

CTENIS CLARNOENSIS SP. N., AN UNUSUAL CYCADALEAN FOLIAGE FROM THE EOCENE CLARNO FORMATION, OREGON

Boglárika Erdei^{1,*} and Steven R. Manchester[†]

*Hungarian Natural History Museum, Botanical Department, PO Box 222, H-1476 Budapest, Hungary, and Montgomery Botanical Center, 11901 Old Cutler Road, Coral Gables, Florida 33156, USA; and †Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611-7800, USA

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Premise of research. Leaves of an extinct kind of cycad are recognized from the middle and late Eocene Clarno Formation of Oregon. Although the pinnately compound leaf is similar in gross form and organization to some other extant and Cenozoic cycads such as *Dioon* Lindl., *Encephalartos* Lehm., and *Dioonopsis* Horiuchi et Kimura, it is readily distinguished from them by its venation, consisting of a closed reticulum of a single order of veins with a frequent dichotomizing and anastomosing pattern.

Methodology. Fossils stored in the Museum of Paleontology (University of California), Florida Museum of Natural History (University of Florida), and Condon Museum of Natural History (University of Oregon) were studied applying conventional macromorphological and micromorphological methods including transmitted light and epifluorescence microscopy.

Pivotal results. The leaves conform in their peculiar venation and epidermal anatomy to the extinct genus *Ctenis* Lindley et Hutton, which previously was known only from Mesozoic occurrences. *Ctenis clarnoensis* Erdei et Manchester sp. n. adds to the diversity of cycads known from the Paleogene of western North America.

Conclusions. The record of the reticulate-veined *C. clarnoensis* and other fossil cycad genera with anastomosing venation patterns from the Paleogene implies that an extinct lineage or lineages of cycads sharing the character of reticulate venation, previously considered to be restricted to the Mesozoic, may have persisted into the Paleogene. Some physiognomic features of leaflets including the involute margin and pointed apex may suggest periodically dry conditions. By the present record the stratigraphic range of *Ctenis* is significantly extended from its previously known latest records in the Early Cretaceous up to as late as the Eocene.

Keywords: *Ctenis*, cycadalean foliage, venation, Eocene, North America, paleobotany.

Introduction

Leaves displaying the general morphology of cycad foliage are encountered only sporadically in Paleogene sediments of North America contrasting with Mesozoic strata in which cycad-like remains are relatively frequent and typical elements of the flora. One of the well-known cycadalean foliage genera of the Mesozoic, *Ctenis* was established by Lindley and Hutton (1834, p. 103) to accommodate leaves with the general character of modern cycads but with abundant vein anastomoses, giving a reticulate venation pattern. Although some early authors (e.g., Raciborski 1894; Staub 1896; Möller 1902; Yokoyama 1906) favored the assignment of *Ctenis* leaves to the pteridophytes, characteristic epidermal traits revealed later by Florin (1933) and Harris (1964) suggested their relation to cycads. Leaves assigned to *Ctenis* were not frequent elements of fossil assemblages; nevertheless, the genus was relatively widespread and reported from mainly Upper Triassic to Mid-

dle Jurassic strata in England (Yorkshire et al. 1834; Harris 1950, 1964); southern Sweden (Nathorst 1886; Florin 1933); Denmark (Möller 1902; Florin 1933); Greenland (Harris 1932, 1937); California, Oregon, and Virginia (Fontaine 1889, 1896, 1898–1899; Ward 1905); Poland (Raciborski 1894); Romania (Staub 1896); the Middle East (Schweitzer and Kirchner 1998); Uzbekistan (Gomolitzky 1974); China (Yokoyama 1906; Zhang and Zheng 1987); Japan (Oishi 1932, 1940; Kimura and Sekido 1972); Korea (Kawasaki 1926); and Argentina (Artabe and Stevenson 1999). In this article we contribute to the fossil record of *Ctenis* with a much younger occurrence of the genus from the Eocene Clarno Formation in Oregon.

The Cenozoic record of cycads in North America includes good examples from the northern Rocky Mountains and Western Interior and the Pacific Northwest including Oregon, Washington, and Alaska (DeVore and Pigg 2010). However, only a few have been well documented and thoroughly investigated with studies including epidermal anatomy as well as leaf architecture, such as *Eostangeria pseudopteris* Kvaček et Manchester from Wyoming and Oregon (Kvaček and Manchester 1999) and *Dioonopsis* species from Alaska and California (Erdei et al. 2012). An isolated zamiod leaflet was

¹ Author for correspondence; e-mail: erdei@bot.nhmu.hu.

recorded from the Republic flora of northeastern Washington (Hopkins and Johnson 1997), but epidermal characters remain unknown. Convergence in gross form and venation of leaves among different extant and extinct genera makes it difficult to confirm the placement of such fossil remains unless epidermal anatomy can also be observed. Differences in epidermal anatomy recorded in the cuticles can be used to distinguish among extant and fossil genera. The nearly whole-plant record of a cycad resembling *Dioonopsis* has been documented from the highly diverse flora of the Early Paleocene Castle Rock locality in central Colorado from the Rocky Mountains (Ellis et al. 2003; Miller et al. 2007; DeVore and Pigg 2010). Although cones are not known for this plant, the growth architecture, leaf form, venation, and epidermal characters are preserved. A thorough review is required, as well, for numerous other specimens previously reported in the literature, such as tiny fragments that were identified by Berry (1916), Hollick (1928), and Brown (1962) as various extinct species of *Zamia* L. (Erdei et al. 2014). The North American Paleogene fossil record and distribution of cycads have recently been discussed by DeVore and Pigg (2010).

Although the systematic relationships of Tertiary cycads are still far from resolved, the importance of extinct lineages among cycads, e.g., *Dioonopsis* (Horiuchi and Kimura 1987; Erdei et al. 2012), *Eostangeria* Barthel (Barthel 1976; Kvaček and Manchester 1999; Uzunova et al. 2001), and *Pseudodioon* Erdei, Akgün et Barone Lumaga (Erdei et al. 2010), seems to be significant in the North American and Eurasian Paleogene floras. A common feature of these extinct cycads is that their leaves display a gross morphology mostly well comparable to modern genera, e.g., *Eostangeria* to extant *Stangeria* T. Moore and *Dioonopsis* to modern encephalartoid members of *Zamiaceae*, e.g., *Dioon*, but their epidermal characters either are not present among modern cycads or represent a combination of traits of various extant genera. In concert with this, DeVore and Pigg (2010) emphasize as well that a mosaic of characters not encountered in modern taxa has been recorded among fossil cycads and the relationships between Cenozoic and modern taxa are unclear. This interpretation seems to be supported by recent molecular studies suggesting surprisingly recent radiation of modern species of cycads (Nagalingum et al. 2011).

The foliage *Ctenis clarnoensis* sp. n. described herein contributes to the Cenozoic morphological diversity of extinct leaf forms assigned to cycads and extends considerably the stratigraphic range of the genus *Ctenis*, which is reported here for the first time from post-Mesozoic floras. We compare it with other species of *Ctenis* based on a comprehensive review of the literature and discuss the significance of the reticulate venation pattern in this and other groups of plants.

Material and Methods

The study is based on foliage material in the collections of the Museum of Paleontology, University of California (catalog numbers prefixed UCMP), Berkeley; Florida Museum of Natural History at the University of Florida (UF); Condon Museum of Natural History, University of Oregon, Eugene (F); and the Oregon Museum of Science and Industry, Portland (OMSI). Specimens from UCMP were collected by R. W.

Chaney with A. W. Hancock and A. D. Vance in 1936 from tuffs of Hancock Canyon in the Clarno Formation and identified as a putative cycad assuming its relation to the modern cycad genus *Dioon* (Chaney 1936). Specimens stored at UF and F were collected at the Clarno Nut Beds by S. Manchester, W. Cox, and D. Mustard in 1981.

The middle portion of two leaves and occasional leaf segments are preserved mainly as impressions (figs. 1A, 1C, 2A). Macroscopic details of the fossil foliage are nicely preserved in some of the fossils showing leaflet margin and venation; also whole pinnae with apices are observable, indicating shape of leaf segments and type of attachment. Remains of the cuticle are preserved in patches showing just faintly the former epidermal patterns.

