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Seed plant diversity in the Triassic of Antarctica: a new anatomically preserved ovule from the Fremouw Formation

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Abstract

A new anatomically preserved ovule is described from the Middle Triassic Fremouw Formation of the Beardmore Glacier area, Antarctica. *Probolosperma antarcticum* gen. et sp. nov. is bilaterally symmetrical and up to 1 cm long and 6 mm wide The integument is characterized by a complex sarcotesta with a palisade-like outer layer and a sclerotesta that forms two small lateral wings and elaborations in the chalazal and apical regions. The vascular system consists of a terete strand that enters the pedicel to form a small cup of tracheids at the base of the nucellus, with two strands that extend distally in the inner part of the sclerotesta. Comparisons with other gymnosperm ovules indicate that *Probolosperma* represents a new taxon, which enhances the diversity of known seed plants from the Triassic of Antarctica.

Key-words: Anisian, Triassic, Antarctica, ovule, anatomy, seed

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1. Introduction

Permineralized peat from the Fremouw Formation of the Transantarctic Mountains is one of the most significant sources of anatomically preserved early Middle Triassic plants. These fossils indicate that Antarctica was covered at that time by diverse high-latitude forests that have no modern analogues (Cúneo et al., 2003). To date, the flora is known to include sphenophytes (Osborn et al., 2000; Ryberg et al., 2008), ferns (Millay and Taylor, 1990; Delevoryas et al., 1992; Phipps et al., 2000), and several groups of seed plants. The latter are particularly abundant and include vegetative and reproductive organs of a cycad, two orders of seed ferns, and possibly three families of conifers (Table 1). These fossils are particularly important to our understanding of seed plant evolution. Indeed, some Triassic taxa correspond to early representatives of modern gymnosperm groups whereas others have been suggested as potential angiosperm ancestors as they illustrate examples of seed enclosure within cupules (Taylor et al., 2009). Making the Triassic permineralized plants especially important is the fact that most floras of this period are preserved as compressions/impressions and thus current phylogenetic hypotheses remain greatly constrained by the paucity of anatomical data. It is in this context that the continuing investigation of permineralized specimens from the Fremouw Formation represents an exceptional opportunity to increase our knowledge of the diversity, biology, and relationships of Triassic seed plants.

Reproductive structures are known for most of the taxa present in the Fremouw Formation. Pollen organs have been described for a cycad, Corystospermales, and Voltziales. Ovulate structures include a conifer cone with cupressaceous affinities (Yao et al., 1997), the dispersed ovule *Ignotospermum monilii* (Perovich and Taylor, 1989), and cupulate structures of Petriellales (Taylor et al., 1994) and Corystospermales (Klavins et al., 2002).
In this paper, we add to the known diversity of seed-plant reproductive structures from the Fremouw Formation by describing a new morphogenus of anatomically preserved ovules characterized by the possession of a thick sarcotesta and a sclerotesta with basal and apical elaborations. This new ovule is compared with taxa previously described from the Triassic of Antarctica and, more generally, Gondwana. Although there is not sufficient evidence to assign this seed to a specific group, the discovery of this interesting ovule further underscores the diversity of seed plants during the Middle Triassic in Antarctica, and thus expands our understanding of high paleolatitude ecosystems during a period of pronounced climate change (e.g. Taylor et al., 2000).

2. Material and methods

The specimens are preserved in peat blocks from the Beardmore Glacier area, Queen Alexandra Range, central Transantarctic Mountains, Antarctica. They were collected at the Fremouw Peak locality (84°17'41" S, 164°21'48" E) and at the base of Mount Falla, (84°21'S, 164°42'E). The permineralized peat occurs in the upper Fremouw Formation (Beacon Supergroup, Barrett et al., 1986) and is early Middle Triassic (Anisian) in age based on palynostratigraphy (Farabee et al., 1990). The blocks were cut into slabs and peeled using the standard technique (Galtier and Phillips, 1999). The polished surfaces were etched in 49% hydrofluoric acid then rinsed and peeled. Selected peels were mounted on microscope slides using Eukitt® for observation and digital imagery. Cell and tissue measurements were made using Wright Cell Imaging Facility's ImageJ software (Rasband, 1997–2008). Specimens, peels, and slides are deposited in the Paleobotanical Collections, Natural History Museum and Biodiversity Research Center, University of Kansas, under the specimen numbers 10827,

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12597, 13587, 14374 and 16105, and slide accession numbers 23747–23888.Where several ovules are present in some blocks they are designated by α, β, etc. in the figure legends.

3. Systematics

Genus *Probolosperma* Decombeix, Klavins, Taylor, et Taylor, gen. nov.

Generic diagnosis: Ovules with bilateral symmetry; integument consisting of three layers; complex sarcotesta, composed of unicellular palisade-like outer layer and multicellular inner layer of large thick walled-cells, commonly with dark contents; multicellular sclerotesta flattened, showing 180° rotational symmetry, with elaboration at the apex, two longitudinal ribs in the primary plane, and basal collar-like elaboration projecting downward around pedicel; endotesta uniseriate and parenchymatous. Nucellus attached to chalaza only at its base. Vascular system a terete strand forming a cup at base of nucellus with a single strand extending into each wing along the inner surface of the sclerotesta; tracheids with scalariform and circular bordered pits

Derivatio nominis: the generic name is derived from *Probolos* (Gr.), projecting prominence, referring to the elaborations of the integument, and *sperma* (Gr.), seed.

