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***DORDRECHTITES* ARCANUS SP. NOV., AN ANATOMICALLY PRESERVED GYMNOSPERMOUS REPRODUCTIVE STRUCTURE FROM THE MIDDLE TRIASSIC OF ANTARCTICA**

Julie A. Bergene,* Edith L. Taylor,^{1,*} and Thomas N. Taylor*

*Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, Kansas 66045, U.S.A.,
and Biodiversity Institute, University of Kansas, Lawrence, Kansas 66045, U.S.A.

The genus *Dordrechtites* is an isolated ovulate structure previously described only from South Africa and Australia as impressions. The discovery of compressed and permineralized specimens of this taxon at the base of Mount Falla (uppermost Fremouw Formation) in the central Transantarctic Mountains extends the geographical and geological distribution of the genus and increases the known floral diversity of the Triassic of Antarctica. The first permineralized species, *Dordrechtites arcanus*, is described using standard acetate peel techniques and includes internal anatomy of an elongate arm that extends over the top of a central cupule containing two elongate, bilaterally symmetrical, orthotropous ovules. An arc-shaped collateral vascular bundle extends from the arm into the top of the cupule, branches, and then extends around the ovule to about halfway down to the micropylar end. The cupule is parenchymatous and includes transfusion tissue with cells that have pitted walls. The sclerotesta of the ovule is up to 200 μm thick, consisting of an outer layer with longitudinally oriented, thick-walled cells and an inner layer one cell thick of rectangular, thick-walled cells. The micropyle is flared at the attenuated tip of the pyramidal cupule. The four previously described species of *Dordrechtites* have uncertain affinities, and although the morphology and anatomy of this taxon is now known, the affinities within the gymnosperms are still uncertain.

Keywords: Triassic, gymnosperm, cupule, ovules, central Transantarctic Mountains.

Introduction

During the Triassic Period (252–201 Ma), floras underwent rapid diversification in Gondwana (Anderson et al. 1999). The significant extinction before and during the transition from the Permian to Triassic was not a simple replacement of the flora between the two periods (McLoughlin et al. 1997), since pioneers and survivors extending into the Triassic diversified, while the so-called victims, such as the Glossopteridales, ended their dominance (Lindström and McLoughlin 2007). The glossopterids may have survived briefly into the Triassic (McLoughlin et al. 1997; McManus et al. 2002 and references therein), and the Corystospermales, a widespread group of seed ferns in the Triassic, appear to have originated in small numbers in the late Permian (Kerp et al. 2006; Abu Hamad et al. 2008). New groups of seed plants arose in the Triassic, while others largely diversified, such as the corystosperms and conifers, to take over the land previously dominated by the Glossopteridales in the Permian (Archangelsky 1996). The Triassic period was an important time in seed plant evolution, and it has been suggested that the Triassic flora was the most diverse ever in terms of gymnosperm orders (Anderson and Anderson 2003).

Many gymnosperm groups were present in the Triassic of Gondwana: the Coniferales, Corystospermales, Cycadales, Pel-

taspermales, and Petriellales (Anderson 1978; Taylor et al. 1994; Axsmith et al. 1998; Klavins et al. 2002, 2003; Holmes and Anderson 2005; Schwendemann et al. 2010; Bomfleur et al. 2011b). The diversity of the known flora of Antarctica during the Triassic includes all of the major seed plant groups as well as ferns, sphenophytes, and lycophytes (Delevoryas et al. 1992; Schwendemann et al. 2010; Bomfleur et al. 2011a). By the early Middle Triassic (Anisian) in Antarctica, corystosperm seed ferns, with *Dicroidium*-type foliage and *Umkomasia* ovulate structures, were the dominant group (Farabee et al. 1990; McLoughlin et al. 1997; Axsmith et al. 2000; Klavins et al. 2002; Escapa et al. 2011); conifers and cycads were also present (Escapa et al. 2011). In the central Transantarctic Mountains, the Fremouw Formation contains fossils of every major plant group that was in existence at the time. Interestingly, and perhaps because of the high polar paleolatitude, there are only one or two representative genera of each group in the flora (Escapa et al. 2011).

Middle Triassic permineralized peat from the Fremouw Formation has provided a wealth of detail about the plant groups present in the flora. Permineralizations of fertile structures have been particularly informative of reproductive architecture and phylogenetic affinities. Sometimes, however, it is difficult to relate permineralized taxa to compression forms, and even with anatomical detail, it is challenging to assign isolated reproductive structures to specific plant groups.

The fossil record for Triassic Gondwanan plants has been investigated for the past hundred years, yet several enigmatic

¹ Author for correspondence; e-mail: etaylor@ku.edu.

reproductive structures have still not been assigned to specific groups with any certainty (Anderson and Anderson 2003). *Dordrechtites* is a gymnospermous reproductive structure that was originally described by Anderson (1978) from the Molteno Formation of South Africa (Carnian, lowest Upper Triassic) as an isolated, T-shaped scale with a robust and woody trunk (central portion) attached to a curving arm. It was considered to be either microsporangiate or megasporangiate. As we now understand it, *Dordrechtites* consists of a central triangular region (scale of Anderson 1978) attached to an elongate arm that extends out from either side of the central region. The type species from South Africa, *Dordrechtites elongatus*, was found on the same bedding plane as strap-shaped leaves now assigned to *Heidiphyllum elongatum* (Retallack 1981).

Anderson and Anderson (2003) subsequently described two additional species of *Dordrechtites* from South Africa (*Dordrechtites cetiparvus* and *Dordrechtites mazocirrus*) and placed them in a new family Dordrechtitaceae and order Dordrechtiales within the Pinopsida, together with the type species *D. elongatus*. They also described *Dordrechtites* attached to an axis. Rigby (in Playford et al. 1982) detailed an additional species, *Dordrechtites dikeressa*, from the Moolayember Formation (Middle Triassic) of Queensland, Australia. This species exhibits a central cupule with protruding spine-like points and a shorter arm than the type material. The cupules of *D. dikeressa* were borne in pairs on secondary axes, which were attached to a robust primary axis. Playford et al. (1982) considered *D. dikeressa* to have corystosperm affinities. *Dordrechtites* sp. has also been noted, but not described, from Argentina (Anderson and Anderson 2003; Artabe et al. 2007; Novas 2009, p. 33; Gnaedinger 2010) and Australia (Anderson and Anderson 2003).

In South Africa and Australia, *Dordrechtites* was found in large numbers, >100 specimens at each site and at multiple localities within the country of origin. In these specimens, the *Dordrechtites* cupules were interpreted to be helically attached to a main axis and assumed to contain ovules, although none has yet been isolated.

In this article, we present the first *Dordrechtites* from Antarctica and one of the oldest described species to date (Anisian), thus expanding the known geographic and stratigraphic range of the taxon. In addition, the Antarctic *Dordrechtites* is preserved as combinations of compressions and permineralizations, permitting the first description of the anatomy of this cupule and the ovules within it.

Material and Methods

Reproductive structures of *Dordrechtites* are preserved as compressions and permineralizations within silicified sediments that were collected from the base of Mount Falla (84°20'50.1"S, 164°39'40.6"E) in the Queen Alexandra Range of the central Transantarctic Mountains, Antarctica (fig. 1A; Buckley Island Quadrangle; Barrett and Elliot 1973). Specimens include three compression-combination fossils and 15 permineralization specimens. The compression specimens represent a combination of preservational types because they appear as compressions on the surface (fig. 2A, 2B) but are partially permineralized and contain cellular detail. The other permineralized specimens were found within silicified blocks.

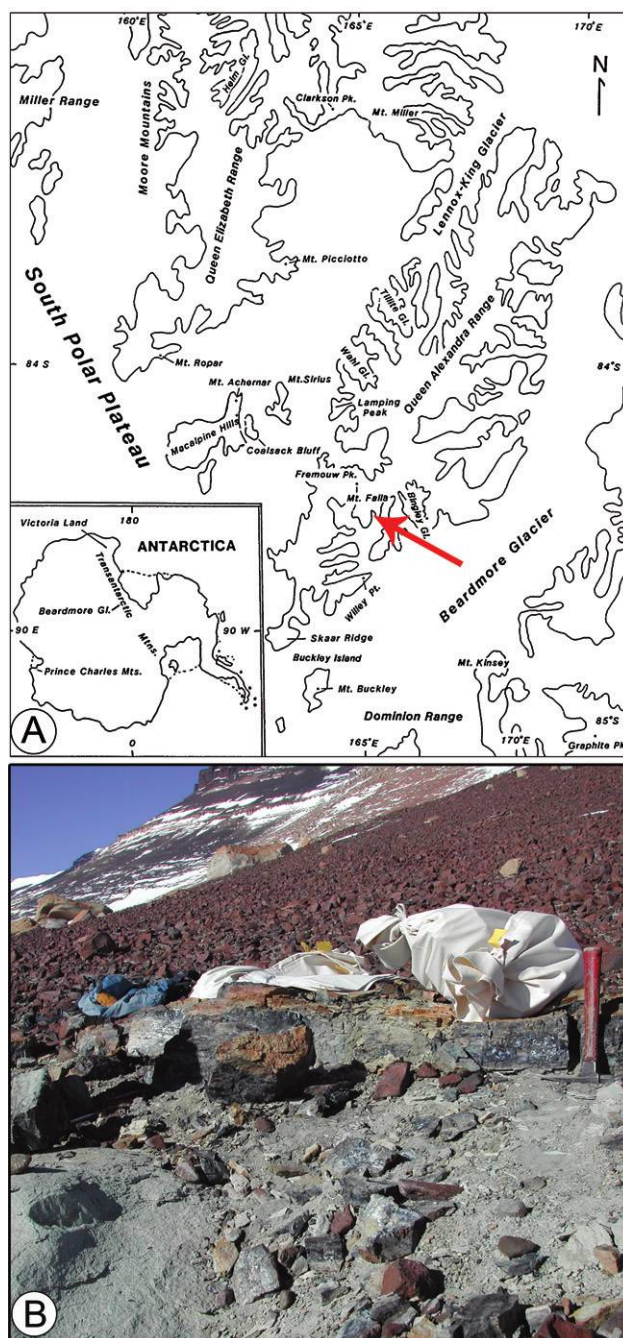


Fig. 1 Locality of *Dordrechtites arcanus*. A, Map of Antarctica (inset) and Beardmore Glacier region. Arrow indicates Mount Falla. Modified from Collinson and Elliot (1984). B, Photograph of locality at base of Mount Falla. Note dark-colored layer of silicified mudstone (next to hammer) above the bluff-forming sandstone. Photograph by C. P. Daghljan, 2003. Hammer = 28 cm.

