SILURIAN CRYPTOSPORES AND MIOSPORES FROM THE TYPE WENLOCK AREA, SHROPSHIRE, ENGLAND

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ABSTRACT. The earliest occurrence of sculptured hilate cryptospores and miospores is near the base of the cf. *protophanus–verrucatus* Sporomorph Zone, now more accurately located within the *lundgreni* Graptolite Biozone in the type Wenlock area. Palynofacies studies indicate that this event is unrelated to changes in the depositional environment. All the Sheinwoodian sporomorphs are laevigate (six species) and have either a crassitate or patinate structure. The oldest known sculptured specimens of trilete miospores (two or three species) and hilate, crassitate/patinate cryptospores (four species) appear almost synchronously in the Homerian (upper part of *lundgreni* Graptolite Biozone). Additional sculptured taxa (two species) appear in the later Homerian but there are no innovations in structure. In North Africa (Gondwana) a closely comparable sequence of structural and sculptural events occurs. Three groups of sporomorphs described from the Buildwas, Coalbrookdale and lower Much Wenlock Limestone Formations are permanently fused cryptospore tetrads (one species), hilate cryptospores derived from dyads (eight species), and trilete miospore (six species). Systematic descriptions of seventeen species in eight genera are provided. Two genera *Laevolancis* and *Artemopyra*, three species *Laevolancis plicata*, *Hispanaediscus wenlockensis*, and *Artemopyra brevicosta*, and one combination are new, and the genera *Hispanaediscus* and *Dyadospora* are emended.

WENLOCK sporomorphs although known from only a few studies provide evidence for the existence of early land plants (Gray 1985) and hold a largely untapped potential for stratigraphical correlation (Richardson and McGregor 1986). Many of these assemblages contain mainly laevigate trilete miospores showing little diversity and have been obtained from poorly dated strata (Smith 1975; Colthurst and Smith 1977; Strother and Traverse 1979). Libyan assemblages are often superbly preserved (Richardson and Ioannides 1973) but although the sequence of spore sculptural patterns is closely similar to that in the Welsh Borderland, and the succession is dated by graptolites, there are samples which may be either Lower Ludlow or Upper Wenlock based on the latter. In some of these cases sporomorph data from the present study support a Wenlock age.

In contrast to North Africa, the geology of the type Wenlock area is well known (Bassett *et al.* 1975) and samples from higher parts of the sequence have yielded sporomorph assemblages of increasing diversity, although frequently spores are comparatively rare (1–20% of assemblage). Spores have been described from the type Wenlock area by Downie (1963), Richardson and Lister (1969), and Mabillard and Aldridge (1985) and from Dudley by Dorning (1983). Most previous works consist solely of records of the miospore genus *Ambitisporites*, but Richardson and Lister (1969) described eight miospore taxa, including some questionable miospores now regarded as cryptospores, and sculptured tetrads in the Much Wenlock Limestone Formation (Wenlock Limestone).

Sections in the type Wenlock area have been resampled (Text-fig. 1) to determine the diversity and stratigraphical ranges of the sporomorph taxa and, as precisely as possible, the horizons where sporomorph events occur, in particular the first appearance of sculpture in 'naked' cryptospores (i.e. those without envelopes) and in miospores. The advent of sculptural types is considered to have biological as well as biostratigraphical significance (Richardson and Lister 1969; Gray 1985;

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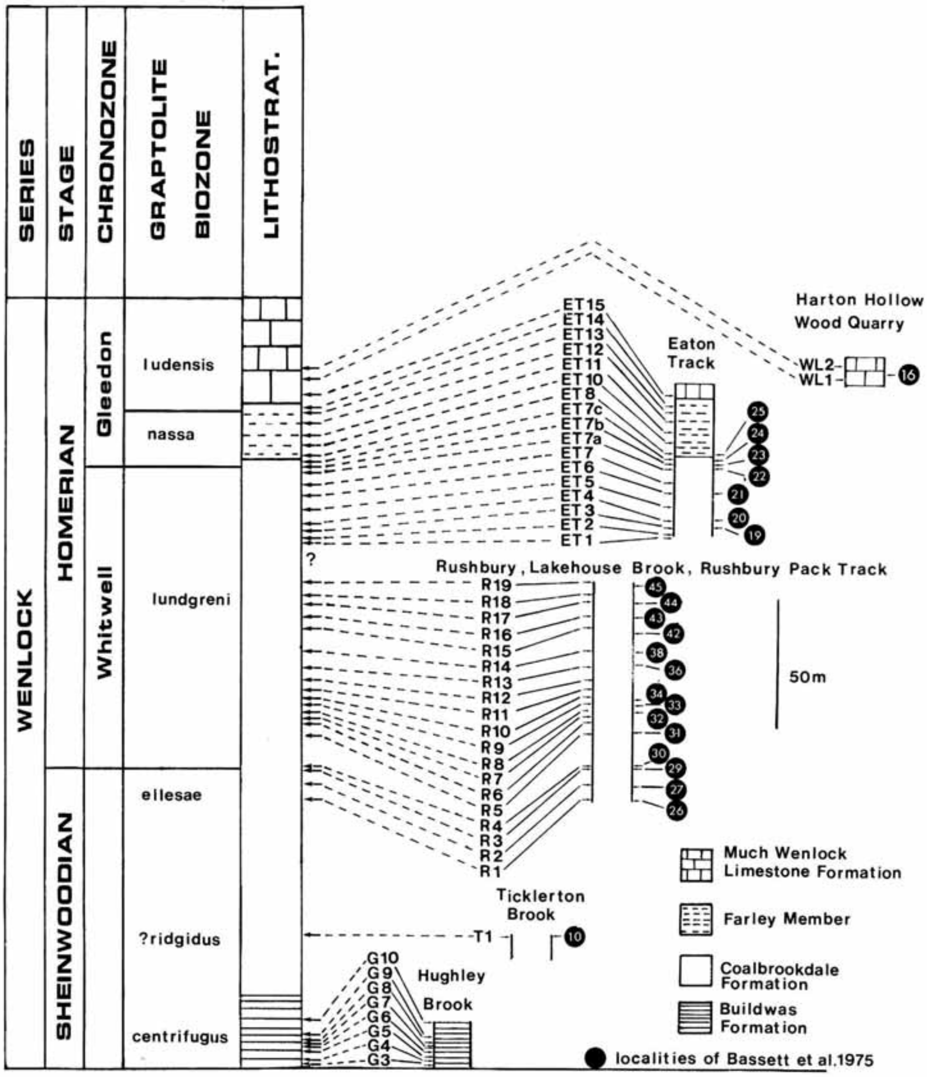


TEXT-FIG. 1. Lithostratigraphic and biostratigraphic position of samples collected from the type Wenlock area, in relation to localities of Bassett *et al.* (1975).

Richardson 1985; Fanning *et al.* 1988). Such studies assist in attempts to understand the colonization of the land by plants because rocks of this age may contain abundant plant microfossils but few megafossils (Richardson and Ioannides 1973; Edwards and Fanning 1985; Gray 1985).

SAMPLING AND TECHNIQUES

Reconnaissance sampling at Eaton Track and Harton Hollow Wood Quarry by Richardson and Lister (1969), and later by the authors with the Ludlow Research Group, revealed laevigate and sculptured sporomorphs at Graptolite locality 24 of Bassett *et al.* (1975), near the top of the Eaton Track Section. For this study a total of forty eight samples were collected from six sections covering a stratigraphical interval of *c.* 240 m (Table 1) from basal Sheinwoodian (basal *centrifugus* Graptolite Biozone) to the late Homerian (lower part of the *ludensis* Graptolite Biozone) but excluding the upper *c.* 20 m of the Much Wenlock Limestone Formation. However, the uppermost part of the section has been sampled independently by both authors in the type Ludlow Area and so far has not yielded any new taxa. Details on the stratigraphy of the type Wenlock Area sections (except for Hughley Brook) are in Bassett *et al.* (1975).

TABLE 1. Locality and horizon of the sections studied

Section	Grid reference	Formation
Hughley Brook *c.* 400 m SW of Gippols Farm	SO 58009920	Buildwas
Ticklerton Brook	SO 48589042	Coalbrookdale
Rushbury	SO 51329173–SO 51329168	Coalbrookdale
Lakehouse Brook	SO 51399164	Coalbrookdale
Rushbury Pack Track	SO 51369146–SO 51679123	Coalbrookdale
Eaton Track	SO 50049001–SO 50509010	Coalbrookdale (Farley Member) – Much Wenlock Limestone
Harton Hollow Wood Quarry	SO 48148788	Much Wenlock Limestone

Samples were all fine-grained buff to olive-green calcareous siltstones and silty limestones. Palynomorphs were extracted and prepared for light microscope observation using standard techniques: HCl–HF–HCl acid treatment followed by zinc bromide solution (S.G. 2·0) heavy mineral separation. Organic residues were washed with distilled water between HCl and HF treatment to remove residual calcium ions and to reduce the formation of calcium fluoride and related compounds during HF treatment. Residues were sieved through a 10 μm sieve, dried on coverslips, mounted in 'Elvacite' mounting medium, and studied in normal transmitted light and Nomarski Interference using a Zeiss Photomicroscope. Photomicrographs were taken on Ilford FP4 film.

From each sample 30 g of rock was processed and a measured amount of the residue from a known mass of rock mounted on a slide. Palynomorphs were then counted from a proportion of the slide and from this the absolute percentage per gram of sample was calculated for prasinophycean 'phycomata' (Tappan 1980) and each acritarch, cryptospore and miospore group. Palynomorph counts were made under oil at × 1000.

SYSTEMATIC PALAEONTOLOGY

The last decade has seen a number of reports showing that Upper Ordovician and Silurian strata contain spore-like microfossils in association with trilete miospores (Strother and Traverse 1979; Miller and Eames 1982; Gray 1985; Johnson 1985; Hill *et al.* 1985; Richardson 1988). We group these atypical spores (cryptospores *sensu* Richardson *et al.* 1984; Richardson 1988) into two major categories which are morphologically distinct and which may reflect macroplant groups and their evolution. In the descriptions below the terminology of Grebe (1971) is used to describe all sporomorphs, included cryptospores, but we have used the term muri for sinuous, sometimes anastomosing, ridges, whether or not they form a reticulum. The stratigraphical distribution refers to the range within this study.

Spore dimensions are given as the maximum diameter in polar compression unless stated otherwise, with the minimum and maximum of the range presented and the mean in brackets. Figured specimens are stored in the Palynology Section, Palaeontology Department, British Museum (Natural History), London and have the prefix FM. Specimen co-ordinates are from a Zeiss Photomicroscope III no. 2562 housed in the Department. All specimens are also located by means of standard England Finder co-ordinates, and are ringed using a permanent red pen.

Anteturma CRYPTOSPORITES Richardson *et al.*, 1984

1. '*Permanently' fused cryptospore tetrads*

This group comprises tetrads and dyads which are not found separated into their individual components and which we therefore believe are 'permanently' fused. Such forms are abundant in the lower Llandovery where well-preserved specimens are enclosed within variously sculptured envelopes (Strother and Traverse 1979; Miller and Eames 1982; Gray 1985, 1988; Johnson 1985; Burgess 1987). Occasionally individual specimens occur with poorly preserved proximal faces which may represent fragmented tetrads (Richardson 1988).

