Research paper

# The 'Orsten'—More than a Cambrian Konservat-Lagerstätte yielding exceptional preservation

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## Abstract

In several areas of southern Sweden, limestone nodules, locally called Orsten occur within bituminous alum shales. These shales and nodules were deposited under dysoxic conditions at the bottom of what was most likely a shallow sea during the late Middle to Upper Cambrian (ca. 500 million years ago). Subsequently, the name 'Orsten' has been referred to particular, mainly arthropod, fossils from such nodules, and, in a wider sense, to the specific type of preservation of minute fossil through secondarily phosphatization. This preservation is exceptional in yielding uncompacted and diagenetically undeformed three-dimensional fossils. 'Orsten'-type preservation resulted from incrustation of a thin external layer and also by impregnation by calcium phosphate and, therefore, mineralization of the surface of the former animals during early diagenesis. Primarily, this type of preservation seems to have affected only cuticle-bearing metazoans such as cycloneuralian nemathelminths and arthropods. 'Orsten' preservation in this sense seems to be limited by size, in having yielded no partial or complete animals larger than 2 mm. On the other end of the scale, even larvae 100 μm long are preserved, often more complete than larger specimens, and details such as setules and pores smaller than 1 μm can be observed. Fossils preserved in such a manner are almost exclusively hollow carcasses, but can be filled secondarily; less common are completely phosphatized compact specimens. The high quality of preservation makes the Swedish 'Orsten' a typical Konservat-Lagerstätte. Yet, its special type of preservation is more widespread in time and geographical distribution than assumed initially, and the origin of the phosphate is not necessarily restricted just to one source. Subsequent to the first discoveries of limb fragments of Cambrian arthropods in 1975, animals in this special preservational type have been discovered in several continents and across a broad stratigraphic range including even Proterozoic strata. The latter have yielded early cleavage and metazoan embryonic stages, expanding knowledge on the preservational capacities of the 'Orsten'. Here, we report the recent status of our research on the

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'Orsten' and give perspectives for future exploration on a worldwide scale, particularly in light of a recently formed international research group named Center of Orsten Research and Exploration (C.O.R.E.).

## 1. Introduction

Investigation of late Cambrian (Furongian) limestone nodules from southern Sweden in the course of work on Scandinavian conodont faunas yielded unexpected discoveries of phosphatized bivalved arthropods by one of the authors (Müller, 1964). One of the species was named *Hesslandona necopina* Müller, 1964, translated as 'the unexpected' accordingly. These first finds did not include fossils with soft-part preservation of ventral body details such as appendages and other cuticular structures. In 1975, etching of subsequently collected material yielded an exceptional three-dimensionally preserved assemblage of 0.1–2 mm sized, secondarily phosphatized arthropod microfossils (Müller, 1979a,b). These activities resulted in a long-term research project with particular emphasis on arthropod fossils in the Swedish material ('Orsten' s. str.; see e.g., Müller, 1982, 1983; Müller and Walossek, 1985; Maas et al., 2003; Waloszek, 2003a,b, for recent summaries). More fossils with this exceptional type of preservation have been discovered in other areas such as Australia, Canada, China, Europe and Russia, and from different geological periods ('Orsten' s.l.; Fig. 1). The discovery of ostracodes and parasitic copepods on fish carcasses (the probable source of phosphate, see below) from the Lower Cretaceous (Bate, 1972; Cressey and Patterson, 1973; Cressey and Boxshall, 1989; Fig. 1) even predate the first Cambrian finds, which represent the bulk of evidence of this preservational type. The range of early Palaeozoic discoveries of 'Orsten'-type fossils extends currently from the upper Lower Cambrian to the Lower Ordovician (Fig. 2).
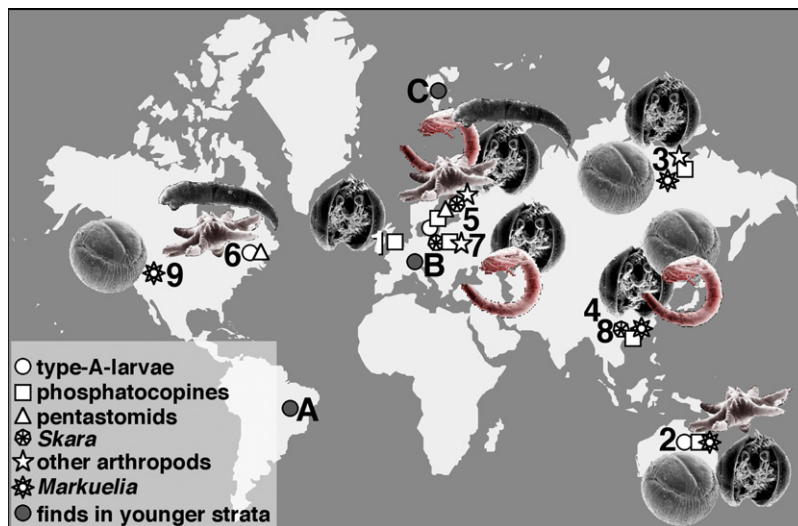


Fig. 1. Occurrences of secondarily phosphatized bilaterian microfossils. Type-A larvae are the oldest eucrustacean nauplii known so far; phosphatocopines are bivalved crustaceans; pentastomids are parasitic, potential stem-lineage derivatives of the Arthropoda s. str. (see Walossek et al., 1994; Maas and Waloszek, 2001); *Skara* is a eucrustacean known from two species; "other arthropods" includes stem arthropods, such as a lobopodian and a tardigrade, and euarthropds such as a pycnogonid chelicerate (Waloszek and Dunlop, 2002), an agnostid (Müller and Walossek, 1987) and various crustaceans (e.g., Müller, 1983; Walossek and Müller, 1990); *Markuelia* = *Markuelia secunda* Val'kov, 1987, is a small scalidophoran nemathelminth worm known from embryonic stages (Bengtson and Yue, 1997; Dong et al., 2004; Donoghue et al., 2006a). Lower Cambrian: (1) Comley, UK (cf. Siveter et al., 2001, 2003; the oldest record so far of Crustacea). Middle Cambrian: (2) Georgina Basin, Australia (cf. Walossek et al., 1993). (3) Siberia, Russia (cf. Müller et al., 1995). (4) Hunan, China (cf. Dong et al., 2005a,b). Uppermost Middle Cambrian to lowermost Ordovician: (5) Sweden (see text). (6) Newfoundland (e.g., Roy and Fåhræus, 1989; Walossek et al., 1994); (7) Poland (cf. Walossek and Szaniawski, 1991; see text); (8) Hunan, China (cf. Dong et al., 2005a,b). Lower Ordovician: (9) Nevada, USA (Donoghue et al., 2006a). Filled circles = 'Orsten'-type preservation in younger localities: (A) Santana Formation, Lower Cretaceous (cf. Bate, 1972; Smith, 2000); (B) Carnic alps, Upper Devonian (cf. Müller, 1979b); (C) Spitzbergen, Triassic (cf. Weitschat, 1983).
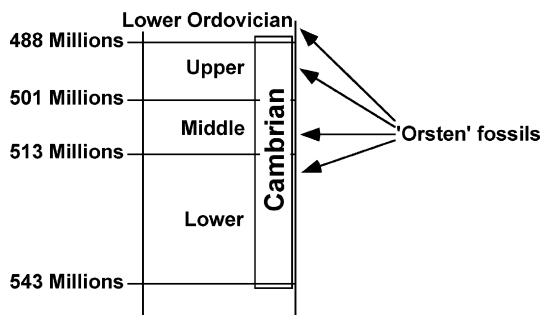
Fig. 2. Stratigraphic range of early Palaeozoic 'Orsten'-type occurrences. Cambrian subdivisions are in the traditional sense; for newer global chronostratigraphic equivalents, see Peng et al. (2006).

Our initial, rather individual co-operation with colleagues in the fields of geology, palaeontology and zoology has led to the establishment of a loose group of researchers with a common interest in the 'Orsten', dubbed Center of 'Orsten' Research and Exploration (C.O.R.E.). The group includes now 20 colleagues from six countries and aims to investigate new finds and localities, and questions of preservation and taphonomy. Herein, we present a review of the current state of our knowledge of the 'Orsten' and its special preservational type, address open questions, and point to perspectives for future work.

## 2. 'Orsten'-type preservation and taphonomic problems

### 2.1. 'Orsten' type of preservation

The term 'Orsten'-type preservation refers to an early, three-dimensionally stabilizing preservation of soft-integument and soft-part structures by calcium phosphate (apatite). 'Orsten' fossils were originally found in nodules of bitumen-rich limestone associated with organic-rich, pyrite-bearing shales in several parts of Sweden (e.g., Müller, 1979a,b). The nodules (Fig. 3A) formed during early diagenesis and certainly prior to compaction and hence, the surrounding shales and limestones often show compaction-related distortion. This

setting is crucial to the understanding of the context within which the fossils were formed and has led to experimental attempts to simulate the 'Orsten' fossilization process (Briggs and Kear, 1993; Briggs et al., 1993).

