Research paper

Linking upper Silurian terrestrial and marine successions—Palynological study from Skåne, Sweden

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ABSTRACT

We have performed a palynostratigraphic study on miospore assemblages from near-shore marine Silurian sedimentary rocks of Skåne, southern Sweden. The material includes both drillcore (from Klintabörningen 1 and Bjärsjölagårdbörningen 2) and outcrop samples from various localities in Skåne. Well-preserved spore assemblages were identified. Long ranging species with a global distribution dominate the spore assemblages, including *Ambitisporites* sp., *Dyadospora* sp., *Laevolancis* sp., and *Tetrahedraletes* sp. and complemented with key taxa including *Emphanisporites neglectus*, *Hispanaediscus lamontii*, *Hispanaediscus verrucatus*, *Scylaspora scripta*, *Synorisporites libycus* and *Synorisporites tripapillatus*. Based on biostratigraphical schemes for early land plant spores, the studied sedimentary rocks of the cores Klintabörningen 1 and Bjärsjölagårdbörningen 2 are interpreted as late Silurian in age, spanning Ludlow to Přídolí. The spore assemblages are compared and correlated to marine fossil schemes including those of conodonts, chitinozoans, graptolites and tentaculitids. Additionally, relative abundance data of specific spore taxa have been used for correlation between the drillcores and the outcrops.

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1. Introduction

Several localities exposing Silurian sedimentary rocks occur in Sweden and many of them are situated in Skåne, southern Sweden. The exposed successions range in age from Llandovery to Přídolí (Grah, 1996). However, many of the outcrop sections are inaccessible today. Over the years these sedimentary rocks have been studied in many aspects, especially with focus on the marine biota and the lithostratigraphic distribution. Whilst there are a vast number of studies on different groups of marine organisms (see next section), none- or very little data exist on the late Silurian terrestrial biota of Sweden (Hagström, 1997; Hagström and Mehlqvist, 2012; Mehlqvist et al., 2012).

This study aims to shed light on the previously poorly investigated Silurian spore assemblages from Sweden and to correlate subsurface samples with exposed Silurian strata. The aim of this paper is to link the marine and terrestrial microfossil assemblages in order to improve the stratigraphical framework for this geographical area by combining the new palynological data with previously published data on marine biota. Our results provide the first palynostratigraphical correlation of upper Silurian strata between outcrops and drillcores in Sweden and provide, for the first time a tie between marine and terrestrial biostratigraphical schemes.

2. Previous works

Numerous stratigraphic and taxonomic studies have been carried out on marine microfossils from Swedish Silurian strata, both from Gotland and Skåne which have led to one of the best resolved Silurian stratigraphical schemes in the world. Larsson (1979) studied the tentaculitids from Gotland and from the Öved-Ramsåsa Group in Skåne, shedding light not only on the taxonomy of this group, adding both to the knowledge on tentaculitids and their morphological variations, their palaeoenvironmental requirements but also on their stratigraphical occurrence in Swedish Silurian strata. Grah (1996) described the chitinozoan assemblages from the Colonius Shale and the Öved-Ramsåsa Group in Skåne and erected a biostratigraphical scheme based on late Silurian chitinozoans. Conodont assemblages from the Öved-Ramsåsa Group in Skåne have been extensively studied and presented by Jeppsson (1974) and Jeppsson and Laufeld (1986) where a Ludlow to Přídolí age was inferred for the Öved-Ramsåsa Group Jeppsson and Laufeld (1986). Stratigraphical and taxonomical data based on Silurian conodont assemblages from Gotland were further presented by Jeppsson (2005) and Jeppsson et al. (2007). Eriksson et al. (2004) and Eriksson (2001) present data on Silurian scolecodonts from Gotland, and from Skåne (Eriksson, 2002). Nilsson (2002) focussed on graptolites from lower Ludlow strata in Skåne, southern Sweden and dated several localities using graptolite biostratigraphy. Vergoossen (1999, 2002a, 2002b, 2003, 2004) included extensive taxonomic and stratigraphic results based on fish scales from upper Silurian deposits from the Öved Sandstone Formation of the Öved-Ramsåsa

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Group in Skåne, Sweden. From coeval assemblages on Gotland, late Silurian acritarchs and prasinophytes and their stratigraphic distribution have been described by Le Hérissé (1989). Additionally, Le Hérissé et al. (2009) described the biodiversity of phytoplankton such as acritarchs and prasinophytes from the late Silurian to the earliest Devonian from a global perspective. These studies have together greatly improved global Silurian stratigraphical schemes.

Data on the late Silurian terrestrial biota of Sweden are however very scarce and, as a matter of fact, data on terrestrial palynology from Baltica are even rarer. The few studies include Gray et al. (1974) who completed the first study on fossil spores from Sweden (Gotland and Skåne), mainly with a palaeoenvironmental angle, describing spores of early land plants. New data were presented more than 20 years later by Steemans (1996) and Hagström (1997) on spore assemblages based on a limited number of samples from the upper Silurian Burgsvik Formation, Gotland. Subsequently, Hagström and Mehlqvist (2012) described plant fossils with in situ cryptospores from the Burgsvik Beds from Gotland. New palynological investigations on Silurian material from Skåne, southern Sweden were initiated in 2008 as part of a Master's thesis (Mehlqvist, 2009) which resulted in the publication Mehlqvist et al. (2012) describing the taxonomical composition of the palynological assemblages of the two drillcores Klintabornningen 1 and Bjärsjölagårdbornningen 2. Extensive work has, however, been performed on Silurian and Devonian spore assemblages from the British Isles that belonged to the palaeocontinent Avalonia at the time (e.g. Richardson and Lister, 1969; Wellman, 1993; Wellman and Richardson, 1993; Wellman et al., 2000). These assemblages are well-described and further work is needed to assess the similarities and differences between the assemblages of Avalonia and Baltica.

3. Geological setting

During the Silurian the palaeocontinents Baltica, Avalonia and Laurentia were located in the tropical climate zone at a low latitudinal position, south of the equator (Moore et al., 1994; Scotese, 2003; Fig. 1). The palaeocontinent Gondwana was located much further south of the equator, separated from Baltica by the Rheic Ocean and even reaching the South Pole (Cocks and Torsvik, 2002). At 440 Mya, Baltica collided with Avalonia and a combined landmass was formed. This combined landmass subsequently collided with Laurentia about 425 to 420 Mya and created the supercontinent Laurasia (Cocks and Torsvik, 2002). Based on palaeomagnetic data, Laurasia then drifted southwards and underwent counter-clockwise rotation (Cocks and Torsvik, 2002).

Fig. 1. Reconstruction of late Silurian palaeogeography showing the position of Baltica. Modified from <http://www.scotese.com/>.

During the Silurian Baltica was partly covered by an epicontinental sea and Silurian deposits have been identified in Norway, mid- and south Sweden, the Baltic Sea (Fig. 2a), the East Baltic States, Denmark and Poland (Jeppsson and Laufeld, 1986). The Silurian strata in Skåne reflect a gradual shallowing-up succession from deepwater graptolitic shales to shallow marine limestones and sandstones, and the sedimentary rocks are divided into the lower and middle Silurian Kallholn Formation, the Cyrtograptus Shale, the Colonius Shale and the upper Silurian Öved-Ramsåsa Group (Fig. 4) (Larsson, 1979; Jeppsson and Laufeld, 1986; Bergström et al., 1999; Märss et al., 1995; Melchin et al., 2004; Verniers et al., 2008).

