

*Dordrechtites arcanus*, an anatomically preserved gymnospermous reproductive structure from  
the Middle Triassic of Antarctica

By

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Submitted to the graduate degree program in Ecology and Evolutionary Biology and the  
Graduate Faculty of the University of Kansas in partial fulfillment of the requirements for the  
degree of Master of Arts.

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Date Defended: April 6, 2012

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Date approved: April 17, 2012

## Abstract

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 Mt. 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 is described, *D. arcanus*, which includes internal anatomy of the two elongate arms and 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  $\mu\text{m}$  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 further the new species described herein is considered *incertae sedis* within the gymnosperms.

## Acknowledgments

I am genuinely grateful to all of those with whom I have collaborated at the University of Kansas. I am especially appreciative of Dr. Edith L. Taylor for supporting me throughout my time at the University of Kansas. From starting my research career as an undergraduate lab assistant and pursuing my secondary education teaching ambitions, to supporting my graduate work in a terminal Masters degree, Edie has encouraged me to be an outstanding woman scientist. Dr. Thomas N. Taylor has also yielded much good advice for the future and has given me the confidence to know I will be successful in whatever I choose to do.

I would also like to thank Dr. Anne-Laure Decombeix and Dr. Sharon Klavins for beginning the work on this project and their preliminary identification of *Dordrechtites* within the Antarctic fossil collection. Dr. Stephen T. Hasiotis was helpful in discussing the depositional environment of the Antarctic material. I am appreciative of Gilbert Ortiz for his collaboration on the reconstruction of this paleobotanical structure. Dr. Rudolph Serbet was also very supportive of this research with his help in the preparation of the specimens and constructive discussions.

I would also like to recognize my family and friends for keeping me grounded and on task to finish this project even though they have no idea what this is all about. This is for you Scott, I will never forget you.

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## Introduction

During the Triassic Period (251–199 Ma) floras underwent rapid diversification in Gondwana. The significant extinction prior to 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). 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 Glossopteridales, however, may have survived into the Triassic period (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, such as the Caytoniales, while others largely diversified, such as the corystosperms and conifers, to take over the land previously dominated by the Glossopteridales in the Paleozoic. The Triassic period was an important time in seed plant evolution; it has been suggested that the Triassic flora was the most diverse ever in terms of gymnosperms (Anderson & Anderson 2003).

Many gymnosperm groups were present in the Triassic of Gondwana: the Caytoniales, Coniferales, Corystospermales, Cycadales, Peltaspermales, and the Petriellales (e.g., Taylor et al. 1994, Barale et al. 1995, Holmes and Anderson 2005, Anderson 1978, Axsmith et al. 1998, Klavins et al. 2002, 2003, Schwendemann et al. 2010, Bomfleur et al. 2011). The diversity of the known flora of Antarctica during the Triassic includes all of these major seed plant groups, as well as ferns and sphenophytes (e.g., Delevoryas et al. 1992, Schwendemann et al. 2010). 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

(CTM), the Fremouw Formation contains fossils of every major plant group that was present at the time. Interestingly, and perhaps due to 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 great deal of detail about the plant groups present in the flora. Permineralizations of reproductive structures have been particularly interesting due to the wealth of knowledge that can be determined from anatomical detail. Yet sometimes 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 researched for the last hundred years, yet a number of enigmatic reproductive structures have still not been assigned to specific groups with any certainty (Anderson & 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) and two curving arms. It was considered to be either microsporangiata or megasporangiata. *Dordrechtites* consists of a central triangular region (scale of Anderson 1978) with an elongate arm extending from either side of the base of the triangle (fig. 2A, 2B). The type species, *D. elongatus*, was found on the same bedding plane as strap-shaped leaves assigned to *Podozamites elongatum*, which are now included in the genus *Heidiphyllum* (*H. elongatum*; Retallack 1981).

Anderson and Anderson (2003) subsequently described two additional species of *Dordrechtites* from South Africa (*D. cetiparvus* and *D. mazocirrus*), and placed them in a new family Dordrechtitaceae and order Dordrechtitales within the Pinopsida, along with the type species *D. elongatus*. They also described *Dordrechtites* attached to an axis. Rigby (in Playford

et al. 1982) detailed an additional species, *D. dikeressa*, from the Moolayember Formation (Upper Triassic) of Queensland, Australia. The latter species exhibits a central cupule with protruding spine-like points and shorter arms than the type species. The cupules 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 the Los Rastros Formation in Argentina (Carnian) (pers. obs. of H. Anderson in Anderson & Anderson 2003), Dubbo district, New South Wales (Anisian) (pers. obs. K. Holmes in Anderson & Anderson 2003), and the Cañadón Largo Formation, El Tranquilo Group of Argentina (Ladinian–Carnian) (Novas 2009, p. 33; Artabe et al. 2007, Gnaedinger 2010).

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 thought to be helically attached to a main axis and assumed to contain ovules, although none have yet been isolated.

In this paper, I present the first *Dordrechtites* from Antarctica and the oldest described species to date (Anisian), thus expanding the known geographic and geologic range of the taxon. In addition, the Antarctic *Dordrechtites* is preserved as a combination of compression and permineralization, allowing for the first description of the anatomy of this cupule and the ovules within it.

## Materials and Methods

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

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* 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 at the base of Mt. 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 due to 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 minutes, 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, GmbH, Freiburg, Germany). All specimens were photographed using a Leica (Allendale, New Jersey, USA) 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 version 11.0 (Adobe Systems, San Jose, California, USA). 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 due to 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) and {12603 A}, {12614 A}, {12930 A, C<sub>top</sub>, D<sub>bot</sub>, D<sub>top</sub>, E}, {13598 C<sub>bot</sub> ( $\alpha$ ,  $\beta$ ), D}, and {13600 A, B} (silicified specimens); slides 24,357–24,376, and 26,749.

## Results

Family and Order—*Gymnospermae incertae sedis*

Genus—*Dordrechtites* Anderson 1978 emend. Bergene et al.

*Emended generic diagnosis.* Isolated T-shaped ovulate reproductive structure consisting of a central pyramidal cupule with two elongated arms that extend out perpendicularly from the wide end (base) of the cupule. Each arm is roughly as long as or slightly longer than the cupule and curves back towards 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 et al. sp. nov.

*Diagnosis.* Isolated ovulate structure consisting of a triangular cupule 8–12 mm long and up to 6.5 mm wide at the base, containing two oblong, bilaterally symmetrical ovules that are attenuated at micropylar end. Arms up to 15 mm long and 1 mm wide at point of attachment to cupule. Epidermis of cupule one cell thick; cells filled with dark contents. Collateral vascular bundle extends from the arm into the top of the cupule, branches and extends around the ovule about halfway down to the micropylar end. Vascular bundle in the arm of ~50 tracheids plus thick-walled sclereids. Tissue of cupule parenchymatous; includes transfusion tissue of rectangular cells with pitted walls. Integument of each ovule bilayered. Sclerotesta up to 200 µm thick, consisting of outer layer with longitudinally oriented, thick-walled cells, and inner layer one cell thick, of rectangular, thick-walled 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<sub>top</sub>, 13598 C<sub>bot</sub>, and surface compression specimen T 5647. 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.

*Type locality.* Base of Mt. 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* due to the generally poor preservation of tissues.

*Description and remarks on species.* The reproductive structure *Dordrechtites arcanus* from Antarctica consists of a central cupule with two arms (fig. 2A, 2B). The elongate arms are 10–15 mm long and attached at the base of the cupule, which on average is 6 mm across. The arms extend up to 15 mm on each side of the cupule. Each arm is approximately 1 mm wide, curving at an angle of about 40° towards the central cupule region. The length of the pyramidal cupule averages 9.5 mm; it is widest at the base, becomes attenuated towards the apex, and exhibits longitudinal striations on the cupule exterior. The cupule contains two ovules (fig. 2C–2G).

No permineralized specimens exhibit two complete arms; the best example is the holotype (12603 A; fig. 2C), which shows one complete arm and a stub of the other. The

specimen measures 25–35 mm across the top from tip to tip, including the middle cupule region. The arms are anatomically comprised of sclerenchymatous cells that are either blocky or ovoid thick-walled sclereids that average 36  $\mu\text{m}$  in diameter (fig. 3A). The sclerenchymatous tissue of the arms extends over the top of the cupule (fig. 2C). The sclerenchyma cells sometimes appear resinous or very degraded.

In cross section, the outline of a single arm is scalloped, suggesting a series of small ridges on the surface of the arm (fig. 3B). Nests of sclereids can be observed in the cortex of the arm in cross section. An arc-shaped collateral vascular bundle with secondary xylem is present in both arms. Based on previous descriptions, one arm presumably connects to a main axis or branch, but no attachment is known for the Antarctic specimens.

Vascular bundles with secondary xylem enter the cupule from the arm and then branch downward. Vascular tissue has been observed at the base and side 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, in the arms and within the cupule, but helical thickenings and circular bordered pits also occur in the arms (fig. 3D, 3E). Tracheids have an average diameter of 10  $\mu\text{m}$ .

Epidermal tissue is present around the exterior of the cupule and the arms on almost all specimens. This layer is 1–3 cells thick and the cells are filled with black contents that appear resinous (fig. 3F). The cells measure 22.5  $\mu\text{m}$  across and are noticeably smaller than adjacent parenchyma cells of the cupule.

The triangular cupule (or trunk of Anderson 1978) ranges from 5–11.5 mm in length (average 9.5 mm) and 2.5–7 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 are considered to be transfusion cells or tracheids. The cells are randomly arranged and range from 25–50  $\mu\text{m}$  wide (average 39.7  $\mu\text{m}$ ). In most sections, they usually appear oval, but some larger cells can be oblong to almost rectangular. The cell walls are thinner than the sclerenchyma cells in the arms and average 6.5  $\mu\text{m}$  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 certain areas of the cupule, there are specific zones of rectangular cells arranged in radial files 3–10 cells deep; cells average 35.5  $\mu\text{m}$  in diameter. The radial files were observed in multiple locations in the cupule (fig. 3C, 4A–4D). In some specimens, they occur surrounding one of the ovules or may occur extending between the two ovules. The cell files also occur in two specimens at the base of the cupule adjacent to the sclerenchyma tissue that extends into the arms.

