

MORPHOLOGY, ULTRASTRUCTURE AND AFFINITY OF BARREMIAN (LOWER CRETACEOUS) MEGASPORES *DIJKSTRAISPORITES* AND *PAXILLITRILETES* FROM BRILON-NEHDEN, GERMANY

VOLKER WILDE

Forschungsinstitut Senckenberg
Palaeobotanik
Senckenberganlage 25
D-60325 Frankfurt am Main
Germany

ALAN R. HEMSLEY

Laboratory for Experimental Palynology
Department of Earth Sciences
University of Wales Cardiff
PO Box 914
Cardiff CF1 3YE, Wales
United Kingdom

Abstract

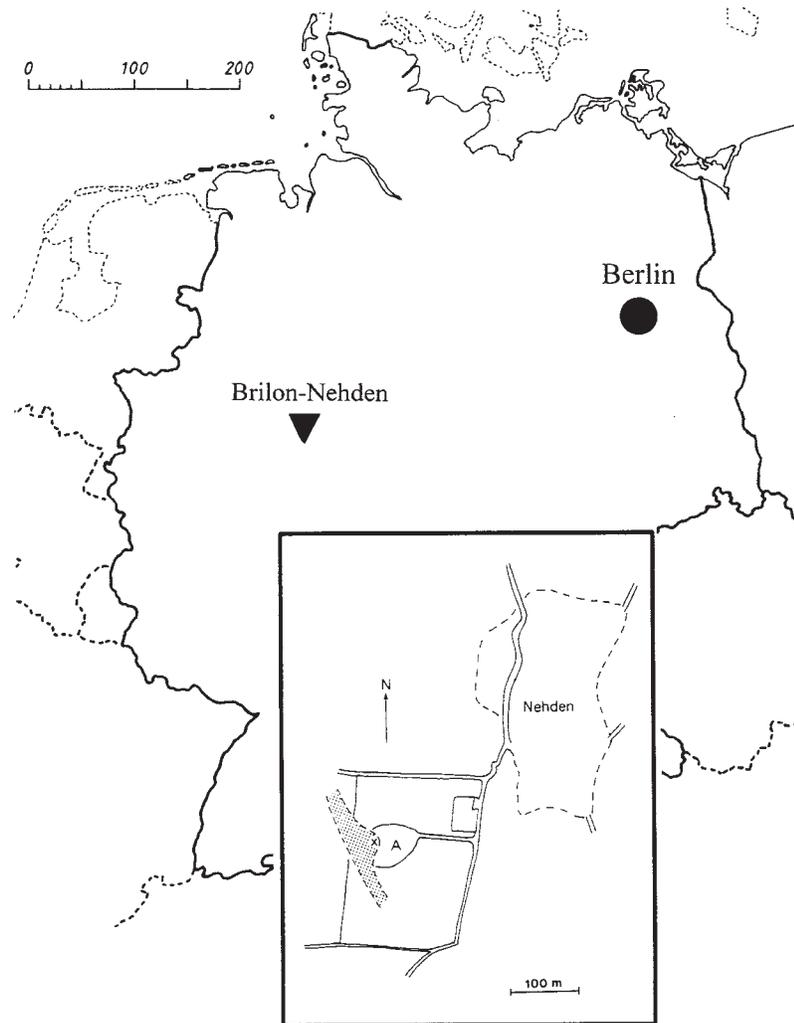
A number of well-preserved megaspores of *Paxillitriletes fairlightensis* (Dijkstra) Potonié & *Dijkstraisorites helios* (Batten) Nicholson & Hall from the terrestrial Barremian (Lower Cretaceous) of Brilon-Nehden (Germany) have been investigated in detail using electron microscopy. Morphology and ultrastructure is compared to that of known examples of Mesozoic megaspores and this, combined with the presence of adherent monolete microspores, indicates an isoetalean affinity for both species. Furthermore, the reticulate body ornament, laesural and equatorial elaboration, and wall ultrastructure suggest a close systematic relationship between these two species. This is new evidence in support of the view that most Mesozoic and Tertiary megaspores with expanded laesural lips and/or zona belong to this order of heterosporous lycopsids.

INTRODUCTION

The clay of a Barremian (Lower Cretaceous) karst infill near Brilon-Nehden (Text-Figure 1) has yielded a diverse assemblage of extremely well-preserved megaspores, including a considerable number of specimens belonging to *Paxillitriletes* Hall & Nicolson 1973 and *Dijkstraisorites* Potonié 1956 (Huckriede, 1982; Kampmann, 1983; Schultz and Noll, 1987). For a comparative study of wall construction in both of these genera, representative material was chosen from that locality.

There are a number of Cretaceous megaspores that are characterized by ridges of the trilete mark that are always connected to the equatorial rim in combination with a more or less elaborate zona along the equatorial to slightly subequatorial curvatures. They may have similar extensions of the ridges of the trilete mark (laesural lips). Depending on size, ornamentation, structure and extension of the zona/laesural lips, they have been grouped into a number of genera, principally *Dijkstraisorites* Potonié 1956, *Henrisporites* (Potonié) Binda & Srivastava 1968, *Herbosisporites* Li Wenben & Batten in Li Wenben et al. 1987, *Minerisporites* Potonié 1956, *Paxillitriletes* Hall & Nicolson 1973, *Sepisporites* Li Wenben & Batten in Li Wenben et al. 1987 and *Tenellisporites* Potonié 1956 (Batten & Koppelhus 1993). Most of the generic and specific descriptions are exclusively based on surface morphology; there is only scarce information on wall ultrastructure in these genera.

Studies utilizing both scanning and transmission electron microscopy (SEM and TEM, respectively) have yielded considerable information regarding the affinity of many fossil megaspores (e.g., Kovach and Dilcher, 1985; Hemsley and Scott, 1989; Taylor, 1994). The use of these techniques is now expected in any detailed documentation of megaspores. The use of SEM images of selectively damaged specimens, especially walls, is advocated as a necessary

