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Were All Devonian Seeds Cupulate? A Reinvestigation of Pseudosporogonites hallei, Xenotheca bertrandii, and Aglosperma spp.

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WERE ALL DEVONIAN SEEDS CUPULATE? A REINVESTIGATION OF *PSEUDOSPOROGONITES HALLEI, XENOTHECA BERTRANDII,* AND *AGLOSPERMA* SPP.

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Premise of research.   Although the most comprehensively known Devonian seeds were borne in a "telomic" cupule, those of some species have been postulated as being borne terminally on naked axes lacking a cupule. Uncertainty remains as to whether such seeds were shed from a cupule before preservation. We reinvestigate the Upper Devonian fossils *Pseudosporogonites hallei* and *Xenotheca bertrandii* from Belgium and the similar ovules *Aglosperma quadrapartita* and *Aglosperma avonensis* from Britain and *Aglosperma* sp. from North America to consider their structure and organization and to determine whether they were cupulate.

Methodology.   Compressions/adpressions of *X. bertrandii* and *Pseudosporogonites* from Belgium and *A. quadrapartita* and *A. avonensis* from the United Kingdom, as well as *Anglosperma* sp. from Pennsylvania, were prepared, mainly by dégagement. Observation and photography were carried out using crossed polarizing filters.

Pivotal results.   *Pseudosporogonites hallei, X. bertrandii,* and *A. quadrapartita* comprise single ovules borne within small, radially symmetrical, uniovulate cupules. Integuments are entire at the chalaza but form flattened lobes distally. While a cupule is unknown in *A. avonensis,* its comparable integument morphology suggests that it was shed from a uniovulate cupule. Although the species are distinct from each other, their similarities show that they are closely related and belong to a single genus, for which the name *Pseudosporogonites* has priority. We emend *P. hallei* in light of our findings and erect the combinations *P. bertrandii* (Stockmans) C. Prestianni, J. Hilton et W. Cressler, *P. quadrapartitus* (J. Hilton et D. Edwards) C. Prestianni, J. Hilton et W. Cressler, and *P. avonensis* (J. Hilton) C. Prestianni, J. Hilton et W. Cressler.

Conclusions.   The uniovulate cupule in *Pseudosporogonites* is distinct from multiovulate telomic cupules of other Devonian seeds and expands the phenotypic diversity seen during the earliest phase of seed plant radiation, which was geologically instantaneous. Hydrasperman pollination in all proven Devonian seeds demonstrates evolution from a common ancestor, but finding morphological intermediates between seed and free-sporing plants remains a significant challenge to evolutionary plant biology.

Keywords: Famennian, gymnosperm, ovule, preovule, uniovulate cupule, hydrasperman, pteridosperm.

Introduction

The origin of the seed during the Devonian period represents one of the most significant events in the history of life on Earth, representing a fundamental change in the way plants overcame the biological and environmental constraints of free-sporing reproduction. The evolutionary development of the seed involved a number of steps that, although known in part in some other plant groups (Bateman and DiMichele 1994*a*), have been combined only by the seed plants into a single structure, namely, the seed (Rothwell 1986; Rothwell and Scheckler 1988; Chaloner and Hemsley 1991; Bateman and DiMichele 1994*b*). The order of acquisition of these steps remains tan-

talizing, as no convincing evolutionary intermediates from the stem group leading to the seed have been found to date, with their origin perhaps being a macroevolutionary (saltational) event for which intermediates may not have existed (Bateman and DiMichele 1994*b*). *Runcaria heinzelinii* Stockmans has been interpreted as a seed plant precursor (Gerrienne et al. 2004) and subsequently was characterized as a proto-ovule (Gerrienne and Meyer-Berthaud 2007). The presence of a single functional megaspore is unknown in this species, and therefore it is difficult to unambiguously interpret it as a member of the stem group leading to seed plants. In seed plants, the integument provided increased protection to the enclosed megagametophyte but also likely served to reduce water loss and ameliorate the effects of desiccation, as well influencing the aerodynamics of pollination to increase pollination potential (Niklas 1983, 1985; Rowe 1997). The origin of the seed was also associated with a general increase in reproductive unit size, providing greater resource investment in individual

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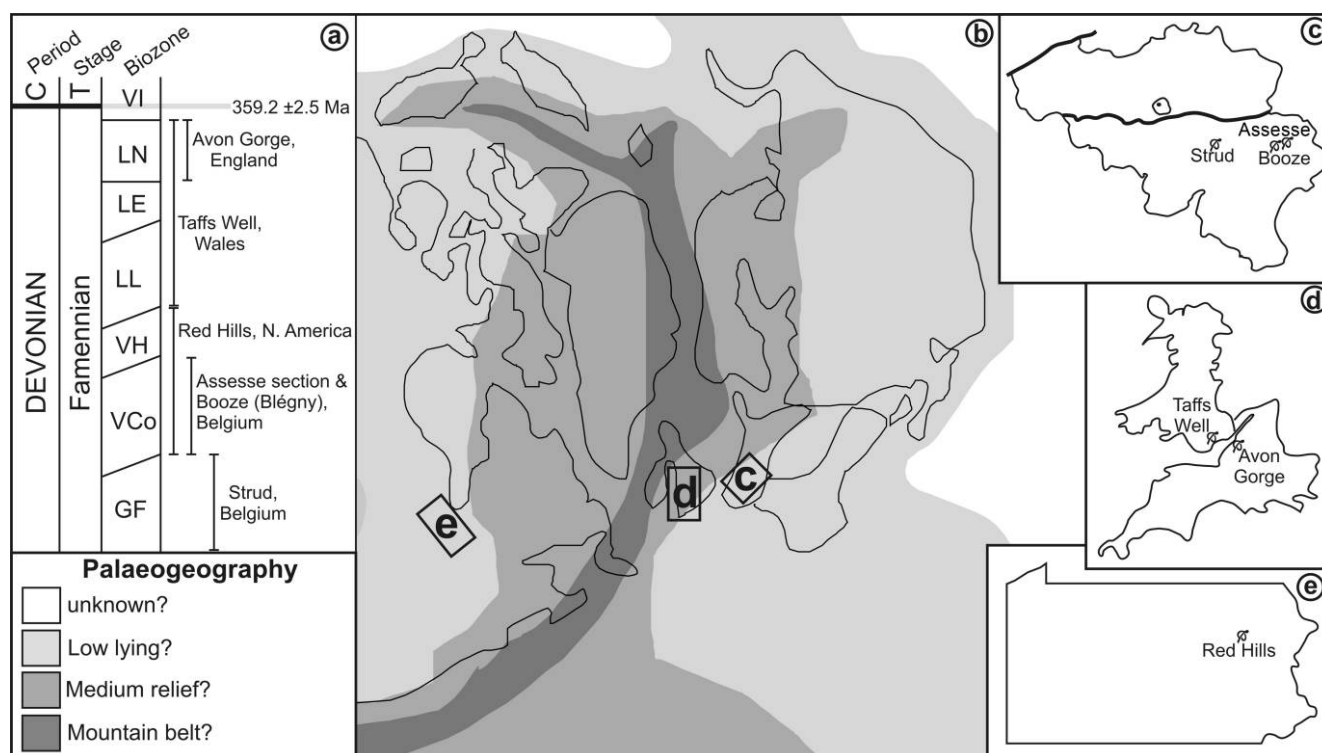
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Fig. 1 Age and location of the fossil plant assemblages containing species of *Pseudosporogonites*. *a*, Miospore biostratigraphy, showing age of assemblages studied. C = Carboniferous, T = Tournaisian, Ma = million years ago. *b*, Outline map of Famennian paleogeography, showing positions of locality maps in *c–e*. Modified from Scotese (1999). *c*, Outline map of Belgium, showing positions of Strud Quarry, the Assesse railway section, and the Booze quarry. *d*, Outline map of Wales and southwestern England, showing positions of Taffs Well and Avon Gorge assemblages. *e*, Outline map of Pennsylvania, showing position of the Red Hills assemblage.

propagules (Sims 2012) and fewer but individually more viable offspring (Bateman and DiMichele 1994*a*). Collectively, the evolution of the seed allowed seed plants to colonize habitats not available to free-sporing plants and to successfully reproduce without available free water (Chaloner and Pettitt 1987; Bateman and DiMichele 1994*a*; Rowe 1997; Prestianni 2005*a*), increasingly dominating terrestrial ecosystems since their origin.

Following the origin of the seed and the seed plant clade, the group underwent a rapid radiation event (Hilton 1998*a*; Prestianni 2005*a*; Prestianni and Gerrienne 2010) that we here consider to be their primary radiation; this appears to be both adaptive and nonadaptive (Bateman and DiMichele 1994*a*; Rowe 1997). Within the first 1–2 Myr of their recognition in the rock record before the Devonian/Carboniferous boundary, the group's diversity was apparent and included forms such as multiple ovules borne in telome-styled cupules (Pettitt and Beck 1968; Fairon-Demaret and Scheckler 1987; Rothwell et al. 1989; Hilton and Edwards 1999; Hilton 2006) and winged ovules (Rowe 1997), species interpreted as acupulate and lacking a cupule (Hilton and Edwards 1996; Hilton 1998*b*), and more enigmatic species with uniovulate cupules (Fairon-Demaret 1996). From this information it remains unclear which, if any, of the currently recognized organizations represent the primitive condition within seed plants (Hilton 1998*a*; Prestianni 2005*a*). Was the ancestral seed cupulate or

acupulate, and if it was cupulate, was it unicupulate or multicupulate? Such elusive questions are important for understanding homologies of the integument and cupule and identifying the early evolutionary history of the seed plants, from which insights into the order of acquisition of individual phenotypic characters and morphological intermediates may be identified. Here, we document additional phenotypic diversity within Devonian ovules through reanalysis of three previously published genera and in doing so demonstrate that the acupulate taxa were borne within small, uniovulate cupules.

Geological Information

Pseudosporogonites hallei from Strud Quarry in Belgium is situated in the Namur Parautochtone and occurs within Upper Devonian deposits attributed to the Evieux Formation (Stockmans 1948; Prestianni et al. 2007; fig. 1). This formation was recently renamed the Bois des Mouches Formation in the Namur Area (Delcambre and Pingot 2000). Fossil plants occur among abundant faunal remains, including the early tetrapod *Ichthyostega* (Clément et al. 2004) and primitive insects (Garrouste et al. 2012). Sediments from Strud were dated palynologically and attributed to the lower GF palynozone, corresponding to the middle Famennian (Prestianni et al. 2007).

Xenotheca bertrandii occurs in the Assesse railway section and the old quarry in Booze (Blégny) in Belgium (fig. 1*c*). The

Assesse railway section is located near Namur, is part of the Dinant synclinorium, and belongs to the Upper Devonian Evieux Formation (Stockmans 1948). No palynological analyses have been performed on samples from this locality. However, correlation with other coeval plant-bearing localities from the Evieux Formation (e.g., Durnal Langlier Quarry) allow it to be dated to the VCo palynozone (Fairon-Demaret and Scheckler 1987). The Booze quarry is part of the Booze/Val Dieu ridge near Liège, which exposes the Evieux Formation (Ancion et al. 1943) and has also been attributed to the VCo palynozone (M. Streel, personal communication, 2010).

Specimens from the Taffs Well assemblage near Cardiff in South Wales (fig. 1d) occur within the Quartz Conglomerate Group of the Old Red Sandstone in the Castel Coch anticline (Gayer et al. 1973). This assemblage contains key miospore taxa from the LL, LE, and LN biozones of late Famennian age (Higgs et al. 1988; Bless et al. 1992).

Fossil plants from the Avon Gorge assemblage (the "*Rhacophyton* bed" of Utting and Neves 1969) near Bristol in west England (fig. 1d) occur in the Shirehampton Beds, which in this area represent the uppermost part of the Upper Old Red Sandstone facies. The Avon Gorge plant bed has been dated to the late Famennian LN miospore biozone (Hennessy and Higgs 1999), a revision of former assessments that it belonged to the basalmost Carboniferous VI miospore biozone (Higgs et al. 1988).

Fossil plants from the Red Hill locality in Pennsylvania occur in sediments of the Duncannon Member of the Catskill Formation that comprise fluvial sandstones, siltstones, and mudstones (Cressler et al. 2010). These sediments occur within the VCo miospore biozone of the Famennian (Cressler et al. 2010).

Material and Methods

Specimens of *Pseudosporogonites hallei* and *Xenotheca bertrandii* were collected by F. Stockmans in 1937–1938 and are deposited in the Paleontological Collections of the Royal Belgian Institute for Natural Sciences (RBINS) in Brussels. These specimens were subsequently included in Stockmans's pioneering monograph on the Upper Devonian flora of Belgium (Stockmans 1948), in which *P. hallei* was illustrated by a single specimen on plate XL, figures 18 and 18a, and *X. bertrandii* was illustrated by four specimens in plate XL, figures 14, 14a, 15, and 17. From the collections at the RBINS, 52 specimens of *Pseudosporogonites hallei* and up to 150 specimens of *X. bertrandii* have been identified. *Pseudosporogonites hallei* is preserved as adpressions and occasional compressions in a gray-green-colored silty sandstone. *Xenotheca bertrandii* is preserved as compressions and partial adpressions in a micaceous sandy siltstone matrix that ranges from green-gray to buff colored.

