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The stem crustacean *Oelandocaris oelandica* re-visited

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The arthropod *Oelandocaris oelandica* from the upper Middle Cambrian "Orsten" of Sweden was recently recognized as a member of the early phase of crustacean evolution based on additional morphological detail from new specimens. Here we present a detailed investigation of all available material. It includes the description of a 400 µm long specimen probably representing an early developmental stage. Variation in size correlated with variation of trunk-segment numbers allowed recognition of different instars. The largest specimens do not exceed an estimated length of about 1 mm, indicating that our material may consist only of immature specimens. The characteristic, extremely long antennula of *O. oelandica* branches into three long rods. It may have served as the major structure to sweep in food, aided by the two subsequent appendages. These and the more posterior limbs were also responsible for locomotion. Minute pores on the outer edges of the posterior limbs and on the trunk tergites possibly contained sensilla originally, which may have served as water-current detectors. The presence of a minute proximal endite only on the third head appendage suggests a rather basal position of this species within Crustacea, because comparable developmental stages of other known stem crustaceans have such an endite on more of their appendages. Reconstruction of *O. oelandica* and its life attitudes (referred to the largest instar known) benefited from the application of 3D modelling. These helped, e.g., in identifying the combination of the plesiomorphic feeding function of the antennulae and the specialisation of the exopods of the next two appendages as a step toward the development of a sweep-net mode of feeding, one of the key novelties in the evolution of Crustacea. Such a mode of feeding coupled with locomotion of the three anterior appendages is still practiced in the naupliar and metanaupliar phases of many extant eucrustaceans, and even some adults.

Key words: Crustacea, Arthropoda, morphology, life habits, sweep-net feeding, evolution, phylogeny, stem lineage, computer-aided 3D modelling.

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Introduction

In 1983 Müller described six Cambrian putative crustacean species on the basis of specimens in an unusual three-dimensional type of phosphatic preservation. Subsequent study of additional arthropod taxa in this "Orsten"-type preservation (Maas et al. 2006) led to the reconstruction of the stem lineage of Crustacea (putative stem taxa: *Cambropachycope clarksoni* Walossek and Müller, 1990, *Goticaris longispinosa* Walossek and Müller, 1990, *Henningsmoenicaris scutula* [Walossek and Müller, 1990], *Martinssonia elongata* Müller and Walossek, 1986; subsequently added: *Cambrocaris baltica* Walossek and Szaniawski, 1991) and identification of the abundant bivalved Phosphatocopina as the sister group of Eucrustacea (crown group Crustacea; Maas et al. 2003; Siveter et al. 2003; Maas and Waloszek 2005). This helped consolidate our understanding of the ground patterns of Crustacea sensu lato, Labrophora (Phosphatocopina + Eucrustacea, possibly also including the myriapods and/or hexapods) and Eucrustacea as the crown group including all taxa with extant derivatives.

Some autapomorphies traditionally proposed for Crustacea, e.g., differentiation of cephalic appendages into two pairs of (sensorial) antennae, mandibles and two pairs of maxillae, could be soundly refuted and demonstrated to be valid only for certain eucrustacean in-group taxa; instead, a new set of autapomorphies was proposed (Walossek and Müller 1990; 1998a, b; Walossek 1999; Maas et al. 2003; Waloszek 2003a, b). Two of the new characters are noteworthy in this context:

– exopods of, at least, the first two post-antennular limbs multi-annulated and with locomotory setae arising from the inner side of the annuli facing the endopod;
– a small setiferous endite, called "proximal endite", located medially below the basipod of the post-antennular appendages (Walossek and Müller 1990).

Multi-annulated exopods form part of a sweep-net feeding and locomotion apparatus and occur in the Cambrian

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phosphatocopines and in extant small-scale eucrustaceans and all free early eucrustacean larvae. The "proximal endite" had been recognized on extant branchiopods almost 90 years earlier (Calman 1909), but remained largely ignored subsequently. We regard its development as a significant step in the change of the locomotory and feeding attitudes along the evolutionary lineage of crustaceans (see also, e.g., Waloszek et al. 2007). Further modification of the "proximal endite" on the second and third appendages, the so-called antennae and mandibles, into a coxa is an autapomorphy of the Labrophora (Siveter et al. 2003). Besides these features, the Labrophora can be distinguished from the stem taxa by more characters associated with the feeding and locomotory apparatus, such as a fleshy labrum behind the original hypostome, fusion of the postoral sternites of the antennal to maxillulary segments (sternal plate, sternum), paragnaths on the mandibular portion of the sternum and the appearance of fine setulae or denticles on setae, parts of the labrum, the sternum and the paragnaths (Maas et al. 2003). These features are also significant in testing proposed atelocerate/tracheate or hexapod relationships (e.g., Wolff and Scholtz 2006 recognized homology between the paragnaths of myriapods, hexapods and crustaceans). Antennular morphology, development of antenna and mandible, exopod morphology, and the occurrence and particularly the ontogenetic development of the "proximal endite" on postantennular limbs, may eventually facilitate further resolution of the relationships among the crustacean stem taxa.

Re-investigations of Müller's original set of taxa (Müller 1983) on the basis of additional material allowed systematic assignment of *Skara anulata* Müller, 1983, *Bredocaris admirabilis* Müller, 1983 and *Rehbachiella kinnekullensis* Müller, 1983 to particular eucrustacean taxa (summary in Walossek and Müller 1998b). *Walossekia quinquespinosa* Müller, 1983 and *Dala peilertae* Müller, 1981 (Müller 1981 treated this species already in sufficient detail to qualify as a valid taxonomic description, accordingly this date has to be used in preference), awaiting detailed restudy, possess features known only from particular crown crustaceans such as cephalocarids, maxillopods and branchiopods, considered to form the monophylum Entomostraca (cf. Walossek 1999).

Oelandocaris oelandica Müller, 1983 was originally known from a single, poorly preserved specimen, but additional material identified subsequently has made a re-investigation tenable. An initial report by Stein et al. (2005) addressed some key features of the new material and concluded that *O. oelandica* is a derivative of the stem lineage of Crustacea. Among the crustacean stem derivatives, *O. oelandica* is unique in having only one "proximal endite", which occurs on the second post-antennular appendage (the mandible of labrophoran crustaceans) and remains up to the latest developmental stage known so far. The aim of our detailed re-investigation of *O. oelandica*, using scanning electron microscopy, morphometrics, and computer-based reconstructions, is to present an in-depth report of its morphology, aspects of ontogeny, morphogenesis of structures, and possible life attitudes. In addition we describe a small specimen, apparently of an early larval stage as the putative earliest stage known of this species, filling the series of instars.

Institutional abbreviation.—UB, University of Bonn, Germany.

Material

All material was etched from bituminous limestone nodules ("Orsten"), isolated and mounted on SEM stubs by the working team of K.J.M. in Bonn, Germany in the 1980s to the mid 1990s. The holotype (UB 649, Fig. 1) of *Oelandocaris oelandica* is derived from the *Olenus gibbosus* Zone (lowermost Furongian Series, Peng et al. 2004; Babcock et al. 2005; Terfelt et al. 2005) of the Alum Shale succession near Degerhamn, Öland, Sweden. The additional material is from the *Agnostus pisiformis* Zone at Gum, Västergötland, Sweden, now representing the uppermost zone of the Middle Cambrian (Babcock et al. 2005). The additional material comprises six specimens, five larger ones (UB W 260–264, size range from more than 660 μm to ca. 1 mm, Table 2) and a considerably smaller specimen (UB W 265), which is ca. 440 μm long. This specimen shares characteristic features with the larger specimens but evidently represents an earlier developmental stage. A brief overview of the preservation of the individual specimens and features they display is given in Table 1. All comparable features among the specimens correspond in structure, topology, and size. Therefore the material is considered conspecific with the holotype despite the stratigraphical and geographic distance between Öland and Västergötland. In the absence of diagnostic differences, establishment of a new species for the material from Västergötland is not tenable.

Due to the poor preservation of the holotype (Table 1), it is difficult to interpret its morphology well, as exemplified by the misinterpretation of segmentation and a miscount of limbs in the original description (Müller 1983, corrected in Stein et al. 2005). The new specimens, though better preserved (Fig. 2), are considerably distorted and incomplete. However, the new material increases our understanding of the holotype, and also allows for comparison of many more specific structures, such as the shield, the overall shape, and the large set of ventral details including the eyes, the hypostome, the mid-ventral surface, and, last but not least, the appendages. This facilitates reconstruction of *Oelandocaris oelandica* at high fidelity and also helps to understand more of the life habits of this tiny early crustacean.

Measurements, though difficult to apply due to the distortion of the specimens (Table 2), revealed considerable variability. Besides the early instar, three size classes can be discriminated, which correlate with an increase in the number of trunk tergites/segments (see section "Ontogeny"). The early developmental stage, represented by UB W 265, has a total length of about 440 μm, with the head region back to the fifth appendages measuring 290 μm. Set 1 of the larger specimens

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Table 1. Specimens studied. Abbreviations: app2, 3, 5, appendages; atl, antennula.

UB 649	Coarsely phosphatized; almost complete length, head shield complete, also with rostral extension; specimen is laterally compressed (inwardly pressed shield flanks), shield somewhat distorted dorsally; cephalic appendages preserved in most cases only by their insertion sockets (partly with infillings); all distal parts of the appendages missing; only app2 has basipod and proximal part of exopod preserved; some proximal limb parts pressed together; hypostome complete, putative eyes preserved, sternal region well recognizable with sternal part of third appendiferous head segment gently elevated; trunk with four segments with short tergites, partly distorted; anterior portion of telson with anus on ventral surface preserved as long tubular structure; shield and trunk tergites seem to have borne lateral spines which are broken off, leaving holes on the surface
UB W 260	Dorso-ventrally flattened, with trunk flexed against the body; head shield almost completely preserved except the rostrum; putative eyes and hypostome well preserved; three tergite-bearing trunk segments preserved, flattened; proximal portions of antennula preserved; basipod and 3 exopod articles preserved in app2; basipod and proximal articles of exopod preserved in other limbs; proximal podomere of endopod of app3 present
UB W 261	Only left half preserved; head shield missing; 4 tergites and part of caudal end recognizable; only proximal portion of eyes preserved; posterior part of hypostome missing; antennula preserved with proximal parts of outgrowths, app2 with basipod and 4 exopod articles, of app3 only basipod preserved, subsequent appendages present with basipod and first podomere of endopod
UB W 262	Head shield fragmentary; putative eyes and hypostome well preserved; 3 trunk tergites preserved; of atl only proximal portions left; app2 with basipods, endopods and exopods, subsequent appendages with basipods, exopods, and first endopodal podomeres
UB W 263	Laterally compressed; anterior and right portions of head shield missing; hypostome and sternal area missing; 5 tergites preserved, tailpiece fragmentary; atl and right appendage series missing; preserved portions of appendages on left side; of app2 only basipod preserved, app3 with basipod and proximal endite within ample joint membrane, proximal endopod podomere, app4 with basipod and first endopod podomere, app5 with basipod, two endopodal podomeres, and part of exopod, first trunk limb with basipod and first endopod podomere; posterior limbs fragmentary
UB W 264	Laterally compressed; anterior portions of head shield missing; only few ventral structures preserved, particularly the posterior end of hypostome; also posterior end only fragmentary
UB W 265	Head shield and trunk fully preserved; hypostome and left appendage series almost entirely preserved, right appendage series fragmentary

Table 2. Morphometric data of selected features of the investigated specimens of *Oelandocaris oelandica* Müller, 1983 (values in μm, values in brackets are estimates; sorted according to the increase in the number of trunk tergites). Total length measured from eyes to start of tail. Head shield measured from eyes. + present but not measured; – absent; ? unclear. Abbreviations: bas, basipod; en, endopod; ts, tergite.

Number of	UB W 265	UB W 262	UB 649	UB W 264	UB W 263	UB W 260	UB W 261
tergites	(1)	3	4	≥4	5	>3	5
total length	440	>670	740	>685	>795	>945	990
head shield length	290	>430	450	>435	–	590	605
head shield height	90	–	125	?	?	+	–
eye length	25	–	30	–	–	50	–
hypostome	120	180 (160)	(150)	?	?	220 (195)	(210)
ts1	–	+	?	95	100	110	+
ts2	–	+	80	85	95	100	+
ts3	–	+	+	60	80	95	100
ts4	–	–	+	+	65	–	80
ts5	–	–	–	?	45	–	80
tailpiece	?	?	?	–	?	–	?
bas2 height	+	60	50	–	65	65	70
bas3 height	+	+	?	–	85	+	100
bas4 height	+	+	?	–	115	110	120
bas5 height	–	+	?	–	120	130	120
bas6 height	–	95	?	–	120	100	+
bas7 height	–	–	?	–	?	90	+
en2.1 height	25	30	?	–	–	–	–
en3.1 height	30	?	?	–	–	–	–
en4.1 height	?	55	?	–	55	60	65
en5.1 height	?	60	?	–	60	–	70
en6.1 height	–	60	?	–	55	–	+
en7.1 height	–	–	?	–	–	–	+

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measures more than 660 µm in total length, with a head shield length greater than 430 µm. Set 2 has a total length of 680 to 740 µm, with a head shield length between 430 and 450 µm. Set 3 measures up to 1mm in total length, and its head shield measures about 600 µm. This size difference of ca. 20–25% between sets 2 and 3 may suggest that more instars might have been present, but the segmental increase of just one trunk segment does not support this view. The holotype falls into set 2. The only major morphological variation between the holotype from Öland and the new material from Västergötland can be found in the size of the caudolateral spines of head shield and trunk tergites. The distance between the two localities is 330 km, so variation might be explained by geographical separation, and possibly also by a slight difference in age, but the limited material does not allow farther-reaching speculations.

