TAXONOMY AND CLASSIFICATION OF SOME NEW EARLY DEVONIAN CRYPTOSPORES FROM ENGLAND

by JOHN B. RICHARDSON

ABSTRACT. Early Devonian cryptospores are described from the Lower Old Red Sandstone (early Gedinnian) of Hereford and Worcester, and Shropshire, England. Two turmae (Nudialetes and Involucraletes), four suprasubturmae (Pseudopolyadi, Eupolyadi, Hilates and Ahilates), one subturma (Hilates), three infraturmae (Laevigati, Synorati and Apiculati), three genera (*Acontotetras*, *Chelinohilates* and *Cymbohilates*), eight species (*Acontotetras inconspicuis*, *Artemopyra*? *scalariformis*, *Cymbohilates horridus*, *C. allenii*, *C. variabilis*, *C. disponerus*, *C. cymosus* and *Chelinohilates erraticus*) and five varieties (*Cymbohilates allenii* vars *allenii* and *magnus*, *C. variabilis* vars *variabilis*, *parvidecus* and *tenuis*) are proposed as new. Cryptospores are divided into two major informal groups: eucryptospores and paracryptospores. Eucryptospore species have only one spore unit configuration and are either 'permanent' tetrads, pseudodyads, dyads or monads. Most have laevigate or apiculate sculpture and are common and widespread in the study area. Paracryptospores have identical sculpture on variable, including abnormal, spore unit configurations (tetrads, triads, dyads and hilate monads). Only one paracryptospore species, *Chelinohilates erraticus* gen. et. sp. nov., is described herein. Paracryptospores may have a separate origin from eucryptospores and similar abnormal spore associations have been found in modern hybrid ferns. If the fossil variable spore units were produced by hybrid parents, and hybridization was a recurrent and common theme, then the impact upon patterns and rates of early land plant evolution would have been considerable.

THE Lower Old Red Sandstone of the Anglo-Welsh Basin is divided into three divisions (traditionally referred to as stages): Downtonian, Dittonian and Breconian. This paper is concerned with some of the new cryptospore taxa from upper Downtonian and Dittonian sections in England. All the spore samples are from an interval of *c*. 383 m ranging from the upper Downtonian (top *c*. 33 m of strata) to the lower upper Dittonian (through 350 m of Dittonian sedimentary rocks). The position of the Silurian/Devonian boundary cannot be recognized with absolute certainty, but on spore and vertebrate evidence is currently placed in the upper Downtonian at about the level of the lowest productive spore sample, that is about 33 m (100 ft) below the base of the Dittonian (Richardson *et al.* in press). The thelodont *Turinia pagei* has been recorded by Turner (1973) at approximately the same level. About 400 m of the Dittonian Formation has been sampled but the highest productive sample found so far is at *c*. 350 m above the Psammosteus Limestones; higher samples were either barren or contained reworked palynomorphs only.

The spores indicate that all the Dittonian assemblages are equivalent in age to Belgian strata of the Gedinnian Stage. Spore evidence from the lowermost Breconian (lower Senni Beds, South Wales) indicates an uppermost Gedinnian age (Richardson *et al.* 1982; J. B. Richardson and A. Hassan, unpublished work); thus the sequences examined in England (upper Downtonian and Dittonian) are all Gedinnian. The upper Downtonian assemblages are divided into two provisional biozones that have not been described so far from Belgium. Spores so far obtained from the Dittonian belong to the *micrornatus-newportensis* palynozone, which has been divided into three subzones (Richardson *et al.* 1984). The highest spore assemblages in Brown Clee Hill, however, are either close to, or may belong to, the overlying *breconensis-zavallatus* palynozone. The cryptospores described in this paper are from all three subzones but mainly from the lower two.

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Lower Old Red Sandstone sedimentary rocks from the Ledbury and Ditton formations of Brown Clee Hill (Shropshire) and from the Raglan Mudstone and St Maughans formations (Hereford and Worcester) have yielded a succession of spore floras consisting of cryptospores and miospores, but dominated by cryptospores.

USE OF GEDINNIAN STAGE NAME

The strata studied are of early Devonian, Gedinnian age (Holland and Richardson 1977; Richardson *et al.* 1984). At this phase of interfacies correlation, the term Gedinnian is preferred to Lochkovian because direct correlation based on spores is possible between some British Lower Old Red Sandstone strata and the Belgian Gedinnian sequence, but not with the type Lochkovian Stage in Bohemia. Spores found so far in lower Lochkovian strata in the Barrandian type area (Czech Republic) are two few and too poor for correlation. In addition there is some uncertainty concerning the correlation between Silurian/Devonian boundary sequences in the type area and other marine sequences. In the boundary type section, two varieties of *Monograptus· uniformis* (*angustidens* and *uniformis*) appear together at the base of the Lochkovian, whereas in Podolia the two graptolite subspecies are separated by 53 m of strata (Nikiforova 1977). Nikiforova stated that 'The position of the Silurian–Devonian boundary in Podolia at the base of *M. uniformis angustidens* (lower subspecies) is proved by the number of species that flourished later'. On the other hand, on the basis of Chitinozoa, Paris and Grahn (1996) concluded that the first appearance of *Monograptus uniformis uniformis*, the subspecies occurring at the higher level, should be correlated with the Silurian/Devonian boundary (Barrandian type area). Although no diagnostic spores are known from the boundary beds in the Czech Republic, and the spores from Podolia lack detailed description and illustration, the first recorded occurrence of spores of the *micrornatus-newportensis* (MN) palynozone in Podolia is at least 250 m above the lower Silurian–Devonian boundary and *c.* 200 m above the higher one (i.e. lowest occurrence of *M. uniformis uniformis*). Thus, to establish accurately the level of first occurrence of *newportensis* and accessory spores of the lower MN Subzone in Podolian graptolitic sequences is important, but the fact that this nominal species occurs above both varieties of *M. uniformis* is evidence for a Devonian, but not basal Devonian, age for the lower MN Subzone.

LOCALITY DATA

Samples from three main areas have been examined: the disused railway cutting at Ammons Hill (Barclay *et al.* 1994); the M50 motorway section near Ross-on-Wye, Hereford and Worcester (Holland and Richardson 1977); and sections on Brown Clee Hill, Shropshire. In the Brown Clee Hill area, most of the stream sections have been investigated and those with moderate to good exposure logged. Over 230 samples have been studied of which 140 proved productive. The longest continuous sections logged and samples are the M50 motorway section, and Hudwick and Newton dingles (Ball and Dineley 1961). In addition, over the last three decades many of the streams and isolated exposures in the Brown Clee Hill have been examined. Productive samples are rare from higher parts of the Ditton Formation.

PALYNOLOGICAL INVESTIGATIONS

Richardson and Lister (1969) described rich miospore assemblages from the lower Downton Formation and Ditton Formation. However at that time only three productive Ditton samples were studied. One of these samples, from the middle of the Ditton Formation, yielded an excellent and varied assemblage. The present paper is part of an ongoing study of material of Early Devonian age using both Nomarksi interference light microscopy and scanning electron microscopy, both unavailable for the previous study.

The taxa described constitute only a small proportion of the species present. It is planned to describe further new taxa and their distribution in subsequent publications.

CRYPTOSPORE AND MIOSPORE MORPHOLOGY

Richardson and Lister (1969) made several tentative generic assignments because it was difficult to determine whether the spores of some taxa had trilete marks (the thin contact area is often crumpled into folds sometimes simulating a trilete mark). For example *Archaeozonotriletes*? cf. *divellomedium* (Chibrikova) Richardson and Lister, 1969 and several similar species were described with thin membranes over the contact are and more or less circular outlines. Further study has shown that most of these species are derived from eudyads. These spores (e.g. *Laevolancis divellomedia*) are now regarded as hilate cryptospore monads.

Representatives of two informal groups of cryptospore are described in the present paper. The first group, eucryptospores, includes permanently adherent tetrads, dyads, and monads. The tetrads may be completely fused, with no lines of attachment (Text-fig. 1A), tightly adherent but with lines of attachment (Text-fig. 1B), or loose with the four units not normally separable. Similarly there are pseudodyads with complete fusion and no line of attachment (Text-fig. 1D), and true dyads (eudyads) with a line of attachment (Text-fig. 1E–F; see also Wellman and Richardson 1993). True dyads are often partially, or completely, detached to form hilate monads (Text-fig. 1G–H). The hilum may be thin with taper pointed folds, or collapsed, i.e. tenuihilate or with a thicker, more rigid, contact area and termed hilate. In both forms a curvatural ridge usually surrounds the hilum (Text-fig. 1G–H; see also Richardson in press). Non-hilate alete forms exist with no differentiation of the exine except for sculpture, and no visible contact features. The eucryptospore group includes most cryptospores, and all regarded here as true cryptospores. They are known from the Ordovician long before the first known occurrence of trilete spores (miospores) in beds of the *sedgwickii* graptolite Biozone (upper Aeronian, Llandovery). Each eucryptospore species consist of one basic type of spore unit, either tetrads, dyads or monads, although hilate monads are derived from eudyads.

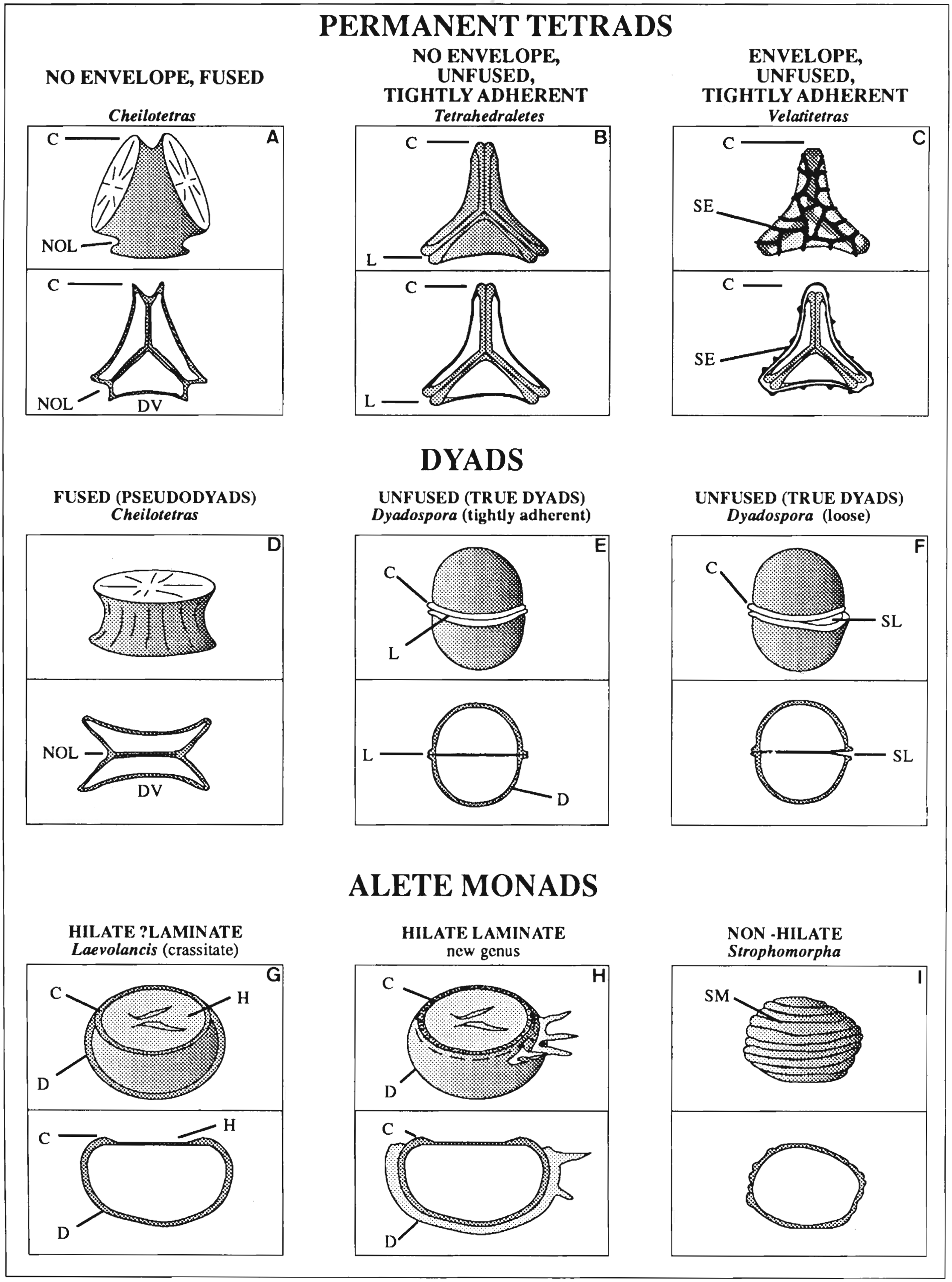
In the second group, paracryptospores, identical sculpture occurs on tetrads, dyads and hilate monads and on triads. The latter occur in lower Gedinnian strata tentatively placed high in the upper part of the Ledbury Formation and so far have not been found below. Trilete spores, derived from freely separating tetrads, may be subtriangular or subcircular in polar view. Some cryptospores and miospores have identical exine sculpture and structure, and it is thus possible that in some cases the same plant species produced both cryptospores and miospores. However, identically sculptured cryptospores and miospores are not always seen in the same bed. Permanently fused spore units (tetrads and dyads) occur regularly in the lower Gedinnian. Trilete (miospore) species are varied but represent only *c.* 40 per cent. of Lower Ditton assemblages. Thus, although there is an evolutionary trend towards the dispersal of monads (both cryptospore and trilete spore) the majority of these are cryptospores. Both in hilate cryptospores and trilete (patinate) spores the proximal faces are often thin, perhaps reflecting derivation from permanently adherent ancestors.

Terminology

In the following taxonomic descriptions, the terminology used is essentially that of Grebe (1971) except for the terms eucryptospore, paracryptospore and hilum (adjective hilate) discussed below, and the modified usage of the term murus (adjective murornate).

Eucryptospore. Cryptospores where each structural/sculptural form usually has only one type of spore unit; that is the spore units are either 'permanent' tetrads, pseudodyads, dyads, or monads (Text-fig. 1). They never include triads. Assemblages of cryptospores covered with an envelope with the same rugulate sculpture on multiple (tetrads and dyads) and single units (monads) occur in Late Ordovician and Early Silurian strata, but in post-Llandovery assemblages eudyads and the hilate monads derived from them are common.

Paracryptospore. Cryptospores with multiple (tetrads, triads and dyads) and single units (monads) and identical structure/sculpture. The units always include triads and one or more units may be



TEXT-FIG. 1. For caption see facing page.

'deformed'. It is possible that such spores have a different origin from eucryptospores and may have had trilete spore-bearing ancestors and descendants.

