What is *Ceratozamia mexicana* (Zamiaceae)?

Andrew P. Vovides[1], Dennis Wm. Stevenson[2], Miguel Angel Pérez-Farrera[3], Sergio López[3], and Sergio Avendaño[1]

Botanical Sciences
94 (2): 419-429, 2016

DOI: 10.17129/botsci.449

Abstract

Explorations in central Veracruz on the Transvolcanic Mexican Belt and regions explored by 19th century botanists we found various populations of *Ceratozamia* whose taxonomic status is not yet completely clear. Especially two populations of *C. mexicana* with distinct morphology; one population at El Esquilón considered as *C. mexicana* by Chamberlain and other authors, and another population at El Mirador that Stevenson found a voucher at the herbarium in Paris with oblanceolate leaflets collected by Ghiesbrecht and designated it as Brongniart's holotype. The plants from El Mirador are comparable to the holotype of *C. mexicana*, but those at El Esquilón do not. Stevenson later also found a voucher at Kew by Thiselton-Dyer as *C. mexicana* var. *tenuis* from Mexico with linear-lanceolate leaflets that is similar to the plants at the El Esquilón population. An analysis of 11 leaflet anatomical characters gave a significant discriminant pattern (Wilk's lambda 0.00015 $P < 0.01$). The squared Mahalanobis distances were also significant ($P < 0.05$) and the first canonic variable showed that 93.4 % of the variation was due to the anatomical characters. A new nomenclatural combination is proposed and Thiselton-Dyer's voucher assigned as the lectotype of *Ceratozamia tenuis*. Epitypes were also designated for the two species in support of the anatomical analysis as well as a description for both species given.

Key words: *Ceratozamia tenuis*, cycad leaflet anatomical analysis, cycad taxonomy.

¿Qué es *Ceratozamia mexicana* (Zamiaceae)?

Resumen

Las exploraciones sobre la Faja Volcánica Transmexicana en la región central de Veracruz y regiones exploradas por los botánicos del siglo XIX permitieron encontrar varias poblaciones de *Ceratozamia* cuyo estatus taxonómico no está completamente claro. En especial, dos poblaciones de *C. mexicana* cuya morfología es distinta; una población en la localidad El Esquilón considerada como *C. mexicana* por Chamberlain y otros autores, así como otra en la localidad El Mirador donde Stevenson encontró un ejemplar en el herbario de París con foliolos oblongo-lanceolados colectada por Ghiesbrecht y lo asignó como holotipo de Brongniart. La población explorada de El Mirador concuerda con el holotipo de *C. mexicana*, pero la población del Esquilón no. Stevenson más adelante encontró también en Kew un ejemplar de Thiselton-Dyer nombrado *C. mexicana* var. *tenuis* proveniente de México con foliolos linear-lanceolados que es semejante con la población de El Esquilón. Un análisis de 11 caracteres anatómicos foliares de especímenes de ambas poblaciones arrojó un patrón de discriminantes significativo (Wilk's Lambda: 0.00015 $P < 0.01$). Las distancias cuadradas de Mahalanobis también fueron significativas ($P < 0.05$), y la primera variable canónico mostró que el 93.4 % de la variación fue debida a los caracteres anatómicos. Se propuso un cambio de combinación nomenclatural y se asignó lectotipo del ejemplar de Thiselton-Dyer como *Ceratozamia tenuis*. Se designó epitipos para las dos especies en apoyo al análisis anatómico y se presenta la descripción para ambas especies.

Palabras clave: Análisis anatómico de foliolos, *Ceratozamia tenuis*, taxonomía de cicadas.

[1]Instituto de Ecología A.C., Xalapa, Veracruz, Mexico
[2]New York Botanical Garden, Bronx, New York, USA
[3]Instituto de Ciencias Biológicas, UNICACH, Tuxtla Gutierrez, Chiapas, Mexico 29039
*Author for correspondence: andrew.vovides@inecol.mx

Botanical excursions over several years into central Veracruz along the transition zone between cloud forest and tropical forest at around 800–1,800 m elevation have resulted in the location of a number of *Ceratozamia* Brongn. populations. The taxonomic status of one of these cycads, *C. brevifrons* Miq. that was considered synonymous with *C. mexicana* Brongn. has been solved by applying numerical analyses to leaflet anatomical characters by Vovides *et al*. (2012). The objective of this study was to elucidate the taxonomic status of the cycads in two of these populations considered as *C. mexicana* that separated significantly in the analyses; at El Esquilón north of the city of Xalapa and at El Mirador to the north east of Huatusco. Details of the other taxa studied, apart from one appearing in the analysis will not be considered further here and can be consulted in Vovides *et al*. (2012). Living specimens were collected and cultivated at the Jardín Botánico Francisco Javier Clavijero (JBC) for several years in order to observe plasticity upon later comparison with habitat plants. Herbarium specimens at XAL, MEXU, NY and especially the type of *C. mexicana* at the herbarium of the National Museum of Natural History, Paris (P) were also examined and compared. Table 1 lists the species and vouchers of the specimens used for the anatomical study and analysis deposited at XAL, MEXU and NY.

