

SPERMATOPHYTE PEOVULES FROM THE BASAL CARBONIFEROUS OF THE AVON GORGE, BRISTOL

by JASON HILTON

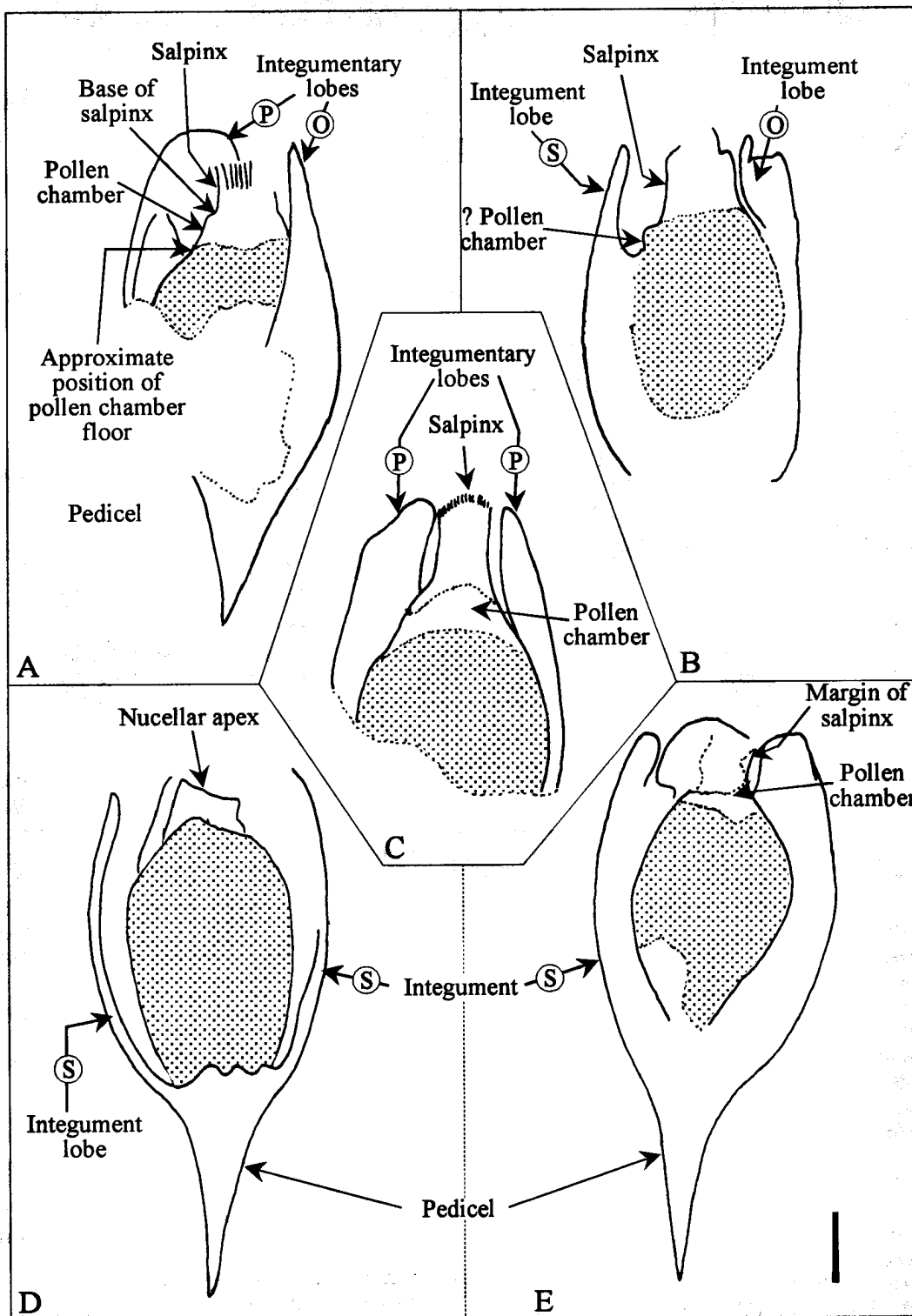
ABSTRACT. *Aglosperma avonensis* is a new acupulate species of Early Carboniferous preovule from the VI miospore biozone of the Avon Gorge near Bristol. It is closest in morphology to the slightly older *Aglosperma quadrapartita* from the Taff Gorge near Cardiff, although distinction can be made on the characteristics of the integument, the nucellus and on general size. The possibility that the new preovule represents an ontogenetic stage of *A. quadrapartita* is discounted. The new species displays characteristics of the nucellar apex not observed in the type species, possessing a distinct pollen chamber and tubular salpinx, most probably evidence of a hydrasperman pollen chamber. The distribution of *Aglosperma* and other similar preovulate structures indicates that acupulate preovules were perhaps as cosmopolitan as the previously more widely known cupulate forms during this early period of spermatophyte radiation.

THE origin and subsequent radiation of the seed-plants has been the focus of much palaeobotanical attention, with evidence frequently based on the structure and organization of the ovulate structures, the only features unique to this group in their early evolution. The evolutionary development of the ovule encapsulated the female gametophyte in an entirely new kind of reproductive structure in which monomegaspority (i.e. a single functional megaspore per tetrad and a single tetrad per sporangium) was accompanied by distal modification of the megasporangium for microspore (pollen or pre-pollen) reception and by integumentation (the enclosure of the megasporangium in an additional sterile layer).

