

## CYCADS FROM THE TRIASSIC OF ANTARCTICA: PERMINERALIZED CYCAD LEAVES

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Permineralized cycad petioles and/or rachides with associated pinnae are described from two Triassic localities in the Queen Alexandra Range, central Transantarctic Mountains, Antarctica. Petiole-rachides display an inverted-omega-shaped arrangement of vascular bundles typical of most genera of extant Cycadales and exarch primary xylem that link them to the modern order. Pinnae associated with the Antarctic petiole-rachides are thin, with regularly spaced vascular bundles. They are similar to those of extant *Zamia* and most other genera of extant Cycadales, whose pinnae lack midribs. Other Mesozoic fossil cycads (e.g., *Charmorgia*, *Lyssoxylon*, *Lioxylon*) have endarch petiole vascular bundles that in some cases were previously considered more similar to those of Bennettitales than those of Cycadales. We suggest, however, that the endarch xylem of these taxa is typical of Cycadales because in extant cycads, the protoxylem changes from endarch to exarch within the base of the petiole. Evolution of cycad leaf form is reviewed based on evidence from the fossil record.

*Keywords:* Antarctica, Cycadales, Fremouw Formation, leaf, Triassic, *Yelchophyllum*.

### Introduction

The Cycadales is an ancient group of gymnosperms represented today by ca. 11 genera and 300 species (Hill et al. 2004) distributed primarily in the tropics (Norstog and Nicholls 1997). Cycads have one of the longest fossil records of all extant seed plant groups, dating at least to the Permian (Zhu and Du 1981; Gao and Thomas 1989a, 1998b), and it has been speculated that they are the most primitive of extant seed plants (e.g., Norstog and Nicholls 1997). However, recent morphological (e.g., Crane 1985; Doyle and Donoghue 1986, 1992; Nixon et al. 1994; Rothwell and Serbet 1994; Doyle 1996, 2006; Hilton and Bateman 2006) and molecular sequence data (e.g., Bowe et al. 2000; Chaw et al. 2000; Rydin et al. 2002; Soltis et al. 2002; Burleigh and Mathews 2004) analyses have failed to definitively resolve relationships among the seed plants, and, thus, the position of Cycadales remains unresolved. While Cycadales are distinctive on the basis of several characters unique to the order (e.g., girdling leaf traces, an inverted-omega-shaped pattern of the petiole vascular bundles, coralloid roots, primary thickening meristems), definitively assigning fossil leaves to Cycadales can be difficult. Often, vegetative leaves of Cycadales are preserved as impression-compression fossils, and leaf architecture may be insufficient to provide a definitive indication of affinities, especially earlier in the fossil record, where it is less likely that leaves can be assigned to extant genera (Pant 1987, 2002). While cuticular anatomy may provide diagnostic features (e.g., of stomata and epidermal cells), cuticle is lacking in many fossil leaves. Compounding the problem is the fact

that leaves of some other groups, such as the extinct Bennettitales, may be difficult to distinguish from those of Cycadales (e.g., Dower et al. 2004).

The reported fossil record of cycad vegetative leaves is extensive, but for the reasons discussed above, much of this record is in need of a detailed reexamination and reevaluation. The record begins in the Carboniferous (with at least one report; Pant 2002), expands in the Permian (e.g., *Yuania*, *Tianbaolimia*; Gao and Thomas 1989b), and increases significantly in the Mesozoic, being composed primarily of extinct genera until the Cenozoic (Pant 1987, 2002). The oldest fossil leaf assigned to an extant genus is *Encephalartos cretaceus* from the Cretaceous (Cenomanian) Dakota Formation of Kansas (Lesquereux 1891). However, because this taxon is based on one partial pinna lacking cuticle (E. J. Hermsen, personal observation, 2006), it seems reasonable to assert that the fossil record of leaves that can plausibly be assigned to extant genera does not begin until the latest Cretaceous, when two pinnate leaves with cuticle from the Cretaceous (Santonian) of Sakhalin Island, Russia, have been assigned to *Cycas* sp. (Krassilov 1978) and cuticle from New Zealand has been assigned to *Macrozamia* sp. (Pole and Douglas 1999). The record of Tertiary leaves includes reports of *Bowenia*, *Ceratozamia*, *Cycas*, *Dioon*, *Encephalartos*, *Lepidozamia*, *Macrozamia*, and *Zamia* (e.g., Yokoyama 1911; Berry 1916; Hollick 1932; Hill 1978, 1980; Carpenter 1991; Liu et al. 1991; however, see Kvaček 2000, concerning *Encephalartos*, and Kvaček 2002, concerning *Ceratozamia* and *Dioon*). Of these genera, at least five (*Bowenia*, *Ceratozamia*, *Cycas*, *Lepidozamia*, and *Macrozamia*) have now been documented on the basis of leaf fossils including or composed solely of cuticle (Hill 1978, 1980; Carpenter 1991; Liu et al. 1991; Liu 1992; Kvaček 2002), and another (*Dioon*) has been linked to the extant genus on the basis of shared derived characteristics

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(Moretti et al. 1993; however, see Kvaček 2002). The remainder of the Mesozoic and Cenozoic leaf record consists of extinct genera (e.g., Pant 1987, 2002).

Structural preservation of fossil leaves of Cycadales is rare. Excluding the Antarctic specimens detailed here, seven specimens representing five distinct taxa are known: one permineralized leaf from the Jurassic of Scotland (Dower et al. 2004), multiple petrified leaves on four specimens from the Early Cretaceous of India (Sharma 1973; Suthar et al. 1986), and two permineralized leaves from the Cretaceous of Japan (Stopes 1910; Nishida et al. 1996). Here, we report the first structurally preserved, Triassic cycad leaves (petioles and/or rachides and pinnae) from the fossil record that do not represent petiole bases attached to a structurally preserved stem taxon. These are among the oldest remains of vegetative leaves that can be definitively linked to a member of the Cycadales on the basis of synapomorphies or autapomorphies unique to the group, and they enrich the sparse Mesozoic record of Cycadales in Antarctica (Plumstead 1962; Hernández and Azcárate 1971; Smoot et al. 1985; Gee 1989; Rees 1993; Webb and Fielding 1993; Cantrill 2000; Hermsen et al. 2006).

### Material and Methods

Most of the specimens described here are preserved in permineralized peat collected from the upper part of the Fremouw Formation (Middle Triassic) at Fremouw Peak in the Beardmore Glacier area, Queen Alexandra Range, Transantarctic Mountains, Antarctica; the fossils have an estimated age of Anisian based on palynology (Farabee et al. 1990). An additional specimen was collected from Triassic Fremouw Formation strata at the base of Mount Falla, also in the Beardmore Glacier area (Barrett et al. 1986). Peat blocks were cut into sections, and the flat surfaces were polished and then etched in 48%–50% hydrofluoric acid. Peels of the etched surfaces were made using the acetate peel technique (Galtier and Phillips 1999), and peels were mounted on slides for study, using Eukitt as a mounting medium. Specimens are housed in the Division of Paleobotany of the Natural History Museum and Biodiversity Research Center (NHMBRC), University of Kansas, Lawrence, Kansas, under accession numbers 22508–22535. Some type specimens occurred adjacent to one another on the peat blocks and thus were mounted together on the same series of slides; therefore, in many cases, multiple type specimens share the same slide number.

Prepared slides of transverse sections of *Zamia integrifolia* (labeled as *Zamia floridana*, now a synonym for *Z. integrifolia*) leaflets were purchased from Triarch (Ripon, WI); illustrated material is housed in the Division of Paleobotany of NHMBRC under slide 22545. Slides of other extant cycads prepared using standard microtechniques are housed in the collections of the New York Botanical Garden, Bronx, New York.

Specimens were photographed using a Leica (Wetzlar, Germany) DC500 digital camera attachment on a Leica MZ16 stereomicroscope or using a Leica DC500 digital camera attachment on a Leica DM5000 B compound microscope. Images were converted from color to gray scale, and plates were composed using Adobe Photoshop CS, version 8.0. Some im-

ages were adjusted using the “brightness/contrast” or “auto contrast” tools in Photoshop after conversion to gray scale. The illustration in figure 4B was produced by tracing over the color version of the image in figure 4A in Photoshop using a WACOM tablet. Measurements of fossil specimens were taken using the program ImageJ (Rasband 1997–2006), calibrated using a micrometer. Measurements have been rounded up or down (as appropriate) to the nearest 0.1 mm if given in millimeters and to the nearest 5  $\mu\text{m}$  if given in micrometers.

Specimens of *Antarcticycas schopfii* illustrated in figure 4A and 4C–4E are housed in the Division of Paleobotany, NHMBRC, under slides 22539–22541. These slides were made from peels of block face 10104C<sub>TOP</sub> and are also from the face upper Fremouw Formation at Fremouw Peak.

