A palynological study from Sweden reveals stable terrestrial environments during Late Silurian extreme marine conditions

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ABSTRACT: A palynological study of the upper Silurian Öved–Ramsåsa Group in Skåne, Sweden yields a well preserved spore assemblage with low relative abundances of marine micro-fossils. In total, 26 spore taxa represented by 15 genera were identified. The spore assemblage is dominated by long-ranging cryptospore taxa, and the trilete spore *Ambitisporites avitus-dilutus*. However, key-species identified include *Artemopyra radiata*, *Hispanaediscus lamontii*, *H. major*, *H. verrucatus*, *Scylaspora scripta* and *Synorisporites* cf. *libycus*. Importantly, *Scylaspora klintaensis* was identified, allowing correlation with the Klinta 1 drillcore (Skåne). A Ludlow age is inferred for the exposed succession, which agrees well with previous conodont stratigraphy. The organic residue is dominated by phytodebris and spores, but with high relative abundances of acritarchs at two levels, possibly related to flooding surfaces.

Based on the palynofacies analysis, a near-shore marine environment is proposed. The close prox-imity to land is inferred by the high proportions of spores, and the dispersed assemblage most likely represents the local flora growing on delta plains. The palynological signal also infers a stable terrestrial environment and vegetation, in contrast to unstable conditions in the marine environment characterised by ooid formation in an evaporitic environment. Comparisons with coeval spore as-semblages from Gotland, Avalonia and Laurentia show relatively close similarities in taxonomic composition at the generic level.

KEY WORDS: cryptospores, early land plants, Klinta, Ludfordian, sea level, stratigraphy

Records of early land plants from Baltica have previously been described from Röstånga, Skåne (Sweden). These Late Ordovician (Katian) spores represent the oldest record of land plants from Baltica (Badawy *et al.* 2014). Other records of cryp-tospores are from Ordovician (latest Katian–Hirnantian) de-posits from the Valga-10 core in southern Estonia (Vecoli *et al.* 2011). Studies concerning terrestrial palynomorphs from the top Ordovician to the Wenlock successions of Baltica are scarce, but middle Llandovery to late Ludlow spore assemb-lages were described by Hagström (1997) from the Närborrnin-gen 1 and Burgsvikborrningen 1 cores and from outcrops on Gotland. A rich and well-preserved palynoflora of crypto-spores, vascular plant spores, fungal spores and hyphae was recovered especially from the Ludfordian Burgsvik Beds by Hagström (1997). Sherwood-Pike & Gray (1985) also reported fungal spores and hyphae from these beds. Silurian spores have also been studied from Skåne and Gotland by Gray *et al.* (1974). Hagström & Mehlqvist (2012) described further early (Ludlow) land plant remains from Gotland. Upper Silurian outcrop sections and bore cores from Skåne have also yielded spore assemblages (Mehlqvist *et al.* 2012, 2014).

The upper Silurian Öved-Ramsåsa Group in Skåne, Sweden has been subjected to numerous investigations over the two last centuries. The strata representing the youngest Palaeozoic are mainly exposed in limestone and sandstone quarries, and along the shore of Lake Ringsjön, the so-called Klinta expo-sure. The first publication, from 1725, is a documentation of the fossil content (Bromell 1725–1729). Succeeding compre-hensive publications concerning the exposed successions at Klinta include, for example, Eichstädt (1888), Grönwall (1897), Hadding (1927, 1933), Regnéll (1960); and detailed studies

comprise research on conodonts (Jeppsson 1975; Jeppsson & Laufeld 1986), tentaculitids (Larsson 1979), chitinozoans (Grahn 1996) and $\delta^{13}C$ composition (Wigforss-Lange 1999; Jeppsson *et al.* 2012). However, all these studies focus on the marine microfossils or sedimentological/geochemical aspects and no contributions concern terrestrial microfossils. Our study focuses on upper Silurian successions from southern Sweden, with the aim of describing the dispersed spore assemblages and other organic debris recovered from exposures at Klinta, providing the first record of terrestrial palynology in these strata. We correlate our results with zonation schemes based on marine microfossils and compare our terrestrial palynological signal to the environmental changes within the marine realm.

