

New fossil records of *Ceratozamia* (Zamiaceae, Cycadales) from the European Oligocene and lower Miocene

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ABSTRACT. New compression leaf material of *Ceratozamia* (Zamiaceae) has been recognised in the European Cenozoic. A leaflet of *Ceratozamia floersheimensis* (Engelhardt) Kvaček was recovered among unidentified material from the Oligocene of Trbovlje, former Trifail, Slovenia, housed in old collections of the Austrian Geological Survey, Vienna. It is similar in morphology and epidermal anatomy to other specimens previously studied from the lower Oligocene of Flörsheim, Germany and Budapest, Hungary. A fragmentary leaflet assigned to *C. hoffmannii* Ettingsh. was recovered in the uppermost part of the Most Formation (Most Basin in North Bohemia, Czech Republic) and dated by magnetostratigraphy and cyclostratigraphy to CHRON C5Cn.3n, that is, the latest early Miocene. It yielded excellently preserved epidermal structures, permitting confirmation of the generic affinity and a more precise comparison with this lower Miocene species previously known from Austria (Münzenberg, Leoben Basin) and re-investigated earlier. Both the Oligocene and Miocene populations of *Ceratozamia* are based on isolated disarticulated leaflets matching some living representatives in the size and slender form of the leaflets. Such ceratozamiaes thrive today in extratropical areas near the present limits of distribution of the genus along the Sierra Madre Orientale in north-eastern Mexico, in particular *C. microstrobila* Vovides & J.D. Rees and others of the *C. latifolia* complex, as well as *C. hildae* G.P. Landry & M.C. Wilson (“bamboo cycad”). The occurrence of *Ceratozamia* suggests subtropical to warm-temperate, almost frostless climate and a high amount of precipitation. The accompanied fossil vegetation of both species corresponds well with the temperature regime. While the Oligocene species in Hungary probably thrived under sub-humid conditions, the remaining occurrences of fossil *Ceratozamia* were connected with humid evergreen to mixed-mesophytic forests.

KEYWORDS: cycads, *Ceratozamia*, lower Oligocene, Germany, Hungary, Slovenia, lower Miocene, Czech Republic, Austria

INTRODUCTION

The cycads were characteristic plants of the Mesozoic. Their later decline and mosaic global distribution are often attributed to geological and environmental changes that took place during cycad evolution over the last 200 million years since their establishment on the Earth (Whitelock 2002). While the early history of cycads has been well explored thanks to extensive studies of fossil records (see e.g. Pott & McLoughlin 2009, 2014, Pott 2014), the later stages of the evolution of this interesting plant group have received less attention until recently. Modern genera, such as *Cycas* (Yokoyama 1911, Su et al. 2014), *Ceratozamia*

(Ettingshausen 1887, 1888), and *Zamia* (Erdei et al. 2014) have only rarely been recognised in the Cenozoic of Eurasia and North America; other genera like *Macrozamia*, *Lepidozamia*, and *Bowenia* have been reported more often in the Southern Hemisphere (see e.g. Cookson 1953, Hill 1978, Pant 1987). Most of the previous fossil records, such as *Zamites* (*Dioon*) *tertiarius* Heer, *Zamia mississippiensis* Berry, *Z. wilcoxensis* Berry, *Z. coloradensis* (Knowlton) R.W. Brown, *Z. wyomingensis* R.W. Brown, and *Ceratozamites vicetinus* Meschinelli, are based on sterile foliage without epidermal anatomy and cannot be assigned reliably to

a modern genus, or they may appear to belong to extinct genera of the Cycadales after revision (Barthel 1976, Kvaček & Manchester 1999, Kvaček & Velitzelos 2000, Erdei et al. 2010, 2012, Erdei B. pers. comm. 2014). The epidermal anatomy may aid in the identification of such fossil records (e.g. Kvaček 2002, 2004, Su et al. 2014, Erdei et al. 2014), complementing the information from fertile specimens of cones, seeds or other organs (wood, pollen), which are much more rarely recovered in the fossil state (see e.g. Pant 1987, Palacios & Rzedowski 1993, Artabe & Stevenson 1999, Artabe et al. 2004).

The leaf epidermal features of cycads are valuable for assessing the systematic positions of fossils based on sterile foliage. Details of stomata, in particular, with conspicuous lamellae and the whole haplocheilic stomatal apparatus (see e.g. Bobrov 1974), are useful for recognising even small fragments of leaf compressions showing epidermal anatomy and for differentiating such leaf fossils from morphologically similar but quite differently allied extinct Bennettites with syndetocheilic stomata (Thomas & Bancroft 1913, Florin 1933, Harris 1964, 1969). Leaf epidermal research focusing on the phylogenetic history of this ancient group of gymnosperms has been done in many palaeobotanical studies of fossil remains recovered mainly from the Mesozoic (e.g. Watson & Sincock 1992, Peppe et al. 2007). Cenozoic records based on sterile leaf fragments have only recently been accepted as a serious basis for deciphering the evolution and dispersal of cycads. The present paper continues a series of studies of Cenozoic Cycadales of North America and Eurasia based on foliage (e.g. Horiuchi & Kimura 1987, Kvaček & Manchester 1999, Kvaček & Velitzelos 2000, Uzunova et al. 2001, Kvaček 2002, 2004, Erdei et al. 2010, Erdei et al. 2012). The fossils recovered so far belong largely to extinct genera (*Dioonopsis* Horiuchi & Kimura, *Eostangeria* Barthel, *Pseudodioon* Erdei et al.), so any new fossil record attributable to a modern cycadalean genus may contribute to our understanding of the largely discontinuous current distribution of the cycads.

In this paper, recently recovered fossil leaflet compressions of *Ceratozamia* are evaluated and the preserved epidermal traits are documented in detail. Previous studies of the leaf epidermal anatomy of living cycads (e.g. Pant & Nautiyal 1963, Greguss 1968) provide

grounds for confirming the occurrence of the genus *Ceratozamia* Brongn. (Zamiaceae), presently endemic to Central America, in the Oligocene and Miocene of Europe.

MATERIAL AND METHODS

The new specimen of *Ceratozamia floersheimensis* was recovered in the collections of the Austrian Geological Survey (Geologische Bundesanstalt), Vienna (courtesy of Barbara Meller). According to the label it comes from Trbovlje, formerly Trifail (ca 46°10'N, 15°03'E). The carbonised leaf lamina firmly adheres to gray marl and only small fragments have been mechanically removed. The accompanying flora includes *Phoenicites* Brongn., Lauraceae, *Comptonia* l'Hérit, *Eotrigonobalanus* Walther & Kvaček, *Ilex castelli* Kvaček & Walther, *Sloanea* L., *Dombeyopsis* Ung., and *Rhodomyrtophyllum* Ruffle & Jähnichen (Kvaček & Walther 2008), and belongs to the early Oligocene Kiscell floral complex sensu Mai (1995) [see Kvaček & Walther (2001), Jungwirth (2003)].

