First cycad seedling foliage from the fossil record and inferences for the Cenozoic evolution of cycads

Boglárka Erdei¹, Mario Coiro², Ian Miller³, Kirk R. Johnson⁴, M. Patrick Griffith⁵ and Vickie Murphy⁵

¹Botanical Department, Hungarian Natural History Museum, Könyves K. krt. 40, Budapest 1087, Hungary
²Department of Systematic and Evolutionary Botany, University of Zürich, Zollikerstrasse, 107 8008 Zürich, Switzerland
³Denver Museum of Nature and Science, 2001 Colorado Boulevard, Denver, CO 80205, USA
⁴Smithsonian National Museum of Natural History, 10th Street, Constitution Avenue North West, Washington, DC 20560, USA
⁵Montgomery Botanical Center, 11901 Old Cutler Road, Coral Gables, FL 33156, USA

The morphology of the early ontogenetic stages of cycad foliage may help resolve the relationships between extinct to extant cycad lineages. However, prior to this study, fossil evidence of cycad seedlings was not known. We describe a compression fossil of cycad eophylls with co-occurring fully developed leaves of adult specimens from the early Palaeocene (ca 63.8 Ma) Castle Rock flora from the Denver Basin, CO, USA and assign it to the fossil genus Dioonopsis (Cycadales) based on leaf morphology and anatomy. The new fossil seedling foliage is particularly important because fully differentiated pinnate leaves of adult plants and the eophylls belong to the same species based on shared epidermal micromorphology, therefore, increasing the number of morphological characteristics that can be used to place Dioonopsis phylogenetically. Significantly, the seedling fossil has a basic foliage structure that is very similar to seedlings of extant cycads, which is consistent with a cycadalean affinity of Dioonopsis. Nevertheless, the set of morphological characters in the seedling and adult specimens of Dioonopsis suggests a distant relationship between Dioonopsis and extant Dioon. This indicates that extinct lineages of cycads were present and widespread during the early Cenozoic (Palaeogene) coupled with the subordinate role of extant genera in the Palaeogene fossil record of cycads.

1. Introduction

The evolution of cycads is a topic that fascinates an increasing number of researchers and avocational cycad enthusiasts. With 355 modern species in 10 genera [1], cycads have long been seen as relics of a once flourishing and diverse group of plants [2]. Recent molecular phylogenetic studies, however, infer a late Palaeogene/Neogene origin and a late Miocene radiation for most extant genera [3,4] with only half of this diversity confirmed in the fossil record [5].

Fossils that show the early ontogenetic stages of plants may preserve important morphological characters to facilitate our understanding of the evolution of and relationships between extinct groups. These early stages, especially seedlings, are rarely fossilized. Among gymnosperms, seedlings have been reported only in few groups including scarce araucariaceous, taxodiaceous and pinaceous seedlings, and a few seedlings inferred as belonging to Welwitschia, ginkgophytes and glycospermapods [6–14].
Herein, we present the first fossil record of a cycad seedling found in close association with a leaf flush of an adult cycad plant of the same species (figure 1). The leaves of two ontogenetic stages, the eophylls (the first foliage) and the fully differentiated pinnate leaves of adult plants, are documented by macromorphological and epidermal features and assigned to the extinct genus, *Dioonopsis*. Based on the gross morphological similarity of the fully differentiated leaves, *Dioonopsis* has traditionally been assigned to the lineage leading to the extant cycad genus, *Dioon* [15,16], which lacks a fossil record. The new fossil seedling sheds light on the evolutionary relationship between *Dioonopsis* and extant cycads (*Dioon*).

