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The Burgess Shale animal *Oesia* is not a chaetognath: A reply to Szaniawski (2005)

SIMON CONWAY MORRIS

The Middle Cambrian *Oesia disjuncta*, a monospecific genus, is known only from the celebrated Burgess Shale of British Columbia. It has been re-interpreted by Szaniawski (*Acta Palaeontologica Polonica* 50:1–8; 2005) as a chaetognath, a distinctive phylum whose exact position in the protostomes is still controversial. Unequivocal chaetognaths, that have no similarity to *Oesia*, are already known to occur in the Chengjiang Lagerstätte (Lower Cambrian, S.W. China), and here I describe the first example of a chaetognath from the Burgess Shale itself. Comparisons between *Oesia* and chaetognaths fail to find any significant homologies. Whilst the phyletic position of *Oesia* is very uncertain, a place in the hemichordates may be worth exploring.

Introduction

Significant advances in metazoan phylogeny (e.g., Philippe et al. 2005; Dunn et al. 2008) continue to have wide-ranging implications for our understanding of evolution, not least in terms of the Cambrian “explosion”. New phylogenetic configurations have brought into evolutionary juxtaposition major groups which classical zoology had long regarded as only distantly related. These new trees are achieving a degree of stability, and necessarily beg the question as to what the common ancestors may have looked like, no easy task given their existing disparity. Important as these advances are, it is important to stress that this area by no means involves a one-way traffic, whereby relevant information is available only from molecular data. In principle, the fossil record can also contribute important, arguably unique, insights. In this context, Burgess Shale-type faunas are well known not only for their extraordinary fossil preservation but also serving as repositories of unfamiliar, even bizarre, animals whose phylogenetic status is a topic of active debate. Phylogenies of early metazoan evolution are drawing on fossil groups which until a few years ago would have simply been treated as “extinct phyla”, but are now realized to be at least potential stem-groups of known phyla and accordingly can throw key, and often unexpected, light on the assembly of bodyplans. Nevertheless, whilst there have been successes, or at least fertile hypotheses, a significant number of Burgess Shale-type taxa are still phylogenetically refractory and therefore a focus of renewed scrutiny.

Institutional abbreviation.—USNM, National Museum of Natural History, Washington, D.C., USA.

Is *Oesia* really a chaetognath?

Of the taxa from Burgess shale-type deposits that are phylogenetically controversial, one such example requiring investigation is *Oesia disjuncta* (hereafter referred to as simply *Oesia*, on account of its monospecificity). To date this animal has only been recorded from the Burgess Shale (Fig. 1A, B, D). The discoverer of this famous deposit, Charles Walcott, described it as a polychaete annelid (Walcott 1911; see also Tarlo 1960), but Lohmann (1922, 1933–1934) reassigned *Oesia* to the appendicularian tunicates. Since then, however, this animal has only received sporadic and passing mention (e.g., Whittington 1971: 1174; Conway Morris 1979: 336), while in *The Fossils of the Burgess Shale* (Briggs et al. 1994) it is not even illustrated (but see p. 221 where it is listed). Based on a re-examination of photographs, but not the original material located in the National Museum of Natural History (Washington, D.C.), Szaniawski (2005) has argued that *Oesia* is best assigned as a chaetognath.

If it were correct, such an interpretation would be important for several reasons. Although the chaetognaths were for long allied to the deuterostomes, with the renaissance in the study of metazoan phylogeny and the major reassessments driven by molecular data, it was to be expected that notwithstanding their very characteristic and distinct bodyplan their place within the deuterostomes (or elsewhere) would have been rapidly resolved. This, however, has not proved to be the case (Bull and Miller 2006), and as Hausdorf et al. (2007: 2727) noted “the phylogenetic position of chaetognaths ... remains elusive”. Thus whilst it is now clear that chaetognaths are protostomes (e.g., Papillon et al. 2004), there remain significant divergences in opinion and it is widely conceded that long branch attraction remains a serious impediment (e.g., Podsiadlowski et al. 2008; see also Halanych 1996). Earlier proposals for a relationship to the ecdysozoans (e.g., Halanych 1996; Zrzavy et al. 1998) continue to receive some support, with a possible relationship to the priapulids being mooted (Helmkamp et al. 2008). Others, however, identify a relationship to the lophotrochozoans as more likely (e.g., Matus et al. 2006; see also Haase et al. 2001), whilst yet others argue that the chaetognaths are more basal and possibly a sister group to all other protostomes (e.g., Marlétaz et al. 2006; Helfenbein et al. 2004; see also Halanych 2004). Continuing work appears to lean in favour of a lophotrochozoan relationship, but unfortunately, these recent studies still make it difficult to distinguish between the two latter alternatives (Matus et al. 2007).

