

†*Henningsmoenicaris scutula*, †*Sandtorpia vestrogothiensis* gen. et sp. nov. and heterochronic events in early crustacean evolution

Joachim T. Haug, Andreas Maas and Dieter Waloszek

Biosystematic Documentation, University of Ulm, Helmholtzstrasse 20, D-89081 Ulm, Germany

ABSTRACT: A detailed account of the morphology and ontogeny of the late Middle Cambrian crustacean †*Henningsmoenicaris scutula* is presented. Ten successive ontogenetic stages could be recognised in the material collected from various localities in Sweden. Morphogenetic changes include the development of a pair of stalked lateral eyes and the increase in the number and size of appendages and their setal armature. Notably, early stages lack ‘proximal endites’ on all post-antennular appendages; such a spine-bearing endite has previously been thought to appear simultaneously on these limbs. In †*H. scutula* a single functional endite appears on the third limb in an advanced stage; an additional endite appears on the second limb and, subsequently, further endites appear on more posterior limbs. Furthermore, a single specimen of †*Sandtorpia vestrogothiensis* gen. et sp. nov. is described. Based on this new information and data of other ‘Orsten’ taxa, particularly those assigned already to the early evolutionary lineage of Crustacea, a small-scale computer-based phylogenetic analysis was performed. This resolved the basal branchings of Crustacea s. l. as follows: †*Oelandocarididae* (= †*Oelandocaris oelandica*+ †*H. scutula*+ †*S. vestrogothiensis*)+ (†*Cambropachycopidae* (= †*Goticaris longispinosa*+ †*Cambropachycope clarksoni*))+ (†*Martinsonia elongata*+ Labrophora (= †*Phosphatocopina*+ Eucrustacea))). Plotting ontogenetic data on the phylogram and comparing the ground pattern at every node led to the detection of three peramorphic heterochronic events in the evolutionary lineage towards Eucrustacea.



KEY WORDS: 4D modelling, ground-pattern reconstruction, morphology, ontogeny, Orsten-type preservation, peramorphosis, phylogeny, ‘proximal endite’

In 1990, Waloszek & Müller described three new arthropod species from the Cambrian of Sweden, †*Goticaris longispinosa*, †*Cambropachycope clarksoni* and †*Henningsmoenicaris scutula*. These taxa, together with another ‘Orsten’ species, †*Martinsonia elongata* Müller & Waloszek, 1986, were identified as derivatives of the stem lineage (‘stem-lineage crustaceans’) leading towards the crown group, the Eucrustacea. Waloszek & Müller (1990) based their description of the new species on two or three (type) specimens for each species, but it was already clear that the ‘Orsten’ material contained more specimens (see Fig. 3 and Supplementary Material). Waloszek & Szaniawski (1991) expanded the unresolved assemblage of stem taxa by including †*Cambrocaris baltica* from the Upper Cambrian of Poland. Identification of †*Oelandocaris oelandica* Müller, 1983 as another derivative of the Eucrustacea stem lineage (Stein *et al.* 2005, 2008; Waloszek *et al.* 2007), and the ongoing discussion about the phylogenetic composition and even validity of Crustacea (e.g. Moura & Christoffersen 1996; Glenner *et al.* 2006) demanded a re-investigation of all currently known species that were originally considered to be ‘stem’ crustaceans.

This is the third recent investigation dealing with this issue. The detailed re-study of †*Oelandocaris oelandica* (Stein *et al.* 2008) and a detailed study of the ontogeny and morphology of †*G. longispinosa* and †*C. clarksoni* (Haug *et al.* 2009), revealed several ontogenetic stages in the known material. The present work re-evaluates †*Henningsmoenicaris scutula* and includes the description of a new species, putatively also a ‘stem-lineage

crustacean’; more precisely, a derivative of the labrophoran stem lineage according to our current understanding of crustacean evolution and phylogeny (Fig. 1; see e.g. Maas *et al.* 2003; Siveter *et al.* 2003; Zhang *et al.* 2007).

In recent years, almost all possible phylogenetic combinations of taxa have been proposed within Arthropoda (in most cases more precisely Euarthropoda; e.g. Dohle 2001; Hwang *et al.* 2001; Pisani *et al.* 2004; Strausfeld *et al.* 2006; Regier *et al.* 2008). The main problem in establishing a stable phylogeny for this group has remained where to place the insects and myriapods or their subunits (Fig. 2). Insects, for example, were proposed to be the sister group to Myriapoda (e.g. Ax 1999) or Progoneata (Kraus 2001), in both cases being members of the Tracheata (=Atelocerata), but were also placed as sister group to Crustacea or crustacean in-groups, like Malacostraca or Remipedia (e.g. Fanenbruck *et al.* 2004), Branchiopoda (Glenner *et al.* 2006) and Ostracoda (Newman 2005). Better knowledge of the crustacean stem lineage is, therefore, seen as an essential issue for helping to resolve relationships within Euarthropoda more precisely.

The aims of the present paper are:

1. To give a detailed description of the ontogeny of †*Henningsmoenicaris scutula* by sorting the material into successive developmental stages and constructing a 4D model (term from Haug *et al.* 2009). A new species, †*Sandtorpia vestrogothiensis*, is also described and a 3D model (the fourth dimension is lacking here) of the single specimen at

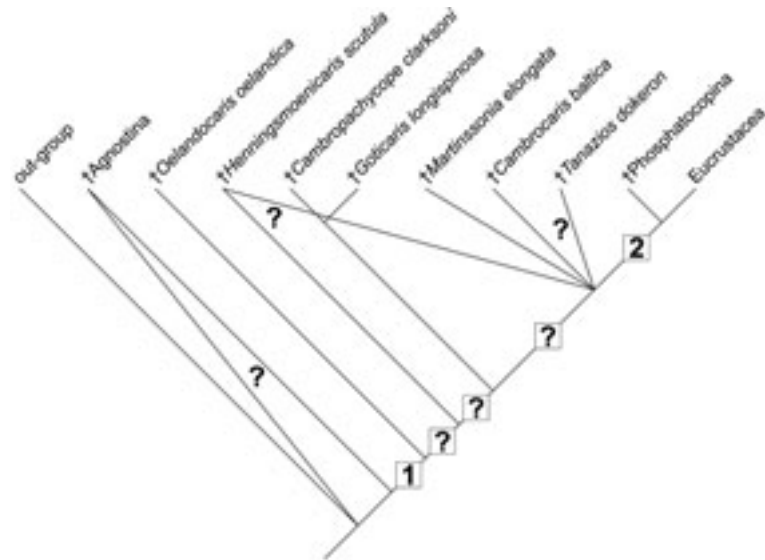


Figure 1 Phylogram summarising current uncertainties in the early evolutionary lineage of Crustacea. Question marks refer to uncertain relationships, question marks in boxes refer to unknown or uncertain autapomorphies. Sets of autapomorphies of recognisable monophyletic units according to Maas *et al.* (2003), Waloszek (2003a) and Zhang *et al.* (2007): (1) Autapomorphies of Crustacea s. l.: presence of a 'proximal endite' on the third appendage, multi-annulated exopods with exclusive median setation on second and third appendage; (2) Autapomorphies of Labrophora: coxae on second and third appendages, labrum with slime glands and sensilla, fused sternum with paragnath and fine setation.

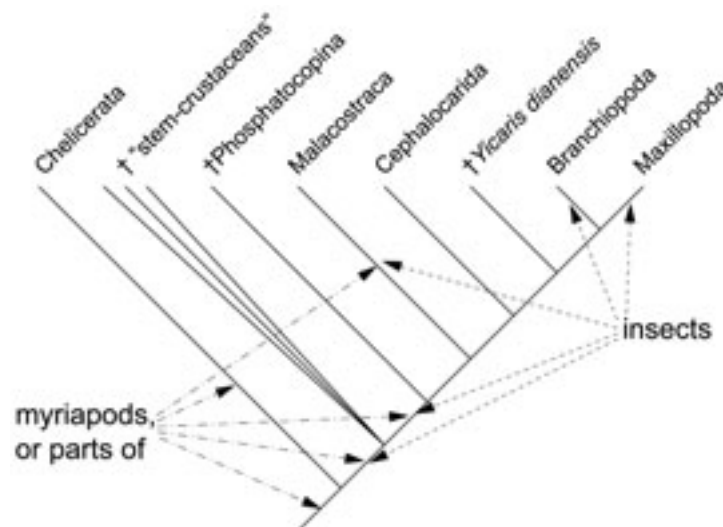


Figure 2 Phylogram of euarthropod phylogeny, displaying the different possible positions of insects and other tracheates that are recently and currently discussed in the literature.

hand is presented, adding to the information on early crustaceans.

2. To use this new information in a phylogenetic analysis of the early branching events within Crustacea.
3. To discuss, based on these results, character evolution along the evolutionary lineage of Crustacea with an emphasis on identifying heterochronic events.

1. Material and methods

1.1. Material

The 40 specimens of †*Henningsmoenicaris scutula* (Fig. 3; Table 1) and the single specimen of †*Sandtorpia vestrogothiensis* gen. et sp. nov. investigated in this study are part of the large collection of material made by Professor Klaus J. Müller, Bonn, during several field trips in Sweden between 1975 and 1980. Specimen UB W 320 is from the †*Ctenopyge tumidal*

affinis/linmarssonibisulcata Zone of the Furongian (the former Zone 5c, d of the Swedish Upper Cambrian, cf. Peng *et al.* 2004). All other specimens are from the former *Agnostus pisiformis* Zone. As the faunas differ significantly between Zones 1 and 5 (for more details see Maas *et al.* 2003), it is likely that the assignment of UB W 320 to Zone 5 might be a sorting error, thus all specimens may better be interpreted as stemming from the former *Agnostus pisiformis* Zone ('late middle Cambrian'). The specimens are part of the collections of the Steinmann Institute of Geology, Mineralogy and Palaeontology, University of Bonn, but are currently kept at the University of Ulm.

1.2. Methods

Collecting, processing of the rock, and isolation of the material had been done already in Bonn in the late 1970s and 1980s (for details see e.g. Müller 1985, 1990; Maas *et al.* 2006). First photographs were done in Bonn using a CamScan SEM.

Further scanning was done at the Central Unit for Electron Microscopy of the University of Ulm using a Zeiss DSM 962. SEM images have been processed using the image-processing software Adobe Photoshop (version CS 1[™]) and the free software GIMP. The depth of focus of some images has been enlarged using the free available image fusion software CombineZM.

Reconstructions of the morphology of all stages were developed using the 3D modelling software Blender (e.g. Haug *et al.* 2009). For the reconstructions, all limbs were first redrawn in anterior view from SEM micrographs, and subsequently adjusted into the missing third dimension. After all limbs had been completed, the body was, likewise, first drawn in lateral view and then adjusted in body width. In the next step, the limbs were assembled to the body proper. All spines/setae, which are mostly broken off close to their base in the actual specimens, were drawn out to achieve their conical shape. However, because the true length could only be estimated, all reconstructed lengths of spines have to be seen as estimates and mostly minimum lengths (numbers are more trustworthy). If limbs or parts of limbs were missing in a stage to be reconstructed, they were obtained from earlier stages. This practice is justified, because limb morphology turned out to vary only slightly between the stages, at least from one stage to the next. The resulting models remain estimates but proved to be very appropriate for general comparisons.

Morphometric data were taken mainly from the head shield, since many specimens are known only from their bowl-shaped shields, often partly preserved with a coarse filling, giving the idea of the position of the former appendages but lacking details. Measurements were made on the SEM images to the nearest 5 µm. This was precise enough to draw conclusions from the data, as experienced from various other such studies on 'Orsten' forms (e.g., Müller & Walossek 1985, 1987, 1988; Walossek 1993; Maas *et al.* 2003; Stein *et al.* 2008; Haug *et al.* 2009). The resulting diagram (Fig. 4) and other line drawings were drawn digitally using Adobe Illustrator CS[™] and processed in the free available software Inkscape 0.45.

1.3. Theoretical concepts

1.3.1. Terms applied to structures. As has been pointed out earlier (Haug *et al.* 2009) the use of specific terms within Euarthropoda can be problematic. Simonetta & Della Cave (1981) once stated: 'Uniform nomenclature for all arthropods is highly desirable so that homologous structures may be designed by the same term'. This, however, is far from being in reach. One problem is that the group-specific terminology is strongly functionally based and often incompatible with that of other groups. Accordingly, the present authors adopted in the main the terminology proposed by Walossek (1993) for Crustacea and Arthropoda in general and discussed and adjusted in Haug *et al.* (2009). All post-antennular appendages are simply numbered consecutively to restrict more specific terms to in-group crustaceans, adopting the arguments of Stein *et al.* (2008) and Haug *et al.* (2009).

1.3.2. The stem-lineage concept. Ax (1984, 1985a) defined two different types of stem lineages, the 'direct' stem lineage and the 'assembled' ('zusammengesetzt') stem lineage. A direct lineage is one which extends from one node to the next. An assembled stem lineage has one or more branchings of species known only as fossils along this lineage. Ax (1985a) also stated that these branchings might branch further to form larger groups, which possess autapomorphic characters. He did not, however, accept any of these branches as a valid sister taxon to the next piece of a lineage leading towards a group that includes extant taxa (crown group, which is automatically a

monophylum; see also Donoghue 2005 for discussion of this matter and references therein).

In the view of the present authors, this restriction leads to an unequal treatment of fossil species, underestimating the value of fossil data. It also neglects the nodes along such an assembled lineage, and the characters (ground pattern) developed in them. All features are simply accumulated in the stem species of the crown group, which prevents resolution of character evolution. To overcome this deficiency, the term 'derivatives of the stem lineage' (somehow equal to the 'plesion' concept as developed by Patterson & Rosen 1977) has been adopted for a number of taxa (†*O. oelandica*, †*H. scutula*, †*Sandtorpia vestrogothiensis* gen. et sp. nov., †*G. longispinosa*, †*C. clarksoni*, †*M. elongata* and †*Cambrocaris baltica*). In our view the stem-lineage concept is only appropriate while exact relationships of fossils remain unclear. As soon as the relationships of a lineage by paired groupings (sister-group relationships) based on synapomorphies are resolved, it is no longer useful, or rather not appropriate, to use the term stem-lineage derivative (or plesion). As a consequence of this, there will be a switching point within this work. The term 'derivative of the stem-lineage of Crustacea' will be used until the phylogenetic analysis resolves the relationships of the taxa; but from that point on, the term will be avoided for those taxa receiving a clear position. Again, it is emphasised that a general distinction in the systematic treatment of fossil and Recent species, as often emphasised with the term 'stem' (see Donoghue 2005 for references), is rejected, also because the often-claimed difference through incomplete knowledge of fossil taxa in fact also holds for most extant species (Wägele 2000).

1.3.3. Ontogeny as a character in phylogenetic systematics and evolution. Hennig (1965) already stated that each 'semaphoront' (i.e. every time slice of an individual), bears valuable phylogenetic information. This concept is easily applicable to arthropods with their distinct moulting stages (=distinct semaphoronts), and it is not surprising that ontogenetic data of fossil and extant crustaceans have been demonstrated to provide a significant phylogenetically informative signal (e.g., Høeg 1992; Walossek 1993; Dahms 2000; Maas & Waloszek 2001; Maas *et al.* 2003; Olesen 2004, 2007; Haug *et al.* 2009). The phylogenetic value of ontogenetic information has been repeatedly highlighted for other metazoans also, for example for molluscs and other spiralian (e.g. Wanninger & Haszprunar 2002; Nielsen *et al.* 2007; Wollesen *et al.* 2007). The present authors regard it as not only important, but indispensable, to include ontogenetic information in any kind of phylogenetic analyses, particularly for Euarthropoda. Yet this has been more or less completely avoided, mainly in computer-based phylogenetic analyses, as it seems to be difficult to code such characters (e.g., Humphries 2002).

Developmental data of fossil species are rarely noted or, if present, they are neglected or hardly recognised. An additional problem is that some data are simply not obtainable from most fossil taxa. The exquisitely preserved 'Orsten' fossils are an exception. Yet, as Wills (1998) stated, 'Orsten' fossils are difficult to include in phylogenetic analyses, as they are mainly preserved in the form of larval stages and their correct evaluation would necessitate the inclusion of larval information from other taxa. Instead of doing so, 'Orsten' fossils are, however, either simply neglected or considered to supply little information because of their larval nature (e.g., Wills 1998; particularly Boxshall 2007). By contrast, the presence of larvae and even series of developmental stages in the 'Orsten' is regarded as one of the greatest strengths of this exceptional palaeontological material, and of enormous value for understanding the phylogeny and evolution of Crustacea and Arthropoda in general. Besides this, small size does not

necessarily imply a larval state (examples: †Skaracarida and †*Bredocaris admirabilis* Müller, 1983; see Müller & Walossek 1985, 1988) and an understanding of morphogenesis is of great significance in understanding evolutionary processes, whether it is the recognition of single structures (e.g., the ‘proximal endite, see Walossek & Müller 1990, or epipodites, see Zhang *et al.* 2007; Maas *et al.* 2009) or structural complexes (e.g., the evolution of the cephalic feeding and locomotory system, e.g., Stein *et al.* 2005; Waloszek *et al.* 2007).

1.3.4. Heterochrony. Heterochrony has been stated to represent one of the driving forces of evolution in a number of biological textbooks (e.g. Wehner & Gehring 1995; Campbell 1998; Futuyma 1998; Freeman & Herron 2004; Kull 2007). Again, heterochrony has had a profound impact on palaeontology, shedding new light on evolutionary pathways for example in trilobites (e.g. McNamara 1978, 1981, 1983, 1986; Edgecombe & Chatterton 1987; Ramsköld 1988). However, it seems that the concept of heterochrony has been quite misunderstood; it is evident that in many textbooks the concept of heterochrony has not been clearly defined (for a summary see, e.g., Webster & Zelditch 2005 and references therein). All in all, the idea of heterochrony is quite well known, especially neoteny, but the methods of identifying heterochronic events in evolution are not well developed. Therefore, this present paper aims to analyse how heterochrony may have affected early crustacean evolution, and discuss how it can be detected and used for phylogenetic analyses.

2. Systematic palaeontology of

†*Henningsmoenicaris scutula* (Walossek & Müller, 1990)

Arthropoda von Siebold & Stannius, 1845
Crustacea Brünnich, 1772
Oelandocarididae tax. nov.

Diagnosis. Small-sized Crustacea. Head comprising five appendage-bearing segments. Antennula large, functioning for swimming and feeding, original median setation directed anteriorly; second and third appendage sub-equal in younger instars, more differentiated in later stages. Exopods of these two appendages multi-annulated, but with only a few elements. Exclusive median setation, two setae on the sub-terminal, three on the terminal element. Proximal endites appear late in ontogeny, at first on the third appendage. Posterior appendages sub-equal from fourth one onward. In later instars these appendages have bipartite exopods. Proximal triangular portion of the exopod is articulated against the proximal endopod portion, the basipod, and the basal arthrodistal membrane of the limb.

†*Henningsmoenicaris scutula* Walossek & Müller, 1991

1990 *Henningsmoenia* n. gen. – Walossek & Müller 1990, p. 425 (non Schallreuter, 1964 [Ostracoda]).

1991 *Henningsmoenicaris* n. gen. – Walossek & Müller p. 138 (pro *Henningsmoenia* Walossek & Müller, 1990 non Schallreuter, 1964 [Ostracoda]).