*Note on terminology.* The petiole and rachis of the leaf of cycads is a continuous structure, petiole denoting the portion of the structure proximal to the point of attachment of the first pinnae and rachis denoting the portion of the structure from the point of attachment of the first pinnae to the distal end of the leaf. The term “petiole-rachis” is used in this article to indicate the whole petiole-rachis structure where ambiguity exists as to where on the continuum a particular section comes from or when the entire structure is being referred to.

### Systematic Paleontology

#### Order—Cycadales

Genus—*Yelchophyllum* gen. nov., Hermsen,  
T. N. Taylor, E. L. Taylor & Stevenson

*Generic diagnosis.* Leaves once pinnate; vascular bundles of petiole-rachides forming a simple (unmodified) inverted-omega-shaped pattern in transverse section; pinnae attached laterally, lacking midribs and mucilage canals.

*Etymology.* The generic name *Yelchophyllum* is proposed in honor of the ship in which the Antarctic explorer Ernest Shackleton returned to rescue the stranded survivors of the *Endurance* expedition in 1916.

*Type species.* *Yelchophyllum omegapetiolaris* sp. nov., Hermsen, T. N. Taylor, E. L. Taylor & Stevenson (fig. 1).

*Specific diagnosis.* Petiole-rachides flattened to rounded on adaxial surface, rounded on abaxial surface; dense layer of sclerenchyma at the periphery of the cortex; pinnae borne laterally and displaced adaxially but insertion not adaxial along the midline of the rachis. Pinnae thickest at point of attachment to rachis and narrowing distally, vascular bundles more or less regularly spaced with adaxial xylem and abaxial phloem, palisade layer indistinct; tracheids with scalariform to circular bordered pitting.

*Holotype* hic designatus. Petiole-rachis with lateral pinna, slides 22508–22519, as well as peels of the same specimen from block faces 10424G<sub>BOT</sub>, 10424G<sub>SIDE1</sub>, and 10424H<sub>1TOP</sub> and any remaining portion of the same specimen in those blocks (fig. 1A, 1E, 1F).

*Paratypes.* Petiole-rachis on slides 22508–22524, as well as peels of the same specimen from block faces 10424G<sub>BOT</sub>, 10424H<sub>1TOP</sub>, and 10424G<sub>SIDE1</sub> and any remaining portion of the same specimen in those blocks (fig. 1B, 1D); large

petiole-rachis (not illustrated) on slides 22508–22524, as well as peels of the same specimens from block faces 10424G<sub>IBOT</sub>, 10424H<sub>ITOP</sub>, and 10424G<sub>ISIDE1</sub> and any remaining portions of the same specimen in those blocks; small petiole-rachis on slides 22508–22516 and 22522–22534, as well as peels of the same specimen from block faces 10424G<sub>IBOT</sub> and 10424G<sub>ISIDE1</sub> and any remaining portion of the same specimen in that block (fig. 1C); small petiole-rachis on slides 22517–22519, as well as peels of the same specimen from block face 10424H<sub>ITOP</sub> and any remaining portion of the same specimen in that block; rachis with lateral pinnae on slides 22525–22528, as well as peels of the same specimen from block face 10424G<sub>IBOT</sub> (fig. 1G, 1H); petiole-rachis without lateral pinnae on slides 22525–22529, as well as peels of the same specimen from block face 10424G<sub>IBOT</sub>; pinna on slides 22508–22516, as well as peels of the same specimen from block face 10424G<sub>IBOT</sub> and any remaining portion of the specimen in that block; pinna on slides 22520–22524, as well as peels of the same specimen from block face 10424G<sub>ISIDE1</sub> and any remaining portion of the same specimen in that block (fig. 1I); pinna (near abaxial surface of holotype) on slides 22517–22519, as well as peels of the same specimen from block face 10424H<sub>ITOP</sub> and any remaining portion of the same specimen in that block (fig. 1J, 1K); petiole-rachis on slides 22530–22531, as well as peels of the same specimen from block face 10104C<sub>TOP</sub> and any remaining portion of that specimen from the same block; petiole-rachis on slide 22532, as well as peels of the same specimen from block face 11252D<sub>TOP</sub> and remaining specimen from the same block; petiole-rachis on slide 22533 and peels of the same specimen from block face 11252D<sub>TOP</sub>, as well as any remaining portion of the specimen from the same block; petiole-rachis on slides 22534–22535 and any peels of the same specimen from block face 12931C<sub>TOP</sub>, as well as any remaining portion of the specimen from the same block.

**Stratigraphic position.** Upper Fremouw Formation (Fremouw Peak); Fremouw Formation (base of Mt. Falla, block 12931C only).

**Age.** Early Middle Triassic (Anisian) for Fremouw Peak (Farabee et al. 1990), Triassic at Mt. Falla (Barrett et al. 1986).

**Localities.** Fremouw Peak (col on north side; lat. 84°17'24.1"S, long. 164°21'24.2"E) and the base of Mt. Falla (lat. 84°20'50.1"S, long. 164°39'40.6"E), Beardmore Glacier area, Queen Alexandra Range, central Transantarctic Mountains, Antarctica.

**Etymology.** The species epithet *omegapetiolaris* refers to the inverted-omega-shaped pattern of vascular bundles in the petioles and/or rachides of this taxon, distinguishing them from other petioles and rachides in the Fremouw flora and linking them to Cycadales.

**Repository.** Division of Paleobotany, NHMBC.

**Description.** Leaves once pinnate. Petiole-rachides flattened to rounded on adaxial surface, rounded on abaxial surface, ca. 0.8–4.1 mm thick and ca. 1.5–4.8 mm wide (fig. 1A–1C), epidermis thin; small thick-walled cells at periphery of petiole-rachides interpreted as dense layer of sclerenchyma (=“cortical armor” of Poole 1923; see fig. 1F). Vascular bundles forming an inverted-omega-shaped pattern in transverse section (fig. 1A–1C), each ca. 65–430  $\mu\text{m}$  thick by 55–315  $\mu\text{m}$  wide, bundles sometimes fused (particularly in the arms

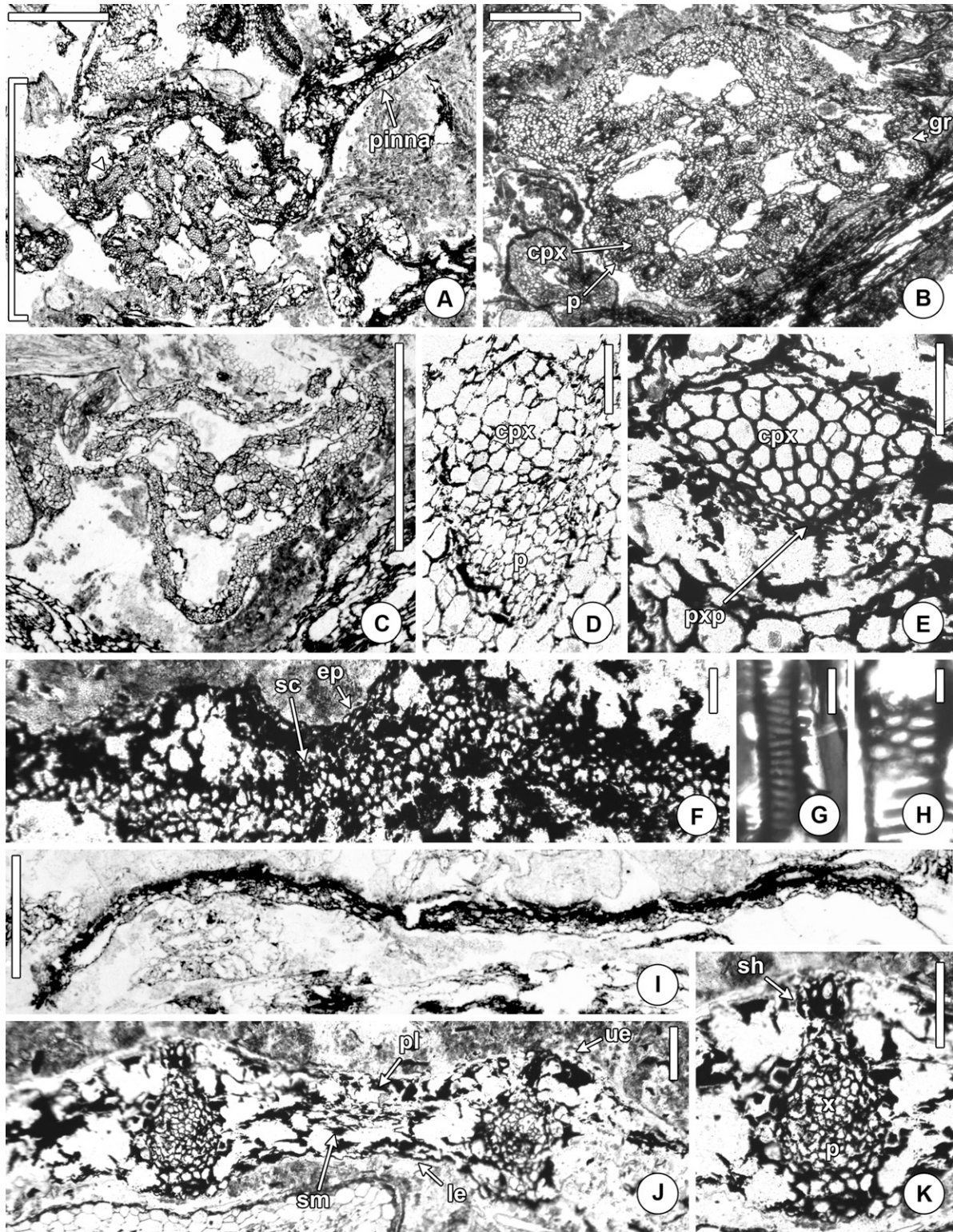
of the omega), xylem exarch and adaxial, phloem abaxial (fig. 1A–1E); pinnae borne laterally and displaced adaxially, but insertion not adaxial along the midline of the rachis (fig. 1A). Pinnae in cross section ca. 645–670  $\mu\text{m}$  thick at point of attachment to rachis; transverse section of pinnae ca. 160–345  $\mu\text{m}$  thick at the veins, 105–195  $\mu\text{m}$  high in intercostal areas, ca. 5.2–7.7 mm in width, length unknown, with multiple regularly spaced veins in transverse section (eight to 13 in three complete transverse sections); vascular bundles ca. 70–145  $\mu\text{m}$  high by ca. 45–120  $\mu\text{m}$  wide, surrounded by a sheath of thick-walled cells. Xylem adaxial, phloem abaxial; epidermis of small cells, palisade mesophyll poorly defined, spongy mesophyll with transversely elongated cells; midribs, mucilage canals, and hypodermis absent (fig. 1I–1K). Tracheids with scalariform to circular bordered pitting (fig. 1G, 1H).

