Bull. nat. Hist. Mus. Lond. (Geol.) **57**(2): 115–162 XY(34002 9-1) Issued 29 November 2001

Palynological zonation of Mid-Palaeozoic sequences from the Cantabrian Mountains, NW Spain: implications for inter-regional and interfacies correlation of the Ludford/Přídolí and Silurian/Devonian boundaries, and plant dispersal patterns

JOHN B. RICHARDSON
Department of Palaeontology, Natural History Museum, Cromwell Road, London SW7 5BD
ROSA M. RODRIGUEZ
Departamento de Ingeniería Minera, Universidad de León, C/Jesus Rubio 2, 24071 León, Spain
STUART J. E. SUTHERLAND
Department of Geology, University of British Columbia, 6339 Stores Road, Vancouver, British Columbia, V6T 1Z4, Canada

CONTENTS

SYNOPSIS. Mid-Palaeozoic strata from the Cantabrian Mountains (north-west Spain) contain rich assemblages of spores, acritarchs and Chitinozoa. Fossil maturation is variable but generally high. The stratigraphical distribution of miospores and cryptospores from four sections through the San Pedro and lower La Vid Formations is sufficiently consistent for the establishment of a sequence of six biozones (including four new biozones). In ascending order the biozones are: 1, ***Scylaspora vetusta*** – ***S.*** sp. B (V) Spore Biozone; 2, ***Artemopyra brevicosta – Hispanaediscus verrucatus*** (**BV**) Spore Biozone; 3, ***Coronaspora reticulata – Chelinospora sanpetrensis*** (**RS**) Spore Biozone; 4, ***Chelinospora hemiesferica*** (**H**) Spore Biozone; 5, ***Scylaspora elegans – Iberoespora cantabrica*** (**EC**) Spore Biozone; 6, ***Streelispora newportensis – Emphanisporites micrornatus*** (**MN**) Spore Biozone. The ***elegans – cantabrica*** (**EC**) Spore Biozone is divided into two sub-biozones based on the first appearance of the genus *Aneurospora* and the lower part of the MN Biozone is distinguished as a separate subzone, namely the ***Streelispora newportensis – Leonispora argovejae*** (**NA**) Spore Assemblage Sub-Biozone (also present in England). The Ludford/Přídolí boundary is probably within the upper part of the ***reticulata – sanpetrensis*** Spore Biozone, and the ***Aneurospora*** Sub-Biozone and succeeding **MN** Biozone, allow inter-regional correlation with basal and Lower Lochkovian strata. Comparisons between England, Spain, and North Africa, show that regional differences in spore floras are most marked in the Přídolí. In the Lower Devonian the differences are less pronounced, and the appearance of variants of the genus *Aneurospora* marks a significant event in both the Laurussian and Gondwanan regions, reflecting wide dispersal of their parent plants. Chitinozoans occur throughout most of the sequence and several species have potential for inter-regional correlation e.g. *Ramochitina villosa* (**RS** Biozone) upper part of the *urna* (lower **EC** Biozone) and *Eisenackitina bohemica* (lower **MN** Biozone).

INTRODUCTION

Because of their abundance and species diversity land plant spores have a much greater potential for the determination of ancient floral regimes than their parent plants. Further, where their fertile parts are known, all Silurian to Lower Devonian (Lochkovian) plants are homosporous with small spores (often *c.* 20 µm, and below 100 µm). Factors which should ensure that their parent plants are widely dispersed. In fact, mid-Palaeozoic spores and marine palynomorphs are found on each of the major drifting continental blocks studied, namely Laurussia and Gondwana. Comparisons of sequences of spores from the Anglo-Welsh area with those from the Cantabrian Mountains and North Africa should aid in the resolution of the nature of these Palaeozoic floras. However, a prerequisite is the study of spore sequences in the three areas. In this study miospores from Southern Britain and the Cantabrian Mountains are studied in detail along with some preliminary work on the chitinozoans of northern Spain. Work on North Africa has been partially published (Richardson & Ioannides, 1973) and additional North African areas are currently being studied. Seward (1931) stated that it is inconceivable that the climate of the Earth was ever uniform, and influences on vegetation might be expected to be profound where crustal pieces drifted through different latitudinal belts. By providing an accurate biozonal framework this work aims to facilitate more accurate comparisons of spore floras in the three areas. The resultant floral dispersal patterns vary through the time interval studied and further work is needed to answer some of the many questions raised.

One of the important features of this study is the completeness of the Přídolí sections in the Cantabrian Mountains in a marine but continentally influenced succession. This probably represents the most complete miospore zonation through the Přídolí Stage. In the continental sections in England there are some of the longest, well-preserved, miospore successions, with a sequence of miospore assemblages from Upper Aeronian to Lower Přídolí and uppermost Přídolí to Lower Lochkovian (Silurian to Lower Devonian). However, there is a gap, equivalent to the upper Lower Přídolí, Middle Přídolí, and lower Upper Přídolí, where no miospore assemblages are known. Between these productive beds of the Lower Devonian (**Aneurospora Subzone** and **MN Zone)** and those from the Lower Downtonian (Lower Přídolí) below, there is, therefore, in England, a considerable gap in the Přídolí spore occurrence. Although there are spores in graptolite-bearing marine sediments in Podolia these spores have been inadequately described and illustrated. The spores illustrated by Shepeleva (1963) from the Lower Devonian of Podolia possibly belong to the **MN Zone** and her species *Lophozonotriletes decoratus* closely resembles *Streelispora newportensis,* the nominal species for the base of the **MN Zone.**

GEOGRAPHICAL & GEOLOGICAL SETTING (FIG. 1)

The Cantabrian Mountains, in the north and northwest of Spain, extend through the Provinces of Asturias, León, Cantabria and Palencia. Geologically, most of the Cantabrian Mountains belong to the 'Cantabrian Zone' of the Iberian Hercynian Massif and occupies the outermost part of it. The 'Cantabrian Zone' is composed of unmetamorphosed Palaeozoic sedimentary rocks deformed during the Variscan Orogeny. The 'Cantabrian Zone' has been divided into five tectono-sedimentary units (Julivert, 1967), arranged in concentric bands parallel to the 'Narcea Anticlinorium', an arch of Precambrian rocks on the western boundary of the 'Cantabrian Zone' (see Fig. 1). Following to the east of the ' Narcea Anticlinorium' is the 'Folds and Nappes Unit' where the most complete Palaeozoic sequences are found. This Unit occupies the western part of the Asturias and the northern part of the León Provinces. Within this structural unit four sections in a Silurian to Lower Devonian clastic succession have been selected for study.

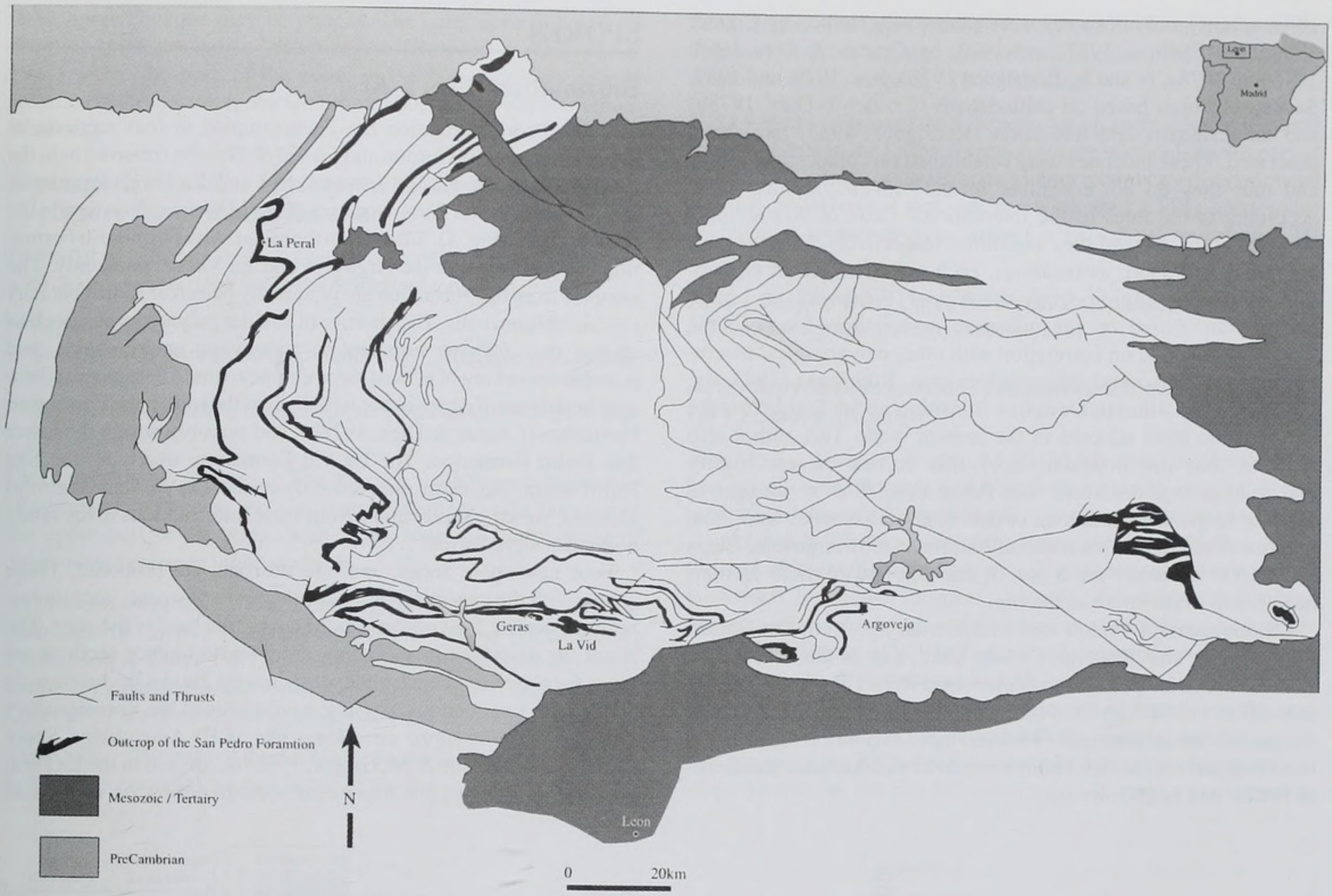


Fig. 1 Simplified geology of the Cantabrian Region, NW Spain (based on Rodriguez, 1983).

San Pedro Formation

This formation was described in two main areas: a, the 'Ferruginous Sandstones of Furada' (Barrois, 1882) on the northern flank of the Cantabrian Mountains, and b, the San Pedro Formation (Comte, 1937) in the south. These two names refer to the Upper Silurian Formations of the 'Folds and Nappes Unit' of the Cantabrian Zone. Three of our sections were originally designated as the San Pedro Formation (Geras de Gordón, La Vid de Gordón and Argovejo). The fourth section was included in the Furada Formation (La Peral). As both formations constitute a single lithostratigraphic unit they are all referred to in the text as San Pedro Formation.

The San Pedro Formation is predominantly sandy and overlies the Formigoso Formation; the latter is Silurian in age. The Formigoso Formation is composed of black shales, with alternating shales and quartzites in the upper part. The San Pedro Formation appears to be in stratigraphical continuity with the underlying Formigoso Formation in the sections near the Precambrian of the 'Narcea Anticlinorium', but the contact is sharp and erosive in the sections situated farther east.

Informally three members can be distinguished in this formation.

The Lower Member consists mainly of red ferruginous, coarse-grained sandstones, sometimes with oolites, having cross-trough stratification. At some localities there are conglomeratic beds, with phosphatic, sideritic and silty clasts and intraclasts; some of these clasts have a volcanic origin (Van den Bosch 1969; Suárez de Centi, 1988).

The Middle Member is composed of medium to fine grained sandstones with current and wave ripples, and grey to green intensively bioturbated mudstones and siltstones.

The Upper Member has fine-grained quartzitic sandstones, with cross stratification, interbedded with dark to black shales.

The San Pedro Formation was deposited in a shallow epeiric sea in intertidal to inner platform conditions (Suárez de Centi, 1988) in a transgressive-regressive cycle (Rodríguez, 1983). In this latter interpretation the middle member represents the deepest conditions.

Age and biozones of the San Pedro Formation

The age of this formation has been established on macrofauna, microplankton and spores. A macrofauna of brachiopods, molluscs, connularia, trilobites and graptolites has been found, but they are not abundant and are restricted to certain beds (Comte, 1934, 1959; Llopis Lladó, 1958, 1960, 1964; Poll, 1962, 1963, 1970). The lower half of the formation is of Ludlow age, based on brachiopods and connularia (Comte, 1934). In some sections, situated to the west of the 'Folds and Nappes Unit' (see Fig. 1), near one of our localities (La Peral), Poll (1963, 1970) found graptolites 20 to 50 m. below the top of the formation: *Saetograptus fristichi fristichi, S. fr. linearis, S. chimaera salweyi* belonging to the *nilssoni*, *scanicus*, and probably *leintwardinensis* Biozones and indicating a Gorstian to Lower Ludfordian age. The highest part was dated as Lochkovian on its macrofauna (Comte, 1934, 1937, 1959; Poll, 1970).

In contrast to the macrofauna, microplankton and miospores are extremely abundant and well preserved. Microplankton (acritarchs, chitinozoans) and miospores were extensively studied by Cramer 1964a, b, 1966b, c, 1967, and 1970; by Cramer & Diez 1968, 1975 and 1978a, b; and by Rodriguez 1978a, b, c, 1979, and 1983. Several biozones based on chitinozoans (Cramer & Diez, 1978b) and on acritarchs and miospores (Rodriguez, 1983) have been described. These biozones were established on composite sections and thus they do not constitute formal biostratigraphical units according to the rules of the International Code of Stratigraphic Nomenclature. Instead they constitute respectively, chitinozoans, acritarchs and spore associations, each one arranged in chronological order, ranging from the Upper Wenlock? to Lower Lochkovian. Based on the miospore associations found in the Geras Section, and on correlation with other palynological assemblages found in several different localities, Rodriguez (1983, fig. 13) placed the Silurian/Devonian transition about 5 m below the stratigraphic level adopted in the present work. This author also showed that the boundaries of this formation are highly diachronous (eg. the upper San Pedro Formation is younger in sections to the south and west of the 'Folds and Nappes Unit' than in those closer to the Precambrian Asturian Arch). Argovejo, Geras and La Vid are in the south part of this unit and all these sections have Lochkovian strata at the top.

Chitinozoans of Přídolí and Lochkovian age from the Carazo Formation, of the 'Pisuerga-Carrión Unit', east of the 'Cantabrian Zone', were described by Schweineberg (1987). The Carazo Formation differs in lithology from the San Pedro Formation but, although the precise lateral continuity between these two formations has not been established, the San Pedro Formation also includes sediments of Přídolí and Lochovian age.

SPORES

Biozonation (Figs 2–6)

The San Pedro Formation has been sampled in four sections: at Argovejo, Geras de Gordón and La Vid de Gordón (referred to in the text as Geras and La Vid respectively) and La Peral. Productive samples from the La Peral section occur at a lower horizon than in the other sections (Fig. 5). Strata from the underlying Formigoso Formation were sampled in the Argovejo and La Vid sections only. The samples from this formation are practically barren of spores but may contain chitinozoans. The absence of smaller palynomorphs, such as spores, may indicate turbulent to winnowing environments, and possible reworking of at least some chitinozoans. Alternatively, there may be a disconformity either within, or at the top of, the Formigoso Formation (Cramer & Diez, 1978b), and possibly within the lower San Pedro Formation. The La Vid Formation, overlying the San Pedro strata, has been sampled only at the La Vid and Argovejo sections, but all samples taken from shale intercalations in the sandy dolomites were barren.

Four new spore zones, and one subzone, are proposed. These zones, with the exception of the *hemiesferica* Biozone, contain two nominal taxa, at least one of which starts at the base of the zone. The zones are described in ascending order and reference sections are given for the base of each zone, or its lowest known occurrence. In addition, in two sections, possible equivalents of the *Synorisporites libycus – Chelinospora poecilomorpha* (**LP**) Assemblage Spore Biozone (Richardson & McGregor, 1986) occur, and in the La Peral Section the *Artemopyra brevicosta – Hispanaediscus verrucatus*

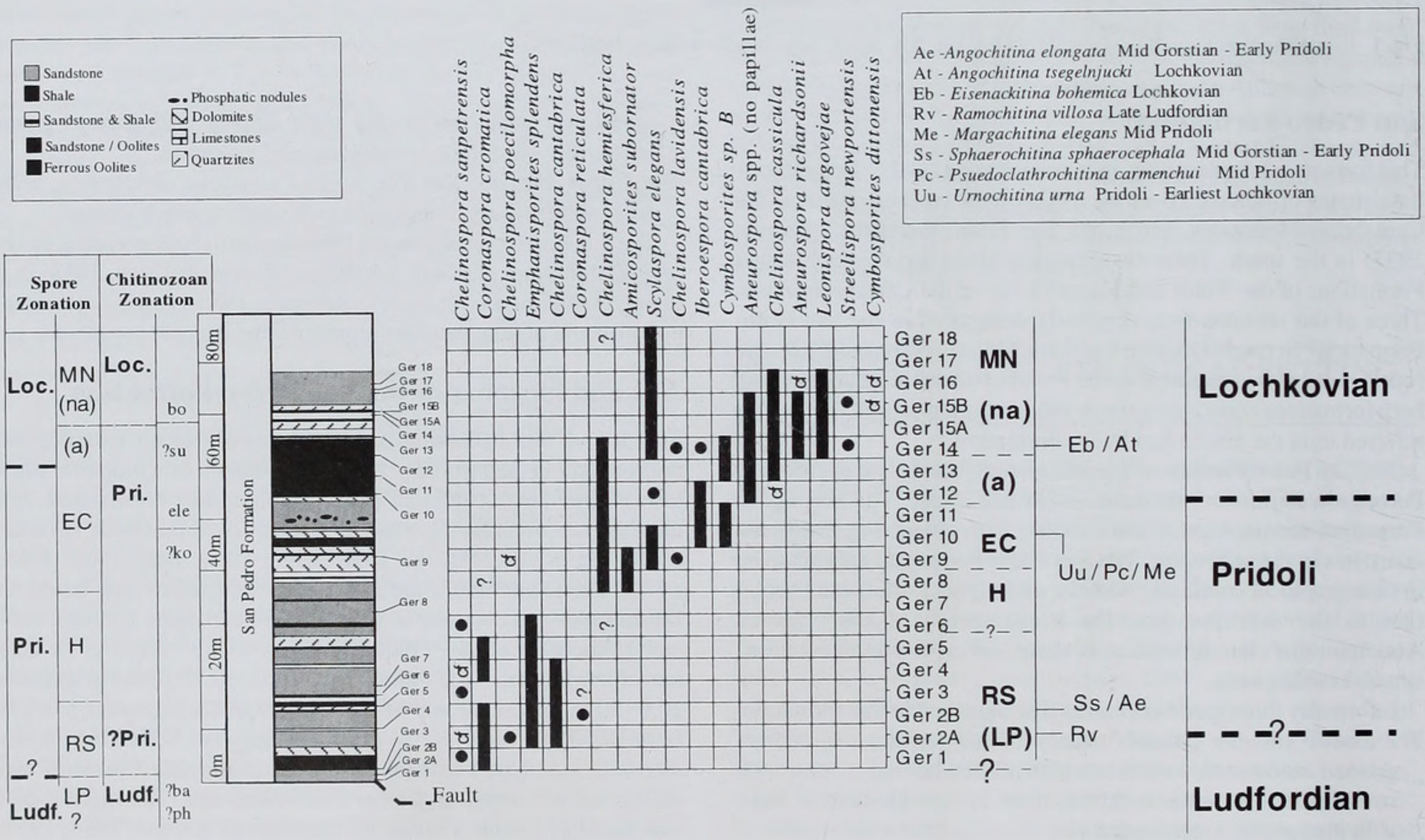


Fig. 2 Selected spore distribution at Geras. Chitinozoan zonation after Verniers *et al.* (1995): **bo**: bohemica, **su**: superba, **ele**: elegans, **ko**: kosovensis, **ba**: barrandei, **ph**: philipi.

(**BV**) Spore Biozone may be present. The latter zone is based on material from the Anglo-Welsh region (Burgess & Richardson, 1991) where the base of the zone, in the type Wenlock area, is recorded in the late *lundgreni* Graptolite Biozone (Lower Homerian, Wenlock).

Scylaspora vetusta – Scylaspora cf. *kozlica* (Dufka) (V) Spore Assemblage Biozone

DEFINITION. Based on the co-occurrence of the two nominal taxa with *Scylaspora scripta* (Burgess & Richardson, 1995).

NOMINAL SPECIES

Scylaspora vetusta (Rodriguez) comb. nov. Rodriguez, 1978b: pl. 1, fig 8.

Scylaspora cf. *kozlica* (Dufka) comb. nov. Dufka 1995: pl. 3, figs 10a–10b.

CHARACTERISTIC SPECIES. The species *Ambitisporites abundo* (Rodriguez) comb. nov. and *Concentricosisporites* (?sp.) appear in the upper part of the zone. Within this zone the morphology of *Scylaspora vetusta* is highly variable.

ACCESSORY SPECIES. Long ranging laevigate species such as *Ambitisporites avitus* Hoffmeister 1959, *A. dilutus* (Hoffmeister) Richardson & Lister 1969, *A. warringtonii* (Richardson & Lister) comb. nov., and *Archaeozonotriletes chulus* (Cramer) Richardson & Lister 1969 are present, along with murornate *Synorisporites* sp.

REMARKS. The base of the *Scylaspora vetusta* Biozone is not seen as both the nomimal species occur in the lowest sample of the La Peral section. The upper boundary is defined by the incoming of the nominal species of the succeeding *Artemopyra brevicosta-Hispanaediscus verrucatus* (**BV**) Biozone.

OCCURENCE. Strata of the *S. vetusta – S.* cf. *kozlica* Spore Biozone are found only in the La Peral section but the nominal species persist into higher zones in other sections. Higher records are discontinuous and may be, at least in part, due to reworking (La Vid *Coronaspora reticulata – sanpetrensis* and lower *Chelinospora hemiesferica* (**H**) Biozones).

AGE. Possibly lower Upper Homerian. Chitinozoa indicate a doubtful Llandovery age and may be reworked.

Artemopyra brevicosta – Hispanaediscus verrucatus (BV) Spore Biozone

REMARKS. Defined in the Anglo-Welsh area (Richardson & McGregor, 1986, Burgess & Richardson, 1995: 26, text-fig. 8) this zone ranges through the middle and upper parts of the Homerian but is unknown in the lower part of the *lundgreni* Graptolite Biozone at the base of this stage in the type area. The spore zone in the type area is divided into three subzones, namely: *Artemopyra brevicosta*, *Hispanaediscus lamontii*, and *Emphanisporites protophanus* (Burgess & Richardson, 1995). In the La Peral sequence the simultaneous appearance of *A. brevicosta* and *H. verrucatus* (sample LP4) is followed by the occurrence of *Hispanaediscus lamontii* in the next higher sample (LP5, 12 m above) and the nominal species persist into the overlying **RS** Spore Biozone. All of these species are typical of the Homerian, but two (*H. lamonti* and *H. verrucatus*) continue

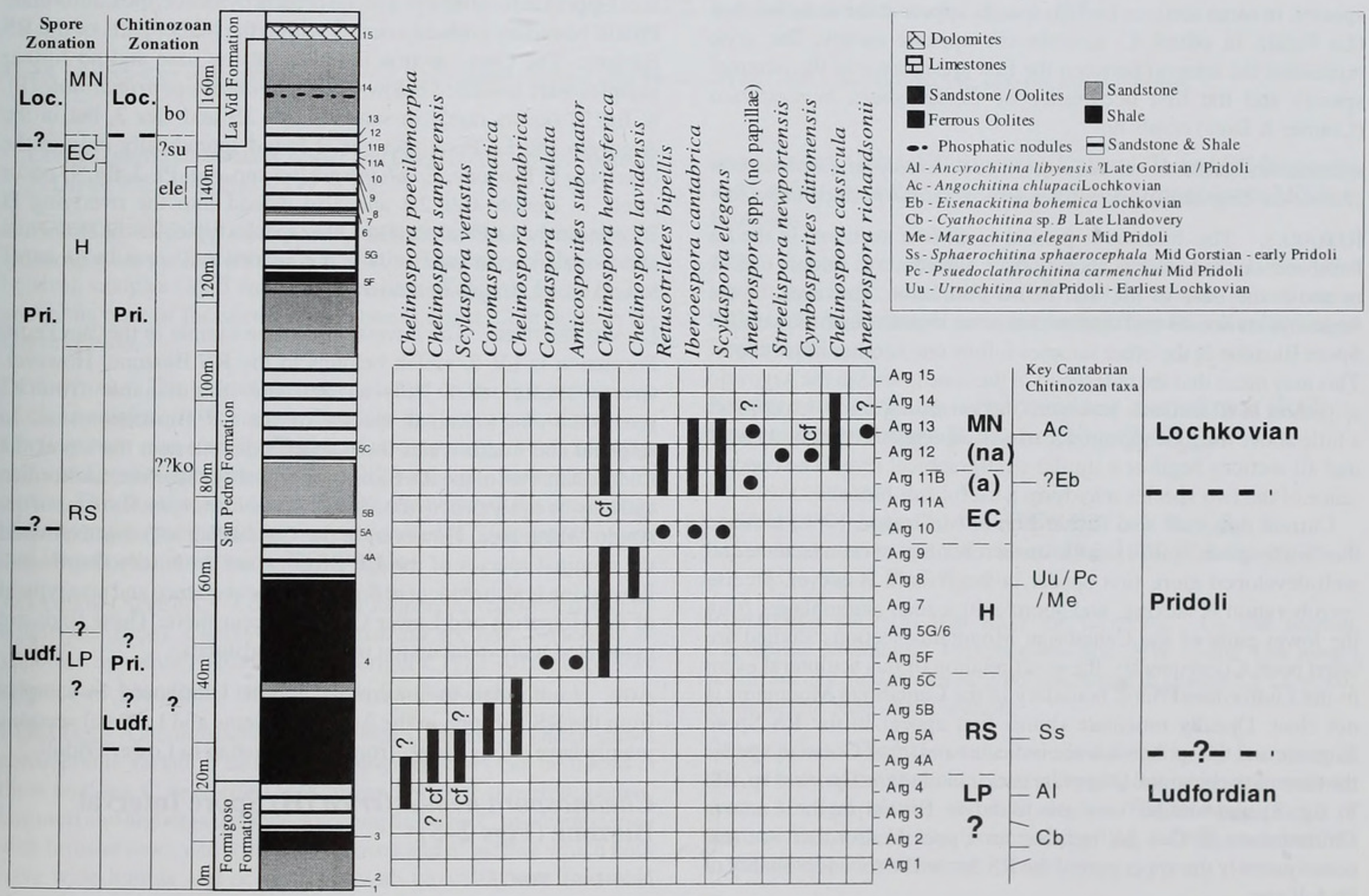


Fig. 3 Selected spore distribution at Argovejo. Chitinozoan zonation after Verniers *et al.* (1995): **bo**: bohemica, **su**: superba, **ele**: elegans, **ko**: kosovensis.

into lower part of the *Synorisporites libycus –Chelinospora poecilomorpha* (**LP**) Spore Biozone in the Anglo-Welsh area. Regarding the age of the La Peral samples, there are two main possibilities: the spores represent either an impoverished Gorstian (**LP**) assemblage with reworked fossils from the Homerian, or b, *in situ* Homerian spores. Since older spores may be reworked and deposited inside clasts in younger rocks, they may be preferentially retained, whereas the lower density of contemporary palynomorphs may cause them to be selectively removed by currents.

OCCURENCE. Found only in the La Peral section.

AGE. Homerian. In the type Wenlock the *brevicosta* and *lamontii* Sub-Biozones are more or less equivalent to the upper *lundgreni* and *nassa* to lower *ludensis* Graptolite Biozones respectively. There is no chitinozoan evidence for sample LP4 but in the underlying sample (LP3) the chitinozoan species *Conochitina rudda* also indicates a Upper Wenlock to Lower Ludfordian age. Therefore, the chitinozoan evidence fits with an assignment to either the upper *brevicosta – verrucatus* (**BV**) Biozone (Middle to Upper Homerian), or to the succeeding spore zone in the Ludlow.

Coronaspora reticulata – Chelinospora sanpetrensis (RS) Spore Biozone (Figs 3–5)

NOMINAL SPECIES

Coronaspora reticulata sp. nov. *Knoxisporites? riondae* Cramer & Diez 1975 (pars): pl. 1, fig. 17.

Chelinospora sanpetrensis (Rodriguez) comb. nov. Rodriguez, 1978c: pl. 1, fig. 13 (figs i, j, l).

DEFINITION. Based on the incoming of either of the two nominal species. In some sections the two species appear at the same horizon (La Peral), in others *C. sanpetrensis* appears earlier. The zone represents the interval between the first appearance of the nominal species and the first occurrence of *Chelinospora hemiesferica* (Cramer & Diez) comb. nov.

ACCESSORY SPECIES. *Chelinospora poecilomorpha*, *Coronaspora cromatica*, *Emphanisporites splendens*, *Chelinospora cantabrica*.

REMARKS. This biozone is present in all four sections. In the La Peral section the base lies above a thick sandstone in sample 6, c.71 m above the base of the San Pedro Formation. However, in the Argovejo section several species that occur together in the lowest RS Spore Biozone in the other samples follow one another in sequence. This may mean that the oldest part of the zone is seen in the Argovejo sequence. In all sections, however, *Chelinospora cantabrica* appears a little above the first appearance of *C. sanpetrensis*, which suggests that all sections begin at a similar stratigraphical level. The concurrence of the two species may form a useful sub-biozone.

Current data (see also Richardson & McGregor, 1986) indicate that trilete spores, with a regular distal reticulum of even lacunae and well-developed muri, first appear in the Přídolí. However, precise corroboration is lacking, and spore/chitinozoan assemblages from the lower parts of the Cantabrian Mountains sections studied are often poor. Consequently, the exact relation of this sculptural event to the Ludfordian/Přídolí boundary in the Cantabrian Mountains is not clear. Distally reticulate spores first appear in the **RS** Spore Biozone and the spore evidence indicates an Upper Gorstian age for the base of the biozone. Other rare taxa include *Insolisporites* sp. (Pl. 3, fig. 3) and similar taxa are found in Britain in the Ludlow. Chitinozoans in Ger 2A indicate an Upper Ludfordian age and consequentely the upper part of the **RS** Spore Biozone is probably of Přídolí age.

REFERENCE SECTION. La Peral, Cordillera Cantabrica, Province of Asturias, NW Spain. The 'base' of the zone is between 49 and 71 m above the base of the San Pedro Formation. The strata in this 22 m interval are dominated by red sandstones and were not sampled. The zone is at least 22 m thick in the La Peral section.

DISTRIBUTION. La Peral, Geras, La Vid and Argovejo sections. In the Argovejo sequence the thickness of the zone is uncertain due to a 40 m interval where samples are barren. In the other sections the thickness of the zone is around 15–25 m.

ARGOVEJO SECTION. The lowest eleven samples are barren or do not contain diagnostic palynomorphs. In sample ARG/4 *poecilomorpha* occurs with cf. *sanpetrensis* and may indicate the presence of the upper part of the **LP** Biozone (Upper Ludfordian in England and Wales). Chitinozoa from the same sample are long ranging from Upper Gorstian to Přídolí and therefore do not conflict with the presence of the upper **LP** Spore Biozone but are insufficiently precise.

GERAS SECTION. *Chelinospora sanpetrensis*, one of the nominal species of the **RS** Spore Biozone, occurs in the basal sample (Ger 1) of the Geras section. *Chelinospora poecilomorpha* and *Stellatispora inframurinatus* var. *cambrensis* appear in the overlying samples (Ger 2A and Ger 3 respectively) and are also found in the upper Gorstian and Ludfordian of England and Wales but are absent from the succeeding Downtonian there. The presence of the chitinozoan *Ramochitina villosa* indicates a Late Ludfordian age for sample Ger 2A within the **RS** Biozone. *Emphanisporites splendens* appears in Ger2A to Ger6. This species is found in North Africa in association with typical lower Downton (Lower Přídolí) species in the upper part of its known range there. Thus, at least part of the **RS** Spore biozone is of Upper Ludfordian age and, on present evidence, the Ludfordian/Přídolí boundary probably occurs within the higher parts of the **RS** Biozone. The Geras section is faulted at the base and no further samples were collected below Ger 1. *Coronaspora primordiale* (Pl. 6, fig. 3) occurs rarely in samples Ger 2B and Ger 3, but in the Argovejo and La Peral sections is found sporadically only in the overlying **H** Biozone. *Emphanisporites* spp. (eg. Pl. 2, fig. 9) occur rarely in sample Ger 2B and also extend into the overlying **H** Biozone in the La Peral section. Other species typical of the Homerian and Gorstian occur erratically in this section and are most probably reworked, eg. *Hispanaediscus lamonti*.

LA VID SECTION. The lowest productive sample in the San Pedro Formation is LV 6, which belongs to the **RS** Biozone. However, spores similar to S. *libycus* and indistinguishable from *C. poecilomorpha* (nominal species of the **LP** Biozone) occur. In England and South Wales these species die out near the top of the Ludfordian. Part of the **RS** Biozone is probably, therefore, Ludfordian and may be equivalent to the *libycus – poecilomorpha* Biozone of the Anglo-Welsh area. However, in the Cantabrian sections examined the nominal species of the **LP** Biozone are erratically distributed. Reworking is also evident in this part of the sequence and taxa typical of the Homerian and Lower Gorstian occur there. These finds are associated with an incursion of thick sandstones.

