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

3
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14
15
16 **Abstract**

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

27
28
29 **Key-words:** Anisian, Triassic, Antarctica, ovule, anatomy, seed
30

31 **1. Introduction**

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

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

63 64 **2. Material and methods**

65 The specimens are preserved in peat blocks from the Beardmore Glacier area, Queen
66 Alexandra Range, central Transantarctic Mountains, Antarctica. They were collected at the
67 Fremouw Peak locality (84°17'41" S, 164°21'48" E) and at the base of Mount Falla, (84°21'S,
68 164°42'E). The permineralized peat occurs in the upper Fremouw Formation (Beacon
69 Supergroup, Barrett et al., 1986) and is early Middle Triassic (Anisian) in age based on
70 palynostratigraphy (Farabee et al., 1990). The blocks were cut into slabs and peeled using the
71 standard technique (Galtier and Phillips, 1999). The polished surfaces were etched in 49%
72 hydrofluoric acid then rinsed and peeled. Selected peels were mounted on microscope slides
73 using Eukitt® for observation and digital imagery. Cell and tissue measurements were made
74 using Wright Cell Imaging Facility's ImageJ software (Rasband, 1997–2008). Specimens,
75 peels, and slides are deposited in the Paleobotanical Collections, Natural History Museum and
76 Biodiversity Research Center, University of Kansas, under the specimen numbers 10827,

77 12597, 13587, 14374 and 16105, and slide accession numbers 23747–23888. Where several
78 ovules are present in some blocks they are designated by α , β , etc. in the figure legends.
79

80 **3. Systematics**

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

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

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

93 *Type species:*

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

95 *Holotype, designated herein:* Specimen in block 16105 Ftop (Plate I, 1; Plate II, 1-3),
96 including six cellulose acetate peels, three of which are mounted on microscope slides
97 (23747–23749)

98 *Paratypes, designated herein:* Two specimens from block 12597 Dbot (Plate I, 3; Plate II, 6-
99 7), including 125 cellulose acetate peels, 32 of which are mounted on microscope slides
100 (23750–2381); one specimen from block 10827 E (Plate I, 5-6; Plate II, 5), including 61
101 cellulose acetate peels, 13 of which mounted on microscope slides (23803–23813, 23889–
102 23890)

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

105 *Formation:* Fremouw Formation, Beacon Supergroup.

106 *Age:* Middle Triassic (Anisian).

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

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

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

120 121 **4. Description**

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

129 4.1. Integument

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

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

155 The most conspicuous part of the integument in *P. antarcticum* is the sclerotic layer (
156 = sclerotesta). Its thickness is variable, typically measuring 100–250 µm in the mid-region of
157 the ovule to more than 1 mm thick in zones where it forms the elaborations that are the
158 distinctive features at the apex and base of the ovule (Fig. 1). The sclerotesta is composed of
159 7–10 layers of sclereids; these are oriented parallel to the long axis of the ovule and are
160 hexagonal to circular in transverse section (Plate II, 1, 3). They are 10–18 µm in diameter, up
161 to 90 µm in length, and have pitted walls. In many cases, only the outline of the cells can be
162 seen where the walls are not preserved and are replaced by amorphous, opaque contents. In
163 the zones where the cell wall is well preserved, it is about 6 µm thick and surrounds a small
164 oval lumen (Plate II, 3).

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

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

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

184 4.2. Nucellus

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

192 4.3. Vascular System

194 A thick (about 85 μm in diameter) terete strand of tracheids enters the base of the
195 ovule (Fig. 1; Plate I, 3; Plate II, 7, 8) and expands to form a small cup where the nucellus is
196 attached (Plate II, 66). In the pedicel, the strand is composed of about 50 tracheids that are 5-
197 25 μm in diameter and up to 150 μm long. Most display scalariform thickenings but a few
198 possess crowded, multiseriate bordered pits (Plate II, 9). The disc at the base of the nucellus is
199 composed of 1-3 layers of tracheids. Successive cross sections through the base of the ovule
200 indicate two lateral vascular strands that extend out from the cup in opposite directions at the
201 base of the nucellus. The strands can be traced in the integument only in the basal third of the
202 ovule. In cross section, a vascular bundle is also present on the inner surface of the small
203 wing-like extensions of the sclerotesta (Plate II, 10). No vascular strands have been observed
204 in the sarcotesta.

