

A second type A-nauplius from the Upper Cambrian 'Orsten' of Sweden

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Among newly sorted material, two specimens at first considered as nauplius-like larva A (Müller & Walossek 1986, *Transactions of the Royal Society of Edinburgh: Earth Sciences* 77) differ from this type in their larger sized body and appendages, much smaller caudal spines, and lack of the dorsal hook-like plates. They are regarded as a similar but distinct type, named 'larva A2'. □ *Crustacea, ontogeny, phosphatization, 3D-preservation.*

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Four different phosphatized and three-dimensionally preserved larvae of euarthropods, which could not be assigned to any of the associated larger stages, have been described by Müller & Walossek (1986b). Of these, larva A (Müller & Walossek 1986b, Fig. 2a–d), about 100 to 130 µm long, is the most abundant form (Fig. 3A).

Larva A is a true ortho-nauplius and is considered to have belonged to a eucarustacean. Its simplicity of form, however, prevents its assignment to any of the larger stages in the material. The smooth, ovoid body has three pairs of simple, 'sausage-like' and unsegmented appendages. A cephalic shield is not developed, and the naupliar eye is not expressed externally. The labrum is prominent, projecting from the ventral surface, and is devoid of setation.

The non-functional, initial mouth at the rear of the labrum, the lack of an anus, and the little-developed medial setation of the appendages, consisting of a few short, sometimes paired spinules, strongly suggest that larva A was not feeding. Again, this low degree of setation on the appendages does not concur with good swimming abilities.

A characteristic feature of larva A is the development of three pairs of hook- or scale-like outgrowths (sc) on the gently convex dorsal surface (Fig. 3A). These obviously correspond to the appendages and may have housed muscles which moved the limbs. The caudal end of the larva (tr) is slightly conical and truncate, terminating in a single spine dorsally (dcs) and a pair of spines

(vcs), representing initial furcal extension, ventrally.

We now have more than 80 specimens of larva A sorted from the residues. In contrast to the other larvae and the majority of larger forms known so far, larva A occurs in all zones of the Upper Cambrian series which yielded soft body preservation, i.e. in zones 1, 2a, 5c, d, and e (zones after Westergård 1947).

Larva A specimens show some but negligible variability in size and shape. During further scanning of the 'Orsten' material, two new specimens, at first assigned to larva A, were recognized as separate. Closer examination brought to light a number of differences from the morphology of larva A. For the new specimens, the name larva A2 is used.

Both individuals are from the *Agnostus pisi-formis* zone 1, Gum at Kinnekulle. UB1 is from sample 6761, one of the most productive samples for larva A, and UB2 is from sample 6757. UB1 is almost complete and well-inflated, except for its dorsal surface which is somewhat deformed (Fig. 1A, C–F). The left side is covered with grains of phosphatic matter. Because of mounting of the specimen on its forehead region (Fig. 1C–E), few structures of the ventral side are recognizable.

UB2 is also almost complete, but more wrinkled, probably due to slight collapsing after death (Fig. 1B). The first antennae are both flexed somewhat posteriorly distal to their bases. Because of this deformation the specimen has not

been used for detailed measurements. Furthermore, thick alien crystals cover the dorsal surface of this specimen, which is mounted on its ventral side.

Description of larva A2

The body of the new type is 140–150 μm long and egg-shaped, with the greatest width at the level of the second antenna. As in larva A, a head shield is lacking. The anterior margin of the body,

between the first antennae (at1), is almost disguised in the glue of the stub (Fig. 1C, E), but may have been slightly more rounded than in larva A (Fig. 3A; Müller & Walossek 1986b, Figs. 1, 2a, c, 3e). Again, the distance between the insertions of the first antennae is 60–70 μm , which is about 15–20% more than in larva A.

Due to mounting, little is known of the ventral surface. Fig. 1D suggests that it is similar to larva A, and also that the labrum may not be very different. Accordingly, much of the ventral surface of this larva has been adopted from larva A for the reconstruction in Fig. 2B.

