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MIDDLE DEVONIAN (GIVETIAN) PLANT MICROFOSSILS FROM GOÉ (BELGIUM) (*)

by K. M. LELE (**) and M. STREEL (***)

(2 figures et 4 planches)

ABSTRACT

Associations of Middle Devonian spores and other plant microfossils recovered from four successive beds of the Brandt quarry, near Goé (Belgium). are studied in detail for their taxonomy and pattern of distribution.

A total of 16 spore genera (including 30 species, 4 of which are new) are described. *Biornatispora* is newly erected. Specialization trends in *Retusotriletes* are discussed with a view to draw attention on its circumscription. The stratigraphic significance, the environmental condition of the microfossil assemblages and their probable relation to the associated megafossil flora are briefly considered.

RÉSUMÉ

Des associations de spores et d'autres microfossiles végétaux du Dévonien moyen ont été isolées de quatre bancs successifs dans la carrière Brandt, près de Goé (Synclinorium de la Vesdre, Belgique). Leur taxonomie est étudiée en détail ainsi que leur distribution dans la séquence sédimentaire.

Seize genres, comprenant 30 espèces dont 4 nouvelles, sont décrites. Un nouveau genre est défini : *Biornatispora*. Les diverses tendances de la spécialisation du genre *Retusotriletes* sont discutées dans le but de mieux comprendre les limites du genre. La valeur stratigraphique et les conditions de dépôt de ces assemblages de microfossiles végétaux sont brièvement esquissées ainsi que leurs relations probables avec la mégaflore associée.

INTRODUCTION

The occurrence of spores in the Middle Devonian (Givetian) of Belgium was first reported by Leclercq (1960) while investigating a rich megaflora in the succession of the Brandt quarry near Goé.

Subsequently Streel (1964) published an account of the spore assemblage recovered from one of the beds of the above quarry which contained *Pseudosporrochnus nodosus* Leclercq and Banks (1962). The small assemblage contained 9 dispersed miospore genera (including two new) distributed in the following species (original list) : *Phyllothecotriletes rotundus* Streel, *P. triangulatus* Streel, *Apiculiretusispora brandtii* Streel (*gen. nov.*), *Apiculiretusispora sp.*, *Verrucosisporites den-*

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(**) Birbal Sahni Institute of Paleobotany, Lucknow (India).

(***) Université de Liège, Laboratoire de Paléontologie végétale, 7, place du Vingt-Août, Liège.

tatus Streel, *V. mucronatus* Streel, *V. pseudospinosus* Streel, *V. apiculatus* Streel, *Hystrichosporites cf. corystus* Richardson, *Aneurospora goensis* Streel (*gen. nov.*), *Ancyrospora ancyrea* var. *ancyrea* Richardson, *Endosporites* cf. *micromanifestus* Hacquebard, *Rhabdosporites* cf. *Langi* Richardson.

In view of the interesting results obtained by Streel from a single sedimentary bed, the present work was undertaken to extend similar investigations to other beds of the Goé succession, which also contain megafossil associations.

The object is to study :

1. the spore taxa in greater morphological details based on a more complete material and to take note of other plant microfossils e.g. cuticles, tracheids, etc.
2. the distribution pattern of the microfossil assemblages in the various layers and,
3. the possible relationship reflected between the microfossil and megafossil associations belonging to the same layer.

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MATERIAL AND METHODS

Rock samples from four successive beds from an exposure in the Brandt quarry were macerated. In general the rocks are silstones, greyish to yellowish brown in colour. In some of the thick rock specimens, the sediments show irregular alternations of thin shaly layers with sandy ones.

A sequence of five such thin layers was separately macerated in the case of the rock specimen n° 178. The results showed that spores were practically confined to the finegrained shaly layers, while the sandy ones only after repeated attempts could yield a few ill-preserved spores (see Table 1 for details).

In other rock specimens of similary thickness, it was therefore preferred to select the shaly layers alone and macerate them separately. In the case of bed n° IV two specimens were particularly chosen to compare the results of spore frequencies.

The 4 rock specimens were thus split into a total of 13 maceration samples.

Details concerning these samples and the megafossil associations of the beds are given in Table 1.

The samples (5 gms in each case) were macerated following the technique described by Streel (1965*a*). In addition, the residues, after the HF treatment were carefully oxided in Schulze mixture for a duration of time ranging from 1/2 hr to 12 hrs. Alkali treatment gave no advantage.

The type and figured slides (Regd. Nos 3101-3120) are preserved in the collection of Plant Paleontology, Université de Liège, Belgium.

For convenience of practice, the assessments, as expressed in this Table, were based on the following criteria :

Population : 1. « Rich » when a single slide (cover-slip area 26 × 21 mm.) was found enough for counting 100 spores. 2. « Moderate » — when two slides were required for the same count and 3. « Scarce » — when more than two slides were necessary.

Preservation : 1. « Good » — when the spores were generally well-preserved, transparent and complete, and could be readily identified. 2. « Satisfactory » — when the spores were generally less well-preserved, translucid, and ± incomplete and could be identified with some effort. 3. « Poor » — when spores were generally ill-preserved, opaque and incomplete, and were difficult to determine.

TABLE 1

Characteristics of samples

Specimen No	No	Sample No Sh = shaly Ss = sandy	Spore population	Preser-vation	Megafossils
177	VI	177	Rich	Good	Very fragmentary plant remains
27	V	27/III	Moderate	Good	Drifted axes
		27/II	Scarce	Poor	
		27/I	Scarce	Poor	
269	IV	269/III	Moderate	Satisfactory	Fragments of *Pseudosporochnus* and *Aneurophyton* ; some large axes of *Pseudosporochnus nodosus* Lecl. and Banks
		269/II	Scarce	Poor	
		269/I	Scarce	Poor	
178	IV	178/V (sh)	Moderate	Satisfactory	
		178/IV (ss)	Scarce	Poor	
		178/III (sh)	Moderate	Satisfactory	
		178/II (ss)	Scarce	Poor	
		178/I (sh)	Moderate	Poor	
583	III	583	Absent	X	Rich in *Pseudosporochnus* and *Aneurophyton* (+ Sporangia)

TAXONOMY

In recent years, the problem of the classification of dispersed spores and pollen has gathered considerable impetus (Dettmann, 1963 ; Richardson, 1965 ; Neves & Owens, 1966 ; Smith & Butterworth, 1967).

Despite certain points of advantages that some of the recent proposals may apparently show over the earlier scheme of Potonié and Kremp (1955), it is not certain if any one of them is exclusively perfect in itself.

The controversy over the problem of spore classification is still under discussion in the C.I.M.P. working groups. Until a final decision is reached it seems wiser to follow the broad scheme of Potonié and Kremp.

Anteturma : *Sporonites* (R. Pot.) Ibrahim, 1933
Genus : *Pilasporites* Balme & Hennelly, 1956
Type species : *P. calculus* Balme & Henn., 1956

Pilasporites cf. *plurigenus* Balme & Henn.
(pl. 1 ; fig. 1)

Some specimens, otherwise appearing like *Punctatisporites* in shape, but devoid of any haptotypic features are accomodated under *Pilasporites*.

They mesure 30-40 μ in diameter, have a moderately thick (less than 1 μ) and occasionally folded exine. They compare generally with *P. plurigenus* Balme and Hennelly, 1956.

Anteturma : *Sporites* H. Potonié, 1893
Turma : *Triletes* (Reinsch) Pot. & Kr., 1954
Subturma : *Azonotriletes* Luber., 1935
Infraturma : *Laevigati* (Benn. & Kidst.) Pot. & Kr., 1954
Genus : *Leiotriletes* (Naum.) Pot. & Kr., 1954
Type species : *L. sphaerotriangulus* (Loose) Pot. & Kr., 1954

Leiotriletes cf. *simplex* Naumova
(pl. 1 ; figs. 2, 3)

Size range 23-25 μ, roundly triangular, angles rounded, sides convex, trilete mark clear, apex ± elevated rays occasionally wavy and associated with folds, about 3/4 of spore radius or more ; exine 1-2 μ thick, infragranulate.

The few specimens encountered seem to be nearest to *L. simplex* Naumova (1953) than any other species.

Leiotriletes cf. *laevis* Naum.
(pl. 1 ; figs. 4, 5)

Size range 18-25 μ ; roundly triangular, angles rounded, sides ± convex, trilete mark simple, rays about 3/4 spore radius, exine about 1 μ thick, smooth to infrapunctate.

In its shape and size range the specimens are closely comparable with *L. laevis* Naumova (1953). Forms similar to those figured here have earlier been referred to *L.* cf. *priddyi* by Streel (1967). We are now inclined to transfer at least some of them (e.g. Streel, pl. 1 ; figs. 1, 2) to *L. laevis* for *L. priddyi* Berry (1927) seems to be characterized by straight to concave interradial margins.

Genus : *Punctatisporites* (Ibr.) Pot. & Kr., 1954
Type species : *P. punctatus* Ibrahim, 1933

Punctatisporites spp.
(pl. 1 ; figs. 6-8)

Form A (fig. 6) — 73 μ average diameter, exine thick (± 2 μ) with an indistinct structure, trilete mark associated with broad secondary folds extending nearly up to the margin.

Form B (fig. 7, 8) — size range 26-36 μ, shape almost circular with a slight triangularity, trilete mark clear, simple, occasionnaly opened ; rays 2/3 of spore radius or longer. Exine 1-2 μ thick ± infragranulate, rarely folded.

This form agrees closely with *Punctatisporites* sp. A recorded by Streel (1967, Pl. 1 ; fig. 6) from the Emsian of Belgium.

Genus : *Retusotriletes* (Naumova) Streel, 1964

Type species : *R. simplex* Naum. (Lectogenotype of Potonié, 1958)

The genus *Retusotriletes* is used here in a wider sense (see Streel, 1967) for spore with discernible curvaturae or/and an apical differentiation of the exine at the proximal pole irrespective of exine thickness. The diverse trends of organizational specialization in the retusoid spore complex are discussed later to bring out the reasonable limits of the genus *Retusotriletes*.

Retusotriletes simplex Naumova, 1953

(pl. 1 ; figs. 9, 10, 11)

Size range 30-40 μ, circular to roundly triangular, exine moderately thick, smooth to infragranulate, fine granules may also be locally present over the exine, trilete mark simple, straight, rays 3/4 of spore radius or longer, bounded by curvaturae, secondary folds rare.

REMARKS : The species seems to be very generalized and may not therefore be homogeneous. The curvaturae are occasionally seen almost touching the equator (fig. 9, 11) for their large part except near the ray extremeties. The exine at the proximal pole does not show any differentiation.