Based on biostratigraphy of various marine fossil groups from exposed sedimentary rocks, the Öved-Ramsåsa Group has been dated to span Ludlow (Ludfordian stage) to Přídolí and include thereby the youngest Palaeozoic strata in Skåne (Jeppsson and Laufeld, 1986). The Öved-Ramsåsa Group is divided into the Klinta and the Öved Sandstone formations and the former is subdivided into the Lunnarna, Bjär, Bjärsjö and Bjärsjölagård Members (Jeppsson and Laufeld, 1986). Exposures of the Öved-Ramsåsa Group can be found in Klinta, Lunnarna, Bjärsjölagård and Ramsåsa (Fig. 2b).

The Öved-Ramsåsa Group is dominated by mudstones, in places tidally influenced, inter-layered with shallow marine carbonates (Wigforss-Lange, 1999, 2007). The sedimentary rocks of the Klinta Formation consist of mudstones interlayered with silt- and limestones. In the Bjärsjölagård Member, which is dominated by limestone, a thick carbonate unit (i.e. the Bjärsjölagård Limestone) occurs, overlain by a sandstone (The Öved Sandstone Formation) present in the Klinta, Bjärsjölagård and Ramsåsa areas (Jeppsson and Laufeld, 1986).

4. Material and methods

Two drillcores, Klintabornningen 1 (K1) and Bjärsjölagårdbornningen 2 (B2), spanning the upper Silurian Öved-Ramsåsa Group in Skåne were sampled for palynology (Tables 1 and 2). Additionally, a range of exposures of Silurian age all over Skåne from the Colonius Shale and Öved-Ramsåsa Group were sampled in order to tie in the exposed successions with those from the drillcores. The exposed sections include Råröd 1, Lunnarna 1, Skarhult 1, Rövarkulan 1, Harlösa 1, Bjärsjölagård 2, Bjärsjölagård sandstone, Vollsjö 1, Järrestadsån 2 and Skillinge 2 (Fig. 2a; Table 3). These localities are described in the Results section. Altogether 78 samples were selected for palynological analysis for this study. The samples were processed according to standard palynological procedures at Global GeoLab Ltd., Alberta, Canada (see Mehlqvist et al., 2012 for more detailed description). A minimum of 150 specimens per slide were counted and identified taxonomically by light- and scanning electron microscope (SEM), and after the count of 150 was reached, the entire slide was further studied for rare taxa. In slides containing less than 150 spores, all the spores in the slide were counted. The taxonomical descriptions of the spores identified in the two drillcores were presented in Mehlqvist et al. (2012). Palynological slides and macerated residues are deposited at the Department of Geology, Lund University, Sweden.

4.1. Stratigraphical schemes applied in this study

For this study, a combination of the following spore zonation schemes have been applied: Richardson and McGregor (1986), Richardson and Edwards (1989), Burgess and Richardson (1995), Richardson (1996) and Richardson et al. (2001). We have further applied the variation in abundance of specific taxa for correlation between the studied sections. The biostratigraphical zonation of Richardson and McGregor (1986) were based on assemblages from the Old Red Sandstone continent (Avalonia, Baltica and Laurentia). Richardson and Edwards (1989) refined the spore zonation of Richardson and McGregor (1986) to include three new zones spanning the entire Silurian up to Upper Devonian. Burgess and Richardson (1995) erected a sporomorph zonation

Fig. 2. a. Map showing the extension of Silurian landmass (dotted pattern), superimposed on modern map of Scandinavia. Distribution of lower Palaeozoic rocks indicated by grey filling. The study area is marked. Map modified after Nielsen, 2004. b. Geological map of the study area with localities for the drillcores marked with circles, sampled exposures with stars.

including four zones and seven subzones for the Homerian to lower Přídolí, based on spore assemblages from successions in the Anglo-Welsh Basin, British Isles. A year later, Richardson (1996) defined

seven phases of major sporomorph evolutionary events through the Cambrian to Upper Devonian. More recently, Richardson et al. (2001) constructed a biozonation based on spores from southern Britain and the Cantabrian Mountains in northern and northwestern Spain.

In our study, existing marine and terrestrial micropalaeontological zonation schemes are tied in with our palynological results. Linking the marine and terrestrial realms will not only provide improved stratigraphical control but will also provide time equivalent comparisons between marine and terrestrial palaeoenvironments during the studied interval.

5. Results—palynology and stratigraphical implications

5.1. General composition of the spore assemblages

The results from this study reveal rich and well preserved palynological assemblages and 36 spore species belonging to 21 genera were identified. The cryptospores are represented by 18 species, and the trilete spores by 18 species. The organic matter is highly dominated by spores and plant debris but marine microfossils, such as prasinophytes, acritarchs, chitinozoans and scolecodont elements occur in some samples. We further identified fungal spores and hyphae in a few samples together with tubular structures of an uncertain affinity but these are discussed elsewhere.

The sedimentary rocks from Råröd 1, Vollsjo 1 and Järrestadsån 2 outcrops are mostly dominated by long-ranging cosmopolitan species, mainly indicative of a mid Silurian age (e.g. Wenlock) but the dearth of biostratigraphically-important species makes a more detailed age estimation difficult (Table 3). Palynostratigraphical interpretations were hampered by low, or no spore recovery in samples from the following sites; Skarhult 1, Lunnarna 1, Harlösa 1, Skillinge 2, Rövarkulan 1 (Table 3).

5.2. Drillcores

5.2.1. Klintaborrningen 1

The sedimentary rocks in K1 are, based on the spore assemblages, dated to span Ludlow to Přídolí age (Fig. 3). The assemblage is strongly dominated by cryptospores but the relative abundance of trilete spores increases upwards. *Laevolancis plicata* is the dominant species (Table 1) followed by *Laevolancis divellomedia* (Fig. 5; Plate I:7). Most of the succession belongs to the *libycus-poecilomorphus* Assemblage Zone of Richardson and McGregor (1986) and miospore Zone 4B to 5A of Richardson (1996); Figs. 3–4, based on the occurrence of the species *Emphanisporites neglectus* together with *Synorisporites* cf. *libycus* and apiculate spores such as *Apiculiretusispora* sp. indicative of a Ludlow age (Fig. 4). A late Silurian (late Ludlow to Přídolí) age is suggested for the topmost part of the Klintaborrningen 1 core based on the first occurrence of *Synorisporites tripapillatus* (Figs. 3–4). This corresponds to the Miospore Zone 5B of Richardson (1996) and to the *Synorisporites tripapillatus*–*Apiculiretusispora spicula* Assemblage Zone of Richardson and McGregor (1986). However, *S. tripapillatus* has been identified in Ludlovian successions (Rubinstein and Steemans, 2002) and these authors argue that *S. tripapillatus* alone is not necessarily indicative of Přídolí age but rather late Ludlow to early Přídolí.

In summary, these results show that the sedimentary rocks of the Klintaborrningen 1 core cover a time interval from Ludlow to early Přídolí (Figs. 3–4). One specimen of *Chelinospora hemiesferica* indicative of early to middle Přídolí (Richardson et al., 2001) was encountered in the lower part of the core (sample 5; 193 m). However, as this single specimen is not consistent with the rest of the palynoflora of the Klintaborrningen 1 assemblage, its occurrence is herein interpreted as a down-core contamination during the drilling process although revealing that Přídolí indeed is represented higher up in the succession.

The sedimentary rocks of the Klintaborrningen 1 are assigned to *Saetograptus fritschi linearis*–*Saetograptus leintwardinensis* to

Fig. 3. Logs of the drillcores; Klintaborrningen 1 and Bjärsjölagårdborrningen 2 showing the lithology and correlation. Depth in metres, arrows with numbers indicates sample levels and sample numbers.