The integument of the ovule consists of a two-parted sclerotesta and endotesta; sarcotesta is not preserved. The outer layer of sclerotesta is comprised of narrow, elongate, longitudinally arranged fibers, with a layer thickness of 40–200  $\mu\text{m}$  (average 140  $\mu\text{m}$ ). The integument thickness is less toward the micropylar end of the ovule. Individual thickened sclerotic cells are not sufficiently preserved to determine the size, but the dense layer is readily defined (fig. 5A, 5B). The inner layer of the sclerotesta is one cell thick (fig. 5C). These cells have thickened walls and are rectangular as well as long and narrow. This layer consists of alternating short and long cells in line, averaging 47.9  $\mu\text{m}$  in length, with a range of 30–70  $\mu\text{m}$  long. Most specimens are degraded and sometimes 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  $\mu\text{m}$

thick and is intact in all specimens. The megaspore membrane extends from the base all the way to the apex and into the micropylar canal.

The two ovules are naturally oriented side by side (arms and ovules in one plane, fig. 2D) and are wider at the base but narrow approaching the apex. However, in almost all specimens, the ovules are observed in a unique orientation. One of the ovules is seen in longitudinal section while the other seems to be at a very oblique angle, almost a cross section in 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 x 27  $\mu\text{m}$  (fig. 6B, 6C). Micropylar cell differentiation was only preserved 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, and possibly more developed megagametophyte, measures 415 x 175  $\mu\text{m}$ . It appears to be 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 be a different form of fungal material that occurs in other specimens.

In most of the specimens, the tissues within one of the two ovules are degraded and the ovule area is filled with fungi (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. Another fungal type with small hyphae is found in the parenchyma cells of the cupule (fig. 6F).

## 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 Triassic of Antarctica. With the preservation being a combination of compression and permineralization, the internal anatomy of the cupule and ovules can now be detailed and related to the morphology of this structure as previously described. As an *incertae sedis* genus, this ovulate structure still has no association to 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, i.e., it was described as a scale (later as an ovuliferous scale; Anderson & Anderson 2003). Whether the structure was part of a microsporangiata or megasporangiata cone was not known, but it was compared to microsporophylls in the Cycadales and Coniferales, as well as the bract-scale complex (megasporophyll of Anderson 1978) of *Cedrus deodara*. Although interpreted as a conifer, there is no evidence of a subtending bract or a fused bract-scale complex. The original diagnosis included T-shaped scales that were an average of 18 mm long and 1 mm wide. In the diagnosis, the central part (“trunk” of Anderson 1978) was approximately 11 mm long and as wide as 5 mm.

The next report on *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 *D. 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), as they are listed as 2-3 mm high, while the seed itself is 5-9 mm long. Each seed bore one prominent spinelike point with three smaller points. The size of this *Dordrechtites* structure was smaller than the dimensions provided in the original generic diagnosis (Anderson 1978), so at this point the genus should have been emended to incorporate the different sizes and the newly found attachment of the cupules to an axis. Rigby (Playford et al. 1982) noted that the word ‘cone’ was used only for convenience. The structure that is pictured (fig. 7C; 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 *Dordrechtites dikeressa* was placed in the Corystospermaceae Thomas 1933, based on Rigby’s observations that there were no bracteoles of any kind present. He compared the paired arrangement of cupules in *D. dikeressa* to *Umkomasia geminata* from the same flora (Playford et al. 1982).

In 2003, Anderson and Anderson added two new species, *D. cetiparvus* and *D. mazocirrus*, also from the Molteno Formation. These species differed from *D. elongatus* in their smaller size (*D. cetiparvus*) and reflexed central region (*D. mazocirrus*), as well as differences in the lengths of the arms compared to 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” (fig. 7A). The genus was placed within a new family Dordrechtitaceae Anderson & Anderson 2003 and order Dordrechtiales Anderson & 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” [sic]. Based on 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 *D. arcanus* from Antarctica) is T-shaped with sterile arms and a winged ovuliferous “trunk” (central part) bearing an ovule/seed (Anderson & Anderson 2003). The interpretation of this “winged trunk” as a single, winged ovule is not well supported, however, as no dispersed seeds were found, either in the Molteno (Anderson & 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 & Anderson 2003) compared to the sterile arms is incorrect as originally reconstructed (fig. 7B vs. fig. 8A, 8C; Anderson & Anderson 2003, p. 60, fig. 4). In the permineralized *D. arcanus*, the arms can be seen in the same plane as the two ovules, in contrast to the original description, which put them in the opposite plane of the central cupule. The permineralized specimens from Antarctica also demonstrate that there is no bract/scale complex or wings and that two ovules (rather than one) sit within the cupule. What were previously thought to represent wings are probably creases and striations on the exterior of the cupule.

Because of these previous nomenclatural irregularities and the presence of new information from our anatomical study, it is important to emend the genus to clarify characteristics of the taxon based on information from South Africa, Australia, and now Antarctica. The following emended generic diagnosis still 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 *Dordrechtites* 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. It is likely that an 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 Mt. Falla specimens. A vascular bundle containing ~50 tracheids and a space where the phloem probably existed extends through the middle of each arm. This collateral vascular bundle gives off branches into the cupule at the base, but the preservation is too fragmentary to fully trace the course of the vasculature. Portions of vasculature with secondary xylem in cross section also extend about halfway down the cupule on the outside of one of the ovules (fig. 3C). Scalariform secondary thickenings are the most common, as seen in the arms and within the cupule, yet helical thickenings and circular bordered pits also occur in the arms.

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 a number of extant conifers, cycads, and gnetophytes and considered an auxiliary conducting system perpendicular to the midvein. Transfusion tissue cells are also frequently arranged in longitudinal rows (Griffith 1957). Transfusion tracheids, historically, 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).

Transfusion tissue is observed throughout the parenchyma in *D. arcanus* in almost every specimen. It was first hypothesized that the pits on the transfusion tracheids 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 localized around the vascular bundle, this tissue occurs throughout the cupule and amounts to many pitted cells visible in a 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. In *D. arcanus*, transfusion tracheids can be seen near a vascular bundle at the base of the cupule and more towards the apex; however, 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, in *Doylea tetrahedrasperma* (Stockey and Rothwell 2009).

The function for a large amount of transfusion tissue in the cupule is not known; however, cells of this type are 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 radial files of cells in the ground tissue of every permineralized specimen. The files are observed both separating the two ovules from each other and surrounding just one

ovule (fig. 4A–4D). 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 throughout the cupule, running vertically between the ovules and then extending out toward the sides of the cupule near the base where the arms connect. These files were originally thought to represent an abscission zone for the ovules; however, they also separate the two ovules. Another hypothesis for these radial files is that they represent some sort of wound response, e.g., 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 the disease explanation for the radial files, however, is that they occur in all but two specimens, even those that show no evidence of fungal hyphae. At the present time, I 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 while the other seems to be at an oblique angle, almost a cross section in cases (fig. 8B). 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 for this orientation is that one of the ovules was re-oriented as it was growing but there is 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 I suggest that they may 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 (Traverse 2007, Balme 1995, Jansson et al. 2008), and it 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 the *Pteruchus* 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 (Traverse 2007). This pollen may be related with *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, based on 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 early Middle and Late Triassic. The Molteno Formation in South Africa is dated as Carnian and the Moolayember Formation of Australia is also Carnian due to palynomorph association, such as *Falcisporites* and *Aratrisporites* (Playford et al. 1982, Anderson & Anderson 2003, McLoughlin et al. 1997). Farabee et al. (1990) suggested that the permineralized peat from Fremouw Peak, Antarctica, was Anisian (early Middle Triassic) based on 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. Anderson pers. obs. in Anderson & Anderson 2003), the Dubbo district, New South Wales, Australia (Anisian) (pers. obs. K. Holmes in Anderson & Anderson 2003), and the Cañadón Largo Formation, El Tranquilo Group of Argentina (Ladinian–Carnian) (Novas 2009, p. 33; Artabe et al. 2007, Gnaedinger 2010).

#### *Comparison of D. arcanus with Other Species*

*Dordrechtites arcanus* is most similar to the type species, *D. elongatus*, based on both morphology and overall size (30 x10 mm for the entire specimen of *D. elongatus*). 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 arms of *D. cetiparvus* are very unequal in length; the distal arm is only 5 mm long and appears stunted (Anderson & Anderson 2003). The cupule is strongly reflexed and angular and is curved proximally, i.e., the cupule apex is pointed towards the point of attachment and not downward.

*Dordrechtites mazocirrus* (Anderson & Anderson 2003) is very similar to *D. cetiparvus* but is slightly larger and its cupule is rounder and fuller. The arms are again unequal in *D. mazocirrus*, but measure about 10 mm (Anderson and Anderson 2003). *Dordrechtites arcanus* exhibits much longer and straighter arms than the reflexed and stunted arms and cupules of *D. cetiparvus* and *D. mazocirrus*. It is difficult to understand the morphology of the cupule from the permineralizations since there is loss of preservation due to degradation, however the cupules do not appear to be reflexed as in *D. mazocirrus* and *D. cetiparvus* (Anderson & Anderson 2003).

