunks to 30 cm) with attenuate leaflet tips. The same pattern of distribution is seen for these two species (Fig. 7): *C. mexicana* in north-central Veracruz, and *C. robusta* ranging from south-central Veracruz into Guatemala and Belize with one disjunct population in Pacific Oaxaca. The latter has the widest range of any species of *Ceratozamia*.

Discussion

There appears to be a correlation between habitat and vegetative morphology of the leaves in *Ceratozamia*. That is, the wetter the habitat the larger and thinner the leaves and leaflets. Because all species of *Ceratozamia* appear morphologically identical in their seedling and juvenile stages, we assume they all have a common ancestor. In our opinion, divergence has occurred along two main lines, one consisting of those species which perpetuate or even elaborate the juvenile characters in the adults and a second in which leaf and leaflet morphology shows a distinct departure from that observed in the juvenile stages.

As pointed out by Moretti et al. (1980), the distribution of *Ceratozamia* is correlated with mountain systems with a prevailing north-south orientation. Moreover, the genus as a whole shows a narrow but essentially continuous distribution from Tamaulipas in the north to Belize in the south even though no single species occupies the entire range. There are two exceptional disjunctions: two populations that appear referable to *C. robusta* in Sierra Madre del Sur in Pacific Oaxaca (Fig. 7); and a population of *C. miqueliana* on the coast of the Gulf of Mexico (Fig. 6).

Within this range, there is one group of species, *C. euryphyllidia*, *C. hildae*, *C.*

latifolia (including *C. microstrobila*), and *C. miqueliana*, with broad, thin leaflets strongly asymmetric and acuminate at the apex, that have north-south distribution closely correlated with moisture and temperature. It is our contention that these taxa have a common origin. Certainly, it would appear that *C. latifolia* and *C. hildae* are related to one another in that they occupy similar habitats and are located in the same area. The systematics of these two species needs to be clarified as it would appear superficially at least that *C. hildae* may be nothing more than a clustered leaflet form of *C. latifolia* and its recognition as a species would appear to rest solely upon the fact that it is not sympatric with *C. latifolia*. The systematic position of *C. microstrobila* is less problematic as it is clearly a part of *C. latifolia* in view of the fact that plants of the former can "become" the latter and *vice versa* when grown in changed environments. In contrast, plants of *C. euryphyllidia* and *C. miqueliana* always maintain their morphological characters both in the field and when raised under differing conditions in cultivation.

There are two equally persuasive but mutually exclusive explanations for the distribution of the taxa in the second line, which includes *C. kuesteriana*, *C. matudae*, *C. mexicana*, *C. norstogii*, *C. robusta*, and *C. zaragozae*. Both of these explanations involve vicariance as there is no known dispersal mechanism for any species of *Ceratozamia*. The first hypothesis calls for one widespread parental species of *Ceratozamia*, perhaps similar to *C. robusta*, which has the largest range in the genus. Populations of this species became isolated from each other as a result of the tertiary formation of the mountain ranges. Subsequent evolution resulted in the formation of new taxa with northern and southern morphological counterparts in similar habitats. Thus, each of the northern species, *C. kuesteriana*, *C. zaragozae*, and *C. mexicana*, has its southern counterpart, *C. matudae*, *C. norstogii*, and *C. robusta*, respectively, in a similar habitat. This explanation assumes similar morphologies developing independently in similar environments.

The second hypothesis, which is more parsimonious, assumes three widespread parental species, each separated by orogenesis into northern and southern populations which subsequently differentiated into northern and southern taxa.

Neither of these two explanations can be proven at this time, but the results of further work, now in progress, on phytochemistry, anatomy, and cytology can be brought to bear upon these explanations.

Vegetative key to the species of *Ceratozamia*¹

- 1 Leaflets inequilateral, oblanceolate to obovate with abruptly acuminate apices.
 - 2 Leaflets clustered along the rachis.....*C. hildae*
 - 2 Leaflets evenly spaced, opposite to subopposite.
 - 3 Leaflets 2-4 cm wide.....*C. latifolia*
 - 3 Leaflets greater than 5 cm wide.
 - 4 Leaflets papyraceous to membranaceous, 5-8 cm wide.....*C. miqueliana*
 - 4 Leaflets translucent, 9-16 cm wide.....*C. euryphyllidia*
- 1 Leaflets equilateral, lanceolate to linear-lanceolate with acute or long attenuate apices.
 - 5 Leaflets strongly rolled adaxially; rachis usually twisted.
 - 6 Leaves of mature plants to 1 m long; restricted to San Luis Potosí, Mexico.....*C. zaragozae*
 - 6 Leaves of mature plants from 1-2 m long; restricted to western Chiapas, Mexico.....
 -*C. norstogii*
 - 5 Leaflets planate, margins sometimes revolute; rachis straight.
 - 7 Leaflets 1-1.5 cm wide. abruptly cuneate basally, symmetrical, margins revolute

¹ Because as discussed in the text, all seedlings and young plants of *Ceratozamia* spp. are similar, this key is only for older plants. The emphasis on vegetative characters is because the genus is dioecious and, moreover, reproductive structures are infrequently encountered either in the field or as herbarium specimens.

- 8 Petiole and rachis unarmed or if armed, sparsely so and the prickles diminutive; restricted to Tamaulipas, Mexico.....*C. kuesteriana*
 8 Petiole and rachis armed with numerous stout prickles.....*C. matudae*
 7 Leaflets 1.5-5 cm wide, gradually tapering basally, falcate to subfalcate, margins not revolute.
 9 Leaflets 1.5-2.5 cm wide, subfalcate, coriaceous; adult plants with leaves to 1.5 m; trunks to 0.5 m.....*C. mexicana*
 9 Leaflets 2.5-5 cm wide, falcate, papyraceous to subcoriaceous; adult plants with leaves to 3 m; trunks to 2 m.....*C. robusta*

Acknowledgments

We would like to thank the reviewers for their time and effort in improving this manuscript. One of us (DWS) particularly appreciated the suggestions that a stronger position be taken regarding systematics. We are indeed indebted to Rupert Barneby for his suggestion of the Greek derived specific epithet and to Elyssa Kellerman for help in mapping.

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