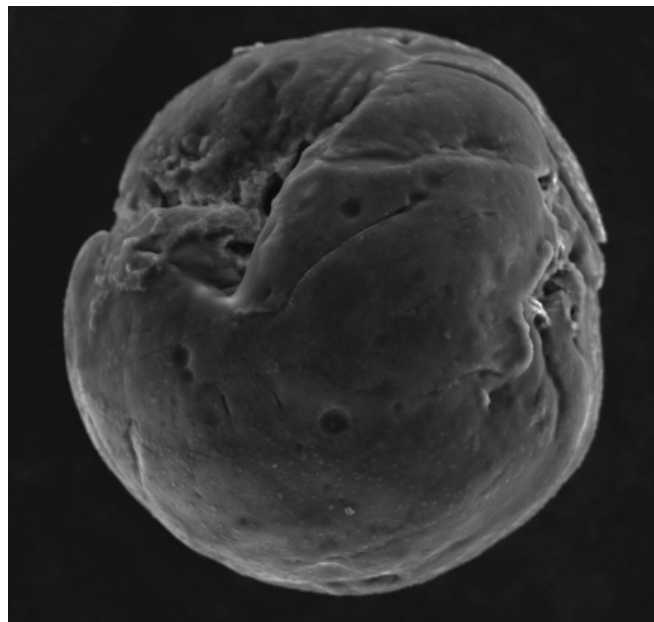


Microspherules from the lowermost Ordovician in Scania, Sweden – affinity and taphonomy

Jan Ulmius

Bachelor thesis in geology at Lund University -
Lithosphere and Paleobiosphere Sciences, no. 271
(15 hskp/ECTS)



Department of Earth- and Ecosystem Sciences
Division of Geology
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Cover Picture: A putative fossil embryo from the *Rhabdinopora flabelliforme parabola* graptolite Zone in the Alum Shale Formation, Södra Sandby, southern Sweden.

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Ulmus, J., 2010: Microspherules from the lowermost Ordovician in Scania, Sweden – affinity and taphonomy
Bachelor thesis in geology at Lund University, no. 271, 21 pp. 15 ECTS credits.

Abstract: Microscopic spherules, 0.1-0.5 mm in diameter, from the lowermost Ordovician *Rhabdinopora flabelliforme parabola* graptolite Zone of the Alum Shale Formation in Södra Sandby, Scania, southern Sweden, have been investigated. The specimens have been studied by light and scanning electron microscopy in order to assess their affinity, taphonomic history, and possible relation to metazoan embryos. Different morphological types could be identified: specimens with a surface of pyrite crystals, black specimens partly enclosed in a pyrite crystal crust, black specimens with a smooth surface with lobes and grooves and also black specimens with a rougher surface. Elemental mapping confirms that the black specimens contain apatite, however, the smooth ones most likely have a surface layer consisting mainly of carbon. The conditions for phosphatisation through degradation of organic material and also pyritisation were favourable in the anaerobic sediments that formed the Alum Shale Formation, however, the formation of carbon films are more difficult to explain. The black spherules could be the result of a chemical process forming a phosphate peloid or grain, or by degradation and concomitant phosphatisation of fecal pellets or metazoan embryos. Especially those specimens with lobes and grooves resemble fossil embryos previously described from the Cambrian and Ordovician. Further studies of their internal structures are needed to confirm a metazoan affinity, however, their outer morphology strongly suggests such a relationship.

Keywords: Ordovician, microfossil, embryo, pyrite, apatite, pyritisation, phosphatisation, carbonisation, Alum Shale Formation, Sweden

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Mikroskopiska sfäruler från understa ordovicium i Skåne, Sverige – ursprung och bevaring

JAN ULMIUS

Ulmus, J., 2010: Mikroskopiska sfäruler från understa ordovicium i Skåne, Sverige – ursprung och bevaring. Examensarbete i geologi vid Lunds Universitet, nr. 271, 21 sid. 15 hp.

Sammanfattning: Ett unikt material av mikroskopiska sfäruler från understa ordovicium i alunskifferformationen utanför Södra Sandby i Skåne har studerats. Möjligt ursprung och samband med tidiga embryor samt bevaringssätt har undersökts med hjälp av ljus- och svepelektronmikroskopi. Några olika morfologiska typer av de 0,1-0,5 mm stora partiklarna kunde identifieras: sfäriska partiklar med en yta av pyritkristaller, svarta sfäriska partiklar delvis inneslutna i pyritkrusta, svarta sfäriska partiklar med en slät yta med lober och fåror samt svarta sfäriska partiklar med en mera skrovlig ytstruktur. Kartläggning av grundämnen visar att de svarta exemplaren innehåller apatit, dock verkar de svarta släta formerna huvudsakligen ha ett ytskikt av kol. I de syrefattiga sediment som sfärulerna bildades var betingelserna gynnsamma för fosfatbildning och pyritisering. Bildningen av ett ytskikt av kol är emellertid svårare att förklara. De svarta sfärulerna kan antingen ha bildats genom en kemisk utfällning av kalciumfosfat till små apatitkorn eller genom mikrobiell nedbrytning av organiskt material under samtidig utfällning av kalciumfosfat. Ursprunget till det organiska materialet kan vara fekal-pellets men också embryor av djur som levde i havet under denna tid. De svarta släta sfärulerna med lober och fåror har stora likheter med tidigare beskrivna fossila embryor från kambrium och ordovicium. Ytterligare studier av de inre strukturerna hos dessa behövs för att bekräfta detta, men den yttre morfologin antyder starkt denna relation.

Nyckelord: Ordovicium, mikrofossil, embryo, pyrit, apatit, pyritisering, fosfatbildning, kolbildning, alunskiffer, Sverige.

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1 Introduction

At the village of Södra Sandby (Scania, southern Sweden) outcrops of Cambrian strata are exposed along the Sularp brook (Fig. 1). The deposits are dominated by kerogen-rich black shales with a few beds and lenses of organic-rich limestone. A recent excavation was made in order to study the Cambrian-Ordovician transition at high resolution (Fig.1C). When searching for conodonts in a limestone bed from the lowermost Ordovician, spherical particles, 0.1-0.5 mm in diameter, were discovered, some of them

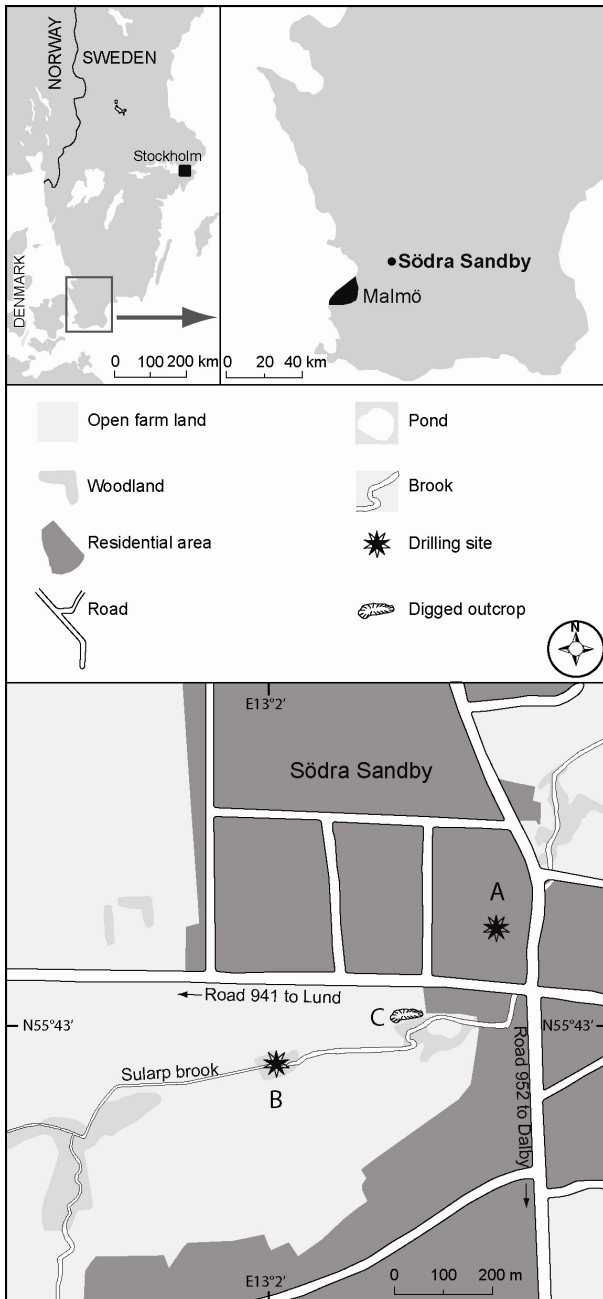


Fig. 1. Drill (A-B) and digging (C) sites in Södra Sandby. A: Westergård (1944), B: Hede (1951). Modified drawing courtesy by Fredrik Terfelt.

remarkably similar to previously reported fossil embryos. Are they of biological origin or are they the result of chemical/geological processes? The aim of this study is twofold: to try to ascertain the nature of these spherical specimens in order to evaluate their affinity and style of preservation, and to present a review on fossil embryos of early metazoans.

