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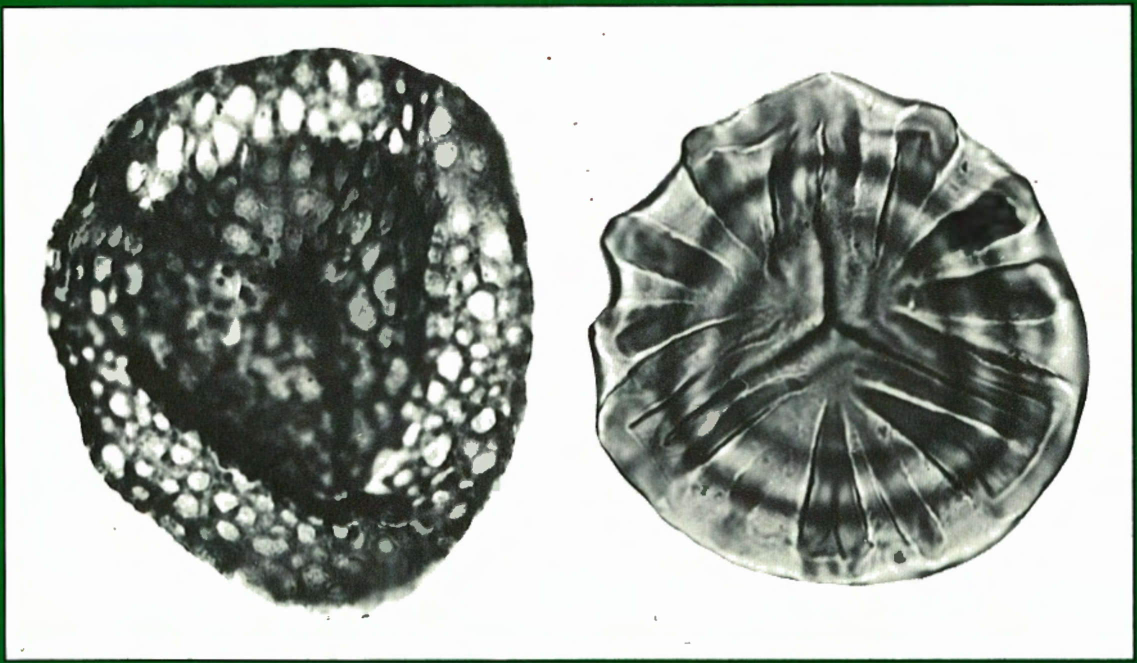
BULLETIN 364

SILURIAN AND DEVONIAN SPORE ZONES OF THE OLD RED SANDSTONE CONTINENT AND ADJACENT REGIONS

J.B. RICHARDSON
D.C. McGREGOR



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the Geological Survey of Canada,
Ottawa and Calgary

Authors' addresses

J.B. Richardson
Department of Palaeontology
British Museum (Natural History)
Cromwell Road
London SW7 5BD, England

D.C. McGregor
Geological Survey of Canada
601 Booth Street
Ottawa, Ontario K1A 0E8

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Cover photos

Left: **Retispora lepidophyta** (Kedo) Playford, enlarged X1000, from the Harrylock Formation, Hook Head, Ireland. It is a near-worldwide zonal indicator of Late Famennian and Strunian age (see p. 22-23). GSC type no. 73310; GSC loc. 99211.

Right: **Emphanisporites annulatus** McGregor, enlarged X1000, from the Stooping River Formation, Moose River Basin, Ontario. It is of near-worldwide occurrence in rocks of Emsian age (see p. 12-14). GSC type no. 41759; GSC plant loc. 8095.

PREFACE

Correlation of rock units is important to the understanding of geological relationships. Spores are among the most useful fossils for this purpose, as evidenced by the fact that they have been valuable tools for hydrocarbon exploration in Canada and abroad for many years.

Spores are widespread in marine and nonmarine rocks of Silurian and Devonian age. However, to date no comprehensive spore zonation for the whole of the Silurian and Devonian systems has been proposed. This report describes such a zonation for North America and Europe. New spore zones are calibrated with zones already established for graptolites, conodonts, ammonoids and tentaculites found exclusively in marine strata. Thus, a basis for direct time correlation of widespread marine and continental rocks of the Silurian and Devonian of Canada is established in this report. It also provides data that may be useful for the international definition of geological boundaries.

R.A. Price
Director General
Geological Survey of Canada

PRÉFACE

La corrélation des unités rocheuses tient un rôle important relatif à l'interprétation géologique. Parmi des fossils qui jouent un rôle majeur à cette fin, les spores prennent une place capitale, fait qui a été déjà mis en évidence au Canada et ailleurs dans l'exploration des hydrocarbures.

Des spores sont répandues dans les roches marines et non-marines du Silurien et du Dévonien. Néanmoins, jusqu'à présent, l'on n'a pas proposé une zonation compréhensive de spores pour l'ensemble des systèmes Silurien et Dévonien. Le présent rapport décrit une telle zonation pour l'Amérique du Nord et l'Europe. De nouvelles zones de spores s'étalonnent aux zones déjà établies de graptolites, de conodontes, d'ammonoïdes, et de tentaculites trouvés dans des strates exclusivement marines. Dès lors, une base pour la corrélation temporelle directe de roches marines et continentales très répandues du Silurien et du Dévonien du Canada se voit établie dans ce rapport. De plus, il présente des données d'utilité potentielle à la définition internationale de limites géologiques.

Le directeur général de la
Commission géologique du Canada
R.A. Price

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SILURIAN AND DEVONIAN SPORE ZONES OF THE OLD RED SANDSTONE CONTINENT AND ADJACENT REGIONS

Abstract

Silurian and Devonian stratigraphic sections from marine and nonmarine strata of the Old Red Sandstone Continent and adjacent basins were studied palynologically and collated. Nineteen spore zones are proposed, some of which may be subdivided regionally. The zones are regarded as assemblage biozones. Each zone is based on the following: two characterizing and widely-occurring species after which the zone is named, at least one of which begins at the base of the zone; an association of other species of spores that typically occur together; and, for some zones, a major morphological "event", such as the first appearance of proximal radial muri (early Gorstian) and the first appearance of bifurcate-tipped spines (latest Emsian). For the bases of most of the zones, reference sections have been selected.

The wide geographical spread of the zones, especially those in the Lower Devonian, testifies to the apparently near cosmopolitan distribution of at least some components of the vegetation that produced the spores. On the other hand, in parts of the Upper Devonian, some spores (and therefore the plants that produced them) show a distinctly regional pattern of distribution. Most of the spore "events" do not coincide temporally with "events" that have been selected independently to delimit Siluro-Devonian plant megafossil zones.

Résumé

Des coupes stratigraphiques du Silurien et du Dévonien provenant de couches marines et non marines du continent des vieux grès rouges et de bassins voisins ont été étudiées d'un point de vue palynologique et elles ont été rassemblées. Dix-neuf zones de spores sont proposées, quelques-unes d'entre elles pouvant être subdivisées dans certaines régions. Ces zones sont considérées comme des biozones d'assemblage. Chaque zone est fondée sur 1) deux espèces caractéristiques à large distribution d'après lesquelles la zone est dénommée, au moins une des deux apparaissant à la base de la zone, 2) un assemblage d'autres espèces de spores qui sont typiquement présentes en même temps; et pour quelques zones 3) un "évènement" morphologique majeur tel que la première apparition de muri radiaux proximaux (Gorstein ancien) et la première apparition d'épines à extrémité bifurquée (Emsien le plus tardif). Des coupes de référence avaient été sélectionnées pour les limites inférieures de la plupart des zones.

La grande distribution géographique des zones, en particulier celles du Dévonien inférieur, atteste une distribution pratiquement cosmopolite d'au moins quelques éléments de la végétation qui a produit les spores. D'autre part, au Dévonien supérieur, quelques spores (et, par conséquent, les plantes qui les ont produites) montrent un schéma de distribution régional bien distinct. La plupart des "évènements" remarqués chez les spores ne coincident pas dans le temps avec des "évènements" qu'avaient été choisis indépendamment à délimiter les zones de mégafossiles végétaux siluro-dévoniens.

INTRODUCTION

Spores with tetrad marks, produced by terrestrial plants, occur abundantly and in considerable variety in Late Silurian (Gorstian) and younger rocks, and in lesser numbers and diversity in strata at least as old as middle Llandovery. Trilete spores have been reported repeatedly from Llandovery rocks, and many have been dated convincingly using marine fossils. A number of authors have described spores and tetrads that they claim are of pre-Llandovery age (e.g. Combaz, 1967, Tremadoc; Timofeev, 1966, Cambrian, Early, Middle and Late Ordovician) but, in these works, either the age or the precise nature of the fossils is in dispute (some may be acritarchs), or the specimens are not adequately described or illustrated.

More recently, Gray, Massa and Boucot (1982) published excellent photographs of "permanent" tetrads, and *Ambitisporites*-like miospores broken out of tetrads, from rocks of supposed Caradoc (Late Ordovician) age. Their assemblage resembles those from the Llandovery of north Africa. In Llandovery rocks, single spores are well known, if sometimes rare, but there is a tendency for the spores to remain in tetrads to a greater extent than in younger rocks. Thus, based on morphology alone, the "Caradoc" spores reported by Gray et al. (1982) could be Silurian. On the stratigraphic evidence presented so far by Gray et al. (1982) and Massa (1980), one must exercise caution in accepting a Caradoc age for them. However, "permanent" miospore tetrads have also been recorded from the Ordovician by Vavrdova (1982, Pl. 1, fig. 1, Pl. 4), from the Kosov Formation, which corresponds approximately to the upper Ashgillian *Glyptograptus bohemicus* Zone.

Fossil spores commonly are divided into two broadly defined types based on size. Megaspores, comprising morphographic species with a mean size of 200 µm or greater, appear in the late Siegenian, become progressively more abundant through the Emsian and Middle Devonian, achieve a remarkable differentiation in the Frasnian, and persist to the present day. Miospores, less than 200 µm in diameter, are first seen in rocks at least as old as the Early Silurian and are the most nearly ubiquitous of identifiable land plant remains in sediments of that age and younger. They occur in various continental facies and, significantly for biostratigraphy, in certain marine facies as well.

Some generalizations may be made regarding the nature of spore assemblages that occur in the principal, broadly categorized sedimentary environments, based on those recovered from Devonian sediments (e.g. Nazarenko, 1974) and from younger deposits (e.g. Stanley, 1969; Tschudy, 1969). The most abundant and diverse assemblages, and the largest and best preserved spores, are found in continental and neritic facies, with the greatest concentration and diversity being in the inner neritic zone but (except at deltas) some distance offshore. Spores may even occur in deep water sediments far from shore, but there they commonly are small, more limited in number and diversity, and less well preserved.

At present there is no internationally accepted spore zonation for the whole of the Silurian and Devonian. This report proposes such a zonation, based mainly on miospores, for the Old Red Sandstone (ORS) Continent and adjacent regions. With some modification, the scheme incorporates zones proposed for parts of the Devonian by Streel (1966, and later papers), Richardson (1974), McGregor and Camfield (1976) and others (see Figure 1 and McGregor, 1979b, figures 2-7), and considerable unpublished information, some of which is included in theses by Ahmed (1978), Ford (1972), Hassan (1982), Karathanasopoulos (1975), Riegel (1975) and Wood (1978). The data are drawn mainly from the authors' work on western European, North African and North American sequences, and from the literature on spores of the European U.S.S.R. An outline of this scheme was presented to the Carboniferous Congress in Moscow in 1975. Comments made at that meeting and subsequently by Soviet palynologists, have been considered in the selection of characteristic species, although the final result is solely the authors' responsibility. Correlation with spore assemblages of the Soviet Union is difficult, largely because Soviet and non-Soviet palynologists use different, independently-developed schemes of taxonomy and nomenclature.

The study of Silurian and Devonian spores is advancing rapidly. Considering the dynamic state of the subject, the zones we are proposing should not be regarded as final. More information is needed regarding the geographical distribution of the zones both within and, especially, beyond the ORS Continent, as well as about the relationship of the scheme to floral provinciality. For example, although little has been known about Devonian spores from China until recently, contemporary Chinese research suggests that some of our zones may be applicable there (see Figure 1). Furthermore, some of the key species and morphological "events" in the spore succession can be recognized in sequences from South America, Antarctica and Australia, and are thus almost worldwide. The present emphasis on the zonation of the ORS Continent and adjacent sedimentary basins, therefore, is not so much a result of known biogeographical constraints as it is of the fact that most of the thoroughly described and precisely dated assemblages are from those regions.

We expect that as work progresses it will be possible to recognize additional zones, as has been true, for example, with conodont zonation. Indeed, this is already possible on an intra-regional basis (see Figure 1). In addition, as more data accumulate, it will be possible to test more fully whether the zones are in fact synchronous over the whole ORS region, or possibly even beyond this region.

The International Union of Geological Sciences Subcommission on Devonian Stratigraphy has defined the bases of the Eifelian, Frasnian and Famennian stages as at the lower boundaries of the *Polygnathus costatus partitus*, Lower *Polygnathus asymmetricus* and Middle *Palmatolepis triangularis* conodont zones, respectively. We accept these recommendations. For those stages with bases that are as yet not defined internationally, we have related the spore zones provisionally to faunally-defined versions of the relevant stage boundaries (see Figure 4).

The Subcommission on Devonian Stratigraphy has also recommended Lochkovian, Pragian and Emsian as the international standard stage nomenclature for the Lower Devonian. As a result of this decision, the Rhenish stages Gedinnian and Siegenian assume the status of regional stages. Although we acknowledge the wisdom of this decision as it applies to faunal correlations, we prefer to retain the Rhenish terminology at this time, as correlations of the spore-bearing Rhenish facies with Lochkovian and Pragian strata of the pelagic facies still are not securely established.

Unless stated to the contrary, all of the proposed zones and spore features discussed on the following pages are based on spores with tetrad marks, i.e. spores thought to have been produced by land plants. Citations of spore nomenclature, including "?" and "cf." designations, are given in the form in which they were originally published. Information on the provenance and repository of the specimens illustrated herein is given in Table 2 and the Appendix.

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ZONAL CONCEPT

Much has been written about the structure, definition, and limitations of biozones (e.g. Teichert, 1958; Hancock, 1977; Holland et al., 1978). However, the theoretical basis for the creation of palynological zones has received relatively little publicity, especially amongst proponents of the traditional, marine, faunal orthochronologies. It therefore seems appropriate to explain the rationale underlying the zonal scheme we are proposing.

Among the most significant characteristics of Recent and fossil spores are their abundance, their relative resistance to destruction, and the extraordinary scope of their dispersal by wind and especially by water. Assemblages of dispersed spores may be preserved in both continental and marine sediments. Except in autochthonous coals, each assemblage as a whole tends to reflect the combined vegetation of various parts of the drainage basin, whereas individual components of the assemblage may vary both qualitatively and quantitatively according to sedimentary factors and local concentrations of the parent vegetation onshore. Assemblages are commonly composed of thirty or more stratigraphically useful species, and many thousands of specimens may be present in a few grams of rock.

Widespread, apparently synchronous "first appearances" of certain taxa and form features of spores occur repeatedly in the geological column, and the Silurian and Devonian are not exceptional in this respect. Such occurrences are assumed to reflect evolution, and morphological antecedents can be suggested for many taxa. Whatever their evolutionary antecedents, certain (but not all) species and structural features seem to have attained widespread geographical distribution instantaneously in terms of geological time. Consequently, we have accorded considerable biochronological significance to first appearances of selected species and form features (Fig. 2). Upper stratigraphical limits (disappearances) may have been affected by such factors as persistence of relict floras, or redeposition, and so are given less weight in the definition of zonal boundaries.

On the other hand, there are some species that apparently do not make their first appearance contemporaneously in the sections that have been studied. A case can be made for significant ecological and hydrodynamic control, in addition to the large-scale geographical controls mentioned below, as an explanation for the seemingly heterochronous appearance of some species. Many authors have discussed this phenomenon. For example, Streel (1967), Richardson (1969) and McGregor (1981) have dealt with several species that occur in the vicinity of the Middle-Upper Devonian boundary. This phenomenon emphasizes the advisability of comparing whole assemblages comprising shared, characteristic taxa for long-distance correlation using spores.

Most of the zones defined here are, to some degree, geographical composites. That is, the lists of characteristic species commonly include certain elements of contemporaneous assemblages that appear to be restricted geographically. *Archaeoperisaccus* spp. in the Frasnian, and *Cornispora* spp. in the Famennian are examples of species with well-defined geographical limits (see McGregor, 1979b). However, each zone has shared, characteristic taxa that permit interregional temporal correlation of the zone.

The zones we are proposing are characterized by species that may have different inherent values for long-distance time-correlation. Some species do not have global distribution but may characterize floral provinces or realms, whereas others may represent more local variations that nevertheless have to be taken into account for interregional correlation.

Recently, some workers have adopted the use of palynological "phases" to facilitate regional correlation (Van der Zwan, 1980; Loboziak and Streel, 1981). Phases are considered to represent successive, evolutionary(?) steps in the gradual compositional development of palynological assemblages (Van der Zwan, 1980, p. 192). The phase concept may be useful, but it needs to be defined more explicitly and distinguished clearly from local and regional zonation.

In view of the foregoing, we believe the most reasonable basis for defining spore zones that can be correlated on an intercontinental scale is a combination of the co-occurrence of whole assemblages comprising several characteristic taxa, and the first appearance of selected species and form features. The earliest records of one or two selected species, observed in a variety of facies and irrespective of relative abundance (which may, however, be significant for local correlations), are used to define the base of each zone in a reference section. Assemblages occurring in consistent order of succession, each characterized by several species, provide the basis for correlations on a global scale. The Oppel zone, as defined in the International Stratigraphic Guide (Hedberg, 1976), which is one variant of the assemblage zone of the recently revised North American Stratigraphic Code (1983, p. 863), closely approximates this approach. The "global zones" of Mamet (1977) are in some ways similar in concept, but differ in being based on supposed phyletic lineages. Johnson (1979) has presented a useful discussion of both of these zonal concepts, which he calls the "overlap range zone" and the "lineage zone". Our zones are not interval zones, as they are defined in part, and correlated, by assemblages of characteristic taxa.

Because we use first occurrence of species rather than maximum abundance or frequency of occurrence to define zone boundaries, some nominal species may have their acme above the zone bearing their name. An example is *Geminospora lemurata*, the acme of which is not in the *lemurata-magnificus* Zone but in the succeeding *optivus-triangulatus* Zone.

We have not attempted to establish spore lineages, although such attempts, based on morphological "successions", might be just as feasible for spores as for other fossils. The most secure basis for recognition of lineages might be the demonstrated relationship of certain spore forms to their parent plants (*vide inter alia* Gensel, 1979). Visscher (1971, p. 27) was of the opinion that the typological concept in palynological taxonomy may be fundamentally unsuited to the recognition of phyletic lineages. He suggested that the "deme" system, which emphasizes the gradation rather than the uniformity of morphological characters, might facilitate the recognition of evolutionary lines. We suspect, however, that the proposal of empirically-based "phyletic" lineages on the data presently available could encourage entrenched thinking and consequent circular reasoning, and would not improve the precision of our correlations.

Silurian and Devonian plant megafossil zones (Banks, 1980) are in part reflected in the proposed spore zonation (Fig. 2). For example, the diversification of land plants (base of Banks's zone II) and the appearance of a group of advanced progymnosperms (near the base of Banks's zone V) approximately correlate with the spore changes that occur at the beginning of our *micrornatus-newportensis* and *lemurata-magnificus* zones. On the other hand, there are other megafossil zones, such as Banks's zone III, whose bases at present do not coincide with the base of any spore zone, although plants within zone III, for example *Dawsonites*, *Sawdonia*, and *Psilophyton*, have produced spores of the *Apiculiretusispora* type, which are most abundant in the upper Siegenian and Emsian (the range of Banks's zone). Some apparent discrepancies between the two zonal systems may stem from the difficulty of correlating continental strata (from which most plant megafossils have been obtained) with marine stages. Spore studies can make a major contribution to the solution of this problem. Other discrepancies between the spore and plant megafossil zonations may be harder to resolve, for the reasons given by Banks (1980, p. 3-5).

NOMENCLATURE OF THE ZONES

The name given to each spore zone comprises (a) the names of two widely-occurring and characteristic taxa, referred to as "nominal species", and (b) a statement of the kind of zone. On its first citation, the name of the zone is given in full, for example the *Contagisporites optivus* var. *optivus-Cristatisporites triangulatus* Assemblage Zone. In subsequent citations, the name of the zone is abbreviated – the *optivus-triangulatus* Zone.

The use of combinations of letters derived from the nominal species, e.g. "OT Zone" for the *optivus-triangulatus* Zone, is not recommended. Such letter designations are hard to remember, convey no information as to the composition of the zone, and may be confused with or duplicated by previously or subsequently established two-letter zonal designations, such as those of Clayton et al. (1977). When two-letter designations are also used for subzones (Clayton et al., 1978), phases (Van der Zwan, 1980), and acritarch zones (Loboziak et al., 1983), even greater confusion is possible.

If the names of the nominal taxa change, the name of the zone should be changed accordingly.

The numbers preceding the headings of the zone descriptions in the text refer to Figure 5, and are not intended to be part of the nomenclature of the zones.

CRITERIA FOR CHARACTERIZING THE ZONES

1. At least one of the nominal species selected for each zone begins at the base of the zone in the reference section. Most of the nominal species are geographically widespread.

2. The zones are recognized by the presence of a substantial number of the characteristic species. They are not circumscribed by the local or total ranges of the nominal species. A nominal species may also occur in stratigraphically higher zones, or may even be absent from its zone in some places. The known stratigraphic ranges of the nominal species and the other characteristic species are given in figures 2 and 3.

3. The bases of some zones are also characterized by the first manifestations of major features of spore morphology, such as the appearance of bifurcate-tipped processes in the late Emsian at the base of the *douglastownense-eurypterota* Zone. We refer to these phenomena as "events" (Fig. 2). Such palynological "events" may transgress conventional taxonomic divisions. They are of greater temporal and geographical magnitude than the "events" referred to by Hughes (1975, p. 142) in relation to his "biorecords".

4. A good zonal base exists if the defining "events" and the first occurrence of characteristic taxa are not accompanied by an observable lithological or structural discontinuity, or associated with mass extinction or renewal of taxa, and if a similar succession of taxa and "events" has been observed in two or more sedimentary basins.

5. The base of each zone is defined with respect to a specified stratigraphic section in which the zone is characteristically developed, and which also contains a zonally significant fauna. The top of each zone is defined by the base of the succeeding zone.

The standards described in the foregoing paragraphs represent ideal conditions for the definition of spore zones. Some of the zones described here do not fit all the established criteria (see Table 1). For example, the bases of the *avitus-dilutus* and *chulus-nanus* zones have not been defined in reference sections. Nevertheless, after some hesitation, we have included these two zones because, whatever their exact limits, they appear to be consistent in composition over a wide geographical area, and they represent the oldest known assemblages of trilete spores.

Figure 2. *Stratigraphic ranges of nominal species of the spore assemblage zones, and comparison of the zones with the floral zones of Banks (1980) and with selected "events" in the evolution of spore morphology. Broken horizontal lines indicate imprecisely defined zonal limits. Broken vertical lines indicate uncertain age and/or identification of species. The dotted line indicates uncertain correlation between the top of the Downtonian and the base of the Gedinnian.*

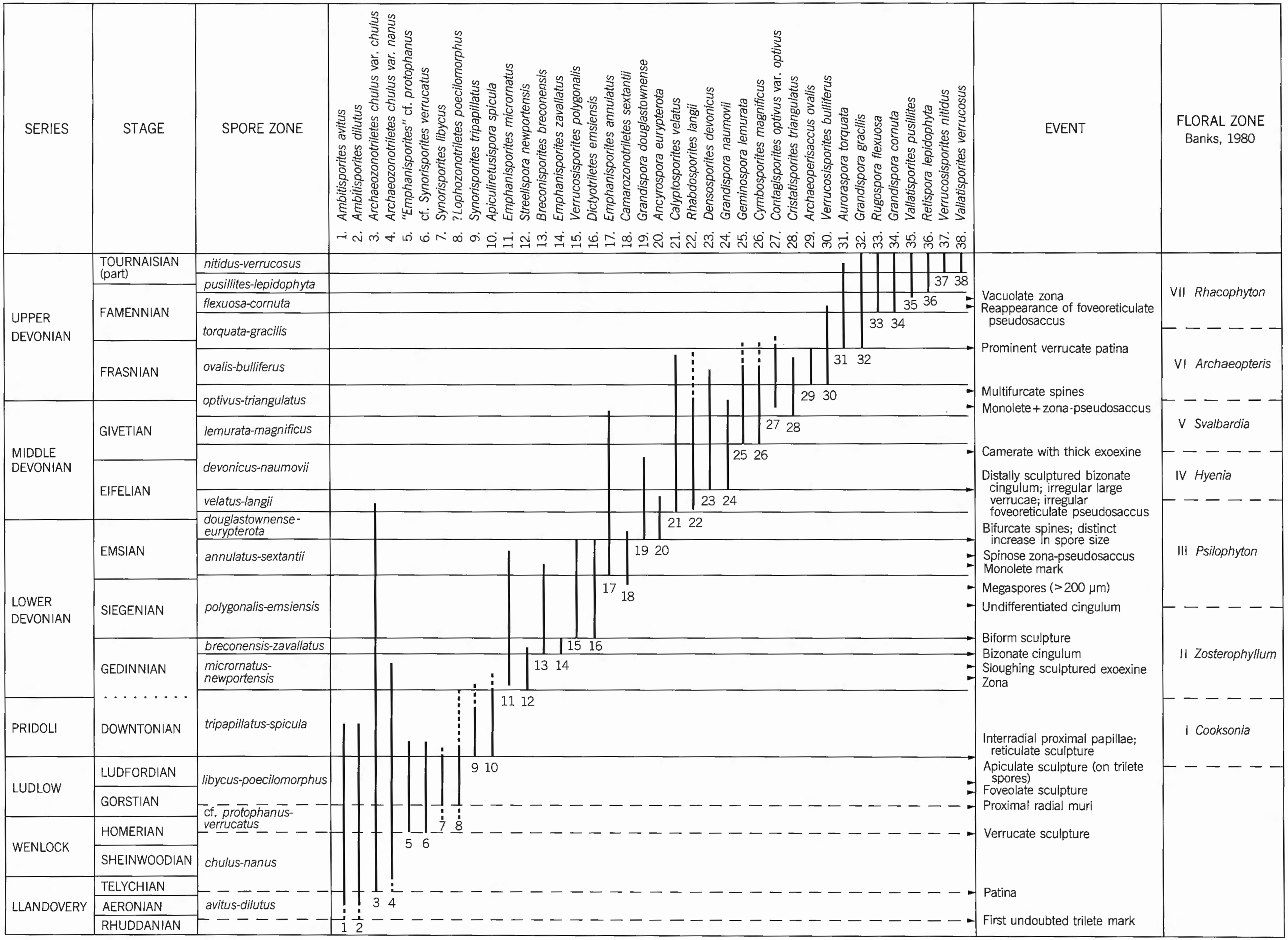
SERIES
STAGE
SPORE ZONE
EVENT
FLORAL ZONE
Banks, 1980
1. Ambitisporites avitus
2. Ambitisporites dilutus
3. Archaeozonotriletes chulus var. chulus
4. Archaeozonotriletes chulus var. nanus
5. "Emphanisporites" cf. protophanus
6. cf. Synorisporites verrucatus
7. Synorisporites libycus
8. ?Lophozonotriletes poecilomorphus
9. Synorisporites tripapillatus
10. Apiculiretusispora spicula
11. Emphanisporites micrornatus
12. Streelispora newportensis
13. Breconisporites breconensis
14. Emphanisporites zavallatus
15. Verrucosisporites polygonalis
16. Dictyotriletes emsiensis
17. Emphanisporites annulatus
18. Camarozonotriletes sextantii
19. Grandispora douglastownense
20. Ancyrospora eurypterota
21. Calyptosporites velatus
22. Rhabdosporites langii
23. Densosporites devonicus
24. Grandispora naumovii
25. Geminospora lemurata
26. Cymbosporites magnificus
27. Contagisporites optivus var. optivus
28. Cristatisporites triangulatus
29. Archaeoperisaccus ovalis
30. Verrucosisporites bulliferus
31. Auroraspora torquata
32. Grandispora gracilis
33. Rugospora flexuosa
34. Grandispora cornuta
35. Vallatisporites pusillites
36. Retispora lepidophyta
37. Verrucosisporites nitidus
38. Vallatisporites verrucosus
UPPER DEVONIAN
MIDDLE DEVONIAN
LOWER DEVONIAN
PRIDOLI
LUDLOW
WENLOCK
LLANDOVERY
TOURNAISIAN (part)
FAMENNIAN
FRASNIAN
GIVETIAN
EIFELIAN
EMSIAN
SIEGENIAN
GEDINNIAN
DOWNTONIAN
LUDFORDIAN
GORSTIAN
HOMERIAN
SHEINWOODIAN
TELYCHIAN
AERONIAN
RHUDDANIAN
nitidus-verrucosus
pusillites-lepidophyta
flexuosa-cornuta
torquata-gracilis
ovalis-bulliferus
optivus-triangulatus
lemurata-magnificus
devonicus-naumovii
velatus-langii
douglastownense-eurypterota
annulatus-sextantii
polygonalis-emsiensis
breconensis-zavallatus
micrornatus-newportensis
tripapillatus-spicula
libycus-poecilomorphus
cf. protophanus-verrucatus
chulus-nanus
avitus-dilutus
37 38
35 36
33 34
31 32
29 30
27 28
25 26
23 24
21 22
19 20
17 18
15 16
13 14
11 12
9 10
5 6
7
8
3 4
1 2
Vacuolate zona
Reappearance of foveoreticulate pseudosaccus
Prominent verrucate patina
Multifurcate spines
Monolete + zona-pseudosaccus
Camerate with thick exoexine
Distally sculptured bizonate cingulum; irregular large verrucae; irregular foveoreticulate pseudosaccus
Bifurcate spines; distinct increase in spore size
Spinose zona-pseudosaccus
Monolete mark
Megaspores (>200 μm)
Undifferentiated cingulum
Biform sculpture
Bizonate cingulum
Sloughing sculptured exoexine
Zona
Interradial proximal papillae; reticulate sculpture
Apiculate sculpture (on trilete spores)
Foveolate sculpture
Proximal radial muri
Verrucate sculpture
Patina
First undoubted trilete mark
VII Rhacophyton
VI Archaeopteris
V Svalbardia
IV Hyenia
III Psilophyton
II Zosterophyllum
I Cooksonia
GSC

TABLE 1

Conformity of spore zone circumscriptions with criteria 3 to 5 for definition of zones

ASSEMBLAGE ZONE	"EVENT" AT BASE	"GOOD" BASE	REFERENCE SECTION	FAUNAL CONTROL
nitidus-verrucosus	-	X	X	-
pusillites-lepidophyta	-	X	X	X
flexuosa-cornuta	-	X	X	-
torquata-gracilis	X	X	X	X
ovalis-bulliferus	-	X	X	X
optivus-triangulatus	-	X	X	-
lemurata-magnificus	-	X	X	-
devonicus-naumovii	X	X	X	X
velatus-langii	-	-	X	X
douglastownense-eurypterota	X	X	X	X
annulatus-sextantii	-	-	X	X
polygonalis-emsiensis	X	X	X	X
breconensis-zavallatus	X	X	X	X
micrornatus-newportensis	-	X	X	X
tripapillatus-spicula	X	-	X	X
libycus-poecilomorphus	X	X	X	X
cf. *protophanus-verrucatus*	X	X	X	X
chulus-nanus	X	X	-	X
avitus-dilutus	X	X	-	X

The first occurrence of a nominal species in the reference section for the zone may not represent the earliest chronostratigraphic record of the species, because of environmental and sedimentological constraints on the movement of spores to the site of deposition. Nevertheless, the stratigraphic level at which the lowest-occurring nominal species appears in the reference section shall be the "anchoring point" for determining the species content of the zone, until redefinition of the zone becomes necessary.