Cuticular details were studied using both epifluorescence and transmitted light microscopy with much more success when applying the former. UV light was applied on cuticles intact on sediment of the megafossil, as well as on pieces of cuticle removed from the megafossil specimens, cleaned in hydrofluoric acid, and subsequently washed in water. For transmitted light microscopy, pieces of cuticle were macerated by oxidation with Schultze's solution and leached by an aqueous solution of potassium hydroxide (5%). Unfortunately, we were able to macerate successfully only the upper cuticle; only epifluorescence revealed features from the poorly preserved lower cuticle. For description of the fossil leaves, we use the term "pinna" following Florin (1933) and Harris (1964). When describing venation, the term "reticulate" was favored in the sense as used by earlier authors (Wagner 1979; Trivett and Pigg 1996; Roth-Nebelsick et al. 2001).

For extant comparisons cycad leaflets were sampled with permission from the living cycad collections at the Montgomery Botanical Center (Coral Gables, FL). Leaflets of extant cycads were cleared for comparison of venation patterns by treatment with 10% solution of potassium hydroxide at room temperature.

Images of fossil cuticles were obtained using a Zeiss Axio-phot microscope equipped with a digital camera (AxioCam). For the purpose of focus stacking of cuticle images, the software Heliconfocus was used. Although the quite robust, three-dimensional leaf rachis seemed to be permineralized in one specimen; our attempts to reveal its anatomy through sectioning revealed it to be a cast lacking preservation of cellular structure.

Geological Settings

The most impressive specimens, large leaves with several segments attached along the rachis, were collected from Stegamonster Hill (lat. 44°55.287'N, long. 120°25.293'W), adjacent to present-day Hancock Field Station in Hancock Canyon (Chaney 1936). These specimens were deposited at UCMP and F. This occurs in siltstone layers interdigitating with lahar deposits of the Clarno Formation, considered to be late Eocene (ca. 44 Ma; Uintan; Hanson 1996). This site was labeled cycad locality within unit C of the Clarno Formation in figure 2 of Hanson (1996). Smaller fragmentary specimens, obtained from the nearby Clarno Nut Beds locality (lat. 44°55.370'N, long. 120°25.930'W; unit B of Hanson 1996) contain remnant cuticle. This locality is considered to

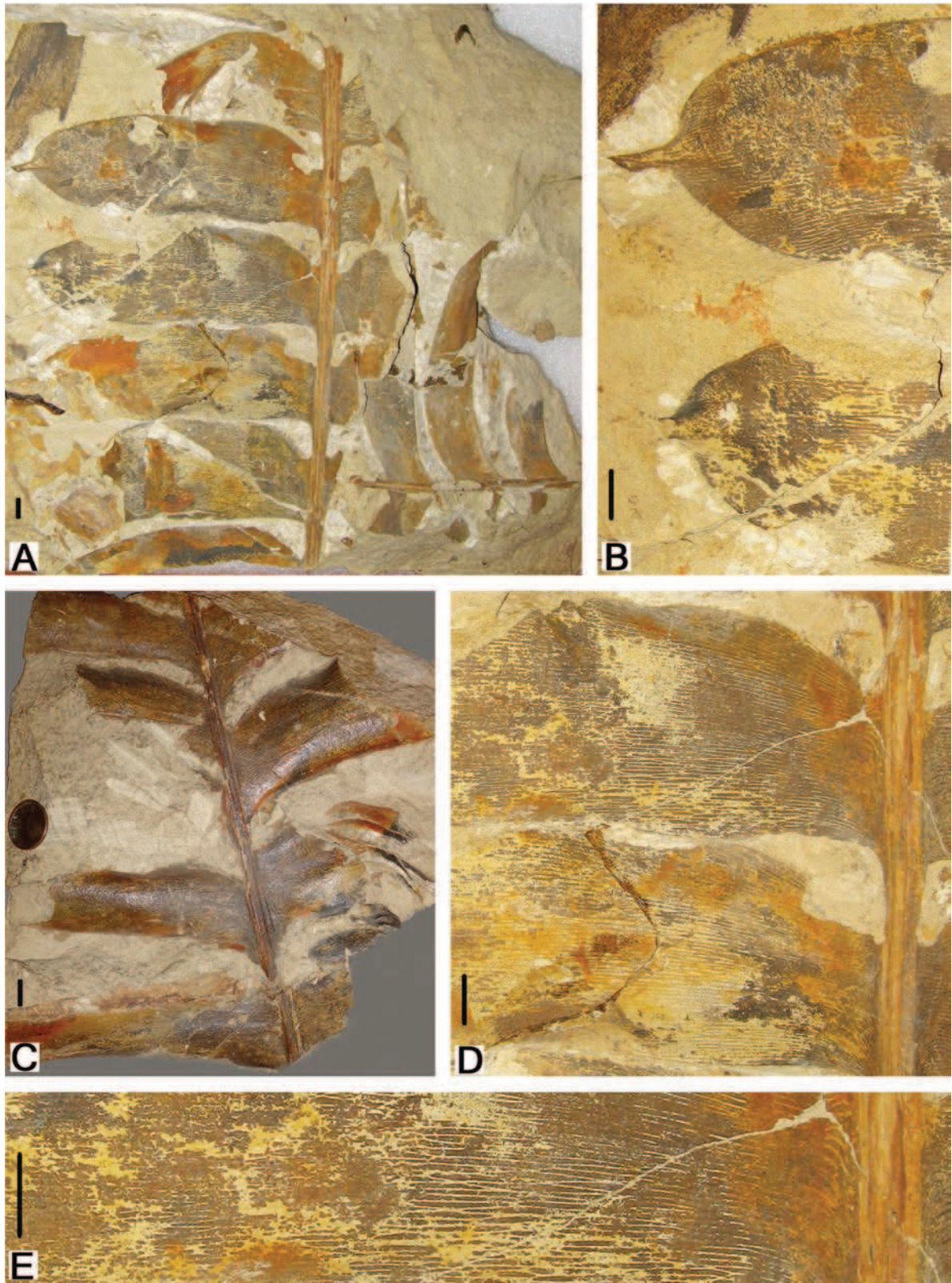


Fig. 1 Macromorphological details of *Ctenis clarnoensis* sp. n. from the Eocene Clarno Formation. Scale bars = 1 cm. *A*, Holotype specimen of *C. clarnoensis* sp. n. (UCMP151989). *B*, Apex of leaf segments of the holotype showing a pointed tubular extension (UCMP151989). *C*, Specimen of *C. clarnoensis* sp. n. cited as “additional specimen,” which is characterized by more elongate pinnae than the holotype (F34381). *D*, Detail of the holotype showing attachment of pinnae to rachis (UCMP151989). *E*, Detail of venation in the holotype. Note the frequent anastomoses forming elongate areoles (UCMP151989).