It is not yet completely resolved how far mineralization by phosphate is exclusively an incrustation or to what extent penetrative impregnation by phosphate has played a role in the Swedish 'Orsten' and other Lagerstätten of that kind. In fact, depending on the locality, age and type of lagerstätte, the relative influence of incrustation versus impregnation seems to vary considerably. The fossil embryos from the Neoproterozoic Doushantuo Formation of South China (approximately 550 million years; Xiao and Knoll, 2000; Donoghue and Dong, 2006) as an example are, unlike the Swedish 'Orsten' fossils, invariably preserved fully impregnated by phosphate. They are hollow in cases of obvious secondary diagenetic alteration (S. Dornbos, comm., 2006). That stresses that phosphate impregnation of soft parts and even cellular and subcellular structures was surely as important, if not more so, than in the 'Orsten' nodules from Sweden.

Concerning 'Orsten' s. str. fossils, phosphatic preservation has hitherto exclusively been found in layers or concretions of bituminous limestone (stinkstone, 'Orsten' that lack any phosphate apart from those in the fossils; Müller, 1985). Braun (2001) and Braun and Wilde (2001) demonstrated that early phosphatization is not necessarily restricted to carbonate rocks, but may also affect fossil preservation in clay-rich and siliceous sedimentary rocks. It is not yet possible to give a substantiated estimate of the timing of phosphatization. 'Orsten' preservation in the Swedish uppermost Middle to Upper Cambrian apparently affected the cuticle above the epidermis only of particular animal groups, but not where the outermost part of the exoskeleton consists of chitin (Figs. 3–6). This is most apparent in the fact that even detailed structures are preserved on the surface, for example of crustaceans, and these are epicuticular (epicuticle, the outermost cuticular layer, does not contain chitin but is made mainly of lipoproteins). Examples of

Fig. 3. Secondary phosphatization of the 'Orsten' type and preservational aspects. (A) 'Orsten' nodule of about 80 cm in length embedded within alum shales, quarry near Falköping, Västergötland, Sweden (from Waloszek, 2003b). (B) Late larva of the phosphatocopine *Falites fala* Müller, 1964 (st 929, UB W 268, sample 975; Zone 5, Upper Cambrian, Stenåsen, Falbygden, Västergötland, Sweden). Part of body and inner lamella of left side preserved, other parts largely decomposed. (C) Detail of the anterior ventral shield of B. Dorsal and ventral cuticle, the doublure broken off (sharp-edged fracture) exposing the void between the cuticles. Arrow: phosphate layer having overgrown the surface. (D) Feathered sensillum on the distal podomere of a trunk limb of the stem crustacean *Dala peilertae* Müller, 1983 as an example of preservation of delicate surface details (st 2090, UB W 269, sample 6393; Zone 5, Upper Cambrian, Falbygden, between Haggården and Marieberg, Kinnekulle, Västergötland, Sweden). (E) Double row of secondary setules on a trunk-limb seta of a specimen of *Hesslandona unisulcata* Müller, 1982 (st 2216, UB W 273, sample 6409; *Agnostus pisiformis* Zone, Gum, Kinnekulle, Västergötland, Sweden). (F and G) Trunk fragment of the stem-lineage crustacean *Goticaris longispinosa* in lateroventral view (F) and turned around (G) to view into the hollow body (body diameter approximately 200 μm; st 4970, UB W 270, sample 6763; *A. pisiformis* Zone, Gum, Kinnekulle, Västergötland, Sweden).