Type species. Type species by original designation: *Henningsmoenia scutula* Walossek & Müller, 1990 [= *Henningsmoenicaris scutula* (Walossek & Müller 1990)]

†*Henningsmoenicaris scutula* (Walossek & Müller, 1990)

- v* 1990 *Henningsmoenia scutula* n. sp. – Walossek & Müller, pp. 413, 414, 416, 417, 419, 422–424, 426; fig. 4 [UB 101, 102, 103], 5, 7; table 2.
- v 1991 *Henningsmoenicaris scutula* (Walossek & Müller 1990) – Müller & Walossek, pp. 289, 291; fig. 7 [UB 101], 15.
- . 1991 *Henningsmoenicaris scutula* – Walossek & Szaniawski, pp. 372, 375.
- . 1992 *Henningsmoenicaris scutula* (Walossek & Müller, 1990) – Walossek & Müller, pp. 305, 307.
- . 1996 *Henningsmoenicaris* Müller & Walossek 1991 – Hou *et al.*, p. 1141.
- . 1998a *Henningsmoenicaris scutula* (Walossek & Müller, 1991) – Walossek & Müller, pp. 193–197, 201, 206.
- . 1998b *Henningsmoenicaris scutula* (Walossek & Müller, 1990) – Walossek & Müller, pp. 140, 142.
- . 1998 *Henningsmoenicaris scultata* – Schram & Hof, pp. 241, 242; table 6.1, 6.3; figs 6.8–6.11 [sic!].
- . 1999 *Henningsmoenia* – Fryer, p. 8 [referred to species].
- . 1999 *Henningsmoenicaris scutula* (Walossek & Müller, 1990) – Walossek, pp. 9, 11; fig. 5
- . 2000 *Henningsmoenicaris* – Dahms, p. 94 [referred to species].
- . 2001 *Henningsmoenicaris* – Chen *et al.*, fig. 4 [referred to species].
- . 2003 *Henningsmoenicaris scutula* (Walossek & Müller, 1990) – Maas *et al.*, pp. 13, 182, 185, 186, 189; table 2; fig. 69.
- . 2003 *Henningsmoenicaris scutula* (Walossek & Müller, 1990) – Siveter *et al.*, p. 24; fig. 7.
- . 2003a *Henningsmoenicaris scutula* (Walossek & Müller, 1990) – Waloszek, pp. 69, 70.
- 2003b *Henningsmoenicaris* – Waloszek, fig. 5–1.
- non 2004 *Henningsmoenicaris scutula* – Schram & Koenemann, fig. 19.9 [= *Cambropachycope clarksoni* Walossek & Müller, 1990].
- . 2005 *Henningsmoenicaris scutula* (Walossek & Müller, 1990) – Maas & Waloszek, fig. 8.
- v 2005 *Henningsmoenicaris scutula* (Walossek & Müller, 1990) – Stein *et al.*, pp. 57, 60, 64, 68; figs 5e [UB W 266, is erroneously labelled as destroyed], 5f, 7.
- v 2005 *Henningsmoenicaris scutula* (Walossek & Müller, 1990) – Waloszek & Maas, p. 517; fig. 3C [UB W 130].
- . 2006 *Henningsmoenicaris scutula* (Walossek & Müller, 1990) – Maas *et al.*, p. 275.
- . 2007 *Henningsmoenicaris scutula* Walossek & Müller – Waloszek *et al.*, figs 3, 5d.
- 2007a *Henningsmoenicaris* – Siveter *et al.*, p. 2105 [referred to species].
- . 2007 *Henningsmoenicaris scutula* – Haug *et al.*, Abstract 75.
- . 2008 *Henningsmoenicaris scutula* (Walossek & Müller 1990) – Stein *et al.*, pp. 461, 464, 466, 470, 481, 483.

Locus typicus. Gum at Kinnekulle (r 03525 h 89250), Västergötland, Sweden.

2.1. Original material

The original description of the species by Walossek & Müller (1990) was based on three specimens. The first specimen (UB 101) is an almost completely preserved representative of the first larval stage. The second one, the holotype UB 102, is the most complete specimen of the tenth stage according to the staging system developed in the present paper and, therefore, represents the ontogenetically oldest known stage preserved with relatively complete information. The third specimen (UB 103) is a trunk fragment that belongs to an even later developmental stage. All three specimens proved to be well chosen as they turned out to mark the outlines of the ontogenetic

Table 1 Known specimens of †*Henningsmoenicaris scutula* (Walossek & Müller, 1990). 1=specimen number; 2=repository number (preface UB . . .); 3=sample number; 4=stratigraphic zone; 5=locality; 6=developmental stage; 7=measured length of shield in μm ; 8=measured width of shield in μm .

1	2	3	4	5	6	7	8
2581	101	6414	1	Falbygden–Billingen, Gum (Kinnekulle)	1		
2991	W 305	6417	1	Falbygden–Billingen, Gum (Kinnekulle)	1		
4057	W 306	6761	1	Gum (Kinnekulle)	1		
4099	W 307	6761	1	Gum (Kinnekulle)	1		
4123	W 308	6761	1	Gum (Kinnekulle)	1		
4356	W 309	6409	1	Falbygden–Billingen, Gum (Kinnekulle)	1		
4577	1572	6763	1	Gum (Kinnekulle)	1	190	125
4578	W 311	6763	1	Gum (Kinnekulle)	1		
8963	W 312	6763	1	Gum (Kinnekulle)	1	180	120
9552	W 130	6750	1	Gum (Kinnekulle)	2	180	125
2992	W 313	6417	1	Falbygden–Billingen, Gum (Kinnekulle)	3	240	170
2995	W 314	6417	1	Falbygden–Billingen, Gum (Kinnekulle)	3		
3565	W 315	6761	1	Gum (Kinnekulle)	3	265	165
4315	W 316	6763	1	Gum (Kinnekulle)	3	280	175
4532	W 317	6784	1	Gum (Kinnekulle)	4		
4555	W 318	6787	1	Gum (Kinnekulle)	4	300	195
9559	W 319	6787	1	Gum (Kinnekulle)	4		
2418	W 320	6141	5c–d	Street between Stenstorp and Dala	5	330	340
2717	W 321	6409	1	Falbygden–Billingen, Gum (Kinnekulle)	5	390	260
2935	W 322	6409	1	Falbygden–Billingen, Gum (Kinnekulle)	5	380	340
2979	W 323	6414	1	Falbygden–Billingen, Gum (Kinnekulle)	5	345	300
4642	W 324	6783	1	Gum (Kinnekulle)	5	365	290
9556	W 325	6750	1	Gum (Kinnekulle)	5	365	275
2044	W 326	6417	1	Falbygden–Billingen, Gum (Kinnekulle)	6	480	365
4023	W 327	6409	1	Falbygden–Billingen, Gum (Kinnekulle)	6	460	400
4069	W 328	6417	1	Falbygden–Billingen, Gum (Kinnekulle)	6	405	290
4554	W 329	6755	1	Gum (Kinnekulle)	6	435	390
3916	W 330	6781	1	Gum (Kinnekulle)	7	455	515
4039	W 331	6783	1	Gum (Kinnekulle)	7		
4065	W 332	6757	1	Gum (Kinnekulle)	7	450	530
4067	W 333	6757	1	Gum (Kinnekulle)	7		
2982	W 334	6416	1	Falbygden–Billingen, Gum (Kinnekulle)	8	595	670
4008	W 266	6760	1	Gum (Kinnekulle)	8		
4377	W 335	6782	1	Gum (Kinnekulle)	8		
4663	W 336	6776	1	Gum (Kinnekulle)	9		
2920	W 337	6409	1	Falbygden–Billingen, Gum (Kinnekulle)	10		
3550	102	6761	1	Gum (Kinnekulle)	10		
4550	W 338	6783	1	Gum (Kinnekulle)	10		
4652	W 339	6757	1	Gum (Kinnekulle)	10		
2424	103	6414	1	Falbygden–Billingen, Gum (Kinnekulle)	11		
4144	W 340	6784	1	Gum (Kinnekulle)	–		

sequence with the first and last stages of the successively known part of the developmental sequence and the significantly older fragmentary specimen.

2.2. New description

It was possible to identify ten successive stages and, additionally, a distinctly older stage represented by a single fragmentary specimen (UB 103, see above). Head shield data could resolve only stages 1 to 8 (Fig. 4), because the shields of larger specimens are either damaged or not preserved. Other measurements, such as on the hypostome, confirmed these stages, but were even more incomplete. Based on morphometric data alone, it was not possible to distinguish between stages 1 and 2 (Fig. 4), but the morphological differences between the specimens in this size area demand, in our view, distinction into two successive earliest stages but with almost the same size.

2.2.1. Stage one. Developmental stage represented by nine specimens, UB 101, UB 1572, UB W 305, UB W 306, UB W 307, UB W 308, UB W 309, UB W 311, UB W 312.

Body ovoid, about 180 μm long, bearing four pairs of appendages inserting ventro-laterally. First pair of appendages uniramous, succeeding three pairs biramous (Fig. 5A, F). Head shield not clearly demarcated from the body, but indicated by a frontal protuberance (Fig. 5F) and a lateral bulge on each side (Fig. 5D, F). Bulges merge posteriorly into the dorso-caudal spine (Fig. 5D). Frontal protuberance smoothly widening ventro-caudally into the bulging hypostome (Fig. 5F). Hypostome being half as broad as the whole animal, about two fifth of its length (i.e. whole length 2.5 times hypostome length) (Table 2, Figs 5A, F, 15, 16); length to width ratio of hypostome is 1.3. Mouth opening situated at the rear of the hypostome, so pointing backwards (Fig. 5A, D). Mouth membrane around the mouth opening forming a

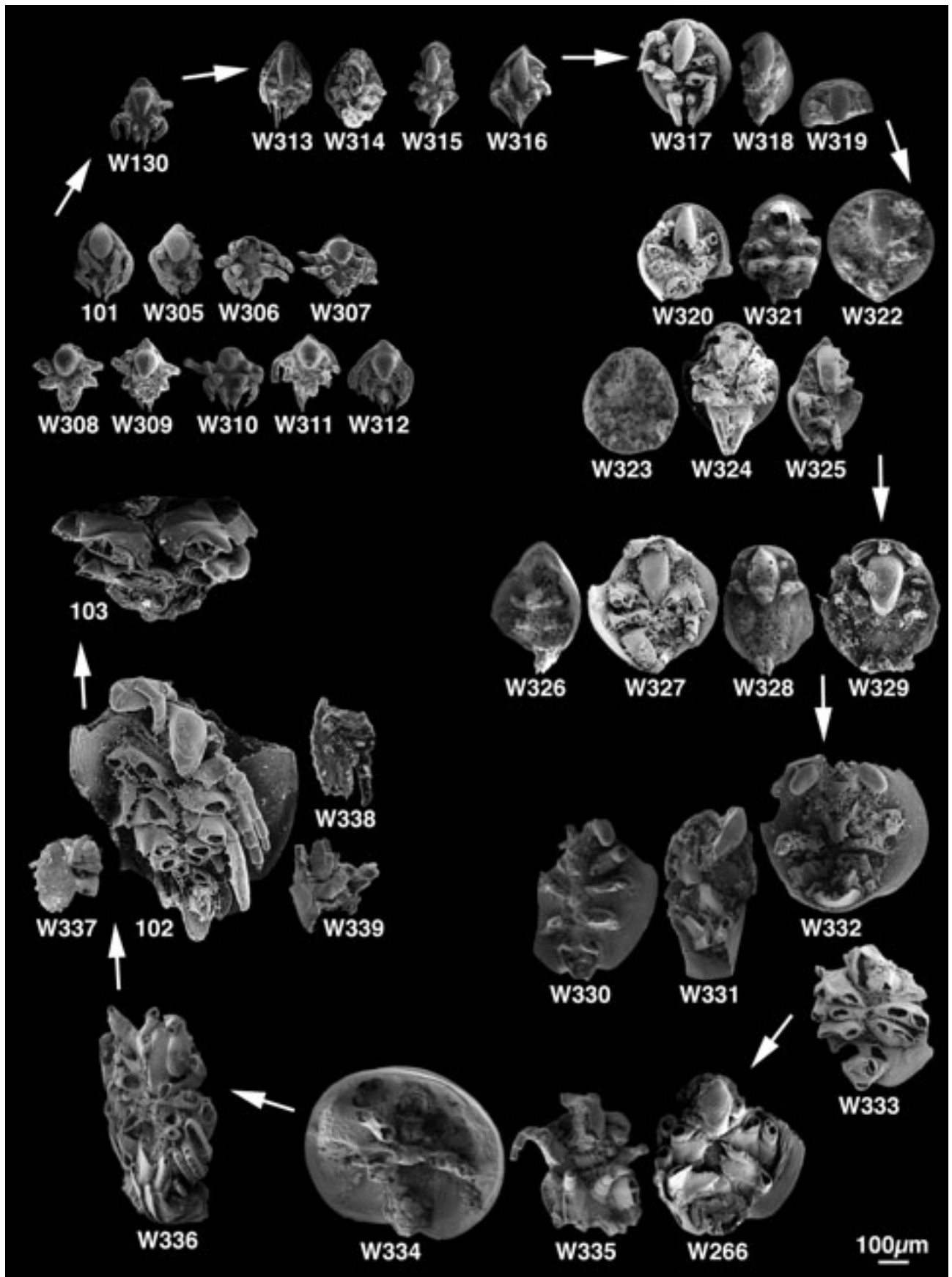


Figure 3 SEM images of all 40 specimens of †*Henningsmoenicaris scutula* (Walossek & Müller, 1990), mostly in ventral aspect and with their repository number (read as UB ...). Specimens grouped according to their developmental stage (starting in upper left corner with first stage and then clockwise).

tri-radiate, lip-like structure, resulting in a y-shaped mouth opening (Fig. 5A). Small tubercle situated in the middle of the base of each of the three lip-like triangles (Fig. 5A). Anus area

indicated by an elongated hump or swelling of soft appearance below the dorso-caudal spine, possibly an anal membrane, but an opening is, most likely, lacking (Fig. 5D).

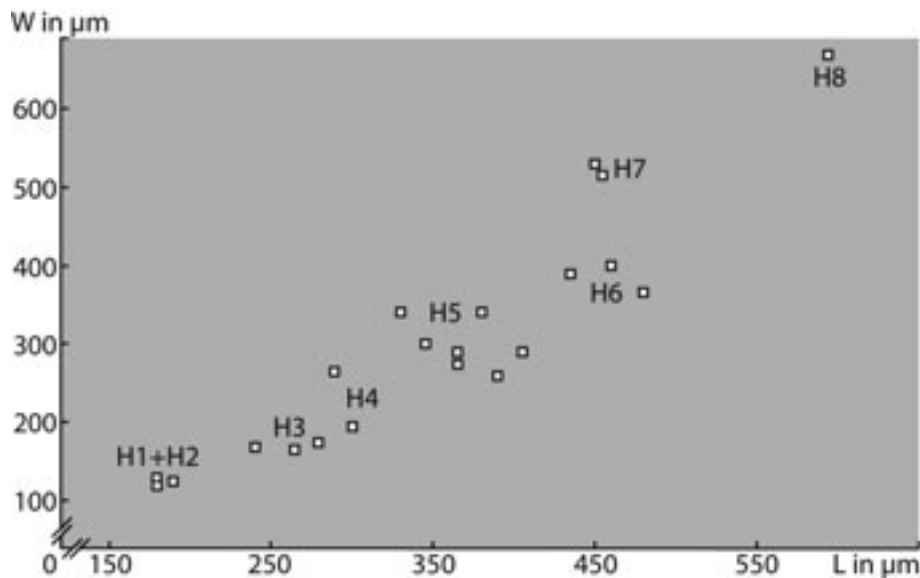


Figure 4 Diagram of width versus length of the head shield measured on 20 specimens of †*Henningsmoenicaris scutula* (Walossek & Müller, 1990). For further explanation see text.

All appendages are more or less soft, as is indicated by their finely wrinkled surface (UB W 312, Fig. 5B). Antennula slender, long, more or less circular in diameter, inserting antero-latero and dorsally of the hypostome, slightly ventrally of the elongate swellings that indicate the future outline of the lateral shield margin (Fig. 5B). No clear transition between membranous joint area and the segmented distal part, which appears rather soft. Distal part with at least three portions. Most proximal portion about three times as long as wide and carrying a robust seta antero-distally. Second portion shorter than the previous one, only slightly longer than wide, also carrying a seta antero-distally, which is more sclerotised than the proximal seta, smaller and inserting more laterally. Third portion about twice as long as the second one, carrying a seta of comparable size and position to that of the second portion (Fig. 5B). Further distal parts are missing in all specimens.

Second pair of appendages articulates ventro-laterally, par- orally to the body, appendages rotated 10°, median edge facing slightly posterior (Table 2; Fig. 15.1). Second limbs composed of a prominent membranous socket, on which the sub-triangularly shaped basipod rests, which carries the two rami, exopod and endopod (Fig. 5B). Insertion of the appendage oval, medio-lateral axis 1.5 times antero-posterior axis (Table 2). Basipod drawn out medio-proximally into two prominent, inwardly pointing spines, one above the other. The two spines have a smaller accessory spine, one located distally of the proximal spine and another one located antero-laterally of the distal spine (Figs 5C, 17). Endopod more or less circular in diameter, consisting of two portions articulating medio-distally on the basipod. Proximal endopodal podomere, possibly a true podomere, slightly longer than wide, tube-shaped and carrying one seta medio-distally (Figs 5C, 17). Distal portion at least twice as long as the proximal one, bottleneck-like decreasing in diameter distally to about half of the basal diameter and remaining as such to extend into three setae, a prominent one distally flanked by two thinner ones medially and laterally (Fig. 5E, F). All three setae pointing more or less distally. Additionally, a small, also distally pointing seta arises from the anterior surface of the distal endopod portion positioned at about two thirds of its length (Fig. 5A). Exopod arising from the outer sloping edge of the basipod, within a small distance from the endopod. Cross-section of the exopod oval, flattened in antero-posterior axis. Exopod composed of

several articles. Proximal article soft, making up approximately 2/5 of the exopod. Distal portion of exopod slightly better sclerotised and divided into three articles (Fig. 5E, F). Exopodal armature: proximal part and first article of distal portion with a medio-distally inserting and obliquely distally pointing seta (Table 2; Fig. 5A, E); seta of proximal part shorter than that of the subsequent article (Fig. 5A). Next distal article with a pair of setae (Fig. 5A, E, F) being apparently more robust than the more proximal ones. Distal exopod article with two terminal setae, one inserting medio-distally and one terminally. A third, but much smaller seta inserts disto-laterally (Table 2; Fig. 5F).

Third appendage oriented perpendicular to the antero-posterior body axis (Table 2; Figs 5C, F, 15.1). Appendage resembling the second one in all major aspects (Fig. 17), particularly the exopod shape and armature, except the size of the associate spine near the proximal one of the basipod spines and the most proximal exopod seta, which are both significantly larger than those of the second limb (Fig. 5A).

Fourth appendage oriented almost parallel to body axis, i.e. its median surface almost facing anteriorly, rotated 85° compared to standard orientation (Table 2; Fig. 15.1). Insertion area almost circular. Appendage biramous, but only with a faint ridge demarcating off the basipod from the rami (Fig. 5E). Endopod made up of two recognisable portions. Two spines arising from the median edge of the proximal portion of the endopod (Fig. 5A, 17). Distal part of endopod short, merely forming a rounded socket for a terminal, distally pointing seta (Fig. 5E). Exopod rod-shaped, circular in cross section, poorly sclerotised, tapering distally. Of the three distal setae, one inserts medio-distally, one terminally, and one latero-distally (Fig. 5E), the latter being smaller than the others (Fig. 5E).