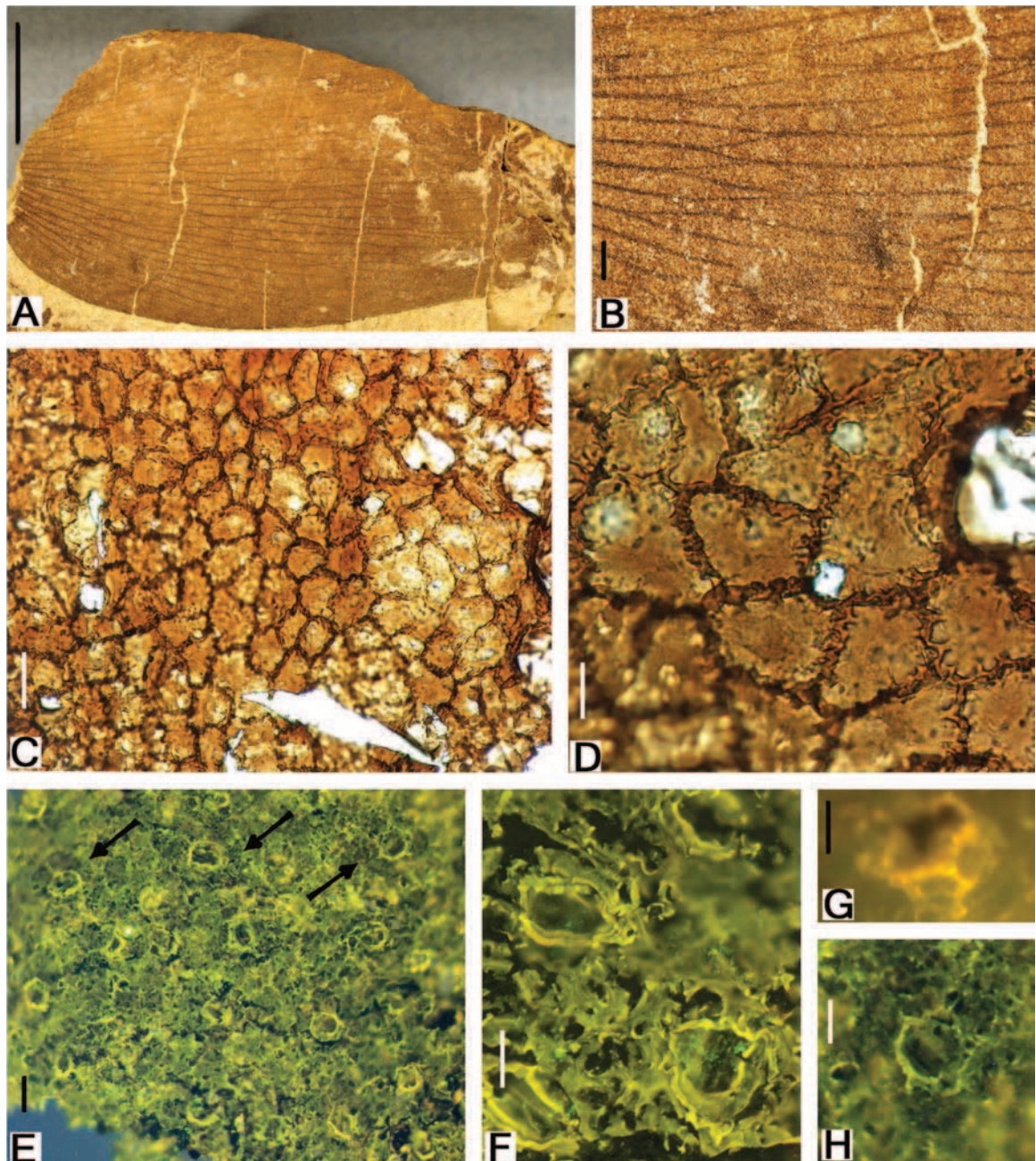


Fig. 2 Macromorphological and cuticular details of *Ctenis clarnoensis* sp. n. from the Eocene Clarno Formation. *A*, Detached pinna with contracted base (1754a); scale bar = 1 cm. *B*, Detail of venation of specimen on *A* showing elongate meshes (1754a); scale bar = 1 mm. *C*, Adaxial cuticle of *C. clarnoensis* sp. n. showing isodiametric cells and thickened cell walls (OMSI-PB 1715), transmitted light microscopy (lm); scale bar = 50 μ m. *D*, Enlargement of *C* (OMSI-PB 1715), lm; scale bar = 50 μ m. *E*, Abaxial cuticle *C. clarnoensis* sp. n. showing scattered, randomly orientated stomata. Arrows indicate stomata with subsidiaries faintly observable (OMSI-PB 1754b), fluorescence microscopy (fm); scale bar = 50 μ m. *F*, Stomata showing sunken guard cells (OMSI-PB 1754b), fm; scale bar = 20 μ m. *G*, Stoma enlarged showing walls of some subsidiaries (OMSI-PB 1754b), fm; scale bar = 20 μ m. *H*, Stoma enlarged from *E* showing cyclocytic arrangement of subsidiaries (OMSI-PB 1754b), fm; scale bar = 20 μ m.

be older, early middle Eocene, ca. 47 million years (Bridge-
rian; Hanson 1996).

The Nut Beds flora contains a diverse subtropical flora docu-
mented by 145 genera of fruits and seeds (Manchester 1994),
66 genera of silicified woods (Wheeler and Manchester 2002),

and a large number of leaf remains (Manchester 1981). Note-
worthy elements of the leaf flora include *Ginkgo* L., *Meliosma*
Blume, *Quercus* L., Lauraceae, Menispermaceae, Juglanda-
ceae, and ferns plus at least two other cycads in addition to
the one presented here (so-called *Dioon* [fig. 5 in Manchester

1981) and *Eostangeria* [fig. 1E in Kvaček and Manchester 1999]). The fruit and seed flora includes members of the Musaceae (*Ensete* Bruce ex Horan.); Cannabaceae (*Celtis* L.); Juglandaceae (*Juglans* L., *Platycarya* Siebold et Zucc., *Engelhardia* Lesch. ex Blume); Tapisciaceae (*Tapiscia* Oliv.); Toricelliaceae (*Toricellia* DC.); Ulmaceae (*Cedrelospermum* Saprota); and diverse Icacinaceae, Menispermaceae, and Vitaceae.

Results: Systematics

Order—Cycadales Dumort

Genus—*Ctenis* Lindley et Hutton

Species—*Ctenis clarnoensis* Erdei et Manchester sp. n.

(Figs. 1, 2A–2G, 3A–3C)

Holotype. UCMP 151989 here designated (figs. 1A, 1B, 1D, 1E, 3A–3C).

Repository. University of California, Museum of Paleontology (UCMP).

Paratypes. UF 225-47241, 47243, OMSI-PB 492, 1754a, 1754b (fig. 2A, 2B, 2E–2G; loose cuticle fragments have been preserved and analyzed), OMSI-PB 1715 (and cuticle slides prepared from OMSI-PB 1715; fig. 2C, 2D).

Repositories. Florida Museum of Natural History (UF).

Additional specimen. F34381 (Condon Museum of Natural History, University of Oregon [F]; fig. 1C).

Type locality. Hancock Canyon, Wheeler County, Oregon.

Stratigraphic horizon. Clarno Formation, Late Eocene (type locality) and middle Eocene (Nut Beds locality yielding the paratypes).

Etymology. Referring to the Clarno Formation (the formation is named after a small settlement Clarno that commemorates with its name Andrew Clarno, an early settler in the area).

Diagnosis. Leaf pinnately compound; pinnae at least six pairs, inserted with broad, slightly contracted base laterally and suboppositely on rachis sides at angles of 80°–85° to rachis. Pinnae falcate, robust, elliptic, margin entire, partly in-