Hilum. This is used essentially in the sense of Erdtman (1952) for the contact area between alete spores, except that hila on monads derived from dyads have distinctly delimited contact areas. Traverse (1988) defines it as an irregular germinal aperture of a spore or pollen grain, formed by the breakdown of the exine in the vicinity of one of the poles. At first I was not certain whether the hilum in these early Devonian spores was proximal or distal, but the presence of contact features and the discovery of complete dyads for many of the species shows that the hilum is proximal wherever it can be directly determined. Therefore the appearance of distal hila may be a later, possibly a post-Palaeozoic phenomenon. A hilum *sensu* Traverse (1988) was not recorded in a recent review of pteridophyte spores (Tryon and Lugardon 1991) but was recorded for the Jurassic spores of the genus *Coptospora* (Dettman, 1963). Dettman commented that polar features comparable to those of *Coptospora* are 'shown by certain modern hepatic spores which germinate by means of a rupture in, and after breakdown of, their polar (distal exine)... and that many of the modern spores borne by the Sphaerocarpaceae, Ricciaceae, and Riellaceae are hilate...'. However, Inoue (1960) has shown that in some hepatics (Marchantiales) the position of rupture of the spore wall on germination is not always polar. Thus, the hilum on bryophyte spores may not be proximal and so is not necessarily a contact feature but is an area of breakdown of the spore exine associated with germination. Nevertheless, if distal or lateral breakdown, of the type described by Inoue, existed in these early Devonian cryptospores it has not been reported; 'permanent' tetrads presumably had distal and/or equatorial germination. Although the germination position is not known in the monads described, there are reasons for assuming that it was proximal, because the contact face is commonly thin and collapsed, or the sculpture is modified in the proximal polar area. In Palaeozoic spores it is often assumed that germination is proximal but direct evidence is scarce, though germinating spores are known from the Rhynie Chert. However, although lacking evidence to the contrary that germination is probably proximal, this is not certain and therefore position of germination is excluded from the definition of a hilum for these spores.

In the spores described below, the term hilum encompasses three conditions: (1) more or less circular area surrounded by a curvatura perfecta but with a contact area only slightly thinner than the subequatorial area; (2) where the outer part of the exoexine is much thinner over the contact area; (3) a contact area consisting of inner exoexine only, this inner layer being thin, diaphanous, and commonly collapsed. Where the contact area is thin as in (2) and (3) the monads are termed tenuihilate (Text-fig. 1G–H). All three conditions essentially fit the Erdtman definition.

Muri. The term is used for sinuous, sometimes anastomosing ridges, whether or not they form a reticulum.

The prefix micro- is used to indicate elements less than 1 μm in size, where the exact shape can be determined accurately only under the SEM (e.g. microconi, microbaculae).

MATERIAL AND METHODS

All material is housed in the Palynology Laboratory, Department of Palaeontology, The Natural History Museum, London. Figured specimens have an FM number and are located on slides. Letters and numbers (e.g. CH/71/TG/2c/3) refer to the sample/slide number, followed by the specimen location co-ordinates taken on a Zeiss Photomicroscope III (no. 2562) housed in the Palynology Section of the Palaeontology Department. E.F. numbers refer to the specimen location

TEXT-FIG. 1. Schematic representation of some eucryptospores (modified after Wellman and Richardson 1993; Richardson in press); C, curvatural line/thickening; D, distally inflated; DV, distally invaginated; H, hilum; L, line of attachment; NOL, no line of attachment; SE, sculptured envelope; SL, separation along line of attachment; SM, spiral muri. The lower half of each diagram shows the spore in section.

on an England Finder slide. BM numbers refer to photographic negatives, held in the archives of The Natural History Museum, London.

Sporomorphs were extracted from rock samples using standard palynological methods. Because of the low maturation of the material, usually no oxidation was needed, but a wash in dilute (5 per cent.) HNO_3 for a few minutes aided separation of spores from small organic particles. Some spores are thick walled; in this case part of the residue was oxidized for 5 minutes. Residues were strewn on a coverslip and dried, covered with Elvacite plastic mounting medium and everted onto a glass slide. Material for SEM study was mounted either on film (emulsion side up) or on circular glass coverslips, mounted on stubs, coated with gold and studied on a Hitachi 8S800 Field Emission SEM.

Preliminary light photomicrographs were taken on a Zeiss Photomicroscope III housed in the Palynology Laboratory. Photographs for the plates were produced by the Museum's Photographic Unit using Zeiss equipment.

SYSTEMATIC PALAEONTOLOGY

Strother (1991) erected turmae on the basis of the number of units in the cryptospore, e.g. turma Tetrasporites. Using his classification, multiple units (tetrads and dyads) that are otherwise identical (sculpturally/structurally) are classified separately at the turma level, whereas in this work species of both paracryptospores and some eucryptospores may include a variety of multiple units, or both multiple and single units. Strother's concept of separating fused and unfused multiple units is incorporated.

DIAGNOSTIC FEATURE	RANK	CATEGORY							
	ANTETURMA	CRYPTOSPORITES							
Stratification	TURMA	NUDIALETES				INVOLUCRALETES			
Nature of attachment of units / nature or absence of unit area (hilum)	SUPRA-SUBTURMA	Pseudopolyadi	Eupolyadi	Hilates	Ahilates	Pseudopolyadi	Eupolyadi	Hilates	Ahilates
Sculpture	INFRATURMA	Laevigati Apiculati Synorati				Laevigati Apiculati Synorati			

TEXT-FIG. 2. Revised scheme for the classification of Cryptosporites.

Cryptospores are divided herein into two turmae. For those cryptospores with an outer envelope (e.g. *Velatitetras*), either sculptured or smooth, the turma Involucraletes is proposed; specimens without an envelope (e.g. *Tetrahedraletes*) are included in Nudialetes. Each turma is subdivided into four suprasubturmae: (1) Pseudopolyadi, multiple fused units (tetrads and dyads); (2) Eupolyadi, multiple unfused units (closely and loosely adherent tetrads and dyads with lines of attachment); (3) Hilates, hilate monads; and (4) Anhilates, monads with no contact features. On the basis of sculpture, all these suprasubturmae are subdivided into three infraturmae: Laevigati, Apiculati and Synorati.

The succession of incoming of each major sculptural type is the same in both monad cryptospores and miospores. The earliest forms are laevigate, and are followed successively by murornate-verrucate, apiculate, and reticulate–murornate ornament. This probably indicates that sculptural type reflects important adaptive responses of their plants in their early evolutionary history, possibly related to water supply (germination in ephemerally wet terrestrial environments (Fanning *et al.* 1988)). However, Perold (1989) reported that, where he had information concerning environmental factors, none of these had an appreciable affect on the sculpturing of *Riccia* spores. On the other hand, Jovet-Ast (1987) proposed a phylogenetic classification and arranged the different ornamentation patterns of *Riccia* spores into seven main types; the tetrad spores with spinose ornamentation were considered as primitive. It is interesting to note that similar 'permanent' spore tetrads occur in the Upper Silurian.

In the suprasubturmae proposed below, the 'permanent' tetrads show distinct lines of attachment, and new taxa are described from Eupolyadi and Hilates.

In the following cryptospore descriptions, dimension figures given in parentheses indicate the mean.

Anteturma CRYPTOSPORITES Richardson, Ford and Parker, 1984

Remarks. Sporomorphs, excluding pollen, of non-marine origin, consisting of 'permanent' tetrahedral and planar tetrads, pseudodyads, dyads, and alete monads. Monads may be derived from unfused or eudyads, in which case they show conspicuous contact features (hilate), or they may lack any contact features (Richardson 1988). Hilate monads were the last of the main cryptospore units to appear and occur in the lower Sheinwoodian of the type area but are more common in higher Silurian strata and are abundant in the Lower Devonian (lower Gedinnian). Most of the other types of spore unit ('permanent' tetrads, pseudodyads, and ahilate monads) are found in Caradoc and later strata, and there is some evidence that at least some of them occurred earlier in the Ordovician (Richardson in press).

Turma INVOLUCRALETES turma nov.

Diagnosis. Multiple or single cryptospore units with a thin envelope covering the entire tetrad, dyad, or monad. Examples include *Velatitetras* Burgess, 1991 and *Segetrespora* Burgess, 1991.

Turma NUDIALETES turma nov.

Diagnosis. Multiple, or single, cryptospore units without external envelopes. Examples include *Tetrahedraletes* Strother and Traverse emend. Wellman and Richardson, 1993.

Suprasubturma PSEUDOPOLYADI suprasubturma nov.

Diagnosis. Cryptospores with fused multiple units. An example is *Pseudodyadospora* Johnson.

Suprasubturma EUPOLYADI suprasubturma nov.

Diagnosis. Cryptospores with multiple, closely adherent units. Examples are *Acontotetras* gen. nov., and *Dyadospora* Strother and Traverse.

Infraturma APICULATI infraturma nov.

Diagnosis. Eucryptospores with apiculate sculpture, i.e. grana, coni, spinae, or a mixture of apiculate/spinose elements as the main ornament.

Genus ACONTOTETRAS gen. nov.

Derivation of name. Greek *aconto*, spear; tetras derived from *tessares* (tettares), four.

Type species. *Acontotetras inconspicuis* sp. nov.

Diagnosis. 'Permanent' tetrahedral tetrads composed of subtriangular to subcircular, closely adhering, eucryptospore units separated from each other by distinct lines of attachment; exine with a sculpture of grana, coni or microconi.

Comparison. These spores are small and lack envelopes. The presence of grana and coni distinguishes the genus from *Tetrahedraletes* which has a laevigate exine. *Rimosotetras* also has a laevigate exine and consists of loose tetrads.

Remarks. Compressional states vary in a similar way to those seen in *Tetrahedraletes* (Strother and Traverse) Wellman and Richardson, 1993. 'Permanent' tetrads without envelopes but with apiculate sculpture occur commonly in the Lower Devonian of the Welsh Borders.

Acontotetras inconspicuis gen. et sp. nov.

Plate 9, figures 6–8; Plate 10, figures 3, 6–7

Derivation of name. Latin *inconspicuus*, not readily visible.

Holotype. FM746 (Pl. 10, figs 6–7 sample CH/SD/88/2C, slide 3S, co-ord. 069 1079; E.F. no. G38; ?upper Downton Formation, Brown Clee Hill; diameter 39 μm, individual spore units 26–29 μm.

Diagnosis. An *Acontotetras* with small wide low grana (microconi).

Description. 'Permanent' tetrads comprising sub-triangular spore units. The individual spores often have an invaginated distal surface and are discrete with a distinct line of attachment at the junctions between adjacent spores. Exine is *c*. 1(2)3 μm thick. Distal exine is sculptured with low wide grana and microconi. The latter are usually evenly spaced so that elements of the same size could be inserted between them, but are sometimes more crowded; elements are $< 0{\cdot}5$ μm high, 0·7–1·4 μm wide and 0·5–1 μm apart.

Dimensions. Tetrads 20(27)46 μm, individual spore units 14(25)36 μm; 30 specimens measured.

EXPLANATION OF PLATE 1

Figs 1–2. *Cymbohilates allenii* var. *allenii* gen., sp. et var. nov.; holotype, FM 715 (slide M50/6/4, co-ord. 164 1220; E.F. no. R53); lower St Maughans Formation, M50 section. 1, proximal focus showing hilum and proximal folds, 2, distal focus showing evenly spaced *grana*.

Figs 3–4. *Cymbohilates disponerus* gen. et sp. nov.; holotype, proximal and distal focus; FM 716 (slide CH/TG/2/79/6, co-ord. 190 0961; E.F. no. T26/3); lower Ditton Formation, Brown Clee Hill.

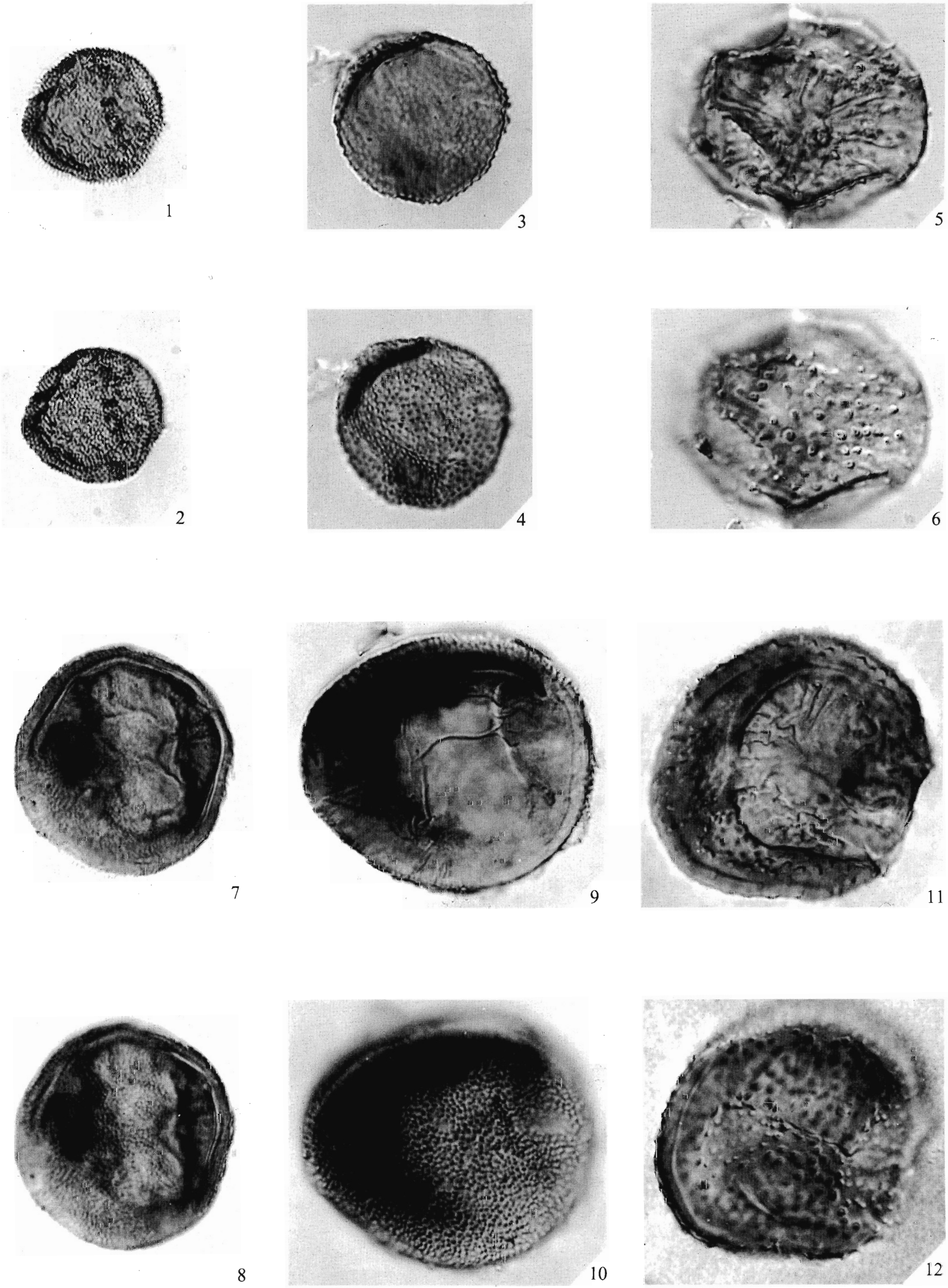
Figs 5–6. *Cymbohilates variabilis* var. *tenuis* gen., sp. et var. nov., holotype, proximal and distal focus; FM 718 (slide CH/81/HD4G/7, co-ord. 200 1121; E.F. no. V43/1), north Brown Clee Hill; lower Ditton Formation.

