



# LUND UNIVERSITY

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

Eriksson, Mats E.; Horn, Esben

*Published in:*  
Earth-Science Reviews

*DOI:*  
[10.1016/j.earscirev.2017.08.004](https://doi.org/10.1016/j.earscirev.2017.08.004)

2017

[Link to publication](#)

*Citation for published version (APA):*

Eriksson, M. E., & Horn, E. (2017). Agnostus pisiformis — a half a billion-year old pea-shaped enigma. *Earth-Science Reviews*, 173, 65-76. <https://doi.org/10.1016/j.earscirev.2017.08.004>

*Total number of authors:*  
2

## General rights

Unless other specific re-use rights are stated the following general rights apply:

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

Read more about Creative commons licenses: <https://creativecommons.org/licenses/>

## Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

LUND UNIVERSITY

PO Box 117  
221 00 Lund  
+46 46-222 00 00

1 **"This is the peer reviewed version of the following article: Eriksson, M.E. & Horn, E. 2017: *Agnostus***  
2 ***pisiformis* — a half a billion-year old pea-shaped enigma. *Earth-Science Reviews* 173, 65-76., which**  
3 **has been published in final form at**  
4 **<https://www.sciencedirect.com/science/article/pii/S0012825217301903?via%3Dihub>.**

5  
6 ***Agnostus pisiformis* — a half a billion-year old pea-shaped enigma**

7  
8 Mats E. Eriksson<sup>a\*</sup>, Esben Horn<sup>b</sup>

9  
10 <sup>a</sup>Department of Geology, Lund University, Sölvegatan 12, SE-223 62 Lund, Sweden.

11 <sup>b</sup>10 TONS ApS, Ved Slusen 34, 2300 København S. V. Denmark.

12  
13  
14 \*Corresponding author.

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

16  
17 **ABSTRACT**

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

36 **Keywords:** *Agnostus pisiformis*; Cambrian; ‘Orsten’; Exceptional preservation; Phosphatization;  
37 Reconstructions

38  
39 **1. Introduction**

40 Ever since the dawn of paleontology it has been of great interest to make interpretative reconstructions  
41 of extinct organisms and ancient ecosystems (e.g., Owen, 1854; Edwards, 1967; Doyle and Robinson,  
42 1993; Mayor, 2000). The process of faithfully doing so, however, is no simple task because of the  
43 illusive paucity of the fossil record combined with the required comprehension of organismal anatomy  
44 (particularly pertaining to those organisms lacking close modern relatives) and consummate artistic

45 skills. Nonetheless, the combination of novel analytical techniques and artistic materials, alongside the  
46 surge of new fossil discoveries prompting continuously increasing knowledge of the diversity of  
47 ancient organisms has made these prospects brighter. The past few decades have indeed witnessed an  
48 increased interest in creating sophisticated and anatomically reliable, three-dimensional  
49 reconstructions of fossil organisms, both in terms of physical replicas and virtual ones (e.g., Eriksson,  
50 2014; Lautenschlager and Rücklin, 2014; Vinther et al., 2016). The exceptionally well-preserved  
51 Konservat-Lagerstätte fossils obviously form a fundamental part of this paleontological iconographic  
52 progression as they provide an unusual array of biological and structural information on non-  
53 biomineralized tissues in addition to the hard parts (Seilacher, 1970; Allison and Briggs, 1993;  
54 Muscente et al., 2017).

55 Some fossil taxa are well-known – if not famous – for their usefulness as scientific tools  
56 (such as for biostratigraphy, paleobiogeography, or determining the thermal maturity of their host  
57 rocks). They can represent exceptional snapshots in time, or ‘rear view mirrors’, for our understanding  
58 of pivotal evolutionary steps (such as the conquest of the air – *Archaeopteryx lithographica* – and the  
59 first steps onto land – *Ichthyostega stensioei* and its allies; e.g., Ostrom, 1976; Ahlberg and Clack,  
60 2006). Yet others are known for their beauty and alluring qualities, and still others for their interesting  
61 and convoluted research history (such as the Burgess Shale celebrity *Hallucigenia sparsa*; e.g.,  
62 Conway Morris, 1977; Gould, 1989; Ramsköld, 1992). Some species, however, easily fit into several  
63 of the above categories and one such example is the Cambrian, trilobite-like arthropod *Agnostus*  
64 *pisiformis*.

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

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

80

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

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

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

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

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

97 Although the species was first formally described by Wahlenberg already in 1818 (at  
98 that time as *E. pisiformis*) its history of research has considerably deeper roots. The first illustrations  
99 of *A. pisiformis* can actually be traced as far back in time as to the early part of the 18<sup>th</sup> century; the  
100 first account being that of Bromell (1729, p. 527) who published an illustration of the species covering  
101 an ‘Orsten’ slab (Fig. 2; see also Regnéll, 1949, p. 19, fig. 11; Ahlberg and Ahlgren, 1996; St. John,  
102 1997, 2007). Perhaps more importantly, or at least better known, Swedish naturalist extraordinaire  
103 Carl von Linné (known also under his latinized name Carolus Linnæus) also mentioned the presence  
104 of *A. pisiformis* in the southern Swedish provinces of Västergötland and Skåne, in his travel accounts  
105 (Linnæus, 1747, p. 24, 1751, p. 122; cf. Ahlberg and Ahlgren, 1996). Linné is actually credited as the  
106 author of the taxon in many literary sources (e.g., Westergård, 1922; Müller and Walossek, 1987; see  
107 also St. John, 1997). However, although Linné gave brief descriptions he never actually named it in a  
108 formal sense and it has subsequently been shown that the earliest valid reference to *pisiformis* appears  
109 to be that of Wahlenberg (1818) (see discussions by Rushton, 1978, p. 258; Ahlberg and Ahlgren,  
110 1996, p. 131; St. John, 1997, 2007).

