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Eriksson, Mats E.; Horn, Esben

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Agnostus pisiformis — a half a billion-year old pea-shaped enigma

Mats E. Eriksson[a*], Esben Horn[b]

[a]Department of Geology, Lund University, Sölvegatan 12, SE-223 62 Lund, Sweden.

[b]10 TONS ApS, Ved Slusen 34, 2300 København S. V. Denmark.

*Corresponding author.
E-mail addresses: mats.eriksson@geol.lu.se (M.E. Eriksson), horn@10tons.dk (E. Horn).

ABSTRACT

The Cambrian arthropod *Agnostus pisiformis* (Wahlenberg, 1818) is not only a beautiful fossil animal, approximately one centimeter in length when adult, but also an extinct species unusually well-known from its 'soft' ventral cuticular structures. It is moreover very useful for biostratigraphic correlation and has a long research history. The species occurs in huge numbers, and in all developmental stages, in rocks belonging to the Alum Shale Formation in Sweden. Here it can be found in both shale and limestone ('Orsten') nodules, sometimes excellently preserved. In this study, we present a review of the species, including an account of its research history, spatio-temporal distribution, biostratigraphic utility, anatomy, ontogeny, and inferred mode of life, together with the characteristics of its host rock. Furthermore, herein science meets art to describe the process of how we successfully were able to 'breathe life' into this important fossil species by constructing greatly enlarged and highly detailed three-dimensional sculptural models. Three different versions were produced, including one with the test completely enrolled (i.e., animal in inferred protective mode), one with test slightly gaping (i.e., animal in active 'swimming' mode) and a 'fake SEM' version (i.e., showing how the actual miniscule fossils are perceived when studied in a scanning electron microscope). Replicas such as these fulfil very important purposes as they can be used for research as well as teaching and outreach, allowing scientists and laymen alike to study minute, extinct organisms first-hand and up close. One of the ultimate and also long-term goals of these *A. pisiformis* sculptures is to include them into a traveling exhibition on life in the Cambrian seas.

Keywords: Agnostus pisiformis; Cambrian; 'Orsten'; Exceptional preservation; Phosphatization; Reconstructions

1. Introduction

Ever since the dawn of paleontology it has been of great interest to make interpretative reconstructions of extinct organisms and ancient ecosystems (e.g., Owen, 1854; Edwards, 1967; Doyle and Robinson, 1993; Mayor, 2000). The process of faithfully doing so, however, is no simple task because of the illusive paucity of the fossil record combined with the required comprehension of organismal anatomy (particularly pertaining to those organisms lacking close modern relatives) and consummate artistic skills. Nonetheless, the combination of novel analytical techniques and artistic materials, alongside the surge of new fossil discoveries prompting continuously increasing knowledge of the diversity of ancient organisms has made these prospects brighter. The past few decades have indeed witnessed an increased interest in creating sophisticated and anatomically reliable, three-dimensional reconstructions of fossil organisms, both in terms of physical replicas and virtual ones (e.g., Eriksson, 2014; Lautenschlager and Rücklin, 2014; Vinther et al., 2016). The exceptionally well-preserved Konservat-Lagerstätte fossils obviously form a fundamental part of this paleontological iconographic progression as they provide an unusual array of biological and structural information on non-biomineralized tissues in addition to the hard parts (Seilacher, 1970; Allison and Briggs, 1993; Muscente et al., 2017).

Some fossil taxa are well-known – if not famous – for their usefulness as scientific tools (such as for biostratigraphy, paleobiogeography, or determining the thermal maturity of their host rocks). They can represent exceptional snapshots in time, or 'rear view mirrors', for our understanding of pivotal evolutionary steps (such as the conquest of the air – *Archaeopteryx lithographica* – and the first steps onto land – *Ichthyostega stensioei* and its allies; e.g., Ostrom, 1976; Ahlberg and Clack, 2006). Yet others are known for their beauty and alluring qualities, and still others for their interesting and convoluted research history (such as the Burgess Shale celebrity *Hallucigenia sparsa*; e.g., Conway Morris, 1977; Gould, 1989; Ramsköld, 1992). Some species, however, easily fit into several of the above categories and one such example is the Cambrian, trilobite-like arthropod *Agnostus pisiformis*.

Being famous primarily from the Alum Shale Formation of Sweden this species is known from several different modes of preservation, ranging from flattened imprints in shale via three-dimensional specimens in limestone and to exquisite, phosphatized and 'soft-tissue-bearing' Lagerstätte specimens, in the so-called 'Orsten' type preservation (which typically preserves all cuticular features, including appendages, setae, spines, and other ventral details; e.g., Müller, 1979; Müller and Walossek, 1987; Waloszek, 2003; Maas et al. 2006). It also has great practical applicability as an indicator of relative geologic time and a long research history, being known since the days of Carolus Linnæus.

In this paper we present a review of *Agnostus pisiformis* and how our knowledge of the species has progressively increased, particularly with the discoveries of exceptionally well-preserved Lagerstätte material (Müller and Walossek, 1987; Waloßek and Müller, 1988). The pristine nature of the secondarily phosphatized fossil material has provided unprecedented insights into its anatomy and ontogeny, allowing also for highly accurate replicas to be produced. Thus, herein we also describe in detail the process of how this (and similar fossils) can be reconstructed as beautiful and life-like sculptures that work as much as art pieces as important tools for understanding ancient organisms.

2. *Agnostus pisiformis* – a key species with a fitting etymology

Everyone working with sedimentary rocks of Cambrian age in Sweden is aware of the characteristic species *Agnostus pisiformis*. Not only because it is an important index fossil, but also because it usually occurs in great abundance and is easily recognized.