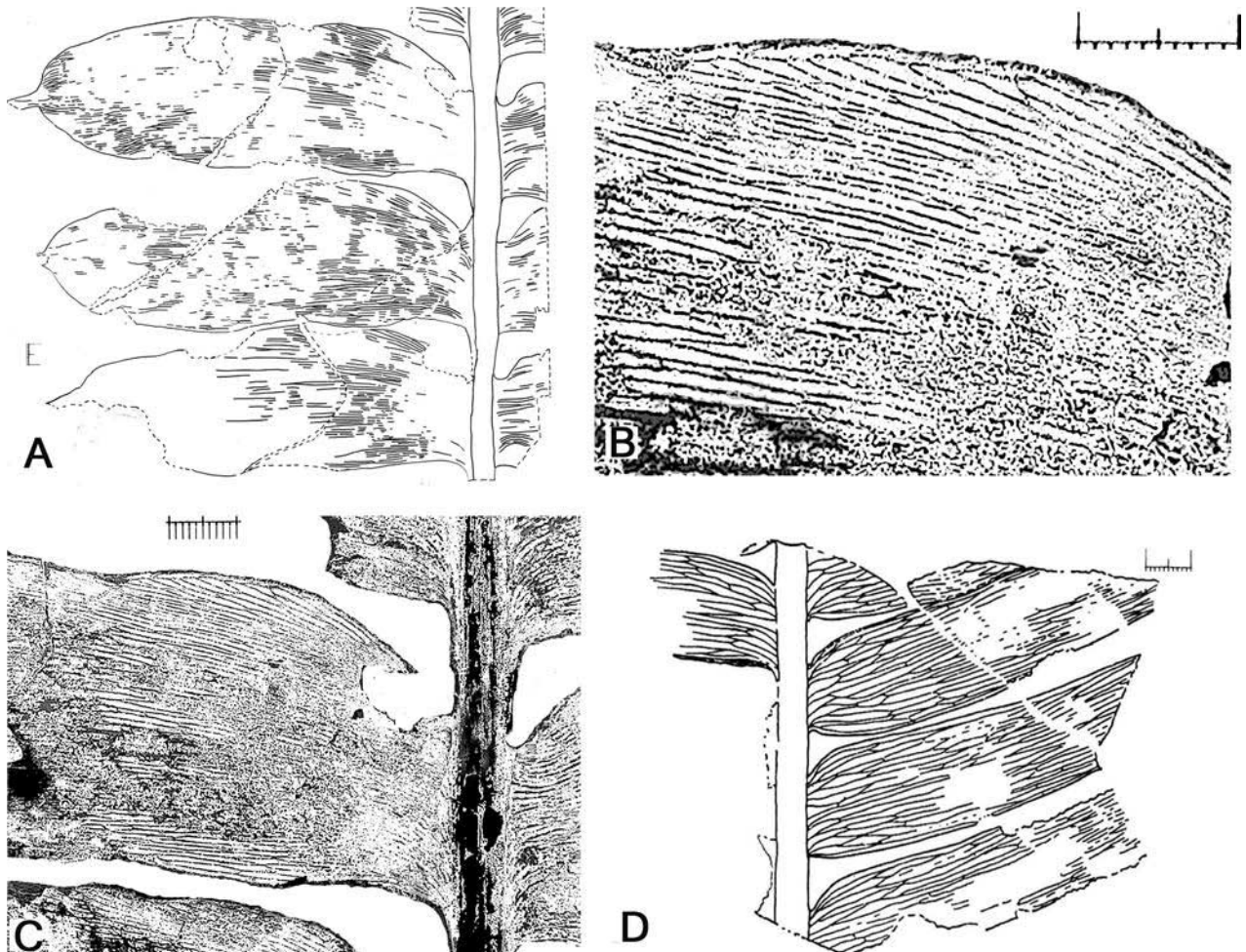


Fig. 3 Line drawings of leaves of *Ctenis clarnoensis* sp. n. and *Ctenis kaneharai* for comparison. Scale bars = 1 cm. A–C, *C. clarnoensis* sp. n. A, Drawing of holotype (UCMP151989). B, Detail of venation (UCMP151989). C, Closer view showing insertion of pinnae (UCMP151989). D, *C. kaneharai* (from Harris 1964, fig. 48D).

volute; basiscopic pinna base decurrent to rachis; apex obtuse with an acuminate tubular tip. Veins frequently forking and anastomosing to form a network. Veins decurrent at pinna base; adjacent veins joining before reaching the margin or the apex. Ordinary epidermal cells on adaxial and abaxial sides isodiametric, anticlinal cell walls thickened, slightly undulate. Leaf hypostomatic, stomata scattered, randomly orientated, cyclocytic, guard cells sunken; subsidiary cell walls thickened, forming a rim around guard cells.

Description. Fragmentary middle portions of pinnately compound leaves, rachis with attached leaf segments, and several detached pinnae form the basis of this study. The length and width of the largest fragmentary leaf (fig. 1A) are 26.5 and 19.5 cm, respectively. Extrapolated complete width of the leaf is 27 cm. Although the original length could not be estimated, it may be assumed that the leaf was significantly larger than its preserved part. The rachis is straight, relatively robust, with a width of 0.8–1.2 cm, and seems to have definite parallel grooves, suggesting that rachis may have displayed a noncircular cross-sectional pattern (fig. 1E). (However, it should be taken into account that such grooves may be taphonomic artifacts, as well.) Five pairs of pinnae (plus fragments of one more pair are observable) are inserted on the rachis, but the number of pinna pairs must have been much higher. The relatively large and robust tongue-shaped lanceolate pinnae are 12.7–15 cm long and 3.8–5 cm wide ($l/w \sim 3.2$). Pinnae are inserted to rachis slightly suboppositely at angles of 80°–85°, laterally on rachis sides with a broad but contracted base right above the place of insertion (fig. 1A, 1D). Pinnae are to some extent falcate and seem not or only slightly overlapping. The leaf was probably keeled because leaflet bases and the main part of the lamina seem to have been in different planes originally. Pinnae are entire margined, and the margin seems to be partly involute, giving a wavy appearance along the middle portion of pinnae (fig. 1A, 1B).

The lamina is decurrent to the rachis and contracted close to the point of insertion (fig. 1D). Contraction mainly occurs by the basal acroscopic part of the lamina. The apex is obtuse and asymmetrical, with the acroscopic margin more rounded. Pinnae apices possess a tubelike, pointed, probably spiny extension (fig. 1B), which is likely to have resulted from the abruptly involute margin, but we cannot rule out that this form was an artifact caused by shape deformation due to drying out of the leaf. Nevertheless, we consider the former interpretation to be more likely.

Vein density is moderate, with 11–15 veins per centimeter in the middle part of the lamina. Up to 40–60 veins are intercepted in a line across the full width of the middle part of the lamina, and they are of the same order, without a differentiated midvein. Veins entering the pinnae fork and anastomose frequently, thus forming a mesh of 5–30-mm-long areoles (figs. 1D, 1E, 2B). Although it is usually faintly observable, veins seem to join adjacent veins close to the margin. This is more conspicuous close to the apex (fig. 1B). Veins are decurrent at the base of pinnae (fig. 1D).

Adaxial cuticle is thick, with large, mostly isodiametric cells of 30–60 μm in diameter (fig. 2C, 2D). Anticlinal cell walls are mostly penta- and hexagonal. No definite rows or grouping of cells is observable. Anticlinal cell walls are thickened and slightly undulate. No stomata or trichome bases were ob-

served, although it should be considered that the cuticle is just partial and very poorly preserved.

Abaxial cuticle is thinner and very poorly preserved in patches around stomata (fig. 2E). Ordinary epidermal cell outlines are hardly observable, probably (observed in one sample) isodiametric, with slightly undulate anticlinal cell walls. Stomata seem to be scattered, based on the brightly fluorescing annular thickenings around stomata (fig. 2E, 2F), but the few available fragments are not large enough to recognize whether they are arranged in bands. Stomata are cyclocytic, with sunken guard cells, and seem randomly orientated (fig. 2E–2G). Guard cells are 30–40 μm in length. The stomatal aperture is narrow, oblong, and about 20–25 μm long. Subsidiary cells are barely observable (fig. 2F, 2G). Probably 5–7 subsidiary cells having thickened cell walls surround the guard cells. Centripetally, the cell walls seem to be more thickened, forming a coronal rim of about 25–30 μm in diameter surrounding the stomatal pit. Trichome bases were not observed, but their absence may be attributable to poor preservation.

It must be noted that some of the leaf remains—one of them right on the same slab with the holotype (fig. 1A) and another cited as an “additional specimen” (fig. 1C)—show slightly different morphology with slender and more elongate pinnae. Pinna apices are not preserved in these cases. Epidermal characters were not available, but the identical venation pattern with frequently dichotomizing and anastomosing veins indicates that these specimens probably represent morphological variation within the species or even individuals.

Discussion

Systematic Position

The gross morphology of the fossil leaves—including the pinnately compound organization with pinnae attached laterally with broad bases to the rachis, basically parallel venation constructed of a single order of veins, and basic micro-morphological traits such as cyclocytic stomata and strongly cutinized epidermis—indicate a most probable affinity to cycads. Other alternatives such as relationship to ferns, pteridosperms, other cycadophytes (Bennettitales), or monocots are not supported by epidermal features, such as strongly cutinized epidermis or scattered, randomly oriented, cyclocytic stomata, or by macromorphological traits, such as pinnate leaves with elongate pinnae attached laterally with a broad base to rachis or the lack of stronger middle vein on pinnae or the uniform order of parallel veins and the lack of perpendicular veinlets connecting major veins.