### 113 2.1. Temporal and geographic distribution

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

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

## 132 3. The *Agnostus pisiformis*-bearing host rock

### 133 3.1. The Alum Shale Formation

134 The rocks hosting *A. pisiformis* in Scandinavia belong to the Alum Shale Formation (e.g., Martinsson,  
135 1974; Andersson et al., 1985; Bergström and Gee, 1985; Buchardt et al., 1997; Nielsen and Schovsbo,  
136 2007; Ahlberg et al., 2016; Rasmussen et al., 2017). During the latter half of the Cambrian Period,  
137 Scandinavia was largely covered by a widespread shallow and tranquil sea. Mud and fine-grained  
138 matter were slowly deposited and since the environment was very rich in organic matter and the  
139 oxygen levels were low, the bottom sediments became oxygen depleted, sometimes anoxic. This  
140 meant that not all organic matter could be broken down and a black mud was formed. With time and  
141 increasing pressure these muddy sediments were compacted and resulted in the dark grey to black,  
142 kerogen-rich shales and mudstones of the Alum Shale Formation. The total organic carbon values of  
143 the Alum Shales are between 2 and 22 wt% (e.g., Thickpenny, 1987; Buchardt et al., 1997; Egenhoff  
144 et al., 2015). This particular rock type occurs stratigraphically from the Cambrian Series 3 through the  
145 Tremadocian (Early Ordovician) (Bergström and Gee, 1985; Nielsen and Schovsbo, 2007) and a

146 maximum thickness of approximately 160 m has been estimated in southern Scandinavia (Nielsen and  
147 Schovsbo, 2007).

148 These rocks are extremely rich in fossils and dominated by different types of  
149 arthropods, with polymerid trilobites and agnostoids occurring *en masse* (e.g., Westergård, 1922,  
150 1946; Ahlberg, 2003; Terfelt et al., 2011; Rasmussen et al., 2017, and references therein). Like an  
151 ancient mass grave the sediments enclose a long vanished marine ecosystem that apparently was  
152 seething with life. The slow sedimentation of fine-grained matter during overall calm conditions  
153 rendered the strata very condensed, and calculations suggest that one to ten millimeters of shale  
154 represent approximately one thousand years of deposition (e.g. Thickpenny, 1987; Buchardt et al.,  
155 1997; Egenhoff et al., 2015). Recent studies have, however, shown that at times very shallow, even  
156 subaerial, conditions prevailed in proximal settings during the deposition of the Alum Shale Formation  
157 (e.g., Lehnert et al., 2012, 2013; Ahlberg et al., 2016).

158 Within these shales there are lenses and beds of another type of rock; a black to  
159 greyish-brown limestone colloquially known as ‘Orsten’ or stinkstone (Figs 1, 3). The latter name  
160 derives from the fact that the rock is so enriched in hydrocarbons that if it is cracked open with a  
161 hammer there is often a pungent stench of kerosene or crude oil. The name ‘Orsten’ (a Swedish name  
162 for stinkstone) is derived from an old veterinary term, as the limestone was processed and used for  
163 curing diseases in pigs and other domestic animals (Bromell, 1729; Regnéll, 1949; Berg-Madsen,  
164 1989). Regardless of the unflattering name, strange odor and dull color, these limestones can contain  
165 magnificently preserved microscopic fossils, known as the ‘Orsten’ fossils.

166

### 167 3.2. The ‘Orsten’ Konservat-Lagerstätte

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

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

185 The ‘Orsten’ Lagerstätte of Sweden is represented mainly by secondarily phosphatized  
186 arthropods (primarily crustaceans), in the size range of 2 mm or less (e.g. Müller, 1979; Walossek,  
187 1993; Waloszek, 2003; Maas et al., 2006; Eriksson et al., 2016). The fossils are impregnated with  
188 calcium phosphate, an excellent medium for preserving fossils in minute detail, including delicate  
189 ‘soft-tissue’ structures (Maas et al., 2006, and references therein). The discovery of this incredible  
190 faunal assemblage by Müller has since been followed by a sequence of investigations disclosing,  
191 among other things, morphological details of utmost interest for the evolution of, and relationships  
192 among, early arthropods (e.g., Maas et al. 2006, and references therein). After being identified in  
193 Sweden, ‘Orsten’ type fossils have been recorded from many parts of the world (Maas et al., 2006). In  
194 Sweden the ‘Orsten’ Lagerstätte spans approximately 10 million years. Taking into account also this  
195 type of deposit from other parts of the world, the ‘Orsten’ type deposits span the upper lower  
196 Cambrian through to possibly the lower Ordovician, thus altogether embracing some 30 million years  
197 (Maas et al., 2006; Eriksson and Waloszek, 2016). This also makes the ‘Orsten’ Lagerstätte quite

198 unique as most other Cambrian Lagerstätten are very restricted geographically as well as  
199 stratigraphically (e.g., Zhu et al., 2006).