Figs 7–10. *C. allenii* var. *magnus* gen., sp. et var. nov. 7–8, holotype, FM 719 (slide CH/TG1b/79/3, co-ord. 098 1055; E.F. no. K36); lower Ditton Formation, Brown Clee Hill. 7, proximal focus showing irregular folds over the hilum; 8, distal focus, slightly tipped specimen. 9–10, FM 720 (slide CH5/71/5A/2a, co-ord. 055 0754; E.F. no. F5); lower Ditton Formation, north Brown Clee Hill. 9, showing almost circular hilum. 10, distal focus showing evenly spaced, closely packed, sculptural elements.

Figs 11–12. *Cymbohilates variabilis* var. *parvidecus* gen., sp. et var. nov.; holotype, slightly tipped specimen; FM 721 (slide CH/HD/4G/7, co-ord. 223 1096; E.F. no. X40), north Brown Clee Hill; lower Ditton Formation. 11, showing approximately circular hilum with irregular approximately radial folds. 12, showing sculpture of spaced low coni.

All × 1000.

PLATE 1



RICHARDSON, *Cymbohilates*

Comparisons. Acontotetras sp. A (Pl. 10, figs 4–5) has a thinner, less rigid, exine with more widely spaced and irregular grana, *Acontotetras* sp. B (Pl. 10, figs 8–9) has a thick, rigid, exine with more widely spaced grana.

Occurrence. Common in the ?Upper Red Marls (Upper Downton) and lower Ditton formations; present in the upper-lower and middle Ditton Formation, Brown Clee Hill; present in the St Maughans Formation, Ammons Hill; ?*Apiculiretusispora* sp. E Assemblage Spore Zone, lower and middle *micrornatus-newportensis* palynosubzones (lower and lower middle Gedinnian).

Suprasubturma HILATES suprasubturma nov.

Diagnosis. Monads derived from eudyads with a distinct proximal contact area (hilum).

Remarks. These cryptospores are provisionally divided into three infraturmae based upon their sculpture or lack of it, as follows: Laevigati with smooth exine, Synorati with verrucate to murornate ornament, and Apiculati with granulate, apiculate to spinose sculpture.

Many species have a clearly laminate exine. The outer layer of several of these laminate species may be degraded, broken or almost entirely lost (e.g. *Cymbosporites horridus*, *Chelinohilates erraticus*). In the latter case, the inner bodies are laevigate and resemble *Laevolancis divellomedia.* Rare dyads have delicate reticulate envelopes, so it is possible that many of the smooth-walled specimens recorded formerly had a thin, delicate, outer exinal layer.

Infraturma LAEVIGATI infraturma nov.

Diagnosis. Eucryptospores with a smooth exine.

Genus ARTEMOPYRA Burgess and Richardson, 1991 emend. herein

Type species. Artemopyra brevicosta Burgess and Richardson, 1991.

Emended diagnosis. Proximally hilate cryptospore monads; originally elliptical to hemispherical in equatorial view. Hilum sculptured with predominantly radial muri. Distal exine laevigate.

Remarks. The genus is herein restricted to distally laevigate forms. In the Gedinnian, there is a wide variety of monad cryptospores with proximal radial sculpture and herein they are separated on the basis of their distal sculpture.

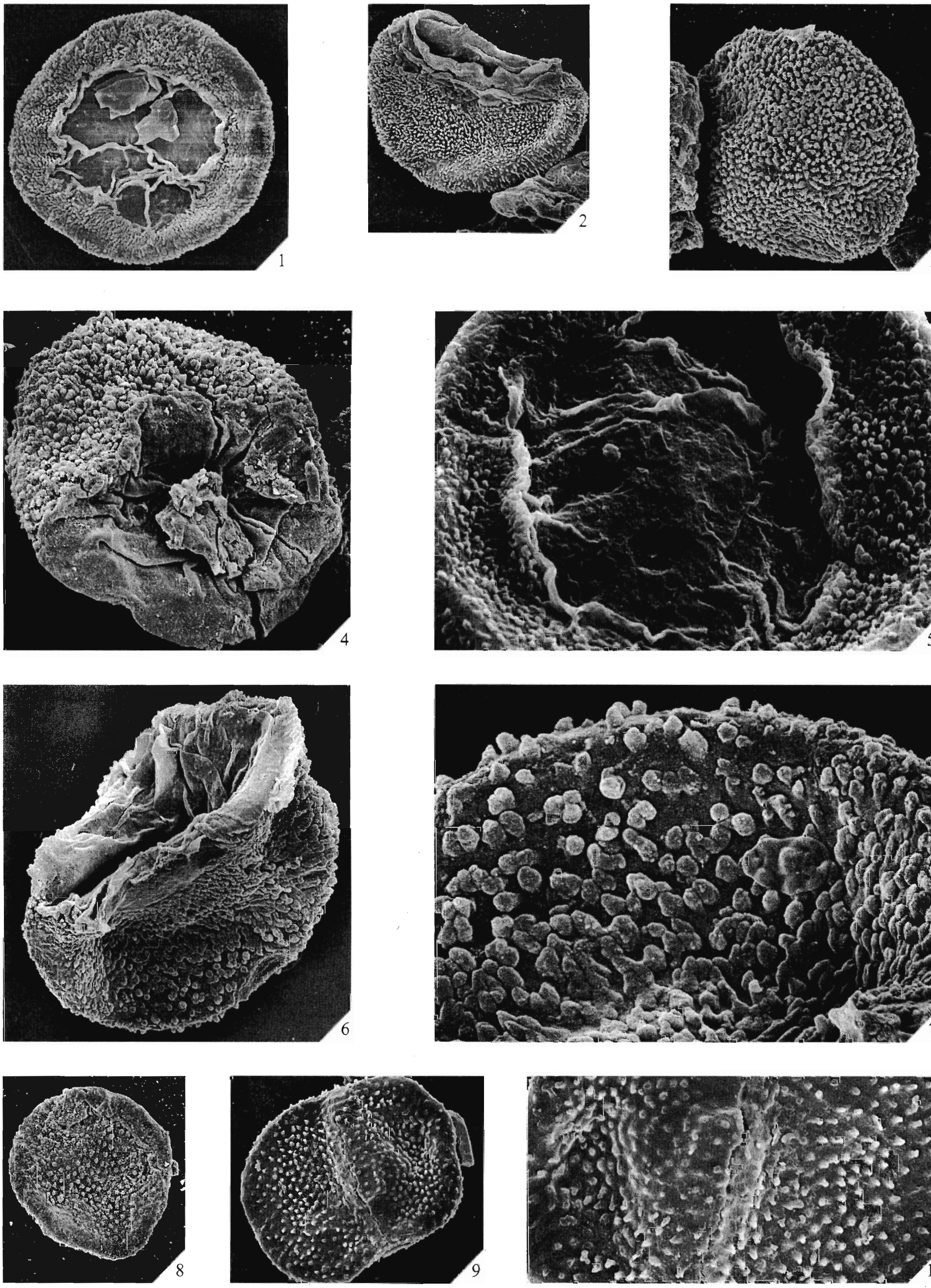
The taxa included in the prologue given by Burgess and Richardson (1991), *Artemopyra brevicosta* and *A.* sp. A, are both distally laevigate and are retained. In addition, a new species is proposed below.

EXPLANATION OF PLATE 2

Figs 1–7. *Cymbohilates allenii* var. *magnus* gen., sp. et var. nov.; lower Ditton Formation. 1, BM033345 (sample CH/TG/1B); proximal polar view showing irregular concentric and tangential folds on the hilum; Brown Clee Hill. 2, BM033890 (sample CH/TG/2); equatorial view; Brown Clee Hill. 3, BM031295 (sample CH/HD/4); distal polar view showing coarse anastomosing sculpture; north Brown Clee Hill. 4, BM031315 (sample CH/HD/4E); tipped specimen, showing coarse distal sculpture; north Brown Clee Hill. 5, BMcp/02445 (sample CH/TG2); detail of hilum: × 5000. 6–7, sample CH/TG/1B; north Brown Clee Hill. 6, BM033590 equatorial view, showing hilate folds; × 2000. 7, BM033591 detail of irregular grana showing discrete and anastomosing elements; × 6000.

Figs 8–10. *Cymbohilates disponerus* sp. nov.; lower Ditton formation. 8, BM031292 (sample CH/HD/4E); distal view; north Brown Clee Hill. 9–10, BM033222 (sample CH/TG/1B); dyad, lateral view; Brown Clee Hill. 10, detail of microconi and line of attachment; × 2000.

All figures × 1000, except where stated otherwise.



RICHARDSON, *Cymbohilates*

Artemopyra? *scalariformis* sp. nov.

Plate 10, figures 10–12

Derivation of name. Latin *scala*, ladder; *forma*, shape.

Holotype. FM 747 (Pl. 10, figs 10–11) sample CH/SD/88/2C, slide 3S, co-ord. 088 0897; E.F. no. J20/1; lower St Maughans Formation, Ammons Hill; diameter 38 μm.

Diagnosis. An *Artemopyra* with a narrow curvaturate zone less than 20 per cent. of the cryptospore radius in width, and consisting of radial subequatorial muri bounded by concentric 'ridges'.

Description. Proximally hilate monads, with circular to sub-circular amb, originally elliptical in cross section with a flattened apical area. The hilum is 25–36 μm wide, and is surrounded by a 'sculptured' curvaturate zone, consisting dominantly of short radial muri but which may also include coni; rarely muri become irregular poleward and form a mesh. Curvatural zone is 1–3 μm wide, radial bars < 1 μm thick. Distal exine is laevigate and *c*. 2 μm thick.

Dimensions. Diameter 32(37)49 μm; 13 specimens measured.

Comparison. The nature of the curvaturate area distinguishes this species from other species of *Artemopyra*.

Remarks. A ladder-like curvaturate area is seen on the inner layer of *Cymbohilates horridus* sp. nov. when the sculptured layer is degraded (Pl. 5, fig. 6) so it is possible that these specimens represent the inner bodies of sculptured spores that have lost their outer layer, although most specimens of *Artemopyra*? *scalariformis* are too small to represent degraded *C. horridus*. The variations seen in the 'sculptured' curvature zone may indicate that the inner bodies of more than one species are represented. Their presence may be due therefore to oxidation both natural and during processing. They were probably derived from loosely attached dyads.

Occurrence. ?Upper Red Marls (upper Downton Formation), Ammons Hill, M50, north Brown Clee Hill; ?*Apiculiretusispora* sp. E Assemblage Miospore Zone, lower *micrornatus-newportensis* palynosubzone (lower Gedinnian).

Infraturma APICULATI infraturma nov.

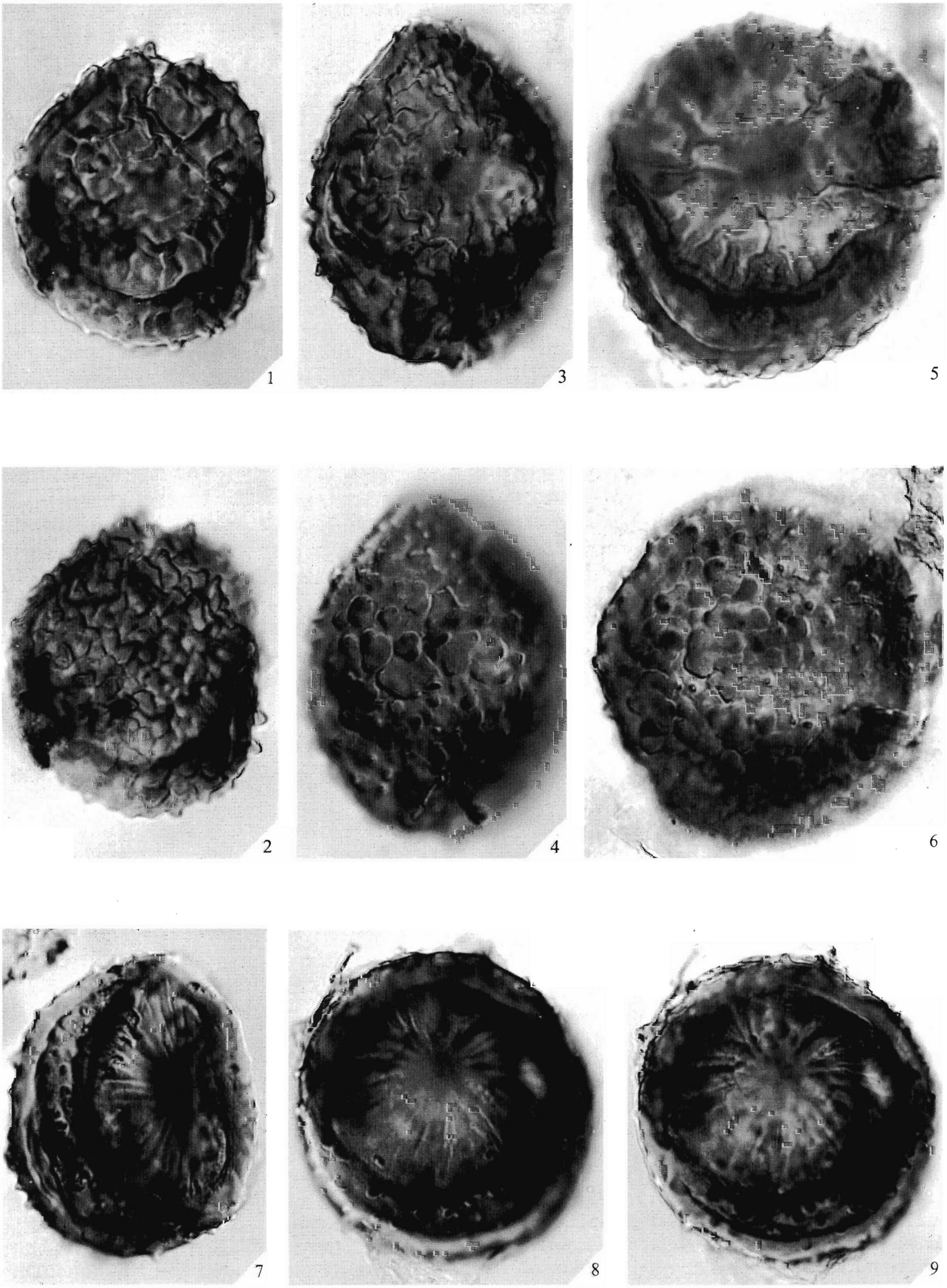
Diagnosis. Eucryptospores with a granulate, apiculate or spinose sculpture as the dominant sculpture.