## Discussion

### *Affinities and Interpretation of Yelchophyllum*

All members of extant Cycadales possess petiole-rachides with an omega-shaped pattern of vascular bundles (fig. 2A), each with exarch protoxylem. These characteristics are considered synapomorphies for the order as a whole and the omega-shaped pattern an autapomorphy for Cycadales with respect to other seed plant groups (Hermesen et al. 2006). Among extant cycads, only *Bowenia*, *Encephalartos*, and *Stangeria* have a pattern of vascular bundles that does not appear clearly omega shaped in transverse section (fig. 2B–2D); however, serial sections of the petiole-rachides show an elaborated inverted omega of trace departure to the pinnae (Matte 1904). *Yelchophyllum* is thus clearly linked to Cycadales by the distinctive inverted-omega-shaped arrangement of vascular bundles in the petiole-rachides (fig. 1A–1C). The modified-omega-shaped petiole-rachis bundle pattern as seen in *Bowenia*, *Encephalartos*, and *Stangeria* is considered a derived character in Cycadales, suggesting that *Yelchophyllum* is characterized by the plesiomorphic pattern (unmodified inverted omega) within the group (e.g., Stevenson 1990; Hermesen et al. 2006). The vascular bundles of the omega in *Yelchophyllum* are often closely spaced and sometimes fused, particularly in the arms (“collar” of Yoshida 2000) of the omega (fig. 1A). Bundle fusion occurs in extant cycads, particularly in the neck of the omega, although also in other regions (Yoshida 2000).

Among other fossil cycads, the Upper Triassic stem taxon *Charmorgia* also has petioles with an inverted-omega-shaped arrangement of vascular bundles (Ash 1985). Bock (1969) suggested that the stem cast *Cycadenia* from the Triassic of Pennsylvania may have an inverted-omega-shaped petiole bundle pattern, although the bundle traces in the sole specimen of that taxon are poorly preserved. In the leaf taxa *Cretocycas* and *Cycadinorachis*, the former clearly has an inverted-omega-shaped arrangement in the petiole-rachis (Nishida et al. 1996), and the latter may have one as well (Sharma 1973; Suthar et al. 1986). The Cretaceous-Tertiary genus *Bororoa* and the Cretaceous genus *Brunoa* lack a clear omega-shaped pattern (Petriella 1972, 1978; Artabe and Stevenson 1999; Artabe et al. 2004), although these taxa are interpreted as having



**Fig. 1** *Yelchophyllum omegapetiolaris* gen. et sp. nov. A, Transverse section of a rachis with attached lateral pinna, showing typical omega-shaped pattern of vascular bundles. Adaxial surface is interpreted as oriented toward the top of the page, as it would be in extant cycads. The extent of the rachis is indicated by the bracket at the left of the figure; the cortex and epidermis are missing from the abaxial side. An example of fused bundles is indicated with an arrowhead. Specimen 22510, scale bar = 1 mm. B, Transverse section of a petiole or rachis showing inverted-omega-shaped pattern of vascular bundles, with phloem (*p*) oriented abaxially and centripetal xylem (*cpx*) adaxially. An indentation on one side of the petiole or rachis (*gr*) may be a lateral groove into which the pinnae are inserted. Slide 22513, scale bar = 1 mm. C, Transverse section of

an elaborated-omega-shaped pattern. Two other structurally preserved taxa, *Menucoa* and *Lioxylon*, have been described as having an unordered arrangement (Petriella 1969) and a poorly developed omega or irregular pattern of petiole bundles (Zhang et al. 2006), respectively. However, reexamination of specimens of *Menucoa* (D. W. Stevenson, personal observation, 2004) and reinterpretation of illustrated transverse sections of petioles attached to *Lioxylon* (Zhang et al. 2006, figs. 4*f*, 5*b*–5*f*) suggest that the vascular bundle arrangement in lateral appendages of these two taxa, although initially appearing random or only poorly omega shaped, is an omega-shaped or elaborated-omega-shaped pattern that has probably been distorted during fossilization. Somewhat analogous to this situation is the seemingly disorderly or random arrangement of vascular bundles in transverse sections of the petiole-rachis of the extant genus *Encephalartos* (fig. 2*D*). Matte (1904) demonstrated, through reconstruction of the vasculature of the petiole-rachis from serial sections, that the vascular bundle pattern in *Encephalartos* is an elaborated omega, or a basic-omega-shaped pattern with anastomosing branches (Matte 1904, pls. 6, 7; see also Yoshida 2000). Similarly, tracing the petiole vasculature in serial sections of fossil specimens while accounting for distortion in shape of the lateral appendages (where applicable) in reconstructing the vasculature might help to expose a basic- or elaborated-omega-shaped pattern in taxa where such a pattern is not immediately apparent, thus providing an important link to extant Cycadales.

Cycads produce three types of lateral appendages: foliage leaves, scale leaves or cataphylls, and sporophylls. Foliage leaves, in addition to being the only lateral appendages that can have a distinct inverted-omega-shaped arrangement of vascular bundles, have well-developed vascular bundles, each with a fascicular cambium, a characteristic also present in sporophylls (Matte 1904; Stevenson 1990). In extant cycads, the protoxylem in the vascular bundles of the petiole-rachides is exarch and occurs at the tip of a wedge of centripetal primary xylem (Le Goc 1914; Marsh 1914; fig. 2*E*, 2*F*). Some xylem (centrifugal xylem) is produced on the opposite side of the protoxylem by a fascicular cambium, giving the bundles a pseudomesarch or diploxylic appearance (fig. 2*F*); this centrifugal xylem has been interpreted to be mostly to completely secondary (e.g., Sinnott 1911; Le Goc 1914; Marsh 1914). The primary and secondary xylem are separated by parenchyma (Le Goc 1914; see also fig. 2*F*). Secondary phloem is produced on the opposite side of the fascicular cambium from the cen-

trifugal xylem, resulting in the presence of arcs of crushed phloem cells toward the periphery of the phloem zone (fig. 2*F*).

