

CRYPTOSPORES FROM THE TYPE AREA OF THE CARADOC SERIES IN SOUTHERN BRITAIN

by CHARLES H. WELLMAN

ABSTRACT. Cryptospores, which are interpreted as subaerially dispersed spores derived from early land plants, are described from the type area for the Caradoc Series in southern Britain. They are present in palynomorph assemblages isolated from a number of horizons in a sequence of predominantly nearshore shallow marine deposits. The cryptospores are described systematically; they comprise monads, dyads and tetrads, many of which are enclosed within an envelope which is either laevigate or sculptured. Difficulties associated with interpretation of cryptospore morphology are discussed and associated implications for systematics outlined. The cryptospore assemblages are similar in composition throughout the type Caradoc sequence, suggesting stasis, and are similar to previously described cryptospore assemblages of Ordovician and early Silurian age. Data on Llanvirn (Ordovician)–Llandovery (early Silurian) sporomorph assemblages indicate little variation in composition (taxa and morphotypes) during this interval, until the inception of trilete spores in the late Llandovery when there was an important change in the nature of sporomorph assemblages. The biostratigraphical, palaeophytogeographical and palaeobiological implications of the new data are discussed. Significant findings include confirmation of the presence of unfused dyads (true dyads) in the Caradoc and documentation of the high abundance of dyads in the assemblages.

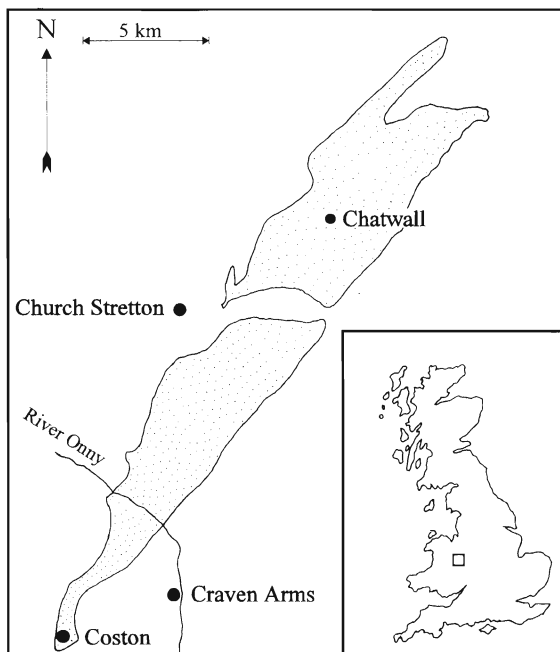
CRYPTOSPORES (*sensu* Richardson *et al.* 1984; Richardson 1988) comprise a group of atypical sporomorphs believed to be subaerially dispersed spores derived from some form of land plant (Gray and Boucot 1971, 1977; Strother and Traverse 1979; Miller and Eames 1982; Vavrdova 1982, 1984, 1988, 1989; Gray 1985, 1991; Johnson 1985; Richardson 1985, 1988; Burgess 1991; Strother 1991; Wellman and Richardson 1993). The earliest reported cryptospores are from the Llanvirn Series (Vavrdova 1984; McClure 1988; Strother *et al.* 1996) and cryptospores are the sole component of Ordovician and earliest Silurian sporomorph assemblages. Miospores (trilete spores) make their inception in the late Llandovery (e.g. Gray 1985; Richardson 1988) but cryptospores often dominate Silurian and earliest Devonian sporomorph assemblages. At some point in the Early Devonian cryptospore abundance diminishes and miospores begin to dominate sporomorph assemblages (Richardson 1992; Wellman 1993a).

It is possible that cryptospores provide the earliest evidence for land plants. However, the nature and affinities of cryptospore-producing plants is controversial. Some authors believe they were derived from embryophytes at a hepatic grade of organization (e.g. Gray 1985 and references therein; Edwards *et al.* 1995) whereas others suggest they were derived from plants that were closer to the green algae (e.g. Strother 1982, 1991; Johnson 1985).

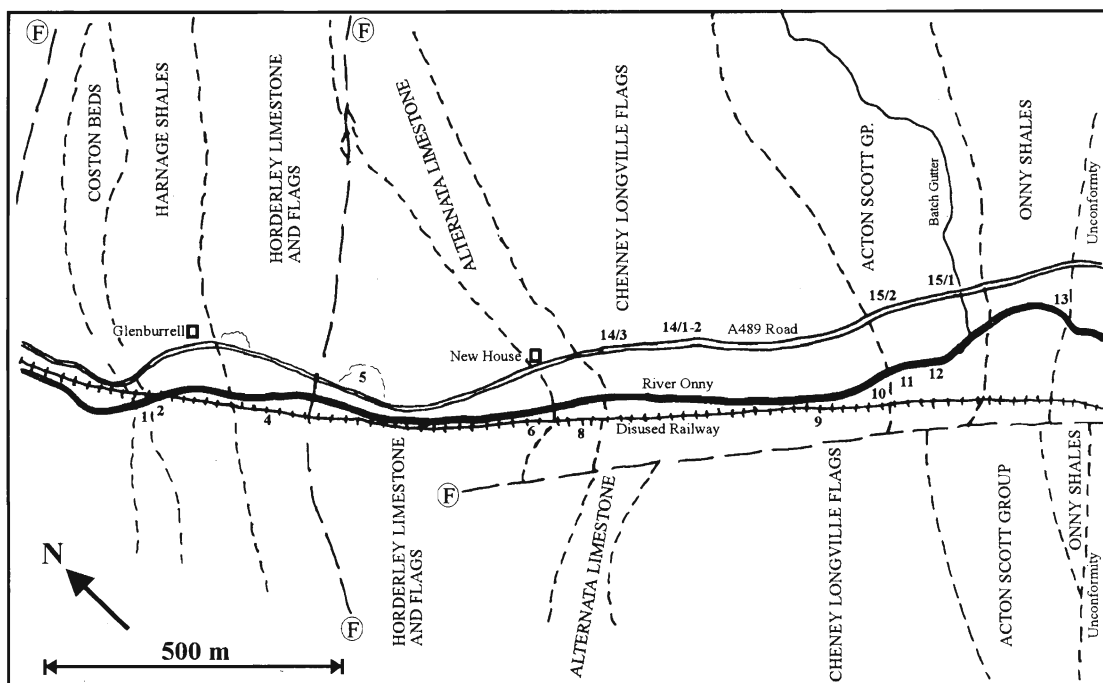
To date, there have been few reports of Ordovician cryptospores. This paper enhances our knowledge of Ordovician cryptospores, shedding light on their morphology and their spatial and temporal distribution. A brief discussion of the palaeobiology of cryptospores is presented in light of the new data.

GEOLOGICAL SETTING AND PREVIOUS PALYNOLOGICAL INVESTIGATION

The type area for the Caradoc in south Shropshire (United Kingdom) comprises two outcrops (Text-fig. 1). The type Caradoc deposits are predominantly nearshore shallow marine in origin and consist largely of calcareous sandstones and siltstones. They contain a rich shelly fauna. Diachronism and lateral facies changes are common. Detailed accounts of the geology and



TEXT-FIG. 1. Location map showing Ordovician outcrop (stippled) in the type area of the Caradoc, Shropshire, UK.



TEXT-FIG. 2. Geological map of the type section of the Caradoc along the River Onny. Sample localities are numbered on the map (see Appendix). Thicker dashed lines marked with an F represent faults. Thinner dashed lines represent geological boundaries.

STAGE	LITHOLOGICAL UNIT	SAMPLE	<i>cf. Strophomorpha</i> sp.	<i>Naked laevigate monads</i>	<i>Dyadospora murusdensa</i>	<i>?Laevolancis divellomedia</i>	<i>Pseudodyadospora laevigata</i>	<i>Tetraedraletes medinensis</i>	<i>Rimosotetras problematica</i>	<i>Cheilotetras</i> sp.	<i>Envelope enclosed laevigate monads</i>	<i>Rugosphaera cerebra</i>	<i>Abditusdyadus laevigatus?</i>	<i>Abditusdyadus histosus?</i>	<i>Segestrespora laevigata</i>	<i>Segestrespora rugosa</i>	<i>Segestrespora</i> sp.A	<i>Velatitetras laevigata</i>	<i>Velatitetras rugulata</i>
ONNIAN	ONNY SHALES	CA13/1-5	?	X	?	X	X	X		X		?			X			X	
ACTONIAN	ACTON SCOTT BEDS	CA12/1		X	X	X	X	X	X		X								
		CA15/2	X	X	X	X	X	X	X	X	X	X			?	?			
		CA15/1		X	X	X	X	X	X	X	X	X	X		X	X		X	X
		CA11/1		X	X	X	X	X	X	X					X	X			
CA11/2		X	X	X	X	X	X	X				X	X		X	X		X	
MARSHBROOKIAN	CHENEY LONGVILLE FLAGS	CA10/1			X	X	X	X				?					?		
		CA9/1			X	X	X	X	X				X			X	X		X
		CA9/2			X	X	X	X	X				X			X	X		
		CA14/1			X	X	X	X	X						X	X			
CA14/2	X	X	X	X	X	X	X							X	X		X	X	
CA14/3	X	X	X	X	X	X	X	X			X	X		X	X		X	X	
LONGVILLIAN	ALTERNATA LIMESTONE	CA8/3		X	X	X	X	X											
		CA8/2		X	X	X	X	X					X			X	X		X
	CA8/1		X	X	X	X	X	X											
	CA6/1		X	X	X	X	X	X		X		X			X			X	X
SOUDLEYAN	HORDERLEY LIMESTONE AND FLAGS	CA5/2			X	X	X	X	X	X		?			X				
		CA5/1			X	X	X	X											
	CA4/1	X	X	X	X	X	X	X	X		X				X	X	X		
	HARNAGIAN	HARNAGE SHALES																	
COSTONIAN	COSTON BEDS	CA2/1			X	X	X	X	X			X	X	X					
		CA1/1																	

TEXT-FIG. 3. Stratigraphy of the type section for the Caradoc illustrating the location of samples and the distribution of cryptospores.

palaeontology of the type Caradoc deposits are provided by Dean (1958, 1960, 1964), Greig *et al.* (1968) and Hurst (1979a, 1979b, 1979c). The history and classification of the Caradoc Series is summarized by Whittington *et al.* (1984), Harland *et al.* (1990) and Fortey *et al.* (1995). A geological map of the type section for the Caradoc in the Onny Valley, of the southern outcrop, is provided in

Text-figure 2. Text-figure 3 illustrates the stratigraphical successions developed in the type Caradoc area.

There are several published palynological investigations of the type Caradoc succession. Jenkins (1967) described the chitinozoans and briefly reported on some of the acritarchs. Subsequently, Turner (1984) provided a full account of the acritarchs. A detailed discussion concerning reworking of acritarchs, which is apparently commonplace, was presented by Turner (1982). Dorning (1986) noted that 'spores of land plant origin' were present in the late Soudleyan of the type Caradoc area but he did not describe or figure the sporomorphs, although he illustrated a permanent tetrad and a dyad. Richardson (1988) provided a preliminary report of cryptospores from the type Caradoc but did not figure material from this area.

SAMPLING AND TECHNIQUES

Samples were collected from a number of horizons at various localities in the type area for the Caradoc (Text-figs 1–3; see Appendix). Recovery was good and preservation excellent in most of the samples. Cryptospores were generally rare but in some samples comprised up to 10 per cent. of the palynomorphs; typical marine palynomorphs such as acritarchs, chitinozoans and scolecodonts comprised the remainder of the assemblages. Thermal maturation was low (Thermal Alteration Index 1–2) and oxidation was unnecessary.

Samples were prepared by standard HCl–HF–HCl acid maceration techniques followed by heavy mineral separation using sodium polytungstate. The organic residue was recovered by sieving using 10 μm mesh. Part of the residue was strew mounted on glass slides, using 'Elvacite' mounting medium, for examination by light microscopy. Additionally, stubs were strew mounted and gold coated for examination by scanning electron microscopy. Some sporomorphs were individually picked and analysed by light microscopy followed by scanning electron microscopy.

CRYPTOSPORE SYSTEMATICS

Comments on cryptospore classification

In this work, cryptospore form-taxa are grouped (classified) under general headings relating to their morphology. Biological affinities and evolutionary relationships of cryptospores are uncertain and one must consider the significance of the form-taxa utilized and the relevance of the artificial, morphology-based, classification in which they are placed, particularly when addressing biological issues. Two relevant matters are discussed below.

Firstly, many of the cryptospores in the assemblages described herein are enclosed within an envelope. However, it has been suggested that taphonomic effects may sometimes destroy envelopes (Strother and Traverse 1979; Gray 1985, 1991; Strother 1991). Therefore, many naked cryptospores may originally have possessed an envelope and consequently the use of presence/absence of an envelope as a diagnostic character, currently used to differentiate at the generic level, may not reflect true biological relationships. However, Johnson (1985) noted the persistence of envelopes and their sculpture following extensive oxidation, even after specimens had begun to disintegrate. Such findings support the use of envelopes and envelope sculpture as morphological characters useful for systematics. Therefore, it was decided to maintain current generic concepts based on presence/absence of an envelope until such time as the nature and significance of the envelope can be clarified.

Secondly, some cryptospore monads, dyads and tetrads exhibit similarities in morphology, particularly those that possess envelopes with identical sculpture. It has been suggested that they may derive from the same plant (Johnson 1985; Richardson 1988, 1992; Strother 1991), either where the plant produced a mixture of morphotypes or the plant produced either monads, dyads or tetrads, perhaps depending on environmental conditions. The number of units (spores) comprising a cryptospore is presently used to differentiate at the generic level. Again, it was decided to maintain present generic concepts until relationships between various cryptospore morphotypes are more fully understood.

