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A CHARCOALIFIED OVULE ADAPTED FOR WIND DISPERSAL AND DETERRING HERBIVORY FROM THE LATE VISÉAN (CARBONIFEROUS) OF SCOTLAND

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Premise of research. Mississippian (Lower Carboniferous) anatomically preserved ovules are pivotal to our present understanding of the Paleozoic primary seed plant radiation, but few are known from the late Viséan stratigraphic interval approximately 330 million years ago. Here, we document an exceptionally well-preserved mesoscopic charcoalified ovule from late Viséan limestones that is adapted for wind dispersal and for deterring herbivory.

Methodology. We use synchrotron radiation X-ray tomographic microscopy (SRXTM) and low-vacuum scanning electron microscopy (LVSEM) to analyze histological features not identifiable through traditional methods.

Pivotal results. The ovule is small, 2 mm long and 1.25 mm in maximum diameter, and has a dense covering of spirally arranged, long, slender, hollow hairs with glandular apices and a distal papilla. The nucellus is fused to the integument up to the nucellar apex, and above this, the integument comprises eight apical lobes, each with a single vascular bundle. The nucellar apex has a domed pollen chamber and large central column characteristic of hydrasperman-type (lagenostomalean) pteridosperms, but it lacks the distal salpinx seen in most hydrasperman ovules, leaving an exposed distal opening to the pollen chamber for pollination. Differences with existing taxa lead to the erection of *Hirsutisperma rothwellii* gen. et sp. nov.

Conclusions. The apical glands presumably functioned as granivory deterrents; coprolites (fossilized feces) from herbivorous arthropods are abundant in the fossiliferous horizon and at this stratigraphic interval. The small ovule size and its dense covering of hairs indicate *Hirsutisperma* was adapted for wind dispersal and was an *r*-selected species, producing large numbers of small offspring in unstable or changing environments. Taphonomic implications are discussed, including preservational biases for charcoalification. *Hirsutisperma* provides the first clear evidence for ecological niche partitioning in Mississippian hydrasperman-type ovules.

Keywords: gymnosperm, seed, hydrasperman reproduction, hairs, herbivory, plant-animal relationships, seed ecology, taphonomy, wildfire.

Online enhancement: video.

Introduction

The Paleozoic origin and primary radiation of seed plants represent key events in Earth history and terrestrialization, leading to the colonization of drier and/or upland (extrabasinal) habitats uninhabitable by free-sporing plants (e.g., Bateman and DiMichele 1994; Bateman et al. 1998), as well as forming diverse communities in Carboniferous wetlands (Dunn et al.

2006). First appearing in the fossil record in the late Devonian (Rothwell et al. 1989; Prestianni et al. 2013), seed plants underwent a rapid adaptive radiation in which they diversified to become dominant in many Carboniferous and stratigraphically younger floras. Particularly important to our present understanding of early seed plants are the Tournaisian-Viséan (Mississippian) anatomically preserved floras of southern Scotland (see Scott et al. 1984, 1986; Scott and Galtier 1996; Galtier and Meyer-Berthaud 2006; Bateman et al. 2016) that include a spectacular range of fossil species often with exceptional levels of anatomical preservation. Foremost of these are the remarkably diverse ovules extensively documented by the pioneering work of A. G. Long (1915–1999; e.g., Long 1960a, 1960b). However, most of these ovules are from the Tournaisian to the middle

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of the Viséan stages; remarkably few are known from the Late Viséan, with only *Sphaerostoma ovale* (Benson 1914) and *Phylostoma* sp. known from this stratigraphic interval in the Pettycur locality in Fife (Scott et al. 1984). Here, we provide a detailed systematic account of an exceptionally well-preserved late Viséan ovule from the Kingswood locality near Pettycur (Meyer-Berthaud and Galtier 1986; Scott et al. 1986) that is preserved as a mesoscopic charcoal (Glasspool and Scott 2013). The fossil is unusual in its morphology, being significantly smaller than contemporaneous species and in having a dense covering of fine, long, integumentary hairs with glandular apices and an exposed nucellar apex. It was briefly illustrated and had a summary description presented by Scott et al. (2009) in a techniques article that used it to introduce the combination of low-vacuum scanning electron microscopy (LVSEM) and synchrotron radiation X-ray tomographic microscopy (SRXTM), but a full systematic investigation was not undertaken at that time. We describe and illustrate the fossil in detail for the first time, then compare it with other Paleozoic ovule taxa and, in doing so, establish a new genus and species based on its unique features. We also consider the evolutionary, ecological, and taphonomic implications of the new ovule.

Geological Setting

On the southern coast of Fife in southern Scotland, the area around Pettycur exposes the Kinghorn Volcanic Formation (Gordon 1914; Allan 1924; Monaghan and Browne 2010) of mid-late Viséan age (Mississippian, Carboniferous; Monaghan and Parrish 2006; Monaghan and Browne 2010; Bateman et al. 2016). These rocks outcrop in cliff sections at Pettycur and at Kingswood End to the west, as well as in the intervening Pettycur Caravan site (Rex and Scott 1987). The nearby Pettycur limestone flora has been described in numerous publications (Scott et al. 1984; Rex and Scott 1987; Neregato and Hilton 2019). Palynological dating of the Kinghorn Volcanic Formation has indicated that it belongs to the *Raistrickia nigra-Triquirites marginatus* (NM) and *Tripartites vetustus-Rotaspora fracta* (VF) miospore zones (Brindley and Spinner 1989) of mid to late Asbian to early Brigantian regional substages of the Viséan stage (Monaghan and Pringle 2004), with absolute ages between 329 and 335 Ma (Monaghan and Pringle 2004; Monaghan and Browne 2010). The succession at Kingswood End (NS 265 864) comprises a sequence of basalt lavas, dolerite sills, ashes, limestones, and coaly shales and is cut by a small agglomerate-filled vent (Rex and Scott 1987). Outcrops just to the east in the Pettycur Caravan site expose a 6-m sequence of agglomerates and ashes, with beds and lenses of limestones at the top (the Kingswood Limestone) that show evidence of slumping. Limestones of bed 9 in this succession at locality 1 of Scott et al. (1986) contain the charcoalified ovule described herein, together with bands of abundant charcoal and calcareous permineralizations (Meyer-Berthaud 1986, 1990; Meyer-Berthaud and Galtier 1986; Scott et al. 1986; Scott 1990a). An additional outcrop (2) of ashes with bedded Kingswood Limestone was later exposed in the upper part of the Caravan site (Scott 1990b).

Palynological data from outcrop 1 (see Scott et al. 1986) of the Kingswood Limestone yielded a rich palynoflora that was consistent with the NM zone (*Tripartites distinctus-Murospora parthenopia* [DP] subzone) of mid-late Asbian age (Mid/late

Viséan). This date is in line with the broader biostratigraphic review undertaken by Brindley and Spinner (1989).

Material and Methods

More than 80 limestone blocks were collected from the original outcrop 1 at Kingswood (Scott et al. 1986). Blocks were sliced into 1-cm-thick slabs, and from each surface, one reference peel was made (Galtier and Phillips 1999), etching surfaces with 10% hydrochloric acid. Selected peels were mounted on glass slides for microscopic examination and photography. Petrographic thin sections, some stained with potassium ferricyanide and Alizarin red S carbonate stain, were prepared of the limestones and some of the lavas. In addition, polished thin sections of selected areas were made to provide data on the permineralization process and on the preservation of the plants. In this study, selected slabs of block KIN957 were dissolved in dilute 20% hydrochloric acid. Residues were then sieved using a 180-mm polypropylene sieve. The charcoal residue was further treated with 40% hydrofluoric acid to remove silica and neutralized. The cleaned residue was stored in distilled water and sorted in water using a binocular microscope with incident lighting. Specimens were separated using 000 hair brushes and mounted on dry-cavity slides (see Pearson and Scott 1999 for techniques). The ovule described herein was picked from residues from dissolving block 9571. The dry specimen was mounted on a 3-mm-diameter brass pin using colloidal carbon in isopropanol.

The specimen was first analyzed uncoated under LVSEM using a Hitachi S3000N variable pressure SEM at Royal Holloway University of London (by A. C. Scott, under low vacuum and in backscatter electron mode; see Scott et al. 2009 for details). Following LVSEM analysis, the specimen was investigated using SRXTM in 2006 at the Tomography Station of the Materials Sciences beamline (predecessor of the TOMCAT beamline; Stampanoni et al. 2006) of the Swiss Light Source, Paul Scherrer Institut, Villigen, Switzerland (Stampanoni et al. 2002), as outlined by Scott et al. (2009). The ovule was too large to fit on a single scan, so the chalazal and apical regions were scanned separately (data set A and B). In 2009, the data was analyzed in Avizo version 5.0 (Mercury Computer Systems, Chelmsford, MA), but at that time, the authors mistakenly thought they had only an incomplete image stack when producing figures 5 and 6 in Scott et al. (2009). In 2018, the original SRXTM data was reanalyzed in detail, with individual images adjusted in ImageJ (<https://imagej.nih.gov/ij/>), using Fiji (<https://imagej.net/Fiji>) for bulk image brightness/contrast editing and to run a despeckle pass to reduce noise. Data was analyzed and manipulated using Avizo version 9.1, and the ovule was reconstructed using Drishti (ver. 2.6.4; <https://sf.anu.edu.au/Vizlab/drishti/index.shtml>). Software improvements since the earlier analyses enabled recognition of additional anatomical features within the data sets.

