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DISTINGUISHING ANGIOPHYTES FROM THE EARLIEST ANGIOSPERMS: A LOWER CRETACEOUS (VALANGINIAN-HAUTERIVIAN) FRUIT-LIKE REPRODUCTIVE STRUCTURE[1]

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A remarkably diverse Lower Cretaceous (Valanginian-Hauterivian) flora at Apple Bay, Vancouver Island, preserves seed plants at an important time of floristic evolutionary transition, about the same time as the earliest flowering plant megafossils. The fossils are permineralized in carbonate concretions and include tetrahedral seeds within cupule- or carpel-like structures. These enclosing structures, composed of elongate sclerenchyma cells with spiral thickenings that grade externally to a few layers of parenchyma, are vascularized by one collateral vascular bundle and lack trichomes. They apparently broke open to release the tightly enclosed seeds by valves. Seeds are similar to those of the Triassic seed fern *Petriellaea*, but are about 100 million years younger and differ in size, vascularization, integumentary anatomy, seed attachment, and number of seeds/cupule. These new seeds are described as *Doylea tetrahedrasperma* gen. et sp. nov., tentatively assigned to Corystospermales. Inverted cupules are reminiscent of an outer angiosperm integument rather than a carpel. Like fruits, cupules opened to release seeds at maturity, thereby foretelling several aspects of angiospermy. They show that nearly total ovule enclosure, a level of organization approaching angiospermy, was achieved by advanced seed ferns during the Mesozoic.

Key words: angiospermy; corystosperms; Cretaceous; cupule; *Petriellaea*; seed ferns.

One of the most diagnostic angiosperm characters is the carpel, an enclosing structure that contains and completely encloses one or more ovules. Enclosure of the ovule at the time of pollination has led to changes in pollination biology from the typical gymnospermous condition in which pollen lands on and usually enters the ovule micropyle, to the angiospermous condition in which pollen lands on a stigma, stigmatic hairs, or a secretion on the carpel surface, and a pollen tube grows down to the ovule. Distinguishing the primitive carpel in the fossil record from a seed fern (pteridosperm) cupule requires not only good preservation of plant tissues, but a knowledge of the development of those tissues and the presence of pollen on or in the reproductive structures (i.e., the mode of pollination). The angiosperm identity of the Jurassic fossil genus *Caytonia* Thomas (Caytoniales; Thomas, 1925) was refuted by Harris (1940) after he macerated the compression/impression seeds from the cupules and found *Vitreisporites* Leschik pollen (the type found in *Caytonanthus* Harris 1933a) in the seed micropyles. Work by Gould and Delevoryas (1977) and subsequently by Nishida et al. (2003, 2004, 2007) resulted in similar finds showing that *Glossopteris* Brongniart (Glossopteridales, also often implicated in angiospermy) had gymnosperm pollination and a reproductive cycle similar to cycads and *Ginkgo*.

Cupules of a number of groups of Mesozoic seed ferns have captured the attention of botanists over the years in the search for angiosperm ancestors (Taylor and Taylor, 1993; Stewart and Rothwell, 1993). Deducing homologies between carpels and organs of other seed plants has been difficult (Taylor and Kirchner, 1996; also see Frohlich and Chase, 2007, for a contemporary neontological perspective). The term "cupule" has been used for more-or-less carpel-like structures surrounding seeds in a number of seed plant groups, from the earliest gymnosperms (e.g., *Elksinia* Rothwell et al., 1989) with hydrasperman reproduction, to a variety of reproductively more complex Paleozoic and Mesozoic forms (Doyle and Donoghue, 1986; Nixon et al., 1994; Rothwell and Serbet, 1994; Doyle, 2006; Hilton and Bateman, 2006). However, with the detailed characterization of well-preserved specimens, it has become apparent that these structures are not necessarily homologous to carpels or to each other and that "cupules" evolved independently several times in the fossil record (Nixon et al., 1994; Rothwell and Serbet, 1994; Doyle 2006; Hilton and Bateman, 2006).

As Doyle (2006) has pointed out, while most workers have concentrated on the enclosure of ovules to indicate angiospermy, little attention has been paid to the other surrounding structure found in most angiosperm ovules, the second integument. We know little from the fossil record, or other sources for that matter, about whether the outer integument evolved from a surrounding structure that was, in turn, surrounded by a carpel or whether the outer integument arose de novo, as suggested by at least some developmental evidence (Sieber et al., 2004). We are uncertain whether the carpel represents a sporophyll (i.e., the "conduplicate carpel") with adaxial ovules or originated from a shoot with a terminal ovule, in which case, the carpel wall was derived from a subtending bract or leaf (e.g., Taylor and Kirchner, 1996). We also have yet to determine whether the evolution of the carpel preceded or followed the evolution of the outer integument in the angiophyte progenitors of flowering plants. Therefore, when considering putative homologies of cupules that surround uni-integumentary ovules, we are uncertain

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whether the cupule may be equivalent to the outer integument or to the carpel. There is some evidence from evolutionary developmental studies that both the outer integument and the carpel wall are foliar in nature and that the abaxial surface of each faces outward (i.e., seeds are attached adaxially [Eshed et al., 1999; McAbee et al., 2006]), but even that evidence is equivocal (summarized by Doyle, 2006). Within this context, new discoveries from the fossil record have great potential for helping to clarify these questions of positional homology, as well as for providing data to document the sequence in which the angiosperm outer integument and carpel have evolved.

A remarkably diverse Lower Cretaceous (Valanginian-Hauterivian) flora at Apple Bay on Vancouver Island, British Columbia, Canada preserves a diverse assemblage of seed plants at an important time of floristic evolutionary transition. While older floras are dominated by ferns and other pteridophytes and by extinct gymnosperms, including conifers, bennettitaleans, gnetophytes and seed ferns, Apple Bay and other roughly contemporaneous Early Cretaceous floras contain specimens that provide new data on some of the outstanding questions of angiosperm gynoecial evolution. The appearance of many modern taxa of gymnosperms (Stockey and Wiebe, 2008) probably occurs around the transition between angiophytes and angiosperms (Stockey and Rothwell, 2007), but both the evolutionary transition to angiospermy and the topology of the seed plant tree remain incompletely understood.

Over the past several years, attempts to characterize the evolution of angiosperms have been framed by the largely tree-based concepts of "crown groups" and "stem groups," in which angiophytes are considered to be extinct stem-group representatives of the clade that includes living angiosperms (Donoghue, 2005). In practice, however, angiophytes remain a poorly defined assemblage of extinct gymnosperms with some, but not all of the characters that define angiosperms (see fig. 4 of Doyle and Donoghue, 1993; fig. 1 of Donoghue, 2005). Within this context some but not necessarily all angiophytes may have led directly to the angiosperms, and it becomes an important challenge for the paleobotanist to determine which is which.

In this paper we describe and discuss the potential phylogenetic significance of a suite of newly discovered fossil cupule- or carpel-like structures that enclose single seeds from the Apple Bay locality. These specimens are evaluated in terms of the fossil record of seed ferns and the origin of both the second integument and carpel of angiosperms. Do the angiosperms show as rapid an evolution as Darwin believed when he wrote about the "abominable mystery"? How do we distinguish true angiosperms from angiophytes in the fossil record? Are the lines beginning to blur? The current study shows that there are additional groups of interest besides the traditional suspects: e.g., Bennettitales, Gnetales, Caytoniales, and Glossopteridales, which have all been implicated at one time or another in angiosperm origins. While several authors, back to Darwin himself, have suggested that the absence of sufficient fossil data is a problem, we attempt to help fill that gap by the description of a new fossil taxon based on seed-bearing reproductive structures.