Methods

Techniques.—Initial SEM investigation of all specimens occurred in the early 1980s to mid 1990s in Bonn (DW). Detailed re-investigations after 2000 were done in Ulm (MS, DW) using a Zeiss DSM 962 scanning electron microscope at the Central Facility for Electron Microscopy, University of Ulm. All specimens had been glued to SEM stubs prior to our re-investigations and could not be re-mounted due to their fragility. Documentation of the morphology in all aspects was greatly facilitated by an electro-mechanic SEM device constructed by the team of the Central Facility. This appliance enabled rotation and tilting of the scanned object up to a full angle of 90°, thus extending by far the limited inclination provided by the SEM.

Measurements were obtained from the SEM images. Since high accuracy was not feasible because of preservational limitations (tilting and wrinkling), we adjusted the values to the nearest 5 µm. This suffices for gross comparisons within the material (Table 2; see also, e.g., Müller and Walossek 1985 and Walossek 1993).

Reconstruction of some structures remains uncertain due to the only partial preservation of, e.g., limb parts and the tail end. In some cases, details from the early developmental stage (UB W 265) were used to complete the reconstruction. Where similarity could be estimated, features were also taken from other stem crustaceans, particularly *Henningsmoenicaris scutula* (Walossek and Müller, 1990) (JTH, AM, and DW unpublished data).

The SEM images were processed with Adobe Photoshop™ CS1, the line drawings were produced with Adobe Illustrator™ CS1 and 3. A plasticine model at 500 times magnification was created in a similar fashion as that of *Bredocaris admirabilis* (Müller and Walossek 1988). Coloured plasticine was used to distinguish different limb parts, adopting the standardized colour scheme introduced by Walossek (1993). We controlled the proportions using enlarged SEM pictures and line drawings of the appendages. Changing the orientation of the limbs of the model helped to improve the understanding of the possible range of movement and interoperability in the whole locomotory and feeding apparatus. Later, a refined 3D reconstruction was created using the modelling software Blender (MS, JTH). A sequence of a possible limb movement cycle was created and the movie is stored in the data repository of *Acta Palaeontologica Polonica* (see Supplementary Online Material at http://app.pan.pl/SOM/app53-Stein_etal_SOM.pdf).

Terminology.—Terminology follows the standardisation of morphological terms for crustaceans and arthropods proposed by Walossek/Waloszek in various papers (e.g. Walossek 1993; Waloszek 2003b), which is considered to provide maximum consistency and terminological stability. Standardisation is particularly important with regard to segmentation, appendage morphology and other ventral structures (e.g., differentiation between "hypostome" and "labrum", see, e.g., Waloszek 2003b). Since we regard homology of the most anterior segmented and pivot-jointed appendages among euarthropods as well established (e.g., Chen et al. 2004; Scholtz and Edgecombe 2005, 2006; Waloszek et al. 2005; but see Budd 2002 for an opposing view) we use the term antennula rather than antenna for this appendage, to avoid confusion with the first postantennular appendage in Crustacea, called antenna. The post-antennular limbs are denoted in neutral terminology, i.e., the "first post-antennular limb" also represents the "second appendage", and so on. The term podomere is restricted to the subdivision of the endopod, but the homology of the subdivisions of the antennula and the exopods of the post-antennular limbs are uncertain. Therefore we apply the neutral term article to these. The terms "anterior and posterior wings" are adopted from trilobite descriptive terminology of the hypostome, as corresponding structures are present in *Oelandocaris oelandica* and other euarthropods such as e.g., *Agnostus pisiformis* (Müller and Walossek 1987), and the phosphatocopines (Maas et al. 2003). Other terms are explained, as necessary, in the text. Terminology of the armature of the appendages was quite difficult to apply due to the fragmentary status. Hence we could not clearly distinguish between setae and spines, setulae or spinulae, denticles, etc. Also the size could often only be estimated from the insertion area, although the available "Orsten" forms provide good proxy in estimating size and form of such cuticular outgrowths.

Morphology of *Oelandocaris oelandica*

Assignment of the different specimens from Västergötland to *Oelandocaris oelandica* rests on the following characters of the holotype from the Isle of Öland:

Fig. 1. Holotype of stem crustacean *Oelandocaris oelandica* Müller, 1983 (UB 649) from Degerhamn, Öland, Sweden. **A**. Lateral view. **B**. Ventral view. **C**. Dorsal view. **D**. Stereo image of ventral view. **E**. Latero-ventral view of the head. Abbreviations: app, appendages; ts, tergites. →

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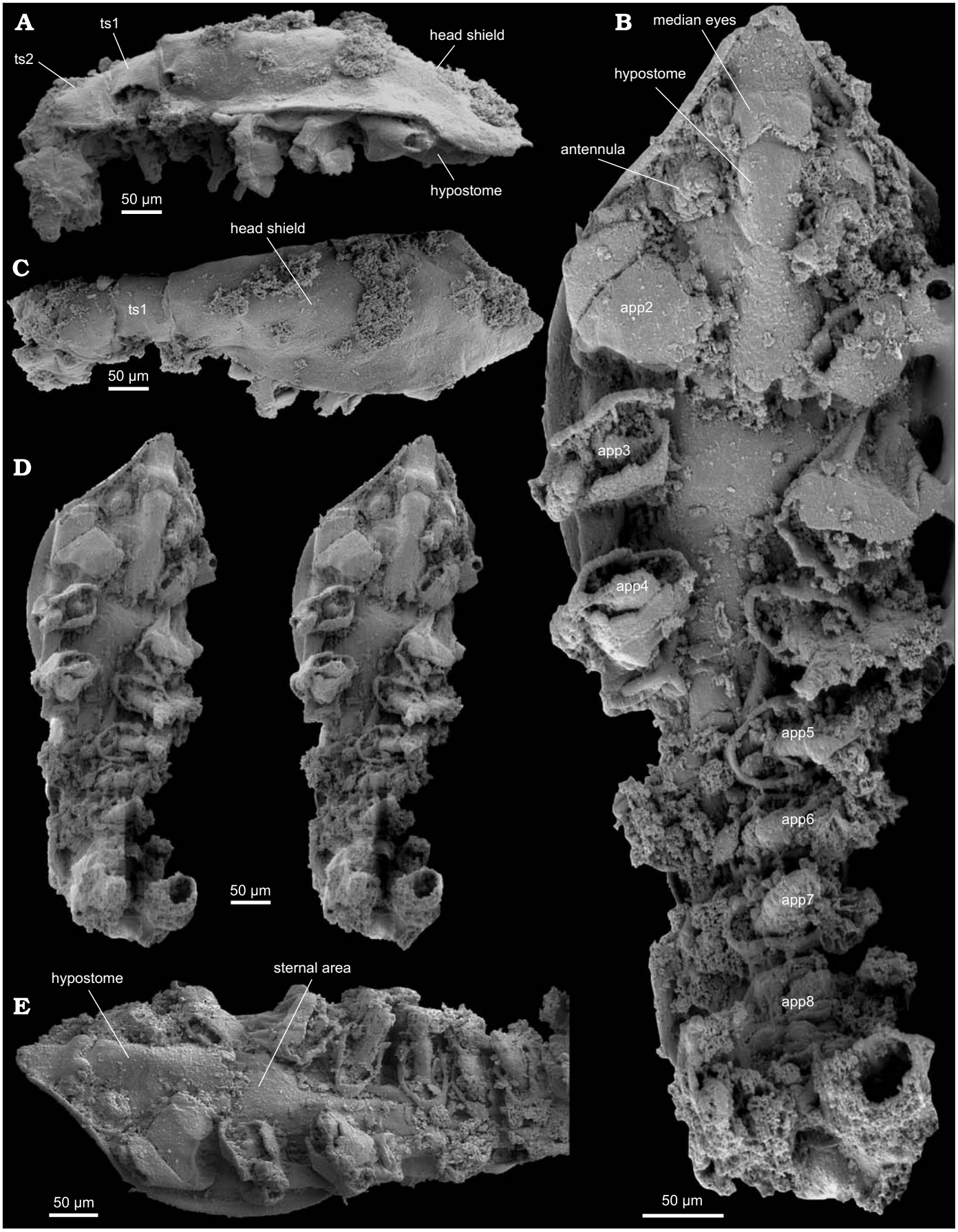

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– simple elongate head shield drawn out anteriorly into short rostrum with flat ventral side;
– head shield bluntly terminated caudally, most likely with lateral spines pointing caudally;
– head incorporates five appendiferous segments;
– elongate, slightly elevated hypostome;
– paired bulbous protrusions (interpreted as eyes) at front of hypostome;
– nearly circular insertion site of antennula;
– proximal limb parts of second appendages in holotype.

The trunk of the holotype comprises four free segments with laterally downward bending tergites extending into short, ill-defined tergopleurae with pointed or spine-bearing posterolateral corners. The maximum number of segments in the larger specimens from Västergötland is five. The general description is based on the largest specimens in the material, with the younger specimens being used as a complement for missing features.

Oelandocaris Müller, 1983

Type species: *Oelandocaris oelandica* Müller, 1983.

Oelandocaris oelandica Müller, 1983

*v1983 *Oelandocaris oelandica* sp. nov.; Müller1983: 93, 107; fig. 11A, B [UB 649], 12.
1985 *Oelandocaris degerhamnensis* Müller, 1983; Müller and Walossek 1985a: 163 [sic!].
2003 *Oelandocaris oelandica*; Maas et al. 2003: table 2 [holotype specimen].
v2005 *Oelandocaris oelandica* Müller, 1983; Stein et al. 2005: 55–57, 60, 62, 64, 67–69; figs. 1 [UB 649], 2, 3A [UB 649], B [UB W 260], C [UB W 261], D [UB W 262], 4A [UB W 261], B–D [UB W 263], E [UB W 262], F [UB W 263], G [UB W 260], 5C [UB W 263], D, 7.
2006 *Oelandocaris oelandica* Müller, 1983; Maas et al. 2006: 275.
v2007 *Oelandocaris oelandica* Müller, 1983; Chen et al. 2007: 264; fig. 11E.
2007 *Oelandocaris oelandica* Müller, 1983; Siveter et al. 2007: 2105.
v2007 *Oelandocaris oelandica* Müller, 1983; Waloszek et al. 2007: 284; figs. 2B [UB W 261, erroneously labelled UB W 263], C [UB W 263], 3, 5C.

General habitus

The body of the largest developmental stage known of *Oelandocaris oelandica* comprises two tagmata: head and trunk. Both are almost equal in length, the head shield measuring about 600 µm, the trunk about 400 µm (see Table 1; Figs. 1–3) including a tailpiece estimated to somewhat more than 100 µm in length (never complete). The nearly semi-circular cross section of both parts and the general appearance —head shield with frontal rostrum-like extension and the segmented tail, most likely extending into a conical end piece—give the animal a shrimp-like appearance. The ventral side of the head is flat, with the shield margins extending only slightly ventrolaterally. The anterior of the trunk is almost as wide as the posterior end of the head shield and tapers gently posteriorly, apparently ending in a longer conical element. This conical element is only partly preserved, but appears to be similar to the tail end of *Henningsmoenicaris scutula* with a medially deepened softer area, accommodating the pre-terminal anus and a pair of lateral, caudally pointing setae. This is also observed in the early developmental stage (UB W 265) assigned to *O. oelandica*.

Head and head shield.—The head shield (Fig. 1) incorporates five appendiferous segments, the antennular segment plus four segments with biramous limbs (Figs. 1, 2). Towards the anterior it narrows rapidly, extending into a short conical rostrum with a bluntly rounded tip (Fig. 1B). The head shield is moderately arched in cross section and has slightly extended lateral flanges. These curve down from the rostrum at about the antennulae (Fig. 1A, B) being almost straight laterally and covering little more of the appendages than the body-joint area. The head shield reaches its maximum width between the first and second post-antennular limbs (Fig. 1B). The flat ventral side of the head is weakly sclerotised (called inner lamella in euarthropods and crustaceans with large shields, e.g., ostracodes). The only elevated structure on the ventral side of the head is the elongate hypostome in the mid line of the anterior half and the sternal region of the third appendiferous segment. The posterolateral corners of the head shield curve upward into a straight posterior margin, which overhangs the anterior trunk tergite only slightly (Fig. 2B, E). This gives the head shield a sharply terminating appearance in lateral view. Caudolaterally directed spines seem to have emerged from the corners. These differ in size individually, from being very conspicuous (Fig. 2B) to being only little protrusions (Fig. $2E_1$).