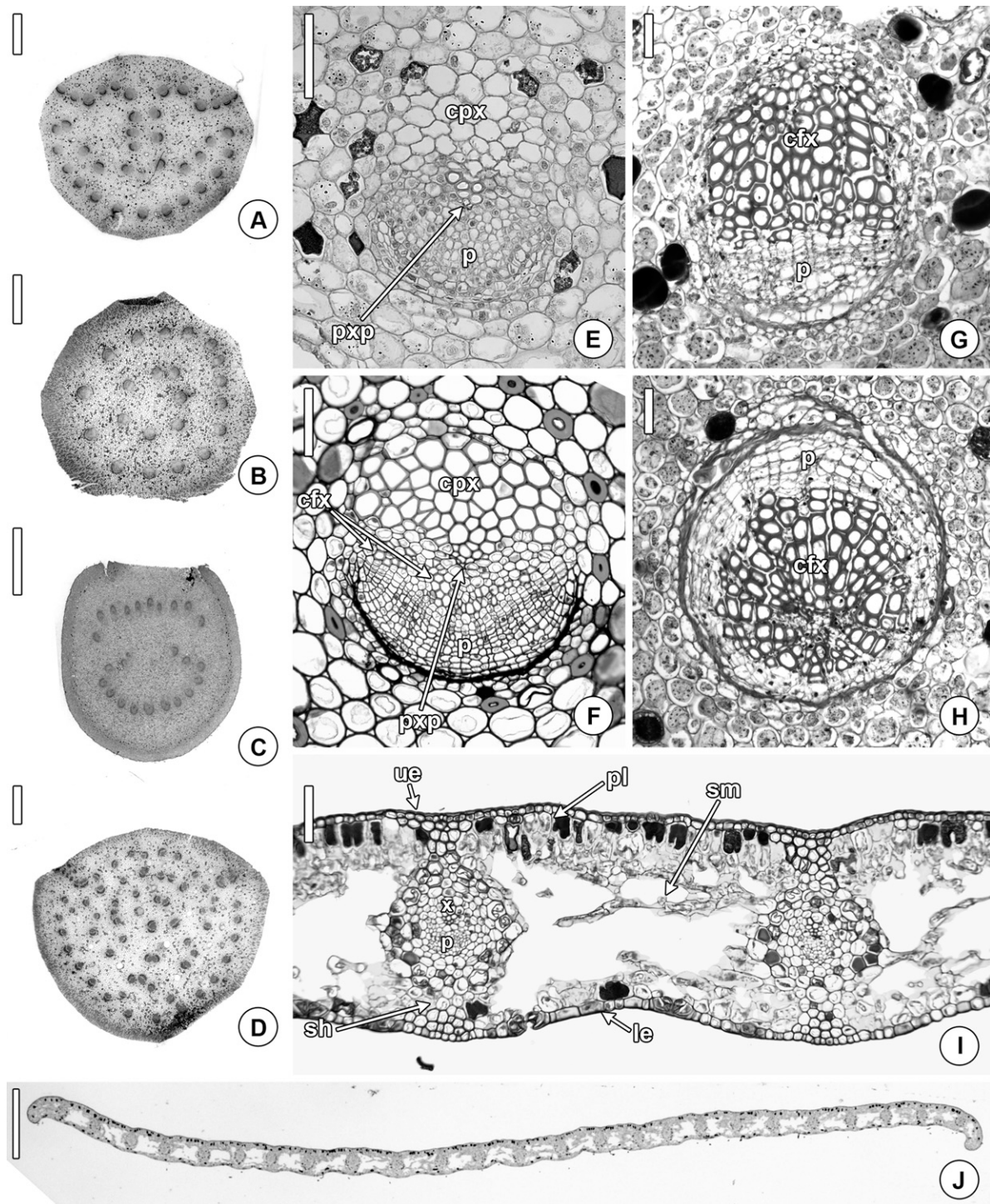
The vascular bundles of *Yelchophyllum* are interpreted as having an arrangement similar to that of extant cycads. The holotype specimen of *Yelchophyllum* has some vascular bundles in which the phloem has degraded, and the wedge shape of the primary xylem is especially apparent (fig. 1*E*); the protoxylem is interpreted to be at the tip of this wedge (fig. 1*E*), in the same position it would occupy in extant cycads (fig. 2*E*, 2*F*). No clearly differentiated centrifugal xylem has been identified in petiole-rachides of *Yelchophyllum* (fig. 1*D*, 1*E*). This may indicate that no centrifugal xylem was produced, although the preservation of the bundles, the age of a petiole or rachis when fossilized, or the position of the section along the length of a petiole or rachis may affect our ability to identify centrifugal xylem. In extant cycads, centrifugal xylem may be represented by a few cells or may be entirely absent in young leaves or closer to the distal end of the rachis (Le Goc 1914; figs. 2*E*, 3). The presence or absence of a parenchyma band is not clear in *Yelchophyllum* petiole-rachides (fig. 1*D*, 1*E*); the phloem is generally poorly preserved although extensively developed (fig. 1*D*, 1*E*).

Whether mucilage canals are present in the ground tissue of the petiole-rachides of *Yelchophyllum* is impossible to discern with certainty, given the lack of preservation of much of the ground tissue in the specimens examined; however, like those of extant cycads, *Yelchophyllum* petiole-rachides have a layer of thick-walled cells interpreted as sclerenchyma or cortical armor (Poole 1923) at the periphery of the cortex (fig. 1*F*; see also Poole 1923, pls. 18, 19, for illustrations of sclerids in extant cycads). Putative prickles (not shown) have been found on a specimen of *Yelchophyllum* preserved in block 11005. If these can be demonstrated unequivocally to be prickles and not simply artifacts of preservation (e.g., caused by cell breakdown), it may suggest that *Yelchophyllum* has affinities to *Ceratozamia* and *Zamia*, which are also characterized by prickles (Stevenson 1990). (In extant cycads, individual plants or leaves on the same plant may or may not be armed [Stevenson 1990], which could explain the apparent absence of prickles in the type series, assuming the presence of prickles could be confirmed in at least one specimen of *Yelchophyllum*.)

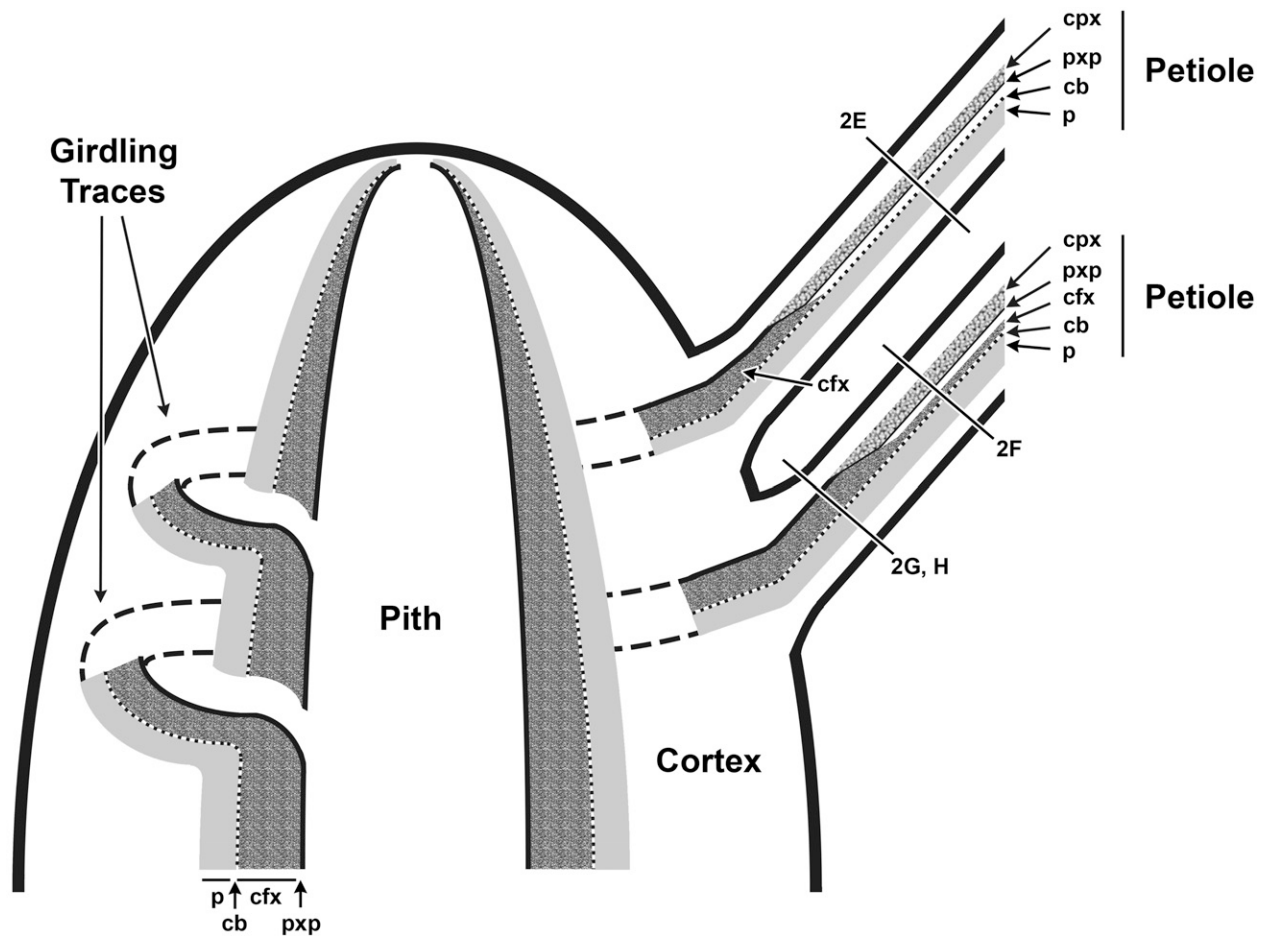
Horiuchi and Kimura (1987) have indicated that rachis shape, in particular whether the rachis is figure eight shaped (bilobed) in cross section (see Horiuchi and Kimura 1987,