The new fragmentary specimen of *C. hofmannii* comes from drill core No. Os 16 (coordinates 50°36'N, 13°40'E) executed in 2012 in the NE part of the Most Basin near the town of Osek (Fig. 1). The fossiliferous rock is firm grey clay or claystone belonging to the Lom Member of the Most Formation of the local lithostratigraphy and recently dated by palaeomagnetostatigraphy and cyclostratigraphy to CHRON C5Cn.3n, 16.5 to 16.7 Ma (Matys Grygar & Mach 2013, Matys Grygar et al. 2013, Mach et al. 2014, Matys Grygar et al. in press); that is, it belongs to the uppermost lower Miocene, uppermost Burdigalian. The exact level of the recovered fossil lies at 79.2 m depth in the drill core, ca 62 m above the roof of the Lom Seam, and belongs to the youngest part of the fill of the Most (formerly North Bohemian) Basin. The fossiliferous facies is typical of the lacustrine deposits that cover the lignite seams there (Mach et al. 2014). The accompanying plant megafossils are very sparse (*Pinus* sp., *Laurophyllum nobile* Kolak. & Shakryl, *Myrica lignitum* (Ung.) Saporta). The flora of the Lom Member, to the extent that it is currently known, was reviewed by Teodoridis & Kvaček (2006) and comes mostly from the Lom Seam in the clay lignite facies (*Azolla*, *Salvinia*, *Pronephrium*, *Glyptostrobus*, *Quasisequoia*, *Potamogeton*, cf. *Alnus*, *Myrica*, *Salix*, *Decodon*, *Nyssa*, *Hemitrapa*). The clay deposit of the Libkovic Member closely underlying the Lom Seam belongs to the same sedimentary cycle (Mach et al. 2014). It yielded a macrofossil plant assemblage consisting of mostly palaeosubtropical elements, such as *Lygodium gaudinii*, *Laurus abchasic*, *Laurophyllum pseudovillense*, *L. pseudoprinceps*, *L. markvarticense*, *Quercus kubinyii*, *Platanus neptuni*, *Cedrelospermum* sp., and *Gordonia hradekensis* (Teodoridis & Kvaček 2006, Kvaček & Teodoridis 2007).

The recovered fossils are incomplete leaflets (impression/compression) whose coaly matter in the case of the North Bohemian specimen peels off when drying from the rock. For observation of venation details in transmitted light, larger fragments of leaf

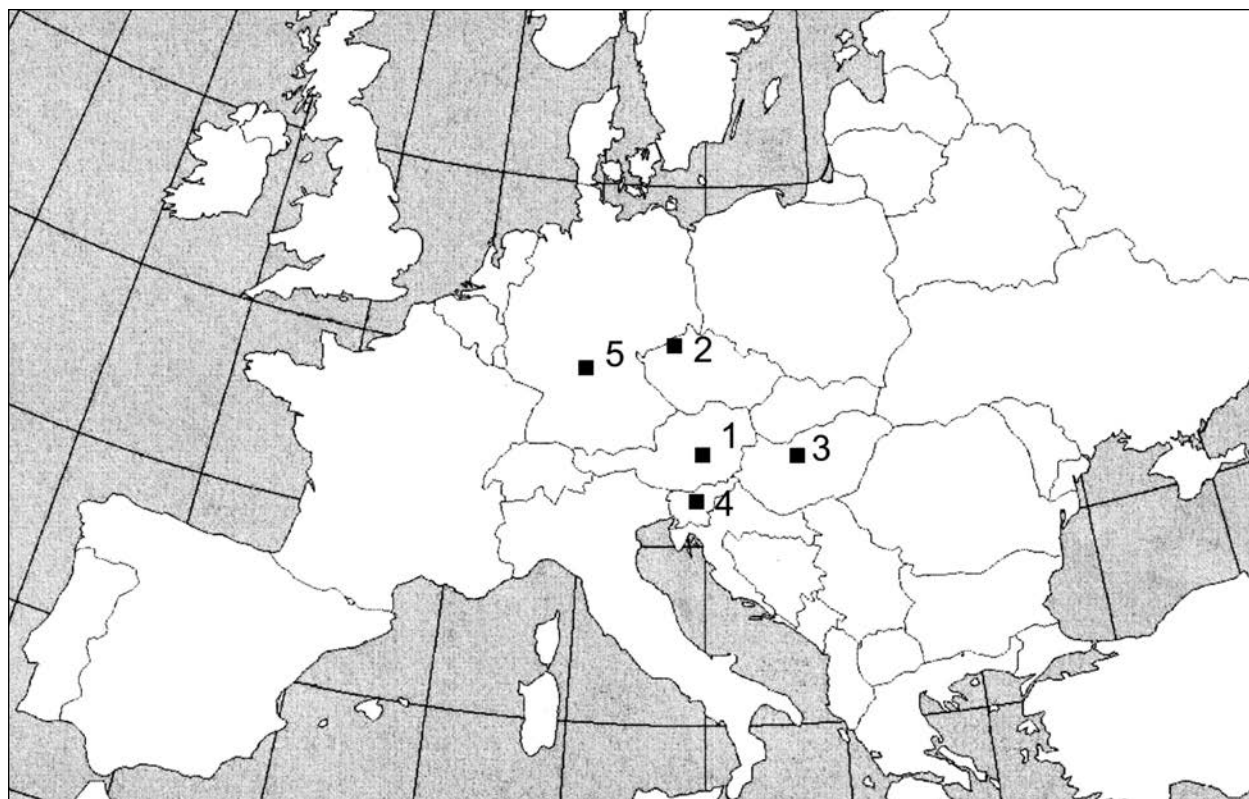


Fig. 1. Distribution of fossil *Ceratozamia* in Europe. 1. *Ceratozamia hofmannii* Ettingsh., Münzenberg (type locality), Leoben Basin, Austria, lower Miocene; 2. *Ceratozamia hofmannii* Ettingsh., Osek, Most Basin, Czech Republic, lower Miocene; 3. *Ceratozamia floersheimensis* (Engelhardt) Kvaček, Budapest, Hungary, lower Oligocene; 4. *Ceratozamia floersheimensis* (Engelhardt) Kvaček, Trbovlje (former Trifail), Slovenia, lower Oligocene; 5. *Ceratozamia floersheimensis* (Engelhardt) Kvaček, Flörsheim (type locality), Hesse, Germany, lower Oligocene

lamina were bleached in 30% peroxide for several days. For preparation of cuticles, portions of the lamina were cleaned in hydrofluoric acid and macerated with Schulze's solution and KOH. A portion of the isolated cuticle was embedded in glycerol and prepared on current microscope slides; other fragments were placed on stubs for SEM observation. Maceration of other fossil foliage, namely other samples of *Ceratozamia floersheimensis* from Flörsheim (Germany), Budapest (Hungary) and the type specimen of *C. hofmannii* (see Kvaček 2002, 2004), proceeded in the same way. Preparations of foliage of modern cycads were also treated with Schulze's solution and KOH, and some were stained with safranin.