Type species:

Probolosperma antarcticum Decombeix, Klavins, Taylor, et Taylor, sp. nov.

Holotype, designated herein: Specimen in block 16105 Ftop (Plate I, 1; Plate II, 1-3), including six cellulose acetate peels, three of which are mounted on microscope slides (23747–23749)

Paratypes, designated herein: Two specimens from block 12597 Dbot (Plate I, 3; Plate II, 6-7), including 125 cellulose acetate peels, 32 of which are mounted on microscope slides (23750–2381); one specimen from block 10827 E (Plate I, 5-6; Plate II, 5), including 61 cellulose acetate peels, 13 of which mounted on microscope slides (23803–23813, 23889–23890)

Repository: The specimens, peels, and slides are housed in the Paleobotany Division of the University of Kansas Natural History Museum and Biodiversity Research Center.

Formation: Fremouw Formation, Beacon Supergroup.

Age: Middle Triassic (Anisian).

Type locality: Fremouw Peak, Queen Alexandra Range, Antarctica (84° 16'S 164° 21'E), Buckley Island Quadrangle (Barrett and Elliot, 1973).

Etymology: The epithet *antarcticum* (L., of Antarctica) is proposed, in reference to the geographical region from which the new species is described.

Specific diagnosis: Ovules approximately up to 1 cm long, 6 mm wide in primary plane and 3 mm in secondary plane. Sarcotesta up to 0.5 mm in thickness, palisade-like cells of outer layer with thickened outer and lateral walls, cells of multiseriate inner layer up to 0.1 mm in diameter, with thick walls. Sclerotesta 0.1-0.3 mm wide in middle region, in some cases with irregular outer surface, composed of about 7-10 layers of cells with pitted walls. Small lateral ribs formed by sclerified layer up to 0.7 mm thick; apical extension forming a rim up to 1 mm thick; basal collar–like extension as long as the pedicel; zone between basal extension and pedicel filled with cells from sarcotesta inner layer; endotesta cells with dark contents. Thick vascular bundle of about 50 tracheids.

4. Description

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The ovules are flattened, showing 180° rotational symmetry, and are 6-10 mm long, up to 6 mm wide in the primary plane and 3 mm in the secondary plane (Fig. 1; Plate I).). In longitudinal section in the primary plane, the ovules are ovate, whereas in the secondary plane they appear vase shaped due to the flattening of their distal portion, perhaps as a result of compression (Fig. 1, A, B; Plate I, 1-3). All demonstrate characteristic elaborations of the sclerotesta at the apex and base (Plate I, 1-4). In transverse section, the ovules are oval at the base and become increasingly flattened toward the apex (Plate I, 5-7).

4.1. Integument

The integument of *P. antarcticum* has a total thickness of 630 µm at mid-level and is composed of a complex sarcotesta, a middle sclerotesta, and a simple, uniseriate endotesta (Plate I, 1; Plate II, 1). The outer part of the integument, recognized as the sarcotesta, is variously preserved. In most specimens, its presence is only indicated by a cavity that surrounds the ovule and contains a few degraded cells, especially around the basal extensions of the sclerotesta (e.g. Plate I, 4). In a single specimen (16105 Ftop), the complete sarcotesta is preserved sufficiently to indicate that the layer ranges from 260–500 µm thick and is composed of two distinct zones (Plate I, 1; Plate II, 1). The outermost zone, corresponding to the epidermis, is unicellular, forming a palisade–like layer of parenchymatous cells with thickened outer and lateral walls (Plate II, 2). These cells are 37-44 µm long and 12-19 µm in diameter with outer walls 3-4 µm thick; most have shrunken dark contents. The inner layer of the sarcotesta is multicellular and composed of a partially degraded tissue (Plate II, 1, 3). The only identifiable cells in this layer are 25-100 µm in diameter, with walls up to 15 µm thick, and commonly with conspicuous dark contents. These cells appear to have thicker walls and are more numerous at the junction with the underlying sclerotesta. In specimen 16105 Ftop, the sarcotesta does not completely surround the sclerotesta but appears to fold back on itself below the level of the apex (Plate I, 1; Plate II, 1). However, the evidence for this feature is limited to this single specimen, which is only partly preserved and the general shape of the sarcotesta remains unknown.

The poor preservation of the sarcotesta compared with the underlying sclerotesta suggests that this tissue was relatively fragile and may have decomposed rapidly prior to fossilization. The consistent presence of a thin coalified layer between the sarcotesta and sclerotesta (Plate II, 3) may also suggest the possibility that the sarcotesta may have been exfoliated naturally during the development of the seed. This hypothesis might explain the nearly consistent absence of the sarcotesta in most specimens.

The most conspicuous part of the integument in *P. antarcticum* is the sclerotic layer (= sclerotesta). Its thickness is variable, typically measuring 100-250 µm in the mid-region of the ovule to more than 1 mm thick in zones where it forms the elaborations that are the distinctive features at the apex and base of the ovule (Fig. 1). The sclerotesta is composed of 7-10 layers of sclereids; these are oriented parallel to the long axis of the ovule and are hexagonal to circular in transverse section (Plate II, 1, 3). They are 10–18 µm in diameter, up to 90 µm in length, and have pitted walls. In many cases, only the outline of the cells can be seen where the walls are not preserved and are replaced by amorphous, opaque contents. In the zones where the cell wall is well preserved, it is about 6 µm thick and surrounds a small oval lumen (Plate II, 3).