MATERIALS AND METHODS

Fourteen specimens of a unique seed plant are preserved in calcium carbonate concretions and the surrounding carbonate-cemented graywacke matrix at the Apple Bay locality on northern Vancouver Island, British Columbia, Canada. The locality is on the beach along Quatsino Sound (50 36′21″N, 127 39′25″W; UTM 9U WG 951068) where material is accessible at low tide (Stockey and Wiebe, 2008). Sediments have been regarded as Lower Cretaceous (Valanginian-Barremian), Longarm Formation equivalents (Jeletzky, 1976; Haggart and Tipper, 1994), corresponding to Jeletzky's Barremian variegated clastic unit (Sweet, 2000). However, recent oxygen isotope analysis has narrowed the age to the Valanginian-Hauterivian boundary (D. R. Gröcke, Durham University, UK, personal communication).

The Apple Bay site is well known for its preservation of mosses, numerous pteridophytes including lycopods, equisetophytes, and at least 10 families of filicalean ferns (Stockey, 2004; Hernandez-Castillo et al., 2006; Little et al., 2006; Rothwell and Stockey, 2006; Stockey et al., 2006; Vavrek et al., 2006). Among the seed plants found here are conifers of modern families (Pinaceae, Cupressaceae) and conifers similar to extinct Voltziales (Sanders et al., 2004; Stockey and Wiebe, 2008). The pollen record includes only one possible angiospermous-type of grain, *Clavatipollenites*-type pollen (Sweet, 2000), a palynomorph found on early chloranthaceous fruits (Friis et al., 1999). Other gymnospermous remains include cycadophyte leaves and reproductive structures of Bennettitales (Rothwell et al., 2009, pp. 296–322 in this issue).

Specimens in this study include seven cupules with enclosed seeds, two empty cupules, and five isolated seeds of the same type that were studied using the well-known cellulose acetate peel technique with 5% hydrochloric acid (Joy et al., 1956). Slides were mounted in Eukitt (O. Kindler GmbH, Freiburg, Germany) xylene-soluble mounting medium. Images were captured using a PowerPhase digital scanning camera (Phase One, Copenhagen, Denmark) and processed using Photoshop 7.0 (Adobe, San Jose, California, USA). Three-dimensional reconstructions were rendered using AMIRA 3.1.1, visualization software (TGS Software, San Diego, California, USA). All specimens and microscope slides are housed in the University of Alberta Paleobotanical Collections, Edmonton, Alberta, Canada (UAPC-ALTA).

RESULTS

Systematics—Order: Corystospermales?

Genus: *Doylea* gen. nov.

Generic diagnosis: Cupule/carpel-like megasporangiate structures, ellipsoidal to globose, glabrous; bearing one, tightly enclosed, orthotropous, tetrahedral seed on abaxial surface; opening by three valves. Ovule attached by cup-shaped zone of transfusion tissue; either completely enclosed or exposed along edges by apparent valvate dehiscence of enclosing structure. Integument unvascularized with three longitudinal ribs, nucellus free from integument to chalaza, apparent pollen chamber with nucellar beak.

Species: *Doylea tetrahedrasperma* sp. nov.

Specific diagnosis: Cupule/carpel-like organs 3–4 mm wide, 5 mm long; outer zone parenchymatous; inner zone sclerenchymatous, cells with helical thickenings. Ovules 2–3 mm wide, 3 mm tall; triangular in cross section; micropyle trifid. Integument parenchymatous, three-layered: outer of small cells, middle of isodiametric cells that are thicker in corners, inner with elongate, flattened, rectangular cells; suture line in corners (angles).

Holotype hic designatus: P13394 A (UAPC-ALTA) (Figs. 1, 11, 12, 16, 25, 27).

Paratypes: P 13021 G bot, H; P 13133 F bot, P13243 A, P13249 B bot, P 13373 I bot, P13396 C bot, P13497 D top, C bot; P13955 A, B; P14221 E top; P14726 C bot, P14741 B top, P14784 B top. (UAPC-ALTA).

Locality: Apple Bay, northern Vancouver Island, British Columbia, Canada (50°36′21″N, 127°39′25″W; UTM 9U WG 951068).

Stratigraphic position and age: Longarm Formation equivalent, Valanginian-Hauterivian boundary, Early Cretaceous.

Etymology: The genus is named for James A. Doyle, University of California at Davis, in honor of the contributions he has made to our understanding of angiosperm evolution through his unrelenting search for the origin of the carpel and outer integument. The specific epithet refers to the distinctive tetrahedral seed found in this taxon.

Description—Fourteen specimens of this unique seed-bearing plant have been found (Figs. 1–10), including both empty cupule/carpel-like seed-enclosing structures and dispersed seeds (Figs. 8–10). One specimen has been found in the graywacke matrix (Fig. 4) in which the concretions are embedded, but the other 13 specimens occur inside the concretions where the tissues are better preserved.

Isolated seed-enclosing structures are 3–4 mm in diameter, up to 5.5 mm long, and ellipsoidal to globose (Figs. 1–5). Reconstructions of three of the most complete specimens were made using AMIRA (see Appendix S1–S5 with the online version of this article and Figs. 25–36). Internally, a triangular locule encloses a single tetrahedral seed, which is triangular in cross section (Figs. 1–4). One of the specimens has a fragment of external tissue attached to the enclosing structure at one end, but this is discontinuous and not well preserved (see online Appendix S3 and Fig. 30). Attachments of the reproductive structures to any additional axes are not known.

The seed-enclosing structures are composed mostly of elongate sclerenchyma cells with spiral thickenings that grade externally to a few rows of parenchyma (Figs. 1, 3). Most appear to be somewhat abraded and often the parenchymatous tissues have been removed (Figs. 2, 4, 5, 8, 9). Both the inner and outer surfaces appear to have lacked trichomes. The wall is very thin at the corners (Figs. 2, 4, 7, 9) and appears to have broken open to release the seeds by means of valves. Two specimens appear to have split open into three valves, one valve that contains vascular tissue and two that do not (Figs. 6, 7). The numerous spiral or helical thickenings on the sclerenchymatous cells of the walls probably facilitated the opening of the structures to release seeds (Figs. 14, 15) in a fashion that is similar to the dehiscence of some modern fruits (Fahn and Werker, 1972).

Seed-enclosing structures have one collateral vascular bundle (Figs. 1, 2, 6–9, 17, 18). In specimens where the vascular bundle is well preserved, it can be determined that ovules were borne on the abaxial surface of a bilateral, modified leaf-like structure. This position is demonstrated by the position of the phloem, which is represented by a tissue gap to the inside of the xylem (Fig. 17). Seeds are attached to this inner (i.e., abaxial) surface, and vascular bundles have been traced by serial sections to the broad ovule bases. Seed bases are vascularized by a cup-shaped zone of transfusion tissue (Figs. 11, 12) composed of short, pitted, tracheary elements (Fig. 19). Tracheary elements in the vascular strands between the collateral bundle of the enclosing structure and the vascular cup at the ovule base have helical secondary wall thickenings (Figs. 13, 16).