preserved structures are the soft inner lamella within the shields of phosphatocopines (Fig. 3B) and intersegmental membranes or membranes around mouth and anal openings, even with tiny folds still present, fine denti-cles on the surface of sternal bars between appendages (sternites), eye lobes in various taxa, sensilla nesting in tiny pores (Fig. 3D), or setules on setae that are less than half a micron thick (Fig. 3E).
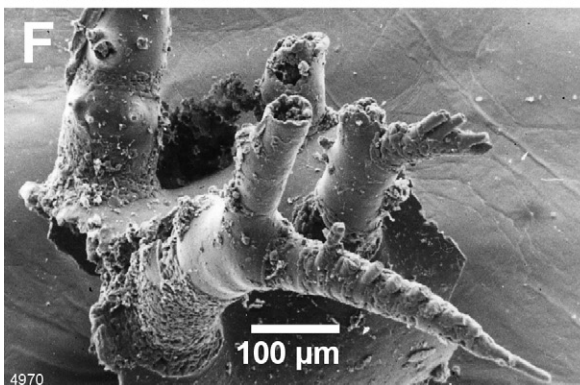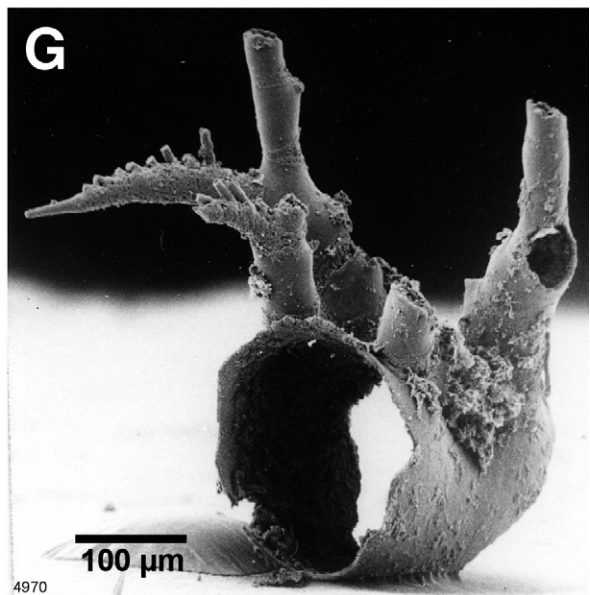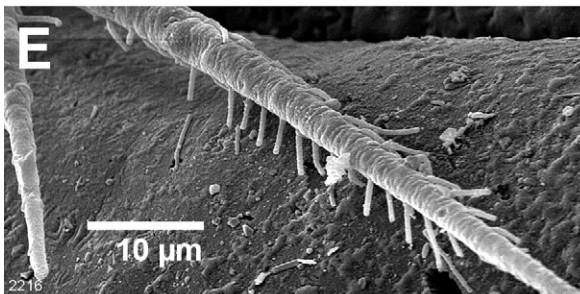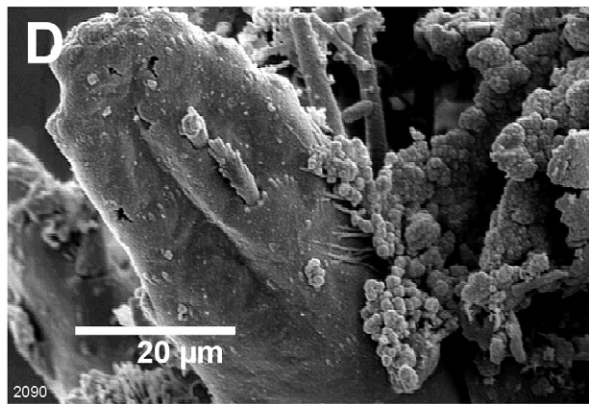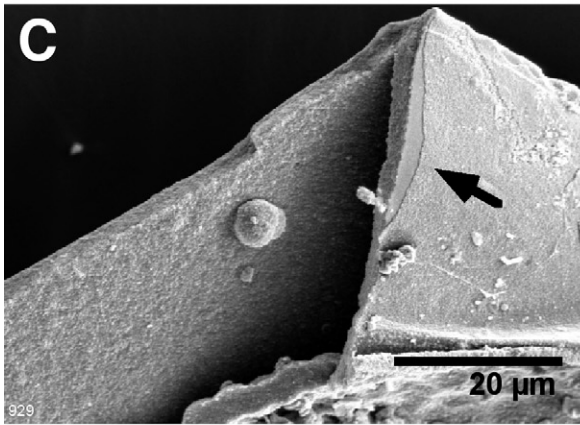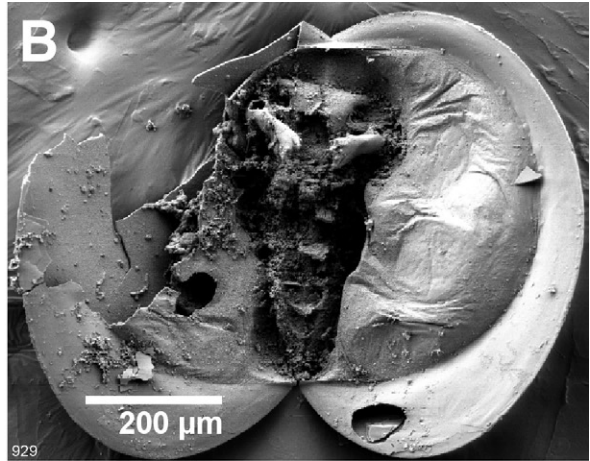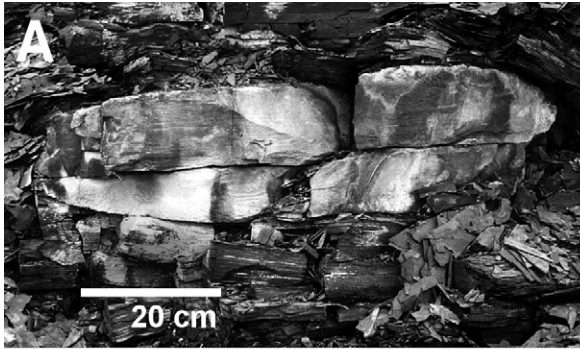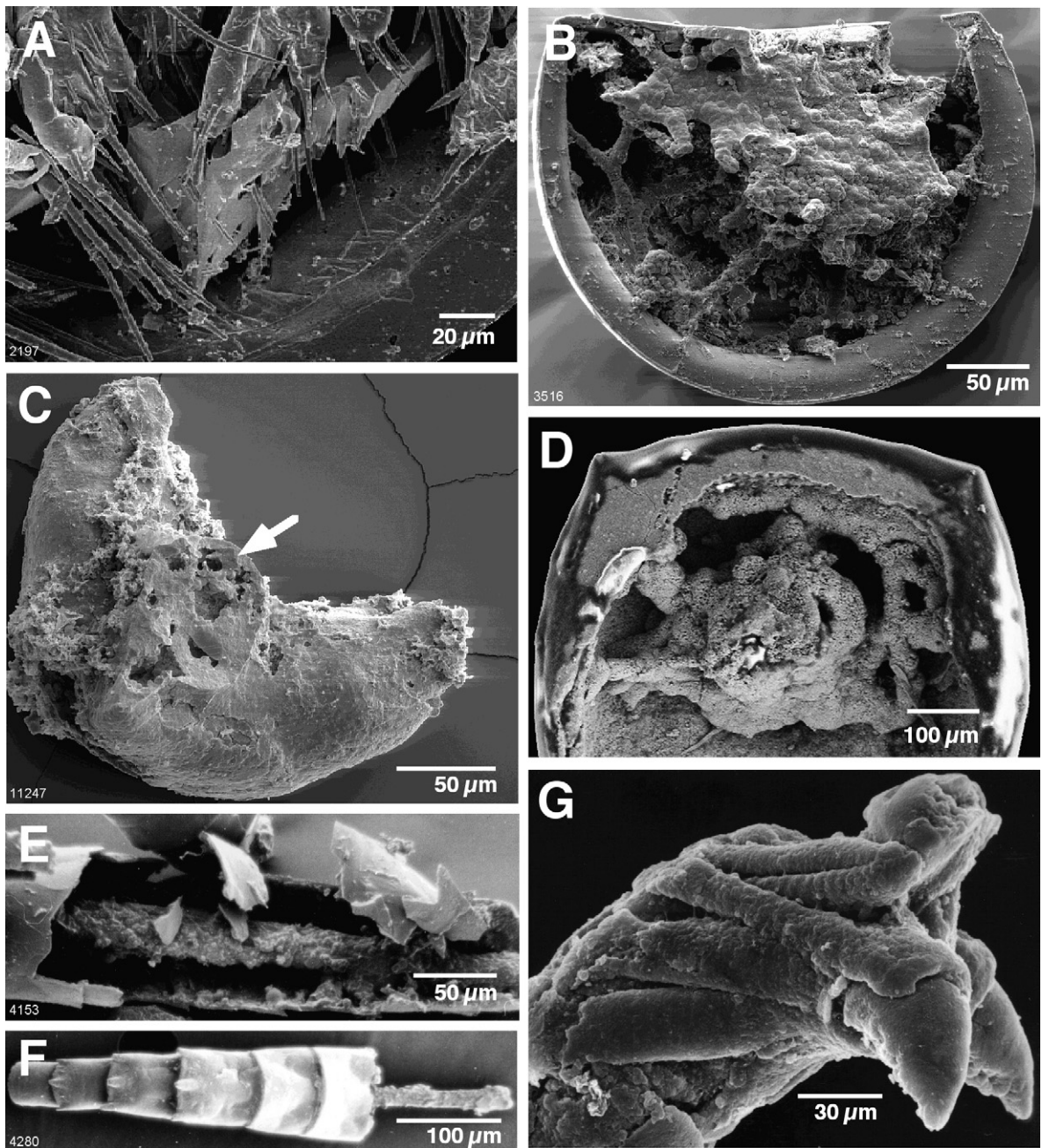
Fig. 4. Preservational aspects. (A) A crystal in the shield space of a specimen of *Hesslandona unisulcata* Müller, 1982, with setae passing through it (st 2197, UB 658, from Müller, 1982, pl. 1, Fig. 1a–d; Müller and Walossek, 1991, Fig. 1; Maas et al., 2003, pl. 7A; *Agnostus pisiformis* Zone, Gum, Kinnekulle, Västergötland, Sweden). (B) Shield valve of another *Hesslandona unisulcata* specimen filled with coarsely phosphatized strands (st 3516, UB W 151, sample 6404; from Maas et al., 2003, pl. 4F; *A. pisiformis* Zone, W Kestad, between Haggården und Marieberg, Kinnekulle, Västergötland, Sweden). (C) Head of a specimen of a hammer-headed larval pentastomid (st 11247, UB W 271; Upper Cambrian/Lower Ordovician of Kinnekulle area, Västergötland, Sweden) from posterior. Arrow: breakage zone of the trunk, with most of the internal space filled by amorphous phosphatic matter. (D) Head of *Proagnostus bulbus* Butts, 1926 with coarse matter roughly indicating the location of hypostome and appendages (repository number GMPKU2203; *P. bulbus* Zone, GSSP Paibi Section, Huayuan, Hunan, China; see also Babcock et al., 2005b, Fig. 1C). (E) *Skara anulata* Müller, 1983 showing possibly shrunken body mass with gut appearance (st 4153, UB 721, sample 6759; *A. pisiformis* Zone, Gum, Kinnekulle, Västergötland, Sweden; from Müller and Walossek, 1985, pl. 17:3). (F) Same structure in a specimen of *S. minuta* Müller and Walossek, 1985 (st 4280, UB W 272, sample 6763; *A. pisiformis* Zone, Gum, Kinnekulle, Västergötland, Sweden). (G) Muscle tissue preserved in a possibly immature pentastomid specimen (by kind permission of D. Andres, Berlin) from the Isle of Öland, Sweden (Andres, 1989, pl. 2:4–8).
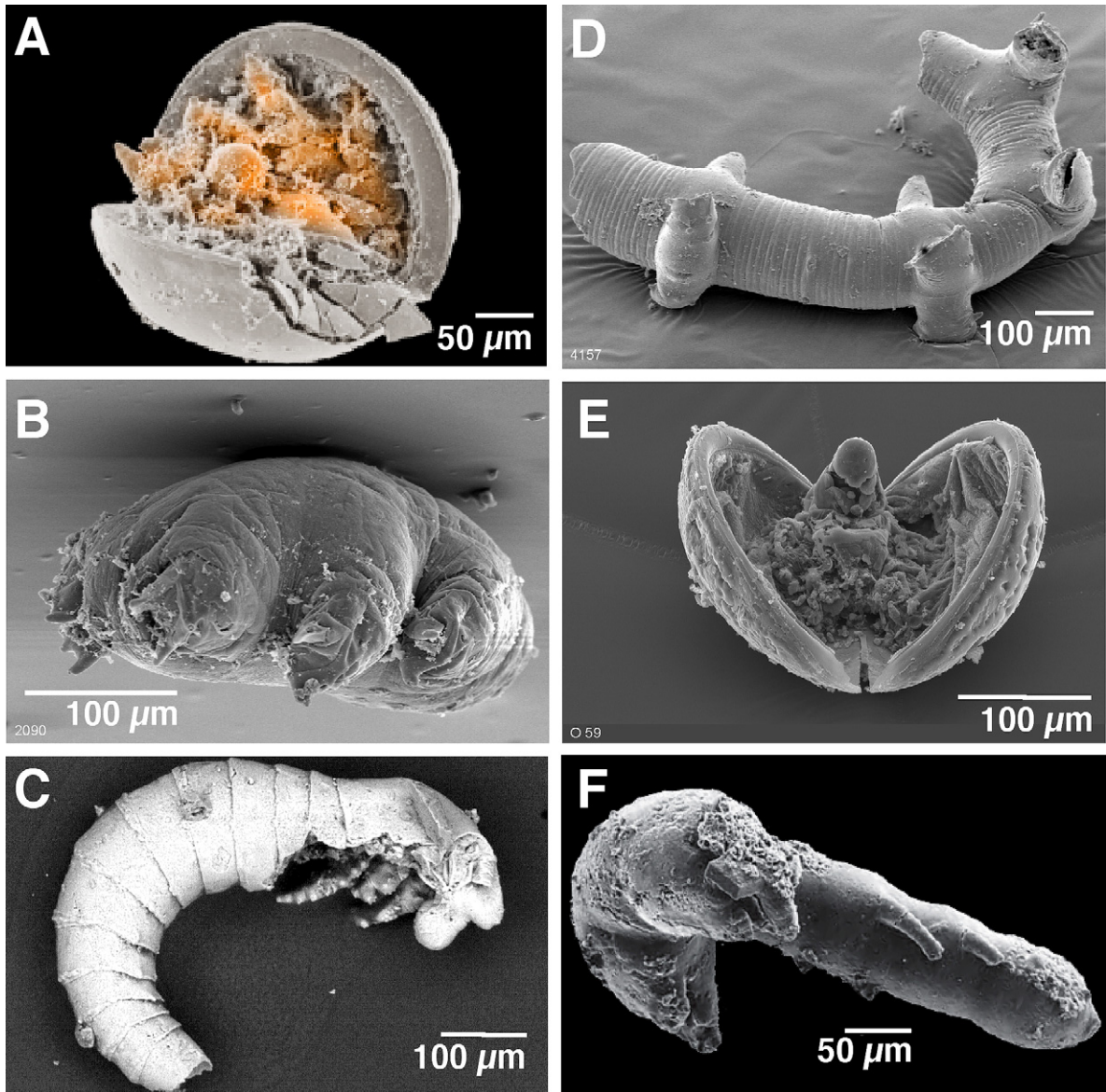
Fig. 5. Taxa demonstrating the taxonomic and geographical range of 'Orsten'-type fossils. (A) Phosphatocopine crustacean *Klausmuelleria salopensis* Siveter, Waloszek and Williams, 2003 (Repository number OUM A.2209; *Protolenus* limestone, Lower Cambrian, Comley, UK; from Siveter et al., 2003, pl. 1:3). (B) Hitherto undescribed tardigrade stem arthropod from the Middle Cambrian, Siberia, Russia (st 9892, UB W 266, sample 7677; Middle Cambrian Kuonamka Formation, Olenek Uplift, West Siberia, Russia). (C) Eucrustacean *Skara* sp. (Upper Cambrian, western Hunan, China; from Dong et al., 2005b, Fig. 4). (D) Hitherto undescribed lobopodian stem arthropod from the Upper Cambrian, Västergötland, Sweden (st 4157, UB W 126, sample 6760; *Agnostus pisiformis* Zone, Gum, Kinnekulle, Västergötland, Sweden; cf. Maas and Waloszek, 2001; Waloszek, 2003b). (E) Phosphatocopine crustacean *Hesslandona* sp. from the Upper Cambrian, Poland (st 59; Upper Cambrian, Debki-2 borehole, northern Poland; EO material). (F) Pentastomid stem arthropod *Heymonsicambria taylori* Walossek, Repetski et Müller, 1994 (GSC 106257; Green Point Formation at Green Point, western Newfoundland, Canada; from Walossek et al., 1994, pl. 1).