Specimens of *Aglosperma quadrapartita*, as documented by Hilton and Edwards (1996), were collected by R. A. Gayer and D. Edwards (Cardiff University) in geological sampling of the Taff Gorge, as documented by Gayer et al. (1973). Specimens of *Aglosperma avonensis* were collected in the 1960s and 1970s by R. H. Wagner, J. Utting, R. Neves, and colleagues at Sheffield University during student fieldwork (Utting and Neves 1969) and in the mid-1990s by Hilton and colleagues from Cardiff University (Hilton 1998b) and are as documented

by Hilton (1998a, 1998b). Specimens of both *A. quadrapartita* and *A. avonensis* are deposited at the National Museums of Wales, Cardiff. Additional (unfigured) specimens from the Avon Gorge plant bed are deposited in Cordoba (Spain) in the research collections of R. H. Wagner. Specimens from Red Hills assemblage (Pennsylvania) are as documented by Cressler et al. (2010) and are deposited at the Academy of Natural Sciences, Philadelphia.

All specimens are preserved as compressions/impressions and were prepared for morphological investigation mainly by dégagement (Fairon-Demaret et al. 1999). Positions of measurements taken and the terminology used are shown in figure 2. Illumination of specimens for both dégagement and photography was provided by a Zeiss Stereo CL 1500 light source. Specimens were photographed dry, using crossed polarizing filters to enhance the contrast. A deltapix camera fixed on a Zeiss Stemi 2000 stereomicroscope was used for all detail photography. Macrophotography was done with a Nikon D70 camera with a Nikon 35-mm macro lens.

Results

Pseudosporogonites hallei *Stockmans*

Description. The majority of specimens comprise isolated ovules (fig. 3a), of which 52 have been identified and 22 are complete. A single specimen shows the distal parts of the fertile branching system, with a terminal cupule that envelops the
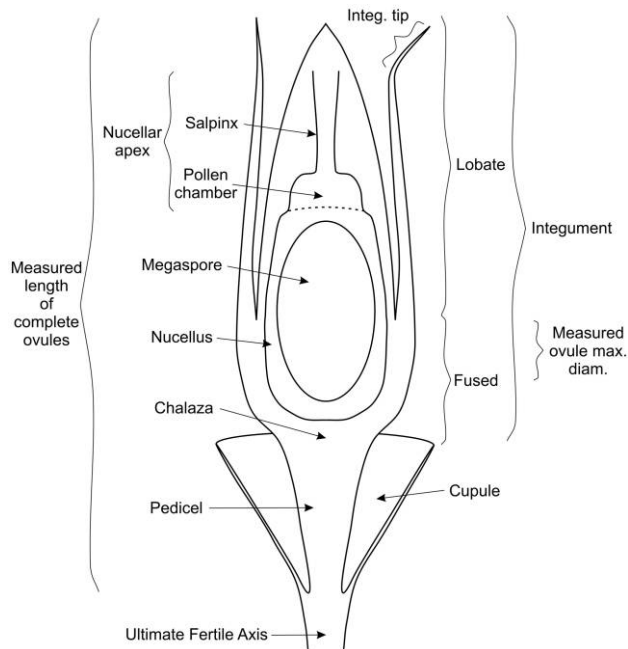
Fig. 2 Diagrammatic reconstruction through midlevel of *Pseudosporogonites*, showing gross morphology of the cupule and ovule. The positions of key measurements taken are indicated, along with the terminology used in the description. "Ultimate fertile axis" represents the distal parts of the plant's fertile branching system, and the dashed line below the pollen chamber represents the position of the membranous pollen chamber floor (or plinth) in hydrasperman ovules.

base of a single, centrally placed terminal ovule (fig. 3b). The axis is incomplete, 10 mm long, and 0.3 mm wide and represents the distal part of an otherwise unknown cupuliferous branching system. Complete ovules, measured from the tips of the attachment of the pedicel to the tips of the integument lobes, are 5.6–7.5 mm long ($\bar{x}$ = 6.4 mm; n = 22) and 1.7–2.7 mm wide ($\bar{x}$ = 2.2 mm; n = 22 specimens) and have a long pedicel and a lobed integument (fig. 3a) surrounding a nucellus with a prominent nucellar apex.

The cupule is particularly difficult to distinguish and is absent or indistinctly preserved in the majority of the specimens. In compression it occurs as a slightly flared structure borne at the end of long, slender pedicels (fig. 3b–3d) and ranges between 1.4 and 1.7 mm wide and between 1.9 and 2.1 mm long. It is shaped like a small collar that we here term a "collaret"; this completely surrounds the pedicel at the base of the ovule (fig. 3c, 3d). Sometimes an inconspicuous longitudinal striation can be observed at its surface, and although imperfectly preserved, the distal margin of the cupule is irregular and seems to be dentate (fig. 3c, 3d). A single specimen (RBINS 31729; fig. 3e) shows an ovule slightly detached from the cupule. This, as well as the abundance of isolated ovules in the sediment, appears to represent the point of facultative abscission of ovules from the cupule, but it may be taphonomic.

The absence of a cupule in most of the specimens allows the base of the ovule to be observed in detail, and the chalaza is visible only when the cupule is absent. The ovule pedicel is typically poorly preserved but characteristically tapers and gives the base of the ovule a pointed shape (fig. 3f, 3g). The tapering shape of the ovule pedicel suggests that the cupule has a similarly shaped hollow central attachment scar after abscission. At the chalaza the integument is entire (fig. 3f–3h), but distally it consists of four elongated, flat lobes (fig. 3a, 3h, 3i). In plan view the integumentary lobes are broad and lanceolate (fig. 3f, 3g) and measure 4.5–7.5 mm long and 2–3 mm wide, and in profile view the lobes are very thin and have a slight flare outward near the apex (fig. 3a, 3f, 3g). The integument is entire for less than one-third of its total length in most specimens (fig. 3f), but in some cases it is entire up to approximately half of the ovule length (fig. 3g) and forms lobes distally. The ovule broadens in the midpart of its length and narrows distally, following the shape of the nucellus. Distally, the integumentary lobes diverge and become separated and either flare outward (fig. 3a, 3f, 3g) or gently taper inward (fig. 3h), where they form an acute tip. The micropylar region is open and surrounded to varying degrees by the lobate integument (fig. 3a, 3f–3i).

The nucellus is visible in only a few specimens, because it is covered in most cases by the integument. Where complete, it is tightly adpressed against the integument. On preparation by dégagement, individual lobes readily detach from the specimen (fig. 3h) to reveal the nucellus below. In the most complete and best-preserved specimen, the nucellus is 4.5 mm long and 2 mm wide (fig. 3h), but in other specimens the nucellus is smaller and typically measures 3 mm long and 2 mm wide. The nucellus has a rounded chalaza and smooth sides. Distally, the nucellus is attenuated and forms a dome-shaped pollen chamber 1.3 mm wide and 0.8 mm high, with a conspicuous floor and a short (0.7 mm high) salpinx with a distal fringe (fig. 3i). At this level the integument is free from the nucellus,

there is a prominent gap between the two, and the nucellar apex is exposed between the integumentary lobes (fig. 3a, 3h, 3i).

Interpretation of P. hallei. *Pseudosporogonites hallei*, as documented here, is shown to possess a small cupule that envelops the base of a single, radially symmetrical ovule that comprises four flattened integumentary lobes surrounding a nucellus with a hydrasperman-type pollen chamber and a salpinx. We interpret the nucellus as being attached only at the chalaza because the integumentary lobes readily detach on preparation, suggesting that the two are unfused. The integument is shown to vary from apically recurved to slightly inwardly curved, but we are uncertain of the causes of this. It may be taphonomic, relating to drying and partial desiccation of some ovules, or it could be ontogenetic, associated with the integument shape changing as the ovules develop, for example, in pre- versus postfertilization stages of maturation. However, there is no correlation of ovule shape and size with the structure of the integumentary apex, which makes ascertaining the likely causes of this variation difficult. We note that the Mississippian ovule genus *Genomosperma* Long (Long 1960), as currently characterized, includes (from the same floral assemblage) one species with short, inwardly curved integumentary lobes (*Genomosperma latens* Long) and another with longer, outwardly flaring integumentary lobes (*Genomosperma kidstonii* Long) that otherwise have virtually identical anatomy. Whatever the cause of this variation within a genus (i.e., *Genomosperma*) or species (i.e., *P. hallei*), it appears that more than one Paleozoic ovule taxon exhibited a similar tendency in variation of integumentary lobe curvature. These ovule species are compared in more detail below.

Comparisons. The description and interpretation of *P. hallei* presented here shows it to be an ovule produced by a hydrasperman-type pteridosperm. The majority of previously recognized Devonian-aged ovules are borne within branched, multiovulate cupules that have varying degrees of fusion between cupule lobes, with individual ovules having varying degrees of integumentary fusion, from almost none (e.g., *Moresnetia*: Fairon-Demaret and Scheckler 1987), to fused midway (*Elkinsia*: Rothwell et al. 1989; *Xenotheca*: Hilton and Edwards 1999), to lobate only distally (e.g., distal-only *Archaeosperma arnoldii*: Pettitt and Beck 1968; *Glamorgania*: Hilton 2006). These differ from *P. hallei* in having multiple ovules laterally positioned within a single larger, "telomic" branched cupule and having terete rather than flattened integumentary lobes; in some species there are trichomes on the ovules (e.g., *Archaeosperma*). Furthermore, ovules in these multiovulate cupules tend to be much smaller, typically 1–5 mm long, as opposed to those of *P. hallei*, which are 5–7.5 mm long. The presence of a shared hydrasperman-type pollen chamber demonstrates that both kinds of morphologies evolved from a common ancestor.

Pseudosporogonites hallei shares some similarities with the uniovulate cupule *Dorinnotheca streelii* Fairon-Demaret from the Famennian of Belgium (Fairon-Demaret 1996). The cupule of *Dorinnotheca* comprises eight basally fused segments that form a large collaret around the base of a single ovule and is 2–5 mm long and 2 mm wide. Both species have an integument with four lobes in the distal two-thirds of ovule length, but those in *P. hallei* are thin and triangular to lanceolate, 5–7.5

Fig. 3 Cupules and ovules of *Pseudosporogonites hallei* (Stockmans) C. Prestianni et al. from the Devonian of Belgium. Scale bars = 1 mm unless otherwise stated. *a*, Holotype with well-preserved ovule having prominent apically recurved integumentary lobes and a pollen chamber. As with the majority of specimens of this species, the cupule is not preserved. Specimen RBINS-31878. *b*, Single ovule enclosed basally in a cupule borne ultimately on a thin ultimate fertile axis (UFA). RBINS-26679b. *c*, Enlargement of the cupule (C) from *b*, showing cup-like structure around the ovule's chalaza. *d*, Detail showing the cupule and the rounded base of the nucellus. RBINS-31823. *e*, Specimen with the cupule (C) slightly detached from the ovule at the chalaza (Ch); while this could be either abscised or taphonomically isolated, it demonstrates the position of weakness along which the two preferentially separate. RBINS-31729a. *f*, Isolated ovule with both a triangular pedicel (P) that widens toward the chalaza and distally recurved integumentary lobes (I). RBINS-31809b. *g*, Isolated ovule with one distally recurved integumentary lobe (I)

mm long, and 1.3–2.5 mm wide, while those of *Dorinnotheca* are thick and triangular, 4.5–7 mm long, 1.1–1.4 mm wide, and on the whole narrower. Both *Dorinnotheca* and *P. hallei* have a hydrasperman pollen chamber, but this is larger in *Dorinnotheca*, where it is 2–2.2 mm long, and the salpinx in *Dorinnotheca* is 2.0 mm long, considerably longer than the 0.7 mm in *P. hallei*. The segmented cupule, the integument shape, and the size of the nucellus, especially the nucellar apex, readily distinguish these species. We conclude that placing them in separate genera is justified.

The Famennian ovule *Condrusia rumex* Stockmans (Stockmans 1948; Fairon-Demaret 1996; Prestianni 2005a; Prestianni and Gerrienne 2010), from the Evieux Formation of Belgium, is very different from *P. hallei*. It possesses a cupule with two laminar segments ∼5.4 mm long and 4.6 mm wide surrounding an ovule with an entire integument and a hydrasperman-type nucellus that is 2.1–3.2 mm long and 1.3–1.9 mm wide and has a salpinx that is ∼2 mm long.

Pseusosporognites hallei is most similar to ovules of *Aglosperma quadrapartita* Hilton et Edwards (Hilton and Edwards 1996), *Aglosperma avonensis* Hilton (Hilton 1998a), and specimens named *Xenotheca bertrandii* by Stockmans (1948). These species lack a telome-style cupule, are typically larger than the ovules borne in telomic cupules, and have integumentary lobes that are flattened rather than terete. However, cupules have not previously been noted in these taxa, leading us to reinvestigate them individually (see below).