Genus TETRAHEDRALETES Strother and Traverse, 1979

Type species. Tetrahedraletes medinensis Strother and Traverse, 1979.

Tetrahedraletes medinensis Strother and Traverse, 1979

Plate 1, figs 12 and 13

Figured specimens. FM 156, Pl. 1, fig. 12, slide S24/3, 040 1210; FM 157, Pl. 1, fig. 13, slide S24/6 060 1240; both specimens from sample G 5, Hughley Brook, lower Buildwas Formation.

EXPLANATION OF PLATE 1

All figures × 1000.

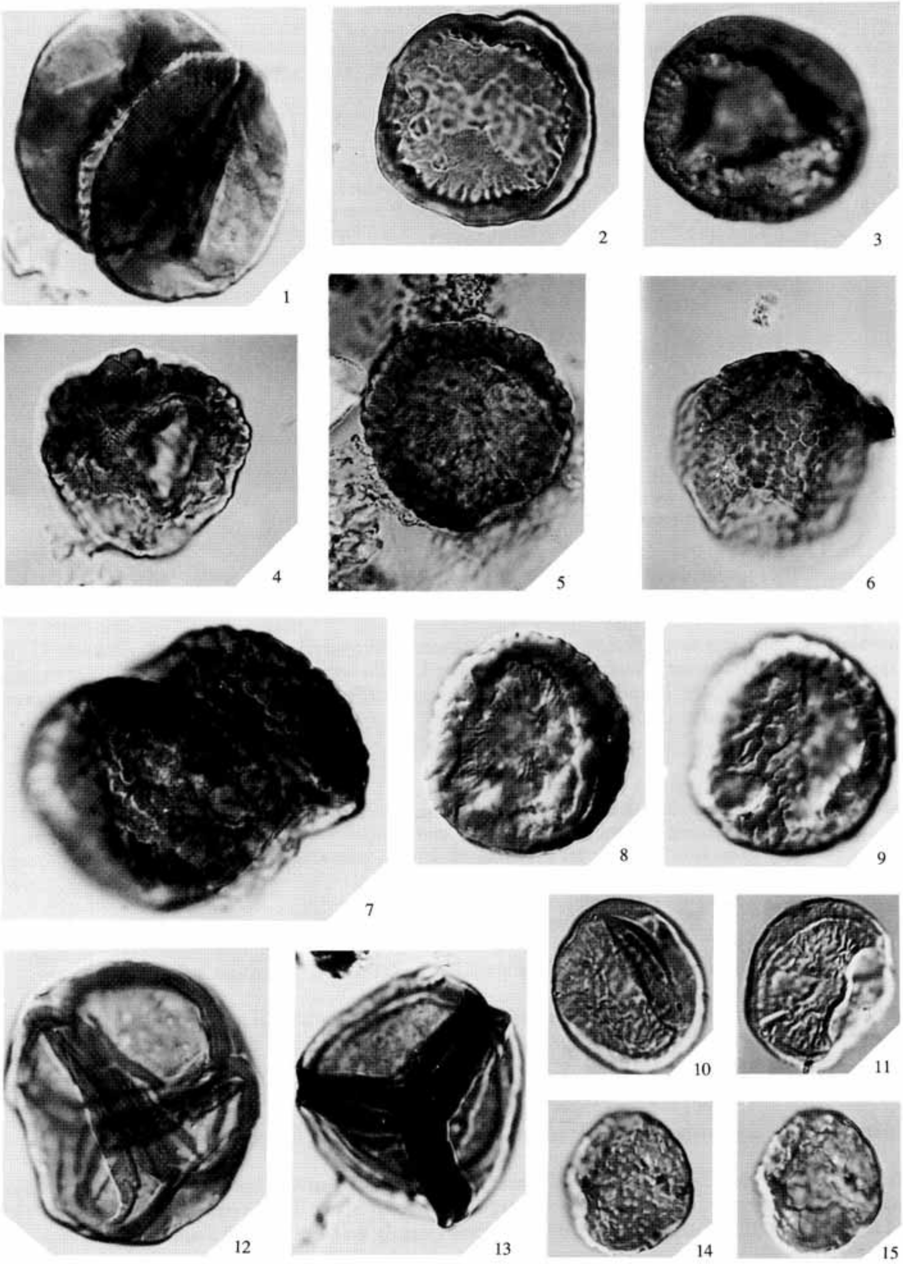
Figs 1–3. *Artemopyra brevicosta* sp. nov. 1, Dyad; FM 147 (slide GL22/1 co-ord 060 1030; England Finder no: F32/3/4), sample ET 7a, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone. 2, FM 148 (slide GL24/26 co-ord 200 1110; E.F. no: U40/4 U41/3), sample ET 7c, upper Coalbrookdale Formation, *nassa* Graptolite Biozone. 3, FM 146, holotype (slide ET 9A/4 co-ord 165 1300; E.F. no: R60), sample ET 10, Farley Member, *nassa* Graptolite Biozone.

Figs 4–9. *Hispanaediscus wenlockensis* sp. nov. 4, FM 150 (slide GL24/23 co-ord 030 1263; E.F. no: C56/2), sample ET 7c, upper Coalbrookdale Formation, *nassa* Graptolite Biozone. 5, Proximal view showing radial muri; FM 151 (slide GL24/5 co-ord 130 1055; E.F. no: N35/3), sample ET 7c, upper Coalbrookdale Formation, *nassa* Graptolite Biozone. 6, Distal view showing verrucae; FM 149 (slide GL24/13 co-ord 100 1290; E.F. no: K59/4), sample ET 7c, upper Coalbrookdale Formation, *nassa* Graptolite Biozone. 7, Dyad; FM 153 (slide ET 9A/1 co-ord 090 1365; E.F. no: J67/2), sample ET 10, Farley Member, *nassa* Graptolite Biozone. 8, FM 152, holotype; proximal view (slide GL 24/24 co-ord 055 1205; E.F. no: E50/4 F50/2), sample ET 7c, upper Coalbrookdale Formation, *nassa* Graptolite Biozone. 9, Holotype, FM 152; distal view.

Figs 10 and 11. *Artemopyra* sp. A. 10, Proximal surface with radial muri and murus marking boundary of proximal hilum; FM 154 (slide ET 16/5 co-ord 078 1088; E.F. no: H38/2), sample ET 15, lower Much Wenlock Limestone Formation, *ludensis* Graptolite Biozone. 11, Specimen showing muri on proximal surface and smooth distal surface; FM 155 (slide ET 16/8 co-ord 144 1050; E.F. no: 034/4 035/3), sample ET 15, lower Much Wenlock Limestone Formation, *ludensis* Graptolite Biozone.

Figs 12 and 13. *Tetrahedraletes medinensis* Strother and Traverse 1979. 12, FM 156 (slide S24/3 co-ord 040 1210; E.F. no: E53), sample G 5, Buildwas Formation, *centrifugus* Graptolite Biozone. 13, FM 157 (slide S24/6 co-ord 060 1240; E.F. no: G54/1/3), sample G 5, Buildwas Formation, *centrifugus* Graptolite Biozone.

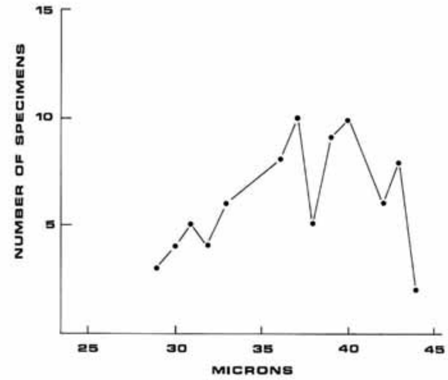
Figs 14 and 15. HILATE CRYPTOSPORE TYPE 1. 14, Sculptured distal surface; FM 158 (slide GL24/7 co-ord 100 1070; E.F. no: K36/4), sample ET 7c, upper Coalbrookdale Formation, *nassa* Graptolite Biozone. 15, Smooth 'proximal' surface of FM 158.



BURGESS and RICHARDSON, Wenlock cryptospores

Description. Laevigate obligate tetrahedral tetrads, subcircular to circular in outline, preserved in many compressional forms relating to the degree of rotation from an apical view prior to compression. Within the tetrads individual 'spores' have a subtriangular to subcircular equatorial outline, and unfused equatorial crassitudes 1–5 μm wide. Distal exine 1–2 μm thick and usually invaginated.

Dimensions. Tetrads 30(37)52 μm in diameter (100 specimens measured from sample G 5; Text-fig. 2).



TEXT-FIG. 2. Size frequency distribution of a hundred *Tetrahedraletes medinensis* (Strother and Traverse, 1979) from sample G 5, Hughley Brook (*centrifugus* Graptolite Biozone); $\bar{x} = 37{\cdot}3$ μm.

Distribution. Throughout the Wenlock, basal Sheinwoodian to late Homerian Stages, *centrifugus* to *ludensis* Graptolite Biozones.

Comparisons. Specimens of *Tetrahedraletes medinensis* recovered in the Wenlock (Text-fig. 2) are larger than those from the Rhuddanian of the type Llandovery area (Burgess 1991) but are similar in size to those from the Llandovery of North America (Pratt *et al.* 1978; Strother and Traverse 1979; Miller and Eames 1982; Johnson 1985).

2. *Hilate cryptospores*

Sporomorphs in this group are alete, hemispherical in equatorial view, have a thin proximal surface (hilum) and an equatorial thickening. In many cases they are seen to be derived from loosely attached dyads and as all have the same basic structure they are probably all derived from dyads.

Genus LAEVOLANCIS gen. nov.

Type species. Laevolancis (*Archaeozonotriletes*) *divellomedium* (Chibrickova) comb. nov.

Diagnosis. Alete proximally hilate cryptospores, originally elliptical to hemispherical in equatorial view with an equatorial to subequatorial crassitude surrounding the hilum; exine laevigate.

Derivation of name. Latin *laevigatus*, smooth; *lancis*, plate or dish.

Remarks. These cryptospores are occasionally seen as loosely attached dyads.

Discussion. The genus *Gneudnaspora* Balme (1988) includes similar spores but is not used here because the Australian spores may be trilete, monolete or alete. The Wenlock spores are all alete and many, if not all, are derived from dyads. Consequently we have erected a new genus *Laevolancis* to accommodate the alete forms in Balme's genus and other alete species of similar structure with a laevigate exine.

Laevolancis divellomedium (Chibrickova) comb. nov.

Plate 2, figs 4 and 6.