After SRXTM analysis, the specimen became fragmented during transportation because of its brittle nature. The remaining fragments were mounted on an SEM stub using a carbon filter pad and analyzed on a Thermofisher Phemon ProX SEM at the Birmingham Electron Analytical Microscope facility (University of Birmingham). The specimen was uncoated and investigated at 15 kV using two backscatter detectors. The

resultant digital SEM images were edited (cropped; brightness, contrast, and intensity levels adjusted) in GIMP (ver. 2.8.16; <http://www.gimp.org>). All figures were constructed in Inkscape (ver. 0.92; <https://inkscape.org>).

Results

Genus—*Hirsutisperma* gen. nov. J. Hilton,
J. Galtier and A.C. Scott

Generic diagnosis. Very small hydrasperman ovule, radially symmetrical and conical. Integument and nucellus adnate except at the apex, where the nucellus forms the pollen chamber. Cylindrical pedicel progressively enlarging into the integument, showing longitudinal lobes. Above the plinth, integument lobes free, each containing a single vascular strand. Entire integumentary outer surface, including free distal lobes, densely covered by long multicellular hairs intertwined and spirally arranged. At nucellar apex, a wide, domed pollen chamber with walls composed of large cells with thickened walls, ranging to smaller cells surrounding a central opening. Pollen chamber floor of small cells with a conical central column.

Etymology. The generic name emphasizes the very distinctive hair covering of this ovule that is interpreted as being of special adaptive significance.

Species—*Hirsutisperma rothwellii* sp. nov. J. Hilton,
J. Galtier and A.C. Scott

Specific diagnosis. Conical ovule 2 mm long, up to 1.25 mm wide immediately above the pollen chamber. Base of ovule 270 μm in diameter, gradually widens in basal two-thirds of ovule length to 800–900 μm wide, reaching up to 1.20 mm below plinth. Integument thickness 180–220 μm ; eight free integumentary lobes, 330 μm in maximum diameter. Hairs at least 0.5 mm long, 10–20 μm in diameter. Glandular tips 35–45 μm long and 20–25 μm wide. Nucellus cavity obconical, up to 1400 μm in maximum length and 625 μm in maximum width, containing only fragments of megaspore wall. Pollen chamber dome shaped, up to 400 μm wide and 200 μm high. Cells of the pollen chamber wall rectangular, 20–25 μm in diameter and 60–80 μm long. Central column up to 240 μm wide and 160 μm high, made of small, thin-walled cells, 15–20 μm wide and 40–60 μm high. Single vascular strand enters ovule at chalaza and divides below nucellus into eight bundles, one in each integumentary lobe. Integumentary bundles 20–30 μm wide, composed of small tracheids 4–8 μm in diameter.

Etymology. The specific epithet is in honour of Gar W. Rothwell for his pioneering studies on the reproductive biology of Paleozoic ovules and for his seminal work piecing together the ontogeny and functional morphology of hydrasperman-type ovules.

Locality. Kingswood, Fife, Scotland (UK National Grid Reference NS 265 864).

Horizon. Kingswood Limestone, Kinghorn Volcanic Formation.

Stratigraphic age. DP subzone of the NM miospore zone; mid-late Asbian British regional substage, corresponding to the middle to late Viséan global stage (Mississippian, Carboniferous).

Holotype. V 68764 (figs. 1–7).

Depository. Palaeontological Collections, Natural History Museum, London.

Remarks. The new genus is distinguished from all other hydrasperman-type ovules by its small size and dense covering of hollow, spirally arranged hairs with apical glands with papillae. Remaining parts of the holotype are mounted on an SEM stub (see “Material and Methods”).

Description

Gross morphology. The following description is based on a single ovule with exceptional preservation that is 2 mm long and has a maximum diameter of 1.25 mm (fig. 1a). The ovule has a dense covering of thin, spirally arranged hairs that envelope the outer body of the integument and give the ovule an asymmetrical appearance (fig. 1a, 1b). Apically, the integument comprises eight terete integumentary lobes that surround an exposed nucellar apex (fig. 1c). The nucellar apex comprises a pollen chamber with a large apical opening and a central column within it (fig. 1c, 1d). In contrast to the asymmetrical hairs on the exterior of the integument, the inner parts of the integument, including the free lobes and the nucellar apex, show the ovule is radially symmetrical in transverse section (fig. 1c). The shape, organization, and tissue compositions of the ovule are best characterized from analysis of the three-dimensional SRXTM data set in longitudinal (fig. 2) and transverse (fig. 3) sections. Longitudinal sections show the integument is conical, widening gradually in the basal two-thirds of the ovule’s length before gradually narrowing (fig. 2a, 2b). Longitudinal paradermal sections show the organization of the integument protruding beyond the apex of the nucellus (fig. 2c, 2d). In transverse sections, the integument is entire in the basal ca. 50% of the ovule, where it gradually widens below the level of the nucellus and the structure of the integument (fig. 3a, 3b). Integumentary lobes develop distally from the chalaza (fig. 3c–3i) and remain attached to the nucellus for some of their length (fig. 3c, 3d) but become free from the nucellus apically (fig. 3e–3h). The nucellar apex is exposed between the projecting integumentary lobes (fig. 3e–3h), with the lobes extending beyond the end of the nucellus (fig. 3i) but taphonomically incomplete with irregular distal margins.

Integument. The most distinctive feature of the integument is the dense covering of long, slender, filamentous hairs on the outside of the integument (fig. 1a, 1b). These originate from the outer epidermis from vertically elongated, rectangular cells that are approximately 50 μm long and 20 μm wide (fig. 4a–4d). Individual hairs are at least 500 μm long (figs. 1a, 4d, 4f) and, where complete, have swollen, glandular terminations, often with a small apical papillae and spiraled rectangular cells (fig. 4e–4g). Hairs are approximately 10–20 μm thick (fig. 4f–4h), with those at the base of the ovule typically slenderer than those positioned apically (fig. 1a, 1b). The hairs appear to be multicellular, evidenced by broken hairs having internal wall divisions (fig. 4h) from very oblique wall endings. Hairs arise in bundles and twist around each other (fig. 4i) and tend to have a dominant vertical trend in their orientation when viewed in longitudinal sections (figs. 1a, 4a). However, when viewed in transverse section, a spiraled arrangement of the hairs is dominant, best seen in the SRXTM data set (fig. 5a–5c) and especially in the SRXTM virtual transverse sections (fig. 6c, 6d). At the