Figure 4 shows the approximate correlation of the spore zones with standard graptolite, conodont, ammonoid and tentaculite zones, based on published and unpublished information from many sources. Figure 4 also gives the stratigraphic position of the reference sections designated herein for the bases of the spore zones. Figure 5 shows the geographical location of the reference sections. Table 3 summarizes the lithology, depositional environments and fossil content of the spore zones in the vicinity of the reference sections.

In the following description of the zones, the plate and figure numbers given in brackets following the names of the characteristic species refer to illustrations in this bulletin.

DESCRIPTION OF THE ZONES

1. *Ambitisporites avitus - A. dilutus* Assemblage Zone

Age. Early and early Late Llandovery (Aeronian and early Telychian).

Reference section for the base of the zone. None.

Characteristic species.

Ambitisporites avitus Hoffmeister, 1959, Pl. 1, figs. 1-8 (Pl. 1, fig. 1).

A. dilutus (Hoffmeister) Richardson and Lister, 1969; Hoffmeister, 1959, Pl. 1, figs. 9-13 (Pl. 1, fig. 2).

Retusotriletes warringtonii Richardson and Lister, 1969, Pl. 37, figs. 7 and 8 (Pl. 1, fig. 3).

Tetrahedraletes medinensis Strother and Traverse, 1979, Pl. 1, figs. 14-17 (Pl. 1, figs. 4, 5).

Description. Laevigate, equatorially crassitate, trilete miospores and laevigate and sculptured monads, dyads and "permanent" tetrads. Spores are mainly small (mostly 20-40 µm in diameter), subtriangular or subcircular.

Distribution. Upper Pentamerus Beds and lower Hughley Shales, Shropshire (Richardson in Aldridge et al., 1979), approximately *Monograptus sedgwickii* and *M. turriculatus* graptolite zones (Hill, 1974); in subsurface, Middle Llandovery of Libya (Hoffmeister, 1959; age determination

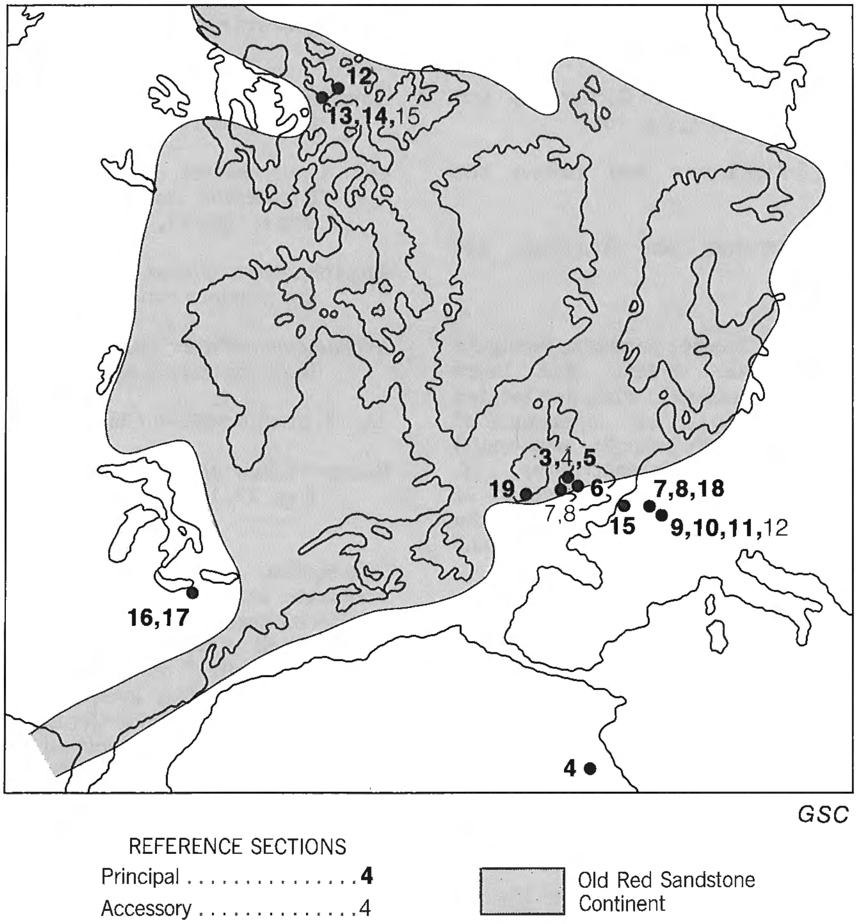

Figure 5. *Geographical location of reference sections. Numbers refer to numbered zones in text. The limits of the Old Red Sandstone Continent are taken from Anderton et al., 1979, with revisions. The continental assembly is provisional.*

by Berry in Gray and Boucot, 1971); lower Massanutten Sandstone, Virginia (Pratt et al., 1978); Tuscarora Formation, Pennsylvania (Strother and Traverse, 1979). The Medina Group, Rhuddanian Stage, Lower Llandovery, New York State (Miller and Eames, 1982) contains a rich assemblage of spore-like fossils, but does not contain the diagnostic species of this zone.

Remarks. "Permanent" tetrads (*Tetrahedraletes*) and dyads (*Dyadospora* Strother and Traverse, 1979) may be present. Some tetrads and dyads are enclosed by a single diaphanous membrane. Sculptured, alete, spore-like fossils, for example *Strophomorpha* Miller and Eames (1982), have been described from New York State and Pennsylvania, where tetrads and dyads along with sculptured alete spore-like fossils (monads) may dominate the assemblage.

2. *Archaeozonotriletes chulus* var. *chulus* – *A. chulus* var. *nanus* Assemblage Zone

Age. Approximately Late Llandovery to late Wenlock (Telychian to late Homerian).

Reference section for the base of the zone. None.

Characteristic species.

Archaeozonotriletes chulus (Cramer) Richardson and Lister var. *chulus*; Richardson and Lister, 1969, Pl. 43, figs. 1-6 (Pl. 1, figs. 6-8).

A. chulus (Cramer) Richardson and Lister var. *nanus* Richardson and Lister, 1969, Pl. 43, figs. 10 and 11 (Pl. 1, fig. 9).

Ambitisporites avitus Hoffmeister; see previous zone.

A. dilutus (Hoffmeister) Richardson and Lister; see previous zone.

?*A.* cf. *divellomedium* Chibrikova 1959; Richardson and Lister, 1969, Pl. 43, fig. 12 (Pl. 1, fig. 10).

Retusotriletes warringtonii Richardson and Lister; see previous zone.

Tetrahedraletes medinensis Strother and Traverse; see previous zone.

Description. First appearance of trilete, patinate, laevigate miospores with a thin proximal surface that bears characteristic compression folds concentric with, and located just inside, the equatorial thickening. First appearance of subcircular, possibly alete spores with polar(?), proximal(?) circular diaphanous area (?*Archaeozonotriletes* cf. *divellomedium*) in the upper part of the zone. Persistence of species from the previous zone, except for many of the sculptured "spore-like microfossils" (see Strother and Traverse, 1979 and Miller and Eames, 1982).

Distribution. Upper Coalbrookdale Beds (*Cyrtograptus lundgreni* graptolite biozone), Shropshire, England (Richardson and Lister, 1969); subsurface of Libya (Richardson and Al-Ameri, unpublished). An assemblage from the Lettergesh Formation of Ireland (Smith, 1975), dated as early Wenlock from graptolite evidence, could belong to either the *chulus-nanus* or the *avitus-dilutus* zone, as it does not contain *Archaeozonotriletes chulus.*

Remarks. Palynomorphs that appear identical to ?*A.* cf. *divellomedium* have been described from marine Silurian rocks of Spain by Cramer (1966a) under the name *Saturnus laevigatus,* a form regarded by Cramer as *incertae sedis.* However, similar forms have been recovered from nonmarine strata, and therefore probably were derived from land plants (Richardson and Lister, 1969). This form ranges into the Lower Devonian.

3. "*Emphanisporites*" cf. *protophanus* - cf. *Synorisporites verrucatus* Assemblage Zone

Age. Late Wenlock and early Ludlow (late Homerian to early Gorstian).

Provisional reference section for the base of the zone. Type area of the Wenlock Series, Much Wenlock Limestone Formation, approximately 4 m above its base, Harton Hollow Wood Quarry, 213.4 m south of Harton Village, Shropshire, England (Richardson and Lister, 1969).*

Range of the zone. Much Wenlock Limestone Formation (*Monograptus ludensis* graptolite zone) to the lower part of the lower Elton Beds [*Neodiversograptus nilssoni* graptolite zone(?)].

Characteristic species.

"*Emphanisporites*" cf. *protophanus* Richardson and Ioannides, 1973, Pl. 2, fig. 7 (Pl. 1, fig. 12).

cf. *Synorisporites verrucatus* Richardson and Lister; Richardson and Ioannides, 1973, Pl. 6, figs. 17-21 (Pl. 1, figs. 11, 13, 14).

Ambitisporites dilutus (Hoffmeister) Richardson and Lister; see previous zone.

Archaeozonotriletes chulus (Cramer) Richardson and Lister (both varieties); see previous zone.

?*A.* cf. *divellomedium* Chibrikova; see previous zone.

Retusotriletes abundo Rodriguez, 1978, Pl. 1, fig. 6 (Pl. 1, figs. 15, 16).

Description. Appearance of patinate alete(?) forms with verrucate sculpture; persistence of trilete spores with an equatorial crassitude. Appearance of spores that are possibly alete and that have incipient proximal ribs ("*Emphanisporites*" cf. *protophanus*). Beginning of retusoid spores with distinctly invaginated curvaturae and circular or subcircular amb (*Retusotriletes abundo*) high in the zone. In comparison, *R. warringtonii* of the preceding zones has a subtriangular amb and equatorial curvaturate thickenings that rarely invaginate onto the proximal surface.

Distribution. Much Wenlock Limestone Formation and lower Elton Beds, Shropshire, England (Richardson and Lister, 1969); calcareous silts and nodular limestones, Much Wenlock Limestone Formation(?), Trostrey Wood, Monmouthshire (Richardson, unpublished); subsurface of Libya (Richardson and Ioannides, 1973; Richardson and Al-Ameri, unpublished); San Pedro Formation, northern Spain (Rodriguez, 1978).

Remarks. Alete spores with "distal" verrucate sculpture, similar to cf. *Synorisporites verrucatus,* were recorded by Cramer (1966a) as *Hispanaediscus verrucatus* (*incertae sedis*).

4. *Synorisporites libycus* - ?*Lophozonotriletes poecilomorphus* Assemblage Zone

Age. Gorstian and Ludfordian. Graptolite zones *Neodiversograptus nilssoni* to approximately *Neocucullograptus kozlowskii* (see Bassett et al., 1982).

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*Recently a research student, Neil Burgess, working at the British Museum (Natural History), located "*Emphanisporites*" cf. *protophanus* and cf. *Synorisporites verrucatus* in the upper Coalbrookdale Formation below Harton Hollow Wood Quarry in the type Wenlock area. Discovery of these specimens necessitates lowering the base of the cf. *protophanus* - *verrucatus* Zone to at least the upper lower Homerian in the graptolite upper *lundgreni* Zone.

Reference section for the base of the zone. British Petroleum borehole B2-34, sample 18, Ghadames Basin, northern Libya (Richardson and Ioannides, 1973). Graptolites in this sequence indicate a late Wenlock or early Ludlow age (*op. cit.*, p. 258). Accessory reference section: top of the lower Elton Beds, junction of Elton Lane with the track to Evenhay Farm, 800 m southeast of Elton village and 6.4 km southwest of Ludlow, Shropshire, England. Spores are rare in this section (Richardson and Lister, 1969). The accessory reference section was chosen because it is in the type area of the Ludlow Series, and because the primary reference section is in a borehole.

Range of the zone. In Shropshire, upper part of the lower Elton Beds to the top of the upper Whitcliffe Beds.

Characteristic species.

Synorisporites libycus Richardson and Ioannides, 1973, Pl. 7, figs. 1-6 (Pl. 2, figs. 1-3).

?*Lophozonotriletes poecilomorphus* Richardson and Ioannides, 1973, Pl. 7, figs. 9-15 and Pl. 8, figs. 1, 4-6 (Pl. 2, figs. 6, 7).

cf. *Brochotriletes* sp. A, Richardson and Ioannides, 1973, Pl. 4, figs. 5-6, 8-10 (Pl. 2, figs. 8, 9).

"*Emphanisporites*" *protophanus* Richardson and Ioannides, 1973, Pl. 2, figs. 8-12 (Pl. 2, fig. 12).

"*E.*" cf. *protophanus* Richardson and Ioannides; see previous zone.

E. neglectus Vigran, 1964, Pl. 1, figs. 14-16 (Pl. 2, fig. 4).

cf. *Synorisporites downtonensis* Richardson and Lister, 1969, Pl. 40, fig. 6 (Pl. 2, fig. 11).

Synorisporites cf. *verrucatus* Richardson and Ioannides, 1973, Pl. 6, figs. 11-16 (Pl. 2, figs. 5, 10).

Tetraletes variabilis Cramer, 1966b, Pl. 1, figs. 7, 8, 10 (Pl. 2, fig. 16).

Description. First appearance of proximal radial muri on trilete spores (*Emphanisporites*), distal murornate sculpture (?*Lophozonotriletes*, cf. *Synorisporites downtonensis*), and apiculate tetragonal tetrads (*Tetraletes*). Beginning of apiculate sculpture on trilete spores. Appearance of foveolate sculpture (cf. *Brochotriletes*). Persistence of all nominal species of the previous zones.

Distribution and regional variation. Acacus Formation of Libya (Richardson and Ioannides, 1973). Middle Elton, Bringewood, Leintwardine and Whitcliffe beds of Shropshire, England (Richardson and Lister, 1969; Richardson, unpublished), based on the first appearance of murornate sculpture; the nominal species were not found. Assemblages described by Aristova and Arkhangelskaya (1976) from the Kuresaare Beds contain *Retusotriletes* with wholly proximal curvaturae, *Emphanisporites*, and possibly *Apiculiretusispora* and *Brochotriletes*. All of these elements occur for the first time in the *libycus-poecilomorphus* Zone. The nominal species of this zone occur in the upper Tarabuco Formation and the lower Santa Rosa Formation of the Tarabuco region, Bolivia (McGregor, 1984). Other possible occurrences of this zone are in the Mississinewa Shale of Indiana (Wood, 1978), and the lower member of the Barlow Inlet Formation of Cornwallis Island, Canada (McGregor and Narbonne, 1978; Thorsteinsson and Uyeno, 1980). In the Ludlow, *Brochotriletes* and similar forms are so far known from Libya (Richardson and Ioannides, 1973), Spain (Rodriguez, 1978), Estonia (Aristova and Arkhangelskaya, 1976), and Bolivia (McGregor, 1984).

Remarks. When further work on the systematic description of upper Gorstian and Ludfordian spores is completed it may be possible to separate the upper part of the *libycus-poecilomorphus* Zone on the basis of *Apiculiretusispora* spp.

5. *Synorisporites tripapillatus* - *Apiculiretusispora spicula* Assemblage Zone

Age. Downtonian, sensu White, 1950; approximately equivalent to the Pridolian (see Cocks et al., 1971, p. 127; Kaljo, 1978; Richardson et al., 1981). A detailed review of the Downton Series is given by Bassett et al. (1982).

Reference section for the base of the zone. Ludford Lane, Ludlow, Shropshire, England, base of the Downton Castle Sandstone Group, immediately above the Ludlow Bone Bed (Richardson and Lister, 1969). In the type area, no spores were recovered from the Ludlow Bone Bed, which is lenslike and, although persistent in many sections in the Welsh Borderland, is absent to the west and southwest of the region. This and the other bone beds in the sequence do not appear to represent marked discontinuities (Martinsson, 1977, p. 49).

Range of the zone. Downton Castle Sandstone Group, Shropshire. Many of the characteristic species have not been found in the Temeside and Ledbury formations, but study of these beds is still preliminary.

Characteristic species.

Synorisporites tripapillatus Richardson and Lister, 1969, Pl. 40, figs. 7-9 (Pl. 2, figs. 17, 18).

Apiculiretusispora spicula Richardson and Lister, 1969, Pl. 38, figs. 3, 4 (Pl. 2, fig. 14).

Ambitisporites sp. B of Richardson and Ioannides, 1973, Pl. 6, figs. 7-9 (Pl. 3, fig. 1).

Amicosporites splendidus Cramer, 1967, Pl. 2, figs. 31, 40, 41 (Pl. 2, fig. 13).

Apiculiretusispora synorea Richardson and Lister, 1969, Pl. 38, figs. 5, 6 (Pl. 2, fig. 15).

Cymbosporites echinatus Richardson and Lister, 1969, Pl. 42, figs. 1-5 (Pl. 3, fig. 2).

C. verrucosus Richardson and Lister, 1969, Pl. 42, figs. 6-8 (Pl. 3, figs. 4, 5).

Emphanisporites neglectus Vigran, 1964; see previous zone.

E. splendens (Richardson and Ioannides) Richardson and Ioannides 1979; 1973, Pl. 3, figs. 12-15; Pl. 4, figs. 1-4, 7 (Pl. 3, fig. 3).

Synorisporites downtonensis Richardson and Lister, 1969, Pl. 40, figs. 4. 5 (Pl. 3, figs. 8, 9).

S. verrucatus Richardson and Lister, 1969, Pl. 40, figs. 10-12 (Pl. 3, figs. 6, 7).

Description. First appearance of interradial proximal papillae (*S. tripapillatus; Ambitisporites* sp. B, ? = *A. tripapillatus* Moreau-Benoit, 1976), distally sculptured patinate spores with thin contact areas (*Chelinospora* and *Cymbosporites*), and reticulate sculpture (*Chelinospora*). Persistence of nearly all species from the previous zone.

Distribution and regional variation. Downton Castle Sandstone Group, England and Wales (Richardson and Lister, 1969); upper Acacus Formation, Libya (Richardson and Ioannides, 1973); upper beds of the Oued Tifist Formation, Algeria (Jardiné and Yapaudjian, 1968). The upper Acacus Formation and the Oued Tifist Formation have not been faunally dated.

The zone may also occur in the Kaugatuma and Okhesaare(?) beds of Estonia (Aristova and Arkhangelskaya, 1976), the Borshchov Horizon of Podolia (Arkhangelskaya, 1980a; Richardson et al., 1981), and the Santa Rosa Formation of the Tarabuco region of Bolivia (McGregor, 1984). It has not been confirmed in North America, but spores possibly of this zone, as yet unstudied, are present in strata of Pridolian age in Canada, for example the Clam Bank Formation of Newfoundland (Martin, 1978, p. 77; McGregor, unpublished), and the Devon Island Formation of Devon Island, Queen Elizabeth Islands (McGregor, unpublished).

Emphanisporites rotatus is present high in the Acacus Formation of Downtonian age (based on spore correlation) in Libya; in parts of the San Pedro Formation assigned to the Ludlow and Downtonian by Rodriguez (1978); and in the poudingue de Fépin (lower Gedinnian) and the Oignies Formation (mid-Gedinnian) of Belgium (Streel et al., 1981). It has not been found below the Senni Beds (Siegenian) in the Anglo-Welsh sequence or the basal Stooping River Formation (early Siegenian) in Canada. *Emphanisporites splendens* is so far only known from Spain, north Africa (Richardson, Rasul and Al-Ameri, 1981) and China (Gao, 1981).

Remarks. Work in progress on Downtonian spores by one of us (JBR) may result in subdivision of this zone.

6. *Emphanisporites micrornatus - Streelispora newportensis* Assemblage Zone

Age. Early (but not earliest) and early late Gedinnian, by indirect correlation (Richardson et al., 1981; Richardson, unpublished; Blieck, 1982). *Pteraspis leathensis* and *Rhinopteraspis crouchi* vertebrate zones.

The base of the Gedinnian in the type area is considered to be, in this paper, approximately equivalent to the Siluro-Devonian boundary. Bultynck (1982) recorded conodonts of the *Icriodus woschmidti* Zone (latest Pridolian and earliest Lochkovian) in the boreholes at Artois, northern France, and also recorded the probable presence of this zone in the lower Gedinne Beds at Naux ("20 km southeast of Gedinne"). Palynological samples (Steemans, 1982a) from the Fépin Conglomerate and Haybes Beds, basal Gedinnian of the type locality (Lahonry Quarry), however, have yielded a *micrornatus-newportensis* assemblage that may be correlated with the Chortkov Beds of the Podolian sequence (Richardson et al., 1981). This assemblage is early but not earliest Devonian, and is younger than the *Monograptus uniformis* and *Icriodus woschmidti* zones. The Fépin Conglomerate is therefore regarded here as early but not earliest Gedinnian.

Reference section for the base of the zone. Ross-Tewkesbury Spur Motorway (M. 50), Hereford and Worcester, England (Holland and Richardson, 1977; Richardson, unpublished). Base of the St. Maughan's Group, immediately above the prominent calcrete that ". . . is close to or encloses the Downtonian-Dittonian boundary and includes the "*Psammosteus*" Limestone . . ." (Allen and Dineley, 1976, p. 13).

Range of the zone. Lower and middle Ditton Group (base sensu White, 1950) Shropshire. The upper part of the zone is not well documented, because, so far, only poor assemblages have been found from the upper Ditton Group in the Clee Hills (Richardson, unpublished).

Characteristic species.

Emphanisporites micrornatus Richardson and Lister, 1969, Pl. 38, figs. 10, 11 (Pl. 4, fig. 1).

Streelispora newportensis (Chaloner and Streel) Richardson and Lister, 1969, Pl. 41, figs. 3-6 (Pl. 3, figs. 10, 11).

Acinosporites salopiensis Richardson and Lister, 1969, Pl. 39, figs. 5, 6 (Pl. 3, figs. 12, 13).

Apiculiretusispora plicata (Allen) Streel, 1967, Allen, 1965, Pl. 94, figs. 6-9 (Pl. 4, fig. 2).

Chelinospora cassicula Richardson and Lister, 1969, Pl. 42, figs. 10-12 (Pl. 4, figs. 6, 7).

Cymbosporites proteus McGregor and Camfield, 1976, Pl. 1, figs. 8-16, 21-23 (Pl. 4, figs. 3, 4).

Emphanisporites epicautus Richardson and Lister, 1969, Pl. 38, figs. 13-15 (Pl. 4, fig. 5).

Perotrilites microbaculatus Richardson and Lister, 1969, Pl. 39, figs. 7-13 (Pl. 4, figs. 8, 9).

Retusotriletes maculatus McGregor and Camfield, 1976, Pl. 1, fig. 6 (Pl. 4, fig. 10).

Description. First appearance of prominent, flimsy zona (e.g. "spore zonée sp. A", Steemans, 1981), this feature rare until the succeeding zone. Beginning of sloughing, sculptured exoexine. Increase in the variety of proximally radially-ribbed spores (*Emphanisporites*), including the appearance and common occurrence of specimens with conate and granulate distal sculpture (*E. micrornatus*). Proliferation of reticulate sculpture (*Chelinospora* and, in the upper part of the zone, *Dictyotriletes*). Persistence of spores with proximal, interradial papillae. Most spores are less than 40 µm in diameter.

Distribution and regional variation. Ditton Group, Clee Hills, Shropshire, and St. Maughan's Group, Herefordshire, England; Red Marl Group, Breconshire, Wales (Richardson and Lister, 1969; Richardson, unpublished); Arbuthnott Group, Scotland (Richardson, 1967; Ford, 1972; Richardson et al., 1984); poudingue de Fépin and lower arkose d'Haybes (Steemans, 1982a) and Fooz Formation (Steemans, 1981), Dinant Synclinorium, Belgium; subsurface of Libya (Richardson et al., 1981; Richardson and Al-Ameri, unpublished); Strypa Horizon of the Dniestr Series (Shepeleva, 1963); the Chortkov and Ivane horizons of the Tiver series and the Ustetko Horizon of the lower Dniestr series (Arkhangelskaya, 1980a) of Podolia. *Emphanisporites micrornatus* and other species consistent with the *micrornatus-newportensis* Zone occur in the Kenogami River Formation of Northern Ontario (McGregor and Camfield, 1976). Some elements of the zone are present in the Massif Armoricain of France: the Saint Cenere section (Moreau-Benoit, 1976) and the Saint-Pierre-sur-Erve section (D'Erceville, 1979). *S. newportensis*, but not *E. micrornatus*, has been recorded from the Lower Devonian of Qujing, Yunnan Province, China (Gao Lianda, personal communication to JBR, 1981).

E. micrornatus first appears 30 to 60 m above the base of the zone in the sections examined in the Brown Clee area, and is common in samples from the lower and middle Dittonian (Richardson, unpublished). It also appears in Podolia somewhat later than *S. newportensis*, in the Ivane Horizon (Richardson et al., 1981), and is not yet present in assemblages containing *S. newportensis* in the basal Gedinnian of the type region of the stage (Steemans, 1982a).

7. *Breconisporites breconensis - Emphanisporites zavallatus* Assemblage Zone

Age. Late Gedinnian (Richardson et al., 1982). Approximately *Althaspis leachi* vertebrate zone.

Reference section for the base of the zone. Belgium, southeastern Dinant Synclinorium, Nonceveux section along the road between Remouchamps and Trois-Ponts (Steemans, 1981, 1982b; Richardson et al., 1982); topographic map I.G.M., 1:25,000, Sheet 49, 3-4; Lambert grid X: 246500 and Y: 129750. The base of the zone is 35 m above the base of the Bois d'Ausse Formation. Accessory reference section, South Wales, Brecon Beacons, Glyn Tarell stream section (Hassan, 1982), map reference SN 9752 2163. The lowest strata known to be in the zone are close to the base of the Senni Beds, that is the lowest productive sample occurs within, but not at, the base of the basal sandstone unit of the Senni Beds (Richardson et al., 1982).

Range of the zone. At Nonceveux, the zone includes at least 270 m of the Bois d'Ausse Formation, beginning at the lowest spore-bearing locality 35 m above the base of the Bois d'Ausse. In the southern part of the Dinant Basin the zone covers at least 400 m of strata. In the Black Mountains and Brecon Beacons, it covers the lower 64 to 90 m, respectively, of the Senni Beds except for the first 3 to 4 m of the basal sandstone unit. It is associated with the heterostracan *Althaspis leachi* (White) in Belgium (Richardson et al., 1982).

Characteristic species.

Breconisporites breconensis Richardson, Streel, Hassan and Steemans, 1982, Pl. 1, figs. 7-11 (Pl. 4, fig. 11).

Emphanisporites zavallatus Richardson, Streel, Hassan and Steemans, 1982, Pl. 1, figs. 1-6 (Pl. 4, fig. 13).

Apiculiretusispora plicata (Allen) Streel; see previous zone.

Camptozonotriletes sp. cf. *C. caperatus* McGregor; Hassan, 1982, Pl. 30, figs. 8, 9, 11 (Pl. 4, fig. 12).

Cirratriradites sp. A, Streel et al., 1981, Pl. 3, figs. 10, 11 (Pl. 4, fig. 14).

Clivosispora verrucata McGregor var. *verrucata*, McGregor, 1973, Pl. 7, figs. 4, 5, 10 (Pl. 4, figs. 15, 16).

Description. First appearance of bizonate spores with distal annulate thickening (*Breconisporites breconensis*), coarsely sculptured *Emphanisporites* (*E. zavallatus*), and cingulate verrucate spores (*Clivosispora*). Appearance of zonate spores with verrucate or murornate sculpture (*Camptozonotriletes*).

Distribution. Lower and middle Bois d'Ausse Formation, southeast part of Dinant Synclinorium, and upper Oignies and St. Hubert formations, southern Dinant Synclinorium in Belgium; lower and middle Senni Beds, Brecon Beacons and Black Mountains, Powys and Gwent, south Wales (Hassan, 1982); subsurface of the Moesian Platform, Romania (Beju, 1967); possibly in the Shyashuvian Suite, Lithuania (Arkhangelskaya, 1978).

8. *Verrucosisporites polygonalis - Dictyotriletes emsiensis* Assemblage Zone

Age. Siegenian (and earliest Emsian?). Approximately *Rhinopteraspis dunensis* vertebrate zone, by indirect correlation with Blieck (1982). The precise relationships between the *polygonalis-emsiensis* Zone and the boundaries of the *dunensis* Zone are not known.

Reference section for the base of the zone. Belgium, the southeastern Dinant Synclinorium, Nonceveux section along the road between Remouchamps and Trois-Ponts (Godefroid et al., 1982); topographic map I.G.M., 1:25,000, sheet 49, 3-4; Lambert grid X:248750 and Y:129750. The base of the zone is in the Bois d'Ausse Formation, 81 m below the base of the Solières Formation. Accessory reference section, middle Senni Beds, Craig Cerrig-gleisiad, Brecon Beacons, South Wales, map reference SN 9610 2200 (Richardson and Hassan, unpublished). The base of the zone is about 15.5 m above the base of the section. Samples from the underlying basal Senni Beds contain a *breconensis-zavallatus* assemblage.

