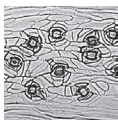# A review of the Cenozoic fossil record of the genus *Zamia* L. (Zamiaceae, Cycadales) with recognition of a new species from the late Eocene of Panama – evolution and biogeographic inferences

BOGLÁRKA ERDEI, MICHAEL CALONJE, AUSTIN HENDY & NICOLAS ESPINOSA

Modern *Zamia* L. is the second largest genus among cycads, however reliably identified fossil occurrences of the genus have so far been missing. Previously, fossil "*Zamia*" species were established in large numbers on the basis of macromorphological similarity of foliage fragments to living *Zamia* species. However, a reinvestigation of specimens assigned formerly to *Zamia* and the relevant literature provided no clear-cut evidence for their assignment to this genus. We investigated a newly recovered fossil specimen from marine sediments of the Gatuncillo Formation, near Buena Vista, Colon Province, Central Panama. It represents the first unequivocal fossil record of the genus confirmed by epidermal as well as macromorphological characters and it is described as *Zamia nelliae* Erdei & Calonje sp. nov. Foraminiferal and nannoplankton biostratigraphy of the locality indicates a late Eocene to earliest Oligocene age. Morphometric comparison of epidermal features of *Z. nelliae* with those of modern *Zamia* species suggests similarity with those of the Caribbean *Zamia* clade. The fossil record of *Zamia* from Panama implies that the genus appeared by the end of the Eocene or earliest Oligocene in the Central American–Caribbean region, however, the origin of the genus is still unresolved. The record of *Z. nelliae* may challenge former concepts on the evolution of *Zamia* and raises an "intermediate" hypothesis on its origin in the Central American–Caribbean region and its subsequent dispersal south- and northwards. • Keywords: cycad, *Zamia*, cuticle, morphometry, Paleogene, Panama.

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Cycads today comprise 349 accepted species in ten genera (Calonje *et al.* 2017). The number of cycad species described during the last decade increased significantly as a result of intense fieldwork by botanists. Recent results of phylogenetic studies of cycads suggested a relatively recent, late Miocene radiation of cycad species along with the Paleogene appearance of most of the major clades (genera excluding *Cycas* L. and *Dioon* Lindl.) and have challenged the theory of "living fossil cycads" (Nagalingum *et al.* 2011, Salas-Leiva *et al.* 2013, Condamine *et al.* 2015). These studies estimated the divergence of *Microcycas-Zamia* to the late Eocene–early Oligocene.

Zamia, with 77 currently accepted species (Calonje *et al.* 2017) is the second largest genus of cycads, and is the most morphologically and ecologically diverse genus in the extant Cycadales (Norstog & Nichols 1997). Furthermore it is the most speciose and broadly distributed cycad genus in the New World. The centre of diversity for the genus appears to be northern South America and Central America, as the highest species diversity occurs in Colombia (21 species) and Panama (17 species). *Zamia* species inhabit a great variety of habitats including areas near mangrove swamps (*Zamia roezlii* Linden), dry desert-like areas (*Zamia encephalartoides* D.W. Stev.), coastal sand dunes (*Zamia lucayana* Britton),

and even occur as obligate cliff dwellers (*Z. meermanii* Calonje) and obligate epiphytes (*Z. pseudoparasitica* J. Yates). *Microcycas* (Miq.) A. DC., a monotypic genus, is well supported as the sister genus to *Zamia* (including *Chigua* D.W. Stev.) in both morphological (*e.g.* Crane 1988, Stevenson 1990) and molecular-based (*e.g.* Hill 2003, Chaw *et al.* 2005) phylogenetic studies. Caputo *et al.* (2004) published a phylogeny of *Zamia* combining morphological characters and sequence data from the internal transcribed spacer 2 (ITS2). They found phylogenetic patterns reflecting geographical distribution, with separate clades resolved for mainly Caribbean, Mexican, Central American, and South American species.

Despite the relative importance of modern *Zamia* among cycads, well documented fossil occurrences of the genus have so far been missing. This situation contrasts with some other extant cycad genera that have been more convincingly recognized in the fossil record, e.g. *Bowenia* Hook ex Hook f. (Hill 1978), *Ceratozamia* Brongn. (Kvaček, Z. 2002, 2004, 2014), *Cycas* (Yokoyama 1911, Su *et al.* 2014), *Lepidozamia* Regel (Hill 1980), and *Macrozamia* Miq. (Carpenter 1991). A large number of purported fossil "*Zamia*" species have been established on the basis of macromorphological similarity of leaflets or leaflet fragments to leaflets of living *Zamia* species. Putative fossil records of *Zamia* were mentioned from both America and Europe, with much higher frequency in North America. Most of these reports were based on solitary leaflets which is congruent with the articulate character of the leaflets in the genus (and in two other closely related genera, *Ceratozamia* and *Microcycas*).

The macromorphological similarity of cycad leaves hinders the systematic treatment, of fossils because these cannot be identified securely based only on gross morphology. However, the assignment of the majority of cycad leaf remains to extant genera can be corroborated with the analyses of epidermal traits combined with gross morphological characters. The shape and arrangement of epidermal cells on the adaxial and abaxial epidermis, the occurrence or absence of cells or group of cells having differently thickened cell walls, and the shape and arrangement of stomata all give clues to differentiate extant zamiaceous cycad genera (see also Greguss 1968) In most *Zamia* species, epidermal traits, *i.e.* elongate, almost linear, epidermal cells with convex, non-angular anticlinals on both the upper and lower epidermis being devoid of cell groups with heavily thickened cell walls, the more or less parallel oriented, isodiametric stomata arranged in bands, complement macromorphological traits. Previous reports of fossil *Zamia* were exclusively based on macromorphological traits, lacking confirmation from epidermal characters. The first author re-examined many specimens that were formerly described as *Zamia* by Berry (1916a, b, 1917, 1930), Brown (1962), and Hollick (1928) during the first half of the 20th century and were available from museum collections

whereas some other specimens have already been revisited and excluded from the genus, and partly transferred to the extinct *Dioonopsis* (*e.g.* Erdei *et al.* 2012, Wilf *et al.* 2014).

Herein, we review the published fossil records of *Zamia* based on reinvestigation of physical specimens and the relevant literature and describe the first fossil evidence of *Zamia* from Paleogene sediments of Panama. In order to assess the morphological relation of the fossil species, *Z. nelliae* Erdei et Calonje to modern *Zamia* species we applied morphometric analyses of the epidermal traits of the fossil and numerous modern *Zamia* species representing all major *Zamia* clades (Calonje, unpublished phylogenetic research).

Geological setting

The fossil described herein as *Zamia nelliae* was collected by A. Hendy from sediments referred to the Gatuncillo Formation exposed in Colon Province, Central Panama (Fig. 1). The Gatuncillo Formation crops out in rolling lowlands to the east of the Panama Canal, overlying Cretaceous basement, and in turn being overlain by either Oligocene or Miocene sediments (Woodring 1973). Historically, workers have considered the Gatuncillo to be middle to upper Eocene on the basis of planktonic foraminifera (Coryell & Embich 1937), large benthic foraminifera (Cole 1949, 1952), and mollusks, corals, and echinoderms (see Woodring 1973 for discussion). Ramírez *et al.* (2016) using U-Pb geochronology found ages for the Gatuncillo Formation at two sites no younger than 36 and 41 Ma, respectively. Strontium isotope analyses ($^{87}Sr/^{86}Sr$) by Tripathi & Zachos (2002) also supported a Priabonian (37.8–33.9 Ma) age, although most samples were likely impacted by diagenetic alteration.

The locality (STRI loc. 290268) is 1.5 km S of Buena Vista, on the NE side of the Madden-Colón road (Transisthmica), and 46 km SE of Colón (9° 16´ 4.80˝ N, 79° 41´ 15.83˝ W). This section has now been destroyed through continued quarrying of rock for construction fill, but previously exposed some 20 m of mudstone and carbonaceous sandstone. Compression fossils of various plants were collected from a steeply dipping carbonaceous sandstone bed, along with infrequent molds of bivalves and gastropods of nearshore affinity. These overlay a thick succession of mudstone, with sparse molluscs, including nuculanid and corbulid bivalves, turrid gastropods, *Dentalium* (Scaphopoda), and *Aturia* (Cephalopoda). This fauna, together with the fine and massive siliciclastic sediments indicate an offshore (mid-shelf to outer shelf) setting for the overlying mudstone facies. Foraminifera in this facies are abundant, and include *Hantkenina alabamensis, Turbotalia cerrozazulensis,* and *Chiloguembelina cubensis*. Characteristic nannoplankton includes *Cribrocentrum reticulatum, Reticulofenestra umbilicus, Helicosphaera euphratis, Pontosphaera multipora.* Nannoplankton and
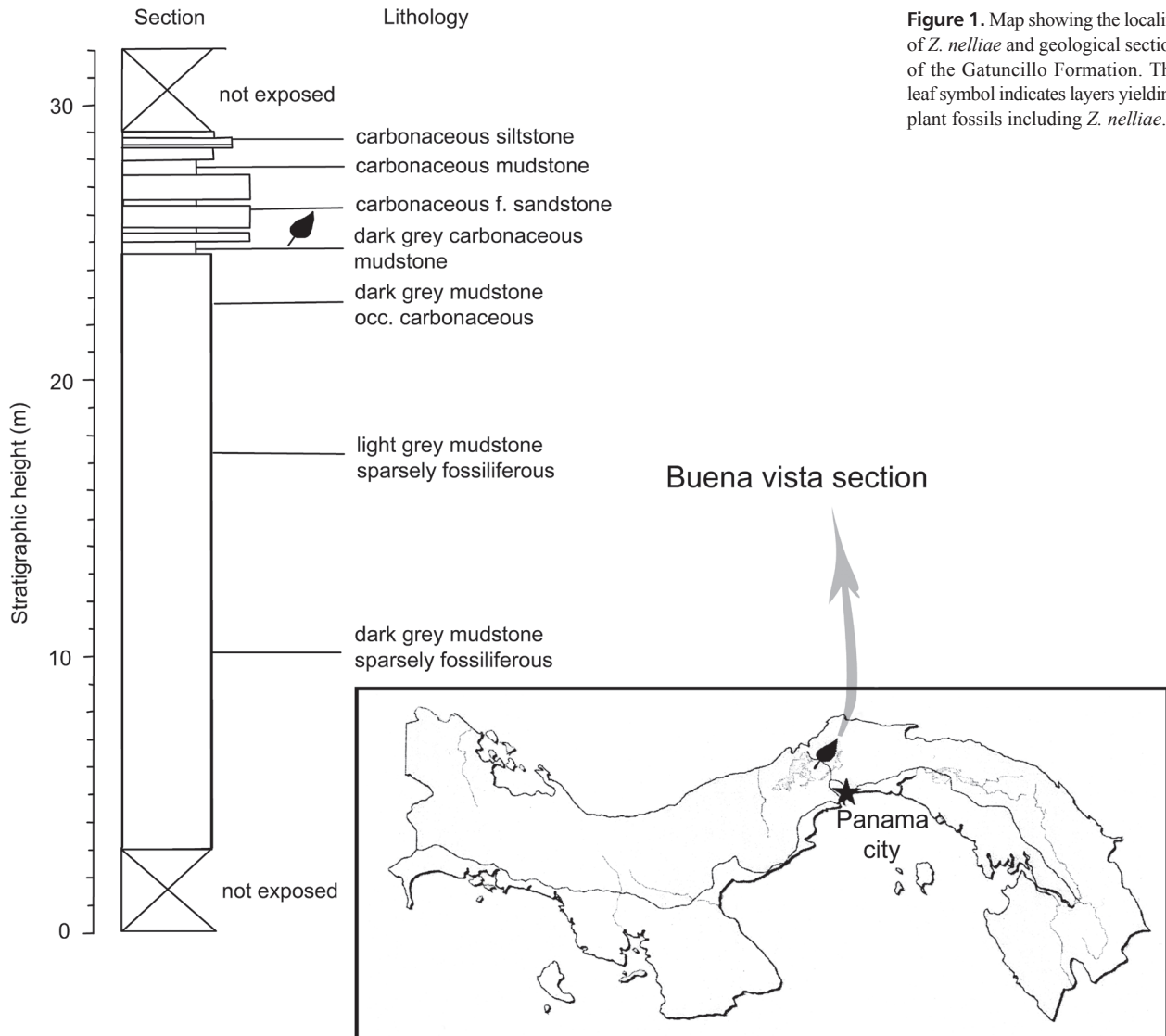
Figure 1. Map showing the locality of *Z. nelliae* and geological section of the Gatuncillo Formation. The leaf symbol indicates layers yielding plant fossils including *Z. nelliae*.