2.2.2. Stage two. Stage represented by a single specimen, UB W 130 (Fig. 6A–E). Morphology and size almost unchanged compared to that of stage one, except for a few but significant changes, which demand the erection of a separate stage. One feature is the head shield, which is now clearly set off from the body proper (Fig. 6B, C, D): its distinct outer rim runs from the anterior (the former anterior protrusion) gently widening in profile to its maximum width in the middle of the body (Fig. 15) and converging again to fade out into the dorso-caudal spine, which gives the body an oval to rounded

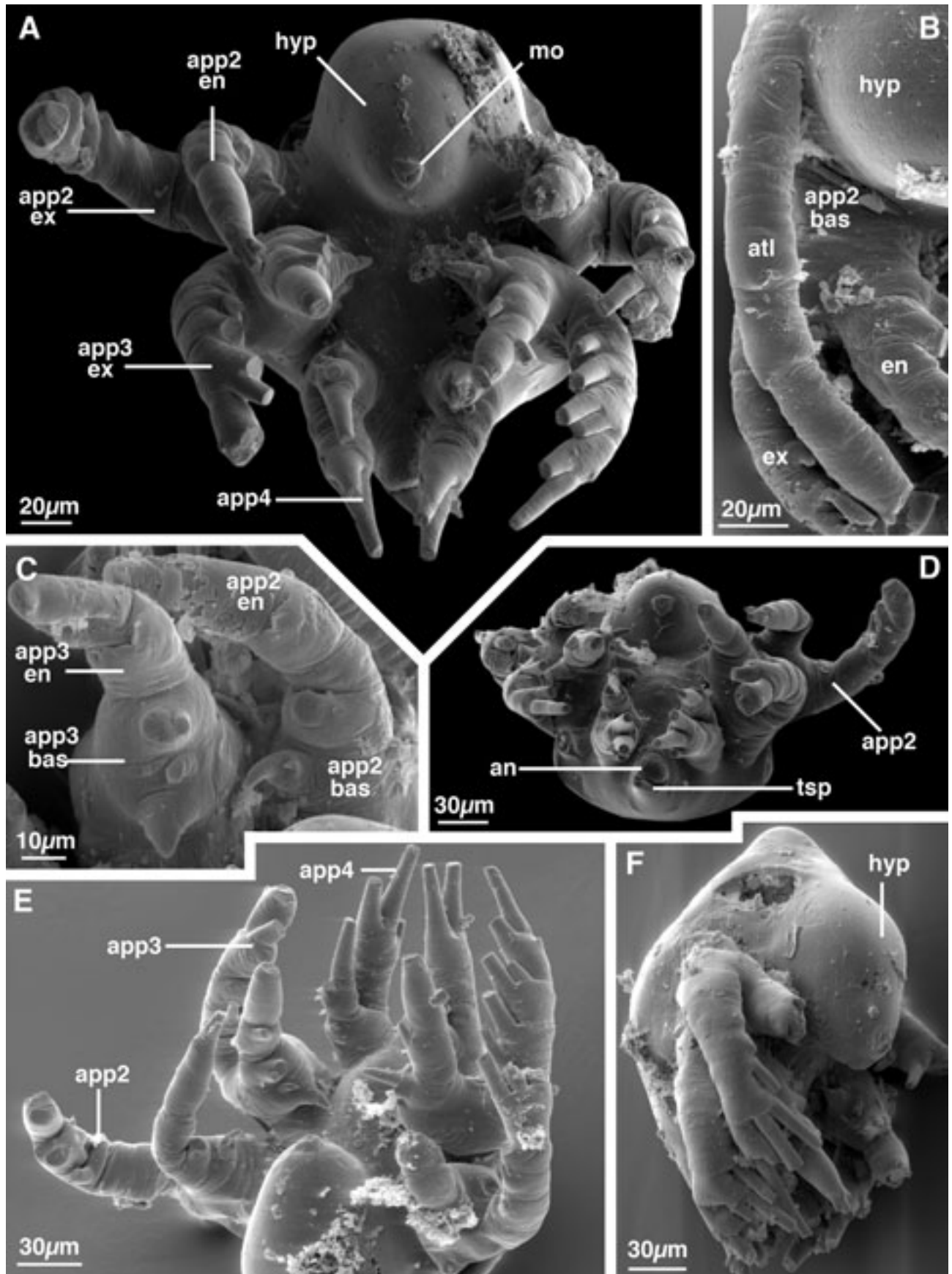


Figure 5 Developmental stage 1 of †*Henningsmoenicaris scutula* (Walossek & Müller, 1990): (A) UB W 1572, ventral view; (B) UB W 312, antero-lateral region. Detailed view of antennula; (C–F) UB 1572: (C) median view of the right second and third appendages; (D) ventro-terminal view, displaying the terminal details; (E) antero-lateral view, showing details of the appendages; (F) latero-ventral view, displaying the hypostome. Abbreviations: an=anus; app=appendage (2–4); atl=antennula; bas=basipod; en=endopod; ex=exopod; hyp=hypostome; mo=mouth opening; tsp=terminal spine.

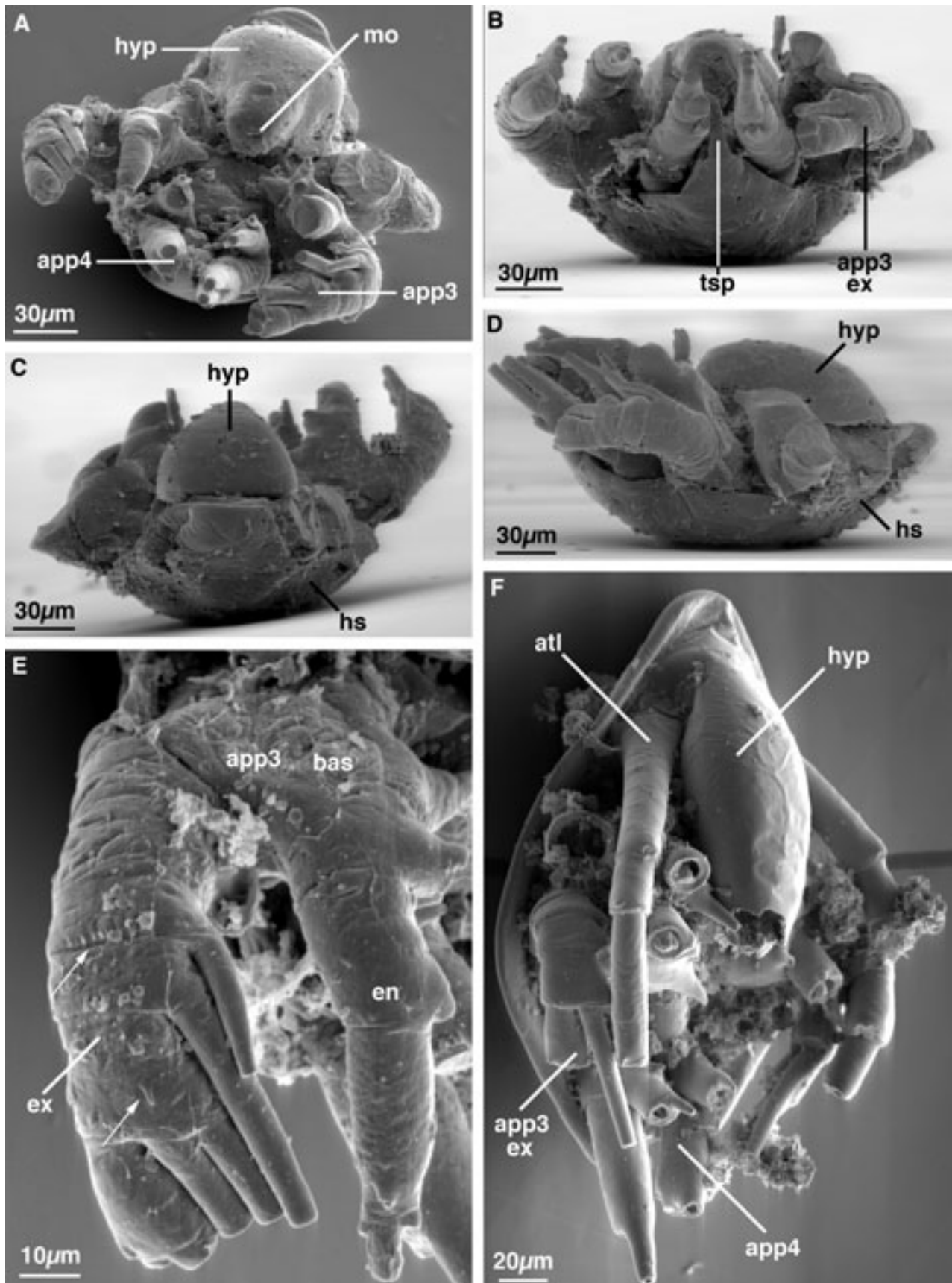


Figure 6 Developmental stages 2 and 3 of †*Henningsmoenicaris scutula* (Walossek & Müller, 1990): (A–E) Developmental stage 2, UB W 130: (A) ventro-terminal view of specimen displaying the tri-radiate mouth opening; (B) animal displayed in terminal view. Sharp rim of the head shield merges into the terminal spine; (C) anterior view of the animal. The hypostome is set off from the cephalic shield; (D) lateral view of the animal displaying again the set off hypostome and the sharp rim of the head shield; (E) detail of the right third appendage from anterior. The exopod shows some ornamentation details marked by arrows. (F) Developmental stage 3, UB W 313. Latero-ventral view of the animal showing general organisation. Abbreviations: app=appendage (3–4); atl=antennula; bas=basipod; en=endopod; ex=exopod; hs=head shield; hyp=hypostome; mo=mouth opening; tsp=terminal spine.

spindle-like shape in dorsal aspect. Ventrally the hypostome is set off from anterior shield margin by a softer area. Posterior part of hypostome more elongated than in preceding stage, with a length to width ratio of 1.8 (1.3 in stage one), now only slightly shorter than half of the length of the whole body (0.4 in stage one) (Table 2, Figs 6A, C, D, 15.2). Anus area represented by an elongated bump below the dorso-caudal spine, apparently lacking an opening as in the preceding stage (Fig. 6A). The surface of the exopod of the third appendage is finely ornamented with rows of tiny scales (Fig. 6E).

2.2.3. Stage three. Stage represented by four more or less complete specimens, UB W 313, UB W 314, UB W 315, UB W 316. Body about 260 μm long, so significantly larger than previous stage (180 μm , see Table 1). Body with a slightly bowl-shaped head shield of oval profile in dorsal/ventral view (Figs 6F, 15.3). Shield length about 1.6 times its maximum width (Table 2). Head shield (Fig. 7A, B) with well-defined rim, which is slightly enhanced but without a clearly demarcated ventral doublure. Caudally, the head shield or dorsal body surface continues into a robust dorso-caudal spine, as in the previous stage. Hypostome more elongate than in previous stage, being twice as long as broad (1.8 in stage two) (Fig. 7B), spindle-shaped, broadest at about one third of the length from posterior. Hypostome half as long as the whole animal as in stage two (Fig. 7B), but on the ventral surface of the hypostome a more or less circular, apparently weakly sclerotised area is slightly set off (marked with an arrow in Fig. 7B). Mouth opening situated at the rear of the bulged hypostome as in preceding stage. Anal opening exposed on the ventral surface of the body between last pair of appendages and base of caudal spine, surrounded by a soft membrane (Fig. 7C).

Four appendages as in previous stages, i.e. the antennulae and three pairs of biramous appendages (Figs 6F, 7B). Morphology as in previous stages, but appearing more rigid and with well-developed demarcation lines between the portions (Figs 6F, 7A). Antennula starting proximally with a weakly set-off conical portion that continues into three elongate distal portions, as in stage one. Terminal end unknown. Length of the preserved articles unchanged, which indicates a proportional decrease in relation to other structures, e.g. the main body (Fig. 7A). Setation unchanged.

Second appendage as that of preceding stage, except the basipodal armature, which is shifted distally along the inner edge of the basipod (Fig. 7B) rotation now -20° compared to standard orientation (10° in preceding stage), median edges facing medio-posteriorly (Table 2). Additionally the insertion of the appendage is now more elongated in medio-lateral axis, this axis measuring twice the antero-posterior axis (1.5 in stage two) (Table 2; Fig. 15). Furthermore, the exopod is now subdivided into six articles being oval in cross-section, the proximal two lacking median setae, but the four distal portions with one to three setae, as in the preceding stage.

Third appendage similar to the second one and that of previous stage, also with the distal shift of its basipod armature and the elongation of the insertion area, but the two prominent basipod spines are separated from each other by a larger distance than in appendage two and in the previous stage (Fig. 7B). Another difference from both the second appendage and the third limb of the previous stage is that the distal prominent basipodal spine points more medio-distally. Again, the associate spine of the proximal spine is located more anteriorly (still larger than the corresponding spine of the second appendage). Endopod unchanged. Exopod has one portion less than that of the second appendage, thus comprising five articles, with the most proximal article lacking a seta (Fig. 7A). Distal exopod article unchanged, also exopod setation (e.g., most proximal seta larger than that of the

exopod of the second appendage). Fourth appendage resembling that of the preceding stage, but insertion area of the appendage now oval (circular in stage two), medio-lateral axis being about 1.3 times antero-posterior axis. Exopod now clearly demarcated off from the basipod and appendages rotated 50° compared to standard orientation, median edges facing medio-anteriorly (Table 2; Fig. 15.3). Demarcation between basi- and endopod weakly developed, setal pattern as before (Figs 4F, 5B). Base of exopod now oval (circular in preceding stage), medio-lateral axis being about 1.3 times antero-posterior axis.

2.2.4. Stage four. Three specimens assigned to this stage: UB W 317, an almost complete specimen; UB W 318, a more damaged one; and UB W 319, a fragment of the anterior body region.

Stage differing little from the preceding one, besides the relation of shield width and length and setation of the fourth appendage. Head shield bowl-shaped, 1.5 times as long as broad (1.6 in preceding stage) (Fig. 15). Shield deeper than in the preceding stage, now with a narrow doublure (Fig. 7D). Anterior shield margin now gently rounded. Hypostome shape almost unchanged, but slightly more elongated than in preceding stage, 2.3 times as long as wide (2 times in stage three) (Table 2; Fig. 15). Appendages 1–3 unchanged compared to preceding stage, besides insertions area of the second appendage now being more elongated, medio-lateral axis being about 2.5 times antero-posterior axis (2 in stage three) (Table 2; Fig. 15). Fourth appendage unchanged, besides exopod now with an elongated base, medio-lateral axis being about 1.5 times antero-posterior axis (1.3 in stage three) and now with step-like indentations for the insertions for four setae. There are no longer two terminal setae on the exopod (as in the preceding stages), but one median, one terminal and two lateral ones (Fig. 7E).

2.2.5. Stage five. Stage represented by six specimens, UB W 320, UB W 321, UB W 322, UB W 323, UB W 324, UB W 325. Body with a large bowl-shaped shield, being 1.3 times longer than wide (Fig. 8A), extending caudally into a terminal spine, and now with five pairs of appendages (Fig. 8C), the antennulae, three pairs of biramous limbs, and a pair of limb rudiments. Two elongated oval and slightly raised blisters are present inwards of the shield margin alongside the rim (Fig. 8A), on either side of the anterior end of the hypostome and anterior to the insertions of the antennulae; about 2.5 times as long as wide. Blisters lying at an angle of 45° to the hypostome, following the outline of the shield.

Antennula unknown apart from its very proximal part, which does not differ from that of preceding stage. Second appendage resembling that of preceding stages in most aspects (Fig. 8A), but the insertion area more elongated, medio-lateral axis being about 2.8 times antero-posterior axis (2.5 before) and with an additional centro-median seta on the most proximal article of the exopod.

Third appendage resembling that of preceding stage in most aspects (Fig. 8A), but insertion area now more elongated, medio-lateral axis being about 2.5 times antero-posterior axis (2 before) (Table 2; Fig. 15), resulting in a more flattened shape of the basipod. Additionally two new spines are present on the median edge of the basipod between the two prominent spines. In total there are four smaller spines, besides the two prominent basipodal spines, two between these, one more anterior, one more posterior, as well as two even smaller spines, one anterior to each prominent basipod spine (Fig. 17).

Fourth pair of appendages differs from that of the preceding stage in the following aspects: appendages rotated 45° compared to standard orientation, median edges facing medio-anteriorly (50° in preceding stage) (Figs 8C, 15.5), the

insertion area is more elongated in medio-lateral axis being about 1.8 times antero-posterior axis (1.3 before). Appendage now with demarcation line separating the two proximal endopodal portions (Fig. 8B, C), thus endopod consisting of at least three portions, being slightly longer than their diameter, the proximal two with a medio-distal spine each (Figs 8C, 17). Further distal portion(s) unknown since they are not preserved in our material.

Exopod paddle-shaped, its base more elongated than before, medio-lateral axis about 2.4 as long as the antero-posterior axis (1.5 before). Exopod with marginal step-like indentations for the insertion of now six setae (four in the preceding stage): two median ones, a terminal one and three lateral ones (Fig. 8B). Terminal seta accompanied by a seta antero-medially to it (Table 2). Possible sensilla being positioned in a symmetrical pattern on both exopods, as indicated by three holes on the anterior surface of the exopods of UB W 324 (Fig. 8B). Central putative sensillum located almost directly proximal to the associate seta of the terminal seta, the more median sensorial seta positioned proximal to the more distal median seta, and the more lateral sensorial seta situated median to the insertion of the most lateral seta.

Fifth pair of appendages inserting between the fourth appendages and the anus. Insertion area oval, oriented almost in long axis of the body, medio-lateral axis being about 1.3 times antero-posterior axis. Accordingly, median side of appendages facing almost anteriorly. Appendages are uniramous, elongated, cone-shaped, tapering to the distal end into a small blunt tip (Fig. 8C).

2.2.6. Stage six. Developmental stage represented by four specimens, UB W 326, UB W 327, UB W 328, and UB W 329. Body now comprising two tagmata, the head, covered by the bowl-shaped shield and the caudal end piece (Fig. 8E). End piece extending into a caudal spine. Head includes five appendage-bearing segments, i.e. those of the antennulae and four pairs of biramous limbs. Caudal end piece carrying a single pair of rudimentary limbs (Fig. 8D). Anal opening exposed on the ventral surface of the body between last pair of appendages and base of caudal spine, surrounded by a soft membrane.

Head shield bowl-shaped, being 1.2 times as long as wide (Table 2; Fig. 15), with a doublure that is broader compared to that of the preceding stage (Fig. 8E). Head shield no longer merging into the terminal spine but having a posterior rim that is straight from dorsally posterior, c-shaped when seen from posterior, being about as wide as one quarter of the maximum head shield width. The caudal end piece is positioned in this c-shaped section. Exact morphology of the caudal end unclear because of the poor preservation in our material.

Blister-like structures left and right of the hypostome more prominent compared to the preceding stage, more recognisable as such, but otherwise unchanged (Fig. 6E). Softer area on the median surface of the hypostome more pronounced than before and reaching further anteriorly on the hypostome (Fig. 8E).

Antennulae not known apart from their proximal-most part. Also of the second appendage only the proximal parts are known, i.e. the basipod and the three proximal articles of the exopod (Fig. 8E), unchanged compared to the preceding stage, besides insertion area of the appendage, which is more elongated in medio-lateral axis being about three times antero-posterior axis (2.8 before). Median seta on the most proximal exopod article being quite robust, about three times as long as wide and curved, starting in a median direction but curving up to point distally. This shape and the blunt tip give the seta a hook-like appearance (Fig. 8F). Third appendage with no changes compared to the preceding stage, besides insertion

area, which is more elongated in medio-lateral axis being about three times antero-posterior axis (2.5 before).

