TERRESTRIAL PLANT MICROFOSSILS FROM SILURIAN INLIERS OF THE MIDLAND VALLEY OF SCOTLAND

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ABSTRACT. Palynomorph assemblages comprising sporomorphs (cryptospores and miospores) and plant fragments (cuticle-like sheets and tubular structures) were recovered from red-bed sequences in the Lesmahagow, Hagshaw Hills and North Esk inliers from the Midland Valley of Scotland. The assemblages all indicate an early Wenlock age and probably belong to the *chulus-nanus* Spore Assemblage Biozone. The cryptospore taxa *Cheilotetras caledonica* gen. et sp. nov. and *Pseudodyadospora petasus* sp. nov. are proposed, and *Tetrahedraletes* is emended. The palynomorph and plant microfossil assemblages consist of entirely land-derived forms except in the North Esk inlier where rare acanthomorph acritarchs were recovered from a single horizon. Palynology thus provides additional evidence that the deposits in the Lesmahagow and Hagshaw Hills inliers accumulated in a non-marine environment, whereas a brief marine incursion interrupted terrestrial fluviatile deposition in the North Esk inlier. This report describes rare examples of Silurian palynomorph assemblages of entirely land-derived forms.

THE red-bed sequences in the Silurian inliers situated along the southern margin of the Midland Valley of Scotland have hitherto been poorly age constrained. This was unfortunate as they contain important faunas associated with fish beds and herald the onset of 'Old Red Sandstone facies' sedimentation in this part of Scotland (Walton and Oliver 1991). The recovery of palynomorph assemblages from these deposits provided an ideal opportunity to initiate a biostratigraphical investigation. The assemblages were recovered from horizons in the purported continental sequences of several of the inliers and are all similar, essentially comprising an identical suite of taxa, except for the presence of rare acanthomorph acritarchs in a single preparation. The assemblages contain cryptospores, miospores, the enigmatic palynomorph '*Moyeria*', and phytoclasts such as cuticle-like sheets and tubular structures.

Recently the distribution of miospores and cryptospores has been described in sequences from the Llandovery and Wenlock type areas (Burgess 1991; Burgess and Richardson 1991). This work complements the miospore zonation scheme for the Silurian which was established by Richardson and McGregor (1986) and expanded by Richardson (*in* Richardson and Edwards 1989). Hence there now exists a working sporomorph zonation scheme for the Silurian with which the Midland Valley assemblages can be correlated. The sporomorph assemblages are systematically described, compared with similar, previously described assemblages, and correlated with sporomorph zonation schemes. Additionally, the plant microfossil assemblages occur in a sequence of strata which has been interpreted as non-marine, and palynofacies analysis provides useful supplementary evidence compatible with the previously published sedimentological and palaeontological data.

Plant macrofossils are rare in strata of this age and consequently the form and evolution of early terrestrial vegetation is not well understood (Edwards and Fanning 1985; Gray 1985; Edwards and Burgess 1990). The sporomorphs and phytoclasts provide an insight into the abundance, distribution and, to a certain extent, morphology of the land plants from which some of the microfossils may have derived. Additionally, certain palynomorphs which occur in the assemblages may have belonged to organisms inhabiting continental water bodies and hence contribute information concerning life in these environments.

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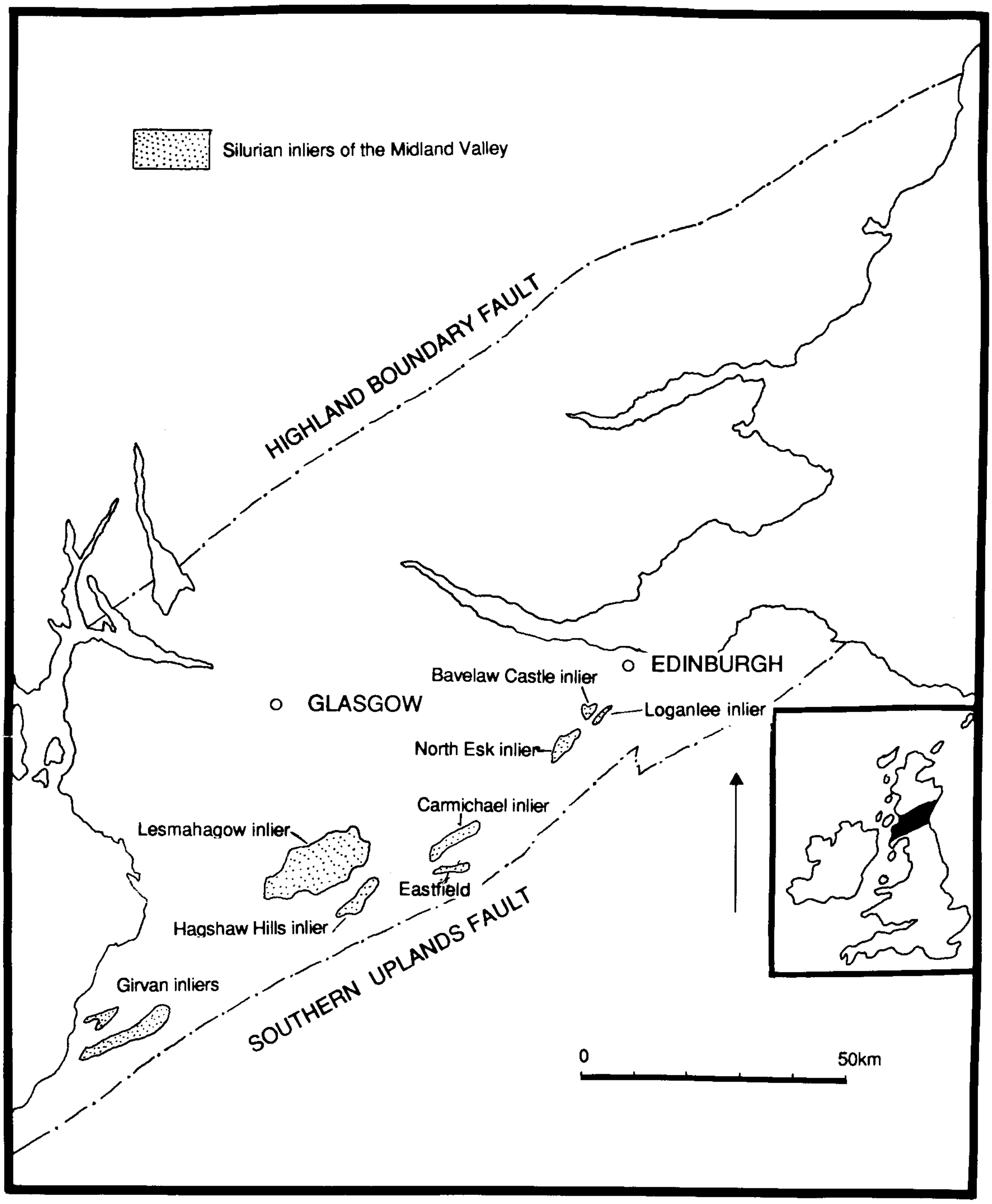
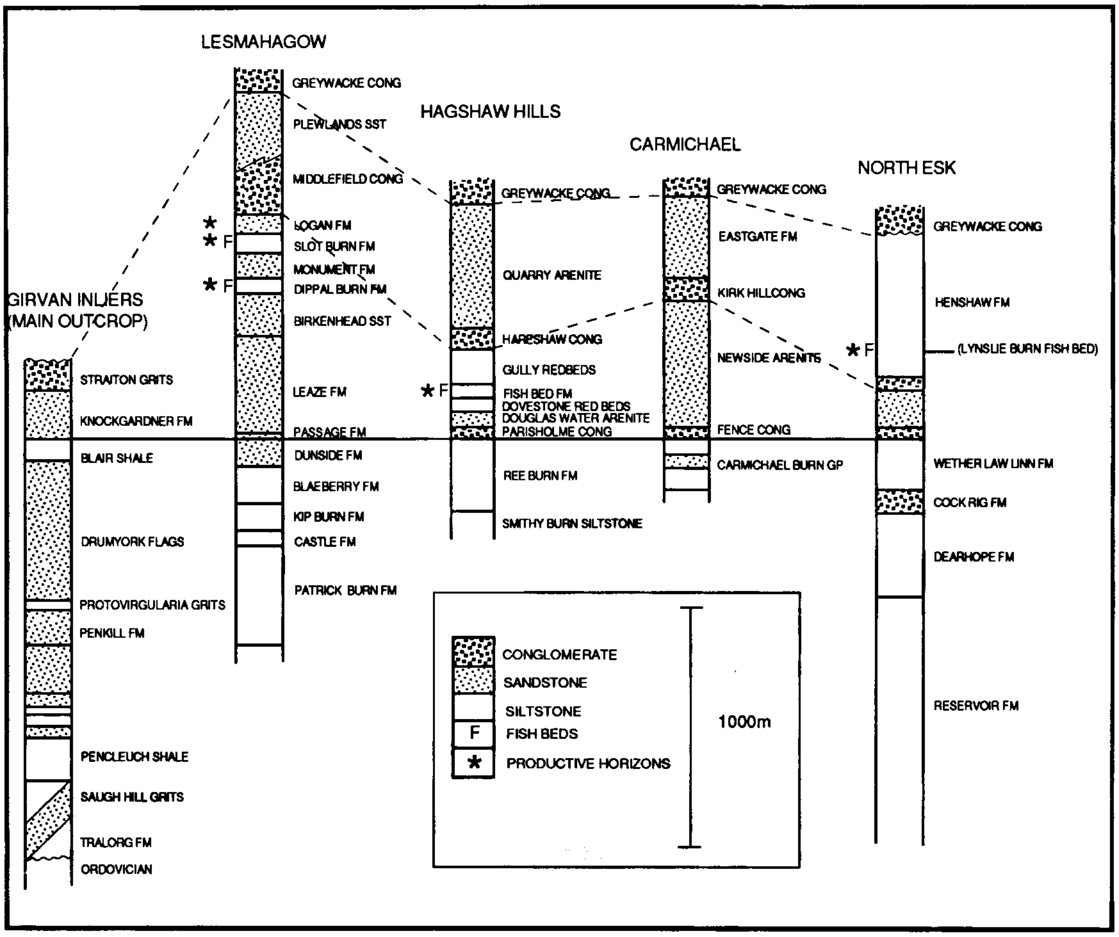


TEXT-FIG. 1. Location map of the Silurian inliers of the Midland Valley of Scotland (after Walton and Oliver 1991).

GEOLOGICAL SETTING

A series of Silurian inliers occurs along the southern margin of the Midland Valley of Scotland (Text-fig. 1). These inliers show marine Llandovery and Lower Wenlock successions which pass up into non-marine sediments that are poorly age constrained, despite the presence of the faunas recovered from the fish beds (Rolfe 1973*a*, 1973*b*; Walton and Oliver 1991) (Text-fig. 2). Graptolites and shelly faunas have been used to date the marine successions (Lamont 1947; Rolfe 1961, 1973*a*, 1973*b*; Rolfe and Fritz 1966; Cocks and Toghill 1973; Bull 1987). The deposits are believed to have accumulated in an elongate basin with landmasses situated to the north and south. The tectonic scenario is contentious, but is clearly intimately related to the complex tectonic events associated with the southern margin of the Laurasian continent which was destructive throughout the Silurian (Bluck 1985; McKerrow 1988*a*, 1988*b*). Leggett (1980) suggested that the basin was an upper slope basin with a landmass to the north and an emergent accretionary prism, represented by the Southern Uplands, to the south. The descending oceanic plate would have been situated to the south beyond the accretionary prism. Alternatively, Bluck (1983) envisaged an interarc basin separated from the accretionary prism by an arc. This model requires that the accretionary prism was at some point thrust northwards into its



TEXT-FIG. 2. Stratigraphical successions with positions of productive samples in the Silurian inliers of the Midland Valley (after Walton 1991): stratigraphical nomenclature after Cocks and Toghill (1973) for the Girvan inliers, Jennings (1961) summarized in Walton and Oliver (1991) for the Lesmahagow inlier, Rolfe (1961) for the Hagshaw Hills inlier, Rolfe (1960) for the Carmichael inlier and Robertson (1989) for the North Esk inlier.

current position where it conceals the arc and fore-arc basin deposits. More recently, it has been suggested that large-scale strike-slip fault movement along the Southern Uplands Fault and Highland Boundary Fault may have been important (McKerrow 1988*a*, 1988*b*; Pickering *et al.* 1988; McKerrow *et al.* 1991).

At Girvan, deposits of Rhuddanian age (*cyphus* Biozone) rest with angular unconformity on Ordovician rocks, and over 1800 m of marine Llandovery strata is developed (Cocks and Toghill 1973). Towards the top of the sequence there is a regression and deep water turbiditic sediments of latest Llandovery age (*crenulata* Biozone) are succeeded by shallow water marine deposits which have been dated using acritarchs as early Wenlock age (Dorning 1982). These beds give way to unfossiliferous strata of red-bed facies presumed to have accumulated in a terrestrial–fluviatile environment. In the other inliers the base of the successions is not seen and the oldest strata are marine and of latest Llandovery and early Wenlock age (Lamont 1947; Rolfe 1961, 1973*a*, 1973*b*; Robertson 1989). Towards the top of the marine strata a regression is developed (Walton and Oliver 1991), which is apparently contemporaneous with the one present in the Girvan area. The deep basinal sediments are succeeded by strata which are believed to have accumulated in a shallowing marine environment, and eventually deposits of red-bed facies are developed.

The red-bed sequences in the inliers comprise a combination of conglomerates, sandstones and siltstones with over 1500 m of red-beds developed in the Lesmahagow inlier. They exhibit sedimentological characteristics indicative of accumulation in terrestrial–fluviatile and lacustrine environments (McGiven 1968; Rolfe 1973*a*). The conglomerates are typical of alluvial fan deposits and many of the siltstones show desiccation cracks and other features characteristic of floodplain deposits. Also, possible channel deposits are developed in the Logan Formation of the Lesmahagow inlier. However, it has recently been suggested that the fish recovered from the fish-beds are marine forms brought in by marine incursions (Blieck and Janvier 1991).

The red-bed sequences are generally unfossiliferous, except for the faunas of the fish beds. The fish beds are present in the Dippal Burn Formation and Slot Burn Formation of the Lesmahagow inlier, the Fish Bed Formation of the Hagshaw Hills inlier and the Henshaw Formation of the North Esk inlier. The fish beds of the Lesmahagow and Hagshaw Hills inliers comprise finely laminated siltstones which occur in a sequence of massive, dark greenish-grey sandstones and siltstones. The paucity of desiccation cracks and the lateral and vertical uniformity suggests that the formations in which these fish beds are located accumulated in permanent bodies of water such as lakes or possibly lagoons. The fish beds have yielded the anaspids *Birkenia elegans*, *Lasanius problematicus* and *L. armatus*, the thelodonts *Logania* (*Thelodus*) *taiti*, *Lanarkia horrida* and *L. spinosa*, the cephalaspid *Ateleaspis tessellata*, eurypterids and rare plant fragments (Ritchie 1963, summarized in Rolfe 1973*a*). The fish beds are laminated and the fossils are usually articulated which suggests an absence of bioturbating organisms. This may indicate that the bottom waters were not oxygenated (Rolfe 1973*a*). However, the fish bed in the North Esk inlier is different in that it comprises massive olive green siltstones and contains a fauna of disarticulated fragments. The fish *B. elegans*, *A. tesselata* and *Lasanius problematicus* are present, in addition to the crinoid *Pisocrinus campana*. This horizon has been interpreted as being due to a minor marine incursion (Robertson 1989).

The fauna of the fish beds is probably strongly facies controlled and therefore of little value biostratigraphically. However, Heintz (1939) tentatively suggested that the fish faunas were of mid to late Ludlow age after comparing them with other faunas, particularly the Oesal fish fauna of the Baltic. Later, Westoll re-evaluated the evidence and suggested that a 'late Wenlock or early to middle Ludlow age would seem reasonable' (Westoll 1951, p. 6).

Other indices which are of value in correlation between the inliers are the distinctive alluvial fan conglomerates. There are three major conglomerates which can be traced between the inliers; these are named the Igneous Conglomerate, the Quartzite Conglomerate and the Greywacke Conglomerate (Text-fig. 2). Each conglomerate is characterized by a distinct clast lithology. The variation in composition probably reflects differences in the lithology of the source area. It is possible that the conglomerates are strongly diachronous but they still provide useful reference points.

In the Pentland Hills the red-bed sequence of the Silurian inliers is overlain with angular unconformity by the Greywacke Conglomerate which is taken as the local base of the Devonian. However, at Lesmahagow the Greywacke Conglomerate succeeds the Silurian red-beds without apparent discordance, although there is almost certainly disconformity. The 'Lower Old Red Sandstone' deposits which overlie the Greywacke Conglomerate have yielded the Early Devonian fish *Cephalaspis* (Mykura 1991).

PREVIOUS PALYNOLOGICAL INVESTIGATIONS

Little has been published concerning the palynology of the Silurian inliers of the Midland Valley. Richardson (1967) reported on assemblages from the Lesmahagow inlier which contained poorly preserved simple, smooth, azonate spores and apiculate bodies which lacked triradiate marks. Later, Jancis Ford investigated the Silurian inliers in more detail in her unpublished Ph.D. studies (Ford 1971). Richardson (*in* Aldridge *et al.* 1979) summarized Ford's findings noting that she had recorded sculptured miospores belonging to *Apiculiretusispora* and *Emphanisporites* from seemingly anomalous levels in the Hagshaw Hills and Lesmahagow inliers. After re-examining Ford's slides and verifying the presence of such spores, Ford's localities were recollected. Assemblages with only smooth-walled trilete spores, similar to those recovered from above and below her sample horizon, were recorded. The only other relevant publication from Girvan (Dorning 1982) described acritarchs and suggested an early Wenlock age for the Knockgardner Formation. He noted the presence of trilete spores referable to *Ambitisporites*. Samples from the Knockgardner Formation were recollected but trilete spores were not found, although permanent tetrads referable to *Tetrahedraletes medinensis* (Strother and Traverse) emend. were present.

SAMPLING AND TECHNIQUES

Samples were collected from throughout the red-bed sequences of the Silurian inliers. Productive samples were confined to the Dippal Burn, Slot Burn and Logan Formations of the Lesmahagow inlier, the Fish Bed Formation of the Hagshaw Hills inlier and the Lynslie Burn fish bed in the Henshaw Formation of the North Esk inlier. Recovery was variable from within these formations, but some well-preserved assemblages were obtained. Thermal maturation was fairly high (Thermal Alteration Index scale 3–4) and the spores are dark brown. Sample details are given in Appendix 1. The stratigraphical terminology utilized throughout this paper is from Robertson (1989) for the North Esk inlier, Rolfe (1961) for the Hagshaw Hills inlier and Jennings (1961), summarized in Walton and Oliver (1991), for the Lesmahagow inlier.