The level containing the fossils is part of the uppermost Fremouw Formation (Beacon Supergroup), which is dated as early Middle Triassic (Anisian; Barrett 1969; Farabee et al. 1990). The nearby type section of the Fremouw Formation is 614 m thick and consists of quartzose sandstone deposits from low-sinuosity, braided streams (Barrett et al. 1986). *Dordrechtites*

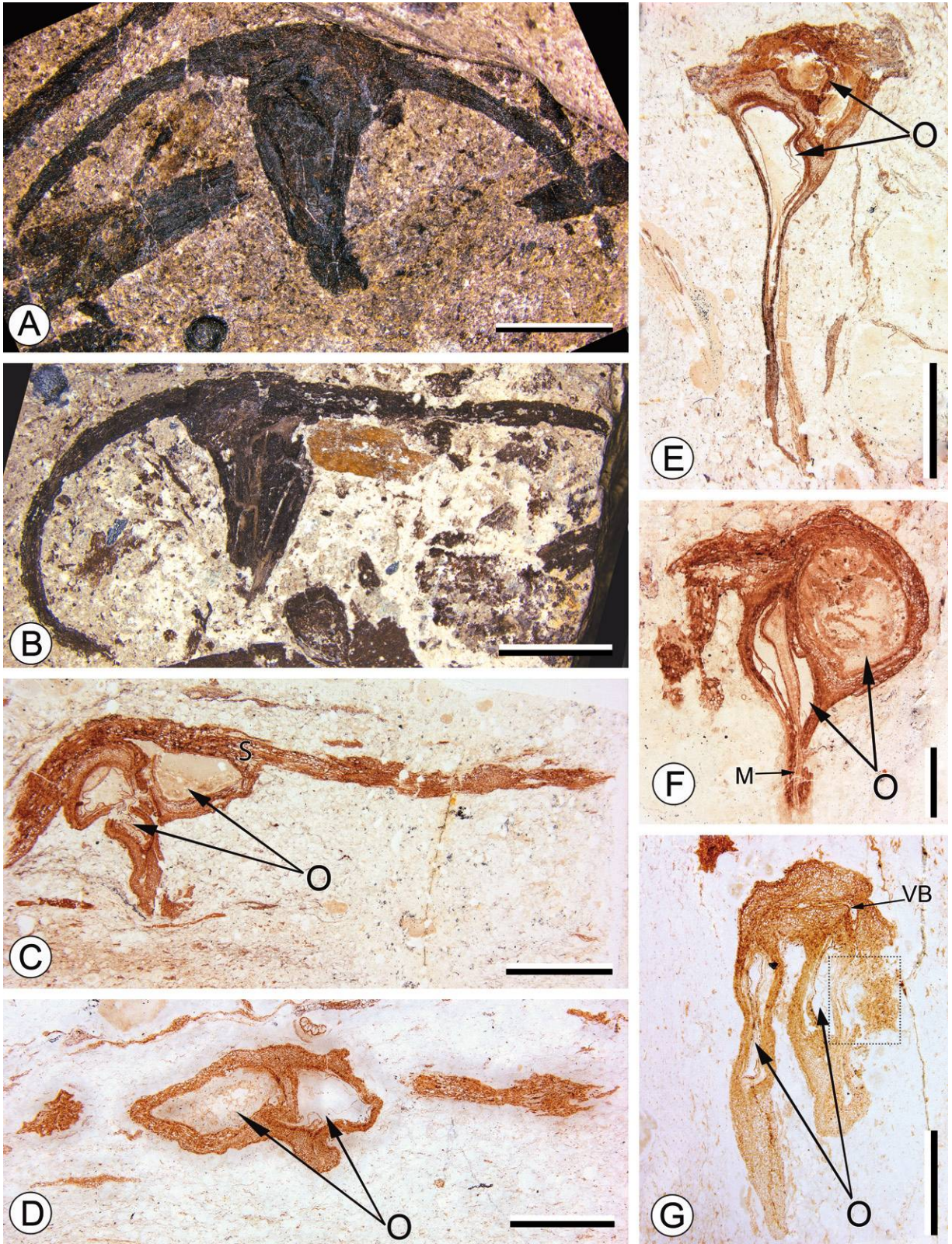


Fig. 2 *Dordrechtites arcanus* nov. sp. from the base of Mount Falla, central Transantarctic Mountains, Antarctica. *A, B*, Compressions. *C–G*, Permineralizations. *A*, *Dordrechtites arcanus* displaying central cupule attached to arm. T 5647. *B*, *Dordrechtites arcanus* with curved arm (left) and organic debris typical of the rock matrix. T 5949. *C*, Longitudinal section showing one side with a complete arm and broken stub on other side; central cupule contains two ovules (arrows). Note sclerenchyma of arm (S) continuing over top of cupule. Holotype, 12603 A 3. *D*, Oblique

was found within Barrett's (1968) section F4 at the base of Mt. Falla in what are interpreted as strata from the uppermost Fremouw Formation (Barrett 1968). The fossils occur within a layer of silicified, carbonaceous mudstone—level 4—that was directly above a massive, bluff-forming sandstone, just above the snow level (as illustrated in Barrett 1968) at the base of Mount Falla (fig. 1B). The mudstone exhibits fine laminations, suggesting deposition in a quiet environment, perhaps an abandoned stream channel. In contrast, the plant material within the mudstone is generally very finely comminuted, suggesting transport in a higher-energy environment. As a result, most specimens are degraded and poorly preserved. Although the deposit resembles a permineralized peat in hand samples (fig. 1B), etched surfaces and peels reveal that most of the plant material is difficult to recognize. In addition, the low proportion of plant material argues against this being termed a peat deposit. Permineralized plant material appears to be relatively widespread in this region, probably as a result of the dissolution of siliceous volcanic detritus that was abundant in the area (Taylor et al. 1989).

Sectioned and polished blocks were etched with 48% hydrofluoric acid for 1–5 min, and cellulose acetate peels (Galtier and Phillips 1999) were made from the prepared surface, with some peels subsequently mounted on microscope slides using Eukitt (O. Kindler, Freiburg). All specimens were photographed using a Leica (Allendale, NJ) DC500 digital camera attachment on a Leica MZ 16 stereomicroscope and a Leica DM 5000B compound microscope. Digital images were minimally processed using Photoshop CS4 (ver. 11.0; Adobe Systems, San Jose, CA). Cell and tissue measurements were taken with ImageJ software (<http://imagej.nih.gov/ij/>). An attempt was made to measure 100 cells of each cell type, but because of poor preservation, this was not always possible. Specimens, peels, and slides are deposited in the Paleobotany Division of the Natural History Museum and Biodiversity Institute at the University of Kansas (KUPB) as T 5647, T 5648, and T 5949 (surface compression specimens); 12603 A; 12614 A; 12930 A, C_{top}, D_{bot}, D_{top}, E; 13598 C_{bot} (α , β), D; 13600 A, B (silicified specimens); and slides 24,357–24,376 and 26,749.

Results

Family and Order—Gymnosperms incertae sedis

Genus—*Dordrechtites* Anderson 1978 Here Emended

Emended generic diagnosis. Isolated T-shaped ovulate reproductive structure consisting of a central pyramidal cupule with an elongated arm that extends out perpendicularly from the wide end (base) of the cupule. The arm is roughly as long as or slightly longer than the cupule and curves back toward the cupule. Two ovules per cupule, each with attenuated apex.

Type species. *Dordrechtites elongatus* Anderson 1978, from the Upper Triassic (Carnian) Molteno Formation, Karoo Basin, South Africa.

Species—*Dordrechtites arcanus* Bergene, E. Taylor et T. Taylor sp. nov.

Diagnosis. Isolated ovulate structure consisting of a triangular cupule 5–12 mm long and up to 6.5 mm wide at the base, containing two oblong, bilaterally symmetrical ovules that are attenuated at micropylar end and attached to an extended, terete arm. Each side of arm up to 15 mm long and 1 mm wide at point of attachment to cupule. Epidermis of cupule one cell thick. Vascular bundle extends through arm and branches into cupule; bundles extend about halfway down the cupule. Vascular bundle in center of arm collateral; nests of sclereids in cortex. Tissue of cupule parenchymatous; includes transfusion tissue of rectangular cells with pitted walls. Integument of endostea and bilayered sclerotesta; outer sclerotesta with longitudinally oriented cells, and inner layer of rectangular cells. Micropyle flared at attenuated tip.

Holotype. Slides and peels of specimen 12603 A (fig. 2C). All described and figured specimens are deposited in the Paleobotany Division of the Natural History Museum and Biodiversity Institute (KUPB), University of Kansas, Lawrence, Kansas, USA.

Paratypes. Slides and peels of specimens 12614 A, 12930 C_{top}, 13598 C_{bot}, and surface compression specimen T 5647, KUPB.