2 The Cambrian-Ordovician transition of Southern Scandinavia

2.1 Palaeogeography and depositional setting of Baltica

During the late Cambrian to the Early Ordovician (499-479 Ma) Baltica was located on the southern hemisphere between 30 and 60°S as an isolated continent (Fig. 2). Present-day south-western Scandinavia

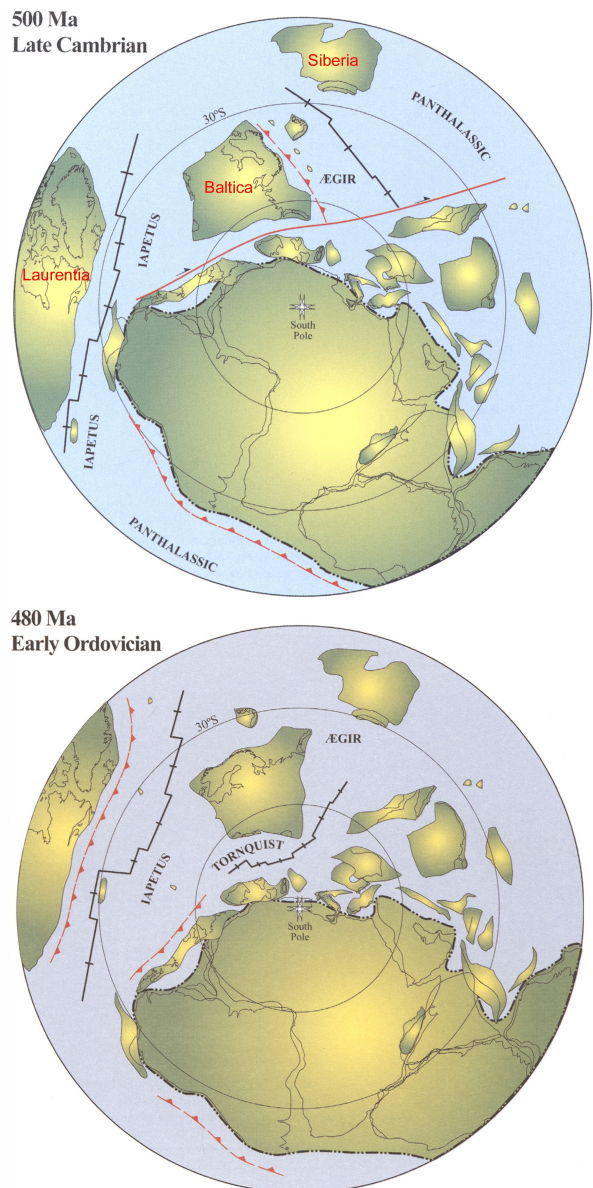


Fig. 2. Palaeogeographic reconstruction of the southern hemisphere in the late Cambrian and Early Ordovician. Adopted from Cocks & Torsvik (2006, figs. 4-5).

was situated at the northern edge at about 40°S during the Furongian. As Baltica rotated anti-clockwise, south-western Scandinavia was facing to the west at about 50°S during the Tremadocian (Cocks & Torsvik 2006). During the Ordovician Baltica travelled northwards towards the equator, docking first with Avalonia and subsequently colliding with Laurentia in the Silurian. One result of this movement was that shelf sediments changed from primarily clastic with limited cold-water carbonates in the Cambrian and Early Ordovician to sediments of progressively warmer-water origin later in the Ordovician (Cocks & Torsvik 2005).

During Cambrian-Ordovician times large parts of Baltica were covered by an epicontinental sea, the Baltoscandian Basin, characterised by an extremely low gradient, flat seabed topography and low sedimentation rate (Fig. 3; Jaanusson 1973). The water depth within the basin decreased from the southwest to the northeast, resulting in a facies zonation, referred to as “confacies belts”, reflecting the spatial distribution of different lithofacies and faunas (Fig. 4; Jaanusson 1976). In the Scanian and Oslo confacies belts, mud deposition was prominent from the middle Cambrian to the Tremadocian, whereas carbonate production was more pronounced further to the east. The long-term sea level shows a gradual rise through the Cambrian Period, reaching the highest level in the Late Ordovician (>200 m above present-day sea level), and followed by a lowering in response to the Hirnantian glaciation (Hag & Schutter 2008). Due to third-order fluctuations in the sea level, the limit for carbonate production in the Baltoscandian Basin varied, e.g. during the Ceraropyge Regressive Event, limestones spread across western Baltoscandia (Nielsen 2004).

The global climate during the early Cambrian through Late Ordovician can be characterized as a greenhouse state or warm mode (Frakes et al. 1992) with low oxygen levels (~50% of present levels) and high carbon dioxide levels (8-18 times the present level) (Barnes 2004). Although sea surface temperatures at low latitudes could have been as high as 40°C (Trotter et al. 2008) the high latitudes of Baltica resulted in more temperate waters, which led to slow carbonate production (Nielsen 2004).

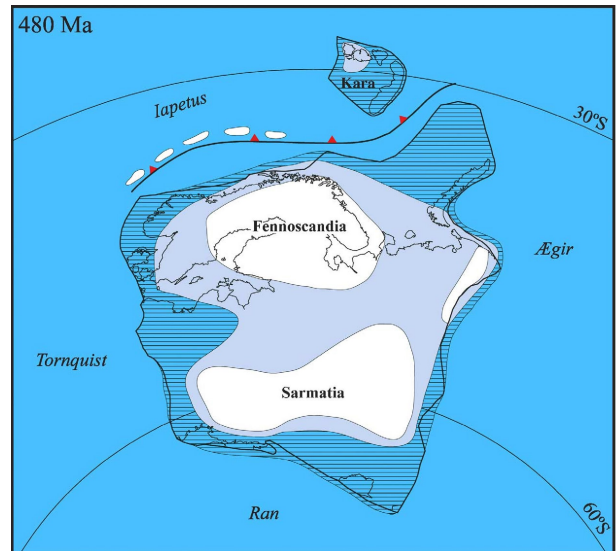


Fig 3. Early Ordovician palaeogeography of Baltica; land (white), shallow shelf (light blue), deeper shelf (hatched blue) and oceans (blue). Adopted from Cocks & Torsvik (2005, fig. 6).

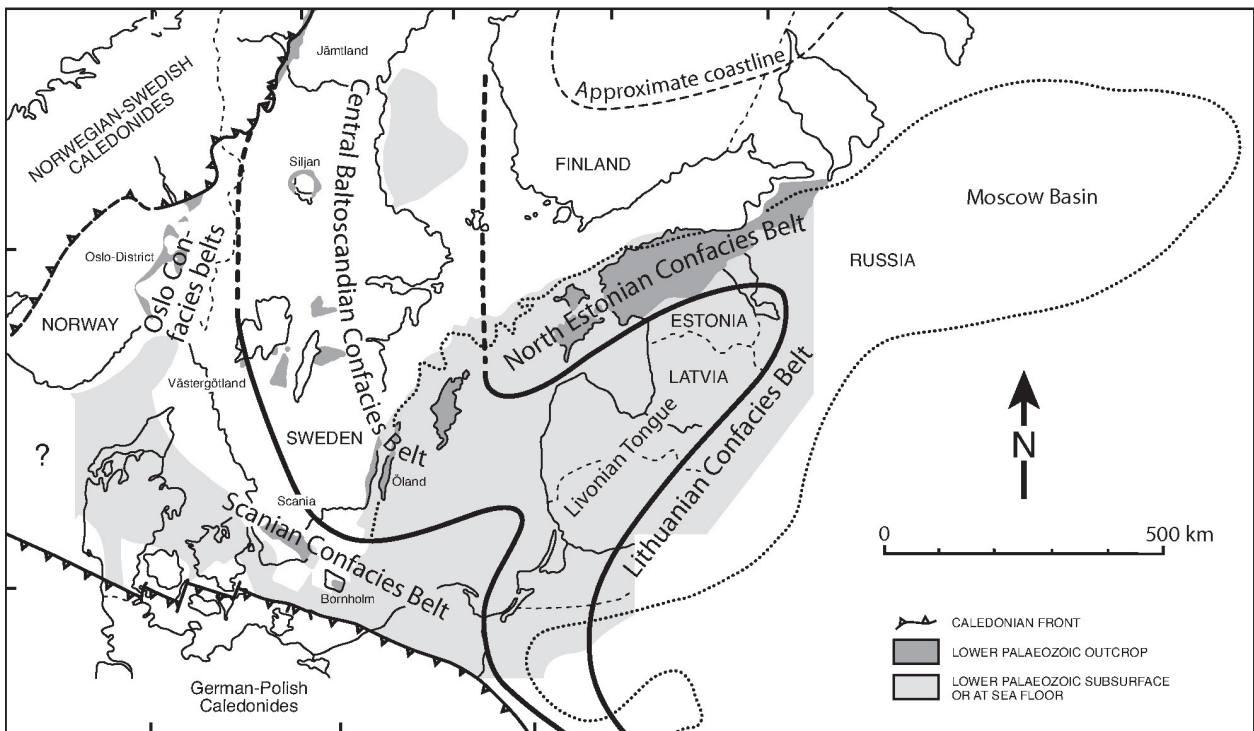


Fig. 4. Distribution of the post-Tremadocian confacies in Baltoscandia. Adopted from Stouge (2004, fig. 2).

2.2 Fauna

During the early Cambrian a sudden appearance of well-skeletonised metazoans with groups such as trilobites, inarticulate brachiopods, hyoliths, monoplacophorans and eocrinoids can be observed in the fossil record. This advent of biomineralised metazoans is generally referred to as the Cambrian explosion (Zhuravlev 2001). The communities were mainly benthic and composed of surface deposit feeders, grazers, carnivores and suspension feeders with low epifaunal and/or infaunal tiering levels. After the Cambrian explosion of animal phyla that ended at about 530 Ma it took more than 40 myr before the initiation of the Early and Middle Ordovician diversification, known as the Great Ordovician Biodiversification Event (GOBE), when the diversification at lower taxonomic levels increased significantly (e.g. Servais et al. 2010). An explanation for this stagnation period could be successive pulses of extinction that limited the build-up of diversity (Zhuravlev 2001). During the GOBE, articulated brachiopods, cephalopods, crinoids, ostracodes and corals appeared and diversified (Webby et al. 2004). The communities of attached epifaunal suspension feeders, deep burrowers and carnivores greatly expanded. Baltica became progressively more isolated during the late Cambrian and Early Ordovician, which led to a more endemic fauna. Many Baltic trilobites and brachiopods, even at the family level, are unknown from other terranes (Cocks & Torsvik 2005).