206 5. Discussion

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

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

216
217 *5.1. Comparison with previously described ovules from the Fremouw Formation*

218 Corystosperms are the most abundant component of the permineralized flora from the
219 Fremouw Formation. Anatomically preserved, cupulate, ovule-bearing organs of
220 corystosperms are represented by the form species *Umkomasia resinosa* (Klavins et al., 2002).
221 Like *P. antarcticum*, ovules of *U. resinosa* are flattened in cross section. However,
222 *Umkomasia* ovules lack a pedicel and differ significantly in the morphology and anatomy of
223 the integument, which is much thinner (150 vs. 630 μm), mostly composed of thin-walled
224 cells, and devoid of sclerotesta extensions. The integument of *U. resinosa* ovules is also
225 characterized by the presence of secretory cavities, a character that links it with other
226 corystosperm organs from the same locality. The lack of a sclereid layer in the *Umkomasia*
227 ovules might be linked to an early developmental stage of the observed specimens (Klavins et
228 al., 2002). In extant gymnosperms, the integument of immature ovules is composed of thin-
229 walled cells with the differentiation of the sclerotesta occurring later in development. A
230 similar phenomenon has also been reported in fossil seeds (e.g. *Callospermarion*, Rothwell,
231 1971). However, while the well-differentiated sclerotestal layer observed in *Probolosperra*
232 might simply reflect a more advanced stage of integument development consistent with the
233 fact that all specimens are found dispersed, other characters indicate the two are distinct seed
234 types. Although the evidence to date suggests the Corystospermales were a diverse group, the
235 morphology and anatomy of their reproductive organs, where known in detail, are quite
236 similar throughout Gondwana. Therefore, we think it unlikely that the new ovules represent a
237 new genus among the corystosperms as the group is currently understood.

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

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

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

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

261
262 5.2. Comparison with taxa from the Fremouw Formation for which ovulate structures are
263 unknown

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

286 Putative podocarpaceous conifers are also represented in the Triassic of Antarctica by
287 stems assigned to *Notophytum krauselii* (Meyer-Berthaud and Taylor, 1991). Permineralized
288 trunks of *Jeffersonioxylon* have been compared to Podocarpaceae based on wood anatomy
289 (Del Fueyo et al., 1995), but were subsequently assigned to the Corystospermales on the basis
290 of an association only with *Dicroidium* leaves (Cúneo et al., 2003). Axsmith and collaborators
291 (1998) demonstrated that leaves of *N. krauselii* are similar to the common compression fossil
292 *Heidiphyllum elongatum* and may in fact be conspecific. Corresponding anatomically
293 preserved reproductive structures are unknown, but evidence from compression fossils
294 indicate that the seed cone *Telemachus elongatus*, originally assigned to the Voltziales
295 (Anderson, 1978), was probably produced by the same plant (Axsmith et al., 1998).
296 Compression specimens of *T. elongatus* are present in Antarctica in the Upper Triassic Lashly
297 and Falla Formations (Yao et al., 1995). While it is difficult to compare the anatomically
298 preserved ovules with compression specimens, the fact that the ovules of *T. elongatus* are
299 small (1.5–2 mm) and nearly spherical suggests that these taxa are distinct.

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

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

311 312 5.3. Other taxa

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

319 With the exception of *Parasciadopitys* from the Fremouw Formation, all other Triassic
320 seed cones that have been described are preserved as compression/impressions. In addition to
321 *Heidiphyllum*, Anderson and Anderson (1985) noted the presence of three types of conifer
322 foliage in the Triassic of Gondwana: *Voltziopsis* Potonié (Voltziaceae), *Rissikia* Townrow
323 (Podocarpaceae), and *Pagiophyllum* Heer (incertae sedis). However, there is insufficient
324 evidence to demonstrate that there were several types of podocarps in Antarctica during the
325 Triassic (Table 1; (Axsmith et al., 1998). Ovules of extant podocarps are characterized by the
326 presence of a fleshy structure (epimatium), probably homologous to a scale (Tomlinson,
327 1992). In *Microstrobis* and *Phyllocladus* there is no ovule supporting structure (Tomlinson et
328 al., 1989) so the absence of an epimatium does not rule out a podocarpacean affinity. The
329 integument of ovules in the Podocarpaceae consists of a thick sclerified middle layer between
330 two fleshy layers, with the inner one becoming membranous during maturation.

