

The background of the cover features three distinct fossil images. The top left shows a dark, branching plant fossil on a light-colored rock matrix. The top right shows a large, white, teardrop-shaped fossil, possibly a seed or fruit, with reddish-brown veins. The bottom half of the cover is dominated by a large, detailed fossil of a plant stem with a prominent vascular network, showing circular and polygonal cells.

TRANSFORMATIVE PALEOBOTANY

PAPERS TO COMMEMORATE THE LIFE AND LEGACY OF THOMAS N. TAYLOR

EDITED BY MICHAEL KRINGS, CARLA J. HARPER, NÉSTOR RUBÉN CÚNEO, AND GAR W. ROTHWELL



Transformative Paleobotany

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Pachytestopsis tayloriorum gen. et sp. nov., an Anatomically Preserved Glossopterid Seed From the Lopingian of Queensland, Australia

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1. INTRODUCTION

Permian plant-bearing deposits of Gondwana contain a broad array of isolated, dispersed seeds with uncertain affinities. Pant et al. (1985) recognized more than 30 genera and more than 90 species of dispersed seeds from the Permian of Gondwana, and several more have been described and illustrated subsequently (e.g., McLoughlin, 1992; Bordy and Prevec, 2008; de Souza and Iannuzzi, 2009; Tewari et al., 2012; Edirisooriya et al., 2018). In most cases, these seeds are preserved as adpressions and provide only very limited information on external morphology, detracting from their systematic appraisal and inhibiting confident association with co-occurring foliage or fructifications. Anatomically preserved Gondwanan Permian seeds are rare and confined to a few exceptional deposits of silicified peat in Antarctica and eastern Australia (Gould and Delevoryas, 1977; McLoughlin, 1990c, 1992; Pigg and Trivett, 1994; Holdgate et al., 2005; Ryberg, 2010; Ryberg and Taylor, 2013). Anatomically preserved seeds recovered from one Lopingian (upper Permian) silicified peat bed at the Homevale locality in the Bowen Basin, Australia, offer an opportunity to resolve the architecture of probable glossopterid disseminules and to infer associations with enigmatic glossopterid fructifications. Recent cladistic analyses of major seed-plant groups highlight seed architectural features (e.g., platyspermy versus radiospermy and number and structure of integumentary layers) as key characters for differentiating

gymnosperm clades (Crane, 1985; Nixon et al., 1994; Rothwell and Serbet, 1994; Doyle, 2006; Hilton and Bateman, 2006). Therefore, a thorough understanding of seed architecture may help clarify the relationships between glossopterids and other seed plants and provide insights into the anatomical diversity and ecological strategies of this enigmatic plant group.

Here, we describe a new anatomically preserved seed that is substantially larger than forms recorded previously from the Homevale permineralized peat deposits. We also document the presence of pollen entrapped in the micropyle of the seeds. Based on these observations, we infer affinities of the seeds and discuss the implications for coding of characters in gymnosperm phylogenies.

2. GEOLOGICAL SETTING

The studied fossil material derives from the Fort Cooper Coal Measures, the middle coal-bearing unit of the Lopingian (upper Permian) Blackwater Group in the Homevale–Hail Creek area of the northeastern part of the Bowen Basin, Queensland, Australia. The Fort Cooper Coal Measures are around 400 m thick in the Homevale and Hail Creek areas and consist predominantly of green, volcanolithic sandstone, carbonaceous and siliceous shale, numerous thin tuff beds, and minor coal, silicified peat, and conglomerate (Goscombe, 1975; Hutton et al., 1991). Exposures are discontinuous and best represented by the more erosion-resistant silicified beds that form low

strike-ridges. The silicified peat hosting the fossil seeds described in this study occurs as a thin lens within a siltstone- and sandstone-dominated succession rich in volcanogenic detritus. Siltstones adjacent to the silicified peat lens are rich in impressions of foliage, stems, and roots of glossopterid gymnosperms and osmundaceous ferns. The abundance of tuffaceous beds is the principal feature used to correlate the upper part of the Fort Cooper Coal Measures with the Burngrove Formation in the central part of the Bowen Basin, the upper Black Alley Shale or lower Bandanna Formation in the southwestern sector of the basin, and the Kaloola Member of the Baralaba Coal Measures in the southeastern part of the basin (Koppe, 1978; Fielding et al., 1990; Matheson, 1990). Equivalent plant macrofossil assemblages are also represented in these units (Rigby, 1972; Gould and Delevoryas, 1977; McLoughlin, 1990c, 1992, 1994a,b). The lower part of the Fort Cooper Coal Measures is possibly correlative with the Fair Hill and upper Peawaddy formations in the central and southwestern Bowen Basin, respectively. A Lopingian (late Permian) age has been proposed for the tuff-rich interval of the Blackwater Group throughout the Bowen Basin based on palynomorph assemblages assignable to the upper Stage 5b–c (*Microreticulatisporites bitriangularis*–*Triplexisporites playfordii*) Palynozone of Price (1983) or the APP5 Zone of Price (1997). Draper et al. (1990), Briggs (1991), and Shi et al. (2010) tentatively assigned these formations to the Maokouan–Wuchiapingian stages. However, recent radiometric dates (CA-IDTIMS U–Pb dating of zircons from tuffs) obtained by Laurie et al. (2016) for these units in the southern Bowen Basin are in the range of 254.10 ± 0.09 – 252.54 ± 0.05 Ma, indicating a Changhsingian age.

The Fort Cooper Coal Measures are interpreted to have been deposited within predominantly small-scale fluvial channels and extensive low-energy, lacustrine and paludal environments subject to regular extensive blanketing by air-fall tuffs (Hutton et al., 1991). Palaeocurrent data from the Hail Creek area indicate variable sediment transport directions to the southwest and southeast (Jensen, 1975).

Silicified peat lenses in the Homevale to Hail Creek areas have been studied since the early 1970s as a source of anatomically preserved plant fossils. Taxa previously described from the silicified peats near Homevale include the osmundaceous fern axis *Palaeosmunda williamsii* Gould (1970), glossopterid root *Vertebraria indica* Royle (Gould, 1975), leaf *Glossopteris homevalensis* Pigg and McLoughlin (1997), an ovuliferous *Dictyopteridium*-like fructification *Homevaleia gouldii* Nishida et al. (2007), and a microsporangiate organ *Ediea homevalensis* Nishida et al. (2013), together with various dispersed, unnamed sporangia (Gould and Delevoryas, 1977) and shoot apices (see Chapter 8). However, significant assemblages of as yet undescribed plant and fungal remains are preserved anatomically in the permineralized peats and as impressions in overlying siltstones at this locality (McLoughlin, 1990c).

3. MATERIAL AND METHODS

The material was collected during field work by S.M. and A.N.D. in February 1994 and is held in the palaeontological collections of the Swedish Museum of Natural History, Stockholm. It appears that material cited to be from Homevale in some previous investigations derives from different peat lenses within the Fort Cooper Coal Measures located approximately 2–3 km to the southwest of the source of material in the present study and close to the operational area of Rio Tinto's Hail Creek Coal Mine (Nishida et al., 2007). Material in our study derives from a lens of silicified peat extending laterally over several meters and with a vertical extent of <1 m located at $21^{\circ}28'16.63''\text{S}$, $148^{\circ}25'56.12''\text{E}$, here designated locality HV6 (Fig. 9.1).

Blocks of the silicified peat were prepared via petrographic thin sectioning and the cellulose-acetate peel technique as outlined by Galtier and Phillips (1999). Optimal results for peels were obtained by etching the polished rock surfaces for 60–90 s in 48% hydrofluoric acid and then bonding a 50- μm -thick cellulose acetate sheet to the etched surface. Peels were then mounted on microscope slides using Histomount (National Diagnostics). In all cases, better resolution of anatomical details was obtained from petrographic thin sections than from acetate peels. Slides were prepared manually to thicknesses of 35–50 μm , depending on the optimal clarity of the plant cell structures, and examined and photographed with the use of Olympus BH-2 and Zeiss Axioskop 2 Plus transmitted light microscopes equipped with an Olympus DP-71 digital camera system. Brightness, contrast, and saturation were adjusted using Adobe Photoshop image processing software. Two specimens (NRMS089696 and NRMS089697) consisting of seed-bearing chert blocks (c. $5 \times 10 \times 10$ mm) were analyzed using synchrotron X-ray tomographic microscopy at the TOMCAT beam-line of the Swiss Light Source, Paul Scherrer Institute (Villigen, Switzerland). However, contrast between the matrix and the fossils was not sufficient to obtain well-resolved anatomical details from these specimens, and images from those analyses are not included here.

4. RESULTS

Order Dictyopteridiales McLoughlin ex Doweld, 2001 (=Glossopteridales sensu Pant, 1982)

Family uncertain

Genus *Pachytestopsis* McLoughlin, Bomfleur et Drinnan gen. nov.

Diagnosis: Seeds platyspermic, medium-sized (c. 5–11 mm long), flattened ovoid, with rounded base, tapered apex, and narrow wing. Seed coat differentiated into three major layers: a multistratified exotesta, a mesotesta incorporating outer thin-walled and inner sclerenchymatous layers separated by an irregular boundary, and a thin endotesta.

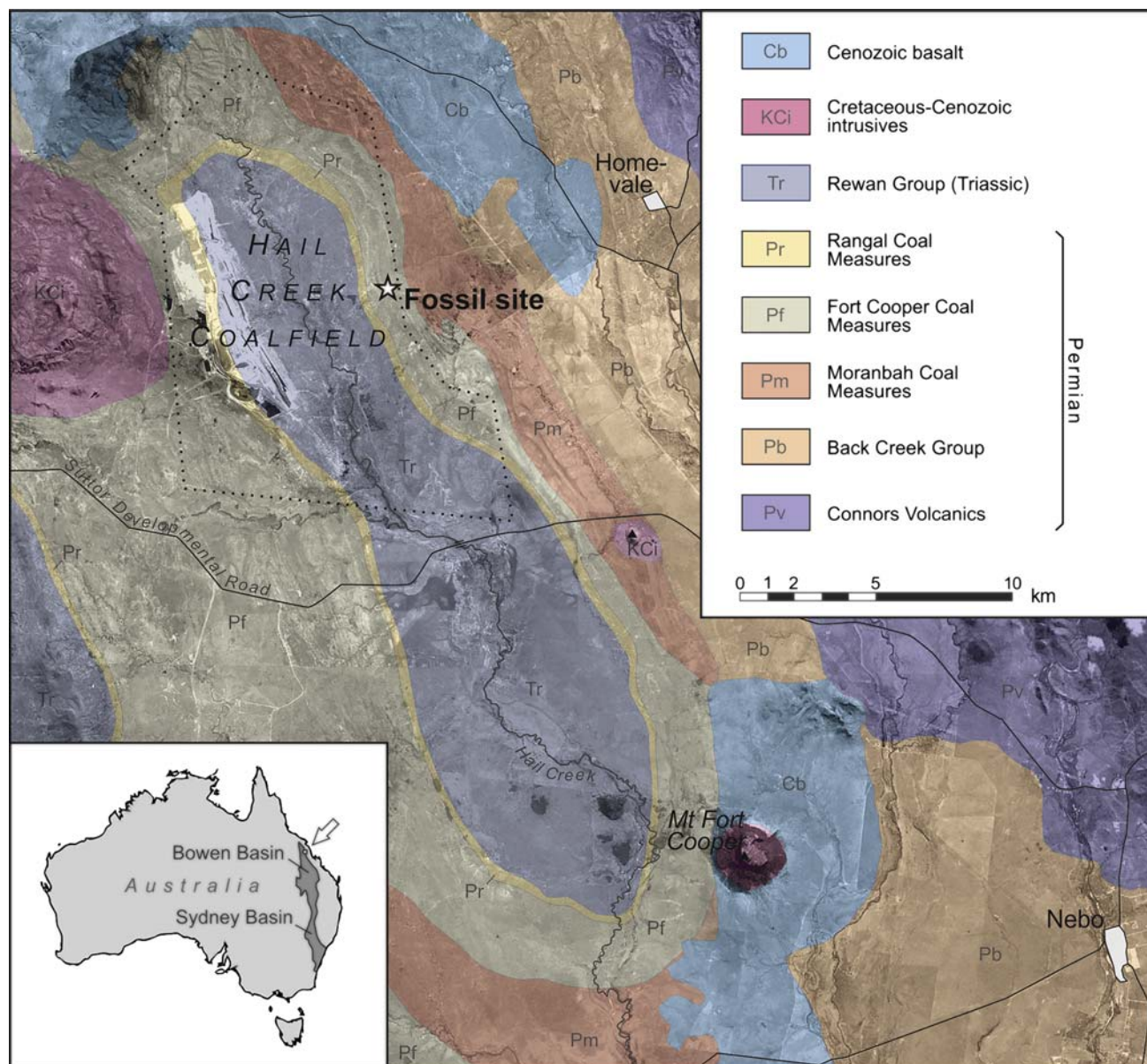


FIGURE 9.1 Geological map of the Hail Creek–Homevale area superimposed on a Landsat-derived Google Earth digital topographic image (Map data: Google, DigitalGlobe: 2018) of the area; the fossil site (designated HV6 in the text) is indicated by a star.

