SPOROMORPH ASSEMBLAGES FROM THE 'LOWER OLD RED SANDSTONE' OF LORNE, SCOTLAND

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ABSTRACT. The basal strata of the 'Lower Old Red Sandstone' in the Lorne area of the Grampian Highlands of Scotland, have yielded plant microfossil assemblages comprising sporomorphs (cryptospores and miospores) and plant fragments (tubular structures and cuticles). The sporomorphs are described systematically, and one genus (*Abditusdyadus*), 19 species (*Artemopyra laevigata*, *A. robusta*, *Chelinohilates lornensis*, *C. sinuosus*, *Cymbohilates amplus*, *Cy. histricosus*, *Cy. microgranulatus*, *Hispanaediscus*? *irregularis*, *Qualisaspora kidstonii*, *Abditusdyadus histosus*, *Ab. chalazus*, *Ab. laevigatus*, *Retusotriletes maccullocki*, *Dibolisporites ardchoircii*, cf. *Amicosporites discus*, cf. *Am. macconochiei*, cf. *Am. symesii*, *Aneurospora geikiei* and *An. hispidica*), two varieties (*C. sinuosus* var. *sinuosus* and *C. sinuosus* var. *angustus*) and one combination *Velatitetras* (*Nodospora*) *retimembrana* are proposed as new. The sporomorph assemblages are all similar and suggest an earliest Lochkovian (earliest Devonian) age. The new biostratigraphical information indicates that the basal strata exposed in the Lorne area on the island of Kerrera and on the mainland at Oban are of similar age. Furthermore, the sporomorph assemblages occur below the Lorne lavas which have been dated radiometrically; combined, these provide a geochronological tie point of value for age determination of the Silurian–Devonian boundary. The plant microfossil assemblages are interpreted as having accumulated in continental, probably lacustrine, environments. This paper describes the first well preserved land plant microfossil assemblages of earliest Devonian age recovered from non-marine deposits and provides an important insight into the nature of terrestrial vegetation at this time. There are a high abundance and diversity of cryptospores, suggesting that cryptospore-producing plants were thriving and co-existed with miospore-producing plants, which were presumably of vascular status. The presence of rare envelope-enclosed cryptospores is intriguing as similar spores have only rarely been reported from post early Silurian strata. Small scale variation in the distribution of vegetation, possibly associated with differences in environment or palaeogeography, is suggested by the presence of *Dibolisporites* and the paucity of patinate miospores and *Synorisporites* spp.

THE 'Lower Old Red Sandstone' of the Lorne area comprises a thin veneer of basal sedimentary rocks overlain by a vertically and laterally extensive development of lavas (Text-figs 1–3). They rest with angular unconformity on Dalradian slates. Until recently the basal sedimentary rocks were not securely age constrained and their relationship with other 'Lower Old Red Sandstone' deposits was unclear. Previous age determinations were based on rare fish and arthropod faunas which were believed to indicate a Downtonian (Přídolí), and in some places Dittonian (Lochkovian), age (Waterston 1965). However, such faunas are not well understood and age designations based on them are not satisfactory. The discovery of plant microfossil assemblages provided an opportunity for independent age determination (Marshall 1991; Wellman 1991). The plant microfossil assemblages comprise sporomorphs and plant fragments (Wellman 1995) and are particularly important as they are the first well preserved land plant microfossil assemblages of earliest Devonian age recovered from non-marine deposits.

GEOLOGICAL SETTING

History of research

The rocks of the Lorne area were first classified by MacCullock (1819) who divided them into the primary, secondary and overlying units. The primary unit included the 'slates' of Kerrera (i.e.

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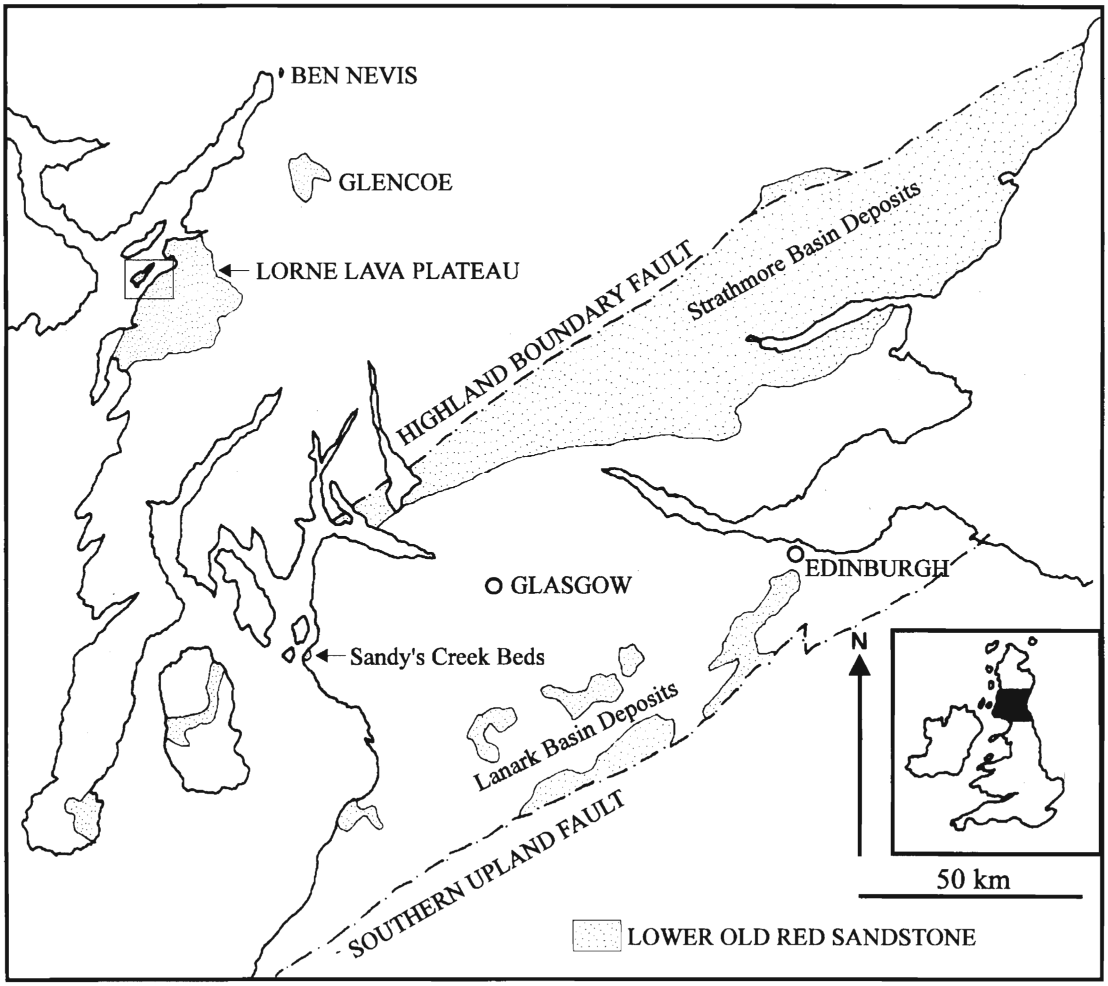
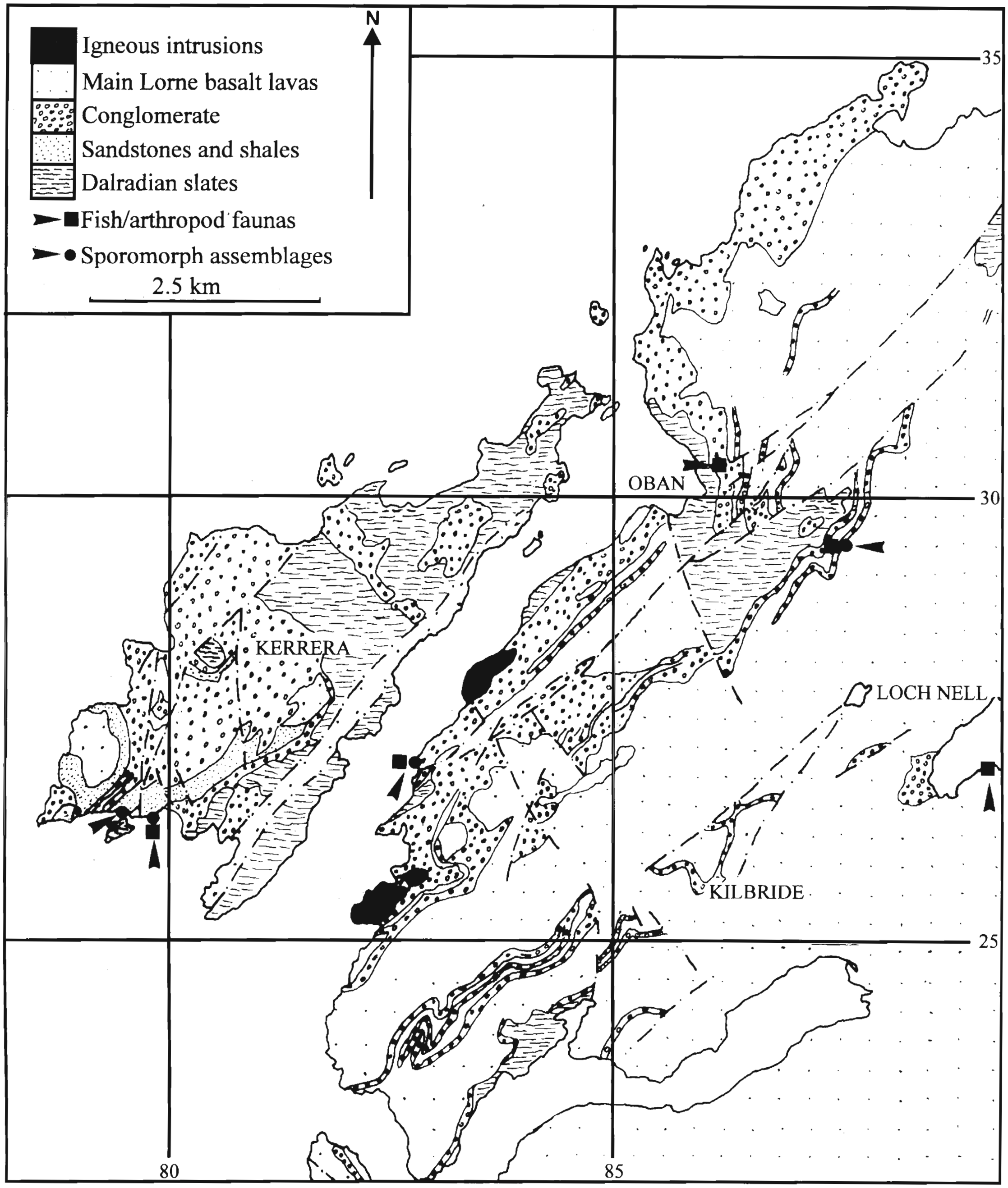


TEXT-FIG. 1. Location map of the 'Lower Old Red Sandstone' in the Midland Valley and Grampian Highlands of Scotland. The area delineated in the Lorne region represents the area of the geological map illustrated in Text-figure 2.

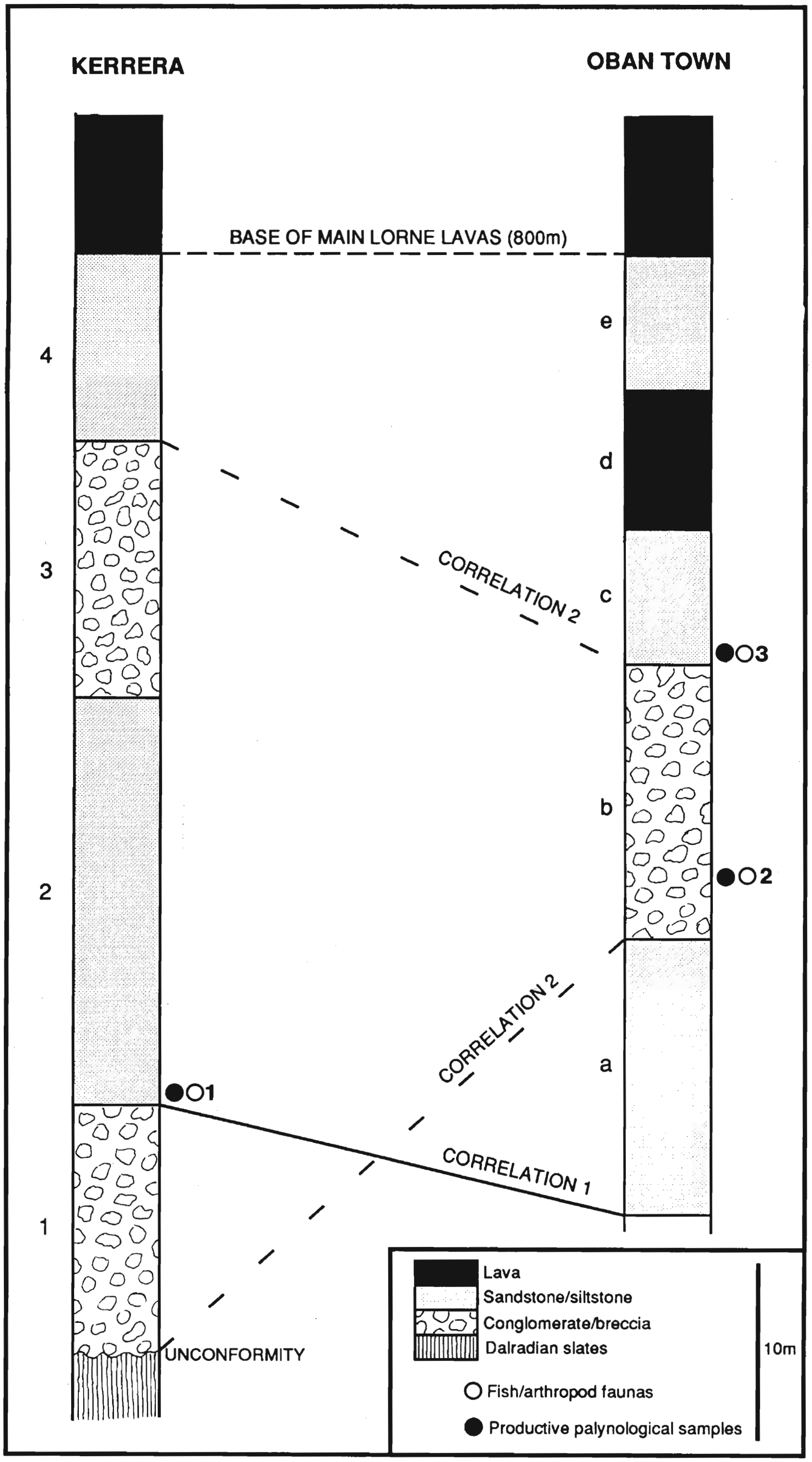
the Dalradian slates), the secondary unit the red sandstone and conglomerate of Kerrera and Oban, and the overlying unit the lavas of Oban and Mull. Boué (1820) suggested that the Lorne lavas may be of 'Lower Old Red Sandstone' age but eventually decided to group them with the Mull lavas, which he considered to be of post *Gryphea* Limestone (Jurassic) age. Geikie initially followed Boué and advocated a Jurassic age for the lavas (Geikie 1861) but subsequently assigned a 'Lower Old Red Sandstone' age to both the lavas and sedimentary rocks (Geikie 1865). Eventually, fossil evidence which proved the general age of the deposits was recovered. During 1897 Macconochie, collecting for the Geological Survey, discovered typical 'Lower Old Red Sandstone' fossil fish and plants from the basal strata of Kerrera (Geikie 1897).

In 1908 the Geological Survey produced a comprehensive geological map of the area along with an associated explanation, *The geology of the country near Oban and Dalmally* (*explanation of sheet 45*). Subsequently, a more detailed description of the geology of the area was published (Lee and Bailey 1925), which included a summary of further fossil finds and a tentative lithostratigraphical correlation of the various exposures. More recently, Waterston (1965) summarized the geology of



TEXT-FIG. 2. Geological map of Kerrera and the area around Oban (adapted from Lee and Bailey 1925).

the area and suggested that the fossils from the basal strata of Kerrera were probably Downtonian (Přídolí) (L. B. H. Tarlo and P. R. Gurr, pers. comm.) and those from the basal strata from Oban town were probably Dittonian (Lochkovian). Subsequently, Morton (1979) undertook a comprehensive sedimentological study of the 'Lower Old Red Sandstone' in the north-east of the Midland Valley and Lorne area and, in interpreting the ages suggested by Waterston (1965),



TEXT-FIG. 3. For caption see opposite.

equated the Kerrera sequence with the Stonehaven Group at Stonehaven (which was at that time believed to be of Přídolí age) and the Oban sequence with the Arbuthnott Group of the Strathmore area (which is late early Lochkovian; Richardson *et al.* 1984). However, it has now been demonstrated that the Stonehaven Group is of late Wenlock–earliest Ludlow age (Marshall 1991; Wellman 1991, 1993*a*) suggesting that it is older than the Lorne deposits. Thirlwall (1988) reported a Rb/Sr age determination of 415–424 Ma for the Lorne lava plateau.

Lorne stratigraphical successions

In the following account, the terminology of Lee and Bailey (1925) is used (Text-fig. 3). Lee and Bailey divided the sedimentary sequences developed below the main Lorne lavas into Groups 1–4 for the sequence exposed on Kerrera and Groups a–e for the sequence exposed near Oban. They attempted to correlate the other exposures with these two sequences, although they accepted that lithostratigraphical correlation was difficult. The most important sequences are on the south coast of Kerrera, in Oban and along the Sound of Kerrera.

On Kerrera, a thin basal breccia (Group 1) rests with angular unconformity on Dalradian slates. The breccia is succeeded by up to 300 m of conglomerates, sandstones and siltstones with local intercalations of lava (Groups 2–4). However, clasts of lava are present in the conglomerates which lie below the first lavas in the succession, suggesting that lava was being extruded into other parts of the basin at an early stage and provided some of the detritus for the lower conglomerates. A siltstone at the base of the Group 2 sandstones and siltstones, exposed on the south-east shore of the island, has yielded plant and fish remains (Lee and Bailey 1925; Waterston 1965). The fauna was interpreted as Downtonian (Přídolí) (Tarlo and Gurr *in* Waterston 1965). Although Tarlo and Gurr (1969) suggested that the fossiliferous siltstones were deposited in a tidal cuvette, a continental, most probably lacustrine, origin has been preferred by most workers (Mykura 1991).

The sequence exposed on the mainland, in the vicinity of Oban, comprises conglomerates and sandstones (Groups a and b) succeeded by intercalations of shales and basalt lava (Groups c–e). A fauna comprising fish, plants, ostracods and a millipede has been recovered from Group c shales exposed in Oban and at an equivalent horizon exposed in the railway cutting 1·5 km east of Oban (Lee and Bailey 1925; Waterston 1965). Waterston (1965) suggested that the fauna 'has a Dittonian aspect... and may well be from a horizon higher than that of Kerrera'.

On the mainland, a further sequence is exposed south of Oban on the coast along the Sound of Kerrera. Fish and plant remains have been recovered from grey siltstones, which are intercalated with conglomerates, and were correlated by Lee and Bailey (1925) with the Group b conglomerates of the Oban town sequence.

The 'Lower Old Red Sandstone' sedimentary sequences developed in the Lorne area are difficult to correlate as there is extensive vertical and lateral variation. Lee and Bailey (1925) accepted this problem but nevertheless attempted tentative lithostratigraphical correlations (Text-fig. 3). They suggested that the lowermost sandstone (2) present in the Kerrera sequence probably corresponds to the basement sandstone (a) in the Oban sequence, and that the basement conglomerate (1) of Kerrera consequently does not occur on the mainland. However, they also stated that 'on the other hand, it must be admitted that the mixed sequence (1–3), of Kerrera, may represent the Oban conglomerate (b), since the latter breaks up into a mixed series of conglomerate and sandstone when traced southwards on the mainland'. These tentative correlations indicate that the fossiliferous horizons of Kerrera and Oban may be at different levels (Text-fig. 3), and this possibly fuelled the

TEXT-FIG. 3. Stratigraphical successions developed on Kerrera and near Oban (data from Lee and Bailey 1925). The numbers/letters to the left of the stratigraphical columns refer to the stratigraphical nomenclature adopted by Lee and Bailey (1925). The two correlations illustrated refer to tentative correlations suggested by Lee and Bailey (1925). The likely horizon of the fish/arthropod faunas and productive palynological samples is illustrated. Fauna 1 is from the south coast of Kerrera, Fauna 2 from the Sound of Kerrera south of Oban (shale interbedded with conglomerate), and Fauna 3 from Oban and the railway cutting at Glen Crutten to the east of Oban (see Appendix).

TABLE 1. Sporomorph taxa reported: occurrence and abundance in selected samples. Locality data (see Appendix): 1, south shore of Kerrera, exposure in west of bay located east of Ardmore Farm; 2, south shore of Kerrera, exposure in foreshore of bay located west of Ardmore Farm; 3, mainland south of Oban, exposure in bay west of Gallanach House Lodge (Port Caraig na Maraig). Sporomorphs from the productive sample from the railway cutting east of Oban (BOB1) are poorly preserved; species are difficult to recognize and consequently a species log was not attempted. However, the microflora shares enough elements in common with the other sporomorph assemblages from Lorne to suggest tentatively that the sporomorph assemblages are similar. Occurrence data: X, present; 0, not reported; ?, possibly present but not positively identified. Abundance data: R, rare (less than 5 specimens per slide), M, medium abundance (5–15 specimens per slide) and C, common (more than 15 specimens per slide). Abundance estimate based on number of specimens encountered. At least six slides were examined for each sample.

Locality				
1	2	3	Abundance:	Sporomorphs
				NAKED ALETE CRYPTOSPORE MONADS
X	X	X	C	Laevigate, naked, alete cryptospore monads
X	0	X	R	*Fustisispora aenigma* Wellman, 1993*b*?
				HILATE CRYPTOSPORES
X	X	X	C	*Laevolancis divellomedia* (Chibrikova) Burgess and Richardson, 1991
X	X	X	C	*Laevolancis plicata* Burgess and Richardson, 1991
X	X	X	M	*Artemopyra laevigata* sp. nov.
X	X	X	C	*Artemopyra robusta* sp. nov.
X	X	X	C	*Chelinohilates lornensis* sp. nov.
X	X	X	C	*Chelinohilates sinuosus* var. *sinuosus* sp. et var. nov.
X	X	X	M	*Chelinohilates sinuosus* var. *angustus* sp. et var. nov.
X	X	X	R	*Cymbohilates amplus* sp. nov.
X	X	X	C	*Cymbohilates allenii* var. *magnus* Richardson, 1996
X	X	0	R	*Cymbosporites hystricosus* sp. nov.
X	X	X	M	*Cymbohilates microgranulatus* sp. nov.
0	X	0	R	*Cymbosporites*? sp. A
X	X	0	M	*Hispanaediscus*? *irregularis* sp. nov.
X	X	X	C	*Hispanaediscus* cf. *verrucatus* Cramer emend. Burgess and Richardson, 1991
				NAKED UNFUSED CRYPTOSPORE DYADS (TRUE DYADS)
X	X	X	C	'dyads of *Laevolancis plicata*' (*Dyadospora murusattenuata*)
X	X	X	C	'dyads of *Laevolancis divellomedia*' (*Dyadospora murusdensa*)
X	X	0	R	'dyads of *Chelinohilates sinuosus* var. *sinuosus*'
X	0	0	R	'dyads of *Chelinohilates sinuosus* var. *angustus*'
0	0	X	R	'dyads of *Chelinohilates lornensis*'
X	X	0	R	'dyads of *Cymbohilates hudwickensis*'
				NAKED UNFUSED CRYPTOSPORE TETRADS
X	X	X	C	*Tetrahedraletes medinensis* Strother and Traverse emend. Wellman and Richardson, 1993
				NAKED FUSED CRYPTOSPORE DYADS (PSEUDODYADS)
X	X	X	M	*Pseudodyadospora petasus* Wellman and Richardson, 1993
				NAKED FUSED CRYPTOSPORE TETRADS
X	X	X	R	*Cheilotetras caledonica*? Wellman and Richardson, 1993
				ENVELOPE ENCLOSED CRYPTOSPORES
?	X	?	R	*Qualisaspora kidstonii* sp. nov.
0	X	0	R	*Abditusdyadus chalazus* gen. et sp. nov.
X	0	0	R	*Abditusdyadus histosus* gen. et sp. nov.
X	X	0	R	*Abditusdyadus laevigatus* gen. et sp. nov.

TABLE 1. (*cont.*)

Locality 1	2	3	Abundance:	Sporomorphs
X	X	X	R	*Velatitetras* (*Nodospora*) *retimembrana*? (Miller and Eames, 1982) comb. nov.
				MIOSPORES
X	X	X	C	*Retusotriletes maccullockii* sp. nov.
X	X	X	M	*Retusotriletes maculatus* McGregor and Camfield, 1976
X	X	X	M	*Retusotriletes rotundus* (Streel) Lele and Streel, 1969
X	X	0	R	*Retusotriletes* sp. A
X	X	X	R	*Retusotriletes* spp.
X	X	X	M	*Apiculiretusispora* sp. A
X	X	X	R	*Apiculiretusispora* spp.
X	X	X	M	*Dibolisporites ardchoricii* sp. nov.
X	X	X	C	*Ambitisporites avitus* Hoffmeister, 1959
X	X	X	C	*Ambitisporites dilutus* (Hoffmeister) Richardson and Lister, 1969
X	X	0	M	*Ambitisporites* sp. A
X	X	X	M	cf. *Amicosporites discus* sp. nov.
X	X	X	R	cf. *Amicosporites macconochiei* sp. nov.
X	X	X	C	cf. *Amicosporites symesii* sp. nov.
X	X	X	C	*Aneurospora geikiei* sp. nov.
X	X	X	C	*Aneurospora hispidica* sp. nov.
X	X	0	R	*Aneurospora* sp. A Wellman, 1993*b*
X	X	X	R	*Aneurospora* sp. B
0	X	0	R	*Emphanisporites* sp. A
X	X	?	R	*Emphanisporites* sp. B
X	X	X	R	*Emphanisporites* spp.
0	X	X	R	*Synorisporites* sp. A
X	X	X	R	*Synorisporites* spp.
X	X	X	R	*Archaeozonotriletes chulus* (Cramer) Richardson and Lister, 1969
X	X	0	R	*Chelinospora* sp. A
X	X	X	R	*Chelinospora* spp.
X	X	X	R	*Cymbosporites* spp.
X	X	X	C	Tetrads of trilete spores

arguments that the faunas are of different age. However, the sedimentary rocks are notoriously difficult to correlate and such proposed lithostratigraphical correlations should not be used to provide evidence relating to the relative age of the faunas.