AGE. Ludfordian to lowermost Přídolí. Chitinozoa in samples from the **RS** Biozone in the Argovejo, Geras and La Peral sections mainly have a long range, from Mid-Gorstian to Lower Přídolí.

Chelinospora hemiesferica (H) Spore Interval Biozone (Figs 2–5)

NOMINAL SPECIES

Chelinospora hemiesferica (Cramer and Díez) comb. nov.; Cramer and Díez 1975: pl. 2, figs 34–36, (Pl. 9, figs 3, 5).

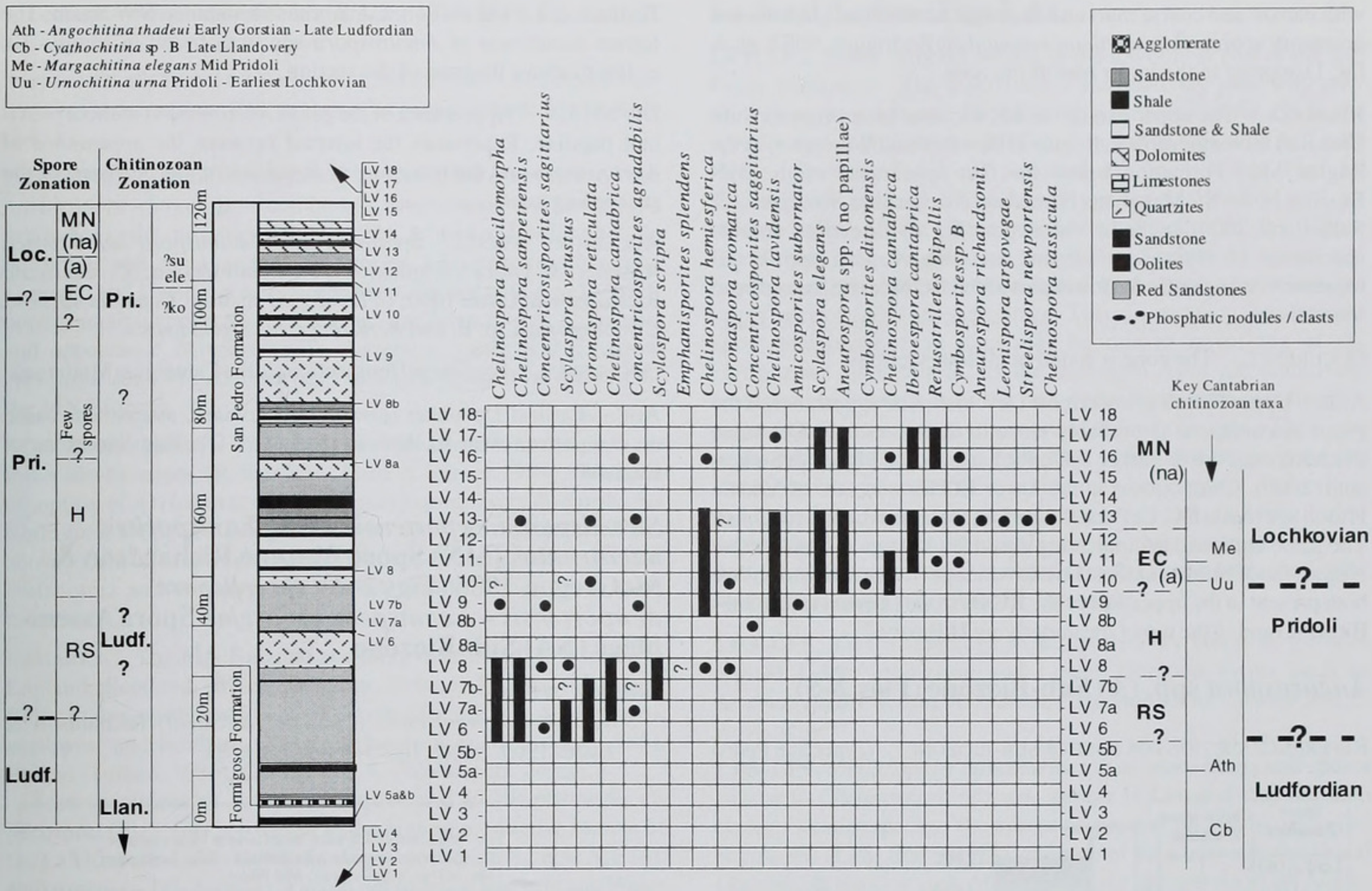


Fig. 4 Selected spore distribution at La Vid. Chitinozoan zonation after Verniers *et al.* (1995): **su**: superba, **ele**: elegans, **ko**: kosovensis.

Coronaspora subornata (Cramer and Díez) comb. nov.; Cramer & Diez 1975: pl. 1, fig. 7, (Pl. 8, fig. 7).

REFERENCE SECTION. San Pedro Formation, Geras, Province of León, Cordillera Cantabrica, NW Spain. The base of the zone is between samples Ger 5 and 6, and the base of sample 6 is c.16.2 m above the base of the section. The zone is about 22 m thick in the Geras section.

DEFINITION. The base of the zone is based on the first appearance of *C. hemiesferica* (Cramer & Diez). In the lower part of the zone *Chelinospora sanpetrensis* (Rodríguez), *Coronaspora reticulata* sp. nov. and *Emphanisporites splendens* (Richardson & Ioannides, 1973) persist. This biozone represents the interval between the appearance of the nominal species and the first occurrence of *Scylospora elegans* and *Iberoespora cantabrica* (**EC**) Biozone.

ACCESSORY SPECIES. *Coronaspora subornata* (occurs erratically within the zone), *Chelinospora canistrata* sp. nov. *Concentricosisporites agradabilis* (Rodriguez) Rodriguez, 1983. All the accessory spores have been found in three of the four sections.

REMARKS. *Chelinospora hemiesferica* (Cramer & Diez) shows considerable variation and a morphological series can be traced in these sections. *C. hemiesferica* (Silurian, Přídolí) has narrow geniculate muri and higher in the zone is accompanied by *C.* cf. *hemiesferica* with broader muri, and then *C. lavidensis* and *C. media,* which both have wide lumina and occur along with typical Lower Devonian (Lochkovian) species *Chelinospora cassicula* Richardson & Lister. So far the variant *C.* cf. *hemiesferica* has been found in three of the four sections: Geras (**EC** Biozone), La Peral (**H**, and **EC** Biozones), and La Vid (upper **EC** (*Aneurospora* Sub-Biozone), lower **MN** Sub-Biozone).

AGE. Lower and Middle Přídolí. The chitinozoan *Urnachitina urna* occurs in the basal sample (LP10) of the *hemiesferica* Biozone in the La Peral section, *U. urna* has a range from Přídolí to lowermost Lochkovian.

Scylaspora elegans – Iberoespora cantabrica (EC) Spore Assemblage Biozone (Figs 2–5)

NOMINAL SPECIES

Scylaspora elegans sp. nov. (Pl. 5, figs 2–4, Pl. 6, fig. 8).

Iberoespora cantabrica Cramer & Diez 1975: pl. 2, figs 24, 26–28 (Pl. 6, fig. 4; Pl. 7, fig. 4).

REFERENCE SECTION FOR BASE OF BIOZONE. La Vid section, Cantabrian Mountains, Province of León, NW Spain. The lowest occurrence of *Scylaspora elegans* was found in sample LV10, *c.* 102 m above the base of the section.

DEFINITION. The base of the zone is defined by the incoming of one, or both, of the nominal species. Usually *Iberoespora cantabrica* occurs stratigraphically above *S. elegans*. The first appearance of *Aneurospora* spp., lacking proximal papillae, defines a sub-biozone in the upper part of the zone.

ACCESSORY SPECIES. *Retusotriletes bipellis* Rodriguez, 1978c, *Cymbosporites* sp. B, and several *Chelinospora* morphs (variants) with narrow and coarse muri and an irregular reticulum are common accessory spores. *Retusotriletes coronadus* (Rodriguez, 1983: pl. 8, fig. 1) appears in the lower part of the zone.

REMARKS. The upper part of the **EC** Biozone (*Aneurospora* Sub-Biozone) is recognisable in England (Hereford and Worcester) in the Raglan Marl Formation below the first appearance of the **MN** Biozone in the St. Maughans Formation (Richardson, Rodriguez & Sutherland, 2000). In the La Vid section (Fig. 4) the earliest definite specimens of *Scylaspora elegans* and *Aneurospora* spp. occur together, consequently the lower part of the **EC** biozone has not been found there.

OCCURENCE. The zone is found in all four sections.

AGE. Upper Přídolí to lowermost Devonian. The appearance of the genus *Aneurospora* is probably close to the base of the Devonian (Richardson, Ford & Parker 1984; Richardson, Rodriguez & Sutherland, 2000). Chitinozoans in the lower **EC** Biozone are of Middle Přídolí age (basal **EC**, La Peral, lower **EC**, Geras and La Vid sections). The same chitinozoans indicating a mid-Přídolí age (*Margachitina elegans*) and Přídolí to earliest Lochkovian age (*Urnochitina urna*) are both present in the upper part of the **EC** Biozone (***Aneurospora*** Sub-Biozone) and in the top of the underlying **H** Biozone.

Aneurospora spp. (A) Sub-Biozone (Figs 2–5)

REFERENCE SECTION FOR BASE OF SUB-BIOZONE. Upper San Pedro Formation, La Vid section, Cantabrian Mountains, NW Spain. The lowest occurrence of *Aneurospora* spp. was found in sample 10, *c.* 106 m above the base of the section.

DEFINITION. Appearance of the genus *Aneurospora* without proximal papillae. Represents the interval between the appearance of *Aneurospora* and the incoming of *Streelispora newportensis* of the succeeding zone.

ACCESSORY SPECIES. Spores of the *Chelinospora hemiesferica* (Cramer & Diez) complex, *C.* cf. *hemiesferica*, *C. cassicula* Richardson & Lister 1969, *C. lavidensis* sp. nov., *C. media* sp. nov., *Cymbosporites* sp. B, and *Retusotriletes coronadus* s.s.

OCCURENCE. Found in all four sections in the Cantabrian Mountains.

AGE. Earliest Devonian (Lower Lochkovian), assessment based on comparison with sections in the Lower Old Red Sandstone of England.

Streelispora newportensis – Emphanisporites micrornatus (MN) Spore Biozone Richardson & McGregor, 1986 (Figs 2–4); *Streelispora newportensis – Leonispora argovejae* Spore Assemblage (NA) Sub-Biozone

NOMINAL SPECIES

Streelispora newportensis (Chaloner & Streel) Richardson & Lister 1969: pl. 41, figs 3–6 (Pl. 7, fig. 8).

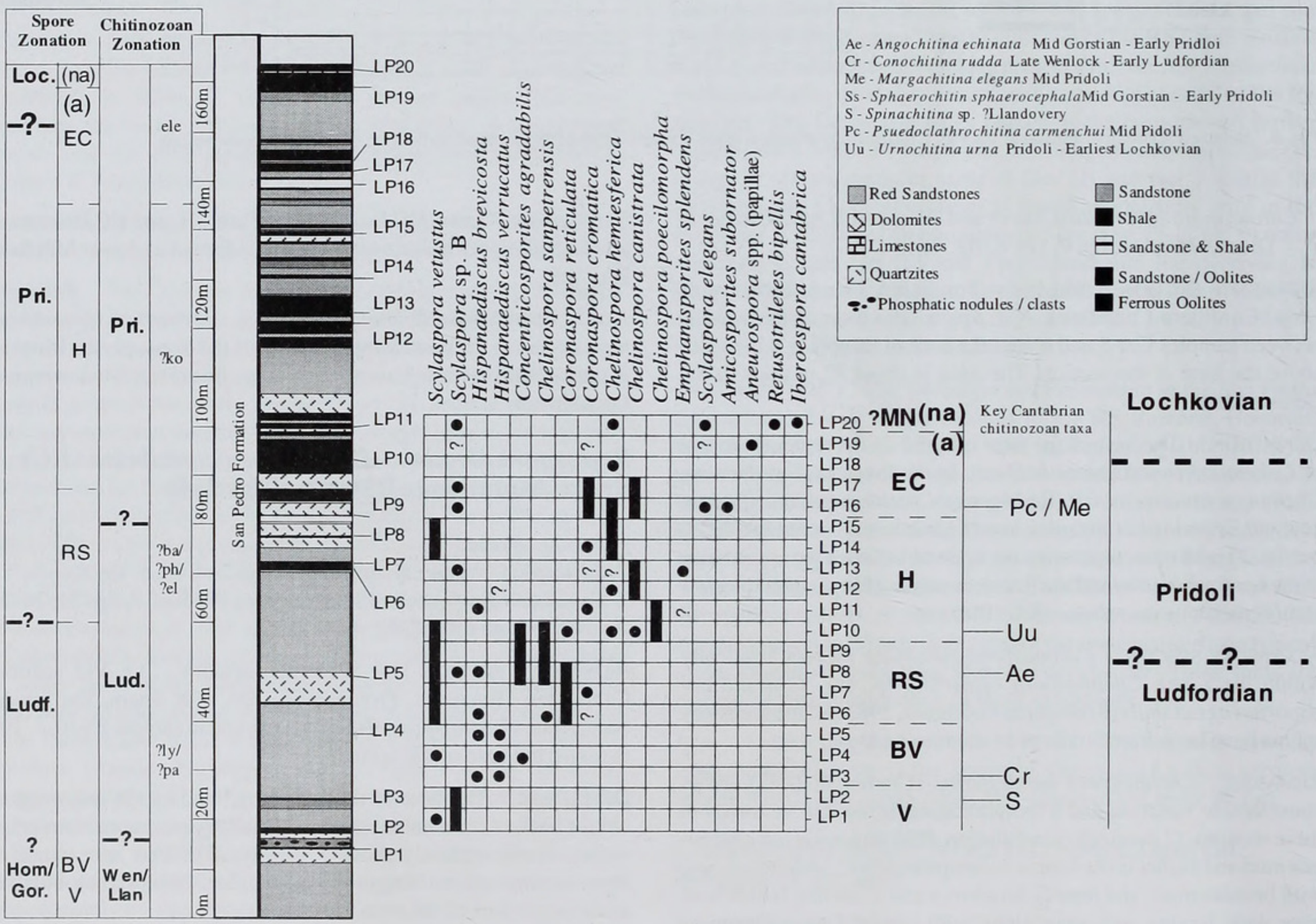


Fig. 5 Selected spore distribution at La Peral. Chitinozoan zonation after Verniers *et al.* (1995): **ele**: elegans, **ko**: kosovensis, **ba**: barrandei, **ph**: philipi, **el**: elongata, **ly**: lycoperdoides, **pa**: pachycephala.

Leonispora argovejae Cramer & Diez 1975: pl. 1, fig. 3 (Pl. 7, fig. 5).

REFERENCE SECTION FOR BASE OF SUB-BIOZONE. San Pedro Formation, Geras section, 70.1 m above the base of the section (sample Ger14).

DESCRIPTION. First appearance of tripapillate species of the *Aneurospora – Streelispora* complex (*S. newportensis* and *Leonispora argovejae*), the non-papillate species *A. richardsonii*, and the murornate and apiculate patinate species, *Chelinospora cassicula*, *C. media* and *Cymbosporites dittonensis*. Spores with a well-developed zona first appear within the zone. Persistence of *R. coronadus* and appearance of spores with curvatural spines and a narrow curvatural zona (*Breconisporites*? sp. C; Pl. 4, fig. 3) at the base of the **MN** Biozone.

ACCESSORY SPECIES. In Britain the **MN** Biozone is divided into three sub-biozones (Richardson, Ford & Parker 1984). With the exception of *A. richardsonii* (Rodriguez) comb. nov., *R. coronadus* Rodriguez 1983, and *Breconisporites*? sp. C all the species listed above occur also in the lower **MN** Sub-Biozone of the Anglo-Welsh area and consequently the **NA** Sub-Biozone can be used there also.

REMARKS. The **MN** Biozone is widely distributed. It is found in England, Scotland, Wales, Belgium, Poland, Podolia (Ukraine), Baltic States, northwest Spain and North Africa (Libya & Morocco), northwest and southern China (Richardson & McGregor, 1986), Poland (Turnau, 1986), and the U.S.A. (Wood, pers. comm.).

Rare specimens of *Telisporites* sp. A and *Emphanisporites* cf. *decoratus* (Pl. 3, figs 2, 6) occur in the highest productive sample of the La Vid section, also high in the Argovejo section (sample Arg 14). *Raistrickia* sp. (Pl. 3, fig. 4), a taxon not found in England and Wales at this level, also occurs in the Geras section.

OCCURENCE. The **MN** Biozone occurs in the upper San Pedro Formation in the Argovejo, Geras, and La Vid sections.

AGE. Lower but not lowermost Devonian (Lochkovian) based on spores, probably lowermost Devonian based on chitinozoans.

AGE OF THE BIOZONES AND INTER-REGIONAL PALYNOLOGICAL CORRELATION

Palynological correlation reveals several anomalies between the ages based on chitinozoans and those on spores in three of the four sections examined from the Cantabrian Mountains. There is evidence for considerable reworking in three of the sections. In other parts of the sections the data are consistent between the two fossil groups and the sequence of spore zones can be traced throughout the study area. All but the lower two zones in La Peral are found in at least three localities.

In spite of regional differences there are a number of species that are found both in the Silurian type area of England and south Wales and the current area of study. Of the four sections, that at La Peral is farthest offshore and perhaps represents a more continuous spore sequence less disturbed by reworking than the sediments in the Argovejo, Geras and La Vid sections where the San Pedro Formation is marginal marine in part. For this reason the La Peral section is taken as our basis for correlation of our sections with those from the Anglo-Welsh type area. and, although the preservation of the spores is not as good in the La Peral section, it is nevertheless sufficient for correlation with Britain up to the *Aneurospora* Sub-Biozone.

La Peral Section (Figs 5, 6)

LP1, LP2. These samples belong to the lowermost part of the San Pedro Formation . The assemblages are relatively poor with only thirteen cryptospore and miospore taxa recorded so far. (N.B. the spore range charts are not published in full at this time and only those important for local zonation are included in Fig. 5). Chitinozoans indicate a Llandovery age for this interval and, although some of the spore species also occur in the Upper Llandovery they are long ranging forms. Sculptured spores e.g. *Scylaspora* spp. have not been found in the type area below the upper part of the Homerian Stage. This discrepancy between the spore and chitinozoan data may be due to reworking of the chitinozoan *Spinachitina,* as the transition from the underlying formation to lower part of the San Pedro Formation constitutes a regressive-transgresive cycle across the whole area. Thus, the lower part of the San Pedro Formation in this area may represent a transgressive cycle where reworking may be prevalent. Reworking of Upper Llandovery spores would be practically invisible in impoverished younger assemblages as the spore records of *Ambitisporites* spp. found in these samples range from the Upper Aeronian (Llandovery) into the Devonian.

LP3–LP5. This assemblage of sculptured cryptospores includes typical Upper Homerian and Lower Gorstian forms such as *Artemopyra brevicosta, A. radiata, Hispanaediscus lamontii* and *H. verrucatus.*

LP6–LP9. *Stellatispora inframurinata* var. *cambrensis* and spores similar to *Chelinospora obscura,* appear in LP6 and they are both typical Gorstian species. The miospore species *Concentricosisporites sagittarius* (LP8) first occurs at the base of the Ludlow Series (basal Gorstian) in the type area. All three taxa are key species in the Anglo-Welsh area. This age is consistent with that indicated by chitinozoans in sample LP8 dated as Middle Gorstian to Middle Přídolí age. *Stellatispora inframurinata* is used as a zonal species in England and Wales and is found in the Upper Gorstian and Ludfordian stages. With the exception of *S. inframurinata,* none of these forms has been found above the Ludlow in the type area. In sample LP 10 (10 m higher than LP 8) *C. hemiesferica* occurs for the first time, marking the base of our **H** Biozone.

LP12–LP16. The first appearance of *Amicosporites splendidus* may mark either the uppermost Ludfordian or the lowermost Přídolí. There were no chitinozoans in sample LP12 but in the overlying sample (LP16) chitinozoans typical of the Middle Přídolí have been found.

LP19. According to our research the genus *Aneurospora* marks a level at, or near, the base of the Devonian. Unfortunately chitinozoan evidence is limited and suggests a Lower to Middle Přídolí age. However, in all the other sections studied the *Aneurospora* Sub-Biozone is followed by the **MN** Biozone, which is found only in Lower, not basal, Lochkovian. LP20 may belong to the MN Biozone but lacks the nominal species.

SPORE BIOZONES

***Scylaspora vetusta* (V) Spore Biozone.** This biozone has been found only in the La Peral Section samples (LP1, LP2). The assemblage is limited but contains *Scylaspora vetusta* and *Retusotriletes abundo.* Both these species were found in North Africa (Richardson & Ioannides, 1973) but the latter occurs 60 m above Wenlock/basal Ludlow graptolites. *Scylaspora* and *Synorisporites* sp. indicate an age not older than late Lower Homerian.

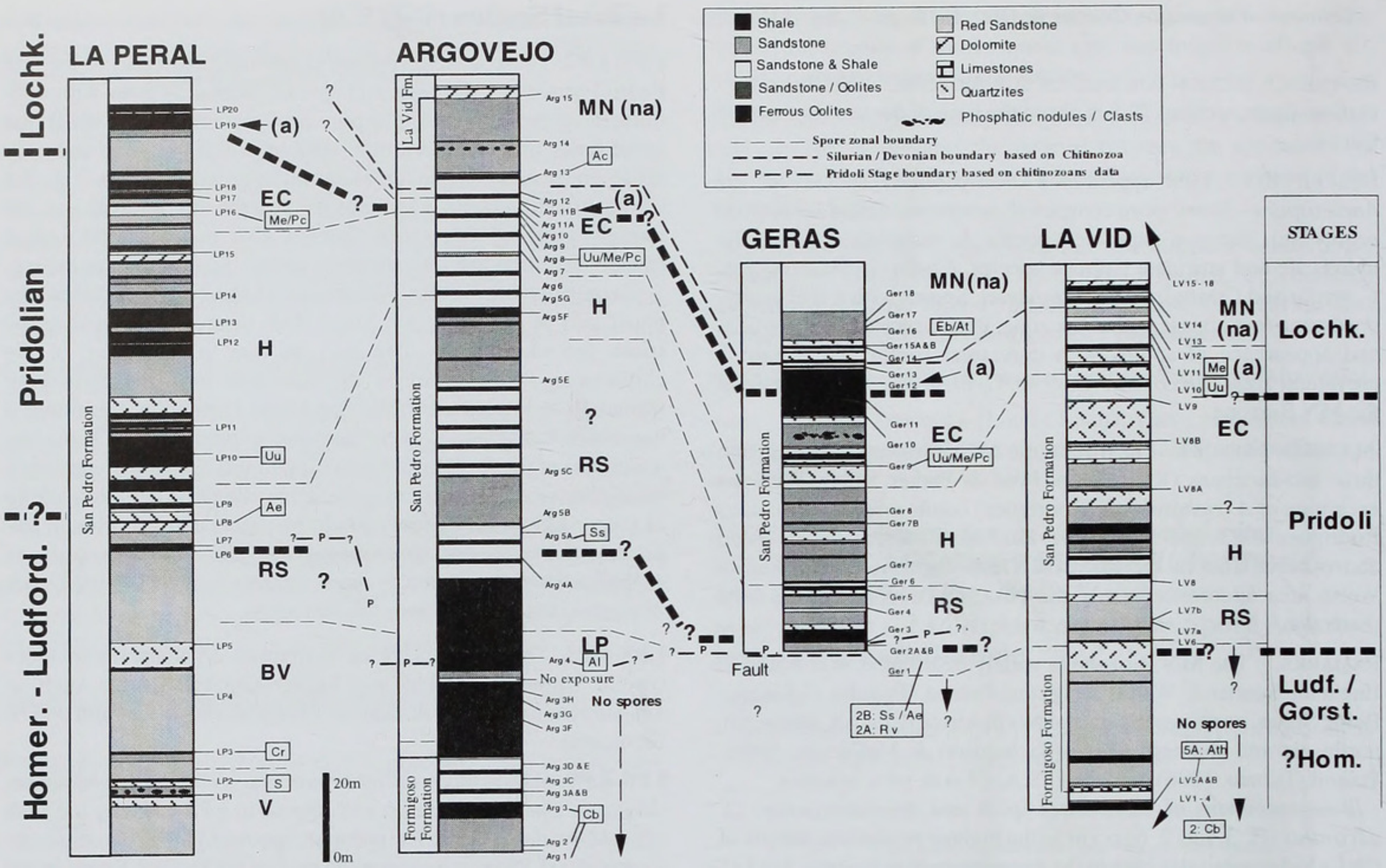


Fig. 6 Correlation of Cantabrian sections. Spore zonation new, except for LP Biozones after Richardson & McGregor (1986), **MN** Biozone after Holland & Richardson (1977) and Richardson & McGregor (1986), and **BV** Biozone after Burgess & Richardson (1995); **MN**: micrornatus – newportensis, **(na)**: newportensis – argovejae Subzone, **(a)**: Aneurospora Subzone, **EC**: elegans – cantabrica, **H**: hemisphaerica, **RS**: reticulata – sanpetrensis, **LP**: libycus – polymorpha, **BV**: brevicosta – verrucatus, **V**: vetusta. Key Cantabrian chitinozoan taxa: **Ac**: *Angochitina chlupaci* Lochkovian, **Ae**: *Angochitina echinata* Mid Gorstian – Lower Přídolí, **Al**: *Ancyrochitina libyensis* Late Gorstian? – Lower Pvrídolí, **Ath**: *Angochitina thadeui* Lower Gorstian-Late Ludfordian, **At**: *Angochitina tsegelnuki* Lochkovian, **Cb**: *Cyathochitina* sp. B Late Llandovery, **Cr**: *Conochitina rudda* Late Homerian-Lower Ludfordian, **Eb**: *Eisenackitina bohemica* Lochkovian, **Me**: *Margachitina elegans* Mid Přídolí, **Pc**: *Pseudoclathrochitina carmenchui* Mid Přídolí, **Rv**: *Ramochitina villosa* Late Ludfordian, **Ss**: *Sphaerochitina sphaerocephala* Mid Gorstian to Lower Přídolí, **S**: *Spinachitina* sp. Llandovery?, **Uu**: *Urnachitina urna* Přídolí-earliest Lochkovian.

***Artemopyra brevicosta – Hispanaediscus verrucatus* (BV) Spore Biozone (Burgess & Richardson 1995).** Both the nominal species are found in samples LP3 and LP5. The fact that *Hispanaediscus lamontii* also occurs in the latter sample may indicate that the junction between the *A. brevicosta* and *H. lamontii* Sub-Biozones lies between these two samples. In south Wales this sub-zonal boundary occurs in the Middle Homerian between the *lundgreni* and *nassa* Graptolite Biozones.

***Chelinospora reticulata – C. sanpetrensis* (RS) Spore Biozone.** This biozone is represented in all four sections. In the La Peral section both the nominal species appear together in sample LP6. Neither species has been found in the type area of England and Wales. However, the **RS** assemblages include *Concentricosisporites sagittarius* and *Stellatisporites inframurinatus* var. *cambrensis* first found in the Lower and lower Upper Gorstian respectively, and spores similar to *Chelinospora obscura* in the Middle Gorstian. All of these species can occur together in the lower part of the *cambrensis* Sub-Biozone. On current data, therefore, we tentatively, regard the lower boundary of the **RS** Biozone as lower Upper Gorstian, approximately lower *incipiens* Graptolite Biozone.

***Chelinospora hemiesferica* (H) Spore Biozone.** The base of the *hemiesferica* Biozone is found in sample LP 10 in the La Peral section. Associated spores are mainly found in the Cantabrian Mountains and North Africa. Several species, however, also occur in the Anglo-Welsh area. One of these, *Chelinospora poecilomorpha* occurs throughout the Ludlow Series in south Wales but has not been found in the Lower Prídolí there. In North Africa this species has a similar range and occurs with *Emphanisporites splendens*, a co-occurrence also found in LP9. In sample LP12 *Amicosporites splendidus* occurs and this species is also found in the uppermost Ludfordian to Downtonian (Lower Přídolí) in England but is rare there. The base of the biozone is placed tentatively, therefore, in the Lower Přídolí but could be also of latest Ludfordian age.

***Scylaspora elegans – Iberoespora cantabrica* (EC) Spore Biozone.** The first appearance of *Scylaspora elegans* occurs in the La Peral section in sample LP 16 coeval with chitinozoans typical of the Middle Přídolí. This is consistent with chitinozoan finds in the sections of Argovejo (Arg 8), Geras (Ger 10), and La Vid (LV 10, LV 11). The base of the zone is therefore placed in the Middle Přídolí with some confidence.

***Aneurospora* (A) Spore Sub-Biozone.** The first occurrence of this genus is found in three of the four sections studied: La Peral (sample

LP19), Geras (sample Ger 12) and La Vid (sample LV 10). This spore event occurs in England in sections from Hereford and Worcester in strata below the ***micrornatus – newportensis* (MN)** Zone. Although the *Aneurospora* Sub-Biozone in the Cantabrian Mountains occurs a little below (*c.* 5 m) the occurrence of the typical Lochkovian chitinozoans *Eisenackitina bohemica* and *Angochitina tsegelnjucki* (Geras), we regard the base of this Sub-Biozone as close to the Silurian/Devonian Boundary (Richardson, Rodríguez & Sutherland, 2000). This correlation is based partly on comparisons with material from Podolia described by Arkhangel'skaya (1980). In Podolia, below the base of the equivalents of the MN Biozone (Chortkov Group), there is distinct spore assemblage in the Mitkov Formation (Borshchov Group). This lower assemblage probably contains non-papillate spores of the genus *Aneurospora* and is above the first occurrence of the graptolite *Monograptus uniformis uniformis* providing support for the idea that the ***Aneurospora* (A)** Sub-Biozone is Devonian. Based on the distribution of key chitinozoan species, Paris & Grahn (1996) used the base of *Monograptus uniformis uniformis*, the higher of the two critical graptolite subspecies, to mark the base of the Devonian. In particular *Eisenackitina bohemica,* also found by us in the Cantabrian Mountains, and other restricted chitinozoan species occur in the upper Tajna Formation along with *M. uniformis uniformis*. Although it is difficult to be certain, because of the nature of the spore illustrations (Arkhangel'skaya, 1980), this Lower Podolian spore assemblage appears to include non-papillate species/varieties of *Aneurospora* and may, therefore, be equivalent to the *Aneurospora* Sub-Zone. Assemblages with tripapillate spores (*Aneurospora/Streelispora*?) occur in the Chortkov Group *c.* 70 m above the Mitkov assemblage. The Silurian/Devonian Boundary is currently placed at the first appearance of *M. uniformis angustidens* at base of the Borshchov Group (Tajna Formation, Nikiforova, 1977) but no spore assemblages have been described from the lower part of the Borshchov Group. Even so, the position of the Silurian/Devonian boundary as determined by Paris & Grahn seems reasonable from the spore evidence currently available.

Fig. 7 Přídolí palaeotectonic-palaeogeographic map. Simplified from Ziegler (1988).

LAURUSSIA – GONDWANA SPORE DISTRIBUTION PATTERNS (FIGS 7–9)

Upper Silurian and Lower Devonian spore floras are diverse and homosporous but little is known of their geographical dispersal. Silurian palaeogeographical maps show Europe and North America at low latitudes, between the Tropic of Capricorn and the equator (Witzke & Heckel, 1988), separated by an ocean from Gondwana (with Iberia in close proximity on its northern flanks) in higher southern latitudes (McKerrow & Scotese, 1990). The map (Fig. 7) based on Ziegler (1988) shows the Cantabrian Terrane separated from Gondwana by Proto-Tethys and on its northern flank the Rheic Ocean lies between the Aquitaine Cantabrian Terrane and northern France and Britain. McKerrow & Scotese show a wedge-shaped ocean narrowing westward to the point where the Americas were in contact. Using this reconstruction, and unless there was a major climatic barrier, there would have been a possible land plant migration route between Laurussia and Gondwana. With favourable winds, airborne transport would have been feasible for many of the spores because of their small size (Mogensen, 1981) and it is worth noting that many moss species have achieved wide dispersal in the northern hemisphere since the last ice age, some 10,000 years ago (Schofield, 1985). Such a time span is negligible in terms of geological time and is essentially instantaneous. Theoretically therefore, since there was no major physical barrier to dispersal apart from the availability of suitable habitats, and possibly climate, large parts of the tropical flora should have been uniform. As size affects dispersal (Mogensen, 1981), smaller spores, corresponding to homosporous plants with spores less than 25 μm, and appearing in the Přídolí and lowermost Lochkovian, should have had the widest distribution. Before the Pridloli, multiple unit cryptospores from the Llandovery and Wenlock, and to a lesser extent in the Upper Ordovician are apparently closely similar and widespread. Such assemblages occur in North America, Europe, North Africa, the Middle East and China. Was this wide dispersal due to efficient spore dispersal mechanisms, closer proximity of the main continents when their parent plants evolved, climate, or some other factors? The Ordovician data may not be representative, as few assemblages have been described in detail, but the uniformity of Lower Silurian cryptospore assemblages form a

Fig. 8 Emsian palaeotectonic-palaeogeographic map. Simplified from Ziegler (1988).