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

211

#### 212 4. Anatomy and life mode of *Agnostus pisiformis*

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

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

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

242 Although much of the general morphology of the adult *A. pisiformis* was captured  
243 already in the meraspid instar stages, morphological changes are observed in both the test and  
244 appendages during ontogeny. The most notable change of the test probably comprises the above-  
245 mentioned separation of the tergites of the two anteriormost trunk segments from the initial pygidium,  
246 the former of which then forms the short thoracic region. In addition, there are changes in morphology  
247 and position of the cephalic and pygidial spines, changes in the horizontal axis of symmetry and  
248 pygidial axis (from a triangular to lanceolate form), a shift in position of the tergites and progressive  
249 development of tergal elevations, slight morphological changes in preglabellar and glabellar areas,

250 change in length/width ratio of the pygidial and cephalic shields, change in pattern and number of  
251 pores, and an overall progressive increase in convexity of the test (Müller and Walossek 1987, p. 26–  
252 27).

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

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

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

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

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

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

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

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

310

## 311 **5. ‘Breathing life’ into *Agnostus pisiformis***

312

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

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

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

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

351

### 352 *5.1. Sculpting process*



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

354 Positive, hand-modeled clay models of the external shields were first meticulously  
355 prepared (Fig. 6A, B, C), with careful reference to scientific descriptions, drawings, and photographs  
356 (Müller and Walossek, 1987; Walošek and Müller 1988). This initial model was made with a smooth  
357 surface (Fig. 6A, B, C). In order to add the walls of the polygonal surface texture visible in some well-  
358 preserved specimens (see Müller and Walossek, 1987, p.10, pls. 7, 8) we made a silicone skin mold  
359 from the smooth original model. Based on this negative mold a positive silicone cast was produced,  
360 which was subsequently used to make a negative wax mold (Fig. 6D–F) of the thoracic segments and  
361 cephalic and pygidial shields. The polygonal surface texture could then be engraved into the wax mold  
362 using a fine-tipped sculpting tool (Fig. 6E, F). Although time-consuming, engraving the pattern is  
363 considerably easier than trying to create such protruding fine structures directly on a positive model.  
364

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

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

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

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

401

402

403 *5.1.1. Enrolled version*

404

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

411

412

### 413 5.1.2. A ‘fake SEM’ version

414 In order to visualize how the actual fossils usually look while being studied in an SEM or in SEM-  
415 micrographs, a unique ‘fake SEM’ sculpture was also produced (Fig. 10C–F). We again used the  
416 existing molds to cast copies from ‘Acrylic One’, a two-component material consisting of a mineral  
417 powder and a water-based acrylic resin, thus basically forming an acrylic gypsum. Fine details such as  
418 hairs and bristles break off during de-molding and this actually mimics the incomplete and somewhat  
419 distorted nature of most fossil specimens. We also compressed and distorted the silicone molds of the  
420 shell-like cuticular cover of the animal late in the curing process of the acrylic gypsum so that the parts  
421 emerged looking exactly like the fossil – with compression features. As noted by Müller and Walossek  
422 (1987, p. 33), the appendages of the fossils are subjected to some *post mortem* distortion and  
423 dislocation. The incomplete legs, parts of the bristles and fragmented parts of the shields were  
424 arranged and glued together with ‘Acrylic One’ mixed with sand. We also brushed on a textile paint  
425 compound called Expantex. Expantex looks like a thick paint but when heated with a blow torch the  
426 paint will ‘pop’, almost like popcorn and transform into peculiar organic ‘coral-like’ structures  
427 resembling micro-crystal structures that is often seen as ‘noise’ (i.e., matrix and/or  
428 secondary/diagenetically grown phosphate) in the SEM micrographs.

429

## 430 6. Conclusions and future plans

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

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

449 We think that *A. pisiformis* is an exemplar in this regard, and a fitting ‘gateway’ into the  
450 world of the ‘Orsten’ fossils because of its alluring morphology, differing modes of preservation,  
451 scientific utility and status as an excellent index fossil, and, last but not least, its long research history.  
452 As a final – if somewhat biased – statement, we think that it is obligatory for today’s working

453 scientists to make research results accessible, understandable, and hopefully interesting, beyond the  
454 often arcane research community.

455

## 456 **Acknowledgements**

457 Grants to MEE from National Geographic (grant #GEFNE 143-15) and the Swedish Research Council  
458 (grant 2015-05084) funded this project. Thanks to Anders Lindskog (Lund), Peter Cederström (Eslöv)  
459 and John Ahlgren (Hällekis) for excellent field work assistance and company and everyone at *10 Tons*,  
460 Copenhagen, involved in the sculpting process. Our sincere thanks also to Dieter Waloszek (Ulm and  
461 Lund) for helpful discussions on the intricate morphology of *A. pisiformis* and for allowing us to use  
462 two images for this article, and to Per Ahlberg (Lund) for kindly providing a photograph used herein.  
463 David A.T. Harper (Durham), D. Waloszek and P. Ahlberg are gratefully thanked also for critically  
464 reading a draft of the manuscript. Finally, reviewers John Laurie and Joachim Haug, and journal editor  
465 André Strasser, made valuable comments that greatly improved the manuscript.