EXPLANATION OF PLATE 3

Figs. 1–6. *Cymbohilates variabilis* var. *variabilis* gen., sp. et. var. nov.; north Brown Clee Hill; lower Ditton Formation; showing variation in this variety; all specimens compressed slightly obliquely; proximal and distal focus of the same specimen illustrated; proximal focus showing hilum with radial and concentric muri/folds and curvatural thickening, distal focus showing variable nature of the sculpture. 1–2, FM 722 (slide CH/HD/4G/7, co-ord. 200 0986; E.F. no. V29/1). 3–4, FM 723 (slide CH/HD/4E/8, co-ord. 104 1024; E.F. no. L32/2). 5–6, holotype, FM 724 (slide CH/HD/4G/9, co-ord. 040 1105; E.F. no. D41).

Figs 7–9. *Cymbohilates variabilis* var. A; north Brown Clee Hill; lower Ditton Formation. 7, FM 725 (slide CH/HD/4G/7, co-ord. 192 0994; E.F. no. U29/2); equatorial view showing hilum, curvatural crassitude, close-packed radial muri and apical thickening. 8–9, FM 726 (slide CH/HD/4G/9, co-ord. 086 1115; E.F. no. J42); showing thick wall. 8, proximal focus showing circular hilum with radial muri. 9, more distal focus showing broad-based coni.

All × 1000.



RICHARDSON, *Cymbohilates*

Genus CYMBOHILATES gen. nov.

Derivation of name. Latin *cymba*, bowl or cup; *hilum*, scar.

Type species. *Cymbohilates horridus* sp. nov.

Diagnosis. Proximally hilate cryptospore monads; exine, sculptured subequatorially and distally with grana, coni, spinae, biform, and occasional baculae, elements sometimes fused in groups. Contact area (hilum) smooth, with random or concentric folds, and/or, radial muri. Hilum, more or less circular, curvatural ridge distinct.

Comparison. *Laevolancis* has a structure similar to some species but is laevigate; specimens of *Laevolancis* resemble the inner exoexine of *C. horridus*. *Hispanaediscus* has a distal sculpture of verrucae, and/or muri but is otherwise similar. Where the hilum is collapsed, specimens of some species may be difficult to distinguish from proximally hilate miospores of the genus *Cymbosporites*, but the species of the latter are all trilete.

Remarks. In some species (e.g. *Cymbohilates horridus* sp. nov.) only the remnants of a thin diaphanous hilum are seen usually, while in others (e.g. *C. allenii* sp. nov.) the exine is thin and laevigate over the contact area, which has irregular and/or concentric folds but probably remains double-layered. The hilum, in contrast to that in *C. horridus*, is usually intact possibly indicating that the exine remains double-layered over the hilum. In these species the contact area is marked by a series of folds in a thin unsculptured part of the outer exine. In *C. variabilis*, most spores show well-defined contact areas with regular 'muri' in the subequatorial part but which breaks down into random and concentric folds towards the proximal polar apex, similar to the situation in some Wenlock specimens of *Hispanaediscus*. Structurally, *C. horridus* is at least two-layered and other species are probably laminate. These monad cryptospores are derived from 'loose' dyads. Spores still associated in dyads are relatively rare but are known for most species.

Cymbohilates horridus gen. et sp. nov.

Plate 5, figures 1–11; Plate 6, figures 1–2

Derivation of name. Latin *horridus*, bristly.

Holotype. FM 727 (Pl. 5, figs 1–3) sample CH5/71/A5, slide 2, co-ord. 0053 0772; E.F. no. E7; lower Ditton Formation, Brown Clee Hill, Shropshire; diameter (excluding spines) 66 μm, hilum width 50 μm, spines 6–7 μm long, width at base 4–5 μm.

EXPLANATION OF PLATE 4

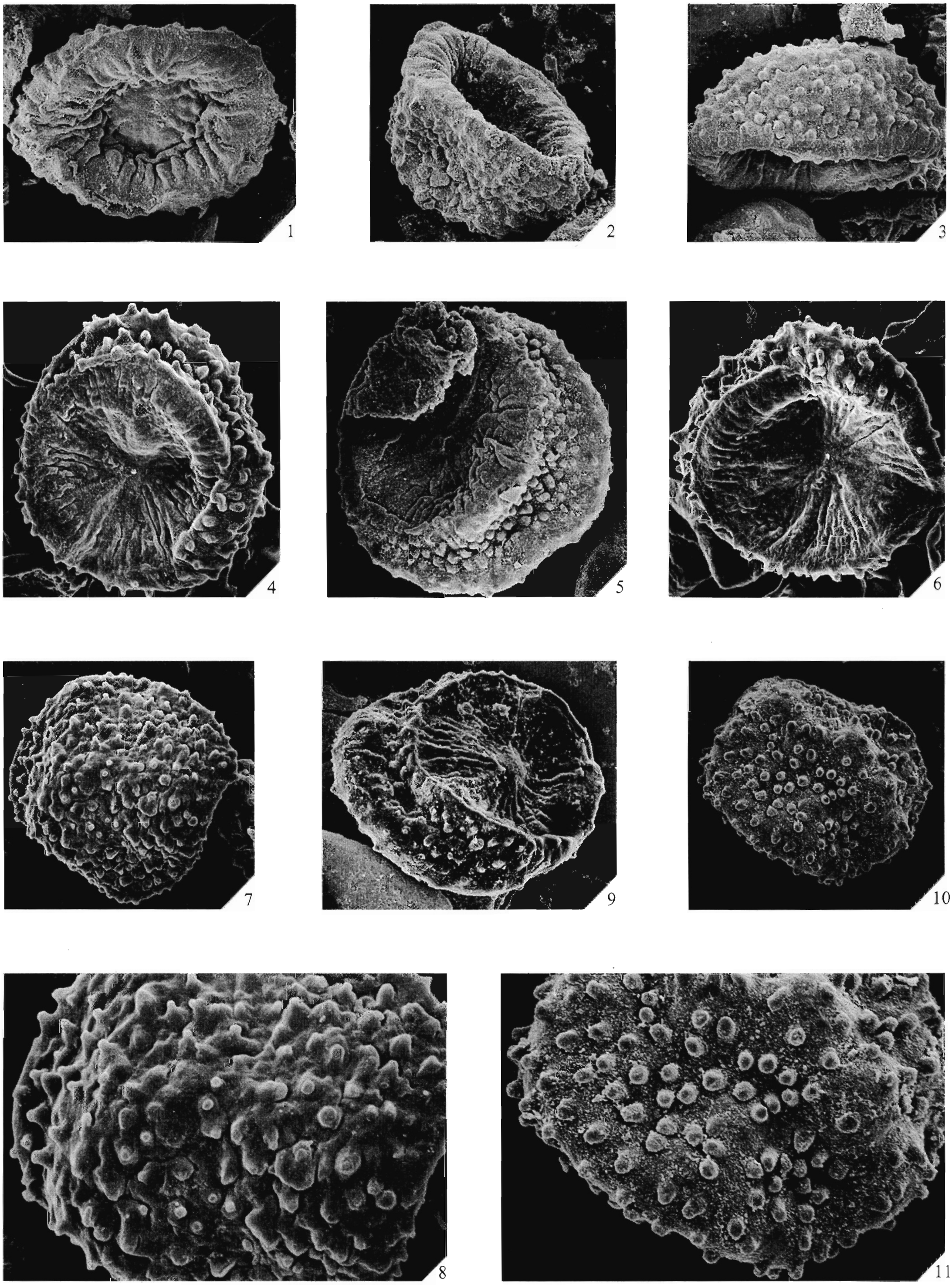
Figs 1–8. *Cymbohilates variabilis* var. *variabilis* gen., sp. et var. nov.; sample CH/71/HD/4E; north Brown Clee Hill; lower Ditton Formation. 1, BM032393; proximal view showing proximal-subequatorial area characterized by radial muri/folds and smoother polar apex. 2, BM030930; lateral compression showing invaginated hilum and distal sculpture. 3, BM032386; lateral view showing distal sculpture. 4, BM117755; oblique proximal view showing hilum with radial muri and sculpture of cones and microbaculae. 5, BM032044; oblique compression showing hilum and distal sculpture. 6, BM117757; proximal view showing coni, many elements with truncated apices. 7–8, BM117765; distal view showing biform elements fused in groups with truncated tips; 8, $\times$2000.

Fig. 9. *Cymbohilates variabilis* var. A; BM032052; laterally compressed specimen showing hilum with radial muri and apical papilla; north Brown Clee Hill; lower Ditton Formation.

Figs 10–11, *Cymbohilates variabilis* var. *parvidecus* gen., sp. et var. nov.; BM032884; distal views showing spaced microbaculae; compare the sculpture on var. *variabilis* (fig. 8); north Brown Clee Hill; lower Ditton formation; 11, $\times$2000.

All $\times$ 1000, except where stated otherwise.

PLATE 4



RICHARDSON, *Cymbohilates*

Diagnosis. A large *Cymbohilates* (over 50 μm, excluding spines), with a thin (< 0·5 μm) diaphanous hilum and a sculpture of prominent pointed spines.

Description. Amb is circular to sub-circular, often preserved in lateral compression; probably originally variably inflated distally from elliptical to hemispherical and with a flat, or flattened, proximal hilum. Spores are two- or three-layered. Hilum is distinct, circular, diaphanous, thin, commonly broken, or collapsed, with only the remnants seen around the margin of the contact area; outside the hilum, the exine is double-layered. Exine is distally 1·5 μm thick (one specimen only measured). Curvatural zone (collar) on inner exoexine is 4–8 μm wide; it consists of an outer (equatorial) narrow 1–1·5 μm thickened zone (crassitude) and an inner (poleward) zone, with thin (< 0·5 μm) radial muri/folds and a punctate wall. The rest of the inner exoexine is *c*. 1 μm thick, laevigate, sometimes crumpled into folds, but usually rigid. Diameter of hilum (inside curvatura) is 26–70 μm. Outer exoexine is thick, sculptured and often fragmentary. Sculpture consists of prominent pointed spines, uniformly tapered but showing a tendency to become biform on some specimens. The spines may be fused in groups of twos or threes, joined together by ridges 0·7–2·0 μm wide. The ridges are sinuous in plan, angular in cross section, often crenulate to cristate in profile, and form an irregular reticulate pattern. Small buttresses (> 1 μm wide) occur at the base of the ridges and more or less at right angles to them, giving a pleated pattern at the margins of the lumina. Spines 5–16 μm long, 2–8 μm wide at their bases.

Dimensions. 50–90 μm (excluding spines), mode 67 μm; 25 specimens measured.

Comparisons. The large size, distinct hilum, and prominent spinose sculpture distinguishes this species from all other members of the genus.

Remarks. This species is frequently found in a fragmentary condition, or with the outer sculptured layer degraded and partly removed.

Occurrence. Rare in the lower Ditton Formation, and present and occasionally relatively common in the middle Ditton Formation, Brown Clee Hill; present in the lower and middle St Maughans Formation, Ammons Hill and M50; lower and middle *micrornatus-newportensis* palynosubzones (lower and middle Gedinnian).

Cymbohilates allenii gen. et sp. nov.

Plate 1, figures 1, 2, 7–10; Plate 2, figures 1–7

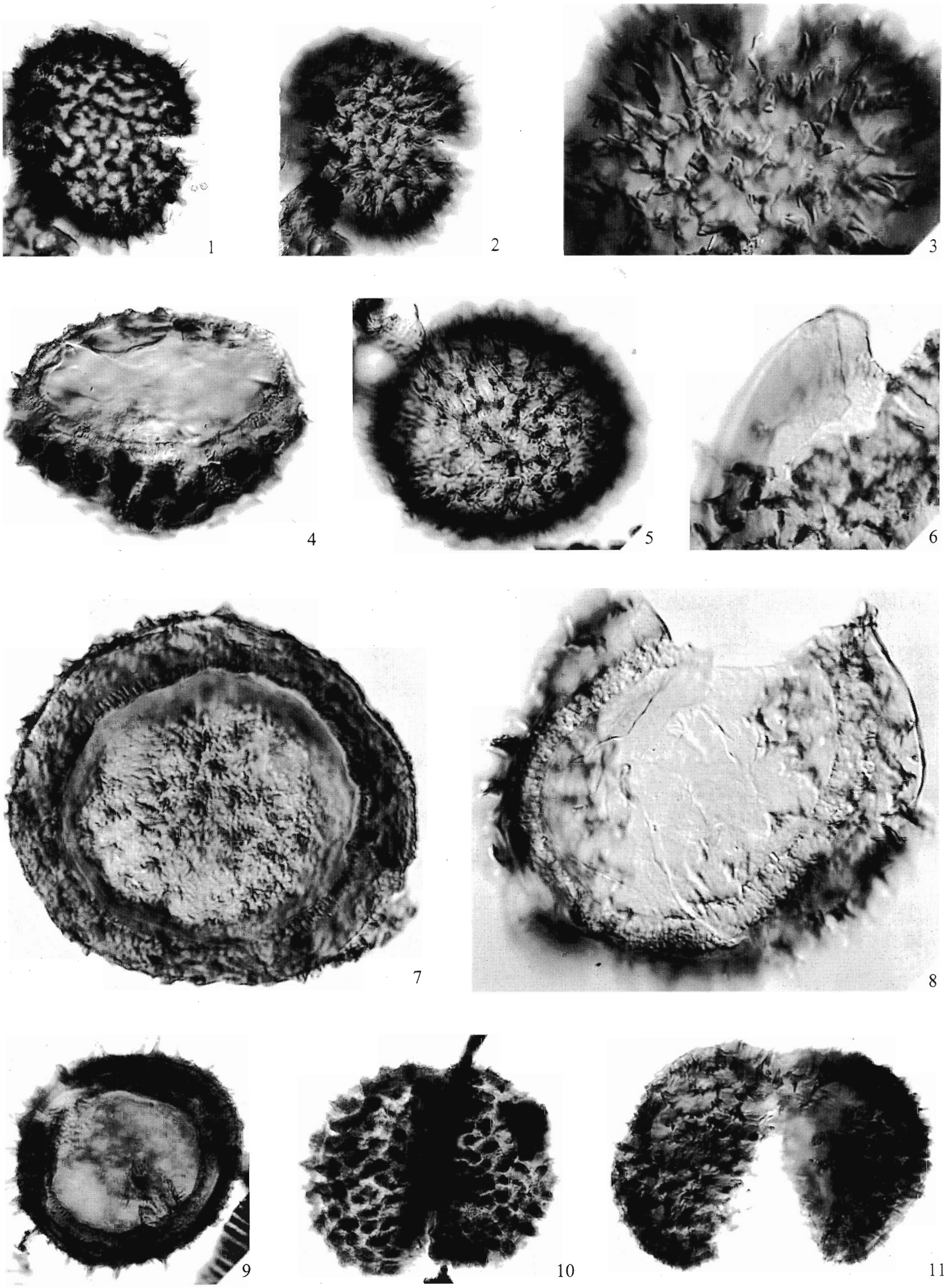
Derivation of name. Named in honour of Professor J. R. L. Allen, who has produced a revolution in the understanding of Old Red Sandstone sedimentology.