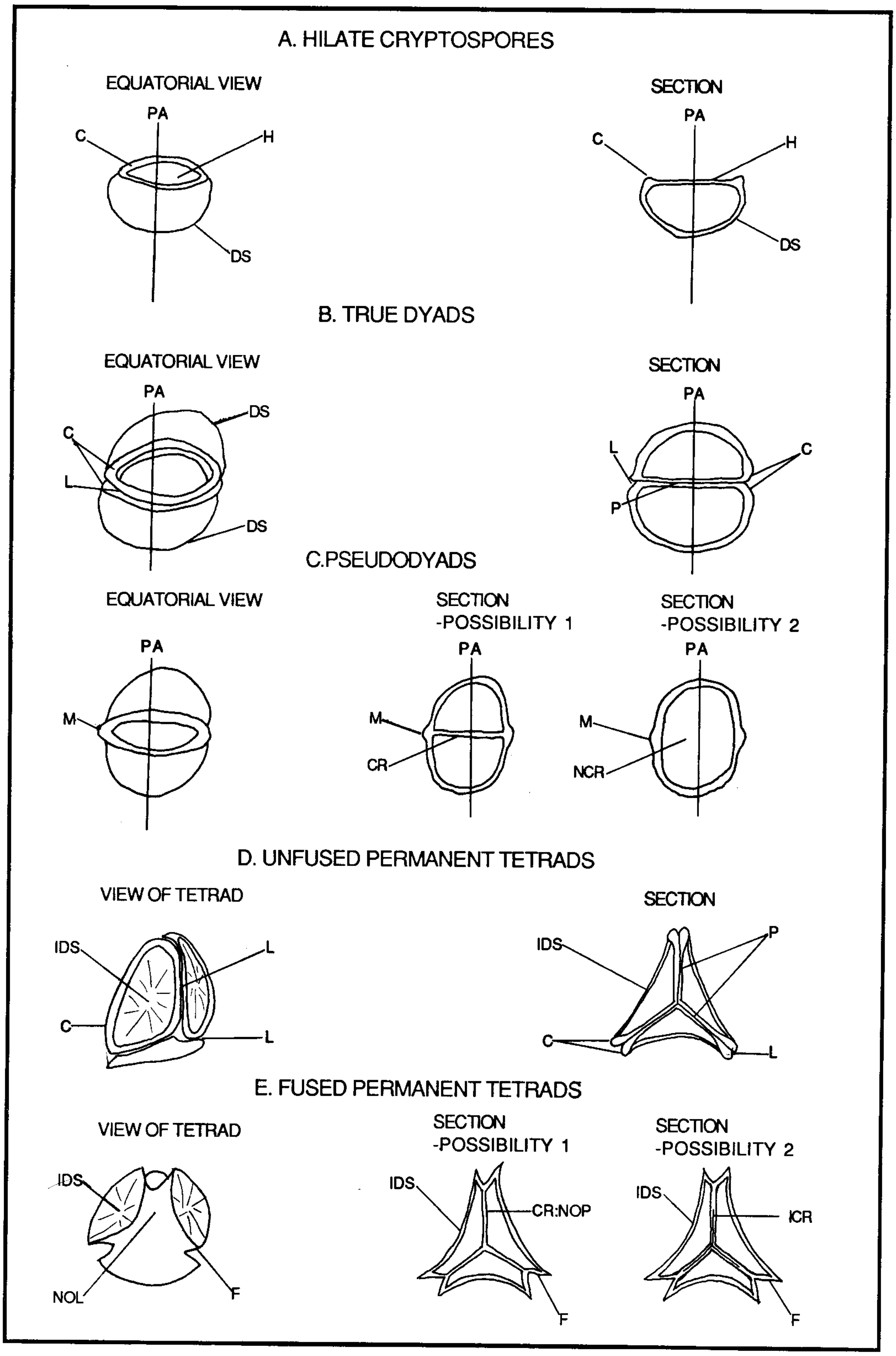
Samples were prepared for palynological investigation using standard HCl–HF–HCl acid maceration techniques followed by zinc bromide heavy mineral separation. The organic residue was sieved through a 10 μm mesh. The residue was strew-mounted using 'Elvacite' mounting medium. Some samples were oxidized for between 10 and 60 minutes in concentrated nitric acid in order to clear them for light microscope observation. Transmitted light investigation with the use of Nomarski interference contrast was carried out on a Zeiss Photomicroscope 111 (no. 2562). Additionally, stubs were strew-mounted and gold coated for scanning electron microscopy using an Hitachi 800 scanning electron microscope.

SYSTEMATIC PALAEONTOLOGY

Discussion. In the twenty years following the first report of permanent tetrads by Gray and Boucot (1971) there has been an increasing awareness of the presence in Lower Palaeozoic deposits of palynomorphs which possess characteristics of subaerially dispersed land plant spores, but are in many respects atypical (Strother and Traverse 1979; Vavrdova 1982, 1984, 1988, 1989; Miller and Eames 1982; Gray, Massa and Boucot 1982; Gray *et al.* 1985; Gray 1985, 1988; Johnson 1985; Gray, Theron and Boucot 1986; Richardson 1988; Burgess 1991; Burgess and Richardson 1991). These spore-like microfossils have been termed cryptospores and the anteturma Cryptosporites erected for their inclusion (Richardson *et al.* 1984; Richardson 1988; Richardson and Edwards 1989). There are several major categories of cryptospore which are morphologically distinct. They include fused permanent tetrads, unfused permanent tetrads, fused permanent dyads (pseudodyads), unfused permanent dyads (true dyads), alete monads and hilate cryptospores. The hilate cryptospores are, in the main, believed to be spores liberated from true dyads which have dissociated (Burgess and Richardson 1991). Most of these cryptospore categories have been reported enclosed within a loose or tight fitting membranous envelope (Gray and Boucot 1971; Strother and Traverse 1979; Miller and Eames 1982; Gray 1985; Johnson 1985; Richardson 1988; Burgess 1991).

The oldest reported cryptospores are permanent tetrads from the Llanvirn (Vavrdova 1984). Abundant and diverse cryptospore assemblages have been described from geographically widespread localities of Caradoc, Ashgill and early Llandovery strata (Strother and Traverse 1979; Gray, Massa and Boucot 1982; Miller and Eames 1982; Vavrdova 1982, 1984, 1988, 1989; Gray 1985, 1988; Gray *et al.* 1985; Johnson 1985; Gray, Theron and Boucot 1986; Richardson 1988; Burgess 1991). Trilete miospores first appear in the Llandovery (Aeronian) (Richardson 1988) and co-exist with cryptospores until at least the Late Devonian, although the upper limit of cryptospore occurrence is not well documented.

Terminology. Suprageneric classification has not yet been proposed for the cryptospores, so the anteturma Cryptosporites is informally subdivided into general sections relating to the morphotypes outlined above.



TEXT-FIG. 3. For legend see opposite.

Wherever possible the terminology of Grèbe (1991) is utilized in the description of both miospores and cryptospores. However, because the morphology of cryptospores differs from that of miospores, the method of orientation of these sporomorphs requires explanation and is illustrated in Text-figure 3. The only new terminology introduced relates to the junctions between spores in cryptospores which comprise more than one spore. Those cryptospores composed of discrete spores and attached across a clear plane of separation are referred to as *unfused* and are united across a *plane of attachment*. The crack or suture which marks the junction between the spores is termed a *line of attachment*. Cryptospores which comprise more than one spore where there is not perceptible line of attachment marking the junction between the spores are termed *fused*. The fused state suggests that the spores probably share a single common wall and lack a plane of attachment. However, it is difficult to ascertain the structure of such cryptospores without the aid of thin sections. Text-figure 3 illustrates the main groups of cryptospore and demonstrates some possible alternatives where the structure is contentious.

Repository of material. Figured specimens are stored in the Palynology Section, Palaeontology Department, British Museum (Natural History), London. Specimen location refers to standard England Finder co-ordinates from the Zeiss Photomicroscope 111 (no. 2562) housed in the same department. Scanning electron micrograph print numbers refer to proof prints stored in the Electron Microscopy Unit of the British Museum (Natural History).

Occurrence of sporomorph taxa. All of the taxa reported were recorded in samples from the Dippal Burn, Slot Burn and Logan Formations of the Lesmahagow inlier, the Fish Bed Formation of the Hagshaw Hills inlier, and the Henshaw Formation of the North Esk inlier, apart from *Dyadospora murusdensa*, *Rimosotetras problematica* and '*Moyeria*' *cabottii* which were not recorded from the Henshaw Formation (see Text-fig. 4). Regarding data concerning figured specimens, FBF = Fish Bed Formation of the Hagshaw Hills inlier, DBF = Dippal Burn, SBF = Slot Burn; LF = Logan Formations of the Lesmahagow inlier; HF = Henshaw Formation of the North Esk inlier.

Anteturma CRYPTOSPORITES (Richardson, Ford and Parker, 1984) Richardson, 1988

1. *Fused cryptospore tetrads.* This group comprises permanent tetrads in which the spores are fused together. There are no lines of attachment on the tetrad surface which mark the position of planes of attachment between the spores.

Genus CHEILOTETRAS gen. nov.

Type species. Cheilotetras caledonica gen. et sp. nov.

Derivation of name. Greek *cheilos*, lip; *tetras*, four.

Diagnosis. Laevigate permanent tetrahedral tetrads composed of subtriangular to subcircular spore-like units. The spores are fused together, there are no visible lines of attachment, and each spore possesses an invaginated distal wall.

Generic comparison. The genus *Tetrahedraletes* (Strother and Traverse) emend. comprises discrete spores with a clear plane of attachment between them.

Discussion. The genus *Cheilotetras* has been proposed for spore tetrads united across entirely fused junctions, with no visible lines of attachment. Such sporomorphs are distinguished from other

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TEXT-FIG. 3. Orientation and morphological nomenclature of cryptospores: PA, polar axis; C, crassitude; H, hilum; DS, distal surface; IDS, invaginated distal surface; L, line of attachment; NOL, no line of attachment; P, plane of attachment; NOP, no plane of attachment; M, medial arcuate thickening; CR, crosswall; ICR, incomplete plane of attachment developed in crosswall; F, 'flange'.

	HAGSHAW HILLS INLIER									LESMAHAGOW INLIER																			NORTH ESK INLIER			
	FISH BED FM									LOGAN FM										SLOT BURN FM			DIPPAL BURN FM					LYNSLIE BURN FISH BED			
SPOROMORPHS / SAMPLES	AH5	AH6	AH10	BH4	BH8	BH9	BH13	BH14	BH15	CL5	CL6	CL7	CL8	CL9	CL10	CL11	CL12	CL13	CL14	BL7	CL16	DL8	BL13	BL15	BL16	DL13	DL14	BP7	CP6	CP7	CP9
Ambitisporites avitus	X	X	X	1	3	1	X	X	X	1	1	2	3	2	X	X	X	X	X	4	X	2	3	X	X	3	2	-	X	X	X
Ambitisporites dilutus	X	X	X	9	9	13	X	X	X	11	5	7	10	8	X	X	X	X	X	13	X	6	8	X	X	16	15	X	X	X	X
Laevolancis divellomedium	X	X	X	9	5	7	X	X	X	3	3	1	4	3	X	X	X	X	X	19	X	5	4	X	X	14	12	X	X	X	X
Laevolancis plicata	-	X	X	3	1	2	X	X	X	2	1	P	1	3	X	X	X	X	X	16	X	8	5	X	X	13	9	X	X	X	X
Dyadospora murusattenuata	-	X	X	3	1	2	X	X	X	P	2	2	2	P	X	X	X	X	X	1	X	1	P	X	X	1	P	-	-	-	X
Dyadospora murusdensa	-	-	-	2	P	P	X	-	X	P	P	P	1	P	X	X	X	X	X	1	X	1	2	X	X	1	1	-	-	-	-
Pseudodyadospora petasus	-	X	X	3	1	2	-	X	X	4	6	8	3	2	X	X	X	X	X	1	X	6	1	X	X	3	4	X	-	X	X
Tetrahedraletes medinensis	X	X	X	9	6	9	X	X	X	16	20	23	20	22	X	X	X	X	X	14	X	24	9	X	X	13	19	X	X	X	X
Rimosotetras problematica	X	X	X	1	P	1	-	-	X	1	P	1	P	1	X	X	X	X	X	1	X	3	P	X	X	P	1	-	-	-	-
Cheilotetras caledonica	X	X	X	4	2	P	-	-	X	5	6	15	5	4	X	X	X	X	X	4	X	7	5	X	X	2	4	-	X	X	-
'Moyeria' cabottii	X	-	X	15	22	7	-	X	X	19	13	7	15	14	X	X	X	X	X	2	-	-	20	X	X	3	1	-	-	-	-
Alete cryptospore monads	X	X	X	35	47	51	X	X	X	38	43	35	36	41	X	X	X	X	X	24	X	37	43	X	X	31	32	X	X	X	X
Acanthomorph acritarchs	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-
PRESERVATION	P	P	P	G	G	G	P	P	P	G	G	G	G	G	G	G	G	G	G	G	G	G	G	P	P	G	G	P	P	P	P

TEXT-FIG. 4. Occurrence of sporomorphs and results of frequency counts: ×, present; –, not recorded. Values refer to percentages recorded from frequency counts of 200 palynomorphs where P = present but not featured in counts. Regarding preservation: P, poor; G, good.

cryptospore permanent tetrads which comprise discrete spores with a clearly perceptible plane of attachment between the spores. There is an analogous situation in dyads, e.g. the true dyad genus *Dyadospora* (Strother and Traverse) Burgess and Richardson, 1991, is distinguished from pseudodyads (*sensu* Johnson 1985) because the spores are separated by a clear plane of attachment. However, the internal structure of such fused tetrads and pseudodyads is difficult to elucidate. Either the spores of the tetrad/dyad shares a common wall, or are discrete, where the plane of attachment is incompletely developed or the line of attachment is masked, perhaps by a tightly adherent membranous envelope.

Cheilotetras caledonica gen. et sp. nov.

Plate 1, figs 1–7

Derivation of name. From the Latin '*Caledonia*', Scotland.

Holotype and type locality. FM 272, Pl. 1, figs 3, 6 (slide CL6/2, co-ord. 1120 109; E.F. no: K42/4), sample CL6, Logan Formation at Logan Water, Lesmahagow inlier.

Paratypes. Pl. 1, fig. 1, (stub CW36, Print P006225), sample CL7, LF. Pl. 1, fig. 2, (stub CW2, Print P004398), sample AH5, FBF. FM 273, Pl. 1, figs 4–5 (slide CL9/1, co-ord. 1319 107; E.F. no: K62/4), sample CL9, LF. FM 274, Pl. 1, fig. 7, (slide CL7/2, co-ord. 1333 062; E.F. no: F64/2), sample CL7, LF.

Diagnosis. A laevigate *Cheilotetras* where the exine of each spore is drawn out beyond the junction with adjacent spores into a distinct flange-like extension.

Description. Permanent tetrahedral tetrad composed of subcircular to subtriangular spore-like units. The individual spores have an invaginated distal surface. The crassitude of each spore is drawn out into a distinct rim 2–8 μm wide, which extends beyond the junction with the adjacent spores. The junction is entirely fused and no line of attachment is evident. The distal exine over the spores is laevigate, rigid and 1–2 μm in thickness.

Dimensions. 29(45)65 μm; 80 specimens measured.

Comparison and remarks. Tetrahedraletes medinensis (Strother and Traverse) emend. comprises discrete spores with distinct lines of attachment which mark the plane of attachment between adjacent spores. Additionally, the crassitudes associated with each spore in *Tetrahedraletes* is not extended into a 'flange'. *Rimosotetras problematica* Burgess, 1991 is composed of discrete spores which are loosely attached.

2. *Unfused cryptospore tetrads.* This group of permanent tetrads comprises discrete spores with planes of attachment between adjoining spores which form distinct cracks or sutures (lines of attachment) on the tetrad surface. The tetrads are not found dissociated and this suggests that they are dispersed intact, and remain permanently attached. Unfused tetrads have been reported naked and enclosed within laevigate or variously ornamented envelopes (Gray and Boucot 1971; Strother and Traverse 1979; Miller and Eames 1982; Gray 1985: Johnson 1985; Richardson 1988; Burgess 1991; Burgess and Richardson 1991).

Genus RIMOSOTETRAS Burgess, 1991

Type species. Rimosotetras problematica Burgess, 1991, p. 586, pl. 1, figs 12, 14–15.

Rimosotetras problematica Burgess, 1991

Plate 1, figs 8–10

?1979	'Spore tetrads, probably *Ambitisporites*', Holland and Smith, pl. 2, figs 5–6.
1985	'loose tetrads', Richardson *in* Hill *et al.*, pl. 15, figs 5–6.
?1987	'spore tetrad', Smelror, fig. 4*c*.

Figured specimens FM 275, Pl. 1, fig. 8 (slide CL7/2, co-ord. 1104 143; E.F. no: 040), sample CL7, DBF. FM 276, Pl. 1, fig. 9 (slide BH8/1, co-ord. 1222 099; E.F. no: K52/2), sample BH8, FBF. Pl. 1, fig. 10 (stub CW11, Print P004559), sample BL7, SBF.

Description. Permanent tetrads comprising subcircular to sub-triangular spore-like units. The individual spores usually have an inflated distal surface and are crassitate. The spores are discrete and a distinct line of attachment, in the form of a shallow cleft, is present at the junctions between adjacent spores. The tetrads are loosely attached but tend to remain bound together, although they are sometimes observed in a state of partial dissociation. The distal exine over the spores is laevigate, approximately 1 μm in thickness and frequently folded.

Dimensions. 32(48)70 μm; 27 specimens measured.

Comparisons. Tetrahedraletes medinensis (Strother and Traverse) emend. is always rigidly intact, and never in a state of partial dissociation, and comprises spores which are usually distally invaginated and have a more prominent equatorial crassitude. The spores of *Cheilotetras caledonica* gen. et sp. nov. are distally invaginated, fused to the adjacent spores of the tetrad and have flange-like extensions.

Genus TETRAHEDRALETES (Strother and Traverse, 1979) emend.

Type species. Tetrahedraletes medinensis Strother and Traverse, 1979, Tuscarora Formation, Pennsylvania, USA.

Emended diagnosis. Permanent tetrahedral tetrads composed of subtriangular to subcircular spore-like units. The spores are crassitate and have a laevigate invaginated distal wall. The spores are discrete and the plane of attachment between adjoining spores forms a distinct line of attachment at the junction between the crassitudes.

Generic comparison. Cheilotetras gen. nov. has been erected for permanent tetrads with fused spores and *Tetrahedraletes* is retained only for those with discrete, unfused spores.

Discussion. Strother and Traverse (1979) proposed two genera of permanent tetrad, *Nodospora* and *Tetrahedraletes*, which were differentiated chiefly on the criteria that *Tetrahedraletes* has a tetrahedral configuration and *Nodospora* a cross-tetrad arrangement. Following intensive study of permanent tetrads, several authors concluded that the type specimens of *Tetrahedraletes* (*T. medinensis*) and *Nodospora* (*N. burnhamensis*) were synonymous as they represented different compressional morphologies of otherwise identical tetrads (Gray *et al.* 1983; Duffield 1985; Burgess 1991; Gray 1991). To account for this Burgess (1991) emended the diagnosis of *Tetrahedraletes* to accommodate naked, laevigate permanent tetrads and *Nodospora* was suppressed. Furthermore, *Velatitetras* Burgess, 1991 was erected to accommodate permanent tetrads that are enclosed within an envelope. Several forms of permanent tetrad with envelopes have previously been described and placed in *Nodospora* (Strother and Traverse 1979; Miller and Eames 1982; Johnson 1985). However, Burgess's emendation of *Tetrahedraletes* differs from the original definition of Strother and Traverse in one important aspect. Burgess stipulated that *Tetrahedraletes* comprised spores which could be either fused or unfused. We consider that the type species of *Tetrahedraletes* and *Nodospora* are synonymous but have emended the diagnosis of Strother and Traverse because we consider that the nature of the junction between the spores, i.e. fused or unfused, is an important character.

Tetrahedraletes medinensis (Strother and Traverse, 1979) emend.

Plate 2, figs 8, 10–12

1971 'spore tetrads in tetrahedral configuration', Gray and Boucot, fig. 1*h*.
1971 tetrad of rather thick walled spore-like alete palynomorphs', Cramer, pl. 4, fig. 1.