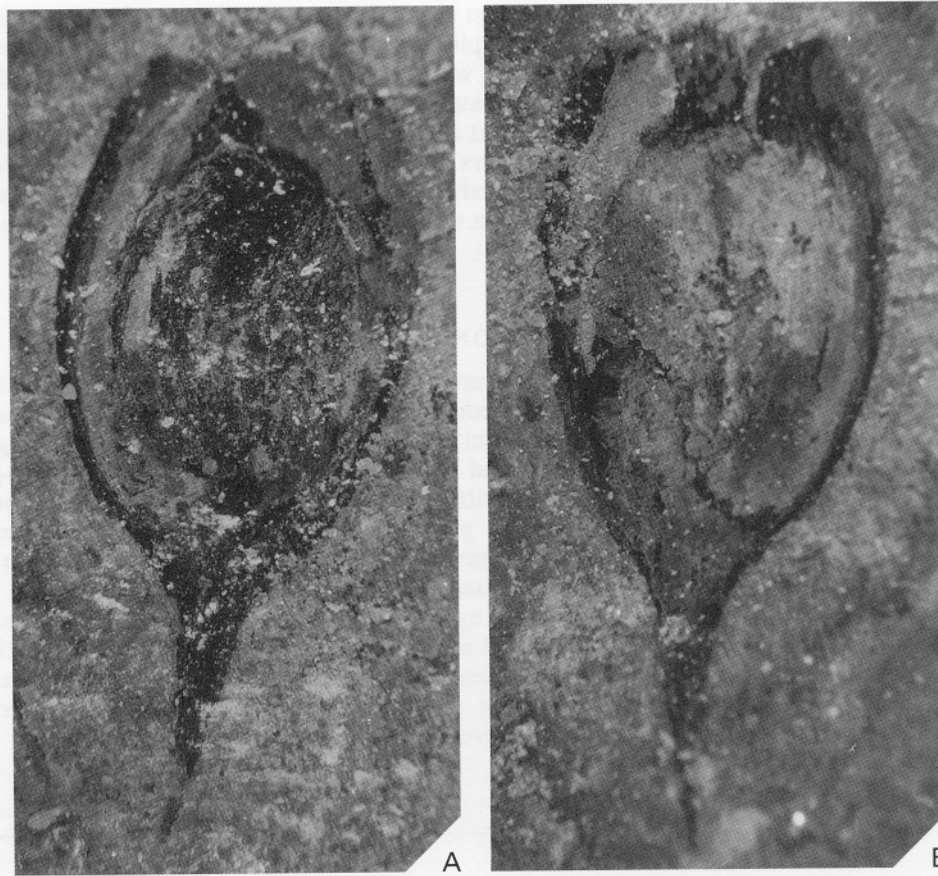
Prior to the first geological occurrence of true 'micropylar' ovules, Palaeozoic ovulate structures exhibited a preovular integument, or pre-integument of some authors. In preovules, the integument is proximally complete and distally divides into lobes. These are thus morphologically distinct from true ovules which have a completely enveloping integument except at a micropyle. To date, all pre-Carboniferous ovulate structures are preovulate (Rothwell and Scheckler 1988; Hilton and Edwards 1996).

Recent research has identified that not all of the earliest preovule morphologies occurred within vegetative cupules as had previously been thought (e.g. Rothwell and Scheckler 1988; Serbet and Rothwell 1992), but that certain preovules terminate long slender axes (Hilton and Edwards 1996). These acupulate preovules are morphologically distinct from the cupulate forms and have so far failed to provide unequivocal evidence concerning their reproductive biologies with respect to post-pollination sealing of the megagametophyte. However, in cupulate morphologies evidence of pollination biology has been used as evidence to support theories relating to the phyletic status of the seed plants. Rothwell (1986) interpreted his 'hydrasperman' pollination biology as diagnostic of all ancestral ovulate structures, inferring monophyly for the seed plants based on the improbability of this kind of elaborate structure having evolved more than once. As yet, the presence of this kind of reproductive biology in the earliest phases of seed plant radiation is only known unequivocally in the cupulate taxa (Rothwell *et al.* 1989; Hilton and Edwards 1996, in press).

During palynological investigations of the Devonian–Carboniferous boundary sequence in the Avon Gorge, Utting and Neves (1969) located plant material within the Shirehampton Beds of the Upper Old Red Sandstone–Lower Limestone Shale transition. The plant megafossils were identified by R. H. Wagner (*in* Utting and Neves 1969) as cf. *Rhacophyton*, and the plant bed was subsequently named the '*Rhacophyton* bed', reflecting the monotypic characteristics of the deposit reported by Utting and Neves (Fairon-Demaret 1986). Subsequent work has identified the presence



TEXT-FIG. 1. For caption see opposite.



TEXT-FIG. 2. *Aglosperma avonensis* sp. nov.; part (A) and counterpart (B) of holotype. NMW.97.10G.1a-b; two preintegumentary lobes are present in section, either side of the central nucellus. The nucellus is as long as the integument and possesses a nucellar apex with pollen chamber and salpinx (attached to the counterpart). The counterpart possesses a mineral film between the nucellus (on the part). The integument is visible, as most of the nucellus (the proximal 85 per cent.) is attached to the part. The long pedicel is clearly visible. Both $\times 13$.

of numerous dispersed acupulate preovules within the original material and re-collection from the site has provided additional preovules, although none in attachment to a parent plant.

MATERIAL AND METHODS

Plant adpressions from the Avon Gorge locality were prepared by *dégagement* (Leclercq 1960), using sharpened tungsten needles to remove matrix (and mud) from specimens while viewed under a Wild M3 binocular microscope. Specimens were reinforced during and after *dégagement* with

TEXT-FIG. 1. Annotated diagrams of four specimens of *Aglosperma avonensis* sp. nov. showing details of gross morphology and characteristics of the nucellar apex. The nucellus of each specimen is shown stippled. Preintegument lobe orientation: P, plan view; S, section view; O, oblique view. A, NMW.97.10G.9 (Pl. 2, figs 4-5); B, NMW.97.10G.2d (Pl. 1, fig. 1; Pl. 2, fig. 7); C, NMW.97.10 (Pl. 2, figs 6, 8); D, NMW.97.10G.1a (Text-fig. 2A); E, NMW.97.10G.1b (Text-fig. 2B). Scale bar represents 1 mm.

Paraloid glue soluble in acetone. Many of the best specimens were revealed by fortuitous fractures through the matrix. Rock splitting was accomplished using triangular tipped, leather-working needles struck with a toffee hammer. Specimens were kept dry at all times as contact with water results in fragmentation of the coalified plant material.

Illumination of specimens for both dégageage and photography was provided by a Schott KL 1500 light source, fitted with twin polarizing filters. A third polarizing filter was attached to either the microscope objective or the camera lens to reduce the glare from the micaceous matrix and to enhance edge definition. An Olympus OM system was used for all photography, using a variety of macro lenses.

LOCALITY INFORMATION AND STRATIGRAPHY

The '*Rhacophyton*' bed of the Avon Gorge occurs at the base of the Shirehampton Beds of the Upper Old Red Sandstone, which are immediately overlain in this locality by the basal Carboniferous Lower Limestone Shale. The exact location of the plant-bearing strata is given in Utting and Neves (1969). The plants are found in two distinct lithologies: green fine-grained sandstones (which represent fluvial channel in-fills) containing abundant plant debris; and green mudstones, containing intact (?autochthonous) plant material, interpreted as being vegetated overbank deposits (flood plain) with the plants having been rapidly covered with sediment during flood events. Further details of the entire plant assemblage will be presented elsewhere.