The material of *C. floersheimensis* is housed in the Senckenberg Museum, Frankfurt/M. (SM-B, type specimen), the Hungarian Natural History Museum, Budapest (BP), and the newly recovered specimen in the Austrian Geological Survey (Geologische Bundesanstalt), Vienna (BAW); some duplicate cuticle preparations are at the Institute of Geology and Palaeontology, Charles University in Prague. The type specimen of *C. hofmannii* was recovered in the Natural History Museum of Leiden (NHML); the new specimen assigned to *C. hofmannii* and recovered in drill core Os16 in North Bohemia has been included in the collections of the National Museum in Prague [specimen numbers NM G 9465 (a–f)], and duplicate cuticle preparations are at present kept in the collections of the Institute of Geology and Palaeontology of the Charles University in Prague.

Foliage of living plants was collected at the Montgomery Botanical Center, Miami (MBC), and the botanical gardens in Prague (PRC) and Kew (K), and received from private collections (courtesy B. Schutzman – BSCH). Cuticle preparations of living cycads are housed at present in the Institute of Geology and Palaeontology, Faculty of Science, Charles University in Prague.

SYSTEMATIC DESCRIPTIONS

The newly recovered leaf fossils from Slovenia and North Bohemia clearly represent cycads on account of the structure of haplocheilic stomata with well-cutinised proximal lamellae, having dorsal cuticular flanges over the guard cells (Pl. 2, figs 2, 3, 10). In spite of its fragmentary nature, the plant fossil from North Bohemia is reasonably explained as a leaflet. Its morphology (parallel venation resembling monocots) permits exclusion of affinity to the Cycadaceae Persoon with the single genus *Cycas* L. characterised by having one-veined leaflets. Stangeriaceae L. Jonson and Zamiaceae Rchb. subfam. Eostangerioideae Kvaček, Palamarev & Uzunova in

Uzunova et al. (2001) differ in having pinnate venation of leaflets. The remaining members of the Zamiaceae have either articulate leaflets characteristic of subfam. Zamioideae J. Schust. or nonarticulate leaflets belonging to Encephalartoideae D. W. Stev. (Stevenson 1992). This feature is not always recognisable in the fossil state when only isolated leaflets or parts of whole compound fronds are recovered. Sometimes leaflets of *Encephalartos* are shed individually (personal communication, B. Erdei 2014).

The fossil leaflets of *Ceratozamia hofmannii*, both the holotype from Austria as well as the present material from North Bohemia, suggest an articulate condition, occurring isolated from the fronds. Those from the European Oligocene described as *C. floersheimensis* (Engelhardt) Kvaček (Kvaček 2002, present paper) show similarly articulate leaflets. The presence of distinct rows of short narrow cells in the adaxial as well as abaxial epidermis seen in the fossil foliage is especially typical of the monotypic tribus Ceratozamia D. W. Stev. and the genus *Ceratozamia* Brongn.

Order: Cycadales Dumort.

Family: Zamiaceae Rchb.

Subfamily: Zamioideae J. Schust.

Tribus: Ceratozamia D. W. Stev.

Genus: *Ceratozamia* Brongn.

***Ceratozamia floersheimensis* (Engelhardt)
Kvaček**

Plate 1, figs 6, 7, Plate 2, fig. 10

- 1911 *Iris floersheimensis* Engelhardt, p. 319, fig. 27.
2002 *Ceratozamia floersheimensis* (Engelhardt) Kvaček, p. 305, figs 1–21.

The three leaflets of *C. floersheimensis* so far recovered from the Oligocene of Germany and Hungary (Kvaček 2002, figs 1–9) and the new one from Slovenia (Pl. 1, fig. 7) are either sessile or broadly attached, thus differing from the Miocene *C. hofmannii* Ettingsh. having a very narrow petiolulate base (Pl. 1, fig. 1, Kvaček 2004, fig. 1). The complete size is known only in the new record from Trbovlje. The leaflet is lanceolate to subfalcate, 200 mm in length and 25 mm in width. All specimens

recovered so far share the epidermal structure typical of many living species (see Kvaček 2002, figs 10–15). In this respect the newly recovered specimen (Pl. 2, fig. 10) also matches the type material from Flörsheim, although preservation of the former is not satisfactory. The texture of all the compressions studied is coriaceous. The formation of the leaflet bases suggests that the leaflets might be attached regularly along the rachis, although more complete leaves or leaf fragments with the rachis are not preserved. The species circumscription thus remains incomplete.

***Ceratozamia hofmannii* Ettingsh.**

Plate 1, figs 1–4, Plate 2, figs 1–9, Plate 3, figs 9, 10

- 1887 *Ceratozamia hofmannii* Ettingshausen, p. 81.
1888 *Ceratozamia hofmannii* Ettingshausen; Ettingshausen, p. 272, pl. 3, fig. 10.
2004 *Ceratozamia hofmannii* Ettingshausen; Kvaček, pp. 111–118, figs 1–5.

The illustration of the type specimen published by Ettingshausen (1888) from the lower Miocene of Münzenberg, Austria (Pl. 1, fig. 1) shows a complete leaflet on which the details of venation (interstitial strands) are visible (Kvaček 2004, fig. 2). A leaf epidermal study of its fragment (now housed in NHML and published by Kvaček 2004, fig. 1) confirmed the affinity of the holotype to *Ceratozamia* (Pl. 2, fig. 9). It is narrow-petiolulate, very different from the previously characterised *C. floersheimensis*. The species description of *Ceratozamia hofmannii* can now be extended by several traits preserved in the material from North Bohemia. This newly recovered fragmentary leaflet (Pl. 1, fig. 2) is slightly broader than the type specimen (max. width 23 mm vs. 17.5 mm in the Austrian material) and incomplete in length (85 mm). The preserved margins are almost parallel, typical of lanceolate leaflet forms. Otherwise it conforms to the type specimen in all venation details: parallel veins 16 in number, not forked, mostly 1.5 mm apart (Pl. 1, fig. 3), vein density only slightly diminishing in the narrower part, interstitial strands present, mostly 3 (Pl. 1, fig. 4). The cuticle of its adaxial epidermis (Pl. 2, figs 4, 6, Pl. 3, fig. 9) is quite thick and reflects two kinds of parallel cells. The broader prosenchymatous cells that leave only thin traces of anticlinal walls on the cuticle are 15–20 µm wide and 100–150 µm long or more, parallel with the veins, with rounded