Type locality. Base of Mount Falla in the Queen Alexandra Range of the central Transantarctic Mountains, Antarctica (84°20'50.1"S, 164°39'40.6"E), Barrett's (1968) section F4, level 4.

Stratigraphic position. Uppermost Fremouw Formation, Beacon Supergroup, lower Middle Triassic (Anisian).

Etymology. *Arcanus* is Latin for mystery and is fitting for the description of the Antarctic *Dordrechtites* because of its obscure affinities.

Description and remarks on species. Although Anderson and Anderson (2003) illustrate *Dordrechtites* attached to an axis by the tip of one arm, the Antarctic specimens are dispersed and broken, and there is no way to distinguish which side represents the site of attachment and which extends beyond the cupule. Since the internal anatomy is the same on both sides, and since the arm can be distinguished anatomically over the top of the cupule (fig. 2C), we have chosen to use the neutral term "arm" for this structure rather than "peduncle" or another term with phylogenetic implications, for example, scale (see "Discussion").

The reproductive structure *Dordrechtites arcanus* from Antarctica consists of a central, pyramidal cupule attached at its base to the adaxial side of an elongate arm (fig. 2A, 2B).

cross section through the base of a cupule showing arm on left in cross section (*far left*) and right side in oblique section, with two ovules in center. 13598 C_{bot} 90. E, Oblique longitudinal section of cupule showing attenuated micropylar tip; arm is broken off on both sides. 12614 A 2. F, Oblique longitudinal section of cupule with possible aborted ovule on the right, smaller ovule on the left with possible micropyle (M). 12930 C_{top} 8. G, Longitudinal section of cupule showing two ovules embedded in tissue of cupule. Cross section of arm with central vascular bundle visible in top left. Box is enlarged in figure 3C. 13598 C_{bot} 20. Scale bars = 5 mm (A, B), 3 mm (C–E), 1 mm (F), 2 mm (G).

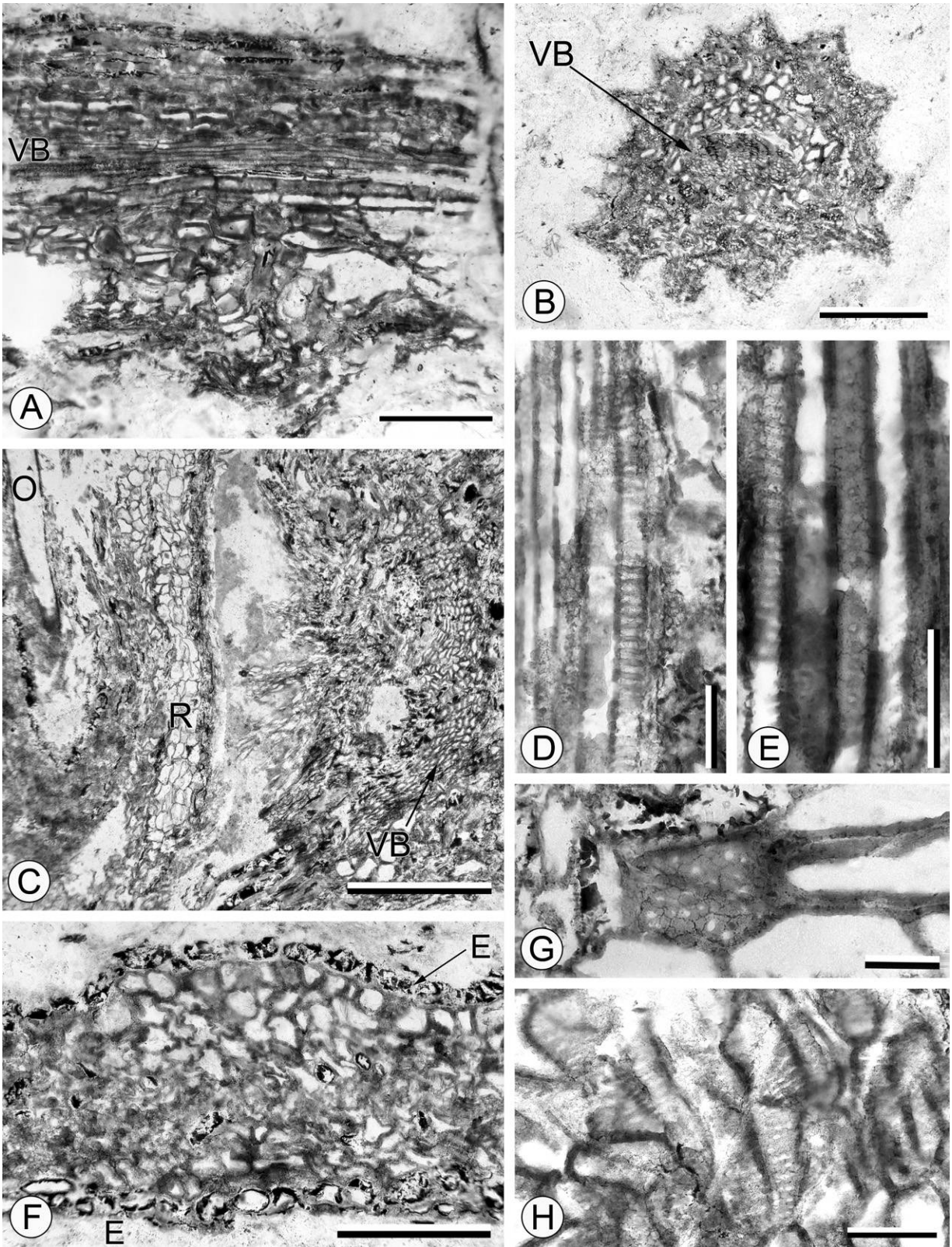


Fig. 3 *Dordrehtites arcanus* detail of arm, epidermis, and vasculature. *A*, Oblique section of arm showing sclerenchyma and vascular bundle (VB) running through the middle. 12603 A 3. *B*, Cross section of arm with central arc-shaped collateral vascular bundle (VB) with secondary xylem and space where phloem should be. Note scalloped exterior and nests of sclereids in the cortex. 13598 C_{bot} 37. *C*, Detail of figure 2G, showing organized files of cells (R) lateral to one of the ovules (O) and a vascular bundle in cross section (VB) on the right. 13598 C_{bot}

The arm extends up to 15 mm on each side of the cupule and is approximately 1 mm wide, variously curving at an angle of about 40° back toward the central cupule region. The cupule averages 9.5 mm long and is widest at the base (average 6 mm), becomes attenuated toward the apex, and exhibits longitudinal striations on the exterior. Each cupule contains two ovules (fig. 2C–2G).

No permineralized specimens exhibit a complete arm on both sides; the best example is the holotype (12603 A; fig. 2C), which shows one complete side but is broken off on the other side. The arm is comprised of sclerenchymatous cells that are either blocky or ovoid, thick-walled sclereids that average 36 μm in diameter (fig. 3A). The sclerenchymatous tissue of the arm extends over the top of the cupule (fig. 2C). The sclerenchyma cells sometimes appear resinous or very degraded. In cross section, the outline of the arm is scalloped, suggesting a series of small ridges on the surface, and nests of sclereids occur in the cortex (fig. 3B). An arc-shaped collateral vascular bundle with ~50 secondary xylem tracheids and a space where the phloem was not preserved occurs in the center (fig. 3B).

Vascular bundles with secondary xylem enter the cupule from the arm and then branch downward. Vascular tissue has been observed at the base and sides of the cupule surrounding the ovule, but the preservation is too fragmentary to fully trace the course of the vasculature (fig. 3C). Tracheids were observed within the integument at the base of the ovule in only one specimen. Scalariform secondary wall thickenings are the most common type found; they occur in the arm and within the cupule, but helical thickenings and circular bordered pits also occur in the arm (fig. 3D, 3E). Tracheids average 10 μm in diameter.

Epidermal tissue is present around the exterior of the cupule and the arm on almost all specimens. The cells measure 22.5 μm across, are noticeably smaller than adjacent parenchyma cells of the cupule, and are filled with black contents that appear resinous (fig. 3F).

The central cupule (or “trunk” of Anderson 1978) is 5–12 mm long (average, 9.5 mm) and 2.5–6.5 mm wide (average, 6 mm). The most common cell type in the cupule is parenchyma with slightly thickened walls. In tangential section, these cells exhibit simple pits that may be randomly arranged or somewhat aligned in rows (fig. 3G, 3H), and most are considered to be transfusion cells or tracheids. The cells are randomly arranged and range from 25 to 50 μm wide (average, 39.7 μm). They are usually oval, but some larger cells can be oblong to almost rectangular. The cell walls are thinner than the sclerenchyma cells in the arm and average 6.5 μm thick. This transfusion tissue is seen throughout the cupule and is the most recognizable and best-preserved tissue within the structure. In most specimens, this layer is 40–60 cells wide but narrows down the side of the ovule toward the tip of the cupule.

In multiple locations in the cupule, there are zones of rectangular cells arranged in organized files 3–10 cells deep; cells average 35.5 μm in diameter (figs. 3C, 4). In some specimens, they surround one of the ovules or extend between the ovules. In two specimens, the files occur at the base of the cupule adjacent to the sclerenchyma that extends into the arm.

The integument of each ovule consists of a two-parted sclerotesta and an endotesta; sarcotesta is not preserved. The outer layer of sclerotesta is 40–200 μm (average, 140 μm) and consists of narrow, elongate, longitudinally arranged fibers. The integument thins toward the micropylar end of the ovule. The size of individual cells in this outer layer cannot be determined because of poor preservation, but the layer is readily defined by its density (fig. 5A, 5B). The inner layer of the sclerotesta is one cell thick (fig. 5A [IS], 5C), consisting of narrow rectangular, alternating short and long cells (30–70 μm ; average, 47.9 μm). Most specimens are degraded, and this layer is not easy to distinguish clearly against the dense outer part of the sclerotesta. Individual cells of the endotesta are indistinguishable, but the endotesta and megaspore membrane are closely associated (fig. 5D). The megaspore membrane averages 8 μm thick and is present in all specimens. It extends from the base to the apex and into the micropylar canal.

