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# EXTERNAL MORPHOLOGY AND POST-EMBRYONIC DEVELOPMENT OF *DEROCHEILOCARIS REMANEI* (MYSTACOCARIDA) REVISITED, WITH A COMPARISON TO THE CAMBRIAN TAXON *SKARA*

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ABSTRACT

A re-description of the post-embryonic development of *Derocheilocaris remanei* Delamare-Debouteville and Chappuis, 1951 (Mystacocarida) is presented. It includes nine stages, not ten as originally described. The first stage already has a maxillula (though not fully developed) and is, therefore, not an ortho-nauplius as previously reported. Particular focus is on the development of the post-mandibular appendages (maxillula, maxilla, maxilliped) that undergo significant changes during ontogeny, and the development of the so-called 'toothed furrows', all of which are good indicators of changes between the stages. The maxilla and maxilliped are quite different from each other in the adult stage, but they develop in a very similar manner, showing very similar morphologies at certain stages. None of the post-mandibular appendages has a fully formed coxa, but only a proximal endite, which is in contrast to some previous interpretations. The development of *D. remanei* was originally considered very different from that of its transatlantic 'sister species', *D. typicus*, but our observations indicate that this is not the case. Rather, the development of *D. typicus* and *D. remanei* is very similar. This implies that not only the adult morphology of Mystacocarida is remarkably conservative, but also the larval sequence. With regard to the feeding system, mystacocaridans have a cephalo-thoracic feeding apparatus including the first pair of trunk limbs modified as maxillipeds, which collaborate with the maxillulae and maxillae in the feeding process. All three limbs are very similar to each other (the main difference is that the maxilliped possesses a vestigial exopod). The feeding system is in both general aspects and in particular details very similar to that of Copepoda and the representatives of the Cambrian taxon *Skara*. This suggests a close relationship between these three taxa, for which we propose the name Copepodoida. The name refers to specific features found exclusively in copepodans and, in our view, mystacocaridans and the three species of *Skara*.

KEY WORDS: Copepodoida, Mystacocarida, ontogeny, SEM

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## INTRODUCTION

Mystacocarida is a species-poor taxon of entomostracan Crustacea comprising only two genera, *Derocheilocaris* Pennak and Zinn, 1943 and *Ctenocheilocaris* Renaud-Mornant, 1976, which comprise just about 13 species currently recognized. Mystacocaridans were discovered rather late (Pennak and Zinn, 1943), which cannot be explained by a lifestyle in dark and hard-to-reach caves like those of other relatively recently discovered groups of Crustacea, such as Spelaeogriphacea (Gordon, 1957), Mictacea (Bowman et al., 1985), and Remipedia (Yager, 1981). Mystacocaridans remained unrecognised for a long time most likely because of their small size, less than one millimetre, and due to their interstitial life habit. In fact, mystacocaridans spend their whole life between sand grains and are almost completely unable to move in a directed manner outside this special environment (Lombardi and Ruppert, 1982, and references therein). Despite their small size mystacocaridans are an important component of the meiofaunal community, often appearing in overwhelming abundances, particularly during the reproductive phase (McLachlan, 1977).

The general appearance of a mystacocaridan can roughly be compared with a (very) small brush (German name: Pinselkrebs, meaning ''brush shrimp,'' Schrehardt and Pross, 1987). This superficial similarity is due to the fact that well-developed, setae-bearing appendages are concentrated in the anterior body (head appendages and maxilliped). The more posterior segments either bear reduced limbs only or are entirely limb-less. One of the unusual characteristics of Mystacocarida is an anterior portion of the head, which is set off and articulated against the rest of the head and carries the massive antennulae (Olesen, 2001). Movable rostral structures are also known from other Crustacea such as Leptostraca (Vannier et al., 1997) or Stomatopoda (Reaka, 1975). In Stomatopoda, the movable anterior area carries both the eyes and the antennulae. However, an ''inter-cephalic joint,'' as it might be called in mystacocaridans, is not developed in any other known crustacean – fossil or extant. Another specialty of mystacocaridans is the occurrence of 'toothed furrows' on both the dorso-lateral posterior area of the head shield, and the dorso-lateral median areas of all post-maxillipedal segments (Hessler, 1971). The rims of these furrows are



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furnished with a row of small 'teeth' on each side. Their function is unknown and no comparable structures are developed in any other crustacean. Within Mystacocarida differences are seen in the exact pattern of teeth along these furrows, which has been used to erect new species (Hessler, 1971). Other morphological peculiarities include the upward bent claw-like furcal rami and the minute second to fifth trunk limbs. The morphological variation within Mystacocarida is very small. Separation of species within a genus is mainly based on differences in the setal pattern of the maxillae and (the above mentioned) arrangement of teeth on the 'toothed furrows' (Hessler, 1971). The only two known genera are very similar to each other but can be distinguished by the presence of a small exopod on the maxilliped in the species of *Derocheilocaris,* which is missing in the species of *Ctenocheilocaris* (Renaud-Mornant, 1976).

Within Crustacea, Mystacocarida represents an enigmatic taxon, and phylogenetic analyses (morphological or molecular) have placed it in various positions. In their classification, Martin and Davis (2001) placed Mystacocarida as one of six subclasses within the class Maxillopoda, reflecting that the taxon has often been viewed as belonging to a monophyletic Maxillopoda (Dahl, 1956; Newman, 1983; Boxshall and Huys, 1989; Walossek and Müller, 1998a; see also Grygier, 1983). Walossek and Müller (1998a) considered Mystacocarida as the sister taxon to either Copepoda, or the Cambrian taxon *Skara* (all of which together comprise the 'copepodan line'; see also Starobogatov, 1988). This view was supported by Olesen (2001). The monophyly of Maxillopoda has, however, found no universal acceptance (Hessler, 1982; Boxshall, 1983; Newman, 2005), and especially molecular data has so far failed to offer support (Giribet et al., 2005; Regier et al., 2005). In a recent, comprehensive analysis of molecular data, Maxillopoda turns out to be polyphyletic, but still with Mystacocarida clustering with some of the maxillopodan taxa (sister taxon to a supposed monophylum consisting of Pentastomida and Branchiura; Reumont et al., 2009, Regier et al., 2010). Also a very basal position within Crustacea (or even Mandibulata) has been suggested (Edgecombe et al., 2000; Fanenbruck, 2003). In cases where an exact placement is not suggested, mystacocaridans are still considered to exhibit potentially a plesiomorphic condition of several features (Brenneis and Richter, 2010).

The rise of molecular phylogenetics has put morphology-based phylogenetics under pressure. However, morphology, including all data from external and internal anatomy, sexuality and reproduction, development and life attitudes, is in our view an at least equally important primary source of data for phylogenetic reconstructions for a number of reasons: 1) morphology provides a large set of mostly complex characters, 2) morphology is necessary when discussing evolutionary changes either as the primary source for phylogeny, or mapped on one, 3) morphology is indispensable when combing extant and fossil taxa into one phylogeny (Reif, 2002; Wirkner and Richter, 2009; Assis, 2009 and references therein). In particular we stress the importance of including fossils because these represent life forms in a historical dimension and, therefore, provide a direct window on evolution. Change through time, or the opposite, stasis, is often clearly represented in the morphology of various fossils such as the Cambrian well-preserved microfossils of the 'Orsten'-type, which therefore provide a huge additional toolbox for any sort of phylogenetic analyses when combined with recent taxa (Walossek, 1993; Walossek and Müller, 1998a, b; Olesen, 2007).

However, morphology-based phylogenetics often suffer from incomplete knowledge, misunderstandings, and/or terminological flaws, but this does not diminish the validity and usefulness of morphology as a whole; it should rather stimulate us to do more research and develop more stringent methods and tools (cf. discussion in Haug et al., 2010).

Given this as a starting point our work is a supplement to the description of *Derocheilocaris remanei* Delamare-Debouteville and Chappuis, 1951 (Mystacocarida) by Olesen (2001) focusing on aspects that, until now, were incompletely known such as the true number of larval stages, the development of the feeding apparatus, and the development of the characteristic 'toothed furrows' laterally on the tergites of the body segments. We expect deeper insights into functional aspects especially about the feeding apparatus, an important base for comparing *D. remanei* to one of its putative sister groups. The special form of the feeding apparatus was postulated as an autapomorphy of a taxon comprising Mystacocarida, the Cambrian *Skara*, and Copepoda.

## Material and Methods

Material of *D. remanei* was collected at the type locality of this taxon at Canet Plage, France, in February 1996 by one of the authors (JO) and was used by Olesen (2001), wherein details of collecting and material processing can be found. The same specimens were re-examined for this study with a JEOL SM-31010 SEM at the Zoological Museum, University of Copenhagen. For some specimens, two images in different focal planes were taken and later combined with the freely available software program 'CombineZM' [http://hadleyweb.pwp.blueyonder.co.uk/CZM/News.htm] in order to obtain an image with a higher depth of field. Because a very high resolution of some specimens was desirable, some images were stitched together from several separate sub-images taken at different x- and y-axis positions in the SEM using either the photomerge function of Adobe Photoshop (CS3), or the freely available software Microsoft Image Composite Editor [http://research.microsoft.com/en-us/um/redmond/groups/ivm/ICE/]. Additionally, some of the single images were combined from two images of different focal planes, therefore resulting in a true composite image in the sense of Haug et al. (2008, 2009a, b). Further image processing was done using Adobe Photoshop (CS3) and freely available software program Gimp [http://www.gimp.org/]. Line drawings were produced as vector graphics in Adobe Illustrator (CS3) and freely available software program Inkscape [http://inkscape.org/].

For *D. remanei* several sub-species have been described. Hessler (1971) mentions at least three sub-species: *D. remanei remanei*, *D. remanei biscayensis*, and *D. remanei katesae*. Following Hessler's suggestion (1971), McLachlan (1979) raised this third subspecies to a full species as *Derocheilocaris katesae* (Noodt, 1954). The specimens from Canet Plage inspected during this study were assumed to be representatives of the subspecies *D. remanei remanei*, which we confirmed with the key of Hessler (1971).

Length measurements were obtained from the two parts of the head shield. Measurements were taken in lateral view of the animals. Selected structures (antenna, maxillula, maxilla, maxilliped, sternal region, 'toothed furrows') were followed through the ontogenetic sequence to document their morphogenetic change.

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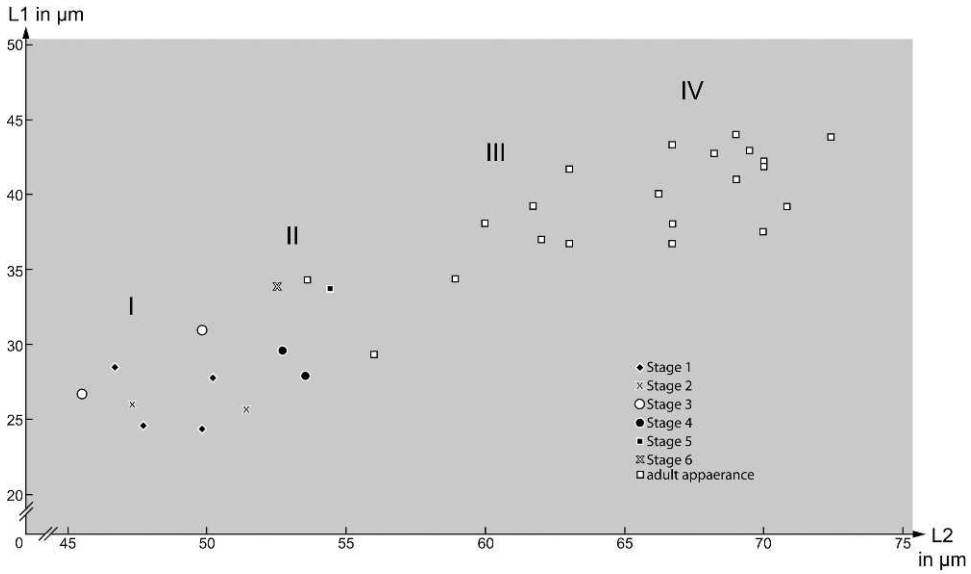


Fig. 1. Scatter plot of lengths of anterior part of head shield (L1) versus posterior part of head shield (L2) of *Derocheilocaris remanei*; different segmental condition of the specimens is indicated via the shape and color of the dots (details in legend); note the apparently four size clusters marked by Roman numerals.

## Results

### Identification of Ontogenetic Stages of *D. remanei* (Figs. 1-3)

Plotting the measured length of the anterior, articulated part of the head shield versus the length of the posterior part of the head shield resulted in four distinct size clusters (Fig. 1). Cluster I comprises three distinct morphological groups, which differ from each other with respect to the number of trunk segments excluding the telson. The telson is not a segment, but rather the non-metameric body end of Arthropoda with another ontogenetic history than body segments or metameres (also called somites) (Schminke, 1976; Walossek, 1993). We interpreted the group with the lowest number of segments as the earliest stage and other groups with more segments as successive stages. One group in cluster I has only three post-cephalic segments and is identified here as developmental stage 1 of *D. remanei* (Fig. 2A); a second group is identified as stage 2 by the possession of five post-cephalic segments with the last one not yet set off distinctly from the telson (Fig. 2B); a third group based on the presence of seven post-cephalic segments with the last one also not yet set distinctly off from the telson is identified as stage 3 (Fig. 2C). Cluster II contains four groups with distinct morphologies. The first group, our stage 4, has nine post-cephalic segments, with the last segment not yet distinctly set off from the telson (Fig. 2D); the second group, stage 5, has ten segments with the last one not yet distinctly set off from the telson (Fig. 2E); the third group, interpreted as stage 6, has ten post-cephalic segments but with a separate last segment (Fig. 2F); the fourth group, stage 7, has again ten post-cephalic segments (Fig. 3A), but stages 6 and 7 differ with respect to the presence of a prominent ''naupliar process'' on the antenna in stage 6, which is absent in stage 7. This feature is known from several larval series of entomostracan crustaceans and seems to be an indicator of a change in the feeding strategies of the larva, thus being likewise an indicator of a stage change. Clusters III and IV both exhibit the same number of trunk segments as stage 7 and are also identical with respect to their segment numbers. Cluster III, is stage 8 (Fig. 3B) and cluster IV is stage 9, the adult (Fig. 3C). The last three stages are only distinguishable by measurements and differences in the 'toothed furrows' (details below), not by differences in segment number. In total there are nine developmental stages of *D. remanei*, eight immature stages and the adult.