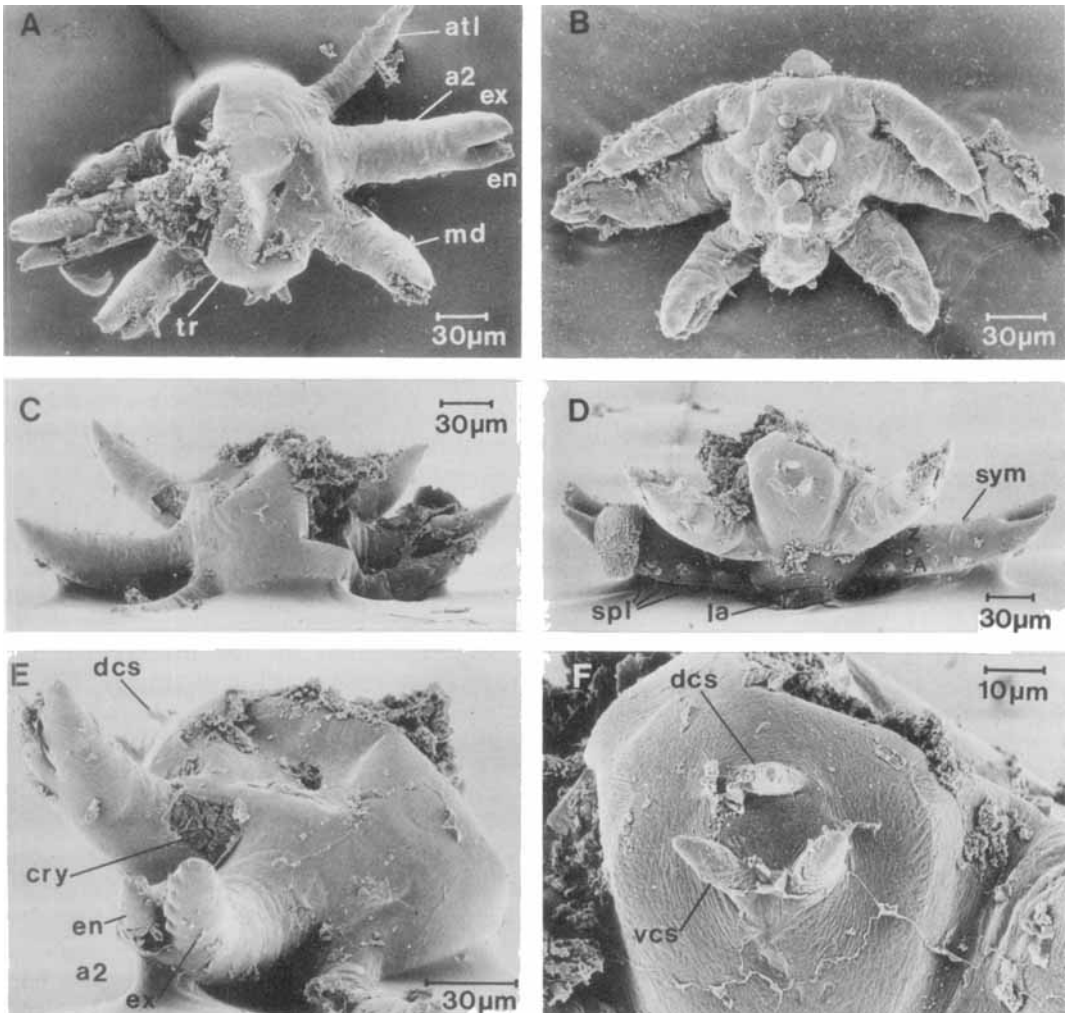


Fig. 1. SEM photographs of larva A2 (for abbreviations in this and the following figures see Table 1). □ A, C–F. UB W1. □ A. Dorsal view. □ C. Anterior view, slightly from the dorsal. □ D. Posterior view, slightly from the ventral. □ E. Lateral view, anterior to the right. □ F. Close up of caudal end; note the fine surface texture. □ B. UB W2 in dorsal view.