2.3 Scania and Södra Sandby

The lithostratigraphy of southern Scandinavia including Scania, for the middle Cambrian to the Lower Ordovician is shown in Fig. 5. The interval of interest for this study contains the Alum Shale Formation capped by the Björkåsholmen Formation (formerly the Ceratopyge Limestone). The Alum Shale Formation consists of kerogeneous black, more or less fissile shales with beds and lenses of limestone, the so-called stinkstone (Nielsen et al. 2007). The thickness of the formation decreases from about 100 m in western Scania to about 50 m on Bornholm and wedges out at the Baltic coast (Bucharadt et al. 1997). The alum shales are dominated by agnostid and olenid trilobites with brachiopods and phospatocopines as minor faunal elements in the Cambrian and graptolites in the Lower Ordovician (Bucharadt et al. 1997). The Björkåsholmen Formation, with a thickness in the order of one metre, consists of interbedded carbonates, shales and glauconitic beds deposited during a sea-level fall (Egenhoff et al. 2010). It contains inter alia agnostid and ptychopariid trilobites, brachiopods and conodonts (Tjernvik 1956).

The present work is based on a digging just north of the Sularp brook immediately west of the centre of Södra Sandby (see Figs. 1C and 6). The digging penetrated about 5 m of the Alum Shale Formation in the lower Tremadocian *Rhabdinopora flabelliforme parabola* graptolite Zone and in the upper Furongian *Acerocare ecorne* trilobite Zone with shales, lime-

stones, stinkstones and pyrite horizons and concretions. The limestone bed in the uppermost part of the section consists of an organic-rich argillaceous limestone with an intercalated bed of shale. About 260 m northeast of this digging a boring was conducted 1941-42 (Fig. 1A; Westergård 1944). Here the *Rhabdinopora* and *Acerocare* yielding strata are between 10 and 15 m below the surface and a limestone bed at 11 m can be correlated with the limestone bed in the digging. Another boring about 450 m west of the digging was conducted by Hede (1951; Fig. 1B). Here the boundary strata are about 48 m below ground surface, however, no limestone is present at this level.

3 Fossil embryos

3.1 Introduction

There is still much controversy concerning the timing of the appearance of the first complex animals, the metazoans, on Earth. According to the molecular clock, it is estimated that they appeared before the Cryogenian (850-635 Ma) and that the phyla Porifera (sponges) and Cnidaria (e.g. corals and jellyfish) separated during the Cryogenian (Peterson et al. 2008). During the subsequent Ediacaran (635-542 Ma) the superphyla Ecdysozoa (e.g. arthropods and some marine worms), Spiralia (e.g. bryozoa, molluscs, brachiopods and annelids) and Deuterostomata (e.g. vertebrates, echinoderms and hemichordates) appeared (Peterson et al. 2008). The chances of finding well preserved body fossils from these periods are limited, partly because the animals probably were soft-bodied and that these strata have been subjected to intense metamorphism and tectonism. The exceptions are the Ediacaran biota from the interval 600-550 Ma from different parts of the world and the approximately 600 Ma old Doushantuo fossils from South China. However, new findings push the record of animal body-fossils further back in time, e.g. the discovery of possible sponge-grade metazoans in pre-Marionan (older than 635 Ma) limestones in South Australia (Maloof et al. 2010).

Evolutionary developmental biology studies have been hampered by the scarce fossil record limited largely to late ontogenetic stages (Donoghue & Dong 2005). However, with the discovery of fossilised embryos from late Neoproterozoic and Cambrian strata, palaeontology can give a better contribution to developmental evolution. The Doushantuo formation is of particular interest because of the discovery of phosphatised microscopic embryos of early metazoans at different developmental stages from the Neoproterozoic (Xiao and Knoll 2000). The first discoveries of fossilised metazoan embryos were made from lower and middle Cambrian strata in China and Siberia (Zhang and Pratt 1994; Bengtson and Zhao 1997). In order to investigate the structure of the fossil embryos, increasingly sophisticated methods have been used, including synchrotron X-ray tomographic microscopy (Donoghue et al. 2006a). Subsequently, fossilised em-

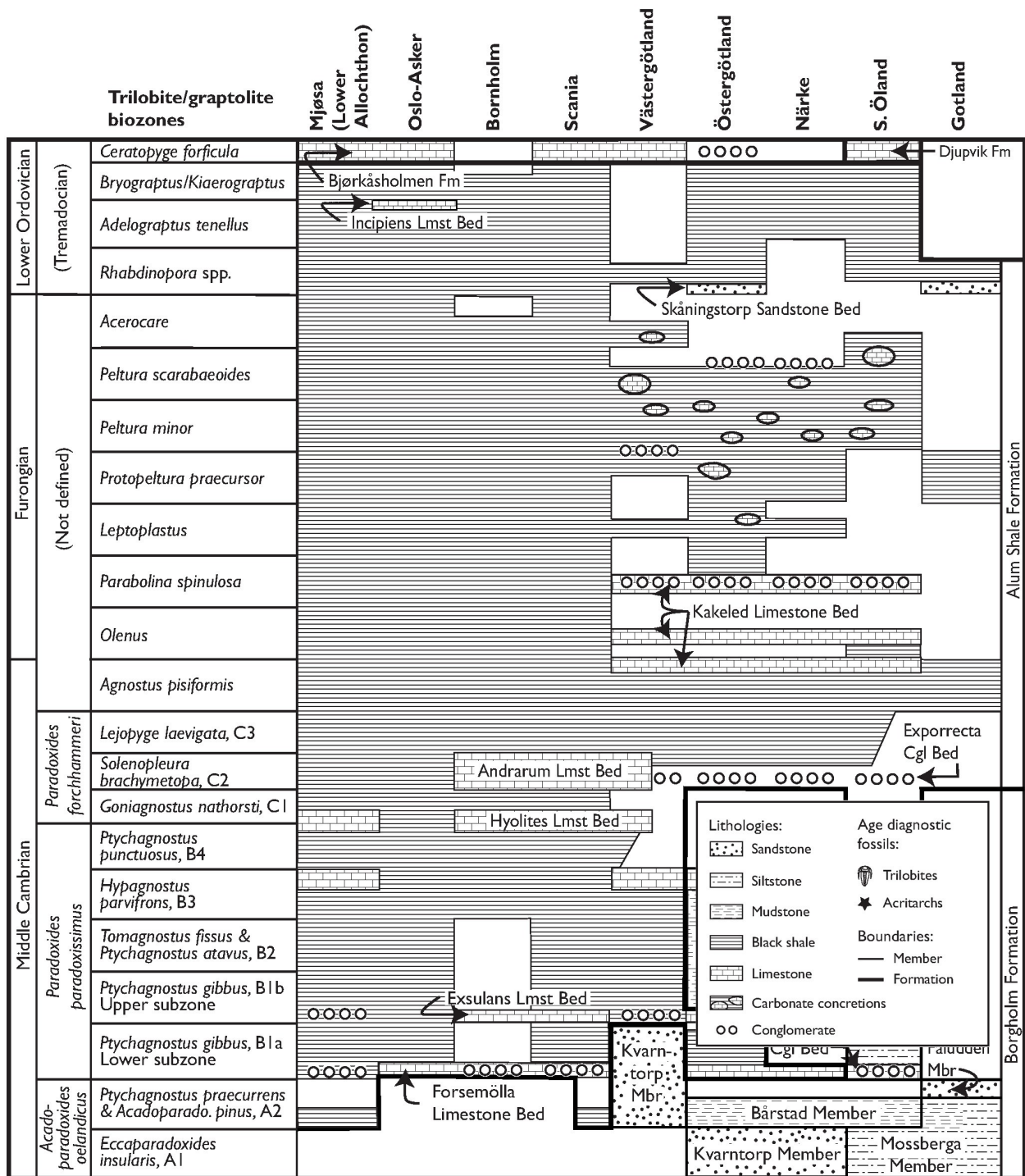


Fig. 5. Lithostratigraphic scheme and biozones for the Middle Cambrian, Furongian and Tremadocian of southern Scandinavia. Adopted from Nielsen et al. (2007, fig.3).

bryos have been discovered in the lower Cambrian of Canada (Pyle et al. 2006), middle Cambrian of Australia and the Lower Ordovician of North America (Donoghue et al. 2006b). It has been speculated that the record of these types of embryos may be limited to the late Neoproterozoic to Early Ordovician because of the closure of the phosphatic window in the Early Ordovician and also because of increased bioturbation and tiering levels in subsequent times (Donoghue et al. 2006b).