1. Geological setting

By the time of the Silurian, Baltica was located south of the Equator in the tropical climate zone (Fig. 1a; Moore *et al.* 1994). The platform was partly covered by an epicontinental sea and remnants of Silurian deposits are found in Norway, mid and south Sweden, the Baltic Sea, the East Baltic States, Denmark and Poland. The Baltoscandian Platform was, during the Palaeozoic, strongly affected by the Caledonian orogenic cycle that resulted in the collision of the continents Laurentia, Baltica and Avalonia (Fig 1a). The Iapetus and Rheic Oceans were closing up and the active fold belts on the western and southeastern margins of the Baltic platform formed the Arctic–North Atlantic Caledonides and the North German–Polish Caledonides (Frost *et al.* 1981; Ziegler 1984; Zeh & Gerdes 2010). The former, wide shelf areas transformed to marginal basins where clastics, derived from the mountain ranges, were
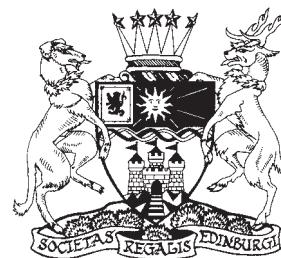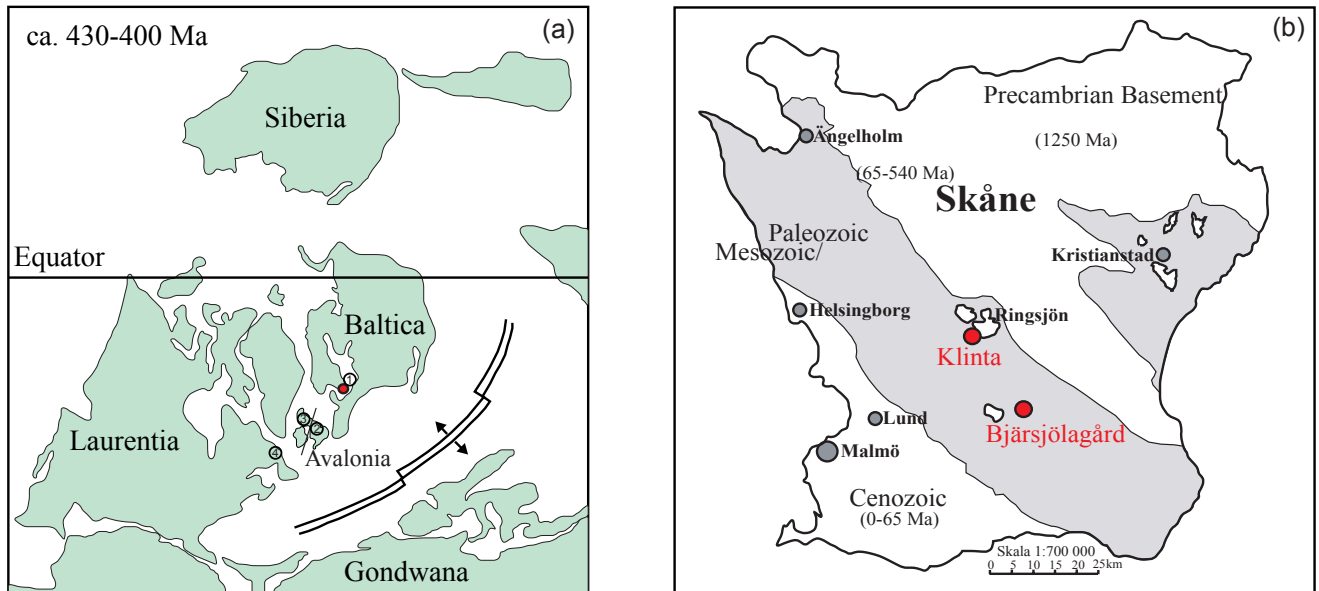
Figure 1 (a) Palaeogeographic map showing the position of Baltica, during the late Silurian to Early Devonian. Red circle marks the study site in Skåne, Sweden. Numbers show the location of other study sites, compared with Klinta: 1 = Gotland; 2 = Wales; 3 = Scotland; 4 = Nova Scotia. (Map modified after Scotese *et al.* 1985). (b) The principal exposures of the Öved Ramsåsa Group are found in Klinta and Bjärsjölagård, Sweden (Locality map modified after Wikman & Bergström 1987).

deposited (Zeh & Gerdes 2010). The sedimentary strata reflect a gradual shallowing-up from deep-water graptolitic shales to shallow marine limestones and sandstones. Following the pro-grading, shoreline marine deposition ceased, as indicated by the onset of early Devonian "Old Red Sandstone" deposition (Bassett 1985).

The youngest Palaeozoic stratum in southern Sweden is the Öved–Ramsåsa Group, which is sub-divided into the Klinta Formation (Jeppsson & Laufeld 1986) and the overlying Öveds Sandstone Formation (Hadding 1927). These sediments are dominated by mudstones, inter-layered with shallow marine carbonates, grading into sandstones in the younger part of the succession. The majority of the outcrops representing the Öved-Ramsåsa Group are found in central Skåne at Klinta and Bjärsjölagård (Fig. 1b). The Klinta exposures are located along the shoreline of the eastern lake Ringsjön (Figs 1b, 2).

In sedimentological and petrographic studies, these deposits have been shown to contain cerebroid ooids and evaporite tracers, which are linked to changes in faunas (Wigforss-Lange 2007; Jeppsson *et al.* 2012). The depositional setting has been interpreted as a near-shore tidally-influenced environment grading from open marine shallow subtidal to lagoonal intertidal conditions (Wigforss-Lange 2007).

The present stratigraphical scheme and nomenclature for the Öved-Ramsåsa Group is primarily based on conodont stratigraphy established by Jeppsson (1975) and Jeppsson & Laufeld (1986), and on spores from land plants studied from the drillcores Klinta 1 and Bjärsjölagård 2 (Mehlqvist *et al.* 2012).

The section at Klinta investigated herein comprises the Bjär and Bjärsjö members containing the conodont faunas *Ozarkodina excavata* (former *Hindeodella excavata*), older

Figure 2 One of the studied exposures at Klinta, located by the shore of the eastern Lake Ringsjön, Sweden.

Table I
Raw data, % of spore taxa identified in each sample. Taxa highlighted in yellow are trilete spore species; the rest are cryptospores.

