LARGE PERMINERALIZED SEEDS IN THE JURASSIC OF HAIDA GWAII, WESTERN CANADA: EXPLORING THE MODE AND TEMPO OF CYCAD EVOLUTION

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Premise of research. Numerous large permineralized fossil seeds from the Jurassic of Haida Gwaii, western Canada, provide evidence for the mode and tempo of cycad evolution.

Methodology. Fossil seed specimens are studied from external morphology and serially sectioned by the classic cellulose acetate peel technique to reveal anatomical features of the integument, vascular system, nucellus, and gametophyte. Fossils are compared to living cycad seeds that are also examined from external views, dissections, and anatomical preparations.

Pivotal results. The fossil seeds are described as *Traskia maahlae* gen. et sp. nov. Features of the integument and vascular system reveal that *T. maahlae* is a stem group cycad that shares seed architecture and mode of germination with living *Cycas* spp.

Conclusions. *Traskia maahlae* adds to a growing body of paleontological data on stem and crown group cycads. Results suggest that modern pollination and postpollination biology and the two contrasting modes of cycad seed germination evolved during the Mesozoic but that crown group cycad species may not have appeared until the Cenozoic.

Keywords: cycad, fossil and living, ovule and seed, paleobotany, *Traskia*, vascular architecture.

Introduction

The discovery of anatomically preserved plant fossils, including remains of cycads, in Jurassic deposits from Haida Gwaii (formerly the Queen Charlotte Islands), off the west coast of continental British Columbia, Canada, initiated anatomical studies of mid-Mesozoic fossil plants from the far west of North America nearly 150 yr ago (Dawson 1873). The original report of these fossils emphasized large cycad seeds described as *Cycadeocarpus columbianus* Dawson, associated cycad foliar fragments, and cupressaceous wood (Dawson 1873). More recent collections from the same source on South Balch Island, just north of Maude Island and south of Queen Charlotte City in Skidegate Inlet, have yielded hundreds of large permineralized cycad seeds and associated plant remains. Such seeds have also been reinvestigated by Chaloner and Hemsley (1992) and in an unpublished MS thesis (King 2000). As a result of those contributions and more recent collections, we now realize that the South Balch Island assemblage includes two distinctly different types of cycad seeds that do not conform to the structure of crown group genera.

In this article, we describe the second species of anatomically preserved Jurassic cycad seeds from the South Balch Island assemblage and name it *Traskia maahlae* gen. et sp. nov. Rothwell, Stockey, Stevenson et Zumajo-Cardona. We compare *T. maahlae* with the seeds of living and previously described fossil cycads and use those data to assess the diversity and tempo of evolution of cycad integumentary histologies, seed vascularization, pollination/postpollination biology, and germination mechanisms. These data expand our understanding of the species richness of Jurassic cycads, establish a minimum age for the divergence of the two major patterns of living cycad seed germination (namely, that of the Cycadaceae and that of the Stangeriaceae/Zamiaceae; Hermsen et al. 2006, 2009), and provide additional data for assessing the pattern of phylogeny for stem and crown group cycads through time.

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Material and Methods

This study is based on more than 100 large seeds of two distinctly different morphologies that are preserved by carbonate

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cellular permineralization in beach deposits along the south shore of South Balch Island in Skidegate Inlet, which is south of Queen Charlotte City in the Haida Gwaii archipelago off the west coast of continental Canada (Chaloner and Hemsley 1992). The exposure is located at lat. 53°13′15″N, long. 132°4′44″W (roughly between lat. 53.222496 and long. 132.0789740 and lat. 53.22798 and long. 132.081318). Surface strata of South Balch Island are part of the Yakoun Formation, Vancouver Group of the Callovian Stage of the earliest Upper Jurassic (Chaloner and Hemsley 1992).

Fossil seeds investigated in this study are from several collections, with a total of 51 specimens of the new genus and species, more than 50 specimens of *Cycadeocarpus columbianus*, and numerous small abraded/eroded specimens that consist primarily of the seed megaspore membrane and internal contents. The last group cannot be assigned to either *Cycadeocarpus* or the new genus because taxonomically diagnostic features are not present in specimens that consist only of megaspore membrane and internal structures. Seeds were sorted, photographed, measured, and studied for external features, and then 12 were selected for serial sectioning (i.e., SBI 10, SBI 13, SBI 18, SBI 36, SBI 39, SBI 40, SBI 41, SBI 42, SBI 45, SBI 46, SBI 48, and SBI 50) using the classic cellulose acetate peel technique (Joy et al. 1956). Peels were mounted on glass microscope slides using Eukitt, a xylene-soluble mounting medium (O. Kindler, Freiburg, Germany). Low-magnification photographs were captured with a MicroLumina digital scanning camera (Leaf Systems, Bedford, MA) focused through a Nikkor 105-mm AF macro lens (Nikon, Melville, NY). Higher-magnification images were captured with a Better Light scanning camera (Precision Digital Imaging System, Placerville, CA) mounted on a Leitz Aristophot stand (E. Leitz, Wetzlar, Germany) and focused either with Summar lenses (E. Leitz, Wetzlar, Germany) or with a Zeiss WL compound microscope (Carl Zeiss, Oberkochen, Germany). Images were processed with Adobe Photoshop CS2 (Adobe Systems, San Jose, CA).

Living cycad ovules and seeds of *Zamia furfuracea* L.f. ex Aiton and *Cycas rumphii* Miq. were collected from Fairchild Tropical Garden (accession numbers FTG 63–424 and FTG 65–416) and from the Montgomery Botanical Center (accession number 98–1804A), respectively, for comparison with the fossils. Specimens were immediately fixed in formalin–propionic acid–alcohol (5 parts 37% formaldehyde, 5 parts propionic acid, and 90 parts 50% ethanol) and stored in 50% ethanol until used. Ovules were dehydrated manually through an alcohol-toluene series and embedded in Paraplast X-tra (Fisher Healthcare, Houston, TX). Specimens were sectioned at 10–14 μm with an AO Spencer 820 rotary microtome. Sections were stained with Johansen's safranin, counterstained with 0.5% Astra Blue (Kraus et al. 1998), and mounted in Canada Balsam (Sigma-Aldrich, St. Louis, MO). They were viewed and digitally photographed with a Zeiss Axioplan compound microscope equipped with a Nikon DXM1200C digital camera with ACT-1 software.

Although integumentary maturation typically occurs late in the development of gymnospermous ovules (Rothwell 1971; Singh 1978), it should be noted here that the sclerotesta of living cycads does not truly differentiate until the megagametophyte has matured with archegonia present and there is a fully developed vascular system. Thus, the incipient sclerotesta of the extant seeds is identifiable in figures 5*b* and 6*e*, but cells are not fully lignified until much later, after mature vascular bundles are present (cf. fig. 6*a*, 6*d*, and 6*e* with 6*b*).

Results

Systematics

Order—Cycadales Pers. ex Bercht. & J.Presl

Family—Incertae Sedis

Genus—Traskia *gen. nov. Rothwell, Stockey, Stevenson et Zumajo-Cardona*

Generic diagnosis. Cycad plants with anatomically preserved seeds having 180° rotational symmetry, longitudinally oriented germination suture in major plane of symmetry, ovate-elliptical in longitudinal section, oval in cross section. Integument of thin endotesta, sclerotesta of sclereids, and thick outer sarcotesta. Nucellus adnate to integument up to level of large pollen chamber. Pollen chamber wall extending through micropylar canal to seed apex as elongated nucellar beak. Two massive, radially oriented, platelike vascular bundles entering chalaza near sides of seed, extending through integument to endotesta, passing basally to terminate below seed cavity, and extending apically as two triangular bundles up to level of pollen chamber in the major plane of symmetry.

Etymology. The generic name *Traskia* is proposed to honor the Trask brothers of Vancouver Island. Mike Trask, geologist, paleontologist, resident of Vancouver Island, and cycad enthusiast, has been an energetic collector and a supporter of our paleobotanical studies and has generously provided several of the specimens used in this study. Pat Trask, paleontologist and curator of natural history at Courtenay and District Museum and Palaeontology Centre, has assisted in field studies, has graciously provided loans of fossil materials, and has accepted the specimens of *Traskia maahlae* for curation at the museum. Both are productive paleontologists in their own right and for many years have been valued supporters of our paleobotanical studies of Vancouver Island fossils.

Type species. *Traskia maahlae* sp. nov. Rothwell, Stockey, Stevenson et Zumajo-Cardona.

Specific diagnosis. Seeds ranging from 3 to 7 cm long and 3 to 7 cm wide in the major plane and 2.4 to 3.2 cm thick in the minor plane. Sarcotesta 7–16 mm thick, of oval cells 120–330 μm in greatest dimension; sclerotesta 0.5–1.1 mm thick, of isodiametric sclereids 35–95 μm in diameter; endotesta of thin-walled cells 40–65 μm in diameter.

Holotype. SBI 46 (figs. 4*a*, 4*b*, 4*d*–4*f*, 5*d*, 5*e*).

Paratypes. SBI 10 (fig. 1*a*), SBI 13.

Stratigraphic position. Yakoun Formation, Vancouver Group of the Callovian Stage.

Locality. Shingle beach along south side of South Balch Island in Skidegate Inlet, south of Queen Charlotte City in the Haida Gwaii archipelago off the west coast of continental Canada; at lat. 53°13′15″N, long. 132°4′44″W (roughly between lat. 53.222496 and long. 132.0789740 and lat. 53.22798 and long. 132.081318).