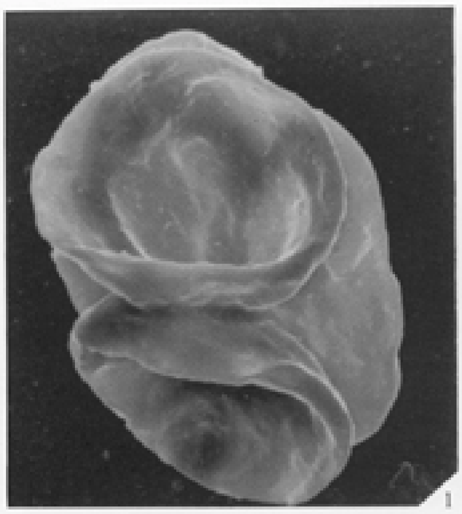
EXPLANATION OF PLATE 1

Figs 1–7. *Cheilotetras caledonica* gen. et sp. nov. 1, (stub CW36, Print P006225) sample CL7; Logan Formation; Logan Water, Lesmahagow inlier, × 1450. 2, (stub CW2, Print P004398) sample AH5; Fish Bed Formation; Glenbuck Loch, Hagshaw Hills inlier, × 1700. 3, 6, FM 272; holotype (slide CL6/2, co-ord. 1120 109; E.F. no. K42/4) sample CL6; Logan Formation; Logan Water, Lesmahagow inlier. 4–5, FM 273 (slide CL9/1, co-ord. 1319 107; E.F. no. K62/4) sample CL9; Logan Formation; Logan Water, Lesmahagow inlier. 7, FM 274 (slide CL7/2, co-ord. 1333 062; E.F. no. F64/2) sample CL7; Logan Formation; Logan Water, Lesmahagow inlier.

Figs 8–10. *Rimosotetras problematica* Burgess and Richardson, 1991. 8, FM 275 (slide CL7/2, co-ord. 1104 143; E.F. no. O40) sample BL13; Dippal Burn Formation; Dippal Burn, Lesmahagow inlier. 9, FM 276 (slide BH8/1, co-ord. 1222 099; E.F. no. K52/2) sample BH8; Fish Bed Formation; Glenbuck Loch, Hagshaw Hills inlier. 10, (stub CW11, Print P004559) sample BL7; Slot Burn Formation, Slot Burn, Lesmahagow inlier. × 1530.

All figures × 1000, except where otherwise stated.

PLATE 1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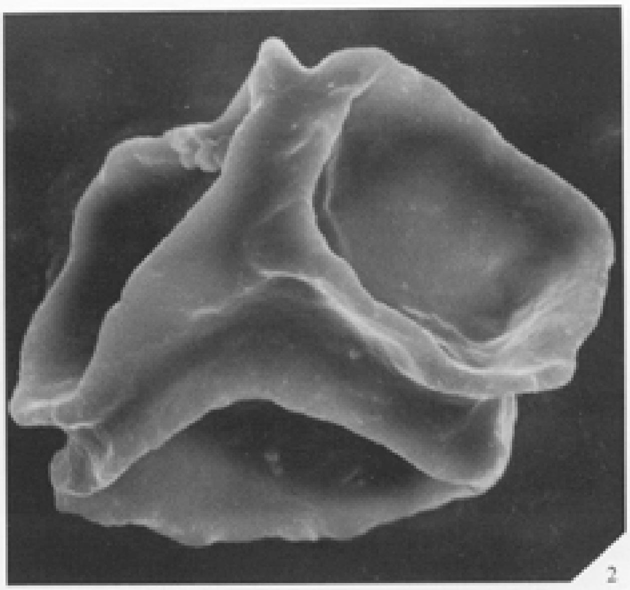
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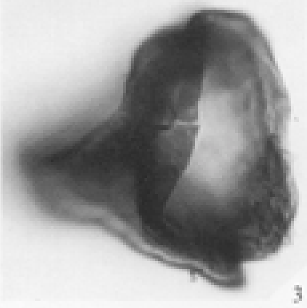
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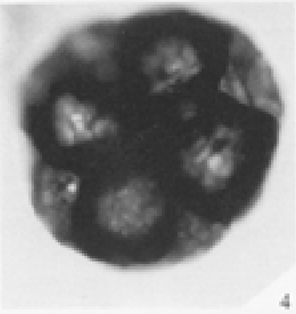
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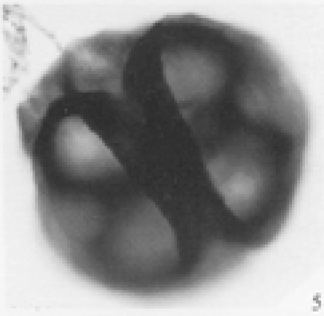
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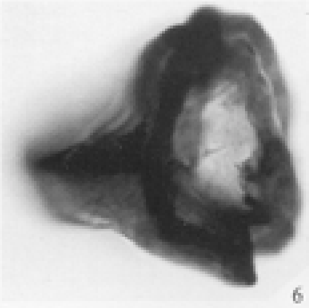
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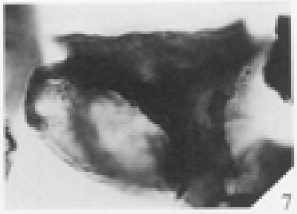
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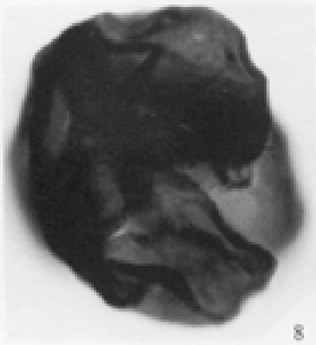
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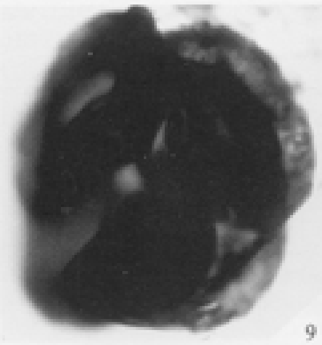
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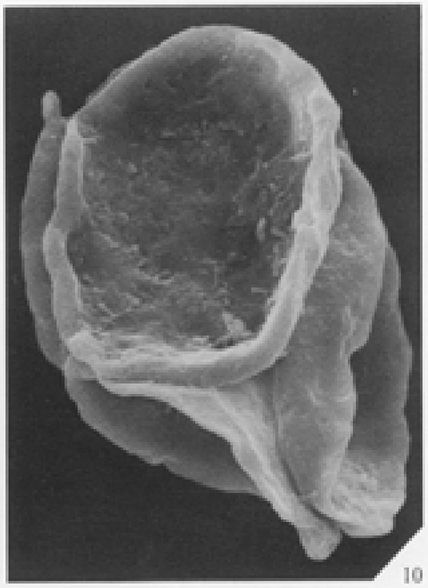
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WELLMAN and RICHARDSON, *Cheilotetras*, *Rimosotetras*

1972	'non-miospore tetradic palynomorph', Cramer and Diez del Cramer, p. 116, pl. 36, figs 79, 84.
1979	*Tetrahedraletes medinensis* Strother and Traverse, p. 8, pl. 1, figs 5, 14–17.
1979	*Nodospora burnhamensis* Strother and Traverse, p. 10, pl. 1, fig. 11; pl. 2, fig. 1.
1982	'tetrahedral tetrads', Gray *et al.*, figs 2A–B, 3, 4, 8, 9, 10A–B.
1982	*Tetrahedraletes medinensis* Strother and Traverse; Miller and Eames, p. 250, pl. 5, fig. 1; pl. 6, fig. 1.
1982	*Nodospora burnhamensis* Strother and Traverse; Miller and Eames, p. 248, pl. 5, fig. 5; pl. 6, fig. 3.
1985	*Tetrahedraletes* cf. *T. medinensis*, Gray *et al.*, fig. 5*f–h*.
1985	*Tetrahedraletes medinensis* Strother and Traverse; Johnson, p. 344, pl. 11, figs 1, 3.
1985	*Nodospora burnhamensis* Strother and Traverse; Johnson, p. 344, pl. 11, fig. 4.
1985	*cf. Tetrahedraletes medinensis* Strother and Traverse; Richardson *in* Hill *et al.*, pl. 15, fig. 1.
1985	'permanent tetrad', Richardson *in* Hill *et al.*, pl. 15, fig. 3.
1985	*Nodospora burnhamensis* Strother and Traverse; Duffield, fig. 1–6 (*non* fig. 8).
1986	*Tetrahedraletes* cf. *T. medinensis*, Gray *et al.*, fig. 6, items 1–7.
1987	*Tetrahedraletes medinensis* Strother and Traverse; Smelror, fig. 4J.
1989	*Tetrahedraletes medinensis* Strother and Traverse; Barron, fig. 6D.
1991	*Tetrahedraletes medinensis* var. *parvus* Burgess, p. 579, pl. 1, figs 1–4.
1991	*Tetrahedraletes medinensis* Strother and Traverse; Burgess and Richardson, p. 604, pl. 1, figs 12–13.

Holotype and type locality. As designated for *Tetrahedraletes medinensis* Strother and Traverse, 1979, Tuscarora Formation, Pennsylvania, USA.

Figured specimens. Pl. 2, fig. 8 (stub CW32, Print P007350), sample CL13, LF. FM 268, Pl. 2, fig. 10 (slide BL13/2, co-ord. 1280 159; E.F. no: Q59/1), sample BL13, DBF. FM 269, Pl. 2, fig. 11 (slide BL13/2, co-ord. 1069 060; E.F. no: F37/1), sample BL13, DBF. FM 270, Pl. 2, fig. 12 (slide BL7/4, co-ord 1153 100; E.F. no. K46/1) sample BL7, SBF.

Emended diagnosis. A *Tetrahedraletes* which is firmly bonded with prominent equatorial crassitudes on the individual spores and distinct lines of attachment at the junctions between adjacent spores. The distal walls of the spores are laevigate, rigid and invaginated.

Description. Permanent tetrahedral tetrads comprising subcircular to subtriangular spore-like units. Individual spores with a rounded crassitude, which is 1–4 μm wide, and an invaginated distal surface. The spores are discrete, and a plane of attachment is present between the junctions of adjacent spores forming distinct sutures (lines of attachment) on the surface of the tetrad between the crassitudes of adjacent spores. The tetrads are

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EXPLANATION OF PLATE 2

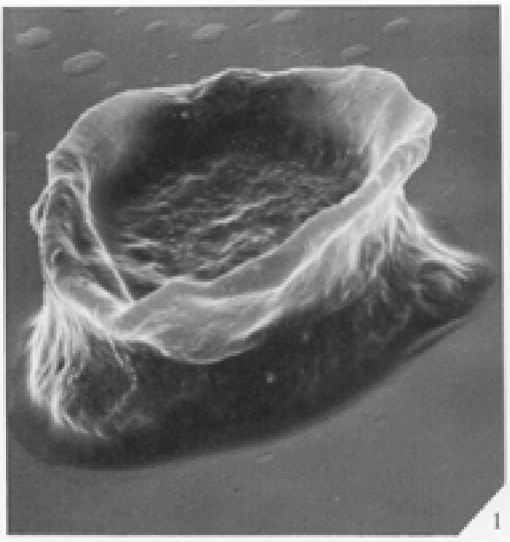
Figs 1–7. *Pseudodyadospora petasus* sp. nov. 1, 4, (stub CW17, Print P004937 and P004938) sample BH4; Fish Bed Formation; Glenbuck Loch, Hagshaw Hills inlier; 1, ×2170; 2, ×5000. 2–3, FM 266; holotype (slide CL6/2, co-ord. 1158 064; E.F. no. F46) sample CL6; Logan Formation; Logan Water, Lesmahagow inlier. 5, FM 267 (slide BL13/2, co-ord. 1293 062; E.F. no. F60/1) sample BL13; Dippal Burn Formation; Dippal Burn, Lesmahagow inlier. 6–7, FM 296 (slide CL7/2, co-ord. 1147 070; E.F. no. F45/3) sample CL7; Slot Burn Formation; Slot Burn, Lesmahagow inlier.

Figs 8, 10–12. *Tetrahedraletes medinensis* (Strother and Traverse) emend. 8, (stub CW32, Print P007350) sample CL13; Logan Formation; Logan Water, Lesmahagow inlier, ×2500. 10, FM 268 (slide BL13/2, co-ord. 1280 159; E.F. no. Q59/1) sample BL13; Dippal Burn Formation; Dippal Burn, Lesmahagow inlier. 11, FM 269 (slide BL13/2, co-ord. 1069 060; E.F. no. F37/1) sample BL13; Dippal Burn Formation; Dippal Burn, Lesmahagow inlier. 12, FM 270 (slide BL7/4, co-ord. 1153 100; E.F. no. K46/1) sample BL7; Slot Burn Formation; Slot Burn, Lesmahagow inlier.

Fig. 9. '*Moyeria*' *cabottii* (Cramer) Miller and Eames, 1982. FM 271 (slide CL5/2, co-ord. 1155 182; E.F. no. S46) sample CL5; Logan Formation; Logan Water, Lesmahagow inlier.

All figures ×1000, except where otherwise stated.

PLATE 2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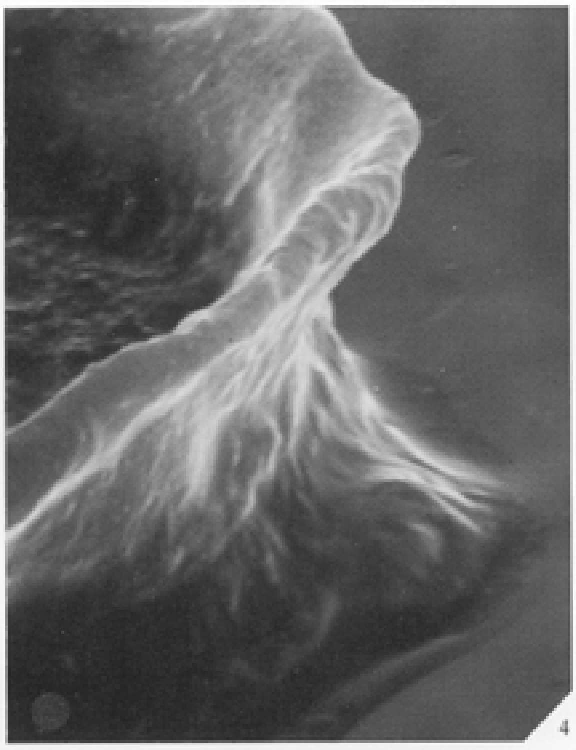
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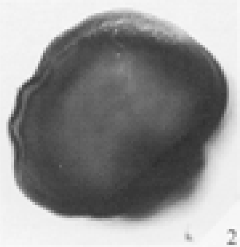
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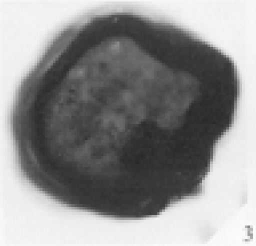
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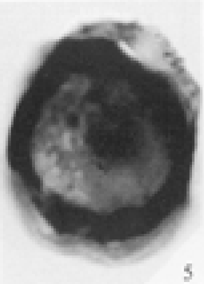
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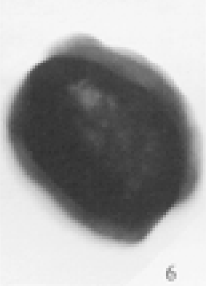
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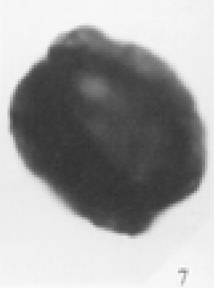
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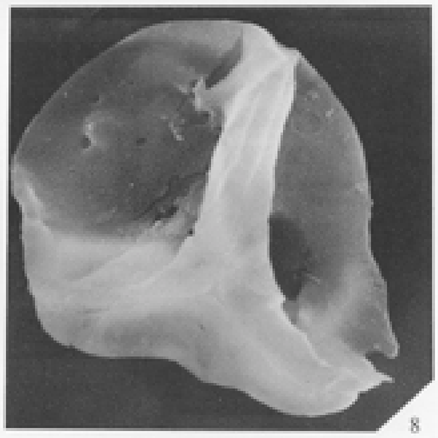
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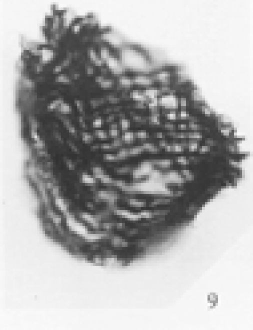
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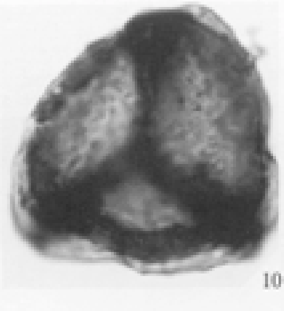
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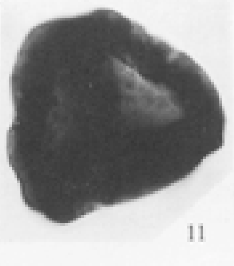
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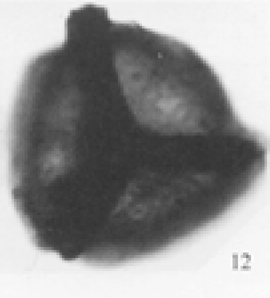
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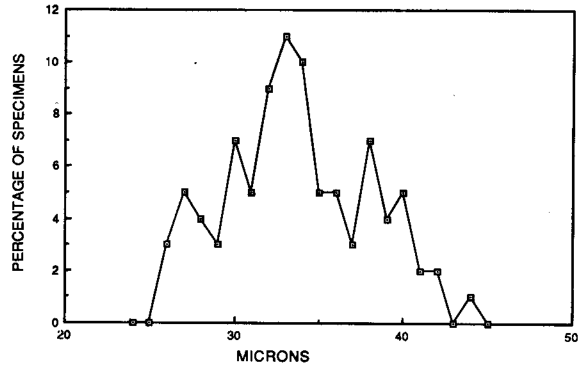
WELLMAN and RICHARDSON, *Pseudodyadospora, Tetrahedraletes*, '*Moyeria*'



TEXT-FIG. 5. Size frequency distribution of 100 *Tetrahedraletes medinensis* (Strother and Traverse) emend. from sample CL7, Logan Formation, Logan Water, Lesmahagow inlier.

securely bonded and none was observed in a state of dissociation. The distal exine is laevigate and 1–2 μm in thickness.

Dimensions. 24(34)50 μm; 100 specimens measured (Text-fig. 5).

Comparison. Cheilotetras caledonica gen. et sp. nov. comprises fused spores with their distal exines with flange-like extensions. The spores of *Rimosotetras problematica* Burgess, 1991 are loosely attached and usually comprises distally inflated spores.

3. *Fused cryptospore dyads* (*pseudodyads*). Permanent dyads of this type were first recognized by Johnson (1985) from strata of Llandovery age from Pennsylvania and are almost certainly equivalent to the 'diacrodoid acritarchs' described by Strother and Traverse (1979) (Gensel *et al.* 1991). Pseudodyads comprise two permanently fused spores joined by an encircling thickened band which may, or may not, be attached to a single crosswall (Text-fig. 3c). If a crosswall is present there is no noticeable plane of attachment between the spores of the pseudodyad and no line of attachment is seen on the exterior of the sporomorphs. Pseudodyads occur naked or enclosed within an envelope (Johnson 1985; Richardson 1988; Burgess 1991).

Genus PSEUDODYADOSPORA Johnson, 1985

Type species. Pseudodyadospora laevigata Johnson, 1985

Pseudodyadospora petasus sp. nov.

Plate 2, figs 1–7

Derivation of name. From the Latin '*petasus*', meaning hat, referring to the shape of each unit.

Holotype and type locality. FM 266, Pl. 2, figs 2–3 (slide CL6/2, co-ord. 1158 064; E.F. no: F46), sample CL6, Logan Formation at Logan Water, Lesmahagow inlier.

Paratypes. Pl. 2, figs 1, 4 (stub CW17, Print P004937 and P004938), sample BH4, FBF. FM 267, Pl. 2, fig. 5 (slide BL13/2, co-ord. 1293 062; E.F. no: F60/1), sample BL13, DBF. FM 296, Pl. 2, figs 6–7 (slide CL7/2, co-ord. 1147 070; E.F. no: F45/3), sample CL7, SBF.

Diagnosis. A *Pseudodyadospora* with an equatorial constriction at the place of attachment. Exine laevigate. Spores have a distinctly invaginated distal wall, and a shorter polar axis than equatorial axis.