Range of the zone. Middle and upper Senni Beds; the overlying Brownstones Group has so far proved barren of spores.

Characteristic species.

Verrucosisporites polygonalis Lanninger, 1968, Pl. 22, fig. 19 (Pl. 5, figs. 1, 2).

Dictyotriletes emsiensis (Allen) McGregor 1973, Pl. 5, fig. 15 (Pl. 5, figs. 4, 5).

Apiculiretusispora arenorugosa McGregor, 1973, Pl. 2, figs. 15, 25 (Pl. 6, fig. 6).

A. cf. *brandtii* Streel, in Edwards, 1968, Pl. 132, figs. 8-10 (Pl. 5, fig. 9).

A. plicata (Allen) Streel; see previous two zones.

Breconisporites breconensis Richardson, Streel, Hassan and Steemans; see previous zone.

Brochotriletes foveolatus? Naumova; McGregor, 1973, Pl. 4, figs. 20, 23, 24 (Pl. 5, fig. 3).

B. hudsonii McGregor and Camfield, 1976, Pl. 3, figs. 1, 2 (Pl. 6, figs. 3, 4).

Camptozonotriletes caperatus McGregor, 1973, Pl. 7, figs. 1, 2 (Pl. 6, fig. 7).

Clivosispora verrucata McGregor var. *convoluta* McGregor and Camfield, 1976, Pl. 2, figs. 13-21 (Pl. 5, figs. 10, 11).

Dibolisporites eifeliensis (Lanninger) McGregor, 1973, Pl. 3, figs. 17-22, 26 (Pl. 5, fig. 6).

D. wetteldorfensis Lanninger; McGregor, 1973, Pl. 3, figs. 23-25 (Pl. 5, figs. 7, 8).

D. n. sp. K, Hassan, 1982, Pl. 12, figs. 1-6, 8-10 (Pl. 6, fig. 5).

Dictyotriletes favosus McGregor and Camfield, 1976, Pl. 2, figs. 5, 6 (Pl. 6, figs. 1, 2).

Emphanisporites decoratus Allen, 1965, Pl. 97, figs. 15-18 (Pl. 5, figs. 12, 13).

Description. Appearance and proliferation of biform sculpture (*Dibolisporites*), including sculptural elements with expanded tips (*D. eifeliensis*). Proliferation of *Apiculiretusispora* spp., and diversification of *Dictyotriletes* spp. and coarsely sculptured *Emphanisporites*. Proximal interradial papillae are rare. First rare megaspores, *Dictyotriletes canadensis*, high in the zone (Grande Grève Formation, McGregor, unpublished).

Distribution. Middle and upper Senni Beds, Brecon Beacons, Breconshire, and Mill Bay Formation (Cosheston Group), Dyfed, South Wales (Richardson, 1967; Richardson and Lister, 1969; Richardson and Thomas in Williams 1978); Grande Grève Formation, Gaspé (McGregor and Owens, 1966; McGregor, unpublished); Stooping River Formation, Northern Ontario (McGregor and Camfield, 1976); Upper Bois d'Ausse Formation and Solières, Acoz, Anor, St. Michel and Petigny formations, Dinant Basin, Belgium (Streel et al., 1981; Steemans, 1981, 1982b; Godefroid et al., 1982); southeast Massif Armoricain, France (Moreau-Benoit, 1976); and possibly the lower part of the Kemeri Series of Lithuania (Arkhangelskaya, 1980a), and the Snowblind Bay Formation of Cornwallis Island, Arctic Canada (McGregor, unpublished).

Dictyotriletes emsiensis appears below *Verrucosisporites polygonalis* in Ontario (McGregor and Camfield, 1976) and in Belgium (Streel, pers. comm., 1984) but above *V. polygonalis* in Gaspé (McGregor, 1977). Neither species has as yet been found in the Brecon Beacons. We have selected the first appearance of *V. polygonalis* to mark the base of the zone in the primary reference section.

9. *Emphanisporites annulatus - Camarozonotriletes sextantii* Assemblage Zone

Age. Early and early late Emsian. Approximately *Polygnathus dehiscens* Zone to *Polygnathus serotinus* Zone inclusive, in the conodont zonation.

Reference section for the base of the zone. Lower Singhofen Group, Beinhausen Formation, Gefell Member, southeast Eifel region (Fuchs, 1974; Riegel and Karathanasopoulos, 1982). Spores have not been found in the lowermost Emsian Ulmen Group, which lies immediately below the Gefell Member. Below the Ulmen Group, the Saxler Schichten (Herdorf Group) of uppermost Siegenian age contains spores, but not the nominal species or other spores typical of the *annulatus-sextantii* Zone, with the exception of *Apiculiretusispora brandtii.* A more suitable reference section, in stratigraphic continuity with underlying spore-bearing beds, may be found as more work is done on strata of this age.

Range of the zone. Base of Beinhausen Formation (Gefell Member) to high Wetteldorf Formation.

Characteristic species.

Emphanisporites annulatus McGregor, 1961, Pl. 1, figs. 5, 6 (Pl. 6, figs. 9, 10).

Camarozonotriletes sextantii McGregor and Camfield, 1976, Pl. 4, 13, 14, 16-18 (Pl. 6, figs. 11, 12).

Acinosporites lindlarensis Riegel var. *lindlarensis*, Riegel, 1968, Pl. 19, figs. 11-16 (Pl. 6, fig. 8).

Apiculatasporites microconus (Richardson) McGregor and Camfield, 1982; Richardson, 1965, Pl. 89, fig. 3 (Pl. 7, fig. 1).

Apiculiretusispora brandtii Streel, 1964, Pl. 1, figs. 6-10 (Pl. 7, fig. 5).

A. plicata (Allen) Streel; see previous two zones.

**Calyptosporites biornatus* (Lanninger) Richardson, 1974; Lanninger, 1968, Pl. 25, fig. 12 (Pl. 7, fig. 4).

Camptozonotriletes cf. *aliquantus* Allen, 1965; Riegel, 1973, Pl. 15, figs. 4, 5 (Pl. 7, fig. 7).

Dibolisporites echinaceus (Eisenack) Richardson, 1965, Pl. 89, figs. 5, 6 (Pl. 7, figs. 2, 3).

Dibolisporites eifeliensis (Lanninger) McGregor; see previous zone.

Dictyotriletes canadensis McGregor, 1973, Pl. 5, figs. 21-23 (Pl. 7, fig. 8).

D. gorgoneus Cramer, 1967, Pl. 3, figs. 69, 72 (Pl. 7, fig. 6).

Emphanisporites schultzii McGregor, 1973, Pl. 6, fig. 14 (Pl. 7, fig. 9).

Verruciretusispora dubia (Eisenack) Richardson and Rasul, 1978, Pl. 1, fig. 6 (Pl. 7, fig. 10).

Description. Greatest abundance and diversification of proximally radially ribbed spores (*Emphanisporites*). First appearance of distally annulate forms of *Emphanisporites*, for example *E. erraticus* and *E. annulatus*, the latter with an indistinctly delimited annulus in early Emsian and sharply delimited annulus in later Emsian. Diversification of biform sculpture (*Dibolisporites*). First appearance of *D. echinaceus* sensu Richardson (1965), *Apiculatasporites microconus* and *Acinosporites lindlarensis*, species that are more common in the succeeding zone. First prominent-spined zonate-pseudosaccates in the upper part of the zone. First rare monolete spores. Diversification of small megaspores.

Distribution and regional variation. Beinhausen Formation, Gefell Member (Riegel and Karathanasopoulos, 1982), Stadtfeld, Klerf, Wiltz and Wetteldorf formations (Lanninger, 1968; Schultz, 1968), and Hunsrück Shale (Karathanasopoulos, 1975), in the Rheinisches Schiefergebirge; subsurface of southern England (Richardson and Rasul, 1978); "Emsian 2-3" of Sart-Tilman, Liège (Streel, 1967) and Wépion and Pesche beds in the Dinant Synclinorium (Streel et al., 1981) in Belgium; subsurface of Romania (Beju, 1967); Daleje Shale, Czechoslovakia (McGregor, 1979a); Ouan Kasa Formation and upper Tadrart Formation of Libya (Massa and Moreau-Benoit, 1976; Moreau-Benoit, 1979, 1980); York River Formation and lower Battery Point Formation of Gaspé (McGregor, 1977), La Garde Formation and Atholville beds of lower Restigouche River, Quebec and New Brunswick (Dineley and Williams, 1968), Sextant and Stooping River formations of Northern Ontario (McGregor and Camfield, 1976), and Vendom Fiord Formation of Ellesmere Island (McGregor, 1974 and unpublished) in Canada; Reuterskiøldfjellet Sandstone of Vestspitsbergen (Allen, 1965, 1967). Possibly in the Horlick Formation of Ohio Range, Antarctica (Kemp, 1972); La Vid Shales, Spain (Cramer, 1967); Danlin Formation, Kueichow, China (Gao and Hou, 1975); Malobachat Horizon of Salair, U.S.S.R. (Andreeva, 1973); and the upper part of the Kemeri Series of Lithuania (Arkhangelskaya, 1980a).

The upper part of this zone may occur in the Takata, Muradymovo, Vanyashkino and Vyazovo deposits of the western slope of the South Urals, where Chibrikova (1978, p. 111) has reported spores similar to the spores from the upper Emsian of the Rhine area, Belgium, Canada, and Spitsbergen. Spores with prominent, bifurcate-tipped spines, that typify the succeeding *douglastownense-eurypterota* Zone, including the upper Wetteldorf-Heisdorf-Lauch sequence of the Rhine region, have not been reported from these beds. According to Chibrikova (1972, p. 33; 1978), the Vanyashkino and Vyazovo are characterized by an influx of large, sculptured zonate-pseudosaccate spores (*Hymenozonotriletes* of the Soviet nomenclature). This event may correlate with the first appearance of similar spores in the upper part of the *annulatus-sextantii* Zone in western Europe and Canada (see Figure 2). The Vyazovo beds contain conodonts of the *Polygnathus inversus* and *P. serotinus* zones (Maslov et al., 1983), which is additional evidence that the Vyazovo deposits are older than the Heisdorf and uppermost Wetteldorf beds of the Eifel region (Weddige, 1977).

In Czechoslovakia, *Camarozonotriletes sextantii* is rare in the Daleje Shale near Srbsko, high in the tentaculite *Nowakia cancellata* Zone (McGregor, 1979a), but *E. annulatus* has not been found, perhaps owing to insufficient study.

The first large, prominent-spined, zonate-pseudosaccate spores appear well up in the *annulatus-sextantii* Zone, but they are not abundant until the succeeding *douglastownense-eurypterota* Zone. Such spores occur in the Wiltz Formation and possibly, if records of *Calyptosporites biornatus* are substantiated, as early as the Klerf Formation of the southeast Eifel region (Riegel and Karathanasopoulos, 1982); high in the *N. cancellata* Zone of the Barrandian region (McGregor, 1979a); and high in the Battery Point Formation of eastern Gaspé (McGregor, 1977).

Camarozonotriletes sextantii is rare in the Battery Point Formation of Gaspé, but is abundant in the Sextant and Stooping River formations of Northern Ontario. T.T. Uyeno comments as follows (personal communication to DCM, 1984): "In the Stooping River Formation it [*C. sextantii*] begins about 65 m above the apparent base of the conodont *dehiscens* Zone. This base cannot be located precisely, because the conodont faunas of the Stooping River Formation consist primarily of icriodontids, not zone-defining polygnathids. The Pragian-Zlichovian boundary occurs within the *dehiscens* Zone (Klapper and Johnson, 1980, p. 403), but as the lower limit of this zone cannot be located, the stadial boundary is similarly elusive." In Belgium, Steemans (1982b) found *C. sextantii* in the Petigny Formation, i.e. in the upper Siegenian. It has not been found in the reference section or in other spore-bearing strata of the Rhineland (Riegel and Karathanasopoulos, 1982), or in the U.S.S.R.

In the Eifel region, the *annulatus-sextantii* Zone can be subdivided in the Lower Emsian by the appearance of *Verruciretusispora dubia* and possibly *Calyptosporites biornatus* in the lower Klerf Formation. However, *V. dubia* has not been recorded below the succeeding *douglastownense-eurypterota* Zone in Gaspé. *Acinosporites lindlarensis*, a characteristic species of the *douglastownense-eurypterota*

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*There is a disagreement between the authors regarding the generic names of some pseudosaccate spores. For those taxa marked with an asterisk DCM would prefer to use *Grandispora* and JBR would prefer *Calyptosporites* or, for some, *Spinozonotriletes*. No new combinations are proposed. For discussion see Richardson (1960, p. 58; 1965, p. 583), Playford (1971, p. 45), Riegel (1973, p. 97), and McGregor and Camfield (1982, p. 43).

Zone in western Europe, occurs high in the *annulatus-sextantii* Zone in the Stooping River Formation. *Emphanisporites annulatus* and some other species of the *annulatus-sextantii* Zone are present in the Icla Formation of the Tarabuco region, Bolivia (McGregor, 1984). However, *E. annulatus* has not been recorded from Arctic Canada or Spitsbergen.

10. ******Grandispora douglastownense* **-** *Ancyrospora eurypterota* **Assemblage Zone**

Age. Late Emsian and earliest Eifelian. Approximately *Polygnathus costatus patulus* Zone to lowermost *Polygnathus costatus costatus* Zone inclusive, of the conodont scale.

Reference section for the base of the zone. Uppermost Wetteldorf Formation, Plein Quarry, west side of Remel-Bach-Tal, 3 km east of Murlenbach, Salmerwald Syncline, Eifel region (Riegel, 1975, p. 62, 258; 1982).

Range of the zone. High in the Wetteldorf Formation to the top of the Lauch Formation.

Characteristic species.

Grandispora douglastownense McGregor, 1973, Pl. 8, figs. 8, 9, 12-14 (Pl. 8, fig. 3).

Ancyrospora eurypterota Riegel, 1973, Pl. 17, figs. 1-5 (Pl. 8, figs. 1, 2).

Acinosporites apiculatus (Streel) Streel, 1967; Streel, 1964, Pl. 1, fig. 13 (Pl. 8, figs. 4, 5).

Ancyrospora kedoae (Riegel) Turnau, 1974; Riegel, 1973, Pl. 15, figs. 1-3 (Pl. 9, fig. 1).

A. nettersheimensis Riegel, 1973, Pl. 17, figs. 6-8 (Pl. 8, figs. 7, 8).

A. loganii McGregor, 1973, Pl. 9, figs. 6, 7, 10-12 (Pl. 8, fig. 6).

Apiculiretusispora gaspiensis McGregor, 1973, Pl. 3, figs. 1-4 (Pl. 9, fig. 2).

**Calyptosporites* sp. nov. Riegel, 1975; 1982, Pl. 1, fig. 4 (? = *Hymenozonotriletes endemicus* Chibrikova, 1959) (Pl. 9, fig. 3).

**Calyptosporites proteus* (Naumova) Allen, 1965, Pl. 103, figs. 10, 11 (Pl. 9, fig. 4).

Dibolisporites echinaceus (Eisenack) Richardson, 1965; see previous zone.

Grandispora eximia (Allen) McGregor and Camfield, 1982, Pl. 10, figs. 2, 6, 7 (Pl, 9, fig. 5).

Hystricosporites cf. *H. corystus* Richardson, 1965; Riegel, 1973, Pl. 12, figs. 3, 4 (Pl. 9, fig. 7).

H. microancyreus Riegel, 1973, Pl. 12, figs. 6, 7 (Pl. 10, figs. 1, 2).

**Spinozonotriletes arduinnae* Riegel, 1973, Pl. 16, figs. 1-3 (Pl. 9, fig. 6).

Description. Appearance of bifurcate appendages (*Ancyrospora, Hystricosporites*). Proliferation of large, apiculate and spinose, zonate-pseudosaccate spores (*Calyptosporites-Grandispora*). Disappearance of most reticulate and tripapillate spores and distally sculptured forms of *Emphanisporites*. Marked increase in spore size. Persistence and proliferation of *Dibolisporites echinaceus*, *Apiculatasporites microconus*, and *Verruciretusispora dubia*.

Distribution and regional variation. Upper Wetteldorf Formation and Heisdorf and Lauch formations of the Eifel region (Riegel, 1973, 1982); uppermost Hierges Formation of the Ardennes (Streel, Demaret-Fairon and Otazo, 1975; Streel et al., 1981); upper Battery Point Formation of Gaspé (McGregor, 1977), Wapske Formation of New Brunswick, McAdam Lake Formation of Nova Scotia, Blue Fiord Formation south of Strathcona Fiord, Ellesmere Island, and unnamed strata in the subsurface of Melville Island and the Grand Banks (McGregor, unpublished) in Canada; Trout Valley Formation of Maine, U.S.A. (Andrews et al., 1977); subsurface of Poland (Turnau, 1974). Possibly in North Africa (Massa and Moreau-Benoit, 1976), the Kuznets Basin and the southwest Urals (Chibrikova, 1977).

Bifurcate spines seem to be less common at this level in asiatic parts of the Soviet Union, but the comparison is of questionable validity owing to uncertain correlation. In the Barrandian region, the strata in which this zone would be expected, that is, the upper part of the Třebotov Limestone and its correlatives, contain only rare, poorly preserved spores (McGregor, unpublished). Spores high in the preceding spore zone have been recovered from the tentaculite upper *N. richteri* Zone of the lower Třebotov Limestone at Praha-Hlubočepy (McGregor, 1979a).

Remarks. If *Calyptosporites* sp. nov. of Riegel (see above) can be equated with *Hymenozonotriletes endemicus*, a link would be established with assemblages from the Ryazhsk Horizon of the central part of the Russian Platform (Arkhangelskaya, 1974) and the *Calceola* Horizon of the South Urals (Chibrikova, 1977, fig. 36).

The upper part of the Ryazhsk on the Russian Platform, including the lower *Periplecotriletes tortus* Zone of Soviet nomenclature (see Figure 1) was correlated with the Heisdorf Formation (i.e. the lower part of the *douglastownense-eurypterota* Zone) of the Eifel by Arkhangelskaya (1983). In contrast, the Ryazhsk and *Calceola* deposits of the South Urals were aligned with a higher part of the Eifel sequence by Chibrikova (1983), possibly with the Lauch and Nohn formations. The Ryazhsk and *Calceola* beds would then correlate at least in part with the *velatus-langii* Zone, a conclusion close to Arkhangelskaya's earlier (1976) opinion on correlation of these beds. From photographs and other information in the paper by Arkhangelskaya (1976) it would seem that the thin, upper part of the Ryazhsk Horizon in the central regions of the Russian Platform, with **Calyptosporites velatus* and ?*Densosporites devonicus*, would be no older than the Nohn Formation (*velatus-langii* Zone, early Eifelian) of the Eifel. This is in contrast to Arkhangelskaya's later (1983) correlation of the upper Ryazhsk with the Heisdorf Formation (late Emsian).

11. *Calyptosporites velatus - Rhabdosporites langii* Assemblage Zone

Age. Early Eifelian. *Polygnathus costatus costatus* Zone of the conodont succession.

Reference section for base of zone. Nohn Formation, Lierberg section, north side of Sötenich Syncline, Eifel region (Paulus, 1961, p. 37; Riegel, 1975). New exposures being investigated in the north Eifel region may provide a more suitable reference section (W. Riegel, pers. comm., 1981).

Range of zone. Base to near top of Nohn Formation.

Characteristic species.

Calyptosporites velatus (Eisenack) Richardson, 1962; Richardson, 1960, Pl. 14, fig. 4 (Pl. 10, fig. 6).

Rhabdosporites langii (Eisenack) Richardson, 1960, Pl. 14, figs. 8, 9 (Pl. 10, fig. 5).

Acinosporites acanthomammillatus Richardson, 1965, Pl. 91, figs. 1, 2 (Pl. 10, figs. 3, 4).

A. macrospinosus Richardson, 1965, Pl. 91, figs. 3-6 (Pl. 10, fig. 9).

Anapiculatisporites petilus Richardson, 1965, Pl. 89, fig. 11 (Pl. 10, fig. 7).

Ancyrospora ancyrea (Eisenack) Richardson var. *ancyrea*; Richardson, 1962, Pl. 25, figs. 6, 7 (Pl. 11, figs. 1, 2).

Corystisporites multispinosus Richardson, 1965, Pl. 89, fig. 10 (Pl. 12, fig. 1).

Densosporites concinnus (Owens) McGregor and Camfield, 1982, Pl. 6, figs. 13, 14, 18, 19 (Pl. 12, fig. 2).

Grandispora longa Chi and Hills, 1976, Pl. 14, figs. 1, 2 only (Pl. 11, figs. 7, 8).

Kraeuselisporites acerosus (Arkhangelskaya) McGregor and Camfield, 1982, Pl. 14, figs. 6, 7, 9, 10 (Pl. 11, figs. 3, 4).

Kraeuselisporites ollii? (Chibrikova) McGregor and Camfield, 1982, Pl. 14, figs. 2-5, 8 (Pl. 10, fig. 8).

Periplecotriletes tortus Egorova, 1974, Pl. 1, fig. 5 (Pl. 11, figs. 5, 6).

Perotrilites bifurcatus Richardson, 1962, Pl. 25, figs. 4, 5 (Pl. 12, fig. 3).

Retusotriletes distinctus Richardson, 1965, Pl. 88, figs. 7, 8 (Pl. 12, fig. 5).

R. rugulatus Riegel, 1973, Pl. 10, figs. 2-4 (Pl. 12, fig. 4).

Description. Proliferation of finely-sculptured zonate-pseudosaccate spores intermediate in size between miospores and megaspores. Beginning of spores that are both zonate and camerate and have a flimsy exoexine (*Perotrilites sensu* Evans, 1970). Diversification of murornate-spinose spores (*Acinosporites*). Persistence of most species from the previous zone.

Distribution and regional variation. Upper Lauch and Nohn formations of the Eifel region (Riegel, 1973, 1975, 1982); Morsovo Horizon, Russian Platform (Arkhangelskaya, 1976); upper Battery Point Formation, Gaspé (McGregor, 1977); McAdam Lake Formation of Nova Scotia (McGregor, unpublished); Cape De Bray Formation and lowest Weatherall Formation, Melville Island, Arctic Canada (McGregor and Camfield, 1982); Strathcona Fiord Formation and lowermost Hecla Bay Formation, Ellesmere Island, Arctic Canada (McGregor, unpublished); Aouinet Ouenine Formation of Libya (Massa and Moreau-Benoit, 1976; Moreau-Benoit, 1980). Both nominal species are important elements of early Eifelian to late Givetian assemblages in southern China and in the ORS region across Arctic and Eastern Canada, Western Europe, North Africa, the Russian Platform and probably Central Asia. *Acinosporites* spp. may have a more restricted geographical distribution, but the spores of this genus are common in the Scottish Old Red Sandstone, parts of Eastern and Arctic Canada, and probably the Russian Platform. *Ancyrospora ancyrea* has not so far been recorded from Soviet Asia but has been reported from southern China (Gao and Hou, 1975).

12. *Densosporites devonicus - *Grandispora naumovii* Assemblage Zone

Age. Mid-Eifelian to early Givetian. Approximately upper *Polygnathus costatus costatus* Zone to upper *Polygnathus xylus ensensis* Zone inclusive in the conodont scale (by indirect correlation).

Reference section for the base of the zone. Type section of the Weatherall Formation, 152 m above its base, 16.2 km east of the east arm of Weatherall Bay, northeastern Melville Island, Arctic Canada (McGregor and Camfield, 1982). Accessory reference section, upper Nohn Formation, Lierberg section, north side of the Sötenich Syncline, Eifel region (Paulus, 1961; Riegel, 1973).

Range of the zone. Near the base to near the top of the Weatherall Formation, eastern Melville Island. Uppermost Nohn to "Fleringer" and Dreimühlen(?) formations, Eifel region (the position of the upper part of the zone is uncertain in the Eifel).

Characteristic species.

Densosporites devonicus Richardson, 1960, Pl. 14, fig. 10 (Pl. 12, fig. 6).

Grandispora naumovii (Kedo) McGregor, 1973; Kedo, 1955, Pl. 4, fig. 8 (Pl. 13, fig. 1).

Acinosporites acanthomammillatus Richardson; see previous zone.

A. macrospinosus Richardson; see previous zone.

Ancyrospora grandispinosa Richardson, 1960, Pl. 14, fig. 7 (Pl. 13, fig. 7).

***Cristatisporites orcadensis* Richardson, 1960, Pl. 14, fig. 2 (Pl. 13, fig. 2).

Densosporites inaequus (McGregor) McGregor and Camfield, 1982, Pl. 7, figs. 1-6 (Pl. 12, fig. 7).

Grandispora inculta Allen, 1965, Pl. 734, figs. 7-9 (Pl. 13, fig. 5).

G. mammillata Owens, 1971, Pl. 14, figs. 1-4 (Pl. 12, fig. 8).

Hystricosporites gravis Owens, 1971, Pl. 8, figs. 1-3 (Pl. 14, fig. 1).

H. reflexus Owens, 1971, Pl. 7, figs. 1-4 (Pl. 14, fig. 7).

Kraeuselisporites rugosus (Owens) McGregor and Camfield, 1982, Pl. 14, figs. 11, 12 (Pl. 13, fig. 6).

Lophotriletes devonicus (Naumova ex Chibrikova) McGregor and Camfield, 1982, Pl. 15, figs. 5-11 (Pl. 13, fig. 3).

Perotrilites conatus Richardson, 1965, Pl. 91, figs. 10, 11 (Pl. 13, fig. 4).

Retispora archaelepidophyta (Kedo) McGregor and Camfield, 1982, Pl. 16, figs. 4-7, 10 (Pl. 14, figs. 3, 4).

Retusotriletes distinctus Richardson, 1965; see previous zone.

R. rugulatus Riegel; see previous zone.

Rhabdosporites langii (Eisenack) Richardson; see previous zone.

Verrucosisporites premnus Richardson, 1965, Pl. 90, figs. 1, 2 (Pl. 14, figs. 5, 6).

V. scurrus (Naumova) McGregor and Camfield, 1982, Pl. 18, figs. 10-17, 22 (Pl. 14, fig. 2).

Description. First appearance and diversification of cingulizonate spores with bifurcate spines (*Densosporites* spp.). First appearance of irregular, large, verrucate sculpture (e.g. *Verrucosisporites premnus, V. scurrus*). Beginning of foveoreticulate sculpture on pseudosaccate spores (*Retispora*). Persistence of all characteristic species of the previous zone. No sharp distinction in size can yet be made between miospores and megaspores.

Distribution and regional variation. Weatherall Formation of eastern Melville Island (McGregor and Camfield, 1982), Bird Fiord Formation of Ellesmere, Helena and Devon islands, lower Hecla Bay Formation of southeastern Ellesmere Island, and subsurface of Bathurst and Cameron islands (McGregor, unpublished) in the Canadian Arctic; upper Battery Point Formation and Malbaie Formation of Gaspé (McGregor, 1977) and Williams Island Formation of Northern Ontario (McGregor and Camfield, 1976) in Eastern Canada; Ahrdorf, Junkerberg, Freilingen, "Fleringer" and Dreimühlen(?) formations of the Prüm Syncline, and upper Nohn Formation of the Sötenich Syncline, Eifel region (Riegel, 1975); upper Lower and Upper Caithness Flagstone, and upper Lower and lower Upper Stromness groups, Orcadian Basin, Scotland (Richardson, 1965; Richardson, unpublished); Mosolovo and Chernoyar horizons of the Russian Platform (Arkhangelskaya, 1974). Possibly in the McAras Brook Formation of St. George's Bay, Nova Scotia, Canada (McGregor, unpublished).

Densosporites devonicus has been found in Scotland, Germany, Arctic and Eastern Canada and central parts of the Russian Platform. In the Rhineland, it is rare and sporadic in the Nohn, Ahrdorf, Junkerberg and Freilingen formations. It is abundant at some localities in the Achanarras Fish Bed, Scotland (Richardson, 1965). In western Europe, *Verrucosisporites premnus* is restricted to the upper part of the zone, and in the Orcadian Basin it has not been recorded below the Eday Group, northeast Scotland (Richardson, 1965).

13. *Geminospora lemurata - Cymbosporites magnificus* Assemblage Zone

Age. Mid-Givetian. Approximately equivalent to the upper *Polygnathus xylus ensensis* Zone to the lower Upper *Polygnathus varcus* Subzone inclusive, of the conodont scale (by indirect correlation).

Reference section for the base of the zone. Uppermost beds of the Weatherall Formation, northeast of Beverley Inlet, southeastern Melville Island, Arctic Canada (Embry and Klovan, 1976; McGregor and Uyeno, 1972; McGregor, 1981).

Range of the zone. Upper Weatherall Formation, from 31.5 m below its contact with the Hecla Bay Formation, to the upper beds of the Hecla Bay Formation.

Characteristic species.

Geminospora lemurata Balme, 1962, emend. Playford, 1983, figs. 1-9 (Pl. 4, figs. 8, 9).

Cymbosporites magnificus (McGregor) McGregor and Camfield, 1982, Pl. 6, figs. 4, 5; McGregor, 1960, Pl. 13, figs. 2-4 (Pl. 14, fig. 11).

Ancyrospora langii (Taugourdeau-Lantz) Allen, 1965, Pl. 106, figs. 5-7 (Pl. 16, figs. 2, 3).

Aneurospora goensis Streel, 1964, Pl. 1, figs. 16-20 (Pl. 16, fig. 4).

A. greggsii (McGregor) Streel, in Becker et al., 1974; McGregor, 1964, Pl. 1, figs. 1-12 (Pl. 15, fig. 10).

Archaeozonotriletes variabilis Naumova, 1953; Allen, 1965, Pl. 100, figs. 3-6 (Pl. 14, fig. 10).

A. timanicus Naumova, 1953, Pl. 12, fig. 14 (Pl. 15, figs. 4, 5).

Biharisporites parviornatus Richardson, 1965, Pl. 90, figs. 12, 13 (Pl. 15, fig. 1).

Corystisporites serratus (Naumova) McGregor and Camfield, 1982; Naumova, 1953, Pl. 1, figs. 19, 20 (Pl. 15, fig. 6).

**JBR prefers to use the name *Samarisporites*.

Geminospora? bislimbata (Chibrikova) McGregor and Camfield, 1982, Pl. 8, figs. 12, 13; Chibrikova, 1959, Pl. 8, fig. 8 (Pl. 15, fig. 2).

