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First evidence of Devonian strata in Sweden — A palynological investigation of Övedskloster drillcores 1 and 2, Skåne, Sweden

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A B S T R A C T

Palynological analyses were carried out on 50 samples from the Övedskloster 1 (Ö1) and 2 drillcores (Ö2), southern Sweden. The study revealed well-preserved palynological assemblages including 77 spore species in 28 genera, and some additional forms retained under open nomenclature. The spore assemblages are collectively dominated by trilete spores in terms of abundance and diversity and have been ascribed to two informal palynozones (Assemblage A and Assemblage B), based on the representation of spore taxa. The presence of the spore species *Acinosporites salopiensis*, *Chelinohilates erraticus*, *Cymbohilates allenii*, *Cymbohilates allenii* var. *magnus*, and *Retusotriletes maccullockii* indicates that the stratigraphic succession spans the Silurian–Devonian boundary (Přídolí–Lochkovian), and thus constitutes the first robust evidence of Devonian strata on the Swedish mainland. These results have implications for the age of fossil faunas (e.g. fish) from the same deposits, previously dated as late Silurian. Palynofacies analyses reveal a shallowing-upward succession with nearshore marine marls at the base of the investigated core, grading into sandstones in conjunction with a decrease in the relative abundance of marine palynomorphs. The uppermost 70 m are mainly represented by red sandstones that are devoid of recognizable palynomorphs and host only phytodebris. We interpret this interval to represent predominantly paralic to fluvial deposits equivalent to facies represented in the Old Red Sandstone of Britain.

1. Introduction

1.1. The Silurian–Devonian of Baltica

During the early Paleozoic, until the end of the Silurian, Baltica formed an independent plate bordered by the Tornquist and Iapetus oceans (Fig. 1). During this time-interval, sediments were deposited across the entire expanse of what is now the Baltic Sea and much of onshore Sweden (Torsvik and Rehnström, 2003). This widespread deposition was related to the extensive transgressions that occurred during the Cambrian and Ordovician (Bjerkéus, 2001). Avalonia collided with Baltica at the end of the Ordovician (Vecoli and Samuelsson, 2001) and a general shallowing is evident from this time onwards, as the Tornquist Sea retreated as a consequence of orogenic uplift (Torsvik and Rehnström, 2003). By the middle Silurian, a shallow marine embayment, extending from the south of Sweden to Gotland and to the Baltic States, was all that remained of the Tornquist Sea. By the latest Silurian the docking of Baltica and Avalonia was complete. Baltica then became incorporated into the continent Laurussia (the Old Red Sandstone Continent) that formed as a consequence of the collision of Baltica, Laurentia and Avalonia (Scotese et al., 1985; Torsvik and Rehnström, 2003). During the late Silurian–Early Devonian the Caledonian orogeny dramatically influenced the sedimentary development towards the west and the south (Bjerkéus, 2001). This is clearly detectable in the sedimentary record as a shift from marine carbonates to more terrestrially influenced sediments, such as sandstones (commonly reddish). The youngest Paleozoic strata of Sweden, apparently marginal marine to continental, are poorly dated due to a dearth of fossils and because past research has focused on the marine macro- and microfossils. Our study integrating the terrestrial (miospores) and marine (acritarchs) palynomorphs allows new interpretations of the depositional setting of these strata. The palynological analysis yields information about changes in relative sea-level, proximity to land and correlation between the marine and terrestrial realms. This study aims to improve resolution of the age of the youngest Paleozoic sedimentary succession in Sweden based on spores from land plants, in sediments that previously have been deemed poorly fossiliferous. By applying palynofacies analyses,

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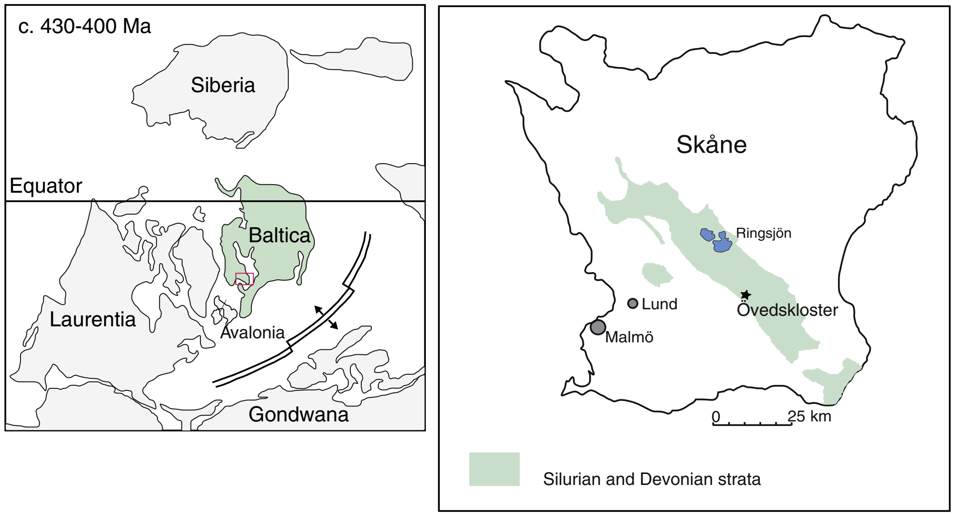


Fig. 1. A. Paleogeographical map showing Baltica 430–400 Ma (after Scotese et al. (1985)). B. Map of southern Sweden indicating Silurian–Devonian deposits and with location of Övedskloster cores marked.

we test the competing hypotheses that these strata were deposited either in marine or terrestrial settings.

1.2. The Silurian–Devonian boundary based on miospores

The Silurian–Devonian stratotype has been defined at Klonk, Czech Republic (Chlupac and Kukal, 1977), where the boundary is based on marine microfauna and fauna including graptolites, conodonts and tentaculitids. Continental fossils (e.g. miospores, land plants, fish) are absent from the stratotype successions making correlation difficult with continental sediments.

Richardson and Lister (1969) were the first to propose a biostratigraphic scheme based on spores across the Silurian–Devonian boundary. The base of the Devonian was traditionally placed in the Welsh Borderland at the Ludlow Bone Bed and its equivalent elsewhere. The Downtonian was, therefore, included within the Devonian. However, the Downtonian is now regarded as approximately equivalent to the Přídolí Series for which the stratotype is defined in marine sequences of the Czech Republic (e.g. Cocks et al., 1971; Kaljo, 1978; Richardson and McGregor, 1986). The Dittonian, overlying the Downtonian in Britain, begins with the Bishop Frome Limestone Group (previously denominated *Psammosteous* Limestone Group); now considered as the possible base of the Devonian. The Přídolí (Downtonian) is characterized by spores including *Apiculiretusispora spicula*, *Cymbosporites verrucosus*, *Synorisporites tripapillatus* and *Synorisporites verrucatus* (see in Richardson and McGregor (1986)). The taxa *S. tripapillatus* and *A. spicula* characterize the Přídolían biozone of Richardson and McGregor (1986). However, Ludlovian layers are rich in marine palynomorphs and poor in miospores, making the first appearance of those taxa doubtful. In the Lochkovian (Dittonian) successions, many new species appear; among the biostratigraphically most important are *Streelispora newportensis*, *Chelinospora cassicula*, *Emphanisporites micrornatus* and *Cymbosporites dittonensis* (see Richardson and McGregor (1986)). The first appearance of *S. newportensis* followed by *E. micrornatus*, has long been considered to mark the base of the Lochkovian; both represent the eponymous species of Biozone MN (Richardson and McGregor, 1986; Streel et al., 1987; Steemans, 1989). Both biozones have broad geographic distributions but are recognized mainly on the Old Red Sandstone Continent. The characteristic species of the MN Biozone are mostly unknown in Gondwana. Only one specimen of *S. newportensis* has been observed in Tunisia (Loboziak et al., 1992), in contrast to peri-Gondwanan localities such as Spain (Richardson et al., 2001) and Brittany (France) (Steemans, 1989). Later, Richardson and Edwards (1989) subdivided the *S. tripapillatus*–*A. spicula* Biozone into three biozones: a narrower *S. tripapillatus*–*A. spicula* Biozone overlain by “biozone A” and the “*Apiculiretusispora* sp. E biozone” (Fig. 2). The latter is spanning the S–D boundary. In this scheme, the first appearance of *S. newportensis* occurs in the lower part of the Lochkovian but not at its base. This has been confirmed by data based on chitinozoans from Spain (Richardson et al., 2001).

2. Geological setting

Mid-Paleozoic deposits are exposed in three areas of the southernmost Swedish province Skåne: south and southwest of the lakes Ringsjön; in the area of Bjärsjölagård and Bosjökloster; and in the Ramsåsa area (Fig. 1b). The strata at Bjärsjölagård and Övedskloster were first mentioned in Bromells “Lithographia Svecana” from, 1725–1729. The Öveds-Ramsåsa succession can be divided into four units based on lithology: 1, the basal Bjärsjölagård Limestone; 2, sandstone (yellow); 3, grey to reddish calcareous shale; and 4, the Öved Sandstone (red sandstone) (Fig. 2). The deposits are estimated to reach a thickness of c. 300–400 m (Anderegg et al., 1968; Larsson, 1979). The strata dip 14° SW in the new quarry at Helvetesgraven (Tullberg, 1882) and it is unclear whether this has been taken into account when assessing the thickness. These units are not exposed as an entire succession but instead occur as isolated outcrops, not always readily correlatable. Some intervals of the Öveds-Ramsåsa Group host rich fossil assemblages and the successions have previously been correlated to the latest Silurian of Britain, although, according to Anderegg et al. (1968) the uppermost part of the Öved Sandstone is possibly of Early Devonian age, based on lithological correlations with successions from the Baltic countries. A Devonian age for the Öved Sandstone was further proposed by Hadding (1929). Tullberg (1882) stated that the Öved Sandstone due to its red color had even been mistaken for representing Triassic strata.