The sclerotesta is elaborated into lateral ridges at the base and micropylar end of the ovule. In section view small ribs extend out from the surface in the primary plane for approximately 700 µm (Plate I, 5, 6). At the chalazal end, the sclerotesta forms a collar-like

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elaboration around the pedicel (Fig.1, C; Plate I, 5). Successive tangential longitudinal sections toward the center of the ovule show the sclerotesta initially as a central thickening at the base of the ovule (Plate I, 1), and then as two downward-oriented lateral projections (Plate I, 2, 4). Towards the center of the ovule, these two projections appear on both sides of the pedicel and have a similar length (Plate I, 3). The pedicel is sclerified, terete in cross section, and measures up to 0.5 mm wide and 1.7 mm long. Remains of tissue comparable to the inner layer of the sarcotesta are present between the pedicel and the collar formed around it by the sclerotesta (Plate I, 4, 5), which indicates that this region was not devoid of cells. At the micropylar end of the ovule, the sclerotesta forms a shallow rim that is bilaterally symmetrical and located about 2 mm below the micropyle (Fig.1; Plate I, 1-3). The rim is expanded in the primary plane and is up to 1 mm in thick. In cross section the apical part of the sclerotesta is flattened with two small ridges at each lateral edge of the ovule (Plate I, 7).

The innermost part of the integument (endotesta) is poorly preserved and generally not present, but in a few cases it is represented by a thin layer on the inner surface of the sclerotesta (Plate II, 4). It is composed of a single layer of thin-walled cells with dark contents.

4.2. Nucellus

The nucellus appears attached to the integument only at the base of the ovule (Plate II, 6) and distally we observed no well-developed pollen chamber in any specimens of *Probolosperma antarcticum* A delicate megaspore membrane is often preserved and appears as a narrow dark line appressed against the nucellus or occasionally shrunken away from it. Remnants of gametophyte cells are present in some specimens but their preservation is not sufficient to suggest any level of organization.

4.3. Vascular System

A thick (about 85 µm in diameter) terete strand of tracheids enters the base of the ovule (Fig. 1; Plate I, 3; Plate II, 7, 8) and expands to form a small cup where the nucellus is attached (Plate II, 66). In the pedicel, the strand is composed of about 50 tracheids that are 5-25 µm in diameter and up to 150 µm long. Most display scalariform thickenings but a few possess crowded, multiseriate bordered pits (Plate II, 9). The disc at the base of the nucellus is composed of 1-3 layers of tracheids. Successive cross sections through the base of the ovule indicate two lateral vascular strands that extend out from the cup in opposite directions at the base of the nucellus. The strands can be traced in the integument only in the basal third of the ovule. In cross section, a vascular bundle is also present on the inner surface of the small wing-like extensions of the sclerotesta (Plate II, 10). No vascular strands have been observed in the sarcotesta.

5. Discussion

Few isolated fossil seeds can be assigned with certainty to the plants that produced them. This is especially true for periods like the Triassic where only a small number of anatomically preserved specimens are known in sufficient detail that affinities with other organs can be hypothesized. To date, we have found no *Probolosperma* ovules in organic connection to vegetative structures, or juxtaposed to structures or organs that could be interpreted as cupules, or in an arrangement that might suggest a cone-like structure. However, when compared to all other detached ovules from the Triassic of Gondwana, *P.*

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antarcticum includes a unique set of characters that requires the establishment of a new morphogenus.

5.1. Comparison with previously described ovules from the Fremouw Formation

Corystosperms are the most abundant component of the permineralized flora from the Fremouw Formation. Anatomically preserved, cupulate, ovule-bearing organs of corystosperms are represented by the form species *Umkomasia resinosa* (Klavins et al., 2002). Like *P. antarcticum*, ovules of *U. resinosa* are flattened in cross section. However, *Umkomasia* ovules lack a pedicel and differ significantly in the morphology and anatomy of the integument, which is much thinner (150 vs. 630 µm), mostly composed of thin-walled cells, and devoid of sclerotesta extensions. The integument of *U. resinosa* ovules is also characterized by the presence of secretory cavities, a character that links it with other corystosperm organs from the same locality. The lack of a sclereid layer in the *Umkomasia* ovules might be linked to an early developmental stage of the observed specimens (Klavins et al., 2002). In extant gymnosperms, the integument of immature ovules is composed of thin-walled cells with the differentiation of the sclerotesta occurring later in development. A similar phenomenon has also been reported in fossil seeds (e.g. *Callospermarion*, Rothwell, 1971). However, while the well-differentiated sclerotestal layer observed in *Probolosperma* might simply reflect a more advanced stage of integument development consistent with the fact that all specimens are found dispersed, other characters indicate the two are distinct seed types. Although the evidence to date suggests the Corystospermales were a diverse group, the morphology and anatomy of their reproductive organs, where known in detail, are quite similar throughout Gondwana. Therefore, we think it unlikely that the new ovules represent a new genus among the corystosperms as the group is currently understood.