Grandispora tomentosa Taugourdeau-Lantz, 1967, Pl. 1, figs. 7, 8 (Pl. 16, fig. 8).

Hymenozonotriletes celeber Chibrikova, 1959, Pl. 13, fig. 3 (Pl. 15, fig. 7).

Perotrilites conatus Richardson; see previous zone.

P. heclaensis McGregor and Camfield, 1982, Pl. 15, figs. 18-21 (Pl. 15, fig. 3).

Description. Appearance of small-sculptured, camerate spores with a thick exoexine (*Geminospora*). Proliferation of spores with highly irregular verrucate to baculate sculpture (*Verrucosisporites* spp. and *Dibolisporites* spp.). Diversification of species of patinate spores (*Archaeozonotriletes* spp., *Cymbosporites* spp.). Clear distinction in size between miospores and megaspores.

Distribution and regional variation. Uppermost Weatherall Formation and Hecla Bay Formation of Melville Island (McGregor and Uyeno, 1972; McGregor, 1981) and correlative strata of Bathurst, Vanier, Cameron, and Ellesmere islands (McGregor, unpublished) in the Canadian Arctic; Vorobyev, Staryi Oskol and Ardatov beds and their correlatives of the European U.S.S.R. (Naumova, 1953; Kedo, 1955; Araslanova, 1973; Raskatova, 1974). Possibly in the upper Mimer Valley Formation of Vestspitsbergen (Allen, 1965, 1967) and the Blacourt Formation of the Boulonnais, France (Loboziak and Streel, 1980).

Remarks. *Archaeozonotriletes basilaris* Naumova (1953), regarded by Soviet palynologists as an indicator of Vorobyev (early Givetian) and younger age, is thought by Medianik (1982) to be a junior synonym of *Geminospora lemurata*. *A. basilaris* reaches its acme in strata of Mullino to Kynov age in the U.S.S.R. (Araslanova, 1973; Medianik, 1982), (mid to late Givetian in terms of the stage definitions used in this paper), and continues up to the late Frasnian in lesser numbers. Its range and acme thus are similar to those known on a world scale for *G. lemurata*. *A. basilaris* may also be at least a partial synonym of *Aneurospora greggsii* (McGregor) Streel, but this is yet to be determined.

14. *Contagisporites optivus* var. *optivus* - ***Cristatisporites triangulatus*** Assemblage Zone

Age. Late Givetian and early Frasnian. Approximately Upper *Polygnathus varcus* Subzone to Lower *Polygnathus asymmetricus* Zone inclusive, in the conodont scale (by indirect correlation).

Provisional reference section for the base of the zone. Hecla Bay Formation, northeast of Beverley Inlet, southeastern Melville Island, Arctic Canada (Embry and Klovan, 1976; McGregor and Uyeno, 1972; McGregor, 1981). Spore-bearing beds are sparse at the base of the zone in this section. A stratigraphic sequence on the east side of Kellett Strait, Melville Island, now being studied by DCM, may be a more suitable reference section.

Range of the zone. Hecla Bay Formation, 872 m above its base, to the Beverley Inlet Formation, 303 m above its base.

Characteristic species.

Contagisporites optivus (Chibrikova) Owens var. *optivus*; Owens, 1971, Pl. 16, figs. 1-3 (Pl. 16, fig. 1).

Cristatisporites triangulatus (Allen) McGregor and Camfield, 1982; Allen, 1965, Pl. 99, figs. 1-6 (Pl. 15, fig. 9).

Ancyrospora involucra Owens, 1971, Pl. 24, figs. 5, 6, Pl. 25, figs. 1, 2 (Pl. 15, fig. 8).

A. langii (Taugourdeau-Lantz) Allen; see previous zone.

A. melvillensis Owens, 1971, Pl. 23, figs. 5-6 (Pl. 16, figs. 6, 7).

Aneurospora goensis Streel; see previous zone.

A. greggsii (McGregor) Streel; see previous zone.

Archaeoperisaccus timanicus Pashkevich, 1964, Pl. 14, figs. 1-4 (Pl. 16, fig. 9).

Chelinospora concinna Allen, 1965, Pl. 101, figs. 12-20 (Pl. 16, fig. 10).

C. ligurata Allen, 1965, Pl. 102, figs. 1-7 (Pl. 16, fig. 5).

Geminospora lemurata Balme emend. Playford, 1983; see previous zone.

Grandispora tomentosa Taugourdeau-Lantz; see previous zone.

Description. First appearance of forms with prominent development of zona in the radial regions (*Cristatisporites triangulatus*). Diversification of small-sculptured camerate spores with a thick exoexine (*Geminospora*) and their dominance in some nearshore marine and external continental facies. Waning of *Rhabdosporites langii*, *Calyptosporites velatus* and *Dibolisporites echinaceus*. Disappearance of *Grandispora naumovii* and *Perotrilites bifurcatus*. Persistence, and abundance in some assemblages, of anchor-spined spores with broad, conical spines that bear small, terminal bifurcations (e.g. *Ancyrospora melvillensis*). Appearance of multifurcate spines high in the zone (Taugourdeau-Lantz, 1971). First monolete camerate spores (*Archaeoperisaccus timanicus*) in the middle of the zone (Medianik, 1980; McGregor, 1981).

Distribution and regional variation. Hecla Bay and Beverley Inlet formations of eastern Melville Island, Weatherall Formation of western Melville Island and Prince Patrick Island (McGregor, 1981), upper Hecla Bay Formation and lower Fram Formation of southwestern Ellesmere Island, Hare Indian Formation of the western District of Mackenzie, lower Flume Formation of east central British Columbia, Escuminac Formation of Quebec, and unnamed strata in the subsurface of the Grand Banks (McGregor, unpublished) in Canada; subsurface of Belgium (Streel, 1972); Blacourt Formation, Boulonnais, France (Loboziak and Streel, 1980); upper Mimer Valley Formation of Vestspitsbergen (Allen, 1965, 1967); and the Mullino, Pashiya, Kynov and Sargaevo beds and their correlatives in the European U.S.S.R. (Chibrikova, 1962; Araslanova, 1973). Possibly in the Nation River Formation of east-central Alaska (Scott and Doher, 1967), the Pine Point Formation of the District of Mackenzie, Canada (Audretsch, 1968), the subsurface of southern England (Mortimer and Chaloner, 1972; McGregor, 1981), the Sherkin Formation of County Cork, Ireland (Clayton and Graham, 1974), and the Bu Ness, Observatory and Ward Hill groups of Fair Isle, Shetland (Marshall and Allen, 1982).

The "Haikou Formation" of Longhuashan, Zhanyi, China contains *Cristatisporites* (al. *Samarisporites*) *triangulatus* and *Chelinospora ligurata*, and a *Stringocephalus* fauna that is taken to indicate Givetian age (Lu, 1980a). It also contains a distinctive monolete spore superficially like *Archaeoperisaccus* but with transverse exinal folds suggesting distal cavation (Lu, 1980b). Spores like it have not been found in the ORS region. Two other species in the same spore assemblage (Lu, 1980b) apparently are similar to *Archaeoperisaccus* spp. of the ORS region and may represent the earliest record of specimens of this genus.

Remarks. The appearance of multifurcate spines and *A. timanicus* may eventually form the basis for subdividing this zone.

Loboziak and Streel (1980) identified *Cristatisporites triangulatus* from near the base of the Blacourt Formation in the Boulonnais, immediately below conodonts of the *Icriodus obliquimarginatus* Zone. As far as we are aware, this is the earliest age claimed for this species. The age of the sample seems to be beyond dispute. If their concept of *C. triangulatus* is the same as ours, and/or as that of the Soviet palynologists (see Pychova, 1960; Volochaev et al., 1979; Kedo and Obukhovskaya, 1981), the documented stratigraphic range of this species would be extended significantly downward by this record, and the base of the *optivus-triangulatus* Zone would need to be redefined.

However, the oldest specimens identified as *C. triangulatus* in the Boulonnais occur three conodont zones below the first record of *Geminospora lemurata* (Loboziak and Streel, 1980) in the same region, whereas in Arctic Canada (McGregor, 1981), and in the European U.S.S.R. (e.g. in Fomina, 1968), their order of appearance is reversed, if one uses the synonymy for *G. lemurata* given in McGregor and Camfield (1982) and suggested by Playford (1983), and the synonymy for *C. triangulatus* given by Allen (1982). The context of the assemblages in which these species first occur in Canada and the U.S.S.R. suggests that *G. lemurata* may occur well below *C. triangulatus* in beds equivalent to the conodont *obliquimarginatus* Zone (Fig. 6). Nevertheless, none of the Canadian or Soviet reports include data on co-occurring faunas that would permit international correlation of the spore ranges. Further work is needed in order to correlate the stratigraphic ranges of both species.

15. *Archaeoperisaccus ovalis - Verrucosisporites bulliferus* Assemblage Zone

Age. Frasnian. Approximately the Middle *Polygnathus asymmetricus* Zone to the *Palmatolepis gigas* Zone inclusive in the conodont scale.

Reference section for the base of the zone. Noces Member, Beaulieu Formation, Caffiers area, Ferques railroad section, Boulonnais, France (Brice et al., 1979; Loboziak and Streel, 1981). The base of this zone is well defined in this section, as it is in stratigraphical continuity with beds below containing spores of the *optivus-triangulatus* Zone. Accessory reference section (for the *Archaeoperisaccus* assemblage), Beverley Inlet Formation, northeast of Beverley Inlet, southeastern Melville Island (Embry and Klovan, 1976; McGregor and Uyeno, 1972; McGregor, 1981).

Range of the zone. In the Boulonnais, from the Noces Member of the Beaulieu Formation to the upper (but not uppermost) Hydrequent Formation inclusive. In the Canadian Arctic, from the Beverley Inlet Formation, 353 m above the base, to about 110 m above the base of the overlying Parry Islands Formation.

Characteristic species.

Archaeoperisaccus ovalis Naumova, 1953, Pl. 14, fig. 13 (Pl. 17, fig. 1).

Verrucosisporites bulliferus n. name; replaced synonym, *V. bullatus* Taugourdeau-Lantz, 1967, p. 50, Pl. 2, figs. 9, 10 (non *V. bullatus* Balme and Hennelly, 1956) (Pl. 17, fig. 2).

Ancyrospora furcula Owens, 1971, Pl. 23, figs. 1-4 (Pl. 17, figs. 4, 5).

A. melvillensis Owens, 1971; see previous zone.

Aneurospora greggsii (McGregor) Streel, 1974; see previous two zones.

Archaeoperisaccus opiparus Owens, 1971, Pl. 22, figs. 1-6 (Pl. 17, fig. 3).

cf. *Archaeozonotriletes laetus* Sergeeva in Nazarenko et al., 1971, Pl. 5, fig. 11 (Pl. 17, fig. 7).

Diaphanospora reticulata Guennel, 1963, figs. 17-19 (Pl. 17, fig. 11).

Geminospora lemurata Balme emend. Playford, 1983; see previous two zones.

Hymenozonotriletes deliquescens Naumova, 1953, Pl. 9, fig. 8 (Pl. 17, fig. 6).

Lophozonotriletes media Taugourdeau-Lantz, 1967, Pl. 2, fig. 6 (Pl. 17, fig. 10).

Nikitinsporites canadensis Chaloner, 1959, Fig. 4, Pl. 55, fig. 5 (Pl. 17, figs. 8, 9).

Description. First appearance and acme of minutely sculptured, monolete, camerate spores (*Archaeoperisaccus* spp). Proliferation of multifurcate-spined spores (e.g. *Ancyrospora furcula*) and small megaspores (e.g. *Nikitinsporites*). Most ancyrospores with broad, conical, bifurcate spines disappear in the upper part of the zone. Continued prominence of *Geminospora* spp. and bifurcate-spined spores. Decline and disappearance of most large, sculptured, zonate-pseudosaccate miospores. Beginning of marked regionalism in the distribution of some elements of the spore floras.

Distribution and regional variation. Beaulieu, Ferques and Hydrequent formations, Boulonnais, France (Loboziak and Streel, 1981); Beverley Inlet Formation and lower Parry

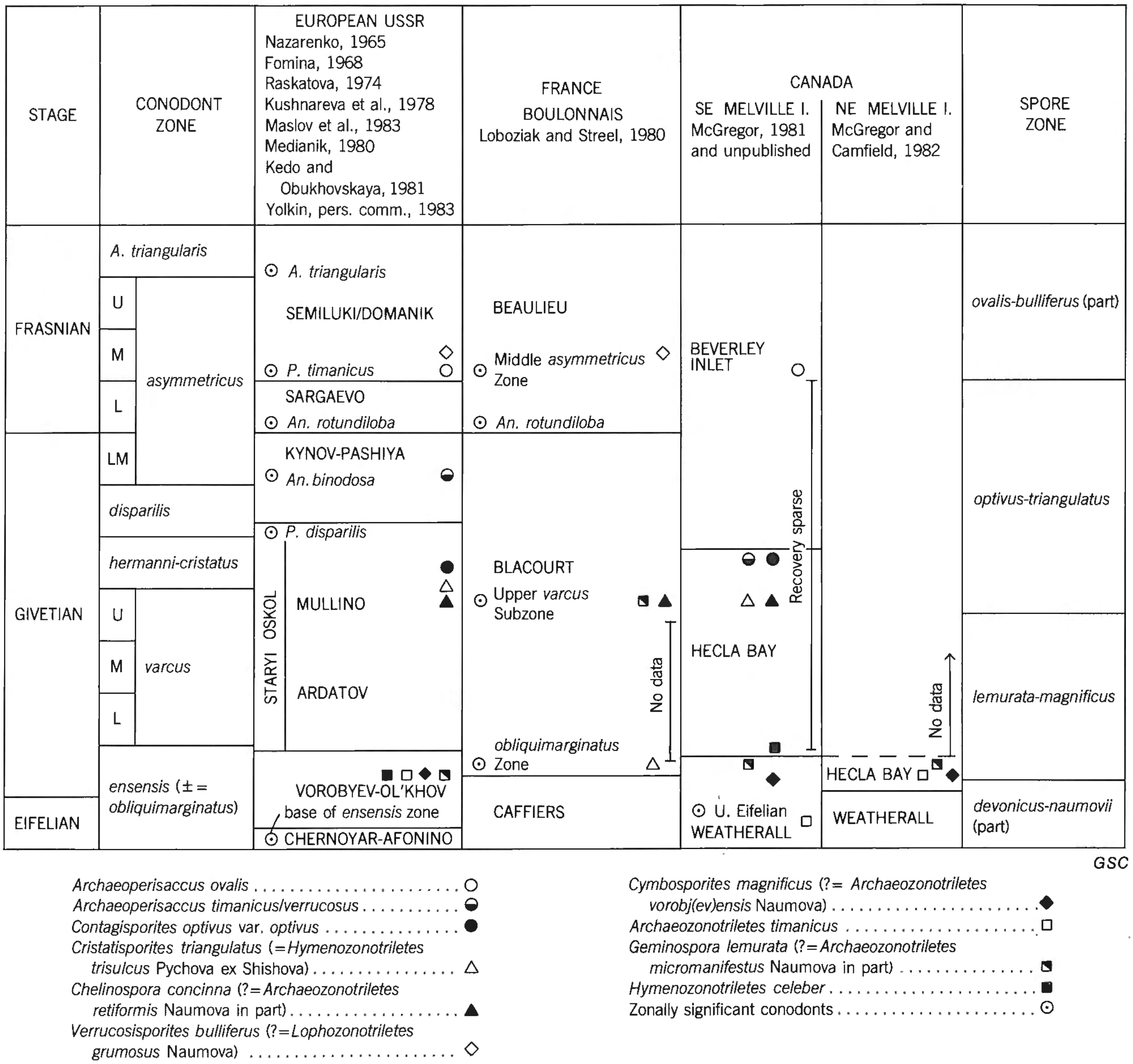

***Figure 6.** Approximate correlation of selected late Givetian and early Frasnian spore-bearing strata of the European U.S.S.R., Western Europe, and Arctic Canada.*

Islands Formation, southeastern Melville Island (Owens, 1971; McGregor and Uyeno, 1972; McGregor, 1981), subsurface of Vanier Island (Whiteley, 1980), Okse Bay Group of Grinnell Peninsula, Devon Island, and subsurface of Banks and Cameron islands (McGregor, unpublished), Fram and Hell Gate formations of southwestern Ellesmere Island (McGregor, 1969 and unpublished), Weatherall Formation of Prince Patrick Island (McGregor, 1981), Imperial Formation of District of MacKenzie (McGregor, 1969; Chi and Hills, 1974), Escarpment Member of Hay River Formation, District of MacKenzie (McGregor and Owens, 1966) and Perdrix Formation of east-central British Columbia (McGregor, unpublished) in Canada; Domanik, Liaiol, Vetlasyan, Bel'gop and Sirachoi strata of the Timan-Pechora region (Sennova, 1972; Medianik, 1980), Goltva and Rudnya strata of the Dnepr-Donets Depression (Sergeeva, 1979), and Semiluki, Petino, Voronezh and Evlanov strata and their correlatives on the Russian Platform (Naumova, 1953; Raskatova, 1974) in the U.S.S.R.; Chemung Group of central Pennsylvania, U.S.A. (McGregor, unpublished). Possibly in the Calmar Formation of western Alberta and the Long Rapids Formation of Northern Ontario, Canada (McGregor, unpublished); the Oneonta, Walton and Rhinestreet formations of central New York State, U.S.A. (Richardson, unpublished); and the subsurface of the Vilyu River region in east-central Siberia (Mikhailova and Fradkina, 1966).

The nominal species ***Verrucosisporites bulliferus***, present in Northern Ontario (McGregor, unpublished), central New York State (Richardson, unpublished) and France (Taugourdeau-Lantz, 1971) may be identical to ***Lophozonotriletes grumosus*** Naumova (1953), which is common in middle and late Frasnian deposits of the Russian Platform.

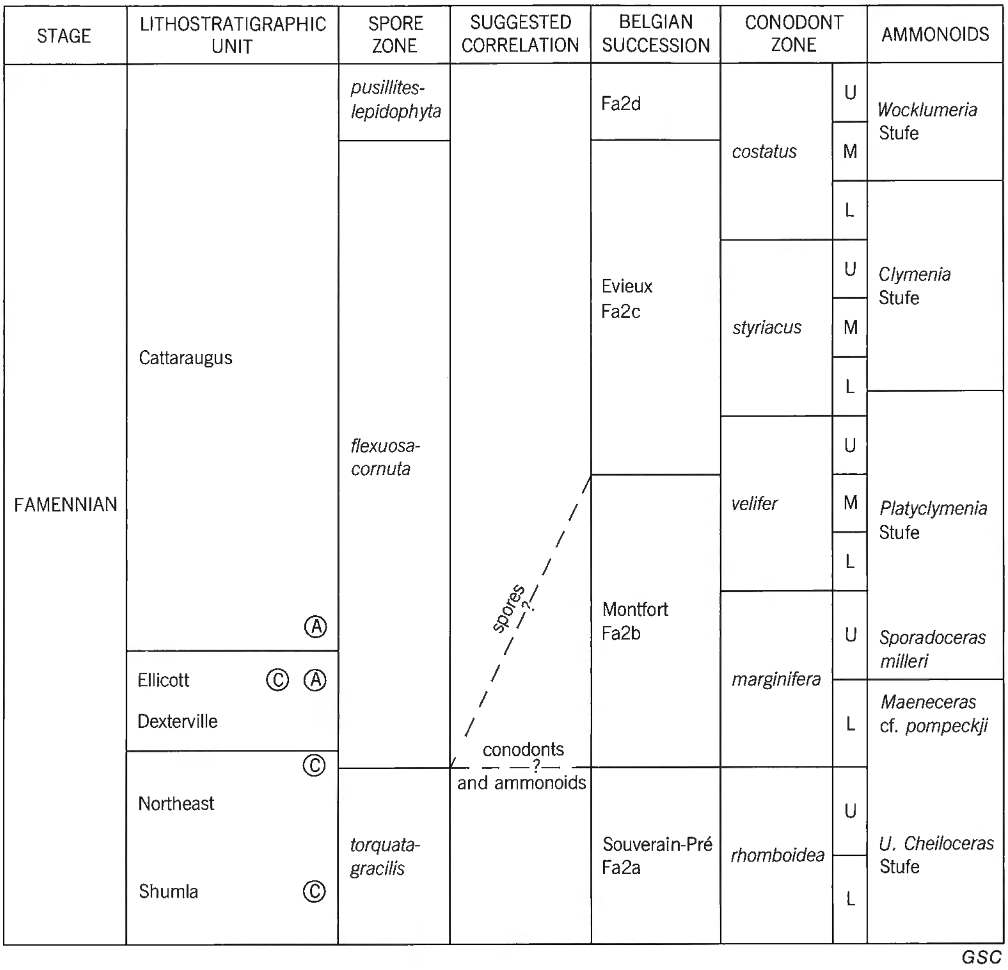

Figure 7. *Approximate correlation of the* ***torquata-gracilis/flexuosa-cornuta*** *boundary in New York State, based on spores and invertebrate faunas. A = ammonoids, C = conodonts, after Rickard (1975) and Kirchgasser and House (1981). The Belgian units Fa2a to Fa2c are diachronous (Becker et al., 1974). We have shown the oldest age for each as indicated by Ziegler (1979).*

Archaeoperisaccus spp. apparently are geographically restricted, as they occur in the eastern, northern and western parts of the ORS region and in eastern Asia (McGregor, 1979b, Fig. 13).

16. *Auroraspora torquata - Grandispora gracilis* Assemblage Zone

Age. Latest Frasnian to early late Famennian. Approximately the lower *Palmatolepis triangularis* Zone to the middle *Scaphignathus velifer* Zone inclusive in terms of the conodont succession (Rickard, 1975; for post-Gowanda formations of New York, unpublished spore correlation by JBR with the Belgian succession). See Figure 7 and comments under the *flexuosa-cornuta* Zone.

Reference section for the base of the zone. Hanover Shale Formation, West Falls Group, Chautauqua County, western New York State, U.S.A., Walnut Creek section (Pepper and de Witt, 1950; Ahmed, 1978; Richardson, unpublished).

Range of the zone. Hanover Shale Formation, 9.8 m above its base, to the lower part of the upper Northeast Shale Formation, inclusive.

Characteristic species.

Auroraspora torquata Higgs, 1975, Pl. 4, figs. 1-3 (Pl. 18, fig. 1).

Grandispora gracilis (Kedo) Streel, in Becker et al., 1974, Pl. 19, figs. 1-3 (Pl. 18, figs. 2, 3).

Aneurospora greggii (McGregor) Streel, 1974; see previous three zones.

Archaeozonotriletes famenensis Naumova, 1953, Pl. 17, figs. 31-34 (Pl. 18, fig. 4).

Auroraspora hyalina (Naumova) Streel, in Becker et al., 1974; Streel, 1965, Pl. 1, figs. 7, 8 (Pl. 18, fig. 6).

A. macra Sullivan, 1968, Pl. 27, figs. 6-10 (Pl. 19, fig. 8).

A. pseudocrista Ahmed, 1980, Pl. 2, figs. 5-9 (Pl. 18, fig. 8).

Cornispora varicornata Staplin and Jansonius in Staplin, 1961, Pl. 1, figs. 6-12 (Pl. 18, fig. 5).

Crassispora catenata Higgs, 1975, Pl. 2, figs. 1-3 (Pl. 19, fig. 5).

Cyrtospora cristifera (Luber) Van der Zwan, 1979, Pl. 1, figs. 1-5; Pl. 2, figs. 1-8; Pl. 3, figs. 1-3 (Pl. 18, fig. 7).

Diducites poljessicus (Kedo) Van Veen, 1981, Pl. 4, figs. 1-4, 6 (Pl. 19, fig. 4).

D. versabilis (Kedo) Van Veen, 1981, Pl. 2, figs. 5, 6; Pl. 3, figs. 1-6, 9 (Pl. 18, fig. 9).

"(?)*Hymenozonotriletes denticulatus* Naumova" of McGregor, 1967, Pl. 1, fig. 25 (Pl. 19, figs. 2, 3).

Hystricosporites multifurcatus (Winslow) Mortimer and Chaloner, 1967; Winslow, 1962, Pl. 12, figs. 8-8b, Pl. 13, figs. 1-9, Pl. 22, fig. 16 (Pl. 18, fig. 10).

Knoxisporites dedaleus (Naumova) Streel, 1977; Naumova, 1953, Pl. 19, fig. 11. [=*K. literatus* (Waltz) Playford, of Clayton et al., 1978)] (Pl. 19, fig. 1).

Lophozonotriletes lebedianensis Naumova, 1953, Pl. 17, fig. 42 (Pl. 19, fig. 6).

Description. Diversification of smooth-walled, pseudosaccate spores (*Auroraspora*) and abundance of *Aneurospora greggsii*. First appearance of broad radial and/or concentric thickenings on cingulate spores (*Knoxisporites*). First appearance of prominent spinose to verrucate distal crassitude (*Cyrtospora cristifera*). Specimens with two or more protrusions on the crassitude (*Cornispora varicornata*) appear about midway in the zone in northern and western regions. Miospores on average smaller than in Middle Devonian and earlier Frasnian zones, commonly less than 100 µm in diameter.

Distribution and regional variation. Parry Islands Formation of Banks, Cameron and Byam Martin islands (McGregor, unpublished) and Bathurst Island (McGregor and Owens, 1966), Kotcho and Imperial formations of western District of Mackenzie, and Memramcook Formation of southeastern New Brunswick (McGregor, unpublished) in Canada; Hanover, Dunkirk, South Wales, Gowanda, Laona, Westfield and lower Northeast Shale formations of western New York State (Ahmed, 1978; Wood, 1978; Richardson, unpublished); Livny, Zadonsk and Elets strata of the Russian Platform (Raskatova, 1973, 1974; Naumova, 1953); Hydrequent Formation, Boulonnais, France (Loboziak and Streel, 1981; Loboziak et al., 1983).

Auroraspora torquata is present in Southern Ontario, New Brunswick and Nova Scotia in Canada (McGregor, unpublished) and in New York State and western Europe, but has not been reported from the Soviet Union or the northern parts of the ORS continent. *Cyrtospora cristifera* does not appear in the southern part of the ORS continent until the *nitidus-vallatus* Zone (latest Devonian).

Remarks. *Hystricosporites multifurcatus* as used herein does not include the specimens described under this name by Mortimer and Chaloner (1967). Nevertheless, the nomenclatural transfer of the species to *Hystricosporites* as proposed by them is retained.

17. *Rugospora flexuosa - Grandispora cornuta* Assemblage Zone

Age. Late Famennian. Approximately Upper *Scaphignathus velifer* Zone to lower part of Middle *Bispathodus costatus* Zone inclusive, in terms of the conodont succession and based on spore evidence. This dating does not agree with the age determined on the basis of sparse conodont and ammonoid evidence in New York State (see below and Figure 7).

Rickard (1975, p. 10) records that conodont species of the *Palmatolepis marginifera* Zone have been recognised in the Northeast Shale Formation and overlying "Chadakoin" (Dexterville and Ellicott formations of the Conneaut Group). Kirchgasser and House (1981) record "fauna 27" in the middle of the Ellicott Shale Formation, including the ammonoid *Maeneceras* cf. *pompeckji*, which in Europe is a "typical Famennian II beta goniatite". According to Ziegler (1979), the upper part of the *Cheiloceras* Stufe (II beta) is equivalent to the *Palmatolepis rhomboidea* and lower part of the *P. marginifera* conodont zones. Thus the conodont and ammonoid evidence, although scanty, is more or less consistent.

In contrast, a correlation (miospore-based) with Belgian strata where conodont sequences are well known, would place the appearance of *Rugospora flexuosa* and *Grandispora cornuta* (as *G. uncata*) at or near the base of Fa2c (Becker et al., 1974), a level which, according to Ziegler (1979, Fig. 7), is not older than the base of the conodont Upper *S. velifer* Zone. In Belgium, the equivalent of the upper part of the *flexuosa-cornuta* Zone (the upper VCo Zone of Streel) has been correlated with the lower part of the conodont Middle *B. costatus* Zone (see enclosure in Paproth et al., 1983). Therefore, on spore evidence, the *flexuosa-cornuta* Zone in Belgium may extend from the Upper *S. velifer* Zone to the Middle *B. costatus* Zone of the conodont succession.

It seems unlikely that the discrepancy in New York between the conodont - ammonoid and miospore correlations is due to the late appearance or incomplete record of the nominal miospore species in Belgium. This conclusion is supported by data on the distribution of two other species that have restricted stratigraphic ranges in both Belgium and New York State. In Belgium, *Retusotriletes phillipsii* is confined to lower Fa2c and *Lagenicula* sp. A is only recorded from Fa2c (Becker et al., 1974). In New York State and northern Pennsylvania, if the conodont - ammonoid evidence were accepted, the ranges of these species would be approximately lower and middle Fa2b (*R. phillipsii*) and Fa2a(?) and lower Fa2b (*Lagenicula* sp. A), not Fa2c.

Clendening et al. (1980) also suggest a correlation between the New York State succession and that of Belgium. On the basis of the appearance of *Retusotriletes phillipsii*, they correlate the Shumla Siltstone and Northeast Shale formations of the upper part of the Canadaway Group (below the *flexuosa-cornuta* Zone) with the Belgian Fa2c. This correlation would lower the base of Fa2c even more, in terms of the New York succession, than would the palynological correlation discussed in the preceding paragraphs. On the other hand, in samples examined by JBR through the western New York State sequence, *R. phillipsii* has not been found below the Dexterville Siltstone Formation, which overlies the Northeast Shale Formation. *Grandispora cornuta* occurs commonly in the Dexterville Formation and above, and a similar form occurs sporadically in the upper part of the underlying Northeast Shale Formation.

Reference section for the base of the zone. North Chautauqua County, New York State, tributary of Canadaway Creek, approximately 2.8 km southeast of Arkwright Falls; upper Northeast Shale Formation (Canadaway Group), 16.8 m above the base of the exposed section, 125 m above the top of the Shumla Siltstone Formation and about 25.6 m below the base of the Dexterville Formation. The exposure is marked on the geological map in Tesmer (1963).

In sections at Chautauqua Creek to the southwest, assemblages belonging to this zone occur in at least the top 17 m of the Northeast Shale Formation (Richardson, unpublished).

No suitable reference section has been found yet for the *Cornispora* assemblage.

Range of the zone. Upper Northeast Shale Formation (Canadaway Group) to the lower Venango and Cattaraugus Formations, western New York State.

Characteristic species.