Lateral wings extending in primary plane from seed base to micropylar apex. Mesotesta c. 0.5 mm thick, with irregular boundary between inner and outer layers. Vasculature restricted to seed base and supplying nucellar pad.

Etymology: The suffix *-opsis* indicates similarity to the genus *Pachytosta* Brongniart; both names refer to the thick and heavily sclerified seed coats (*G. pachys*, thick; Lat. *testa*, shell).

Type species: *Pachytostopsis tayloriorum* McLoughlin et al. sp. nov. (here designated).

Remarks: The new genus is erected to accommodate platyspermic, winged seeds with a notably thick mesotesta incorporating a distinctly sculptured boundary between the inner and outer layers. Other anatomically preserved Gondwanan platyspermic seeds have markedly thinner seed coats,

are much smaller, or have apparent radial symmetry or minimal development of the lateral wings (Gould and Delevoryas, 1977; Smoot and Taylor, 1986; Taylor and Taylor, 1987; McLoughlin, 1992; Klavins et al., 2001; Holdgate et al., 2005; Nishida et al., 2007; Ryberg, 2010; Ryberg and Taylor, 2013).

***Pachytostopsis tayloriorum* McLoughlin et al. sp. nov.**
Holotype: NRMS089801-01-01 (here designated).

Type locality, unit, and age: Fossil site HV6, northern Bowen Basin, Queensland, Australia (Fig. 9.1); Fort Cooper Coal Measures; Changhsingian.

Additional material: See Appendix 1.

Type locality: Small, roadside outcrop (HV6: Fig. 9.1) near the central eastern boundary of the Hail Creek Coalfield, situated c. 10 km WSW of Homevale and c. 35 km NW of Nebo (Queensland, Australia).

Type stratum and age: Fort Cooper Coal Measures (Blackwater Group), Bowen Basin; Changhsingian (late Permian).

Etymology: The specific epithet is chosen in honour of Professors Thomas and Edith Taylor (University of Kansas) for their contributions to our knowledge of the anatomy and biology of glossopterid gymnosperms.

Diagnosis: Seed coat consisting of lignified exotesta with epidermis and hypodermis c. 2–3 cell layers thick composed of thickened prismatic cells; mesotesta of longitudinally arranged cells differentiated into narrow outer layer of thin-walled cells and inner layer of sclereids; and parenchymatous endotesta. Exotesta forming a pair of thin lateral wings in primary plane, of more-or-less even width from base to micropyle, containing a narrow core of outer mesotestal parenchyma. Inner mesotesta up to 600 μm thick with an outer boundary of irregular projections or ridges. Vasculature consisting of a terete strand entering straight through the chalaza and bifurcating and abruptly terminating in a discoidal to cup-shaped nucellar pad; testa is otherwise unvascularized. Basal nucellar pad up to 230 μm thick, tapering distally into cutinized nucellar wall with straight longitudinal anticlinal cell walls and oblique end walls. Megaspore membrane <10 μm thick.

Description: Seed 5–11 mm long, 5–10.1 mm wide in the primary plane (incorporating narrow wings), 1.2–3.5 mm thick in the secondary plane, typically flattened ovoid with 180-degree rotational symmetry (Plate I, 1–5). All specimens are detached from other organs. Seed integument consists of robust exotesta, two-layered mesotesta, and thin endotesta.

Exotesta consisting of a single layer of epidermal cells underlain by a robust hypodermis two or three cells thick (Plate II, 1–4). Epidermal cells rectangular prismatic, 14–(20)–26 μm wide and deep, 80–(110)–300 μm long, slightly bulbous on the outer surface, and covered by a 3- μm -thick cuticle (Plate II, 3 and 5). Epidermal cells having strongly thickened walls, with the lumen almost entirely occluded (Plate II, 3). Hypodermal cells in well-regimented layers; cells increasing in diameter with each layer towards the seed interior (Plate II, 1–4). Outermost hypodermal layer consisting of cylindrical or rectangular prismatic cells 19–(30)–43 μm wide and deep, and 150–(195)–420 μm long with transverse or tapered end walls. Cell sizes increasing to a maximum of 90 μm wide, 52 μm deep, and 320 μm long in innermost hypodermal layer. Hypodermal cell walls incorporating robust lamellar thickenings that typically occlude most of lumen (Plate II, 3).

Mesotesta typically 0.5–0.6 mm thick, consisting of two layers: an outer layer of delicate, spongy parenchyma cells and an inner layer of sclereids (Plate II, 1 and 2). Boundary between mesotesta layers sharp but irregular or ragged, giving both layers variable thickness (Plate I, 1–5). Outer layer of mesotesta typically 80–150 μm thick, locally reduced to single cell or absent, well developed along winged flanks of seeds, and expanded near apex up to

300 μm thick; consisting of oblong cells, variably shaped in cross-section, up to 260 μm long and 14–(40)–80 μm in diameter with walls c. 0.6 μm thick; cells are commonly compressed or degraded, leaving a cavity (Plate II, 1, 2, 4, and 5). Inner layer of mesotesta very robust, commonly with intense mineral staining, and 250–600 μm wide (locally representing the entire thickness of mesotesta); cells of inner layer of mesotesta are cylindrical, rectangular, or hexagonal prismatic, aligned longitudinally, 25–75 μm in diameter and 60–190 μm long, generally short and broad near contact with outer layer, and narrow and elongate near contact with endodermis; walls are thickened with concentric lamellae to almost complete occlusion of lumen (Plate II, 1, 2, and 6–8). Lamellar thickenings commonly delaminated from the outer cell wall, giving an “exploded” appearance (Plate II, 6). Cells of the inner layer of the mesotesta traversed by numerous radial pores up to 2 μm in diameter and 30 μm long (i.e., extending through the full width of cell wall; Plate II, 7 and 8). Inner layer of mesotesta expanded basally up to 0.92 mm wide, flanking chalazal vascular strand (Plate I, 1 and 2).

Endotesta 30–60 μm thick, best developed at winged flanks of seed (Plate II, 9), parenchymatous, composed of longitudinally orientated, rectangular to hexagonal prismatic (but commonly compressed) cells, 10–(20)–50 μm wide in tangential transverse dimension, 5–(10)–20 μm wide in radial transverse dimension, up to 100 μm long, and with walls c. 0.5 μm thick (Plate II, 6). Boundary between endotesta and mesotesta sharp, but endotestal cells commonly degraded.

Marginal wings well developed from base to apex of seed, reaching maximal width around mid-length. Wings consisting of an extension of the exotesta together with a thin, commonly compressed or degraded core of outer mesotestal tissue two or three cells thick (Plates I, 4, 5 and III, 2). Wing hypodermis generally reduced to single-cell thickness. Wings typically c. 0.75 mm wide and up to 300 μm thick (wedge shaped in transverse section) basally (Plate IV, 1), 1.2 mm wide, and of even thickness (200 μm) medially (Plate I, 4 and 5), 0.7 mm wide, and consistently thin (c. 60 μm) apically.

Micropyle ill preserved, represented by a narrow (10–20 μm wide) apical canal through seed integument leading to a pollen chamber apical to a contracted nucellus (Plate V, 4). Up to 20 pollen grains preserved in pollen chamber (Plate VI, 1–3 and 12). No obvious elaboration of exotesta around micropyle.

Base of the seed rounded with a 500- μm -wide, 250- μm -deep, chalazal pocket representing detachment scar (Plate I, 2). Vascular supply to seed represented by terete strand entering straight through thickened chalazal integument (Plate IV, 1), then forking and terminating abruptly in nucellar pad (Plate IV, 3 and 4). Integument otherwise unvascularized. Xylem strand 26–77 μm wide, surrounded by a zone of transfusion tissue 48–66 μm wide consisting of thin-walled cells 9–20 μm in diameter, c. 175 μm long