### Changes in Feeding Apparatus as a Basis for Stage Identification

Many structures appear to undergo no or only rather slight changes throughout ontogeny. Here we have focused on structures affiliated with the feeding apparatus, which exhibit the most significant changes during development. Another reason for focusing on the feeding apparatus is that this area of the body has proven to be of particular evolutionary/phylogenetic importance within Arthropoda (see Waloszek et al., 2007). The head shield has in its posterior area a pair of 'toothed furrows', which are documented in detail below because of their significant ontogenetic changes. Other parts of the shield and its general shape appear, however, not to change significantly throughout ontogeny and are therefore not described here. The antennula undergoes only slight changes in its setation pattern (see Olesen, 2001) and is also not considered in the following. Also the (second) antenna does not change its morphology much apart from a prominent median structure on the median edge, the ''naupliar process'', which gets lost later in ontogeny. Of the so-called mouthparts, the mandible appears, remarkably, to exhibit the fewest changes throughout ontogeny. It is already well developed in the hatching stage, which possesses trunk segments and can therefore be considered advanced. Accordingly, the

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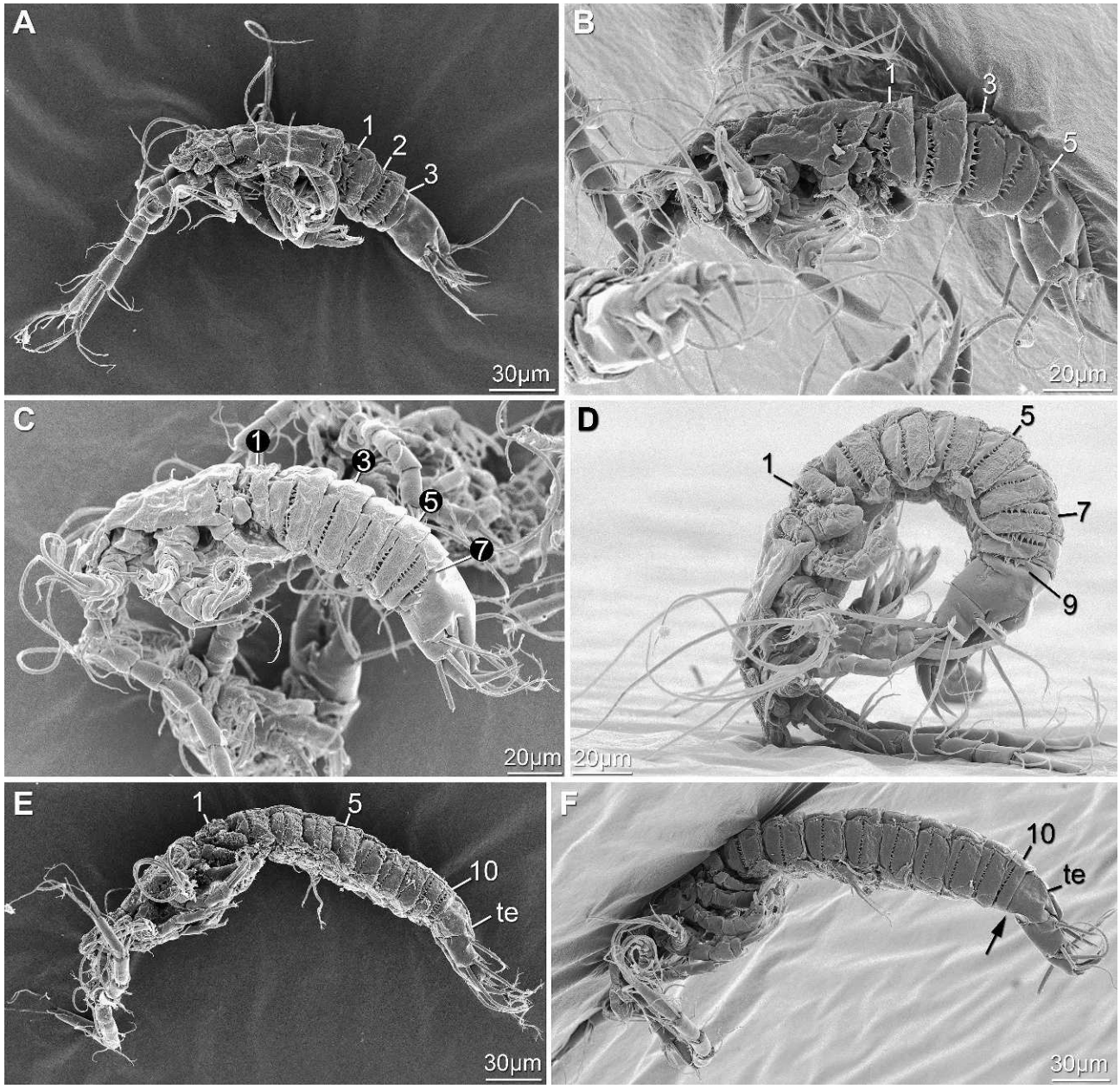


Fig. 2. *Derocheilocaris remanei*, developmental stages 1 to 6, all in lateral view; numbers indicating the trunk segments. A, Stage 1 with three trunk segments; B, Stage 2 with five trunk segments; C, Stage 3 with seven trunk segments; D, Stage 4 with nine trunk segments; E, Stage 5 with ten trunk segments; the tenth segment (10) is not yet completely set off from the telson (te); F, Stage 6; the arrow marks the clear demarcation lines between segment ten (10) and the telson (te).

early set of naupliar and metanaupliar stages in which the morphogenesis of the mandible occurs in a number of other crustacean taxa, has been skipped in the development of mystacocaridans (for general description of larval sequences in crustaceans see Walossek, 1993; Olesen et al., in press). After the hatching stage, the development of the mandible seems to stop; thus the adult still has a mandible of larval morphology. More changes occur in the maxillula, maxilla, and maxilliped, which are described in detail below. The rudimentary trunk limbs have also not been described here, and neither has the morphogenesis of the furca because it was described in detail already by Olesen (2001). Other prominent structures like the labrum and the sternal region of the head were documented at least for several of the developmental stages. Although not involved in the feeding apparatus, we documented the morphogenesis of the 'toothed furrows' of the tergites and the head shield as these undergo changes throughout ontogeny and have been used as diagnostic characters at the species level (Hessler, 1971).

Morphology of the Antennal ''Naupliar Process'' (Figs. 4, 5).—The so-called ''naupliar process'' of the (second) antenna is an elongate, branched, medially directed

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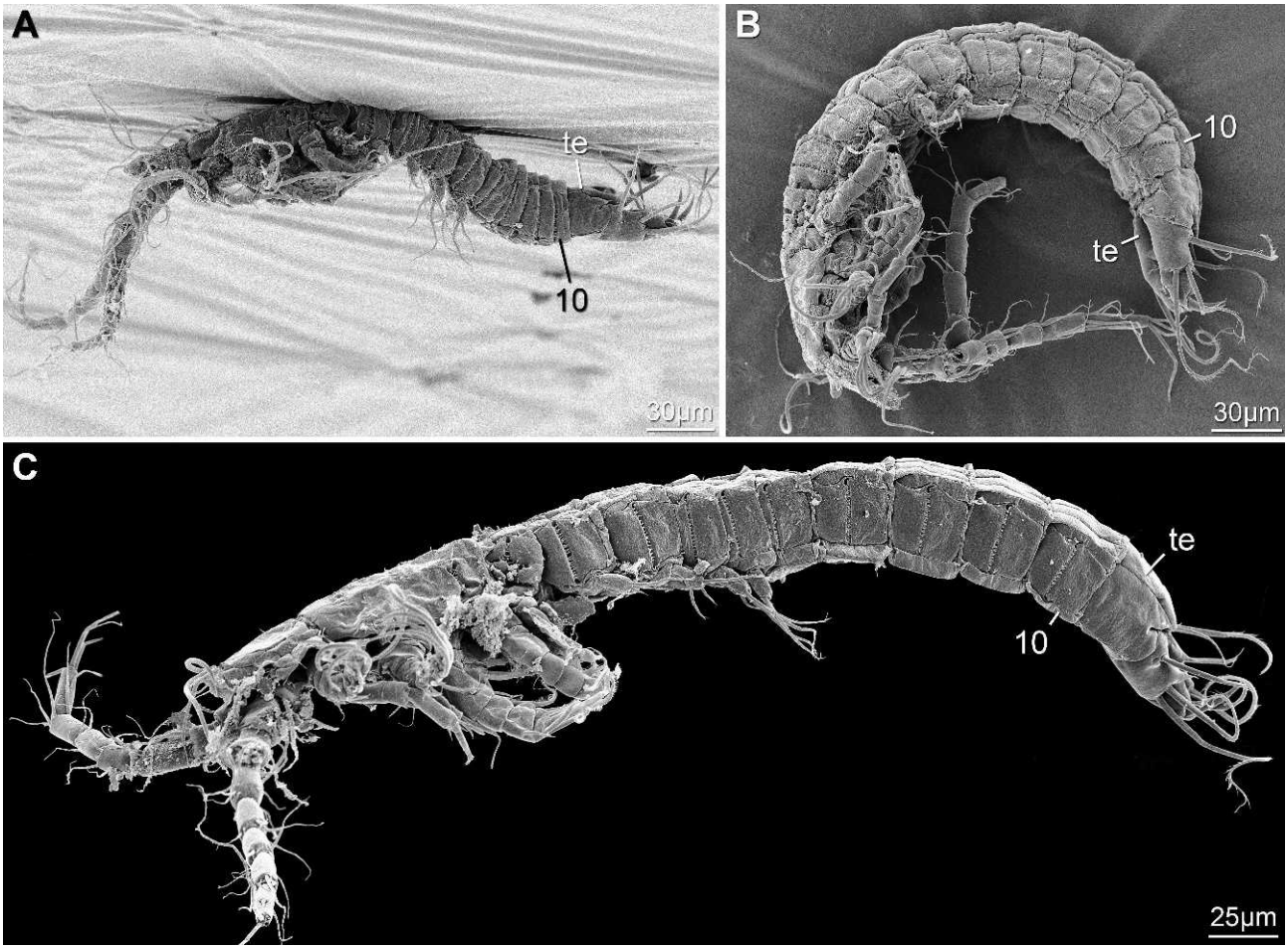


Fig. 3. *Derocheilocaris remanei*, developmental stages 7 to 9; all possess ten trunk segments anterior to the telson (te). A, Stage 7; B, Stage 8; C, Stage 9, i.e., adult stage.

structure, which probably plays a role in both collecting and handling of food items. In most specimens, the ''naupliar process'' is hidden by other structures, particularly the large labrum. Therefore, the morphology of the naupliar process had to be reconstructed from several specimens that were partly dissected exhibiting different parts of the process (Fig. 5).

The ''naupliar process'' of the antenna is present only in the first six developmental stages. It arises medially from the antennal coxa, thus representing the median armature (enditic protrusion). First, it bifurcates a short way distally into two rods named proximal (npp) and distal arms (npd) (Figs. 4A, B, 5), both running in parallel in an oblique posterior direction. Half way the length of the naupliar process each arm bifurcates further into long inwardly curved spines resulting in four spines in total; the spines are flattened in antero-posterior aspect and appear to be rather soft and almost look like ribbons (Fig. 4D). The distal two spines are furnished with a comb of fine setae, which can be relatively long (Figs. 4C, D, 5). The tips of the proximal two spines are usually lying right beneath the labrum (Fig. 4E, F) and bear one stronger spine proximally and more than a dozen small setules forming a comb more distally (Figs. 4E, 5).

While the naupliar process does not undergo recognizable changes throughout the early larval phase, i.e., in the first six developmental stages, it is absent from stage 7 onward. A pair of knoblets on the adult antenna in the corresponding position has been identified as remains of the naupliar process (Olesen, 2001).

Morphogenesis of the Maxillula (Figs. 6, 7A, 9; Table 1).—A general difficulty in describing the limbs is the limited access to both sides (anterior and posterior). As recognized in other entomostracan Crustacea, e.g., in cephalocarids (Olesen et al., in press), these two sides can differ significantly in their patterns of sclerotizations. Whenever both sides were accessible these differences are mentioned.

The maxillula is present already in the smallest, first developmental stage of *D. remanei* recognized herein (Fig. 6A, cf. Fig. 9), which is indicative of the advanced nature of this larva (see discussion below). Unfortunately, it is only accessible from the anterior side. The outline of the maxillula is paddle-shaped and it is approximately 20 µm long and about 10 µm wide. No subdivisions of the appendage are apparent on the anterior side, in particular no endopod-basipod boundary is present. Five blunt lobes of about 2 µm in proximo-distal length arise along the median

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margin of the maxillula. Based on the later developmental stages it is most likely that the most proximal lobe corresponds to the proximal endite, the next three lobes to the future basipodal endites, and the most distal one to the future endopodal elements, but this must remain an assumption. An exopod is missing.

The maxillula at stage 2 could not be well documented in the present material. The description is, therefore, mainly based on earlier observations of Olesen (2001). By the second stage, the maxillula is more-or-less differentiated into three distinct parts from proximal to distal, but is only slightly larger in dimensions than the previous stage (Fig. 6B, cf. Fig. 9). Again the limb is only accessible from the anterior side. The proximal part, the proximal endite (about one quarter of the total limb length) rests medio-proximally within the arthrodial membrane of the limb. Since it merges with the surrounding membrane, it lacks a well-defined outline. Medially, the proximal endite carries four spines pointing medially. The second limb part is the basipod, also measuring about one quarter of the total length. It is rectangular in anterior view and flattened in the anterior-posterior axis. It is also only weakly bordered, but is separated from the more proximal membrane through a fold on the lateral side. Three spines arise from the median edge of the basipod, having a diameter of about 2 μm and an approximate length of 12 μm. They appear softer than the 'spines' of the proximal endite and are flattened in the anterior-posterior axis; such structures are in the following better referred to as 'spine-like setae'. These spine-like setae appear to correspond to the three future basipodal endites. The third and most distal part is the uniform endopod. It is about 10 μm long, slightly curved medially and 6-7 μm in width, and extends into a small knob at the tip.

At the third stage, the maxillula (Figs. 6C, 7A, 9) is about 30 μm long. Both sides of the maxillula have been examined for this developmental stage, but the anterior side is only incompletely known. The proximal endite is accessible from posterior. It is better set off from the surrounding membrane and the basipod than in the preceding stage. It carries three well-developed spine-like setae now (they appear now to be softer, therefore the terminology is changed here) with a diameter of about 2 μm, but being anterior-posteriorly flattened. The length of the spine-like setae is about 5 μm. It is unclear whether there is a fourth spine-like seta corresponding to the fourth spine of the preceding stage.

Lateral to the proximal endite an area of the arthrodial membrane of the limb is more strongly sclerotized than the rest of the membrane, forming a more or less well-defined lateral sclerite (ls), but this is not connected with the median proximal endite so it does not form a distinct ''coxal portion.'' The lateral sclerite is visible from posterior as well as from anterior. It appears to reach further towards the median edge, i.e., closer to the proximal endite, on the posterior side than on the anterior side.

The rectangular basipod appears to be weakly subdivided on the posterior side (Fig. 7A) into two parts, a triangular area and a more L-shaped element that surrounds the triangular portion from behind. Medially the basipod is drawn out into three enditic lobes, the two more proximal ones being larger than the distal one, and with the distal two endites arising from the triangular part of the basipod. The proximal basipodal endite bears at least two spine-like setae (not properly visible due to unfavorable mounting on the SEM stub). One is longer and weakly sclerotized, most likely corresponding to the proximal one of the three basipodal spines of the last stage, and almost of the same dimensions. The second spine is shorter and more rigid, about 2 μm in diameter and 5 μm in length. The two more distal basipodal endites are set off from the more proximal one through folds around a slightly stronger sclerotized area embracing the endites. The proximal of the two distal endites has at least three spine-like setae; the distal basipodal endite carries one or two spine-like setae. The third, distal part of the maxillula is the endopod, which now is slightly inwardly curved and subdivided into four elements. The elements are rectangular in shape and wider than high in anterior view, the proximal three are drawn slightly out medio-distally into enditic protrusions. The proximal three elements have folds running from proximal to distal, indicating stronger sclerotized lateral areas on the posterior side (Fig. 7A), while the median areas appear softer. The anterior side is well sclerotized entirely. The sclerotized area appears to reach around each element, from the median edge across the anterior side and then around the lateral edge to the midline of the posterior side. This leaves only the median half of the posterior side less sclerotized and softer appearing due to its wrinkled surface. The second and third elements each carry one spine-like seta medio-distally. The distal element is well separated from the penultimate element on the anterior side (Fig. 6C), but no clear fold between the two is apparent on the posterior side (Fig. 7A). The distal endopod element has three spine-like setae inserting distally.