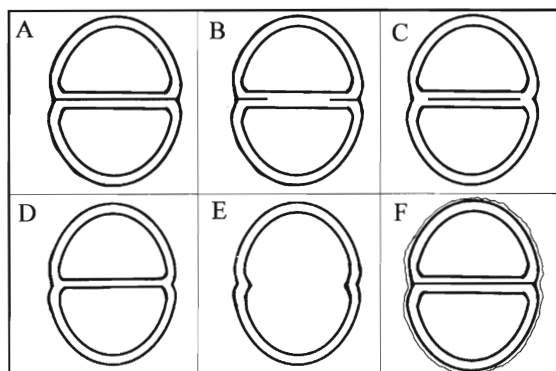
In summary, the present system of cryptospore systematics developed as an effective working classification and one must remember that we are essentially dealing with form-taxa placed in an artificial morphology-based classification. Scientists should carefully consider the use of taxa derived from this classification when they are applied to biological/evolutionary issues. It is anticipated that, as our understanding of cryptospores is enhanced, the cryptospore classification system will be manipulated in order to provide an acceptable working system that reflects biological and evolutionary relationships.

Comments on the nature of cryptospore junctions

Many polyad cryptospores (e.g. permanent tetrads and permanent dyads) were clearly dispersed intact and did not dissociate following dispersal. The nature of the junction between the spores comprising such permanent polyad cryptospores is unclear. Campo and Guinet (1961) recognized two different types of permanent tetrad among extant pollen: calymmate tetrads in which the ectexines of the spores comprising the tetrad exhibit complete fusion; and acalymmate tetrads in which the ectexines of the spores comprising the tetrads exhibit partial, sometimes extremely tenuous, fusion. Blackmore and Crane (1988) noted that among extant pollen permanent tetrads 'the degree of cohesion between tetrad members varies considerably between taxa' and 'although there are clear examples of both calymmate tetrads and acalymmate tetrads, these two conditions intergrade and every intermediate degree of ectexine fusion may be encountered'. In order to describe the nature of fusion between spores comprising permanent polyad cryptospores Wellman and Richardson (1993) introduced the terms fused and unfused, which are used in a similar way to the terms calymmate and acalymmate respectively. Wellman and Richardson introduced the new terminology in order to differentiate between cryptospores, where permanent polyads are probably primitive, and extant pollen, where permanent polyads are almost certainly derived.

The actual structure of fused/unfused permanent polyad cryptospores is unclear and it is possible that, as in extant pollen permanent tetrads, the degree of fusion between spores varies considerably. Probably the best method of determining the nature of junctions in permanent polyad cryptospores is to section them. However, sectioning techniques are difficult and time-consuming. Taylor (1995) initiated such work and his preliminary results demonstrate that in some late Ordovician specimens of *Tetrahedraletes medinensis* Strother and Traverse emend. Wellman and Richardson, 1993 the spores comprising the tetrad exhibit fusion over much of their distal surface, but not at the periphery of the distal surface, thus forming lines of attachment at the surface of the tetrad (i.e. similar to the case illustrated in Text-fig. 4c). However, Taylor admits that the fusion may be diagenetic, a problem that may plague future research of this type.

I believe that the nature of the junctions in polyad cryptospores will prove to be useful systematically and may well have biological significance. Therefore, in following Wellman and Richardson (1994), I recommend that permanent polyad cryptospores are described as fused or unfused. Cryptospores are recognized as fused if a line of attachment (*sensu* Wellman and Richardson 1993) is absent or unfused if a line of attachment is present. The terms fused and unfused often provide an indication of the nature of the junctions in cryptospores. For example, in fused cryptospores such as *Cheilotetras caledonica* Wellman and Richardson, 1993 the junctions between the component spores probably exhibit complete fusion. Also, certain unfused dyads often occur partially dissociated and the junctions between the dyad members probably exhibit very tenuous fusion. However, it must be emphasized that the terms fused and unfused do not always inform us of the nature of a junction as different structures can produce forms with complete or partial fusion (Text-fig. 4). If a line of attachment is present (i.e. unfused) there are two likely scenarios. Either the cryptospore has a complete plane of attachment and the spores are independent, in which case the cryptospore essentially lacks any fusion (Text-fig. 4A), or the plane of attachment is incomplete, in which case the cryptospore in essence exhibits only partial fusion (Text-fig. 4B). If a line of attachment is not present (i.e. fused) there are several likely scenarios. Firstly, the spores may share a common crosswall and no plane of attachment is present, in which case the cryptospore essentially exhibits complete fusion (Text-fig. 4D). Secondly, the crosswall may



TEXT-FIG. 4. Possible structures for fused and unfused cryptospores illustrated using a dyad (see text for details).

have an incompletely developed plane of attachment, in which case the cryptospore in essence exhibits partial fusion (Text-fig. 4c). Thirdly, the cryptospore may lack any fusion with a complete plane of attachment but the corresponding line of attachment is concealed, perhaps by a tight fitting envelope (Text-fig. 4f). Finally, the cryptospore may not have a crosswall (Text-fig. 4e) (Johnson 1985), although I consider this unlikely.

Problems associated with interpretation of cryptospore morphology.

Some of the morphological features used to define certain cryptospore taxa can only be ascertained in well preserved specimens or using evidence derived from chance observation, e.g. broken specimens that reveal features not normally discernible. Routine observation, particularly when dealing with poorly preserved material or a limited number of specimens, may not enable morphological observations which permit designation to such taxa. In this case the use of open nomenclature is essential. Occasionally, however, a serendipitous observation may reveal a diagnostic feature which allows a specimen to be assigned to a particular taxon. Other specimens which are identical in every other respect to this specimen, but do not display the diagnostic feature, can often be assumed also to belong to the taxon in question, although the use of open nomenclature is again advised. When examining cryptospores there are several areas where difficulties can arise regarding interpretation of morphology.

Identifying the number of spores in envelope-enclosed cryptospores. Cryptospore envelopes can obscure the enclosed cryptospore, making it difficult to determine the number of spores contained within the envelope. This causes particular difficulties if the cryptospores are of high thermal maturation and are not fully translucent. Is the cryptospore a monad, dyad or tetrad? Often the shape of the cryptospore provides evidence as to the number of spores, although this is not an infallible test, particularly if the spores comprising the cryptospore are tightly packed. At present the number of units comprising the cryptospore is used as a diagnostic character at the generic level. Liberal use of open nomenclature is advised.

Ascertaining the nature of sculpture in envelope-enclosed cryptospores. It is often difficult to ascertain the nature of sculpture on envelope-enclosed cryptospores. Is the inner body sculptured, the envelope sculptured, or both? This is a particular problem if the cryptospores are poorly preserved or the envelope is closely adherent to the inner body. However, analysis of well preserved material and specimens in which the envelope is partially removed, revealing the nature of the inner body, suggests that Ordovician–early Silurian envelope-enclosed cryptospores usually possess laevigate inner bodies. It is generally only the envelope that bears sculpture.

Identifying fused/unfused junctions. Although the structure of cryptospore junctions is not well understood the nature of the junctions may be an important characteristic. I therefore suggest that

junctions are identified as fused or unfused using absence/presence of a line of attachment as evidence, although one must remember that a number of different structures can produce both fused and unfused junctions. However, in practice it can be difficult to ascertain if a cryptospore junction is fused or unfused (i.e. whether or not a line of attachment is present) when it is not possible to observe the junction adequately, either because the cryptospore is poorly preserved, lies in a difficult orientation, or is enclosed in an envelope that obscures the junction. In the case of naked cryptospores, if they are well preserved and abundant, usually enough specimens are preserved in an orientation conducive to recognition of the presence/absence of a line of attachment. Furthermore, SEM observation can often reveal the presence/absence of this line. However, one must be wary of thin, tightly adherent envelopes which may be mistaken for the spore wall and give the impression that an unfused junction is in fact fused. Consequently, there is only a problem in recognizing the nature of junctions in naked cryptospores if the spores are poorly preserved, or few specimens are available for study and they are preserved in an unsuitable orientation. In the case of envelope enclosed cryptospores, it is often very difficult to ascertain the nature of the junction by light microscope work, particularly if the specimens are poorly preserved, and SEM observation is only of assistance if the envelope is partially removed. Nevertheless, in well preserved specimens or in rare specimens with their envelope partially removed, the nature of the junction may be revealed.

SYSTEMATIC PALAEOLOGY

Terminology outlined by Grebe (1971), Richardson (1988), Wellman and Richardson (1993) and Richardson (1996) is used in the description of the cryptospores. Figured specimens (slides and SEM stubs) are stored in the Palynology Section, Palaeontology Department, The Natural History Museum, London. Light microscope specimen location refers to England Finder coordinates from the Zeiss Photomicroscope III (no. 2562) housed in the same department.

Anteturma CRYPTOSPORITES Richardson *et al.* 1984 (see also Richardson, 1988)

NAKED ALETE CRYPTOSPORE MONADS

Genus STROPHOMORPHA Miller and Eames, 1982

Type species. Strophomorpha ovata Miller and Eames, 1982.

cf. *Strophomorpha* sp.

Plate 3, figures 1–2

Description. Monad elliptical and with thick walls. Naked and without a contact area. Sculpture comprises straight muri which extend between the poles forming a striate pattern. The muri are *c.* 1 μm wide, exhibiting slight variation in width, less than 0.5 μm apart and *c.* 0.75 μm tall. Some of the muri are split.

Dimensions. Length 34 μm , maximum width 22 μm ; one specimen measured.

Remarks. In previously described specimens of *Strophomorpha* the muri are arranged helically (see Miller and Eames 1982; Burgess 1991).

NAKED LAEVIGATE MONADS

Plate 3, figures 3–4

Description. Circular to sub-circular monads. Walls > 1 μm thick and rarely folded. Naked and without contact features. Spores entirely laevigate.

Dimensions. 22(29)60 μm ; 29 specimens measured.

Remarks. Similar monads, only enclosed within a laevigate envelope, are reported (Pl. 3, figs 18–20).

It is possible that some of the naked forms were originally enclosed in an envelope but the envelope has been removed.

NAKED CRYPTOSPORE UNFUSED DYADS (TRUE DYADS)

Genus *DYADOSPORA* Strother and Traverse, 1979 emend. Burgess and Richardson, 1991

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

Remarks. This genus accommodates naked, laevigate, unfused dyads. In this work, dyads are only included in *Dyadospora* if a clearly perceptible line of attachment is present.

Dyadospora murusdensa Strother and Traverse, 1979 emend. Burgess and Richardson, 1991

Plate 1, figures 16–20, 25; Plate 2, figures 11–16, 20

Dimensions. Dyad length 23(30)33 μm , dyad width 22(25)30 μm ; 45 specimens measured.

Comparison. The specimens from the type Caradoc are essentially identical to previously described specimens of this long ranging and widely reported taxon. The dyads generally have thick walls and are placed with the thick-walled species *D. murusdensa* rather than the thin-walled species *D. murusattenuata*.

Remarks. The type Caradoc specimens are usually tightly adherent and are only very rarely observed in a state of partial dissociation. In the latter case, it is unclear if dissociation is due to the spores naturally separating or if they have been physically forced apart (see discussion following description of *L. divellomedia*?).

EXPLANATION OF PLATE 1

Figs 1–3. *Cheilotetras* sp.; A489 roadcut exposure, River Onny Valley; Acton Scott Beds. 1, FM811 (slide CA15/1/D, E.F. no. S44). 2–3, FM812 (slide CA15/1/C, E.F. no. N55/1); two planes of focus are illustrated revealing the fused nature of the tetrad.

Figs 4–5. *Rimosotetras problematica* Burgess, 1991; A489 roadcut exposure, River Onny Valley; Acton Scott Beds. 4, FM813 (slide CA15/1/B, E.F. no. D53). 5, FM814 (slide CA15/1/A, E.F. no. O41/3).

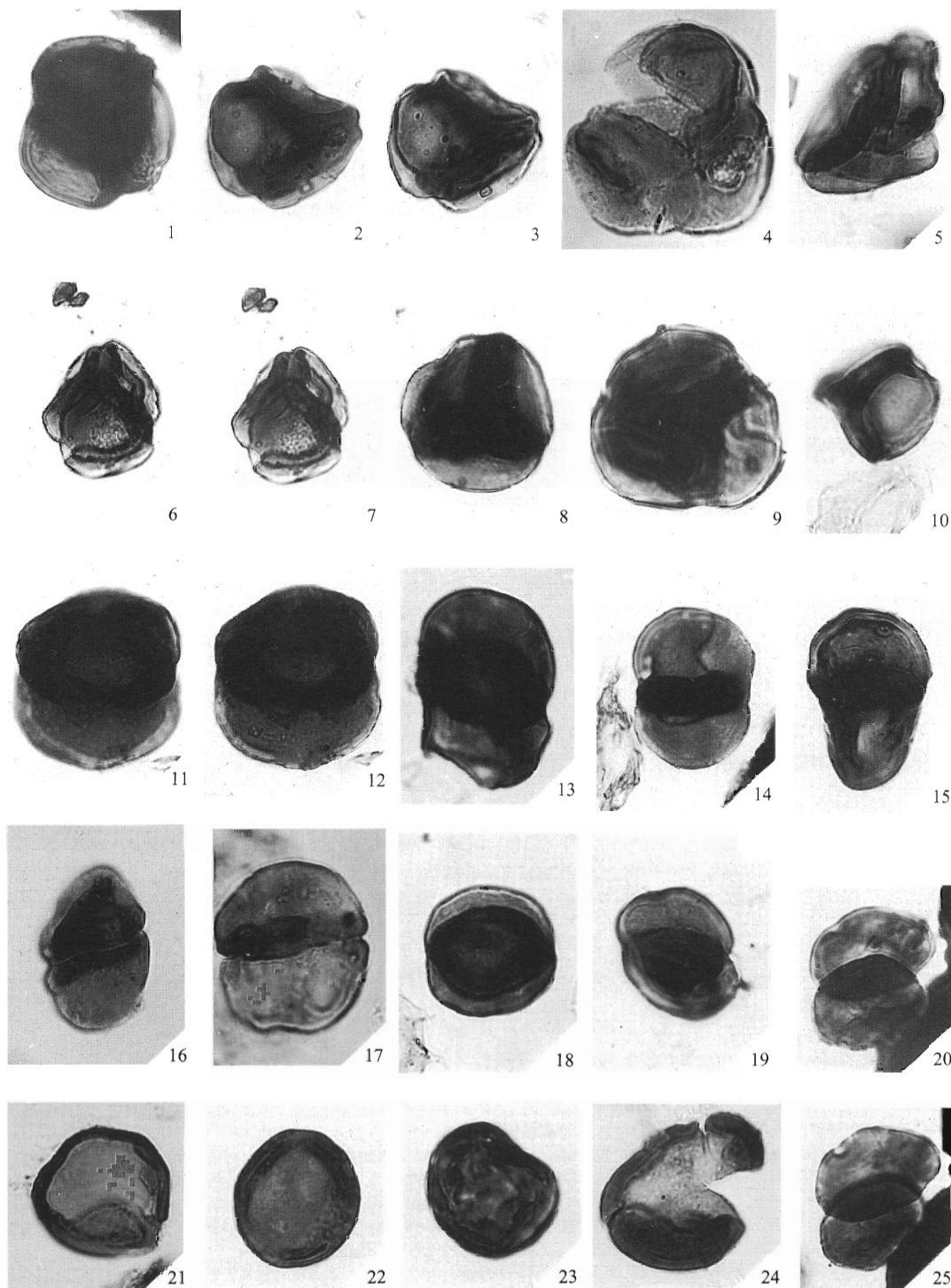
Figs 6–10. *Tetrahedraletes medinensis* Strother and Traverse emend. Wellman and Richardson, 1993; A489 roadcut exposure, River Onny Valley; Acton Scott Beds. 6–7, FM815 (slide CA15/1/A, E.F. no. F37); two planes of focus are illustrated revealing the unfused nature of the tetrad. 8, FM816 (slide CA15/1/A, E.F. no. H61/2). 9, FM817 (slide CA15/1/B, E.F. no. T35/1). 10, FM818 (slide CA15/1/C, E.F. no. M57).