466

## 467 **References**

- 468 Ahlberg, P., 2003. Trilobites and intercontinental tie points in the Upper Cambrian of Scandinavia.  
469 *Geologica Acta* 1, 127–134.
- 470
- 471 Ahlberg, P., Ahlgren, J., 1996. Agnostids from the Upper Cambrian of Västergötland, Sweden. *GFF*  
472 118, 129–140.
- 473
- 474 Ahlberg, P., Eriksson, M.E., Lundberg, F., Lindskog, A., 2016. Cambrian stratigraphy of the Tomten-  
475 1 drill core, Västergötland, Sweden. *GFF* 138, 490–501.
- 476
- 477 Ahlberg, P.E., Clack, J.A., 2006. A firm step from water to land. *Nature* 440, 747–749.
- 478
- 479 Allison, P.A., Briggs, D.E.G., 1993. Exceptional fossils record: distribution of soft-tissue  
480 preservation through the Phanerozoic. *Geology* 21, 527–530.
- 481
- 482 Andersson, A., Dahlman, B., Gee, D., Snäll, S., 1985. The Scandinavian Alum Shales. *Sveriges*  
483 *Geologiska Undersökning Serie Ca* 56, 1–50.
- 484
- 485 Babcock, L.E., Peng, S., Ahlberg, P. 2017. Cambrian trilobite biostratigraphy and its  
486 role in developing an integrated history of the Earth system. *Lethaia*, DOI: 10.1111/let.  
487 12200.
- 488
- 489 Berg-Madsen, V., 1989. Origin and usage of the geological terms orsten, stinkstone, and anthraconite.  
490 *Archives Nat. Hist.* 16, 191–208.
- 491
- 492 Bergström, J., Gee, D.G., 1985. The Cambrian in Scandinavia. In Gee, D.G., Sturt, B.A. (Eds.), *The*  
493 *Caledonide Orogen – Scandinavia and Related Areas*, 247–271. Wiley, Chichester.
- 494
- 495 Bromell, M. von., 1729. *Lithographia Svecana. Acta Literaria (et Scientiarum) Sveciae Upsaliae*  
496 *publicata*, 2, continens annos 1725—29. Upsaliae & Stockholmia s.a.
- 497
- 498 Brongniart, A., 1822. Les Trilobites. In Brongniart, A., Desmarest, A.-G., *Histoire naturelle des*  
499 *crustacés fossiles, sous les rapports zoologiques et géologiques*, 1–65. F.G. Lavrault, Paris, 154 pp.
- 500
- 501 Buchardt, B., Nielsen, A.T., Schovsbo, N.H., 1997. Alunskiferen i Skandinavien. *Geologisk Tidsskrift*  
502 3, 1–30.

503  
504 Caron, J.-B., Rudkin, D., (Eds.), 2009. A Burgess Shale Primer. History, Geology, and Research  
505 Highlights. The Burgess Shale Consortium, Toronto. 108 pp.  
506  
507 Conway Morris, S., 1977. A new metazoan from the Cambrian Burgess Shale of British Columbia.  
508 Palaeontology 20, 623–640.  
509  
510 Cunningham, J.A., Rahman, I.A., Lautenschlager, S., Rayfield, E.J., Donoghue, P.C.J., 2014, A virtual  
511 world of paleontology. Trends Ecol. Evol. 29, 347–357.  
512  
513 Doyle, P., Robinson, E., 1993. The Victorian 'Geological Illustrations' of Crystal Palace  
514 Park. Proc. Geol. Assoc., 104, 181–194.  
515  
516 Edwards, W.N., 1967. The early history of palaeontology. Trustees Brit. Mus. (Nat. Hist.), London. 58  
517 pp.  
518  
519 Egenhoff, S.O., Fishman, N.S., Ahlberg, P., Maletz, J., Jackson, A., Kolte, K., Lowers, H., Mackie, J.,  
520 Newby, W., Petrowsky, M., 2015. Sedimentology of SPICE (Steptoean positive carbon isotope  
521 excursion): a high-resolution trace fossil and microfabric analysis of the middle to late Cambrian  
522 Alum Shale Formation, southern Sweden. The Geological Society of America Special Paper 515, 87–  
523 102.  
524  
525 Eriksson, M.E., 2014. Master of Puppets: sculpting ancient worlds. Geology Today 30, 98–104.  
526  
527 Eriksson, M.E., Terfelt, F., Elofsson, R., Marone, F., 2012. Internal soft-tissue anatomy of Cambrian  
528 'Orsten' arthropods as revealed by synchrotron X-ray tomographic microscopy. PLoS ONE 7(8):  
529 e42582. doi:10.1371/journal.pone.0042582.  
530  
531 Eriksson, M.E., Terfelt, F., Elofsson, R., Maas, A., Marone, F., Lindskog, A., Waloszek, D., Schmitz,  
532 B., Stampanoni, M., 2016. Baring it all: undressing Cambrian 'Orsten' phosphatocopine crustaceans  
533 using synchrotron radiation X-ray tomographic microscopy. Lethaia 49, 312–326.  
534  
535 Eriksson, M.E., Waloszek, D., 2016. Half a billion year old microscopic treasures – the Cambrian  
536 'Orsten' fossils of Sweden. Geology Today 32, 115–120.  
537  
538 Gould, S.J., 1989. Wonderful Life: The Burgess Shale and the nature of history. W.W. Norton &  
539 Company. New York. London. 347 pp.  
540  
541 Haug, J.T., Maas, A., Waloszek, D., 2010 (for 2009). †*Henningsmoenicaris scutula*, †*Sandtorpia*  
542 *vestrogothiensis* gen. et sp. nov. and heterochronic events in early crustacean  
543 evolution. Earth Environ. Sci. Trans. Royal Soc. Edinburgh 100, 311–350.  
544  
545 Jeppsson, L., Anehus, R., Fredholm, D., 1999. The optimal acetate buffered acetic acid technique for  
546 extracting phosphatic fossils. J. Paleontol. 73, 957–965.  
547  
548 Kaesler, R.L., (ed.) 1997. Treatise on Invertebrate Paleontology, Part O, Arthropoda 1, Trilobita,  
549 Revised. Volume 1. Geological Society of America and University of Kansas Press, Lawrence.  
550  
551 Lautenschlager, S., Rücklin, M., 2014. Beyond the print—virtual paleontology in science publishing,  
552 outreach, and education. J. Paleontol. 88, 727–734.  
553  
554 Lehnert, O., Calner, M., Ahlberg, P., Ebbestad, J.O., Harper, D.A.T., Meinhold, G., 2013. Palaeokarst  
555 formation in the early Palaeozoic of Baltoscandia – evidence for significant sea-level changes in a  
556 shallow epicontinental sea. Proceedings of the 3rd IGCP 591 Annual Meeting, 169–171. Lund,  
557 Sweden.