Retusotriletes goensis sp. nov.

(pl. 1 ; figs. 12-16)

HOLOTYPE : pl. 1 ; fig. 12. 38 μ.
PARATYPE : pl. 1 ; fig. 13. *ca* 41 μ.

DIAGNOSIS : Size range 38-80 μ, shape subcircular to roundly triangular, exine moderately thick, smooth to infragranulate, proximal polar region differentiated as a denser, ± thick, roundly triangular area (hereafter called « Apical area ») extending for 1/3-1/2 of spore radius, outline of apical area diffused to well-defined ; trilete mark clear, rays generally well seen up to 3/4 of spore radius and are bounded by perfect curvaturae ; secondary folds may be present.

COMPARISON. *R microgranulatus* (Vigran) Streel (1967), probably stands nearest to *R. goensis* sp. nov. than any other species. However, *R. microgranulatus* is distinguishable by the fact that it has a smaller apical area (1/3-1/4 of spore radius) and the rays are clear only within the confines of this area : beyond that they are apparently reduced to bare traces. Besides, the curvaturae in *R. microgranulatus*, if at all present, are very obscure. On the contrary, in *R. goensis* sp. nov. the apical area shows a wider range in its extent and degree of prominence (see figures 14-16) and the rays are longer and generally well seen up to their contact with the curvaturae, the latter being also well-defined. Additionally, the apical area, when sharply developed has also a somewhat elevated appearance.

R. biarealis McGregor (1964) differs in its much larger size and the scabrate proximal ornament. In our opinion, the specimen in Pl. 1, fig. G, of Mortimer (1967) shows features similar to *R. goensis* rather than to *R. rotundus* emend. The latter species, as will be pointed out later, has a different kind of apical area.

Retusotriletes confossus (Richardson) Streel, 1967
(pl. 1 ; fig. 17)

Specimens few ; the one figured measures 58 μ ; subcircular, exine thick with clear infra-punctate structure characteristic of the species ; Rays clear up to 1/2 spore radius but are traceable for 3/4 distance, curvaturae discernible ; apical area ± deltoid in shape, 1/3 of spore radius, outline diffused, infra-elements apparently more densely packed.

Retusotriletes rotundus (Streel) emend.
(pl. 1 ; figs. 18-20)

HOLOTYPE : Streel, 1964, Pl. 1 ; fig. 1.

EMENDED DIAGNOSIS. Size range 36-64 μ, shape roundly triangular to circular exine moderately thick, trilete mark clear, rays ± straight, ± well seen up to 4/5 of spore radius, bounded by curvaturae perfectae ; apical area ± roundly triangular extending up to 1/2 spore radius, differentiated into two zones : an inner lighter zone with a relatively thinner exine than elsewhere, and an outer darker zone with a relatively thicker and ± diffused outline exine ; relative proportion and prominence of the two zones variable ; local granulation on exine may be present ; few folds common.

REMARKS : The species is emended in view of the details available in regard to the apical area. The specimens illustrated by Streel (1964) and those figured here demonstrate the variability in the extent of the apical area as well as the proportion of the lighter zone to the darker zone. In general it has been observed that as the inner lighter zone increases in extent, the outer darker zone tends to become relatively thinner and ill-defined. In extreme cases, the inner margin of the darker zone may appear somewhat scalloped resembling that of *R.* (al. *Calamospora*) *whitneyanus* (Chaloner, 1963) Streel (1967, p. 27).

The present diagnosis now permits the inclusion of a specimen referred to *R. triangulatus* Streel (1964, Pl. 1, fig. 3) under *R. rotundus*. The following specimens might also belong to *R. rotundus* :

1. *Phyllothecotriletes* (al. *Retusotriletes*) *distinctus* (Richardson) Mortimer (1967, Pl. 1, fig. H).
2. *Retusotriletes* sp. Richardson (1967, Pl. 2, fig. A).

Retusotriletes triangulatus (Str.) Streel, 1967
(pl. 1 ; fig. 21)

Examples rare, figured specimen 50 μ in diameter, circular ; apical area like a dark, thicked roundly triangular zone (about 5 μ wide) surrounding the pole ; exine at the pole (enclosed by apical area) is unspecialized and similar to the rest of the spore exine in thickness ; outer limit of apical area extending up to ± 1/2 spore radius ; trilete rays clear within the apical area but traceable up to 4/5 spore radius, bounded by curvaturae. A reexamination of the holotype confirms these observations.

Comparison : The species is distinguishable from *R. rotundus* by the absence of the inner lighter zone in the apical area. The rays are not uniformly well-defined for their whole extent and the curvaturae are imperfect. The distinction between the two species is however not very evident without a clever scrutiny of several specimens. A specimen figured by Richardson (1967, Pl. 3, fig. A) shows what appears like a single thickened apical area completely covering the proximal polar region. Its assignment to *R. triangulatus* is therefore questionable. On the other hand, the specimen seems to bear more resemblance with the figures of *R. biarealis* McGregor (1964).

Genus : *Aneurospora* Streel, 1964
Type species : *A. goensis* Streel, 1964 ; p. 16

Aneurospora goensis, Streel, 1964

(pl. 1 ; figs. 22-26)
(pl. 2 ; figs. 27, 28)

Size range 30-60 μ, specimens abundant, agreeing in all essential respects with the diagnosis of the genus and species.

It may be summarized that *A. goensis* is an anisopolar spore, the proximal part being ± pyramidal, the distal one ± hemispherical. The proximal pyramid appears to make a slightly angular contact with the proximo-equatorial part of the exine. At this contact, the subequatorial proximal region is especially rigid and probably thickened so as to appear like a dark band. The inner limits of the band are ill-defined and its width is also ± variable even in the same specimen. The trilete rays which are slightly elevated are seen to merge into the band with occasionally a slight expansion. Where the band is less perfect, a thin line may be discernible. Obliquely preserved specimens are not uncommon (figs. 25-26) which help to confirm that the dark band is only a proximal feature and is of the nature of banded curvaturae (see « specialisation trends in *Retusotriletes* »).

The ornament, which is mostly distal, shows a wide range of variation in size and distribution as illustrated in the figures. Some small specimens (measuring 30 μ) but with apparently identical features, are also found which serve to increase the lower size-range of the species. The loop-like structure in the expanded ray ends as shown by Streel (1964, Text, fig. 6, p. 16) is not typical to the species. Compression folds are occasionally seen distally. There is no appreciable difference in the thickness of the proximal and distal exines. No internal layer has been noticed.

Comparisons : *Retusotriletes greggsii* McGregor (1964, p. 8) also shows a distal ornament of distinct coni or apiculae. This character, together with the presence of banded curvaturae, bring the species undoubtedly within the circumscription of *Aneurospora*. The canadian species however, differs from *A. goensis* in the closer and relatively finer distal ornament.

Geminospora-bearing material from the type locality, kindly sent to us by Dr. Balme, was examined for comparison with *Aneurospora goensis*. *Geminospora* seems to be sufficiently distinct in the absence of banded curvaturae and the common development of a mesosporoid. Besides, it has in general a thicker exine (up to 3 μ) but the difference between the thickness of the proximal and distal exines does not appear to be appreciable.

Geminospora (al. *Lycospora*) *svalbardiae* (Vigran) Allen (1965) and *Geminospora Huberculata* Allen (1965) seem to be interesting in that despite the presence of an inner layer, they have haptotypic features more comparable with those of *Aneurospora*. Their taxonomic position, therefore, remains rather open.

Aneurospora (*Retusotriletes*) *semizonalis* McGregor, nov. comb.

(pl. 2 ; fig. 29)

1964 — *Retusotriletes semizonalis* McGregor, p. 10.

Specimens rare, figured example roundly triangular, 39 μ in diameter, rays reaching close to equator, curvaturae associated with a dark equatorial band (banded curvaturae) 2-3 μ wide, as is characteristic of the species ; exine finely granulate as also seems to be the case in the specimens figured by McGregor (1964, pl. 2, fig. 4).

REMARK : The generic diagnosis of *Aneurospora* does not exclude laevigate forms, although the type species is distinctly ornamented. With this broad concept in mind, *Retusotriletes semizonalis* of McGregor (1964) deserves accomodation under *Aneurospora*. *Retusotriletes incohatus* Sullivan (1964) may also appear to fall within the limits of *Aneurospora*.

Genus : *Apiculiretusispora* (Streel) Streel 1967.

Type species : *A. brandtii* Streel, 1964, p. 8.

Apiculiretusispora brandtii Streel

(pl. 2 ; figs. 30-31)

Size range 53-78 μ ; specimens agreeing well with the type species, except for the general lack of an apical area. Several fragmentary specimens, probably of this species, are also encountered in the preparation.

Genus : *Dibolisporites* Richardson, 1965.

Type species : *D. echinaceus* (Eisenack) Richardson, 1965.

Dibolisporites cf. *gibberosus* (Naum.) var. major (Kedo) Richardson, 1965

(pl. 2 ; fig. 33)

Size range 75-97 μ, complete specimens few ; several fragmentary ones probably belonging to this species being noticeable ; circular or flattened to various shapes with common secondary folds ; proximal surface smooth or with reduced coni, ornament tending to gain prominence near proximo-equatorial region and well-developed over the distal part, being composed of regularly placed coni, pila or bacula often with a conate apex or bearing a fine, spine « biform » ; apical area or curvaturae not well-developed.

Comparable specimens are figured by Streel (1967) from the Emsian of Belgium.

Dibolisporites sp. A.

(pl. 1 ; fig. 34)

Several fragmentary specimens, showing *Dibolisporites* type of ornament are not uncommon. While the majority of these undoubtedly belonged to *D.* cf. *gibbe-*

rosus, some others seem to represent another type, apparently large in size, with well-developed, thick trilete mark, surrounded usually by dark apical area (fig. 35) and well-defined curvaturae. They do not compare with the known species, but are not enough complete for erecting a new one.

Genus : *Granulatisporites* (Ibr.) Pot. et Kr., 1954

Granulatisporites Stockmansi Streel, 1967
(pl. 1 ; fig. 32)

Specimens rare, figured one 25 μ, roundly triangular, exine 1-2 μ thick, mostly distal ornament of small rounded or slightly conical grana up to 0,5 μ high and as wide. The present specimens compare with the species recorded from the Emsian of Belgium (Streel, 1967).

Genus : *Verrucosisporites* (Ibr.) Smith, 1957
Type species : *V. verrucosus* Ibrahim, 1933

Verrucosisporites spp.
(pl. 2 ; figs. 35, 36)

Form A (fig. 35) — Rare specimens, ± 60 μ in diameter, trilete obscure, verrucae ± regular in size (up to about 2 μ high) and distribution, closely spaced.