Figs 11–15. *Pseudodyadospora laevigata* Johnson, 1985. 11–12, FM819 (slide CA4/1/A, E.F. no. C55/3); quarry in section along the River Onny; Horderley Sandstones and Flags; two planes of focus are illustrated revealing the fused nature of the dyad. 13, FM820 (slide CA15/1/B, E.F. no. H42/3); A489 roadcut exposure, River Onny Valley; Acton Scott Beds. 14, FM821 (slide CA5/1/A, E.F. no. K38/3); quarry beside A489, River Onny Valley; Horderley Sandstones and Flags. 15, FM822 (slide CA15/1/C, E.F. no. V41/4); A489 roadcut exposure, River Onny Valley; Acton Scott Beds.

Figs 16–20, 25. *Dyadospora murusdensa* Strother and Traverse emend. Burgess and Richardson, 1991. 16–17, 19–20, 25, A489 roadcut exposure, River Onny Valley; Acton Scott Beds. 16, FM823 (slide CA15/1/C, E.F. no. T56/1). 17, FM824 (slide CA15/1/A, E.F. no. C61/4). 19, FM826 (slide CA15/1/A, E.F. no. G60/3). 20, 25, FM827 (slide CA15/1/A, E.F. no. Q41); two planes of focus are illustrated revealing the unfused nature of the dyad. 18, FM825 (slide CA4/1/A, E.F. no. F34/4); quarry in section along the River Onny; Horderley Sandstones and Flags.

Figs 21–24. *Laevolancis divellomedia* (Chibrikova) Burgess and Richardson, 1991? 21, FM828 (slide CA15/1/A, E.F. no. Q40/2); A489 roadcut exposure, River Onny Valley; Acton Scott Beds. 22, FM829 (slide CA4/1/A, E.F. no. 066/4); quarry in section along the River Onny; Horderley Sandstones and Flags. 23, FM830 (slide CA15/1/C, E.F. no. H52); A489 roadcut exposure, River Onny Valley; Acton Scott Beds. 24, FM831 (slide CA15/1/A, E.F. no. H57/1); A489 roadcut exposure, River Onny Valley; Acton Scott Beds.

All $\times 1000$.



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 21–24; Plate 2, figures 17–19

Description. Amb circular to sub-circular. Equatorial to subequatorial crassitude $1(1.5)4\ \mu\text{m}$ wide delimits a circular to sub-circular hilum. Hilum thinner than distal exine. Hilum nearly always collapsed and torn, or missing. Distal exine rigid and usually unfolded. Spores entirely laevigate.

Dimensions. $18(25)33\ \mu\text{m}$; 39 specimens measured.

Comparison. Specimens assigned to *L. divellomedia*? from the type Caradoc appears more-or-less identical to previously described specimens of *L. divellomedia* except in that the hilum is usually torn or missing. They differ from *Ambitisporites? vavrdovii* Richardson, 1988 which has irregular trilete cracks on the proximal surface.

Remarks. The vast majority of specimens of *L. divellomedia*? from the type Caradoc have a torn or missing proximal hilum. It is likely that these specimens are similar to *A.? vavrdovii* in that they both represent spores which have been physically separated from permanent polyad cryptospores. However, rare specimens of *L. divellomedia*? from the type Caradoc have a complete proximal hilum. These specimens may represent the products of natural dissociation of polyad cryptospores, probably loose dyads or loose tetrads such as *Rimosotetras problematica*, and thus represent true *L. divellomedia*.

NAKED UNFUSED CRYPTOSPORE TETRADS

Genus *TETRAHEDRALETES* Strother and Traverse, 1979 emend. Wellman and Richardson, 1993

Type species. Tetrahedraletes medinensis Strother and Traverse, 1979.

Remarks. This genus accommodates naked, laevigate, unfused permanent tetrads. In this work tetrads are only included in *Tetrahedraletes* if a clearly perceptible line of attachment is present.

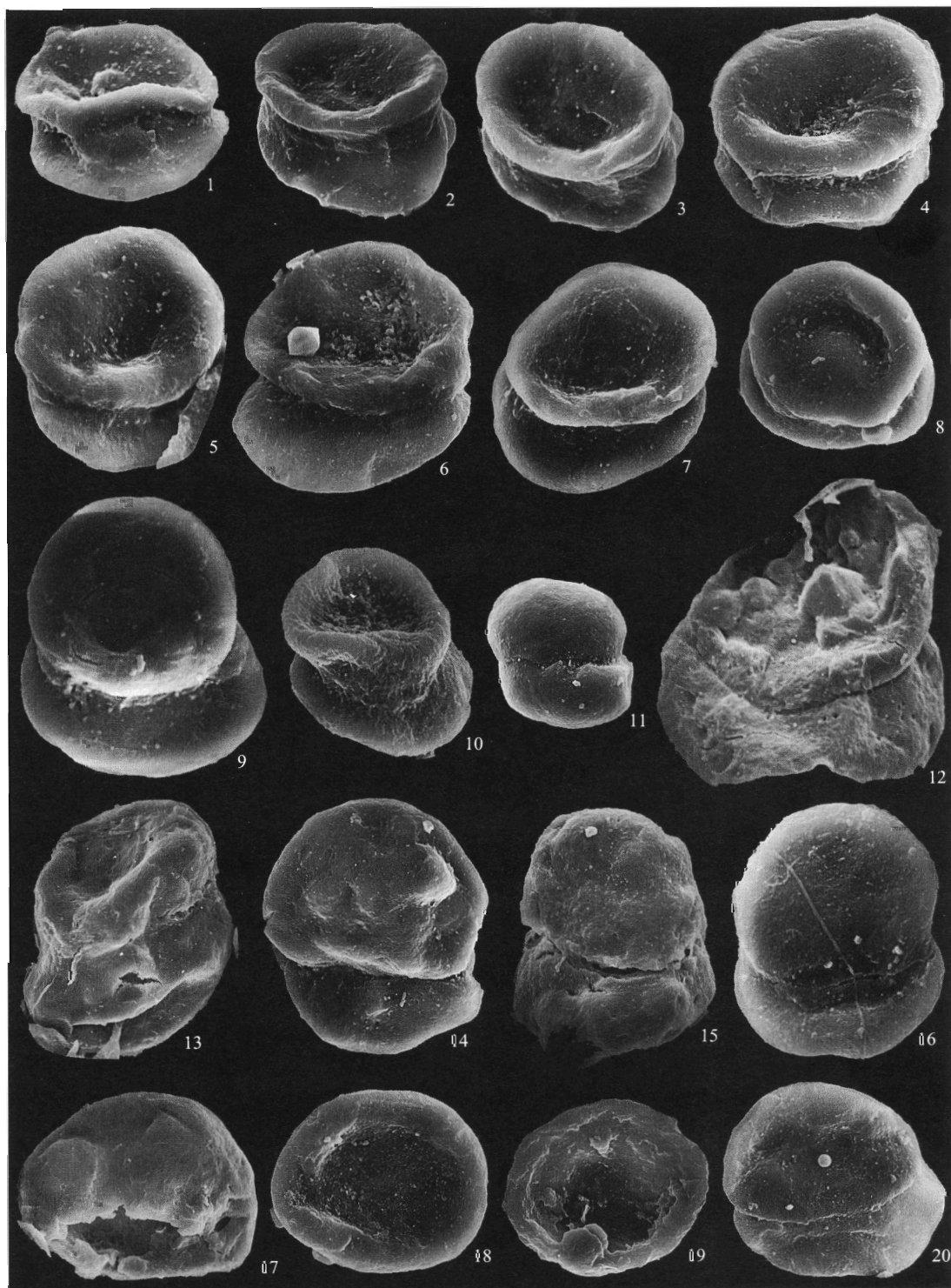
EXPLANATION OF PLATE 2

Figs 1–10. *Pseudodyadospora laevigata* Johnson, 1985. 1, 10, (Stub CW119) sample CA15/1; A489 roadcut exposure, River Onny Valley; Acton Scott Beds. 2–7, 9, sample CA9/1; river exposure, River Onny Valley; Cheney Longville Flags. 2–4, 6, Stub CW125. 5, 7, 9, Stub CW126. 8, (Stub CW120) sample CA15/1; A489 roadcut exposure, River Onny Valley; Acton Scott Beds.

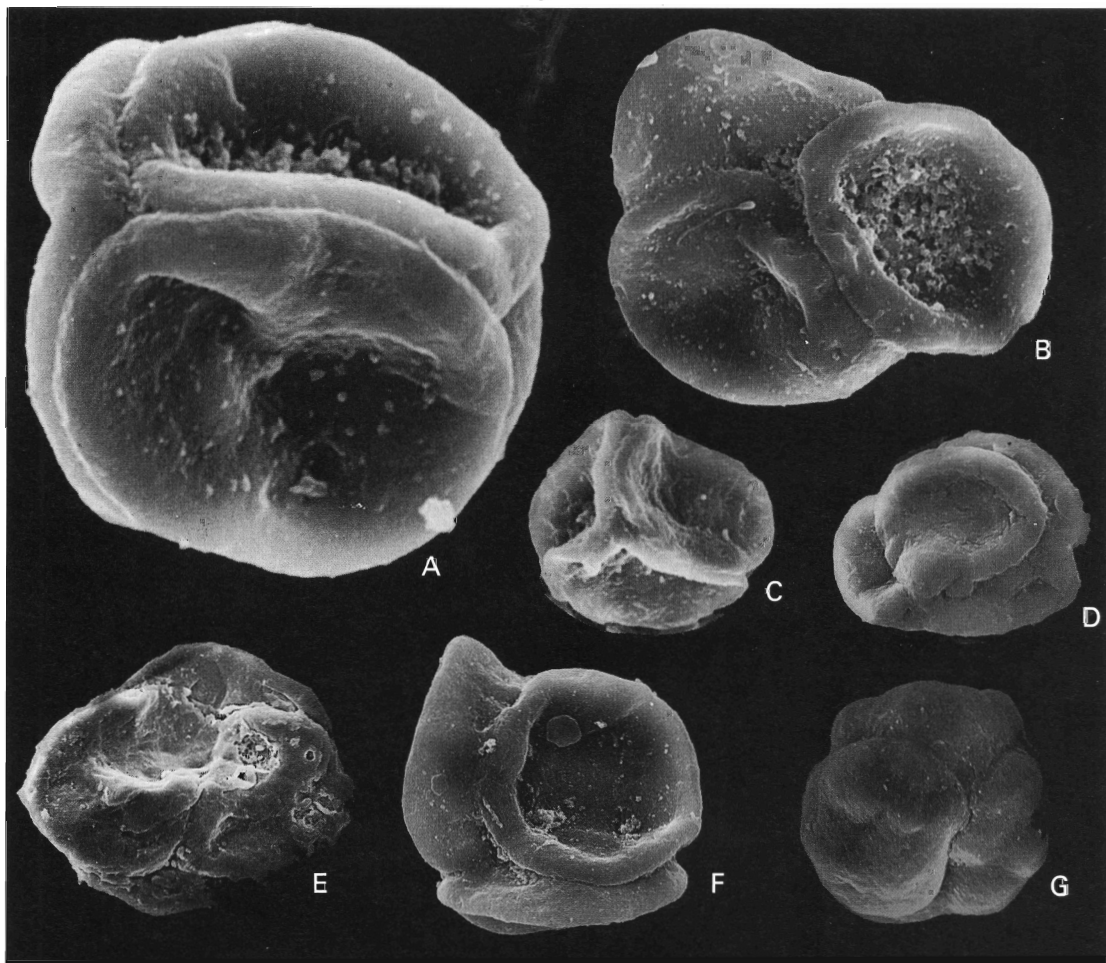
Figs 11–16, 20. *Dyadospora murusdensa* Strother and Traverse emend. Burgess and Richardson, 1991. 11, 14, (Stub CW125) sample CA9/1; river exposure, River Onny Valley; Cheney Longville Flags. 12–13, 15, (Stub CW121) sample CA15/1, A489 roadcut exposure, River Onny Valley; Acton Scott Beds. 16, (Stub CW120) sample CA15/1; A489 roadcut exposure, River Onny Valley; Acton Scott Beds. 20, (Stub CW126) sample CA9/1; river exposure, River Onny Valley; Cheney Longville Flags.