Secondary overgrowth by phosphate layers may also occur. This resulted in fine layers on top of the original cuticular surface, as, for example, seen on the shields of phosphatocopines. The layers may partly be peeled off, possibly during the preparation process (arrowed in Fig. 3C). Overgrowth may also result in a thickening of structures, such as in setae on limbs of specimens of the Upper Cambrian eucrustacean *Skara annulata* Müller, 1983 (Müller and Walossek, 1985, pl. 15:1). Contamination and overgrowth of the surfaces by different crystals, phosphate or calcite, results in coarse granules attached to the surface, fine ridges, rectangular
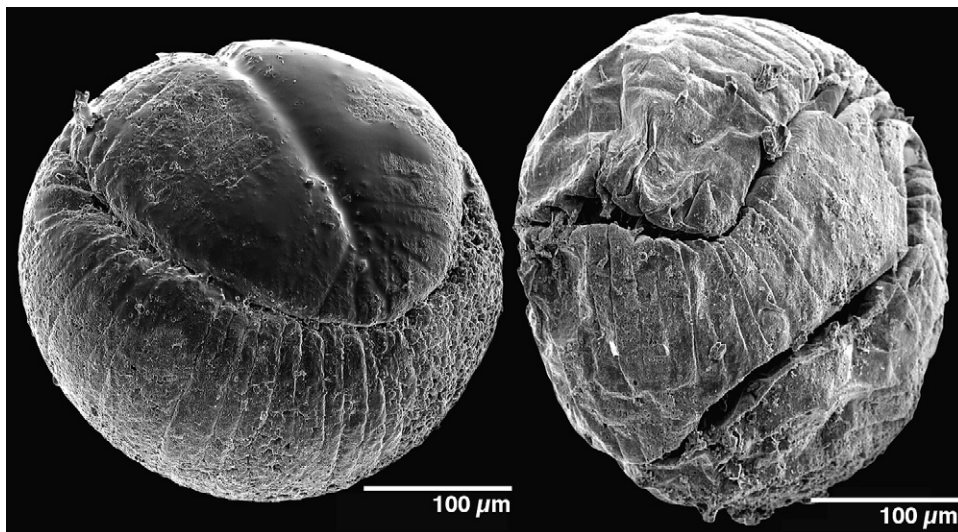
Fig. 6. Enrolled embryo of the cycloneuralian nemathelminth *Markuelia* sp. from the Middle Cambrian, Australia (courtesy "BMR" Australia). Egg shell missing. (A) Specimen (st 9260, UB W 132, sample 7313; Middle Cambrian Monastery Formation, N Rogers Ridge, Georgina Basin, Australia) displaying the curved trunk part. (B) Specimen (st 9261, UB W 133, sample 7313; stratigraphy as in A) displaying head (h) and tail end with curved spines (t), seen next to each other but in reverse position (Donoghue et al., 2006a).

holes or even huge blocks of crystals with setae passing through them (Fig. 4A). Sometimes differences in thickness/softness can be recognized when structures like joint membranes are incompletely phosphatized, while firmer parts of the cuticle are smoothly preserved, as in the appendages of *Goticaris longispinosa* Walossek et Müller, 1990 (Fig. 3F and G).

Most of the 'Orsten' specimens are hollow carcasses (Fig. 3F and G). This suggests that a kind of limited incrustation is more likely the dominant mode of preservation. Less common, but not exclusively for the parasitic pentastomids (Figs. 4C, G and 5F), are solid specimens; although we cannot validate if this is a complete filling of the specimens or a complete impregnation into the centre of the body (arrow in Fig. 4C). A few specimens of *Skara minuta* Müller et Walossek, 1985 also show this kind of preservation (Müller and Walossek, 1985, pl. 9:4). The void in hollow specimens can be filled with phosphatic crystalline matter, but this is difficult to interpret. For example, we have found structures that may be strands of organic origin in shields of phosphatocopine crustaceans and agnostoids in Swedish and also Chinese material (Fig. 4B and D). These may perhaps be bacterially-mediated phosphatized remnants of strands of soft tissue (Babcock et al., 2005a). Their irregularity in appearance may be caused by the crystallization process, while the regularity in topology of the phosphate may indicate that internal matter has accumulated at particular places and caused phosphatic crystallization to occur along this same matter. Such coarse, bubble-

like matter also occurs, for example in the hypostome of *Agnostus pisiformis* Wahlenberg, 1818 (Fig. 4D; see also Wilmot, 1990), while strands run toward the shield margin roughly matching the position of the appendages there. They are probably only the internal, formerly fluid- and muscle filled space, and do not represent the cuticle. Similar phosphatic strands have been observed between elements in a fused cluster of conodont elements from the Ordovician (Lower Tremadocian) (Figs. 2.3 and 2.5 in Smith et al., 2005).