From stage 4 onward the morphology of the maxillula does not undergo significant further changes, and the general organization described here refers, therefore, just to a ''late'' stage. The limb has only been studied from the anterior. Differences from the previous stage are mainly in the number of setae and in the presence of more apparent subdivisions of the different limb elements (Fig. 6D, E, cf. Fig. 9). The proximal endite now has at least five spine-like setae. The basipod is weakly sub-divided on the anterior side, which differs from the subdivision of the posterior side known for the previous stage: a smaller rectangular area carries the proximal basipodal endite, a larger rectangular part gives rise to two distal endites. The first basipodal endite bears at least one spine-like seta in the specimens at hand, but most likely there are more, as indicated by earlier developmental stages. The second basipodal endite bears two spine-like setae, the distal one three such setae. The endopod elements are now all well separated from each other and carry more spines on their median edges than before; they carry two, one, two, and eight spines from proximal to distal, respectively. The areas where these spines arise are drawn out medially forming enditic protrusions. The endopod elements are also larger compared to the basipod than in the preceding stage. An

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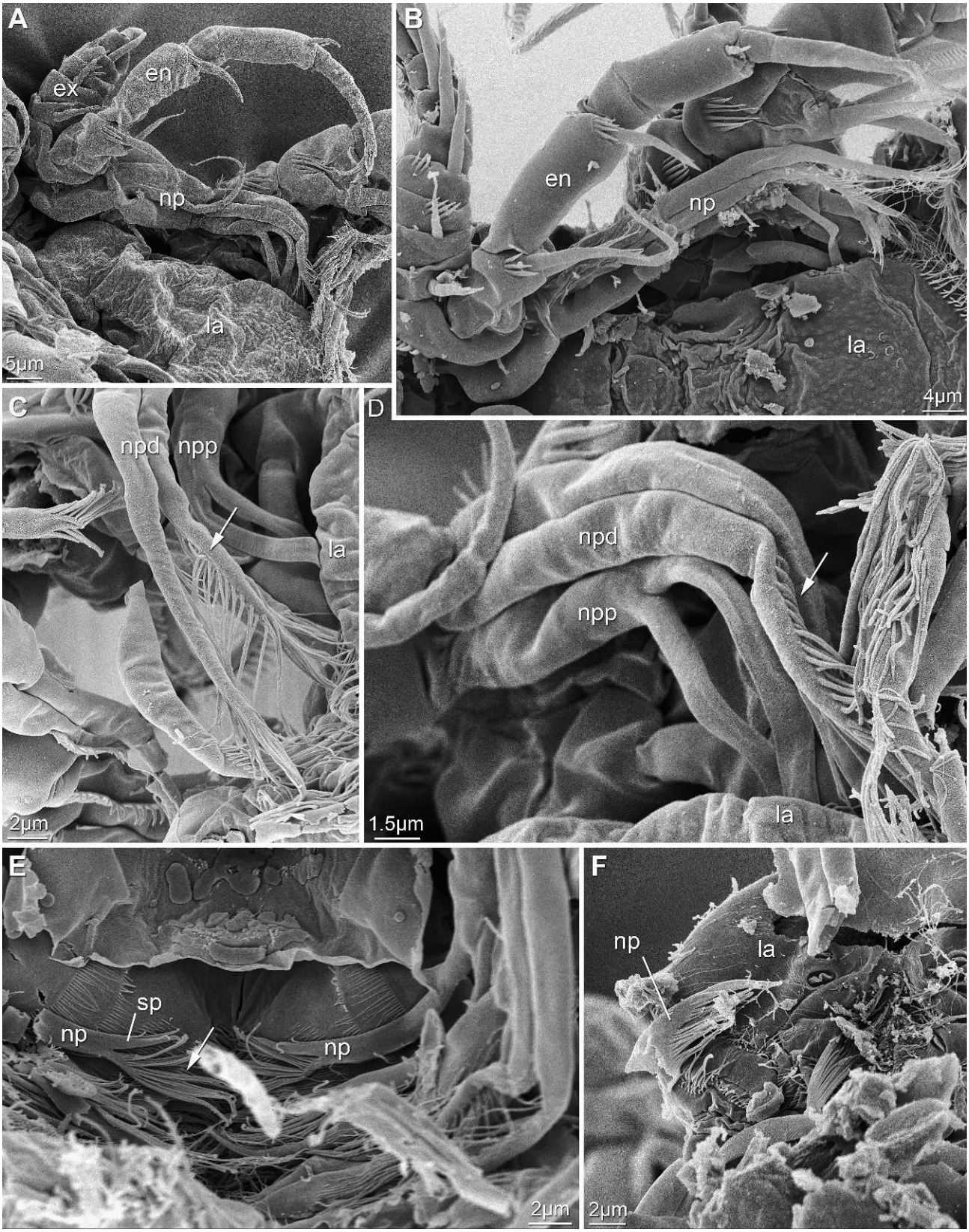


Fig. 4. ''Naupliar process'' of the antenna of *Derocheilocaris remanei*. A, Complete left antenna seen from median side of an earlier developmental stage; besides the two rami (exopod, ex and endopod, en) the ''naupliar process'' (np) is a very prominent structure; note how the distal part is concealed by the labrum (la); B, ''Naupliar process'' (np); note that the distal part of the proximal part of the naupliar process curves under the labrum; C, Tips of the distal ends of the distal two setae of the ''naupliar process'' (npd); also here it is apparent how the proximal part of the ''naupliar process'' (npp) curves under the labrum (la); arrow marks the long setae on the distal part; D, The four spines of the ''naupliar process'', two distal ones (npd), two proximal ones (npp);

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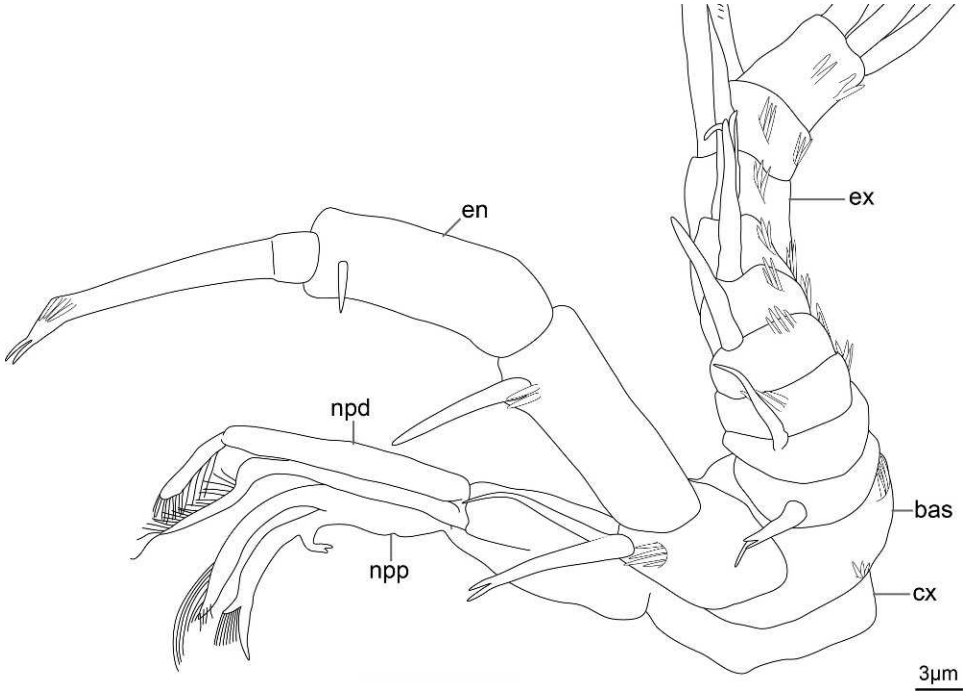


Fig. 5. Right antenna of a larval specimen of *Derocheilocaris remanei*; the appendage is seen from the anterior, but slightly from above; the distal setae of the exopod are cut off to save space; the coxa (cx) carries the ''naupliar process'' with its proximal (npp) and distal (npd) part; endopod (en) and exopod (ex) arise from the basipod (bas).

exopod is never developed during morphogenesis of the maxillula.

Morphogenesis of Maxilla (Figs. 7B, 8A-C, 9; Table 1).—The maxilla appears first in stage 4 in the form of a rather undifferentiated limb bud of about 15 µm in length and 10 µm in width (Figs. 8A, 9). Three parts can be recognized along the limb axis. The proximal part is identified as the proximal endite. It is set off proximally and laterally from the arthrodial membrane of the limb and distally from the basipod, and is therefore not considered a coxa. Medially the proximal endite protrudes into a hook-like spine. The next limb element is the basipod, which carries a single median spine pointing medio-distally. The distal part, probably the initial endopod, is only weakly set off from the basipod and forms just a simple lobe.

At the fifth stage, the maxilla is about 30 µm long and better differentiated (Figs. 8B, 9). The proximal endite carries three median spines. The membrane lateral to the proximal endite appears stronger sclerotized than the more median membrane, indicating a future lateral sclerite, as seen on the maxillula (see above). The basipod is rectangular in anterior view, slightly higher in the proximo-distal axis (about 10 µm in total) than in the medio-lateral axis, and flattened in the anterior-posterior axis. Medially it carries four distinct endites, each carrying a single medially pointing spine-like seta. A fold running from proximal to distal separates a more strongly sclerotised lateral area of the basipod from a softer appearing median one. The endopod is distinctly set off from the basipod, but is still lobe-like and now longer in proximal-distal aspect (about 15 µm long, less than 10 µm wide). Faint folds are indicative of the future subdivision of the endopod.

In stage 6 the maxilla reaches its definite form, i.e., its morphology does not undergo significant changes in following stages (Figs. 8C, 9). From this stage on the proximal endite is distinctly set off from the arthrodial membrane and from the basipod, both on the anterior and posterior side. At least five spine-like setae arise from this endite. The lateral area of the arthrodial membrane forms a defined scleritic structure (cf. maxillula), which appears to be restricted to the lateral area (also visible from anterior), but in posterior view only a soft membrane is apparent lateral to the proximal endite. The basipod is more elongate along its proximo-distal axis than in the earlier stages, its median edge being drawn out into five endites (total of six endites in the maxilla). Four basipodal endites are apparent from the posterior side only. The proximal basipodal endite appears to be concealed by the large proximal endite. On the anterior side the proximal basipodal endite forms a defined sclerite, which is well separated from the proximal endite. A single proximo-distally running fold on the posterior side separates a better sclerotized lateral area of the basipod from a weakly sclerotized median area from which the endites arise. Each endite carries at least one

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arrow marks the long setae on the distal part; E, Tips of the proximal spine of the ''naupliar process'' (np), on the ventral surface close to the mouth, labrum removed; proximal spine (sp) and a distal comb of setae (arrow) are apparent; F, Removed labrum (la); one tip of the proximal spine of the ''naupliar process'' (np) still sticking to it, indicating the original position.

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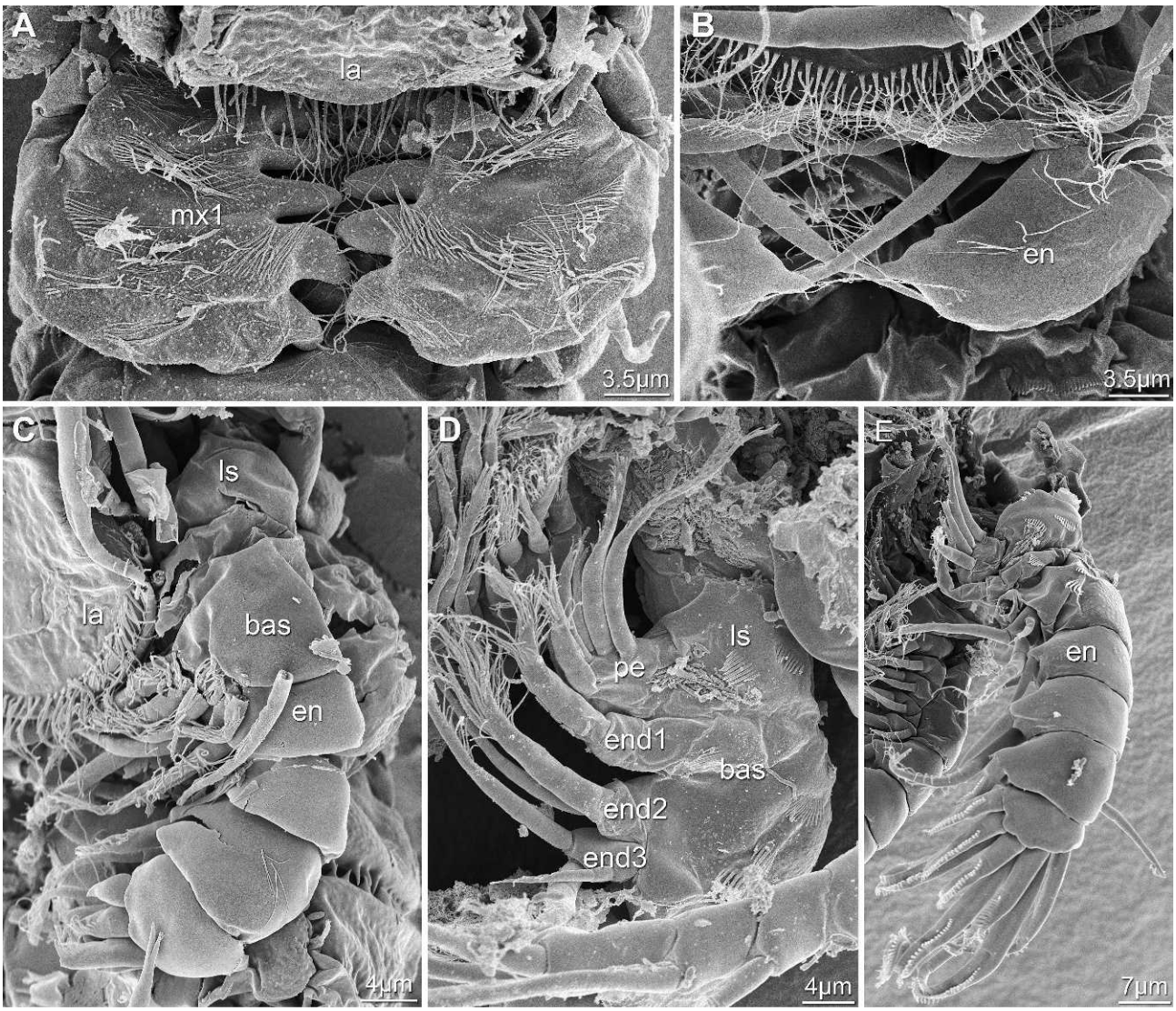


Fig. 6. Morphogenesis of maxillula of *Derocheilocaris remanei*, all in anterior view. A, Stage 1; the maxillula (mx1) is partly concealed by the large labrum (la); B, Stage 2; note the special shape of the endopod (en); C, Stage 3; in this stage the subdivision of the endopod is very apparent; basipod (bas) well separated from endopod and lateral sclerite (ls); labrum concealing medio-proximal structures; D, Later developmental stage, proximal part; subdivision less well apparent than before, but still recognisable; proximal endite (pe) and three endites (end1–end3) of the basipod on the median side, lateral sclerite and basipod; E, Later developmental stage, distal part, mainly the endopod (en).

large and one small spine-like seta; the fifth endite bears an additional one. The endopod (less than 20 µm measured without setae) is distinctly subdivided into four elements. The proximal three elements are of asymmetric trapezoidal shape; their rectangular to square shape in apparent in anterior view is medio-distally extended into an enditic protrusion bearing the spine-like setae. The distal element does not possess such a protrusion. The proximal element bears three spine-like setae arising medio-distally, the second element has one, the third two such spines. The distal endopod element carries five spines. The lateral side of the three proximal endopod elements is stronger sclerotised than the posterior side; this is indicated by folds that extend from proximal to distal and separate the two areas (Fig. 7B). On the anterior side all elements are well sclerotized. The sclerotized area, as observed on the maxillula, appears to stretch around each element from the median edge around the anterior side and the lateral edge reaching to the midline of the posterior area. This leaves only the median half of the posterior side less sclerotized and softer appearing, recognizable through the wrinkled surface. Also as in the maxillula, the maxilla does not bear an exopod at any time during its development.