Figs 17–19 *Laevolancis divellomedia* (Chibrikova) Burgess and Richardson, 1991? 17, (Stub CW122) sample CA15/2; A489 roadcut exposure, River Onny Valley; Acton Scott Beds. 18–19, (Stub CW125) sample CA9/1; river exposure, River Onny Valley; Cheney Longville Flags.

All $\times 1500$.



WELLMAN, Caradoc cryptospores



TEXT-FIG. 5. Specimens of *Tetrahedraletes medinensis* Strother and Traverse emend. Wellman and Richardson, 1993. A, (Stub CW119) sample CA15/1; A489 roadcut exposure, River Onny Valley; Acton Scott Beds. B, (Stub CW125) sample CA9/1; river exposure, River Onny Valley; Cheney Longville Flags. C, (Stub CW126) sample CA9/1; river exposure, River Onny Valley; Cheney Longville Flags. D, (Stub CW122) sample CA15/2; A489 roadcut exposure, River Onny Valley; Acton Scott Beds. E, (Stub CW122) sample CA15/2; A489 roadcut exposure, River Onny Valley; Acton Scott Beds. F, (Stub CW125) sample CA9/1, river exposure, River Onny Valley; Cheney Longville Flags. G, (Stub CW137) sample CA9/1, river exposure, River Onny Valley; Cheney Longville Flags. All $\times 1500$, except A which is $\times 4000$.

Tetrahedraletes medinensis Strother and Traverse, 1979 emend. Wellman and Richardson, 1993

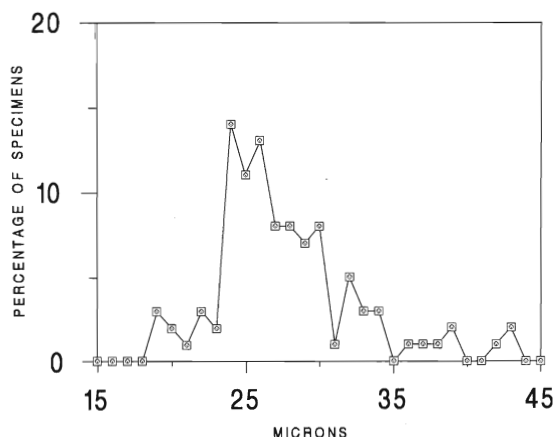
Plate 1, figures 6–10; Text-figure 5

Dimensions. 19(28)43 μm ; 100 specimens measured

Comparison. The specimens reported herein are typical examples of the widely reported taxon *T. medinensis*. Burgess (1991) erected two varieties of *T. medinensis* distinguished on tetrad size: var. *medinensis* with diameter greater than 35 μm and var. *parvus* with diameter less than 35 μm . If this size-based distinction is employed the majority of the type Caradoc specimens can be accommodated in var. *parvus*. *Tetrahedraletes grayae* Strother, 1991 is thin-walled and lacks equatorial crassitudes, whereas the tetrads from the type Caradoc are thick-walled and usually have thickenings (crassitudes) at the margins of the individual units.

Remarks. Gray (1988) measured average tetrad size in sporomorph assemblages of Late Ordovician and early Silurian age. She noted an increase in average tetrad size with time, finding that Ordovician sporomorph assemblages have average tetrad size less than 30 μm with average tetrad size increasing to nearly 50 μm by the mid-late early Silurian. The type Caradoc specimens have an average tetrad size of 28 μm (see Text-fig. 6) and therefore conform with Gray's data.

TEXT-FIG. 6. Size frequency distribution of 100 *Tetrahedraletes medinensis* from sample CA15.



Genus RIMOSOTETRAS Burgess, 1991

Type species. *Rimosotetras problematica* Burgess, 1991.

Rimosotetras problematica Burgess, 1991

Plate 1, figures 4–5

Dimensions. 27(30)38 μm ; ten specimens measured.

Comparison. These specimens are identical to *R. problematica*, described from the Llandovery of southern Britain (Burgess 1991) and the Wenlock of Scotland (Wellman 1993b; Wellman and Richardson 1993). They are similar to *Tetrahedraletes medinensis* but are loosely attached, often in a state of apparent partial dissociation.

Remarks. It is possible that some of these tetrads naturally dissociated producing alele spores. Some of the spores described as *Laevolancis divellomedia*? may derive from this source.

NAKED FUSED CRYPTOSPORE DYADS (PSEUDODYADS)

Genus PSEUDODYADOSPORA Johnson, 1985

Type species. *Pseudodyadospora laevigata* Johnson, 1985.

Remarks. This genus accommodates naked, laevigate, fused dyads. In this work, spores are included in *Pseudodyadospora* if they lack a clearly perceptible line of attachment.

Pseudodyadospora laevigata Johnson, 1985

Plate 1, figures 11–15; Plate 2, figures 1–10

Dimensions. Dyad length 22(30)42 μm , dyad width 21(25)40 μm ; 48 specimens measured.

Comparison. *P. laevigata* from the type Caradoc is essentially identical to previously described specimens of this long ranging and widely reported taxon. Sporomorphs assigned to *Dyadospora murusdensa* are clearly unfused with a discernible line of attachment at the junction between the two spores.

Remarks. Many of the specimens of *P. laevigata* have their distal surfaces invaginated. This is probably a result of collapse. Specimens of *Dyadospora murusdensa* occasionally exhibit this feature but much less commonly.

NAKED FUSED CRYPTOSPORE TETRADS

Genus CHEILOTTETRAS Wellman and Richardson, 1993

Type species. *Cheilotetras caledonica* Wellman and Richardson, 1993

Remarks. This genus accommodates naked, laevigate, fused permanent tetrads. In this work, tetrads are included in *Cheilotetras* only if they lack a clearly perceptible line of attachment.

Cheilotetras sp.

Plate 1, figures 1–3

Description. Permanent tetrahedral tetrads comprising subtriangular to subrounded spores, usually with invaginated distal walls. The spores are joined at thickened equatorial crassitudes. The junctions between spores are fused with no line of attachment. Spores entirely laevigate.

Dimensions. 21(28)39 μm ; ten specimens measured

Comparison. In *Cheilotetras caledonica* Wellman and Richardson, 1993 the equatorial crassitudes of the individual spores are drawn out into distinct extended flanges. *Tetrahedraletes medinensis* has discernible lines of attachment between the spores.

ENVELOPE ENCLOSED CRYPTOSPORES

Genus RUGOSPHAERA Strother and Traverse, 1979 emend. Strother, 1991

Type species. *Rugosphaera tuscarorensis* Strother and Traverse, 1979.

Rugosphaera cerebra Miller and Eames, 1982

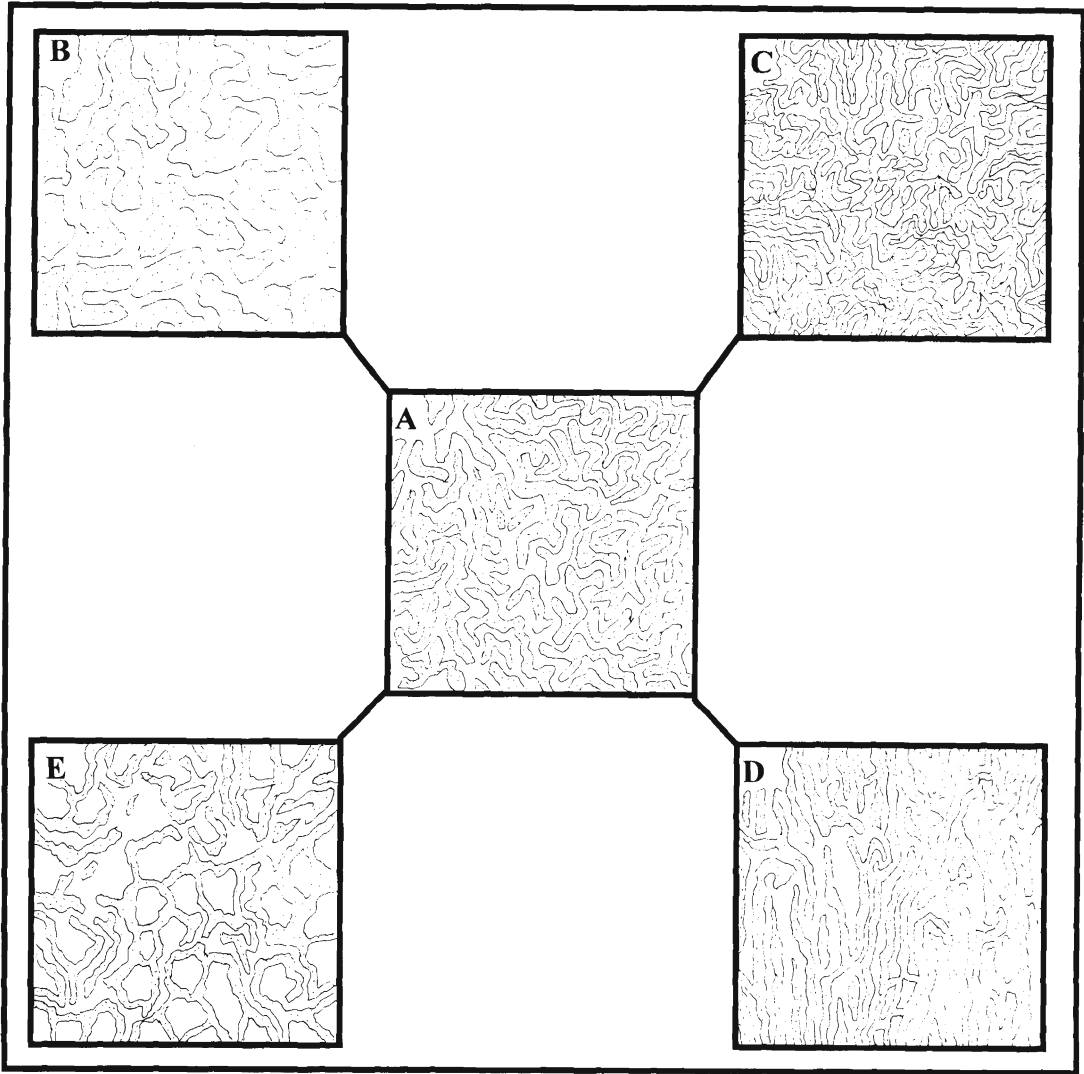
Plate 4, figures 16–20; Plate 5, figures 8–9, 11–12

- 1982 *Rugosphaera?* *cerebra* Miller and Eames, p. 249, pl. 5, fig. 4; pl. 6, figs 10–12.
- ?1985 'Rugose spore (?)'; Duffield, p. 1007, fig. 3(7).
- 1988 *Rugosphaera?* *cerebra* Miller and Eames; Richardson, p. 95.
- 1991 *Rugosphaera* cf. *R.?* *cerebra* Miller and Eames; Burgess, p. 593, pl. 2, figs 11–12.

Comparison. *Rugosphaera tuscarorensis* Strother and Traverse, 1979 is sculptured with rugulae which are 1.5 μm wide, and are more widely spaced and less sinuous than the muri in *R. cerebra*. Additionally, the description of *R. tuscarorensis* suggests that the inner body is sculptured and is enclosed within a tight fitting, laevigate, membranous envelope.

Remarks. Miller and Eames (1982) questionably assigned *R. cerebra* to *Rugosphaera*. However, in the light of the emendation of this genus by Strother (1991), *R. cerebra* can now be accommodated in *Rugosphaera*. The envelopes of *Rugosphaera cerebra*, *Segestrespora* (*Pseudodyadospora*) *rugosa* and *Velatitetras rugulata* bear identical sculpture. It is evident from examination of specimens with broken envelopes that the inner body is laevigate and it is the envelope that is sculptured. SEM images (e.g. Pl. 5, fig. 12) confirm that the sculpture represents true sculpture and is not an effect

of folding or degradation in the envelope. In general the envelope is relatively thick (c. $0.75\ \mu\text{m}$ thick without the sculpture) and the sculpture is in the form of closely spaced muri which form a murornate ornament. The muri are generally $0.5\text{--}1.5\ \mu\text{m}$ wide, up to $1.5\ \mu\text{m}$ tall and are usually less than $0.5\ \mu\text{m}$ apart. However, there is considerable variation in the appearance of the sculpture forming a set of morphological gradational series (Text-fig. 7). In the most common form of



TEXT-FIG. 7. Sculptural variation exhibited by *Rugosphaera cerebra*, *Segestrespora rugosa* and *Velatitetras rugulata* (each square represents $30\ \mu\text{m}$ square). A, standard sculpture. B, with broad muri verging on rugulae. C, narrow muri. D, muri partially aligned. E, muri forming partial reticulum.

sculpture the muri are tightly packed, sinuous with angular (geniculate) bends and often dichotomize. However, in some specimens the sculpture comprises muri which are relatively straight, in others the muri are broader and resemble verrucae or rugulae, and in other specimens the muri form a partial reticulum.

LAEVIGATE MONADS ENCLOSED WITHIN A LAEVIGATE ENVELOPE

Plate 3, figures 18–20

Description. Circular to sub-circular thick-walled monads. No contact features. Spores entirely laevigate. Enclosed within a tight fitting or relatively loose laevigate envelope. The envelope is thin ($< 0.75 \mu\text{m}$ thick) and usually folded.

Dimensions. 22(29)35 μm ; six specimens measured.

Remarks. It is possible that some of the naked alele monads reported, which are identical except for the absence of an envelope, represent comparable spores where the envelope has not been preserved.

Genus *ABDITUSDYADUS* Wellman and Richardson, 1996

Type species. *Abditusdyadus histosus* Wellman and Richardson, 1996.

Remarks. This genus accommodates envelope-enclosed unfused dyads (true dyads). In this work, spores are only placed with *Abditusdyadus* if a line of attachment is clearly perceptible.

Abditusdyadus laevigatus Wellman and Richardson, 1996?

