

High-level phylogenetic analysis using developmental sequences: The Cambrian †*Martinssonina elongata*, †*Musacaris gerdgeyeri* gen. et sp. nov. and their position in early crustacean evolution

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ABSTRACT

The ontogenetic sequence of †*Martinssonina elongata*, a derivative of the stem lineage of Eucrustacea, has been re-investigated. Morphological and morphometric data provide a revision of the original description of this species. Specimens originally assigned to second and third developmental stages have been removed from the †*M. elongata* sequence and assigned, together with several larger specimens, to an entirely new species, †*Musacaris gerdgeyeri* gen. et. sp. nov. having a completely unsegmented body, giving the appearance of a giant euarthropod head larva. This is interpreted either as a hypertrophied larva or a late developmental stage of a neotenic species. Only the earliest unsegmented larvae and segmented instars of the original sequence are ascribed to †*M. elongata*. The two species are apparently closely related and are closer to Labrophora (†Phosphatocopina + Eucrustacea) than to other Cambrian “‘Orsten’ crustacean stem derivatives”. The ontogenetic sequences of the two taxa and those of the other derivatives of the recently investigated labrophoran stem lineage indicate several heterochronic peramorphic (‘adultising’) events during early crustacean evolution. This is most evident in the development of the proximal parts of the appendages.

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1. Introduction

This present study is the fourth to reinvestigate larval development of “stem”-Crustacea that belong to the ‘Orsten’ fauna from the late Middle to Upper Cambrian of Sweden (Stein et al., 2008; Haug et al., 2009, in press). ‘Orsten’ fossils are uncompressed, three-dimensional, and have been preserved with fragile elements, such as eyes, various membranes, such as around the mouth, and anal and genital openings (Maas et al., 2007). Resolution of fine structures is to 0.2 μm. Preservation of specimens below one or two millimetres has some limitations but these are outweighed by their unique advantage of allowing comparisons between adult and larval forms.

†*Martinssonina elongata* Müller and Walossek, 1986 was the first ‘Orsten’ species to provide a developmental sequence. This included three early larval stages, a late developmental stage almost resembling the assumed adult, and the assumed adult (Müller and Walossek, 1986). Originally described as a crustacean-

like euarthropod, this informal position was more precisely determined since †*M. elongata* was identified as a derivative of the stem lineage of Crustacea by Walossek and Müller (1990). It has since become one of the most cited of all ‘Orsten’ taxa (cf. synonymy list), accepted generally as phylogenetically basal to other Crustacea, but also proposed as related to in-group eucrustaceans (Wills, 1998; Wills et al., 1998).

Recent studies by Stein et al. (2005, 2008) and Haug et al. (2009, in press) have focused on morphological and developmental patterns of taxa that are also identified as derivatives of the stem lineage of Crustacea; namely †*Oelandocaris oelandica* Müller, 1983 (Stein et al., 2005, 2008), †*Goticaris longispinosa* Walossek and Müller, 1990 and †*Cambropachycope clarksoni* Walossek and Müller, 1990 (Haug et al., 2009), as well as †*Henningsmoenicaris scutula* (Walossek and Müller, 1990) and †*Sandtorpia vestrogothiensis* nom. nud. (Haug et al., in press). Developmental studies providing additional characters have further contributed to understanding taxonomic evolution relating to heterochronic events (Haug et al., in press). Continuing this approach, we have re-investigated all material pertaining to †*M. elongata* and some unstudied specimens of similar appearance. This has resulted in the discovery of a new, apparently closely related species, †*Musacaris gerdgeyeri* gen. et sp. nov.

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Haug et al. (in press) confirmed earlier assumptions that †*M. elongata* is closely related to the Labrophora (for labrophoran autapomorphies see Maas et al., 2003). We have here tested if this affinity still holds when adding †*Mus. gerdgeyeri* gen. et sp. nov., since its features are likely to bear on a reconstruction of the labrophoran ground pattern. The aim of the present re-evaluation is to provide additional data pertaining to heterochronic events and the reconstructions of ground patterns, to provide an evolutionary scenario that reveals sequential acquisition of novel characters.

Wills and co-workers (Wills, 1998; Wills et al., 1998) have proposed that †*M. elongata* and the maxillopodan †*Skaracarida* should be closely related. In our opinion, these two taxa are superficially alike in gross morphology only (cf. Müller and Walossek, 1985a, see their Fig. 5a,b). As will be demonstrated, the morphological differences between the two taxa clearly reflect the phylogenetic distance between a stem derivative and an entomos-tracan in-group taxon.