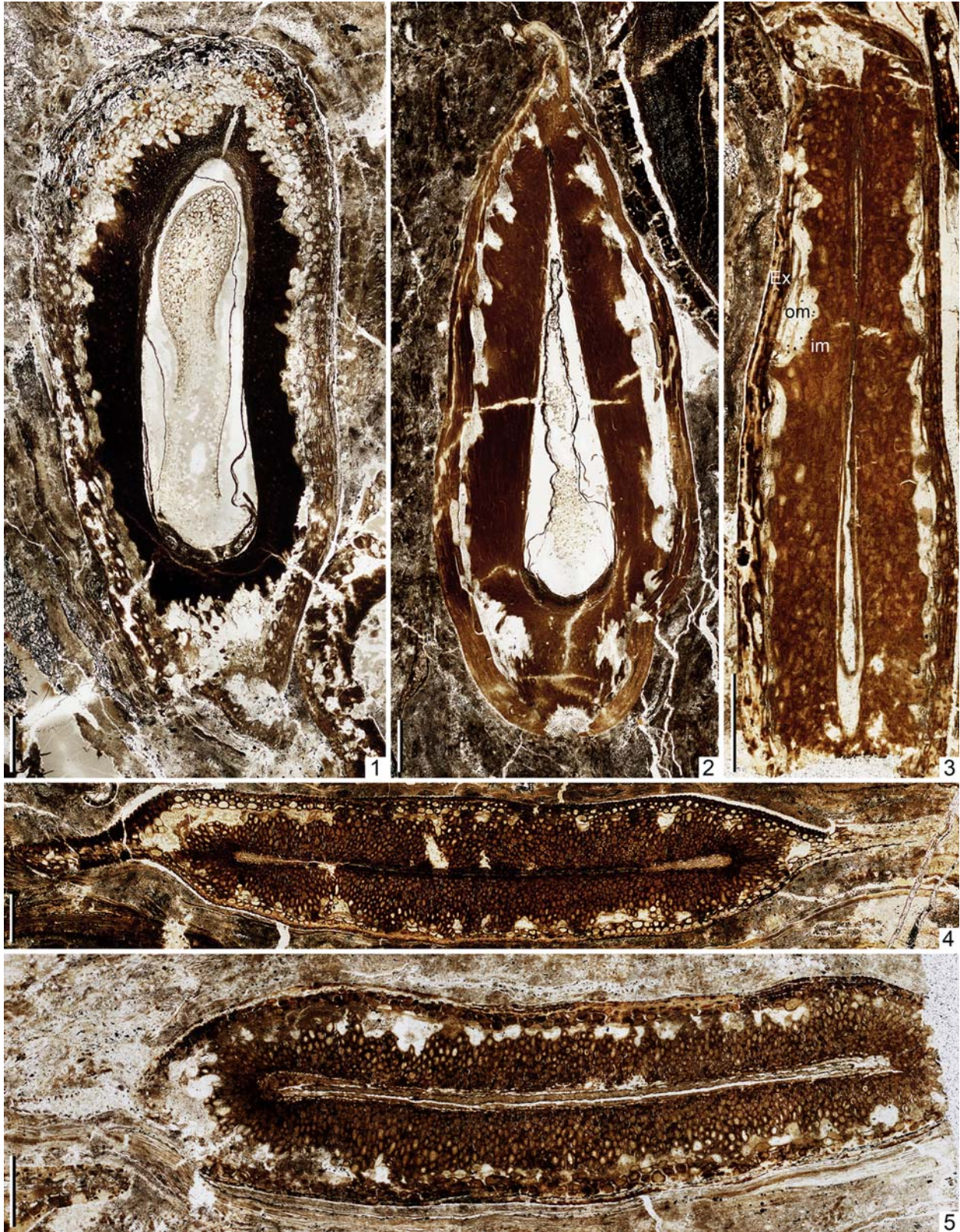


PLATE 1 *Pachytestopsis tayloriorum* gen. et sp. nov. (1) Holotype: oblique to near-longitudinal section of seed with well-developed gametophyte and sarcotesta expanded into a wing in the upper part; NRMS089801-01-01. (2) Near-longitudinal section of seed with well-differentiated integument layers, chalazal pocket, and remnants of nucellus and megagametophyte; NRMS089801-01-02. (3) Longitudinal section of seed in plane of narrowest dimension, *ex*, exotesta; *im*, inner mesotesta, *om*, outer mesotesta; NRMS089799-04-01. (4) Transverse section of seed showing well-developed wings; NRMS089799-02-01. (5) Transverse section of seed showing differentiation of integumentary layers; NRMS089799-04-02. Scale bars = 500 µm.

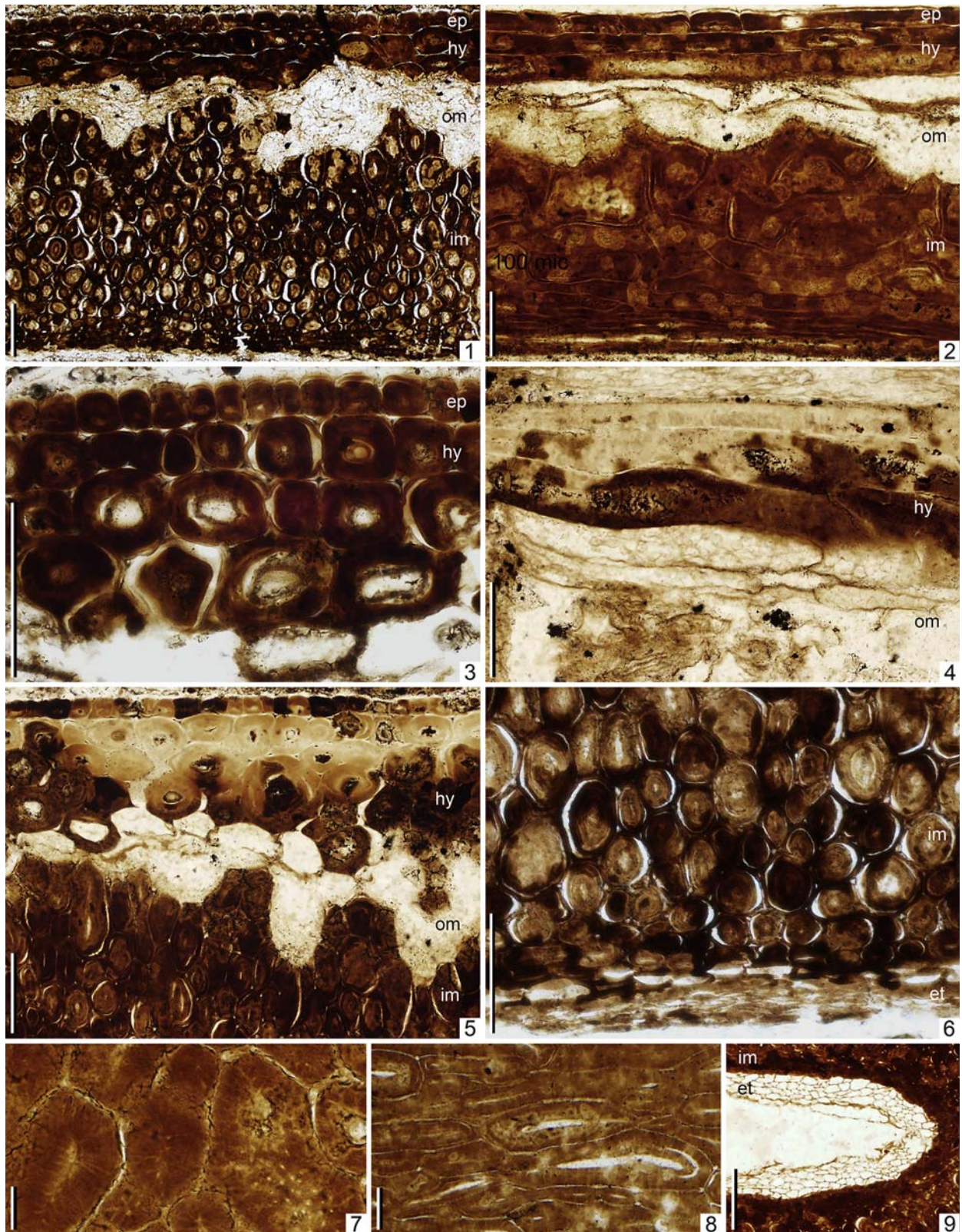


PLATE II Details of *Pachytestopsis tayloriorum* gen. et sp. nov. integument. (1) Exotesta (epidermis and hypodermis), and two-layered mesotesta in transverse section; NRMS 124914-05. (2) Exotesta and two-layered mesotesta in longitudinal section; NRMS089799-04-01. (3) Exotesta in transverse section; NRMS089799-06-01. (4) Exotesta and thin-walled cells of outer mesotesta in longitudinal section (seed axis horizontal); NRMS089799-03-01. (5) Remnant cells of outer mesotesta between portions of exotesta (top) and inner mesotesta (bottom); NRMS089799-03-02. (6) Concentrically thickened cells of inner mesotesta (top) and thin endotesta cells (bottom); NRMS089799-04-02. (7) Enlargement of inner mesotesta cells with radial pitting in transverse section; NRMS124926-03-01. (8) Enlargement of inner mesotesta cells with radial pitting in longitudinal section; NRMS124926-03-01. (9) Portion of compressed seed showing well-preserved endotesta; NRMS089799-03-03. For all figures: *ep*, epidermis; *et*, endotesta; *hy*, hypodermis; *im*, inner mesotesta; *om*, outer mesotesta. Scale bars for 1–6, 9 = 100 μ m; for 7 = 20 μ m; for 8 = 50 μ m.

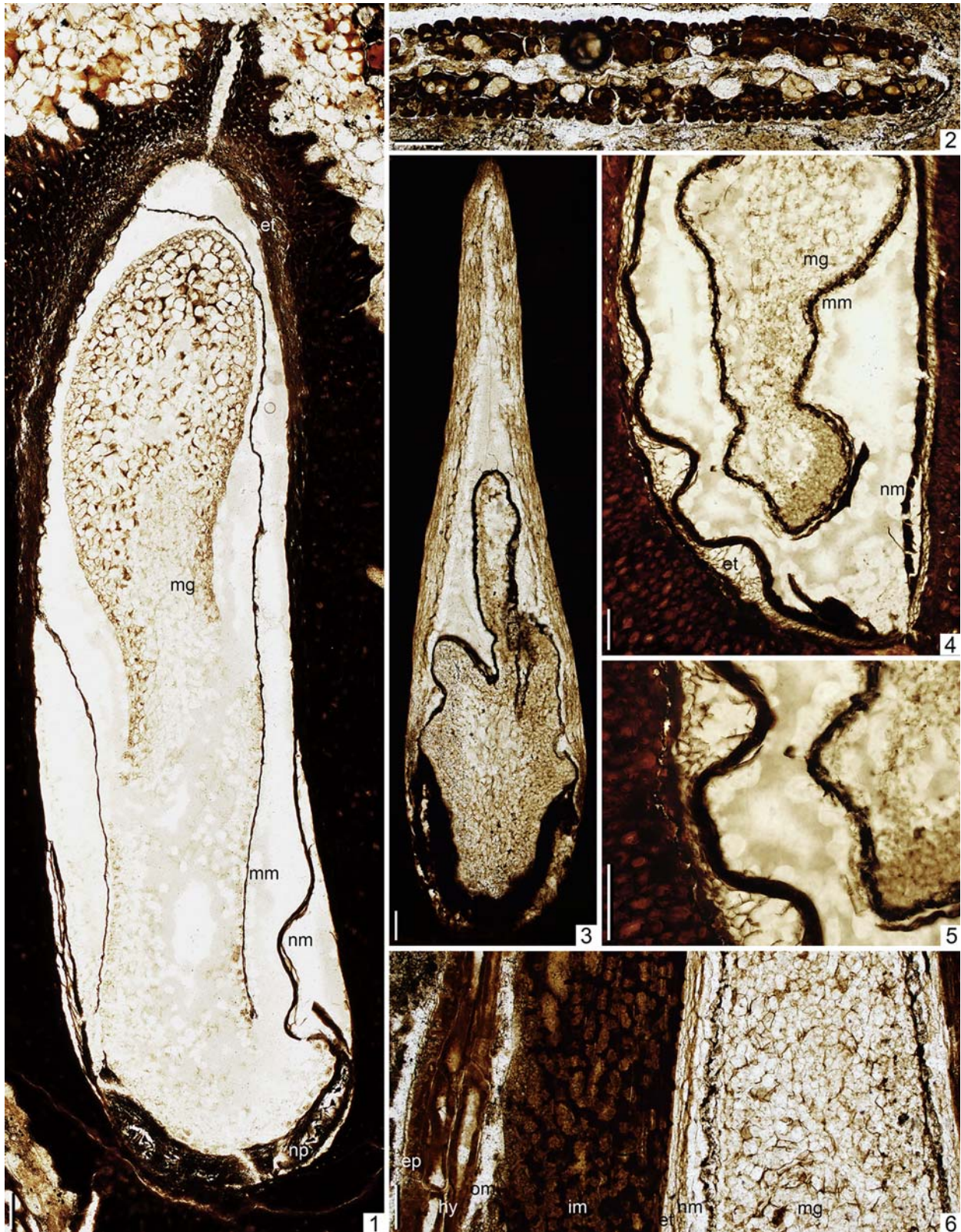


PLATE III Details of inner portions of *Pachytetopsis tayloriorum* gen. et sp. nov. seeds. (1) Enlargement of nucellus and megagametophyte tissues within the holotype; NRMS089801-01-01. (2) Transverse section of seed wing; NRMS124914-05-01. (3) Enlargement of gametophyte and surrounding well-developed endotesta; NRMS124932-02. (4) Portion of seed inner mesotesta, endotesta, nucellus, and gametophyte; NRMS089799-06-02. (5) Enlargement of portion of inner mesotesta, endotesta, nucellus, and gametophyte; NRMS089799-06-02. (6) Longitudinal section of portion of seed showing layers of the integument and gametophyte; NRMS124914-05-02. For all figures: *ep* = epidermis; *et* = endotesta; *hy* = hypodermis; *im* = inner mesotesta; *mg* = megagametophyte; *mm* = megaspore membrane; *nm* = nucellar membrane; *np* = nucellar pad; *om* = outer mesotesta. Scale bars = 100 μ m.