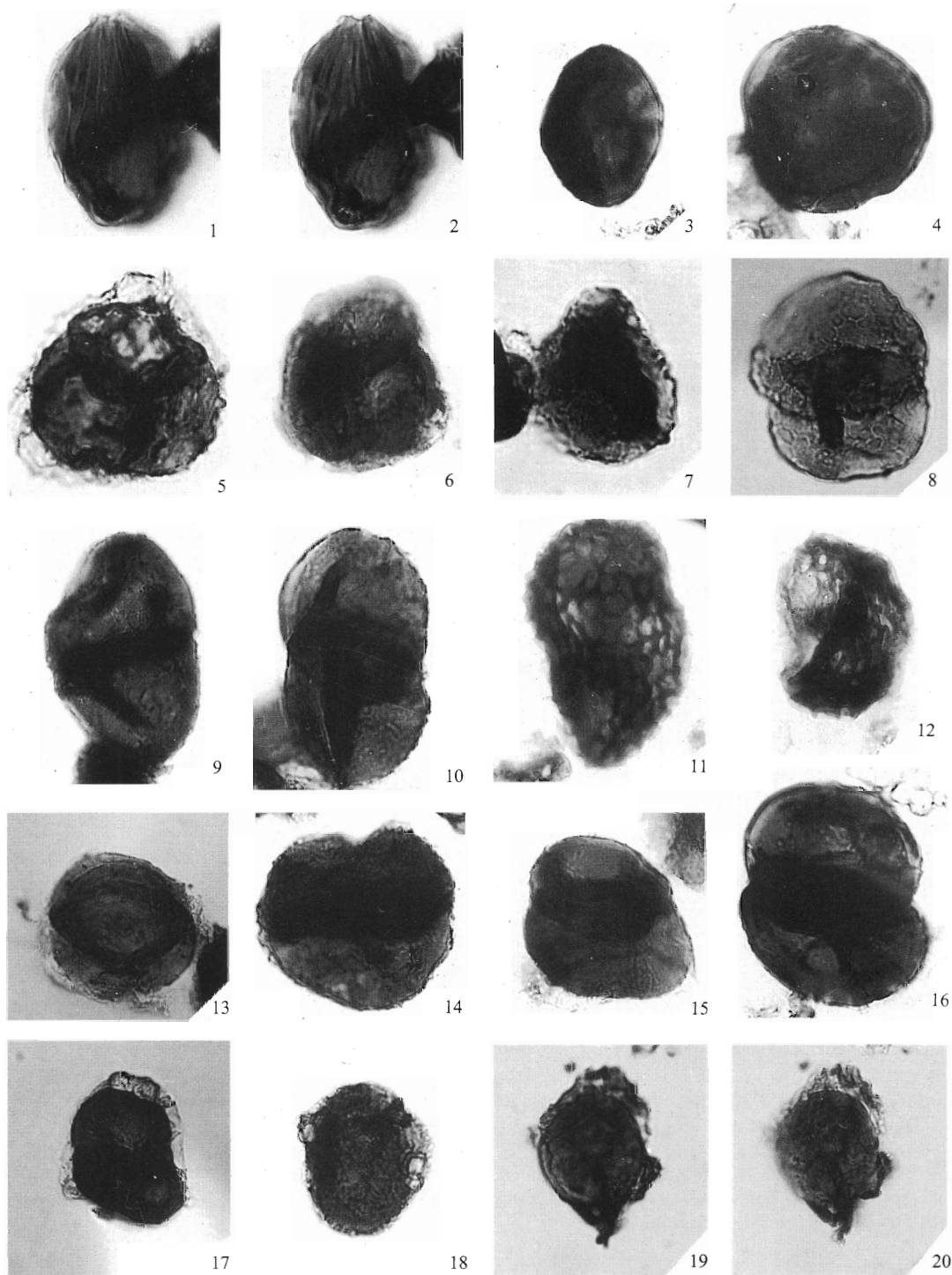
Plate 3, figures 9, 13

Dimensions. Dyad length 26(35)42 μm , dyad width 24(28)32 μm ; five specimens measured.

Comparison. *A. laevigatus* reported by Wellman and Richardson (1996) is larger (73(79)89 μm long). *Segestrespora laevigata* Burgess, 1991 comprises fused dyads enclosed within a laevigate envelope.

EXPLANATION OF PLATE 3

- Figs 1–2. *Strophomorpha* sp.; FM832 (slide CA15/1/C, E.F. no. V58/1); A489 roadcut exposure, River Onny Valley; Acton Scott Beds; the two planes of focus illustrated demonstrate the nature of the ornament.
- Figs 3–4. Naked alele cryptospore monads. Quarry in section along the River Onny; Horderley Sandstones and Flags. 3, FM833 (slide CA4/1/A, E.F. no. U62/1). 4, FM834 (slide CA4/1/A, E.F. no. J57).
- Figs 5–7. *Velatitetras laevigata* Burgess, 1991; A489 roadcut exposure, River Onny Valley; Acton Scott Beds. 5, FM835 (slide CA15/1/C, E.F. no. M42). 6, FM836 (slide CA15/1/A, E.F. no. S53). 7, FM837 (slide CA15/1/C, E.F. no. E35/2).
- Fig. 8. *Abditusdyadus histosus* Wellman and Richardson, 1996?; FM838 (slide CA2/1/A, E.F. no. J48/1); quarry in section along the River Onny; Harnage Shales.
- Figs 9, 13. *Abditusdyadus laevigatus* Wellman and Richardson?, 1996. 9, FM839 (slide CA4/1/A, E.F. no. G49); quarry in section along the River Onny; Horderley Sandstones and Flags. 13, FM840 (slide CA15/1/D, E.F. no. 045/4); A489 roadcut exposure, River Onny Valley; Acton Scott Beds.
- Figs 11–12. *Segestrespora*? sp. A; quarry in section along the River Onny; Horderley Sandstones and Flags. 11, FM841 (slide CA4/1/A, E.F. no. W53). 12, FM842 (slide CA4/1/A, E.F. no. S60/4).
- Figs 10, 14–17. *Segestrespora laevigata* Burgess, 1991. 10, 14, 16–17, quarry in section along the River Onny; Horderley Sandstones and Flags. 10, FM843 (slide CA4/1/A, E.F. no. N66/1). 14, FM844 (slide CA4/1/A, E.F. no. G40). 16, FM846 (slide CA4/1/A, E.F. no. K42). 17, FM847 (slide CA4/1/A, E.F. no. C58). 15, FM845 (slide CA4/1/A, E.F. no. U54/1); A489 roadcut exposure, River Onny Valley; Acton Scott Beds.
- Figs 18–20. Alele cryptospore monads enclosed in a laevigate envelope. 18, FM848 (slide CA4/1/A, E.F. no. S44/1); quarry in section along the River Onny; Horderley Sandstones and Flags. 19–20, FM849 (slide CA15/1/A, E.F. no. N48); A489 roadcut exposure, River Onny Valley; Acton Scott Beds; the two planes of focus illustrated reveal the surface ornament of the envelope and inner body.
- All $\times 1000$, except where stated otherwise.



Abditudyadus histosus Wellman and Richardson, 1996?

Plate 3, figure 8

Dimensions. 34 μm long by 28 μm wide and 36 μm long by 24 μm wide; two specimens measured.

Remarks. The specimens from the type Caradoc are similar to those described by Wellman and Richardson (1996) but are smaller (34–36 μm long compared with 62(73)83 μm).

Genus *SEGESTRESPORA* Burgess, 1991

Type species. *Segestrespora (Dyadospora) membranifera* (Johnson) Burgess, 1991.

Remarks. This genus accommodates envelope-enclosed fused dyads (pseudodyads). In this work, spores are placed with *Segestrespora* if a line of attachment is not discernible.

Segestrespora laevigata Burgess, 1991

Plate 3, figures 10, 14–17

Dimensions. Dyad length 21(32)44 μm , dyad width 21(26)38 μm ; 34 specimens measured.

Remarks. These spores are more-or-less identical to those described by Burgess (1991). Sometimes the envelope is folded, presenting an appearance of haphazardly arranged muri.

Segestrespora (Pseudodyadospora) rugosa (Johnson) Burgess, 1991

Plate 4, figures 5–15; Plate 5, figures 1–7, 10

1988 *Pseudodyadospora* sp. C Richardson, p. 95.

Dimensions. Dyad length 24(34)48 μm , dyad width 20(26)33 μm ; 61 specimens measured.

Remarks. These spores are more-or-less identical to *Segestrespora (Pseudodyadospora) rugosa* as described by Burgess (1991). The envelopes of *S. rugosa*, *Rugosphaera cerebra* and *Velatitetras rugulata* bear identical sculpture.

Segestrespora? sp. A

Plate 3, figures 11–12

Description. Probable dyad, longer than wide, enclosed within a relatively thick envelope. Envelope with a reticulate ornament. Reticulum is regular and comprises muri which are *c.* 1 μm tall and 1 μm wide. Lumina equidimensional and rounded-subpolygonal, 1.5–2.5 μm in maximum diameter.

Dimensions. Dyad length 34(38)42 μm , dyad width 26(29)30 μm ; three specimens measured.

Comparison. *Abditudyadus histosus?* is similar but has a thinner envelope with a reticulate ornament consisting of narrower muri (< 0.75 μm) which form lumina which are, on average, slightly larger than those in *Segestrespora?* sp. A. *Segestrespora (Dyadospora) membranifera* (Johnson) Burgess, 1991 has less prominent muri which do not form a reticulum.

Remarks. The thickness of the envelope prevents reliable observation of the enclosed spores. It is unclear if they are fused or unfused and it is possible that in some specimens more than two spores may be present, although the elongate shape of the spores suggests that they comprise dyads.

Genus VELATITETRAS Burgess, 1991

Type species. Velatitetras laevigata Burgess, 1991.

Remarks. This genus accommodates envelope-enclosed permanent tetrads which are either fused or unfused (Burgess 1991). Current taxonomic practice encourages the use of separate genera for fused and unfused cryptospores. There is a case for creating separate genera for envelope-enclosed fused and unfused tetrads because, in well preserved material, or where the specimens are preserved with part of the envelope removed, the nature of the junctions may be revealed. For example, Gray (1985, pl. 2, figs 21–22) illustrated a permanent tetrad enclosed within a laevigate envelope where the envelope is partially removed, revealing a probable line of attachment, suggesting that the tetrad is unfused. However, too few specimens were available from this study to justify emending *Velatitetras* and creating a new genus, and it was decided to place all envelope enclosed tetrads with *Velatitetras*.

Velatitetras laevigata Burgess, 1991

Plate 3, figures 5–7

Dimensions. 25(35)53 μm ; 22 specimens measured.

Comparison. The type Caradoc spores are essentially identical to those described by Burgess (1991).

Remarks. In the cases where it is possible to ascertain the nature of the tetrads they appear to be unfused. In some specimens the envelope is folded and the folds resemble haphazardly arranged muri.

Velatitetras rugulata Burgess, 1991

Plate 4, figures 1–4

1988 *Nodospora* sp. A Richardson. p. 94.

Dimensions. 26(34)56 μm ; seven specimens measured.

Comparison. The specimens from the type Caradoc are more-or-less identical to those described by Burgess (1991). *Nodospora rugosa* Strother and Traverse, 1979 probably belongs within *Velatitetras* and has similar sculpture to *V. rugulata*. However, *N. rugosa* has been reported by Strother and Traverse (1979) and Johnson (1985) and in both cases is considerably larger than *V. rugulata*.

Remarks. The envelopes of *V. rugulata*, *Rugosphaera cerebra* and *Segestrespora* (*Pseudodyadospora*) *rugosa* bear identical sculpture.

CRYPTOSPORE DISTRIBUTION IN THE TYPE CARADOC

The occurrence of cryptospore taxa reported from the type Caradoc sequence is outlined in Text-figure 3 and the results of morphotype abundance counts are presented in Table 1. As expected, taxonomic diversity appears to be directly proportional to cryptospore abundance. Samples with abundant cryptospores belonging to numerous taxa probably represent sediments which received a high terrestrial input and incorporated a more representative sample of the land-derived sporomorphs. However, it is possible that reworking may have influenced the distribution of cryptospores in the type Caradoc. Turner (1982) described the abundance of reworked acritarchs in palynological preparations from the type Caradoc sequence and it could be argued that many of the cryptospores may also have been reworked. Nevertheless, there are several lines of evidence which suggest that the cryptospores are not reworked and consequently the observed distribution probably reflects their true stratigraphical distribution. Firstly, the cryptospores are of uniform preservation and are all of low thermal alteration index, suggesting a single source. Secondly, the reworked acritarchs fall into three distinct groups of Tremadoc, Arenig and Llanvirn age.

Cryptospores are not known from pre-Caradoc strata in southern Britain, so there is no obvious source for reworked cryptospores. Furthermore, cryptospores are unknown until the Llanvirn so the reworked Tremadoc and Llandeilo sediments are unlikely to have provided cryptospores for reworking, although the reworked Llanvirn sediments may have provided a source. However, examination of the regional geology suggests that the Llanvirn, and also the Tremadoc and Arenig, deposits from which the acritarchs were reworked were almost certainly offshore marine deposits and probably contained few, if any, cryptospores.

The distribution of cryptospores in the type Caradoc is noteworthy for two reasons. Firstly, cryptospore assemblages from throughout the sampled sequence are similar in taxonomic composition (Text-fig. 3) which may be interpreted as indicating stasis over this interval. Secondly, dyads are abundant and are the dominant morphotype in the cryptospore assemblages (Table 1). More counts need to be undertaken using cryptospore assemblages from a variety of ages and environments in order to test the general validity of these findings.

STRATIGRAPHICAL DISTRIBUTION OF ORDOVICIAN–EARLY SILURIAN SPOROMORPHS

Previous reports of Ordovician sporomorphs

There are few reports of Ordovician sporomorphs. The reports considered herein to be genuine describe only cryptospores. The occasional reports of miospores (trilete spores) from Ordovician deposits are believed to be erroneous because either the age of the deposits is incorrect, the spores are contaminants, or the authors have described palynomorphs which resemble miospores but are, for example, folded acritarchs or spores physically broken out of permanent tetrads (i.e. *Ambitisporites? vavrdovii* Richardson, 1988; see Chaloner 1967; Schopf 1969). A recent example is that of Nøhr-Hansen and Koppelhus (1987) who reported ornamented trilete spores from marine shelf deposits from the Troedsson Cliff Formation from Greenland (Ashgill). Palynological preparations from the Troedsson Cliff Formation have been examined by Gray who could not confirm the presence of trilete spores and suggested that they were 'artefactual' (Gray 1991).