foraminiferal biostratigraphy place this underlying succession in to zones P14–P17 (Bartonian–Priabonian) and NP18–NP21 (Priabonian–Rupelian), respectively (Hendy & Machado unpublished data). Since there is no major unconformity at the base of the *Zamia*-bearing strata, it is assumed that the *Zamia*-bearing horizon is no older than the Priabonian, but more likely to be latest Priabonian–earliest Rupelian in age.

Material and methods

Material

The fossil described herein as *Zamia nelliae* is deposited in the Paleobotany collection of the Florida Museum of Natural History (UF 19531-70503 /STRI 36903/). Repositories for other material from the section which yielded the fossil

Zamia include the Invertebrate Paleontology collection of the Natural History Museum of Los Angeles County for macrofossils (LACMIP loc. 41768), and the Smithsonian Tropical Research Institute Center for Tropical Paleontology and Archaeology for microfossils (STRI loc. 290268).

Specimens formerly assigned to *Zamia* and re-examined here include those of *Z. australis* Berry (Berry 1928, Argentina; USNM 37857/holotype), *Z. mississippiensis* Berry (Berry 1916a, 1917, Wilcox flora; USNM35473, 35501, 35502/types), *Z. tennesseeana* Berry (Berry 1930, Tennessee; USNM39727/holotype), *Z. (?) wilcoxensis* Berry (Berry 1916b, Wilcox flora; USNM35474/holotype), *Z. collazoensis* Hollick (Hollick 1928, Puerto Rico; YPM25440, 27131/holotype/, 27141, 27144), *Z. noblei* Hollick (Hollick 1928, Puerto Rico; YPM25445ab/paratype/, 27140, 27152, 27169/type/, 27170, 27498/?type/), *Podozamites latipennis* Heer /Z. coloradensis (Knowlton) Brown (Brown

1962, Wyoming; USNM40155/?lectotype), *Z. wyomingensis* Brown (Brown 1962, Wyoming; USNM167487/holotype), *Zamia washingtoniana* Ward (Ward 1895, Potomac, Cretaceous; USNM31768a,b, 31769a,b/types).

The following extant species of *Ceratozamia* (24 species) and *Microcycas* (1 species) were studied for comparison: *Ceratozamia alvarezii* Pérez-Farr., Vovides & Iglesias (MBC 20010258A, FTG D. Little & D.W. Stevenson 1102), *C. becerrae* Pérez-Farr., Vovides & Schutzman (MBC 20010249)*, C. brevifrons* Miq. (MBC 98618E), *C. chimalapensis* Pérez-Farr. & Vovides (MBC 20020073F), *C. decumbens* Vovides, Avendaño, Pérez-Farr. & Gonz.-Astorga (MBC 20010924A)*, C. euryphyllidia* Vázq.Torres, Sabato & D.W. Stev. (FTBG89334A), *C. fuscoviridis* Moore ex R. Osborne, D.W. Stev. & Vovides (MBC20010167A), *C. hildae* G.P. Landry & M.C. Wilson (MBC 88339), *C. kuesteriana* Regel (MBC 931202A), *C. latifolia* Miq. (MBC 931178A), *C. matudae* [Stevenson *et al.*, 681 (FTG)], *C. mexicana* Brongn. (FTBG 67881), *C. microstrobila* Vovides & J.D. Rees (MBC 931220A), *C. miqueliana* H. Wendl. (MBC 20010235A), *C. mirandae* Vovides, Pérez-Farr. & Iglesias (MBC 20020252), *C. mixeorum* Chemnick, T.J. Greg. & Salas-Mor. [J. Chemnick & T.J. Gregory 51 (FTG)], *C. morettii* Vázq. Torres & Vovides (MBC 20010161A), *C. norstogii* D.W. Stev. (MBC 93944G), *C. robusta* Miq. (MBC 20120345A), *C. sabatoi* Vovides, Vázq.Torres, Schutzman & Iglesias (MBC 20010176A), *C. vovidesii* Pérez-Farr. & Iglesias, (MBC 20020826F), *C. whitelockiana* Chemnick & T.J. Greg. [J. Chemnick & T.J. Gregory 51 (FTG)], *C. zaragozae* Medellín (MBC 20010182A), *C. zoquorum* Pérez-Farr., Vovides & Iglesias, (MBC 20011365A), *Microcycas calocoma* (Miq.) A. DC. (MBC RM384A).

Zamia species adopted for comparison and morphometric measurements are listed in Table 1. (39 species in total, 32 species in morphometry plus samples of selected Caribbean clade species from various localities). Additional information on the macro- and micromorphology of *Zamia* leaves was obtained from Greguss (1968) and Schutzman (1998). Greguss (1968) provided a key to the genera of cycads based on epidermal features, however its usefulness is partly limited since having at that time only a fragment (18 *Zamia* species) of the currently recognized cycad species (349 cycad species, 77 *Zamia* species, Calonje *et al.* 2017).

Studies of epidermal details in additional cycad genera include *Bowenia serrulata* (W.Bull) Chamb. (MBC 20040865R), *Cycas revoluta* Thunb. (Herbarium of the Szafer Institute, Krakow), *Dioon edule* Lindl. (fresh material, Botanical Garden of the University of Naples), *D. mejiae* Standl. & L.O. Williams (fresh material, Toowong Botanical Gardens, Brisbane), *D. purpusii* Rose (fresh material, Toowong Botanical Gardens, Brisbane), *D. rzedowskii* De Luca, A. Moretti, Sabato & Vázq. Torres (fresh material, Botanical Garden of the University of Naples), *D. spinulosum* Dyer ex Eichler (fresh material, Botanical Garden of the

University of Naples), *Encephalartos eugene-maraisii* I. Verd. (fresh material, Botanical Garden of the University of Naples), *E. ferox* G. Bertol (MBC 78357F), *E. gratus* Prain (MBC 64561F), *E. hildebrandtii* A. Braun & C.D. Bouché (MBC 651375A), *E. inopinus* R.A. Dyer (fresh material, Botanical Garden of the University of Naples), *E. manikensis* (Gilliland) Gilliland (MBC 971643A), *E. sclavoi* A. Moretti, D.W. Stev. & De Luca (fresh material, Toowong Botanical Gardens, Brisbane), *Lepidozamia peroffskyana* Regel (MBC 651328A), *Macrozamia communis* L.A.S. Johnson (MBC 60385A), *M. moorei* F. Muell. (MBC 59302B), *M. lucida* L.A.S. Johnson (MBC 59691C), *Stangeria eriopus* (Kunze) Baill. (MBC 651325K). Additional information on epidermal details of *Dioon* was obtained from Barone Lumaga *et al.* (2015).

Abbreviations. – FTBG – Fairchild Tropical Botanical Garden, Florida, USA; FTG – Herbarium of the Fairchild Tropical Botanical Garden, Florida, USA; MBC – Montgomery Botanical Center, Florida, USA; Nong Nooch – Nong Nooch Tropical Botanical Garden, Thailand; Selby – Marie Selby Botanical Gardens, Florida, USA; USNM – Smithsonian Institution, Washington DC, USA; YPM – Yale Peabody Museum of Natural History, Connecticut, USA.

Methods

Epidermal characters of fossil specimens were studied using transmitted light, epifluorescence, and scanning electron microscopy. For these purposes cuticle fragments were removed from the specimen and cleaned in hydrofluoric acid. In addition, epifluorescence was applied on cuticles that were intact on the shale. For studies with transmitted light and electron microscopy, cuticle samples were macerated following the conventional method (Jones & Rowe 1999) and were stained with safranin. Cuticles were studied using Zeiss Axiophot microscope equipped with an Axiocam digital camera. Scanning electron microscopy was performed on a Hitachi S-4000 FE-SEM. Microscopic slides of fossil material are stored in the Florida Museum of Natural History (Gainesville).

Leaf material of extant cycads for comparison was treated with 20% CrO_3 for 48–72 h or more as required, at room temperature and stained with safranin when desired. For consistency, samples were taken from the centre of leaflet lamina and the leaflets were collected from the middle part of each sampled leaf.

Microscopic slides of extant leaf material are stored in the Hungarian Natural History Museum, Botanical Department (Budapest, Hungary).

Morphometric analyses of epidermal characters were carried out for 35 extant *Zamia* samples (including *Z.* aff. *portoricensis* Urb. and samples of *Z. pygmaea* Sims

Table 1. List of *Zamia* species used for comparison. Bold face indicates species included in morphometric analysis. Abbreviations of clades: C – Caribbean; F – Fischeri; I – Isthmus; M – Megamexico; S – South America.