2. Material and methods

2.1. Material

Twenty-one specimens of †*M. elongata* and 13 specimens herein assigned to the new species †*Mus. gerdgeyeri* gen. et sp. nov. derive from material collected during several field trips by K.J. Müller in Sweden in the 1970s. All are exclusively from the “*Agnostus pisiformis* Biozone” (see electronic supplement) of Epoch 3 of the Cambrian (for new zonation of the Cambrian see Peng et al., 2004). One specimen UB W 341/SPEC 1455 was labelled as being from Biozone 5 of the former Upper Cambrian (now referred to the late Furongian). The faunas, however, differ significantly between Biozone 1 and 5 (for more details see Maas et al., 2003) without any faunal overlap (with the exception of type-A larvae, the range of which is even larger). Accordingly we regard this as a sorting error, and both species should be regarded as occurring only in the *Agnostus pisiformis* Biozone. All specimens are part of the collection of the Steinmann Institute of the University of Bonn, but currently housed at the Biosystematic Documentation, University of Ulm.

2.2. Methods

Processing rock, sorting and preliminary analysis of the selected specimens was undertaken in Bonn (see Müller, 1985, 1990; Maas et al., 2006 for details). Photography of the material was

originally done in Bonn (by DW) using a CamScan SEM and standard photography producing greyscale negatives. Re-scanning at Ulm (mainly by JTH) at the Central Unit for Electron Microscopy using a Zeiss DSM 962 yielded digital images for further handling. Several of the original specimens were found to be destroyed or heavily damaged in the meantime. For these we could only use original photographs for our restudy. A customized tilting unit that permits tilting up to 90° was developed by the Central Unit for Electron Microscopy. This allowed observation of features hitherto inaccessible for final reconstruction of larval stages. Digital SEM images were processed using Adobe Photoshop (version CS 3) on an Apple Macintosh and the free software GIMP (www.gimp.org). The depth of focus of some images was improved using the freely available image fusion software “Combine ZM” (<http://www.hadleyweb.pwp.blueyonder.co.uk/CZM/combinezm.htm>).

Models of all instars were made using the 3D-modelling software Blender (<http://www.blender.org>). These can be rotated in any desired direction, which enables and facilitates comparison between different instars and the other ‘Orsten’ taxa using the same method. For reconstructions, all limbs were first redrawn in anterior view from SEM photographs, then adjusted in the missing third dimension for subsequent modelling in Blender. After all limbs had been completed, the body was likewise first drawn in a lateral view and then adjusted for body width. In the next step, the limbs were connected to the body proper. All spines/setae, which are mostly broken off close to their base in the specimens, were drawn assuming a standard conical shape. Because the true length of spines and setae can only be estimated, all lengths are minimum estimates. If limbs or parts of limbs are missing in a particular instar, these were reconstructed on the basis of what is known from earlier instars. Limb structures vary only gradually from growth stage to growth stage. The final models have been used to compare different morphological aspects.

Morphometric data (Figs. 1, 2) were generated using the SEM images measured to the nearest 5 µm. As known from various studies on ‘Orsten’ specimens this is a sufficient approximation for reliable morphometric analyses (Müller and Walossek, 1985b, 1987, 1988; Walossek, 1993; Stein et al., 2008; Haug et al., 2009, in press). The diagram in Fig. 2 was produced using Adobe Illustrator CS 3 and processed in the free available software Inkscape 0.45.

Here, we have adopted most of the terminology proposed by Walossek (1993) for Crustacea and Arthropoda in general to attempt terminological stability: see also Waloszek, 2003a,b; Haug et al., in press for discussion of terms. All post-antennular

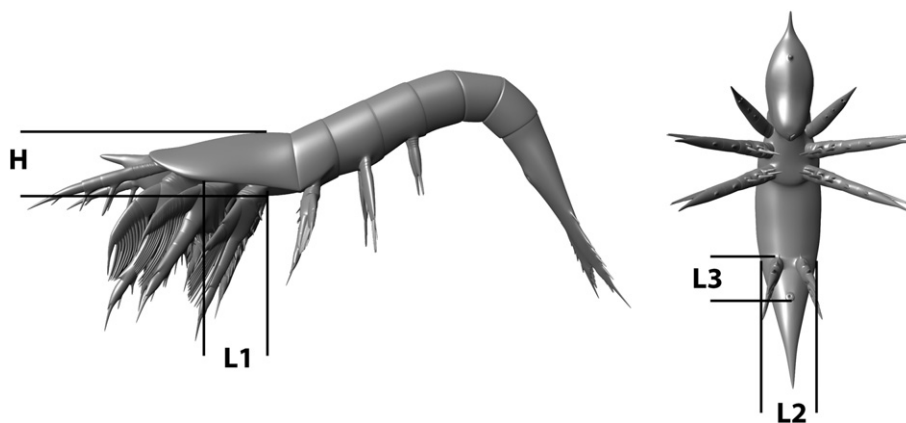


Fig. 1. Measurements for obtaining morphometric data. H: Height of the body in lateral view. L1: Distance from the anterior edge of the insertion area of the third appendage to the posterior edge of the insertion area of the fourth appendage. L2: Width of the body in ventral view measured at the level of the fourth appendage. L3: Distance from the anterior edge of the insertion area of the fourth appendage to the posterior edge of the anal membrane.

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