Among other Cenozoic cycads, *Dioonopsis* (Horiuchi and Kimura 1987) and *Pterostoma* R. S. Hill (Hill 1980) have leaflets of comparable gross morphology, and even some anastomosing veins of the same type as in the Clarno fossils are observable. Furthermore, *Dioonopsis* leaves were recorded from coeval floras of North America (Erdei et al. 2012); therefore, it might seem to be straightforward to assign the Clarno leaves to *Dioonopsis*. However, the much more frequent anastomoses forming meshes all over the leaf lamina in the Clarno leaves do not justify their inclusion in *Dioonop-*

sis (or *Pterostoma*). Among modern cycads, anastomoses of veins occur in leaves of some genera (e.g., *Encephalartos*) close to the leaflet apex. Anastomosis of veins in extant cycads is basically different, in as much as these always result in the decrease of the number of veins.

Morphologically similar leaves known from Mesozoic floras have been assigned to the genus *Ctenis* (Lindley and Hutton 1834; for an extensive list of references, see below). *Ctenis* was established by Lindley and Hutton (1834, p. 103; *Ctenis falcata* Lindley et Hutton) based on Phillips's leaf remains from the Mesozoic flora of Gristhorpe Bay, Yorkshire (*Cycadites sulcicaulis* Phillips 1829, p. 148, pl. 7, fig. 21). Lindley and Hutton disputed the assignment of Phillips's leaf to *Cycadites* Sternberg and established the genus *Ctenis* to accommodate cycad-like simply pinnate leaves with parallel, frequently anastomosing venation—practically a reticulate venation pattern. Later, Ward (1905) noted that according to nomenclatural rules Lindley and Hutton's binomial should be corrected as *Ctenis sulcicaulis* (Phillips) Ward. De Zigno (1856, p. 190) published a more detailed formal diagnosis of the genus; then Harris (1964, p. 102) presented an emended diagnosis based on descriptions by Florin (1933). Certain epidermal features of leaves assignable to *Ctenis* were mentioned first by Seward (1917) but were extensively revealed in works of Harris (1932, 1950, 1964) and Florin (1933). Consequently, the distinction of some species was based primarily on the micromorphological details preserved in the cuticles.

Earlier there was some debate as to whether *Ctenis* leaves belonged to cycads or ferns. In his study of the Bjuv flora of Sweden, Nathorst (1878) compared leaf remains that were described as simple leaves of *Anthrophyopsis* to some poly-podiaceous ferns. Additional findings indicated later that it is a heterogenous group representing in part pinnate leaves assignable to Lindley and Hutton's genus, *Ctenis* (Nathorst 1886; Harris 1932; Florin 1933; Florin gave a detailed discussion on the topic). Assignment of *Ctenis* leaves to pteridophytes was favored later by others based on structures resembling sori on some of the pinnae (e.g., Raciborski 1894, p. 196; Staub 1896, p. 332; Möller 1902, p. 14; Yokoyama 1906, p. 26; see details in Seward 1917). Seward (1917, p. 578) noted, however, that no sporangia had ever been found on *Ctenis* leaves and classified *Ctenis* species under the heading "cycadophytes." Disputing the earlier proposed relationship with ferns, Florin (1933, p. 62) argued that the sorus-like structures were formed by parasitic organisms and emphasized that the characteristic epidermal traits of the leaves suggested their relation to cycads. Harris (1964, p. 102) supported Florin's view, adding other characters as evidence of cycad affinity of *Ctenis* leaves. Later, Florin's view has been adopted, and *Ctenis* remains have been attributed to the cycads by various authors. We conclude that, among modern and so-far-known extinct groups of plants, cycads serve as the best comparisons for leaf remains accommodated in the genus *Ctenis*.

A large number of *Ctenis* species have been established in the fossil record (more than 50; see Kimura and Sekido 1972). The majority of these were diagnosed using macromorphological details and were often based on overlapping characters. Species distinctions are frequently poorly grounded and need future revision beyond the scope of this study.

Leaves assigned to *Ctenis* have been reported just sporadically from Mesozoic localities in North America, although additional records may be expected based on unpublished material in museum collections (B. Erdi, personal observation). Fontaine and Ward (Fontaine 1889, 1896, 1898–1899; Ward 1905) assigned foliage remains from the Mesozoic of California (Oroville), Virginia (Potomac), and Oregon to various *Ctenis* species, including *C. sulcicaulis* (Phillips) Ward (syn. *C. falcata*, Lindley and Hutton 1834), *C. orovillensis* Fontaine, *C. grandifolia* Fontaine, *C. auriculata* Fontaine, and *C. imbricata* Fontaine. These leaves mostly resemble each other in having somewhat slender, strap-shaped pinnae. *Ctenis grandifolia* has relatively broader leaf segments, but these are of irregular width (Fontaine 1898–1899, pl. 57). Pinnae of *C. auriculata* (California, Oroville flora; Fontaine 1898–1899, pl. 58, figs. 1–3) show a contracted base and a slightly rounded form comparable to some specimens of *C. clarnoensis* (PB1754a,b; fig. 2A); however, pinna apices are not preserved.

The Eurasian record of *Ctenis* is abundant as compared to the North American. *Ctenis kaneharai* Yokoyama from the Jurassic of China (Yokoyama 1906) has relatively broad pinnae; its width is sometimes close to that of *C. clarnoensis*, but leaf segments are more elongated and not tongue shaped in the Chinese species. *Ctenis kaneharai* was later described from Japan (Oishi 1940) and England, Yorkshire (Harris 1950, 1964), as well. Specimens from the Jurassic of Yorkshire (Harris 1950, 1964) have somewhat more slender leaf segments but agree in the contracted base of pinnae with a slightly rounded acroscopic margin (for a comparison fig. 3 shows line drawings of *C. clarnoensis* sp. n. and *C. kaneharai*). Other *Ctenis* species from the Mesozoic of Japan include *C. japonica* Oishi, *C. yabei* Oishi, and *C. takamiana* Oishi and Huzioka (Oishi 1932, 1940; Oishi and Huzioka 1938). Those from Korea are *C. yamanarii* Kawasaki (Kawasaki 1926) and from China *C. chaoi* Sze (Sze 1933) and *C. uwatokoii* Toyama et Oishi (Toyama and Oishi 1935). None of these conform to the morphological features of the leaves from Clarno. The species *C. yabei* (Oishi 1932) and *C. takamiana* (Oishi and Huzioka 1938) possess short and broad pinnae that are distinct from other species of the genus *Ctenis*, and even the authors note the resemblance of the leaves of the latter species to *Anomozamites* Schimper and *Nilssonina* Brongn. Nevertheless, the type specimens of these species do not correspond to the pectinated character of the genus *Ctenis* as noted by Lindley and Hutton (1834, p. 64): "we venture to propose the name of *Ctenis* in reference to its pectinated character."

Among the *Ctenis* species reported by Raciborski (1894) from the Polish and Staub (1896) from the Hungarian (locality now in Romania) Mesozoic, pinnae of *C. zeuschneri* Raciborski show an overall shape more or less comparable to *C. clarnoensis*. However, they differ in being basally less contracted and in having obtuse but not pointed apices. Another *Ctenis* species, *C. potockii* Raciborski (Raciborski 1894), has broad leaf segments but with a less or uncontracted base.