The basal sedimentary rock/lava intercalations are overlain, with overlap to the east and west, by up to 800 m of lava. The lavas cover an area of 300 km^2. They consist chiefly of basalts and andesites, although minor flows of dacite and rhyolite exist. Two distinctive ignimbrites are present high in the succession (Roberts 1966) which have been correlated with similar ignimbrites in the 'Lower Old Red Sandstone' sequence at Glen Coe to the north-east (Text-fig. 1).

PREVIOUS PALYNOLOGICAL INVESTIGATION

Marshall (1991) reported briefly on sporomorphs recovered from the 'Lower Old Red Sandstone' of the Lorne area. He outlined the overall characteristics of the assemblages but did not describe the sporomorphs systematically. He noted that spore associations from sedimentary rocks exposed on Kerrera and at Oban were similar and suggested an age range of latest Silurian to earliest Devonian, possibly more specifically earliest Devonian.

SAMPLING AND TECHNIQUES

Samples were collected from siltstones in the 'Lower Old Red Sandstone' successions exposed on Kerrera, from the mainland coast south of Oban, and also from scattered inland exposures. Palynologically productive samples were obtained from the south coast of Kerrera, the mainland coast south of Oban and the railway cutting 1·5 km east of Oban (Text-fig. 2) (see Appendix for locality details). Preservation is variable, but poor in most of the productive samples. However, certain horizons yielded exceptionally well preserved and diverse plant microfossil assemblages. The spores are dark brown (TAI 3–4), although it was possible to clear the residues by treatment with Schulze's solution. The assemblages are similar and comprise entirely land-derived forms (sporomorphs and plant fragments).

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 using a 10 μm mesh. The residue was strew mounted in 'Elvacite' mounting medium. The samples were oxidized for between 10 and 60 minutes using concentrated Schulze's solution in order to clear them and facilitate light microscope observation. For many preparations this treatment was highly effective. Transmitted light investigation with the use of Nomarskii interference contrast was carried out on a Zeiss Photomicroscope III. Additionally, stubs were strew mounted and gold coated for scanning electron microscopy using an Hitachi 800 Scanning Electron Microscope.

SYSTEMATIC PALAEONTOLOGY

Terminology

The descriptions of the miospores are organized in accordance with a standard morphology-based turma system of classification. The descriptions of cryptospores are organized under general headings relating to their gross morphology. The terminology of Grebe (1971), Wellman and Richardson (1993) and Richardson (1996) is used in the description of sporomorphs.

Repository of material and occurrence of taxa

Figured specimens are stored in the Palynology Section, Palaeontology Department, The Natural History Museum, London. Specimen location refers to standard England Finder co-ordinates from the Zeiss Photomicroscope III (no. 2562) housed in the same department. Scanning Electron Microscope print numbers refer to negatives stored in the Electron Microscopy Unit of The Natural History Museum, London. All of the taxa described and figured were recovered from the basal strata of the 'Lower Old Red Sandstone' of Lorne, either from Kerrera or the coast south of Oban (see Appendix). Data on the occurrence of taxa are outlined in Tables 1–2.

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

NAKED ALETE MONADS

Genus FUSTISISPORA Wellman, 1993*b*

Type species. *Fustisispora aenigma* Wellman, 1993*b*.

Fustisispora aenigma Wellman, 1993*b*?

Plate 1, figure 3; Plate 12, figure 2

?1993*b* *Fustisispora aenigma* Wellman, p. 130, fig. 8h–l.

Dimensions. 31(36)40 μm; eight specimens measured.

Remarks. These specimens are similar to those described by Wellman (1993*b*) from a late early–early late Lochkovian sporomorph assemblage from the Sandy's Creek Beds, Scotland. However, the

TABLE 2. Percentage frequency of sporomorph morphotypes in selected samples, based on counts of 200 determinate palynomorphs. Indeterminate palynomorphs were ignored. p = present, but not in sufficient quantities to feature in the count. See Appendix for details of assemblages.

	AK1	AK6	AOB5
Trilete spores	**17·5**	**17·5**	**23**
Laevigate	10	11	15
Retusoid	1	2	4·5
Crassitate	8·5	8·5	10
Patinate	0·5	0·5	0·5
Ornamented	7·5	6·5	8
Retusoid	0·5	3·5	3
Emphanisporites spp.	p	p	0·5
Equatorially crassitate	6·5	3	4·5
Patinate	0·5	p	p
Tetrads of trilete spores	**0·5**	**2**	1·5
Cryptospores	**82**	**80·5**	**75·5**
Laevigate alete monads	57·5	50·5	40
Sculptured alete monads	0·5	1·5	1
Laevigate hilate cryptospores	8·5	10	12·5
Sculptured hilate cryptospores	5·5	9·5	12·5
True dyads	3·5	3·5	3
Pseudodyads	p	0·5	0·5
Fused permanent tetrads	p	0·5	p
Unfused permanent tetrads	6·5	4·5	6
Envelope enclosed cryptospores	p	p	p

Lorne specimens are poorly preserved and are questionably assigned to this taxon because the nature of the main body of the spore is unclear.

NAKED UNFUSED DYADS (TRUE DYADS) AND HILATE CRYPTOSPORES

Genus LAEVOLANCIS Burgess and Richardson, 1991

Type species. *Laevolancis divellomedia* (Chibrikova) Burgess and Richardson, 1991.

Laevolancis divellomedia (Chibrikova) Burgess and Richardson, 1991

Plate 1, figures 4, 7; Plate 4, figures 1–2

Dimensions. 36(43)50 μm; 40 specimens measured.

Remarks. The Lorne specimens are typical examples of this laevigate hilate cryptospore species, which has been described from numerous localities of Silurian and Devonian age. *L. divellomedia* is sometimes present united in true dyads (placed with the taxon *Dyadospora murusdensa* Strother and Traverse emend. Burgess and Richardson, 1991). The dimensions of the dyads are: length = 57(69)85 μm, width = 42(57)75 μm (15 specimens measured). The hilate cryptospores are more abundant than the associated dyads, suggesting that the propagules were habitually shed following dyad dissociation.

Laevolancis plicata Burgess and Richardson, 1991

Plate 1, figure 8; Plate 5, figures 8, 11; Plate 13, figure 3

Dimensions. 33(37)43 μm; 20 specimens measured.

Remarks. The Lorne specimens are typical examples of this laevigate hilate cryptospore species which has been widely described from localities of Silurian and Devonian age. *L. plicata* is also present united in true dyads (placed with the taxon *Dyadospora murusattenuata* Strother and Traverse emend. Burgess and Richardson, 1991). The dimensions of the dyads are: length = 32(41)54 μm, width = 28(38)49 μm (35 specimens measured). In most samples the hilate cryptospores are more abundant than the associated intact dyads, suggesting that the propagules were habitually dispersed following dyad dissociation.

Genus ARTEMOPYRA Burgess and Richardson emend. Richardson, 1996

Type species. *Artemopyra brevicosta* Burgess and Richardson, 1991.

Artemopyra laevigata sp. nov.

Plate 3, figures 3–4, 6; Plate 12, figure 7

Derivation of name. Refers to the laevigate distal surface; *laevigatus* = smooth (Latin).

Holotype and type locality. Plate 3, figure 6, FM503 (slide AK6/2, co-ord. 030 1305; E.F. no. D61/3), sample AK6, basal strata of the 'Lower Old Red Sandstone', near Eilean Orasaig, Kerrera.

Paratypes. Plate 3, figures 3–4, FM502 (slide AOB1/3, co-ord. 093 1173; E.F. no. L47/2), sample AOB1, Oban. Plate 12; figure 7, SEM stub CW46, print P007891, sample AK6, Kerrera.

Diagnosis. A distally laevigate *Artemopyra*. Hilum sculptured with 25–40 radially disposed, narrow muri of variable character. The length of the muri is variable within specimens, extending from the crassitude for one-third to all of the way to the proximal pole.

Description. Amb circular to sub-circular. Sub-equatorial crassitude 0·75–1·5 μm wide delimits a more or less circular hilum. Hilum sculptured with radially disposed muri. The form of the radial muri is variable within and between specimens. There are usually between 25 and 40 muri, which may be straight or sinuous, extending from the crassitude for between one-third to all of the way to the proximal pole. The muri are less than 1 μm wide and 0·5 μm high, up to 2 μm apart, and occasionally bifurcate. On some specimens the muri thin and begin to meander and bifurcate in an erratic manner towards the proximal pole. The spores are distally laevigate.

Dimensions. 33(39)48 μm; 17 specimens measured.

EXPLANATION OF PLATE 1

Figs 1–2, 5. *Qualisaspora kidstonii* sp. nov.; sample AK6; near Eilean Orasaig, Kerrera. 1, FM475 (slide AK6/2, co-ord. 037 1289; E.F. no. E59/2). 2, FM476 (slide AK6/2, co-ord. 150 1185; E.F. no. R48/4). 5, FM474 (slide AK6/4, co-ord. 043 1224; E.F. no. F53/1); holotype.

Fig. 3. *Fustisispora aenigma* Wellman, 1993*b*?; FM477 (slide AOB4/2, co-ord. 151 1250; E.F. no. R55/2), sample AOB4; Port Caraig na Maraig, Oban.

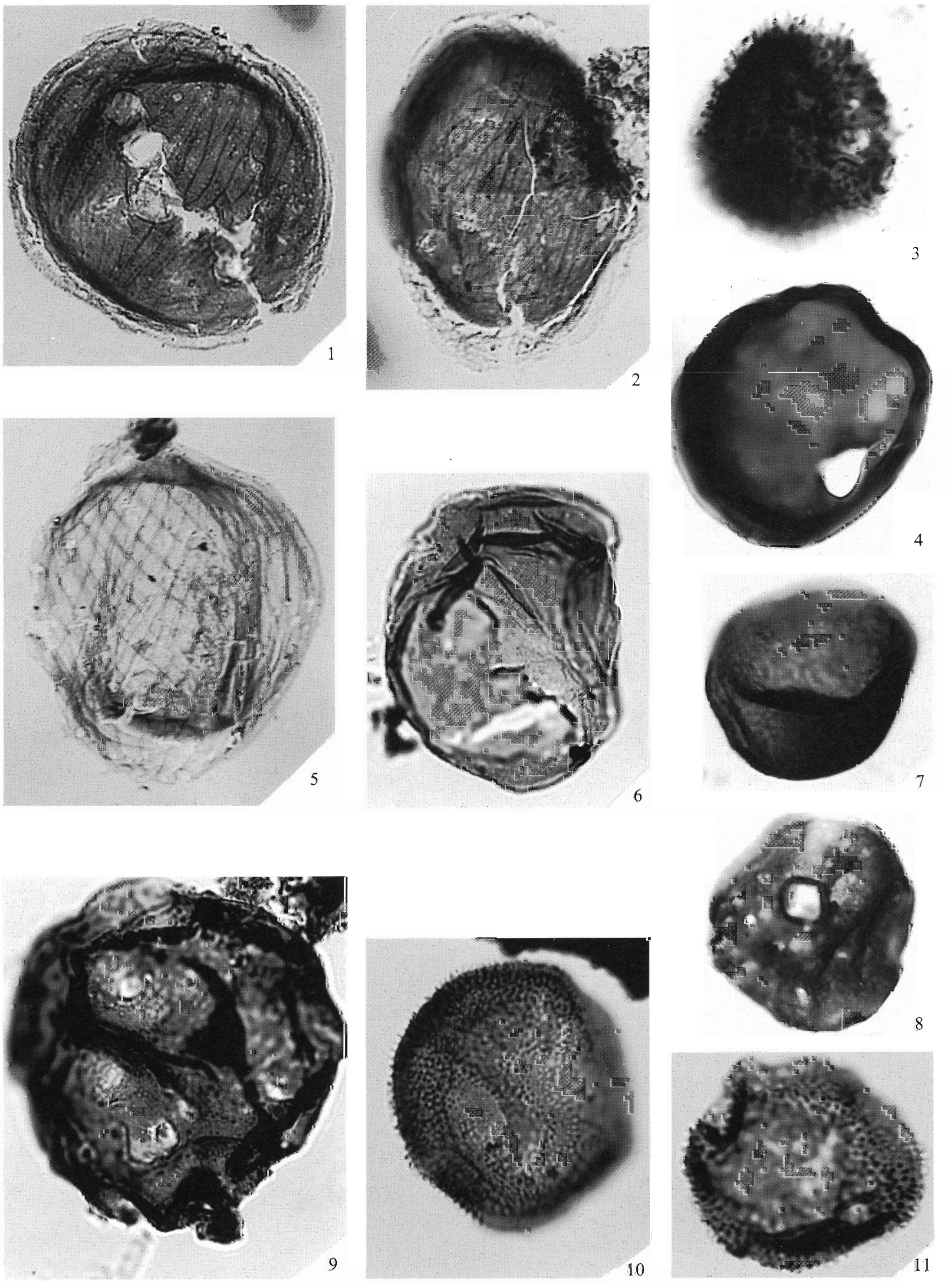
Figs 4, 7. *Laevolancis divellomedia* (Chibrikova) Burgess and Richardson, 1991; sample AOB4; Port Caraig na Maraig, Oban. 4, FM478 (slide AOB4/2, co-ord. 120 1326; E.F. no. N63/4). 7, FM479 (slide AOB4/2, co-ord. 150 1147; E.F. no. Q45/3).

Figs 6, 9. Laevigate alete cryptospore monads; sample AK6; near Eilean Orasaig, Kerrera. 6, FM480 (slide AK6/7, co-ord. 058 1291; E.F. no. G60/1). 9, FM481 (slide AK6/4, co-ord. 069 1070; E.F. no. H37/1).

Fig. 8. *Laevolancis plicata* Burgess and Richardson, 1991; FM482 (slide AK6/2, co-ord. 182 1201; E.F. no. U50/2), sample AK6; near Eilean Orasaig, Kerrera.

Figs 10–11. *Cymbohilates allenii* var. *magnus* Richardson, 1996; near Eilean Orasaig, Kerrera. 10, FM483 (slide AK6/2, co-ord. 060 1269; E.F. no. G57), sample AK6/2. 11, FM484 (slide AK1/4, co-ord. 182 1155; E.F. no. U45/2), sample AK1.

All × 1000.



WELLMAN and RICHARDSON, 'Lower Old Red Sandstone' sporomorphs

Comparison. *A. brevicosta* Burgess and Richardson possesses proximal radial muri which are confined to the equatorial region of the contact area. *Artemopyra* sp. A Burgess and Richardson, 1991 has proximal radial muri which become highly convoluted and anastomosing in the central region of the hilum, but this feature is developed to a much greater extent than in specimens of *A. laevigata*.

Artemopyra robusta sp. nov.

Plate 3, figures 10–11; Plate 12, figures 4–5

Derivation of name. Refers to the thick distal wall; *robustus* = hard and strong (Latin).

Holotype and type locality. Plate 3, figure 11, FM507 (slide AK1/2, co-ord. 064 1089; E.F. no. H39/1), sample AK1, basal strata of the 'Lower Old Red Sandstone', near Eilean Orasaig, Kerrera.

Paratypes. Plate 3, figure 10, FM506 (slide AK1/2, co-ord. 138 1118; E.F. no. P42), sample AK1, Kerrera, Plate 12, figure 4, SEM stub CW33, print P009556, sample AK1, Kerrera. Plate 12, figure 5, SEM stub CW34, print P009557, sample AK1, Kerrera.

Diagnosis. An *Artemopyra* with a thick and differentially thickened laevigate distal exine. The hilum is sculptured with 24–36 straight and robust radial muri which are up to 2·5 μm wide, *c*. 0·75 μm high and less than 0·75 μm apart.

Description. Amb circular to sub-circular. Equatorial or, more usually, subequatorial crassitude 1·5 μm wide delimits a more or less circular hilum. Hilum sculptured with radially disposed muri which are relatively straight, less than 0·75 μm apart, *c*. 0·75 μm high, and up to 2·5 μm wide at the equator, tapering to 0·75 μm wide towards the centre of the hilum. There are usually between 24–36 muri. Distal surface laevigate but differentially thickened, therefore imparting an uneven, blotchy appearance (see Plate 12, figures 4–5).

Dimensions. 44(51)62 μm; 66 specimens measured.

Comparison. *Artemopyra laevigata* sp. nov. is generally smaller (33(39)49 μm), has a thinner distal exine which is laevigate but not differentially thickened, and possesses proximal radial muri which are highly variable in appearance.

EXPLANATION OF PLATE 2

Figs 1, 6. *Cymbohilates microgranulatus* sp. nov. 1, FM485 (slide AOB1/2, co-ord. 039 1166; E.F. no. E47/3), sample AOB1; Port Caraig na Maraig, Oban; holotype. 6, FM486 (slide AK6/2, co-ord. 082 1187; E.F. no. J49/3), sample AK6/2; near Eilean Orasaig, Kerrera.

Figs 2–4. *Cymbohilates allenii* var. *magnus* Richardson, 1996. 2–3, sample AK1; near Eilean Orasaig, Kerrera. 2, FM487 (slide AK1/3, co-ord. 145 1178; E.F. no. Q48). 3, FM488 (slide AK1/3, co-ord. 137 1189; E.F. no. P49). 4, FM489 (slide AOB5/2, co-ord. 110 1185; E.F. no. M49/3), sample AOB5; Caraig na Maraig, Oban.

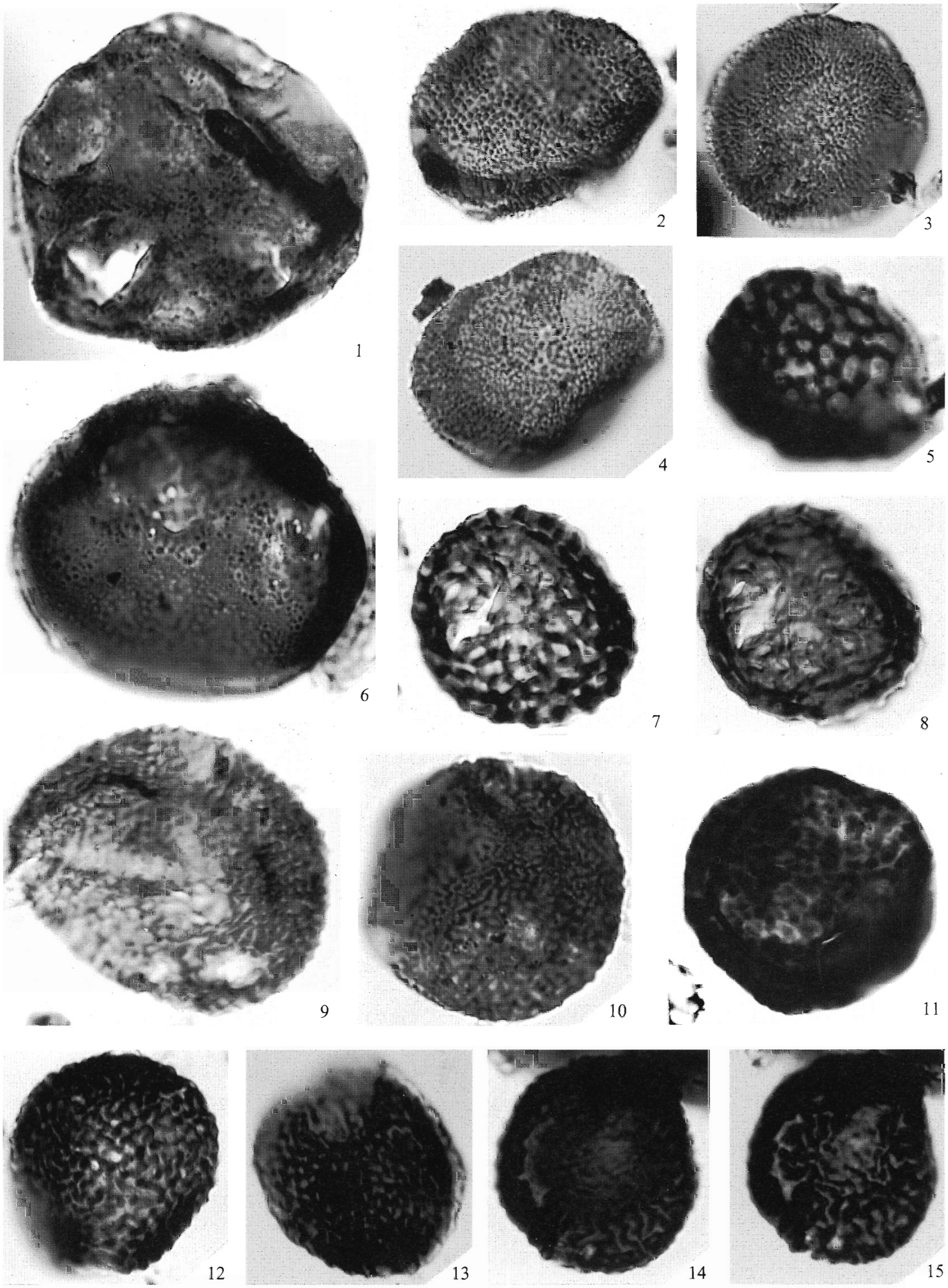
Figs 5, 7–8. *Chelinohilates lornensis* sp. nov.; near Eilean Orasaig, Kerrera. 5, FM490 (slide AK6/2, co-ord. 027 1187; E.F. no. D49/1), sample AK6. 7–8, FM491 (slide AK1/2, co-ord. 118 1099; E.F. no. N40/3), sample AK1; holotype.

Figs 9–10. *Chelinohilates sinuosus* var. *angustus* sp. et var. nov.; sample AK1; near Eilean Orasaig, Kerrera. 9, FM492 (slide AK1/2, co-ord. 149 1103; E.F. no. Q40/4); holotype. 10, FM493 (slide AK1/2, co-ord. 066 1066; E.F. no. H36/2).

Fig. 11. *Hispanaediscus* cf. *verrucatus* Cramer emend. Burgess and Richardson, 1991. 11, FM494 (slide AK6/5, co-ord. 140 1154; E.F. no. P45/4), sample AK6; near Eilean Orasaig, Kerrera.

Figs 12–15. *Chelinohilates sinuosus* var. *sinuosus* sp. et var. nov.; sample AK6; near Eilean Orasaig, Kerrera. 12, FM495 (slide AK6/3, co-ord. 120 1267; E.F. no. N57/4). 13, FM497 (slide AK1/3, co-ord. 102 1145; E.F. no. M44/3); holotype. 14–15, FM496 (slide AK6/4, co-ord. 030 1179; E.F. no. D48/3).

All × 1000.



WELLMAN and RICHARDSON, 'Lower Old Red Sandstone' sporomorphs

Genus CHELINOHILATES Richardson, 1996

Type species. Chelinohilates erraticus Richardson, 1996.

Chelinohilates lornensis sp. nov.

Plate 2, figures 5, 7–8; Plate 4, figure 3; Plate 12, figure 12

1991 *Brochotriletes ?foveolatus* Naumova; Marshall, fig. 3(7).

Derivation of name. After the Lorne area where these specimens were obtained.

Holotype and type locality. Plate 2, figures 7–8, FM491 (slide AK1/2, co-ord. 118 1099; E.F. no. N40/3), sample AK1, basal strata of the 'Lower Old Red Sandstone', near Eilean Orasaig, Kerrera.

Paratypes. Plate 2, figure 5, FM490 (slide AK6/2, co-ord. 027 1187; E.F. no. D49/1), sample AK6, Kerrera. Plate 4, figure 3, FM512 (slide AOB5/2, co-ord. 063 1319; E.F. no. H62/4), sample AOB5, Oban. Plate 12, figure 12, SEM stub CW46, print P009420, sample AK6, Kerrera.

Diagnosis. A *Chelinohilates* sculptured outside of the contact area with muri which form a regular polygonal reticulum. Muri 1·0–1·5 μm wide, lumina 1·5–2·5 μm in maximum diameter. The hilum has an irregular ornament of radially disposed muri/folds.

Description. Amb circular to sub-circular. Subequatorial crassitude *c*. 1 μm wide delimits a more or less circular hilum. Hilum with an irregular sculpture of sinuous radial muri/folds. The muri/folds are up to 1 μm wide and of irregular length, although they commonly extend from the proximal pole to the crassitude. Distal surface *c*. 2 μm thick and sculptured with muri which form a regular polygonal reticulum. Muri 1·0–1·5 μm wide, lumina 1·5–2·5 μm in maximum diameter.

Dimensions. 27(36)42 μm; 43 specimens measured.

Comparison. Illustrations of *Dictyotriletes gorgoneus* Cramer, 1966*c* suggest that this species, which has similar sculpture to *C. lornensis*, may be alete. In fact, Cramer noted that laesurae were not observed. However, Cramer's specimens are smaller (16–26 μm) than those described above.

Remarks. A specimen of *C. lornensis* united in true dyad configuration is reported ('dyad of *C. lornensis*') (Pl. 4, fig. 3). It is 44 μm long by 29 μm wide.