The Mississippian-aged ovules *G. kidstonii* and *G. latens* are similar to *P. hallei* in having flattened integumentary lobes with the distal half of the integument length being lobate. These species are anatomically preserved, unlike *P. hallei*, which prevents a full comparison, but species of *Genomosperma* are somewhat larger (*G. kidstonii*, 10–15 mm long; *G. latens*, ∼7–10 mm long) and typically have eight integumentary lobes. A cupule is unknown in *Genomosperma*, but these specimens are currently under investigation (Z. Wickens, personal communication, 2011). Our interpretation here is that *Genomosperma* is closely related to *Pseudosporogonites* but a distinct genus, with *Pseudosporogonites* appearing to represent a more basal member of the family Genomospermaceae sensu Long (1975).

The Pennsylvanian hydrasperman-type ovule *Lagenostoma lomaxii* Will. is borne in uniovulate cupules and has some similarities to *P. hallei*; detailed comparisons are restricted because *L. lomaxii* is anatomically preserved and anatomy is unknown in *Pseudosporogonites*. The cupule and integument of *Lagenostoma* are glandular (Williamson 1877), but the apex of *Lagenostoma* is open, with short integumentary lobes unlike the extended lobes in *P. hallei*.

Pseudosporogonites hallei shares some similarities with *Runcaria*, which was documented by Gerrienne and Meyer-Berthaud (2007) as a proto-ovule. In *P. hallei* the presence of a hydrasperman pollen chamber demonstrates it to be a seed plant, but in *Runcaria* there is no described distal opening of

the sporangium, and the presence of a single functional megaspore has not been proven. *Runcaria* may be an intermediate on the lineage leading to the seed, but its relationship with true seeds is uncertain, although in lacking a hydrasperman-type nucellar apex it is distinct from the stratigraphically younger *Pseudosporogonites*. Similarly, we remain unconvinced that *Spermolithus devonicus* represents a Devonian ovule (see Hilton 1998a) and conclude that it must be reinvestigated before detailed comparisons are possible.

As *P. hallei* has the greatest similarity to the contemporaneous species *X. bertrandii* and the younger species *A. quadrapartita* and *A. avonensis*, these have been reinvestigated in our study, along with the recently documented occurrence of *Aglosperma* sp. from North America (Cressler et al. 2010). For *X. bertrandii*, our intention is to determine whether it is an ovule and, if so, to determine its organization, structure, and relationship with *P. hallei*. As both species of *Aglosperma* are already well characterized as ovules, our investigation focuses on whether they, too, were cupulate.

Xenotheca bertrandii *Stockmans*

Description. The description of *X. bertrandii* is based on 141 specimens, of which 46 are complete. The most complete specimen (fig. 4a) comprises a small cupule (fig. 4b) that encloses the ovule pedicel and has four prominent, elongated integumentary lobes. The integument surrounds a nucellus that has an apex consisting of a small pollen chamber and a long, tubular salpinx (fig. 4a).

The cupule is difficult to distinguish and is present only on the best-preserved specimens. Cupules are highly variable in size, ranging from 2.25 to 5.2 mm long ($\bar{x} = 4.4$ mm; $n = 9$) and from 1.4 to 2 mm wide ($\bar{x} = 2.1$ mm; $n = 9$), and consist of a trumpet-shaped structure surrounding the pedicel (fig. 4a–4c). There is no distinct base to the cupule, with the apical part of the ultimate fertile axis gently widening to form the cupule. Cupules do not extend to the level of the ovule chalaza, and they end abruptly with an irregular, dentate distal margin (fig. 4a). In the best-preserved specimen, dark, longitudinally orientated strands can be seen in the cupule, and the dark, longitudinally oriented strands of the integument are visible through the thin and delicate structure of the cupule.

Complete ovules, measured from the pedicel immediately above the point of attachment of the cupule to the apex of the integument, are 7–11 mm long ($\bar{x} = 9.53$ mm, $n = 46$) and 1.7–2.9 mm wide ($\bar{x} = 2.2$, $n = 46$) but are best characterized from examples that are isolated from the cupule (fig. 4d–4h), as the cupule often obscures features of the pedicel. The basal region of the ovule consists of up to four small, diverging terete strands that arise from the same point at the base of the ovule (fig. 4d, 4f, 4g). It is uncertain whether these strands are from individual lobes or represent part of the entire (nonlobate) part of the integument where the tissue between the strands has decayed. Quite reduced in most specimens (fig. 4f), the basal

and another in plan view that has a truncated apex where it is recurved (IR). RBINS-31822. *h*, Ovule lacking a cupule and two integumentary lobes, showing the ovate shape of the nucellus. RBINS-31830c. *i*, Enlargement from *h*, showing ovule apex with integumentary lobes (I), a pollen chamber (PC), a pollen chamber plinth (PL), and a salpinx (S) present. Scale bar = 0.5 mm.
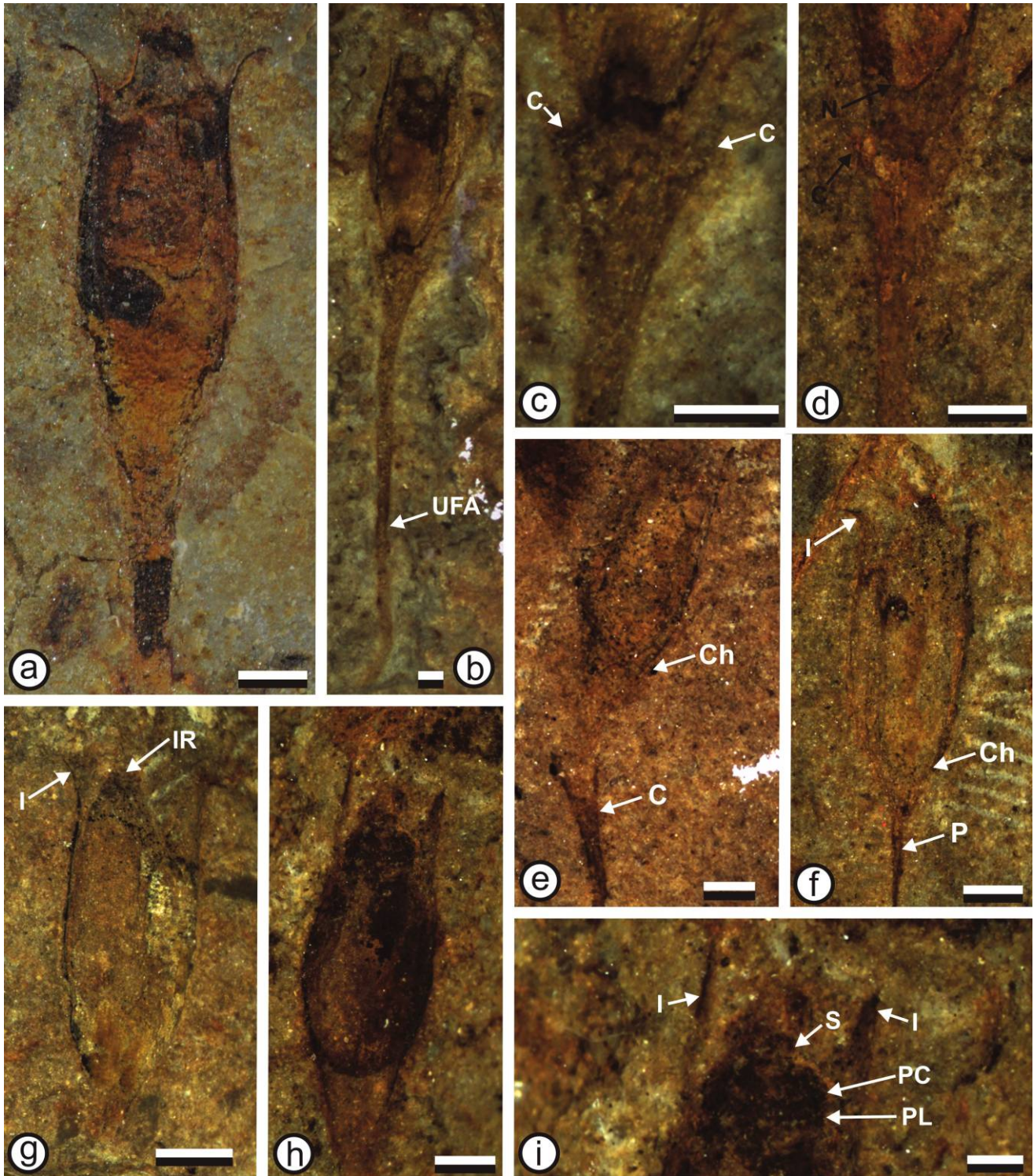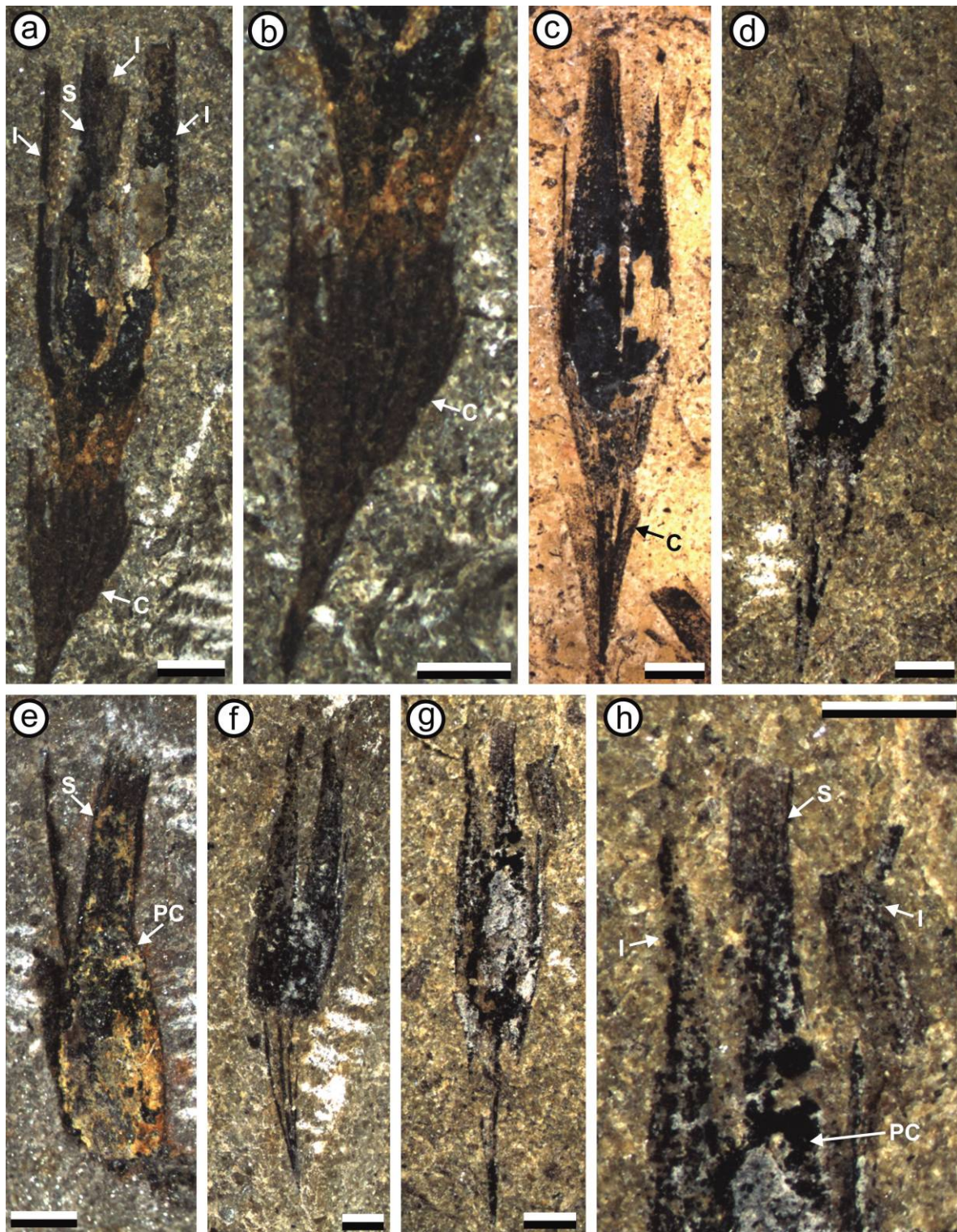
Fig. 4 Cupules and ovules of *Pseudosporogonites bertrandii* (Stockmans) C. Prestianni et al. from the Devonian of Belgium. Scale bars = 2 mm unless otherwise stated. *a*, Collaret cupule (C) with a dentate margin enveloping the base of a single ovule with long integumentary lobes (I) and a central nucellus with an elongated salpinx (S). Scale bar = 1 mm. Specimen RBINS-40697. *b*, Enlargement from *a*, showing the cupule (C) with dentate margin and faint longitudinal ribs. Scale bar = 1 mm. *c*, Triangular cupule (C) with incomplete apex basally enveloping a single ovule with acutely pointed integumentary lobes. Resin-transferred specimen; RBINS-40719. *d*, Complete ovule with imperfectly preserved triangular pedicel with prominent dark ribs. Scale bar = 1 mm. RBINS-40764. *e*, Basally incomplete ovule with one elongate integumentary

strands can occupy half of the integument's total length (fig. 4g). We consider the basal strands to be the remaining part of the pedicel and consider the junction where the pedicel widens into the body of the ovule to be the chalaza.