Rugospora flexuosa (Jushko) Streel in Becker et al., 1974, Pl. 21, figs. 8-11 (Pl. 19, fig. 7).

Grandispora cornuta Higgs, 1975, Pl. 4, figs. 4-6 (Pl. 20, fig. 1).

Auroraspora hyalina (Naumova) Streel; see previous zone.

A. macra Sullivan; see previous zone.

A. torquata Higgs; see previous zone.

Cornispora varicornata Staplin and Jansonius; see previous zone.

Cyrtospora cristifera (Luber) Van der Zwan; see previous zone.

Diducites poljessicus (Kedo) Van Veen; see previous zone.

D. versabilis (Kedo) Van Veen; see previous zone.

Grandispora gracilis (Kedo) Streel; see previous zone.

Hystricosporites multifurcatus (Winslow) Mortimer and Chaloner, 1967; see previous zone.

Lagenicula sp. A Streel, in Becker et al., 1974, Pl. 23, figs. 3-7 (=*Hymenozonotriletes immensus* Nazarenko and Nekryata, in Kedo et al., 1971, Pl. 16, figs. 1-4) (Pl. 19, fig. 9).

Retispora cassicula (Higgs) Higgs and Russell, 1981; Higgs, 1975, Pl. 5, figs. 1-3 (Pl. 20, fig. 2).

Retusotriletes phillipsii Clendening, Eames and Wood, 1980, Pl. 1, figs. 1-9 (Pl. 20, fig. 3).

Description. Reappearance of pseudosaccate spores with foveoreticulate exoexine (*Retispora*; see Zone 12). Continuation of most species from the previous zone, some in greater abundance (e.g. *Auroraspora hyalina*, *A. macra*, *A. poljessica*, *A. torquata*, *Grandispora gracilis*, *Cyrtospora cristifera*, and *Rugospora versabilis*). Diversification of simple-spined and laevigate pseudosaccates (*Grandispora* and *Auroraspora*).

Distribution and regional variation. Northeast Shale, Dexterville and Ellicott Formations (upper Canadaway and Conneaut Groups) and lower Venango and Cattaraugus Formations (lower Conewango Group), New York State (Ahmed, 1978; Richardson, unpublished), and an unspecified stratigraphic unit in West Virginia (McGregor, unpublished) in the U.S.A.; Imperial Formation of the Yukon Territory and western District of Mackenzie (Van der Zwan and Walton, 1981; McGregor, unpublished) and Parry Islands Formation of Bathurst and Banks islands, and unnamed strata of Antigonish County, Nova Scotia (McGregor, unpublished) in Canada; Misery Series of Bear Island (Kaiser, 1971); Assise d'Evieux, Belgium (Becker et al., 1974); Purple Sandstone Group of southern Ireland (Higgs and Russell, 1981); subsurface of North Africa (Massa and Moreau-Benoit, 1976); subsurface of Poland (Turnau, 1979); Dankov-Lebedyan beds of the Russian Platform (Raskatova, 1973, 1974; Byvsheva, 1980), the Pripyat Depression (e.g. Kedo et al., 1971; Avkhimovich, 1974), the Dniepr-Donets Depression (Sorokina, 1968) and northern Timan (Pashkevich, 1971; Sennova, 1972) in the U.S.S.R. *Cornispora* spp. and *Cyrtospora cristifera* are restricted to the eastern, northern and western parts of the ORS Continent, as in the previous zone.

18. *Vallatisporites pusillites* (sensu lato) - *Retispora lepidophyta* Zone

Age. Strunian (Conil and Lys, 1980). Approximately Middle *Bispathodus costatus* Zone to lower part of the "Lower *Protognathodus* fauna" in terms of the German conodont succession.

Reference section for the base of the zone. Chanxhe Section, eastern Dinant Basin, Ourthe Valley, Belgium (Bless et al., 1974; Streel, Bless et al., 1975).

Range of the zone. Fa2d to lower Tn1b. For more extensive discussion of the range of this zone, see Clayton et al. (1977, p. 6).

Characteristic species.

Vallatisporites pusillites (Kedo) Dolby and Neves, 1970, Pl. 2, figs. 1-4 (Pl. 20, fig. 5).

Retispora lepidophyta (Kedo) Playford, 1976, Pl. 10, figs. 1-15 (Pl. 20, fig. 4).

Diducites poljessicus (Kedo) Van Veen; see previous two zones.

D. versabilis (Kedo) Van Veen; see previous two zones.

Discernisporites micromanifestus (Hacquebard) Sabry and Neves, sensu Higgs, 1975, Pl. 5, fig. 13 (Pl. 20, fig. 7).

Grandispora echinata Hacquebard, 1957, Pl. 3, fig. 17 (Pl. 20, fig. 6).

Knoxisporites literatus (Waltz) Playford, 1963, Pl. 90, figs. 7, 8 (Pl. 21, fig. 5).

Raistrickia variabilis Dolby and Neves, 1970, Pl. 1, fig. 6 (Pl. 21, fig. 1).

Rugospora flexuosa (Jushko) Streel; see previous zone.

Tumulispora malevkensis (Kedo) Turnau, 1978; Kedo, 1963, Pl. 10, figs. 240, 241 (Pl. 21, fig. 4).

T. rarituberculata (Luber) Turnau, 1975, Pl. 4, figs. 1, 2, 4, 6 (Pl. 21, figs. 2, 3).

Description. Acme of pseudosaccate spores with a foveoreticulate exoexine (*Retispora*). Widespread occurrence of vacuolate zona (*Vallatisporites*). Persistence of most of the species characteristic of the previous zone.

Distribution and regional variation. This zone is of near worldwide occurrence (see McGregor, 1979b). In the standard North American succession in western New York State, *Vallatisporites pusillites* begins in the upper part of the preceding *flexuosa-cornuta* Zone, in the lowermost parts of the Venango and Cattaraugus formations about 79 m below the appearance of *Retispora lepidophyta*. It also begins in the upper part of the *flexuosa-cornuta* Zone in the Lower Sandstone Member of the Pocono Formation of Pennsylvania (Streel and Traverse, 1978). In Belgium, *V. pusillites* and *R. lepidophyta* make their first appearance together, at the base of the *pusillites-lepidophyta* Zone. The two species also occur together in Kazakhstan (Grishina and Klenina, 1981), Tibet (Gao, 1983) and Kwangsi, South China (Wang et al., 1978), but *V. pusillites* is absent from synchronous strata in Hunan (Hou, 1982). On the other hand, in the European U.S.S.R. both *V. pusillites* and *Rugospora flexuosa* appear high in the range of *R. lepidophyta*, probably in the *lepidophyta-nitidus* Subzone (Byvsheva, 1980). *Tumulispora malevkensis* first occurs in this zone in eastern Europe (Byvsheva, 1980; Raskatova, 1974; Turnau, 1978) but not until the succeeding *nitidus-vallatus* zone in western Europe (Clayton et al., 1977).

Hymenozonotriletes explanatus is first seen near the top of the zone in southern Ireland, and is used by Clayton et al. (1978) to define the boundary between two subzones in that region: the *lepidophyta-literatus* Subzone and the *lepidophyta-explanatus* Subzone. The *lepidophyta-explanatus* Subzone is characterized by the same species as the *lepidophyta-literatus* Subzone, with the addition of *H. explanatus*. It has been recognized in southern Ireland (Clayton, in Naylor, 1975; Higgs, 1975), the Ardennes-Rhine region, and western New York State and northern Pennsylvania (Richardson, unpublished). However, as *H. explanatus* occurs only in the highest beds of the *pusillites-lepidophyta* Zone, it does not seem reasonable to regard it as a characteristic species of this zone.

Remarks. It may be possible to separate a new zone in the upper part of the *pusillites-lepidophyta* Zone based on *H. explanatus*, *Grandispora echinata*, *Knoxisporites literatus*, *Tumulispora* spp. and other species that have not been found in the lower part of the zone.

19. *Verrucosisporites nitidus* - *Vallatisporites verrucosus* Assemblage Zone

Retispora lepidophyta - *Verrucosisporites nitidus* Subzone

Age. Late Strunian. Approximately equivalent to all but the basal part of the "Lower *Protognathodus* fauna" of the German conodont succession.

Reference section for the base of the zone. Old Head of Kinsale, South Munster Basin, southwestern Ireland (Clayton et al., 1974). The base of the zone is about two thirds of the way up the Holeopen Bay Member of the Old Head Sandstone Formation.

Range of the subzone. Upper third of the Holeopen Bay Member to the top of the Old Head Sandstone Formation.

Characteristic species.

Verrucosisporites nitidus (Naumova) Playford, 1964, Pl. 3, figs. 3-6 (Pl. 21, fig. 7).

Vallatisporites verrucosus Hacquebard, 1957, Pl. 2, fig. 13 (Pl. 21, fig. 8).

Retispora lepidophyta (Kedo) Playford; see previous zone.

Cyrtospora cristifera (Luber) Van der Zwan; see *torquata-gracilis* and *flexuosa-cornuta* zones.

Discernisporites micromanifestus (Hacquebard) Sabry and Neves, sensu Higgs, 1975; see previous zone.

Grandispora echinata Hacquebard, 1957; see previous zone.

Hymenozonotriletes explanatus (Luber) Kedo, 1963, Pl. 6, figs. 144-147 (Pl. 21, fig. 6).

Knoxisporites literatus (Waltz) Playford; see previous zone.

Raistrickia corynoges Sullivan, 1968, Pl. 25, figs. 6-8 (Pl. 21, fig. 9).

Tumulispora malevkensis (Kedo) Turnau; see previous zone.

T. rarituberculata (Luber) Turnau; see previous zone.

Description. Decline of grapnel-tipped spines (*Ancyrospora*, *Hystricosporites*) and foveoreticulate exoexine (*Retispora*), and their disappearance at the top of the zone. Diversification of coarsely verrucate, cingulate spores (*Tumulispora*). Appearance of *Cyrtospora cristifera* in southern parts of the ORS Continent (eastern North America and western Europe).

Distribution. Old Head Sandstone Formation, southern Ireland (Clayton et al., 1974; Holland, 1981); highest Hangenberg Shales, Germany (Paproth and Streel, 1970); unnamed strata on St. George's Bay, Nova Scotia, Banff Formation of Alberta and southwestern District of Mackenzie, and Besa River Formation of east central British Columbia in Canada (McGregor, unpublished); Knapp Formation of western New York State and northern

Pennsylvania (Richardson, unpublished) and Pocono Formation of Pennsylvania, U.S.A. (Streel and Traverse, 1978); Malevka Horizon of the Russian Platform (Byvsheva, 1976). Possibly in the subsurface of Poland (Turnau, 1979), the Sappington Member of Three Forks Formation of Montana (Sandberg et al., 1972) and the Berea Formation of Ohio (Winslow, 1962).

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APPENDIX

Locality register for specimens figured herein,
for which descriptions of localities have not been published

Plate 1, figure 4. Pennsylvania State University "Mill Hall locality", 1.1 m southeast of Mill Hall, Clinton County, Pennsylvania; outcrop at a level 250 m above US Route 220.

Plate 11, figures 5 and 6. GSC locality C-84874. Southwestern Ellesmere Island, District of Franklin, NTS 49C, UTM zone 16, 519550E, 8569100N, east of Bird Fiord; outcrop 8 m above base of Strathcona Fiord Formation.

Plate 14, figure 13. GSC plant locality 7013. Northwestern Cornwallis Island, District of Franklin, NTS 58G/5; outcrop on Rookery Creek, Locality 32 ("Pennsylvanian") of Thorsteinsson (1958, p. 111).

Plate 15, figure 6. GSC locality C-84874 (same as Plate 11, figures 5 and 6).

Plate 15, figure 7. GSC locality C-28109. Western District of Mackenzie, NTS 96E/11, 65°30'20"N, 127°13'26"W, Banff Aquit GPD Oscar Creek H-71 well; cuttings from 640-730 ft (195-222.5 m), spore-bearing member of Hare Indian Formation (see Tassonyi, 1969).

Plate 16, figure 4. GSC locality C-33961. Banks Island, District of Franklin, NTS 98A/16, 72°47'51"N, 120°44'48"W, Elf Texaco Tiritchik M-48 well; cuttings from 3100-3140 ft (945-957 m), 884-924 ft (269.5-282 m) above base of Weatherall Formation.

Plate 16, figure 5. GSC locality C-91916. Southwestern Ellesmere Island, District of Franklin, NTS 49C/6, UTM zone 16, 505250E, 8562675N; outcrop on east side of inner part of southeast arm of Bird Fiord; Fram Formation.

Plate 16, figures 6 and 7. GSC locality C-91913 (same as Plate 16, figure 5, but 50.5 m lower stratigraphically).

Plate 17, figure 6. GSC locality C-91918 (same as Plate 16, figure 5, but 17.9 m higher stratigraphically).

Plate 17, figure 7. GSC locality 97081. East-central British Columbia, NTS 93H/16, Monkman Pass area, 53°52'34"N, 120°01'08"W; outcrop 19 m below top of Perdrix Formation.

Plate 18, figure 6. GSC locality D1726. Antigonish County, Nova Scotia, NTS 11F/12, 45°44'24.4"N, 61°53'28.46"W, west side of St. George's Bay, north of McIsaac Point.

Plate 18, figure 7. GSC plant locality 5436. Northwestern District of Mackenzie, NTS 106M, about 48 km southwest of Fort McPherson; outcrop along Vittrekwa River, Imperial Formation.

Plate 18, figure 9. Richardson locality NY96/1965. McKean County, Pennsylvania; road cut on U.S. Route 6 at Bush Hill, 5 km east of Smethport.

Plate 19, figure 1. GSC plant locality 5436 (same as Plate 18, figure 7).

Plate 19, figure 5. Richardson locality US6/1968. Pope Hollow section, along boundary between Caroll and South Valley townships, Jamestown Quadrangle near Chautauqua, New York.

Plate 19, figure 9. Richardson locality PA19/1966. Warren County, Pennsylvania, road cut on State Highway 59, 19.3 km east of Warren and 2.25 km northeast of Kinzua Dam.

Plate 20, figure 1. Richardson locality NY95/1965. McKean County, Pennsylvania, Hanley Quarries, east of Lewis Run.

Plate 20, figure 3 (same as Plate 19, figure 5).

Plate 20, figure 5. Richardson locality NY25/1965. Cattaraugus County, New York State, road cut on State Highway 16A, 4.8 km south of Olean.

Plate 20, figure 7. GSC locality D1726 (same as Plate 18, figure 6).

Plate 21, figure 4. GSC plant locality 6496. Yukon Territory, NTS 106L, Caribou River; Imperial Formation.

Plate 21, figure 6. GSC locality D1726 (same as Plate 18, figure 6).

Plate 21, figure 7. GSC locality 97057. Northernmost tip of Western Australia, Amax Ellendale well, 1750.5 m; Fairfield Formation(?).

PLATES 1-21

Illustrations of spores

Letter-number designations following descriptions of figures are type specimen numbers. For further explanation, see Table 2 (in pocket)

PLATE 1

(All figures are X1000, unless stated otherwise)

Figure	1.	*Ambitisporites avitus* Hoffmeister. FM 1.
Figure	2.	*Ambitisporites dilutus* (Hoffmeister) Richardson and Lister. FM 2.
Figure	3.	*Retusotriletes warringtonii* Richardson and Lister. FM 3.
Figures	4, 5.	*Tetrahedraletes medinensis* Strother and Traverse; 4, FM4; 5, Scanning Electron Micrograph, X2000.
Figures	6-8.	*Archaeozonotriletes chulus* (Cramer) Richardson and Lister var. *chulus*; 6, 7, FM 5; 8, two specimens, one laterally compressed, FM 6.
Figure	9.	*Archaeozonotriletes chulus* (Cramer) Richardson and Lister var. *nanus* Richardson and Lister. GSC 41705.
Figure	10.	?*Archaeozonotriletes* cf. *divellomedium* Chibrikova. FM 8.
Figures	11, 13, 14.	cf. *Synorisporites verrucatus* Richardson and Ioannides; 11, X1500, FM 12; 13, 14, FM 13.
Figure	12.	*Emphanisporites* cf. *protophanus* Richardson and Ioannides. FM 11.
Figures	15, 16.	*Retusotriletes abundo* Rodriguez; 15, FM 9; 16, FM 10.


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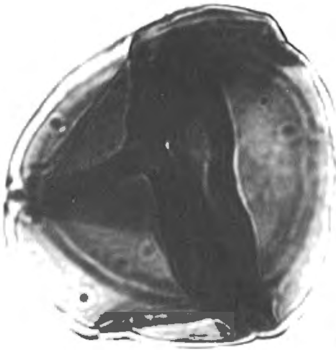
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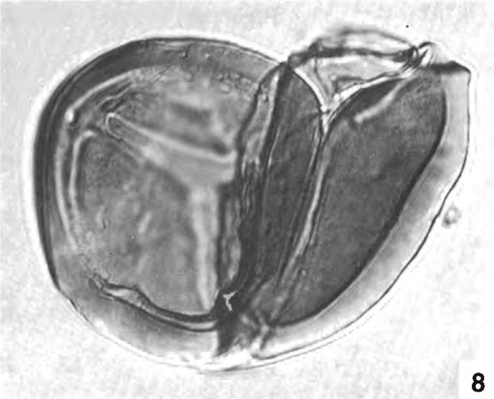
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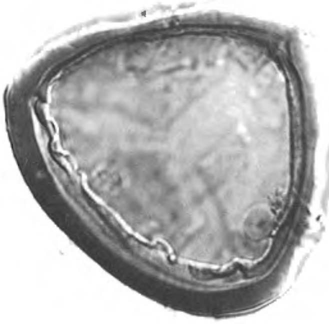
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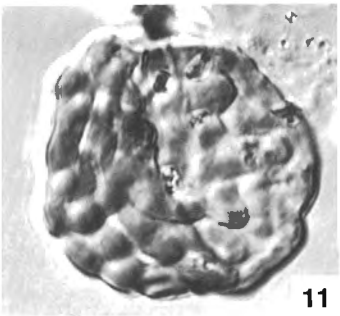
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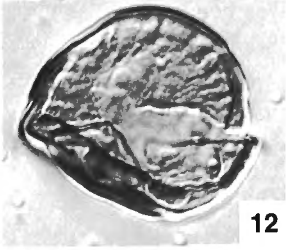
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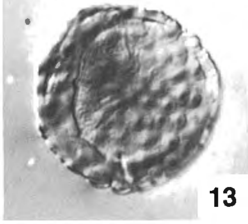
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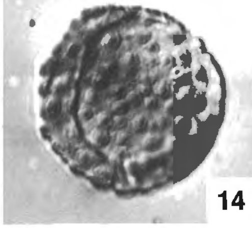
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PLATE 2

(All figures are X1000, unless stated otherwise)

Figures	1-3.	*Synorisporites libycus* Richardson and Ioannides; 1, X2000, FM 14; 2, 3, FM 15.
Figure	4.	*Emphanisporites neglectus* Vigran. FM 19.
Figures	5, 10.	*Synorisporites* cf. *verrucatus* Richardson and Ioannides; 5, FM 17; 10, X1500, FM 16.
Figures	6, 7.	?*Lophozonotriletes poecilomorphus* Richardson and Ioannides. FM 21.
Figures	8, 9.	cf. *Brochotriletes* sp. A of Richardson and Ioannides, 1973, X1500. FM 22.
Figure	11.	cf. *Synorisporites downtonensis* Richardson and Lister. IGS MPK 10.
Figure	12.	*Emphanisporites protophanus* Richardson and Ioannides. FM 20.
Figure	13.	*Amicosporites splendidus* Cramer. FM 26.
Figure	14.	*Apiculiretusispora spicula* Richardson and Lister, holotype. FM 24.
Figure	15.	*Apiculiretusispora synorea* Richardson and Lister. FM 25.
Figure	16.	*Tetraletes variabilis* Cramer. FM 23.
Figures	17, 18.	*Synorisporites tripapillatus* Richardson and Lister, holotype, X2000. FM 18.

PLATE 2


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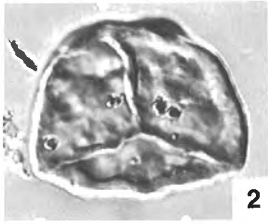
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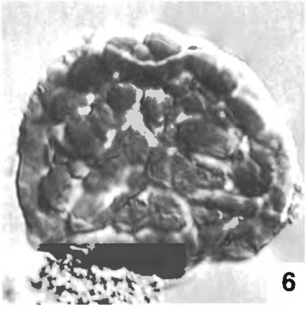
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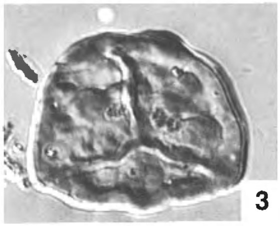
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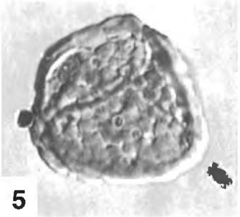
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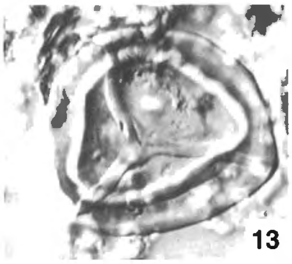
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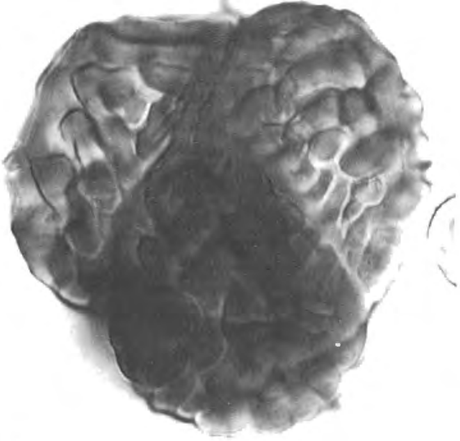
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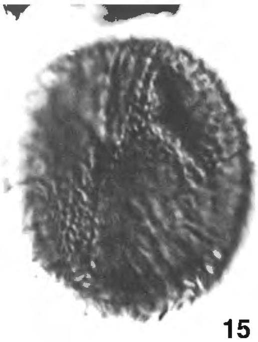
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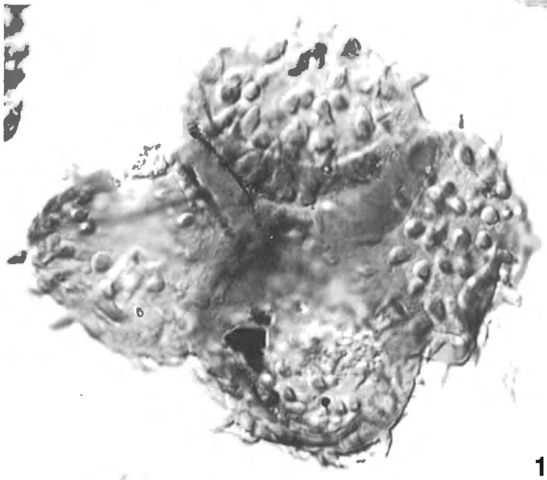
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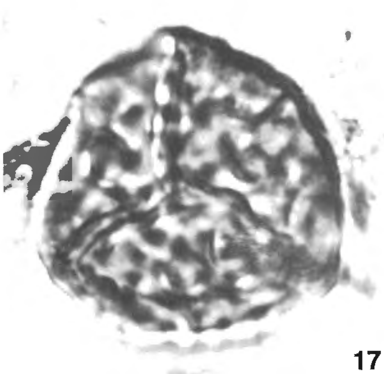
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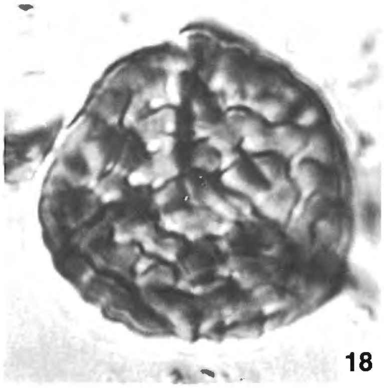
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PLATE 3

(All figures are X1000, unless stated otherwise)

Figure 1. *Ambitisporites* sp. B of Richardson and Ioannides, 1973. FM 27.

Figure 2. *Cymbosporites echinatus* Richardson and Lister. FM 28.

Figure 3. *Emphanisporites splendens* Richardson and Ioannides, holotype. FM 30.

Figures 4, 5. *Cymbosporites verrucosus* Richardson and Lister, holotype. FM 29.

Figures 6, 7. *Synorisporites verrucatus* Richardson and Lister, holotype. FM 32.

Figures 8, 9. *Synorisporites downtonensis* Richardson and Lister. FM 31.

Figures 10, 11. *Streelispora newportensis* (Chaloner and Streel) Richardson and Lister, X2000. FM 33.

Figures 12, 13. *Acinosporites salopiensis* Richardson and Lister, holotype, X2000. FM 34.


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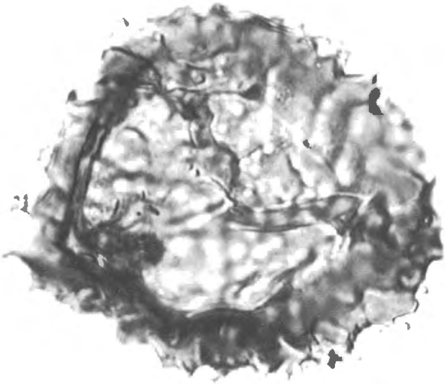
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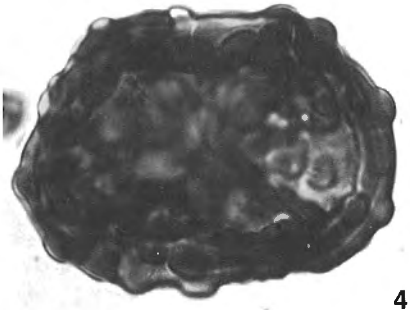
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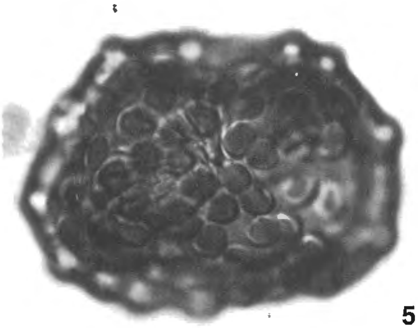
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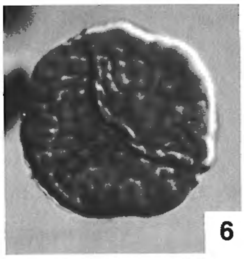
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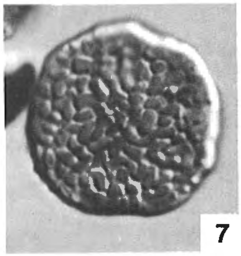
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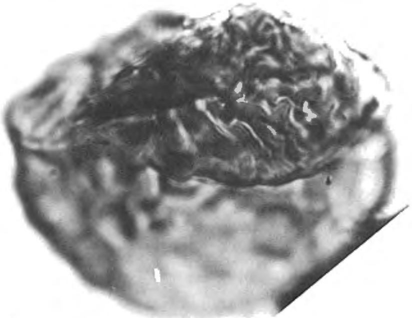
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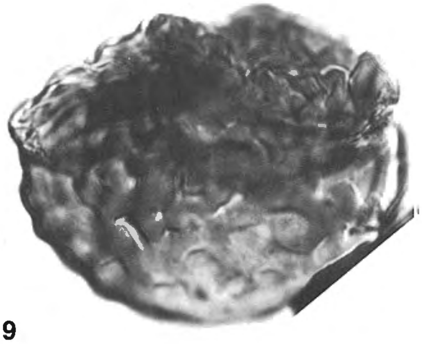
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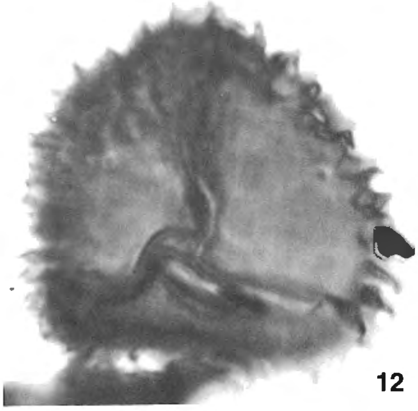
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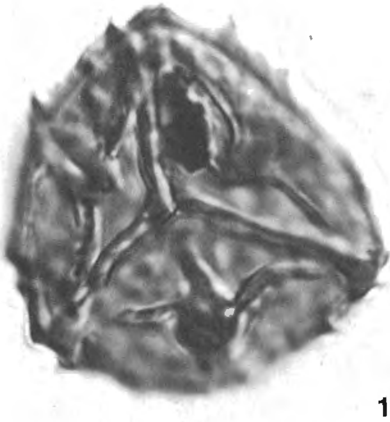
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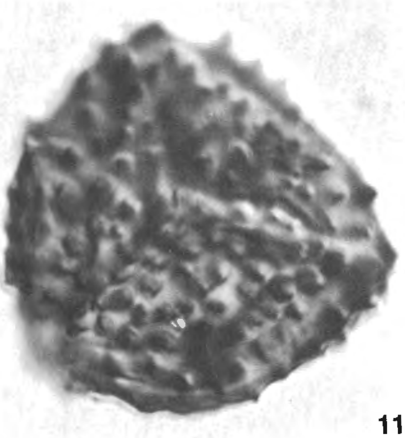
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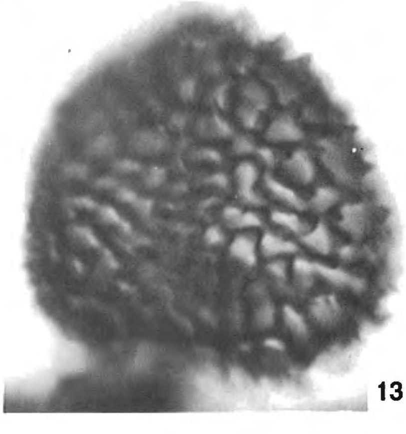
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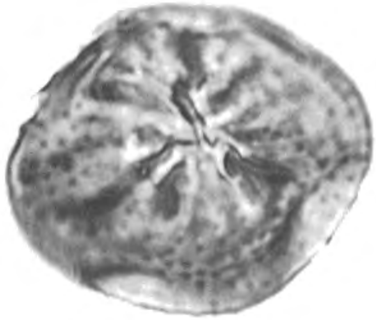
PLATE 4

(All figures are X1000, unless stated otherwise)