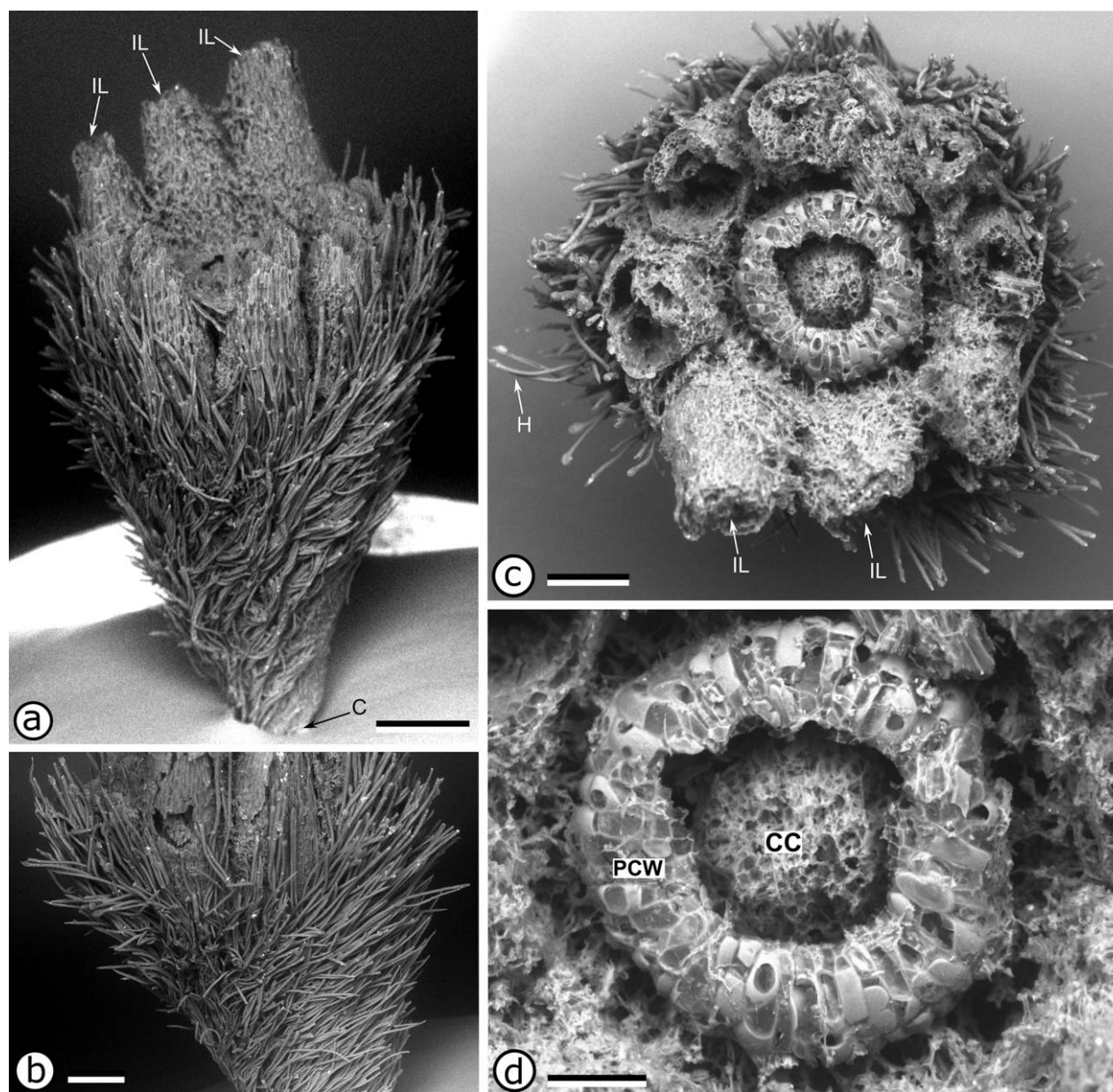


Fig. 1 Low-vacuum SEM images of *Hirsutisperma rothwellii* gen. et sp. nov. showing gross morphology. All images of the holotype (V 68764). *a*, Entire ovule in semioblique lateral view showing narrow chalaza (C) at pedicel level, apically free integumentary lobes (IL) and nucellar apex, and prominent integumentary hairs. *b*, Chalazal region of ovule showing dense covering of counterclockwise-twisting, long, slender integumentary hairs. *c*, Apical transverse view showing long hairs (H) on exterior of the integument and eight apically incomplete integumentary lobes surrounding the exposed central nucellar apex. *d*, Enlargement of *c* showing large rectangular cells of the pollen chamber wall (PCW) with apical opening and revealing cellular central column (CC) within. Scale bars = 500 μm (*a*), 200 μm (*b*, *c*), 100 μm (*d*).

base of the ovule where lobes are absent (fig. 1*a*), hairs appear to be uniformly distributed judging from SEM images (figs. 1*a*, 1*b*, 4*a*–4*c*) and in transverse sections from the SRXTM data (fig. 5*a*, 5*b*). Where hairs are absent at the base of the ovule, it is most likely due to taphonomic loss, as broken hair bases or gaps in the epidermal cells where individual hairs originate are clearly visible (fig. 4*a*). By contrast, where the integument is lobate, hairs are distributed on the external faces of the integumentary lobes only (fig. 5*d*, 5*e*), with no hairs occurring in the zone between adjacent lobes, where they start to separate from each other. Hairs arise in bunches (figs. 4*i*, 5*d*–5*f*) and intertwine with one another (fig. 4*i*).

The integument is differentiated into distinct tissue zones, with a uniseriate external epidermis (figs. 4*a*–4*d*, 5*a*–5*e*) of rectangular cells, 3.5–5 μm thick, and zones of thick-walled and thin-walled cells apparent inside the epidermis. Immediately

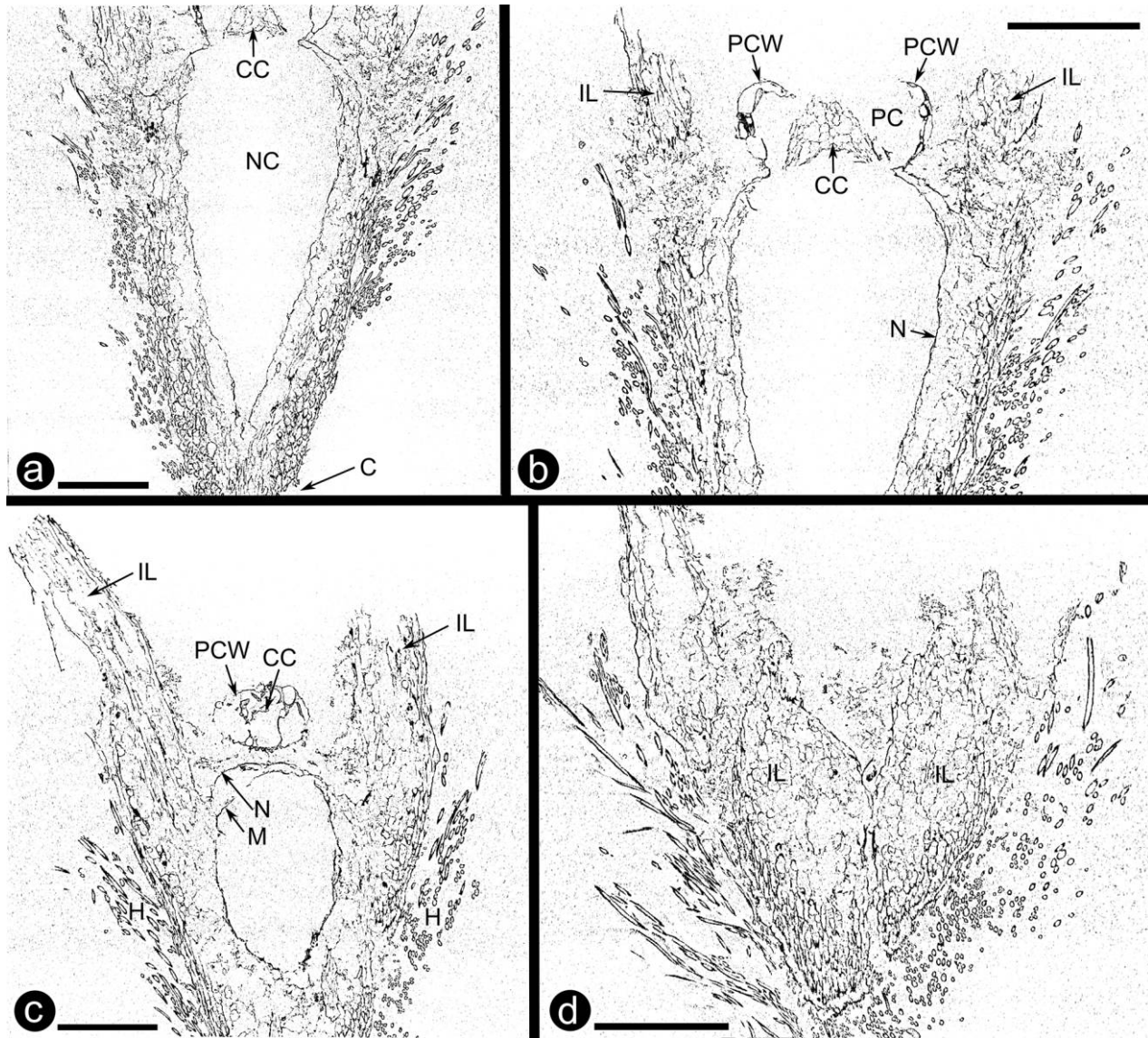


Fig. 2 Virtual longitudinal tomographic sections from the SRXTM data of *Hirsutisperma rothwellii* gen. et sp. nov. showing internal organization and anatomy. All images of the holotype (V 68764). *a*, Section through chalaza (C) to base of the nucellar apex showing maximum height of the conical nucellar cavity (NC). *b*, Section through distal part of ovule with integumentary lobes (IL) and nucellar apex showing small-celled central column (CC) and pollen chamber (PC) with decreasing cell size toward the distal opening. *c*, Vertical paradermal view of the side of the domed pollen chamber wall (PCW) above the nucellus (N) and megaspore (M) and longitudinal section of two integumentary lobes (IL). *d*, Vertical and oblique to paradermal section of three integumentary lobes (IL). Scale bars = 250 μm .

within the external epidermis is a thin zone, 10–15 μm thick, comprising two or three rows of small, thick-walled cells (fig. 5*d–5f*) that appear to represent sclerotesta. Individual sclerotesta cells are 4–6 μm in transverse direction and 6–8 μm wide, with thick cell walls that the scanned data (fig. 7*c*) do not allow us to characterize further. On the inner surface of this zone occurs larger, irregularly spaced cells (fig. 5*e, 5f*), typically 20–40 μm in diameter, with thin walls that appear to be parenchymatous and represent endotesta. Vascular bundles are situated in the center of each integumentary lobe and are surrounded by large, thin-walled cells that, in some sections, ap-

pear to be radially organized (fig. 5*f*) or often decayed (fig. 7*c*) but, in other sections, are less clear, and the entire lobe appears to be bilaterally symmetrical (fig. 5*h*). In paradermal views through the integument (fig. 2*d*), the thick-walled cells on the exterior of the integument are longitudinally elongated, 40–60 μm long.

In the previous report of the Kingswood ovule, Scott et al. (2009) considered the inner surface of the integument to have a covering of fine hairs. Here, we reinterpret these features (fig. 7*a, 7b*) either as decayed tissues of the integument or as microbial filaments draped over the tissues of the integument.