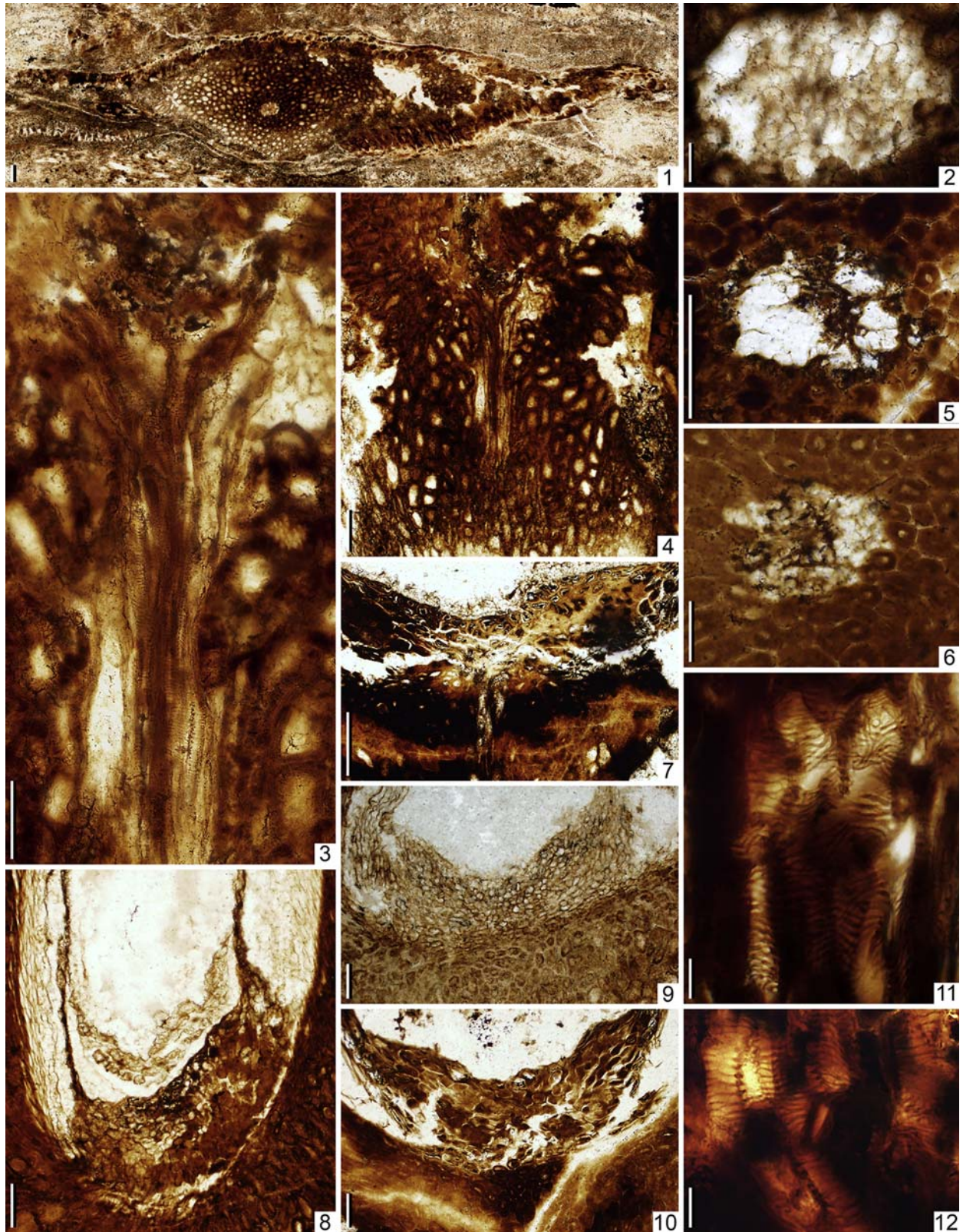


PLATE IV Details of vasculature of *Pachytetopsis tayloriorum* gen. et sp. nov. seeds. (1) Transverse section through seed base showing vascular supply; NRMS089799-05. (2) Enlargement of vascular strand and surrounding transfusion tissue in transverse section of seed base; NRMS089799-05. (3 and 4) Longitudinal section of seed base showing bifurcating vascular strand; NRMS089799-04-03. (5) Enlargement of vascular strand surrounded by degraded transfusion tissue in transverse section of seed base; NRMS 124915-02-01. (6) Vascular strand surrounded by degraded transfusion tissue and inner mesotesta cells in transverse section of seed base; NRMS 124957-03. (7) Vein supplying nucellar pad at base of seed; NRMS 124953-02. (8) Well-developed nucellar pad at base of seed; NRMS089799-02-02. (9) Nucellar pad at base of seed; NRMS 124937-02. (10) Nucellar pad at base of seed; NRMS 124919-02. (11 and 12) Scalariform-pitted tracheids in chalazal vascular strand; NRMS089828-05-01. Scale bars for 1, 4, 5, 7–10 = 100 μ m; for 3, 6 = 50 μ m; for 2 = 20 μ m; for 11, 12 = 10 μ m.

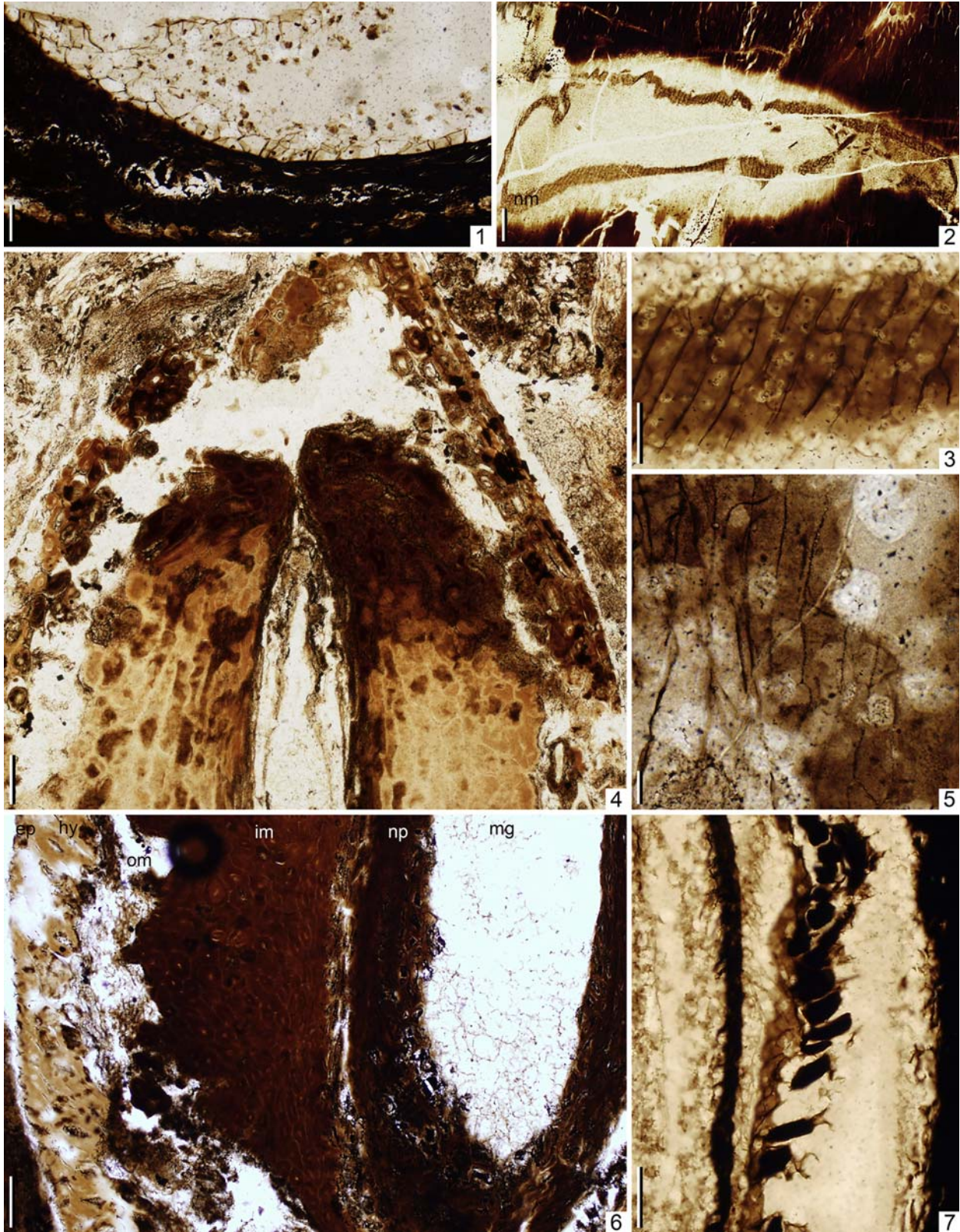


PLATE V Details of nucellus, megagametophyte and micropyle of *Pachytestopsis tayloriorum* gen. et sp. nov. seeds. (1) Megagametophyte tissue with cellular contents at base of seed; NRMS 124918-02-01. (2) Oblique section through inner seed showing cellular pattern on nucellus; NRMS089799-06-03. (3) Enlargement of nucellus showing arrangement of cells; NRMS089799-06-03. (4) Micropylar region of seed; NRMS089799-04-04. (5) Enlargement of nucellus cuticle showing cell pattern; NRMS 124918-02-01. (6) Basal part of seed showing integument layers, nucellar pad, and remnant megagametophyte tissue; NRMS 124923-05. (7) Enlargement of nucellus, megaspore membrane, and megagametophyte in longitudinal section—with intervening fungal hyphae; NRMS089828-05-02. For all figures: *ep* = epidermis; *hy* = hypodermis; *im* = inner mesotesta; *mg* = megagametophyte; *nm* = nucellar membrane; *np* = nucellar pad; *om* = outer mesotesta. Scale bars for 2 = 200 μm ; 1, 4, 6, and 7 = 100 μm ; for 3 = 50 μm ; for 5 = 20 μm .

