Reinterpretation of an alleged marine hexapod stem-group representative

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Abstract

The appendages of the recently described lower Devonian arthropod *Devonohexapodus*, originally assigned to the stem group of Hexapoda, probably have been misinterpreted. There is no convincing evidence for the evolutionary loss of the first post-antennal pair of appendages and the post-mortem loss of another two pairs of anterior appendages. Three pairs of particularly long appendages in the anterior body portion possibly are not homologous to the thoracic legs of insects. The fossil does not belong in the stem group of Hexapoda.

Keywords: Hexapoda; Arthropod phylogeny; Devonian

Introduction

Haas et al. (2003) described a marine fossil from the lower Devonian Hunsrück Shales, which they believed to be a member of the hexapod stem lineage. Their main reason for the assignment is the anterior body portion resembling a thorax due to three pairs of long, possibly 6-segmented legs. Additional evidence are the alleged lack of a limb corresponding to the first post-antennal appendage (homologous with the 2nd antenna of Crustacea), the presence of uniramous legs (both listed as apomorphies the fossil is said to share with the Atelocerata; Haas et al. 2003, p. 48), and alleged synapomorphies of *Devonohexapodus* and Insecta: “thoracopods” slender and stenopodial; “thoracopods” with no more than six podomeres; “abdomen” with short, stout leglets and a pair of cerci.

However, it is unlikely that Haas’ et aliorum interpretation of those structures that appear to be especially important for determining the systematic position of the fossil is correct.

Discussion

Anterior body portion

The fossil exhibits fine and finest structures firmly fixed to the body and more or less loosely articulating with it. Especially noteworthy are the long and well preserved filiform antennae, the long and slender legs in the anterior body portion, and the series of small hind legs. The authors claim that the first two pairs of mouthparts are missing and that this is a preservational artefact. If the authors are correct in stating that the fossil is an atelocerate, a strong and short mandible must have been present in the living animal (see Haas et al. 2003, Fig. 5). In the Atelocerata, the mandible, which is the first pair of mouthparts said to be missing, is a structure which is tightly attached to the head capsule.
A state of preservation with both long antennae and an alleged labium present but the mandibles and maxillae absent is highly unlikely. Therefore, I conclude that all anterior appendages are preserved and that the first pair of appendages preserved behind the antennae indeed is the first morphological pair of post-antennal appendages. The eyes are large and ovoid and are set apart from the first pair of appendages by what Haas et al. (p. 42) described as an unsegmented cuticular bridge. Separation of the eyes from the rest of the body by the bridge may have supported vision. I do not interpret the bridge as a structure that once bore additional appendages now missing from the fossil. To some degree, its narrowness would be in conflict with an extensive musculature that one should expect from mandibles and maxillae.

Under this view, the first post-antennal pair of appendages in the fossil is not the labium. Instead, it would correspond to the crustaceans' second antennae. An alternative view is that, if the euarthropodan labrum derives from a pair of appendages and is the true first pair of appendages (Popadić et al., 1998; Scholtz 1998, p. 329), it is homologous to that structure. Either possibility implies that the following three pairs of long appendages are not homologous to the hexapodan thoracic legs.

Haas et al. (2003, p. 46) claim that Devonohexapodus has entirely reduced first postantennal appendages (the homologues of the crustaceans' 2nd antennae). The authors consider this to be additional evidence of their conclusion that it belongs in the Atelocerata. However, their interpretation was determined by their assumption that it is an atelocerate which in turn was based on their view that it is a hexapod. The fossil itself does not provide any evidence for an evolutionary loss of the structure. As the authors believed that the first two pairs of mouthparts are not preserved in the fossil, one may ask why they excluded the possibility of preservational loss for the first post-antennal appendage (= 2nd antenna in Crustacea).

Thus, it appears that the anterior region of living Devonohexapodus bore one pair of long antennae, one pair of short and three pairs of long appendages. According to this interpretation, the latter appendages might be the undifferentiated equivalent of the three pairs of mouthparts of the ateloceratan head. This implies that the head capsule of the fossil consisted of three segments at most, as the segments bearing the three long appendages were not fused to form a solid entity. If the present description of the head structure is correct, the animal does not belong in one of the extant subgroups of the Euarthropoda.

If Haas et al. are right in stating that several appendages immediately posterior of the antennae are missing due to preservational circumstances, those probably would not have resembled mandibles or maxillae for the reasons given above. This would also exclude the specimen from the stem lineage of hexapods. Devonohexapodus has very long antennae. Antennae of such a structure are generally not believed to pertain to the ateloceratan and hexapodan ground patterns.