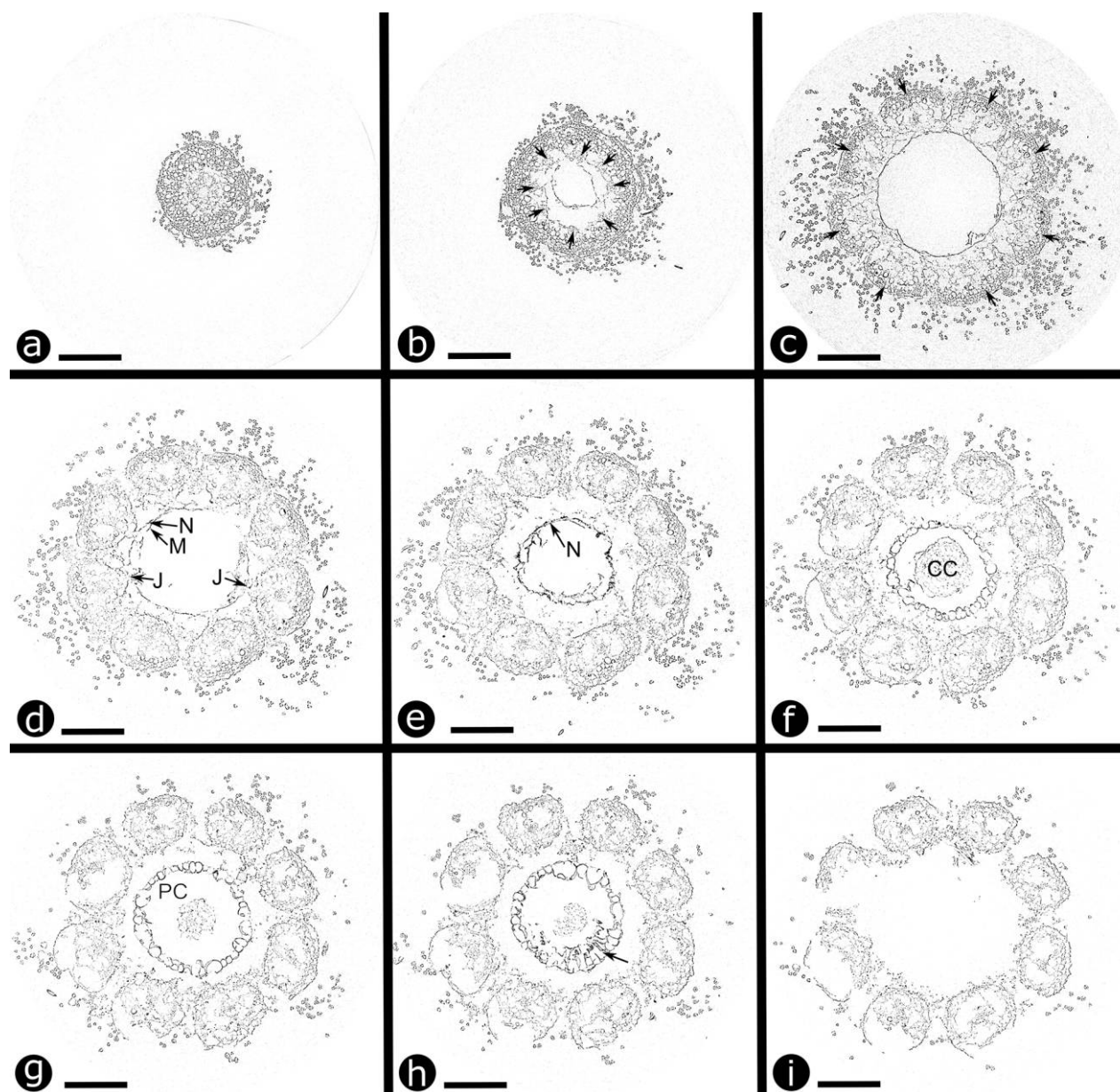


Fig. 3 Virtual transverse tomographic sections from the SRXTM data of *Hirsutisperma rothwellii* gen. et sp. nov. showing internal organization and anatomy. All images of the holotype (V 68764) and at same scale for comparison. *a*, Ovule pedicel with central vascular strand (section a900). *b*, Base of nucellar cavity with initiation of eight integumentary vascular strands (arrows) surrounded by hairs (a700). *c*, Maximum diameter of the nucellar cavity and lateral fusion of integumentary lobes (arrows; a220). *d*, Coalescence of nucellus and integumentary lobes (b550); conjoined (J) integument and nucellus (N) and distinct megaspore (M). *e*, Nucellus (N) free from integument lobes below pollen chamber (b510). *f*, Maximum diameter of the central column (CC; b470). *g*, Maximum diameter of the pollen chamber (PC) with uniseriate wall (b420). *h*, Paradermal view of top of the pollen chamber (arrow; b400). *i*, Free integumentary lobes above pollen chamber with few exterior hairs (b350). Scale bars = 200 μ m.

Nucellus, nucellar apex, and megaspore. The nucellus is thin and fused to the integument for the bottom half of the ovule, becoming free from the integument where the lobes start to separate from one another. At this level, the nucellus and integument are conjoined only at the innermost parts of the lobes (figs. 3*d*, 5*f*). The nucellar apex comprises a plinth, at which level the nucellus narrows below the pollen chamber (figs. 2*b*,

3*e*, 5*g*). The pollen chamber forms a wide dome, 280 μ m wide at its base and widening to 400 μ m apically, that is up to 200 μ m high. It comprises rectangular, thick-walled cells, 20–25 μ m wide and 60–80 μ m high, that are readily distinguished from the SRXTM data set (figs. 2*b*, 2*c*, 5*i*–5*l*). Cells of the nucellus get smaller toward the apical opening and bend inward into the center of the pollen chamber when viewed from above

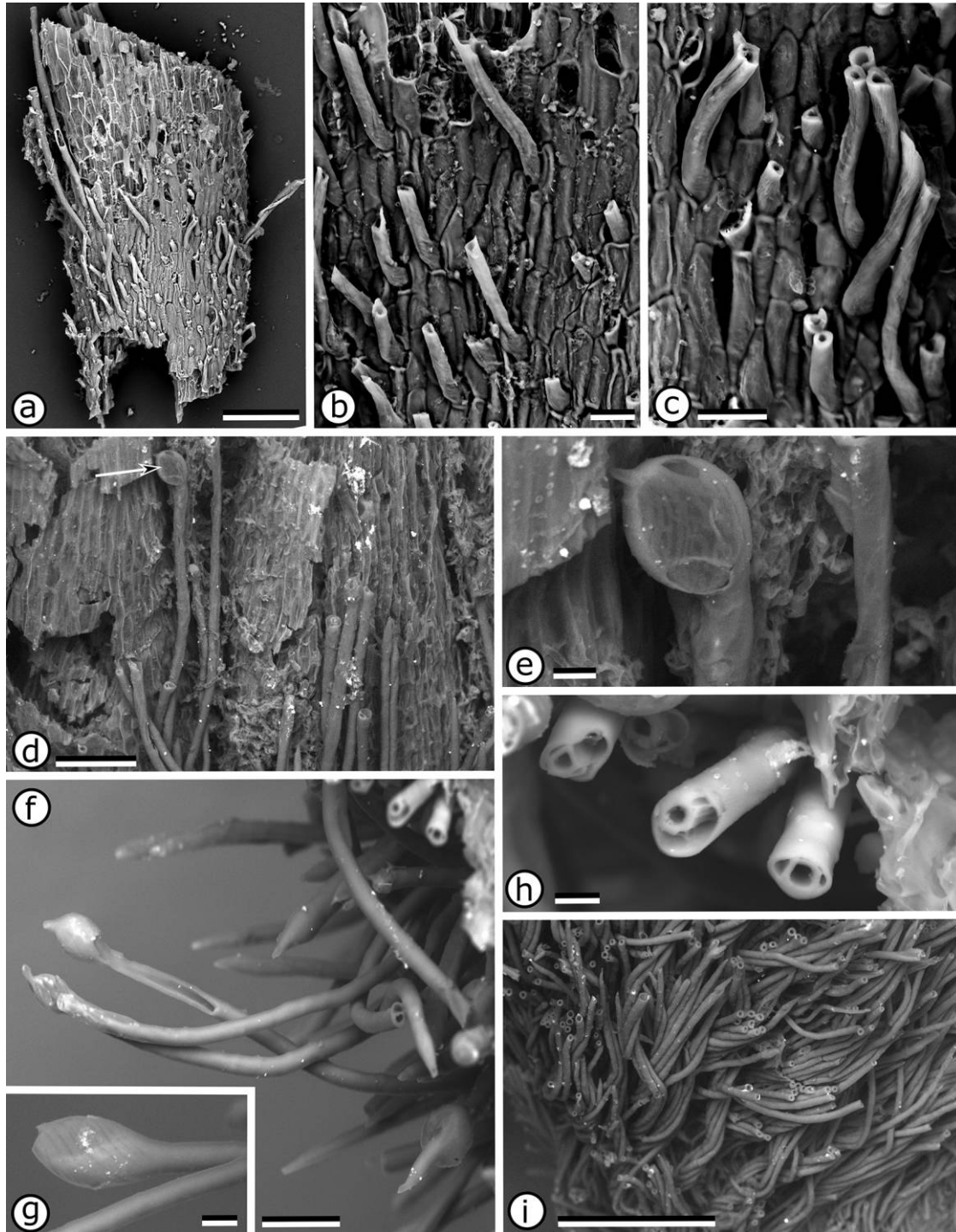


Fig. 4 Low-vacuum SEM images of *Hirsutisperma rothwellii* gen. et sp. nov. showing organization of the hairs on the exterior of the integument. All images of the holotype (V 68764). *a*, Portion of an integumentary lobe with many hairs removed, revealing epidermal cells and hair bases. *b*, Enlargement of *a* showing epidermal cells and basal regions of hollow hairs with twisted structure. *c*, Enlargement of *a* revealing elongate epidermal cells and hollow hairs with spiraled structure. *d*, Outer epidermis of an integumentary lobe with vertically elongated rectangular cells and a complete hair with glandular tip (arrow). *e*, Enlargement of *d* showing glandular apex of hair with spirally organized thickenings. *f*, Hairs with hollow centers and spiraled glands with pointed, nipple-like apices. *g*, Incomplete apical gland with prominent spiraling. *h*, Broken hairs with central bodies and divisions. *i*, Spirally arranged broken hairs organized in bundles. Scale bars = 100 μm (*a*, *d*), 20 μm (*b*, *c*), 10 μm (*e*, *g*, *h*), 50 μm (*f*), 200 μm (*i*).