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rachis assumed to be more distal than in *A* and *B*, based on the small size of the section and compressed shape of the omega pattern of the vascular bundles. Slide 22510, scale bar = 1 mm. *D*, Higher magnification of a vascular bundle from different section of petiole or rachis in *B*, showing centripetal primary xylem (*cp**x*) and phloem (*p*). Presence or absence of parenchyma or cambial tissue within the bundle is unclear. Slide 22511, scale bar = 100  $\mu$ m. *E*, Higher magnification of vascular bundle from *A*, clearly showing a wedge of centripetal xylem (*cp**x*) with protoxylem pole (*pxp*); the phloem would have been in the degraded area below xylem. Specimen 22510, scale bar = 100  $\mu$ m. *F*, Detail of periphery of rachis in *A*, showing layer of small, thick-walled cells (*sc*) near the periphery of the rachis, interpreted as sclerenchyma or "cortical armor," and thin epidermis (*ep*). Slide 22510, scale bar = 50  $\mu$ m. *G*, Tracheids from pinna attached to rachis, showing scalariform thickenings. Slide 22525, scale bar = 50  $\mu$ m. *H*, Tracheids from rachis, showing circular bordered pitting. Specimen 22525, scale bar = 10  $\mu$ m. *I*, Transverse section of *Yelchophyllum* pinna. Note regularly spaced vascular bundles. Slide 22523, scale bar = 1 mm. *J*, Detail of *Yelchophyllum* pinna in transverse section, showing vascular bundles with well-developed sheaths of thick-walled cells and structure of pinna, including upper epidermis (*ue*), lower epidermis (*le*), indistinct palisade layer (*pl*), and spongy mesophyll (*sm*). Slide 22518, scale bar = 100  $\mu$ m. *K*, Detail of vascular bundle from *J*, showing well-developed sheath of thick-walled cells (*sb*) and tissues interpreted to be xylem (*x*) and phloem (*p*) based on positional similarity to extant cycad leaves (see fig. 2*I*). Slide 22518, scale bar = 100  $\mu$ m.



**Fig. 2** Extant cycad petioles, rachides, and pinnae. *A*, Transverse section of *Ceratozamia mexicana* petiole, showing typical inverted-omega-shaped vascular bundle pattern, phloem (dark stain) abaxial, xylem (lighter stain) adaxial. Periphery of petiole has been removed. Scale bar = 2 mm. *B*, Transverse section of *Bowenia spectabilis* petiole, showing pattern of vascular bundles. Phloem external, xylem internal. Periphery of petiole has been removed. Scale bar = 2 mm. *C*, Transverse section of *Stangeria* petiole-rachis, showing pattern of vascular bundles. Phloem external, xylem internal. Scale bar = 2 mm. *D*, Transverse section of *Encephalartos villosus* rachis, showing complex arrangement of vascular bundles. Periphery of rachis has been removed. Scale bar = 2 mm. *E*, Transverse section of developing vascular bundle in petiole-rachis of *Zamia furfuracea*, showing phloem (*p*), protoxylem pole (*pxp*), and centripetal xylem (*cpx*) in which most tracheids still have relatively thin walls. Scale bar = 100  $\mu$ m. *F*, Transverse section of vascular bundle in petiole of *Bowenia spectabilis* from *B*, showing extensive xylem and phloem development, including phloem (*p*) with crushed outer cells, centrifugal xylem (*cfx*), protoxylem pole (*pxp*), and characteristic wedge of centripetal xylem (*cpx*). Scale bar = 100  $\mu$ m. *G*, Transverse section of collateral vascular bundle near the base of the petiole of *Macrozamia moorei*, showing phloem (*p*) and



**Fig. 3** Schematic diagram of cycad stem and petiole showing relative arrangement of xylem and phloem in the leaf traces as they diverge from the vascular cylinder of the stem, traverse the cortex, and enter the petiole of the leaf. The stem and cortical traces show phloem (*p*), a cambium (*cb*), and centrifugal xylem (*cfx*). In the petioles, the primary xylem is initially fully centrifugal (*cfx*), but, after passing through a transition zone, it becomes centripetal (*cpx*), although centrifugal xylem can be produced by a cambium (*cb*) in more distal portions of the petiole. The position of the protoxylem pole (*pxp*) is represented by the solid line. Transverse sections marked on petioles (marked 2E–2H) correspond to petiole-rachis bundle anatomy shown in fig. 2E–2H. Image modified after the text figure of Le Goc (1914).

fig. 2), may be a distinguishing morphological feature in some cycad taxa. They observed figure eight-shaped rachides among extant *Cycas*, *Ceratozamia*, *Dioon*, and *Encephalartos* and the Paleogene taxon *Dioonopsis*; they also speculated on the basis of published data that bilobed rachides may have occurred in some species of the fossil leaf taxa *Paracycas*, *Pseudoctenis*, *Ctenis*, and *Ctenozamites* (Horiuchi and Kimura 1987). Further observations for this study from living cycad plants and published illustrations (e.g., Stevenson 1990) indicate that leaflets of taxa with decurrent pinnae can occur in grooves (sometimes subtle) oriented parallel to the length of the rachis, thus confirming that this character deserves further exploration to determine whether it has systematic significance

at the generic level. The petiole-rachis of *Yelchophyllum* is not bilobed in cross section (fig. 1A–1C). The presence or absence of a groove into which the pinnae are inserted is difficult to discern with certainty, although at least one paratype shows a lateral indentation in some sections that may be a groove (fig. 1B). However, as pointed out by C. J. Chamberlain (unpublished data; see Norstog and Nicholls 1997), when fresh, a cycad leaf may be round in transverse section, but when dried, the same leaf may appear to have longitudinal grooves into which the pinnae are inserted. Thus, it is important that fresh material be the basis for observation of this feature (Norstog and Nicholls 1997), and it remains possible that the “groove” in this specimen is an artifact.

centrifugal xylem (*cfx*). Scale bar = 100  $\mu$ m. *H*, Transverse section of concentric vascular bundle near the base of the petiole of *M. moorei*, showing phloem (*p*) and centrifugal xylem (*cfx*). Scale bar = 100  $\mu$ m. *I*, Detail of transverse section of *Zamia integrifolia* pinna, showing two vascular bundles with sheaths extending adaxially and abaxially. Note internal structure, including upper epidermis (*ue*), palisade layer (*pl*), xylem (*x*), phloem (*p*), lower epidermis (*le*), sheath around bundle (*sb*), and spongy mesophyll (*sm*). Slide 22545, scale bar = 100  $\mu$ m. *J*, Transverse section of *Zamia integrifolia* pinna, showing regularly spaced vascular bundles. Slide 22545, scale bar = 1 mm.

Pinnae associated with the *Yelchophyllum* petiole-rachides and interpreted as representing the same leaf taxon are small and thin (fig. 1I, 1J). The structures are interpreted as pinnae rather than simple laminae because of their narrow width in transverse section (fig. 1I) and because of the absence of lateral laminae on sections of rachides that may reasonably be inferred to be nearer the distal end of the leaf based on their size and anatomy, suggesting that the lamina was not continuous on either side of the rachis (fig. 1C). Pinnae lack midribs and are characterized by a series of relatively regularly spaced vascular bundles (fig. 1I, 1J). Pinnae within Cycadales generally lack midribs, although four extant and additional fossil genera are interpreted as having pinnae with midribs. Of those taxa with midribs, the midribs are of three different types: (1) the *Cycas* type, confined to *Cycas*—a simple midrib with one vascular bundle and exarch-to-slightly-mesarch protoxylem pole; (2) the *Chigua* type, found in *Bowenia*, *Stangeria*, and *Chigua*—a compound midrib with two or more vascular bundles, each with an exarch-to-slightly-mesarch protoxylem pole (because *Bowenia* leaves are bipinnate, however, the midveins of other genera are considered homologous to the rachillae, or secondary rachides of *Bowenia*; these bear the pinnules, which lack midribs; see Stevenson et al. 1996); and (3) the *Marattia* type, found only within extinct members of Cycadales—a single large arch-shaped midrib with several vascular bundles, each with a mesarch-to-endarch protoxylem pole (Stevenson et al. 1996). In taxa lacking midribs, the pinnae are characterized by dichotomizing venation with multiple, more or less regularly spaced veins in transverse section (Brashier 1968; Stevenson et al. 1996). The pinnae of *Yelchophyllum* (fig. 1I, 1J), therefore, are most similar to those of *Zamia* (fig. 2I, 2J; see also Stevenson et al. 1996, fig. 4) and other cycads with dichotomizing venation (see Brashier 1968, figs. 1, 3–7). As in some extant cycads (Brashier 1968), the lamina of the pinna is thinner in the intercostal areas in *Yelchophyllum* (fig. 1I, 1J). Although the possibility that *Yelchophyllum* had bipinnate leaves like *Bowenia* (thus, the pinna anatomy alone is deceptive regarding the presence of a midrib) cannot be completely eliminated, the anatomy of the petiole-rachides of *Yelchophyllum* does not suggest that any are homologous to the midribs of pinnae in other cycads, as in *Bowenia* (Matte 1905; Stevenson et al. 1996). The vascular bundles in the pinnae of *Yelchophyllum* are interpreted as collateral with adaxial xylem and abaxial phloem by comparison with vascular bundles in the pinnae of extant *Zamia integrifolia* (figs. 1K, 2I).