Fourth appendage rotated 30° compared to standard orientation, median edges facing medio-anteriorly (45° before) (Figs 8E, 15; Table 2). Basipod longer in medio-lateral axis than before, medio-lateral axis being about 2.5 times antero-posterior axis (1.8 before). Endopod not known. Insertion of the exopod now more elongate, medio-lateral axis being about 3.3 times antero-posterior axis (2.4 before). Exopod paddle-shaped with step-like indentations for the insertion of eight setae (six before): three (two before) medially, one terminal with an antero-median situated associate seta and four lateral (three before) (Fig. 8E).

Fifth appendage now biramous (uniramous rudiments in preceding stage), insertion area more elongate, medio-lateral axis being about 2 times antero-posterior axis (1.3 before). Appendages rotated 75° compared to standard orientation, median edges facing medio-anteriorly. Endopod not demarcated off from basipod, only proximal parts known. Exopod only faintly demarcated off, base elongate, medio-lateral axis being about 2.3 times antero-posterior axis. Exopod paddle-shaped, with step-like indentations for the insertion of four setae along its outer margin, one situated medially, one terminally and two laterally (Fig. 8D).

Sixth appendages uniramous, small and cone-shaped (Fig. 8D), inserting posteriorly to the fifth appendage on the caudal end piece and anteriorly to the anus. Insertion areas oval medio-lateral axis being about 1.3 times antero-posterior axis, median surfaces almost facing anteriorly.

2.2.7. Stage seven. Stage represented by four specimens, UB W 330, UB W 331, UB W 332, and UB W 333. Head covered by a large bowl-shaped shield (length to width ratio 0.9), comprising five appendage-bearing segments (Table 2; Fig. 15.7). Trunk consisting of a single portion covered by a shield extending into the terminal spine dorsally and two pairs of appendages ventrally (Fig. 9A). First pair of trunk appendages biramous, second pair uniramous and apparently poorly developed (Fig. 8F). Anus posterior to the last pair of appendages on the caudal end.

Blisters left and right of the hypostome, posterior to the anterior rim of the shield, not only again larger than in the preceding stage, but also free posteriorly and at that point slightly uplifted (Fig. 9A). Hypostome not changed noticeably in shape. Soft area larger compared to the preceding stage and now covering almost the complete ventral (distal) side of the hypostome.

Antennulae only known by their very proximal parts, showing no changes. Second appendages apparently changed against preceding stage. Appendages rotated -30° compared to standard orientation (-20° before), median edges facing medio-posteriorly. Distal portion of basipod, indicated by the distal basipodal spine, is no longer part of the basipod, as it is separated by a clear joint demarcation (Fig. 7B); thus, it now forms the most proximal portion of the endopod. Former proximal prominent basipod spine now with two accessory spines, one antero-distally, one postero-distally (Fig. 7B). These associate spines are almost as large as the prominent spine. All three spines are pointing medially into the median food area. Antero-distally to these three spines an additional small spine is situated. Proximal to the three basipodal spines, an area is to some degree demarcated off from the basipod, but not completely. This area carries a small slightly upward curved spine centrally (Figs 9B, 17)

Third appendage resembling that of preceding stages in many aspects. A small cuticular plate, medio-proximal to the basipod and surrounded completely by arthroal membrane, carrying two small medially pointing setae (Figs 9C, 17). This

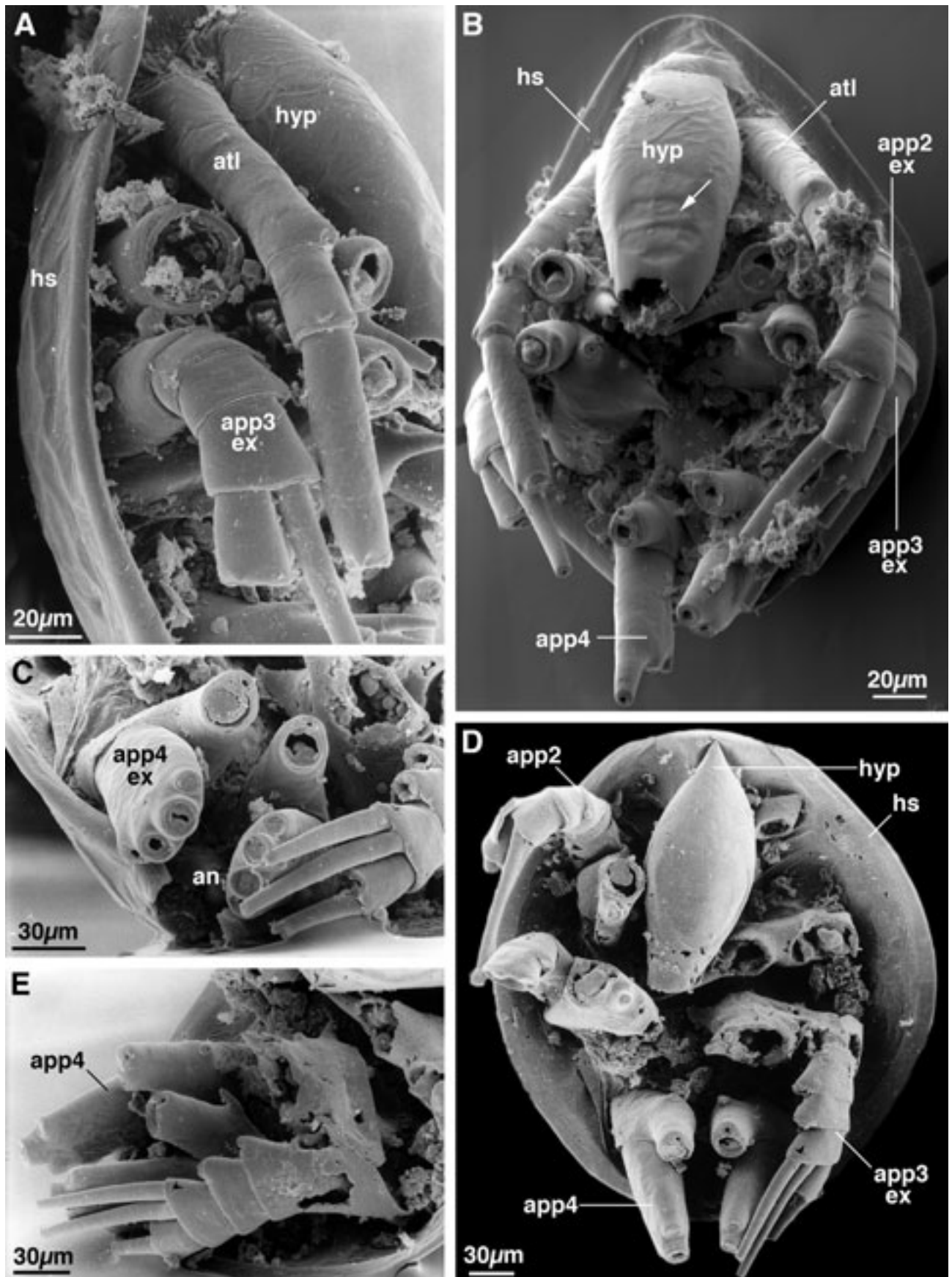


Figure 7 Developmental stage 3 continued and 4 of †*Henningsmoenicaris scutula* (Walossek & Müller, 1990): (A, B) Developmental stage 3, UB W 313: (A) ventro-lateral view of the anterior region. Details of the antennula displayed. Note the distinct margin of the head shield; (B) ventral view displaying details of the appendages. (C–E) Developmental stage 4, UB W 317: (C) details of terminal aspects displaying the anus and the insertion areas of four spine-like setae on the exopod of the fourth appendage; (D) ventral view showing general organisation, and length of spine-like setae on the exopod of the second appendage and third appendage; (E) detail of terminal area seen from lateral displaying details of fourth appendage. Abbreviations: an=anus; app=appendage (2–4); atl=antennula; en=endopod; ex=exopod; hs=head shield; hyp=hypostome.

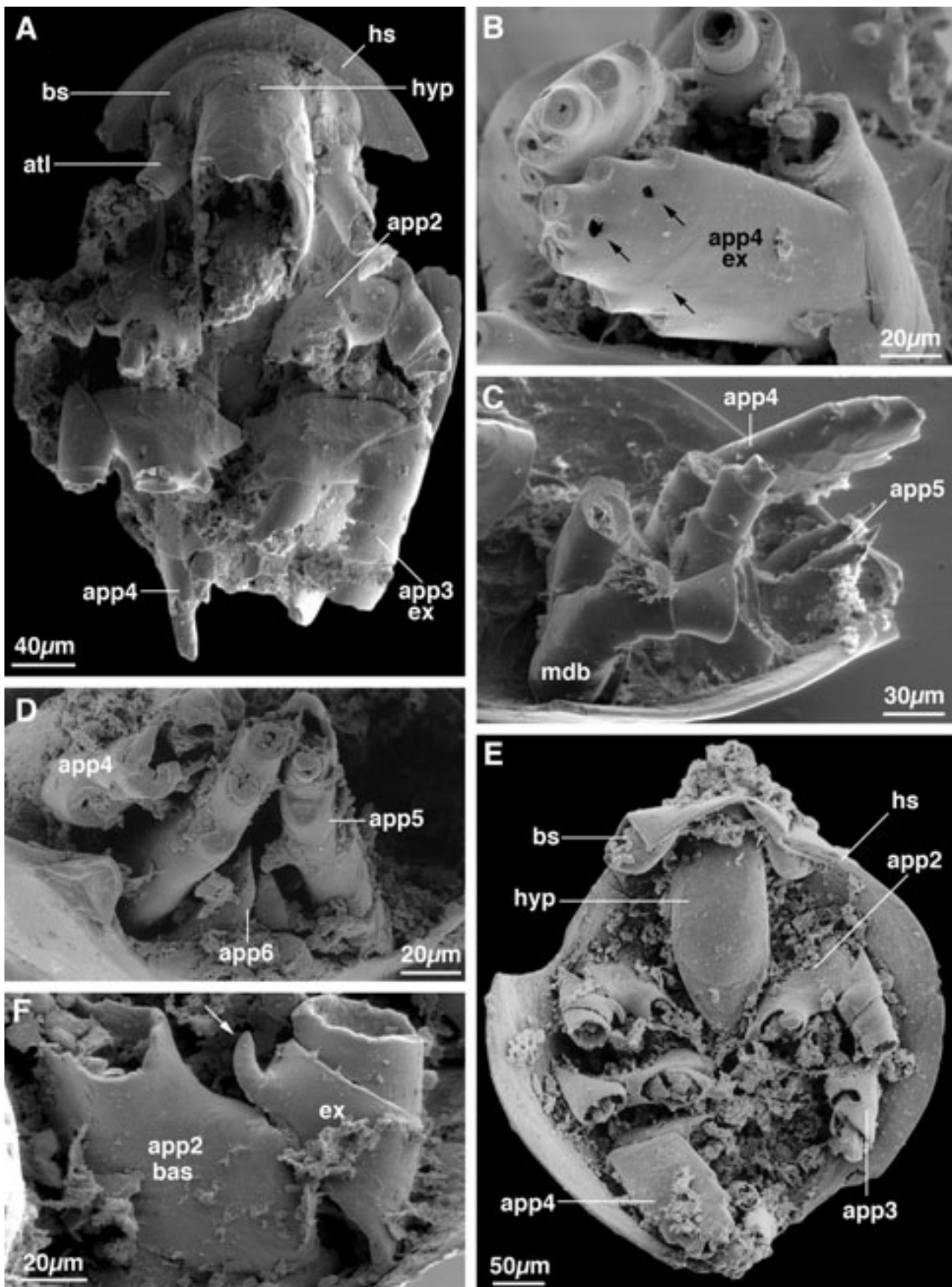


Figure 8 Developmental stages 5 and 6 of †*Henningsmoenicaris scutula* (Walossek & Müller, 1990): (A–C) Developmental stage 5: (A) UB W 321, ventral view, showing general organisation; (B) UB W 324, details of the exopod of the fourth appendage. Arrows mark the insertion areas of putative sensorial setae; (C) UB W 325, detailed view of the rudimentary fifth cephalic limb. (D–F) Developmental stage 6, UB W 327: (D) details of terminal appendages displaying the rudimentary sixth appendage; (E) ventral view, giving an overview of the general organisation; (F) details of the exopod of the right second appendage from anterior. Hook-shaped seta marked by arrow. Abbreviations: app=appendage (2–6); atl=antennula; bas=basipod; bs=blister; ex=exopod; hs=head shield; hyp=hypostome; mdb=??.

portion is identified as the proximal endite (*sensu* Walossek & Müller 1990). Posterior to the distal prominent basipodal spine is now an additional spine almost on the posterior surface. Exopod with two new setae on the disto-lateral rim and medio-laterally on the most proximal article. A single seta is preserved on the disto-lateral rim of the next proximal article, suggesting the presence of comparable seta on the insertion areas of the most proximal article, thus three new setae in total. The single preserved seta appears rather soft. It is curved proximally thus distally pointing (Fig. 9E).

Fourth appendages rotated 20° compared to standard orientation, median edges facing medio-anteriorly (Fig. 15.7), insertion area further elongated medio-lateral axis being about three times antero-posterior axis (2.5 before). Appendage with significant changes with regard to the previous shape: exopod is now divided into two parts, proximal exopod portion elongated, triangular in shape, articulating on the lateral side of the most proximal endopod podomere, the lateral side of the basipod and reaching into the arthrodival membrane of the appendage (Fig. 9G). Base of the exopod more elongated in medio-lateral axis being about 4.3 times the antero-posterior axis (3.3 before).

Basipod now with three spines medio-distally, one prominent one medially, the other two slightly smaller ones further anteriorly (only a single spine before) (Figs 8D, 17). A smaller single new spine is positioned posteriorly to the mid axis of the median surface and right in the middle between distal and proximal rim of the basipod. Proximal endopod podomere now with four spines on its medio-distal rim (one spine before). One spine is median, one is anterior, the other two more to the posterior. Furthermore, the proximal endopod podomere has a small hump antero-laterally, carrying a distally pointing seta anterior to the articulation of the exopod. More distal parts of the endopod are unknown. Details of exopod setation are also unknown.

Fifth appendage only known from its insertion area, being more elongate in medio-lateral axis than in preceding stage, about two times antero-posterior axis (2.5 before) (Fig. 9F). Appendages rotated 45° compared to standard orientation (75° in preceding stage), median edges facing medio-anteriorly. Appendage six, the first trunk limb, now biramous but distal parts of the two rami unknown, appendages rotated 55° compared to standard orientation, median edges facing medio-anteriorly. Seventh appendage present as a club-shaped bud (Fig. 9F).

2.2.8. Stage eight. Stage represented by three specimens, UB W 266, UB W 334, and UB W 335. Head and shield as before. Trunk (Fig. 10A) with one free appendage-bearing segment with a tergite, and the caudal end, covered by a small shield, extending into the terminal spine, with two pairs of appendages. Blisters, formerly left and right to the anterior end of the hypostome now entirely raised from the body surface onto stalks, which insert antero-laterally to the hypostome (Fig. 10F).

Antennulae known only from their two most proximal articles (Fig. 8E), which are oval in diameter. Proximal article carrying a small seta anteriorly on its distal margin. Two holes on distal article are interpreted as insertions of next article and seta: the larger, posterior hole presumably representing the insertion of the next distal article, which is significantly smaller in diameter compared to the two preserved articles. Smaller anterior hole, based on its size, presumably being the insertion of a prominent seta (Fig. 17).

Second appendage resembling that of the previous stage in most aspects, but appendages rotated -40° compared to standard orientation (-30° in preceding stage), median edges facing medio-posteriorly, and the distinct offset of the medio-

proximal area of the basipod now completely surrounded by membrane and carrying a pair of spines: one anteriorly, the other posteriorly, both pointing medially (Fig. 17) (only one spine verified for preceding stage). This portion is identified as the proximal endite (*sensu* Walossek & Müller 1990; Fig. 10C).

Third appendage similar to that of the preceding stage in most aspects, other than the following differences: median edge of basipod with five spines (three before) between the two large prominent spines, three in a more posterior proximo-distal axis (one before), two in a more anterior one (Fig. 17). Anterior part of median edge of basipod with a single spine pointing medially (as before), posterior side with two, one more distally, one more proximally (proximal one new) (Figs 10G, 17). Basipod now with a small hump antero-medially to the insertion of the exopod, which carries a distally pointing seta. Proximal endopod portion with four spines (one before), a large median spine, two spines anterior to it, of these one antero-distally, one antero-proximally, and one spine arising postero-distally to the prominent spine. Exopod unchanged compared to preceding stage.

Fourth appendage resembling that of the preceding stage in most aspects (Fig. 10A), besides insertion area now being more elongate, medio-lateral axis being about 3.3 times antero-posterior axis (3.0 before) (Table 2; Fig. 15). Additionally, basipod with four spines on its medio-distal rim (three in the preceding stage). The median and two more anterior ones are also present in stage 7. The posterior one is new at this stage (Figs 10A, 17). Proximal to these four spines, there are now six spines (one before). They form a row of two smaller spines distally and a row of three slightly larger setae are situated more proximally, all pointing medially. The sixth spine is situated proximo-posteriorly close to the medio-proximal rim of the basipod (Fig. 17). Endopod with four portions, slightly shorter than their diameter compared to preceding stage. Next portion with a prominent median seta medio-distally, also present in stage seven, but now flanked by two smaller setae anteriorly and posteriorly (Fig. 17). Penultimate portion with a single spine medio-distally. Terminal portion short and extending distally into a seta (only insertion of this seta preserved in UB W 335). Exopod unchanged, besides insertion area being more elongate, medio-lateral axis being about five times antero-posterior axis (4.3 before).

Fifth appendage differing from preceding stage, now resembling the fourth appendage of this stage in having a bipartite exopod articulating to the proximal endopod portion, the lateral side of the basipod and reaching further laterally into the arthrodival membrane of the appendage. Appendages rotated 30° compared to standard orientation (45° in preceding stage, Fig. 15), median edges facing medio-anteriorly. The insertion area of the appendage is elongate in medio-lateral axis, being about 2.8 times antero-posterior axis (2.0 before). Basipod sub-rectangular, with four spines on its disto-median rim (not exactly known for earlier stages), one inserting medially, two more anteriorly and one more posteriorly (Fig. 10D), exactly as in appendage 4 (Fig. 17). Two additional new spines are situated more proximal on the median edge of the basipod, one more anteriorly, one more posteriorly, both pointing medially (Fig. 17). Endopod consisting of at least four portions (three preserved at most), but the second portion is made up of two not (yet?) demarcated articles as indicated through the setation pattern and a bulge (Fig. 10D) running around the portion.