331 Vascularization of the integument is highly variable within the family (Mill et al., 2004).

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

338 The presence of sclerotesta elaborations in *Probolosperra* distinguishes these seeds
339 from all other Triassic ovules described to date. Two Late Triassic taxa from the Molteno
340 Formation, however, must be mentioned here because of their unusual shape. *Alexia urceolus*
341 (Anderson and Anderson, 2003) is a putative gymnospermous ovulate strobilus bearing
342 pitcher-shaped structures that have been interpreted as cupules. The shape of these putative
343 cupules is somewhat similar to that of *Probolosperra*, but they are significantly smaller, less
344 than 3 mm long (Anderson and Anderson, 2003, p. 318) versus 6–10 mm for *Probolosperra*.
345 Anderson and Anderson also illustrate an unnamed seed (Anderson and Anderson, 2003, p.
346 388, figs 1-3) that has an elongated shape, a ridged testa, and lateral extensions around the
347 micropyle. The seed is a little more than 1 cm long and thus comparable in size to
348 *Probolosperra*. The lateral extensions around the micropyle are, however, less developed
349 than in *Probolosperra*.

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

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

373 374 5.4. Diversity of gymnosperms in the Fremouw Formation

375 The number of reproductive structures versus vegetative structures known for each
376 gymnosperm group in the Fremouw Formation is variable (Table 1). Stems assigned to the
377 Corystospermales include *Kykloxylon*, with attached leaf bases, *Jeffersonioxylon* trunks (Del
378 Fueyo et al., 1995; Cúneo et al., 2003) and a *Rhexoxylon*-like fragment of trunk (Taylor,
379 1992). The latter two genera are assigned to the corystosperms based on co-occurrence with
380 *Dicroidium* foliage (Archangelsky and Brett, 1961; Cúneo et al., 2003; Bodnar, 2008), an
381 exclusive association in the case of *Jeffersonioxylon* (Cúneo et al., 2003). This contrasts with
382 the single species of ovulate structure described for the group. A reverse situation is found
383 with the conifers in the Fremouw permineralized peat for which a single type of stem assigned
384 to the Podocarpaceae, *Notophytum* (Archangelsky and Brett, 1961; Cúneo et al., 2003;
385 Bodnar, 2008), has been described whereas the reproductive structures indicate the presence
386 of other groups. The ovulate structures of *Antarcticycas* have not been identified to date, and
387 the vegetative structures of *Petriellaea* and *Ignotospermum* remain unknown. *Probolosperra*
388 represents a new taxon with novel architecture that enhances the known diversity of
389 gymnosperms from the Triassic of Antarctica. The identification of corresponding vegetative
390 structures might help resolve the affinities of this peculiar seed

391 392 393 **Acknowledgments**

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521 **Table legend.**

522 **Table 1.** Anatomically preserved spermatophytes previously documented from the Middle
523 Triassic Fremouw Formation of Antarctica. 1: Meyer-Berthaud et al., 1993; 2: Taylor, 1992;
524 3: Del Fueyo et al., 1995, 4: Pigg, 1990; 5: Yao et al., 1995; 6: Klavins et al., 2002, 7: Taylor
525 et al., 1994; 8: Smoot et al., 1985; 9: Hermsen et al., 2007a; 10: Klavins et al., 2003; 11:
526 Meyer-Berthaud and Taylor, 1991; 12: Yao et al., 1997, 13: Hermsen et al., 2007b, 14:
527 Perovich and Taylor, 1989.

528

529

530 **Figure legend**

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

537
538 **Plate legends**

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

- 542 1. Longitudinal section of ovule showing complete integument (left), with folded sarcotesta
543 (Sa) and sclerotesta elaborations at the base and apex (arrows). Peel 16105 Ftop #1 still on
544 block. Holotype.
- 545 2. Longitudinal section of ovule showing sclerotesta elaboration at the apex and base. Slide
546 #23846 (peel 13587 Hbot #7)
- 547 3. Median longitudinal section of ovule sectioned in secondary plane, showing the entry of the
548 vascular strand through the pedicel (arrow), basal elaboration of the sarcotesta surrounding
549 the pedicel, and apical elaborations. Slide #23773 (peel 12597 Dbot #60, specimen α).
- 550 4. Longitudinal section through the base of an ovule showing the transition between the basal
551 elaborations of the sarcotesta illustrated in 1 and 2. See text for detailed explanation. 4: slide
552 #23796 (peel 10827 Ctop #80)
- 553 5. Transverse section of the ovule chalaza showing pedicel (P), basal collar-like elaboration of
554 the sclerotesta, and lateral wings (arrows). Slide #23810 (peel 10827E#45)
- 555 6. Transverse section of the middle region of the ovule showing distinct flattening and small
556 lateral wings (arrows). Slide #23803 (peel 10827E #5).
- 557 7. Transverse section of the apical region of an ovule showing the distinct flattening and
558 bilaterally symmetrical elaboration of the sclerotesta. Slide # 23868 (peel 14374Gtop#1)