Ctenis nathorstii Möller reported by Möller (1902), and later by Florin (1933) from the Jurassic of Sweden, has a much more delicate structure than leaves of *C. clarnoensis*, with elongate, slender leaf segments. Antevs (1919) and later

Florin (1933) described foliage remains as *Ctenis* species from the Jurassic flora of Sweden, with Florin (1933) providing detailed epidermal descriptions. Some of these species have basically similar morphology except for the pointed apex of pinnae in *C. clarnoensis*. Leaves assigned by Florin (1933) to Harris's species, *C. nilssonii* (Nath.) Harris, have pinnae broader than 3 cm, but venation is less dense than in *C. clarnoensis*. *Ctenis latepinnata* Florin (Florin 1933) has leaves with very broad pinnae, exceeding 7 cm, and a large number of densely packed veins, although veins are spaced more widely than in the leaf from Clarno. Pinnae have obtuse rounded apices comparable to *C. clarnoensis*, except for the pointed apex of the latter. However, epidermal features are clearly distinct; in Florin's species, the stomata are arranged in groups, and epidermal cells are elongate rather than isodiametric, as in *C. clarnoensis*. Harris (1964) noted that *Ctenis* species display conspicuous striations on the cuticle, a feature that had already been noted by Florin (1933) in most species descriptions. Probably due to poor preservation, this character is not observable on the cuticles of *C. clarnoensis*. Another species from Sweden, *C. laxa* Florin (Florin 1933), possesses pinnae broader than 3 cm, but its venation is less dense (4–5 per cm) than in *C. clarnoensis*.

Species identified by Harris (1932, 1937) from Scoresby Sound East Greenland, *C. minuta* Florin, *C. nilssonii* (Nathorst) Harris, and *C. stewartiana* Harris, were all reported from Sweden as well (Florin 1933). The Jurassic flora of Yorkshire (England) included a great number of foliage remains assigned to various species of *Ctenis* by Harris (1964); he even provided a dichotomous key of the species using both macromorphological and cuticular details. Harris (1964) published extensive synonym lists and detailed comparisons for all the species, from which it is obvious that characters of the numerous species described formerly are often overlapping. Most species (*C. sulcicaulis*, *C. kaneharai*, and *C. stewartiana*) reported from Yorkshire are shared by other Mesozoic floras. As partly discussed above, none of the species described from Yorkshire is closely comparable with the Clarno species.

Later on, numerous accounts of *Ctenis* foliage remains have been published, including those from the Mesozoic of Argentina (Artabe and Stevenson 1999); the Jurassic of Uzbekistan (Gomolitzky 1974), Oxfordshire, United Kingdom (Cleal and Rees 2003), Antarctica (Rees and Cleal 2004), and China (Zhang and Zheng 1987); the Cretaceous of Japan (Kimura and Sekido 1972); the Jurassic and Cretaceous of USSR/Russia (Vakhrameev 1966; Samylina 1983); the Jurassic of the Middle East (Schweitzer and Kirchner 1998); and so on. Kimura and Sekido (1972) gave an account on *Ctenis* species and summarized shortly their main macromorphological traits. Some of these show unusual morphology, e.g., *Ctenis* sp. cf. *exilis* Harris (Rees and Cleal 2004) and *C. angrenica* Gomolitzky (Gomolitzky 1974; resolution of figures is too low to observe the exact venation pattern), with narrow, lobed, or toothed leaf segments. For more examples see Kimura and Sekido (1972) and Rees and Cleal (2004).

Schweitzer and Kirchner (1998) related some fossil leaf impressions from the Middle East to *Ctenis* species that were formerly described from England, China, and Japan (*C. cf. sulcicaulis*, *C. cf. kaneharai*, *C. cf. takamiana*) and also provided a brief review of those that had been described earlier

from the region. None of these records corresponds to the macromorphological traits of the leaves from Clarno.

Kimura and Sekido (1972) described some fronds with broad pinnae as *Ctenis nipponica* Kimura et Sekido and *Ctenis* sp. from the Lower Cretaceous of Japan and compared it with other species having similarly robust leaf segments described from England, Greenland, and Sweden by Florin and Harris (see above), from Oregon (*C. grandifolia* Fontaine; Ward 1905), Afghanistan (*C. approximatus* Jacob et Shukla, *C. constrictus* Jacob et Shukla; Jacob and Shukla 1955), Romania (locality formerly in Hungary; *C. asplenioides* [Ettingshausen] Schenk; in Seward 1917; *C. hungarica*; Staub 1896), Russia (*C. burejensis* Prynada; Vakhramejev and Doludenko 1961; Samylina 1963; *C. pleschkovii* Genkina, *C. uralensis* Genkina; Genkina 1963), and China and Mongolia (*C. chaoi* Sze; Sze 1933; *C. uwatokoii* Toyama et Oishi; Toyama and Oishi 1935). Although *C. uwatokoii* displays more or less tongue-shaped leaf segments (Toyama and Oishi 1935, pl. 3, fig. 3; figure poor quality, details hardly observable) comparable to the leaves from Clarno, none of the above species (including *C. nipponica*) have pinnae with apices, if preserved, characterized by a pointed apex as in the Clarno leaves.

None of the *Ctenis* records discussed above matches the combination of distinct characters of the *Ctenis* leaves from the Clarno Formation at the specific level, although comparison has often been hindered by the rather fragmentary leaf remains lacking important leaf traits or by the occasional lack or poor quality of documentation in the literature. Finally, it should be noted that most of the formerly described *Ctenis* species have been established on fragmentary leaf records mostly with important characters such as pinna apices either not or just poorly preserved, limiting appropriate comparisons. Many of the species were distinguished using characters (e.g., width of pinnae) that may vary depending on the position on the plant or on the leaf (basal, medial, or apical portion).

As a summary, based on macromorphological traits and the shape and form of pinnae and pinna apices, we establish a new species for the here described leaves from the Clarno Formation. With regard to the leaves having slender and more elongate leaflets (F34381 and a leaf from the holotype's slab), we presume that these represent the same species. It may be noted that none of the leaflets of the above two leaves have apices preserved that could enable a complete assignment. These leaves may originate from other parts of the plant or the leaf, resulting in a slightly different morphology.

The marginal termination of veins is usually not discussed in detail by authors; they just mention that veins run to the margin. Florin (1933, p. 79), noting as well that veins reach the margin in pinnae of some *Ctenis* species, gave no more details. However, some figures (e.g., Ward 1905, pl. 27, figs. 1–4) suggest that veins do not end freely by the margin; instead, neighboring veins join, resulting in the pattern seen in *C. clarnoensis*.

Harris (1964, pp. 102, 105, 117) provided a more detailed description of the venation of *Ctenis* species from the Jurassic of Yorkshire. Based on well-preserved specimens of *C. sulcicaulis*, the type species of *Ctenis*, he found that margin is thickened by a fiber bundle. According to his description, at the margins of the pinnae, the outermost vein runs parallel

with the marginal fiber bundle but usually do not anastomose with it. Toward the apex, marginal veins end separately in or near the fiber bundle. The pinnae of the Clarno leaves show a similar pattern (fig. 1B); however, the marginal fiber bundle is not identifiable—possibly due to limitations of preservation.

Some leaves display a large triangular apical segment, e.g., *C. nilssonii* (Florin 1933, taf. 4, fig. 5), *C. nathorstii* (Florin 1933, taf. 8, fig. 5.); however, there is no information on the form of the apical segment in *C. clarnoensis*. None of the leaves assigned so far to *Ctenis* displays an involute margin and pointed apex of pinnae comparable to that in *C. clarnoensis*. The cuticular details of *C. clarnoensis*, although just faintly observable, are comparable to species so far described with micromorphology (e.g., Harris 1932, 1964; Florin 1933), i.e., cuticle relatively thick, haplocheilic stomata randomly distributed, sunken on the abaxial side. Unfortunately, due to poor preservation, finer details are not comparable. Striations described in species of *Ctenis* (Florin 1933; Harris 1964) are not conspicuous in the cuticle of *C. clarnoensis*.