or oblique ends. The shorter cells show darker anticlinal walls in transmitted light, are elongate-quadrangular to rounded in outline, typically 2–3 μm wide and 3–6 μm long, and form simple rows interspaced between the long cells. No stomata were observed on the macerated portions of the adaxial epidermis (Pl. 2, fig. 4). The cuticle of the abaxial epidermis (Pl. 2, figs 5, 6, Pl. 3, fig. 10) is similar in thickness and shows narrow, ca 50 μm wide costal areas and ca 300 μm wide intercostal areas with 10 irregular and incomplete rows of stomata. The long and broad cells in nonstomatal areas are of the same kind as in the adaxial epidermis. The short cells are apparently less elongate than in the adaxial epidermis, serially arranged in the same kind of rows irregularly disposed between stomata. Row length varies between 50 and 200 μm (Pl. 2, fig. 7). The stomata are haplocheilic, mostly longitudinally oriented, consisting of a pair of sunken guard cells ca 25 μm wide and 28 μm long with thickly cutinised dorsal lamellae and surrounded mostly by 2 polar and 4 lateral, partly isodiametric or occasionally elongate subsidiary cells, so that the complete apparatus may reach 90 μm or more in diameter (Pl. 2, figs 2, 3). The stomata are only slightly sunken into very shallow crypts whose openings are polygonal-rounded, slightly swollen on the margins (Pl. 2, fig. 1) and vary in size negligibly. In the size variation of stomata, *C. hofmannii* matches *C. floersheimensis* (Kvaček 2002), and most studied living species.

COMPARISONS

FOSSIL REPRESENTATIVES OF *CERATOZAMIA*

Most of the fossils previously assigned to *Ceratozamia* have been rejected as representatives of this genus. For example, the Eocene *C. wrightii* Hollick from North America (e.g. Hollick 1932, Jones 1993, Whitelock 2002) was transferred together with other cycads from the same locality to the fossil genus *Dioonopsis* on account of the revealed epidermal anatomy (Erdei et al. 2012). The Cretaceous *Jirusia* Bayer was also once considered similar to *Ceratozamia* on account of the associated seed cones of *Microzamia gibba* (Reuss) Corda but revision of it did not confirm this affinity (Kvaček J. 1995, 1997). Its spiny leaflets

are not articulate, remaining attached to the rachis, and its epidermal structure deviates considerably from *Ceratozamia* in having isodiametric polygonal cells rather than elongate cells on both sides of the leaf. *Ceratozamites vicentinus* Meschinelli from the Oligocene of Monte Piano in Italy has not been revised so far, but according to the illustration it likely represents a monocot in Kräusel's opinion (Kräusel 1928, Kvaček 2002). A definitive judgment is impossible because the fossils from Monte Piano and Monte Berico were completely destroyed during a bomb attack in 1944 (Kustatscher et al. 2014).

Thus the only fossil records confirmed by epidermal anatomy and gross morphology to belong to *Ceratozamia* are those noted above from the European lower Oligocene of Germany, Hungary (Kvaček 2002) and Slovenia (Trbovlje – Pl. 1, fig. 7, Pl. 2, fig. 10) as *C. floersheimensis* (Engelhardt) Kvaček, and from the European lower Miocene as *C. hofmannii* (Ettingshausen 1887, 1888, Kvaček 2004). The studied material from North Bohemia is comparable in morphology (almost parallel-sided leaflet fragment) and in the pattern of the epidermal cell structure of the adaxial cuticle with the type specimen of *C. hofmannii* from the Miocene of Austria (re-illustrated in Pl. 1, fig. 1, Pl. 2, fig. 9), a fragment of which was recovered at NHML (Kvaček 2004, fig. 1). The abaxial cuticle newly obtained from the North Bohemian material corresponds in all details of nonstomatal areas with the structures of the holotype (Pl. 2, fig. 9). The Miocene records match the above-mentioned Oligocene fossils in morphology and venation except for the much narrower petiolulate leaflet base (Ettingshausen 1888, pl. 3, fig. 10, Kvaček 2004, fig. 1). The only known more or less complete leaflet of *C. hofmannii* is 170 mm in length when restored and 17 mm in width. Leaflets of *C. floersheimensis* are either sessile (Pl. 1, fig. 7) or broadly attached (Kvaček 2002, fig. 7). The full size is known only in the record from Trbovlje; this lanceolate subfalcate leaflet is 200 mm in length and 25 mm in width (Pl. 1, fig. 7) and shows the epidermal structure (Pl. 2, fig. 10) matching the type material from Flörsheim (Kvaček 2002, figs 10–18). The leaflet attachment shows only a subtle difference between the two species but it may support the proposal to keep the two fossil species apart, suggested also by geobotanical differences

(different accompanying vegetation, geological age) and considering the restricted size and limited areas known for the populations of living species (Whitelock 2004).

COMPARISON WITH EXTANT CYCADS

A wider comparison of leaf epidermal data in the Zamioideae confirms that the only diagnostic trait of foliage in living *Ceratozamia* is the presence of rows of short cells between broader thick-walled prosenchymatous cells in both leaf sides, as previously suggested by Pant & Nautiyal (1963) and Greguss (1968) and confirmed by Kvaček (2002). In no other genus of the Zamioideae, that is, *Zamia* L. (including *Zamia restrepoi*, formerly *Chigua* D. H. Stev.) and *Microcycas* (Miquel) DC, has such a pattern of cell structure been observed. *Microcycas* shows rows of thick-walled and thin-walled cells but differs in the lack of rows of short cells (Pl. 3, figs 15, 16). In *Zamia*, non-modified epidermal cells are very uniformly elongate (Pl. 3, fig. 11) and stomata are also on the level of the epidermis (Pl. 3, fig. 12). Differences in species are expressed in inner anatomical characters (Acuña-Castillo & Marín-Méndez 2012, 2013) as well as epidermal cell patterns (Erdei et al. 2014). As noted above, the Encephalartoideae differ in having non-articulate leaflets. In *Dioon* the short and long cells in the adaxial epidermis are clearly distinguished, as in *Ceratozamia*, but unlike *Ceratozamia* they usually show slightly wavy anticlinal walls and quadrangular outlines. The stomata on the abaxial side of the leaf are deeply sunken in stomatal crypts (Pl. 3, figs 13, 14). *Encephalartos* differs from *Ceratozamia* in having more uniform cell patterns of the adaxial epidermis and nonstomatal areas of the abaxial epidermis. Some species tend to have more isodiametric cells (Erdei et al. 2012). Differences between the species are well expressed in inner anatomical characters and stomatal topography (Koeleman et al. 1981).