Description. Pseudodyads circular in polar view and distally invaginated. In equatorial view the sporomorph has the profile of two shallow bowls attached by their undersides. The junction between the two spores is entirely fused and no line of attachment is present on the pseudodyad surface. The pseudodyads are generally isomorphic and usually preserved in polar compression. The exine is laevigate, 1–2 μm in thickness, and is rigid or occasionally folded.

Dimensions. 26(32)44 μm; 55 specimens measured.

Comparison. Pseudodyadospora laevigata Johnson, 1985 is distally inflated rather than invaginated and the spores are generally not joined across a marked constriction.

Comments. Pseudodyadospora petasus sp. nov. has a shape which distinguishes it from all other species of pseudodyad that have been described. In many respects the morphology is reminiscent of the cryptospore permanent tetrad *Cheilotetras caledonica* gen. et sp. nov. and it may be that the two are in some way related. However, like *Cheilotetras caledonica*, the internal structure of *Pseudodyadospora petasus* is unclear. It seems likely that the spores share a common crosswall, but the possibility exists that it comprises discrete spores where the plane of attachment is incompletely developed or the line of attachment is masked. Sporomorphs that can be assigned to *P. petasus* have been reported over a wide stratigraphical range including records from the Stonehaven Group at Stonehaven, Scotland which is of late Wenlock age (Wellman 1991) and the Downton and Ditton Groups of southern Britain, of Přídolí and Gedinnian age respectively (Richardson unpublished data).

4. *Unfused cryptospore dyads* (*true dyads*). These dyads comprise two distinct spores with a clear plane of attachment between them forming a line of attachment on the surface of the dyad. The dyads exhibit different degrees of dissociation across the contact area between the spores. Separated spores appear to be identical to hilate cryptospores, which generally co-occur with the dyads, and it is likely that the dyads are the source of most, if not all, of these sporomorphs (Burgess and Richardson 1991). True dyads are usually naked but there are reports of some enclosed in envelopes (Johnson 1985; Richardson 1988; Wellman 1991).

Genus DYADOSPORA (Strother and Traverse, 1979) Burgess and Richardson, 1991

Type species. Dyadospora murusattenuata (Strother and Traverse) Burgess and Richardson, 1991.

Dyadospora murusattenuata (Strother and Traverse) Burgess and Richardson, 1991

Plate 3, figs 9, 12

1979	*Dyadospora murusattenuata* Strother and Traverse, p. 15, pl. 3, figs 9–10.
1982	*Dyadospora murusattenuata* Strother and Traverse; Miller and Eames, p. 247, pl. 6, fig. 8.
1985	*Dyadospora murusattenuata* Strother and Traverse; Johnson, p. 334.
1991	*Dyadospora* cf. *murusattenuata* Strother and Traverse; Burgess, p. 592, pl. 2, fig. 10.
1991	*Dyadospora murusattenuata* (Strother and Traverse) Burgess and Richardson, p. 614, pl. 2, figs 7, 9.

Figured specimens. FM 262, Pl. 3, fig. 9 (slide DL13/2, co-ord. 1227 224; E.F. no: W53/4), sample DL13, DBF. FM 263, Pl. 3, fig. 12 (slide DL13/2, co-ord. 1274 133; E.F. no: N58), sample DL13, DBF.

Description. The dyads are circular to sub-circular in polar and equatorial view and generally isomorphic. They consist of two distally inflated spores which are normally slightly shorter than they are wide in equatorial view. Dyads usually preserved in oblique compression. The spores are joined at contact areas which are surrounded by an equatorial crassitude. There is a distinct plane of attachment between the spores identified by a line of attachment between the two crassitudes. The two spores are often partly separated. Distal exine laevigate, 1 μm or less in thickness, and almost invariably folded.

Dimensions. Total dyad length 30(37)48 μm, equatorial width 27(32)40 μm; 40 specimens measured.

Comparisons. Dyadospora murusdensa (Strother and Traverse) Burgess and Richardson, 1991 comprises spores with a thicker, more rigid exine which is not normally folded.

Comments. This true dyad species is believed to comprise two hilate cryptospores of the species *Laevolancis plicata* Burgess and Richardson, 1991. It is possible that many, if not all, of the specimens of *L. plicata* which co-occur with *D. murusattenuata* in the assemblages are derived from dissociation of such dyads. Because specimens of *L. plicata* are more abundant than *D. murusattenuata* in most preparations (Text-fig. 4), it seems likely that these sporomorphs are habitually dispersed in the dissociated form.

Dyadospora murusdensa (Strother and Traverse, 1979) Burgess and Richardson, 1991

Plate 3, figs 10, 13

1979	*Dyadospora murusdensa* Strother and Traverse, p. 15, pl. 3, figs 6–7
1982	*Dyadospora murusdensa* Strother and Traverse; Miller and Eames, p. 247, pl. 6, fig. 7.
1985	*Dyadospora murusdensa* Strother and Traverse; Johnson, p. 334, pl. 7, fig. 9.
1985	*Dyadospora murusdensa* Strother and Traverse; Richardson *in* Hill *et al.*, pl. 15, figs 8–9.
1988	*Dyadospora murusdensa* Strother and Traverse; Richardson, p. 94, pl. 16, fig. 2.
1989	*Dyadospora murusdensa* Strother and Traverse; Barron, p. 84, fig. 6F.

Figured specimens. FM 264, Pl. 3, fig. 10 (slide DL14/2, co-ord. 1161 156; E.F. no. P46/4), sample DL14, DBF. FM 265, Pl. 3, fig. 13 (slide DL13/2, co-ord. 1350 203; E.F. no. U66/3), sample DL13, DBF.

EXPLANATION OF PLATE 3

Figs 1–3. *Ambitisporites avitus* Hoffmeister, 1959. 1, (stub CW17, Print P004939) sample BH4; Fish Bed Formation; Glenbuck Loch, Hagshaw Hills inlier, × 2000. 2, FM 256 (slide BL7/4, co-ord. 1295 139; E.F. no. 060/1/2) sample BL7; Slot Burn Formation; Slot Burn, Lesmahagow inlier. 3, FM 257 (slide BL13/2, co-ord. 1093 189; E.F. no. T39/2) sample BL13; Dippal Burn Formation; Dippal Burn, Lesmahagow inlier.

Figs 4–6. *Ambitisporites dilutus* (Hoffmeister) Richardson and Lister, 1969. 4, FM 258 (slide CL9/4, co-ord. 1275 071; E.F. no. G58/1) sample CL9; Logan Formation; Logan Water, Lesmahagow inlier. 5, FM 259 (slide BL13/2, co-ord. 1095 190; E.F. no. T40/1) sample BL13; Dippal Burn Formation; Dippal Burn, Lesmahagow inlier. 6, (stub CW11, Print P005069) sample BL7; Slot Burn Formation; Slot Burn, Lesmahagow inlier, × 2000.

Fig. 7. *Laevolancis plicata* Burgess and Richardson, 1991. FM 260 (slide BL7/5, co-ord. 1119 123; E.F. no. M42) sample BL7; Slot Burn Formation; Slot Burn, Lesmahagow inlier.

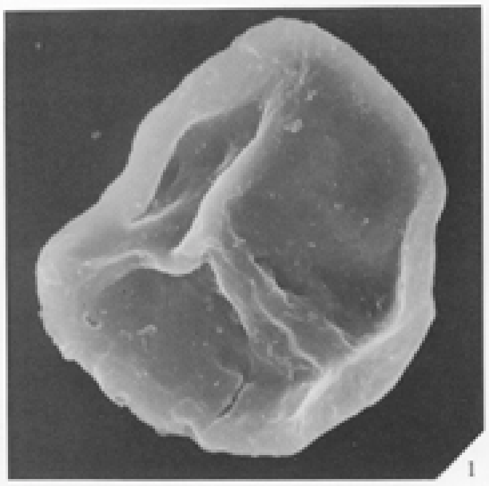
Figs 8, 11. *Laevolancis* (*Archaeozonotriletes*) *divellomedium* (Chibrikova) Burgess and Richardson, 1991. 8, FM 261 (slide DL14/2, co-ord. 1095 206; E.F. no. U39/4) sample DL14; Dippal Burn Formation; Dippal Burn, Lesmahagow inlier. 11, (stub CW26, Print P005115) sample BH9; Fish Bed Formation; Glenbuck Loch, Hagshaw Hills inlier, × 2000.

Figs 9, 12. *Dyadospora murusattenuata* (Strother and Traverse) Burgess and Richardson, 1991. 9, FM 262 (slide DL13/2, co-ord. 1227 224; E.F. no. W53/4) sample DL13; Dippal Burn Formation; Dippal Burn, Lesmahagow inlier. 12, FM 263 (slide DL13/2, co-ord. 1274 133; E.F. no. N58) sample DL13; Dippal Burn Formation; Dippal Burn, Lesmahagow inlier.

Figs 10, 13. *Dyadospora murusdensa* (Strother and Traverse) Burgess and Richardson, 1991. 10, FM 264 (slide DL14/2, co-ord. 1161 156; E.F. no. P46/4) sample DL14; Dippal Burn Formation; Dippal Burn, Lesmahagow inlier. 13, FM 265 (slide DL13/2, co-ord. 1350 203; E.F. no. U66/3) sample DL13; Dippal Burn Formation; Dippal Burn, Lesmahagow inlier.

All figures × 1000, except where otherwise stated.

PLATE 3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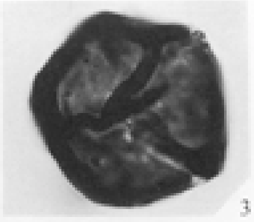
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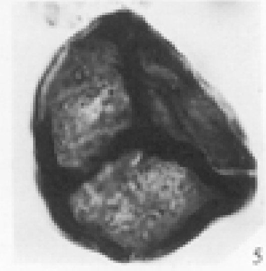
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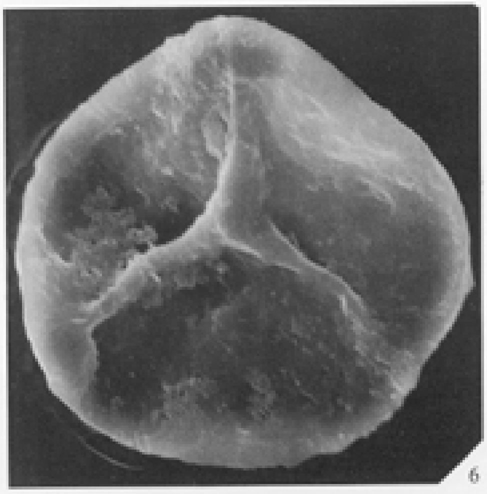
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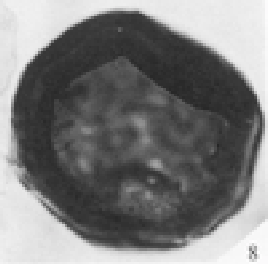
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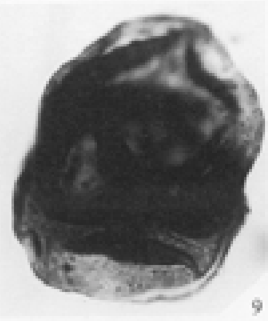
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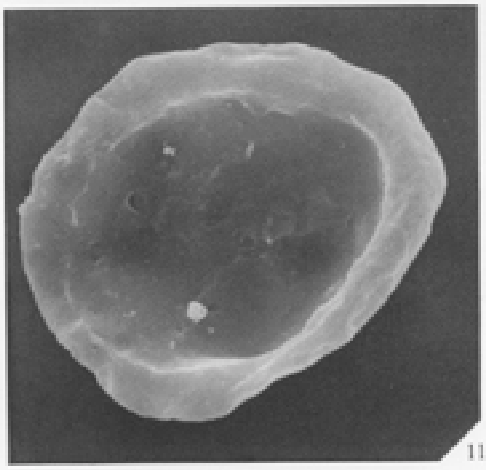
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WELLMAN and RICHARDSON, *Ambitisporites*, *Laevolancis*, *Dyadospora*

Description. Dyads consist of two spores which are distally inflated and, in equatorial view, are usually slightly shorter than they are wide. Dyads usually preserved in oblique compression and are circular to subcircular in polar and equatorial view and generally isomorphic. The spores are joined at contact areas which are surrounded by a prominent equatorial crassitude, and a distinct plane of attachment forms of a line of attachment, usually in the form of a cleft, between the two crassitudes. Spores frequently partly separated. Exine distally laevigate, rigid, *c.* 2 μm in thickness, and usually without folds.

Dimensions. Total dyad length 30(39)56 μm, equatorial width 32(35)48 μm; 26 specimens measured.

Comparisons. The exine of *Dyadospora murusattenuata* (Strother and Traverse) Burgess and Richardson, 1991 is thinner, less rigid, and usually folded.

Comments. Burgess and Richardson (1991) suggested that *Dyadospora murusdensa* comprises two hilate cryptospores of the species *Laevolancis* (*Archaeozonotriletes*) *divellomedium* (Chibrikova) Burgess and Richardson, 1991. It is possible that many, if not all, of these hilate cryptospores are derived from dissociated specimens of *D. murusdensa.* As is the case with *L. plicata* and *D. murusattenuata*, *L. divellomedium* is more abundant than *D. murusdensa* in most preparations (Text-fig. 4), and it seems likely that these sporomorphs are habitually dispersed in the dissociated form.

5. *Hilate cryptospores.* These cryptospores consist of a solitary spore (monad) which possesses a roughly circular contact area (hilum) often defined by an equatorial, or subequatorial, crassitude or a change in ornament. The contact area is usually thinner than the distal exine. The exine, including the contact area, may be laevigate or variously ornamented. Closely similar monads have been observed partly united at the contact area as a loose dyad.

Genus LAEVOLANCIS Burgess and Richardson, 1991

Type species. Laevolancis (*Archaeozonotriletes*) *divellomedium* (Chibrikova) Burgess and Richardson, 1991, p. 607, pl. 2, figs 4, 6.

Laevolanics (*Archaeozonotriletes*) *divellomedium* (Chibrikova) Burgess and Richardson, 1991

Plate 3, figs 8, 11

1959 *Archaeozonotriletes divellomedium* Chibrikova, p. 65, pl. 9, fig. 4.
1966 *Hispanaediscus bernesgae* Cramer, p. 82, pl. 2, fig. 4.
1969 ?*Archaeozonotriletes* cf. *divellomedium* Chibrikova; Richardson and Lister, p. 238, pl. 43, fig. 12.
1973 ?*Archaeozonotriletes* cf. *divellomedium* Chibrikova; Richardson and Ioannides, p. 280, pl. 8, figs 10–11.
1979 *Archaeozonotriletes* cf. *chulus nanus* Richardson and Lister; Holland and Smith, pl. 2, figs 7–9.
1979 'smooth-walled inaperturate spore', Strother and Traverse, p. 14, pl. 3, fig. 5.
1984 ?*Stenozonotriletes irregularis* Schultz; McGregor, p. 37, pl. 1, fig. 26.

Figured specimens. FM 261, Pl. 3, fig. 8 (slide DL14/2, co-ord. 1095 206; E.F. no. U39/4), sample DL14, DBF., Pl. 3, fig. 11 (stub CW26, Print P005115), sample BH9, FBF.

Description. Amb circular to subcircular in polar compression. Equatorial to subequatorial crassitude 1–2 μm wide delimits a circular to subcircular contact area (hilum). Exine laevigate over contact area, appears thinner than the distal exine, and is sometimes folded, ruptured or collapsed. Distal exine laevigate, rigid and usually unfolded, *c.* 2 μm in thickness.

Dimensions. 28(36)46 μm; 100 specimens measured.

Comparison and remarks. Laevolancis plicata Richardson and Burgess, 1991 has a thinner, less rigid wall and a less prominent crassitude. *L. divellomedium* is probably derived from thick-walled true dyads, similar, if not identical to, *Dyadspora murusdensa* (Strother and Traverse) Burgess and Richardson, 1991.

Laevolancis plicata Burgess and Richardson, 1991

Plate 3, fig. 7

1991 *Laevolancis plicata* Burgess and Richardson, p. 607, pl. 2, fig. 8.

Figured specimen. FM 260, Pl. 3, fig. 7 (slide BL7/5, co-ord. 1119 123; E.F. no. M42), sample BL7, SBF.

Description. Amb circular to subcircular. Equatorial to subequatorial crassitude *c.* 1 μm wide delimits a more or less circular contact area (hilum). Exine over contact area laevigate, thin, less than 1 μm in thickness, and often collapsed or absent. Distal exine laevigate, thin, *c.* 1 μm in thickness, and usually folded.

Dimensions. 30(34)40 μm; 40 specimens measured.

Comparison and remarks. Laevolancis (*Archaeozonotriletes*) *divellomedium* (Chibrikova) Burgess and Richardson, 1991, has a more prominent crassitude and a thicker, more rigid distal exine. Specimens of *L. plicata* are closely similar to spores to *Dyadospora murusattenuata* (Strother and Traverse) Burgess and Richardson, 1991

Anteturma SPORITES 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.

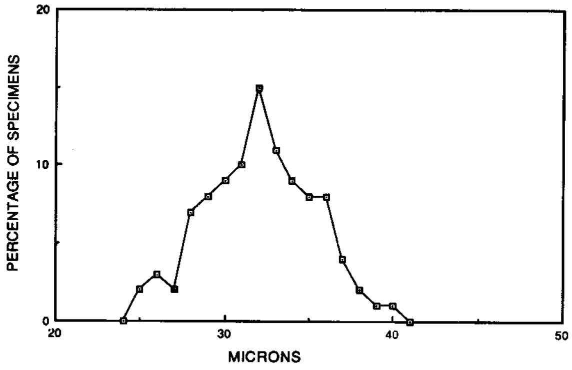
Ambitisporites avitus Hoffmeister, 1959

Plate 3, figs 1–3

1959 *Ambitisporites avitus* Hoffmeister, p. 332, pl. 1, figs 1–8.
1969 *Ambitisporites* cf. *avitus* Hoffmeister; Richardson and Lister, p. 228, pl. 40, fig. 2.
1973 *Ambitisporites avitus* Hoffmeister; Richardson and Ioannides, p. 277, pl. 5, figs 1–8.
?1975 'single spore showing equatorial thickening', Smith, pl. 1*e*.
1977 *Ambitisporites avitus* Hoffmeister; Colthurst and Smith, pl. 2, fig. 15.
1978 *Ambitisporites avitus* Hoffmeister; Emo and Smith, pl. 1, fig. 4.
1978 *Ambitisporites avitus* Hoffmeister; Rodriguez, p. 412, pl. 1, fig. 4.
1983 *Ambitisporites avitus* Hoffmeister; Rodriguez, p. 28, pl. 1, fig. 1.
1987 *Ambitisporites avitus* Hoffmeister; Smelror, fig. 4A–B.
1989 *Ambitisporites avitus* Hoffmeister; Barron, fig. 6A.

Figured specimens. Pl. 3, fig. 1 (stub CW17, Print P004939), sample BH4, FBF. FM 256, Pl. 3, fig. 2 (slide BL7/4, co-ord. 1295 139; E.F. no. 060/1/2), sample BL7, SBF. FM 257, Pl. 3, fig. 3 (slide BL13/2, co-ord. 1093 189; E.F. no. T39/2), sample BL13, DBF.

Description. Amb subcircular to subtriangular. Trilete mark distinct and simple with straight laesurae which usually extend to the equator of the spore. Laesurae diverge into curvaturae which are coincident with the equator of the spore and form a distinct and prominent equatorial crassitude which is 1·5–2·5 μm wide. In



TEXT-FIG. 6. Size frequency distribution of 100 *Ambitisporites avitus* Hoffmeister, 1959 from sample CL7, Logan Formation; Logan Water, Lesmahagow inlier.

obliquely compressed specimens the curvaturae can sometimes be seen to invaginate. Exine laevigate, distally 1–2 μm in thickness.

Dimensions. 25(32)39 μm; 100 specimens measured (Text-fig. 6).