Hypostome, putative eyes, and sternal region.—The elongate, more or less rectangular hypostome extends medially from slightly behind the rostrum backwards and ends bluntly at two thirds of the length of the head shield (Figs. 1B, D, E, 2C, 3). It is straight sagittally, only slightly elevated, and gently sloping laterally. The first post-antennular limbs are inserted at the posterolateral corners of the hypostome (Fig. 1B, D, E). The anterior hypostomal wings extend to the antero-lateral margin of the head shield (Fig. $8B_2$, arrow). They are overlain by a paired structure, which is composed of a medially connected peduncle and an ovoid swelling on top of it (Figs. 1B, D, E, 4A, C), possibly representing the median eyes. Behind the putative eyes, the hypostome is slightly swollen. Posterior to that, the hypostomal flanks are slightly constricted to widen again at the posterior margin. The posterior wings of the hypostome are little pronounced

Fig. 2. Specimens of later developmental stages of the stem crustacean *Oelandocaris oelandica* Müller, 1983 from Gum, Västergötland, Sweden. **A**. UB W 260, ventral view. **B**. UB W 264, lateral view. **C**. UB W 261, lateral view. **D**. UB W 262, ventral view, specimen slightly distorted. **E**. UB W 263, lateral view from the left side, left set of appendages broken off, exposing the right limbs (E_1) and lateral view of the right side (E_2). Arrows point to postero-lateral corners/spines on head shield and tergites. Abbreviations: app, appendages; ts, tergites. →

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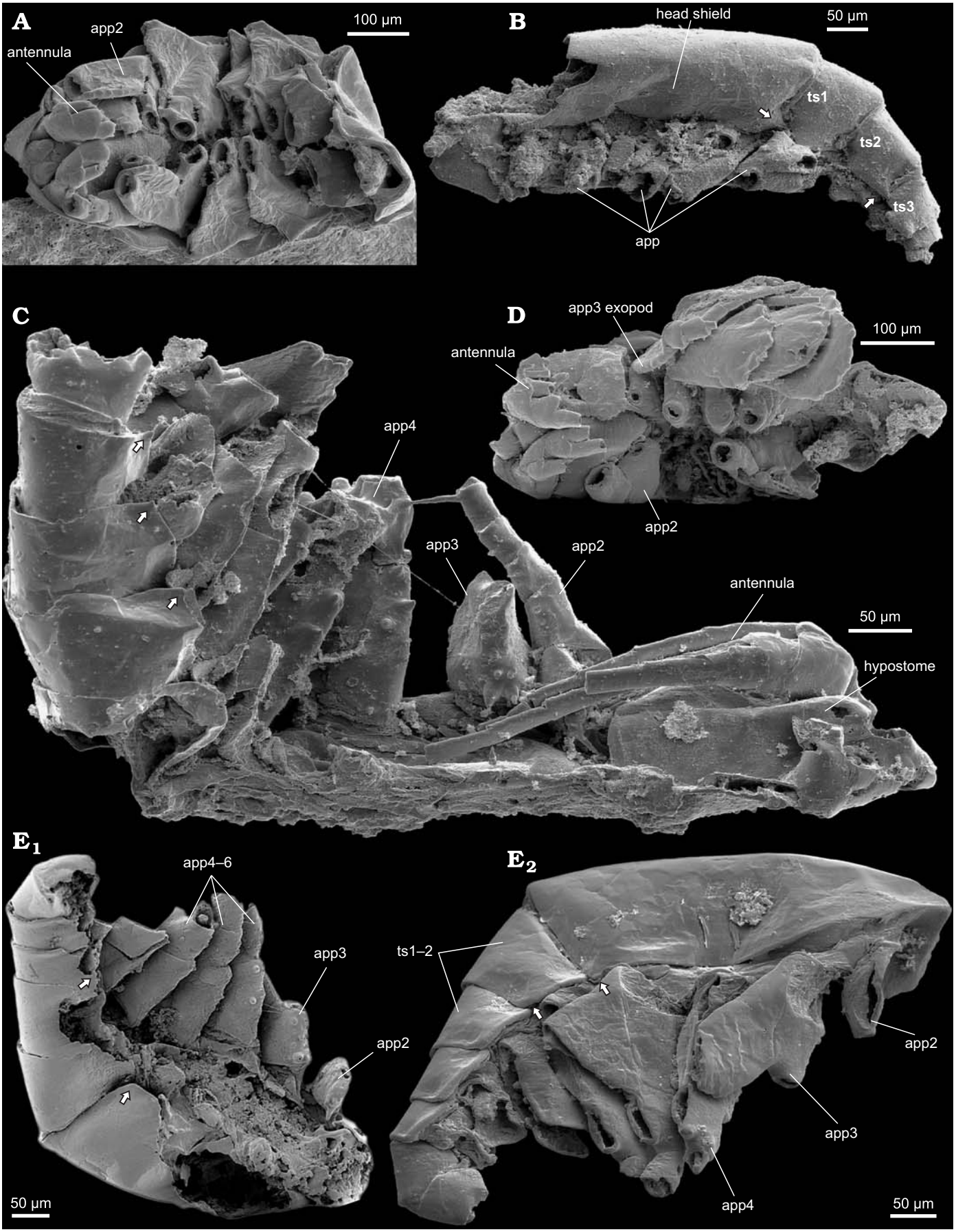

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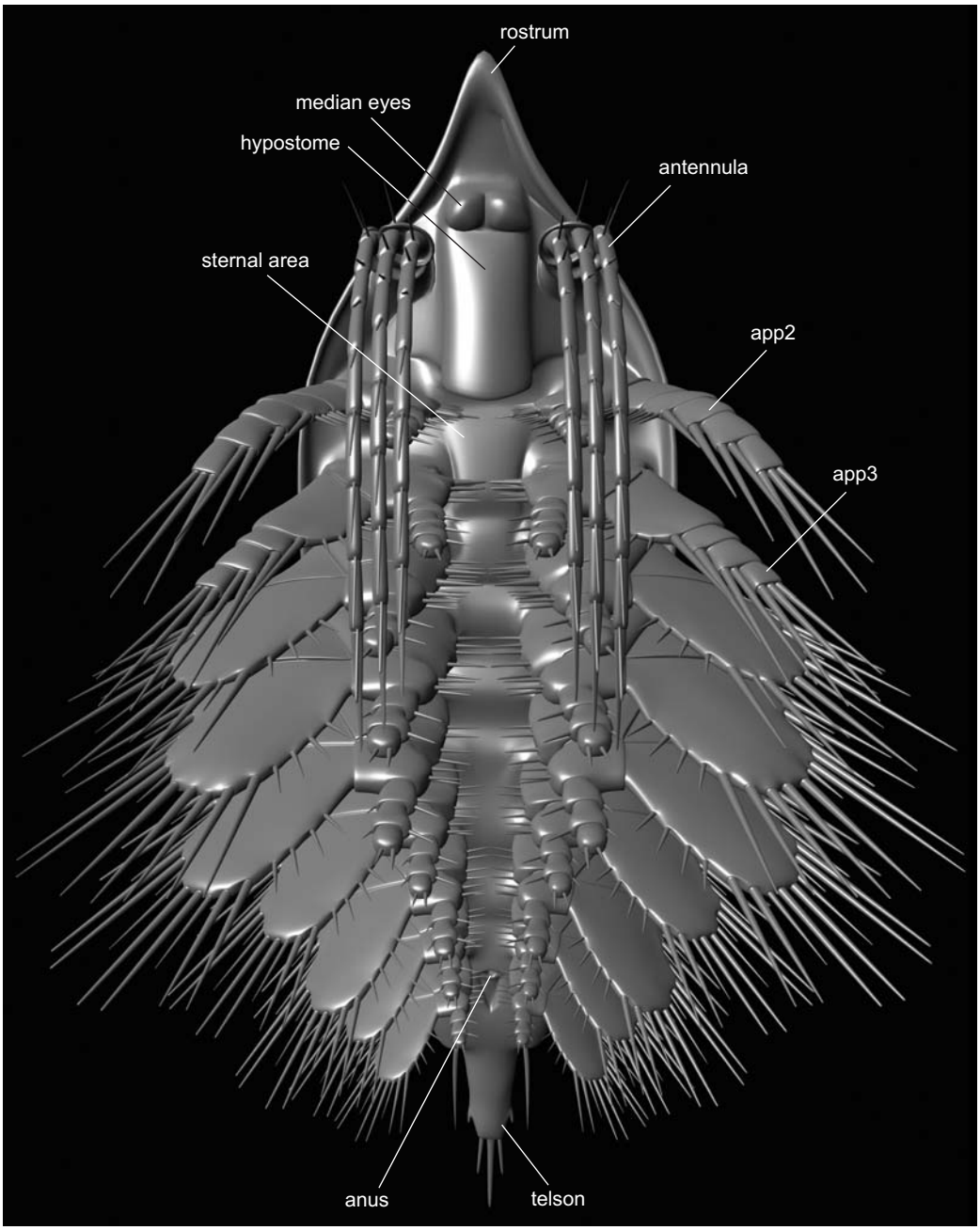

Fig. 3. Reconstruction of the morphology of the latest known developmental stage of stem crustacean *Oelandocaris oelandica* Müller, 1983 in ventral view. Abbreviation: app, appendages.

and seem to merge into the antero-median edge of the insertions of the second limb (Fig. 1B). The mouth opening is located below the posterior margin of the hypostome (Fig. 4C). It seems to be overhung to some degree by the rounded end of the hypostome. A mouth membrane, a soft lip-like structure around the actual opening, may be present, but is only preserved in the earliest developmental stage (Fig. 9F). From the elevation of the hypostome it is clear that the mouth opens above the ventral surface.

A sternite belonging to the first post-antennular segment (antennal segment in labrophoran terminology) could not be identified. The sternal region between the second post-anten-

Fig. 4. Details of specimens of later developmental stages of the stem crustacean *Oelandocaris oelandica* Müller, 1983 from Gum, Västergötland, Sweden. **A**. UB W 260; A_1, ventral view of anterior head region; A_2, latero-ventral view of putative median eyes; A_3, close-up of head with antennula and the anteriorly bent third appendage. **B**. UB W 261, latero-ventral view displaying antennula. Setal sockets marked by arrows. **C**. UB W 264, ventral view of head region. Specimen considerably squeezed. Abbreviations: atl, antennula; am, arthrodial membrane; app, appendages; hs, head shield; hyp, hypostome; me, median eyes; ped, peduncle. →

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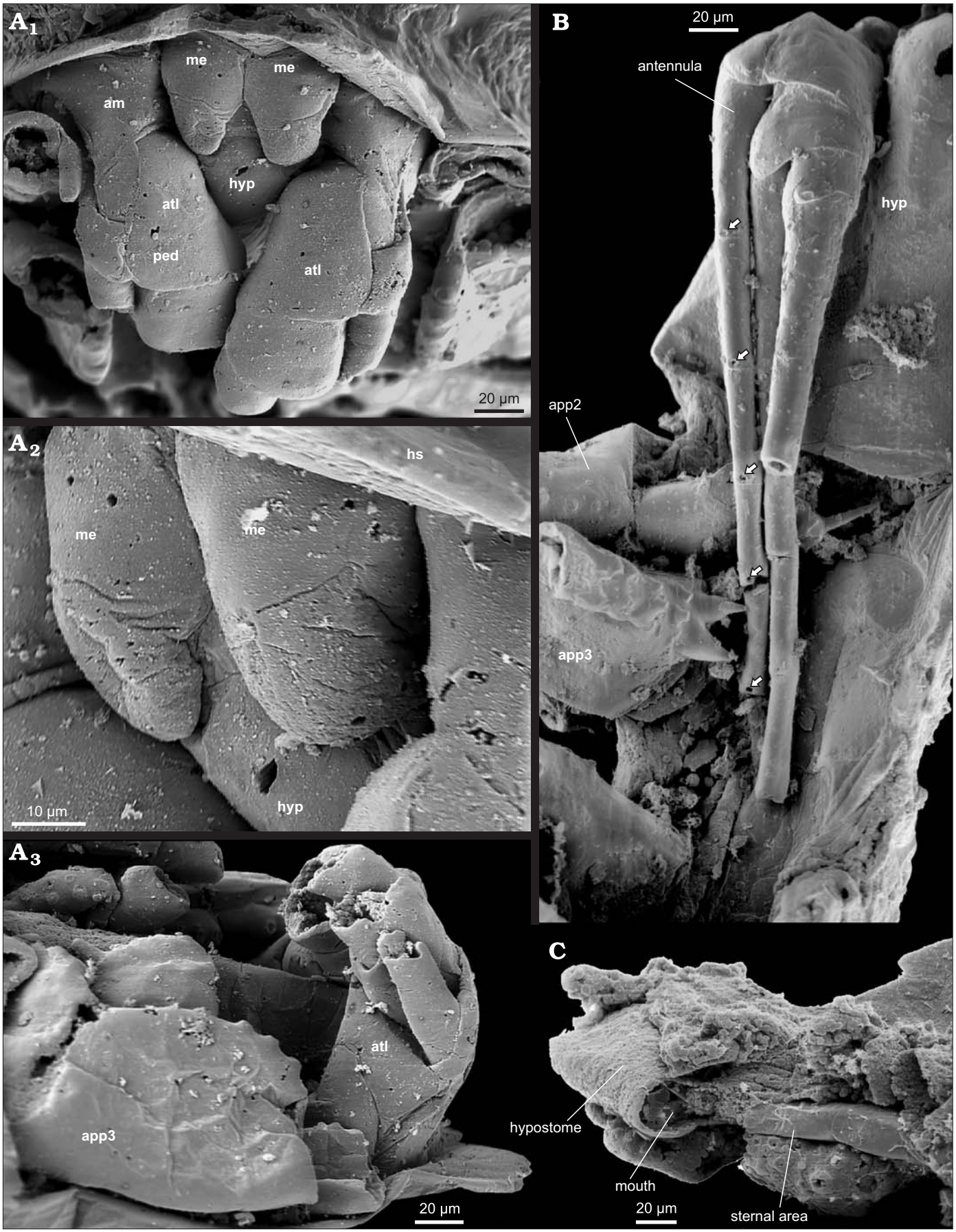

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nular appendages may be slightly more sclerotised than the surface surrounding the appendages, being moderately elevated (best preserved in the holotype, see Fig. 1E). Towards the hypostome the surface is slightly deepened and may be softer than in its surrounding. A median segmental boundary toward the narrower sternite of the third post-antennular segment is present, but weakly developed, so this sternite is separate (Figs. 4B, 5E). The last cephalic sternite is also separate, again narrower than the preceding sternite. The trunk segments have even narrower spaces between their limbs. Therefore, the food chamber may be limited to the head (Fig. 3).