Collecting within the Avon Gorge is hampered by the locality being situated under approximately 2 metres of estuarine mud and being submerged at each high tide. As a consequence of the tidal nature of the estuary, rapidity in collecting is essential. It has proved impossible to remove all the mud from the rock surfaces at the field exposure, making sedimentological observations virtually impossible as bedding related features are obscured.

EXPLANATION OF PLATE 1

Figs 1–7. *Aglosperma avonensis* sp. nov.; Avon Gorge plant assemblage. 1, four isolated preovules at varying stages of dégageage, aligned on the same slab but each faces a different direction suggesting a random arrangement. This slab lacks a counterpart and the specimens are generally not well preserved or intact. The preovule to the left (NMW.97.10G.2a) lacks an uppermost preintegumentary lobe but its impression can be noted by the darker coloured imprint on the sediment below. The left middle preovule (NMW.97.10G.2b) possesses two preintegumentary lobes whilst the right middle preovule (NMW.97.10G.2c) is distally incomplete but has a well preserved pedicel and chalaza. The preovule to the right (NMW.97.10G.2d) is proximally incomplete and is enlarged in Pl. 2, fig. 7, showing the details of the nucellar apex; $\times 3.6$. 2, NMW.97.10G.3; isolated preovule showing details of the long pedicel which tapers to a point; little of the integument remains in this poorly preserved specimen, although the positions of two preintegumentary lobes, one with a rounded apex, are visible; $\times 8.7$. 3, NMW.97.10G.4; three preovules in close proximity to each other and to a short axis (right centre). The uppermost preovule has its distal apex pointing upwards, the central preovule is orientated towards the right and the lowermost preovule is orientated towards the upper right. None of these preovules or the axis are attached to each other. The pedicel on the central preovule is typical of this species when complete, tapering to a point; $\times 4.2$. 4–5, part and counterpart of NMW.97.10G.5. 4, preovule with an entire pedicel and three well preserved preintegumentary lobes. At the distal apex the nucellar apex is visible. 5, details of the nucellar apex beside the distally recurved preintegumentary lobe on the right hand side. The distal extremes of both part and counterpart of this preovule are enlarged in figs 6–7; $\times 9$. 6–7, enlargement of the distal areas of NMW.97.10G.5 (figs 4–5). 6, nucellar apex comprising a pollen chamber and salpinx which protrudes beyond the distal reaches of the two preintegumentary lobes visible at each side. The tips of the preintegumentary lobes are slightly recurved, each tapering to a point and are observed in section; $\times 35$. All specimens are illuminated by multi-directional, low angled, polarized light to reveal features otherwise not visible with conventional lighting.



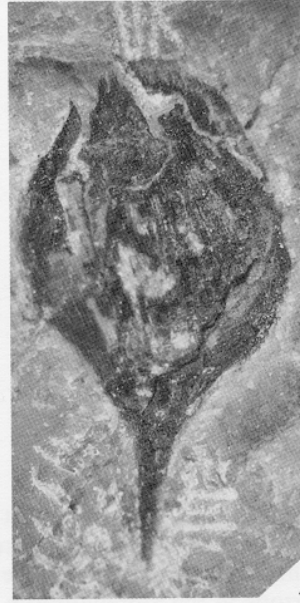
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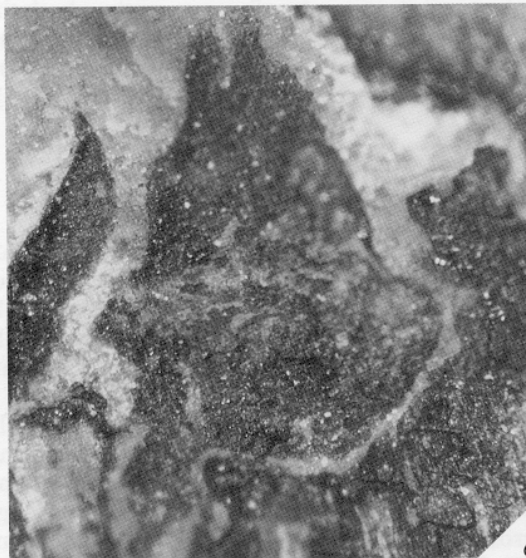
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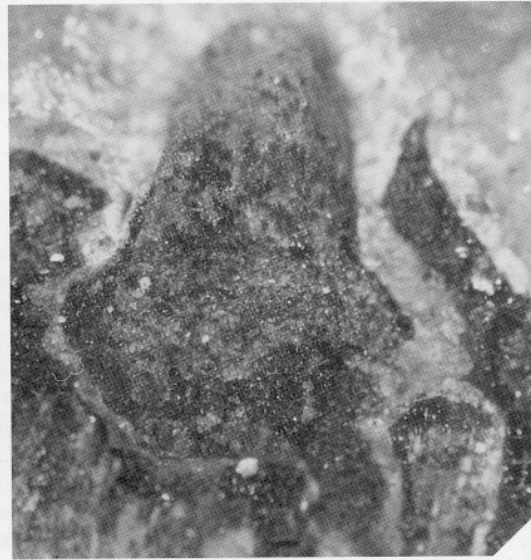
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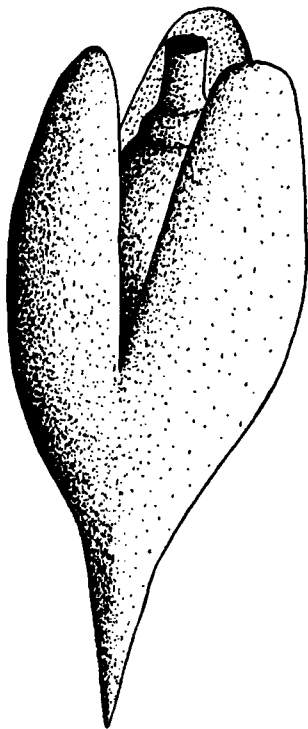


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7

TEXT-FIG. 3. Reconstruction of *Aglosperma avonensis* sp. nov. Scale bar represents 1 mm.



Utting and Neves (1969) dated the Avon Gorge plant bed palynologically as within the VI spore zone (basal Tournaisian). This has been confirmed by re-examination of the palynoflora by Higgs *et al.* (1988), who assigned the Portishead Beds of the Avon Gorge to their LL biozone, whilst noting a change to the VI biozone in the Shirehampton Beds, including the plant-bearing strata in this younger biozone. This places the Avon Gorge plant bed stratigraphically younger than both the latest Devonian Taffs Well plant assemblage in Tongwynlais, Cardiff and the assemblage from Croyde Hoe Quarry on Baggy Point, north Devon (Fairon-Demaret 1986; Higgs *et al.* 1988; Hilton and Edwards 1996, in press), both of which contain abundant preovulate remains (Hilton 1996).