One tetrahedral, orthotropous ovule is very tightly enclosed inside each cupule/carpel-like structure. Ovules are 2–3 mm in diameter and 3 mm long with an integument of at least three zones of small parenchymatous cells, 4–8 cells thick on the flat sides, that increase to 24–28 cells in the angles or corners (Figs. 20–23). Cell size increases in the corners (angles) of the seed (Figs. 7 at left, 20–22). The innermost cells of the integument are more elongate and flattened (Fig. 21). In the reconstruction of specimen P13243A (Fig. 5), the micropylar end of the ovule shows three arms of integument, two of which are incurved (Fig. 33). Both enclosed and isolated seeds show what appears to be a suture line in the angles (Figs. 6, 7, 10, 20, 21). Thus, like the cupule/carpel-like organ, the seeds probably also split along three lines—the enclosing structures at the time of dispersal, the seeds at the time of germination.

The nucellus is attached only at the base of the seed (Figs. 1, 2, 5, 10–12, 20, 24, 25). The cuticle covering the nucellus is quite prominent and thick, and outlines of former cells are discernable where the cuticle extended between the cells of the outer layer (Figs. 25, 26). So far, no pollen chamber has been identified with certainty, leaving the nature of the nucellar apex in question. However, one seed cut in oblique section shows what may be prominent rectangular nucellar cells at one at one side (Fig. 2, at arrow) that are similar to cells of the nucellar beak in other fossils that have a pollen chamber (e.g., Rothwell, 1971, fig. 18; 1980, figs. 17, 21, 23). Because more distal levels of the seed were lost in the saw cut, the identification of a pollen chamber in *Doylea* remains uncertain.

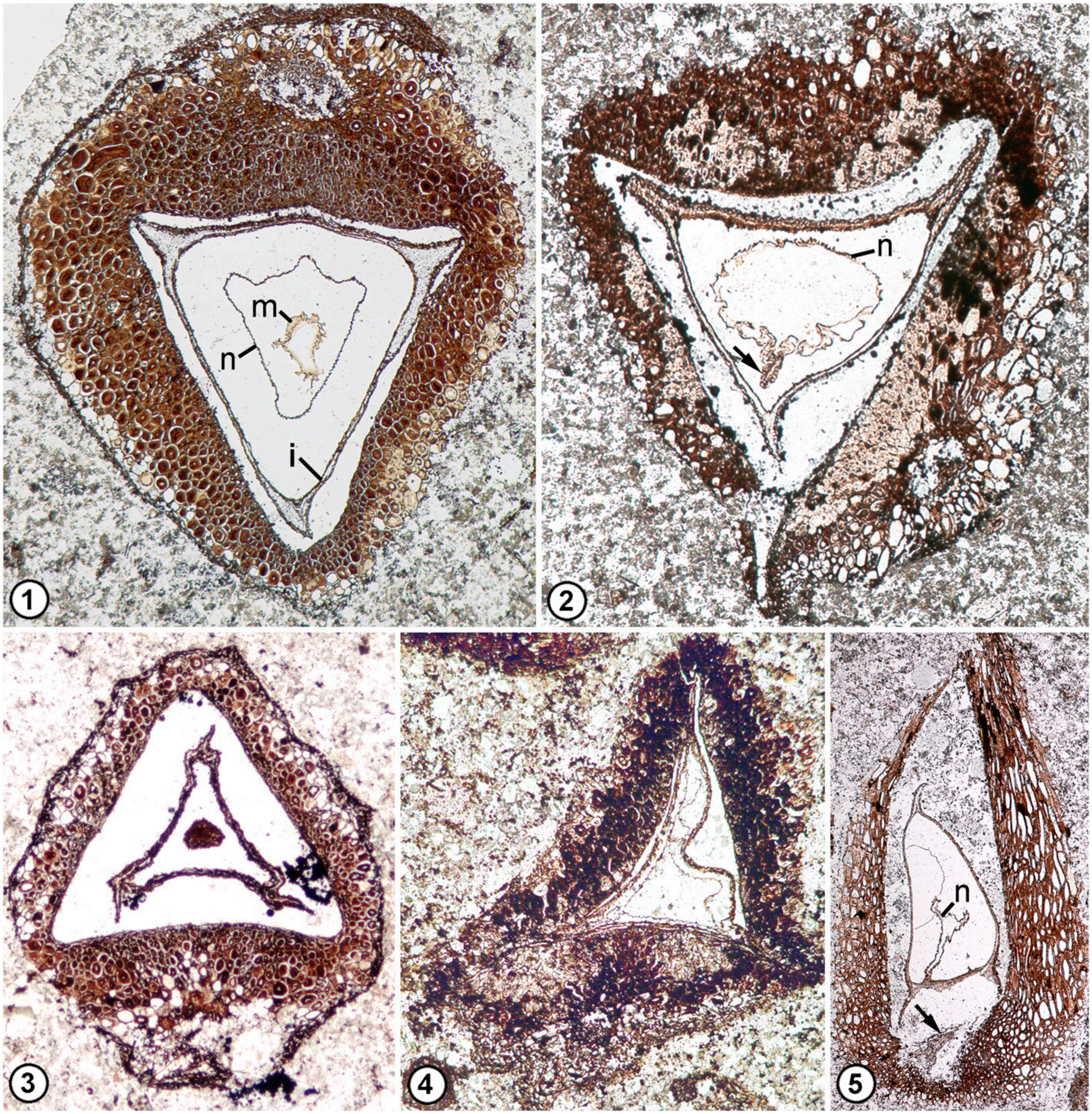
The megaspore membrane is thick and shrunken in the ovules (Figs. 1, 25, 27). In some seeds, there is light-colored material inside the megaspore membrane that may represent megagametophyte, but tissues are not well preserved (Figs. 1, 25, 27). In one of the smaller ovules (Fig. 24), the shrunken nucellus and megagametophyte form a trilobed structure with a hollow center (Fig. 24) that appears similar to gymnosperm ovules with megagametophytes in the free-nuclear phase of development (see e.g., Stockey, 1978, figs. 22, 23, 38). So far, no embryo tissues have been identified.

Closure of the reproductive structures—To determine the morphology and extent of the ovule enclosing structure and the three-dimensional configuration of the seeds, several of the most complete specimens were reconstructed using AMIRA (Figs. 25–32, also see Appendix S1–S5 in online Supplemental Data). The most complete specimen in longitudinal section (Figs. 5, 28, 31) reveals that the ovule is orthotropous and completely enclosed. Although small areas of the enclosing tissue remain open along one edge (Figs. 5, 31, at top), this surface of the enclosing structure has been abraded. Therefore, it is probable that seed enclosure may have been even more complete in life than in the fossils. Other reconstructions of the most complete specimens with enclosed seeds do not preserve the micropylar end because it was lost in the saw cuts (Figs. 30, 31). The only ovule in which the micropylar end is intact occurs in the specimen illustrated in Figs. 5, 28, 30, 33). In this specimen, the micropylar arms are situated directly beneath the small holes in the enclosing tissue (see also online Appendix S1–S5). Because of the tightness of the fit of the enclosing tissue to the ovule, these holes may have provided an entry point for pollination. So far, no pollen grains have been identified in the Apple Bay specimens.