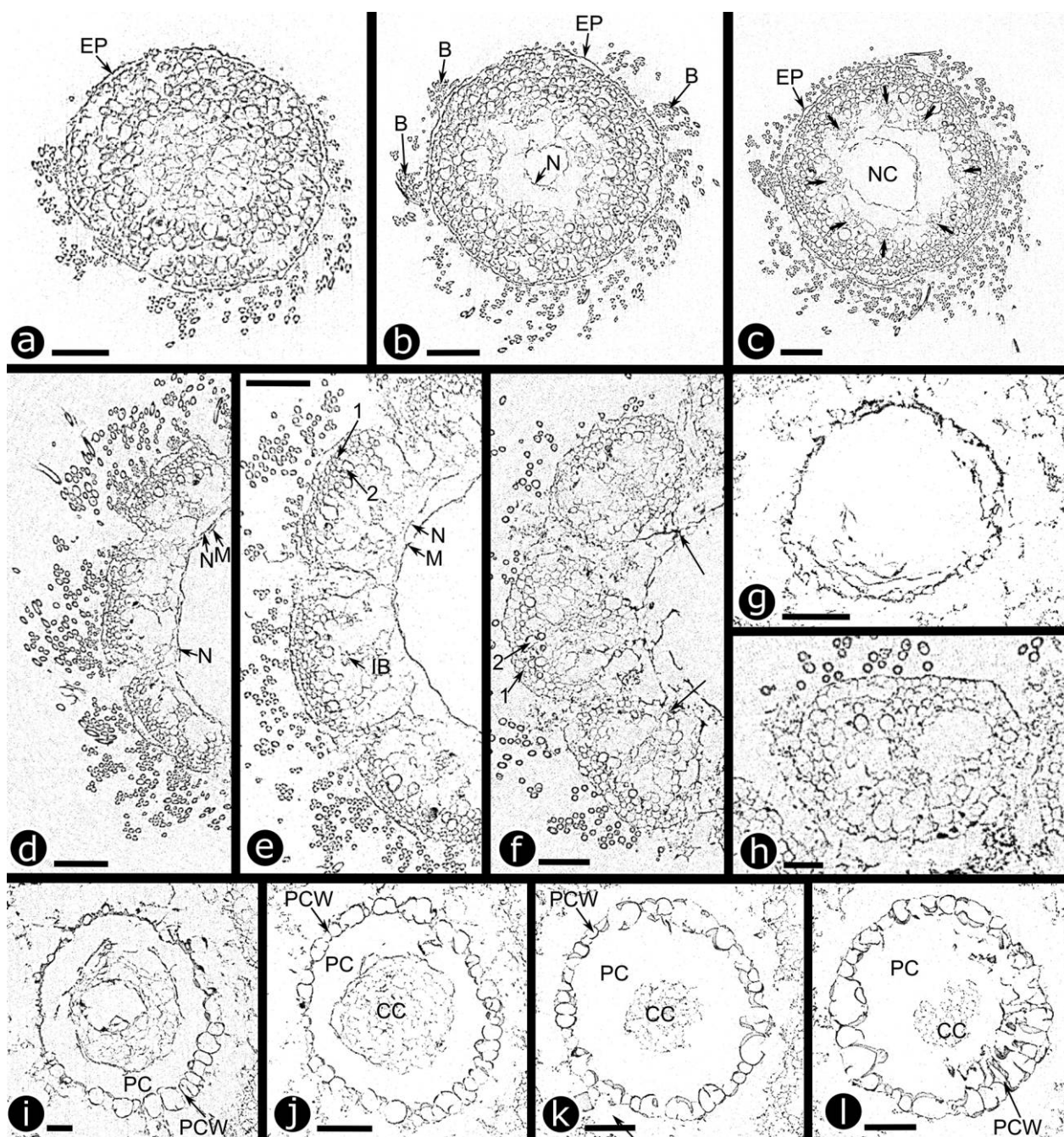


Fig. 5 Anatomy of the integument and nucellus of *Hirsutisperma rothwellii* gen. et sp. nov. from transverse SRXTM data of the holotype (V 68764). Section numbers indicated in parentheses. *a*, Pedicel showing bundles of hairs, uniseriate epidermis (EP), and single vascular strand (a0933). *b*, Base of nucellus (N) with two layered integuments and with uniseriate epidermis (EP) and bundles (B) of radiating hairs (a0801). *c*, Denser covering of hairs envelops uniseriate epidermis and integument with outer zone of small cells and inner zone of larger cells. Integumentary lobes starting to develop, with eight integumentary vascular bundles (arrows) and a small nucellar cavity (NC; a0700). *d*, Incipient integumentary lobes with hairs restricted to lobe exteriors and nucellus (N) fused to integument and megaspore (M) visible (a0413). *e*, Four integumentary lobes with uniseriate epidermis, exterior zone of small cells (1) bounded by larger cells on the interior (2). Nucellus fused to integument and megaspore in places attached to nucellus (b0633). *f*, Incipient integumentary lobes (still in narrow contact with the nucellus; arrows) with central zone (2) of radiating large, thin-walled cells and outer zone of small cells (1; a0127). *g*, Basalmost section of the free nucellus corresponding to the constricted “plinth” region (b510). *h*, Single integumentary lobe showing central vascular stand surrounded by thick-walled cells and radiating small cells (a0080). *i*, Base of the pollen chamber (PC) showing domed central area and thick, rectangular cells of the pollen chamber wall (PCW; a0053). *j*, Widest part of the central column (CC) with uniseriate pollen chamber wall (PCW; b0470). *k*, Widest section of the pollen chamber with smaller central column (CC) and large space (or annular cavity) inside the pollen chamber (PC; b0420). *l*, View from above of the pollen chamber with central column (CC) approaching apical opening, with smaller rectangular cells near the opening at right (b400). Scale bars = 100 μ m (*a-d, f*), 50 μ m (*e, g-l*).

(figs. 1*c*, 1*d*, 5*l*) or in longitudinal section (figs. 2*b*, 6*b*), and the pollen chamber opening appears to have a complete margin. The pollen chamber lacks a distal, tubular salpinx emanating from the roof, with the apical opening of the pollen chamber 95–110 μm in diameter. Centrally within the pollen chamber occurs a large central column comprising small, variably sized, polygonal, thin-walled cells (figs. 2*b*, 5*i*–5*l*) that are elongated longitudinally and appear to be parenchymatous. The conical central column has a concave base, with a maximum diameter of 240 μm , and is up to 160 μm high (figs. 2*b*, 5*i*). The apex of the central column sits immediately below the pollen chamber opening, leaving a gap 20–70 μm wide for pollen to enter. Pollen has not been identified in the nucellar apex. The megaspore membrane is in most places adnate, but in some places, the nucellus has separated from it (figs. 3*d*, 5*c*, 5*e*). The megaspore wall is extremely thin and impossible to measure from the SRXTM data set. Tissues of the megagametophyte are absent.

Vascularization. A single vascular strand enters the ovule centrally at the chalaza (figs. 2*a*, 3*a*, 5*a*) and divides below the nucellus (figs. 3*b*, 5*b*) into eight radially organized integumentary bundles, with each bundle corresponding to the position of a single integumentary lobe. Integumentary bundles extend to the end of the preserved length of the lobes (figs. 1*c*, 5*e*, 7*c*, 7*d*), but as the lobes are in each case incomplete, their full length, like the length of the integumentary lobes themselves, is unknown. At the apex of the integument, integumentary lobe bundles are terete and approximately 20–30 μm wide in transverse section, comprising 15–25 hexagonal tracheids varying in size from 4 to 8 μm wide (fig. 7*c*, 7*d*). The smallest (?protoxylem) tracheids are abaxially mesarch. In longitudinal section (fig. 7*d*), tracheids are approximately 2–4 μm wide with scalariform pitting.