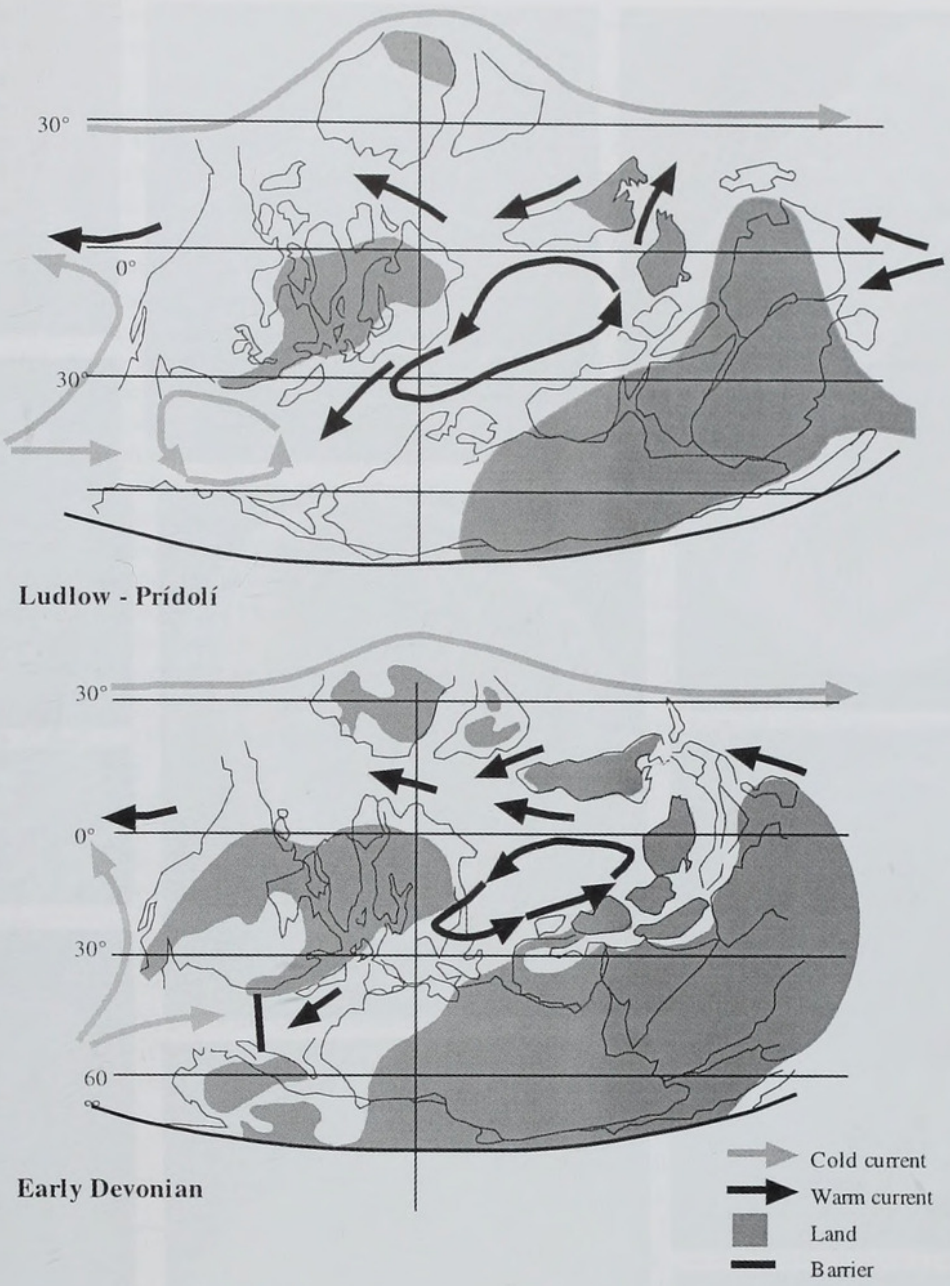
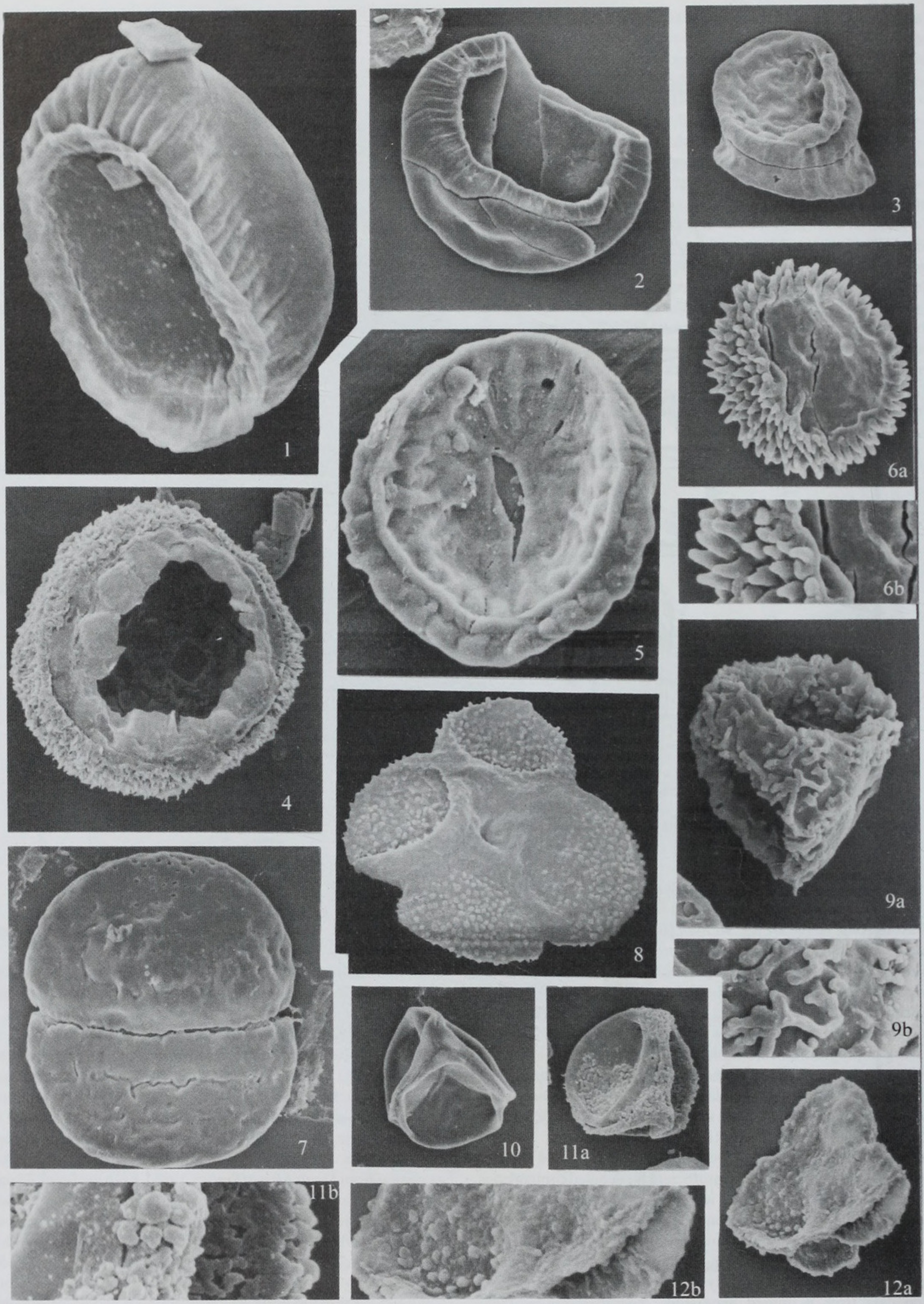


Fig. 9 Oceanic circulation through the Ludlow-Lower Devonian. Based on Le Hérissé *et al.* (1997).

contrast to some of the Upper Silurian trilete associations showing regional variations in species distribution.

Well illustrated accounts of spore data from Upper Silurian-Lower Devonian sequences are limited to comparatively few areas, viz. Britain (Richardson & Lister, 1969), the Cantabrian Mountains (Rodriguez, 1983), and North Africa (Richardson & Ioannides 1973, and work in progress). More limited stratigraphical data are available from Belgium, France, Poland, and China. Upper Silurian and Lower Devonian spore assemblages have been described from graptolite-bearing sequences only in England and Wales (Richardson & Lister, 1969, Burgess & Richardson, 1995) and Podolia (Arkhangel'skaya, 1980). However, many of the published illustrations of the Podolian material are insufficient for detailed comparisons and key taxa cannot be identified with certainty at the species level. Nevertheless the assemblages enable general correlation of these important graptolite-bearing sequences with Britain. The following discussions are therefore based mainly upon the authors' previous and current work, and consequently the present discussion is dependent on data from a limited geographic area representing three separate blocks, namely Laurussia, Iberia-Aquitaine and northern Gondwana.

Several spore taxa (eg. *Streelispora newportensis)*, although rare in parts of Gondwana, appear to be geographically widespread. Some cryptospore taxa, eg. *Tetraletes variabilis* Cramer 1966a, may have a restricted distribution and so far have been recorded only from Gondwana, Iberia and Brittany, whereas other cryptospores (Pl. 1, figs 1, 7, 9–11) occur in Laurussia as well. The planar tetrads of *Tetraletes* occur in Silurian-Lower Devonian sections from northwest Spain and North Africa, with a single specimen recorded from Brittany (d'Erceville, 1979). It is interesting to note that similar planar tetrads are found in the modern thalloid liverwort *Riccia perssonii* from South Africa (Perold, 1989). Both the fossil *Tetraletes* and the modern *Riccia* spores are permanently adherent and are joined by more or less smooth bands of attachment separating areas of spinose sculpture. Many cryptospore taxa are found in the Silurian of North America, Britain, Western Europe, the Baltic States, Podolia, Spain, and North Africa, whereas others are apparently regionally confined. As more records are forthcoming it should be possible to


1
2
3
6a
6b
4
5
9a
8
7
10
11a
9b
11b
12b
12a

determine how many of these ubiquitous spores had evolved before the break-up of the southern continent. On the other hand, trilete species, which evolved after many of the regionally dispersed cryptospores (e.g. *Tetrahedraletes medinensis* (Strother & Traverse), Pl. 1, fig. 10), apparently show a dichotomy with several distinctive trilete species currently known only from the Cantabrian Mountains and North Africa. As more spore data accumulates, therefore, the dispersal patterns of early land floras may provide constraints to palinspastic reconstructions. In addition, new insights into the correlation of marine with non-marine plant-bearing strata, will help to date more accurately events in land plant evolution, recorded in greatest detail in continental rocks. Further, the joint study of chitinozoans and spores in the same sequences will eventually permit an understanding of inter-facies correlation, not only in marine shelf environments, but also with stratotype sequences mainly established in sediments deposited in distal marine environments where spores are often rare and badly preserved.

There is some support from the chitinozoan data for the changing regional differences in the spore data outlined above. Though the nature of sampling for chitinozoans (see below) makes any direct comparisons difficult. However, there does appear to be an increasing similarity between chitinozoan assemblages of northwest Spain and North America/Europe in the upper/later parts of all four sections studied. Due to a lack of data it is not possible to determine if there is a corresponding 'dissimilarity' with Gondwanan assemblages. Paris *et al.* (1995) noted similarities between chitinozoan assemblages in northern Spain and Gondwana and dissimilarity with coeval assemblages in Baltica during the Llandovery. This evidence was used to support the existence of a wide mid-European Rheic Ocean during the Llandovery.

Such temperal changes in our assemblages, i.e. a greater similarity with Gondwanan spore floras in the Lower Silurian, and increasing similarity with Baltic/Avalonian assemblages in the Upper Silurian/Lower Devonian, would be consistent with a drift of northwest Spain away from Gondwana and towards Laurentia/Avalonia through this period.

CHITINOZOA

General distribution

In sections where the Formigoso Formation is represented (Argovejo and La Vid) chitinozoans belonging to the genera *Cyathochitina* and *Conochitina* are common. The lower parts of the San Pedro Formation often contain *Angochitina* and *Sphaerochitina* with species belonging to *Plectochitina* (e.g. *Plectochitina caminae* Cramer & Diez 1978a, figs 8q, 8r and *Plectochitina rosendae* Cramer & Diez 1978a, fig. 8p) and heavily ornamented species such as *Ancyrochitina javieri* Schweineberg 1987 (figs 8f, g) becoming more common in the central parts of the formation. Certain species such as *Calpichitina velata* Wrona (1980: figs 6i, j) and *Margachitina catineria* Obut (1973: fig. 6r) occur in 'blooms' at certain horizons, for example *C. velata* at La Vid (LV6) and *M. catenaria* (Pl. 11, fig. 13) at Geras (Ger16, 17 and 18). In addition, the chitinozoans *Vinnalochitina horrentis* (Wrona, 1980), *Cingulochitina ervensis* (Paris, 1979) and *Cingulochitina serrata* (Taugourdeau & de Jekhowsky, 1960) form common components of assemblages in the San Pedro Formation (see Pl. 11, figs 8, 11a, 11b and Pl. 12, fig. 9 respectively).

Geras (Fig. 10)

Unlike the other three sections, no Llandovery chitinozoans were recovered. *Sphaerochitina sphaerocephala* (Eisenack 1932) and *Angochitina echinata* Eisenack 1932 (Pl. 12, figs 6 and 10 respectively) were used as accompanying species in the Global Chitinozoan Biozonation of Verniers *et al.* (1995). Their presence in Ger 2b, 1.5 metres above the base of the section, suggests a mid-Gorstian to Lower Přídolí age for the lower part of the San Pedro Formation at Geras. Greater resolution is provided by *Ramochitina villosa* (Laufeld, 1974) (recovered from sample Ger 2a, 2.4 metres above the base of the section and Ger 2b; Pl. 13, fig. 7) which has been reported from the top of the Lower Leintwardine Formation and the Upper Whitcliffe Formation of the type Ludlow, UK (Sutherland 1994: 65) and from strata of similar Upper Ludfordian age on Gotland (Hamra and Sundre Beds, Laufeld, 1974: 96) and Estonia (Kuressaare Regional Stage, Nestor, 1990: 85). *Ancyrochitina valladolitana* Schweineberg 1987 (figs 8d, e) was recovered from Ger 4, 10 m above the base of the section within the San Pedro Formation. This species was described from the Palencia region of Northern Spain by Schweineberg (1987) and assigned to graptolite biozones 34/35 (Gorstian) of Elles & Wood (1901–18). However, it was noted that the chitinozoan species probably ranges into the Přídolí (Schweineberg 1987: 77).

Ancyrochitina javieri Schweineberg (1987: figs 8f, g) has also been recovered from Ger 4. This species was described as occurring between graptolite biozones 32 to 35 (late Homerian-Lower Gorstian) of Elles & Wood (1901–18) in the Palencia Region of Northern Spain

PLATE 1

Figs 1, 2 *Artemopyra*? sp. A. **1,** BM 137698, oblique compression showing radial folds on the proximal and distal surfaces adjacent to the curvatural ridge, × 2000, stub Ger92/9/1; **2,** BM 130612, specimen with more delicate muri than that in Fig. 1, oblique compression, × 2000, sample Ger92/8.

Fig. 3 *Chelinohilates* sp. BM 137155, dyad showing distal and subequatorial muri, sample Geras 92/9/1.

Fig. 4 *Cymbohilates* cf. *allenii* var. *magnus* Richardson 1996. BM 115329, proximal view showing remnants of hilum, sample Arg92/14.

Fig. 5 *Hispanaediscus* cf. *lamontii* Wellman 1993. BM 135296, proximal view, × 2000, sample Ger92/2B/2.

Fig. 6 *Cymbohilates* cf. *horridus* Richardson 1996. BM 130858, sample LV92/13; **6a,** proximal view; **6b,** detail of spines; × 2500.

Fig. 7 *Hispanaediscus lamontii* Wellman 1993. BM 137471, dyad, sample Arg13/D1.

Fig. 8 *Tetraletes variabilis* Cramer 1966a. BM 137848, tetragonal (cruciform) tetrad, sample Ger92/6.

Fig. 9 *Velatitetras rugulata*? Burgess 1991. BM 465, LV92/6; **9a**, tetrad, lines of attachment probably covered by closely adherent envelope; **9b**, detail of geniculate disjointed muri, × 2000.

Fig. 10 *Tetraletes medinensis* (Strother & Traverse) emend. Wellman & Richardson 1993. BM 130623, showing lines of attachment and microgranulate distal surfaces, sample Ger92/8/1.

Fig. 11 *Pachytetras* sp. BM 138111, LV92/8/DD; **11a**, unfused tetrad showing sculpture sloughing off revealing lines of attachment; **11b,** BM 138113, detail of microverrucate-murornate sculpture, × 5000.

Fig. 12 *Tetraletes variabilis*? Cramer 1966a. BM 132691, LV92/10; **12a**, BM 132691; **12b**, detail of microverrucate sculpture, × 2000.

All are Scanning Electron Photomicrographs at × 1000 unless otherwise stated; BM numbers refer to photographic negatives in the archives of the Natural History Museum, London.

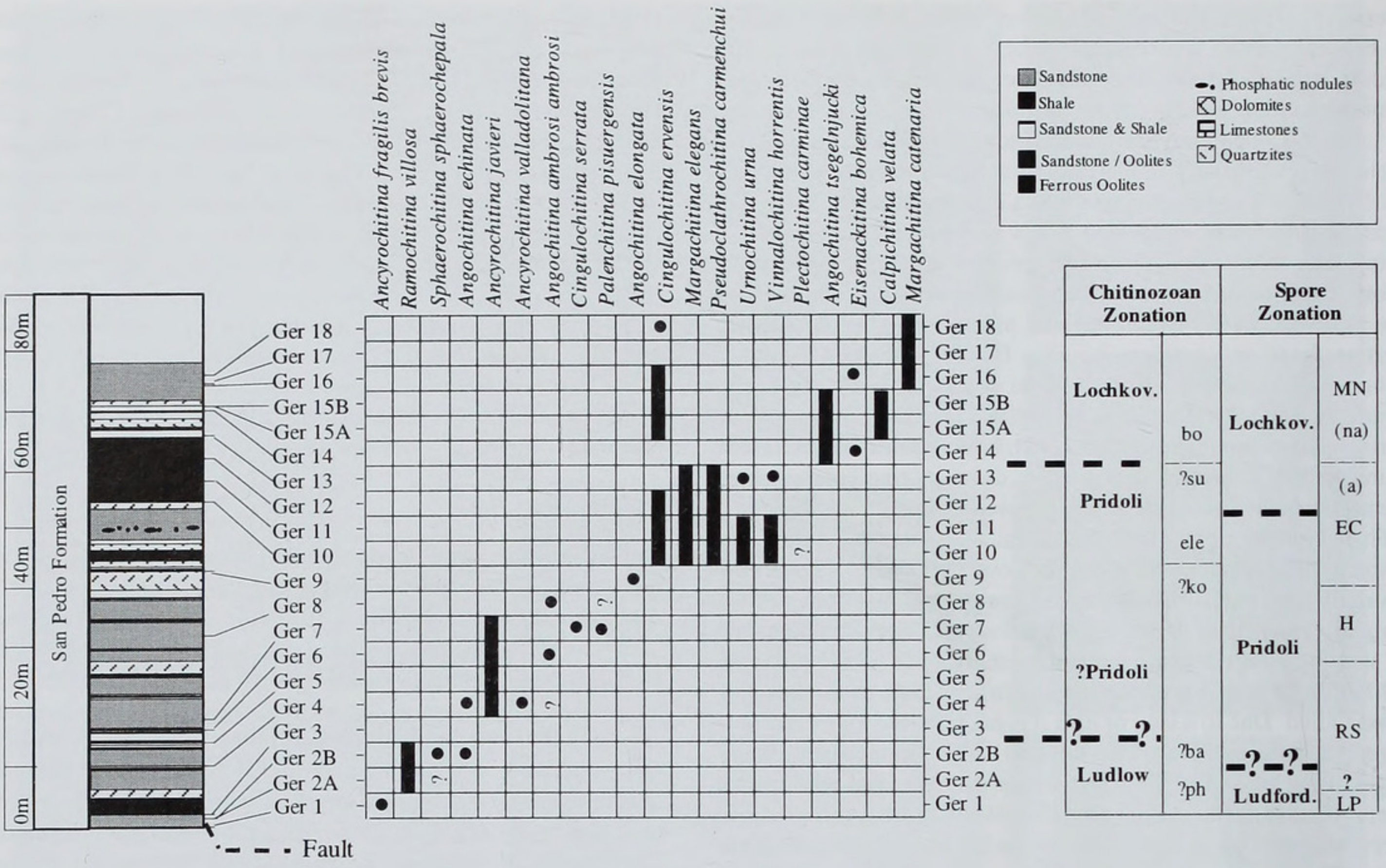


Fig. 10 Selected chitinozoan distribution at Geras. Chitinozoan zonation after Verniers *et al.* (1995): **bo**: bohemica, **su**: superba, **ele**: elegans, **ko**: kosovensis, **ba**: barrandei, **ph**: philipi.

(Schweineberg, 1987: 70). A similar species, *Ancyrochitina* sp. A, was described by Paris from the Formation du Val in the section at Heuzé, Brittany (Paris, 1981) and is associated with *Pterochitina perivelata* Eisenack (1937), a chitinozoan with a well established range from the Upper Ludfordian to the Upper Přídolí (*barrandei* Biozone to early part of the *superba* biozone of Verniers *et al.* (1995). The presence of *Angochitina elongata* Eisenack (1931, figs 8h, i) in sample Ger 9 may be the result of reworking.

Urnochitina urna (Eisenack, 1934) is a very useful Přídolí marker in the stratotype area (Barandian region, Central Bohemia). *U. urna* occurs very close to (within 50 cm) or at the base of the Přídolí (although some atypical specimens do occur a few centimetres below the first occurrence of *Monograptus parultimus* (Kríz *et al.*, 1986). *U. urna* is recovered from the Geras section at Ger 10, 55 metres above the base of the section in the San Pedro Formation. In addition to *U. urna, Pseudoclathrochitina carmenchui* Cramer (1964b) and *Margachitina elegans* (Taugourdeau & de Jekhowsky, 1960: pl. 7, figs 92, 93) also occur in Ger 10. Both species are important markers for the mid-Přídolí *elegans* Biozone of Verniers *et al.* 1995.

In Bohemia, *Eisenackitina bohemica* (Eisenack, 1934) occurs 50cm above the base of the Devonian at Klonk, the Silurian/Devonian boundary stratotype, and Karlstejn (Paris *et al.*, 1981). At Geras, *E. bohemica* is recovered from Ger 14, 70 metres above the base of the section in the San Pedro Formation (Pl. 11, fig. 14). It is found associated with *Angochitina tsegelnjucki* Paris & Grahn (1996, fig. 7r) (Pl. 12, fig. 8). In Podolia this species is reported from the upper part of the Mitkov Formation which, on the basis of its association with *E. bohemica* and *Margachitina catenaria* Obut (1973), was assigned to the Lochkovian by Paris & Grahn (1996).

In the highest part of the section, between 74 and 76 m above the base (samples Ger 16, 17 & 18), significant numbers of a species resembling *M. catenaria* of Lochkovian age occur consistently (see p. 134). However, only a tentative assignment is made here to the Cantabrian forms as no individuals were recovered that demonstrated a convincing peduncle.

Stage and Series Boundaries

On the basis of chitinozoans the Silurian/Devonian boundary would be placed below the first occurrence of *E. bohemica* at Ger 14. The Ludlow/Přídolí boundary is less easy to define but will occur somewhere between the first occurrence of typical Přídolí chitinozoans (*U. urna, P. carmenchui* and *M. elegans*) in Ger 10 but above the last occurrence of *R. villosa* in Ger 2b.

Argovejo (Fig. 11)

An Upper Llandovery age for the Formigoso Formation at Argovejo (Argovejo 1–3; 21–10.5 metres below the base of the San Pedro Formation) is suggested by the presence of *Cyathochitina* sp. B Paris (1981: pl. 11, fig. 11) (Pl. 11, fig. 12). This species is reported from Upper Llandovery strata in the Massif Armorican by Paris (1981: 299). The discovery of the Llandovery chitinozoan *Cyathochitina elenitae* Cramer (1964b) in sample Arg 3 (Pl. 11, fig. 6) supports this age assignment. The latter species (Pl. 11, fig. 5) was also recovered with another Llandovery chitinozoan, *Conochitina alagarda* Cramer 1967 in Arg 4 (Pl. 11, fig. 2). However, as both of these species are found associated with spores from the **RS** Biozone (late Ludfordian-Lower Přídolí) they may represent reworking.

Ancyrochitina libyensis Jaglin (1986) was recovered from Arg 4,

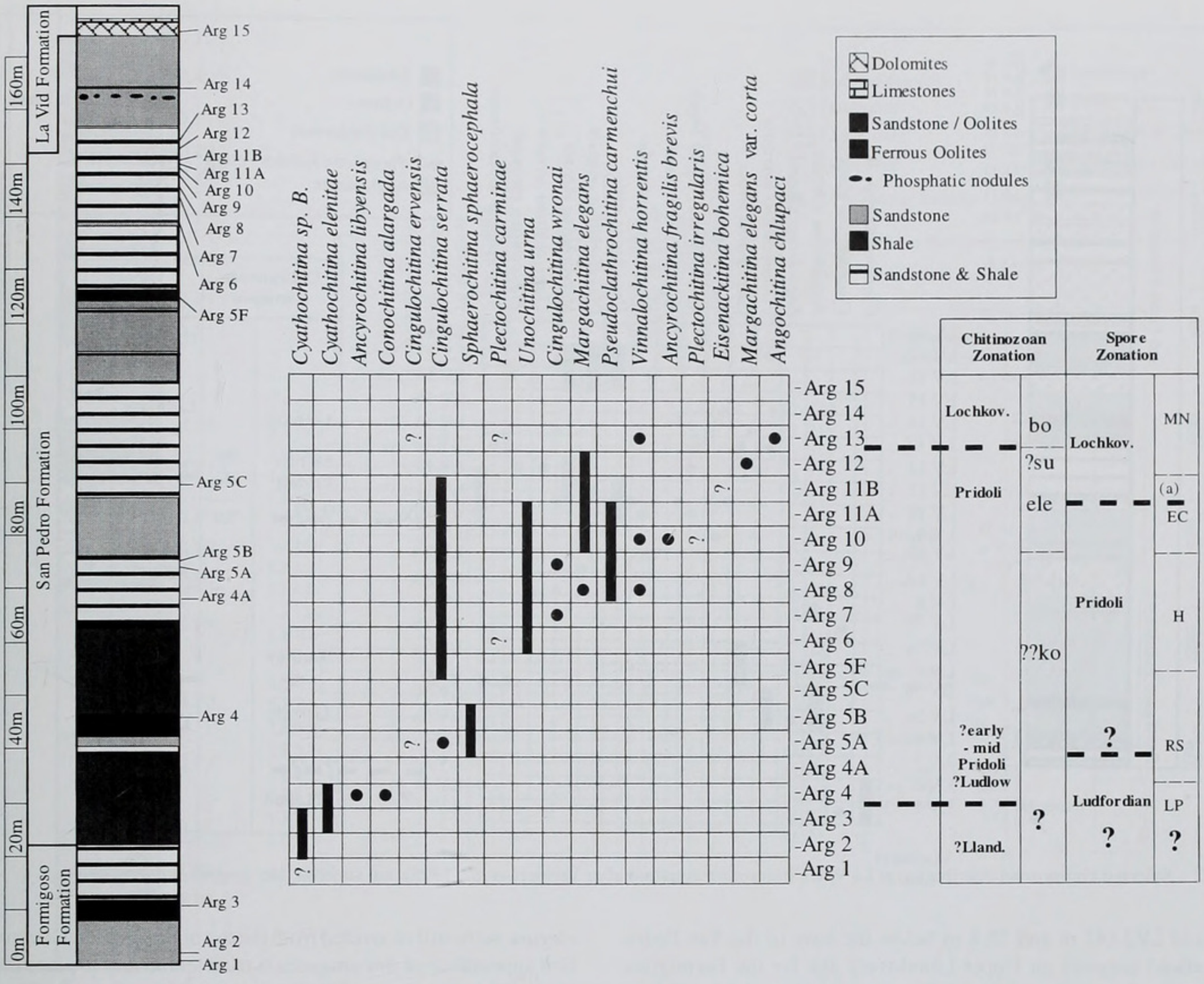


Fig. 11 Selected chitinozoan distribution at Argovejo. Chitinozoan zonation after Verniers *et al.* (1995): **bo**: bohemica, **su**: superba, **ele**: elegans, **ko**: kosovensis.

20 metres above the base of the San Pedro Formation (Pl. 13, fig. 6). Although *A. libyensis* was originally described by Jaglin (1986: 51) as a Přídolí species, Schweineberg (1987: 71) has subsequently recovered the same species from Ludlow strata of the Palencia Region of Northern Spain (Graptolite Biozones 34, 35 of Elles & Wood (1901–18), Upper Gorstian). *Sphaerochitina sphaerocephala* ((Pl. 12, fig. 6) common in the Přídolí but also ranging down into the Upper Ludlow) is recovered from Arg 5a, 52 metres above the base of the San Pedro Formation, but it is not until Arg 8, 123.5 metres above the base of the San Pedro Formation, that a typical Přídolí assemblage is encountered. Species such as *M. elegans* (associated with *Margachitina elegans* var. *corta* Cramer (1964b) in Arg 12 – Pl. 12, fig. 3), *U. urna* and *P. carmenchui* (Pl. 12, fig. 1) are common components of the assemblage. *Cingulochitina wronai* Paris & Kríz (1984) is often reported as forming an important component of Přídolí assemblages. It is recorded (Pl. 11, fig. 9) in Arg 7, 121.5m above the base of the San Pedro Formation. However, the species is also reported from the Upper Ludlow (Paris in Kríz *et al.*, 1986), Paris & Grahn (1996) and Schweineberg (1987).

Possible *E. bohemica* was recorded from Arg 11b, 128.1 metres above the base of the San Pedro Formation but a more reliable Devonian signature is provided by *Angochitina chlupaci* Paris *et. al* (1981) in Arg 13, 132.1 metres above the base of the San Pedro Formation (Pl. 12, fig. 13). In Bohemia this species occurs within 50 cm of the base of the Lochkovian at Klonk and Karlstejn (Paris *et al.*, 1981).

Stage and Series boundaries

The base of the Devonian is drawn below Arg 13. The base of the Přídolí is more difficult to identify but lies between Arg 4 and Arg 7 with the first occurrence of typical Přídolí chitinozoans such as *U. urna*. The base of the Ludlow will lie somewhere below the first occurrence of *S. sphaerocephala* in Arg 5a. This leaves around 57 metres of section between possible Upper Ludlow/Lower-Middle Přídolí as suggested by the recovery of *S. sphaerocephala* and the Upper Llandovery chitinozoans recovered from the Formigoso Formation in Arg 3. There are four possible explanations: 1, the Wenlock and Ludlow are very condensed in the lower part of the San Pedro Formation; 2, there is a large disconformity somewhere above Arg 3; 3, the Wenlock/Ludlow have been tectonically reduced; 4, the Llandovery chitinozoans present in the Formigoso Formation are reworked.

La Vid (Fig. 12)

Like Argovejo, the presence of *Cyathochitina* sp. B, Paris (1981) in

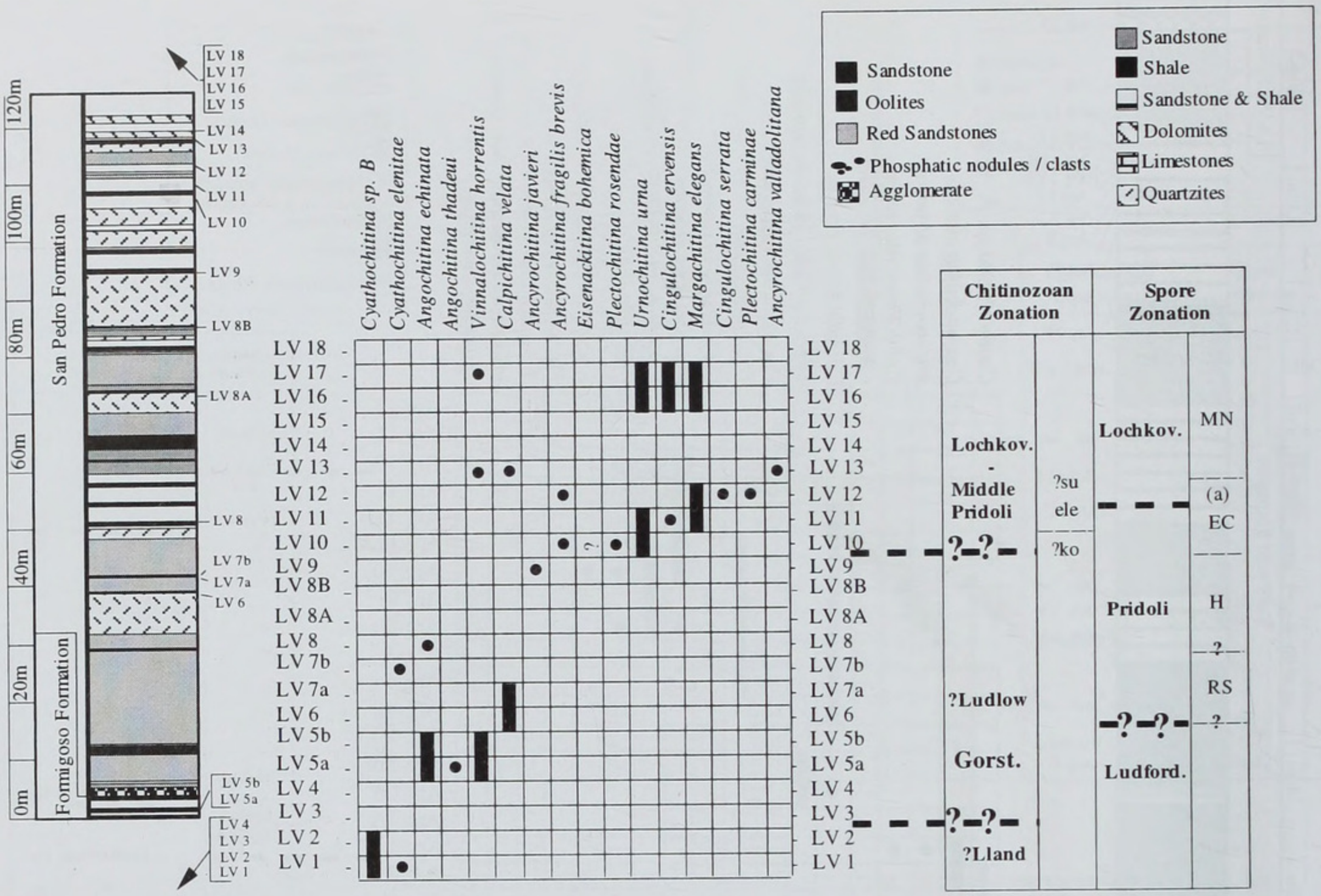


Fig. 12 Selected chitinozoan distribution at La Vid. Chitinozoan zonation after Verniers *et al.* (1995): **su**: superba, **ele**: elegans, **ko**: kosovensis.