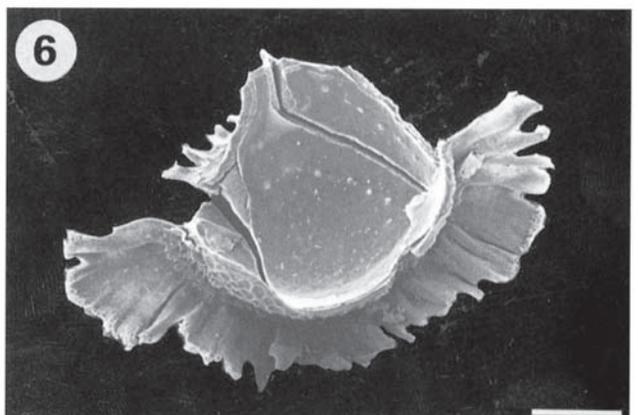
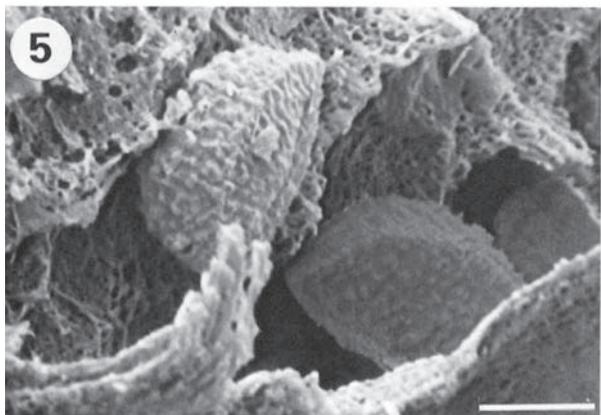
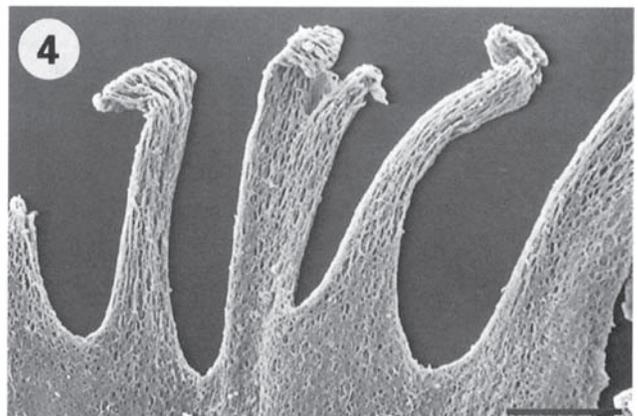
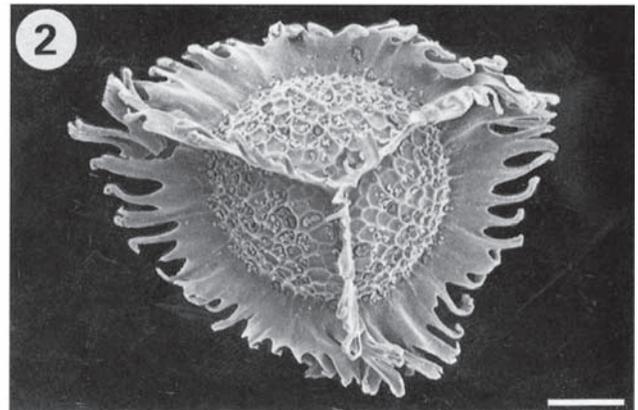
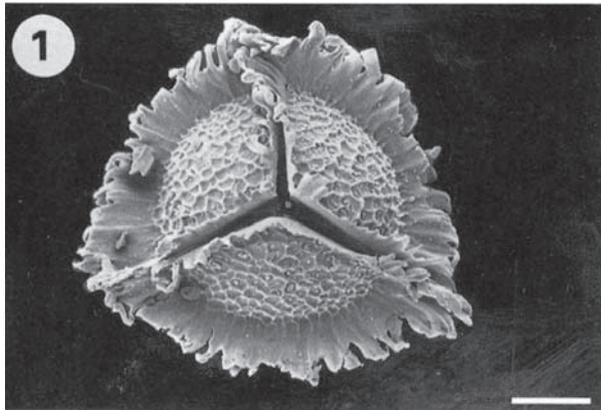


Text-Figure 1. Locality map showing position of Brilon-Nehden within Germany. Inset shows details of the locality with respect to Nehden.

PLATE 1

Dijkstrastrisporites helios (SEM).

- | | | | |
|---|---|---|---|
| 1 | Proximal view of a megaspore with an extensive zona. The laesural lips have separated along the lines of suture. Occasional microspores can be found lodged between the spore body and the zona or laesurae. Scale bar = 100 μ m. | 4 | The fimbriate zona exhibits an anastomosing fibrous microtopography with clear radial tendency to the component fibres. Scale bar = 25 μ m. |
| 2 | Proximal view of another megaspore showing a more extensive zona and raised laesural lips. Scale bar = 100 μ m. | 5 | Monolete microspores (possibly <i>Perinomonoletes</i> ; see Kovach and Dilcher, 1985) are sometimes found lodged between surface features such as the reticulate sculpture and laesural lips. Scale bar = 10 μ m. |
| 3 | Detail of the reticulate sculpture occupying the surface of the megaspore body. To the left is the laesurae. Residual sporopollenin is sometimes found (as here) within the cells of the reticulum. Scale bar = 20 μ m. | 6 | The inside of the basal lamina of a broken megaspore exhibits a series of papillae which run parallel to the suture marks, 60 μ m to each side. Scale bar = 100 μ m. |



supplement to information obtained by TEM (e.g., Koppelhus and Batten, 1992), and is critical in the establishment of a complete picture of the internal wall structure. This philosophy has been pursued in the examination of these two species of megaspores from Brilon-Nehden.

LOCALITY DATA

There are a number of scattered localities with Lower Cretaceous terrestrial sediments known from the northern stretches of the Rhenish–Ardennic Shield (Pelzer and Wilde, 1987), including Bernissart with its particularly famous *Iguanodon*-bearing clays (Casier, 1978; Bultynck, 1987). The sediments are for the most part confined to depressions and cavities of karstic origin (Bultynck, 1987). Accordingly, the Lower Cretaceous clays of Nehden survived later erosion as cave-infill which was exposed by quarrying calcite veins cutting the adjacent Middle Devonian limestones. The locality soon became well known for a great number of *Iguanodon*-remains recalling the situation in Bernissart (Norman and Hilpert, 1987). Whereas only scarce plant fragments have been described from Bernissart (Seward, 1900), a number of exquisitely preserved plant remains including megaspores have been found and cursorily described from Nehden (Huckriede, 1982; Kampmann, 1983; Schultz and Noll, 1987). Due to the protected nature of a cavity, the material is exceptionally well-preserved, and most of the megaspores are hardly compressed.

There was some initial debate with respect to the exact age of the plant-bearing sediments at Nehden. When comparing the megaspores to respective associations previously described from the uppermost part of the English Wealden, Huckriede (1982) favored an Aptian age. This is in accordance with the statements of Grebe (1982) who studied microspores and pollen. A more detailed analysis

of the megaspore flora by Schultz and Noll (1987) resulted in the same conclusion. Detailed comparisons of charalean gyrogonites from Nehden with well dated charophyte floras from other areas left Schudack (1987) in favor of a Barremian age for the Nehden-clays. His critical review of the previous arguments made clear that there is no obvious contradiction to a Barremian age for the sediments with respect to the associations of megaspores and microspores as described by Huckriede (1982), Grebe (1982), Kampmann (1983), and Schultz and Noll (1987). Accordingly, a Barremian age is well established for the material of the present study.