Living ceratozamas exceed 25 species (Osborn et al. 2012, Calonje 2013) distributed from wet tropical to warm temperate regions of Mexico along the Sierra Madre Orientale, extending also to Belize, Guatemala, and Honduras (see Vovides et al. 2004a). They are currently divided into several groups and their ecology is partly reflected in the gross morphology of leaves and leaflets (Vovides et al. 2004b). The

type specimen of *C. hofmannii* matches most subfalcate long-acuminate leaflets of the extant group of *C. latifolia*, including *C. kuesteriana* Regel, *C. matudae* Lundell., *C. robusta* Miq., *C. sabatoi* Vovides et al. (Pl. 1, fig. 8), *C. vovidesii* Pérez-Farrera et al., and *C. zaragozae* Medelin (see Pérez-Farrera et al. 2007), and does not compare with species with broad leaflets such as *C. miqueliana* H. Wendland (Pl. 1, fig. 5), *C. becerrae* Vovides et al. (2004c), and *C. zoquorum* Pérez-Farrera et al. Several species with slender-lanceolate leaflets, such as *C. sabatoi*, *C. kuesteriana*, and *C. hildae*, were at first compared with *C. hofmannii* (Kvaček 2004), but the length/width index reveals perhaps a better morphological relationship between the fossil and living species. Of the available living species, *C. microstrobila* Vovides & J.D. Rees (Pl. 1, fig. 5, Pl. 3, figs 1, 2), *C. morettii* Vázquez-Torres & Vovides, *C. latifolia* Miquel (Table 1), and *C. delucana* Vázquez-Torres, Moretti & Carvajal-Hernández (2013) bear leaflets most similar to *C. floersheimensis* and *C. hofmannii*; to the latter also *C. hildae*, a hardy species, which is almost extinct in nature, and also bears leaflets resembling *C. hofmannii*. The mentioned living species also correspond well in their ecological conditions: occupying NE areas of *Ceratozamia* in the Sierra Madre Orientale (states of Tamaulipas, San Luis Potosi and Veracruz), they thrive as understory shrubs in cloud forest and pine-oak forest in the subtropical to warm-temperate zones (14–17°C mean annual temperature), receiving high amounts of precipitation (800–2000 mm) throughout the year. For instance, *Ceratozamia delucana* has been described as undergrowth in habitats of mountain cloud forest, in some aspects similar to the mixed mesophytic and evergreen forests of the European early Miocene. Vázquez-Torres et al. (2013) list as the most representative species of woody elements *Pinus pseudostrobus* Lindl., *P. chiapensis* (Martinez) Andersen, *Clethra mexicana* DC, *Alnus jorullensis* Kunth., *Rapanea myricoides* (Schltdl.) Lundell, *Citharexylum mocinnii* D. Don, *Oreopanax echinops* Decne. & Planch., *Oreopanax xalapensis* Decne. & Planch., *Quercus crassifolia* Bonpl., *Persea schiedeana* Nees, *Smilax bona-nox* L., *Liquidambar macrophylla* Oerst., *Trema micrantha* (L.) Blume and ferns, *Alsophila firma* (Baker) D.S.Conant, *Cyathea bicrenata* Liebm., *Lophosoria quadripinnata* (J.F.Gmel.) C.Chr., and *Polystichum hartwegii* (Klotzsch) Hieron.

Table 1. Mean leaflet size and form in various living species of *Ceratozamia* (adapted from published data and author's observations), compared with leaflets of *Ceratozamia hofmannii* shown in Pl. 1, figs 1, 2 and *C. floersheimensis* from Trbovlje shown in Pl. 1, fig. 7

Taxon	Leaflet length (cm)	Leaflet width (cm)	L/w index	Leaflet form
<i>Ceratozamia alvarezii</i>	16–32.5	0.5–0.9	32–36	linear
<i>Ceratozamia becerrae</i>	17–30	5.2–10	3	broad obovate
<i>Ceratozamia delucana</i>	30–45	2–4	10.2–15	lanceolate, subfalcate
<i>Ceratozamia euryphyllidia</i>	18–31	9–16	2	oblanceolate – broad obovate
<i>Ceratozamia hildae</i>	9–15	1–3	5–9	lanceolate
<i>Ceratozamia kuesteriana</i>	10–22	0.6–1.5	14.6–16.6	narrow lanceolate
<i>Ceratozamia latifolia</i>	20–30	3.3–4.3	6–7	lanceolate, falcate
<i>Ceratozamia matudae</i>	20–38	0.7–1.5	25.3–28.5	linear
<i>Ceratozamia mexicana</i>	28–40	1.5–2	18.6–20	narrow lanceolate – subfalcate
<i>Ceratozamia microstrobila</i>	15–18	2.8–3.2	5.3–5.6	lanceolate
<i>Ceratozamia miqueliana</i>	20–30	5–7	4–4.3	broad oblanceolate
<i>Ceratozamia mirandae</i>	20–50	0.3–0.7	66.6–71.5	linear
<i>Ceratozamia mixeorum</i>	24–39	2.1–2.9	11.4–13.5	narrow lanceolate – subfalcate
<i>Ceratozamia morettii</i>	25–35	2.7–4.8	7.3–9	lanceolate, subfalcate
<i>Ceratozamia norstogii</i>	34–57	0.3–0.5	113–114	linear
<i>Ceratozamia robusta</i>	25–40	2.5–4	10	lanceolate, falcate
<i>Ceratozamia sabatoi</i>	9–29	0.7–2.4	12–12.8	lanceolate
<i>Ceratozamia whitelockiana</i>	30–50	3–3.8	10–13	lanceolate, subfalcate
<i>Ceratozamia zaragozae</i>	5–28	0.4–0.6	12.5–47	linear lanceolate
<i>Ceratozamia zoquorum</i>	23–38.5	3.2–6.5	7.2–5.9	oblong, broad – oblanceolate
<i>Ceratozamia hofmannii</i> , Münzenberg	17	1.75	10	lanceolate, subfalcate
<i>Ceratozamia hofmannii</i> , North Bohemia	(8.5<)	2.3	?	? lanceolate
<i>Ceratozamia floersheimensis</i> , Trbovlje	20	2.6	7.5	lanceolate, subfalcate

However, the morphological traits of leaflets in *Ceratozamia* vary with maturity and the wetness of habitats (Whitelock 2002). Having only isolated fossil leaflets at hand, a more detailed morphological comparison with extant foliage is possible only in part. In fact, the isolated fossil leaflets may not even reflect the mean size, as the variation of whole leaves is not known. The complete leaflets of

C. floersheimensis exceed the Miocene species in length, reaching ca 20 cm. In any case, the living ceratozamia differ by having larger leaflets and mostly exceeding both *C. floersheimensis* and *C. hofmannii* in size (Table 1), although the position of the recovered fossil leaflets within the frond is unknown.