Trunk.—The maximum number of trunk segments encountered in the largest specimens is five (Fig. 2E, Table 1). Apart from the transversely oriented, elliptical limb insertions, the ventral surface of the trunk is not sufficiently well preserved to allow a detailed description. It seems that the median path between the limbs becomes progressively narrower towards the posterior (Fig. 2A, D). If sternites were present, they must have been small.

The trunk tergites are of the same shape, except for a decrease in size towards the posterior (Fig. 2B, E_2). They are roughly U-shaped in cross section. The postero-lateral areas are slightly imbricated (anterior one overlapping the next). There are no distinctive tergopleurae (Fig. 2C, E_2). The curved lateral margins are thickened, possibly bearing setae or sensilla, as is indicated by the presence of corresponding holes and setal sockets in several of our specimens (Fig. $6C_1$, see also the chapter on special details below). One prominent seta may insert close to the postero-lateral tergal corner, as is indicated by a socket being larger than the others (Fig. $8B_1$, arrow). In a similar fashion as the shield, each tergite is extended into a spine at its postero-lateral corner (Fig. 2B, C).

An elongate tailpiece is present, but is known only from fragments in our material of the older developmental stages (Figs. $6B_2$, $8B_1$, D). Part of it is preserved in the holotype, where it was reconstructed as a rod in the original description of the species, though not fully understood (Müller 1983: fig. 12). New photographs show at least the remains of the anus between the enrolled sides (Fig. 8C, see also Fig. 3), proving that this rod-like end is indeed a telson (or a pleotelson depending on the number of further segments included in this portion). The anterior portion of the tailpiece is elliptical in cross section, being slightly depressed in dorso-ventral aspect, bearing an indentation on the ventral side (Fig. 8C) and a pair of lateral step-like ridges with attachment sites for setae (Figs. 2C, $8B_1$ arrow). Presumably the tail is more or less a truncated cone with a flattened ventral side, as is inferred from the morphology of the earlier developmental stage (below) and a similar morphology of this region in *Henningsmoenicaris scutula* (Walossek and Müller 1990; JTH, AM, and DW unpublished data). The anterior ventral side is slightly depressed and may be pliable, with the anus located in this soft area (Fig. 8C).

Appendages

Antennula.—The antennula (Figs. 2C, 7A) inserts directly postero-laterally to the anterior wing of the hypostome (Fig. 1B). The insertion area is circular to sub-triangular. The antennula rests on a prominent, socket-like truncated-conical arthrodial membrane (Fig. $4A_1$). The appendage itself is composed of a relatively short three-divided peduncle, each of the articles carrying a multi-segmented outgrowth disto-laterally (Figs. $4A_1$, A_3, 7A). The structure of the peduncle is complex, with many structures involved. All articles are narrowest at their proximal end and widen distally. The first article is two-divided in the long axis of the appendage, the smaller lateral portion carrying the outgrowth and a seta on its anterior surface. The larger median portion is slightly constricted proximally and indented postero-distally allowing a wide flexure of the entire distal part of the antennula and its own outgrowth (Fig. $4A_3$). The subsequent article inserts mediodistally on the first article. It is uniform, inverted conical as the first article, but smaller in extension and width, carrying a seta on its antero-distal surface, an outgrowth latero-distally, and the third article mediodistally (Fig. 4B). The third article is barrel to cone shaped, continuing into an outgrowth distally. Even this article bears a seta on its antero-distal surface (Fig. 4B).

All outgrowths are composed of tubular articles. The first outgrowth consists of at least five articles; the second and third outgrowths consist of at least two articles. Presumably all three outgrowths are at least half as long as the entire animal, as suggested by additional isolated parts found between the basipods of the fifth cephalic appendage pair in one of the specimens (Fig. 3). The most proximal article of each of the outgrowths is wide at its base and narrows rapidly distally. The other articles are ca. five times as long as wide and are slightly laterally compressed and oval in cross section. All carry a seta on their antero-distal surface, as is indicated by the preserved insertion areas (arrowheads in Fig. 4B). The setae may point distally, as is indicated by the position of their insertion areas (Fig. 2C).

Second cephalic appendage (app2).—The first post-antennular limb (Fig. 7B) is biramous and is inserted at the postero-lateral edge of the hypostome. The limb is rotated postero-me-

Fig. 5. Details of specimens of later developmental stages of the stem crustacean *Oelandocaris oelandica* Müller, 1983 from Gum continued. **A**. UB W 262; A_1, lateral view exhibiting the exopod of third appendage; A_2, second appendage nestling to the hypostome viewed from the posterior. **B**. UB W 263; B_1, third appendage viewed from the anterior, endopod and tip of exopod missing, small arrows point to setal attachments on median edge of exopod, large arrows mark basipod-exopod articulation; B_2, median view of appendages 2 to 4 from postero-lateral, only the arthrodial membranes and the basipods are preserved of the appendages; note the proximal endite of the third appendage. Mirrored for correct view of the mouth area of the animal. **C**. UB W 261; C_1, view from antero-ventral onto the ventral body surface with appendages 2 to 4 and the tips of the antennula; C_2, close-up of proximal part of second appendage exhibiting various setae. Arrow points to bifid seta. Abbreviations: alt, antennula; am, arthrodial membrane; app, appendages; bas, basipod; ex, exopod; hyp, hypostome. →

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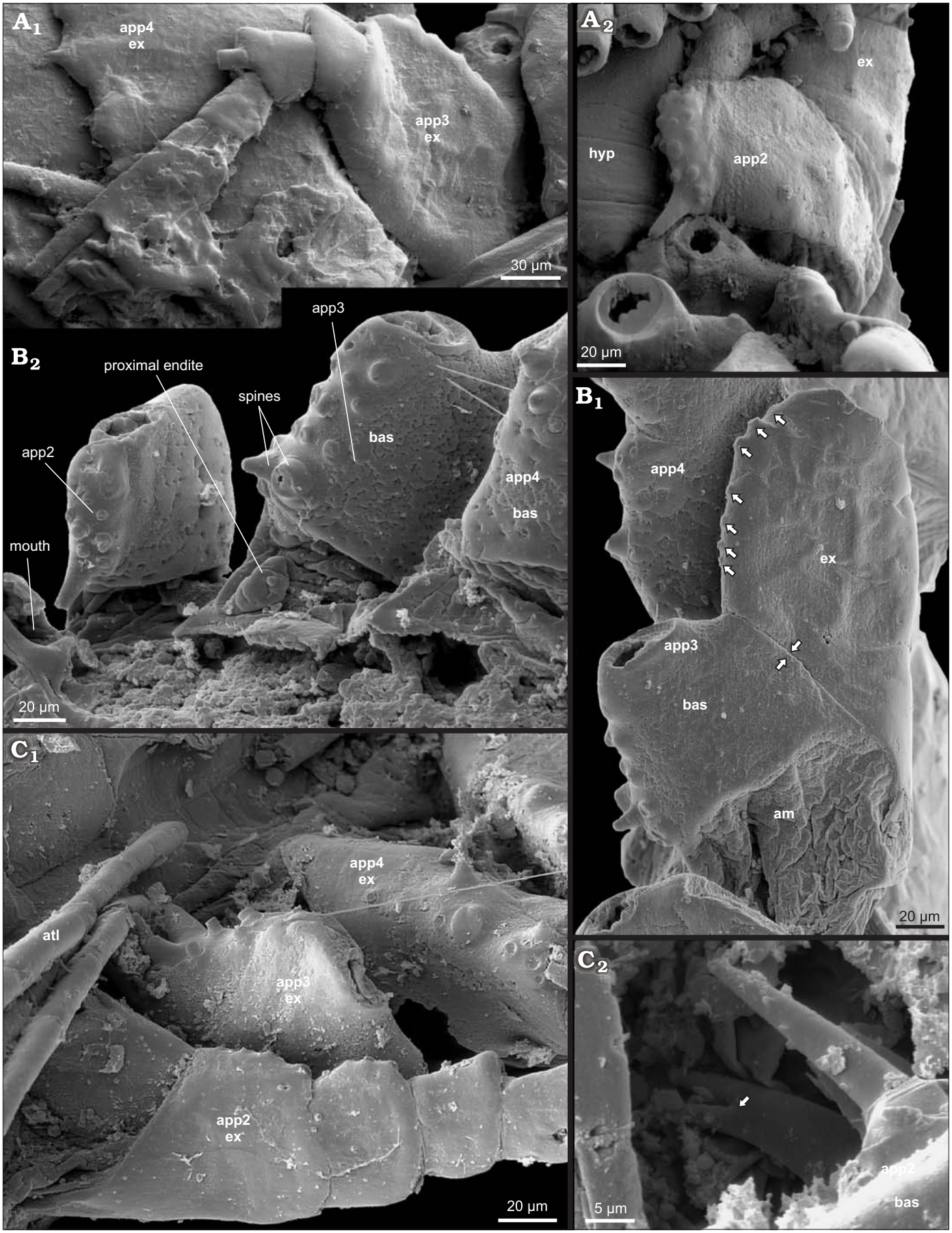

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dially, with the median edge of the antero-posteriorly flattened basipod being more posterior than the insertion of the exopod. The arthrodial membrane forms a limb socket. The posterior face of the basipod is shorter than the anterior. Along its median edge, the basipod carries a bi-serial armature of setae or fine spines that point toward the mouth. The most proximal of the anterior row is a prominent spine with a bifid tip that reaches underneath the distal portion of the hypostome. Distal to it, the anterior series consists of eight equally large setae arranged in a meandering row. The posterior series consists of seven setae, the two most proximal of which are smaller than the distal ones.

The endopod is attached to the medio-distal portion of the basipod. It comprises four sub-cylindrical podomeres. Each of the three proximal podomeres widens slightly distally and possibly carries a seta on each side of the articulation with the subsequent podomere. The distal podomere is a short conical element probably bearing two setae (Fig. $5A_2$). The exopod comprises five antero-posteriorly-compressed articles. With roughly double the size of the basipod, it is the dominant ramus of this appendage. The proximal portion articulates along the slanting lateral edge of the basipod (Fig. 1B). The second exopodal portion is shorter, trapezoidal to rectangular in outline. Both portions carried a series of four to five setae along their median edges, opposing the endopod. Exopodal articles 3 to 5 decrease in size distally. They are trapezoidal in outline and widen distally. All lack setae along their median edges. Distally, the second to fourth exopodal articles each give rise to a subsequent article and carry one and two setae medio-distally respectively. The fifth exopodal article bears 3 setae along its distal margin (indicated by the specimen of the earliest stage, UB W 265, see Fig. 9B).

Third cephalic appendage (app3).—As the previous limb and all following ones, the second post-antennular limb (Fig. 7C) is biramous. It inserts behind the posterior margin of the hypostome, lateral to the elevation of the sternal area (Fig. 1E). Its basipod is about 30% longer than that of the second cephalic appendage. Its posterior face is shorter than the anterior. The extensive arthrodial membrane forms the limb socket. Medially, the proximal endite, a small sclerotised element, rests within this socket. It is sub-triangular and carries a single seta close to its posterior edge. The armature on the median edge is principally bi-serial, but the proximal elements of the series are prominent spines (Fig. 4B). The distal setae are arranged in two distinct rows each with four setae along the median edge plus two setae on the posterior face (Fig. $5B_2$). In addition, there is a series of three small setae anterior to the larger spines.

The endopod of this limb is unknown except for its articulation site on the medio-distal edge of the basipod (the reconstruction is based on the endopod of the first post-antennular limb, see Fig. 7C). The exopod inserts along the slanting outer edge of the basipod and comprises four portions or articles. The proximal portion is elongatedly paddle-shaped. Proximally, it forms a shaft that extends some way down the lateral body wall as part of the body-limb joint (Fig. $5B_1$). The free inner margin carries a series of six setae, opposing the endopod; medio-distally there is a long seta in addition. Posteriorly, the joint between this portion and the basipod is rather wide medially, suggesting the possibility of a wider back swing of the exopod (Fig. 8D). The subsequent two articles are shorter and narrower than the proximal portion and distinctly trapezoidal in anterior view; the elongation of their median faces relative to the exterior faces pre-forms an outward turn of the entire distal part of the exopod (possibly also reflecting its maximum outward flexure, see Fig. $5A_1$). Medio-distally, the second article carries one long seta, the third article two slightly smaller setae (Fig. $5A_1$). The terminal, fourth article is slender, subrectangular and carries a set of three setae terminally.

Fourth and fifth cephalic appendages.—The third (Fig. 7D) and fourth (Fig. 7E) post-antennular limbs are similar with one another and their basipods are about 20% longer than that of the second post-antennular limb (Fig. 2C, E_1). The arthrodial membrane forms a prominent socket, which is less extensive than in the preceding two post-antennular limbs; also, the armature on the median edge with setae or spines is less well developed. One cluster of setae, including a large spine-like one, is situated about two-thirds up from the proximal edge of the basipod, and a triplet of setae arises near the medio-distal margin (Fig. 2C).