558  
559 Lehnert, O., Calner, M., Ahlberg, P., Harper, D.A.T., 2012. Multiple palaeokarst horizons in the  
560 Lower Palaeozoic of Baltoscandia challenging the dogma of a deep epicontinental sea. Geophysical  
561 Research Abstracts 14 EGU2012-11362-1, 2012. EGU General Assembly 2012.  
562  
563 Linnæus, C., 1747. Wästgöta-Resa, på Rikens högloflige Ständers befallning förrättad år 1746. Med  
564 anmärkningar uti oeconomien, naturkunnogheten, antiquiteter, inwånames seder och lefnads-sätt. Lars  
565 Salvius, Stockholm. (12)+284+(20) pp. [Several later eds.]  
566  
567 Linnæus, C., 1751, Skånska resa, på höga öfwerhetens befallning förrättad år 1749. Med rön och  
568 anmärkningar uti oeconomien, naturalier, antiquiteter, seder, lefnadssätt. Lars Salvius, Stockholm.  
569 (10)+xiv+434+(34) pp. [Several later eds.]  
570  
571 Maas, A., Braun, A., Dong, X.-P., Donoghue, P.C.J., Müller, K.J., Olempska, E., Repetski, J.E.,  
572 Siveter, D.J., Stein, M., Waloszek, D., 2006. The ‘Orsten’—more than a Cambrian Konservat-  
573 Lagerstätte yielding exceptional preservation. *Palaeoworld*  
574 15, 266–282.  
575  
576 Maas, A., Waloszek, D., Müller, K.J., 2003. Morphology, ontogeny and phylogeny of the  
577 Phosphatocopina (Crustacea) from the Upper Cambrian ‘Orsten’ of Sweden. *Fossils/Strata* 49, 1–238.  
578  
579 Martinsson, A., 1974. The Cambrian of Norden. In Holland, C.H. (Ed.), *Lower Palaeozoic rocks of the*  
580 *world, Vol. 2, Cambrian of the British Isles, Norden, and Spitsbergen*, 185–283. Wiley-Interscience,  
581 London.  
582  
583 Mayor, A. 2000. *The first fossil hunters*. Princeton University Press, Princeton, 361 pp.  
584  
585 Muscente, A.D., Schiffbauer, J.D., Broce, J., Laflamme, M., O'Donnell, K., Boag, T.H., Meyer, M.,  
586 Hawkins, A.D., Huntley, J.W., McNamara, M., MacKenzie, L.A., Stanley Jr., G.D., Hinman, N.W.,  
587 Hofmann, M.H., Shuhai Xiao, S., 2017. Exceptionally preserved fossil assemblages through geologic  
588 time and space. *Gondwana Res.* 48, 164–188.  
589  
590 Müller, K.J., 1964. Ostracoda (Bradiorina) mit phosphatischen Gehäusen aus dem Oberkambrium von  
591 Schweden. *Neues Jahrb. Geol. Paläontol., Abhandlungen* 121(1), 1–46.  
592  
593 Müller, K.J., 1979. Phosphatocopine ostracodes with preserved appendages from the Upper Cambrian  
594 of Sweden. *Lethaia* 12, 1–27.  
595  
596 Müller, K.J., 1982. Weichteile von Fossilien aus dem Erdaltertum. *Die Naturwissenschaften* 69, 249–  
597 254.  
598  
599 Müller, K.J., Hinz, I., 1991. Upper Cambrian conodonts from Sweden. *Fossils/Strata* 28, 1–153.  
600  
601 Müller, K.J., Walossek, D., 1987. Morphology, ontogeny, and life habit of *Agnostus pisiformis* from  
602 the Upper Cambrian of Sweden. *Fossils/Strata* 19, 1–124.  
603  
604 Müller, K.J., Walossek, D., 1988. External morphology and larval development of the Upper  
605 Cambrian maxillopod *Bredocaris admirabilis*. *Fossils/Strata* 23, 1–70.  
606  
607 Nielsen, A.T., Schovsbo, N.H., 2007. Cambrian to basal Ordovician lithostratigraphy in southern  
608 Scandinavia. *Bull. Geol. Soc. Denmark* 53, 47–92.  
609  
610 Ostrom, J.H., 1976. *Archaeopteryx* and the origin of birds. *Biol. J. Linnean Soc.* 8, 91–182.  
611  
612 Owen, R., 1854. *Geology and inhabitants of the ancient world*. Crystal Palace