Morphogenesis of Maxilliped (Figs. 8D-F, 9; Table 1).—Stage 5 is the first stage, at which the maxilliped appears (Figs. 8D, 9) as a lobe-like bud. The limb bud has a total length of almost 20 µm and a width of about 10 µm, and is made up of three elements: the future proximal endite, the basipod, and the endopod. All elements are only weakly bordered by latero-medially running folds. Proximo-distally running folds on all three elements separate more weakly sclerotized (slightly collapsed in the preserved specimens) median areas from more strongly sclerotized

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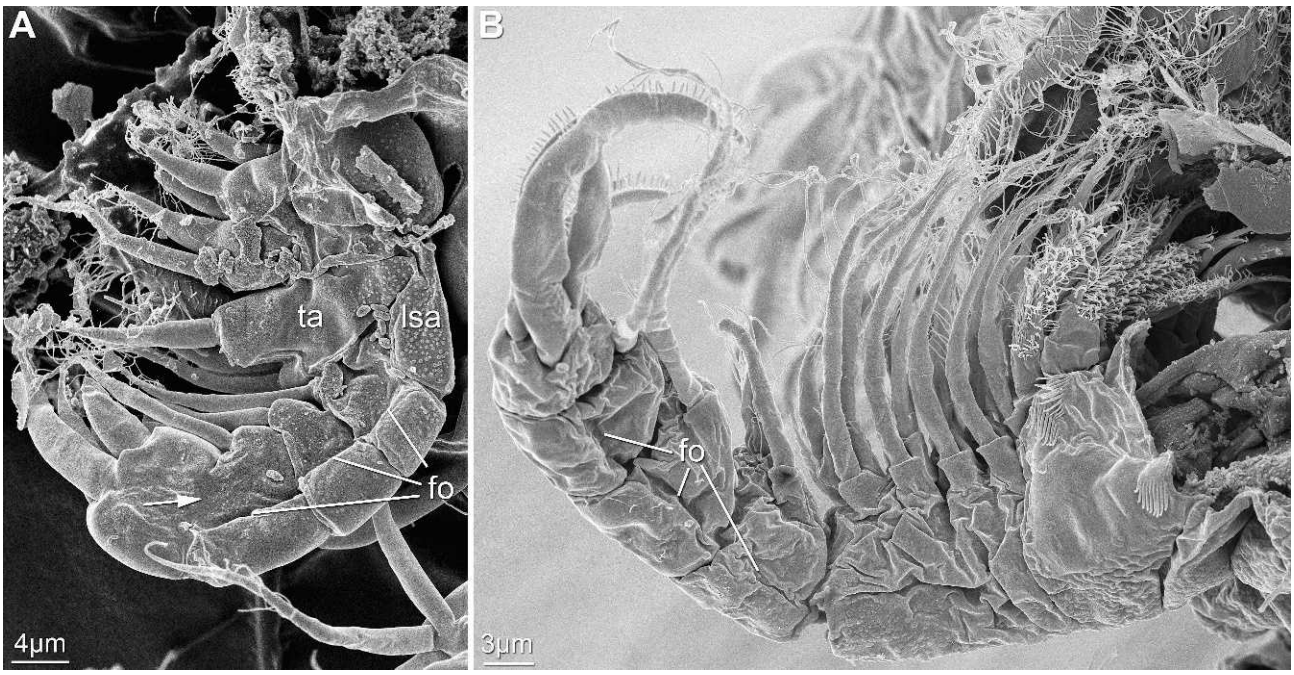


Fig. 7. ''Mouth parts'' of *Derocheilocaris remanei* in posterior view. A, Posterior side of a maxillula of a stage 3 specimen; fo = fold, lsa = l-shaped area of the basipod, ta = triangular area of the basipod; arrow marks not well-developed border between the ultimate and penultimate endopod element; B, Posterior side of a (second) maxilla of a specimen of a late developmental stage.

areas laterally. At stage 6, the maxilliped is more differentiated than in the previous stage (Figs. 8E, 9). Its proximal element, the proximal endite, has now three medially pointing spine-like setae. The lateral area of the arthrodial membrane appears more strongly sclerotized than before, forming a lateral sclerite (cf. maxillula and maxilla). The basipod is weakly set off from the proximal endite and the more proximal arthrodial membrane. It has four endites along its median edge, each with a medially pointing spine-like seta. The distal endite carries a small additional associate seta. The lateral side of the basipod is still separated by a proximo-distally running fold. This lateral area appears more strongly sclerotized (due to no visible shrinkage wrinkles), in contrast to the other, more weakly-sclerotized area (more collapsed). The endopod is (still) lobe-like and not clearly set off from the basipod. Its future subdivision into at least two elements is indicated by an indentation close to the tip of the lobe.

There is additionally a separate, spine-like limb part at the latero-distal 'shoulder' of the basipod (Fig. 8E). This structure could represent the precursor of the exopod or the seta adjacent to it, which are both developed in the next stage. An exact identification is not possible at the moment.

Table 1. Growth pattern of *Derocheilocaris remanei*; abbreviations: ex = exopod, mx1 = maxillula, mx2 = maxilla, mxp = maxilliped, o = present, not yet completely developed, • = limb in definitive state, TSx = number of trunk segments.

| stage | TS3 1 | TS5 2 | TS7 3 | TS9 4 | TS10 5 | TS10 6 | TS10 7 | TS10 8 | TS10 9 |
|---|---|---|---|---|---|---|---|---|---|
| mx1 | o | o | o | • | • | • | • | • | • |
| mx2 | – | – | – | o | o | • | • | • | • |
| mxp | – | – | – | – | o | o | • ex | • ex | • ex |

The maxilliped reaches its definite morphology in stage 7 and does not undergo further changes. The exact morphology is only known for the posterior side of the limb at this stage. From this stage on the proximal endite of the maxilliped (Fig. 8F, 9) appears well developed and of the final shape. It carries four spine-like setae medially. One of these is heavily setulose. As before, the lateral area of the arthrodial membrane exhibits a stronger sclerotisation, i.e., it forms a sclerite-like structure, but it appears to be restricted mostly to the lateral and anterior side, only a small part being visible in posterior view (cf. maxilla). The basipod is triangular with four median endites, as before, but the proximal basipodal endite as well as the second endite now bears three spine-like setae. The third endite bears four spine-like setae and the fourth endite only two. The endopod is subdivided into three elements. The first appears to lack setae, the second element bears a pair of spine-like setae medio-distally, and the terminal one has two setae. The two proximal endopodal elements have more weakly sclerotized median areas than the equivalent region in the two more anterior limbs. The maxilliped has now an exopod developed (cf. above). It articulates laterally on the slope of the triangular basipod. The exopod is made up of a single square-shaped element, only about 5 µm high. It carries two setae distally. A single seta arises laterally from the basipod proximal to the exopod, which, relative to exopods of many other crustaceans, appears rather vestigial.

## Hypostome-labrum Complex (Fig. 10)

The ''labrum'', more precisely the hypostome-labrum complex (for clarification of this see e.g., Maas et al.,

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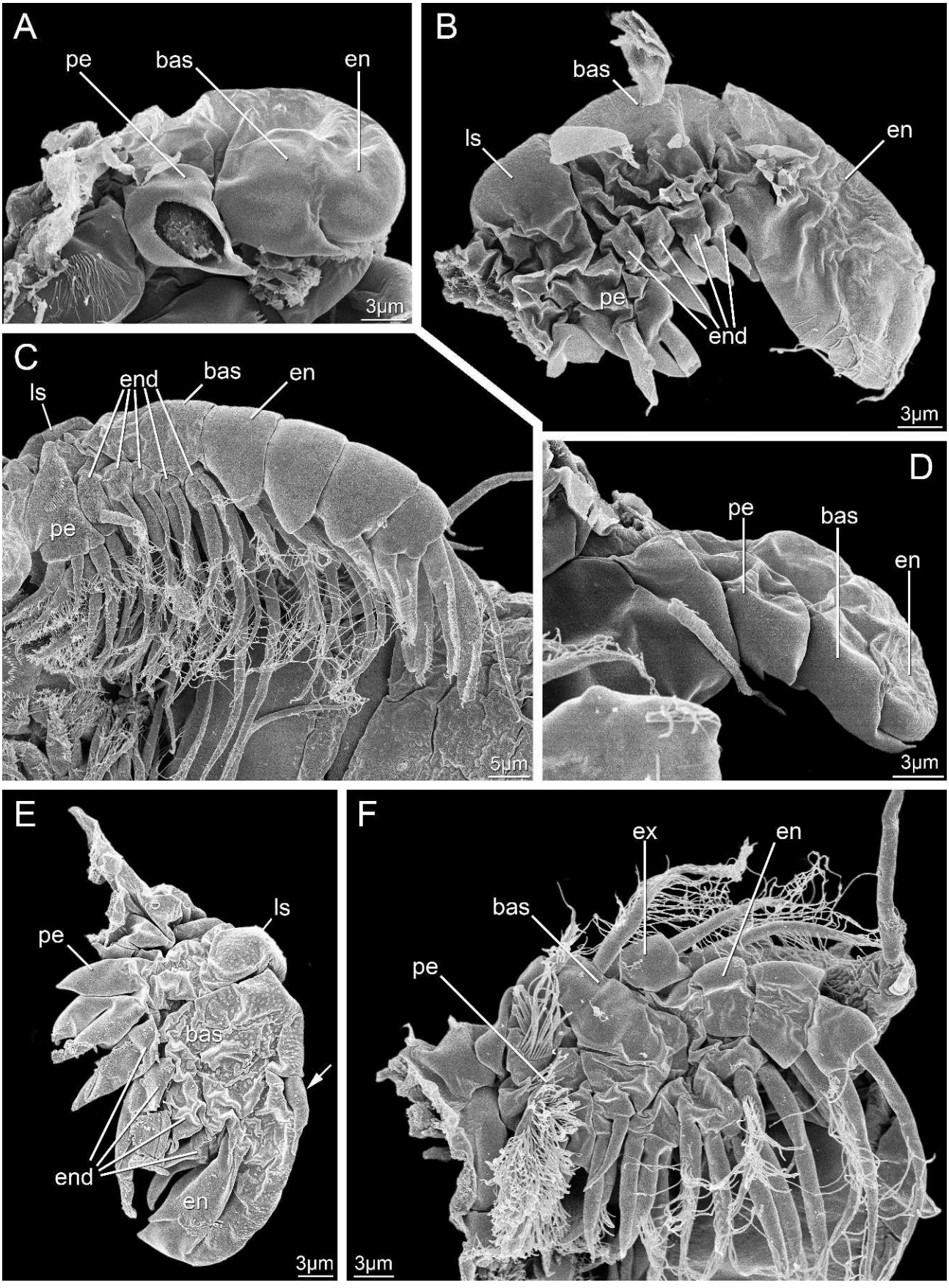


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2003), starts medio-posteriorly between the antennal insertions and reaches back to the posterior rim of the head. Accordingly, it is extremely large in the anterior-posterior dimension – about three times as long as wide in the adult – but is rather flat in the dorso-ventral aspect (Fig. 10A). In the adult, the hypostome-labrum complex conceals almost the complete feeding apparatus, i.e., the entire mid-ventral area of the animal. The gross shape is that of a spoon or scoop, i.e., straight rectangular in the anterior two thirds, but widening into a rounded form on the posterior third (Fig. 10A). When viewed ventrally a subdivision into a labrum and a hypostome is not clearly visible (Fig. 10A). However, such a separation can be more clearly seen in a labrum removed and oriented to expose its inner surface (Fig. 10B). The hypostome occupies the anterior third of the hypostome-labrum complex. It appears almost square; but actually it is trapezoidal in dorso-ventral aspect, tapering slightly anteriorly. In ventral view, i.e., the morphological anterior surface, the labrum is relatively smooth (Fig. 10B; details in Fig. 10A) with only the posterior rim bearing fine setae. The inner side of the labrum, i.e., the morphological posterior surface, bears many fine setae including two rows of medially oriented setae (Fig. 10B, C) and fine forward-pointing setae arising from the posterior margin. More fine setae are arranged in less strict patterns. There are also six pores on the posterior surface (Fig. 10C, D) – not simple openings, but soft tubes each in a depression (Fig. 10D). A comparable pair of pores is present medio-anteriorly. The surface of the area between the rows of setae, which also comprises the pores, appears finely wrinkled and is therefore interpreted as being softer than the ''outer'' surface of the labrum (Fig. 10D). The function of these pores is unknown, but these may be slime-secreting papillae.

The ontogeny of the hypostome-labrum complex and its details could not be followed throughout ontogeny; it proved to be difficult to detach the labrum from the body in order to view its posterior side, especially in small specimens. A single example of a detached larval labrum was found in the material (Fig. 10E). The larval status was recognized through the tip of the ''naupliar process'' still sticking to it. The structure is damaged, but we could observe that the pores are not arranged in the same pattern as in adult specimens – only four pores, two are close together, not six as in the adult. Two further pores are present, but more anteriorly and also more tilted than in the adult.

## Ventral Post-labral Sternal and Post-maxillular Sternite Surfaces (Figs. 11, 16A)

The exact morphology of the sternites, which is a part of the feeding apparatus, could be best observed in late developmental stages, mainly adults (cf. Fig. 16A). The sternum is a sclerotisation of the ventral cuticle posterior to the mouth opening, comprising the ventral area of the segments of the mandibles and maxillules. Whether it reaches further anteriorly and includes also parts of the sternitic area of the antennae could not be observed. The paragnath humps, structures of the mandibular sternite (cf. Walossek, 1993), are raised into small blade-like structures of about 5 μm in length and width that are directed antero-laterally (Fig. 11A-C). These distal parts are shaped so that they follow the convexity of the posterior side of the mandibles and wrap around the posterior edge of the coxal blade (C-shaped when viewed from laterally) (Fig. 11A, C). It is possible that this close association limits the backward movements of the mandibles. Medially the paragnaths flank a groove in antero-posterior direction, the so-called paragnath channel (Fig. 11B). The sternum, although not completely devoid of setae, is relatively smooth compared to the ''normal'' sternum of other eucrustaceans, which is covered by fine hairs (cf. Waloszek, 2003; Maas et al., 2003).