Usually, only more or less decay-resistant soft tissues, like chitin and cellulose, are fossilised. However, there are many examples of exceptional preservation of less resistant soft tissue in Konservat-Lagerstätten (Selden & Nudds 2004). In the most spectacular cases, soft tissue such as muscle fibres may be preserved (Martill 1990). Since eggs and embryos usually are soft-bodied, exceptional processes and environmental conditions are required in order to preserve them. Even if they do become preserved and can be recovered by

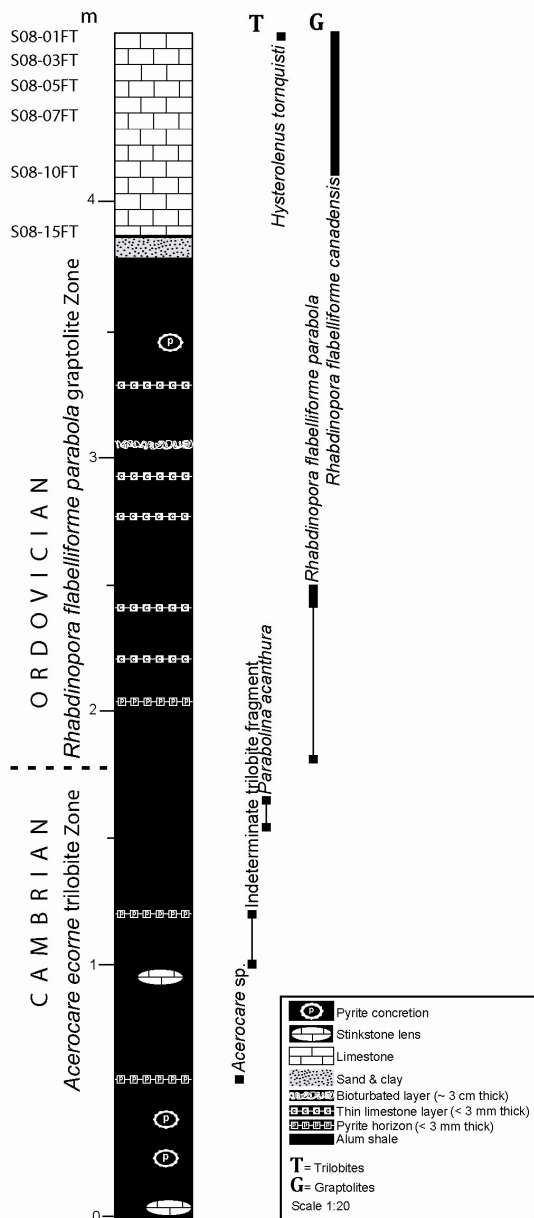


Fig. 6. Stratigraphy and lithology of the *Acerocare ecorne* and *Rhabdinopora flabelliforme parabola* zones (Cambrian-Ordovician transitional interval) in the Alum Shale Formation at Södra Sandby. The sampled limestone bed is indicated by sample numbers. Modified drawing courtesy by Fredrik Terfelt.

standard micropalaeontological techniques it can be easy to overlook the due to their inconspicuous appearance.

3.2 Fossilisation processes of soft tissues

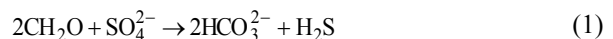
Mineralisation of soft tissue is a means to preserve the structure. The resulting state of preservation is a race between the rate of decay and the rate of mineralisation. Soft tissue mineralisation can occur in three

major ways according to Allison & Briggs (1991):

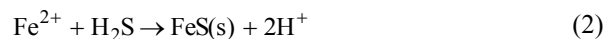
- Permineralisation
- Replication of morphology by means of authigenic mineralisation
- Mineral casts or moulds

Permineralisation is a chemical process that occurs when mineral-rich water rapidly permeates the tissues and precipitates within their pore spaces. Permineralisation of soft tissue is less common in animals than in plants. Authigenic mineralisation is the product of decay bacteria which form a mineral coating on the tissue, preserving an exact replica of the original soft tissue that subsequently decay and disappears. Casts and moulds result from diffuse early diagenetic cementation in the surrounding sediments. The type of mineral that precipitates depends on the chemical composition of the sediment and the conditions created by the decay process. Minerals most commonly involved in these processes include pyrite, apatite and calcite or aragonite.

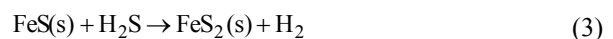
Soft-tissue mineralization is driven by bacterial decomposition under anaerobic conditions (Briggs 2003). The major process of organic matter oxidation in marine sediments is bacterial sulphate oxidation. An overall reaction for the oxidation-reduction reaction can be written:



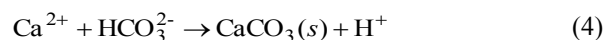
The hydrogen sulphide can combine with reactive iron-bearing minerals to produce iron monosulphides:



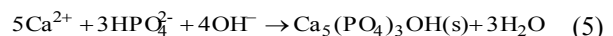
The iron monosulphides can react further with hydrogen sulphide to produce pyrite:



Ca^{2+} in pore waters can combine with the bicarbonate in reaction (1) to produce calcium carbonate (calcite or aragonite):



If phosphorous is included in the organic material in reaction (1), phosphate can be produced. Phosphate from this source or external sources can combine with Ca^{2+} to produce apatite:



Calcium phosphate precipitation is favoured increasingly over calcium carbonate as pH decreases from neutral to acidic. Fluoride also favours apatite formation and magnesium should be absent as it inhibits apatite formation (Allison & Briggs 1991).

According to reactions (1-3) the formation of pyrite requires dissolved sulphate, organic matter and an iron source. However, in euxinic environments pyrite can form without any organic matter because hydrogen sulphide is present everywhere in the bottom waters

(Flügel 2010). Soft-tissue pyritisation could thus happen when iron and sulphate diffuse toward a decaying organ where bacterial sulphate reduction occurs and iron is in a reactive state.

The frequent association of pyrite and phosphorites in the sediments indicates that apatite also can form in oxygen-depleted environments. The concentration of P must be high enough close to the decaying tissue in order for phosphatisation to take place and preserve the tissue. If the organic production in the water column is high, the sediment will contain large amounts of such material, which will start decaying and releasing phosphate into the pore waters (Föllmi 1996). Microbial mats are thought to help trap these pore waters. Also the presence of particulate FeOOH in the water column can bind phosphate and deliver it to the sediment (Briggs 2003). The bacterial decay processes also lowers the pH of the pore waters, which favour the precipitation of calcium phosphates over calcium carbonate. This is also the mechanism by which calcium carbonate is replaced by apatite in calcareous shells.

Another way of preserving soft tissues is through carbonisation, which is common for plant remains (Allison & Briggs 1991). The tissue is preserved as a carbon residue forming an outline or film. The conditions required for carbonisation are not well known, however, decay must have been halted.

3.3 Distribution

Fossil embryo findings have been reported from an interval embracing the Ediacaran to the Early Ordovician, representing a 150 million year window, and from most continents (see Table 1). Preservation is almost solely through phosphatisation. The embryo-bearing rocks represent shallow water settings, except perhaps for the Bititao and Haoqiao formations in Hunan province of China, which are inferred as being formed in deeper water environments (Dong 2009). All sites except for South China in the Ediacaran were situated at $\pm 30^\circ$ from the equator.

3.4 Affinity and characteristics

It has only been possible to establish the taxonomic affinity of fossil embryos in a few cases. *Olivoooides* was first described by Zhang & Pratt (1994) as a globular fossil embryo of uncertain affinity but has later been interpreted as the prehatching stages of *Punctatus*, which, in turn, has been interpreted as a scyphozoan cnidarian (jellyfishes) (Bengtson & Zhao 1997). *Punctatus* can be related to the extinct conulariids (Zhao & Bengtsson 1999). From the fossil material a full life cycle has been reconstructed, from the blastula of different cleavage states, showing the blastomere boundaries (Fig. 7A-

Table 1. Fossil embryos findings

Period (Ma)	Site	Litology (Preservation)	Name (Affinity)	Reference
Ediacaran (632)	Doushantuo Formation, Yichang, Hubei, China	Dolostone with phosphorite concretions (Phosphatisation)	<i>Tianzhushania</i> (Embryos inside acritarchs)	Yin et al. 2007
Ediacaran	Chambagahat Formation, Himachal Lesser Himalaya, India	Phosphatic chert lenticles associated with quartz arenite	(Cnidarians, bilaterians?)	Mathur et al. 2009
Late Neoproterozoic (580-570)	Doushantuo Formation, Weng'an, Guizhou, China	Dolomitic phosphorite (Phosphatisation)	<i>Megasphaera</i> <i>Parapandorina</i> (Cnidarians) <i>Tianzhushania</i> = <i>Megasphaera</i> (Copepods) <i>Megasphaera ornata</i> (Poriferan, cnidarian, protostomial, deuterostomial)	Xiao et al 1998 Xiao & Knoll 2000 Chen et al. 2000 Yin et al. 2004 Xiao et al. 2007 Chen et al. 2009

Cont.