Brongniart (1846) described *Ceratozamia mexicana* from a cultivated plant in Paris as having coriaceous, oblong-lanceolate, subfalcate, entire, acuminate smooth leaflets with partly sunken parallel veins that corresponds to the holotype in Paris (P!, Figure 1A) Brongniart s.n. This was collected by Ghiesbrecht in Mexico from El Mirador (Schuster, 1932) also mentioned by Thiselton-Dyer (1884), and an illustration in Brongniart (1846, Figure 1B), see also Stevenson and Sabato (1986). Thiselton-Dyer (1884) described *C. mexicana* var. *tenuis* Dyer very briefly with no illustration referring to Mexico as the provenance, but at the time of typification by Stevenson and Sabato (1986) no extant specimens were known so they typified with the description (no longer legal in the International Code of Nomenclature for algae, fungi, and plants). Thus, the true nature of this taxon was enigmatic until Stevenson in 1999 discovered oversized sheets of cycads at the Kew herbarium that were far removed from the normal-sized collections. In those collections are three sheets of a single leaf of a specimen labelled *C. mexicana* var. *tenuis* collected from a cultivated plant at Kew (no longer alive) in 1881 (K-3 sheets!, Figure 2) that we consider to be the lectotype. Thus, with an established type, we have a better concept of the morphology of this taxon. Coupled with this discovery, Vovides and Avendaño visited the El Mirador population northeast of Huatusco and it does correspond to the holotype of *C. mexicana*; thus, we refer to this as the El Mirador population. Chamberlain (1919) located a population about 11 km north of the city of Xalapa in a broad valley on the road to Naolinco that he considered *C. mexicana*, and subsequently was recognized as *C. mexicana* var. *mexicana* in the Flora of Veracruz by Vovides *et al*. (1983) and *C. mexicana* by Whitelock (2002). There are still stands of this cycad in this area in localities such as El Esquilón, and it is more abundant in

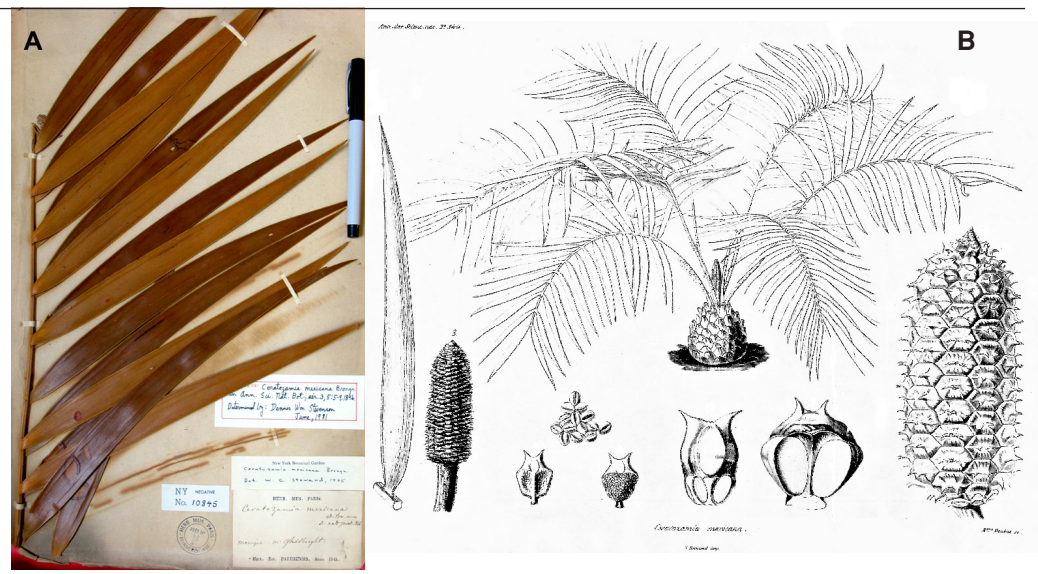

Figure 1. *Ceratozamia mexicana*. **A)** Holotype of *C. mexicana* Brongniart. **B)** Illustration from Brongniart's original 1846 paper describing *C. mexicana*.