Figure	1.	*Emphanisporites micrornatus* Richardson and Lister, X2000. FM 35.
Figure	2.	*Apiculiretusispora plicata* (Allen) Streel. GSC 15153.
Figures	3, 4.	*Cymbosporites proteus* McGregor and Camfield, holotype, X500. GSC 41710.
Figure	5.	*Emphanisporites epicautus* Richardson and Lister. FM 37.
Figures	6, 7.	*Chelinospora cassicula* Richardson and Lister, holotype. FM 36.
Figures	8, 9.	*Perotrilites microbaculatus* Richardson and Lister. FM 38.
Figure	10.	*Retusotriletes maculatus* McGregor and Camfield, holotype. GSC 41706.
Figure	11.	*Breconisporites breconensis* Richardson, Streel, Hassan and Steemans, holotype, X1100. V61174/FM 39.
Figure	12.	*Camptozonotriletes* sp. cf. *C. caperatus* McGregor. FM 40.
Figure	13.	*Emphanisporites zavallatus* Richardson, Streel, Hassan and Steemans, holotype. V61170/FM 41.
Figure	14.	*Cirratriradites* sp. A of Streel et al., 1981. FM 42.
Figures	15, 16.	*Clivosisporа verrucata* McGregor var. *verrucata*, holotype, X500. GSC 15179.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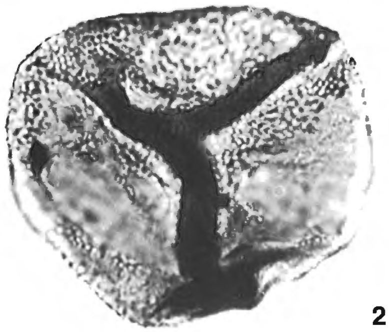
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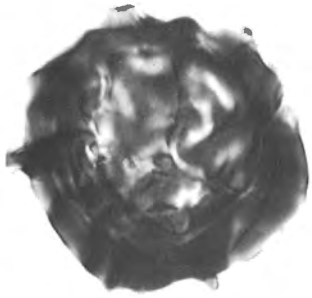
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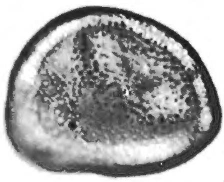
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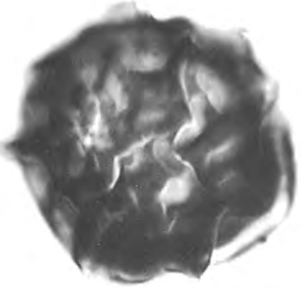
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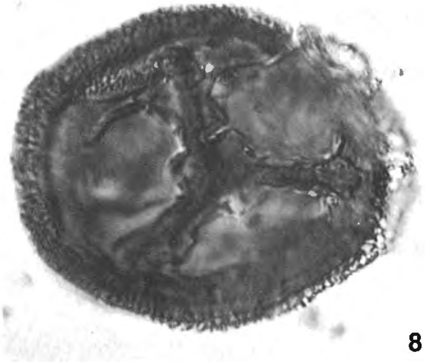
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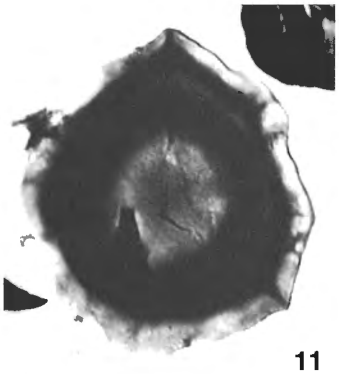
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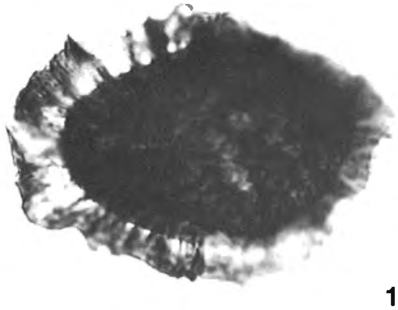
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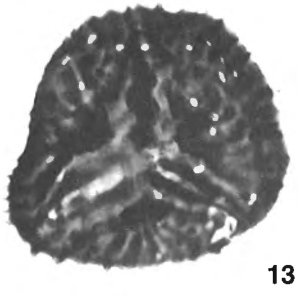
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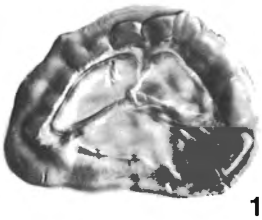
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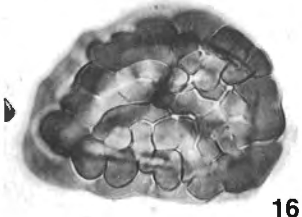
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PLATE 5

(All figures are X1000, unless stated otherwise)

Figures 1, 2. *Verrucosisporites polygonalis* Lanninger. GSC 31989.

Figure 3. *Brochotriletes foveolatus*? Naumova. GSC 31990.

Figures 4, 5. *Dictyotriletes emsiensis* (Allen) McGregor. GSC 41734.

Figure 6. *Dibolisporites eifeliensis* (Lanninger) McGregor, X500. GSC 49817.

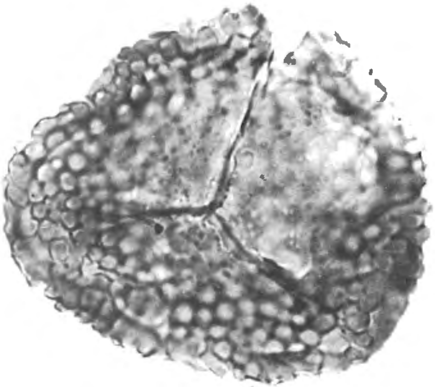
Figures 7, 8. *Dibolisporites wetteldorfensis* Lanninger. GSC 15161.

Figure 9. *Apiculiretusispora* cf. *brandtii* Streel. IGS MPK 1895.

Figures 10, 11. *Clivosispora verrucata* McGregor var. *convoluta* McGregor and Camfield, X500. GSC 27081.

Figures 12, 13. *Emphanisporites decoratus* Allen. GSC 27076.

PLATE 5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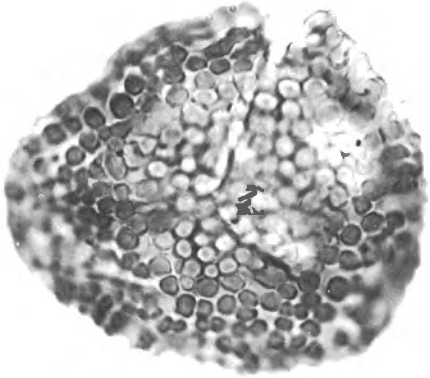
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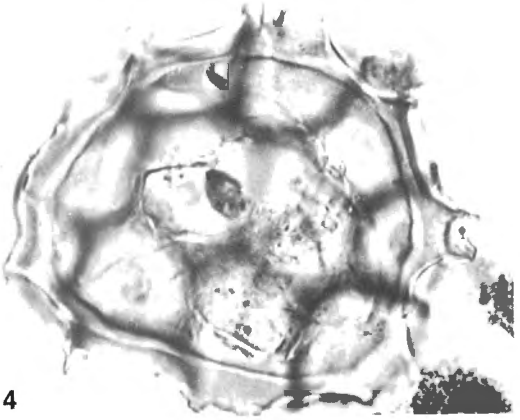
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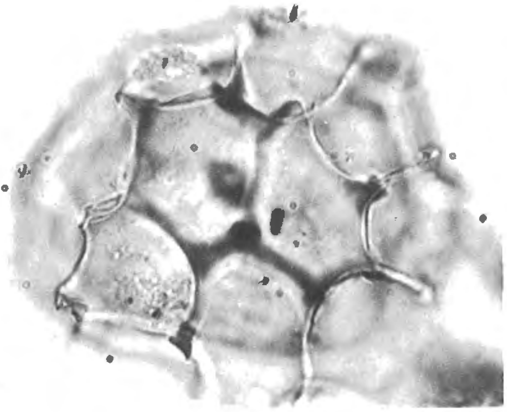
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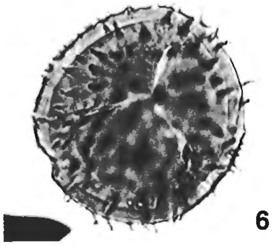
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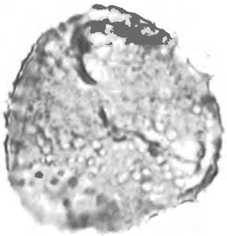
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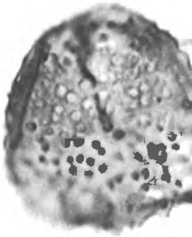
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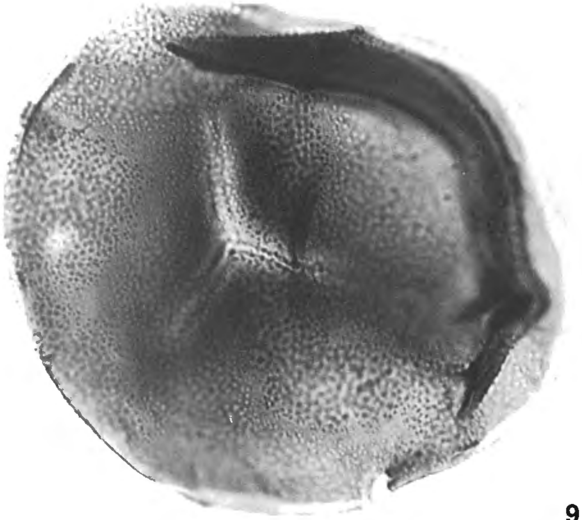
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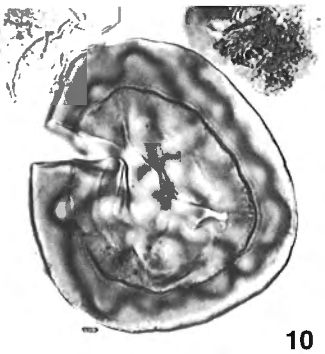
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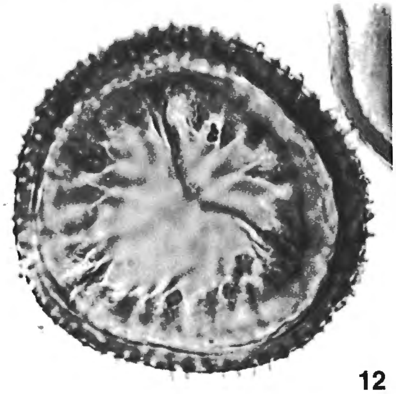
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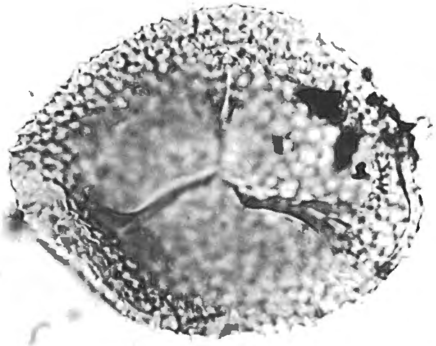
PLATE 6

(All figures are X1000, unless stated otherwise)

Figures	1, 2.	*Dictyotriletes favosus* McGregor and Camfield, X500. GSC 15181.
Figures	3, 4.	*Brochotriletes hudsonii* McGregor and Camfield, holotype, X500. GSC 41729.
Figure	5.	*Dibolisporites* n. sp. K of Hassan, 1982. FM 43.
Figure	6.	*Apiculiretusispora arenorugosa* McGregor, holotype, X500. GSC 31961.
Figure	7.	*Camptozonotriletes caperatus* McGregor, holotype, X500. GSC 15197.
Figure	8.	*Acinosporites lindlarensis* Riegel var. *lindlarensis*. GSC 73289.
Figures	9, 10.	*Emphanisporites annulatus* McGregor. GSC 32002.
Figures	11, 12.	*Camarozonotriletes sextantii* McGregor and Camfield. GSC 27083.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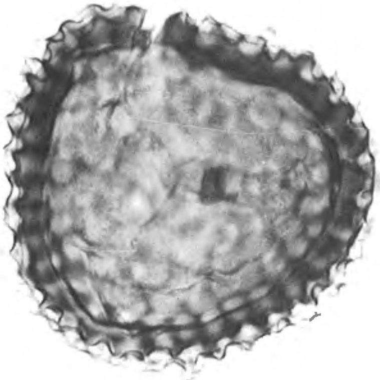
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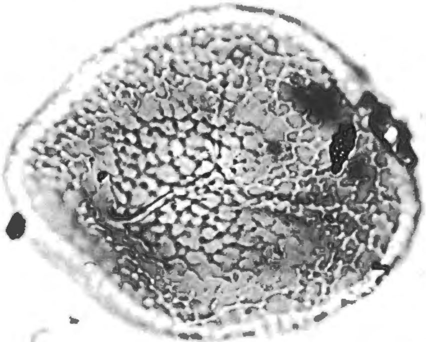
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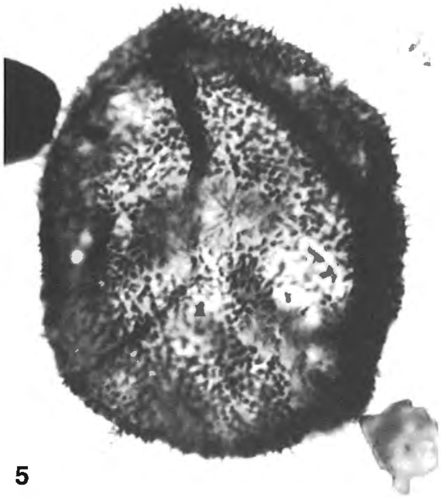
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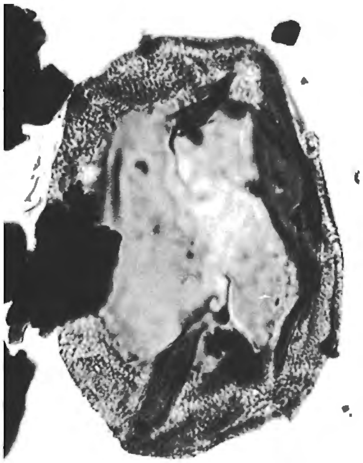
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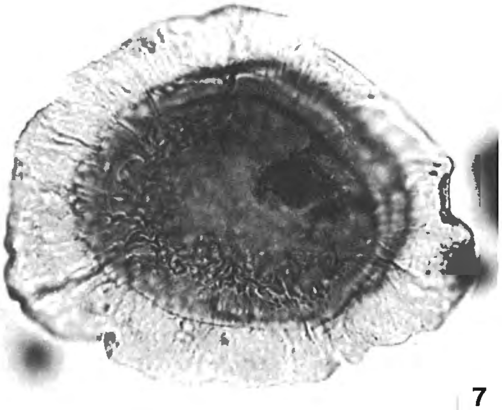
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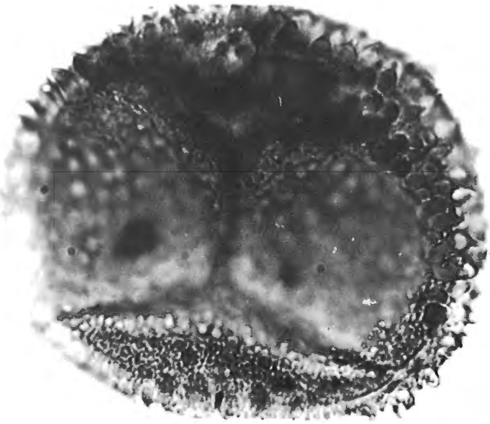
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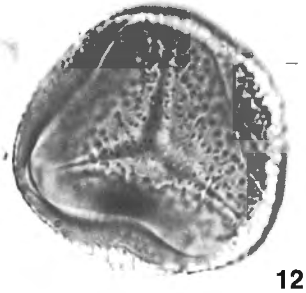
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PLATE 7

(All figures are X500, unless stated otherwise)

Figure 1. *Apiculatasporites microconus* (Richardson) McGregor and Camfield. FM 44.

Figures 2, 3. *Dibolisporites echinaceus* (Eisenack) Richardson; 3, X1200. GSC 31972.

Figure 4. *Calyptosporites biornatus* (Lanninger) Richardson.

Figure 5. *Apiculiretusispora brandtii* Streel.

Figure 6. *Dictyotriletes gorgoneus* Cramer, X1000. GSC 31997.

Figure 7. *Camptozonotriletes* cf. *aliquantus* Allen, X1000.

Figure 8. *Dictyotriletes canadensis* McGregor. GSC 32001.

Figure 9. *Emphanisporites schultzii* McGregor, X1000. GSC 32008.

Figure 10. *Verruciretusispora dubia* (Eisenack) Richardson and Rasul. IGS MPK 1897.


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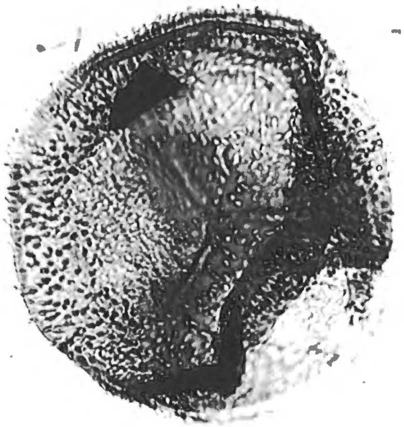
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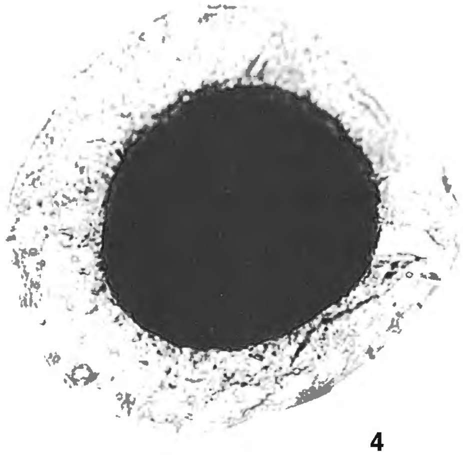
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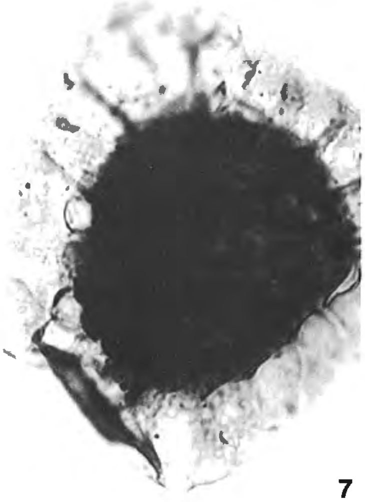
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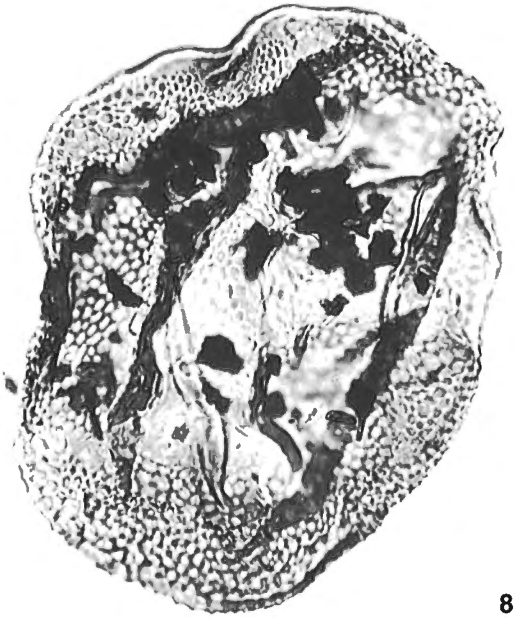
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PLATE 8

(All figures are X500, unless stated otherwise)

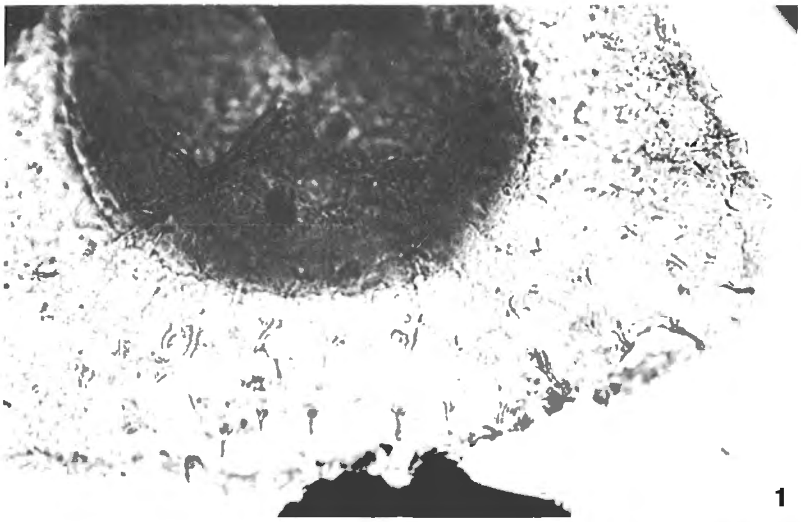
Figures 1, 2. *Ancyrospora eurypterota* Riegel; 2, X1000.

Figure 3. *Grandispora douglastownense* McGregor, holotype. GSC 32034.

Figures 4, 5. *Acinosporites apiculatus* (Streel) Streel; 4, X2000.

Figure 6. *Ancyrospora loganii* McGregor. GSC 15282.

Figures 7, 8. *Ancyrospora nettersheimensis* Riegel; 8, X1000.



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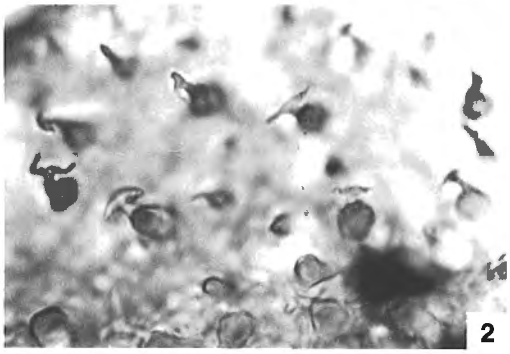

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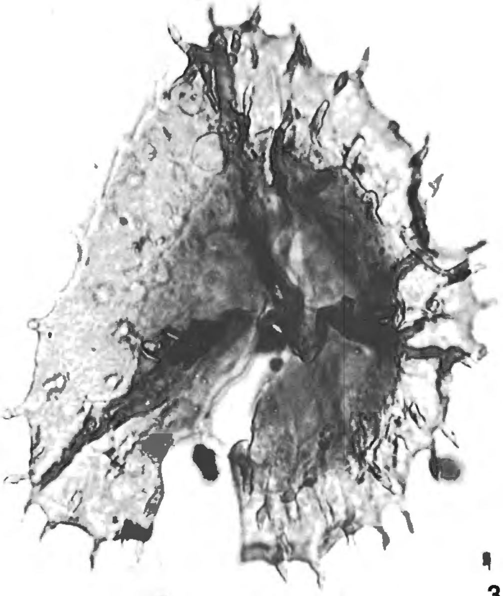

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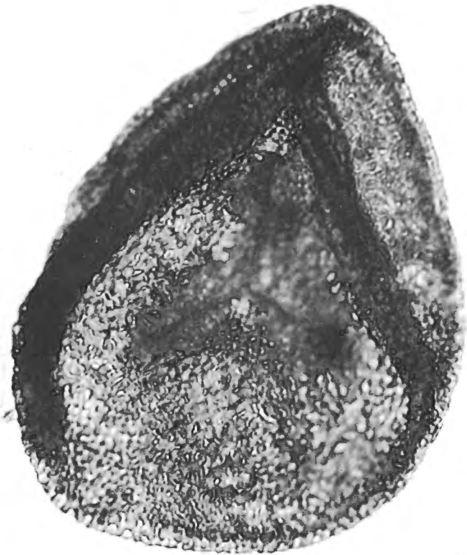

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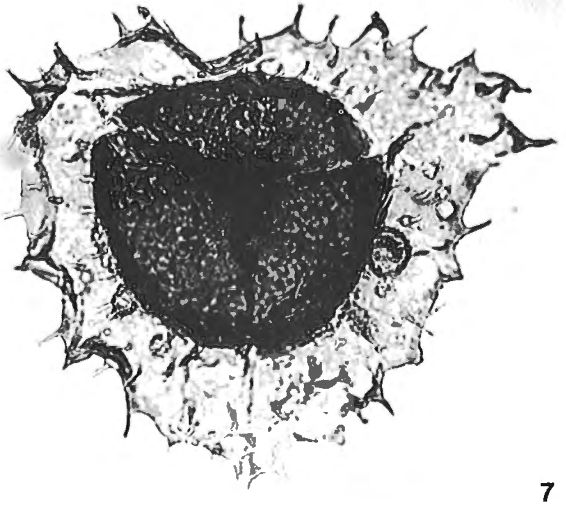

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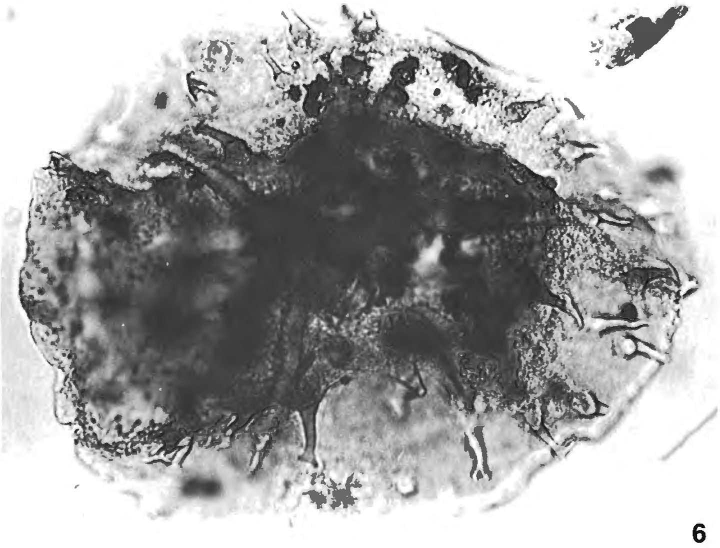

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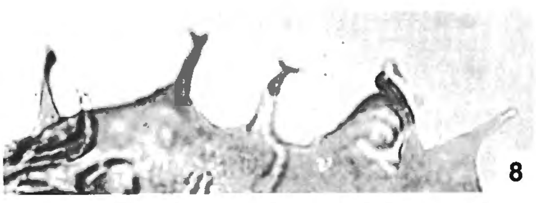

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PLATE 9

(All figures are X500, unless stated otherwise)

Figure 1. *Ancyrospora kedoae* (Riegel) Turnau.

Figure 2. *Apiculiretusispora gaspiensis* McGregor, X1000. GSC 31968.

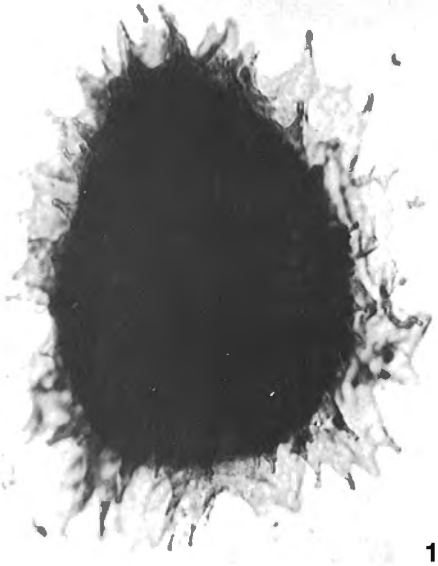
Figure 3. *Calyptosporites* sp. nov. of Riegel, 1975.

Figure 4. *Calyptosporites proteus* (Naumova) Allen. GSC 49834.

Figure 5. *Grandispora eximia* (Allen) McGregor and Camfield. GSC 66310.

Figure 6. *Spinozonotriletes arduinnae* Riegel, holotype.

Figure 7. *Hystricosporites* cf. *H. corystus* Richardson.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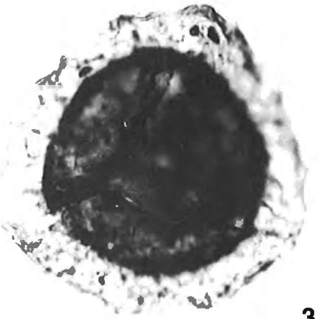
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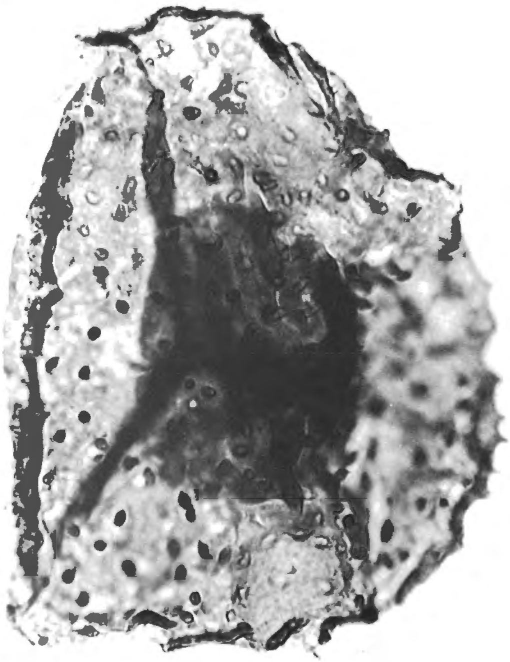
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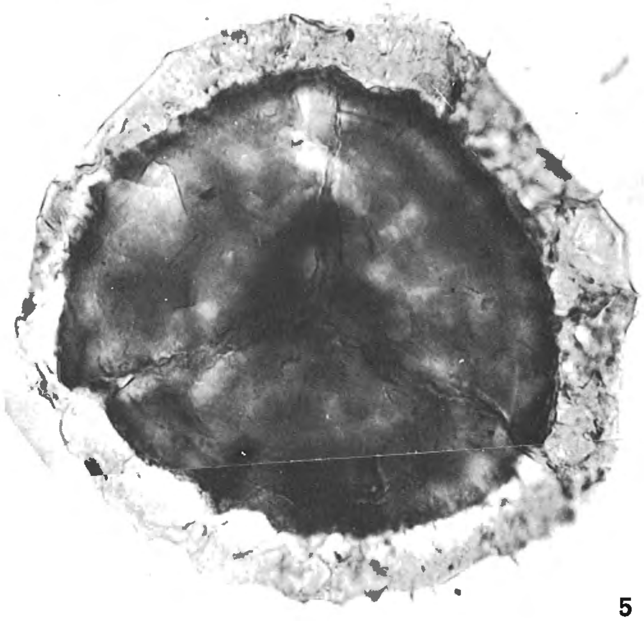
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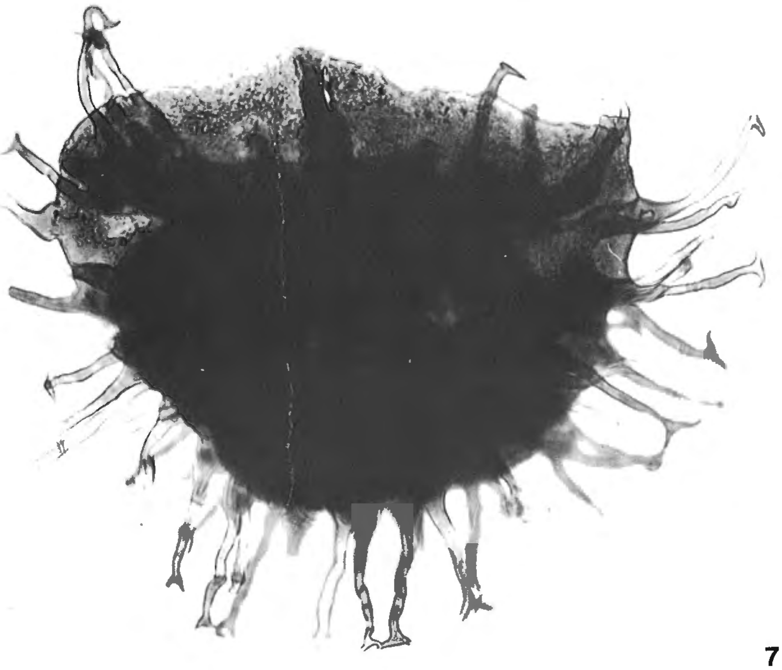
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PLATE 10

(All figures are X500, unless stated otherwise)

Figures 1, 2. *Hystricosporites microancyreus* Riegel.