The pinnae of *Yelchophyllum* have little internal structure (fig. 1I, 1J), appearing similar in cross section to pinnae of *Zamia* (Lamb 1923; see also fig. 2I, 2J). There are thick-walled cells extending abaxially and adaxially from the vascular bundles forming a sheath (fig. 1K), as observed in leaves of *Z. integrifolia* (fig. 2I). The poorly preserved upper and lower epidermis is composed of small cells, with a distinct layer of larger cells beneath the upper epidermis (fig. 1J). Although pinnae of most cycad genera show a distinct palisade layer below the upper epidermis (Lamb 1923), the palisade layer in *Yelchophyllum* is similar to that in some *Zamia* species in that it has “a more or less palisade region, but the cells are scarcely elongated or regular enough to constitute a true palisade” (Lamb 1923, p. 201). The spongy mesophyll,

as in extant cycads (Lamb 1923), appears to be composed of cells that are elongated transversely (fig. 1J, 2I). There is no evidence of a hypodermis or any indication that the pinnae had mucilage canals (fig. 1I, 1J). Mucilage canals have been noted in pinnae of *Dioon* and some species of *Cycas*, *Encephalartos*, *Macrozamia*, and *Stangeria*, although in most extant cycads, as in *Yelchophyllum*, they are absent (Lamb 1923; Pant 2002).

Pinnae of *Yelchophyllum* are borne laterally and displaced adaxially on the rachis, differentiating them from those of the extant genus *Lepidozamia*, which has pinnae borne adaxially along the midventral line (Stevenson 1990). The pinnae of *Yelchophyllum* are markedly thicker at the point of attachment to the rachis than they are in transverse sections taken more distally (cf. fig. 1A with fig. 1I, 1J). It is not known whether the pinnae are articulate, as in *Ceratozamia*, *Chigua*, *Microcycas*, and *Zamia*, or decurrent, as in other cycads (Stevenson 1990).

#### Other Structurally Preserved Cycadalean Leaf Taxa

Few other anatomically preserved leaf fossils attributed to Cycadales have been described. *Yelchophyllum* appears to be the sole Triassic representative, with only seven other specimens known. Two of these, one assigned to “*Nilssonsonia cf. tenuinervis*” (a name no longer valid for this specimen; see Cleal et al. 2006) from the Jurassic (Aalenian-Bajocian) of Scotland (Dower et al. 2004) and one assigned to *Nilssonsonia orientalis* from the Cretaceous of Japan (Stopes 1910), differ from *Yelchophyllum* in being simple leaves. The structure of the midrib (equivalent to the rachis of *Yelchophyllum*) has not been described in either specimen. The leaf from Scotland is similar to *Yelchophyllum* in having an outer cortex of sclerenchyma in its midrib and in likely lacking mucilage ducts in the lamina, but it differs in having well-defined layers of palisade and spongy mesophyll in the lamina (Dower et al. 2004). The lamina of *N. orientalis* has vascular bundles with adaxial exarch xylem but differs from that of *Yelchophyllum* in having an undifferentiated internal structure, resin ducts, and poorly developed bundle sheaths (Stopes 1910).

The remaining five anatomically preserved specimens represent two taxa for which the petiole-rachis structure is known. The first, *Cycadinorachis omegoides*, encompasses one petrified petiole-rachis with an omega-shaped pattern of vascular bundles from the Amarjola locality (Sharma 1973) and three specimens, each with two to five petrified leaves, from the Sonajori locality (Suthar et al. 1986), both located in intertrappen beds of the Rajmahal Formation, Rajmahal Hills, India (Sengupta 1988; Banerji 2000). The Rajmahal Traps are considered Early Cretaceous (Aptian, ca. 118 Ma according to recent  $^{40}\text{Ar}/^{39}\text{Ar}$  dating) in age (Kent et al. 2002). Sharma (1973) described the holotype from Amarjola as having concentric vascular bundles with mesarch xylem and could not link the petiole-rachis definitively to Cycadales, suggesting that the vascular bundles could also represent petiolar meristemes of a fern. Suthar et al. (1986) described additional material from Sonajori that differs from the holotype in having collateral vascular bundles, mucilage ducts, and small medullary bundles within the loop of the omega formed by the larger vascular bundles. Interestingly, the bundles in the rachides described by Suthar et al. (1986) have a distinct triangular wedge of xylem and phloem arranged to the centrifugal side of the xylem, as in Cycadales. The lamina of *C. omegoides*



from Sonajori shows a homogenous mesophyll and sheaths around the bundles with sclerenchyma connecting the bundles to the upper and lower epidermis. The omega-shaped pattern of petiole-rachis vascular bundles is clear in the *Amarjola* specimen, but it is less distinct in the Sonajori material, resembling a simple loop more than an omega (Suthar et al. 1986, fig. 1a–1c, pl. 1, figs. 1, 2, 5). While the omega-shaped pattern of petiole-rachis vascular bundles (particularly in the *Amarjola* material) appears to link *Cycadinorachis* to the Cycadales, the presence of mesarch vascular bundles and, in the Sonajori material, the presence of medullary bundles within the venter (see Yoshida 2000) of the omega differentiate *Cycadinorachis* from *Yelchophyllum* and extant members of Cycadales.

*Cretocycas yezonakajimae* is a taxon based on a single cycad petiole-rachis preserved as a permineralization in a calcareous nodule from the Upper Cretaceous (Turonian-Coniacian) of Japan (Nishida et al. 1996). This specimen is clearly cycadalean, exhibiting the characteristic inverted-omega-shaped pattern of vascular bundles, with adaxial xylem and abaxial phloem. This petiole-rachis is similar to that of *Yelchophyllum* in features where the two taxa can be compared (arrangement of bundles, arrangement of xylem and phloem within the bundles, outer cortex of thick-walled cells). Interestingly, while *Cretocycas* is otherwise well preserved, its phloem is nearly obliterated, as in some specimens of *Yelchophyllum*. Likewise, no evidence of secondary centrifugal xylem is known from either taxon. The ground tissue of *Cretocycas* includes nests of fibers and mucilage canals, and the laminar portion of the leaf is unknown.

Nishida et al. (1996) considered *Cretocycas* intermediate between *Cycadinorachis* and the petiole-rachides of extant cycads in the anatomy of its vascular bundles. Along this proposed character gradient, *Cycadinorachis* has centrarch xylem development with relatively evenly developed metaxylem around the protoxylem. *Cretocycas* has centrarch xylem development with disproportionately developed centripetal metaxylem; extant cycads are mesarch, with parenchyma separating centripetal and centrifugal xylem. However, as noted above, the structure of the vascular bundles in extant Cycadales is considered to be pseudomesarch, with centripetal primary xylem and centrifugal secondary xylem produced by a fascicular cambium (Le Goc 1914; Marsh 1914; fig. 2F).

*Cretocycas* has primary xylem that occurs in a distinct wedge similar to that formed by the primary xylem in extant cycads (fig. 2E, 2F). In a transverse section of a vascular bundle of *Cretocycas*, Nishida et al. (1996) interpreted the protoxylem as occurring near but not at the apex of the primary xylem wedge; instead, they considered it to be surrounded by centripetal and centrifugal metaxylem but with no parenchyma band separating centripetal and centrifugal xylems as in extant cycads (Nishida et al. 1996, fig. 6). Accompanying longitudinal sections of two vascular bundles, however, show protoxylem (tracheids with annular or helical thickenings) abutting the degraded zone where the phloem would have occurred, as well as metaxylem centripetal to the protoxylem (see especially Nishida et al. 1996, fig. 7), thus suggesting that the bundles may be entirely exarch as in extant Cycadales. Unfortunately, although Nishida et al. (1996) compared the anatomy of *Cretocycas* to that of extant members of Cycadales, *Cretocycas* possesses no characters (e.g., spines, prickles, dis-

tinctive hairs) that are of demonstrable importance in ascertaining its systematic position within Cycadales.