Discussion

Taphonomy

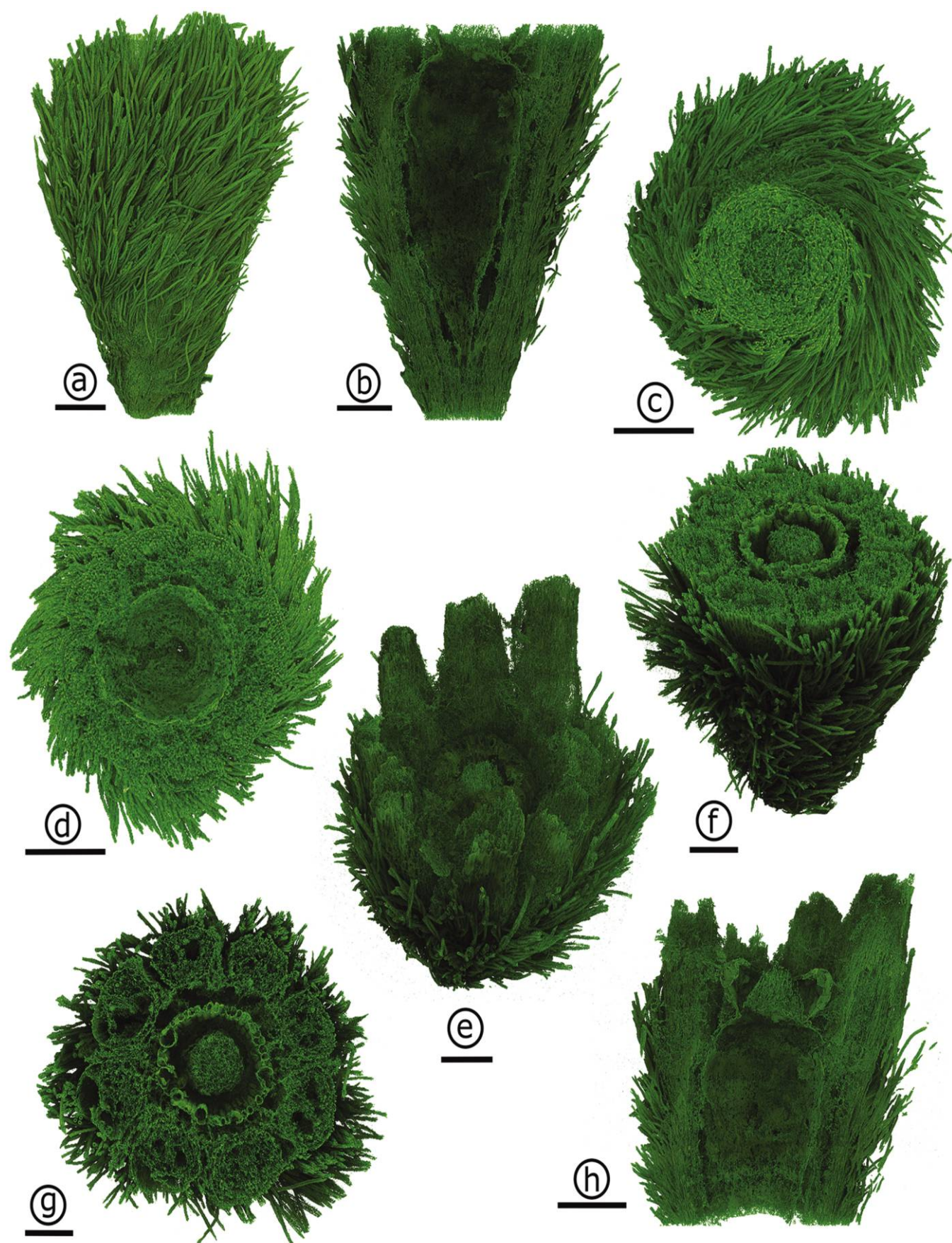
The Kingswood Limestone occurs as slumped blocks in a succession of volcanic ashes exposed in a faulted block within the Pettycur Caravan site. The base of the section comprises a series of coarse and fine ashes, but the top of the unit also contains limestone layers that range from 5 to 50 cm thick and in some cases are lens shaped. These show evidence of crude bedding but also evidence of slumping. The limestone blocks are supported within a matrix of mud, silt, ash, and basalt fragments and have a calcite micritic groundmass, with some areas containing scattered permineralized plants (Scott 1990*b*). There may also be scattered charcoal fragments. However, most of the charcoal is found in distinctive zones within the limestone. The charcoal ranges in size from a few millimeters to larger charcoalified wood fragments up to 1 or 2 cm in length. The charcoal fragments were well mixed in terms of size and comprise a range of plant organs—pollen organs, leaves, stems, wood, and the ovule described herein, together with abundant arthropod coprolites. Rare arthropod cuticles are also found, as well as occasional fish bones (Scott et al. 1986).

Charcoal may be produced both from the activity of wildfire (Scott 2010) and from plants being entombed in hot volcanic ashes (Scott and Glasspool 2005; Scott 2010). However, in the case of plants charred by entombment in hot volcanic ashes such as pyroclastic flows, the wood charcoal is often

found as whole stems or trunks, in some cases tens or hundreds of centimeters in length (Scott 2010). In wildfire charcoal, the size range is much smaller (Scott 1989), as the charcoal is formed by incomplete combustion (Scott 2010). The Kingswood charcoal is most likely to have been formed by the activity of wildfire. At Kingswood, it has been previously noted that the taxa preserved as charcoal are quite different from those preserved as calcareous permineralizations (Scott et al. 1986). Charcoalified fragments were produced from the activity of wildfire and could form from plants subjected to fire as part of the living vegetation or as litter. The occurrence of large numbers of charred coprolites suggests that the litter has been charred, as the coprolites are typical of arthropod coprolites produced by detritivores in the litter layer (Scott and Taylor 1983; Scott et al. 1992). However, the large number of pollen organs present that still contain pollen (Meyer-Berthaud 1989) suggests that living vegetation was also subjected to fire, possibly low-temperature surface fires. The ovule is also likely to have been charred while still attached to the living plant. If this was the case, the effect of the fire on the morphology and anatomy of the ovule needs to be considered.

Change in the dimensions of plant tissues in experimental charcoalification suggests that increasing the temperature of the wildfire can cause plant tissues to shrink, perhaps up to 50% (Lupia 1995; Belcher et al. 2005; McParland et al. 2007; Henry and Théry-Parisot 2014). However, many of these experiments expose the plants to high temperatures >450°C for one or several hours. In the case of low-temperature surface fires, temperatures may have been between 300° and 400°C for minutes rather than hours (Scott et al. 2000; Belcher and Hudpith 2016), and hence, plant tissues may not have undergone such a significant level of shrinkage. In hotter crown fires, leaves and fertile organs from the living plants tend to be consumed by the fire, and any leaf charcoal is predominantly produced in the litter (Scott 2010). By contrast, in long charring experiments (>1 h) with flowers and seeds, shrinkage has been observed up to 50% (Lupia 1995). In the case of the ovule described here, it is unlikely that this level of shrinkage took place, as there is no evidence of any residual high-temperature features such as bubbling (Scott 1989). However, it has been noted in nonwoody plant axes that even at 500°C different plant tissues may char differently, causing separation and differential shrinkage (McParland et al. 2007). In wet specimens of wood, rapid heating may cause instantaneous evaporation of water, and this may cause the sudden expansion of tissues (Harris 1958). We conclude that the measurements provided for the ovule here are likely to be within 80% of the original size and that the morphological features seen have not been significantly modified from their original condition. As such, *Hirsutisperm* would still have been a very small seed prior to charcoalification, possibly up to 2.5 mm long and 1.5 mm wide, assuming an 80% size reduction. However, an interesting possibility might be that different tissues in *Hirsutisperm* reacted differently to charcoalification. For instance, the parenchymatous central column may have shrunk more than the robust cells of the pollen chamber wall surrounding it because of taphonomy, potentially making an ontogenetically mature ovule in which the pollen chamber was sealed by the central column appear to be in a pollination configuration with a gap for pollen to enter the pollen chamber.

The limestone at Kingswood has been interpreted as being deposited at the margins of a crater lake (Scott et al. 1986; Scott



1990b). In such a case, the plants preserved as charcoal may have been living higher on the flanks of the crater or on the crater rim, and following a wildfire, postfire erosion washed the slurry of sediment and charred plants (Scott 2010; Scott et al. 2014) into the lake. This fits with the interpretation of *Hirsutisperma* being an *r*-selected species living in an unstable environment with low competition pressures as outlined below. The range of charcoal sizes and organ types suggests that the plants have not been subjected to extensive transport (see Nichols et al. 2000; Scott 2010), and the evidence of distinct bands of charcoal that also contain charred litter and coprolites together with rock fragments supports this conclusion.

Comparisons

The gross morphology of the ovule and in particular its exposed nucellar apex, with a central column and dome-shaped pollen chamber, and lobate integument firmly place the Kingswood ovule within the hydrasperman (=lagenostomean-type) pteridosperms (Rothwell 1986; Hilton and Bateman 2006). Features that separate it from previously recognized hydrasperman ovules are its small size and its dense covering of long, slender, intertwined, twisted hairs. The very dense spiral arrangement of hairs is especially striking in figure 6c and 6d and is unlike all other recognized Paleozoic ovules. Other Mississippian ovules have hairs on the exterior of the integument, but in each case, these are interpreted as straight and solid and lacking glandular apices, as in, for example, *Salpingostoma* (Gordon 1941), *Dolichosperma* (Long 1975), and *Tantalosperma* (Barnard and Long 1973). *Stannostoma oliveri* is small, 3.1 mm long and 1.5 mm wide, and is reported to have short papillae (Rothwell and Scott 1992), but again, the nature of its preservation and method of study may make this difficult to interpret. The stratigraphically younger ovule *Physostoma elegans* (Oliver 1909) has a dense growth of club-shaped hairs on the external surface of the integument and lobes, but its hairs are considerably thicker and are not helically arranged and lack glandular apices. Like the Kingswood ovule, *P. elegans* appears to lack a salpinx (Oliver 1909), but the ovule is larger at 5.5–6 mm long and up to 2 mm wide and has 10 integumentary lobes.

From the Mississippian of Scotland, there are three previously known ovule species that, like *Hirsutisperma*, have longitudinal ridges on the seed body that develop apically into integumentary lobes: *Salpingostoma* (Gordon 1941), *Tantalosperma* (Long 1973), and *Dolichosperma* (Long 1961). All

are considerably larger than *Hirsutisperma* (table 1) and have integuments with sparse hairs, with *Salpingostoma* distinguished by its trumpet-shaped salpinx, while *Tantalosperma* and *Dolichosperma* each have a wide, funnel-shaped salpinx. Although less well preserved in comparison to *Hirsutisperma*, the integument of *Tantalosperma* (Long 1973) also comprises a multi-seriate endotesta lacking secretory and a thin zone of sclerotesta comprising one or two rows of small, dense cells on the external margin of the ovule (see Long 1973, fig. 33). We consider *Hirsutisperma* to be more closely related to *Tantalosperma*, *Salpingostoma*, and *Dolichosperma* than to other hydrasperman-type ovules based on the presence of longitudinal ridges below the level of the integumentary lobes and their integumentary hairs.