Taxon	Provenance	Clade	Accession / Voucher
Z. erosa O.F. Cook & G.N. Collins	Puerto Rico	C	MBC 20030275*D
Z. integrifolia L.f.	Florida (USA)	C	MBC 20050880*B
Z. lucayana Britton	Long Island, Bahamas	C	MBC 20090823
Z. portoricensis Urb.	Puerto Rico	C	MBC 20030469A
Z. pumila L. (Puerto Rico)	Puerto Rico	C	MBC 20080285B
Z. pygmaea Sims	Cuba	C	Calonje *et al.* CU13-003(FTG)
Z. pygmaea (formerly *Z. silicea*)	Cuba	C	Calonje *et al.* CU13-007(FTG)
Z. aff. *portoricensis*	Jamaica	C	MBC 20030357
Z. angustifolia Jacq. (Cuba)	Cuba	C	MBC 20110318
Z. angustifolia (Bahamas)	Eleuthera, Bahamas	C	FTBG 9548*A
Z. stricta Miq.	Cuba		MBC 20110318
Z. fischeri Miq.	Tamaulipas, Mexico	F	MBC 20010205*A
Z. inermis Vovides, J.D. Rees & Vázq. Torres	Mexico	F	MBC 92143*D
Z. nelliae (fossil)	Panama		STRI 36903
Z. acuminata Oerst. ex Dyer	Costa Rica	I	MBC 20041004
Z. dressleri D.W. Stev.	Panama	I	Selby1996-0009
Z. elegantissima Schutzman, Vovides & R.S. Adams	Panama	I	MBC 2000775*G
Z. imperialis A.S. Taylor, J.L. Haynes & Holzman	Panama	I	MBC 2000265*A
Z. lindleyii Warsz. ex A. Dietr.	Panama	I	MBC 20010802*A
Z. nana A. Lindstr., Calonje, D.W. Stev. & A.S.Taylor	Panama	I	MBC 20020234*B
Z. nesophila A.S. Taylor, J.L. Haynes & Holzman	Panama	I	MBC 20010123*A
Z. obliqua A. Braun	Colombia	I	FTG 89162
Z. pseudoparasitica J. Yates	Panama	I	MBC 2000319*A
Z. cremnophila Vovides, Schutzman & Dehgan	Mexico	M	FTBG 87339
Z. decumbens Calonje, Meerman, M.P. Griff. & Hoese	Belize	M	MBC 20080715
Z. furfuracea L.f.	Mexico	M	MBC 20010214*H
Z. lacandona Schutzman & Vovides	Mexico	M	MBC 93939*A
Z. loddigesii Miq.	Mexico	M	MBC 99801*A
Z. onan-reyesii C. Nelson & Sandoval	Honduras	M	MBC 20030877Q
Z. purpurea Vovides, J.D. Rees & Vázq. Torres	Mexico	M	FTBG 93928*N
Z. soconuscensis Schutzman, Vovides & Dehgan	Mexico	M	MBC 20030717*A
Z. variegata Warsz.	Guatemala	M	FTBG 73196*B
Z. amplifolia W. Bull ex Mast.	Colombia	S	FTG 91596/Bogler 1223
Z. disodon D.W. Stev. & Sabato	Colombia	S	cult. Nong Nooch
Z. encephalartoides D.W. Stev.	Colombia	S	MBC 94910*A
Z. ipetiensis D.W. Stev.	Panama	S	MBC 2000279*A
Z. lindenii Regel ex André	Ecuador	S	MBC 20001000*F
Z. manicata Linden ex Regel	Panama	S	FTBG 84272*V
Z. restrepoi (D.W. Stev.) A. Lindstr.	Colombia	S	MBC 20100026A
Z. pyrophylla Calonje, D.W. Stev. & A. Lindstr.	Colombia	S	MBC 20100027*A
Z. roezlii Linden	Colombia	S	MBC 94635*B
Z. urep B. Walln.	Peru	S	cult. Nong Nooch
Z. wallisii A. Braun	Colombia	S	MBC 20010301*A

and *Z. angustifolia* Jacq. from various localities) and the fossil *Zamia* by taking various measurements using ImageJ v. 1.47 (Rasband WS. ImageJ, U.S. National Institutes of Health, Bethesda, Maryland, USA; *https://imagej.nih.gov/ ij/*, 1997–2012) on spatially calibrated slide photographs. Modern species were selected to include all the major *Zamia* clades (Calonje unpublished phylogenetic data; Tab. 1).

For abaxial surfaces, the following characters were measured: stomatal index, mean stomatal pore length, standard deviation of stomatal pore angle, mean interstomatal band width (the width of the area between two stomatal bands), mean stomatal band width, mean stomatal band to interstomatal band width ratio. For adaxial surfaces, the following characters were measured: mean adaxial cell area, standard deviation of adaxial cell angle, mean adaxial cell length, mean adaxial cell width, mean adaxial cell circularity = $4\pi(Area/Perimeter^2)$, mean adaxial cell aspect ratio, mean adaxial cell roundness = $4 \times [Area]/\pi \times [Major\ axis]^2$, and mean adaxial cell solidity = $[Area]/[Convex\ area]$.

Stomatal index was estimated by counting stomata and epidermal cells occurring in an area of approximately 0.25 mm^2 within stomatal bands and by using the formula *[number of stomata/(number of stomata + number of epidermal cells)] ×100* and measurements were made by averaging 3 measurements taken in different regions of the slide preparations. A recent study by Haworth *et al.* (2011) showed that selected cycad species (six cycad genera including *Zamia*, each represented by one species) showed no significant stomatal density or index response to changes in ambient CO_2 or O_2. Thus, it may be inferred that varying atmospheric CO_2 level does not influence stomatal density/ index of the fossil *Zamia* species.

Stomatal angle (orientation of stomata) was calculated in Image J by drawing the long axis of the stomatal lit and calculating the angle of this line to the stomatal band. Stomatal and interstomatal bands were measured by averaging 5 measurements taken in different regions of the slide preparations. Adaxial cell measurements were taken by selecting between 40 and 67 individual cells along a transect for every species, and thresholding them for particle analysis in ImageJ. Individual cell measurements were averaged except for angular measurements in which the standard deviation was recorded to measure the variation in the angles. All measurements were used in a Principal Coordinate Analysis executed in SPSS (IBM Corp. Released 2012. IBM SPSS Statistics for Windows, Version 21.0. Armonk, NY: IBM Corp.).

Systematic palaeobotany

Order Cycadales Dumortier, 1829
Family Zamiaceae Horaninow, 1834

Genus *Zamia* Linnaeus, 1763

Zamia nelliae Erdei & Calonje sp. nov.
Figures 2A–E, 3A–D

Holotype. – Inventory number UF 19531-70503 (STRI 36903), Florida Museum of Natural History (FLMNH); (Fig. 2A).

Type horizon and locality. – Gatuncillo Formation, middle Eocene to lower Oligocene. Buena Vista, Colon Province, Central Panama; locality numbered STRI loc. 290268; 9° 16′ 4.80″ N, 79° 41′ 15.83″ W.

Etymology. – In honour of Nell Montgomery Jennings (1905–1990) who envisioned and established the Montgomery Botanical Center as a botanical research centre emphasizing palms and cycads.

Material. – Cuticle preparation: inventory number UF 19531-70503 (STRI 36903), stored at FLMNH.

Diagnosis. – Pinna lanceolate, tapering toward the apex; Apex acute; Margin entire; Venation parallel, veins closely spaced, more than twenty veins close to leaflet apex; Lamina hypostomatic; Stomata cyclocytic, in narrow bands of two to three ill-defined rows of stomata. Stomata arranged predominantly parallel, but often oblique or perpendicular to the long axis of the leaflet; Stomata isodiametric; Guard cells sunken surrounded by four to seven subsidiary cells; Abaxial ordinary epidermal cells parallel, elongated, in costal areas more elongated, anticlinals convex, non-angular; Adaxial ordinary epidermal cells parallel, elongated, linear, convex, non-angular with rounded corners; Rare one-celled trichome bases on both epidermis.

Description. – Lamina of the fragmentary leaflet is lanceolate, slightly asymmetrical and seems to be coriaceous (Fig. 2A). Preserved length and width of the lamina are 7 and 2.2 cm, respectively. Less than half of the leaflet is preserved therefore the entire length and maximum width are estimated to be larger than 14 cm and 2.2 cm. Apex is

Figure 2. Morphological details of *Zamia nelliae* Erdei et Calonje sp. nov. from the Paleogene of Panama (holotype, STRI 36903). Abbreviations: lm – transmitted light microscopy; SEM – scanning electron microscopy. A – leaflet showing entire margin and parallel venation. Scale bar = 1 cm; B – adaxial cuticle displaying parallel arranged linear epidermal cells (lm). Scale bar = 50 µm; C – abaxial cuticle showing stomatal bands. Bands are composed of two-three ill-defined rows of stomata (lm). Scale bar = 100 µm; D – two stomatal bands with linear, parallel arranged epidermal cells between bands (SEM). Scale bar = 100 µm; E – closer view of a stomatal band. Some of the stomata are arranged obliquely or even perpendicularly to the band (SEM). Scale bar = 50 µm.
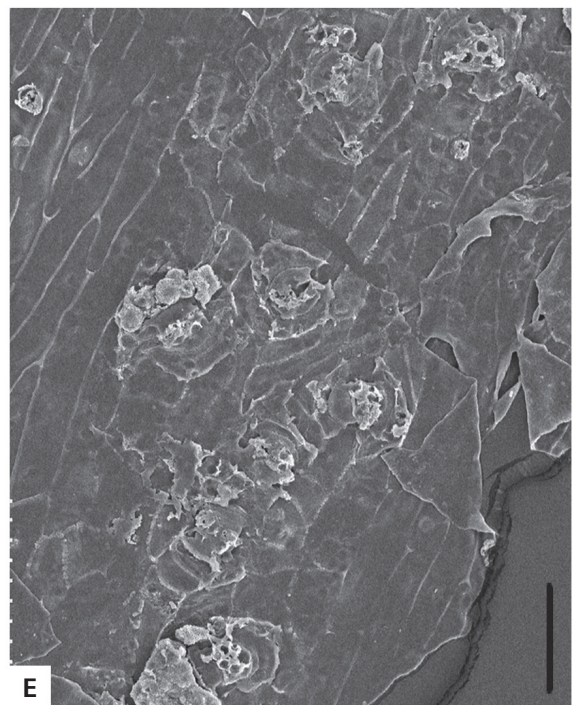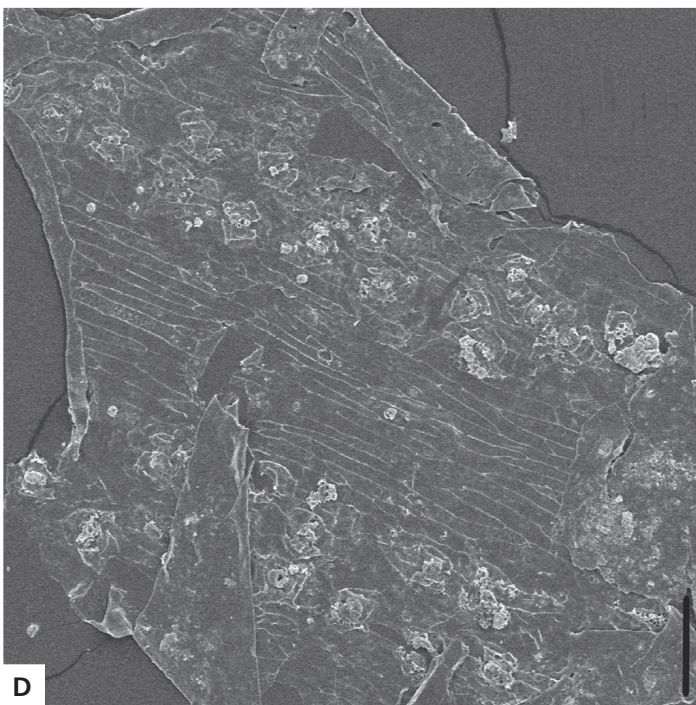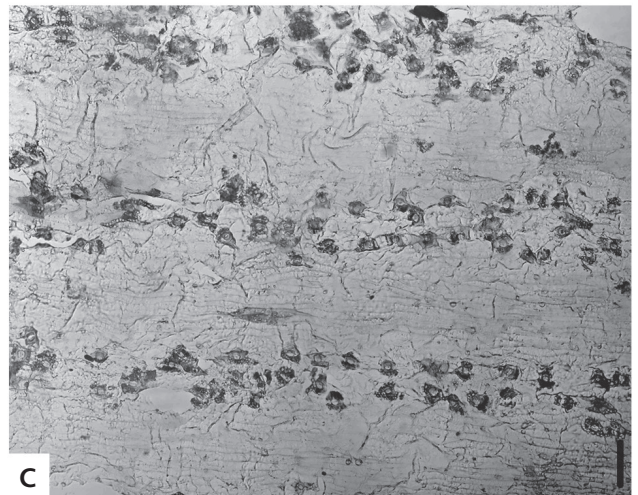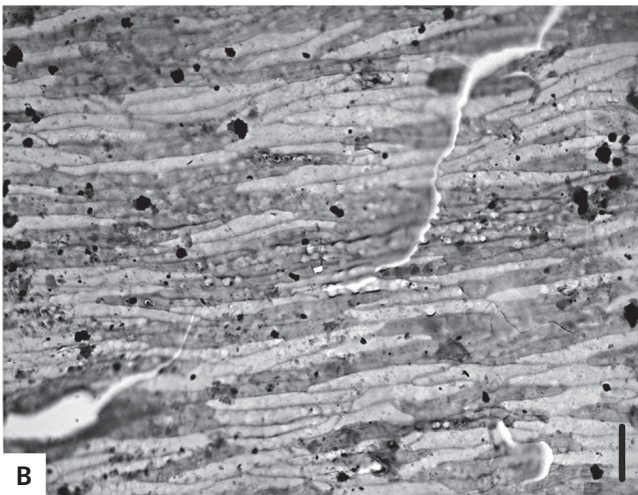
acute; base is not preserved. The margin is entire. Venation is parallel, with strong veins, spaced at 0.3–0.5 mm from each other measured in the apical part of the lamina. The number of veins is estimated about 25 near the apical part of the leaflet. No forkings or anastomoses of veins are observable. Veins seem to terminate at the margin (open venation).