The transition between the pedicel and the chalaza is particularly distinct (fig. 4d, 4f, 4g), with the chalaza being ovate and entire at this level, but after 2–3 mm, approximately half of the integumentary length, splits are observed (fig. 4f, 4g). They mark the beginning of the apical integumentary lobes. Four lobes are present, but in most cases only two (fig. 4f–4h) or three (fig. 4a) are visible. Individual lobes are elongate, typically 7–11 mm long and 1–1.5 mm wide, and lanceolate (fig. 4c, 4d), with a smooth exterior surface, and their upper part thins out and slightly flares outward (fig. 4h).

The nucellus is visible between the integumentary lobes or where individual lobes have been removed by dégagement. The nucellus is bottle shaped, ranges from 5.92 to 8.2 mm long ($\bar{x} = 7.1$ mm; $n = 17$) and from 1 to 1.53 mm wide ($\bar{x} = 1.3$ mm; $n = 16$), and has a smooth surface. The nucellus has two distinct parts: (1) the central body, which is oval in shape, 3–5.5 mm long ($\bar{x} = 3.89$; $n = 16$), and has a rounded base (fig. 4f, 4g), and (2) distally the nucellar apex width is ~50% that of the base of the nucellus and comprises a small, dome-shaped pollen chamber and an elongate salpinx that is 3 mm high and 1 mm wide (fig. 4a, 4e, 4h). In the best-preserved specimens the distal margin of the salpinx is fringed (fig. 4h).

Interpretation of X. bertrandii. *Xenotheca bertrandii*, as documented here, comprises a cupule subtending the base of a single ovule that has a distally lobate integument surrounding a nucellus with a hydrasperman-type pollen chamber and an elongate, tubular salpinx. As most of the ovules are isolated from the cupule, it is likely that they were shed and then dispersed. The basal strands of an ovule are interpreted as vascular tissue that has divided and diverged into each integumentary lobe. The outer layers of the ovule chalaza are imperfectly preserved but show these resistant strands and possibly an abscission zone where tissue decay facilitated detachment of the ovule from the cupule and aided in dispersal.

Comparison. Cupules of *Xenotheca devonica* range from 8 to 15 mm long and from 4 to 10 mm wide and divide dichotomously to produce 16 distal cupule lobes. Cupules bear multiple ovules on the inwardly facing surface of the cupule, with up to four ovules per cupule. Individual ovules vary between 3 and 5.5 mm long and between 0.8 and 1.1 mm wide and consist of four to seven terete integumentary lobes in the distal two-thirds of the integumentary length. This organization is distinct from Stockmans's (1948) species *X. bertrandii*, which is here shown to be uniovulate, with the cupule being small and collaret shaped rather than branched and telome-style. We conclude that Stockmans's species *X. bertrandii* cannot be assigned to the multiovulate-cupule genus *Xenotheca*, as diagnosed by Hilton and Edwards (1999), and is more similar to *P. hallei*, *A. quadrapartita* (Hilton and Edwards 1996),

A. avonensis (Hilton 1998a), and *Aglosperma* sp. of Cressler et al. (2010).

Stockmans's *X. bertrandii* and *P. hallei* both have cupules that subtend the base of a single ovule, leaving the medial and distal portions of the ovule exposed. Both species are interpreted to have shed their ovules from the cupule, but in neither species have isolated cupules from which ovules were shed been identified. Ovules in both species are radially symmetrical, with an integument that is entire proximally but lobate distally. Individual lobes are flattened, laminar in transverse section, and lanceolate in longitudinal section. Both species have an open micropylar region in which the nucellar apex is exposed, and each possesses a hydrasperman-type pollen chamber with a distal tubular salpinx that is considered symplesiomorphic within seed plants as a whole. Our conclusion is that *X. bertrandii* readily conforms to the genus *Pseudosporogonites* as emended here, and it is here considered to be a second species of that genus, resulting in the creation of *P. bertrandii* (Stockmans) Prestianni et al. comb. et emend. nov. However, it also shares similarities with *Aglosperma* spp. that must be considered.

Aglosperma quadrapartita *Hilton et Edwards*

Aglosperma quadrapartita has a long, tapering pedicel, a rounded chalaza, and an integument with four flattened, lanceolate lobes in the distal two-thirds of ovule length, with an open micropylar region and an exposed hydrasperman-type nucellar apex (Hilton and Edwards 1996). This organization is similar to the structure of Stockmans's *X. bertrandii*, although a cupule has not previously been noted in *A. quadrapartita*. Hilton and Edwards (1996) determined that five specimens had small protrusions below the chalaza that they interpreted as taphonomic splintering of the pedicel. These features are of a size and in a position similar to those of the cupules of *P. hallei* and *P. bertrandii*, as documented here, and they require reinvestigation to determine their nature. *Aglosperma avonensis* Hilton is, as the genus-level attribution suggests, very similar to *A. quadrapartita*, but it is typically shorter and wider and has a shorter pedicel that widens into a broad triangle below the chalaza (Hilton 1998b). In *A. avonensis*, the integument comprises three or four lobes that are flattened and have rounded apices. A cupule is not known in *A. avonensis*, but the tapering, triangular pedicel and overall morphology of the ovule are similar to those of the ovules of Stockmans's *X. bertrandii*. Here we reinvestigate both species of *Aglosperma* and specimens recently described as *Aglosperma* sp. by Cressler et al. (2010) to reconsider whether they were cupulate or not and to consider their potential relationships with the Belgian species originally documented by Stockmans (1948).

Description. This species was characterized by Hilton and Edwards (1996), and here we provide only additional infor-

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lobe, a pollen chamber (PC), and an elongate salpinx (S) with an irregular apex. RBINS-40750. *f*, Dispersed ovule with triangular pedicel with visible dark strands. RBINS-40831. *g*, Dispersed ovule with poorly preserved triangular pedicel with dark strands, a rounded chalaza, and two integumentary lobes surrounding a nucellus with a long, tubular salpinx. RBINS-40772. *h*, Enlargement from *g*, showing the ovule apex with integumentary lobes (I), a pollen chamber (PC), and a salpinx (S).

mation that has come to light during our investigation. Hilton and Edwards (1996, p. 244) noted that five specimens had projections protruding from the pedicel below the chalaza, of which the best preserved are shown here in figure 4. The most complete specimen (fig. 5a) has a wide chalaza with two lateral projections emanating to either side of the pedicel. These end abruptly below the level of the chalaza, where they form a cup-like structure in which the ovule chalaza is inserted centrally. Other specimens are less compete (fig. 5b) or less well preserved (fig. 5c) and show much smaller, thinner projections up to 0.9 mm long in the same relative position. These end below the point at which the chalaza widens. Rarely in this species is the pedicel complete, typically comprising up to four small, terete strands (see pl. II, fig. 7 of Hilton and Edwards 1996).

Interpretation.   Hilton and Edwards (1996) concluded that the chalazal projections in *A. quadrapartita* were taphonomic changes to structure resulting from splitting and fracturing of the pedicel. However, they are extremely similar to the cupules in *P. hallei* and *P. bertrandii*, which are more complete and better preserved, supporting another interpretation, namely, that the projections in *A. quadrapartita* represent the remains of a small, uniovulate cupule. In the most complete specimen, the cupule forms a cup-like structure that has a rounded apex situated below the level of the chalaza, but in less well-preserved examples it is preserved as thin tissues emanating below the level of the chalaza. Thus, the extended ovule pedicel in these specimens, as described by Hilton and Edwards (1996), is in fact an axis bearing a terminal cupule that in turn envelops the base of the ovule. Here we emphasize that the presence of a cupule in *Pseudosporogonites* was unknown to Hilton and Edwards at the time of their investigation. Specimens from Taffs Well are imperfectly preserved, and the cupule has only recently been recognized, after better-preserved examples of Belgian ovules were seen. Like *Pseudosporogonites*, *A. quadrapartita* is cupulate and bears a single ovule centrally, with the cupule covering only the basal region of the ovule and ending below the level of the chalaza.

The information presented in this article on the nature of *P. hallei* and *P. bertrandii* and the documentation of a cupule assigned to *A. quadrapartita* reduce the distinction between these species, which all comprise uniovulate cupules bearing a single ovule with a pronounced chalaza, four flattened integumentary lobes, and an exposed hydrasperman-type pollen chamber with a distal salpinx. *Aglosprema quadrapartita* differs from *P. hallei* in having a finely longitudinally ribbed integument and in having straight integumentary lobes that differ from the consistently apically recurved integumentary lobes of *P. hallei*. Also, in terms of their size, *P. hallei* occupies a much smaller size range than is seen for the stratigraphically younger species *A. quadrapartita* (see "Systematic Paleontology"), with only minimal overlap. We therefore consider these to represent distinct biological species within a single genus. As *Pseudosporogonites* was validly established by Stockmans (1948), it has nomenclatural priority. We therefore formally transfer *A. quadrapartita* Hilton et Edwards into *Pseudosporogonites quadrapartitus* (Hilton et Edwards) C. Prestianni, J. Hilton et W. Cressler comb. et emend. nov. (see below). We also emend the specific diagnosis to include the cupule.

Discussion.   The dominance of shed ovules lacking a cu-

pule in *P. quadrapartitus* suggests that dispersal from the parent plant was facilitated primarily by shedding the ovule from the cupule, but in some instances the cupule was shed with an ovule. No specimens have yet been identified that may represent isolated cupules from which ovules have been shed, and intact branching systems for this species are at present unknown.

Aglosperma avonensis *Hilton*

Description.   This species was characterized by Hilton (1998b), who documented the ovule to have a prominent triangular pedicel (fig. 6), with an integument comprising three or four flattened integumentary lobes (fig. 6a, 6b) surrounding a hydrasperman-type pollen chamber and with a short, wide salpinx (fig. 6c). Reinvestigation of the specimens of this species shows each to be isolated and where complete to comprise a prominent, triangular pedicel that widens toward the chalaza. No evidence of a cupule or an attachment scar where the cupule was borne has been observed.

Interpretation.   The triangular pedicel and the overall similarity to *P. quadrapartitus*, *P. bertrandii*, and *P. hallei* lead us to speculate that *A. avonensis* too was borne in a uniovulate cupule. We consider that this species conforms to the generic diagnosis of *Pseudosporogonites* presented here and is distinct from the other recognized species, leading to its formal transfer into *Pseudosporogonites* as *P. avonensis*. While we accept that a cupule is not observed in *P. avonensis*, its features are consistent with an ovule borne in a uniovulate cupule, especially the shape of the pedicel, which is unique to ovules borne in this way. An alternative hypothesis is that the cupule was extremely reduced and no longer visible in *P. avonensis*, but with the tapering nature of the pedicel we consider it more likely that this ovule was shed from a cupule rather than being acupulate. Isolated cupules have not been identified from this assemblage to date.