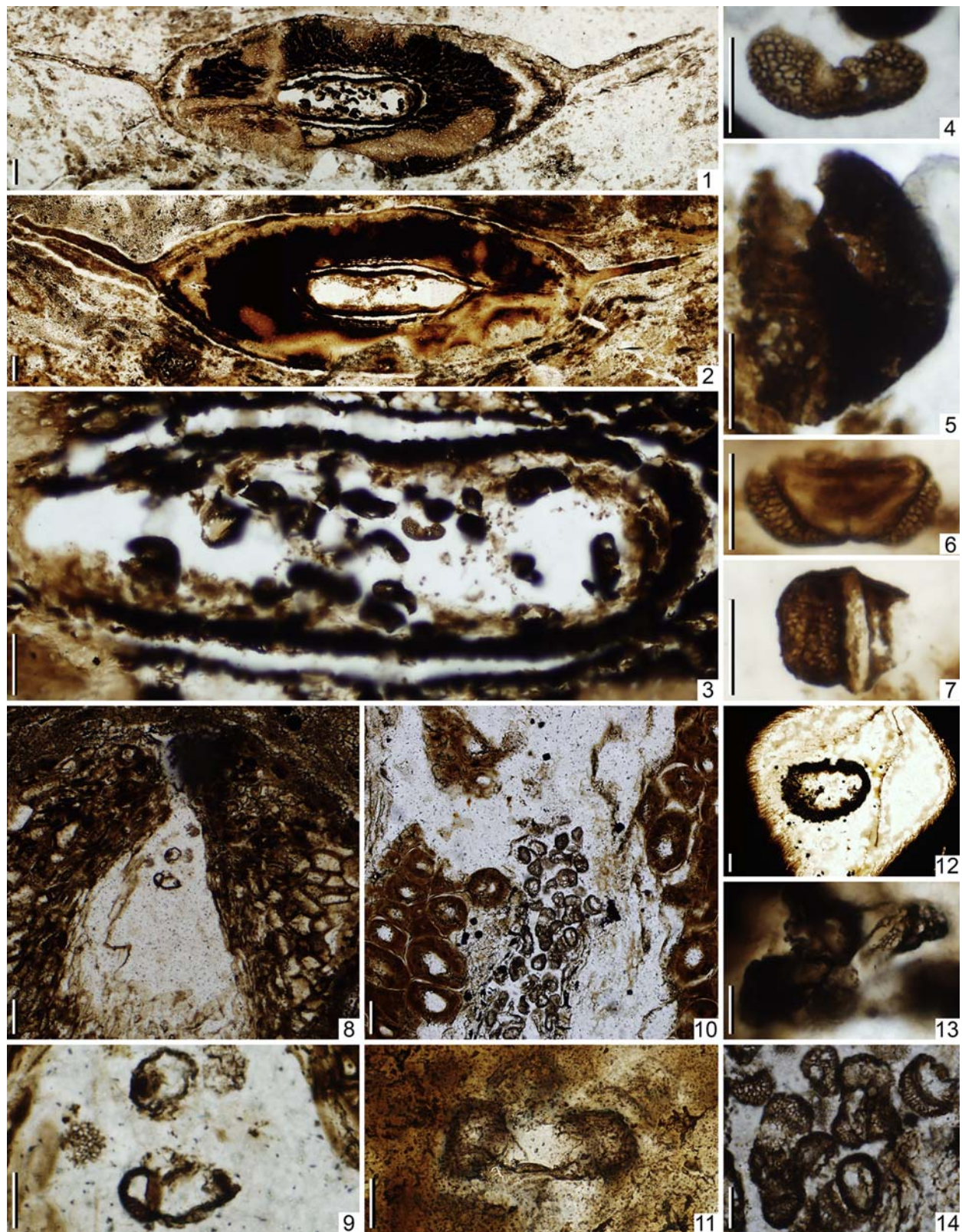


PLATE VI Pollen preserved in the micropyle and pollen chamber of *Pachytestopsis tayloriorum* gen. et sp. nov. seeds. (1) Transverse section through a seed pollen chamber containing numerous taeniate bisaccate pollen (cellulose acetate peel); NRMS 124927-02. (2) Slightly more proximal transverse section through the same pollen chamber showing a few pollen grains; NRMS 124927-05. (3) Enlargement of pollen chamber from 1 showing variation in pollen size; NRMS 124927-02. (4) Saccate pollen grain in equatorial view; NRMS 124927-02. (5) Large bisaccate pollen grain with taeniate corpus in latero-equatorial view; NRMS 124927-02. (6) Taeniate bisaccate pollen in oblique view; NRMS 124927-05. (7) Bisaccate pollen in distal view; NRMS 124927-05. (8) Longitudinal section of micropylar region of seed showing pollen in pollen chamber; NRMS 124942-03. (9) Cross-sections of bisaccate pollen; NRMS 124942-03. (10) Large mass of pollen preserved within the integumentary layers of a seed; NRMS 124915-02-02. (11) Degraded bisaccate pollen grain in the micropyle of a seed; NRMS124926-03-02. (12) Transverse section through the micropylar region of a seed with a few pollen grains and degraded nucellus and megagametophyte tissue; NRMS089797-04. (13) Degraded taeniate bisaccate pollen grains in the micropyle of a seed; NRMS089797-04. (14) Enlargement of bisaccate pollen from 10; NRMS 124915-02-02. Scale bars = 100 μ m in 1, 2, and 12; 50 μ m in 3, 8, and 10; 20 μ m in 4–7, 9, 11, 13, and 14.

(Plate IV, 2, 5, and 6). Tracheids c. $9\ \mu\text{m}$ in diameter, exceeding $200\ \mu\text{m}$ long, with scalariform to reticulate pitting (Plate IV, 11 and 12).

Nucellus consisting of basal flattened disc or shallow to deeply cup-shaped nucellar pad (Plate IV, 7–10) attenuating distally into a one-cell-thick nucellar membrane that is variably free or fused to the endotesta or to the megagametophyte (Plate III, 1 and 3–6). Nucellar pad up to 15 cells thick ($160\text{--}230\ \mu\text{m}$ thick); cells lenticular to rectangular prisms, $15\text{--}30\ \mu\text{m}$ wide and deep, $15\text{--}40\ \mu\text{m}$ long (Plate IV, 7–10). Nucellar membrane with well-developed cuticle preserving longitudinally arranged cell outlines $80\text{--}100\ \mu\text{m}$ long and $18\text{--}25\ \mu\text{m}$ wide, with straight lateral anticlinal walls and transverse to oblique end walls (Plate V, 2, 3, and 5). Nucellus typically contracted slightly from seed apex, forming a small pollen chamber (Plate III, 1 and 3).

Megagametophyte tissue variably preserved, typically consisting of isodiametric cells, $35\ \mu\text{m}$ in diameter with $0.8\text{-}\mu\text{m}$ -thick walls (Plates III, 1,3,6 and V, 6). Margin of megagametophyte consisting of regular brick-shaped epidermal cells $16 \times 16 \times 23\ \mu\text{m}$, in some cases enclosed by a dark featureless megaspore membrane $4\text{--}8\ \mu\text{m}$ thick (Plate III, 1, 4, and 5). In many cases, megagametophyte tissue is degraded into featureless brown detritus (Plate III, 4). A few examples retain possible remnant organelles preserved within megagametophyte cells (Plate V, 1). No archegonia or embryos detected.

Pollen preserved in the micropyle bisaccate, haploxylonoid, and taeniate (Plate VI, 4–14): $33\text{--}79\ \mu\text{m}$ wide; sacci and corpus $16\text{--}57\ \mu\text{m}$ long; $4\text{--}7$ taeniae on corpus; taeniae $3\text{--}4\ \mu\text{m}$ wide; cappula $5\text{--}6\ \mu\text{m}$ wide; and sacci $12\text{--}24\ \mu\text{m}$ wide, hollow with reticulate ornament.

Remarks: Several dozen seeds of this type are present in the studied samples (Appendix 1). The broad (twofold) variation in the dimensions of *Pachytetopsis tayloriorum* specimens is not unexpected for glossopterid seeds in this size category. For example, *Samaropsis minniensis* from coeval strata in the central Bowen Basin similarly varies in the range of $6\text{--}12\ \text{mm}$ wide and $6\text{--}10\ \text{mm}$ long (McLoughlin, 1992).

All of the Homevale seeds have some deficiencies in the preservation of cellular details, especially of the thin-walled outer mesotesta and megagametophyte tissues. In some cases, fungal saprotrophism appears to have contributed to the breakdown of the seed tissues (Plate V, 7). In other cases, bacterial decay and other attrition processes in the early stages of peatification appear to have particularly degraded tissues composed of thin-walled cells and deposited amorphous organic matter in the lumens of some robust cells. Despite these degradational factors, preservation of the seeds is commonly better than for other plant organs in the assemblage, and sufficient anatomical details are available to provide a detailed reconstruction of the seed (Fig. 9.2).

We note that there are differences in the terminology used for various wall layers of fossil seeds and that some authors may have alternative interpretations of the homologies of some wall components. We adopt a simple

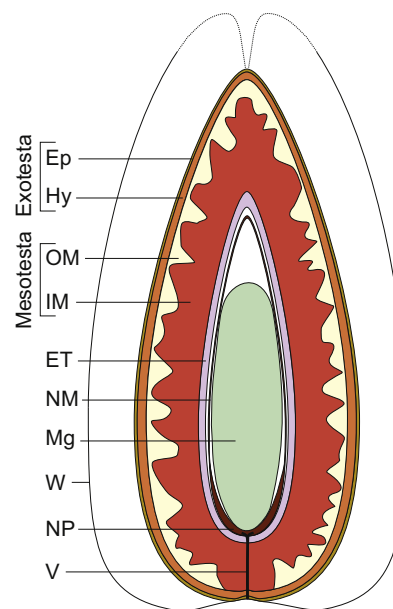


FIGURE 9.2 Schematic longitudinal section of *Pachytetopsis tayloriorum* gen. et sp. nov. showing the distribution of tissue types in the seed. Ep, epidermis; ET, endotesta; Hy, hypodermis; IM, inner mesotesta; Mg, megagametophyte; NM, nucellar membrane; NP, nucellar pad; OM, outer mesotesta; V, vascular trace. Seed length $5\text{--}11\ \text{mm}$.

three-layer model for the integument and group the prominent sclereid layer and adjacent contiguous band of thin-walled cells collectively as the mesotesta (Fig. 9.2) on the basis of their radially interdigitating arrangement and abrupt differentiation from adjacent layers. Other authors might recognize these two discrete integumentary layers or only the inner sclereid band as the sclerotesta (see discussion by Rothwell and Serbet, 1994).

The presence of a true pollen chamber is equivocal. A gap between the megagametophyte and the endotesta is apparent in several specimens, but this might also be a consequence of postmortem shriveling of the megagametophyte. Nevertheless, because a pollen chamber preserving pollen tubes has been identified previously in other glossopterid seeds from this deposit, we interpret the distal cavity to represent a true pollen chamber.

5. DISCUSSION

5.1 Affinities of the Seeds

Although none of the Homevale seeds was found attached to a megasporophyll, an affinity with glossopterids is strongly favoured. Glossopterid foliage and fructifications overwhelmingly dominate almost all Australian Lopingian fossil plant assemblages, and we assume that the majority of dispersed seeds found in such deposits are affiliated with that group. Apart from glossopterids, a relatively narrow range of gymnosperm foliage is represented in Australian Guadalupian to Lopingian deposits, including (in decreasing order of abundance) cordaitaleans, voltzialean conifers, cycadaleans, and a few enigmatic gymnosperms, such as

Bergiopteris, *Dunedoonia*, and *Blechnoxylon* (Holmes, 1977, 1995; White, 1981, 1986; Rigby, 1983; McLoughlin, 1992, 1995; Pigg and Trivett, 1994). Of these, cordaitaleans typically produced monosaccate pollen (Balme, 1995); the only known eastern Australian Permian conifer (*Walkomiella*) has small, tight, globose cones that probably bore diminutive seeds (White, 1981); cycads have radiospermic seeds (Meyen, 1987); *Blechnoxylon* may represent an immature glossopterid (Pant and Nautiyal, 1984); and *Dunedoonia* and *Bergiopteris* are extremely rare (Holmes, 1977; McLoughlin, 1995). Ginkgoalean leaves reported by White (1986) are probably misidentified *Schizoneura* (sphenophyte) leaf whorls. To date, several species of *Glossopteris* and a single species of *Noeggerathiopsis* (Cordaitales) are the only gymnosperm leaves recognized from the Homevale silicified peats and associated siltstones (Gould and Delevoryas, 1977; Pigg and McLoughlin, 1997; McLoughlin, personal observations). Given that *Pachytetopsis tayloriorum* is platyspermic and has taeniate bisaccate pollen in the micropyle, we infer that this seed was produced by a glossopterid gymnosperm.

Dispersed seeds from the Permian of Gondwana generally fall into three broad size categories. The largest seeds, such as *Samaropsis milleri* (Feistmantel) Seward, 1917, *S. dawsonii* Walkom, 1922, “Seed gen. A, sp. A” of Anderson and Anderson (1985), and *Samaropsis gigas* Souza and Iannuzzi, 2012, are ovate forms up to 55 mm long and 40 mm wide, with poorly to well-developed wings (Millan, 1977; McLoughlin and McNamara, 2001; Bernardes-De-Oliveira et al., 2007).