LV1 and LV2 (42 m and 38.8 m below the base of the San Pedro Formation) suggests an Upper Llandovery age for the Formigoso Formation. *Angochitina echinata* Eisenack (1931) and *Angochitina thadeui* Paris (1981) (Pl. 12, fig. 11) were recovered from LV 5a. The latter has been reported from strata assigned to Graptolite Biozones 32 and 33 (Homerian to Lower Gorstian) of Elles & Wood (1901–18) by Schweineberg (1987: 59). A Llandovery age is also supported by the presence of *C. elenitae* in LV1. The recovery of this species (39 metres above the base of the San Pedro Formation at the level of sample LV 7b) is probably the result of reworking. *A. echinata* is a common species in the Middle Gorstian to Lower Přídolí (Verniers *et al.* 1995).

Typical Přídolí chitinozoans (e.g. *Urnochitina urna* – Pl. 12, fig. 4), associated with *Plectochitina* (Pl. 13, fig. 8), are not recovered until LV 10, 102.2 metres above the base of the San Pedro Formation. *Margachitina elegans* (Pl. 12, fig. 5), used as an index species for the mid-Přídolí by Verniers *et al.* (1995), is first encountered in LV11, 107.8 m above the base of the San Pedro Formation. *Ancyrochitina fragilis brevis* Taugourdeau & de Jekhowsky (1960) was recovered from LV10 (Pl. 13, fig. 5). This species was regarded as a 'late Ludlow' species by Cramer & Diez (1978a). Samples LV 10, 11, and 12 are regarded as lowermost Devonian based on the spores but no chitinozoans were recovered that could be positively identified as Devonian. The spores in sample LV 13, *c.* 1 m above LV 12, are typical of the lower **MN** Biozone (**NA** Subzone) of Lower Lockhovian age.

Stage and Series boundaries

No Devonian chitinozoans were recovered from La Vid and typical Přídolí forms such as *Pseudoclathrochitina carmenchui* and *M. elegans* were still recovered from the top of the section. However, the first appearance of *Aneurospora* is used tentatively to place the base of the Devonian below LV10 (see also Richardson, Rodriguez & Sutherland, 2000). The base of the Přídolí is placed somewhere below LV10 with the first occurrence of *U. urna*. As with Argovejo, the presence of Upper Llandovery chitinozoans in the Formigoso Formation may suggest the presence of a disconformity or the reworking of Lower Silurian faunas. The spacing of some samples, because of unsuitable lithology and poor recovery from others, makes a more precise biostratigraphy difficult at this time.

La Peral (Fig. 13)

Because *Spinachitina* has not been reported above the Llandovery, the presence of *Spinachitina* sp. in LP2 (Pl. 11, fig. 4) 18 meters above the base of the San Pedro Formation may suggest either a pre-Wenlock age for this part of the section or possibly evidence for reworking. *Conochitina rudda* Sutherland (1994), present in LP3, 24.6 metres above the base of section, has been described from the Upper Wenlock/Lower Ludlow of the type area in the Welsh Borderlands (Sutherland, 1994: 48). *Conochitina pachycephala* Eisenack 1964, present in LP3 (Pl. 11, fig. 1), is used as an index species for the mid-Upper Wenlock but also ranges well into the Gorstian (Verniers *et al.* 1995). The presence of *Cyathochitina elenitae* (Pl. 11, fig. 3) in the same sample may be the result of reworking. The recovery of *Angochitina echinata* (Pl. 12, fig. 10) suggests an age of at least Middle Gorstian to Lower Přídolí (Verniers *et al.,* 1995) for LP 8, 77.5 m above the base of section. *A. elongata*, recovered from the same sample, was used as a mid-Ludlow zonal indicator in the biozonation of

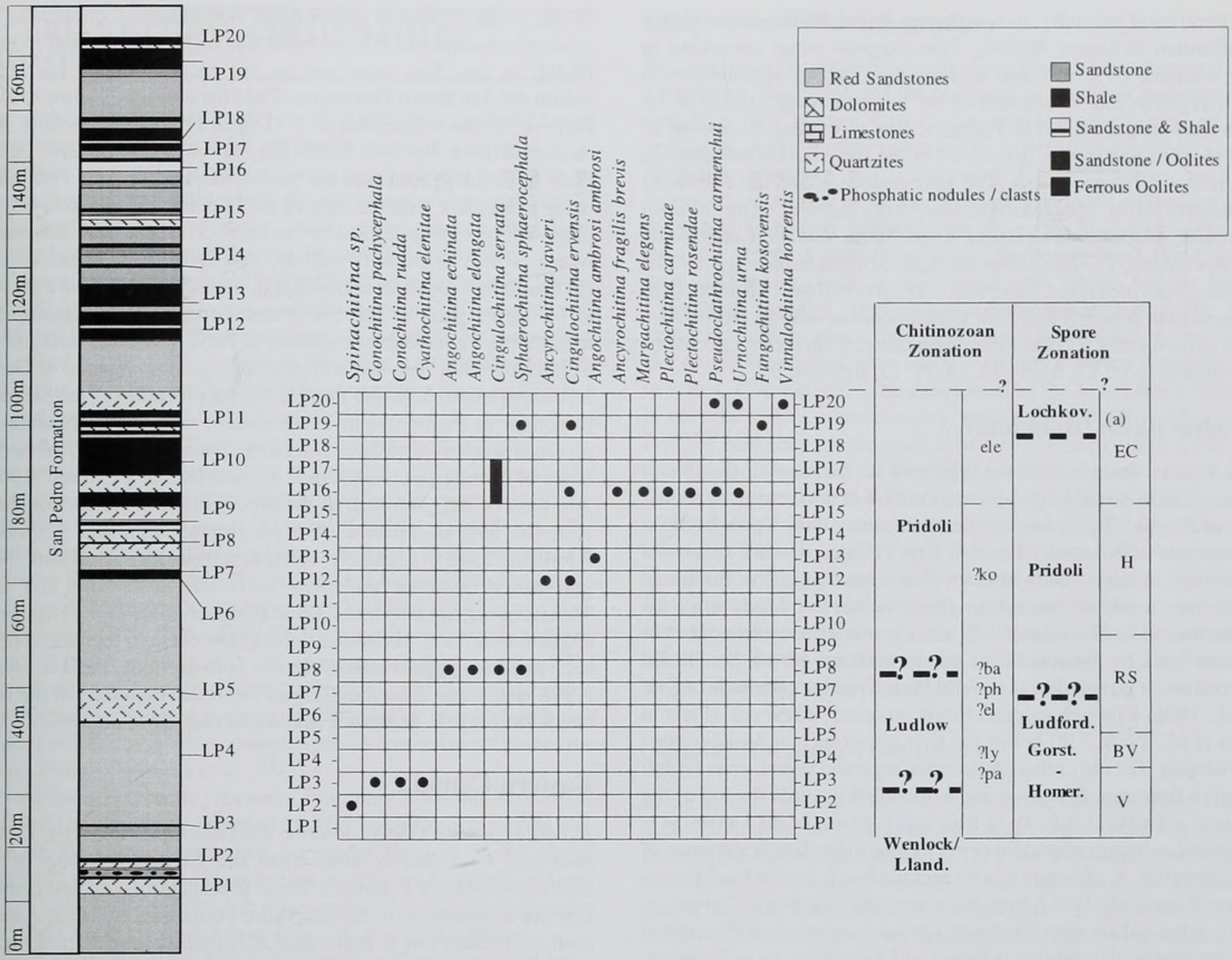


Fig. 13 Selected chitinozoan distribution at La Peral. Chitinozoan zonation after Verniers *et al.* (1995): **ele**: elegans, **ko**: kosovensis, **ba**: barrandei, **ph**: philipi, **el**: elongata, **ly**: lycoperdoides, **pa**: pachycephala.

Verniers *et al.* (1995). Not until LP16, 149.5 metres above base of section, is a Přídolí chitinozoan assemblage containing *U. urna*, *M. elegans* and *P. carmenchui*, recovered. *Fungochitina kosovensis* Paris & Kríz (1984), is found in LP19, 169 meters above the base of the section (Pl. 12, fig. 7) but is more commonly described from the Lower- mid-Přídolí (Paris & Kríz, 1984, Verniers *et al.*, 1995). The uppermost sample LP 20 at La Peral contains *Urnachitina urna* (Pl. 11, fig. 10) associated with *Pseudoclathrochitina carmenchui* (Pl. 12, fig. 2). As with La Vid, chitinozoan evidence for a Přídolí age contradicts the interpretation based on spore data, which places the base of the Lochkovian between LP 18 and 19 from the presence of *Aneurospora* in LP 19.

Stage and Series boundaries

It is not possible to suggest a base for the Devonian on the basis of the chitinozoans recovered from this section. The base of the Přídolí is tentatively placed somewhere below LP 16 (although it must be noted that *A. echinata*, present in LP 8, can also be recovered from the Přídolí). As with La Vid, additional sampling should increase the resolution of chitinozoan biostratigraphy in this section.

COMPARISON OF THE CHITINOZOANS FROM THE CANTABRIAN MOUNTAINS WITH COEVAL SECTIONS AND THE GLOBAL BIOZONATION SCHEME

Direct statistical comparisons are not made here as samples were not prepared specifically for Chitinozoa and the rarest forms may have been overlooked or destroyed. However, it is possible to make general comparisons with coeval sections.

Palencia Province, northern Spain

Palencia is located in the Cantabrian Mountains to the east of our sections in Northern Spain and demonstrates many similarities in chitinozoan assemblages. Schweineberg (1987) noted the presence of *Cyathochitina* spp. in the Las Arroyacas Formation (possibly equivalent to the Formigoso and the lower part of the San Pedro Formations) in Palencia, which he regarded on the basis of graptolites as Wenlock (*lundgreni* Biozone). In our material we find *C. elenitae* in the lower part of the San Pedro Formation. Firstly in the **V** Biozone (Homerian to Lower Gorstian, La Peral) and secondly an occurrence in the **RS** Biozone (Upper Ludfordian to Lower Přídolí). This suggests some reworking in our sections. *U. urna* forms an important part of assemblages in both regions and is considered by Schweineberg (1987) to be restricted to the Přídolí in Palencia. See preceding discussion of our sections and further discussion of the Asturias-León/Palencian chitinozoan ranges below. The two regions share the following Ludlow/Přídolí species: *Ancyrochitina javieri, Angochitina echinata, Angochitina elongata, Angochitina thadeui, Conochitina pachycephala, Cyathochitina elenitae, Margachitina elegans* var. *corta, Ancyrochitina libyensis, Ancyrochitina valladolitana, Angochitina ambrosi ambrosi, Cingulochitina wronai, Palenchitina pisuergensis, Plectochitina carminae;* Cantabrian specimens are figured in Pl. 12, figs 3, 12, 14, Pl. 13, figs 1–4, 9.

Prague Basin (Bohemia)

The Prague Basin is both the type area for the base of the Přídolí (Pozary, 1km east of Reporyje) and the base of the Devonian (Klonk, SW of Prague). The characteristic chitinozoan of the Upper Ludlow, *Eisenackitina barrandei* Paris & Kríz (1984), was not recovered from our sections. Only species that extend into the Přídolí in Bohemia were recovered in the Cantabrian Mountains (*S. sphaerocephala, C. wronai*). *U. urna* is a common component of assemblages in the middle to upper portions of the San Pedro Formation. It is regarded as a useful Přídolí marker (see Paris *in* Kríz *et al.*, 1986) although atypical forms do occur 'a few cm' (Paris in Kríz *et al.*, 1986: 338) below the first occurrence of *Monograptus parultimus*. The only other chitinozoan regarded as an Lower Přídolí form in Bohemia, *F. kosovensis,* is recorded towards the top of the section at La Peral (LP19). In Bohemia the base of the Devonian is regarded as being coincident or very close to the first occurrence of *E. bohemica*. *A. chlupaci* is also regarded as a Lower Lochkovian form (Paris *et al.*, 1981). Both these species occur in the Cantabrian Mountains and are associated with Devonian spores (see description of chitinozoan distribution in Geras and Argovejo). As in Bohemia, *C. velata* (chitinozoan indet. n. gen? in Paris *et al.*, 1981) occurs close to the top of the Silurian in the Cantabrian Mountains (Pl. 11, fig. 7).

The Type Ludlow Sections

Sutherland (1994) described chitinozoans from the type Ludlow in the Welsh Borderlands of the UK. The Lower Ludlow in the type area is characterized by *Conochitina* Eisenack (1931) species and in particular *C. rudda* and *C. pachycephala*. Both these species are recognized in our sections, but only from one sample at La Peral (LP3) in the San Pedro Formation. *Angochitina echinata* is a common component of mid-Ludlow assemblages in the Welsh Borderlands and occurs sporadically through the San Pedro Formation. In the Ludfordian, *R. villosa* is the only species we find in common with the type area where this species is a useful marker for the mid- to upper Ludfordian. Due to poor chitinozoan recovery from the latest Ludlow and Lower Přídolí in the Welsh Borderlands (probably as a result of an increasing fresh water influence) any further comparisons are difficult.

Podolia, Ukraine

A provisional study of Silurian and Devonian sections of this area was detailed in Paris & Grahn (1996). Six assemblages were defined, the age controlled with reference to chitinozoan index taxa in Bohemia (Kríz *et al.*, 1986; Paris *et al.*, 1981). Assemblage 1 from Podolia, characterized by *E. barrandei* was not encountered in our study. Podolian chitinozoan assemblage 2 containing *U. urna, M. elegans* and *F. kosovensis* was regarded as Lower to mid-Přídolí in age. The same species are encountered in our study within the San Pedro Formation. The characteristic chitinozoan of Paris & Grahn's assemblage 3 (Upper Přídolí), *C. velata,* was recovered from the San Pedro Formation at La Vid and Geras. Paris & Grahn (1996) take the base of the Devonian in Podolia as being coincident with the base of the Podolian chitinozoan assemblage 4. The zone is defined by the first occurrence of *E. bohemica*, which is also associated with *M. catenaria*. Both these species (although *M. catenaria* somewhat dubiously in Geras) are present in the upper parts of the San Pedro Formation. *A. tsegulnjucki*, regarded as a characteristic species of Paris & Grahn's assemblage 5 (Lochkovian) coincides with the range of *E. bohemica* in Geras. It is important to note that Paris & Grahn's location of the Silurian/Devonian in Podolia is in disagreement with the assignment of previous workers who have placed the boundary at the first occurrence of *Monograptus uniformis angustidens* (e.g., Koren' 1968). The base of the Devonian at the type section at Klonk coincides with the first occurrence of *Monograptus uniformis uniformis* (Holland, 1985), a closely related subspecies. At Klonk both graptolites occur at the same level but in Podolia the first *Monograptus. u. uniformis* occurs higher than *Monograptus u. angustidens*. As *E. bohemica* occurs very close to the first appearance of *Monograptus u.uniformis* in both sections, Paris & Grahn (1996) elected to draw the Silurian/Devonian boundary at the base of the range of *E. bohemica* and *Monograptus u. uniformis*.

Eastern Canada

Achab & Asselin (1993) describe *Cingulochitina ervensis, C. serrata* and *Urnochitina urna* from the Chaleurs Group in the northeastern Gaspé Peninsula. These species form common components of assemblages in the San Pedro Formation. Achab & Asselin used the presence of *E. bohemica, M. catenaria and A. chlupaci* to define the base of the Devonian in this area of Canada. In the Cantabrian Mountains, the same species are found associated with or at a level above the first occurrence of *Aneurospora*, taken by Richardson, Rodriguez & Sutherland (2000) to represent the base of the Devonian.

North Africa

Taugourdeau & Jekhowsky (1960) published data from core material from the Sahara. It is difficult to compare the material from our area with that of North Africa with any great certainty, due to the relative lack of stratigraphical control and difficulty in positively identifying chitinozoans from the silhouettes presented in the plates of the paper. However, *C. serrata. M. elegans* and *E. bohemica* are recorded by Taugourdeau & Jekhowsky (1960) in a broad zone defined as 'Gothlandian' (approximately equivalent to the Silurian) to Lower/Middle Devonian.

Jaglin (1986) examined core material from the Upper Silurian (mostly Přídolí) of Libya. Jaglin made age determinations based on well-known Přídolí chitinozoans such as *U. urna, P. perivelata, M. elegans* and *P. carmenchui*. Many of the species recorded from the Přídolí by Jaglin (1986) were also encountered in the Cantabrian Mountains. These include: *A. libyensis, V. horrentis, C. serrata, F. kosovensis, R. villosa, M. elegans, P. carminae, P. carmenchui, S. sphaerocephala* and *U. urna*. Of these, only the ranges of *A. libyensis* and *V. horrentis* were detailed by Jaglin, all of which were shown as being present close to the base of the Přídolí in borehole A1–61.

SILURIAN GLOBAL CHITINOZOAN BIOZONATION

The global scheme of Verniers *et al.* (1995) was calibrated with reference to chitinozoan index species in global stratotype sections and other localities, or by reference to graptolite, conodont or trilobite biozonal schemes where this information was not available. To be included in the scheme, index species had to have been recorded from at least two major Silurian palaeocontinents.

Conochitina pachycephala was used as the index species for the Middle-Upper Wenlock *pachycephala* Biozone. This species was recovered in our study from one sample close to the base of section at La Peral (LP3). As *C. pachycephala* ranges well into the Gorstian and because the succeeding Upper Homerian *lycoperdoides* Biozone was not encountered, it is not possible to increase the resolution of this part of the San Pedro Formation with chitinozoan data.

Angochitina elongata was used as the index species for the Middle Ludlow biozone in the global scheme but was only recorded sporadically from La Peral and Geras. At Geras (Ger 9) it is possible that the species is reworked as it is found associated with spores attributed to the lower **EC** Biozone, which is regarded as Upper Přídolí in age. At La Peral, *A. elongata* occurs in sample LP8 and is associated with spores attributed to the Ludlow **RS** Biozone. *A. echinata* is noted as an accompanying species in the *elongata* biozone of the global scheme and was recovered from La Peral, La Vid and questionably from Geras. Although a common component of many Middle and Upper Ludlow chitinozoan assemblages it is known to range into the Lower Přídolí (Verniers *et al.* 1995).

No chitinozoans were recovered from the Cantabrian Mountains that could be directly attributed to the Middle Ludfordian *philipi* Biozone or the Upper Ludfordian *barrandei* Biozone of the global scheme. *S. sphaerocephala*, recovered from Geras, La Peral and Argovejo, is shown to range through the *barrandei* Biozone by Verniers *et al.* (1995), but is also noted as ranging into the Middle Přídolí.

The Lower Přídolí *kosovensis* biozone is well represented in most areas globally by the presence of *U. urna,* which was recovered from all four sections studied. The index species *Fungochitina kosovensis* is recorded from La Peral, but in only one sample (LP 19) at a level well above the base of the following *elegans* Biozone.

The *elegans* Biozone is well represented in our sections by the index species, *Margachitina elegans,* in all sections, often associated with *P. carmenchui* and *U. urna.*

The index taxa for the Upper Přídolí *superba* Biozone (*Anthochitina superba* Eisenack, 1971) has not been recorded in this study, with only the accompanying species *U. urna* encountered. The top of the *superba* Biozone and the base if the first biozone in the Devonian is defined by the first occurrence of *E. bohemica*, regarded as being coincident with the base of the Devonian (Paris, Winchester-Seeto & Grahn, 2000) *E. bohemica* has been identified from Geras in samples Ger 14 and 16.

BIOSTRATIGRAPHICAL CONCLUSIONS

The **vetustus** (**V**) and **brevicosta – verrucatus** (**BV**) Spore Biozones indicate an age no earlier than Homerian. Chitinozoan evidence is sparse but the range of *Conochitina rudda* in sample LP3 includes the Upper Homerian. There is thus a possible disconformity between the **BV** spore assemblage (Upper Homerian) in the La Peral section and the **reticulata – sanpetrensis** (**RS**) assemblage (Ludfordian to Lower Přídolí). The base of the **RS** Biozone is not seen in the sections studied with the possible exception of La Peral.

Ludfordian/Přídolí boundary

Because of differences in chitinozoan assemblages between the Cantabrian Mountains and the type area in Bohemia, and possibly sampling deficiencies due to the coarseness of some of the sediments, it is currently not possible to define this boundary with precision. However, the occurrence of several forms, such as *Ramochitina villosa* at Geras, indicate a Upper Ludfordian age, consistent with spore evidence that places the boundary in the **RS** Biozone. Spore assemblages from the Welsh Borderland show many species in common with those from Spain, but the lower Cantabrian samples (Formigoso and the lower part of the San Pedro Formation) often yield poor results and the key forms from the Anglo-Welsh area are usually missing or have a sporadic distribution. Consequently, the exact level of the lower **RS** boundary is uncertain. The approximately equivalent **LP/TS** (Ludfordian/ Přídolí) boundary in the type area has not been located but the spore assemblages below the **RS** Biozone have some comparable features to the lower **LP** Biozone (mid- Gorstian to Ludfordian) and spores similar to the nominal species of the *Chelinospora obscura* Sub-Biozone (mid-Gorstian) and the overlying *cambrensis* and *inframurinatus* Sub-Biozones occur in the **RS** Biozone. Few other independently dated sections have been studied palynologically across the Ludfordian/Přídolí boundary elsewhere, so the location of the lower boundary of the Přídolí Stage must remain provisional.

Silurian/Devonian boundary

In the Silurian/Devonian boundary stratotype (Klonk section, Bohemia), *Eisenackitina bohemica* and *Angochitina chlupaci* appear close to the base of the Devonian. They are also found in the Geras and Argovejo sections respectively, where the base of the Devonian (based on spore data – Richardson, Rodriguez & Sutherland, 2000) is also a little lower than the appearance of these two chitinozoan species, and close to the base of the *Aneurospora* spp. Sub-Biozone. This latter assemblage is found in three of the four Cantabrian sections studied, and occurs also in the Anglo-Welsh area above the thelodont *Turinia pagei* at a level 30 m below the base of the **MN** Biozone. The **MN** Biozone occurs near the base of the Gedinnian in Belgium and above the basal Devonian graptolites in Podolia (Ukraine). Consequently, although further work needs to be done on sections (e.g. Podolia) containing spores, chitinozoa, and key macrofossils, the *Aneurospora* spp. Sub-Biozone has potential for inter-regional correlation, and its base, on current evidence, including chitinozoan work in this paper, is near, if not coincident with, the Silurian/Devonian Boundary.

Radiometric dates and Přídolí basal Devonian timescales

Recently construed radiometric dates (Tucker *et al.,* 1998) give ages for the Upper Ludfordian (Whitcliffe) and basal Devonian (Lochkovian) as 420 ± 4 Ma and 417.6 ± 1 Ma respectively. This leaves a minimum of 2.4 Ma for the duration of the Přídolí. Our researches on sequences from the Cantabrian Mountains indicate one spore zone in this interval with parts of two others. Previously, Richardson *et al.* (1984) estimated duration of *c.* 3 Ma for each spore zone. Using roughly 1 2/3 zones this would give a figure of approximately 5 Ma for the duration of the Přídolí Stage. This seems more realistic for the biological changes involved. The maximum interval (7.4 Ma) indicated by the radiometric dates would allow for at least 2.5 biozones of average duration.

MATERIALS AND METHODS

Type and figured palynomorphs for this paper are housed in the Palynology Laboratory, Department of Palaeontology, The Natural History Museum, London. Figured specimens have either FM numbers (spores) or FC numbers (chitinozoa). Spores are located on slides, while for SEM images the number refers to the relevant stub. Letters and numbers (eg. LV 92/17 (DE) 3, 179 0914) refer to section, year of collection, sample, (maceration), slide number and lastly the specimen location co-ordinates taken on a Zeiss Photomicroscope III (n. 2562) housed in the Palynology Section of the Palaeontology Department. E.F. numbers are the England Finder co-ordinates (e.g. J33/1) of the specimen location. BM numbers refer to SEM photographic negatives held in the archives of The Natural History Museum, London. SEM stubs and strew, or picked specimens, were coated with gold palladium. Spores were studied on Hitachi S800 and Phillips XL 30 field emission SEM's and, in addition, some chitinozoans were studied on a Hitachi S2500. Mounting methods for the chitinozoa are as described by Sutherland (1994); spores are strewn, mainly on mica, secured to the stub with araldite S2. Numbering of chitinozoan specimens follows the same pattern as described for the spores, eg. sample number ARG11A, slide number 508/12, stub box reference SB4/45, England Finder reference (Q27/4).

The light photomicrographs were taken on a Zeiss photomicroscope using Normarski differential interference with × 60 or × 100 objectives and a plate camera and were all taken by Mr. Peter York of the Natural History Museum.

Sporomorphs and chitinozoa were extracted from rock samples using standard palynological methods. Because of the high maturation of much of the material schultze's solution was usually used but light microscope and SEM studies revealed that even very fine sculptural detail was preserved, comparable with that seen in English Lower Devonian material with low maturation (Richardson, 1996b). Residues were strewn on slides and dried and covered with either elvacite or epoxy resin.

A duplicate set of samples is preserved in the Mining and Engineering Department, University of León.

TAXONOMY OF SELECTED SPORE TAXA

Anteturma **SPORITES** H. Potonié 1893
Turma **TRILETES** (Reinsch 1881) Potonié & Kremp 1954
Subturma **AZONOTRILETES** Luber 1935
Genus ***RETUSOTRILETES*** (Naumova) Richardson 1965

TYPE SPECIES. *Retusotriletes pychovii* Naumova 1953 (lectotype species of Richardson 1965).

REMARKS. The great variability of smooth taxa is illustrated by Rodríguez (1983). Two genera in particular show a great deal of variation. The genus *Archaicusporites* has a thin proximal face with an apical triangular thickening, but otherwise is similar in structure to the genus *Archaeozonotriletes*. There is also a complex of retusoid spores and, in particular, the spores placed in the species *R. coronadus* Rodríguez 1983 include laevigate forms, and forms with apiculate sculpture which herein are placed in two genera.

Retusotriletes bipellis Rodriguez, 1978 Pl. 2, fig. 1

Rodriguez, 1978c: pl. 3, fig. 2; San Pedro Formation, Torrestio, Province of León, Cantabrian Mountains, northwest Spain.

DIMENSIONS. Rodriguez 1978c, 40–70 µm; present study 30–48 µm (based on 10 specimens).

REMARKS. These miospores have a thin proximal exine and may grade into species of *Archaicusporites*.

OCCURRENCE. Found in all sections, occurring from the **EC** Biozone to the **NA** Sub-Biozone (**MN** Biozone), Upper Přídolí and Lower Lochkovian.

Retusotriletes coronadus (Rodriguez, 1983) emend

1978 *Retusotriletes communis* Naumova; Rodriguez: pl. 4, fig. 12.
1983 *Retusotriletes coronadus* Rodriguez (pars): pl. 9, figs 1, 10? (non pl. 8, figs 1, 8).

DIAGNOSIS. Trilete retusoid azonate spores with relatively thin contact areas and a thickened proximal triangle surrounding a thin apical area.

COMPARISONS. *Archaicusporites asturicus* and *A. torrestionensis* (Rodriguez, 1983) (Pl. 10, fig. 8) are similar but have thicker equatorial and distal walls.

REMARKS. Spores originally placed in this taxon show considerable morphological diversity. The figure of the holotype (Rodriguez, 1983: pl. 9, fig. 1) is different from the other specimens illustrating the original description, and appears to have a dark triangle on the proximal surface similar to *Archaicusporites asturicus* (Rodriguez, 1983: pl. 7, fig. 3). The epithet *R. coronadus* is retained pending re-examination of the holotype. Other spores belong to two separate morphologies, the first (Form 1) with a highly distinctive double curvaturate structure (Rodriguez, 1983: pl. 8, fig. 1), the second

PLATE 2

Fig. 1 *Retusotriletes bipellis* Rodriguez 1978c, FM 1496. **1a,** shows Y-mark and folded proximal membrane; **1b,** double ridged curvaturae and laevigate distal exine, Ger92/15a, (469) 3, 213 0959.

Figs 2, 3 *Retusotriletes? saturnus* sp. nov. **2a,** FM 1498, proximal view shows distinct triangular area at the spore apex; **2b,** shows concentric curvatural thickenings, LV92/17 (D3) 3, 152 0928; **3,** FM 1497, proximal view showing trilete folds, LV92/17 (D3) 3, 179 0914.

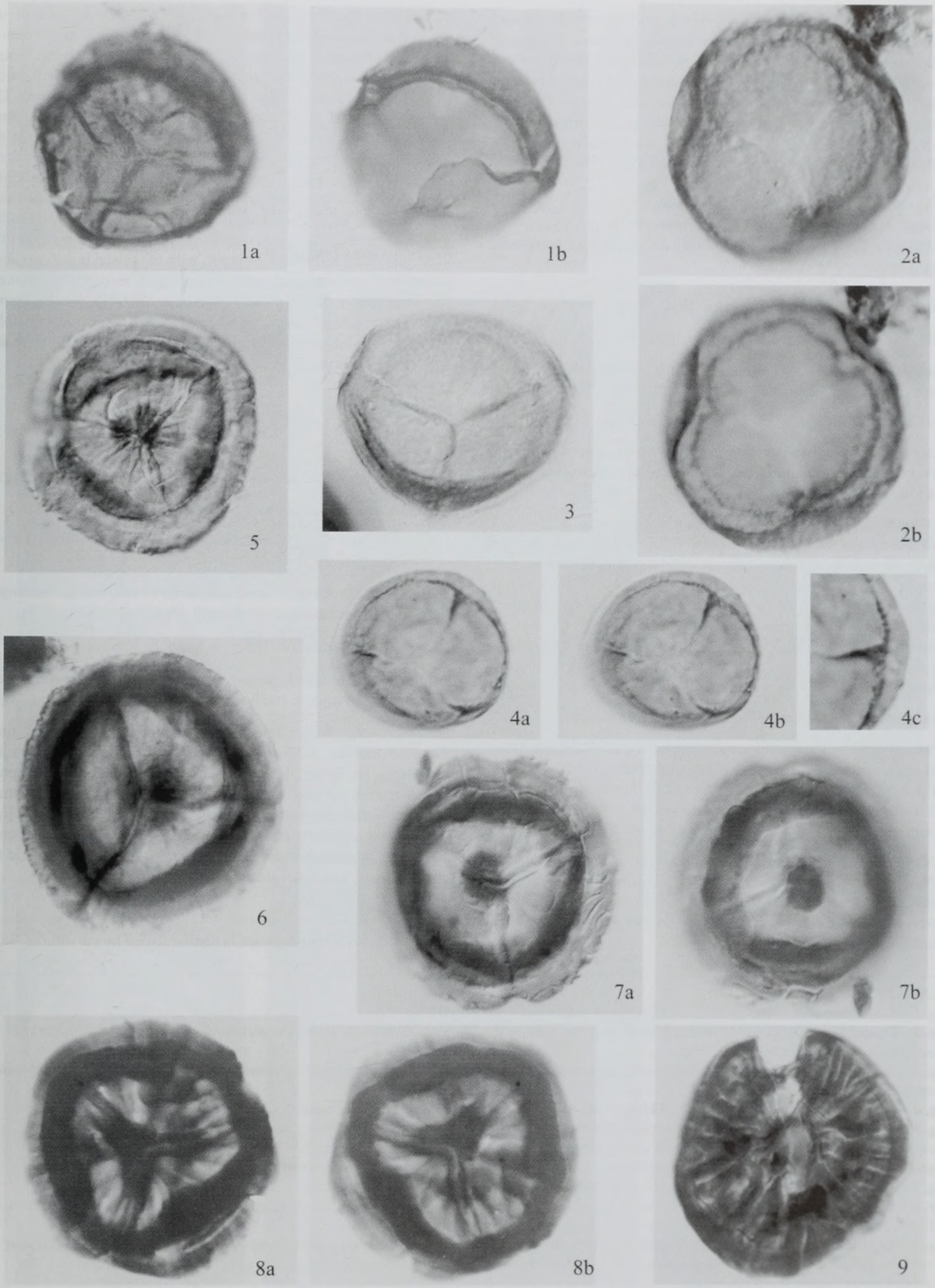
Fig. 4 *Apiculiretusispora arcidecus* sp. nov. FM 1499. **4a, 4b,** proximal view, showing grana and microconi forming the curvaturae perfectae; **4c**, detail of curvaturae at radial apex, × 1,500, LV92/13 (D3) 1, 066 0952.