Fig. 1 External views of permineralized seeds from South Balch Island, all × 1.0. *a–h*, *l*, *m*, *Traskia maahlae*. *j*, *k*, *Cycadeocarpus columbianus*. *a*, Lateral view of specimen SBI 10 in the major plane of symmetry. Note the apparent wing accentuated by sediment (gray; *lower right*). *b*, Lateral view of SBI 62 showing suture (arrow). *c*, SBI 36, with irregular longitudinal ribs and furrows. *d*, Somewhat eroded specimen SBI 5 in apical view, showing 180° rotational symmetry, the position of the pollen chamber (white arrow), and the lateral sutures (black arrows). *e*, Lateral view of the somewhat abraded specimen SBI 3 in the major plane of symmetry. *f*, Lateral view of SBI 13, showing longitudinal suture (arrows). *g*, Apical view of the highly abraded specimen SBI 61. *h*, Lateral view of the highly abraded SBI 61 in the major plane of symmetry. *i*, Lateral view of the major plane of SBI 42. Arrows indicate the suture. *j*, Apical view of highly abraded *C. columbianus*. Arrowheads indicate channels of coronula. SBI 60. *k*, Lateral view of the highly abraded specimen of *C. columbianus* in *j*. SBI 60. Arrowheads indicate canals of coronula. *l*, Lateral view of an abraded specimen. SBI 48. *m*, Lateral view of the abraded specimen SBI 59's surface, with irregular ridges and furrows. Scale bar = 2 cm.

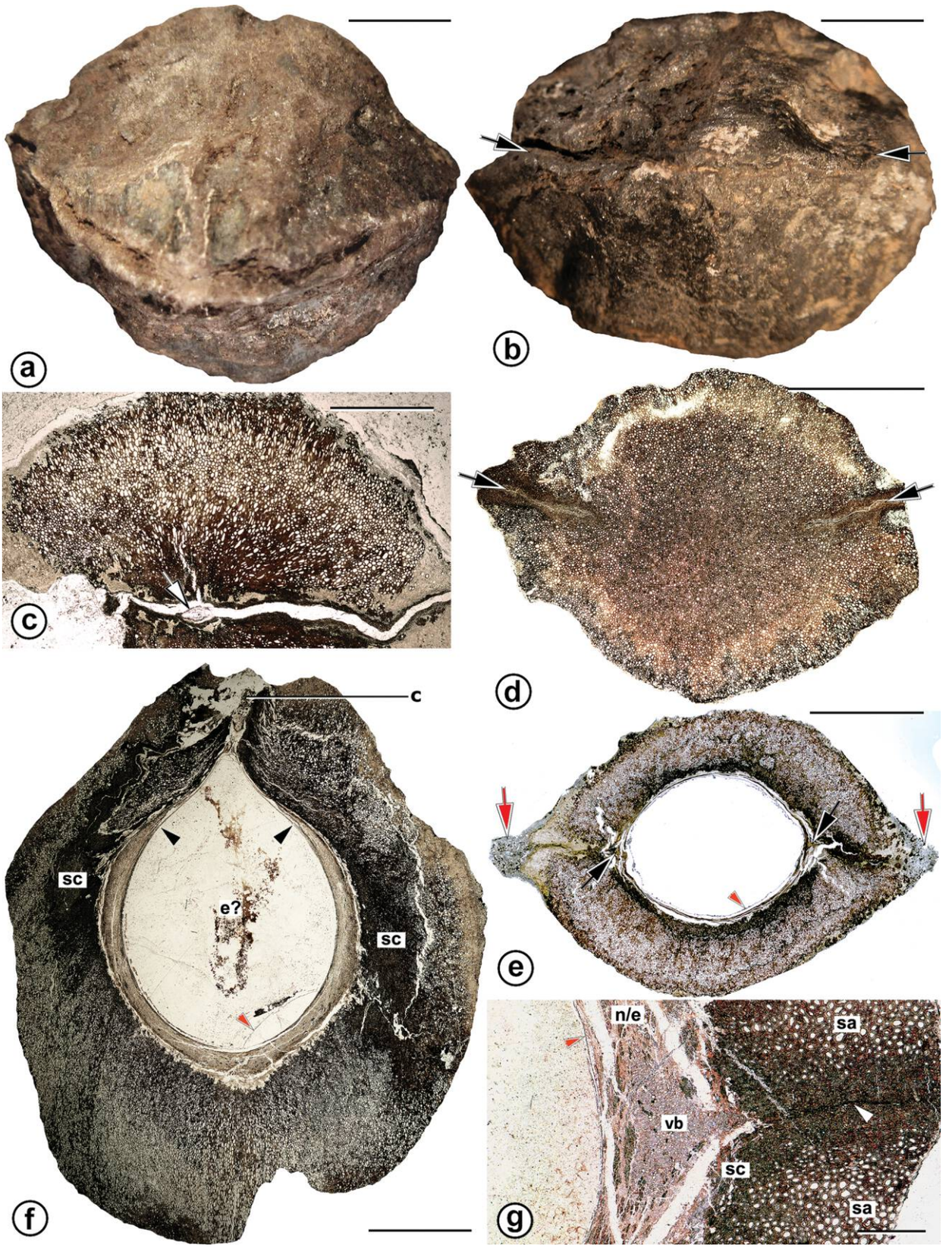

Fig. 2 *Traskia maahlae* gen. et sp. nov. *a*, Exterior view of apex, showing 180° rotational symmetry and longitudinal suture. SBI 39. ×4.1. Scale bar = 5 mm. *b*, Exterior view of chalaza, showing 180° rotational symmetry and positions where vascular bundles enter the chalaza (arrows).

Stratigraphy and age. Yakoun Formation, Vancouver Group of the Callovian Stage of the earliest Late Jurassic (Chaloner and Hemsley 1992).

Etymology. The specific epithet *maahlae* (from *máahl*, seed, in the native Haida language) acknowledges the origin of the specimens in the lands of the Haida people, who are the aboriginal residents of the Haida Gwaii (literally "Islands of the Haida People") archipelago.

Repository. Paleobotanical collections of the Courtenay and District Museum and Palaeontology Centre, Courtney, Vancouver Island, British Columbia, Canada.

Systematic discussion. In an unpublished thesis, King (2000) described and named specimens of *T. maahlae* as *Dawsonocarpus haidorum*. However, according to the International Code of Botanical Nomenclature (Turland et al. 2018), that name is not effectively published. Therefore, as a nomen ineditum, *D. haidorum* must be regarded as an invalid name.

Results

Gross Seed Morphology

Seeds of *Traskia maahlae* show a wide range of size, shape, and external features, but all are roughly elliptical in longitudinal view with a rounded base and taper to the micropyle (fig. 1*a*–1*c*, 1*e*, 1*f*, 1*h*, 1*l*, 1*m*). Specimens are typically oval or flattened in end view, displaying 180° rotational symmetry (figs. 1*d*, 1*g*, 2*e*), and all sectioned specimens have a common suite of histological features. Many seeds are relatively complete (fig. 1*a*–1*f*, 1*i*, 1*m*). Others are broken in half in the major plane of symmetry or are abraded to varying degrees and therefore are smaller than the complete specimens (fig. 1*g*, 1*h*). Nevertheless, such seeds can often be distinguished from abraded specimens of *Cycadeocarpus columbianus* by their symmetry (i.e., 180° rotational symmetry rather than radial symmetry), overall shape, histological features, and the absence of the characteristic ring of canals that surrounds the micropyle of *C. columbianus* (fig. 1*j*, 1*k*, arrowheads).

Relatively unabraded specimens of *T. maahlae* typically show a longitudinal suture in the major plane of symmetry that extends over the apical region of the seed (figs. 1*d* [black arrows], 2*a*) and basally to near the chalaza (fig. 1*f*, arrows). Some specimens have a relatively smooth outer surface (fig. 1*b*). Others have a lumpy appearance (fig. 1*d*, 1*f*), irregular longitudinal ridges and furrows (fig. 1*a*, 1*c*, 1*i*), and/or a winglike rim in the major plane of symmetry (fig. 1*a*, 1*c*, 1*e*) that is accentuated by (or consists primarily of) rock matrix that adheres to the margin of the integument (fig. 2*e*, red arrows). We believe that these variations represent taphonomic effects of differential decay, compaction, and/or predepositional abrasion experienced by individual specimens.

Specimens range from 2.8 to 7.1 cm long (mean = 5.23 cm; $n = 29$), from 3.2 to 7.5 cm wide in the major plane of symmetry (mean = 4.67 cm; $n = 27$), and from 2.4 to 3.2 cm thick in the minor plane of symmetry (mean = 3.36 cm; $n = 27$). They are oval in cross section (figs. 1*d*, 1*g*, 2*a*, 2*b*, 2*e*), as is the seed cavity (fig. 2*e*). The integument is roughly ovate in longitudinal section, with a bluntly rounded chalaza, and often tapers to a pointed apex (figs. 1*a*–1*c*, 1*e*, 1*f*, 1*l*, 1*m*, 2*f*). There is a large seed cavity that in longitudinal section is also rounded at the chalaza and tapers to a point at the base of the micropylar canal (fig. 1*f*).

Integument

As is characteristic for the seeds of living cycads, the integument of *T. maahlae* is quite thick and prominent (fig. 2*e*, 2*f*). It is up to 16 mm thick in relatively unabraded specimens, consisting of an endotesta, sclerotesta, and broad outer sarcotesta (figs. 2*g*, 3). The endotesta is continuous with the nucellus except in the apical region (i.e., n/e in figs. 2*g*, 3), and the combined endotestal/nucellar tissues form a 0.5–1.0-mm-thick zone of small thin-walled cells with golden-colored walls (figs. 2*g*, 3, 4*c*, 4*d*). Cell walls are incompletely preserved, appear to be longitudinally oriented along the sides of the seed, and are more isodiametric at the chalaza. Within this tissue there are darker scattered or clustered isodiametric cells 40–80 μm in diameter with more prominent walls (figs. 2*g*, 3, 4*a*, 4*c*, 4*d*). Most of the latter are easily identified by their black contents (fig. 3*d*, arrow), but others intergrade with cells that lack contents (fig. 4*d*).