Aglosperma *sp. from North America*

Description.   The identity of ovules assigned to *Aglosperma* sp. by Cressler et al. (2010) from the Late Devonian of North America is reconsidered following the transfer of these two species of *Aglosperma* to *Pseudosporogonites*. Cressler et al. (2010) provided a comprehensive description of the fossils from which only the salient points are included here, along with representative illustrations of the specimens (fig. 7). Specimens include ovules attached to cupules terminal on a fertile branching system as well as isolated ovules. The fertile axes divide dichotomously and have a small terminal cupule bearing a single, centrally inserted ovule (fig. 7a, 7b). In more complete specimens adjacent ultimate fertile axes may overlay one another, such that additional divisions can be seen below the level of the cupule (fig. 7b); these will be the subject of a future paper documenting the ovulate branching systems. The cupule covers the ovule pedicel and does not extend to the chalaza. Ovules range from 8 to 11 mm long, measured from the attachment of the cupule to the tip of the integument, and comprise an integument that is entire in the basal third of its ovule length and distally forms four flattened, lanceolate integumentary lobes. The integument surrounds an oval nucellus with a distal nucellar apex comprising a small pollen chamber
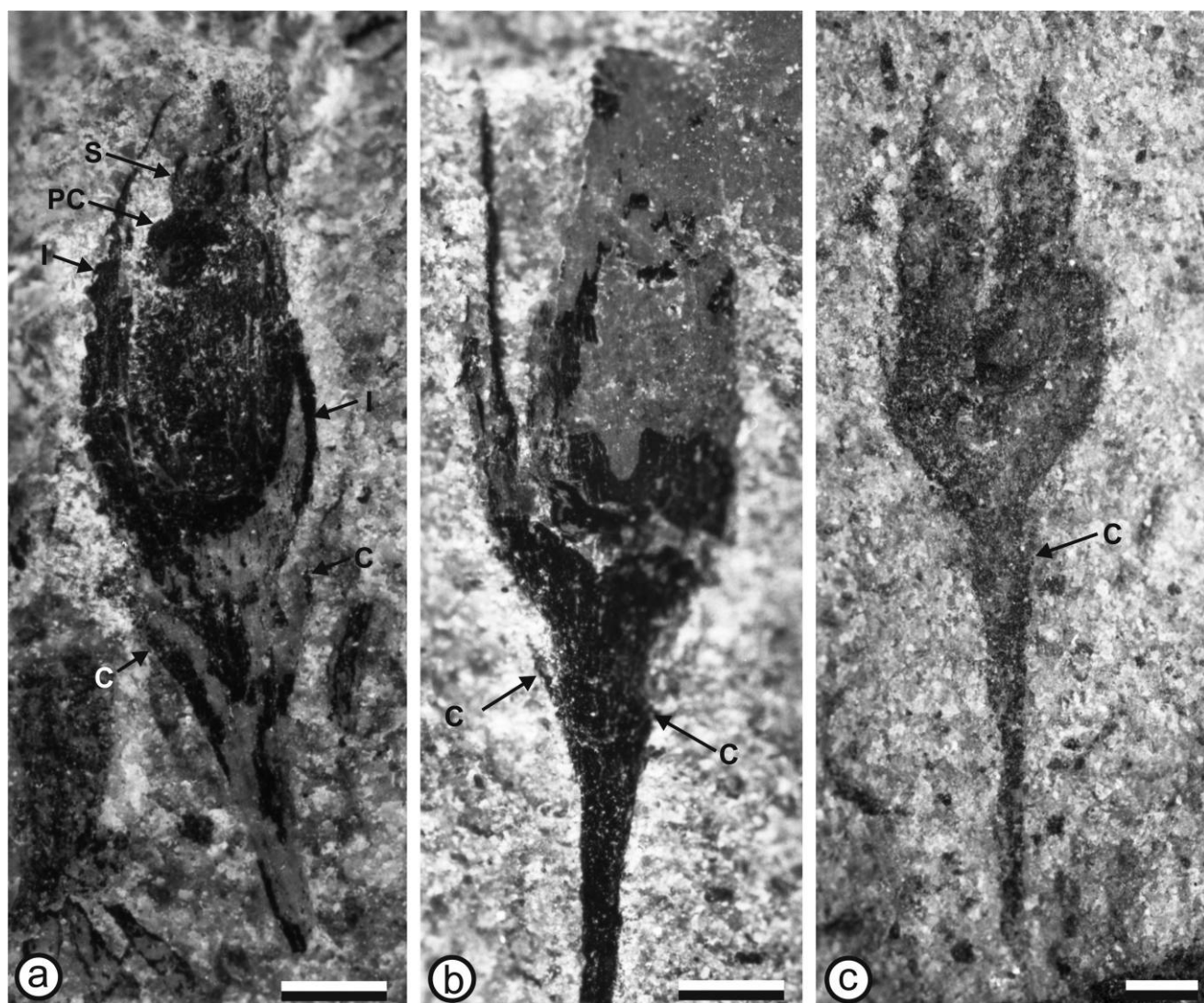
Fig. 5 *Pseudosporogonites quadrapartitus* (J. Hilton et D. Edwards) C. Prestianni et al. comb. nov. from the Devonian of Britain, showing cupule and ovule morphology. All scale bars = 1 mm. *a*, Entire specimen, with large cupule (C) basally enclosing a single ovule with a lobed integument (I) and a prominent nucellus comprising a nucellar apex with a pollen chamber (PC) and a salpinx (S). NMW 94.75G.8. *b*, Large ovule with vestigial remains of the cupule attachment (C). NMW 94.75G.9. *c*, Poorly preserved specimen with position of cupule attachment (C) faintly visible. NMW 94.75G.

and a long, tubular salpinx (fig. 7*b*, 7*c*). Distally, the integumentary lobes may be slightly recurved (fig. 7*c*), with the distal two-thirds of the integumentary length being lobate.

Interpretation. In terms of their morphology, the specimens from the Red Hills are closest in morphology and structure to *P. bertrandii* from the Late Devonian of Belgium and have the same organization and structure, comprising a small cupule that subtends the pedicel and bears a single, centrally placed terminal ovule. The ovule in both the Belgian and North American specimens is basally entire but in the distal two-thirds forms elongate, flattened lobes that surround a hydraspeman-type nucellus with a small pollen chamber and a long salpinx. When the size ranges of the Belgian and North American specimens are compared (fig. 8), they have considerable overlap, but with the North American specimens occupying a

wider part of the range occupied by the Belgian species. We conclude that the North American specimens represent a second occurrence of the species *P. bertrandii* and see no reason to establish them as a distinct species, as they fall within the range of variation seen in *P. bertrandii* from Belgium.

Discussion

Species Recognition and Size Ranges within Pseudosporogonites

In this account we consider *Pseudosporogonites* to include four species, namely, *P. hallei*, *P. bertrandii*, *P. quadrapartitus*, and *P. avonensis*, that can be distinguished from one another on the basis of their morphology and structure (table 1). *Pseu-*
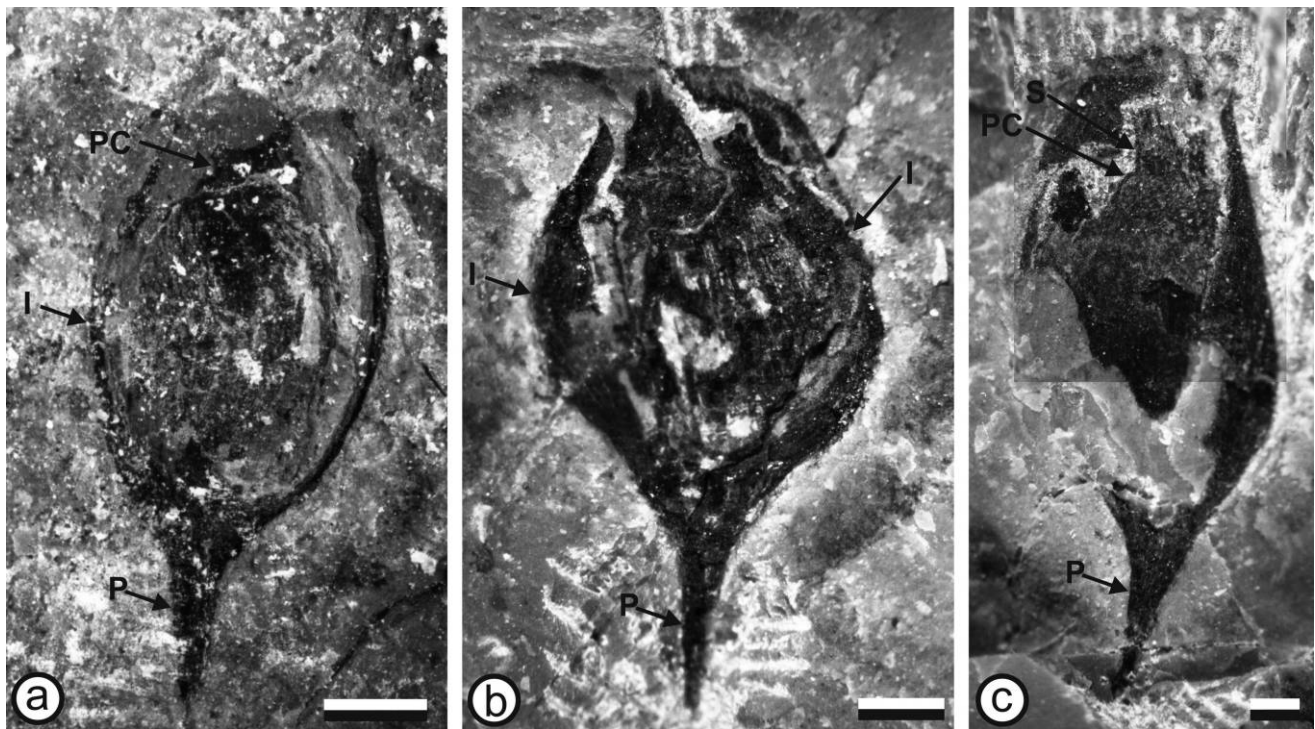
Fig. 6   Isolated ovules of *Pseudosporogonites avonensis* (J. Hilton) C. Prestianni et al. comb. nov., with the prominent short, triangular pedicels characteristic of this species. All scale bars = 1 mm. *a*, Holotype with pedicel and integumentary lobes in section and plan view with rounded apices. NMW.97.10G.1a. *b*, Ovule with integumentary lobes having recurved apices and an exposed nucellar apex. NMW.97.10G.5. *c*, Partial specimen in which integumentary lobes have been removed to reveal the enclosed nucellar apex with broad, tubular salpinx. Image composite of two photographs at different focal planes, as the specimen is not preserved in a single level. NMW.97.10G.9. I = integument, P = pedicel, PC = pollen chamber, S = salpinx.

dosporogonites avonensis has three or four integumentary lobes, whereas the other species consistently have four, and its lobes are lanceolate but with the apex more rounded than those of the other species; integumentary lobes are triangular to lanceolate in *P. hallei*, triangular in *P. bertrandii*, and lanceolate in *P. quadrapartitus* (table 1). The salpinx varies between species and is longest in *P. bertrandii* (3 mm) and shortest in *P. quadrapartitus* (0.6 mm) and *P. hallei* (0.7 mm); in *P. bertrandii* it is distinguished by its fringed apex. Integumentary lobes are apically recurved outward in specimens of *P. hallei*, but the lobes of the other species are consistently straight or curve inward, where they more fully envelop the nucellar apex.

Species of *Pseudosporogonites* have overlapping size ranges; each occupies a distinct part of the total size range (fig. 8) of the genus. Interestingly, the sizes of *P. hallei* and *P. bertrandii* from Belgium do not overlap, but the size of the North American specimens of *P. bertrandii* overlaps part of the range of the same species from Belgium, and the North American specimens are typically wider (fig. 8). *Pseudosporogonites quadrapartitus* has the greatest size range, which overlaps that of each of the other species to some extent but includes the range of the older species *P. hallei*. An apparent trend is observed in which the stratigraphically older species *P. bertrandii* and *P. hallei* tend to be thinner and somewhat longer (e.g., *P. hallei*) than the younger species *P. avonensis* (fig. 7). The species of *Pseudosporogonites* are reconstructed in figure 9.

Comparison with Other Devonian Ovule Genera

The trumpet- or collar-shaped uniovulate cupule with a dentate margin in species of *Pseudosporogonites* distinguishes it from other genera of Devonian ovule, as does the structure of the integument. The majority of recognized Devonian ovules are borne in multiovulate cupules that range from telome-style, cruciately dividing, terete axes, such as those of *Elkinsia polymorpha* (Rothwell et al. 1989), *Moresnetia zalesskyi* (Fairon-Demaret and Scheckler 1987), and *Xenotheca devonica* (Hilton and Edwards 1999), to structures with varying degrees of fusion between adjacent lobes but with free tips, such as in *Archaeosperma arnoldii* (Pettitt and Beck 1968) and *Glamorgania gayerii* (Hilton 2006; table 2). These multiovulate cupules are larger than the cupules in *Pseudosporogonites* (table 2) and bear smaller ovules on the inwardly facing surface of the cupule rather than singly and centrally on an undivided cupule. Ovules in multiovulate cupules tend to have integuments with varying levels of fusion basally and form terete lobes proximally (*Moresnetia*), medially (*Elkinsia, Xenotheca, Archaeosperma*), or distally (*Glamorgania*; table 2). These are readily distinguished from the flattened, lanceolate lobes in *Pseudosporogonites*, which can also be finely ribbed (*P. quadrapartitus*).