The oldest reported sporomorphs considered to be genuine are from the Llanvirn. Corna (1970) reported land plant remains, including trilete spores, from the Sarka Formation of Bohemia which is securely dated as Llanvirn. Subsequently, Vavrdova (1984) reported 'cruciate thick walled tetrads' and figured a permanent tetrad (Vavrdova 1984, pl. 4, fig. 1) from the same horizon. It is likely that the trilete spores reported by Corna are spores physically separated from permanent tetrads (*A.? vavrdovii* Richardson, 1988). Another report of Llanvirn sporomorphs is by McClure

EXPLANATION OF PLATE 4

Figs 1–4. *Velatitetras rugulata* Burgess, 1991; A489 roadcut exposure, River Onny Valley; Acton Scott Beds. 1–2, FM850 (slide CA15/1/A, E.F. no. T36). 3–4, FM851 (slide CA15/1/B, E.F. no. L49/2); two planes of focus are illustrated.

Figs 5–15. *Segestrespora (Pseudodyadospora) rugosa* (Johnson) Burgess, 1991; A489 roadcut exposure, River Onny Valley; Acton Scott Beds. 5–6, FM852 (slide CA15/1/B, E.F. no. N55/3); two planes of focus are illustrated. 7–8, FM853 (slide CA15/1/C, E.F. no. N42); two planes of focus are illustrated. 9–10, 14, FM854 (slide CA15/1/D, E.F. no. F38/1); three planes of focus are illustrated. 11–12, FM855 (slide CA15/1/D, E.F. no. U41); two planes of focus are illustrated. 13, FM856 (slide CA15/1/D, E.F. no. X45). 15, FM857 (slide CA15/1/A, E.F. no. F62/4).

Figs 16–20. *Rugosphaera cerebra* Miller and Eames, 1982; A489 roadcut exposure, River Onny Valley; Acton Scott Beds. 16, FM858 (slide CA15/1/A, E.F. no. W49/4), 17, FM859 (slide CA15/1/C, E.F. no. N58/1). 18, FM860 (slide CA15/1/B, E.F. no. E55/4). 19, FM861 (slide CA15/1/D, E.F. no. U48). 20, FM862 (slide CA15/1/C, E.F. no. F55).

All $\times 1500$, except where stated otherwise.

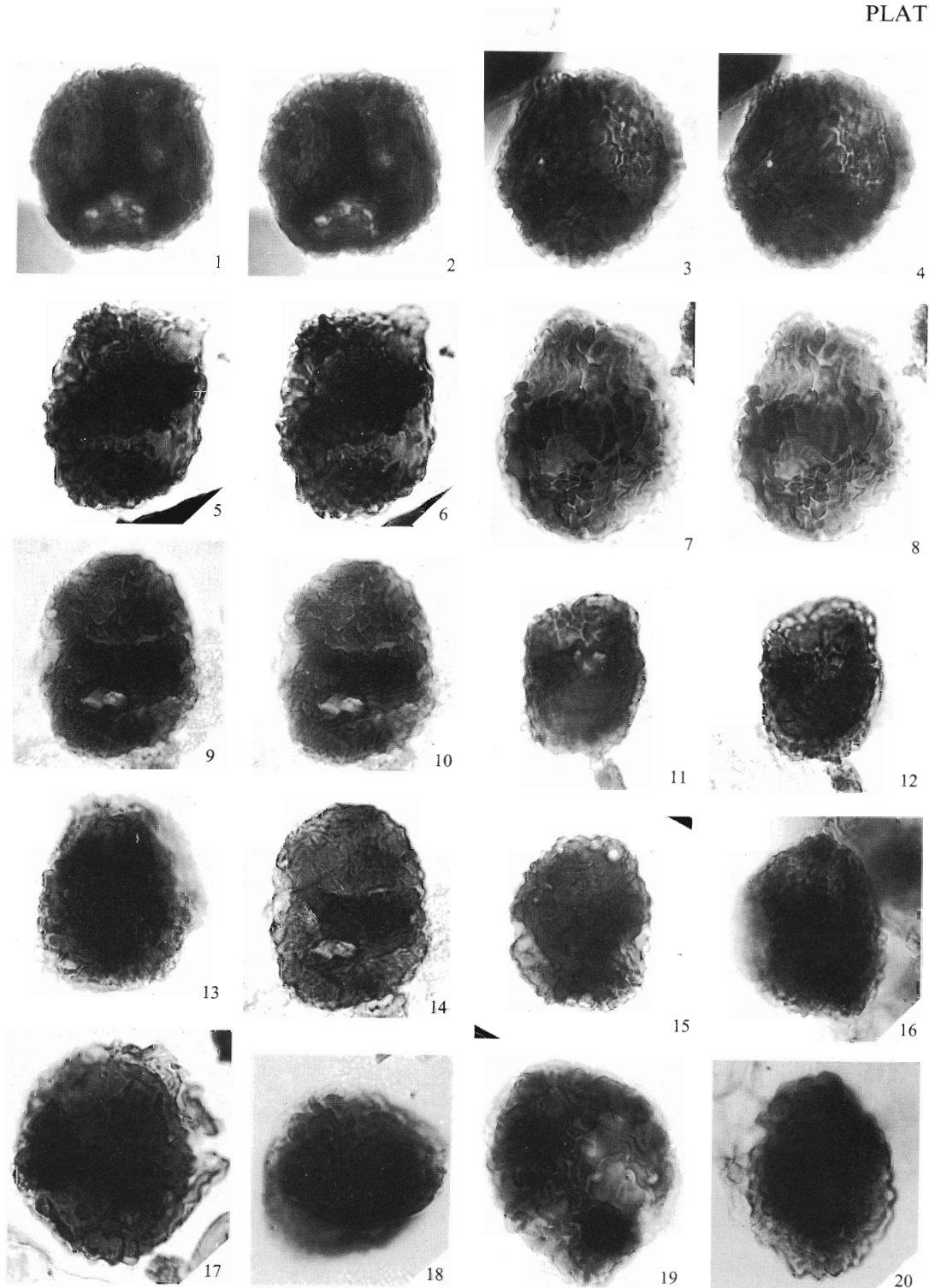


TABLE 1. Abundance of cryptospore morphotypes in selected samples (based on counts of 200 sporomorphs).

Cryptospore morphotype	Percentage abundance for selected samples		
	4/1	11/2	15/1
Naked fused tetrads	0.5	0.5	—
Naked unfused tetrads	7.5	25.5	13.0
Naked fused dyads	41.0	28.5	15.9
Naked unfused dyads	19.0	10.0	11.0
Naked monads	14.0	15.0	15.0
<i>Laevolancis divellomedia</i> ?	4.0	1.5	1.5
Envelope enclosed tetrads	0.5	5.0	7.5
Envelope enclosed dyads	10.5	7.0	21.0
Envelope enclosed monads	3.0	7.0	16.0
Total tetrads	8.5	31.0	20.5
Total dyads	74.5	47.0	48.5
Total monads	17.0	22.0	31.0
Total naked	86.0	81.0	57.5
Total envelope enclosed	14.0	19.0	42.5

TABLE 2. Spore taxa reported by Richardson (1988) from the type area for the Caradoc in southern Britain. X, present; —, not reported; 1, *Alternata* Limestone; 2, Middle Acton Scott Beds.

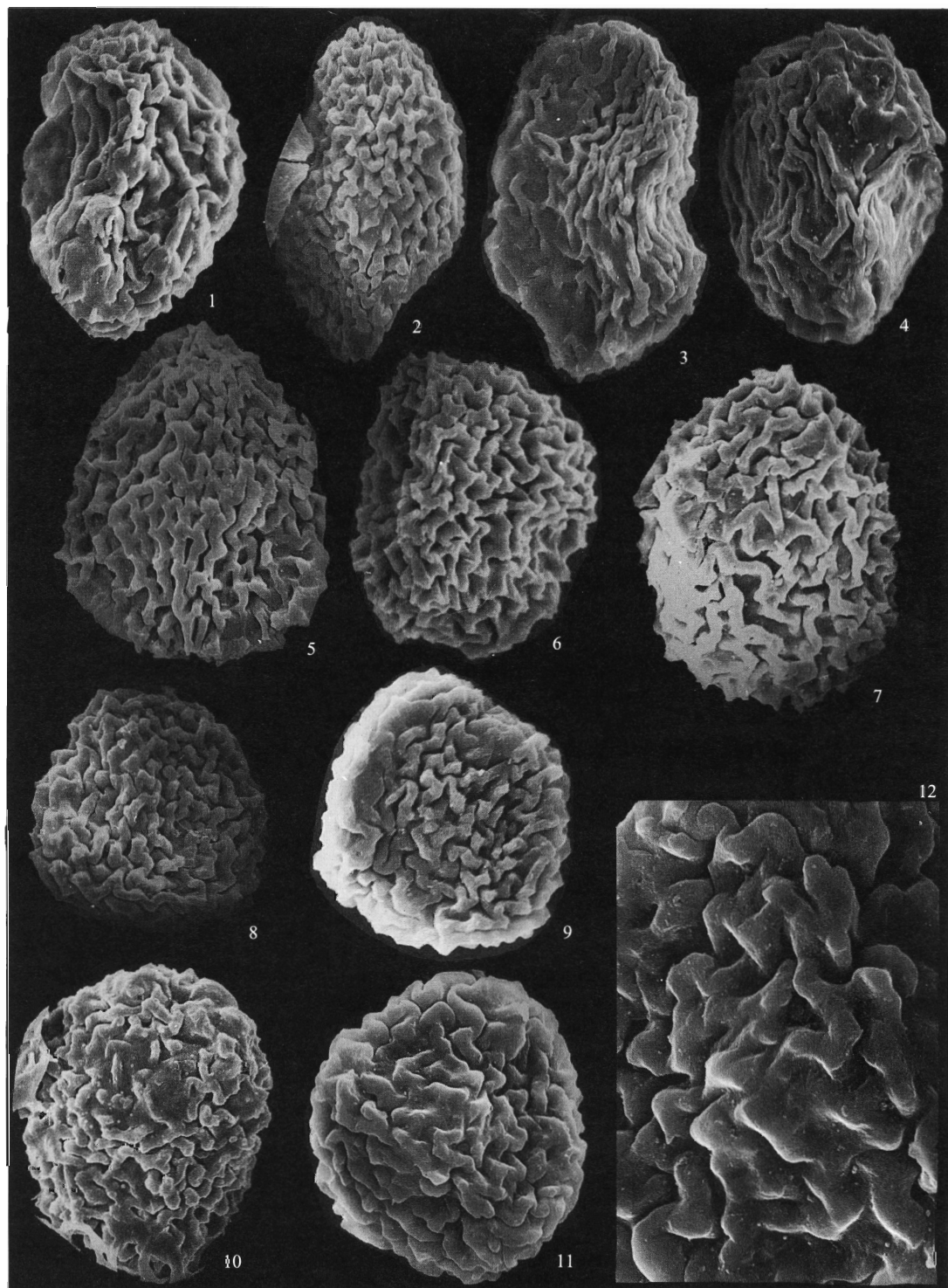
Occurrence		Cryptospore taxa
1	2	
?	—	<i>Strophomorpha</i> sp. (as <i>Striatomorpha</i> sp. [sic])
X	X	<i>Tetrahedraletes medinensis</i> (as <i>T. medinensis</i> and <i>Nodospora burnhamensis</i>)
X	X	<i>Tetrahedraletes grayae</i> ? (as <i>Nodospora-Tetrahedraletes</i> sp. A)
X	—	<i>Rimosotetras problematica</i> (as 'Loose tetrads')
X	X	<i>Pseudodyadospora</i> cf. <i>laevigata</i>
X	—	<i>Rugosphaera tuscarorensis</i> ?
?	X	<i>Rugosphaera cerebra</i> (as <i>Rugosphaera</i> ? <i>cerebra</i>)
X	X	<i>Segestrespora rugosa</i> (as <i>Pseudodyadospora</i> sp. C)
X	X	<i>Velatitetras rugulata</i> (as <i>Nodospora</i> sp. A)
X	?	<i>Velatitetras laevigata</i> (as <i>Nodospora</i> sp. B)
?	—	<i>Velatitetras</i> sp. A Burgess, 1991 (as <i>Nodospora</i> sp. E)

EXPLANATION OF PLATE 5

Figs 1–7, 10. *Segestrespora* (*Pseudodyadospora*) *rugosa* (Johnson) Burgess, 1991; A489 roadcut exposure, River Onny Valley; Acton Scott Beds. 1–4, 6–7, 10, (Stub CW121) sample CA15/1. 5, (Stub CW122) sample CA15/2.

Figs 8–9, 11–12. *Rugosphaera cerebra* Miller and Eames, 1982. 8, (Stub CW121) sample CA15/11; A489 roadcut exposure, River Onny Valley; Acton Scott Beds. 9, 11–12, (Stub CW137) sample CA9/1, roadcut exposure, River Onny Valley; Cheney Longville Flags; close-up of ornament; $\times 2700$.

All $\times 1500$, except where stated otherwise.



WELLMAN, *Segestrespora* (*Pseudodyadospora*), *Rugosphaera*

TABLE 3. Spore taxa reported by Richardson (1988) from the upper Ashgill of Libya. X, reported; —, not reported; 1, well E1-1 at 2552–2574 ft; 2, well E1-1 at 2520–2550 ft.