Gut preservation or preservation of matter in the centre of the trunk has been observed so far only in skaracarids (Fig. 4E and F). At least in some specimens, there are ridges corresponding to the trunk segments, but shrunken as if it was originally matter in a colloidal state that condensed in the course of diagenesis (Müller and Walossek, 1985, pl. 17:3, 4). Andres (1989) illustrated pentastomids partly lacking cuticle and, thus, with exposed muscle tissue. This is the only known example of unequivocally internal matter in 'Orsten'-type preservation. These muscle strands in the head region leading to the limb portions and in the trunk (four strands) preserve even the striations typical of cross-striated musculature (Fig. 4G).

## 2.2. Recovery of 'Orsten' fossils

'Orsten' fossils are usually recovered by careful sorting of a large residue that remains after etching kilogram-sized samples in dilute (approximately 10%) acetic

acid (K.J.M. preferred to crack the samples to pieces of walnut size). Fossils may also be recovered from the limestone using weak formic acid. Buffering may also be applied to ensure that the calcium phosphate remains insoluble. This is achieved by introducing calcium acetate, either by seeding the reaction with about 20 g of limestone, synthetic calcium carbonate, or in the case of formic acid, a cocktail of calcium carbonate and tricalcium diphosphate (Müller, 1985; Jeppsson and Anehus, 1995; Jeppsson et al., 1999). Separation and concentration of well-preserved 'Orsten' fossils is a material- and time-consuming procedure. Weitschat and Guhl (1994) similarly applied dilute acid in the processing of their Lower Triassic material from Spitsbergen. In contrast to our "bulk maceration" technique, they etched single calcareous internal moulds of their ostracodes by repeatedly adding small drops of acid until the calcareous cement was dissolved and the phosphatic pieces remained. Using this careful technique, these authors were able to discover delicate symphoriont ciliates on parts of the extremities of phosphatized ostracodes.

### 2.3. Problems of taphonomy

Despite the generally good quality of preservation of 'Orsten'-type fossils and overall similarity of the fossil preservation and faunal content (Fig. 1), there seems to be no uniform taphonomic process that has led to the origin of 'Orsten'-type lagerstätten. Autochthonous phosphatization without subsequent displacement of phosphatized fossils occurred in the vicinity of decaying larger soft body material (near carcasses of bony fish or in the living chambers of cephalopods; see Bate, 1972; Weitschat, 1983). Such processes are known from Triassic and Lower Cretaceous material, but cannot yet be invoked for the lower Palaeozoic 'Orsten' of Sweden. Evidence of in situ phosphatization of sea-bottom layers, including their infaunal components, is also lacking. It may have occurred during an initial phase, but nothing like a complete life-community of the flocculent layer been discovered in the Alum Shale succession of the Swedish Cambrian. There is, however, evidence of a concentration of phosphatized fossils in particular layers of the sedimentary rock, possibly due to minor scale reworking and re-sedimentation. Concentration of phosphatic particles by water currents (winnowing) in the upper layers of the sediment or at the water–sediment interface may have played an important role in the origin of the typical 'Orsten' lagerstätten in Sweden. This has still to be demonstrated to be the case for other localities. Extensive winnowing, possibly

connected with reworking is likely to have occurred in the case of the lower Tremadocian material from Sweden, and possibly also in Newfoundland, where the fossils (pentastomids; Figs. 4G and 5F) occur as individual grains (mostly solid) in impure limestones that are quite rich in phosphatic microfossils (e.g., conodonts), many of which show evidence of physical abrasion and represent several faunal zones (Andres, 1989; Walossek et al., 1994; Waloszek et al., 2006).

Our current interpretation is that delicate preservation, at least in the hollow 'Orsten' fossils from the Upper Middle to Upper Cambrian of Sweden, must have taken place soon after death and without significant decay. Indeed, considering the high fidelity of preservation of structures by phosphate, most authors assumed a period of a few hours up to a few days after death for the process of post-mortem phosphatization to have taken place (e.g., Weitschat and Guhl, 1994). Yet, our preliminary decay experiments (A.M.; D.W.) have shown that it takes 1–2 weeks for the filtering limbs of water fleas to decompose completely, up to which time they conserve their shape and setal arrangement. This would exclude the possibility of rapid decay by bacterial action (in contrast to the internal body mass) and subsequent transformation into other substances such as in other types of preservation (for example in the Tertiary Konservat-Lagerstätte Messel; cf. Schmitz, 1992). Another indicator that impregnation occurred before decay is the peculiar cell-like surface patterning, possibly indicating the epidermal cells underneath the impregnated cuticle in a tiny, still unnamed lobopodian from the Upper Cambrian of Sweden (Fig. 5A). Briggs et al. (1993) demonstrated in their experimental studies that fine phosphatization still occurs after weeks or even months, provided that decay of soft parts and soft integument structures is inhibited. Briggs et al. (1993) also showed that it is not necessary to postulate a higher than normal phosphate content of the sediment pore water for phosphatization as long as only small bodies or small amounts of soft parts are present. For the process of mineralization by phosphate, the presence and activity of anaerobic bacteria seem to have played a major role. The presence of high concentrations of decaying organic matter is crucial to the process, promoting anoxia, which inhibits the activity of aerobic bacteria that would otherwise rapidly destroy the carcass of a dead organism (Briggs and Kear, 1994). Yet bacteria involved in the mineralization process do not seem to be replicated by phosphate in every case. Instead, they may biochemically induce phosphate mineralization; a process which is not necessarily associated with bacterial preservation. In principle, the meiofaunal fossils of the 'Orsten' s. str. may have been

preserved by such a bacterially-induced phosphatization, showing no traces of preservation of the bacteria themselves.

Decaying organic matter also leads to a reduction in pH which precludes the authigenic precipitation of calcium carbonate $CaCO_3$ by anaerobic bacteria, and calcium phosphate $Ca_2(PO_4)_2$ is produced preferentially (Briggs and Wilby, 1996). Thus, paradoxically, decay is a necessary element of preservation (Briggs, 1996), a factor that becomes increasingly important where organic matter is sparse within an environment. Within the microenvironment of decay and preservation (i.e. that immediately surrounding the carcass), pH levels eventually rise and $CaCO_3$ is precipitated in preference to $Ca_2(PO_4)_2$. It is during this stage that the limestone (nodules in the case of 'Orsten' s. str.) that entomb phosphatized organic tissues are precipitated, protecting and preserving the 'Orsten' fossils during compaction.

Not all 'Orsten'-type fossils have been found in nodules, as is the case in the material from Sweden. In fact, occurrences outside Sweden reveal aspects of taphonomy and preservation that differ from the original 'Orsten' material and, therefore, add significant new data to our knowledge of the taphonomy and origin of this type of preservation. It can be assumed that any limestone showing phosphatization, not only the "typical" 'Orsten'-type nodules, is a potential source for 'Orsten'-type fossils (Müller, 1979b). Phosphatization in non-calcareous sedimentary rocks may well prove to be a significant additional source for 'Orsten'-type preservation in the future (Braun, 2001, 2004; Braun and Wilde, 2001). Similar types of fossil preservation, but not necessarily resulting from the same type of preservational processes, are known from the Proterozoic, and Early Cambrian (embryonic stages; e.g., Chen et al., 2004), from the Triassic (Weitschat, 1983; Weitschat and Guhl, 1994, showing even preservation of stalked ciliates) and Lower Cretaceous rocks (e.g., Bate, 1972; Cressey and Boxshall, 1989; Smith, 2000). The fossilized embryos from the Ediacaran Doushantuo Formation at Weng'an (Xiao et al., 1998), and the Lower Cambrian Kuanchuanpu Formation at Shizhonggou (Bengtson and Yue, 1997; Yue and Bengtson, 1999; Chen et al., 2004; Steiner et al., 2004a,b), were recovered from coarse-grained dolomitic phosphorite (phosphate grains in a dolomitic matrix), although it is likely that they are reworked. Andres' (1989) material from the Lower Ordovician of the Isle of Öland, Sweden is likewise not from nodular limestone. The same is true for the Siberian and the Australian material from the Middle Cambrian, but still the facies of the Doushantuo fossils is remarkably different from that of 'Orsten' s. str. fossils.

The 'Orsten'-type fossils and *Markuelia* Val'kov, 1984, including all the figured specimens (Dong et al., 2004; Babcock et al., 2005a) from the Middle to Upper Cambrian (Furongian) of Hunan (entire Cambrian sequence approximately 2000 m thick), were recovered from dark grey, medium to thick-bedded micrite intercalated with dark grey, thin-bedded laminated, dolomitic calcisiltite, containing organic matter and scattered pyrite. Burrows and bioturbation may occur. A different mechanism may have been involved in the 'Orsten'-type and *Markuelia*-bearing rocks of Middle Cambrian age in Hunan. There, the fossils were recovered from dark grey, thin- to medium-bedded bio-microsparite. The environment is interpreted as a deeper water setting along the marginal areas of the Cambrian sea (Yangtze Platform). This facies is quite unlike the Upper Cambrian 'Orsten' s. str. in Sweden. Taphonomic processes, leading to 'Orsten'-type preservation in this deeper water environment have not yet been studied in detail.