Holotype. FM 715 (Pl. 1, figs 1–2) sample M50/6, slide 4, co-ord. 164 1220; E.F. no. R53; lower St Maughans Formation, M50 motorway section, Hereford and Worcester; diameter 20 μm, hilum width 15 μm.

EXPLANATION OF PLATE 5

Figs 1–11. *Cymbohilates horridus* gen. et sp. nov.; lower Ditton Formation. 1–3, holotype, FM 727 (slide CH5/71/A52, co-ord. 053 0770; E.F. no. E7/1); distal view showing spinose sculpture; north Brown Clee Hill; 3, × 1000. 4, FM 728 (slide WB8/155 single grain mount; E.F. no. L35); equatorial view showing thin hilum; north Brown Clee Hill. 5, FM 729 (CH/HD4G/9 co-ord. 090 1100; E.F. no. J40/4); distal polar view; north Brown Clee Hill. 6, FM 730 (slide CH5/71/6B/3, co-ord. 113 1125; E.F. no. L43/3); broken specimen showing smooth inner exine; north Brown Clee Hill; × 1000. 7, FM731 (slide CH5/71/5A/2a, co-ord. 151 1096; E.F. no. P40/3/4); proximal polar view showing hilum and striate curvaturate band on outer exine; Brown Clee Hill; × 1000. 8, FM 732 (slide CH5/71/5A/2, co-ord. 075 0810; E.F. no. H10); degraded specimen showing microreticulate curvaturate zone on inner exinal layer; Brown Clee Hill; × 1000. 9, FM 733 (slide CH/HD 4G/7, co-ord. 206 1125; E.F. no. V43); proximal polar view; north Brown Clee Hill. 10, FM 734 (slide CH/HD/71/6B/3, co-ord. 142 1175; E.F. no. P48); dyad in equatorial view; north Brown Clee Hill. 11, FM 735 (slide CH5/71/5A/1, co-ord. 112 0765; E.F. no. L6/3); ?dyad showing crenulate ridges connecting the spine bases; north Brown Clee Hill.
All × 500, except where stated otherwise.

PLATE 5



RICHARDSON, *Cymbohilates*

Diagnosis. A *Cymbohilates* with a double wall except possibly for the hilum; amb circular to sub-circular, hilum more or less circular, with an irregular frequently folded margin; hilum unsculptured but characterized by a series of folds; sculpture over distal and subequatorial proximal surfaces consists of small closely packed granules as seen under the light microscope.

Comparison. The small, closely packed, granular sculpture, nature of the hilum and structure differentiate this species from others of the genus.

Remarks. It is not known whether the inner layer of the exine is present in the hilum, but the optical density is similar to the rest of the spore.

Cymbohilates allenii var. *allenii* gen., sp. et var. nov.

Plate 1, figures 1–2

Diagnosis. A *Cymbohilates allenii* with a maximum size of less than 30 μm.

Description. Amb is circular to sub-circular, invariably compressed in polar view, and was originally probably flattened–elliptical in shape. The hilum is 14–24 μm wide, with an irregular but more or less circular margin. The hilum is laevigate but typically shows a series of folds, usually roughly concentric around the equatorial margin, and random or sometimes arranged in a radial fashion across the hilum. The exine is two-layered. The outer exinal layer is thin and diaphanous where separated, sculptured uniformly over the entire surface by closely packed minute grana or microconi, with the exception of the hilum. The sculpture is less than 1 μm high and *c*. 0·5 μm wide, and more or less parallel-sided and isodiametric; under the SEM, elements often appear in groups, or interconnected by fine mural strands, usually at their bases.

Dimensions. 14–29 μm; 25 specimens measured.

Comparisons. The small size and less rigid wall distinguishes this variety from var. *magnus*.

Remarks. Similar specimens (14–24 μm, five specimens) but with radial muri/folds (emphanoid) are referred to as *Cymbohilates allenii* var. A.

Occurrence. Upper Raglan Marl and St Maughans Formations, M50 section; lower and middle Ditton Formation, Brown Clee Hill; ?*Apiculiretusispora* sp. E Assemblage Miospore Zone, lower and lower middle *micrornatus-newportensis* palynosubzones (lower Gedinnian).

Cymbohilates allenii var. *magnus* gen., sp. et var. nov.

Plate 1, figures 7–10; Plate 2, figures 1–7

Derivation of name. Latin *magnus*, great, large.

Holotype. FM 719 (Pl. 1, figs 7–8) sample TGIB/79, slide 3, co-ord. 098 1055; E.F. no. K36; lower Ditton Formation (*leathenensis* vertebrate zone), Brown Clee Hill; diameter 34 μm, hilum width 25 μm.

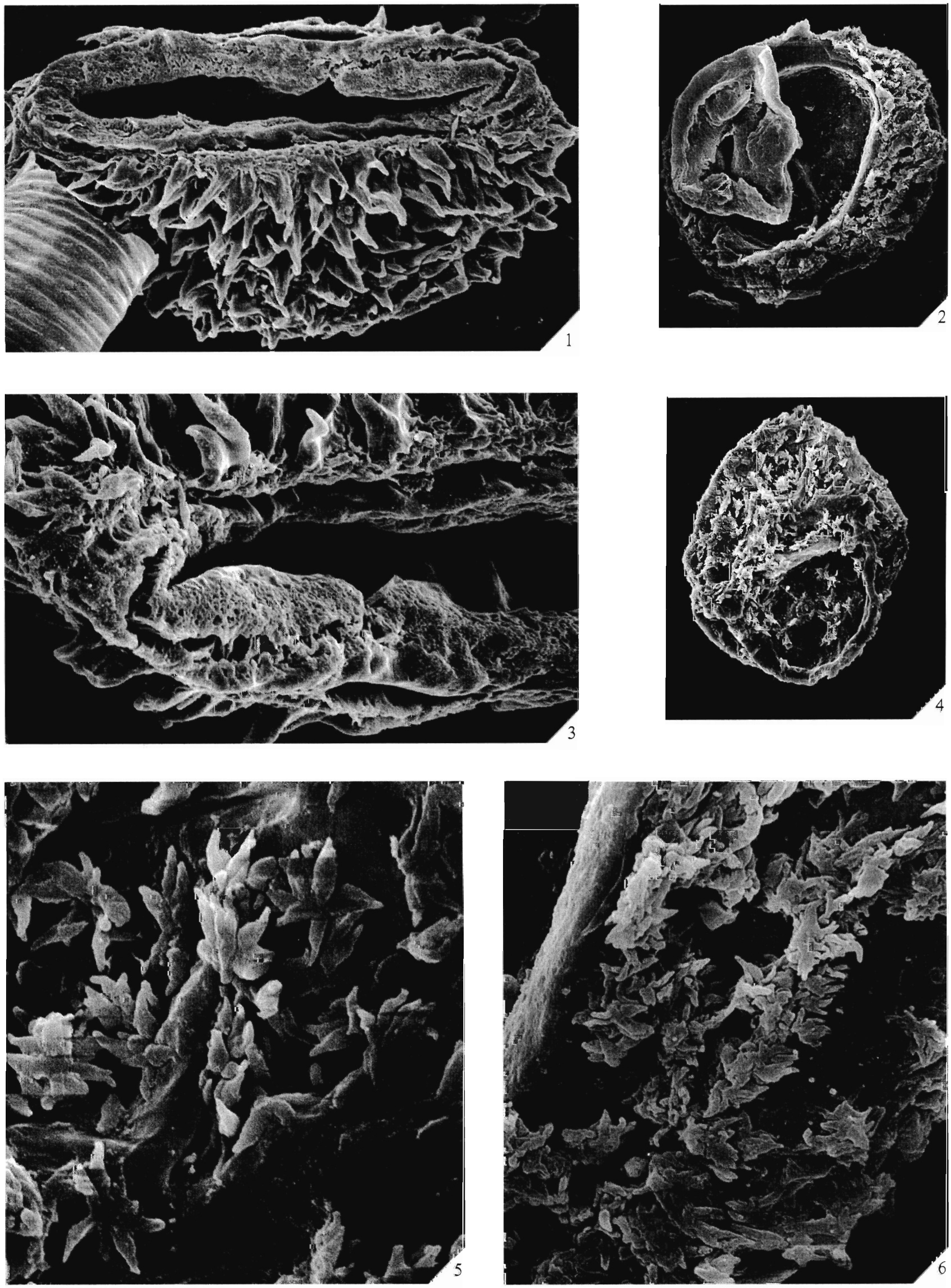
EXPLANATION OF PLATE 6

Figs 1–2. *Cymbohilates horridus* gen. et sp. nov.; (sample CH/HD/4E); north Brown Clee Hill; lower Ditton Formation. 1, BM11776; equatorial view showing hilum area, subequatorial and distal spines. 2, BM11777; showing two-layered (?three-layered) exine, outer exinal layer with sculpture not present over the contact area, inner exine layer puctate invaginated over the contact area; × 2000.

Figs 3–6. *Cymbohilates cymosus* gen. et sp. nov.; (sample M50/5G); Ross on Wye; lower St Maughans Formation. 3, BM088159; oblique proximal view showing invaginated hilum and inner smooth exine. 4, BM088160; detail of fig. 3 showing irregular distribution of partly degraded sculpture; × 6000. 5, BM16796; tetrad. 6, BM16797; detail of fig. 5 showing some of the short spines in star-shaped rosettes; × 6000.

All × 1000, except where stated otherwise.

PLATE 6



RICHARDSON, *Cymbohilates*

Diagnosis. A *Cymbohilates allenii* with a size of 30 μm or greater.

Description. Amb is circular to sub-circular, moderately inflated distally so that spores are commonly compressed obliquely. Hilum is more or less circular, 22–32 μm wide. Exine is double-walled, the thin outer layer of the exine closely adhering to the inner, thick (1–3 μm) exine layer, except over the contact area (hilum), where it is thrown into a series of tangential and radial folds. The outer exinal layer is diaphanous and sculptured uniformly except over the contact area. The sculpture consists of grana, coni, or microbaculae as seen under the light microscope; elements are *c*. 0·5 μm high and wide.

Dimensions. 30–50 μm; 33 specimens measured.

Comparisons. It is distinguished from *C. allenii* var. *allenii* by its greater size range, greater distal inflation, pattern of proximal folds and thicker inner layer of the exine. In gross morphology it is similar to *Perotrilites microbaculatus*, but is hilate and alete.

Occurrence. St Maughans Formation, M50; lower Ditton Formation, Brown Clee Hill, occasionally common; lower and middle *micrornatus-newportensis* palynosubzones (lower and lower middle Gedinnian).

Cymbohilates variabilis gen. et sp. nov.

Plate 1, figures 5–6, 11–12; Plates 3–4

Derivation of name. Latin *variabilis*, changeable; referring to the variable sculpture.

Holotype. FM 724 (Pl. 3, figs 5–6) sample HD 4G, slide 9, co-ord. 042 1105; E.F. no. D41; Ditton Formation, *c*. 60 m above Psammosteus Limestone (lower *crouchi* vertebrate zone, Gedinnian), Brown Clee Hill; diameter (excluding sculpture) 52 μm, hilum width including crassitude 43 μm, distal wall 4 μm thick, sculpture mainly fused in groups, *c*. 1 μm high and 2–3·5 μm wide, apical area 13 μm wide.

Diagnosis. A *Cymbohilates* with a thick equatorial and distal exine, with sculptural elements of variable size and shape on the same spore.

Comparison. The thick equatorial and distal wall and mixture of biform, verrucose, apiculate and spatulate tipped spinose elements distinguish *C. variabilis* from other *Cymbohilates* species.

Remarks. The hilum, though flattened or depressed, is always present and this suggests that the exine over the contact area is not markedly thinner than over the rest of the spore.

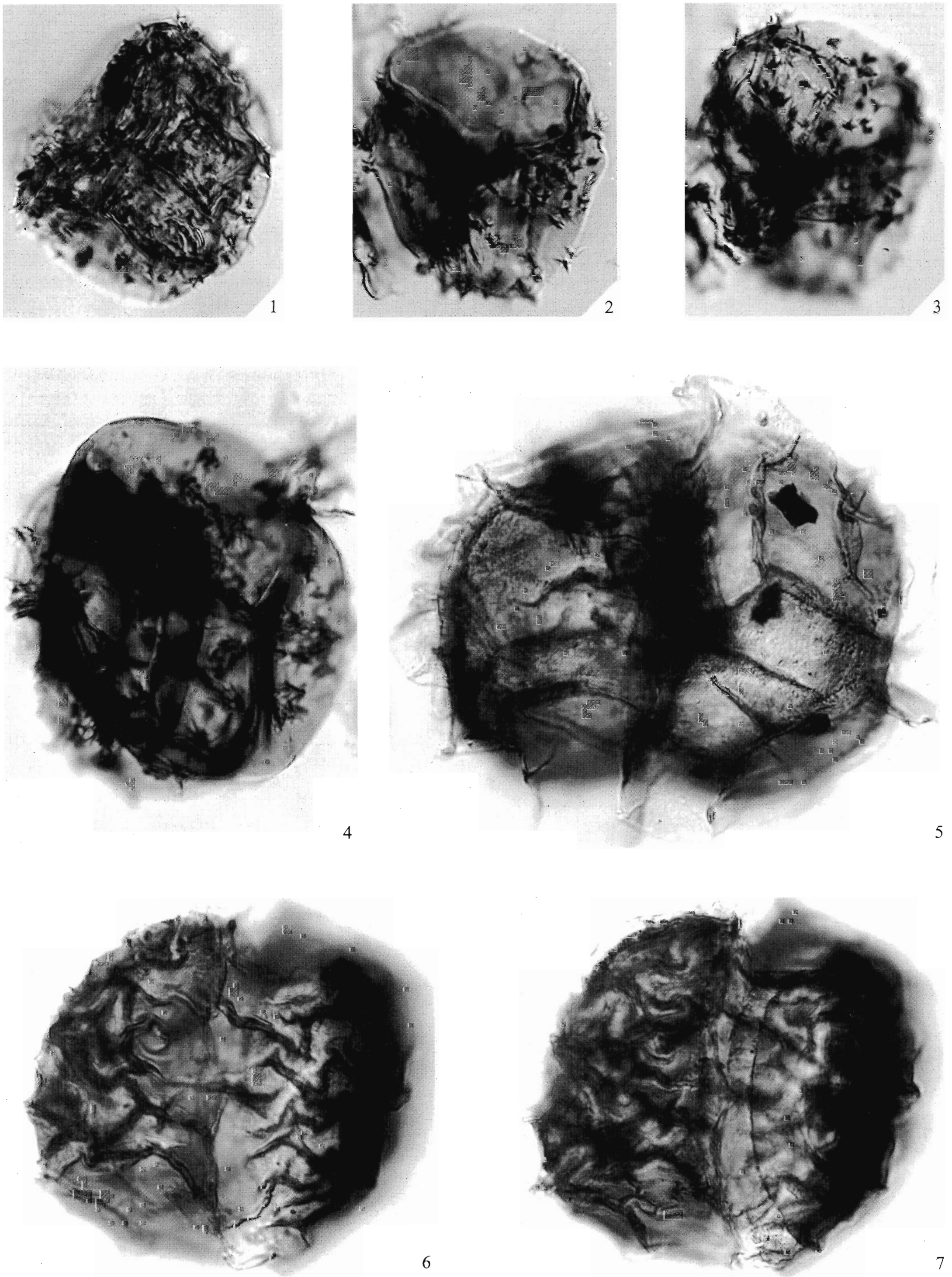
Botanical affinity. Unknown. Occurs in elongate sporangia in north Brown Clee.