613 Library and Bradbury & Evans, London.  
614  
615 Peng, S.C., Babcock, L.E., Geyer, G., Moczydlowska, M., 2006. Nomenclature of Cambrian epochs  
616 and series based on GSSPs. Comments on an alternative proposal by Rowland and Hicks. *Episodes* 29,  
617 130–132.  
618  
619 Peng, S.C., Babcock, L.E., Robison, R.A., Lin, H.L., Rees, M.N., Saltzman, M.R., 2004. Global  
620 Standard Stratotype-section and Point (GSSP) of the Furongian Series and Paibian Stage (Cambrian).  
621 *Lethaia* 37, 365–379.  
622  
623 Peng, S.C., Babcock, L.E., Zuo, J.X., Lin, H.L., Zhu, X.J., Yang, X.F., Robison, R.A., Qi, Y.P.,  
624 Bagnoli, G., Chen, Y., 2009. The Global boundary Stratotype Section and Point of the Guzhangian  
625 Stage (Cambrian) in the Wuling Mountains, northwestern Hunan, China. *Episodes* 32, 41–55.  
626  
627 Peng, S.C., Robison, R.A., 2000. Agnostoid biostratigraphy across the Middle-Upper Cambrian  
628 boundary in Hunan, China. *Mem. Paleontol. Soc.*, 53, 1–104.  
629  
630 Ramsköld, L., 1992. The second leg row of *Hallucigenia* discovered. *Lethaia* 25, 221–224.  
631  
632 Rasmussen, B.W., Rasmussen, J.A., Nielsen, A.T., 2017. Biostratigraphy of the Furongian (upper  
633 Cambrian) Alum Shale Formation at Degerhamn, Öland, Sweden. *GFF* 139, 92–118.  
634  
635 Regnéll, G., 1949. On the position of palaeontology and historical geology in Sweden before 1800.  
636 *Arkiv Mineral. Geol.* 1, 1–64.  
637  
638 Robison, R.A., 1975. Species diversity among agnostoid trilobites. *Fossils Strata* 4, 219–226.  
639  
640 Rushton, A.W.A., 1978. Fossils from the Middle-Upper Cambrian transition in the Nuneaton district.  
641 *Palaeontology* 21, 245–283.  
642  
643 Seilacher, A., 1970. Begriff und bedeutung der Fossil-Lagerstätten. *Neues Jahrb. Geol. Paläontol.*  
644 *Monatshefte* 1970, 34–39.  
645  
646 Stein, M., Waloszek, D., Maas, A., Haug, J.T., Müller, K.J., 2008. The stem crustacean *Oelandocaris*  
647 *oelandica* re-visited. *Acta Palaeontol. Pol.* 53, 461–484.  
648  
649 St. John, J., 1997. Who is the author of *Agnostus pisiformis*?: The Trilobite Papers 9, 14–17.  
650  
651 St. John, J., 2007. The earliest trilobite research (antiquity to the 1820s). In Mikulic, D.G., Landing,  
652 E., Kluesendorf, J. (Eds.), *Fabulous Fossils—300 Years of Worldwide Research on Trilobites*. New  
653 York State Museum Bulletin 507, 201–211.  
654  
655 Terfelt, F., Ahlberg, P., Eriksson, M.E., 2011. Complete record of Furongian polymerid trilobites and  
656 agnostoids of Scandinavia – a biostratigraphical scheme. *Lethaia* 44, 8–14.  
657  
658 Thickpenny, A., 1987. Palaeo-oceanography and depositional environment of the Scandinavian Alum  
659 Shales: sedimentological and geochemical evidence. In Leggett, J.K., Zuffa, G.G. (Eds.): *Marine*  
660 *clastic sedimentology – concepts and case studies*, pp. 156–171. Graham & Trotman, London.  
661  
662 Vinther, J., Nicholls, R., Lautenschlager, S., Pittman, M., Kaye, T.G., Rayfield, E., Mayr, G., Cuthill,  
663 I.C., 2016. 3D Camouflage in an Ornithischian Dinosaur. *Current Biol.* 26, 2456–2462.  
664  
665 Wahlenberg, G., 1818. *Petrificata telluris svecanae*. *Nova Acta Regiae Societatis Scientiarum*  
666 *Upsaliensis* 8, 1–116. [The title page of the volume is dated 1821, but Wahlenberg's memoir was  
667 printed 1818, as stated on p. 293 in the same volume.]

668  
669 Walossek, D., 1993. The Upper Cambrian *Rehbachella kinnekullensis* Müller, 1983, and the  
670 phylogeny of Branchiopoda and Crustacea. *Fossils Strata* 32, 1–202.  
671  
672 Walossek, D., Müller, K.J., 1990. Upper Cambrian stem-lineage crustaceans and their bearing upon  
673 the monophyletic origin of Crustacea and the position of *Agnostus*. *Lethaia* 23, 409–427.  
674  
675 Waloßek, D., Müller, K.J., 1988. Über die ventralmorphologie und Ökologie von *Agnostus*. *Der*  
676 *Geschiebesammler* 22, 11–38.  
677  
678 Waloszek, D., 2003. The 'Orsten' window – a three-dimensionally preserved Upper Cambrian  
679 meiofauna and its contribution to our understanding of the evolution of Arthropoda. *Paleontological*  
680 *Research* 7, 71–88.  
681  
682 Westergård, A.H., 1922. Sveriges olenidskiffer. Sveriges Geologiska Undersökning Ca 18, 1–205.  
683  
684 Westergård, A.H., 1946. Agnostidea of the Middle Cambrian of Sweden. Sveriges Geologiska  
685 Undersökning Serie C 477, 1–141.  
686  
687 Whittington, H.B., 1985. The Burgess Shale. Yale University Press, New Haven, 151 pp.  
688  
689 Zhu, M.Y., Babcock, L.E., Peng, S.C., 2006. Advances in Cambrian stratigraphy and paleontology:  
690 integrating correlation techniques, paleobiology, taphonomy and paleoenvironmental reconstruction.  
691 *Palaeoworld* 15, 217–222.  
692