1959 *Archaeozonotriletes divellomedium* Chibrickova, p. 65, pl. 9, fig. 4.
1966 *Hispanaediscus bernesgae* Cramer, p. 82, pl. 1, fig. 1; text-fig. 2, figs 2 and 11.
1968 Spore no. 2651, Magloire, pl. 1, fig. 6.
1969 *?Archaeozonotriletes* cf. *divellomedium* Chibrickova; Richardson and Lister, p. 238, pl. 43, fig. 12.
1973 *?A.* cf. *divellomedium* Chibrickova; Richardson and Ioannides, p. 280, pl. 8, figs 10 and 11.
1974 *Zonaletes* (?) *divellomedium* (Chibrickova); Arkhangelskaya, pl. 6, figs 3 and 4.
1974 *?A. divellomedium* Chibrickova; McGregor, pl. 1, figs 35 and 40.
1978 *Hispanaediscus* sp., McGregor and Narbonne, p. 1296, pl. 1, figs 20–22.
1979 'Smooth-walled inaperturate spore', Strother and Traverse, p. 14, pl. 12, fig. 9.
1984 *?Stenozonotriletes irregularis* McGregor, p. 37, pl. 1, fig. 26.
1986 *Tholisporites divellomedium* Turnau, p. 349, pl. 2, fig. 12.
1980 *Zonaletes* (?) *divellomedium* (Chibrickova) Arkhangelskaya, pl. 5, fig. 34.
1988 *Gneudnaspora divellomedium* (Chibrickova) Balme, p. 125 [*partim*], pl. 3, figs 1–7.

Holotype and type locality. Chibrickova, 1959, prep. 977, collections of the Gorno-Geological Institute, Bashkir Filial, Academy of Sciences, USSR; Takata Beds, Emsian.

Figured specimens. FM 163, Pl. 2, fig. 4, slide S24/3, 145 1290, sample G5, Hughley Brook, Buildwas Formation; FM 164, Pl. 2, fig. 6, slide ET 8/5, 133 1265, sample ET 6, Eaton Track, upper Coalbrookdale Formation.

Diagnosis. A *Laevolancis* with a rigid wall and a 1(1·5)4 μm wide subequatorial crassitude.

Description. Cryptospores occasionally preserved in loosely attached dyads in a variety of compressional morphologies but are usually separated. Separated spores: amb subcircular, or occasionally circular, specimens frequently tipped, originally roughly hemispherical in equatorial view with ±flattened proximal polar area. An equatorial to subequatorial crassitude surrounds the proximal hilum; hilum flattened to concave in equatorial view, laevigate, occasionally folded, or ruptured, optically appears thinner than the distal exine; distal exine laevigate *c.* 2 μm thick.

Dimensions. Maximum diameter 30(38)49 μm, minimum diameter 18(30)38 μm (30 specimens measured from sample G 5, Hughley Brook, Buildwas Formation).

Distribution. Present and often common throughout the sequence, Buildwas to Much Wenlock Limestone Formations; basal *centrifugus* to lower *ludensis* Graptolite Biozones.

Comparisons. The size range of Chibrickova's specimens (35–50 μm; Chibrickova 1959) overlaps with that of the Wenlock specimens. Balme's specimens from the Devonian Gneudna Formation (Balme 1988) also overlap but are mostly larger (44–68 μm); otherwise the alete forms described by Balme are identical (J. B. R., examination of the Australian material). *Hispanaediscus bernesgae* Cramer, 1966 is regarded as synonymous but the genus *Hispanaediscus* is restricted herein to verrucate hilate cryptospores similar to the type species.

Laevolancis plicata sp. nov.

Plate 2, fig. 8

Holotype and type locality. FM 167; Pl. 2, fig. 8; slide Rush S14/5, 170 1150; sample R 17, Rushbury Pack Track (Text-fig. 1; Table 1), Coalbrookdale Formation, late Wenlock *lundgreni* Graptolite Biozone.

Diagnosis. A *Laevolancis* with thin, often folded, walls.

Derivation of name. Latin *plicatus*, folded.

Description. Cryptospores occasionally preserved in loosely attached, often partially separated, dyads but spores are most frequently found separated as single grains. Amb sub-circular to circular; distally slightly convex in equatorial view. Crassitude equatorial to sub-equatorial, 0·5–1·5 μm wide, surrounds a proximal hilum; proximal hilum usually concave, laevigate and frequently folded. Distal exine *c*. 1 μm thick, laevigate.

Dimensions. Maximum diameter 22(27)35 μm, minimum diameter 14(21)27 μm (30 specimens measured from sample ET 7c); Eaton Track Section, Coalbrookdale Formation.

Distribution. Present throughout the sequence, Buildwas to Much Wenlock Limestone Formations; basal *centrifugus* to lower *ludensis* Graptolite Biozones.

Comparisons. *Laevolancis divellomedium* (Chibrickova) comb. nov. is larger, more inflated distally and has a thicker, more rigid wall (*c*. 2 μm). Many of these spores are separated from dyads of the genus *Dyadospora* (Strother and Traverse, 1979) emend. and possibly solely from *D. murusattenuata*.

Genus HISPANAEDISCUS (Cramer) emend.

Type species. *Hispanaediscus verrucatus* Cramer, 1966.

Emended diagnosis. Alete proximally hilate cryptospores; originally elliptical to hemispherical in equatorial view; equatorial to sub-equatorial crassitude surrounding the hilum. Hilum laevigate, or

EXPLANATION OF PLATE 2

All figures × 1000.

Figs 1–3, 5. *Dyadospora murusdensa* (Strother and Traverse) emend. 1, FM 159 (slide Tick S1/7 co-ord 063 1209; E.F. no: F51/1/3), sample T 1, lower Coalbrookdale Formation, *ellesae* Graptolite Biozone. 2, Partially separated specimen with pyrite damage, FM 161 (slide Rush S 10/8 co-ord 200 1204; E.F. no: U50/4), sample R 14, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone. 3, FM 160 (slide ET 5A/5 co-ord 152 1053; E.F. no: P35/3), sample ET 3, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone. 5, partially separated specimen; FM 162 (slide Rush S10/1, co-ord 070 1220; E.F. no: G52/2/G53/1), sample R 14, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone.

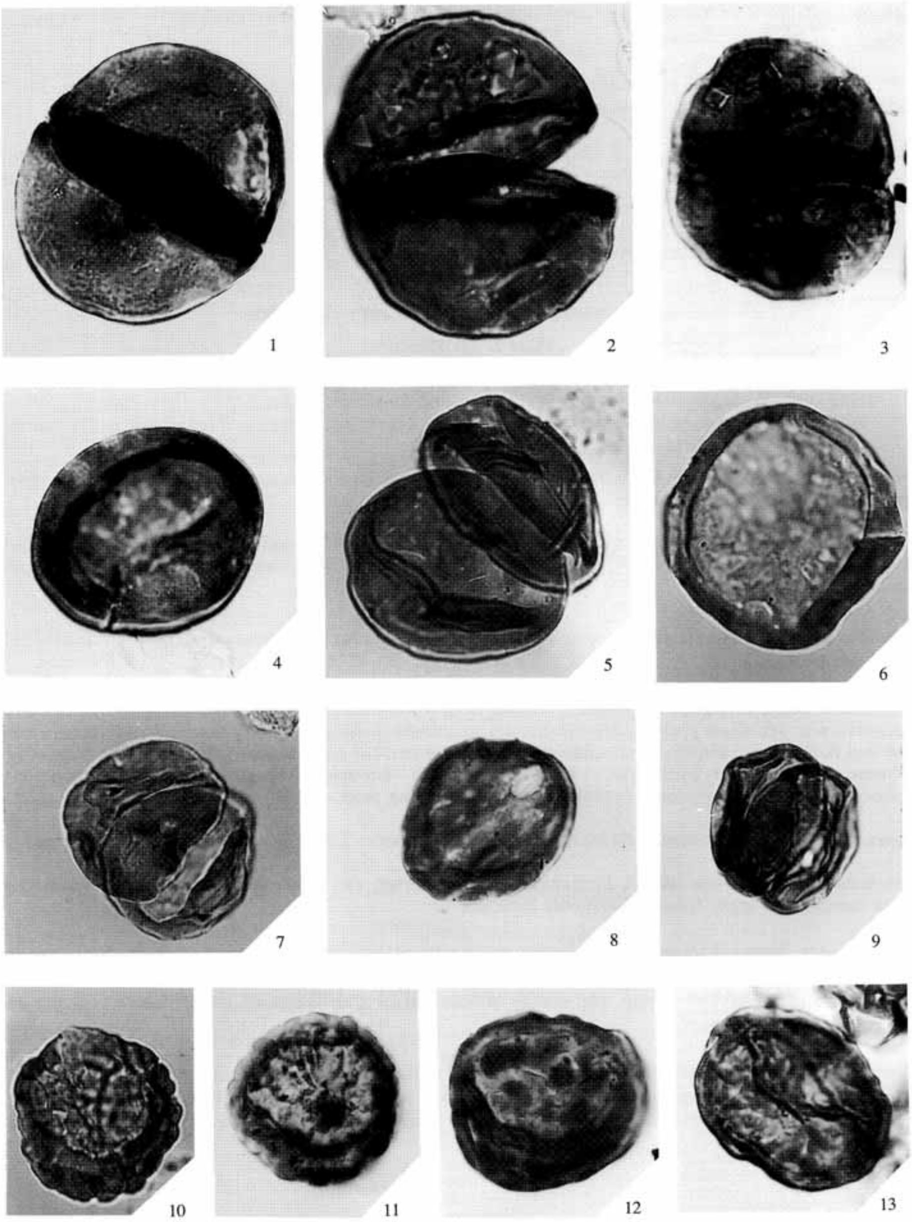
Figs 4 and 6. *Laevolancis divellomedium* (Chibrickova) comb. nov. 4, FM 164, holotype (slide ET 8/5 co-ord 133 1265; E.F. no: N56/4/N57/3), sample ET 6, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone. 6, FM 163 (slide S24/3 co-ord 145 1290; E.F. no: P59/2/P60/1), sample G 5, Buildwas Formation, *centrifugus* Graptolite Biozone.

Figs 7 and 9. *Dyadospora murusattenuata* (Strother and Traverse) emend. 7, FM 165 (slide GL24/25 co-ord 098 1202; E.F. no: K50), sample ET 7c, upper Coalbrookdale Formation, *nassa* Graptolite Biozone. 9, FM 166 (slide Rush S10/8 co-ord 153, 1204: E.F. no: P50), sample R 14, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone.

Fig. 8. *Laevolancis plicata* sp. nov. FM 167, holotype (Rush S14/5 co-ord 170 1150: E.F. no: Q44), sample R 17, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone.

Figs 10 and 11. cf. *Hispanaediscus* sp. A. 10, FM 168 (slide ET 16/5 co-ord 090 1140; E.F. no: J44/1/2), sample ET 15, lower Much Wenlock Limestone Formation, *ludensis* Graptolite Biozone. 11, FM 169 (slide ET 16/2 co-ord 160 1210; E.F. no: Q51/3), sample ET 15, lower Much Wenlock Limestone Formation, *ludensis* Graptolite Biozone.

Figs 12 and 13. *Hispanaediscus verrucatus* (Cramer) emend. 12, FM 170 (slide Rush S14/5 co-ord 065 1040: E.F. no: F33), sample R 17, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone. 13, FM 171 (slide ET 8/6 co-ord 017 1350; E.F. no: A65/2), sample ET 6, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone.



BURGESS and RICHARDSON, Wenlock cryptospores with radial and/or randomly orientated muri/folds. Distal exine ornamented with verrucae and or muri.

Comparison. Artemopyra gen. nov. has the same structure and radial proximal muri/folds, but is distally laevigate, apiculate or spinose.