Spore species/sample	Depth (m)	Artemopyra brevicosta	Artemopyra radiata	Artemopyra sp.	Cymbohilates sp. A	Cymbohilates sp. B	Dyadospora murusdensa-murusattentata	Hispanaediscus lamontii	Hispanaediscus major	Hispanaediscus verrucatus	Imperfectotriletes sp.	Laevolancis divellomedia-plicata	Pachytetras rugosa	Tetrahedraletes grayii	Tetrahedraletes medinensis	Ambitisporites avitus-dilutus	Ambitisporites parvus	Apiculiretusispora burgsvikensis	Apiculiretusispora sp. B	Archeozonotriletes sp.	Retusotriletes goensis	Retusotriletes cf. warringtonii	Synorisporites cf. libycus	Scylaspora scripta	Scylaspora klintaensis	Scylaspora cf. vetusta	Chelinospora sp.
93-3	14.08	0	0	0	0.7	0	5.3	0	0	0	4.6	81.6	0	0	0	2.0	1.3	0	0	0	0	2.6	0	0	2.0	0	0
93-16	13.83	0	0	0	0	0	6.3	0	0	0	0	89.9	0	0	0	3.8	0	0	0	0	0	0	0	0	0	0	0
93-2	13.36	0	0	0	0.7	0,7	2.6	0	0	0	4.6	82.2	0	0	0,7	7.2	0.7	0	0	0	0	0	0	0	0	0	0.7
93-96	12.56	0	0	0	0	1,3	8.6	0.7	0	0	0	76.3	0	0.7	0	9.9	0	0	0.7	0	0	0.7	0	1.3	0	0	0
93-8	11.18	0	0	0	1.3	0	9.3	0	0.7	2.0	0	62.3	8.6	0.7	3.3	9.3	0	0	0.7	0	0	2.0	0	0	0	0	0
93-91	11.06	0	0,7	0	0	0	11.2	0	0	0.7	1.3	75.7	0.7	0.7	0	9.2	0	0	0	0	0	0	0	0	0	0	0
93-80	9.73	0	0	0	4.0	0	3.2	0	2.4	30.6	4.0	28.2	3.2	7.3	0.8	8.9	0.8	0	0	0.8	0.8	4.8	0	0	0	0	0
93-76	9.07	0	0	0	0	0	1.3	0	0	0	0	58.9	0	1.3	19.9	8.6	0	4.6	0	0	0	5.3	0	0	0	0	0
93-23	8.87	0	0	0	0	0	9.2	0.7	0	0	1.3	82.4	0	2.6	0	2.0	0	0	0	0	0	2.0	0	0	0	0	0
93-22	8.30	0	0	0	0	0	5.2	0	0	3.9	0	87.6	0	0.7	0	2.6	0	0	0	0	0	0	0	0	0	0	0
93-35	6.54	0	0	0	0.7	0	14.5	1.3	0	0	0	76.3	0	0	0.7	5.3	0.7	0.7	0	0	0	0	0	0	0	0	0
93-33	6.25	0	0,7	0	0	0,7	11.9	7.9	0	0	0	64.2	0	2.6	0	7.9	0.7	0	0	0	0	2.6	0	0.7	0	0	0
93-49	4.75	1.3	0	1.9	0	0	7.0	0	0	1.3	0	85.4	0	0	0.6	1.3	0.6	0	0	0	0	0	0	0	0	0,6	0
93-48	4.26	0	0	0	0	0	15.5	0	0	0	0	78.0	0	0	2.4	2.4	1.8	0	0	0	0	0	0	0	0	0	0
93-71	3.95	0	0	0	0.6	0	14.8	1.3	0.6	0	3.2	64.5	0	4.5	0	2.6	0	0	4.5	0	0	3.2	0	0	0	0	0
93-47	3.85	0	0	1	0.6	0	10.3	0	0	0	0	79.5	0	0	1.9	6.4	0	0	0	0	0	0	0.6	0	0	0	0
93-46	2.58	0	0	0	0	0	2.0	0	0	1.3	0	89.9	0	0	0	4.7	0	0	0	0	0	1.3	0.7	0	0	0	0
93-45	1.75	0	0	0	1.2	0	1.2	0	0	0	0	87.7	0	3.7	1.2	2.5	0.6	0	0	0	0	1.2	0	0	0	0	0.6
93-42	1.08	0	0	0	1.3	0	1.3	0	0	0	0	87.3	0	0	4.4	5.1	0	0	0	0	0	0.6	0	0	0	0	0
93-37	0.00	0	0	0	0.7	0	0.7	0	0	0	0	69.1	0	2.7	4.7	8.7	0	12.1	0	0	0	1.3	0	0	0	0	0

and younger *Ozarkodina scanica* (former *Hindeodella steinhornensis scanica*) of the *Polygnathoides siluricus* Zone and the Icriodontid Zone (Jeppsson 1975, table 1; Jeppsson *et al.* 2012, fig. 2). These faunas indicate a Ludlow (Ludfordian) age.

2. Material and methods

2.1. Sampling
The Klinta outcrop (55.8640°N, 13.5110°E) is a 600 m-long exposure along the shoreline of eastern Lake Ringsjön (Figs 1b; 2). The cliff face is 6 m high, but since the strata dip 18° to the south, the succession becomes progressively younger in that direction. In 1996, one of the authors (W-L) excavated the cliff face and sampled five stratigraphic sections each separated by 30 m. The resulting composite log, based on correlations outlined by Wigforss-Lange (1999, 2007), represents a continuous section with a thickness of 14 m.

2.2. Palynology
Twenty samples were selected for palynological analysis and the samples were processed according to standard palynological procedures at Global GeoLab Ltd., Canada. About 20 g of sediment were first treated with dilute hydrochloric acid (HCl) to remove calcium carbonate, and further macerated in 45 % hydrofluoric acid (HF). No oxidation of the residues was performed, since the palynomorphs are of low thermal maturity. The organic residue was sieved using a 10-μm mesh and mounted in epoxy resin on two microscopic slides. 150 spores were identified per slide and the percentage of each spore taxa was calculated (Fig. 3; Table I). Some morphotaxa and similar taxa have been combined in the diagrams (Figs 3, 4).

2.3. Palynofacies
Palynofacies analysis involved counting the relative abundance of organic particles based on 1,000 counts per slide. Classification of palynological matter was based on Batten's (1996) scheme adjusted to the local palynofacies, therefore not all sub-groups from Batten's classification system are represented within this study: I. Spores (from early land plants); II. Black phytodebris; III. Brown phytodebris; IV. Cuticle-like sheets; V. Tubular structures; VI. Acritarchs; VII. Scolecodonts; and VIII. Chitinozoans (Fig. 5). The slides and residues are deposited at the Department of Geology at Lund University and illustrated specimens are identified by LO numbers.

3. Results

3.1. Palynology and age determination
A well preserved spore assemblage represented by 26 spore taxa in 15 genera was identified. Marine microfossils are represented by acritarchs (Fig. 6) that occur in all samples, together with low relative abundances of chitinozoans and scolecodonts occurring in a few samples (Fig. 5).