In addition to the leaf epidermal characteristics already known for living species of

Table 2. Stomata density of *Ceratozamia hofmannii* (sample Os16–2, Osek) and selected living Zamiaaceae

Taxon (sample)	Range of stomata number per 0.2 mm ²	Mean number of stomata per 0.2 mm ²
<i>Ceratozamia hofmannii</i> (Os16–2)	5–8	6.5
<i>Ceratozamia microstrobila</i> (cult. MBC – 93790)	6–10	7.5
<i>Ceratozamia zaragozae</i> (cult. MBC – 01183)	6–10	7.8
<i>Ceratozamia hildae</i> (cult. MBC – 937885)	4–6	5.1
<i>Ceratozamia hildae</i> (cult. K – 1978 1827)	4–7	5.5
<i>Ceratozamia norstogii</i> (cult. MBC – 010257)	5–8	6.6
<i>Ceratozamia latifolia</i> (cult. K – Yates s.n.)	4–6	4.7
<i>Ceratozamia sabatoi</i> (BSCH – BD 86 652, Queretaro)	5–8	6.5
<i>Ceratozamia robusta</i> (cult. PRC – s.n. 1)	4–7	5.3
<i>Ceratozamia robusta</i> (cult. PRC – s.n. 2)	5–8	6.8
<i>Ceratozamia kuesteriana</i> (BSCH – BP 86–61.2)	5–9	7.5
<i>Ceratozamia mexicana</i> (cult. K – 1969 – 12158)	4–8	5.9
<i>Microcycas calocoma</i> (cult. MBC – 77404)	8–11	9.4
<i>Zamia standleyi</i> (BSCH – S30)	10–11	10.4
<i>Zamia paucijuga</i> (BSCH – S-937)	11–15	13.3

Ceratozamia (Kvaček 2002), some others are added here (Pl. 3, figs 1–8). In leaf epidermal pattern, some living species differ at first sight in the distribution and length of rows containing short cells. In this respect *C. hofmannii* is typical in having densely set long rows on both the adaxial and abaxial sides of the leaf. However, it is very difficult to identify individual species of *Ceratozamia* on the basis of epidermal structure alone. With the newly obtained data it becomes clear that the living and fossil *Ceratozamia* species show very consistent anatomical features (Pl. 3), and I have not attempted to follow the variation of epidermal features statistically.

Stomatal density, a trait often employed in palaeoclimatic studies (e.g. Kuerschner 1997, Kuerschner et al. 2008), does not vary greatly between species throughout the geographic area of living *Ceratozamia*. A brief survey of *C. hofmannii* and selected living species (Table 2) shows little variation and consistent density, in contrast to the higher stomatal density in *Zamia* and *Microcycas*. Erdei et al. (2014) measured stomatal densities in *Zamia* species cultivated in MBC and found differences showing a relation to phylogeny. A more detailed study of material from the natural habitat is needed to produce more objective datasets.

The external micromorphology in living *Ceratozamia* often shows an epicuticular wax coating forming reticulate ridges or granules (Erdei et al. 2010, Barone Lumaga et al. 2012). This feature was not observed in the studied fossil material.

COMMENTS ON OTHER FOSSIL CYCADS

Besides *Ceratozamia*, only extinct genera or uncertain taxa are known in the fossil state in the European Cenozoic, unlike in Asia, where fossils belonging to *Cycas* have also been found (Yokoyama 1911, Su et al. 2014), and unlike in the Southern Hemisphere with diverse fossil representatives of *Macrozamia*, *Lepidozamia*, and *Bowenia* (see e.g. Cookson 1953, Hill 1978, Pant 1987). Not all of the previously described *Zamia*-like fossils could be corroborated as *Zamia*. However, a new fossil is going to be described as *Zamia* from the Eocene of Panama (Erdei et al. 2014). The European records belong mostly to groups with nonarticulate leaflets. *Pseudodioon* Erdei et al. (2010) from the Miocene of Turkey shares isodiametric

cells in the adaxial epidermis with *Dioonopsis* Horiuchi & Kimura (1987) known from the Palaeogene of Japan and the USA (Erdei et al. 2012) but differs in having a coronal rim around the stomata. In Europe a few records belong to the Zamiaceae with pinnate venation of the leaflets, namely *Eostangeria* Barthel (Eocene of Germany – Barthel 1976, Miocene of Austria – Jechorek & Kovar-Eder 2004, Bulgaria – Uzunova et al. 2001). Other foliage remains and other organs of cycads recovered in the Cenozoic of Europe (Kräusel 1928) have not been revised yet and have not yielded epidermal traits (see e.g. Kvaček & Velitzelos 2000, Kvaček & Walther 2004). Fossil wood from the Miocene of Poland and assigned to *Cycadoxylon czeczottiae* Zalewska (1956) was recognised, together with similar wood from the Miocene of Germany, as cupressoid by Greguss (1973, as *Pseudotaxodioxylon*). Outside Europe, *Eostangeria* was also present in the North American Eocene (Kvaček & Manchester 1999).

A full review of the cycad records will not be given here. However, it is worth noting that an extinct Argentinian cycad, *Almargemia incrassata* Archangelsky (1966) from the Lower Cretaceous, shows rows of short cells in the epidermis of either leaf side in a manner similar to *Ceratozamia*.

CONCLUSIONS ON PHYTOGEOGRAPHY AND PALAEOCLIMATE

Ceratozamia represents one of the rare Cenozoic plant disjunctions between Central America and Europe, besides, for example, *Matudaea* – Walther 1980, *Engelhardia* sect. *Palaeocarya* and *Oreomunnea* – Jähnichen et al. 1977, *Tetrapterys* – Hably & Manchester 2000, *Anacardium* – Collinson et al. 2012, *Cyclanthus* – Smith et al. 2008 or *Sabal* – see Manchester 1999, proving that these two land masses were once so near or so connected with island chains that cycads and other plants were able to migrate between them (Denk et al. 2011). The latest fossil record of *Ceratozamia* in Europe comes from the late early Miocene, although extinct cycads (*Eostangeria* – Uzunova et al. 2001, Jechorek & Kovar-Eder 2004, Erdei et al. 2012) persisted there still later to the middle Miocene. According to leaflet morphology and texture as well the accompanying vegetation, the European representatives

of *Ceratozamia* may have thrived there under climatic conditions similar to those of living *Ceratozamia* species presently occupying the northern parts of the distribution of the genus in extratropical Mexico (e.g. *C. microstrobila* in San Luis Potosi State and adjacent regions – Vovides et al. 2004 a, b). However, the nearest living relatives may deviate from the fossil equivalents in autecology (Kvaček 2007). The record of *Ceratozamia* in the lower Miocene of North Bohemia well fits the early stage of the Miocene Climatic Optimum in Central Europe, as suggested by accompanying plant assemblages of pine-laurel evergreen forest (Mach et al. 2014). The Oligocene populations, in particular those in Hungary (Hably & Fernandez Marron 1998), were likely adapted to less humid conditions. The presented fossil records may challenge estimates made from the molecular clock, giving the time of diversification for *Ceratozamia* as the late Miocene (Nagalingum et al. 2011, Renner 2011, Rull 2012).