Remarks. Hilate cryptospores in *Hispanaediscus* are occasionally seen as loosely attached dyads. This genus was originally erected by Cramer (1966) for alete palynomorphs with laevigate, verrucate/murornate and foveolate sculpture. The type species is verrucate and we have restricted the genus to forms with verrucate distal sculpture where the proximal exine is not markedly thinner than the distal and included species with proximal sculpture.

Hispanaediscus verrucatus (Cramer) emend.

Plate 2, figs 12 and 13

1966 *Hispanaediscus verrucatus* Cramer, p. 82, pl. 2, fig. 7 [*partim*], *non* fig. 2.
?1969 cf. *Synorisporites verrucatus* Richardson and Lister, pl. 40, fig. 13.
1973 cf. *Synorisporites verrucatus* Richardson and Lister; Richardson and Ioannides, p. 278, [*partim*] pl. 6, figs 17, 18, 20, *non* pl. 6, fig. 19.

Holotype. Cramer, 1966, pl. 2, fig. 7; F: 22354-5-2. San Pedro Formation, near Valporquero, Léon, northwest Spain. Probably of late Silurian age.

Figured specimens. FM 170, Pl. 2, fig. 12, slide Rush 13/14, 065 1040, sample R 16, Rushbury Pack Track, Coalbrookdale Formation; FM 171, Pl. 2, fig. 13, slide ET 8/6, 017 1350, sample ET 6, Eaton Track, upper Coalbrookdale Formation.

Emended diagnosis. An *Hispanaediscus* with a smooth, diaphanous hilum and verrucate – murornate distal sculpture.

Description. Hilate cryptospores probably derived from loosely attached, partially separated, dyads, but all specimens seen are single grains. Amb sub-circular to circular, originally distally hemispherical in equatorial view and flattened proximally. Distal exine more or less convex, *c.* 1 μm thick, sculpture consists mainly of low verrucae and/or muri 1–5 μm wide, *c.* 1 μm high and 0·5–3 μm apart. The groups of fused elements may coalesce into longer occasionally convolute and anastomosing muri.

Dimensions. Maximum diameter 23(28)32 μm, minimum diameter 22(25)30 μm (15 specimens measured).

Distribution. Upper Coalbrookdale Formation, Farley Member, and Much Wenlock Limestone Formation; upper *lundgreni* to lower *ludensis* Graptolite Biozones.

Comparisons. Some of Cramer's specimens appear identical to those from the Wenlock of the type area and Wenlock–Ludlow of North Africa. The spores from England, Spain and North Africa all have size ranges less than 35 μm, and means of between 24 and 28 μm. *H. wenlockensis* is larger and has proximal radial muri.

Remarks. Cramer's material appears to include trilete spores with a more triangular outline, similarly the material described by Richardson and Ioannides includes tetrads with comparable sculpture. Herein *H. verrucatus* is restricted to alete hilate cryptospores with a circular or subcircular amb.

Hispanaediscus wenlockensis sp. nov.

Plate 1, figs 4–9

Holotype and type locality. FM 152, Pl. 1, figs 8 and 9, slide GL 24/24, 055 1205, sample ET 7c, Eaton Track (Text-fig. 1 and Table 1), Coalbrookdale Formation, late Wenlock *nassa* Graptolite Biozone.

Paratypes. FM 149, Pl. 1, fig. 6, GL24/13, 100 1290, sample ET 7c; FM 150, Pl. 1, fig. 4, slide GL24/23, 030 1263, sample ET 7c; FM 151, Pl. 1, fig. 5, slide GL24/5, 130 1055, sample ET 7c; FM 152, Pl. 1, fig. 8, slide GL24/24, 055 1205, sample ET 7c, Coalbrookdale Formation; FM 153, Pl. 1, fig. 7, ET 9A/1, 090 1365, sample ET 8, Farley Member; all specimens from Eaton Track.

Diagnosis. An *Hispanaediscus* with short proximal radial muri and distal sculpture dominated by verrucae which occasionally coalesce into muri.

Description. Cryptospores derived from loosely attached, partially separated, dyads (only 1 found, Pl. 1, fig. 7) but most spores found separated as single grains. Amb sub-circular to circular; spores weakly convex distally in equatorial view. Crassitude equatorial to sub-equatorial, 0·5(1)1·5 μm wide, surrounds a proximal hilum. Proximal hilum sculptured by closely packed radial muri, up to 7 μm long and *c.* 1 μm wide which never reach the proximal pole. Distal exine *c.* 2 μm thick, sculptured with closely packed verrucae usually appearing hexagonal in plan view, elements 1(2)3 μm wide at the base, 1–1·5 μm high and 1 μm or less apart; rare elements composed of coalescent verrucae (muri) up to 17 μm long.

Dimensions. Maximum diameter 35(39)47 μm, minimum diameter 19(34)39 mm (27 specimens measured from sample ET 7c, Coalbrookdale Formation, Eaton Track.

Distribution. Uppermost Coalbrookdale Formation and lower Farley Member, lower *nassa* Graptolite Biozone.

Comparisons. Hispanaediscus verrucatus Cramer (1966) is smaller (*c.* 25 μm), laevigate proximally and has more widely spaced distal verrucae.

cf. *Hispanaediscus* sp. A

Plate 2, figs 10 and 11

Figured specimens. FM 168, Pl. 2, fig. 10, slide ET 16/5, 090 1140, sample ET 15, Eaton Track, Much Wenlock Limestone Formation; FM 169, Pl. 2, fig. 11, slide ET 16/2, 160 1210, sample ET 15, as above.

Description. Cryptospores seen only as separate grains. Amb circular, rarely subcircular; originally distally hemispherical and ±flattened proximally. Proximal hilum thin, usually absent or fragmentary; sculptured with low convolute to straight, radial muri or folds 0·5–1·5 μm wide and 7–10 μm long; muri/folds taper from margin of hilum to proximal pole. Distal exine *c.* 2 μm thick at the distal pole and slightly thickened, up to 3 μm thick at the equator; most specimens sculptured with closely spaced, convolute and anastomosing muri, rounded in profile, 0·5(2)4 μm wide, $<$ 1–3 μm apart and $<$ 1 μm high; elements usually composed of coalescent verrucae but may be more regular forming narrow irregular ridges or rugulae.

Dimensions. Maximum diameter 19(25)36 μm, minimum diameter 17(22·5)29 μm (13 specimens measured from samples ET 15, WL1 and WL2).

Distribution. Upper Coalbrookdale Formation, Farley Member and Much Wenlock Limestone Formation; lower *nassa* to lower *ludensis* Graptolite Biozones.

Comparison. Specimens of *Cymbosporites verrucosus* Richardson and Lister, 1969 are similar but larger (29–52 μm), some specimens have trilete folds or indistinct trilete marks, and the verrucae are larger and do not form ridges. cf. *Hispanaediscus* sp. A has a thin proximal hilum, and therefore is not typical of the genus *Hispanaediscus*. Too few specimens have been found to warrant further taxonomic separation.

Genus ARTEMOPYRA gen. nov.

Type species. *Artemopyra brevicosta* sp. nov.

Derivation of name. Greek *artema*, ear-ring, pyr = fire.

Diagnosis. Alete proximally hilate cryptospores; originally elliptical to hemispherical in equatorial view. Proximal hilum sculptured with predominantly radial muri. Distal exine laevigate or sculptured with grana, coni, biform elements or spinae.

Remarks. Specimens have been found in loosely attached dyads.

Artemopyra brevicosta sp. nov.

Plate 1, figs 1–3

1973 *?Emphanisporites* cf. *protophanus* Richardson and Ioannides, pl. 2, fig. 7.
1979 ? 'Spore with radial thickenings on one surface', Strother and Traverse, p. 14.

Holotype and type locality. FM 146, Pl. 1, fig. 3, slide ET 9A/4, 165 1300; sample ET 8, Eaton Track (see Text-fig. 1 and Table 1), Farley Member, late Wenlock *nassa* Graptolite Biozone.

Paratypes. FM 147, Pl. 1, fig. 1, slide GL 22/1, 060 1030, sample ET 7a; FM 148, Pl. 1, fig. 2, slide GL 24/26, 200 1110, sample ET 7c; both Eaton Track, upper Coalbrookdale Formation.

Derivation of name. Latin *brevis*, short; *costa*, rib.

Diagnosis. An *Artemopyra* with simple proximal subequatorial radial muri < half spore radius in length; distal exine laevigate.

Description. Proximally hilate cryptospores derived from loosely attached, partially separated, dyads; dyads frequent (Pl. 1, fig. 1), but most spores found separated as single grains. Amb circular to sub-circular, cryptospores originally hemispherical with flattened proximal pole. A more or less equatorial crassitude, distinct to indistinct, surrounds the hilum and and is roughly circular and concentric with the amb; hilum sculptured with straight or slightly sinuous muri < 1(3)6 μm long, < 1(1)2 μm maximum width and < 1–2 μm apart; muri taper polewards. Distal exine laevigate, *c*. 1·5 μm thick.

Dimensions. Maximum diameter 22(35)49 μm, minimum diameter 21(28)44 μm (90 specimens measured from sample ET 7c).

Distribution. Upper Coalbrookdale Formation, Farley Member, upper *lundgreni* to lower *nassa* Graptolite Biozones.

Comparison. *?Emphanisporites* cf. *protophanus* Richardson and Ioannides, 1973 from the Tannezuft and Acacus Formations of western Libya (probably upper Wenlock, Ludlow and Downton (Pridoli) equivalents) is slightly smaller but includes synonymous spores. Wenlock(?) material of Strother and Traverse (1979) has been examined and contains specimens of *A. brevicosta*, including dyads. *Artemopyra* sp. A has narrower, longer and more convolute radial muri.

Remarks. This species is distinctive and abundant and, in the type Wenlock Area, its first appearance is a good indicator of the late Homerian.

Artemopyra sp. A

Plate 1, figs 10 and 11

Figured specimen. FM 154, Pl. 1, fig. 10, slide ET 16/5, 078 1088; FM 155, Pl. 1, fig. 11, slide ET 16/8, 144 1050; both specimens from sample ET 15, Eaton Track, lower Much Wenlock Limestone Formation.

Description. Amb circular to sub-circular, cryptospores originally elliptical with flattened proximal pole. Crassitude equatorial to sub-equatorial, forms a narrow ring *c.* 1 μm wide surrounding the proximal hilum. Proximal hilum concave, sculptured with low, more or less radial muri and/or folds 2(4)7·5 μm long, *c.* 1 μm wide, < 1–1 μm apart and < 1 μm high; muri taper gradually to the proximal pole, becoming more convolute and anastomosing. Distal exine *c.* 1 μm thick and laevigate.

Dimensions. Maximum diameter 28 μm, minimum diameter 23 μm (two specimens measured from samples ET 15 and WL1).

Distribution. Found in two samples, Much Wenlock Limestone Formation, lower *ludensis* Graptolite Biozone.

Comparisons. Artemopyra brevicosta sp. nov. has shorter, more robust, radial muri.

HILATE CRYPTOSPORE type 1

Plate 1, figs 14 and 15

?1966 *Hispanaediscus leonensis* Cramer, p. 83, pl. 2, fig. 8
?1979 'Perforated palynomorph', Strother and Traverse, p. 14.