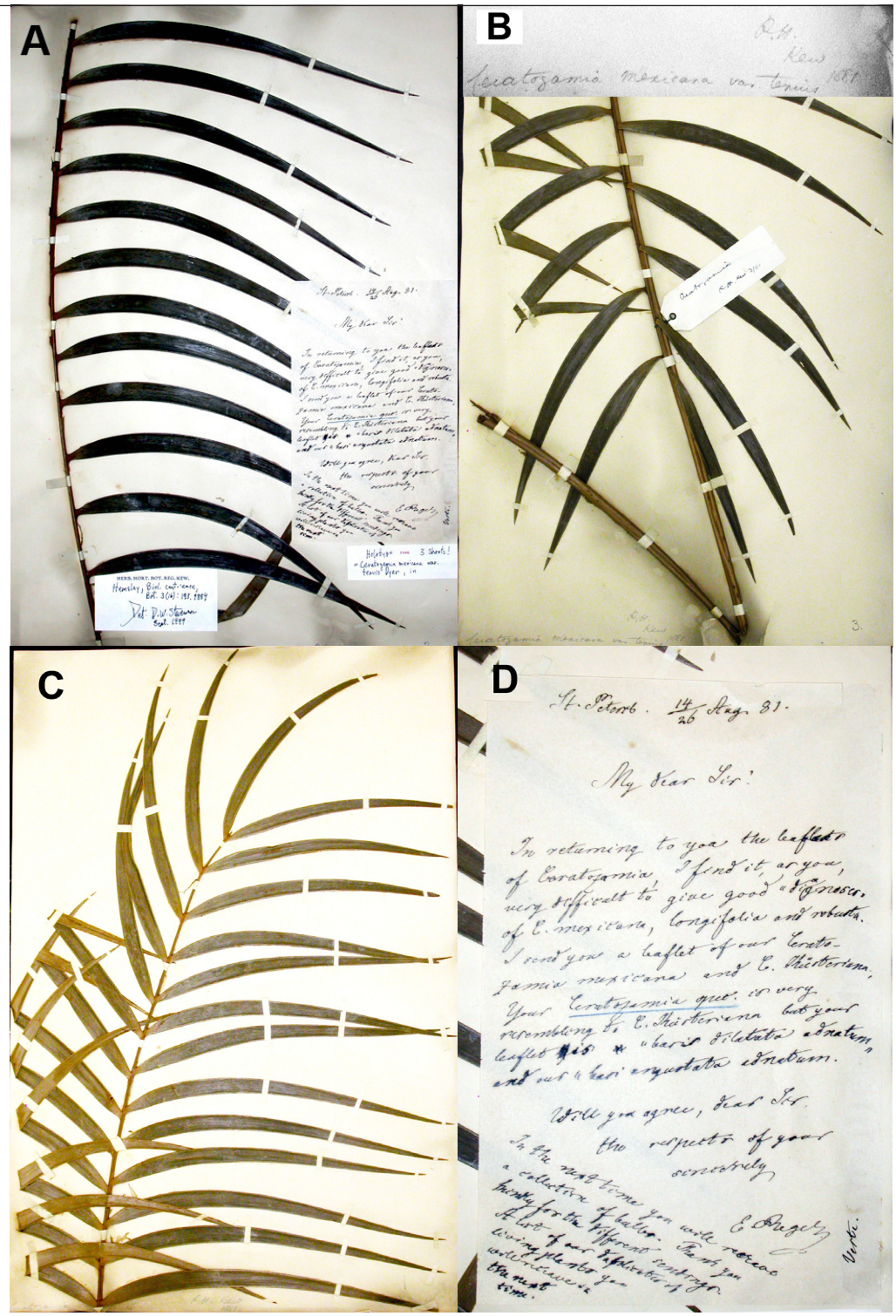

Figure 2. Holotype of *Ceratozamia mexicana* var. *tenuis*. **A)** Sheet 2 of 3. **B)** Sheet 3 of 3, insert above, enlarged portion of text at base of Sheet 3. **C)** Sheet 1 of 3. **D)** Enlargement of letter attached to Sheet 2 in Thiselton-Dyer's handwriting.

the surrounding forests near Coacoatzintla. *Ceratozamia mexicana sensu* Chamberlain, which we refer to as the El Esquilón population, differs from the type specimen (El Mirador) in that the El Esquilón population has linear lanceolate, falcate to subfalcate leaflets whereas the leaflets of the type specimen of *C. mexicana* are oblong-lanceolate, subfalcate (Brongniart, 1846; Figure 1). The Esquilón population has leaflet morphology consistent with the cultivated plant of *C. mexicana* var. *tenuis* as represented by the lectotype (Figure 2). Thiselton-Dyer (1884) comments that *C. mexicana* var. *tenuis* leaflets resemble those of *C. kuesteriana* Regel, but the

Table 1. El Esquilón and El Mirador, Veracruz populations of *Ceratozamia mexicana* vouchers deposited at XAL of the specimens used for the anatomical analysis.