Comparison. *Ambitisporites dilutus* (Hoffmeister) Richardson and Lister, 1969 is similar but has a less prominent equatorial crassitude. However, there is probably intergradation between the two species (see Richardson and Ioannides 1973, p. 277). In this investigation, the size range of the two species proved to be virtually identical (Text-figs 6–7).

Ambitisporites dilutus (Hoffmeister) Richardson and Lister, 1969

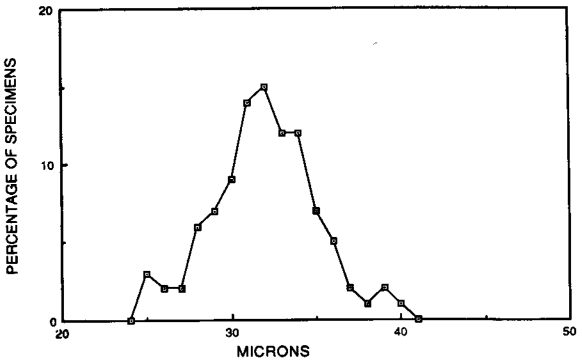
Plate 3, figs 4–6

1959	*Punctatisporites dilutus* Hoffmeister, p. 334, pl. 1, figs 9–13.
1969	*Ambitisporites* cf. *dilutus* (Hoffmeister) Richardson and Lister, p. 229, pl. 40, fig. 3.
1973	*Ambitisporites dilutus* (Hoffmeister) Richardson and Lister; Richardson and Ioannides, p. 277, pl. 6, figs 1–5.
1977	*Ambitisporites avitus* Hoffmeister; Colthurst and Smith, pl. 2, fig. 17.
?1978	*Ambitisporites*, Pratt *et al*., pl. 3, figs 7–10.
1978	*Ambitisporites dilutus* (Hoffmeister) Richardson and Lister; Rodriguez, p. 412, pl. 1, fig. 5.
1979	*Ambitisporites* sp. Strother and Traverse, pl. 3, figs 1–4.
1979	*Ambitisporites avitus* Hoffmeister; Holland and Smith, pl. 2, figs 1–4.
1983	*Ambitisporites dilutus* (Hoffmeister) Richardson and Lister; Rodriguez, p. 29, pl. 1, figs 3, 7.
1984	*Punctatisporites*? *dilutus* Hoffmeister; McGregor, p. 33, pl. 1, fig. 14.
1985	*Ambitisporites dilutus* (Hoffmeister) Richardson and Lister; Richardson *in* Hill *et al*., pl. 16, figs 3, 5–6.
1987	*Ambitisporites dilutus* (Hoffmeister) Richardson and Lister; Smelror, fig. 4D, 4K.
1989	*Ambitisporites dilutus* (Hoffmeister) Richardson and Lister; Barron, fig. 6B.
1991	*Ambitisporites dilutus* (Hoffmeister) Richardson and Lister; Burgess and Richardson, p. 615, text-fig. 3D–H.
1991	*Ambitisporites dilutus* (Hoffmeister) Richardson and Lister; Burgess, p. 594, pl. 2, fig. 15.

Figured specimens. FM 258, Pl. 3, fig. 4 (slide CL9/4, co-ord. 1275 071; E.F. no. G58/1), sample CL9 LF. FM 259, Pl. 3, fig. 5 (slide BL13/2, co-ord. 1095 190; E.F. no. T40/1), sample BL13, DBF., Pl. 3, fig. 6 (stub CW11, Print P005069), sample BL7, SBF.

Description. Amb circular to subtriangular. Triradiate mark distinct and simple with straight sutures which extend to the spore equator. The laesurae diverge into curvaturae which are coincident with the equator of the spore and form an equatorial crassitude. The crassitude varies from 0·5 to 1·5 μm in width. The curvaturae can be seen to invaginate in obliquely preserved specimens. The spores are smooth walled. Distal exine 1–2 μm in thickness.

TEXT-FIG. 7. Size frequency distribution of 100 *Ambitisporites dilutus* (Hoffmeister) Richardson and Lister, 1969 from sample CL7, Logan Formation; Logan Water, Lesmahagow inlier.



Dimensions. 25(32)40 μm; 100 specimens measured (Text-fig. 7).

Comparison. Ambitisporites avitus Hoffmeister, 1959, has a more prominent crassitude.

6. *Indeterminate.* According to Fensome *et al.* (1991) the genus '*Moyeria*' is a junior synonym of *Dactylofusa*. However, we provisionally retain the genus '*Moyeria*' to accommodate atypical palynomorphs like '*Moyeria*' *cabottii* pending further detailed taxonomic work. '*Moyeria*' differs from typical acritarchs and alete cryptospore monads, e.g. *Strophomorpha ovata* Miller and Eames, 1982. *Strophomorpha* is of similar general morphology to '*Moyeria*' but has a thicker, more rigid, wall which resembles that of cryptospore tetrads and dyads and appears to differ from that of '*Moyeria*' (see also Miller and Eames 1982). Thus, in order to highlight the differences between '*Moyeria*' *cabottii*, acritarchs, and cryptospores we prefer to categorize '*Moyeria*' as indeterminate. In a comprehensive review, Gray and Boucot (1989) proposed that '*Moyeria*' inhabited freshwater environments and may have euglenoid affinities. Whilst we regard the latter as unproven, our paper also reports '*Moyeria*' *cabottii* from deposits interpreted as non-marine.

Genus 'MOYERIA' Thusu, 1973

Type species. Moyeria uticaensis Thusu, 1973.

Moyeria cabottii (Cramer) Miller and Eames, 1982

Plate 2, fig. 9

1970 *Eupoikilofusa cabottii* Cramer, p. 87, pl. 4, figs 66–67.
1974 *Schizaeoisporites* sp. 1, Martin, p. 32, pl. 4, figs 115–116, 123; pl. 7, figs 233, 236.
1978 *Moyeria uticaensis* Thusu; McGregor and Narbonne, pl. 1, figs 29–31.
?1979 *Moyeria* sp. Holland and Smith, pl. 2, fig. 10.
1982 *Moyeria cabotti* (Cramer) Miller and Eames, p. 242, pl. 3, fig. 3.
1983 *Eupoikilofusa cabottii* Cramer; Rodriguez, p. 63, pl. 10, figs 5–6.
1984 *Eupoikilofusa cabottii* Cramer; Turner, p. 109, pl. 12, figs 3, 6.
1985 *Moyeria cabottii* (Cramer) Miller and Eames; Johnson, p. 330, pl. 3, fig. 5.
1989 *Moyeria cabottii* Cramer; Gray and Boucot, figs 1A–E, 2A–B.

Figured specimen. FM 271, Pl. 2, fig. 9 (slide CL5/2, co-ord. 1155 182, E.F. no. S46), sample CL5, LF.

Description. Body ellipsoidal to ovoidal and hollow. Externally ornamented with muri arranged in a bihelical pattern, that is, the muri originate at one pole of the body from where they spiral in the same direction until they reach the pole at the opposite end of the body. The muri are less than 0·5–1·0 μm high, less than 0·75 μm wide and 0·5–1·0 μm apart. The body wall is relatively thin.

Dimensions. 29(45)73 μm; 85 specimens measured.

Comparison. *Qualisaspora fragilis* Richardson, Ford and Parker, 1984 has a similar ornament but comprises two layers: a laevigate, thick-walled inner body enclosed within an ornamented, thin-walled outer layer. *Strophomorpha ovata* Miller and Eames, 1982 is thick walled and is ornamented with broader and more closely space muri than those in '*Moyeria*' *cabottii*.

Remarks. As '*Moyeria*' *cabottii* occurs in non-marine deposits it seems reasonable to suppose that it either represents subaerially dispersed reproductive propagules derived from a terrestrial plant or the remains of an organism which inhabited non-marine water bodies. The dissimilarity of '*Moyeria*' *cabottii* to other sporomorphs, mainly because of its thin wall, may indicate that it was not subaerially dispersed. Therefore it seems likely that '*Moyeria*' *cabottii* represents the remains of some form of organism which inhabited continental water bodies. The possibility that the specimens of '*Moyeria*' *cabottii* are reworked from older marine strata is ruled out because no typical marine palynomorphs, such as chitinozoans and acritarchs, which would also be expected to be reworked are present.

COMPOSITION OF THE PALYNOMORPH ASSEMBLAGE

Palynomorph assemblages consisting entirely of land-derived forms were recovered from the Fish Bed Formation (Hagshaw Hills inlier) and the Dippal Burn, Slot Burn and Logan Formations (Lesmahagow inlier). In the Henshaw Formation (North Esk inlier) rare marine acritarchs are also present (Pl. 4, fig. 6). The assemblages contain cryptospores, miospores, cuticle-like sheets, tubular structures and the enigmatic palynomorph '*Moyeria*'. The suite of palynomorphs is almost identical in each of the formations, except for the presence of acritarchs in the Henshaw Formation. Among the microfossils, cryptospores are dominant in variety and relative abundance but miospores are present in all of the samples. The relative abundances of the palynomorphs and a species list is presented in Text-figure 4. In the following synopsis, results of frequency counts are expressed in the form of three figures, for example 2(6)11 per cent, where the first and last numbers refer, respectively, to the minimum and maximum percentage frequency encountered in the counts, and the number in parentheses refers to the mean of all of the counts.

The cryptospores included permanent tetrads, pseudodyads, true dyads, hilate cryptospores and alete cryptospore monads. The permanent tetrads consist of forms with discrete spores (*Tetrahedraletes medinensis* and *Rimosotetras problematica*) and fused spores (*Cheilotetras caledonica*). None of the tetrads was observed enclosed within an envelope. Permanent tetrads comprise between 8 and 34 per cent of the total palynomorph content with *Tetrahedraletes medinensis* constituting 6(16)24 per cent, *Cheilotetras caledonica* 0(5)15 per cent and *Rimosotetras problematica* always less than 3 per cent.

True dyads comprise 0(2)5 per cent of the total palynomorphs and are represented by the smooth-walled forms *Dyadospora murusattenuata* and *Dyadospora murusdensa*. None has an envelope. They are occasionally seen separated into two laevigate hilate cryptospores and many, if not all, the hilate cryptospores are probably derived from them. The only pseudodyad recognized was the rather atypical form *Pseudodyadospora petasus* which is fused and has extended 'flanges' protruding from each spore. It comprises 0(3)8 per cent of the palynomorph assemblages.

All the hilate cryptospores are laevigate, crassitate forms referable to the species *Laevolancis divellomedium* and *Laevolancis plicata*. These two species constitute 1(13)35 per cent of the assemblage.

Alete cryptospore monads comprise a group of palynomorphs which consist of a discrete body which may, or may not, be enclosed within a membranous envelope. They are often thick walled and possess ornament comparable to that of cryptospore tetrads and dyads. The origin of most cryptospore monads is unknown but the similarity to other cryptospores suggests that some are subaerially dispersed propagules of land plants, although others may be derived from aqueous organisms such as protists and algae. Laevigate, alete cryptospore monads (Pl. 4, fig. 1) are usually the most common palynomorph in the Midland Valley sporomorph assemblage and comprise 24(38)51 per cent of the total palynomorph content. This collection of palynomorphs is nondescript and no attempt was made to classify them formally. However, the alete cryptospore monads vary dramatically in size and probably originate from more than one source (Text-fig. 8). Many of the alete cryptospore monads in the Midland Valley assemblages are relatively thin walled, although not as thin walled as typical marine sphaeromorphs, which suggests that they may not be subaerially dispersed reproductive propagules but are possibly derived from freshwater protists or other organisms which inhabited the body of water in which the sediment accumulated.

Only two species of trilete spores are present, *Ambitisporites avitus* and *Ambitisporites dilutus*, the latter being more common. The size range of each species is similar and narrow and there seems to be complete intergradation between them (see p. 174). Both are crassitate and laevigate and they comprise 6(12)19 per cent of the total palynomorphs.

The enigmatic palynomorph '*Moyeria*' is present in most of the samples studied and constitutes 0(11)22 per cent of the palynomorphs.

DESCRIPTION OF OTHER ORGANIC FRAGMENTS

All the productive samples contain abundant fragmentary organic remains in the form of tubular structures, cuticle-like sheets, and rare cuticle fragments probably of arthropod origin. The affinities of these structures have been intensely debated in recent years (Banks 1975; Gray and Boucot 1977; Pratt *et al.* 1978; Strother and Traverse 1979; Edwards 1982, 1986; Edwards and Rose 1984; Gray 1985; Johnson 1985; Strother 1988; Burgess and Edwards 1991; Gensel *et al.* 1991). Because the tubular structures and cuticle-like sheets have been recovered from unequivocal non-marine deposits and they show remarkable similarities to structures in extant and fossil land plants they are generally considered to be derived from land plants (Gray 1985; Strother 1988; Edwards and Burgess 1991; Gensel *et al.* 1991). In order to facilitate the study of these fragments, attempts have recently been made to classify them in an artificial morphological classification (Edwards 1982, 1986; Edwards and Rose 1984; Burgess and Edwards 1991). A brief description of these remains isolated from the Midland Valley Silurian inliers follows.

Tubular structures

The tubular structures are dominated by straight, parallel-sided, smooth-walled, diaphanous forms which appear identical to tubes described as *Laevitubulus plicatus* Burgess and Edwards, 1991 (Pl. 4, figs 3, 7). These tubes are 18–50 μm wide and up to 200 μm long, are always preserved flattened and have smooth walls with a corroded appearance. Constrictions, septae and branching are not observed, but rare specimens with a tapering termination have been recorded (Pl. 4, fig. 3). Other smooth-walled forms include those with thick, smooth, opaque walls which can be equated with *L. crassus* Burgess and Edwards, 1991 (Pl. 5, fig. 3). They are parallel-sided, 7–14 μm wide, up to 100 μm long and usually have a curved or helical organization. Terminations, branching, constrictions and septae were not recorded. Rare monospecific wefts of loosely aggregated and randomly orientated smooth tubes that can be assigned to *L. laxus* Burgess and Edwards, 1991 were also recorded (Pl. 5, fig. 1). The individual tubes have thin diaphanous walls, are straight with parallel sides and are 2–9 μm wide, up to 96 μm long and usually branch at acute angles. Constrictions are sometimes present but septae and terminations were not observed. *L. tenuis* Burgess and Edwards, 1991 is also present (Pl. 4, fig. 8). They comprise straight, parallel sided, flattened, smooth, opaque tubes. Specimens are 12(18)36 μm wide and up to 320 μm long. Terminations, septae or branching were not observed.

Less common are tubes which are externally smooth but have an internal ornament of annular, or less commonly spiral, thickenings (Pl. 4, figs 4–5; Pl. 6, fig. 2). Scanning electron microscope studies have illustrated that the internal thickenings are homogeneous with the walls. The tubes are straight with parallel sides, 15–45 μm wide and up to 146 μm long, and have not been observed branching or with septae or terminations. The internal thickenings are 0·5–1·5 μm wide, 0·5–1·0 μm high and 1·0–5·0 μm apart. The thickenings sometimes diminish in size and eventually disappear or may dichotomize at an acute angle (Pl. 6, fig. 2). The thickenings are most commonly arranged in an annular manner with rare dichotomies and can be assigned to *Porcatitubulus annulatus* Burgess and Edwards, 1991. Forms with spiral thickenings are less common and are assigned to *P. spiralis* Burgess and Edwards, 1991. Usually there is one helix, but occasionally more than one helix is present. Tubes with a pattern of very fine, closely packed striations which are arranged in an annular or spiral pattern were also recorded (Pl. 4, figs 9–10). This pattern is either formed by an internal ornament of closely packed minute thickenings or represents fibres within the wall of the tube. Burgess and Edwards (1991) illustrated similar tubes and included them in the taxon *P. spiralis* Burgess and Edwards, 1991, thereby implying that the tubes possess internal thickenings. However, the internal thickenings are much smaller than the size range Burgess and Edwards stipulated for this species. Similar tubes have also been illustrated by Pratt *et al.* (1978, pl. 2, fig. 9) from the Lower Massanutten Sandstone of Llandovery age from Virginia, and by Strother and Traverse (1979, pl. 3, fig. 14) from ?Wenlock age strata of Pennsylvania. Both Pratt *et al.* and Strother and Traverse suggest that the walls of these tubes possessed an internal fibrillar structure giving the impression of spiral striations when the light passed through the tubes. It is difficult to interpret the structure using light microscopy, although SEM observation of similar tubes from Lochkovian material suggests that the tubes may possess an internal ornament of thickenings (Wellman 1991). Similar tubes with an internal ornament of closely spaced, low thickenings which are up to 2 μm wide were also recovered (Pl. 5, fig. 2).

In addition to isolated tubular structures, rare associations of tubes were recorded (Pl. 4, fig. 6). These comprised straight, unbranched, wide tubes with a mesh of narrow, branched tubes adhering to their surface. The wide tubes are smooth-walled, 20–30 μm wide and up to 230 μm long, and are preserved flattened. The narrow tubes generally run more-or-less parallel to the wide tubes and are regularly branched with offshoots at 90 degrees. The branches are usually 4–12 μm long and frequently terminate in closed ends. The narrow tubes are unornamented and 1·5–2·5 μm wide.

EXPLANATION OF PLATE 4

Fig. 1. Alete cryptospore monad. FM 277 (slide BL7/4, co-ord. 1167 214; E.F. no. V47/3) sample BL7; Slot Burn Formation; Slot Burn, Lesmahagow inlier, × 1000.

Fig. 2. Acanthomorph acritarch. FM 278 (slide CP6/1, co-ord. 1221 085; E.F. no. H52/4) sample CP6; Lynslie Burn Fish Bed; Henshaw Formation, North Esk inlier, × 1000.

Figs 3, 7. *Laevitubulus plicatus* Burgess and Edwards, 1991. FM 279 (slide CL8/1, co-ord. 1165 172; E.F. no. R47) sample CL8; Logan Formation; Logan Water, Lesmahagow inlier, × 500. 7, FM 280 (slide BH8/1, co-ord. 1275 160; E.F. no. Q58) sample BH8; Fish Bed Formation; Glenbuck Loch, Hagshaw Hills inlier, × 315.

Fig. 4. *Porcatitubulus spiralis* Burgess and Edwards, 1991. FM 281 (slide BL13/2, co-ord. 1253 128; E.F. no. M56/3) sample BL13; Dippal Burn Formation; Dippal Burn, Lesmahagow inlier, × 500.

Fig. 5. *Porcatitubulus annulatus* Burgess and Edwards, 1991. FM 282 (slide BH8/1, co-ord. 1237 169; E.F. no. R54/2) sample BH8; Fish Bed Formation; Glenbuck Loch, Hagshaw Hills inlier, × 500.