Sclerotesta surrounds the endotesta (figs. 2*e*, 2*g*, 3), extends toward the periphery of the integument adjacent to the longitudinal suture in the major plane of symmetry (figs. 2*e*, 2*f*, 4*a*), and accompanies the vascular bundles in the chalazal zone (fig. 2*d*). At low magnification, the sclerotesta is distinctly darker than the endotesta and sarcotesta (fig. 2*e*, 2*f*), but at higher magnifications it resolves as relatively small isodiametric cells with thick walls (figs. 2*g*, 3) that measure 35–59 μm in the greatest dimension. At the inner margin of the sclerotesta in some longitudinal sections, there are patches of thin-walled cells that alternate with the sclereids (figs. 3*e* [arrows], 4*d*).

The sarcotesta that forms the thick outer zone of the integument consists of oval to isodiametric cells that are larger than those of the sclerotesta (figs. 2*c*–2*g*, 3, 4*c*) and that measure 120–330 μm in diameter. Sarcotestal cells tend to have thicker walls toward the inner margin of the zone and thinner walls toward the periphery (figs. 2*c*, 2*e*, 4*c*), but the transition is inconsistent, and there are areas of thicker-walled cells that

SBI 39. ×4.1. Scale bar = 5 mm. *c*, Cross section of the apical region, showing the histology of the integument, a split at the suture, and the tip of the nucellar beak (arrow) within the micropylar canal. SBI 10 B bot #44. ×4. Scale bar = 5 mm. *d*, Cross section of chalaza below the nucellus, showing vascular bundles entering the seed (arrows) and the histology of the integument at this level. SBI 10 B top #3. ×2.5. Scale bar = 1 cm. *e*, Cross section at midregion, showing symmetry, histological features of the integument and nucellus, and megaspore membrane (arrowhead). Note the gray sediment forming narrow wings of the seed (red arrows). SBI 10 B top #3. ×2.0. Scale bar = 1 cm. *f*, Midlongitudinal section in the major plane, showing the seed shape, micropylar canal, sclerotesta lining of sutures (sc), level where the nucellus (pollen chamber wall) separates from the endotesta (black arrowheads), and position of the megaspore membrane (red arrowhead). The horizontal line at c marks the level at which the section in *c* was made. SBI 46 A #103. ×3.8. e? = embryo? Scale bar = 2 cm. *g*, Cross section in the midregion, showing an integument with a suture (white arrowhead), vascular bundle (vb), histology, and megaspore membrane (red arrowhead) adjacent to the nucellar tissue. n/e = nucellus and endotesta; sa = sarcotesta; sc = sclerotesta. SBI 13 A bot #8. ×13. Scale bar = 1 mm.

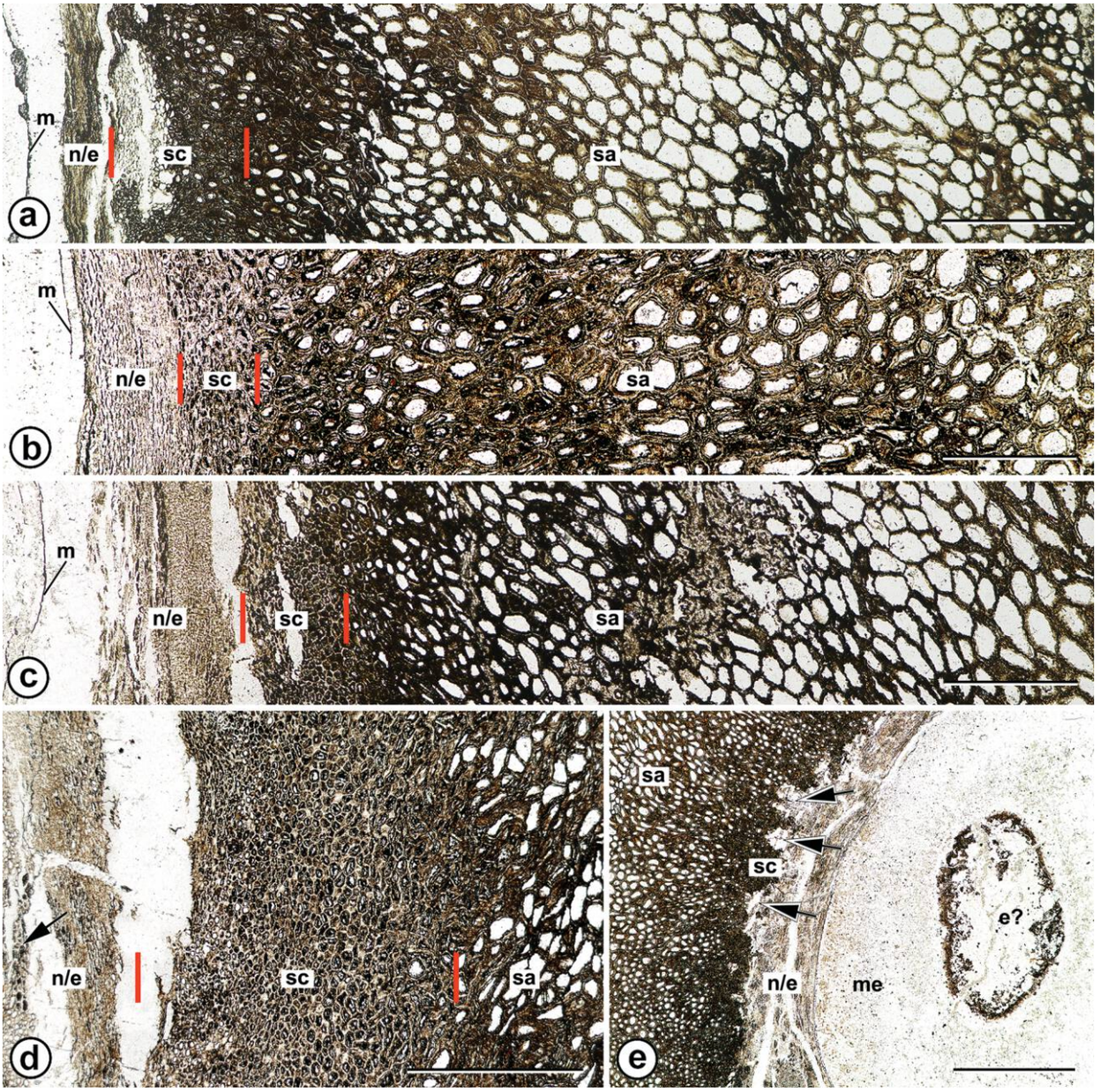

Fig. 3 *Traskia maahlae* gen. et sp. nov. *a–c*, Variation in the anatomy of the integument and nucellus, as seen in transverse (*a*, *b*) and longitudinal (*c*) views. Megaspore membrane (m) at the left, nucellus adnate to the endotesta (n/e), sclerotesta (sc), and sarcotesta (sa) at the far right. Red lines are placed at the margins of various tissues. *a*, SBI 10 B top #4. × 22. Scale bar = 1 mm. *b*, SBI 39 B bot #12. × 22. Scale bar = 1 mm. *c*, SBI 48 A #31. × 22. Scale bar = 1 mm. *d*, Enlargement of nucellus-endotesta (n/e), sclerotesta (sc), and sarcotesta (sa), showing features of the cells in each zone. The arrow indicates a patch of the nucellus made up of cells with dark contents. SBI 48 A #50. × 30. Scale bar = 1 mm. *e*, Cross section of a seed showing features of the nucellus-endotesta (n/e), sclerotesta (sc), sarcotesta (sa), megagametophyte (me), and probable embryo (e?) in the midregion. Arrows indicate parenchymatous areas inside the sclerotesta. SBI 13 A bot #16. × 10. Scale bar = 2 cm.

alternate with areas of thinner-walled cells throughout much of the outer part of the sarcotesta (figs. 2*c*, 3*a*). The inconsistent distribution of thin- and thicker-walled cells accounts for the irregular longitudinal ridges and furrows at the surface of some taphonomically altered specimens (fig. 1*a*, 1*c*, 1*i*).

In the apical region, the integument narrows toward the tip of the micropylar canal (fig. 2*a*, 2*f*), and the thickness of the sarcotesta also diminishes apically. As seen in section views near the seed apex, the micropylar canal is surrounded by sclerotesta and has a distinct internal palisade epidermis (figs. 2*c* [arrow], 2*f*, 5*g*). At successively more proximal levels of the micropylar canal (fig. 5*g–5k*), the palisade becomes less distinct, and a progressively thickening zone of thinner-walled cells is present between the sclerotesta and the palisade (fig. 5*h–5k*).