Of the endopod, only the proximal podomeres (first one and parts of the second one) are known. The proximal podomere is almost as broad as the basipod and carries a set of setae medially and a row of denticles medio-distally (Fig. $6C_1$). The outer margin articulates with the second article of the exopod (Fig. 1F). The second endopodal podomere inserts on the medio-distal end of the proximal podomere and is roughly 30% narrower than the latter. It is too poorly known for further description.

The exopod consists of two portions. Together they form a paddle and are separated by a fine hinge joint, which extends from the boundary of the basipod and the first endopodal podomere to the lateral margin of the exopod (Fig. 8D). The proximal exopodal portion is subtriangular. Laterally, it is somewhat extended and dipped into the membranous cuticle between shield margin and body proper, form-

Fig. 6. Details of specimens of later developmental stages of the stem crustacean *Oelandocaris oelandica* Müller, 1983 from Gum continued. **A**. UB W 263, close-up median view of appendages 4 to 6 exhibiting denticle rows on the distal area of the podomeres (arrows). **B**. UB W 260; B_1, lateral close-up view of specimen exhibiting appendages posterior to the third cephalic appendage; note the exopod shaft being articulating with body wall (arrows); B_2, posterior to ventral view of strongly bent specimen; tips of limbs broken off rather proximally. **C**. UB W 261; C_1, close-up lateral view of the exopods of appendages five and six displaying putative attachment sites of delicate setae or sensillae (arrows), and such sensillae at the tergite (arrow heads); C_2, dorsal view of trunk segments; arrows point to attachment sites of delicate setae or sensillae; C_3, dorso-lateral and close-up view of the posterior tergite displayed in C_2; arrows point to attachment sites of delicate setae or sensillae. Abbreviation: an, anus. →

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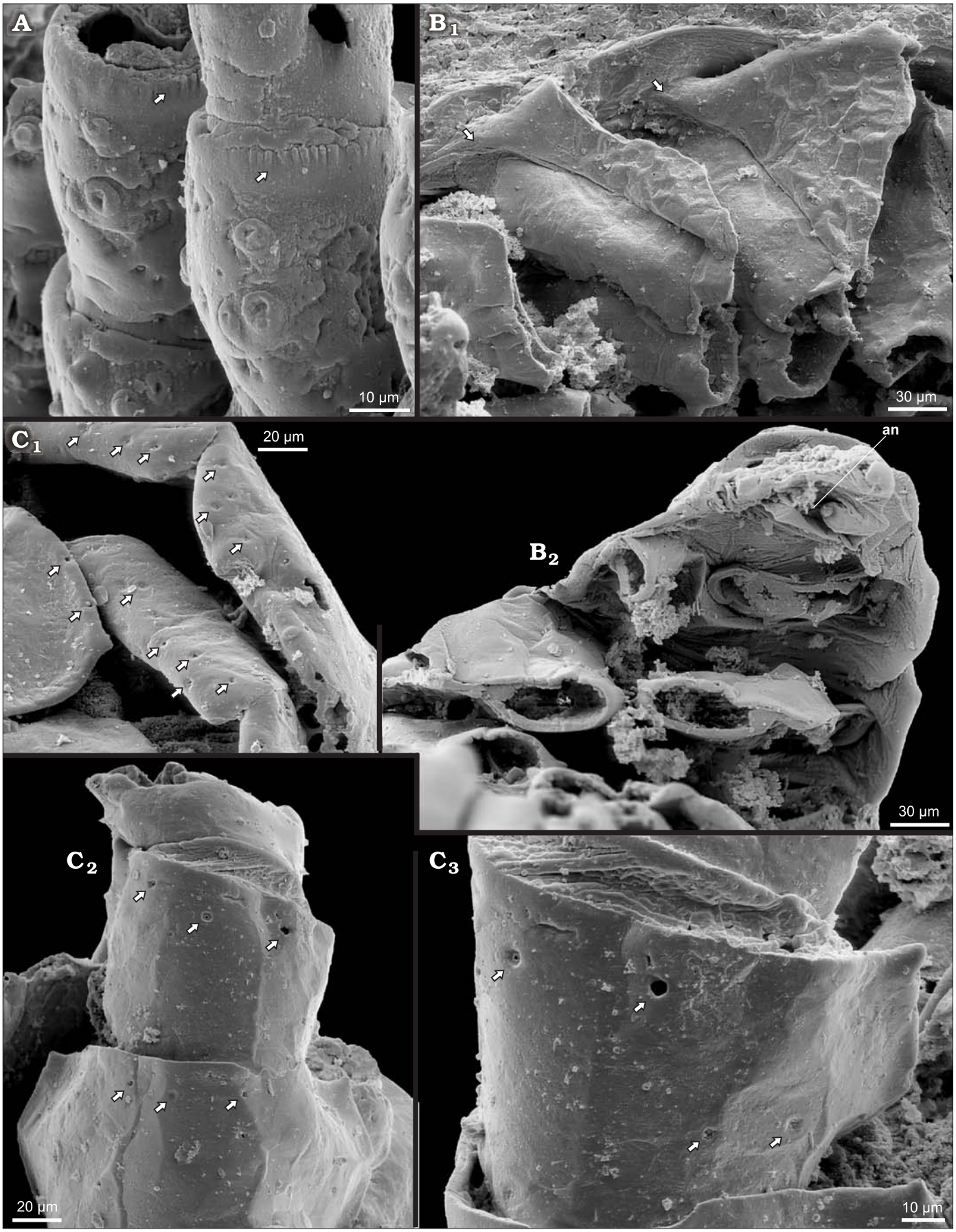

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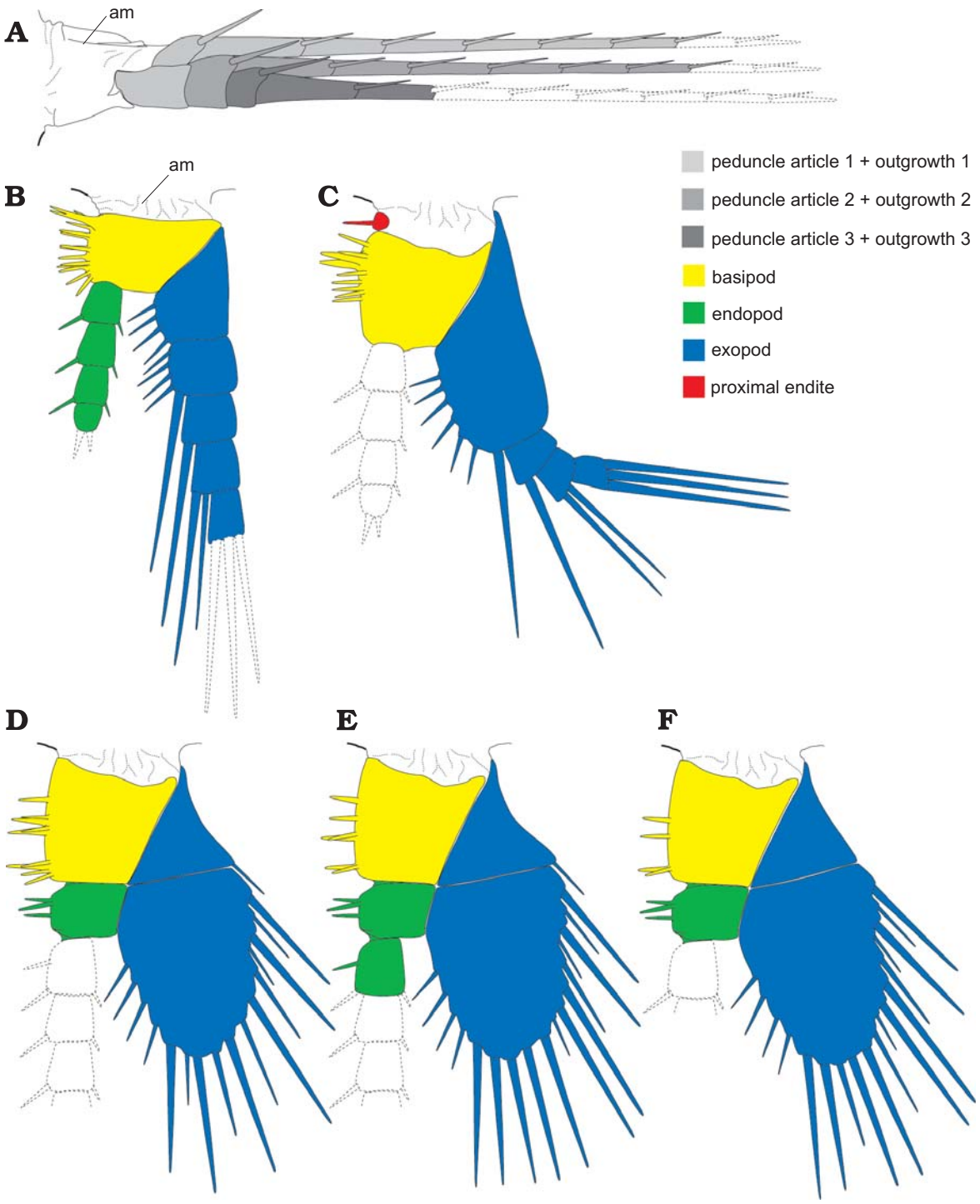

Fig. 7. Reconstruction of the appendage morphology of later developmental stages of *Oelandocaris oelandica* Müller, 1983. **A**. Antennula. **B–F**. Second to sixth appendages. Note that the first three appendages differ from each other and from the sub-equal fourth to sixth appendages.

ing a monocondylic limb joint (Fig. $2E_2$). Along almost the entire margin, the paddle carries prominent setae intercalating with finer setae (reconstructed in Fig. 7D–E, see also Fig. 8A). In addition, the lateral edge of the proximal triangular portion carries one seta far distally (known by its socket; Fig. 8D). The outer rim of the exopod appears more strongly sclerotised than the anterior and posterior surfaces (possibly stabilizing the rather soft ramus; arrowed in Fig. 8D).

Trunk appendages.—The anterior trunk appendages are known to some degree (Figs. 2A, C, E_1, 7F), whereas the posterior ones are known only from fragments of their proximal parts. From what is preserved, it seems that the anterior ones are similar to the third and fourth post-antennular limbs, but have progressively narrower basipods and decrease in overall size towards the posterior. Additionally, the space between the basipods of each appendage pair becomes progres-

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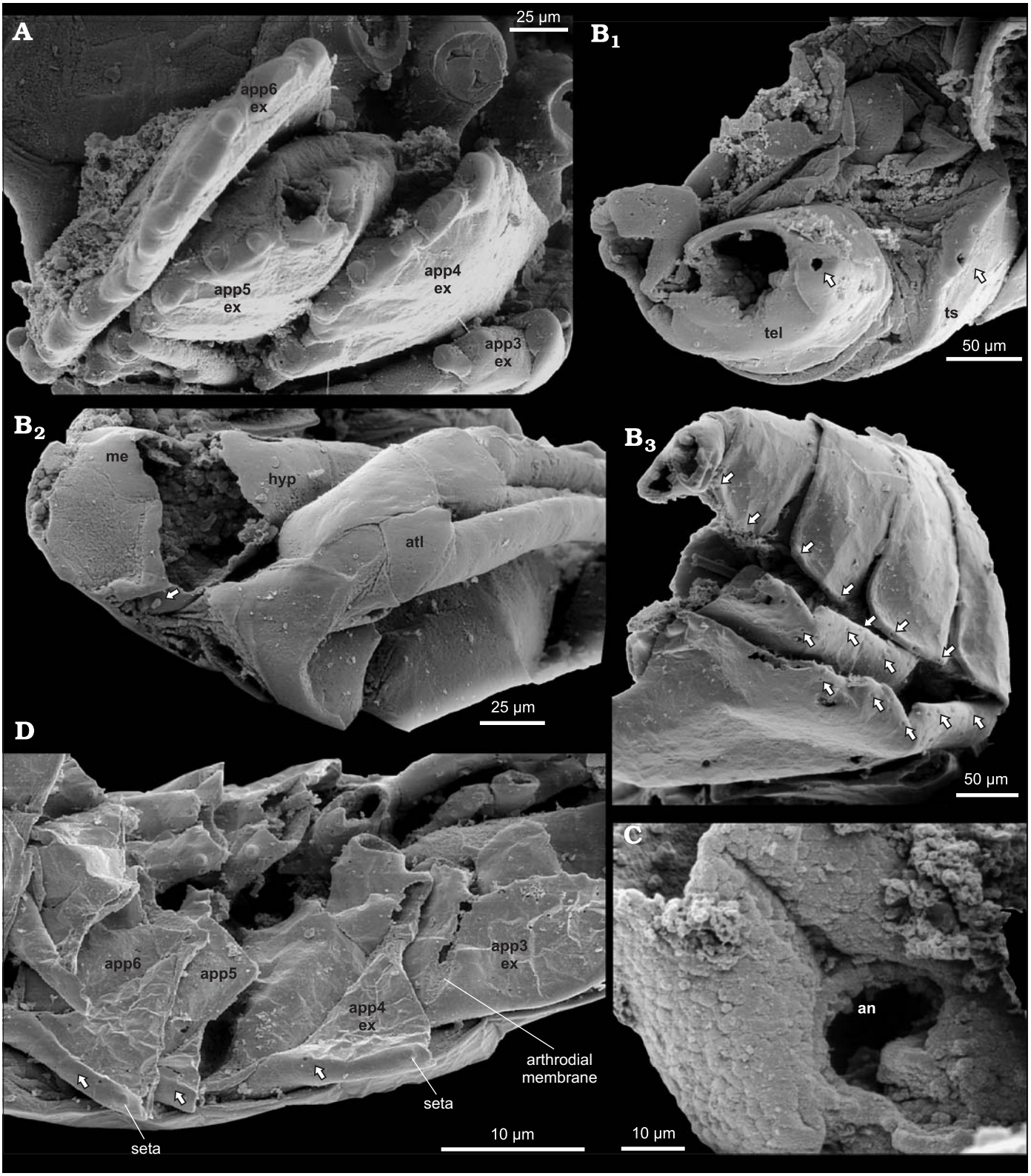

Fig. 8. SEM photographs of additional important details of the stem crustacean *Oelandocaris oelandica* Müller, 1983. **A**. UB W 262, exopods of appendages posterior to the third cephalic appendage, showing insertion of setae; note the weak sclerotisation of the exopod surface as demonstrated by the deformed exopod of the fifth appendage. **B**. UB W 261; B_1, tail piece with marginal spines on last tergite and caudal end (arrows); B_2, anterior wings of hypostome (arrow); B_3, insertion sites of sensillae on tergite borders and exopods (arrows). **C**. UB 649, anal opening with displaced membrane on ventral side of caudal end. **D**. UB W 260, basipods and exopods of third to sixth limbs, showing the more strongly sclerotised lateral margin of the exopod (arrows) with seta distally, and the membranous area at the articulation of the exopod of the third limb with the basipod. Abbreviations: alt, antennula; an, anus; app, appendages; bas, basipod; ex, exopod; hyp, hypostome; me, median eyes; tel, telson; ts, tergites.