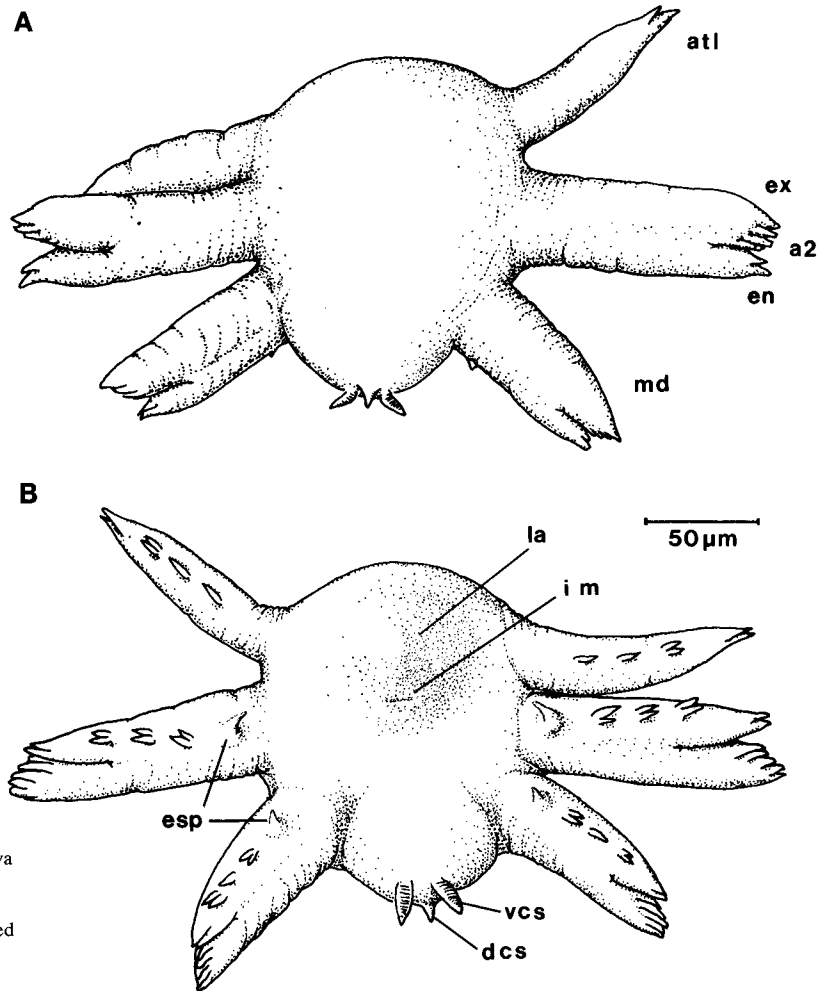


Fig. 2. Reconstruction of larva A2 in dorsal (A) and ventral views (B). Details of the ventral surface in part adopted from larva A (Müller & Walossek 1986b, Fig. 4d).

The most significant distinction between larva A and larva A2 is the lack of dorsal outgrowths of the latter, which has a smooth and gently convex dorsal surface (Figs. 1A–C, E, 2A, to be compared with larva A in Fig. 3A).

In their gross design the appendages are similar to those of larva A, being plump and devoid of a distinct segmentation. The lengths of the appendages of UB W1 are about 100 µm for the first antenna (at1), 110 µm for the second antenna (a2), and 80 µm for the mandible (md), which is about 10% longer than in larva A. As in larva A, the protopods (sym = sympod) of the second antenna and mandible are very long, being about 80 µm for the former and 50 µm for the latter.

In both appendages, the distal rami (en, ex) are 30 µm long, the endopod being slightly shorter than the exopod. The medial setation of the inner

Table 1. List of symbols.

app 4	– fourth appendage of the earliest larva of <i>Martinssonia elongata</i>
at1	– first antenna, antennula
a2	– second antenna
dcs	– dorsocaudal spine
en	– endopod
esp	– enditic spine
ex	– exopod
i m	– initial mouth
la	– labrum
md	– mandible
sc	– scale-like outgrowths on the dorsal surface of larva A
spl	– spinule
sym	– sympod (undivided protopod)
tr	– trunk bud
UB	– repository number at Institut für Paläontologie, Universität Bonn
vcs	– ventrocaudal spine (initial furcal extension)