The two ovules can be oriented side by side (the arm and ovules in one plane; fig. 2D) and are wider at the base but narrow approaching the apex. In most specimens, however, the ovules occur at different angles; when one is in longitudinal section, the other is at a very oblique angle, almost a cross section in some cases (fig. 2E, 2F). The ovules are orthotropous, and multiple specimens show an attenuated apex with finger-like projections that presumably funneled pollen into the micropyle. Bisaccate pollen, which would be assigned to the *sporae dispersae* genus *Alisporites*, occurs within the micropyle in one specimen (fig. 6A). This pollen has a single germination furrow and measures approximately 50 $\mu\text{m} \times 27 \mu\text{m}$ (fig. 6B, 6C). Micropylar cell differentiation was preserved only in one instance, but a micropylar canal was present in two specimens at the attenuated apex (fig. 2F).

A mass of parenchyma cells inside the ovule in two specimens may represent a possible megagametophyte (fig. 6D). The larger (more developed?) megagametophyte measures 415 $\mu\text{m} \times 175 \mu\text{m}$ and is composed of parenchyma cells that are slightly smaller than those in the cupule. It is not possible to clearly identify the mass as a gametophyte, and it could also represent degraded tissue.

In most of the specimens, the tissues within one of the two ovules are degraded, and the ovule area is filled with fungal hyphae. In some sections, there are hyphae disposed along the inside of the megaspore membrane in various planes of section (fig. 6E). This feature is consistent enough (occurring in five specimens) that it may be related to the possible regular abortion of the second ovule. There is a wide range of hyphal sizes (5–35 μm) in the degraded ovule

35. D, Tracheid with scalariform secondary thickenings, found within arm. 12603 A 9. E, Tracheid with circular bordered pits (rare), found within arm. 12603 A 6. F, Section through part of a cupule showing upper and lower epidermis (E) and underlying parenchyma; note dark, possibly resinous contents of epidermal cells. 13598 C_{bot} 52. G, H, Simple circular (G) and elongate (H) pits on transfusion tracheids in cupule. 13598 C_{bot} 71, 12930 E 3. Scale bars = 200 μm (A), 300 μm (B, C), 50 μm (D, G, H), 30 μm (E), 100 μm (F).

(fig. 6E). Another fungus with smaller-diameter hyphae (3.5–15 μm) occurs within the parenchyma cells of the cupule (fig. 6F). Since there are no observable host responses, we are uncertain whether these fungi represent parasites or saprobes.

Discussion

This is the first description of *Dordrechtites* from Antarctica and thus extends the geographical distribution of the genus and increases the known floral diversity in the Middle Triassic of Antarctica. Since the preservation is a combination of compression and permineralization, it is now possible to detail the internal anatomy of the cupule and ovules and relate these to the morphology of the previously described impression-compression specimens. As an *incertae sedis* genus, this ovulate structure still has no association with a parent plant. Other species descriptions from South Africa and Australia have shed little light on the possible affinities of *Dordrechtites*.

Taxonomic History of *Dordrechtites*

The initial diagnosis of *Dordrechtites* (Anderson 1978), from the Upper Triassic (Carnian) Molteno Formation of South Africa, described the unit as an isolated scale. Because it was assumed to represent a conifer, the terms used to describe the sporophyll were those used for conifers; that is, it was described as a scale (later as an ovuliferous scale; Anderson and Anderson 2003). Whether the structure was part of a microsporangiate or megasporangiate cone was not known, but it was compared with microsporophylls in the Cycadales and Coniferales as well as the bract/scale complex (megasporophyll of Anderson 1978, p. 62) of *Cedrus deodara*. The original diagnosis included T-shaped scales that were an average of 18 mm long and 1 mm wide, “arms of T gracile and curving downwards to varying degree . . . trunk of T robust and woody, tapering to point” (Anderson 1978). In the diagnosis, the central part (“trunk” of Anderson 1978) was approximately 11 mm long and as wide as 5 mm. Anderson and Anderson (2003) later described the isolated structures attached by one of the arms to a cone axis. The structures were grouped together into fascicles, with each fascicle attached to a short, stout pedicel. The presence of pedicels on the main axis showed that each *Dordrechtites* structure dehisced as a single, intact unit. Anderson and Anderson (2003) described the *Dordrechtites* unit as an ovuliferous scale and each fascicle of 3–4 scales as a megasporophyll.

The next account of *Dordrechtites* was that of Playford et al. (1982), in which Rigby described a new species from the Middle Triassic Moolayember Formation of the Bowen Basin in Australia as *Dordrechtites dikeressa*. This species was diagnosed as a compound ovulate fructification consisting of a central cone axis bearing helically arranged secondary axes. Each secondary axis bore pairs of what were termed cupules, each with two prominent horns (Playford et al. 1982). The cupules apparently covered only the top of the seed (i.e., not enclosing it), since they are listed as 2–3 mm high, while

the seed itself is 5–9 mm long. Each seed bore one prominent spine-like point and three smaller points. This species was smaller than the dimensions in the original generic diagnosis (Anderson 1978), so presumably the generic diagnosis should have been emended to incorporate the different sizes (or remove sizes altogether) and to include the attachment of the cupules to an axis, but this was not done. Rigby (Playford et al. 1982) noted that the word “cone” was used only for convenience. The structure that is pictured (Playford et al. 1982, pl. 6, fig. 6) has a massive central axis and irregularly spaced secondary axes (2–10 mm apart). Although the term “cone” was used, *D. dikeressa* was placed in the Corystospermaceae Thomas 1933, on the basis of Rigby’s observations that there were no bracteoles of any kind present. He compared the paired arrangement of cupules in *D. dikeressa* with *Umkomasia geminata* from the same flora (Playford et al. 1982).

In 2003, Anderson and Anderson added two new species, *Dordrechtites cetiparvus* and *Dordrechtites mazocirrus*, also from the Molteno Formation. These species differed from *Dordrechtites elongatus* in their smaller size (*D. cetiparvus*) and reflexed central region (*D. mazocirrus*) as well as differences in the lengths of the arm compared with the central region. This publication listed a generic diagnosis, rather than an emended diagnosis, of “a pinopsid female cone bearing fascicles of gracile, T-shaped, ovulate scales that detach readily from short stout pedicels” (Anderson and Anderson 2003, p. 60). The genus was placed within a new family, Dordrechtitaceae Anderson and Anderson 2003, and order, Dordrechtitales Anderson and Anderson 2003, within the Pinopsida Meyen 1984. Similarly, a specific diagnosis (not emended) was listed for the type species, *D. elongatus*: “A *Dordrechtites* species bearing relatively large scales with long, gracile, roughly equal arms and gently arching fertile trunk” (Anderson and Anderson 2003, p. 64). On the basis of impression specimens, the type species is described as a simple strobilus with clusters of “scales” attached suboppositely and subdecussately to a main axis, although this attachment was not included in the diagnosis. The ovuliferous “scale” (or the entire specimen of *Dordrechtites arcanus* from Antarctica) is T-shaped with sterile arms and a winged ovuliferous “trunk” (central part) bearing an ovule/seed (Anderson and Anderson 2003). The interpretation of this “winged trunk” as a single, winged ovule is not well supported, however, since no dispersed seeds were found either in the Molteno (Anderson and Anderson 2003) or in the material from Australia (Playford et al. 1982).

The anatomical information from *D. arcanus* shows that the orientation of the central cupule (winged trunk of Anderson and Anderson 2003) compared with the arms is incorrect as originally reconstructed (Anderson and Anderson 2003, p. 60, fig. 4). In the permineralized *D. arcanus*, the arm is in the same plane as the two ovules, in contrast to the original description, which put the broader plane of the cupule at right angles to the arms. The permineralized specimens from Antarctica also demonstrate that two ovules (rather than one) sit within the cupule. What were previously thought to represent wings are probably creases or striations on the exterior of the cupule.

Because of these previous nomenclatural irregularities and the presence of new information from our anatomical study,