2. Material and methods

Seedling foliage, a slab with numerous fully differentiated leaves of an adult plant, and many detached leaves assigned to cycads were reported among the fossils from the early Palaeocene (Danian; radiometrically dated at 63.84 ± 0.06 Ma) Castle Rock flora in the Denver Basin, CO, USA ([17–19]; electronic supplementary material, figures S1 and S2). The detailed investigation of these fossils is presented here for the first time. The specimens are housed in the palaeobotanical collection of the Denver Museum of Nature and Science, Denver, CO, USA (seedling fossil and its counterpart—DMNH15662, locality DMNH1200; fossil foliage of adult plants—DMNH15683 (leaf flush), DMNH15674, DMNH8993, locality DMNH1200).
Seedling macromorphology of extant cycad genera was examined for comparison (electronic supplementary material, table S1). Epidermal characters of the fossil foliage were studied using epifluorescence and transmitted light microscopy. The geology of the locality, the associated Castle Rock megafossil, detailed descriptions, inventories, storage and additional images of studied fossil cycad material and the methods applied for the investigation of epidermal characters on the fossils are discussed in the electronic supplementary material.

A matrix including 15 leaf morphological and cuticular characters, 10 characters modified from Martinez et al. [20] and five new characters (electronic supplementary material, note S1 and table S2), was scored for all extant genera of cycads and Dioonopsis based on new character observations from the Castle Rock fossils and data from previous matrices and observations [21]. The most parsimonious placement of Dioonopsis on a phylogenetic tree based on [4] was tested by moving the taxon by hand in Mesquite [22] on a backbone phylogeny based on the results of the analyses of Salas-Leiva et al. [4], testing all possible placements of the fossil. Moreover, we conducted a maximum-parsimony analysis using PAUP v. 4.10 [23]. Most parsimonious trees were obtained using exhaustive enumeration of the trees compatible with the backbone constraint topology from Salas-Leiva et al. [4], and 1000 bootstrap replicates were run using the same constraint and a heuristic search strategy. A consensus network of the bootstrap trees was generated using SplitsTree [24] applying a 15% cut-off. We also conducted a Bayesian analysis using MrBayes v. 3.2.6 [25]. The Markov-k model with correction for variable characters and a gamma-distributed rate variation was applied. The topology from Salas-Leiva et al. [4] was used as a backbone constraint. Two independent runs with four chains (one cold, three heated) were run for 10 000 000 generations. After discarding 25% of each run as burn-in, the runs were combined and a consensus network was generated using SplitsTree applying a 15% cut-off.

3. Results and discussion

We assign the fossil foliage of adult specimens, including approximately 25 whole leaves in a single flush and many detached whole and partial leaves, to Dioonopsis praespinulosa described previously from the Palaeogene of Alaska [16] based on both macro- and micromorphology of the leaves (figure 1; electronic supplementary material, figures S3 and S4). The following characters support this taxonomic assignment: pinnate leaves; sub-opposite leaflets inserted with broad, decurrent bases laterally on rachis sides; a single order of parallel veins, which frequently dichotomize and locally form N-shaped anastomoses (i.e. neighbouring parallel veins traversed by a steep vein); isodiametric epidermal cells, cycloptic stomata randomly arranged on the lower side of the leaves with four to seven radially arranged subsidiary cells. The 25 associated fully differentiated pinnate leaves (figure 1f), which presumably represents one leaf flush, indicate a plant with approximately 1-m-long generated using SplitsTree applying a 15% cut-off. Finally, the extinct foliage type, Ctenis, typically reported from Mesozoic floras, but also found in early Cenozoic floras of North America [26], is distinguished by having leaves with, in many cases, irregularly segmented leaflets with a high frequency of vein anastomoses. Compared to extant members of Cycadales, Dioonopsis is distinguished by its N-shaped vein anastomoses.

The eophylls are paripinnate having two pairs of leaflets, which bear teeth on the apical margin and frequently dichotomizing parallel veins (figure 1; electronic supplementary material, figure S3). Veins sporadically anastomose as well, forming N-shape cross-connections similar to those of fully differentiated pinnate leaves of adult plants. Based on shared venation characteristics (anastomoses) and epidermal features (figure 1; electronic supplementary material, figure S5), the eophylls represent the juvenile stage of D. praespinulosa. Detailed descriptions of the fossil specimens and additional photo documentation are given in the electronic supplementary material.