Whilst the exact position of the chaetognaths in the scheme of metazoan phylogeny may be difficult to pin down, a broadly basal position evidently has major implications for both the nature of ancestral triploblasts as well as their functional morphology and ecology. Thus chaetognaths might be informative as to key ancestral characters within the bilaterian metazoans, including embryology (e.g., Shimotori and Goto 2001), the nature of the mesoderm (e.g., Shinn 1994) and also the musculature (e.g., Casanova and Duvert 2002), as well as coelomic body cavities and the fate of the blastopore. In addition, the spinose protoconodonts which appear at the dawn of the Cambrian explosion, are reliably attributed to the chaetognaths (e.g., Szaniawski 2002). This is consistent with this group being amongst the earliest effective predators in the pelagic realm (e.g., Hu et al. 2007), and has important implications for the exploitation of higher trophic levels by basal lophotrochozoans, if not basal triploblasts.

Nevertheless, as with a few other phyla e.g., sipunculans, the chaetognaths have a very conservative bodyplan, and even the specialized denizens of the hydrothermal vent community show little modification (Casanova and Moreau 2005). Similarly the few innovations, notably the development of limb-like appendages, are evidently autapomorphic novelties and have no wider phylogenetic context (Casanova et al. 2003). Given this anatomical uniformity, then clearly any palaeontological data relevant to the origin and early history of chaetognaths would be of very considerable interest.

Here I suggest that the claim for *Oesia* being material to this argument (Szaniawski 2005) is difficult to substantiate. Whilst this assignment by Szaniawski has already been treated with considerable skepticism (Vannier et al. 2006), other authors have evidently either kept an open mind (Hu et al. 2007; in passing I might note that their claim that I have reinterpreted the Burgess Shale fossil *Nectocaris* as a chaetognath (Conway Morris 1998) is a misunderstanding) or more significantly have supported this proposal to the extent of annotating illustrations of *Oesia* with ostensible chaetognathic descriptors (Bull and Miller 2006). Accordingly, it is timely to assess the evidence for and against *Oesia* being any sort of chaetognath. While a full redescription of *Oesia* is still necessary, the thesis put forward by Szaniawski can be questioned on the basis of two lines of evidence. First, on the basis of my investigations I argue that *Oesia* has no meaningful similarity to any known chaetognath. Nor does there appear to be any compelling to identify this taxon as either a stem-group chaetognath or some other basal protostome that might be allied to this enigmatic phylum. In fairness this begs the question of what any such stem-group would actually look like given the morphological isolation of the chaetognath bodyplan, but as suggested below there is little a priori evidence from *Oesia* to support this view. Second, and more tellingly, unequivocal chaetognaths are known from Burgess Shale-type localities, and to date those described have no significant similarity to *Oesia*.

The basis of Szaniawski's (2005: 4) analysis is, of course, that there are "numerous close structural similarities" between *Oesia* and chaetognaths.