The genus name *Agnostus* obviously has the same word stem as the 'religious' doctrine of agnosticism. This derives from ancient Greek and literally means 'without knowledge'. The fitting reason with regards to this genus was that the early scholars were oblivious as to what type of organisms they were looking at while working on agnostoids. Therefore, when first formally described in 1822, Brongniart appropriately named it *Agnostus* (Brongniart, 1822, p. 38). Brongniart thereby also transferred *A. pisiformis* from Wahlenberg's (1818) earlier combination *Entomostracites pisiformis.*

The species epithet – *pisiformis* – literally translates into 'pea-shaped'. There is no surprise here either, as it is simply an excellent reference to the general appearance of the fossil; when the specimens are found articulated and enrolled, they strongly resemble peas. Some rock surfaces in

Scandinavia can be completely covered by the head- and tail shields of this fossil species, making the rock surfaces appear 'bubbly' by their presence (Fig. 1).

Although the species was first formally described by Wahlenberg already in 1818 (at that time as *E. pisiformis*) its history of research has considerably deeper roots. The first illustrations of *A. pisiformis* can actually be traced as far back in time as to the early part of the 18th century; the first account being that of Bromell (1729, p. 527) who published an illustration of the species covering an 'Orsten' slab (Fig. 2; see also Regnéll, 1949, p. 19, fig. 11; Ahlberg and Ahlgren, 1996; St. John, 1997, 2007). Perhaps more importantly, or at least better known, Swedish naturalist extraordinaire Carl von Linné (known also under his latinized name Carolus Linnæus) also mentioned the presence of *A. pisiformis* in the southern Swedish provinces of Västergötland and Skåne, in his travel accounts (Linnæus, 1747, p. 24, 1751, p. 122; cf. Ahlberg and Ahlgren, 1996). Linné is actually credited as the author of the taxon in many literary sources (e.g., Westergård, 1922; Müller and Walossek, 1987; see also St. John, 1997). However, although Linné gave brief descriptions he never actually named it in a formal sense and it has subsequently been shown that the earliest valid reference to *pisiformis* appears to be that of Wahlenberg (1818) (see discussions by Rushton, 1978, p. 258; Ahlberg and Ahlgren, 1996, p. 131; St. John, 1997, 2007).

2.1. Temporal and geographic distribution

Agnostus pisiformis is known as an excellent index fossil for biostratigraphy and is thus used to mark a specific time interval in the Cambrian Period. It obviously means that if you find rocks hosting *A. pisiformis* you know that those particular beds should belong to the biozone with the same name. Stratigraphically this belongs to the topmost part (the global Guzhangian Stage) of the informal Cambrian Series 3 (e.g., Peng et al., 2004, 2006, 2009). The first appearance datum (FAD) of *A. pisiformis* marks the base of the eponymous biozone. This is, in turn, succeeded by the *Glyptagnostus reticulatus* Biozone; the FAD of that agnostoid species also marks the base of the global Paibian Stage and the Furongian Series, traditionally known as the 'Upper' Cambrian in Sweden (Peng et al., 2004). *Agnostus pisiformis* is however not entirely confined to its biozone. Based on material collected on Billingen in the province of Västergötland, Sweden, Ahlberg and Ahlgren (1996, p. 131) noted that *A. pisiformis* ranges slightly farther upwards stratigraphically, beyond its biozone, and thus into the succeeding *G. reticulatus* Zone.

Agnostus pisiformis is by far most common and characteristic in strata of its appropriate age in Sweden and other parts of Scandinavia. It has, however, been recorded also outside Scandinavia in coeval rocks from, e.g., England (Avalonia), Novaya Zemlya (Russia) and eastern Canada (Rushton, 1978; Peng and Robison, 2000; Ahlberg, 2003). Adding to these are possible occurrences also in Poland, Kazakhstan and Siberia (P. Ahlberg, Lund, personal communication, 2016).

3. The *Agnostus pisiformis*-bearing host rock

3.1. The Alum Shale Formation

The rocks hosting *A. pisiformis* in Scandinavia belong to the Alum Shale Formation (e.g., Martinsson, 1974; Andersson et al., 1985; Bergström and Gee, 1985; Buchardt et al., 1997; Nielsen and Schovsbo, 2007; Ahlberg et al., 2016; Rasmussen et al., 2017). During the latter half of the Cambrian Period, Scandinavia was largely covered by a widespread shallow and tranquil sea. Mud and fine-grained matter were slowly deposited and since the environment was very rich in organic matter and the oxygen levels were low, the bottom sediments became oxygen depleted, sometimes anoxic. This meant that not all organic matter could be broken down and a black mud was formed. With time and increasing pressure these muddy sediments were compacted and resulted in the dark grey to black, kerogen-rich shales and mudstones of the Alum Shale Formation. The total organic carbon values of the Alum Shales are between 2 and 22 wt% (e.g., Thickpenny, 1987; Buchardt et al., 1997; Egenhoff et al., 2015). This particular rock type occurs stratigraphically from the Cambrian Series 3 through the Tremadocian (Early Ordovician) (Bergström and Gee, 1985; Nielsen and Schovsbo, 2007) and a maximum thickness of approximately 160 m has been estimated in southern Scandinavia (Nielsen and Schovsbo, 2007).

These rocks are extremely rich in fossils and dominated by different types of arthropods, with polymerid trilobites and agnostoids occurring *en masse* (e.g., Westergård, 1922, 1946; Ahlberg, 2003; Terfelt et al., 2011; Rasmussen et al., 2017, and references therein). Like an ancient mass grave the sediments enclose a long vanished marine ecosystem that apparently was seething with life. The slow sedimentation of fine-grained matter during overall calm conditions rendered the strata very condensed, and calculations suggest that one to ten millimeters of shale represent approximately one thousand years of deposition (e.g. Thickpenny, 1987; Buchardt et al., 1997; Egenhoff et al., 2015). Recent studies have, however, shown that at times very shallow, even subaerial, conditions prevailed in proximal settings during the deposition of the Alum Shale Formation (e.g., Lehnert et al., 2012, 2013; Ahlberg et al., 2016).