Based on the observation that pinnae are preserved dominantly in attachment to the rachis, it may be assumed that they were not deciduous from (or articulated on) the rachis. Preservation of intact leaves may be attributable to taphonomical factors, as well; however, it is much more likely that leaves fossilized as a whole reflect the nonarticulate character of pinnae. Most species of present-day cycads have nonarticulate leaflets. Three genera, *Ceratozamia* Brongn. (27 species), *Zamia* (75 species), and *Microcycas* (Miq.) A.DC. (1 species), possess deciduous leaflets. That means that less than one-third of the presently recognized modern cycad species (335; Osborne et al. 2012; Calonje et al. 2013 [the World List of Cycads]) have articulate/deciduous leaflets. Considering the high number of both Cenozoic and Mesozoic cycadalean leaf forms that are fossilized with pinnae attached (e.g., Cenozoic: *Dioonopsis*, *Pseudodioon*, *Pterostoma* R.S. Hill, and numerous other *Dioon*-like leaves; Mesozoic: *Almargemia* Florin [Florin 1933], *Ctenis*, *Jirusia* Bayer [Bayer 1914], *Mesodescolea* Archangelsky [Archangelsky 1963], *Mesosingera* Archangelsky [Archangelsky 1963], *Pseudoctenis* Seward [Seward 1911], *Ticoa* Archangelsky [Archangelsky 1963]), it is probable that the proportion of fossil cycad forms with nonarticulated pinnae was likewise relatively high.

The most conspicuous characters of leaf segments in *C. clarnoensis* are venation pattern and the pointed pinna apices with a tubular ending unknown among both modern cycads and fossil cycads. This feature may indicate somewhat xerophytic conditions attributable to either a seasonally dry climate or certain habitat conditions causing physiological drought. Another plausible explanation may be that, on the contrary, the leaflet apices represent drip tips that were distorted due to desiccation after being shed from the parent plant.

Venation of Fossil Cycadalean Foliage and Modern Cycads

Venation of *Ctenis* pinnae is characterized by a reticulate pattern whereby the basically parallel, uniform-order veins frequently fork and anastomose, thus forming loose meshes. This venation pattern is not seen among any of the modern cycads. Based on Brashier (1968) and the authors' observations,

the following notes can be made on the venation of modern cycads. Dichotomous branching of veins is relatively frequently observable in the lower half of the lamina of most genera except for *Dioon* (*Cycas* L. is an exception, having just a midrib and no side veins). In *Stangeria* the side veins departing from the midvein form frequent dichotomies. The few anastomoses, rarely observable in the minority of the extant genera (fig. 4A–4D), display a pattern different from that of *Ctenis* (fig. 3B, 3D); e.g., veins steeply join apically (*Dioon*, *Macrozamia* Miq.; fig. 4A) or veins join close to the margin (forming a marginal vascular system in *Stangeria* leaflets; Brashier 1968; fig. 4B). Anastomoses are observable in somewhat higher number in leaflets of *Encephalartos*; however, this is confined mostly in the upper, more apical part of leaflets where the lamina begins to taper (fig. 4C, 4D). Eventually, vein anastomoses observable in leaflets of modern cycads occur close to the margin or apex, contrasting with anastomoses relatively evenly distributed on the entire lamina of *Ctenis*. Furthermore, anastomoses are formed in basically different forms in *Ctenis* and extant genera. In the former, neighboring parallel veins are usually traversed by a steep vein forming an N shape (figs. 2B, 3B, 4E), whereas in extant genera, neighboring parallel veins are joined (fig. 4A–4D), by which mean number of veins is decreased, e.g., when the lamina is tapering.

Among previously described Tertiary fossil cycad records, *Pterostoma* (Hill 1980) from Australia and *Dioonopsis* from Japan (Horiuchi and Kimura 1987) and North America (Erdei et al. 2012) show the same kind of vein anastomoses as seen in *Ctenis* (fig. 4E). In leaflets of both of these genera, however, anastomoses are described as rare or occasional (Hill 1980; Erdei et al. 2012). Horiuchi and Kimura (1987) noted that the anastomoses of *Dioonopsis* are similar to those of *Ctenis* but much fewer in number and pointed out epidermal similarities of *Dioonopsis* and certain *Ctenis* species. Hill (1980) assumed a finer network of venation between major parallel veins in pinnae of *Pterostoma anastomosans* R.S. Hill based on the shape and orientation of epidermal cells. However, this would presume a different evolutionary stage of venation development, a hierarchical reticulate venation pattern not known among any fossil or modern cycads.

The venation of *Ctenis* leaves shows a simple reticulate pattern. The term “simple” is used here as defined by Roth-Nebelsick et al. (2001). Contrasting with the hierarchical reticulate pattern of veins (e.g., angiosperms), the veins of *Ctenis* are of uniform order, without hierarchical ranking. The term “closed” or “reticulate” versus “open” or “dichotomous” has been used to differentiate venation types with or without anastomoses of veins (Wagner 1979; Trivett and Pigg 1996; Roth-Nebelsick et al. 2001).

The open venation pattern is often regarded to be the primitive architecture, and this type of venation is encountered dominantly among early land plants with fernlike leaves (Roth-Nebelsick et al. 2001). It should be noted that dichotomizing venation pattern (with occasional anastomoses) occurs even among angiosperms, e.g., *Circaea* Maxim. and *Kingdonia* Balf.f. et W.W.Sm. (Ren et al. 1998), but it is interpreted by Ren et al. (1998) as a reduced character showing adaptation to moist and shady habitat.

Closed or reticulate venation pattern appeared in nearly all groups of land plants, among ferns and various gymno-