While ovules of *Dorinnotheca streeli* are also borne singly and centrally within a cupule, the cupule of *Dorinnotheca* is
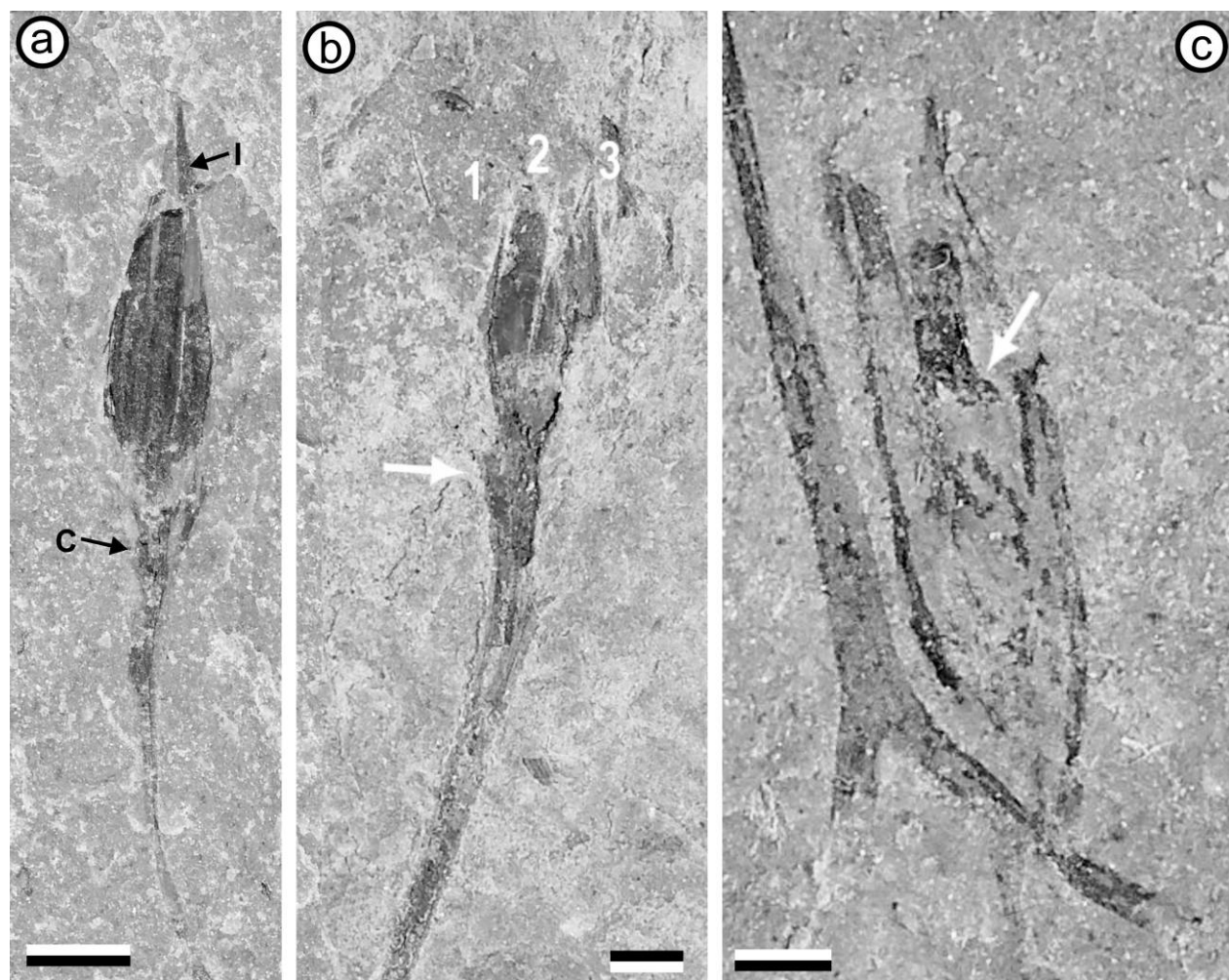
Fig. 7 Uniovulate cupules of *Pseudosporogonites bertrandii* Prestianni et al. from the Late Devonian of North America. *a*, Distal part of ovuliferous branching system with a uniovulate cupule (C) surrounding an ovule chalaza and an ovule with lanceolate integumentary lobes. Specimen ANSP 4525, scale bar = 2 mm. *b*, Distal part of ovuliferous branching system with uniovulate cupule (arrow) surrounding ovule chalaza, and ovule with impressions of three (1–3) lanceolate integumentary lobes visible. ANSP 4538; scale bar = 2 mm. *c*, Isolated ovule, showing nucellus and nucellar apex (arrow) and surrounding integumentary lobes. ANSP 4525, scale bar = 1 mm.

larger than that of *Pseudosporogonites*, typically 5–6 mm long and 1–1.5 mm wide, highly branched, and recurved to cover the ovule to the level of the chalaza (Fairon-Demaret 1996; table 2). *Dorinnotheca* is further distinguished by the thick triangular and pyramid-shaped integumentary lobes which are very different from the flattened, lanceolate lobes in *Pseudosporogonites* (table 2).

The Famennian ovule *Condrusia rumex* Stockmans (Stockmans 1948; Fairon-Demaret 1996; Prestianni 2005*a*, 2005*b*; Prestianni and Gerrienne 2006; Prestianni et al. 2007), from the Evieux Formation of Belgium, is very different from *Pseudosporogonites* in possessing a cupule with two laminar segments enclosing the ovule. This is very different from the small, radial funnel or collaret cupules in *Pseudosporogonites*.

Ovules of *Warsteinia paprothii* Rowe are easily distinguished from *Pseudosporogonites* spp. by their smaller size (typically 2.3–3.0 mm wide and 3.3–3.7 mm long), pointed chalaza that lacks a pedicel, and possession of a laterally ex-

tended, winged integument that forms lobes above the level of the nucellar apex (Rowe 1997). *Warsteinia* is known only in isolated condition, so the presence of a cupule is unknown.

Specimens of *Pseudosporogonites* where the cupule is absent have a prominent pedicel that may be entire and triangular in profile, gradually widening to the chalaza (*P. hallei*, *P. avonensis*, most specimens of *P. quadrapartitus*), or is incomplete and comprises up to four strands (*P. bertrandii*, occasional specimens of *P. quadrapartitus*). We consider the shape of the pedicel to be a distinctive feature of the genus that is absent in all other Devonian genera, with this shape presumably relating to the position of facultative ovule abscission from the cupule.

Age of the Strud Locality and *P. hallei*

Preliminary dating of Strud Quarry using palynolostratigraphy has assigned the plant-bearing sediments to the GF pal-
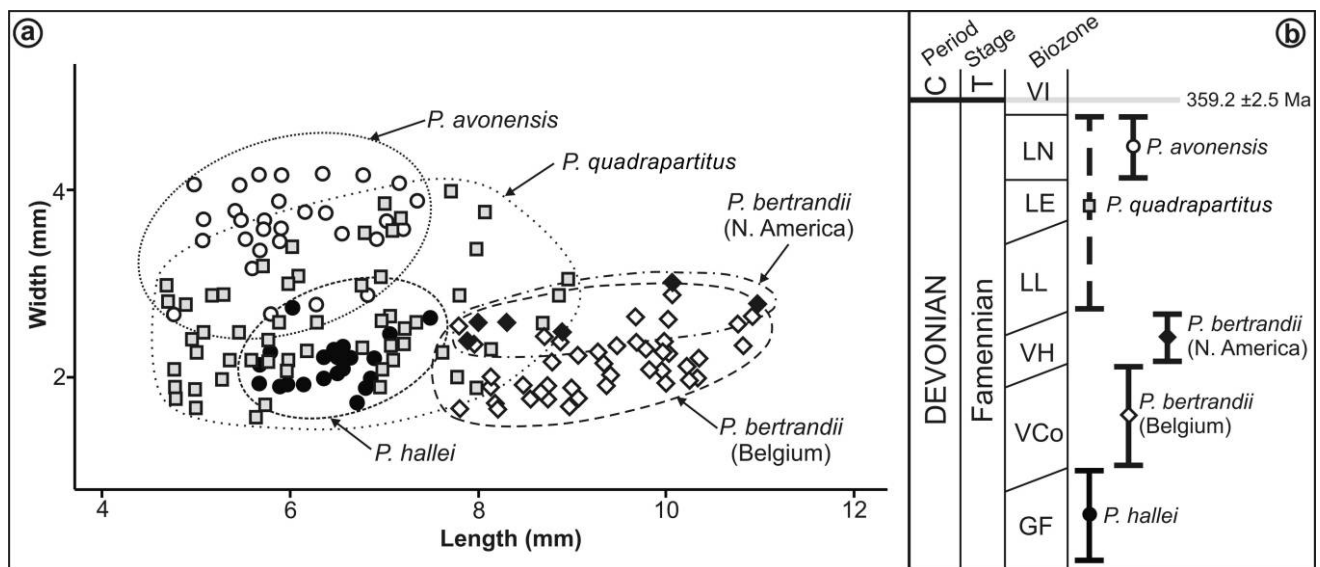
Fig. 8 Size and age ranges of species of *Pseudosporogonites*. *a*, Length and width measurements for complete specimens of each species, with occurrences of *P. bertrandii* from Belgium and North America differentiated. Note that the species have overlapping sizes and are distinguished by other features of their morphology (see text and table 1). *b*, Stratigraphic ages of species showing, in combination with figure 1*a*, (1) that the oldest species (*P. hallei*) occupies the smallest size range, (2) that the younger species *P. bertrandii* is typically longer than but similar in width to *P. hallei*, and (3) that the stratigraphically younger species *P. quadrapartitus* and *P. avonensis* display an overall trend of increasing width and reduction in length when compared with the older species. C = Carboniferous, T = Tournaisian, Ma = million years ago.

ynozone (Prestianni et al. 2007). If correct, this is important and demonstrates that the locality represents the stratigraphically oldest occurrence of seed plants, predating the currently recognized oldest species, *E. polymorpha* (Rothwell et al. 1989). However, this palynostratigraphic result contradicts regional lithological interpretations in which Strud Quarry exposes the Bois des Mouches Formation, which is laterally equivalent to the Evieux Formation, which is uniformly attributed to the VCo palynozone (Thorez et al. 2006). The GF and VCo palynozones differ from each other in the occurrence of the marker taxa *Grandispora cornuta* Higgs and *Rugospora flexuosa* (Jushko) Byvsheva; otherwise, they are similar (Streel et al. 1987). Following Streel et al. (1987), we consider the boundary between these biozones to be diachronous and in our stratigraphic charts (figs. 1, 7) represent the boundary as a sloping line along which the absolute ages of the different palynozones overlap to some extent. Also, considering the reported continental depositional facies interpreted at Strud (Prestianni et al. 2007; Garrouste et al. 2012), a strong ecological bias is probable, and we cannot exclude the absence of these two marker taxa as being related to factors other than age. Therefore, we err on the side of caution and conclude that the GF palynozone at Strud could represent facies contemporaneous with the VCo palynozone but with different ecological conditions. The level of precision available in palynostratigraphy is, in our view, unable to determine which of the GF and CVo palynozones is older; as a consequence, we consider them to be age equivalent.

Symplesiomorphy in Basal Seeds: Were All Devonian Seeds Cupulate?

The origin of the seed remains one of the most contentious issues in paleobotany, perhaps second only to the subsequent origin of the angiosperms. A key issue for each of these events is that from their first occurrence in the fossil record, species are recognizable as fully formed members of the group to which they are assigned and that convincing morphological intermediates remain to be found. For the origin of the ovule, the stratigraphically oldest representatives from the Late Devonian are botanically functioning ovules, and intermediates with their progymnopermous (free-sporing) ancestors are inferred from traditional systematics (Beck 1970; Beck and Wight 1988) or cladistic analyses of lignophytes (Rothwell and Serbet 1994; Hilton and Bateman 2006) rather than being based on putative intermediates from the fossil record. An exception is *Runcaria heinzelinii* from the Mid-Devonian, which was postulated as a seed plant precursor by Gerrienne et al. (2004) and later characterized as a "proto-ovule" comprising indehiscent, integumented megasporangia that have not achieved a hydrasperman nucellar organization (Gerrienne and Meyer-Berthaud 2007). *Runcaria* is interpreted as having a laminar cupule bearing a single fertile structure comprising a highly divided integument surrounding a megasporangium with elongated distal extension. Its identification as part of the seed plant lineage is hypothetical. Gerrienne et al. (2004) interpreted the integumented megasporangia as containing a single functional megaspore, but this feature has not been dem-

Table 1

Comparison of Species of *Pseudosporogonites* from the Famennian of Europe and North America, Based on Data Presented in This Article

	P. hallei	*P. bertrandii*	*P. quadrapartitus*	*P. avonensis*
Location	Strud Quarry, Belgium	Assesse and Booze, Belgium	Taffs Well, Wales	Avon Gorge, England
Miospore biozone	GF	VCo	LL–LN	LN
Authors	Stockmans 1948	Stockmans 1948	Hilton and Edwards 1996	Hilton 1998*b*
Cupule:				
Fusion	Fused	Fused	Fused	?
Shape	Collaret	Collaret	Collaret	?
Length (mm)	2.0–2.7	2.3–5.2	1.4–2.2	?
Width (mm)	1.4–1.7	1.4–2.7	1.2–1.8	?
Integument:				
Number of lobes	4	4	4	3–(4)
Fusion	1/3	1/3	<1/3	<1/3
Lobe shape	Triangular/lanceolate	Triangular	Lanceolate	Rounded lanceolate
Lobe length (mm)	5.5–7.5	7.0–11.0	6.0–9.0	6.0–9.0
Lobe width (mm)	1.3–2.5	1.4–2.1	~1.3–2.5	~1.8–2.9
Overall diameter (mm)	1.5–4.2	1.7–2.9	1.6–4.0	3.0–5.5
Nucellus:				
Length (mm)	4.0–4.8	2.0–5.2	2.2–3.8	3.9–5.5
Width (mm)	1.5–2.0	1.0–1.5	1.0–1.6	2.1–2.8
PC width (mm)	1.3	1.5	1.1	.7–1.1
PC height (mm)	.8	1.0	.7	.3–.8
Salpinx length (mm)	.7	3.0	.6	1.1

Note. PC = pollen chamber.

onstrated. Our conclusion is that *Runcaria* could lie on the evolutionary stem lineage leading to seed plants, but the lack of a convincing single megaspore leads us to consider a detailed discussion on the homologies with structures in *Runcaria* to be too difficult to attempt in this article.