### Lengths of three anterior pairs of appendages

Contrary to the statements of Haas et al. (e.g., p. 48, Fig. 5), slender thoracic legs do not necessarily pertain to the insectan ground pattern. In fact, the leg bauplan of the stem species of the Insecta is uncertain, and thoracic legs were stout in Monura and are comparatively short in Archaeognatha, Zygentoma, Diplura and Protura. Long and slender legs were mentioned as a possible apomorphy of Carbotoiriurida + Pterygota, i.e. of a subordinate taxon of Insecta (Willmann 2003).

### Posterior body region

The legs of the posterior body are short and said to consist of 4–5 podomeres. Under the Devonohexapodus-as-hexapod view this was said to be a derived character (reduction in number of podomeres). However, it should be noted that in arthropods differences in podomere number often have evolved independently.

**“Thorax”**

The authors (p. 42) state that the animal has a three-segmented thorax. However, the fossil has three pairs of very long appendages, whereas the corresponding segments hardly differ from the posterior ones except in that they are narrow (p. 47) and become smaller with increasing proximity to the anterior end of the animal. In many authors’ views a thorax in the sense of a particularly pronounced tagma consisting of enlarged segments is one of the hexapodan apomorphies. Such a thorax does not exist in Devonohexapodus. The presence of three pairs of long walking appendages is not characteristic for an insect thorax, because multi-segmented abdominal appendages must also have existed among early insects. Moreover, such a thorax does not pertain to the Ellipind and many basal Ectognatha, and therefore may be apomorphic to some subordinate insect group. It possibly did not exist in the insectan ground plan representative.

### Uniramous appendages

The members of the Atelocerata have uniramous appendages. This is generally accepted as being derived as compared to the situation in the ground patterns of Crustacea and Chelicerata (e.g. Hemig 1986). Given that Onychophora, Tardigrada and Linguatulida, and
related Cambrian taxa such as *Xenusion*, *Aysheia*, etc., are Arthropoda but not euarthropods (for the Linguatulida see Waloszek and Müller 1994; Maas and Waloszek 2001), uniramous appendages (as a plesiomorphy) possibly also belong in the arthropodian ground pattern. This view implies that biramous appendages were not among the first euarthropodian apomorphies, and that early Euarthropoda had uniramous appendages as well (but note that several soft-bodied early arthropods may have had appendages with dorsal branches which were, however, divergently interpreted; Delle Cave et al. 1998). Hence, the leg structure of *Devono*hexapodus* may be interpreted in two different ways: as a plesiomorphy or as a derived character. Haas et al. (2003), led by their *Devono*hexapodus- as-hexapod view, preferred the latter interpretation. But as the stenopodial appendages of various arthropod groups are the result of repeated losses of exopodites, stenopodial legs did not necessarily evolve as homologous characters.

The terminal leglet is said to be subdivided into at least 4–5 elements, and thus to resemble short cerci. However, it is unclear if cerci belong in the hexapodan ground plan, as their presence is certain only for the ground patterns of Diplura and Ectognatha (Kristensen 1998), and might be autapomorphic of the Euentomata (= Diplura + Ectognatha; Klass and Kristensen 2001, p. 268; Willmann 2003).

Tergites and sternites

In lateral view, the central area of each trunk segment of the fossil is not well preserved. It is possible that tergites and sternites left the lateral portions of the segments largely uncovered. This is not to be expected for an animal belonging in the stem group of Hexapoda.

Conclusions

There is no evidence that mouthparts or any other appendages are lacking in the foremost portion of the fossil due to preservational loss. Furthermore, there is no evidence for the evolutionary loss of the first postantennal pair of appendages (complete reduction as in atelocerates). Consequently, the six long and slender appendages in the anterior body portion of *Devono*hexapodus and Insecta are not regarded as homologues here. With this view in mind, most structures can be interpreted phylogenetically in a way that differs from the opinion of Haas et al. (2003). The head appears to be three-segmented at most, which excludes *Devono*hexapodus from the insectan stem group. The homonomous body segments, the short uniramous legs, small-sized tergites and sternites (?), and the high number of metameres are not convincing evidence for a position among the Atelocerata, as similar character states occur in other arthropod taxa as well. The remarkable lengths of the six anterior appendages, the huge eyes and a “sclerotized bridge” between the eyes and the body portion bearing the foremost pair of appendages are interpreted here as autapomorphies of the taxon. Therefore, the assumption that *Devono*hexapodus* belongs in the Atelocerata is rejected, and any implication derived earlier from the fossil’s alleged phylogenetic position, or reference to it as evidence for the origin and early evolution of Hexapoda (e.g. Thomas 2003), is considered to be unfounded.

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Dieter Waloszek reminded me of the fact that 10 years ago I had been asked for an opinion on the then only partly prepared specimen, based on a photograph. At that time I had also not reached a conclusion as to where the fossil belongs systematically. I thank Gert Tröster for valuable discussion, and Wolfgang Wägele and Dieter Waloszek for comments on an earlier draft of this paper.

References