METHODOLOGY

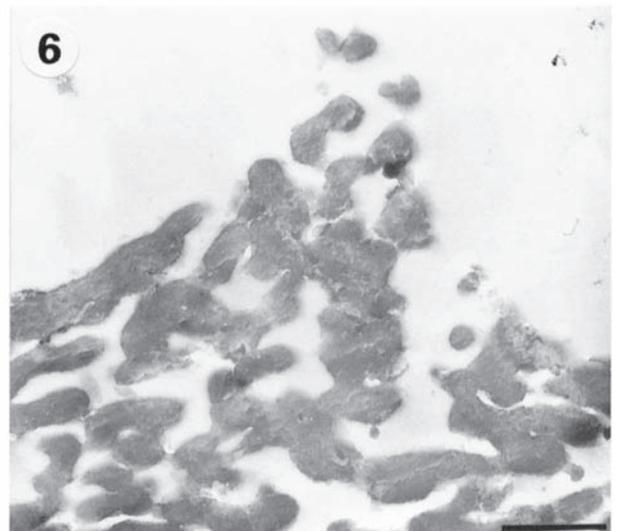
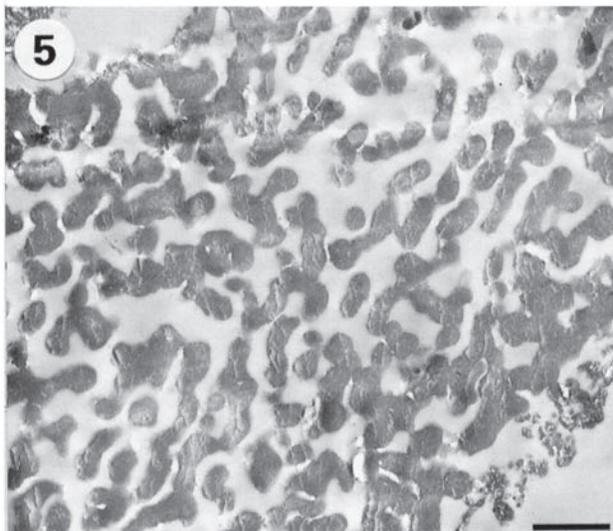
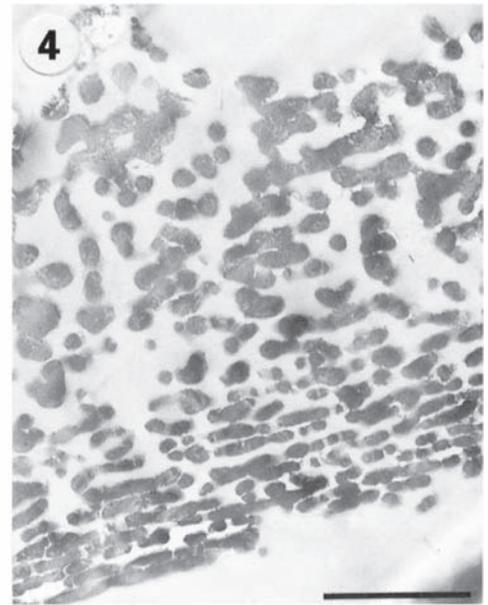
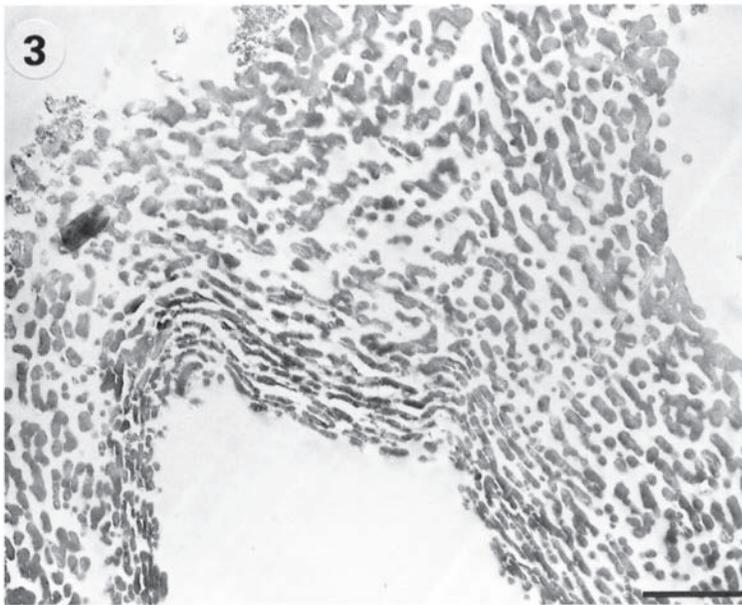
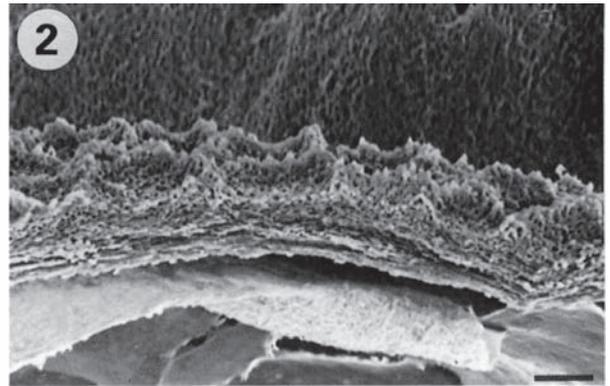
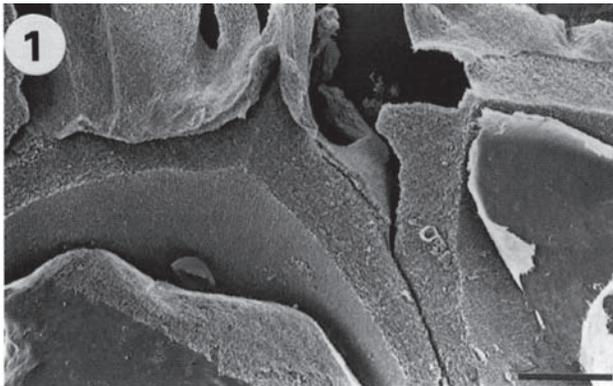
Megaspores and other plant material of similar size have been concentrated from the sediment by soaking lumps of the clay in water followed by sieving with a mesh-size of 150 μm or 200 μm as available. In some instances, disaggregation of the clayey matrix was aided by adding some hydrogen peroxide. The megaspores were subsequently isolated from the residue using a dissecting microscope. To avoid any shrinkage and potential damage by drying, specimens were picked out of water and transferred to glycerol for permanent storage.

Megaspores selected for SEM-studies were first individually picked from the glycerol, rinsed in distilled water and subsequently air dried before mounting on stubs. When it became clear that still adhering clay particles tended to obscure details of the surface, additional specimens were treated with hydrochloric and hydrofluoric acid (at least 24 hours each) previous to air drying. Details of the spore walls have been exposed by more or less controlled damage of individual specimens already mounted on stubs under a dissecting microscope.

PLATE 2

Dijkstraisporites helios.

- | | | | |
|---|--|---|---|
| 1 | Inside view of a broken triletem (SEM). Note separating basal lamina. Scale bar = 50 μm . | 4 | Generalized wall structure by TEM. The transition from inner laminate units to outer rounded units is apparent. Scale bar = 5 μm . |
| 2 | Broken wall (SEM). Transitional structure from detached basal lamina through laminate units to outer globular units comprising the reticulum. Scale bar = 10 μm . | 5 | Detail of the internal structure of the zona (TEM). Scale bar = 1 μm . |
| 3 | Perpendicular TEM-section through the equator showing internal lamellate units and zona base (top). Scale bar = 5 μm . | 6 | Outermost rounded units forming a wall of the reticulum (TEM). Scale bar = 1 μm . |



All megaspores examined by TEM were removed from stubs using amyl acetate and further cleaned by immersion in 20% hydrofluoric acid for 48 hours, principally to remove any remaining siliceous material. The spores were then removed, neutralized and thoroughly washed in distilled water. Megaspores were then dehydrated in acetone and infiltrated/embedded in a hard mixture of Spurr resin (for details see Hemsley and Scott, 1989; Hemsley and Glasspool, 1999). Ultrathin sections of approximately 100 nm were obtained using glass knives and subsequently observed with a JEOL 100S TEM. No staining of sections was required.

RESULTS

Dijkstraia sporites helios (Dijkstra) Potonié 1956 (Plates 1 and 2)

Lenticular megaspores of around 400–500 μm diameter and subtriangular outline and consisting of a spore body (circular in outline) and an encircling equatorial zona (Plate 1, figs 1, 2). The proximal and distal surfaces are covered by a reticulate ornament with lacunae of 20–30 μm diameter and segregating muri of around 5 μm width and up to 10 μm in extension from the surface; this being greatest at the junctions of the muri (Plate 1, fig. 3). The equator supports a massive fimbriate zona which may account for almost half of the total spore radius (100–120 μm) (Plate 1, fig. 1). It usually shows a gentle proximal concavity. The reticulum merges with the zona and extends part way across its radius. The zona is greatest in extension at the extremities of the raised fimbriate laesural lips which also extend to 50 μm above the proximal surface of the spore. The lacunae of the reticulum are larger in the vicinity of the laesurae. The zona and laesural lips exhibit a fibrous, spongy microtopography, much of which appears to show at least some radial orientation (Plate 1, fig. 4). Laesural lips and zona merge at the

periphery. Internal proximal views of broken specimens consistently show single rows of faint papillae on both sides of the suture (Plate 1, fig. 6). The papillae protrude inwards from the inside of the basal lamina. Individual papillae are about 15 μm in diameter and 25–30 μm apart and around 60–70 μm from the suture.