3. Material and methods

Two drillcores have been sampled in this study: Övedskloster 1 (Ö1) and Övedskloster 2 (Ö2) (Fig. 3). They were drilled in the late 1960s by the Swedish Geological Survey, directly south of the Helvetesgraven (hell-hole) sandstone quarry c. 10 km NW of Sjöbo in Skåne. The drilling of the Ö1 well failed due to technical reasons and reached only 117.6 m and subsequently Ö2 was drilled only 100 m north of Ö1, reaching a depth of 210.3 m (Anderegg et al., 1968). The drilling aimed to reach

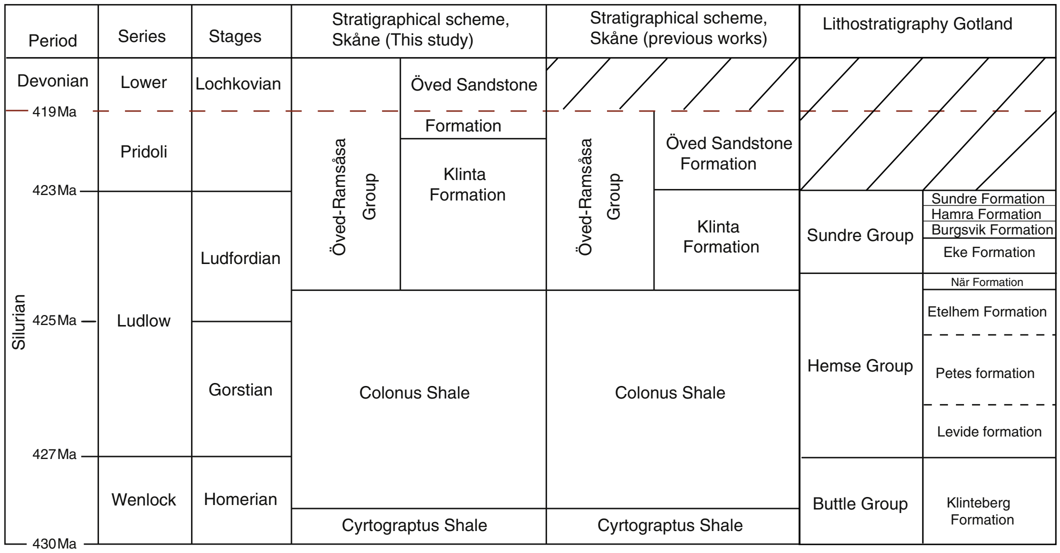


Fig. 2. Chrono- and lithostratigraphical chart of the late Silurian and basal Devonian correlating global series and stages with local groups, formations and members of Skåne and Gotland (sensu Jeppsson and Laufeld (1986); Jeppsson et al. (2006)).

the successions of underlying strata correlative with the Bjärsölagård 2 core and to assess the thickness and fossil content of the Öved Sandstone (Anderegg et al., 1968). According to Anderegg et al. (1968) this goal was not achieved as the Övedskloster drillcores did not reach depths sufficient to penetrate strata correlative with the successions represented in Bjärsjölagård 2 (Mehlqvist et al., 2012, 2014).

As the Ö2 drillcore penetrates a thicker succession, this core has been the focus of our study and 45 samples were processed for palynology, of which 36 were productive. Additionally, six samples were processed also from the less complete Ö1 core with the aim to correlate with the palynological assemblages recovered from Ö2.

3.1. Palynology

The samples included in this study were processed according to standard palynological procedures at Global Geolab Ltd., Alberta, Canada. The samples were first treated with dilute hydrochloric acid (HCl) to remove calcium carbonate, and subsequently macerated by leaving the sample in 75% hydrofluoric acid (HF) overnight. The organic residue was sieved through a 20 μm mesh and mounted in epoxy resin on glass slides. One hundred and fifty land plant spores per slide were counted where possible and identified taxonomically by light microscopy (Plates I, II, IV) and Scanning Electron Microscopy (SEM; Plate III). After the count of 150 was reached, the entire slide was further studied for rare taxa. All the spores were counted in slides containing less than 150 spores. The palynological slides and macerated residues from this study are deposited at the Department of Geology, Lund University, Sweden. Palynofacies analysis involved counting the relative abundance of organic particles based on 300 counts per slide. The organic matter was divided into fourteen palynofacies groups; I, Spores (from early land plants); II, Phytodebris; III, *Nematothallus*; IV, *Cosmochlaina*; V, Chitinozoans; VI, Arthropod cuticle; VII, Tubular structures; VIII, Charcoal; IX, Fungal spores; X, Acritarchs; XI, Green algae; XII, Graptolite remains; XIII, AOM; and XIV, Unidentified remains.

4. Results

A diverse, abundant and well-preserved spore assemblage was identified in the Övedskloster drillcores. The assemblages include 77 species belonging to 28 genera (of which several taxa are retained under open nomenclature). Trilete spores are represented by 44 taxa and cryptospores 33. The assemblages are collectively dominated by trilete spores in terms of abundance and diversity when calculating the means from the total assemblage, but the differences between individual samples may vary considerably. In general, the most common taxa include *Ambitisporites avitus-dilutus*, *Archaeozonotriletes chulus*, *Gneudnaspora divellomedia*, *Retusotriletes* spp. and *Tetrahedraletes medinensis* (Fig. 4).

Two assemblages are distinguished, a Přídolían assemblage between 208.45 and 135.0 m and a Lochkovian assemblage starting with a transitional zone with successive appearances of Lochkovian taxa from 135 to 130.95 m (Fig. 5A). The late Silurian assemblage includes 36 taxa and the Lochkovian interval (including the transitional zone) incorporates 73 taxa (Fig. 5A, B).

4.1. Biostratigraphical interpretations

4.1.1. Övedskloster 2

The assemblages in the samples from Övedskloster 2 drillcore are dominated by long-ranging taxa in terms of abundance. Nevertheless, a significant number of key-taxa occur and the spore succession has been subdivided into two informal assemblages based on the First Appearance Datum (FAD) of spore taxa (Fig. 5B).

4.1.1.1. Assemblage A. 208.45–145.30 m. Thirty–six taxa were identified in this interval: 16 cryptospore taxa, 20 trilete spore taxa and one unidentified specimen. Based on the spore content, Assemblage A is dated as Přídolí, which agrees with observations based on tentaculitids (K. Larsson pers. com). The FAD of *Apiculiretusispora spicula* (199 m) and *Synorisporites tripapillatus* (208.45 m) are indicative of a Přídolí age and the assemblage is correlated with the *Synorisporites tripapillatus–Apiculiretusispora spicula* Assemblage Zone (Richardson and McGregor, 1986). *Artemopyra scalariformis* identified in the basal sample (208.45 m), has previously been recovered from the Upper Downton Formation in Britain within the *Apiculiretusispora* sp. E Assemblage Miospore Zone of Přídolí age, and in the lower *micronatus-newportensis* Zone of Lochkovian age (Richardson, 1996a, 1996b).

4.1.1.2. Assemblage B. 135.00–top core. Assemblage B commences with an interval, 135–130.95 m, herein characterized as “transitional”. While the composition of the palynoflora significantly differs from Assemblage A, there are no key-taxa clearly indicating a Lochkovian age (Fig. 5B).

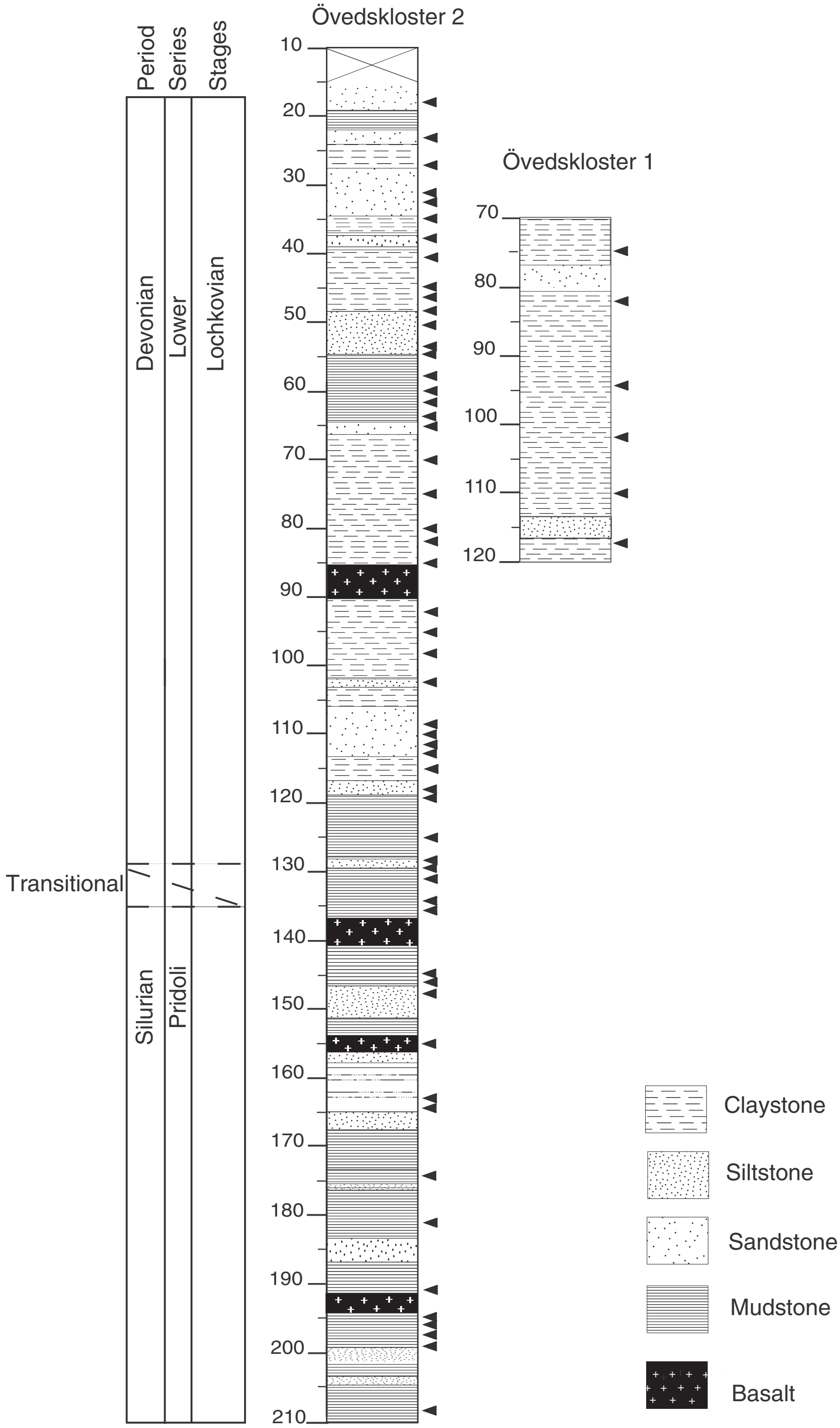
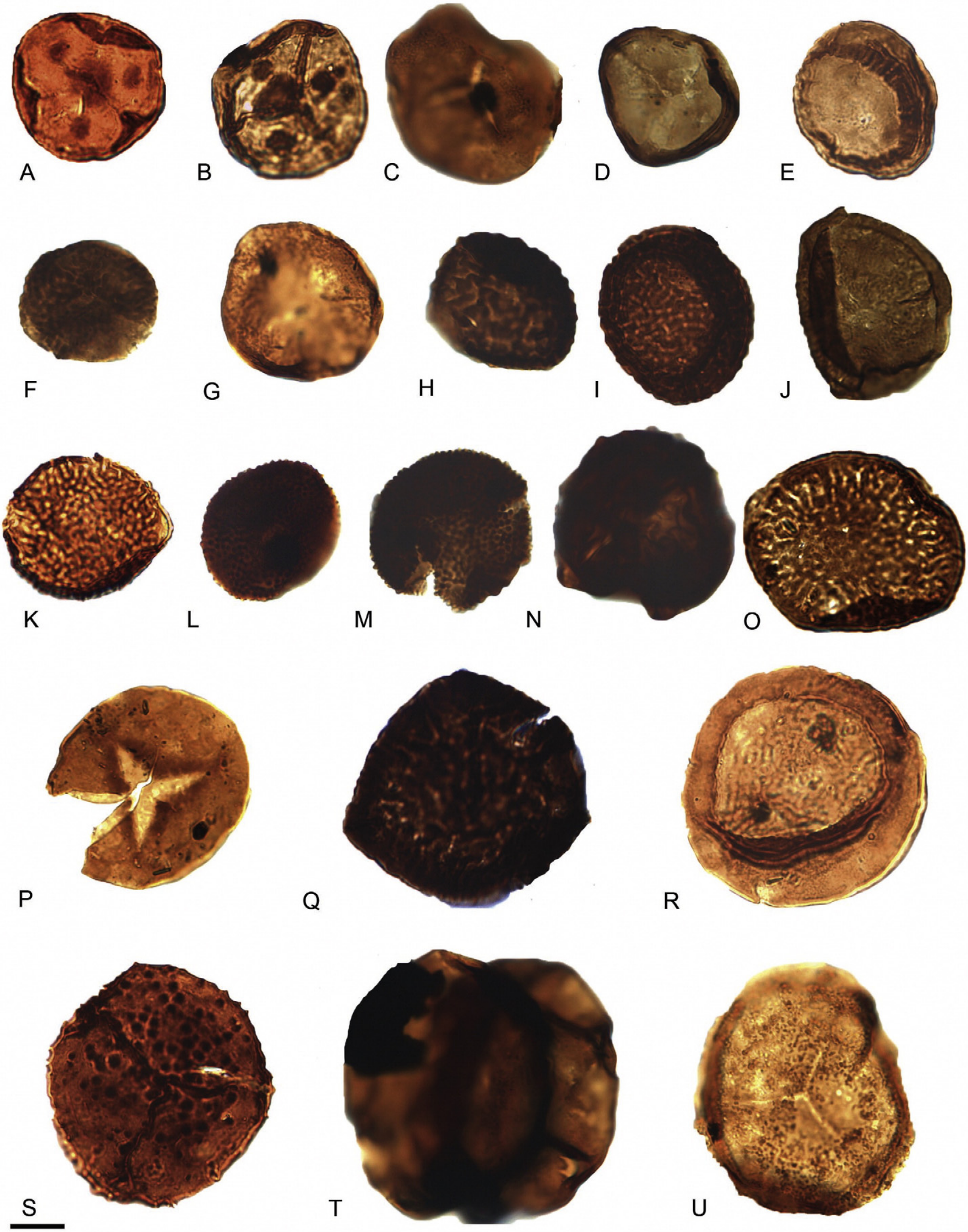