DESCRIPTION OF SPECIMENS

The description is based on 68 complete specimens and more than 30 incomplete ones. All specimens are detached from the parent plant and most show evidence of a highly prominent pedicel (Text-figs 1–2; Pl. 1, figs 1–4; Pl. 2, figs 1–4). The pedicel widens towards the chalaza of the preovule which is not clearly distinguishable because there is no distinction between the base of the preovule and the end of the pedicel. The pedicel is up to 5.1 mm long and tapers proximally to a point, presumably marking the place of preovule detachment (e.g. Text-fig. 1; Pl. 1, figs 1–3).

The overall outline of the preovule is ovate (Pl. 1, figs 1–4; Pl. 2, figs 1–3). Specimens typically have similarly convex outermost integumentary surfaces in all orientations encountered, indicating that the preovules were radially isodiametric prior to compression. The chalazal third of the integument is entire and the distal two-thirds are divided into three (rarely four) lobes (Pl. 1, figs 1, 4–5; Pl. 2, figs 1–4, 6). Each lobe is laminar in cross section and is curved around the outside of the nucellus and tapers distally to an obtuse apex (Pl. 2, figs 1–3). Both the inner and outer surfaces

of the preintegument are glabrous except for fine surface ribbing that is seen only on better preserved specimens, with ribs typically 1–2 μm wide and 5–10 μm apart from each other.

The nucellus is often visible between the preintegumentary lobes. The thin mineral film present between the preintegument and the nucellus indicates that the nucellus is free except for basal attachment where the nucellus is adnate to the chalazal portion of the preintegument (Text-fig. 1; Pl. 1, figs 1–7). This mineral film is similar to that described by Hilton and Edwards (1996), occurring between the preintegument and the nucellus of *Aglosperma quadrapartita* Hilton and Edwards, 1996. The outline of the nucellus follows the inner surface of the preintegument for approximately two-thirds of preovule length with the nucellar apex occurring above this point (Pl. 1, fig. 1; Pl. 2, fig. 6). The outer surface of the nucellus is usually glabrous. One specimen has preserved cellular detail, indicating that the outer layer of the nucellus consists of elongated epidermal cells which have a striated appearance. Another specimen possesses distinct ornamentation on the outer surface of the nucellus reminiscent of desiccation cracks, but this is not considered to be an original characteristic of the preovule.

Twelve specimens show well preserved nucellar apices and hence the form of the distal apparatus for microspore (pre-pollen/pollen) capture. The nucellus tapers towards the apex, presumably outlining the position of the functional megaspore (Text-fig. 1; Pl. 1, figs 4–7; Pl. 2, figs 6–8) although the latter has not been observed. The nucellar apex is cylindrical in form, comprising a dome-shaped pollen chamber where the approximate position of the pollen chamber floor can be discerned (Text-fig. 1; Pl. 1, figs 6–7; Pl. 2, figs 3–7). Above the pollen chamber is an elongate cylindrical salpinx (Text-fig. 1; Pl. 1, figs 6–7) the distal extremity of which commonly is irregular, suggesting it to be either incomplete or more probably with an irregular apex in life (Pl. 2, fig. 5). In some cases it flares outwards distally (Text-fig. 1A; Pl. 2, fig. 5) whilst in others it tapers distally (Text-fig. 1B; Pl. 1, figs 6–7; Pl. 2, figs 6–8). In certain specimens the salpinx protrudes beyond the exterior of the integument through the distal integumentary aperture (Text-fig. 1A, D–E; Pl. 1, figs 6–7) whilst in other specimens the nucellar apex is contained within the length of the integument (Text-fig. 1C; Pl. 2, figs 4–8). *Aglosperma avonensis* is reconstructed in Text-figure 3 showing the more commonly occurring three lobed form.

SYSTEMATIC PALAEONTOLOGY

Class LAGENOSPERMOPSIDA *sensu* Cleal, 1994

Order LAGENOSTOMALES Seward, 1917

Family GENOMOSPERMACEAE Long, 1975

Genus AGLOSPERMA Hilton and Edwards, 1996, nov. emend.

Type species. *Aglosperma quadrapartita* Hilton and Edwards, 1996.

Emended diagnosis. Acupulate preovule situated singly and terminally on long axis (pedicel). Preintegument lobate, fused in approximately basal third or less of preovule length, and widest at point where integumentary fusion ends. Preintegument vascularized with one strand per lobe. Micropyle absent. Nucellus free from the integument except at basal attachment. Nucellus glabrous and ovate in outline below pollen chamber. Distal nucellar apex with pollen chamber and long salpinx.

Remarks. The generic diagnosis is emended very slightly from that in Hilton and Edwards (1996) to incorporate characteristics of the new material and to remove characters which, with the discovery of an additional species, are now considered specific. Thus, characters relating to the number and shape of the preintegumentary lobes have been removed from the original diagnosis of the genus.

Aglosperma avonensis sp. nov.

Plates 1–2; Text-figures 1–3

Derivation of name. *Avonensis* from the Avon area, relating to the source of the material from the Avon Gorge, Bristol.

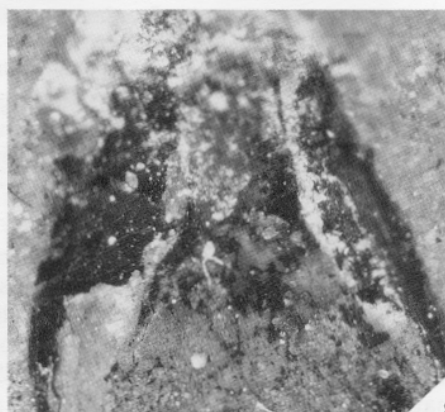
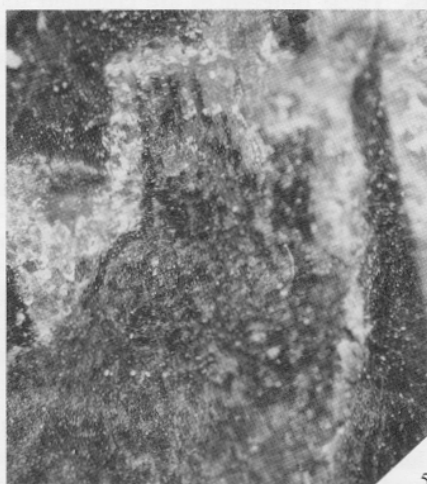
Holotype. NMW.97.10G.1a (part) NMW.97.10G.1b (counterpart), a complete addressed preovule, National Museums and Galleries of Wales, Cardiff, Wales, UK.