Table 1

Quantitative palynological data for the samples in the drillcore Klintabornningen 1.

Sample number	1	2	3	4	5	6	8	9	10	12	13	17	19	20	21	22	23	24	25	27	35	36	37	38	39	40
Taxa/depth (m)	205.31	204.98	202.20	200.89	193.09	178.24	156.37	153.41	151.76	143.33	138.83	122.96	117.42	116.28	112.28	107.71	103.58	101.95	100.45	96.02	80.12	61.62	55.11	47.91	40.03	35.90
<i>Artemopyra radiata</i>	7	2			1				1																	
<i>Cheilotetras caledonica</i>		3	6	1	3	1																	1			1
<i>Cymbohilates</i> sp. A												1					1									
<i>Cymbohilates</i> sp. B													3	1												
<i>Dyadospora murusdensa-murusattenuata</i>	0	0	0	0	0	4	34	59	25	26	74	100	82	14	14	6	22	25	25	1	0	1			9	0
<i>Hispanaediscus lamontii</i>	1																									
<i>Hispanaediscus verrucatus</i>																	2				1	1				
<i>Imperfectotriletes vavrdovae</i>			6	5	4																	30	4		12	2
<i>Laevolancis divellomedia-plicata</i>	71	95	86	97	74	29	116	87	136	124	54	40	70	110	111	128	95	78	76	115	86	85	4	1	42	68
<i>Rimosotetras problematica</i>																									1	1
<i>Tetrahedraletes grayii</i>	5		2	1	3	8																1				
<i>Tetrahedraletes medinensis</i>	57	44	23	20	13	84		5			10	5	3	12	6	5	3	6	12	14	3	15	3		11	25
<i>Ambitisporites avitus-dilutus</i>	4	1	8	5	5	1	0	1	1	9	12	3	5	13	32	11	26	35	36	24	36	10	1	1	37	1
<i>Ambitisporites parvus</i>								2	1	1	1	1							1							
<i>Amicosporites discus</i>					1																					
<i>Apiculiretusispora? burgsvikensis</i>	2	3	11	13	38	23			1			1		1				6		1	1					25
<i>Archeozonotriletes chulus morphon</i>	1		6	7	6																		6	1	25	3
<i>Chelinospora hemiesferica</i>					1																					
<i>Dictyotriletes</i> sp.						1																				
<i>Emphanisporites neglectus</i>									1																	
<i>Retusotriletes goensis</i>																	1					1	6			
<i>Retusotriletes</i> cf. <i>warringtonii</i>	4	3	1	1	2																	6			14	7
<i>Scylaspora klintaensis</i>															10											1
<i>Scylaspora scripta</i>							1																			
<i>Synorisporites</i> cf. <i>libycus</i>																				3						
<i>Synorisporites tripapillatus</i>																						11				
<i>Synorisporites verrucatus</i>						1																1				1
Total sum of spores counted	152	151	149	150	151	153	150	154	166	160	151	151	163	151	173	150	150	150	150	158	138	151	25	3	152	134

Table 2
Quantitative palynological data for the samples in the drillcore Bjärsjölagårdborringen 2.

Sample numbers	2	3	4	5	6	9	10	11	12	13	14	15	18	19	20
Taxa/depth (m)	69.65	60.72	57.94	52.93	48.83	31.9	28.9	27.55	25.3	23.11	20.34	17.97	10.03	4.73	2
<i>Artemopyra rugaticosta</i>		4													
<i>Cymbohilates</i> sp. A			1	1											
<i>Cymbohilates</i> sp. B			2	1	2	1			2						
<i>Dyadospora murusattenuata</i>	19	33	35	28	46	57	9	14	1	8	26			11	1
<i>Dyadospora murusdensa</i>	33	23	32	41	34	55	11	14	17	23	23		9	14	4
<i>Hispanaedisca lamontii</i>													1		
<i>Hispanaedisca major</i>														4	
<i>Hispanaedisca verrucatus</i>				1	2	4	5		1	6			2	1	
<i>Laevolancis divellomedia</i>	29	29	21	27	6	10	10	54	58	27	28	1	36	33	46
<i>Laevolancis plicata</i>	24	31	42	42	31	15	18	37	37	59	28		53	39	44
<i>Rimosotetras problematica</i>								1			1		1		
<i>Tetrahedraletes grayii</i>										1	2				
<i>Tetrahedraletes medinensis</i>	3	7	2	1	1	2	6	7	4	7	7		9		2
<i>Ambitisporites avitus</i>	2	8	7	7	8		15	9	17	9	15		21	25	26
<i>Ambitisporites dilutus</i>		12	5	5	10	7	17	14	12	11	17		11	18	18
<i>Ambitisporites parvus</i>	2			1							1		1		1
<i>Apiculiretusispora? burgsvikensis</i>	33		1	1										3	
<i>Apiculiretusispora</i> sp. A					1									1	
<i>Apiculiretusispora</i> sp. B			1												
<i>Emphanisporites neglectus</i>	1												1		
<i>Retusotrilites goensis</i>	1	3	2		1				1		2		4	1	
<i>Scylaspora scripta</i>											2				
<i>Synorisporites tripapillatus</i>									1						3
Total sum of spores counted	147	150	151	156	142	151	91	150	151	151	152	1	149	150	145

Monograptus parultimus graptolite zones, as defined by Jaeger (1991), corresponding to the topmost part of the *Angochitina echinata*–*Sphaerochitina sphaerocephala* chitinozoan zone (Grahn, 1996; Fig. 4) and the Icriodontid–*Ozarkodina crisa* conodont zones (Jeppsson et al., 2006). These all indicate a Ludlow age for the sedimentary rocks (Fig. 3). It should be noted, however, that correlation to standard graptolite zones in post-leintwardinensis successions in Skåne must be considered tentative as diagnostic graptolites are very rare in the Öved-Ramsåsa Group.

The sedimentary rocks of the Klintabörningen 1 are dominated by the cryptospore *Laevolancis divellomedium* morphon (Steemans, 1996), *Dyadospora murusdensa*–*murusattenuata* morphon (Steemans, 1996) and *Ambitisporites avitus*–*dilutus* morphon (Steemans, 1996), however significant changes in relative abundance are seen throughout the succession. The assemblages from the basal part of the core are dominated by *Laevolancis divellomedium* morphon, *Tetrahedraletes medinensis*, and by *Apiculiretusispora? burgsvikensis* reaching 25% of the total spore content in sample 5. Taxa occurring in low portions within the basal part of the core include *Artemopyra radiata*, *Scylaspora scripta* and *Synorisporites verrucatus* (Fig. 5 and 6).

The assemblage in the middle part of the drill core is dominated by *Dyadospora murusdensa*–*murusattenuata* and *Laevolancis divellomedium* reaching maximum values of relative abundance of 66% and 85%, respectively. Taxa occurring in low abundances comprise *Emphanisporites neglectus*, *Scylaspora klintaensis* and *Retusotrilites goensis* (Fig. 5).

The assemblage within the topmost part of the core shows prominent changes in that *Ambitisporites avitus*–*dilutus* increase significantly in abundance. Together with *L. divellomedium* they dominate. *Hispanaedisca verrucatus*, *Tetrahedraletes medinensis*, *Retusotrilites goensis* and *Synorisporites* spp. occur as minor components.