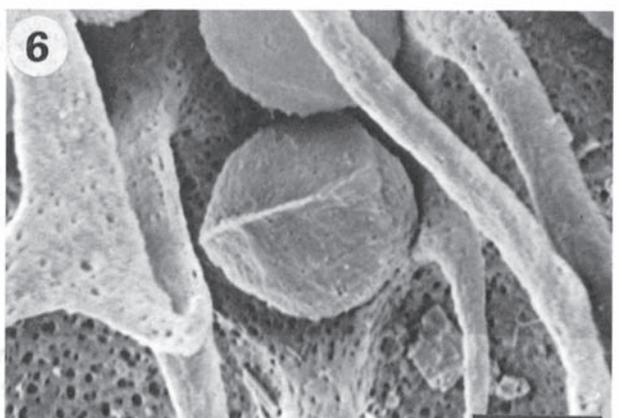
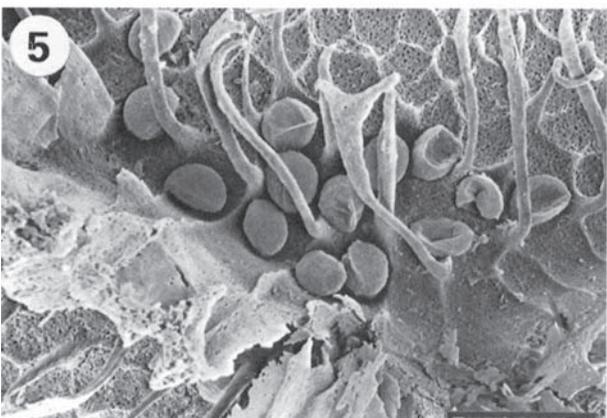
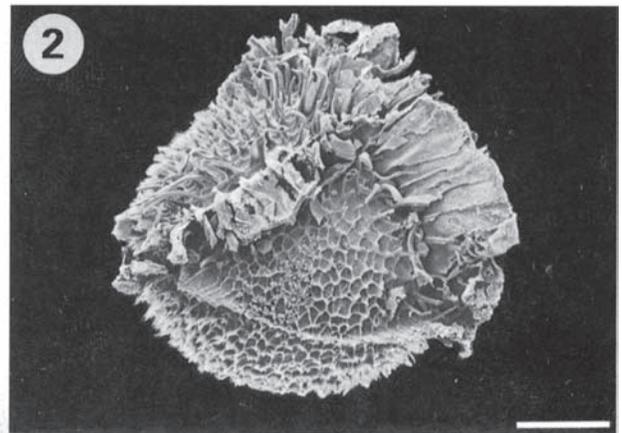
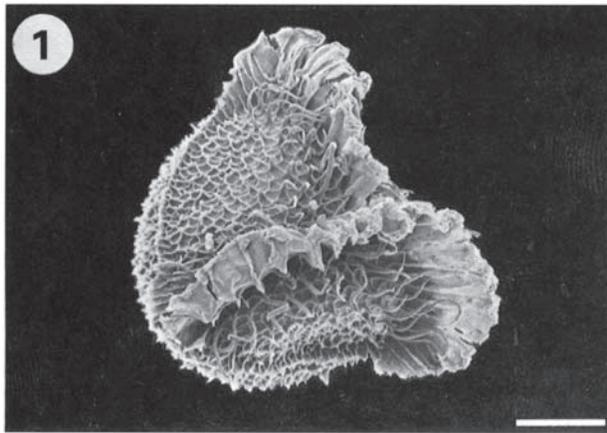
Monolete microspores are sometimes adherent to the surface sculpture (Plate 1, fig. 5). They appear similar to those compared to *Perinomonoletes* Krutzsch 1967 by Kovach and Dilcher (1985) which were adherent to their *Paxillitriteles vittatus*. Each microspore is about 20 μm in length and finely granulate to verrucate.

SEM photomicrographs of broken specimens (Plate 2, figs. 1, 2) and TEM (Plate 2, figs. 3–6) examination of megaspore walls show these to consist of a mesh of sporopollenin units which form more extensive laminate structures (lying parallel to the inner surface) toward the inside (Plate 2, figs. 3, 4). The diameter of units/laminae increases radially from 0.25–0.5 μm (forming the innermost units) to 0.5–0.75 μm at the outer boundary where the units lack any particular orientation. Unit packing density is high at the inner wall margin, low in the middle of the wall, and high again toward the outer margin where the degree of interconnection of laminae is greatest. The entire wall (Plate 2, fig. 4) ranges from 15 to 20 μm in thickness, the latter measurement incorporating the height of the muri forming the polygonal, reticulate surface ornament. Here, the outer units of the wall appear less closely-packed and may show some tangential alignment (Plate 2, fig. 6). The zona and laesural lips consist of an ‘outgrowth’ of the middle and outer parts of the wall, and hence do not contain distinctly laminate units (Plate 2, fig. 5). The centre of these structures consists of loosely-packed units lacking particular orientation whereas the outer boundaries are more densely-packed and may appear more or less continuous in section. An inner lamina (membrane) is present, but is often detached from the innermost units of the wall (Plate 2, fig. 2).

PLATE 3

Paxillitriteles fairlightensis (SEM).

- | | | | |
|---|--|---|---|
| 1 | Typical specimen showing prominent crested laesural lips (right). Scale bar = 100 μm . | 4 | Similar to 3, but illustrating details of the expanded laesurae. Scale bar = 50 μm . |
| 2 | Typical specimen in lateral view of the proximal face showing limited development of a zona. Scale bar = 100 μm . | 5 | Abundant monolete microspores entangled at the base of spines near the junction of the laesurae. Scale bar = 50 μm . |
| 3 | Detail of elongate spines arising close to the junction of the laesurae. Scale bar = 20 μm . | 6 | Detail of spine apex with perforated microstructure and entangled monolete microspore. Scale bar = 10 μm . |



Paxillitriletes fairlightensis (Batten) Hall & Nicolson 1973
(Plates 3 and 4)

More or less spherical megaspores of around 300–400 μm diameter and with a reticulate ornament on both distal and proximal hemispheres (Plate 3, figs. 1, 2). The lacunae forming the reticulum are up to 40 μm in diameter surrounded by muri of 5 μm width and of up to 10 μm extension from the surface, especially at junctions and toward the laesural lips where they may extend into filaments up to 70 μm in length (Plate 3, figs. 3, 4). The laesural lips are extended into prominent apical crests (120 μm in height) with fimbriate, rounded margins which appear fluted and undulating (Plate 3, figs. 1, 2). The crest merges at the curvature with a narrowing, more or less equatorial zona that extends only 10–15 μm from the spore surface at the midpoint between laesural lips. Crests and muri exhibit a fibrous, spongy microtopology (Plate 3, fig. 4). Again, the constituent fibrous units appear radially oriented.

Monolete microspores very similar to *Perinomonoletes* (see above) are commonly abundant, entangled at the base of the spines adjacent to the triletum (Plate 3, figs. 5, 6). Each spore is around 20 μm in length, with a scabrate to granulate surface (Plate 3, fig. 6).

SEM photomicrographs of broken specimens (Plate 4, fig. 1) and TEM (Plate 4, figs. 2–6) examination of megaspore walls reveal a structure composed of essentially laminate units with an orientation mostly parallel to the inner surface of the wall (Plate 4, fig. 3). The thickness of the laminae increases from 0.25–0.5 μm (innermost) to as much as 2.5 μm (outermost). The degree of interconnection of laminate units increases radially although the packing density decreases (Plate 4, fig. 4). Muri and laesural lips are formed from less densely-packed middle and outer wall units which are less strongly laminate, but which retain an ornamentation parallel to the surface of the extension (Plate 4, fig. 5). An extremely thin (0.1 μm) continuous lamina (membrane) is adherent to the inside of the innermost wall units (Plate 4, fig. 6). The total wall thickness is around 17 μm beneath the lacunae of the reticulum, increasing to as much as 30 μm under muri.