Proximal endopodal portion about as long as its diameter, second portion almost twice as long as its diameter (each of the two articles about as long as its diameter), third portion elongated about 1.5 times as long as its diameter, more distal portions smaller in diameter than proximal portions

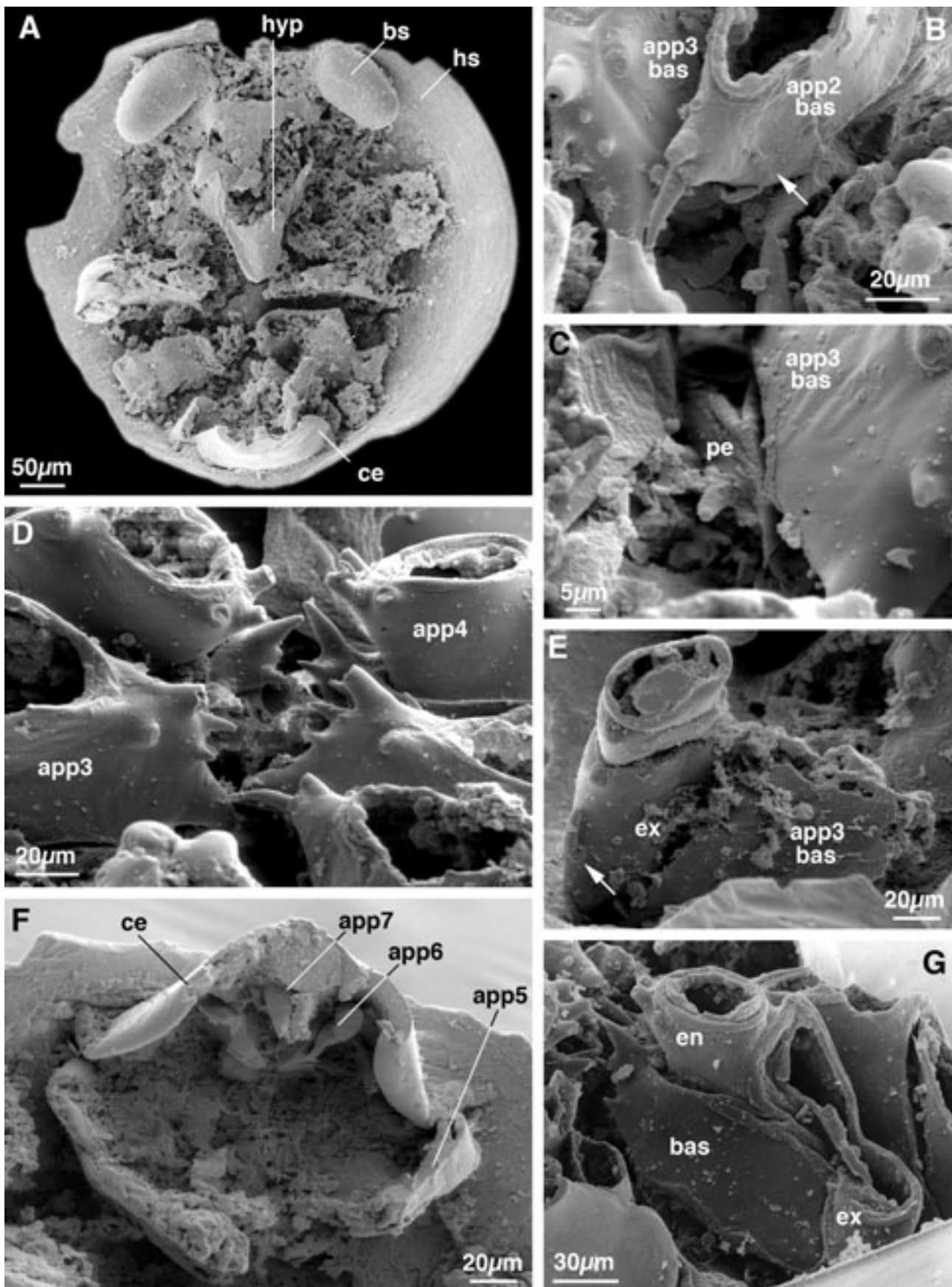


Figure 9 Developmental stage 7 of †*Henningsmoenicaris scutula* (Walossek & Müller, 1990): (A) UB W 332, ventral view displaying general body organisation. (B–D) UB W 333: (B) median details of right second appendage. Small setiferous plate (future proximal endite) marked by arrow; (C) median details of right third appendage displaying the proximal endite; (D) anterior view of the third and fourth appendages. (E, F) UB W 332: (E) details of the exopod of the third appendage. Banana-shaped soft seta marked by arrow; (F) detail of the trunk displaying the rudimentary seventh appendage. (G) UB W 333. View from posterior on the left fourth appendage. Abbreviations: app=appendage (2–7); bas=basipod; ce=caudal end; en=endopod; ex=exopod; hs=head shield; hyp=hypostome; pe=proximal endite.

(Fig. 10D). Most proximal portion carrying four spines on its disto-median rim (single spine before), one spine medially, two more posteriorly and one more anteriorly, exactly as in appendage 4 (Fig. 17). At the lateral side of the portion, anterior to the articulation of the proximal exopod portion, is a small hump with a distally pointing seta. Proximal part of second endopodal portion with three spines on the median part of the bulge separating this part from the distal one. On the disto-median rim of the distal part two spines are present. Probable penultimate portion with a single seta on its disto-median rim. Further portions unknown.

Exopod now bipartite with a proximal and a distal part. Proximal part articulated on the most proximal podomere of the endopod, the lateral side of the basipod and the arthroal membrane of the appendage. Distal part of exopod unknown.

Further appendages are not preserved in any specimen, apart from the insertion areas of two more, i.e. appendages six and seven, in UB W 266 indicative of the presence of more trunk limbs in the advanced stages of †*H. scutula*. Sixth appendages rotated 55° compared to standard orientation (as in preceding stage), median edges facing medio-anteriorly, seventh appendages rotated 65° compared to standard orientation (before unknown), median edges also facing medio-anteriorly, as indicated by the insertion areas. An eighth appendage is present but cannot be characterised due to its poor preservation in the material.

2.2.9. Stage nine. Stage represented by a single, but remarkably complete, specimen, UB W 336. Head with five pairs of appendages, trunk with an apodous shield-covered caudal end preceded by three free tergite-bearing segments (Figs 11H, 17) carrying biramous appendages (Fig. 11A). Tergites are drawn out latero-terminally into stout spines (Fig. 11H). The specimen shows exquisite preservations like setules on spines of the third appendage and a sixth and seventh appendage.

Antennula only known from its most proximal two articles with no changes compared to the preceding stage. Second appendage almost the same to the preceding stage, besides an additional seta on the disto-lateral rim of the most proximal exopod article. Third appendage similar to that of the preceding stage, besides an additional soft seta on the lateral side of the exopod, thus now four such setae (three before). It is situated on the proximo-lateral rim of the exopod (Fig. 11B).

Fourth appendage resembling that of preceding stage, besides the more elongated insertion area, medio-lateral axis being about 3.5 times antero-posterior axis (3.3 before) (Table 2; Fig. 15). Basipod and endopod of fifth appendage unchanged compared to the preceding stage, besides a demarcation separating the second endopod portion into two (Fig. 11D) and the more elongated insertion area of the appendage, the medio-lateral axis being about 3.8 times antero-posterior axis (2.5 before) (Table 2; Fig. 15). Distal part of exopod a large paddle with step-like indentations for the insertion of 11 spine-like setae and six associate setae along the outer margin (Fig. 11A) (last known status: fifth stage with four spine-like setae), one terminal seta, four setae insert medially and six laterally. The associate setae insert antero-laterally to the two most distal median setae, the terminal seta and the three most distal lateral setae.

Sixth appendage now resembling the fourth and fifth appendage in having a bipartite exopod articulating to the proximal part of the proximal endopod portion, the lateral side of the basipod, and reaching further laterally into the arthroal membrane on the appendage (Fig. 11A). Insertion area oval, elongate, medio-lateral axis being about five times antero-posterior axis (1.5 in stage seven). Basipod carries four

spines on its medio-distal rim: one medially, two more anteriorly, one more posteriorly.

Proximal endopodal portion consists of two (still?) unseparated articles, as indicated by a bulge and two setae, dividing the portion into two parts of more or less equal length, each about as long as their diameter. One of the two setae on the disto-median rim of the proximal part is set medially, the other one more anteriorly. Distal part with two setae on its disto-median rim, also one set medially, the other one more anteriorly. Second portion elongated, about 1.5 times as long as the diameter and with two medially pointing setae on its disto-median rim. Further distal parts unknown. Exopod paddle-shaped, bipartite. Proximal article elongated triangular in shape. It articulates with the proximal of the two articles of the proximal endopodal portion, the lateral side of the basipod, and reaches laterally into the arthroal membrane of the appendage. Distal part with step-like indentations for the insertion of 10 spine-like setae and three associate setae on its margin, one seta terminally, six laterally and three medially (status before unknown) (Table 2). Associate setae insert antero-laterally to the most distal median spine-like seta, the terminal seta and the most distal lateral seta.

Seventh limb with basipod, endopod and exopod (Fig. 11A). Insertion of appendage oval, elongate, medio-lateral axis being about six times antero-posterior axis (1.3 in stage seven, unknown for stage 8). Basipod setation not known. Endopod at least consisting of three portions (two preserved at most). Setation of the most proximal podomere unknown. Next distal podomere carries a single seta at its disto-median rim. Further distal parts unknown. Exopod bipartite, insertion oval, elongate, medio-lateral axis being about 5.8 times antero-posterior axis (status unknown before). Proximal part of exopod articulates with the lateral side of the basipod, but reaches further laterally into the arthroal membrane of the appendage. Distal part of exopod paddle-shaped with step-like indentations for the insertion of eight setae, one terminally, two medially and five laterally (status unknown before) (Table 2).

Eighth appendage with basipod, endopod and exopod (Fig. 11G). Basipod and endopod are not (yet?) clearly demarcated from each other. Single median seta presumably on to the most proximal endopod portion, thus the endopod would be made up of three portions, the two proximal ones only distinguished by the presence of the seta. Terminal portion is club-shaped, extends into a distally pointing seta. Exopod articulates laterally on the basipod, insertion area being oval, medio-lateral axis being about 2.5 times antero-posterior axis. Exopod paddle-shaped and carrying four setae, one terminally, two laterally and one medially.

2.2.10. Stage ten. Stage represented by four specimens: one relatively complete specimen, holotype UB 102; two isolated appendages, UB W 337, UB W 338; and an isolated trunk fragment UB W 339. Body comprising a head with five limb-bearing segments and a trunk with three free segments and a caudal end (Figs 15, 16). Tergite-bearing trunk segments carrying biramous appendages, shield-covered caudal end with a pair of uniramous limb buds. Membranous connections between the bubble-like structures formerly left and right of the hypostome and their stalks, as well as that between stalks and body being very elaborate. Hypostome unchanged.

Antennula preserved from its two most proximal parts, now showing changes (Fig. 12A). Second appendage resembles that of preceding stages in many aspects. Triangle of three strong spines (as before), but proximal to these a new, fourth strong spine occurs (Fig. 17). As before, postero-distally to the triangle of spines a smaller spine is situated. Two new smaller medially pointing spines are present on the more posterior area

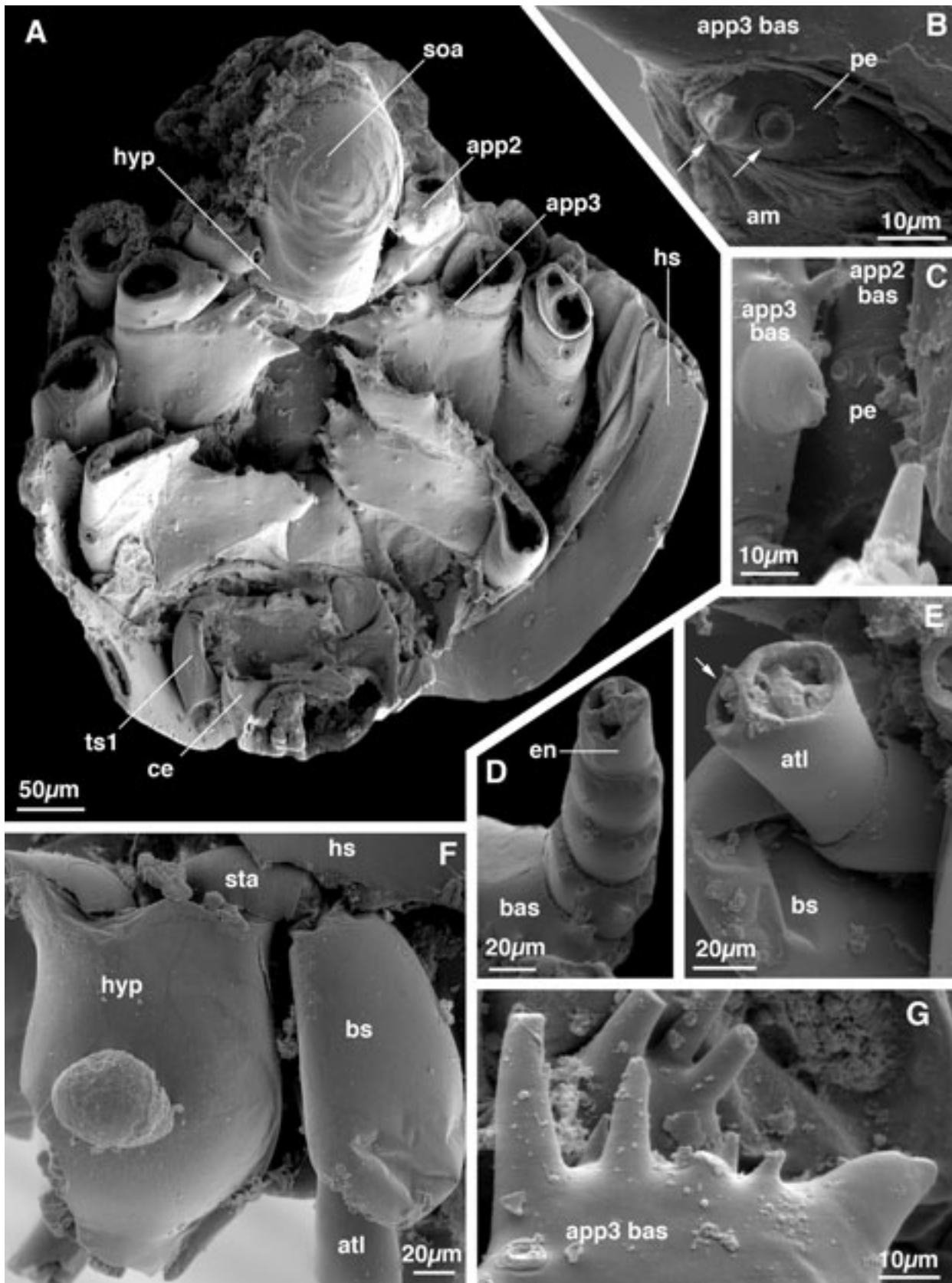


Figure 10 Developmental stage 8 of †*Henningsmoenicaris scutula* (Walossek & Müller, 1990): (A–C) UB W 266: (A) ventral view displaying general organisation; (B) details of medio-proximal aspects of the right third appendage displaying the proximal endite. Remnants of two setae marked by arrows; (C) details of medio-proximal aspects of the right second appendage displaying the proximal endite. (D–F) UB W 335: (D) details of basipod and endopod of the left fifth appendage from median; (E) details of the antennula. Arrow indicates the insertion area of a large probably spine-like seta; (F) details of the blisters, i.e. the initial lateral eyes seen from anterior. Eye stalk exhibits a strongly sclerotised area. (G) UB W 266, details of the basipod of the right third appendage from posterior. Image tilted compared to A. Abbreviations: am=arthrodial membrane; app=appendage (2–3); atl=antennula; bas=basipod; bs=blister; ce=caudal end; en=endopod; hs=head shield; hyp=hypostome; pe=proximal endite; soa=softer area on hypostome; sta=sclerotised region of the eye stalk; ts=trunk segments.

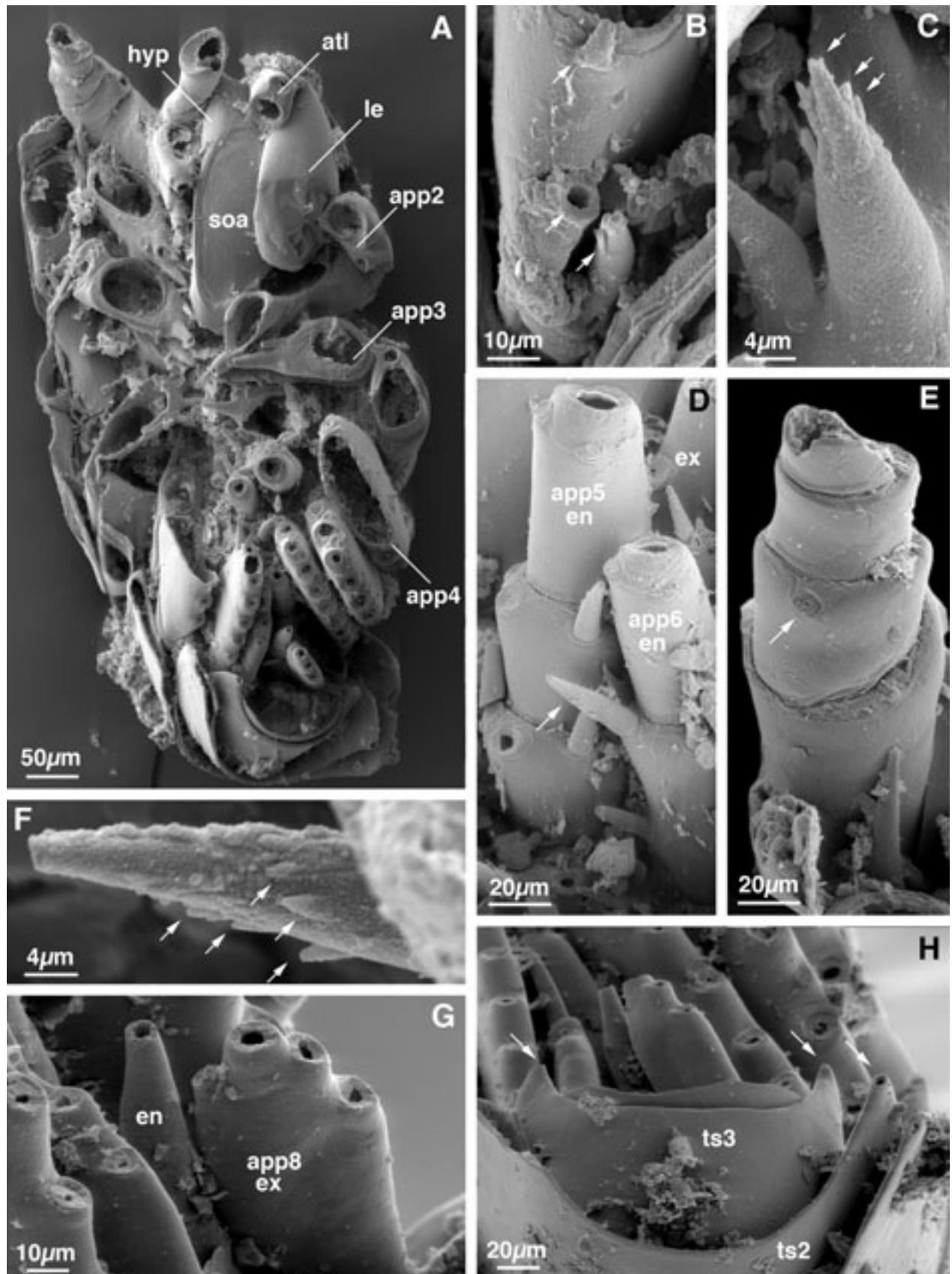


Figure 11 Developmental stage 9 of †*Henningismoenicaris scutula* (Walossek & Müller, 1990), UB W 336: (A) ventral view showing general organisation; (B) details of the most proximal article of the exopod of the right third appendage. Arrows indicate the soft setae on the lateral margin; (C) details of a median basipodal spine showing setules indicated by arrows; (D) median view of the endopods of the fifth and sixth appendages. Arrow indicates the seta that is displayed in detail in F; (E) lateral view of the exopod of the second appendage displaying a lateral insertion on the second article; (F) detail of a single seta from the sixth appendage displayed in D, image slightly rotated. Arrows indicate setules; (G) close-up of the eighth appendage; (H) details of the dorsal aspects of the tergites. Arrows indicate stout spines. Abbreviations: app=appendage (2–6, 8); atl=antennula; en=endopod; ex=exopod; hyp=hypostome; le=lateral eye (was referred to as bs, blister in earlier stages); soa=softer area on hypostome; ts=trunk segments.

of the basipod, one on the level of the two distal spines of the triangle, the other one between the level of the proximal spine of the triangle and the level of the more proximal strong spine (Fig. 17). Other details of the second appendage unchanged (Fig. 12C).