Chelinohilates sinuosus sp. nov.

Plate 2, figures 9–10, 12–15; Plate 4, figures 5–6; Plate 12, figures 8–9

Derivation of name. With reference to the distal ornament of sinuous muri; *sinuosus* = sinuous (Latin).

Holotype and type locality. Plate 2, figure 13, FM497 (slide AK1/3, co-ord. 102 1145; E.F. no. M44/2), sample AK1, basal strata of the 'Lower Old Red Sandstone', near Eilean Orasaig, Kerrera.

Diagnosis. A *Chelinohilates* sculptured outside of the contact area with closely spaced, meandering and bifurcating muri which give the sporomorph a brain-like appearance. Hilum usually with radially disposed folds.

Comparison. *C. lornensis* sp. nov. is similar in construction but has a distal sculpture comprising muri which form a highly regular reticulum.

Chelinohilates sinuosus var. *sinuosus* sp. et var. nov.

Plate 2, figures 12–15; Plate 4, figure 6; Plate 12, figure 9

Holotype. Same as species.

Paratypes. Plate 2, figure 12, FM495 (slide AK6/3, co-ord. 120 1267; E.F. no. N57/4). Plate 2, figures 14–15, FM496 (slide AK6/4, co-ord. 030 1179; E.F. no. D48/3). Plate 4, figure 6, FM515 (slide AK6/4, co-ord. 065 1170; E.F. no. H47). Plate 12, figure 9, SEM stub CW46, print P009370. All from sample AK6, Kerrera.

Diagnosis. A *Chelinohilates sinuosus* with distal muri 1·0–1·5 μm wide, up to 0·75 μm high and up to 1·5 μm apart.

Description. Amb circular to sub-circular. Subequatorial crassitude *c*. 1 μm wide delimits a more or less circular hilum. Hilum sculptured with radially disposed folds which are erratic and often bifurcate and meander. Sculptured outside the contact area with closely spaced muri which meander and bifurcate. The muri are 1·0–1·5 μm wide, up to 0·75 μm high and up to 1·5 μm apart. The muri form a brain like pattern, in places developed into an irregular reticulum. The muri are often slightly thickened where they bifurcate.

Dimensions. 32(36)48 μm; 39 specimens measured.

Comparison. *C. sinuosus* var. *angustus* sp. et var. nov. has a distal sculpture comprising more slender muri.

Remarks. A true dyad comprising *C. sinuosus* var. *sinuosus* is reported (Pl. 4, fig. 6). It is 39 μm long by 34 μm wide.

Chelinohilates sinuosus var. *angustus* sp. et var. nov.

Plate 2, figures 9–10; Plate 4, figure 5; Plate 12, figure 8

Derivation of name. Refers to the distal ornament of narrow muri; *angustus* = narrow (Latin).

Holotype and type locality. Plate 2, figure 9, FM492 (slide AK1/2, co-ord. 149 1103; E.F. no. Q40/4), sample AK1, basal strata of the 'Lower Old Red Sandstone', near Eilean Orasaig, Kerrera.

Paratypes. Plate 2, figure 10, FM493 (slide AK1/2, co-ord. 066 1066; E.F. no. H36/2), sample AK1, Kerrera. Plate 4, figure 5, FM514 (slide AK1/2, co-ord. 117 1231; E.F. no. N53/4), sample AK1, Kerrera. Plate 12, figure 8, SEM stub CW46, print P007947, sample AK6, Kerrera.

Diagnosis. A *Chelinohilates sinuosus* with distal muri less than 1 μm wide, less than 0·75 μm high and usually less than 1 μm apart.

Description. Amb circular to sub-circular. Subequatorial crassitude *c*. 1 μm wide delimits a more or less circular hilum. Hilum sculptured with radially disposed folds which are erratic and often bifurcate and meander. Sculptured outside of the contact area with closely spaced muri which bifurcate and meander. The muri are less than 1 μm wide, less than 0·75 μm high and usually less than 1 μm apart. The muri form a brain-like pattern, in places developed into an irregular reticulum.

Dimensions. 27(39)52 μm; 13 specimens measured.

Comparison. *C. sinuosus* var. *sinuosus* is similar but the distal muri are broader.

Remarks. A true dyad comprising *C. sinuosus* var. *angustus* is reported (Pl. 4, fig. 5). It is 44 μm long by 29 μm wide.

Genus CYMBOHILATES Richardson, 1996

Type species. *Cymbohilates horridus* Richardson, 1996.

Cymbohilates amplus sp. nov.

Plate 10, figures 1–3

Derivation of name. Refers to the large size of these spores; *amplus* = large (Latin).

TABLE 3. Characteristics of species of *Cymbohilates* present in the Lorne assemblages. C, coni; MC, microconi; MG, microgarana; MS, microspinae; S, spinae. Element height, width and spacing refer to the dimensions of the elements comprising the distal sculpture.

Taxon	Spore diameter	Distal sculpture	Element height	Element width	Element spacing	Radial proximal muri
Cy. amplus	73(87)104 μm	S and C	0·75–1·5	0·5–1 μm	2–4 μm	no
Cy. allenii var. *magnus*	30(38)56 μm	MS, S, MC and C	0·5–1 μm	0·5–0·75 μm	< 0·5 μm	no
Cy. hystricosus	38(43)50 μm	C	*c.* 1 μm	2–2·5 μm	< 0·75 μm	yes
Cy. microgranulatus	44(57)74 μm	MG with some MC and MS	0·5–0·75 μm	0·5–0·75 μm	< 1 μm	no
Cy. sp. A	48 μm	S	1·5–2 μm	0·5–0·75 μm	< 0·5 μm	yes

Holotype and type locality. Plate 10, figures 2–3. FM565 (slide AOB1/4, co-ord. 190 1068; E.F. no. U36/4), sample AOB4, basal strata of the 'Lower Old Red Sandstone', Port Caraig na Maraig, Oban.

Paratype. Plate 10, figure 1, FM564 (slide AK1/3, co-ord. 056 1314; E.F. no. G62), sample AK1, Kerrera.

Diagnosis. Large (73–104 μm) *Cymbohilates* sculptured outside of the contact area with evenly distributed but widely spaced spinae and coni 0·75–1·5 μm high, 0·5–1·0 μm wide and 2–4 μm apart. Hilum laevigate.

Description. Amb circular. Subequatorial crassitude 1·0–2·5 μm wide delimits a circular hilum. Hilum laevigate. There is significant folding on the proximal and distal surface including large concentric folds near, and merging with, the crassitude. Sculptured outside of the contact area with fairly evenly distributed but widely spaced spinae and coni which are 0·75–1·5 μm high, 0·5–1·0 μm wide and 2–4 μm apart.

Dimensions. 73(87)104 μm; seven specimens measured.

Comparison. *Cy. amplus* is the species most similar to *Cy. microgranulatus* sp. nov. (see Table 3). However, *Cy. microgranulatus* is smaller (diameter 44–74 μm) and has distal sculpture comprising primarily micrograna 0·5–0·75 μm high which are more closely packed (< 1 μm apart).

Cymbohilates allenii var. *magnus* Richardson, 1996

Plate 2, figures 2–4; Plate 4, figure 4; Plate 12, figures 3, 6

Description. Amb circular to sub-circular. Equatorial to subequatorial crassitude *c*. 1 μm wide delimits a more or less circular hilum. Hilum laevigate. Sculptured outside of the contact area with evenly distributed and crowded microconi and microspinae (0·5–0·75 μm high), often also with small coni and spinae (up to 1·0 μm high). The elements are 0·5–0·75 μm wide and are usually less than 0·5 μm apart.

Dimensions. 30(38)56 μm; 37 specimens measured.

Comparison. Table 3 outlines the major differences between *Cy. allenii* var. *magnus* and other species of *Cymbohilates*.

Remarks. Two true dyads comprising *Cy. allenii* var. *magnus* are recorded (Pl. 4, fig. 4). One is 50 μm long by 42 μm wide and the other 48 μm by 40 μm.

Cymbohilates hystricosus sp. nov.

Plate 3, figures 9, 12

Derivation of name. Refers to the ornament; *hystricosus* = prickly, thorny (Greek).

Holotype and type locality. Plate 3, figure 9, FM508 (slide AK6/4, co-ord. 198 1114; E.F. no. V41/4), sample AK6, basal strata of the 'Lower Old Red Sandstone', near Eilean Orasaig, Kerrera.

Paratypes. Plate 3, figure 12, FM509 (slide AK6/3, co-ord. 058 1192; E.F. no. G49/4), sample AK6, Kerrera.

Diagnosis. A *Cymbohilates* with robust radially disposed muri adorning the proximal hilum. Sculptured outside the contact area with evenly distributed coni which are *c*. 1 μm high, 2·0–2·5 μm wide and up to 0·75 μm apart.

Description. Amb sub-circular. Subequatorial crassitude 1·5 μm wide delimits a more or less circular hilum. Hilum ornamented with approximately 32 robust, radial, muri. Muri straight to slightly sinuous, 1·5 μm wide and 1·5–2·0 μm apart at the crassitude, extending to the centre of the proximal pole. Sculptured outside of the contact area with an evenly distributed coni which are *c.* 1 μm high, 2·0–2·5 μm wide at the base, and up to 0·75 μm apart.

Dimensions. 38(43)50 μm; seven specimens measured.

Comparison. Cymbohilates? sp. A is similar but has distal sculpture comprising spinae which are 1·5–2·0 μm high (see Table 3).

Cymbohilates microgranulatus sp. nov.

Plate 2, figures 1, 6; Plate 12, figure 11

Derivation of name. Refers to the ornament of micrograna; *mikros* = small (Greek).

Holotype and type locality. Plate 2, figure 1, FM485 (slide AOB1/2, co-ord. 039 1166; E.F. no. E47/3), sample AOB1, basal strata of the 'Lower Old Red Sandstone', Port Caraig na Maraig, Oban.

Paratypes. Plate 2, figure 6, FM486 (slide AK6/2, co-ord. 083 1187; E.F. no. J49/3), sample AK6/2, Kerrera. Plate 12, figure 11, SEM stub CW64, print P009316, sample BK2, Kerrera.

Diagnosis. A *Cymbohilates* sculptured outside of the contact area predominantly with evenly distributed micrograna 0·5–0·75 μm high, 0·5–0·75 μm wide and up to 1 μm apart. Proximal hilum laevigate, occasionally with folds.

Description. Amb circular to sub-circular. Subequatorial crassitude *c.* 1 μm wide delimits a more or less circular hilum. Hilum laevigate, often with folds which are usually radially arranged. Sculptured outside of the contact area predominantly with evenly distributed micrograna, but occasionally also with microconi and microspinae. Sculpture elements 0·5–0·75 μm high, 0·5–0·75 μm wide and fairly widely spaced (up to 1 μm apart). Distal wall up to 2·5 μm thick.

Dimensions. 44(57)74 μm; 19 specimens measured.

Comparison. Cy. microgranulatus is most similar to *Cy. amplus* (see Table 3). However, *Cy. amplus* is larger (73–104 μm) and has distal sculpture comprising evenly distributed but widely spaced spinae and coni which are 0·75–1·5 μm high, 0·5–1·0 μm wide and 2–4 μm apart.

EXPLANATION OF PLATE 3

Figs 1–2, 5. *Hispanaediscus*? *irregularis* sp. nov.; sample AK6; near Eilean Orasaig, Kerrera. 1, FM499 (slide AK6/3, co-ord. 208 1190; E.F. no. X49). 2, FM500 (slide AK6/5, co-ord. 082 1167; E.F. no. K47/1). 5, FM501 (slide AK6/3, co-ord. 144 1123; E.F. no. Q42); holotype.

Figs 3–4, 6. *Artemopyra laevigata* sp. nov. 3–4, FM502 (slide AOB1/3, co-ord. 093 1173; E.F. no. L47/2), sample AOB1; Port Caraig na Maraig, Oban. 6, FM503 (slide AK6/2, co-ord. 030 1305; E.F. no. D61/3), sample AK6; near Eilean Orasaig, Kerrera; holotype.

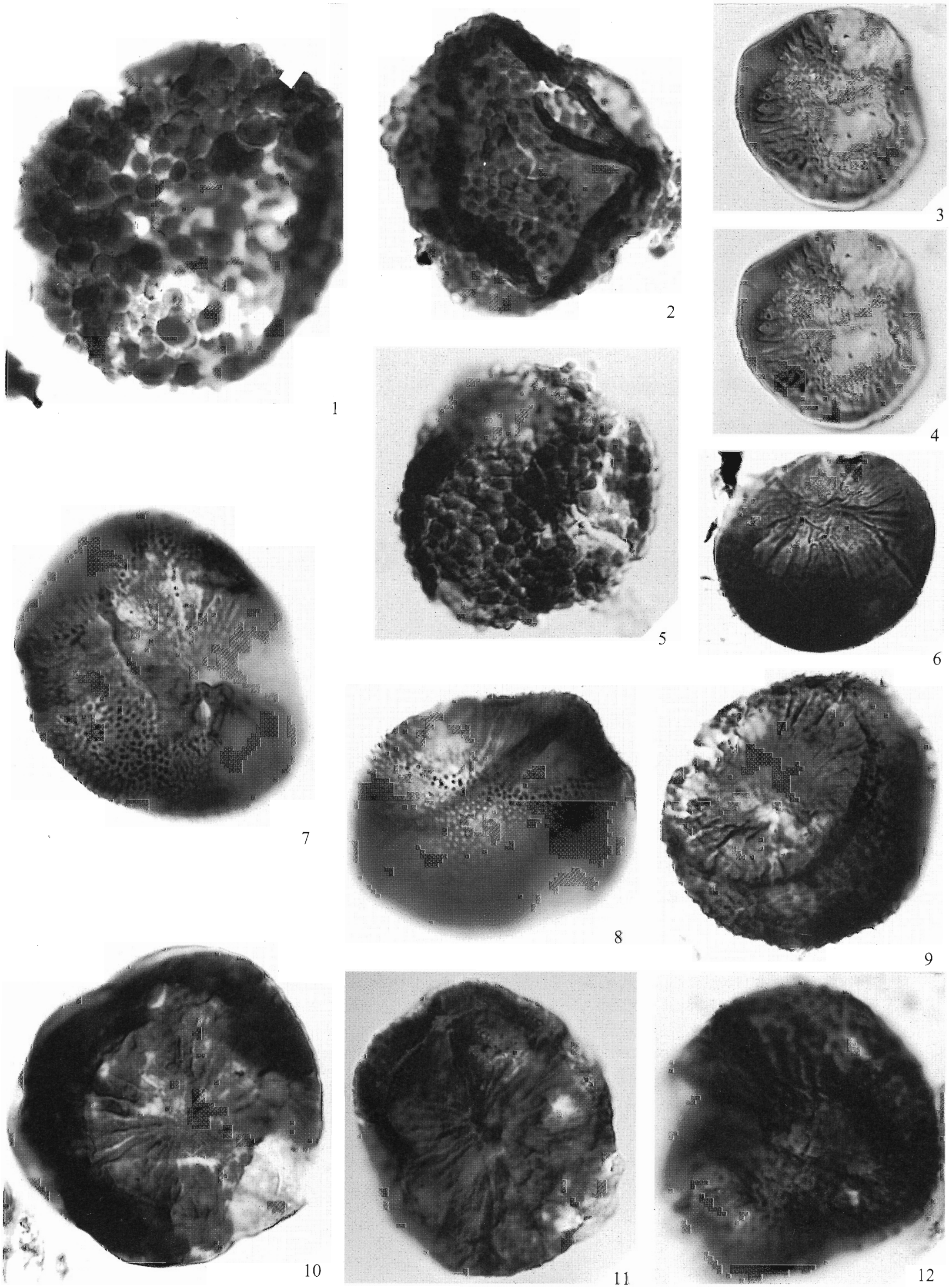
Figs 7–8. *Cymbohilates*? sp. A; sample AK6; near Eilean Orasaig, Kerrera. 7, FM504 (slide AK6/4, co-ord. 164 1131; E.F. no. S43). 8, FM505 (slide AK6/5, co-ord. 116 1276; E.F. no. N58).

Figs 9, 12. *Cymbohilates hystricosus* sp. nov.; sample AK6; near Eilean Orasaig, Kerrera. 9, FM508 (slide AK6/4, co-ord. 198 1114; E.F. no. V41/4); holotype. 12, FM509 (slide AK6/3, co-ord. 058 1192; E.F. no. G49/4).

Figs 10–11. *Artemopyra robusta* sp. nov.; sample AK1; near Eilean Orasaig, Kerrera. 10, FM506 (slide AK1/2, co-ord. 138 1118; E.F. no. P42). 11, FM507 (slide AK1/2, co-ord. 064 1089; E.F. no. H39/1); holotype.

All × 1000.

PLATE 3



WELLMAN and RICHARDSON, 'Lower Old Red Sandstone' sporomorphs

Cymbohilates? sp. A

Plate 3, figures 7–8

Description. Amb sub-circular. Equatorial crassitude *c*. 1 μm wide delimits a more or less circular contact area (?hilum). There is no evidence of a trilete mark. The contact area is sculptured with numerous, crowded radial muri which extend from the proximal pole to the crassitude. Muri straight and low, up to 1·5 μm wide with rounded tops. Sculptured outside of the contact area with evenly distributed and densely packed straight-sided or slightly tapering spinae 1·5–2·0 μm high, 0·5–0·75 μm wide and less than 0·5 μm apart.

Dimensions. Two specimens measured; both 48 μm.

Remarks. Table 1 outlines the major differences between *Cy*.? sp. A and other species of *Cymbohilates*. This species is assigned questionably to *Cymbohilates* as the proximal face is not well preserved and it is possible that the spores are trilete. However, a trilete mark has not been observed and if present is indistinct.

Genus HISPANAEDISCUS Cramer emend. Burgess and Richardson, 1991

Type species. *Hispanaediscus verrucatus* Cramer emend. Burgess and Richardson, 1991.

Hispanaediscus? *irregularis* sp. nov.

Plate 3, figures 1–2, 5; Plate 12, figure 10

Derivation of name. Refers to the irregular ornament; *irregularis* = not regular (Latin).

Holotype and type locality. Plate 3, figure 5, FM501 (slide AK6/3, co-ord. 144 1123; E.F. no. Q42), sample AK6, basal strata of the 'Lower Old Red Sandstone', near Eilean Orasaig, Kerrera.

Paratypes. Plate 3, figure 1, FM499 (slide AK6/3, co-ord. 208 1190; E.F. no. X49), sample AK6, Kerrera. Plate 3, figure 2, FM500 (slide AK6/5, co-ord. 082 1167; E.F. no. K47/1), sample AK6, Kerrera. Plate 12, figure 10, SEM stub CW62, print P008892, sample BK1, Kerrera.

Diagnosis. A ?hilate cryptospore with densely packed distal sculpture, comprising irregularly shaped verrucae which are 2–4 μm wide and 1·5–3·0 μm high.

Description. Amb circular to sub-circular. A faint circular subequatorial crassitude, which probably delimits a hilum, has been discerned in some specimens. Outside of the ?hilum the sporomorph is sculptured with

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EXPLANATION OF PLATE 4

Figs 1–2. 'Dyad of *Laevolancis divellomedia*', (*Dyadospora murusdensa* Strother and Traverse emend. Burgess and Richardson, 1991); near Eilean Orasaig, Kerrera. 1, FM510 (slide AK1/2, co-ord. 220 1210; E.F. no. Y52/1), sample AK1. 2, FM511 (slide AK6/2, co-ord. 078 1111; E.F. no. J41), sample AK6.

Fig. 3. 'Dyad of *Chelinohilates lornensis*'; FM512 (slide AOB5/2, co-ord. 069 1319; E.F. no. H62/4), sample AOB5; Port Caraig na Maraig, Oban.

Fig. 4. 'Dyad of *Cymbohilates allenii* var. *magnus*'; FM513 (slide AK6/7, co-ord. 044 122; E.F. no. F52/2), sample AK6; near Eilean Orasaig, Kerrera.

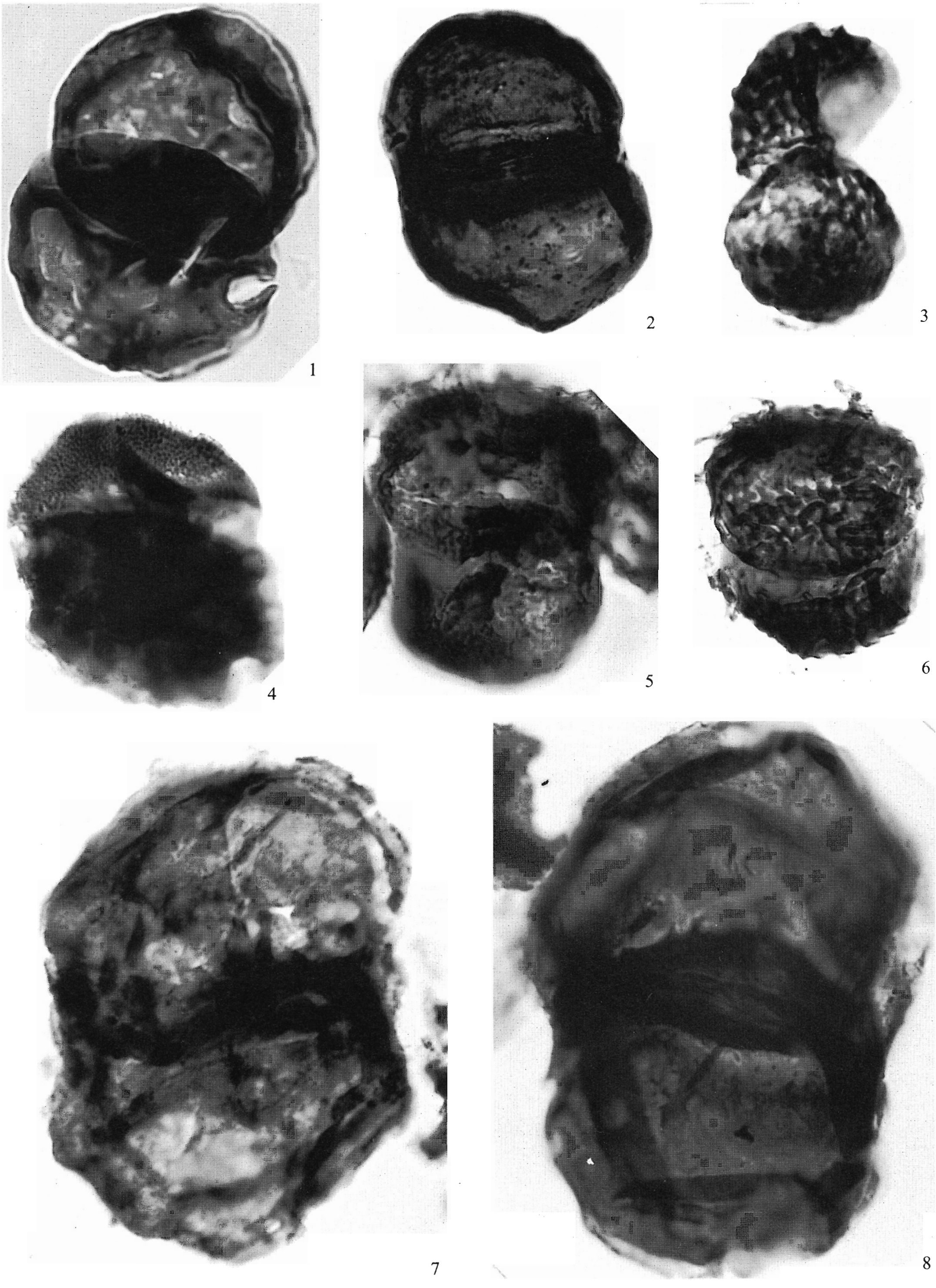
Fig. 5. 'Dyad of *Chelinohilates sinuosus* var. *angustus*'; FM514 (slide AK1/2, co-ord. 117 1231; E.F. no. N53/4), sample AK1; near Eilean Orasaig, Kerrera.

Fig. 6. 'Dyad of *Chelinohilates sinuosus* var. *sinuosus*'; FM515 (slide AK6/4, co-ord. 065 1170; E.F. no. H47), sample AK6; near Eilean Orasaig, Kerrera.

Figs 7–8. *Abditidyadus laevigatus* gen. et sp. nov.; near Eilean Orasaig, Kerrera. 7, FM516 (slide AK1/3, co-ord. 169 1249; E.F. no. T55/2), sample AK1. 8, FM517 (slide AK6/7, co-ord. 070 1204; E.F. no. H51/3), sample AK6; holotype.

All × 1000.

PLATE 4



WELLMAN and RICHARDSON, 'Lower Old Red Sandstone' sporomorphs

crowded verrucae, which are irregular in shape and variable in size. The elements are 2–4 μm wide, generally with roughly circular bases, 1·5–3·0 μm high, and round or flat topped. The elements are always less than 0·5 μm apart but do not merge or combine.

Dimensions. 36(49)56 μm; 11 specimens measured.

Remarks. It is difficult to ascertain the nature of the contact area delimited by the crassitude as it is masked by the dense distal sculpture. However, the crassitude bears no indication of invaginated points which would be expected if the sporomorph possessed a trilete mark. This suggests that these sporomorphs are probably hilate cryptospores with a thin-walled hilum. Hilate cryptospores with similar sculpture comprising large, crowded, highly irregular verrucae have not previously been reported.

Hispanaediscus cf. *verrucatus* Cramer emend. Burgess and Richardson, 1991

Plate 2, figure 11; Plate 13, figures 6–7

Description. Amb circular to sub-circular. Equatorial or subequatorial crassitude *c*. 1 μm wide delimits a more or less circular hilum. Hilum laevigate, often folded or collapsed. Sculptured outside of the contact area with verrucae 1·0–2·5 μm in maximum diameter and up to 1 μm high. The verrucae are either flat or round topped and the bases are usually sub-rounded in plan. In some specimens the verrucae coalesce in places forming muri up to 4 μm long by 1·5 μm wide. The sculpture elements are 0·5–1·0 μm apart.