The spore assemblages are dominated by cryptospores, which are represented by 14 species in eight genera, and by trilete spores, represented by 12 species in seven genera. The morphotaxa *Laevolancis divellomedia* and *L. plicata* are the overall dominant taxa and together make up c.28–90 %. *Dyadospora murusdensa-murusattenuata* makes up 0.7–15.5 % (average 5 %); and *Ambitisporites avitus* reaches a maximum relative abundance of 10 % of the total spore count. Biostratigraphically important species include *Artemopyra brevicosta,*
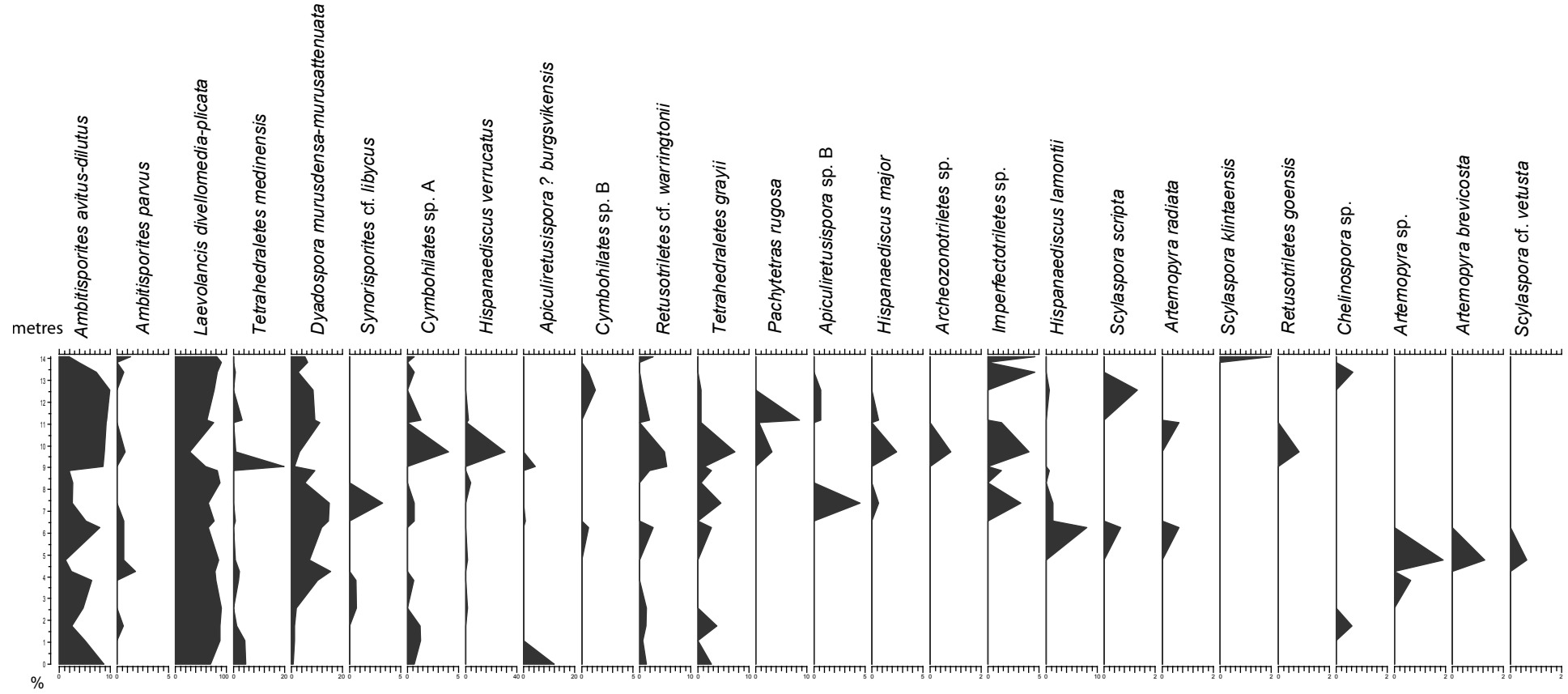
Figure 3   Spore diagram illustrating the relative abundance of selected spore taxa identified in the studied samples from the Klinta exposure. Note the different % scales on x-axes.
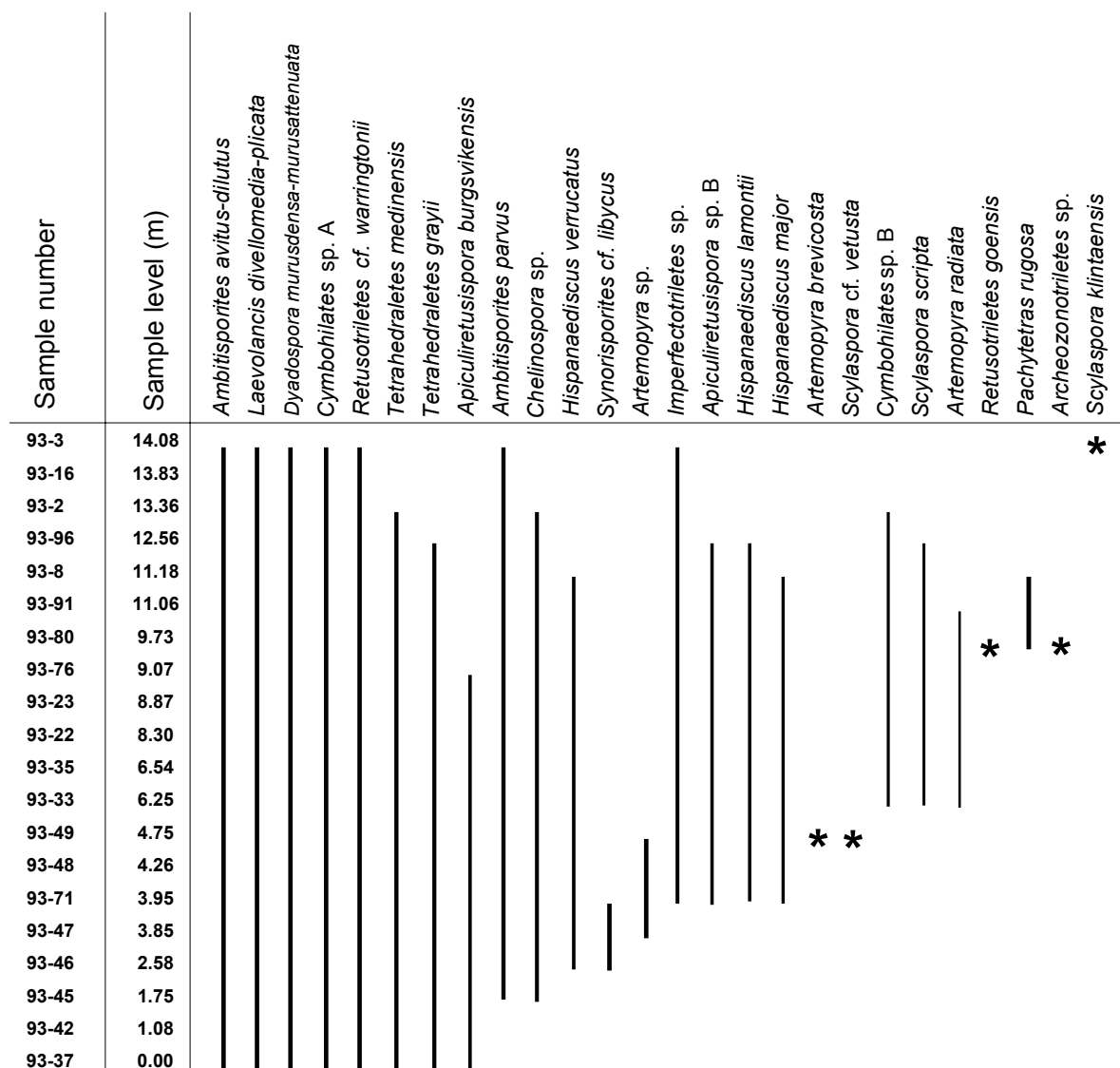
Figure 4 Range-chart for selected spore taxa through the Klinta outcrop succession. Stars represent occurrence in only one sample.