Horizon and age. Shirehampton Beds, Upper Old Red Sandstone, Bristol district: VI miospore biozone of the Tournaisian, Lower Carboniferous.

Diagnosis. As for genus. Preovule excluding pedicel 4.7–7.1 mm long (\bar{x} = 5.78 mm, n = 34), 2.6–4.2 mm wide (\bar{x} = 3.56 mm, n = 34). Pedicel tapers, widening towards junction with preovule, up to 2.4 mm wide and < 5.1 mm long. Integument lobate in distal two-thirds or more with typically three preintegumentary lobes and less commonly four. Each preintegument lobe laminar in cross section and curved around the outside of the nucellus. Preintegument lobes tapering to an obtuse apex and with fine surface ribbing on inner and outer surfaces. Preintegument thickness 0.35 mm towards chalaza and thinning to 0.1 mm distally. Nucellus 3.9–5.5 mm long (\bar{x} = 4.5 mm, n = 16) and 2.1–2.8 mm (\bar{x} = 2.4 mm, n = 16) with maximum diameter towards the point of attachment. Pollen chamber with distinct pollen chamber floor 0.3–0.8 mm long (\bar{x} = 0.7 mm, n = 12) and 0.7–1.1 mm wide (\bar{x} = 0.85 mm, n = 12). Cylindrical salpinx *c.* one-third of pollen chamber width at distal end of pollen chamber.

EXPLANATION OF PLATE 2

Figs 1–8. *Aglosperma avonensis* sp. nov.; Avon Gorge plant assemblage. 1, NMW.97.10G.6; poorly preserved preovule where much of the organic material has lifted off. Two preintegumentary lobes are visible, each in approximate plan view, although only the right hand lobe has a complete rounded apex; $\times 8$. 2, NMW.97.10G.7; single preovule with three preintegumentary lobes, each with a rounded apex and fused in the chalazal one-third of the preovule or less. The lobe to the right is in section while the central one is in plan view and the one to the left is obliquely orientated. The pointed pedicel is prominent; $\times 8$. 3, NMW.97.10G.8; preovule with three preintegumentary lobes, the central one in plan view with a rounded apex and two lateral lobes each in an oblique orientation with the outer surface exposed. The integument is fused only towards the chalaza for approximately one-quarter of the preovule's length. The pedicel is incomplete but has the characteristic tapering appearance; $\times 9$. 4, NMW.97.10G.9; preovule with long tapering pedicel and an incomplete preintegument. The nucellar apex is well preserved comprising a dome-shaped pollen chamber with a distally broadening salpinx situated distally from the pollen chamber. One integumentary lobe is visible to the right of the nucellus and another present to the left, below the nucellus. The third lobe has been removed to reveal the nucellus. The nucellar apex is enlarged in fig. 5; $\times 9$. 5, NMW.97.10G.9; enlargement of the nucellar apex shown in fig. 4, showing the position of the pollen chamber and the salpinx and the irregular distal margin of the salpinx; $\times 27$. 6, NMW.97.10G.10; basally incomplete preovule with two preintegumentary lobes beneath the central nucellus. A third lobe has been removed by dégageement to reveal the nucellus below, enlarged in fig. 8. The nucellar apex does not extend beyond the tips of the integumentary lobes; $\times 8$. 7, NMW.97.10G.2d; enlargement of the right-most preovule in Pl. 1, fig. 1. This specimen displays two preintegumentary lobes, one either side of the nucellus. The lobe to the left is revealed in section whilst the one to the right is obliquely oriented. The nucellar apex comprises a cylindrical salpinx extending distally from a dome-shaped pollen chamber; $\times 15$. 8, NMW.97.10G.10; enlargement of the nucellar apex shown in fig. 6 with long, cylindrical salpinx situated distally on a dome-shaped pollen chamber; $\times 14$. All specimens are illuminated by multi-directional, low angled, polarized light to reveal features otherwise not visible in conventional lighting.



HILTON, *Aglosperma*

DISCUSSION

Comparison with other taxa

This new preovule is distinct from *Aglosperma quadrapartita* Hilton and Edwards, 1996 in a number of ways despite the presence of certain shared characteristics. Both *A. quadrapartita* and the new specimens are isodiametric in cross section and comprise a nucellus enveloped by a preintegument. Both species have similar levels of preintegumentary lobe fusion (fused in approximately the chalazal one-third) and have similar low levels of fusion of the preintegument to the nucellus. The preintegument of both species is finely striated, without hairs or glands, and is laminar when viewed in compressed transverse section. The size range of the two species overlap, although *A. quadrapartita* is typically longer and thinner. Preintegumentary size comparisons of the two species are shown in Text-figure 4.

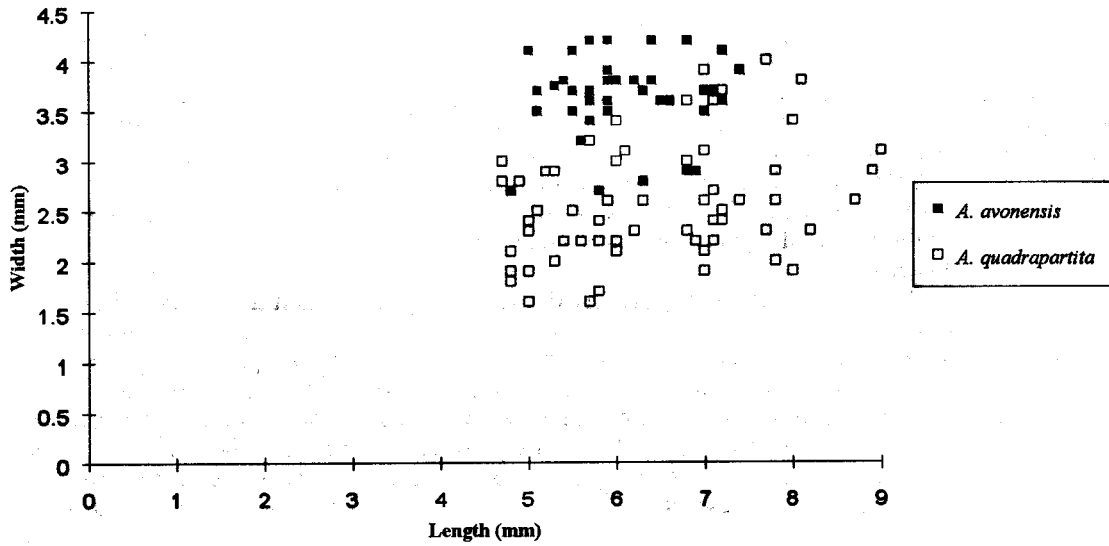
The pedicel of *A. quadrapartita* is longer, and does not taper to a point as observed in the new material, with the detachment surface typically being an irregular fracture. *A. quadrapartita* has four preintegumentary lobes whilst the new preovules typically have three lobes, with only two specimens having four lobes. Therefore, the number of preintegumentary lobes between the two preovules is on the whole different, although the number of lobes observed in each species is not mutually exclusive. A further distinction relating to the preintegument is that in *A. quadrapartita* the lobes are lanceolate in outline, tapering to a distal point, whilst in the new species they are more obtuse and lack distinct pointed tips. These differences are confined to specimens at each locality. The nucellus of the new material is typically larger than in *A. quadrapartita* (Text-fig. 5) measured both in absolute terms and in size relative to the preintegument. Both species have a distinct nucellar apex, although in the new specimens the pollen chamber floor and pollen chamber are better defined than in *A. quadrapartita*. Features of the two species are compared in Table 1.