Figs 5–7 *Breconisporites*? spp. **5,** FM 1500, proximal view with an equatorial crassitude, arcuate zones of thickening, thinnest in the radial areas surrounding a thin apical triangular area with radial folds, and a distal polar thickening, Arg92/14 (468) 11, 138 0893; **6,** FM 1501, similar specimen with distinctly granulate equator, LV92/13 (495) 2, 195 0960; **7a, b,** FM 1502; **7a** proximal view; **7b** distal focus showing annulus and polar thickening, slide Arg92/14 (468) 11, 083 1072.

Fig. 8 *Emphanisporites splendens* Richardson & Ioannides 1979. **8a, 8b** FM 1503, showing radial ribs, distinct annulus and large inter-radial thickenings, Ger92/2B (477) 2, 165 0961.

Fig. 9 *Emphanisporites* sp. FM 1504, Ger92/2B (477) 2, 166 0898.

All figs × 1000, unless stated otherwise.


1a
1b
2a
5
3
2b
4a
4b
4c
6
7a
7b
8a
8b
9

(Form 2) with curvaturae formed from bands of sculpture (Rodríguez, 1983: pl. 8, fig. 8). In England the spores with arcuate lines of sculpture (curvaturae) show a morphological sequence of increasing complexity through the Přídolí and into the Lochkovian. The same trend to a lesser extent is seen in spore assemblages from the Cantabrian Mountains. Two azonate species are illustrated in Rodriguez (1983). Form 3 is zonate and new but the curvaturate sculptural pattern is similar to that seen in Form 2. The three forms are referred to in the text as follows.

Form 1: *Retusotriletes*? *saturnus* sp. nov.

Form 2: *Apiculiretusispora arcidecus* sp. nov.

Form 3: *Breconisporites*? spp. (cf. *Retusotriletes coronadus* Rodriguez).

Retusotriletes*? *saturnus sp. nov. Pl. 2, figs 2, 3; Pl. 3, fig. 1

1983 *Retusotriletes coronadus* Rodriguez: 46: pl. 8, fig. 1 only.

Derivation of name. Latin m. Saturnus, Saturn, referring to the concentric rings, i.e. double curvaturae surrounding the spore.

Holotype. Rodriguez, 1983: figs 3, 43, pl. 8, fig. 1.

Diagnosis. Distally laevigate retusoid trilete spores with two curvaturate bands; the inner band forms a raised wedge-shaped band and joins with the trilete folds.

Description. Amb +/– circular, hemispherical in lateral view with more flattened proximal surface. Exine distally laevigate and proximally microrugulate to scabrate; rugulae often more pronounced between the two curvaturate bands, inner band *c.* 5/8 spore radius, slightly invaginated at the radial apices, outer band +/– equals spore radius, although often markedly invaginated radially. Curvaturate bands distinct, equatorial margin of inner curvaturae minutely irregular, outer curvaturate band with smoother margin, forming a distinct narrow extension, trilete rays with slightly sinuous low lips.

Dimensions. 30–49µm (16 specimens measured).

Comparisons. The double curvaturate band and distinctive proximal microsculpture distinguish these spores from other species of the genera *Retusotriletes* and *Scylaspora*. *R. bipellis* does not have the scalloped inner 'curvaturae' and the proximal surface appears to be smooth. The type material was not available for comparison.

Occurrence. Upper San Pedro Formation, upper **EC** and lower **MN** Sub-Biozones, Argovejo; upper **EC** (*Aneurospora* Sub-Biozone) Geras; uppermost **EC** (*Aneurospora* Sub-Biozone), La Peral; and lower **MN** Sub-Biozone La Vid; uppermost Přídolí and Lower Lochkovian.

Remarks. *Retusotriletes*? *saturnus* sp. nov. forms part of the original *R. 'coronadus'* complex of Rodriguez (1983) and occurs in the highest Přídolí and Lower Lochkovian in the Cantabrian Mountains. So far this species has not been found in the Anglo-Welsh area, where few sections of this interval have produced spores. The proximal surface of *R. saturnus* is quite distinctive. The inner curvaturae form a wedge-shaped thickening and invaginate at the contact with the often indistinct trilete folds. The proximal surface is scabrate to microrugulate (under SEM), a feature that is specially marked between the inner and outer curvaturate zones. The outer curvaturae are coincident with the equator except in the inter-radial areas and the distal surface is smooth. In equatorial view, under the SEM, the spore resembles a limpet, with the raised inner curvatura resembling a mantle, and the outer curvatura resembling the shell. The structure of *R. 'coronadus'* however, with its wedge-shaped inner curvatural band, revealed by SEM studies, is distinct both from the species holotype figured by Rodriguez (1983: pl. 9, fig.1) and from *A. archidecus.*

Genus ***APICULIRETUSISPORA*** Streel, 1964

Apiculiretusispora arcidecus sp.nov Pl. 2, fig. 4

Basionym. *Retusotriletes coronadus* Rodriguez, 1983 (*pars*) .

1983 *Retusotriletes coronadus* Rodriguez (*pars*); Rodriguez: 46, pl. 8, fig. 8.

Derivation of name. Latin *arc*, arch or arc, *decus*, ornament; referring to the curvatural sculptured zones.

Holotype. Rodriguez, 1983: pl. 8, fig. 8.

Diagnosis. Retusoid spores with scupture of grana and coni confined to the curvaturae and borders of the trilete mark.

Description. Amb circular to sub circular, trilete mark distinct, laesurae labrate, 4/5ths radius, sculptural elements form the curvaturae perfectae, may connect with broad bands of sculpture which border the lips, and can also occur on the lips. Sculptural elements variable from barely discernible to distinct under the light microscope; elements consist of micrograna, microconi and coni, >1–1.5µm high and wide. Proximal equatorial areas, outside the contact areas, and distal surface laevigate.

Dimensions. 28–43 µm.

Comparisons. This species is distinguished by curvaturae

PLATE 3

Fig. 1 *Retusotriletes*? *saturnus* sp. nov. BM 129970, proximal view, sample Arg92/10.

Fig. 2 *Telisporites* sp. A. LV92/13; **2a**, BM 130849, proximal view, × 500; **2b** BM 130850, distal spines and curvatural ridge; **2c** BM 130851, distinct sculpture on contact area, × 2500.

Fig. 3 *Insolisporites* sp. Ger92/2B; **3a,** BM 134643, proximal view showing distal sculpture and proximal apical cones; **3b,** BM 134644, detail of proximal apical sculpture, × 2000.

Fig. 4 *Raistrickia* sp. Ger15B; **4a,** BM 130714, proximal view, × 2000; **4b,** BM 130713, detail of baculate sculpture and labrate laesurae, × 2500.

Fig. 5 *Scylaspora vetusta* (Rodriguez) comb. nov. Ger2B/1; **5a,** BM 135149, obliquely compressed specimen with proximal crenulate muri near the equator; **5b** BM 135150, detail of proximal sculpture × 2000.

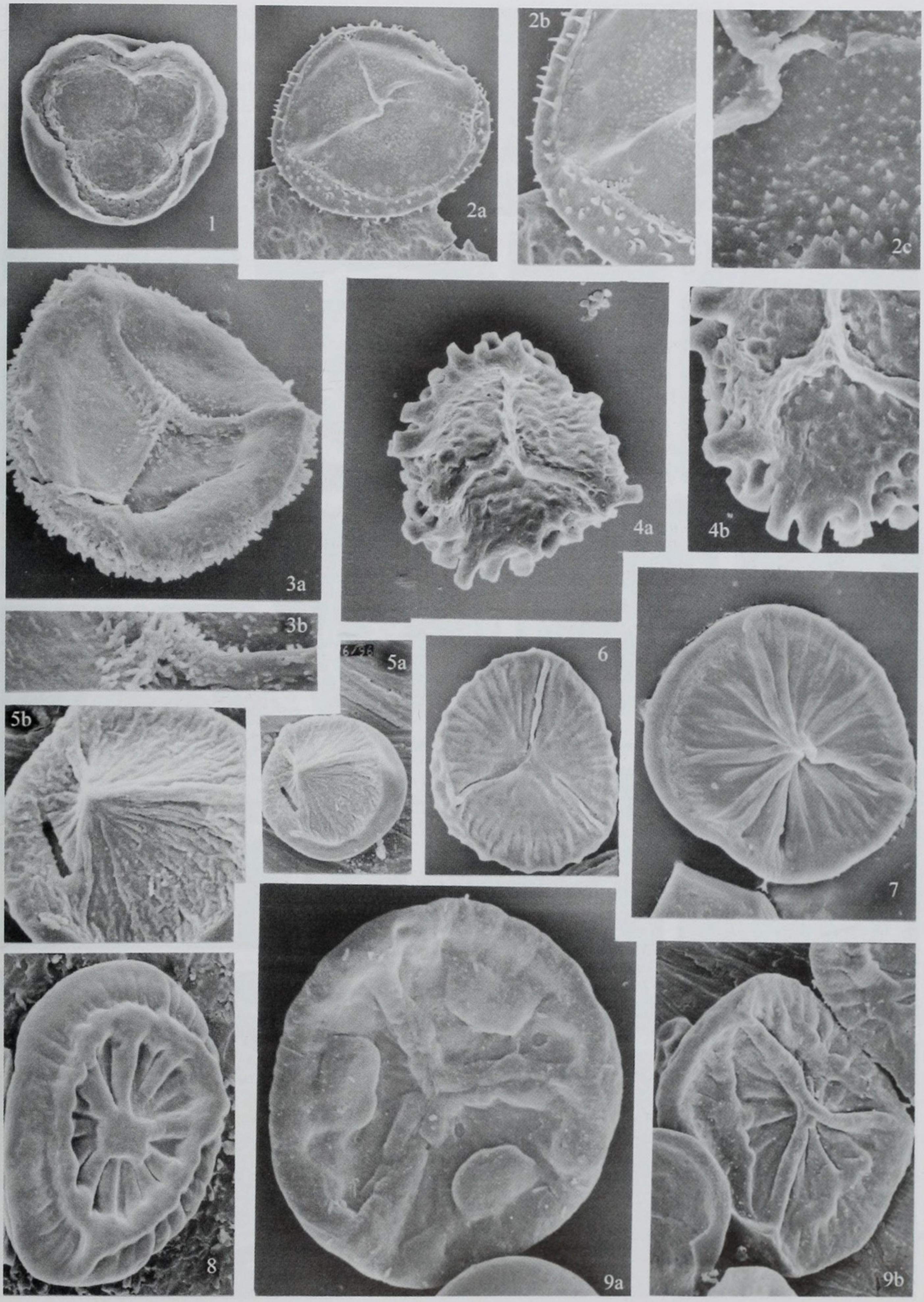
Fig. 6 *Emphanisporites* cf. *decoratus* Allen 1965. BM 132902, slightly oblique proximal view showing spaced distal cones, sample LV13/1.

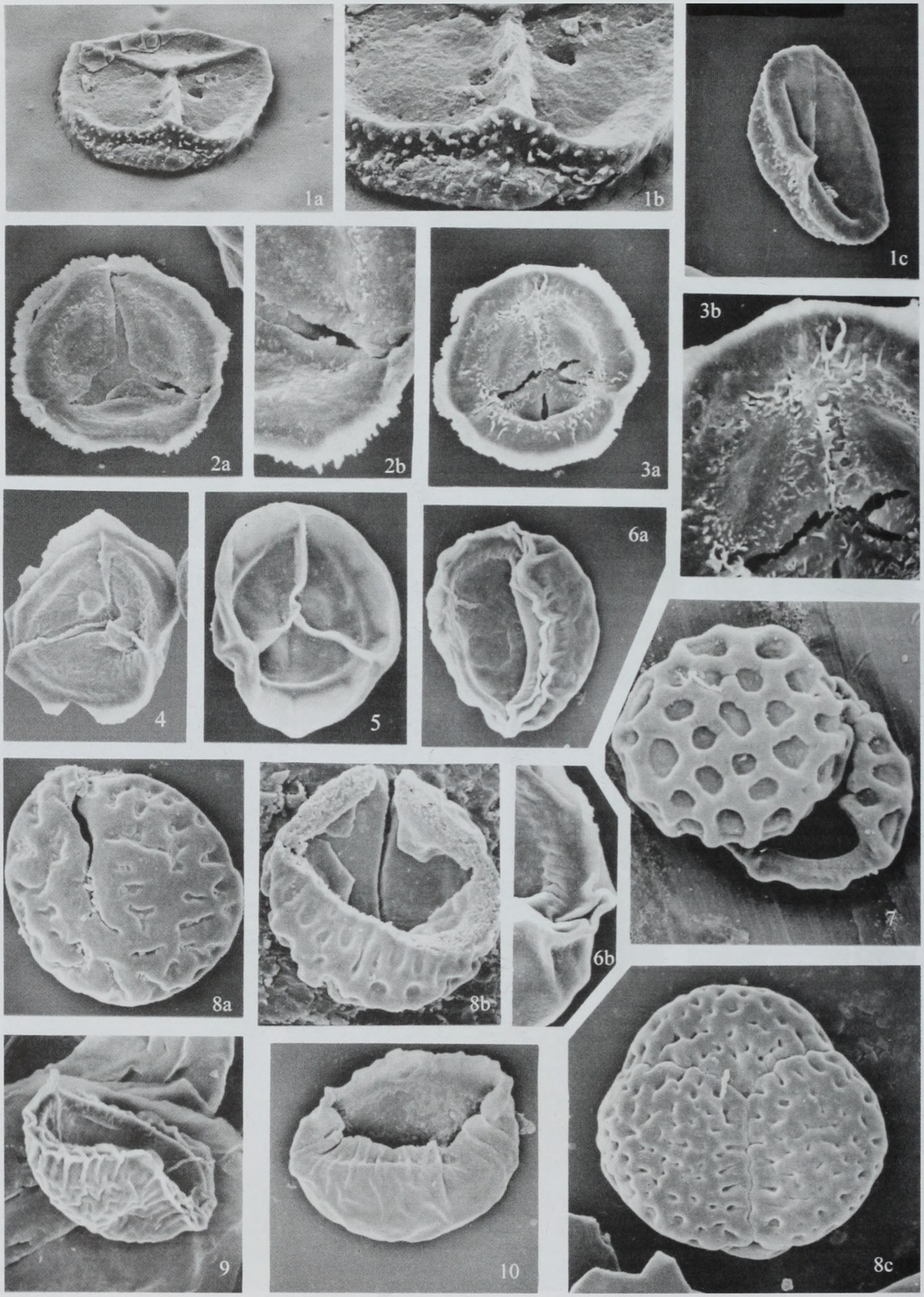
Fig. 7 *Emphanisporites rotatus* McGregor 1961. BM 134062, proximal view, Arg92/5A.

Fig. 8 *Emphanisporites* cf. *splendens* Richardson & Ioannides 1979. BM 134633, proximal view?, showing annulus, apical thickening and radial muri, Ger92/2B.

Fig. 9 *Emphanisporites splendens* Richardson & Ioannides 1979. **9a,** BM 140339, proximal view showing well-developed paired lips, faint radial muri and three prominent inter radial thickenings, × 2000, LP10/DD; **9b,** BM136882, proximal view showing a kyrtome-like structure, Ger2B/1, × 1000.

All figs × 1000, unless stated otherwise.


1
2a
2b
2c
3a
3b
4a
4b
5a
5b
6
7
8
9a
9b


1a
1b
1c
2a
2b
3a
3b
4
5
6a
7
8a
8b
6b
9
10
8c

perfectae formed from sculptural elements and absence of sculpture outside the contact areas towards the amb and over the distal surface.

OCCURRENCE. Rare in the Cantabrian Mountains, Argovejo, La Vid, **hemiesferica (H)** to **micrornatus – newportensis (MN)** Biozones. Přídolí to Lochkovian. In England (Shropshire & Herefordshire) where this species occurs in the Lower Přídolí and spores of this type have been found also in sporangia (Fanning *et al.*, 1991: 3.2 b). Similar spores are found higher in the sequence in the Lower Lochkovian but the higher spores have a variably greater cover of apiculate to spinose sculpture; in extreme forms the spore is completely covered with cones/spines (Richardson, unpublished).

REMARKS. In the case of Form 2 the curvatural bands are defined by sculpture, sometimes barely discernible, sometimes forming broad bands of variable grana and coni paralleling the trilete mark and merging radially into curvatural sculpture. This species, *Apiculiretusispora arcidecus* sp. nov. occurs in the Lower Přídolí of England and has been found in sporangia (Fanning *et al.*, 1991). Stratigraphically higher spores are variable but include specimens with more pronounced sculpture. There is considerable variation; variants in the Lower Devonian have dense distal sculpture, whereas the proximal surface is completely covered with cones, or short spines, with only three small inter-radial areas remaining smooth (interradial papillae). A third species, *Breconisporites*? cf. *coronadus* shows that zonate spores may also have a distinct proximal pattern of sculpture similar to that of *A. arcidecus* sp. nov.

Genus ***BRECONISPORITES*** Richardson *et al.* 1982

***Breconisporites*? spp.** (cf. *Retusotriletes coronadus* Rodriguez, 1983, *pars*) Pl. 2, figs 5–7; Pl. 4, figs 2–4

This form has equatorial wedge-shaped curvaturae extending equatorially (into a zona?). On the proximal surface there is a band of spines and cones in each of the inter-radial areas. These sculptured bands parallel the curvaturae and join with the sculpture which parallels the lips. The 'curvatural' sculpture is composed of fimbriae, spines and cones. Sculpture size *c.* 1–6 µm. The proximal central area, within the arcuate sculpture, may be depressed. There is a +/– circular thickening over the distal polar area.

REMARKS. Specimens of *Breconisporites* from South Wales (locus typicus) (Richardson *et al.*, 1982) have a bizonate cingulum and some species have a proximal area of coni; the Cantabrian spores have some similarities but are not distinctly bizonate. Rare laevigate or proximally rugulate zonate spores that are more clearly bizonate occur near the top (sample LV 13) of the sampled part of the La Vid Section (Pl. 4, fig. 5). In specimens with prominent proximal spines (Pl. 4, fig. 3) the distribution of the spines, in arcuate, 'curvaturate' zones, linked to areas of spines bordering the lips, is similar to the pattern of sculpture seen in *Apiculiretusispora arcidecus* sp. nov. where the sculpture is much finer. The curvatural thickening is extended to form a zona and there are three arcuate bands of spines and cones on the proximal face. The latter spores, and the heavily sculptured spores of type 2, have been found only in the Devonian so far, and form part of a complex morphon, which is being further, investigated.

Infraturma **MURORNATI** Potonié & Kremp 1954
Genus ***EMPHANISPORITES*** McGregor 1961

TYPE SPECIES. *Emphanisporites rotatus* McGregor 1961 (Pl. 3, fig. 7).

Emphanisporites splendens Richardson & Ioannides 1979 Pl. 2, fig. 8, Pl. 3, fig. 9

1973 *Emphanisporites? pseudoerraticus* Richardson & Ioannides: 275–76, pl. 3, figs 12–15; pl. 4, figs 1–4, 7.
1978c *Emphanisporites? pseudoerraticus* Rodriguez: 417, pl. 2, fig. 17.
1979 *Emphanisporites splendens* Richardson & Ioannides: 111.
1983 ?*Emphanisporites pseudoerraticus* Rodriguez: 40, 41, pl. 3, fig. 20.

DIMENSIONS. 26–63µm (17 specimens); 50–78µm (24 specimens) (Richardson & Ioannides 1973).

REMARKS. The Cantabrian and North African specimens are highly variable, but the specimens in this study include much smaller forms than any found in North Africa. Also the 'annulus' is sometimes formed of three inter-radial tangential thickenings which together form a triangle resembling a proximal kyrtome. However, in some of the Cantabrian and the previously described North African specimens, there is no annulus but only irregular inter-radial thickenings. In other specimens (Pl. 3, fig. 8) with an annulus, radial ribs, and polar, or near polar, thickenings that may be proximal, there is no clear trilete mark. These are referred to herein as *Emphanisporites* cf. *splendens*.

PLATE 4

Fig. 1 *Aneurospora richardsonii* (Rodriguez) comb. nov. Tilt 45°, Arg97/13/1P; **1a,** BM 2118, oblique proximal compression; **1b,** BM 2119, showing distal coni, × 2000; **1c,** BM130290, specimen in oblique compression showing rigid equatorial crassitude, Arg/92/13.
Fig. 2 *Breconisporites* sp. A. Sample La Vid 92/13/1; **2a,** BM 132895, proximal view; **2b,** BM 132896, distal proximal sculpture, × 2000.
Fig. 3 *Breconisporites* sp. C. LV92/13/1; **3a,** BM 132899, proximal view; **3b,** BM 132900, spinose proximal sculpture forming zones parallel with the equator and paralleling the trilete sutures, × 2000.
Fig. 4 *Breconisporites* sp. B. BM 130860, proximal view showing rugulate sculpture, × 500, LV92/13.
Fig. 5 Zonate spore. Proximal view, specimen with laevigate contact face, BM 130859, LV92/13.
Figs 6, 10 *Chelinospora* cf. *hemiesferica* (Cramer & Diez) comb. nov. **6,** BM 130308, Arg92/10; **6a,** BM 130307, oblique compression; **6b,** detail of radial folds around the hilum, × 2000; **10,** BM 132469, oblique view with spaced uncluttered distal muri, LP92/19.
Fig. 7 *Chelinospora cantabrica* sp. nov. BM 135304, partial tetrad, upper specimen distal view showing large broad lacunae, lower specimen giving a partial proximal view of the equator surrounding hilate area and subequatorial sculpture, Ger92/2B/2.
Fig. 8 *Chelinospora sanpetrensis* (Rodriguez) comb. nov. **8a,** BM 136891, distal view showing low murornate sculpture and narrow, occasionally branching lumena, Ger92/2B/3; **8b,** BM 135042, proximal/oblique view showing granulate – micro rugulate curvatural sculpture, thin broken hilum, and subequatorial radial lacunae, Ger92/2A; **8c,** BM 134063, spore tetrad showing sub-equatorial radial lacunae, sample Arg92/5A.
Fig. 9 *Chelinospora hemiesferica* (Cramer & Diez) comb. nov. BM 132687, oblique view, LV92/10.
All figs × 1000, unless stated otherwise.

OCCURRENCE. Lower and Middle San Pedro Formation, **RS** and **H** Biozones; Upper Ludfordian and Lower Přídolí, possibly some specimens are reworked.

Subturma **ZONOTRILETES** Waltz 1935 in Luber & Waltz 1938
Infraturma **CRASSITI** Bharadwaj & Venkatachala 1961
Genus ***AMBITISPORITES*** Hoffmeister 1959

Ambitisporites warringtonii (Richardson & Lister, 1969) comb. nov.

BASIONYM. *Retusotriletes warringtonii* Richardson & Lister 1969.

1969 *Retusotriletes warringtonii* Richardson & Lister 1969: pl. 37, figs 7, 8.

REMARKS. The curvaturae are thickened and form a crassitude that is more or less coincident with the equator. These forms are closely similar to *A. avitus* except for the size and thickness of the crassitude.

Ambitisporites? eslae (Cramer & Diez, 1975) comb. nov. Pl. 5, fig. 1

BASIONYM. *Retusotriletes eslae* Cramer & Diez 1975 (*pars*), 343, pl. 1, fig. 11 only.

1973 *Ambitisporites* sp. B, Richardson & Ioannides: 277, pl. 6, fig. 8 only.
1975 *Retusotriletes eslae* Cramer & Diez (*pars*): 343, pl. 1, fig. 11 only (see discussion under *Scylaspora elegans* sp. nov.).
?1976 *Retusotriletes maculatus* McGregor & Camfield: 26, pl. 1, fig. 6.
?1995 *Ambitisporites tripapillatus* Moreau-Benoit; Burgess & Richardson: 16, pl. 6, fig. 16.

HOLOTYPE. Cramer & Diez 1975: pl. 1, fig. 11.

COMPARISON AND REMARKS. *A. tripapillatus* Moreau-Benoit (1976: 37, pl. 7, figs 2–4) has a darkened area along the Y-rays at the spore apex with straight to concave sides. *Scylaspora elegans* has a large darkened apical area and proximal rugulate sculpture. *Retusotriletes maculatus* McGregor & Camfield (1976) and, in part, *Ambitisporites* sp. B (McGregor & Camfield, 1976: pl. 6, fig. 8 only), appear to have a narrow equatorial crassitude, but are otherwise similar to *A. eslae* (Cramer & Diez). They all show an equatorial crassitude except at the radial apices where the curvaturae invaginate. A similar feature is seen in some specimens of *Ambitisporites*, eg. *A. avitus*. Several Lower Devonian laevigate spores are proximally retusoid (McGregor & Camfield, 1976) and from the limited data available these spores appear to be pandemic, although many of the records are from Spain, North Africa and South America. The age of similar spores to this species is varied. *A. eslae, A. tripapillatus* and *R.. maculatus* are all from the Lower Devonian but the Burgess & Richardson record is of Lower Přídolí age.

OCCURENCE. Argovejo, **EC** (**a**) subzone and **MN** zone (Lower Lochkovian).

Genus ***SCYLASPORA*** Burgess & Richardson 1995

TYPE SPECIES. *Scylaspora scripta* Burgess & Richardson 1995.

REMARKS. Some of the spores placed in the genus *Rugosisporites* by Dufka (1995) resemble those of *Scylaspora*; however, the type species of *Rugosisporites* is *Retusotriletes chartulatus* McGregor (1978) which is retusoid with distinct invaginations at the radial apices. McGregor's species is similar, but not identical, to some Middle and Upper Devonian species also placed in the genus *Retusotriletes*, namely *R. rugulatus* and *R. phillipsii*. Consequently, since the type species of *Rugosisporites* is regarded here as belonging to *Retusotriletes*, as McGregor determined, then removal of the type species necessitates the invalidation of the genus *Rugosisporites* by placing it in synonymy with the genus *Retusotriletes*.

Scylaspora elegans sp. nov. Pl. 5, figs 2–4, Pl. 6, fig. 8

1975 *Retusotriletes eslae* Cramer & Diez (pars): 343, pl. 1, fig. 12 only.
1983 *Retusotriletes eslae* Cramer & Diez; Rodriguez, 1983: 47, pl. 5, figs 14, 19, 20.

HOLOTYPE. FM 1490 (Pl. 5, fig. 2), diameter 43 µm; sample La Vid 13, slide D3/2, co-ord. 090 1036; E.F. no. J34/3; upper San Pedro Formation, La Vid section, Cantabrian Mountains, Province of León, northwest Spain.

DERIVATION OF NAME. Latin a. elegans, refined, elegant, referring to the delicate proximal sculpture.

DIAGNOSIS. A *Scylaspora* with a narrow +/– equatorial curvatural crassitude, three distinct proximal inter-radial papillae, Y-sutures bordered by darkened (?thickened) narrow areas tapering to the equator, proximal surface with contorted microrugulae, accompanied by short radial microrugulae near the curvaturae, microrugulae become less distinct polewards; distal exine laevigate.

DESCRIPTION. Amb rounded to subtriangular. Proximal surface with straight to sinuous microrugulae adjacent to the curvaturae, <0.5 µm wide and high, and decreasing in height towards the proximal pole; straight microrugulae confined to the curvatural area. Under the SEM the microrugulae are close-packed and contorted

PLATE 5

Fig. 1 *Ambitisporites? eslae* (Cramer & Diez) comb. nov. FM 1505, Arg92/12 (510) 3, 206 1169.

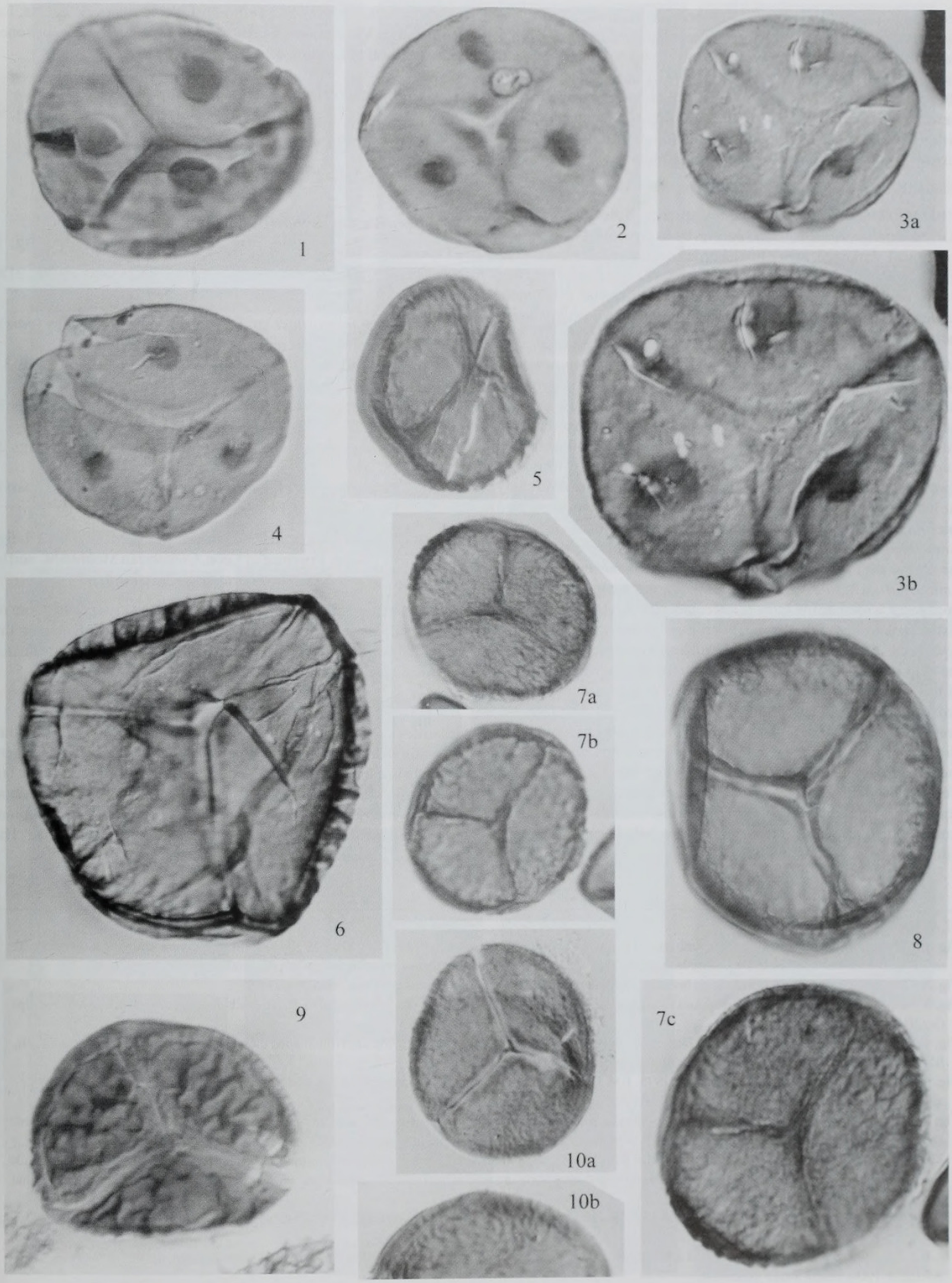
Figs 2–4 *Scylaspora elegans* sp. nov. **2**, FM 1490 (**holotype**), proximal view showing dark apical triangle, narrow crassitude, curvaturae perfectae and inter-radial papillae, LV92/13 (D3) 2, 0901036; **3a, 3b**, FM 1506, **3b,** × 1500 showing minute radial ridges outside the curvatural crassitude, Ger92/12 (371) 3, 100 1131; **4**, FM 1507, LV92/17 (D3) 3, co-ord. 207 0908, E.F.V21/3.

Figs 5–8 *Scylaspora vetusta* (Rodriguez) comb. nov. showing variations. **5,** FM 1508, oblique compression showing +/– radial muri around the curvatural crassitude, LV92/8 (D3) 2, 106 0991; **6,** FM 1509, proximal view, thin-walled specimen showing equatorial radial thickenings becoming indistinct towards the proximal pole, LP92/8 (D2) 1, 025 1014; **7a–c,** FM 1510, proximal view showing irregular and anastomosing proximal muri; **7c**, × 1500; LV92/8 (D3) 2, 058 1127; **8,** FM 1511, specimen showing paired lips, Arg92/5a (473) 3, 029 0910.

Fig. 9 *Scylaspora* cf. *scripta* Burgess & Richardson 1995. FM 1512, × 1500, LV97/8a (D16) 2, 096 1123.