Another group of seed ferns with anatomically preserved ovules from the Fremouw Formation of Antarctica is the Petriellales, an order created for cupules containing seeds (Taylor et al., 1994). This order has also been suggested as containing vegetative and fertile specimens of the Kannaskoppiaceae from the Late Triassic Molteno Formation in South Africa (Anderson and Anderson, 2003); however, these latter specimens are only represented by impressions and thus their anatomy remains unknown. Ovules of *Petriellaea triangulata* from Fremouw are much smaller than *Probolosperma*, only 2-3 mm long, and lack a pedicel. *Petriellaea* also differs in that it is triangular in cross section and lacks a distinctive sclerified layer, although, as discussed above, this may reflect seed development.

Reproductive organs showing affinities with the former Taxodiaceae (Cupressaceae; Sequoioideae) are represented in the Fremouw Formation by the seed cone *Parasciadopitys aequata* (Yao et al., 1997). Like *Probolosperma*, ovules of *Parasciadopitys* are distinctly flattened in cross section. In these ovules the integument is tripartite and forms a small wing on either side in primary plane. The seeds are sessile and smaller than the new specimens, with a maximum length of 4.4 mm. The sclerotesta is thinner and shows no extensions at the micropylar end or at the base. There are also distinct differences in the thickness and anatomy of the sarcotesta.

Another morphotaxon of dispersed ovules from the Fremouw Formations is *Ignotospermum monilii* (Perovich and Taylor, 1989).Specimens of *I. monilii* co-occur with the new ovules in several peat blocks, but are clearly different based on the absence of a pedicel, their radial symmetry, and a smaller size. The anatomy of the integument is also distinct, with

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the sclerotesta organized in three distinct layers and showing no extensions. Nothing is known about the sarcotesta of *Ignotospermum.*

5.2. Comparison with taxa from the Fremouw Formation for which ovulate structures are unknown

Cycadales are represented in the Fremouw Formation by *Antarcticycas schopfii* as reconstructed by Hermsen et al. (2009) from stems and roots (Smoot et al., 1985), *Yelchophyllum omegapetiolaris* leaves (Hermsen et al., 2007a), and *Delemaya spinulosa* pollen cones (Klavins et al., 2003).Although *Antarcticycas* is one of the best-documented Mesozoic cycads, the ovulate organs remain unknown. Putative cycad fossils have been described from the Pennsylvanian (e.g. Taylor, 1969; Leary, 1990) but the best-known fossil cycad ovules are Jurassic compressions, which limits comparisons and understanding of the evolution of cycad ovules. Cycad ovules are usually larger than those of *Probolosperma*, but there are some extant forms less than 1 cm long (Chamberlain, 1935). Ovule symmetry is radial in all extant cycads except *Cycas* (Stevenson, 1992). Bilateral symmetry is also documented in the fossil record, for example, in *Primocycas* from the Permian of China (Zhu and Du, 1981). Modern cycad ovules are characterized by an integument composed of an outer fleshy layer, a conspicuous stony layer, and an inner layer that is initially fleshy but shrinks during development to form a thin membrane adpressed against the stony layer (Chamberlain, 1935, p.109). Cells of the outer layer are commonly filled with tannin. An elaborate sclerotesta occurs in some extant species with radial symmetry (Zamiaceae) in the form of a ring of small teeth at the micropylar end (coronula). In *Dioon mejiae* the sclerotesta also forms a collar in the chalaza (Caputo et al., 1985). Cycad ovules have a complex vascular system in the integument that consists of vascular bundles in both the outer and inner fleshy layers. Although the size, symmetry, and integument anatomy of *Probolosperma* are compatible with a cycad affinity, the difference in vascularization remains a major obstacle in attributing them to this group.

Putative podocarpaceous conifers are also represented in the Triassic of Antarctica by stems assigned to *Notophytum krauselii* (Meyer-Berthaud and Taylor, 1991). Permineralized trunks of *Jeffersonioxylon* have been compared to Podocarpaceae based on wood anatomy (Del Fueyo et al., 1995), but were subsequently assigned to the Corystospermales on the basis of an association only with *Dicroidium* leaves (Cúneo et al., 2003). Axsmith and collaborators (1998) demonstrated that leaves of *N. krauselii* are similar to the common compression fossil *Heidiphyllum elongatum* and may in fact be conspecific. Corresponding anatomically preserved reproductive structures are unknown, but evidence from compression fossils indicate that the seed cone *Telemachus elongatus*, originally assigned to the Voltziales (Anderson, 1978), was probably produced by the same plant (Axsmith et al., 1998). Compression specimens of *T. elongatus* are present in Antarctica in the Upper Triassic Lashly and Falla Formations (Yao et al., 1995). While it is difficult to compare the anatomically preserved ovules with compression specimens, the fact that the ovules of *T. elongatus* are small (1.5-2 mm) and nearly spherical suggests that these taxa are distinct.

The most recently recognized group of gymnosperms from the Fremouw Formation is the voltzialean conifers, represented by the pollen cone *Leastrobus fallaea* from the base of Mount Falla (Hermsen et al., 2007b). Historically, voltzialeans have been interpreted as an intermediate between the cordaites and conifers, but probably represent a grade of cone evolution at the base of the conifer complex rather than a natural group (Taylor and

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Grauvogel-Stamm, 1995; Rothwell et al., 2005; Hilton and Bateman, 2006, fig. 4). Ovules found in voltzialean cones are characterized either by bilateral or 180° rotational symmetry; some may have narrow wings and vascular bundles in the major plane of the integument (example *Hanskerpia hamiltonensis*, Rothwell et al., 2005). The size range of voltzialean ovules is compatible with that of the new ovules; however, to date none of these have been described with similar integument extensions.