TABLE 1. Comparison of selected features of *Aglosperma quadrapartita* and *Aglosperma avonensis* sp. nov.

Character	<i>Aglosperma quadrapartita</i>	<i>Aglosperma avonensis</i> sp. nov.
Attachment	Pedicel max. length 12 mm, attenuated apex	Pedicel max. length 6 mm Tapering and with rounded apex
Form	Acupulate, radial symmetry	Acupulate, radial symmetry
Overall length	6–9 mm	6–9 mm
Overall diameter	2.3–4 mm	3–5.5 mm
Integument	4 lobes Fused basal one-third or less Laminar and ribbed Pointed apex 1 vascular strand per lobe	3 (rarely 4) lobes Fused basal one-third or less Laminar and ribbed Rounded apex ?1 vascular strand per lobe
Nucellus	Free from integument Small pollen chamber Long thin salpinx	Free from integument Large pollen chamber Long wide salpinx

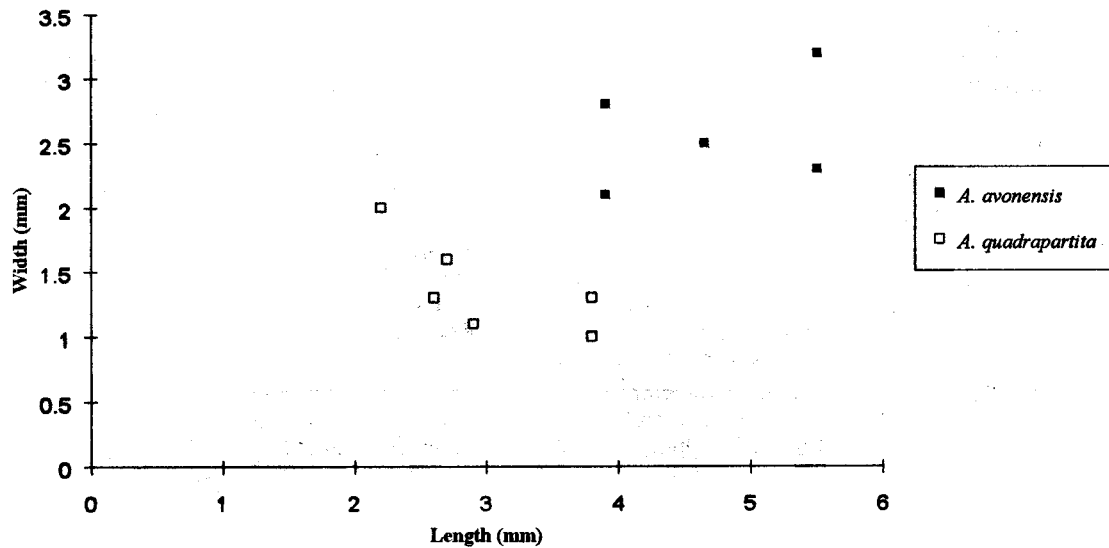
The possibility that the new material represents an ontogenetic progression of *Aglosperma quadrapartita* is considered unlikely based on what is known about developmental sequences in other Late Devonian preovules. Rothwell and Scheckler (1988) showed an ontogenetic series in both *Moresnetia zalesskyi* (Stockmans) Fairon-Demaret and Scheckler, 1987 and *Elkinsia polymorpha* Rothwell, Scheckler and Gillespie, 1989, characterized by increases in overall dimensions with maturation post-pollination. If the two sets of specimens were conspecific, but represent different ontogenetic stages, based on size alone it would be expected that the new material would be a more

Integumentary dimensions



TEXT-FIG. 4. Graph comparing the integumentary dimensions of *Aglosperma quadrapartita* and *Aglosperma avonensis* sp. nov.

Nucellus dimensions



TEXT-FIG. 5. Graph comparing the nucellar dimensions of *Aglosperma quadrapartita* and *Aglosperma avonensis* sp. nov.

mature form of *A. quadrapartita*. Although it is possible that the greater overall nucellar dimensions of the new material could be explained through ontogenetic variation, the combination of other differences, in particular those relating to the form of the preintegument, suggests that this is not

the case. Whilst both species have a similar low degree of preintegumentary fusion at the chalazal end, the new material typically possesses three obtusely tipped integumentary lobes rather than the four lanceolate integumentary lobes observed in *A. quadrapartita*. This quantitative and morphological variation in preintegumentary lobe characteristics is very different from that reported through developmental sequences in other ovulate structures, where changes are in size rather than lobe shape and number (Rothwell and Scheckler 1988). Therefore, the combined differences of the integument and the nucellus are here considered sufficient to discount the new material as being an ontogenetic variant of *A. quadrapartita* resulting in the erection of a second species of the genus. For further comparison of the genus *Aglosperma* with other Palaeozoic preovule taxa, see Hilton and Edwards (1996).

