Discussion

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Fossil chaetognaths from the Burgess Shale: A reply to Conway Morris (2009)

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Walcott (1911) erected the new genus and species *Oesia disjuncta* and assigned them to the polychaete annelids, based on a small collection of similar fossils from the famous Middle Cambrian Burgess Shale. In 2002 I suggested that the species is "possibly related to chaetognaths" (Szaniawski 2002: 405). Later, after obtaining new photos of the specimens and making comparative investigations with the extant chaetognaths, I was able to describe many significant similarities, and came to the conclusion that *O. disjuncta* indeed is an ancestral chaetognath (Szaniawski 2005). This interpretation already has been accepted in several publications (Vannier et al. 2005; Ball and Miller 2006; Hu et al. 2007. Giribet 2008). Ball and Miller (2006: 594) confirmed not only its "... remarkable resemblance to modern chaetognaths" but also correctness of recognition of all its organs. They even reproduced a part of my illustration showing them (Ball and Miller 2006: fig. 2). Vannier et al. (2006: 629) combined the problem with the open question of the systematic position of another Burgess Shale fossil *Amiskwia sagittiformis* Walcott, 1911, and expressed their reservation based on "...the lack of clear evidence of a grasping apparatus...". Only Conway Morris (2009) firmly disagreed with this diagnosis and even devoted a special "discussion" article addressing the issue. However, that article contains several ambiguities and misunderstandings which need clarification.

On the second page of the discussion paper Conway Morris (2009: 176) made the following definitive statement: "I argue that *Oesia* has no meaningful similarity to any known chaetognath". However on the next column of the same page he presents quite a different opinion: "It can be concluded that the similarities between *O. disjuncta* and the chaetognaths certainly merit discussion". Nevertheless, according to this author the lack of recognizable grasping spines in *O. disjuncta*, as well as its dissimilarity to the two specimens of chaetognaths recently found in the Lower Cambrian of Chengjiang locality (Chen and Huang 2002; Chen et al. 2002; Chen 2004) and to the unnamed specimen of grasping apparatus newly reported by him from the Burgess Shale (Conway Morris 2009: fig. 1C) proves the lack of its affinity with chaetognaths.

Presenting the first of the arguments, the author did not take into account that the grasping apparatus of chaetognaths can be seen well only in specimens in which the spines are spread for action (Fig. 1D). This is because in the natural resting position almost the entire head of chaetognaths is covered by a fold of body wall, termed a hood (Fig. 1A). Grasping spines are then not only covered by the hood but they also stick tightly to each other and individual spines are not well discernible (Fig. 1B, C, F). In the fossils of chaetognaths with preserved remnants of soft tissue, as in the case of *O. disjuncta*, remnants of the covering hood should be also preserved. Thus, the grasping spines in the chaetognath body fossils can be visible only exceptionally, for example when the apparatus is preserved in the acting position, or when the hood became damaged. However, even in the specimens in which the hood is pulled down or damaged, the grasping spines can be seen only from the ventral side (Fig. 1E, F and Szaniawski 2005: fig. 3B, F, G). The two hitherto known specimens of chaetognaths from Chengjiang represent such exceptions. In my opinion, the original existence of the grasping apparatus in specimens of *O. disjuncta* is shown in the characteristically differentiated shape of their head. That shape depends on the arrangement of the grasping apparatus. In dead extant chaetognath bodies it is often arranged more or less crosswise to the body axis, which causes the head to be very wide (Fig. 1E and Szaniawski 2005: fig. 3B, F, G). Most probably, a similar arrangement is seen in some specimens of *Oesia* (see specimens USNM 57630 and 57631 in Walcott 1911; Szaniawski 2005 and Conway Morris 2009).

The argument based on the alleged lack of similarity between *O.disjuncta* and the Chengjiang specimens also is not justified, because the whole bodies of the latter are poorly preserved. The only difference in shape which can be definitively established is the comparatively more narrow tail part in the Chengjiang specimens. However, this difference is uninformative because in extant chaetognaths the proportions of tail and trunk width are strongly differentiated.