5.3. Other taxa

Two groups of Mesozoic seed ferns are yet to be identified in the Fremouw Formation: the Caytoniales and Peltaspermales. Both groups occur in the Triassic of Gondwana but only as impression/compressions. Ovules of Caytoniales are small (2 mm), radial, and lack sclerotesta elaborations. Peltasperm ovules are also small and bilateral. The micropylar end of the seed is generally pointed, but may be rounded. The seed surface shows some ribs and strong folds, perhaps suggesting sclerified cells.

With the exception of *Parasciadopitys* from the Fremouw Formation, all other Triassic seed cones that have been described are preserved as compression/impressions. In addition to *Heidiphyllum*, Anderson and Anderson (1985) noted the presence of three types of conifer foliage in the Triassic of Gondwana: *Voltziopsis* Potonié (Voltziaceae), *Rissikia* Townrow (Podocarpaceae), and *Pagiophyllum* Heer (incertae sedis). However, there is insufficient evidence to demonstrate that there were several types of podocarps in Antarctica during the Triassic (Table 1; (Axsmith et al., 1998). Ovules of extant podocarps are characterized by the presence of a fleshy structure (epimatium), probably homologous to a scale (Tomlinson, 1992). In *Microstrobus* and *Phyllocladus* there is no ovule supporting structure (Tomlinson et al., 1989) so the absence of an epimatium does not rule out a podocarpacean affinity. The integument of ovules in the Podocarpaceae consists of a thick sclerified middle layer between two fleshy layers, with the inner one becoming membranous during maturation. Vascularization of the integument is highly variable within the family (Mill et al., 2004).

Compression specimens of ovule-bearing structures assigned to the ginkgophytes are documented in the Late Triassic Molteno Formation of South Africa (Anderson and Anderson, 2003). *Ginkgo* ovules have a tripartite integument comparable to that of cycads. The vascular system is different from both the cycads and *Probolosperma* since it consists only of two, rarely three, non-branching strands located in the inner fleshy layer (Chamberlain, 1935, p.203).

The presence of sclerotesta elaborations in *Probolosperma* distinguishes these seeds from all other Triassic ovules described to date. Two Late Triassic taxa from the Molteno Formation, however, must be mentioned here because of their unusual shape. *Alexia urceolus* (Anderson and Anderson, 2003) is a putative gymnospermous ovulate strobilus bearing pitcher-shaped structures that have been interpreted as cupules. The shape of these putative cupules is somewhat similar to that of *Probolosperma*, but they are significantly smaller, less than 3 mm long (Anderson and Anderson, 2003, p. 318) versus 6–10 mm for *Probolosperma*. Anderson and Anderson also illustrate an unnamed seed (Anderson and Anderson, 2003, p. 388, figs 1-3) that has an elongated shape, a ridged testa, and lateral extensions around the micropyle. The seed is a little more than 1 cm long and thus comparable in size to *Probolosperma*. The lateral extensions around the micropyle are, however, less developed than in *Probolosperma*.

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The morphology most similar to *Probolosperma* is found in Pennsylvanian trigonocarpalean (Medullosales) seeds. In *Pachytesta stewartii*, for example, the sclerotesta forms a basal chamber (Taylor and Delevoryas, 1964). In *Stephanospermum akenoides* from the Grand-Croix cherts of France, the sclerotesta forms a crown at the micropylar end (Combourieu and Galtier, 1985),whereas in *Polylophospermum stephanense*, also from Grand-Croix, teeth of the sclerotesta form a collar around both the micropyle and pedicel (Combourieu and Galtier, 1985). In noting these similar features we do not wish to imply any taxonomic affinity for *Probolosperma*, but rather to note a convergence of integumentary organization that may be related to some ecological or environmental pressures (e.g., pollination, dispersion mechanism, spatial arrangement of seeds, or habitat). A major difference is that the sclerotesta of trigonocarpaleans has radial symmetry whereas that of the new ovules is distinctly bilateral. Another similarity shared with the Medullosales is the presence of a pedicel in *Probolosperma,* a structure found in no other ovules from the Fremouw Formation. This may reflect the fact that they are the largest ovules in this flora and thus a stronger mechanism of attachment was needed. The presence of pitted tracheids in the vascular strands that enter the pedicel might also be linked to the large size of the strand.

Mitrospermum leeanum is a cordaitean seed from the Pennsylvanian of Iowa. It has a sclerotesta in the form of lateral wings and a large basal chamber that has been interpreted as a floating mechanism for dispersal in water (Kern and Andrews, 1946; Baxter, 1971). It differs from trigonocarpalean seeds by its strong bilateral symmetry, free nucellus, and thick integument, a set of characters also found in *Probolospermum.* It also is comparable in size. However *Mitrospermum leeanum* lacks a pedicel and differs from the new ovules by the anatomy of its integument which has a sclerified outer layer.