Occurrence		Cryptospore taxa
1	2	
—	?	<i>Dyadospora murusdensa</i>
X	X	<i>Tetrahedraletes medinensis</i> (as <i>T. medinensis</i> and <i>Nodospora burnhamensis</i>)
X	X	<i>Tetrahedraletes grayae</i> ? (as <i>Nodospora-Tetrahedraletes</i> sp. A)
—	X	<i>Tetrahedraletes</i> sp. C (as <i>Nodospora</i> sp. C)
—	X	<i>Tetrahedraletes</i> spp. indet. (as <i>Nodospora</i> spp. indet.)
—	X	<i>Tetrahedraletes</i> sp. indet. 1 (as <i>Nodospora</i> sp. indet. 1)
—	X	<i>Tetrahedraletes</i> sp. indet. 2 (as <i>Nodospora</i> sp. indet. 2)
X	X	<i>Rimosotetras problematica</i> (as 'Loose tetrads')
X	X	<i>Pseudodyadospora</i> sp. A
X	X	<i>Tetraletes laevigatus</i>
—	X	<i>Ambitisporites</i> ? <i>vavrdovii</i> (as ? <i>Ambitisporites imperfectus</i>)
—	X	<i>Rugosphaera tuscarenensis</i> ?
—	X	<i>Rugosphaera cerebra</i> (as <i>Rugosphaera</i> ? <i>cerebra</i>)
—	X	<i>Segestrespora rugosa</i> (as <i>Pseudodyadospora</i> sp. C)
X	X	<i>Velatitetras rugulata</i> (as <i>Nodospora</i> sp. A)
X	—	<i>Velatitetras</i> sp. A Burgess, 1991 (as <i>Nodospora</i> sp. E)

(1988) who reported 'distinct tetrahedral tetrad type of suspected land plant origin' from the Hanadir Shale, deposited as part of a nearshore marine prograding delta system, in the Tabuk section from Saudi Arabia. Graptolites indicate that the Hanadir Shale can be correlated with the *murchisoni* graptolite zone (Llanvirn). Strother *et al.* (1996) also report cryptospores from the Hanadir Shale. They reported *Laevolancis*-type monads in addition to dyads and tetrads which were either naked or enclosed in a thin laevigate envelope. The dyads and tetrads included both fused and unfused forms.

Caradoc sporomorphs were first reported by Gray *et al.* (1982) who described and figured permanent tetrads and single spores, physically broken out of permanent tetrads, from the Melez Chograne Formation from the Murzuk and southern Rhadames basins of Libya. Dorning (1986) noted that 'the earliest confirmed spores of land plant origin are recorded from the late Soudleyan of the Type Caradoc area', from southern Britain. He did not describe or figure the sporomorphs but illustrated a permanent tetrad and a dyad. Subsequently, Richardson (1988) described, but did not figure, sporomorphs from the *Alternata* Limestone and Middle Acton Scott Beds from the type area of the Caradoc in southern Britain. The distribution of the cryptospores reported is outlined in Table 2. Another report of sporomorphs from the Ordovician of Britain is by Millward and Molyneux (1992), who illustrated a cryptospore permanent tetrad (fig. 3m) and a probable cryptospore pseudodyad (fig. 3n) from the Over Water Formation (Eycott Volcanic Group) of the English Lake District, northern Britain. These deposits are interpreted as Llandeilo–Caradoc.

There is a number of reported sporomorph assemblages of Ashgill age. Gray and Boucot (1972) mentioned permanent tetrads from the Elkhorn Formation, Kentucky, USA and Gray *et al.* (1982) and Gray (1985) figured some of these tetrads, including naked permanent tetrads, permanent tetrads enclosed within a reticulate envelope and permanent tetrads enclosed within a smooth envelope. Subsequently, Gray (1988) reported and figured permanent tetrads from the Preacherville Member (Drakes Formation) of the Ohio Brush Creek section, Kentucky, USA. The figured tetrads included naked forms, forms enclosed in a reticulate envelope and forms enclosed in a smooth, or possibly degraded reticulate, envelope. Other occurrences of Ashgill sporomorphs from North America were reported by Gray (1988) who documented permanent tetrads from a number of localities: a palaeokarst from Manitoulin Island, Ontario, Canada; the Sesquatchie Formation of

TABLE 4. Spore taxa reported by Vavrdova from the Kosov Formation, Czech Republic.

<i>Strophomorpha</i> aff. <i>ovata</i>
Laevigate monads
<i>Acinosporites</i> ? <i>kosovensa</i> Vavrdova, 1989 (probable cryptospore monad)
? aff. <i>Emphanisporites protophanus</i> (probable cryptospore monad)
? <i>Virgatisporites</i> sp. (probable cryptospore monad)
<i>Dyadospora murusattenuata</i>
<i>Dyadospora murusdensa</i>
<i>Tetrahedraletes medinensis</i>
<i>Pseudodyadospora laevigata</i>
<i>Pseudodyadospora</i> spp.
<i>Ambitisporites</i> ? <i>vavrdovii</i> Richardson, 1988 (as <i>Ambitisporites imperfectus</i>)
<i>Aneurospora</i> ? <i>fragilis</i> Vavrdova, 1989 (Probably <i>A.?</i> <i>vavrdovii</i> Richardson, 1988)
<i>Archaeozonotriletes chulus</i> (Probably <i>Laevolancis divellomedia</i> ? <i>sensu</i> Wellman, herein)
<i>Chaetosporites pollensimilis</i> (? not figured)
Pentads
<i>Tritonialetes vacuolus</i>
<i>Quadrисporites horridus</i>
<i>Quadrисporites variabilis</i> (as <i>Tetraletes variabilis</i>)
<i>Vallatiales aureolatus</i>
<i>Rugosphaera cerebra</i>
<i>Rugosphaera tuscarorensis</i>
<i>Dyadospora membranifera</i>
<i>Nodospora retimembrana</i>
<i>Nodospora rugosa</i>
<i>Stegambiquadrella contenta</i>

the Green Gap section and the Shellmound formation of the Nickajack Dam section, Tennessee, USA; and the Sesquatchie and Red Mountain formations of the Ringgold section, Georgia, USA. Additionally, Strother (1991) described a new species of naked permanent tetrad, *Tetrahedraletes grayae*, from the Fort Atkinson Dolomite, McQuokata Group of Illinois, USA, which is of Ashgill age.

From southern Africa, Gray *et al.* (1986) described and figured *Tetrahedraletes* cf. *T. medinensis* from the Ashgill Soom Shale Member (Cedeberg Formation), of Cape Province, South Africa. From northern Africa, Gray *et al.* (1982) reported, but did not figure, permanent tetrads from the Ashgill Djeffara Formation of the Rhadames basin, and the Memouniat Formation of the Murzuk and southern Rhadames basins. Richardson (1988) reported sporomorph assemblages, believed to be late Ashgill on the basis of palynological evidence (acritarchs and chitinozoans), from two intervals from a well in north-east Libya. His taxon list is reproduced in Table 3.

In a series of papers Vavrdova described sporomorphs from the Kosov Formation (Ashgill) at Hlásná Třebaň, Czech Republic (Vavrdova 1982, 1984, 1988, 1989). The assemblage contains monads, dyads (true dyads and pseudodyads), tetrads and polyad cryptospores (with three, five or seven units, including cryptospores with possible dwarf units). Some of the cryptospores are enclosed within an envelope. Additionally, Vavrdova reported spores which have been physically torn out of polyad cryptospores (e.g. *Ambitisporites*? *vavrdovii* Richardson, 1988). The sporomorphs described as trilete spores by Vavrdova are probably of similar origin. Gray (1988) noted that she examined a preparation from the Kosov Formation but did not encounter tetrads with varied ornamentation as described by Vavrdova. Table 4 lists the taxa reported by Vavrdova with various comments and interpretations by the present author.

From Europe, Burgess (1991) reported sporomorphs from the shallow sub-tidal, or possibly intertidal, deposits of the Scrach Formation, which is latest Ordovician (latest Ashgill, *persculptus* graptolite zone), from south-west Wales. He reported the following cryptospores: *Tetrahedraletes*

medinensis var. *parvus*, *Velatitetras reticulata* Burgess, 1991, *V. laevigata*, *Pseudodyadospora* cf. *laevigata*, *Segestrespora laevigata*, *S. rugosa*, *S. membranifera* and *Rimosotetras problematica*. Reitz and Heuse (1994) described cryptospores from the upper Ordovician Lederscheifer Formation of southern Thuringia and northern Bavaria. These deposits are interpreted as nearshore shallow marine in origin. The cryptospores figured were assigned to ?*Rugosphaera tuscarorensis*, *R. tuscarorensis*, cf. *Nodospora burnhamensis* and *Dyadospora murusdensa*. Some cryptospore monads were also figured.

Cryptospores which are possibly of Ordovician age were described in two other reports. Foster and Williams (1991) reported *Tetrahedraletes medinensis* from the Mallova Salt of the Carribuddy Group, Canning Basin, Western Australia. They suggested that the presence of these permanent tetrads indicates a late Ordovician–early Silurian age. Lakova *et al.* (1992) reported monads, dyads, *Tetrahedraletes medinensis*, and tetrads ‘with a reticulate membrane’ from late Ordovician to Llandovery metasediments, in the Derwent Heights of south-east Bulgaria.

Summary of the stratigraphical distribution of Ordovician–early Silurian sporomorphs

It is clear from the above literature review that Ordovician sporomorph assemblages are all similar in composition (Text-fig. 7). They comprise entirely cryptospores and are dominated by monads, dyads (fused and unfused) and tetrads (fused and unfused). All of these morphotypes may occur enclosed within a membranous envelope which is either laevigate or ornamented. The polyad cryptospores generally remain firmly attached and do not dissociate. However, the presence of *Laevolancis divellomedia*? and *Ambitisporites? vavrdovii* suggests that some of the polyad cryptospores may have dissociated, although it is likely that most of these spores represent spores physically broken out of cryptospores. Moving up the geological column, a literature survey of reported early Silurian sporomorph assemblages, prior to the inception of miospores in the late Llandovery, indicates that sporomorph assemblages of this age are similar in general character to Ordovician assemblages and contain many taxa in common (e.g. Gray and Boucot 1971; Strother and Traverse 1979; Miller and Eames 1982; Johnson 1985; Gray 1988 and references therein; Richardson 1988; Burgess 1991).

Miospores (trilete spores) first appear in the late Llandovery (e.g. Richardson 1988; Burgess 1991; Gray *et al.* 1992). Reported late Llandovery and Wenlock sporomorph assemblages contain cryptospores in addition to miospores, and the cryptospores are often more abundant than miospores (e.g. Wellman 1993b; Wellman and Richardson 1993). The cryptospores include monads, dyads (fused and unfused) and tetrads (fused and unfused), but loosely attached dyads and hilate cryptospores derived from them are also present and are usually abundant (Burgess and Richardson 1991; Wellman 1993b; Wellman and Richardson 1993). Envelope-enclosed cryptospores are usually absent.

It is apparent that there was a major change in the character of sporomorph assemblages in the late Llandovery–early Wenlock interval (Gray 1985, 1991 and references therein; Richardson 1988; Burgess 1991). Unfortunately there is a paucity of reported late Llandovery sporomorph assemblages and the nature of the turnover in sporomorph assemblages is unclear. Gray (1985, 1991, 1993) suggested that, following their inception in the late Llandovery, miospores rapidly rose to prominence and dominated sporomorph assemblages throughout the latest Llandovery and Wenlock. Gray (1991) suggested that post late Llandovery sporomorph assemblages that are dominated by cryptospores are either caused by reworking, a consequence of relic floras, or are the outcome of spores derived from local vegetation swamping out spores derived from the regional vegetation. However, data published to date indicate that, in many cases, cryptospores dominate sporomorph assemblages at least until the earliest Devonian (Wellman 1993a; Wellman and Richardson 1996).

TEXT-FIG. 8. Stratigraphical distribution of Ordovician–Lower Devonian sporomorphs. A, first appearance of sculptured miospores and hilate cryptospores, B, first appearance of miospores. Dashed lines signify possible occurrence.

Sporomorph zonation of the Ordovician–lower Silurian

Sporomorph zonation schemes which encompass the Ordovician–lower Silurian have been proposed by Gray (see Gray 1985 and subsequent papers) and Richardson (Richardson 1988; Richardson and Edwards 1989). Gray (1985) proposed three Microfossil Assemblage Zones (MA Zones) for the Ordovician and Silurian. The base of MA Zone 1 is defined by the first appearance of cryptospores in the lower Llanvirn and at the top is defined by the first appearance of miospores in the Upper Llandovery. Gray *et al.* (1992) modified the upper limit of MA Zone 1 when they recognized rare trilete spores in the upper part of that zone and redefined its upper boundary as the point where trilete spores first begin to dominate assemblages, in the mid-Telychian (Upper Llandovery).

Richardson and Edwards (1989) proposed the *Dyadospora murusattenuata*–*Dyadospora murusdensa* Assemblage Biozone (AB), which is similar to Gray's MA Zone 1 in that the base is defined by the first occurrence of cryptospores and the top by the first occurrence of miospores. However, Richardson and Edwards tentatively subdivided this zone into an upper (1a) and lower (1b) unit based on the increase in diversity in the upper part. Richardson (1988) modified the concept of the *murusattenuata*–*murusdensa* AB. Firstly, he suggested that the nominal species for the zone were not suitable, as *Dyadospora* might not extend down into the Caradoc, so he renamed the zone the *Velatitetras rugulata* (as *Nodospora* sp. A)–*Dyadospora murusdensa* AB. Secondly, Richardson subdivided the *Velatitetras rugulata*–*Dyadospora murusdensa* AB into three Assemblage Biosubzones (ABS). The oldest subzone, the *Rugosphaera? cerebra*–*Pseudodyadospora* cf. *laevigata* ABS, was based on Caradoc (Actonian and Longvillian) material from the type area in southern Britain. The middle subzone, the *Ambitisporites? vavrdovii*–*Pseudodyadospora* sp. A ABS, was based on late Ashgill material from subsurface north-east Libya. The youngest subzone, the *Dyadospora membranifera*–*Pseudodyadospora* sp. B ABS, was based on early Silurian material.