In terms of cladistic understanding of seed plants, the only comprehensively known Devonian seed plant is *E. polymorpha* (Rothwell and Scheckler 1988; Serbet and Rothwell 1992). This taxon has been widely accepted as the basalmost member of the seed plant clade from which a symplesiomorphic condition has been interpreted (Rothwell and Serbet 1994; Serbet and Rothwell 1992, 1995; Hilton and Bateman 2006). However, other Devonian seeds are now known that present different morphologies and suggest that *Elkinsia* is one of several plausible primitive arrangements within the seed plant clade. The question then arises, What is less derived within seed plants? Here we consider the structure of Devonian ovules to evaluate this question, on the assumption that features shared by all Devonian ovules are likely to be plesiomorphic, as comparable to later fossil taxa.

All basalmost seed plants are characterized by a hydrasperman-type nucellus surrounded by a lobate integument, with some, but not all, taxa borne in a cupule. The hydrasperman-type nucellus has an apex comprising a membranous pollen chamber floor, a domed pollen chamber containing a parenchymatous central column, and a distal salpinx. The nucellar apex serves for reception and retention of pollen before fertilization, with the central column pushing into the base of the salpinx after pollination to seal off the nucellus (Rothwell 1986; Rothwell and Serbet 1992; Serbet and Rothwell 1995). Variation within Devonian ovules is demonstrated by the shape and size of the respective features of the nucellus. Species with

a short salpinx include *E. polymorpha*, *Xenotheca devonica*, *M. zalesskyi*, and *P. hallei*, while other species, such as *P. bertrandii* and *D. streelii*, have a longer salpinx (table 2). The stratigraphically earliest ovule species display both short (*Elkinsia*) and long (*P. bertrandii*) salpinx morphologies, but we consider the longer salpinx to be a derived condition; development from a rounded apex of a sporangium to a nucellar apex appears to be aggregative and represents an overall increase in size rather than a reduction from a larger ancestral condition. However, if *Runcaria* is correctly interpreted as a seed plant ancestor, then the tubular apical extension of the sporangium in that species (Gerrienne et al. 2004; Gerrienne and Meyer-Berthaud 2007) may indicate that the longer salpinx is primitive, although the ovoid termination in *Runcaria* is puzzling and difficult to interpret.

The integument of Devonian ovules varies considerably in terms of its morphology and degree of fusion to the nucellus. Integument shape ranges from terete lobes that may be free from each other for the majority of the ovule length (e.g., *Morenetia*) or fused distally from the chalaza but free apically to varying degrees (*Elkinsia*, *Archaeosperma*, *Xenotheca*, *Kerryia*, *Glamorgania*) to those that are flattened and lanceolate (*Pseudosporogonites* spp.) or triangular in section and pyramidal (*Dorinnotheca*) or laterally extended and winged (*Warsteinia*; table 2). Fusion of the integument to the nucellus also varies, from species where the nucellus is free except at the chalaza (*Pseudosporogonites*, *Moresnetia*) to species in which it is fused for one-third to one-half (*Elkinsia*) or two-thirds to three-quarters (*Kerryia*, *Warsteinia*) of the ovule length or entirely fused (*Archaeosperma*; table 2). In terms of their stratigraphic appearance in the fossil record, a clear trend is difficult to identify; integumentary lobes that are terete, lanceolate, and
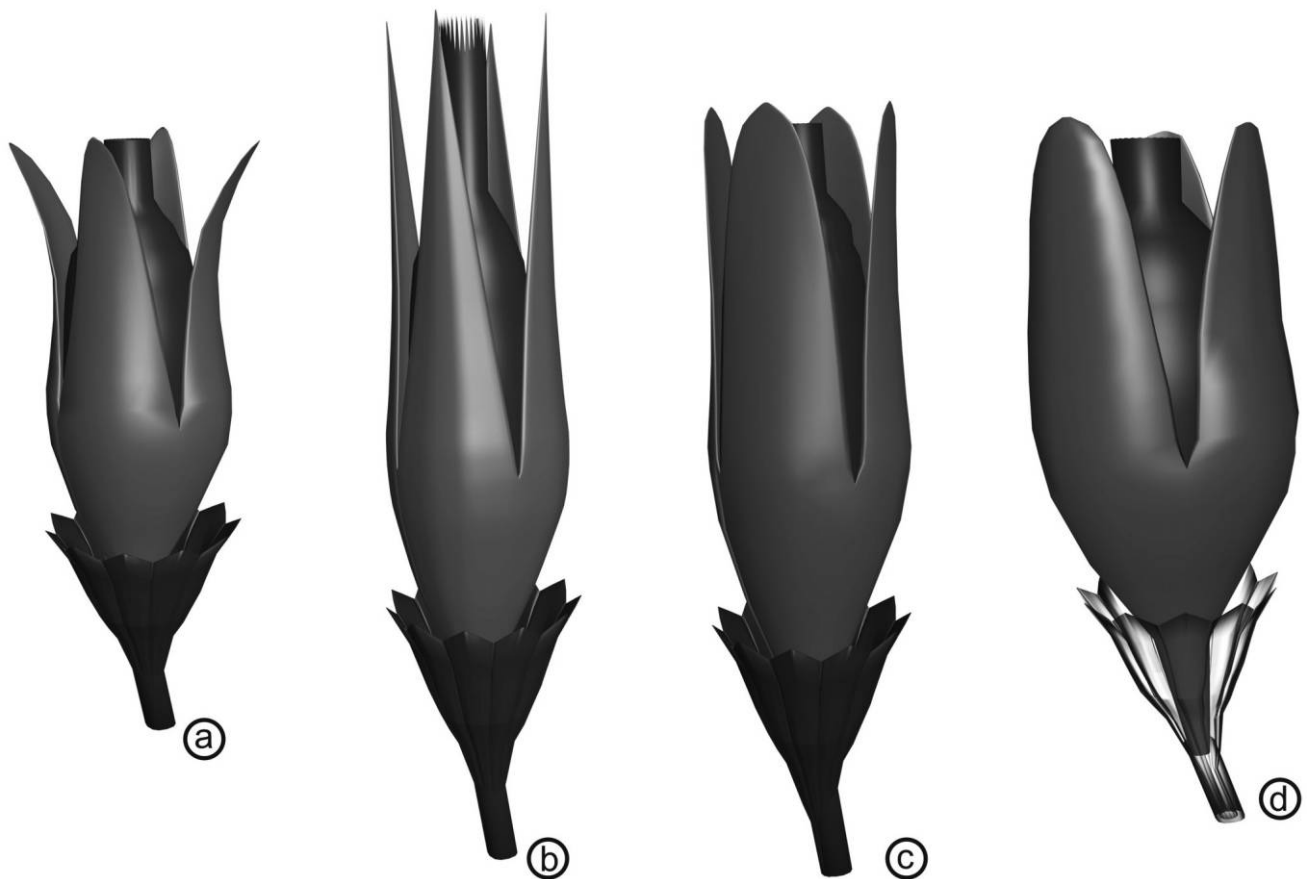
Fig. 9   Reconstruction of species of *Pseudosporogonites* from the Famennian of Europe and North America. *a*, *P. hallei* from Belgium. *b*, *P. bertrandii* from Belgium and North America. *c*, *P. quadrapartitus* from Wales. *d*, *P. avonensis* from England.

triangular in transverse section are more or less contemporaneous with each other (table 2), but winged integuments, as seen in *Warsteinia*, appear comparatively late and may represent a derived condition (Rowe 1997).

Cupules of Devonian seed plants are of three kinds, namely, (1) telomic, branched cupule varieties containing multiple ovules, such as those of *Elkinsia* and related taxa (*Moresnetia*, *Xenotheca*, *Kerryia*, *Glamorgania*), (2) branched, recurved uniovulate cupules, as in *Dorinnotheca*, and (3) small, unbranched uniovulate cupules, as seen in *Pseudosporogonites* (table 2). Stratigraphically, it is difficult to determine which kind, if any, are primitive or derived, as none of these arrangements is significantly older than the others and none compares well with the laminate "cupule" in *Runcaria*. Ovules are known to have been shed in some species with telomic branched cupules (e.g., *Moresnetia*; Fairon-Demaret and Scheckler 1987) and also from cupules in *Pseudosporogonites*. But cupules of *Dorinnotheca* each contain a single ovule, and neither isolated ovules nor cupules have been observed; this suggests that they may not have been abscised (Fairon-Demaret 1996). It is unknown whether ovules of *Warsteinia* were borne in a cupule, as this species has been found only isolated (Rowe 1997). However, we consider it likely that *Warsteinia* was cupulate, like all other recognized Devonian ovules, and we spec-

ulate that it was borne in a multiovulate cupule rather than in a uniovulate cupule like *Pseudosporogonites*, in which ovules consistently have a distinctive triangular pedicel after dispersal. Stratigraphically younger winged medullosan ovules were borne on dichotomous branching systems and lack a cupule (Drinnan et al. 1990), but such ovules are derived from the ancestral hydrasperman condition (Serbet and Rothwell 1995; Seyfullah et al. 2010).

Functional Traits of the Cupule and Integument in Pseudosporogonites

The range of phenotypic variation in Famennian-aged ovules demonstrates that the earliest phase of seed plant diversification was well underway by the onset of the Carboniferous period, with different taxa adapted to different environmental conditions starting to develop subtly different reproductive strategies. The development of the hydrasperman-type pollination mechanism is, as far as we know, universal in the most primitive ovule taxa and allowed for improved reception of pollen grain in pollination, retention of the pollen grains before fertilization, and postpollination sealing off of the nucellus (Rothwell 1986; Bateman and DiMichele 1994*a*; Serbet and Rothwell 1995; Rowe 1997). Hydrasperman-type pollination

Table 2

Comparison of Cupule and Ovule Features of Devonian Ovule Genera

Genus	Cupule				Integument					Ovule	
	Type	No. ovules	Morphology	No. segments	Type	No. lobes	Lobe fusion	Shape	Other	Length (mm)	Width (mm)
Xenotheca	Multiovulate	<4	Telomic	4	Lobed	4–8	1/3	Telomic	Smooth	2.7–5.5	1.6–2.5
Moresnetia	Multiovulate	<4	Telomic	4	Lobed	8–11	Free	Telomic	Smooth	1.0–5.0	1.0
Elkinsia	Multiovulate	<4	Telomic	4	Lobed	4–5	1/3	Telomic	Smooth	3.5–6.5	1.0–2.6
Glamorgania	Multiovulate	>1	Telomic	4	Entire	NA[a]	Entire	Telomic	Smooth	1.8–3.1	1.1–1.8
Archaeosperma	Multiovulate	4	Telomic	4	Lobed	5–6	3/4	Telomic	Hairy	4.2	1.4–1.7
Duodimidia	Multiovulate	2	Telomic	4	?	?	?	?	?	?	?
Kerryia	Multiovulate	2–6	Telomic	<6	Lobed	8–10	1/2	Telomic	Smooth	3.15–4.4	1.0–1.6
Pseudosporogonites	Uniovulate	1	Collaret	1	Lobed	3–4	1/3	Flat	Ribbed	5.5–11.0	1.5–5.5
Dorinnotheca	Uniovulate	1	Collaret	8 (fused)	Lobed	4	Free	Flat	Thick, triangular	4.5–7.0	1.1–1.3
Condrusia	Uniovulate	1	Laminar	2	?	?	?	?	?	?	?
Warsteinia	?	?	?	?	Lobed	4	3/4	Telomic	Winged	3.3–4.7	2.3–3.0

Sources. *Xenotheca*: Hilton and Edwards (1999) and Hilton (2006); *Moresnetia*: Fairon-Demaret and Scheckler (1987); *Elkinsia*: Rothwell et al. (1989); *Glamorgania*: Hilton (2006); *Archaeosperma*: Pettitt and Beck (1968); *Duodimidia*: Cressler et al. (2010); *Kerryia*: Rothwell and Wight (1989); *Pseudosporogonites*: this article; *Dorinnotheca*: Fairon-Demaret (1996); *Condrusia*: Prestianni and Gerrienne (2006); *Warsteinia*: Rowe (1997).

[a] Not applicable.

enabled seed plants to jump the adaptive valley separating water-dependent free-sporing heterospory and the seed habit. The combination of an increased size of the megagametophyte, the development of fewer but larger propagules, and the increased protection offered by an integument, was central to the long-lasting evolutionary success of the clade (Chaloner and Hemsley 1991; Bateman and DiMichele 1994; Rowe 1997). While an entire integument would provide increased protection from herbivory, desiccation, and microbial attack, it would also play an important role in increasing pollination effectiveness (Niklas 1983, 1985; Rowe 1997). Lobed integument may have offered little or no protection to the exposed nucellus (Rowe 1997). Rowe (1997) concluded that lobate integuments may have been initially nonadaptive but were essentially preadapted for a number of functions following structural modifications, including (1) fusion (protection), (2) centripetal differentiation (air-mediated dispersal), (3) development of air spaces (water-mediated dispersal), and (4) entire integuments (aerodynamic optimization of pollination). Ovules of *Pseudosporogonites* are among the largest of the Famennian-aged ovules, perhaps suggesting that they represent an ecologically established rather than a pioneering plant species, in comparison to species with smaller ovules. The level of fusion of the integumentary lobes in *Pseudosporogonites* in the basal one-third to one-half of ovule length also suggests that increased protection was becoming more important evolutionarily. While the cupule in multiovulate seed plants would have been likely to influence the aerodynamics of pollination in these species because it completely surrounded the ovule (Niklas 1985), in *Pseudosporogonites* the form of the ovule and the overall exposed nature of the integument suggest that in this genus the cupule did not serve to increase anemophilous pollination potential but was associated with facilitating dispersal of the diaspore in a predetermined way via facultative abscission. Ovule abscission from cupules is known to have occurred in *Moresnetia* (Fairon-Demaret and Scheckler 1987)

but may have been more widespread in basal seed plants than previously thought.