Cuticle of both upper and lower surfaces is well-preserved. On the adaxial cuticle ordinary cells are serially arranged, elongate, linear (Fig. 2B). Cells are of 75–250 μm in length and 10–20 μm in width (l/w ~ 7–12). Anticlinal walls are convex, non-angular, their corners are definitely rounded. The anticlinal cell walls seem to be uniformly thickened. The different staining of cell groups (Fig. 2B) may indicate variably thickened periclinal walls. On the abaxial cuticle ordinary cells are arranged parallel to the long axis of the lamina (Fig. 2C–E). Distinct costal and intercostal areas are differentiated. Cells in costal areas are elongate, linear, with similar dimensions as cells on the adaxial side, 60–230 μm long and 10–20 μm wide. Ordinary epidermal cells in intercostal areas are shorter. Stomata are cyclocytic (haplocheilic) and are arranged in bands (Figs 2C; 3A–D). Bands are mostly composed of two to three indefinite rows of stomata (Fig. 2C). Stomata are oriented variously, mainly parallel but often obliquely or even perpendicularly to the long axis of the leaflet (Fig. 2E). Stomata are broad oval, even rounded. Guard cells are 25–30 μm wide, 18–25 μm long, seem slightly sunken and have strong thickened ledges (Fig. 3B–D). Stomatal pore is oval and 12–15 μm long. Guard cells are surrounded by four to seven subsidiary cells organized more or less irregularly. One-celled trichome bases are rarely observable on both the abaxial and adaxial epidermis, on the former first of all in costal areas.

Discussion. – Comparison of *Zamia nelliae* with extant and extinct members of the Cycadales: The combination of macromorphological (lanceolate shape of the lamina, parallel veins of uniform order) and epidermal features of the fossil leaflet (elongate, non-isodiametric, slightly irregularly arranged ordinary epidermal cells of the adaxial and abaxial epidermis, cyclocytic type of stomata, thickened dorsal ledges of guard cells, irregular pattern of subsidiary cells, stomata arranged in bands) seen in this fossil lamina resembles the features of modern cycads. Extinct cycad genera hitherto described from the Cenozoic and established on fossil foliage (having both macro- and micromorphological details), e.g. *Austrozamia* Wilf, D. Stevenson et Cuneo (Wilf *et al.* 2016), *Ctenis* Lindley et Hutton (Erdei & Manchester 2015), *Dioonopsis* Horiuchi et Kimura (Horiuchi & Kimura 1987, Erdei *et al.* 2012), *Eostangeria* Barthel (Barthel 1976; Palamarev & Uzunova 1992; Kvaček, Z. & Manchester 1999), *Pseudodioon* Erdei, Akgün et Barone Lumaga (Erdei *et al.* 2010), *Pterostoma* R. S. Hill (Hill 1980), have isodiametric ordinary epidermal cells contrasting the linear cells of the epidermis of *Z. nelliae*. Stomata of the fossil cycads mentioned above (excluding *Austrozamia* since lacking information on stomata) display a more regular arrangement of the subsidiary cells than those of the fossil from Panama. *Ctenis*, *Dioonopsis,* and *Pterostoma* all have scattered, randomly arranged stomata definitely contrasting the distinct stomatal bands of the fossil described here. In *Pseudodioon* stomata are arranged in bands however guard cells are surrounded by much higher number of subsidiaries (8–11) than in the fossil from Panama. As regards macromorphology, the venation of most of the above extinct cycads differs from that of *Zamia nelliae* in displaying forkings and anastomoses of veins (*Ctenis, Dioonopsis, Pterostoma*) or having a midrib (*Eostangeria*).

Mesozoic foliage assigned to cycads (or cycadophytes) differs either in macro- (leaflet/pinna shape, venation) or micromorphology (epidermal cells, arrangement of stomata) or in both, e.g. *Almargemia* Florin (Florin 1933) – stomata irregularly arranged, sunken guard cells; *Apoldia* Wesley (Zijlstra *et al.* 2009, Kustatscher *et al.* 2010) – pinna shape, isodiametric epidermal cells; *Ctenis* Lindley et Hutton (Lindley & Hutton 1834) – anastomosing veins, isodiametric epidermal cells, scattered stomata; *Eobowenia* M. Coiro et C. Pott (Coiro & Pott 2017) – short rows of heavily cutinised epidermal cells; *Jirusia* Bayer (Kvaček, J. 1995) – isodiametric epidermal cells; *Mesenea* Kvaček (Kvaček, J. 1999) – venation, isodiametric epidermal cells, scattered stomata; *Mesodescolea* Archangelsky (Archangelsky & Petriella 1971, Artabe & Stevenson 1999) – pinna shape, epidermal cells; *Mesosingeria* Archangelsky (Archangelsky 1963, Villar de Seoane 2005) – pinna/pinnule morphology