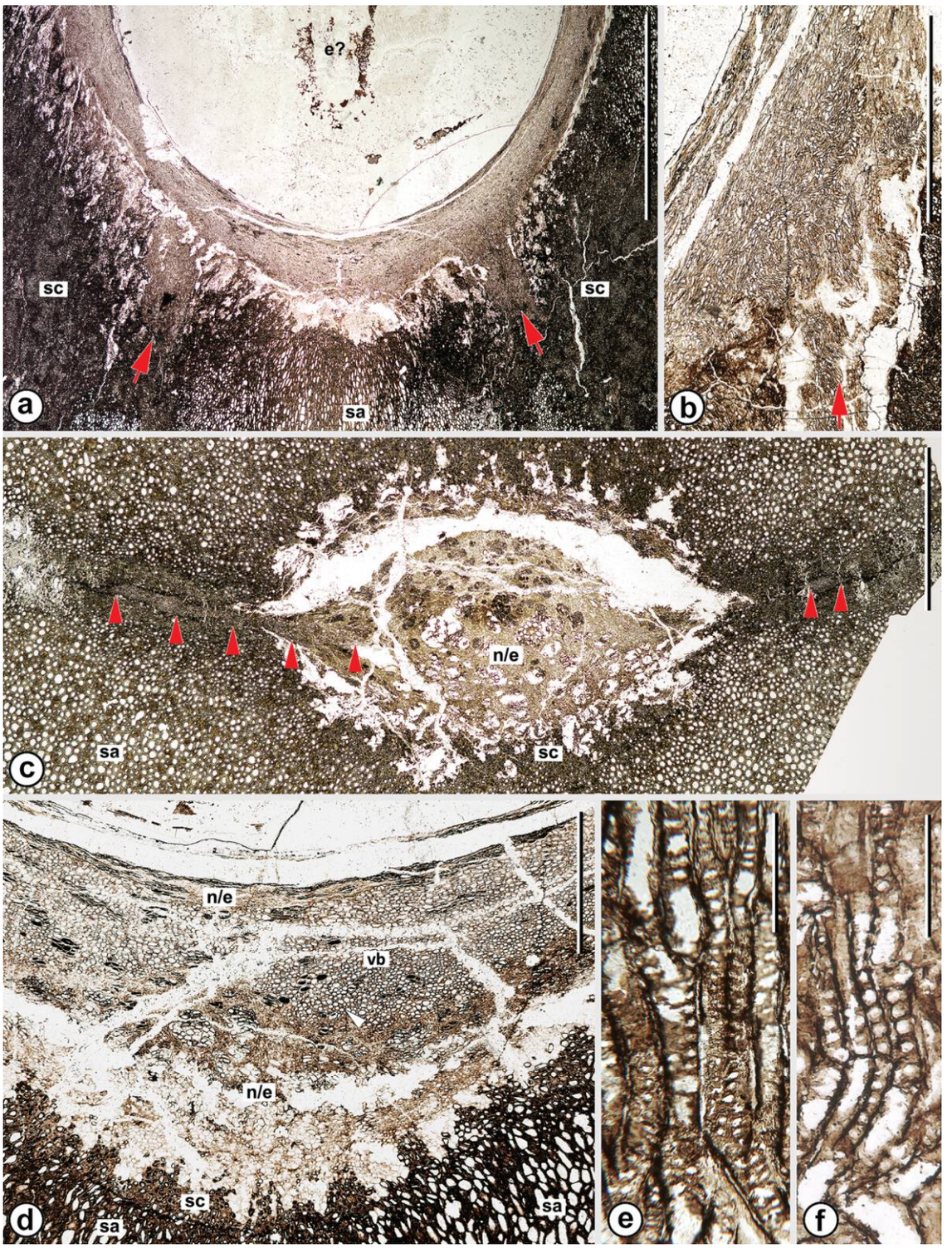

Fig. 4 *Traskia maahlae* gen. et sp. nov. *a*, Midlongitudinal section in the major plane of the chalazal region of the seed, showing vascular bundles (arrows) passing through the sarcotesta (sa) and sclerotesta (sc) to extend both apically and basally within the nucellus/endotesta. Note the probable embryo (e?) within the seed cavity. SBI 46A #6. × 4. Scale bar = 1 cm. *b*, Enlargement of a view comparable to that in the lower right of *a*, showing a massive bundle of tracheids entering the endotesta/nucellus. SBI 45A #32. × 20. Scale bar = 2 mm. *c*, Cross section of the chalaza, showing tissue of the nucellus/endotesta (n/e) at the center and a massive vascular bundle (arrowheads). SBI 13b bot #153. × 8. Scale bar = 4 mm. *d*, Enlargement of tissues at the base of a seed cavity in cross section, showing sarcotesta (sa), sclerotesta (sc), and nucellus/endotesta (n/e) containing tracheids of a vascular bundle (vb). Megaspore membrane is present at the top of the figure. Note the nests of secretory cells with black contents among the tracheids and within the nucellus/endotesta. SBI 46A #106. × 14. Scale bar = 2 mm. *e*, Tracheids with bordered pits in longitudinal section. SBI 46A #76. × 230. Scale bar = 100 μm. *f*, Tracheids with bordered pits in longitudinal section. SBI 45A #53. × 250. Scale bar = 100 μm.

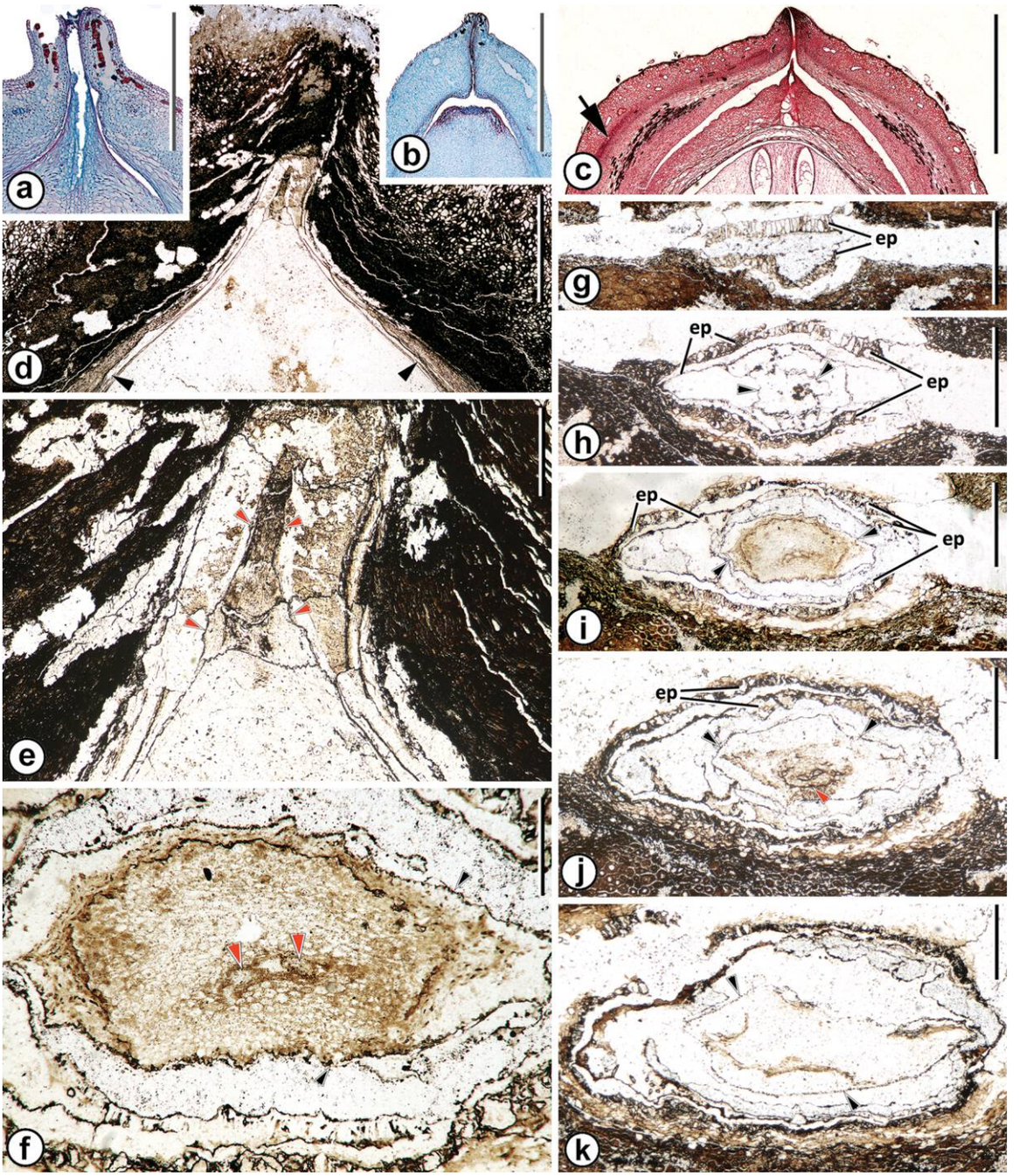

Fig. 5 Apical region of *Traskia maahlae* gen. et sp. nov. and seeds of living cycads. *a*, Longitudinal section of *Zamia furfuracea* with a developed micropyle. Note the degeneration of the nucellus at an early stage of pollen chamber development. × 50. Scale bar = 500 μm. *b*, Longitudinal section of *Z. furfuracea* with a cellular nucellar apex after nucellar degeneration and formation of the pollen chamber. Red arrows indicate bundles of the inner and outer vascular system. × 25. Scale bar = 1 mm. *c*, Longitudinal section of *Ceratozamia* sp. with two archegonia, an open micropyle, and a degenerating nucellus. The arrow indicates procambial tissue of the vascular bundle. × 6. Scale bar = 5 mm. *d–k*, *Traskia maahlae* gen. et sp. nov. *d*, Midlongitudinal section showing the pollen chamber and micropylar canal. Arrowheads indicate the level where the nucellus separates from the endotesta to form a pollen chamber wall. SBI 46A #116. × 4. Scale bar = 1 cm. *e*, Enlargement of the pollen chamber tip at the base of the micropylar canal, showing the apex of the pollen chamber wall (arrowheads) surrounded by small cells with golden walls that occlude the micropylar canal. SBI 46 A #116. × 16. Scale bar = 1 mm. *f*, Cross section near the base of the micropylar canal. Note the membranous pollen chamber wall (black arrowheads), cellular contents of the micropylar canal, and oval objects (red arrowheads) that may be pollen tubes. SBI 10 B bot #57. × 90. Scale bar = 200 μm. *g–k*, Basipetal series of sections from near the apex (*g*) to the base (*k*) of the micropylar canal. Note the inner epidermis of the integument (ep), from which the cuticle has separated in *h–j*, and the membranous pollen chamber wall at the arrowheads in *h–k*. *g–k*, All SBI 10 B bot. *g*, #28. × 30. *h*, #44. × 33. *i*, #57. × 29. *j*, #62. × 32. *k*, #69. × 29. Scale bars = 1 mm (*g–k*).