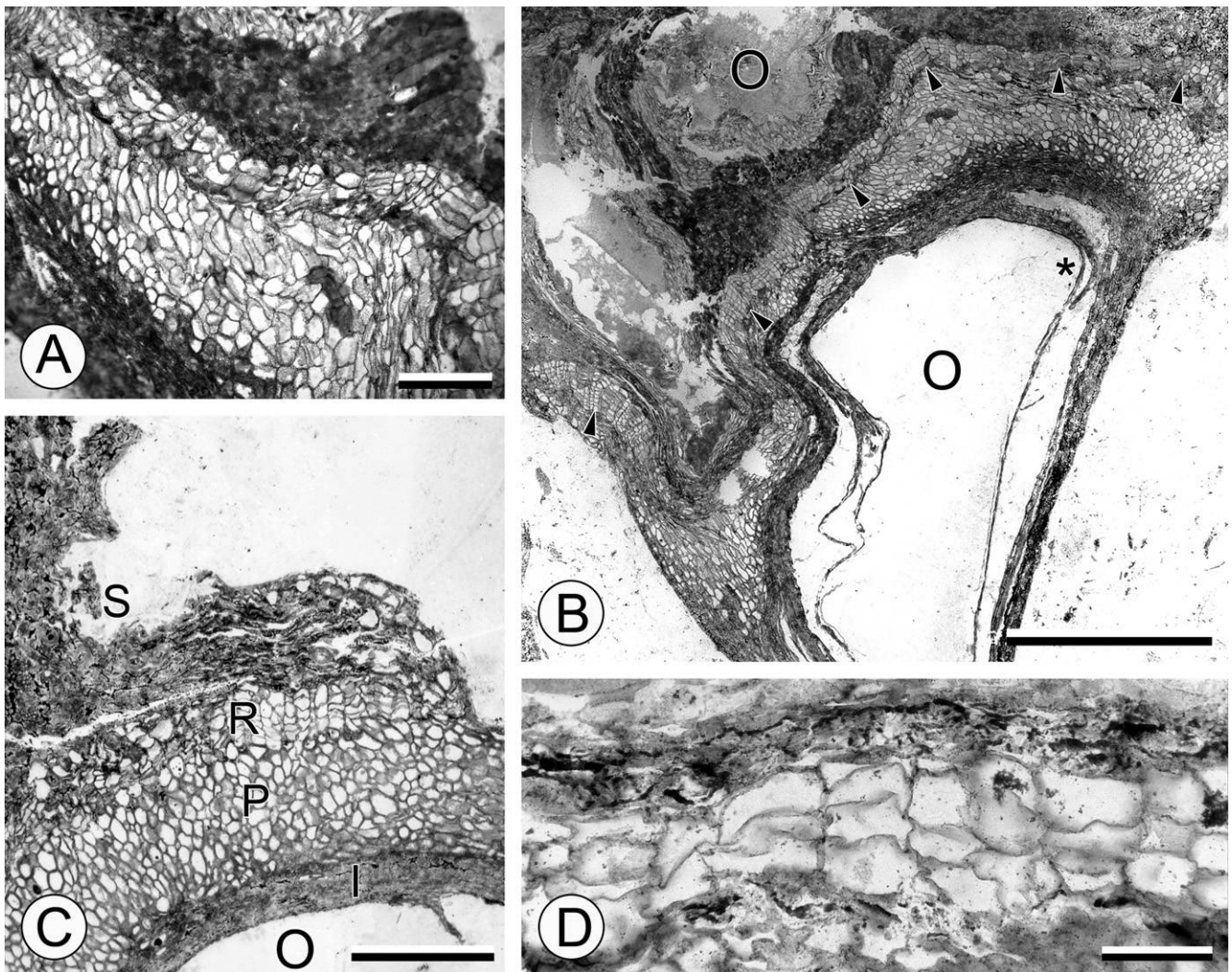


Fig. 4 *Dordrechtites arcanus* cupule tissue. A, Files of cells (center) forming a distinct line against more randomly oriented transfusion parenchyma (detail of B). 12614 A 2. B, Section through the bases of two ovules showing files between the two ovules (arrowheads); endotesta is preserved inside right-hand ovule. 12614 A 2. C, Section through base of cupule (ovule below) showing various tissues: sclerenchyma (S), which also extends into the arm, files of cells (R) below the sclerenchyma, transfusion parenchyma of the cupule (P), sclerotesta of the integument (I), and the endotesta addressed to the sclerotesta (asterisk). 12930 E 30. D, Detail of cells in files showing thin-walled, probable meristematic (cambial) cells. 13598 C_{bot} 35. Scale bars = 50 μm (A, D), 200 μm (B), 400 μm (C).

it was important to emend the genus to clarify characteristics of the taxon on the basis of information from South Africa, Australia, and now Antarctica. Our emended generic diagnosis lists the taxon as an isolated ovulate structure, since this was the original diagnosis, and will allow for the broadest inclusion of fossil specimens.

New Anatomical Data from Dordrechtites arcanus

Dordrechtites arcanus is similar in size and morphology to the type species, *D. elongatus*, but a new species was created to reflect the additional information available from anatomical detail. Information on the ovules of *Dordrechtites* was not known from any previously described species, including the number or orientation of ovules. This new species of *Dor-*

drechites is preserved as compressions and permineralizations; no other specimens show a combination of preservation types.

Transverse sections of the arm of *D. arcanus* reveal that the exterior appearance is scalloped (fig. 3B), a unique morphological feature that has not been seen in the compression-impression specimens. The arm would have to be preserved in a cross-sectional orientation in a compression, however, in order to show this feature. It has been difficult to reconstruct the vasculature of *D. arcanus* because of the differential preservation in the Mount Falla specimens. A vascular bundle extends through the middle of each arm and gives off branches into the cupule at the base, but the preservation is too fragmentary to fully trace the course of the vasculature.

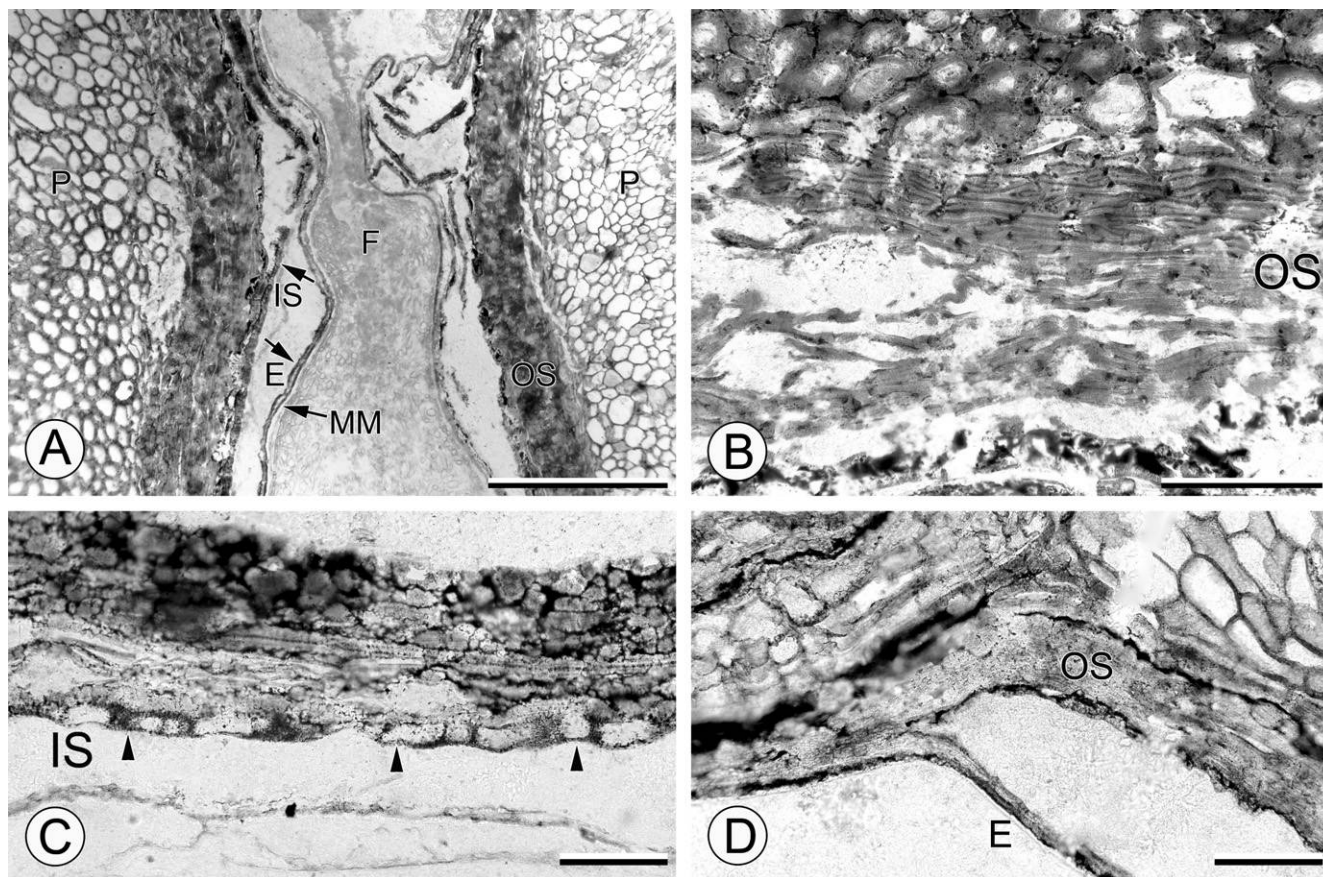


Fig. 5 *Dordrechtites arcanus* cupule and ovule anatomy. *A*, Section through ovule (*center*) and cupule transfusion parenchyma (*P*; *left and right*). Note dense outer layer of sclerotesta (*OS*), degraded inner layer of sclerotesta (*IS*), endotesta (*E*), megaspore membrane (*MM*), and fungus (*F*) confined within megaspore membrane. 12930 A 43. *B*, Longitudinal section through outer layer of sclerotesta (*OS*), showing longitudinally arranged fibers. 13598 C_{bot} 35. *C*, Section showing inner layer of sclerotesta (*IS*), one cell thick. 12614 A 25. *D*, Section through base of ovule showing separation of sclerotesta (*OS*) and endotesta (*E*). Note files of cells (*left, above*) and transfusion parenchyma to the right. 12930 E 3. Scale bars = 100 μm (*A*, *C*, *D*), 50 μm (*B*).