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PLATES

Plate 1

1. *Ceratozamia hofmannii* Ettingsh., holotype re-illustrated from Ettingshausen (1888, pl. 3, fig. 10; fragmentary part preserved at NHML – see Kvaček 2004, fig. 1), Münzenberg, Austria, lower Miocene, scale bar = 10 mm
- 2–8. *Ceratozamia hofmannii* Ettingsh., Osek, drill core Os 16, depth 79.2 m, North Bohemia, Czech Republic, uppermost lower Miocene
 2. Preserved part of recovered leaflet impression/compression, coll. NM G 9465 a, scale bar = 10 mm
 3. Magnified surface of specimen in fig. 2, showing venation pattern with costal and intercostal areas, scale bar = 5 mm
 4. Detail of middle part of leaflet lamina separated from specimen in fig. 2, showing parallel veins and interstitial strands in transmitted light, coll. Charles University, Faculty of Science, Os16–2, scale bar = 2 mm
5. *Ceratozamia microstrobila* Vovides & J.D. Rees, leaflet of species group with slender leaflets from NE Mexico, cult. MBC, scale bar = 10 mm
6. *Ceratozamia floersheimensis* (Engelhardt) Kvaček, holotype, lignified compression of leaflet (re-illustrated from Kvaček 2002) Flörsheim, Germany, lower Oligocene, coll. SM B 17228, scale bar = 10 mm
7. *Ceratozamia floersheimensis* (Engelhardt) Kvaček, newly recognised record, lignified compression of leaflet, Trbovlje (former Trifail), Slovenia, lower Oligocene, coll. GBA 2006/84/501, scale bar = 10 mm
8. *Ceratozamia sabatoi* Vovides et al., leaflet of species group with linear leaflets, Querétaro, coll. *Schutzmann BD 86-65.2*, scale bar = 10 mm
9. *Ceratozamia miqueliana* H. Wendland, leaflet of species group with broad leaflets from tropical habitats in S Mexico, cult. MBC, scale bar = 10 mm

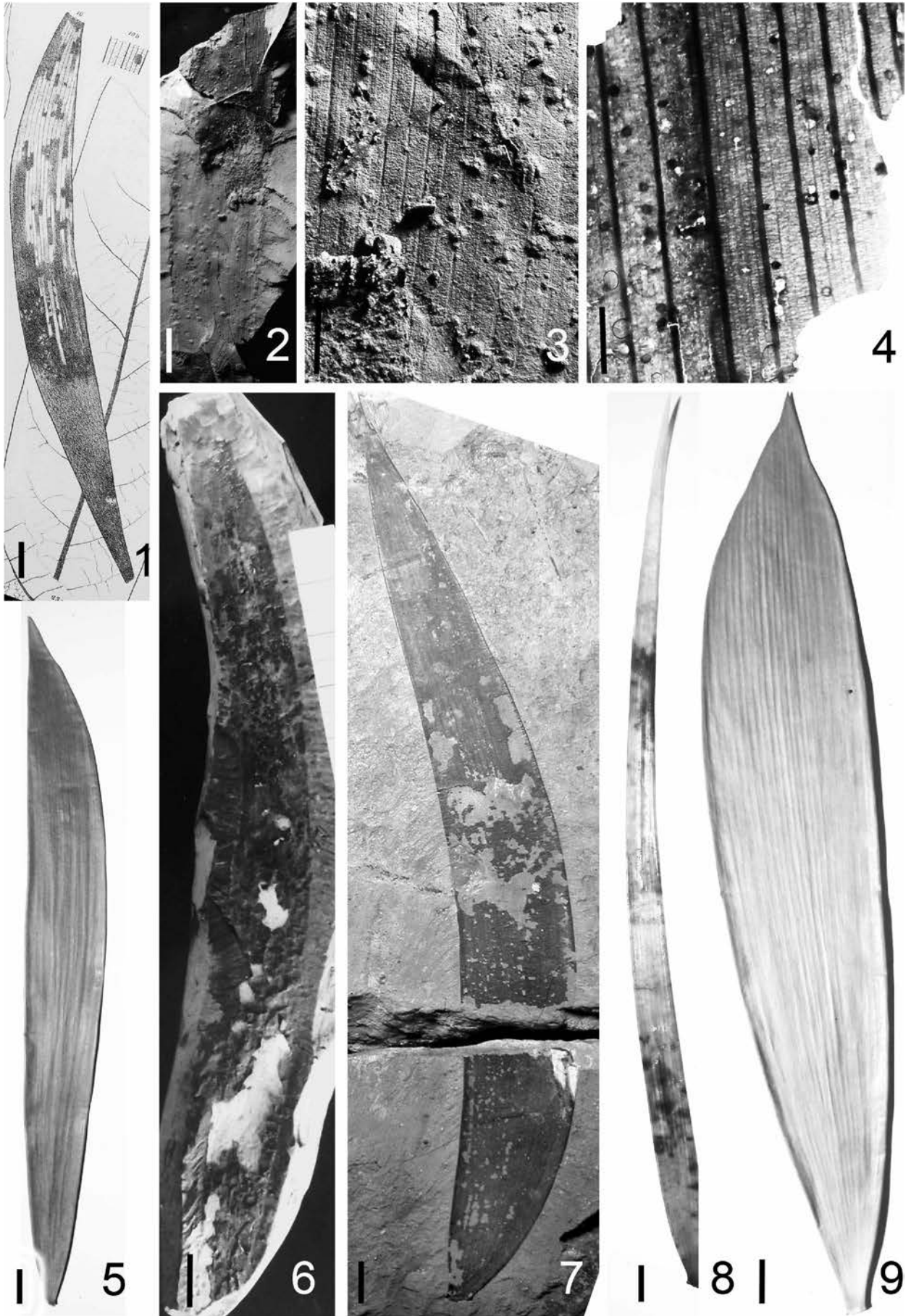


Plate 2

- 1–8. *Ceratozamia hofmannii* Ettingsh., Osek, drill core Os 16, depth 79.2 m, North Bohemia, Czech Republic, uppermost lower Miocene (NM G 9465)
 1. Outer surface of abaxial cuticle with openings of stomatal crypts, SEM micrograph, scale bar = 20 μm
 2. Inner view of stoma, showing inner lamellae, subsidiary cells and adjacent cell pattern, scale bar = 20 μm
 3. Inner view of stoma, showing inner lamellae, scale bar = 10 μm
 4. Outer surface of adaxial cuticle, scale bar = 100 μm
 5. Inner surface of abaxial cuticle with stomata and cell patterns over intercostal areas, scale bar = 100 μm
 6. Adaxial cuticle in transmitted light, showing characteristic pattern of short and long cell structure, scale bar = 100 μm
 7. Abaxial cuticle in transmitted light with stomata and rows of short cells, scale bar = 100 μm
 8. Overall view of abaxial cuticle with distinctly demarcated costal and intercostal areas, scale bar = 300 μm
9. *Ceratozamia hofmannii* Ettingsh., adaxial cuticle, duplicate preparation from holotype (NHML), scale bar = 100 μm
10. *Ceratozamia floersheimensis* (Engelhardt) Kvaček, abaxial cuticle from specimen shown in Pl. 1, fig. 7, scale bar = 100 μm