Figured specimen. FM 158, Pl. 1, figs 14 and 15, slide GL 24/7, 100 1070; sample ET 7c, Eaton Track, Coalbrookdale Formation.

Description. Proximally hilate cryptospores. Amb circular to sub-circular; cryptospores originally elliptical with flattened proximal pole. Crassitude equatorial to sub-equatorial, forms a narrow ring *c.* 1·5 μm wide surrounding the proximal hilum which is concave and laevigate. Distal exine *c.* 1·5 μm thick, foveolate; foveolae regularly spaced *c.* 1 μm × 0·5 μm and *c.* 1 μm apart.

Dimensions. Maximum diameter 18(21)25 μm (2 specimens recorded in sample ET 7c).

Distribution. As for figured specimen.

Comparison. Hispanaediscus leonensis Cramer, 1966 has a similar structure and may be synonymous with this type. However, the genus *Hipanaediscus* is used here for verrucate/murinate hilate cryptospores and hence could not be used for this type. Material from Pennsylvania described by Strother and Traverse (1979) has been re-examined by N. D. B. and contains specimens which are closely comparable.

3. *Dyads of hilate cryptospores*

In rocks of Llandovery age cryptospore tetrads and dyads are common and in most cases the tetrad or dyad condition is 'permanent'. For these propagules separate genera have been created. In younger Silurian strata intact dyads become increasingly rare although the hilate cryptospores derived from them are common. In this work the separated cryptospores are named whereas usually their dyad counterparts are not. This parallels the standard treatment of dispersed miospores and their tetrads. Because this is a gradational phenomenon the hilate cryptospore genus *Dyadospora* Strother and Traverse, 1979 is retained, though emended, pending further investigations.

Genus DYADOSPORA Strother and Traverse emend.

Type species. Dyadospora murusattenuata Strother and Traverse, 1979 emend.

Emended diagnosis. Dyads composed of two laevigate hilate cryptospores. Individual spores not strongly mutually attached, a clear line of separation is always seen; in equatorial compression the two spores are often partially separated.

Remarks. The diagnosis of the genus *Dyadospora* has been restricted to include only non-'permanent' dyads which separate to give two laevigate hilate cryptospores. Pseudodyads, characteristic of the early Silurian, are retained in the genus *Pseudodyadospora* Johnson, 1985. With careful observation the two genera can be distinguished and their stratigraphical distribution and biological significance assessed.

Dyadospora murusattenuata Strother and Traverse emend.

Plate 2, figs 7 and 9

1979 *Dyadospora murusattenuata* Strother and Traverse, p. 15, pl. 6, figs 8 and 10.
1982 *Dyadospora murusattenuata* Strother and Traverse; Miller and Eames, p. 247, pl. 6, fig. 8.
1985 *Dyadospora murusattenuata* Strother and Traverse; Johnson, p. 334.

Figured specimens. FM 165, Pl. 2, fig. 7, slide GL24/25, 098 1202, sample ET 7c, Eaton Track; FM 166, Pl. 2, fig. 9, slide Rush S10/8, 153 1204, sample R 14, Rushbury Pack Track, upper Coalbrookdale Formation.

Emended diagnosis. A *Dyadospora* with thin folded walls.

Description. Dyads, usually isomorphic, circular to subcircular in equatorial view, usually preserved in oblique compression, each spore is distally convex; crassitudes at the point of contact between the two cryptospores; a cleft is always present between the crassitudes of each spore. Distal exine laevigate, *c*. 1 μm thick over the distal pole and usually folded.

Dimensions. Dyad length 22(28)39 μm, equatorial width 20(27)37 μm (35 specimens measured) from sample ET 7c, Coalbrookdale Formation, upper Wenlock *nassa* Graptolite Biozone.

Distribution. Throughout the sequence, Buildwas to Much Wenlock Limestone Formations; lower *centrifugus* to lower *ludensis* Graptolite Biozones.

Comparisons. The holotype of *Dyadospora murusattenuata* Strother and Traverse, 1979 (? Wenlock, pl. 3, fig. 9) is closely similar to the specimens found in this study. In both cases the specimens are thin-walled, folded and show partially separated dyads. Slides of the material from Pennsylvania described by Strother and Traverse have been examined for comparison and contain abundant dyads identical to those described herein. *D. murusdensa* Strother and Traverse, 1979 emend. is larger and thicker-walled. *Pseudodyadospora laevigata* Johnson, 1985 is more elongate, and often anisomorphic (i.e. the two parts of the dyad are of unequal size, Richardson 1988; Burgess 1991) and the individual 'spores' are joined by a single fused thickening, or crassitude.

Remarks. Separation of these dyads is believed to produce spores of the species *Laevolancis plicata* gen. et sp. nov.

Dyadospora murusdensa Strother and Traverse emend.

Plate 2, figs 1–3, 5

1979 *Dyadospora murusdensa* Strother and Traverse, p. 15, pl. 3, figs 6 and 7.
1982 cf. *Dyadospora murusdensa* Strother and Traverse; Miller and Eames, p. 247, pl. 6, fig. 7.
1985 cf. *Dyadospora murusdensa* Strother and Traverse; Johnson, p. 334, pl. 7, fig. 9.
1985 *Dyadospora murusdensa* Strother and Traverse; Richardson in Hill *et al*., p. 29, pl. 15, figs 8 and 9.

Figured specimens. FM 159, Pl. 2, fig. 1, slide Tick 1/7, 063 1209; sample T 1, Ticklerton Brook, Coalbrookdale Formation; FM 160, Pl. 2, fig. 2, slide ET 5A/5, 152 1053, sample ET 3, Eaton Track, upper Coalbrookdale Formation; FM 161, Pl. 2, fig. 3, slide Rush S10/8, 200 1204, sample R 14; FM 162, Pl. 2, fig. 5, slide Rush S10/1, 070 1220, sample R 14, Rushbury Pack Track, upper Coalbrookdale Formation.

Emended diagnosis. A *Dyadospora* with unfolded walls.

Description. Dyads, usually isomorphic, circular to subcircular in equatorial view, usually preserved in oblique compression, each spore is distally convex; crassitudes 2(3)4 μm thick, equatorial to sub-equatorial, the two cryptospores are usually loosely attached or almost separated (Pl. 2, figs 2 and 5). In equatorial view the length is equal to, or slightly greater than the width at the equator; exine laevigate, 1(2)3 μm thick over the distal pole and usually without folds.

Dimensions. Dyad length 23(39)47 μm, equatorial diameter 21(34)46 μm (13 specimens measured from various samples).

Comparison. The holotype of *Dyadospora murusdensa* Strother and Traverse (1979, pl. 3, fig. 9) is closely similar to the dyads described above. Slides of material described by Strother and Traverse from Pennsylvania have been examined for comparison and contain dyads identical to those described here. *Dyadospora murusattenuata* Strother and Traverse emend. is thinner-walled and generally smaller.

Anteturma SPORITES H. Potonié, 1893
Turma TRILETES Reinsch, 1891
Subturma ZONOTRILETES Waltz, 1935 in Luber and Waltz (1938)
Infraturma CRASSITI Bharadwaj and Venkatachala, 1961
Genus AMBITISPORITES Hoffmeister, 1959

Type species. *Ambitisporites avitus* Hoffmeister, 1959

Ambitisporites dilutus (Hoffmeister) Richardson and Lister, 1969

Text-fig. 3D–H

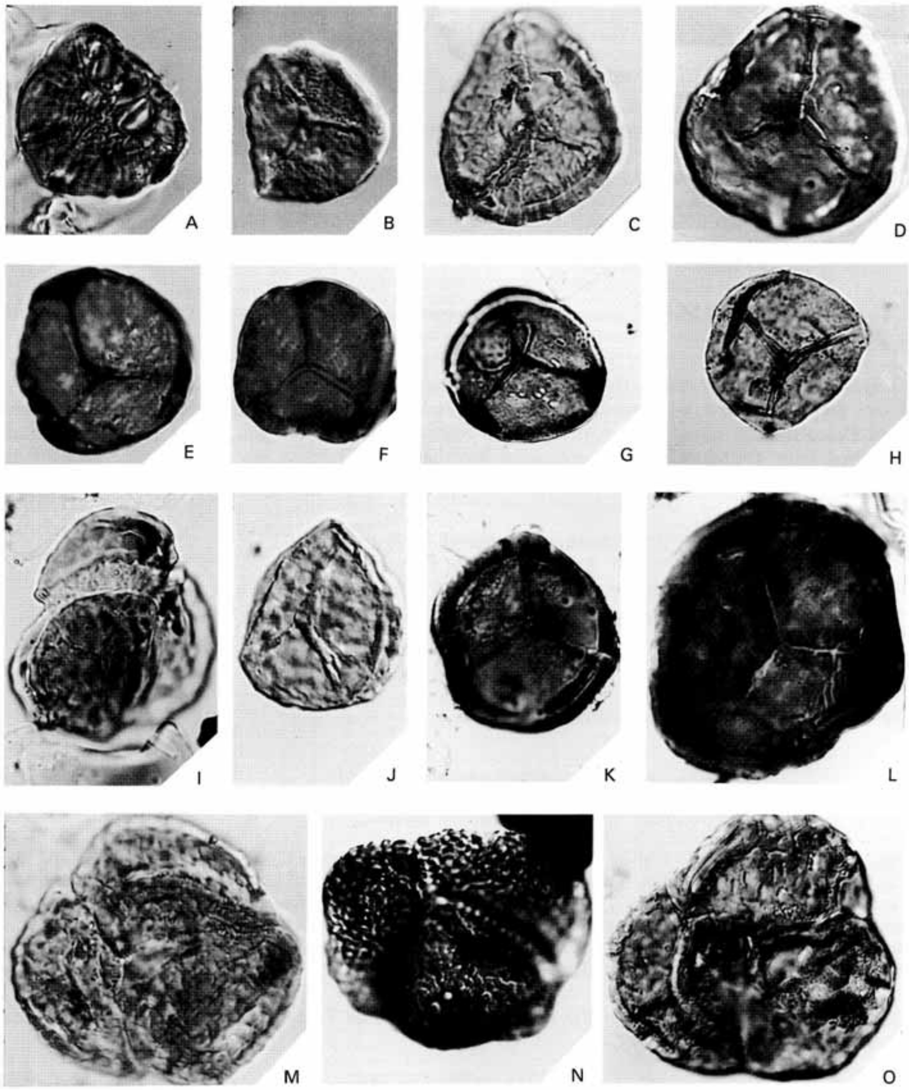
Figured specimens. FM 175, Text-fig. 3D, slide ET 16/2, 100 1205; sample ET 15, Eaton Track, Much Wenlock Limestone Formation; FM 176, Text-fig. 3E, slide Rush Vill S1/3, 182 1223, sample R 2, Rushbury, lower Coalbrookdale Formation; FM 177, Text-fig. 3E, slide ET 8/5, 130 1240, sample ET 6; FM 178, Text-fig. 3G, slide Rush Vill S1/3, 180 1050, sample R 2; FM 179, Text-fig. 3H, slide ET 8/5, 123 1380, sample ET 6, Rushbury and Eaton Track; specimens FM 177 and FM 179 are from the upper Coalbrookdale Formation and FM 178 from the lower Coalbrookdale Formation.