Figure 3. Stomatal details of *Zamia nelliae* Erdei et Calonje sp. nov. from the Paleogene of Panama (holotype, STRI 36903) and epidermal anatomy of extant *Ceratozamia* Brongn. species for a comparison. Abbreviations: lm – transmitted light microscopy; SEM – scanning electron microscopy. • A – closer view of a stomatal band of *Zamia nelliae* with a stoma arranged perpendicularly to the band axis. Epidermal cells in stomatal bands are less elongated than cells between the bands (lm). Scale bar = 50 μm; B – two stomata of *Zamia nelliae* showing sunken guard cells and well developed cuticular ledges (lm). Scale bar = 50 μm; C – stoma of *Zamia nelliae* enlarged showing cyclocytic arrangement of subsidiaries (SEM). Scale bar = 30 μm; D – stoma of *Zamia nelliae* enlarged showing well developed cuticular ledges (SEM). Scale bar = 30 μm. • E – abaxial epidermis of *Ceratozamia microstrobila* Vovides et J.D. Rees showing a stomatal band. Note the parallel arranged stomata and the rows of short cells (indicated by arrow), MBC 931220A (lm). Scale bar = 50 μm; F – adaxial epidermis of *Ceratozamia microstrobila* showing parallel arranged elongate cells and rows of short cells (indicated by arrow), MBC 931220A (lm). Scale bar = 50 μm. • G – abaxial epidermis of *Ceratozamia sabatoi* Vovides, Vázq.Torres, Schutzman et Iglesias. Note the parallel arranged stomata and the rows of short cells (indicated by arrow), MBC 20010176 (lm). Scale bar = 50 μm; H – adaxial epidermis of *Ceratozamia sabatoi* showing parallel arranged elongate cells and rows of short cells (indicated by arrow), MBC 20010176 (lm). Scale bar = 50 μm.
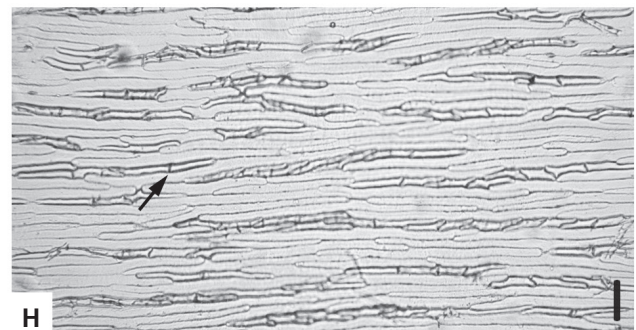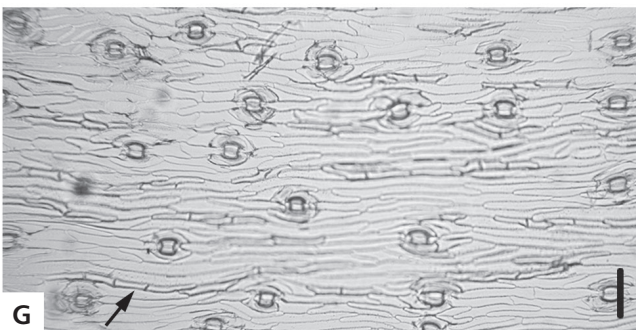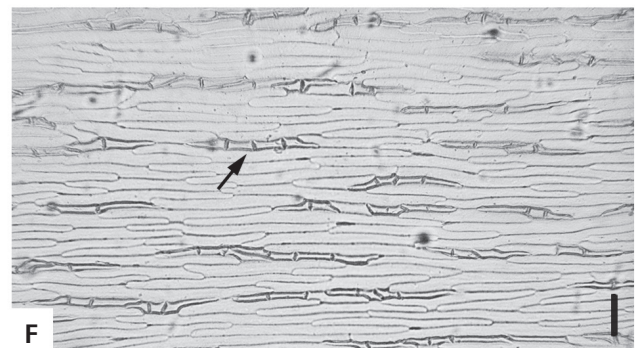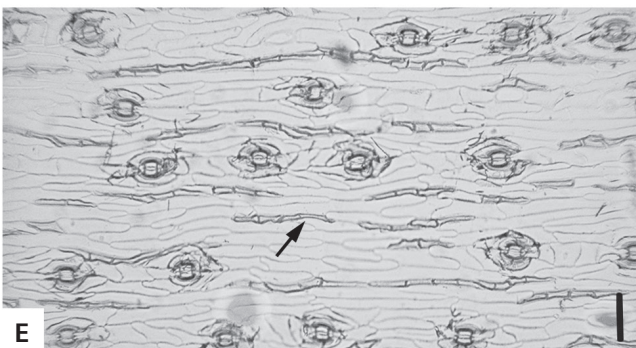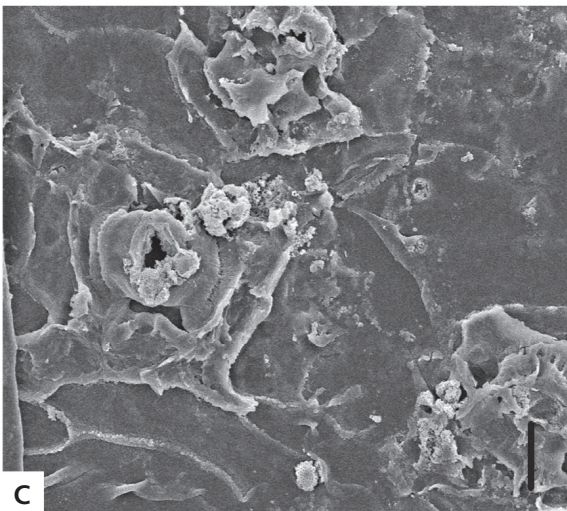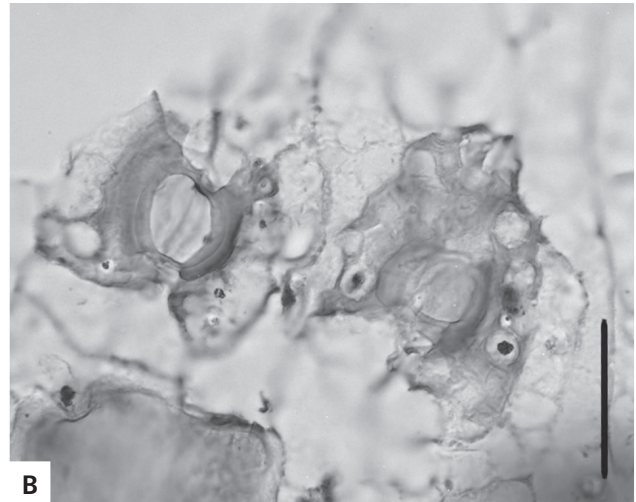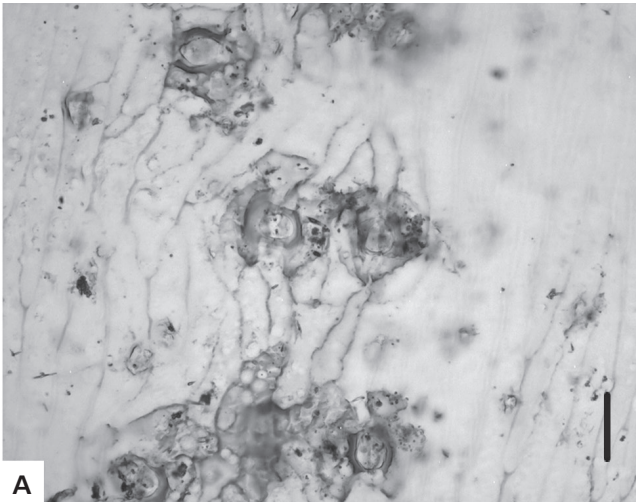
(shape), isodiametric epidermal cells, scattered, deeply sunken stomata; *Nilssonia* Brongniart (Brongniart 1825; Harris 1964; Kvaček, J. 1995; Watson & Cusack 2005; Pott *et al.* 2007a, 2012) – venation, scattered stomata; *Pseudoctenis* Seward (Seward 1911, Pott *et al.* 2007b) – isodiametric epidermal cells; *Restrepophyllum* Passalia, Del Fueyo et Archangelsky (Passalia *et al.* 2010) – pinna morphology (shape, venation), isodiametric epidermal cells, scattered stomata; *Sueria* Menéndez (Menéndez 1965) – pinna shape, epidermal cells; *Ticoa* (Archangelsky 1963, Villar de Seoane 2005) – pinna morphology (shape, venation), isodiametric epidermal cells, scattered, deeply sunken stomata.

Macro- and micromorphology of the fossil leaflet recalls genera of the Zamiaceae – first of all those of the Zamioideae. In Cycadaceae, species of *Cycas* develop leaflets with a midrib but no other veins. As regards genera in Zamiaceae, *Stangeria* T. Moore (also having midrib) is well-known for its feather-like venation. *Bowenia* develops broader and shorter leaflets than the fossil, and the anticlinal walls of its epidermal cells show a concave, angular pattern and stomata are non-sunken (see also Coiro & Pott 2017). Members of subfamily Encephalartoideae, i.e. *Dioon*, *Encephalartos*, *Macrozamia* and *Lepidozamia* species, develop leaflets which are usually elongate (all the above genera) or even linear (*Macrozamia*, *Lepidozamia*), and epidermal cells do not display the linear arrangement shown by the fossil. Anticlinal walls of the epidermal cells in *Dioon* show a definite concave, angular pattern and stomata are deeply sunken (see in Greguss 1968, Erdei *et al.* 2010, Barone Lumaga *et al.* 2015). In the other three genera epidermal cells are not of the linear type as in the fossil and anticlinal cell walls show a more pronounced concave pattern. In *Encephalartos* and *Lepidozamia* the long axis of epidermal cells is frequently oblique to the veins (this is also well observable in the extinct genus *Austrozamia*, assigned to the Encephalartoideae, Wilf *et al.* 2016), cells of triangular shape occur, and epidermal cells are usually non-elongate (l/w less than 5–7) displaying a distinct concave pattern (Greguss 1968, Hill 1980). In *Macrozamia* anticlinal walls of epidermal cells display a concave pattern, stomata are parallel to the long axis of leaflet, and encircling/subsidiary cells give an angular (pentagonal, hexagonal) outline of the stomatal pore (see Greguss 1968, Carpenter 1991), unlike our fossil.

Members of subfamily Zamioideae, i.e. *Ceratozamia*, *Microcycas* (Miq.) A. DC. and *Zamia* develop leaflets

with epidermal details more comparable to the fossil (Figs 3E–H, 4A–H) however species of the first two genera can be easily distinguished from the fossil. The single species of *Microcycas* has quite elongate, linear leaflets unlike the fossil. As regards epidermal details, cells with heavily thickened walls form rows (Fig. 4B) unlike in the fossil. Stomata are arranged parallel to the long axis of the leaflet in *Ceratozamia* (Fig. 3E, G), and *Microcycas* (Fig. 4A), unlike the often obliquely arranged stomata of the fossil. In contrast, numerous *Zamia* species display stomata oriented obliquely (e.g. *Z. erosa* O. F. Cook & G. N. Collins, *Z. pumila* L., *Z. stricta* Miq., *etc.*) or even perpendicular (e.g. *Z. dressleri* D. W. Stev., *Z. urep* B. Walln., *Z. wallisii* A. Braun) to the long axis of the leaflet (Fig. 4C, E, G). Stomata of *Microcycas* are more elongate (longer than wide), than those of the fossil and of modern *Zamia* species (Fig. 4A; see also Greguss 1968).

In *Ceratozamia* stomatal bands are broad; practically stomata are dispersed in intercostal areas between the veins. However, the most obvious distinctive character is the occurrence of serial rows of short cells with heavily thickened cell walls on both the adaxial and abaxial epidermis of leaflets in species of *Ceratozamia* (Fig. 3E–H) (see also Greguss 1968); these are absent in species of *Zamia* as well as in the fossil (Fig. 4C–H). The significance of short cell rows in identifying *Ceratozamia* is also supported by its fossil remains. Rows of short cells similar to those of modern *Ceratozamia* species were observed in leaves of the genus described from Europe, i.e *Ceratozamia floersheimensis* (Engelhardt) Kvaček, Z. from early Oligocene sites in Germany, Hungary and Slovenia (Kvaček, Z. 2002). Darker staining cell groups occur on the adaxial cuticle of the fossil (Fig. 2B) showing similarity to some modern *Zamia* species (Fig. 4H). However the importance of this trait is subordinate since possibly occurring in other cycad genera, as well (e.g. *Macrozamia*; Greguss 1968, Carpenter 1991).

Based on the above considerations and the highly comparable epidermal details and macromorphological traits of the fossil and modern *Zamia* species we assign the fossil leaflet to *Zamia*.

Morphometric analysis of epidermal traits of modern Zamia species and the fossil Z. nelliae: Morphometric analysis of the epidermal details of modern *Zamia* species (35 samples including 32 species) and the fossil species, *Z. nelliae* was carried out to assess the morphological