DISCUSSION

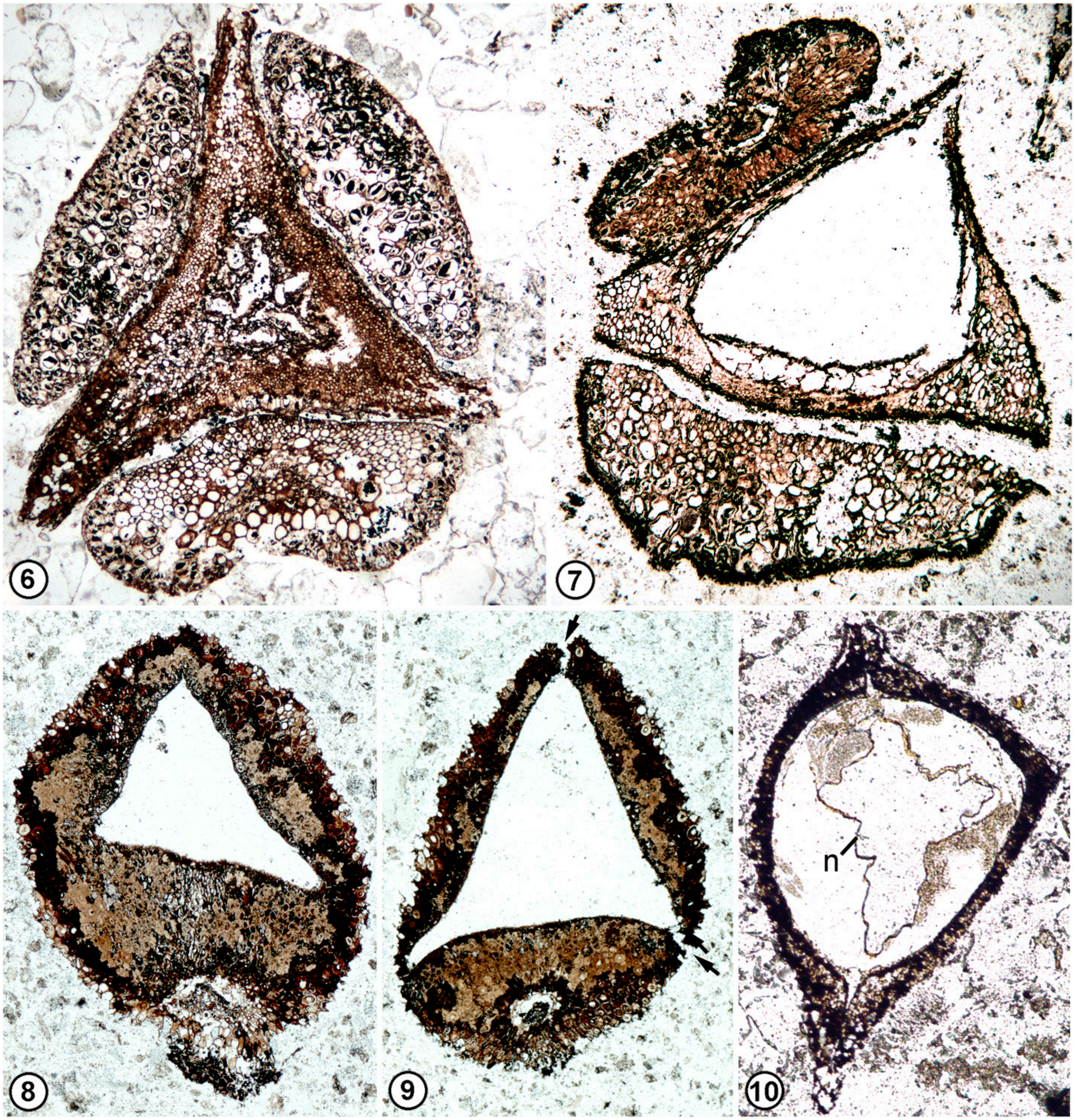
The isolated seed-enclosing structures are ellipsoidal to globose, lack trichomes, and contain one tetrahedral, orthotropous ovule on the abaxial surface of a leaf homologue (i.e., the phloem of the vascular bundle in the enclosing tissue faces the seed). The degree of seed enclosure varies from specimen to specimen, but is more complete than for virtually all known cupulate seed ferns. We compare these reproductive structures with those of angiosperms and cupulate seed ferns.

Comparison of seed-enclosing structure of* Doylea *to the carpel of angiosperms—Several specimens of the most extensively



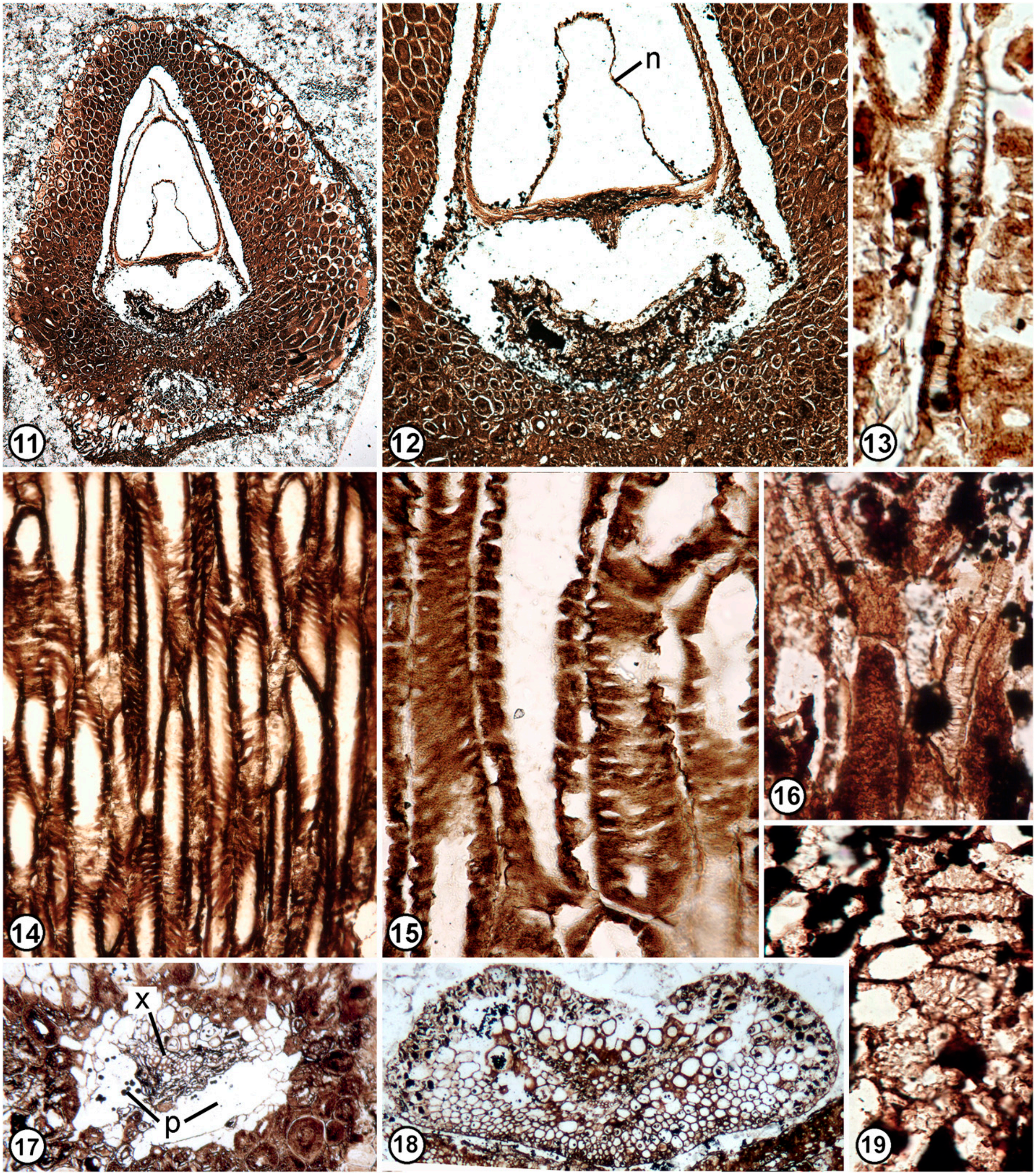
Figs. 1–5. *Doylea tetrahedrasperma* gen. et sp. nov. cupulate seeds. **1.** Transverse section through cupule showing one tightly enclosed seed with nucellus and megagametophyte. Note sclerotic cupule wall with small amounts of parenchyma in outer wall and vascular tissue, near top. Holotype P13394 A #25 ×30. **2.** Transverse section of cupule with tightly enclosed seed showing cracks in cupule wall and possible nucellar beak (arrow). Note cupule vascular tissue at lower right. P13249 Bbot #4 ×33. **3.** Transverse section of cupule with enclosed immature ovule. P14726 Cbot #1 ×45. **4.** Transverse section of cupule from the graywacke matrix with tightly enclosed seed P13133. Fbot #8 ×38. **5.** Longitudinal section of abraded cupule with orthotropous seed showing basal attachment of nucellus and remains of vascular cup (arrow). P13243 A #6 ×16. i = integument; m = megagametophyte; *N* = nucellus