4. Nomenclature

Dioonopsis praespinulosa (Hollick) Erdei, Manchester et Kvaček, emend. nov. Erdei

Genus: Dioonopsis Horiiuchi et Kimura, Review of Palaeobotany and Palynology, 51:217, 1987. Species: Dioonopsis praespinulosa (Hollick) Erdei, Manchester et Kvaček, International Journal of Plant Sciences 173(1):83, figs 1–3a, 4 and 5, 2012, lectotype USNM38688b, figs 2d–e, 4a–d.

The emended diagnosis of Dioonopsis praespinulosa, given by Erdei, Manchester and Kvaček, International Journal of Plant Sciences 173(1):83, is completed by adding the description of the eophylls (DMNH15662, Denver Museum of Nature and Science, Denver, CO, USA; figure 1a–d, electronic supplementary material, figures S3d,e and S5a–e).

Emendation of the diagnosis: Eophyll paripinnate, with few pairs of leaflets, leaflets obovate, apex slightly rounded, base decurrent, acute teeth on the apical one-third of lamina; 8–10 parallel veins entering leaflets, veins frequently dichotomize in the apical half of lamina, some veins sporadically anastomose forming N-shape; lamina hypostomatic, stomata cycloptic, scattered, guard cells sunken, surrounded by four to seven subsidiaries, coronal rim formed around stomata, anticlinal walls isodiametric.

We surveyed the macromorphology of extant cycad seedlings and compared them to the seedling of Dioonopsis praespinulosa (figure 2; electronic supplementary material, table S1). The basic morphology of the D. praespinulosa eophylls closely resembles the eophylls of several extant cycads (e.g. Encephalartos), which is consistent with the cycadalean affinity of Dioonopsis. The eophylls of D. praespinulosa differ most strongly from those of Cycas and Stangeria, which have prominent midribs. In the majority of the extant members of Zamiaceae, which includes all extant cycad genera except Cycas, the eophylls and the fully differentiated leaves of adult plants of the same species have similar gross morphology. For instance, the eophyll and the fully differentiated leaves of adult specimens of most Dioon species are nearly indistinguishable. When differences do occur, they usually involve the shape of the leaflet (e.g. the eophylls of some Zamia and Encephalartos...
species, i.e. E. ferox, Z. furfuracea, are more ovate) or the frequency of teeth or spines on the leaflet margins as in some Dioon and Encephalartos species (e.g. D. merolae, E. kisambo). Finally, as seen in some Ceratozamia, Encephalartos and Zamia species, eophylls have considerably fewer leaflet pairs than the fully differentiated foliage of adult specimens has.

In contrast to many species of Zamiaceae, the seedling of Dioonopsis has eophylls that differ markedly in leaflet shape, margin and number of leaflets from the fully differentiated leaves of adult plants. The morphological disparity of the seedling and the adult foliage of Dioonopsis may be compared to that of some Encephalartos species (figure 2).

The venation of both eophylls and the fully differentiated leaves of Dioonopsis differs significantly from all extant cycads. In particular, the veins anastomose to form an N-configuration—a consistent and distinctive character of both eophylls and fully differentiated foliage of adult plants of Dioonopsis [16,28]. Although this venation pattern does not appear in extant cycads, it is shared by fossil foliage assigned to Cycadales (e.g. Ctenis [28] and Pterostoma [27]) implying that an extinct lineage or lineages of cycads with similar venation patterns lived during the Mesozoic (Ctenis) and persisted into the Palaeogene (Dioonopsis, Pterostoma).

Among extant cycads, Dioon has been inferred to be related to the extinct Dioonopsis based on their shared gross morphology of leaves (parallel-veined leaflets with broad bases inserted laterally to the rachis) [15]. However, these genera are easily distinguished by leaf venation and epidermal characters (electronic supplementary material, table S2; [29]) and by the morphology of their seedlings. In fact, the contrasting morphological characters of the seedlings and adult specimens of Dioonopsis and Dioon suggest a distant relationship between these genera.

When considered in a phylogenetic context, our analysis indicates the placement of Dioonopsis outside Zamiaceae with both MP bootstrap and Bayesian posterior probability supporting this placement (figure 2). Similar results are obtained looking at the most parsimonious placement of the fossil, with only a placement close to Stangeria, being one step less parsimonious, which is due mostly to a reversal of typical zamiaceous characters in the lineage leading to Stangeria (loss of elongate cells, irregular orientation of the stomata).