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sively narrower towards the posterior, and the setal armature becomes less developed (Figs. $2E_1$, 8D).

Special morphological details

Setation.—Preservation of setae and spines in the available material is incomplete. Prominent and possibly large setae or spines have a higher preservational potential than delicate ones, but often are broken off distally. In most cases, only the sockets of the more delicate setae are preserved. Therefore, reconstruction of the setation of *Oelandocaris oelandica* relies largely on size, form and distribution of these sockets and experience from other "Orsten" taxa.

There are, at least, three kinds of sockets to be distinguished pointing to the presence of different setae or spines arising from these. One is an extension of the general cuticle. This type is the predominant type found, e.g., along the median edges of the basipods, at least some possibly having masticatory function (Fig. $5B_2$, C). A second type is a socket at the edge of the exopod flaps of the fourth and successive limbs. These suggest the insertion of long and prominent setae, often used for locomotion (Fig. $5A_1$). Another, most likely more delicate type of setae occurs on the antennular outgrowths (Fig. 4B), the median edges of the basipods, and along the inner edges of the exopods opposing the endopods (Fig. $5B_1$). Those on the inner edges of the basipods are preserved only rarely and never in full length. The function of this type of setae is unclear; a function as part of the feeding apparatus is possible, though not obvious for those setae on the antennular outgrowths. A third type of sockets found on the tergites and outer edges of the proximal exopod podomeres is a much smaller one, having a circular depression in the centre (Fig. 6C; for details see next section).

Possible sensilla.—The tergites are covered with holes of about 5 μm in diameter (Fig. $6C_1$,C_2). In some cases a recessed central socket is preserved (Fig. $6C_3$), suggestive of a sensillum arising there. Such holes occur in rows parallel to the anterior and posterior margins of each tergite. Additional sockets occur in a row along the lateral margins of the tergites (Fig. $6C_1$). Some sockets in this row are larger, particularly the most posterior which probably give rise to a more prominent sensillum or seta. Several similarly small pores, filled by a membrane except for a tiny hole in the centre (Figs. $6C_1$, $8B_3$), are located on the anterior surface of the triangular exopod portion and the proximal part of the paddle-shaped distal exopod portion close to the lateral margin. These may have been the insertions of fine sensilla, such as are known from "Orsten" and extant eucrustaceans.

Denticles.—Tiny cuticular spines, called denticles, occur in rows along the mediodistal edge of the first endopodal podomeres of the fourth and fifth appendage and all post-cephalic limbs (Fig. 6A). Denticles are otherwise known so far only from labrophoran crustaceans (see, e.g., Müller and Walossek 1988: pl. 4: 3), but the recent report from the stem chelicerate *Leanchoilia illecebrosa* (Hou, 1987) by Liu et al. (2007) suggests that they possibly represent a rather ancient feature.

Ontogeny

Early developmental stage.—One specimen, UB W 265, considered to belong to *Oelandocaris oelandica*, is considerably smaller (440 μm total length, reconstruction in ventral aspect in Fig. 10A) than the other specimens (660 μm to more than 990 μm total length). Its head shield (Fig. 9A, B) incorporates five appendiferous segments as in the larger specimens, has similarly little extended margins, but has a more oval shape in dorsal view, with a truncated posterior midline. The hypostome (Fig. 9B, C, E; mouth in F) differs in shape from in the larger specimens in being more oval in ventral view and posteriorly pointed. Another difference is in the antennula, which has presumably only two outgrowths arising from the proximal part (Fig. 9G). Assignment to *Oelandocaris oelandica* is supported by the paired structure overlapping the anterior wings of the hypostome (Fig. 9D, E as compared with Fig. $8B_2$), multi-annulated exopods of second and third cephalic appendages with the terminal portion of the third cephalic appendage carrying three setae (Fig. 9G) and paddle-shaped exopods of the posterior limbs having robust marginal setae, although fewer in number (Fig. 9H). A further indication of its inclusion into this species is the presence of a lateral step-like ridge on either side of the conical, slightly depressed tail end representing the insertion points of, most likely, postero-laterally pointing spines (arrows in Fig. 9B, C). The divergent morphology of the hypostome is bridged by the next larger specimen UB W 262 (more than 670 μm total length), which possesses a hypostome of intermediate shape.

Apart from its size, the specimen differs from later developmental stages in the:
- morphology of the head shield;
- antennula that has only two outgrowths;
- basipod morphology;
- shape of the trunk;
- number of trunk segments.

Morphology of the early stage in detail.—The specimen has a bowl-shaped head shield incorporating five appendiferous segments. Anteriorly, the head shield margin appears to be amply rounded (Fig. 9A–C), but it is deformed in the

Fig. 9. Earliest known developmental stage of the stem crustacean *Oelandocaris oelandica* Müller, 1983, specimen UB W 265 from Gum, Västergötland, Sweden. **A**. Dorsal view. **B**. Lateral view, arrow marks step-like ridge on tail, arrow head marking small seta. **C**. Ventral view, arrows mark step-like ridges on tail. **D**. Close-up ventral view of the paired structures interpreted as median eyes. **E**. Close-up ventral view of the forehead, arrow marks posterior wing of hypostome. **F**. View into the mouth opening. Note the possible sensory structures surrounding it (arrows). **G**. Latero-ventral view of posterior head region. **H**. Close-up posterior view of posterior limbs. Abbreviations: app, appendages; me, median eyes; ex, exopod; hyp, hypostome. →

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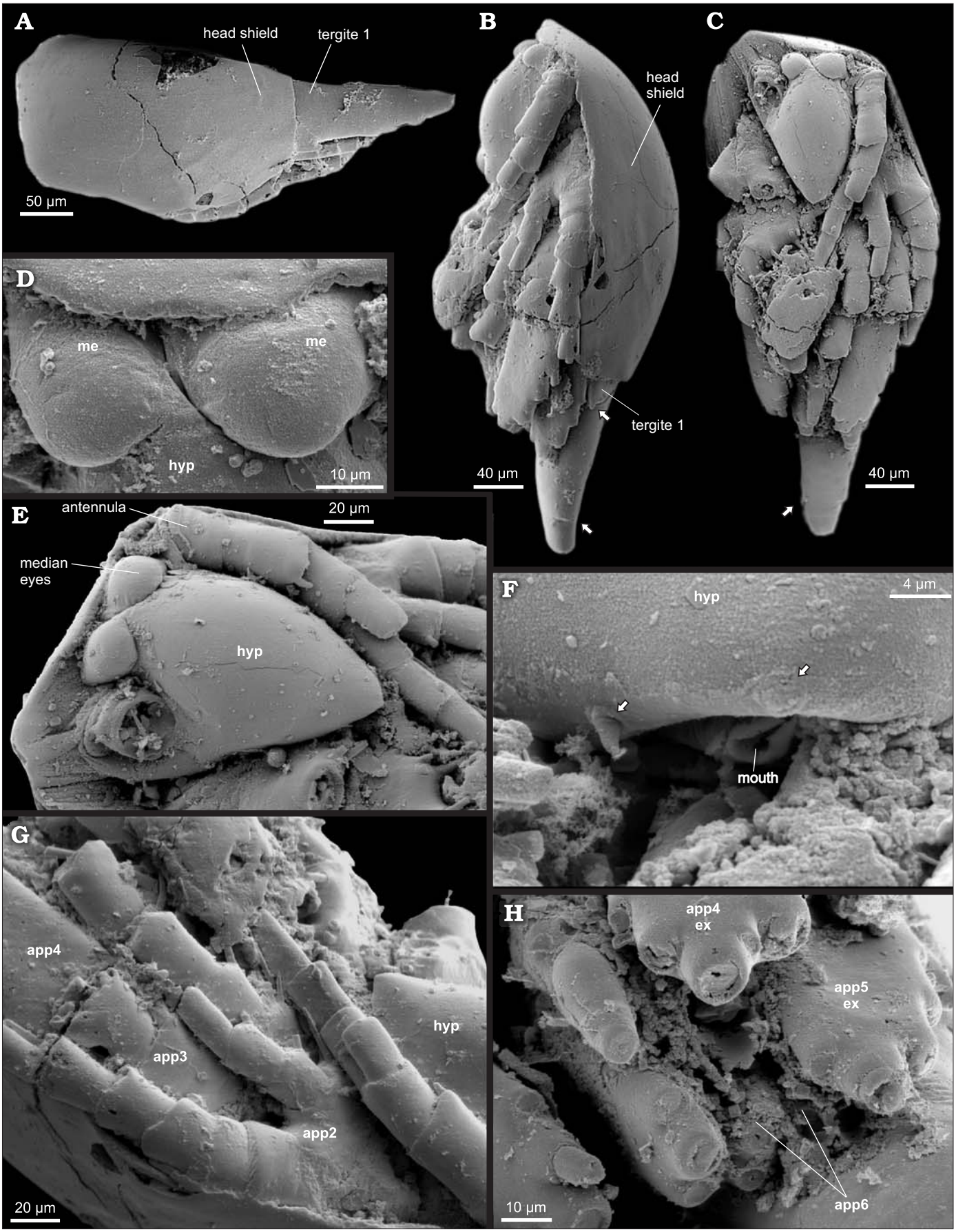

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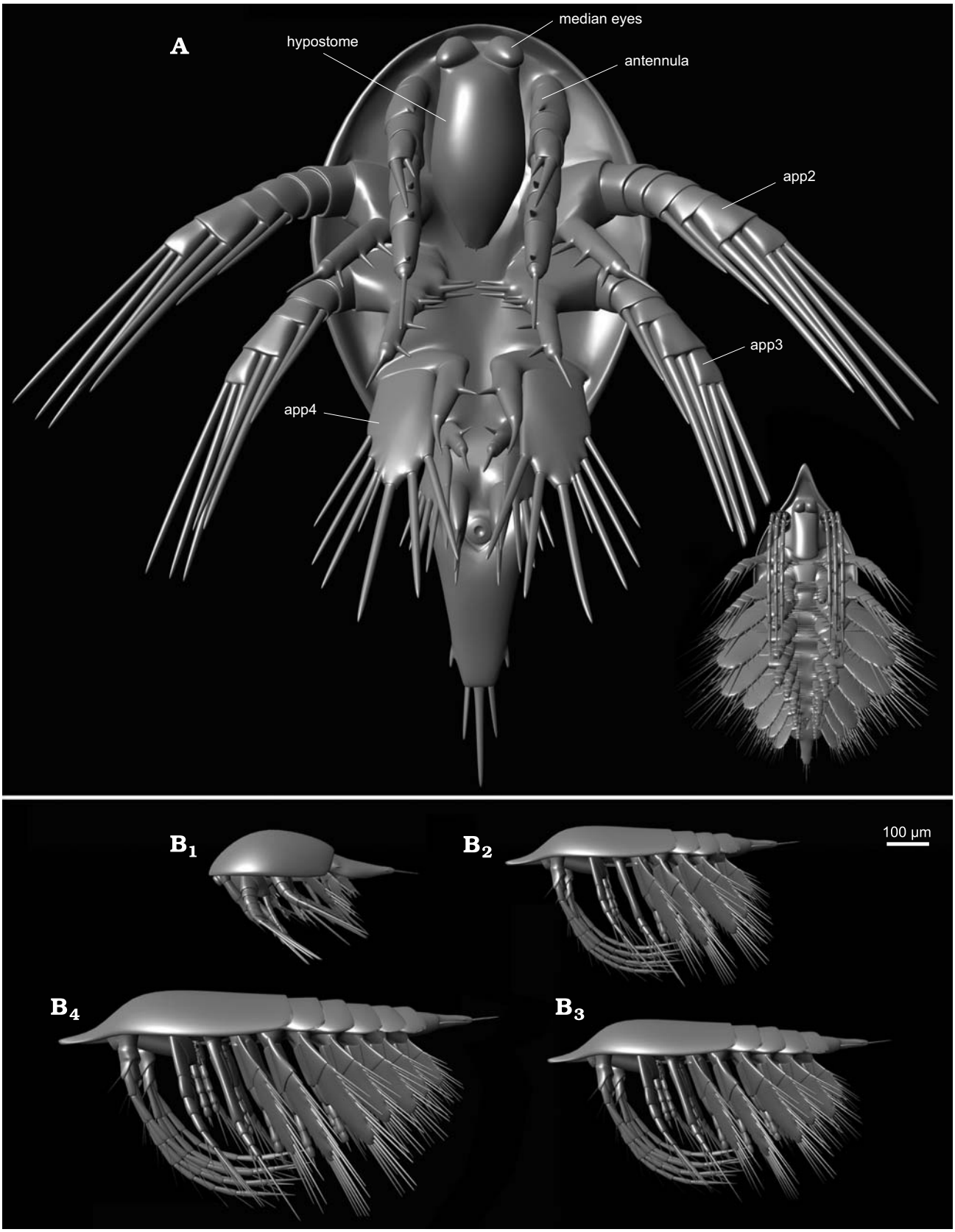

Fig. 10. 3D model of the morphology of the early developmental stage and the ontogenetic sequence of *Oelandocaris oelandica*, with four developmental stages known. **A**. Early developmental stage in ventral view, for comparison, but not to scale the ventral view of the oldest developmental stage known is shown. **B**. Reconstruction of stages in lateral view. Early developmental stage (B_1), first next older set (B_2), second next older set (B_3), and third, apparently, oldest stage (B_4). Abbreviations: app, appendages.