EXPLANATION OF PLATE 7

Figs 1–4. *Cymbohilates cymosus* gen. et sp. nov.; tetrads; north Brown Clee Hill; lower Ditton Formation. 1, FM 736 (slide CH/HD/4G/7, co-ord. 212 1128; E.F. no. W43/2). 2–3, holotype, FM 737 (slide CH/HD/4E/8, co-ord. 055 1048; E35/3); different focal levels of the same specimen showing star-shaped clusters of spines. 4, FM 738 (slide CH/HD/4E/8, co-ord. 180 1057; E.F. no. S36/3).

Figs 5–7. *Chelinohilates erraticus* gen. et sp. nov.; dyads in equatorial view; north Brown Clee Hill; ?upper Ledbury Formation. 5, FM 739 (CH/SD/2C/3/5, co-ord. 089 1058; E.F. no. J36); muri form large polygonal fields. 6–7, holotype, FM 740 (CH/SD/2C/3/5, co-ord. 065 1074; E.F. no. G38/1); specimen in different focal planes. 6, muri forming an irregular reticulum. 7, showing layered exine and anisopolar nature of the dyad.

All × 1000.



RICHARDSON, *Cymbohilates*, *Chelinohilates*

Cymbohilates variabilis var. *variabilis* gen., sp. et var. nov.

Plate 3, figures 1–6; Plate 4, figures 1–8

Diagnosis. A *Cymbohilates variabilis* with variable sculptural elements, consisting of discrete coni, biform coni, irregular broad-based coni fused into groups, or a mixture of elements. Elements with rounded, pointed, or flattened apices, irregularly sinuous in plan, include occasional single elements; hilum surrounded by a narrow curvatural ridge, and with proximal radial, or radial and concentric muri/folds; hilum invaginated but optically similar in density to distal area.

Description. Amb is circular to sub-circular, originally probably flattened–hemispherical in equatorial view. Exine is 3–4 μm thick outside the contact area. Hilum is 26–30 μm wide, circular to sub-circular, and differentiated from the rest of the spore by a sinuous subequatorial curvatural ridge, 1–2 μm wide. The hilum is often densely packed with radial muri, which are *c*. 2 μm subequatorially and taper to less than 1 μm. The muri eventually die out into a darkened (?thickened) smooth area (?apical papilla) *c*. 6 μm across, or sometimes become more spaced and terminate about three-fifths of the way from the equator, where they join concentric folds. Polewards, there may be a further set of spaced radial folds. Distal elements are dominantly fused in groups and consist of broad-based coni and biform coni (i.e. broad-based coni with small apical terminations $< 0{\cdot}5$ μm), *c*. 0·5–2·0 μm high, 1–8 μm wide; smaller elements are less than 1 μm. Elements are usually conical or biform and may have truncated apices. The density and distribution of the fused elements are variable, but they are mainly densely packed, discrete elements, which are often subequatorial.

Dimensions. 35–54 μm; mode 52 μm; 20 specimens measured.

Comparison. The relatively large (basal width > 2 μm), frequently coalescent sculptural elements distinguish this variety. *C. allenii* has small, evenly spaced grana, a thin exine, and a sharply contrasting proximal hilum.

Remarks. Specimens with the coarser sculptural elements of variety *variabilis* show a rigid smooth area 4–9 μm across at the proximal pole. Under the SEM this area is invaginated whereas the papilla in *C. variabilis* var. A is a rounded projection (compare Pl. 4, figs 1 and 9).

Occurrence. Upper-lower (*c*. 60 m above Psammosteus Limestone) and middle Ditton Formation, north Brown Clee Hill; middle *micrornatus-newportensis* palynosubzone (lower-middle Gedinnian).

Cymbohilates variabilis var. *parvidecus* gen., sp. et var. nov.

Plate 1, figures 11–12; Plate 4, figures 10–11

Derivation of name. Latin *parvus*, little; *decus*, ornament.

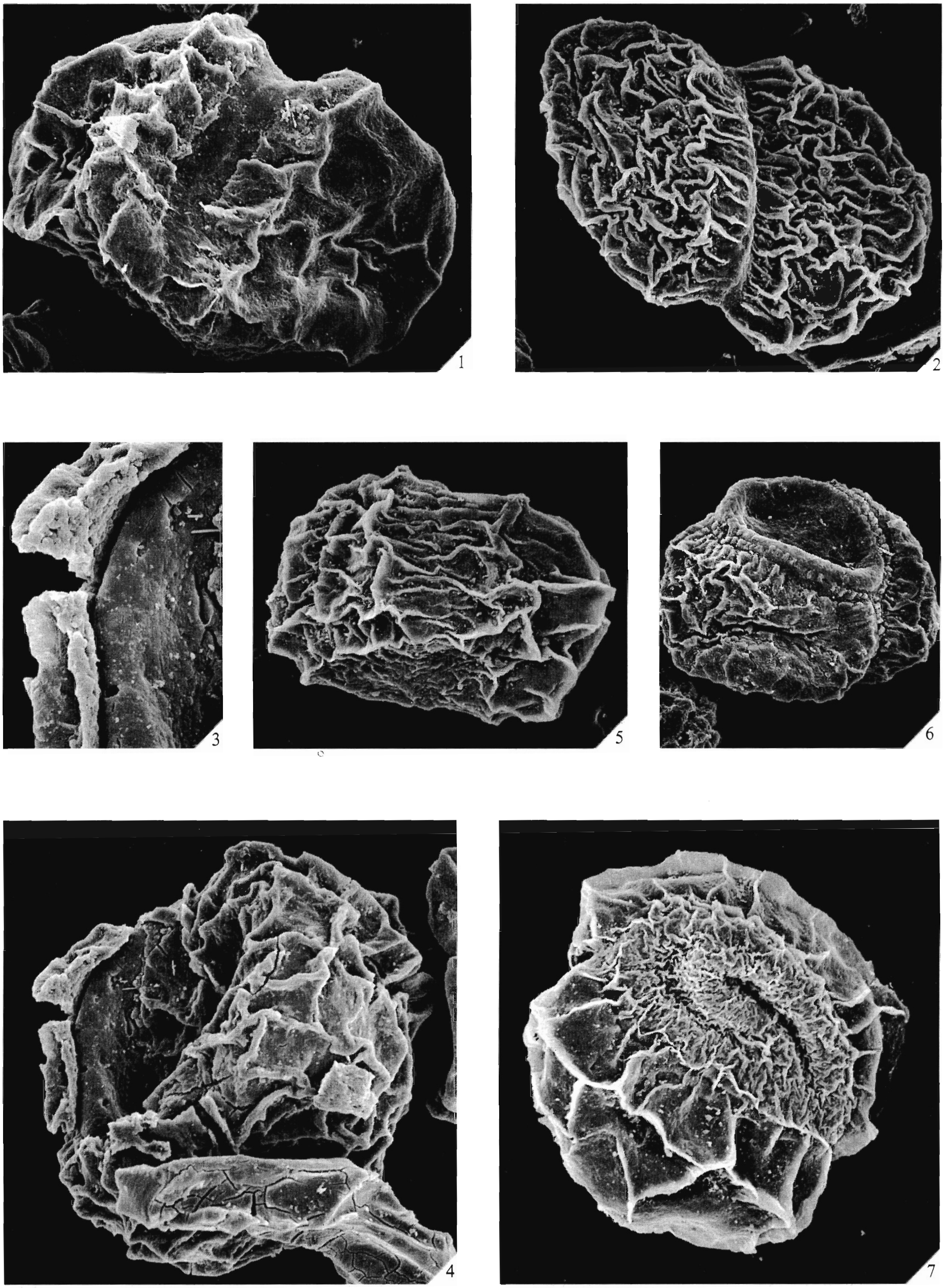
Holotype. FM 721 (Pl. 1, figs 11–12) sample HD4G, slide 7, co-ord. 223 1096; E.F. no. X40; Ditton Formation (*leathensis* to lower *crouchi* vertebrate zones), Brown Clee Hill, Shropshire; diameter 27 μm, hilum width 26 μm, distal wall 2 μm thick, sculpture *c*. 1 μm high, 1–1·5 μm wide.

EXPLANATION OF PLATE 8

Figs 1–7. *Chelinohilates erraticus* gen. et sp. nov.; (sample CH/SD/88/2C); ?upper Ledbury Formation. 1, BM118304; dyad in equatorial view showing separation of the sculptured outer exine and fusion of inner exine. 2, BM118320; dyad in equatorial view showing irregular reticulum and muri normal to the contact between the two units. 3, BM118333; wall fragment of monad in fig. 4 showing outer sculptured exine layer partially separated from smooth inner exine layer; ×2000. 4, BM118332; monad with outer exine not extending over the hilum. 5, BM118293; triad with an ?aborted spore at right angles. 6, BM118202; triad with one invaginated, ?aborted, spore not covered with outer sculptured exine layer. 7, BM118318; triad with abnormal third spore.

All × 1000, except where stated otherwise.

PLATE 8



RICHARDSON, *Chelinohilates*

Diagnosis. A *Cymbohilates variabilis* with coni, grana or microbaculae; width of elements at base less than 2 μm, and typically *c*. 1 μm.

Description. Amb is circular to sub-circular with some distal inflation, commonly obliquely compressed, originally probably flattened–hemispherical in equatorial view. Exine is distally and equatorially 1–4 μm thick. Hilum is circular to sub-circular, differentiated from the rest of the spore by wall thickness and sculpture, and commonly has densely packed radial muri that fuse towards the polar apex, or sometimes terminate about one-third of the way from the equator where they join concentric folds. Exine outside the hilum is ?1–4 μm thick. Distal elements are more or less isodiametric to slightly elongate, *c*. 0·5 μm high and wide; coarser elements are less than 2 μm in size. The elements may be conical or more or less parallel-sided with truncated apices. The density of elements is variable; some are spaced so that elements of equal size could easily be accommodated between them, in other cases they are densely packed. Under the SEM, the parallel-sided and flat-topped nature of some of the sculptural elements may be clearly seen (Pl. 4, fig. 11).

Dimensions. 22–47 μm (including sculpture), mode 42 μm,; 30 specimens measured.

Comparison. *Cymbohilates variabilis* var. *variabilis* has larger more densely packed sculpture; the thicker wall, nature of the hilum and the sculptural elements distinguish this form from *C. allenii*.

Occurrence. Lower and middle Ditton Formation, Brown Clee Hill; lower and lower middle *micrornatus-newportensis* palynosubzones (lower and middle Gedinnian).

Cymbohilates variabilis var. *tenuis* gen., sp. et var. nov.

Plate 1, figures 5–6

Derivation of name. Latin *tenuis*, thin.

Holotype. FM 718 (Pl. 1, figs 5–6) sample HD4G, slide 7, co-ord. 200 1121; E.F. no. B43/1; Ditton Formation (lower *crouchi* vertebrate zone), Brown Clee Hill, Shropshire; diameter 41 μm, hilum width 30 μm, distal wall *c*. 1 μm thick, sculpture *c*. 0·5 μm high, 0·5–1·0 μm wide.

Diagnosis. A *Cymbohilates variabilis* with a relatively thin exine and a sculpture of spaced, broad-based coni and microbaculae.