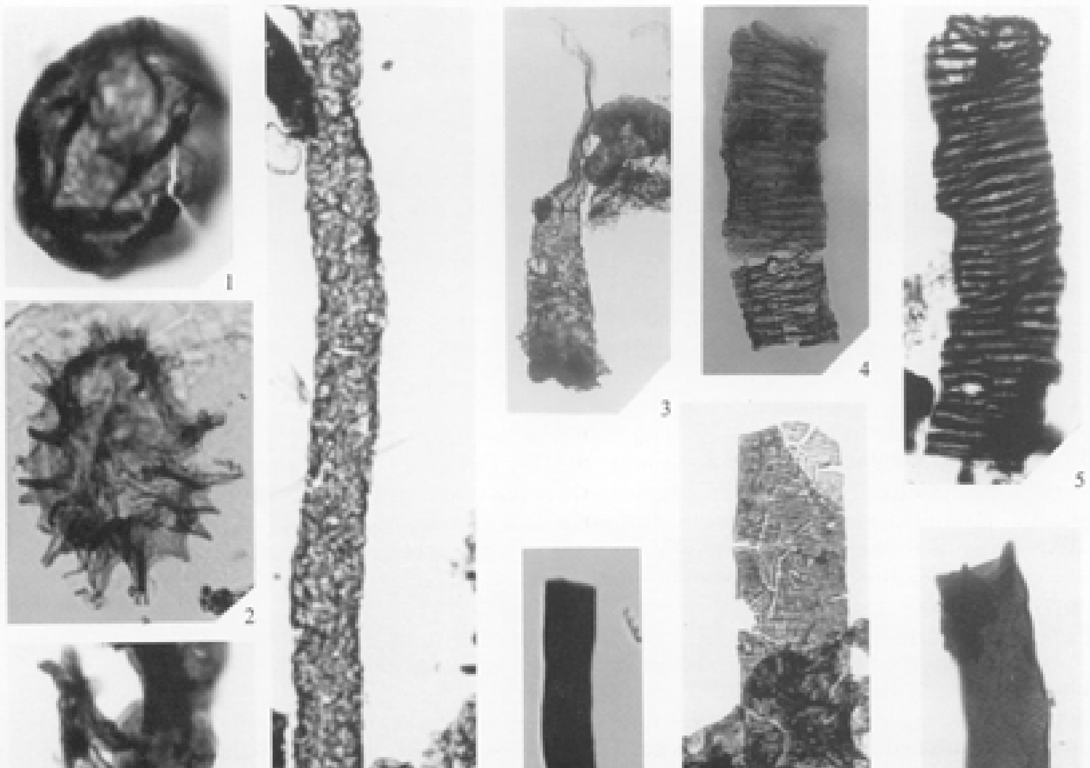
Fig. 6. Fragment of ?*Prototaxites* sp. FM 283 (slide BL7/4, co-ord. 1116 125; E.F. no. M41/3) sample BL7; Slot Burn Formation; Slot Burn, Lesmahagow inlier, × 1000.

Fig. 8. *Laevitubulus tenuis* Burgess and Edwards, 1991. FM 284 (slide CL8/1 co-ord. 1277 136; E.F. no. N58) sample CL8; Logan Formation; Logan Water, Lesmahagow inlier, × 500.

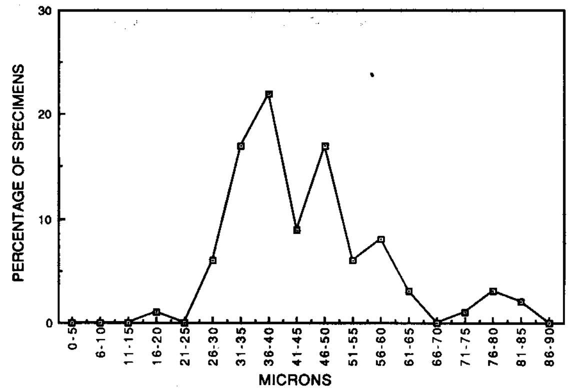
Fig. 9. Tube with annular internal microthickenings. FM 285 (slide DL8/2, co-ord. 1290 090; E.F. no. J60) sample DL8; Slot Burn Formation; Slot Burn, Lesmahagow inlier, × 540.

Fig. 10. Tube with spiral internal microthickenings. FM 286 (slide DL8/2 co-ord. 1280 070; E.F. no. F58/4) sample DL8; Slot Burn Formation; Slot Burn, Lesmahagow inlier, × 500.

PLATE 4



WELLMAN and RICHARDSON, palynomorphs and tubes



TEXT-FIG. 8. Size frequency distribution of 200 alete cryptospore monads from sample CL7, Logan Formation, Logan Water, Lesmahagow inlier.

Similar associations of tubes have been illustrated by Edwards (1982) from deposits of Ludlow age from Wales. Edwards noted the similarity between the organization of the fragmented tube associations and structures present in *Prototaxites*, a nematophyte known from plant megafossils. We also find the similarity striking and refer the associations to ?*Prototaxites* sp.

Cuticle-like sheets

The cuticle-like sheets show little diversity. They are smooth on one surface and have an irregular reticulate pattern of ridges (muri) on the other. The units are either predominantly circular (Pl. 5, fig. 6; Pl. 6, fig. 5), or polygonal (Pl. 5, figs 4–5, 7–8; Pl. 6, fig. 1), vary in size on an individual sheet and do not form any recognizable patterns. Maximum unit size varies from 2 to 25 μm, average 10 μm. The sheets are up to 350 μm in maximum diameter but margins have not been observed. Perforations in the sheets are usually a result of abrasion as the edges of the holes are irregular and show signs of tearing. Infrequently almost perfectly circular perforations with clear-cut margins puncture the cuticle between muri (Pl. 6, figs 4, 6). It seems that these perforations are not a result of abrasion and may be primary, in which case they perhaps mark the position of some type of aerating structure (see Edwards and Rose 1984, p. 52), or may be the result of some form of infection or wounding.

EXPLANATION OF PLATE 5

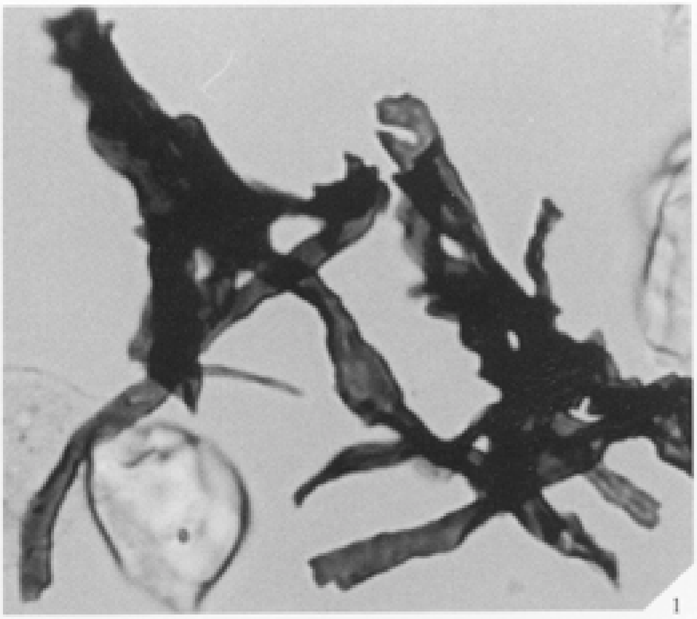
Fig. 1. *Laevitubulus laxus* Burgess and Edwards, 1991. FM 287 (slide CL9/1, co-ord. 1205 105; E.F. no. K51) sample CL9; Logan Formation; Logan Water, Lesmahagow inlier, × 850.

Fig. 2. Tube with wide 'strap-like' internal thickenings. FM 288 (slide DL8/2, co-ord. 1260 100; E.F. no. K57/1) sample DL8; Slot Burn Formation; Lesmahagow inlier, × 1200.

Fig. 3. *Laevitubulus crassus* Burgess and Edwards, 1991. FM 289 (slide DL8/2, co-ord. 1180 095; E.F. no. J48/4) sample DL8; Slot Burn Formation; Slot Burn, Lesmahagow inlier, × 625.

Figs 4–8. Cuticle-like sheets. 4, 8, FM 290 (slide CL6/3, co-ord. 1260 090; E.F. no. J56/2) sample CL6; with polygonal units; Logan Formation; Logan Water, Lesmahagow inlier; 4, × 270; 8, × 600. 5, FM 291 (slide CL6/3, co-ord. 1240 150; E.F. no. P54/2) sample CL6; with polygonal units; Logan Formation; Logan Water, Lesmahagow inlier, × 270. 6, FM 292 (slide CL5/2, co-ord. 1216 150; E.F. no. P52) sample CL5; with rounded units; Logan Formation; Logan Water, Lesmahagow inlier, × 350. 7, FM 293 (slide CL5/3, co-ord. 1274 127; E.F. no. M58/3/4) sample CL5; with polygonal units; Logan Formation; Logan Water, Lesmahagow inlier, × 250.

PLATE 5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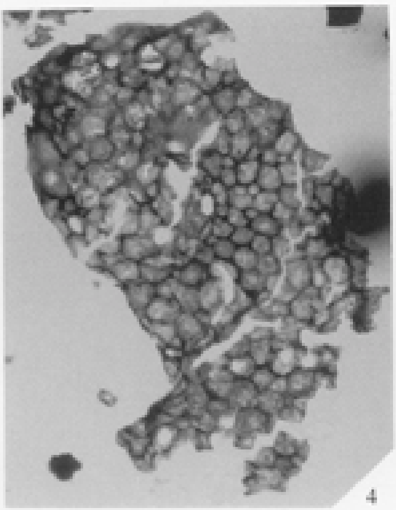
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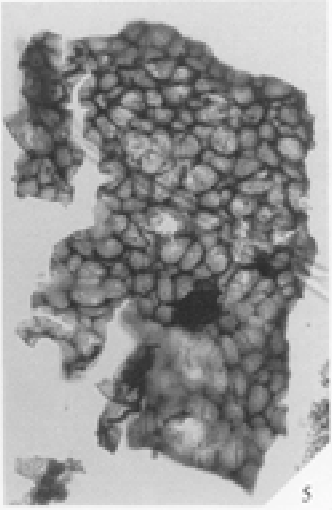
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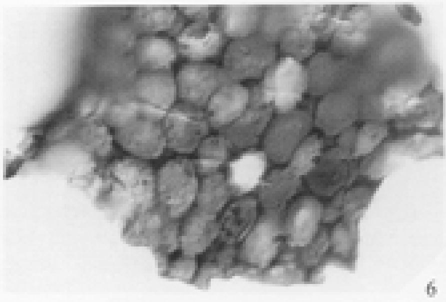
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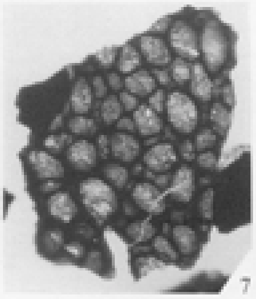
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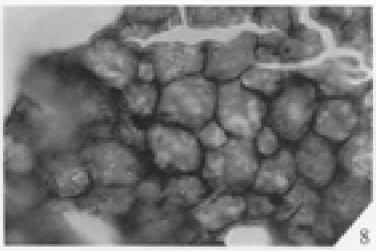
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WELLMAN and RICHARDSON, tubes and cuticles

AGE OF THE ASSEMBLAGES

The salient features of the assemblages utilized in age dating are the presence of unsculptured trilete spores and hilate cryptospores, the absence of trilete spores and hilate cryptospores with ornament, and the general character of the assemblage.

In the type area of the Llandovery in South Wales, unequivocal laevigate trilete spores referable to *Ambitisporites* appear in the late Aeronian (upper *sedgwickii* Biozone) (Richardson 1988; Burgess 1991). However, Richardson (1988) noted that spore recovery is variable in this sequence and the first appearance of *Ambitisporites* may eventually prove to be slightly earlier. The earliest record of hilate cryptospores is a species of the laevigate genus *Laevolancis* from the early Wenlock (lower *centrifugus* Biozone) from the type area of the Wenlock (Burgess and Richardson 1991). The inception of sculptured miospores and hilate cryptospores is slightly later and the earliest reported examples are also from the type area of the Wenlock where they first appear in the Homerian (upper *lundgreni* Biozone) (Burgess and Richardson 1991). However, another occurrence of the same, or possibly earlier age, is cf. *Synorisporites verrucatus* from strata of *ellesae* to *lundgreni* Biozone ages from the Greyhound Law inlier in the Cheviot Hills of northern England which has been age constrained using graptolites (Barron 1989).

Thus the presence of laevigate hilate cryptospores suggests a lower age bracket of earliest Sheinwoodian (early *centrifugus* Biozone) and the absence of ornamented spores indicates an upper age bracket of Homerian (upper *lundgreni* Biozone) or possibly latest Sheinwoodian (*ellesae* Biozone) age. Therefore the assemblages are assigned an early Wenlock age. The spore-based age determination corresponds with biostratigraphical evidence derived from macrofaunas which indicates that strata which lie below the plant microfossil assemblages are of Telychian and possibly early Sheinwoodian age (Lamont 1947; Rolfe 1961, 1973*a*, 1973*b*; Rolfe and Fritz 1966; Bull 1987).

COMPARISONS WITH SPOROMORPH ZONAL SCHEMES

In the scheme of Richardson and McGregor (1986) (see also Richardson 1988; Richardson and Edwards 1989) the Midland Valley assemblages can be accommodated in the *chulus-nanus* Assemblage Biozone which is of ?Telychian–early Homerian (upper *lundgreni* Biozone) age. This spore biozone is characterized by smooth-walled trilete spores, naked permanent tetrads and true dyads, and laeviage hilate cryptospores. The preceeding *avitus-dilutus* Assemblage Biozone contains the earliest laevigate trilete spores but hilate cryptospores have not been reported. Miospores and hilate cryptospores with sculpture appear at the base of the *protophanus-verrucatus* Assemblage Biozone which succeeds the *chulus-nanus* Assemblage Biozone.

The absence of laevigate patinate miospores from the Midland Valley assemblages, and hence the nominal species of the *chulus-nanus* Assemblage Biozone, may be a consequence of palaeo-

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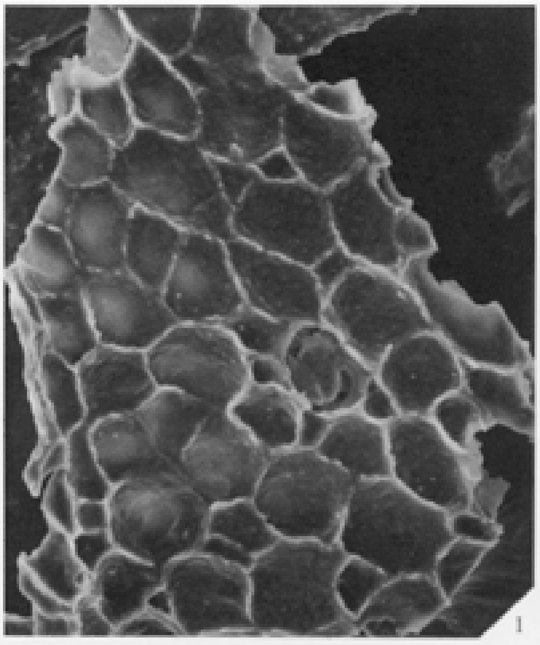
EXPLANATION OF PLATE 6

Figs 1, 4–6. Cuticle-like sheets. 1, (stub CW6, Print P004401) sample BL7; with polygonal units; Slot Burn Formation; Slot Burn, Lesmahagow inlier, × 570. 4, (stub CW6, Print P004407) sample BL7; smooth external surface with perforations; Slot Burn Formation; Slot Burn, Lesmahagow inlier, × 580. 5, (stub CW48, Print P008556) sample DL8; with circular units; Slot Burn Formation; Slot Burn, Lesmahagow inlier, × 150. 6, FM 295 (slide CL6/3, co-ord. 1294 085; E.F. no. H60) sample CL6; with polygonal units, several of which are punctured by circular perforations; Logan Formation; Logan Water, Lesmahagow inlier, × 550.

Fig. 2. *Porcatitubulus* sp. Burgess and Edwards, 1991. (stub CW30, Print P007354) sample CL5; fractured specimen showing the internal thickenings; Logan Formation; Logan Water, Lesmahagow inlier, × 1670.

Fig. 3. ?Arthropod cuticle. FM 294 (slide CL5/2, co-ord. 1215 110; E.F. no. L52) sample CL5; Logan Formation; Logan Water, Lesmahagow inlier, × 250.

PLATE 6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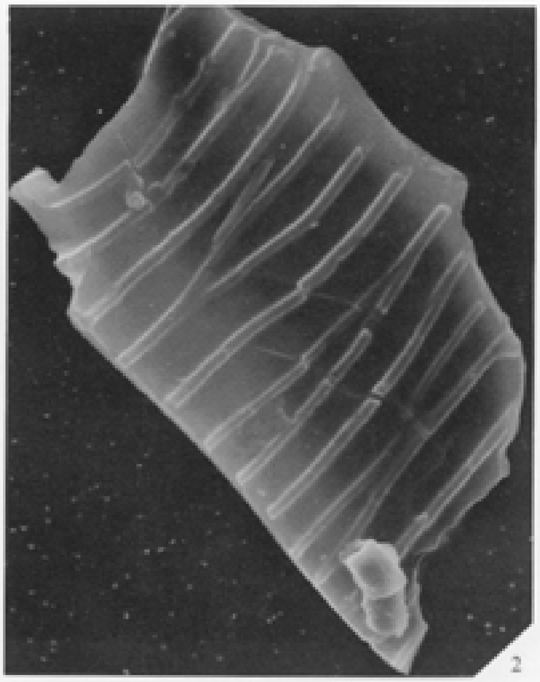
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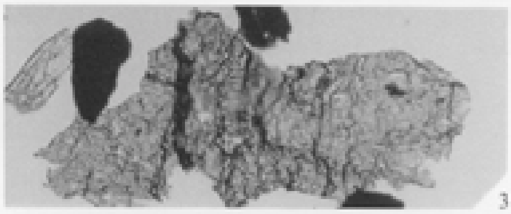
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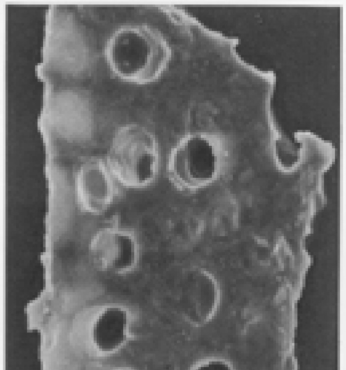
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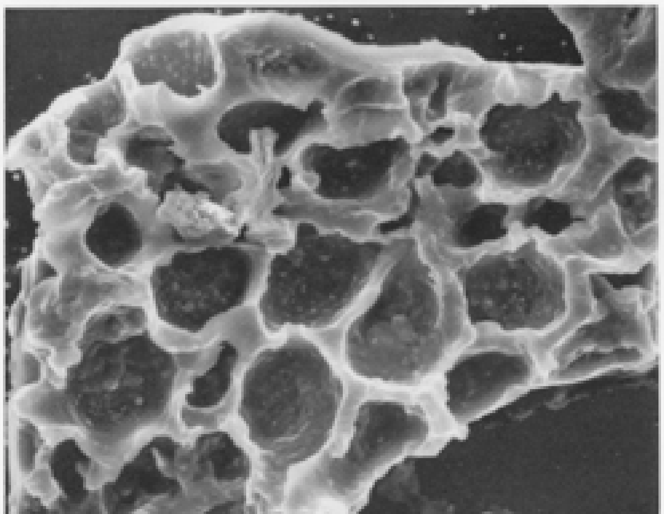
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6

WELLMAN and RICHARDSON, tubes and cuticles geographical or palaeoenvironmental factors. The *chulus-nanus* Assemblage Biozone is based largely on work in the marine and marginal marine deposits of southern Britain which are of different facies and palaeogeographical province from the Midland Valley deposits. Richardson and McGregor (1986) noted a similar situation in that the assemblage described by Smith (1975) from the Lettergesh Formation of Ireland is confidently dated as early Wenlock age, and therefore falls within the age range of the *chulus-nanus* Assemblage Biozone, but lacks patinate spores. However, it is noteworthy that there are remarkable similarities between the Midland Valley sporomorph assemblages and those described by Burgess and Richardson (1991) from early Wenlock strata of the type area (see below). Such observations support an early Wenlock age and inclusion in the *chulus-nanus* Assemblage Biozone.

COMPARISON WITH PREVIOUSLY DESCRIBED SPOROMORPH ASSEMBLAGES OF LATE LLANDOVERY AND EARLY WENLOCK AGE

Sporomorph assemblages have been described from the type areas for the Llandovery and Wenlock in southern Britain and also from Llandovery and Wenlock strata in North Africa, North America, South America and various localities in Europe. The essence of these reports is outlined below.