5.2.2. Bjärsjölagårdborringen 2

A late Silurian (late Ludlow to Přídolí) age is suggested for the topmost part (25.3 m–2 m) of the Bjärsjölagårdborringen 2 based on the first occurrence of *Synorisporites tripapillatus* (Figs. 3–4). This interval corresponds to the *Synorisporites tripapillatus*–*Apiculiretusispora spicula* Assemblage Zone of Richardson and McGregor (1986) and to the Miospore subphase 5B of Richardson (1996). The assemblage is

dominated by the cryptospore species *Laevolancis plicata*, *Dyadospora murusdensa*, *Dyadospora murusattenuata* and *Laevolancis divellomedia*.

The sedimentary rocks from B2 are assigned to the *Saetograptus fritschii linearis*–*Saetograptus leintwardinensis* to *Monograptus P. parultimus* graptolite zones (Ludfordian to Přídolí). This corresponds to the top of the *Angochitina echinata* up to *Sphaerochitina sphaerocephala* chitinozoan zone and to the Icriodontid–*Ozarkodina crisa* conodont zones (Fig. 4). These age assessments inferred from the marine microfossils agree perfectly with the age assessments of the spore assemblages from B2.

The dominant components i.e. *Laevolancis divellomedium* morphon and *Dyadospora murusdensa*–*murusattenuata* morphon reach top values of 100% and 70% respectively (Fig. 5). *Ambitisporites avitus*–*dilutus* varies in abundance between 10 and 35% and peaks at c. 28 m. Other spore taxa occurring in lower relative abundances include *Hispanaedisca lamontii*, *Hispanaedisca major* and *Synorisporites tripapillatus* (Fig. 5).

5.3. Outcrop sections

The outcrop samples are less diverse but dominated by the same long-ranging cryptospore species as in the assemblages from the drillcores. Additional spore taxa that are not encountered in the drillcore assemblages include; *Pachytetras rugosa* and *Chelinohilates* spp. Positions for the localities are given according to the reference system SWEREF 99TM.

5.3.1. Early Ludlow–Gorstian

5.3.1.1. Vollsjö 1. Dark mudstones belonging to the Colonius Shale are exposed along the Vollsjöän rivulet. An exposure in the rivulet was sampled below the old railway bridge close to Solgården (6173796 N/423334 E). Only 10 spore taxa were identified in this single sample. The assemblage is dominated by *Laevolancis divellomedia* but also contains *Laevolancis plicata*, *Tetrahedraletes medinensis*, *Ambitisporites avitus*, *Chelinohilates* sp. and *Tetrahedraletes grayii* (Fig. 6). This assemblage shows a similar species composition as the sample from Råröd 1, also dominated by the same long ranging species. Additionally, chitinozoans, scolecodont elements and acritarchs occur in the sample and these sedimentary rocks have previously been dated to Ludlow (Gorstian) and assigned to the *Colonograptus colonus* graptolite zone, corresponding to the top of *Sphaerochitina lycoperdoides* chitinozoan

Plate I. The scale bars on all figures represent 10 µm. 1. *Ambitisporites avitus* Hoffmeister, 1959. 2. *Artemopyra radiata* Strother, 1991. 3. *Apiculiretusispora? burgsvikensis* Hagström, 1997. 4. *Chelinohilates* sp. 5. *Dyadospora murusdensa* (Strother and Traverse) Burgess and Richardson, 1991. 6. *Hispanaediscus verrucatus* (Cramer) Burgess and Richardson, 1991. 7. *Laevolancis divellomedia* (Chibrikova) Burgess and Richardson, 1991. 8–11. *Pachytetras rugosa* Hagström, 1997. 10. SEM photograph 11. SEM magnification of the exine and the ornament. 12. *Retusotriletes goensis* Lele and Streeel, 1969.

Period	Series	Stages	Skåne	Outcrop positions	Spore zonation			Graptolite Zonation (Melchin et al. 2004/ Verniers et al. 2008)	Conodont Zonation (Jeppsson et al. 2006)	Local Chitinozoan Zonation (Grahn 1996)	Chitinozoan Zonation (Verniers et al. 1995/ Melchin et al. 2004)	Vertebrate Zonation (Märss et al. 1995/ Melchin et al. 2004)		
					(Richardson & McGregor 1986)	Sub-Zones (Burgess & Richardson 1995)	(Richardson 1996)							
Silurian	Pridoli		Öved Sandstone Formation	Öved Ramsåsa Group	5	Synorisporites tripapillatus- Apiculiretusispora spicula	5B	Istrograptus transgrediens Monogr. bouceki-perneri	Sphaerochitina sphaerocephala		Angochitina superba	Katoporus timanicus- K.lithuanicus		
								Monogr. lochkovensis Monogr. branikensis				Poracanthodes punctatus		
								Monogr. parultimus-ultimus						
								Monograptus formosus				Margachitina elegans Fungochitina kosovensis	Nostolepis gracilis	
								Neocucullo. kozlowskii B.comuatus- P.podoliensis						
	Ludfordian		Klinta Formation	Öved Ramsåsa Group	4	Synorisporites libycus- Lophozonotriteles poecilomorphus	S. inframurinata var. inframurinata	5A	O. crispa	Eisenackitina philipi	Eisenackitina barrandei	Thelodus sculptilis		
									O. snajdri				Andreolepis hedei	
									Neocucullo. kozlowskii B.comuatus- P.podoliensis					
									Saetogr. leintwardinensis Saetograptus linearis					
	Gorstian		Colonus shale		3	Synorisporites libycus- Lophozonotriteles poecilomorphus	S. inframurinata var. inframurinata	4B	K.v. variabilis	Angochitina echinata	Eisenackitina phillipi	Eisenackitina phillipi	Phlebolepis elegans	
									A. ploeckensis					Phlebolepis ornata
									'O. ex'. hamata					
									K.v. variabilis					
									Lobograptus scanicus					
	Homerian		Cyrtograptus Shale		2	Artemopyra brevicosta- Hispanaedisca verrucatus	S. inframurinata var. cambrensis	4A	K. crassa	Sphaerochitina lycoperdoides	Unzoned	Sphaerochitina lycoperdoides	Paralogania martinssoni	
									Neodiversograptus nilssoni					
									Colonograptus ludensis					
									Colo. praedeubeli-deubeli					
									Pri. parvus-Gothogr. nassa					
	Sheinwoodian		Cyrtograptus Shale		1	Artemopyra brevicosta- Hispanaedisca verrucatus	S. inframurinata var. cambrensis	4A	O. bohemica longa	Unzoned		Conochitina pachycephala	Loganellia grossi	
									Cyrtograptus lundgreni					
									Cyrtogr. perneri					
									Cyrtogr. rigidus					
									Monogr. beloph.					
Ludlow				2	Synorisporites libycus- Lophozonotriteles poecilomorphus	S. inframurinata var. cambrensis	4B	K.v. variabilis	Angochitina echinata	Eisenackitina phillipi	Eisenackitina phillipi	Phlebolepis ornata		
								'O. ex'. hamata						
								K.v. variabilis						
								Lobograptus scanicus						
								Neodiversograptus nilssoni

Fig. 5. Spore species abundances of selected taxa from Klintaborrningen 1 and Bjärsjölagårdborrningen 2. Abundance is shown in % and the depths are indicated in metres.

Fig. 6. Range chart of spore species identified in Klintabornningen 1 and in the outcrop samples.

of Ludlow (Gorstian) age. The marine microfossil schemes further correspond to *Chelinospora obscura* and *Stellatispora inframurinata* var. *cambrensis* spore sub-zones within the base of the *libycus-poecilomorphus* spore zone.