## 3. Taxonomic range of the 'Orsten' fossils

Phosphatization is usually assumed to be selective in the size range of fossils preserved as well as in a taxonomical sense (e.g., Walossek, 1993; Waloszek, 2003b). So far, we have clear evidence only of specimens smaller than 1–2 mm. Records of secondarily phosphatized parts of animals preserved by phosphate larger than this are uncertain at best: Weitschat and Bandel (1991) described phosphatized organic components in the phragmocones of cephalopods from the Triassic of Spitsbergen. These are in the centimetre range, but it is unclear if this can be added to the type we are discussing here. Concerning arthropods, adult animals may be much larger, as, for example, phosphatocopines or agnostoids, both of which live inside an extended dorsal cuticle. Only specimens smaller than 1 mm are preserved. Furthermore, small specimens, mostly larvae, are usually better preserved the smaller they are. Our smallest animals are the type-A larvae with a body length of 100 μm (Fig. 1).

Besides ciliates (Weitschat and Guhl, 1994) – even smaller than our larvae – and embryonic stages showing putative affinities with various metazoan taxa (see below) we have a clear record of secondarily phosphatized organisms of only two metazoan groups: scalidophoran nemathelminths and the arthropods. Both taxa have a somewhat firm and layered cuticle, but it is important to stress again that chitin is not the trigger of phosphatization. The record of nemathelminths so far is limited to embryos of *Markuelia* species (see below and Donoghue et al., 2006a), a few (still unpub-

lished) loricae with striking resemblance to those of the larval Recent priapulid *Tubiluchus corallicola* van der Land, 1968, and a single tiny tubular larva with an annulated anterior body part and a hairy posterior body part ending in a pair of short extensions (also taxonomically unpublished). Müller and Hinz-Schallreuter (1993) described 10 species of palaeoscolecids having 3d-phosphatic preservation. Several specimens of this material are thin but several millimetres long.

The record of described arthropods includes:

- Stem arthropods: A still undescribed lobopodian from the Upper Cambrian, Sweden, the smallest of its kind (Fig. 5B); a tardigrade (water bear) from the Middle Cambrian, Siberia (Fig. 5C); and several pentastomids from the uppermost Cambrian in Sweden, Cambro-Ordovician boundary beds in Newfoundland to the Lower Ordovician, Öland, Sweden (Fig. 5F); example taxa: *Aengapentastomum andresi* Waloszek, Repetski et Maas, 2006, *Heymonsicambria repetskii* Walossek et Müller, 1994, *Heymonsicambria taylori* Walossek, Repetski et Müller, 1994.
- Chelicerates: A small, early larva of a pycnogonid, *Cambropycnogon klausmuelleri* Waloszek et Dunlop, 2002.
- Agnostoids: Several successive larval stages of *A. pisiformis* from the traditionally termed lowermost zone of the Upper Cambrian Alum Shale succession, now top of the Middle Cambrian; one *Proagnostus* from the Cambrian of China.
- Stem crustaceans: Six taxa from the Upper Cambrian of Sweden and Poland; *Cambrocaris baltica* Walossek et Szaniawski, 1991, *Cambropachycope clarksoni* Walossek et Müller, 1990, *G. longispinosa* Walossek et Müller, 1990, *Henningsmoenicaris scutula* (Walossek and Müller, 1990), *Martinssonia elongata* Müller et Walossek, 1986, *Oelandocaris oelandica* Müller, 1983.
- Phosphatocopines: This is the most abundant group, with more than 50,000 specimens and about 15 species in the Swedish material, and with the longest record: from the Lower Cambrian of Comley, UK (*Klausmuelleria salopensis* Siveter, Waloszek et Williams, 2003; Fig. 5A); Middle Cambrian records are from China and Australia (empty carcasses also in the Siberian material); and the Upper Cambrian of Sweden, Poland and China (Fig. 5D); example taxa: *Falites fala* Müller, 1964, *H. necopina* Müller, 1964, *Hesslandona suecica* Maas, Waloszek et Müller, 2003, *Hesslandona unisulcata* Müller, 1982, *Vestrogothia spinata* Müller, 1964 (see Maas et al., 2003, for a comprehensive study of Phosphatocopina).

- Eucrustaceans: Six taxa have been described from the Swedish Upper Cambrian material so far: *Bredocaris admirabilis* Müller, 1983, *Dala peilertae* Müller, 1983, *Rehbachiella kinnekullensis* Müller, 1983, *Skara anulata* Müller, 1983, *Skara minuta* Müller et Walossek, 1985, *Walossekia quinquespinosa* Müller, 1983; skaracarids have also been recorded from Australia (Middle Cambrian), Poland and China (both Upper Cambrian; Fig. 5E).

The Swedish material is from two different zones of the alum shale sequence, with a gap of two biozones in between. The taxa are almost exclusive to very narrow stratigraphical windows, which helps greatly to discriminate the forms. Most species from Sweden and also from Poland (unpublished) occur in Zones 1 and 2 of the Upper Cambrian in the traditional sense. Zone 1 is the *A. pisiformis* Biozone, the latest Middle Cambrian according to the latest subdivision and global chronostratigraphic correlation of the Cambrian (Peng et al., 2004; Babcock et al., 2005b; Terfelt et al., 2005). Many fossils are known only from this single stratigraphical interval. *A. pisiformis* itself is present in rock-forming abundances in the Swedish Biozone 1 (Müller and Walossek, 1987; Waloszek, 2003b). Other taxa occur in Zone 2 in Sweden and Poland. The investigated material from Biozones 2 and 5 contains significantly fewer species, while no individuals have been found in Biozones 3, 4 and 6 of the Upper Cambrian succession in Sweden (cf. Maas et al., 2003; Furongian according to the global chronostratigraphic subdivision). Younger forms are fewer (only *D. peilertae* Müller, 1983 and *Bredocaris admirabilis* Müller, 1983 described so far) and all pentastomids are from this time period. Only type-A larvae – presumably true orthonauplii of unknown eucrustaceans – occur in both time intervals, and they have also been reported from the Middle Cambrian of Australia and the Lower Ordovician of Newfound (Fig. 1). Thus they are similarly widespread compared to skaracarids, but even longer ranging. The entire Swedish material totals approximately 1450 specimens "with soft parts" of non-phosphatocopine taxa and 2000 specimens of phosphatocopines. In all, of the estimated number of 90 nemathelminth and arthropod taxa in an 'Orsten'-type preservation (not counting the embryos), 65 are from Sweden. We have described only a fraction of the material so far, mainly, because most taxa are known only from one, or a few, often badly wrinkled and distorted fragments. Many isolated appendages, apparently from different arthropods await description. The 'Orsten' material also contains numerous phosphatized problematic fossils, many known as "small shelly

fossils" from many localities worldwide. Of these, the four species of the Cambrogeorginidae from the Middle Cambrian of Australia (Müller and Hinz, 1992) demonstrate soft-part preservation in the sense discussed here.

As noted above, animals preserved in an 'Orsten' type of preservation are rather small, even considering variation in the source of the phosphate. Accordingly, it is not surprising that many specimens comprise larval stages (examples: Fig. 5A, B, E and F). This holds true for the bulk of the material, but is not necessarily the case for all of them. In fact, several forms are, most likely miniature adults of typical meiofaunal forms (e.g., the eucrustacean Skara, Fig. 5C). Such animals – and this is our current model of at least the Swedish 'Orsten' faunal assemblages – lived on or in a soft-bottom environment, either temporarily or in a particular phase of their life cycle (cf. Müller and Waloszek, 1991). Recent meiofauna may show adaptations particularly to oxygen-depleted environments, which would explain its record in bituminous limestones indicative of dysoxic conditions at the time of formation. At least in the case of the Swedish record, the 'Orsten' trapped a particular meiofaunal biota and, therefore, provides us with an exceptional and so far unique window into the soft-bottom sea life of minute animals 500 million years ago.