Fig. 3. Lithology and correlation of the drillcores Övedskloster 1 and Övedskloster 2. Depth in meters, arrows indicating sample levels (modified from Hagin (1991)).

A prominent increase in diversity is noted at 135.00 m where the following species appear; *Chelinohilates sinuosus* var. *sinuosus*, *Concentricosiporites sagittarius*, *Confossuspora reniforma*, *Ambitisporites eslae*, *Aneurospora geikiei* and *C. sinuosus*. These are all described from an early Lochkovian assemblage from the "Lower Old Red Sandstone" in Lorne (Scotland) by Wellman and Richardson (1996). However, *Concentricosiporites sagittarius* has previously also been recovered from upper Ludfordian and lower Přídolí strata (Burgess and Richardson, 1995). At 134.20 m *Cymbohilates allenii* var. *allenii* (also described from Lorne in Wellman and Richardson (1996)) appears together with *Apiculiretusispora synorea*, *Chelinospora cantabrica* and *Retusotriletes triangulatus* among others. *Apiculiretusispora synorea* is one of the indicative species of the Přídolían *tripapillatus-spicula* Assemblage Zone of Richardson and McGregor (1986). While *Retusotriletes triangulatus* is common in Devonian (especially Early–Middle Devonian) assemblages in Gondwana (Breuer and Steemans, 2013). *Chelinospora cantabrica* identified at 134.2 m has previously been described from the *Coronaspora reticulata–Chelinospora*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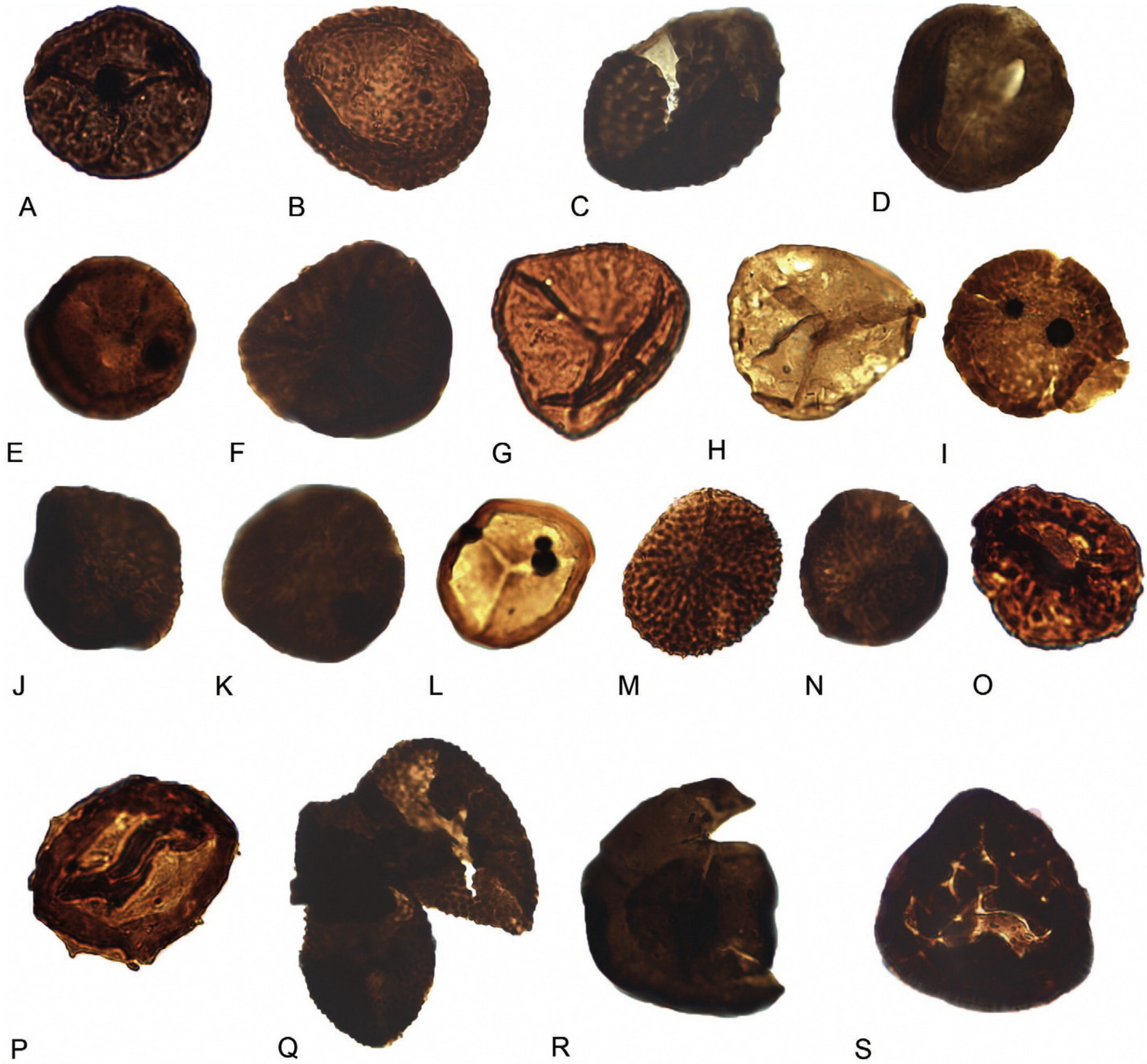


Plate II. Scale bar = 10 μm. A. *Scylaspora downiei* Burgess and Richardson (1995). B. *Cymbohilates* sp. C. *Chelinohilates* cf. *sinuous* Wellman and Richardson (1996). D–E. *Cymbohilates microgranulatus* Wellman and Richardson (1996). F. *Emphanisporites rotates* McGregor, 1973. G. *Emphanisporites* sp. H. *Retusotriletes maccullockii* Wellman and Richardson, 1996. I. Sp. indet. J–K. *Hispanaediscus* sp. A *in* Burgess and Richardson (1995). L. *Retusotriletes* cf. *goensis* Richardson and Ioannides (1973). M. *Emphanisporites* sp. N. *Scylaspora downiei* Burgess and Richardson (1995). O. Sp. indet. P. Sp. indet. Q. *Cymbohilates* cf. *hystricosus* Wellman and Richardson (1996). R. *Concentricosisporites sagittarius* (Rodriguez) Richardson et al. (2001).

sanpetrensis (RS) and lowermost H biozones of Richardson et al. (2001) of Ludfordian to earliest Přídolí age in the Cantabrian Mountains, Spain, and within the H biozone of early to mid-Přídolí age.

The interval 130 m and upwards, is dated as Lochkovian and comprises 61 taxa of which 24 represent cryptospore and 37 trilete spore taxa (Fig. 5a). This assemblage is characterized by the appearance of Devonian-type key taxa with more pronounced ornamentation in addition to the long-ranging species persisting from the lower part of the core including *Ambitisporites avitus/dilutus*, *Archaeozonotriletes chulus*, *Gneudnaspora divellomedia* and *Tetrahedraletes medinensis*.

Taxa that indicate an Early Devonian (Lochkovian age) include e.g. *Chelinohilates erraticus*, *Cymbohilates allenii*, *Chelinospora pseudoreticulata*

Plate I. Scale bar = 10 μm A–B. *Ambitisporites eslae* (Cramer & Diez) Richardson et al. (2001). C. *Apiculiretusispora* sp. D. *Archaeozonotriletes chulus* (Cramer) Richardson and Lister (1969). E. *Artemopyra* spp. F. cf. *Streelispora granulata* Richardson and Lister (1969). G. cf. *Scylaspora downiei* Burgess and Richardson (1995). H. *Chelinohilates* cf. *sinuous* Wellman and Richardson (1996). I. *Chelinohilates sinuosus* var. *sinuous* Wellman and Richardson (1996). J. cf. *Scylaspora scripta* Burgess and Richardson (1995). K. *Chelinohilates sinuosus* var. *angustus* Wellman and Richardson (1996). L–M. *Cymbohilates allenii* Richardson (1996a, 1996b). N. *Chelinohilates erraticus* Richardson (1996a, 1996b). O. *Chelinohilates lornensis* Wellman and Richardson (1996). P. *Retusotriletes triangulates* Streel, 1976. Q. *Chelinohilates* sp. R. *Artemopyra scalariformis* Richardson, 1996a, 1996b. S. cf. *Aneurospora geikiei* Wellman and Richardson (1996). T. *Pseudodyadospora petasus* Wellman and Richardson (1993). U. cf. *Apiculiretusispora asperata* Burgess and Richardson (1995).