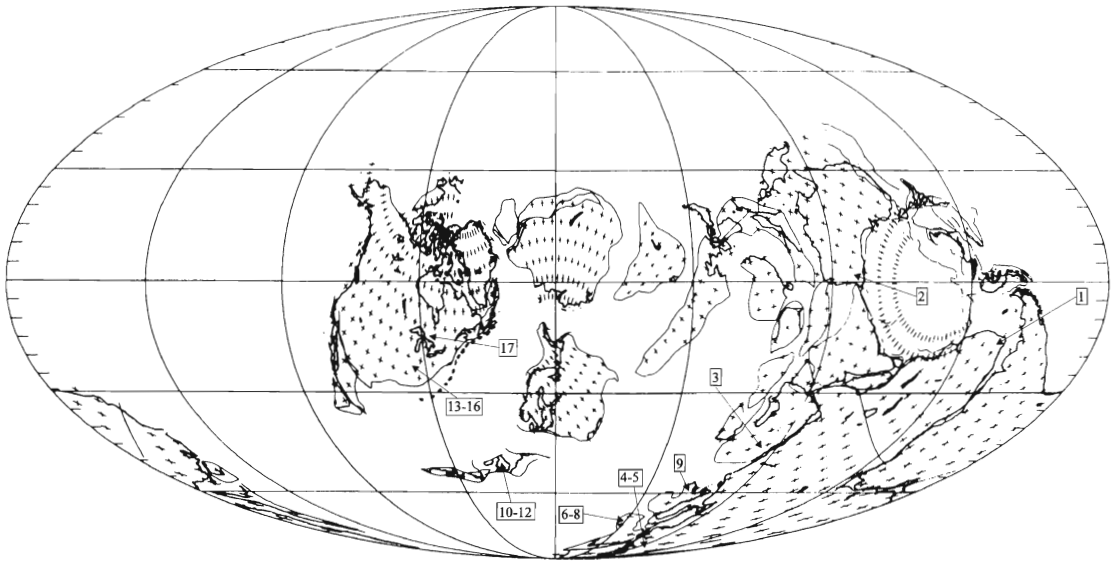
The type Caradoc cryptospore assemblages can be accommodated in Gray's MA Zone 1 or Richardson's *rugulata*–*murusdensa* AB (*cerebra*–cf. *laevigata* ABS). However, the new data indicate that true dyads (in the form of *Dyadospora murusdensa*) do in fact occur in the Caradoc (see Richardson 1988, p. 89) and are now known to extend down into the Llanvirn (Strother *et al.* 1996).

CRYPTOSPORE PALAEOPHYTOGEOGRAPHY IN THE ORDOVICIAN–EARLY SILURIAN

Gray *et al.* (1992) suggested that variation in the distribution of ornament types, displayed by envelope-enclosed tetrads from Ordovician–early Silurian sporomorph assemblages, provides the first evidence for phytogeographical differentiation of land plants. They suggested that sporomorph assemblages from the cool Malvinokaffric Realm contain only tetrads enclosed within laevigate envelopes, whereas assemblages from warmer extra-Malvinokaffric Realms (North Silurian Realms) contain tetrads enclosed in ornamented envelopes. Their spore tetrad data for the Malvinokaffric realm come from Africa (Ghana, Libya and South Africa), South America (Parana and Amazon basins) and Arabia, and their data for the extra-Malvinokaffric Realm from eastern North America and Britain.

Data inconsistent with Gray's findings are the reports by Richardson (1988) of ornamented tetrads from Libya and by Vavrdova (1982, 1984, 1988, 1989) of ornamented tetrads from the Czech Republic. Gray, however, discounted both reports. Gray *et al.* (1992) questioned the tetrad status of the ornamented spores described by Richardson and suggested that 'a number of problems relate to Richardson's interpretation of ornament'. Gray (1988) noted that she had examined a preparation from the Kosov Formation but did not encounter tetrads with varied ornamentation as reported by Vavrdova.

The type Caradoc cryptospore assemblages can be incorporated into Gray's phytogeographical scheme. The assemblages contain permanent tetrads enclosed within ornamented envelopes and are therefore, according to Gray's scheme, equated with assemblages from the extra-Malvinokaffric Realm. This does not conflict with palaeogeographical reconstructions by Scotese and McKerrow



TEXT-FIG. 9. Location of reported Ordovician cryptospore assemblages marked on a palaeogeographical reconstruction for the Caradoc (after Scotese and McKerrow 1990). 1, Cedeberg Formation, South Africa; 2, Carribuddy Group, Australia; 3, Hanadir Shale, Saudi Arabia; 4, Murzuk and Rhadames Basin, Libya; 5, north-east Libya; 6, Kosov Formation, Czech Republic; 7, Sarka Formation, Bohemia; 8, Lederscheifer Formation, southern Thuringia and northern Bavaria; 9, south-east Bulgaria; 10, type area for the Caradoc, Welsh Borderland, UK; 11, Over Water Formation, Lake District, UK; 12, Scrach Formation, south-west Wales, UK; 13, Elkhorn and Drakes Formation, Kentucky, USA; 14, McQuokata Group, Illinois, USA; 15, Sesquatchie and Red Mountain formations, Georgia, USA; 16, Sesquatchie and Shellmound formations, Tennessee, USA; 17, Manatoulin Island, Ontario, Canada.

(1990; Text-fig. 9) who place the type Caradoc area near the boundary between the Malvinokaffric and extra-Malvinokaffric realms, where it might therefore be associated with either realm. However, more data is needed in order to test further Gray's phytogeographical scheme, particularly in view of the conflicting data presented in the reports by Richardson (1988) and Vavrdova (1982, 1984, 1988, 1989).

CRYPTOSPORE AFFINITIES AND EVOLUTION

It is now generally accepted that cryptospores represent subaerially dispersed spores produced by land plants. New evidence from *in situ* cryptospores, albeit from Upper Silurian–Lower Devonian fossils, is shedding some light on the nature of the parent plants (Fanning *et al.* 1991; Edwards *et al.* 1994, 1995). Firstly, permanent tetrads, similar to those reported from the Llanvirn to at least the Lower Devonian, have recently been reported from two interconnecting lobes of a bifurcation at one end of a small axial fossil (Edwards *et al.* 1995). This specimen shows similarities with extant thalloid hepatics and may represent a plant at a bryophyte grade of organization. Secondly, loose dyads and associated hilate cryptospores, characteristic of post late Llandovery sporomorph assemblages, have been reported *in situ* from rhyniophytoid plants (Fanning *et al.* 1991; Edwards *et al.* 1994). However, many rhyniophytoid plants are known to have produced trilete spores similar to those produced by rhyniophyte plants (e.g. Fanning *et al.* 1991). The affinities of rhyniophytoid plants is conjectural. Many may represent true vascular plants (i.e. rhyniophytes) in which tracheids have not been demonstrated. Others may not have been true vascular plants, but were probably closely related, or even ancestral, to the tracheophytes.

The new evidence from *in situ* spore studies may be integrated with data derived from dispersed spore studies to provide a tentative hypothesis for the evolution of early land plants. It is possible that cryptospores derive from two sources. Typical cryptospore monads, dyads and tetrads, characteristic of sporomorph assemblages from the Llanvirn–upper Llandovery, but extending to at least the lower Devonian, may be related to the *in situ* tetrads described by Edwards *et al.* (1995) and derive from plants at an hepatic grade of organization (see also Gray 1985). However, loose dyads and associated hilate cryptospores, which first appear in the Upper Llandovery and are abundant in sporomorph assemblages until at least the Lower Devonian, may derive from rhyniophytoid plants. The change in the nature of sporomorph assemblages which occurs in the Upper Llandovery may therefore be equated with the rise of rhyniophytoid plants (see Gray 1985). Rhyniophytoid plants are known from at least the upper Wenlock (Edwards and Feehan 1980), but have low fossilization potential, and it is quite possible they extend down into the Upper Llandovery. The loose dyads, associated hilate cryptospores, and trilete spores which appear in the Upper Llandovery may have derived from early rhyniophytoid plants. Such plants went on to dominate plant assemblages throughout the remainder of the Silurian. However, it is clear that the plants which produced the cryptospore monads, dyads and tetrads which were characteristic of the pre-late Llandovery persisted, although the scarcity of envelope-enclosed cryptospores after the late Llandovery suggests some changes (extinction or evolution).

In summary, it is possible that the tightly attached permanent dyads (fused and unfused), that were habitually dispersed attached, are not closely related to the loose dyads which were, in the main, dispersed after dissociation into hilate cryptospores. The loose dyads and associated hilate cryptospores appear to be more closely related to trilete spores, as both morphotypes are known to have been produced by rhyniophytoid plants. Clearly, some rhyniophytoid plants produced trilete spores via normal meiosis, whereas others produced loose dyads. There is a number of different mechanisms which could account for the formation of dyads (Fanning *et al.* 1991; Strother 1991; Gray 1993; Hemsley 1994). These mechanisms generally involve either some form of abnormal meiosis or normal meiosis with shifts in the timing of meiotic cleavages and/or sporopollenin deposition.

CONCLUSIONS

Cryptospore studies are still in their infancy. Well documented reports of cryptospores are few and, consequently, their distribution in time and space is not well known. Furthermore, cryptospore morphology is not yet fully resolved and, because of the paucity of specimens, little is known about cryptospore-producing plants. Therefore, the relationships between the various cryptospore morphotypes and the affinities of cryptospores remain uncertain. These problems will only be countered by more work. Detailed reporting of more cryptospore assemblages is required in order to shed light on their temporal and spatial distribution; more sectioning work, and detailed morphological analysis are needed in order to resolve cryptospore morphology; and further finds of *in situ* cryptospores are necessary in order that their parent plants can be described, which may, it is hoped, shed light on the affinities of cryptospores.

The occurrence of abundant and well preserved cryptospores in the type Caradoc sequence has several important implications. Firstly, it demonstrates that well preserved cryptospore assemblages are preserved in Ordovician deposits. Future palynological investigations of deposits of this age will it is hoped reveal additional material, the study of which will increase our knowledge and understanding of Ordovician cryptospores. Secondly, the description of cryptospores from a continuous stratigraphical sequence in the type Caradoc has revealed much new information about them. New information is presented regarding cryptospore morphology, the composition of cryptospore assemblages, and the temporal and spatial distribution of cryptospores in the Ordovician. There are several particularly noteworthy findings. The occurrence of true dyads in the Caradoc is confirmed and it is demonstrated that dyads (fused and unfused) are abundant and dominate the type Caradoc assemblages. Furthermore, cryptospore assemblages appear to exhibit stasis during the Caradoc and, in fact, during the period from the Llanvirn to the early Llandovery.

This suggests that early land plant evolution was fairly static. However, taxonomic diversity is relatively high in the Caradoc, as well as in the Llanvirn, and this may imply a period of prior evolution.

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APPENDIX

Sample locations (see Text-figs 1–3). Stratigraphical (Strat.) abbreviations: AL, *Alternata* Limestone; ASB, Acton Scott Beds; CB, Coston Beds; CLV, Cheney Longville Flags; HLAf, Horderley Limestone and Flags; HS, Harnage Shales; OS, Onny Shales. Spore abundance abbreviations: R, rare; A, average abundance; C, common.

Sample	Strat.	Location	Grid Ref.	Spore Abundance
CA1/1	CB	Type section in River Onny valley; siltstone lens c. 3 m from western end of quarry.	MM41168615	Barren
CA2/1	HS	Type section in River Onny valley; siltstone procured by sinking a trench c. 1 m east of eastern end of the quarry.	MM41198614	R
CA4/1	HLAF	Type section in River Onny valley; narrow, near vertical, siltstone bed in the centre of the quarry.	MM41348600	C
CA5/1	HLAF	A489 roadcut; cutting to the north of the road, directly opposite the milestone.	MM41528596	A

CA5/2	HLAF	A489 roadcut; cutting to the north of the road, 10 m west of the milestone.	MM41518596	C
CA6/1	HLAF	Type section in the River Onny valley; small exposure in the grass bank south of the dismantled railway.	MM41758571	R
CA8/1	AL	Type section in the River Onny valley; small exposure in the grass bank, 17 m east of CA7/1.	MM41768570	R
CA8/2	AL	Type section in the River Onny valley; small exposure in the grass bank, 5 m east of CA8/1.	MM41778570	R
CA9/1	CLF	Type section in the River Onny valley; quarry to the south of the dismantled railway; eastern end of exposure, 2 m west of the large tree.	MM42098545	A
CA9/2	CLF	Type section in the River Onny valley; quarry to the south of the dismantled railway; eastern end of exposure, 1 m east of the large tree; 1 m stratigraphically higher than CA9/1.	MM42098545	R
CA10/1	CLF	Type section in the River Onny valley; cliff in the south bank of the river c. 5 m west of large tree; 1 m above the base of the exposure.	MM42338540	R
CA11/1	ASB	Type section in the River Onny valley; cliff in the south bank of the river; c. 2 m east of large tree, at the base of the exposure.	MM42348539	R
CA11/2	ASB	Type section in the River Onny valley; 10 mm thick bed of pale grey fine siltstone c. 1 m above CA11/1.	MM42348539	C
CA12/1	ASB	Type section in the River Onny valley; 1.5 m above CA11/2.	MM42358538	A
CA13/1	OS	Type section in the River Onny valley; cliff in north bank of the Onny River; eastern end of exposure at the base.	MM42638528	R
CA13/2	OS	Type section in the River Onny valley; 0.3 m above CA13/1.	MM42638528	R
CA13/3	OS	Type section in the River Onny valley; 0.5 m above CA13/1.	MM42638528	R
CA13/4	OS	Type section in the River Onny valley; 0.7 m above CA13/1.	MM42638528	R
CA14/1	CLF	A489 roadcut; exposure to the north of the road, c. 200 m east of Newhouse.	MM41998572	R
CA14/2	CLF	A489 roadcut; 1 m above CA14/1.	MM41998572	R
CA14/3	CLF	A489 roadcut; 1 m below junction with the <i>Alternata</i> Limestone.	MM41918575	A
CA15/1	ASB	A489 roadcut; exposure, c. 100 m west of gate.	MM42458548	C
CA15/2	ASB	A489 roadcut; 150 m west of CA15/1 and c. 20 m lower stratigraphically.	MM42378551	C