Pollination biology

The material described here presents clear evidence from the external shape of the nucellar apex of *Aglosperma avonensis*, and shows a pollen chamber and tubular salpinx. This combination of characters is in general agreement with the external features present in other early seed plant ovulate structures, in particular those Late Devonian and Early Carboniferous forms displaying hydrasperman reproduction (Rothwell 1986). The distribution of the latter has been given considerable phylogenetic importance, implying monophyly of the spermatophytes based on its ubiquitous distribution within the earliest seed plants and the improbability of this kind of elaborate reproductive structure having evolved independently more than once (Rothwell 1986; Rothwell and Scheckler 1988; Rothwell and Serbet 1994). In pre-Carboniferous spermatophytes this type of reproduction has previously been verified only in cupulate taxa (e.g. *Moresnetia* (Stockmans) Fairon-Demaret and Scheckler, 1987; *Elkinsia* Rothwell, Scheckler and Gillespie, 1989; *Kerryia* Rothwell and Wight, 1989). Thus, the presence of hydrasperman reproduction in ovulate structures with different architectural models (i.e. the acupulate taxa) has not been ascertained and currently adds no support to theories on the monophyly of the spermatophytes.

Rothwell (1986) and Rothwell and Scheckler (1988) considered evidence from the exterior morphology of the nucellar apex insufficient to demonstrate the presence of hydrasperman reproduction. In the absence of permineralized preservation it is impossible to observe features within the nucellar apex characteristic of hydrasperman ovules, including a membranous pollen chamber floor and a central column. The demonstration of internal morphology is essential because a nucellar apex comprising both a pollen chamber and salpinx (= nucellar beak) is not unique to hydrasperman ovules, with similar forms being observed in both medullosan and callistophytalean ovules also of Palaeozoic age (Serbet and Rothwell 1995). The presence of Late Devonian or basal Carboniferous examples of both of these other kinds of pollen chamber organizations is not supported by the fossil record (Serbet and Rothwell 1995).

Hydrasperman, medullosan and callistophytalean patterns of reproduction differ from each other primarily through the processes of post-pollination sealing of the megagametophyte (Serbet and Rothwell 1995). In hydrasperman ovules, sealing is achieved by the pollen chamber floor being pushed outwards by the developing megagametophyte so that the central column seals the base of the spine (Rothwell 1986; Rothwell and Scheckler 1988; Serbet and Rothwell 1995). In ovules displaying the medullosan pattern, sealing off is accomplished by a combination of reduction in the size of the opening of the nucellar beak and the deposition of mucilaginous or resinous substances at the tip of the nucellar beak (Serbet and Rothwell 1995). Therefore, the functioning of the central column characteristic of hydrasperman reproduction has become redundant in medullosan ovules (more typically absent), playing no part in post-pollination sealing off of the megagametophyte. In both hydrasperman and medullosan patterns, sealing of the megagametophyte is entirely through tissues of the nucellus. In the megagametophyte of callistophytalean ovules it occurs from the combination of the closure of the nucellar beak (either through deposition of mucilaginous/resinous substances or through enlargement of the cells at the nucellar beak) and closure of the micropyle of the integument around the nucellus.

To date, hydrasperman reproduction has been ascertained in all permineralized Devonian and basal Carboniferous ovulate structures where the combination of characteristics include both a pollen chamber and salpinx. Furthermore, only one preovulate structure of the same age has been proven to be non-hydrasperman, possessing a parenchymous nucellar beak rather than a hydrasperman-type pollen chamber (*Coumaisperma*; Galtier and Rowe 1989, 1991). In this regard it seems most probable that *Aglosperma avonensis* too was hydrasperman although further evidence in the form of permineralized anatomy is necessary to confirm this important point. Rather than presenting evidence for a diphyletic origin for the spermatophytes (as suggested by Hilton and Edwards 1996) it is here suggested that *Aglosperma* more probably presents evidence for a rapid morphological radiation of the seed-plants from a common ancestor. However, whether this hypothetical ancestor was cupulate or acupulate is a matter of considerable debate.

Further considerations

In the absence of evidence of the morphology of the parent plant, both species of *Aglosperma* have been interpreted as being acupulate (*sensu* Hilton and Edwards 1996). This implies that, beyond the known length of the pedicel, the preovule was attached directly to the parent plant and not enclosed within a cupule. The preintegument of *Aglosperma* is clearly distinct from definite cupulate preovules in being considerably larger (up to twice the size) and the free integumentary lobes of both species of *Aglosperma* are laminate in transverse section, rather than the terete cylindrical lobes observed in cupulate forms. This feature of preintegumentary lobe shape is so far unique to *Aglosperma* among contemporaneous spermatophytes. Furthermore, *Aglosperma* occurs terminally on a slender axis rather than on a short pedicel adnate to the cupule. From these distinguishing features Hilton and Edwards (1996) separated *Aglosperma* from contemporaneous cupulate morphologies and subsequently advocated an acupulate nature for the genus.

The discovery of *A. avonensis* indicates that the genus is not limited to a single location as previously thought (Hilton and Edwards 1996). As both the Avon Gorge and the Taff Gorge were situated on the southern margin of St George's land in the Late Devonian (Cope *et al.* 1992), the new discovery suggests that the genus (amongst other spermatophytes) was possibly common in this palaeogeographical region (Hilton 1996). Furthermore, from the stratigraphical occurrences of the two species of *Aglosperma* it may be deduced that the three lobed forms are derived from the older four lobed forms, although further species and occurrences would be desirable to verify this point.

Evidence for the cosmopolitan distribution of the genus comes from identification (by the author) of *Aglosperma quadrapartita* from a Late Devonian locality in Russia, dated on miospores as VCo miospore zone (M. Fairon-Demaret, pers. comm. 1995). This occurrence places acupulate preovules contemporaneous with the earliest cupulate forms and indicates that acupulate preovules were geographically widespread by the end of the Devonian. However, based on current evidence, acupulate preovules were not as widely distributed as cupulate forms, which have been recorded from North America (*Elkinsia polymorpha* Rothwell, Scheckler and Gillespie, 1989 and *Archaeosperma arnoldii* Pettit and Beck, 1968), Europe (*Moresnetia zalesskyi* (Stockmans) Fairon-Demaret and Scheckler, 1987; *Xenotheca devonica* (Arber and Goode) *emend.* Hilton and Edwards, in press and *Kerryia mattenii* Rothwell and Wight, 1989) and Russia (*Moresnetia* sp., Pettitt and Beck, 1968; *Lenlogia kryshstofovichii* (Radtchenko) Krassilov and Zakharova, 1995).

The distribution of *Aglosperma* has consequences for phylogenetic analyses of the seed plants (e.g. Crane 1985; Doyle and Donoghue 1986, 1992; Nixon *et al.* 1994; Rothwell and Serbet 1994) which identify the cupulate morphologies (i.e. those with the moresnetian architectural model *sensu* Hilton and Edwards in press) as characteristic of the earliest seed plants. In such analyses there is now the need to identify an additional (although lesser known) seed plant morphotype.