Dimensions. Diameter 22(28)47 μm (100 specimens measured, see Text-fig. 4 for spread of measurements), distal exine 1–2 μm thick.

Distribution. Common throughout the sequence. Buildwas to Much Wenlock Limestone Formations; basal *centrifugus* to lower *ludensis* Graptolite Biozones.

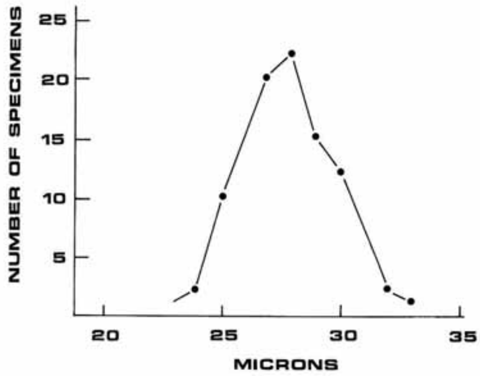
Comparison. *Ambitisporites avitus* Hoffmeister, 1959 has a well-defined crassitude.

Remarks. *Ambitisporites dilutus* is the most abundant spore in the samples studied, up to 10,000 specimens per gram of sediment were present in some residues. The size-distribution of these spores



TEXT-FIG. 3. All figures × 1000. A–C. TRILETE MIOSPORE TYPE 1. A, FM 172 (slide Rush S10/4 co-ord 135 1090; E.F. no: 039/1), sample R 14, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone. B, FM 173 (slide GL22/1 co-ord 063 1048; E.F. no: F34), sample ET 7a, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone. C, FM 174 (slide ET 9A/1 co-ord 070 1145; E.F. no: G44/4), sample ET 8, upper Coalbrookdale Formation, *nassa* Graptolite Biozone. D–H, *Ambitisporites dilutus* (Hoffmeister) Richardson and Lister, 1969. D, FM 175 (slide ET 16/2, co-ord 100 1205; E.F. no: K50/2), sample ET 15, lower Much Wenlock shows a classic normal distribution (Text-fig. 4), perhaps indicating the spores were produced by a single population of one or only a few species.

TEXT-FIG. 4. Size frequency distribution of a hundred *Ambitisporites dilutus* (Hoffmeister) Richardson and Lister, 1969 from sample R 2, Rushbury (*ellesae* Graptolite Biozone); $\bar{x} =$ 27·9 μm.



Genus SYNORISPORITES Richardson and Lister, 1969

Type species. Synorisporites downtonensis Richardson and Lister, 1969.

Synorisporites cf. *S.*? *libycus* Richardson and Ioannides, 1973

Text-fig. 3I, J

Figured specimens. FM 180, Text-fig. 3I, slide GL 22/1, 130 1030, sample ET 7a; FM 181, Text-fig. 3J, slide ET 8/3 180 1264, sample ET 6, both samples from the Eaton Track, upper Coalbrookdale Formation.

Description. Amb sub-triangular with convex sides and rounded apices. Distally originally elliptical in equatorial view with a flattened pyramidal proximal surface. Equatorial crassitude narrow, 0·5(1·5)3 μm wide, and may be indistinct. Contact surface laevigate. Distal exine *c.* 1μm thick, sculptured with low, rounded and relatively broad muri and discrete verrucae or muri often composed of coalescent verrucae, 2(4)6 μm long,

Limestone Formation, *ludensis* Graptolite Biozone. E, FM 176 (slide Rush Vill S1/3 co-ord 182 1223; E.F. no: S54/5/T54/2), sample R 2, lower Coalbrookdale Formation, *ellesae* Graptolite Biozone. F, FM 177 (slide ET 8/5, co-ord 130 1240; E.F. no: N54/4/054/2), sample ET 6, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone. G, FM 178 (slide Rush Vill S1/3 co-ord 180 1050; E.F. no: T35/2), sample R2, lower Coalbrookdale Formation, *ellesae* Graptolite Biozone. H, FM 179 (slide ET 8/5 co-ord 123 1380; E.F. no: N69/1), sample ET 6, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone. I, J. *Synosporites* cf. *S.*? *libycus* Richardson and Ioannides, 1973. I, Tetrad; FM 180 (slide GL22/1 co-ord 130 1030; E.F. no: 032/2/4), sample ET 7a, upper Coalbrookdale Formation, *ludgreni* Graptolite Biozone. J, isolated spore showing trilete mark; FM 181 (slide ET 8/3, 180 1264; E.F. no: S56), sample ET 6, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone. K. *Archaeozonotriletes chulus* (Cramer) var. *nanus* Richardson and Lister, 1969. FM 182 (slide S29/3 co-ord 040 0950; E.F. no: C23/2/C24/1), sample G 9, Buildwas Formation, *centrifugus* Graptolite Biozone. L. *Archaeozonotriletes chulus* (Cramer) var. *chulus* Richardson and Lister, 1969. FM 183 (slide ET 8/3 co-ord 225 1390; E.F. no: X69/X70), sample ET 6, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone. M–O. MURORNATE TETRADS. M, FM 184 (slide ET 7/4 co-ord 150 1087; E.F. no: P38/4), sample ET 5, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone. N, FM 185 (slide ET 15/1 157 1312; E.F. no: Q61/2), sample ET 14, Farley Member, *ludensis* Graptolite Biozone. O, FM 186 (slide WL 2/5 co-ord 006 1364; E.F. no: A66), sample WL 2, lower Much Wenlock Limestone Formation, *ludensis* Graptolite Biozone.

1(2)5 μm wide, < 1 μm high and 0·5(1)4 μm apart. Trilete mark distinct, with straight to slightly sinuous sutures which extend to the equator or nearly so, and are accompanied by low lips, *c.* 1 μm high and wide.

Dimensions. Maximum diameter 18(26)32 μm (4 specimens measured).

Distribution. Upper Coalbrookdale Formation and lower Farley Member, upper *lundgreni* to lower *nassa* Graptolite Biozones.

Comparisons. Synorisporites? libycus Richardson and Ioannides, 1973 is of similar size (19–42 μm) but includes some spores with broader verrucae (2–8 μm). *S. verrucatus* Richardson and Lister, 1969 from the lower Downton Group (= Pridoli age) has smaller and more prominent verrucae.

TRILETE MIOSPORE type 1

Text-fig. 3A–C

Figured specimens. FM 172, Text-fig. 3A, slide Rush S10/4 135 1090, sample R 14, Rushbury Pack Track, upper Coalbrookdale Formation; FM 173, Text-fig. 3B, slide GL22/1 063 1048, sample ET 7a, Eaton Track, upper Coalbrookdale Formation; FM 174, Text-fig. 3C, slide ET 9A/1, 070 1145, sample ET 8, Eaton Track, Farley Member.

Description. Amb sub-triangular with convex sides and rounded apices. Equatorial crassitude narrow, 0·5–3·5 μm wide. Proximal surface sculptured with convolute and anastomosing muri *c.* 1 μm wide and 0·5 μm apart; muri are radially aligned near the equator but are predominantly randomly orientated over the remainder of the proximal surface. Distal exine *c.* 1 μm thick; laevigate in two specimens, and with scattered grana in one specimen.

Dimensions. Maximum diameter 28(35)40 μm (three specimens measured from samples ET 7c and ET 8).

Distribution. Upper Coalbrookdale Formation to lower Farley Member. Lower *nassa* Graptolite Biozone.

Comparisons. Emphanisporites McGregor, 1961 has proximal muri which are predominantly radial whereas in Trilete Miospore type 1 the muri are mainly randomly oriented.

Infraturma PATINATI (Butterworth and Williams) emend. Smith and Butterworth, 1967
Genus ARCHAEOZONOTRILETES (Naumova) Allen, 1965

Type species. *Archaeozonotriletes variabilis* (Naumova) Allen, 1965.

Archaeozonotriletes chulus (Cramer) var. *chulus* Richardson and Lister, 1969

Text-fig. 3L

Figured specimen. FM 183, Text-fig. 3L, slide ET 8/3, 225 1390, sample ET 6, Eaton Track, upper Coalbrookdale Formation.

Dimensions. Diameter 36(39)43 μm (17 specimens measured). Equatorial exine width 2–6 μm; exine 1·5–4 μm thick at distal pole.

Distribution. Throughout the Wenlock, Buildwas to Much Wenlock Limestone Formations; basal *centrifugus* to lower *ludensis* Graptolite Biozones.

Comparisons. The genus *Archaeozonotriletes* is preferred for these spores because the distal patina is either the same as, or similar in thickness to, the equatorial thickness (Table 2). *Tholisporites*

TABLE 2. Exine thickness in spores of the *Archaeozonotriletes chulus* var. *chulus* type from the Welsh Borderland (Richardson and Lister 1969).

	Distal pole	Equator	
		Inter-radial	Radial
Wenlock	1·5–4 μm	2–6 μm	?
Downton	4–5 μm	4–6 μm	3–6 μm
Ditton	2·0–2·5 μm	2·5–5 μm (3·5–4·5)	?

Butterworth and Williams, 1958 has a 'Patina thickest in the equatorial region, thinning slightly towards the distal pole.' Although Smith and Butterworth (1967) report a distal thickness for *T. scoticus* (the type species) 'usually less than the equatorial thickness', they compare *Tholisporites* with a cingulate genus *Densosporites*. Further, *A. chulus* (Cramer) is elliptical in equatorial view and usually preserved in polar compression whereas the type species of both *Tholisporites* and *Archaeozonotiletes* are more inflated, hemispherical in lateral view, and commonly compressed in lateral orientation (Allen 1965, p. 721; Smith and Butterworth 1967, p. 268). Thus *A. chulus* differs in basic shape/structure from both the genera with which it has been compared. The genus *Archaeozonotriletes* has priority over *Tholisporites* and it remains to be seen whether these two genera can be separated on a satisfactory basis and whether spores with a less inflated distal hemisphere should be accommodated in a new genus.

Remarks. JBR is a member of an international working group looking at species of the *chulus* type and pending its results we prefer to leave this species in the genus *Archaeozonotriletes*.

Archaeozonotriletes chulus (Cramer) var. *nanus* Richardson and Lister, 1969

Text-fig. 3K

Figured specimen. FM 182, Text-fig. 3K, slide S29/3, 040 0950, sample G 9, Hughley Brook, Buildwas Formation.

Dimensions. Diameter 21·5(28)35 μm (14 specimens measured from various samples); equatorial exine width 2–6 μm; exine 1·5–4 μm at distal pole.

Distribution. Throughout the Wenlock, Buildwas to Much Wenlock Limestone Formations; basal *centrifugus* to lower *ludensis* Graptolite Biozones.

Comparison. A bimodal size distribution was demonstrated for the two varieties of *A. chulus* by Richardson and Lister (1969) for Upper Silurian (Downtonian) and Lower Devonian (Dittonian) specimens. The present work shows that in the lower Wenlock (Buildwas Formation) *A. chulus* var. *nanus* is dominant whereas *A. chulus* var. *chulus* dominates higher in the Wenlock.