The structure of the nucellar apex in the Kingswood ovule is unusual among hydrasperman taxa that typically have an elongate, tubular salpinx emanating from the apex of the pollen chamber (Rothwell 1986; Hilton and Bateman 2006). In the Kingswood ovule, the pollen chamber terminates abruptly with a large opening through which the central column is visible but does not protrude. The apical cells of the pollen chamber are complete (figs. 1d, 2b, 5l), from which we consider it unlikely that the salpinx has been lost taphonomically. The occurrence of thickened walls in the epidermal cells of the pollen chamber showing a gradient in decreasing size toward the opening (see figs. 2b, 5l) is a strong argument supporting a mature stage rather than inferring the nucellar apex to be immature, from which a salpinx has yet to develop. Further development of such a tissue composed of thickened (?lignified) cells is hardly conceivable.

Despite the evidence presented above, we cannot fully exclude the possibility that a tubular salpinx in *Hirsutisperma* was destroyed taphonomically; this is discussed below. Ovules of *Salpingostoma* are somewhat comparable to *Hirsutisperma*; in his description of *Salpingostoma* ovules contained in *Calathospermum* cupules, Walton (1949, pl. III, fig. 22) illustrated details of the pollen chamber with thickened dome cells similar to those of our specimen, but these are in continuity with a central tubular salpinx. In *Salpingostoma*, the salpinx is very thin, with cells hardly distinguishable, and would certainly be very fragile if not protected by the surrounding integument lobes (Gordon 1941; Walton 1949).

A similarly broad, dome-shaped pollen chamber lacking a salpinx, as seen in *Hirsutisperma*, is known in other Mississippian ovules including the stratigraphically contemporaneous species *Sphaerostoma ovale* from Pettycur (Benson 1914; table 1). Our views from above the pollen chamber (e.g., figs. 1d, 5l) are similar to Benson's text-figure 2b and plate II, figures 7 and 10, that show the roof of the pollen chamber in surface view

Fig. 6 External morphology virtual reconstruction of *Hirsutisperma rothwellii* gen. et sp. nov. from the three-dimensional SRXTM data set using Drishti (by A. R. T. Spencer). All images of the holotype (V 68764) and from data set A. *a*, External lateral view of the basal-medial part of the ovule, showing dense exterior covering of long, slender hairs with spiral arrangement. *b*, Virtual longitudinal section through the ovule showing conical form. *c*, Virtual transverse section through chalaza and base of the nucellus showing the dense mat of spirally arranged hairs. *d*, Virtual transverse section through midpoint of ovule showing spirally arranged hairs at level with incipient integumentary lobes. *e*, Apical view of ovule showing three more complete integumentary lobes and more fragmentary remains of the others. *f*, Oblique view of ovule with virtual transverse section through the nucellar apex showing central column, pollen chamber, and integumentary lobes surrounded by thin mat of hairs. *g*, Virtual transverse section through pollen chamber showing irregular, large cells in the pollen chamber wall and base of the pollen chamber adjacent to the central column. *h*, Virtual longitudinal section through apex of ovule revealing central column protruding from the apex of the pollen chamber opening but with a gap between it and the pollen chamber roof. Scale bars = 250 μ m.

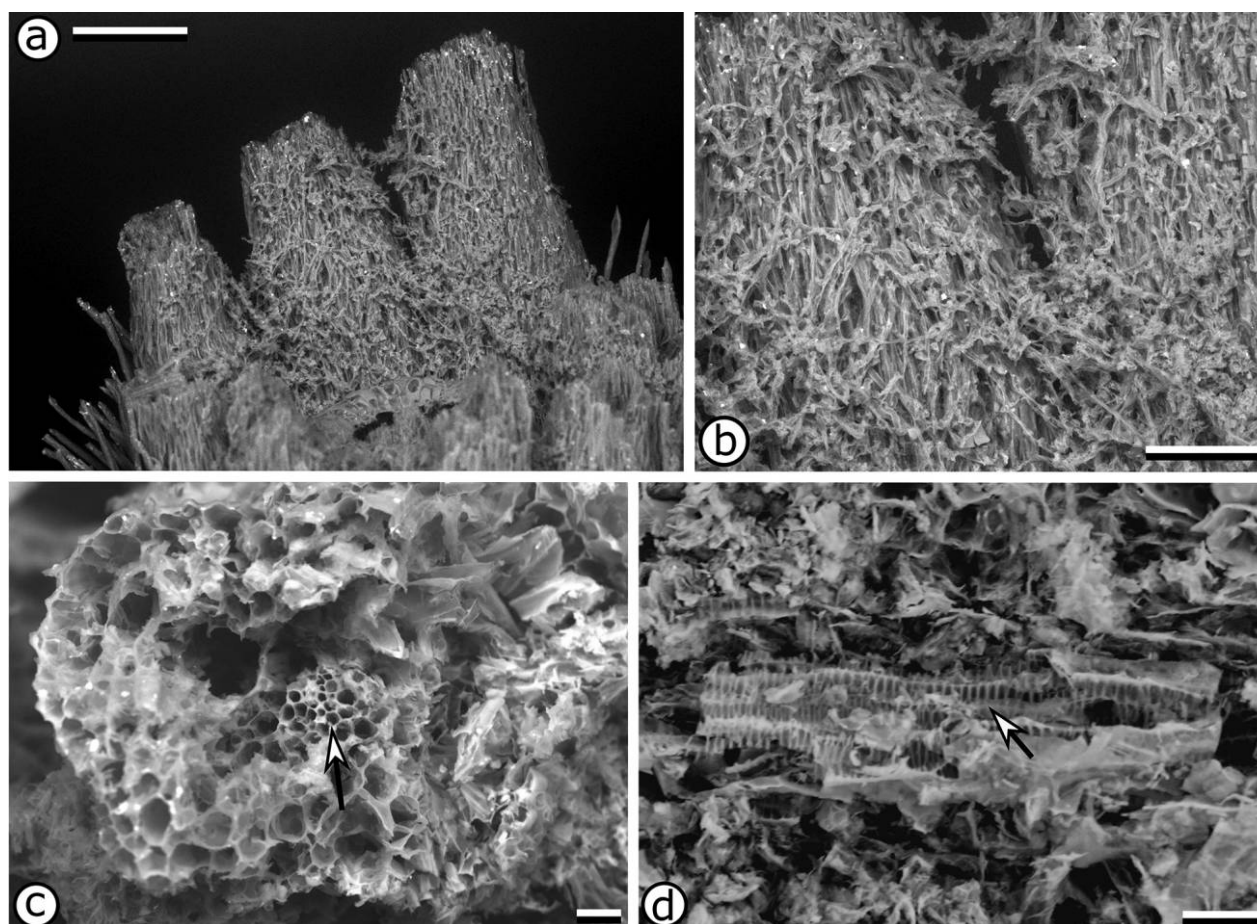


Fig. 7 Low-vacuum SEM images of *Hirsutisperma rothwellii* gen. et sp. nov. showing inner surface of the integumentary lobes and integumentary bundles. All images of the holotype (V 68764). *a*, Internal surface of the integumentary lobes showing fibrous texture; no hairs are attached to the internal surface. *b*, Enlargement from *a* showing detail of the fibrous texture. *c*, Fractured integumentary lobe apex revealing transverse section through an integumentary xylem bundle (arrow) with mesarch organization, surrounded by thin-walled cells. *d*, Fractured integumentary lobe showing a xylem bundle in longitudinal section with scalariform thickening of tracheids (arrow). Scale bars = 200 μm (*a*), 100 μm (*b*), 20 μm (*c*, *d*).

and the central column. In *Sphaerostoma*, like in the Kingswood ovule, the pollen chamber cells possessed thickened walls, which have been compared by Benson (1914) to a fern “multiseriate annulus.” Most importantly, Benson (1914) was able to compare ontogenetically mature and younger ovules from *Sphaerostoma*; in younger ovules, epidermal cells are thin walled, and the overlying parenchyma is undergoing lysigenic degeneration. She proposed a summary of developmental stages; namely, “special thickening of the roof-cells of the pollen chamber. Concomitant lysigenic degeneration of the subjacent tissue leading to the excavation of the pollen chamber. Circumsessile dehiscence and consequent formation of a stomium by the upward movement of the free margin of the roof. The retention of the pollen by the downward curvature of the roof” (Benson 1914, p. 12). Such an interpretation may be applied to our new ovule, which would represent a distinct condition within the hydrasperman pollination syndrome and indicate a close relationship of the Kingswood ovule with *Sphaerostoma*.

Sphaerostoma is larger than the Kingswood ovule at 3.5 mm long and 2.2 mm wide and is further distinguished by its apical integument comprising eight short integumentary lobes composed of large cells constituting a crest or “frill” surrounding the micropyle (table 1). A further difference is that *Sphaerostoma* was borne inside a uniovulate cupule and, thus, at the time of its description, was considered comparable to the stratigraphically younger genus *Lagenostoma* (Oliver and Scott 1904).