Species	Herbarium vouchers (XAL)				
C. mexicana (El Esquilón)	A.V.015	A.V.018*	A.V.72	S.A. 5628	S.A.5619
C. mexicana (El Mirador)	A.V.730	A.V.747	J.R.1688*	S.A.5205	S.A.5206

*epitype also at MEXU, NY

Table 2. Eleven leaflet anatomical characters used for statistical analyses of the *Ceratozamia* taxa.

Character	Character type and cross sectional measurements
1	Abaxial epidermal cell length
2	Macrolumen epidermal cell length
3	Adaxial cuticle thickness
4	Adaxial epidermal cell length
5	Palisade parenchyma cell length
6	Palisade parenchyma cell width
7	Perivascular fibre diameter
8	Intervascular fibre length
9	Intervascular fibre width
10	Number of perivascular fibres (surrounding vascular bundle)
11	Number of intervascular fibres (between vascular bundles)

general habit is different. *Ceratozamia kuesteriana* has consistently reddish brown emergent leaves (a character that is lost on herbarium vouchers), elongate linear-lanceolate leaflets that are strongly caniculate adaxially, mentioned in the German description shown in Figure 22 of Tafel 4 by Regel (1857a) and can be seen in the illustration in Figure 2 of Moretti *et al*., (1982), in Figure 2 of Vovides (1985), and most obviously in Figures 24-25 Tafel 186 of Regel (1857b). Leaflets in *C. mexicana* from El Mirador are consistently reddish brown emergent and flat whereas those in *C. mexicana* from El Esquilón are consistently light green emergent and only slightly caniculate.

Methods for anatomical study

Leaflets for used for sectioning were taken from plants growing in habitat as well as those cultivated in the Jardín Botánico Francisco Javier Clavijero over several years. The central portion of leaflets taken from the median leaflets of leaves from five individuals of each taxon from each of the populations were fixed in FAA and hand sectioned with the aid of a sliding microtome. Fixed sections were subjected to the phloroglucinol HCl test for lignin also permanent preparations were made, double-stained with safranin and fast green, cleared and mounted according to Purvis *et al*. (1966). Photomicrographs taken with a digital camera using clear field light microscopy. Cross-sectional measurements were taken from 11 characters (Table 2) using a calibrated eyepiece micrometer; where cells were not isodiametric the measurements were expressed as length and width. Twentyfive replicate measurements were taken for each character from each

Table 3. Diagnostic vegetative and anatomical features separating *C. mexicana* from *C. tenuis*

Feature*	*Ceratozamia mexicana*	*Ceratozamia tenuis*
Leaf emergent color	Reddish brown	Green
Leaflets	Oblong-lanceolate	Linear-lanceolate
Girder sclerenchyma	Present	Absent

*Not used in analyses

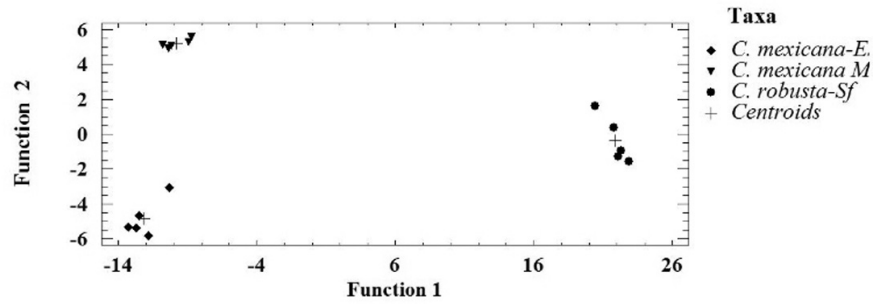

Figure 3. Scatter plot score derived from the functions produced by stepwise discriminant analysis of 11 anatomical characters occurring in *Ceratozamia tenuis* from El Esquilón, *C. mexicana* from El Mirador, and *C. robusta* from San Fernando, Chiapas.

Table 4. Summary of analysis of variance of the 11 anatomical characters R^2 (correlation coefficient), F (F value), P (Probability).

Character	R^2	*F*	*P*
1	0.70	13.70	0.0008
2	0.30	2.35	0.1378
3	0.65	11.07	0.0002
4	0.63	10.02	0.0028
5	0.33	2.98	0.0889
6	0.80	23.74	<0.0001
7	0.80	23.96	<0.0001
8	0.80	23.56	<0.0001
9	0.83	28.66	<0.0001
10	0.98	283.80	<0.0001
11	0.97	198.14	<0.0001

of the five leaflet samples of the two taxa as described in Vovides *et al*. (2012), **the additional species *C. robusta* Miq. was included order to satisfy requirements for a discriminant reanalysis** of the data on three taxa. Analysis of variance (ANOVA) and Tukey multiple range analyses were done using JMP version 3.2 statistical software. Discriminant analyses (McCune & Mefford, 1997) were done with Statgraphics software version 2.0. Data were transformed to log10 and Mahalanobis distances were obtained.