Artemopyra radiata, *Hispanaediscus lamontii*, *H. major*, *H. verrucatus*, *Scylaspora scripta* and *Synorisporites* cf. *libycus* (Fig. 7). Further, *Scylaspora klintaensis* occurs in the uppermost sample 93-3 at 14.08 m (Figs 3, 4; Table 1). This species was previously described from the Klinta 1 drillcore with a first appearance datum (FAD) at 112 m (Mehlqvist *et al.* 2012). This provides a tentative correlation between the outcrop section and the drillcore Klinta 1.

3.2. Palynofacies analysis
The organic matter is, in most samples, dominated by either black and brown phytoclasts or spores (Fig. 5). However, acritarchs reach high relative abundances at two levels through the sampled succession, reaching 64 % at 11 m. Chitinozoans and scolecodonts only occur in low numbers and do not exceed 2 % in any sample. Cuticle-like sheets and tubular structures are present with a few specimens in the basal part of the succession, not exceeding 1 %.

4. Geological and palaeoenvironmental implications
The succession has previously been dated to Ludfordian, based on the presence of the mid-Ludfordian conodont zones *Polygnathoides siluricus* and Icriodontid (Jeppsson *et al.* 2012)

and by the presence of chitinozoans representing the *Angochitina echinata* chitinozoan zone (Grahn 1996). For a detailed biostratigraphic zonation scheme, see Mehlqvist *et al.* (2014).

The age assessments previously performed on marine microfossils are supported by our palynological study revealing a Ludlow age, as the spore assemblage can be equated with the *Synorisporites libycus–Lophozonotriletes poecilomorphus* Assemblage Zone of Richardson & McGregor (1986). It should, however, be noted that the Assemblage Zone of Richardson & McGregor (1986) was established in Avalonia and, whilst the zone can be broadly correlated between Avalonia and Baltica, a more precise correlation is perhaps not possible. Importantly, our results can now be used for a spore zonation scheme for Baltica, representing a typical Ludfordian spore assemblage.

We have compared our results with a coeval spore assemblage from nearby drillcore successions (Klinta 1 and Bjärsjölagård 2) previously described by Mehlqvist *et al.* (2012, 2014). *Scylaspora klintaensis* has its FAD in the Klinta 1 drillcore at 112 m, where the succession is dated as Ludfordian (Mehlqvist *et al.* 2012). In the Klinta section, the same species occur at 14.08 m (Fig. 4). This correlation also agrees well with chemostratigraphic data (Wigforss-Lange 1999, 2007; Jeppsson *et al.* 2012).
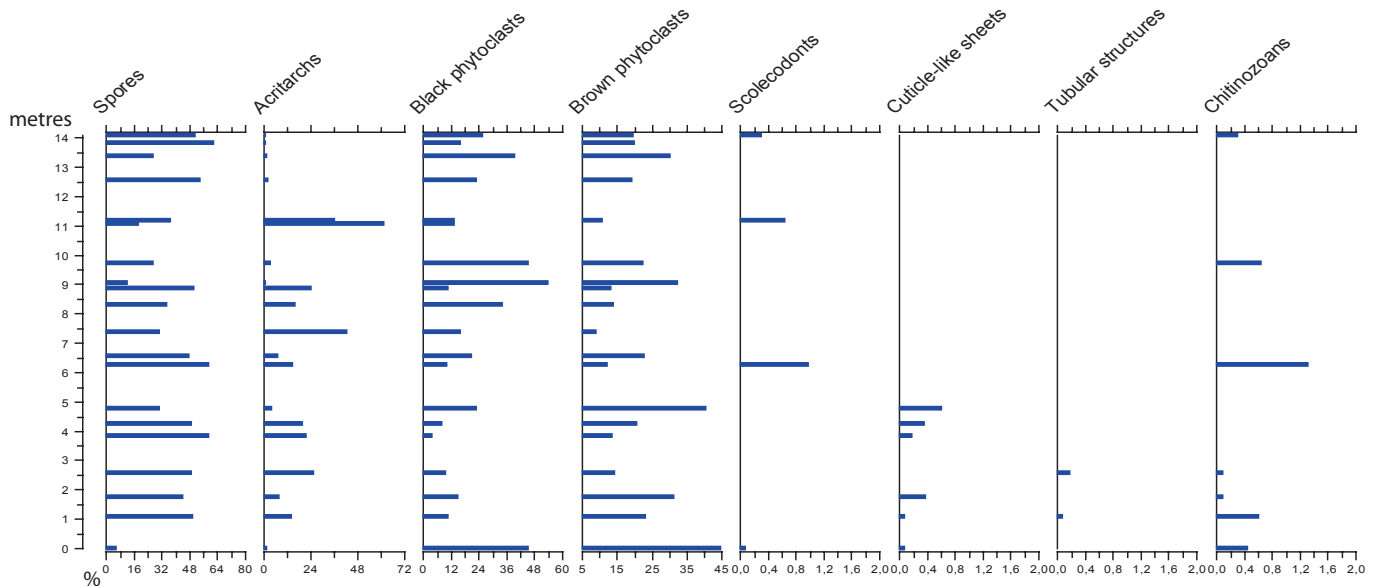
Figure 5 Palynofacies results, showing the relative abundance of the different components of organic matter in the residues from the studied samples. Note that x-axes for marine microfossils only represent 2 %.