*Dordrechtites dikeressa* 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 which contains the seed below, and then two slender horns continue on the other side of the cupule up to 15 mm (fig. 7C, 7D; Playford et al. 1982). The measurement across the top of the structure is relatively the same as *D. arcanus* (~ 30 mm), but *D. arcanus* does not have a dichotomy within the extending arms. As described, the cupule of *D. arcanus* envelops the entire ovule region. This is unlike *D. dikeressa*, in which the cupule sits on top of the single seed that is 5–9 mm in length.

*Dordrechtites dikeressa* from Australia also exhibits noticeable spikes or points on the exterior of the cupule which are not observed in *D. arcanus*. On the Antarctic compressions there are bumps and striations preserved but this is most likely due to preservation of the presumed fleshy cupule. No spikes are observed in *D. arcanus*, however 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.

*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 & Anderson 2003) were described as a lax cone bearing fascicles of three to four gracile scales. Anderson and Anderson (2003) illustrate attachment to the central axis via one of the curving arms of the cupule, with the other arm curving around the cupule (fig. 7A). *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 (fig. 7C; 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 that in turn is connected to the main axis. Rigby suggests a completely different morphology, one 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 & Anderson 2003), the connection to a main axis for the isolated structure is via one of the arms. This is borne out by the anatomical detail from *D. arcanus*, which has arc-shaped vascular tissue in both arms. It is not possible to determine, however, which arm represented the site of attachment since no specimen exhibited two complete arms. In all cases, the arms appear broken off and do not taper to a point as in previously described impression-compression 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 Mt. Falla site.

#### *Fungal Activity*

In virtually all specimens of *Dordrehtites arcanus* fungal activity is present (fig. 6E, 6F). The most noticeable evidence occurs within one of the two ovules in the cupule; many specimens show a single, infected ovule. Even more unusual is the almost complete absence of the integumentary layer in this ovule in two specimens (fig. 2C, 2F). Only shredded, degraded sclerotesta is observed with no megaspore membrane or endotesta. Other fungi are present as hyphae in different ovule specimens and also in the parenchyma of the cupule. 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 (2–3 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

cupule parenchyma cells (fig. 6F) consists of individual hyphae. It is unknown if this was a mutualistic or saprobic relationship because the tissues and cells seem well-developed, but it is more likely to have been an infection after *Dordrechtites* fell into a 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, Caytoniales, Cycadales, Peltaspermales, and Petriellales all produced ovulate structures, although only some have been positively identified (e.g., Seward 1908, Thomas 1933, Banerji and Lemoigne 1987, Holmes 1982, Taylor et al. 1994, Yao et al. 1993, 1995; Barale et al. 1995, Klavins et al. 2002, 2003, Bomfleur et al. 2011) 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 Mt. 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 & Anderson (2003) concluded that the isolated form of *Dordrechtites* represented a single scale of a conifer cone; however, there is no evidence of a bract/scale complex in the anatomically preserved specimens from Antarctica, nor in the impressions from South Africa. There is no differentiation of cell tissues or an abscission zone in the Antarctic fossils as might be expected at the base of a bract/scale complex in a conifer cone. The permineralized material demonstrates no similarities to a cone or scale; therefore this genus should not be considered a conifer.

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. *Umkomasia* is conserved in its morphology throughout Gondwana and has been studied both in impression-compressions (Thomas 1933, Holmes and Anderson 2005) and in permineralizations (Klavins et al. 2002). Based on anatomical detail, *U. resinosa* (Klavins et al. 2002) included fleshy cupules which fully enclosed one or two ovules. The cupule partially covered the seed and a bifid integumentary tip extended beyond the cupule, which is similar to compression-impression specimens. The cupules are approximately 8 mm long and 3 mm wide (Holmes 1987, Klavins et al. 2002). The *Dordrechtites* cupule in comparison is approximately 8 mm in length from base to tip and 5 mm across the base. *Umkomasia* cupules are also referenced as individual sporophylls (i.e., not part of a cone; Axsmith et al. 2000) and are helically arranged on an axis that is connected, at least in one instance, to a short shoot with attached *Dicroidium* foliage (Axsmith et al. 2000). It has been possible to reconstruct the corystosperm plant from Fremouw Peak, Antarctica based on the presence of particular secretory cells in the foliage (*Dicroidium*), stems (*Kykloxylon*), pollen organs (*Pteruchus* organ), and ovulate cupules (*Umkomasia*). 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 may still represent an ovulate structure of the corystosperms that is different from *Umkomasia*.

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). *Heidiphyllum elongatum*, as it is now interpreted, was originally

described as *Podozamites elongatus* (Anderson 1978) and considered to be affiliated with *Telemachus elongatus* and possibly *D. elongatus*. Retallack (1981) erected the genus *Heidiphyllum* (Morris) Retallack to include apetiolate leaves from Gondwana, which he separated from *Podozamites*, a primarily Laurasian taxon with distinct petioles and transversely oriented paracytic stomata. Anderson & Anderson (2003) considered *Dordrechtites* to be a voltzialean conifer due to 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). This morphology is completely unlike the central cupule with two lateral arms seen in *Dordrechtites*. While both taxa occur with *Heidiphyllum* leaves in South Africa, in Antarctica, *H. elongatum* occurs only readily with *T. antarcticus* seed cones. Axsmith et al. (1998) suggested that *Heidiphyllum* leaves may have been borne by *Notophytum* stems based on cuticular similarities. Hermsen et al. (2007) described a permineralized voltzialean pollen cone, *Leastrobus fallae*, from the same site as *Dordrechtites*, and 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* seed cones, and *Leastrobus* pollen cones. Later Bomfleur et al. (2011) also attributed compressed pollen cones of *Switzianthus* sp. to the same plant, based on cuticular similarities. If correct, then it seems unlikely that *Dordrechtites* can be correlated with the conifers, at least in Antarctica.

Another seed plant group present in Antarctica during the Triassic is the Peltaspermales. The peltasperms occur over a wide range of localities in Gondwana and extend from the Carboniferous to the Triassic (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; each sporophyll 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, like *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 is only one peltasperm currently known from Antarctica. Bomfleur et al. (2011) described a new peltasperm from the Upper Triassic Falla Formation based on ovulate structures of *Matatiella*, leaves of *Dejerseya*, and a branching pollen-bearing structure assigned to *Townrovia*. Although there are some similarities between the ovules of *Peltaspermum* and *Dordrechtites*, the morphology of the sporophyll is different and therefore *D. arcanus* is not considered to be related to this group.

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

The Caytoniales are relatively widespread during the Mesozoic (e.g., Thomas 1925, Clifford 1998), but have yet to be identified from the Fremouw Formation, although they have been observed elsewhere in Antarctica (Rees 1993; Barale et al. 1995). The ovules of *Caytonia* are borne within leaf-like cupules that recurve towards the main axis (Thomas 1933; Reymanówna 1973). They average 4.5 mm in diameter and produce 8–13 orthotropous ovules along the midrib (Taylor et al. 2006). *Dordrechtites* and *Caytonia* differ in the number of ovules within the cupule, the morphology of the cupule, and its orientation to the axis. There are no arms or extensions in the *Caytonia* cupules and the fine details of the micropyle and cuticular canals are not observed in *Dordrechtites*.

Few ginkgophytes are known from the central Transantarctic Mountains, and these are all Late Triassic (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). *Hamshawvia* in South Africa is 15–40 mm long and bears two megasporophylls that may have been longitudinally folded and held 8–20 ovules (Anderson & Anderson 2003). The strobilus was borne on a short shoot that also held *Sphenobaiera* leaves (Anderson & Anderson 2003). While *Hamshawvia* bears some resemblance to *Caytonia* or *Umkomasia*, it is not comparable to *Dordrechtites* based on morphology and number of ovules per sporophyll.

Since *Dordrechtites arcanus* occurs in the upper part of the Fremouw Formation, it can be compared with 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 from Fremouw Peak are borne on a dichotomizing axis in clusters and their basal attachment occurs in the form of a short pedicle; each cupule contains two to six orthotropous ovules (Taylor et al. 1994). *Kannaskoppia* is an impression genus that was described from the Molteno Formation of South Africa and placed in the Petriellales, as but was placed in its own family, Kannaskoppiaceae (Anderson & Anderson 2003). *Kannaskoppia* consists of an axis bearing megasporophylls arranged in two rows; each megasporophyll contains a single ovule but the cupule may separate into several lobes upon maturity (Anderson and Anderson 2003). The similarities between *Petriellaea* and *Kannaskoppia* are few except in reconstructions of morphology. Although these taxa are still relatively poorly known, they are not similar to *Dordrechtites*.

*Probolosperma* is an anatomically preserved, isolated ovule with uncertain affinities from the Fremouw Formation (Decombeix et al. 2010). The ovule (6–10 mm long) is elongate and

bilaterally symmetrical. *Probolosperra antarcticum* has a three-layered integument with a complex sarcotesta and sclerotesta that extends out to form two lateral wings and elaborations at the micropylar and chalazal ends (Decombeix et al. 2010). Organic attachment is not preserved in the permineralization but there is a pedicle area where the vascular system enters the ovule. The nucellus is only fused to the integument at the base. Some oblique tangential sections of *Dordrechtites* can look very similar to *Probolosperra*, but the sclerotestal elaboration at the apex and base of *Probolosperra* is not observed in *Dordrechtites*.

*Ignotospermum* is a dispersed ovule from the Middle Triassic permineralized peat from Fremouw Peak (Fremouw Formation). It is radially symmetrical with an integument composed of a simple endotesta and complex sclerotesta (Perovich and Taylor 1989). The sclerotesta consists of three distinct layers of thick walled cells and the vascular strand that extends into the sclerotesta. Overall, *I. monilii* is about 3.5 mm long and 2.75 mm in diameter. This species is not attached by a pedicle but ends bluntly at the chalazal end of the ovule. It is also not enclosed in a cupule or other structure. Primarily, the radial symmetry of ovule does not allow a comparison to *Dordrechtites*.