Within these shales there are lenses and beds of another type of rock; a black to greyish-brown limestone colloquially known as 'Orsten' or stinkstone (Figs 1, 3). The latter name derives from the fact that the rock is so enriched in hydrocarbons that if it is cracked open with a hammer there is often a pungent stench of kerosene or crude oil. The name 'Orsten' (a Swedish name for stinkstone) is derived from an old veterinary term, as the limestone was processed and used for curing diseases in pigs and other domestic animals (Bromell, 1729; Regnéll, 1949; Berg-Madsen, 1989). Regardless of the unflattering name, strange odor and dull color, these limestones can contain magnificently preserved microscopic fossils, known as the 'Orsten' fossils.

3.2. The 'Orsten' Konservat-Lagerstätte

As indicated above, fossils are common in both the shale and the limestone ('Orsten') of the Alum Shale Formation, but because the shale is considerably more compressed, the fossils are more flattened therein than in the limestone, where they are often beautifully and three-dimensionally preserved (Fig. 1). However, the fossils embedded in some 'Orsten' nodules would prove to be even more amazing than first perceived through studies by the naked eye or through a hand lens. A spectacular and hitherto unknown, miniscule biota only appear when the rock is etched in acetic acid (Eriksson and Waloszek, 2016).

It was the late German paleontologist Klaus J. Müller who in the 1960s and 1970s was hunting for conodonts and shields of small crustaceans known as phosphatocopines in the Cambrian (e.g., Müller, 1964; Müller and Hinz 1991, and references therein); he dissolved huge quantities of 'Orsten' in acid in search of these microfossils (cf. Müller, 1979; Jeppsson et al., 1999). It was in such sample residues that Müller serendipitously discovered something that would prove to be far more interesting and scientifically novel than conodonts (Müller, 1979). Among the microscopic fossil remains, he observed minute arthropods in an exceptional state of preservation. The fossils not only preserved the usual hard parts and external shells in three dimensions, but also internal and delicate 'soft cuticular tissue' structures, in magnificent detail. Ventral appendages are still present and in such a pristine state of preservation that the organisms look almost modern.

The 'Orsten' Lagerstätte of Sweden is represented mainly by secondarily phosphatized arthropods (primarily crustaceans), in the size range of 2 mm or less (e.g. Müller, 1979; Walossek, 1993; Waloszek, 2003; Maas et al., 2006; Eriksson et al., 2016). The fossils are impregnated with calcium phosphate, an excellent medium for preserving fossils in minute detail, including delicate 'soft-tissue' structures (Maas et al., 2006, and references therein). The discovery of this incredible faunal assemblage by Müller has since been followed by a sequence of investigations disclosing, among other things, morphological details of utmost interest for the evolution of, and relationships among, early arthropods (e.g., Maas et al. 2006, and references therein). After being identified in Sweden, 'Orsten' type fossils have been recorded from many parts of the world (Maas et al., 2006). In Sweden the 'Orsten' Lagerstätte spans approximately 10 million years. Taking into account also this type of deposit from other parts of the world, the 'Orsten' type deposits span the upper lower Cambrian through to possibly the lower Ordovician, thus altogether embracing some 30 million years (Maas et al., 2006; Eriksson and Waloszek, 2016). This also makes the 'Orsten' Lagerstätte quite unique as most other Cambrian Lagerstätten are very restricted geographically as well as stratigraphically (e.g., Zhu et al., 2006).

It was from the acid-resistant ‘Orsten’ residues that the exceptionally preserved, phosphatized specimens of *Agnostus pisiformis* were also recorded (Fig. 4; Müller, 1982; Müller and Walossek, 1987; Waloßek and Müller, 1988). Although it is not the most commonly found ‘Orsten’ species (the Phosphatocopina is by far the most common and species-rich taxon; Maas et al., 2003; Eriksson et al., 2016), it is noteworthy that most of the ‘Orsten’ type fossils known from Sweden derive from the *A. pisiformis* Zone (Maas et al., 2006). Thus, for the first time, and despite being known as a fossil since the time of Linnæus, the ventral ‘soft tissue’ parts of *A. pisiformis* were found preserved and could be studied in stunning detail (Figs. 4, 5; Müller and Walossek, 1987). Those specimens also allowed an assessment of its early ontogeny and complete anatomy. This, in turn, allowed for a much better understanding of the mode of life and functional morphology of the species (Müller and Walossek, 1987; Waloßek and Müller, 1988; Eriksson and Waloszek, 2016).

4. Anatomy and life mode of *Agnostus pisiformis*

Seemingly insignificant and contrasting with the polymerid trilobites, agnostoids are characterized by a head region (cephalon) and a tail region (pygidium) of nearly equal size (e.g., Robison, 1975; Kaesler 1997; Babcock et al., 2017). These are, in turn, separated by two thoracic segments with tergites. Although the trunk tergum of *Agnostus pisiformis* consists of two tergites and the large pygidal shield, there is no distinctive subdisvision into a ‘thorax’ and a ‘pygidium’ on the ventral side of the animal (Müller and Walossek, 1987). The horseshoe-shaped cephalic and pygidial shields in *A. pisiformis* closely resemble each other in size and broad morphology (outline, convexity and height), a feature known as isopygy (see Müller and Walossek, 1987).