Results

Two qualitative morphological and one anatomical variable separate *Ceratozamia mexicana*, El Mirador and *C. mexicana*, El Esquilón (Table 3). Furthermore the ANOVA test on the11 anatomical variables of the leaflets of the *Ceratozamia* species tested were significantly different at $P < 0.001$ (Table 4) except for macrolumen epidermal cell and palisade parenchyma cell length (characters 2 and 5 respectively). The Tukey multiple range test showed that the number of perivascular fibres (character 10) were significantly different for the two *C. mexicana* populations, separating the groups with no overlap. *Ceratozamia robusta* is separated from the two *C. mexicana* populations by the number of intervascular fibres character (character 11). Data derived from the discriminant function analysis of anatomical characters separate the three populations; two of *C. mexicana* (Esquilón and El Mirador populations) and *C. robusta* coordinately in bidimensional space and do not present any overlapping between groups (Figure 3). The Wilks

Table 5. Summary of the discriminant analysis results from the analysis of three taxa in *Ceratozamia* χ^2 = Chi square test, DF: Degrees of freedom, P = Probability

Derivate Functions	Wilks λ	χ^2	DF	P-Value
1	0.000149	61.6679	22	0.0000
2	0.045107	21.6911	10	0.0168

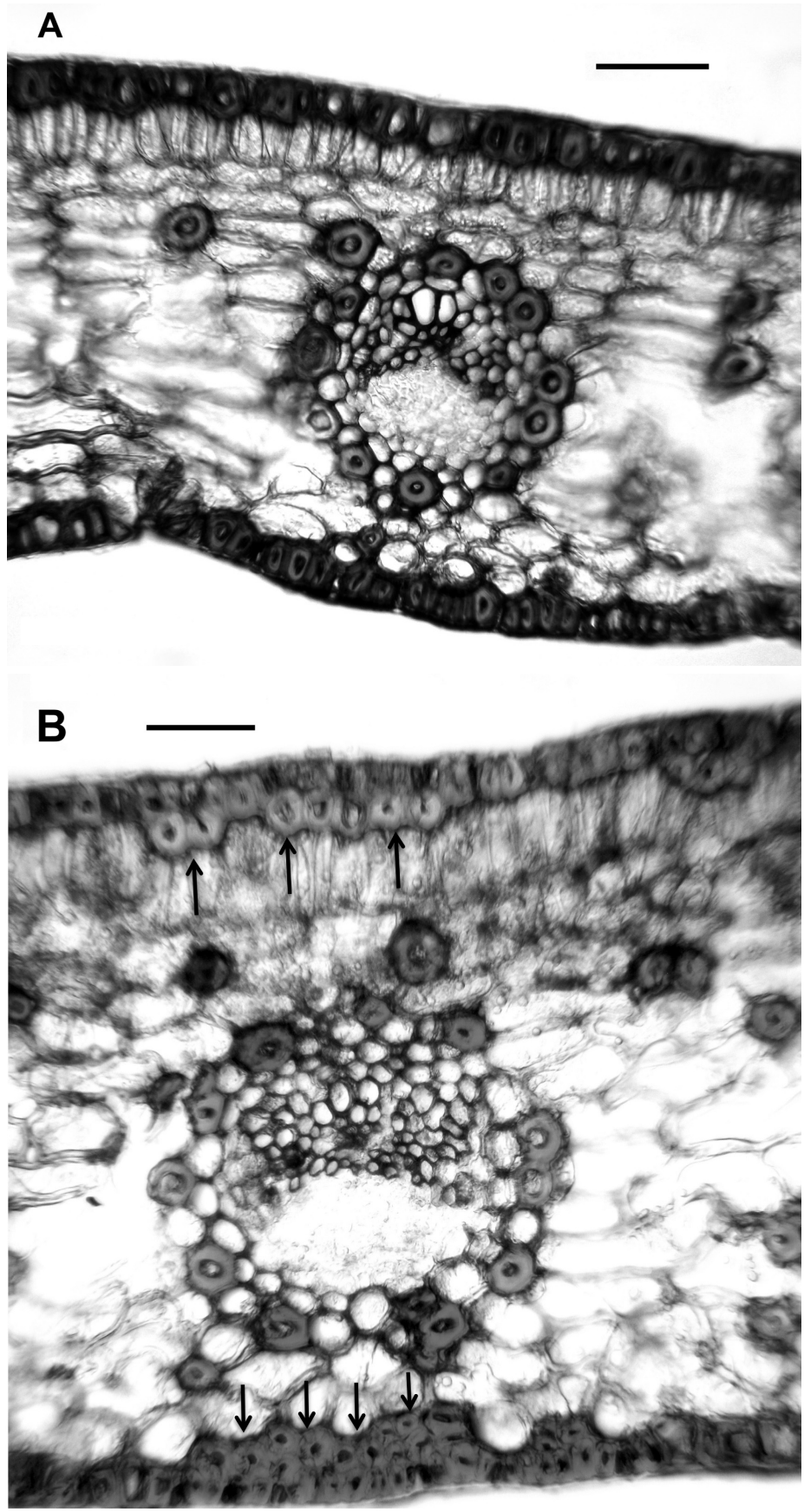

Figure 4. Transverse sections of leaflets treated with phloroglucinol HCl. **A)** *Ceratozamia tenuis* from El Esquilón. **B)** *Ceratozamia mexicana* from El Mirador with girder sclerenchyma (arrows). Scale Bars = 100 μm.