The argument concerning dissimilarity of *O. disjuncta* to the specimen newly illustrated by Conway Morris (2009: fig. 1C) is mostly irrelevant because that specimen represents only a grasping apparatus, which obviously is not comparable with the body of the whole animal in which the apparatus is not visible. The specimen confirms only the occurrence of chaetognaths in this locality. However, it is not clear why the author did not mention even that the specimen is very similar to the well known species of early chaetognaths *Phakelodus tenuis* (Müller, 1959) and the very similar *P. elongatus* (Zhang in An et al. 1983). These species were originally established based on individual spines and were assigned to the conodonts (Müller 1959; An et al. 1983). Bengtson (1976) included *Phakelodus* in the informal group of primitive conodonts that he named protoconodonts. Some years later, after

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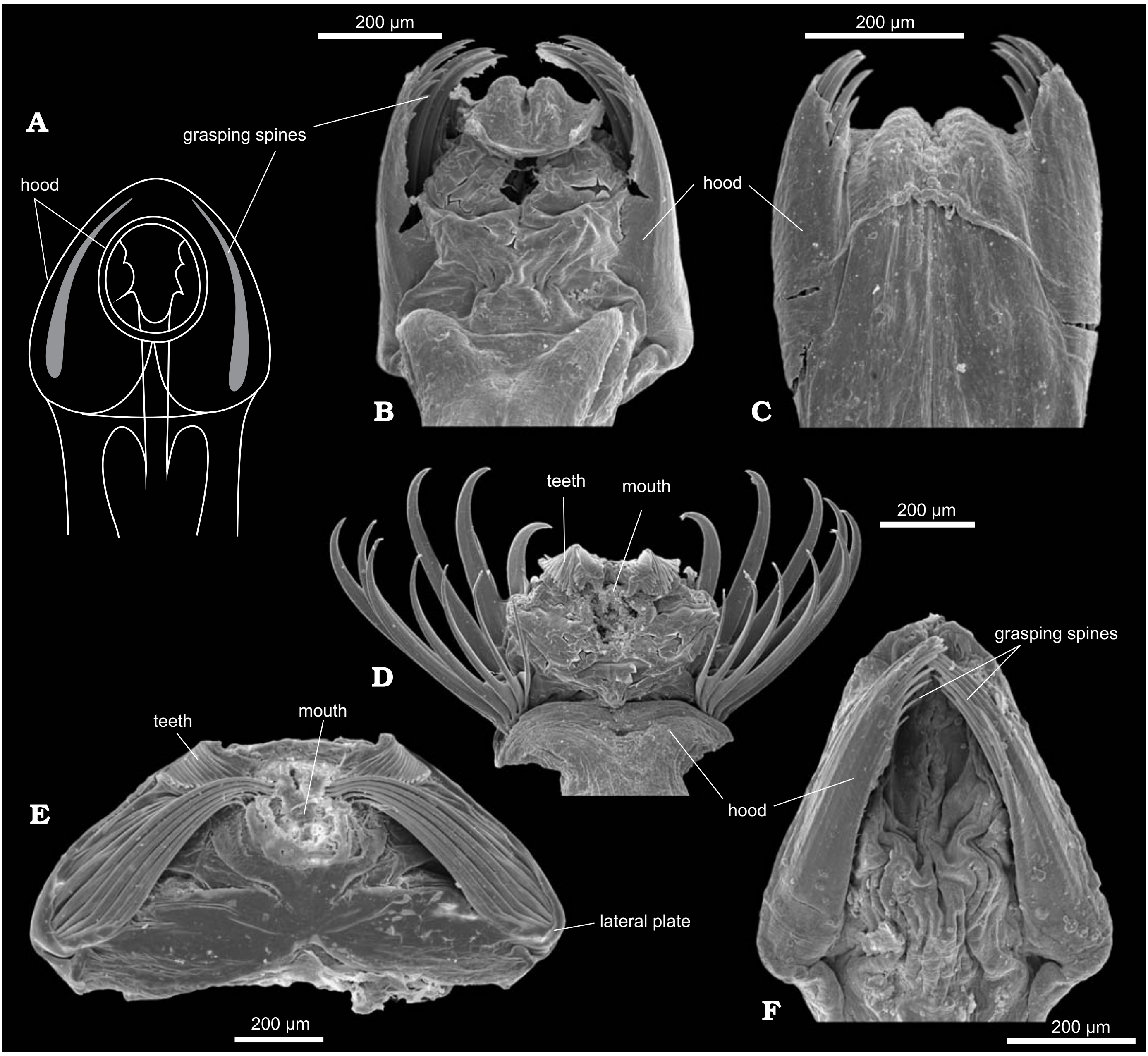