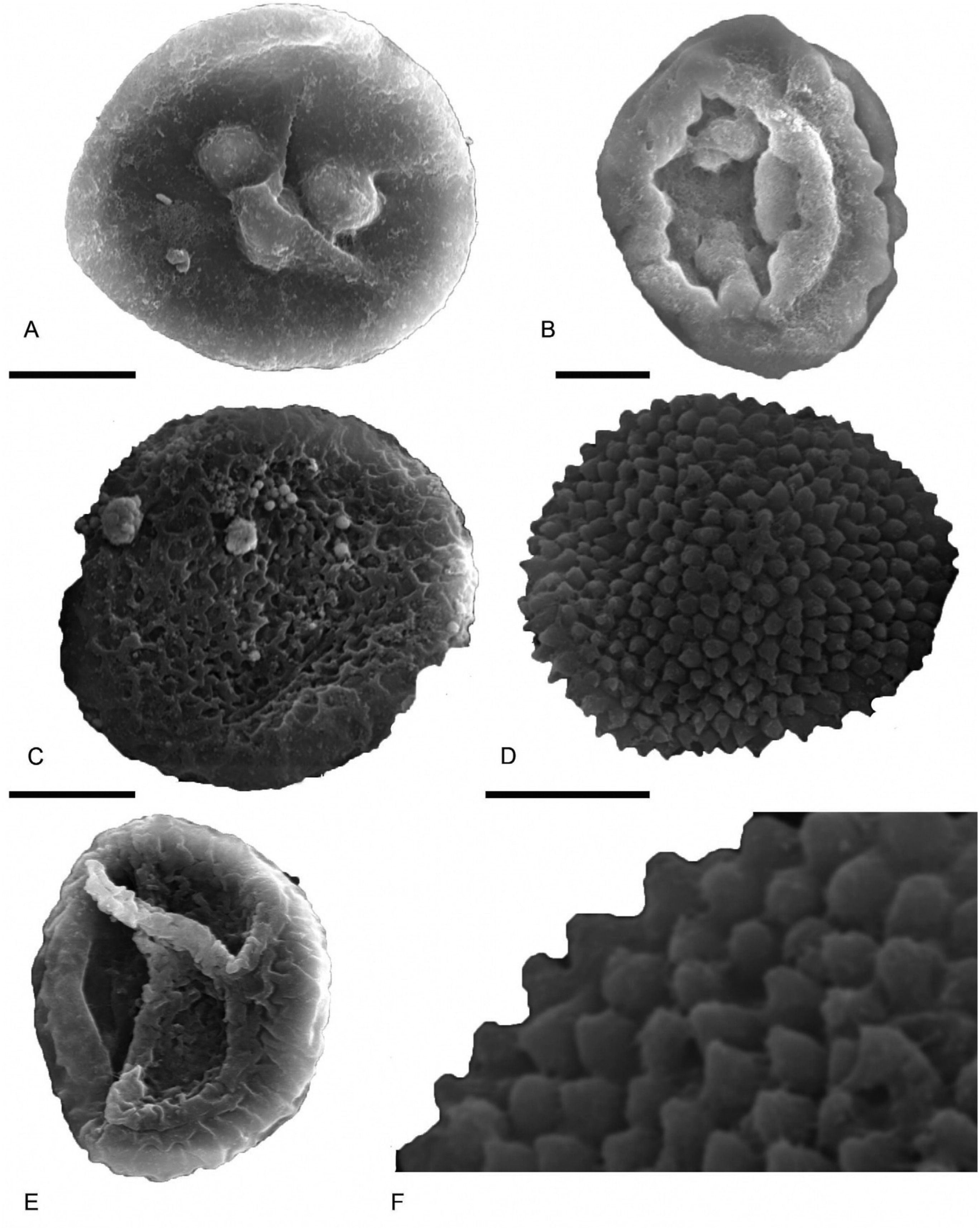


Plate III. SEM photographs, Scale bar = 10 μm if not otherwise stated A. *Ambitisporites tripapillatus* B. cf. *Chelinospora* (*Lophozonotrilites*)*poecilomorpha* (Richardson & Ioannides) Richardson et al. (2001). C. cf. *Chelinohilates sinuous* Wellman and Richardson (1996). D. cf. *Aneurospora geikiei*. E. cf. *Scylaspora* sp. F. Closeup on the spines on D. Scale bar = 5 μm.

and *Cymbohilates microgranulatus*. Previous stratigraphic ranges of the species are described below.

Cymbohilates allenii has previously been identified in strata of early to middle Lochkovian age, both below and within the *Emphanisporites micrornatus–Streelispora newportensis* (MN) palynosubzones (Fig. 6.; Richardson et al., 2001; Wellman and Richardson, 1996). Important to note is that the MN zone ranges from the early but not the earliest Lochkovian. *Chelinohilates erraticus* (95.0 m) is common in Britain ranging from Přídolí to early Lochkovian, represented both within the *Apiculiretusispora* sp. E. Assemblage Miospore Zone and the *Emphanisporites micrornatus–Streelispora newportensis* Zone (Richardson, 1996a, 1996b; Fig. 6).

Cymbohilates microgranulatus (100.00 m and 92.10 m) has been reported from upper Přídolí to the lowermost Lochkovian strata from the "Lower Old Red Sandstone" of Lorne, Scotland from the *Apiculiretusispora* sp. E palyno-subzone; (Wellman and Richardson, 1996). *Chelinospora pseudoreticulata*, recorded at 130 and 129.78 m has a known range from Lochkovian to late Pragian or early Emsian in Belgium and Germany (Steemans, 1989).

The trilete spore *Scylaspora elegans* occurs at 81.68 m in the Övedskloster 2 drillcore. This species has been reported from the *Scylaspora elegans–Iberoespora cantabrica* (EC) spore assemblage biozone of Richardson et al. (2001), which corresponds to late/latest Přídolí–early Lochkovian in the Cantabrian Mountains. *Chelinospora hemiesferica* occurs at 130 and 129.78 m and was described to occur in the *Chelinospora hemiesferica* (H) Spore Interval biozone to early *S. newportensis–E. micronatus* (MN) spore biozone of an early and mid-Přídolí to Early (but not earliest) Devonian age (Lochkovian; Richardson et al., 2001).

Additionally, the assemblage at 199.00 m is characterized by a high abundance of *Tetrahedraletes medinensis* (40%). As pointed out by Lavender and Wellman (2002) this feature that has been reported only in a few studies suggested to indicate a consistent feature of Lochkovian spore assemblages. Important to note is that most of the tetrads in sample 199.00 m show a quadrahedric cross configuration and may be related to the old genus *Nodospora* Strother and Traverse (1979); in contrast to the tetrahedric tetrads which are related to *Tetrahedraletes* Strother and Traverse (1979). Gray (1991) demonstrated in rotating glass ball that the spore arrangements in the tetrad may be either quadrahedric or tetrahedral. They concluded that *Nodospora* and *Tetrahedraletes* constitute a single genus; their configuration being due to the taphonomic processes or they may reflect the different ways spores compress depending upon their orientation during compression. However, the four spores in a tetrad are not really spherical but show a planar contact. In addition, the spore may have a distal spherical or ovoid face. Typically, spores of the "*Nodospora*" configuration are elongate and bean-shaped in contrast to the spores of *Tetrahedraletes* arrangement which have a hemispherical distal face. This observation reinstates the question as to whether these represent indeed two different genera or only one.

4.1.1.3. Reworking. Additionally, taxa previously reported only from older successions are intermixed with incoming younger (Lochkovian) taxa. This possibly implies that reworking of older sediments has occurred.

Examples of spores identified in the Lochkovian part of the drillcore Ö2 (130–65 m) that previously only have been described from Přídolían or older sediments include *Coronaspora cromatica* recorded at 130 and 75 m in Ö2 is considered as a marker for the lower boundary of Přídolí in the Cantabrian Mountains (Richardson et al., 2001). *Chelinospora sanpetrensis* identified at 129.78 and 111 m has previously been identified within the RS and early to mid-H biozone (Ludfordian to mid-Přídolí) in Cantabrian Mountains as described by Richardson et al. (2001). *Concentricosiporites sagittarius*, identified at 92.1 m in Ö2, has previously been recovered from late Ludfordian and early Přídolí strata (Burgess and Richardson, 1995). *Coronaspora reticulata* identified at 81.68 m has previously been described from upper Ludfordian and Přídolían successions in the Cantabrian Mountains (Richardson et al., 2001). There are also some taxa in the studied cores that previously only have been recorded from Homerian strata such as: *Confossuspora reniforma* and *Scylaspora scripta* (Burgess and Richardson, 1995). *Hispanaediscus lamontii* has a known range of Homerian to Gorstian (Burgess and Richardson, 1995) but occurs in Ö2 within Assemblage B at 95.00 m. *Apiculiretusispora* cf. *A. asperata* recorded at 97, 95 and 68 m has previously been recorded only in sediments of Gorstian to Ludfordian age (Burgess and Richardson, 1995). We interpret the presence of these taxa as a result of reworking of older sediments.

A complication is that most stratigraphical schemes for spores from this interval have been based on British material. Occurrences of Lochkovian successions comprising well-preserved miospore assemblages are scarce in Britain, which might be a reason why the taxa outlined below have not been recorded in Lochkovian successions there.

The biostratigraphic interpretation of the Övedskloster drillcore 2 implies that the lower part, hosting Assemblage A (208.45 m to 145.3 m depth) is of the latest Ludlow to Přídolí age based on the occurrences of species such as *Ambitisporites parvus*, *Artemopyra scalariformis*, *Apiculiretusispora spicula*, *Synorisporites tripapillatus*, *S. verrucatus* and *Hispanaediscus major*. This is further supported by tentaculitids identified in samples at the base of the Övedskloster drillcore 2, clearly indicating a Přídolí age (K. Larsson, pers. comm.)