Based on the palynofacies analysis, with an extremely high relative abundance of terrestrially-derived organic matter (spores and phytoclasts), a paralic environment is proposed for the basal and the topmost part of the succession. The close proximity to land is inferred by the high proportions of spores, which reflect a restricted catchment area, and the assemblage most probably represents the local flora growing on delta plains and with spores transported into the marine setting.

Relatively high abundances of acritarchs occur at 7 m and 11 m above the base of the section (Figs 5, 6). Considering the characteristics of the depositional environment, these deviations represent episodes of higher flood surges. In the shallow tide-dominated environment, even minor oscillations in water energy and/or water level will undoubtedly affect the sedimentation. The oxygen isotope composition also shows a minor depletion of ^{18}O at the upper level of acritarchs abundance (at 11 m; Fig. 6). This may reflect climate changes signalling higher temperatures (melting ice sheets); but it may also reflect diagenesis, as the oxygen isotope is extremely sensitive to diagenetic alteration under the influence of meteoric waters. The carbon isotope composition shows no corresponding excursion (Fig. 6).

The extreme conditions in the marine environment characterised by an increase of cyanobacteria, cerebroid ooids and evaporite tracers, combined with extinctions of conodont faunas and fish (Jeppsson & Aldridge 2000; Eriksson et al. 2009), are not reflected in the terrestrial vegetation. The terrestrial palynological signal reflects, instead, a robust, well-established and stable early flora throughout the studied succession, which contradicts results proposed by Stricanne et al. (2006) suggesting that both marine and terrestrial realms were synchronously affected during the Lau Event. We argue that the extinction during the Lau event is partly due to regression affecting local marine faunas, which seemingly didn't affect the terrestrial environments.

5. Comparison with other assemblages

Here, we compare the Klinta assemblage with coeval palynomorph suites from Baltica, Avalonia and that part of Laurentia presently represented in Scotland. The relevant intervals for comparison were selected from those publications that provide

data sets spanning larger intervals than the Ludlow. Numerous publications have dealt with late Silurian miospore assemblages from areas further afield, but those studies are beyond the scope for detailed comparisons in this paper and will be addressed in a future study comparing larger Swedish datasets. Examples of assemblages and miospore zonations for further comparisons from other palaeocontinents include those from Pennsylvania (Laurentia: Beck & Strother 2008) and the Cantabrian Mountains (northern Spain: Richardson et al. 2001).

Gondwanan assemblages have been documented in many publications; e.g., Rubinstein & Steemans (2002) comprehensively dealt with miospore assemblages spanning the Silurian–Devonian boundary from the Ghadamis Basin in Libya, and Spina & Vecoli (2009) described a coeval spore assemblage from the Tunisian part of the same basin. Other studies of somewhat younger (Devonian) spore assemblages from Tunisia were presented by, e.g., Loboziak et al. (1992). Additionally, there is a range of publications on miospore assemblages from the Precordillera Basin, Argentina; one of the latest examples being that of Garcia Muro et al. (2014), who described upper Silurian miospore suites.

Late Silurian spore assemblages from China were described by Wang & Li (2000) from northern Jiangsu, and Wang et al. (2005) documented a spore assemblage from Guamgyuan, Sichuan.

5.1. Baltica
Hagström (1997) describes miospore assemblage from Gotland, from material comprising middle Llandovery to upper Ludlow strata representing a shallowing-up sequence. Marine deposits prevail in the lowermost part of the drillcores and more nearshore, possibly deltaic, deposits in the uppermost part of the succession represented by the Burgsvik Beds of Ludfordian age. The Burgsvik beds are coeval to the Klinta succession and is the interval hosting the most abundant spore assemblages from Gotland (Gray et al. 1974; Hagström 1997). Fourteen species, notably the tetrad *Pachytetras rugosa* and the trilete spores *Apiculiretusispora* ? *burgsvikensis, Artemopyra brevicosta, Cymbohilates* sp., *Hispanaediscus verrucatus* and *Synorisporites* cf. *libycus*, are shared between the present study and the coeval assemblages from Gotland. Species that occur
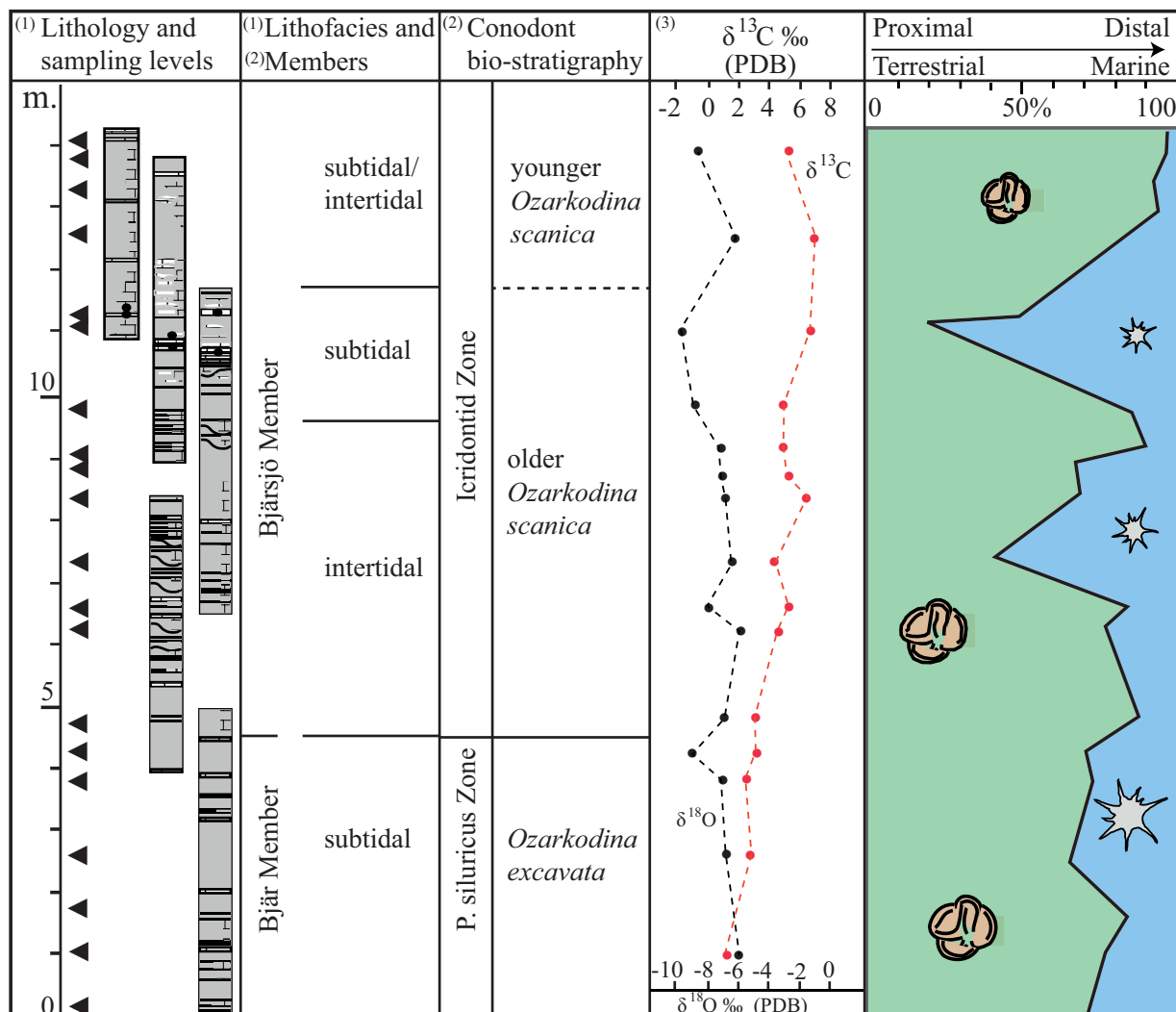
Figure 6 A compilation of data from this study and previously published results from the studied interval. The chart records the proportion of terrestrial vs. marine palynomorphs in relation to lithofacies, conodont stratigraphy and carbon and oxygen isotope composition. The data have been obtained from the following publications: (1) Wigforss-Lange 2007; (2) Jeppsson 1975; Jeppsson & Laufeld 1986; Jeppsson *et al.* 2012; (3) Wigforss-Lange 1999; Jeppsson *et al.* 2012).