Trilobites, an abundant group of euarthropods in the Cambrian and lower Palaeozoic in general, seemingly escaped soft-part preservation. Secondarily phosphatized olenid trilobites have been reported recently (Ahlberg et al., 2003, 2005), but in that case, only the calcified dorsal portions of the cuticle were replaced by phosphatic matter. So far, it is not clear why the ventral features of trilobites were not affected by phosphatization. Likewise, in *A. pisiformis*, a member of another taxon with a calcified dorsal cuticle – possibly more closely affiliated with Crustacea than Trilobita (Waloszek and Müller, 1990; Stein et al., 2005) – only the youngest stages, most likely without calcite in their cuticle (still), are preserved with cuticular details, both dorsally and ventrally. Adults are always preserved as "empty shells" (cf. Müller and Waloszek, 1987) and such shells virtually make up the limestone nodules of the relevant Biozone (e.g., Waloszek, 2003b, Fig. 2:1b). Furthermore, from other agnostids, sometimes as abundant in the rock as *A. pisiformis*, not a single trace of uncalcified cuticular parts is known. Cotton and Fortey (2005) and Bruton and Nakrem (2005) upheld the traditional view that agnostoids are trilobites and closely related to the equally small-sized eodiscids. The two author groups base their arguments exclusively on dorsal features, i.e. the tergites, and neglect the ventral body and appendage details completely, although this feature

is as specialized as in Crustacea already in the immature specimens of *A. pisiformis* (Müller and Waloszek, 1987; Stein et al., 2005). Particularly the 'Orsten' fossils have demonstrated and underlined the importance of soft-part details, especially limb morphology in arthropods, as phylogenetically relevant structures. The convergently developed bivalved shield in, for example, Phosphatocopina and Ostracoda clearly indicates that mere shield characters do not necessarily imply relationship (Maas and Waloszek, 2005).

## 4. 'Orsten' on a worldwide scale (also Fig. 5)

Discoveries of 'Orsten'-type fossils have now been recorded from all over the world (Fig. 1). Remarkably, they are all from the coastal areas of smaller continents arranged in a bow close to the equator at the beginning of the Cambrian period. Records from the coastal zones of the southern Gondwana continent are, so far, lacking. The current state of knowledge on the global occurrence of 'Orsten' s. str. fossils is given in Table 1.

## 5. Orsten-type preservation preserves embryos and cleavage stages

Perhaps the most exciting of recent palaeontological discoveries has been the recovery of fossilized embryos in a three-dimensional preservation of the 'Orsten' type (being phosphatized). These embryos are remarkable for three reasons:

 (i) the fact that structures so delicate and transient as embryos could be preserved at all;
 (ii) the greatest failing of the fossil record – an absence of embryological data – would be overcome; and
(iii) that this insight into embryology would be available for this critical period of metazoan diversification.

Despite an inauspicious beginning (Zhang and Pratt, 1994), convincing embryos have now been recovered from the Ediacaran (Xiao et al., 1998), Cambrian (Bengtson and Yue, 1997; Yue and Bengtson, 1999; Steiner et al., 2004a,b; Chen et al., 2004; Dong et al., 2004, 2005a,b; Donoghue and Dong, 2006) and Early Ordovician (Donoghue et al., 2006a), and from widespread geographical areas (Donoghue and Dong, 2006; Donoghue et al., 2006a). Embryos from the Ediacaran Doushantuo Formation are all at the cleavage stage, exhibiting up to several hundred blastomeres (Xiao et al., 1998; Xiao and Knoll, 2000; contrary to the popular view that they are limited to no more than the 16 cells—Conway Morris, 1998, 2004; see also Raff

Table 1
Current distribution of Orsten-type fossils

| Period | Locality | Example references |
| --- | --- | --- |
| Lower Cambrian | *Great Britain*: *Protolenus* Limestone, Comley area of Shropshire, UK; a few specimens of the phosphatocopine crustacean *Klausmuelleria salopensis*; representing, at the time of its description, the oldest known occurrence of a crustacean, an arthropod – and a metazoan in general – with its body and complement of limbs preserved in three dimensions. Thus, the 'Orsten'-type Konservat-Lagerstätte in Shropshire (Botomian to Toyonian in age) represents an early stratigraphical source for exceptionally well-preserved metazoan fossils. Contains also various other phosphatocopines and "small shelly fossils" | Siveter et al. (2001, 2003), Hinz (1987) |
| Middle Cambrian | *Australia*: Monastery Creek Phosphorite Fm., Gowers Fm., Inca Shale Fm., and Devoncourt Limestone Fm., Georgina Basin, western Queensland; contains: eucrustacean nauplii ("type-A" larvae, Fig. 1), phosphatocopines, isolated appendages, Small Shelly Fossils and Problematica, palaeoscolecids | Müller and Hinz (1992), Müller and Hinz-Schallreuter (1993), Walossek et al. (1993) |
| | *Russia*: Kuonamka Formation, Olenek-Uplift, West-Siberia; contains: smooth to strongly deformed shields of phosphatocopines (no soft parts), palaeoscolecids and other nemathelminths, small shelly fossils, and four specimens of a tardigrade (Fig. 5B) | Müller et al. (1995), Donoghue et al. (2006a) |
| | *China*: Wangcun section, Taoyuan County, western Hunan and Wa'ergang section, Huayuan County, western Hunan. Both sections yielded fossilized embryos, trilobites, brachiopods, small shelly fossils, sponge spicules and radiolarians | Dong et al. (2004, 2005b) |
| Upper Cambrian | *Sweden*: Zones 1–5 in different localities in Västergötland; larval stages of the rock-forming *Agnostus pisiformis*, a pycnogonid chelicerate larva, mainly crustaceans of different phylogenetic positions, stem-lineage derivatives of Crustacea, various phosphatocopines and a set of eucrustaceans with affinities to maxillopod and branchiopod entomostracans, few specimens of different species of pentastomids. Finds on the Isle of Öland, Zone 5, include phosphatocopines and a stem crustacean | For example, Müller (1979a, 1982, 1983), Müller and Walossek (1985), Walossek and Müller (1990, 1994), Maas et al. (2003), Stein et al. (2005) |
| | *Poland*: Zone 5, Hel Peninsula; a single specimen of the stem-lineage crustacean *Cambrocaris baltica*. The recent investigation of borehole samples from northern Poland has yielded a still unpublished number of phosphatocopines, ranging from Zones 1 to 5 (material of EO) | Walossek and Szaniawski (1991) |
| | *China*: Bitiao Formation, Wangcun section, Yongshun County, western Hunan; several specimens of *Markuelia hunanensis*; one unnamed specimen of a hesslandonid phosphatocopine and a specimen of *Skara* sp. sensu Dong et al. (2005); Wa'ergang and Paibi sections, Huayuan County; both sections yielded fossilized embryos, trilobites, brachiopods, small shelly fossils, sponge spicules and radiolarians | Dong et al. (2004, 2005b) |
| Lower Ordovician | *Sweden*: Isle of Öland; more than 1000 specimens of pentastomids and a few other arthropods, small shelly fossils, conodonts | Andres (1989) |
| | *Canada*: Middle-Arm Point Fm., Bay of Islands, western Newfoundland, "type-A" larvae; Green Point Fm. at Green Point, Newfoundland; single specimen of the pentastomid *Heymonsicambria taylori* | Roy and Fåhræus (1989), Walossek et al. (1994) |
| | *USA*: Nevada; specimens of the cycloneuralian nemathelminth *Markuelia secunda* | Donoghue et al. (2006a) |

et al., 2006, for taphonomy experiments and a discussion on the feasibility of these embryos). These fossils are remarkable for their preservation, but little more can be drawn from them because they are not found in association with later stages that might provide some evidence of their affinity. The Cambrian record is much richer, with a range of embryos such as *Olivooides multisulcatus* Qian, 1977, a putative scyphozoan cnidarian, and *Pseudooides prima* Qian, 1977, a possible arthropod, preserved from cleavage stages through to hatchlings (Bengtson and Yue, 1997; Yue and Bengtson, 1999; Steiner et al., 2004a,b; Chen et al., 2004). However, by far best understood are species of *Markuelia* Val'kov, 1984, known from the Lower Cambrian of Siberia, the Middle Cambrian of China and Australia (Fig. 6), the Late Cambrian of China and the Lower Ordovician of the USA (Bengtson and Yue, 1997; Dong et al., 2004, 2005a,b; Donoghue et al., 2006a). *Markuelia* specimens are known from cleavage stages, but also from sufficiently late stages such that it is possible to constrain hypotheses of their affinity. Dong et al. (2004, 2005a,b) discussed *Markuelia* as a member of the scalidophoran cycloneuralians within Nemathelminthes (=Aschelminthes).