SYSTEMATIC PALEONTOLOGY

It is not the aim of this paper to present a complete systematic revision of the species included. Therefore, synonymy is restricted to references of nomenclatural significance, and to material that has been described previously from Nehden.

Class LYCOPODIOPSIDA
Order ISOETALES
Family *incertae sedis*

Genus *Dijkstraisporites* Potonié 1956

Dijkstraisporites helios (Dijkstra) Potonié 1956
Plate 1, figs. 1–6 ; Plate 2, figs. 1–6

Triletes helios Dijkstra, 1951, p. 11, pl. 3, fig. 17.
Dijkstraisporites helios (Dijkstra) Potonié, 1956, p. 74, pl. 10, figs. 99, 100; Huckriede, 1982, pp. 189, 190, pl. 9, figs. 4, 5, 6; Kampmann, 1983, p. 24, pl. 5.
Dijkstraisporites ustoides Kampmann, 1983, p. 22, pl. 4.

Remarks. The first megaspores initially extracted from the sediments at Nehden were correctly placed in *Dijkstraisporites helios* by Huckriede (1982). Later, Kampmann (1983) described a second species, *Dijkstraisporites ustoides*, from the same locality. Based on our own observations of a great number of specimens from Nehden, the figured type specimen of Kampmann (1983) should fit into the spectrum of variation within *Dijkstraisporites helios*.

Genus *Paxillitriletes* Hall & Nicolson 1973

Paxillitriletes reticulatus (Mädler) Hall & Nicolson 1973
Plate 3, figs. 1–6 ; Plate 4, figs. 1–6

Thomsonia reticulata Mädler, 1955, p. 150, pl. 5, figs. 14–19.
Paxillitriletes reticulatus (Mädler), Hall and Nicolson, 1973, p. 319; Schultz and Noll, 1987, pp. 95, 96, pl. 7 figs. 4–6.
Paxillitriletes lindstroemi Huckriede, 1982, p. 190, pl. 12, fig. 3, pl. 13, figs. 1, 2, pl. 14, figs. 1–4.

DISCUSSION

Despite immediately apparent differences in gross morphology, these two spore forms show many common characteristics, the reticulate main spore body ornament, fibrous/spongy microtopography, raised laesural lips and equatorial zona. Ultrastructural similarities also exist; laminate inner wall units, radially increasing diameter of units, utilisation of middle and outer wall units in the extension of zona and laesural lips. These characteristics, with reference to their distribution amongst other megaspore genera, can provide support for a pre-

sumed isoetalean affiliation for the two genera investigated herein.

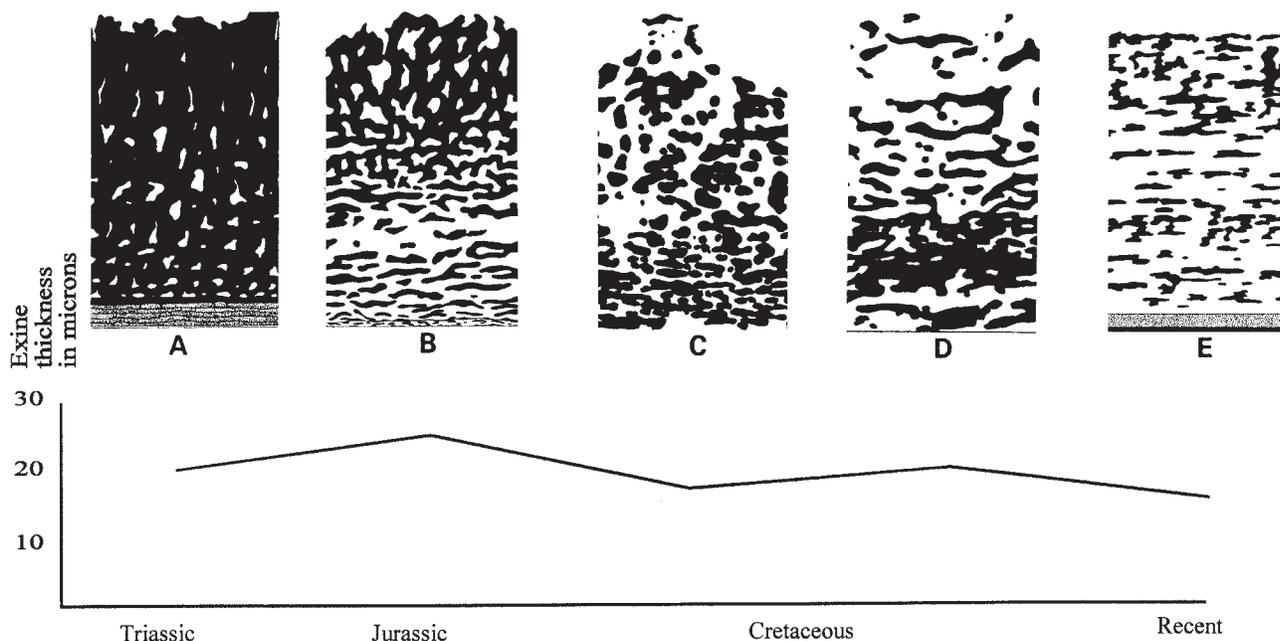
Reticulate surface patterning is common in lycopsid megaspores of all ages (e.g., Karczewska, 1976; Taylor and Taylor, 1988; Tryon and Lugardon, 1991) and is of only minimal use in indicating affiliation. The similarity in scale, and the distinct polygonal outlines formed by the muri in *Dijkstraisporites* and *Paxillitriletes* are, however, perhaps indicative of a close relationship and may serve to differentiate them from reticulate selaginellalean megaspores in which the lacunae and muri are often of larger scale. Surface microtopology is highly variable, but among extant and Tertiary lycopsid megaspores, those of presumed isoetalean affinity exhibit a surface mesh or spongy structure (foam), often with a distinct orientation. Conversely, megaspores of selaginellalean affinity tend to possess surface microtopology consisting of aggregations of fused particles which form a porous, but more dense surface covering (see Minaki, 1984; Hickey, 1986; Kovach, 1989; Tryon and Lugardon, 1991).

Raised laesural lips have been widespread amongst the differing groups of lycopsid megaspores and may have had various functions such as aerodynamic guides, apical weighting devices or microspore capture mechanisms (Kovach and Dilcher, 1985; Collinson, 1991; Hemsley, Scott and Collinson, 1999). Extensions of the type seen in

Paxillitriletes are similar to those of *Minerisporites* (e.g., Bergad, 1978; Kovach and Dilcher, 1985; Batten and Koppelhus, 1993) but those of *Paxillitriletes* are more divided at the extremities and with a more fluted appearance. The isoetalean affinity of at least some *Minerisporites* is not in doubt (Hickey, 1977; Melchior, 1977), however, raised laesural lips are present in some selaginellalean megaspores, particularly those with a pronounced equatorial zona (Taylor, 1989; Tryon and Lugardon, 1991). Fimbriation of raised laesural lips or zona has not been recorded in any megaspores referable to the Selaginellales.

Internal papillae have been considered an important taxonomic feature in Permian megaspore species (Høeg et al. 1955) where they were used as a diagnostic character in the creation of *Duosporites*. Such papillae have not been reported from other Cretaceous megaspores. The significance of internal papillae still remains obscure although their development is likely to be associated with that of the suture.