The sternite of the maxillary segment, i.e., the ventral sclerotisation between the maxillae, is clearly set off from the sternum by a fold (Fig. 11D), which means it is not part of the sternum (a plesiomorphy retained from the ground pattern of Labrophora and Eucrustacea, see e.g., Maas et al., 2003). The maxillary sternite is triangular to heart-shaped, with the tip pointing anteriorly (Fig. 11D). Its width is slightly smaller than that of the sternum. In contrast to the sternum, a rather dense layer of small hairs directed mainly antero-medially covers the maxillary sternite (Fig. 11D).

The width of the hexagonal sternite of the maxillipedal segment is comparable to that of the maxillary segment, but it is almost twice as long (Fig. 11D). From anterior to posterior, a median groove runs through the sternite. The rims of this groove are furnished with medially directed fine hairs (Fig. 11D). The groove of the maxillipedal sternite is not directly continuous with the paragnath channel, since the intervening segment lacks a median groove (cf. Fig. 16A). Possibly the antero-medially directed hairs on the maxillary sternite fulfill a similar function as the median grooves found both anterior and posterior to it. The whole complex of grooves and hairs is a part of the feeding apparatus, and probably assists in guiding the food particles to the mouth.

Morphogenetic changes of the sternitic area were difficult to follow, but apparently the adult morphology is not present before the limbs of the corresponding sternite are functional. For example, in stage 4 the maxillulary sternite has only few hairs and these appear to be more postero-medially directed, while they are

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Fig. 8. Morphogenesis of maxilla and maxilliped of *Derocheilocaris remanei*, all in anterior view. A-C. Maxilla. A, Stage 4; three recognizable parts: proximal endite (pe), basipod (bas) and probable endopod (en?); B, Stage 5; laterally to the proximal endite (pe) a lateral sclerite (ls) is now present; the basipod (bas) has now four endites (end) and the endopod (en) is now recognisable, but yet not subdivided; C, Later developmental stage; proximal endite (pe) and lateral sclerite (ls) still recognizable; basipod (bas) now with five endites (end); endopod (en) now subdivided; D-F, Maxilliped. D, Stage 5; three recognizable parts: proximal endite (pe), basipod (bas) and the probable endopod (en?); E, Stage 6; laterally to the proximal endite (pe) a lateral sclerite (ls) appears; the basipod (bas) has now four endites (end) and the endopod (en) is recognizable, but not subdivided yet; arrow points to possible future exopod; F, Later developmental stage; besides proximal endite (pe), basipod (bas) and endopod (en), one new element, the exopod (ex) occurs.

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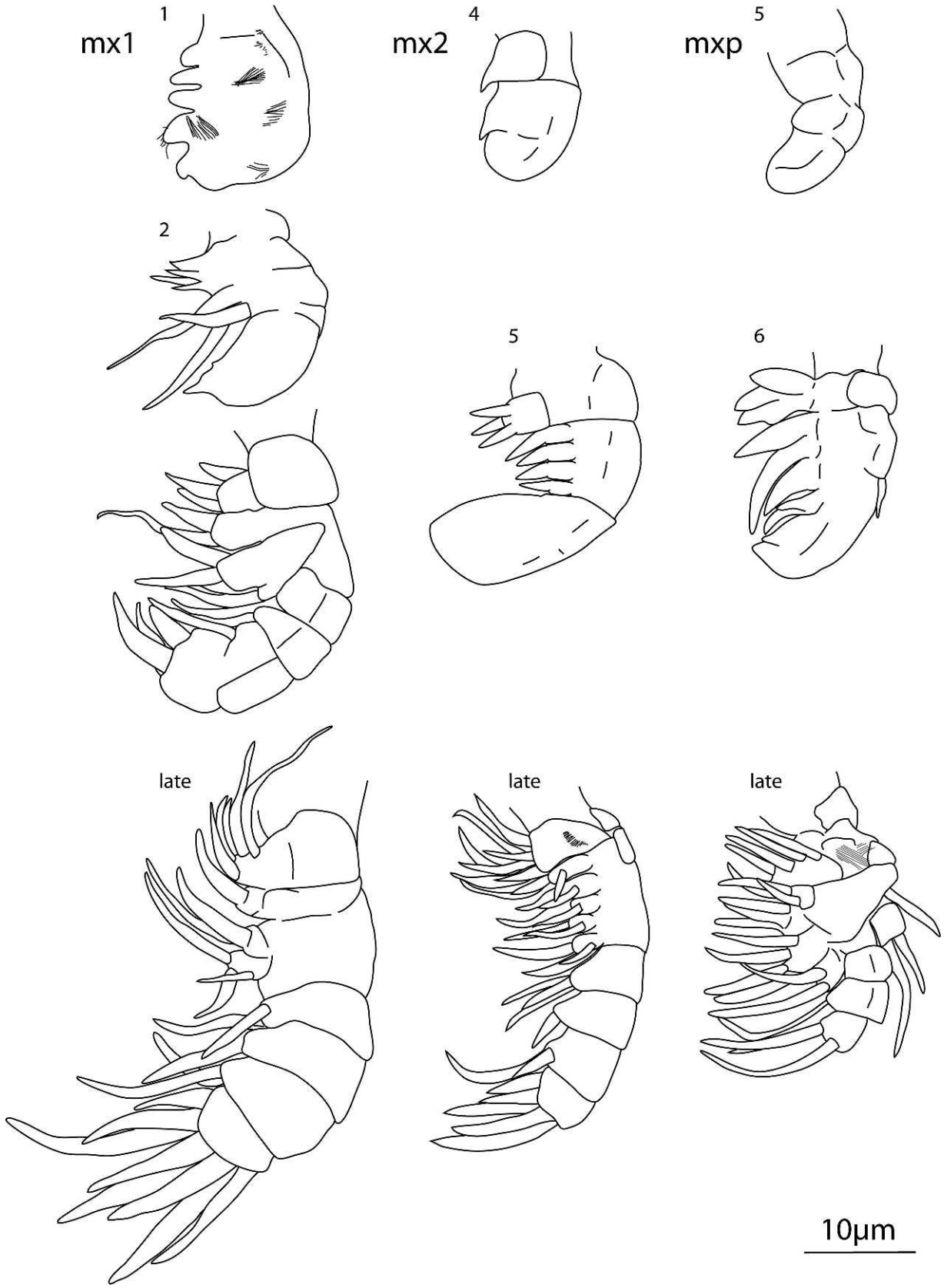


Fig. 9. Comparison of the morphogenesis of maxillula (mx1), maxilla (mx2) and maxilliped (mxp) of *Derocheilocaris remanei*; parts redrawn from the anterior sides of actual specimens, but in some cases combined from different specimens; note the similarities of the early two developmental stages of maxilla and maxilliped; numbers refer to developmental stages.

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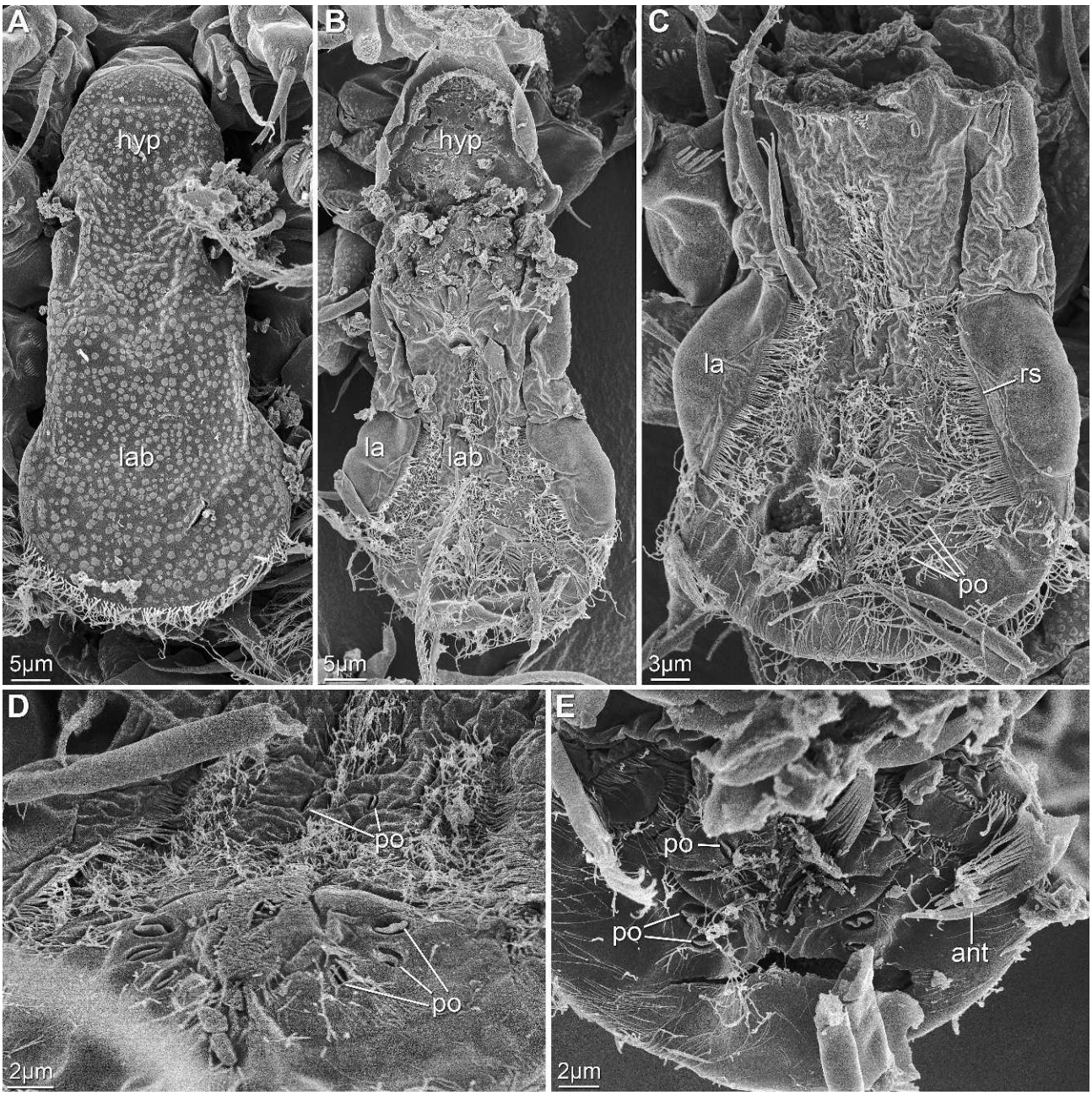


Fig. 10. Hypostome-labrum complex of *Derocheilocaris remanei*. A, Anterior side; hypostome (hyp) and labrum (lab) hardly distinguishable; B, Posterior side; hypostome and labrum apparently separated; on the labrum part a lateral area (la) is set off; C, Close-up on the labrum part, posterior side; observable details are the rows of setae (rs) and the pores (po); D, Close-up on the anterior region of the labrum, posterior side; E, Comparable region as in D, but on a larval specimen; the larval status is indicated by the broken off tip of a ''naupliar process'' of the antenna (ant) (same image as Fig. 4F, but different image detail and rotated).

antero-medially directed in the adults. An unusual structure can be observed in stage 4. Here the maxillipedal sternite bears two pairs of backward pointing spiny combs (Fig. 11E), but these are absent in the subsequent stages (Fig. 11F). These combs appear to be present already earlier but here they are less distinct and partly concealed by the large maxillula so they could be not documented adequately. They might fulfill a grooming function, but this is unclear.

## Morphogenesis of the 'Toothed Furrows' (Figs. 12-15)

Rows of so-called 'toothed furrows' located laterally on the body are characteristic for all mystacocaridans. Their specific morphologies have been used as diagnostic characters for various species (Hessler, 1971) but their function is still unknown. Here we present a detailed study of the morphogenesis of the 'toothed furrows' in *D. remanei.*

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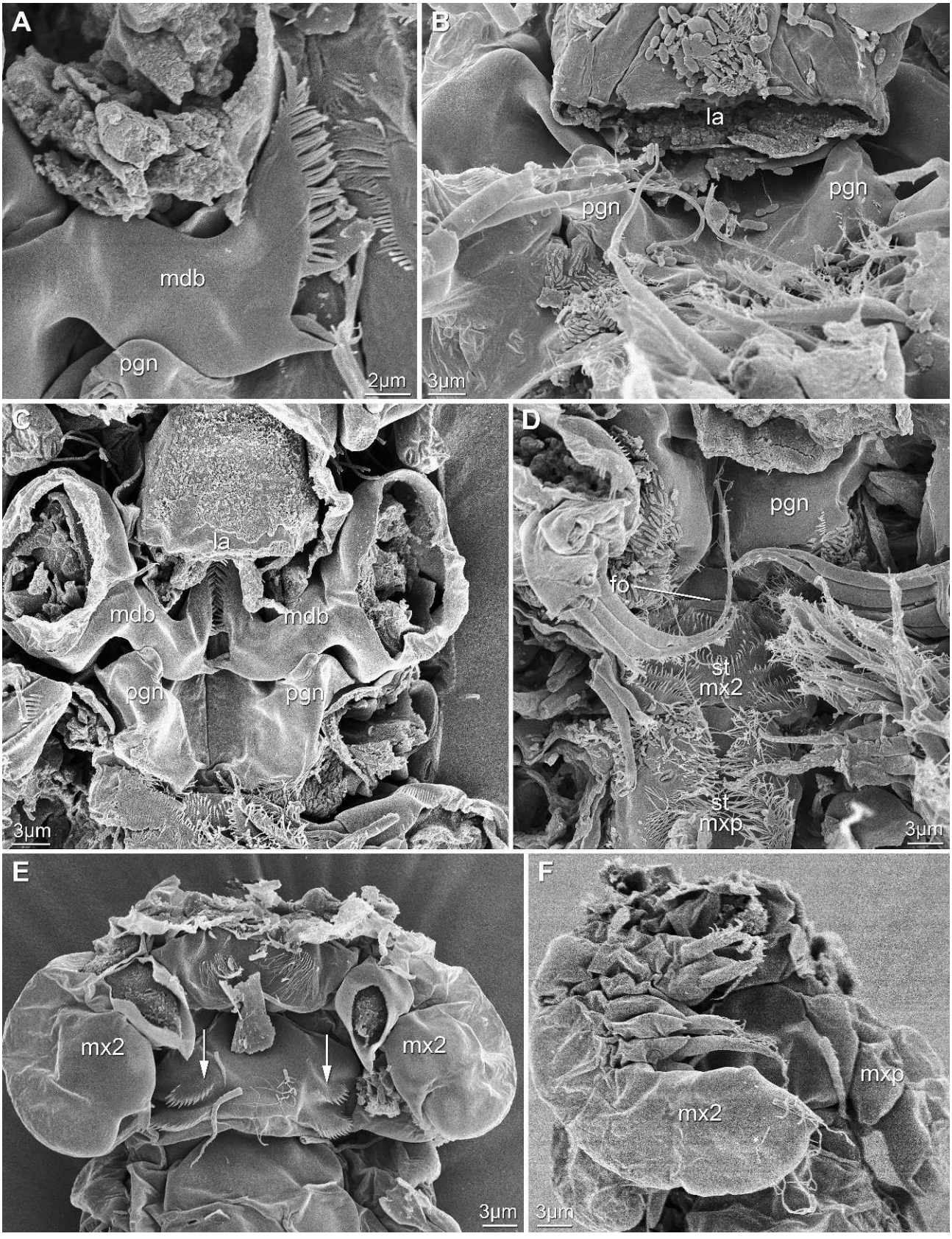