In the parenchyma, transfusion tissue is identified throughout by the simple pits on the cell walls (fig. 3G, 3H). Common in gymnosperms, transfusion tissue usually surrounds the vascular bundle and is composed of tracheids and living parenchyma cells. Described in detail by Worsdell (1897), transfusion tracheids and transfusion tissue are found in the leaves of many extant conifers, cycads, gnetophytes, and some angiosperms and considered an auxiliary conducting system perpendicular to the midvein. Transfusion tissue cells are also frequently arranged in longitudinal rows (Griffith 1957). Historically, transfusion tracheids are almost always seen surrounding the vascular bundle. Although transfusion tracheids are mostly observed with bordered pits and thin secondary walls, *Casuarina* stems contain transfusion tissue with simple pits and lignified walls that are formed directly from parenchyma cells and are independent from the xylem, similar to *D. arcanus* (Worsdell 1897; Griffith 1957; Dickison 2000). It was first hypothesized that the pits on the transfusion tracheids in *Dordrechtites* were primary pit fields in parenchyma cells, but the simple pits are too large for this explanation. The amount of this tissue is unusual because, instead of being local-

ized around the vascular bundle, the transfusion tissue occurs throughout the cupule, with many pitted cells visible in each single section (~200 cells). Parenchyma cells, in which the transfusion tissue is located, are arranged randomly (see parenchyma description above) and not in longitudinal rows, as Griffith (1957) described. Transfusion cells occur near a vascular bundle at the base of the cupule and more toward the apex, but they also appear elsewhere, even if some distance from the known vascular trace. Transfusion tissue has been described in other Mesozoic plants, but it is normally seen in only one area, such as a vascular cup or disc near the base of the ovule (e.g., *Petriellaea triangulata*; Taylor et al. 1994) or centrally located near the vascular bundle, as in *Doylea tetrahedrasperma* (Stockey and Rothwell 2009).

The function for the large amount of transfusion tissue in the cupule is not known; however, cells of this type are generally present in areas where a large amount of solutes are being translocated. Perhaps because of the limited growing time at these high latitudes, translocation to the developing seeds proceeded very rapidly, and this additional tissue augmented the vasculature in the cupule.

One of the most puzzling aspects of the anatomy of *D. arcanus* cupules is the presence and distribution of files of cells in the ground tissue of every permineralized specimen. The files are evident between the two ovules and surrounding just one ovule (fig. 4). There are generally 2–8 files of cells in each occurrence, and they can be followed for some distance within the cupule. The files appear to be in a T orientation in the cupule, running vertically between the ovules and then extending out toward the sides of the cupule near the base where the arm connects. These files were originally thought to represent an abscission zone for the ovules; however, they also separate the two ovules. Another hypothesis for the cells is that they represent some sort of wound response, for example, a method to wall off healthy from diseased tissue. There are fungal hyphae present in some of the specimens, even replacing the ovule in one case (fig. 6E). In this specimen, the space occupied by the fungi was originally thought to represent an air pocket (Bergene et al. 2011), but subsequent discovery of degraded sclerotesta proves that it is a heavily degraded ovule. The problem with a postulated wound response, however, is that the files of cells occur in all but two specimens, even those that show no evidence of fungal hyphae. At the present time, we do not have a good explanation for the distribution of these zones of what appears to be cambial activity.

In almost all specimens, one of the ovules is seen in longitudinal section whereas the other is at an oblique angle, almost a cross section in cases (fig. 7B). It is not clear why this distinctive orientation occurs in all but one specimen. It does not appear to be a result of preservation because the cell layers are intact and do not show major tearing or shredding. One hypothesis is that one of the ovules was reoriented as it was growing, but there are no morphological data that yet support this idea. Morphologically, there is also no obvious protrusion from the cupule wall, and the cupule is relatively oval and not oddly shaped, so the arrangement of ovules is contained within the overall pyramidal shape of the cupule.

The ovules exhibit long, finger-like projections made of parenchyma at either side of the micropyle. Projections such as these have not been described from other species of *Dordrechtites*, but we suggest that they may have functioned in pollen capture. There are only a few specimens that display a micropylar canal within the protruding tips of the cupule apex. A few, very degraded pollen grains of the *Alisporites* type were found within the micropyle, but better-preserved grains were found in the surrounding matrix and within the outer tissues of a degraded cupule. This type of pollen has been considered to be indicative of conifers and corystosperms (Balme 1995; Traverse 2007; Jansson et al. 2008) and is also ubiquitous within the Fremouw Formation permineralized peat matrix (Osborn and Taylor 1993; Taylor et al. 1994; Yao et al. 1995). Similar grains have been found within *Pteruchus*, the pollen organ of the Corystospermales (Yao et al. 1995), and in the conifers, it has been found in the pollen chamber of *Compsostrobus* (Delevoryas and Hope 1973) and in pollen cones of *Willsiostrobus* and *Lelestrobus* (Grauvogel-Stamm 1978; Srivastava 1984). *Alisporites* occurs in many formations around the world and is considered a notable Triassic pollen type, with particular abundance in the Gondwanan Triassic (Helby et al. 1987; Traverse 2007). This pollen may be related to *Dordrechtites* just by bedding plane

association within the matrix. No high concentration of pollen has been found at the micropylar end of the cupules, but since they were apparently transported, on the basis of the finely ground plant debris in the matrix, it is not surprising that only a few grains have been found.

Dordrechtites Distribution

To date, *Dordrechtites* has been found in the Middle and Late Triassic. The Moolayember Formation of Australia is dated as Anisian-Ladinian because of palynomorph association, such as *Falcisporites* and *Aratrisporites parvispinosus* (Playford et al. 1982; Helby et al. 1987), and the Molteno Formation of South Africa is Carnian (Anderson and Anderson 2003). Farabee et al. (1990) suggested that the permineralized peat from Fremouw Peak, Antarctica, was Anisian (early Middle Triassic) on the basis of palynomorphs in the peat. The fossils described herein occur at approximately the same level in the Fremouw Formation as the peat, and this represents the earliest occurrence of the genus. *Dordrechtites* has also been noted—but not described—from the Upper Triassic Los Rastros Formation of the Ischigualasto region of Argentina (Carnian; H. M. Anderson, personal observation, in Anderson and Anderson 2003); the Dubbo district, New South Wales, Australia (Anisian; K. Holmes, personal observation, in Anderson and Anderson 2003); and the Cañadón Largo Formation, El Tranquilo Group of Argentina (Ladinian-Carnian; Artabe et al. 2007; Novas 2009, p. 33; Gnaedinger 2010).

Comparison of *Dordrechtites arcanus* with Other Species

Dordrechtites arcanus is most similar to the type species, *D. elongatus*, on the basis of both morphology and overall size. The Antarctic compressions could be considered *D. elongatus*; however, anatomical detail found in the specimens and the unique dual preservation does not link these species together.

Dordrechtites arcanus differs from *D. cetiparvus* in the orientation of the cupule to the arm. The sides of the arm in *D. cetiparvus* are very unequal in length; the distal part of the arm is only 5 mm long and appears stunted (Anderson and Anderson 2003). The cupule is strongly reflexed and angular and is curved proximally; that is, the cupule apex is pointed back toward the point of attachment and not downward. *Dordrechtites mazocirrus* (Anderson and Anderson 2003) is very similar to *D. cetiparvus* but is slightly larger, and the cupule is more spherical and fuller. The arm is also unequal in *D. mazocirrus*, but each side measures about 10 mm long (Anderson and Anderson 2003). The arm in *D. arcanus* is longer and straighter than those in *D. cetiparvus* and *D. mazocirrus*, and the cupules of *D. arcanus* are not reflexed as in these two South African species (Anderson and Anderson 2003).

Dordrechtites dikeressa from Australia is the species that is most unlike *D. arcanus*. According to Rigby (Playford et al. 1982), a 5–6-mm petiole is attached to an arched cupule 6–8 mm long, with the seed attached below; two slender “horns” extend up to 15 mm beyond the distal margin of the cupule (Playford et al. 1982). The measurement across the top of the structure is similar to *D. arcanus* (~30 mm), but there is no dichotomy of the distal arm in *D. arcanus*. In addition, the cupule of *D. arcanus* completely surrounds the ovules, whereas the cupule is described as encircling only the base