Diversity of Plant Assemblages Containing Pseudosporogonites

Species of *Pseudosporogonites* come from five different floral assemblages of Famennian age in Europe and North America and co-occur with a diversity of other plants, including basal seed plants. *Pseudosporogonites hallei* from Strud Quarry and *P. bertrandii* from the Assesse railway section and the old quarry in Booze (Blégny) in Belgium are part of the classical Belgian Upper Devonian assemblage (Stockmans 1948), with *Pseudosporogonites* co-occurring with *Archaeopteris*, *Rhacophyton*, *Barinophyton*, *Moresnetia*, *Condrusia*, and *Sphenopteris*. From the Red Hills assemblage in North America, ovules of *P. bertrandii* co-occur with cupules of the seed plant *Duodimidia pfefferkornii* and sphenopteroid-type foliage (Cressler et al. 2010); thus, at least two species of seed plant were present (ovules are not known in *D. pfefferkornii*, and therefore it remains unclear whether one or more biological species are present that had similarly structured cupules). Also in the assemblage occur remains of the progymnosperm *Archaeopteris*, along with the ferns *Rhacophyton* and *Gillespiea*, lycopsids, and the zosterophyll *Barinophyton* (Cressler 2006; Cressler et al. 2010). *Pseudosporogonites bertrandii* from Belgium and North America co-occurs with the progymnosperm *Archaeopteris* and *Barinophyton* as well as with the early fern *Rhacophyton*, although the North American assemblage is not as diverse as the Upper Devonian floras of Belgium.

From the Taffs Well assemblage in Wales, *P. quadrapartitus* co-occurs with multiovulate cupules of *X. devonica* and *G. gayerii*, collectively indicating the presence of three species of seed plant (Hilton 2006). This assemblage is fragmentary but

also includes leaves of two species of *Platyphyllum*, pollen organs of two species of *Telangiopsis* sp., and fertile units bearing lateral sporangia that resemble those of archaeopterids (Hilton 1996). From the Avon Gorge in England, *P. avonensis* occurs as part of a diverse floral assemblage dominated by the fern *Chlidanophyton dublinensis*, leaves of *Platyphyllum* sp., and pollen organs of *Telangium* sp., but no other species of seed plant has been identified (Hilton 1999). Both of the British assemblages in which *Pseudosporogonites* occurs lack *Barinophyton* and *Rhacophyton*.

At present, *Pseudosporogonites* is the only known Devonian seed plant genus to occur in both Europe and North America, and its co-occurrence with *Archaeopteris*, *Rhacophyton*, and *Barinophyton* suggests that the plants characteristic of the Evieux flora are snapshots of a more diverse Late Devonian flora that spanned this paleogeographic region; floristic analysis of the plants from the *Rhacophyton* plant megafossil biozone (VII) sensu Edwards and Berry (1991) is now required to fully characterize this flora, to identify co-occurring taxa more fully, and to consider environmental variation within it.

Early tetrapods coexist with *P. hallei* at Strud in Belgium (Clément et al. 2004) and with *P. bertrandii* and *Duodimidia* in the Red Hill flora of North America (Cressler et al. 2010). Insects also occur at Strud Quarry (Garrouste et al. 2012), making this an important locality that marks the dawn of a new era in life on Earth, including early representatives of biological groups that subsequently evolved to dominate terrestrial biotas and represent the starting point for the later evolution of complex terrestrial ecosystems dominated by seed plants, insects, and vertebrates. In this earliest phase of radiation within terrestrial vertebrates and seed plants, their coadaption is likely to have been significant (Cressler 2006; Prestianni and Gerrienne 2010).

Systematic Paleontology

Genus—Pseudosporogonites (*Stockmans*) Prestianni,
J. Hilton et Cressler emend. nov.

Synonomy. *Pseudosporogonites* Stockmans 1948. Mémoires du Musée Royal d'Histoire Naturelle de Belgique 110: 1–85, pl. XI, fig. 18.

Aglosperma Hilton and Edwards 1996. Review of Palaeobotany and Palynology 93:235–252, pls. 1–III.

Emended generic diagnosis. Small cupule bearing single, radially symmetrical ovule, positioned centrally on an axis that widens at the chalaza. Ovule pedicel characteristically pointed. Integument unlobed in approximately the basal third of ovule length and widest at point where integumentary lobation starts. Integumentary lobes lanceolate and laminar in transverse section. Micropyle absent. Nucellus free from the integument except at chalaza. Nucellus glabrous and ovate in outline below pollen chamber. Distal nucellar apex with pollen chamber and salpinx.

Type. *Pseudosporogonites hallei* Stockmans, 1948 emend. C. Prestianni, J Hilton et W. Cressler.

Species—Pseudosporogonites hallei *Stockmans,*
Here Emended

Emended specific diagnosis. Cupulate ovules 5.5–7.5 mm long ($\bar{x}$ = 6.4 mm, n = 22), 1.5–4.2 mm wide ($\bar{x}$ = 2.2 mm, n = 22). Cupule collaret shaped, bearing single ovule with long, tapering pedicel. Cupule covering basalmost part of ovule, up to 2.0–2.7 mm long ($\bar{x}$ = 2.4 mm, n = 8) and 1.4–1.7 mm wide ($\bar{x}$ = 1.59 mm, n = 8). Pedicel widening toward junction with ovule. Integument lobate in distal two-thirds or less, with typically four integumentary lobes. Integumentary lobes strongly tapering outward, with typically short tips. Nucellus including nucellar apex 4.6–5.3 mm long ($\bar{x}$ = 4.8 mm, n = 4) and 1.5–2.0 mm wide ($\bar{x}$ = 1.6 mm, n = 4). Nucellar apex comprising dome-shaped pollen chamber with prominent pollen chamber floor, 1.3 mm wide and 0.8 mm long, and distally bearing a short, cylindrical salpinx up to 0.7 mm long.

Holotype. RBINS-31878, Royal Belgian Institute of Natural Sciences, Brussels (fig. 3a).

Type locality. Strud, Belgium, a small quarry at the beginning of the road of Labas.

Stratigraphic horizon and age. Bois des Mouches Formation, Condroz Group, GH miospore biozone of the Upper Famennian, Upper Devonian (Prestianni et al. 2007).

Remarks. The genus and species *P. hallei* were established by Stockmans (1948) who provided a brief diagnosis and figured one specimen (Stockmans 1948, pl. XL, fig. 18 and 18a; specimen RBINS-31878); a detailed description was not provided. Following the International Code of Botanical Nomenclature, this specimen is the holotype (art. 9.1, n. 1, McNeill et al. 2006). Here we provide a detailed description and further illustrations of *P. hallei* based on the original materials available to Stockmans as well as additional specimens from the type locality. We consequently emend the generic and specific diagnoses to incorporate our findings. Stockmans (1948) did not discuss the affinities of *P. hallei* but mentioned the occurrence of dehiscence and noted an overall resemblance to, but not a relationship with, the genus *Sporogonites* Halle, which is now interpreted to be the sporophyte generation of a bryophyte (Kenrick and Crane 1997). In comprising a uniovulate cupule in which the ovule has a lobate integument surrounding a nucellus that has apical modification for pollen reception and retention before fertilization and postpollination sealing off of the megagametophyte, *P. hallei* is here identified as a seed plant and is interpreted to be a member of the basal hydrasperman pteridosperm grade (Serbet and Rothwell 1995; Hilton and Bateman 2006).

Species—Pseudosporogonites bertrandii (*Stockmans*)
C. Prestianni, J. Hilton et W. Cressler comb. et emend. nov.

Basionym. *Xenotheca bertrandii* Stockmans 1948. Mémoires du Musée Royal d'Histoire Naturelle de Belgique 110: 59–60, pl. XL, figs. 14–17.

Synonomy. *Aglosperma* sp. Cressler et al. 2010. International Journal of Coal Geology 83:91–102, figs. 1–5.

Emended specific diagnosis. Small cupule bearing single

ovule centrally. Cupule collaret shaped, 2.3–5.2 mm long ($\bar{x}$ = 4.4 mm, n = 9), 1.4–2.7 mm wide ($\bar{x}$ = 2 mm, n = 9), and enveloping base of ovule pedicel. Ovule with long pedicel, widening toward junction with ovule, where it forms a rounded chalaza. Ovules 7–11 mm long ($\bar{x}$ = 9.5 mm, n = 46) and 1.7–2.9 mm wide ($\bar{x}$ = 2.2 mm, n = 46). Integument lobate in distal two-thirds or less of ovule length, with typically four integumentary lobes. Integumentary lobes tapering and straight, with long tips. Nucellus including nucellar apex 5.9–8.2 mm high ($\bar{x}$ = 7.1 mm, n = 17) and 1–1.5 mm wide ($\bar{x}$ = 1.3 mm, n = 16). Nucellar apex comprising small, dome-shaped pollen chamber with distinct pollen chamber floor, 1.5 mm wide and 1 mm high. Nucellar apex with short cylindrical salpinx up to 3 mm high with fringed distal margin.

Lectotype. Here designated RBINS-40785, Royal Belgian Institute of Natural Sciences, Brussels, Belgium.

Type locality. Carrière de Booze à Trembleur (Blégny), Belgium.

Stratigraphic horizon and age. Evieux Formation, Condroz Group, VCo miospore biozone of Upper Famennian, Upper Devonian and the Duncannon Member of the Catskill Formation, VCo-VH miospore palynozones of the Upper Famennian (Cressler et al. 2010).

Remarks. Of the material studied by Stockmans (1948), we have selected specimen RBINS-40785 as lectotype, as it is the only one to clearly show the different parts characterizing *P. bertrandii* as described here. Other illustrated specimens were badly preserved and gave incomplete information.

*Species—*Pseudosporogonites quadrapartitus (*J. Hilton et D. Edwards*) C. Prestianni, J. Hilton et W. Cressler *comb. et emend. nov.*

Basionym. *Aglosperma quadrapartita* J. Hilton et D. Edwards 1996. Review of Palaeobotany and Palynology 93: 237–241, pls. I–III.

Emended specific diagnosis. Ovule borne singly and centrally within a small uniovulate cupule on long stalk. Stalk 0.6–0.8 mm wide, <12.4 mm long. Ovule 4.7–9.0 mm long ($\bar{x}$ = 6.4 mm), 1.6–4.0 mm wide ($\bar{x}$ = 2.58 mm). Integument with fine surface ribbing on inner and outer surfaces. Integument thickness 0.4 mm toward chalaza and thinning to 0.1 mm distally. Nucellus 2.2–3.8 mm long ($\bar{x}$ = 3.0 mm) and 1.0–1.6 mm wide ($\bar{x}$ = 1.38 mm). Pollen chamber 0.1 mm wide and 0.15 mm high. Salpinx at least 0.6 mm long.

Remarks. We have expanded the specific diagnosis to include the presence of a small cupule, as demonstrated above, in this species and have changed the description of the pedicel to relate it to an extended stalk bearing the cupule. We have also changed the interpretive term "preovule" to the botanically correct term "ovule." As the generic name *Pseudosporogonites* is masculine, the feminine epithet *quadrapartita* has been changed to *quadrapartitus*. Other parts of the diagnosis are unmodified from that of Hilton and Edwards (1996).

Holotype. NMW 94.75G.2a (part) and 2b (counterpart), National Museum of Wales, Cardiff, Wales, United Kingdom.

Type locality. Taffs Well, Mid-Glamorgan, Wales. Grid reference ST131825.

Stratigraphic horizon and age. Quartz Conglomerate Group, Upper Old Red Sandstone, LL–LN miospore zones, Famennian stage of the Devonian.

*Species—*Pseudosporogonites avonensis (*J. Hilton*) C. Prestianni, J. Hilton et W. Cressler *comb. nov.*

Basionym. *Aglosperma avonensis* J. Hilton 1998*b*. Palaeontology 41: 1084–1087, pls. 1–2 and text figs. 1–2.

Holotype. NMW.97.l0G.la (part), NMW.97.l0G.1b (counterpart), a complete ovule, National Museum of Wales, Cardiff, Wales, United Kingdom.

Type locality. Avon Gorge, Bristol, England.

Stratigraphic horizon and age. Shirehampton Beds, Upper Old Red Sandstone, Bristol district: LN miospore biozone, Famennian, Late Devonian (Hennessy and Higgs 1999).

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