Table 1 cont. Fossil embryos findings

Period (Ma)	Site	Litology Preservation	Name (Affinity)	Reference
Earliest Cambrian (530)	Dengying Formation, Kuanchuanpu, Shaanxi, China	Limestone-phosporites (transported) (Phosphatisation)	<i>Olivoooides, Punctatus</i> (Scyphozoans)	Bengtson & Zhao 1997
			<i>Pseudoooides</i> (Arthropod)	Steiner et al. 2004
			(Phosphatisation- Kerogen)	Chen et al. 2007
Lower Tommotian (530)	Pestrotsvet Formation, Aldan River, Siberia	Marine limestones (Phosphatisation)	<i>Markuelia</i>	Bengtson & Zhao 1997
Tommotian (530)	Pestrotsvet Formation, Gonam-Aldan Rivers, Siberia	Marine limestones (Phosphatisation)	<i>Markuelia</i>	Donoghue et al. 2006b
Lower Cambrian (520)	Manykay Formation, Bol'shaya Kuonamka River, Siberia	Carbonate packstone (Phosphatisation)	(Cnidarians)	Kouchinsky et al. 1999
	Ingta Formation, Wernecke Mountains, Yukon, Canada	Parted and nodular lime- stone, phosphate (Phosphatisation)	<i>Olivoooides</i> <i>Archaeoooides</i>	Pyle et al. 2006
Middle Cambrian (510)	Gaotai Formation, Duyun, China	(Phosphatisation)	<i>Pseudoooides</i> (Arthropod)	Zhang & Pratt 1994
Late Templetonian (508)	Inca shale, Beetle- Monastery Creek For- mation, Georgina Ba- sin, Australia	Shales, siltstones, phosporite (Phosphatisation)	<i>Markuelia</i>	Donoghue et al. 2006b
Middle Cambrian (513-501)	Kaili Formation, Guizhou, China	Silty mudstone (Silica replacement)	(Marine invertebrate eggs and embryos)	Lin et al. 2006
Middle-Late Cambrian (500)	Bititao Formation, Haoqiao Formation, Wangcun, Hunan, China	Biomicrosparite, nodular micrite (Phosphatisation)	<i>Markuelia hunanensi</i> , <i>Markuelia elegans</i> (Scalidophoran)	Dong et al. 2004 Dong 2009
Tremadocian (480)	Vinini Formation, Battle Mountin, Nevada, USA	Siltstone, Limestone (Phosphatisation)	<i>Markuelia</i>	Donoghue et al. 2006b

B), through the stellate embryo (Fig. 7C) to the adult stage (Fig. 7D). The interior of the blastula is also well preserved which is evident from Fig. 8, where elongated wedge-shaped blastomers are arranged around a central cavity resembling a coeloblastula (Zhao & Bengtson 1999). The phosphate in *Olivoooides* is either in the form of acicular crystals, approximately 1 μm wide or small spheroids 1-3 μm in diameter that probably were formed under the influence of bacteria (Zhao & Bengtson 1999). The internal soft tissue is usually not preserved in the same detail as the cuticle (Fig. 7). Instead they have a thread-like structure, which could indicate partially decomposed soft tissue or filamentous bacteria according to Zhao & Bengtson (1999).

Another fossil embryo with more robust affinity is

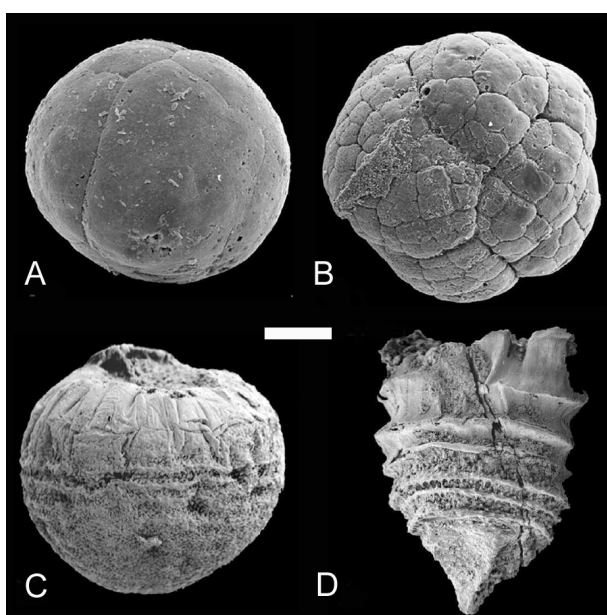


Fig. 7. Embryonic and adult stages of *Olivoooides*. A: Eight-cell stage blastula, B: Later stage blastulae, C: Stellate embryo, D: Adult *Punctatus*. Relative scale bar: 43 μm (A), 82 μm (B), 156 μm (C), 424 μm (D). Adopted from Donoghue & Dong (2005, fig. 2).

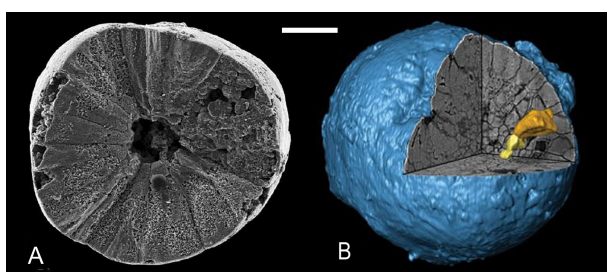


Fig. 8. A: Fractured embryo of *Olivoooides* (adopted from Donoghue & Dong 2005, Fig. 2); B: Tomographic reconstruction of embryo of *Olivoooides*, the yellow structure is a rendering of the morphology of a column of blastomers. Scale bar 103 μm (A) and 119 μm (B). Adopted from Donoghue et al. (2006a, fig 1).

Markuelia, which also is the most widely distributed fossil embryo taxon hitherto known, with records from the lower Cambrian to the Lower Ordovician in Australia, South China, Siberia and North America (Donoghue et al. 2006b). *Markuelia* is established as a scalidophoran which includes the now living phyla Kinorhyncha (mud dragons), Pripulida (penis worms) and Loricifera (Dong et al. 2004). Many exquisitely preserved specimens of *Markuelia* have been found (e.g. Fig. 9). The embryo in Fig. 9 is coiled in an inverted S-shaped loop with the head to the upper right and the tail with spines in the centre. Also for *Markuelia* the phosphatisation varies in fidelity from structures less than 0.3 μm to just a general outline of the embryo. The texture indicates a bacterially mediated replacement (Dong et al. 2004).

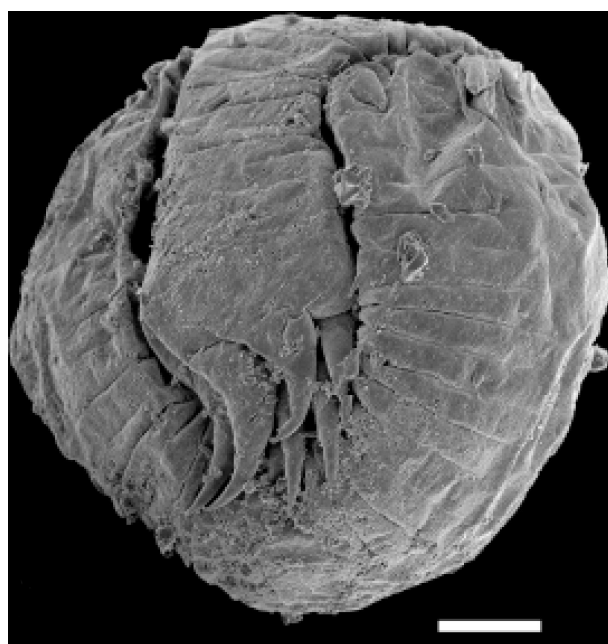


Fig. 9. Fossil embryo of *Markuelia*, scale bar 59 μm . Adopted from Donoghue et al. (2006b, fig 1).

Spectacular fossil embryos from the late Neoproterozoic of the Doushantou Formation in South China have been described, although their affinity is unknown. *Parapandorina* is interpreted as an early cleavage stage metazoan embryo with equal and radial cleavage (Fig. 10; Xiao & Knoll 2000). However, the embryo interpretation has been questioned and instead the fossils could represent giant sulphur bacteria similar to present-day *Thiomargarita*, which has a size and morphology similar to the Doushantou microfossils and is also capable to control phosphate mineral precipitation (Bailey et al. 2007). Using phase contrast synchrotron X-ray microtomography, Chen et al. (2009) maintained a metazoan origin based on presence of e.g. macromeres and micromeres, polar lobes, blastulation and gastrulation and chorionic protection. However, it was not possible to differentiate between poriferan, cnidarian, protostomial or deuterostomial affinity. Permineralisation and replication by phos-

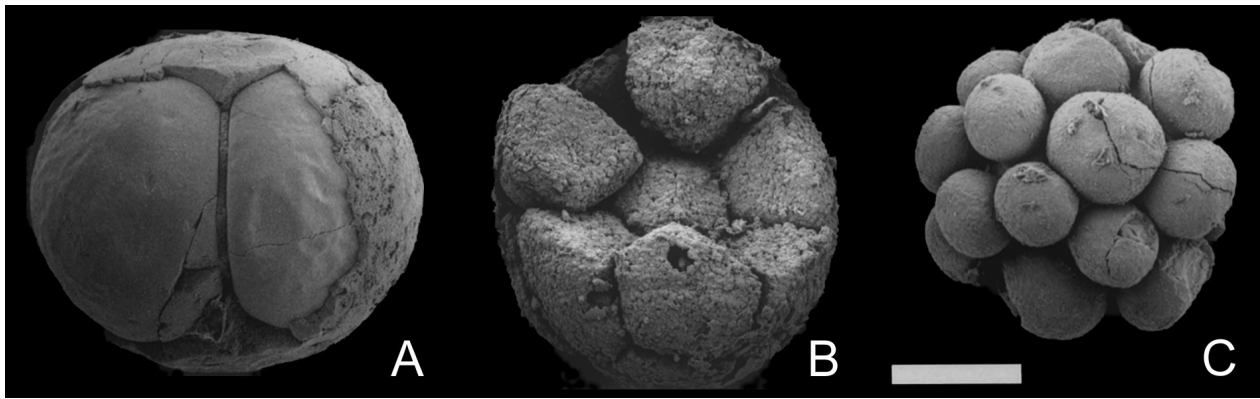


Fig. 10. Fossil embryos of *Parapandorina* from the Doushantou Formation at different cleavage stages. Scale bar 168 μm for (A), 233 μm for (B) and 200 μm for (C). Adopted from Xiao et al. (1998, fig 5).

phate are the two mechanisms responsible for the soft tissue preservation in the Doushantuo Lagerstätte (Xiao & Knoll 1999). The Doushantuo embryo envelopes can be coated on both the outer and inner sides with a few micrometers thick isopachous crust of crystalline apatite or with phosphatic spherules. Permineralisation can fill blastomere interiors with randomly oriented phosphate minerals, and phosphatic filaments can also be observed in the interior of the embryos. Both the filaments and spherules are thought to reflect phosphatic encrustation of infesting bacteria. In the Doushantuo phosphorites, pyritised spheroids 400-900 μm in diameter also can be found, which can have been templated by biological structures (Xiao & Knoll 1999).