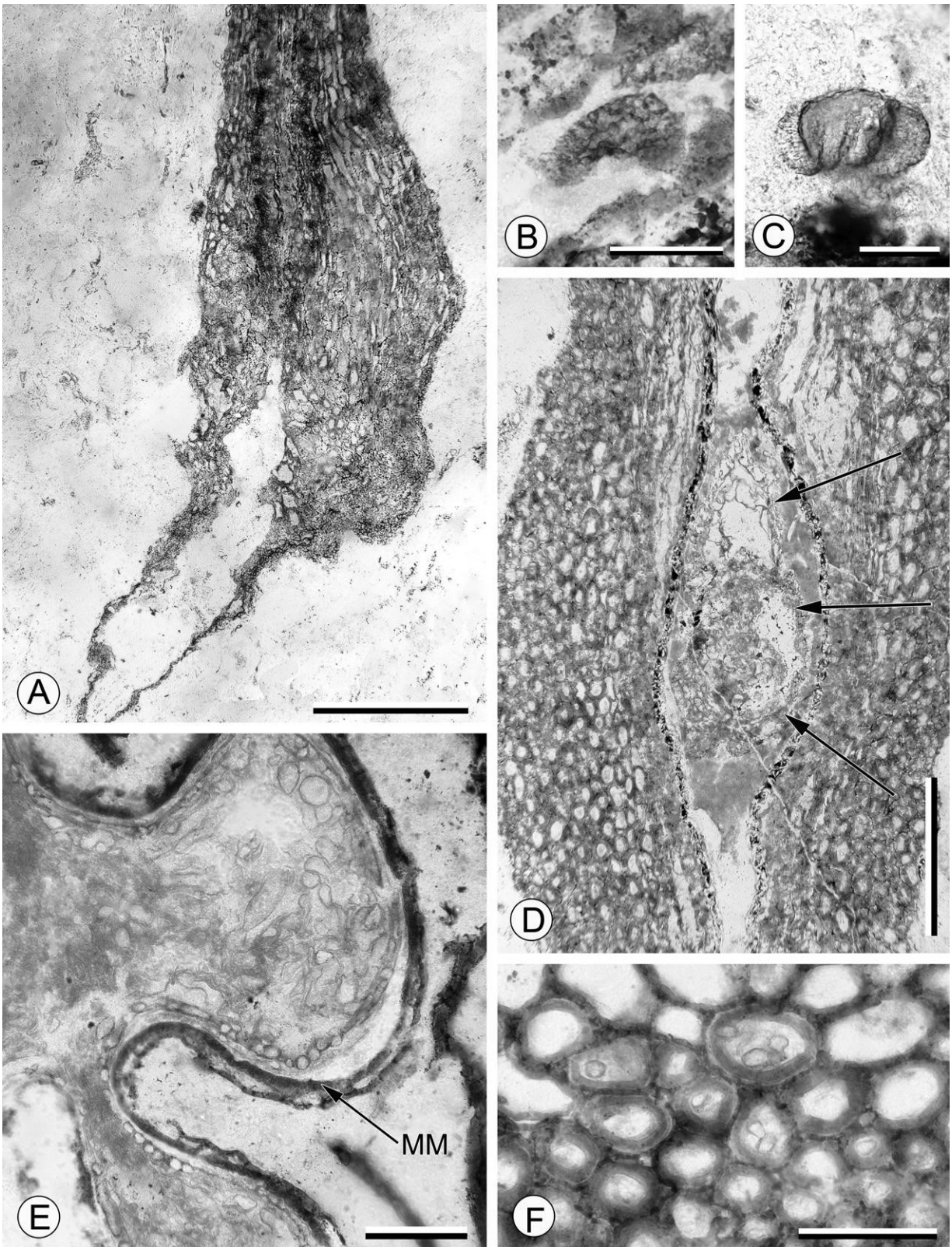


Fig. 6 *Dordrechtites arcanus* ovule anatomy and fungus. *A*, Flared micropylar tip at apex of ovule. 12930 D_{top} 58. *B*, Pollen grain similar to *Alisporites* pollen found within the micropyle; only part of the saccus of the grain is visible. 12930 D_{top} 55. *C*, Oblique view of well-preserved *Alisporites* pollen found near specimen in matrix. 12603 A 75. *D*, Possible megagametophyte (arrows) enclosed within endotesta. 13598 C_{bot}

of the single seed in *D. dikeressa*. *Dordrechtites dikeressa* also exhibits noticeable spikes or points on the exterior of the cupule that are not evident in *D. arcanus*. Bumps and striations are preserved on the Antarctic compressions, but these are most likely preservational artifacts from compression of the presumably fleshy cupule. There are bumps near the connection of the arm and cupule on all three compression specimens; these are considered to be related to the transition from arm to cupule or spikes, as in *D. dikeressa*.

Dordrechtites from Antarctica occurs only as dispersed cupules, but previous descriptions have observed the cupulate structures attached to an axis. These descriptions have differed, however, in the attachment of the cupules. The species from South Africa (*D. elongatus*, *D. cetiparvus*, *D. mazocirrus*; Anderson and Anderson 2003) were described as lax cones bearing fascicles of three to four gracile scales. Anderson and Anderson (2003) illustrated attachment to the central axis via one of the curving arms of the cupule, with the other arm curving around the cupule. *Dordrechtites dikeressa* from Australia displays attachment in a different orientation, with each unit attached to a secondary axis as part of a cluster of three or four cupules, with the secondary axis then attached to the main (primary) axis (Playford et al. 1982). According to this reconstruction, the axes from one or two pairs of cupules fuse together into a branch that acts as a fascicle, and this in turn is connected to the main axis. Rigby suggested a morphology that may have “corystosperm affinities in its lack of scales and bracts, [the presence of] cupulate seeds and open branching habit” (Rigby in Playford et al. 1982, p. 9).

According to previous descriptions (Playford et al. 1982; Anderson and Anderson 2003), the connection to a main axis for the isolated structure is via one side of the arm. This is borne out by the anatomical detail from *D. arcanus*, which has arc-shaped vascular tissue in both sides of the arm. It is not possible to determine, however, which side of the arm represented the site of attachment, since no specimen retains a complete arm. In all cases, the arm is broken off and does not taper to a point as in previously described impression specimens. Although the gracile nature of *D. arcanus* and the other species in the genus might suggest adaptation for wind dispersal, it must have been a very robust and woody structure in order to survive transport to the Mount Falla site of deposition.

Fungal activity. Fungal activity is present in virtually all specimens of *Dordrechtites arcanus* (fig. 6E, 6F). The most noticeable evidence occurs within the space occupied by one of the two ovules in the cupule, where many specimens show a fungal infection. In two specimens, the integument is almost completely degraded (fig. 2C, 2F), and no megaspore membrane or endotesta is preserved. Fungal hyphae are present in other ovules as well as in cupule parenchyma. The hyphae appear to fill in the space within the megaspore membrane in one specimen (fig. 6E), presumably replacing the ovule. This occurrence may represent an aborted ovule that has been infected. The large size of the area (two to three times the adjacent ovule) is unusual and suggests that if the ovule did abort, it was late in development. The fungus that occurs within the cells of

the thick-walled cupular parenchyma cells (fig. 6F) consists of individual hyphae. It is unknown whether this was a mutualistic or saprobic relationship because the tissues and cells seem well developed, but it is more likely to have been a saprobic infection after *Dordrechtites* fell into the depositional environment.

Affinities of *Dordrechtites*. In addition to *Dordrechtites*, there are other seed plant reproductive structures that occur in the Triassic of Gondwana. Other plant groups such as Corystospermales, Coniferales, Cycadales, Peltaspermales, and Petriellales all produced ovulate structures, although only some have been positively identified (Seward 1908; Thomas 1933; Holmes 1982; Yao et al. 1993, 1995; Taylor et al. 1994; Klavins et al. 2002, 2003; Bomfleur et al. 2011b) or included in whole-plant reconstructions. It remains impossible at this time to associate *D. arcanus* with any particular foliage type because *Dordrechtites* is not directly associated with any other plants in the matrix. Within the silicified material from the base of Mount Falla, other seed-plant foliage has been identified, including *Dicroidium* (most common), *Notophytum* leaves (Axsmith et al. 1998), *Sphenobaiera*, and only a couple of examples of *Heidiphyllum*.

Anderson and Anderson (2003) concluded that the isolated form of *Dordrechtites* represented a single scale of a conifer cone. As noted above, we chose to not use the terms “scale” or “bract/scale” for *Dordrechtites*, since this term implies a phylogenetic relationship within the conifers. At the present time, there is not enough evidence to assign *Dordrechtites* to any higher group.

The other hypothesis, as put forward by Rigby (Playford et al. 1982), is that *Dordrechtites* is a corystosperm seed fern. If correct, then *Dordrechtites* represents the second ovulate morphotype of the corystosperms known from Antarctica. The corystosperm ovulate structure, *Umkomasia*, is conservative in its morphology throughout Gondwana and has been studied both in impression-compressions (Thomas 1933; Holmes and Anderson 2005) and permineralizations (Klavins et al. 2002). Gondwanan *Umkomasia* is also very similar in morphology to Laurasian occurrences (Kirchner and Müller 1992; Zan et al. 2008). On the basis of anatomical detail, *Umkomasia resinosa* from the Fremouw Formation (Klavins et al. 2002) included fleshy cupules (~8 mm × 3 mm), which almost completely enclosed one or two ovules; a bifid integumentary tip extended beyond the cupule, which is similar to compression-impression specimens. The *Dordrechtites* cupule is similar in size, but *Umkomasia* cupules are reflexed around the ovule and attached singly to an axis (i.e., not part of a cone; Axsmith et al. 2000). The permineralized corystosperm from Fremouw Peak, Antarctica, has been reconstructed on the basis of the presence of particular secretory cells in the foliage (*Dicroidium*), stems (*Kykloxylon*), pollen organs (*Pteruchus*), and ovulate cupules (*Umkomasia*; Taylor 1996). A whole-plant reconstruction was also made for the *Dicroidium* plant from the Ischigualasto Formation of Argentina (Petriella 1978, 1981), including stems of *Rhexoxylon* with *Dicroidium*, *Pteruchus*, and *Umkomasia*. The Corystospermales have been well resolved in compressions and permineralizations, and their ovulate organs are easily recognized throughout Gondwana. No secretory cells occur in *D. arcanus*, but it

66. E, Fungus within megaspore membrane (MM); note hyphae in multiple orientations. 12930 A 25. F, Fungus within transfusion parenchyma cells. 13598 C_{bot} 33. Scale bars = 500 μm (A), 30 μm (B, C), 300 μm (D), 50 μm (E, F).