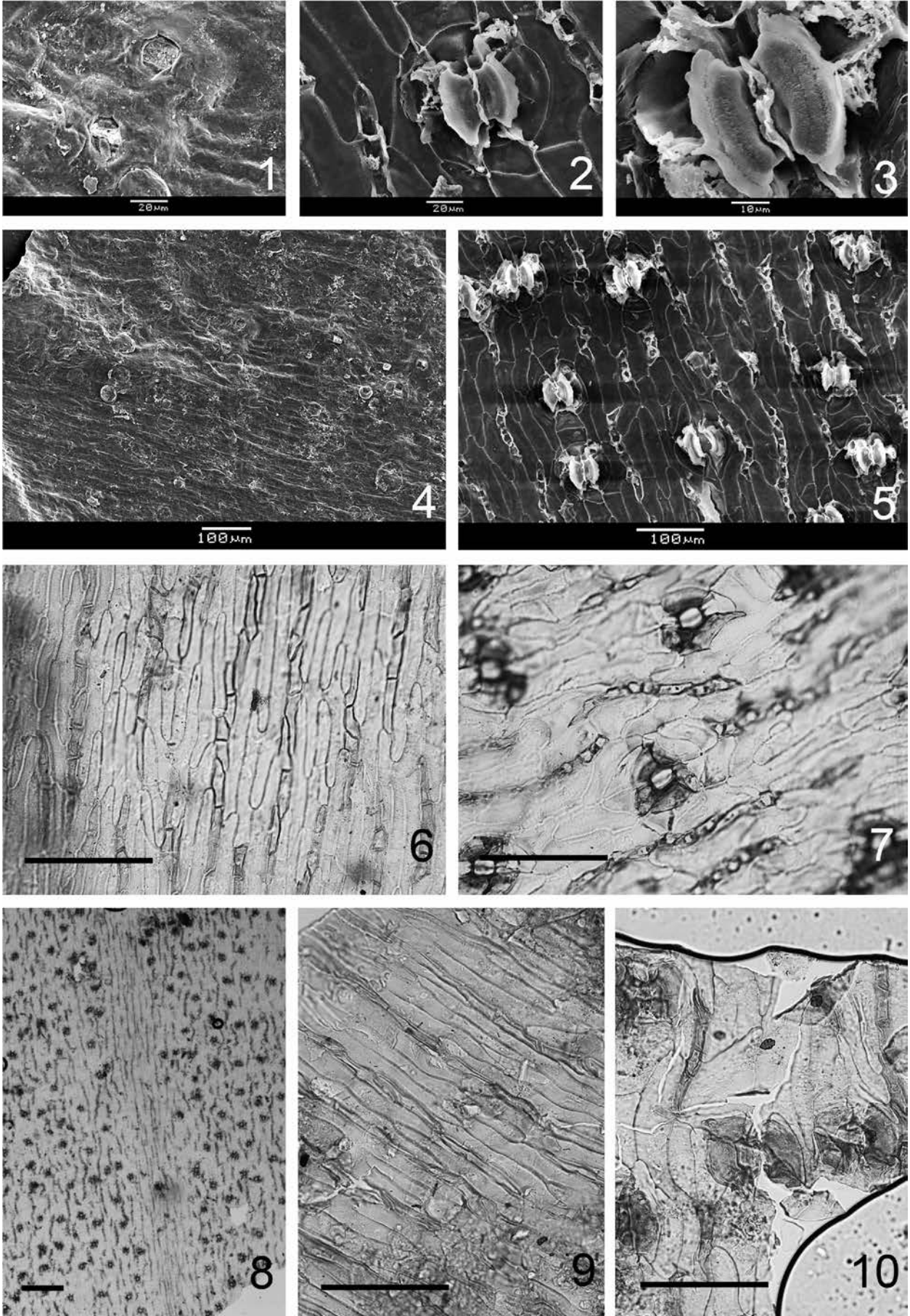


Plate 3

1, 2. *Ceratozamia microstrobila* Vovides & J.D. Rees, cult. MBC

1. Adaxial epidermis with long thick-walled cells and narrower rows of short cells
2. Abaxial epidermis with amphicyclic stomata and rows of long and short narrower cells

3, 4. *Ceratozamia mexicana* Brongn., cult. K

3. Adaxial epidermis with long thick-walled cells and narrower rows of short cells
4. Abaxial epidermis with incompletely amphicyclic stomata and rows of long and short narrower cells

5, 6. *Ceratozamia sabatoi* Vovides et al., Querétaro, coll. *Schutzmann* BD 8665.2

5. Adaxial epidermis with long thick-walled cells and narrower rows of short cells
6. Abaxial epidermis with monocyclic stomata and rows of long and short narrower cells

7, 8. *Ceratozamia norstogii* D. W. Stev., cult. MBC

7. Adaxial epidermis with long cells and rows of short cells
8. Abaxial epidermis with incompletely amphicyclic stomata and rows of long and short narrower cells

9, 10. *Ceratozamia hofmannii* Ettingsh., Osek, Os16-2

9. Adaxial epidermis with long cells and rows of short cells
10. Abaxial epidermis with incompletely amphicyclic stomata and rows of long and short narrower cells

11, 12. *Zamia paucijuga* Wieland, coll. *Schutzman* S-55, Mexico

11. Adaxial epidermis with uniform pattern of narrow elongate cells
12. Abaxial epidermis with incompletely amphicyclic stomata and rows of nondifferentiated cells

13, 14. *Dioon edule* Lindl., cult. PRC

13. Adaxial epidermis with rows of shorter quadrangular and longer thick-walled cells
14. Abaxial epidermis with incompletely amphicyclic, deeply sunken stomata in crypts and rows of nondifferentiated cells

15, 16. *Microcycas calocoma* (Miq.) DC., cult. MBC

15. Adaxial epidermis with long elongate thick-walled and narrower thin-walled cells
16. Abaxial epidermis with incompletely amphicyclic stomata and rows of thick-walled and thin-walled cells

Scale bar = 100 μ m