Tianzhushania was originally described as an acritarch, however, it is now considered as a taphonomic variant of *Megasphaera*, interpreted as a resting egg of animal origin (Fig. 11; Yin et al. 2004). These embryos, at different cleavage stages within a cyst or hull, have been found in rocks as old as 630 Ma (Yin et al. 2007). *Tianzhushania* is preserved through both phosphatisation and silicification.

A classical idea is that indirect development is ancestral in metazoans (Jägersten 1972), i.e. a pelagobenthic life cycle (pelagic larva + benthic adult).

From the known fossil record of embryos presented above direct development is indicated, however, this could be a taphonomic artefact as preservation of larvae may be even more unlikely than preservation of embryos (Budd 2004; Donoghue & Dong 2005), or that larval development is associated with free spawning and eggs and embryos are not likely to be deposited below the sediment-water interface (Gostling et al. 2008). The embryos of *Markuelia*, *Olivoides* and *Pseudoides* are also large, which could have been beneficial for preservation (Donoghue et al. 2006b).

3.5 Taphonomy of fossil embryos

Decay and mineralisation have been investigated by experimental taphonomy using living invertebrate eggs and embryos in artificial seawater (Martin et al. 2003, 2005; Raff et al. 2006). The results show that mineralisation is mediated by bacteria that generate anoxic conditions and reduce pH. Even in the absence of e.g. decaying carcasses as a source of phosphorous or calcium, mineralisation with calcium carbonate or a combination of calcium carbonate and calcium phosphate occur. This mineralisation process can be very rapid, taking only weeks and varies between embryo taxa (Martin et al. 2003, 2005). Bacteria can also form biofilms on the tissues, thereby retaining the original

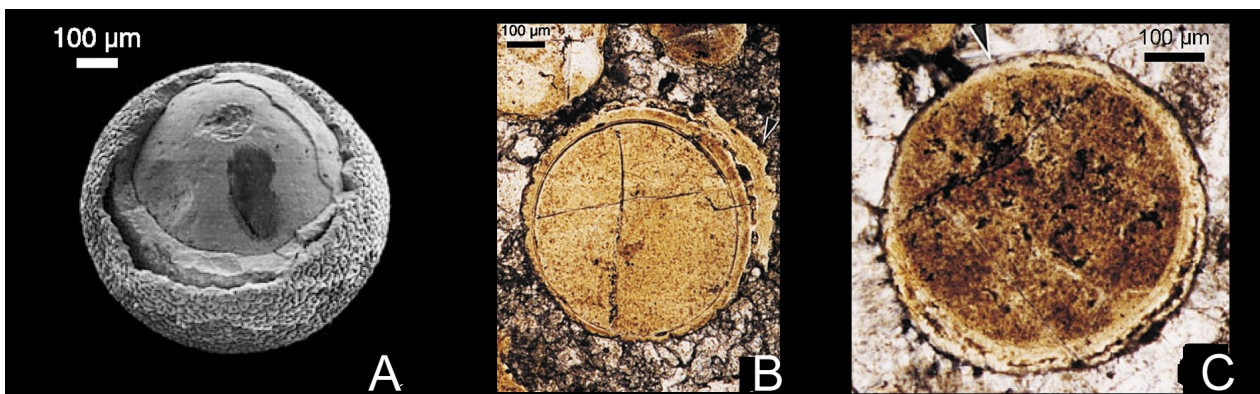


Fig. 11. A: SEM micrograph of *Tianzhushania* with internal body with membrane and secondary overgrowth. B: Thin section of *Tianzhushania* with ornamented middle wall and a part of the outer covering. C: Thin section of *Tianzhushania* lacking the outer covering. Adopted from Yin et al. (2004, figs. 4-6).

structure of the tissue during the decay and then catalysing mineralisation of the films (Raff et al. 2008).

The fossil record of microscopic embryos seems to be restricted to the interval spanning the late Neoproterozoic to the Early Ordovician (Donoghue & Dong 2005). There also seems to be a reduction in the degree of phosphatisation from the early embryos to specimens in the late Cambrian and Early Ordovician (Donoghue & Dong 2005). The high degree of phosphatisation during the late Neoproterozoic and the early Cambrian is usually attributed to higher levels of phosphorous in the oceans at this time, whereas these levels are thought to have declined after the Cambrian (Donoghue et al. 2006b). Formation of phosphorites is assumed to take place by upwelling of cold nutrient-rich water on continental shelves (Sheldon 1981). Episodes of phosphogenesis can be related to palaeoceanography and palaeogeography, relative sea level, palaeocurrents, and palaeoclimate. Although the formation of phosphorites on continental shelves was high during the Cambrian and Ordovician it was also high in the Permian, the Upper Jurassic-Lower Cretaceous, the Upper Cretaceous-Lower Tertiary and the Miocene (Shields et al. 2000). Obviously the phosphorous levels in the oceans is not the sole explanation and the decrease in preservation of embryos from the Cambrian to the Ordovician can probably also be attributed to the increase in bioturbation during this period (Droser & Bottjer 1989; Donoghue et al. 2006b).

4 Materials and methods

4.1 Literature review

A thorough literature review was made covering fossil embryos from the Precambrian, Cambrian and Ordovician and also on the environmental setting at the Cambrian-Ordovician transition for Baltica and Scania in particular.

4.2 Sample preparation and analysis

The studied limestone bed (Fig. 6) was sampled in about 5 cm thick intervals. About 1-2 kg of each sample was digested in buffered acetic acid according to the methods described by Jeppsson (2005). After drying, the residues were sieved and split into three different size fractions (>250, 125-250 and <125 μm) that were picked for microfossils, including putative embryos, under an optical stereomicroscope. Spherical specimens were sorted into different categories based on morphology and photomicrographs were taken. Selected specimens were mounted on stubs using carbon adhesive tape and without coating investigated in a Hitachi S-3400N scanning electron microscope (SEM) using an acceleration voltage of 15 kV at high vacuum or at pressure of 80 Pa. Elemental analysis and mapping were performed with an energy-dispersive spectrometer (INCA X-sight, Cambridge Instruments) in backscatter mode.

Six specimens of different morphotypes were prepared for thin sectioning by placing them on adhesive

tape in a mould, covering the specimens in epoxy resin, polishing the cast on the side with microfossils, and mounting with epoxy onto a glass slide. The cast on the slide was then cut as thinly as possible with a diamond saw and polished until the specimens became translucent. The thin section was investigated in plane- and cross-polarised light in a microscope and photographed. For analyses in SEM the thin section was coated with carbon.

All figured specimens and the remaining collection (courtesy of Mats Eriksson and Fredrik Terfelt) are stored at the Department of Earth and Ecosystems Sciences, Division of Geology, Lund University.

5 Results

5.1 Description of the material

Selected samples from the limestone bed were picked for microspherules, see Table 2. They are approximately 0.1-0.5 mm in diameter. The specimens can be sub-divided into three morphological types (see Fig. 12):

1. Specimens with a micro-granular surface of tiny yellowish-brown mineral grains, probably pyrite crystals
2. Dull to glossy black specimens, sometimes with a mottled appearance and occasionally also an onion-like outer layer. These specimens are not necessarily as spherical as the ones in category 1. Grooves and lobes are also visible on the surface.
3. Specimens with fragments of the yellow-brown crust of category 1, partially enclosing a black core of category 2.

From these observations it seems likely that the specimens consist of black cores enclosed by a yellow-brown crust of pyrite crystals, and that the category 3 particles have lost some of this layer. The microspherules are conspicuously concentrated in the upper part of the limestone bed (Samples S08-01FT, S08-03FT and S08-05FT). Microfossils such as conodont elements and brachiopod fragments and also some acid-resistant mineral grains are also observed in the samples.

The size of the specimens with a pyrite crust (complete or partial) is in the range 200-500 μm and the size of the naked black specimens is in the range 100-400 μm .

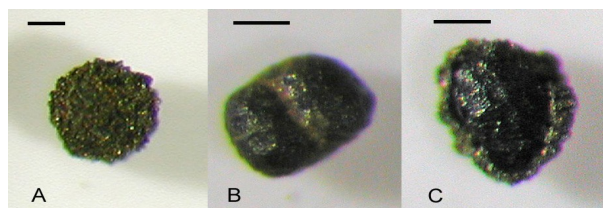


Fig. 12. Light microscope photographs of the three morphological types distinguished, all from sample S08-05FT. A: morphotype 1, B: morphotype 2, C: morphotype 3. Scale bar 100 μm .

Table 2. Samples picked for putative fossil embryos.

Sample number	Sieve fraction	Observations	
		Spherical particles	Other
S08-01FT	>250 μm	Some category 1 specimens	Euhedral pyrite crystals and aggregates
	125-250 μm	Many category 2 specimens	
	<125 μm	None	
S08-03FT	>250 μm	Some category 1 and 3 specimens	Pyrite aggregates, greyish needle-shaped grains
	125-250 μm	Some category 2 specimens	Euhedral pyrite crystals and aggregates, greyish needle-formed particles, some quartz grains
	<125 μm	None	
S08-05FT	¹⁾	Category 1, 2 and 3 specimens	Other microfossils
S08-07FT	>250 μm	Isolated rounded rust-coloured particles,	Pyrite aggregates
	125-250 μm	Isolated rounded rust-coloured particles	
	<125 μm	None	
S08-10FT	>250 μm	None	Pyrite aggregates
	125-250 μm	None	Isolated quartz and feldspar grains
	<125 μm	None	
S08-15FT	>250 μm	None	Pyrite aggregates
	125-250 μm	None	Isolated quartz and feldspar grains
	<125 μm	None	

¹⁾Sample S08-05FT had already been picked for microfossils by Mats Eriksson.