The ultrastructural detail of megaspore walls has been investigated in a wide range of taxa. It has been suggested that affinity may be determined by considering the orientation of the wall units in relation to the inner surface of the wall (Kovach and Dilcher, 1988; Kovach, 1989; Taylor, 1994). However, this would appear inapplicable to forms older than the Cretaceous. Because megaspores



Text-Figure 2. Diagrammatic representations of wall sections of probable isoetalean megaspores comparable with *Paxillitriletes* and *Dijkstraisporites* described herein. Diagrams are arranged in chronological order (left to right, not to scale). Below, the graph depicts the possible trend in wall thickness over this period, based on measurements from the literature and figured examples. (A) *Nathorstisporites muricatus* from Hemsley and Scott (1989). (B) *Nathorstisporites hopliticus* redrawn from Kempf (1971). (C) *Dijkstraisporites helios*. (D) *Paxillitriletes fairlightensis*. (E) Generalized *Isoetes* drawn from Lugardon (1986).

of selaginellalean affinity are considered as possessing a weaker tangential orientation of units, and units consisting principally of particles rather than laminae (as in the isoetaleans, e.g., Text-Figure 2), the affinity of *Paxillitriletes* and *Dijkstraisporites* would on this basis appear to be isoetalean. Recent investigations into isoetalean megaspore wall diversity (Taylor, 1993) have further strengthened the view that the essentially laminate wall structure is characteristic of at least the more recent isoetaleans (see also Text-Figure 2) and is in contrast to the particulate walls of the selaginellales where diversity of particulate arrangements may result in distinct layering within the wall (Minaki, 1984; Taylor, 1989; Collinson, Hemsley and Taylor, 1993). The laminate nature of the innermost exine units is exacerbated by expansion of the megaspore sporocyte subsequent to the bulk of wall development. Expansion appears to have its greatest effect within the inner layers of the megaspore wall (Taylor, 1990, 1992; Hemsley, 1997). It would seem therefore, that these features taken in combination support an isoetalean affinity for *Paxillitriletes* and *Dijkstraisporites*.

The essential difference between *Dijkstraisporites* and *Paxillitriletes* rests largely upon the degree of exaggeration of either the laesural lips or zona. Where expanded laesural lips or zona are absent, or where these features have become abraded or detached, megaspores with this form of reticulate body ornament could be assigned to *Minerisporites* (Kozur, 1979) or *Pavlovisporites* (see Batten and Koppelhus, 1993). Similarly, were expansion of both laesural lips and zona to occur, megaspores could be assigned to *Capillisporites* Kozur 1979.

A number of megaspores with similar expansion of the laesural lips and comparable megaspore body ornament have been investigated by SEM and TEM. Many have already been putatively assigned to the Isoetales using similar criteria to those discussed above (Collinson, 1991; Hemsley, Scott and Collinson, 1999). Ultrastructure is known for two species of *Nathorstisporites* Jung 1958,

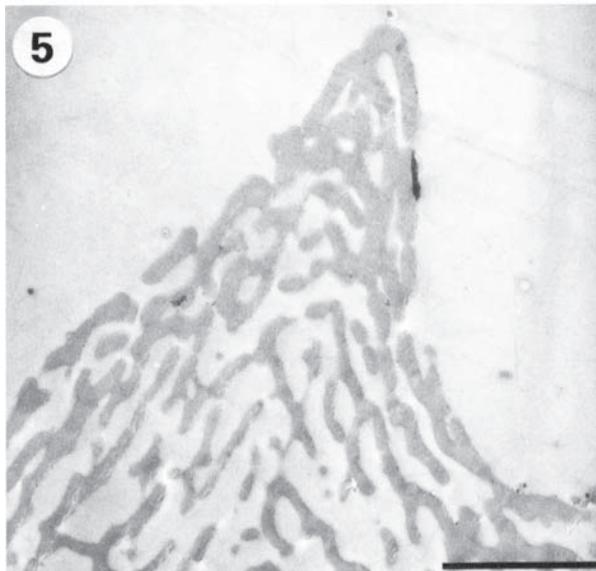
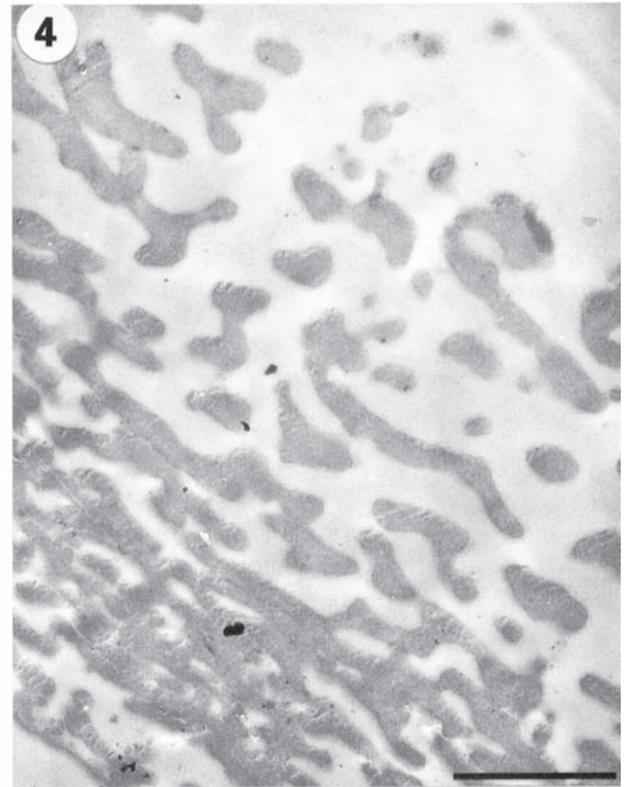
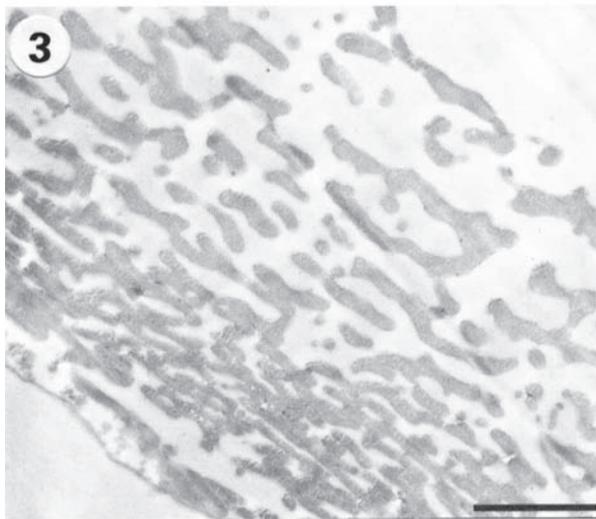
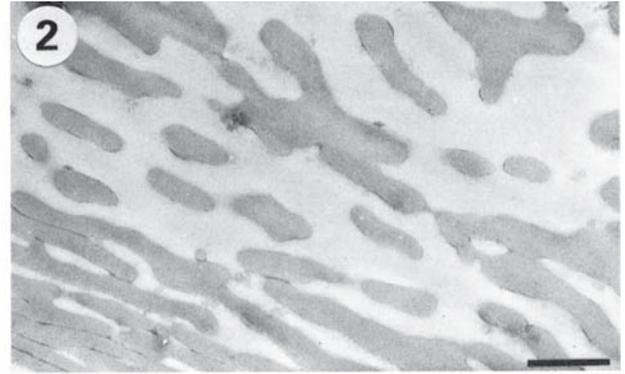
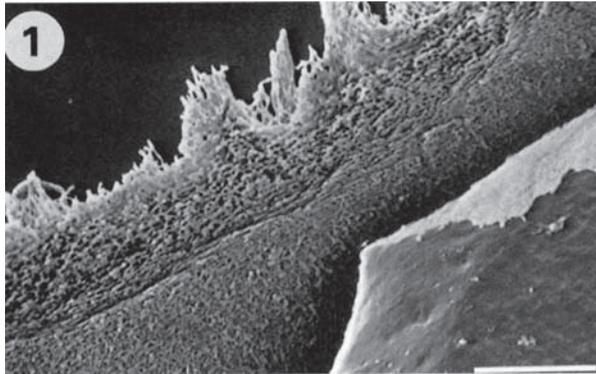
which has a laesural lip expansion similar to that of *Paxillitriletes*. The Lower Triassic *N. muricatus* Scott and Playford 1985 examined by Hemsley and Scott (1989) is of Australian origin and may not be directly comparable with Northern hemisphere isoetalean megaspores. It is, however, noteworthy in having a wall structure recalling that of many Carboniferous rhizomorphic lycopsid megaspores (Text-Figure 2A). *N. hopliticus* Jung 1958, as figured by Kempf (1971) (Lower Jurassic), has a less dense outer wall ultrastructure and is similar in many respects to that of *Dijkstraisporites helios* described here (Text-Figures 2B, 2C). The wall structure of *Paxillitriletes fairlightensis* (Text-Figure 2D) is indistinguishable from that of *P. vittatus* as originally described by Kovach and Dilcher (1985) (Mid Cretaceous) which, according to these authors, bears a strong resemblance in its ultrastructure to *Minerisporites dissimilis* Tschudy 1976 (Cretaceous) illustrated by Bergad (1978). Living *Isoetes* L. exhibits a remarkably consistent ultrastructure (Taylor, 1993) comprising many lamellae with an orientation parallel to the inner surface of the wall (Text-Figure 2E). This type of ultrastructural organisation is clearly similar to that of *Paxillitriletes*. All of the above examples (Text-Figure 2) serve to emphasize those megaspore characters considered indicative of an isoetalean lineage and which differentiate them from the selaginellales.