5.4. Diversity of gymnosperms in the Fremouw Formation

The number of reproductive structures versus vegetative structures known for each gymnosperm group in the Fremouw Formation is variable (Table 1). Stems assigned to the Corystospermales include *Kykloxylon* , with attached leaf bases, *Jeffersonioxylon* trunks (Del Fueyo et al., 1995; Cúneo et al., 2003) and a *Rhexoxylon*-like fragment of trunk (Taylor, 1992). The latter two genera are assigned to the corystosperms based on co-occurrence with *Dicroidium* foliage (Archangelsky and Brett, 1961; Cúneo et al., 2003; Bodnar, 2008), an exclusive association in the case of *Jeffersonioxylon* (Cúneo et al., 2003). This contrasts with the single species of ovulate structure described for the group. A reverse situation is found with the conifers in the Fremouw permineralized peat for which a single type of stem assigned to the Podocarpaceae, *Notophytum* (Archangelsky and Brett, 1961; Cúneo et al., 2003; Bodnar, 2008), has been described whereas the reproductive structures indicate the presence of other groups. The ovulate structures of *Antarcticycas* have not been identified to date, and the vegetative structures of *Petriellaea* and *Ignotospermum* remain unknown. *Probolosperma* represents a new taxon with novel architecture that enhances the known diversity of gymnosperms from the Triassic of Antarctica. The identification of corresponding vegetative structures might help resolve the affinities of this peculiar seed

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Table legend.

Table 1. Anatomically preserved spermatophytes previously documented from the Middle Triassic Fremouw Formation of Antarctica. 1: Meyer-Berthaud et al., 1993; 2: Taylor, 1992; 3: Del Fueyo et al., 1995, 4: Pigg, 1990; 5: Yao et al., 1995; 6: Klavins et al., 2002, 7: Taylor et al., 1994; 8: Smoot et al., 1985; 9: Hermsen et al., 2007a; 10: Klavins et al., 2003; 11: Meyer-Berthaud and Taylor, 1991; 12: Yao et al., 1997, 13: Hermsen et al., 2007b, 14: Perovich and Taylor, 1989.

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Figure legend

Fig. 1 Idealized reconstruction of *Probolosperma* seen from the side and from the base of the ovule. Since the shape of the sarcotesta is unknown, only the general aspect of the sclerotesta is represented here. A. Longitudinal section in primary plane. B. Longitudinal section in secondary plane, equivalent to Plate I, 3. C. Transverse section through the base of the ovule showing the sclerotesta forming a collar around the pedicel and small lateral expansions, equivalent to Plate I, 5.

Plate legends

Plate I. *Probolosperma antarcticum* gen. et sp. nov., permineralized ovules from the Middle Triassic of Antarctica. General features in longitudinal (1-4) and transverse (5-7) sections. Scale bar = 1 mm, except Fig. 7 = 500 µm. Sa: sarcotesta, P: pedicel.

1. Longitudinal section of ovule showing complete integument (left), with folded sarcotesta (Sa) and sclerotesta elaborations at the base and apex (arrows). Peel 16105 Ftop #1 still on block. Holotype.
2. Longitudinal section of ovule showing sclerotesta elaboration at the apex and base. Slide #23846 (peel 13587 Hbot #7)
3. Median longitudinal section of ovule sectioned in secondary plane, showing the entry of the vascular strand through the pedicel (arrow), basal elaboration of the sarcotesta surrounding the pedicel, and apical elaborations. Slide #23773 (peel 12597 Dbot #60, specimen α).
4. Longitudinal section through the base of an ovule showing the transition between the basal elaborations of the sarcotesta illustrated in 1 and 2. See text for detailed explanation. 4: slide #23796 (peel 10827 Ctop #80)
5. Transverse section of the ovule chalaza showing pedicel (P), basal collar-like elaboration of the sclerotesta, and lateral wings (arrows). Slide #23810 (peel 10827E#45)
6. Transverse section of the middle region of the ovule showing distinct flattening and small lateral wings (arrows). Slide #23803 (peel 10827E #5).
7. Transverse section of the apical region of an ovule showing the distinct flattening and bilaterally symmetrical elaboration of the sclerotesta. Slide # 23868 (peel 14374Gtop#1)

Plate II. *Probolosperma antarcticum* gen. et sp. nov., permineralized ovules from the Middle Triassic of Antarctica. Integument and vascularization.

1-4. Longitudinal sections of integument with the center of the ovule on the right in all images, Sa: sarcotesta, Sc: sclerotesta. 1-3. Holotype.

1. Integument showing the two layers of the sarcotesta, the sclerotesta, and the position of the endotesta (arrow). Surface of specimen in block 16105 Ftop before peel #1.
2. Outer layer of the sarcotesta showing palisade-like cells with thick outer and lateral walls. Scale bar = 20 µm. Slide #23748 (peel 16105 Ftop#2).
3. Transition area between sarcotesta and sclerotesta. Note the dark layer (center) between. Scale bar = 20 µm. Slide #23748 (peel 16105 Ftop#2).
4. Inner region of the sclerotesta, along with endotesta (E) and nucellus. Scale bar = 10 µm. Slide #23846 (peel 13587 Hbot#7).
5. Detail of the distal end of the nucellus. Scale bar = 250 µm. Slide #23749 (peel 16105 Ftop#3)
6. Base of the ovule showing attachment of the nucellus (arrows) and the cup of tracheids (T). Scale bar = 500 µm. Slide #23846 (peel 13587 Hbot #7)

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7. Transverse section of the pedicel showing the central vascular bundle. Note remains of sarcotesta (arrow) surrounding the pedicel. Scale bar = 250 µm. Slide #23811 (peel 10827 E#50).
8. Detail of the base of the ovule illustrated on Plate I, 3 showing the vascular strand extending through the pedicel. Scale bar = 250 µm. Slide #23773 (peel 12597 Dbot #60, specimen α).
9. Detail of tracheid pitting. Slide #23773 (peel 12597 Dbot #60).
10. Cross section showing a small bundle (arrow) in the inner region of the sarcotesta. Scale bar = 500 µm. Slide #23806 (peel 10827 E#20).