Seed Vascularization

Traskia maahlae is vascularized by two large bundles of tracheids that enter the ovule near the sides of the chalaza in the major plane of symmetry (fig. 2*b*, arrows). Each bundle forms a radially oriented massive plate of tracheids (fig. 2*d*) that passes distally through the sarcotesta and sclerotesta (fig. 4*a*, 4*b*, arrows), and then tracheids of each bundle extend (fig. 4*b*) toward both the apex and the chalaza. The basally extending tracheids pass within the nucellar/endotestal tissue before terminating toward the center of the chalaza (fig. 4*c*, right arrowheads). The two apically extending bundles are also located within the endotestal/nucellar tissue in the major plane of symmetry (figs. 2*e*, 2*g*, 6*f*). They lie inside the sutures, are distinctly triangular in cross sections (fig. 2*g*), and extend distally to about the level of the pollen chamber. Tracheids of the vascular bundles appear twisted and distorted in longitudinal sections (fig. 4*b*, 4*f*). They measure 17–36 μm in diameter and have wall thickenings that range from bordered reticulate to uniseriate and biseriate bordered pits (fig. 4*e*, 4*f*).

Nucellus and Pollen Chamber

For most of the length of the seed cavity, the nucellus is contiguous with the endotesta and has the histological features described above for the endotesta (fig. 3). In the apical region of the seed cavity, the nucellus separates from the endotesta to form a large pollen chamber (figs. 2*f*, 5*d*, arrowheads). The pollen chamber wall extends distally, narrows toward the seed apex, and enters the micropylar canal (fig. 5*d*, 5*e*). It consists of one or two layers of elongated thin-walled cells proximal to the micropylar canal. More distally, it appears as a dark line in sectional views (fig. 5*d*, 5*e*). Within the micropylar canal, the nucellar beak narrows further (fig. 5*e*, red arrowheads) and is occluded by an amber substance (fig. 5*d*). In this same region, the nucellar beak is surrounded by isodiametric cells with golden-brown walls (fig. 5*e*, 5*f*, 5*i*) that are preserved within the epidermis of the integument (fig. 5*e*–5*j*).

The micropylar canal contains several membranous layers as well as cellular contents that vary in composition from level to level (fig. 5*d*–5*k*). As viewed in cross sections from the apex to the base of the micropylar canal, the integument and its contents consist of an intergrading series of cell layers, membrane-like lines, and cellular tissue (fig. 5*g*–5*k*). The apicalmost sections show a uniseriate palisade-like epidermis of the integument that has separated from the remainder of the integument (fig. 5*g*). In more proximal sections, the inner margin of the epidermal cells remains partly (fig. 5*h*, lower right) or completely (fig. 5*i*, 5*j*) separated from the rest of that layer (fig. 5*g*–5*j*, at ep). Inside the epidermis is a membrane-like line (fig. 5*f*, 5*h*–5*k*, arrowheads) that surrounds closely packed isodiametric cells with golden-brown walls 15–20 μm in diameter (fig. 5*f*, 5*i*, 5*j*). In some sections and parts of other sections, those cells appear to form two zones (fig. 5*f*, 5*i*, 5*j*), but in other areas, they clearly form a single zone (fig. 5*f*, bottom). This suggests that the apparent zonation is the result of taphonomic compression. At the center of the micropylar canal in the specimen seen in figure 5*f*–5*k*, there are two oval structures (55–77 μm in greatest diameter) within the nucellar beak (fig. 5*f* [red arrowheads], 5*i*, 5*j*) that may represent pollen tubes.

Megaspore Membrane, Megagametophyte, and Possible Embryos

The megagametophyte consists of the megaspore membrane (figs. 2*e*–2*g* [red arrowheads], 3*a*–3*c*, at m) and what appear to be poorly preserved cells in some areas of some specimens (e.g., fig. 3*e*, at me). There are also longitudinally oriented cylindrical structures ~2 mm in diameter (figs. 2*f*, 3*e*, at e?) that may represent embryos in the globular stage and/or are not mature enough or preserved well enough to show cotyledons and other embryonic organs.

Structure of Extant Cycad Ovules and Seeds

Gymnosperm ovules are typically orthotropous, have one integument covering the nucellus, and have the micropyle at the apex (Stevenson 2013). Despite the fact that gymnosperms do not have a carpel to protect the ovules or fruit to disperse the seeds, many extinct and living species have modifications in the tissues of the ovule or have associated structures surrounding the ovule that fulfill those functions (Stewart and Rothwell 1993; Norstog and Nicholls 1997; Stockey et al. 2021; Klymiuk et al. 2022). Anatomically, in the ovules of living cycads, the integument undergoes a series of ontogenetic transformations before and after fertilization, forming a fleshy seed coat with an increase in the number of cell layers, differentiation of mucilage canals, and gold cell accumulations (figs. 5, 6*a*; Chamberlain 1935; Norstog 1987; Brenner et al. 2003). At the time of fertilization, the integument has three clearly differentiated tissue zones similar to those of many Paleozoic fossil seeds (Taylor 1965; Rothwell 1971). In many fossil gymnosperms and in living cycads, those zones become (1) the outermost sarcotesta, (2) a middle sclerotesta, and (3) a fleshy inner zone that is fused to the nucellus over most of the length of the ovule (figs. 5*a*–5*c*, 6*a*, 7*a*; Rothwell 1971; Singh 1978; Schmid 1986; Sánchez-Tinoco and Engleman 2004; Sánchez-Tinoco et al. 2007; Zumajo-Cardona et al. 2021) and that is referred to as endotesta. These three zones can be identified in living cycads as the young ovules increase in size. However, not until after fertilization and after the seeds have reached maximum size do the cells in each of these zones mature (Chamberlain 1909, 1935; Rothwell 1971). In living cycads, the mature sarcotesta is parenchymatous, with mucilage canals, gold cells, an epidermis, and the outer vascular system (fig. 6*a*–6*d*; Chamberlain 1935; Singh 1978). The mature sclerotesta is composed exclusively of sclereids that appear in two zones that are perpendicular to each other (fig. 6*c*), with the cells of the inner one oriented vertically and those of the outer one oriented horizontally, like the ovules of Paleozoic medullosan seed ferns (Stopes 1904; Hoskins and Cross 1946*a*, 1946*b*; Taylor 1965; Combourieu and Galtier 1985; Serbet and Rothwell 1995). This is obvious in some genera of cycads with living species but less developed in others, such as *Bowenia* (Kershaw 1912). The inner fleshy zone consists of parenchyma with mucilage canals, gold cells and other idioblasts, and the inner vascular system (figs. 5*c*, 6*a*–6*c*). When completely mature, this zone becomes what is called the papery layer because the cells become crushed and die (Coulter and Chamberlain 1903, 1917; Chamberlain 1935). Nevertheless, the inner vascular system can still be identified in the papery layer as a system of dichotomizing vascular bundles