Form B (fig.36) — One specimen, 24 μ in diameter, verrucae ± 2 μ high with rounded to flat tops, about 10 elements in 1/3 of the circumference of spore.

Genus : *Biornatispora* gen. nov.
Type species : *Biornatispora* (*Verrucosisporites*) *dentata* (Streel) n. comb.

HOLOTYPE : Streel, 1964, pl. 1, fig. 14.

COTYPE : pl. 2, figs. 37, 38.

DIAGNOSIS : Trilete spores, roundly triangular to circular, exine covered with two kinds of sculpture viz. an apiculate ornament which is superimposed over and occasionally intermixed with low muri ; ornamented muri ± anastomose to form a reticuloid pattern ; sculpture mostly well-developed on distal side but may encroach on the proximo-equatorial region ; trilete mark simple, rays 2/3-3/4 spore radius, often obscured by ornament ; secondary folds uncommon.

DESCRIPTION : The spores are characterized by two kinds of sculptural elements. The first kind of sculpture consists of low ridges (muri) of variable height which show a strong tendency to anastomose forming a ± reticuloid pattern. The other kind of sculpture is composed of apiculate elements (coni, verrucae or baculae) of variable size and shape which are superimposed over the ridges and may be sometimes intermixed.

The study of the large number of specimens reveals a wide range of variation in both kinds of sculptural elements. For instance, all transitions from scattered ± unconnected ridges leading towards the formation of a ± complete reticuloid pattern are observable. Similarly, the apiculate elements also show considerable variation in their distribution, size and shape and may sometimes bear a fine tip at the apex.

The apiculae are generally superimposed over the ridges and can also occur separately between them. At the same time a tendency is noticeable in the apiculae to become decurrent at their bases which may laterally connect to form low ridges. The two kinds of sculpture (ridges and apiculae) thus seem to be closely associated with each other although one of the sculptural types usually dominates over the other.

The sculpture is very well-developed on the distal side. A few reduced elements, specially of the apiculate type, may be present on the proximal side, particularly near the equator. The spores derive various shapes on flattening which suggests that they lack preferred orientation.

COMPARISON : *Acinosporites* Richardson (1965) is distinguished by the *convoluted* pattern of the muri which characteristically bear « biform » ornament elements i.e., verrucae surmounted by spines, spinose projections or cones. The present spores, which were earlier referred to *Acinosporites* do not possess such characters.

Camptotriletes differs in having sparsely spaced cristate ridges which are ± concentrically arranged and do not form a reticuloid pattern through anastomosis.

Dictyotriletes has, in the strict sense, only muri which form a complete reticulum, there being no associated apiculate ornament.

The following species warrant transfer under *Biornatispora* : *Acinosporites lanceolatus* Streel, 1967.

Biornatispora (*Verrucosisporites*) *dentata* (Streel) nov. comb.

(pl. 2 ; figs. 37-43)

Synonyms : *Verrucosisporites dentatus* Streel, 1964
Acinosporites dentatus (Str.) Streel, 1967
Acinosporites mucronatus (Str.) Streel, 1967

EMENDED DIAGNOSIS : Size range 36-58 μ, shape typically circular to roundly triangular, but other shapes may be derived by compression ; trilete mark often obscured by the dense ornament ; rays straight, simple, 2/3-3/4 spore radius, muri thin, ± 0,5 μ wide, forming a ± complete reticuloid pattern with lumina up to 6 μ wide ; surmonted by densely packed and ± regular ornament usually composed of pointed to blunt coni. Some elements may also bear fine tips at the apex. Elements, up to 2 μ high and as broad or broader, may be decurrent and fused near bases ; random elements may be present in between muri ; ornamentation better developed distally ; but few elements may be found on proximal side, about 30-56 elements along equator.

DESCRIPTION : The variability in the shape of compressed specimens indicates the nature of the spores. The reticuloid pattern of thin muri is often obscured by the dense cover of the dominant apiculate ornament but with careful focal analysis it is detectable. Figures 37 and 38 represent the same spore in two different foci to demonstrate both kinds of sculptural elements. Broken specimens (fig. 43) as well as more eroded ones (figs. 41, 42) further confirm the reticuloid appearance of the muri and show that it is not a negative reticulum. The ornament elements are mostly coni or some verrucae and their size and distribution is more or less regular.

Towards base, the elements often tend to be decurrent or fused. The proximal side has reduced elements near the equator.

REMARKS : The species *Verrucosisporites mucronatus* Streel (1964) is considered a junior synonym of *Biornatispora dentata* because the features of the former are found to be insufficient for sharp demarcation. When the ornamentation is very regular and the reticuloid pattern finer the specimens approach the *mucronatus*-type (pl. 2, fig. 40) but the abundant material now examined shows all transitions towards the *dentatus*-type.

Biornatispora (*Verrucosisporites*) *pseudospinosa* (Streel, 1964) nov. comb.
(pl. 2 ; figs. 44-47)

Verrucosisporites pseudospinosus Streel, 1964
Acinosporites pseudospinosus (Str.) Streel, 1967

EMENDED DIAGNOSIS : Size range 26-64 μ circular to oval ; trilete often obscured by ornament, rays straight, simple, 2/3-3/4 of spore radius ; muri up to 1 μ wide, anastomosed to form reticuloid pattern, lumina 3-1 μ wide ; muri surmounted by coni or verrucae of very variable shape and size, up to 8 μ high, ± sparse and irregular in distribution ; elements often decurrent and fused at base forming ridges, reduced ornament may be present between muri ; about 10-26 elements along equator.

DESCRIPTION : Specimens are often flattened to a subcircular or oval shape. The apiculate ornament shows considerable irregularity in size, shape and distribution. The majority of elements are conate, but a few verrucate or baculate elements may also occur. They are generally superimposed on the muri, a few reduced ones being present between. The bases of the apiculae are often decurrent and connected. The degree of anastomosis between the muri is variable so that the resulting reticuloid pattern is generally incomplete.

COMPARISON : *B. pseudospinosa* is distinguishable from *B. dentata* by its very irregular, sparser and variable nature of the ornament elements as well as by the more open and imperfect appearance of the reticuloid pattern of muri. The number of projections seen along the equator is also smaller.

Biornatispora (*Verrucosiporites*) *apiculata* (Streel, 1964), nov. comb.

Verrucosisporites apiculatus Streel, 1964
Acinosporites apiculatus (Str.) Streel, 1967

The examination of the holotype confirms its assignment to the genus *Biornatispora*. Several specimens, although in rather fragmentary state, are present in the material which agree to the species.

Biornatispora reticulata sp. nov.
(pl. 2 ; figs. 48-52)

HOLOTYPE : pl. 2 ; fig. 48. 42 × 36μ.
PARATYPE : pl. 2 ; figs. 49, 50. 48 × 33μ.

DIAGNOSIS : Size range 40-45 μ, circular, oval or roundly triangular, trilete mark simple, often weakly developed, rays ± 2/3 (rarely 3/4) spore radius, distal side with a ± perfectly developed and fairly open reticuloid pattern of thin, moderately high muri, lumina about 4 μ - 15 μ wide, few reduced coni superimposed on muri. Exine of lumina smooth to infragranulate and may have some reduced coni.

DESCRIPTION : In this species, the reticuloid pattern has attained much greater perfection than in the previous ones. The muri appear to be thicker at base and taper towards top. Often they are higher at their junction. When projected outside the equator they are about 2-4 μ high.

On the contrary, the apiculate ornament is rather sporadic and reduced. Much reduced elements can be detected in the lumina.

COMPARISON : This species is readily distinguishable from the other species of *Biornatispora*, by its fairly open and almost complete reticulum and the reduced nature of the apiculate elements. Some extreme forms, where the ornament is hard to discover, may be mistaken for *Dictyotriletes* which lacks apiculate ornament.

Genus : *Convolutispora* Hoff., Stap. & Malloy, 1955
Type species : *C. florida* Hoff., Stap. & Malloy, 1955

Convolutispora sp.
(pl. 3 ; fig. 53)

Two specimens, about 46 μ, ± circular, trilete mark imperceptible, about 0,8-1,5 μ wide convoluted ridges anastomosing here and there, channels between ridges norrower than the width of muri, exine moderately thick.

Subturma : *Perinotriletes* Erdtman, 1947

Genus : *Perotrilites* (Erdtman) Couper, 1953
Type species : *Perotrilites granulatus* Couper

Perotrilites mutabilis sp. nov.
(pl. 3 ; figs. 54-57)

HOLOTYPE : pl. 3 ; fig. 54.
30 μ, body 28 μ.

DIAGNOSIS : Size range 28-40 μ, circular to roundly triangular, central body smooth may be slightly darker than perispore ; perispore lighter yellow, thin, ± transparent, usually only slightly greater than the body, often only partly separated along equator, ornamented with minute bacula or pila of variable shape and size (up to 1 μ high and as broad), elements tend to be closer and thicker on the distal polar region ; trilete mark simple, weekly developed, rays ± 1/2 of body radius, apical area occasionally slightly darker.

DESCRIPTION : The perispore is rather tight-fitting and is only partially separated in favourably preserved specimens. The ornament of the perispore shows coni to bacula or pila, some bearing a fine spine at the apex. The distribution of ornament is not uniform : it tends to be more concentrated near the distal polar region where it is also comparatively stouter (fig. 57).

COMPARISON : The new form differs from all known species by its much smaller size, its verry narrow and ill-separated perispore and the variability in the nature and distribution of the ornamentation. The separation of the perispore in this species seems to be a prevailing feature which enables its assignment to *Perotrilites* rather than to *Apiculiretusispora* (see Streel, 1967, p. 33).

Subturma : *Zonotriletes* Waltz, 1935

Infraturma : *Zonati* Pot. & Kr., 1954

Genus : *Samarisporites* Richardson, 1965

Type species : *S. orcadensis* Richardson, 1965.

Samarisporites Leclercqi sp. nov.

(pl. 3 ; figs. 58-60)

HOLOTYPE : pl. 3 ; fig. 58, 51 μ, zona ± 2 μ, C. area 46 μ.

PARATYPE : pl. 3 ; fig. 59.

DIAGNOSIS : Size range 38-72 μ ; roundly triangular to subcircular ; central body of ± conformable shape, 28-60 μ ; relatively darker than zona ; zona 2-10 μ wide (1/5-1/6 of body radius), occasionally a little wider at the three corners ; trilete simple, rays occasionally thick (up to 2 μ), reaching equator of body and may be prolonged as folds into zona ; proximal surface smooth, distal side irregularly microverrucate to granulate, occasionally small ridges of folds may be additionally present.

