Enalikter aphson is more likely an annelid than an arthropod: a comment to Siveter et al. (2014)

Torsten H. Struck1, Carolin Haug2, Gerhard Haszprunar2,3, Nikola-Michael Prpic4 and Joachim T. Haug2

1 Zoological Research Museum Alexander König, Leibniz-Institute for Animal Biodiversity, Adenauerallee 160, Bonn 53113, Germany
2 LMU Munich, Biocenter, Department of Biology II and GeoBio-Center, Großhaderner Str. 2, Planegg-Martinsried 82152, Germany
3 Bavarian State Collection of Zoology, Münchhausenstr. 21, Munich 81247, Germany
4 Department of Developmental Biology, GZMB Ernst-Caspari-Haus, Georg August University, Johann-Friedrich-Blumenbach-Institute for Zoology and Anthropology, Justus-von-Liebig-Weg 11, Göttingen 37077, Germany

Siveter et al. [1] recently described a new putative megacheiran arthropod, Enalikter aphson, from the Silurian Herefordshire Lagerstaette and discussed its impact on arthropod phylogeny and the survival of megacheirans beyond the Cambrian Period.

In this comment, we should like to suggest an alternative interpretation of the new fossil. We think that the evidence for arthropod affinities of E. aphson is not compelling, and we argue that all features of this species are more compatible with an annelid affinity of E. aphson. Accordingly, the supposed impact of E. aphson on arthropod phylogeny and longevity of early megacheirans is questioned.

The body of E. aphson is composed of segments that bear appendages, some of which are interpreted as biramous or multiramous. The segments lack a well-delineated tergite on the dorsal side; as pointed out by Siveter et al. [1] tergo-pleurae are also not visible in the material. Siveter et al. [1] identify a ‘dome-like’ tergite on the dorsal side of the first ‘trunk’ segment, but this is not visible in lateral aspect and thus the nature of this structure is unclear. The same is true for structures interpreted by the authors as ‘button-like sternites’. There is no sign of partially overlapping, sclerotized structures, which is otherwise the typical appearance of tergites in all megacheiran fossils [2,3].

The trunk of E. aphson appears to be extremely flexible as evidenced by specimen OUMNH C.29632 (Siveter et al. [1, fig. 1t–w]), which is in that degree unusual for typical megacheirans, but would be compatible with trunks of certain other arthropods (e.g. centipedes and remipede crustaceans). However, the curvature of the trunk is very smooth and continuous, unlike an arthropod trunk, which can only be bent at the segmental borders; it is much more reminiscent of the continuous flexibility of the skin-muscle tube pressurized by the coelomic system in annelids.

The anterior end of E. aphson is a slightly swollen bulb that bears an unpaired frontal filament and three pairs of multi-branched appendages, which are morphologically distinct from the appendages of the trunk. The authors interpret this body region as a head covered by a cephalic shield. However, this ‘head shield’ is morphologically much less distinct than the different colours employed by the authors in the virtual reconstruction seem to suggest. There is no evidence for a separate dorsal structure comparable to a cephalothoracic shield or a carapace in arthropods: in lateral view it can be seen that the anterior portion is a uniform swelling, without morphologically separate sclerotized coverings. The surface structure of the ‘head shield’ viewed from dorsal is identical to the surface of the following segments, and the only difference of the anterior part is that it is slightly wider than the rest of the body. The uniform appearance of this anterior portion is fully compatible with the notion that it represents the head of an annelid body organization, which includes the prostomium, the peristomium and the two following segments. Fusion of the prostomium with the following segments is
known from different annelid taxa (e.g. pisoniids, onuphids, sabellids). Hence, given the position of the mouth and the head appendage 1 (Siveter et al. [1, fig. 1d]), the so-called disc-like oral surface would represent the frontal end of the prostomium, and the frontal end of the so-called head shield would represent the peristomium overarching the prostomium. A peristomium overarching the prostomium is also known from different annelid taxa (e.g. eunicids, onuphids, sabellids).

Reinterpretation as an annelid head is also supported by the distinct morphology of the appendages of this part: in annelids the head appendages always differ from the segmental appendages. The unpaired frontal appendage (figure 1a), though previously unseen in any arthropod, is typical for a large number of annelid species as a median antenna (e.g. hesionids, scale worms, onuphids, oenonids, eunicids or amphinomids; figure 1b; [6]). In several of these annelid species the median antenna occurs at a frontal position on the prostomium rather than in a more posterior position close to the peristomium (e.g. hesionids, syllids, scale worms), as is the case in E. aphson (Siveter et al. [1, fig. 1d]). The first paired head appendages with their three branches were homologized by Siveter et al. [1] with the great appendages of leachicolid megacheirans. There is no basis for this homology assumption other than the fact that there are three flagella in both groups. The distinct organization seen in leachicolids, the appendages of which are divided into two peduncle elements and three to four multichela elements (figure 1c) [2], is not present in the material of E. aphson. Furthermore, proximally to the flagellar parts in the great appendages of leachicolids are stiff elongate spine-like elements [2], which appear to be absent in E. aphson. Additionally, there are also other arthropod groups in which tri-flagellate anterior appendages occur, e.g. malacostracan crustaceans (figure 1d) [7] and pauropod myriapods [8]. Instead, the multi-branched anterior appendages occurring in a lateral position in the reconstruction of E. aphson are very similar to the branched prostomial appendages in annelids like fabricids (e.g. Manayunkia and Fabricia) [9]. The head appendages 2 and 3 would then be modified parapodia of the two following segments fused to the head as can be found in several annelid taxa (e.g. nereids, hesionids, onuphids).