enclosed seeds are nearly completely isolated from the outside environment by the enclosing tissue (e.g., Figs. 1–4, 29), while other specimens have openings along the corners of the seed (e.g., Fig. 6). The enclosing structure tightly covers the seed, but it apparently dehisced at the corners at maturity by means of three distinct valves, thus releasing seeds into the environment. This interpretation is supported by the occurrence of isolated seeds (e.g., Fig. 10) and also by two specimens that have partially open enclosing structures with seeds still inside (Figs. 6, 7). The existence of such a dispersal mechanism would

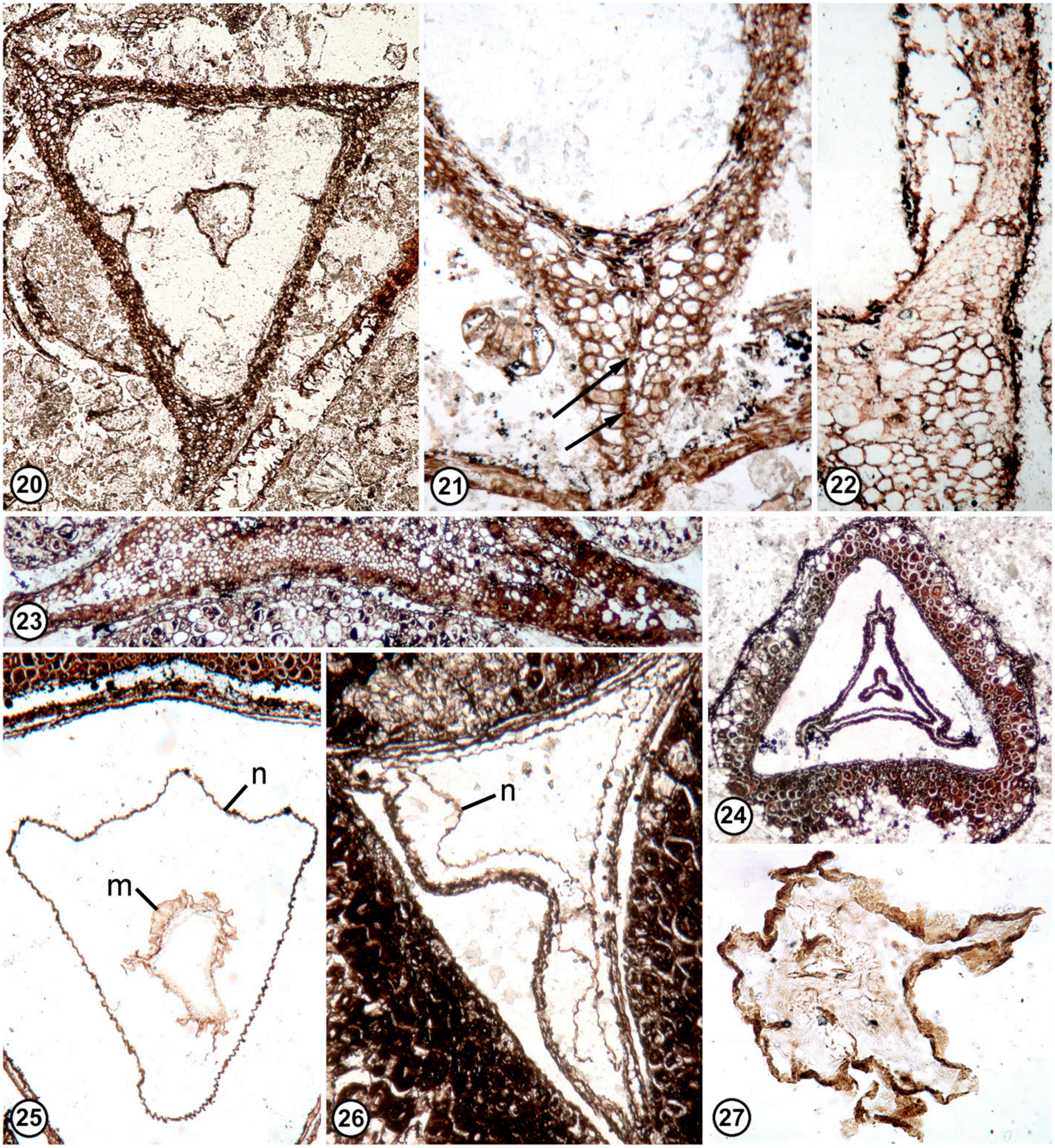


Figs. 6–10. *Doylea tetrahedrasperma* gen. et sp. nov. cupules and seeds. **6.** Transverse section of enlarged seed with three cupule lobes. Segment with vascular tissue at bottom. P13503 Ctop #3 ×44. **7.** Transverse section of seed still enclosed by two of three cupule lobes. Segment with vascular tissue on upper left. P14221 Etop #12 ×29. **8.** Empty cupule with vascular tissue at bottom. P13497 Dtop #1 ×20. **9.** Empty abraded cupule showing suture openings (arrows). P13497 Cbot #20 ×23. **10.** Isolated seed showing free nucellus (n) and suture lines in both upper and lower angles. P13393 Ibot #2 ×52.