Whilst agnostoids could grow to a maximum length exceeding a centimeter, they usually are less than 10 millimeters long (e.g., Robison, 1975; Kaesler, 1997; Babcock et al., 2017). Adult specimens of *A. pisiformis* may reach approximately 10 mm in total length (c. 4.5 mm for each shield). As with polymerid trilobites and other arthropods, *A. pisiformis* shed its exoskeleton repeatedly during growth. Therefore, most fossil remains encountered are molted exuviae whereas articulated specimens, representing deceased individuals, are considerably less common. As opposed to the test (the dorsal area of the cuticle), the ventral parts were less sclerotized – a feature inherited from the ancestor of all sclerotized arthropods.

The ontogenetic development of *A. pisiformis* is unusually well-documented (for a meticulously detailed description of the ontogeny, the reader is referred to Müller and Walossek 1987) although the ‘soft’ integument of later stages than the first holaspid stage has not been recognized. *Agnostus pisiformis* went through several molt stages (or instars), starting off as a minute larva, the first of a set of so-called meraspid instar stages. Seven distinct molting stages have been identified within the meraspid instar, three belonging to the first meraspid degree and four to the second (Müller and Walossek, 1987). After passing the meraspid stage, the animal reached the first holaspid stage, which had liberated both tergites of the thoracic segments (which thus allows for easy discrimination between holaspids and meraspids). In the holaspids, nine pairs of appendages are developed: four cephalic pairs and five pairs in the trunk region (Müller and Walossek, 1987). Because the largest of the eight developmental stages recorded in ‘Orsten-type’ preservation did not reveal structures that might have been involved in reproduction, Müller and Walossek (1987) suggested that the smaller holaspids were still immature.

Although much of the general morphology of the adult *A. pisiformis* was captured already in the meraspid instar stages, morphological changes are observed in both the test and appendages during ontogeny. The most notable change of the test probably comprises the above-mentioned separation of the tergites of the two anteriormost trunk segments from the initial pygidium, the former of which then forms the short thoracic region. In addition, there are changes in morphology and position of the cephalic and pygidial spines, changes in the horizontal axis of symmetry and pygidial axis (from a triangular to lanceolate form), a shift in position of the tergites and progressive development of tergal elevations, slight morphological changes in preglabellar and glabellar areas, change in length/width ratio of the pygidal and cephalic shields, change in pattern and number of pores, and an overall progressive increase in convexity of the test (Müller and Walossek 1987, p. 26–27).

The ventral side of the animal also alters during ontogeny. In the cephalic region many features actually do not change significantly except for an overall size increase. With increasing test convexity the testal cavity is enlarged, and changing flexure of the trunk body against the cephalon is accompanied by a slight change in appendage positions. Rear of the postoral feeding chamber the median part of the ventral body becomes more gently curved and U-shaped in cross-section. The appendages change slightly and gradually with a size increase and elongation of the podomeres (Müller and Walossek, 1987, fig. 11), and the setation alters somewhat with increasing number of setae and spines. While the trunk body elongates, the trunk limbs successively develop from rudimentary to fully functioning. From the meraspid stage 2a the final number of five trunk appendages had developed.

Whilst 'final', adult holaspid, instars are unknown in 'Orsten' type preservation, the external shield morphology of adults is very well known from masses of specimens found in the Alum Shale Formation. Collectively, the degree of detailed insights into its anatomy makes *A. pisiformis* one of the best-known fossil arthropods in the world.

For a long time, agnostoids were regarded as trilobites. However, the 'soft tissue' (appendage) structures discovered from the 'Orsten' Lagerstätte rather suggested a crustacean (*sensu lato*) affinity (Müller and Walossek, 1987). Although this conclusion was drawn from empirical evidence from the fossil records and was based on uniquely well-preserved material, contrasting opinions with regard to the evolutionary relationship between polymerid trilobites and agnostoids do still persist (for a recent summary, see Babcock et al., 2017, and references therein). However, as noted by Haug et al. (2010), a sister group relationship of the Agnostina and Crustacea does not exclude a close relationship to the Trilobita.

Agnostus pisiformis lacks dorsal eyes and was long thought to be blind. However, it does have ventral and probably light sensitive eye structures associated with the hypostome in later ontogentic stages (Müller and Walossek, 1987; Walossek and Müller, 1990). Thus, it was probably able to see while the shields were gaping, though not as well as many polymerid trilobites with their dorsal compound eyes. *Agnostus pisiformis* probably lived alongside most known 'Orsten' taxa of the meiofauna, but more above than within the flocculent zone in the Cambrian Alum Shale sea (Müller and Walossek, 1987; Maas et al., 2006). Although it was most likely not able to open up fully (outstretch) it could achieve complete enrolment with a tight fit of the shields, presumably for protection against predators while resting or escaping unsuitable environmental conditions (Müller and Walossek, 1987). When enrolled the animal appears nut or pea-shaped.

It comes as little surprise that the mode of life and feeding habit of *A. pisiformis* have been as enigmatic as most other aspects of the animal. Prior to the discovery of the exceptionally well-preserved 'Orsten' specimens, the species had been suggested to, for example, have a benthic or a passive (planktonic) pelagic life style, that received nutrition through parasitism or as a filter feeder (Müller and Walossek, 1987, p. 39–40). The ventral 'soft' cuticle structures and appendages suggest that *A. pisiformis* could actively swim (mainly with the outer rami, exopodites of the second and third cephalic appendages), albeit not very well or rapidly. While swimming, the shields were slightly open. The morphology of the antennulae suggests that they were involved in the process of gathering food, which likely consisted of suspended organic/detrital matter floating in the water column in or near the flocculent zone. While swimming or floating, the animal was more or less horizontally oriented with the head shield probably situated downward. For additional information on the anatomy and inferred life style of *A. pisiformis*, see the monograph by Müller and Walossek (1987) complemented by Waloßek and Müller (1988).