Dimensions. 31(41)54 μm; 28 specimens measured.

Remarks. *H. verrucatus* Cramer emend. Burgess and Richardson, 1991 has the same structure but is generally smaller and is sculptured with verrucae which are more widely spaced and less distinct.

Ornament is higly variable between specimens in the group of spores described above and they may not comprise a natural group. However, they are described together because they all have an identical structure and all possess an ornament dominated by verrucae. The variation in sculpture is manifested in the size, shape and spacing of the verrucae. Further subdivision would have been confusing and probably somewhat arbitrary.

EXPLANATION OF PLATE 5

Figs 1, 5. *Abditusdyadus histosus* gen. et sp. nov.; sample AK1; near Eilean Orasaig, Kerrera. 1, FM518 (slide AK1/4, co-ord. 156 1191; E.F. no. R49). 5, FM519 (slide AK1/2, co-ord. 045 1133; E.F. no. F43/2); holotype.

Figs 3–4, 7. *Tetrahedraletes medinensis* Strother and Traverse emend. Wellman and Richardson, 1993; sample AK6; near Eilean Orasaig, Kerrera. 3, FM520 (slide AK6/5, co-ord. 099 1216; E.F. no. L52/3). 4, FM521 (slide AK6/2, co-ord. 052 1283; E.F. no. F59/3). 7, FM522 (slide AK6/2, co-ord. 041 1146; E.F. no. E44/4).

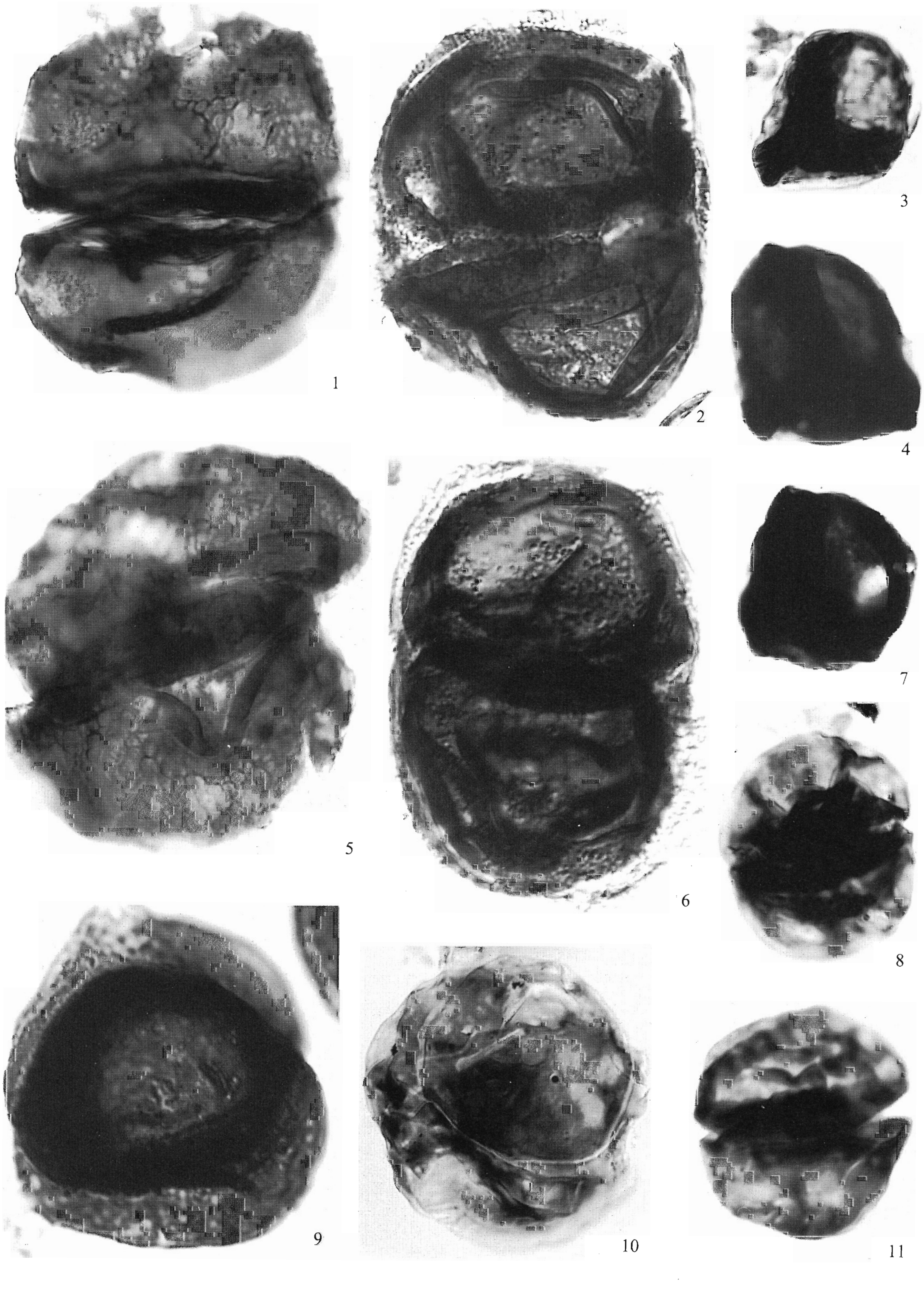
Figs 2, 6. *Abditusdyadus chalazus* gen. et sp. nov.; sample AK6; near Eilean Orasaig, Kerrera. 2, FM523 (slide AK6/2, co-ord. 070 1299; E.F. no. H60/4), 6, FM524 (slide AK6/2, co-ord. 162 1335; E.F. no. S64); holotype.

Figs 8, 11. 'Dyad of *Laevolancis plicata* Burgess and Richardson, 1991' (*Dyadospora murusattenuata* Strother and Traverse, 1979 emend. Burgess and Richardson, 1991); sample AK1; near Eilean Orasaig, Kerrera. 8, FM526 (slide AK1/3, co-ord. 025 1087; E.F. no. D38/2). 11, FM525 (slide AK1/4, co-ord. 014 1273; E.F. no. C58/1).

Fig. 9. *Pseudodyadospora petasus* Wellman and Richardson, 1993; FM527 (slide AOB5/2, co-ord. 220 1354; E.F. no. Y66), sample AOB5; Port Caraig na Maraig, Oban.

Fig. 10. ?Tetrad of trilete spores; FM528 (slide AK1/2, co-ord. 133 1218; E.F. no. P52), sample AK1; near Eilean Orasaig, Kerrera.

All × 1000.



WELLMAN and RICHARDSON, 'Lower Old Red Sandstone' sporomorphs

NAKED UNFUSED TETRADS

Genus TETRAHEDRALETES Strother and Traverse emend. Wellman and Richardson, 1993

Type species. Tetrahedraletes medinensis Strother and Traverse, 1979.

Tetrahedraletes medinensis Strother and Traverse *emend.* Wellman and Richardson, 1993

Plate 5, figures 3–4, 7

Dimensions. 23(34)49 μm; 65 specimens measured.

NAKED FUSED DYADS (PSEUDODYADS)

Genus PSEUDODYADOSPORA Johnson, 1985

Type species. Pseudodyadospora laevigata Johnson, 1985.

Pseudodyadospora petasus Wellman and Richardson, 1993

Plate 5, figure 9; Plate 13, figure 2

Dimensions. 45(55)65 μm in diameter; 23 specimens measured.

Remarks. The Lorne specimens are essentially identical to previously described specimens of *P. petasus* except that they are larger. Previously reported specimens have diameters of 26(32)44 μm (Wellman and Richardson 1993 – early Wenlock) and 32(42)51 μm (Wellman 1993*a* – late Wenlock, or possibly earliest Ludlow).

NAKED FUSED TETRADS

Genus CHEILOTETRAS Wellman and Richardson, 1993

Type species. Cheilotetras caledonica Wellman and Richardson, 1993.

Cheilotetras caledonica Wellman and Richardson, 1993?

Plate 13, figure 1

Dimensions. 49(58)77 μm; 17 specimens measured.

Remarks. Rare fused permanent tetrads similar to *Ch. caledonica* were recovered. However, the flanges associated with the fused junctions are not as pronounced as they are in the type material.

ENVELOPE-ENCLOSED CRYPTOSPORES

Genus QUALISASPORA Richardson, Ford and Parker, 1984

Type species. Qualisaspora fragilis Richardson, Ford and Parker, 1984.

Qualisaspora kidstonii sp. nov.

Plate 1, figures 1–2, 5; Plate 12, figure 1

Derivation of name. After Dr Robert Kidston, in recognition of his contribution to palaeobotanical studies of the Scottish Old Red Sandstone.

Holotype and type locality. Plate 1, figure 5, FM474 (slide AK6/4, co-ord. 043 1224; E.F. no. F53/1), sample AK6, basal strata of the 'Lower Old Red Sandstone', near Eilean Orasaig, Kerrera.

Paratypes. Plate 1, figure 1, FM475 (slide AK6/2, co-ord. 037 1289; E.F. no. E59/2), sample AK6, Kerrera. Plate 1, figure 2, FM476 (slide AK6/2, co-ord. 150 1185; E.F. no. R48/4), sample AK6, Kerrera. Plate 12, figure 1, SEM stub CW34, print P007324, sample AK1, Kerrera.

Diagnosis. A *Qualisaspora* with a flimsy, membranous, loose envelope.

Description. Thick-walled, laevigate, inner body rounded-oval in outline. Outer membranous envelope diaphanous and flimsy, less than 0·75 μm thick, sculptured with muri arranged in a bihelical pattern. Muri less than 0·75 μm high and wide, and 3–4 μm apart midway between the two foci. The muri occasionally bifurcate. The two layers are separated by up to 8 μm, usually 2–4 μm.

Dimensions. 32(40)48 μm; 12 specimens measured.

Comparison. *Q. fragilis* Richardson, Ford and Parker, 1984 is similar to the Lorne specimens except in that it possesses a thicker, more rigid, envelope which is sculptured with more prominent muri up to 1 μm high. '*Moyeria*' *cabottii* (Cramer) Miller and Eames, 1982 is unilayered.

Genus ABDITUSDYADUS gen. nov.

Derivation of name. Refers to the envelope enclosing the dyad; *abditus* = hidden, concealed (Greek).

Type species. *Abditusdyadus histosus* sp. nov.

Diagnosis. Unfused dyads (i.e. true dyads) enclosed within a loose or tight fitting membranous envelope. The envelope may be laevigate or variously ornamented.

Comparison. *Dyadospora* Strother and Traverse emend. Burgess and Richardson, 1991 encompasses smooth-walled, unfused dyads (true dyads) which lack an enclosing envelope. *Segestrespora* Burgess, 1991 was erected for fused dyads (pseudodyads) which are enclosed within an envelope.

Remarks. Current systematic practice differentiates between cryptospores at the generic level depending on whether they are naked or enclosed within an envelope. For example, Burgess (1991) created new genera for envelope-enclosed pseudodyads (*Segestrespora*) and envelope-enclosed permanent tetrads (*Velatitetras*) in order to distinguish them from naked forms. However, polyad cryptospores are also differentiated at the generic level depending on the nature of the junction between units, i.e. whether they are fused (without a line of attachment) or unfused (with a line of attachment) (see discussion in Wellman and Richardson 1993). We follow current systematic practice in proposing a new genus for unfused dyads (true dyads) which are enclosed within an envelope, thus differentiating them from naked unfused dyads and envelope-enclosed fused dyads. However, we recognize that it is often difficult to ascertain if an envelope-enclosed polyad cryptospore is fused or unfused, particularly if the specimen is poorly preserved. We recommend that in cases where it is impossible to determine if envelope-enclosed dyads are fused or unfused, open nomenclature is used and the specimens are assigned questionably to either *Segestrespora* or *Abditusdyadus*. Envelope-enclosed true dyads are generally rare. However, despite the small number of specimens available for study, we believe it is logical and beneficial to erect a new genus and describe the included species, in order to follow current taxonomic practice and differentiate between envelope-enclosed unfused and fused dyads. Furthermore, although the specimens are rare, they are easily recognized as comprising true dyads and fall into morphologically distinct sets which are readily divided into the species proposed.

Abditusdyadus histosus gen. et sp. nov.

Plate 5, figures 1, 5

Derivation of name. Refers to the envelope sculpture; *histos* = web (Greek).

Holotype and type locality. Plate 5, figure 5, FM519 (slide AK1/2), co-ord. 045 1133; E.F. no. F43/2), sample AK1, basal strata of the 'Lower Old Red Sandstone', near Eilean Orasaig, Kerrera.

Paratype. Plate 5, figure 1, FM518 (slide AK1/4, co-ord. 156 1191; E.F. no. R49), sample AK1, Kerrera.

Diagnosis. An *Abditusdyadus* comprising a laevigate true dyad enclosed within an envelope sculptured with muri which form a regular polygonal reticulum. Muri $< 0{\cdot}75\ \mu$m high and $< 0{\cdot}75\ \mu$m wide, lumina 1–3 μm in maximum diameter.

Description. True dyads comprising two laevigate hilate cryptospores with thick, generally unfolded walls. The individual spores are attached across a clearly perceptible plane of attachment and may be partially separated. The dyad is enclosed within a loose or tight fitting membranous envelope which is less than 0·5 μm thick. Envelope sculptured with muri which are less than 0·75 μm high and wide, being slightly wider at the junctions where they meet. The muri form a regular reticulum with sub-polygonal lumina of fairly regular size with a maximum diameter of 1·5–3·0 μm.

Dimensions. Length = 62(73)83 μm, width = 57(64)76 μm; 15 specimens measured.

Comparisons. *A. laevigatus* sp. nov. has a laevigate envelope. *A. chalazus* sp. nov. has an envelope sculptured with grana. The envelope sculpture of *A. histosus* is identical to that on the envelope-enclosed permanent tetrad *Velatitetras* (*Nodospora*) *retimembrana* (Miller and Eames, 1982)? comb. nov. which is also present in the Lorne assemblage.

Abditusdyadus chalazus gen. et sp. nov.

Plate 5, figures 2, 6

Derivation of name. Refers to the envelope sculpture; *chalaza* = pimple, tubercle (Greek).

Holotype and type locality. Plate 5, figure 6, FM524 (slide AK6/2, co-ord. 162 1335; E.F. no. S64), sample AK6, basal strata of the 'Lower Old Red Sandstone', near Eilean Orasaig, Kerrera.

Paratype. Plate 5, figure 2, FM523 (slide AK6/2, co-ord. 070 1299; E.F. no. H60/4), sample AK6, Kerrera.

Diagnosis. An *Abditusdyadus* comprising a laevigate true dyad enclosed within an envelope sculptured with grana which are less than 0·75 μm high, up to 0·75 μm wide and 0·5–1·5 μm apart.

EXPLANATION OF PLATE 6

Figs 1–2. *Velatitetras* (*Nodospora*) *retimembrana* (Miller and Eames, 1982)? comb. nov.; sample AK1; near Eilean Orasaig, Kerrera. 1, FM529 (slide AK1/3, co-ord. 046 1128; E.F. no. F43/1). 2, FM530 (slide AK1/3, co-ord. 030 1232; E.F. no. D53).

Figs 3–4. *Retusotriletes rotundus* Streel emend. Lele and Streel, 1969?; sample AOB4; Port Caraig na Maraig, Oban. 3, FM531 (slide AOB4/2, co-ord. 190 1213; E.F. no. U51/4). 4, FM532 (slide AOB4/2, co-ord. 186 1250; E.F. no. U55/4).

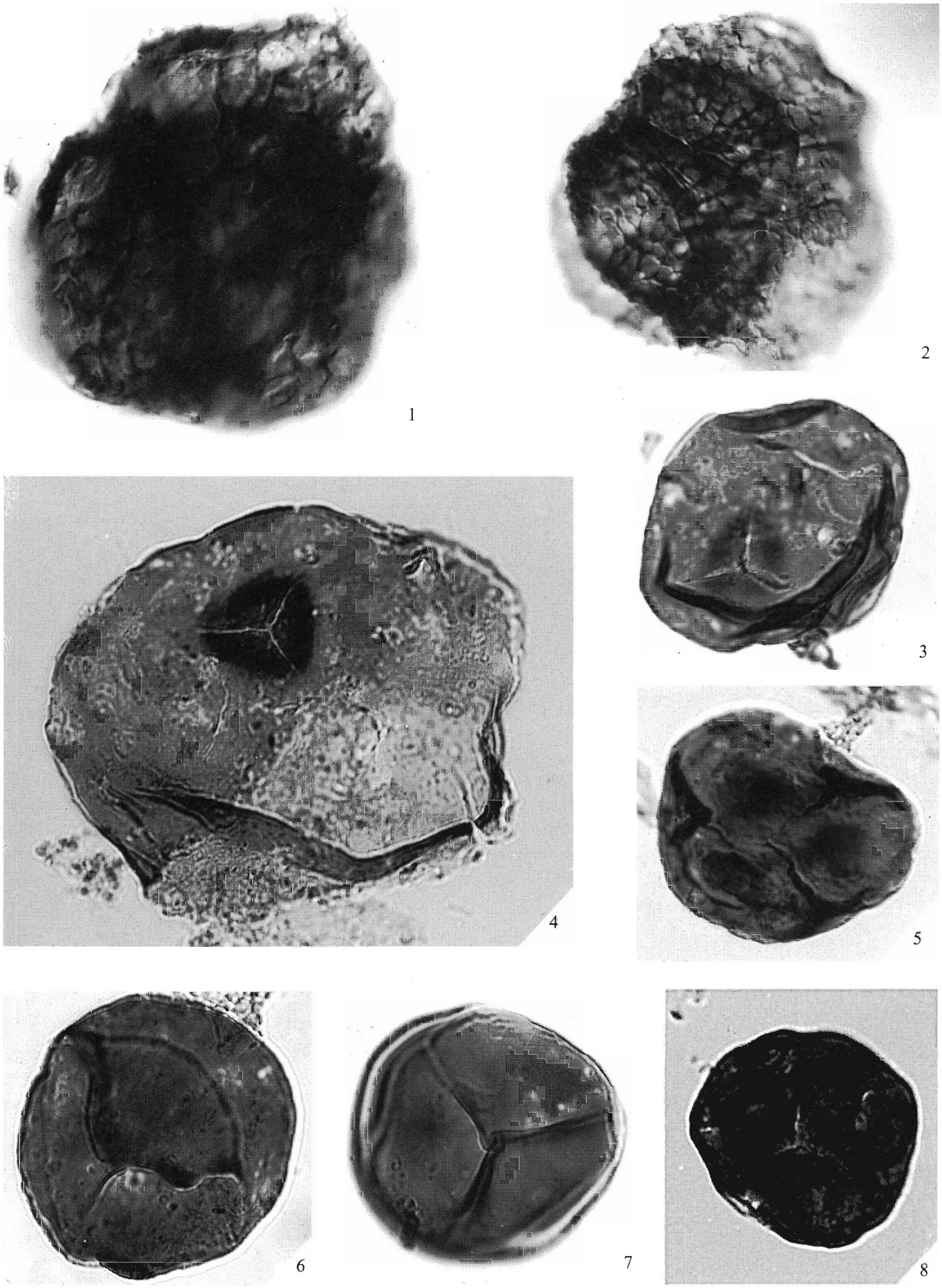
Fig. 5. *Retusotriletes maculatus* McGregor and Camfield, 1976; FM533 (slide AK1/3, co-ord. 158 1164; E.F. no. R46/4), sample AK1; near Eilean Orasaig, Kerrera.

Figs 6–7. *Retusotriletes maccullockii* sp. nov. 6, FM534 (slide AK1/2, co-ord. 109 1114; E.F. no. M41/1), sample AK1; near Eilean Orasaig, Kerrera. 7, FM535 (slide AOB4/2, co-ord. 060 1343; E.F. no. G65), sample AOB4; Port Caraig na Maraig, Oban; holotype.

Fig. 8. *Retusotriletes* sp.; FM536 (slide AK6/5, co-ord. 140 1246; E.F. no. P55/3), sample AK6; near Eilean Orasaig, Kerrera.

All ×1000.

PLATE 6



WELLMAN and RICHARDSON, *Velatitetras* (*Nodospora*), *Retusotriletes*

Description. True dyads comprising two laevigate hilate cryptospores with thick, usually unfolded walls. The individual spores are attached across a clearly perceptible plane of attachment and may be partially separated. The dyad is enclosed within a loose fitting or tightly adherent membranous envelope which is less than 0·5 μm thick and is diaphanous. The envelope is sculptured with grana which are less than 0·75 μm high and up to 0·75 μm wide. The grana are usually fairly evenly distributed and are 0·5–1·5 μm apart.

Dimensions. Length = 64(72)77 μm, width = 50(57)66 μm; six specimens measured.

Comparison. A. laevigatus sp. nov. has a laevigate envelope. *A. histosus* has an envelope with reticulate sculpture.

Abditusdyadus laevigatus gen. et sp. nov.

Plate 4, figures 7–8

Derivation of name. Refers to the laevigate envelope; *laevigatus* = smooth (Latin).

Holotype and type locality. Plate 4, figure 8, FM517 (slide AK6/7, co-ord. 070 1204; E.F. no. H51/3), sample AK6, basal strata of the 'Lower Old Red Sandstone', near Eilean Orasaig, Kerrera.

Paratypes. Plate 4, figure 7, FM516 (slide AK1/3, co-ord. 169 1249; E.F. no. T55/2), sample AK1, Kerrera.

Diagnosis. An *Abditusdyadus* comprising a laevigate true dyad enclosed within a laevigate envelope.

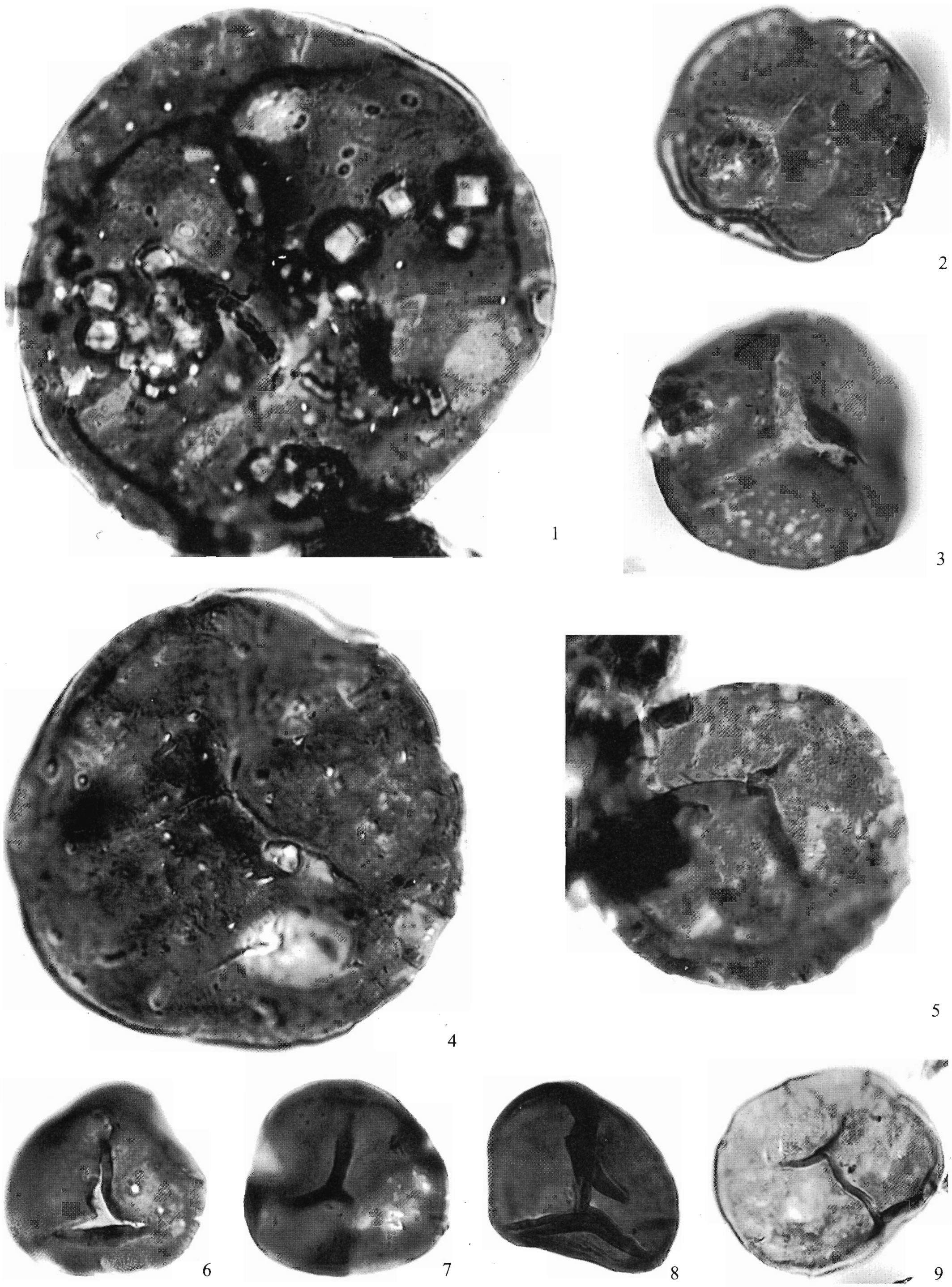
Description. Dyads composed of two laevigate hilate cryptospores with thick, generally unfolded walls. The individual spores are attached across a clearly perceptible plane of attachment and are occasionally partially separated. The dyad is enclosed within a loose or tightly adherent membranous envelope which is less than 0·5 μm thick. The envelope is diaphanous and entirely laevigate.