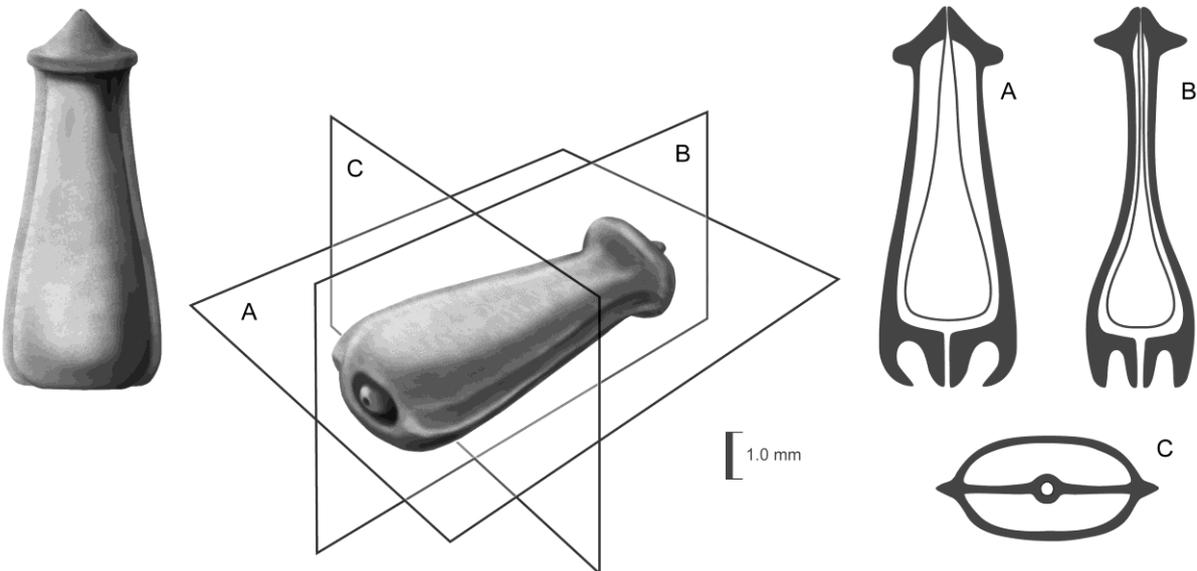
559
560 **Plate II.** *Probolosperma antarcticum* gen. et sp. nov., permineralized ovules from the Middle
561 Triassic of Antarctica. Integument and vascularization.

- 562 1-4. Longitudinal sections of integument with the center of the ovule on the right in all
563 images, Sa: sarcotesta, Sc: sclerotesta. 1-3. Holotype.
- 564 1. Integument showing the two layers of the sarcotesta, the sclerotesta, and the position of the
565 endotesta (arrow). Surface of specimen in block 16105 Ftop before peel #1.
- 566 2. Outer layer of the sarcotesta showing palisade-like cells with thick outer and lateral walls.
567 Scale bar = 20 μ m. Slide #23748 (peel 16105 Ftop#2).
- 568 3. Transition area between sarcotesta and sclerotesta. Note the dark layer (center) between.
569 Scale bar = 20 μ m. Slide #23748 (peel 16105 Ftop#2).
- 570 4. Inner region of the sclerotesta, along with endotesta (E) and nucellus. Scale bar = 10 μ m.
571 Slide #23846 (peel 13587 Hbot#7).
- 572 5. Detail of the distal end of the nucellus. Scale bar = 250 μ m. Slide #23749 (peel 16105
573 Ftop#3)
- 574 6. Base of the ovule showing attachment of the nucellus (arrows) and the cup of tracheids (T).
575 Scale bar = 500 μ m. Slide #23846 (peel 13587 Hbot #7)

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