Microspores found adhering to the surface of a megaspore need not necessarily be the complimentary microspore produced by the same plant species. However, there is strong precedent for the belief that within the Isoetales, such examples of adherence do represent cases of compatible mega- and microspores in attachment (Kovach and Dilcher, 1985; Collinson, 1991). It would appear that the tendency for micro- and megaspores to become firmly attached has been a feature of isoetalean spore functional biology for a considerable period (Collinson, 1991; Hemsley, Scott and Collinson, 1999). The presence of abundant monolete microspores on these specimens of *Paxillitriletes* and *Dijkstraisporites* further confirms this

PLATE 4

Paxillitriletes fairlightensis.

- | | | | |
|---|---|---|--|
| 1 | Obliquely broken megaspore wall showing spongy internal structure and detached basal lamina (SEM). Scale bar = 20 µm. | 4 | Detail of the central part of the megaspore wall (TEM). Scale bar = 5 µm. |
| 2 | Detail of the outer units of the wall as viewed by TEM. Scale bar = 2 µm. | 5 | Tangential section through the base of a spine showing fusion of many of the laminate surface units (TEM). Scale bar = 5 µm. |
| 3 | A TEM section through the entire thickness of the megaspore wall showing a gradual radial change in size of the constituent laminate units and a distinct basal lamina (bottom left). Scale bar = 5 µm. | 6 | Detail of the inner laminate units and tiny basal globules adjacent to the basal lamina (TEM). Scale bar = 2 µm. |



scenario since this unusual microspore morphology is consistently shown by living and many fossil isoetaleans (Chaloner and Boureau, 1967; Tryon and Lugardon, 1991; Pigg, 1993). The adherence of microspores, like the expanded zona and laesural lips, is a function of the reproductive biology of isoetalean megaspores, discussed in detail by Kovach and Dilcher (1985), Collinson (1991) and Hemsley et al. (1999).

Monolete microspores found in association and sometimes adherent to many types of isoetalean megaspores have previously been assigned to the genus *Aratrisporites* Leschik. The megaspores include *Nathorstisporites* and *Banksisporites* Dettmann which are probably of pleuromeiacean affinity as well as other megaspores from more *Isoetes*-like plants (Collinson, 1991). *Perinomonoletes* has been suggested by Kovach and Dilcher (1985) as the spore type found adherent to *Paxillitriletes vittatus* and as such, this may be a more precise determination of the companion microspore genus to *P. fairlightensis* than *Aratrisporites* microspores which might otherwise be considered similar. *Perinomonoletes* was erected by Krutzsch (1967) to include smooth monolete spores with a more or less folded perispore which are effectively identical to microspores produced by living *Isoetes*. The presence of similar microspores in *Dijkstrastrisporites* is not unexpected in view of the similarities shown by the megaspores.

CONCLUSIONS

Specimens of *Dijkstrastrisporites helios* and *Paxillitriletes fairlightensis* are abundant and exceptionally well-preserved at the Brilon-Nehden locality. Morphology and wall ultrastructure, together with adherent microspores strongly suggest an isoetalean affinity for both megaspores and greatly support the view that most Mesozoic and Tertiary megaspores with expanded laesural lips and/or zona belong to this group (Batten and Koppelhus, 1993). Megaspore body microtopology and reticulate ornament suggest a relatively close relationship between these two species, a view confirmed by the similarities of wall ultrastructure. The virtual identity of the wall structure of *P. fairlightensis* with those of *P. vittatus* (see Kovach and Dilcher, 1985) is encouraging with regard to the belief that similar wall structure can be expected in megaspores with similar morphology. Our results also support the contention that orientation of wall units can be used as a guide to group affiliation in lycopsids as old as the Lower Cretaceous (Kovach and Dilcher, 1988). Further investigation of wall ultrastructure in (probably) related genera (listed in our introduction) may well result in an understanding of the interrelationships within this complex of Cretaceous isoetalean megaspores.

ACKNOWLEDGMENTS

Access to the site was provided by courtesy of the Westfälisches Museum für Archäologie — Amt für Bodendenkmalpflege — in Münster (Westfalen, Germany) and supported by the Forschungsinstitut Senckenberg, Frankfurt am Main in 1985. Most of the SEM-work was done by K. Schmidt in Frankfurt am Main. We thank L. Axe, J. Crawley, M. Turner, V. Williams and C. Winters for technical assistance. ARH is grateful to the Royal Society for a University Research Fellowship during the tenure of which this work was undertaken as VW is to the DFG (Deutsche Forschungsgemeinschaft/German Research Foundation) tenured in Göttingen where some of his work was completed.

References Cited

- BATTEN, D.J., and KOPPELHUS, E.B.
1993 Morphological reassessment of some zonate and coronate megaspore genera of mainly post-Palaeozoic age. *Review of Palaeobotany and Palynology*, 78: 19–40.
- BERGAD, R.D.
1978 Ultrastructural studies of selected North American Cretaceous megaspores of *Minerisporites*, *Erlansonisporites*, *Horstisporites*, and *Ricinospora*, n. gen. *Palynology*, 2: 39–51.
- BULTYNCK, P.
1987 *Bernissart en de Iguanodons*. Koninklijk Belgisch Instituut voor Natuurwetenschappen. Brussel. 117 pgs.
- CASIER, E.
1978 *Les Iguanodons de Bernissart*, 2nd ed. Institut Royal des Sciences Naturelles de Belgique. Bruxelles. 166 pgs.
- CHALONER, W. G., and BOUREAU, E.
1967 Lycophyta. In: E. Boureau (ed) *Traité de Paléobotanique, II*. pp. 437–781. Masson et C^{ie}, Paris.
- COLLINSON, M.E.
1991 Diversification of modern heterosporous pteridophytes. In: Blackmore, S., and Barnes, S.H. (eds.), *Pollen and Spores*. Systematics Association Special Volume, 44. Clarendon Press, Oxford, pp. 119–150.
- COLLINSON, M.E., HEMSLEY, A.R., and TAYLOR, W.A.
1993 Sporopollenin exhibiting colloidal organization in spore walls. *Grana Supplement*, 1: 31–39.
- DIJKSTRA, S.J.
1951 Wealden megaspores and their stratigraphical value. *Mededelingen Geologische Stichting N.S.*, 5: 7–21.
- GREBE, H.
1982 Die unterkretazische Karsthöhlen-Füllung von Nehden im Sauerland. 2. Die Mikrosporen-