Third appendage similar in most aspects to that of preceding stage, but now with more spines in the two rows of smaller spines between the two prominent spines of the median edge, the anterior row with four smaller spines (two before), the posterior row also with four spines (three before). On the medio-anterior edge of the basipod there is a row of three spines pointing medially (one in stage 8). Another row of comparable spines occurs on the posterior side of the basipod (two in stage 8) (Fig. 17). Exopod carries now three new associate setae, on the two proximal exopodal articles, which carry one median seta each and on the next distal article that carries a pair of setae (Table 2). These three new associate setae insert medially to the larger spine-like setae (Fig. 12C).

Fourth appendage as in preceding stages, but exopod setation comprising nine spine-like and eight associate setae (eight spine-like setae in stage six and at least three associate setae in stage nine; Fig. 10D; Table 2), one seta terminally, three medially and five (four in stage six) laterally. All setae but the most proximal median seta have an associate seta antero-medially. Eight most likely sensorial setae close to the strong seta on the margin are represented by small holes in the anterior surface of UB 102 (Fig. 12D).

Fifth to seventh appendages unchanged compared to preceding stages as far as preserved (Fig. 12E for fifth, 12F for sixth appendage), but appendages rotated 45° compared to standard orientation (55° before), median edges facing medio-anteriorly. Seventh appendages rotated 50° compared to standard orientation (65° before), median edges facing medio-anteriorly (Fig. 15.10). Eighth appendages rotated 65° compared to standard orientation (70° before), median edges facing medio-anteriorly (Table 2; Fig. 15.10). Terminal portion of endopod of fifth appendage short and globular, distally extending into a seta. Eighth appendage now with a single seta on the disto-median rim of the penultimate endopodal portion and an exopod with step-like indentations for the insertion of five setae (four in preceding stage): one of these setae medially, one terminally, three laterally (two in preceding stage) (Fig. 12G). A ninth appendage is present, developed as a club-shaped, uniramous limb bud (Fig. 12G).

2.2.11. Advanced developmental stage. A single specimen, UB 103, is interpreted as a trunk fragment of a significantly older stage (Fig. 13). The fragment comprises three segments with broad tergites and the proximal parts of three pairs of appendages. Unfortunately, the specimen has been damaged since the original description, so that the description given herein is based on photographs taken before this restudy.

Tergites only fragmentarily preserved. Appendages of the trunk, as noted for earlier stages, made up of basipod, endopod and, presumably, bipartite exopod, but proximal to the median side of the basipod with an additional structure, a lobate spine-bearing sclerotisation, the proximal endite. The most anterior appendage with six stout spines on the proximal endite (arrangement of spines shown in Fig. 17), next posterior appendage with four stout spines (Fig. 17). Third appendage not known in detail. Basipod sub-rectangular in anterior view, carrying the endopod medio-distally and the exopod laterally. The basipod has a pronounced line running from the latero-distal edge to the proximo-median edge on the anterior side (Fig. 13). Posterior surface unknown. Median edge with a number of stout spines. The more anterior appendage carrying 15 stout spines (arrangement displayed in Fig. 17), next posterior appendage with 11 stout spines (arrangement dis-

played in Fig. 17). Endopod known only from its proximo-lateral parts. The joint of the exopod runs into the latero-distal side of the endopodal portion. Antero-laterally to this, an elaborate, distally drawn out hump carries a distally pointing seta. Exopod bipartite: proximal part forms a joint with the proximal endopodal portion on the lateral side of the basipod and reaches further into the arthro-dial membrane of the appendage. The distal part of the exopod is not preserved.

2.3. Development of specific structures

2.3.1. Terminal size. The maximum size of †*Henningsmoenicaris scutula* has to be re-evaluated against the original description in the light of the new data. The holotype specimen, the largest of the fully preserved specimens, but not representing a representative of the largest stage, is about 1 mm long. As can be estimated from the large fragment of a later stage, a maximum length of about 2.5 mm for this stage seems realistic, assuming an isometric growth of head and trunk (Fig. 14), but it remains unclear if this was the final, i.e. adult, stage.

2.3.2. Addition of segments. The first stage known has four appendage-bearing segments (1 in Figs 14–16), thus being a head larva *sensu* Walossek & Müller (1990). No segment addition seems to happen in the next three stages (2–4 in Figs 14–16). When the fifth appendage appears in ontogeny (stage five; 5 in Figs 14–16), its segment is incorporated within the head shield, thus the fifth appendage is a head appendage (Fig. 8C). The sixth appendage that appears in stage six (6 in Figs 14–16) inserts in a distinctly set-off area, the rather small caudal end, covered by a shield that merges into the terminal spine that is now longer on the head shield. This portion also carries the anus.

By the seventh stage, a seventh pair of appendages appears (7 in Figs 14–16) on the caudal end, which now carries two pairs of appendages (6th and 7th trunk limbs) but is still covered by a single dorsal shield (Fig. 9F), terminally extending into the terminal spine (7 in Figs 14–16). At stage eight, the trunk is made up of two portions, a free tergite-bearing segment with the sixth pair of limbs, and the caudal end carrying now two pairs of limbs (7th and 8th, see previous stage; Fig. 10A; 8 in Figs 14–16). Stage nine, again, bears three free tergite-bearing trunk segments each carrying limbs, and the apodous caudal end (Fig. 11A, H; 9 in Figs 14–16). The caudal end carries a pair of rudimentary appendages by stage ten (Fig. 12G; 10 in Figs 14–16), indicating that it is a compound of trunk region (at least one segment) and telson. Whether this portion is later subdivided into another free tergite and a terminal portion cannot be stated.

The condition of the caudal end in stage seven and stage eight fulfils the definition of a pygidium according to Hughes *et al.* 2006: ‘. . . conjoined segments posterior to the last trunk articulation, regardless of ontogenetic stage, specific identity or ultimate fate.’, as the portion posterior to the last trunk articulation carries two pairs of appendages, thus these segments are ‘conjoined’. Further reminiscence of a (typical trilobite) pygidium is the developmental fate of the segments carrying the seventh and eighth appendages, which are at first conjoined (see above) to the next anterior one and the caudal end, and become free later in development. Therefore the terminal structure furthermore fulfils the developmental based definition of a pygidium given by Ramsköld *et al.* (1997). See discussion for more details on this aspect.

2.3.3. Lateral eyes. †*Henningsmoenicaris scutula* develops a pair of blister-like structures lateral (5 in Figs 14–16), and later antero-lateral to the anterior end of the hypostome (8 in Figs 14–16). The blisters are interpreted as the lateral (compound) eyes. The lateral eyes are clearly recognisable at stage

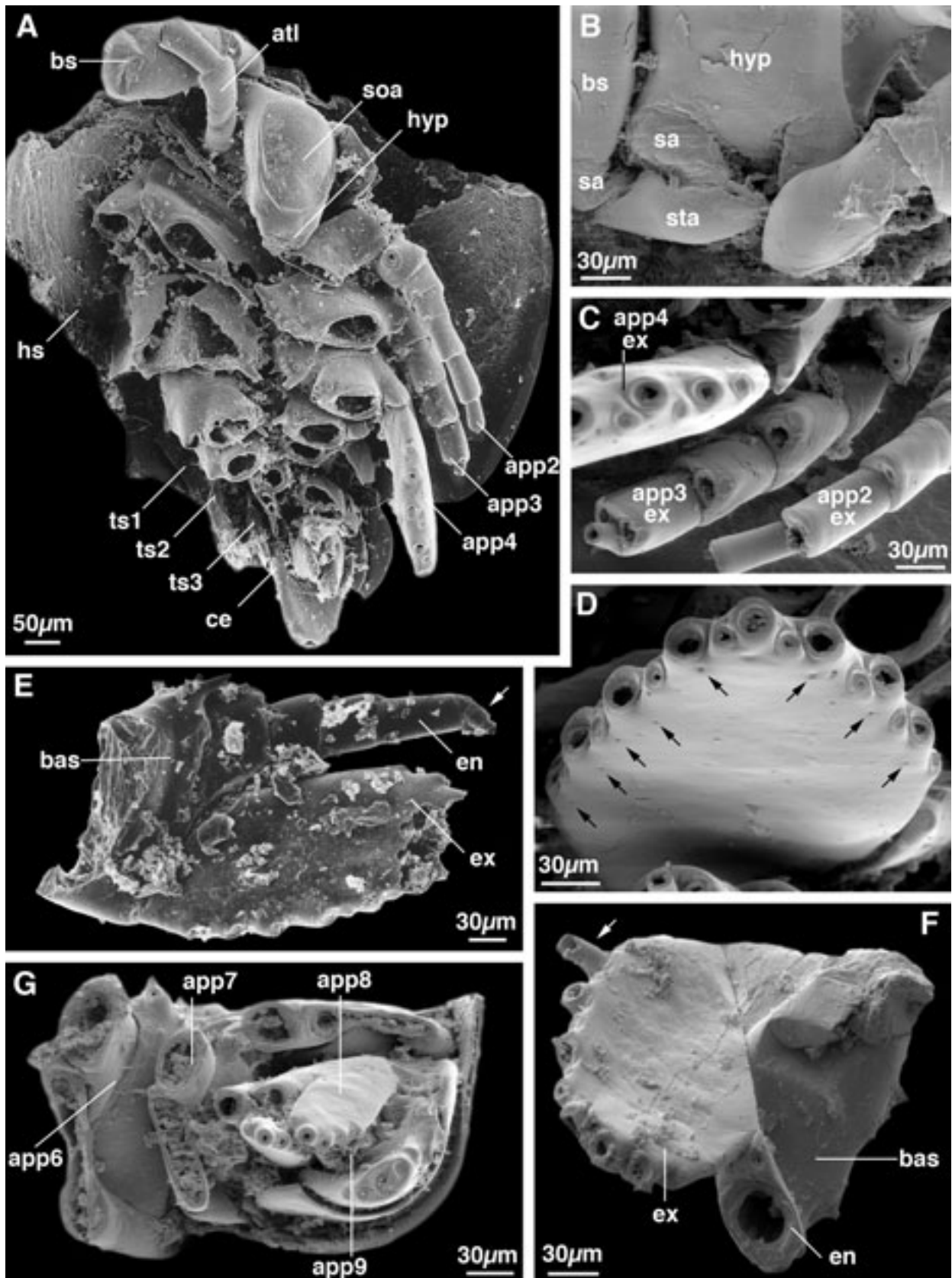


Figure 12 Developmental stage 10 of †*Henningmoenicaris scutula* (Walossek & Müller, 1990): (A–D) Holotype UB 102: (A) ventral view displaying general organisation; (B) detail of the anterior region of the hypostome. The lateral eye has two soft areas distally and proximally to the strongly sclerotised eye stalk; (C) details of the exopod of the third appendage; (D) Detailed view of the exopod of the fourth appendage. Arrows point to holes probably marking the original insertion of sensorial setae. (E) UB W 338, Isolated fifth appendage from posterior. Arrow marks the most distal portion of the endopod. (F) UB W 337, isolated and distorted sixth appendage, more or less from anterior. Arrow indicates one of the broken-off spine-like setae emerging from the exopod. (G) UB W 339, isolated trunk seen from posterior. Ninth appendage present as anlagen. Abbreviations: app=appendage (2–4, 6–9); atl=antennula; bas=basipod; bs=blister; ce=caudal end; en=endopod; ex=exopod; hs=head shield; hyp=hypostome; sa=membranous area of the stalk; soa=softer area on hypostome; sta=sclerotised region of the eye stalk; ts=trunk segments.

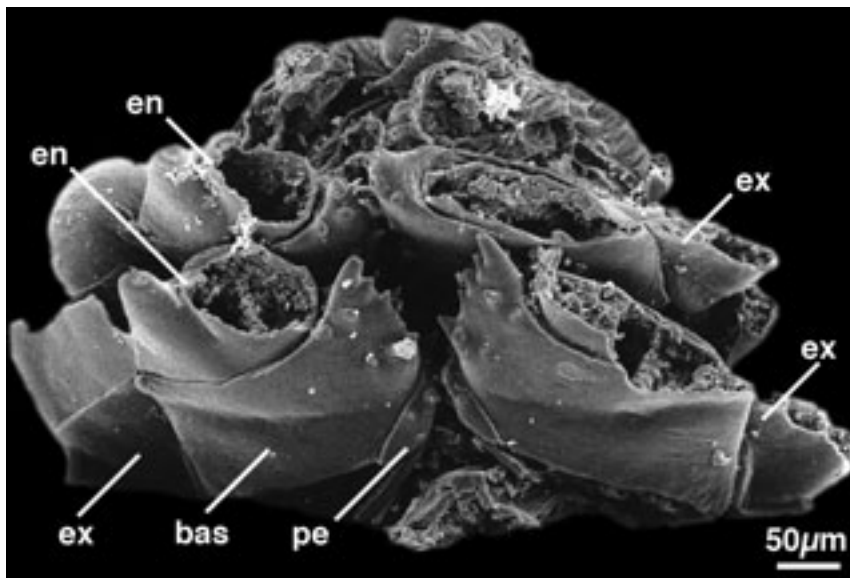


Figure 13 Fragment representing a late developmental stage of †*Henningsmoenicaris scutula* (Walossek & Müller, 1990), UB 103. The isolated trunk is shown in anterior view displaying details of the appendages. Abbreviations: bas=basipod; en=endopod; ex=exopod; pe=proximal endite.

five (Fig. 8A; 5 in Figs 14–16). They start as oval elevations directly inwards of the shield margin antero-laterally of the hypostome, so clearly separate from both structures (Fig. 8A). Progressively, the blisters become more prominent and bulbous (Fig. 8E). The lateral eyes are free from the body surface at stage 7 on their lateral side and only attached directly right and left next to the hypostome (Fig. 9A). The lateral eyes are stalked from stage eight on (Fig. 10F; 8 in Figs 14–16). The stalks are tube-like sclerotised structures that seem to insert right on the anterior of the hypostome. In stage ten the stalks have pronounced membranes, both proximal and distal, i.e. on the body-stalk connection and the stalk-eye-bubble connection (Fig. 12B; 10 in Figs 14–16).

2.3.4. Hypostome. The hypostome (Table 2; Fig. 15) becomes more elongate throughout development. At stage one the approximate length to width ratio is 1:3; it increases to 1:8 in stage three, 2 in stage three and reaches 2:3 in stage four. This ratio remains unchanged later in development. The soft area on the ventral (distal) side of the hypostome is interpreted as a possible median eye. The area first becomes faintly visible in stage three (Fig. 7B), but is not clearly visible before stage five, where the area is circular close to the posterior end of the hypostome. It reaches further anteriorly in stage six, and even further in stage seven, until it covers almost the complete ventral (distal) surface of the hypostome from stage eight onwards (Fig. 10A).

2.3.5. Appendages. The development of the appendages can be traced in great detail throughout the ontogenetic sequence. The antennula in the earlier stages appears soft, but is more strongly sclerotised in later stages. Of the three anterior setae present in earlier stages (Figs 5B, 6F), only the most proximal one can be recognised by its large insertion in older stages (Fig. 10E). This large seta becomes distinctly offset, jointed and very large in diameter (Fig. 10E). More distal portions of the antennulae are not preserved for older stages. All post-antennular appendages/limbs change the shape of their insertions from being oval in young to more elongated in older stages. Another general observation is the increase of spines on the median surfaces of the basipod, the endopod portions and possibly also of the proximal endite during ontogeny (Fig. 17). Another significant increase can be detected in the number of setae of the exopods, especially on the appendages 4–8 (Table 2; Fig. 20).

In the first two larval stages, the second and third limbs look quite similar to each other (Figs 18, 19). By the third stage, the exopod of the second appendage, now with clear demarcations of its articles, comprises one more article (Fig. 18.3) than before (Fig. 18.1, 2). By stage four the distance between the two prominent basipodal spines of the third limb has increased, and additional spines appear at stage five and the following stages in this gap, starting to form a strong gnathal edge on the basipod (Fig. 18.4). In stage five there is also an additional difference in the appearance of the hook-shaped spine on the most proximal exopod article of the second limb (Fig. 18.5). In stage seven more complex organisational changes occur by offsetting the distal part of the basipod, which is from then on freely articulated and appears like an endopod podomere. Additionally, the proximal endites appear on both limbs, but they are connected to the basipod in the second limb and free and, possibly, functional in the third already (Fig. 17). During further development of the basipod the gnathal edge of the third limb becomes more and more defined (Fig. 19), and the basipod of the second limb becomes more and more elongated. Additionally the second limbs are rotated from -10° to -40° during ontogeny, i.e. their median edges facing further posteriorly, while the third appendage remains perpendicular to the body axis, i.e. in standard orientation. The tenth stage shows another difference to the early stage in that the articles of the exopod of the third appendage gain an associate seta on the proximal three setiferous articles (Fig. 12E), which are not seen in the second cephalic limb.

The fourth cephalic limb shows a distinctive re-organisation of its morphology during ontogeny (Fig. 20). These changes are, in a shortened form, also seen in the more posterior limbs. It starts as a biramous limb with the basipod and rami not clearly demarcated. The exopod is a simple paddle with distal setation at first. Up to the sixth larval stage the basipod becomes more elongated. This is coupled with the enlargement of the exopod paddle and thus the elongation of the insertion area. With the seventh stage major changes occur in that the exopod is now divided in two, with its proximal part being joined to the basipod, to the proximal endopodal podomere and reaching beyond the proximo-lateral rim of the basipod into the arthrochial membrane of the appendage.