Figures 3, 4. *Acinosporites acanthomammillatus* Richardson, holotype. FM 45.

Figure 5. *Rhabdosporites langii* (Eisenack) Richardson. FM 46.

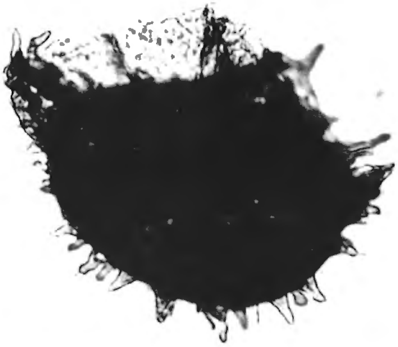
Figure 6. *Calyptosporites velatus* (Eisenack) Richardson. FM 47.

Figure 7. *Anapiculatisporites petilus* Richardson, holotype, X1000. FM 48.

Figure 8. *Kraeuselisporites ollii*? (Chibrikova) McGregor and Camfield. GSC 29391.

Figure 9. *Acinosporites macrospinosus* Richardson, holotype. FM 49.

PLATE 10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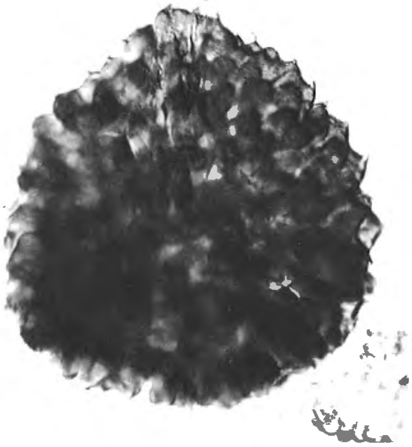
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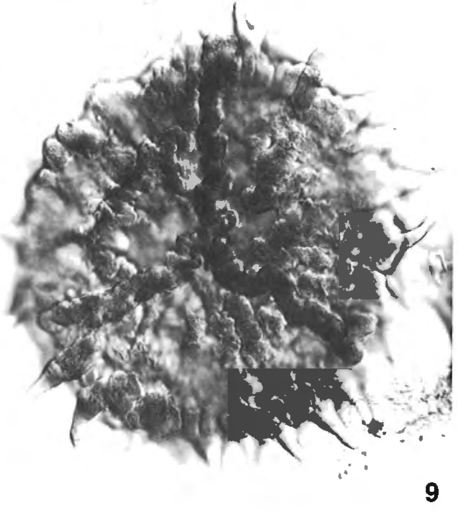
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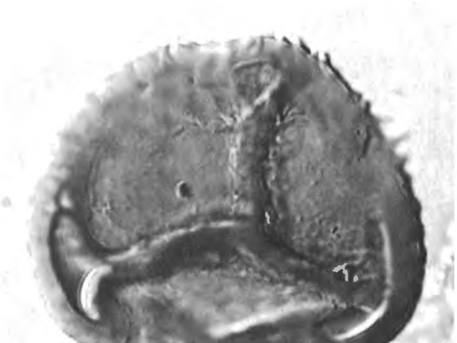
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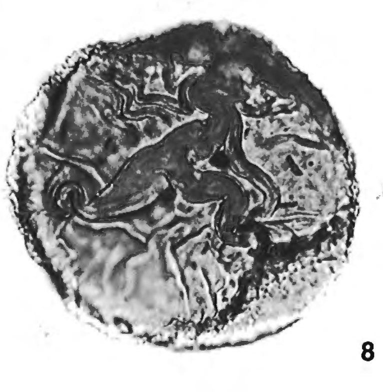
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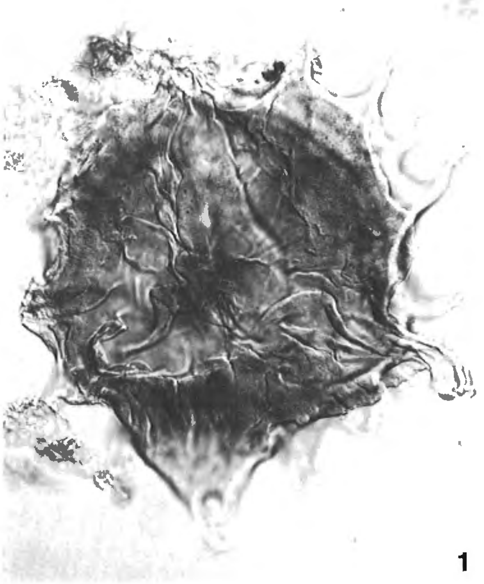
PLATE 11

(All figures are X500)

Figures	1, 2.	*Ancyrospora ancyrea* (Eisenack) Richardson var. *ancyrea.* FM 50.
Figures	3, 4.	*Kraeuselisporites acerosus* (Arkhangelskaya) McGregor and Camfield. GSC 66349.
Figures	5, 6.	*Periplecotriletes tortus* Egorova. GSC 73290.
Figures	7, 8.	*Grandispora longa* Chi and Hills. GSC 15305.

PLATE 11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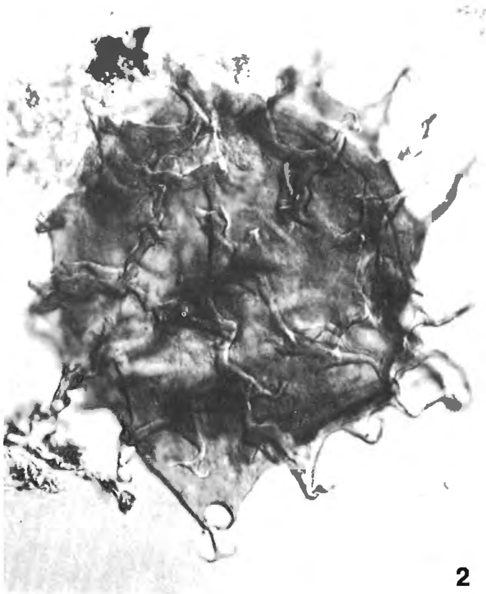
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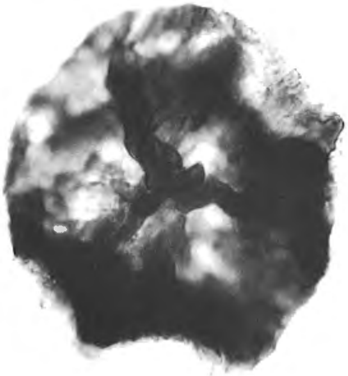
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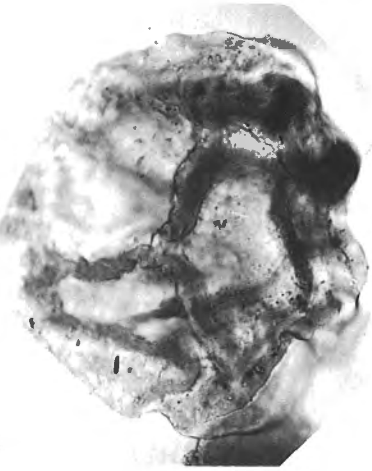
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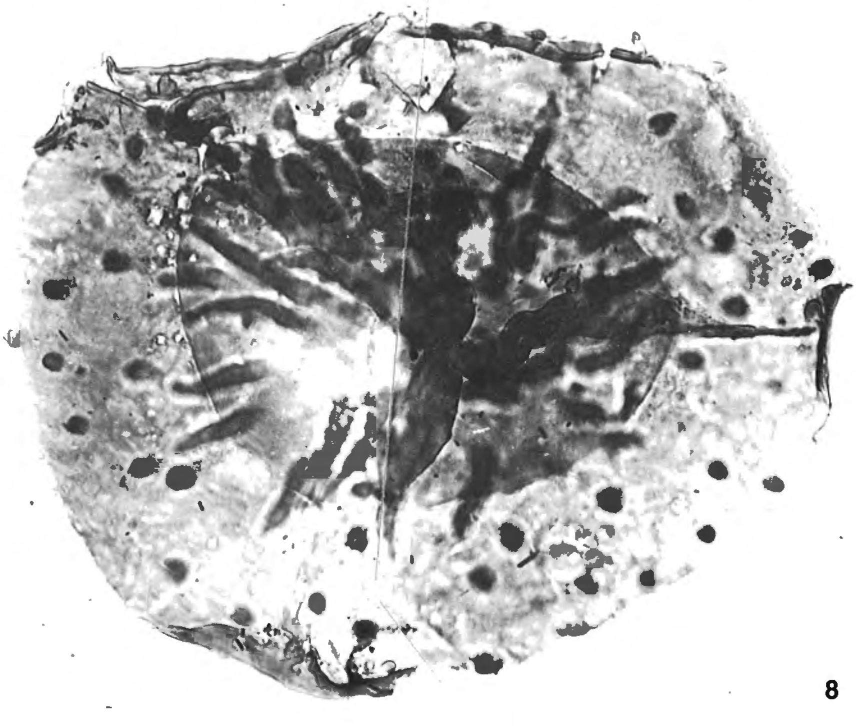
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PLATE 12

(All figures are X500, unless stated otherwise)

Figure 1. *Corystisporites multispinosus* Richardson, holotype. FM 51.

Figure 2. *Densosporites concinnus* (Owens) McGregor and Camfield, X1000. GSC 73291.

Figure 3. *Perotrilites bifurcatus* Richardson, holotype. FM 52.

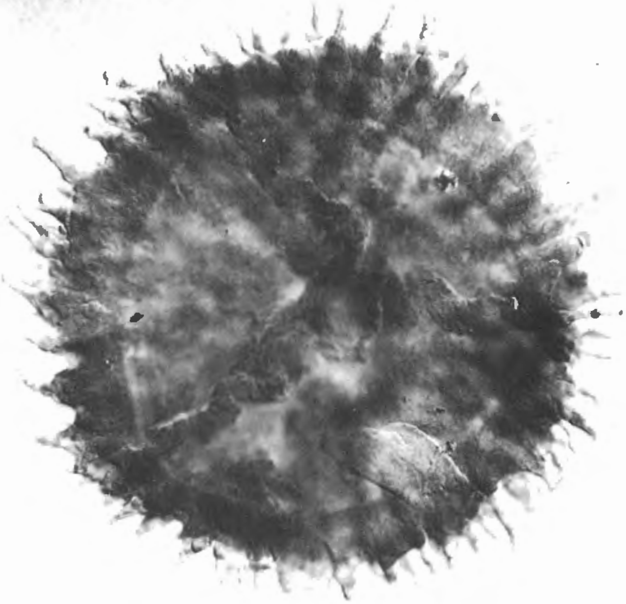
Figure 4. *Retusotriletes rugulatus* Riegel, X1000. GSC 66379.

Figure 5. *Retusotriletes distinctus* Richardson. FM 53.

Figure 6. *Densosporites devonicus* Richardson. FM 54.

Figure 7. *Densosporites inaequus* (McGregor) McGregor and Camfield. GSC 66274.

Figure 8. *Grandispora mammillata* Owens. GSC 66320.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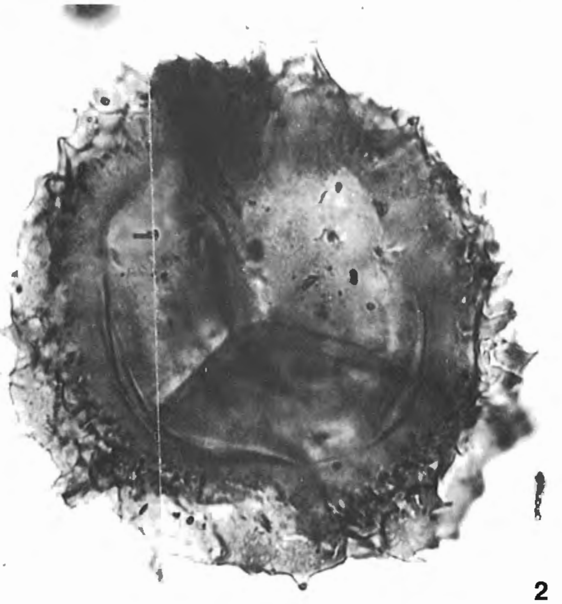
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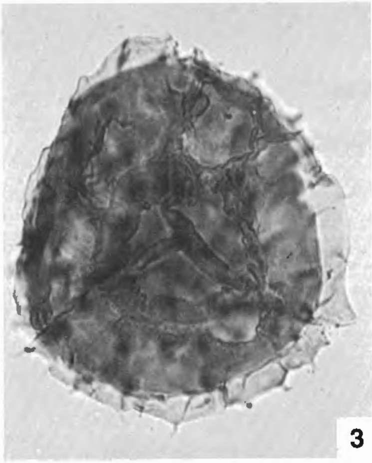
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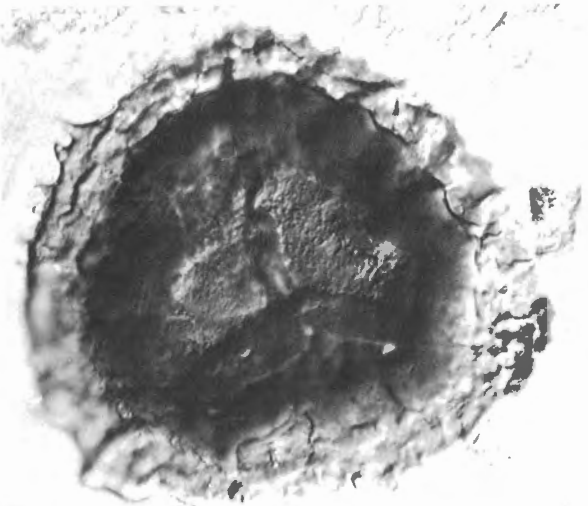
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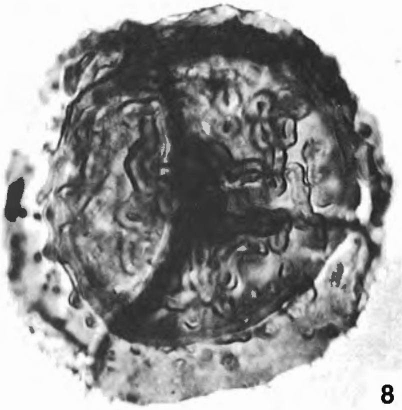
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PLATE 13

(All figures are X500, unless stated otherwise)

Figure 1. *Grandispora naumovii* (Kedo) McGregor. FM 55.

Figure 2. *Cristatisporites orcadensis* Richardson, holotype. FM 56.

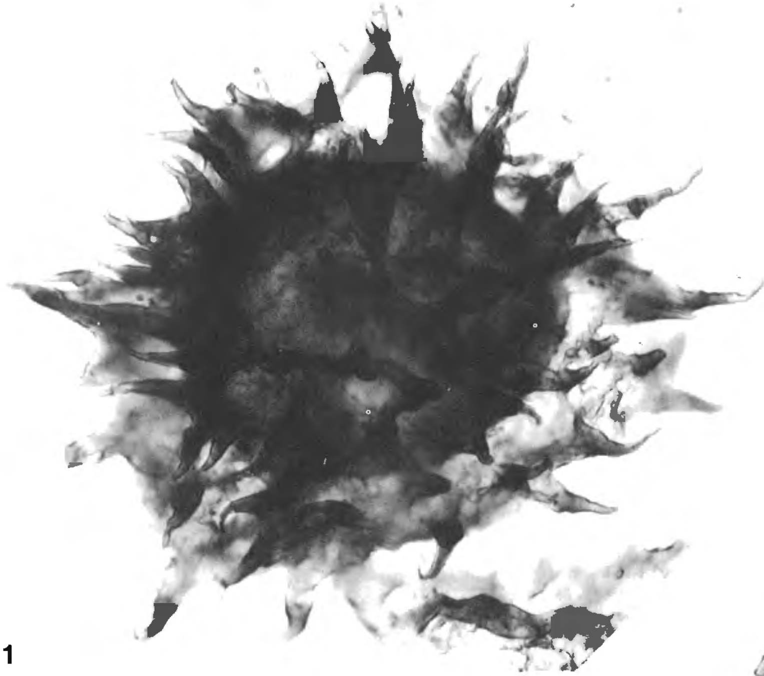
Figure 3. *Lophotriletes devonicus* (Naumova ex Chibrikova) McGregor and Camfield, X1000. GSC 66356.

Figure 4. *Perotrilites conatus* Richardson. FM 57.

Figure 5. *Grandispora inculta* Allen, X1000. GSC 66317.

Figure 6. *Kraeuselisporites rugosus* (Owens) McGregor and Camfield. GSC 29387.

Figure 7. *Ancyrospora grandispinosa* Richardson, X300. FM 58.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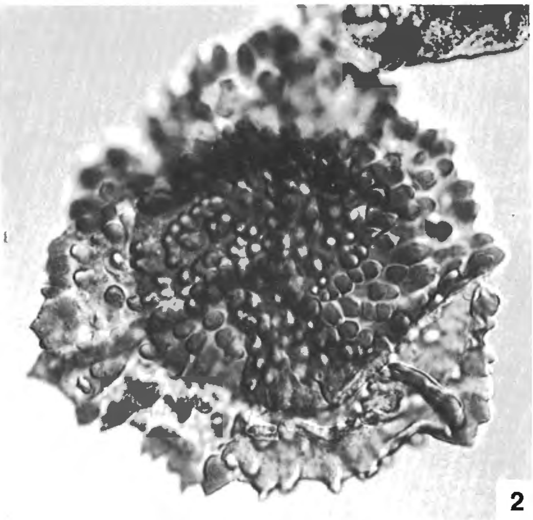
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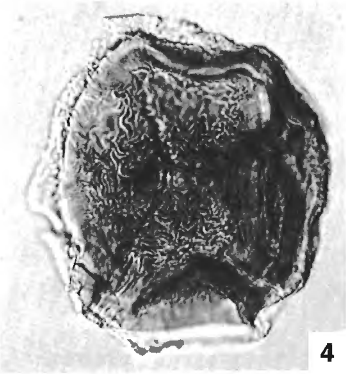
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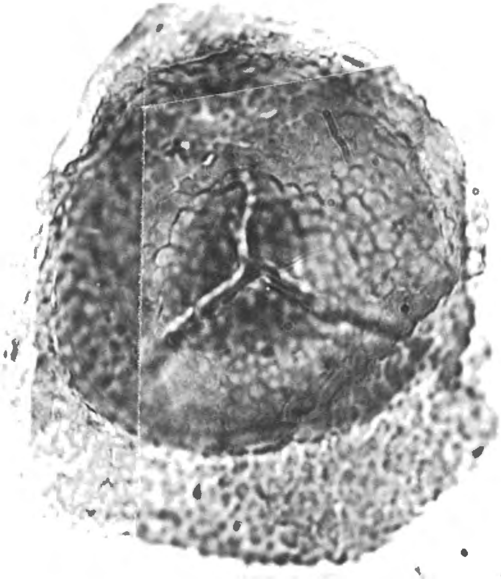
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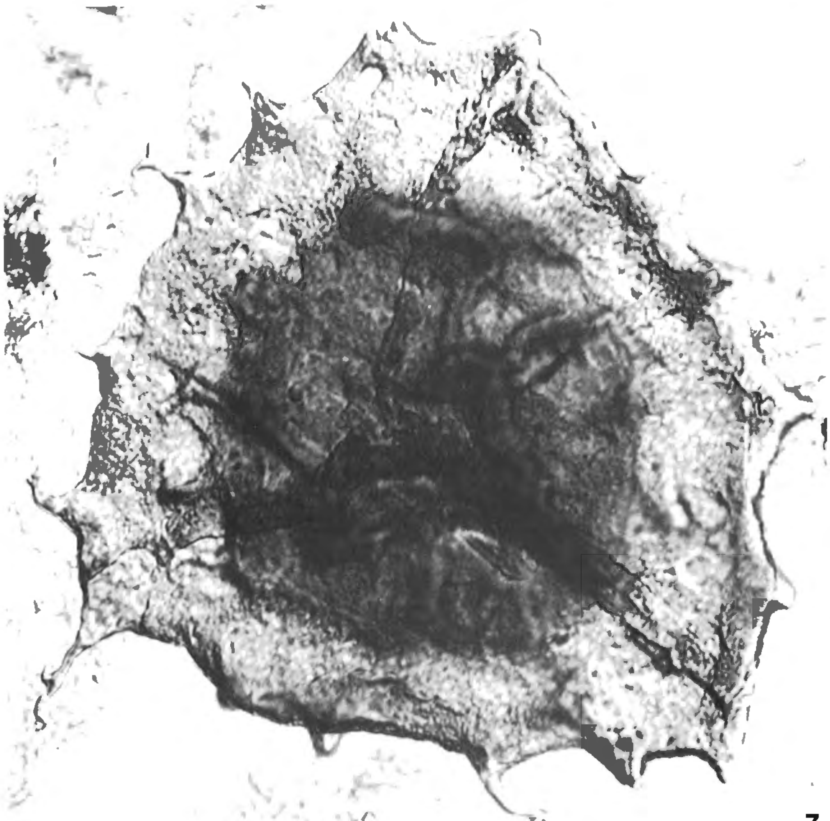
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PLATE 14

(All figures are X500, unless stated otherwise)

Figure 1. *Hystricosporites gravis* Owens. GSC 15550.

Figure 2. *Verrucosisporites scurrus* (Naumova) McGregor and Camfield, X1000. GSC 66396.

Figures 3, 4. *Retispora archaelepidophyta* (Kedo) McGregor and Camfield; 3, GSC 49843; 4, X1000, GSC 66372.

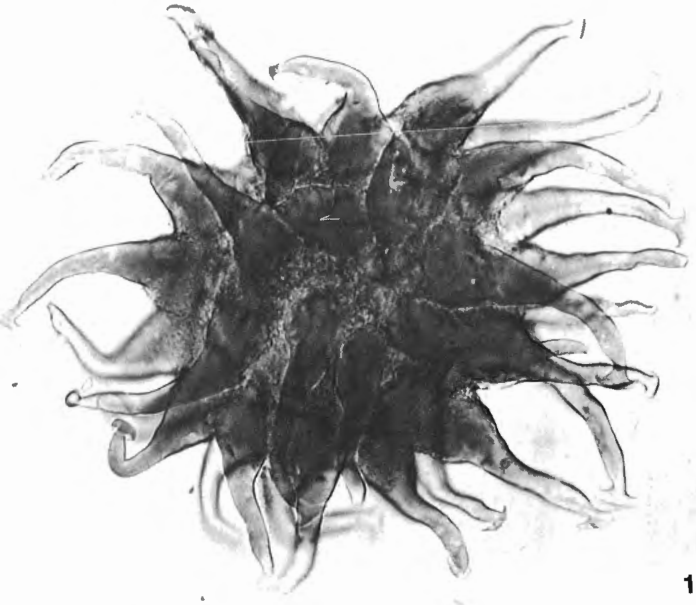
Fiugres 5, 6. *Verrucosisporites premnus* Richardson; 6, X1000. GSC 66394.

Figure 7. *Hystricosporites reflexus* Owens, holotype. GSC 15546.

Figures 8, 9. *Geminospora lemurata* Balme, X1000. GSC 66296.

Figure 10. *Archaeozonotriletes variabilis* Naumova. GSC 13624.

Figure 11. *Cymbosporites magnificus* (McGregor) McGregor and Camfield, holotype. GSC 13036.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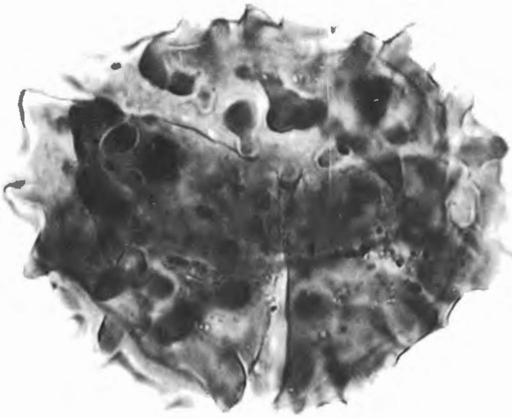
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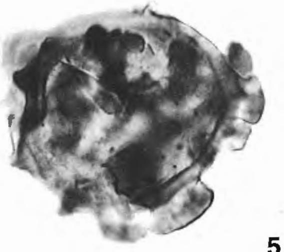
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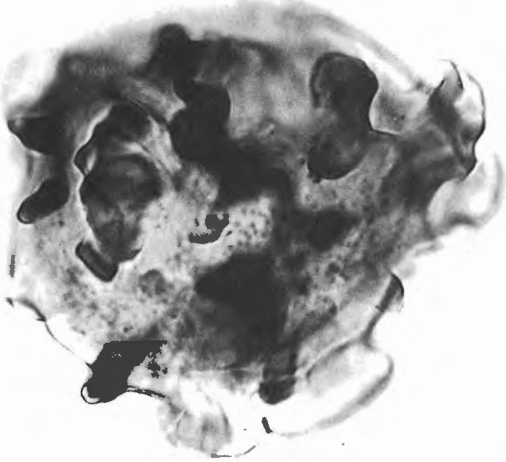
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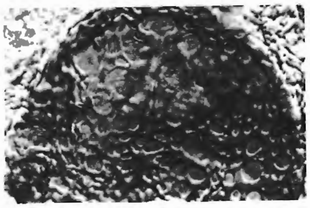
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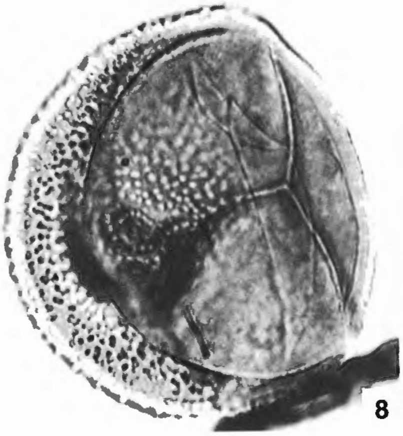
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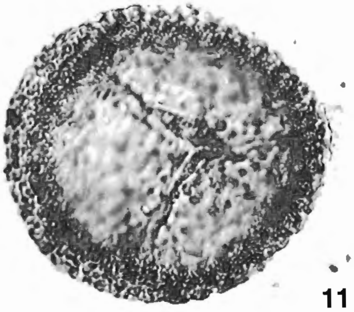
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PLATE 15

(All figures are X500, unless stated otherwise)

Figure 1. *Biharisporites parviornatus* Richardson, holotype. FM 59.

Figure 2. *Geminospora? bislimbata* (Chibrikova) McGregor and Camfield. GSC 66295.

Figure 3. *Perotrilites heclaensis* McGregor and Camfield, X1000. GSC 66362.

Figures 4, 5. *Archaeozonotriletes timanicus* Naumova. GSC 66216.

Figure 6. *Corystisporites serratus* (Naumova) McGregor and Camfield, X1000. GSC 73292.

Figure 7. *Hymenozonotriletes celeber* Chibrikova. GSC 49845.

Figure 8. *Ancyrospora involucra* Owens. GSC 15684.

Figure 9. *Cristatisporites triangulatus* (Allen) McGregor and Camfield. GSC 49842.

Figure 10. *Aneurospora greggsii* (McGregor) Streel, holotype. GSC 13184.