Fig. 1. Heads of chaetognaths. **A**. Schematic drawing of the head of *Sagitta elegans* Verrill in ventral view, grasping apparatus in natural, resting position, almost whole head covered by a hood, (modified after Kuhl 1938). **B**–**F**. Heads of undetermined extant chaetognaths from the North Sea and Antarctica, SEM photos of the air dried specimens, soft parts contracted. **B**. Ventral view, grasping apparatus in resting position, hood partly damaged as a result of drying (the same specimen as in Szaniawski 2002: fig. 2B, new photo). **C**. Dorsal view, grasping apparatus in resting position, hood partly damaged as a result of drying (the same specimen as in Szaniawski 1982: fig 2C, new photo). **D**. Ventral view, grasping apparatus in acting position, hood pulled down. **E**. Ventral view of compressed specimen, hood pulled down, not visible, grasping apparatus in resting position, extended laterally. **F**. Ventral view, hood partly damaged, grasping apparatus in resting position.

finding whole apparatuses composed of such spines, I recognized that *Phakelodus tenuis* (and now also *P. elongatus*, following the work of Müller and Hinz (1991) represents the grasping apparatus of chaetognaths (Szaniawski 1980a, b, 1982, 2002; Repetski and Szaniawski 1981). These still are the only commonly occurring species of fossil chaetognaths. Individual spines and apparatuses of these species are widely distributed in the Cambrian and Lower Ordovician (Tremadocian) deposits and are known showing the three-dimensionally preserved form and the compressed form, which are very similar to the specimen from the Burgess Shale (Fig. 2C). The compressed form has long been known from the Upper Cambrian of Great Britain (Miller and Rushton 1973; Bergström and Orchard 1985) and from Sweden (Müller and Andres 1976; Andres 1981, 1988). One of the specimens found in Great Britain has even been illustrated in the revised version of the conodont volume of the Treatise (Miller 1981). Upper Cambrian and Tremadocian apparatuses and clusters of *Phakelodus*, preserved in the three-dimensional form, are known from many local-