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Figure 4. Epidermal anatomy of extant species of *Microcycas (*Miq.) A. DC. and *Zamia* L. for a comparison. Abbreviation: lm – transmitted light microscopy. • A – abaxial epidermis of *Microcycas calocoma* (Miq.) A. DC. showing a stomatal band, MBC RM384A (lm). Note the parallel arrangement of stomata. Scale bar = 50 µm; B – adaxial epidermis of *Microcycas calocoma* with slightly elongated but not linear cells, MBC RM384A (lm). Scale bar = 50 µm. • C – abaxial epidermis of *Zamia erosa* O.F. Cook et G.N. Collins showing stomatal bands, MBC 20030275D (lm). Note the small-sized stomata and some stomata arranged obliquely. Scale bar = 100 µm; D – adaxial epidermis of *Zamia erosa* showing elongate cells, MBC 20030275D (lm). Scale bar = 100 µm. • E – abaxial epidermis of *Zamia pumila* L. showing stomatal bands, MBC 20080285B (lm). Note the sometimes obliquely arranged, small-sized stomata. Scale bar = 100 µm; F – adaxial epidermis of *Zamia pumila* showing elongate cells. Scale bar = 100 µm; G – closer view of stomata of *Zamia pumila*, MBC 20080285B (lm). Scale bar = 50 µm; H – closer view of adaxial epidermis of *Zamia pumila*, MBC 20080285B (lm). Scale bar = 50 µm.
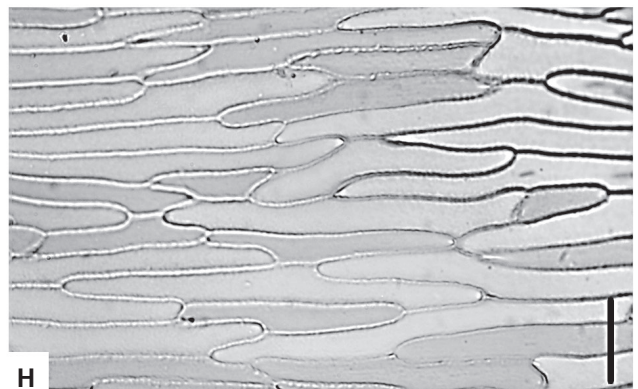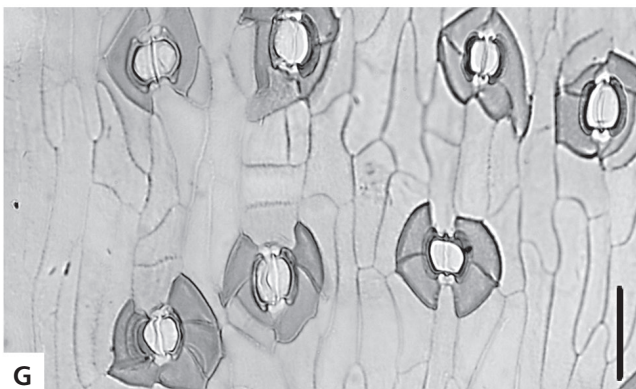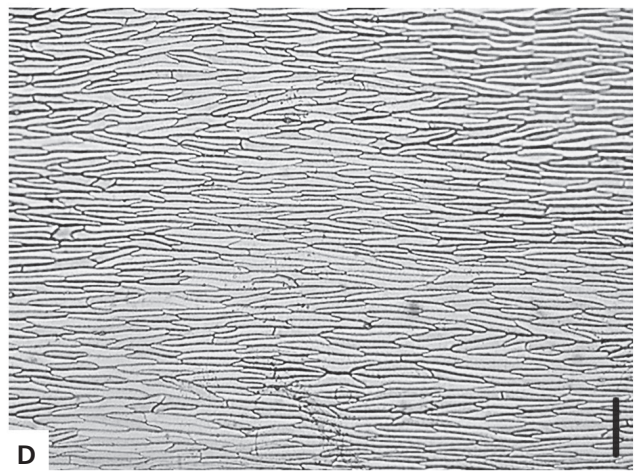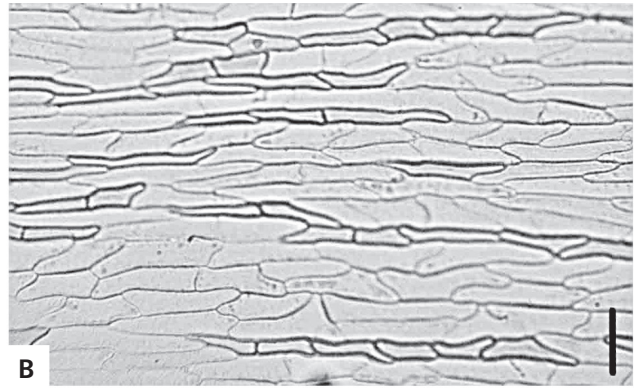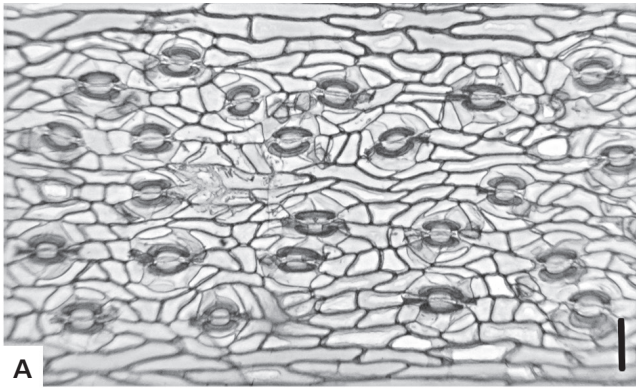
Table 2. Variance from PCA analysis of *Zamia* epidermal traits.

Component	Initial Eigenvalues		
	Total	% of Variance	Cumulative %
1	6.133	43.806	43.806
2	2.487	17.764	61.571
3	1.978	14.125	75.696
4	1.011	7.222	82.918

similarity and relation of the fossil to the modern members of the genus. Results of the first two components of the principal coordinate analysis (PCA) are shown in Figure 5. The first and second components of the PCA explain 43.81% and 7.76% of the variance, respectively (Tab. 2). Values of the various variables estimated for the fossil epidermal cells are within the range represented by extant *Zamia* species. Species of the Caribbean clade are obviously grouped together thus demonstrating a definite uniformity as regards their epidermal traits. The epidermal details of *Z. nelliae* show the highest similarity to species belonging to the Caribbean clade. Most members of this clade possess small, relatively high number of stomata and small-sized epidermal cells. Among species of this clade, *Z. erosa* is most comparable to the fossil; similarities include stomatal and interstomatal band widths and ratios, adaxial cell shape. The *Z. erosa* sample was collected from a plant of Puerto Rican provenance, but the species is also currently considered to occur in Jamaica and Puerto Rico. Other members of this clade displaying definitely elongate, or even linear epidermal cells are *Z. integrifolia* L.f., *Z. pumila, Z. portoricensis* Urb., and *Z. stricta* (Fig. 4C–H).

Review of previously published fossil reports of *Zamia*

Most of the specimens assigned formerly to *Zamia* are cited here as "*Zamia*" to indicate that these botanical assignments are either not proven or false. The specimens are either devoid of enough diagnostic traits to identify them as a species of *Zamia* or undoubtedly do not represent the *Zamia* genus (or even cycads). It should be noted, however, that all the specimens re-examined are too poorly preserved to identify them with certainty.

Order Cycadales Dumortier, 1829
Family Zamiaceae Horaninow, 1834

?*Zamia collazoensis* Hollick, 1928

> 1928 *Zamia collazoensis*; Hollick, p. 184, pl. 53, figs 1 (type), 3, 5, (7?).

> 1932 *Zamia collazoensis* Hollick. – Hollick, p. 173, pl. 7, figs 5, 6.

Remarks. – Hollick (1928) established two *Zamia* species from the Paleogene Collazo Shales of Puerto Rico and distinguished them on the basis of the shape of the lamina. *Z. collazoensis* was established for broader and more rounded leaflets. Based on macromorphological details Hollick's two species may be conspecific. All the specimens figured by Hollick were re-examined. The poorly preserved foliage fragments showing faintly observable macromorphological details, *i.e.* entire margin and parallel venation, provided heavily coalified cuticles with no cellular details preserved. Although the fossils themselves provide not such clear-cut morphological details as implied by the diagrams of Hollick, the fossils may represent *Zamia* leaflets based on their shape, venation (and cuticular details given below for ?*Z. noblei*).

?*Zamia noblei* Hollick, 1928
Figure 6A–C

> 1928 *Zamia noblei*; Hollick, p. 185, pl. 53, figs 9, 10, pl. 54, figs 1, 3a (type), pl. 55, figs 1–3, 4a, 5a.
> 1932 *Zamia noblei* Hollick. – Hollick, p. 174, pl. 6, figs 3, 4.

Remarks. – Hollick's other *Zamia* species from Puerto Rico is distinguished by its slender leaflets. Cuticular details were preserved on one leaflet from among the specimens figured by Hollick (1928: pl. 55, fig. 1, YPM27152; Fig. 6A). A fragment of the abaxial cuticle shows elongate, somewhat irregular ordinary epidermal cells (Fig. 6B, C) and a stomatal band constructed of 4 ill-defined rows of stomata. Stomatal structure, though faintly observable, seems to be of cycadalean, cyclotypic type. The adaxial cuticle is not preserved. The overall cuticular structure suggests a zamiaceous cycad; the lack of short cell rows and the slightly irregular arrangement of stomata are consistent with *Zamia*. However due to poorly preserved cuticular details and the lack of adaxial cuticle we are unable to confirm that the leaflets are *Zamia*.

"*Zamia*" *coloradensis* (Knowlton) Brown, 1962
Figure 6D

> 1962 *Zamia coloradensis*; (Knowlton) Brown, p. 47, pl. 10, figs 6, 9.

Remarks. – Brown (1962) described two *Zamia* species from the flora of Wyoming (Paleocene, Fort Union Formation). Some of the specimens had previously been assigned by Brown (1939) to *Podozamites latipennis* Heer but Brown concluded later (1962) based on new collections that the fossils represent the genus *Zamia*, and made a new combination *Zamia coloradensis*. Knowlton (1930: p. 40,

Figure 5. Principal coordinate analysis results of *Zamia* epidermal characters. The epidermal morphology of extant *Zamia* species and of the fossil *Z. nelliae* were analyzed. Major *Zamia* clades (the component species of major clades are indicated in Tab. 1) are indicated by different symbols. Data points represent species and are indicated by the symbol of the clade the species belongs to. Values of the various variables estimated for the epidermal cells of the fossil *Z. nelliae* are within the range represented by extant *Zamia* species. The epidermal details of *Z. nelliae* show the highest similarity to species belonging to the Caribbean clade.
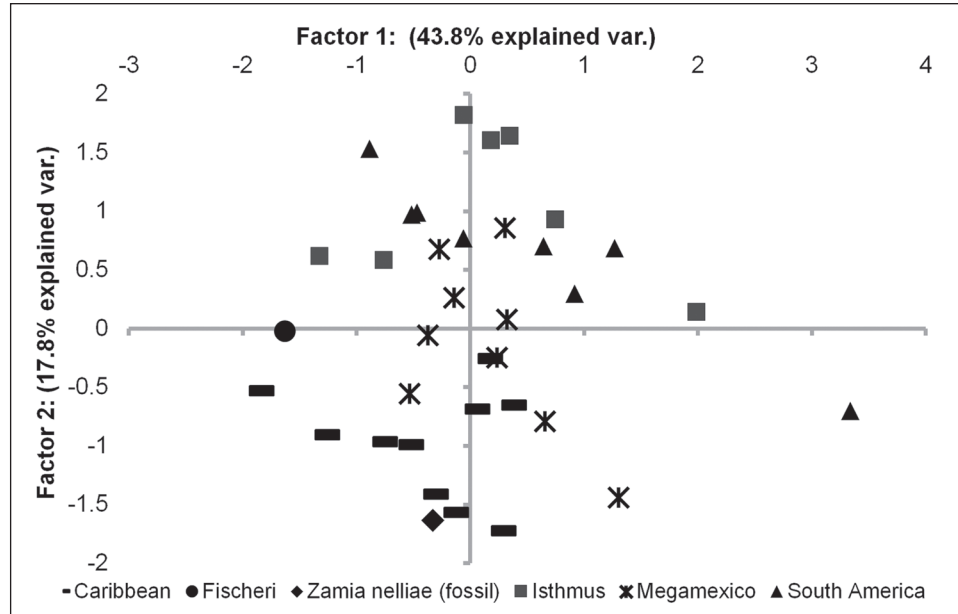
pl. 10, fig. 3) had assigned a specimen, collected by George L. Cannon, in 1889, from Middle Park Formation, Colorado, to the palm genus *Chamaedorea*?, as *Chamaedorea*? *coloradensis* Knowlton, however Brown noted (1962) that this, as well as the other cited remains, do not represent palms owing to the forkings and anastomoses of veins. For a discussion see "*Zamia*" *wyomingensis* below.

"*Zamia*" *wyomingensis* Brown, 1962
Figure 6E

 1962 *Zamia wyomingensis*; Brown, p. 47, pl.10, fig.1.