A close relationship between Dioonopsis and Dioon retrieved in some previous phylogenetic analyses [20,21,30] is due mostly to the coding of Dioonopsis as having two layers of encircling cells (an autapomorphy of Dioon [29]), longitudinally

---

**Figure 2.** Comparison of eophylls of extant cycads and extinct Dioonopsis (a–h). (a) Dioon merolae. (b) Encephalartos ferox. (c) Encephalartos transvenosus. (d) Zamia furfuracea. Line drawings of cleared eophyll leaflets of extant cycads and extinct Dioonopsis showing venation details. (e) Zamia furfuracea. (f) Dioon spinulosum. (g) Encephalartos hildebrandtii. (h) Dioonopsis praespinulosa. Scale bars: (a–h) 1 cm. (i) Number of steps needed for placing Dioonopsis on the molecular backbone topology. MP indicates the most parsimonious placements. (j) Consensus network showing support for the placement of Dioonopsis from the maximum-parsimony bootstrap and the Bayesian inference posterior probability. The two stronger splits are shown. (Online version in colour.)
oriented stomata (a potential synapomorphy of Zamiaceae [21]) and anticlinal plugs. These characters are clearly absent from all species of Dioonopsis and were probably originally miscoded based on some ambiguity in the original description [15].

The fossil genus and species, Dioonopsis nipponica, were established to accommodate cycad leaves with well-preserved epidermal details from the Palaeocene Noda Group of northeast Honshu, Japan [15]. Following the description of this material, Eocene cycad fossils from Alaska and California that were previously argued to be related to Cenotazamia and Dioon were found to belong to Dioonopsis [16]. The disjunct biogeographic distribution of Dioonopsis was interpreted as the consequence of spreading via the Beringia phytogeographic pathway [16]. The occurrence of D. prae_spinulosa in the Castle Rock flora (ca 63.8 Ma) further expands the North American distribution of Dioonopsis during the Palaeogene. Nevertheless, it does not offer additional clues about the place of origin of the genus because Dioonopsis appears roughly simultaneously, during the Palaeocene, in the fossil record of Japan and North America. However, the megafossils accompanying Dioonopsis do provide information on the ecological tolerance of the genus. In particular, the Castle Rock flora has been argued to be a high diversity, subtropical rainforest [31], whereas the Alaskan floras, although the Yakutat tectonic block was probably located further south [32], suggest more temperate conditions [16]. Assuming that, during the Palaeocene, Dioonopsis achieved higher palaeolatitudes (the Beringian passage) estimated at 75°–80° N, its adaptation to extreme light variations [16] was probably established, similarly to some extinct Southern Hemisphere cycads [33]. Considering these ecological factors, Dioonopsis had an ecological tolerance greater than any extant cycad genus.

Although there are rare examples of fossil cycads for which organs of the same genus or species were reported as associated (e.g. Antarctica cycas [33]), the early and late ontogenetic stages of Dioonopsis prae_spinulosa that are preserved in the early Palaeocene Castle Rock flora are unprecedented. Even though there is an extensive record of extinct cycads [15,16,26–28,34–39], fossil data are commonly limited to adult leaves making a comparison to extant genera challenging. The co-occurring eophylls and fully developed adult foliage of D. prae_spinulosa allow for a much more complete analysis of Dioonopsis and its phylogenetic placement in Cycadales. Our work confirms that Dioonopsis belongs to an extinct lineage of cycads outside Zamiaceae. This pattern corroborates that today unknown cycad lineages flourished during the early Cenozoic (Palaeogene) [5]. The apparent scarcity of modern forms in both the Palaeogene and Mesoozoic fossil record of cycads may be interpreted by a younger evolutionary radiation of modern cycads [3]. Nevertheless, the Cenozoic history of cycads is far from being resolved and requires additional fossil data.