Dimensions. Length = 73(79)89 μm, width = 52(58)62 μm; eight specimens measured.

Remarks. A. histosus has an envelope with reticulate sculpture. *A. chalazus* has an envelope sculptured with grana. Burgess (1991) suggests that *Dyadospora membranifera* Johnson, 1985 is an envelope-enclosed pseudodyad and placed it with *Segestrespora* (*Dyadospora*) *membranifera* (Johnson) Burgess, 1991. However, Johnson's illustrations suggest that at least some of the specimens she placed with *Dyadospora membranifera* (e.g. pl. 7, figs 5–6), but not the type specimen, may be true dyads. However, Johnson's spores are smaller (length = 23(38)47 μm, width = 27(37)47 μm) than the Lorne specimens.

EXPLANATION OF PLATE 7

Figs 1, 4. *Retusotriletes* sp. A; sample AK1; near Eilean Orasaig, Kerrera. 1, FM537 (slide AK1/2, co-ord. 177 1167; E.F. no. T47). 4, FM538 (slide AK1/5, co-ord. 118 1120; E.F. no. N42).
Figs 2–3. *Retusotriletes* spp.; near Eilean Orasaig, Kerrera. 2, FM539 (slide AK1/3, co-ord. 180 1191; E.F. no. T49/4), sample AK1. 3, FM540 (slide AK6/5, co-ord. 125 1114; E.F. no. O41), sample AK6.
Fig. 5. *Apiculiretusispora* sp. A; FM541 (slide AK1/2, co-ord. 085 1165; E.F. no. K47/1), sample AK1; near Eilean Orasaig, Kerrera
Figs 6–8. *Ambitisporites* sp. A; sample AK6; near Eilean Orasaig, Kerrera. 6, FM543 (slide AK6/2, co-ord. 113 1190; E.F. no. N49). 7, FM542 (slide AK6/2, co-ord. 137 1200; E.F. no. P50). 8, FM544 (slide AK6/3, co-ord. 081 1119; E.F. no. J42/3).
Fig. 9. *Ambitisporites dilutus* (Hoffmeister) Richardson and Lister, 1969; FM545 (slide AK1/3, co-ord. 117 1169; E.F. no. N47), sample AK1; near Eilean Orasaig, Kerrera.
All × 1000.



WELLMAN and RICHARDSON, 'Lower Old Red Sandstone' sporomorphs

Genus VELATITETRAS Burgess, 1991

Type species. *Velatitetras laevigata* Burgess, 1991

Velatitetras (*Nodospora*) *retimembrana* (Miller and Eames, 1982) comb. nov.

Holotype and type locality. *Nodospora retimembrana* Miller and Eames (1982, pl. 6, fig. 4; OSU 35848). Power Glen Formation, (WPL-6), 1·5 m (5 ft) below the top of the Whirlpool Sandstone, Niagara Gorge, Lewiston, New York, USA.

Remarks. Burgess (1991) erected the genus *Velatitetras* to include envelope-enclosed cryptospore permanent tetrads. *Nodospora retimembrana* Miller and Eames, 1982 comprises envelope-enclosed cryptospore permanent tetrads and is transferred to *Velatitetras* from *Nodospora*. Burgess (1991) placed *Nodospora* in synonymy with *Tetrahedraletes*, a genus which encompasses naked, laevigate, cryptospore permanent tetrads.

Velatitetras (*Nodospora*) *retimembrana* (Miller and Eames, 1982)? comb. nov.

Plate 6, figures 1–2

Description. Large, smooth walled tetrahedral tetrad with distinct lines of attachment at the junctions between the spores. The distal walls of the spores comprising the tetrads are 2–3 μm thick. Tetrad enclosed within a tightly adherent envelope which is fairly sturdy, *c*. 1 μm thick, and not generally highly folded. Envelope sculptured with muri which are less than 0·75 μm high and wide, being slightly wider at the junctions where they meet. The muri form a regular reticulum with sub-polygonal lumina of fairly regular size with a maximum diameter of 1·5–2·5 μm.

Dimensions. 54(67)72 μm; four specimens measured.

Remarks. *Velatiteras* (*Nodospora*) *retimembrana* from the Medina Group, New York State (Llandovery age) is smaller (diameter 34(43)60 μm) but is otherwise identical. However, Johnson (1985) reports *Nodospora retimembrana* from the Tuscarora Formation in central Pennsylvania (Llandovery age) with a diameter range 52(62)81 μm. *Velatitetras reticulata* Burgess, 1991 from the Llandovery type area, Wales is smaller (diameter 22(27)35 μm), and the reticulum is ill-defined and often irregular.

Anteturma SPORITES Potonié, 1893
Turma TRILETES Reinsch, 1891
Subturma AZONOTRILETES Luber, 1935

Genus RETUSOTRILETES Naumova, 1953 emend. Richardson, 1965 (*non* Streel, 1964)

Type species. *Retusotriletes pychovii* Naumova, 1953 (lectotype of Richardson 1965).

EXPLANATION OF PLATE 8

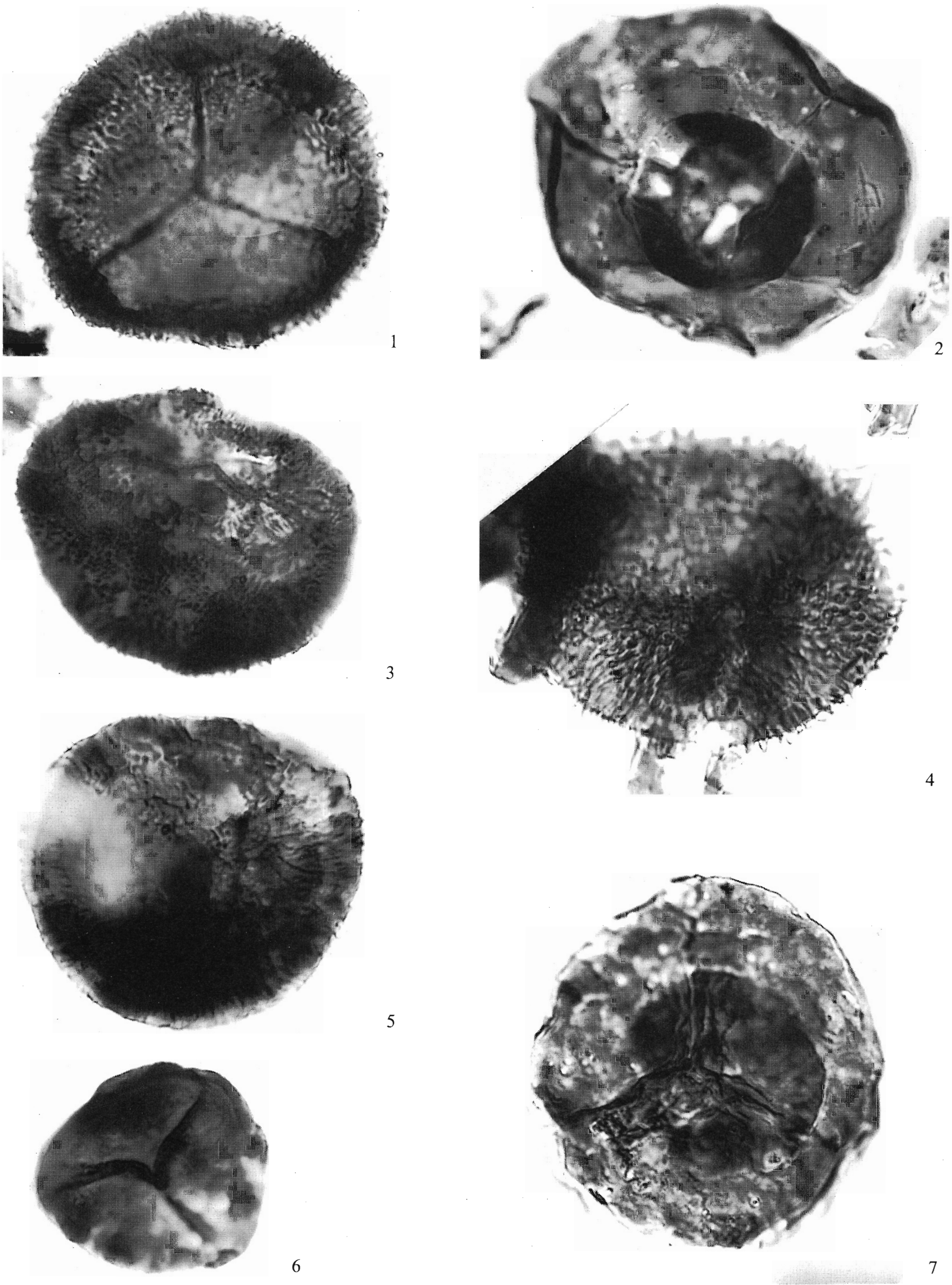
Figs 1, 3–5. *Dibolisporites ardchoircii* sp. nov. near Eilean Orasaig, Kerrera. 1, FM546 (slide AK6/7, co-ord. 018 1227; E.F. no. C53), sample AK6; holotype. 3, FM547 (slide AK6/5, co-ord. 043 1154; E.F. no. E45/4), sample AK6. 4, FM548 (slide AK1/3, co-ord. 144 1238; E.F. no. Q54), sample AK1. 5, FM549 (slide AK1/3, co-ord. 075 1242; E.F. no. J54/2), sample AK1.

Figs 2, 7. cf. *Amicosporites discus* sp. nov.; sample AK1; near Eilean Orasaig, Kerrera. 2, FM550 (slide AK1/3, co-ord. 068 1100; E.F. no. H40). 7, FM551 (slide AK1/3, co-ord. 037 1279; E.F. no. E58/2); holotype.

Fig. 6. *Ambitisporites avitus* Hoffmeister, 1959; FM552 (slide AOB4/2, co-ord. 187 1072; E.F. no. U37), sample AOB4; Port Caraig na Maraig, Oban.

All × 1000.

PLATE 8



WELLMAN and RICHARDSON, 'Lower Old Red Sandstone' sporomorphs

Retusotriletes maccullockii sp. nov.

Plate 6, figures 6–7

Derivation of name. After J. MacCullock who first classified the rocks of Lorne in 1819.

Holotype and type locality. Plate 6, figure 7, FM535 (slide AOB4/2, co-ord. 060 1343; E.F. no. G65), sample AOB4, basal strata of the 'Lower Old Red Sandstone', Port Caraig na Maraig, Oban.

Paratype. Plate 6, figure 6, FM534 (slide AK1/2, co-ord. 109 1114; E.F. no. M41/1), sample AK1, Kerrera.

Diagnosis. A *Retusotriletes* with distinct laesurae accompanied by prominent lips which taper in height from the equator towards the pole. The lips are up to 3 μm high at the equator tapering to 1 μm high at the proximal pole.

Description. Amb sub-circular. Trilete mark distinct with laesurae which extend for two-thirds to four-fifths of the spore radius. Laesurae straight and accompanied by lips which are up to 1 μm wide and taper from the equator towards the pole. Maximum height of lips is 3 μm at the equator and 1 μm at the pole. Contact areas delimited by distinct curvaturae perfectae up to 1 μm wide which lie entirely within the equator of the spore when observed in polar compression. There is little or no invagination at the junction between the curvaturae and the trilete rays. Exine entirely laevigate.

Dimensions. 37(43)50 μm; 24 specimens measured.

Remarks. There are many described species of *Retusotriletes*. However, none of these, to the knowledge of the authors, possess such distinct lips which taper so dramatically toward the pole.

Retusotriletes maculatus McGregor and Camfield, 1976

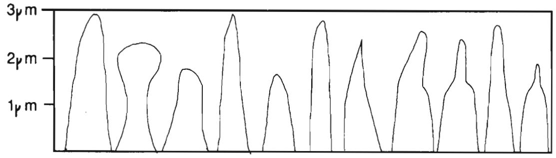
Plate 6, figure 5

Description. Amb sub-circular. Trilete mark distinct with sinuous or straight laesurae which are accompanied by narrow lips up to 1 μm wide. Laesurae diverge into curvaturae perfectae and there is prominent invagination. The curvaturae are concordant, or nearly concordant, with the equatorial margin for much of the interradial circumference and in some specimens form an equatorial crassitude up to 1·5 μm wide. In the centre of each interradial area is an oval to rounded papilla 8–12 μm in maximum diameter. Exine entirely laevigate.

Dimensions. 40(48)67 μm; 18 specimens measured.

Comparison. The Lorne specimens are similar to the holotype of *Retusotriletes maculatus* but have lips associated with the laesurae and the interradial papillae are less distinct. *Ambitisporites tripapillatus* Moreau-Benoit, 1976 and *Ambitisporites* sp. B. Richardson and Lister, 1969 are tripapillate but have prominent equatorial crassitudes.

Remarks. In the vast majority of specimens the curvaturae are distinctly invaginated and are coincident with the equator of the spore only in the central portion of each interradial area. However, in some specimens the curvaturae are coincident with the equator for a considerable portion of each interradial area and form an equatorial crassitude. Clearly there is a degree of intergradation between fully retusoid sporomorphs in which the curvaturae lie entirely within the equator of the spore and equatorially crassitate spores. This situation makes it difficult to decide whether to place the spores with the azonate genus *Retusotriletes* or the crassitate genus *Ambitisporites*. *Retusotriletes* is probably most convenient since the majority of specimens have curvaturae which fall entirely within the proximal surface and, in the specimens which appear to be crassitate, the crassitude is in no way persistent due to the invagination in the radial areas.



TEXT-FIG. 4. Range of variation in the ornament of *Dibolisporites ardchoircii* sp. nov. (lateral view).

Retusotriletes rotundus (Streel) Lele and Streel, 1969?

Plate 6, figures 3–4

Description. Amb sub-circular. Trilete mark distinct with straight, simple laesurae which occasionally gape slightly near the proximal pole. The laesurae extend for *c.* five-sixths of the spore radius. The contact areas are delimited by distinct curvaturae perfectae which are invaginated but extend to nearly reach the equator in the interradial areas. There is a prominent thickened triangular area situated at the proximal pole which is observed as a darkened region. The thickening is 18–25 µm in maximum diameter, usually less than one-third of the spore diameter. The innermost zone of the thickening (up to 10 µm in diameter) is lighter in colour (?thinner). Exine beyond the thickened region is thin (*c.* 1 µm) and commonly folded into prominent concentric folds. Exine entirely laevigate.

Dimensions. 33(58)76 µm; 24 specimens measured.

Remarks. There are numerous species of *Retusotriletes* described from the Silurian and Devonian which possess thickened proximal apical areas (see Lele and Streel 1969). The species most similar to the Lorne specimens in *R. rotundus* (Streel) Lele and Streel, 1969 which has a similar apical thickening differentiated into a thick/dark outer zone and a thin/pale inner zone.

Retusotriletes sp. A

Plate 7, figures 1, 4

Description. Amb sub-circular to sub-triangular. Trilete mark distinct with straight, simple laesurae which extend for two-thirds to seven-eighths of the spore radius and occasionally gape slightly. Contact areas delimited by distinct curvaturae perfectae. Curvaturae invaginated at the extremities of the laesurae but extend to nearly reach the equator in the interradial areas. Exine entirely laevigate.

Dimensions. 73 and 85 µm; two specimens measured.

Remarks. Because of their large size these spores are conspicuous in the Lorne assemblages. However, they are rare and consequently are not formally named.

Genus APICULIRETUSISPORA Streel emend. Streel, 1967

Type species. Apiculiretusispora brandtii Streel, 1964.

Apiculiretusispora sp. A

Plate 7, figure 5

Description. Amb sub-circular. Trilete mark distinct with straight laesurae which commonly gape. The rays extend from one-half to three-quarters the distance to the equator, and are usually accompanied by lips 0·5–1·0 µm wide. In some specimens the height of the lips appears to decrease from the equator to the proximal pole. Curvaturae perfectae are developed and lie entirely within the spore equator. The proximal face is smooth. Sculptured distally with micrograna, microconi and rare microspinae which are usually less than 0·75 µm high. The elements are usually fairly crowded and are less than 1 µm apart.

Dimensions. 44(50)57 µm; 14 specimens measured.

Remarks. There are numerous described spore taxa, usually assigned to *Apiculiretusispora*, which are grossly similar to *Apiculiretusispora* sp. A. However, we believe too few specimens were recovered to justify designation to one of these species, particularly considering the vast stratigraphical range of spores with similar rudimentary morphology.

Genus DIBOLISPORITES Richardson, 1965

Type species. Dibolisporites echinaceus (Eisenack, 1944) Richardson, 1965.

Dibolisporites ardchoircii sp. nov.

Plate 8, figures 1, 3–5

Derivation of name. After Ardchoirc, a dwelling on the Isle of Kerrera.

Holotype and type locality. Plate 8, figure 1, FM546 (slide AK6/7, co-ord. 018 1227; E.F. no. C53), sample AK6, basal strata of the 'Lower Old Red Sandstone', near Eilean Orasaig, Kerrera.

Paratypes. Plate 8, figure 3, FM547 (slide AK6/5, co-ord. 043 1154; E.F. no. E45/4), sample AK6 Kerrera. Plate 8, figure 4, FM548 (slide AK1/3, co-ord. 144 1238; E.F. no. Q54), sample AK1, Kerrera. Plate 8, figure 5, FM549 (slide AK1/3, co-ord. 075 1242; E.F. no. J54/2), sample AK1, Kerrera.

Diagnosis. A tripapillate *Dibolisporites* with densely packed distal sculpture comprising a mixture of sculptural types including spinae, biform elements and spatulate elements.

Description. Amb sub-rounded. Trilete rays straight, accompanied by narrow lips less than 1 μm high and wide. Laesurae culminate in curvaturae perfectae which lie entirely within the proximal face and are invaginated in the radial areas. In the centre of each contact area is a smooth, sub-circular interradial papilla which measures 10–12 μm long by 5–7 μm wide. The contact areas beyond the papillae have reduced sculpture comprising micrograna or minute muri which are less than 0·5 μm high and wide, and less than 2 μm long. The muri are convoluted and anastomosing, and curved in a geniculate fashion. It is possible that the muri may actually be folds in an exoexinal layer. Sculptured distally and equatorially by a varied and dense ornament of spinae with subsidiary pila, bacula, biform elements and spatulate elements. The elements are 0·75–3·0 μm high, generally less than 1·0 μm wide and rarely more than 1·5 μm apart. The variation exhibited by the sculpture is illustrated in Text-figure 4.

Dimensions. 45(57)64 μm; 32 specimens measured.

Remarks. These spores are azonate, with the curvaturae perfectae lying entirely within the equator of the spore, and clearly possess sculptural elements of *Dibolisporites*-type. However, they differ

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EXPLANATION OF PLATE 9

Figs 1–2. cf. *Amicosporites macconochiei* sp. nov.; sample AK6; near Eilean Orasaig, Kerrera. 1, FM553 (slide AK6/4, co-ord. 150 1145; E.F. no. Q44/4); holotype. 2, FM554 (slide AK6/3, co-ord. 093 1149; E.F. no. L45/1).

Figs 3, 6. cf. *Amicosporites symesii* sp. nov.; sample AOB5; Port Caraig na Maraig, Oban. 3, FM555 (slide AOB5/2, co-ord. 200 1084; E.F. no. V38/4). 6, FM556 (slide AOB4/2, co-ord. 197 1282; E.F. no. V59/3); holotype.

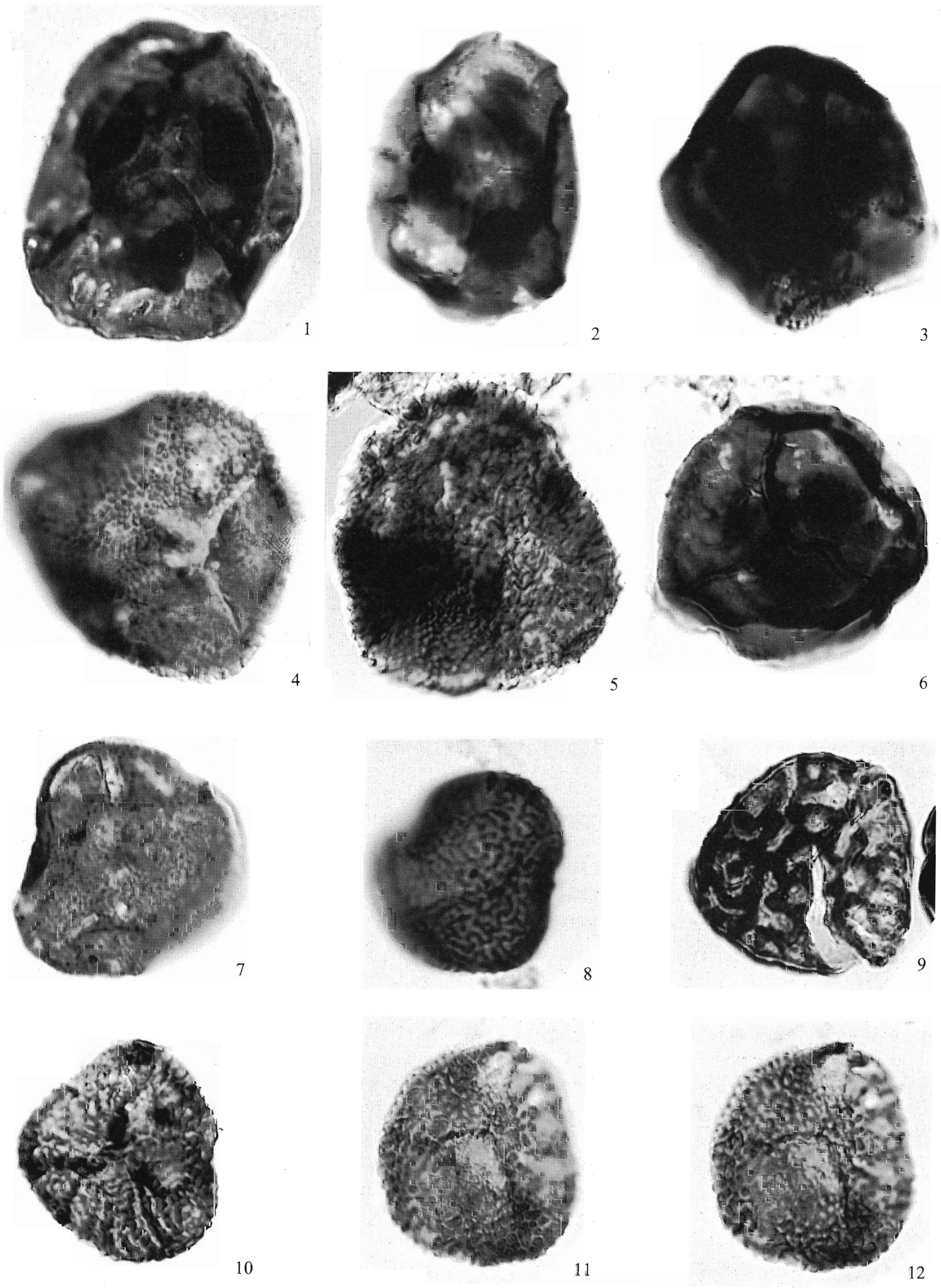
Figs 4–5. *Aneurospora* sp. B; sample AK1; near Eilean Orasaig, Kerrera. 4, FM557 (slide AK1/3, co-ord. 026 1280; E.F. no. D58/2). 5, FM558 (slide AK1/3, co-ord. 184 1321; E.F. no. U63/3).

Fig. 7. *Aneurospora* sp. A Wellman, 1993*b*; FM559 (slide AK1/2, co-ord. 110 1194; E.F. no. M50/3), sample AK1; near Eilean Orasaig, Kerrera.

Figs 8–12. *Synorisporites* spp. 8, 10–12, near Eilean Orasaig, Kerrera. 8, FM560 (slide AK6/3, co-ord. 084 1166; E.F. no. K47/1), sample AK6. 10, FM562 (slide AK6/5, co-ord. 150 1168; E.F. no. Q47/3), sample AK6. 11–12, FM563 (slide AK1/3, co-ord. 015 1136; E.F. no. C43/2), sample AK1. 9, FM561 (slide AOB5/2, co-ord. 143 1218; E.F. no. Q52), sample AOB5; Port Caraig na Maraig, Oban.

All × 1000.

PLATE 9



WELLMAN and RICHARDSON, 'Lower Old Red Sandstone' sporomorphs

from other species of *Dibolisporites* because they have distinct interradial papillae, although the distal ornament is similar to that in other species of this genus, for example *D. quebecensis* McGregor, 1973.

Subturma ZONOTRILETES Waltz *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 8, figure 6

Dimensions. 30(39)56 μm; 25 specimens measured.

Ambitisporites dilutus (Hoffmeister) Richardson and Lister, 1969

Plate 7, figure 9

Dimensions. 28(41)63 μm; 56 specimens measured.

Ambitisporites sp. A

Plate 7, figures 6–8

Description. Amb sub-circular to sub-triangular. Trilete mark distinct, straight and accompanied by prominent lips 1·5 μm wide and 1 μm high. Laesurae extend to the spore equator but the lips do not always extend the entire length of the laesurae. Occasionally the lip associated with one of the laesurae is noticeably shorter than those of the other rays. The laesurae diverge into curvaturae perfectae, but are not usually invaginated. Curvaturae coincident with the equator form a prominent, clearly defined and persistent equatorial crassitude 2·0–2·5 μm wide. Exine entirely laevigate.

Dimensions. 32(42)53 μm; 14 specimens measured.

Remarks. Ambitisporites sp. C Richardson and Ioannides, 1973 is superficially similar but is large and has folds associated with the laesurae rather than true lips. *Ambitisporites avitus* Hoffmeister, 1959 is similar but usually has less prominent lips.

Genus AMICOSPORITES Cramer, 1966*c*

Type species. Amicosporites splendidus Cramer, 1966*c*.