Considering the extreme numbers of specimens found at some levels of its eponymous biozone in the Alum Shale Formation, *A. pisiformis* must have occurred in the many millions, even if the overall low sedimentation rate might bias this. No other fossils occur in anywhere like the same abundance – virtually coquinas – which are packed with *A. pisiformis*. This may also suggest that the

A. pisiformis carcasses caused significant decay and was an important factor for the low oxygen and high biomass accumulation which eventually led to bitumen production in these strata.

Given its biozonal and most likely ecological importance, as one of the most abundant animals in the Alum Shale sea, as well as its fascinating scientific history and morphology – which is known in significant detail and through ontogeny – *A. pisiformis* forms the perfect candidate for an enlarged sculpture. A sculpture that enables also the general public to become aware of the minute evolutionary wonders of the 'Orsten' in particular and those of the Cambrian Period in general (see below).

5. 'Breathing life' into *Agnostus pisiformis*

The process of making sculptures out of long extinct organisms is a daunting one, riddled with obstacles and pitfalls (see Eriksson, 2014, and references therein). The fossil record is frustratingly incomplete and even among exceptionally well-preserved Konservat-Lagerstätten fossils there are still features usually missing, such as original color, various 'soft' tissues, external creases and wrinkles and other such fine textural attributes; attributes that greatly contribute to how we perceive organisms in life and which obviously are crucial in a reconstructive sculpting process. However difficult the art of reconstructing ancient biotas might be, it can nonetheless be both rewarding and stimulating. The resulting three-dimensional replicas can be used for multiple purposes, such as research (e.g., to facilitate our understanding of the functional morphology of extinct animals), teaching and outreach (e.g., used in exhibitions and/or for promotion). Thus, if successful, such fossil reconstructions, alongside the growing number of virtual ones, can fill very important functions (see, e.g., Müller and Walossek 1988; Stein et al., 2008; Haug et al., 2010; Eriksson et al., 2012, 2016; Eriksson, 2014; Lautenschlager and Rücklin, 2014; Cunningham et al., 2014; Vinther et al., 2016).

For this project, we aimed to make meticulously detailed, dramatically posed and greatly enlarged, three-dimensional reconstructions of *A. pisiformis*. Our sculpting process was performed at *10 Tons Studios*, located on the outskirts of Copenhagen, Denmark; they are a firm specialized in making sculptures of extinct, but also extant, organisms. *10 Tons* was founded and is owned by one of the authors (EH). The philosophy of *10 Tons* is to combine superior craftsmanship with an utmost respect for science and of the organisms' detailed anatomy; collectively this results in fascinating and truly life-like sculptures (Eriksson, 2014).

This entire process was a collaborative effort between EH and his team at *10 Tons*, executing the hands-on sculpting, and first author (MEE) acting as scientific supervisor and sparring partner. Because *A. pisiformis* is one of the most intricate and anatomically complicated organisms known from the 'Orsten' of Sweden, substantial time and devotion was put into making a life-like and authentic replica. We decided to make two separate reconstructions; one showing the species in its inferred 'active' or swimming life mode, i.e., with semi-open shields, and the other showing it with the test in a completely enrolled position. In addition to these, a third, and less detailed version was made with the aim of mimicking a view of an actual fossil through a scanning electron microscope (SEM), the main instrument of choice for studying 'Orsten' fossils in detail.

Relying on first hand fossil material and data, alongside the published literature (in particular Müller and Walossek, 1987; Waloßek and Müller 1988), we first evaluated and discussed in-depth the pit-falls, choice of materials, and optimal ontogenetic growth stage that was to be made into a sculpture (a late meraspid degree was chosen). The actual sculpting and construction phase is a step-wise process including various different techniques and materials (Figs. 6–10; see also below). Typically, this differs from project to project and new problems encountered may entail coming up with novelty solutions. Moreover, the materials and techniques finally used are usually a result of 'trial and error' and vary considerably depending on size, area of use and mode of display of the final sculpture (Eriksson, 2014).

5.1. Sculpting process

For *A. pisiformis*, the sculpting process involved the following steps:

Positive, hand-modeled clay models of the external shields were first meticulously prepared (Fig. 6A, B, C), with careful reference to scientific descriptions, drawings, and photographs (Müller and Walossek, 1987; Waloßek and Müller 1988). This initial model was made with a smooth surface (Fig. 6A, B, C). In order to add the walls of the polygonal surface texture visible in some well-preserved specimens (see Müller and Walossek, 1987, p.10, pls. 7, 8) we made a silicone skin mold from the smooth original model. Based on this negative mold a positive silicone cast was produced, which was subsequently used to make a negative wax mold (Fig. 6D–F) of the thoracic segments and cephalic and pygidal shields. The polygonal surface texture could then be engraved into the wax mold using a fine-tipped sculpting tool (Fig. 6E, F). Although time-consuming, engraving the pattern is considerably easier than trying to create such protruding fine structures directly on a positive model.

Having this negative wax mold with the engraved surface texture, we proceeded to make the final, positive prototype out of silicone. In order to do so, a negative skin mold was made, in which we 'slush cast' a thin shell casting from 'Easy Flow' – a polyurethane resin. The 'soft' internal, or ventral, body parts that were enclosed by the carapace in life were then sculpted in the 'Easy Flow' carapace cast, using artificial clay ('Monster Clay'; Fig. 6G, H, I), a re-useable sulfur free, professional oil/wax based sculpting medium. Once both the inner and outer sides of the carapace were finished, we finally made the negative silicone mold of the carapace. Using this mold, positive versions were cast from strong and durable translucent polyurethane resin. Additives such as talc and dry pigments are mixed into the polyurethane resin while still soft in order to achieve the desired semi-translucent appearance (Fig. 7). Whether the shields of *A. pisiformis* were translucent (and/or to what degree) is uncertain and modern organisms, such as ostracods and copepods, were used for reference.