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single specimen at hand. A rostrum-like protrusion of the shield, as in the later stages, is lacking. The trunk is a single, dorso-ventrally slightly depressed cone-shaped portion, but must include at least one segment, as is indicated by the sixth pair of appendages inserting ventrally (Fig. 9B). The future tergite of this trunk segment, laying partly underneath the posterior border of the head shield, is also indicated by the presence of a small spine at its weakly demarcated postero-lateral corners (arrowhead in Fig. 9B), similar to the situation in the head shield and tergites of the larger specimens. The trunk is approximately half as long as the head shield. Posteriorly, it bends slightly dorsally. Laterally in this part of the trunk there is a step-like ridge on either side at about three-quarters of the length of the trunk. These ridges form the insertion points of fine, most likely postero-laterally projecting setae or spines (Fig. 9B, C).

The main body of the hypostome is ovoid, with a wider front and a tapering rear. The pointed posterior midline bore a spine, which is broken off in the specimen at hand (Fig. 9E). This spine is flanked on either side by a spine arising from the posterior margin of the hypostome. The mouth opening is visible below the posterior of the hypostome (Fig. 9F). The anterior wings of the hypostome are overlain by the paired bulbous structure (Fig. 9D, E) also known from the larger specimens and tentatively interpreted there as median eyes. Due to some degree of deformation, the insertion of the right antennula is contorted and the posterior wing of the hypostome pushed anteriorly (arrowed in Fig. 9E). The location of the second cephalic appendage indicates that the original position of the posterior wings was farther back, about two-thirds the length of the hypostome. Accordingly, only the pointed posterior end of the hypostome slightly overhung part of the postoral sternal area.

The left antennula is largely complete. Its shows an ample arthrodial membrane, which is rather squeezed together, and several tubular articles. The first article bears a short spine or seta antero-distally on a slight swelling of the margin (Fig. 9E), the second gives rise to a tubular, but preservationally flattened outgrowth latero-distally, while the third article gives rise to two more portions, the proximal one carrying a seta antero-distally and the distal portion being a rounded cone, possibly continuing into a terminal seta (Fig. 9G). This morphology resembles that of the antennula of older stages, suggesting that the proximal outgrowth is still missing—possibly the seta on the first article, while the second is present, and the third outgrowth consisting of the distal portions of the antennula (Fig. 9E).

In all post-antennular limbs, setation of the basipod of the small specimen is less developed than in the larger specimens. A "proximal endite" could not be observed. The exopodal articles of the second and third cephalic appendages increase in length from proximal to distal and are, in all, more cylindrical (longer than wide) than those of the same limbs in larger stages (Fig. 9B, C, G). Only two exopodal portions and two endopodal podomeres are preserved of the third cephalic appendage. The exopodal portions lack setae on their inner margins (Fig. 9B, C, G). The endopods are cylindrical elements with one stout seta medio-distally (Fig. 9E). The exopods of the following two appendages are paddle-shaped as in the larger specimens, but differ from those of the older ones in that the paddles are made up of a single portion only. Furthermore, the outer joint is formed by the basipod and it seems that the first endopod podomere of the fourth limb is not articulating with the exopod. The exopod of the third post-antennular limbs carries six setae along its margin, two inserting disto-medially, one terminally (the most prominent one), and three disto-laterally. A smaller associate seta is present antero-laterally to the terminal seta. The exopod of the fourth post-antennular limb carries five setae along its margin, one inserting disto-medially, one terminally (the most prominent one) and three disto-laterally. The single pair of trunk limbs is almost completely hidden under the exopods of the fifth appendage. It appears to be uniramous, carrying three setae distally, the anterior one being smaller than the other two. This seta may be the precursor of the endopod.

Later developmental stages, i.e,. rostrum-bearing instars.—The six larger specimens (670–990 μm) all have head shields that incorporate five appendiferous segments, a rostrum-like anterior projection of the shield, and three to five trunk segments free from the tailpiece. Possibly three (rostrum-bearing) stages can be identified:

- smallest stage: total length slightly longer than 670 μm, three tergites (UB W 262; the total length can not be measured, as the anterior part of the head shield and posterior portion of the tail are missing);
- median stage: total length estimated to be between 680 and 740 μm, four tergites (UB 648, holotype, UB W 264; total length of the latter can not be measured, as the anterior portion of the head is missing);
- largest stage: total length almost 1mm, five tergites (UB W 260, 261, 263).

The difference in size and number of tergites between the smallest rostrum-bearing instar, having three pairs of fully developed limbs posterior to the third cephalic appendage, and the early larva UB W 265 indicates a gap in preserved ontogenetic stages (Fig. 10B). The most apparent difference between the smallest of the rostrum-bearing instars and the two larger rostrum-bearing instars is that the posterior end of the hypostome is pointed (Fig. 2D), as in the early developmental stage (Fig. 9E). The head shield of the holotype has a weak boundary between the fourth and fifth appendiferous segments, which cannot be seen in UB W 264, the other specimen of this instar. In the smaller UB W 262, the head shield is broken dorsally and the remainder is bent in several places. Therefore, it cannot be assessed whether this demarcation is present also in the smallest rostrum-bearing instar. As can be judged from the limited material, morphological differences within the largest two instars reflect a further increase in size and a larger number of tergites (5), the latter feature being the most convincing feature for stage discrimination. All three instars can be clearly ordered or distinguished by the progressive increase in the number of free trunk segments.

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Discussion

Morphological features

Eyes.—Early and later stages of *Oelandocaris oelandica*, or more precisely the largest instar at hand, possess a pair of bulbous structures at the front of their hypostomes. Such structures are unknown from any fossil other than in "Orsten" type of preservation or extant euarthropods and their larvae. Comparisons with fossil taxa are, therefore, limited, more or less, to "Orsten" taxa. Among these, several taxa bear paired frontal, lobe-like structures, at least in early stages of their development. Within Eucrustacea these are *Bredocaris admirabilis* Müller, 1983, *Rehbachiella kinnekullensis* Müller, 1983, and *Walossekia quinquespinosa* Müller, 1983. The lobes of *B. admirabilis* are fairly large and separated by a bar with a median pit or pimple-like structure (Müller and Walossek 1988: pl. 8:2). *R. kinnekullensis* has a pair of large lobes initially which can be followed during ontogeny (Walossek 1993: pls. 21: 1, 28: 4). Similar to *B. admirabilis*, there is a median structure, but more bulging than in the latter. *W. quinquespinosa* has a pair of rather pointed and closely spaced lobes at the front of the hypostome/labrum complex (Müller 1983: "fo" in his fig. 6) which are similar to those of *O. oelandica*.

Phosphatocopina, the sister taxon of Eucrustacea according to Siveter et al. (2003) and Maas et al. (2003), is characterised by paired lobes with probably an associated third part posterior to the lobes on the anterior part of the hypostome, interpreted as median eyes because of their position (Maas et al. 2003: fig. 3A–D). Within the stem-lineage derivatives of Labrophora recovered from the "Orsten" (Waloszek 2003a), a pair of lobes, possibly median eyes, is located between the unpaired compound eye and forehead in *Goticaris longispinosa* Walossek and Müller, 1990 (Walossek and Müller 1990: fig. 3A, B); *Cambropachycope clarksoni* Walossek and Müller, 1990 only possesses the compound eye (Walossek and Müller 1990). A pair of lobes of *Henningsmoenicaris scutula* (Walossek and Müller, 1990) rests on stalks and has been interpreted as the compound eyes (Walossek and Müller 1990). Other "Orsten" taxa have been described as eyeless, such as the eucrustacean skaracarids (Müller and Walossek 1985b) and the euarthropod *Agnostus pisiformis* (Wahlenberg, 1818) (Müller and Walossek 1987), but the two have indeed paired lobes in the frontal area: in *Skara anulata* these occur antero-ventrally on the hypostome-labrum complex (Müller and Walossek 1985b: pl. 4: 2, 3), and *A. pisiformis* possesses small humps on the pliable cuticular area in front of the hypostome (Müller and Walossek 1987: pl. 13).

Another euarthropod species recently discovered in China is *Yicaris dianensis* Zhang, Siveter, Walossek, and Maas, 2007 from the Lower Cambrian of Xiaotan section, Yongshan, Yunnan Province (Zhang et al. 2007). *Y. dianensis* is known from material preserved in "Orsten" type of preservation and, therefore, is easily comparable with the other "Orsten" material. The species is interpreted as a eucrustacean since it shares various features with cephalocarids, branchiopods and "Orsten" crustaceans *R. kinnekullensis, Dala peilertae* and *W. quinquespinosa* (Zhang et al. 2007). All are considered as members of the Eucrustacea (cf. Walossek 2003b). *Y. dianensis* has a pair of immense lobes extending from the forehead in early stages, similar to those of *R. kinnekullensis*, and a smaller median lobe slightly more posteriorly located than the pair.

Two species cannot be compared in detail at present: the fragmentary head preservation does not allow assessment of eyes in *Dala peilertae* Müller, 1983. The material known of *Cambrocaris baltica* Walossek and Szaniawski, 1991 is too coarsely preserved (Walossek and Szaniawski 1991). Unfortunately, the specimen is now destroyed and therefore cannot be re-scanned.

In all, only a few of the mentioned eye-like structures could be demonstrated to be compound eyes, e.g., on the basis of characteristic facet patterns of the original ommatidia (although this cannot be visualised in an SEM, and even present ommatidia must not necessarily display a facet pattern on the surface), an elaborate eye-stalk that is unknown for median eyes, or less so by the topology. With respect to *O. oelandica*, it seems appropriate, therefore, to follow Müller (1983) and Stein et al. (2005) in interpreting the paired structure at the anterior end of its hypostome as a the median (naupliar) eye rather than as vestiges or rudiments of the lateral compound (= facetted) eyes. Thus, compound eyes are evident only for the "Orsten" taxa *Henningsmoenicaris scutula* and the two one-eyed species *Goticaris longispinosa and Cambropachycope clarksoni*. Occurrence of compound eyes, however, is a plesiomorphic character since they are part already of the ground pattern of Arthropoda sensu stricto (Waloszek et al. 2005).

Head segments.—A feature that requires further investigation in other taxa derived from the stem lineage of the Labrophora is the number of appendiferous segments in the head. The holotype (UB 648) of *Oelandocaris oelandica* shows a weak boundary between the fourth and fifth appendiferous head segments (see above). The reasonably well preserved head shields of other specimens (UB W 264 of the same stage as the holotype and UB W 263 representing the latest stage at hand) do not show this split, suggesting that the line on the holotype may be interpreted as a preservational feature. From a phylogenetic perspective it is clear, though, that the fifth appendiferous segment was added independently in the different euarthropod lineages. One instance occurred in the stem lineage at least of the Labrophora, another in the chelicerate stem-lineage.

The addition of original trunk segments to a head tagma can be recognised during the ontogeny of Eucrustacea as demonstrated by their larvae attaining more segments progressively. Ontogeny within Eucrustacea starts with a nauplius larva with three appendiferous segments. This feature is regarded as an autapomorphy of the taxon (Maas et al. 2003;

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Waloszek 2003a). Among Recent eucrustaceans, the smallest metanauplius has four appendiferous segments incorporated in the head, and this status is retained for a period of stages until the fifth segment is included seamlessly (cf. Müller and Walossek 1988 for *Bredocaris admirabilis*; Walossek 1993 for *Rehbachiella kinnekullensis*; Jens Høeg, personal communication 2003 for cirripede cyprid larvae).