693

## 694 **Figures**

695

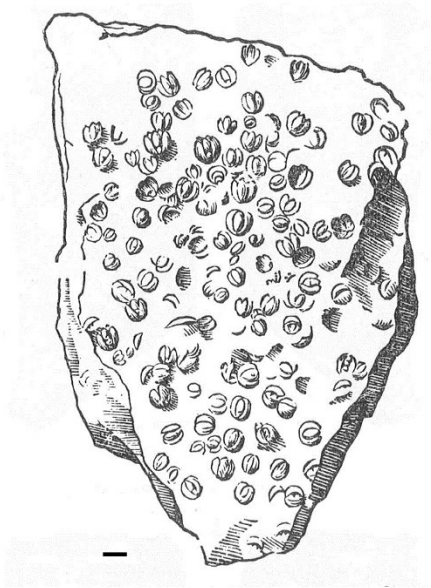


696

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



701 Photograph courtesy of P. Ahlberg (Lund University) and used with kind permission. [Single-column  
702 image]  
703

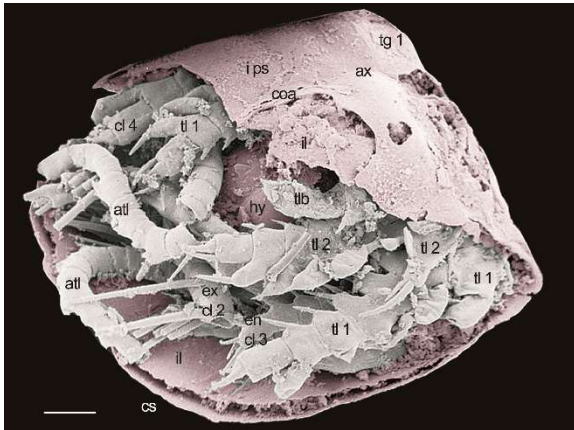


704  
705  
706 **Fig. 2.** The very first illustration of *Agnostus pisiformis* from the Swedish Alum Shale Formation. The  
707 specimens are preserved on the bedding plane surface of an ‘Orsten’ rock slab from Varnhem in the  
708 province of Västergötland, southern Sweden. Scale bar is ca. 3.5 mm. From Bromell (1729, p. 527; cf.  
709 Regnéll, 1949). [Single-column image]  
710



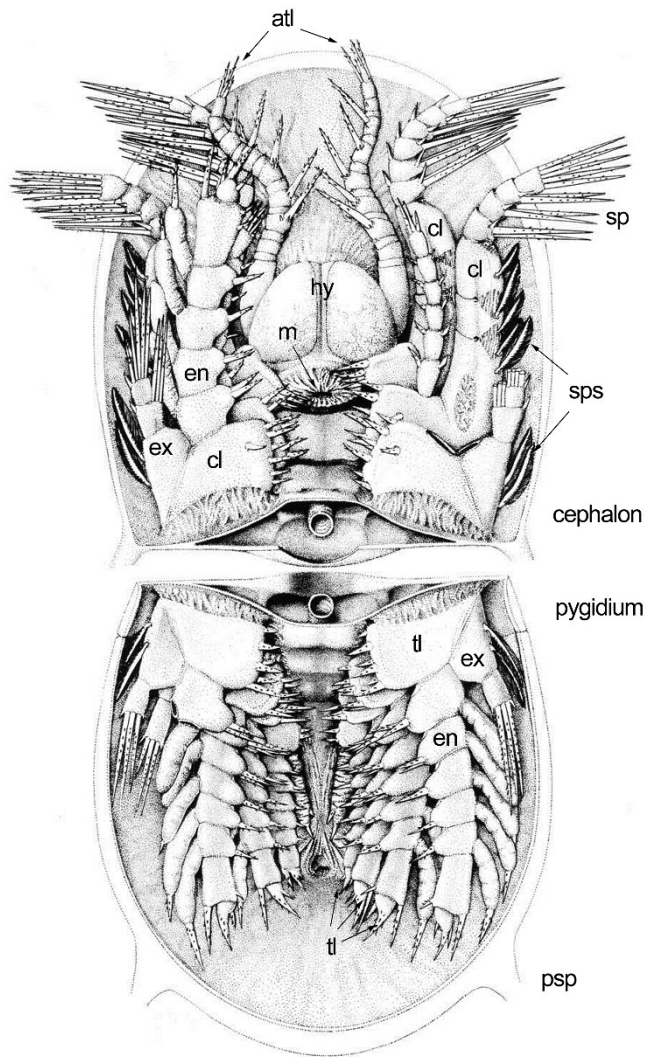
711  
712  
713 **Fig. 3.** An lens-shaped ‘Orsten’ nodule (ca. 0.7 m in diameter) enveloped by the paper thin black  
714 layers of Alum shale from the abandoned quarry at Andrarum in Skåne, the southernmost province of  
715 Sweden. The greenish-brown tint seen on the convex ‘Orsten’ nodule is a consequence of weathering  
716 combined with some lichen, and the yellowish tint seen in some patches on the surrounding shale is a  
717 result of weathered iron and sulphur compounds [Single-column image]  
718





719  
 720  
 721  
 722  
 723  
 724  
 725  
 726  
 727  
 728  
 729  
 730  
 731

**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 (pygidial) shield (artificially colored pink to distinguish it from the ‘soft integument’ structures). Abbreviated descriptive terms: atl = antennulae; 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 1 = 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]