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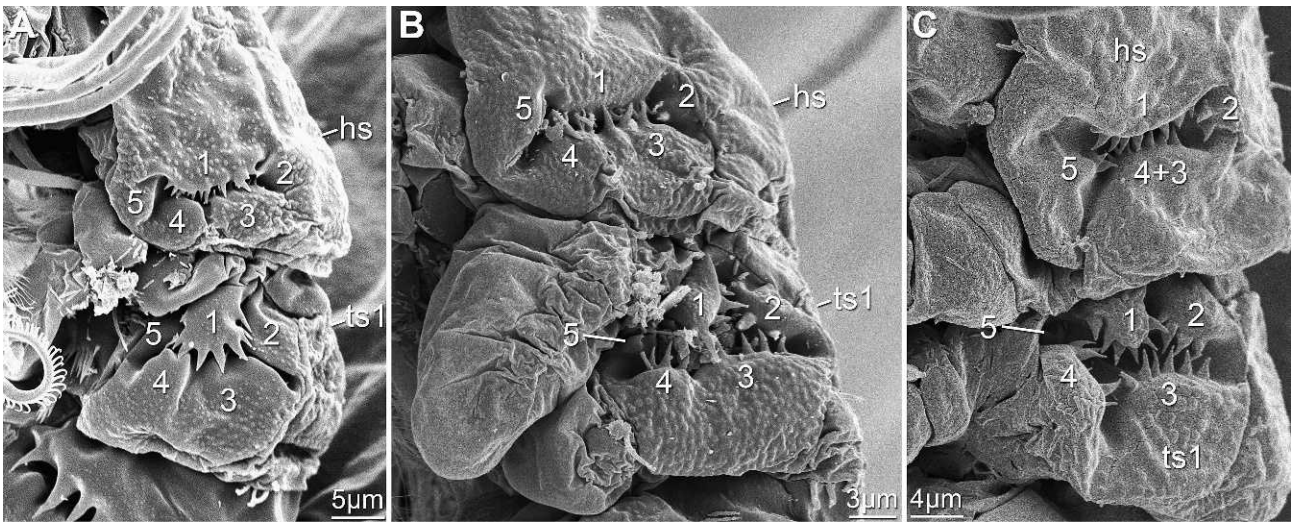


Fig. 12. Development of the ''X-shaped'' 'toothed furrows' of *Derocheilocaris remanei*; specimens oriented anterior up and dorsal right. A, Stage 1; both ''furrows'' are surrounded by five lobes, indicated by the numbers; B, Stage 4; both grooves are surrounded by five lobes, but these are less apparent; for details, see text; C, Adult stage; only four lobes are apparent on both ''X-shaped'' furrows; for details, see text.

The 'toothed furrows' are grooves on the dorso-lateral area of the body and are armed with spines along their margins, which are often termed teeth. The head shield (above the maxillary segment) as well as all trunk segments possesses a pair of these grooves. The grooves are in-folds of the cuticle running from dorso-medially to laterally, leaving a mid-area of the dorsal area of about one third without the grooves. Spines arising from the rims of the groove often partly cover the groove cavities. The grooves are right in the middle of the trunk segments in the anterior-posterior axis. They are not as well defined as often drawn (cf. Hessler, 1971) towards their median and lateral ends, fading smoothly out especially in earlier developmental stages. We can distinguish between two principal types of these grooves. Type 1 is present on the head shield and on the tergite of the maxillipedal segment; type 2 is present on all other tergites. The grooves change significantly throughout development. Although two general types of grooves can be distinguished, significant differences are also present within the two categories.

The grooves of type 1 are often described as being X-shaped (Olesen, 2001). This is indeed the appearance in adults, in which these grooves are surrounded by four bounding structures (anterior, posterior, lateral, and median), which together impart the impression of an X-shaped groove. However, ontogenetic information reveals a more complicated situation. For example, in stage 1 specimens, there are five (not only four) spine-bearing lobes surrounding the grooves of type 1 (Fig. 12A), namely the anterior lobe 1, the antero-medial lobe 2, the postero-medial lobe 3, the postero-lateral lobe 4, and the antero-lateral lobe 5, which together yield a groove shape dissimilar to the letter X.

Differences are apparent already in stage 1 between the groove of the head shield and that of the maxillipedal segment (Fig. 12A). On the head shield, lobe 1 is more elongate on latero-median dimension than it is on the maxillipedal segment, lobe 2 is therefore placed almost medial and lobe 5 almost lateral. Lobe 1 of the head shield carries more than 10 spines along its rim, lobe 2 one spine, and lobe 3 at least four spines. The other two lobes lack spines. The spines of lobe 1 cover the ones of lobe 3, reaching beyond the rim of lobe 3. On the maxillipedal segment, lobe 1 is very dominant but does not extend far laterally and medially. It is equipped with less than ten spines. The spines merge near the edge of the lobe leaving no well-defined rim-spine border; the whole lobe therefore almost appears like a hand with opened fingers covering the groove. The spines reach onto lobe 2, 3, and 4. Two incipient humps on both lobes 3 and 4 indicate future spines.

In stage 4, five lobes are still apparent on both the grooves of the head shield and of the tergite of the maxillipedal segment (type 1 groove) (Fig. 12B). On the groove of the head shield, lobe 1 appears to carry not more spines than in the preceding stages, but this is difficult to judge since the spines do not arise from the direct rim but from slightly inside the groove. The spines appear relatively shorter than before and no longer reach onto lobe three. Lobe 2 appears to carry two spines. Lobe 3 now bears five or six spines, which now cover the spines of lobe 1 and reach the rim of that lobe. Lobe 4 carries at least three

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Fig. 11. Details of the sternitic region of *Derocheilocaris remanei*. A-D. Later developmental stages. A, Close up on the anterior part of the right paragnath (pgn) gripping around the edge of the mandible (mdb); B, Sternum with a median channel surrounded by the two paragnath humps (pgn) and the labrum (la); C, Arrangement of paragnaths (pgn), mandibles (mdb) and anterior part of the labrum (la) (posterior part removed); D, Sternum with paragnaths (pgn) and more posterior ventral region with clearly set off sternites between the maxilla (st mx2) and the maxilliped (st mxp); E, Stage 4; sternite of maxillipedal segment equipped with two pairs of backward oriented spiny combs (arrows); F, Stage 5; the spiny combs are absent.

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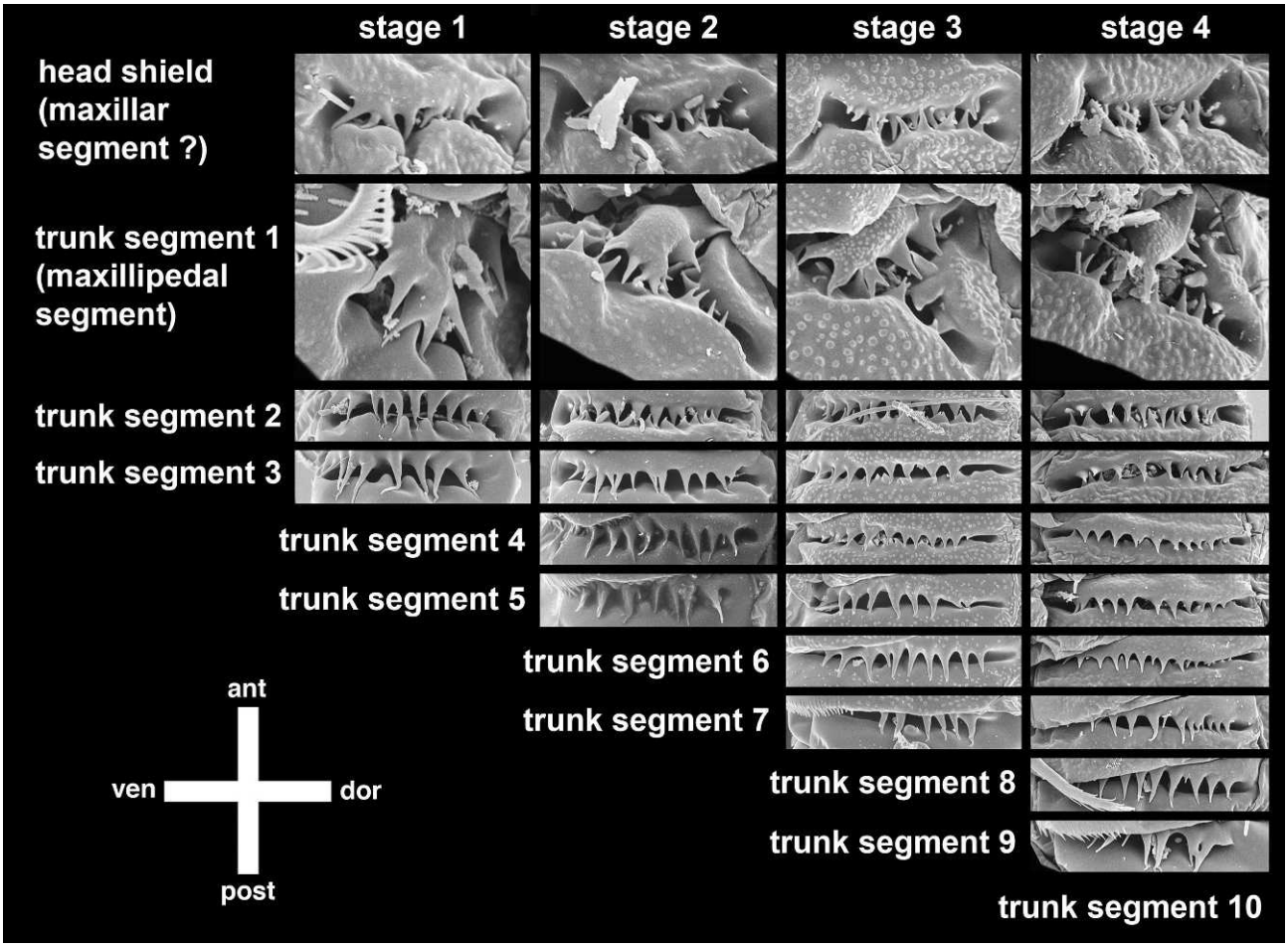


Fig. 13. Morphogenesis of the 'toothed furrows' from stages 1 to 4 of *Derocheilocaris remanei*; the cross indicates the orientation of the grooves: ant = anterior, post = posterior, ven = ventral, dor = dorsal.

spines that overreach the groove and touch lobe 1. Lobes 3 and 4 are almost continuous, the groove separating the two now being very reduced. Also the groove of the maxillipedal segment has changed. Lobe 1 is less dominant. It appears to have not more spines than before, but their positions are different. A well-defined rim boundary is now apparent, and the spines appear slightly shorter than before, only one of them touching the rim of lobe 3. Lobe 2 bears two spines, lobe 3 four spines, and lobe 4 three spines. Lobe 5 is small, with two spines, and is partly concealed by the antero-lateral area of the tergite, which is partly folded over it.

In stage 7 both type one grooves have reached their X-shape (Fig. 12C). The groove of the head shield appears to be surrounded by only four lobes. Based on the number of spines it can be concluded that the anterior lobe is still lobe 1, now with about eight spines, the medial lobe is lobe 2 (with two spines), but the posterior lobe appears to be a fusion product of lobe 3 and 4 (with seven spines together). Lobe 5 is still small and with two spines. The groove on the tergite of the maxilipedal segment looks different. Lobe 1 is more or less unchanged compared to stage 4, lobe 2 has now four spines; lobe 3 (with six spines) and lobe 4 (with four spines) are still well separated. Lobe 5 on the other hand is in fact no longer a functional lobe confining the groove. Instead two spines appear to arise from inside the groove between lobes 4 and 1.

In summary, both grooves of type one start from a rather similar condition of a complex folded groove surrounded by five lobes, after which both reach a condition where the groove is surrounded by four lobes giving the groove the typical X-shaped appearance. Yet the ontogenetic pathways of the two grooves are very different. While on the head shield two lobes fuse into a single one, on the maxilipedal segment one lobe becomes reduced.

The grooves on the tergites of the more posterior segments are simple, slit-shaped openings with marginal spines (type 2 groove) (Figs. 13, 14). During ontogeny the shape of the grooves changes relatively little, although they appear more "open" in earlier stages and more "closed" in later ones. This is coupled to the increase of the number of spines along the anterior and posterior margins of the grooves.

The grooves are quite different in appearance from anterior to posterior. These differences occur gradually along the trunk, yet for descriptive reasons the segments will be discussed in groups. The differences are not only apparent in the larvae, but also upon close inspection in the

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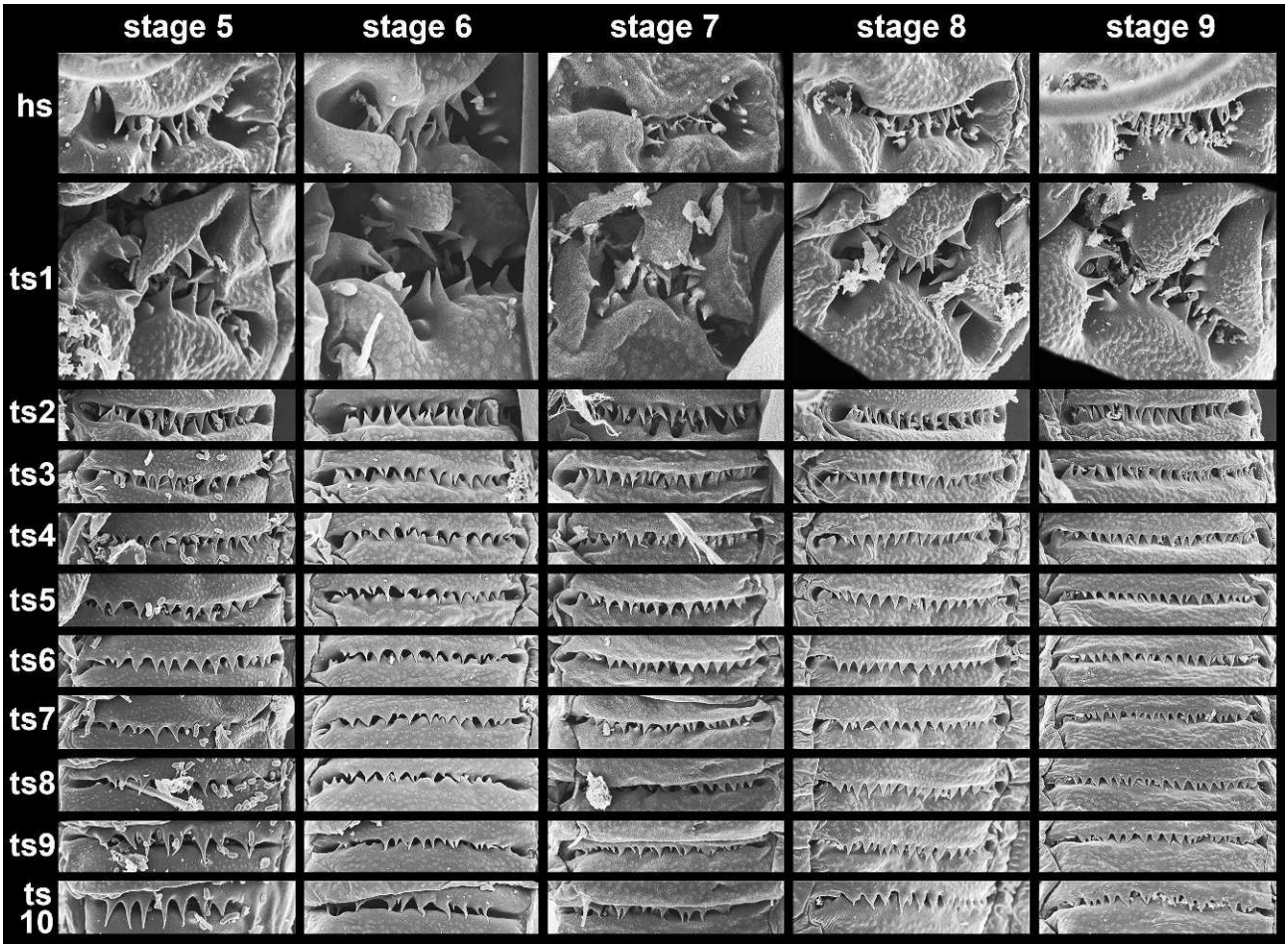


Fig. 14. Morphogenesis of the 'toothed furrows' from stages 5 to 9 of *Derocheilocaris remanei*; orientation of the grooves like in Fig. 13.

adult. The grooves of the trunk segments 2 through 4 are similar. The spines on the anterior and the posterior rim of the groove arise from ''inside'' the groove, below the ''edge''. The spines are arranged so that a spine from the posterior rim fit in the gap between two spines of the anterior and vice versa, which gives the entire arrangement a zipper-like appearance. This is best developed in the groove of trunk segment 2. In trunk segments 3 and 4, the spines on the anterior rim of the grooves are placed less deep into the groove, i.e., closer to its edge. Consequently, spines on the anterior rim cover the spines of the posterior rim partly.