COMPARISON : The species of *Samarisporites* described by Richardson (1965) differ widely in respect of the body/zona proportion as well as in the size and nature of ornamentation.

Samarisporites sp.

(pl. 3 ; fig. 61)

Roundly triangular, 66 μ, central body 56 μ, body periphery relatively darker (? as a band), trilete rays seen up to the dark zone ; distal side with scattered larger coni (2-3 μ high) sometimes coalescing at base ; a few also seen on the zona.

REMARKS : Specimens are not sufficient to decide whether the peripheral dark zone of the body is a structural feature like a crassitude associated with cingulum or is due to preservation. In *Samarisporites Leclercqi* also a similar but less distinct peripheral darkness is occasionally noticed (fig. 59) but in clear specimens it is not present. If the darkness is due to preservation and maceration factors, the equatorial structure is more likely to be a zona.

Anteturma : *Pollenites R.* Pot., 1931
Turma : *Saccites* Erdtman, 1947
Subturma : *Monosaccites* (Chitaley) Pot. & Kr., 1954
Infraturma : *Extornati* Butt. & Will., 1958

Genus : *Calyptosporites* Richardson, 1962
Type species : *C. velatus* (Eisen.) Richardson, 1960

Calyptosporites sp. cf. *C. velatus* (Eisen.) Richard.

(pl. 3 ; figs. 62-63)

Specimens rare ; saccus generally eroded and broken. Size about 108 μ, subtriangular saccus up to ± 22 μ wide, distal side with minute, sparse coni (less than 1 μ high) ; body darker than saccus, subtriangular, 60-66 μ ; trilete mark clear, extending into the saccus as folds ; secondary folds on body present.

The size range of *C. velatus* accomodates the present specimens, but the former has comparatively larger ornament and shorter mark.

Calyptosporites sp.

(pl. 3 ; fig. 64)

One specimen, size 120 μ, body dark, subtriangular, 68 μ ; saccus about 26 μ wide, trilete not clear, scattered ornament of rod-like elements (up to 2,5 μ high) some with conate tips. Despite the rather eroded nature of the specimen, its ornament is not comparable with that of the known species of *Calyptosporites*.

Genus : *Rhabdosporites* Richardson, 1960
Type species : *R. Langi* (Eisen.) Richardson, 1960

The genus is stated to have a bladder characterized by parallel-sided, closely packed and evenly distributed rods with truncated tips. Observation of some well-preserved specimens of *R. Langi* from the Cromarty region however reveal that there may be conical elements among the bacula. In the present material also the specimens, otherwise similar to *Rhabdosporites*, show mostly cones and seldom bacula, so that the forms derive an appearance of *Geminospora*.

It is not certain whether the ornament of coni is a primary feature or a result of erosion. In view of this we prefer to assign the specimens doubtfully to *Rhabdosporites*.

? *Rhabdosporites Langi* (Eisen.) Richardson, 1960

(pl. 3 ; fig. 65)

Examples rare, figured specimen 104 μ, subcircular, saccus moderately thick, about 12-20 μ wide, prominent saccus-folds extending beyond body limits ; body 77 μ, subcircular, trilete mark obscured, bladder ornament consisting mostly of densely packed minute coni and some rod-like elements.

The specimen bears evidence for a three-layered exine. The middle layer is thin and seen at some places (indicated by arrow). Richardson (1965, p. 589 ; pl. 93, fig. 7) described *Rhabdosporites* sp. with three layers ; the spore is otherwise similar to *R. Langi*.

Spores similar to *Rhabdosporites Langi* have recently been discovered in the sporangia of *Tetraxylopteris*, Bonamo & Banks, 1967.

? *Rhabdosporites parvulus* Richardson, 1965

(pl. 3 ; figs. 66-68)

Size range 42-75 μ, subtriangular to subcircular, central body 39-45 μ conformable with overall outline, smooth, distinct, occasionally darker ; saccus width 2-8 μ, variable in same specimen ; secondary folds seen in the body region but rarely beyond its limits ; trilete mark distinct, occasionally thick and with lips (fig. 67) ; bladder ornament of minute, densely packed coni, microverrucae and occasionally bacula.

The present spores differ from *R. parvulus* in having a smaller body and overall size-range and in the preponderance of coni over bacula in the bladder ornament. To a certain extent, the specimens would also recall *Geminospora*, where the mesosporoid has well separated.

Sporae Incertae Sedis

Genus : *Ancyrospora* Richardson, 1960.

Type species : *A. ancyrea* Richardson, 1960

Ancyrospora sp. cf. *A. ancyrea* var. *brevispinosa* Rich. 1962

(pl. 4 ; figs. 69-71)

Size range 58-66 μ (excluding spines) subcircular to roundly triangular, central body usually darker, 50-59 μ, zona up to 6 μ wide, narrower in relation to body (± 1/4 of body radius) ; trilete mark not visible ; spines broad-based, up to 12 μ wide and 8 μ high, tips presumably not preserved, about 15 spines along equator.

The specimen are smaller than those of *A. ancyrea* var. *brevispinosa* (75-106 μ) and are not sufficiently well-preserved to show undoubted bifurcate appendages.

It is, however, interesting to note that some fragments showing long bifurcate appendages have been encountered in the material (fig. 72) which may indirectly support the presence of *Ancyrospora* or *Hystricosporites*. Besides, there is another incomplete specimen with broken long appendages (fig. 73) which shows the peculiar radiating bands on the body strongly recalling *Ancyrospora trocha* (Allen, 1965, pl. 107, fig. 1) or *Hystricosporites* (McGregor and Owens, 1966, pl. IX, fig. 7).

Other Plant Microfossils

FILAMENTS (pl. 4 ; figs. 74-77).

Fragments of tubular filaments have been commonly encountered in all the samples. They are particularly more abundant in sample 178/V (bed IV) where, incidently, the spore population is scarce and the occurrence of fine organic débris is striking.

Two distinct types of filaments are recognisable : one with smooth external wall (fig. 74) and the other with a dense ornament of minute grana, bacula or microverrucae (figs. 75, 76). More commonly the filaments are 5 μ - 10 μ wide, but narrower or wider ones also occur. They have a brown colour. Some of them show clear evidence of branching (fig. 74) and possess transverse partitions recalling septa (figs. 74, 76). Several examples apparently representing terminal parts of these filaments are also found. Figure 77 shows a smooth walled specimen with a slightly swollen termination. That these filaments are related to some Algae or fungi seems likely.

STOMA (pl. 4 ; fig. 78).

Cuticles are generally absent. However, an exceptionally well-preserved stoma (fig. 78) was found in the sample 177 (bed VI). The apparatus shows two large, kidney-shaped guard cells, enclosing a wide elliptical pore. The guard cells are more cutinized than the surrounding cells. The latter do not reveal their outlines due to ill-preservation and their number cannot be ascertained.

TRACHEIDS (pl. 4 ; figs. 79-81).

A variety of tracheids is present. Some show pits in single or several rows (figs. 80, 81). A thin border may appear to surround the pits in the specimen in fig. 80. In other examples the pits may apparently grade into scalariform or reticulate elements (fig. 79).

Incertae Sedis

(pl. 4 ; figs. 82, 83)

A few very small, smooth-walled and rather thin, circular bodies have been found in samples 178/V (bed IV) and 269/III (bed IV). They occur singly or in groups (figs. 82, 83). No tetrad mark is noticeable. Some of the bodies occurring in group (fig. 82) show a slightly peripheral zone. A similar, but more conspicuous darker peripheral dark zone is seen in the other specimen (fig. 83) and in addition, there is also a small circular thickening near the centre. The affinities of these objects are uncertain. However, the bodies in groups (fig. 82) recall some of the leiospheroids figured by Combaz (1967, pl. 2 ; fig. G).

SPECIALIZATION TRENDS IN RETUSOTRILETES

Retusotriletes is an important constituant of the Devonian spore assemblages. In the Goé material, there are five recognizable species which show significant distribution. While assessing the morphological peculiarities of the species in relation to each other, it became evident that the genus reflected certain interesting trends in its organizational specialization. A close scrutiny of all the relevent material described under *Retusotriletes* or allied genera was hence followed which indicated considerable diversity in the specialization trends in the retusoid spore complex as a whole. It is therefore, considered important to evaluate all the significant facts bearing on this subject in order to resolve the limits of the genus *Retusotriletes*. The ideas expressed below, were also presented by one of us at the C.I.M.P. meeting (Sheffield, 1967) to serve as a contribution to the seminar in the Working Group on « Devonian Laevigate Genera ».

Species referred to *Retusotriletes* possess the following important characters which warrant consideration for the interpretation of organizational specialization in the retusoid complex.

I. TRILETE MARK

A. Perfect rays : when they are uniformely defined up to their junction with the curvaturae. The entire tetrad mark may have been functional.
e. g. : *R. simplex, R. semizonalis, R. goensis* sp. nov.

B. Imperfect rays : when they are not uniformely defined up to their junction with the curvaturae. Normally part of rays in the vicinity of the pole is clear (laesurae), while the remaining part is reduced to bare traces up to the junction with the curvaturae. An apical area, when present, is coextensive with the well-defined ray portions. It is probable that the entire tetrad mark may not have been functional.
e. g. : *R. triangulatus, R. microgranulatus, R. confossus.*

II. CURVATURAE

A. Simple curvaturae : when perfectly developed (Curvaturae perfectae) they are normally noticeable as continuous lines or slightly elevated ridges connecting the extremities of the rays.
e. g. : *R. simplex, R. biarealis, R. goensis* sp. nov. etc.
When imperfectly developed (Curvaturae imperfectae) they are barely traceable as interrupted lines.
e. g. : *R. microgranulatus, R. triangulatus, R. confossus.*

B. Banded curvaturae : The term is used to designate a type where a part of the proximal exine near the equator is noticeably darker, rigid and probably thickened so as to appear like a ± wide band. This structure may replace the simple curvaturae or may be associated with them.
e. g. : *R. semizonalis, R. pichovii* (particularly Pl. 18, fig. 19 of Naumova, 1953).
It is suspected that ? *Punctatisporites dilutus* Hoffmeister (1959) which may be a variant of *Ambitisporites,* shows what appears likes banded curvaturae. *R. incohatus* Sullivan (1964) may also possess similar features. *R. avonensis* Playford (1962, p. 9) may have banded curvaturae but the occurrence of a mesosporoid and thick exine seems to render it somewhat exclusive.