Remarks. A notable characteristic of the Lorne assemblages is the presence of a set of closely similar taxa which are crassitate and have prominent proximal and/or distal thickenings of the exine. These spores are similar to *Amicosporites splendidus* Cramer, 1966*c* and other species placed with *Amicosporites* (see for example Cramer and Diez 1975). Unfortunately, the genus *Amicosporites* cannot accommodate some of the Lorne taxa under consideration; a distal thickening in the form of an annulus is diagnostic for the genus, a feature not present in all of the Lorne taxa. However, it was decided to place the Lorne taxa within cf. *Amicosporites* because firstly, they all have similar morphology and are probably closely related, and secondly, they appear to be closely related to other species assigned to *Amicosporites*. We consider it undesirable to emend *Amicosporites* or create a new genus to accommodate such spores until more data is available.

cf. *Amicosporites discus* sp. nov.

Plate 8, figures 2, 7

Derivation of name. Refers to the distal circular thickening; *diskos* = circular plate (Greek).

Holotype and type locality. Plate 8, figure 7, FM551 (slide AK1/3, co-ord. 037 1279; E.F. no. E58/2), sample AK1, basal strata of the 'Lower Old Red Sandstone', near Eilean Orasaig, Kerrera.

Paratype. Plate 8, figure 2, FM550 (slide AK1/3, co-ord. 068 1100; E.F. no. H40), sample AK1, Kerrera.

Diagnosis. Laevigate, equatorially crassitate, trilete spores with a large (18–31 μm in diameter), distinct, circular thickening located on the distal surface and centred on the distal pole.

Description. Amb sub-circular. Trilete mark distinct, with straight or slightly sinuous laesurae which are accompanied by narrow lips less than 0·75 μm wide. Laesurae extend nearly to the equator, where they diverge into curvaturae. The curvaturae are commonly invaginated opposite the laesurae but follow the equator for the rest of the circumference forming a narrow equatorial crassitude which is usually less than 2 μm wide. There are often folds on the proximal surface which run parallel to the laesurae. A regular and distinct circular thickening is centred on the pole of the distal surface. The thickening has a diameter of 18–31 μm, generally about half the diameter of the spore. The exine is entirely laevigate.

Dimensions. 40(50)63 μm; 16 specimens measured.

Remarks. Rodriguez (1978*a*, 1978*b*) described two spores with circular thickenings centred around the polar regions, *Leiotriletes socorridus* Rodriguez, 1978*a* which has a distal thickening, and *Stenozonotriletes sagittarius* Rodriguez, 1978*b* which has a proximal thickening. Subsequently, Rodriguez (1983) proposed a new genus, *Concentricosisporites*, with *Concentricosisporites* (*Stenozonotriletes*) *sagittarius* as the type species. However, Jansonius and Hills (1990) suggested that *Co. sagittarius* may possess an inner body rather than an exinal thickening. Both of the species described by Rodriguez are similar to cf. *A. discus* but *Co. sagittarius* has a more prominent crassitude and the thickening is situated proximally, and *L. socorridus* apparently lacks an equatorial crassitude and has simple laesurae.

Additionally, there are several species of *Retusotriletes* which have circular thickenings, for example *R. rotundus* (Streel) Streel, 1967 and *R. goensis* (Streel) Lele and Streel, 1969. However, in these species the thickening is situated proximally. Cf. *Amicosporites macconochiei* sp. nov. and *Amicosporites splendidus* Cramer, 1966*c* have a distal annulus rather than a solid circular thickening.

cf. *Amicosporites macconochiei* sp. nov.

Plate 9, figures 1–2

Derivation of name. After Mr A. Macconochie, who discovered the first fossils from the 'Lower Old Red Sandstone' of the Lorne area.

Holotype and type locality. Plate 9, figure 1, FM553 (slide AK6/4, co-ord. 150 1145; E.F. no. Q44/4), sample AK6, basal strata of the 'Lower Old Red Sandstone', near Eilean Orasaig, Kerrera.

Paratype. Plate 9, figure 2, FM554 (slide AK6/3, co-ord. 093 1149; E.F. no. L45/1), sample AK6, Kerrera.

Diagnosis. Laevigate, equatorially crassitate, trilete spores with prominent oval proximal interradial papillae, and a distinct annulus situated on the distal surface and centred around the distal pole.

Description. Amb sub-circular. Trilete mark distinct with straight laesurae which are either simple or more usually accompanied by narrow lips up to 1 μm wide. Laesurae extend to near the equator where they diverge into curvaturae perfectae which are invaginated. The curvaturae are thickened and coincident with the equator for most of its length forming a narrow equatorial crassitude up to 1 μm wide. There is a distinct oval papilla in the centre of each interradial area 8–15 μm long by 5–11 μm wide. On the distal surface a concentric ridge 4–7 μm wide forms an annulus of diameter 20–31 μm which is centred around the distal pole. The exine is entirely laevigate.

Dimensions. 45(52)58 μm; 19 specimens measured.

Comparisons. *Amicosporites splendidus* Cramer, 1966*c* has a more prominent and better defined distal annulus and lacks interradial papillae. Cf. *A. discus* has a distal solid circular thickening rather than an annulus and lacks interradial papillae.

cf. *Amicosporites symesii* sp. nov.

Plate 9, figures 3, 6; Plate 13, figure 8

Derivation of name. After Mr R. G. Symes who undertook much of the early mapping of the 'Lower Old Red Sandstone' in the Lorne area.

Holotype and type locality. Plate 9, figure 6, FM556 (slide AOB5/2, co-ord. 197 1282; E.F. no. V59/3), sample AOB5, basal strata of the 'Lower Old Red Sandstone', Port Caraig na Maraig, Oban.

Paratype. Plate 9, figure 3, FM555 (slide AOB5/2, co-ord. 200 1084; E.F. no. V38/4), sample AOB5, Oban. ?Plate 13, figure 8, SEM stub CW47, print P009512, sample AK6, Kerrera.

Diagnosis. Equatorially crassitate, laevigate, trilete spores with prominent lips associated with the triradiate mark. The lips taper from the equator towards the proximal pole. In each of the interradial areas there is a large thickened region with poorly defined margins.

Description. Amb sub-triangular to sub-circular. Trilete mark distinct with straight laesurae which are accompanied by prominent lips. The lips are up to 1·5 μm wide and taper from the equator towards the pole. The lips are up to 4 μm high at the equator. The laesurae generally extend to the spore equator where they diverge into prominent curvaturae perfectae without any appreciable invagination. The curvaturae are coincident with the equator forming a distinct equatorial crassitude 2–4 μm wide. The equatorial crassitude is often accompanied by concentric folds in the proximal exine. Each interradial area possesses an indistinctly delimited thickening which is subcircular to subtriangular in shape and 11–17 μm in maximum diameter. The thickenings often extends to cover most of the interradial area. Exine entirely laevigate.

Dimensions. 34(46)56 μm; 28 specimens measured.

Remarks. Several species, reported from the Lorne assemblage and from elsewhere, have a similar construction to cf. *A. symesii*. However, the prominent lips and diffuse areas of interradial thickening serve to distinguish cf. *A. symesii*. *Ambitisporites* sp. B Richardson and Lister, 1969 and *A. tripapillatus* Moreau-Benoit, 1976 have smaller, discrete interradial thickenings, as does

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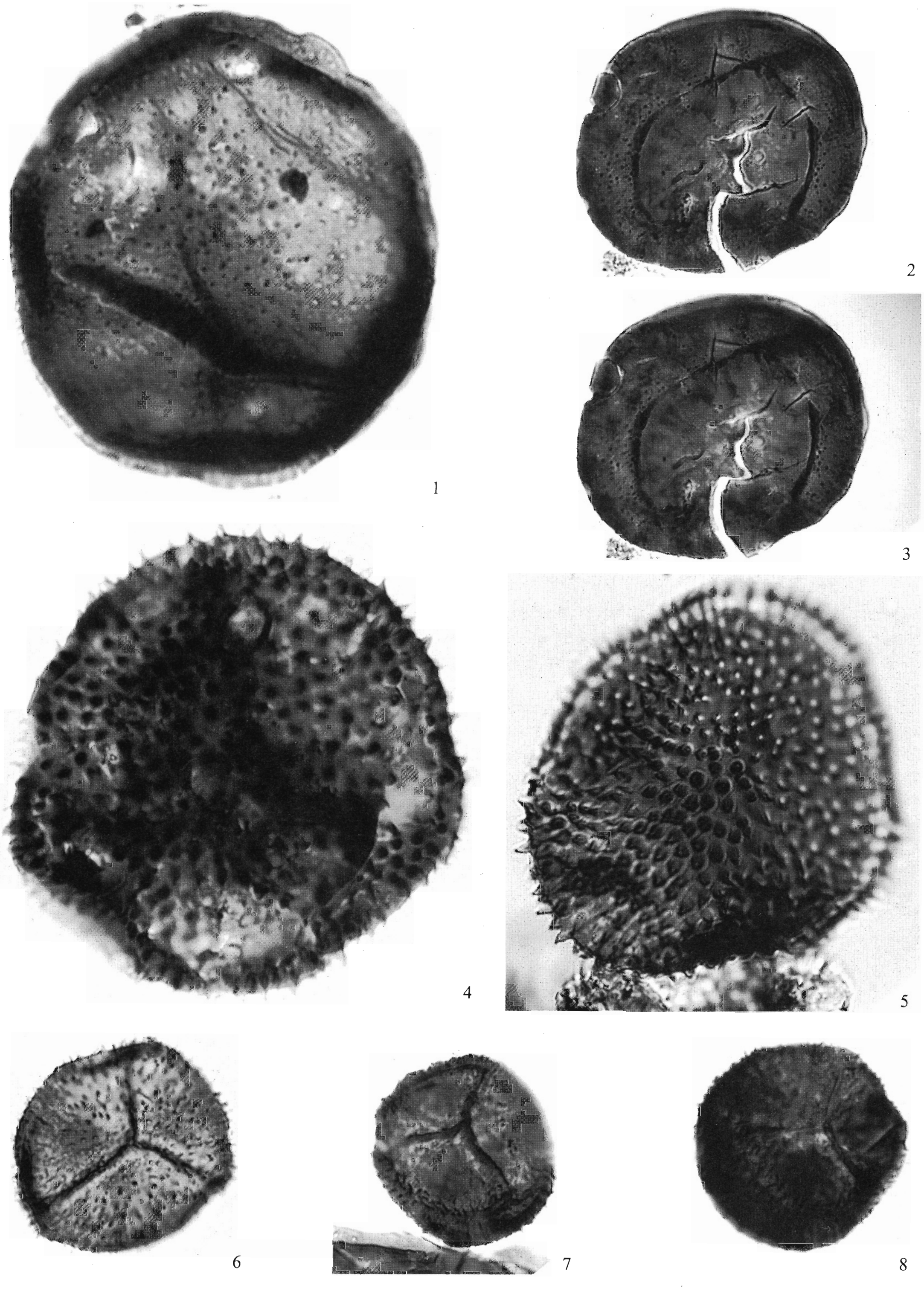
EXPLANATION OF PLATE 10

Figs 1–3. *Cymbohilates amplus* sp. nov. 1, FM564 (slide AK1/3, co-ord. 056 1314; E.F. no. G62); sample AK1, near Eilean Orasaig, Kerrera. 2–3, FM565 (slide AOB1/4, co-ord. 190 1068; E.F. no. U36/4), sample AOB1; Port Caraig na Maraig, Oban; holotype; ×500.

Figs 4–5. *Aneurospora geikiei* sp. nov.; sample AK1; near Eilean Orasaig, Kerrera. 4, FM566 (slide AK1/3, co-ord. 069 1085; E.F. no. H38); holotype. 5, FM567 (slide AK1/2, co-ord. 163 1165; E.F. no. S46/2).

Figs 6–8. *Aneurospora hispidica* sp. nov.; sample AK6; near Eilean Orasaig, Kerrera. 6, FM568 (slide AK6/5, co-ord. 186 1166; E.F. no. U47/3); holotype. 7, FM570 (slide AK6/2, co-ord. 175 1047; E.F. no. T34/2). 8, FM569 (slide AK6/3, co-ord. 090 1196; E.F. no. K50/3).

All ×1000 (except figs 2–3).



WELLMAN and RICHARDSON, *Cymbohilates*, *Aneurospora*

Retusotriletes maculatus McGregor and Camfield, 1976 and the specimens from Lorne assigned to this species. Cf. *A. discus* and cf. *A. macconochiei* are similar in construction but possess distal thickenings. Although, cf. *A. symesii* lacks distal thickenings, in terms of its structure and the nature of the proximal thickenings it appears to be closely related to cf. *A. discus* and cf. *A. macconochiei*, and for this reason is placed within cf. *Amicosporites*.

Genus ANEUROSPORA Streel emend. Richardson *et al.*, 1982

Type species. *Aneurospora goensis* Streel, 1964.

Aneurospora geikiei sp. nov.

Plate 10, figures 4–5; Plate 13, figures 10–12

1991 *Cymbosporites* sp.; Marshall, fig. 3(2).

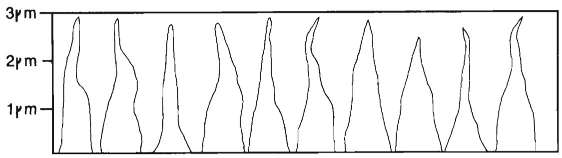
Derivation of name. After Sir Archibald Geikie, in recognition of his contribution toward the study of the 'Old Red Sandstone' of Scotland.

Holotype and type locality. Plate 10, figure 4, FM566 (slide AK1/3, co-ord. 069 1085; E.F. no. H38), sample AK1, basal strata of the 'Lower Old Red Sandstone', near Eilean Orasaig, Kerrera.

Paratypes. Plate 10, figure 5, FM567 (slide AK1/2, co-ord. 163 1165; E.F. no. S46/2), sample AK1, Kerrera. Plate 13, figure 10, SEM stub CW64, print P009313, sample BK2, Kerrera. Plate 13, figure 11, SEM stub CW33, print P007356, sample AK1, Kerrera. Plate 13, figure 12, SEM stub CW33, print P007357, sample AK1, Kerrera.

Diagnosis. An *Aneurospora* with an indistinct trilete mark, a laevigate or microgranulate proximal surface and distal sculpture comprising evenly distributed prominent spinose elements which are 1·5–3·0 μm tall, 0·7–1·0 μm wide at their base, and 1–4 μm apart. Spines occasionally biform.

Description. Amb sub-circular. Trilete mark indistinct and often difficult to discern. Laesurae straight and simple, usually slightly gaping, extending to, or nearly to, the equatorial crassitude. Proximal surface laevigate or with a faint microgranulate sculpture. In some specimens there is a slightly darkened, ?thickened, triangular area which surrounds the trilete mark and extends for one-third to one-half of the spore radius. Equatorial crassitude clearly defined and 1·5–3·5 μm wide. The proximal surface is somewhat thinner than the distal surface (1–2 μm as opposed to *c.* 4 μm) and is often fractured at the margin with the rigid crassitude. Distal surface and equatorial margin sculptured with spines and biform elements. Biform elements with a straight to slightly tapering basal portion tipped by a rapidly tapering spine. Elements 1·5–3·0 μm high, 0·7–1·0 μm wide at their base, and 1–4 μm apart (see Text-fig. 5).



TEXT-FIG. 5. Range of variation in the ornament of *Aneurospora geikiei* sp. nov. (lateral view).

Dimensions. 53(69)86 μm; 54 specimens measured.

Comparison. *Streelispora riegelensis* Rodriguez, 1978*c* is similar to *A. geikiei* but the spines are shorter (0·5–15 μm) and are not usually biform. Furthermore, *S. reigelensis* is smaller, with a diameter of 20–30 μm.

Aneurospora hispidica sp. nov.

Plate 10, figures 6–8; Plate 13, figure 9

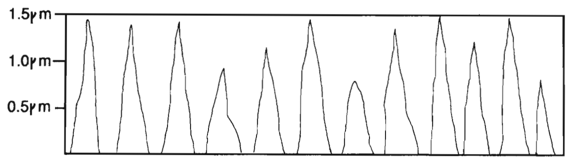
Derivation of name. Refers to the ornament; *hispidicus* = hairy (Latin).

Holotype and type locality. Plate 10, figure 6, FM568 (slide AK6/5, co-ord. 186 1166; E.F. no. U47/3), sample AK6, basal strata of the 'Lower Old Red Sandstone', near Eilean Orasaig, Kerrera.

Paratypes. Plate 10, figure 7, FM570 (slide AK6/2, co-ord. 175 1047; E.F. no. T34/2), sample AK6 Kerrera. Plate 10, figure 8, FM569 (slide AK6/3, co-ord. 090 1196; E.F. no. K50/3), sample AK6, Kerrera. Plate 13, figure 8, SEM stub CW46, print P009374, sample AK1, Kerrera.

Diagnosis. An *Aneurospora* sculptured distally and equatorially with slender spines 0·7–1·0 μm high, less than 0·5 μm wide and 0·5–2·0 μm apart. A 'bald patch' is located in the centre of each contact area, outside of which reduced proximal sculpture is developed.

Description. Amb sub-circular. Distinct trilete mark with laesurae that are straight and simple and extend to the equatorial crassitude. At the spore equator the laesurae join the equatorial crassitude which is 1·0–2·5 μm wide, but there is no invagination. On the proximal surface a reduced sculpture of grana and coni occurs in a narrow strip which extends outwards for up to 3 μm on either side of the laesurae. The reduced sculpture defines a sub-circular smooth ('bald') area in the centre of each contact area that is 8–10 μm long and 5–8 μm wide. These 'bald' areas resemble interradial papillae but do not appear to be significantly thickened. Spores sculptured equatorially and distally by spines 0·7–1·5 μm high, less than 0·5 μm wide and 0·5–2·0 μm apart (see Text-fig. 6).



TEXT-FIG. 6. Range of variation in the ornament of *Aneurospora hispidica* sp. nov. (lateral view).

Dimensions. 27(33)44 μm; 50 specimens measured.

Comparison. The ornament of *A. hispidica* resembles that of *Apiculiretusispora spicula* Richardson and Lister, 1969, but the latter is fully retusoid.

Aneurospora sp. A Wellman, 1993*b*

Plate 9, figure 7

Dimensions. 37(46)54 μm; four specimens measured.

Comparison. These spores are identical to *Aneurospora* sp. A, described from the Sandy's Creek Beds of the Midland Valley of Scotland (late early–early late Lochkovian; Wellman 1993*b*).

Aneurospora sp. B

Plate 9, figures 4–5

Description. Amb sub-triangular. Trilete mark simple and indistinct, with laesurae extending to the inner margin of the crassitude. Proximal surface sculptured with small convolute and anastomosing muri which are less than 0·5 μm high and wide. In places the muri form an irregular reticulum with lumina of maximum diameter *c.* 2·5 μm. Equatorial crassitude *c.* 2 μm wide. Sculptured distally and equatorially by closely spaced round or flat-topped tuburcula that are 0·5–1·0 μm wide, 0·5–1·5 μm high and less than 0·5 μm apart.

Dimensions. 45(47)48 μm; three specimens measured.

Comparison and remarks. The distal ornament of flat-topped tuburcula is distinctive and serves to distinguish these specimens from other species of *Aneurospora*. The proximal ornament appears to consist of true sculptural elements, rather than being a product of the folding of a thin exoexinal layer.

Genus EMPHANISPORITES McGregor, 1961

Type species. Emphanisporites rotatus McGregor, 1961.

Emphanisporites sp. A

Plate 11, figures 7–8

Description. Amb sub-triangular. Trilete mark distinct with more-or-less straight laesurae which extend to the equator and are accompanied by narrow lips less than 0·5 μm high and wide. Equatorial crassitude 1·5 μm wide. Contact areas ornamented with seven to ten radially arranged muri which are straight, 1·5 μm wide at the equator, tapering to less than 0·5 μm wide before terminating a few micrometres short of the polar axes. Distal sculpture comprises densely packed, relatively straight-sided, microspinae which are less than 0·5 μm high and 0·5–1·5 μm apart.

Dimensions. 29 μm; one specimen measured.

Comparison. E. micrornatus Richardson and Lister, 1969 has more robust proximal ribs and a distal sculpture comprising micrograna, and microconi which are wider than the microspinae adorning *Emphanisporites* sp. A.

EXPLANATION OF PLATE 11

Figs 1–2. *Synorisporites* sp. A; sample AK6; near Eilean Orasaig, Kerrera. 1, FM571 (slide AK6/3, co-ord. 099 1100; E.F. no. L40). 2, FM572 (slide AK6/2, co-ord. 030 1261; E.F. no. D56/4).

Fig. 3. *Emphanisporites* sp.; FM573 (slide AOB5/2, co-ord. 070 1297; E.F. no. H60/4), sample AOB5; Port Caraig na Maraig, Oban.

Figs 4–6. *Emphanisporites* sp. B; sample AK6; near Eilean Orasaig, Kerrera. 4, FM574 (slide AK6/3, co-ord. 149 1260; E.F. no. P56/4). 5–6, FM575 (slide AK6/4, co-ord. 217 1269; E.F. no. Y57/2).

Figs 7–8. *Emphanisporites* sp. A; FM576 (slide AK6/5, co-ord. 060 1094; E.F. no. G39/4), sample AK6; near Eilean Orasaig, Kerrera.

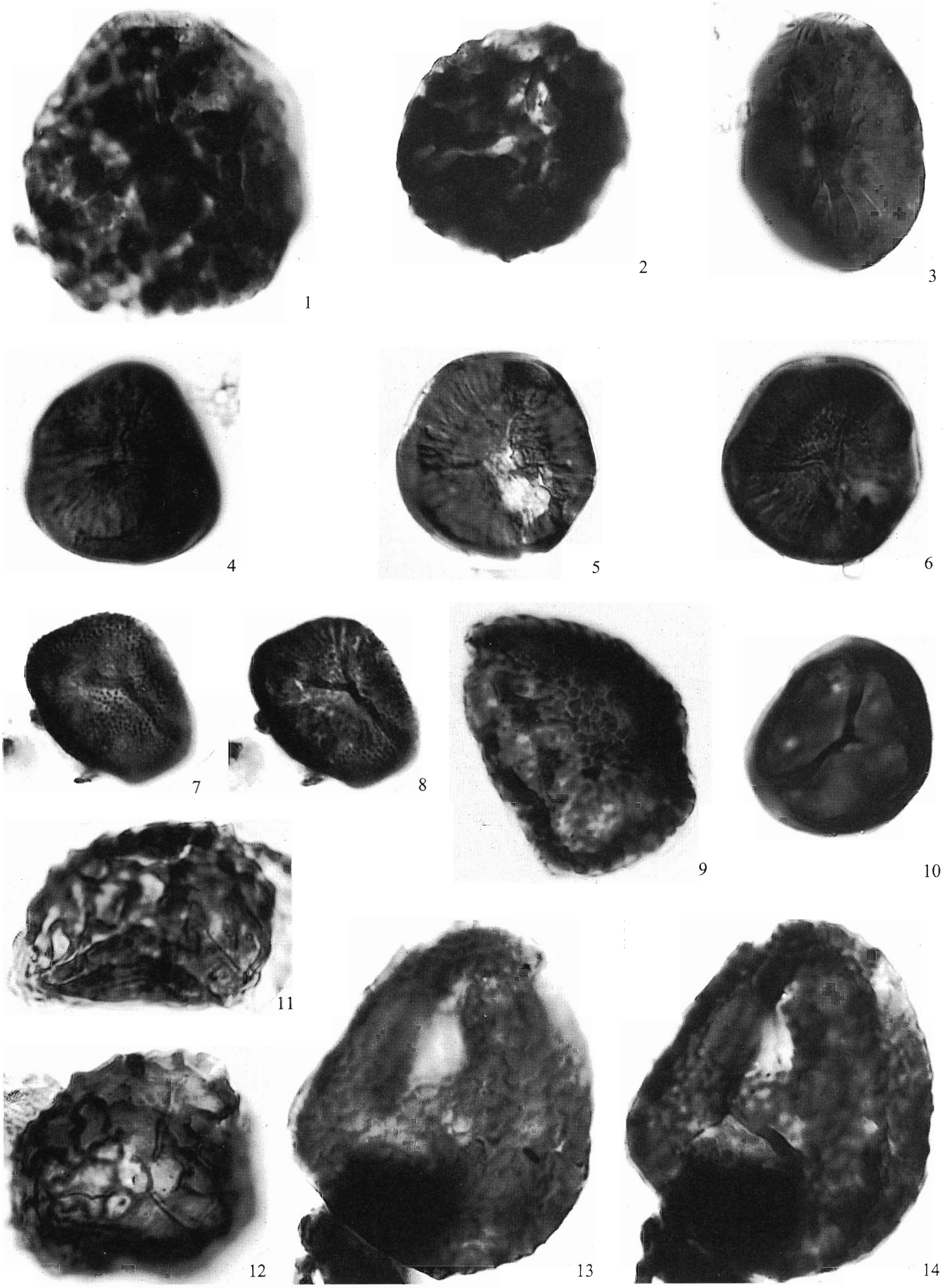
Fig. 9. *Cymbosporites* sp.; FM577 (slide AK1/2, co-ord. 175 1247; E.F. no. T55), sample AK1; near Eilean Orasaig, Kerrera.

Fig. 10. *Archaeozonotriletes chulus* (Cramer) Richardson and Lister, 1969 var. *chulus* Richardson and Lister, 1969; FM578 (slide AOB4/2, co-ord. 090 1319; E.F. no. K62/4), sample AOB4; Port Caraig na Maraig, Oban.

Figs 11–12. *Chelinospora* sp. A; near Eilean Orasaig, Kerrera. 11, FM498 (slide AK1/3, co-ord. 027 1313; E.F. no. D62/1), sample AK1. 12, FM350 (slide AK6/3, co-ord. 092 1148; E.F. no. K45/3), sample AK6.