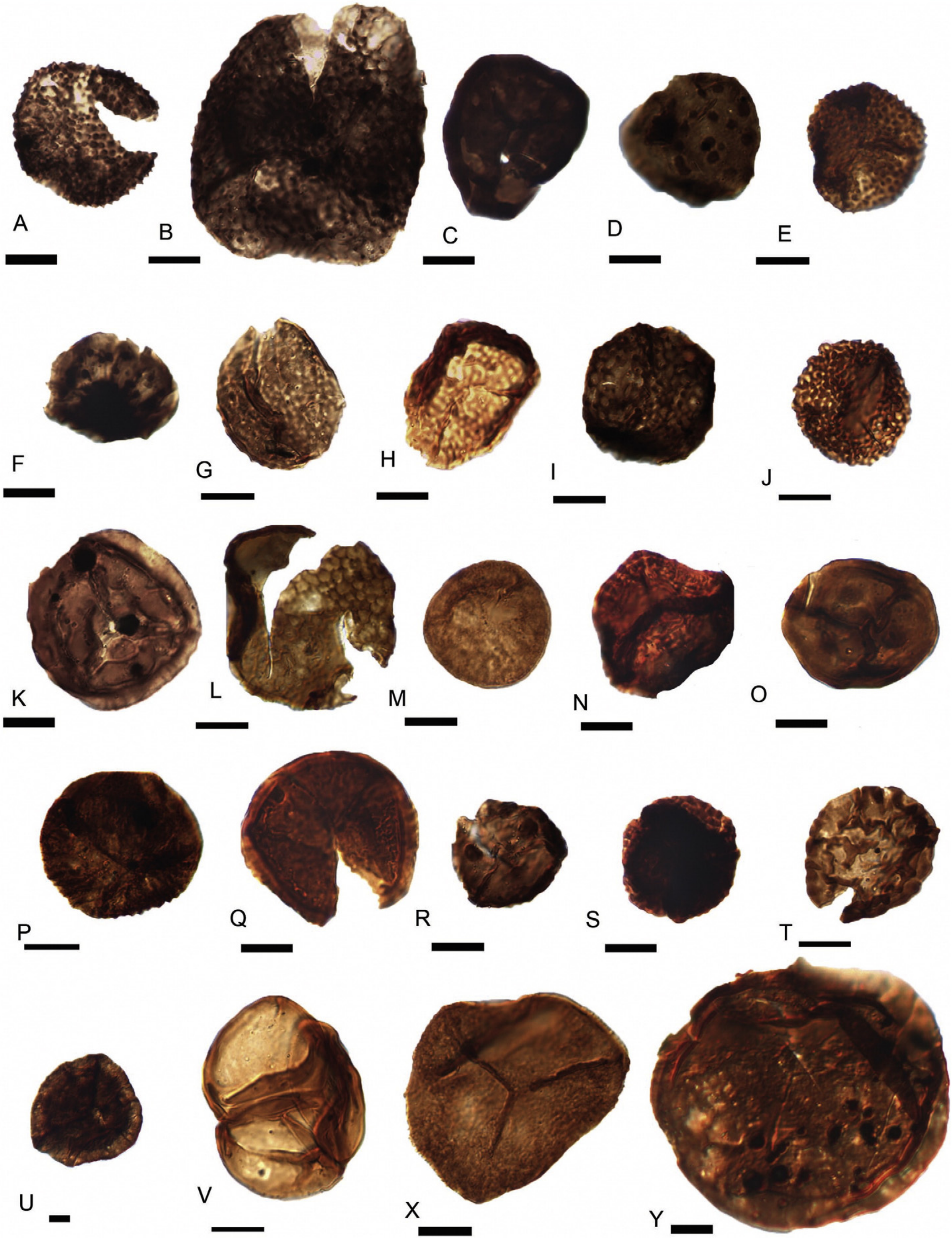
4.1.1.4. Palynofacies: Övedskloster 2. In the samples from the Övedskloster 2 core, phytodebris and spores generally dominate (Fig. 7) reaching c. 80% in the interval 105–75 m. Marine microfossils occur in lower relative abundances (Fig. 8) although attaining 30% at 85 m, where also chitinozoans reach their acme of nearly 20%. Acritarchs reach an abundance between 0 and 15%, while arthropod cuticles, graptolite remains and green algae occur in low relative abundances throughout the core (<5%; Fig. 8).

When calculating the ratio between terrestrial/marine organic matter, a general pattern is evident in that marine microfossils occur only up to c. 70 m in the core, while the upper part (70–20 m) probably represents paralic conditions and contains chiefly non-marine organic matter including phytodebris, small amounts of charcoal and fungal spores (Fig. 7). Interestingly, a spike of *Nematothallus* and charcoal is identified in the shallower marine paralic interval of the core (60–40 m).

4.1.2. Övedskloster 1 and correlation with Övedskloster 2

Only six samples were processed from the Övedskloster 1 drillcore, of which five samples were productive (Fig. 5b). The assemblage is poor mainly comprising long-ranging taxa, hampering biostratigraphic assessments. The species identified include: *Ambitisporites avitus*/*dilutus* morphon, *Archaeozonotriletes chulus*/*nanus*, *Apiculiretusispora* spp., *Apiculiretusispora* sp. B, *Cheilotetras caledonica*, *Cymbohilates* sp. cf. *C. hystricosus*, *Gneudnaspora divellomedia*, *Hispanaediscus lamontii*, *Hispanaediscus verrucatus*, *Hispanaediscus* sp. A, *Imperfectotriletes* sp., *Retusotriletes* sp. *Synorisporites verrucatus*, *Tetrahedraletes medinensis* and *Tetrahedraletes grayii*. Although dating is not possible based on the spore content, correlation with the strata intersected in the nearby drillcore Ö2 is based on combined lithostratigraphy and palynofacies results (Figs. 3, 9) and the age of the successions within this core is herein interpreted as Lochkovian.

4.1.2.1. Palynofacies: Övedskloster 1. The palynofacies results of the samples in Övedskloster 1 (Fig. 9) show the same general trend as for the upper part of Övedskloster 2 with a dominance of terrestrially derived organic matter. The interval 111 to 95 m is dominated by spores (with maximum relative abundance of 80%) followed by a phytodebris-dominated interval, 88–75 m (Fig. 9). Other categories of organic matter occur in low abundance throughout the core with acritarchs representing 6% at 111 m and chitinozoans reaching nearly 10% at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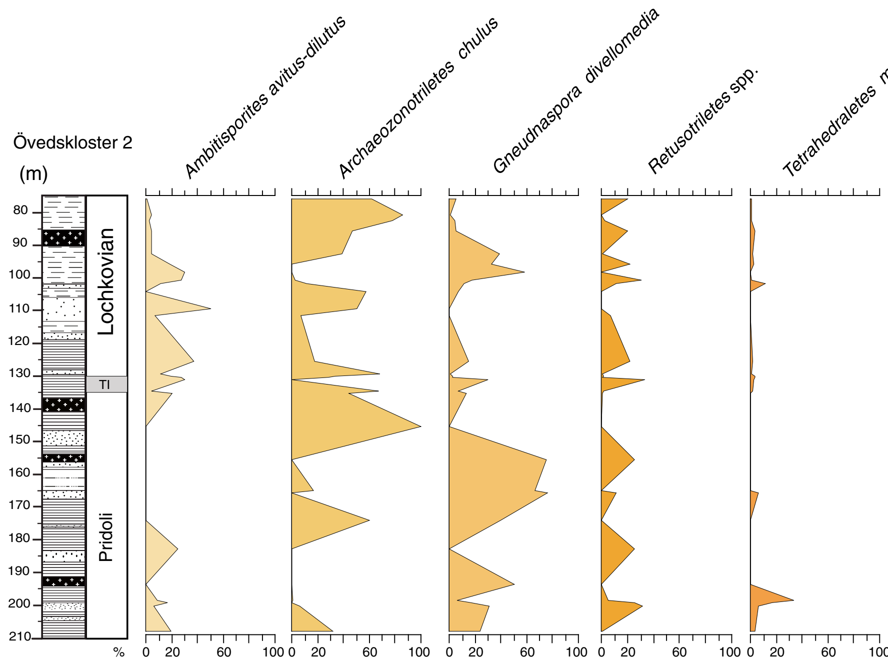

Fig. 4. Relative abundance diagram of the most common taxa identified in the drill core Övedskloster 2, expressed in %. TI = Transitional Interval.

95 m. The ratio between terrestrial and marine organic matter indicates that the rather prominent change from marine to terrestrial environment occurs at 88 m, providing a level for correlation with the Ö2 core (Fig. 3). In most samples, the terrestrial palynofacies components dominate with 80–100%. Interestingly, charcoal particles occur mainly in the top of the core (Fig. 9).

5. Discussion

5.1. Comparison with other assemblages

In comparison to other miospore suites from Sweden, such as those from the Klinta 1 and Bjärsjölagård 2 drillcores outlined by Mehlqvist et al. (2012), the Öved Sandstone assemblage is notably more diverse, with 77 species belonging to 28 genera, compared to assemblages from the drillcores intersecting the older successions, where a diversity of 34 taxa was identified by Mehlqvist et al. (2012). The species composition is also broadly different. Although a few species are shared, these are long-ranging forms, and the general differences in the assemblages indicate a younger age for the Öved Sandstone. These differences probably reflect the increasing abundance and diversity of trilete spores during the late Silurian and Early Devonian globally (Steemans, 1999; Rubinstein and Steemans, 2002; Steemans et al., 2007). However, local environmental factors may influence assemblage composition. For example, cryptospore-producing plants are supposed to have been more common in moist biotopes and with a high tolerance to climatic changes, whereas trilete-spore producing plants were more sensitive to climatic changes but could grow in a greater variety of biotopes (Steemans et al., 2007).

Compared to the somewhat older miospore assemblage (Ludlow) from Gotland studied by Hagström (1997), the assemblages from Övedskloster are clearly more diverse. The Gotland assemblages are instead more similar (in species composition and dominance of cryptospores) to the Ludfordian strata in the Klinta and Bjärsjölagård drillcores (Mehlqvist et al., 2012) and those from the Klinta exposure (Mehlqvist et al., 2015). Other miospore associations resembling the Övedskloster assemblages have been outlined by Burgess and Richardson (1995) from south and southwest Wales. Approximately 22 species are shared between the Welsh (dated to late Wenlock–early Přídolí) and Övedskloster assemblages. The Welsh assemblages include key taxa such as: *Apiculiretusispora asperata*, *Apiculiretusispora synorea*, *Concentricosiporites sagittarius*, *Confossuspora reniforma*, *Scylaspora downiei* and *Synorisporites tripapillatus*. In a comprehensive work on miospore assemblages from four sections in the Cantabrian Mountains (northern Spain) a detailed miospore zonation was presented by Richardson et al. (2001). The successions belong to the San Pedro Formation and span the Ludfordian/Přídolí and Silurian–Devonian boundaries. The San Pedro Formation assemblages share nine species with the Övedskloster palynosuite: *Ambitisporites eslae*, *Chelinospora cantabrica*, *C. hemiesferica*, *Chelinospora* (*Lophozonotrilites*) *poecilomorpha*, *C. sanpetrensis*, *Concentricosiporites sagittarius*, *Coronaspora cromatica*, *C. reticulata*, *Scylaspora elegans* and *S. vetusta*. Rubinstein and Steemans (2002) presented a comprehensive study of miospore assemblages spanning the Silurian–Devonian boundary from the Ghadamis Basin in Libya. The samples derive from a drillcore from an entirely marine succession where age control is also based on acritarchs and chitinozoans. The Libyan assemblage is well preserved and diverse with c. 80 taxa, dominated by trilete spores (both in diversity and abundance), and with cryptospores as a minor element. Interestingly, *S. tripapillatus* appears earlier in the Libyan succession than in the material from the Welsh Borderland, as they have been identified in samples dated as early Ludlow. Twenty-two species are shared between the Libyan and Övedskloster assemblages, including: *Archaeozonotriletes chulus*, *Apiculiretusispora synorea*, *Concentricosiporites sagittarius*, *Confossuspora*

Plate IV. Scale bar = 10 μm. A. *Apiculiretusispora synorea* Richardson and Lister (1969). B. *Acinosporites* sp. C. *Acinosporites salopiensis* Richardson and Lister (1969). D. *Apiculiretusispora hispidica* E. *Apiculiretusispora spicula* Richardson and Lister (1969). F. *Brochotriletes* cf. *foveolatus* Naumova, 1953. G. *Chelinospora* (*Brochotriletes*) *sanpetrensis* (Rodriguez) Richardson, Rodriguez, Sutherland (2001). H. *Chelinospora hemiesferica* (Cramer & Diez) Richardson et al. (2001). I. *Chelinospora psedoreticulata* Steemans (1989). J. *Chelinospora* sp. K. *Coronaspora cromatica* (Rodriguez) emend. Richardson et al. (2001) L. *Coronaspora reticulata* Richardson et al. (2001). M. *Emphanisporites micronatus* Richardson and Lister (1969). N. *Emphanisporites concentricus* Burgess and Richardson, 1995. O. *Scylaspora elegans* Richardson et al. (2001). P. *Scylaspora vetusta* (Rodriguez) Richardson et al. (2001).Q. *Stellatispora inframurinata* R. *Synorisporites tripapillatus* Richardson and Lister (1969). S. *Pachytetras rugosa* Hagström (1997). T. Sp. indet U. Sp. Indet V. Tetrad. X. *Apiculiretusispora* sp. Y. *Zonotriletes* sp.