5.2 Scanning electron microscopy (SEM) analyses

Eighty specimens of the three morphological types were investigated in SEM, for a selection see Fig. 13. The type 2 specimens sometimes have a very smooth surface (and look lustrous in the optical microscope) (Fig. 13D-I) and are denoted type 2a. Other specimens in this category seem to have a rougher, microgranular surface and are more porous (when transporting the cores with a moist brush, the cores absorb the water quickly) (Fig. 13J-L), and are denoted type 2b. Many of the type 2a specimens have lobes, grooves and indentations (Fig. 13D-I). In some of the type 2b specimens different layers are visible (Fig. 13K).

From the elemental mapping of a type 3 specimen it is evident that the crust is composed of pyrite (Fig. 14). The pyrite crystals are mostly euhedral and can vary between 5 and 20 μm in size. The black core consists primarily of calcium and phosphorous, which indicates calcium phosphate or apatite. In specimens with damaged pyrite coating it sometimes looks as if the black core does not fill up the entire volume (Fig. 13B, C).

The elemental mapping of type 2a specimens with a smooth surface gives the surprising result that at least the surface contains a lot of carbon and almost no calcium, phosphorous, iron or sulphur (Fig. 15). Since the sample preparation includes acetic acid the carbon cannot be in the state of carbonate. A spot elemental analysis is not unambiguous, however, in cases where it is possible to analyse cracks of type 2a specimens with a smooth surface, calcium and phosphorous can be detected. The type 2b specimens with the rougher, microgranular surface have much less carbon on the surface and consist mainly of calcium and phosphorous, i.e. apatite.

5.3 Thin section analyses

The specimens investigated in thin section belong to category 1 and 2b. The thin section had to be polished to a few micrometers in order to become transparent. The cross section of a type 2b specimen shows some granularity with darker and paler areas and also an indication of an outer layer (Fig. 16). Elemental spot analysis shows almost pure apatite ($\text{Ca}_5(\text{PO}_4)_3\text{F}$) in the darker areas and this is also true for the paler

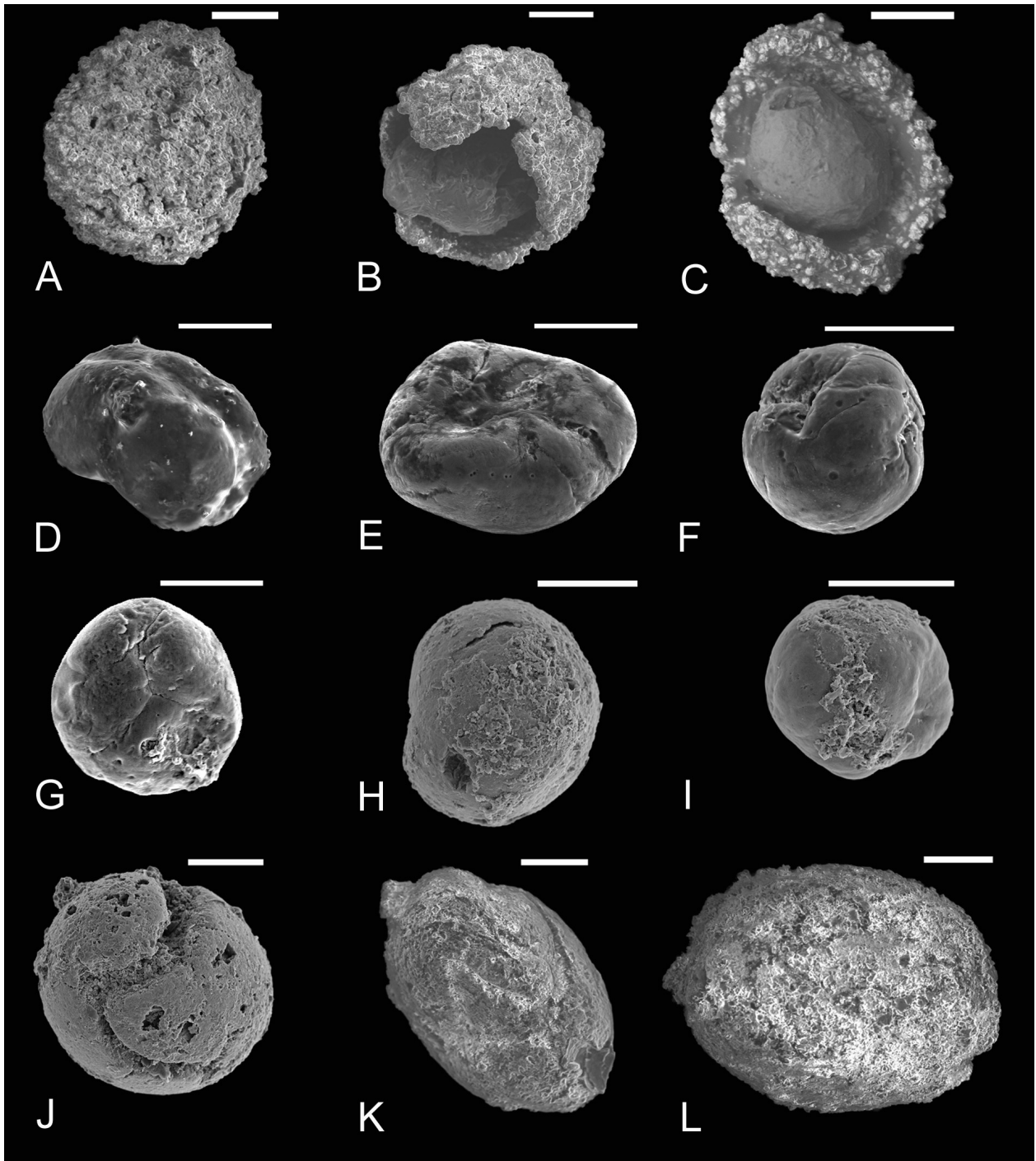


Fig. 13. SEM photomicrographs of microspherules, some of which are putative embryos, from the limestone bed in Södra Sandby. A: Morphotype 1 (Sample S08-05FT), B-C: Morphotype 3 (Sample S08-05FT), D-I: Morphotype 2 (Sample S08-01FT), J-K: Morphotype 2 (Sample S08-05FT), L: Morphotype 2 (Sample S08-05FT, used for thin-section in Fig. 16). Scale bars 100 μm . Photo G courtesy by Fredrik Terfelt and photos H-J courtesy by Mats Eriksson (the specimens H-J are gold coated).

areas with a slightly different composition. One of the other type 2b specimens also shows internal heterogeneity with apatite and traces of an outer layer. The other type 2b specimens have a more compact, homogeneous cross-section with apatite. The thin section of the type 1 specimens reveals a translucent to opaque pyrite crust, one of which seems to be empty.

6 Discussion

The section investigated belongs to the Alum Shale Formation, which was formed under dysoxic to anoxic conditions (Buchardt et al. 1997). Bituminous limestone nodules (orsten or stinkstones) are common throughout the entire formation (Buchardt et al. 1997).

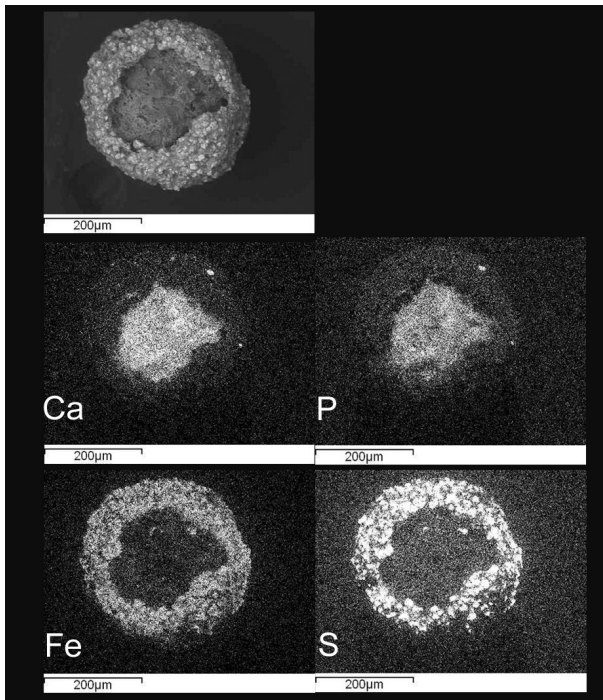


Fig. 14. Elemental mapping of a category 3 specimen from sample S08-05FT. Backscatter image and selected element maps. Relative amounts of an element is indicated by the brightness; the brighter the image the higher level of a certain element.

The sampled limestone is not part of a major, laterally continuous limestone bed, and is not typical for a stinkstone either. It might be a limestone bed with local lateral extension. The Alum shales also contain horizons of pyrite concretions and phosphorite nodules revealing that conditions for phosphatisation and/or pyritisation of organic matter were present. The samples at hand contain pure euhedral pyrite crystals and aggregates, which could indicate euxinic environments in the sediments, i.e., H_2S is present everywhere in the bottom waters (Flügel 2010). The euhedral appearance also indicates that the formation of pyrite was a slow process.