Table 6. Summary of the squared Mahalanobis distance (above asterisk), F values (below asterisk) and statistical significance (P). Esq = Esquilón population, Mir = Mirador population. P < 0.05 for all cases.

	***C. mex* Esq**	***C. mex* Mir**	***C. robusta***
C. mex Esq	*	106.76	1178.93
C. mex Mir	4.04	*	1035.15
C. robusta	44.66	39.21	*

Lambda (λ) test was highly significant (Wilk's $\lambda = 0.00015$ $P < 0.0091$) (Table 5), thus showing that all the species were classified correctly. Additionally, the squared Mahalanobis distances (Table 6) were statistically significant in all cases ($P < 0.05$). Of the 11 variables included in the standardized discrete canonical function, the two variables with the highest values in discriminant functions 1 and 2 were the cross sectional length of the thin walled macrolumen epidermal cells (character 2) and the cross sectional width of intervascular fibers (character 9) for function 1. The first and second canonic variable showed that 93.43 % of the variation is largely due to anatomical characters. The positive correlations (Table 7) of all the variables show differences between species. Additional to this analysis microscopic examination of leaflet cross sections revealed that *C. mexicana* (El Mirador) presents incipient girder sclerenchyma (not used in analysis) whereas those of El Esquilón do not (Figure 4).

We therefore consider the plants from El Esquilón to match Thiselton-Dyer's concept of *Ceratozamia mexicana* var. *tenuis*, and consider this taxon distinct enough to merit species rank. In following the guidelines for cycad classification proposed in Walters and Osborne (2004) that discourages the use of infraspecific units, we propose a change in rank of *C. mexicana* var. *tenuis* to *C. tenuis*, and based upon handwriting and origin a lectotype was assigned for this species. Epitypes were assigned for *C. tenuis* (AV-018) and for *C. mexicana* [JR-1688 (XAL, MEXU, NY)].

Table 7. Standardized discriminant function values for each of three factors used in the analysis of taxa for 11 leaflet anatomic characters.

Function	**1**	**2**
Character		
1	-0.33	-0.56
2	255.40	261.23
3	0.53	0.78
4	0.60	0.58
5	0.95	-104.51
6	163.43	202.40
7	-0.55	133.45
8	-306.49	-0.61
9	534.27	0.87
10	-235.42	0.65
11	-133.34	-138.78
Eigenvalue	301.17	21.17
Among group variance	93.43	6.57
Canonical correlation	0.99	0.97

Description

Ceratozamia tenuis (Dyer) D. W. Stev. *et* Vovides **stat. and comb. nov.** (Figure 5A) Basionym: *Ceratozamia mexicana* var. *tenuis* Dyer Biol. Cent.-Amer., Bot. 3: 193. 1884. Type: Hort. Kew Palm House *Thistleton-Dyer s.n.* 1881 (Lectotype, here designated, K! 3 sheets). Epitype, here designated *A. Vovides* 018 (XAL, NY).

Figure 5. *Ceratozamia* living plants. **A)** *C. tenuis*. **B)** *C. mexicana*.

Trunk epigeous, globose becoming cylindrical with age, up to one meter tall or more in very old plants, up to 20 cm diameter or more when mature. Leaves 1–15 forming a terminal crown, pinnate, 80–280 cm long, 50–100 cm wide; leaflets 20–30 pairs, linear-lanceolate to lanceolate, falcate to subfalcate, 22–50 cm long, 1.3–1.8 cm wide but up to 2.5 cm or more wide in juveniles, apex acuminate to sub-acuminate, base attenuate; petiole and rachis ascending to descending, armed with short to long stout prickles. Pollen strobili cylindrical to narrowly conical, erect, 17–25 cm long or more, 2.5–4.5 cm diameter; peduncle short, tomentose; ovulate strobili olive green, cylindrical, 10–31 cm long, 5–10 cm diameter; peduncles 9–13 cm long, 1–2 cm diameter, erect, tomentose. Seeds angular to ovoid, 1.7–2 cm long, 1.4–1.6 cm diameter, sarcotesta fleshy, creamy white turning brown at maturity. Chromosome number $2n = 16$ (this study).