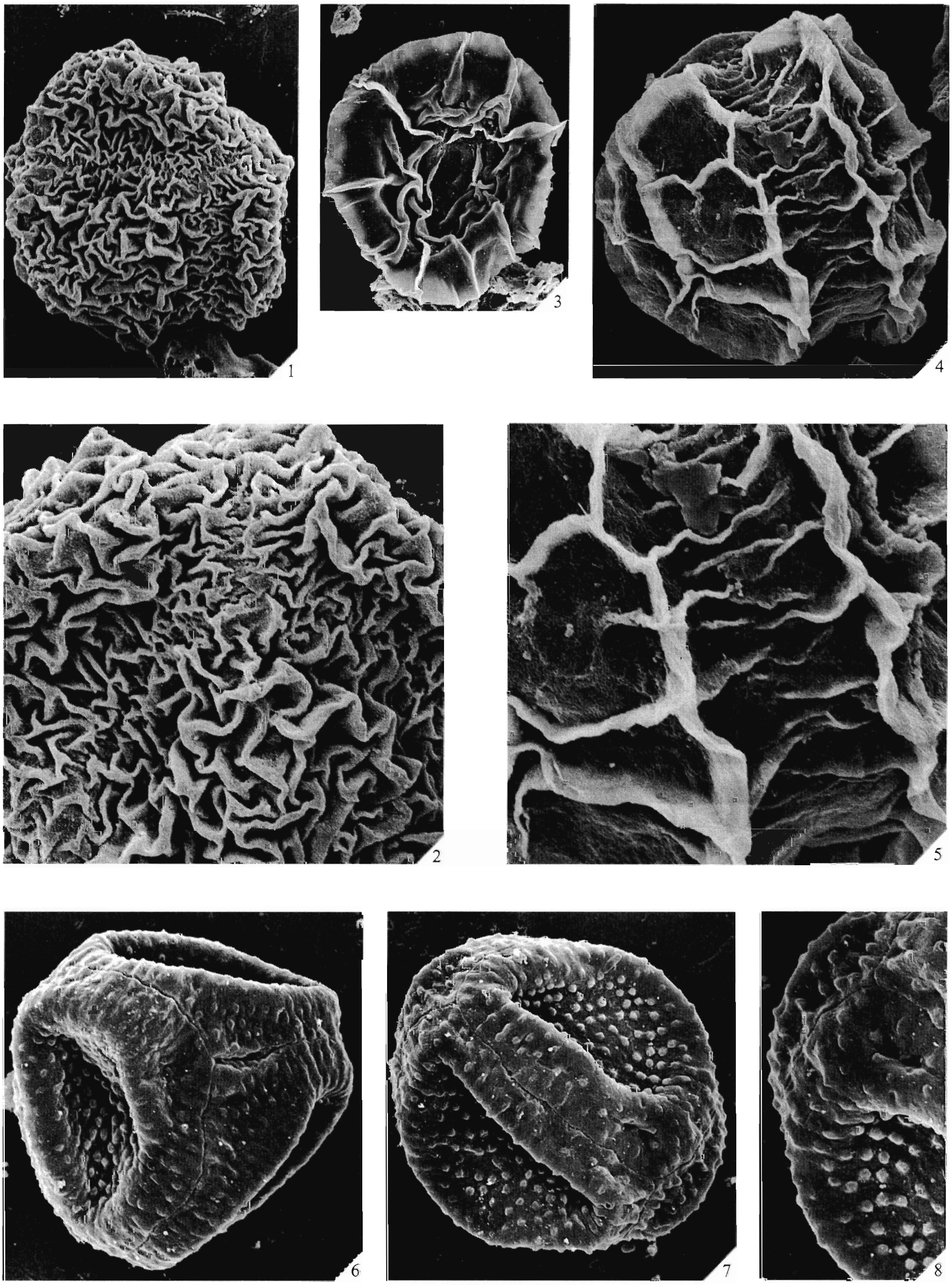
Description. Amb is circular to sub-circular, and commonly tipped. The hilum is surrounded by a narrow crassitude in some specimens. The exine is commonly folded. Structurally, it is the same as var. *parvidecus* but the sculpture tends to be dominated by broad-based coni with rounded to pointed apices, occasionally fused in pairs; parallel-sided elements with flat tops also occur.

EXPLANATION OF PLATE 9

Figs 1–5. *Chelinohilates erraticus* gen. et sp. nov. 1–2, Sample CH/81/4c; lower Ditton Formation; Brown Clee Hill. 1, BM115109; tetrad showing closely spaced muri. 2, BM115107; specimen with closely packed muri, detail of modified muri along curvatural bands; ×2000. 3–5, Sample 50/5G; lower St Maughans Formation. 3, BM088153; distal view of a monad. 4–5, BM088414. 4, triad, showing two anisomorphic spores and the top of a third spore at right angles to them. 5, detail, showing curvatural band with muri at right angles to the distal reticulum; ×2000.

Figs 6–8. *Acontotetras inconspicuis* gen. et sp. nov.; sample CH/88/2c; ?upper Ledbury Formation. 6–7, showing two tetrads in different compressional state, spore units with invaginated distal areas; ×2000. 6; BM109915. 7, BM109918. 8, detail of sculpture on fig. 7; ×3000.

All × 1000, except where stated otherwise.



RICHARDSON, *Chelinohilates*, *Acontotetras*

Dimensions. 21–46 μm (including sculpture); 12 specimens measured.

Comparison. Distinguished from var. *parvidecus* by the thinner, frequently folded exine and dominantly conate sculpture.

Occurrence. Lower and middle Ditton Formation, Brown Clee Hill; lower and middle *newportensis-micrornatus* palynosubzones (lower and lower-middle Gedinnian).

Cymbohilates variabilis var. A

Plate 3, figures 7–9; Plate 4, figure 9

Description. Hilate monad cryptospores with no marked thinning over the proximal hilum. Amb is circular to sub-circular with some distal inflation, commonly obliquely compressed, originally probably flattened–hemispherical in equatorial view. Hilum is circular to sub-circular, and differentiated from the rest of the spore by curvatural zone 0·5–5 μm wide. The wall thickness is distally 2·5–4·0 μm; the hilum is rigid and not markedly thinner. Sculpture distally consists of broad based coni 0·5–1·5 μm high, 1·0–3·5 μm wide, 1–4 μm apart; proximal sculpture consists of close-packed, straight, radial muri, *c.* 1 μm wide, reaching from the curvatural ridge to the margin of a smooth papilla at the spore apex. This papilla is 4–9 μm wide. Muri taper slightly to the pole, or occasionally broaden poleward and fuse near the apical papilla.

Dimensions. Maximum diameter, 21–47 μm, hilum 17–39 μm; five specimens measured.

Remarks. This is similar to *C. variabilis* var. *variabilis* distally, but has close-packed radial muri almost to the apex; apical papillae at polar apex are variably developed. In one specimen (diameter 27 μm) no radial muri were observed, although there was an apical papilla.

Cymbohilates disponerus gen. et sp. nov.

Plate 1, figures 5–6; Plate 2, figures 8–10

Derivation of name. Latin *disponere*, to space out. It refers to the spaced sculptural elements.

Holotype. FM 716 (Pl. 1, figs 5–6) sample TG/2/79, slide 6, co-ord. 190 0958; E.F. no. T26/3; lower Ditton Formation (lower *crouchi* vertebrate zone, middle *micrornatus-newportensis* palynosubzone), Brown Clee Hill, Shropshire; diameter 27 μm, hilum width 22 μm, sculpture *c.* 0·5 μm high, 0·5–0·7 μm wide.

Diagnosis. A *Cymbohilates* sculptured with evenly spaced microconi to coni; sculptural elements isodiametric to broader than high.

EXPLANATION OF PLATE 10

Figs 1–2. *Chelinohilates erraticus* gen. et sp. nov. 1, FM 741 (slide CH5/71/5A/2A, co-ord. 052 0754; E.F. no. E5/4); distal view of monad showing irregular reticulum showing broad lumina. 2, FM 742 (slide CH/71/6B/3, co-ord. 191 1197; E.F. no. U50/2); broken specimen showing two-layered exine, inner layer thin, smooth and with narrow curvatura.

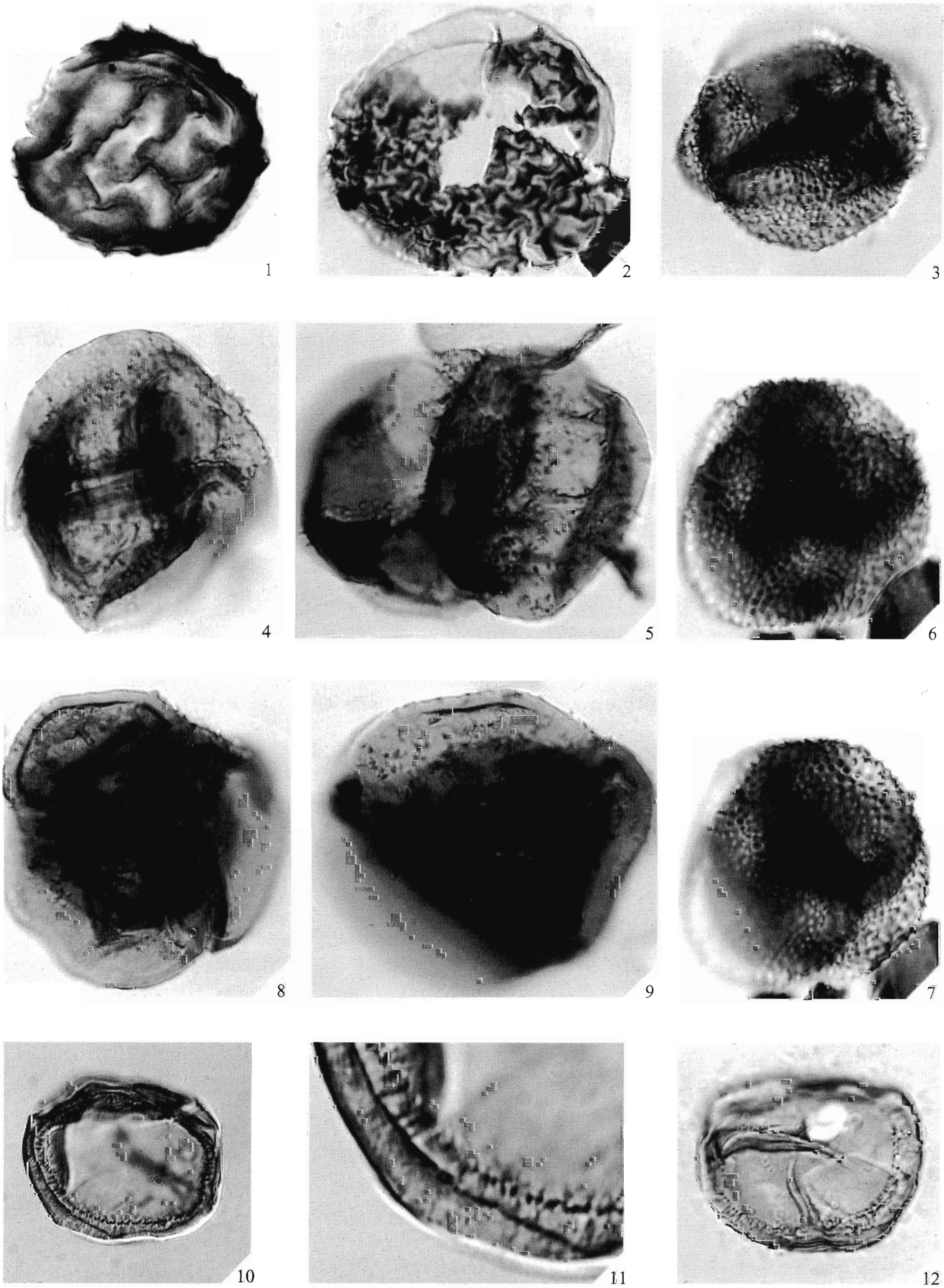
Figs 3, 6–7. *Acontotetras inconspicuis* gen. et sp. nov. 3, F743 (slide CH/88/2c/3S, co-ord. 093 1029; E.F. no. K33/2). 6–7, FM 746 (slide CH/88/2c/3S, co-ord. 069 1079; E.F. no. G38); in different focal planes.

Figs 4–5. *Acontotetras* sp. A; showing thin-walled spore units and sparse small sculptural elements. 4, FM 744 (slide CH/4E/8, co-ord. 138 1047; E.F. no. N35). 5, FM 745 (CH/4E/8, co-ord. 094 1097; E.F. no. K40/2).

Figs 8–9. *Acontotetras* sp. B.; showing thick-walled spore units and sparse sculptural elements. 8, FM 748 (slide CH/4E/8, co-ord. 200 1060; E.F. no. U36/4). 9, FM 749 (slide CH/4E/8, co-ord. 160 1073; E.F. no. R38/1).

Figs 10–12. *Artemopyra*? *scalariformis* sp. nov.; proximal view. 10–11, holotype FM 747 (slide CH88/2c/3S, co-ord. 088 0897; E.F. no. J20/1). 11, detail of fig. 10, showing curvatural zone; × 3000. 12, (slide MPA 25198/2/3, co-ord. 210 0932; E.F. no. W23).

All × 1000, except where stated otherwise. All samples from north Brown Clee Hill; lower Ditton Formation.



RICHARDSON, *Chelinohilates*, *Acontotetras*, *Artemopyra*?

Description. Hilate, alete monads with a circular to sub-circular, distally, inflated amb. Specimens are occasionally preserved in equatorial compression, or tipped. The exine is 0·5(0·7)1·5 μm thick. The hilum (contact area) is 14(17)23 μm thick, but is thinner, sometimes with concentric folds, just inside the hilum margin. A narrow band, *c.* 3 μm wide, of radial ?folds is sometimes seen around the hilum. Sculpture consists of microconi/coni typically spaced 1·0–1·5 μm apart, more rarely 2 μm apart. Coni are usually wider than high, but occasionally more or less isodiametric, < 0·5–0·7 μm high, 0·5(0·7)1·0 μm wide.

Dimensions. 16–30 μm (including sculpture); 22 specimens measured.

Comparisons. This differs from *Cymbohilates variabilis* by the small regular and evenly distributed coni. *C. allenii* is distinguished by close-packed, minute grana.

Remarks. Hilate cryptospores very similar to *C. disponerus* occur in elongate sporangia of the *Salopella* type (Edwards *et al.* 1994). The macrofossils occur in the same beds as the dispersed spores. Specimens of the same size with apparently identical sculpture occur in tetrads. Specimens with smaller sculpture and radial hilate folds and an apical papilla are referred to *C.* sp. B.

Occurrence. Lower and middle Ditton Formation, Brown Clee Hill; lower and middle *micrornatus-newportensis* palynosubzones (lower and lower middle Gedinnian).

Cymbohilates cymosus gen. et sp. nov.

Plate 6, figures 3–6; Plate 7, figures 1–4

Derivation of name. Latin *cymosus*, full of shoots.

Holotype. FM 737 (Pl. 7, figs 2–3) sample HD4E, slide 8, co-ord. 055 1407; E.F. no. E35/3; lower Ditton Formation, Brown Clee Hill, Shropshire; diameter tetrad 46 μm, spore units 33, 38 μm, distal wall < 1 μm thick, clusters of sculptural elements 1–3 μm high, 1·5–2·0 μm wide.

Diagnosis. A *Cymbohilates* sculptured with short spines in star-shaped clusters.

Description. Hilate monads and tetrads with a circular to sub-circular distally inflated amb. Specimens are occasionally preserved in equatorial compression, or tipped. The exine is double layered, the inner layer 1·0–1·5 μm thick. The hilum (contact area) is thinner and sometimes shows fine radial folds; a concentric fold occurs just inside the hilum margin. Sculpture consists of closely packed, short spines in 3–7 rayed clusters, or occasionally as single-rayed elements; pila and short bifid spines are *c.* 1–3 μm wide, 1–4 μm high.

Dimensions. 28–52 μm, mode 37 μm; 18 specimens measured.

Remarks. The clusters of short spines are diagnostic. Spore units occur mainly in tetrads but also as hilate monads, possibly indicating derivation from dyads, but no definite dyads have been seen.

Occurrence. ?Uppermost Red Downton and lower Ditton formations, Brown Clee Hill; Ammons Hill, St Maughans Formation; ?*Apiculiretusispora* sp. E Assemblage Miospore Zone, lower and middle *micrornatus-newportensis* palynosubzones (lower and lower-middle Gedinnian).

Infraturma SYNORATI infraturma nov.

Diagnosis. Cryptospores with a verrucate and/or murornate sculpture as the dominant type of ornament.

Genus CHELINOHILATES gen. nov.