732  
 733  
 734  
 735  
 736  
 737  
 738  
 739  
 740  
 741  
 742

**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 Waloszek 1987). Abbreviated descriptive terms: atl = antennulae; 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]



743  
 744  
 745  
 746  
 747  
 748  
 749  
 750  
 751

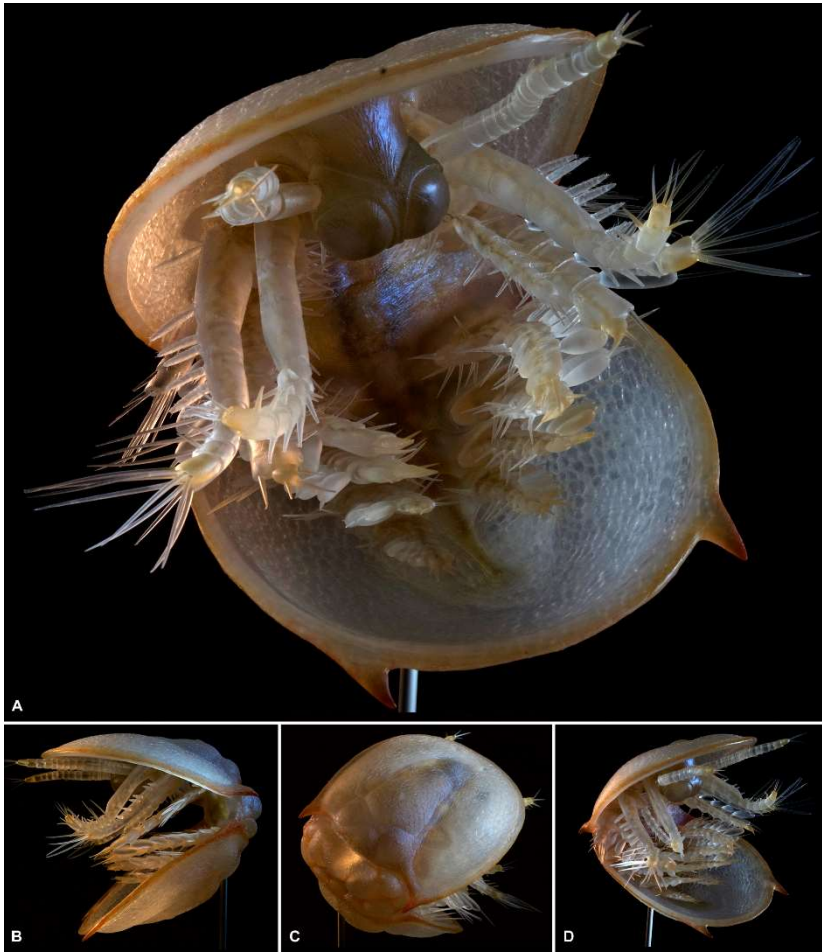
**Fig. 6.** The meticulous step-wise process of sculpting an enlarged reconstruction of *Agnostus pisiformis*. A–C. The initial, hand-sculpted clay model. D–F. Negative wax mold versions into which the polygonal surface texture is engraved. G–H. Monster clay versions of the inner side of the cephalic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



752  
753  
754  
755  
756  
757  
758  
759

**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 pygidial 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]





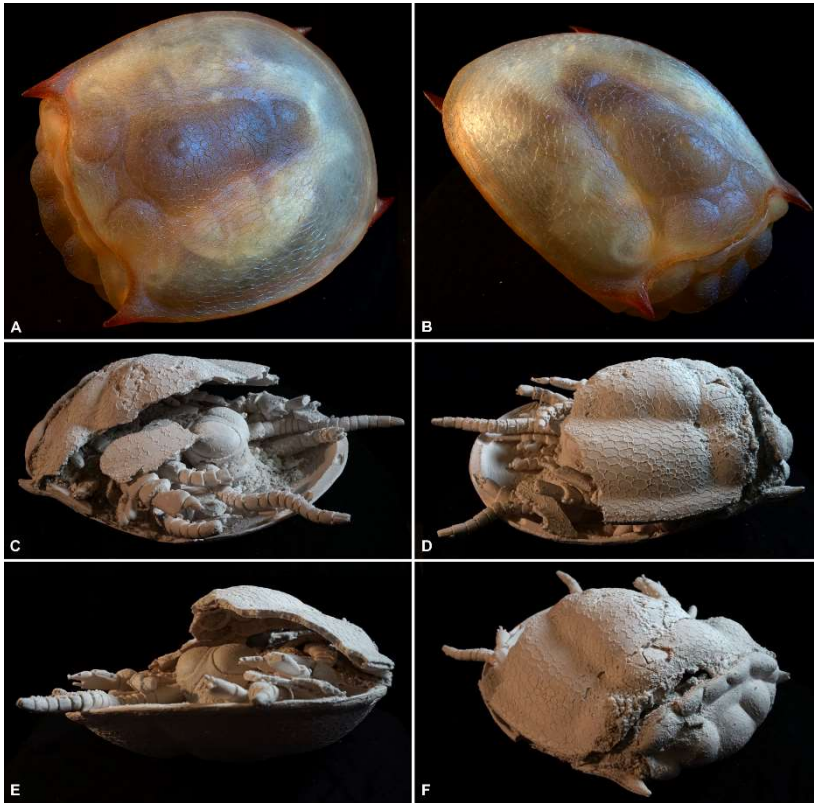
760  
761  
762  
763  
764

**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]



765  
766  
767  
768

**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]



770  
 771  
 772  
 773  
 774

**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]