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

## Conclusions

The genus *Dordrechtites* and a new species, *D. arcanus*, is described from combined compressions and permineralizations, providing the first report of anatomical information on this enigmatic Triassic ovulate structure and the first account from Antarctica. This is also the earliest described occurrence 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, there is no well-defined pollen receiving structure. 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 as a conifer cone scale or was allied with the corystosperm seed ferns. Since there is no evidence of a bract-scale complex in the anatomically preserved specimens, a conifer relationship is unlikely. The presence of a cupule and an elongate micropyle suggests affinities with the corystosperms.

## Literature Cited

- Abu Hamad A, H Kerp, B Vörding, K Bandel 2008 A Late Permian flora with *Dicroidium* from the Dead Sea region, Jordan. *Rev Palaeobot Palynol* 149: 85–130.
- Anderson HM 1978 *Podozamites* and associated cones and scales from the Upper Triassic Molteno Formation, Karoo Basin, South Africa. *Palaeontologia Africana* 21: 57–77.
- Anderson JM, HM Anderson 2003 Heyday of the gymnosperms: systematics and biodiversity of the Late Triassic Molteno fructifications. National Botanical Institute, Pretoria, South Africa.
- Artabe AE, EM Morel, DG Ganuza 2007 Las floras triásicas de la Argentina. *Asociación Paleontológica Argentina, Publicación Especial* 11: 75–86.
- Axsmith BJ, Taylor TN, Taylor EL 1998 Anatomically preserved leaves of the conifer *Notophytum krauselii* (Podocarpaceae) from the Triassic of Antarctica. *Amer J Bot* 85: 704–713.
- Axsmith BJ, EL Taylor, TN Taylor, NR Cuneo 2000 New perspectives on the Mesozoic seed fern order Corystospermales based on attached organs from the Triassic of Antarctica. *Am J Bot* 87: 757–768.
- Balme BE 1995 Fossil in situ spores and pollen grains: An annotated catalogue. *Rev Palaeobot Palynol* 87: 81–323.
- Banerji J, Y Lemoigne 1987 Significant additions to the Upper Triassic flora of Williams Point, Livingston Island, South Shetlands (Antarctica). *Géobios* 20: 469–487.
- Barale G, M Philippe, T Torres, F Thévenard 1995 Reappraisal of the Triassic flora from Williams Point, Livingston Island (South Shetland Islands, Antarctica): Systematical, biostratigraphical and paleogeographical implications. *Instituto Antártico Chileno, Serie Científica* 45: 9–38.

- Barrett PJ 1968 The post-glacial Permian and Triassic Beacon Rocks in the Beardmore Glacier Area, central Transantarctic Mountains, Antarctica. PhD thesis, Ohio State University, (unpublished).
- Barrett PJ 1969 Stratigraphy and petrology of the mainly fluvial Permian and Triassic Beacon rocks, Beardmore Glacier area, Antarctica. Institute of Polar Studies Report 34. Ohio State University Research Foundation, Columbus.
- Barrett PJ, DH Elliot, JF Lindsay 1986 The Beacon Supergroup (Devonian-Triassic) and Ferrar Group (Jurassic) in the Beardmore Glacier area, Antarctica. *Antarct Res Ser* 36: 339–428.
- Bergene J, EL Taylor, TN Taylor 2011 Anatomically preserved *Dordrechtites* from the Middle Triassic of Antarctica. Botany 2011 (Botanical Society of America Meeting, 9–13 July 2011, St. Louis) Abstract 303 p. 123.
- Bomfleur B, EL Taylor, TN Taylor, R Serbet, M Krings, H Kerp 2011 Systematics and paleoecology of a new peltaspermalean seed fern from the Triassic polar vegetation of Gondwana. *Int J Plant Sci* 172: 807–835.
- Clifford HT 1998 First record of *Caytonia* in Australia. *Memoirs of the Queensland Museum* 42: 448.
- Collinson JW, DH Elliot 1984 Geology of Coalsack Bluff, Antarctica. Pages 97–102 in MD Turner, JF Spletstoesser, eds. *Geology of the Central Transantarctic Mountains*. American Geophysical Union, Washington, DC.
- Crane PR 1985 Phylogenetic analysis of seed plants and the origin of angiosperms. *Ann Mo Bot Gard* 72: 716–793.
- Decombeix A-L, SD Klavins, EL Taylor, TN Taylor 2010 Seed plant diversity in the Triassic of Antarctica: A new anatomically preserved ovule from the Fremouw Formation. *Rev Palaeobot Palynol* 158: 272–280.

- Delevoryas T, RC Hope 1973 Fertile coniferophyte remains from the Late Triassic Deep River Basin, North Carolina. *Am J Bot* 60: 810–818.
- Delevoryas T, TN Taylor, EL Taylor 1992 A marattialean fern from the Triassic of Antarctica. *Rev Palaeobot Palynol* 74: 101–107.
- Dickison WC 2000 Integrative plant anatomy. San Diego: Harcourt/Academic Press.
- Escapa IH, A-L Decombeix, EL Taylor, TN Taylor 2010 Evolution and relationships of the conifer seed cone *Telemachus*: evidence from the Triassic of Antarctica. *Int J Plant Sci* 171: 560–573.
- Escapa, I, EL Taylor, NR Cúneo, B Bomfleur, J Bergene, R Serbet, TN Taylor 2011 Triassic floras of Antarctica: Plant diversity and distribution in high paleolatitude communities: *PALAIOS* 26: 522–544.
- Farabee MJ, EL Taylor, TN Taylor 1990 Correlation of Permian and Triassic palynomorph assemblages from the central Transantarctic Mountains, Antarctica. *Rev Palaeobot Palynol* 65: 257–265.
- Galtier J, TL Phillips 1999 The acetate peel technique. Pages 67–70 in TP Jones, NP Rowe, eds. *Fossil Plants and Spores: Modern Techniques*. The Geological Society, London, UK.
- Gnaedinger S 2010 Estructuras reproductivas en el Grupo El Tranquilo (Triásico tardío), provincia de Santa Cruz, Argentina. X Congreso Argentino de Paleontología y Bioestratigrafía–VII Congreso Latinoamericano de Paleontología. September 20–24, 2010, abstract 73.
- Grauvogel-Stamm L 1978 La flore du Grès à *Voltzia* (Buntsandstein supérieur) des Vosges du Nord (France): Morphologie, anatomie, interprétations phylogénique et paléogéographique. *Sci Géol Mém* 59: 1–225.

- Griffith MM 1957 Foliar ontogeny in *Podocarpus marcophyllus*, with special reference to transfusion tissue. *Am J Bot* 44: 705–715.
- Harris TM 1937 The fossil flora of Scoresby Sound East Greenland Part 5. Stratigraphic relations of the plant beds. *Medd om Grønland* 112: 3–104.
- Hermesen EJ, TN Taylor, EL Taylor 2007 A voltzialean pollen cone from the Triassic of Antarctica. *Rev Palaeobot Palynol* 144: 113–122.
- Hermesen EJ, EL Taylor, TN Taylor 2009 Morphology and ecology of the *Antarcticycas* plant. *Rev Palaeobot Palynol* 153: 108–123.
- Holmes WBK. 1982. The Middle Triassic flora from Benolong, near Dubbo, central-western New South Wales. *Alcheringa* 6: 1–33.
- Holmes WBK 1987 New corystosperm ovulate fructifications from the Middle Triassic of eastern Australia. *Alcheringa* 11: 165–173.
- Holmes WBK, HM Anderson 2005 The Middle Triassic megafossil flora of the Basin Creek Formation, Nymboida Coal Measures, New South Wales, Australia, Part 4. Umkomasiaceae, *Dicroidium* and affiliated fructifications. *Proc Linn Soc N S Wales* 126: 1–37.
- Jansson IM, S McLoughlin, V Vajda, M Pole 2008 An Early Jurassic flora from the Clarence-Moreton Basin, Australia. *Rev Palaeobot Palynol* 150: 5–21.
- Kerp H, A Abu Hamad, B Vörding, K Bandel 2006 Typical Triassic Gondwanan floral elements in the Upper Permian of the paleotropics. *Geology* 34: 265–268.
- Klavins SD, TN Taylor, EL Taylor 2002 Anatomy of *Umkomasia* (Corystospermales) from the Triassic of Antarctica. *Am J Bot* 89: 664–676.

- Klavins SD, EL Taylor, M Krings, TN Taylor 2003 Gymnosperms from the Middle Triassic of Antarctica: the first structurally preserved cycad pollen cone. *Int J Plant Sci* 164: 1007–1020.
- Lindström S, S McLoughlin 2007 Synchronous palynofloristic extinction and recovery after the end-Permian event in the Prince Charles Mountains, Antarctica: Implications for palynofloristic turnover across Gondwana. *Rev Palaeobot Palynol* 145: 89–122.
- McLoughlin S, S Lindström, AN Drinnan 1997 Gondwanan floristic and sedimentological trends during the Permian–Triassic transition: New evidence from the Amery Group, northern Prince Charles Mountains, East Antarctica. *Antarctic Science* 9: 281–298.
- McManus HA, EL Taylor, TN Taylor, JW Collinson 2002 A petrified *Glossopteris* flora from Collinson Ridge, central Transantarctic Mountains: Late Permian or Early Triassic?. *Rev Palaeobot Palynol* 120: 233–246.
- Novas, FE 2009 *The age of dinosaurs in South America*. Bloomington: Indiana University Press.
- Osborn JM, TN Taylor 1993 Pollen morphology and ultrastructure of the Corystospermales: Permineralized in situ grains from the Triassic of Antarctica. *Rev Palaeobot Palynol* 79: 205–219.
- Petriella B 1978 La reconstrucción de *Dicroidium* (Pteridospermopsida, Corystospermaceae). *Obra del Centenario del Mus de La Plata* 5: 107–110.
- Petriella B 1981 Sistemática y vinculaciones de las Corystospermaceae H. Thomas. *Ameghiniana* 18: 221–234.
- Perovich NE, EL Taylor 1989 Structurally preserved fossil plants from Antarctica. IV. Triassic ovules. *Am J Bot* 76: 992–999.
- Playford G, JF Rigby, DC Archibald 1982 A Middle Triassic flora from the Moolayember Formation, Bowen Basin, Queensland. *Geol Surv Qnsld Publ* 380: 1–52.