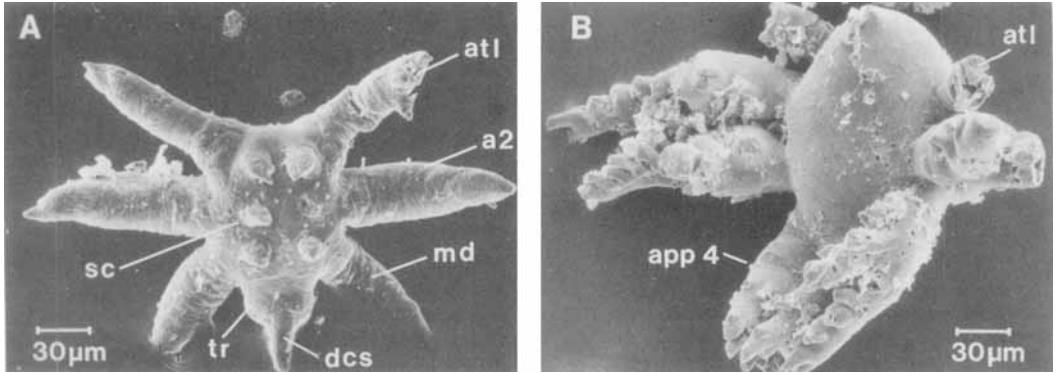


Fig. 3. SEM photographs of Upper Cambrian larva A and the earliest stage of *Martinssonella elongata*. □ A. Dorsal view of larva A, showing the scale-like outgrowths there (UB 793, also illustrated in Müller & Walossek 1986b, Fig. 1m). □ B. Ventral view of instar one of *Martinssonella* (UB 755, also illustrated in Müller & Walossek 1986a, Fig. 11A).

edge is known only in part (Fig. 1D), suggesting a similar design as in larva A, but the exopods of the second antenna and mandible both carry five to six, most probably short, setae which are medially directed distally against the endopod. By contrast there are one to two setae less in larva A (Fig. 1E, compare with Müller & Walossek 1986b, Fig. 4a–c).

Another important difference between the two larvae is the caudal end. In larva A this portion behind the mandibles is as long as it is wide (30–35 µm) and slightly conical. Thus it can be clearly identified as the initial trunk (Fig. 3A; see also Müller & Walossek 1986b, Fig. 2). In larva A2, however, the caudal end is rounded, 60–65 µm wide (measured behind the mandibles) but only slightly less than 30 µm long (Figs. 1A, 2A; due to shrinkage the caudal end appears slightly better defined in UB2; see Fig. 1B).

Again, in larva A the three caudal spines (dcs, vcs) are rigid and about 15–25 µm long. By contrast, in larva A2 these spines are less than 10 µm, the more acute dorsocaudal one being even shorter (Figs. 1F, 2; spines broken off in UB2).

The apparent lack of the anus (Fig. 1F) and the poor setation of the appendages (as far as is known) indicates that larva A2 was a non-feeding nauplius, as was larva A.

In respect of the larger size of various structures (c. 10–20% increase) and better development of the exopods in larva A2 it may be suspected that the two larvae represent successive growth stages of the same animal. The lack of dorsal outgrowths could be explained by their reduction after moulting from larva A to larva A2.

However, an argument against such an assumption is in the caudal end: the initial trunk is better defined in the smaller larva A than in larva A2 and has much longer terminal spines. As a rule, in crustacean larvae the initial trunk elongates progressively during ontogeny, accompanied by the progressive development of furcal rami from paired setae (e.g. Izawa 1987, Fig. 2), or short humps with few terminal spines or setae (e.g. see Müller & Walossek 1988 for the ontogeny of the Upper Cambrian maxillopod *Bredocaris admirabilis*). Even if naupliar larvae do not grow during development, as in certain parasitic copepods, the furca gains structure progressively (Izawa 1975, Figs. 1–5). This led us to regard the two specimens as representatives of a distinct larval form which is still closely allied to larva A.

Comparisons of type A-larvae with other 'Orsten' larvae

Considering relationships between type A-larvae and early instars of other 'Orsten' forms, only the early instars of *Martinssonella elongata* (Müller & Walossek 1986a), described from zone 1 of the 'orsten' sequence, show some similarity, mainly in their simplicity of form.

The first stage of *Martinssonella* is egg-shaped and about 190 µm long (Fig. 3B). Similar to type A-larvae, it lacks a head shield and has no distinct initial trunk. However, the earliest larva of *Martinssonella* is already a metanauplius with three functional postantennular appendages. The

exopods of all postantennular appendages are well-segmented and bear few rigid setae, indicating that the earliest larva of *Martinssonina* was much more mobile than type A-larvae.

