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

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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 18th 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

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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**

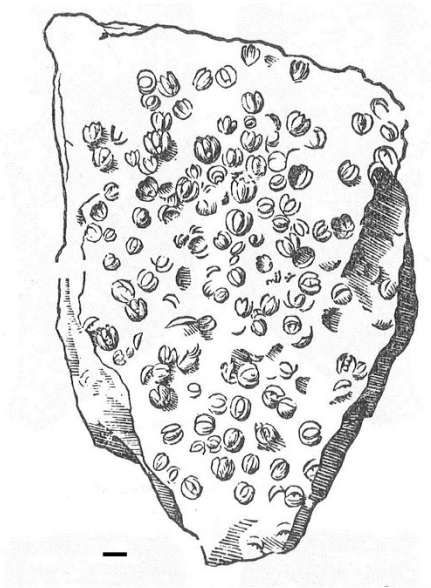
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696

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.

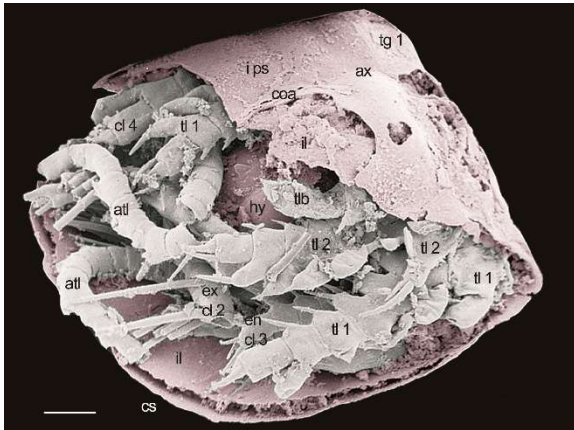
701 Photograph courtesy of P. Ahlberg (Lund University) and used with kind permission. [Single-column
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706 **Fig. 2.** The very first illustration of *Agnostus pisiformis* from the Swedish Alum Shale Formation. The
707 specimens are preserved on the 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]
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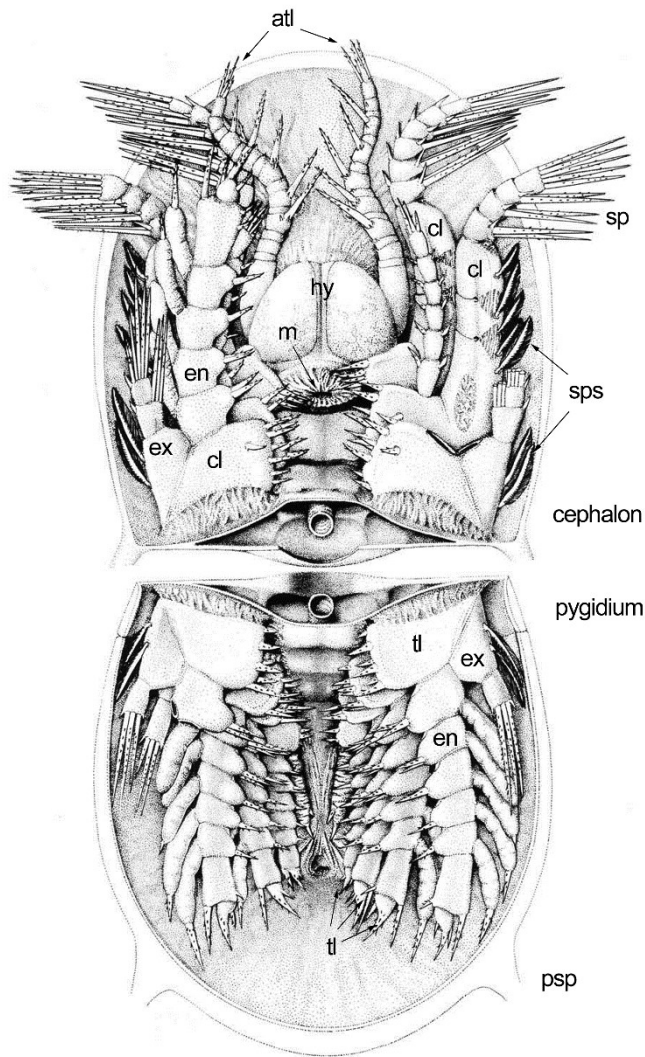


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713 **Fig. 3.** An lens-shaped ‘Orsten’ nodule (ca. 0.7 m in diameter) enveloped by the paper thin black
714 layers of Alum shale from the abandoned quarry at Andrarum in Skåne, the southernmost province of
715 Sweden. The greenish-brown tint seen 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]
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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; ips = 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]



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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]



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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]



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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]



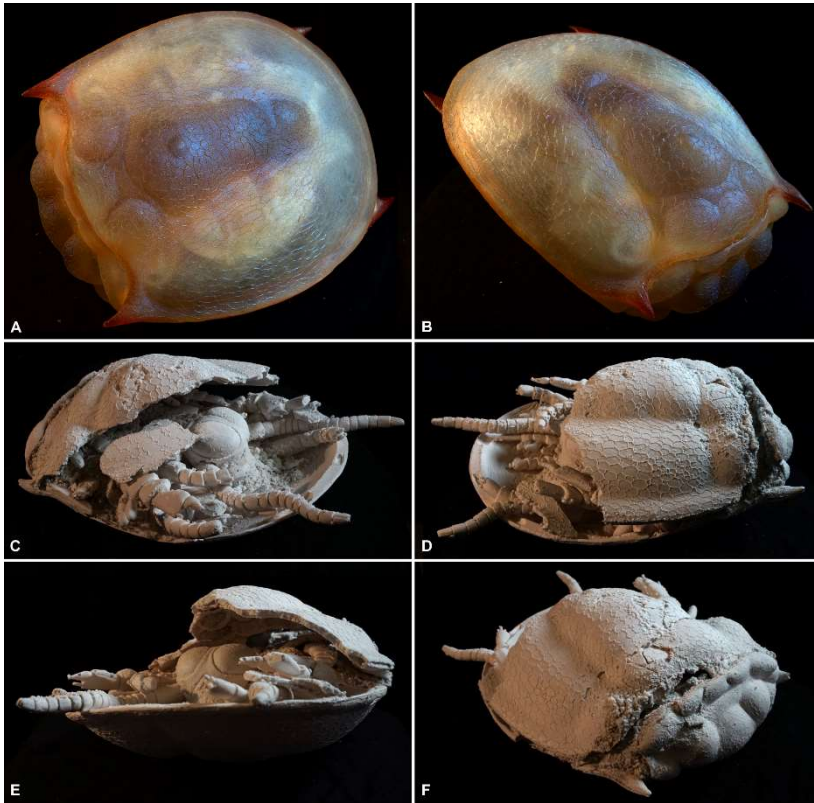
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Fig. 8. The final, life-like sculpture of a late meraspid instar stage of *Agnostus pisiformis* with shields in semi-open ('swimming') position; seen from different views (A–D). [double-column image]



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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]



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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]