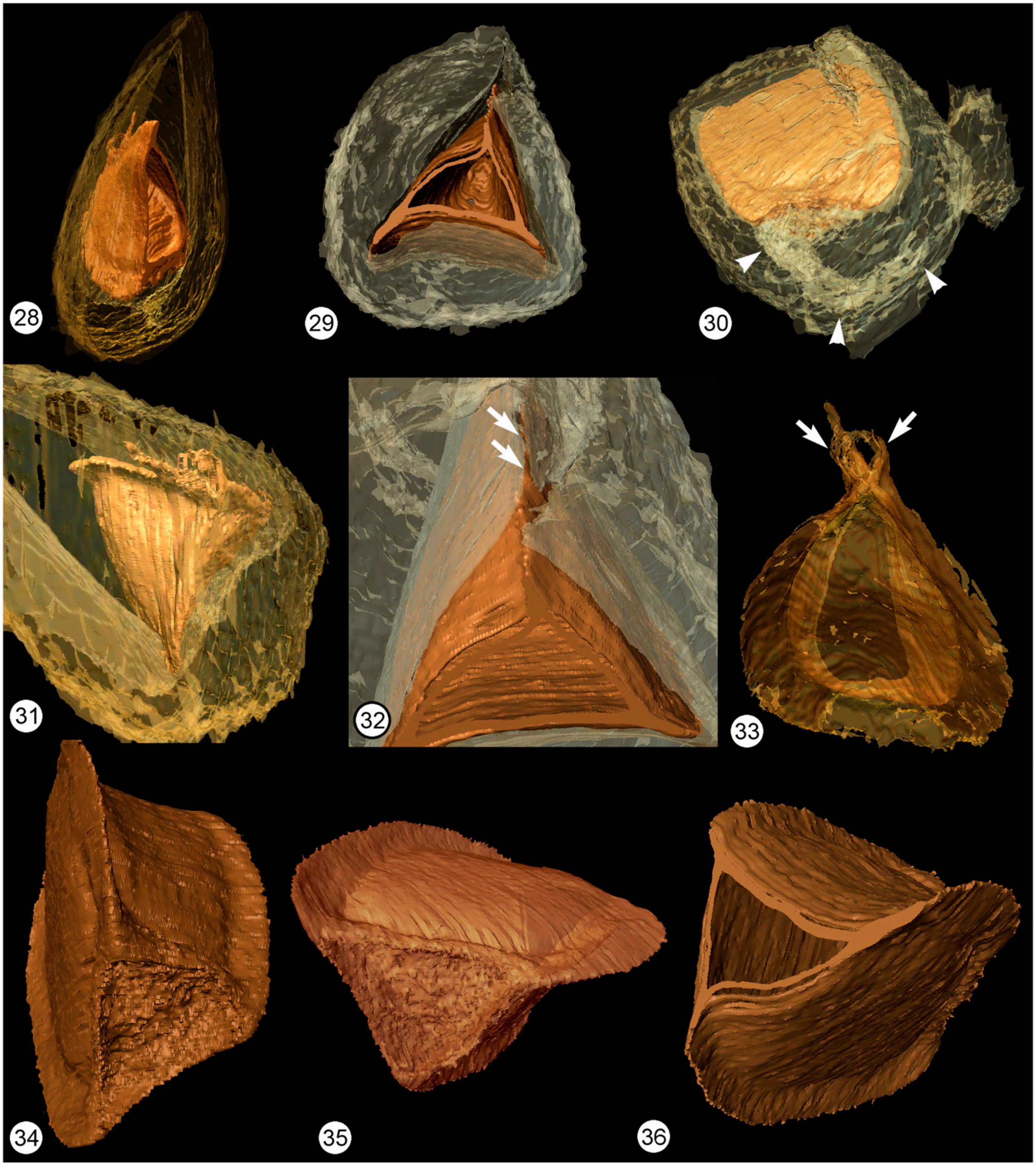
also account for the range of variation that is present in the degree of seed enclosure from specimen to specimen. The enclosing structure appears to have nearly completely surrounded the seed in at least some stages of development, with only small openings near the micropylar end of the cupule being potentially available for the possible entry of pollen (see Appendix S1–S5 with online Supplemental Data). Unlike carpels of most living angiosperms, in which tissue completely isolates seeds from the external environment at the time of pollination, several living "basal" angiosperms have carpels that are partly closed



Figs. 11–19. *Doylea tetrahedrasperma* gen. et sp. nov. **11.** Transverse section of cupule with tightly enclosed seed showing vascular disc at seed base and vascular tissue near bottom. Holotype P13394 A #44 ×24. **12.** Vascular disc at base of ovule showing basal nucellar attachment Note sclerotic tissues of cupule wall. Holotype P13394 A #44 ×60. **13.** Tracheary element between cupule and vascular disc at seed base showing helically secondary wall thickenings. Holotype P13394A #78 ×524. **14.** Sclerenchyma fibers of inner cupule wall showing helical thickenings. P13243 A #47 ×120. **15.** Helical thickenings on fibers of inner cupule wall. P13243 A #2 ×283. **16.** Vascular tissue between cupule trace and vascular cup at base of seed. Holotype P13394 A #80 ×458. **17.** Collateral vascular bundle in cupule. (x = xylem; p = phloem gap) P13497 Cbot#3 × 80. **18.** Vascularized segment of cupule lobe from Fig 6. P13503 Ctop #3 ×60. **19.** Transfusion tissue in vascular cup at base of seed showing short tracheary elements with numerous pits. P13243 A #1 ×333. *N* = nucellus.



Figs. 20–27. *Doylea tetrahedrasperma* gen. et sp. nov. **20.** Isolated seed. P13396 Cbot #2 ×29. **21.** Seed showing integumentary layers and suture line (at arrows) where seed probably split open at germination P13396 Cbot #2 ×47. **22.** Seed integumentary layers. P14221 Etop #12 ×70. **23.** Seed integumentary layers. P13503 C top #3 ×54. **24.** Immature seed in cupule showing triangular, collapsed zone of tissue in center. P14726 Cbot #2 ×43. **25.** Nucellus (n) showing thick cuticle and megagametophyte (m). Holotype P13394 A #25 ×71. **26.** Seed showing nucellus (n) with thick cuticle. Holotype P13133 Fbot #8 98. **27.** Probable remains of megagametophyte. Holotype P13394 A #30 ×583.



Figs. 28–36. *Doylea tetrahedrasperma* gen. et sp. nov. AMIRA reconstructions; cupule transparent and seed opaque. **28.** Longitudinal view based on 70 sections of seed in cupule. Note space above micropylar end of seed, at top. P13243 A series ×20. **29.** Transverse sectional view based on 135 sections showing one tightly enclosed tetrahedral ovule. P13249 Bbot series ×15. **30.** View through cupule showing seed attachment; arrows indicate vascular tissue. Note extraneous tissue at right. P13249 Bbot series ×16 **31.** Top view of seed in cupule. Note series of small holes in cupule. P13243 A series ×27. **32.** Ovule in cupule showing crack on one side (arrows). P13249 B bot series ×26. **33.** Longitudinal view of ovule showing micropylar arms at top. P13243A series ×32. **34**. View of seed at base showing three flanges at corners and triangular area of attachment to cupule. P13249 Bbot series ×29. **35.** Triangular seed base. P13249 Bbot series ×27. **36.** Transverse section of tetrahedral seed showing three corner flanges. P13249 Bbot series ×27.

by secretions, rather than by postgenital tissue fusion (Endress and Igersheim, 2000). So far, we have no way of determining whether such a secretion occurred in the fossil specimens.

The prominent nucellus attached only at the base, an apparently single integument, a megaspore membrane with enclosed thin-walled tissue, a surrounding cupule-like structure that was probably at least partially open near the micropylar end, and a trifid micropyle indicate that these plants were probably gymnospermous rather than angiospermous. A developmental sequence for these plants and attachment to some sort of branching system would be of great help in determining the exact affinities of the Apple Bay seed plant. It should be noted that while no pollen has been found in or associated with these reproductive structures, the small openings at the micropylar end of the enclosing structure and the trifid micropyle could indicate that these plants had a pollination droplet. In living gymnosperms such as pinaceous conifers (e.g., Owens et al., 1998, 2001), micropylar arms are common in ovules that produce pollination droplets, and these taxa usually have saccate pollen (e.g., Tomlinson, 1994). Thus, it appears likely that these reproductive structures were ovulate cupules borne by an extinct gymnosperm.