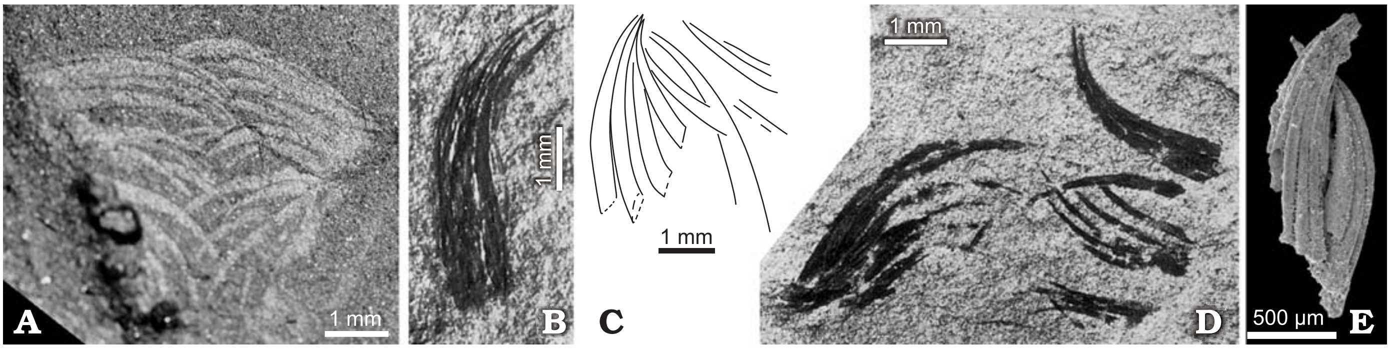

Fig. 2. Natural assemblages of the compressed grasping spines of chaetognaths. **A**. Unnamed assemblage, Middle Cambrian, Burgess Shale, British Columbia, Canada, USNM 199540 (after Conway Morris 2009: fig. 1C). **B**, **D**. *Phakelodus tenuis* (Müller, 1959), Upper Cambrian, Hunneberg, Sweden (after Andres 1981: figs. 3, 5). **C**. Unnamed assemblage, Upper Cambrian, borehole core in Warwickshire, central England, magnification approximate (after the unpublished drawings of Adrian Rushton, the specimen nr. Ca 467 is preserved in the British Geological Survey, Nottingham England. **E**. Three-dimensionally preserved grasping apparatus *Phakelodus tenuis* (Müller, 1959), subsurface Upper Cambrian of northern Poland (after Szaniawski 1982: fig. 1A, new photo).

ities and have been reported in numerous publications (see e.g., Müller and Hinz 1991; Dubinina 2000).

I believe that some of the other controversial arguments of Conway Morris are based on misunderstandings. The author suggested, for instance, that my diagnosis of the systematic position of *Oesia disjuncta* was based on the belief that it has preserved recognizable grasping spines. To support that, the author quoted a fragment of my sentence that they “are not [...] well preserved” (Conway Morris 2009: 176). However, the full cited sentence reads as follows: “The specimens of *O. disjuncta* do not have well preserved feeding apparatuses” (Szaniawski 2005: 4). Obviously, this has a different meaning, because the feeding apparatuses of chaetognaths are composed not only of grasping spines but also of other elements—the lateral plates, to which the grasping spines are attached, and the small spines termed anterior and posterior teeth. Possible traces of the grasping spines and the lateral plate are shown (with question marks) in figs. 1 and 2G of my paper. However I wrote clearly that “... the feeding apparatus of *O. disjuncta* is preserved only in the form of unconvincing remnants...” (Szaniawski 2005: 4). In my opinion, the more important feature supporting the original existence of grasping apparatus in the specimens of *O. disjuncta* is the very characteristically differentiated shape of their heads. In the dead bodies of extant chaetognaths, the shape depends on the arrangement of the grasping apparatus. In many specimens it is arranged more or less crosswise to the body axis, and then the head is very wide (Fig. 1E and Szaniawski 2005: fig. 3B, F). Some specimens of *Oesia* have similar shapes (see specimens, USNM 57630 and 57631 in Walcott 1911; Szaniawski 2005 and Conway Morris 2009).

Another misunderstanding concerns my tentative explanation of the lack of isolated chaetognath grasping spines from the Burgess Shale locality. I tried to explain that their phosphatisation was nearly impossible because “the depositional setting of the Burgess Shale was different from setting that favor phosphatization” (Petrovich 2001: 705), while preservation of their remnants together with the soft body is rather improbable because of the different fossilization process of the chitinous grasping spines and soft tissue. Conway Morris (2009: 176), in discussing this opinion, mentions the “... well preserved chitinous bodies of the numerous arthropods” in the Burgess Shale. However, the author probably did not take into account that original chitin usually does not preserve longer than 25 Ma (Stankiewicz et al. 1997), which means that in Cambrian deposits only its chemically altered remnants can be preserved. The chitin of grasping spines is composed of the fibrous alfa-chitin crystallites and is structurally different from the chitin of the exoskeleton of arthropods, in which it is usually embedded in a hardened proteinaceous matrix. Its chemical alteration also can be different than in arthropods and does not have to preserve similarly well. Moreover, the grasping spines do not have to be preserved together with the whole chaetognath’s body, not only because of the difference in chemical composition but also because of their different mechanical resistance. As I have establish experimentally, as a result of pressing and drying of whole specimens, the rigid grasping spines are often pulled out of their softer cuticular pockets and thus can be isolated (Szaniawski 2005: fig 3C, E).