in the Gotland assemblage, but are lacking from the current study, include *Abditusdyadus chalazus, Cymbohilates microgranulatus* and *C. variabilis.* The abundance data in Hagström (1997) is focused on the palynofacies and the relation between marine and terrestrial palynomorphs. The lack of percentage data for the spores hampers abundance comparison with the present study.

5.2. Avalonia and present-day Scotland

5.2.1. *Avalonia.* A late Wenlock to early Přídolí assemblage presented by Burgess & Richardson (1995) from the Rumney Inlier (south Wales) and Towy Anticline (southwest Wales) has been compared to the Klinta assemblage. The Welsh successions comprise near-shore marine sediments and in the Ludfordian interval 16 spore taxa were identified (11 trilete spores and five cryptospore taxa), making the Klinta assemblage the more diverse. When comparing the relation between cryptospores and trilete spores, major differences exist between the two assemblages, as the Welsh Ludfordian assemblage is highly dominated by trilete spores (69 %). Some shared taxa, such as *Laevolancis* and *Ambitisporites*, are long-ranging, but shared stratigraphically important species include *Artemopyra brevicosta, A. radiata, Hispanaediscus*

lamontii, H. major, *H. verrucatus, Scylaspora scripta* and *Synorisporites* cf. *libycus*. However, the presence of *A. brevicosta,* characteristic of slightly older assemblages in Avalonia, might signify that this taxon appears later in Baltica than in Avalonia and this agrees with previous observations (Wellman *et al.* 2013).