#### *Anatomy of Petiole Vascular Bundles in Structurally Preserved Fossil Stem Taxa*

Other anatomically preserved petioles attributed to the Cycadales occur as leaf bases attached to structurally preserved cycad stem taxa and can be assigned to the order with confidence. Little special attention has been given to the structure of the vascular bundles in leaf bases associated with structurally preserved fossil stems, with the exception of the leaf bases of *Charmorgia*, a petrified stem taxon from the Upper Triassic Chinle Formation of Arizona (Ash 1985). Vascular bundles in the petiole bases of *Charmorgia* were interpreted as endarch with centrifugal metaxylem and possibly some secondary xylem (Ash 1985). Ash (1985, p. 29) considered the arrangement of tissues in the bundles “noteworthy because they differ so radically from those of the living cycads,” being, in his opinion, more comparable to bundles of *Cycadeoidea dacotensis* (Bennettitales) than to those of *Cycas*. He also noted that the illustrated leaf base vascular bundles of *Lyxoxylon* (Gould 1971, figs. 19–21), another structurally preserved stem taxon from the Upper Triassic Chinle Formation in the southwestern United States, have the same organization as those of *Charmorgia*. A petiole vascular bundle illustrated from *Bororoa* (Petriella 1972, pl. 7, fig. f), from the Tertiary of Argentina, also appears to lack the classic diploxylic arrangement of the Cycadales and does not have an obvious centripetal xylem wedge. Zhang et al. (2006) similarly described a structurally preserved fossil cycad stem, *Lioxylon liaoningense* from the Jurassic of China, as having petiole vascular bundles with endarch protoxylem and some secondary xylem (see Zhang et al. 2006, fig. 4d, 4e).

While it may seem that the petiolar vascular bundles of these other extinct taxa differ significantly from those of *Yelchophyllum* and extant members of the Cycadales, the arrangement of vascular tissues in these taxa may actually be much like their arrangement in extant Cycadales. Le Goc (1914, p. 184–185) described the structure of the bundles in extant cycads (species of *Ceratozamia*, *Cycas*, *Dioon*, *Encephalartos*, and *Stangeria*) as follows, beginning with their divergence from the stele, traversing the cortex, and then moving from the proximal toward the distal end of the petiole-rachis. The xylem of the stele and of the leaf traces in the cortex is endarch; at ca. 1 cm from the junction of the leaf and stem, the bundles in the petiole take on the characteristic omega-shaped pattern. For the first 2 cm of the petiole, although the bundles may be variable in form (collateral or concentric), the xylem in the bundles is still “entirely endarch or centrifugal” (fig. 2G, 2H; this centrifugal growth was interpreted by Le Goc as largely secondary). A transition zone occurs over the next 3–4 cm of the petiole, so that the typical centripetal-centrifugal structure of the vascular bundles can be observed ca. 5–6 cm from the base of the petiole (fig. 3). The centrifugal xylem is longitudinally continuous, beginning with the divergence of the leaf traces from the stele, through the cortex, and into the petiole-rachis, but the centripetal primary xylem apparent in transverse sections of the more distal regions of the petiole-rachis is independent (Le Goc 1914). Marsh (1914) came to largely similar conclusions in a study

of *Stangeria*, except that all centrifugal bundles at the base of the specimen he examined were collateral, and the transition from centrifugal to centripetal primary xylem took place within the most basal centimeter of the petiole; further, he noted that the amount of centrifugal xylem did not simply decrease distally but actually increased just below the level of insertion of the first pinna and persisted into the terminal leaflet.

According to Ash (1985), the maximum extent of the leaf bases of specimens of *Charmorgia* is ca. 6 cm, suggesting that it is possible that the vascular bundles in the sections he observed represent the typical cycad anatomy near the petiole base. Likewise, only the basal parts of the petioles in *Lioxylon* are preserved (Zhang et al. 2006). The illustrated vascular bundle of *Bororoa* may similarly be near the petiole base; however, since cataphylls have been reported from *Bororoa* (Artabe et al. 2005), this bundle may also be a cataphyll vascular bundle (see figs. 15, 17 in Hermsen et al. 2006 for comparative illustrations of a cataphyll and petiole vascular bundles in extant cycads). While the length of the petioles of *Lyssoxylon* is not recorded, the illustrated leaf traces referred to by Ash (Gould 1971, figs. 19–21) occur in the cortex. Le Goc (1914, p. 189–190) noted that the centrifugal xylem of the petioles “is a continuation of the normal centrifugal xylem of the stele and the girdles” (fig. 3), and, thus, the arrangement of the bundles passing through the cortex of *Lyssoxylon* is also typical of Cycadales.

The endarch-to-exarch arrangement of protoxylem in the extant Cycadales is especially interesting in the context of a possible connection between *Antarcticycas* and *Yelchophyllum*, the only known cycad stem taxon and the only known cycad leaf taxon, respectively, occurring at the same locality. If indeed these two taxa are part of the same plant, then that plant has the same unique anatomy characteristic of extant members of Cycadales. Xylem in the vascular cylinder of *Antarcticycas* is endarch (fig. 4C), and the vascular traces traversing the cortex have endarch primary xylem (fig. 4D), as in extant Cycadales. The vascular bundles in *Yelchophyllum*, however, are exarch, similar to those in extant Cycadales (figs. 1E, 2F). Notably, a lateral appendage that may represent a petiole diverging from the *Antarcticycas* stem (fig. 4A, 4B) has vascular bundles with anatomy similar to that found in *Charmorgia* and *Lioxylon* (fig. 4E).

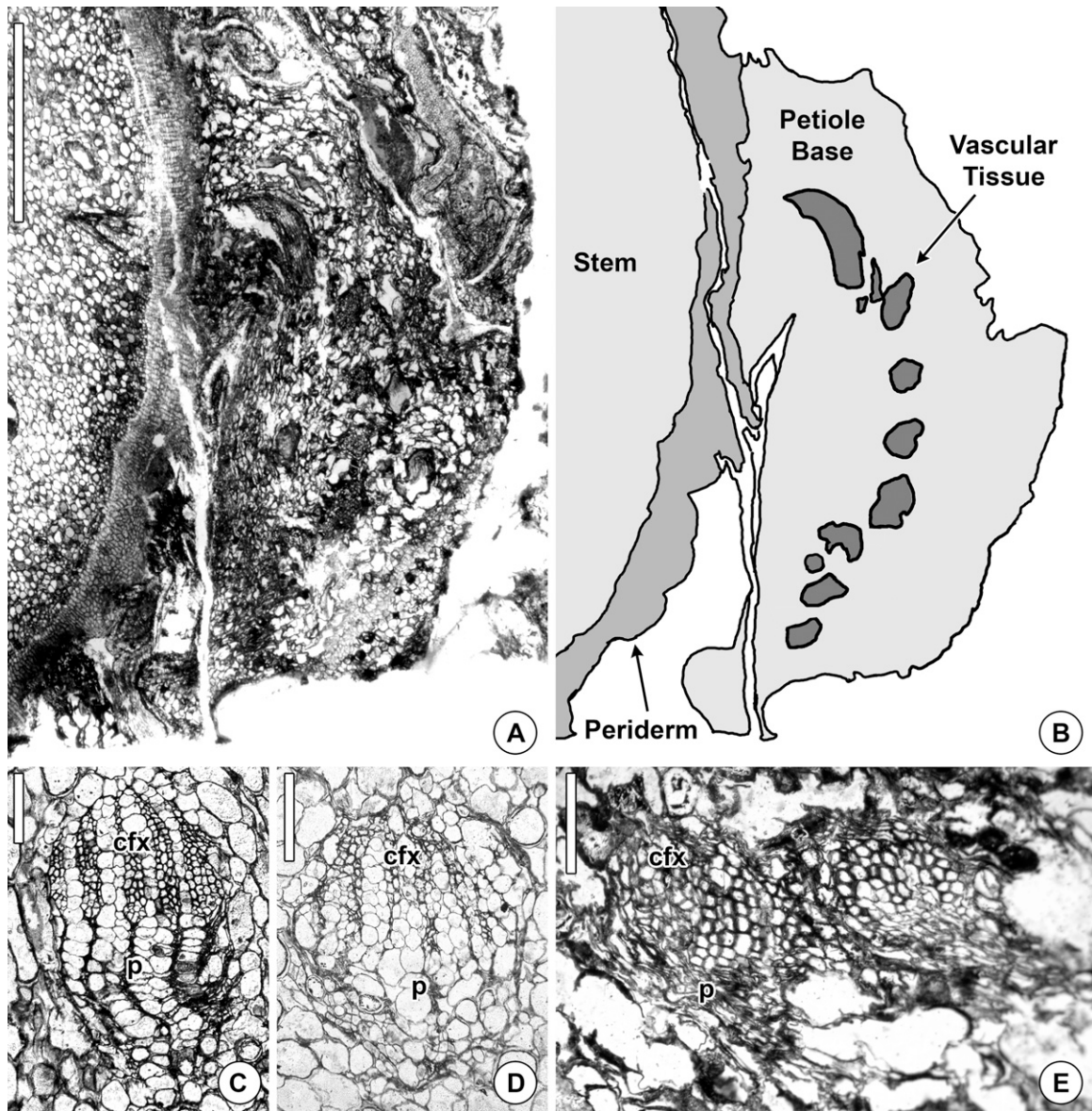
### Conclusions

Although it was once suggested that *Dicroidium* leaves in the permineralized peat from Fremouw Peak might belong to *Antarcticycas* stems (Delevoryas 1990a), this conjecture was based on the absence of typical cycadophytic leaves and recognizable corystosperm stems at the site. We now know that *Dicroidium* leaves were borne on *Kykloxylon* stems, and both are assigned to the Corystospermales (Meyer-Berthaud et al. 1993). The discovery of *Yelchophyllum* now clearly indicates that leaves with characteristic cycad anatomy are present in the Middle Triassic permineralized peat.