5.3.1.3. Skarhult 1. This locality is situated in the proximity of the city of Eslöv (6185232 N/398598 E). Silurian grey mudstones belonging to the Odarslöv Sandstone (lower-middle part of the Colonius Shale) are exposed at the bottom of the Bråån Creek. The exposure along the creek by the bridge was sampled. The sedimentary rocks at the Skarhult 1 locality are at some levels rich in fossils (Hede, 1919) and contain the earliest tentaculitid fauna in Skåne along with the assemblage identified in Röddinge (Larsson, 1979). No spores were found in this sample but phytodebris and minor occurrences of chitinozoans and scolecodont elements were encountered. The sedimentary rocks exposed at Skarhult 1 have previously been assigned to the *Colonograptus colonus* graptolite zone (Nilsson, 2002) and to the top of the *Sphaerolithina lycoperdoides* chitinozoan zone (Grahn, 1996) and the *Kockelella crassa* conodont zone of Ludlow (Gorstian) age (Jeppsson et al., 2006). This interval corresponds to the *Chelinospora obscura* and *Stellatispora inframurinata* var. *cambrensis* spore sub-zones within the base of the *libycus-poecilomorphus* spore zone.

5.3.1.4. Järrestadsån 2. At this locality, mudstones (light grey to green and dark grey to brown) of the Colonius Shale are exposed in the valley between Gärarp and Tommarp (6154334 N/453392 E). Three samples were collected from an exposed section along the small rivulet, Tommarpsån, in a meadow from a vertical section and with a sample resolution of 0.5 m (Plate II: 2–3). In the lowermost sample (sample 1), only one specimen was identified (*Tetrahedraletes medinensis*) whilst sample 2 contains 37 spores dominated by *T. medinensis*. Sample 3 is rich in spores and is also dominated by *T. medinensis* together with other permanent tetrads such as *Tetrahedraletes grayii*. The composition of the miospore assemblage, highly dominated by permanent tetrads lacking envelope (Cheilotetras caledonica, *T. medinensis* and *T. grayii*) together with genera such as *Laevolancis*, *Dyadospora* and *Ambitisporites* suggests an early to mid Silurian age (Fig. 6). Minor occurrences of chitinozoans were found in sample number 2. Grahn (1996) assigned the sedimentary rocks of this locality to the *Colonograptus colonus* Zone of Ludlow (Gorstian) age (Fig. 3). In the terrestrial realm this corresponds to the *Chelinospora obscura* and *Stellatispora inframurinata* var. *cambrensis* spore sub-zones within the base of the *libycus-poecilomorphus* spore zone.

5.3.1.5. Skillinge 2: new locality. This locality has previously not been described. Sedimentary rocks consisting of grey mudstones representing

Plate II. Outcrop localities. 1. Harlösa 1, sample levels marked. 2–3. Järrestadsån 2, close up of sampled section. 3. Järrestadsån 2, overview. 4. Råröd 1, grey shales exposed along the rivulet.

the top of the *Colonus* Shale are exposed along the beach northeast of Skillinge harbour (6148092 N/455184 E). One sample was collected from the loose slabs on the beach. In this sample, only two *Dyadospora murusdensa* spores were identified. Additionally, sparse marine microfossils such as scolecodont elements and chitinozoans were identified. The sedimentary rocks exposed at Skillinge 1 is in [Grahns \(1996\)](#) assigned to the *Saetograptus chimaera* graptolite zone corresponding to the lower part of the *Angochitina echinata* chitinozoan zone and the 'O. ex'. *hamata* to *K.v. variabilis* conodont zones of Ludlow (Gorstian) age ([Grahns, 1996](#); [Nilsson, 2002](#); [Jeppsson et al., 2006](#)).

This interval corresponds to the *Apiculiretusispora? asperata* spore subzone within the *libycus-poecilomorphus* zone (Fig. 3).

5.3.1.6. Rövarekulan 1. At this locality (6184014 N/405979 E), parts of the *Colonus* Shale is exposed in a narrow valley eroded by the Bråån Creek and the sedimentary rocks comprise light grey to light green siltstones and mudstones. Two samples were collected from the exposed section along the Bråån in the Rövarekulan nature reserve, one from the darker mudstone and the other from a siltstone lens. Only the siltstone sample yielded spores whilst the sample from the darker shale

contains poorly preserved algae of unknown affinity. The spores identified include *Laevolancis divellomedia* and *Tetrahedraletes medinensis* (Fig. 6). Marine microfossils such as acritarchs, chitinozoans and scolecodont elements were further encountered. The succession at this locality belongs to the *Saetograptus chimaera* graptolite zone corresponding to the lower part of the *Angochitina echinata* chitinozoans zone and the 'O. ex'. *hamata* to *K.v. variabilis* conodont zones dated as Ludlow (Gorstian) ([Grahns, 1996](#); [Jeppsson et al., 2006](#)). This interval corresponds to the spore subzone *Apiculiretusispora? asperata* within the *libycus-poecilomorphus* Zone (Fig. 3).

5.3.2. Late Ludlow (Ludfordian)—Přídolí

5.3.2.1. Lunnarna 1. Lunnarna 1 is located in the Ringsjö area close to the village of Snogeröd (6188674 N/406589 E). Here the succession consisting of grey to green mudstones is exposed in a canalized brook and one sample was collected from this locality. Only eight spores were identified in this single sample including the taxa *Retusotriletes* cf. *warringtonii*, *Laevolancis divellomedia* and *Laevolancis plicata*. The low recovery of spores hampers a biostratigraphical assessment. No marine

Table 3
Quantitative palynological data for the outcrop samples.

Taxa	Vollsjö 1	Harlösa: A	Harlösa 1: C	Järrestadsån 2:1.	Järrestadsån 2:2.	Järrestadsån 2:3.	Skillinge 2	Rövarkulan 1	Råröd 1	Bjärsjölagård 2: 1,65 m	Bjärsjölagård 2: 1,45 m	Bjärsjölagård 2: 0,5 m
<i>Artemopyra radiata</i>									4			
<i>Cheilotetras caledonica</i>						3						
<i>Chelinohilates</i> sp.	8								6			
<i>Cymbohilates</i> sp. A									2			
<i>Dyadospora murusattenuata</i>	1					3					2	3
<i>Dyadospora murusdensa</i>	2				1	9	1					6
<i>Hispanaedisca verrucatus</i>										4	11	12
<i>Imperfectotrites vavrdovae</i>	2								7		2	2
<i>Laevolancis divellomedia</i>	109	1	3			11		1	79	54	64	62
<i>Laevolancis plicata</i>	15		1			7			46	38	53	46
<i>Pachytetras rugosa</i>										6	8	
<i>Rimosotetras problematica</i>												1
<i>Tetrahedraletes grayii</i>	2	1		1	3	39			1	2	1	2
<i>Tetrahedraletes medinensis</i>	17	1		1	12	67		1	14	5	4	1
<i>Ambitisporites avitus</i>	2					3			2	9	20	18
<i>Ambitisporites dilutus</i>						5						
<i>Ambitisporites parvus</i>						1					4	2
<i>Apiculiretusispora?</i>											1	
<i>burgsvikensis</i>												
<i>Apiculiretusispora</i> sp. B										1		
<i>Retusotrites</i> cf. <i>warringtonii</i>	1											1
Number of specimens	159	3	4	2	16	148	1	2	161	123	170	156

microfossils were identified in this sample. The sedimentary rocks in Lunnarna 1 have, based on marine microfossils, been dated to late Ludlow and assigned to *Saetograptus fritschi linearis*–*Saetograptus leintwardinensis* graptolite zone corresponding to the top of the *Angochitina echinata* and the lower part of *Eisenachitina philipi* chitinozoan zone coeval with the Icriodontid to *Ozarkodina crisa* conodont zones.