Intermediate-sized seeds, in the range of 6–15 mm long, include forms with variable wing development. For example, from the Bowen Basin, *Nummulospermum bowenensis* Walkom, 1922 has wings that are well developed only in the distal part of the seed and extend into a horned micropyle. In contrast, *Samaropsis minniensis* (McLoughlin, 1992) and several other platyspermic seeds illustrated by Walkom (1935) have lateral wings of consistent moderate width, whereas *Samaropsis pincombei* Walkom, 1928 and *Alatocarpus indicus* Lele, 1969 have pairs of lateral wings that are extraordinarily broad (extending up to 12 mm beyond the sclerotesta on either side of the seed). Some strongly compressed seeds in this size range, such as *Samaropsis etheridgei* Walkom, 1922, have narrow lateral flanges that may represent either true wings or crushed and laterally splayed sarcotestal (exotestal) rims.

The smallest class of seeds associated with glossopterids is represented by forms less than 5 mm long. In the Bowen Basin, this group includes *Samaropsis carinata* McLoughlin, 1992 and *S. minima* McLoughlin, 1992, which both have very narrow lateral wings. This category of small seeds includes the most abundant forms in most Australian upper Permian deposits. In some cases, they have been found attached to multiovulate scutiform glossopterid reproductive structures, such as *Plumsteadia* (White, 1964), *Austroglossa* (Holmes, 1974, 1995),

Senotheca (McLoughlin, 1990a, 2012a), and *Dictyopteridium* (McLoughlin, 1990c). Based on their size and shape, it is likely that the permineralized fructifications bearing small seeds described by Gould and Delevoryas (1977) from Homevale, and later assigned to *Homevaleia* Nishida et al. (2007), are anatomically preserved examples of *Dictyopteridium* fructifications. Several other glossopterid ovuliferous organs are known from the Australian Permian (Rigby, 1963, 1978, 1983; White, 1964, 1978; Holmes, 1974; McLoughlin, 1990a,b, 1995, 2012a,b,c, 2016), but in most cases they have not been found with attached seeds.

Based on the size of the reproductive organs and on the density of ovule attachment points on the receptacle, it is likely that scutiform fructifications, such as *Dictyopteridium*, *Plumsteadia*, *Ottokaria*, *Senotheca*, *Ottokaria*, *Karingbalia*, and *Scutum*, bore numerous (in some cases up to 400) seeds of the smallest size category. Flabellate or cupulate organs, such as *Lidgettonia*, *Rigbya*, and *Nogoa*, in contrast, generally have fewer (2–10) and considerably larger (2–5 mm) ovule attachment scars, indicating that they probably produced seeds of the intermediate-size category. Glossopterid fructifications with a clear affinity to seeds of the largest category (15–30 mm) have not yet been recorded from Australia. It is possible that these largest seeds were borne on glossopterid fructifications of a type not yet discovered. Some South American Permian seeds falling into this size category have been considered affiliates of the fructification *Arberia*, which has been variously linked to glossopterids or cordaitaleans (Millan, 1967; de Souza and Iannuzzi, 2012). Alternatively, such large seeds may belong to one of the rarer non-glossopterid elements in the Australian Permian flora.

Pachytetopsis tayloriorum falls into the intermediate-size category. Although no fructifications have been recorded thus far from the Homevale flora that would support seeds of this size, coeval deposits in the central Bowen Basin and contiguous Sydney Basin host *Rigbya*, *Nogoa*, and *Lidgettonia* species that have seed scars and cupules that would accommodate such seeds (White, 1978; McLoughlin, 1990a, 1995, 2012c).

5.2 Comparison With Other Permian Gondwanan Seeds

Eight permineralized seed/ovule types, not all of which have been formally named, have now been described or illustrated from deposits associated with glossopterid foliage (Table 1). *Pachytetopsis tayloriorum* differs from the other forms in several key characters. It is markedly larger than all previous forms described, reaching 11 mm in maximum dimension—around twice the size of most other forms (Table 9.1). Its 180-degree rotational symmetry and prominent wings differ from the small glossopterid seeds assigned to *Lonchiphyllum aplopermum* Ryberg and Taylor, 2013 and *Homevaleia gouldii* Nishida et al., 2007, which appear to lack wings and possess radial symmetry.

TABLE 9.1 Comparison of Morphological and Anatomical Characters Among Permian Gondwanan Permineralized Seeds

Taxon	<i>Plectilosperrum elliotii</i>	<i>Choanostoma verruculosum</i>	Seeds of <i>Lakkosia kerasata</i>	Seeds of <i>Lonchiphylum aplosperrum</i>	Un-named Silicified Seeds	Seeds of <i>Homevaleia gouldii</i>	Un-named Silicified Seeds	<i>Pachytetopsis tayloriorum</i>
Formation; age; locality	Buckley Formation; Changhsingian; Skaar Ridge, Transantarctic Mountains	Buckley Formation; Changhsingian; Skaar Ridge, Transantarctic Mountains	Buckley Formation; Changhsingian; Skaar Ridge, Transantarctic Mountains	Buckley Formation; Changhsingian; Skaar Ridge, Transantarctic Mountains	Uppermost Toploje Member, Bainmedart Coal Measures; Roadian—Wordian; Prince Charles Mountains, Antarctica	Fort Cooper Coal Measures; early Changhsingian; northern Bowen Basin, Australia	Burngrove Formation or Rangal Coal Measures; Changhsingian; Blackwater Mine, Bowen Basin, Australia	Fort Cooper Coal Measures; early Changhsingian; Bowen Basin, Australia
Length	4.8 mm	c. 2 mm	2–3.5 mm	1.1 mm	1.6–5.4 mm	0.8–1.5 mm	Uncertain	5–11 mm
Max. width	3.1 mm in primary plane; 2.2 mm in secondary plane	c. 1.5 mm in primary plane, slightly compressed in secondary plane	1–3.7 mm in primary plane	0.97 mm	1.2–5.1 mm in primary plane	0.8–1 mm wide in primary plane; 0.4–0.7 mm in secondary plane	7.5 mm in primary plane	5–10.1 mm wide in primary plane (incorporating narrow wings), 1.2–3.5 mm in secondary plane
Shape	Ovoid to narrowly ovoid	Circular to elliptical in lateral view	Described as obovoid, but possibly pyriform	Ovoid	Ovoid—globose	Ovoid or pyriform.	Uncertain	Flattened ovoid
Vascularization	Single terete strand extending into chalazal tracheal disc, then forking to vascularize spongy zone of integument within primary plane	Vascular bundle of tracheids 5–9 μ m in diameter with annular or helical thickenings at chalaza; vascular strand 2–3 cells wide	No veins evident in sclerotesta; no indication of a chalazal disk of vascular tissue	Seeds borne on short vascularized stalks; clusters of thick-walled cells at chalazal end may indicate vascular bundles in integument	Ambiguous; apparently a single strand entering the seed base and supplying nucellar pad	Ovules sit at ends of short vascular traces; veins extend into inner zone of sclerotesta	Uncertain	Terete strand surrounded by transfusion tissue entering straight through thickened chalazal integument then forking and terminating abruptly in nucellar pad
Seed symmetry	Bilateral or 180-degree rotational symmetry	180-degree rotational symmetry	180-degree rotational symmetry	Radial or 180-degree rotational symmetry	Uncertain	Radial or weak 180-degree rotational symmetry	180-degree rotational symmetry	180-degree rotational symmetry
Exotesta/sarcotesta and surface ornament	Three layered; innermost zone 3–7 small (c. $15 \times 18 \mu$ m), thin-walled, longitudinally orientated isodiametric cells, 208 μ m long, filled with opaque	Consisting of thin-walled, isodiametric to elongate cells, overlain by epidermal layer of smaller rectangular cells; distally expanded into blunt-tipped fleshy	Moderate thickness (0.15 mm); forming short extensions or horns around base (around micropyle in original description)	Composed of single layer of large rectangular cells ($19 \times 12 \mu$ m in longitudinal section) with walls 5 μ m thick with the exterior and anticlinal walls much thicker than	Outer layer consisting of spongy cells, c. 200 μ m thick, locally expanding to around 300 μ m near micropyle	Three to four layers of thin-walled, elongate parenchymatous cells contiguous with inter-seed cellular meshwork enclosing large intercellular spaces	50–100 μ m thick, appressed to mesotesta or locally separated by a gap left by degraded tissue; extending laterally to form wings; locally bearing sparse spinulate ornament	Consisting of single layer of rectangular prismatic epidermal cells 14–(20)–26 μ m wide and deep, 80–(110)–300 μ m long with strongly thickened walls,

Continued

TABLE 9.1 Comparison of Morphological and Anatomical Characters Among Permian Gondwanan Permineralized Seeds—cont'd

Taxon	<i>Plectilospermum elliotii</i>	<i>Choanostoma verruculosum</i>	Seeds of <i>Lakkosia kerasata</i>	Seeds of <i>Lonchiphylum aplospermum</i>	Un-named Silicified Seeds	Seeds of <i>Homevaleia gouldii</i>	Un-named Silicified Seeds	<i>Pachytestopsis tayloriorum</i>
	material; middle zone spongy, mostly comprising large spaces and cell wall fragments (complete cells 35–40 µm in diameter); outer zone of thick-walled rectangular cells with dark contents, usually 2 cells thick covered by cuticle c. 60 µm thick.	appendages comprising 4–5 layers of thin-walled, elongate cells; apical lobes extending above apex of nucellus; blunt-tipped protuberances measuring up to 150 µm high randomly cover surface of lower half of ovule		the interior wall; no external ornamentation				underlain by 2–3 well-regimented layers of strongly thickened cells of hypodermis; hypodermal cells rectangular prismatic varying from 19–(30)–43 µm wide and deep, and 150–(195)–420 µm long in inner layer to 90 µm wide, 52 µm deep in outer layer
Mesotesta/ Sclerotesta	Broad; inner portion with longitudinally aligned cells, isodiametric in cross-section. Walls thickened with concentric layers, lacking conspicuous pits and with clear lumen; innermost 4–5 cell layers isodiametric in cross-section (11.5–20.7 µm in diameter), outermost 2–3 cell layers c. 18.9 × 45.4 µm.	Up to 12 cells wide at micropyle, elsewhere 3–5 cells wide (up to 96 µm wide), heterogeneous, constructed of clusters of isodiametric to slightly elongate, sclerified cells intermixed with clusters of unsclerified cells; Walls of the sclerified cells 5–13 µm thick, lamellar with both simple and ramifying pits	None obvious	c. 20 µm thick, 10 cells wide, consisting of uniform, heavily sclerified cells; slightly thickened and with pitted cells around micropyle	Relatively broad (c. 300 µm thick), consisting of inner layer of thick-walled, dark, radially elongate cells and outer layer of thin-walled or degraded cells	Inner zone of fibrous cells, 2–3 cells thick, vascularized by a strand of tracheids with bordered pits towards micropyle; outer zone of polygonal sclereids 3–4 cells thick, thickening towards micropyle and containing scattered mucilage cells near base	Mesotesta up to 900 µm wide basally, thinning to <100 µm distally, composed of thick-walled cells 45 × 90 × 180 µm, arranged longitudinally	0.5–0.6 mm thick, consisting of outer layer of parenchymatous cells 260 µm long and 14–(40)–80 µm in diameter with walls c. 0.6 µm thick, and an inner layer of longitudinally aligned cylindrical or rectangular to hexagonal prismatic sclereids, 25–75 µm in diameter, 60–190 µm long bearing numerous radial pores up to 2 µm in diameter
Endotesta	Usually dark layer, 1 cell thick, comprising cells 15 × 77 µm in cross-section	40-µm-thick (half thickness of sclerotesta); 3–4 layers of thin-walled, narrowly rectangular parenchyma cells lining inner surface of sclerotesta;	Thin (0.1 mm), except at base (apex in original description) where it expands into two large hemispherical pads	Fibrous, 2–3 cells thick with walls 3 µm thick; commonly crushed	<150 µm thick consisting of a few layers of longitudinally elongate dark cells	Up to four layers of thin-walled parenchymatous cells	Dense and mineral-stained (<100 µm thick)	30–60 µm thick, consisting of rectangular to hexagonal prismatic (but commonly compressed) longitudinal cells, 10–(20)–50 µm