Following Conway Morris (2009: 176), *O. disjuncta* differs from chaetognaths also by its tail fin, because “... this posterior-most region appears to have had a three-dimensional arrangement composed of a series of plate-like structures.” However such apparent structure of the fin may represent only one specimen (USNM 57630, see Walcott 1911; Szaniawski 2005; Conway Morris 2009), and most probably this is a misleading appearance resulting from post-mortem folding of the flexible fin. The alleged structure of the tail fin would be very unusual.

I fully agree with the remark of Conway Morris (2009: 209) concerning the dubious identification of lateral fins in *Oesia*, but this comment does not differ much from my own expressed opinion (Szaniawski 2005: 6). The lateral fins of extant chaetognaths are very flexible and in some species are rayless. After taking a whole specimen out from the liquid the fins usually became “glued” to the body and are almost invisible. Their identification in the fossil state must be very tenuous.

Referral of *O. disjuncta* to chaetognaths does not exclude the possibility that *Amiskwia sagittiformis* Walcott, known from the same locality and originally described as a chaetognath (Walcott 1911), also belongs to the phylum. It may represent a benthic form, but that problem is beyond the scope of this paper.

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References

An, T.-X., Zhang, F., Xiang, W., Zhang, Y., Xu, W., Zhang, H., Jiang, D., Yang, C., Lin, L., Cui, Z., and Yang, X. 1983. *The Conodonts of North China and the Adjacent Regions*. 223 pp. Science Press, Beijing.

Andres, D. 1981. Beziehungen zwischen kambrischen Conodonten und Euconodonten [in German]. *Berliner geowissenschaftliche Abhandlungen A* 32: 19–31.

Andres, D. 1988. Struktur, Apparate und Phylogneie primitiver conodonten. *Paläontographica A* 200 (4–6): 1–105.

Ball, E.E and Miller, D.J. 2006. The continuing classificatory conundrum of chaetognaths. *Current Biology* 16: R59–R596.

Bengtson, S. 1976. The structure of some Middle Cambrian conodonts, and the early evolution of conodont structure and function. *Lethaia* 9: 185–206.

Bergström, S.M. and Orchard, M.J. 1985. Conodonts of the Cambrian and Ordovician System from the British Isles. *In*: A.C. Higgins and R.L. Austin (eds.), *A Stratigraphical Index of Conodonts*, 32–67. Ellis Horwood Limited, Chichester.

Briggs, D.E.G. 1999. Molecular taphonomy of animal and plant cuticles: selective preservation and diagenesis. *Philosophical Transactions of the Royal Society, London B* 354: 7–17.

Chen, J.-Y. 2004. *The Dawn of Animal World* [in Chinese]. xii + 366 pp. Jiangsu Science and Technical Press, Nanjing.

Chen, J.-Y. and Huang, D.-Y 2002. A possible Lower Cambrian chaetognath (arrow worm). *Science* 298: 187.

Chen, L.-Z., Luo, H-L., Hu, S.-X., Yin, J.-Y., Jiang, Z.-W., Wu, Z.-L., Li, F., and Chen, A.-L. 2002. *Early Cambrian Chengjiang Fauna in Eastern Yunnan, China* [in Chinese]. 199 pp. Yunnan Science and Technology Press, Kunming.

Conway Morris, S. 2009. The Burgess Shale animal *Oesia disjuncta* is not a chaetognath: A reply to Szaniawski (2002). *Acta Palaeontologica Polonica* 54 (1): 175–179.

Dubinina S.V. 2000. *Konodonty i zonalnaâ stratigrafiâ pograničnych otloženij kembriâ i ordovika*. 239 pp. Geologičeskij Institut, Rosijskaâ Akademiâ Nauk, Trudy, vypusk 517, Nauka, Moskva.

Giribet, G. 2008. Assembling the lophotrochozoan (= spiralian) tree of life. *Philosophical Transactions of the Royal Society B* 363: 1513–1522.