Fig. 10 *Scylaspora* cf. *kozlica* (Dufka) comb. nov. FM 1513, LV92/8 (D3) 1, 163 0983; **10a**, proximal polar compression, showing proximal microrugulae and grana; **10b,** × 1500, showing detail of proximal sculpture.

All figs × 1000, unless stated otherwise.


1
2
3a
4
5
3b
7a
7b
6
8
9
10a
7c
10b

becoming sinuous, and less distinct, poleward. Trilete sutures +/– equal the spore radius or slightly less, accompanied by raised, often darkened areas, tapering towards the amb. A wider thinner proximal triangular area reaches *c.* 4/5ths of the spore radius and inter-radially often reaches the papillae; papillae distinct, rounded to ovoid in plan view, with a slightly raised profile, maximum diameter 4–9 µm. Trilete-folds, or smooth lips, occur in some specimens and are narrow over the apical area and expand towards the equator.

DIMENSIONS. 27–58 µm (59 specimens measured).

COMPARISONS. *Scylaspora elegans* sp. nov. differs from proximally tripapillate *Ambitisporites* species by its proximal microrugulae and apical darkened area (lips) bordering the trilete mark. The photograph of the holotype of *Ambitisporites? eslae* Cramer & Diez (1975: pl. 1, fig. 11) lacks this feature and has a wide crassitude. *Retusotriletes maculatus* has proximal curvaturae invaginated at their radial apices.

REMARKS. The current investigation revealed that *Retusotriletes eslae* Cramer & Diez includes two distinct forms. The original holotype has a broad equatorial crassitude, trilete folds and appears to lack the apical, gradually tapering and darkened areas that flank the trilete mark. Specimens with a broad crassitude are rare in the samples studied (eg. Pl. 5, fig. 1) and it is not known whether such forms have a proximal microverrucate sculpture. It has not been possible to study the holotype for this purpose and, although Cramer & Diez described microrugulae, their diagnosis states that the proximal surface is 'smooth to microrugulate'. Pending re-examination of the type material the forms with a broad crassitude are retained but referred to as *Ambitisporites? eslae* (Cramer & Diez). The more commonly occurring spores, with a narrow, more or less equatorial, curvatural crassitude, distinct trilete area and proximal microrugulae, are transferred to the new species *Scylaspora elegans*. The microrugulae can be seen under the light microscope in some specimens but under the SEM all spores of this species show microrugulae that decrease in size towards the proximal pole. Both species occur in all sections but data from the present study shows that *S. elegans* sp. nov. occurs at the base of the **EC** Biozone whereas *A? eslae* (Cramer & Diez) comb. nov. occurs first in the *Aneurospora* Subzone at the top of the **EC** Biozone. In the Cantabrian Mountains *Scylaspora elegans* sp. nov. occurs in strata equivalent to the Upper/uppermost Přídolí and extends into the Lower Lochkovian (Devonian) and may, therefore, help in establishing the Silurian/Devonian boundary.

OCCURRENCE. Upper San Pedro Formation, Argovejo, Geras, La Peral and La Vid sections, **EC** Biozone to Lower **MN** Sub-Biozone, Upper Přídolí to Lower Lochkovian.

Scylaspora* cf. *scripta Burgess & Richardson 1995
Pl. 5, fig. 9

DIMENSIONS. 23–29µm (3 specimens measured).

OCCURRENCE. La Vid, samples 6, 7B, 8A.

Scylaspora vetusta (Rodriguez) comb. nov.
Pl. 3, fig. 5; Pl. 5, figs 5–8; Pl. 6, fig. 1

BASIONYM. *Archaeozonotriletes vetustus* Rodriguez, 1978b: 219, pl. 1, fig. 8.

1973 *Emphanisporites*? sp. D, Richardson & Ioannides (*pars*): 276, pl. 3, fig. 9 only.
1978b *Archaeozonotriletes vetustus* Rodriguez: 219, pl. 1, fig. 8.
1978c *Archaeozonotriletes chulus* Rodriguez: pl. 1, fig. 14.
1978c *Archaeozonotriletes vetustus* Rodriguez: 414, pl. 2, figs 7, 8.
1983 *Archaeozonotriletes vetustus* Rodriguez: 32, pl. 1, figs 2, 18, 20.
1995 *Rugosisporites* cf. *chartulatus* (McGregor); Dufka (pars): 71, pl. 2, figs 9–14.

HOLOTYPE AND TYPE LOCALITY. Rodriguez, R.M. 1978b: pl. 1, fig. 8; Corniero village, Province of León, Cantabrian Mountains, northwest Spain, lower San Pedro Formation, ?Ludfordian.

EMENDED DIAGNOSIS. A *Scylaspora* with closely spaced, more or less radial, anastomosing, irregularly sinuous, muri/rugulae on the proximal surface; distally laevigate apart from a narrow subequatorial area with +/– radial muri.

DIMENSIONS. 28–72 µm (60 specimens measured).

REMARKS. Spores of this species are highly variable. In some cases there are irregular muri/rugulae that reach the pole, in others cuneiform elements are prominent over the equatorial crassitude but sculpture is faint to indistinguishable over the rest of the proximal surface. Intermediates occur where distinct equatorial sculpture becomes increasingly faint leaving a laevigate apical zone. The equatorial crassitude is variable in width.

PLATE 6

Fig. 1 *Scylaspora vetusta* (Rodriguez) comb. nov. **1a**, BM 140019, proximal view, LP92/10/DP; **1b**, BM 134179, proximal view showing subequatorial radial muri and scabrate apical area, sample Geras 92/7; **1c**, BM 134195, proximal view, showing irregular proximal sculpture, Arg92/4A/1.

Fig. 2 *Scylaspora* sp. BM 135151, strong broad equatorial crassitude and coarse sinuous proximal muri, Ger2B/2.

Fig. 3 *Coronaspora primordiale* (Rodriguez) Rodriguez 1983. BM 137485, proximal view showing inter-radial thickenings, grooved crassitude and lips, Ger2B/2.

Fig. 4 *Iberoespora cantabrica* Cramer & Diez 1975. **4a**, BM 116051, proximal view showing chevron-shaped elements forming the labra, Arg92/7; **4b**, BM 137480, proximal view showing inter-radial thickenings, Arg13/Dii.

Fig. 5 *Iberoespora glabella*? Cramer & Diez 1975. BM 129724, distal view showing concentric furrow inside equatorial crassitude and foveolate-murornate sculpture over central area, Arg92/11B.

Fig. 6 *Coronaspora cromatica* (Rodriguez) Jansonius & Hills 1979. **6a**, BM 134510, proximal view showing variably developed verrucate lips, kyrtome and inter-radial muri, Ger92/2B; **6b**, BM 134199, proximal view, showing kyrtome, inter-radial thickenings and verrucate labra, Arg5A/1; **6c**, BM 137269, distal view showing annulus and irregular muri in polar area, Ger92/2B/2; **6d**, BM 135144, oblique compression showing equatorial crassitude and distal annulus, Ger92/2B/1; **6e**, BM 134634, proximal view showing well-developed verrucate labra, Ger92/2B; **6f**, BM 134634, detail of proximal apical area in Fig. 6e, × 2000.

Fig. 7 *Coronaspora reticulata* sp. nov. **7a**, BM 138958, oblique proximal view showing kyrtome, LV92/7b/DD1; **7b**, BM 138395, proximal view showing kyrtome and thin apical area.

Fig. 8 *Scylaspora elegans* sp. nov. **8a**, BM 2548, proximal view, Arg 92/11B/2; **8b**, BM2551, detail of proximal microrugulae, tilt 45°, × 4000.

All figs × 1000, unless stated otherwise.


1a
1b
1c
2
3
4a
4b
5
6a
6b
6c
6d
6e
6f
7a
7b
8a
8b

Scylaspora* cf. *kozlica (Dufka) comb. nov. Pl. 5, fig. 10

Cf. 1995 *Rugosisporites kozlicus* Dufka (*pars*): 72, pl. 2, figs 15–17.

DESCRIPTION. Amb circular to subcircular. Equatorial crassitude 1–2 µm wide. Trilete mark labrate, *c*. 4/5 spore radius, lips less than 1µm wide, merge with curvaturae perfectae which form a narrow equatorial crassitude with a thicker inner portion and a narrow (< 0.5 µm), apparently membranous, extension. Proximal surface covered with narrow irregular rugulae *c*. 0.5 µm wide and possible micrograna. Sculpture less distinct near the proximal pole. Distal surface laevigate except for sub-equatorial rugulae with scattered micrograna.

DIMENSIONS. 31–44 µm (30 specimens measured).

COMPARISONS. Similar to *S. scripta* in having radially aligned muri near the equator and distal sculpture, but has more radial geniculate and anastomosing robust muri. *S. kozlicus* (Dufka) is similar but is distally laevigate and lacks the paired lines of thickening on either side of the Y-mark. *S.* sp. A (this study) has geniculate muri on the proximal and distal surfaces and is rare.

REMARKS. *Scylaspora* cf. *scripta* is similar to forms described from the Homerian and may be reworked. The spores have a membranous extension, seen at the equator on some specimens, and may be double-layered with the thin outer part of the exoexine forming the rugulae over the proximal surface. *S. vetusta* has coarser rugulae but is otherwise closely similar.

OCCURRENCE. La Vid section, upper **RS** and lower **H** Biozones (Upper Ludfordian – Přídolí).

Genus *CONCENTRICOSISPORITES* Rodriguez 1983

TYPE SPECIES. *Concentricosisporites sagittarius* (Rodriguez) 1983.

REMARKS. Jansonius & Hills (1990: card 4630) considered that the central dark area in the type species may represent an inner body.

Concentricosisporites agradabilis (Rodriguez) Rodriguez 1983 Pl. 7, fig. 2

1978c *Stenozonotriletes agradabilis* Rodriguez: 421, pl. 3, figs 7, 8, 11.
1983 *Concentricosisporites agradabilis* Rodriguez: 35, pl. 4, figs 7, 11, 13.

HOLOTYPE AND TYPE LOCALITY. Rodriguez, 1978b: pl. 3, fig. 8; Torrestio, Province of León, Cantabrian Mountains, northwest Spain, lower San Pedro Formation.

DIAGNOSIS. See Rodriguez, 1978c: 421.

DIMENSIONS. 26–39 µm (18 specimens measured); Rodriguez, 1978b, 24–35 µm.

COMPARISONS. This species shows some resemblance to spores of the genus *Emphanisporites* but the proximal radial ribs are not always distinct and the equatorial crassitude is relatively wide (3–6 µm) in relation to the spore radius.

OCCURRENCE. Lower San Pedro Formation; upper **RS** and lower **H** Biozones; sporadically occurs in **EC** and lower **MN** Biozones where they may represent reworking. In the higher specimens the distal annulus is lobed and the radial 'muri' more distinct. Upper Ludfordian and Lower Přídolí.

Concentricosisporites sagittarius (Rodriguez) Rodriguez, 1983 Pl. 7, fig. 1

1978b *Stenozonotriletes sagittarius* Rodriguez: 219, pl. 1, fig. 7.
1978c *Stenozonotriletes sagittarius* Rodríguez: 421, pl. 2, figs 13, 14.
1983 *Concentricosisporites sagittarius* (Rodriguez); Rodriguez: 36, pl. 3, fig. 21.
1995 *Concentricosisporites sagittarius* Rodriguez; Burgess & Richardson: 17, pl. 6, figs 14, 15.

HOLOTYPE. Rodriguez, 1978b: pl. 1, fig. 7.

DIAGNOSIS. See Rodriguez, 1978b: 219.

DIMENSIONS. 29–44 µm (10 specimens measured); 25–40 µm (Rodriguez, 1978).

OCCURRENCE. San Pedro Formation, Upper **RS** & **H** Biozones La Vid, upper **RS** & lower **H** Biozones La Peral, lower **MN** Biozone Geras (? reworked). Upper Ludfordian and Lower Přídolí.

Genus *IBEROESPORA* Cramer & Diez 1975

TYPE SPECIES. *Iberoespora cantabrica* Cramer & Diez 1975.

Iberoespora cantabrica Cramer & Diez 1975 Pl. 6, fig. 4; Pl. 7, fig. 4

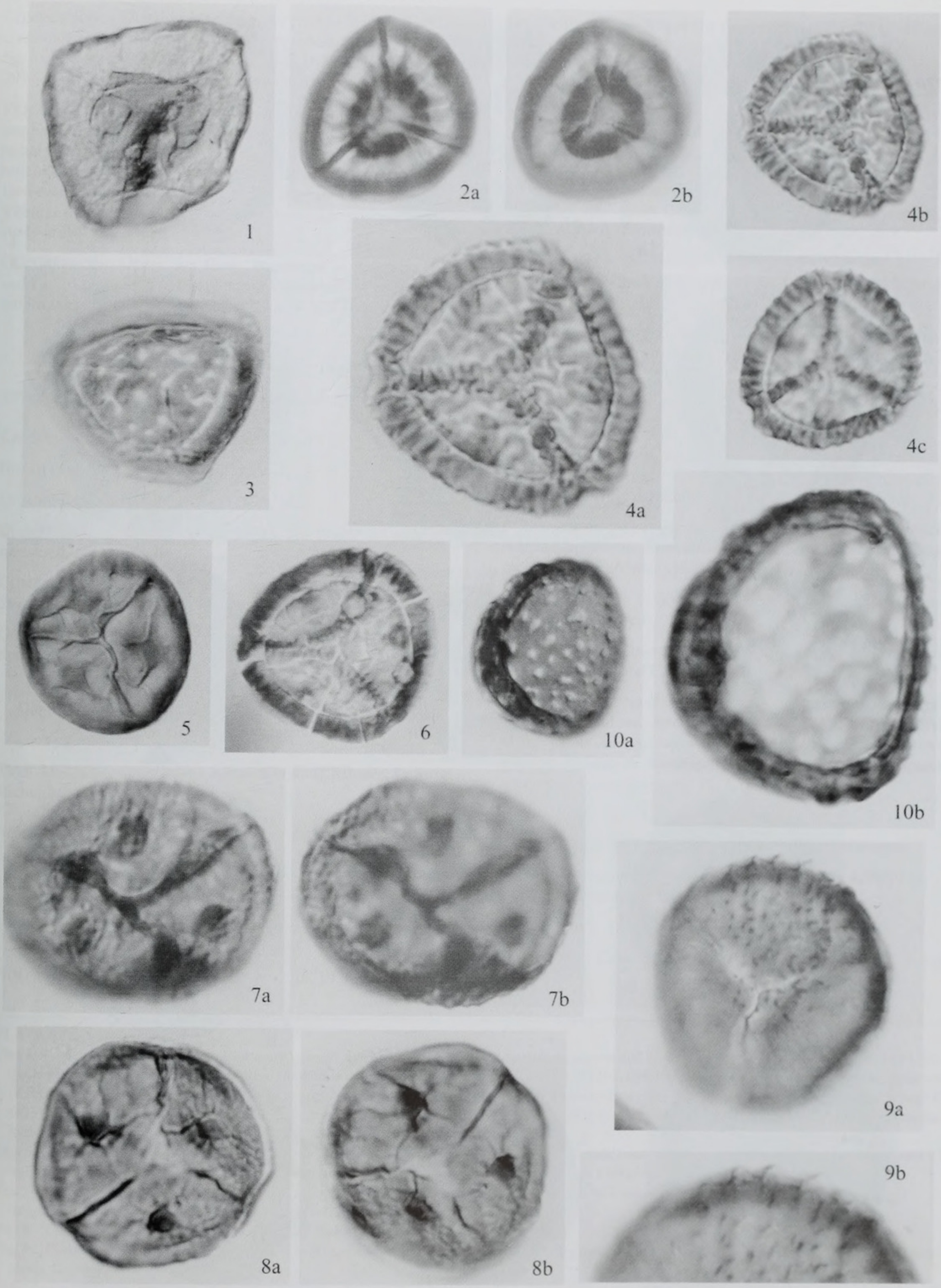
HOLOTYPE. Cramer & Diez 1975: pl. 2, fig. 24.

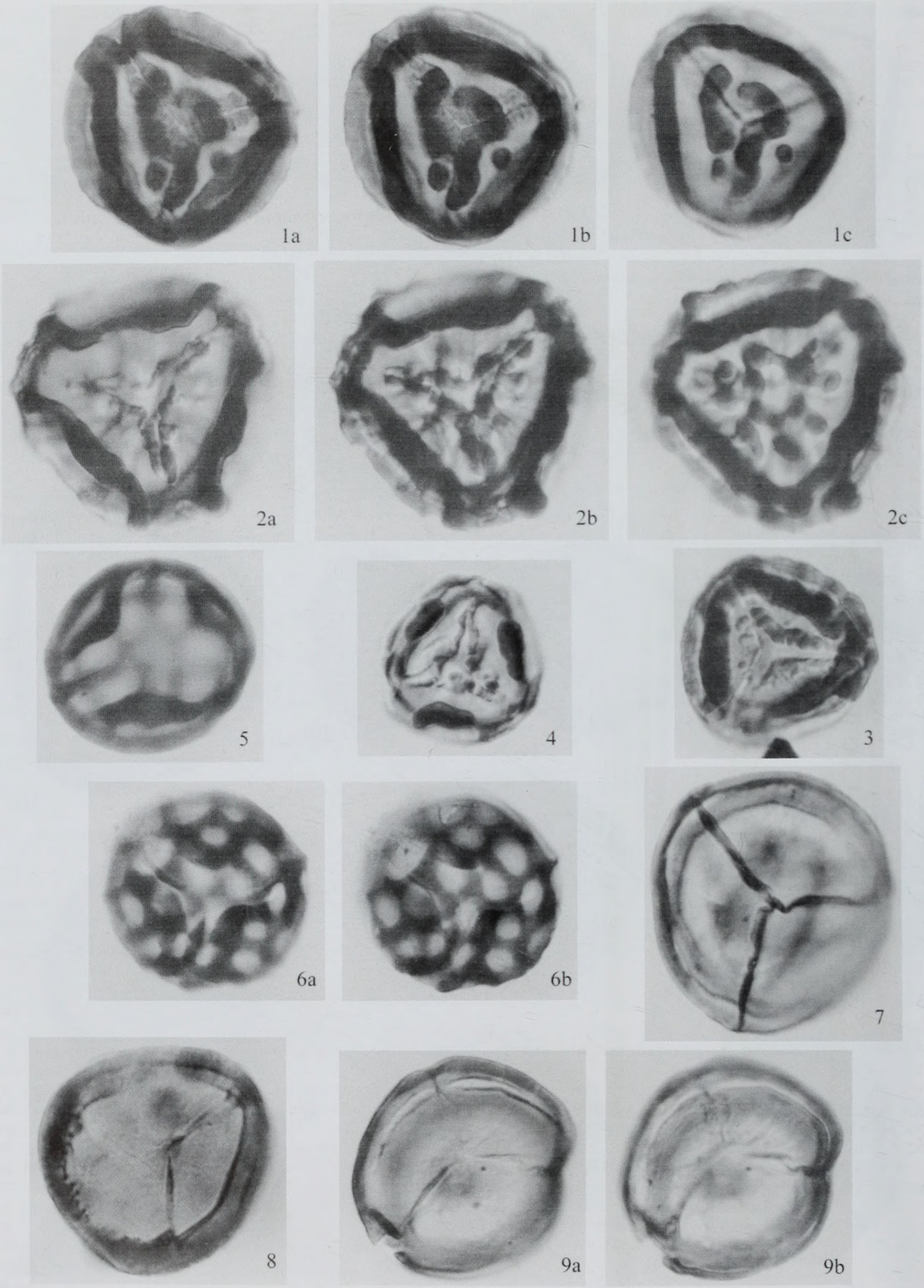
DIAGNOSIS. See Cramer & Diez 1975: 339, pl. 2, figs, 24, 26–28, 30, 31.

DIMENSIONS. 30 to 45 µm (Cramer & Diez, 1975); 27 to 42 µm (40 specimens measured).

PLATE 7

Fig. 1 *Concentricosisporites sagittarius* (Rodriguez) Rodriguez 1983. FM 1514, Ger92/15a (475) 1, 044 1032.
Fig. 2 *Concentricosisporites agradabilis* (Rodriguez) Rodriguez 1983. FM 1515, LV92/13 (495) 2, 098 0982; **2a,** proximal focus; **2b,** distal focus, showing annulus.
Fig. 3 *Iberoespora glabella*? Cramer & Diez 1975. FM 1516, Argovejo 92/12 (510) 3, 139 0874.
Fig. 4 *Iberoespora cantabrica* Cramer & Diez 1975. FM 1517, Arg92/12 (510) 3, 212 0962; **4a, 4b**, showing verrucate lips, distal geniculate muri, and inter-radial thickenings; **4a**, × 1500; **4c**, median focus showing margin of the central body invaginated.
Fig. 5 *Leonispora argovejae* Cramer & Diez 1975. FM 1519, LV92/13 (D3) 1, 051 0913.
Fig. 6 *Iberoespora mariae* Rodríguez 1983. FM 1518, LP92/20 (D8) 2, Geras 92/11 (D8) 1, 030 0969 (see Fig.2, sample GER 11).
Fig. 7 *Aneurospora* sp. Tripapillate form. FM 1520, Ger92/14 (468) 7, 132 0975; **7a,** proximal focus; **7b,** proximal focus, showing curvaturae perfectae.
Fig. 8 *Streelispora newportensis* (Chaloner & Streel) Richardson & Lister 1969. FM 1521, LV13 (D3) 1, 082 0986; **8a, 8b**, × 1500.
Fig. 9 *Aneurospora richardsonii* (Rodriguez) comb. nov., FM 1522, Ger14 92/14 (468) 7, 135 0838; **9b**, shows sculpture in detail, × 1500.
Fig. 10 *Chelinospora sanpetrensis* (Rodriguez) comb. nov. FM 1523, Arg92/5a (473) 3, 123 1092; **10a,** distal focus showing foveolate exine; **10b**, with narrow arcuate fold around proximal hilum, × 1500.
All figs × 1000, unless stated otherwise.


1
2a
2b
4b
3
4a
4c
5
6
10a
10b
7a
7b
9a
9b
8a
8b


1a
1b
1c
2a
2b
2c
5
4
3
6a
6b
7
8
9a
9b

COMPARISON. Distally foveolate specimens with a laevigate crassitude are referred to as *Iberoespora glabella*? (Pl. 6, fig. 5; Pl. 7, fig. 3). The original illustrations (Cramer & Diez, 1975: pl. 2, figs 22, 29) do not show the distal surface clearly.

REMARKS. Cramer & Diez do not explain how they differentiate *I. guzmani* from *I. cantabrica*. Both species have the same structure, radial muri on the crassitude, crenulate lips, a distal sculpture of reticulate to convolute muri, and thickenings in the inter-radial areas. However, the size range given for *I. guzmani* is only 10–20 μm whereas that for *I. cantabrica* is 30–45 μm. The specimens in this study are all larger than 26 μm.

OCCURRENCE. Upper San Pedro Formation in Argovejo, Geras and La Vid sections in the Province of León and La Peral section in the Province of Asturias, upper **EC** – lower **MN** Biozones.

Genus *LEONISPORA* Cramer & Diez 1975

TYPE SPECIES. *Leonispora argovejae* Cramer & Diez 1975.

Leonispora argovejae Cramer & Diez 1975 Pl. 7, fig. 5

HOLOTYPE. Cramer & Diez 1975, pl. 1, fig. 3.

DESCRIPTION. Cramer & Diez (1975: 342).

DIMENSIONS. 25–35 μm (ibid. 1975); 30–38 μm (14 specimens measured, present study).

COMPARISONS. The genus is closely similar in structure to *Streelispora* but is laevigate.

OCCURRENCE. Upper San Pedro Formation, Geras, La Vid sections; **MN** Miospore Biozone, **NA** Subzone.

Genus *STREELISPORA* (Richardson & Lister) Richardson, Streel, Hassan & Steemans 1982

TYPE SPECIES. *Streelispora newportensis* (Chaloner & Streel); Richardson & Lister 1969.

Streelispora newportensis (Chaloner & Streel); Richardson & Lister 1969 Pl. 7, fig. 8

1968 *Granulatisporites newportensis* Chaloner & Streel: 92, pl. 19, figs 7, 8, 11.
1969 *Streelispora newportensis* (Chaloner & Streel); Richardson & Lister: 230–31, pl. 41, figs 3–6.

HOLOTYPE. Chaloner & Streel 1968: 92, pl. 19, figs 7, 8, 11.

DIMENSIONS. 28–39 μm (13 specimens measured), 17–48 μm (80 specimens measured) Richardson & Lister 1969.

OCCURRENCE. Upper San Pedro Formation, Argovejo, Geras, La Vid, **MN** Biozone, **NA** Sub-Biozone.

Genus *ANEUROSPORA* Streel 1964

TYPE SPECIES. *Aneurospora goensis* Streel 1964

Aneurospora richardsonii (Rodriguez) comb. nov. Pl. 4, fig. 1; Pl. 7, fig. 9

BASIONYM. *Streelispora richardsonii* Rodriguez, 1983: 50, pl. 8, figs 6, 7, pl. 9, fig. 3.

1978c *Geminospora spinosa* Allen; Rodriguez: 416, pl. 5, figs 7, 8.
1983 *Streelispora richardsonii* Rodriguez: 50, pl. 8, figs 6, 7, pl. 9, fig. 3.

HOLOTYPE AND LOCUS TYPICUS. See Rodriguez, 1983: 50, pl. 8, fig. 3.

EMENDED DIAGNOSIS. An *Aneurospora* with no proximal papillae, distal sculpture consists of spaced slender spines (fimbriae), elements dominantly parallel-sided with blunt, rounded apices.

COMPARISON. The slender fimbriae distinguish this species. *Anapiculatisporites raistrickiaeformis* Schultz (1968) has coarser, more irregular elements (see also Steemans 1989).

DIMENSIONS. 38 to 50 μm (Rodriguez, 1983); 32 to 47 μm (28 specimens measured).

OCCURRENCE. Lower part of lower **MN** Biozone, NA Subzone, Argovejo, Geras and La Vid sections.

REMARKS. The species *Aneurospora richardsonii* lacks the proximal papillae and associated tangential folds and is herein transferred to the genus *Aneurospora*. Tangential folds around the proximal papillae distinguish *Streelispora* and *Leonispora* from tripapillate species of *Aneurospora* (eg. Pl. 7, fig.7).

Genus *CORONASPORA* Rodriguez 1979 emend.

1978b *Coronaspora mariae* Rodriguez: 218, pl. 1, figs 1–3.
1979 *Coronaspora mariae* Rodriguez: 232.

TYPE SPECIES. *Coronaspora mariae* Rodriguez, 1978.

HOLOTYPE. *Coronaspora mariae* Rodriguez, 1978b: pl. 1, figs 1, 2.

PLATE 8

Figs 1–4 *Coronaspora cromatica* (Rodriguez) emend. **1,** FM 1524; **1a,** showing proximal kyrtome and broad verrucate lips, **1b**, intermediate focus, **1c**, distal view showing annulus and sculpture of sinuous muri and rounded verrucae; Ger92/5 (542) 2, 098 1006; **2,** FM 1525; **2a–c,** proximal to distal levels of focus; **2a** with narrow lips and distinct kyrtome; **2b** relatively narrow crassitude; **2c,** distal sculpture of small interconnected narrow verrucae Arg92/5a, (473) 3, 023 0983; **3,** FM 1526, proximal view, Arg92/5a (473) 3, 139 1133; **4,** FM 1527, proximal view, specimen with inter-radial thickenings on the kyrtome, Arg92/5a (473) 3, 099 0938.

Figs 5, 6 *Coronaspora reticulata* sp. nov. **5,** FM 1528, proximal focus showing kyrtome with wide inter-radial thickenings, LV92/7b (D3) 3, 156 0917; **6a, b,** FM 1491 **(holotype)**, showing distal reticulum (the radial extremities are visible in Fig. 6a), LV92/7b (D3) 3, 043 0965.

Fig. 7 *Coronaspora subornata* (Cramer & Diez) comb. nov. FM 1529, specimen showing narrow Y-folds, equatorial crassitude, distal annulus and irregular distal thickening; Ger92/9 (456) 1, 035 0472.

Fig. 8 *Chelinospora canistrata* sp. nov. FM 1492 **(holotype)**, Ger92/5 (542) 2, 083 1024.

Fig. 9 *Coronaspora infraornata* (Rodriguez) comb. nov. FM 1530, showing curvatural crassitude, distal annulus and distal polar thickening at two focal levels, Ger92/9 (456) 1, 066 0942.

All figs × 1000.

EMENDED DIAGNOSIS. Equatorial crassitate miospores with rounded or convexly triangular amb, a proximal kyrtome of thickened arcuate ridges extending to the radial apices where it is flat-topped and joins with the trilete lips; distal surface with, or without, a distal annulus; distal exine laevigate, verrucate, irregularly murornate, or reticulate.

COMPARISON. The rounded amb and distinct kyrtome distinguish this genus. There is no kyrtome on the type species of *Amicosporites* (*A. splendidus*) but two other species, *A. infraornatus* Rodríguez 1978b and *A. subornator* Cramer and Díez 1975 have this structure and are herein transferred to *Coronaspora*. The kyrtome in *Ahrensisporites* Potonié & Kremp, 1954 and *Concavisporites* Pflug in Thomson and Pflug, 1953 are distinct because the radial parts are prominent and inter-radially the amb is straight to concave. The kyrtome tapers evenly towards the equator in *Kyrtomisporis* Mädler 1964 (see also Achilles, 1981) whereas in *Coronaspora* the kyrtome is a radially broad and flattened (truncated) thickening where the inter-radial branches of the kyrtome meet, and may invaginate to become confluent with the lips. In cross-section the Silurian kyrtomes have a semicircular-shape.

REMARKS. Rodriguez validated the genus in 1979 when she designated *Coronaspora mariae* as type species.

Coronaspora cromatica (Rodriguez) emend Pl. 6, fig. 6; Pl. 8, figs 1–4

1978b *Coronaspora cromatica* Rodríguez: 218, pl. 1, fig. 4.
1979 *Coronaspora cromatica* (Rodriguez) Jansonius & Hills: card number 3543.
1983 *Coronaspora cromatica* Rodriguez: pl. 3, fig. 4.

HOLOTYPE. Rodriguez, 1978b: 218, pl. 1, fig. 4.

EMENDED DIAGNOSIS. A *Coronaspora* with distinct labra, a proximal kyrtome with inter-radial thickenings, distal annulus, and variable muri and verrucae in the distal polar region.

DESCRIPTION. Amb subcircular to subtriangular with convex sides. Spores preserved in polar compression suggesting an original of more or less lenticular shape. Exine proximally with a distinct complete kyrtome with inter-radial thickenings, radial 'bars', connecting these to a narrow (*c.* 3 μm), +/– smooth to irregularly thickened, equatorial crassitude. Kyrtome distinct, formed by raised ridges (+/– semi-circular in profile) paralleling the lips in the inter-radial areas, flattened at radial extremities where it may show distinct invaginations; lips variably developed, may be broad and verrucate often taper sharply to the apices, or may be laevigate and sinuous; in forms with verrucate lips sutures distinct. Distally an annulus has smooth to irregular margins *c.* 9 μm wide, outer border of annulus reaches to 2/3 of the spore radius. Distally polar area sculptured by broad muri 3–7μm wide, 9–18 μm long, muri highly variable in shape and orientation, forming linear or sinuous bars which may be smooth-sided, or show a series of constrictions giving a beaded appearance, due to the mixture of verrucae and short muri, or coalescent verrucae.

DIMENSIONS. 28–47 μm (58 specimens measured); Rodriguez, 1978b, 20–30 μm; width of the cingulum *c.* 2 μm.

COMPARISONS. *Coronaspora mariae* also has a distal annulus and is closely similar but has large rounded verrucae over the distal pole.

REMARKS. Rare specimens with sinuous laevigate lips, like the type material (Rodriguez, 1978b), occur in the Upper part of the San Pedro Formation. So far the forms with smooth lips have only been found in the upper **H** to **EC** Zones. Specimens with verrucate lips occur in the upper **RS** Zone and may prove to be a useful marker for the lower boundary of the Přídolí.

OCCURRENCE. Forms with verrucate lips (Pl. 6, fig. 6, Pl. 8, figs 1–4) occur in the Lower San Pedro Formation; lower upper **RS** Biozone Geras, Argovejo, lower **H** La Vid and La Peral sections; spores with laevigate lips, *C.* cf. *cromatica*, Upper San Pedro Formation, upper **H** & **EC** Biozone La Peral, **EC** & lower **MN** Biozones La Vid.

Coronaspora reticulata sp. nov. Pl. 6, fig. 7; Pl. 8, figs 5, 6

1975 *Knoxisporites? riondae* Cramer & Diez (*pars*): 341, pl. 1, fig. 17 only.
1978c *Knoxisporites? riondae* Cramer & Diez; Rodriguez : 42, 43, pl. 2, figs 18, 19.
1983 *Knoxisporites*? *riondae* Cramer & Diez; Rodriguez (*pars*): 42, 43, pl. 4, figs 2, 3.

HOLOTYPE. FM 1491 (Pl. 8, fig. 6), diameter 36 μm; sample La Vid 7B, slide D3/3, co-ord. 043 0965; E.F. no. E27/1; lower San Pedro Formation, La Vid section, Province of León, Cantabrian Mountains, northwest Spain.

DIAGNOSIS. A *Coronaspora* with broad distal muri forming a reticulum; kyrtome thickened especially in the inter-radial areas; kyrtome surrounds a clover-leaf shaped area of thin exine; laesurae labrate, labra narrow, smooth and sinuous.