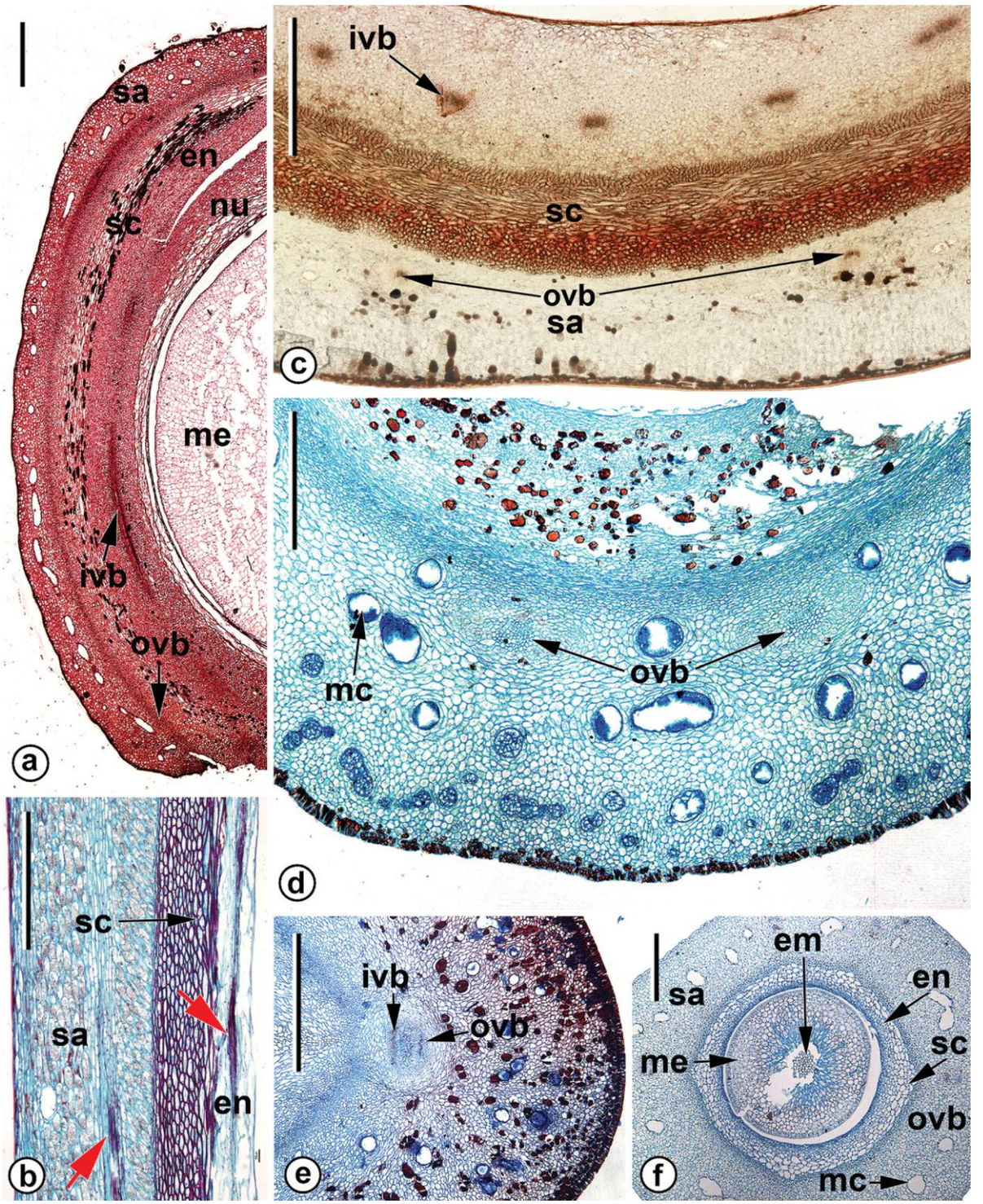

Fig. 6 Histological features of living cycad seeds. *a*, *Ceratozamia* sp. l.s. of seed after pollination but before fertilization, with immature sclerotesta. × 12. Scale bar = 1 mm. *b*, *Dioon edule* x.s. of seed, showing differentiated integumentary zones, including mature sclerotestal sclereids, and a double vascular system. The red arrows indicate vascular bundles. × 25. Scale bar = 1 mm. *c*, *Dioon edule* x.s. of ovule, showing integument and vascularization of the specimen, with only partly differentiated sclerotestal sclereids. × 25. Scale bar = 1 mm. *d*, *Dioon edule* x.s., showing vascular bundle at the level of radial division to produce inner and outer systems. × 25. Scale bar = 1 mm. *e*, *Cycas rumphii* x.s., showing the inner and outer systems. × 50. Scale bar = 500 μm. *f*, Cross section of *Zamia furfuracea* at the stage where the megagametophyte is cellular and the embryo has begun to differentiate but sclerotestal cells have not yet differentiated into sclereids. × 25. Scale bar = 0.5 mm. en = endotesta; ivb = inner vascular bundle; me = megagametophyte; nu = nucellus; ovb = outer vascular bundle; sa = sarcotesta; sc = sclerotesta.

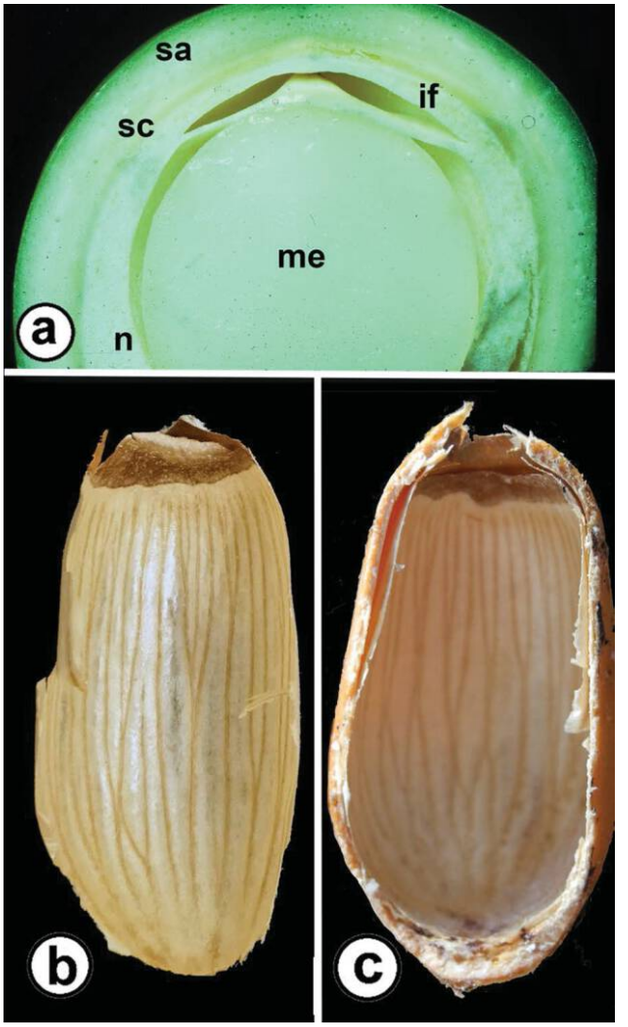

Fig. 7 *a*, Near midlongitudinal section of *Cycas seemannii*. *b*, *c*, *Dioon spinulosum* papery layer (endotesta and nucellus), showing dichotomizing bundles of the inner vascular system. *b*, Exterior view. *c*, Interior view. if = inner flesh or endotesta; me = megagametophyte; n = nucellus; sa = sarcotesta; sc = sclerotesta.

with occasional anastomoses, as in *Dioon edule* (fig. 7*b*, 7*c*). This is a feature also noted by Stopes (1904) for *Cycas revoluta* in her figure 14 and by Warming (1877) for *Ceratozamia mexicana* in his tabula II, figure 24.

Extant Cycad Seed Vasculature

The vascular architecture of extant cycads has been thoroughly examined by Warming (1877), Lang (1902), Stopes (1904, 1905), Kershaw (1912), and Lawson (1926), and the observations summarized here are consistent with the accounts of those authors. In all extant cycads, the ovule has at least two sets of vascular bundles (table 1) originating from a single vascular bundle in the megasporophyll that bears it. For example, in *Cycas*, that bundle dichotomizes in the base of the ovule to produce two bundles for the outer set. Each of those bundles in turn dichotomizes radially to produce the inner vascular system (fig. 6*e*), where repeated branching produces the multiple bundles that are found in the integument. By contrast, in *Ceratozamia* (figs. 5*c*, 6*a*) only the two bundles making up the outer set are present in the free portion of the integument.

Although the basic pattern of vascularization is the same for all living cycads, there are two variations of that pattern. In all living cycads, a single megasporophyll bundle supplies the ovule, and the first two dichotomies give rise to the outer and inner vascular systems of endarch to mesarch bundles, with the outer bundles in the free portion of the integument and the inner bundles terminating in the zone where the integument is free from the nucellus. In some living cycads (e.g., *Dioon*), the bundles of the outer vascular system undergo a series of dichotomies resulting in 6–12 outer strands that enter the free micropylar region of the integument (Stopes 1904). In others, several outer bundles dichotomize radially to produce an inner vascular system of dichotomizing bundles with occasional anastomoses (Stopes 1904; fig. 7*b*, 7*c*).

After fertilization in fossil and living gymnosperms, including cycads, the ovule becomes a seed (Singh 1978; Gifford and Foster 1989; Werker 1997), and the various tissues and cell types of the mature seed begin to differentiate (fig. 6). There are only two types of mature seed morphologies in cycads in terms of symmetry (Stevenson 1990). *Cycas* has bilaterally symmetrical ovules with 180° rotational symmetry (fig. 8*a*, 8*b*), whereas all other cycad genera have radially symmetrical ovules with 360° rotational symmetry sensu Rothwell (1986; fig. 8*c*–8*f*; Stevenson 1990). As a result of these differences, seed germination is quite different in the two types (fig. 8*a*, 8*c*; table 1). The seeds of *Cycas* germinate by splitting open longitudinally from the micropyle to the chalaza into equal halves (fig. 8*a*, 8*b*). This split follows along the two large outer vascular bundles in the major plane of symmetry (Stevenson 1990; Zumajo-Cardona et al. 2021). In contrast, the other genera all have several outer vascular bundles and have a micropylar coronula, as shown for *Encephalartos*, *Zamia*, and *Dioon* (fig. 8*c*–8*f*, respectively). These seeds germinate by splitting open along the veins of the outer set of vascular bundles in a starlike fashion (fig. 8*c*; Zumajo-Cardona et al. 2021). Thus, in all instances, the sclerotesta is ruptured along the outer veins of the ovule, reflecting the vascular architecture of the outer set of bundles.

Discussion

Comparison of Traskia *with Seeds of Extant Cycads*

As is also characteristic of living cycads, *Traskia maahlae* has large seeds (fig. 1*a*–1*f*, 1*i*, 1*l*, 1*m*) with a multizoned integument (fig. 3*a*–3*e*) and a nucellus that is adnate to the integument up to about the level of the pollen chamber (figs. 2*f*, 5*d*). In all, the integument consists of a massive sarcotesta (figs. 2*f*, 2*e*, 3*a*–3*c*, 5*a*–5*c*, 6*a*–6*f*, 7*a*), a sclerotesta of thick-walled sclereids (figs. 3*a*–3*e*, 6*a*–6*d*), and a thin endotesta of thin-walled cells (figs. 3*a*–3*d*, 6*a*–6*d*; table 1).

Most living cycads have radial seeds that germinate as a result of the radical emerging from an apical opening, which is facilitated by the breakdown of cells in a ring of vascularized canals, the coronula, that surrounds the micropyle (fig. 8*c*–8*e*).