C. Winged (or flanged) curvaturae : Represented by a conspicuous, wedge-shaped thickness of the exine appearing like a wing or flange dipping below the spore outline in lateral compression.
e. g. : *R. distinctus* Richardson (1965 ; p. 565) and *R. dubius,* Richardson (1965).

III. APICAL AREA

It is represented by a special differentiation of the exine at the proximal polar region. It may have been only part of the contact area.

A. Specialized apical area may be absent in some species which have, otherwise, ± well-defined curvaturae : e. g. : *R. simplex, R. semizonalis.*

B. Where present, it may show diverse patterns. Three such patterns are so far noticeable :

1. A single dark, thickened area completely covering the proximal polar region. e. g. : *R. goensis* sp. nov., *R. microgranulatus, R. confossus, R. biarealis.*

In *R. goensis* sp. nov. it has been observed that the apical area may be sharply delimited or diffused and may also show a tendency to reduce in size and prominance.

Evidently, the extreme forms, with very inconspicuous apical dark area (see figs. 14 et 15) tend to approach a *R. simplex* type of construction which is characterized by the absence of a dark apical area (Text — fig. 1).

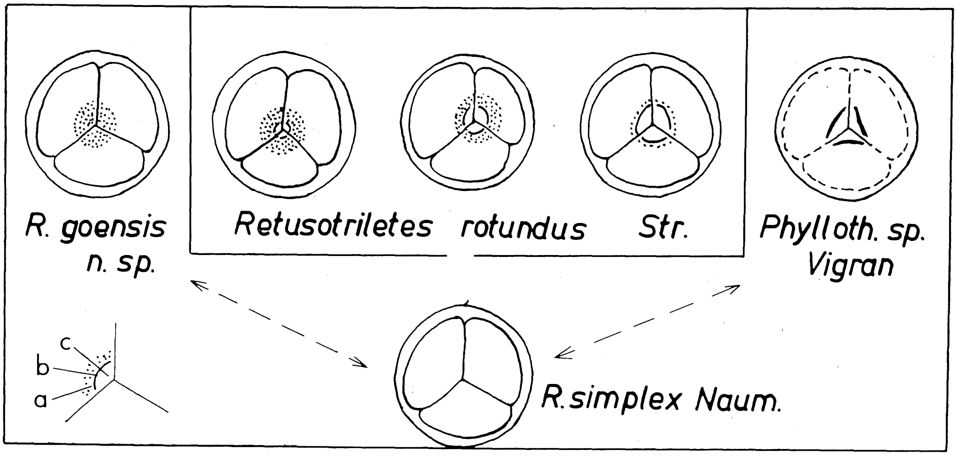


Fig. 1

Organisation trends in R. rotundus and associated species.

a. darker area.
b. margin of inner lighter area.
c. inner lighter area, thinner than rest of spore exine (*Phylloth.* sp. Vigran — Voir Vigran 1964, Pl. 1, Fig. 13).

2. Two concentric areas : inner is lighter and thinner than rest of spore exine, outer is darker and thicker. e. g. : *R. rotundus*.

Critical observation of *R. rotundus* in the present material has shown that the relative proportion between the two areas is variable and seems to have a reversible relationship. Thus, extreme forms, with a very minute lighter area surrounded by a wider dark, thicknened area tend to approach a *R. goensis* type of construction (Text — fig. 1).

3. A single annular ± triangular, dark, thickened area surrounding the pole. Exine at the pole is unspecialized and similar to the rest of the spore. e. g. : *R. triangulatus*.

We assume here that the darkness of the exine at the proximal pole is a structural and sufficiently constant feature of the whole population of the species.

IV. EXINE

Majority of species (including those of Goé) have a moderately thick exine (1-2 μ), but thick forms are also known e. g. *R. distinctus* Richardson (1965, p. 565).

The exine is generally smooth or infrastructured or may also have fine ornamentation. Local deposition of irregular granules is also frequently noticeable. It must be pointed out that *R. semizonalis* McGregor (1964, p. 8) is here excluded from *Retusotriletes* and transfered under *Aneurospora* Streel (see p. 86).

Folds are rare or absent ; where present, located near the equator and aften arcuate. The rigidity of the equatorial or/and proximal surface of the exine seems to be a common feature of the retusoid group of spores (here, *Aneurospora* and *Retusotriletes*) which are typically anisopolar and are, for that reason, generally flattened within the sediment in perfect proximodistal compressions.

This important characteristic separates these genera from *Calamospora*, *Punctatisporites* and *Leiotriletes* which can be irregularly folded (especially in *Calamospora* which has a thin exine), are more or less isopolar and thus lack preferential orientation in flattening within the sediment.

In summary it may be expressed that :

1. The more significant trends are noticeable in the specialization of the exine near the proximal pole on the one hand and near the equator on the other. The former relates to the development of an apical area while the latter to the banded and winged (or flanged) curvaturae.

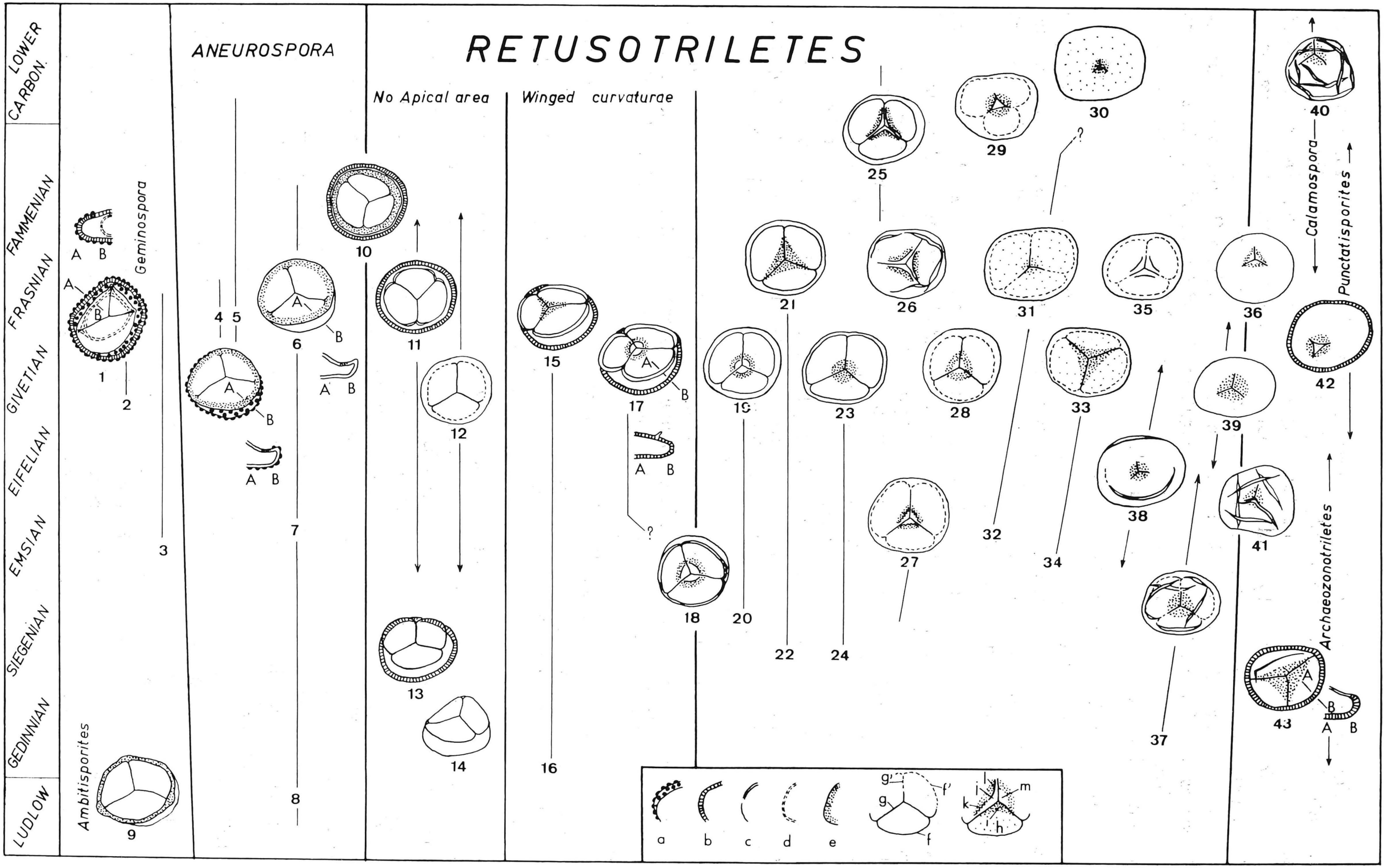
2. It is significant to observe that as far as our present knowledge goes species with an apical area appear to be devoid of banded curvaturae. Stratigraphical records also indicate that in the retusoid spore complex the apical area appeared later as compared to the banded curvaturae (Text-fig. 2). We have, therefore, the impression that the two features may be mutually exclusive and of taxonomic value. If this interpretation was correct, then moderately thick-walled species sharing simple curvaturae (imperfectae or perfectae) but with or without apical area would constitute what is here conceived as *Retusotriletes*. Within this set, the development of an apical area may appear to have originated from simpler types like *Retusotriletes simplex* through specialization (Text-fig. 1).

3. On the other hand, forms with apparently banded curvaturae are traceable as early as the Silurian (e. g. ?*Punctatisporites dilutus* Hoffmeister, 1959). They seem to have followed an independent trend which might have radiated in diverse direction with the passage of time.

For example, one such direction is apparently reflected in the acquisition of mostly distal ornament as in *Aneurospora* which may include both ornamented and laevigate forms. We, therefore, believe that forms with banded curvaturae could be excluded from *Retusotriletes* as here interpreted.

4. Another point of interest is that *Retusotriletes* species possessing an apical area could be arranged in two groups : one associated with perfect rays and curvaturae perfectae while the other associated with imperfect rays and curvaturae imperfectae. Although enough is not yet known ; the majority of species belonging to the second group seem to be stratigraphically younger than those of the first group (Table 2). This might convey the impression as if there was a probable reduction in the trilete mark and the curvaturae during passage of time.

The conceivable end product of such a trend, would be a rather distinct-looking spore-type which has lost its curvaturae and where the mark is reduced to short lasurae confined within the apical area. Indeed, *Phyllothecotriletes rigidus* Playford (1963) from Tournaisian and *Phyllothecotriletes golatensis* Staplin (1960) from Visean which are stratigraphically much younger than the bulk of *Retusotriletes* species, seems to match such a type. Keeping the above idea in mind as well as the fact that truely non-retusoid forms could also develop an apical area independently (see text-fig. 2), it seems safe to contend that all such taxa which are devoid of curvaturae connecting the ray-extremities and lack rigidity of proximal exine (i. e. non-retusoid) would fall beyond the scope of *Retusotriletes* as understood here.