Remarks. – The other species established by Brown (1962) from the Paleocene flora of Wyoming, "*Zamia*" *wyomingensis,* was based on a specimen from the same strata as "*Z.*" *coloradensis*. The reinvestigation of the type specimens of "*Z.*" *wyomingensis* and "*Z.*" *coloradensis* showed that these do not represent extant *Zamia* (see also Watt 1971, Manchester 2014). The specimens may represent a group of extinct cycads related to *Ctenis* or *Dioonopsis* based on characteristic anastomoses of veins shared by these extinct taxa (Erdei *et al.* 2012, Erdei & Manchester 2015). The specimen of "*Z.*" *wyomingensis* shows just the basal part of leaflets therefore details on leaflet venation from the apical region are not available. It should also be noted that the leaflet bases of the specimen of "*Z.*"*coloradensis* figured by Brown (1962: pl.10, fig. 9; Fig. 6D herein) show a somewhat distorted character and are not clearly observable. None of the reinvestigated specimens have epidermal details preserved which could help a more precise identification. It may also be assumed that the fossil described by Knowlton as *Chamaedorea*? is related to these extinct cycads as well,

however Knowlton's figure (1930: pl. 10, fig. 3) seems to indicate a specimen different from those figured *in* Brown (1962), and the figure itself does not allow the proper reassessment of the specimen. Nevertheless, Brown (1962) referred to the specimen as possessing vein forkings and anastomoses similarly to Brown's "*Zamia*" species.

"*Zamia*" (?) *wilcoxensis* Berry, 1916
Figure 6F

 1916b *Zamia* (?) *wilcoxensis*; Berry, p. 169, pl. 114, fig. 2.
 1932 *Zamia* (?) *wilcoxensis* Berry. – Hollick, p. 173, pl. 6, fig. 6.

Remarks. – Berry described "*Z.*" (?) *wilcoxensis* Berry (1916b) from the Eocene Wilcox flora of Louisiana in the SE United States. The species was established on the basis of a poorly preserved impression. The holotype is a basal portion of a linear, entire-margined leaflet with parallel, uniform order of veins which recalls leaflets in Zamiaceae. The base of the leaflet is comparable to the morphology observable among cycads with non-articulated leaflets (Encephalartoideae D. W. Stev.).

?Order Cycadales

"*Zamia*" *tennesseeana* Berry, 1930
Figure 6G

 1930 *Zamia tennesseeana* Berry; Berry, p. 51, pl.32, fig. 8.
 1932 *Zamia tennesseeana* Berry. – Hollick, p. 173, pl. 13, fig. 4.

Remarks. – Berry described another species, "*Z.*" *tennes-seeana* Berry (Berry 1930) from the Eocene Wilcox flora (SE United States). The holotype of this species seems to be comparable to zamiaceous leaflets based on its gross morphology, *i.e.* linear lamina, entire margin and parallel, uniform order of veins. Berry (1930) noted that he hesitated to relate it to the modern *Nageia* (Podocarpaceae) which has somewhat similar leaves. Hollick (1932) accepted Berry's identifications and cited the modern counterparts proposed by Berry and also added other *Zamia* species for comparison. Cuticular details, which would be required to verify cycadalean affinity are not preserved.

"*Zamia*" *washingtoniana* Ward, 1985
Figure 6H

> 1895   *Zamia washingtoniana*; Ward, p. 349, pl. 2, fig. 6.
> 1905   *Zamia washingtoniana* Ward. – Fontaine, p. 503, pl. 111, figs 1, 2.
> 1911   *Zamites tenuinervis* Fontaine. – Berry, p. 345, pl. 54, fig.1.

Remarks. – Ward (1895) established *Zamia washingtoniana* based on a leaf and a seed-like remain preserved on the same slab from the Mount Vernon flora (Potomac Formation, Cretaceous).

Fontaine (1905) mentioned that 11 specimens altogether could be assigned to this species and figured two of the specimens. Later Berry (1911) synonymized Ward's species in *Zamites tenuinervis* Fontaine, however pinnae in *Zamites* Brongniart are attached to the upper surface of the rachis which trait is not traceable in Ward's specimens (only fragmentary pinnae/leaflets). The type specimens reinvestigated here (two specimens with counterparts; figured on pl. 111, figs 1, 2 in Fontaine 1905) are entire margined linear leaflets with parallel venation which is comparable to most cycads in the Zamiaceae. Since epidermal details are not preserved, the systematic relationship of the foliage cannot be supported.

"*Zamia*" sp. Berry, 1929

> 1929   *Zamia* sp.; Berry, p. 2, pl. 1, fig. 6.

Remarks. – Berry (1929) assigned a leaf fragment from Tertiary deposits of Colombia (from sandstones associated with coal at Montserrat near Bogota) to *Zamia*. Berry's figure shows the basal fragment of a parallel-veined leaf(let) which may belong to a cycad but epidermal details are not available for a precise identification.
Other unidentified remains

"*Zamia*" *australis* Berry, 1928

> 1928   *Zamia* australis; Berry, p. 11, pl. 2, fig. 1.

> 1932   *Zamia australis* Berry. – Hollick, p. 176, pl. 6, fig. 2.

Remarks. – Berry described "*Zamia*" *australis* Berry from Rio Negro, Argentina. Although Hollick (1932) accepted Berry's identification, the reinvestigation of the holotype specimen done by the first author (BE) did not reveal evidence of a cycad affinity. It appears to be a poorly preserved unidentifiable foliage fragment.

"*Zamia praecedens*" Ett.

> 1903   *Zamia praecedens* Ett. – Krasser, p. 853. [*nomen nudum*]

Remarks. – Krasser (1903) mentioned a new species by Ettingshausen, "*Zamia*" *praecedens* in his work on the fossil flora from Ouricanga, Brasil, however the species was not validly published since no description or figure of the specimen was included. Berry (1928: p.11) noted that the putative *Zamia* ("*Z.*" *praecedens* Ett. nomen nudum) from Krasser (1903) was not represented in the collection he obtained later from the locality in Brasil. The specimen which is currently stored in the Natural History Museum, Wien (NHMW1905/0017/0004) is an impression fossil without cuticle preserved. Although, at first glance the fossil shows cycad characters, *i.e.* entire margined, linear leaf(let) and parallel venation, it seems to have at least two order of veins which contrasts cycads having a uniform order of veins.

Specimen revisions published in earlier works

Some of the fossil specimens formerly assigned to the genus *Zamia* were reviewed and revised in earlier works. Erdei *et al.* (2012) investigated specimens of "*Zamia*" *mississippiensis* Berry described from the Eocene Wilcox flora, SE United States (Berry 1916a: p. 177, fig. 1.; 1917: p. 63, fig. 17; Hollick 1932: p. 173, pl. 6, fig. 1a–c). The re-examination of Berry's type specimens from Meridian, Mississippi, indicated that they are coniferous twigs, probably Taxodioid Cupressaceae (Erdei *et al*. 2012). The occasionally forking parallel veins mentioned by Berry (1916a) are not observable on the poorly preserved specimens. Leaflets from the Eocene flora of La Porte, California were assigned by Potbury (1935) to *Zamia* and were identified as a variety of Berry's species, "*Z.*" *mississippiensis* Berry var. *macrophylla* Potbury (Potbury 1935: p. 60, pl. 1, fig. 7). However, the leaflets, with well-preserved epidermal characters, were reassigned by Erdei *et al*. (2012) to an extinct cycad genus as *Dioonopsis macrophylla* Erdei, Manchester et Kvaček, Z.

"*Zamia*" *tertiaria* Engelhardt (1891: p. 646, pl. 2, fig. 16) was described on the basis of a single fragmentary leaf from the Eocene of Coronel, Chile. Unfortunately, as Wilf *et al.* (2014) noted, the holotype of the species has been lost along
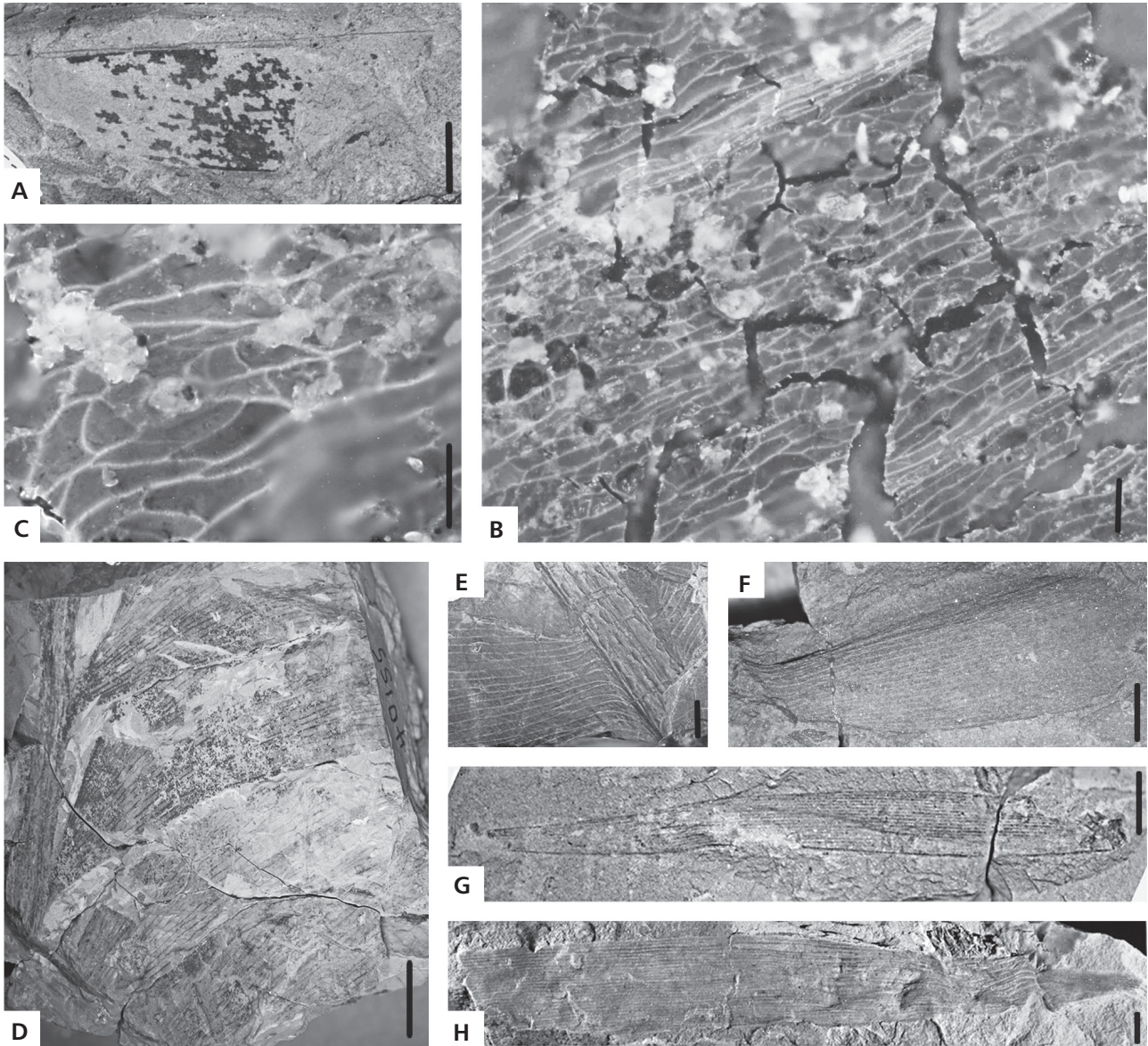
Figure 6. Fossil specimens described formerly as *Zamia* and re-examined in the scope of this study. Abbreviation: fm – fluorescence microscopy. • A, B, C – ?*Zamia noblei*; A – foliage fragment of ?*Zamia noblei* Hollick from the Paleogene of Puerto Rico, (YPM27152), scale bar = 1 cm; B – abaxial cycadalean type cuticule of ?*Zamia noblei* showing stomatal bands, (YPM27152), fm, scale bar = 50 µm; C – closer view of a stoma of ?*Zamia noblei* displaying cyclocytic arrangement of subsidiary cells, (YPM27152), fm, scale bar = 50 µm. • D – leaf fragment of "*Zamia*" *coloradensis* (Knowlton) Brown from the Paleocene flora of Wyoming. Note the cycadalean type leaf and leaflets inserted laterally on rachis, (USNM40155/type), scale bar = 1 cm. • E – leaf fragment of "*Zamia*" *wyomingensis* Brown from the Paleocene flora of Wyoming showing leaflets inserted with a broad base on rachis, (USNM167487 /holotype), scale bar = 0.5 cm. • F – leaflet fragment of "*Zamia*" *wilcoxensis* Berry described from the Eocene Wilcox flora, (USNM35474), scale bar = 0.5 cm. Note the broad base of the leaflet. • G – foliage fragment of "*Zamia*" *tennesseeana* Berry from the Eocene Wilcox flora showing parallel venation, (USNM39727), scale bar = 0.5 cm. • H – foliage fragment of "*Zamia*" *washingtoniana* Ward from the Cretaceous Mount Vernon flora showing parallel venation, (USNM31768), scale bar = 0.5 cm.