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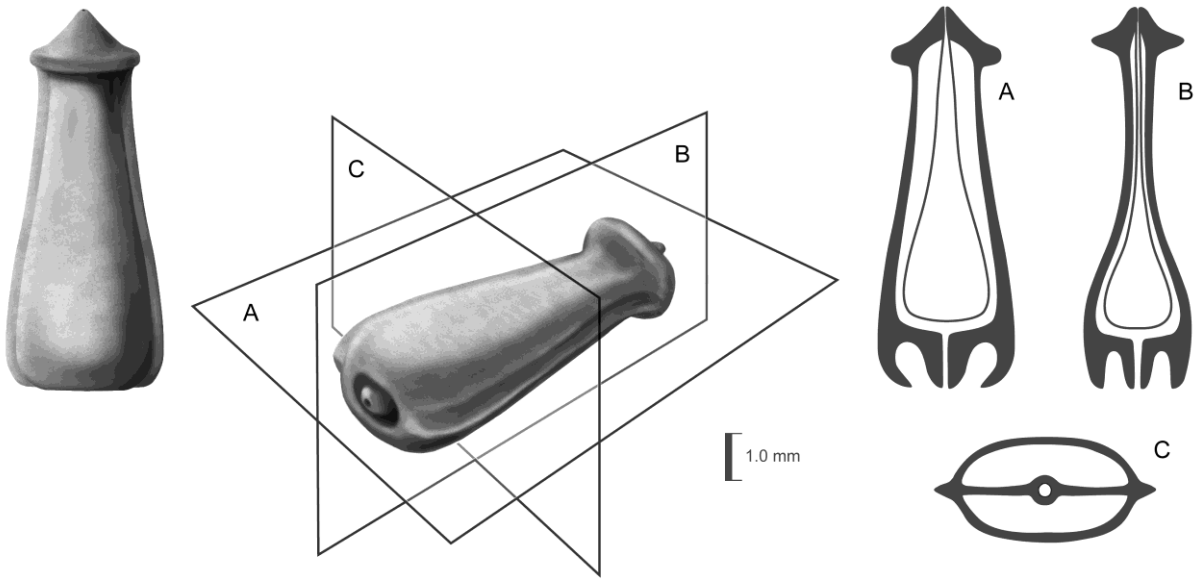

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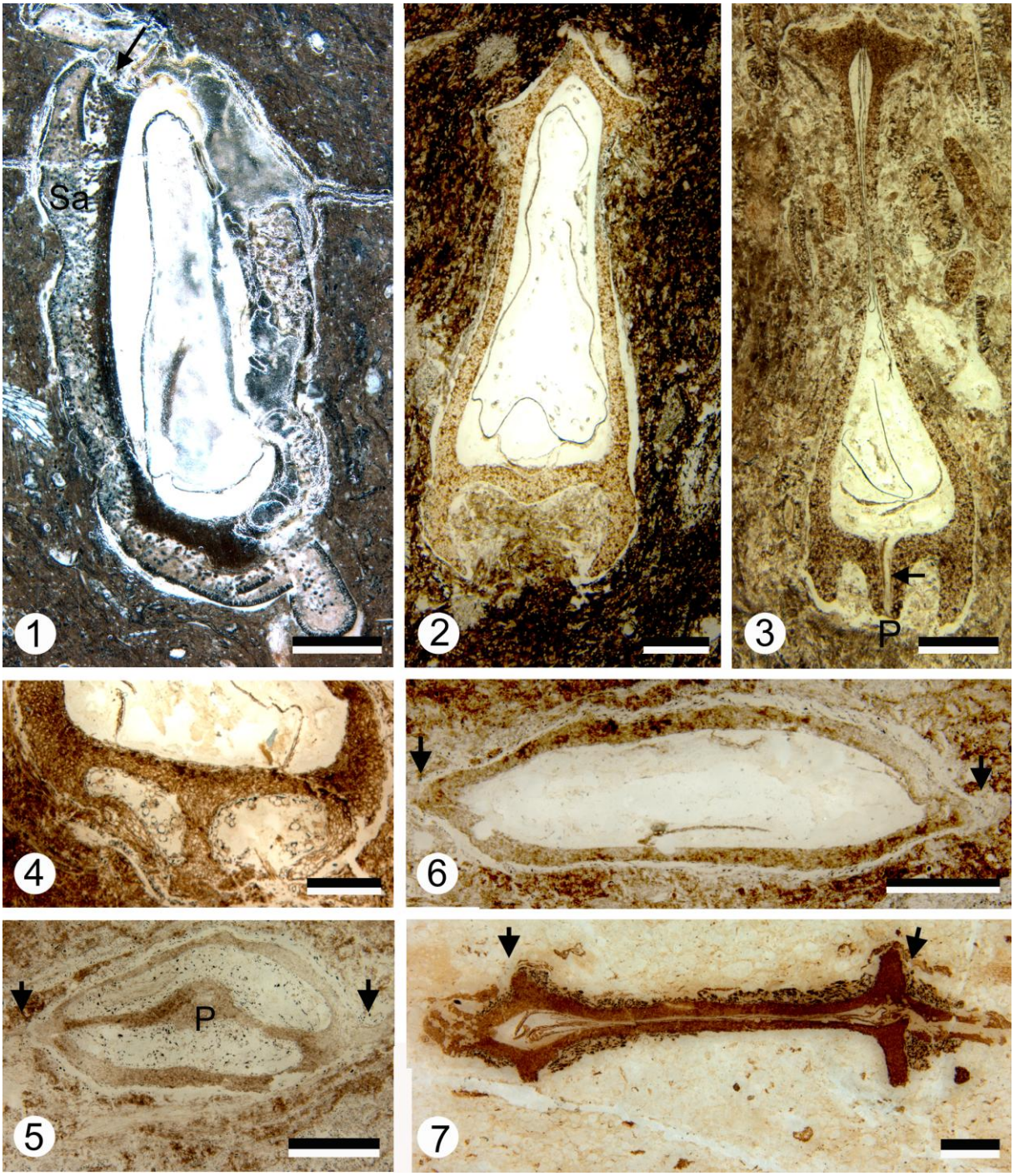