		cells 14–23 µm long and 4–5 µm wide in longitudinal section, oriented parallel to long axis of ovule						wide in tangential dimension, 5–(10)–20 µm wide in radial dimension, up to 100 µm long, with walls c. 0.5 µm thick
Base	Truncate; formed by an expansion of spongy sarcotesta and twofold increase in thickness of sclerotesta from its size in the ovule's mid-region	Borne on very short stalk but otherwise rounded	Broad, with a concavity between basal horns (narrowly tapered in original description)	Broadly rounded on a short stalk	Truncate or broadly rounded	Broadly rounded; supplied by narrow vascular trace of tracheids with helical or scalariform thickenings, surrounded by transfusion tissue cells (17–27 µm in diameter) with scalariform thickenings	Not exposed	Rounded with a 500 µm wide, 250 µm deep, chalazal pocket representing detachment scar
Micropyle	Rounded to slightly pointed	Micropylar extension at apex of nucellus up to about half height of the sarcotesta appendages	Narrowly tapered apex with narrow micropyle possibly with two short horns. (Broad, with a large pollen chamber between apical horns in original description)	Simple	Forming a weak (200 µm) extension at seed apex	Narrow and flanked by slightly thickened integument; space between seeds filled with delicate network of cellular filaments continuous with outer surface of integument and formed into conical web or funnel extending from micropyle	Unavailable	Ill-preserved, represented by 10–20-µm-wide apical canal leading to pollen chamber apical to contracted nucellus; no obvious elaboration of exotesta around micropyle
Wing	1 mm wide	None developed	Possibly developed basally (apically in original description), 0.5 mm wide	Absent	Absent or weakly developed	Absent or weakly developed	Consistently 1.2 mm wide	Well developed from base to apex c. 0.75 mm wide and up to 300 µm thick of consistent width; consisting of extension of exotesta and thin, compressed outer mesotestal tissue 2–3 cells thick. Wing hypodermis reduced to 1 cell thick

Continued

TABLE 9.1 Comparison of Morphological and Anatomical Characters Among Permian Gondwanan Permineralized Seeds—cont'd

[illegible]

Associated or attached megasporophyll	Unknown	Unknown (only glossopterid leaves preserved in the same deposit)	<i>Lakkosia kerasata</i> (possibly equivalent to cupulate or flabellate fructifications such as <i>Rigbya</i> or <i>Lidgettonia</i>)	Lanceolate, laminar with 150 ovules attached to (?adaxial surface; of <i>Dictyopteridium</i> or <i>Plumsteadia</i> type fructification	Unknown	Borne on short stalk on one side of a thick laminar organ with the lateral margins infolded and slightly overlapping, thus enclosing seeds within a flattened or cylindrical envelope (= <i>Homevaleia</i> fructification)	Unknown (only glossopterid leaves and roots preserved in the same deposit)	Unknown
Associated pollen	Bisaccate grains, c. $62 \times 35 \mu\text{m}$ with conspicuously ornamented sacchi; corpus details unclear	Bisaccate grains preserved within the micropyle	<i>Protohaploxypinus</i> sp.	Associated pollen within integument of <i>Protohaploxypinus</i> type	Unknown	Bisaccate, $32\text{--}54 \mu\text{m}$ wide, with corpus diameter of $14\text{--}28 \mu\text{m}$	Unknown	<i>Protohaploxypinus limpidus</i>
Other features			Interpreted here in a manner inverted to that of Ryberg (2010)		Few specimens available; most sections probably do not intersect the marginal wings (if present)		Broadly elliptical in transverse section	Seed size matches scars of cupulate or flabellate reproductive organs (e.g., <i>Rigbya</i> , <i>Nogoa</i> , <i>Lidgettonia</i>)
Authors	Taylor and Taylor (1987)	Klavins et al. (2001)	Ryberg (2010)	Ryberg and Taylor (2013)	Holdgate et al. (2005) and Slater et al. (2015)	Gould and Delevoryas (1977) and Nishida et al. (2007)	McLoughlin (1990c, 1992)	This study

The presence of a hypodermis comprising several well-regimented layers of thick-walled cells is unique to *P. tayloriorum*. Pitting appears to be a common feature of sclereids in the mesotesta of glossopterid seeds, but *P. tayloriorum* is unique in its very thick inner mesotestal layer of sclereids and variable thickness of the outer mesotesta consisting of thin-walled cells. *Pachytestopsis tayloriorum* lacks the proximal micropylar elaborations evident in some other glossopterid seeds, such as *Choanostoma verruculosum* Klavins et al., 2001 and *Samaropsis pincombei* Walkom, 1928.

All glossopterid seeds so far described with pollen in the micropyle or preserved within the integument host taeniate bisaccate pollen of *Protohaploxylinus* or *Striatopodocarpites* type, although in some cases, the grains have been illustrated in distal view in which the taeniae are commonly not distinct (Pant et al., 1985; Table 9.1). The wide distribution of these pollen types among various seeds and fructifications and the occurrence of multiple pollen forms in single glossopterid sporangia (Lindström et al., 1997) suggest that such pollen taxa are diagnostic of glossopterids only at the family or order level. That is, individual glossopterid taxa appear to have plasticity in pollen form, such that similar grain morphologies were produced by numerous species or genera.

Based on the tabulated characters (Table 9.1), *P. tayloriorum* is readily distinguishable from all previously documented permineralized forms. However, it shares some dimensional similarities to *Samaropsis minniensis* McLoughlin 1992, described only from impressions in coeval deposits of the central Bowen Basin. These species have similar size ranges, but *S. minniensis* bears prominent longitudinal striae on the seed coat and the base is cordate in some cases—features that we have not detected in *P. tayloriorum*. The discovery of attached reproductive organs for both species, and pollen in the micropyle of *S. minniensis*, would aid future appraisal of the relationships between these species.

5.3 Glossopterid Seed Character States

Most major analyses of seed plant phylogeny incorporating fossil information have included glossopterids (based on composite characters from various taxa) within the data matrix. Several key characters within the data matrices relate to features of the seeds. Here, we assess the character states relating to glossopterid seeds in three of the major phylogenetic analyses of seed plants (Table 9.2)—those of Rothwell and Serbet (1994), Doyle (2006), and Hilton and Bateman (2006). Of the glossopterid seed characters used in these studies, at least nine have incorrect codings or the character definitions are ambiguous based on the results of this study and recent analyses of other permineralized seeds from Australia and Antarctica (Table 9.2). Based on these

results, a review of vegetative characters of glossopterids is warranted and the segregation of this group into several families might be beneficial for future phylogenetic analyses.

Key among the characters used in phylogenetic analyses of spermatophytes is seed symmetry. Glossopterid seeds have generally been coded as having 180-degree rotational symmetry (Rothwell and Serbet, 1994; Doyle, 2006; Hilton and Bateman, 2006). *Pachytestopsis tayloriorum* has obvious marginal wings and a bifurcating vascular supply that impose 180-degree rotational symmetry on the seed. However, the other seed type described from the Homevale deposit, found in attachment to the fructification *Homevaleia*, lacks wings and has apparent radial symmetry (Gould and Delevoryas, 1977; Pigg and Trivett, 1994; Nishida et al., 2007). It seems likely that both radiospermic and platyspermic architectures are represented in glossopterids, with this character undergoing a series of state reversals within various seed-plant groups.

The coding of the character state for the sarcotesta in glossopterid seeds is problematic. The character definition is ambiguous and its coding is also dependent on how seriation is perceived within this layer. Because *P. tayloriorum* seeds have a prominent exotesta that extends into the wings and incorporates an epidermis and hypodermis of multiple cell strata, we interpret this layer to be equivalent to a multiseriata sarcotesta of other authors. This is opposed to the absent or uniseriate coding for the glossopterid sarcotesta by Doyle (2006) and Hilton and Bateman (2006). We clearly show vascular supply to the base of the nucellus and bifurcation of the vascular strand within the nucellar pad of *P. tayloriorum*, thus providing clarification of an unresolved character in previous analyses of glossopterids. The use of qualitative terms (“thick” and “thin”) for evaluating the nucellus and megaspore walls introduces ambiguity into the interpretation of character states. We recommend that future phylogenetic analyses use more quantitative definitions of such characters.

5.4 Associated Pollen

Several examples of *P. tayloriorum* preserve fossil pollen in the micropyle (Plate VI, 11) or pollen chamber (Plate VI, 1–9, 12, and 13), as masses within the body of damaged seeds (Plate VI, 10 and 14), or as isolated grains in the surrounding peat matrix. In many cases, the pollen grains are opaque or degraded but, where well preserved, all appear to represent taeniate haploxytonoid bisaccate forms with reticulate-ornamented sacchi. In distal view, the taeniae can be indistinct, giving the impression of a non-taeniate grain (Plate VI, 4 and 7), which may account for the apparent absence of taeniae on some grains recovered by Townrow (1962) from glossopterid sporangia. The grains

TABLE 9.2 Comparison and Re-evaluation of Coded Character States for Glossopterid Seeds Used in the Phylogenetic Analyses of Rothwell and Serbet (1994), Doyle (2006), and Hilton and Bateman (2006)

Character Number and Authors	Character States	Rothwell and Serbet (1994)	Doyle (2006)	Hilton and Bateman (2006)	Character State Interpretation and Comments Based on This Study
Char. 41—Rothwell and Serbet (1994); char. 94—Doyle (2006); char. 61—Hilton and Bateman (2006)	Anatomical symmetry of ovule: (0) radial (radiospermic), (1) 180-degree rotational symmetry (platyspermic), (2) with bilateral symmetry, (3) asymmetrical	1	1	1	Should be both 0 (based on the ovules of <i>Homevaleia gouldii</i> and possibly <i>Lonchophyllum aplosperrum</i>) and 1 (based on other seeds)
Char. 36—Rothwell and Serbet (1994)	Integument: (0) absent, (1) as whorl of pre-integumentary lobes (“telomes”) more or less adnate proximally, but not forming a micropyle at apex, (2) completely enclosing nucellus and forming micropyle at apex	2			2
Char. 63—Hilton and Bateman (2006)	Integument: (0) absent, (1) lobate pre-integument, (2) with simple apex, (3) with bifid apex, (4) with straight, tubular micropyle, (5) inverted micropyle orientation in relation to strobilus axis			2	2
Char. 39—Rothwell and Serbet (1994)	Integument: (0) with selerotesta and sarcotesta, (1) simple	0			0
Char. 100—Doyle (2006); char. 64—Hilton and Bateman (2006)	Sarcotesta: (0) absent or uniseriate, (1) multiseriate		0	0	Character ambiguous—dependent on definition of sarcotesta and how seriation is interpreted. As <i>P. tayloriorum</i> seeds have multiple cell layers in their exotesta, the character could be re-scored as 1
Char. 74—Hilton and Bateman (2006)	Exotesta (0) normal, (1) palisade			?	Ambiguous (definitions unclear as above)
Char. 75—Hilton and Bateman (2006)	Ruminations in the seed coat (0) absent, (1) present			?	Can probably be coded 0 but definition is ambiguous
Char. 95—Doyle (2006)	Apex of integument: (0) free lobes, (1) simple, (2) bifid, (3) straight, tubular		1		1
Char. 96—Doyle (2006); char. 62—Hilton and Bateman (2006)	Integument: (0) free from nucellus, (1) fused more than half way up from the base		0	0	Ambiguous (variably free or adnate in <i>P. tayloriorum</i>) — 0 or 1
Char. 43—Rothwell and Serbet (1994); char. 97—Doyle (2006); char. 66—Hilton and Bateman (2006)	Lagenostome (nucellar beak): (0) present, (1) absent	1	1	1	1
Char. 42—Rothwell and Serbet (1994); char. 98—Doyle (2006); char. 68—Hilton and Bateman (2006)	Pollen chamber: (0) hydrasperman (with central column), (1) prominent but with no central column, (2) rudimentary to absent	1	1	1	1