From the microscopic (optical and SEM) investigations at least three different morphological types of spherical particles can be identified. The category 1 specimens (Fig. 13A) with a pyrite crust probably contain a black core like the category 3 specimens (Fig. 13B-C). At least one of the type 1 specimens investigated in thin section contains a core. The pyrite crystals in the crust are mostly large and euhedral, however, it is difficult to decide if the crust also contains smaller framboidal crystals. At first glimpse it appears that the primary spherules are black specimens that subsequently have been enclosed in a crust of pyrite. Reworking of the sediments has later resulted in the different morphological types. However, there is also the possibility that the different morphological types have formed independently of each other. There are some possible different origins for the spherules:

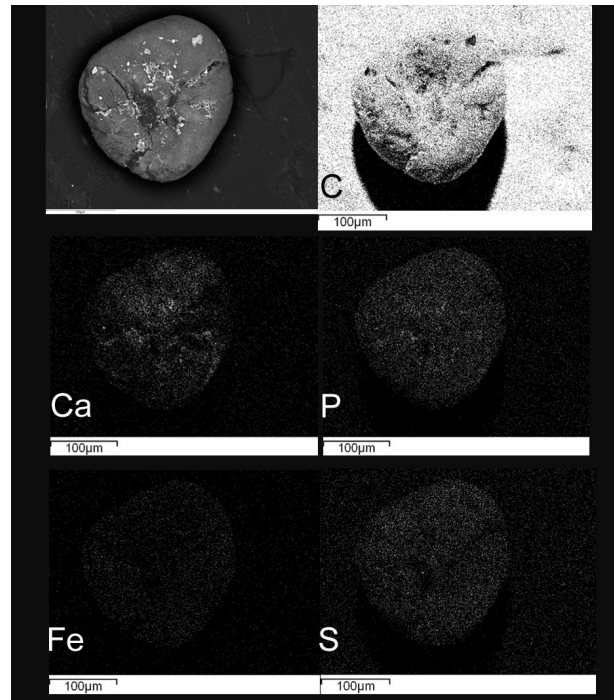


Fig. 15. Elemental mapping of a category 2a specimen from sample S08-05FT. Backscatter image and selected element maps. Relative amounts of an element is indicated by the brightness; the brighter the image the higher level of a certain element.

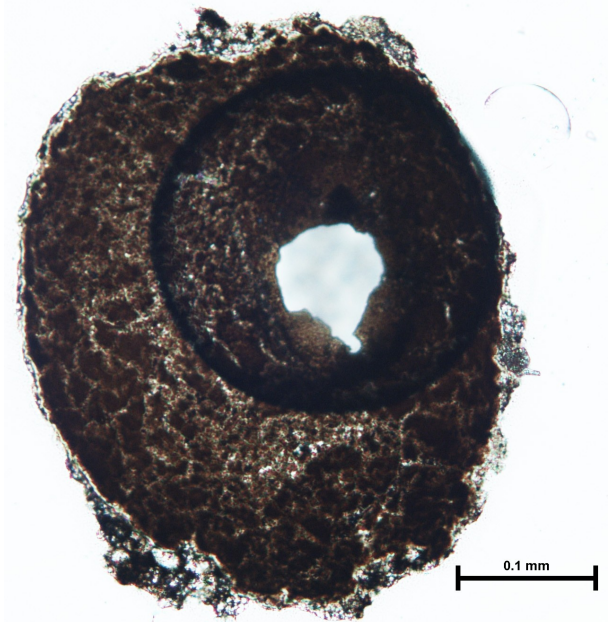


Fig. 16. Thin section of a morphotype 2 particle from sample S08-05FT. The darker ring is an air bubble.

- Chemical
 - Ooids
 - Peloids
- Biological
 - Eggs and embryos
 - Fecal pellets

Phosphate grains can form in situ in the “zone of phosphogenesis” in the upper 5-20 cm of the sediment (Pufahl & Grimm 2003). Usually such grains have concentric laminae and therefore belong to ooids although massive grains (peloids) also occur. The high pore water concentration of phosphate in the sediment needed for precipitation, originates from the microbial degradation of sedimentary organic matter as described in section 3.2. At the Cambrian-Ordovician transition upwelling water on the western parts of Baltica provided a supply of nutrients that resulted in high primary productivity with subsequent organic-rich sediments (Ilyin 1998). Further increased organic matter production and sedimentation may shift redox interfaces upwards in the sediment through the zone of phosphogenesis and instead pyrite can precipitate and form a lamina around the apatite core. These processes can be repeated and result in ooids with concentric laminae of apatite and pyrite (Pufahl & Grimm 2003). Theoretically an apatite core with a single pyrite layer would be possible if the process halts after the first pyrite layer is formed.

If an embryo or a fecal pellet has become buried in the sediment close to the sediment/water interface, microbial degradation of tissues in the embryo or organic matter in the fecal pellet can produce phosphate and together with the phosphate in the pore water induce formation of the apatite core. Subsequent pyrite precipitation on the core surface may then take place as a result of high H₂S concentrations in the sediment close to the core (from decaying organic material and from still ongoing processes in the core) plus sufficient concentrations of reactive Fe in the sediment.

The smooth black specimens which are rich in carbon (at least on the surface) could have resulted from a halted decay with residual tissue and/or degradative bacteria degrading through pressure/heat leaving a carbon film (Allison & Briggs 1991). Alternatively, this type of specimens could represent an organism with some type of recalcitrant envelope that has degraded to a carbon film (Allison & Briggs 1991; Briggs 2003).

The yield of microspherules decreases downwards in the limestone bed (Table 2; Fig 6). Samples S08-01FT to S08-05FF contain specimens in abundance, whereas samples S08-07FT to S08-15FT are practically devoid of such. This could either mean that there was no deposition of spherules in the earlier sediments or, more likely, that the preservation potential subsequently changed. The presence of pyrite in all samples indicates anoxic environment and also conditions suitable for microbial phosphate formation. However, phosphatisation requires, besides sufficient supply of phosphate, also a low pH, supply of fluoride and absence of magnesium ions. If any of these conditions is not fulfilled, apatite formation will not take place.

Is it possible to draw any conclusions regarding the nature and affinity of the microspherules from the limestone bed at Södra Sandby? Phosphate ooids can

be excluded since concentric layers are not observed in the specimens. Phosphate peloids or grains are usually spherical (0.1-0.5 mm) and homogeneous without internal structure (Flügel 2010), which is in accordance with some of the black rough specimens.

Fecal pellets are usually also homogeneous without internal structure but with a more rod-shaped form, size <100 µm to mm (Flügel 2010). The observed specimens are not rod-shaped, but it cannot be excluded that some of the type 2 specimens have a fecal origin, particularly since the vast majority of coprolites are phosphatic. A fecal pellet can have undergone both phosphatisation and carbonisation.

Eggs and embryos from the same oviparous species are relatively uniform in size and shape (Steiner et al. 2004). Embryos can, however, have variable morphology depending on development stage. Depending on the taphonomy, fossilised embryos can have an internal structure or be homogenous. It appears as the degree of phosphatisation was reduced from the earliest found embryos, which often were solid spherules of apatite, to embryos with only the margin preserved in phosphate in late Cambrian and Early Ordovician (Donoghue & Dong 2005). The type 2 specimens share many features with previously described embryos. The specimen in Fig. 13D can be interpreted as a two- or four-stage embryo similar to a two-cell embryo of *Pseudoooides* (see Steiner et al. 2004, fig. 2B) or a two-cell stage of *Olivoooides* (see Pyle et al. 2006, fig. 2:6). The specimens in Fig. 13E-F and H-J could be coiled embryos, e.g. compare Fig. 13J with the fossil embryo of *Markuelia* of similar size in Fig. 9. The specimen in Fig. 13G shows a 120° division similar to a four-cell stage of *Parapandorina raphospissa* (see Xiao & Knoll 2000, fig. 7:4). The specimen in Fig. 13K seems to have been an envelope around a core. The size of the particles is also in the range observed for eggs and embryos, 150-400 µm. What speaks against this interpretation is the great variation in shape; there are not two identical specimens, which could indicate a random process. However, it could also indicate that the type 2 specimens represent embryos from several different groups of animals.

If the type 2 specimens are fossil embryos it would add Baltica to the palaeocontinents where fossil embryos have been found. The specimens from Södra Sandby are roughly of the same age as the *Markuelia* embryos from the Vinini Formation in Nevada, USA (Donoghue et al. 2006b). A difference compared to other embryo-yielding localities is that the Baltica locality represents temperate water at 50°S, while all other localities are within ±30° from the equator (except for South China in the Ediacaran).

7 Conclusions

The spherules found in the limestone bed from the *Rhabdinopora flabelliforme parabola* Zone in Södra Sandby are probably of different origin and may include:

- Phosphate peloids or grains that have formed through a chemical process and subsequently coated by pyrite
- Fecal pellets that have undergone phosphatisation and possibly carbonisation and pyritisation
- Embryos that have undergone phosphatisation, carbonisation and possibly pyritisation

For better securing the nature of the type 2 specimens, further investigations are necessary. The interior of the smooth specimens should be investigated for structures, either by expanding the number of thin sections or by using non-destructive techniques like synchrotron X-ray tomographic microscopy. Only 6 specimens were prepared for thin section and two of these showed internal heterogeneity. The interpretation of these internal structures is ambiguous. However, together with the outer morphology and comparisons with previous studies, they suggest a metazoan embryo origin.

8 Acknowledgements

First of all thanks to Mats Eriksson for suggesting and introducing me to the subject and for showing a genuine interest in the development of the project, including providing material and instruments, running SEM and for meticulous proofreading. Also thanks to Fredrik Terfelt for introduction to thin section techniques and for many suggestions and comments. Thanks also to Anders Lindahl, Johan Lindgren and Anders Lindh for help with microscopes and SEM.

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