References

1. Calonje M, Stevenson DW, Stanberg L. 2017 The World List of Cycads. See http://www.cycadlist.org.
2. Norstog KJ, Nichols TJ. 1997 The biology of the cycads. Ithaca, NY: Cornell University Press.
3. Nagalisingum NS, Marshall CR, Quental TB, Rai HS, Little DP, Mathews S. 2011 Recent synchronous radiation of a living fossil. Science 334, 796–799. (doi:10.1126/science.1209926)
4. Salas-Leiva DE, Meerow AW, Calonje M, Griffith MP, Francisco-Ortega J, Nakamura K, Stevenson DW, Lewis CE, Namoff S. 2013 Phylogeny of the cycads and evolutionary relationships of the Cerro Azul fossil cycad seedling. Am. J. Bot. 100. 1294–1310. (doi:10.3732/ajb.120123)
5. B. E. led the acquisition, made fossil analysis and interpretation of data and drafted the manuscript, M.C. contributed to phylogenetic analysis and its interpretation, I.M. and K.J. made fossil collections and provided field data and figures. P.G. and V.M. provided and studied available fresh seedling material. All authors helped draft the manuscript, made substantial contributions to writing the paper, gave final approval for publication and agree to be held accountable for the work performed.
6. Acknowledgements. B.E. is grateful to the Montgomery Botanical Center for hosting this research and providing modern cycad material for comparisons, Steven Manchester (Florida Museum of Natural History) for access to laboratory infrastructure, Agnieszka Sojka for technical assistance and to anonymous referees for their helpful comments.

Data accessibility. Specimens studied are housed in the palaeobotanical collection of the Denver Museum of Nature and Science, Denver, CO. Full details of studied material, methodology and the associated fossil data are provided in the electronic supplementary material. The matrix used in this study is available on FigShare (https://figshare.com/s/5fa006b87655e89bb619e).

Authors’ contributions. B.E. led the acquisition, made fossil analysis and interpretation of data and drafted the manuscript, M.C. contributed to phylogenetic analysis and its interpretation, I.M. and K.J. made fossil collections and provided field data and figures. P.G. and V.M. provided and studied available fresh seedling material. All authors helped draft the manuscript, made substantial contributions to writing the paper, gave final approval for publication and agree to be held accountable for the work performed.

Funding. Research was supported by an HAESF long-term fellowship and NKFIH project (K108664, K120123) to B.E. and by NSF awards (DBI 1205242 and DBI 1561346) to M.P.G.

Acknowledgements. B.E. is grateful to the Montgomery Botanical Center for hosting this research and providing modern cycad material for comparisons, Steven Manchester (Florida Museum of Natural History) for access to laboratory infrastructure, Agnieszka Sojka for technical assistance and to anonymous referees for their helpful comments.

References

1. Calonje M, Stevenson DW, Stanberg L. 2017 The World List of Cycads. See http://www.cycadlist.org.
2. Norstog KJ, Nichols TJ. 1997 The biology of the cycads. Ithaca, NY: Cornell University Press.
3. Nagalisingum NS, Marshall CR, Quental TB, Rai HS, Little DP, Mathews S. 2011 Recent synchronous radiation of a living fossil. Science 334, 796–799. (doi:10.1126/science.1209926)
4. Salas-Leiva DE, Meerow AW, Calonje M, Griffith MP, Francisco-Ortega J, Nakamura K, Stevenson DW, Lewis CE, Namoff S. 2013 Phylogeny of the cycads and evolutionary relationships of the Cerro Azul fossil cycad seedling. Am. J. Bot. 100. 1294–1310. (doi:10.3732/ajb.120123)
5. B. E. led the acquisition, made fossil analysis and interpretation of data and drafted the manuscript, M.C. contributed to phylogenetic analysis and its interpretation, I.M. and K.J. made fossil collections and provided field data and figures. P.G. and V.M. provided and studied available fresh seedling material. All authors helped draft the manuscript, made substantial contributions to writing the paper, gave final approval for publication and agree to be held accountable for the work performed.