It is important to consider the ontogenetic stage of *Hirsutisperma* in relation to other Mississippian ovules to determine whether this explains the unusual features of its nucellar apex and the absence of the salpinx. Differences in size of the pollen chamber of the ovules shown in table 1 do not result from different degrees of ontogenetic development; in all cases, the pollen chamber is “mature,” with pollen chamber wall cells thickened. Comparison of the size of the pollen chamber in relation to the size of the ovule (or of its nucellar cavity) is about the same (table 1), suggesting that the smaller ovules will not increase

Table 1
Comparison of Mississippian-Aged Ovules Most Similar to *Hirsutisperma* gen. nov.

	<i>Hirsutisperma</i> gen. nov.	<i>Dolichosperma</i> <i>sexangulatum</i>	<i>Salpingostoma</i> <i>dasu</i>	<i>Tantaloosperma</i> <i>setigera</i>	<i>Sphaerostoma</i> <i>ovale</i>
Ovule length	2	20	50	6	3.5
Ovule diameter	.8–1.25	2.6	6	1.2	2.2
Integument and nucellus thickness	.22	.3–.4	1–1.4	.2	.15
Integument lobe and vascular bundle number	8	6	6	4	8
Integument:					
Lobe length	>1	7.5	25	>2	? <.5
Lobe diameter	.3	.4	1.4	.4	? .2
Hair length	>.5	>1.15	>2–3	>1	
Nucellar cavity:					
Shape	Obconical	Obconical	Obconical	Obconical	Ovoid
Length	1.4	8	12	>3	>2
Diameter	.6	2	4	<1	1.4
Pollen chamber:					
Width	.4	1.5	1.6	.6	.75
Height	.2	.8	1	.2–.29	.23
Central column:					
Width	.24	.7	?	.2	<.3
Height	.16	.3	?	.1	.2
Salpinx length	Absent?	.5	6	.3	Absent
Reference	This article	Long 1975	Gordon 1941	Barnard and Long 1973	Benson 1914

Note. All measurements in millimeters.

significantly in size on becoming “fully mature.” The next ontogenetic steps for maturity concern megagametophyte and archegonia development. As the taxa in table 1 lack cellular megagametophytes and archegonia, all are in an immature growth stage, as demonstrated by Rothwell (1986), and hence at a similar ontogenetic stage.

Seed Ecology

Hirsutisperma appears to be in the pollination configuration of its hydrasperman reproduction life cycle (Rothwell 1986), in which the distal opening of the pollen chamber remains open for pollen reception and retention prior to fertilization. This is distinct from the hydrasperman postpollination configuration, in which the central column is pushed outward by the developing megagametophyte and seals the opening to the pollen chamber from within (Rothwell 1986). This, combined with the absence of tissues of the megagametophyte, would suggest that the ovule was ontogenetically immature, contradicting our earlier interpretation that it was mature. The opening to the pollen chamber is 95–110 μm in diameter, but with the central column in its current position, a gap of 20–70 μm exists between the two that would present a size barrier for (pre)pollen of larger diameter to enter the pollen chamber.

Although we do not know how *Hirsutisperma* was borne on the parent plant as it was found isolated, existing evidence supports all hydrasperman-type ovules being borne within a cupule; where hydrasperman-type ovules are known in attachment to the parent plant, they are cupulate. Cupules were uniovulate such as *Pseudosporogonites* (Prestianni et al. 2013), *Spha-*

erostoma (Benson 1914), and *Lagenostoma* (Oliver and Scott 1904), uni- or biovulate such as the minute *Ruxtonia* (Galtier et al. 2007), or multiovulate such as *Elkinsia* (Rothwell et al. 1989), *Xenotheca* (Hilton and Edwards 1999), *Stammnostoma* (Long 1960b), and *Calathospermum* (Barnard 1960) among others. In most well-documented cupules, the ovule pedicel is very short and narrow, if not absent. This is in contrast with *Calathospermum* that bear ovules of *Salpingostoma dasu* (Gordon 1941) with thin and long pedicels similar to *Genomosperma kidstonii* (Long 1960a) and probably our new ovule. This is of interest because the organization of the *Calathospermum* cupule is quite distinct and may eventually suggest a dispersal of the mature pedicellate ovules. If this was the case for the new ovule, the hairy integument would represent an adequate adaptation. Our small new ovule was certainly very light, and the very dense and spirally arranged covering of hairs would have presented a highly efficient adaptation to wind dispersal. An interesting possibility might be that the spirally arranged hairs are in some way related to dispersal of the ovule from a cupule or perhaps for stopping arthropods from entering the cupule. However, we have no way of assessing these concepts based on the single specimen available.

The small size of ovules of *Hirsutisperma* suggests that its parent plant was, in terms of the traditional ecological *r/K* selection continuum (Taylor et al. 1990), an *r*-selected species, producing large numbers of small propagules, each with a low potential of surviving to adulthood. The *r*-selected species are adapted to life in less crowded ecological niches with low competition pressure and are considered pioneering species, often living in unstable or changing environments (MacArthur and Wilson 1967), as

previously interpreted for the Kingswood flora (Scott 2010; Scott et al. 2014). By contrast, based on evidence from size, larger hydrasperman ovules such as *Genomosperma* (Long 1960a) and *Salpingostoma* borne in cupules of *Calathospermum* (Gordon 1941; Walton 1949; Barnard 1960) were more likely to have been *K*-selected species, living in more established ecological settings with higher competition pressures. For *K*-selected species, it is advantageous to produce fewer but larger propagules, providing each with a higher potential to reach maturity and produce the next generation. *Hirsutisperma* suggests that ecological niche partitioning existed in Mississippian hydrasperman-type ovules.

Plant-Animal Relationships

The ovule is characterized by spirally arranged glandular hairs that also have spirally twisted groups of hair. It is pertinent to ask what the function of these would be and how this might provide further paleoecological data. We see three alternatives:

1. The glands contain repellent such as resin or other phytochemicals (see Farmer 2014) to deter feeding arthropods from granivory. During the Mississippian, there are no records of flying insects, but herbivores included millipedes, springtails (Collembola), and mites (see Scott and Taylor 1983; Scott et al. 1992; Labandeira 1998, 2002, 2006, 2007). Millipedes are centimeters in size and tend to feed on dead plant material; certainly some of the coprolites from Kingswood could have come from them (Rothwell and Scott 1988; Scott et al. 1992). Collembola are much smaller and could have been responsible for feeding on the living plants but would have been unlikely to eat entire seeds, even seeds as small as *Hirsutisperma*. Finally, mites are still smaller (see Scott and Taylor 1983; Labandeira 2007) and might have bored into the living plant tissues but would have been too small to eat it. We consider this the most likely function for the glands, especially if the plant was living in an active volcanic terrain in which removing toxins from the plant taken up through growth may have been important. We consider it unlikely that these glands contained resin, as there does not appear to be any solid residue preserved. It has been shown (de Oliveira et al. 2018) that if herbivory pressure is high enough, then the plant may have evolved glandular trichome secretions in response to it. This is even the case for very small plant organs, where there may be pressure from spider mites or other herbivores (Walters 2017). Many secretions also have dual roles (Schnetzler et al. 2017) as both antiherbivore and antimicrobial (Farmer 2014). The tip of the gland could act as a physical defense but when broken, for instance, by an arthropod, could release its toxins (Walters 2017).

2. The glands contain an attractant (for an example, see Aranguren et al. 2018) to promote visitation of an arthropod carrying pollen. We have no evidence of this. It is difficult to imagine one of these groups acting as a pollinator (see comments about the larger *Arthropleura* during the Pennsylvanian by Scott and Taylor 1983 and Labandeira 2002), and this contradicts existing evidence that suggests hydrasperman-type ovules were wind pollinated (see below).

3. The glands contain a sticky substance that is exuded either to help catch arthropod-carried pollen or, more likely, to help catch wind-borne pollen. Although hydrasperman-type ovules were anemophilous (see Niklas 1981, 1985), pollen needed to

enter the nucellar apex to facilitate pollination, for which a pollen drop mechanism would have been beneficial. Pollen drops are widespread in extant seed plants (e.g., Gelbart and von Aderkas 2002) and have been reported in the fossil record in callistophytalean (Rothwell 1978) and medullosan ovules (Combourieu and Galtier 1985), but they are unknown in hydrasperman ovules. We consider that, in very hirsute integuments, only pollen received on the inner surface of the integument lobes and above the pollen chamber had any chance of being trapped and subsequently playing any role in pollination.

The balance of probability is that these glandular trichomes, which are hollow inside, may have produced a toxin or even acyl-sugars (Luu et al. 2017) that acted as an antiherbivore or even against pathogenic fungi.

Concluding Remarks

Since the original studies of Scott et al. (1986), Meyer-Berthaud (1986), and Meyer-Berthaud and Galtier (1986), the Kingswood flora was recognized as an assemblage dominated by fusainized seed plant remains including stems, rachides, distal parts of fronds, and pollen organs, as well as fragments of gymnospermous wood. We present here the first description of a female gymnosperm organ as a minute ovule attributed to a new taxon. The whole-plant relationship with one of the stems, one of the five types of rachides, or one of the two pollen organs already described from the assemblage remains to be resolved. However, it is of interest that dislocated segments of a *Calathospermum*-type cupule have previously been identified from the site; considering the similarity of *Salpingostoma* ovules borne in *Calathospermum* cupules to *Hirsutisperma*, this may represent another part of the same whole-plant species. Of particular note is the presence of spirally arranged glandular hairs (trichomes) that may have contained phytochemicals that could have acted as an antiherbivore or an antifungal agent. The parent plant may have lived on well-drained volcanic soil and was subjected to wild-fire that preserved the ovule as charcoal.

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