In their preliminary investigation of the spores from the Silurian strata of the Anglo-Welsh basin, Richardson and Lister (1969) recorded *Ambitisporites* cf. *avitus* Hoffmeister, 1959, *A. dilutus* (Hoffmeister) Richardson and Lister, 1969, *Archaeozonotriletes chulus* Cramer var. *nanus* Richardson and Lister, 1969, *Retusotriletes* cf. *warringtonii* Richardson and Lister, 1969 and *Laevolancis divellomedium* Burgess and Richardson, 1991 (as ?*Archaeozonotriletes* cf. *divellomedium* Chibrikova, 1959) from the Coalbrookdale Formation of Sheinwoodian and early Homerian age. The earliest ornamented spores were recorded from the Much Wenlock Limestone Formation of Homerian age (*ludensis* Biozone). Following the recognition of cryptospores, the type Llandovery and type Wenlock were studied by Burgess (1991) and Burgess and Richardson (1991) respectively. Burgess recorded the inception of trilete spores, *Ambitisporites dilutus* (Hoffmeister) Richardson and Lister, 1969, in the *sedgwickii* Biozone. It occurred in an impoverished assemblage with the cryptospores *Tetrahedraletes medinensis* Strother and Traverse, 1979, *Velatitetras reticulata* Burgess, 1991 and *Pseudodyadospora* cf. *laevigata* Johnson, 1985. Compared with older assemblages in the Llandovery, the younger assemblages exhibit a lack of variety of cryptospore species. In the type Wenlock strata, Burgess and Richardson (1991) recovered *Ambitisporites dilutus* (Hoffmeister) Richardson and Lister, 1969, *A. avitus* Hoffmeister, 1959, *Archaeozonotriletes chulus* var. *chulus* and *nanus* Richardson and Lister, 1969, *Tetrahedraletes medinensis* Strother and Traverse, 1979, *Dyadospora murusdensa* (Strother and Traverse) Burgess and Richardson, 1991, *D. murusattenuata* (Strother and Traverse) Burgess and Richardson, 1991, *Laevolancis divellomedium* (Chibrikova) Burgess and Richardson, 1991 and *L. plicata* Burgess and Richardson, 1991 throughout the sequence. Higher assemblages in strata of early Homerian age (upper *lundgreni* Biozone) and younger contain ornamented hilate cryptospores and miospores in addition to these species. The Midland Valley assemblages are remarkably similar to the pre-upper *lundgreni* Biozone spore assemblages described by Burgess and Richardson from the type area of the Wenlock. All of the taxa reported by Burgess and Richardson were recovered in the Midland Valley, except for *Archaeozonotriletes chulus*. The only additional species recorded in the Midland Valley assemblage are *Cheilotetras caledonica* gen. et sp. nov. and *Pseudodyadospora petasus* sp. nov., and the latter has now been recognized in preparations of early Wenlock age (early *centifugus* Biozone) from the Wenlock type area.

The first report of trilete spores from Llandovery strata was by Hoffmeister (1959) from possible early Aeronian deposits from Libya (Hoffmeister 1959; Gray and Boucot 1971; Richardson 1988). Richardson (1988) re-examined Hoffmeister's material and noted that the trilete spores co-occurred with cryptospores. He recorded naked permanent tetrads (probably mainly *Tetrahedraletes medinensis* (Strother and Traverse) emend.), permanent tetrads enclosed within a laevigate envelope, possible true dyads, naked pseudodyads and *Ambitisporites*? *vavrdovii* Richardson, 1988.

Other publications concerning Silurian sporomorphs from North Africa include Richardson and Ioannides (1973), Al-Ameri (1980), Richardson (*in* Hill *et al.* 1985), Richardson (1988) and Richardson and Edwards (1989). Richardson and Ioannides (1973) described a sequence of spore assemblages from two wells in Libya. At several positions in the sequence graptolite faunas have been recovered which suggest a Wenlock or early Ludlow age. Richardson (in Richardson and Edwards 1989) compared the spore associations with better age-constrained assemblages from southern Britain and suggested that the oldest assemblage, which lies beneath the graptolite-bearing horizons and comprises only smooth-walled miospores, belongs to the *chulus-nanus* Assemblage Biozone, which suggests a late Llandovery or early Wenlock age. Younger samples in the well are markedly different in that they contain ornamented spores. It is noteworthy that the Libyan succession of 'spore first appearances' is closely comparable to that observed in the southern British sequences.

Richardson (1988) expanded preliminary work in which he had investigated cryptospore and miospores distribution in Silurian strata from several wells in Libya (Richardson *in* Hill *et al.* 1985). In a sample which contained the miospores *Ambitisporites avitus* Hoffmeister, 1959 and *A. dilutus* (Hoffmeister) Richardson and Lister, 1969 he recorded cryptospores including naked permanent tetrads (probably mostly referable to *Tetrahedraletes medinensis* (Strother and Traverse) emend.), loose tetrads (probably *Rimosotetras problematica* Burgess, 1991), permanent tetrads enclosed in smooth and ornamented envelopes, the naked true dyads *Dyadospora murusattenuata* Strother and Traverse, 1979 and *D. murusdensa* Strother and Traverse, 1979, true dyads enclosed in a smooth envelope, pseudodyads enclosed within a rugose envelope and *Ambitisporites*? *vavrdovii* Richardson, 1988. On the basis of correlation with assemblages described from elsewhere he suggested a late Aeronian–early Telychian age. Like the Llandovery assemblages from the type area, these spore associations have much in common with the Midland Valley assemblage but again the major difference is the presence, in the Llandovery-age material, of rare cryptospores enclosed within envelopes.

From elsewhere in Europe, land-derived sporomorphs have been recovered from Silurian deposits in Ireland from both sides of the presumed Iapetus suture. Spores in strata which range from Telychian (*crispus* Biozone) to earliest Homerian (*lundgreni* Biozone) are composed exclusively of laevigate trilete spores, hilate cryptospores and tetrads (Doran 1974; Smith 1975, 1979; Colthurst and Smith 1977; Emo and Smith 1978; Holland and Smith 1979). The trilete spores are generally of the *Ambitisporites* complex, with rare *Retusotriletes* sp. and *Archaeozonotriletes* sp. The reported tetrads are almost certainly cryptospore permanent tetrads, and probable hilate cryptospores have been figured as species of smooth-walled, patinate miospores. In Scotland *Ambitisporites* sp. has been reported from the shallow-water marine Knockgardner Formation of the Girvan area which is of early Wenlock age (Dorning 1982) and in Norway, Smelror (1987) recorded *Tetrahedraletes medinensis* Strother and Traverse, 1979, *Ambitisporites avitus* Hoffmeister, 1959 and *A. dilutus* (Hoffmeister) Richardson and Lister, 1969 from the marine Steinsfjorden Formation of Sheinwoodian age from the Ringerike district.

From North America, Pratt *et al.* (1978) described an important sporomorph assemblage from the Lower Massanutten Sandstone in Virginia. They assigned a probable Llandovery age, based on field relations, and suggested a fluvial origin. They recorded rare *Ambitisporites* sp., 'tetrads of alete spores' (probably *Tetrahedraletes medinensis* (Strother and Traverse) emend.), alete spores (probably *Laevolancis* sp.) and sphaeromorphs. Also in North America, assemblages in which the trilete spores consist entirely of species of the *Ambitisporites* complex have been reported from deposits of Llandovery and Wenlock age by Cramer (1968, 1969, 1971). Additionally, assemblages dominated by a wide diversity of cryptospores, with possible trilete spores, have been described by Gray and Boucot (1971), Strother and Traverse (1979) and Johnson (1985) from deposits of Llandovery age. However, it appears that the rare trilete spores are probably *Ambitisporites*? *vavrdovii*, which mimics a miospore but is probably derived from a fragmented or loose permanent tetrad. These assemblages all contain cryptospores which are enclosed within envelopes.

Finally, from South America, McGregor (1984) noted the presence of rare, small, retusoid, equatorially thickened, unsculptured spores from the middle part of the Tarabuco Formation of Bolivia. Spores in the upper part of the formation suggested a Ludlow age and McGregor proposed a pre-Ludlow age for the older samples. It is probable that they are of late Llandovery or early Wenlock age. There are as yet no reports of late Llandovery or early Wenlock spore assemblages from Australia, Antarctica, Asia or Africa south of the Sahara Desert.

Other palynomorphs which co-occur with the sporomorphs in the Midland Valley assemblages are of less biostratigraphical value as they are long-ranging or their stratigraphical distribution is uncertain. The alete cryptospore monads which dominate the assemblages are long-ranging and can also be confused with marine forms such as prasinophycean cysts and sphaeromorph acritarchs, although the latter are usually thinner walled. Reports of the enigmatic palynomorph '*Moyeria*' *cabottii* so far extend to marine and continental strata of Caradoc to Ludlow age (Gray and Boucot 1989).

COMPARISON WITH PREVIOUS REPORTS OF TUBULAR STRUCTURES AND CUTICLE-LIKE SHEETS FROM THE LOWER PALAEOZOIC

Burgess and Edwards (1991) outlined the stratigraphical distribution of tubular structures from latest Ordovician to earliest Devonian deposits from the Anglo-Welsh Basin. They identified two assemblages. The first ranges from the latest Ordovician to the latest Llandovery and consists almost exclusively of *Laevitubulus plicatus*. Filamentous types and internally thickened forms are absent. The second assemblage first occurs in the earliest Wenlock and persists into the Early Devonian. It is much more diverse and comprises the internally thickened forms *Porcatitubulus spiralis* and *P. annulatus*, the smooth forms *Laevitubulus plicatus*, *L. laxus*, *L. crassus* and the filament *Ornatifilum granulatum*. All of these species range from the early Wenlock to the Early Devonian. In the late Wenlock they are joined by the externally ornamented form *Constrictitubulus cristatus* and the smooth form *Laevitubulus tenuis* which persist until the Early Devonian. However, Burgess and Edwards suggested that the younger and more diverse assemblage of tubular structures might make its inception prior to the early Wenlock in the late Llandovery, but this is masked by sampling bias in the Anglo-Welsh Basin. The late Llandovery samples analysed by Burgess and Edwards were all from distal marine facies, an environment in which the land-derived tubes are very scarce. Pratt *et al.* (1978) reported internally thickened tubes from strata which are probably of late Llandovery age from North America.

The assemblage of tubular structures recovered from the Midland Valley inliers conforms closely with the distribution of tubular structures observed by Burgess and Edwards in the early Wenlock strata of the Anglo-Welsh Basin. However, filaments of the *Ornatifilum granulatum* type are not recorded in the Midland Valley assemblage, and the laevigate tube *Laevitubulus crassus*, which is not recorded in strata older than late Wenlock in southern Britain, is present.

There are few detailed descriptions of Silurian culticle-like sheets and hence their stratigraphical distribution is poorly understood. However, examples similar to those recorded from the Midland Valley are known to range from possibly the Caradoc to the Early Devonian (Gray *et al.* 1982; Edwards 1982, 1986; Edwards and Rose 1984; Edwards and Burgess 1991; Gensel *et al.* 1991).

PALYNOFACIES

The red-bed sequences in the Silurian inliers of the Midland Valley have long been regarded as being entirely non-marine in origin, except for the Lynslie Burn Fish Bed in the North Esk inlier which contains crinoids and has been interpreted as being due to a brief marine incursion. Recently, however, certain fish workers have expressed doubts concerning this interpretation and have proposed that the fish are marine forms and that all the fish beds represents marine incursions (Blieck and Janvier 1991).

The strata have been interpreted as non-marine because the sedimentology of the deposits suggests that they accumulated in terrestrial–fluviatile and lacustrine environments and because unequivocal marine fossils are absent. The fish-bearing horizons are interspersed in red-bed sequences with sedimentological characteristics, e.g. desiccation cracks and alluvial fan conglomerates, typical of terrestrial–fluviatile deposition (McGiven 1968; Rolfe 1973*a*). Furthermore, the formations containing the fish beds exhibit certain characteristics typical of lacustrine deposits and although they contain well-preserved fossils, diagnostic marine forms are absent. Hence the fish beds, except for the Lynslie Burn Fish Bed, were generally accepted as being of lacustrine origin, although the possibility that they were rather atypical lagoonal or deltaic deposits was not completely dismissed (Rolfe 1973*a*).

Palynological preparations from the Slot Burn, Dippal Burn, Logan and Fish Bed Formations comprise palynomorphs presumed to be entirely of continental origin. Marine palynomorphs such as acritarchs or chitinozoans were not recorded. This is also true for samples collected from the fish-bearing horizons, which gives a strong indication that the deposits accumulated in an environment without marine influence. However, palaeoenvironmental interpretation based on palynofacies analysis is not infallible. It is possible for abnormal circumstances to result in the absence of marine palynomorphs from marine deposits. For example, freshwater wedges may profoundly affect marine environments. Gray (1988) discussed abnormal conditions which may result in confusion of both marine and non-marine environments. However, such possibilities rely on unusual conditions, and are probably remote. Considering all of the evidence, it seems most probable that the red-bed deposits accumulated in a terrestrial–fluviatile environment, and the fish-bearing horizons, represent accumulation in freshwater lacustrine environments, except for the Lynslie Burn Fish Bed.

The Lynslie Burn Fish Bed of the North Esk inlier is also situated in a red-bed sequence which is interpreted as accumulating in a terrestrial–fluviatile environment. However, preparations from this horizon contain rare acanthomorph acritarchs (Pl. 4, fig. 2). The possibility that the acritarchs have been reworked from older marine strata has been examined but is considered unlikely as acritarchs are absent from preparations from similar stratigraphical levels in the other inliers. Furthermore, the Lynslie Burn Fish Bed differs from the fish beds in the other inliers because it is unlaminated, the fish remains are disarticulated and crinoid ossicles are present. Therefore it seems likely that this horizon represents a minor and transitory marine incursion. The Lynslie Burn Fish Bed overlies the 'Quartzite Conglomerate' and it is noteworthy that evidence of marine influence has not been recognized at this level in the other inliers.

GEOLOGICAL AND PALAEOBOTANICAL SIGNIFICANCE

The age constraint suggested by the Midland Valley sporomorph assemblages has several implications relating to the geology of the inliers. Firstly it gives a reliable age for the important faunas associated with the fish-beds. Sporomorph assemblages which indicate an early Wenlock age have been recovered from above, below and from the fish-bearing horizons. Secondly, palynofacies analysis provides further evidence that the red-bed sequence in the Hagshaw Hills and Lesmahagow inliers is entirely non-marine and that they are probably lacustrine and fluviatile rather than marginal marine deposits, but the Lynslie Burn Fish Bed may indeed represent a brief marine incursion. Thirdly, regarding tectonics and palaeogeography, the distribution of the samples which indicate an early Wenlock age clearly establishes that a large proportion of the red-bed sequences accumulated during early Wenlock times. At least 500 m of strata of red-bed facies in the Lesmahagow inlier is of early Wenlock age. Such evidence requires detailed consideration when formulating tectonic models for the Midland Valley during Silurian times.

The plant microfossil assemblages of the Midland Valley inliers have immense palaeobotanical significance. They are one of the few Llandovery or Wenlock palynomorph assemblages that has been interpreted as being of continental origin. Other examples are from the Lower Massanutten Sandstone in Virginia (Pratt *et al.* 1978), ?Clinton Strata, Pennsylvania (Strother and Traverse 1979) and possibly the Tuscarora Formation of Pennsylvania (Strother and Traverse 1979; Johnson 1985). Consequently, the Midland Valley palynomorph assemblages offer invaluable information concerning the nature of early Wenlock terrestrial plant microfossil associations and provide evidence pertinent to the study of early land plants.

Land-derived material in marine environments is obviously allochthonous and has probably undergone sorting during transportation. Therefore plant microfossils in marine palynomorph assemblages generally do not provide a true reflection of the composition and relative abundances of plant microfossils derived from continental vegetation. However, lacustrine and fluvial palynomorph assemblages are composed almost entirely of material which is derived exclusively from local vegetation and has generally not been transported far, and is consequently less likely to have been sorted. Therefore such assemblages provide a more accurate reflection of the composition of plant microfossil associations derived from local vegetation. The material can be compared with modern and fossil analogues and also with the record of similar microfloras described from elsewhere. This enables reasoned deductions regarding the nature and distribution of the vegetation and, to a certain extent, permits speculation concerning the physiology and evolution of the plants.

Text-figure 4 outlines the composition of the Midland Valley sporomorph assemblages and tabulates the results of frequency counts. The Midland Valley assemblages are remarkably constant in composition as the same species are present in nearly all of the samples and the frequency counts indicate little variation in abundance. This suggests that there was little or no variation in the composition of the local vegetation. Likewise but on an interregional scale, the Midland Valley assemblages are remarkably similar in composition to sporomorph assemblages described from strata of early Wenlock age from southern Britain, North America, North Africa and elsewhere. This indicates that the flora was not only well established, abundant and geographically widespread, but also cosmopolitan (see also Gray 1991). However, the lack of diversity shown by the sporomorph assemblages, only ten species, suggests that the vegetation comprised few forms. Recent *in situ* sporomorph studies may provide evidence concerning the nature of this simple flora. Fanning *et al.* (1991) have demonstrated that at least some late Silurian trilete spores are derived from rhyniophytoid plants, and certain cryptospores, namely true dyads and their related hilate cryptospores, are also derived from similar upright plants with terminal sporangia. This suggests that the early Wenlock flora from which the Midland Valley plant microfossils were derived may have contained similar rhyniophytoid plants. However, the derivation of other cryptospore morphotypes such as permanent tetrads and pseudodyads remains conjectural although their morphological similarities may be construed as reflecting similar relationships.

The cuticle-like sheets and tubular structures from the Midland Valley assemblages are remarkably similar to those described from other assemblages of early Wenlock age from elsewhere. This suggests that the ?land plants from which these enigmatic structures were derived were also geographically widespread and cosmopolitan. Furthermore, the abundance of such remains suggests that these ?land plants constituted an integral component of the vegetation. However, the precise affinities of the culticle-like sheets and tubular structures remain uncertain, although their overall form and facies relationships indicate that they are probably derived from some form of thalloid land plant (Edwards 1981; Strother 1988; Edwards and Burgess 1990; Burgess and Edwards 1991; Gensel *et al.* 1991). The nature of the reproductive propagules associated with these putative land plants remains unknown.

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REFERENCES

AL-AMERI, T. K. 1980. Palynology, biostratigraphy and palaeoecology of subsurface mid-palaeozoic strata from the Ghadames Basin, Libya. Unpublished Ph.D. thesis, University of London, King's College.

ALRIDGE, R. J., DORNING, K. J., HILL, P. J., RICHARDSON, J. B. and SIVETER, D. J. 1979. Microfossil distribution in the Silurian of Britain and Ireland. 433–438. *In* HARRIS, A. L., HOLLAND, C. H. and LEAKE, B. E. (eds). *The Caledonides of the British Isles – Reviewed. Special Publication of the Geological Society, London*, **8**. Scottish Academic Press, Edinburgh, 768 pp.

BANKS, H. P. 1975. The oldest vascular land plants: a note of caution. *Review of Palaeobotany and Palynology*, **20**, 13–25.

BARRON, H. F. 1989. Mid-Wenlock acritarchs from a Silurian inlier in the Cheviot Hills, NE England. *Scottish Journal of Geology*, **25**, 81–98.

BHARADWAJ, D. A. and VENKATACHALA, B. S. 1961. Spore assemblage out of a Lower Carboniferous shale from Spitsbergen. *Palaeobotanist*, **10**, 18–47.

BLIECK, A. and JANVIER, J. 1991. Silurian vertebrates. 345–388. *In* BASSETT, M. G., LANE, P. D. and EDWARDS, D. (eds). *The Murchison Symposium: proceedings of an international conference on the Silurian system. Special Papers in Palaeontology*, **44**, 1–397.

BLUCK, B. J. 1983. Role of the Midland Valley of Scotland in the Caledonian Orogeny. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **74**, 119–136.

—— 1985. The Scottish paratectonic Caledonides. *Scottish Journal of Geology*, **21**, 437–464.

BULL, E. E. 1987. Upper Llandovery dendroid graptolites from the Pentland Hills, Scotland. *Palaeontology*, **30**, 117–140.

BURGESS, N. D. 1991. Silurian cryptospores and miospores from the type Llandovery area, south-west Wales. *Palaeontology*, **34**, 575–599.