Acknowledgements. B.E. is grateful to the Montgomery Botanical Center for hosting this research and providing modern cycad material for comparisons, Steven Manchester (Florida Museum of Natural History) for access to laboratory infrastructure, Agnieszka Sojka for technical assistance and to anonymous referees for their helpful comments.

References

1. Calonje M, Stevenson DW, Stanberg L. 2017 The World List of Cycads. See http://www.cycadlist.org.
2. Norstog KJ, Nichols TJ. 1997 The biology of the cycads. Ithaca, NY: Cornell University Press.
3. Nagalisingum NS, Marshall CR, Quental TB, Rai HS, Little DP, Mathews S. 2011 Recent synchronous radiation of a living fossil. Science 334, 796–799. (doi:10.1126/science.1209926)
4. Salas-Leiva DE, Meerow AW, Calonje M, Griffith MP, Francisco-Ortega J, Nakamura K, Stevenson DW, Lewis CE, Namoff S. 2013 Phylogeny of the cycads and evolutionary relationships of the Cerro Azul fossil cycad seedling. Am. J. Bot. 100. 1294–1310. (doi:10.3732/ajb.120123)
5. B. E. led the acquisition, made fossil analysis and interpretation of data and drafted the manuscript, M.C. contributed to phylogenetic analysis and its interpretation, I.M. and K.J. made fossil collections and provided field data and figures. P.G. and V.M. provided and studied available fresh seedling material. All authors helped draft the manuscript, made substantial contributions to writing the paper, gave final approval for publication and agree to be held accountable for the work performed.

Acknowledgements. B.E. is grateful to the Montgomery Botanical Center for hosting this research and providing modern cycad material for comparisons, Steven Manchester (Florida Museum of Natural History) for access to laboratory infrastructure, Agnieszka Sojka for technical assistance and to anonymous referees for their helpful comments.
15. Hortuchi J, Kimura T. 1987 Dioonopsis gen. et sp. nov., a new cycad from the Palaeogene of Japan. Rev. Palaeobot. Palynol. 51, 213 – 225. (doi:10.1016/0034-6667(87)90031-5)

16. Erdei B, Manchester SR, Kvacˇ Z. 2012 Dioonopsis Hortuchi et Kimura leaves from the Eocene of Western North America: a cycad shared with the Palaeogene of Japan. Int. J. Plant Sci. 173, 81 – 95. (doi:10.1086/662654)

17. Ellis B, Johnson KR, Dunn RE. 2003 Evidence for an in situ early Paleocene rainforest from Castle Rock, Colorado. Rocky Mount. Geol. 38, 73 – 100. (doi:10.2113/gyrocky.38.1.173)

18. Miller IM, Johnson KR, Ellis B. 2007 A complete cycad plant from the Castle Rock rainforest: implications for the evolution and paleodistribution of American Zamiaceae. In Abstract 24th Annual Mid-Continent Paleobotanical Colloquium, Southern Methodist University, March 16 – 18.

19. Kowalczyk JB et al. 2018 Multiple proxy estimates of atmospheric CO2 from an early Paleocene rainforest. Palaeoecol. Palaeoclim. 33, 1427 – 1438. (doi:10.1029/2018PA003356)

20. Martinez LCA, Artabe AEE, Bodnar J. 2012 A new cycad from the Palaeogene of Japan. J. Geol. 119, 254 – 267. (doi:10.1093/mobio/mjs030)

21. Ronquist F, Huelsenbeck JP. 2003 MRBAYES 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19, 1572 – 1574. (doi:10.1093/bioinformatics/btg180)

22. Erdei B, Akgu¨n F, Barone Lumaga MR. 2010 Pseudodioon akyoli gen. et sp. nov., an extinct member of Cycadales from the Turkish Miocene. Plant. Syst. Evol. 285, 33 – 49. (doi:10.1007/s00606-009-0253-x)

23. Hill RS. 1980 Three new Eocene cycads from eastern Australia. Austr. J. Bot. 28, 105 – 122. (doi:10.1071/BT9800105)

24. Erdei B, Manchester SR. 2015 Ctenis clarnoensis sp. n., an unusual cycadalean foliage from the Eocene Clarno Formation, Oregon. Int. J. Plant Sci. 176, 31 – 43. (doi:10.1086/678467)