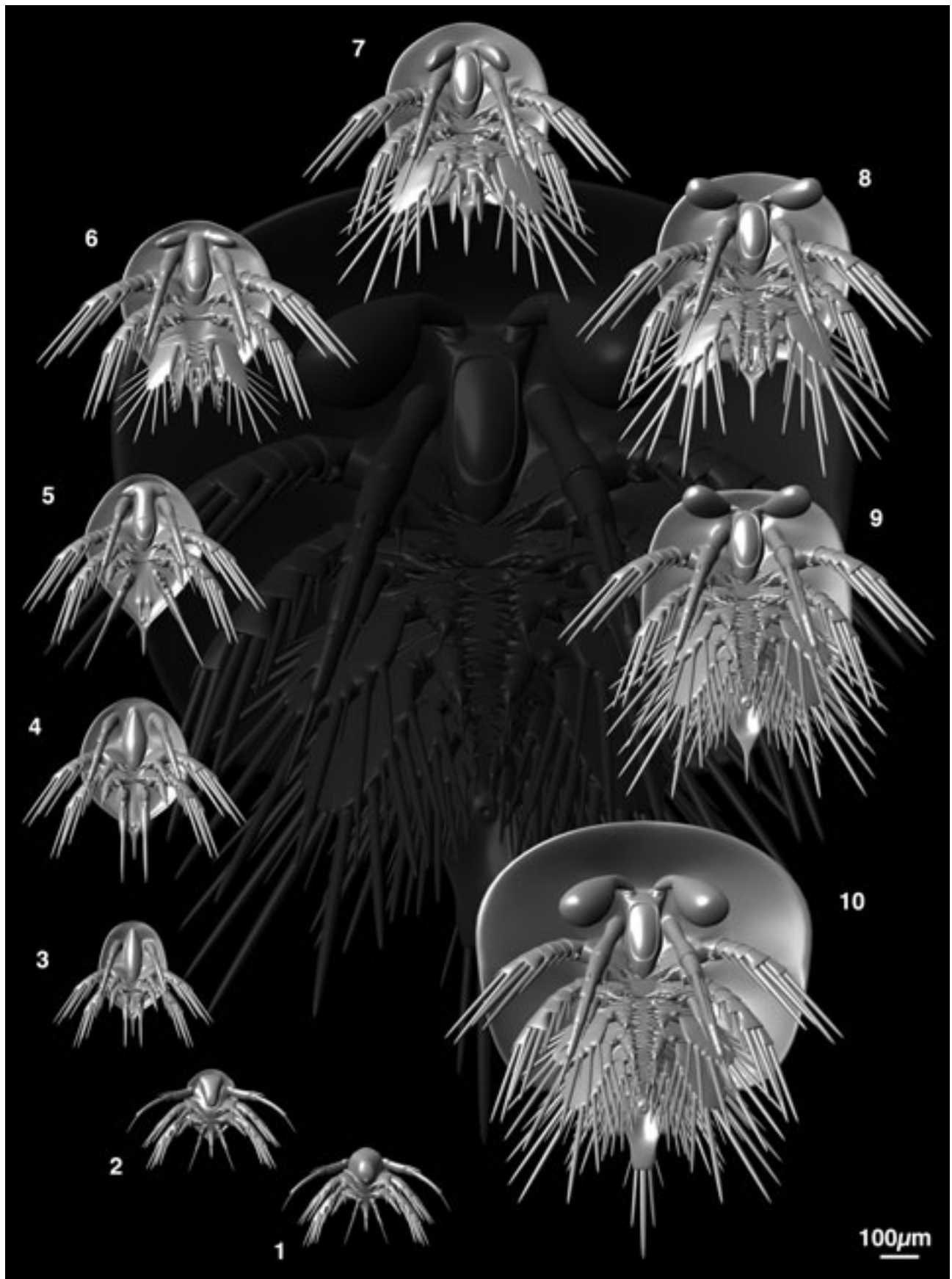


Figure 14 4D model of †*Henningsmoenicaris scutula* (Walossek & Müller, 1990). The ten successive developmental stages are marked with numbers. A putative model of the later developmental stage represented by UB 102 (see Fig. 13) is displayed in the background to show the possible size.

The fifth cephalic limb resembles in its development that of the fourth in many aspects and also the sixth limb shows the same developmental pattern. The seventh limb shows some differences

in not having a connecting joint between endopod and exopod, but shares the bipartite exopod and the laterally not closed basipod. The more posterior limbs are not known in enough

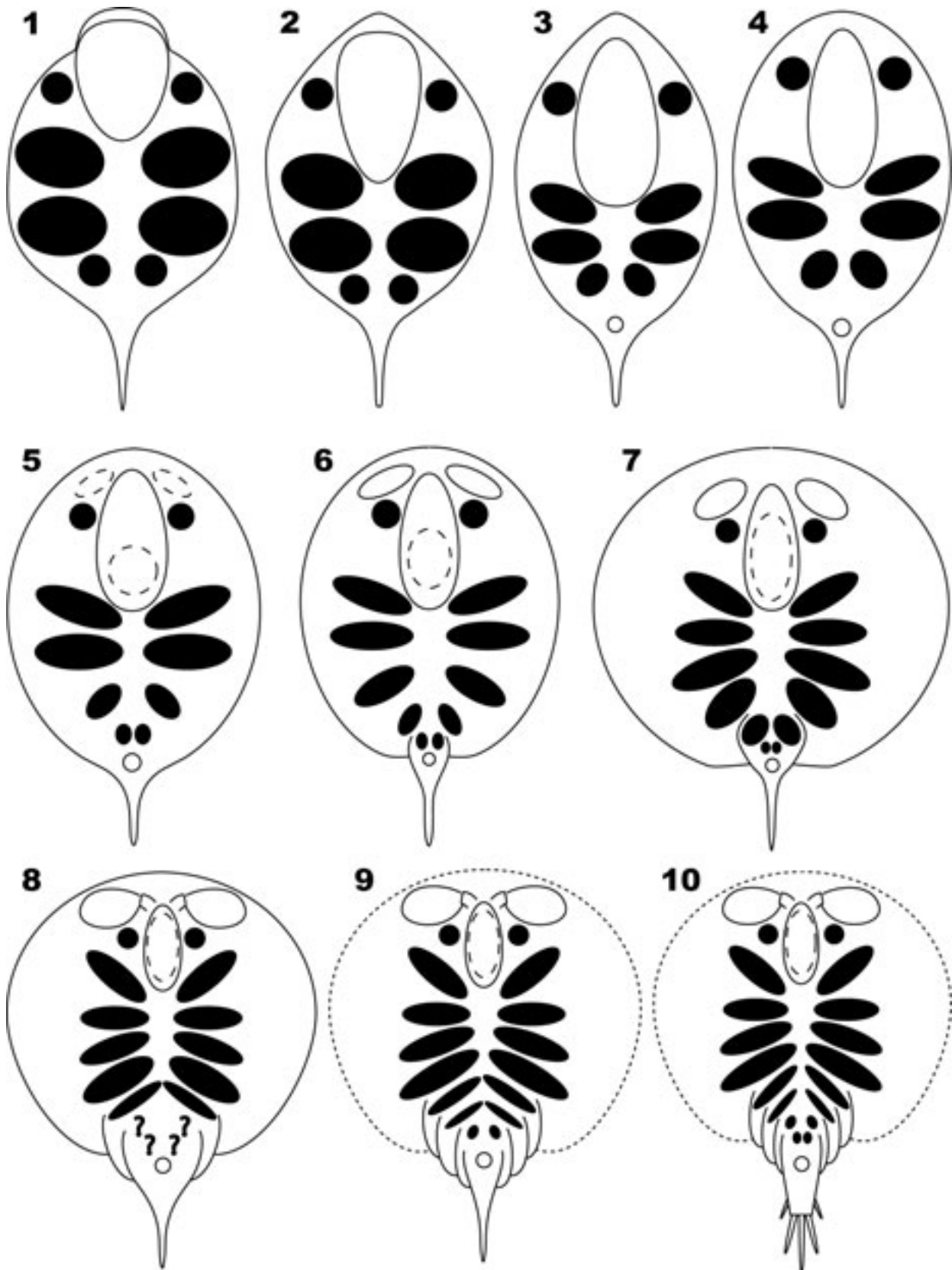


Figure 15 Simplified and schematised ventral view of the ten developmental stages of †*Henningismoenicaris scutula* (Walossek & Müller, 1990) displaying ratio lengths and angles but not exact outlines. Appendages omitted, only insertions shown. Stages marked by numbers. Not to scale. Stippled outlines of bubble-like structures and softer area on the hypostome indicate the not sharply demarcated edge. Dotted lines of the shields of stage nine and ten refer to the incomplete knowledge of these structures in these two stages. Shield in stage ten possibly larger (see Fig. 14) but kept small here to save space.

detail. The fifth limb seems to be the largest of the whole limb series. This is congruent with other finds in euarthropods and, therefore, may possibly be a rather plesiomorphic trait.

Later development of all limbs seems to include the appearance of a large proximal endite, as it is documented for the second and third but also indicated for the more posterior

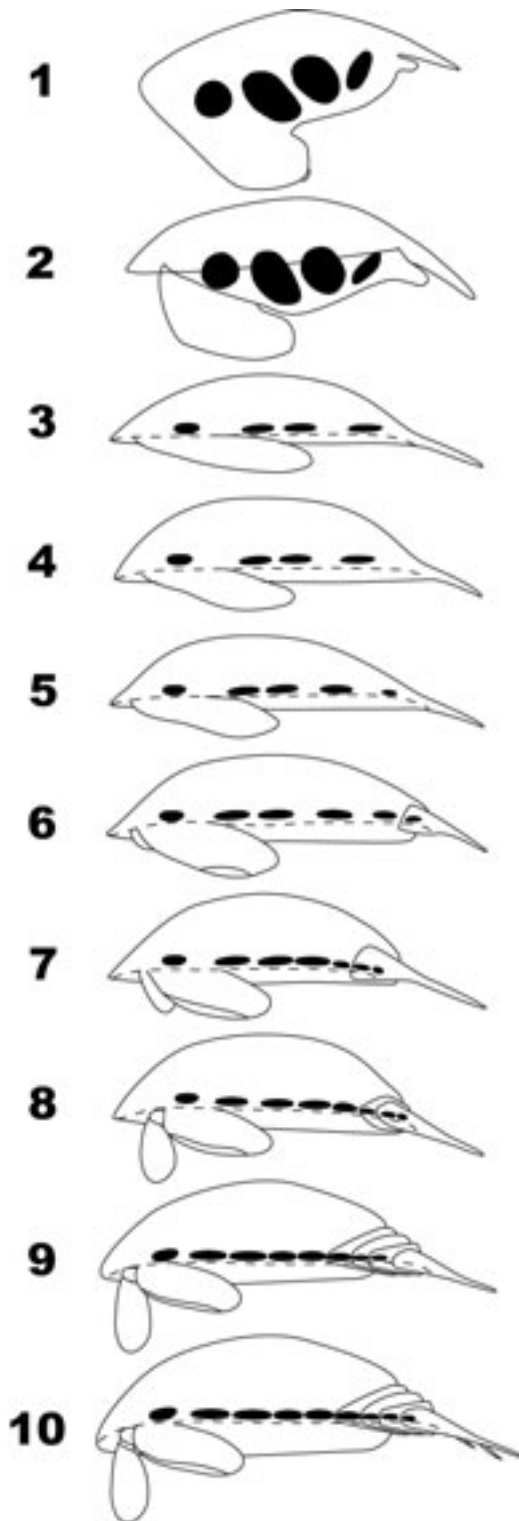


Figure 16 Simplified schematic lateral views of all ten developmental stages of †*Henningsmoenicaris scutula* (Walossek & Müller, 1990). Appendages omitted, only insertions shown. Stages marked by numbers. Not to scale.

trunk by the large trunk fragment, representing a significantly older stage. Based on this, it may be assumed that all post-antennular appendages eventually gain a proximal endite later in development.

3. Systematic palaeontology of †*Sandtorpia vestrogothiensis* gen. et sp. nov.

Arthropoda von Siebold & Stannius, 1845
Crustacea Brünnich, 1772

Oelandocarididae taxon nov.

†*Sandtorpia* gen. nov.

Derivation of name. After Sandtorp, a small assemblage of houses at the Kinnekulle, a shallow hill near lake Vänern in Västergötland, Sweden.

Type species. *Sandtorpia vestrogothiensis* sp. nov.

†*Sandtorpia vestrogothiensis* gen. et sp. nov.

Derivation of name. After Västergötland (the Latin name of Västergötland), the Swedish area where the locality is situated.

Holotype. Single specimen representing an immature stage of the species, UB W 340/SPEC 4144. The holotype is the only known specimen of the species. It is an immature stage composed of the head, no articulated trunk is (yet?) developed. Head with at least four, possibly five, appendage-bearing segments (see section 3.2 for discussion of this issue).

Proximal two portions of antennula present, third portion of antennula broken off distally. Second appendage, distal part of endopods and almost complete exopod missing. Third appendage, distal part of endopods missing. Massive terminal spine broken off after 115 µm, but presumably much longer.

Locus typicus. Gum at the Kinnekulle, Västergötland, Sweden (sample number 6784).

Material. The species is exclusively represented by the holotype.

Diagnosis. Crustacean with a triangular backwardly pointing hypostome. First appendage made up of at least three portions, with anteriorly inserting setae on the two proximal portions. Seta of the more distal portion much more massive. Most distal article of exopod of third appendage with five setae, three of them terminally, most lateral smaller than the other two terminal ones, two other seta along side inner margin. Both separated by a small step-like indentation. Massive terminal spine with a random pattern of smaller backward pointing spinules.

3.1. Description

(Remarks: The description refers to that specific developmental stage represented by the only known specimen.) Arthropod, head covered by a simple bowl-shaped shield merging posteriorly into a pronounced terminal spine. Length of shield approximately 365 µm, width approximately 250 µm. Terminal spine ornamented by high number of backwardly pointing spinules. Anterior on the ventral side triangular hypostome (about 110 µm length and width) with backwardly pointing tip. Posterior to the hypostome ventral stronger sclerotised area of 115 µm length and 95 µm width. Sclerotised area followed by a softer area of 25 µm. Posterior to that again a stronger sclerotised area of about 50 µm length. Behind this area the anus surrounded by soft membrane is positioned right anterior to the base of the terminal spine.

The antennulae insert left and right of the anterior edges of the hypostome (Fig. 21B). Antennula strong, limb-like, circular in diameter, made up of at least three portions. Most proximal portion twice as long as the diameter. Second portion slightly shorter. Antero-medially on the base of the second portion small set-off area carrying an antero-medio-distally pointing seta. Antero-medio-distally second portion drawn out to form a socket for an antero-medio-distally pointing seta, larger than the more proximal seta.

Second appendage inserting right posterior to the hypostome, left and right at the anterior edge of the stronger sclerotised ventral area (Fig. 21B). Appendage with basipod carrying the endopod medio-distally and the exopod latero-distally. Basipod sub-triangular, medio-lateral axis about 2.5

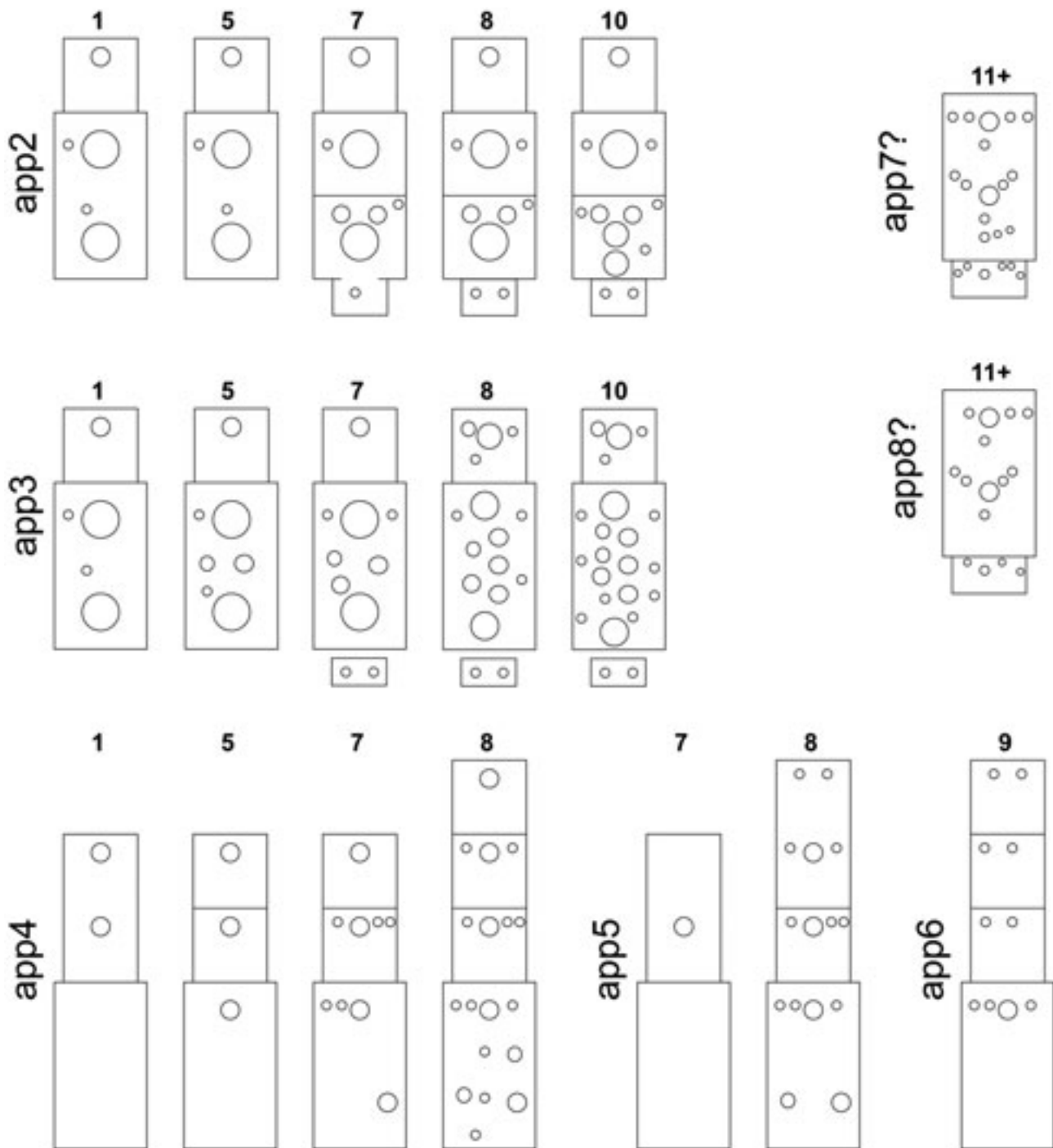


Figure 17 Scheme of the arrangement of spines on the median surfaces, i.e. proximal endite basipod and proximal endopod portions of the appendages throughout ontogeny; omitted are the distal endopod portions lacking median setation. Note that size and shape of endopod portions is schematised and not to scale. Appendages 2–8 numbered as app2–8, number indicating the developmental stage. For stages that are not shown, no changes occurred compared to preceding stage, or stage is not preserved. The identity of the appendages of the late developmental stage (named 11+) is unclear; most parsimonious to assume that they are appendage 7 and 8.

times as large proximo-distal axis (Fig. 21C). Medio-distally drawn out distally into a tube-shaped portion where the endopod inserts. Medially two large medially pointing spines, one proximally, one distally. Distal spine with a small associate spine anterior to it. The endopod with at least three podomeres (Fig. 21C). Proximal two podomeres circular in diameter (Fig. 21B) about twice as long as the diameter. Distal part unknown. Exopod only preserved with proximal article, articulating latero-distally on the slope of the basipod. (Fig. 21B)

Third appendages inserting left and right to the middle of the stronger sclerotised ventral area. Third appendage very

similar to the second appendage. Basipod also sub-triangular, medio-lateral axis about 2.5 times as large proximo-distal axis (Fig. 21C). The drawn out medio-distal part is more elongated than in the second appendage. Medially two prominent spines, one proximal one distal, both with antero-distal associate spines. Proximal spine more massive than distal one. Distal part may represent the undemarcated region of proximal endopod, as it is drawn out very far distally. Endopod with at least two portions (one preserved). Exopod with four articles of oval cross section flattened in antero-posterior axis. Proximal article without seta, next two with a single spine-like seta medially.