Figs 13–14. *Chelinospora* sp.; FM579 (slide AK1/3, co-ord. 176 1136; E.F. no. T43/4), sample AK1; near Eilean Orasaig, Kerrera.

All × 1000.



WELLMAN and RICHARDSON, 'Lower Old Red Sandstone' sporomorphs

Emphanisporites sp. B

Plate 11, figures 4–6

Description. Amb sub-triangular to sub-circular. Trilete mark simple and distinct. Laesurae straight or sinuous extending two-thirds to seven-eighths of the way to the equator where they terminate in curvaturae which are invaginated but merge with the equator forming an equatorial crassitude. Equatorial crassitude 1·0–1·5 μm wide. Proximal surface sculptured with radially disposed muri. The muri are *c*. 1 μm high and wide and are straight in the zone which extends from the spore equator to approximately midway towards the spore apex. From this point the ribs narrow to 0·5 μm or less in height and width and become sinuous forming an haphazard, crowded, meandering pattern which covers the central zone of the proximal surface. There are eight to ten ribs per interradial area. Distal surface smooth.

Dimensions. 30(32)35 μm; six specimens measured.

Comparison. The proximal radial muri of *E. protophanus* Richardson and Ionannides, 1973 are confined to the radial region of the spore and terminate abruptly, leaving the central portion of the spore smooth. *Artemopyra* sp. A Burgess and Richardson, 1991 has a similar proximal sculpture but is alete.

Genus SYNORISPORITES Richardson and Lister, 1969

Type species. *Synorisporites downtonensis* Richardson and Lister, 1969.

Synorisporites sp. A

Plate 11, figures 1–2

Description. Amb sub-circular. Trilete mark distinct with straight laesurae which extend to the equator. Equatorial crassitude 1·5 μm wide. Proximal surface smooth with distinct rounded papillae *c*. 4 μm in diameter situated in the centre of each interradial area. Sculptured distally and equatorially with sub-rounded and

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EXPLANATION OF PLATE 12

Fig. 1. *Qualisaspora kidstonii* sp. nov.; SEM stub CW34, print P007324, sample AK1; near Eilean Orasaig, Kerrera.

Fig. 2. *Fustisispora aenigma* Wellman, 1993*b*?; SEM stub CW34, print P009558, sample AK1; near Eilean Orasaig, Kerrera.

Figs 3, 6. *Cymbohilates allenii* var. *magnus* Richardson, 1996; near Eilean Orasaig, Kerrera. 3, SEM stub CW34, print P007335, sample AK1. 6, SEM stub CW46, print P009428, sample AK6.

Figs 4–5. *Artemopyra robusta* sp. nov.; sample AK1; near Eilean Orasaig, Kerrera. 4, SEM stub CW33, print P009556; ×625. 5, SEM stub CW34, print P009557.

Fig. 7. *Artemopyra laevigata* sp. nov.; SEM stub CW46, print P007891, sample AK6; near Eilean Orasaig, Kerrera.

Fig. 8. *Chelinohilates sinuosus* var. *angustus* sp. et var. nov.; SEM stub CW46, print P007947, sample AK6; near Eilean Orasaig, Kerrera.

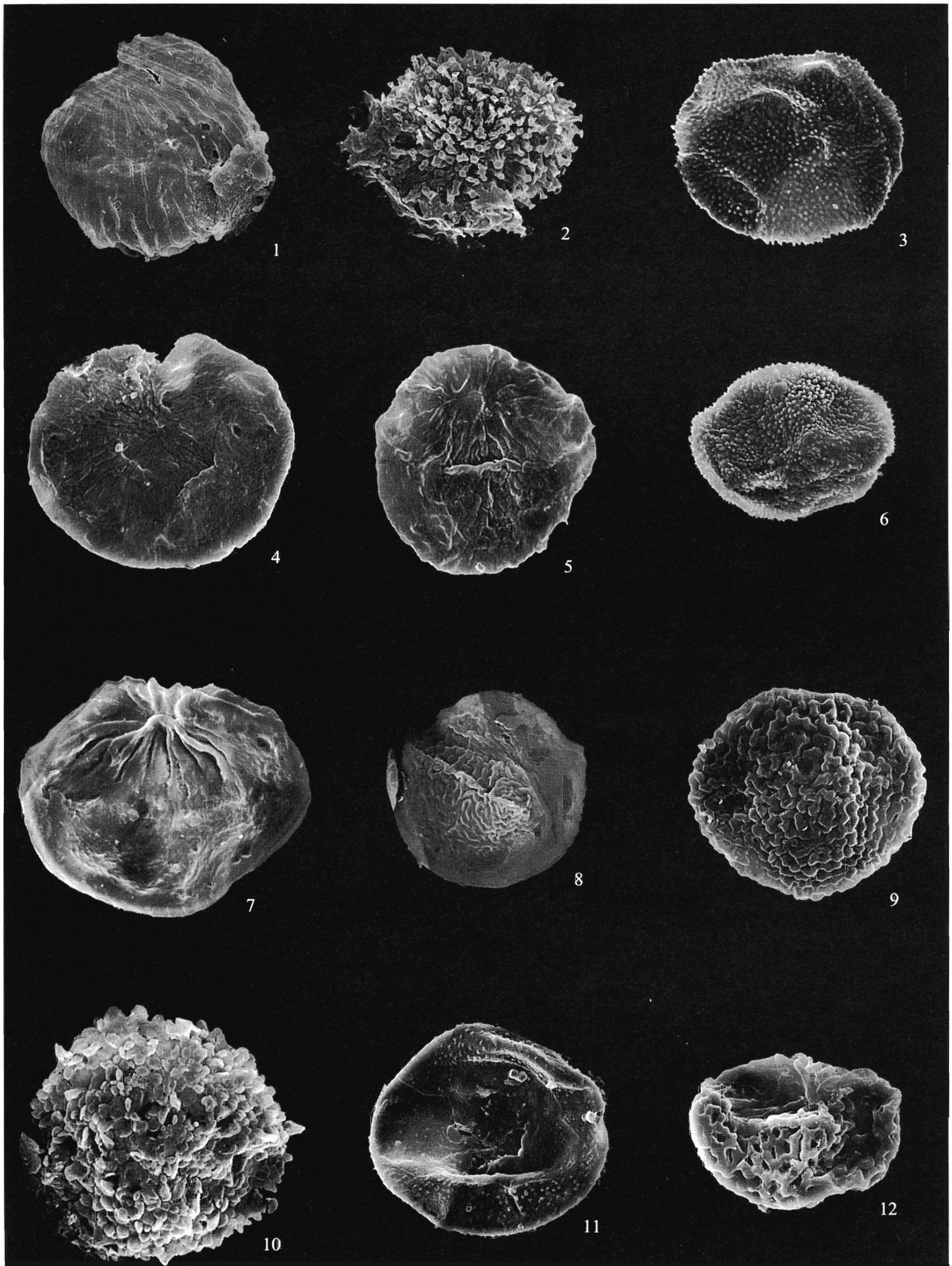
Fig. 9. *Chelinohilates sinuosus* var. *sinuosus* sp. et var. nov.; SEM stub CW46, print P009370, sample AK6; near Eilean Orasaig, Kerrera.

Fig. 10. *Hispanaediscus*? *irregularis* sp. nov.; SEM stub CW62, print P008892, sample BK1; near Eilean Orasaig, Kerrera.

Fig. 11. *Cymbohilates microgranulatus* sp. nov.; SEM stub CW64, print P009316, sample BK2; near Eilean Orasaig, Kerrera; ×500.

Fig. 12. *Chelinohilates lornensis* sp. nov.; SEM stub CW46, print P009420, sample AK6; near Eilean Orasaig, Kerrera.

All ×1000 (except figs 4 and 11).



WELLMAN and RICHARDSON, 'Lower Old Red Sandstone' sporomorphs

irregular rugulae and verrucae 3–6 μm in maximum diameter and *c.* 0·75 μm apart. The rugulae/verrucae are rounded in profile and 0·7–1·5 μm high.

Dimensions. 37(41)49 μm; three specimens measured.

Comparisons. Synorisporites sp. A Richardson and Lister, 1969 is similar but has distal sculptural elements which are slightly shorter (0·4–1·0 μm high).

Synorisporites spp.

Plate 9, figures 8–12

Remarks. Rare spores which belong to the genus *Synorisporites* (i.e. they are equatorially crassitate and possess distal sculpture comprising verrucae, rugulae and/or muri) are present in the Lorne assemblage. However, although this set of spores clearly comprise a number of distinct species, they are present in too few numbers to warrant formal description. A selection of these spores is illustrated on Plate 9, figures 8–12.

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

Type species. Archaeozonotriletes variabilis Naumova, 1953 emend. Allen, 1965.

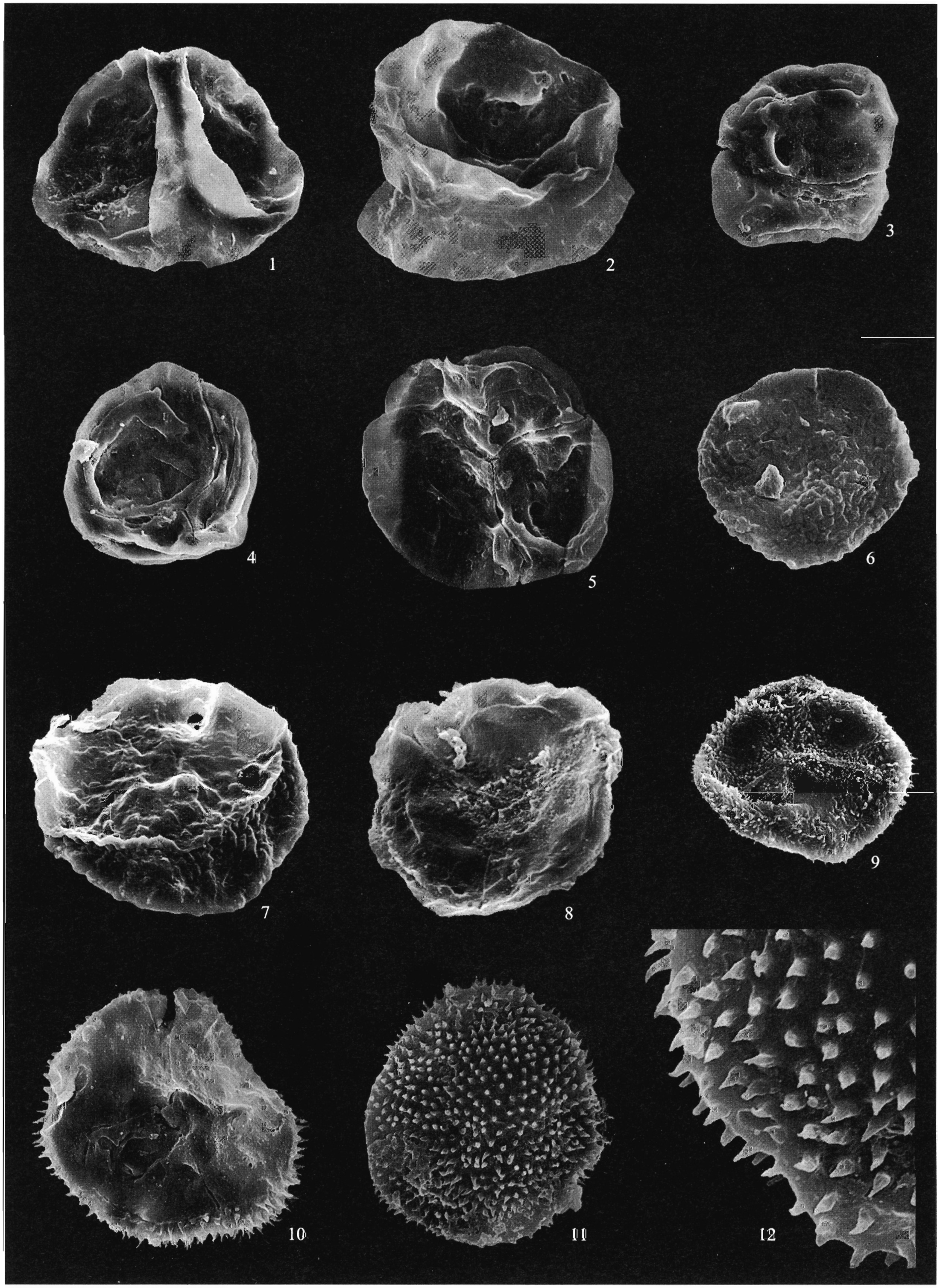
Archaeozonotriletes chulus var. *chulus* Richardson and Lister, 1969

Plate 11, figure 10

Dimensions. 36(39)45 μm; seven specimens measured.

EXPLANATION OF PLATE 13

Fig. 1. *Cheilotetras caledonica* Wellman and Richardson, 1993?; SEM stub CW62, print P008895, sample BK1; near Eilean Orasaig, Kerrera; ×666.
Fig. 2. *Pseudodyadospora petasus* Wellman and Richardson, 1993; SEM stub CW63, print P008954, sample BK1; near Eilean Orasaig, Kerrera.
Fig. 3. 'Dyad of *Laevolancis plicata* Burgess and Richardson, 1991' (*Dyadospora murusattenuata* Strother and Traverse emend. Burgess and Richardson, 1991); SEM stub CW46, print P009368, sample AK6; near Eilean Orasaig, Kerrera.
Figs 4–5. Tetrads of Trilete spores?; sample AK6; near Eilean Orasaig, Kerrera. 4, SEM stub CW46, print P009426. 5, SEM stub CW46, print P009372.
Figs 6–7. *Hispanaediscus* cf. *verrucatus* Burgess and Richardson, 1991; near Eilean Orasaig, Kerrera. 6, SEM stub CW33, print P007338, sample AK1. 7, SEM stub CW47, print P009516, sample AK6; note laevigate proximal hilum.
Fig. 8. cf. *Amicosporites symesii* sp. nov.?; SEM stub CW47, print P009512, sample AK6; near Eilean Orasaig, Kerrera; ×625.
Fig. 9. *Aneurospora hispidica* sp. nov.; SEM stub CW46, print P009374, sample AK1; near Eilean Orasaig, Kerrera.
Figs 10–12. *Aneurospora geikiei* sp. nov.; near Eilean Orasaig, Kerrera. 10, SEM stub CW64, print P009313, sample BK2; ×666. 11, SEM stub CW33, print P007356, sample AK1; ×666. 12, SEM stub CW33, print P007357; same specimen as Fig. 11; ×2000.
All ×1000 (except figs 1, 8, 10–12).



WELLMAN and RICHARDSON, 'Lower Old Red Sandstone' sporomorphs

Genus CHELINOSPORA Allen, 1965 emend. McGregor and Camfield, 1976

Type species. Chelinospora concinna Allen, 1965.

Chelinospora sp. A

Plate 11, figures 11–12

Description. Amb sub-triangular. Trilete mark distinct with simple straight laesurae which extend to the inner margin of the patina. Proximal surface laevigate. Patina 4 μm wide at the equator. Sculptured equatorially and distally by convolute and anastomosing muri *c.* 0·75 μm wide and 1 μm high. The muri form a reticulum of lumina of irregular shape and size. Lumina 2·5–5·0 μm in maximum diameter.

Dimensions. 39(45)54 μm; three specimens measured.

TETRADS OF TRILETE SPORES

Plate 5, figure 10; Plate 13, figures 4–5

Description. Tetrahedral tetrads comprising sub-triangular–sub-circular spores 20–30 μm in diameter. Individual spores generally equatorially crassitate, occasionally azonate. There is always a distinct line of attachment between adjoining spores and the tetrads are often partially separated, occasionally revealing the trilete marks on the proximal faces. The exine over the distal surface is laevigate, 0·7–1·5 μm thick and may be folded.

Dimensions. 37(46)69 μm; 23 specimens measured.

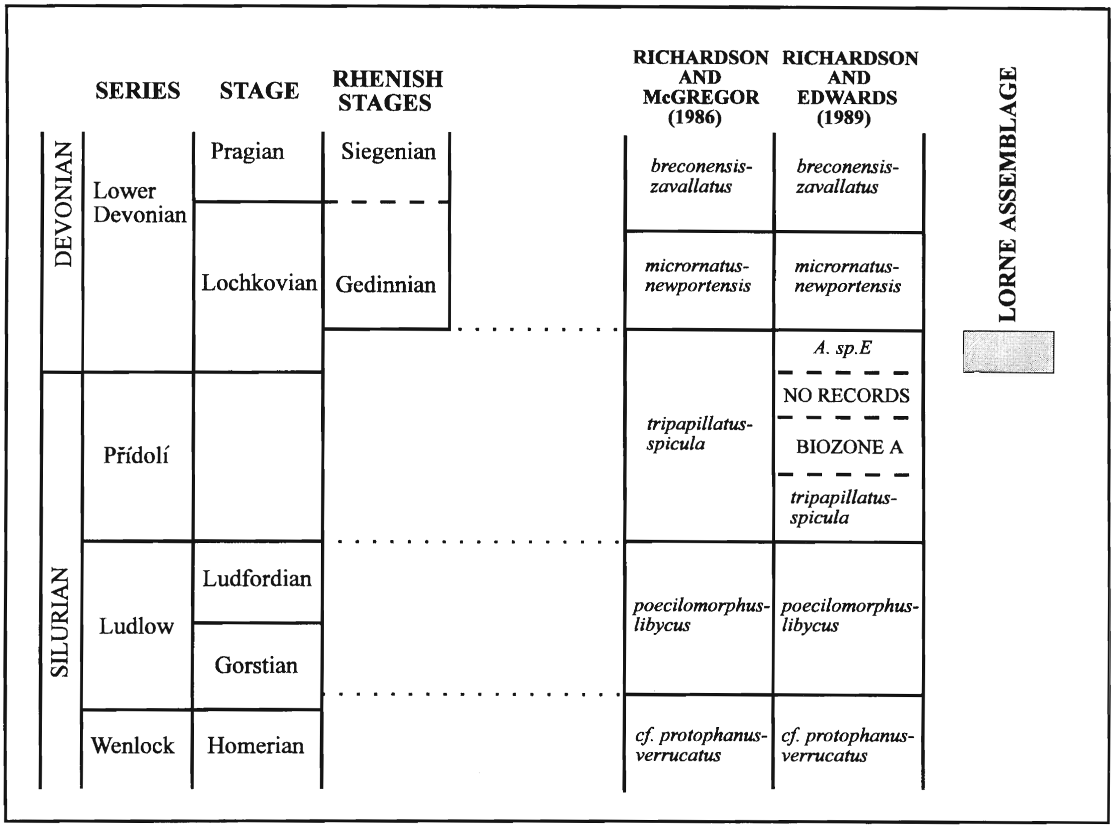
Remarks. These almost certainly represent tetrads of trilete spores. Such tetrads usually dissociate into trilete spores prior to dispersal. These examples have uncharacteristically failed to dissociate and were dispersed intact. They may represent immature spores dispersed prematurely or they may have failed to dissociate for another reason. They probably represent distally laevigate species of *Retusotriletes* and *Ambitisporites*.

BIOSTRATIGRAPHY

All of the sporomorph assemblages examined from Lorne are similar (see Table 1). The general characteristics of the sporomorph assemblages suggests a late Silurian or early Devonian age. More precise age determination poses difficulties because the Lorne assemblages lack taxa with well documented and limited stratigraphical distribution and appear at first sight to be somewhat atypical when compared with the majority of previously described sporomorph associations of late Silurian–early Devonian age (see below). However, these problems may reflect the published fossil record, in which there are gaps in our knowledge of sporomorph distribution over the late Silurian–early Devonian interval, particularly for the latest Přídolí and earliest Lochkovian.

However, certain characteristics of the assemblages provide potential age constraints. A lower age limit is supplied by the presence of crassitate trilete spores with an ornament of large, distinct apiculate elements (e.g. *Aneurospora geikiei*). Spores adorned with such sculptural elements are not known below the Silurian-Devonian boundary (Richardson and Edwards 1989; J. B. Richardson, unpublished work in southern Britain). Thus a lower age bracket of earliest Lochkovian seems probable. An upper age limit is suggested by the absence of various taxa and morphological characteristics, notably zonate miospores and miospores which have a multilayered exine where the exine exhibits a tendency to detach partially (for example *Streelispora* spp.). These features first appear in sporomorph associates of early, but not earliest, Lochkovian age (*micrornatus-newportensis* Sporomorph Assemblage Zone) and have been well documented in sequences of independently age-constrained sporomorph associations in southern Britain (Richardson and

McGregor 1986), the Ardennes–Rhenish region (Steemans 1989), and several other localities (Richardson *et al.* 1981; Richardson and McGregor 1986; Streel *et al.* 1987; Steemans 1989). Therefore an upper age limit of pre-early (but not earliest) Lochkovian is most likely. Considering the lower and upper age brackets the assemblage is assigned an earliest Lochkovian (pre-Gedinnian) age (Text-fig. 7).



TEXT-FIG. 7. Correlation of the Lorne assemblage with respect to sporomorph zonation schemes. Data from Richardson *et al.* (1984), Richardson and McGregor (1986), Richardson and Edwards (1989) and J. B. Richardson (unpublished work in southern Britain).

It is important to recognize that an age determination for the Lorne assemblage is problematical. The paucity of previously described taxa and the absence of species known to have limited stratigraphical range creates particular difficulties. In order to determine the age of the assemblage, one has to rely on comparisons of level of organization (i.e. how advanced/evolved an assemblage is); comparisons of taxa present are effectively ruled out.

COMPARISON WITH SIMILAR AGED SPOROMORPH ASSEMBLAGES

Late Silurian–early Devonian sporomorph assemblages are best documented from sequences in southern Britain, Scotland, the Ardennes–Rhenish region, the Armoricain Massif, the Cantabrian Mountains, and a handful of other scattered localities. These occurrences are discussed briefly below.

TAXON/MORPHOTYPE		southern Britain *tripapillatus-spicula* AB early Přídolí	southern Britain BiozoneA late early Přídolí	southern Britain *Apiculiretusispora* sp.E AB (Biozone B) earliest Lochkovian (pre-Gedinnian)	Lorne, Scotland ?Biozone B equivalent earliest Lochkovian (pre-Gedinnian)	southern Britain *micrornatus-newportensis* AB (lower subzone) early, but not earliest, Lochkovian	Scotland *micrornatus-newportensis* AB (lower subzone) early, but not earliest, Lochkovian	Ardennes-Rhenish region *micrornatus-newportensis* AB (lower subzone) early, but not earliest Lochkovian	southern Britain *micrornatus-newportensis* AB (middle subzone) late early-early late Lochkovian	Scotland *micrornatus-newportensis* AB (middle subzone) late early-early late Lochkovian	Ardennes-Rhenish region *micrornatus-newportensis* AB (middle subzone) late early-early late Lochkovian
		REGION, SPOROMORPH ASSEMBLAGE BIOZONE AND AGE									
OCCURRENCE	*Dibolisporites*	-	-	-	X	-	X	-	-	-	-
OCCURRENCE	*Aneurospora with prominent spines*	-	-	X	X	X	X	X	X	X	X
OCCURRENCE	*Perotrilites*	X	X	X	-	X	X	X	X	X	X
OCCURRENCE	*Streelispora newportensis*	-	-	-	-	X	X	X	X	X	X
OCCURRENCE	*Emphanisporites micrornatus*	-	-	-	-	-	-	-	X	X	X
OCCURRENCE	*Zonate miospores*	-	-	-	-	-	X	X	-	X	X
ABUNDANCE	*Abundance of patinate miospores*	C	C	C	R	C	C	C	C	C	C
ABUNDANCE	*Abundance of Aneurospora*	-	-	R	C	C	R	C	C	R	C
ABUNDANCE	*Abundance of Synorisporites*	C	C	C	R	C	R	C	C	R	C

TEXT-FIG. 8. Occurrence and/or abundance of important taxa/morphotypes in late Silurian–early Devonian sporomorph assemblages from Scotland, southern Britain and the Ardennes–Rhenish region. Data from Richardson *et al.* (1984), Richardson and McGregor (1986), Richardson and Edwards (1989), Steemans (1989), Wellman (1993*b*) and J. B. Richardson (unpublished data).

Southern Britain

The following summary of sporomorph distribution over the late Silurian–early Devonian interval in southern Britain is derived from the work of Chaloner and Streel (1968) Richardson and Lister (1969), Richardson *et al.* (1981, 1984), Richardson and McGregor (1986), Richardson and Edwards (1989), Fanning *et al.* (1991) and Barclay *et al.* (1994).

In the southern British sequences the *tripapillatus-spicula* zone (early Přídolí age) is succeeded by Biozone A (late early Přídolí age), both zones being recorded from the lower part of the Downton Group. A considerable gap in recovery follows and the next productive horizons are from the uppermost Downton Group (earliest Devonian age) which yield rather poorly preserved sporomorph assemblages which have been assigned to the *Apiculiretusispora* sp. E zone, the description of which is still to be published. Succeeding the *Apiculiretusispora* sp. E zone, in the lower part of the Ditton Group directly above the '*Psammosteus*' Limestone, typical *micrornatus-newportensis* zone sporomorph assemblages are present.

Richardson (*in* Fanning *et al.* 1991) lists the sporomorph taxa recorded from the Lower Downton Group of the Welsh Borders (*tripapillatus-spicula* zone and Biozone A). Of the 44 taxa recorded, 28 are miospores and 16 cryptospores. However, counts indicate that cryptospores are more abundant than miospores; for example cryptospores comprise 62 per cent. of the sporomorphs from Perton Lane. The miospores belong to the genera *Retusotriletes*, *Apiculiretusispora*, *Emphanisporites* (distally laevigate except for *E.* cf. *micrornatus*), *Dictyotriletes*?, *Ambitisporites*, *Amicosporites*, *Aneurospora*?, *Streelispora*?, *Synorisporites*, *Archaeozonotriletes*, cf. *Chelinospora*, *Cymbosporites* and *Perotrilites*. Some of the miospores have proximal interradial papillae. The cryptospores consist of laevigate, apiculate and verrucate alete cryptospore monads; laevigate, apiculate-granulate and murinate-verrucate hilate cryptospores; laevigate, apiculate-granulate and murinate dyads; and laevigate and apiculate 'permanent' tetrads.