with many other specimens from Engelhardt's monograph (see Wilf *et al.* 2014 for a detailed discussion on the topic). The drawing of the holotype does not give definite clues to identify the leaf fragment with certainty as a cycad.

Wilf *et al.* (2014) reinvestigated some of the specimens assigned by Berry (1922: p. 120, pl. 1, fig. 4, pl. 2, figs 1–3) to "*Zamia*" *tertiaria* from Chile (Arauco Mine, Curanilahue)

and stored in the Smithsonian Institution (USNM 320640-43). The authors noted that the foliage remains are somewhat different from the drawings (which show densely packed, parallel, occasionally forking veins) and display monocot features including at least two order of veins.

Berry (1922: p. 120) assigned another specimen to "*Zamia*" *tertiaria* from Engelhardt's monograph (1891:

p. 686, pl. 1, fig. 4) that was originally identified by Engelhardt as a monocot remain. Nevertheless, the cycad affinity of foliage remains published by Engelhardt (1891) and Berry (1922) had already been discussed by Hollick (1932: p. 175) and subsequently by Wilf *et al.* (2014).

Specimens described and figured as "*Zamia*" *tertiaria* Engelhardt by Berry (1938: p. 57, pl. 9, USNM 40378h; pl. 8, figs 4, 5, USNM 40378d, f) alongside with the historical collection of "*Zamia*" *tertiaria* from the Eocene Río Pichileufú flora of Río Negro Province, Argentina and stored in the Smithsonian Institution were reinvestigated by Wilf *et al.* (2014) and assigned to *Agathis* (*A. zamunerae* Wilf) demonstrating the first record of the genus from South America. The authors recovered numerous additional specimens recalling Berry's "*Zamia*" *tertiaria* from sites in Río Pichileufú and Laguna del Hunco, including leafy branches and twigs however, as stated by the authors, with such a high relative abundance which is highly unlikely in the case of a cycad. Furthermore, the twigs showed terminal buds and decussate phyllotaxy suggesting a conifer with simple leaves, not a pinnate cycad leaf (Wilf *et al.* 2014).

Conclusions

The review presented herein leads us to conclude that fossil specimens formerly assigned to *Zamia* either show characters not shared by modern *Zamia* species or suffer from poor preservation hindering proper identification of the genus. The fossil foliage from Paleogene sediments in Panama, described here as *Zamia nelliae*, represents the first convincing fossil evidence of *Zamia*. Thus, species representing *Zamia* must have appeared by the end of the Eocene or earliest Oligocene. If Hollick's fossils from Puerto Rico, ?*Z. collazoensis* and ?*Z. noblei*, do represent the genus *Zamia* then the distribution and probable diverse occurrence of the genus (the specimens from Puerto Rico are clearly distinct from *Z. nelliae*) may be postulated in the Caribbeanen–Central American region by the Oligocene.

The morphometric analysis of epidermal micro-morphology of 32 modern and the fossil *Zamia* species showed high similarity of the fossil epidermal traits with those of the Caribbean species group. As most members of the Caribbean clade share epidermal details and form a group more or less distinct from species belonging to other *Zamia* clades, grouping of the fossil with the Caribbean clade may imply a phylogenetic relationship.

The palaeogeographic settings of the Panama isthmus, the Caribbean and northern South America during the Paleogene are of pivotal importance in assessing the early evolution of *Zamia*. Paleogeography and biogeography of Central America and the Caribbean are highly complex issues and tectonic history of this region is still far from settled. The evolution of the Panama isthmus was influenced by numerous overlapping tectonic interactions (Farallon, Caribbean, and South America plates) since the Late Cretaceous. Tectonic reconstructions constrained by palaeomagnetic and thermochronologic data of Montes *et al.* (2012a, b), and zircon geochronology of Ramírez *et al.* (2016) suggest that significant parts of the Panamanian volcanic arc were above sea level from the middle Eocene onwards. There is also support for an emerged Panamanian landmass in Eocene time among palaeobotanical studies. Graham *et al.* (1985) found pollen fossil from mangroves (*Rhiziphora* and *Pelliceria*) from the Gatuncillo Formation and suggested the presence of a series of volcanic islands of moderate to low relief, with shallow seas protected by coral reefs. Fossil fruits and seeds from the middle–late Eocene Tonosí Formation also suggest presence of nearby lowland rainforests (Herrera *et al.* 2012). This evidence suggests that there was a landmass supporting terrestrial vegetation in close proximity to the site of deposition of *Zamia nelliae*. Such a landmass would have been located to the south of the present-day Panama isthmus.

As noted earlier, other putative fossils of *Zamia* are recorded from the Paleogene of the Caribbean Antilles. Since the early Paleogene this island chain, the proto-Antilles, may have migrated eastwards to occupy the position of the present-day Antilles (Perfit & Williams 1989). The proto-Antillean island arc may have more or less connected North and South America during the Late Cretaceous (100–70 Ma). However, it is still poorly known which areas were above sea level during the Late Cretaceous and Paleogene history of the region (Hedges 2001). Given its preservation in marine sediments, the origin of the *Zamia nelliae* material described here is unclear; components of the Gatuncillo fossil plant assemblage might have been transported into the sedimentary basin.

The unique taxonomic composition and high endemism of the Caribbean biota were subjected to numerous studies, though more data are available on vertebrate groups. It is estimated that about $1/3$ of vascular plants native to the West Indies are endemic (Adams 1972, Gentry 1992). The various biogeographic models explaining this specific diversity were established on zoological data (Perfit & Williams 1989, Hedges 2001). The vicariance model (Rosen 1975) postulates that a Proto-Antillean biota connecting North and South America was fragmented during the Late Cretaceous by plate tectonic movement and formed the current island biotas. In contrast the dispersal model (Hedges 1996) suggests that organisms dispersed over water during the Cenozoic to reach the islands. Another theory presumes that a dry land bridge connected the Greater Antilles and South America for a short time during the mid-Cenozoic (Iturralde-Vinent & MacPhee 1999) facilitating dispersal into the Antilles.

Concerning the origin and biogeography of *Zamia* some ideas have already been presented mostly in the context of fossil remains that share some characters with *Zamia*

(and former *Chigua*). Uzunova *et al.* (2001) described *Eostangeria ruzinciniana* Uzunova, Palamarev et Kvaček, Z., the youngest species of the extinct genus *Eostangeria* Barthel from the middle Miocene of Bulgaria. Contrasting other members of the genus, i.e. *E. saxonia* Barthel (Eocene, Germany; Barthel 1976) and *E. pseudopteris* Kvaček, Z. et Manchester (Paleogene of North America; Kvaček, Z. & Manchester 1999), which share general leaflet macromorphology with modern *Stangeria*, i.e. fern-like leaflet with a midrib and forking lateral veins departing at about 60 degrees from the midrib. Leaflets of *E. ruzinciniana* display a macromorphology more reminiscent to that of *Zamia* (*Chigua*) *restrepoi*, with lateral veins arising more steeply from the midrib. Furthermore, all members of *Eostangeria* share epidermal features with modern genera of subfam. Zamioideae, including *Zamia*. Uzunova *et al.* (2001) concluded that a lineage probably comprising *Eostangeria* and *Chigua* originated in North America and migrated to South America during the late Tertiary. Accordingly, this theory puts the origin of a lineage including also *Zamia* (*Chigua*) to North America (and/or Europe). Nevertheless, evidence for this theory is incomplete; fossils undoubtedly representing modern *Zamia* have been recorded neither from North, nor from South America, and fossils of *Eostangeria* have not been reported from South America. Another theory on the origin of *Zamia* is related to *Restrepophyllum* Passalia, Del Fueyo et Archangelsky described recently from the Early Cretaceous of Patagonia, Argentina (Passalia *et al.* 2010). Contrasting with the theory of North American origin, the authors postulate the South American origin of *Zamia* and its migration northwards during the Paleogene. Although in leaflet macromorphology *Restrepophyllum* is reminiscent of modern *Zamia restrepoi* (and as the authors note, also of *Eostangeria ruzinciniana*) its epidermal traits shows some differences from those of *Zamia* as well as other Zamiaceae. The strikingly uniform, epidermal, details of members of Zamioideae subfamily (the non-isodiametric, mostly elongate, somewhat irregular epidermal cells) contrast the isodiametric epidermal cells in *Restrepophyllum*. In this respect *Restrepophyllum* is more reminiscent of other extinct cycads, e.g. *Ctenis*, *Dioonopsis*. Whether the similar leaflet macromorphology of *Zamia restrepoi*, *Eostangeria ruzinciniana*, and *Restrepophyllum* is attributable to the phylogenetic relation of these groups remains an open question. Based on fossil floras possible migration routes during the Oligocene were suggested by Graham & Jarzen (1969) who postulated a Caribbean land bridge through the Antilles and the Yucatan peninsula and an exchange of plant species between northern South America and the Caribbean. However, fossil evidence of *Zamia* supporting this model is still missing from South America.

Although the current study provides evidence that the *Zamia* genus appeared by the end of the Eocene or earliest Oligocene in the Central American–Caribbean region, the origin of the genus is still an unresolved issue. Moreover, the fossil from Panama may indicate an "intermediate" hypothesis in which *Zamia* originated in the Central American–Caribbean region and experienced subsequent south- and northward range expansion. However, it should be noted that data are presently insufficient to support any of the above ideas.

Acknowledgements

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