- Rees PM 1993 Caytoniales in Early Jurassic floras from Antarctica. *Géobios* 26: 33–42.
- Retallack GJ 1981 Middle Triassic megafossil plants from Long Gully, near Otematata, north Otago, New Zealand. *Journal of the Royal Society of New Zealand* 11: 167–200.
- Reymanówna M 1973 The Jurassic flora from Grojec near Kraków in Poland Part II: Caytoniales and anatomy of *Caytonia*. *Acta Palaeobotanica* 14: 1–87.
- Schwendemann AB, TN Taylor, EL Taylor, M Krings, JM Osborn 2010 Modern traits in early Mesozoic sphenophytes: the *Equisetum*-like cones of *Spaciinodum collinsonii* with *in situ* spores and elaters from the Middle Triassic of Antarctica. Pages 15–33 in C Gee, ed. *Plants in Mesozoic time: morphological innovations, phylogeny, ecosystems*. Indiana University Press, Bloomington.
- Seward AC 1908 On a collection of fossil plants from South Africa. *Quart J Geol Soc Lond* 64: 83–108.
- Smoot EL, TN Taylor, T Delevoryas 1985 Structurally preserved fossil plants from Antarctica. I. *Antarcticycas*, gen. nov., a Triassic cycad stem from the Beardmore Glacier area. *Am J Bot* 72: 1410–1423.
- Stockey RA, GW Rothwell 2009 Distinguishing angiosperms from the earliest angiosperms: a Lower Cretaceous (Valanginian–Hauterivian) fruit-like reproductive structure. *Am J Bot* 96: 323–335.
- Srivastava SC 1984 *Lelestrobis*: A new microsporangiate organ from the Triassic of Nidpur, India. *Palaeobotanist* 32: 86–90.
- Taylor EL, TN Taylor 2009 Seed ferns from the late Paleozoic and Mesozoic: any angiosperm ancestors lurking there?. *Am J Bot* 96: 237–251.

- Taylor EL, TN Taylor, JW Collinson 1989 Depositional setting and paleobotany of Permian and Triassic permineralized peat from the central Transantarctic Mountains. *Int J Coal Geol* 12: 657–679.
- Taylor EL, TN Taylor, H Kerp, EJ Hermsen 2006 Mesozoic seed ferns: Old paradigms, new discoveries. *J Torrey Bot Soc* 133: 62–82.
- Taylor TN, GM del Fueyo, EL Taylor 1994 Permineralized seed fern cupules from the Triassic of Antarctica: Implications for cupule and carpel evolution. *Am J Bot* 81: 666–677.
- Thomas HH 1925 The Caytoniales, a new group of angiospermous plants from the Jurassic rocks of Yorkshire. *Phil Trans R Soc Lond B Biol Sci* 213: 299–363.
- Thomas HH 1933 On some pteridospermous plants from the Mesozoic rocks of South Africa. *Phil Trans R Soc Lond B Biol Sci* 222: 193–265.
- Traverse A 2007 *Paleopalynology*. Springer, Dordrecht.
- White ME 1965 Report on 1964 plant fossil collections. Bureau of Mineral Resources, Australia, Record 1965/101, 8 pp. (unpublished).
- Worsdell WC 1897 On the origin of "transfusion tissue" in the leaves of gymnospermous plants. *J Linn Soc, Bot* 33: 118–122.
- Yao X, TN Taylor, EL Taylor 1993 The Triassic seed cone *Telemachus* from Antarctica. *Rev Palaeobot Palynol* 78: 269–276.
- Yao X, TN Taylor, EL Taylor 1995 The corystosperm pollen organ *Pteruchus* from the Triassic of Antarctica. *Am J Bot* 82: 535–546.

## Figures

### Figure 1

Locality of *Dordrehtites arcanus*. *A*, Map of Antarctica (inset) and Beardmore Glacier region. Arrow indicates Mt. Falla; modified from Collinson and Elliot 1984. *B*, Photograph of locality at base of Mt. Falla, note thin layer of silicified mudstone (next to hammer) above the bluff-forming sandstone. Photo by C.P. Daghlian, 2003; hammer = 28 cm.

### Figure 2

*Dordrehtites arcanus* nov. sp. from the base of Mt. Falla, central Transantarctic Mountains, Antarctica. *D. arcanus* morphology, *A,B*: Compression, *C-G*: Permineralization. *A*, *Dordrehtites arcanus* displaying two arms and central cupule; T 5647. *B*, Isolated ovulate structure showing curved arm (left) and organic debris typical of the rock matrix; T 5949. *C*, Longitudinal section with one complete arm and broken stub; central cupule region displays two ovules (arrows). Note sclerenchyma of arm (*S*) continuing over top of cupule; Holotype, 12603 A #3. *D*, Oblique cross section through the base of a cupule showing left arm in cross section, right arm in oblique section, and two ovules in center; 13598 C<sub>bot</sub> #90. *E*, Oblique longitudinal section of cupule showing attenuated tip, broken arms; 12614 A #2. *F*, Oblique longitudinal section of cupule with the possible aborted ovule on the right, smaller ovule on the left with possible micropyle (*M*); 12930 C<sub>top</sub> #8. *G*, Longitudinal section of cupule showing two ovules, and parenchymatous (transfusion) tissue of cupule. Cross section of arm with central vascular bundle visible in top left; 13598 C<sub>bot</sub> #20. Scale bars = 5 mm (*A, B*), 3 mm (*C–E*), 1 mm (*F*) 2 mm (*G*).

### Figure 3

*Dordrechtites arcanus* detail of arms, epidermis and vasculature. *A*, Oblique section of arm containing sclerenchyma, vascular bundle (VB) running through middle; 12603 A #3. *B*, Cross section of arm with central arc-shaped collateral vascular bundle with secondary xylem; note scalloped exterior and nests of sclereids in the cortex; 13598 C<sub>bot</sub> #37. *C*, Detail of Fig. 2F, showing radial files of cells separating the two ovules and cross section of vasculature on the right side of cupule; 13598 C<sub>bot</sub> #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<sub>bot</sub> #52. *G, H*, Simple circular (*G*) and elongate (*H*) pits on transfusion tracheids in cupule; 13598 C<sub>bot</sub> #71, 12930 E #3. Scale bars = 200  $\mu\text{m}$  (*A*), 300  $\mu\text{m}$  (*B, C*), 50  $\mu\text{m}$  (*D*), 30  $\mu\text{m}$  (*E*), 100  $\mu\text{m}$  (*F*), 50  $\mu\text{m}$  (*G, H*).

### Figure 4

*Dordrechtites arcanus* cupule tissue. *A*, Radial files of cells forming a distinct line against more randomly oriented transfusion parenchyma (detail of Fig. 4*B*); 12614 A #2. *B*, Section through the bases of two ovules showing radial files separating the two ovules; endotesta is preserved in right ovule; 12614 A #2. *C*, Section through cupule (ovule below) showing various tissues: sclerenchyma (S) and extending into arms, radial files (arrowheads) below sclerenchyma (R), transfusion parenchyma of cupule (P), integument of dense layer of sclerotesta (I), and endotesta adpressed to sclerotesta (\*); 12930 E #30. *D*, Detail of cells in radial files showing probable meristematic (cambial) cells; 13598 C<sub>bot</sub> #35. Scale bars = 50  $\mu\text{m}$  (*A*), 200  $\mu\text{m}$  (*B*), 400  $\mu\text{m}$  (*C*), 50  $\mu\text{m}$  (*D*).

**Figure 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) and 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<sub>bot</sub> #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 radial files just above and transfusion parenchyma to the right; 12930 E #3. Scale bars = 100  $\mu\text{m}$  (*A*, *C*, *D*), 50  $\mu\text{m}$  (*B*).

**Figure 6**

*Dordrechtites arcanus* ovule anatomy and fungus. *A*, Flared micropylar tip at apex of ovule; 12930 D<sub>top</sub> #58. *B*, Preserved pollen (proximal view) similar to *Alisporites* pollen found within the micropyle; 12930 D<sub>top</sub> #55. *C*, Well-preserved distal surface of *Alisporites* pollen found near specimen in matrix; 12603 A #75. *D*, Possible megagametophyte (arrows) enclosed within endotesta; 13598 C<sub>bot</sub> #66. *E*, Fungus within megaspore membrane (MM); note hyphae in multiple orientations; 12930 A #25. *F*, Fungus within transfusion parenchyma cells; 13598 C<sub>bot</sub> #33. Scale bars = 500  $\mu\text{m}$  (*A*), 30  $\mu\text{m}$  (*B*, *C*), 300  $\mu\text{m}$  (*D*), 50  $\mu\text{m}$  (*E*, *F*).

**Figure 7**

Reconstructions and line drawings of previous *Dordrechtites* descriptions. *A*, Suggested reconstruction of *D. elongatus* in a lax cone (Anderson & Anderson 2003). *B*, Isolated scale of *D. elongatus*, note incorrect orientation with “wings” in different plane than arms (Anderson & Anderson 2003). *C*, Suggested reconstruction of *D. dikeressa* as clusters of scales attached to secondary axis on a branch (Playford et al. 1982). *D*, Isolated specimen of *D. dikeressa*, note spines and arched cupule on top of seed (Playford et al. 1982).