Comparison of* Doylea *to the cupules of fossil seed ferns—The cupule of the Apple Bay specimens is an abaxially enrolled leaf-like structure as evidenced by the single collateral vascular bundle with the phloem zone oriented toward the ovule. In the Paleozoic seed ferns such as *Elkinsia* Rothwell, Scheckler & Gillespie (1989), evidence shows that cupules probably evolved by fusion of terete distal segments of foliar branching systems (Stewart and Rothwell, 1993; Taylor and Taylor, 1993). In "Mesozoic" or post-Carboniferous pteridosperms, however, cupules are usually interpreted as modified leaves or leaflets that enclose the ovules (Crane, 1985, 1988; Nixon et al., 1994; Rothwell and Serbet, 1994; Doyle, 1996, 2006; Hilton and Bateman, 2006). In addition, it has been suggested that cupules in the various "Mesozoic" or post-Carboniferous seed fern groups probably had several separate origins (e.g., Nixon et al., 1994; Rothwell and Serbet, 1994; Hilton and Bateman, 2006; Doyle, 2006).

The post-Carboniferous seed ferns are usually treated in three or four orders (minus the very distinctive glossopterids): Peltaspermales, Caytoniales, Petriellales and Corystospermales, which are known mostly from compression/impression fossils (Stewart and Rothwell, 1993; Taylor and Taylor, 1993; Taylor et al., 1994; Klavins et al., 2002). All these groups are reviewed by Taylor and Taylor (2009, pp. 237–251 in this issue). Of these so-called "Mesozoic" seed ferns, the peltasperms have seeds borne abaxially on peltate, umbrella-like discs or fan-shaped megasporophylls (Harris, 1937; Townrow, 1960; Kerp, 1982, 1988; Poort and Kerp, 1990; Naugolnykh and Kerp, 1996; Kerp et al., 2001; Naugolnykh, 2001; Karasev and Krassilov, 2007) arranged in cones that appear distinct from the seed-enclosing structures from Apple Bay.

While the seed-bearing reproductive structure of the Caytoniales, *Caytonia*, first described from the Jurassic flora of Yorkshire (Thomas, 1925; Harris, 1933b, 1940, 1958, 1964) has received substantial attention, it also represents one of the more poorly known seed ferns (Taylor et al., 2006). Although several species have been described, all are known from compression/impression specimens, and internal detail is generally lacking. The cupules of *Caytonia* have been reported to have 8–30 seeds (Table 1). Seeds of *Caytonia* are ovoid with an outer epidermis and an inner integumentary layer of thick-walled cells (Harris, 1958), unlike the tetrahedral seeds from Apple Bay, which have only thin-walled integumentary layers (Table 1). Evidence provided by Reymanówna (1973) further suggests that *Caytonia* cupules enclosed a series of elongate canals from the outside, leading to the seed micropyles. This type of structure is completely lacking in *Doylea*, where the single seed nearly fills the cupule and is tightly enclosed over all surfaces except the micropylar area (see reconstructions in Appendix S1–S5 with online Supplemental Data and Figs. 28–31).

The most recently described pteridosperm order, the Petriellales, is based on permineralized cupules with enclosed seeds from the Triassic of Antarctica (Taylor et al., 1994). Similarities of *Petriellaea* Taylor, del Fueyo & Taylor to the Apple Bay reproductive structures include cupulate orthotropous seeds with a vascular disc that are triangular in cross section with a parenchymatous integument (Table 1). However, *Petriellaea* cupules are bilateral with a dorsal groove, contain 5–6 seeds about half the size of those from Apple Bay, and appear elliptical in longitudinal view rather than tetrahedral (Table 1). The integumentary cells of the outer layer in *Petriellaea* have dark contents and a vascular disc is reported at the base of the nucellus (Taylor et al., 1994). The Apple Bay seeds lack dark contents and the vascular disc- or cup-shaped zone of tracheids is in a completely different position, outside of the seed integument where the seed is attached to the cupule. The cupule in *Petriellaea* contains many vascular strands to the seeds that are attached on the adaxial surface, while in the Apple Bay material there is a single vascular strand and the seed is attached on the abaxial surface. The nucellus is described as completely attached to the integument in *Petriellaea*, while the nucellus in the Apple Bay seeds is attached to the integument only at its base. Cupules of *Petriellaea* may be borne in groups of up to seven (Taylor et al., 1994). Attachment of the cupules described here is thus far unknown.

The most recent occurrence of pteridosperms is that of *Ktalenia* described by Archangelsky (1963) from the Cretaceous (early Aptian) of Argentina (assigned to Caytoniales, Archangelsky and Taylor, 1985). Cupules, now known to be attached to *Ruflorinia* Archangelsky foliage, contain one or two orthotropous seeds with a prominent nucellar beak (Table 1; Taylor and Archangelsky, 1985). Although these cupules are compression/impressions, cuticles are well preserved and the outer surfaces are papillate, unlike the structures from Apple Bay (Table 1). Like *Caytonia, Petriellaea*, and the structures from Apple Bay, it appears that seed micropyles in *Ktalenia* may have been enclosed inside the cupules. These cupules appear to have been fleshy and unlobed like those of *Caytonia* (Table 1).

Among the Mesozoic seed ferns, the cupules from Apple Bay most closely resemble taxa in the Corystospermales. Corystosperms typically have only one or two ovules per cupule (Table 1), and in those where anatomy is known, the seeds are attached to the abaxial surface of the cupule as in the material described here (Klavins et al., 2002). Unlike the cupules described here, however, they usually have seeds with exposed bifid micropyles (Table 1). Only a few specimens of *Spermatocodon* Thomas are known; however, its cupules are spherical to campanulate (Thomas, 1933), unlike the globose structures from Apple Bay. *Pilophorosperma* Thomas has more distinctly helmet-shaped cupules and conical seeds with curved exposed micropyles that differ from the enclosed tetrahedral seeds of the Apple Bay material. It has long been speculated that the corystosperm cupule was at least somewhat fleshy, as evidenced by

Table 1. Comparison of Apple Bay cupules to those of some Mesozoic seed ferns.

Taxon	Cupule size (mm) width × length	Cupule shape	No. of lobes	No. ovules/ cupule	Seed shape	Seed size (mm)	Micropyle exposed	Seed attachment	Cupule surface bearing seeds	Cupule surface ornamentation	Preservation mode	Age
Doylea	3–4 × 5.5	Ellipsoidal to globose	3	1	Tetrahedral, triangular in xs	2–3 × 3	No	Orthotropous	Abaxial	Glabrous	Permineralization	Cretaceous
Corystospermales												
Kannaskoppia	2.5 × 2	Ovoid to globose	3	?	?	?	?	?	?	?	Compression	Triassic
Karibacarpon	14–18 × 14–38	Fan-shaped–flattened	5–9	1	Ovate, ridged	12–25 × 8–15	Yes	Orthotropous	?	?	Compression	Triassic
Pilophorosperma	3–4 × 2.5–3.5	Ellipsoidal, spherical, helmet-shaped	?	1	Conical	3–3.5 × 4–6.5	Yes	Orthotropous	?	Papillate	Compression	Triassic
Spermatocodon	3.5 × 4	Spherical-campanulate	3–4	1	Flattened?, elliptical	3.5	Yes	Orthotropous	?	Glabrous	Compression	Triassic
Unkomasia	5–8 × 5–9	Spherical, elliptical, hemispherical	2–3	1–2	Elliptical, flattened	1.3 × 4–5	Yes	Orthotropous	Abaxial	Papillate or glabrous	Compression and permineralization	Triassic
Petriellales												
Petriellaea	1.2–2 × 3 × 1.5	Bilateral with dorsal groove	2	5–6	Elliptical, triangular in xs	0.3–1 × 1.5	No	Orthotropous	Adaxial	Glabrous	Permineralization	Triassic
Caytoniales												
Caytonia	3–4 × 2–3	Spherical	0	8–30	Ovoid-elliptical	0.3–1 × 2	No	Orthotropous	?	Papillate	Compression	Triassic-Jurassic
Ktalenia	3–4 × 3–4	Ellipsoidal	0	1–2	Ovoid	1–2.8	No	Orthotropous	?	Papillate	Compression	Cretaceous