During this process, the antennules and appendages (Fig. 7A) were carved from 'Ciba Tool' – a dense epoxy foam board, also known as artificial (or chemical) wood, due to its wood-like properties. We then made the fine setae and/or spines ('hairs' and bristle-like structures) for the appendages. Steel needles were first made from pieces of piano wire that were sanded into shape and molded in silicone. Using a proprietary technique, developed by *10 Tons*, allows casting very natural-looking hairs from crystal-clear polyurethane resin. The hairs were then individually mounted onto the 'Ciba Tool' antennules and appendages. Then silicone molds were made over each new structural element and cast, using the same resin that was used for the carapace casts. Then the outermost ca. 3 mm thick layer was sanded off the casts. After having sprayed a thin layer of 'Motip Plastic Primer' and an additional primer developed by *10 Tons*, the structures were painted to give an illusion of veins and muscle tissue, using a combination of acrylic paint and crayons (Fig. 7A). When this was completed, the sanded and painted parts were put back into their respective negative mold and a thin layer of crystal clear resin was cast. The result is sub-surface scattering and a perfect illusion of veins and muscle tissue residing deep inside the appendages (Fig. 7A).

The final and highly satisfying stage of the process, and the one that really brings the sculpture to life, is the paint application. The shield-like cuticular cover, hypostome and appendages were given a subtle layer of paint using various airbrushing techniques as well as using regular brushes (Fig. 7D, H). The final color scheme chosen was subject to discussion during this process. As we do not know the actual color of *A. pisiformis* in life, there is clearly some artistic freedom involved when making a replica. We did, however, use extant marine crustaceans with a similar size and mode of life (such as copepods and ostracodes) as reference materials and for inspiration.

When all parts of the sculpture were painted, we began to carefully assemble the complete model by gluing the different parts together with cyanoacrylate, a strong and fast-acting adhesive. Then it was mounted on a metal rod in a specially designed, illuminated acrylic display case (Figs 8,9).

5.1.1. Enrolled version

Having the molds for all parts of *A. pisiformis* available makes it relative easy to create additional copies. These were produced in order to make the enrolled version of the animal (Fig. 10A, B). The wrap-around, shield-like cuticle was cast from the same semi-translucent resin as used for the first sculpture with gaping shields, and was painted using the same techniques. Within the closed shields some hair-like structures and curled up plastic film were arranged in order to mimic the effect of seeing ‘something’ (i.e., ventral, ‘soft’ cuticular structures) within the closed test (Fig. 10A, B).

5.1.2. A ‘fake SEM’ version

In order to visualize how the actual fossils usually look while being studied in an SEM or in SEM-micrographs, a unique ‘fake SEM’ sculpture was also produced (Fig. 10C–F). We again used the existing molds to cast copies from ‘Acrylic One’, a two-component material consisting of a mineral powder and a water-based acrylic resin, thus basically forming an acrylic gypsum. Fine details such as hairs and bristles break off during de-molding and this actually mimics the incomplete and somewhat distorted nature of most fossil specimens. We also compressed and distorted the silicone molds of the shell-like cuticular cover of the animal late in the curing process of the acrylic gypsum so that the parts emerged looking exactly like the fossil – with compression features. As noted by Müller and Walossek (1987, p. 33), the appendages of the fossils are subjected to some *post mortem* distortion and dislocation. The incomplete legs, parts of the bristles and fragmented parts of the shields were arranged and glued together with ‘Acrylic One’ mixed with sand. We also brushed on a textile paint compound called Expantex. Expantex looks like a thick paint but when heated with a blow torch the paint will ‘pop’, almost like popcorn and transform into peculiar organic ‘coral-like’ structures resembling micro-crystal structures that is often seen as ‘noise’ (i.e., matrix and/or secondary/diagenetically grown phosphate) in the SEM micrographs.

6. Conclusions and future plans

The true significance of this project is that science meets art by producing authentic, high-end sculptures of a remarkable Cambrian organism that can be used for multiple purposes; research, scientific outreach, and teaching. One of our ultimate goals is to develop maximum societal benefit by incorporating the *Agnostus pisiformis* sculptures with those (existing and in preparation) of other organisms from the Cambrian seas, in a traveling exhibition that spreads our knowledge of early life during one of the most exciting times in Earth history. Perhaps to some extent we also feel inclined at showing the general public that paleontology is not just about dinosaurs and that the considerably older ecosystems of the Cambrian also hosted quite remarkable organisms, when animal communities first dominated the seas.

This project also aims to draw more attention to the ‘Orsten’ fossils in particular. Although not as well-known as the ‘weird wonders’ of the Burgess Shale (e.g., Whittington, 1985; Gould, 1989; Caron and Rudkin, 2009), the ‘Orsten fossils’ are at least as well preserved – if not better – and have provided significant insights into Cambrian biotas and early animal evolution (Waloszek, D., 2003; Maas et al., 2006; Eriksson et al., 2016). Moreover, the ‘Orsten fossils’ comprise the temporally and spatially most widespread Lagerstätte known, not only from the Cambrian System (e.g., Zhu et al., 2006) but from the entire Phanerozoic fossil record (cf. Maas et al., 2006). Thus, another main objective of this project is to display the magnificent ‘Orsten’ fossils also to the general public, as they deserve recognition outside of the scientific community.

We think that *A. pisiformis* is an exemplar in this regard, and a fitting ‘gateway’ into the world of the ‘Orsten’ fossils because of its alluring morphology, differing modes of preservation, scientific utility and status as an excellent index fossil, and, last but not least, its long research history. As a final – if somewhat biased – statement, we think that it is obligatory for today’s working scientists to make research results accessible, understandable, and hopefully interesting, beyond the often arcane research community.