CONCLUSIONS

The possibility that the new material represents an ontogenetic stage of *Aglosperma quadrapartita* is discounted based on the overall morphological distinction from *A. quadrapartita*. This has led to

the taxonomic separation of the two sets of preovules although, due to their overall morphological similarity, they have been placed within the same genus. However, it is evident that without permineralized preservation it is impossible to ascertain unequivocally whether *Aglosperma* possessed hydrasperman pollination biology although this seems the most likely interpretation of the nucellar organization observed.

Aglosperma avonensis adds to the morphological diversity of the early seed plants and indicates that they were both widespread and numerous, constituting an increasingly more common component of earliest Carboniferous floras. Furthermore, new information on the distribution of the genus *Aglosperma* indicates that it was contemporaneous with the earliest cupulate preovules.

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REFERENCES

- CLEAL, C. J. 1994. Gymnospermophyta. 795–808. In BENTON, J. J. (ed.). *The fossil record 2*. Chapman and Hall, London, 845 pp.
- COPE, J. C. W., INGHAM, J. K. and RAWSON, P. F. 1992. Atlas of palaeogeography and lithofacies. *Memoir of the Geological Society of London*, **13**, 1–153.
- CRANE, P. R. 1985. Phylogenetic analysis of seed-plants and the origins of the angiosperms. *Annals of the Missouri Botanical Garden*, **72**, 716–793.
- DOYLE, J. A. and DONOGHUE, M. J. 1986. Seed plant phylogeny and the origin of angiosperms: an experimental cladistic approach. *Botanical Review*, **52**, 321–431.
- — — 1992. Fossils and seed plant phylogeny reanalyzed. *Brittonia*, **44**, 89–106.
- FAIRON-DEMARET, M. 1986. Some uppermost Devonian megafloras: a stratigraphical review. *Annales de la Société Géologique de Belgique*, **109**, 43–48.
- — — and SCHECKLER, S. E. 1987. Typification and redescription of *Moresnetia zalesskyi* Stockmans, 1948, an early seed plant from the Upper Famennian of Belgium. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, **57**, 183–199.
- GALTIER, J. and ROWE, N. P. 1989. A primitive seed like structure and its implications for early gymnosperm evolution. *Nature*, **340**, 225–227.
- — — 1991. A new permineralized seed-like structure from the basal-most Carboniferous of France. *Neues Jahrbuch für Geologie und Paläontologie*, **183**, 103–120.
- HIGGS, K., CLAYTON, G. and KEEGAN, J. B. 1988. Stratigraphic and systematic palynology of the Tournasian rocks of Ireland. *Special Paper of the Geological Survey of Ireland*, **7**, 1–47.
- HILTON, J. 1996. Famennian–Tournaisian plant assemblages from south-west Britain. Unpublished Ph.D. Thesis, University of Wales, Cardiff.
- — — and EDWARDS, D. 1996. A new Late Devonian acupulate preovule from Taffs Well, South Wales. *Review of Palaeobotany and Palynology*, **93**, 235–252.
- — — in press. New data on *Xenotheca devonica* Arber and Goode, an enigmatic early seed plant with cupulate preovules. In KURMANN, M. and HEMSLEY, A. R. (eds). *The evolution of plant architecture*. Royal Botanic Gardens, Kew, London.
- KRASSILOV, V. A. and ZAKHAROVA, T. V. 1995. *Moresnetia*-like plants from the Upper Devonian of Minusinsk basin, Siberia. *Palaeontological Journal*, **29**, 35–43.
- LECLERCQ, S. 1960. Refendage d'un reche fossilifère et dégagement de ses fossiles sous binoculaire. *Senckenberg Lethiaea*, **41**, 483–487.
- LONG, A. G. 1975. Further observations on some Lower Carboniferous seeds and cupules. *Transactions of the Royal Society of Edinburgh*, **69**, 278–293.

- NIXON, K. C., CREPET, W. L., STEVENSON, D. and FRIIS, E. M. 1994. A reevaluation of seed-plant phylogeny. *Annals of the Missouri Botanical Garden*, **81**, 484–533.
- PETTITT, J. M. and BECK, C. B. 1968. *Archaeosperma arnoldii* – a cupulate seed from the Upper Devonian of North America. *Contributions to the Paleontological Museum, University of Michigan*, **22**, 139–154.
- ROTHWELL, W. G. 1986. Classifying the earliest gymnosperms. 137–162. In SPICER, R. A. and THOMAS, B. A. (eds). *Systematic and taxonomic approaches in palaeobotany*. Systematics Association Special Volume No. 31. Clarendon Press, Oxford, 321 pp.
- and SCHECKLER, S. E. 1988. Biology of ancestral gymnosperms. 85–134. In BECK, C. B. (ed.). *Origins and evolution of gymnosperms*. Columbia University Press, New York, 504 pp.
- and GILLESPIE, W. H. 1989. *Elkinsia* gen. nov., a late Devonian gymnosperm with cupulate ovules. *Botanical Gazette*, **150**, 170–189.
- and SERBET, R. 1994. Lignophyte phylogeny and the evolution of spermatophytes: a numerical cladistic analysis. *Systematic Botany*, **19**, 443–482.
- and WIGHT, D. C. 1989. *Pullaritheca longii* gen. nov. and *Kerryia mattenii* gen. et sp. nov., Lower Carboniferous cupules with ovules of the *Hydrasperma tenuis*-type. *Review of Palaeobotany and Palynology*, **60**, 295–309.
- SERBET, R. and ROTHWELL, G. W. 1992. Characterising the most primitive seed ferns. 1. A reconstruction of *Elkinsia polymorpha*. *International Journal of Plant Science*, **53**, 602–621.
- — 1995. Functional morphology and homologies of gymnospermous ovules: evidence from a new species of *Stephanospermum* (Medullosales). *Canadian Journal of Botany*, **73**, 650–661.
- SEWARD, A. C. 1917. *Fossil plants*. Cambridge University Press, Cambridge, 318 pp.
- STOCKMANS, F. 1948. Végétaux du Dévonien Supérieur de la Belgique. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, **110**, 1–85.
- UTTING, J. and NEVES, R. 1969. Palynology of the Lower Limestone Shale Group (Basal Carboniferous Limestone series) and Portishead Beds, (Upper Old Red Sandstone) of the Avon Gorge, Bristol, England. *Colloque sur la Stratigraphie du Carbonifère, Congrès et Colloques, Université Liège*, **55**, 411–422, pl. 2.

JASON HILTON

Department of Earth Sciences
Cardiff University
PO Box 914
Cardiff CF1 3YE, UK

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