Beck & Strother (2001) described a miospore assemblage from Nova Scotia (western Avalonia) from the Arisaig Group. The sediments comprise silisiclastic mudstone and siltstone deposits and represent an almost complete succession of Silurian strata. The assemblage from the Arisaig Group shows similarities to type sections in the Anglo–Welsh Basin (East Avalonia). In total, 36 different spore species were identified from the Arisaig Group, but the assemblage is less diverse than assemblages from the Anglo–Welsh Basin. We compare our Klinta assemblage with the interval represented by the McAdam Brook and Moydart formations of the Arisaig Group (dated to Ludlow and represented by the *libycus–poecilomorphus* Assemblage Zone). It should be noted that the Arisaig assemblage seems to have a larger catchment area with deposition more distal as compared to our study. The mentioned interval in the Arisaig Group contains 25 taxa, some of which are in open nomenclature, a diversity similar to the 26 taxa recorded from the Klinta assemblage. However, out of 13 spore genera
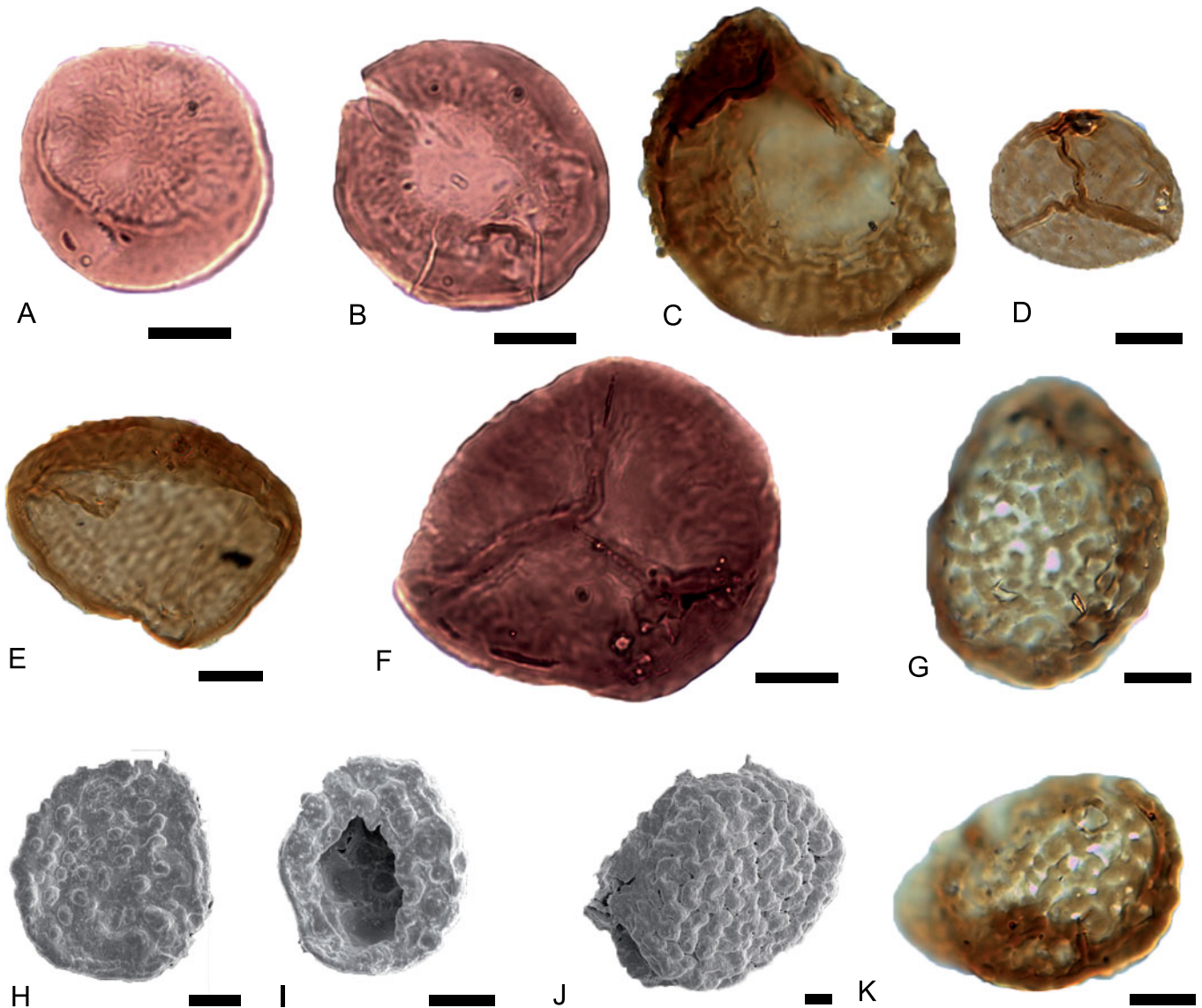
Figure 7 Light microscope images of dispersed spores from the Klinta outcrops, Skåne. Selected spore taxa: (A) *Artemopyra brevicosta* Burgess & Richardson, 1991, LO11917t; (B–C) *Artemopyra radiata* Strother, 1991, LO11918t, LO11919t; (D) *Synorisporties* cf. *libycus* Richardson & Ioannides, 1973, LO11920t; (E) *Hispanaediscus major* Burgess & Richardson, 1995, LO11921t; (F) *Scylaspora* cf. *vetusta* (Rodriguez) Richardson *et al.*, 2001, LO11922t; (G, J–K) *Hispanaediscus lamontii* Wellman, 1993, LO11923t, LO11924t, LO11925t; (H–I) *Hispanaediscus verrucatus* (Cramer) Burgess & Richardson, 1991, LO11926t, LO11927t. Scale bars = 10 μm.

in the *libycus–poecilomorphus* Assemblage Zone of the Arisaig Group, only four are shared with those of this study. The following species are in common with the Klinta assemblage: *T. medinensis*, *A. avitus*, *A, dilutus*, *L. divellomedia*, *L. plicata*, *H. verrucatus*, *H. major*, *A. parvus*, *D. murusattenuata* and *D. murusdensa*.

5.2.2. Scotland. Wellman (1993) described a late Wenlock or early Ludlow spore assemblage from the Stonehaven Group in Scotland. The Stonehaven Group, exposed in the Midland Valley of Scotland, comprises continental sediments overlying Cambro–Ordovician deposits and is followed by a sequence of Lower Old Red Sandstone deposits (Wellman 1993). The spore assemblages are highly dominated by cryptospores (c. 88 %), and trilete spores only make up 8 % of the assemblage, very similar to the numbers observed from Klinta. The trilete spores in the Scottish assemblage are dominated by *A. avitus* and *A. dilutus* (just as in Klinta), whilst ornamented trilete spores are rare. Cryptospores are dominated by the genera *Laevolancis*, *Tetrahedraletes* and *Dyadospora*; this is also consistent with the Klinta assemblage.

At species level, ten species are shared with the present study (*Artemopyra brevicosta* and *Hispanaediscus lamontii* and representatives of the genera *Ambitisporites*, *Archaeozonotriletes*, *Dyadospora, Laevolancis* and *Tetrahedraletes*). Species occurring in the Scottish assemblage, but lacking in this study, include *Cheilotetras caledonica*, *Hispanaediscus wenlockensis* and *Psedodyadospora petasus*. In conclusion, the Stonehaven assemblage shows great similarities to the Klinta assemblage.

5.2.3. Summary. In summary, our comparison of the Klinta assemblage not surprisingly reveals the closest similarities with the Gotland flora with respect to the representation of taxa. Regarding the Avalonian assemblages outlined above, significant similarities occur at generic level, whilst the abundance data show major discrepancies in that most coeval assemblages are strongly dominated by trilete spores. A very close match is evident with the slightly older assemblage (described as Wenlock or early Ludlow) from the Stonehaven Group in Scotland.

6. Conclusions

- Samples from the upper Silurian Öved–Ramsåsa Group in Klinta, Sweden are dominated by the long-ranging cryptospores *Laevolancis divellomedia-plicata* and *Dyadospora murusdensa-murusattenuata* and the trilete spore *Ambitisporites avitus-dilutus*.
- Key taxa include *Synorisporites* cf. *libycus*, *Hispanaediscus verrucatus* and *H. major*, indicating a Ludlow age. This is consistent with marine biostratigraphic schemes.
- The palynofacies results imply a tidally influenced environment, strongly supporting previous interpretations based on sedimentological observations. The high proportions of spores infer a close proximity to land and the spores reflect the local flora inhabiting delta plains or the hinterland.
- The dominance of generally the same taxa throughout the studied interval indicates a steady flora on land, despite significant environmental changes in the marine environment.
- Comparisons with coeval assemblages elsewhere show a relatively high portion of shared taxa with Gotland and slightly older Welsh assemblages.

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8. References

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