LOWER CARBON.
FAMMENIAN
FRASNIAN
GIVETIAN
EIFELIAN
EMSIAN
SIEGENIAN
GEDINNIAN
LUDLOW
Geminospora
Ambitisporites
ANEUROSPORA
RETUSOTRILETES
No Apical area
Winged curvaturae
Calamospora
Punctatisporites
Archaeozonotriletes
A
B
?
1
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3
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Fig. 2

Organisation trends in Retusotriletes
and associated genera during Devonian times.

1. *Geminospora lemurata* Balme 1962.
2. *Geminospora tuberculata* (Kedo) Allen 1965.
3. *Geminospora svalbardia* (Vigran) Allen 1965.
4. *Aneurospora goensis* Streel 1964.
5. *Retusotriletes greggsii* Mc Gregor 1964.
6. *Aneurospora* (al. *Retusotriletes*) *semizonalis* (Mc Gregor) comb. nov., from Mc Gregor 1964.
7. Idem, in Streel 1967.
8. ? *Punctatisporites dilutus* Hoffmeister 1959.
9. *Ambitisporites avitus* Hoffmeister 1959.

10, 11, 12 : No attempt of stratigraphic range.

10. *Retusotriletes pychovii* Naum. var. *major* in Naumova 1953, XVIII, 19.
11. *Retusotriletes pychovii* Naum. in Naumova, 1953, Pl. XIV, fig. 5.
12. *Retusotriletes simplex* Naum. in Naum. 1953, Pl. II, fig. 9.
13. *Retusotriletes* (Naumova) in Richardson 1967, Pl. III, fig. B.
14. *Retusotriletes* cf. *simplex* Naum. in Chaloner et Streel 1968, Pl. II, fig. 4.
15. *Retusotriletes dubius* (Eisenack) Richardson 1965.
16. *Retusotriletes* cf. *dubius* Rich. in Richardson 1967, Pl. I, fig. A.
17. *Retusotriletes distinctus* Richardson 1965.
18. *Phyllothecotriletes distinctus* (Rich.) Mortimer 1967, Pl. I, fig. H.
19. *Retusotriletes rotundus* (Streel) emend.
20. *Retusotriletes* (Naumova) in Richardson 1967, Pl. II, fig. A.
21. *Retusotriletes biarealis* Mc Gregor 1964.
22. *Retusotriletes triangulatus* (Streel) Streel 1967 in Richardson 1967, Pl. III. fig. A.
23. *Retusotriletes goensis* sp. nov.
24. *Phyllothecotriletes rotundus* Streel in Mortimer 1967, Pl. I, fig. G.
25. cf. *Punctatisporites irrasus* Hacquebard 1957 in Streel 1966, Pl. II, fig. 26.
26. *Calamospora atava* (Naumova) Mc Gregor 1964.
27. *Retusotriletes witneyana* (Chaloner) Streel 1967.
28. *Retusotriletes triangulatus* (Streel) Streel 1967.
29. *Phyllothecotriletes nigritellus* Luber 1955.
30. *Phyllothecotriletes golatensis* Staplin 1960.
31. *Retusotriletes microgranulatus* (Vigran) Streel 1967.
32. Idem in Streel 1967, Pl. I, fig. 14.
33. *Retusotriletes confossus* (Rich.) Streel 1967.
34. *Retusotriletes* cf. *confossus* (Rich.) Streel in Streel 1967, Pl. I, fig. 10.
35. *Phyllothecotriletes* sp. in Vigran 1964.
36. *Leiotriletes microdeltoidus* Mc Gregor 1960.
37. *Phyllothecotriletes* cf. *golatensis* Staplin in Mortimer 1967, Pl. I, fig. F.

38 à 43 : No attempt of stratigraphic range.

38. *Leiotriletes nigratus* Naum. in Naumova 1953, Pl. I, fig. 9.
39. *Leiotriletes atavus* Naum. in Naumova 1953, Pl. I, fig. 8.
40. *Calamospora exigua* Staplin 1960.
41. Idem in Mortimer 1967, Pl. I, fig. E.
42. *Stenozonotriletes recognitus* Naum. in Naumova 1953, Pl. X, fig. 8.
43. *Archaeozonotriletes* (Naum.) Allen 1965 in Richardson 1967, Pl. II, fig. B.
44. a. Ornamented exine ; b. thick exine ; c. thin exine ; d. intexine ; e. banded curvaturae ; f. curvaturae perfectae ; f′. curvaturae imperfectae ; g. perfect ray ; g′. imperfect ray ; h. infrapunctate exine ; i. single dark, thickened apical area ; j. inner lighter area, thinner than rest of spore exine ; k. scalloped margin of inner lighter area ; l. straight margin of inner lighter area ; m. inner area, similar to the rest of spore exine.

5. Very little is yet known about forms which are rather peculiar in possessing winged (or flanged) curvaturae e. g. *R. distinctus*. The presence of an apical area in them only strengthens the probability that apical specialization could have been shared by several otherwise distinct trend-lines at the same or different times in the stratigraphical record (see Text-fig. 2).

DISCUSSION

The spore assemblages recovered from the Goé samples contain a total of 16 genera distributed in 30 taxa. All the genera (except *Endosporites*) and the majority of species earlier recorded by Streel (1964) have been found.

In addition, the presence of *Pilasporites*, *Leiotriletes*, *Punctatisporites*, *Granulatisporites*, *Verrucosisporites*, *Samarisporites* and *Calyptosporites* is newly reported. Of these new elements, *Samarisporites* is also found in the sample 173 (Streel, 1964) and, therefore, included here in the frequency chart (Table 2).

Retusotriletes, *Aneurospora* and *Biornatispora* gen. nov. are by far the most important constituents of the various samples.

In view of the abundant material available for study, it was possible to go into the details of certain taxa from the morphological viewpoint. Of special interest is the retusoid spore complex which is well represented in the material particularly by *Retusotriletes* (5 species) and *Aneurospora* (2 species).

A close observation of the diversity in the morphological pattern of the present species as well as those described elsewhere led to the evaluation of the more precise limits of *Retusotriletes* and *Aneurospora* and to the interpretation of the probable trends of specialization arising in the retusoid spore complex as a whole. We are of the opinion that *Retusotriletes* should be enlarged to contain such spores which have a smooth exine and essentially simple curvaturae connecting the ray extremities and an equatorial or/and proximal rigid exine. The development of an apical area in some species is conceived as a specialization trend within the genus and it seems probable that similar specialization appeared in other taxa at the same or different times.

Another significant result emerged out of the study of the specimens previously assigned to *Verrucosisporites* and later to *Acinosporites* (Streel, 1964, 1967).

Our investigations reveal that these spores possess a two-fold sculptural pattern of the exine, viz. an apiculate ornamentation superimposed over or intermixed with a reticuloid pattern of muri. As such the spores are distinct from both *Verrucosisporites* and *Acinosporites sensu stricto* and a new genus *Biornatispora* is erected to accomodate them.

The important megafossil contents of the various beds are given in Table 1. When these are compared with the corresponding microfossil associations, it is striking to notice that the spore population is rather scarce and not so well-preserved in those beds (e. g. 178 bed IV, sample) where large plant fossils are found in abundance often showing fertile and sterile portions in connection.

Sample 583 (bed III), is particularly interesting as it contains an abundance of fertile plant remains but no spores. On the contrary, rich and well-preserved spore associations are present in beds where the megafossil material is very fragmentary (e. g. Bed VI, sample 177).

This rather inverse relationship may probably suggest a kind of sorting of organic debris during course of sedimentation.

Table 2 shows the quantitative destribution of the genera in the samples where

TABLE 2

Proportion of genera in each sample

IV (Base)				V	VI (Top)		Bed
178/I	178/III	178/V	269/III	27/III	177	173	Sample (173 = Streel, 1964)
7	2	3	2		3		Pilasporites
1	2	2	2	2	4		Leiotriletes
2		+	4	7	3		Punctatisporites
24	28	20	11	14	10	9	Retusotriletes
25	38	32	53	38	11	15	Aneurospora
8	3	2	3	4	+	5	Apiculiretusispora
5	3	1	3	?+	4	1	Dibolisporites
			2				Granulatisporites
					+		Verrucosisporites
					+		Convolutispora
12	14	29	15	30	62	65	Biornatispora
		1	1	+	+	1	Perotrilites
		+	2	2	2	+	Samarisporites
+	1	2			+		Calyptosporites
1	1	1	+	+	+	+	? Rhabdosporites
1	+			1	+	1	Ancyrospora
13	6	7	2	2		3	Indeterminable
100	100	100	100	100	100	100	Total

+ indicates presence of the genus in a Sample, although it does not appear in the count.

the spore population is « rich » to « moderate ». The count is based on hundred specimens for each sample. The results of the quantitative study of the sample 173 (Streel, 1964) are included in the table for comparison.

In the table, two assemblages, very similar in composition but different in quantitative respects, may be distinguished. The first, confined to bed VI, is dominated by *Biornatispora* ; the second, found in beds IV and V is dominated by *Aneurospora*. Both assemblages are poor in zonate forms (about 1 %), which in other regions characterize the Givetian spore floras. It is also noticeable that these zonate elements seem to be a little more diversified in the *Aneurospora*-assemblage than in the *Biornatispora*-assemblage.

The quantitative study of each fine layer of sample 178 (layers 178/I, 178/III and 178/V) shows relatively minor variations within the *Aneurospora*-assemblage.

However, another sample (269/III) which represents the same bed as sample 178 (Bed IV) indicates a relatively higher count for *Aneurospora* and a rather lower count for *Biornatispora*. Such variations may be local, probably occurring along the lateral or vertical extent of the bed. Similar variations have been observed in the *Biornatispora*-assemblage described by Streel (1964) in the two very close layers of the sample 173.

Despite the fact that the material studied in this paper (which has a taxonomic purpose) is still insufficient for stratigraphical conclusions, some points seem to emerge. Keeping in view the rather homogeneous distribution of the assemblages in the beds as well as in the fine layers in general, it is striking to note that the assemblages dominated by *Aneurospora* in the lower part are replaced towards the top of the sequence by the assemblages dominated by *Biornatispora*. This change may not necessarily correspond with changes in local environnement but may as well have a regional stratigraphical value. The present results therefore encourage the study of this problem with more detailed and complete sampling.