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Figures

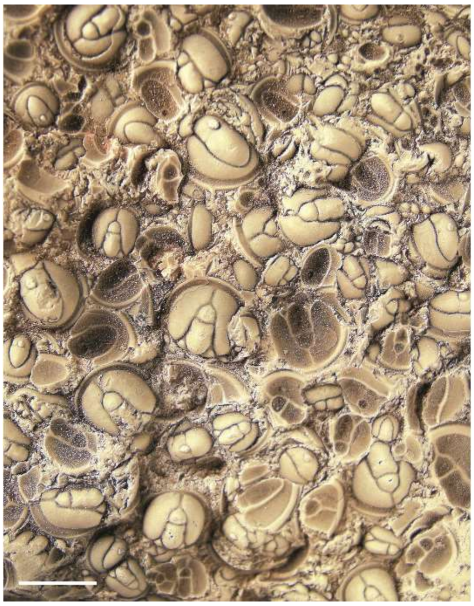

Fig. 1. Specimens almost exclusively belonging to *Agnostus pisiformis* on a slab surface of a lighter brownish variety of the ‘Orsten’ from the eponymous Cambrian biozone in Västergötland, Sweden. The fossils in the ‘Orsten’ are beautifully preserved in 3D as opposed to the generally highly flattened specimens in the surrounding shale. Scale bar (lower left corner) corresponds to ca. 3.5 mm.

Photograph courtesy of P. Ahlberg (Lund University) and used with kind permission. [Single-column image]

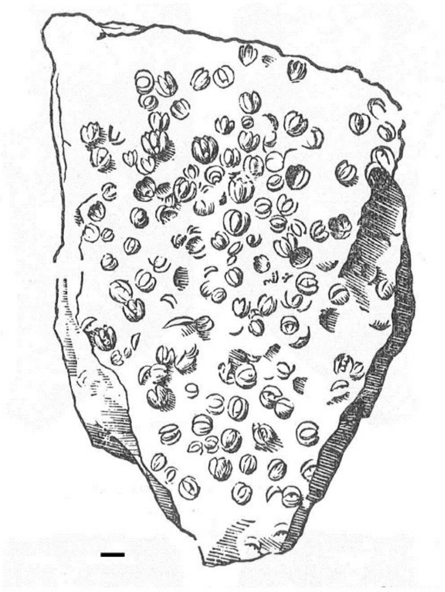

Fig. 2. The very first illustration of *Agnostus pisiformis* from the Swedish Alum Shale Formation. The specimens are preserved on the bedding plane surface of an 'Orsten' rock slab from Varnhem in the province of Västergötland, southern Sweden. Scale bar is ca. 3.5 mm. From Bromell (1729, p. 527; cf. Regnéll, 1949). [Single-column image]

Fig. 3. An lens-shaped 'Orsten' nodule (ca. 0.7 m in diameter) enveloped by the paper thin black layers of Alum shale from the abandoned quarry at Andrarum in Skåne, the southernmost province of Sweden. The greenish-brown tint seen on the convex 'Orsten' nodule is a consequence of weathering combined with some lichen, and the yellowish tint seen in some patches on the surrounding shale is a result of weathered iron and sulphur compounds [Single-column image]

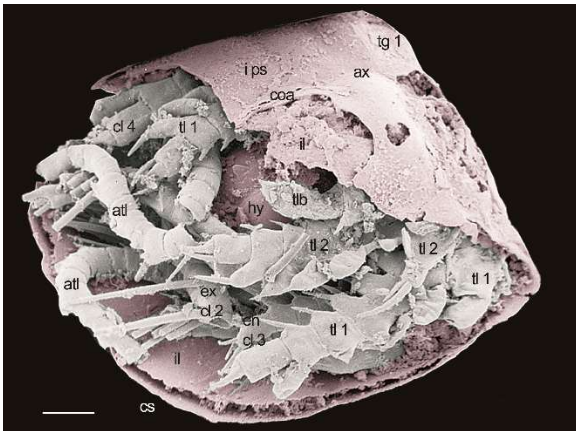

Fig. 4. A phosphatized and exceptionally well-preserved, enrolled specimen (stage 2a) of *A. pisiformis,* which has been extracted from an 'Orsten' by means of acid digestion. Note the finely preserved limbs and antennae visible underneath the broken outer (pygidal) shield (artificially colored pink to distinguish it from the 'soft integument' structures). Abbreviated descriptive terms: atl = antenullae; ax = axis; cl 2–4 = postantennular cephalic appendages, or limbs; coa = secondary coating; = cs = cephalic shield; en = endopodite; ex = exopodite; hy = hypostoma; il = inner lamella; i ps = posterior part of incipient pygidial shield; tg l = first thoracic tergite; tlb = trunk limb bud, lobate rudimentary limb; tl 1–2 = trunk limbs. Scale bar is ca. 60 µm. SEM-micrograph courtesy of D. Waloszek (Ulm and Lund) and used with kind permission (see also Müller and Walossek, 1987, specimen UB 855). [Single-column image]