25. Barone LMR, Coiro M, Truernit E, Erdei B, De Luca P. 2015 Epidermal micromorphology in Antarcticycas and new insights into cycad evolution. Am. J. Bot. 93, 724 – 738. (doi:10.3732/ajb.93.5.724)

26. Ronquist F, Huelsenbeck JP. 2003 MRBAYES 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19, 1572 – 1574. (doi:10.1093/bioinformatics/btg180)

27. Barone LMR, Coiro M, Truernit E, Erdei B, De Luca P. 2015 Epidermal micromorphology in Antarcticycas and new insights into cycad evolution. Am. J. Bot. 93, 724 – 738. (doi:10.3732/ajb.93.5.724)

28. Johnson KR, Ellis B. 2002 A tropical rainforest in Antarcticycas and new insights into cycad evolution. Am. J. Bot. 89, 1427 – 1438. (doi:10.1111/j.0003-6670.2002.tb00191.x)

29. Barone LMR, Coiro M, Truernit E, Erdei B, De Luca P. 2015 Epidermal micromorphology in Antarcticycas and new insights into cycad evolution. Am. J. Bot. 93, 724 – 738. (doi:10.3732/ajb.93.5.724)

30. Hermsen EJ, Taylor EL, Taylor TN. 2009 Morphology and ecology of the Antarcticycas plant. Rev. Palaeobot. Palynol. 153, 108 – 123. (doi:10.1016/j.revpalbo.2008.07.005)

31. Hill RS, Pole MS. 1994 Two new species of Pterostoma R.S. Hill from the Cenozoic sediments in Australasia. Rev. Palaeobot. Palynol. 80, 123 – 130. (doi:10.1016/0034-6667(94)90097-3)

32. White T, Bradley D, Haeussler P, Rowley DB. 2017 Late Paleocene—early Eocene paleosols and a new measure of the transport distance of Alasaka's Yakutat Terrane. J. Geol. 125, 113 – 123. (doi:10.1086/690198)

33. Hermsen EJ, Taylor EL, Taylor TN. 2009 Morphology and ecology of the Antarcticycas plant. Rev. Palaeobot. Palynol. 153, 108 – 123. (doi:10.1016/j.revpalbo.2008.07.005)

34. Hill RS, Pole MS. 1994 Two new species of Pterostoma R.S. Hill from the Cenozoic sediments in Australasia. Rev. Palaeobot. Palynol. 80, 123 – 130. (doi:10.1016/0034-6667(94)90097-3)

35. Barthel M. 1976 Farne und Cycadeen. Eozäne Floren des Geiseltales. Abhandlungen des Zentralen Geologischen Instituts 26, 439 – 490.

36. Kvacˇ Z, Manchester SR. 1999 Eastangaria Barthel (extinct Cycadales) from the Palaeogene of western North America and Europe. Int. J. Plant Sci. 160, 621 – 629. (doi:10.1086/314152)

37. Palamarev E, Uzunova K. 1992 Beiträge zur Entwicklung der Cycadeen in der Tertiärflora Europas. Courier Forschungsinstut Senckenberg 147, 287 – 293.

38. Uzunova K, Palamarev E, Kvacˇ Z. 2001 Eastangaria ruzinckiniana (Zamiaceae) from the Middle Miocene of Bulgaria and its relationship to similar taxa of fossil Eastangaria, and extant Chigua and Stangeria (Cycadales). Acta Palaeobot. 41, 177 – 193.

39. Wilf P, Stevenson DW, Cúneo NR. 2016 The last Patagonian cycad, Austrozamia stockeyi gen. et sp. nov., early Eocene of Laguna del Hunco, Chubut, Argentina. Botany 94, 817 – 829. (doi:10.1139/qjb-2016-0038)

30. Hermsen EJ, Taylor EL, Taylor TN. 2009 Morphology and ecology of the Antarcticycas plant. Rev. Palaeobot. Palynol. 153, 108 – 123. (doi:10.1016/j.revpalbo.2008.07.005)