- Assoziationen, Altersaussage und Versuch eines Vegetationsbildes. *Geologica et Palaeontologica*, 16: 243–258.
- HALL, J.W., and NICOLSON, D.H.
1973 *Paxillitriletes*, a new name for fossil megaspores hitherto invalidly named *Thomsonia*. *Taxon*, 22: 319–320.
- HEMSLEY, A.R.
1997 Teratisms in living and fossil megaspores of the Lycopsidea: tetrad arrangement and exine ontogeny. *Botanical Journal of the Linnean Society*, 125: 1–24.
- HEMSLEY, A.R., and GLASSPOOL, I.J.
1999 Megaspore ultrastructure. In: Jones, T.P., and Rowe, N.P. (eds.), *Fossil Plants and Spores: Modern techniques*. The Geological Society, London, pp. 121–125.
- HEMSLEY, A.R., and SCOTT, A.C.
1989 The ultrastructure of four Australian Triassic megaspores. *Pollen et Spores*, 31 (1–2): 133–154.
- HEMSLEY, A.R., SCOTT, A.C., and COLLINSON, M.E.
1999 The architecture and functional biology of freely-dispersed megaspores. In: Kurmann, M.H., and Hemsley, A.R. (eds.), *The Evolution of Plant Architecture*. Royal Botanic Gardens, Kew, pp. 253–277.
- HICKEY, L.J.
1977 Stratigraphy and palaeobotany of the Golden Valley Formation (Early Tertiary) of Western North Dakota. *Memoirs of the Geological Society of America*, 150: 1–183.
- HICKEY, R.J.
1986 *Isoetes* megaspore surface morphology: nomenclature, variation, and systematic importance. *American Fern Journal*, 76: 1–16.
- HØEG, O. A., BOSE, M.N., and MANUM, S.
1955 On double walls in fossil megaspores. With description of *Duosporites congoensis* n. gen., n. sp. *Nytt Magasin for Botanikk*, 4: 101–107.
- HUCKRIEDE, R.
1982 Die unterkretazische Karsthöhlen-Füllung von Nehden im Sauerland. 1. Geologische, paläozoologische und paläobotanische Befunde und Datierung. *Geologica et Palaeontologica*, 16: 183–242.
- KAMPMANN, H.
1983 Mikrofossilien, Hölzer, Zapfen und Pflanzenreste aus der unterkretazischen Sauriergrube bei Brilon-Nehden. Beitrag zur Deutung des Vegetationsbildes zur Zeit der Kreidesaurier in Westfalen. *Geologie und Paläontologie in Westfalen*, 1: 146.
- KARCZEWSKA, J.
1976 Megaspores of the Turma Zonales from the Carboniferous of Poland. Part II — Reconsideration of the genus *Triangulatisporites*. *Acta Palaeontologica Polonica*, 21 (4): 333–363.
- KEMPF, E.K.
1971 Electron microscopy of Mesozoic megaspores from Denmark. *Grana*, 11: 151–163.
- KOPPELHUS, E.B., and BATTEN, D.J.
1992 Megaspore assemblages from the Jurassic and lowermost Cretaceous of Bornholm, Denmark. *Danmarks Geologiske Undersøgelse*, Serie A, 32: 1–81.
- KOVACH, W.L.
1989 Quantitative methods for the study of lycopod megaspore ultrastructure. *Review of Palaeobotany and Palynology*, 57: 233–246.
- KOVACH, W.L., and DILCHER, D.L.
1985 Morphology, ultrastructure and paleoecology of *Paxillitriletes vittatus* sp. nov. from the Mid-Cretaceous (Cenomanian) of Kansas. *Palynology*, 9: 85–94.
- 1988 Megaspores and other dispersed plant remains from the Dakota Formation (Cenomanian) of Kansas, U.S.A. *Palynology*, 12: 89–199.
- KOZUR, H.
1979 *Pavlovisporites uralicus* n. gen. n. sp., eine neue Megaspore aus dem Kungurian (Leonardian) des Vorurals. *Geologisch Paläontologische Mitteilungen Innsbruck*, 9: 175–177.
- KRUTZSCH, W.
1967 *Atlas der mittel- und jungtertiären dispersen Sporen- und Pollen- sowie der Mikroplanktonformen des nördlichen Mitteleuropa, Lieferung IV und V*. Gustav Fischer, Jena.
- LUGARDON, B.
1986 Ultrastructural data of the exospore function in pteridophyte spores. In: Blackmore, S., and Ferguson, I.K., (eds.), *Pollen and Spores: Form and Function*, Linnean Society, London, pp. 251–264.
- MÄDLER, K.
1955 *Azolla* aus dem Quartär und Tertiär sowie ihre Bedeutung für die Taxonomie älterer Sporen. *Geologisches Jahrbuch*, 70: 143–158.
- MELCHIOR, R.C.
1977 On the occurrence of *Minerisporites mirabilis* in situ. *Scientific publication of the Science Museum of Minnesota*, New Series, 3 (4): 3–11.
- MINAKI, M.
1984 Macrospore morphology and taxonomy of *Selaginella* (Selaginellaceae). *Pollen et Spores*, 26: 421–480.
- NORMAN, D.B., and HILPERT, K.-H.
1987 Die Wirbeltierfauna von Nehden (Sauerland, Westdeutschland). *Geologie und Paläontologie in Westfalen*, 8: 1–77.
- PELZER, G., and WILDE, V.
1987 Klimatische Tendenzen während der Ablagerung der Wealden-Fazies in Nordwesteuropa. *Geologisches Jahrbuch*, A, 96: 239–263.
- PIGG, K.B.
1993 Evolution of isoetalean lycopsids. *Annals of the Missouri Botanical Garden*, 79: 589–612.
- POTONIÉ, R.
1956 Synopsis der Gattungen der Sporae dispersae. I. Teil: Sporites. *Beihefte Geologisches Jahrbuch*, 23: 1–103.

SCHUDACK, M.

- 1987 Charophytenflora und Alter der unterkretazischen Karsthöhlen-Füllung von Nehden (NE-Sauerland). *Geologie und Paläontologie in Westfalen*, 10: 7–44.

SCHULTZ, G., and NOLL, H.

- 1987 Die Megasporen-Assoziation in den unterkretazischen Sedimenten einer Paläokarsthöhle bei Nehden im Sauerland (Rheinisches Schiefergebirge). *Palaeontographica Abteilung B*, 203: 83–107.

SEWARD, A.C.

- 1900 La flore Wealdienne de Bernissart. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, 1: 1–37.

TAYLOR, W.A.

- 1989 Megaspore wall ultrastructure in *Selaginella*. *Pollen et Spores*, 31 (3–4): 251–288.
- 1990 Comparative analysis of megaspore ultrastructure in Pennsylvanian lycophytes. *Review of Palaeobotany and Palynology*, 62: 65–78.
- 1992 Megaspore wall development in *Isoetes melanopoda*: morphogenic post-initiation changes accompanying spore enlargement. *Review of Palaeobotany and Palynology*, 72: 61–72.
- 1993 Megaspore wall ultrastructure in *Isoetes*. *American Journal of Botany*, 80 (2): 165–171.
- 1994 Tests and applications of a method of quantitative analysis of fossil and extant lycopsid megaspore walls. In: Kurman, M.H., and Doyle, J.A. (eds.), *Ultrastructure of fossil spores and pollen*. Royal Botanic Gardens, Kew, pp. 39–52.

TAYLOR, W.A., and TAYLOR, T.N.

- 1988 Ultrastructural analysis of selected Cretaceous megaspores from Argentina. *Journal of Micropaleontology*, 7: 73–87.

TRYON, A.F., and LUGARDON, B.

- 1991 *Spores of the Pteridophyta*. Springer-Verlag, New York.

TSCHUDY, R.H.

- 1976 Stratigraphic distribution of species of the megaspore genus *Minerisporites* in North America. *Geological Survey Professional Paper*, 743-E: 1–10.