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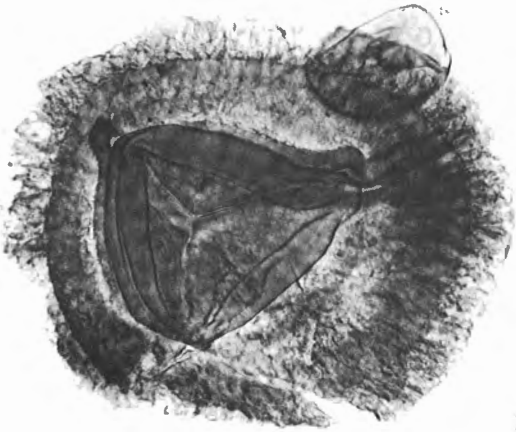

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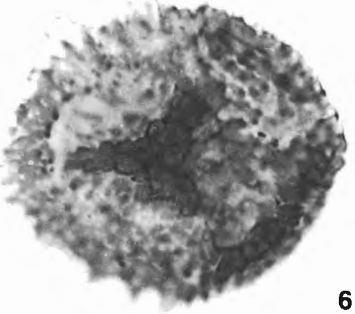

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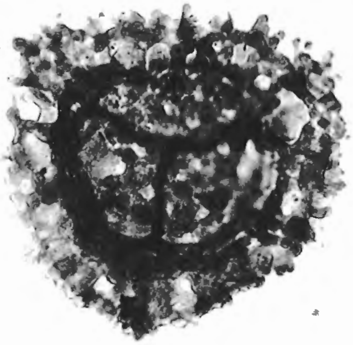

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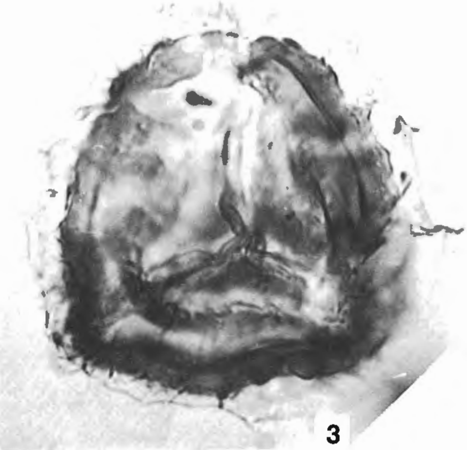

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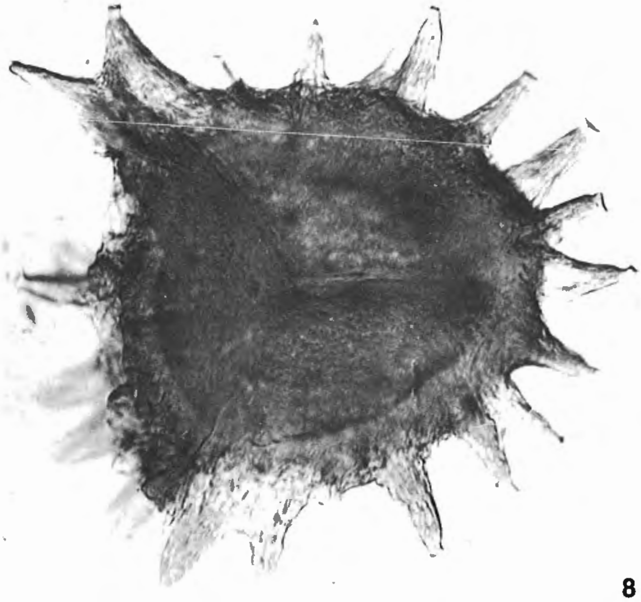

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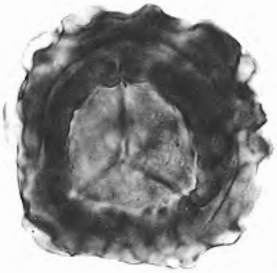

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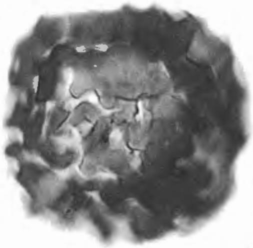

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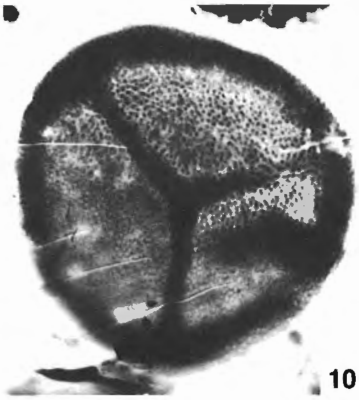

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PLATE 16

(All figures are X500, unless stated otherwise)

Figure 1. *Contagisporites optivus* (Chibrikova) Owens var. *optivus*. GSC 49848.

Figures 2, 3. *Ancyrospora langii* (Taugourdeau-Lantz) Allen. GSC 73293.

Figure 4. *Aneurospora goensis* Streel. GSC 49838.

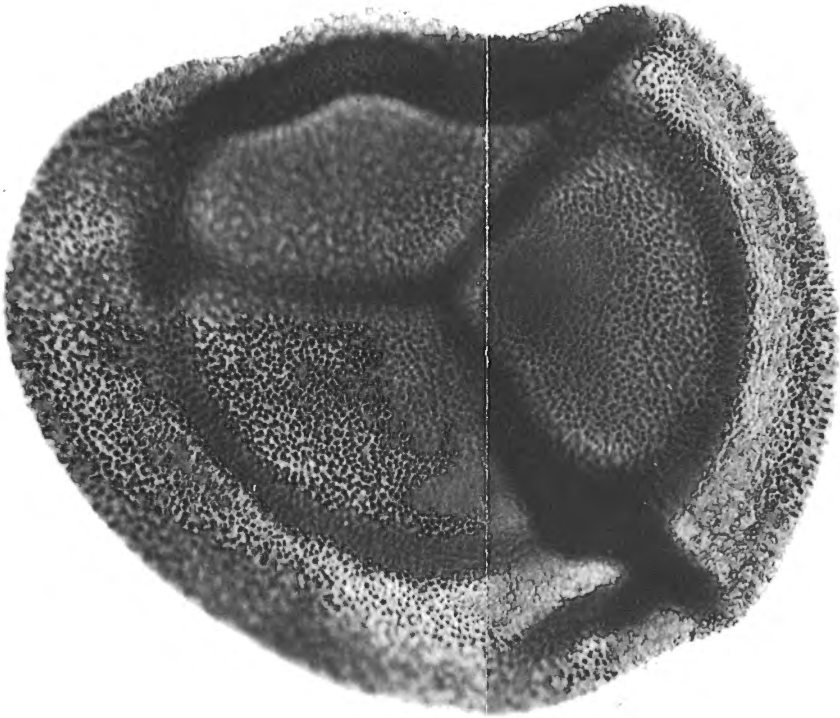
Figure 5. *Chelinospora ligurata* Allen. GSC 73294.

Figures 6, 7. *Ancyrospora melvillensis* Owens. GSC 73295.

Figure 8. *Grandispora tomentosa* Taugourdeau-Lantz. GSC 41770.

Figure 9. *Archaeoperisaccus timanicus* Pashkevich. GSC 29412.

Figure 10. *Chelinospora concinna* Allen, X1000. GSC 49839.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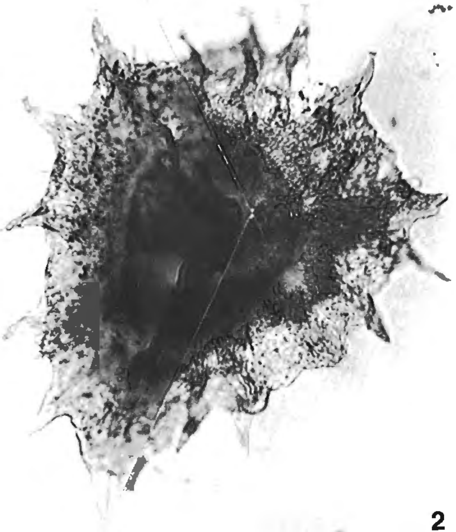
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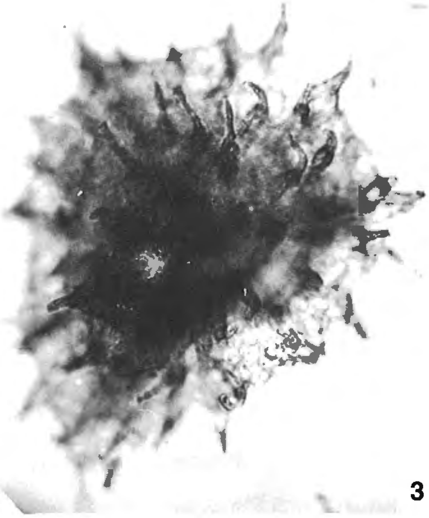
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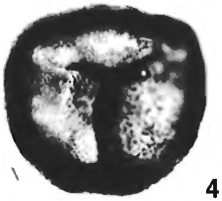
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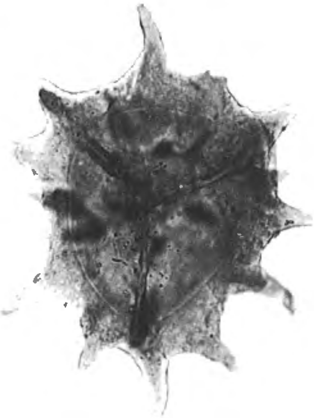
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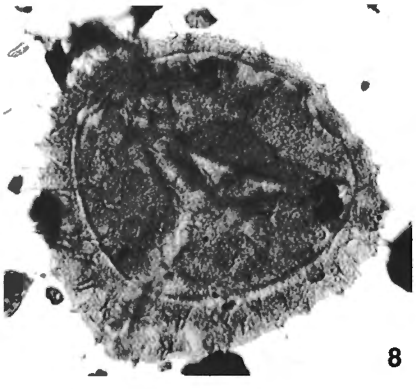
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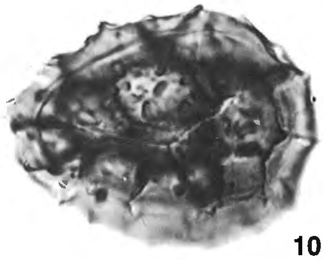
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PLATE 17

(All figures are X500, unless stated otherwise)

Figure 1. *Archaeoperisaccus ovalis* Naumova, X1000. GSC 73296.

Figure 2. *Verrucosisporites bulliferus* nom. nov., X1000. GSC 73297.

Figure 3. *Archaeoperisaccus opiparus* Owens. GSC 73298.

Figures 4, 5. *Ancyrospora furcula* Owens; 5, X1000. GSC 49847.

Figure 6. *Hymenozonotriletes deliquescens* Naumova. GSC 73299.

Figure 7. cf. *Archaeozonotriletes laetus* Sergeeva, X1000. GSC 73300.

Figures 8, 9. *Nikitinsporites canadensis* Chaloner; 8, GSC 73301; 9, X150, GSC 43732.

Figure 10. *Lophozonotriletes media* Taugourdeau-Lantz. GSC 73302.

Figure 11. *Diaphanospora reticulata* Guennel, X1000. GSC 73303.


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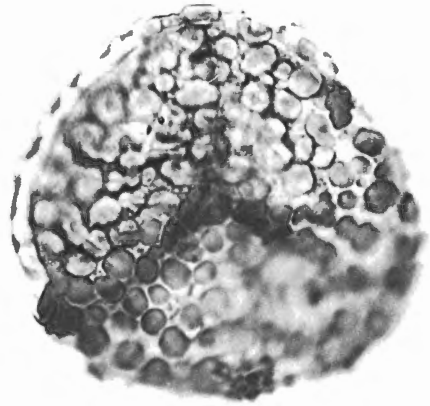
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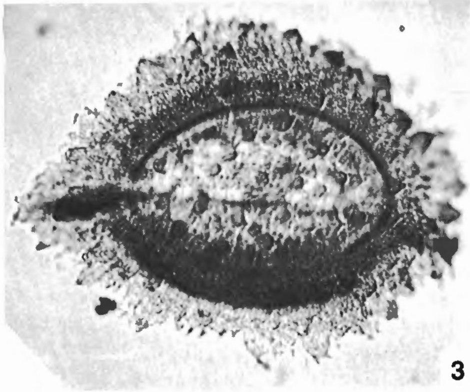
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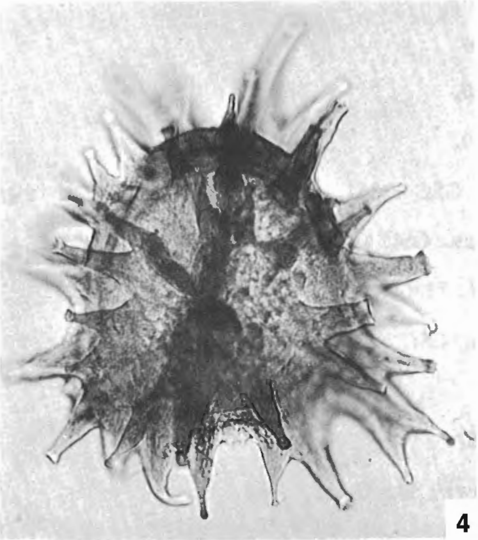
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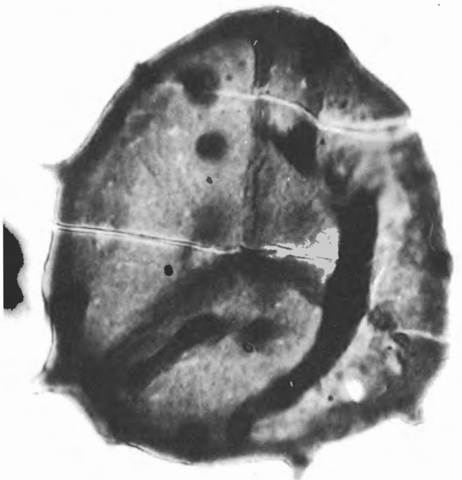
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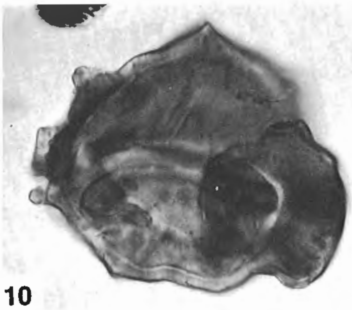
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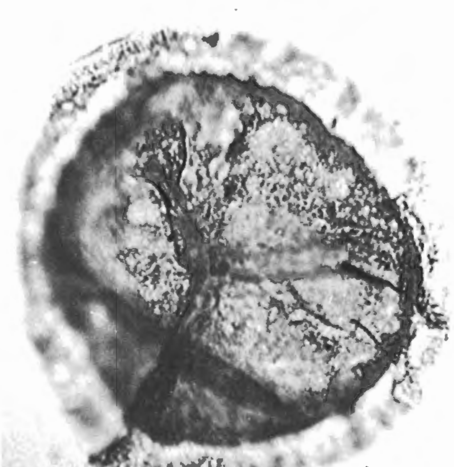
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PLATE 18

(All figures are X1000, unless stated otherwise)

Figure 1. *Auroraspora torquata* Higgs, holotype, X500.

Figures 2, 3. *Grandispora gracilis* (Kedo) Streel; 3, X5000.

Figure 4. *Archaeozonotriletes famenensis* Naumova. GSC 49851.

Figure 5. *Cornispora varicornata* Staplin and Jansonius. GSC 49852.

Figure 6. *Auroraspora hyalina* (Naumova) Streel. GSC 73304.

Figure 7. *Cyrtospora cristifera* (Luber) Van der Zwan. GSC 49853.

Figure 8. *Auroraspora pseudocrista* Ahmed. FM 60.

Figure 9. *Diducites versabilis* (Kedo) Van Veen. FM 67.

Figure 10. *Hystricosporites multifurcatus* (Winslow) Mortimer and Chaloner, X500. GSC 73305.


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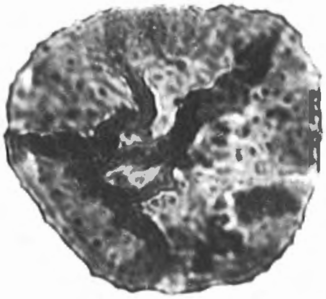
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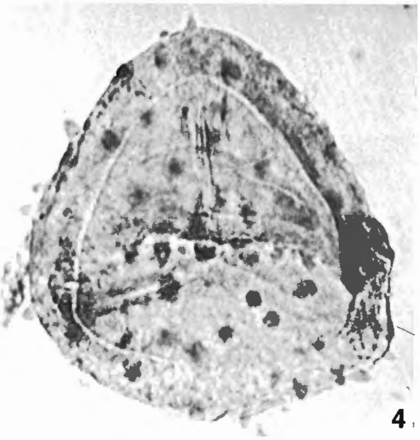
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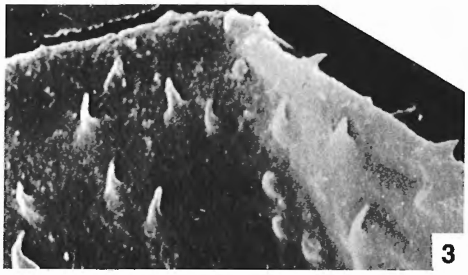
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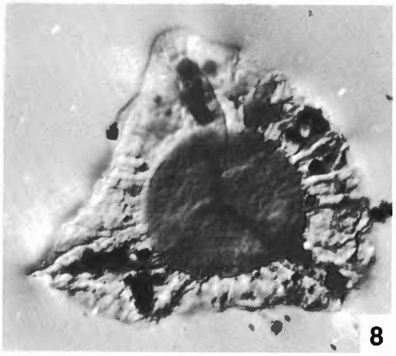
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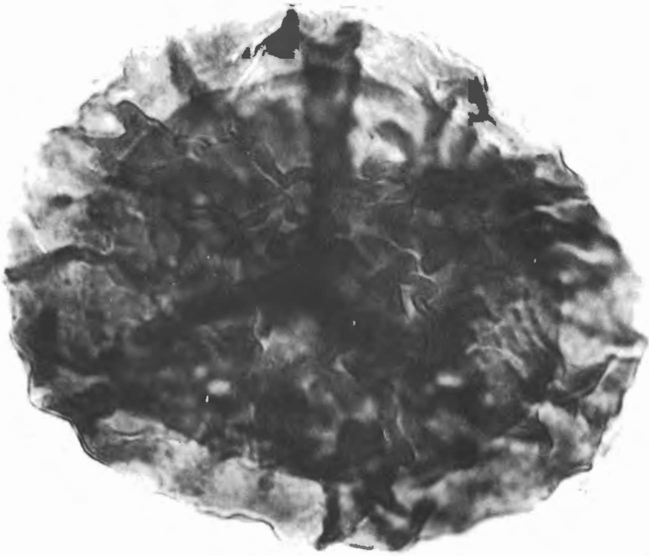
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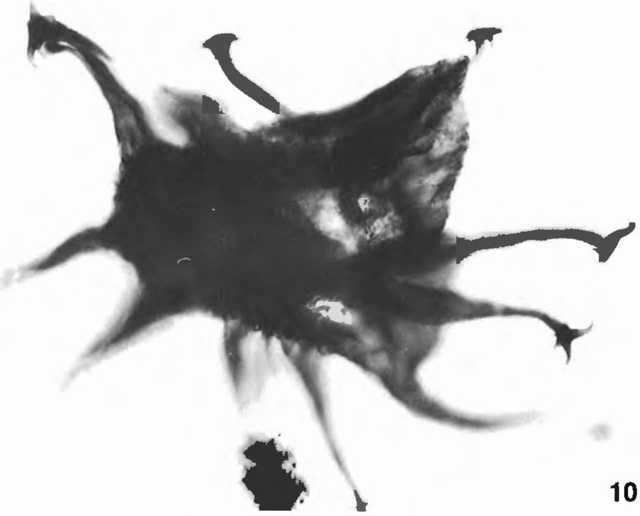
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PLATE 19

(All figures are X1000, unless stated otherwise)

Figure 1. *Knoxisporites dedaleus* (Naumova) Streel. GSC 73306.

Figures 2, 3. "(?)*Hymenozonotriletes denticulatus* Naumova" of McGregor, 1967. GSC 49850.

Figure 4. *Diducites poljessicus* (Kedo) Van Veen.

Figure 5. *Crassispora catenata* Higgs. FM 62.

Figure 6. *Lophozonotriletes lebedianensis* Naumova. GSC 15422.

Figure 7. *Rugospora flexuosa* (Jushko) Streel. GSC 73308.

Figure 8. *Auroraspora macra* Sullivan. GSC 73309.

Figure 9. *Lagenicula* sp. A of Streel in Becker et al., 1974, X500. FM 61.


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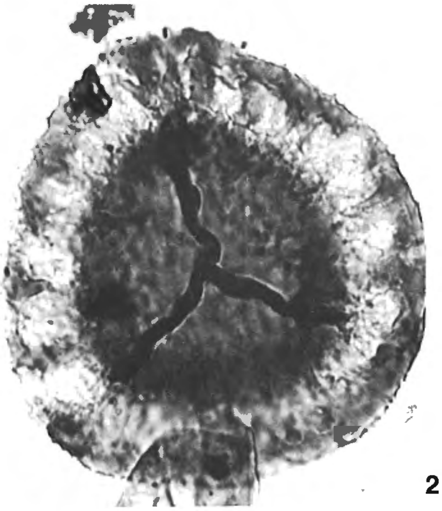
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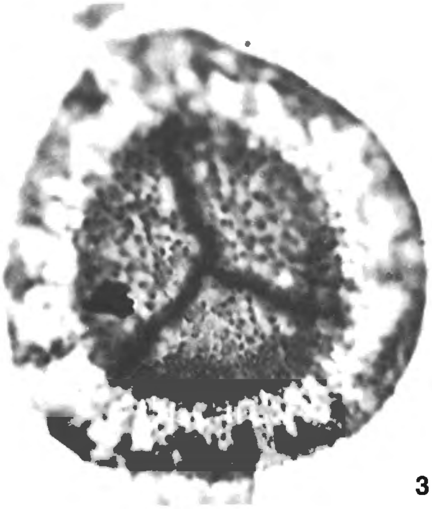
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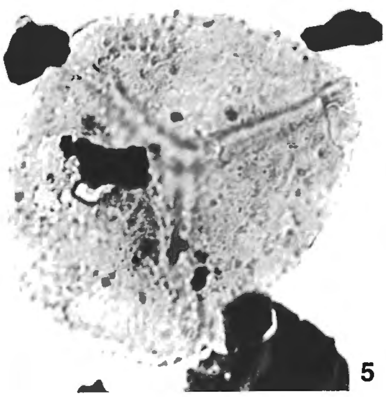
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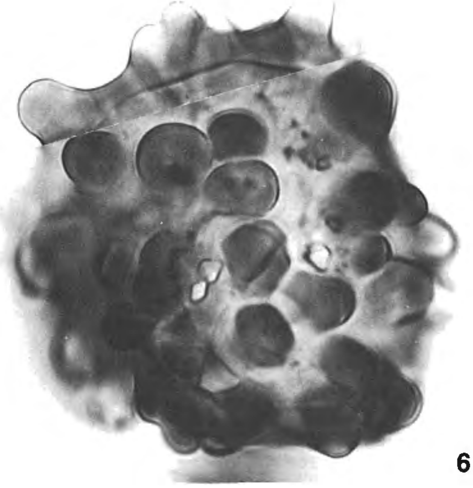
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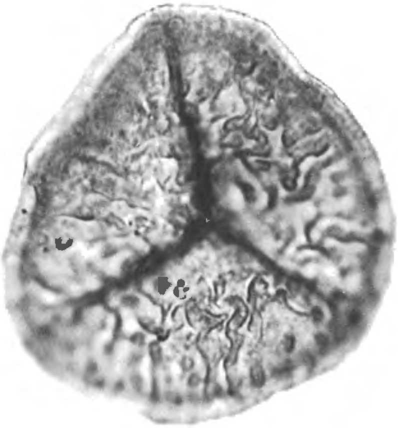
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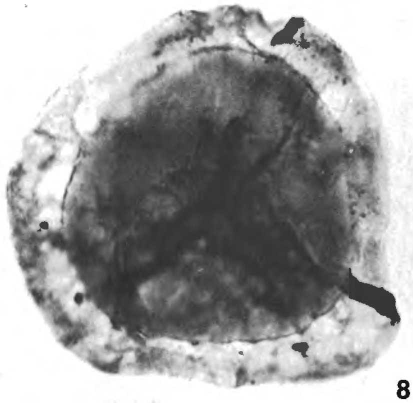
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PLATE 20

(All figures are X1000, unless stated otherwise)

Figure 1. *Grandispora cornuta* Higgs. FM 63.

Figure 2. *Retispora cassicula* (Higgs) Higgs and Russell, X500.

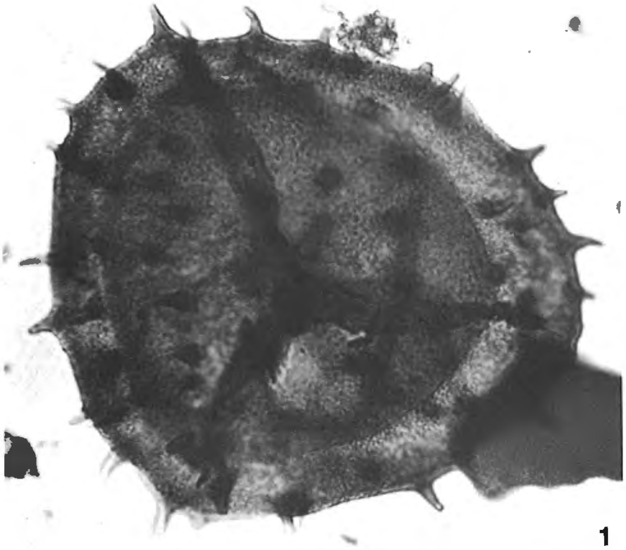
Figure 3. *Retusotriletes phillipsii* Clendening, Eames and Wood. FM 64.

Figure 4. *Retispora lepidophyta* (Kedo) Playford. GSC 73310.

Figure 5. *Vallatisporites pusillites* (Kedo) Dolby and Neves. FM 65.

Figure 6. *Grandispora echinata* Hacquebard. GSC 25496.

Figure 7. *Discernisporites micromanifestus* (Hacquebard) Sabry and Neves. GSC 73311.



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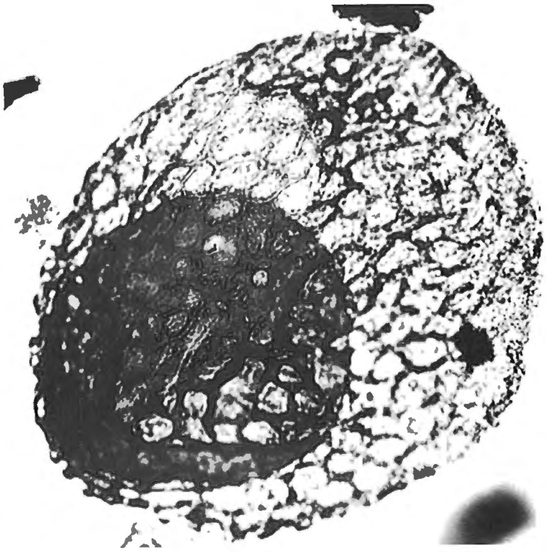

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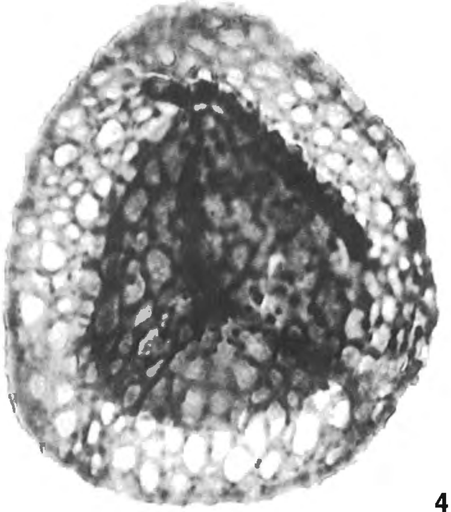

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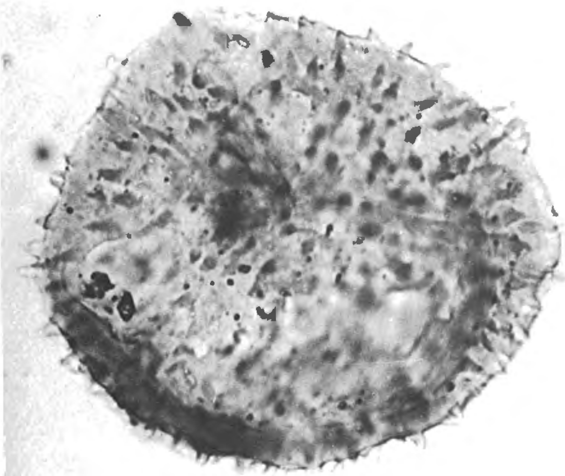

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PLATE 21

(All figures are X1000, unless stated otherwise)

Figure 1. *Raistrickia variabilis* Dolby and Neves. GSC 73312.

Figures 2, 3. *Tumulispora rarituberculata* (Luber) Turnau. FM 66.

Figure 4. *Tumulispora malevkensis* (Kedo) Turnau. GSC 49854.

Figure 5. *Knoxisporites literatus* (Waltz) Playford. GSC 25450.

Figure 6. *Hymenozonotriletes explanatus* (Luber) Kedo, X500. GSC 73313.

Figure 7. *Verrucosisporites nitidus* (Naumova) Playford. GSC 73314.

Figure 8. *Vallatisporites verrucosus* Hacquebard, X500.

Figure 9. *Raistrickia corynoges* Sullivan. GSC 73315.

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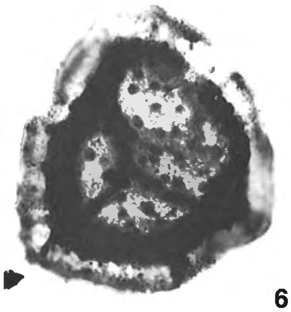

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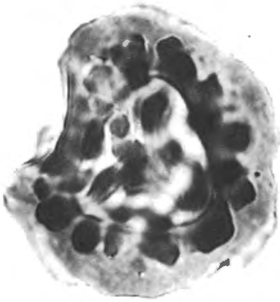

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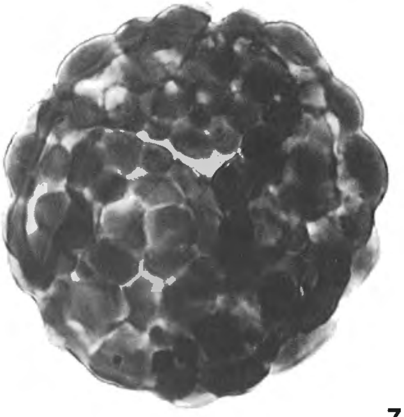

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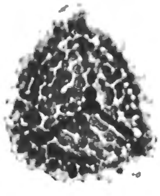

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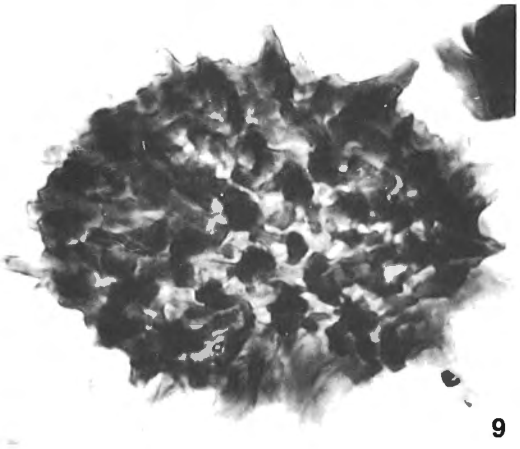

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