Givetian spore assemblages are known from various parts of the world (Streel, 1967, Table 5). To this knowledge, we can add the information provided by the Givetian assemblage from Goé which is characterized by *Aneurospora*, *Biornatispora*, and *Retusotriletes*. Our study which does not prove any assemblage rich in zonate forms, confirms the opinion expressed previously (Streel, 1964) that the zonate assemblages correspond in all probability to different ecological conditions. It may, indeed, seem that the zonate spore assemblages and those dominated by spores with simple structural features as *Aneurospora*, *Retusotriletes* and *Biornatispora* are mutually exclusive.

As proposed earlier, the assemblages of spores with simple structure could correspond to the plant communities represented by the many fossil-remains discovered in the littoral marine sediments like those of Goé by Prof. Leclercq (1940).

More recent investigations on *Sporae in situ* seem to stenghthen this suggestion. For example, *Aneurospora goensis* is a spore of *Aneurophyton germanicum* Kr. & Weyland (see Streel, 1964) ; *Dibolisporites* cf. *gibberosus* is very similar to the spores of *Calamophyton bicephalum* (see Bonamo & Banks, 1966) ; *Retusotriletes greggsii* ; *Geminospora* (al. *Lycospora*) *svalbardiae* and *Aneurospora* sp. (Streel, 1965) — these three forms belonging to the complex of the genera *Aneurospora* and *Geminospora* may have been produced by *Svalbardia polymorpha* (see Greggs, McGregor & Rouse, 1962 ; McGregor, 1964 ; Vigran, 1964 ; Streel, 1965*b*).

By contrast, the assemblages dominated by zonate forms, especially those of Scotland (Richardson, 1960, 1962, 1965) seem to have very poor relation with the megaflora. This indicates a more continental position of the source area. The distinction between upland assemblages and « littoral assemblages » (Streel, 1964) or better « marginal assemblages » (Streel, 1967) is also suggested by Richardson (1965, 1967).

The best characteristic species of both upland and marginal assemblages of Middle Devonian and partly Frasnian age seems to be *Rhabdosporites Langi*. These spores have now been found in *Tetraxylopteris* (*T. Schmidti*) by Bonamo & Banks (1967) a genus close to *Protopteridium*. The spores of *Protopteridium* (Obrhel, 1961) are also strikingly comparable with *Rhabdosporites Langi*. It is significant in this connection to observe that Leclercq (1940) proposed to designate the Middle Devonian vegetation as the « Protopteridium flora » in view of the wide geographical distribution of the genus. This proposal appears to find support from the palynological evidence.

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EXPLANATION OF PLATE 1

(All photomicrographs are from unretouched negatives. The magnification is × 500.)

1 : *Pilasporites cf. plurigenus* Balme et Henn., slide 3105/245.

2, 3 : *Leiotriletes* cf. *simplex* Naumova. 2 : slide 3110/338 ;
3 : slide 3110/513.

4, 5 : *Leiotriletes* cf. *laevis* Naumova. 4 : slide 3107/495 ;
5 : slide 3103/434.

6, 7, 8 : *Punctatisporites* spp. 6 : Form A, 3107/595 ; Form B : 7 and 8 ; 7 : slide 3106/718 ; 8 : slide 3107/575.

9, 10, 11 : *Retusotriletes simplex* Naumova. 9 : slide 3106/304 ; 10 : slide 3103/80 ; 11 : slide 3106/99.

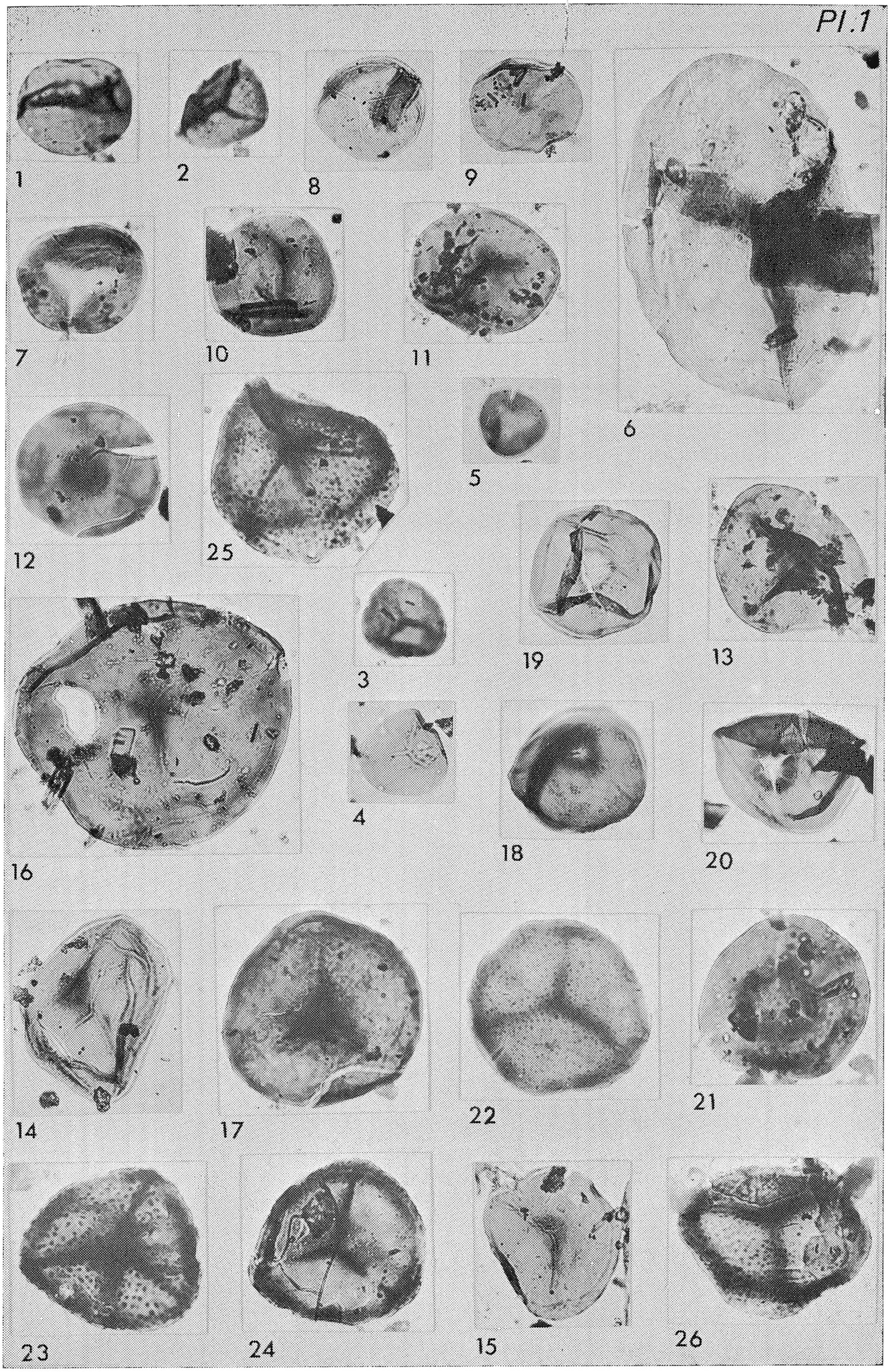
12 to 16 : *Retusotriletes goensis* sp. nov. 12 : holotype : slide 3114/155 ; 13 : paratype : slide 3106/342 — 14, 15, 16 : Variations in extent and degree of prominence of the apical area : 14 : slide 3107/503 ; 15 : slide 3107/394 ; 16 : 3103/349.

17 : *Retusotriletes confossus* (Richardson) Streel. slide 3107/606.

18, 19, 20 : *Retusotriletes rotundus* (Streel) emend. 18, slide 3116/264 ; 19, slide 3114/408 ; 20, slide 3115/524.

21 : *Retusotriletes triangulatus* Streel. slide 3107/496.

22 to 26 : *Aneurospora goensis* Streel. 22 : slide 3115/171 ; 23 : slide 3112/599 ; 24 : slide 3112/704 ; 25 : slide 3107/722 ; 26 : slide 3107/418.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EXPLANATION OF PLATE 2

(All photomicrographs are from unretouched negatives. The magnification is × 500).

27, 28 : *Aneurospora goensis* Streel. 27 : slide 3118/365 ; 28 : slide 3115/235.

29 : *Aneurospora* (*Retusotriletes*) *semizonalis* (Mc Gregor) emend. slide 3103/598.

30, 31 : *Apiculiretusispora brandtii* Streel. 30 : slide 3116/116 ; 31 : slide 3107/236.

32 : *Granulatisporites Stockmansi* Streel. slide 3112/529.

33 : *Dibolisporites* cf. *gibberosus* (Naum.) var. *major* (Kedo) Richardson. slide 3109/706.

34 : *Dibolisporites* sp. A. slide 3101/625.