The anatomical characteristics of *Yelchophyllum*, including the distinctive inverted-omega-shaped pattern of vascular bundles, exarch xylem in the petiole-rachides, and pinnae lacking midribs, clearly demonstrate that leaf anatomy similar to that of extant Cycadales was present by the Middle

Triassic. Evolution of the elaborated-omega-shaped petiolar vascular pattern from the simple (unmodified) inverted-omega pattern appears to have taken place sometime after the Triassic, no later than the Jurassic to Cretaceous (Artabe et al. 2004; Zhang et al. 2006), although direct fossil evidence for the evolution of the elaborated-omega-shaped vascular bundle pattern is sparse. Interestingly, similar timing occurs in the evolution of stem anatomy from the plesiomorphic monoxyle to derived polyxyle types, the former first documented in the Middle Triassic (Smoot et al. 1985), the latter definitively in the Jurassic (centripetal polyxyle; Zhang et al. 2006) to Cretaceous (centrifugal polyxyle; Nishida et al. 1991; Artabe et al. 2004, 2005).

The evolution of pinna midribs, which occur today only in *Cycas*, *Stangeria*, *Chigua*, and *Bowenia*, is difficult to discern in the fossil record. Given their different anatomies, midribs appear to be independently derived in each of these genera. Pinnate leaves with pinnae lacking midribs are definitively documented from the Triassic to the Recent (e.g., Florin 1933; Harris 1964; Anderson and Anderson 1989; Kvaček 2000, 2002). *Yuania chinensis*, a leaf of this type associated with the cycad megasporophyll *Crossozamia* from the Permian of China (Du and Zhu 1982), suggests that cycads with pinnae lacking midribs may have originated in the Paleozoic, although some other species of *Yuania* have been linked by association with *Discinites* in the Noeggerathiales (Wang and Shen 2000; Wang et al. 2004), casting some uncertainty on the *Crossozamia*-*Yuania* connection. Notably, *Y. chinensis* may show features intermediate between the “typical” cycad leaf type (pinnae without midribs, conduplicate ptyxis) and the leaf type characteristic of extant *Cycas*, since its proposed juvenile form, *Tianbaolinia*, exhibits circinate vernation of the pinnae (Gao and Thomas 1989a, 1989b). *Cycas*-like leaves with a single midrib, presumably (but not necessarily demonstrably) of the *Cycas* type (Stevenson et al. 1996), including *Aricycas*, *Paracycas*, and *Cycas*, are known from the Triassic to recent (e.g., Yokoyama 1911; Holden 1914; Harris 1964; Krassilov 1978; Ash 1991; Liu et al. 1991; Liu 1992); they may occur as early as the Permian (Cycadites in Pant et al. 1995). Other Triassic to Cretaceous pinnate leaves, including *Ticoa*, *Mesodescolea*, and *Kurtziana* (however, see Herbst and Gnaedinger 2002 on Triassic *Kurtziana*), have pinnae with midribs of the *Marattia* type (Stevenson et al. 1996), a type of midrib not found within extant Cycadales. Fossil forms assigned to *Bowenia*, which has a *Chigua*-type midrib (Stevenson et al. 1996), have been documented only back to the Eocene (Hill 1978, 1998; however, see Pant 2002 on *Boweniaeocenica*). Although *Eostangeria*, considered similar to *Chigua* in morphology and epidermal structure, is known as early as the Paleocene (Kvaček and Manchester 1999), the anatomy of its midribs is unknown. Additional reports of leaves similar to *Chigua* and *Stangeria* are known from the Permian, but these are questionable (Pant et al. 1995; Pant 2002). Thus, based on the available fossil evidence, it appears that pinnate leaves with or without midribs on the pinnae may have been present by the Permian, and at least three types of pinnae—no midrib, *Cycas* type, and *Marattia* type—probably occurred on pinnately compound leaves by the Triassic to Jurassic. The *Marattia* type is not represented in extant Cycadales, and variations on the *Chigua*-type midrib



**Fig. 4** Vascular bundles in *Antarcticycas*. *A*, Transverse section of lateral appendage possibly representing a petiole attached to stem with vascular tissue (see *B*); vascular bundles are not yet forming a distinct omega shape. Part of the abaxial surface of the lateral appendage has been cut off by a crack in the specimen. Slide 22540, scale bar = 2 mm. *B*, Tracing of putative petiole and stem shown in *A*, clarifying position of vascular tissue. Scale approximately the same as that in *A*. *C*, Vascular bundle in vascular cylinder of *Antarcticycas* stem, showing centripetal xylem (*cfx*) and phloem (*p*). Slide 22540, scale bar = 200  $\mu\text{m}$ . *D*, Vascular bundle traversing cortex of *Antarcticycas* stem, showing centrifugal xylem (*cfx*) and phloem (*p*). Slide 22539, scale bar = 200  $\mu\text{m}$ . *E*, Vascular bundles from another section of lateral appendage shown in *A*, showing centrifugal xylem (*cfx*) and phloem (*p*). Slide 22541, scale bar = 200  $\mu\text{m}$ .

may have evolved in the Cenozoic, where *Eostangeria* and *Bowenia* leaves are first documented.

The evolution of the pinnate cycad leaf is also enigmatic. Mamay (1976) once hypothesized that the pinnate cycad leaf had evolved from an entire-margined *Taeniopteris*-type leaf and that it did not evolve until the Jurassic, where a variety of cycad leaf morphologies co-occur. The purported correlation between time and degree of dissection—younger leaves evolving greater dissection of the margins until a fully pinnate leaf type evolved in the Mesozoic—continues to persist

in the literature (e.g., Zheng et al. 2005), although, as noted by Delevoryas (1990b), pinnate leaf forms thought to represent Cycadales have been described from sediments as old as the Permian (Du and Zhu 1982; Gao and Thomas 1989b) and are abundant by the Triassic (e.g., Anderson and Anderson 1989; Artabe et al. 1991; Ash 1991; Artabe and Stevenson 1999). Bipinnate to tripinnate forms (e.g., *Mesodescolea*, *Ticoa*) appear by the Jurassic to Cretaceous (e.g., Gee 1989; Artabe and Archangelsky 1992; Rees 1993; Artabe and Stevenson 1999). Simple leaves of the *Taeniopteris* type that

have been attributed to Cycadales (e.g., *Bjuvia*, *Doratophyllum*, *Glandulataenia*, *Lepingia*, some *Macrotaeniopteris*, *Sueria*, some *Taeniopteris*, *Yixianophyllum*) occur from the Permian to Cretaceous (e.g., Harris 1932; Florin 1933; Mamay 1976; Gillespie and Pfefferkorn 1986; Gao and Thomas 1989b; Pant 1990; Artabe 1994; Liu and Yao 2002; Ash 2005; Zheng et al. 2005). However, at least one of the Permian forms is now considered unlikely to be cycadalean (Axsmith et al. 2003), and only the Cretaceous taxon *Sueria* has been demonstrated to have features, such as perforated epidermal cells and accessory cell coronas (Artabe 1994; Artabe and Stevenson 1999), hypothesized to be unique to Cycadales (Hermsen et al. 2006, table 1). Thus, simple and pinnate leaves may precede bi- to tripinnate forms, and diversity in leaf morphol-

ogy may peak sometime in the Mesozoic (after which simple and tripinnate leaves disappear), well after the first documentation of putative simple and pinnate forms in the Permian to Triassic. The possibility that the *Taeniopteris*-type leaf is the primitive morphology in the Cycadales can be fully explored only through a better accounting and contextualization of the Paleozoic leaf record of the group.

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