A

Stratigraphy		Depth (m)	Tetrahedraletes medinensis	Retusotriletes spp.	Gneudnaspora divellomedia	Archaeozonotriletes chulus	Tetrahedraletes grayae	Ambitisporites avitus-dilutus	Hispanaediscus verrucatus	Retusotriletes triangulatus	Chelinohilates spp.	Rimosotetras problematica	Scylaspora downiei	Chelinohilates lornensis	Artemopyra scalariformis	Imperfectotriletes patinatus-vavrdovae morphon	Retusotriletes warringtonii	Apiculiretusispora burgsvikensis	Synorisporites tripapillatus	Ambitisporites parvus	Retusotriletes goensis	Emphanisporites rotatus
Devonian	Lochkovian	33.05	1																			
Devonian	Lochkovian	35.00																				
Devonian	Lochkovian	38.03		1																		
Devonian	Lochkovian	41.00		1																		
Devonian	Lochkovian	45.00			1																	
Devonian	Lochkovian	47.22																				
Devonian	Lochkovian	50.00				1																
Devonian	Lochkovian	51.61																				
Devonian	Lochkovian	55.00																				
Devonian	Lochkovian	56.08				1																
Devonian	Lochkovian	58.77																				
Devonian	Lochkovian	60.00			1	3	1															
Devonian	Lochkovian	62.18																				
Devonian	Lochkovian	65.00																				
Devonian	Lochkovian	66.03				1																
Devonian	Lochkovian	70.00				2																
Devonian	Lochkovian	75.00	1	33	9	104	1	1	1	1	1	1										
Devonian	Lochkovian	80.00	1		2	144		7		1			1	1	1							
Devonian	Lochkovian	81.68	1	5	8	131	1	4	1						1							
Devonian	Lochkovian	85.00	5	30	8	68		7		1		1				25						
Devonian	Lochkovian	92.10	3	1	53	53	2	6	1	1							1					
Devonian	Lochkovian	95.00	3	22	33			19		1							1	13				
Devonian	Lochkovian	97.68			31			16														
Devonian	Lochkovian	100.00	1	44	25	4	1	39	1				1			21		4				
Devonian	Lochkovian	103.50			1	8																
Devonian	Lochkovian	108.78				2		2														
Devonian	Lochkovian	125.00	3	30	20	24		51									3			1	1	
Devonian	Lochkovian	129.12	1	1	2	121	6	21		2				2					1			
Devonian	Lochkovian	129.78	7	3	5	67	11	39		3		2									3	
Devonian	Lochkovian	130.00	7	1	4	51	8	50		2									1		5	
Transitional		130.95	1	11	10			10												1		
Transitional		134.20	3	4	13	125	6	9		6									1			1
Transitional		135.00		1	21	68		32								7	2		1		2	
Silurian	Pridoli	145.30				3																
Silurian	Pridoli	155.42		1	3																	
Silurian	Pridoli	164.92			12	3														1		
Silurian	Pridoli	165.75	1	2	13																	
Silurian	Pridoli	174.20			2	3																
Silurian	Pridoli	183.00		1				1													1	
Silurian	Pridoli	194.05			1																	
Silurian	Pridoli	199.00	66	11	12	2	38	18		1		2					11			1	13	
Silurian	Pridoli	199.79	2	3	2		3	2														
Silurian	Pridoli	200.69	1	5	5	1	2	1														
Silurian	Pridoli	208.45	5	1	32	43	7	26	1	1	1	1	1	1	1	4	1	2	1	1	1	1

Depth (m)	Hispanaediscus spp.	Hispanaediscus sp. A	Hispanaediscus major	Synorisporites libycus	Apiculiretusispora spp.	Pseudodyadospora petasus	Apiculiretusispora spicula	Artemopyra radiata	Hispanaediscus lamontii	Scylaspora scripta	Retusotriletes maccullockii	Synorisporites verrucatus	Chelinospora spp.	Synorisporites sp. S	Velatitetras laevigata	Emphanisporites concentricus	Chelinohilates sinuosus var. sinuosus	Artemopyra spp.	Cymbohilates spp.	Concentricosisporites sagittarius
33.05																				
35.00																				
38.03																				
41.00																				
45.00																				
47.22																				
50.00																				
51.61																				
55.00																				
56.08																				
58.77																				
60.00				1	1															
62.18																				
65.00																				
66.03																				
70.00																				
75.00					1	1	1				1	2					1			
80.00						2		1	1			1					1			
81.68					2		1		1	1		1	2					1	1	
85.00																				
92.10										1										1
95.00				1					1											
97.68				1						1	1									
100.00																				
103.50					5															
108.78																				
125.00						1														
129.12					9				1	1		3					1	1		
129.78				3	33		1		3	4	1	1							1	
130.00					34		4		1	1	1	1								
130.95																				
134.20					9															
135.00					9	1						1					1	1	1	1
145.30																				
155.42																				
164.92					2															
165.75					1															
174.20																				
183.00											1									
194.05											1									
199.00				1	5	2	2	2	2	1		2	1	1	1	1				
199.79																				
200.69			1																	
208.45	1	1																		

Depth (m)	Confossuspora reniforma	Ambitisporites eslae	Streelispora granulata	Aneurospora geikiei	Emphanisporites spp.	Cymbohilates allenii	Chelinohilates sinuosus	Pachytetras rugosa	Apiculiretusispora synorea	Acinosporites spp.	Cymbohilates allenii var. allenii	Chelinospora cantabrica	Coronaspora cromatica	Chelinospora poecilomorpha	Chelinospora pseudoreticulata	Chelinospora hemiesferica	Chelinospora sanpetrensis
33.05																	
35.00																	
38.03																	
41.00																	
45.00																	
47.22																	
50.00																	
51.61																	
55.00																	
56.08																	
58.77																	
60.00																	
62.18																	
65.00																	
66.03						1											
70.00																	
75.00						1							1				
80.00																	
81.68							2							1			
85.00																	
92.10	1					9	2										
95.00		1				1											
97.68							1										
100.00																	
103.50																	
108.78																	
125.00			2														
129.12							1	1									
129.78								1	1						2	2	2
130.00													1	2	3	1	1
130.95																	
134.20						2	1	1	1	1	2	1					
135.00	1	1	1	1	2												
145.30																	
155.42																	
164.92																	
165.75																	
174.20																	
183.00																	
194.05																	
199.00																	
199.79																	
200.69																	
208.45																	

Fig. 5. A. Presence/absence data presented as a range chart including all identified taxa from drill core Övedskloster 2.

B

Stratigraphy		Depth (m)	Tetrahedraletes medinensis	Ambitisporites avitus/dilutus morphon	Gneudnaspora divellomedia	Archaeozonotriletes chulus	Imperfectotriletes patinatus-vavrdovae morph.	Retusotriletes spp.	Hispanaediscus verrucatus	Hispanaedisucs lamontii	Synorisporites verrucatus	Cheilotetras caledonica	Cymbohilates hystricosus	Tetrahedraletes grayae	Apiculiretusispora spp.	Apiculiretusispora sp. B	Hispanaediscus sp. A	Retusotriletes triangulatus	Rimosotetras problematica	Chelinohilates lornensis	Synorisporites tripapillatus	Pseudodyadospora petasus	Cymbohilates allenii	Pachytetras rugosa	Chelinospora sanpetrensis	Ambitisporites tripapillatus	Aneurospora hispidica
Devonian	Lochkovian	74.9	x																								
		82.9		x	x																						
		94.9		x	x	x	x	x	x		x				x	x	x										
		101	x		x		x	x			x	x	x	x				x		x		x				x	
		111	x	x	x	x	x	x	x	x	x							x	x		x		x	x	x	x	x

Fig. 5. B. Presence/absence data presented as a range chart including all identified taxa from drill core Övedskloster 1.

reniforma, *Emphanisporites rotatus*, *Retusotriletes triangulatus*, *Scylaspora downiei* and *Synorisporites verrucatus*.

Richardson and Lister (1969) described spore assemblages from upper Silurian and Lower Devonian strata from the Welsh borderland and south Wales from which nine species are shared with the Övedskloster assemblages including: *Acinosporites salopiensis*, *Apiculiretusispora spicula*, *A. synorea* and *Streelispora granulata*.

A study of Early Devonian cryptospores from England (Richardson, 1996b) revealed four species shared with the Övedskloster assemblages, including *Artemopyra scalariformis*, *Chelinohilates erraticus*, *Cymbohilates allenii* and *Cymbohilates allenii* var. *magnus*. Another study from Britain targeted the earliest Devonian non-marine deposits of the lower Old Red Sandstone of Lorne, Scotland (Wellman and Richardson, 1996) and twelve species are shared with the assemblages of this study, including e.g. *Chelinohilates lornensis*, *Chelinohilates sinuosus* var. *angustus*, *Chelinohilates sinuosus* var. *sinuosus*, *Cymbohilates allenii* var. *magnus* and *Retusotriletes maccullocki*.

Spina and Vecoli (2009) recorded Silurian–Devonian miospore assemblages from one drillcore from the Ghadamis Basin, North Africa, in which 24 species are shared with Övedskloster including: *Apiculiretusispora spicula*, *A. synorea*, *Coronaspora cromatica*, *Emphanisporites rotatus* and *Retusotriletes maccullockii*.