Note: Modified and condensed from Taylor et al., 1994; other sources: Archangelsky, 1963; Taylor and Archangelsky, 1985; Axsmith et al., 2000; Klavins et al., 2002; Anderson and Anderson, 2003.

the wrinkled surfaces on many compressions of *Umkomasia* Thomas, *Pilophorosperma*, and *Spermatocodon* (Table 1; Thomas, 1933; Zan et al., 2008). The cupules described here have a thin parenchymatous outer zone that is underlain by a very sclerotic inner zone.

Umkomasia resinosa Klavins, Taylor et Taylor (2002) from the Triassic of Antarctica is, thus far, the only known anatomically preserved corystosperm cupulate structure. Cupules are recurved and attached to a branching system. In *U. resinosa*, there are usually two orthotropous ovules (occasionally one) per cupule (Table 1). *Umkomasia resinosa* also had a rugose, glabrous surface like that in the Apple Bay structures, but *U. resinosa* cupules are typically bilobed rather than trilobed and have prominent secretory cavities (Klavins et al., 2002) that are not found in the material from Apple Bay.

Many corystosperm cupules have been described as "lobed" (Table 1; see Taylor et al., 1994, for summary). In *Umkomasia resinosa*, these appear to be naturally occurring lobes in cupules that contain two seeds, and there is some indication of a possible abscission layer for the seeds, which could allow them to just drop out of the cupules at maturity without the need for the cupule to open. It has also been suggested that some seed fern cupules may have had valvate dehiscence or that the ribs in the cupule may indicate that they dehisced (e.g., Holmes and Ash, 1979; Anderson and Anderson, 2003). *Karibacarpon* Lacey (1976; Holmes and Ash, 1979; Holmes 1987) has been described with 5–9 lobes that opened to leave large star-shaped structures (Table 1). The cupules from Apple Bay like those of *Kannaskoppia* Anderson et Anderson (2003), a Triassic gymnosperm (treated by these authors as a possible ginkgophyte) from the Molteno Formation of South Africa, had three valves. However, in these compression specimens the anatomy of the cupules is not clear, and seeds are unknown. This type of cupule opening mimics the dispersal of angiosperm seeds from a dehiscent fruit. Thus, there appears to be a variety of different types of seed dispersal in corystosperms and related taxa. It is unclear at the present time whether all of these taxa, should be included in the corystospermalean seed ferns. It was reported that ovules of corystosperms probably contained no fibrous cells (Thomas, 1933), based on macerations of compression fossils. However, some tabular, thick-walled cells have been reported now in the permineralized *Umkomasia* from Antarctica (Klavins et al., 2002). Most of the seeds known are flattened (both in compressed and permineralized material). These characters contrast with the Apple Bay seeds, which are distinctly tetrahedral and do not contain any thick-walled integumentary cells. Therefore, we have described the Apple Bay cupules in a new taxon, *Doylea tetrahedrasperma* gen. et sp. nov., in recognition of its distinctive characters.

A description of *Umkomasia* from the Triassic of northern China (Zan et al., 2008) recently brought attention to the occurrence of corystosperms, formerly thought to be mostly Southern Hemisphere taxa, in the Northern Hemisphere at this time. Further occurrences in the Northern Hemisphere include pollen organs of *Pteroma* Harris and foliage of *Pachypteris* Brongniart from the Yorkshire Jurassic flora (Harris, 1964), *Umkomasia* and *Pteruchus* from the Jurassic of Germany (Kirchner and Müller, 1992), and foliage types from the Triassic of Eurasia (Dobruskina, 1994; Zan et al., 2008). The fossils from Apple Bay also show that not only were corystosperm-like plants more common in the Northern Hemisphere in the past, but also that they may have extended up into the Lower Cretaceous of North America. This group, which has had relatively little attention compared to other Mesozoic pteridosperms, is now beginning to be better known and clearly has much more diversity than was previously recognized.

Comparison of* Doylea *to the outer integument of angiosperms—The cupule vasculature in the Apple Bay material tracks the course of a raphe in an anatropous double-integumented angiosperm ovule (see Fig. 30), and there is sometimes a slight bulge to the cupule on that side (see Figs. 1, 3). Recently, Doyle (2006) discussed the origin of the second integument in angiosperms as potentially arising from a seed fern cupule like that of *Caytonia.* This idea originated with Gaussen (1946) and later with Stebbins (1974) and Doyle (1978). *Caytonia*, however, has from 8 to 30 seeds per cupule (Table 1), so evolution of the angiospermous outer integument would require the reduction in the number of ovules per cupule to one (Doyle, 2006). Assuming that the seeds of *Caytonia* are borne on the adaxial surface of the cupule wall (a character that has not been documented), evolution of an angiosperm carpel through the cupule of *Doylea* from that in a *Caytonia*-like ancestor would require not only the reduction of the number of ovules but a complete turning inside-out of the cupule. Unlike the carpels of extant angiosperms (e.g., Eshed et al., 1999, 2001; McAbee et al., 2006), seeds of *Doylea* were borne on the abaxial (rather than the adaxial) surface of the enclosing structure.

Doylea had single seeds that were tightly enclosed in tissue of the cupule like the outer integument of angiosperms, showing that this level of organization was present in pteridosperms in the Lower Cretaceous. The inner integument of angiosperms is attached to the adaxial surface of the outer integument (Eshed et al., 1999; Doyle, 2006; McAbee et al., 2006), while the seed inside the tight cupule of *Doylea* is attached abaxially, making the enclosing tissue analogous rather than homologous with the second integument of flowering plants. *Doylea* seeds were dispersed from the cupules by three valves like those of some dehiscent carpels (fruits) of angiosperms. However, again, these are analogous, rather than homologous to the carpels of flowering plants.

While we know that seed ferns are very diverse in the late Paleozoic and early Mesozoic, *Doylea* provides evidence that far from dying out, corystosperm-like plants may have become increasingly specialized through time to a point of near convergence with angiosperms in terms of their reproductive morphology. *Doylea tetrahedrasperma* was probably one of several angiophytes that combined gymnospermous pollination with angiospermous protection of the seeds and flowering plant-type dehiscence for seed dispersal. The biotic pressures for specializations that we usually consider to be limited to angiosperms have led to convergent evolution and provide a cautionary note about the need to distinguish analogy from homology when probing the fossil record for answers to the mystery of angiosperm origins. As more well-preserved material is described and gaps in the fossil record filled, we look forward to coming closer to understanding the evolutionary pathways that led to angiospermy.

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