Derivation of name. Greek *chelinos*, net; Latin *hilum*, scar.

Type species. Chelinohilates erraticus sp. nov.

Diagnosis. Eucryptospores or paracryptospores with an exine differentiated into at least two layers; outer layer sculptured, diaphanous, variably appressed to the inner exinal layer (inner exoexine), and does not extend over the well-marked contact area (hilum); the inner exoexine may be folded over the contact area, or collapsed; outer exinal layer (outer 'exoexine') sculptured; sculpture consists of muri, mural folds, or rugulae, muri forming irregular, convolute, or reticulate patterns.

Comparison. The distal sculpture of *Hispanaediscus* (Cramer) Burgess and Richardson is dominantly verrucate or verrucate-murornate, but the contact area as redefined by Burgess and Richardson (1991) is not thin and diaphanous. *Cymbohilates* has a similar structure, but a distal sculpture of grana, coni or spinae. *Artemopyra* has proximal radial muri over part of the contact area, but is distally laevigate. *Segestrespora* Burgess has a similar wall construction with a variably adherent envelope, sometimes sculptured by muri, but forms 'permanent' dyads. Species of *Chelinohilates* may consist of a combination of tetrads, triads, dyads, and hilate monads (paracryptospores), or more usually hilate monads alone (eucryptospores).

Remarks. Where the hilum is collapsed individual specimens of some species may be difficult to distinguish from *Chelinospora*, but the latter has a trilete mark and often a sub-triangular amb. *Chelinohilates erraticus* is found in tetrads, triads, loose dyads but more commonly as dissociated monads.

Chelinohilates erraticus gen. et sp. nov.

Plate 7, figures 5–7; Plate 8, figures 1–7; Plate 9, figures 1–5; Plate 10, figures 1–2

Derivation of name. Latin *erraticus*, wandering, shifting; referring to sinuous and irregular nature of the sculpture and variability of specimens.

Holotype. FM 740 (Pl. 7, figs 6–7) sample SD/2C, slide 3S, co-ord. 065 1074; E.F. no. G38/1; lower Ditton Formation (?*leathensis* vertebrate zone, *micrornatus-newportensis* palynozone), Brown Clee Hill, Shropshire; dyad, length 59 μm, individual units length 32 and 33 μm, width 60 and 62 μm, muri 3–6 μm high, *c*. 1 μm wide.

Diagnosis. A *Chelinohilates* with a distinct proximal hilum surrounded by a narrow subequatorial zone of more or less radial muri; outer exoexine loosely to firmly appressed, equatorially and distally sculptured by flexuous muri forming an irregular reticulate pattern.

Description. Alete, hilate cryptospores with a more or less circular amb, elliptical in equatorial view with a membranous elevated annulus (collar) surrounding a thin (< 1 μm), more or less circular hilum, 30–41 μm wide. The hilum is depressed and often lost. Exine is double-layered with a thick, smooth inner layer and a sculptured, thin outer layer which is absent over the hilum; ?inner exoexine thins abruptly to form the hilum. Outer exoexine $< 1{\cdot}0$ μm thick; inner exinal layer 3·0–3·5 μm thick. Outer exoexine translucent and markedly punctate, sculptured by narrow sinuous and geniculate muri/folds < 1–1·4 μm wide at base and < 1–4 μm high; on a few specimens, the outer exoexine is extended at the equator into a membranous zone 8–10 μm high. Muri taper to pointed, membranous crests, sometimes uneven in distribution; they usually form a reticulum with polygonal, usually rectangular meshes, but which are sometimes not completely enclosed by the muri. The muri sometimes radiate from the distal pole and continue as more or less radial muri. The lumina are irregular, rectangular, or triangular in shape, of variable size on an individual specimen with a shorter axis 2–12 μm and a longer axis 5–22 μm. Muri are 0·5(1·5)2 μm wide and 1(3)4 μm high. Equatorial to subequatorial sculpture consists of more or less radial muri *c*. 1·5 μm thick and up to 4 μm long, sometimes branching. The muri form an annulate zone concentric with the hilum, *c*. 4 μm wide; distally, muri are interconnected by a murus more or less concentric with the hilum.

Dimensions. 24–77 μm, mode 42 μm; 50 specimens measured.

Remarks. This taxon is seen in dyads with the adjacent muri in the annulate zone aligned at right angles to the equator (see Pl. 8, fig. 2) and a closely similar subequatorial collar also occurs in triads and tetrads (Pl. 9, figs 4–5). It is interesting to note that in some of the tetrads and triads there is a major dyad with one or two smaller spores (Pl. 8, fig. 5), which may account for the wide size range of spores encountered for this species. In higher parts of the Ditton Formation *Chelinospora cassicula*, trilete but otherwise closely similar spores, are common.

A subequatorial collar, similar to that described here on *Ch. erraticus*, is seen on Visean tetrads *Sagenotetradites* (Satterthwait and Playford 1986, figs 8–10), a genus that Satterthwait and Playford compared to modern liverwort spores of the order Sphaerocarpales.

Occurrence. ?Upper Raglan Marl and lower St Maughans Formations, Ammons Hill and M50; ?upper Red Marl and lower and lower-middle Ditton formations, Brown Clee Hill. Most common high in the ?upper Red Downton Formation; ?*Apiculiretusispora* sp. E Assemblage Spore Zone, lower and middle *micrornatus-newportensis* palynosubzones (lower and lower middle Gedinnian).

Genus HISPANAEDISCUS (Cramer) Burgess and Richardson, 1991

Type species. *Hispanaediscus verrucatus* (Cramer) Burgess and Richardson.

Hispanaediscus cf. *verrucatus* (Cramer) Burgess and Richardson, 1991

Description. Alete, hilate eucryptospores with a circular to sub-circular amb, originally elliptical in cross section. The hilum is thin and diaphanous, and usually collapsed; it is more or less circular, with (a) narrow compression fold(s) around the subequatorial margin. The hilum may be surrounded by an indistinct curvaturate crassitude. Outside the hilum, the exine is thicker and covered by low, broad, sinuous muri with constricted bands separating verrucate projections. The muri are 2–7 μm wide and 1–2 μm high; elements are < 1 μm apart.

Dimensions. 13–19 μm (three specimens measured); 27–33 μm (ten specimens measured).

Comparison. The verrucate-murornate sculptural elements are larger and more closely spaced, but the sculpture is otherwise similar to that of *H. verrucatus* (Cramer 1966).

Occurrence. Rare; lower Ditton Formation, Brown Clee Hill; lower St Maughans Formation, M50; lower and middle *micrornatus-newportensis* palynosubzones (lower and lower-middle Gedinnian).

BIOLOGICAL CONSIDERATIONS

Two major types of dispersed spore are found in Lower Old Red Sandstone sequences of England, namely cryptospores and miospores. Cryptospores and miospores are useful not only for zonation and correlation of non-marine and marine sediments, but also for the insights they are providing on the nature, distribution, diversity and evolution of early land floras (Fanning 1987; Fanning *et al.* 1988, 1991; Richardson 1992). Spores must have played a vital role in increasing the diversity and distribution, and in the evolution and adaptive radiation of land plants. In spite of these recent advances in knowledge, data on the parent plants of *in situ* spores are limited, but at present indicate that trilete spores and eucryptospores were produced by two different types of plant. The third type of spore (paracryptospore) has some physical characteristics of eucryptospores but may represent a plant hybrid with normally trilete spores. The paracryptospores described above are apparently abnormal spore associations (tetrads, triads, dyads, hilate monads and distorted versions of these) with more or less identical sculpture (in the example described above murornate-reticulate) and are regarded as one morphospecies. Trilete miospores with similar sculpture also occur but these are rare below the lower Ditton Formation. It is possible that all these particular paracryptospores (*Chelinohilates erraticus*) and trilete spores (*Chelinospora cassicula* and *Ch.* sp B) were derived from the same, or related, plants.

Spores with these abnormal configurations (i.e. in tetrads, triads, dyads, and monads) are recorded for hybrids of the water fern *Ceratopteris* (Hickok and Klekowski 1973) and these unusual fossil spores may represent Devonian hybrids. Hickok and Klekowski (1973) recorded that 'hybrids exhibited massive spore abortion and pairing abnormalities at meiotic prophase, characteristic of sterile diploids and triploids.' Such abnormalities were also reported in hybridization studies of other fern genera. However, a small proportion of viable spores was also produced by the hybrids. These authors considered that meiotic adaptations are present in other fern genera and may play a significant role in evolution through hybridization. The presence in hybrids of *Asplenium* of apparently viable triads, dyads and monads, with their varied abnormal chromosome numbers, provides a possible mechanism for increasing plant variability. If the presence at some horizons in the Lower Devonian of abnormal spore associations of identically sculptured tetrad, triad, dyad, and monad spores (paracryptospores) indicates the presence of early Devonian hybrids, then it is possible that hybridization and polyploidy may have played a significant role in the diversification and evolution of early land floras. The main supporting evidence is two-fold. Firstly, the associations of abnormal fossil spores resemble only those described from modern fern hybrids. Secondly, the stratigraphical occurrence of *Chelinohilates erraticus* and trilete spores with similar sculpture (*Chelinospora cassicula* and *Ch.* sp. B). The best sequence is at Brown Clee Hill, where there are three assemblages: the lowest (?upper Ledbury Formation) with *Ch. erraticus* and *Ch.* sp. B; a middle one (lower Ditton Formation 0–60 m, lower and lower-middle *micrornatus-newportensis* palynosubzones) with all three taxa; and an upper one (Ditton Formation *c.* 100–*c.* 250 m) where no abnormal spores of this kind (*Ch. erraticus*) have been found and there are only trilete representatives with this sculpture (*Ch. cassicula*). The occurrence of these taxa in the two main sections in the Hereford and Worcester area follows a similar pattern, but the lowest assemblage (with only *Ch. erraticus* and rare. *Ch.* sp. B) occurs above the base of the St Maughans Formation at Ammons Hill. However, now that paracryptospores have been recognized, further searches are necessary to determine the exact distribution of these taxa. Possibly, therefore, plants of the same or closely related species produced either spores in tetrads, triads and dyads (dividing into hilate monad cryptospores) or loose tetrads separating into patinate/hilate miospores. The paracryptospores show some of the features exhibited by spore tetrads described from the Lower Carboniferous of Australia (Satterthwait and Playford 1986), namely reticulate sculpture and a curvaturate zone of short radial ridges normal to the lines of attachment. However, *Ch. erraticus* includes not only tetrads, but triads, dyads and hilate monads. Further, some of the dyads (Pl. 8, figs 5, 7) show a scar at right angles to the line of attachment of the other two spores. This scar may represent either an aborted third spore, or the contact scar left by a separating third spore. One of these scars shows a probable 'monolete' mark (Pl. 8, fig. 7) a feature found in *Ceratopteris* triads (Hickok and Klekowski 1973). In another triad, two spores in dyad configuration have normal sculpture while the third is smooth and smaller in size. This combination of tetrads, triads, dyads and monads has only been found so far in the upper Ledbury, lower St Maughans and Ditton formations. Commonly, especially in the dyads, the spores are anisomorphic, i.e. one of the spores in the pair is smaller than the other. This tendency is often marked. If the occurrence of tetrads, triads and dyads corresponds with interspecific hybridization followed by normal intraspecific variation, then higher strata might be expected to contain tetrads and trilete miospores only. Apparently reticulate evolution – interspecific hybridization followed by polyploidy – is a recurrent theme in the evolution of some homosporous ferns (Hickok and Klekowski 1973). It is possible that it also occurred in early Devonian plants too but so far triads have been found only in the upper Ledbury Formation and lower Ditton Formation at three localities.

Many Early Devonian true cryptospores (eucryptospores) closely resemble bryophyte spores, especially those of liverworts. The basic structure and sculpture of some hepatic spores are often remarkably similar to these fossils. Several hepatics, for example some species of the genus *Riccia*, have 'permanent' tetrads. Perold (1989) illustrates five out of 48 species of this genus with spiny spores 'permanently adherent in tetrads'. *R. personii* has tetrads with the four spores all in one plane, joined together by smooth bands ('connecting bands') and showing no line of attachment as in *Cheilotetras caledonica* (tetrahedral laevigate, Text-fig. 1A). *R. personii* apparently has an unusual configuration (tetragonal) but one that is also found in the Silurian dispersed spiny spore *Tetraletes variabilis* Cramer. How far this represents convergence because of adaptation to similar life strategies and habitats is unknown, but there is no doubt of the similarities of the unit 'packages' of cryptospores and their sculpture to the spores of some liverworts. There are also differences; as in some *Riccia* species the spores are trilete and have well-developed proximal sculpture, closely similar if not identical to that over the distal surface – a feature not seen in the Silurian or Early Devonian. The closeness of some Lower Devonian cryptospores to those of some hepatics does not necessarily indicate affinity but could indicate a similar life strategy, and also that Early Devonian vegetation included plants with some liverwort characteristics. Other plants of this age had tracheophyte features but on present evidence it cannot be assumed that either plant group had exact modern counterparts. Further, individual plant parts appear to have been undergoing evolution at variable rates. The spores were undergoing rapid evolution while sporangia and their axes appear to exhibit stasis (Fanning *et al.* 1988).

The Downtonian (approximately equivalent to the Přídolí) and lower Gedinnian sedimentary rocks of England and Wales contain a remarkable abundance of eucryptospores, especially monads, but dyads and 'permanent' tetrads are also present and locally abundant.

The similarity of eucryptospores to some modern hepatic spores, and the lack of evidence for their parent plants, apart from sporangia, may indicate that, in the Early Devonian and earlier, there was a group of plants with a poor preservation potential, probably inhabiting ephemerally wet habitats, and with similar environmental strategies to some liverworts. The type of dominant spore unit changed through time. In the Caradoc and Llandovery 'permanent' tetrads, pseudodyads and dyads are dominant and, apart from one possible occurrence, hilate monads are unknown. This contrasts with the Lower Devonian, where 'permanent' tetrads and dyads, 'permanent' tetrads with envelopes, pseudodyads, and loose dyads occur and are occasionally common, especially in the lowest Devonian, but the most abundant and varied cryptospores are monads both hilate and non-hilate. Evidence so far indicates that cryptospores show greatest abundance and variety in the upper Ledbury Formation and equivalent horizons whereas, although 'permanent' tetrads and dyads are still present in the Ditton Formation, the most common cryptospores are hilate monads and pseudodyads. Few good assemblages have been found in higher parts of the Ditton Formation but cryptospores occur in the Senni Beds of South Wales (uppermost Gedinnian and Siegenian, J. B. Richardson and A. Hassan, unpublished data). This general trend from multiple, tightly adherent units to single hilate spores perhaps indicates adaptive response possibly to changing climate or even to the nature and interactions with an evolving plant cover and competition with increasingly large rhyniophytes.

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