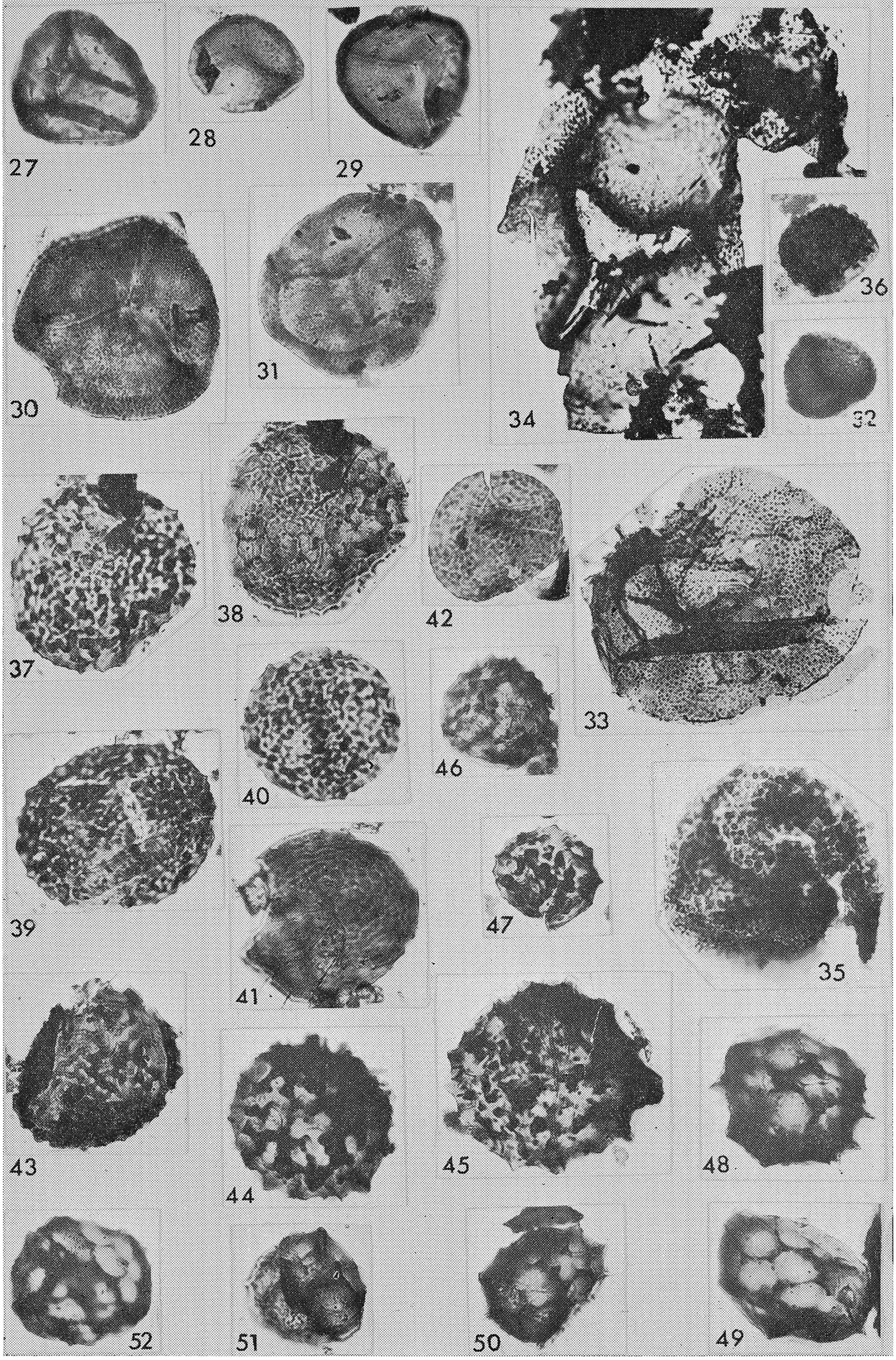
35, 36 : *Verrucosisporites* spp. 35 : form A : slide 3104/415 ; 36 : form B : slide 3103/187.

37 to 43 : *Biornatispora* (*Verrucosisporites*) *dentata* (Streel) n. comb. 37, 38 : cotype : two different foci : slide 3107/284 ; 39 : slide 3107/424 ; 40 : slide 3107/639 ; 41 : slide 3107/248 ; 42 : slide 3104/264 ; 43 : slide 3105/347.

44 to 47 : *Biornatispora* (*Verrucosisporites*) *pseudospinosa* (Streel) n. comn. 44 : slide 3105/708 ; 45 : slide 3107/487 ; 46 : slide 3115/565 ; 47 : slide 3107/318.

48 to 52 : *Biornatispora reticulata* sp. no. — 48 : holotype ; slide 3114/440 ; 49, 50 : paratypes : 49 : slide 3116/199 ; 50 : slide 3114/484 ; 51, 52 : other specimens : 51 : slide 3117/713 ; 52 : slide 3108/378.

Pl. 2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EXPLANATION OF PLATE 3

(All photomicrographs are from unretouched negatives. The magnification is × 500.)

53 : *Convolutispora* sp. slide 3105/557.

54 to 57 : *Perotrilites mutabilis* sp. nov. — 54 : holotype : slide 3116/459 ; 55 to 57 : other specimens : 55 slide 3110/602 ; 56 : slide 3103/223 ; 57 : slide 3107/168.

58, 59, 60 : *Samarisporites Leclercqi* sp. nov. — 58 : holotype : slide 3110/304 ; 59 : paratype : slide 3106/131 ; 60 : other specimens : slide 3103/701.

61 : *Samarisporites* sp. — slide 3106/428.

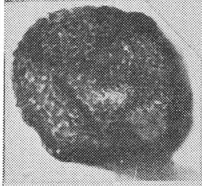
62, 63 : *Calyptosporites* sp. cf. *C. velatus* (Eisen.) Richardson. 62, slide 3109/407 ; 63 : slide 3107/638.

64 : *Calyptosporites* sp. slide 3101/591.

65 : ? *Rhabdosporites Langi* (Eisen.) Richardson. slide 3103/204.

66, 67, 68 : ? *Rhabdosporites parvulus* Richardson. 66 : slide 3106/673 ; 67 : slide 3104/213 ; 68 : slide 3116/459.

Pl. 3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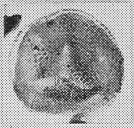
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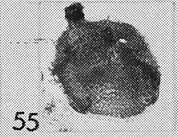
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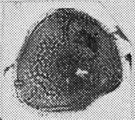
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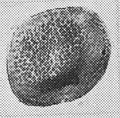
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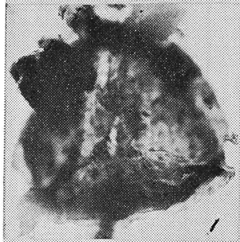
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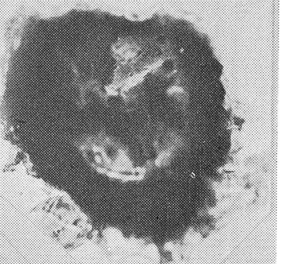
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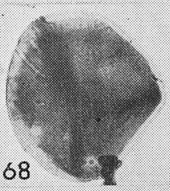
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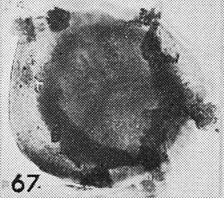
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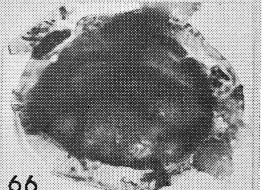
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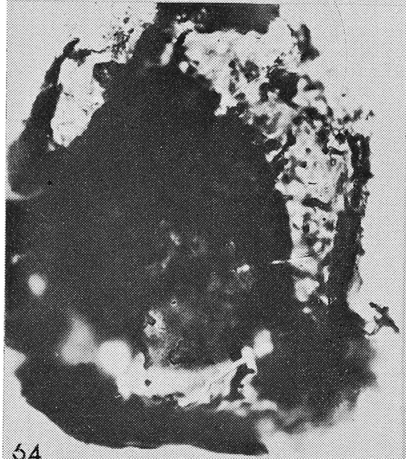
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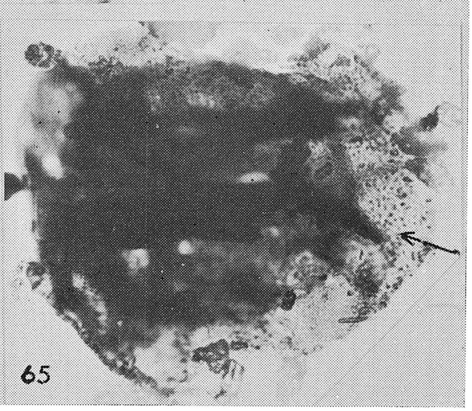
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EXPLANATION OF PLATE 4

(All photomicrographs are from unretouched negatives. The magnification is × 500.)

69, 70, 71 : *Ancyrospora* sp. cf. *A. ancyrea* var. *brevispinosa* Richardson. 69 : slide 3120/314 ; 70 : slide 3106/204 ; 71 : slide 3105/514.

72, 73 : Fragments of presumed spores bearing bifurcate appendages. 72 : slide 3103/92 ; 73 : slide 31.

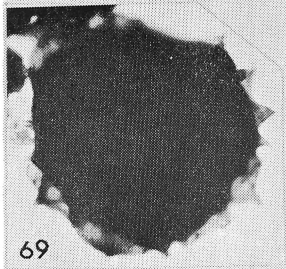
74 to 77 : Filaments — 74 : slide 3109/477 ; 75 : slide 3109/553 ; 76 : slide 3109/452 ; 77 : slide 3110/550.

78 : Stoma — slide 3107/417.

79 to 81 : Tracheids — 79 : slide 3114/560 ; 80 : slide 3117/625 ; 81 : slide 3108/582.

82, 83 : *Incertae sedis* : 82 : slide 3117/378 ; 83 : slide 3110/776.

Pl. 4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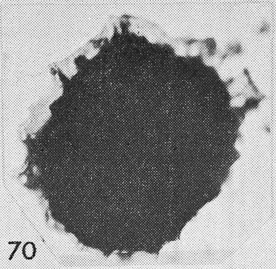
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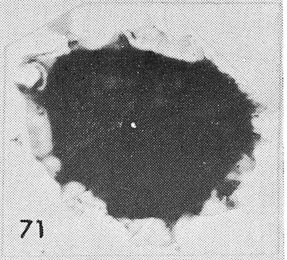
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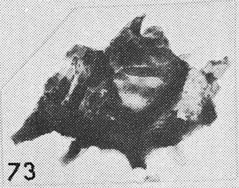
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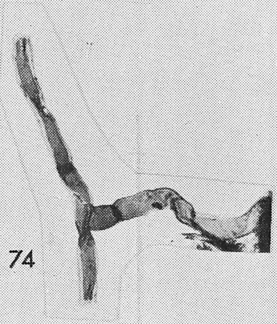
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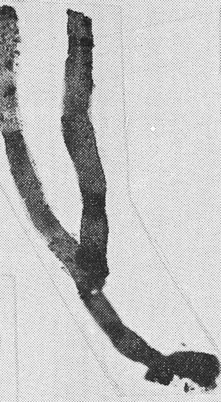
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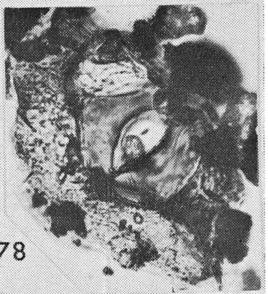
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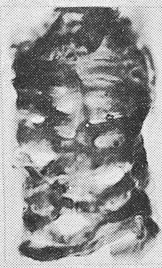
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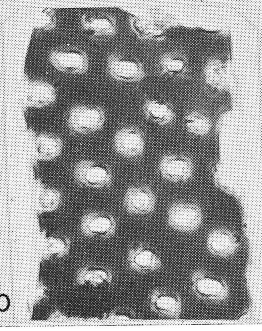
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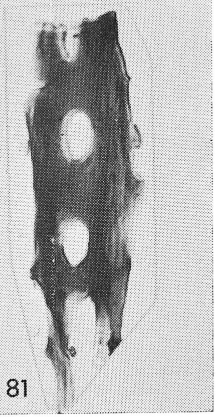
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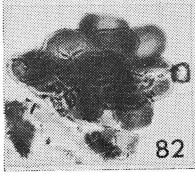
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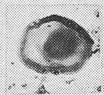
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