Other vouchers examined:
MEXICO: Veracruz; Cuacuatzintla, *Castillo-Campos 118* (XAL); Naolinco, *Chamberlain 13* (F); Chiconquiaco, *Hernández 385A, 1507* (MEXU, XAL); Jilotepec, El Esquilón *Ortega 525* (MEXU, XAL), El Esquilón *Rees 1620* (XAL), El Esquilón *A. Vovides 018, 470, 471, 635, 735* (XAL).

Ceratozamia mexicana Brong. (Figure 5B) Ann. Sci. Nat. Bot., ser. 3, 5: 7-8, Tab. 1. 1846. Type: Mexico, from Ghiesbrecht, cult. in Hort. Bot. Parisiensis, 1845, Brongniart s.n. (Holotype, P!). Epitype (here designated): *J. Rees 1688* (XAL).
Trunk partially subterranean to epigeous, globose to ovoid, becoming cylindrical with age, up to one meter tall or more in very old plants, up to 35 cm diameter or more when mature. Leaves 1–16 or more forming a terminal crown, pinnate, 80–300 cm long, 50–90 cm wide; leaflets 20–50 pairs or more, leaflets oblong-lanceolate, subfalcate, entire, acuminate, smooth 25.8–45.5 cm long, 2–3.4 cm wide, apex acuminate, base attenuate; petiole and rachis ascending to descending, armed with short to long stout prickles. Pollen strobili cylindrical to narrowly conical, erect, 17–25 cm long or more, 2.5–4.5 cm diameter; peduncle short, tomentose; ovulate strobili olive green, cylindrical, 20–45 cm long, 5–10 cm diameter; peduncles becoming decumbent when ovulate strobilus matures, 9–13 cm long, 1.5–2.5 cm diameter, tomentose. Seeds angular to ovoid, 1.7–2 cm long, 1.4–1.6 cm diameter, sarcotesta fleshy, creamy white turning brown at maturity. Chromosome number $2n = 16$ (this study).

Other vouchers examined:
MEXICO: Veracruz; Totutla, El Mirador *A. Vovides 730, 731, 732, 733* (XAL), *Walters 2-1, 2-3, 2-5* (XAL, FTG); Totutla, Zacuapan *C. A. Purpus 6362* (XAL).

Key to species:
Leaflets linear lanceolate to lanceolate, shallowly caniculate, 1.3–1.8 cm wide…...….*C. tenuis*
Leaflets oblong lanceolate, flat, 2–3.4 cm wide……..……...…*C. mexicana*

Discussion

Recent botanical explorations at mid elevations (800 to 1,800 masl) in central Veracruz on the Transvolcanic Mexican Belt revealed populations of related *Ceratozamia* spp. including *C. tenuis* that we consider to form part of the *C. mexicana* species complex that is comprised of *C. morettii* Vázq. Torres and Vovides, *C. brevifrons* Miq., *C. decumbens* Vovides, Avendaño, Pérez-Farr.& Gonz.-Astorga, *C. delucana* Vázq.Torres, A.Moretti & Carvajal-Hern. *Ceratozamia tenuis* differs from its congeners within the complex by having long, narrow, linear-lanceolate, slightly caniculate leaflets and occurs in small, restricted populations in the Xalapa region, although plants may be locally abundant within these populations. Molecular phylogenetic studies by González and Vovides (2002, 2012) and an overall review by Vovides *et al*. (2004) reported that the *C. mexicana* species complex may be of recent speciation along with the *C. kuesteriana* species complex in northeastern México above the Transvolcanic Mexican Belt also known as the Mexican transition zone (Contreras-Medina *et al*., 2007). Molecular phylogenetic relationships among closely related plant species are problematic, both nuclear ribosomal DNA

ITS and chloroplast DNA *trn*L-F non-coding region (González and Vovides, 2002) and a modification to the Sequence Characterized Amplified Region (SCAR) method (González and Vovides, 2012) on the genus *Ceratozamia* showed a similar and unresolved topology in the clade grouping both the *C. mexicana* and the *C. zaragozae* species complexes at and to the north of the Mexican Transvolcanic Mexican Belt respectively. However the morphological and anatomical data were found to be useful in elucidating the species, rather than the molecular studies alone that showed clear geographical differences but not interspecific. That modern cycad species are of recent speciation (Miocene) has been demonstrated by Morettii *et al*. (1993) and Nagalingum *et al*. (2011) and is in agreement with our hypothesis (González and Vovides, 2002, 2012). Furthermore, we regard populations of *C. mexicana*, *C. tenuis*, *C. morettii*, and *C. brevifrons* as forming the *Ceratozamia mexicana* species complex that may be of hybrid origin similar to that found by Johnson (1963) for the *Macrozamia communis* L.A.S. Johnson complex. Further research combining morphological, anatomical and molecular data may throw more light on the speciation processes in *Ceratozamia*.