A key feature would be the diagnostic grasping spines, yet Szaniawski (2005: 4) concurs that these are "not [...] well-

preserved". My close examination of the available suite of *Oesia* leads me to conclude that no trace of grasping spines is evident (Fig. 1A₃, B, D₃), and their highly tentative identification in one specimen (Szaniawski 2005: figs. 1C, 2C; see also Tarlo 1960: fig. 3) cannot be substantiated. Szaniawski (2005) explains this difficulty by using a taphonomic explanation, specifically suggesting that the grasping spines might have been vulnerable to selective destruction in the sediments of the Burgess Shale. Such selectivity is, of course, common-place in taphonomy, but it is less plausible in the context given that the putative spines would be chitinous, and thus presumably similar to otherwise well-preserved chitinous bodies of the numerous arthropods. To be sure, Szaniawski's (2005) proposal echoes the earlier hypothesis of Butterfield (2003) who argued that the principal taphonomic filter in the Burgess Shale is destruction of non-extracellular structures. On this basis he argued that a chaetognath affinity for the worm *Amiskwia* was far more probably than hitherto thought (see Conway Morris 1977). There appears, however, to be no meaningful similarity between *Amiskwia* and *Oesia*, and so no compelling reason to accept *Amiskwia* (or indeed *Oesia*) as a chaetognath.

The identification of other purported chaetognathan features in *Oesia* are also questionable. There is, for example, little evidence for lateral fins (Fig. 1A₅), although one needs to note that in the definitive Cambrian chaetognaths (see below) the evidence for fins (most likely originally delicate and apparently lacking fin rays) is tenuous. A stronger argument might be made on behalf of the identification of the supposed tail fin. It is difficult to see, however, any close similarity to the equivalent area in chaetognaths. This is because in *Oesia* this posterior-most region appears to have had a three-dimensional arrangement composed of a series of plate-like structures (Fig. 1A₂). Whilst one cannot dismiss such an arrangement typifying a stem-group chaetognath, at the least this configuration begs a radical re-organization of the posterior region. Finally, although putative "seminal vesicles" are identified in one specimen, and conceivably represent reproductive tissue, given the general lack of correspondence between *Oesia* and any chaetognath this comparison would seem to carry less weight. So too other similarities would appear to be generalized and lack specificity. This applies particularly to the transverse structures, whilst I regard the identification of a ventral ganglion and the possible location of the anus as, at best, equivocal.

Cambrian chaetognaths

It can be concluded that the similarities between *Oesia* and the chaetognaths certainly merit discussion, but in no case can a diagnostic comparison e.g., unequivocal cephalic spines, be arrived at that would serve to support the affinity as proposed by Szaniawski (2005). This conclusion is reinforced by the existence of unequivocal chaetognath material from Burgess Shale-type deposits. Szaniawski (2005) is dismissive of the Lower Cambrian taxon *Eognathacantha ercainella* from the Chengjiang Lagerstätte of Yunnan, SW China (Chen and Huang 2002). Whilst the illustrations in this short report are not entirely satisfactory, and combined