INCERTAE SEDIS

MURORNATE TETRADS

Text-fig. 3M–O

Figured specimen. FM 184, Text-fig. 3M, slide ET 7/4, 150 1087, sample ET 5, Eaton Track, upper Coalbrookdale Formation; FM 185, Text-fig. 3N, slide ET 15/1, 157 1312, sample ET 14, Eaton Track, Farley Member; FM 186, Text-fig. 3O, slide WL2/5, 006 1364, sample WL 2, Harton Hollow Wood Quarry, lower Much Wenlock Limestone Formation.

Description. Tetrads of closely adherent spores with murornate sculpture. Individual spores with triangular to subtriangular amb. Proximal surface not seen. Distal exine sculptured with elongate, narrow (0·5(1)1·5 μm wide), sinuous to convolute and anastomosing, low (< 1 μm high) and rounded muri; elements discrete but occasionally closely spaced, and fused, < 0·5–3 μm apart.

Dimensions. Tetrads 31(38)50 μm in diameter; individual spores 21·5(31)36 μm in width (20 specimens measured).

Distribution. Upper Coalbrookdale Formation, Farley Member, and Much Wenlock Limestone; *nassa* to lower *ludensis* Graptolite Biozones.

Comparison. Nodospora rugosa Strother and Traverse, 1979 from the Llandovery of North America is a permanent cryptospore tetrad with superficially similar sculpture. However, in *N. rugosa* this sculpture is present on an envelope surrounding the cryptospore tetrad whereas in this species the spore exine is sculptured. Tetrads of rugulate trilete miospores would also appear similar, but one might expect to recover isolated miospores in the same samples; this has not occurred with this species. We are therefore unsure if these tetrads are cryptospores or the tetrads of trilete miospores and hence have included them under *Incertae sedis* pending further investigations.

COMPARISONS WITH OTHER ASSEMBLAGES

Most records of early sporomorphs and plant megafossils have come from Baltica (Britain, Scandinavia and European USSR, Livermore *et al.* 1985). Other sporomorph records for the Silurian come from Laurasia (USA) and Gondwana (North Africa and South America) but so far there are none from Australia, Siberia, Antarctica or China. Even fewer of these assemblages are represented by diverse microfloras (see Table 3).

BIOSTRATIGRAPHY

A spore zonal scheme for the Silurian and Devonian of the northern hemisphere has been proposed by Richardson and McGregor (1986). In this inter-regional scheme Wenlock strata encompass two assemblage biozones: the *chulus–nanus* (Late Llandovery to Late Wenlock, Telychian to Late Homerian) and cf. *protophanus–verrucatus* (Late Wenlock and Early Ludlow, Late Homerian to Early Gorstian). In the Wenlock of the type area characteristic species of the cf. *protophanus–verrucatus* Biozone first appear in upper *lundgreni* Graptolite Biozone of the Eaton Track and Rushbury Pack Track sections (Text-fig. 5). Thus all the Sheinwoodian and lowermost Homerian probably belong to the *chulus–nanus* Biozone. The nominal species of the upper zone are the hilate cryptospores, ?*Emphanisporites* cf. *protophanus* (= *Artemopyra brevicosta* of this work) and cf. *Synorisporites verrucatus* (= *Hispanaediscus verrucatus* of this work). As a result of these new data, the base of the zone is redefined in the Eaton Track Section.

cf. *protophanus–verrucatus* Assemblage Biozone.

The new reference section for the base of this zone is defined in the Upper Coalbrookdale Formation of the type area of the Wenlock Series. The base is taken as sample ET 5 (approximately midway between localities 20 and 21 of Bassett *et al.* 1975) in the Eaton Track Section, of upper *lundgreni* Graptolite Biozone age. The nominal species ?*Emphanisporites* cf. *protophanus* (= *Artemopyra brevicosta*) is rare at this horizon but both nominal species occur *c.* 4 m above in sample ET 6 (approximately locality 21 of Bassett *et al.* 1975) and become more common higher in the *lundgreni* Graptolite Biozone, sample ET 7a (locality 22 of Bassett *et al.* 1975), and above in the Eaton Track Section.

Remarks. In the Rushbury Pack Track, the nominal species cf. *Synorisporites verrucatus* (=

TABLE 3: Homerian and Sheinwoodian spores from the type Wenlock area and around the world

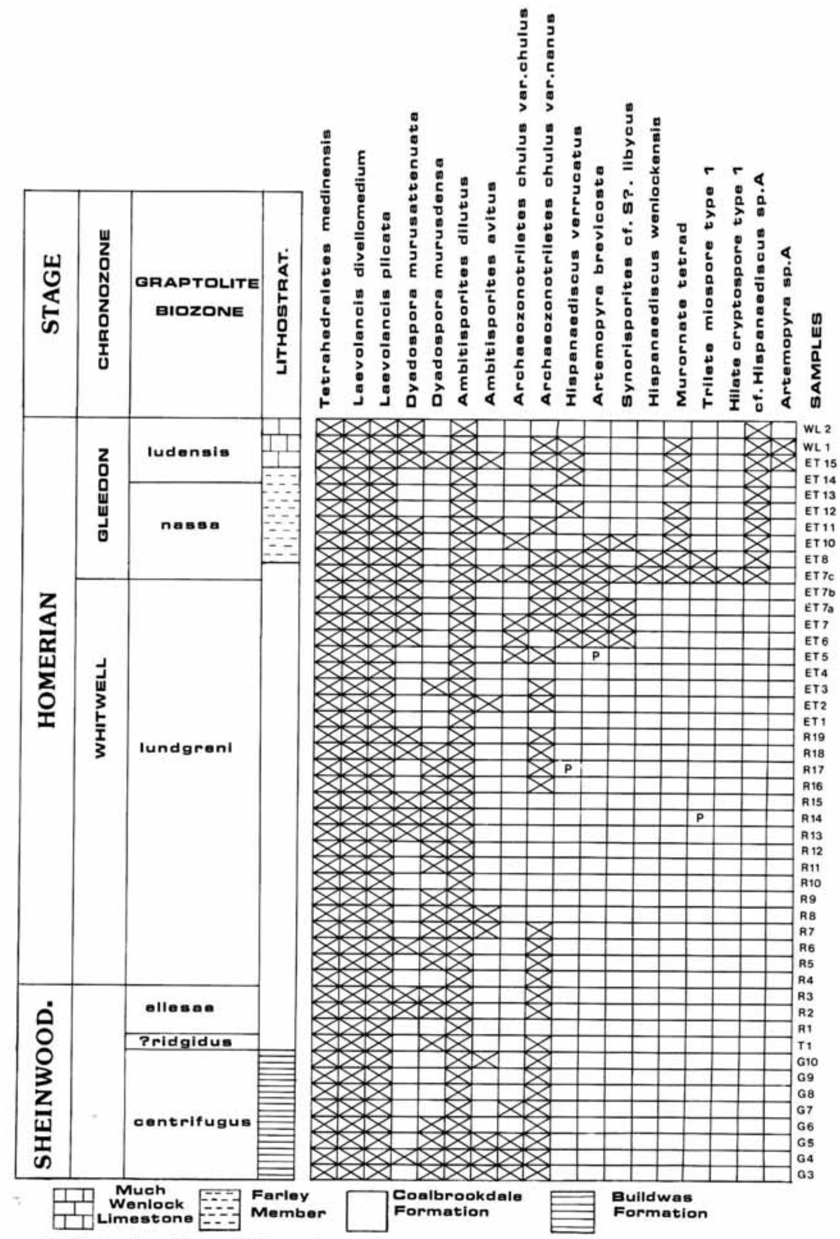
	Great Britain and Ireland (Baltica)						North Africa (Gondwana)			North America (Laurentia)
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
HOMERIAN										
Ambitisporites dilutus	+	+	+	.	+	+	+	+	+	+
A. avitus	+	+	+	.	+	+	+	+	+	+
Archaeozonotriletes chulus var. *chulus*	+	–	–	.	+	–	+	–	–	–
A. chulus var *nanus*	+	–	–	.	+	–	+	–	–	–
Synorisporites cf. *S.? libycus*	+	?	–	.	–	–	+	–	–	–
Murornate tetrads	+	–	–	.	+	–	–	–	–	–
Trilete miospore type 1	+	–	–	.	–	–	–	–	–	–
Emphanisporites protophanus	–	–	–	.	–	–	+	–	–	–
Laevolancis divellomedium	+	+	+	.	+	–	+	+	–	+
L. plicata	+	–	–	.	–	–	–	–	–	–
Artemopyra brevicosta	+	–	–	.	–	–	+	–	–	+
A. sp. A	+	–	–	.	–	–	–	–	–	–
Hispanaediscus wenlockensis	+	–	–	.	–	–	–	–	–	–
H. verrucatus	+	–	–	.	+	–	+	–	–	+
cf. *H.* sp. A	+	–	–	.	–	–	–	–	?	–
Hilate cryptospore type 1	+	–	–	.	–	–	–	–	–	+
Dyadospora murusattenuatta	+	–	–	.	–	–	–	–	–	+
D. murusdensa	+	–	–	.	–	–	–	–	–	+
Tetrahedraletes medinensis	+	–	–	.	–	+	–	–	–	.
SHEINWOODIAN										
Ambitisporites dilutus	+	+	.	+	.	+				
A. avitus	+	+	.	–	.	+				
Archaeozonotriletes chulus var. *chulus*	+	–	.	–	.	+				
A. chulus var. *nanus*	+	–	.	–	.	–				
Laevolancis divellomedium	+	+	.	–	.	–				
L. plicata	+	–	.	–	.	–				
Dyadospora murusattenuatta	+	–	.	–	.	–				
D. murusdensa	+	–	.	–	.	–				
Tetrahedraletes medinensis	+	–	.	–	.	–				

(1) This study; (2) Downie (1963); (3) Dorning (1981*b*, 1983); (4) Mabillard and Aldridge (1981); (5) Richardson and Lister (1969); (6) Smith (1979); (7) Richardson and Ioannides (1973)†; (8) Magloire (1968)†; (9) Jardiné and Yapaudjian (1968)†; (10) Strother and Traverse (1979)†*.

* Assessment of species not described by Strother and Traverse is by personal observation of paratype material in the BM(NH) by N. D. B.

† Studies with poor dating.

. Strata not studied.



TEXT-FIG. 5. Biostratigraphic and lithostratigraphic occurrence of sporomorphs in the type Wenlock area. The base of the cf. *protophanus-verrucatus* Zone occurs below samples R17 (Rushbury Pack Track Section) and ET 5 (Eaton Track Section). Note that the top *c.* 20 m of the Wenlock Limestone was not sampled. P = occurrence of only one specimen.

Hispanaediscus verrucatus) occurs in sample R17 (approximately locality 44 of Bassett *et al.* 1975). This sample is also from the upper *lundgreni* Graptolite Biozone and is probably at a similar horizon to the Eaton Track Reference Section occurrences, but may be slightly lower. The Eaton Track is preferred as the zonal reference section because the spore record is better there. A single specimen of Trilete Miospore type 1 was also found in sample R14, approximately equivalent to locality 38 of Bassett *et al.* (1975) in the upper *lundgreni* Graptolite Biozone. This specimen represents the oldest sculptured miospore dated independently by graptolites.