**Figure 8**

Suggested reconstruction of *Dordrechtites arcanus*. *A*, Reconstruction with cutaway to show orientation of ovules and vasculature in arms and cupule. *B*, Ovules isolated to show skewed orientation of most specimens. *C*, Reconstruction of assumed natural ovule position.

Reconstruction by Gilbert Ortiz.

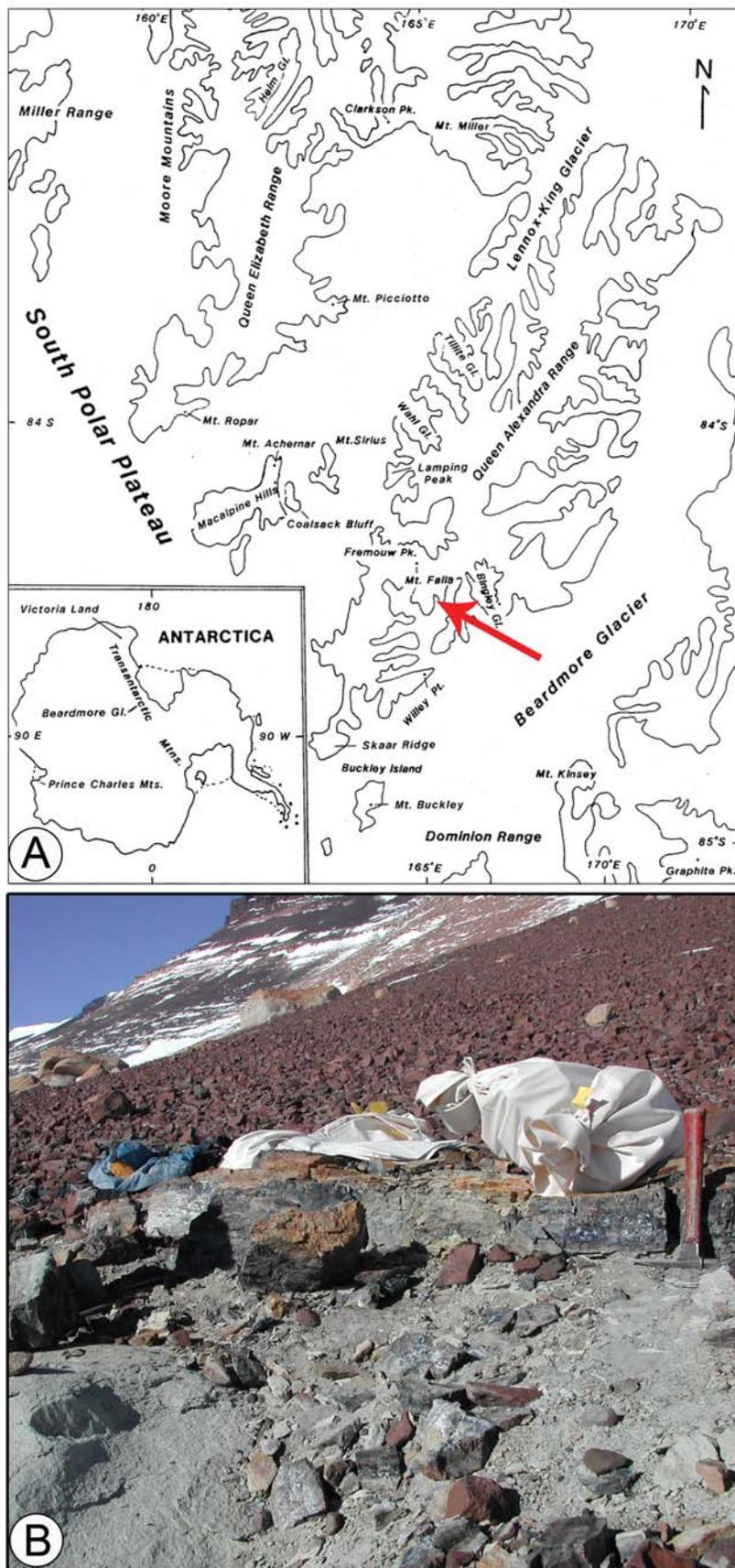


Figure 1

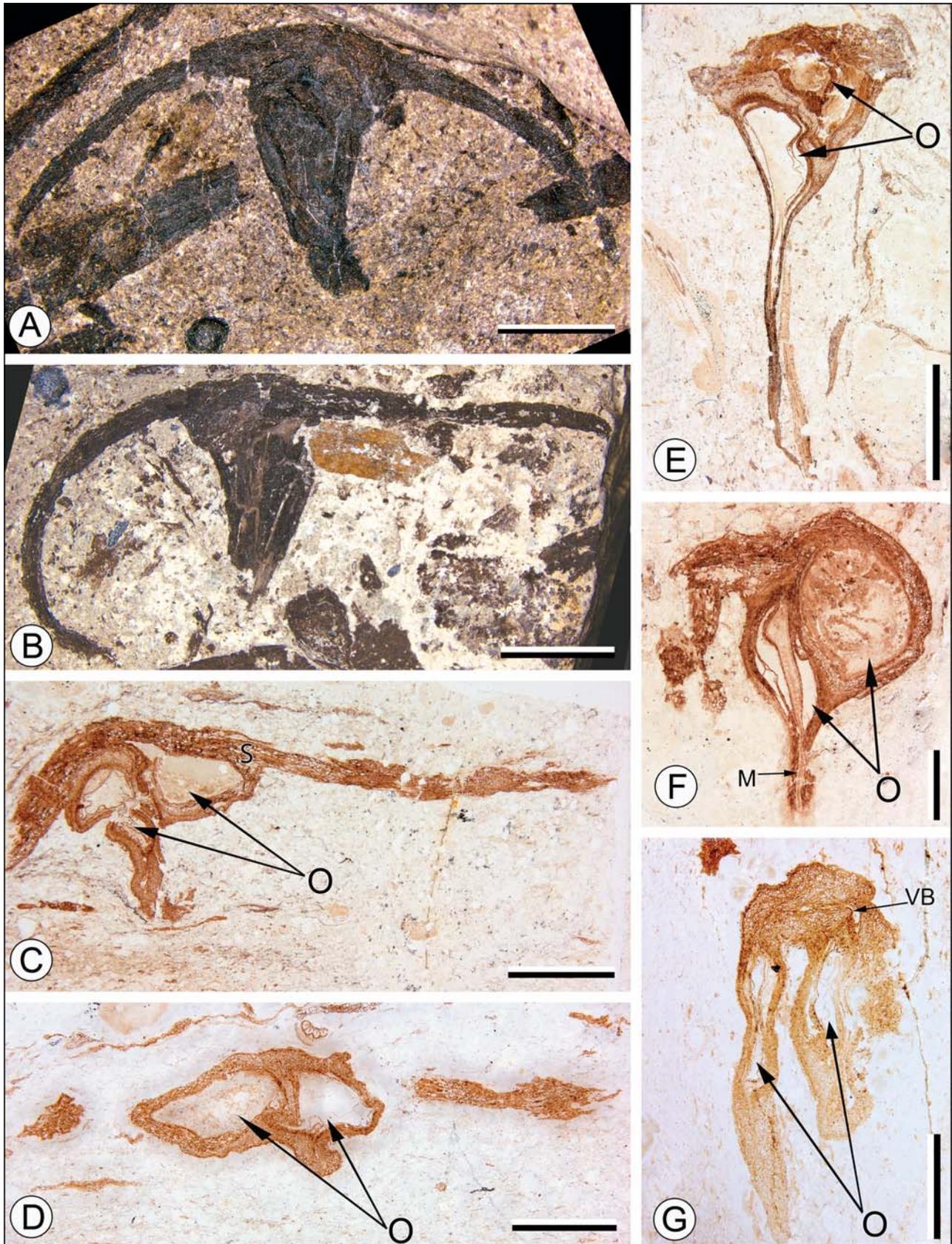


Figure 2

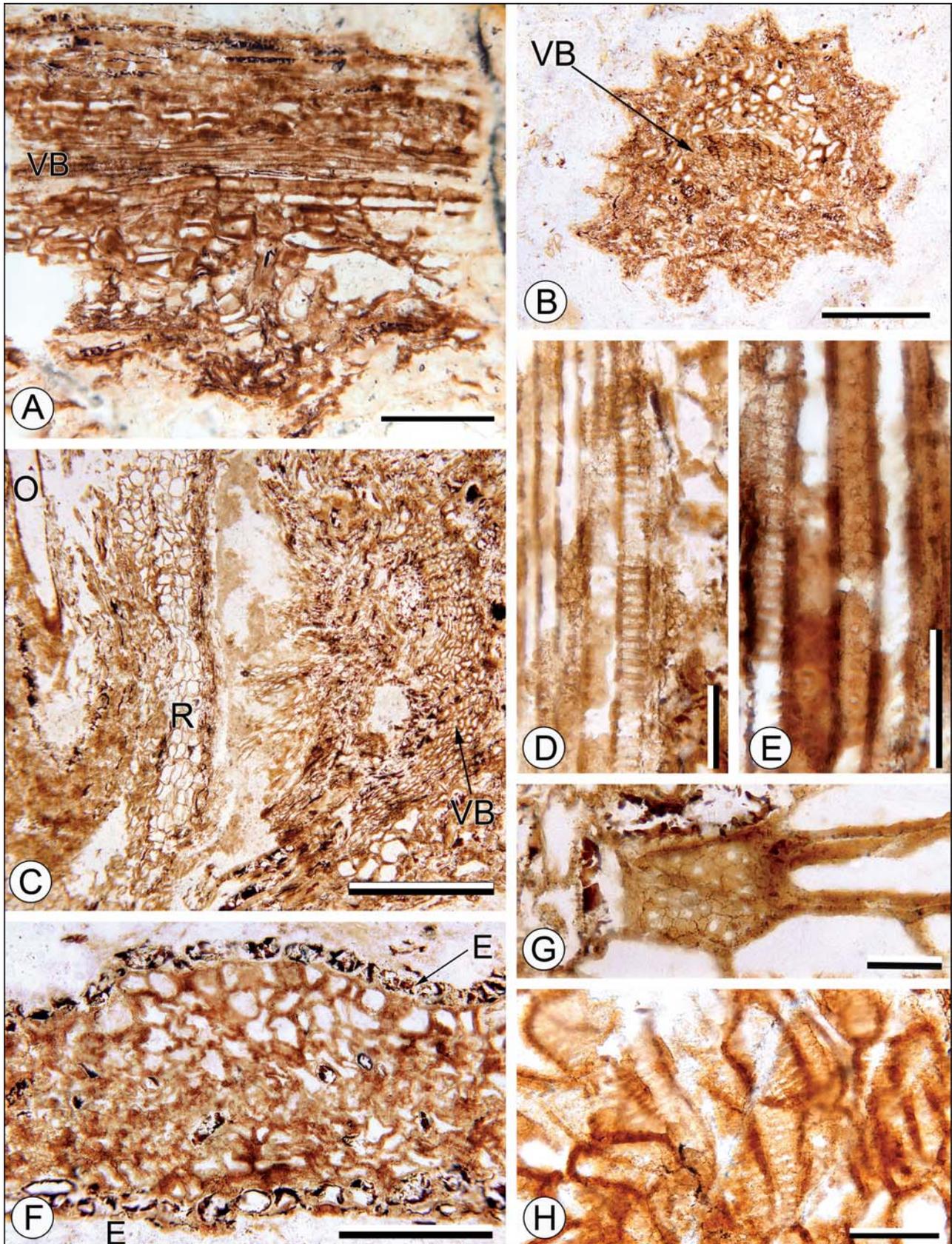


Figure 3