The trunk appendages are branched and thus are superficially reminiscent of the biramous limbs of crustacean arthropods. However, none of the appendages in E. aphson shows distinctly jointed elements. Moreover, the individual branches of the trunk appendages are fan-shaped and appear to derive their rigidity from inner turgor pressure, rather than from an external skeleton, as indicated by the preservation in specimen OUMNH C.29632 (Siveter et al. [1, fig. 1y]) and pointed out already by Siveter et al. [1]. The morphology of the trunk appendages is also reminiscent of the biramous parapodia of errant annelids. The multiple dorsal rays in E. aphson are very similar to dorsal gill fans growing from the notopodial base in species of e.g. Eunicidae. The two stronger branches in E. aphson then correspond to the nato- and neuropodium of a typical annelid parapodium. However, we acknowledge that the virtual reconstruction of E. aphson does not show indications of chaetae. Whether this is due to the resolution of the reconstruction precluding the visualization of such delicate structures or not has to be seen in future analyses of the original material. Also the morphology of the posterior trunk end resembles the pygidium with its two cirri of certain annelids (e.g. eunicids, lumbrinerids, oenonids or onuphids) [6].

Siveter et al. [1] discuss the absence of a sclerotized hypostome in E. aphson and name three arthropod examples allegedly showing a comparable condition. However, all three of these examples, namely Agnostus pisiformis, Hommesquenooxicaris scultula and Martinssonia elongata, in fact possess a well-developed and prominent sclerotized hypostome [10–12].

The phylogenetic analysis by Siveter et al. [1] places E. aphson among megacheirans, and places the entire group outside Euarthropoda. Although the phylogenetic position of the megacheirans is debated and they have previously been placed outside the euarthropods by some authors, there is a growing body of evidence that Megacheira are an ingroup of Euarthropoda, with Chelicerata (s. str.) as an ingroup of Megacheira [3,13]. The result of the analysis by Siveter et al. [1] (which is unfortunately not discussed by the authors) might result from unsupported homology assumptions (with the first appendage as one example). While the dataset forming the basis for the phylogenetic analysis is impressively large, it unfortunately lacks any discussion of the a priori homology assumptions.

Siveter et al. [1] state that E. aphson is especially similar to Bundenbachiellus giganteus from the Lower Devonian Hunsrück Slate. B. giganteus is for sure an arthropod, especially when considering the appendages consisting of jointed elements, which
remains unclear whether E. aphson (e.g. [14, fig. 4]). It does not become clear why E. aphson should be very similar to B. giganteus, partly due to the incomplete knowledge on the morphology of the latter. The main mentioned shared character is the tri-flagellate anteriormost appendage, yet it remains unclear whether B. giganteus really has such an appendage. The proximal region is not accessible; thus the exact structure of the supposed tri-flagellate anterior appendage in B. giganteus is unknown.

In summary, we argue that the available material of E. aphson lacks unequivocal evidence for key arthropod features such as chitinized segmental body armour plates, jointed appendages, and a hypostome, but is compatible with annelid body organizations. Therefore, we reject the further-reaching conclusions of Siveter et al. [1]: megacheirans as falling outside Euarthropoda is likely an artefact, caused by probably erroneous a priori homology assumptions in some characters of the data matrix. The interpretation of B. giganteus (undoubtedly an arthropod) as a megacheiran also lacks support, as this was entirely based on the comparison to E. aphson interpreted as an arthropod. Thus, early megacheirans (before the node of Chelicerata sensu stricto) remain restricted to the Cambrian.

We emphasize here that careful comparison of features in fossil material to the full diversity seen in extant counterparts in both arthropods and annelids is necessary for interpreting segmented fossils, including well-preserved ones, in cases where the fossil does not exhibit clear-cut evidence for the placement in a certain taxon. Furthermore, the discussion of possible pitfalls in the primary homology assumptions of the crucial characters relevant for the placement of the investigated taxon should be part of the phylogenetic interpretations (for a longer discussion, see Mooi & Gill [15]).

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References