—— and EDWARDS, D. 1991. Classifications of uppermost Ordovician to Lower Devonian tubular and filamentous macerals from the Anglo-Welsh Basin. *Botanical Journal of the Linnean Society*, **106**, 41–66.

—— and RICHARDSON, J. B. 1991. Silurian cryptospores and miospores from the type Wenlock area, Shropshire, England. *Palaeontology*, **31**, 601–628.

CHIBRIKOVA, E. V. 1959. [Spores of the Devonian and older rocks of Bashkiria]. 3–116. *In* [*Data on Palaeontology and stratigraphy of Devonian and older deposits of Bashkiria*], Academy of Sciences of USSR, Bashkirian Branch, 247 pp. [In Russian].

COCKS, L. R. M. and TOGHILL, P. 1973. The biostratigraphy of the Silurian rocks of the Girvan district, Scotland. *Journal of the Geological Society, London*, **129**, 209–243.

COLTHURST, J. R. J. and SMITH, D. G. 1977. Palaeontological evidence for the age of the lower Palaeozoic rocks of the Slievenamon inliner, County Tipperary. *Proceedings of the Royal Irish Academy, Series B*, **77**, 143–158.

CRAMER, F. H. 1966. Hoegispheres and other microfossils *incertae sedis* of the San Pedro Formation (Siluro-Devonian boundary) near Valporquero, Léon, NW Spain. *Notas y Comunicaciones del Instituo Geológico y Minero de España*, **86**, 74–94.

—— 1968. Palynologic microfossils of the middle Silurian Maplewood Shale in New York. *Revue de Micropaléontologie*, **11**, 61–70.

—— 1969. Possible implications for Silurian paleogeography from the phytoplankton assemblages of the Rose Hill and Tuscarora Formations of Pennsylvania. *Journal of Paleontology*, **43**, 485–491.

—— 1971. Implications from mid-Palaeozoic palynofacies transgressions for rates of crustal movements, especially in the Wenlockian. *Anals da Academia Brasileira de Ciencias*, **43**, 51–66.

—— and DIEZ, M. DEL C. R. 1972. North American Silurian palynofacies and their spatial arrangement: acritarchs. *Palaeontographica, Abteilung B*, **138**, 107–180.

DORAN, R. J. P. 1974. The Silurian rocks of the southern part of the Slieve Phelim Inlier, County Tipperary. *Proceedings of the Royal Irish Academy*, **74**, 193–202.

DORNING, K. J. 1982. Early Wenlock acritarchs from the Knockgardner and Straiton Grit Formations of Knockgardner, Ayrshire. *Scottish Journal of Geology*, **18**, 267–273.

DUFFIELD, S. L. 1985. Land-derived palynomorphs from the Jupiter Formation (upper Llandoverian), Anticosti Island, Quebec. *Journal of Paleontology*, **59**, 1005–1010.

EDWARDS, D. 1982. Fragmentary non-vascular plant microfossils from the late Silurian of Wales. *Botanical Journal of the Linnean Society*, **84**, 223–256.

—— 1986. Dispersed cuticles of putative non-vascular plants from the Lower Devonian of Britain. *Botanical Journal of the Linnean Society*, **93**, 259–275.

—— and BURGESS, N. D. 1990. Terrestrialization: plants. 60–64. *In* BRIGGS, D. E. G. and CROWTHER, P. R. (eds). *Palaeobiology: a synthesis*. Blackwell Scientific Publication, Oxford, 583 pp.

—— and FANNING, U. 1985. Evolution and environment in the late Silurian–early Devonian: the rise of the pteridophytes. *Philosophical Transactions of the Royal Society of London, Series B*, **309**, 147–165.

EDWARDS, D. and ROSE, V. 1984. Cuticles of *Nematothallus*: a further enigma. *Botanical Journal of the Linnean Society*, **88**, 35–54.

EMO, G. T. and SMITH, D. G. 1978. Palynological evidence for the age of the lower Palaeozoic rocks of the Slieve Aughty, counties Clare and Galway. *Proceedings of the Royal Irish Academy, Series B*, **78**, 281–294.

FANNING, U., RICHARDSON, J. B. and EDWARDS, D. 1991. A review of *in situ* spores in Silurian land plants. 25–47. *In* BLACKMORE, S. and BARNES, S. H. (eds). *Pollen and spores. Systematics Association Special Volume*, **44**, Clarendon Press, Oxford, 391 pp.

FENSOME, R. A., WILLIAMS, G. L., SEDLEY BARSS, M., FREEMAN, J. M. and HILL, J. M. 1991. Acritarchs and fossil prasinophytes: an index to genera, species and intraspecific taxa. *American Association of Stratigraphic Palynologists, Contributions Series No. 25*, 771 pp.

FORD, J. H. 1971. Palynology of some upper Silurian and Lower Old Red Sandstone sediments in the Midland Valley of Scotland. Unpublished Ph.D. thesis, University of London, King's College.

GENSEL, P. G., JOHNSON, N. G. and STROTHER, P. K. 1991. Early land plant debris (Hooker's 'waifs and strays'?). *Palaios*, **5**, 520–547.

GRAY, J. 1985. The microfossil record of early land plants: advances in understanding of early terrestrialization, 1970–1984. *Philosophical Transactions of the Royal Society of London, Series B*, **309**, 167–195.

—— 1988. Evolution of the freshwater ecosystem: the fossil record. *Palaeogeography, Palaeoclimatology and Palaeoecology*, **62**, 1–214.

—— 1991. *Tetrahedraletes, Nodospora*, and the 'cross' tetrad: an accretion of myth. 49–87. *In* BLACKMORE, S. and BARNES, S. H. (eds). *Pollen and spores. Systematics Association Special Volume*, **44**, Clarendon Press, Oxford, 391 pp.

—— and BOUCOT, A. J. 1971. Early Silurian spore tetrads from New York: earliest new world evidence for vascular plants. *Science*, **173**, 918–921.

—— —— 1977. Early vascular land plants: proof and conjecture. *Lethaia*, **10**, 145–174.

—— —— 1989. Is *Moyeria* a euglenoid? *Lethaia*, **22**, 447–456.

—— COLBATH, G. K., ALVARO DE FARIA, COUCOT, A. J. and ROHR, D. M. 1985. Silurian-age fossils from the Paleozoic Parana Basin, southern Brazil. *Geology*, **13**, 521–525.

—— MASSA, D. and BOUCOT, A. J. 1982. Caradocian land plant microfossils from Libya. *Geology*, **10**, 197–201.

—— —— —— 1983. Comment and reply on 'Caradocian land plant microfossils from Libya'. *Geology*, **11**, 316–318.

—— THERON, J. N. and BOUCOT, A. J. 1986. Age of the Cedarberg Formation, South Africa and early land plant evolution. *Geological Magazine*, **123**, 445–454.

GRÈBE, H. 1971. A recommended terminology and descriptive method for spores. 7–34. *In* ALPERN, B. and NEVES, R. (eds). *Microfossiles organiques du Paléozoique, CIMP special volume 4*, 87 pp.

HEINTZ, A. 1939. Cephalaspida from the Downtonian of Norway. *Skrifter Utgitt Av Det Norske Videnskaps Akademi I Oslo*, **1**, 1–119.

HILL, P. J., PARIS, F. and RICHARDSON, J. B. 1985. Silurian palynomorphs. *Journal of Micropalaeontology*, **4**, 27–48.

HOFFMEISTER, W. S. 1959. Lower Silurian plant spores from Libya. *Micropaleontology*, **5**, 331–334.

HOLLAND, C. H. and SMITH, D. G. 1979. Silurian rocks of the Capard inlier, County Laois. *Proceedings of the Royal Irish Academy, Series B*, **79**, 99–110.

JENNINGS, J. S. 1961. The geology of the eastern part of the Lesmahagow inlier. Unpublished Ph.D. thesis, University of Edinburgh.

JOHNSON, N. G. 1985. Early Silurian palynomorphs from the Tuscarora Formation in central Pennsylvania and their palaeobotanical and geological significance. *Review of Palaeobotany and Palynology*, **45**, 307–360.

LAMONT, A. 1947. Gala–Tarannon beds in the Pentland Hills, near Edinburgh. *Geological Magazine*, **84**, 193–208, 289–303.

LEGGETT, J. K. 1980. The sedimentological evolution of a Lower Palaeozoic accretionary fore-arc in the Southern Uplands of Scotland. *Sedimentology*, **27**, 401–407.

LUBER, A. A. and WALTZ, I. E. 1938. Klassifikatsiya i stratificheskoe zhachenie spor nekotovich kamennougl'nich mestorojdenii SSSR. *Trudy TSNIGRI, Moscow*, **105**, 1–45. [In Russian].

MCGIVEN, A. 1968. Sedimentation and provenance of post-Valentian conglomerates up to and including the basal conglomerates of the Lower Old Red Sandstone in the southern part of the Midland Valley of Scotland. Unpublished Ph.D. thesis, University of Glasgow.

MCGREGOR, D. C. 1984. Late Silurian and Devonian spores from Bolivia. *Miscelánea. Academia Nacional de Ciencias, Cordoba*, **69**, 57 pp.

MCGREGOR, D. C. and NARBONNE, G. M. 1978. Upper Silurian trielete spores and other microfossils from the Read Bay Formation, Cornwallis Island, Canadian Arctic. *Canadian Journal of Earth Sciences*, **15**, 1292–1303.

MCKERROW, W. S. 1988*a*. The development of the Iapetus Ocean from the Arenig to the Wenlock. 405–414. *In* HARRIS, A. L. and FETTES, D. J. (eds). *The Caledonian–Appalachian orogen. Special Publication of the Geological Society, London*, **38**, 643 pp.

—— 1988*b*. Wenlock and Givetian deformations in the British Isles and the Canadian Appalachians. 437–448. *In* HARRIS, A. L. and FETTES, D. J. (eds). *The Caledonian–Appalachian orogen. Special Publication of the Geological Society, London*, **38**, 643 pp.

—— DEWEY, J. F. and SCOTESE, C. R. 1991. The Ordovician and Silurian development of the Iapetus. 165–178. *In* BASSETT, M. G., LANE, P. D. and EDWARDS, D. (eds). *The Murchison Symposium: proceedings of an international conference on the Silurian system. Special Papers in Palaeontology*, **44**, 1–397.

MARTIN, F. 1974. Ordovicien Supérieur et Silurien Inférieur à Deelijk (Belgique), palynofacies et microfacies. *Institut Royal des Sciences Naturelles de Belgique, Mémoire*, **174**, 1–71.

MILLER, M. A. and EAMES, L. E. 1982. Palynomorphs from the Silurian Medinna Group (lower Llandovery) of the Niagara Gorge, Lewiston, New York, U.S.A. *Palynology*, **6**, 221–254.

MYKURA, W. 1991. Old Red Sandstone. 297–342. *In* CRAIG, G. Y. (ed.). *Geology of Scotland* (third edition). Scottish Academic Press, Edinburgh, 612 pp.

PICKERING, K. T., BASSETT, M. G. and SIVETER, D. J. 1988. Late Ordovician–early Silurian destruction of the Iapetus Ocean: Newfoundland, British Isles and Scandinavia – a discussion. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **79**, 361–382.

PONTONIÉ, H. 1983. Die Flora des Rotligenden von Thuringen. *Abhandlungen der Königlich Preussischen Geologisdchen-Landesanstalt*, **9**, 1–298.

PRATT, L. M., PHILLIPS, T. L. and DENNISON, J. M. 1978. Evidence of non-vascular land plants from the early Silurian (Llandovery) of Virginia, U.S.A. *Review of Palaeobotany and Palynology*, **25**, 121–149.

REINSCH, P. E. 1891. Neue Untersuchugen über die Mikrostrukt Steinkohle des Carbon, Dyas und Trias. T. O. Weigel, Leipzig, 124 pp.

RICHARDSON, J. B. 1967. Some British lower Devonian spore assemblages and their stratigraphic significance. *Review of Palaeobotany and Palynology*, **1**, 111–129.

—— 1988. Late Ordovician and early Silurian cryptospores and miospores from northeast Libya. 89–109. *In* EL-ARNAUTI, A., OWENS, B. and THUSU, B. (eds). *Subsurface palynostratigraphy of northeast Libya*. Garyounis University Publications, Benghazi, Libya, 276 pp.

—— and EDWARDS, D. 1989. Sporomorphs and plant megafossils. 216–226. *In* HOLLAND, C. H. and BASSETT, M. G. (eds). *A global standard for the Silurian system. National Museum of Wales Geological Series No. 9*, Cardiff, 325 pp.

—— and IOANNIDES, N. 1973. Silurian palynomorphs from the Tanezzuft and Acacus Formations, Tripolitania, North Africa. *Micropaleontology*, **19**, 257–307.

—— and LISTER, T. R. 1969. Upper Silurian and lower Devonian spore assemblages from the Welsh Borderland and South Wales. *Palaeontology*, **12**, 201–252.

—— and MCGREGOR, D. C. 1986. Silurian and Devonian spore zones of the Old Red Sandstone continent and adjacent regions. *Bulletin of the Geological Survey of Canada*, **364**, 79 pp.

—— FORD, J. H. and PARKER, F. 1984. Miospore correlation and age of some Scottish Lower Old Red Sandstone sediments from the Strathmore region (Fife and Angus). *Journal of Micropalaeontology*, **3**, 109–124.

RITCHIE, A. 1963. Palaeontological studies on Scottish Silurian Fish Beds. Unpublished Ph.D. thesis, University of Edinburgh.

ROBERTSON, G. 1989. A palaeoenvironmental interpretation of the Silurian rocks in the Pentland Hills, near Edinburgh. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **80**, 127–141.

RODRIGUEZ, R. M. 1978. Miospores de la formación San Pedro/Furada (Silúrico Superior-Devónico Inferior), Cordillera Cantábrica, España. *Palinología, Número Extraordinario*, **1**, 407–433.

—— 1983. *Palinología de las formaciones del Silúrico Superior–Devónico Inferior de la Cordillera Cantábrica.* Publicaciones de la Universidad de Léon (España), 231 pp.

ROLFE, W. D. I. 1961. The geology of the Hagshaw Hills Silurian inlier, Lanarkshire. *Transactions of the Edinburgh Geological Society*, **18**, 240–269.

—— 1973*a*. Excursion 14. The Hagshaw Hills Silurian inlier. 105–119. *In* BLUCK, B. J. (ed.). *Excursion guide to the geology of the Glasgow district*. The University Press, Glasgow, 181 pp.

—— 1973*b*. Excursion 15. Silurian arthropod and fish assemblages from Lesmahagow, Lanarkshire. 119–126. *In* BLUCK, B. J. (ed.). *Excursion guide to the geology of the Glasgow district*. The University Press, Glasgow, 181 pp.

ROLFE, W. D. I. and FRITZ, M. A. 1966. Recent evidence for the age of the Hagshaw Hills Silurian inlier, Lanarkshire. *Scottish Journal of Geology*, **2**, 159–164.

SMELROR, M. 1987. Llandovery and Wenlock miospores and spore-like microfossils from the Ringerike district, Norway. *Norsk Geologisk Tidsskrift*, **67**, 143–150.

SMITH, D. G. 1975. Wenlock plant spores and tetrads from County Mayo, Ireland. *Geological Magazine*, **112**, 411–414.

SMITH, D. G. 1979. The distribution of trilete spores in Irish Silurian rocks. 423–431. *In* HARRIS, A. L., HOLLAND, C. H. and LEAKE, B. E. (eds). *The Caledonides of the British Isles – reviewed. Special Publication of the Geological Society, London*, **8**. Scottish Academic Press, Edinburgh, 768 pp.

STROTHER, P. K. 1988. New species of *Nematothallus* from the Silurian Bloomsburg Formation of Pennsylvania. *Journal of Paleontology*, **62**, 967–982.

—— and TRAVERSE, A. 1979. Plant microfossils from Llandovery and Wenlock rocks of Pennsylvania. *Palynology*, **3**, 1–21.

THUSU, B. 1983. Acritarches provenant de l'Ilion shale (Wenlockien), Utica, New York. *Revue de Micropaléontologie*, **16**, 137–146.

TURNER, R. E. 1984. Acritarchs from the type area of the Ordovician Caradoc Series, Shropshire, England. *Palaeontographica, Abteilung B*, **190**, 87–157.

VAVRDOVÁ, M. 1982. Recycled acritarchs in the uppermost Ordovician of Bohemia. *Časopis pro Mineralogii a Geologii*, **27**, 337–345.

—— 1984. Some plant microfossils of possible terrestrial origin from the Ordovician of central Bohemia. *Věstník Ústředního Ústavu Geologického*, **59**, 165–170.

—— 1988. Further acritarchs and terrestrial plant remains from the late Ordovician at Hlásná Třebaň (Czechoslovakia). *Časopis pro Mineralogii a Geologii*, **33**, 1–10.

—— 1989. New acritarchs and miospores from the late Ordovician of Hlásná Třebaň, Czeckoslovakia. *Časopis pro Mineralogii a Geologii*, **34**, 403–420.

WALTON, E. K. and OLIVER, G. J. H. 1991. Lower Palaeozoic – stratigraphy. 105–137. *In* CRAIG, G. Y. (ed.). *Geology of Scotland* (third edition). Scottish Academic Press, Edinburgh, 612 pp.

WELLMAN, C. H. 1991. Land-derived palynomorphs from Silurian and Lower Devonian deposits of Scotland. Unpublished Ph.D. thesis, University of Wales.

WESTOLL, T. S. 1951. The vertebrate-bearing strata of Scotland. *Report of the XVIIIth International Geological Congress, London, 1948*, **XI**, 5–21.

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APPENDIX 1

FORMATION	SAMPLE NUMBER	NATIONAL GRID REFERENCE	LOCATION
DBF	BL13	2691663138	Section on north bank of Dippal Burn near derelict footbridge
DBF	BL15	2693063181	North bank of Dippal Burn at the eastern end of the large gorge
DBF	BL16	2692763174	North bank of Dippal Burn at the western end of the large gorge
DBF	DL13	2691663138	Section on north bank of Dippal Burn near derelict footbridge
DBF	DL14	2691663138	Section on north bank of Dippal Burn near derelict footbridge
SBF	BL7	2677263193	Exposure in south bank of Slot Burn
SBF	CL16	2692763173	Exposure in north bank of Logan Water
SBF	DL8	2680263206	Exposure in north bank of Slot Burn west of the gulley
LF	CL5	2763363780	Channel deposit on north bank of the hairpin bend in Logan Water
LF	CL6		
LF	CL7		
LF	CL8		
LF	CL9		
LF	CL10		
LF	CL11	276563778	Channel deposit in north bank of Logan Water
LF	CL12	276563778	Channel deposit in north bank of Logan Water
LF	CL13	2761663776	South bank of Logan Water
LF	CL14	2761663776	South bank of Logan Water
FBF	AH5	2761362838	East shore of Glenbuck Loch (Rolfe 1973, locality 9)
FBF	BH4	2761462850	East shore of Glenbuck Loch (Rolfe 1973, locality 9)
FBF	BH8	2761462840	East shore of Glenbuck Loch (Rolfe 1973, locality 9)
FBF	BH9	2761462840	East shore of Glenbuck Loch (Rolfe 1973, locality 9)
FBF	AH6	2777262905	Headwaters of Sheil Burn (Rolfe 1973, locality 12)
FBF	AH10		
FBF	BH13		
FBF	BH14		
FBF	BH15		
HF(LBFB)	BP7	3131775746	Exposure on south bank of Lynslie Burn (Robertson 1986, locality 29)
HF(LBFB)	CP6		
HF(LBFB)	CP7		
HF(LBFB)	CP9		

Key:

DBF = Dippal Burn Formation, Lesmahagow inlier; SBF = Slot Burn Formation, Lesmahagow inlier; LF = Logan Formation, Lesmahagow inlier; FBF = Fish Bed Formation, Hagshaw Hills inlier; HF(LBFB) = Henshaw Formation (Lynslie Burn Fish Bed), North Esk inlier.