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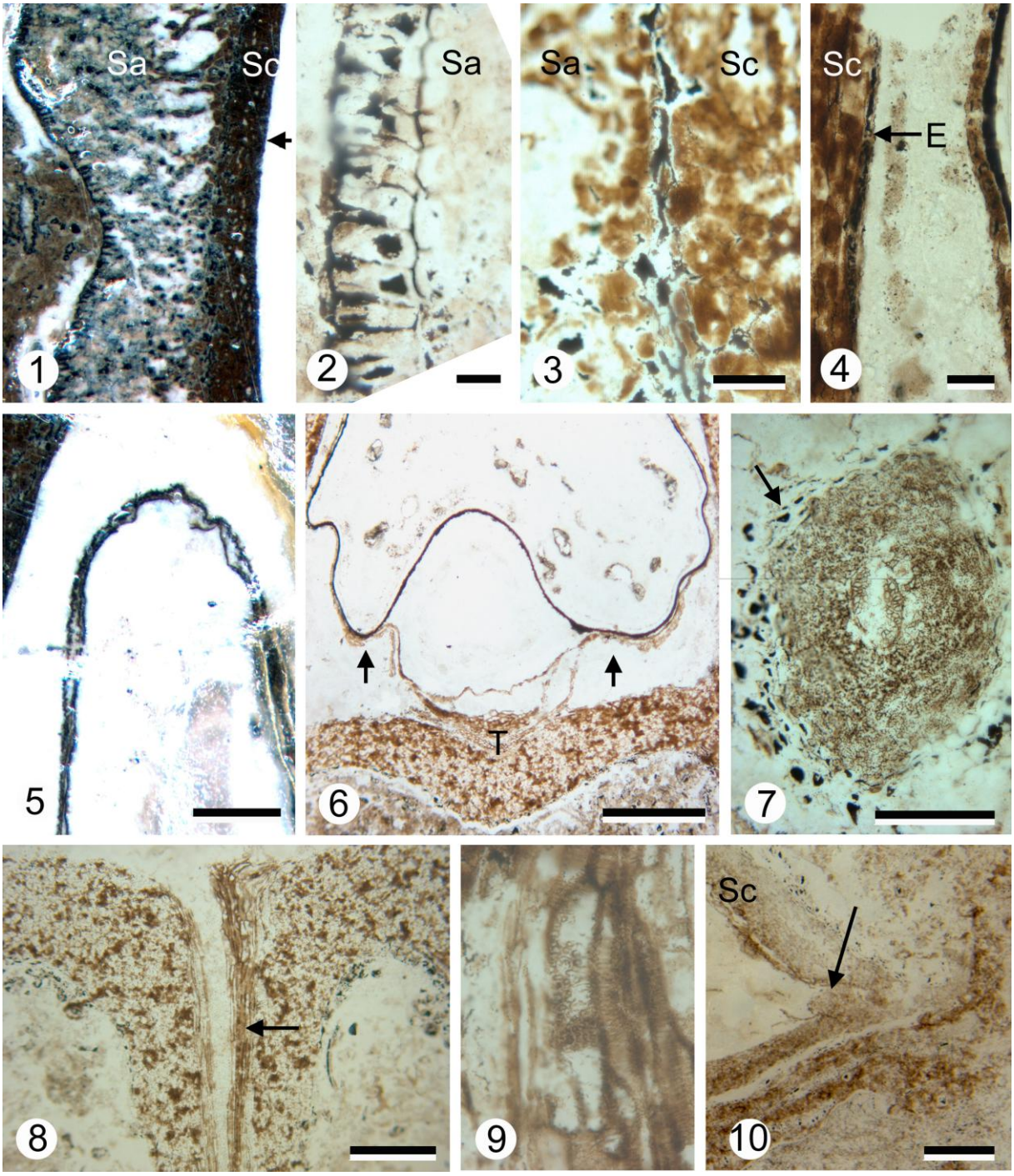

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