Hu, S.-X., Steiner, M., Zhu, M.-Y., Erdtmann, B.-D., Luo, H.-L., Chen, L.-Z., and Weber, B. 2007. Diverse pelagic predators from the Chengjiang Lagerstätte and the establishment of modern-style pelagic ecosystems in the early Cambrian. *Palaeogeography, Palaeoclimatology, Palaeoecology* 254: 307–316.

Kuhl, W. 1938. Chaetognatha. *In*: H.G. Bronn (ed.), *Klassen und Ordnungen des Tierreichs Band IV Vermes. Abteilung IV, Buch 2, Teil 1*, 1–226. Akademische Verlagsgesellschaft, Leipzig.

Miller, J.F. 1981. Superfamily Amphigeisinacea Miller, new. *In*: R.A. Robison (ed.), *Treatise on Invertebrate Paleontology, Part W Miscellanea, Supplement 2 Conodonta*, W11–W115. The Geological Society of America and the University of Kansas, Boulder, Colorado and Lawrence, Kansas.

Miller, J.F. and Rushton, A.W.A. 1973. Natural conodont assemblages from the Upper Cambrian of Warwickshire, Great Britain. *Geological Society of America, Abstracts with Programs* 5 (4): 337–338.

Müller, K.J. 1959. Kambrische Conodonten. *Zeitschrift der Deutschen Geologischen Gesellshaft* 111: 424–485.

Müller, K.J. and Andres, D. 1976. Eine Conodontengruppe von *Prooneotodus tenuis* (Muller) 1959 in Natürlichen Zusammenhang aus dem oberen Kambrium von Schweden. *Palaeontologische Zeitschrift* 50 (3/4): 193–200.

Müller, K.J. and Hinz, I. 1991. Upper Cambrian conodonts from Sweden. *Fossils and Strata* 28: 1–153.

Petrovich, R. 2001. Mechanisms of fossilization of the soft-bodied and lightly armored faunas of the Burgess Shale and of some other classical localities. *American Journal of Science* 301: 683–726.

Repetski, J.E. and Szaniawski H. 1981. Paleobiologic interpretation of Cambrian and Earliest Ordovician conodont natural assemblages. *In*: M.E. Taylor (ed.), Short Papers for the 2nd International Symposium on the Cambrian System. *US Geological Survey, Open-File Report* 81-743: 169–172.

Stankiewicz, B.A. Briggs, D.E.G., Evershed, R.P., Flannery, M.B., and Wuttke, M. 1997. Preservation of chitin in 25 million-year-old fossils. *Science* 276: 1541–1543.

Szaniawski, H. 1980a. Conodonts from the Tremadocian Chalcedony beds, Holy Cross Mountains (Poland). *Acta Palaeontologica Polonica* 25 (1): 101–121.

Szaniawski, H. 1980b. Fused clusters of paraconodonts. *In*: H.P. Schönlaub (ed.), Abstracts for the 2nd European Conodont Symposium (ECOS II). *Abhandlungen der Geologischen Landestalt Wien* 35: 211.

Szaniawski, H. 1982. Chaetognath grasping spies recognized among Cambrian protoconodonts. *Journal of Paleontology* 56 (3): 806–810.

Szaniawski H. 2005. Cambrian chaetognaths recognized in Burgess Shale fossils. *Acta Palaeontologica Polonica* 50 (1): 1–8.

Vannier, J., Steiner, M., Renvoisé, E., Hu, S.-X., and Casanova, J.-P. 2005. Arrow worms: small marine predators from "deep time" *Acta Micropalaeontologica Sinica* 22 (Supplement): 189–190.

Vannier, J., Steiner, M. Renvoisé, E., Hu, S.-X., and Casanova, J.-P. 2006. Early Cambrian origin of modern food webs: evidence from predator arrow worms. *Proceedings of the Royal Society of London B* 274: 627–633.

Walcott, C.D. 1911. Middle Cambrian annelids. *Smithsonian Miscellaneous Collections* 57 (2): 109–144.

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