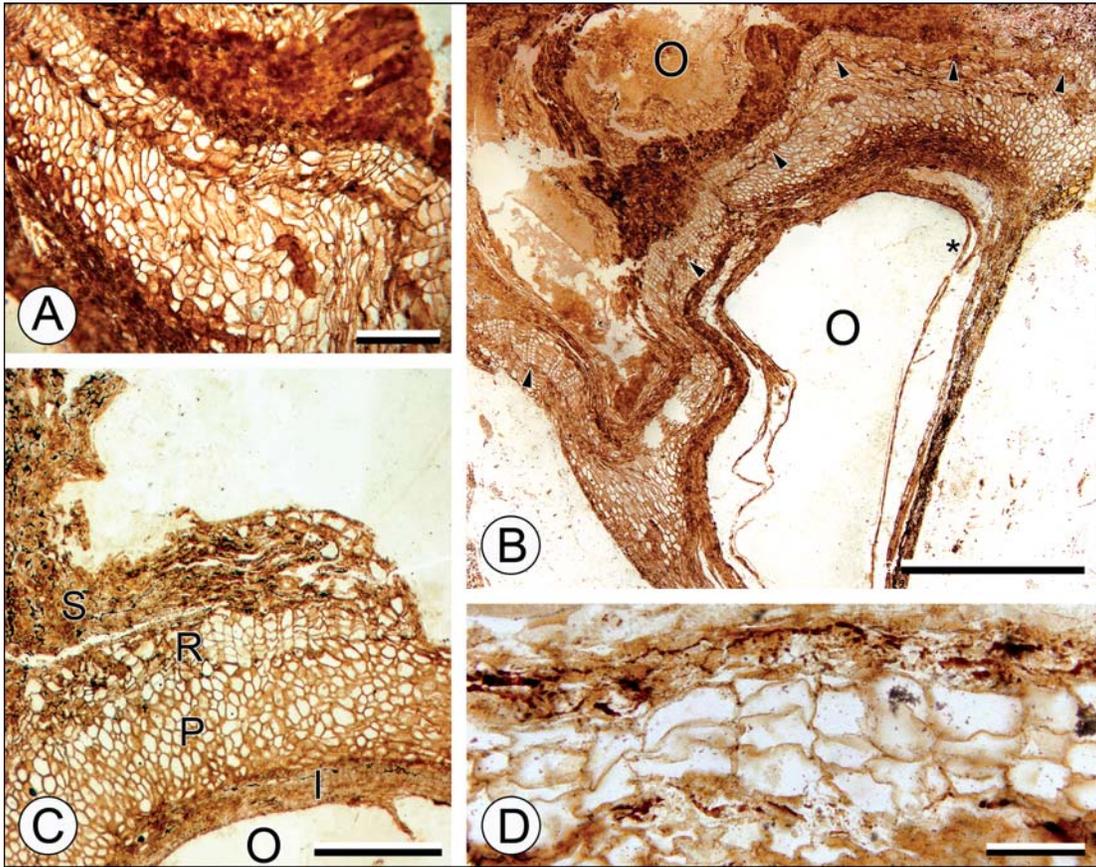


Figure 4

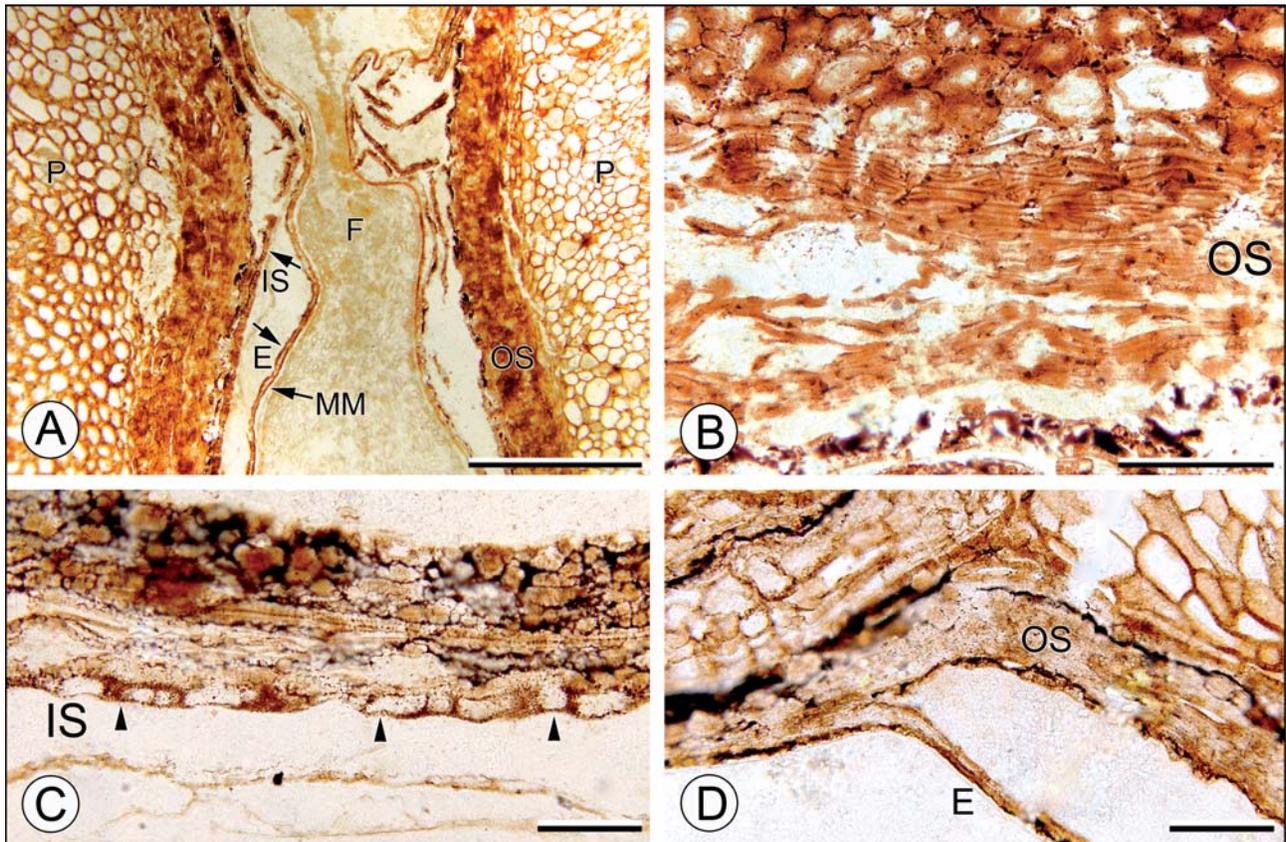


Figure 5

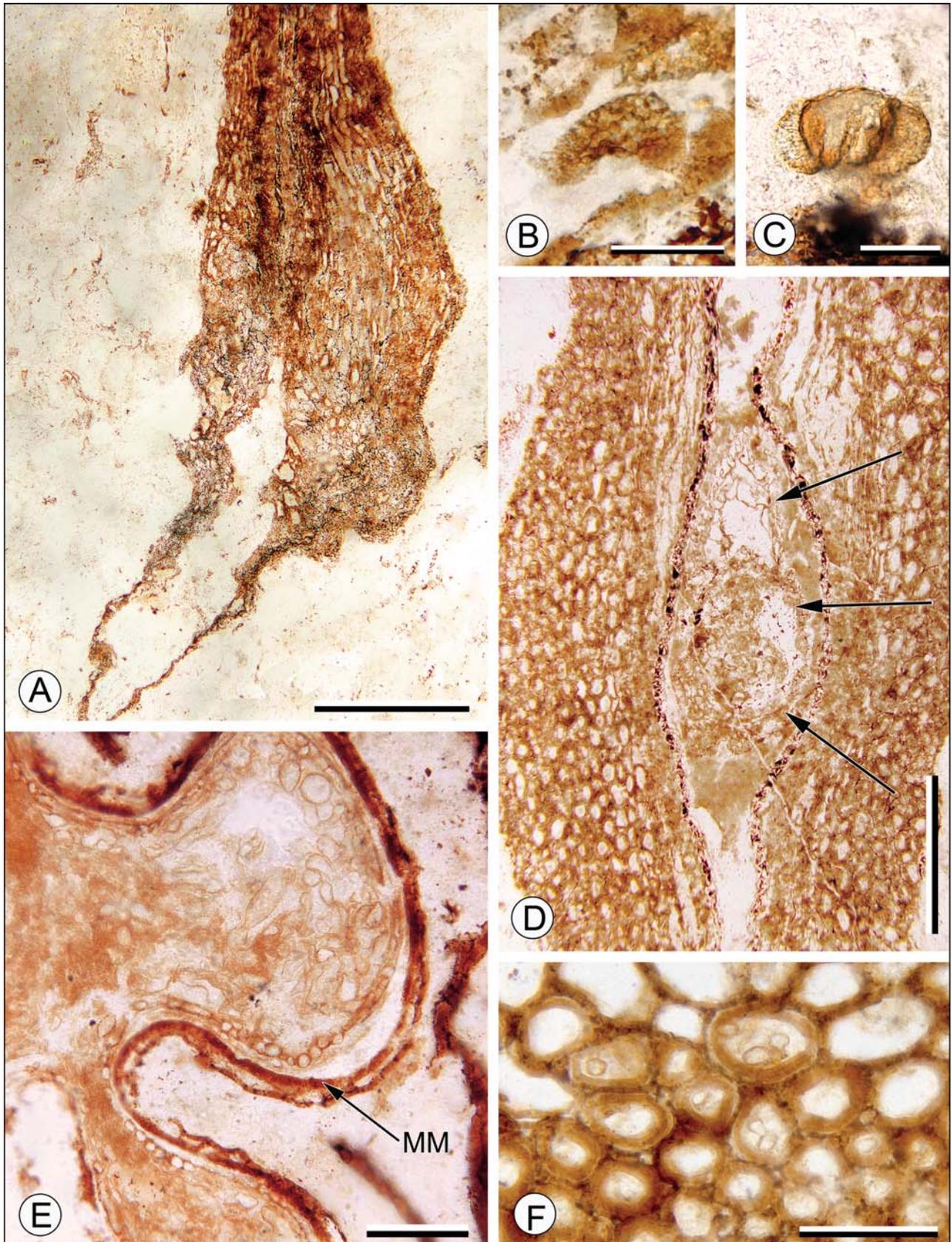


Figure 6

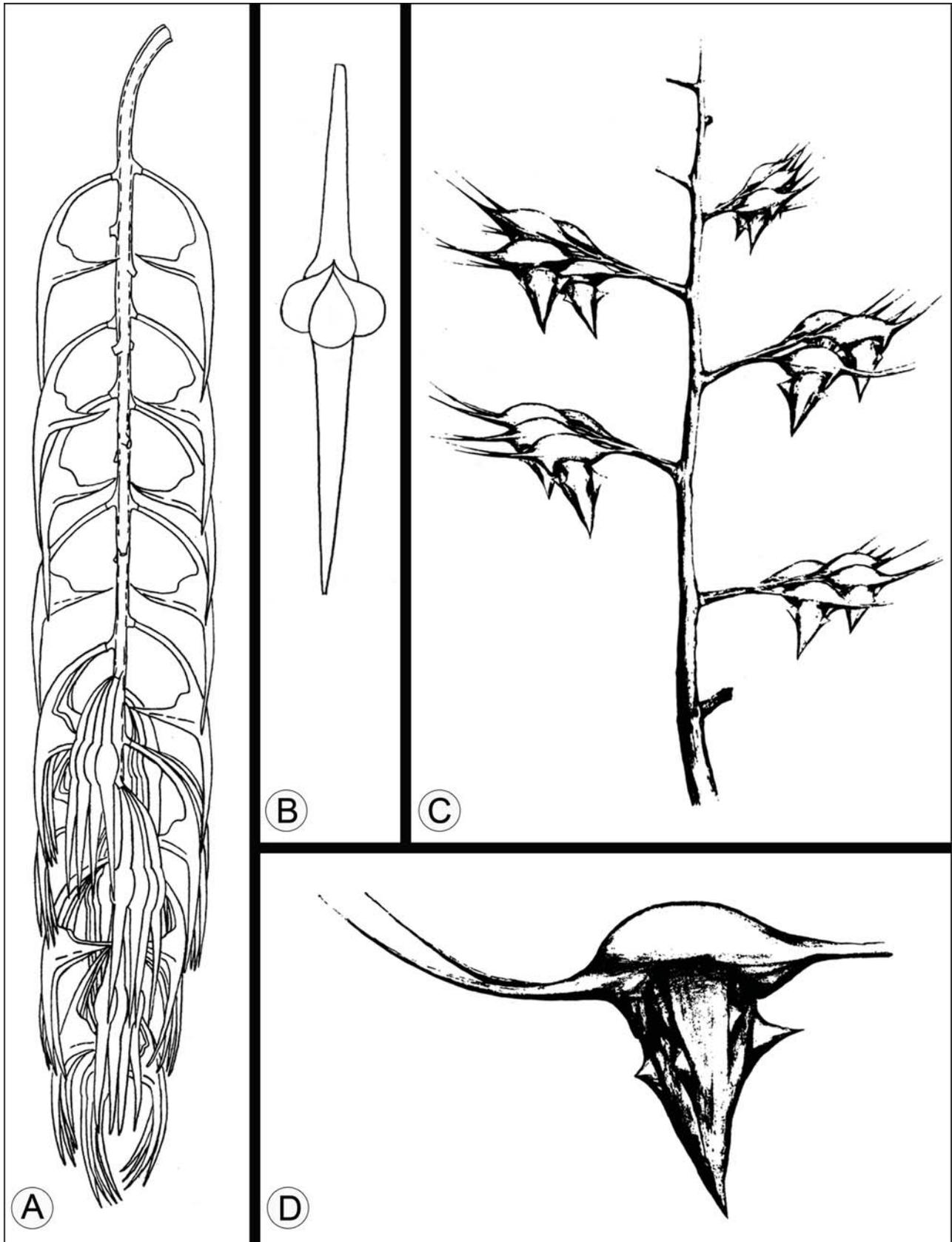


Figure 7

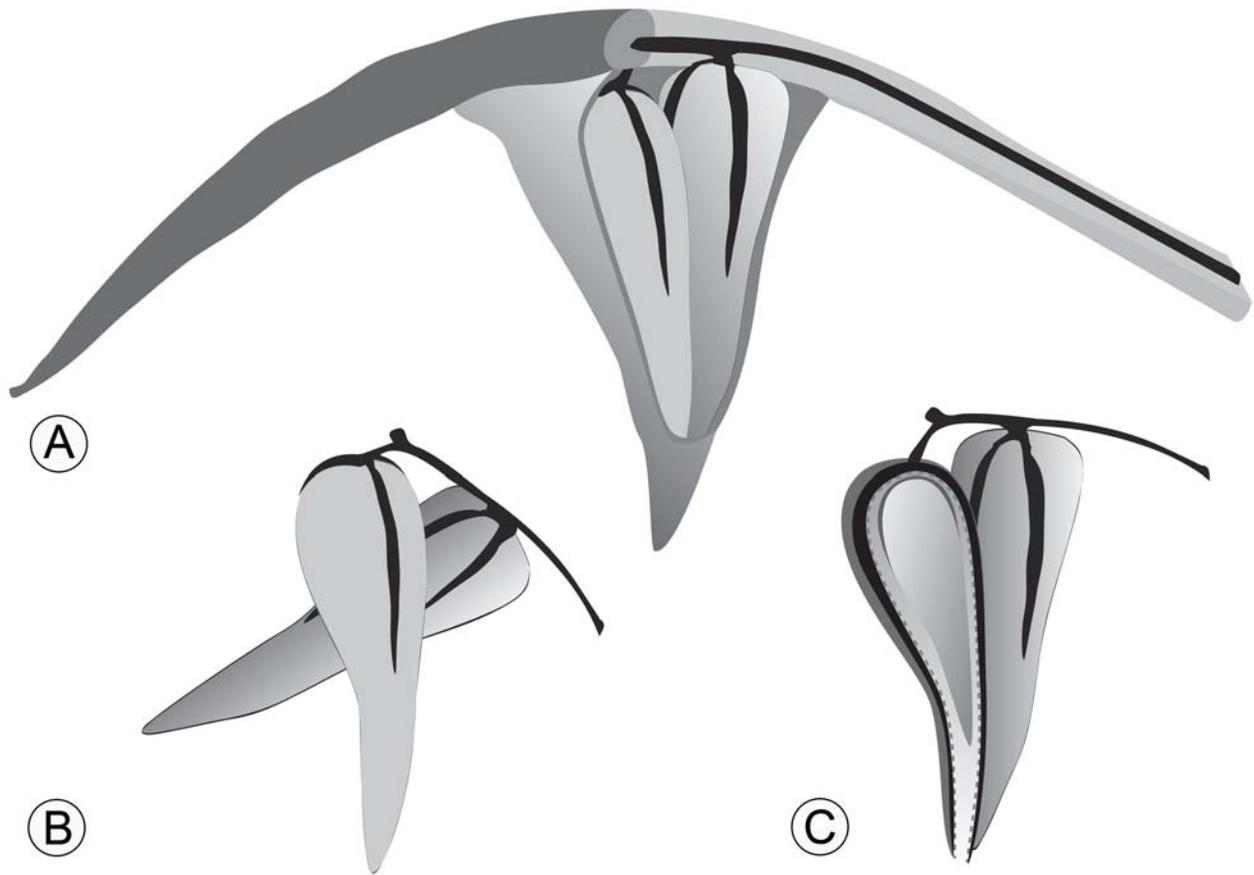


Figure 8