The grooves of trunk segments 5 through 7 resemble the ones on trunk segment 3. The spines on the anterior rim of the groove arise from the outer edge, and cover almost entirely the spines arising from the posterior rim of the groove. The spines of the anterior rim reach over the groove and over the edge of the posterior rim. This is most apparent in the groove of trunk segment 7. Trunk segments 8 through 10 are again similar to the preceding segments, but here the spines of the anterior rim cover most of the groove so that almost no teeth of the posterior rim can be seen and the grooves appear almost closed.

Not only in the adult stage can differences be observed between the grooves of the posterior trunk segments, but also their developmental pattern is different. The development of the grooves of trunk segments 2 and 3 are similar. Grooves on both segments are present already from stage 1. The anterior rim is armed with 10 long, irregular spines reaching over the groove and the posterior rim (Fig. 15A, B). The spines are approximately cone-shaped with soft appearing slightly bent tips. About 3 incipient humps occur on the posterior rim. In stage 2, the spines of the anterior rim are slightly shorter than in stage 1. The anterior rim of the grooves is now invaginated slightly so that the spines insert below the edge, slightly inside the groove. On the posterior rim still only incipient humps are developed. Over the next two stages (3 and 4), the spines on the anterior become shorter and more triangular in shape. Their tips reach the posterior rim of the groove, but do not overlap it any longer. The number has increased slightly to about twelve. On the posterior rim the incipient humps have developed into about eight triangular spines. From stage 5 to 9 the number of spines increases further and the spines become strictly triangular in shape. Finally the entire arrangement appears like a zipper with the spines from the anterior and posterior rim interlocking.

The grooves of trunk segments 4 and 5 appear in stage 2. They largely resemble the grooves of trunk segments 2 and 3 in stage 1, but the anterior rim has only eight spines. In

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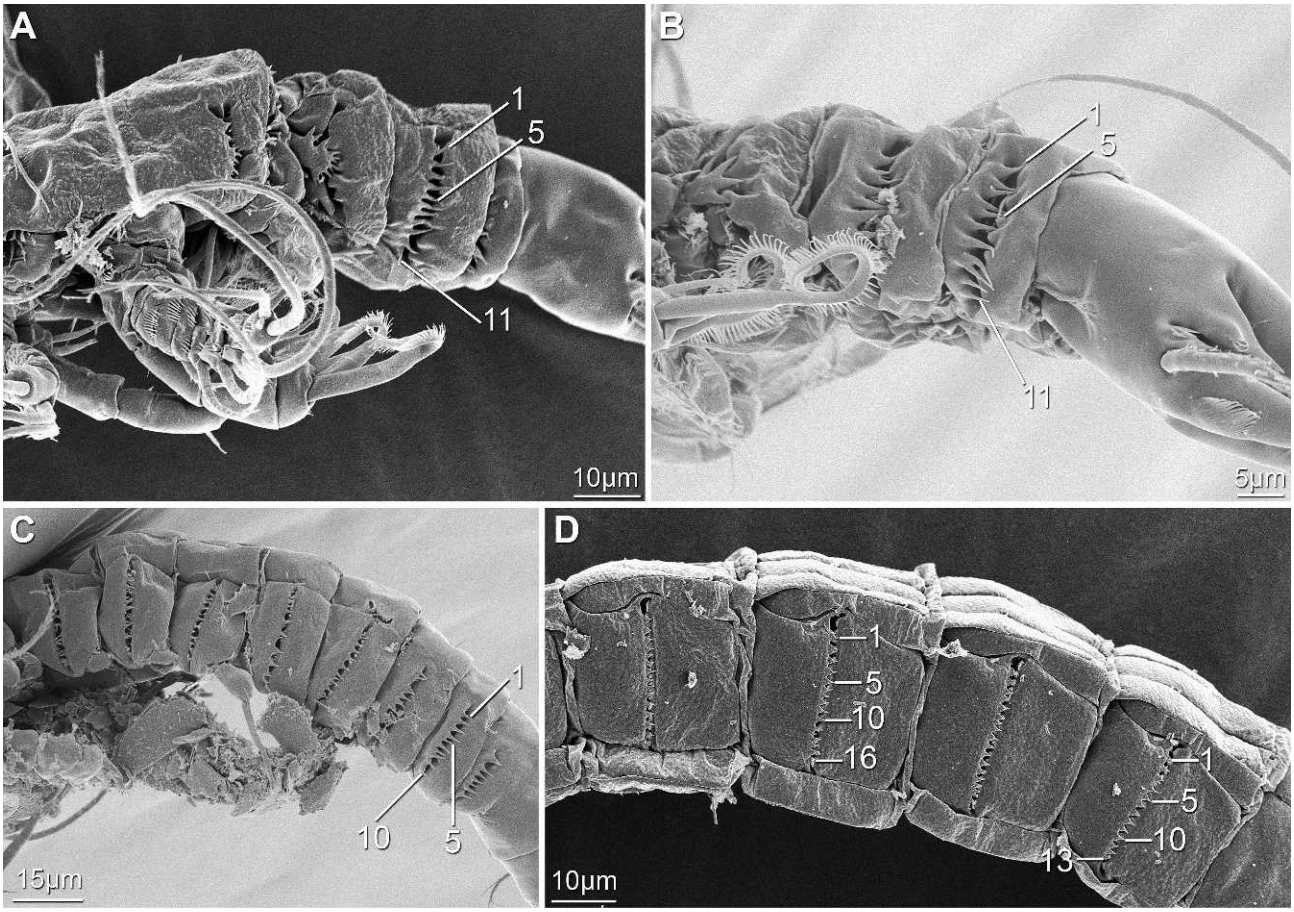


Fig. 15. Examples of 'toothed furrows' of *Derocheilocaris remanei* with deviating numbers of spines. A, Stage 1; on the furrow of the second trunk segment eleven spines are present compared to ten (Fig. 13); B, Stage 1; on the furrow of trunk segment three eleven spines are present instead of ten (Fig. 13); C, Specimen of stage 5; it has ten spines instead of eight on the groove on the ninth segment (Fig. 14); D, Adult specimen; it has 16 spines instead of 19 on the groove of trunk segment eight and 15 instead of 14 on trunk segment 10.

stage 3, the groove of trunk segment 4 reaches a state comparable to the more anterior grooves in the same stage. The groove of trunk segment 5 develops more slowly with its spines becoming strictly triangular one stage later than those of trunk segment 4.

Grooves 6 and 7 appear in stage 3. They resemble that of trunk segment 5 in stage 2, except for the less distinct humps on the posterior rim. The spines of the anterior rim reach over the rim of the posterior side during the entire ontogeny. Spines on the posterior rim reach their triangular shape in stage 7, but are difficult to spot as they are partly covered by the spines of the anterior rim.

Trunk segments 8 and 9 appear at stage 4, trunk segment 10 one stage later. At their first appearance the spines on the anterior rim of the grooves are relatively long and slender, but in the following stage they have already transformed into the triangular shape typical for later stages. The posterior rim remains covered by the spines of the anterior rim throughout the complete ontogeny. Distinct spines on the posterior rim are never developed.

The spine pattern exhibits a certain degree of variation between various specimens of the same stage in the examined material. We present here some examples where spines number deviate from what is shown in the overview figures (Figs. 13, 14). In the specimen of stage 1 shown in Fig. 13, the anterior rim of the second trunk segment is armed with nine spines, but there are also specimens with for example 11 spines (Fig. 15A, B, two specimens). Another example is a specimen of stage 5 that has 10 spines on the anterior rim of the trunk segment 9 (Fig. 15C) instead of 8 as seen in the overview figure (Fig. 13). Adults also exhibit variation. One specimen (Fig. 15D) bears 16 spines on the anterior rim of the 'toothed furrow' of trunk segment 8, instead of 19 in the specimen depicted in the overview figure (Fig. 14), and 15 on the anterior rim of the 'toothed furrow' of trunk segment 10 instead of 14 in the specimen in the overview table (Fig. 14). Such variation is important to register as spine patterns of the furrows have been used as diagnostic characters (cf. Hessler, 1971).

## Discussion

### Developmental Patterns in Mystacocarida

Mystacocaridans of the genus *Derocheilocaris* have been considered to be highly conservative in their adult morphology, while exhibiting significant variation in their ontogenetic sequences. This idea was founded on alleged

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Table 2. Correspondence of new and old staging systems and stage numbers for the ontogeny of *Derocheilocaris remanei*.

| Present investigation | Delamare-Deboutteville (1954) |
|---|---|
| 1 | 1?, 2? |
| 2 | 2?, 3 |
| 3 | 4, 5? |
| 4 | 6 |
| 5 | 7, 8 |
| 6 | ? |
| 7 | 9? |
| 8 | 9? |
| 9 | 10 |

differences between the ontogeny of *D. typica*, described by Hessler and Sanders (1966) and the ontogeny of *D. remanei*, described by Delamare-Deboutteville (1954). However, Cals and Cals-Usciati (1982) and Olesen (2001) pointed out that the validity of this difference, more precisely, the correctness of details of the ontogenetic sequence of *D. remanei*, might be questioned; they found no difference to the ontogeny of *D. typica* in their re-investigations of certain ontogenetic stages. Our results confirm this. Yet comparisons are slightly complicated due to different sets of terms applied by the various authors. For example, McLachlan (1977) (for *D. katesae*) apparently counted the (non-segmental) telson as a segment. He reported, therefore, stages with 4, 6, 8, 10, 11 post-cephalic segments instead of 3, 5, 7, 9, 10, which would be the numbers when not counting the telson as a segment. The latter manner of counting is preferred (see above).

The developmental sequence described here for *D. remanei* is basically the same as that found in three other species of Mystacocarida: *D. algoensis, D. typica,* and *D. katesae*. One difference is that McLachlan (1977) reports a lack of stage 5 for *D. katesae,* but this may be due simply to missing specimens of this stage in the samples. In general, the larval stages of *D. remanei* differ only from *D. algoensis* and *D. typica* with respect to certain setal patterns; the size differences of *D. katesae* may be due to latitudinal differences (cf. Rieger and Ruppert, 1978 and references therein). In conclusion, the ontogeny appears to be highly conserved within *Derocheilocaris*, but whether this applies to Mystacocarida as a whole is unknown since nothing is known about the development of the other mystacocaridan genus, *Ctenocheilocaris.*

The re-established larval sequence of *Derocheilocaris remanei* facilitates a direct comparison to the sequence of *D. remanei* described by Delamare-Deboutteville (1954) from which our observations differ in significant ways (Table 2).

Delamare-Deboutteville (1954) was an important work as it was the first attempt to describe the larval development of a mystacocaridan, yet it suffers from several misinterpretations. The first stage by Delamare-Deboutteville (1954) was described as lacking maxillulae. However, Cals and Cals-Usciati (1982) found that what appears to be the earliest stage indeed does possess a pair of unmodified maxillulae. We agree with Olesen (2001) and support the observations of Cals and Cals-Usciati (1982) since all examined specimens which segmentally correspond to the first stage of Delamare-Deboutteville (1954) have a pair of clear, but undeveloped maxillulae, as has been described also for other species of *Derocheilocaris* (see below). Delmare-Deboutteville's ''first stage'' does not exist; it was most likely a specimen of our stage 1 with the maxillulae concealed by the large labrum. The third stage of Delamare-Deboutteville corresponds to our stage 2. This is based on body segment number and developmental status of the maxillulae (cf. his fig. 3). Therefore, the second stage described by Delamare-Deboutteville must be interpreted as not existing as a separate stage. The few data given on the specimens assigned to this stage does not allow us to judge whether they might have belonged to our stages 1 or 2. The fourth stage of Delamare-Deboutteville is, unfortunately, not described in detail, but from the segmental condition it can only correspond to our stage 3. The fifth stage of Delamare-Deboutteville should have one segment more than his stage 4. There is no specimen in our material exhibiting such a segmental status. It probably also corresponds to our stage 3, as does his stage 4. The sixth stage of Delmare-Deboutteville corresponds segmentally to our stage 4. Also the developmental status of the maxillula reported by Delamare-Deboutteville (1954) is congruent with our stage 4 and, thus, supports this correlation. Stage 7 of Delamare-Deboutteville is described as having gained one segment more than stage 6. This most likely corresponds to our stage 5. The depicted morphology of stage 8 clearly corresponds to our stage 5, based on the morphology of maxilla and the maxilliped. The developmental stage 9 of Delamare-Deboutteville has the definitive (adult) segment number. It could, therefore, correspond to our stages 7 or 8. Delamare-Deboutteville's stage 10 probably corresponds to our stage 9, as both appear to represent the adult stage.

Given our new findings on *D. remanei*, the developmental pattern for Mystacocarida, or more accurately for *Derocheilocaris*, lacking as we do data for *Ctenocheilocaris*, appears to be as conserved as the adult morphology. Although we have to correct some terminological misunderstandings (the term 'coxa', see below), the sequence described for *D. typica* by Hessler and Sanders (1966) is applicable to all species of the genus, as we here present the exact same developmental pattern for *D. remanei*.

We have at least some data for other species of *Derocheilocaris*. Hessler (1971) reported that the first larva of *D. delamarei* Hessler, 1971 looks exactly like that of *D. typica*, except for a single seta at the third antennulary segment. The first two larvae of *D. angolensis* are similar to those of *D. typica* except for stage 2, in which the fourth antennular segment of *D. angolensis* lacks setae (Hessler, 1971).