Continued

TABLE 9.2 Comparison and Re-evaluation of Coded Character States for Glossopterid Seeds Used in the Phylogenetic Analyses of Rothwell and Serbet (1994), Doyle (2006), and Hilton and Bateman (2006)—cont'd

Character Number and Authors	Character States	Rothwell and Serbet (1994)	Doyle (2006)	Hilton and Bateman (2006)	Character State Interpretation and Comments Based on This Study
Char. 67—Hilton and Bateman (2006)	Pollen chamber (0) absent (solidly cellular apex), (1) with membranous floor, (2) without membranous floor			2	2? (but definition of membranous floor in context of pollen chamber is ambiguous)
Char. 44—Rothwell and Serbet (1994); char. 69—Hilton and Bateman (2006)	Post-pollination sealing of pollen chamber: (0) by central column (from pollen chamber floor), (1) at apex of pollen chamber (by nucellar beak or homologous structure, and/or by occlusion from non-cellular substance), (2) not sealed	1		1	1 (presumably); (similar to character 65 of Hilton and Bateman, 2006)
Char. 37—Rothwell and Serbet (1994)	Micropyle (0) normal, (1) tubular	0			0
Char. 38 of Rothwell and Serbet (1994); char. 99—Doyle (2006); char. 65—Hilton and Bateman (2006)	Micropyle: (0) not sealed after pollination, (1) sealed	1	1	1	1 (presumably)
Char. 45—Rothwell and Serbet (1994); char. 101—Doyle (2006); char. 71—Hilton and Bateman (2006)	Nucellus: (0) not vascularized, (1) vascularized at least at base	?	?	?	1
Char. 46—Rothwell and Serbet (1994); char. 102—Doyle (2006); char. 72—Hilton and Bateman (2006)	Nucellar cuticle: (0) thin, (1) thick	1	1	1	The definition of “thick” is ambiguous but because <i>P. tayloriorum</i> has prominent cell patterning on the darkened nucellar cuticle this character's state is retained as 1
Char. 106—Doyle (2006)	Mesotesta: (0) unspecialized, (1) sclerotic		?		Should be scored as 1 based on sclerenchymatous inner mesotesta of <i>P. tayloriorum</i>
Char. 107—Doyle (2006); char. 76—Hilton and Bateman (2006)	Megaspore tetrad: (0) tetrahedral, (1) linear		?	?	?
Char. 108—Doyle (2006)	Cutinized megaspore membrane: (0) present, (1) absent		0		Uncertain (possibly weakly cutinized)
Char. 77—Hilton and Bateman (2006)	Megaspore wall: (0) thick, (1) thin			0	Ambiguous qualitative state definition, but probably 0
Char. 73—Hilton and Bateman (2006)	Testa (0) multiplicative, (1) non-multiplicative.			?	?

Question marks refer to unresolved character state

within *P. tayloriorum* seeds are all consistent with the circumscription of *Protohaploxylinus* (a fossil-genus used for dispersed pollen). A few approach the form of *Protohaploxylinus haigii* Foster, 1979 in having a transversely elliptical corpus, but the Homevale forms are markedly smaller than the dimensions indicated for examples of that species from the same basin (Foster, 1979). *Protohaploxylinus hartii* Foster, 1979 has similar dimensions but differs from the Homevale pollen by its longitudinally elongate corpus typically with eight taeniae. The Homevale pollen grains most closely match the characters of *Protohaploxylinus limpidus* (Balme et Hennelly) Balme et Playford, 1967, in terms of corpus and sacchi dimensions, number of taeniae, and gross shape (Foster, 1979).

Pollen matching the description of *P. limpidus* has a long stratigraphic range and geographic distribution in the Permian of Gondwana (Foster, 1975, 1979; Anderson, 1977; Lindström and McLoughlin, 2007). Pollen of this type has been recovered from glossopterid sporangia in India (Pant and Bhatnagar, 1973), Australia (Gould and Delevoryas, 1977), South Africa (Zavada, 1991), and Antarctica (Lindström et al., 1997) that are referable to *Arberiella vulgaris* (Pant and Nautiyal, 1960) and borne on *Eretmonia*-type reproductive bracts (Ryberg et al., 2012) or in larger, loose, cone-like structures referred to *Ediea* (Nishida et al., 2013). Moreover, apparently equivalent small taeniate bisaccate pollen grains have been identified in the micropyles/pollen chambers of several types of glossopterid seeds (Gould and Delevoryas, 1977; Taylor and Taylor, 1987; Ryberg, 2010; Ryberg and Taylor, 2013). This broad distribution and linkage with multiple seed types suggest that *P. limpidus* encompasses pollen forms derived from a wide spectrum of glossopterid parent plants.

5.5 Taphonomy

All of the studied seeds are detached from other organs. They are dispersed as isolated examples through the permineralized peat matrix or, more commonly, occur as closely spaced masses on particular bedding planes suggestive of seasonal detachment. None of the seeds bears any evidence of herbivory, and this is consistent with this form of damage being one of the few terrestrial arthropod functional feeding types not yet recorded among high-palaeolatitude glossopterids (Prevec et al., 2009; Slater et al., 2012). Other common elements in the permineralized peat are matted leaves of at least two forms of *Glossopteris*, smaller radiospermic seeds and associated *Homevaleia* fructifications, woody axes, *Palaeosmunda* petioles, charcoalified plant organs, fungal hyphae, and dispersed pollen, microspores, and megaspores. *Vertebraria* (glossopterid roots) are sparse. The plant remains typically occur in well-defined laminae, and no significant quantities of siliciclastic

grains are evident in the peat profile. The peat deposit probably represents a laminated accumulation of subaerial plant parts and differs most notably from Permian Antarctic peats by the scarcity of root fossils. Significantly, none of the seeds shows the development of an embryo or emergence of a radicle; hence, it is probable that, even if the ovules were fertilized (representing seeds), development and germination were inhibited by rapid burial by tuffs and entombment in silica.

Most plant remains in the deposit show a considerable degree of compression. Only the thick-walled *P. tayloriorum* seeds and woody axes with sclerenchymatous pith partitions show strong resistance to compression. Although fossil fungi are scattered through the deposit, many leaf, seed, and wood tissues did not undergo significant biological degradation before entombment in silica. Initial permineralization must have occurred relatively soon after deposition, with silica sourced from the alteration of tuffaceous material in overlying beds. At least three generations of chalcedonic to opaline silica veining subsequently penetrated the peat deposit, and this has caused damage to many individual fossils. Strong red–yellow–black staining has also locally affected the plant remains, and this has commonly accentuated the contrast between the plant matter and the surrounding siliceous cement. The thick-walled cells of the inner mesotesta, hypodermis, and epidermis of *P. tayloriorum* seeds typically absorbed rich red (ferric) staining.

6. CONCLUSIONS

Pachytestopsis tayloriorum gen. et sp. nov. is established for permineralized glossopterid seeds with dimensions that might have been accommodated on fructifications of either Rigbyaceae or Lidgettoniaceae. Although not attached to a megasporophyll, a glossopterid affinity is inferred based on the presence of taeniate bisaccate (*Protohaploxylinus*-type) pollen in the pollen chamber of the seeds. The seeds are dated as Changhsingian (latest Permian) based on lithostratigraphic correlation of the host formation (Fort Cooper Coal Measures) with units in the southern Bowen Basin that have been dated radiometrically. The new species is distinguished from other permineralized glossopterid seeds by its greater dimensions, thick mesotesta incorporating an inner layer of very robust sclereids and an outer layer of parenchymatous cells, and an exotesta incorporating thick-walled cells differentiated into a single epidermal and several hypodermal layers. The single vein entering the chalazal integument consists of a terete strand surrounded by a zone of transfusion tissue; this strand bifurcates and terminates abruptly in the nucellar pad. The seeds occur isolated or concentrated in particular laminae within permineralized peats dominated by matted leaves that probably reflect seasonal shedding of plant organs or

defoliation events caused by volcanic ash falls. Structural evaluation of *P. tayloriorum* and other permineralized seeds from the Permian of Gondwana indicates that various characters used in previous phylogenetic analyses are wrongly scored or ambiguous in their definition. Therefore, a thorough review of both reproductive and vegetative characters of glossopterids is warranted for future phylogenetic analyses.

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APPENDIX 1

List of specimens containing *Pachytestopsis tayloriorum* in the collections of the Department of Palaeobiology, Swedish Museum of Natural History.

More than 100 individual seeds distributed in 284 peat blocks, mounted cellulose acetate peels, and thin sections are available under the following registration numbers: (NRM)S089790-01, -02, S089791-01, S089792-01, S089793-01, S089794-01 to -03, S089795-01 to -04, S089796-01, -02, S089797-01 to -06, S089798-01, S089799-01 to -06, S089800-01, -02, S089801-01 (holotype) to -06, S089802-01, S089803-02, S089804-01, S089805-01, S089806-01, -02, S089807-01, S089808-01, S089809-01 to -05, S089810-01, -02, S089811-01, -02, S089812-01, -02, S089813-01, -02, S089814-01, S089815-01, -02, S089816-01 to -03, S089817-01 to -03, S089818-01, S089819-01, -02, S089820-01, -02, S089821-01, -02, S089822-01 to -03, S089823-01, -02, S089824-01, -02, S089825-01, -02, S089826-01, S089827-01, -02, S089828-01 to -05, S089829-01, -02, S089830-01, -02, S089831-01, S089832-01 to -08, S089833-01 to -03, S089834-01 to -03, S089835-01, S089836-01, S089837-01 to -05, S089838-01 to -03, S089839-01, S089840-01 to -03, S089841-01 to -03, S089842-01 to -03, S089843-01, -02, S089844-01 to -04, S089845-01 to -03, S089846-01, -02, S089847-01, S089848-01, S089849-01, S089850-01, S124900-01, S124900-02, S124901-01, -02, S124902-01, S124903-01, -02, S124904-01 to -03, S124905-01 to -04, S124906-01, -02, S124907-01, -02, S124909-01, S124913-01 to -06, S124914-01 to -05, S124915-01, -02, S124916-01, -02, S124917-01, -02, S124918-01, -02, S124919-01, -02, S124920-01 to -03, S124921-01 to -05, S124922-01 to -11, S124923-01 to -05, S124924-01 to -03, S124925-01, -02, S124926-01 to -03, S124927-01 to -06, S124928-01, -02, S124929-01, S124931-01 to -03, S124932-01, -02, S124933-01, -02, S124934-01, -02, S124936-01 to -03, S124937-01, -02, S124938-01, -02, S124939-01, S124940-01, -02, S124941-01 to -04, S124942-01 to -03, S124944-01, -02, S124945-01, -02, S124946-01, -02, S124947-01 to -03, S124948-01, -02, S124949-01, S124950-01, S124951-01 to -03, S124952-01 to -03, S124953-01, -02, S124956-01, S124957-01 to -03, S124958-01 to -03, S124962-01.