Further zonal refinement may be possible, at least in the Anglo-Welsh Area. For example, the presence of *Artemopyra brevicosta* appears to be a good, though possibly only local, marker for the upper *lundgreni* to lower *nassa* Graptolite Biozones in that it has not yet been found from the later *nassa* or *ludensis* Biozones. Also, cf. *Hispanaediscus* sp. A was not recorded in samples from the upper *lundgreni* Graptolite Biozone but is increasingly common in samples from the *nassa* and lower *ludensis* Biozones. Thus with further work this species may prove to be a useful indicator for the later Homerian. In the Libyan borehole sequences the miospore *Emphanisporites protophanus* appears higher in the sequence than ?*Emphanisporites* cf. *protophanus* (= *Artemopyra brevicosta*) but has not been found in the type Wenlock sequence examined. The first appearance of *E. protophanus* is placed in the overlying *libycus–poecilomorphus* Miospore Biozone by Richardson and McGregor (1986) and may prove to be an indicator of the latest Homerian or earliest Gorstian.

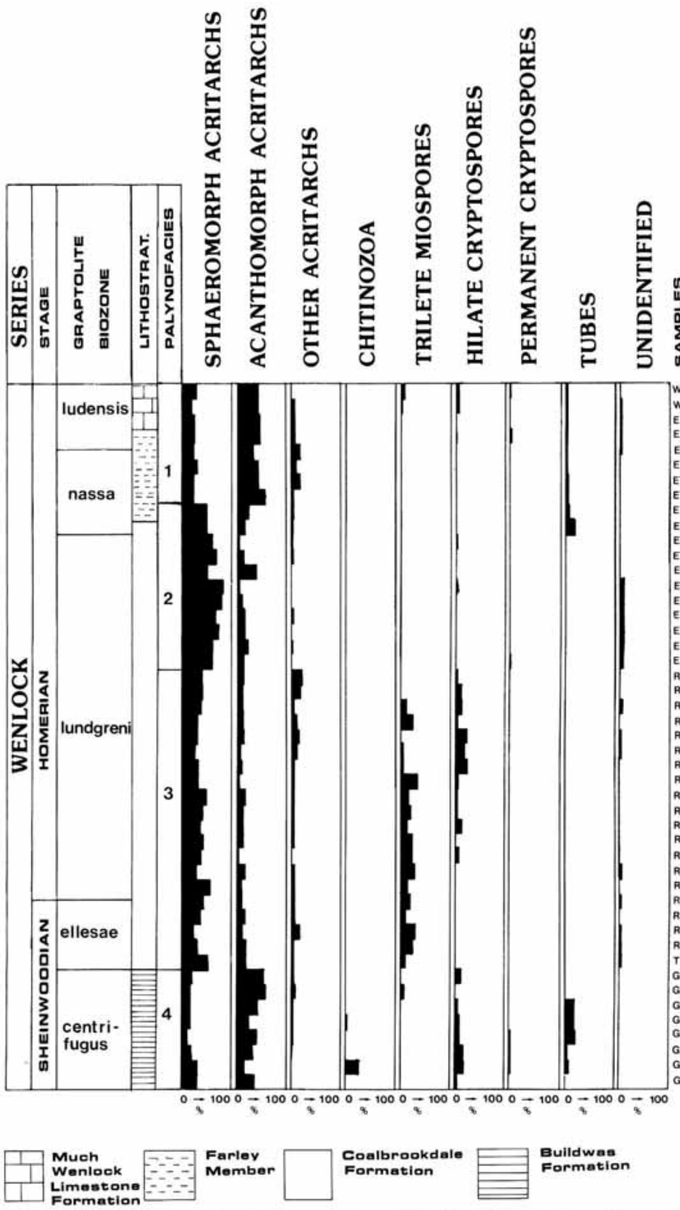
PALYNOFACIES

The appearance of sculpture on hilate cryptospores and trilete miospores is an event of biostratigraphical, biological and evolutionary significance. This event is useful for interregional stratigraphical correlation, and may relate to the primary diversification of land plants (rhyniophytoids). Consequently it is important to ascertain if the appearance of sculptured sporomorphs in the late *lundgreni* Graptolite Biozone of the type Wenlock area is a true 'evolutionary event' representing the first appearance of sculptured miospores and hilate cryptospores, or whether it is a preservational or depositional artifact. Several aspects of marine environments may be determined by studying the types and abundance of marine phytoplankton on the one hand and amounts of land-derived sporomorphs on the other. To this end organic-walled microphytoplankton (prasinophycean cysts and acritarchs), cryptospores and miospores, and organic-walled tubes (Burgess and Edwards in press) were counted from all samples, and used to produce a palynofacies profile of the sequence (Text-fig. 6).

The assemblages of palynomorphs and fragments of plant megafossils recognized fall into four distinct palynofacies, which can be related to changes in the depositional environment and the first appearance of sculptured sporomorphs.

Palynofacies 4 was recorded from samples of the Buildwas Formation in the Hughley Brook Section. The predominant palynomorphs are acanthomorph acritarchs (15–55 %) but there are also significant numbers of hilate cryptospores (5–10 %) and tubes (up to 15 %); trilete spores are rare (< 1 %). Using existing palynofacies models, the Buildwas Formation samples appear to have been deposited in an offshore shelf environment with significant terrestrial input (Dorning 1981*a*; Al-Ameri 1983; Burgess 1987; Richardson and Rasul 1990). Sculptured palynomorphs were not recovered from this palynofacies.

Palynofacies 3 was recorded from samples of the Coalbrookdale Formation from sections around Rushbury. The assemblages are composed predominantly of prasinophyceae (sphaeromorph acritarchs) (30–55 %), trilete miospores (up to 20 %) and, near the top of the section, hilate cryptospores (up to 20 %). Studies of Recent Sediments (Muller 1959) show that the proportion of land derived sporomorphs normally increases shorewards. In addition the proportion of prasinophycean 'phycomata' increases relative to acritarchs in inshore environments (Richardson and Rasul 1990). Thus the palynofacies indicates a shoreward shift in the environment of deposition. In contrast macrofossil studies (Bassett and Cocks pers. comm.) indicate that these beds were deposited in offshore shelf environments. Despite the common occurrence of sporomorphs in



TEXT-FIG. 6. Composition of palynological assemblages (%) through the type Wenlock area and the stratigraphical distribution of four palynofacies.

this palynofacies (up to 25% of the assemblage) sculptured specimens are rare with only two specimens being recovered towards the top of the sequence (Text-fig. 5).

Palynofacies 2 typifies the Coalbrookdale Formation of the Eaton Track Section and is characterized by a dominance of sphaeromorph acritarchs (50–90%). Acanthomorph acritarchs are considerably less abundant (5–25%) and sporomorphs are relatively rare (0–2%). Using our palynofacies model, this palynofacies represents the most distal phase of sedimentation in the type area and probably the deepest water, but it is within this part of the succession that sculptured sporomorphs become increasingly common (though $< 1\%$ of the assemblage).

Palynofacies 1 typifies the upper part of the Coalbrookdale Formation, Farley Member and lower Much Wenlock Limestone Formation of the Eaton Track Section and Harton Hollow Wood Quarry. This palynofacies is dominated by acanthomorph acritarchs (40–60%), with prasinphycean 'phycomata' (20–30%) and increased percentages of sporomorphs (0–3%) and tubes (5–10%). This palynofacies indicates an outer shelf environment and nearer to the shore than that indicated by Palynofacies 2. Sculptured sporomorphs become increasingly diverse through this part of the sequence but are still rare ($< 1\%$ of the total assemblage).

These palynofacies studies show that sporomorphs are most abundant in the late Sheinwoodian and early Homerian (*ellesae* to late *lundgreni* Graptolite Biozones) where they were all laevigate. The earliest sculptured sporomorphs found are from the late *lundgreni* Zone where the palynofacies indicates deposition in offshore, deeper water, environments and where sporomorphs are rare and generally form $< 1\%$ of the assemblage. Sculptured sporomorphs become increasingly diverse in samples from the upper most *lundgreni* to lowermost *ludensis* Zones, where palynofacies studies indicate deposition in slightly more proximal, but still offshore, shelf environments and sporomorphs form only around 1% of the assemblage. In conclusion, the appearance of sculptured sporomorphs in the late *lundgreni* Graptolite Biozone of the Wenlock Type Area does not appear to have been caused by a change in the depositional environment to a more proximal one, but appears to be a true event. Sediments from inshore environments would yield larger numbers of sporomorphs but would not be expected to affect the horizon of this event substantially.

DISCUSSION AND PALAEOBOTANICAL SIGNIFICANCE

Trilete miospores of the genera *Ambitisporites* and *Synorisporites* have been recorded in situ from specimens of *Cooksonia pertoni* in the Upper Silurian (Fanning *et al.* 1988). These spores are comparable to some of the dispersed miospores described above and indicate that similar rhyniophytoid plants may have been present in the Wenlock. The increasing diversity of trilete miospores noted from the late *lundgreni* Graptolite Biozone, especially the appearance of sculpture, strongly suggests that such plants began to diversify in the Homerian. The studies of Fanning *et al.* (1988) on *Cooksonia pertoni* indicate that some of these plants, although they produced both laevigate and sculptured spores, may have looked remarkably similar and the main differences between them may have related to characters of their spores.

The derivation of hilate cryptospores is poorly known. However, smooth-walled hilate cryptospores have been recorded from *Salopella*-like sporangia in the Lower Devonian (Fanning *et al.* in press) and the distribution of these spores shows that they were undoubtedly produced by land-plants. Hilate cryptospores are found throughout the Wenlock of the type area but the first sculptured species occur in the upper *lundgreni* Graptolite Biozone, at a similar horizon to the first sculptured trilete miospores. Thus the evidence from the hilate cryptospores also suggests that the late Wenlock was a time of major importance in the diversification of early land-plants.

Only one species of 'permanent' cryptospore tetrad (*Tetrahedraletes medinensis*) was recovered from the type Wenlock area. It ranges throughout the sequence and represents the youngest published record of the group (Gray 1985). They are also present in strata from the Rumney Inlier of South Wales which ranges from late Wenlock through to the early Downtonian (= Pridoli) (Burgess 1987), and J. B. R. (unpublished) has recorded them in studies of the Downtonian and Dittonian of the Welsh Borderland. However, higher in the sequence they are erratic in their distribution, usually rare, and therefore may be reworked. The type(s) of plants producing these enigmatic palynomorphs are unknown although Gray (1985) has suggested that they may have been similar to some extant hepatics. The nature of the record of 'permanent' cryptospore tetrads in this study indicates that their parent plants were still extant in the Wenlock although their diversity had greatly declined when compared with early Llandovery assemblages (Burgess 1991).

Smooth-walled and internally thickened tubes (Burgess and Edwards in press), which may represent the remains of nematophytalean land plants have also been recovered throughout the sequence in the type Wenlock area. In addition, unornamented cuticles (*sensu* Edwards 1982), believed to form part of the nematophytalean land-plant *Nematothallus* Lang, also occur throughout the succession. The Wenlock records suggest to us that nematophytalean plants and possible nematophytalean, tube-bearing plants were widespread at this time but the nature of any contained spores remains unknown.

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