The absence of mouth and anus in the first two instars of *Martinssonina* and the little defined median setation of their appendages (Müller & Walossek 1986a, Fig. 2A–D) clearly indicate that these larvae were non-feeding, as the type A-larvae. In the third stage (Müller & Walossek 1986a, Fig. 2E, F), mouth, a small postoral sternum, and anus appear, accompanied by a better armature of the postantennular appendages with setae and spines on the inner edges. Further appendages, however, are not added between the first and the third stages.

In striking contrast to type A-larvae, a labrum is not developed at any developmental stage of *Martinssonina*. Again, throughout ontogeny the forehead region bears into a rostrum-like but unjointed spine, while the caudal end continues into a single spine in the early larval stages. With progressively elongating trunk the subsequent two metanaupliar larvae attain a more spindle-shaped habit (Müller & Walossek 1986a, Fig. 2B, C, E). Furcal outgrowths do not appear throughout development.

Recently, Izawa (1987) compared copepod nauplii with larva A and *Martinssonina* larvae. This author concludes that the pair of caudal spines of larva A may represent the initial maxillules of the first larva of *Martinssonina*. This assumption seems to be based on interpretations of Lang (1948, *vide* Vincx & Heip 1979) that a pair of setae at the caudal end of the nauplius of certain harpacticoid copepods are the initial maxillules, rather than the initial furca (see also Onbe 1984). As it makes a great difference whether a structure develops anterior or posterior of the growth zone, this implies that not only the development of these harpacticoids starts already with a metanauplius, uniquely among Copepoda, but also type A-larvae would be metanauplii accordingly.

On the other hand, Vincx & Heip (1979) in their description of the postembryonic development of the harpacticoid copepod *Canuella perplexa* clearly demonstrate that in the first stage the pair of caudal setae refers to the position of the future furca (as is the case in all other copepods). The maxillules appear as a pair of setae anterior to the furcal setae in the second stage (Vincx & Heip 1979, p. 283 and Fig. 1A, B). Vincx & Heip (1979), describing the fate

of these structures throughout ontogeny, suspect that in other harpacticoids the caudal setae may have been misinterpreted too and suggest revision.

Their observations, which are questioned by Izawa (1987), are now corroborated by Dahm (pers. comm.). He found an intermediate stage between the first and second larvae of *Canuella perplexa* in which the initial maxillulae appear *de novo* under the cuticle, slightly anterior to the furcal setae, which are retained.

Furthermore, in the Upper Cambrian maxillopod *Bredocaris admirabilis* (Müller & Walossek 1988; first larva is a metanauplius) and also in *Rehbachella kinnekullensis* (Walossek in prep.; first larva is a true ortho-nauplius), the maxillules appear either as a bilobed structure or as a pair of setae on the ventral side of the larval trunk. Furcal development starts in both forms in the first stage with a pair of rigid spines at the trunk end below the dorsocaudal spine. With this, the pair of ventrocaudal spines of the type A-larvae are considered as initial furcal spines and these larvae regarded as true ortho-nauplii.

Summed up, it would necessitate considerable morphological changes when assuming that larva A could, on moulting, change to the metanauplius larva of *Martinssonina*. These would include the:

- (a) formation of a rostrum, *but*
- (b) reduction of the prominent labrum, *and*
- (c) reduction of the initial mouth opening at its rear, *and*
- (d) reduction of the ventrocaudal spines, i.e. the initial furcal rami.

On the basis of various morphological details (in particular appendage morphology and missing labrum), *Martinssonina* cannot be considered as a eucrustacean but to belong to a group at a lower evolutionary level. The lack of furcal rami may be another indication for this interpretation: several forms in the 'Orsten' material, probably related to *Martinssonina*, also have only a single caudal process. Their description is under way.

As was already assumed for larva A by Müller & Walossek (1986b), the type A-larvae are, on the other hand, nauplii of true eucrustaceans, which are still unknown, however. Accordingly, similarities between their larval stages and even details shared are regarded as plesiomorphic. This makes it unlikely that type A-larvae could represent the naupliar stages of the larval sequence

of *Martinssonina elongata*, as has been assumed by Izawa (1987).

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