The function of the 'toothed furrows' is still unclear, and the detailed documentation of the development of these structures provided here does not answer this question. We could speculate that the ''protected grooves'' might fulfill a function in respiration or osmoregulation. The interstitial environment is often subject to changes in salinity due to rain from above and saltwater in the pore system. The ability to osmoregulate should be important in such

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circumstances. Ultrastructural investigations of these surfaces could validate such a hypothesis by revealing epidermal layers specialized for such functions. Another possibility is that the furrows simply enhance the flexibility of the body, which is highly appropriate adaptation to the interstitial lifestyle of mystacocaridans. This is supported by the presence of oblique, longitudinal muscles that insert on the internal, cuticular invaginations of the furrows (Hessler, 1964; his fig. 33). The external spines along the rims of the furrows may then reduce the risk of detritus or other particles from entering these.

The fact that the furrows become more and more closed during the ontogenetic sequence raises the question as to whether the function of these structures changes throughout ontogeny. The serial homology of these structures along the body is beyond doubt because of the special morphology as in-foldings equipped with teeth. This is even true for the anterior two furrows that differ in shape from the more posterior ones. The similarities between the anterior and posterior furrows include: 1) spines at the anterior rim in a rather irregular pattern with more teeth added in the following stages, 2) teeth on the posterior rim that appear later, 3) teeth arrangement becoming more regular in later stages, and 4) teeth almost close the furrow in the latest stages. Because of these developmental and structural similarities, these furrows must be understood as serially homologous to the posterior ones despite any differences. Especially so since the furrow of the head shield in adults is more similar to the post-maxillipedal ones, differing only in the slight bifurcations at its very terminal end. The furrow of the maxillipedal segment differs from all other in exhibiting a pronounced X-shape with teeth also on the dorsal and ventral edges. As all Mystacocarida are very uniform in appearance and closely related groups do not possess 'toothed furrows', the evolution of these structures remains unknown, e.g., whether the furrows evolved originally in a stricter homonomous pattern, or whether the three different types of furrows (head shield, maxillipedal segment, and the series of more posterior ones) evolved at the same time.

## Taxonomic Status of Species

Since we have now established that no major developmental differences exist between the various species of *Derocheilocaris* for which developmental data is available, the available characters for differentiating between species decrease. Characters used by Hessler (1971) are, for example, tooth patterns at the furrows. As our observations on the development of the 'toothed furrows' demonstrate, not only the morphology of these furrows changes during development, but also even the number of teeth is variable (cf. Figs. 13-15). Furthermore, mystacocaridans have been studied in the past mainly with light microscopy, which does not allow a detailed view of tiny structures as does SEM. The reliability of the characters used for determining species of Mystacocarida so far may thus be questioned.

The basic difference between the two known genera, even though the descriptions of *Ctenocheilocaris* appear rather sketchy, is the presence of a small exopod of the maxilliped of *Derocheilocaris*, which is absent in *Ctenocheilocaris*. Dahl (1952) described the maxilliped of *Derocheilocaris galvarini* Dahl, 1952 as lacking both the endopod and exopod (cf. his fig. 2). This might mean that *D. galvarini* is in fact a species of *Ctenocheilocaris*, or alternatively that *Derocheilocaris* is paraphyletic with respect to *Ctenocheilocaris*. Also, a convergent loss of the exopod cannot be excluded. In any case, use of this character alone to differentiate *Derocheilocaris* from *Ctenocheilocaris* makes it likely that *Derocheilocaris* is paraphyletic with respect to *Ctenocheilocaris*, since only the latter is characterized by an apomorphy.

In summary, mystacocaridans are very distinct in their morphology when comparing them to other Crustacea, but identifying the individual species appears to be largely only possible if the locality is known. No proper phylogenetic analysis of mystacocaridans has been attempted and even the monophyly of the genera may be questioned. Based on the existing data it appears to be impossible to make any meaningful phylogenetic analysis without re-investigating all described species, especially the species of *Ctenocheilocaris* wherein developmental information is entirely lacking.

## "Coxal" Structures on Post-mandibular Appendages

The post-mandibular limbs of Mystacocarida have sometimes been referred to as possessing a coxa (Hessler and Sanders, 1966; Boxshall, 1997), but based on our SEM observations we find no support for this. The maxillula, maxilla, and maxilliped all exhibit a well-developed proximal endite, which is set off distally from the basipod and laterally from the arthrodial membrane. Laterally, there appears to be another sclerotised area within the arthrodial membrane, proximal to the basipod. Taken together these two sclerotised areas may be mistaken for a coxa, but since they are separate from each other, we believe it is not justified to name the proximal limb part a coxa. A coxa is usually defined as a separate, distinct limb segment, which is not present here. Also there is no evidence of a "precoxa" (contrary to Boxshall, 1997).

We question the assignment of the endites of the maxillula as given by Hessler and Sanders (1966) for *D. typica*. They assign two endites to what they call the coxa (which in our view does not exist) and two to the basipod. In contrast, the proximal endite is being set off from the rest of the series, while the remaining three all are part of the basipod (see Fig. 5D). The maxillula possesses 1 + 3 endites as seen not only on the maxillula of various Cambrian taxa such as the species of *Skara*, *Bredocaris admirabilis*, and *Rehbachiella kinnekullensis*, but also in extant species such as the cephalocaridan *H. macracantha* or the copepodan taxon *Thalestris* (see Walossek and Müller, 1998b, their fig. 12.11). Therefore, we conclude it was already present in the ground pattern of the Entomostraca sensu Walossek and Müller, 1998a (Waloszek, 2003; Maas et al., 2003).

Hessler (1971) described the maxilla as possessing five endites for *D. remanei remanei.* Olesen (2001) interpreted a maxilla as possessing four endites, but this assumption was based on a misleading specimen. The maxilla shown by Olesen (2001) only showed a weak differentiation between

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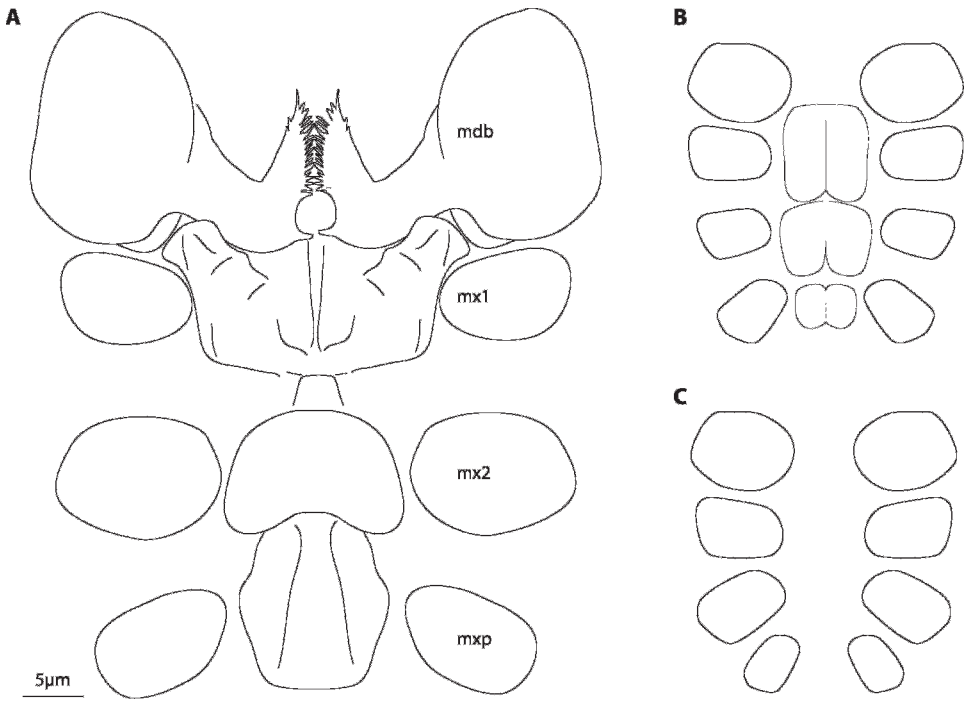


Fig. 16. Comparison of feeding apparatus arrangement of representatives of Copepodoida. A, Reconstructed arrangement of sternitic elements of the ventral region of the feeding apparatus of *Derocheilocaris remanei*.; partial areas redrawn from actual specimens; abbreviations: mdb = mandible, mx1 = maxillula, mx2 = maxilla, mxp = maxilliped; B, Principal arrangement of the feeding apparatus of †*Skara*; C, Principal arrangement of the feeding apparatus of copepodans; sternite details largely unknown. Note the position of the last limb (maxilliped) in A compared to the rotated position in B and C.

endites four and five, which had, therefore, been overlooked. We have based our investigation on more specimens and therefore re-establish the presence of five basipodal endites on the maxilla.

### Cephalo-thoracic Feeding Apparatus of the 'Copepodan Line' sensu Walossek and Müller (1998a)

The maxilla and maxilliped show interesting similarities in their development (Fig. 7), the earliest limb buds of the appendages (stage 4 for maxilla and stage 5 for maxilliped) are somewhat similar in appearance, but this might be explained by both manifesting an undifferentiated status. In the next stage (stage 5 for maxilla and stage 6 for maxilliped), the appendages are not only similar in shape, but also both have four basipodal endites. While there are obvious differences between the fully developed limbs, these developmental similarities point to a serial homology of these appendages, which we interpret as demonstrating the ''mouthpart'' nature of the maxilliped, i.e., the presence of the cephalo-thoracic feeding apparatus. Walossek and Müller (1998a) suggested such an apparatus as a synapomorphy for Mystacocarida, Copepoda, and *Skara*. For this cluster of taxa we propose the name Copepodoida. The name highlights specific features found exclusively in copepodans, and, we think, mystacocaridans and *Skara*.

The orientation of the maxillipeds might help to resolve the basal trichotomy of Copepodoida (cf. Walossek and Müller, 1998a). While the cephalo-thoracic apparatus is ''closed'' in *Skara* (Fig. 16B) and copepodans (Fig. 16C), it ''remains (plesiomorphically?) open'' in mystacocaridans (Fig. 16A). This means that the maxilliped, which is incorporated into the cephalo-thoracic feeding apparatus in Mystacocarida, is positioned (almost) with its functional axis in line with its real axis, i.e., its anterior surface is truly facing anteriorly (Fig. 16A). In *Skara* and Copepoda, the maxillipeds are rotated (Fig. 16B, C). Their median surface almost faces anteriorly, while the anterior side faces more laterally. Additionally, the maxillipeds in *Skara* and Copepoda are shifted closer together, i.e., the distance between the median surfaces is smaller than in the maxillae. In contrast, the maxillipeds are widely separated in *D. remanei*, being inserted lateral to a broad sternitic area.

Therefore, the cephalo-thoracic feeding apparatus incorporating a specialised maxilliped characterizes the ground pattern of Copepodoida, but the positional shift and rotation of the maxilliped might be an apomorphic condition uniting *Skara* and Copepoda, while Mystacocarida retain the plesiomorphic position of this appendage (for other supposed arrangements cf. Walossek and Müller, 1998a; Olesen, 2001). Another similarity of *Skara* and Copepoda is the loss of the exopod of the maxilliped.

Schram et al. (1997) suggested a position of Cycloida close to some of the taxa mentioned above. They proposed a sister group relation between Copepoda and Cycloida, with Mystacocarida being the sister group to the unnamed monophylum formed by both. *Skara* was not placed closely to this group, as it was coded as not possessing a maxilliped in the matrix for the phylogenetic analysis. The status of the last limb of *Skara* as a maxilliped is, in our view, convincing since the similarity to the maxillula and maxilla is even closer than in Mystacocarida. But, admittedly, the total absence in *Skara* of limbs posterior to the maxillipeds, or the presence of

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simple limb buds only (Mystacocarida), complicates the interpretation as a maxilliped in both taxa. Whether Cycloida can be placed either as a sister taxon to Copepodoida, or even as a member of the in-group, is seen by us as highly dubious. The enigmatic cycloids have been interpreted in diverse ways (see for example Dzik, 2008), and even its assignment to Maxillopoda must be seen as uncertain.

### Naupliar Process of the Antenna

The coxal naupliar process in *Derocheilocaris* (Mystacocarida) has a special morphology and appears in some respects similar to the coxa exhibited by the different representatives of the Cambrian taxon *Skara*. In *D. remanei,* the process comprises two spines arising medially from the coxal body, both bifurcating about halfway to the tip that in turn leads to four spine tips distally. In *S. anulata* Müller, 1983 and *S. minuta* Müller and Walossek, 1985 there are four spines arising directly from the antennal coxa (the exact condition is unclear for *S. hunanensis* Dong, 2007 in Liu and Dong, 2007). Whether these four spines are truly homologues of the naupliar process in *D. remanei* remains problematic. Not only the structural difference of four spines versus two bifurcating spines must be considered here, but also the ontogenetic component. In *D. remanei* the process is only present in the larval stages, while it is present in the assumed adult stages in the species of *Skara*. This could also hint at a paedomorphic condition for *Skara*, but that remains speculative. Further investigations of the phylogeny of Copepodoida are necessary before judging this issue.

### Paragnath Morphology as a Character of Possible Phylogenetic Relevance

The paragnaths are autapomorphic structures at the evolutionary level of Labrophora. They arise from the sternum. The humps of the paragnath form a channel between them and function as guiding structures for the mandibles (Maas et al., 2003; Waloszek, 2003; Waloszek et al., 2007).

The paragnaths can be almost appendage-like, for example in Lophogastrida (Richter, 2003) or Amphipoda (Wolff and Scholtz, 2006; Mayer et al., 2008, 2009), and have therefore occasionally been interpreted as true appendages. However, the developmental fate of the paragnaths indicates their evolutionary origin to have been as outgrowths of the sternum (see Wolff and Scholtz, 2006). The paragnaths are possibly homologous to the superlingua of Insecta and Myriapoda (Wolff and Scholtz, 2006). Documenting paragnath morphology might, therefore, prove to be important for inferring the exact systematic position of these taxa.

The special morphology of the paragnaths of mystacocaridans has not been reported previously. The paragnaths of *D. remanei* seemingly fulfil the guiding function of the mandibles as in other Crustacea, but their special C-shaped morphology must serve to restrict the movement of the mandibles more than in any other crustacean that we know of. We could find no precise descriptions of the morphology of the paragnaths in the literature for the presumably closely related Copepoda. In *S. anulata* and *S. minuta*, which has been described in detail [the third described species, *S. hunanensis*, has not yet been depicted in enough detail to obtain such information, cf. Liu and Dong, 2007], the paragnaths appear to have a simple, probably plesiomorphic morphology, being developed as simple humps on the sternum (Müller and Walossek, 1985, their fig. 16.). The paragnaths are again an example of some aspects of the 'Orsten'-type fossils being documented in more detail than many extant species.

## Conclusions

The result of our investigation of the developmental sequence of *D. remanei* can be summarized as follows:

- The developmental pattern of the different mystacocaridan species does not differ significantly (as previously thought); it is as conservative as the adult morphology.
- Certain characters, which previously have been used to distinguish species within Mystacocarida, such as the tooth arrangement of the 'toothed furrows', are subject to intra-specific variation and ontogenetic change.
- The development of the specialized cephalo-thoracic feeding apparatus of Mystacocarida is similar to those of the Cambrian taxon *Skara* as well as Copepoda. Based on this complex apomorphic character, the inclusion of Mystacocarida into the 'copepodan line' sensu Walossek and Müller (1998a) is supported herein, and a taxon Copepodoida is erected embracing Copepoda, Mystacocarida, and *Skara*.

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