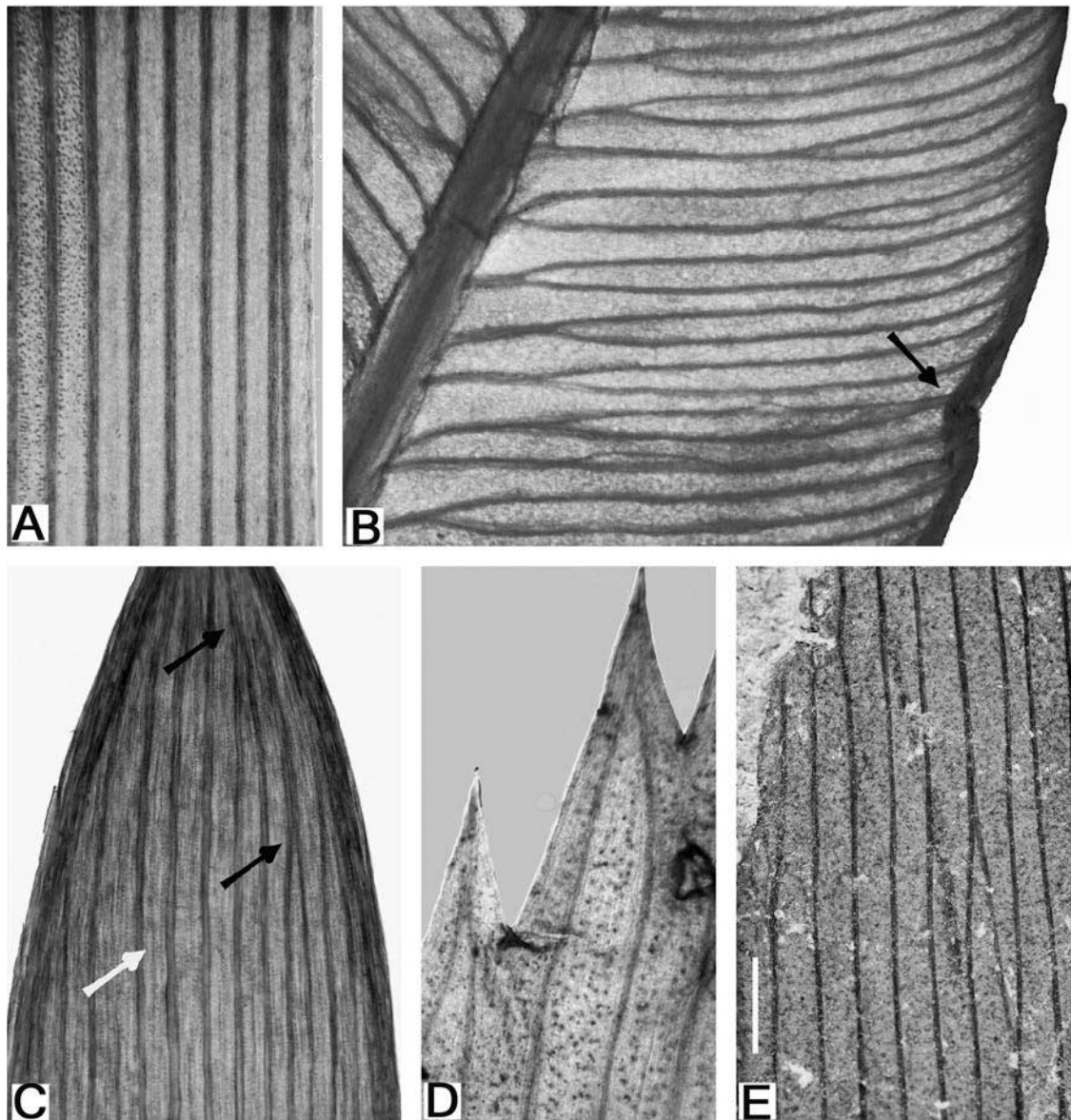


Fig. 4 Venation details of extant cycads and fossil cycadalean foliage. A, Detail of venation from the apical part of a leaflet of *Macrozamia moorei* F. Muell. Anastomosis is formed by joining neighboring veins (cleared leaflet, MBC 59302B). B, *Stangeria eriopus* (Kunze) Baill leaflet; arrow indicates anastomosis (cleared leaflet, MBC 651325B). C, Venation close to the apex of an *Encephalartos horridus* (Jacq.) Lehm. leaflet. Arrows indicate anastomoses; the white arrow marks fibers between veins (cleared leaflet, MBC 64755D). D, Seedling leaflet of *Encephalartos hildebrandtii* A. Braun et C.D. Bouché showing anastomoses of neighboring veins close to apical teeth (cleared leaflet, MBC without number). E, Venation detail of *Dioonopsis macrophylla* (Potbury) Erdei, Manchester et Kvaček. Note the anastomosis forming an N shape (UCMP 876). A color version of this figure is available online.

sperms, and as the characteristic branching pattern of leaf vasculature among angiosperms. It seems undoubted that reticulate venation has been established repeatedly several times in various plant lineages. For instance, the development of network pattern from an open, dichotomous one was suggested to have occurred among ferns more than 50 times (Wagner 1979). Simple reticulate venation pattern was recognized in the fossil record as early as the Late Carboniferous

(Zodrow and Cleal 1993; Kull 1999) and was reported among various groups of plants, both modern and fossil (Tri-vett and Pigg 1996), e.g., ferns (Wagner 1979), cycads (e.g., Brashier 1968), Gnetales (Rodin 1967), and even in *Ginkgo*, manifested by rare anastomoses (Arnott 1959), and fossil groups such as Paleozoic and Mesozoic pteridosperms (e.g., glossopterids, Caytoniales), gigantopterids, and many pinna or pinnule forms with unknown affinity (Taylor et al. 2009).

Medullosan pteridosperms, putative ancestors of cycads, may have possessed leaf types with simple reticulate venation as well (Trivett and Pigg 1996). The fern genus *Acrostichum* L., which co-occurs with *C. clarnoensis*, is another example of reticulate venation. The distant relationships of these groups support the conclusion that evolution of reticulate venation may be driven by ecological constraints as noted by many authors (Hickey and Doyle 1977; Trivett and Pigg 1996; Roth-Nebelsick et al. 2001). Diverse theories have been developed to explain why reticulate venation appeared in various groups of plants. Some authors presume that among monocots there may be a positive correlation between anastomosing venation pattern and climbing habit or the network pattern is more frequent in shaded forest environment (Cameron and Dickson 1998). Others, on the contrary, argue that open venation pattern is more prone to water deficit caused by, e.g., damage; a closed venation can compensate for the failure of some veins (Wagner 1979; Roth-Nebelsick et al. 2001). Zedrow and Cleal (1993) noted that development of reticulate venation patterns in seed ferns may have been induced by physiological stress caused by reduced water availability.

The functional background of the evolution of a closed venation type is unclear and may be different in the various plant groups; however, it has obvious advantages and adaptive significance (see Roth-Nebelsick et al. 2001). Hypotheses usually focus on the main functions of venation as a transporting and mechanical system. In modern cycads, transporting and mechanical functional aspects of the basically open venation (dichotomous or containing just a midrib) are complemented by thick cuticle, an extensive fiber system (most genera), and/or a transfusion tissue in the mesophyll (first of all in *Cycas*; Worsdell 1897; Takeda 1913; Brashier 1968; Norstog and Nicholls 1997; Griffith et al. 2014).

Harris (1964, p. 102) noted that “the lamina in *Ctenis* (at least in species from Yorkshire) seems to be rather more delicate than in most recent cycads” and lacks hypodermal fibers. This seems to be supported by the seemingly nonleathery leaves from Clarno. One of the better-preserved Yorkshire specimens showed the remnants of the mesophyll parenchyma directly attached to the cuticle, but no fibers were observable. Based on this, Harris (1964) concluded that the characteristic fibers strengthening modern cycad leaves may have not been developed in *Ctenis* leaves. The reticulate venation of *Ctenis* leaves may have had a mechanical function as well, fulfilling the role of a fiber system. The pinnae of *C. clarnoensis* show a more dense venation than in most modern cycads.

Reticulate venation with evenly distributed areoles does not occur among modern cycads despite the fact that fairly broad leaflets evolved in some, mainly *Zamia* species, e.g., *Zamia imperialis* A.S. Taylor, J.L. Haynes et Holzman, *Z. nesophila* A.S. Taylor, J.L. Haynes et Holzman, *Z. skinneri* Warsz. ex A. Dietr., with a relatively high average interveinal distance (the distance of two neighboring veins in the middle lamina) of 2–3 mm contrasting the 0.6–0.9 mm in the leaves from Clarno. Furthermore, most modern cycads grow in habitats with some seasonality of rainfall (Norstog and Nicholls 1997), and many extant species occupy a relatively harsh environment with significant water stress (which was supposed as a trigger-

ing factor for the development of reticulate venation in certain fossil groups).

Based on the plant taxa accompanying *C. clarnoensis* in the flora of the Clarno Formation, a humid subtropical climate may be assumed. If interpreting the form of pinna apices in *C. clarnoensis* as adaptation to drier conditions (and assuming that reticulate venation formed as a response to water stress), we may presume some seasonality of rainfall. This is in accordance with the observation that some of the woods of the Clarno flora show semi-ring porous condition (Wheeler and Manchester 2002).

Conclusions

The record of the reticulate-veined *Ctenis clarnoensis* and other fossil genera attributed to cycads with traits of anastomosing venation pattern from both the Mesozoic (*Ctenis*) and the Cenozoic (*Dioonopsis*, *Pterostoma*) implies that an extinct lineage or lineages of cycads with reticulate venation may have persisted from the Mesozoic up to the Paleogene. This is the first time that *Ctenis* leaves have been reported from sediments younger than Mesozoic. In addition, leaf remains collected from Eocene strata of Kupreanof Island, Alaska (K. Johnson and I. Miller, personal communication), show characters of *Ctenis* (pinnate leaf, reticulate venation), providing further support to the survival of the genus up to the Paleogene. The recognition of *Ctenis* in the Tertiary of North America is not the only case of typical Mesozoic taxa being reported in post-Cretaceous strata. Two recent reports noted the unexpected Cenozoic occurrence of some members of putative bennettitalean and pteridosperm taxa, i.e., *Ptilophyllum* Morris from the Oligocene of Australia (McLoughlin et al. 2011) and *Komlopteris* Barbacka in the Oligocene of Tasmania (McLoughlin et al. 2008). Moreover, other fragmented leaf remains from the early Miocene of New Zealand (Pole 1992) recall the reticulate venation of *Ctenis*; however, poor preservation and the lack of epidermal traits hinder a proper identification. Cycads have not been recorded from the Neogene of North America (north of Mexico), which may indicate that the group disappeared from the flora and vegetation, probably driven by climatic change during the later Paleogene.

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