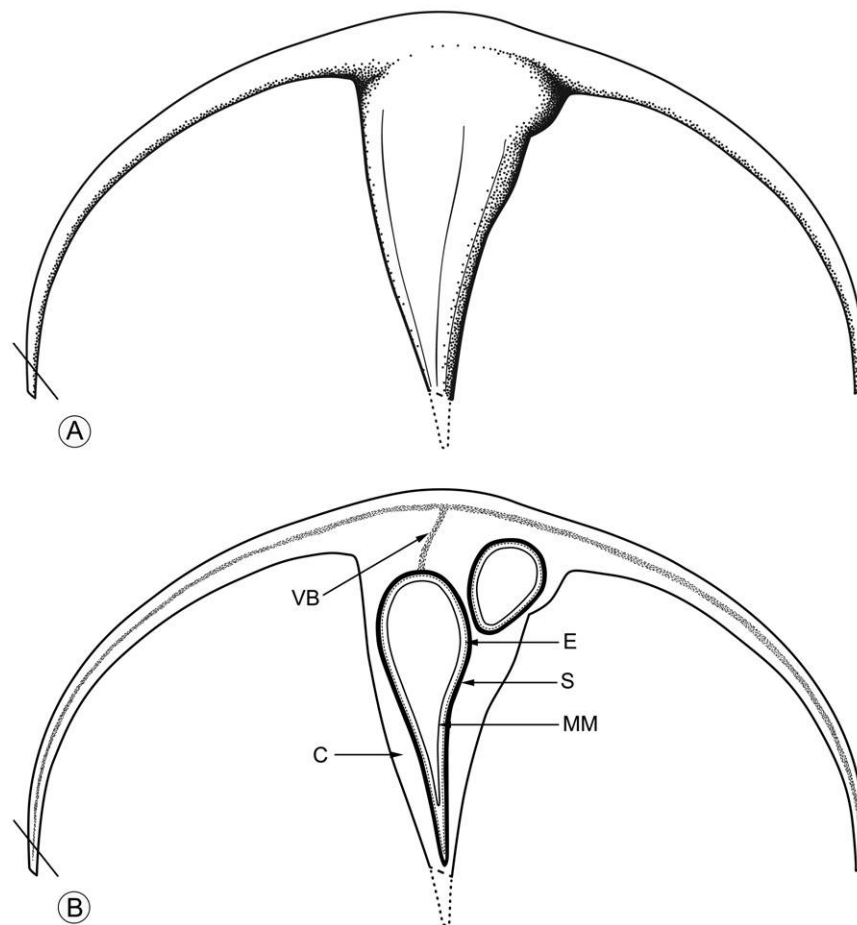


Fig. 7 Suggested reconstructions of *Dordrechtites arcanus*. A, Exterior view of isolated specimen. B, Cutaway to show orientation of ovules and vasculature in arm and cupule. Longitudinal section of ovule showing vascular bundle (VB), cupule (C), endotesta (E), sclerotesta (S), and megaspore membrane (MM). Presumed attachment of structure to plant axis is shown by a slanted line.

may still represent an ovulate structure of the corystosperms that is different from *Umkomasia*. The lack of associated or attached foliage makes it difficult to resolve this question.

In the Molteno Formation of South Africa, the strap-shaped compressed leaf genus *Heidiphyllum* appears on the same bedding planes as *Dordrechtites*. In Australia, *Heidiphyllum* occurs within the Moolayember Formation (White 1965) but not at the same locality as *D. dikeressa* (Playford et al. 1982). Anderson and Anderson (2003) considered *Dordrechtites* to be a voltzialean conifer because of the co-occurrence of *Telemachus* cones, *Heidiphyllum* leaves, and *Dordrechtites* at multiple sites. *Telemachus* is an ovulate cone with a woody axis that bears lobed ovuliferous scales with sterile and fertile bracts (Anderson 1978; Escapa et al. 2010), which is completely unlike *Dordrechtites*. Although both taxa occur with *Heidiphyllum* leaves in South Africa, in Antarctica, *Heidiphyllum elongatum* occurs consistently only with *T. antarcticus* Escapa et al. (2010) seed cones. Axsmith et al. (1998) demonstrated that the conifer stems *Notophytum* bore permineralized leaves with the same morphology as compressed *Heidiphyllum*. Escapa et al. (2010) suggested that there was a single conifer taxon present in the Triassic of Antarctica, consisting of *Heidiphyllum* foliage, *Notophytum* stems, *Telemachus/Parasciadopitys*

seed cones, and *Leastrobus* Hermsen et al. (2007) pollen cones. Later, Bomfleur et al. (2011b) also attributed compressed pollen cones of *Switzianthus* sp. to the same plant, on the basis of cuticular similarities. Thus, on the basis of our current knowledge of the flora from the Fremouw Formation, it seems unlikely that *Dordrechtites* can be correlated with the conifers in this region. Although *Dordrechtites* has superficial similarities to the Mesozoic conifer cone *Palissyia* (Parris et al. 1995), this genus has been described as a typical compound conifer cone (Wang et al. 2012), and the anatomical information from *Dordrechtites* does not support a comparison.

The peltaspermalean seed ferns were also present in Antarctica during the Triassic. The Peltaspermales occur over a wide range of localities in Gondwana and extend from the Carboniferous to the Triassic worldwide (Taylor et al. 2006, 2009). *Peltaspermum rotula* Harris (1937), the type species from the Triassic of Greenland, has multiple ovules arranged in a ring on the abaxial surface of a disk-like megasporophyll, which is attached to the main axis by a peltate stalk. Megasporophylls are helically arranged into a simple strobilus that may be up to 175 mm long (Anderson and Anderson 2003). The ovules are flattened and, similar to *D. arcanus*, exhibit a long, bilobed micropylar tube and a nucellus that is free from the integument

except at the base (Crane 1985). Although relatively common in the Northern and Southern Hemispheres, there are few peltasperms currently known from Antarctica. Bomfleur et al. (2011b) described a new peltasperm from the Upper Triassic Falla Formation on the basis of ovulate structures of *Matatiella*, leaves of *Dejerseya*, and a branching pollen-bearing structure assigned to *Townrovia*. McLoughlin et al. (1997) described pinnules of *Lepidopteris*, a typical peltaspermalean foliage type, from just above the Permian-Triassic boundary in the Prince Charles Mountains of East Antarctica. Although there are some similarities between the ovules of *Peltaspermum* and *Dordrechtites*, the morphology of the sporophyll is different; therefore, *D. arcanus* is not considered to be related to this group.

Cycads were also present during this time period, and a permineralized example has been described from the Fremouw Formation, that is, *Antarcticycas schopfii* (Smoot et al. 1985; Hermsen et al. 2009). This species is very small compared with the *Dordrechtites* reproductive structure (stems only 5.5 cm in maximum diameter). Although the vegetative parts of *Antarcticycas* are relatively well known, no megasporangiate cone has been found to date.

The Caytoniales were relatively widespread during the Mesozoic (Thomas 1925; Turner et al. 2009) but have yet to be identified from the Triassic of Antarctica, although they have been observed elsewhere in Antarctica in younger (Jurassic) rocks (Rees 1993). Previous reports from the Triassic (Banerji and Lemoigne 1987; Barale et al. 1995) are from a flora that has been redated as Cretaceous (Rees and Smellie 1989). *Dordrechtites* and *Caytonia* differ in the number of ovules within the cupule, the morphology of the cupule, and its orientation to the axis.

Few ginkgophytes are known from the central Transantarctic Mountains, and these are all of Late Triassic age (Escapa et al. 2011). Remains consist mostly of foliage types (*Sphenobaiera*, *Baiera*, *Ginkgophyllum*, and *Ginkgo*) and a single specimen of the ovuliferous structure *Hamshawvia*, also known from the Molteno Formation of South Africa (Escapa et al. 2011). Although *Hamshawvia* bears some resemblance to *Caytonia* or *Umkomasia*, it is not similar to *Dordrechtites*, on the basis of morphology and number of ovules per sporophyll.

Since *D. arcanus* occurs in the upper part of the Fremouw Formation, it can be compared with anatomically preserved seed plants described from the permineralized peat from nearby Fremouw Peak. There are several taxa of isolated reproductive structures from the peat that have not yet been assigned to particular plant groups. *Petriellaea triangulata* cupules are leaflike and bear five ovules each (Taylor et al. 1994), which is unlike *Dordrechtites* (Taylor et al. 1994). *Probolosperma antarcticum* is an isolated ovule in which the sclerotesta extends out to form two lateral wings and elaborations at the micropylar and chalazal ends (Decombeix et al. 2010). Some oblique tangential sections of *Dordrechtites* look very similar to *Probolosperma*, but the sclerotestal elaboration is not present in *Dordrechtites*. *Ignotospermum* is a radially symmetrical dispersed ovule (Perovich and Taylor 1989) that is markedly different from *Dordrechtites*.

Initial observations of *Dordrechtites* have assumed seeds enclosed in a cupule; however, another possible affinity is that

of a lycopsid. The described specimens could represent a megasporangium with two megaspores enclosed. There are not many positive reasons for identifying this structure as a lycopod, such as an adaxial sporangium or the presence of a ligule. There is negative evidence, however, such as the absence of an observed pollen chamber within *Dordrechtites*. In addition, the presence of secondary growth and the woody nature of *Dordrechtites* is uncharacteristic of the Lycopphyta. Although scalariform secondary thickenings are seen in both *Dordrechtites* and members of the Lycopphyta, well-defined circular-bordered pits are observed in this new species, a trait that does not occur in lycopsids.

Since the ovules of *D. arcanus* are enclosed within a cupule, it is probable that the affinities are within the seed ferns, but there is no suite of characters that precisely defines the group. Without more knowledge of attachment, we have placed the genus into *incertae sedis* gymnosperms, because there are no associations that would justify placing it within the Corystospermaceae. At this point, we contend that it should not be allied with the conifers, since the morphology of the cupule is unlike anything in that group.

Conclusions

A new species of *Dordrechtites* (*Dordrechtites arcanus*) is described from combined compressions and permineralizations, providing the first report of anatomical information from this enigmatic Triassic ovulate structure and the first account from Antarctica. This is also one of the earliest described occurrences of the genus with an Anisian age. *Dordrechtites arcanus* consists of isolated cupules, each enclosing two bilaterally symmetrical seeds; tissue inside the cupule is dominated by transfusion tracheids. The orthotropous seeds have a bilayered integument, and *Alisporites*-type pollen was found within the micropyle in one specimen. The nucellus is fused to the integument only at the base; no well-defined pollen chamber has yet been observed. Although the preservation is generally somewhat poor, tracheids most commonly have scalariform thickenings, with helical and circular bordered pits also present. Previously, *Dordrechtites* was suggested to represent a conifer cone scale or was allied with the corystosperm seed ferns, but the presence of a cupule and an elongate micropyle suggests affinities with the seed ferns.

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