Steemans et al. (2007) described a miospore assemblage of the earliest Devonian age (Lochkovian) from Saudi Arabia in which 35 species are shared with the Övedskloster assemblages including *Apiculiretusispora spicula*, *Chelinohilates erraticus*, *C. lornensis*, *C. sinuosus* var. *sinuosus*, *Chelinospora cantabrica*, *C. hemiesferica*, *C. sanpetrensis*, *Concentricosiporites sagittarius*, *Coronaspora cromatica*, *C. reticulata*, *Cymbohilates allenii* var. *magnus*, *Emphanisporites rotatus*, *Retusotriletes triangulatus* and *Scylaspora elegans*.

Steemans et al. (2008) described a miospore assemblage from the Silurian–Devonian in northern Brazil (Urubu River, western Amazon area) and identified 64 well-preserved spore species. Twenty-two of those spore species are shared with this study including: *Ambitisporites tripapillatus*, *Chelinohilates sinuosus* var. *sinuosus*, *Chelinospora cantabrica*, *C. sanpetrensis*, *Coronaspora cromatica*, *Retusotriletes maccullockii*, *R. triangulatus* and *Scylaspora downiei*.

The comparisons show that the assemblages most similar to those at Övedskloster are surprisingly from northern Gondwana; Saudi Arabia and Libya. The assemblage from Saudi Arabia with 35 shared species is most similar and dated to the Early Devonian (Lochkovian) (Steemans et al., 2007). The Libyan assemblage spans the Silurian–Devonian boundary and shares 22 taxa. Another assemblage that resembles the assemblage of this study is described from Wenlock–lower Přídolí successions of Wales (Burgess and Richardson, 1995) where 22 taxa are shared. Other assemblages described from Avalonia and Baltica are less similar to the assemblages from the present study.

5.2. Paleogeographical implications

During the middle Silurian, the Baltica–Avalonia continent collided with Laurentia and formed a new paleocontinent, Laurussia, while Gondwana continued its course towards Baltica (Cooks and Torsvik, 2002). The Rheic Ocean reached its widest extent during the late Silurian and Early Devonian (Cooks and Torsvik, 2002) during which present day Sweden was located in the Southern Hemisphere, directly south of the equator (Cooks and Torsvik, 2002). The studied assemblages appear to share most similarities with coeval assemblages from Wales, which belonged to the Avalonian paleo-continent, and with those from Saudi Arabia and Libya (northern Gondwana) revealing an influence from Gondwana, an influence that seems to have increased from the late Silurian to the Early Devonian. This agrees with the fact that Gondwana was getting geographically closer to Baltica and Laurassia, probably enhancing the ease of species interchange. This agrees with the theory of Steemans et al. (2007) that Gondwana and the Old Red Sandstone Continent were much closer than portrayed on many paleogeographical reconstructions, allowing migration of cryptospore-producing plants during the latest Silurian and earliest Devonian.

However, several of the recorded species in the Övedskloster assemblage have only previously been reported from the Cantabrian Mountains of Spain and not in other Old Red Sandstone continent sequences such as Britain.

Archaeozonotriletes chulus is abundant in Přídolían and Lochkovian samples (175.00 m and above) strata. According to Richardson (1996b), this patinate spore is proportionally more abundant offshore. In Wellman and Richardson (1993) there is an absence of laevigate patinate miospores from the Midland Valley assemblages and the authors discuss that this may be a consequence of paleogeographical or paleoenvrionmental factors. The samples in which *A. chulus* are abundant are also rich in marine palynomorphs (Figs. 4, 8). In contrast, the samples richest in continental palynomorphs are also the poorest in *A. chulus* (see p. 96 in Wellman and Richardson (1996)). Similarities in

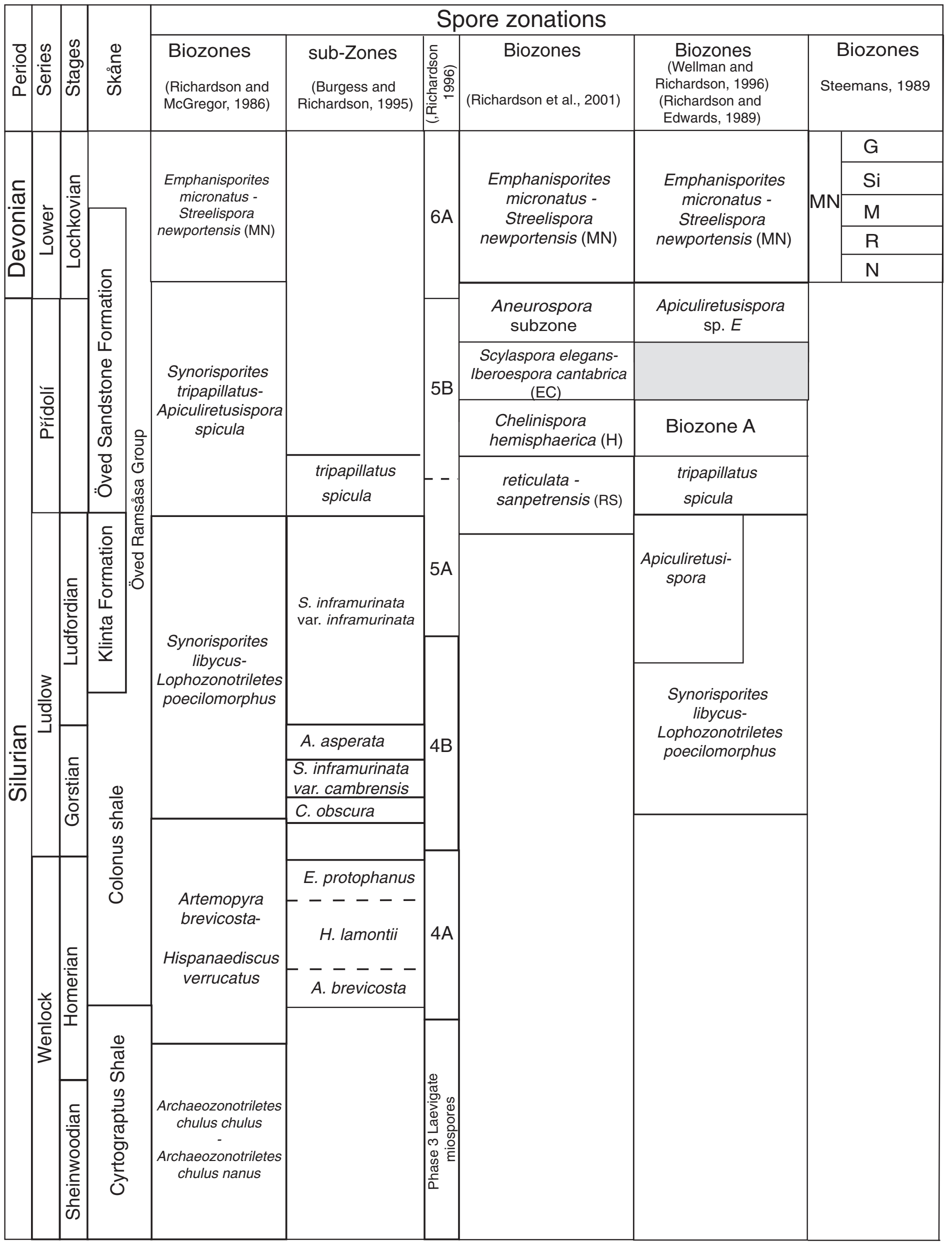

Fig. 6. Correlation of late Silurian and Early Devonian spore-schemes tied to global and local chrono- and lithostratigraphical charts. The spore zonations are based on Richardson and McGregor (1986), Steemans (1989), Richardson and Edwards (1989), Richardson (1996a, 1996b) and Wellman and Richardson (1996).

cryptospore assemblages indicate taxon exchange between the continents that cannot easily be explained by migration of cryptospore-producing plants and raise the question of long distance transport.

6. Conclusions

- This study provides the first confirmation of Devonian strata in Sweden. The age of the Öved Sandstone has been revised based on palynostratigraphy to also include the earliest Devonian successions in the upper part.
- In total, 77 spore species were identified in the two drillcores Övedskloster 1 and 2 and the results reveal a diverse and well-preserved spore assemblage for strata of this age.
- Two distinct assemblages were recognized in the Övedskloster 2 drillcore; Assemblage A of Přídolí age and Assemblage B of Lochkovian age.
- The palynofacies is dominated by terrestrial organic matter, such as spores and phytodebris. Marine microfossils constitute a lesser part of the assemblage and are absent in the upper part of the succession.
- The lack of amorphous organic matter (AOM) in the palynofacies documented from the Övedskloster cores possibly signifies well-oxygenated marine conditions for the lower part of the succession.

7. List of species

Acinosporites salopiensis Richardson and Lister (1969)
Acinosporites spp.
Ambitisporites avitus-dilutus morphon Steemans et al. (1996)
Ambitisporites eslae (Cramer and Diez) Richardson et al. (2001)
Ambitisporites parvus Burgess and Richardson (1995)
Ambitisporites tripapillatus Moreau-Benoit, 1976
Aneurospora geikiei Wellman and Richardson (1996)
Aneurospora hispidica Wellman and Richardson (1996)