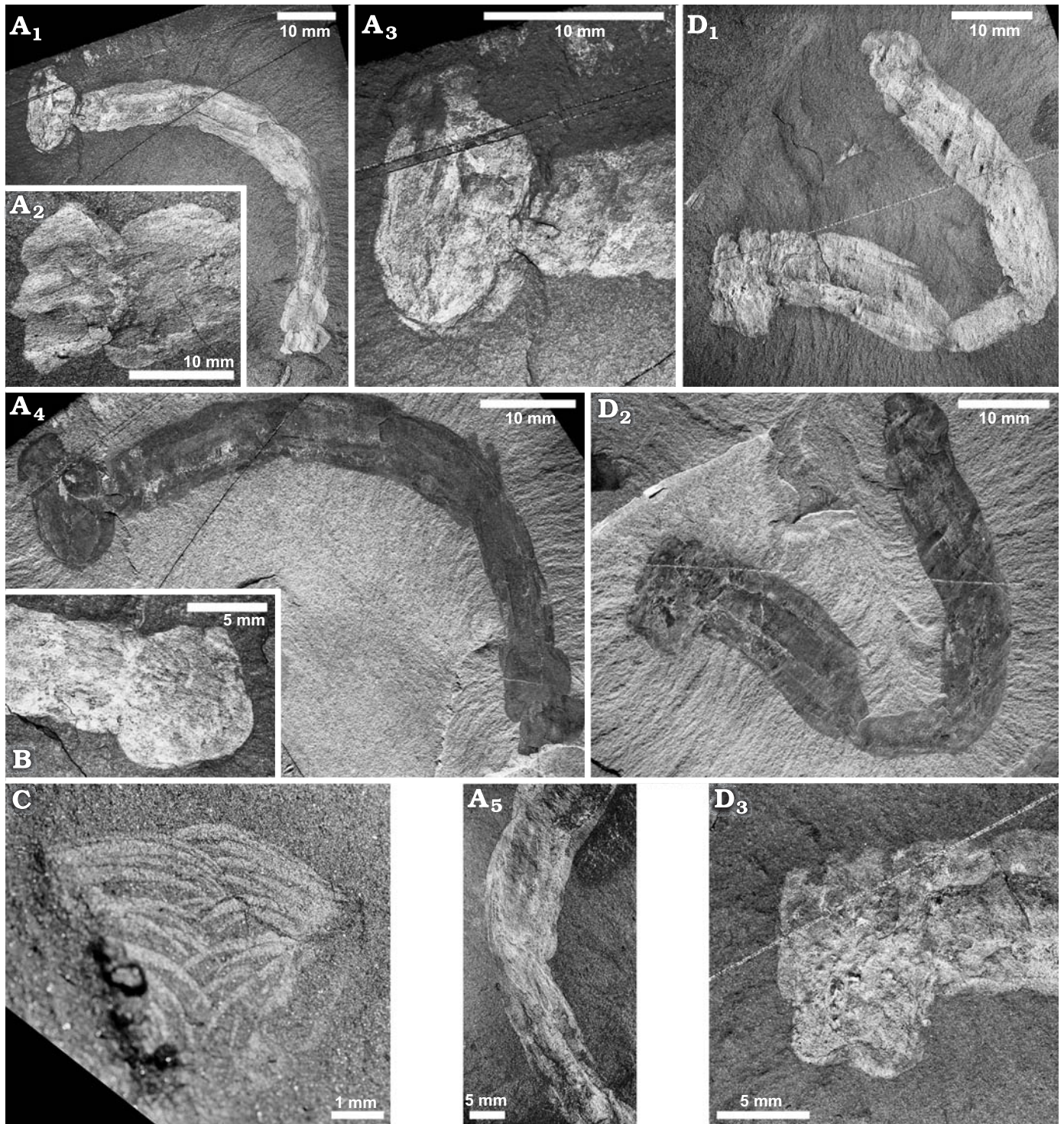


Fig. 1. A possible hemichordate *Oesia disjuncta* Walcott, 1911 (A, B, D) and an undescribed chaetognath (C), both from the Burgess Shale (Phyllopod bed), Middle Cambrian, British Columbia, Canada. A. USNM 57630 (part A₁, A₃, A₄; counterpart A₂, A₅), showing entire specimen in high (A₁) and low (A₄) angle light, and details of posterior (A₂), anterior (A₃) and mid-sections (A₅). B. USNM 57632, details of anterior end. C. USNM 199540, showing array of feeding spines, interlocking, in bilateral arrangement. D. USNM 57631, showing entire specimen in high (D₁) and low (D₂) angle light, and detail of anterior (D₃). Scale bars 10 mm (A₁–A₄, D₁, D₂), 5 mm (A₅, B, D₃), and 1 mm (C).

with the fact that Chen and Huang (2002) are relatively cautious in their assessment, so Szaniawski's (2005) scepticism has some basis. However, better illustrations of the same specimen (Chen 2004: figs. 347–348) are again consistent with the chaetognath in-

terpretation. Moreover, although not mentioned by Szaniawski (2005) there is an independent report of a Chengjiang chaetognath (*Protosagitta spinosa*) by Hu (in Chen et al. 2002: 166–167, text-fig. 8-1.3, pl. 17: 6). Here too the diagnostic grasping appara-

tus is visible, and subsequent research (Vannier et al. 2005, 2006) confirms the systematic position of this fossil. Both *Eognathacantha* and *Protosagitta* are described on the basis of unique specimens, and the relationships between these two taxa (including possible synonymy) remain to be established. Whilst Vannier et al. (2005) accept Szaniawski's (2005) placement of *Oesia*, they add no new information nor attempt to explain the manifest differences between this taxon and *Protosagitta* (and *Eognathacantha*).