Table 1

Comparative Features of Living and Better-Known Fossil Cycad Seeds

Taxon character	*Oxfordia motturii*[a]	*Cycadeocarpus columbianus*[b]	*Traskia maahlae*	*Beania gracilis*[c]	*Cycas* spp.	*Zamia* spp.
Stratigraphy and age	Callovian-Oxfordian boundary of the Middle–Upper Jurassic	Callovian Stage of the Middle Jurassic	Callovian Stage of the Middle Jurassic	Ravenscar Group, Aalenian-Bathonian Stages of the Middle Jurassic	Living	Living
Geography	Southern England	Haida Gwaii, Pacific coast of western Canada	Haida Gwaii, Pacific coast of western Canada	Yorkshire, United Kingdom	Southern Asia/Australasia/Madagascar	Southern North America, Central America, northern South America
Seed symmetry	Bilateral (180° rotational)	Radial	Bilateral (180° rotational)	Radial	Bilateral (180° rotational)	Radial
Seed size (cm)	1.68–2.16 long, 1.79–2.19 maximum width in major plane	4.0–6.5 long, 3.6–5.5 maximum diameter	4.0–5.25 long, 4.25–4.5 maximum width in major plane	1.6 long, 4.25–1.3 maximum diameter	1.5–5.0 long, 1.8–3.5 wide in major plane	1.5–3.0 long, 0.9–1.5 in diameter
Seed surface	12 longitudinal ribs	Smooth	Smooth-irregular, irregularly ribbed	Smooth	Smooth	Smooth
Integument	Multizoned	Multizoned	Multizoned	Multizoned	Multizoned	Multizoned
Sarcotestal histology	Thin outer fibrous zone, thick inner zone of parenchyma	Thin outer dark zone of small cells grading into wide zone of parenchyma, grading into thicker-walled cells inside	Outer parenchymatous zone, inner parenchymatous zone	Parenchymatous with inclusions	Parenchymatous with mucilage canals and thick cuticle	Parenchymatous, with mucilage canals and thick cuticle
Sarcotestal secretory cavities	Absent	Absent	Absent	Present?	Present	Present
Sarcotestal-sclerotestal transition	Abrupt	Subtle	Subtle	?	Abrupt	Abrupt
Sclerotestal histology	One zone of sclereids	One zone of sclereids	One zone of sclereids	Sclereids, possible zonation unknown	Two zones of sclereids	Two zones of sclereids
Endotestal histology	Thin-walled cells	Thin-walled cells	Thin-walled cells with secretory nests	?	Thin-walled cells with secretory nests	Thin-walled cells with secretory nests
Integument-nucellus	Free from chalaza but adjacent to integument[d]	Adnate below pollen chamber	Adnate below pollen chamber	Adnate up to midregion	Adnate below pollen chamber	Adnate below pollen chamber
Vascularization	?; none found in available specimens	Few tracheids only in channels of coronula	Two massive bundles within endotesta/nucellus of major plane	Two systems?; evidence for inner vascular strand	Two systems of small bundles; one in sarcotesta, the other in endotesta/nucellus	Two systems of small bundles; one in sarcotesta, the other in endotesta/nucellus
Pollen chamber	Small	Large	Large, with apex extending through micropylar canal	Large, with apex extending into micropylar canal	Large, with apex extending to base of micropylar canal	Large, with apex extending to base of micropylar canal

[a] Spencer et al. (2017).
[b] Dawson (1873); Chaloner and Hemsley (1992); King (2000).
[c] Harris (1941, 1961).
[d] There is uncertainty about whether the nucellus is free from the integument naturally or because of incomplete preservation (Spencer et al. 2017).

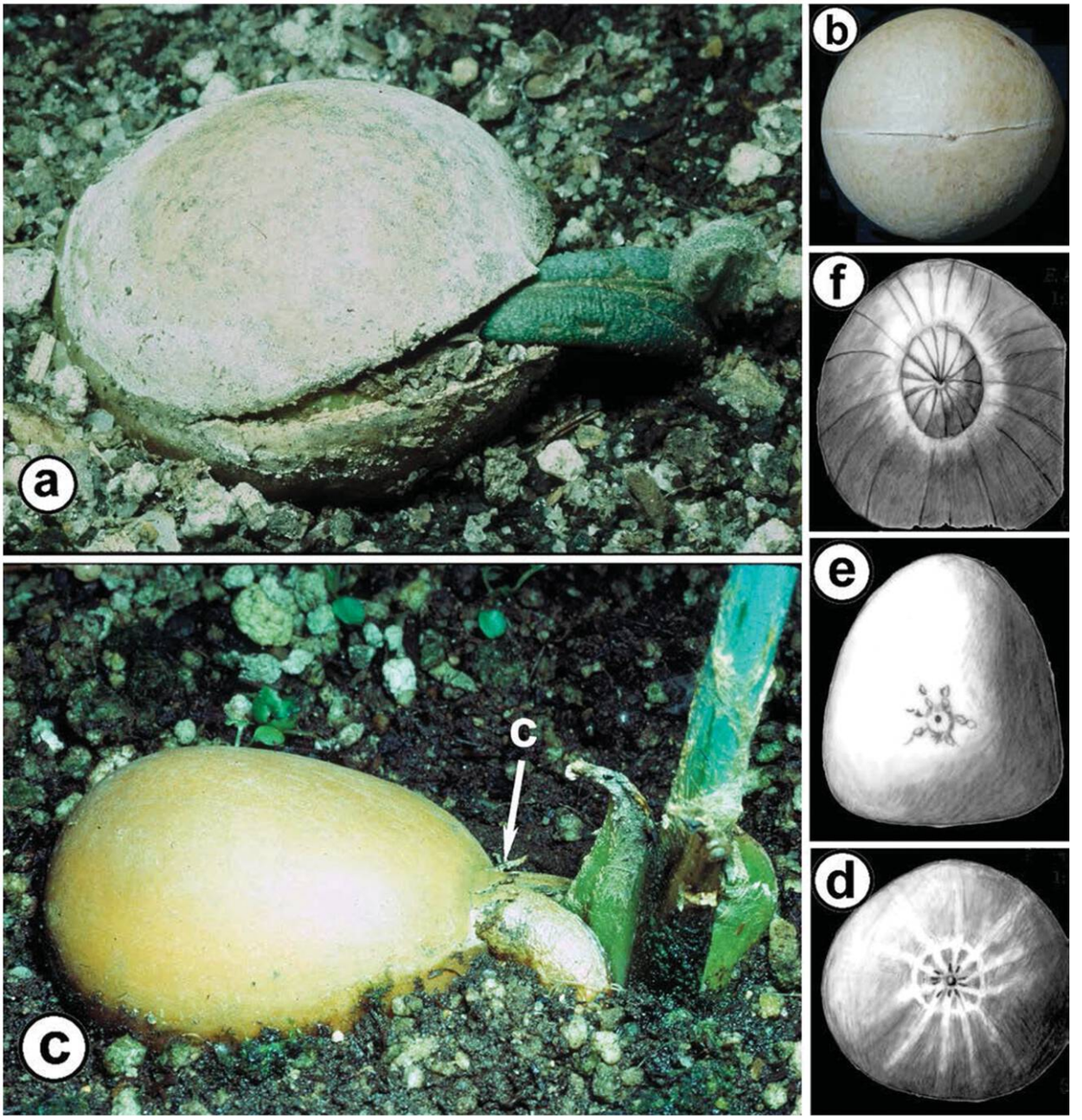

Fig. 8 Contrasting apical morphologies and mechanisms of germination in seeds of living cycads. *a*, *b*, *Cycas revoluta*. *a*, Bivalve seed germination. *b*, Micropyle view of a seed. *c*, *d*, *Dioon spinulosum*. *c*, Coronular germination. *d*, Micropyle view of a seed with a coronula. *e*, *Zamia furfuracea* with an indistinct coronula. *f*, *Encephalartos hildebrandtii* with a distinct coronula. c = coronula. *b* and *d–f* are based on Zumajo-Cardona et al. (2021).

By contrast, seeds of *Cycas* spp. are bilateral, with 180° rotational symmetry (fig. 8*b*); lack a coronula; and split longitudinally along the apical suture that occurs in the major plane of symmetry to facilitate germination (fig. 8*a*). *Traskia maahlae* shares the latter distinctive suite of characters (figs. 1*d*, 1*f*, 2*a*, 2*e*; table 1), which reveals a mode of seed germination in this extinct species similar to that of extant *Cycas*.

The ovules of living cycads are vascularized by two sets of terete strands (fig. 6*a*–6*c*) that originate from a single sporophyll bundle that divides within the chalaza, in both the radial (fig. 6*e*) and tangential planes, to produce a double vascular system (fig. 6*a*–6*d*). In *T. maahlae* two massive platelike bundles enter the chalaza (figs. 2*b*, 2*d*, 4*a*, 4*c*) and do not branch. Therefore, in *T. maahlae*, there is a single vascular system of

only two massive bundles (fig. 2*e*, black arrows), rather than the double vascular system of branching terete strands that characterizes living species (table 1).

In both *T. maahlae* and living cycads, there is a large pollen chamber with a wall that is free from the integument (figs. 2*f*, 5*a*–5*d*, 6*a*) and that narrows toward the base of the micropyle (fig. 5*a*–5*d*). Whereas at most developmental stages in living cycads the pollen chamber wall often terminates near the base of the micropyle (fig. 5*a*, 5*c*), in *T. maahlae* the nucellar beak extends more distally, to the apex of the micropylar canal (fig. 5*d*–5*k*).

In living cycads, the nucellar apex does extend nearly to the tip of the micropylar canal before pollination (Chamberlain 1935; Singh 1978; Norstog and Nicholls 1997; Zumajo-Cardona et al. 2021). After pollination, the apical region of the nucellus begins to degenerate (fig. 5*a*, 5*c*), and this proceeds basipetally until the mature megagametophyte is exposed (Zumajo-Cardona et al. 2021). Simultaneously, the micropyle begins to close basipetally and loses its identity (fig. 5*b*) until it is no longer anatomically recognizable as a canal. The mechanism of the disappearance of the canal and the epidermal cells lining it is unknown (Zumajo-Cardona et al. 2021).