Yet, ontogenetic and evolutionary changes have to be regarded separately. So far, only *Martinssonia elongata* Müller and Walossek, 1986 as a representative of the labrophoran stem lineage has been investigated in detail (Müller and Walossek 1986). In this species all instars show a demarcation of the fifth segment dorsally, while the lateral margin is continuous. Thus, it remains unclear whether this is a specialisation of the fifth head segment in being a demarcation as a joint within the head to lift the anterior part (such kinetics occur especially in stem arthropods; cf. Waloszek et al. 2005) or a retained plesiomorphy with a "not yet" completely included status of the segment. Even the largest specimens of *Cambropachycope clarksoni* and *Goticaris longispinosa* have no more than four appendiferous segments. Re-study of *Henningsmoenicaris scutula* is under way and it seems clear that the largest specimens have a head showing five appendiferous segments as stated by Walossek and Müller (1990). The presence of a head with five appendiferous segments may therefore be a parallel development of *O. oelandica* comparable with the clearly convergent evolution of six or more-segmented cephalothoracic shields among eucrustaceans, but a definitive judgement of this issue has to await further details on the other derivatives of the labrophoran stem lineage.

"Proximal endite".—The "proximal endite" as a movable, setose element in the arthrodial membrane medially underneath the basipod of the postantennular limbs has been regarded as an autapomorphy for Crustacea sensu lato since 1990 (Walossek and Müller 1990; Walossek 1999; Maas and Waloszek 2003; Waloszek 2003a). After the re-study of material from *Oelandocaris oelandica* by Stein et al. (2005) it became clear that the evolutionary origin of the proximal endite is more complicated than hitherto assumed. In fact *O. oelandica* has only one proximal endite on its third cephalic appendage (the mandible of labrophoran crustaceans); all other limbs, the second appendage and more posterior ones, lack a proximal endite and there is no evidence that it has been lost or modified into another structure. New investigations of known "Orsten" taxa (JTH, AM, and DW unpublished data) indicate that the proximal endite may develop ontogenetically on a single limb first, and more proximal endites occur progressively on additional limbs during later ontogeny; but it may even not appear on all postantennular limbs throughout the known ontogeny of "Orsten" fossils assigned to stem-lineage derivatives of Labrophora. Phylogenetically, the appearance of the proximal endite seems to occur not on all but being restricted to a single or at least a few post-antennular limbs only, as demonstrated by *O. oelandica*. Further detailed investigation on other stem-lineage derivatives of the Labrophora is needed to clarify this matter.

Furthermore, it is established that, not before the ground pattern of the Labrophora, the proximal endites of the antenna and the mandible autapomorphically became modified into coxae, forming a ring-shaped structure underneath and articulating against the basipod. Medially, this ring-shaped structure is drawn out into an endite with marginal spines (gnathobase) on the second limb or antenna, which is slightly turned against the labrum (Maas et al. 2003; Siveter et al. 2003). In Labrophora, all postmandibular limbs bear a proximal endite, as exemplified by the Phosphatocopina (Maas et al. 2003) and many extant Eucrustacea (Calman 1909 who called the proximal endite "arthrite" in his work on branchiopods; see also Walossek 1993, 1999 and Walossek and Müller 1998a, b for an overview of the fate of the proximal endite within Eucrustacea).

Recently, Siveter et al. (2007) described a new arthropod, *Tanazios dokeron* Siveter, Sutton, Briggs, and Siveter, 2007, from the famous Silurian Herefordshire Lagerstätte, UK, and interpreted the fossil as a putative stem crustacean. However, the rather coarse preservation of the material with respect to the 3D reconstruction does not allow for the detection of any of the critical features of Crustacea, particularly the "proximal endite" or its derivative, the "coxa". At least, the interpretations made by Siveter et al. (2007) are not in conflict with our interpretation of *O. oelandica* as an early offshoot of the crustacean lineage.

It is of significance that Crustacea sensu lato lack coxae on what are called "antennae" and "mandibles" in labrophoran crustaceans, terms that we would rather restrictedly use for this evolutionary level. Consequently, there was no coxal gnathobase for mastication on the third cephalic appendage early in the crustacean lineage, which developed only subsequently in the stem species of the Labrophora. It is also clear that *O. oelandica* (and the rest of the labrophoran stem-lineage taxa) is not simply a euarthropod, but is associated with the labrophoran stem lineage, in other words is a crustacean sensu lato. Nonetheless, plesiomorphies such as the hypostome with the mouth at its rear, lack of a labrum, specialized second and third limbs without coxal portions and serially uniform limbs posterior to the third cephalic appendage clearly determine the basal phylogenetic position of *O. oelandica* on the early stem lineage of Labrophora.

Possible life habits of the oldest known instar of *Oelandocaris oelandica*

The most probable life habit of *Oelandocaris oelandica*, referring to the latest developmental stage known so far, of course, seems to have been that of an active swimmer. That assumption is supported mainly by its limb morphology. The large paddle-shaped exopods of the limbs posterior to the third cephalic appendage seem to be organs well suited

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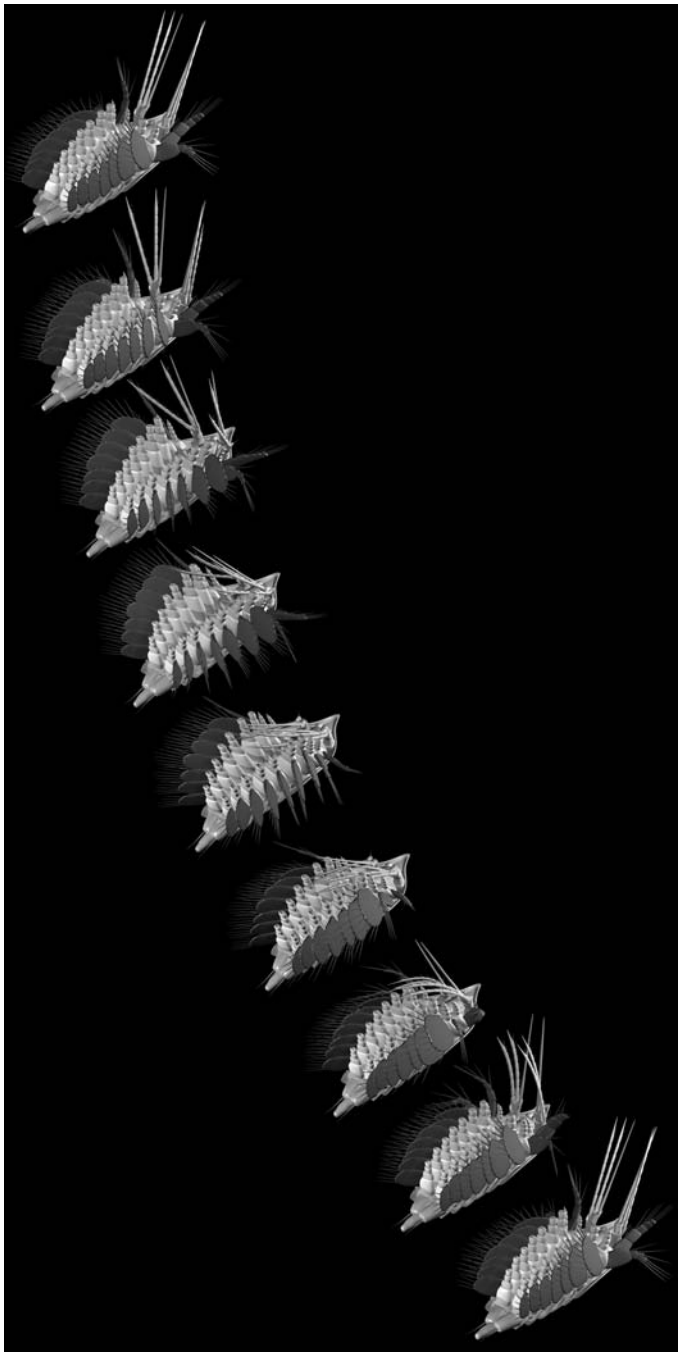

Fig. 11. Reconstruction of sequence of appendage-movement of the stem crustacean *Oelandocaris oelandica* Müller, 1983, captured in succeeding steps from above towards below. Please watch movie at data repository of *Acta Palaeontologica Polonica* (http://app.pan.pl/SOM/app53-Stein_etal_SOM.pdf).

for locomotion. Such exopods are possibly retained from the euarthropod ground pattern (cf. Chen et al. 2004; Waloszek et al. 2005). The connection between the proximal endopodal podomere and the exopod, possibly even another plesiomorphy retained from the euarthropod ground pattern (see Liu et al. 2007 for the stem chelicerate *Leanchoilia illecebrosa*), both reduced the flexibility of the endopods and enhanced the ability for a more forceful stroke of the exopods. The extensive arthrodial membrane forming limb sockets increased agility of the limb as a whole. It seems that the limb as a whole was swung backwards during the swimming stroke. The subdivision of the exopod probably enabled reduction of drag during the recovery stroke by bending the distal portions backwards. The basic posture of the large antennula clearly was directed postero-ventrally. Given posture and articulation of the antennula, a sweeping movement seems most plausible, during which it was swung backwards from a ventrally directed starting position during stroke. In that movement, the antennula would have raked food particles into the ventral food grove. During the recovery stroke it would have moved back into the starting position. This would pose problems for bottom living habits, where the sediment surface would hinder such a movement. Even in a potential posteriorly directed resting position, the antennula would have interfered with the endopods of the post-antennular limbs. It seems therefore most reasonable to assume that *O. oelandica*, at least up to the latest stage known so far, actively swam in the water column and, if closer to the bottom, possibly upside down, as many small crustaceans do, namely brine shrimps, fairy shrimps or tadpole shrimps.

We assume that all limbs acted in concert in a metachronal movement; a putative sequence of movement is presented in Fig. 11. During the stroke, the postantennular limbs are moved outward and backwards, opening the ventral food groove. Simultaneously, the antennula was swung back, initially spreading the long outgrowths, to sweep a large area. Towards the end of the stroke sequence, the outgrowths are drawn together to allow sweeping down into the ventral groove. During the recovery stroke, the antennula swings anteriorly, in the posteroventral starting position. The postantennular limbs simultaneously swing back anteriorly and inwardly. The setation of the basipods then functions in transporting food particles anteriorly towards the mouth opening. The inward facing setae on the exopods of the second and third postantennular limbs may have functioned in retaining escaping particles in the general cephalic area, to be brought in the food groove with the next stroke.

Conclusions

Refining the description of *Oelandocaris oelandica* much of the data presented by Stein et al. (2005) could be confirmed. In addition we can identify the presence of four different instars even in the limited material. This significant new observation indicated by size increase between the stages and a stepwise addition of trunk tergites (reflecting somite addition) from one in the earliest larva-like stage to three, four and five in the rostrum-bearing stages allowed also for an account of aspects of ontogeny. During growth few other details are modified significantly, enabling a combination of all information into a reconstruction of the general morphology of the species (Fig. 3). Importantly, no more proximal endites

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than the one on the third cephalic appendage are added up to the latest stage identified so far.

The new data revealed by the new specimens of *O. oelandica*, confirm the view of Stein et al. (2005) that this "Orsten" species cannot have branched off from the evolutionary lineage of the Crustacea after, e.g., *Cambropachycope clarksoni*, *Goticaris longispinosa*, *Henningsmoenicaris scutula*, and *Martinssonia elongata*. There is growing evidence that in early developmental stages some of the other stem crustaceans lack the "proximal endite" on appendages other than the third one. Accordingly, the appearance and specific fate of the proximal endite may prove to be eventually even a significant tool to resolve the interrelationships between the stem crustaceans, leading to a reconstruction of the beginning of the crustacean evolutionary lineage. Such a step awaits the detailed description of all available taxa but the data available already now help to firmly fix the position of *O. oelandica* on the stem lineage toward the labrophoran Crustacea (cf. Siveter et al. 2003), as suggested already by Stein et al. (2005). This interpretation is supported by the:

– presence of at least one proximal endite;
– exopods of the second and third cephalic appendages being multi-annulated and having medially oriented setae;
– presence of a bi-partite locomotive apparatus consisting of an anterior set, the antennulae acting in conjunction with the subsequent two pairs of head appendages, and a posterior set of more or less homonomous limbs working together in a metachronal beat.

Again, the long and prominent antennula with its three rod-like outgrowths of *O. oelandica* was clearly not a sensorial device, but was, most likely, used for food gathering, as suggested already by Stein et al. (2005). This supports interpretations of the primary function of the antennula already in the crustacean ground pattern as a food-gathering device (Waloszek et al. 2005, 2007). Assumptions concerning the relationships of insects and myriapods, both taxa bearing feeler-like antennulae, with the Crustacea sensu lato, the Labrophora or any of the eucrustacean in-groups (e.g., Glenner et al. 2006) must take this into consideration. If advocating the assumption that insects are crustaceans, one has to explain at which node (in which stem species) particular similarities occurred (developed) to be transferred into synapomorphies of particularly insects and a specific crustacean in-group. It also needs to be explained when and how specific modifications (autapomorphies) occurred in the specific lineage toward the insects and the according eucrustacean in-group. No fossils are available as yet to bridge gaps for any of these lineage sections. Again, the fate of features that crustaceans retained from earlier nodes and features that are acquired by the stem species of Crustacea sensu lato, Labrophora and Eucrustacea have to be explained for crustacean in-group taxa. That means one needs to give reason for the lack of such features in insects if one considers them to be Eucrustacea. Until then, relationship hypotheses about insects, myriapods and crustaceans remain, at best, uncertain.

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