In addition, there are additional records of soft-bodied chaetognaths from the slightly younger Burgess Shale of British Columbia. A number of specimens that are strikingly similar to the Chengjiang material were collected by the Royal Ontario Museum excavations (Desmond Collins, personal communication 2000) and they are presently under investigation by Jean-Bernard Caron and Derek E.G. Briggs. Independently, and many years ago, I noticed in the collections of the USNM a fossil that I interpret as a part of the anterior of a chaetognath. This specimen (USNM 199540; see also Conway Morris (1998: 115) is now illustrated here (Fig. 1C). The specimen was evidently collected by Charles Walcott, and clearly comes from the celebrated Phyllopod bed. I deliberately leave the specimen in open nomenclature, given that more complete material is in the process of description by others.

The specimen (Fig. 1C) displays the following features. The most striking component is the two sets of grasping spines that overlap. Those of the left-hand side are relatively expanded in configuration, and about 12 spines are identifiable. On the right-hand side the arrangement is more crowded with extensive overlapping, but at least 16 spines can be counted. So far as can be discerned the spines of either side originated in a single row. The individual spines are all similar, of about the same size, have a recurved shape, and are relatively slender, albeit expanding towards the points of insertion. There are also some traces of soft tissue to the posterior, but the nodule-like structures are foreign to the specimen and presumably diagenetic.

The specimen is most likely somewhat decayed, but it is similar to the grasping apparatus of extant chaetognaths. This would explain the juxtaposition of right and left sides, as well as the absence of softer tissue. Moreover, their overall morphology and arrangement is directly comparable to the equivalent spines in the chaetognaths from the Chengjiang Lagerstätte (see, in particular, Vannier et al. 2007: fig. 1d, e). So too the shape of the individual spines is strongly reminiscent of the protoconodont elements which are plausibly identified as derived from chaetognaths (e.g., Doguzhaeva et al. 2002; Szaniawski 2002). This specimen, however, has no similarity to *Oesia*, and is further evidence against assigning this animal to the chaetognaths. The well-preserved grasping spines seen in this specimen also directly contradict Butterfield's (2003) taphonomic hypothesis, and provide no support for *Amiskwia* being a chaetognath (see Conway Morris 1977).

Study of the Cambrian "explosion" and especially Burgess Shale-type faunas has been shaken up by various attempts to assign supposedly "bizarre" fossils to stem-groups, even though they have bodyplans (e.g., halkieriids, vetulicolians, vetulicystids, yunnanozoans) radically at odds with popular assumptions as to the supposed, albeit hypothetical, appearance of ancestors of familiar phyla. In the case of the chaetognaths it needs to be

acknowledged that their conservative bodyplan, combined with an enigmatic phylogenetic position, makes it sensible to re-assess critically the fossil record in the hope of finding forms that might potentially elucidate the wider relationships and deeper origins of this intriguing group. To a limited extent this has already been achieved with the soft-part record of Lower Cambrian chaetognaths from the Chengjiang Lagerstätte, notably the evidence (albeit tentative) for the more or less continuous lateral fin-fold and the apparent absence of fin-rays (Chen 2004). To include *Oesia* in this schema is not only hypothetical, but demands a set of arbitrary transformations. Similar remarks apply with equal force to *Amiskwia*.

If *Oesia* is excluded from the chaetognaths, it will be important to resolve its wider relationships. Its overall morphology is vaguely reminiscent of a balanoglossid hemichordate, with the anterior and swollen region conceivably comparable to the diagnostic proboscis. So too the sometimes prominent transverse structures that are generally regarded as segmental divisions and/or musculature conceivably housed gill openings. New material collected by the Royal Ontario Museum (Jean-Bernard Caron, personal communication 2007) may help to resolve some of these issues.

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