DESCRIPTION. Amb circular to subcircular. Spores usually preserved in polar compression, suggesting an original, more-or-less lenticular cross-section. Equatorial crassitude smooth +/– 2 μm. Kyrtome smooth, invaginated and increasing in width towards the spore apex in the inter-radial areas, 2–4 μm, joined at the radial apices where they may be slightly invaginated at the junction with

PLATE 9

Fig. 1 *Chelinospora cantabrica* sp. nov. FM 1493, **(holotype)**; **1a**, distal focus showing a reticulum of broad muri, several with characteristic narrow restrictions; **1b**, shows equatorial margin and muri in plan, Arg92/5a (473) 3, 144 1082.

Fig. 2 *Chelinospora lavidensis* sp. nov. FM 1494 **(holotype)**, showing narrow muri forming an irregular reticulum with subequatorial muri normal to the equator, Arg92/12 (510) 3, 093 1019.

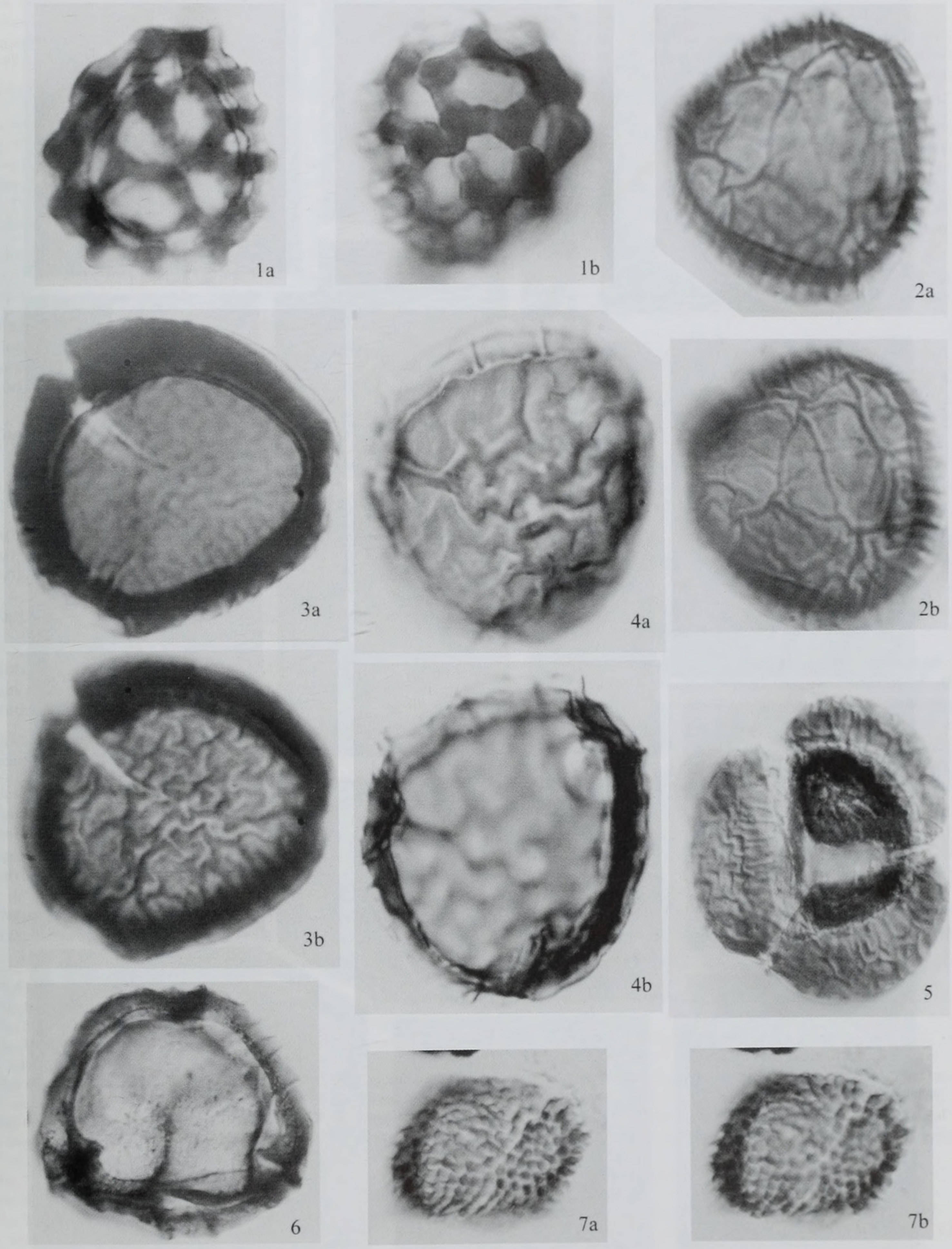
Figs 3, 5 *Chelinospora hemiesferica* (Cramer & Diez) comb. nov. **3,** FM 1531; **3a**, proximal view showing thick crassitude and narrow concentric fold at the equatorial edge of the hilum; **3b**, distal surface showing close-packed narrow geniculate muri, Ger92/9 (450) 1, 147 1050; **5,** FM 1532 tetrad, showing parallel subequatorial muri normal to the equator and geniculate muri over the distal patina, Arg92/14 (468) 11, 080 1069.

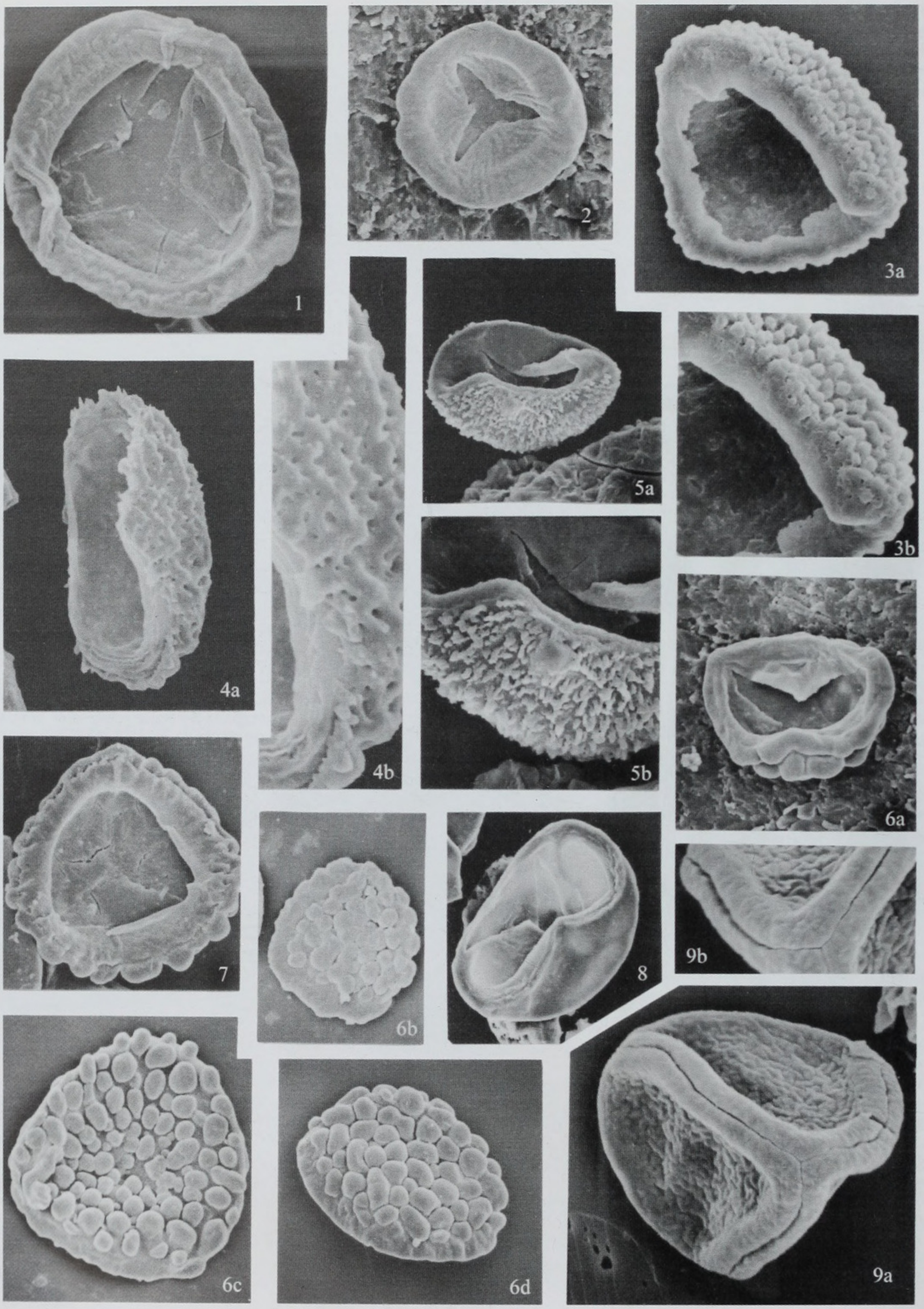
Fig. 4 *Chelinospora* cf. *hemiesferica* (Cramer & Diez) comb. nov. **4,** FM 1533; **4a**, distal view, muri geniculate, but broader and more spaced than in the species; **4b**, proximal focus showing margins of the hilum, Arg92/11a (441) 4, 074 0915.

Fig. 6 *Chelinospora media* sp. nov. FM 1495, holotype, Arg92/12 (510) 3, 093 1019.

Fig. 7 *Cymbosporites* cf. *dittonensis* Richardson & Lister 1969. FM 1534, Arg92/13 (455) 1, 049 1014.

All figs × 1000.


1a
1b
2a
3a
4a
2b
3b
4b
5
6
7a
7b


1
2
3a
4a
4b
5a
3b
5b
6a
7
6b
8
9b
6c
6d
9a

the laesurae, lips smooth, narrow, decreasing in width over the thinner polar area, <1 μm wide. Distal surface with a reticulum of broad muri c.1–4 μm wide and *c.* 1 μm high, surrounding +/– polygonal lumine 3–6 μm maximum width.

DIMENSIONS. 26–44 μm (52 specimens measured).

COMPARISONS. The presence of an equatorial crassitude, proximal kyrtome and distal reticulum, distinguish this species from *Knoxisporites? riondae* Cramer & Diez 1975, the latter has a 'marked concentrical ring' around the distal pole and distal warts (see Cramer & Diez 1975: 341, reconstruction fig. 2.3, and distal focus of holotype pl. 1, fig. 16).

REMARKS. The proximal surface is seen best under the SEM (Pl. 6, fig. 7b) but the kyrtomal thickenings and thin trilobed proximal apical area are also seen under the light microscope.

OCCURRENCE. La Peral **RS** and lowermost **H** Biozone, La Vid **RS** Biozone, and doubtful, poorly preserved specimens in upper **EC** and lower **MN** Biozones; Upper Ludfordian and Přídolí; possibly reworked in Upper Přídolí and Lower Lochkovian, Argovejo.

Coronaspora subornata (Cramer & Diez) comb. nov.

Pl. 8, fig. 7

BASIONYM. *Amicosporites subornator* Cramer & Díez 1975: 338, pl. 1, fig. 7.

1973 Spore type D; Richardson & Ioannides: 281, pl. 9, fig. 2.
1975 *Amicosporites subornator* Cramer & Díez: 338, pl. 1, fig. 7.
1978c *Amicosporites subornator* Cramer & Diez; Rodriguez: 412–13, pl. 2, fig. 2.
1983 *Amicosporites subornator* Crame & Diez; Rodriguez: 30, pl. 3, fig. 13.

HOLOTYPE. Cramer & Diez 1975; pl. 1, fig. 7; San Pedro Formation, Argovejo section, Province of León, Cantabrian Mountains, northwest Spain.

DIAGNOSIS. A *Coronaspora* with a distal annulus and smooth exine.

Description. Amb subcircular to subtriangular with convex sides. Spores preserved in polar compression, suggesting an original of more or less lenticular shape. Exine with a distinct proximal kyrtome, equatorial crassitude +/– smooth to irregularly thickened, and a narrow distal annulus (*c.* 3 μm wide); annulus smooth, and reaches to *c.* 4/5 of the spore radius. Distal? pole surrounded by a dark ring (?annulus). Trilete sutures reach the crassitude, which is invaginated at the radial apices; lips smooth, distinct, and parallel-sided.

DIMENSIONS. 30–40 μm (Cramer & Diez, 1975); 31–44 μm (14 specimens measured, present study).

COMPARISONS. Differs from other members of the genus, with the exception of *C. infraornata*, in having a laevigate exine, *C. infraornata* has a dark distal polar area.

REMARKS. Cramer & Diez (1975: 338) refer to the kyrtome as 'three segments of a circular inspissation' and a dark polar ring as a proximal inspissation. The spores differ from typical members of the genus *Amicosporites* because they have a distinct proximal kyrtome (Cramer & Diez, 1975; fig. 2, 2) similar, if not identical, to those of *C. mariae* and *C. cromatica*. We therefore transfer this species to *Coronaspora*.

OCCURRENCE. La Peral **EC** Biozone, La Vid, uppermost **H**, or lowermost **EC** Biozone, Argovejo, **H** Biozone; Middle and Upper Přídolí.

Coronaspora infraornata (Rodriguez) comb. nov.

Pl. 8, fig. 9

BASIONYM. *Amocosporites infraornatus* Rodríguez 1978b: 217, pl. 1, figs 5, 6.

1978b *Amocosporites infraornatus* Rodríguez: 217, pl. 1, figs 5, 6.
1978c *Amocosporites infraornatus* Rodriguez: 412, pl. 2, fig. 3.
1983 *Amocosporites infraornatus* Rodriguez: 29, pl. 2, figs 14, 16.

HOLOTYPE. Rodriguez, 1978b: 217–18, pl. 1, figs 5, 6; San Pedro Formation, Corniero section, Province of León, Cantabrian Mountains, northwest Spain.

EMENDED DIAGNOSIS. A *Coronaspora* with a distal annulus, smooth exine, and a dark circular area over the distal pole.

DESCRIPTION. Amb subcircular to subtriangular with convex sides. Spores preserved in polar compression, suggesting an original of more or less lenticular shape. Exine with a distinct proximal kyrtome, equatorial crassitude +/– smooth to irregularly thickened, and a narrow distal annulus; annulus smooth and 2–3 μm wide, reaches to *c.* 4/5 of the spore radius. Distal pole surrounded by a circular dark area. Trilete sutures reach the crassitude, which is invaginated at the radial apices; lips smooth, distinct, and parallel-sided.

DIMENSIONS. 15–35 μm Rodriguez (1978b); 25–47 μm (25 specimens measured, present study).

COMPARISONS. Differs from *Coronaspora subornata* in having the circular dark area at the distal pole. In the present study, forms with a dark ring can be distinguished from those with a circular dark area

PLATE 10

Fig. 1 *Chelinospora hemiesferica*? (Cramer & Diez) comb. nov. BM 137697, proximal view, × 2000, Ger92/9/D1.
Fig. 2 ?*Cymbosporites* sp. A. BM 134646, proximal view, Ger92/2A.
Fig. 3 *Cymbosporites* sp. B. Arg92/10; **3a,** BM 130309, proximal/oblique view, × 2000; **3b,** BM 130310, detail of sculpture showing some grana fused into groups, × 2500.
Figs 4, 5 *Cymbosporites* sp. **4a,** BM 133533, Ger92/14, equatorial view; **4b,** same specimen showing detail of multi-layered wall structure and acinoform sculpture of muri and microconi, × 2000; **5,** sample Geras 92/8; **5a,** BM 130610, equatorial view; **5b,** BM 130611, detail of irregular distal coni, × 2000.
Fig. 6 *Chelinospora (Lophozonotriletes?) poecilomorpha* (Richardson & Ioannides) comb. nov. **6a,** BM 135046, oblique compression showing hilum and large distal verrucae, Ger92/2A; **6b,** BM 141007, proximal view, LP10/DD2; **6c,** BM 132242, distal view, Arg92/13, BM 116097; **6d,** distal view showing discrete, rounded to flat-topped verrucae variable in size, LP92/16.
Fig. 7 *Chelinospora (Lophozonotriletes?) poecilomorpha* (Richardson & Ioannides) comb. nov. BM 141007, proximal view, LP92/10/DD2.
Fig. 8 *Archaicusporites torrestionensis*? Rodriguez 1983. BM 130522, proximal/oblique view, Ger92/9.
Fig. 9 Cf. *Pachytetras* sp. Possible permanent cryptospore tetrad, Ger92/2B/2; **9a,** BM 137274, tetrad showing rugulate distal sculpture; **9b,** BM137275, triple contact.
All figs × 1000, unless stated otherwise.


1
2
3
4a
4b
5
6a
6b
7a
7b
8a
8b
9
10
11a
11b
12a
12b
13
14

but in the original description Rodriguez separated *Amicosporites infraornator* from *A. subornata* on the distal position of the dark area. Cramer & Diez (1975) on the other hand thought that the dark ring in *A. subornator* was proximal. If further specimens show that in *A. subornator* the dark ring is distal then the two species may have to be combined.

REMARKS. The spores differ from typical members of the genus *Amicosporites* in having a proximal kyrtome (see under *C. cromatica*). Rodríguez (1978b) included in her species both spores with a distal annulus, not well defined at the inner margin, and others where the annulus was dissected into a series of verrucate-like structures (Rodríguez, 1978b: pl. 1, fig. 12).

OCCURRENCE. Geras, upper **RS, H** and lower **EC** Biozones, La Vid, upper **RS** to top **H** Biozones, Argovejo, **RS**, **H**, **EC** and **MN** Biozones, La Peral upper **H** and lower **EC** Biozones; Přídolí and lowermost Devonian.

Infraturma **PATINATI** Butterworth & Williams 1958 emend. Smith & Butterworth 1967

Genus ***CHELINOSPORA*** Allen 1965

TYPE SPECIES. *Chelinospora concinna* Allen 1965.

Chelinospora canistrata sp. nov. Pl. 8, fig. 8.

DERIVATION OF NAME. Latin *canistrum* n. wicker basket, canistrata resembling a basket.

HOLOTYPE. FM 1492, sample Geras 92/5, slide 2 (542), co-ord. 0831024, E.F. no. J33/1; Lower San Pedro Formation, Geras section, Province of León, Cantabrian Mountains, northwest Spain.

DIAGNOSIS. A *Chelinospora* with low large verrucae-muri and closely packed convolute microrugulae.

DESCRIPTION. Proximally hilate, distally patinate miospores; hilum thin, sometimes diaphanous, frequently torn, or may be collapsed or lost, with a narrow concentric fold just inside the crassitude; narrow equatorial curvatural crassitude with short proximal radial muri extending to the hilum margin seen on a few specimens; distal sculpture of low verrucae and muri, often indistinct, and closely packed sinuous microrugulae < 1 μm wide. Y-mark with narrow 'folds' extend *c.* 2/3 spore radius and merge into crassitude at the hilum margin.

DIMENSIONS. 25–43 μm (based on 18 specimens).

COMPARISONS. The sculpture of low verrucae-muri and microrugulae distinguish *Chelinospora canistrata* sp. nov. from other *Chelinospora* species.

OCCURRENCE. Found in all sections apart from La Vid, uppermost **RS**, **H**, and lower **EC** Biozones.

Chelinospora cantabrica sp. nov. Pl. 4, fig. 7; Pl. 9, fig. 1

DERIVATION OF NAME. Named after the Cantabrian region, NW Spain.

HOLOTYPE. FM 1493 (Pl. 9, fig. 1), diameter 39 μm, sample Argovejo 92/5a, slide 3 (473), co-ord. 1441082, E.F. no. P39/1; Lower San Pedro Formation, Argovejo section, Province of León, Cantabrian Mountains, northwest Spain.

DIAGNOSIS. A *Chelinospora* with a reticulum composed of broad muri with occasional constrictions and narrow sutures, lumina wide, polygonal to irregular.

DESCRIPTION. Proximally hilate miospores, equatorially 2–4 μm thick, distal exine thick (not measured); amb subcircular to subtriangular. Proximal exine thin, frequently broken, or absent, trilete mark not seen. Equatorially and distally sculptured with a broad reticulum, muri 1–10 μm wide, 1–3 μm high, lumina wide and polygonal 2.5–10 μm wide; muri show constrictions broken by narrow sutures at the junction with adjacent polygonal fields.

DIMENSIONS. 5–51 μm (based on 20 specimens).

COMPARISONS. The broad muri with distinct constrictions and sutures, and wide +/– polygonal lumina, distinguish this species from other species of *Chelinospora*. *Coronaspora reticulata* sp. nov. has similar reticulate sculpture but has an equatorial crassitude and a proximal kyrtome.

OCCURRENCE. Argovejo, Geras, and La Vid sections, Lower San Pedro Formation, **RS** and lowermost **H** Biozones, occasional finds in higher zones in the La Vid section.

Chelinospora cassicula Richardson & Lister 1969

1969 *Chelinospora cassicula* Richardson & Lister: 242–43, pl . 42, figs 10–12.

1978a *Chelinospora mariae* Rodriguez (pars); Rodriguez: 10, pl. 1, fig. 3 only.

REMARKS. Rodriguez, 1978a (pl. 1, figs 3–5) placed several spore morphologies in this taxon but from the illustration the holotype belongs in *C. cassicula*.

In the Spanish material examined for this paper several *Chelinospora* species with an equatorial band of radial muri form an evolving 'lineage' (morphon) beginning with *C. hemiesferica*,

PLATE 11

Fig. 1 *Conochitina pachycephala* Eisenack 1964. FC 90l, lateral view, × 170, LP3/SB4/45.

Fig. 2 *Conochitina alargada* Cramer 1967. FC 91, lateral view, × 220, Arg4/SB7/3.

Figs 3, 5, 6 *Cyathochitina elenitae* Cramer 1964. **3,** FC 92, lateral view, × 200, LP3/SB4/48; **5,** FC 93, lateral view × 200, Arg4/SB7/3; **6,** FC 94, Arg3/SB7/1; **6a**, lateral view × 150; **6b**, detail of carina, × 750.

Fig. 4 *Spinachitina* sp. FC 95, LP2/SB4/43; **4a**, lateral view, × 300; **4b**, basal margin detail, × 1750.

Fig. 7 *Calpichitina velata* (Wrona 1980). FC 96, Ger15b/SBGeras-1; **7a**, apertural view, × 500; **7b**, detail of operculum × 1000.

Fig. 8 *Vinnalochitina horrentis* (Jaglin 1986). FC 97, Ger13/SBGeras-2; **8a**, apertural view, × 500; **8b**, detail of operculum × 1000.

Fig. 9 *Cingulochitina wronai* Paris & Kríz 1984. FC 98, lateral view, × 500, Arg7/541/2, (R/34).

Fig. 10 *Urnochitina urna* Eisenack 1934. FC 99, lateral view, × 300, LP20/SB5/55.

Fig. 11 *Cingulochitina ervensis* (Paris 1979). FC 100, Ger11/458/7, (N31/2); **11a**, lateral view, × 250; **11b**, detail of carina, × 1000.

Fig. 12 *Cyathochitina* sp. B, Paris 1981.FC 101, Arg3/SB7/1; **12a**, lateral view, × 300; **12b**, detail of carina, × 800.

Fig. 13 ?*Margachitina catenaria* Obut 1973. FC 102, apertural view, × 400, Ger16/471/3.

Fig. 14 *Eisenackitina bohemica* (Eisenack 1934). FC 103, lateral view, Ger14/468/14, (Q26/4).

followed by *C.* cf. *hemiesferica* in the **H** Biozone, accompanied by *C. lavidensis* in the upper part of the **H** zone. *Chelinospora media* and *C. cassicula* are confined to the higher parts of the section studied Lower Lochkovian (upper **EC** & lower **MN** Biozones).

OCCURRENCE. Argovejo, Geras, and La Vid sections Upper San Pedro Formation, lower **MN** (**NA**) Sub-Biozone.

Chelinospora hemiesferica (Cramer & Diez) comb. nov. Pl. 4, fig. 9; Pl. 9, figs 3, 5

BASIONYM. *Iberoespora hemiesferica* Cramer & Diez, 1975: 341, pl. 2, figs 34–36.

1978c *Cymbosporites dittonensis* Richardson & Lister; Rodriguez: pl. 3, fig. 18.

HOLOTYPE AND LOCUS TYPICUS. Cramer & Diez 1975: 334, 336; pl. 2, figs 34, 35: 'base of a thick green shale 10 m below the exposed top of the San Pedro Formation at the westernmost outcrop in the village of Argovejo in the province of León, Spain'.

EMENDED DIAGNOSIS. A *Chelinospora* with closely spaced narrow muri, geniculate in plan, over the distal hemisphere and an equatorial to subequatorial area, where the muri become radial. Proximal exine thin, trilete mark labrate, labra narrow.

DIMENSIONS. 30–40µm (Cramer & Diez, 1975); 29–44 µm (based on 75 specimens, present study), muri <1 µm wide and high.

REMARKS. The spores may be double-layered and on some specimens a membranous curvatural zone is seen bearing radial extensions of the distal muri.

COMPARISON. The tightly packed geniculate narrow distal muri distinguish this species. Cramer & Diez (1975) refer to a 'pronounced sculpture of brain-like muri' distally.

OCCURENCE. Distributed through the **H** to lower **MN** Biozone (**NA** Sub-Biozone).

Chelinospora cf. *hemiesferica* (Cramer & Diez) comb. nov. Pl. 4, figs 6, 10; Pl. 9, fig. 4; Pl. 10, fig. 1

DESCRIPTION AND COMPARISON. As for *C. hemiesferica,* but with broader, more widely spaced distal muri; muri more than 1–3 µm wide and 1–2 µm apart.

OCCURRENCE. Found in all sections, Argovejo, Geras, La Peral and La Vid sections, Upper San Pedro Formation; range *hemiesferica*, **EC** Biozones to lower **MN** (**NA**) Sub-Biozone; found in the *hemiesferica* Biozone only in the La Peral Section.

Chelinospora lavidensis sp. nov. Pl. 9, fig. 2

1978c *Iberoespora hemiesferica* Cramer & Diez; Rodriguez: 418, pl. 3, fig. 15.

1983 *Dictyotriletes geriense* Rodriguez: pl. 6, fig. 6 only.

DERIVATION OF NAME. Named for the La Vid locality.

HOLOTYPE. FM 1494 (Pl. 9, fig. 2), diameter 33 µm; sample Ger 9, slide D1/1, co-ord. 195 1056; E.F. no. U/36, upper San Pedro Formation, Geras section, Province of León, Cantabrian Mountains, northwest Spain.

DIAGNOSIS. A *Chelinospora* with narrow low muri, 1 µm or less wide and >1µm high, forming an irregular reticulum with broad lumina.

DESCRIPTION. Proximally hilate miospores, equatorially 2–4 µm thick, distal exine thick (not measured), amb subcircular to subtriangular. Proximal hilum thin, frequently broken or absent, trilete mark not seen. Equatorially and distally sculptured with an irregular reticulum, muri 1 µm or less wide, <1 µm high, lumina highly variable in shape and size on a single spore, at the distal pole large and polygonal 8–10 µm wide, subequatorially *c.* 1–2 µm wide; muri become radial at the equator. Y-mark with narrow 'folds' extends *c.* 2/3 spore radius and merge into crassitude at the hilum margin, frequently gape over much of the hilum forming a distinct triangular area.

DIMENSIONS. 29–43 µm (based on 17 specimens).

COMPARISON. *Chelinospora hemiesferica* (Cramer & Diez) comb. nov. has a distal sculpture of closely packed geniculate muri but resembles *C. lavidensis* sp. nov. because both species have an equatorial band of radial muri.

REMARKS. Several species of *Chelinospora* (*C. hemiesferica, C. sanpetrensis, C. media* and *C. lavidensis*) have a subequatorial band of muri normal to the equator, which may indicate affinity or possibly represents a feature related to the development of the tetrad in muronate spores.

OCCURRENCE. Upper part of **H** and **EC** Biozones, rare in lower **MN** (**NA**) Sub-Biozone, Upper Přídolí and lowermost Devonian, Argovejo, Geras and La Vid sections.

PLATE 12

Figs 1, 2 *Pseudoclathrochitina carmenchui* (Cramer 1964). **1,** FC 104, lateral view, × 350, Arg11A/508/12, (Q27/4); **2,** FC 105, LP20/SB5/54; **2a**, lateral view × 400; **2b**, basal margin detail, × 1100.

Fig. 3 *Margachitina elegans* var. *corta* (Cramer 1964). FC 106, lateral view, × 300, Arg12/510/8, (K30/4).

Fig. 4 *Urnochitina urna*, Eisenack 1934. FC 107, chain of 3 individuals, lateral view, × 220, LV10/492/9, (N34).

Fig. 5 *Margachitina elegans* Taugourdeau & de Jekhowski 1960. FC 108, lateral view, × 300, LV12/494/8, (N25).

Fig. 6 *Sphaerochitina sphaerocephala* (Eisenack 1932). FC 109, lateral view, × 700, Arg5A/SB7/4.

Fig. 7 *Fungochitina kosovensis* Paris & Kríz 1984. FC 110, LP19/SB5/57; **7a**, lateral view, × 200; **7b**, basal margin detail, × 1250.

Fig. 8 *Angochitina tsegelnjucki* Paris & Grahn 1996. FC 111, lateral view, × 200, Ger14/468/8, (P31/4).

Fig. 9 *Cingulochitina serrata* (Taugourdeau & Jekhowski 1960). FC 112, LV12/494/8, (N24), **9a,** chain of 11 individuals, lateral view, × 130; **9b,** detail of connection, × 500.

Fig. 10 *Angochitina echinata* Eisenack 1931. FC 113, LP8/CSB1/1; **10a,** lateral view, × 350; **10b,** neck detail, × 750.

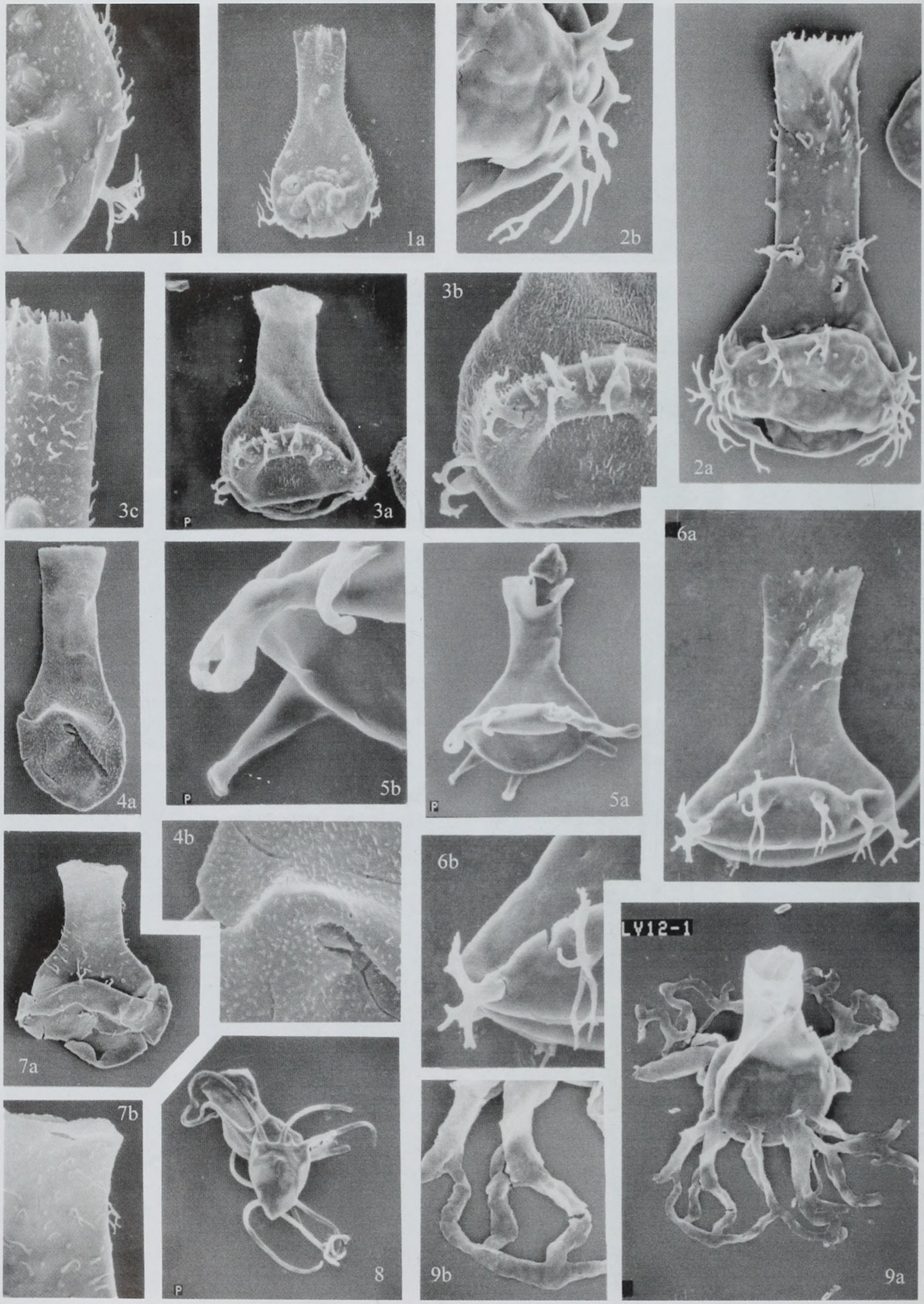
Fig. 11 *Angochitina thadeui* Paris 1981. FC 115, LV5a/CSB1/8; **11a,** lateral view, × 200; **11b**, apertural detail, × 650.