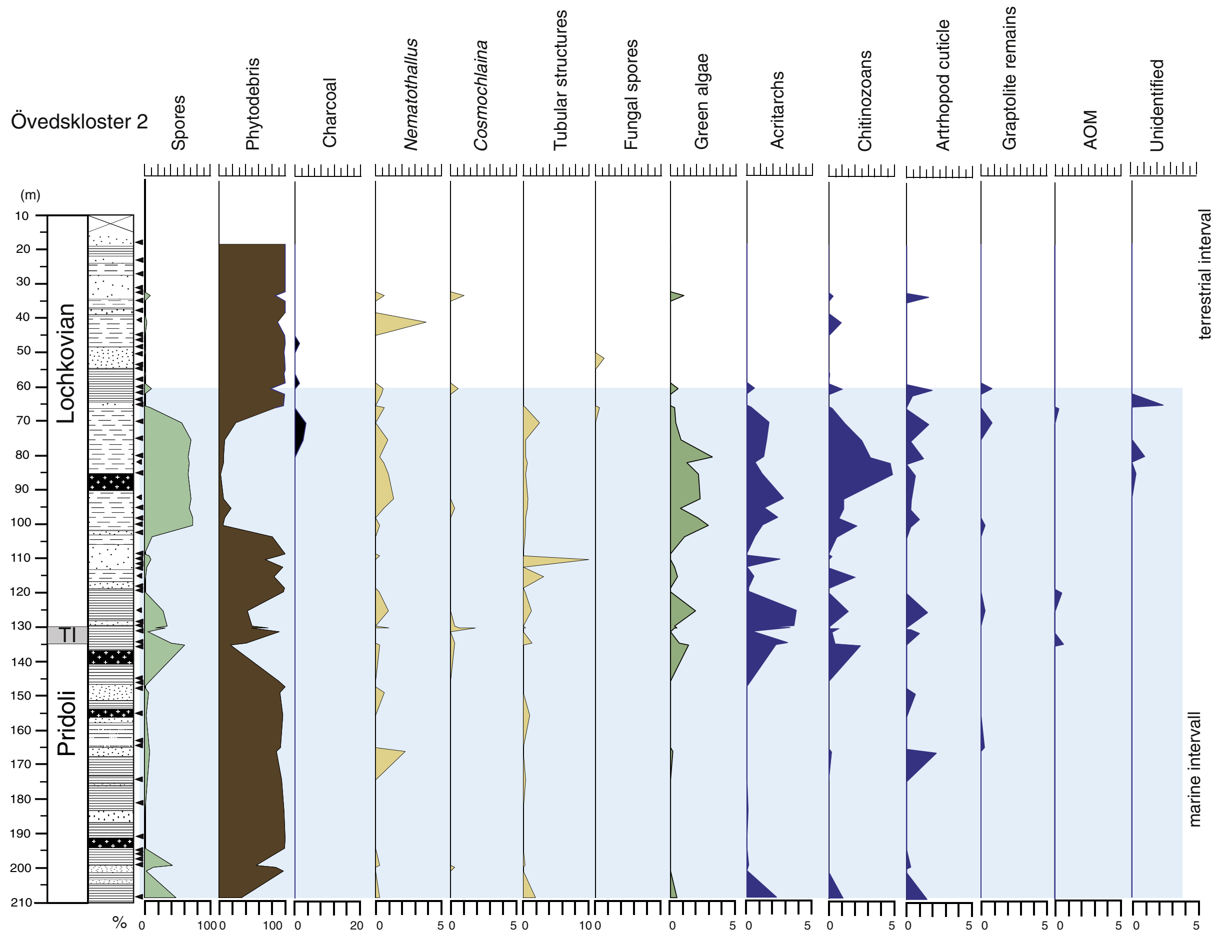

Fig. 7. Palynofacies results from Övedskloster 2 illustrating relative abundance of the different palynofacies categories.

Apiculiretusispora asperata Burgess and Richardson (1995)
Apiculiretusispora burgsvikensis Hagström (1997)
Apiculiretusispora spicula Richardson and Lister (1969)
Apiculiretusispora synorea Richardson and Lister (1969)
Apiculiretusispora sp. B *in* Burgess and Richardson (1995)
Apiculiretusispora spp.
Archaeozonotriletes chulus (Cramer) Richardson and Lister (1969)
Artemopyra radiata Strother, 1991
Artemopyra scalariformis Richardson (1996)
Artemopyra spp.
Brochotriletes cf. *foveolatus* Naumova, 1953
Cheilotetras caledonica Wellman and Richardson (1993)
Chelinohilates erraticus Richardson (1996a, 1996b)
Chelinohilates lornensis Wellman and Richardson (1996)
Chelinohilates sinuosus Wellman and Richardson (1996)
Chelinohilates sinuosus var. *angustus* Wellman and Richardson (1996)
Chelinohilates sinuosus var. *sinuosus* Wellman and Richardson (1996)
Chelinohilates spp.
Chelinospora cantabrica Richardson et al. (2001)
Chelinospora hemiesferica (Cramer & Diez) Richardson et al. (2001)
Chelinospora poecilomorpha (Richardson and Ioannides) Richardson et al. (2001)
Chelinospora pseudoreticulata Steemans (1989)
Chelinospora sanpetrensis (Rodriguez) Richardson et al. (2001)
Chelinospora spp.
Concentricosiporites sagittarius (Rodriguez) Richardson et al. (2001)
Confossuspora reniforma Strother, 1991
Coronaspora cromatica (Rodriguez) emend. Richardson et al. (2001)
Coronaspora reticulata Richardson et al. (2001)
Cymbohilates allenii Richardson (1996)
Cymbohilates allenii var. *allenii* Richardson (1996)
Cymbohilates allenii var. *magnus* Richardson (1996)
Cymbohilates hystricosus Wellman and Richardson (1996)
Cymbohilates micrograngulatus
Cymbohilates sp. A *in* Wellman and Richardson (1996)
Cymbohilates spp.
Dyadospora murusdensa-murusattenuata morphon Steemans, 1996
Emphanisporites concentricus Burgess and Richardson (1995)
Emphanisporites micrornatus Richardson and Lister (1969)
Emphanisporites neglectus Vigran, 1964
Emphanisporites protophanus Richardson and Ioannides, 1973
Emphanisporites rotatus McGregor, 1973
Emphanisporites spp.
Gneudnaspora divellomedia (Chibrikova) Balme, 1988 var. *minor* Breuer et al., 2007
Hispanaediscus lamontii Wellman, 1993
Hispanaediscus major Burgess and Richardson (1995)
Hispanaediscus sp. A in Burgess and Richardson (1995)
Hispanaediscus verrucatus (Cramer) Burgess and Richardson (1991)
Hispanaediscus spp.
Imperfectotriletes patinatus-vavrdovae morphon Steemans, 1996
Pachytetras rugosa Hagström (1997)
Pseudodyadospora petasus Wellman and Richardson (1993)
Retusotriletes goensis (Richardson and Ioannides, 1973) Lele and Streel, 1969
Retusotriletes maccullockii Wellman and Richardson (1996)
Retusotriletes triangulatus (Streel) Streel, 1967
Retusotriletes warringtonii Richardson and Lister (1969)
Retusotriletes spp.
Rimosotetras problematica Burgess, 1991
Scylaspora downiei Burgess and Richardson (1995)
Scylaspora elegans Richardson et al. (2001)
Scylaspora scripta Burgess and Richardson (1995)
Scylaspora vetusta (Rodriguez) Richardson et al. (2001)
Streelispora granulata Richardson and Lister (1969)
Synorisporites libycus Richardson and Ioannides, 1973
Synorisporites sp. S in Wellman and Richardson (1996)
Synorisporites tripapillatus Richardson and Lister (1969)
Synorisporites verrucatus Cramer emend. Burgess and Richardson, 1991
Tetrahedraletes grayae Strother, 1991

(continued on next page)

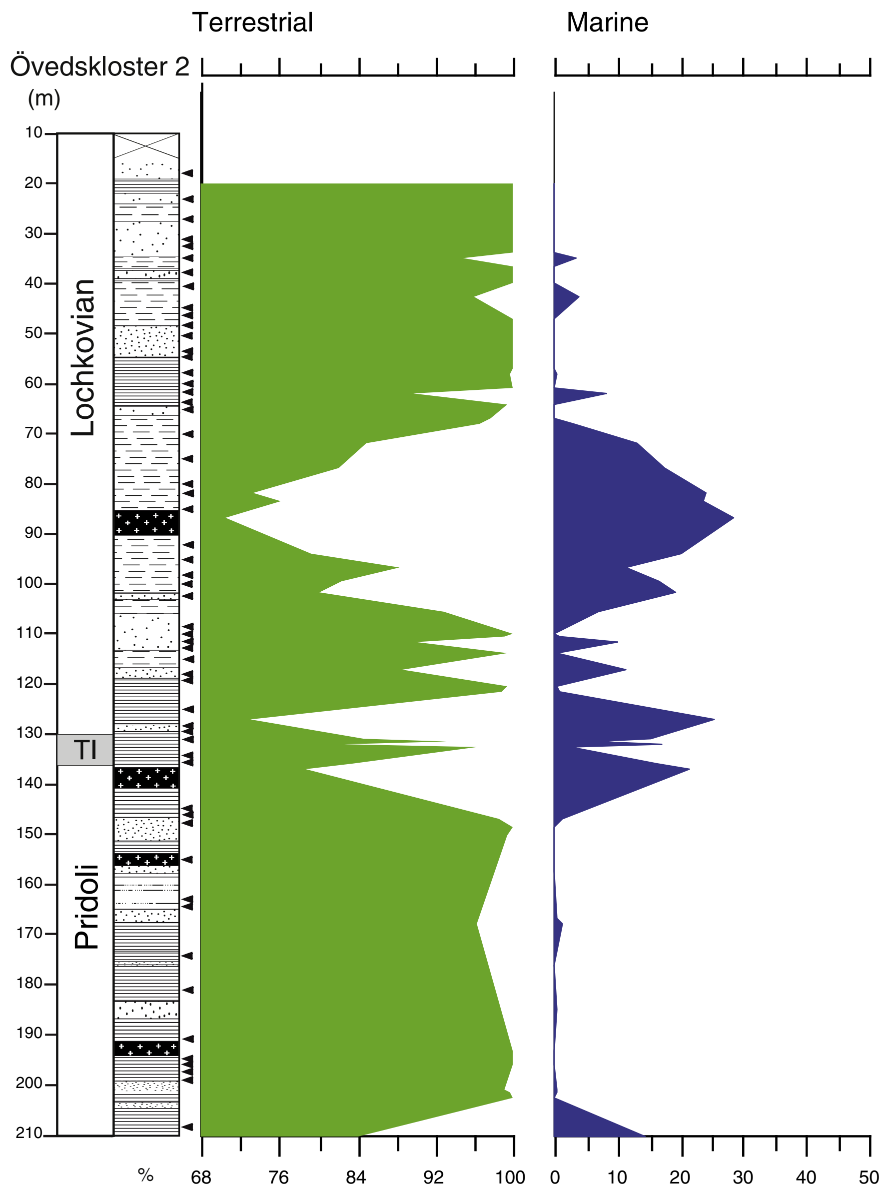

Fig. 8. Relative abundance of terrestrial vs. marine organic content of Övedskloster 2.

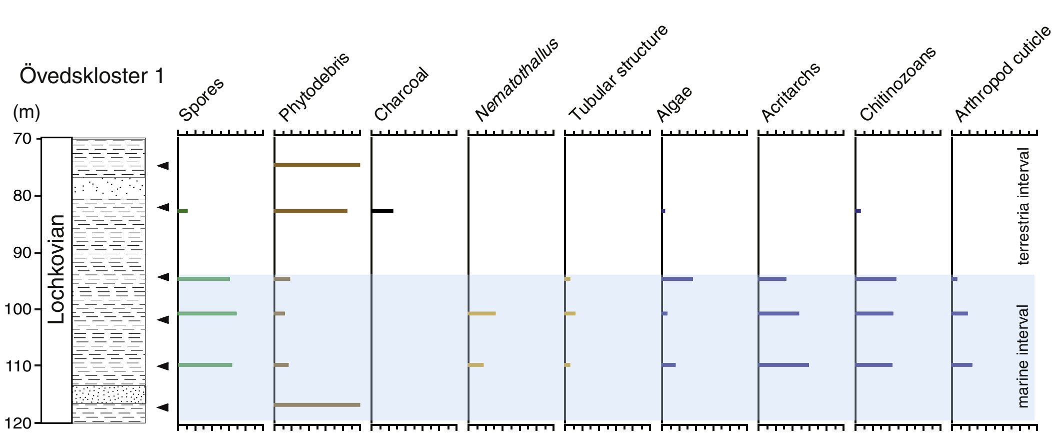

Fig. 9. Palynofacies results from Övedskloster 1 illustrating relative abundance of the different palynofacies categories.

Tetrahedraletes medinensis Strother and Traverse (1979)
Velatitetras laevigata Burgess, 1991

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