Several *T. maahlae* specimens have a pollen chamber apex that extends to the apex of the micropylar canal, which otherwise is completely occluded by cellular tissue (fig. 5*e*, 5*f*). Within the tip of the nucellar beak, as viewed in cross sections, there are also oval structures ~150 μm in maximum diameter at the center of the cellular tissue (fig. 5*f* [red arrowheads], 5*i*, 5*j*). These structures are intriguingly similar to the pollen tubes that occur within the pollen chamber and apical nucellar tissues of *Zamia furfuracea* L.f. ex Aiton. Pollen tubes of *Z. furfuracea* are described as being ~25–65 μm in diameter near their emergence from the pollen grain (Choi and Friedman 1991). Those pollen tubes expand to as much as ~135 μm at more distal levels (e.g., figs. 10, 12 in Choi and Friedman 1991) and therefore are comparable in size to the putative pollen tubes present in the micropylar canal of *T. maahlae* (fig. 5*f*, 5*i*, 5*j*).

Pollen grains of living cycads enter the ovule and germinate to produce a pollen tube that penetrates the cellular apex of the nucellus and facilitates pollen chamber development by enzymatic and mechanical intracellular penetration and destruction of nucellar tissue (Singh 1978; Friedman 1987; Johri 1992). This mode of pollination may have also characterized at least some extinct cycads, as Chaloner and Hemsley (1992) describe objects in the pollen chamber of a *Cycadeocarpus columbianus* seed as pollen grains that are basically similar to those of living species (pl. 1, figs. 7, 8 in Chaloner and Hemsley 1992). We have found no comparable objects in the specimens of either *C. columbianus* or *T. maahlae* investigated in this study.

By contrast, the occurrence of possible pollen tubes within the tip of the pollen chamber within the base of the micropylar canal suggests that pollination of *T. maahlae* resulted in pollen grains being deposited at or near the tip of the micropylar canal. Pollen tubes growing into the ovule from the positions of those grains to facilitate fertilization of *T. maahlae* would account for the absence of such grains within the fossils and also for the presence of putative pollen tubes within the micropylar canal (fig. 5*f*, 5*i*, 5*j*). Beyond recognizing that there are differences in the position of pollen grains within the seeds of *Traskia* and living species, we have no evidence to suggest that pollination/fertilization mechanisms differ. This includes an extended period of time between pollination and fertilization in all.

Comparison of Traskia *with Seeds of Extinct Cycads*

Fossilized putative cycads have been described from as early as the Pennsylvanian, but most ovulate structures are preserved as coalified compressions, impressions, and/or mold casts (e.g., *Crossozamia minor* [Permian; Gao and Thomas 1989]; *Eophyllogonium* [Permian; Mei et al. 1992]; *Primocycas chinensis* [Permian; Zhu and Du 1981]; *Dioonitocarpidium liliensternii* [Triassic; Pott 2019]; *Cycadocarpidium macrozamioides* Schuster [Triassic; Schuster 1911]; *Zamioidea macrozamioides* [Jurassic; Schuster 1911]; *Beania gracilis* Carruthers [Jurassic; Harris 1941, 1961]) that display few characters for critical comparison with *T. maahlae*. The most completely known of these is *B. gracilis*, for which some features of internal structure and histology have been determined (Harris 1941, 1961, 1964; table 1).

Seed macerations of *B. gracilis* show an outer cuticle and inner cuticles of the integument and a nucellus in the apical region. These demonstrate that the nucellus was confluent with the integument below the pollen chamber, which was free from the integument, as it is in living cycads (Harris 1941). Macerated seeds reveal the presence of an inner zone of sclereids that represent the sclerotesta and an outer "flesh" (Harris 1941; sarcotesta) made up of apparently more isodiametric thinner-walled cells in which elongated cells with thicker dark walls and internal contents are embedded. There are also tracheids in the apical region of the seed that may be located within the nucellar tissue (Harris 1941).

Given the wide stratigraphic range of cycad fossils, it is surprising that only a small number of anatomically preserved seeds have thus far been described. Previously described anatomically preserved cycad seeds include *C. columbianus* Dawson from the same Upper Jurassic locality as *T. maahlae* (Dawson 1873; Chaloner and Hemsley 1992; King 2000) and *Oxfordiana motturii* A.R.T. Spencer & J. Hilton from the latest Callovian (Middle Jurassic) to earliest Oxfordian (Middle–Upper Jurassic) Stage of the Jurassic (Spencer et al. 2017; table 1). While we do not know why there has been such a paucity of permineralized cycad seeds recovered from the fossil record, cycads tend to grow in dry environments outside the window of high-fidelity preservation in wetland settings. All three permineralized cycad ovule taxa are from marine sediments in the Callovian-Oxfordian Stages of the Jurassic, which suggests that they were produced by plants that grew adjacent to basins of deposition and that their seeds may have been specialized for dispersal by ocean currents.

All three of these seeds are large, with a thick integument differentiated into outer sarcotesta, sclerotesta, and endotesta, as well as a large pollen chamber. In *T. maahlae*, the sarcotesta consists of thin-walled parenchyma at the periphery, grading irregularly into thicker-walled cells toward the sclerotesta (fig. 2*e*). The sarcotesta of *C. columbianus* consists of small thin-walled parenchyma cells at the periphery grading into larger parenchyma cells and then back into smaller cells toward the inner margin of the zone (table 1; Chaloner and Hemsley 1992). *Oxfordiana motturii* A.R.T. Spencer and J. Hilton has a narrow zone of thick-walled sclereids at the outer periphery and a thicker zone of large thin-walled parenchyma toward the inside (Spencer et al. 2017; table 1). *Traskia maahlae* and *O. motturii* have a single zone of prominent sclerotestal sclereids inside the sarcotesta,

but in *C. columbianus* the sclerotesta is less distinct and may not be well developed in many seeds (Chaloner and Hemsley 1992; table 1). As in living cycad seeds, *T. maahlae* and *C. columbianus* have the nucellus adnate to the endotesta up to the level of the pollen chamber, but these tissues appear to be only pressed together in *O. motturii* (Spencer et al. 2017). Whether this last feature is biological in nature or merely taphonomic in origin remains to be determined.

In agreement with living cycads that have radial seeds, our observations of *C. columbianus* have allowed us to identify tracheids with sclariform wall thickenings adjacent to the canals of the coronula, but we were unable to find vascular tissue at more proximal levels like that of living species. This observation supplements previous descriptions of *C. columbianus* where tracheids of vascular tissues were not identified (Dawson 1873; Chaloner and Hemsley 1992).

Cycadeocarpus columbianus is radial, with a distinct coronula that facilitated seed germination as it does in living species of zamioid cycads (fig. 8*c*; Zumajo-Cardona et al. 2021), while *O. motturii* and *T. maahlae* have 180° rotational symmetry and a longitudinal suture like that which facilitates seed germination in living species of the genus *Cycas* (fig. 8*b*; table 1; Zumajo-Cardona et al. 2021). Vascular tissues are hard to identify and apparently not well developed in *C. columbianus* and *O. motturii* (Chaloner and Hemsley 1992; Spencer et al. 2017). By contrast, the distinctive vascular system of *T. maahlae* consists of two massive bundles that are positioned in the major plane of symmetry (table 1).

As detailed above, all three extinct permineralized cycad seeds lack the double vascular system that characterizes all living cycad species (Zumajo-Cardona et al. 2021). Furthermore, the sarcotestal histology of *O. motturii* is distinctly different from that of all other living and extinct cycad seeds (Spencer et al. 2017). Given these structural differences from the seeds of living species, it is clear that all three Jurassic fossil species represent stem group cycads. Given the extremely small number of extinct species characterized thus far, we do not know whether the two distinctive modes of seed germination evolved before the divergence of Cycadaceae and Zamiaceae or whether the modes of seed germination evolved separately within the respective families. Resolution of this question awaits much denser sampling of permineralized fossil cycad seeds.

Mode and Tempo of Cycad Evolution

The paleontological record documents that cycad-like plants originated no later than the Pennsylvanian or Early Permian (Taylor 1970; Zhu and Du 1981; Gao and Thomas 1989; Delevoryas 1993; Pott et al. 2010) and that modern growth forms were well established by the Triassic (Smoot et al. 1985; Klavins et al. 2003; Hermsen et al. 2006, 2007, 2009; Taylor et al. 2009). Early cycad diversification is documented primarily by the compression fossil record of stems, foliage, and sporophylls (e.g., Delevoryas and Hope 1971; Taylor et al. 2009; Cúneo et al. 2010; Pott et al. 2010); by taxa of permineralized stems (e.g., Jain 1964; Gould 1971; Ash 1985; Lutz et al. 2003; Cúneo et al. 2010); and by permineralized seeds (Dawson 1873; Chaloner and Hemsley 1992; Spencer et al. 2017; this article) that reveal important features of internal anatomy and reproductive biology. Up to the present, a paucity of whole-plant concepts for extinct species of cycads has impeded the furthering of our understanding of the organismal phylogeny of the Cycadales. Only a small number of whole-plant reconstructions have thus far been developed for fossil cycads, including the Triassic *Antarcticycas schopfii* Smoot, the Taylor & Delevoryas plant (Smoot et al. 1985; Klavins et al. 2003; Hermsen et al. 2006, 2007, 2009), *Leptocycas gracilis* Delevoryas and Hope (1971), and a composite concept for a Jurassic plant that consists of *Nilssonia* Brogn. sp. fronds, *Androstrobus wonnacottii* Harris pollen cones, and *Beania mamaya* Carruthers seed cones with seeds (Harris 1961). Evidence from both paleontology and molecular systematics (Hill et al. 2003) reveals a pulse of diversification for living species during the Miocene (Nagalingum et al. 2011), which suggests that evolution within the clade was highly episodic, a pattern that was predicted for general organismal evolution more than 45 yr ago by Eldredge and Gould (1972). However, confirmation and full characterization of the pattern of cycad phylogeny await a much denser sampling of the cycad fossil record.

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