Fig. 12 *Angochitina ambrosi ambrosi* Schweineberg 1987. FC 116, Ger8/461/8, (N38/3); **12a,** lateral view, × 200; **12b,** apertural detail, × 750.

Fig. 13 *Angochitina chlupaci* Paris, Laufeld & Chlupac 1981. FC 117, lateral view, × 250, Arg13/455/2, (J28/2).

Fig. 14 *Angochitina echinata* Eisenack 1931. FC 114, Ger9/456/7, (K31/1); **14a,** lateral view, × 300; **14b,** spiny ornament detail, × 850.


1
2a
3
4
5
6
7a
7b
11a
11b
8
9b
10a
12a
2b
13
10b
9a
12b
14b
14a


1b
1a
2b
2a
3c
3a
3b
4a
5b
5a
6a
4b
6b
7a
LV12-1
7b
8
9b
9a

Chelinospora media sp. nov. Pl. 9, fig. 6

1978a *Chelinospora mariae* Rodríguez (pars): 10, pl. 1, fig. 4.

DERIVATION OF NAME. Latin *medius* a., intermediate.

HOLOTYPE. FM 1495, sample Argovejo 92/12 (510) 3, 093 1019, E.F. no. K32/2 J32/4; Lower San Pedro Formation, Argovejo section, Province of León, Cantabrian Mountains, northwest Spain.

DIAGNOSIS. A *Chelinospora* with low muri, <1 μm wide and < 1μm high, forming a regular reticulum with broad lumina of more or less even size.

DESCRIPTION. Proximally hilate miospores, equatorially 2–4 μm thick, distal exine thick (not measured); amb subtriangular. Proximal hilum thin, frequently broken, or absent, trilete mark not usually seen. Exine equatorially *c.* 5 μm, distally thick equatorially, but not measured. Equatorially and distally sculptured with a reticulum, muri 1 μm or less wide, 1–2 μm high, lumina relatively large, polygonal and 6–14 μm wide; muri become radial at the equator. A few specimens show a Y-mark, with sutures to the inner margin of the patina.

DIMENSIONS. 31–60 μm (based on 12 specimens); England, 37–67 μm (based on 37 specimens).

COMPARISON. Differs from *Chelinospora lavidensis* by the more regular reticulum with broad, more or less even, lumina. The holotype of *Chelinospora mariae* Rodriguez (1978a: pl. 1, fig. 3) appears to be conspecific with *C. cassicula* Richardson & Lister 1969, but other specimens figured by Rodriguez (1978a: pl. 1, fig. 4) appear identical to *C. media* sp. nov.

REMARKS. There appears to be a morphological gradation between *Chelinospora lavidensis*, *C. media*, and *C. cassicula* with some overlap in the ranges of the species. *C. lavidensis* occurs in the uppermost Přídolí and Lower Devonian (upper **H**, **EC** Biozones and lower **MN** Sub-Biozone) of the Cantabrian Mountains. *C. media* occurs near the Silurian/Devonian Boundary and in the lower **MN** Sub-Biozone, and is rare in the middle **MN** Sub-Biozone; *C. cassicula* occurs both in Spain and England in the lower **MN** Sub-Biozone, and especially the middle **MN** Sub-Biozone in England.

Two tryads/dyads (Richardson, 1996a: pl. 3, figs 1, 2) show such close similarities in sculpture to *C. media* that they probably were derived from the same, or closely similar, plants. All these *Chelinospora* species represent part of an evolving spore morphon and were probably derived from a group of closely related plants. The dyads of the species *Chelinohilates erraticus* Richardson 1996b: pl. 7, figs 5–7, have identical sculptural patterns.

OCCURRENCE. Upper San Pedro Formation, La Vid **EC** Biozone, Argovejo and Geras sections, lower **MN** Biozone, uppermost Silurian and Lower Lochkovian. Occurs in the lower part of the lower **MN** (**NA**) Sub-Biozone, Shropshire and Herefordshire in England.

Chelinospora (Lophozonotriletes?) poecilomorpha (Richardson & Ioannides) comb. nov. Pl. 10, figs 6, 7

BASIONYM. *Lophozonotriletes? poecilomorpha* Richardson & Ioannides, 1973: pl. 7, figs 9–15; pl. 8, figs, 1, 4–6.

HOLOTYPE. Richardson & Ioannides, 1973: pl. 7, fig. 10, BP10/22-831060, C1-34 borehole, Libya.

REMARKS. This taxon is transferred to the genus *Chelinospora* because specimens studied under SEM and light microscopy show a distinct distal pattern with a thin polar proximal membrane.

Chelinospora sanpetrensis (Rodriguez) comb. nov. Pl. 4, fig. 8; Pl. 7, fig. 10

BASIONYM. *Brochotriletes sanpetrense* Rodriguez, 1978c: 414, pl. 1, fig. 13.

1983 *Brochotriletes sanpetrensis* Rodriguez: 34, pls 1, 10, 19.

HOLOTYPE AND LOCUS TYPICUS. Rodriguez, 1978c: pl. 1, fig. 13; Torrestio, Province of León Cantabrian Mountains, northwest Spain, lower part of San Pedro Formation.

EMENDED DIAGNOSIS. A *Chelinospora* with a densely murornate, foveolate, and irregular foveo-reticulate sculpture with broad, sinuous, low muri, and narrow lumina.

DESCRIPTION. As in Rodriguez, 1978c: 414, but forms with a reticulum of wide muri and large rounded, polygonal and irregular lumina are classified as a separate species (*C. cantabrica* sp. nov.).

DIMENSIONS. 24, 29–49 μm (based on 60 specimens); 30–45 μm. (Rodriguez, 1978c).

REMARKS. The structure is patinate and consists of a thick distal exine and a thin proximal hilum, frequently ruptured, with a narrow fold on the inner margin of the curvaturae. Under the SEM some specimens show a sculpture of microrugulae and micrograna in the curvaturate zone. Specimens with a dominantly foveolate sculpture are referred to as *Chelinospora* cf. *sanpetrensis* but probably grade into the reticulate forms.

OCCURRENCE. Argovejo, Geras, La Peral and La Vid sections, lower and middle San Pedro Formation; range **RS** and lower to middle **H** Biozones; isolated specimens found in lower **EC** Sub-Biozone (Geras) and lower **MN** (**NA**) Sub-Biozone (La Vid).

Genus ***CYMBOSPORITES*** Allen 1965

TYPE SPECIES. *Cymbosporites cyathus* Allen 1965.

Cymbosporites* cf. *dittonensis Richardson & Lister 1969 Pl. 9, fig. 7

DIMENSIONS. 22–35 μm (based on 6 specimens).

PLATE 13

Figs 1, 3c *Palenchitina pisuergensis* Schweineberg 1987. FC 118, Ger7/SB7/6; **1a,** lateral view, × 300; **1b,** ornament detail, × 1000; **3c,** enlargement of part of Fig. 1a, × 1000.

Fig. 2 *Ancyrochitina valladolitana* Schweineberg 1987. FC 119, Ger4/CSB3/5; **2a,** lateral view, × 355; **2b,** appendix detail, × 750.

Fig. 3 *Ancyrochitina javieri* Schweineberg 1987. FC 120, Ger7/SB7/6; **3a,** lateral view, × 300; **3b,** basal margin detail, × 650.

Fig. 4 *Angochitina elongata* Eisenack 1931. FC 121, Ger9/456/7, (M32/1); **4a,** lateral view, × 300; **4b,** ornament detail, × 850.

Fig. 5 *Ancyrochitina fragilis brevis* Taugourdeau & Jekhowski 1960. FC 122, LV10/492/9, (L36/4); **5a,** lateral view, × 300; **5b,** appendix detail, × 1000.

Fig. 6 *Ancyrochitina libyensis* Jaglin 1986. FC 123, Arg4/SB7/3; **6a,** lateral view, × 500; **6b,** appendix detail, × 850.

Fig. 7 *Ramochitina villosa* (Laufeld 1974). FC 124, Ger2B/CSB3/3; **7a,** lateral view, × 400; **7b,** apertural detail, × 500.

Fig. 8 *Plectochitina rosendae* Cramer & Diez 1978. FC 125, lateral view, × 400, LV10/492/9, (H35/1).

Fig. 9 *Plectochitina carminae* Cramer 1964. FC 126, LV12/494/7, (P22/4); **9a,** lateral view, × 300; **9b,** appendix detail, × 600.

REMARKS. The Cantabrian material has close-packed wide based coni to spinose elements, some biform. The elements are not mixed with minute cone as in typical forms of the species.

OCCURRENCE. Rare, Upper San Pedro Formation, Argovejo, Lower **MN (NA)** Sub-Biozone.

Cymbosporites **sp. B** Pl. 10, fig. 3

DESCRIPTION. Amb subtriangular to subcircular, usually preserved in polar compression. Proximal surface laevigate, contact areas covered by a thin diaphanous exine (hilum), near the periphery of the contact areas are distinct arcuate folds, which form a constant character, usually destroyed except near the margin. Outside the contact areas the exine is much thicker, equatorially and distally, 1.5–2 µm (measured equatorially). Sculpture confined to the equatorial margin and distal hemisphere; consists of broad based coni rounded in plan and evenly tapered in profile, *c.* 1.5 µm wide and >1 µm high; sculptural elements spaced, but with insufficient distance between them for elements of a similar size. Triradiate mark not seen apart from curvatural invaginations at the radial apices.

DIMENSIONS. 26–31 µm (based on 11 specimens).

COMPARISONS. Similar to *Cymbosporites* cf. *catillus* Allen 1965 in Richardson & Lister 1969 except that the coni are broad-based and larger.

REMARKS. Other specimens which may belong to the genus have been found in the Argovejo and Geras sections, namely ?*Cymbosporites* sp. A (Pl. 10, fig. 2) and *Cymbosporites* sp. (Pl. 10, figs 4, 5).

OCCURRENCE. Upper San Pedro Formation, Argovejo, Geras, and La Vid, **EC** Biozone and rare lower **MN (NA)** Sub-Biozone.

TAXONOMY OF CHITINOZOA

As the main purpose of this paper is to define a spore biozonation for the Cantabrian region, only *Ramochitina villosa* (formerly *Gotlandochitina* Laufeld 1974) is described briefly here. A more detailed investigation of the chitinozoans from the Cantabrian Area is to be presented in a forthcoming publication. All material is deposited in the collections of the Natural History Museum, London.

Order **PROSOMATIFERA** Eisenack 1972
Family **LAGENOCHITINIDAE** Eisenack 1931, emend Paris 1981
Subfamily **ANGOCHITININAE** Paris 1981
Genus ***RAMOCHITINA*** Sommer & van Boekel 1964, emend. Paris *et al.* 1999

TYPE SPECIES. *Ramochitina ramosi* Sommer & van Boekel, 1964: 426, pl. 1, fig. 3.

Ramochitina villosa (Laufeld 1974) Pl. 13, fig. 7

1974 *Gotlandochitina villosa* Laufeld: 95, figs 7a, b.
1994 *Gotlandochitina villosa* Laufeld; Sutherland: 65, pl. 17, figs 7–14.

HOLOTYPE. LO 4587 T, figured Laufeld, 1974: fig 56a.

DIAGNOSIS. (After Laufeld, 1974: 95). Body spheroidal, neck cylindrical to subcylindrical; broadly rounded flexure. Ornament of spines which may exhibit simple branching; spines on apertural portion of vesicle curved in aboral direction and in opposite direction on the apertural portion of vesicle; spines on neck decrease in size towards oral pole.

DISCUSSION. In the generic revision of Paris, Winchester-Seeto, & Grahn (2000) *Gotlandochitina* Laufeld 1974 is considered a junior synonym of *Ramochitina* Sommer & van Boekel 1964. *G. villosa* is here transferred to *Ramochitina*.

ACKNOWLEDGEMENTS. We are indebted to the Natural Environment Research Council for research grant GR3/09624; to Katie Bagshaw and Denise Darwin for technical assistance and for preparing material and picking spores for light and SEM microscopy; Peter York is thanked for the light photomicrographs, Chris Jones and Alex Ball for help with SEM studies; and Derek Adams, Natural History Museum Photographic Unit, who composed the plates electronically.

REFERENCES

Achab, A. & Asselin, E. 1993. Upper Silurian and Lower Devonian chitinozoan microfaunas in the Chaleurs Group, Eastern Canada. *Special Papers in Palaeontology*, **48**: 7–15, pl. 1.
Achilles, H. 1981. Die rätische und liassiche Microflora Frankens *Palaeontographica*, B **179**: 1–86, pls 1–17.
Allen, K. C. 1965. Lower and Middle Devonian spores of North and Central Vestspitsbergen. *Palaeontology*, **8**: 687–748, pls 94–108.
Arkhangel'skaya, A. D. 1980. Plant spores from some Lower Devonian sections of the western regions of the Russian Platform (in Russian). *In*, Urvanova, V. N. & Nemtinova, G. I., *Palynological research in the Proterozoic and Phanerozoic of oil- and gas-bearing regions of the USSR. Trudy Vnigni, Moscow*, **217**: 26–46, 140–44, pls 5–11.
Barrois, Ch. 1882. Récherches sur les terrains des Asturies et la Galice. *Memoires de la Société Géologique du Nord, Lille*, **2**: 630 pp., 20 pls.
Burgess, N.D. 1991. Cryptospores and miospores from the Type Llandovery Area, south-west Wales. *Palaeontology*, **34**: 565–99, pls 1, 2.
Burgess, N. D. & Richardson, J. B. 1991. Silurian cryptospores and miospores from the type Wenlock area, Shropshire, England. *Palaeontology*, **34:** 601–28, pls 1, 2.
—— & —— 1995. Late Wenlock to Early Přídolí cryptospores and miospores from south and south-west Wales, Great Britain. *Palaeontographica*, B **236**: 1–44, pls 1–10.
Chaloner, W. G. & Streel, M. 1968. Lower Devonian spores from South Wales. *Argumenta Paleobotanica*, **1**: 87–101, pls 19, 20.
Comte, P. 1934. Sur les couches intermédiares entre le Silurien de Dévonien dans les Asturies. *Comptes Rendu de l'Academie des Sciences*, **198**: 1–166.
—— 1937. La série Cambrienne et Silurienne de León. *Compte Rendu de l'Academie de Sciences*, **204**: 604 pp.
—— 1959 Recherches sur les terrains anciens de la Cordillère Cantabrique. *Memorias Instituto Geológico y Minero de España*, Madrid, **60**: 13–425.
Cramer, F.H. 1964*a*. Some acritarchs from the San Pedro Formation (Gedinnian of the Cantabric Mountains in Spain). *Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie*, **73**: 33–38, pls 1, 2.
—— 1964*b*. Microplankton from three Palaeozoic formations in the province of León (NW Spain). *Leidse geologische mededelingen*, **30**: 255–361, pls 1–24.
—— 1966*a*. Palynomorphs from the Siluro-Devonian boundary in NW Spain. *Notas y Comunicaciónes del Instituto Geológico y Minero de España*, **85**: 71–82, pls 1–3.
—— 1966*b*. Chitinozoans of a composite section of Upper Llandovery to basal Lower Gedinnian sediments in northern León, Spain. A preliminary report. *Bulletin de la Société Belge de Géologie*, **75** (1): 69–129, pls 1–5.
—— 1966*c*. Hoegispheres and other microfossils *incertae sedis* of the San Pedro Formation (Siluro-Devonian Boundary) near Val porquero, León, NW Spain. *Notas y Comunicaciones, del Instituto Geológico y Minero de España*, **86**: 69–129, pls 1, 2.
—— 1967. Palynology of Silurian and Devonian rocks in northwest Spain. *Boletín del Instituto Geológico y Minero de España*, **77**: 223–286, pls 1–4.
—— 1970. Distribution of selected Silurian acritarchs. *Revista Española de Micropaleontologia Número extraordinario*, **1**: 203 pp., 23 pls.
—— & Diez, M. d. C. R. 1968. Consideraciones taxonómicas sobre los acritarcos del Silúrico medio y superior del Norte de España. Los acritarcos acantomorfíticos. *Boletín del Instituto Geológico y Minero de España*, **79**: 541–574, 21 pls.
—— & —— 1975. Earliest Devonian miospores from the Province of León, Spain. *Pollen et Spores*, **17**: 331–344, pls 1–2.

—— & —— 1978*a*. Iberian chitinozoans. 1. Introduction and summary of pre-Devonian strata. *Palinología Número extraordinario,* **1**: 149–201, pls 1–10.

—— & —— 1978*b*. Iberian Chitinozoans. 2. Lower Devonian forms (La Vid Shales and equivalents). *Palinología Número extraordinario,* **1**: 203–217, pls 1, 2.

D'Erceville, M. A. 1979. Les spores des formations Siluro-Dévoniennes de la coupe de Saint-Pierre sur-Erve (synclinorium median Amoricain). *Palaeontographica,* **171 B**: 79–121, pls 1–7.

Dufka, P. 1995. Upper Wenlock miospores and cryptospores derived from a Silurian volcanic island in the Prague Basin (Barrandian area, Bohemia) *Micropalaeontology,* **14**: 67–79, pls 1–3.

Eisenack, A. 1931. Neue Mikrofossilien des baltischen Silurs I. *Paläontologische Zeitschrift,* **13**: 74–118, 5 pls.

—— 1932. Neue Mikrofossilien des baltischen Silurs II. *Paläontologische Zeitschrift,* **14**: 257–277, 2 pls.

—— 1934. Neue Mikrofossilien des baltischen Silurs III. Und neue Mikrofossilien des böhmischen Silurs. *Paläontologische Zeitschrift,* **16**: 52–76, 2 pls.

—— 1937. Neue Mikrofossilien des baltischen Silurs IV. *Paläontologische Zeitschrift,* **19**: 217–243, 2 pls.

—— 1964. Mikrofossilien aus dem Silur Gotlands. Chitinozoen. *Neues Jarbuch fuer Geologie und Paläontologie Abhandlungen,* **120**: 308–342, 30 pls.

—— 1971. Weitere Mikrofossilien aus dem Beyrichienkalk (Silur). *Neues Jarbuch fuer Geologie und Paläontologie Abhandlungen,* **8**: 449–460, 3 pls (Abt. 1–33).

—— 1972. Beitrage zur chitinozoen forschung. *Palaeontographica,* A **140**: 117–130, pls 32–37.

Elles, G. L. & Wood, E. M. R. 1901–1918. British Graptolites. *Monographs of the Palaeontographical Society, London.* 539 pp.

Fanning, U., Richardson, J. B. & Edwards, D. 1991. A review of *in situ* spores in Silurian land plants. *In,* Blackmore, S. & Barnes, S. H. (editors), Pollen and spores, patterns of diversification. *Systematics Association Special Volume,* **44**: 25–47, 2 pls.

Holland, C. H. 1985. Series and stages of the Silurian System. *Episodes,* **8**: 101–103.

—— **& Richardson, J. B.** 1977. *The British Isles. In,* Martinsson, A. (editor), *The Silurian/Devonian boundary*: 355–44. Stuttgart.

Jaglin, J. C. 1986. Nouvelles espéces de Chitinozoaires du Přídolí de Libye. *Révue de Micropaléontologie,* **29**: 44–54, 1 pl.

Jansonius, J. J. & Hills, L. V. 1979. Genera file of fossil spores, supplement. *Special publication, Department of Geology,* University of Calagary, Canada.

—— & —— 1990. Genera file of fossil spores, supplement. *Special publication, Department of Geology,* University of Calagary, Canada. Supplement **10**, card 4630.

Julivert, M. 1967. La ventana del Rio Monasterio y la terminación meridional del Manto del Ponga. *Trabajos de Geologia, University of Oviedo,* **1**: 59–76.

Koren, T. N. 1968. The first occurrence of early Devonian monograptids in the Borshchov horizon of Podolia. *Doklady Akademiya Nauk, SSSR,* **182**: 938–940, 1 pl. [In Russian].

Kriz, J., Jaeger, H., Paris F. & Schonlaub, H. P. 1986. The Přídolí – the fourth subdivision of the Silurian. *Jahrbuch der Geologischen Bundestalt, Vienna, 129*: 291–360, pls 5–6.

Laufeld, S. 1974. Silurian Chitinozoa from Gotland. *Fossils and strata,* **5**: 130 pp, figs 4–74.

Le Herisse, A., Gourvennec, R. & Wicander, R. 1977. Biogeography of Late Silurian and Devonian acritarchs and prasinophytes. *Review of Palaeobotany and Palynology,* **98**: 105–124, 2 pls.

Llopis-Llado, N. 1958. Las bases estratigráficas del Devónico de Asturias. *Breviora Geológica Astúrica* **2**: 13–21.

—— 1960. Estudio geológico de las Sierras de la Corxera, Mostayal y Monsacro. *Instituto de Geología Aplicada, Oviedo, Monografia Geológica,* **14**: 1–132, 5 pls.

—— 1964. Sur le Dévonien inférieur des Asturies (Espagne).*Mémoire du Bureau de Recherches Géologiques et Minières,* **33**: 57–58.

Mädler, K. 1964. Die geologische Verbreitung von Sporen und Pollen in der Deutschen Trias, *Beihefte zum Geologischen Jahrbuch,* **65**: 147 pp, 12 pls.

McGregor, D. C. 1961. Spores with radial pattern from the Devonian of Canada, *Geological Survey of Canada,* Bulletin, **76**: 11pp, 1 pl.

—— **& Camfield, M.** 1976. Upper Silurian(?) to Lower Devonian spores of the Moose River Basin, Ontario. *Geological Survey of Canada,* Bulletin, **263**: 63 pp, 8 pls.

McKerrow, W. S. & Scotese, C. R. 1990. Palaeozoic palaeogeography and biogeography. London: Geological Society, **12**: 435 pp.

Mogensen, G. S. 1981. The biological significance of morphological characters in bryophytes: the spore. *The Bryologist,* **84**: 187–207.

Moreau-Benoit, A. 1976. Les schistes et calcaires Eodevoniens de Saint-Céneré (Massif Amoricain, France). *Mémoires Société géologique minéralogique Bretagne,* **19** (328): 27–58, pls 4–9.

Nestor, V. 1990. Silurian Chitinozoans. Field meeting Estonia 1990. *In,* Kaljo, D. & Nestor, H. (editors), An excursion guidebook, pp. 80–83, pls 14, 15. Institute of Geology, Estonian Academy of Sciences, IUGS, IGCP. Tallin.

Nikiforova, O. I. 1977. Podolia. *In,* Martinsson, A. (editor), The Silurian-Devonian boundary IUGS Series A, **5**: 52–64. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

Obut, A. M. 1973. On the geographical distribution, comparative morphology, ecology, phylogeny and the taxonomic position of Chitinozoa. *In,* Betekhtina O. A. & Zhuravleva I. T. (editors), *Environment and life in the geologic past.,* pp. 72–84, 148–152, 166–174. Institut Geologii i Geofiziki, Novosibirsk. [In Russian].

Paris, F. 1979. 2 Chitinozaires. *In,* Babin, C., Deunff, J., Melou, M., Paris, F., Pelhate, A., Plusquellec, Y. & Racheboeuf, P., La coupe de Porz-ar-Vouden (Přídolí de la Press' Ilea de Crozon), Massif armoricain, France. Lithologie et biostratigraphie. *Palaeontographica,* A **164**: 52–84, 3 pls.

—— 1981. Les Chitinozaires dans le Paléozoïque du sud-ouest de l'Europe (cadre géologique – étude systématique – biostratigraphie). *Mémoire de la Société Géologique et Minéralogique de Bretagne,* **26**: 496 pp., pls 1–41.

—— **& Grahn, Y.** 1996. Chitinozoa of Silurian-Devonian boundary sections in Podolia, Ukraine. *Palaeontology,* **36** (3): 629–649, pls 1–4.

——, ——, **Nestor, V. & Lakova, I.** 1999. A revised chitinozoan classification. *Journal of Paleontology,* **73** (4): 549–70.

—— **& Kriz, J.** 1984. Nouvelles Especes de chitinozoaires a la limite Ludlow/Přídolí en Tchecoslovaquie. *Review of Palaeobotany and Palynology,* **43**: 155–177, 3 pls.

——, **Laufeld, S. & Chlupac, I.** 1981. Chitinozoa of the Silurian-Devonian boundary stratotypes in Bohemia. *Sveriges Geologiska Undersökning, Series,* C **51**: 29, pls 1–3.

——, **Verniers, J., Al-Hajri, S. & Al-Tayyar, H.** 1995. Biostratigraphy and palaeogeographic affinities of Early Silurian chitinozoans from central Saudi Arabia. *Review of Palaeobotany and Palynology,* **89**: 75–90, 1 pl.

——, **Winchester-Seeto, T. & Grahn, Y.** 2000. Toward a global biozonation of Devonian chitinozoans. *Courier Forschungsinstitut Senkenberg,* **220**: 35–55.

Perold, S. M. 1989. Spore-wall ornamentation as an aid in identifying the southern African species of Riccia (Hepaticae). *Journal Hattori Botanical Laboratory,* **67**: 109–201, figs 1–48.

Poll, K. 1962. *Die Furada-Zone als Silurium/Devon (Grenze) mit westlichen Kantabrischen Gebirge (Nordspanien),* 158 pp. Dissertation, Munster.

—— 1963. Zur Stratigraphie des Altpaläozoikums von Belmonte (Asturien, Nordspanien), N. Iberien. *Geologische und Paläontologische Abhandlungen,* **117**: 235–250, pl. 16.

—— 1970. Stratigraphie und Tektonik an der Wende Silurium/Devon im westlichen Kantabrischen Gebirge (Nordspanien). *Sitzungsberichte Physikalisch-medizinschen Sozietat zu Erlangen,* **83/84**: 33–113, pls 1–10.

Potonié, R. & Kremp, G. O. W. 1954. Die Gattungen der paläozoischen Sporae dispersae und ihre Stratigraphie. *Geologischen Jahrbuch,* **69:** 111–194, pl. 20.

Richardson, J. B. 1996a. Abnormal spores and possible interspecific hybridization as a factor in the evolution of Early Devonian land plants. *Review of Palaeobotany and Palynology,* **93**: 333–340, 3 pls.

—— 1996b. Taxonomy and classification of some new Early Devonian cryptospores from England. *Special Papers in Palaeontology,* **55**: 7–40, 10 pls.

——, **Ford, J. H. & Parker, F.** 1984. Miospores, correlation and age of some Scottish Lower Old Red Sandstone sediments from the Strathmore region (Fife and Angus). *Journal of Micropalaeontology,* **3**: 109–124, 4 pls.

—— **& Ioannides, N. S.** 1973. Silurian palynomorphs from the Tanezzuft and Acacus Formations, Tripolitania, North Africa. *Micropaleontology,* **19**: 257–307, pls 1–13.

—— & —— 1979. *Emphanisporites splendens,* a new name for *Emphanisporites pseudoerraticus* Richardson & Ioannides, 1973 (preoccupied). *Micropaleontology,* **25**: 111.

—— **& Lister, T. R.** 1969. Upper Silurian and Lower Devonian spore assemblages from the Welsh Borderland and South Wales. *Palaeontolgy,* **12**: 201–252, pls 37–43.

—— **& McGregor, D. C.** 1986. Silurian and Devonian spore zones of the Old Red Sandstone continent and adjacent regions. *Geological Survey of Canada, Bulletin,* **364**: 1–79, 21 pls.

——, **Rodriguez, R. M. & Sutherland, S. J. E.** 2000. Palynology and recognition of the Silurian/Devonian boundary in some British terrestrial sediments by correlation with Cantabrian & other European sequences – a progress report. *Courier Forschungsinstitut Senkenberg,* **220**: 1–7, 1 pl.

——, **Streel, M., Hassan, A. & Steemans, P. H.** 1982. A new spore assemblage to correlate between the Breconian (British Isles) and the Gedinnian (Belgium). *Annales de la Société Géologique de Belgique* **105**: 135–143, 1 pl.

Rodriguez, R. M. 1978a. Nuevas miosporas de la Formación San Pedro en Geras de Gordón, Cordillera Cantábrica (Provincia de León, Noroeste de España). *Breviora Geológica Astúrica,* **22**: 9–16, 1 pl.

—— 1978b. Miospores de la Formation San Pedro (Silurien-Dévonien) a Corniero (Province de León, Espagne). *Revue de Micropaéontologie,* **20**: 216–221, 1 pl.

—— 1978c. Miosporas de la Formación Furada/San Pedro (Silúrico superior-Devónico inferior), Cordillera Cantábrica, noroeste de España. *Palinología Número Extraordinario.* **1**: 407–433, 5 pls.

——1979. [Loose-leaf Addendum slip]. *Revue de Micropaéontologie,* **20**: facing p. 232.

—— 1983. Palinologia de las formaciones del Silurico superior-Devonico inferior de la Cordillera Cantabrica, Noroeste de España. *Publicatión conjunta de la Institución Fray Bernardino de Sahagún, de la Excelentísima Diputación provincial de León y del Sericio de Publicaciones de la Universidad de León,* 231 pp., 21 pls.

Schofield, W. B. 1985. *Introduction to Bryology,* New York: Macmillan, 431 pp.

Schultz, G. 1968. Eine Unterdevonische mikroflora aus den schichten der Eifel (Rheinisches Schiefergebirge). *Paleontographica,* **B 123**: 5–42, pls 1–4.

Schweineberg, J. 1987. Silurische Chitinozoen aus der Provinz Palencia (Kantabrisches

Gebirge, N-Spanien). *Göttinger Arbeiten zur Geologie und Paläontologie*, **33**: 209–224, 13 pls.

Seward, A. C. 1931. *Plant life through the ages*. 1st edition. 601 pp. Cambridge University Press.

Shepeleva, E. D. 1963. Spores from the Lower Devonian beds of the Podolian Dneister River area. *Regional stratigraphy SSSR:* 98–101. Moscow. [In Russian].

Sommer, F. W. & van Boekel, N. W. 1964. Quitinozoarios do Devoniano de Goias. *Anais Da Academia Brasileria De Ciencias*, **36**: 423–431, 2 pls.

Steemans, P. 1989. Etude palynostratigraphique du Dévonien inferieur dans l'ouest de l' Europe. *Mémoires pour servir à l'Explication des Cartes Géologiques et Miniéres de la Belgiques*, **27**: 453 pp., 47 pls.

Streel, M. 1964. Une association de spores du Givétien inférieur de la Vendre, á Goé (Belgique). *Annales Societé Géologique de Belgique*, **87**: 1–30, 2 pls.

Suárez de Centi, C. 1988. *Estratigrafia sedimentologia y paleogeografia de la Formación Furada/San Pedro, Zona Cantábrica (NW España)*. Tésis Doctoral, Oviedo, 530 pp.

Sutherland, S. J. E. 1994. Ludlow chitinozoans from the type area and adjacent regions (Part 1). *Monograph of the Palaeontographical Society, London*: 1–104, 18 pls.

Taugourdeau, P. & de Jekhowsky, B. 1960. Répartition et description des Chitinozoaires Siluro-Dévoniens de quelques sondages de la C.R.E.P.S., de la C.F.P.A. et de la S.N. Repal au Sahara. *Revue de l'Institut Français du Pétrole, Paris*, **15**: 1199–1260, 13 pls.

Thompson, P. W. & Pflug, H. 1953. Pollen und Sporen der mittel-europäischen Tertiärs. *Palaeontographica*, **B 94:** 1–138, pls 1–15.

Tucker, R. D., Bradley, D. C., Ver Straeten, C. A., Harris, A.G., Ebert, J. R. & McCutcheon, S.R. 1998. New U-Pb zircon ages and the division of Devonian time. *Earth and Planetary Science Letters*, **158:** 175–186.

Turnau, E. 1986. Lower to Middle Devonian spores from the vicinity of Pionki (Central Poland). *Review of Palaeobotany Palynology*, **46:** 311–354, 8 pls.

Van den Bosch, W. J. 1969. Geology of the Luna-Sil Region, Cantabrian Mountains (NW Spain). *Leidse Geologische Mededelingen*, **44**: 137–225.

Verniers, J., Nestor, V., Paris, F., Dufka, P., Sutherland, S. & Van Grootel, G. 1995. A global Chitinozoa biozonation for the Silurian. *Geological Magazine*, **132**: 651–666, figs 5, 6.

Wellman, C. 1993. A land plant microfossil assemblage of Mid Silurian age from the Stonehaven Group, Scotland. *Journal of Micropalaeontology*, **12**: 47–66, 5 pls.

Witzke, B. J., & Heckel, P. H. 1988. Paleoclimatic indicators and inferred Devonian palaeolatitudes of Euramerica. *In*, McMillan, N. J., Embry, A. F. & Glass, D. J. (editors), *International Symposium on the Devonian System, Calgary*, **1**: 49–63. Canadian Society of Petroleum Geologists, Calgary, Canada.

Wrona, R. 1980. Upper Silurian-Lower Devonian Chitinozoa from the subsurface of southeastern Poland. *Palaeontologia Polonica*, **41**: 103–165, pls 24–37.

Ziegler, P. A. 1988. Laurussia – The Old Red Continent. *In*, McMillan, N. J., Embry, A. F. & Glass, D. J. (editors), *International Symposium on the Devonian System* Calgary, **1**: 15–48. Canadian Society of Petroleum Geologists, Calgary, Canada.