Despite their differences, the entire suite of embryos can be attributed to *Markuelia*, based on comparative material described previously from a number of sites in the Lower Cambrian of Siberia, but interpreted first as fossilized embryos by Bengtson and Yue (1997). Three species are known, *M. prima* Val'kov, 1984, and *M. secunda* Val'kov, 1984 (*M. prima* is probably a junior synonym of *M. secunda*), from a number of localities in the Lower Cambrian of Siberia (Bengtson and Yue, 1997), and *M. hunanensis* Dong et Donoghue, 2004 from the Middle Cambrian Huaqiao and Chefu formations, and the Late Cambrian Bitiao Formation, at Wangcun, Hunan, South China (Dong et al., 2004, 2005; Donoghue and Dong, 2006). The key similarities to specimens hitherto assigned to *Markuelia* are the profusely annulated trunk coiled in an 'S'-shaped double loop into a sphere, and the paired terminal appendages.

# 6. Morphological, palaeo-ecological and evolutionary aspects

'Orsten' fossils show, due to their exceptional preservation, structures in comparable detail to Recent material, which requires consideration of evidence from related Recent animals too. Even early ontogenetic stages are preserved in the same quality. Both preservation of structures in topological order and ontogenetic stages make the 'Orsten' fossils an extremely valuable source for the reconstruction of ancient morphologies

and phylogenies, and for the understanding of the early evolution of structural complexes (e.g., the development of tagmosis, segment patterning or the feeding apparatus), of life strategies and adaptation of animals to particular ecological niches. The Phosphatocopina are taken as an example below to demonstrate this.

## 6.1. Phosphatocopina

This group is an example of the wide stratigraphical and geographical occurrence of a taxon of 'Orsten'-type fossils (Fig. 1, Table 1). Phosphatocopines are small bivalved crustaceans, which superficially share some aspects of the shield morphology with the similarly small, ostracode eucrustaceans. The 14 phosphatocopine species from Sweden have a stratigraphic range from Zones 1 to 5 of the traditional Upper Cambrian (Maas et al., 2003; Zone 1 is now assigned to the top of the Middle Cambrian (Peng et al., 2004; Terfelt et al., 2005). Besides this occurrence, phosphatocopines are known from all over the world (e.g., Müller et al., 1995, for Siberia; Hou et al., 2002), yet "soft parts" have only been found in 'Orsten'-type lagerstätten in Europe; e.g., UK (Fig. 5A), Poland (Fig. 5E), Australia (Walossek et al., 1993) and China (Dong et al., 2005a,b). Investigation of the morphology and ontogeny of these animals including a computer-based phylogenetic analysis revealed that the Phosphatocopina are a monophyletic taxon, based on a set of autapomorphies in its ground pattern (Maas et al., 2003; Maas and Waloszek, 2005). Furthermore, it has now been demonstrated that this group is not even remotely related to the ostracodes, but in fact, represents the sister taxon to the crown group of Crustacea, i.e. the Eucrustacea, both united in the taxon Labrophora (named after their characteristic large, so-called upper lip overhanging the mouth; Siveter et al., 2003). This systematic assignment is derived in particular from several features shared with eucrustaceans, but new features when compared to older nodes or other lineages. These new features are involved in a novel design of the cephalic feeding apparatus, thus inducing a new strategy of capturing and manipulating food in the now recessed mouth, which aided in developing a model of the evolution of the cephalic feeding apparatus in the Arthropoda (Stein et al., 2005; Waloszek et al., in press). The ontogeny, on the other hand, remained conservative in retaining a plesiomorphic 'head larva' (Fig. 5A); a larval type developed in the stem species of Euarthropoda having a body made of the eye segment and four segments bearing functional appendages. Eucrustacea modified this type by reducing the number of postoral segments by one. The new larval type,

called the 'nauplius' – a 'short-head larva' – uses the complete new feeding apparatus, also seen in phosphatocopines (newly developed in the Labrophora) and their larvae, demonstrating that the nauplius cannot simply be a plesiomorphic "precursor" of the head larva with fewer segments (Maas et al., 2003; Waloszek, 2003a,b). This example demonstrates the high value of palaeontological data and exceptionally preserved specimens representing ancient species for ordering character states, which would otherwise be impossible based only on data from Recent species.

### 6.2. Ontogeny and evolution

The set of Early Cambrian to Early Ordovician 'Orsten' fossils have informed our current views particularly of arthropod and crustacean evolution considerably. These three-dimensionally preserved fossils document ancient morphologies and provide substantiated arguments for hypotheses of life styles. This is in contrast to purely hypothetical/speculative models. In general, 'Orsten' fossils provide us with an unparalleled insight into the morphogenesis of body somites ('terminal addition') and their structural equipment (e.g., Waloszek and Maas, 2005). The variety of evolutionary levels represented in the 'Orsten' includes lobopodians (Fig. 5D), tardigrades (Fig. 5B) and pentastomids (Fig. 5F), permitting phylogenetic interpretations far beyond the Crustacea alone. The principal strategy of arthropods is apparently the simultaneous development of head somites, as expressed in the 'head larva' (Waloszek and Müller, 1990), and a successive addition of post-cephalic somites from a pre-terminal budding zone with progressive maturation of metameric structures. This can be recognized in the developmental patterns of extant and fossil representatives of several euarthropod taxa, particularly the crustaceans, chelicerates, but also in trilobites (Hughes, 2003a,b) and allied exclusively fossil forms. The development of these taxa points to an early somite-poor and free-living hatching stage, the above-mentioned 'head larva'. From the morphology of the 'Orsten' fossils and their phylogenetic position, it can be concluded that embryonic development to a late stage within an egg, as occurs in Recent stem-arthropods such as onychophorans and certain ingroup euarthropods, has been achieved several times convergently (Waloszek and Maas, 2005).

### 6.3. Meiofaunal life

The size of 'Orsten' fossils suggests that, at least for the 'Orsten' of Sweden, many, if not all, of the animals were part of the so-called meiofauna. This means that these animals lived on or in soft sediment (=flocculent layer, see Müller and Walossek, 1991). There they could move around, search for food, and mate. In some cases the adult forms of particular 'Orsten' species are not known; only their larvae are documented. An explanation might be that these forms left the meiofaunal regime at a specific stage of their life cycle and moved into the water column to enter a pelagic phase. In some cases, we have found only forms that can be considered adults, but their young are lacking. Such animals may have had pelagic larvae and went on the bottom to continue life as meiofaunal organism.

## 7. Conclusions and perspectives

'Orsten' does not refer to a specific time interval or location but it means a specific kind of type of preservation, which yields three-dimensionally preserved fossils. 'Orsten' fossils in a wider sense occur worldwide and potentially throughout the Neoproterozoic, Palaeozoic and Mesozoic eras. Thus, 'Orsten' is more than just a simple type of Konservat-Lagerstätte or an ordinary type of preservation. Progressively it becomes apparent that 'Orsten' in its wider sense is not restricted to particular times, to particular localities, to particular rocks, or even to particular organisms. 'Orsten' fossils provide access to meiofaunal small-scale organisms, a regime that has never previously been amenable for study in the fossil record. Again, such fossils can be used as a toolbox for any kind of larger-scale comparisons, either taxonomical, morphological or, in a broader approach, to uncover evolutionary pathways. The new data have added substantially to our knowledge on the 'Orsten'-type preservation for future explorations in other geological periods and areas. Stratigraphically, new worldwide occurrences of 'Orsten'-type preservation will surely improve our picture of the time and facies limits of this unusual type of preservation as much as of its biological content. 'Orsten' research is a successful discipline at the interface of palaeontological and biological studies and has led to new hypotheses of the phylogeny of animal taxa and a better understanding of the evolution of structures and structural systems. Besides their systematic and phylogenetic (biological) significance, fossils from 'Orsten'-type lagerstätten may significantly contribute to biostratigraphical as well as palaeo-ecological and palaeo-environmental interpretations of the Cambrian System. Lastly, evidence from 'Orsten' fossils can be combined with Recent evidence and also with evidence from fossils of other preservational types, horizons or Lagerstätten, for example from the Lower Cambrian

Maotianshan Shale of South China (e.g., Chen et al., 2004; Maas et al., 2004; Waloszek et al., 2005, in press).

Continuation of investigations on 'Orsten' material has been guaranteed and centralized through the establishment of the C.O.R.E. in January 2005 in Ulm, Germany. This is a group of international scientists either adding their own 'Orsten' material from different sources or expertise in 'Orsten'-related fields. The group not only aims in making progress in research on the existing material of 'Orsten' lagerstätten but also in targeting potential new lagerstätten yielding similar exceptionally preserved 3d fossils. We also aim to explore and apply new techniques of investigation on whole rock samples and individually selected fossils (see technical aspects mentioned in Braun, 2004; Braun et al., 2005; see Donoghue et al., 2006b). One of the major aspects within the taphonomic work on the 'Orsten' in the future is whether mineralization is exclusively an incrustation or an impregnation or a mixture of both conditions. It also has to be investigated whether and how much winnowing played a role in the origin of 'Orsten' fossils from non-Swedish localities.

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