This corresponds to *Stellatispora inframurinata* var. *inframurinata* spore sub-zone within the *libycus-poecilomorphus* zone (Fig. 3).

5.3.2.2. Råröd 1. This site is located in the proximity of the Stehag village (Fig. 2b) (6193826 N/402691 E). Here, Silurian light grey to green shales are exposed along a small rivulet from where one sample was taken. This sample is dominated by long ranging cosmopolitan spore species including, *Laevolancis divellomedia*, *Laevolancis plicata* and *Tetrahedraletes medinensis*. Additionally, *Artemopyra radiata* and the cryptospore *Chelinohilates* sp. were identified. The lack of biostratigraphically important species makes it difficult to determine the exact age of this sample. The sample is dominated by spores but, marine microfossils such as acritarchs, chitinozoans, graptolite fragments and scolecodonts are present in low relative abundances. The succession at Råröd 1 has been assigned to the *Saetograptus fritschi linearis*–*Saetograptus leintwardinensis* graptolite zone of Ludlow age which corresponds to the top of the *Angochitina echinata* and lower part of *Eisenachitina philipi* chitinozoan zone (Grahn, 1996; Fig. 4.). This corresponds to the Icriodontid to *Ozarkodina crisa* conodont zones (Jeppsson et al., 2006). The marine biota has been dated as Ludlow (Ludfordian) age. This corresponds to *Stellatispora inframurinata* var. *inframurinata* spore sub-zone within the *libycus-poecilomorphus* zone (Fig. 3).

5.3.2.3. Bjärsjölagård 2. Three samples from the old, partly water-filled, limestone quarry in Bjärsjölagård were collected (from the levels 0.5 m, 1.45 m and 1.65 m from the first ledge above the water level, Plate II: 4). All samples host rich and well-preserved spore assemblages and the dominant species are *Laevolancis divellomedia* and *Laevolancis plicata*, along with *Ambitisporites avitus*, *Hispanaedisca verrucatus* and *Pachytetras rugosa*. The latter species was described as being present in Ludfordian sedimentary rocks on Gotland (Hagström, 1997). Minor occurrences of scolecodont elements and chitinozoans were observed. The age of these units has, based on marine microfossils, been

interpreted to late Ludlow–Přídolí corresponding to the *Sphaerochitina sphaerocephala* chitinozoan zone (Grahn, 1996) and the *Hindeodella wimani* conodont fauna (Jeppsson, 1974).

This corresponds to the top of *Stellatispora inframurinata* var. *inframurinata* spore sub-zone within the top of the *libycus-poecilomorphus* zone (Fig. 3).

5.3.2.4. Bjärsjölagård sst. Sandstone sediments from Bjärsjölagård are exposed along a canalized brook from the quarry in a forested area east of the old limestone quarry (Plate II). The sedimentary rocks comprise heavily cemented, very hard quartz arenites with a sugary texture. One sample was collected from loose rocks along the brook in the forest 200 m from the old limestone quarry. In the palynological residue, a few acritarchs and 11 spores (only *Tetrahedraletes grayii* identified) were encountered representing the first microfossils ever found in this sandstone interval (Table 3). This sandstone corresponds to the siltstone/sandstone unit encountered in the core of Bjärsjölagårdborrningen 2 in the interval 11.36–19.70 m (Fig. 3). The sandstone represents basal Přídolí, corresponding to the *Synorisporites tripapillatus* – *Apiculiretusispora spicula* spore zone (Fig. 3). Interestingly, Tullberg (1882) noted possible plant remains in the same sandstone from adjacent outcrops.

6. Discussion

6.1. Correlation of the studied drillcores

The drillcores Klintaborrningen 1 and Bjärsjölagårdborrningen 2 cover Ludlow and the base of Přídolí where the latter core is shorter and corresponds to the upper part of the Klintaborrningen 1 core (Fig. 3). The lithology differs in the two cores; the sedimentary rocks in K1 are more siliciclastic with mudstone, siltstone and sandstone layers whereas B2 is more biogenic with carbonates and corals. The drillcores are correlated, based on the first appearance datum (FAD) of *Synorisporites tripapillatus*, where the middle part of K1 (80 m) is correlated to the lower part of B2 (72–25 m) (Fig. 3). The upper part of K1 (80–35 m) and the upper part of B2 (25–2 m) are correlated and assigned to the *Synorisporites tripapillatus*–*Apiculiretusispora spicula* Assemblage Zone of Richardson and McGregor (1986) with a Přídolí age. It needs to be emphasized that the presence of *S. tripapillatus* in itself

cannot convincingly pin point a Přídolí age but rather the Ludlow–Přídolí transition. However, based on the correlation with the marine biostratigraphy a Přídolí age is most probable. The sedimentary rocks from the drillcores correlate to the succession exposed in the Bjärsjölagård quarry. The studied samples from Bjärsjölagård 2 are correlated to the Limestone interval occurring at c. 30 m in Bjärsjölagårdborrningen 2 of late Ludfordian age. The Bjärsjölagård Sandstone is correlated to the sandstone unit at c. 19–14 m in the drillcore B2 of Přídolí age (Fig. 3).

6.2. Comparison with the marine biostratigraphical zonation schemes

The age of the studied succession from the Bjärsjölagårdborrningen 2, agrees well with previous studies on tentaculitids identified from the same drillcore (Larsson, 1979), and this is the only other microfossil group that has been used as a biostratigraphical tool in these drillcores. The spore zones *brevicosta-verrucatus* to *libycus-poecilomorphus* (Homerian–Ludfordian) coincide with the presence of the typical late Silurian tentaculitid species *Lonchidium scanicum*, *Lonchidium ogmotum*, *Tentaculites hisingeri* and *Odessites portensis* outlined in Larsson (1979). The sedimentary rocks assigned to the slightly younger spore zone *tripapillatus-spicula* of Přídolí age host the tentaculitid species *Lonchidium groenwalli*, *Tentaculites scalaris*, *Lonchidium mobergi*, *Odessites lebiensis* and *Tentaculites loxus* (Larsson, 1979). Among these, *T. scalaris* is known from upper Přídolí in the Ohesaare Beds of Estonia, whilst *O. lebiensis* is represented in the basal part of the Podlasiian beds in Poland, i.e. the lower Přídolí (Larsson, 1979) and these two species are confined to the interval 0–10.2 m in B2 and 39–57 m in K1.

Studies on other fossil groups such as conodonts (Jeppsson, 1974), and chitinozoans (Grah, 1996), have been performed on coeval, exposed sedimentary rocks in Skåne. Jeppsson (1974) described conodonts from the Öved-Ramsåsa Group in Skåne and Grah (1996) described late Silurian (late Wenlock–early Přídolí) chitinozoans from the Colonius Shale and the Öved-Ramsåsa Group from Skåne, Sweden. Grah (1996) also erected a biostratigraphical zonation of chitinozoans from the late Silurian of Sweden and correlated it to biozonations of graptolites. However, correlations between the outcrop and drillcore successions have been based merely on lithology as the marine microfossils were only studied from the exposed sections due to the large sample size required (Jeppsson et al., 2006). The studied spore assemblages range from the top of the *brevicosta-verrucatus* Zone to the lower part of the *tripapillatus-spicula* Zone, corresponding to the conodont zones *K. crassa* up to at least *Ozarkodina crassa* (Fig. 4). The spore assemblages further correlate with the *Neodiversograptus nilssoni* graptolite zone up to at least the *Monograptus parultimus-ultimus* Zone and with the local chitinozoan zones *Sphaerochitina lycoperdoides* up to *Sphaerochitina sphaerocephala* (Fig. 4). The *libycus-poecilomorphus* spore zone coincides with the occurrence of the following polychaetan species of the family *Ramphoprionidae*: *Protarabellites rectangularis*, *Protarabellites staufferi*, *Protarabellites triangularis* and *Ramphoprion gotlandensis* described from the Bjärsjölagård Limestone Member of the Klinta Formation, Skåne (Eriksson, 2002).