Acknowledgements

This research was partly financed by SEP-CONACyT project No. CB-2011-01-169468 awarded to A.V., and NSF Grants BSR-8607049 and EF-0629817 to DWS. We thank Sonia Galicia for assistance in the laboratory the Jardín Botánico Fco. J. Clavijero for the living cycad material used for this study. Finally the authors thank especially the two anonymous reviewers whose excellent comments and suggested changes greatly improved the manuscript.

Literature cited

Brongniart A.T. 1846. Note sur un nouveau genre de Cycadées du Mexique. *Annales des Sciences Naturelles, Partie Botanique series* **5**:5-9.

Chamberlain C.J. 1919. *The living cycads*. The University of Chicago Press, Chicago.

Contreras-Medina R., Luna-Vega I. and Morrone J.J. 2007. Gymnosperms and cladistic biogeography of the Mexican Transition Zone. *Taxon* **56**:905-915.

González D. and Vovides A.P. 2012. A modification to the SCAR (Sequence Characterized Amplified Region) method provides phylogenetic insights within *Ceratozamia* (Zamiaceae). *Revista Mexicana de Biodiversidad* **83**:929-938.

González D. and Vovides A.P. 2002. Low intralineage divergence in the genus *Ceratozamia* Brongn. (Zamiaceae) detected with nuclear ribosomal DNA ITS and chloroplast DNA *trnL-F* non-coding region. *Systematic Botany* **27**:654-661.

Johnson L.A.S. 1963. Cytological and taxonomic notes on Zamiaceae. *Contributions from the New South Wales National Herbarium* **3**:235-240.

McCune B. and Mefford M.J. 1997. PC-ORD: Multivariate analysis of ecology data Version 3.17. MJM Software, Gleneden Beach.

Moretti A., Sabato S. and Vázquez Torres M. 1982. The rediscovery of *Ceratozamia kuesteriana* (Zamiaceae) in Mexico. *Brittonia* **34**:185-188.

Moretti A., Caputo P., Cozzolino S., de Luca P., Gaudio L., Siniscalco Gigliano G. and Stevenson D.W. 1993. A phylogenetic analysis of *Dioon* (Zamiaceae). *American Journal of Botany* **80**:204-214.

Nagalingum N.S., Marshall C.R., Quental T.B., Rai H.S., Little D.P. and Mathews S. 2011. Recent Synchronous Radiation of a Living Fossil. *Science* **334**:796-799.

Purvis M.J., Collier D.C. and Walls D. 1966. *Laboratory Techniques in Botany*. Butterworths, London.

Regel E. 1857a. Zwei neue cycadeen, die im Botanischen Garten zu Petersburg kultivirt warden, nebst Beiträgen zur Kenntniss dieser Familie. *Bulletin de la Société des naturalistes de Moscou* **30**:163-191, Fig. 22.

Regel E. 1857b. Die cycadeen des botanischen gartens in Petersburg. *Gartenflora* **6**:5-16, Pl. 186.

Schuster J. 1932. Cycadaceae. *Das Pflanzenreich*. A. Engler. Liepzig, Engelmann. **4**: 130-131.

Stevenson D.W. and Sabato S. 1986. Typification of names in *Ceratozamia* Brongn., *Dion* Lindl., and *Microcycas* A. DC. (Zamiaceae). *Taxon* **35**: 578-584.

Thiselton-Dyer W.T.T. 1884. Order CXXXVII. Cycadaceae. *Biologia Centrali-Americana, Botany* **3**:193-195.

Vovides A.P. 1985. Systematic studies on Mexican Zamiaceae II. Additional notes on *Ceratozamia kuesteriana* from Tamaulipas, Mexico. *Brittonia* **37**:226-231.

Received:
November 13rd, 2014

Accepted:
March 9th, 2015

Vovides A.P., Rees J.D. and Vázquez Torres M. 1983. Zamiaceae. Flora de Veracruz, Fascículo. 26. Instituto Nacional de Investigaciones sobre Recursos Bióticos, Xalapa.

Vovides A.P., Pérez-Farrera M.A., González D. and Avendaño S. 2004. Relationships and phytogeography in *Ceratozamia* (Zamiaceae). In: Walters T. and Osborne R. Eds. *Cycad classification: concepts and recommendations*, pp 109-125, CABI Publishing, Wallingford.

Vovides A.P., Avendaño S., Pérez-Farrera M.A. and Stevenson D.W.M. 2012. What is *Ceratozamia brevifrons* (Zamiaceae)? *Brittonia* **64**:35-42.

Walters T. and Osborne R. 2004. *Cycad Classification: Concepts and Recommendations*. CABI Publishing, Wallingford.

Whitelock L.M. 2002. *The Cycads*. Timber Press, Portland.