In general aspect, the Lorne assemblages exhibit more advanced characters than the *tripapillatus-spicula* zone and Biozone A spore associations (notably *Dibolisporites* with biform sculptural elements and *Aneurospora* with large, prominent spines) and are probably therefore younger. Interestingly, there are also differences in the relative abundance of certain sporomorph morphotypes, for example patinate miospores and species of *Synorisporites* are very rare in the Lorne assemblages but are more abundant in the Downton Group assemblages (Text-fig. 8).

A description of the *Apiculiretusispora* sp. E zone has not yet been published. However, Barclay *et al.* (1994) recently discussed sporomorph assemblages from a sequence in the St Maughans Formation at Ammons Hill, Hereford and Worcester. All of the sporomorph assemblages belonged to the *micrornatus-newportensis* zone (lower subzone) except for the oldest assemblage which they believed was 'either of lowermost *micrornatus-newportensis* age, or, more probably of pre-*micrornatus-newportensis* Zone, but still of early Devonian age'. This sporomorph assemblage is similar to the Lorne assemblage in that firstly, it includes abundant cryptospores including *Cymbohilates* spp. (as genus A) and *Chelinohilates* spp. (as genus B), secondly, envelope-enclosed cryptospores are present (e.g. *Velatitetras retimembrana*), and thirdly, the miospores reported are at a similar grade of organization to those in the Lorne assemblage. However, it differs from the Lorne assemblage in that patinate miospores are abundant, *Perotrilites* is present and *Dibolisporites* is absent.

Sporomorph assemblages belonging to the *micrornatus-newportensis* zone make their inception in the lower Ditton Group and equivalent horizons (Richardson *et al.* 1981; Richardson and McGregor 1986). The *micrornatus-newportensis* zone in southern Britain is characterized by the presence of the following miospore genera: *Retusotriletes*, *Apiculiretusispora*, *Emphanisporites* (including the distally ornamented species *E. micrornatus*, except at the base of the zone), *Ambitisporites*, *Streelispora*, *Aneurospora*, *Synorisporites*, *Archaeozonotriletes*, *Chelinospora*, *Cymbosporites*, *Perotrilites* and *Acinosporites*. A noteworthy feature of the zone is the presence of spores with a multilayered exine, which is manifested in either a sloughing exoexine, proximal folding of a thin exoexinal layer, or a 'perine'. Cryptospores have only recently been reported from *micrornatus-newportensis* zone sporomorph assemblages but are diverse and abundant (Barclay *et al.* 1994; Richardson 1996).

In overall character the Lorne assemblages are not as advanced/evolved as the southern British *micrornatus-newportensis* zone assemblages and are therefore probably older (Text-fig. 8). For example, the Lorne assemblage lacks spores with multilayered exines (e.g. *Streelispora*), zonate miospores and spores with *Acinosporites*-type ornament. Further differences involve proportions of sporomorph morphotypes. Certain morphotypes which are common in the southern Britain *micrornatus-newportensis* zone assemblages, namely patinate spores and species of *Synorisporites*, are very rare in the Lorne assemblage. A further point of interest is the presence in the Lorne assemblage of *Dibolisporites*, a spore that does not appear in the southern British sequence until the Siegenian.

Scotland

The Early Devonian sporomorph associations which are in closest geographical proximity to the Lorne assemblages are from continental strata of the Arbuthnott Group, and its correlatives, from the Midland Valley of Scotland (Richardson *et al.* 1984; Wellman 1993*b*). These are younger than the Lorne assemblages and have been assigned to the *micrornatus-newportensis* zone. The Arbuthnott Group assemblages are very different, in both composition and relative abundance of morphotypes (Text-fig. 8). The differences in composition probably reflect age differences, with the younger Arbuthnott Group assemblages containing typical *micrornatus-newportensis* zone taxa, including advanced forms such as zonate spores, which are not present in the Lorne assemblage. However, the differences in morphotype abundance is intriguing and it is difficult to determine whether it reflects age difference or another cause. The Arbuthnott Group assemblages are rich in patinate miospores and are impoverished with respect to miospores of the *Aneurospora-Streelispora* complex, whereas the Lorne assemblages contain very few patinate miospores but are rich in *Aneurospora*. However, patinate miospores and spores of the *Aneurospora-Streelispora* complex are known to vary in abundance in late Silurian–early Devonian sporomorph assemblages and their distribution/abundance may relate to either facies effects or regional variation in the composition of vegetation (Richardson *et al.* 1984; Richardson and McGregor 1986; Wellman 1993*b*).

Ardennes–Rhenish region

The oldest Devonian deposits in the Ardennes–Rhenish region are of early, but not earliest Devonian age (early Gedinnian; Steemans 1989). The oldest spore associations from the Devonian strata of this region can be assigned to the earliest *micrornatus-newportensis* zone and a sequence of spore assemblages from throughout this biozone exists (Steemans 1989 and references therein). The *micrornatus-newportensis* zone sporomorph assemblages from the shallow marine strata of the Ardennes–Rhenish region are very similar to those from this zone from southern Britain and Scotland (Richardson *et al.* 1984; Richardson and McGregor 1986; Streel *et al.* 1987; Steemans 1989; Wellman 1993*b*). Consequently, the Lorne assemblage differs from the Ardennes–Rhenish assemblages in lacking certain advanced features characteristic of the *micrornatus-newportensis* zone (see discussion above and Text-fig. 8).

Armoricain Massif

Erceville (1979) described the sporomorph component of palynomorph assemblages derived from marine strata from the Saint-Pierre-Sur-Erve region of the eastern part of the Armoricain Massif, northern France. Evidence derived from invertebrate fossils and lithostratigraphical correlation with other localities in the Armoricain Massif suggests that the assemblages are of earliest Lochkovian age. Sporomorphs dominate the palynomorph assemblages, generally comprising in excess of 70 per cent. of the palynomorphs. However, as the palynomorphs are of high thermal maturity, designation to the species level is very difficult and comparisons are therefore severely hampered.

The sporomorph assemblages are dominated by laevigate forms, attributed to the genera *Leiotriletes*, *Retusotriletes*, *Ambitisporites* and *Archaeozonotriletes*. It is noteworthy that the laevigate spores include tripapillate forms and spores with proximal thickenings associated with the triradiate mark. Ornamented spores consist of apiculate forms assigned to the genera *Apiculiretusispora*, *Anapiculatisporites*, *Dibolisporites* and *Streelispora* and murornate forms assigned to the genera *Brochotriletes*, *Dictyotriletes*, *Lophozonotriletes*, *Synorisporites* and *Cymbosporites*. Species of the genera *Iberoespora*, *Amicosporites* and *Emphanisporites* are also reported. It is possible that some of the figured specimens represent hilate cryptospores, particularly those referred to *Brochotriletes* and *Dictyotriletes* which are similar to hilate cryptospores described from the Lorne assemblage.

A feature of interest is the presence in Erceville's material of distinct specimens of *Dibolisporites*, a genus which seems to have sporadic distribution in the Lower Devonian, but is present in the Lorne assemblage. Another noteworthy feature is the reported occurrence of *Streelispora newportensis* (Chaloner and Streel) Richardson and Lister, 1969 which has been widely reported as making its first appearance in strata of early, but not earliest, Lochkovian age and marks the base of the *micrornatus-newportensis* zone (Richardson and McGregor 1986; Streel *et al.* 1987; Steemans

1989). It is possible that, due to the poorly preserved nature of the spores, this report represents a misidentification.

Cantabrian Mountains

Rodriguez (1978*a*, 1978*b*, 1978*c*, 1983) described sporomorph associations from Silurian and early Devonian marine deposits from the Cantabrian Mountains of northern Spain and erected a series of spore zones (see also Cramer 1966*a*, 1966*b*, 1966*c*). Unfortunately there is currently little independent age control for these deposits which probably range from the early Wenlock to the Lochkovian, although work in progress by Rodriguez and Richardson should improve this situation. Furthermore, numerous previously unknown taxa are present in the Spanish material and comparisons with other sporomorph assemblages are difficult. However, many of the spores present in Rodriguez's younger material are similar to spores recovered from the Lorne assemblage, for example *Aneurospora* spp., tripapillate forms, as well as miospores with thickenings of the exine which are reminiscent of spores such as cf. *Amicosporites discus* and cf. *Amicosporites macconochiei*. Unfortunately it is unclear if these spores are from Přídolí or Lochkovian assemblages.

Podolia

Spore assemblages from Podolian sequences which straddle the Silurian–Devonian boundary have been described by Arkhangelskaya (1980). The sporomorphs occur in assemblages dominated by marine palynomorphs and are poorly preserved, to the extent that specific identification is not possible from the illustrations provided. Richardson *et al.* (1981) suggest that assemblages from the Borschov Horizon, for which graptolite evidence indicates an earliest Devonian age, are of a pre-*micrornatus-newportensis* zone level of organization. The sporomorphs are fairly simple and comprise retusoid, equatorially crassitate and patinate forms which are either laevigate or have a simple apiculate, verrucate or murornate sculpture. Additionally, Richardson *et al.* (1981) suggested that the overlying Chortkov and Ivanov horizons contain typical *micrornatus-newportensis* (lower subzone) spore assemblages.

The sporomorphs from the Borschov Horizon are very simple when compared with both the sporomorph assemblages from the overlying Chortkov and Ivanov horizons and the Lorne assemblage. Furthermore, the sporomorphs from the Chortkov and Ivanov horizons are more complex and advanced than those from the Lorne assemblage. However, comparisons are limited because few specimens are illustrated and the spores are poorly preserved.

Bolivia

McGregor (1984) tentatively attributed a Downtonian age to spore associations from the lower part of the Santa Rosa Formation of Bolivia. The assemblages contain spores with interradial papillae, a diversity of sculptured crassitate forms that can be attributed to *Synorisporites* and *Aneurospora*, including conate specimens of *Aneurospora*, rare distally ornamented examples of *Emphanisporites* (*E. novellus*) and rare spores with reticulate sculpture (*Chelinospora cassicula* and *Dictyotriletes* cf. *D. gorgoneus*). However, McGregor noted that the assemblages contained species of *Aneurospora* with prominent cones and spores with a reticulate ornament, features which at this time had not been reported in pre-Gedinnian sporomorph assemblages from elsewhere. Therefore, he suggested that the assemblages might possibly be younger than Downtonian (Gedinnian).

COMPARISONS WITH SPOROMORPH ZONAL SCHEMES

In the system of Richardson and McGregor (1986) the *tripapillatus-spicula* Assemblage Biozone (Přídolí and earliest Devonian) is succeeded by the *micrornatus-newportensis* Assemblage Biozone (early, but not earliest, Devonian). Richardson and Edwards (1989) refined this scheme (Text-fig.

8), based largely on work in southern Britain, by subdividing the *tripapillatus-spicula* Assemblage Biozone into the *tripapillatus-spicula* Assemblage Biozone (early Přídolí), Biozone A (late early Přídolí) and Biozone B (*Apiculiretusispora* sp. E Assemblage Biozone; earliest Devonian); Biozone B is succeeded by the *micrornatus-newportensis* Assemblage Biozone. Biozone A is so far known only from southern Britain and is characterized by crassitate miospores with rugulate-murornate sculpture, hilate cryptospores with distal rugulate sculpture, irregularly granulate *Apiculiretusispora*, *Retusotriletes* spp. and *Archaeozonotriletes chulus*. Biozone B (*Apiculiretusispora* sp. E Assemblage Biozone) has not been described in detail, although it has been discussed by Richardson *et al.* (1981, 1984).

The Lorne assemblage appears to be more evolved than the *tripapillatus-spicula* Assemblage Biozone and Biozone A as it contains crassitate trilete spores with a well-developed sculpture of large, discrete spines. The succeeding Biozone B–*Apiculiretusispora* sp. E Assemblage Biozone is as yet undescribed so comparison is not possible. However, the succeeding *micrornatus-newportensis* Assemblage Biozone is well documented (Richardson and McGregor 1986; Streel *et al.* 1987; Steemans 1989). The absence of the nominal species does not preclude the Lorne assemblage from this biozone, but certain characteristic features of the zone are not represented, namely zonate miospores and spores which possess a multilayered exine (either with a thin exoexine folded over a rigid intexine, a sloughing sculptured exoexine, or as a 'perine'). This suggests that the Lorne assemblage does not belong to the *micrornatus-newportensis* Assemblage Biozone but is less evolved and consequently older. Therefore it seems likely that the Lorne assemblage falls between Biozone A and the *micrornatus-newportensis* Assemblage Biozone and might possibly belong with the undocumented Biozone B.

GEOLOGICAL SIGNIFICANCE

The new age determination suggests that certain previously proposed age determinations and lithostratigraphical correlations are incorrect. Lee and Baily (1925) tentatively suggested that the basal strata of Kerrera might be older than those from mainland Oban, a hypothesis seemingly supported by age determinations based on fish/arthropod faunas (Waterston 1965). Partly on the basis of these suggested age determinations and lithostratigraphical correlations, Morton (1979) correlated the basal strata of Kerrera with the Stonehaven Group at Stonehaven and those at Oban with the Arbuthnott Group from the north-eastern Midland Valley. However, the new biostratigraphical data indicates that the basal strata throughout the Lorne region are all of the same age. Furthermore, it has recently been demonstrated that the Stonehaven Group is late Wenlock–earliest Ludlow (Marshall 1991; Wellman 1991, 1993*a*) and is therefore much older than the Lorne deposits, and the Arbuthnott Group is late early Lochkovian (Richardson *et al.* 1984), and is consequently younger than the Lorne deposits.

The age of the Lorne deposits is especially significant because they underlie the Lorne lavas which have been dated radiometrically (Thirlwall 1988). The new biostratigraphical data suggests that the Silurian-Devonian boundary is slightly older than the lavas. Consequently the biostratigraphical/radiometric data may be integrated to provide an important geochronological tie-point (Marshall 1991).

All the productive palynological preparations from Lorne comprise entirely land-derived palynomorphs suggesting that they accumulated in a non-marine environment. The Lorne deposits are typical 'Lower Old Red Sandstone' facies, which is usually interpreted as terrestrial-fluviatile in origin. The laminated grey shales from which the productive samples were obtained are interspersed within the 'Lower Old Red Sandstone' sequence and exhibit sedimentological characteristics typical of lacustrine deposits. Interestingly, this suggests that the fish and arthropod faunas, obtained from the shales from which the palynomorph assemblages derive, represent animals which inhabited a continental environment. However, one should note that Tarlo and Gurr (1969) suggested that the grey shales present on Kerrera accumulated in a tidal cuvette. The new palynological data suggest that this interpretation is unlikely.

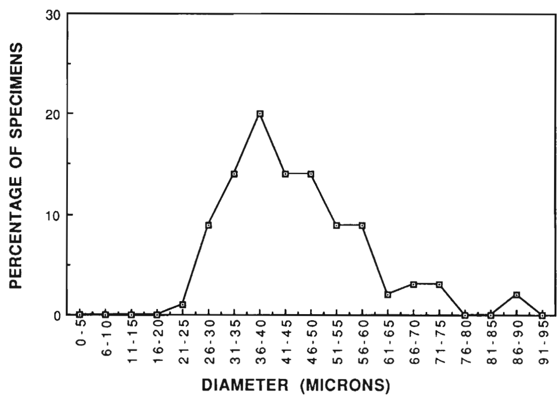
PALAEOBOTANICAL SIGNIFICANCE

Composition of earliest Devonian sporomorph assemblages

Spore data are sparse for the earliest Lochkovian, the age assigned to the Lorne sporomorph assemblage. The large number of new taxa reported herein probably reflects ignorance of sporomorph assemblages of this age. Analysis of the Lorne assemblage thus provides valuable information regarding the nature (presence and abundance of taxa/morphologies) of sporomorph associations of this age. Furthermore, the Lorne assemblage is interpreted as having accumulated in a continental lacustrine environment and the plant microfossils were probably derived predominantly from local vegetation. Therefore, it is anticipated that the Lorne assemblage may provide a fairly accurate reflection of the relative abundance of the various sporomorph morphotypes produced by the local flora (see Table 2).

Regarding the composition of the Lorne assemblages, particularly noteworthy features are (1) cryptospores are abundant and diverse, (2) hilate cryptospores are more abundant than intact true dyads from which they derive, (3) patinate miospores are extremely rare, (4) *Synorisporites* spp. are uncommon, (5) *Dibolisporites* is present, and (6) envelope-enclosed cryptospores are present.

In terms of diversity, the numbers of cryptospore and miospore taxa reported are approximately equal (Table 1). However, the nature of many of the reported taxa is uncertain and some of the morphologically simple taxa, for example permanent tetrads assigned to *Tetrahedraletes medinensis*, may have been produced by more than one plant species. Cryptospores are far more abundant then miospores (Table 2). However, laevigate alete monads comprise between 40·0 and 57·5 per cent. of the Lorne assemblages. Such monads are enigmatic and, although many are thick walled and may represent subaerially dispersed land plant spores, many are thin walled and may derive from other sources, for example from organisms which inhabited continental water bodies (Text-fig. 9). Excluding the laevigate alete monads, cryptospores are still more abundant than miospores, but not as dramatically. These data suggest that cryptospore-producing plants were thriving and co-existed with miospore-producing plants. The miospore-producing plants probably consisted largely of rhyniophytes of vascular staus (Fanning *et al.* 1991); the nature of the cryptospore-producing plants is less certain.



TEXT-FIG. 9. Size frequency distribution of 200 alete cryptospore monads from Sample BK2.

Another noteworthy feature of the assemblages is that dissociated hilate cryptospores are generally far more abundant than the intact true dyads from which they derive. This suggests that such spores were habitually dispersed following dissociation of the dyad. The relatively uncommon intact true dyads possibly represent spores which, uncharacteristically, did not dissociate. It appears to be a characteristic of Silurian–early Devonian sporomorph assemblages that dyads exhibit an increasing tendency to occur dissociated in younger assemblages.

The paucity of patinate miospores in the Lorne assemblage is surprising. Patinate spores first appear in the earliest Wenlock and are relatively common in early and late Wenlock nearshore marine deposits (e.g. Richardson and Lister 1969; Burgess and Richardson 1991), but are absent or rare in inland continental deposits of the same age (Wellman 1993*a*; Wellman and Richardson 1993). Patinate spores are also relatively common in Ludlow and Přídolí nearshore marine deposits (e.g. Richardson and Lister 1969; Fanning *et al.* 1991), but there are, as yet, no reported non-marine sporomorph assemblages of this age. Numerous sporomorph assemblages are known from early Devonian marine and non-marine deposits (*micrornatus-newportensis* zone) and patinate spores are usually common in assemblages from both palaeoenvironments. A possible explanation for the reported distribution of patinate spores, as outlined above, is that during the Wenlock–earliest Lochkovian the plants which produced patinate spores thrived in lowland, nearshore areas but were uncommon inland, but by post earliest Lochkovian times patinate spore producing plants had migrated inland. More data is required in order to test this hypothesis.

The scarcity of *Synorisporites* spp. in the Lorne assemblage may also be a consequence of the plants which produced these spores flourishing only in lowland, nearshore environments (Edwards 1990; Wellman 1993*b*). For example, *Synorisporites* spp. are common in Přídolí–Lochkovian lowland, nearshore assemblages from southern Britain (Richardson and Lister 1969; Fanning *et al.* 1991) but are rare in inland continental assemblages of the same age from Scotland (Richardson *et al.* 1984; Wellman 1993*b*).

The presence of *Dibolisporites* in the Lorne assemblage is intriguing. In the southern British sequences *Dibolisporites* does not appear until the Siegenian (Richardson *et al.* 1984). However, it has been reported from Gedinnian strata from Scotland (Richardson *et al.* 1984) and the Ardennes–Rhenish region (Steemans 1989) and the basal Lochkovian (pre-Gedinnian) of France (Erceville 1979). A possible explanation for the seemingly erratic occurrence of *Dibolisporites* is that the plants which produced these spores were present since at least earliest Devonian times but flourished only under specific conditions and, consequently, the spatial and temporal occurrence of *Dibolisporites* is variable (see discussion in Richardson *et al.* 1984; Edwards 1990; Wellman 1993*b*).

Envelope-enclosed cryptospores

An additional aspect of interest is the presence of envelope-enclosed cryptospores (monads, dyads and tetrads). Such spores are relatively common in Ordovician and early Llandovery cryptospore assemblages (Gray 1985, 1991; Burgess 1991) but have rarely been reported in younger assemblages (Burgess and Richardson 1991; Barclay *et al.* 1994). The envelope-enclosed cryptospores in the Lorne assemblage are morphologically identical to the Ordovician and early Llandovery forms, although the Lorne specimens generally are slightly larger. It is possible that these specimens are reworked, but it is difficult to envisage a suitable source. Assuming that the envelope-enclosed cryptospores are not reworked, there are several possible explanations for their presence in early Devonian deposits. One is that reproductive strategies altered with time. Many, if not all, cryptospores may have formed enclosed within an envelope. During the Llanvirn–early Llandovery, reproductive strategies may have been such that the envelopes were commonly retained after dispersal and hence are often preserved. However, reproductive strategies may have altered post the early Llandovery such that cryptospores tended to lose their envelopes prior to dispersal and consequently envelopes are not commonly preserved. In this scenario post early Llandovery envelope-enclosed cryptospores would represent specimens which uncharacteristically retained their envelope, perhaps due to atypical environmental factors. On the other hand, post early Llandovery envelope-enclosed cryptospores may have derived from plants which retained (i.e. relic flora), or possibly reverted to the primitive habit of envelope retention; or envelope-enclosed cryptospores from the Llanvirn–early Llandovery and earliest Devonian may have evolved this character independently and are unrelated.

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APPENDIX: SAMPLING DETAILS FOR PRODUCTIVE SAMPLES

Sample	Locality	Grid Ref.	Preservation
AK1	South shore of Kerrera, exposure in west of bay located east of Ardmore Farm (Lee and Bailey 1925, fig. 6); northern end of exposure, base of cliff.	NM798267	G
AK2	South shore of Kerrera, exposure in west of bay located east of Ardmore Farm (Lee and Bailey 1925, fig. 6); 50 m south of AK1, 2 m above base of cliff.	NM798267	M
AK3	South shore of Kerrera, exposure in west of bay located east of Ardmore Farm (Lee and Bailey 1925, fig. 6); 50 m south of AK1, top of cliff.	NM798267	M
AK4	South shore of Kerrera, exposure in foreshore, bay located west of Ardmore Farm (Lee and Bailey 1925, fig. 6); edge of wave cut platform.	NM795267	M
AK5	South shore of Kerrera, exposure in foreshore, bay located west of Ardmore Farm (Lee and Bailey 1925, fig. 6); edge of wave cut platform, 40 mm above AK4.	NM795267	M
AK6	South shore of Kerrera, exposure in foreshore, bay located west of Ardmore Farm (Lee and Bailey 1925, fig. 6); edge of wave cut platform, 40 mm below AK4.	NM795267	G
BK1	South shore of Kerrera, exposure in west of bay located east of Ardmore Farm (Lee and Bailey 1925, fig. 6); northern end of exposure, 0·3 m above base of cliff.	NM798267	M
BK2	South shore of Kerrera, exposure in west of bay located east of Ardmore Farm (Lee and Bailey 1925, fig. 6); northern end of exposure, 1 m above BK1.	NM798267	M
BK3	South shore of Kerrera, exposure in west of bay located east of Ardmore Farm (Lee and Bailey 1925, fig. 6); northern end of exposure, 1·05 m above BK1.	NM798267	M
BK4	South shore of Kerrera, exposure in west of bay located east of Ardmore Farm (Lee and Bailey 1925, fig. 6); northern end of exposure, 1·10 m above BK1.	NM798267	M
BK5	South shore of Kerrera, exposure in west of bay located east of Ardmore Farm (Lee and Bailey 1925, fig. 6); 10 m south of northern end of exposure, 1 m above base of cliff.	NM798267	M
AOB1	Mainland south of Oban, exposure in bay west of Gallanach House Lodge (Port Caraig na Maraig) (Lee and Bailey 1925, fig. 4); 2·70 m above top of conglomerate unit.	NM826271	M
AOB2	Mainland south of Oban, exposure in bay west of Gallanach House Lodge (Port Caraig na Maraig) (Lee and Bailey 1925, fig. 4); 2·50 m above top of conglomerate unit.	NM826271	M
AOB3	Mainland south of Oban, exposure in bay west of Gallanach House Lodge (Port Caraig na Maraig) (Lee and Bailey 1925, fig. 4); 5·60 m above top of conglomerate unit.	NM826271	M
AOB4	Mainland south of Oban, exposure in bay west of Gallanach House Lodge (Port Caraig na Maraig) (Lee and Bailey 1925, fig. 4); 2·60 m above top of conglomerate unit.	NM826271	M

APPENDIX (*cont.*)

Sample	Locality	Grid Ref.	Preservation
AOB5	Mainland south of Oban, exposure in bay west of Gallanach House Lodge (Port Caraig na Maraig) (Lee and Bailey 1925, fig. 4); 6·40 m above top of conglomerate unit.	NM826271	M
BOB1	Railway cutting, near Glen Cruitten, 1·5 km east-south-east of Oban town; cliff in south-east of cutting. 0·5 m above base of cliff.	NM873295	P

Preservation: G = good, M = mediocre, P = poor.