7. Depositional environment and the terrestrial ecosystem

The general pattern that emerges when compiling all the studied successions and their palynological content is the shallowing upwards trend where the dark Colonius Shales grade into mudstones and subsequently lighter coloured carbonates. This shows a gradual change from anoxic, deep-water conditions to deposition in well-oxygenated marine ecosystems within the photic zone. Our interpretations are in accordance with results presented in Wigforss-Lange (2007) stating that the Klinta succession shows an upward transition from open marine to lagoonal environments whilst the Bjärsjölagård limestone has been interpreted as deposited in a coastal environment on a mixed

carbonate-siliciclastic shelf in an open-marine setting with freshwater input (Nilsson, 2006).

However, within the marine carbonates, the terrestrial flora has left its signatures and substantial information about the terrestrial ecosystem can be deduced from the palynology also in the marine carbonates. We further interpret the sandstones in the top of the Bjärsjölagårdborrningen 2 (also exposed in the Bjärsjölagård quarry) as terrestrially deposited due to the dearth of marine microfossils but with presence of root fragments (Tullberg, 1882) indicative of a regolith formation. The plants responsible for the spore dispersal probably grew along distributary channels and their spores could spread by rivers and subsequently accumulated in the near-shore to off-shore environments of the inner shelf. Richardson (1996) argues that some spores can have been dispersed by the wind since some are below 25 µm in size. However most of the specimens of this study range up to 60 µm and are thus too heavy for wind dispersal. As most spores in this study exceed 30 µm, they were most probably transported by water into the basin.

The assemblage is numerically dominated by cryptospores, mostly long-ranging cosmopolitan species making a biostratigraphic assessment difficult. The assemblages are moderately diverse with the same diversity of cryptospores and trilete spores. The studied assemblages are similar in composition to the coeval Gotland assemblage from the Burgsvik Beds described in Hagström (1997). However the late Silurian spore assemblages of Skåne reveal an endemic flora dominated by liverwort-like embryophytes and early vascular plants.

8. Conclusions and summary

This palynological study from Skåne, Sweden includes two drillcore successions, Klintaborrningen 1 and Bjärsjölagårdborrningen 2, comprising 205 and 75 m respectively. Additionally, 10 exposures were sampled for palynology, of which all but one contained spores.

In summary, the study reveals rich and well preserved late Silurian spore assemblages. In total (including drillcore and outcrop sections) 36 spore species belonging to 21 genera were identified. The cryptospores (produced by now extinct, primitive land plants) and trilete spores (produced by vascular plants) are represented by 18 species each.

The quantitatively dominating species are the cryptospores *Laevolancis plicata* followed by *Laevolancis divellomedia*. The organic matter is highly dominated by spores and plant phyto-debris but marine microfossils, such as prasinophytes, acritarchs, chitinozoans and scolecodont elements occur in some samples.

Although the recovery of terrestrial palynomorphs is poor in some of the outcrop samples, these results are important as they provide the first evidence of terrestrial spores in these successions.

The studied interval spans the lower Ludlow (Gorstian) to Přídolí. We have based the age assessments on a combination of previously published marine microfossil and, for the younger successions, on spore zonations. Importantly the marine microfossil zonation has been tied to spore assemblages of this study, linking the marine and terrestrial succession of these late Silurian ecosystems.