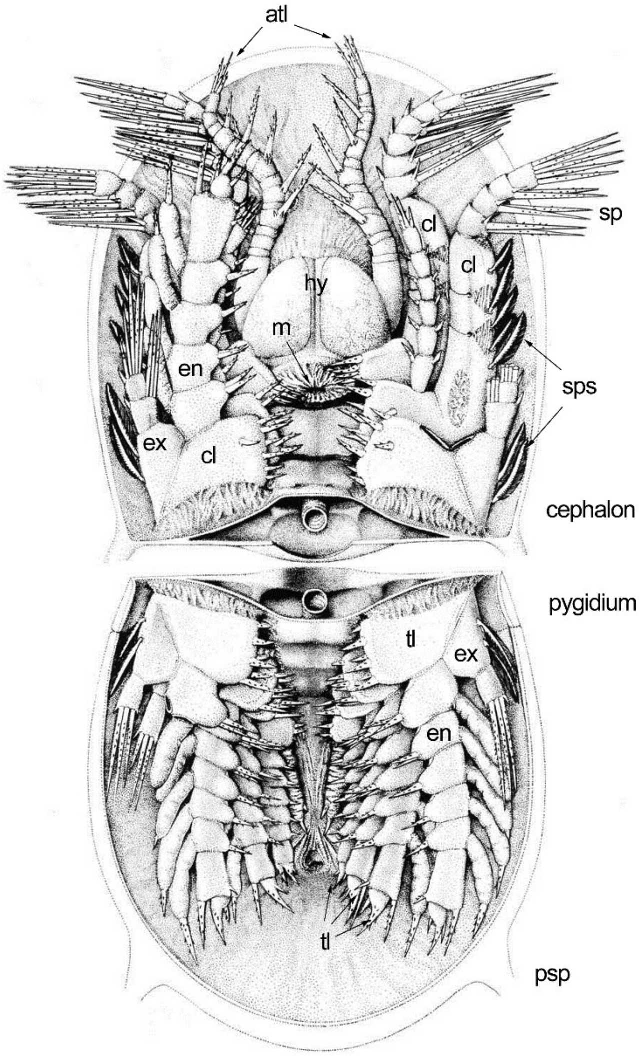

Fig. 5. Illustration showing the ventral morphology of a late meraspis instar stage of *Agnostus pisiformis*, as reconstructed from exceptionally preserved 'Orsten' material. Note that the body is drawn as disconnected between the cephalon and pygidium (see Müller and Walossek 1987). Abbreviated descriptive terms: atl = antenullae; cl = postantennular cephalic appendages, or limbs; en = endopodite; ex = exopodite; hy = hypostoma; m = mouth; psp = spine, posteriorly directed outgrowth of the posterolateral part of the pygidial border; sp = spine-like setae; sps = soft plumose seta of the outer side of the exopodites of the postoral appendages; tl = trunk limbs. Illustration courtesy of D. Waloszek (Ulm and Lund) and used with kind permission. [Single-column image]

Fig. 6. The meticulous step-wise process of sculpting an enlarged reconstruction of *Agnostus pisiformis*. A–C. The initial, hand-sculpted clay model. D–F. Negative wax mold versions into which the polygonal surface texture is engraved. G–H. Monster clay versions of the inner side of the cephalic and pygidal shields. I–K. Intermediate positive casts (before final translucent versions) for hand-modeling of thoracic segments. I. External (dorsal) view of pygidal shield. J. External (dorsal) view of cephalic shield. K. External view of an enrolled version in progress. [double-column image]

Fig. 7. Additional steps towards finalizing the *A. pisiformis* sculpture. A. Appendages ready to be mounted. B. Ventral view of the cephalic shield. D–E. Horn working on gluing appendages in place (Horn also for scale). C, F–G. External views of pygidal and cephalic (F) shield, respectively, showing the polygonal texture pattern and the translucency of the shields. H. Horn applying finishing touches of paint job. [double-column image]

Fig. 8. The final, life-like sculpture of a late meraspid instar stage of *Agnostus pisiformis* with shields in semi-open ('swimming') position; seen from different views (A–D). [double-column image]

Fig. 9. The final sculpture (with shields open) mounted into the specially designed, illuminated display cases. A. Overview. B. Close-up of sculpture. [double-column image]

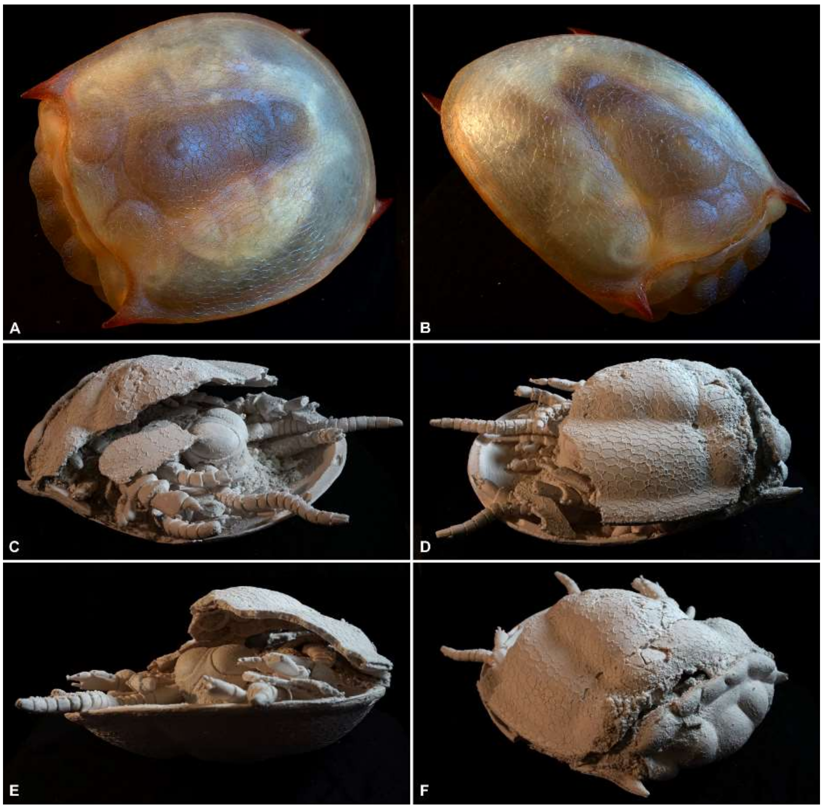

Fig. 10. The final enclosed sculpture version of a late meraspid stage of *Agnostus pisiformis* in different views (A, B). Note the semi-translucent shields that allows for the ventral 'soft tissue' structures to be suggested. C–F. A 'fake SEM' version in different views. [double-column image]