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References

- Bergström, S.M., Huff, W.D., Koren, T., Larsson, K., Ahlberg, P., Kolata, D.R., 1999. The 1997 core drilling through Ordovician and Silurian strata at Röstänga, S. Sweden: preliminary stratigraphic assessment and regional comparison. *GFF* 121, 127–135.
- Burgess, N.D., Richardson, J.B., 1991. Silurian cryptospores and miospores from the type Wenlock area, Shropshire, England. *Palaeontology* 34, 601–628.
- Burgess, N.D., Richardson, J.B., 1995. Late Wenlock to Early Přídolí cryptospores and miospores from south and southwest Wales, Great Britain. *Palaeontographica* 236, 1–44.
- Cocks, L.R.M., Torsvik, T.H., 2002. Earth geography from 500 to 400 million years ago: a faunal palaeomagnetic review. *J. Geol. Soc. Lond.* 159, 631–644.
- Eriksson, M., 2001. Silurian ramphoprioid polychaetes from Gotland, Sweden. *J. Paleontol.* 75, 993–1015.
- Eriksson, M., 2002. The palaeobiogeography of Silurian ramphoprioid polychaete annelids. *Palaeontology* 45, 985–996.
- Eriksson, M.E., Bergman, C.F., Jeppsson, L., 2004. Silurian scolecodonts. *Rev. Palaeobot. Palynol.* 131, 269–300.
- Grahn, Y., 1996. Upper Silurian (Upper Wenlock–Lower Přídolí) Chitinozoa and Biostratigraphy of Skåne, Southern Sweden. *GFF* 118 (4), 237–250.
- Gray, J., Laufeld, S., Boucot, A.J., 1974. Silurian trilete spores and spore tetrads from Gotland: their implications for land plant evolution. *Science* 185, 260–263.
- Hagström, J., 1997. Land-derived palynomorphs from the Silurian of Gotland, Sweden. *GFF* 119, 301–316.
- Hagström, J., Mehlqvist, K., 2012. The dawn of terrestrial ecosystems on Baltica: first report on land plant remains and arthropod coprolites from the Upper Silurian of Gotland, Sweden. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 317–318C, 162–170.
- Hede, J.E., 1919. Om en förekomst av colonusskiffer vid Skarhult i Skåne. *Geol. Fören. Stockh. Förh.* 41, 113–160.
- Hoffmeister, W.S., 1959. Lower Silurian plant spores from Libya. *Micropaleontology* 5, 331–334.
- Jaeger, H., 1991. Neue Standard-Graptolithen Zonenfolge nach der “Großen Krise” an der Wenlock/Ludlow-Grenze (Silur). *Neues Jahrb. Mineral. Geol. Palaeontol. Abh.* 182, 303–354.
- Jeppsson, L., 1974. Aspects of Late Silurian conodonts. *Fossils Strata* 6, 1–54 (Oslo, Pls. 1–12).
- Jeppsson, L., 2005. Conodont-based revisions of the Late Ludfordian on Gotland, Sweden. *GFF* 127, 273–282.
- Jeppsson, L., Laufeld, S., 1986. The Late Silurian Öved-Ramsåsa Group in Skåne, southern Sweden. *Sver. Geol. Unders.* 58, 1–45 (Ca).
- Jeppsson, L., Eriksson, M.E., Calner, M., 2006. A latest Llandovery to latest Ludlow high-resolution biostratigraphy based on the Silurian of Gotland—a summary. *GFF* 128, 109–114.
- Jeppsson, L., Talent, J.A., Mawson, R., Simpson, A.J., Andrew, A.S., Calner, M., Whitford, D.J., Trotter, J.A., Sandström, O., Caldon, H.-J., 2007. High-resolution Late Silurian correlations between Gotland, Sweden, and the Broken River region, NE Australia: lithologies, conodonts and isotopes. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 245, 115–137.
- Larsson, K., 1979. Silurian tentaculitids from Gotland and Scania. *Fossils Strata* 11, 1–180.
- Le Hérisse, A., 1989. Acritarches et kystes d’algues Prasinophycées du Silurien de Gotland, Suède. *Palaeontogr. Ital.* 76, 57–302.
- Le Hérisse, A., Dorning, K.J., Mullins, G.L., Wicander, R., 2009. Global patterns of organic-walled phytoplankton biodiversity during the late Silurian to earliest Devonian. *Palynology* 33 (1), 25–75.
- Lele, K.M., Streel, M., 1969. Middle Devonian (Givetian) plant microfossils from Goé (Belgium). *Ann. Soc. Geol. Belg.* 92, 89–121.
- Märss, T., Fredholm, D., Talimaa, V., Turner, S., Jeppsson, L., Nowlan, G.S., 1995. Silurian vertebrate biozonal scheme. In: Lelievre, H., Wenz, S., Blicke, A., Cloutier, R. (Eds.), *Premiers vertébrés et vertébrés inférieurs. Géobios*, 19, pp. 369–372.
- Mehlqvist, K., 2009. The Spore Record of Early Land Plants from Upper Silurian Deposits in Klinta 1 Well, Skåne, Sweden. (MSc thesis) Department of Geology, Lund University, Sweden.
- Mehlqvist, K., Vajda, V., Steemans, P., 2012. Early land plant spore assemblages from the Late Silurian of Skåne, Sweden. *GFF* 134, 133–144.
- Melchin, M.J., Cooper, R.A., Sadler, P.M., 2004. The Silurian period. In: Gradstein, F.M., Ogg, J.G., Smith, A.G. (Eds.), *A Geologic Time Scale 2004*. Cambridge University Press, Cambridge, pp. 188–201.
- Moore, G.T., Jacobson, S.R., Ross, C.A., Hayashida, D.N., 1994. A paleoclimate simulation of the Wenlockian (Late Early Silurian) world using a general circulation model with implications for early land plant paleoecology. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 110, 115–144.
- Nielsen, A.T., 2004. Ordovician sea level changes: a Baltoscandian perspective. In: Webby, B.D., Paris, F., Droser, M., Percival, I. (Eds.), *The Great Ordovician Diversification Event*. Columbia University Press, New York, pp. 84–93.
- Nilsson, A., 2002. Early Ludlow (Silurian) Graptolites from Skåne, southern Sweden. (MSc thesis) Lund University, Sweden.
- Nilsson, S., 2006. Sedimentary Facies and Fauna of the Late Silurian Bjärsjölagård Limestone Member (Klinta Formation), Skåne, Sweden. (MSc thesis), 195 (25).
- Richardson, J.B., 1996. Lower and middle Palaeozoic records of terrestrial palynomorphs. In: Jansonius, J., McGregor, D.C. (Eds.), *Palynology: Principles and Applications*, vol. 2. American Association of Stratigraphic Palynologists Foundation. Publishers Press, Salt Lake City, UT, pp. 555–574.
- Richardson, J.B., Edwards, D., 1989. Sporomorphs and plant megafossils. In: Holland, C.H., Bassett, M.G. (Eds.), *A Global Standard for the Silurian System*. National Museum of Wales, Cardiff, Geological Series, 9, pp. 216–226.
- Richardson, J.B., Lister, T.R., 1969. Upper Silurian and Lower Devonian spore assemblages from the Welsh Borderland and South Wales. *Palaeontology* 12, 201–252.
- Richardson, J.B., McGregor, D.C., 1986. Silurian and Devonian spore zones of the Old Red Sandstone continent and adjacent regions. *Geol. Sur. Can. Bull.* 364, 1–73.
- Richardson, J.B., Rodriguez, R.M., Sutherland, S.J.E., 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. *Bull. Nat. Hist. Mus. Lond. (Geol.)* 57, 115–162.
- Rubinstein, C., Steemans, P., 2002. Miospore assemblages from the Silurian–Devonian boundary, in borehole A1–61, Ghadamis Basin, Libya. *Rev. Palaeobot. Palynol.* 118, 397–421.
- Scotese, C.R., 2003. PALEOMAP project. <http://www.scotese.com/>.
- Steenmans, P., 1996. Palynology of the Ludlovian Burgsvik Formation of Gotland, Sweden. Abstract IX IPC Meeting, Houston, Texas, USA, p. 151 (June 23–28).
- Strother, P.K., 1991. A classification for the cryptospores. *Palynology* 15, 4–20.
- Tullberg, S.A., 1882. Beskrifning till Kartbladet Övedskloster. *Sver. Geol. Unders.* 86, 1–50 (Aa).
- Vergoossen, J.M.J., 1999. Late Silurian fish microfossils from Helvetesgraven, Skåne (southern Sweden) (I). *Geol. Mijnb.* 78, 267–280.
- Vergoossen, J.M.J., 2002a. Late Silurian fish microfossils from Ramsåsa, locality H, Scania, southern Sweden, with some remarks on the body zonation scheme used in thelodont studies. *Scr. Geol.* 123, 41–69.
- Vergoossen, J.M.J., 2002b. Late Silurian fish microfossils from Klinta and Rinneback’s Bro (Scania, southern Sweden), with some remarks on the morphology of *Nostolepis striata* trunk scales. *Scr. Geol.* 123, 71–92.
- Vergoossen, J.M.J., 2003. First record of fish microfossils from Ramsåsa, site C, Skåne, southern Sweden. *Scr. Geol.* 126, 1–78.
- Vergoossen, J.M.J., 2004. Fish microfossils from Ramsåsa, site E, Scania, southern Sweden (mid Palaeozoic). *Scr. Geol.* 127, 1–70.
- Verniers, J., Maletz, J., Kříž, J., Žigaitė, Ž., Paris, F., Shönlau, H.P., Wrona, R., 2008. Silurian. In: McCann, T. (Ed.), *The Geology of Central Europe, Precambrian and Palaeozoic*, 1, 784. The Geological Society of London, pp. 249–302 (Bath).
- Wellman, C.H., 1993. A land plant microfossil assemblage of Mid Silurian age from the Stonehaven Group, Scotland. *J. Micropaleontol.* 12, 47–66.
- Wellman, C.H., Richardson, J.B., 1993. Terrestrial plant microfossils from Silurian inliers of the Midland Valley of Scotland. *Palaeontology* 36, 155–193.
- Wellman, C.H., Habgood, K., Jenkins, G., Richardson, J.B., 2000. A new plant assemblage (microfossil and megafossil) from the Lower Old Red Sandstone of the Anglo-Welsh Basin: its implications for the palaeoecology of early terrestrial ecosystem. *Rev. Palaeobot. Palynol.* 109, 161–196.
- Wigforss-Lange, J., 1999. Carbon isotope ^{13}C enrichment in Upper Silurian (Whitcliffian) marine calcareous rocks in Scania, Sweden. *GFF* 121, 273–279.
- Wigforss-Lange, J., 2007. Tidal facies in the Upper Silurian Öved Ramsåsa Group of Scania, Sweden: linkages of radial and cerebroid ooids and evaporite tracers to subtidal lagoonal environment. *GFF* 129, 8–15.