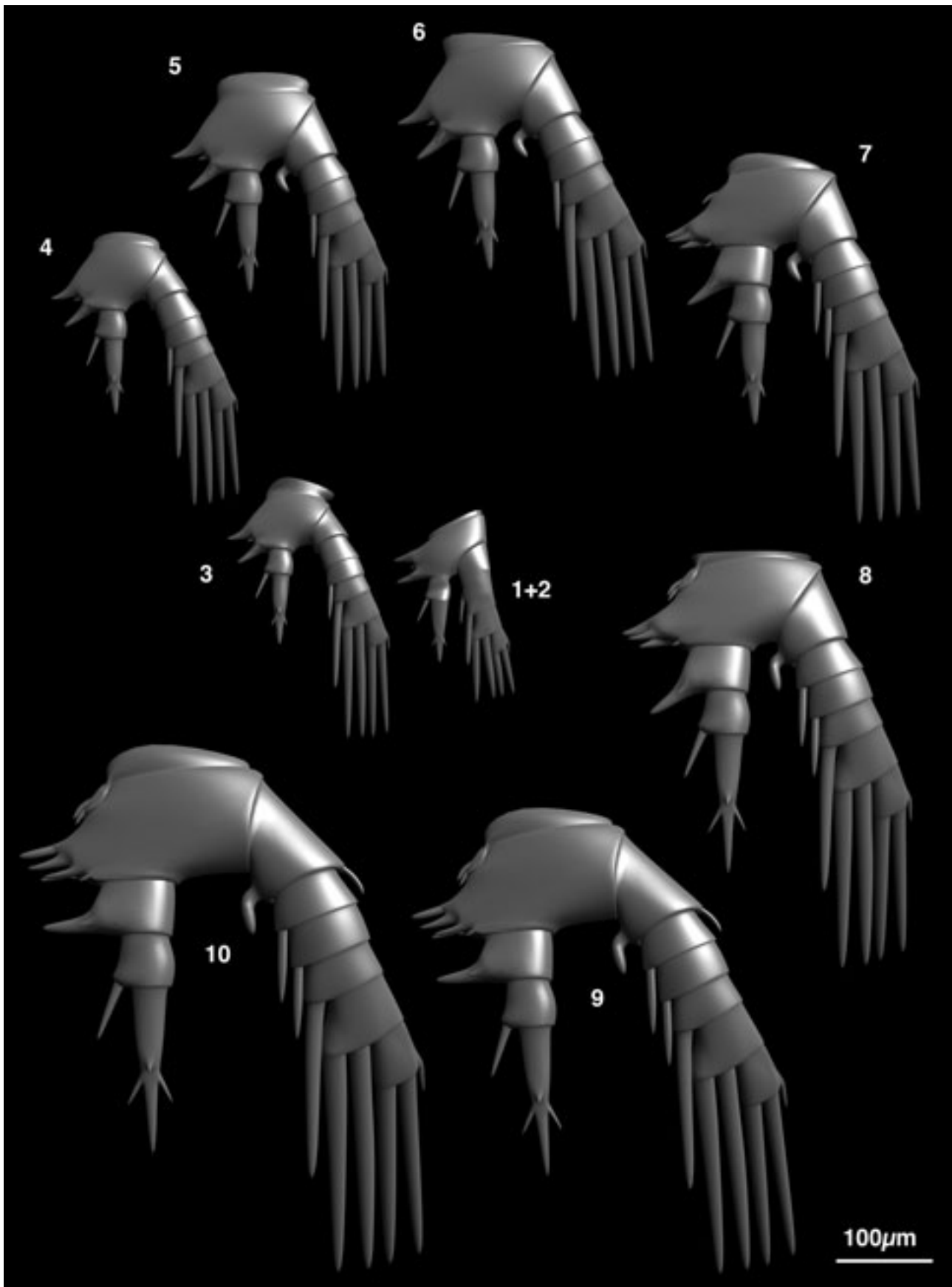


Figure 18 4D model of the second cephalic appendage of †*Henningsmoenicaris scutula* (Walossek & Müller, 1990). Appendages are shown in anterior view. Stages are marked by numbers. Note the elongation of the basipod in latero-medial axis during ontogeny.

The terminal article carries a total of five setae. Three of them insert terminally, the most lateral one being rather small, the other two large. Their diameter is almost as large as the

antero-posterior axis of the exopod. The other two setae insert medially further proximal. The two setae are close to each other but do not form a pair, as one seta is separated by a

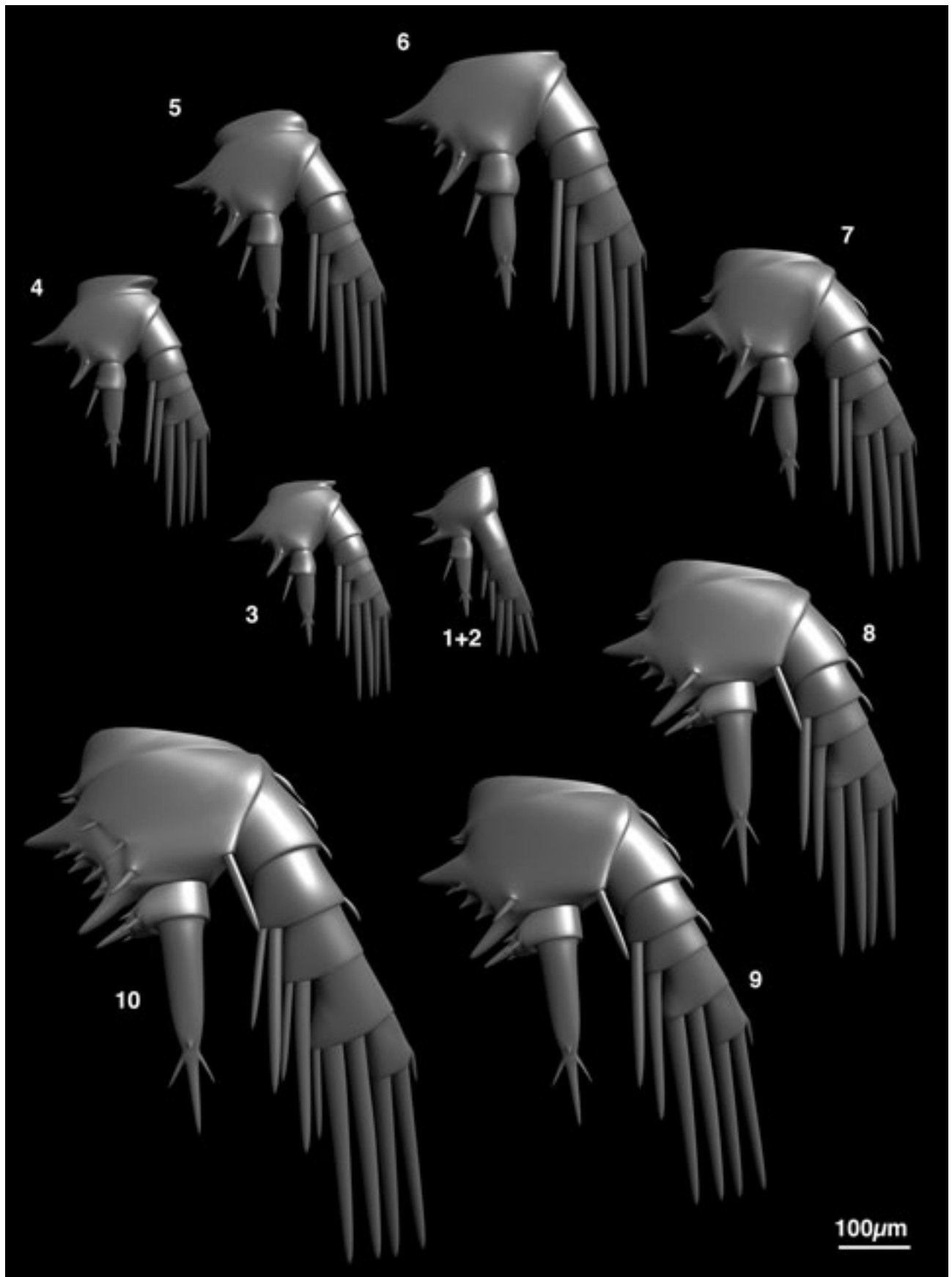


Figure 19 4D model of the third cephalic appendage of †*Henningsmoenicaris scutula* (Walossek & Müller, 1990). Appendages are shown in anterior view. Stages are marked by numbers. Note the change of the median gnathal edge of the basipod during ontogeny.

small step-like indentation, which leads to a slightly more proximal insertion (Fig. 21A). The lateral side of the article is double S-shaped (Fig. 21A).

Fourth appendages insert posterior to the more strongly sclerotised ventral area. Limb comprising basipod, endopod and exopod; demarcation of basipod and endopod unclear.

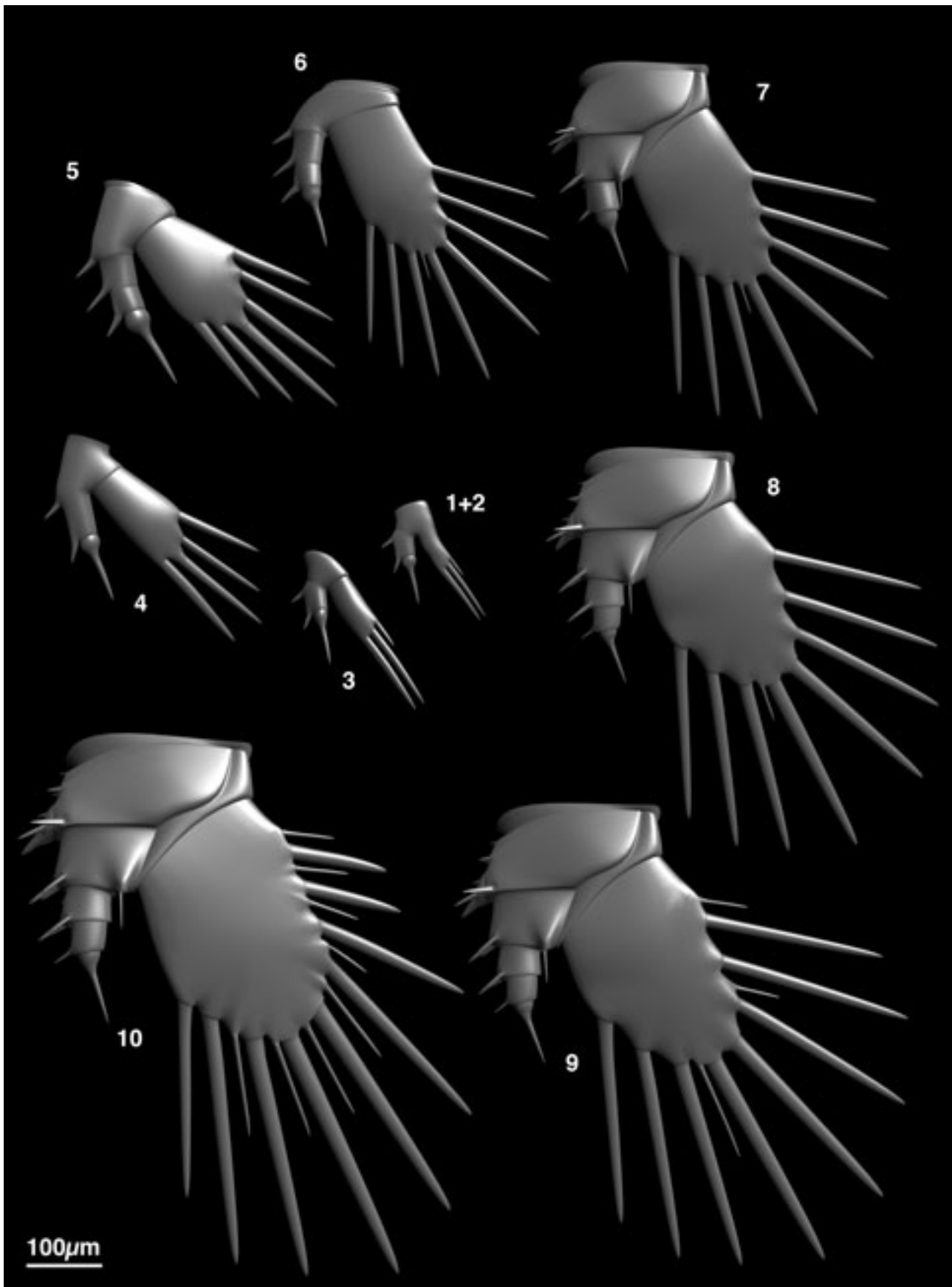


Figure 20 4D model of the fourth cephalic appendage of †*Henningsmoenicaris scutula* (Walossek & Müller, 1990). Appendages are shown in anterior view. Stages are marked by numbers.

Endopod with two portions (Fig. 21B), proximal one unarticulated from basipod, terminal one bullet-shaped, drawn out into long distally pointing seta; a small associate spine latero-

posteriorly at its base. Exopod tube-shaped and of oval cross section, with carries three setae on its distal margin. Two setae are quite prominent, the most lateral one is significantly

smaller than the others. On the posterior stronger sclerotised area a pair of strong club-shaped structures extending into distally pointing seta. These structures point postero-distally.

3.2. Comparison of †*Sandtorpia vestrogothiensis* and †*Henningsmoenicaris scutula*

For a better understanding of †*Sandtorpia vestrogothiensis*, the developmental status of the single specimen of †*Sandtorpia vestrogothiensis* is roughly correlated with a certain developmental stage of †*Henningsmoenicaris scutula*. The shield is not preserved with many details in †*S. vestrogothiensis*. Its size correlates with the single specimen of a stage five larva of †*H. scutula* (Fig. 3). †*H. scutula* bears a pair of rudimentary appendages anterior to the anus in stage five (Fig. 8C) that appear quite similar in shape to the structures anterior to the anus in †*S. vestrogothiensis* (Fig. 21B). These structures might, therefore, be interpreted also as rudimentary appendages. †*S. vestrogothiensis* shows certain similarities to †*H. scutula*, especially in the morphology of the antennula that has a few robust portions with a slightly anteriorly orientated setation (Figs 5B, 10E, 21C), and the exopod of the third appendage with a few portions bearing a spine-like seta and a distal set of three setae, with the most lateral one being smaller than the others (Figs 5F, 6E, 19, 21A).

In spite of this resemblance, these structures differ in detail, as in the antennula of †*H. scutula*, where the most basal seta is very pronounced; in †*S. vestrogothiensis* it is the second (Figs 5B, 21C). Also, the exopod morphology of the third appendages shows differences. In †*H. scutula* the set of three distal setae rests on a separate portion; in †*S. vestrogothiensis* two more setae are present on the terminal portion, which may correspond to the pair of setae on the sub-terminal portion of the exopod of †*H. scutula*, but unlike these they are not a true pair, as they are separated by a small step-like indentation (Figs 5F, 6E, 19, 21A).

More differences can be detected in various other structures. The terminal spine is very pronounced in †*S. vestrogothiensis* (Fig. 21B). Although the spine is not preserved in a stage five †*H. scutula*, the terminal ends of later stages indicate a smaller size in stage five than in †*S. vestrogothiensis*. Also, the backwardly pointing spinules are not present in †*H. scutula*.

The triangular hypostome of †*S. vestrogothiensis* (Fig. 21B, D) differs significantly from the elongated shape present in †*H. scutula* (Fig. 15). There are no eyes developed in †*S. vestrogothiensis*, but in the corresponding stages of †*H. scutula* eyes are initial (Fig. 15). Second and third appendages differ significantly in their basipod morphology. In †*H. scutula* the basipod is a massive sub-triangular structure (Figs 18, 19), whereas in †*S. vestrogothiensis* its proximo-distal dimensions are rather small (Fig. 21C). The fourth appendages of †*S. vestrogothiensis* (Fig. 21B) are, compared to a stage five †*H. scutula*, 'under-developed', as they resemble the fourth appendages of a stage three †*H. scutula* (Fig. 20).

In summary, although there are some similarities between the two forms, they differ in too many details to be considered as conspecific. Thus, in our view, the erection of a separate species for the single specimen of †*S. vestrogothiensis* appears valid. Yet, the various similarities between the two suggest a close relationship, which will be discussed in more detail below.

4. Phylogenetic analysis

4.1. Taxa chosen for the analysis

The analysis was especially designed to explore the basal branchings within Crustacea s. l. and their derivatives, namely

†*Henningsmoenicaris scutula*, †*Sandtorpia vestrogothiensis* (based on data presented in detail herein), †*Oelandocaris oelandica* (based on Stein *et al.* 2005, 2008), †*Gotiscaris longispinosa*, †*Cambropachycope clarksoni* (based on Haug *et al.* 2009) and †*Martinssonsonia elongata* (based on Müller & Waloszek 1986a).

For terminal polarisation, the coded ground patterns of †Phosphatocopina and Eucrustacea have been mainly based on Maas *et al.* (2003), Waloszek (2003), Maas & Waloszek (2005) and Waloszek & Maas (2005). Data availability is more problematic for other Euarthropoda. †*Agnostus pisiformis* (Wahlenberg, 1818) was chosen as it is also preserved in 'Orsten'-type preservation and provides ontogenetic data (coded on the basis of Müller & Waloszek 1987). †*Olenoides serratus* (Rominger, 1887) was included as a representative of 2D-preserved euarthropod taxa as its morphology was well described by Whittington (1975). As an out-group we chose †*Fuxianhuia protensa* Hou, 1987 as a member of Arthropoda s. str. but not of Euarthropoda (coding based in parts on Hou & Bergström 1997 but mainly on Waloszek *et al.* 2005). It is beyond the scope of this present work to clarify relationships within Eucrustacea, particularly the situation of Insecta/Tracheata or Crustacea s. l. within Euarthropoda. This is planned for a later, more comprehensive investigation that will consider all the basal branches of Crustacea, including the still to be re-described ontogeny of †*Martinssonsonia elongata* and description of another, probably closely related, new species, and the description of ontogenetic data of more species of the †Phosphatocopina, which is still under way. In total 10 taxa were included and 30 characters coded (see Supplementary Material for matrix and settings).

Coding of the characters was mainly undertaken using presence ('1') absence ('0') binary coding (Pleijel 1995), or distinguishing between two different conditions. This proved to be especially useful when coding characters for taxa that are not known from all developmental stages, where more characters would have to have been coded as equivocal ('?') than if it had been done as multi-character-state coding. Inapplicable characters are marked by '-'. The analyses were performed with equal weighting using the programs PAUP* and PHYLIP pars (for exact settings see Supplementary Material).

Coding ontogenetic data is in general regarded as problematic (e.g. Humphries 2002) and thus in many cases avoided for both phylogenetic analyses (e.g. Wills 1998) and discussing evolutionary scenarios (Boxshall 2007). Hennig (1965) pointed out that all semaphoronts carry information of phylogenetic value ('holomorph'), but that comparisons must be made amongst corresponding semaphoronts. For judging according stages we relied on segment numbers (cf. Waloszek 1993), for example segmental equivalent to euarthropod head-larva (three-post-antennular segments present).

4.3. Result of the analysis (Figs 22, 23)

PAUP* found nine trees of equal length (Fig. 22A–I), PHYLIP pars two (Fig. 22J–K). One of the latter two trees is equal to the strict consensus tree produced by PAUP* based on the nine single trees. This tree includes two polytomies. The second tree produced by PHYLIP pars has one polytomy less, because one is resolved into two dichotomies. This single tree is preferred over the others (see below).

The preferred tree is given in the following short notation: †*Fuxianhuia protensa*+ (†*Olenoides serratus*+ (†*Agnostus pisiformis*+ ((†*Oelandocaris oelandica*+ †*Henningsmoenicaris scutula*+ †*S. vestrogothiensis*))+ (†*Cambropachycopidae*+ (†*Martinssonsonia elongata*+ (†Phosphatocopina+ Eucrustacea)))))).

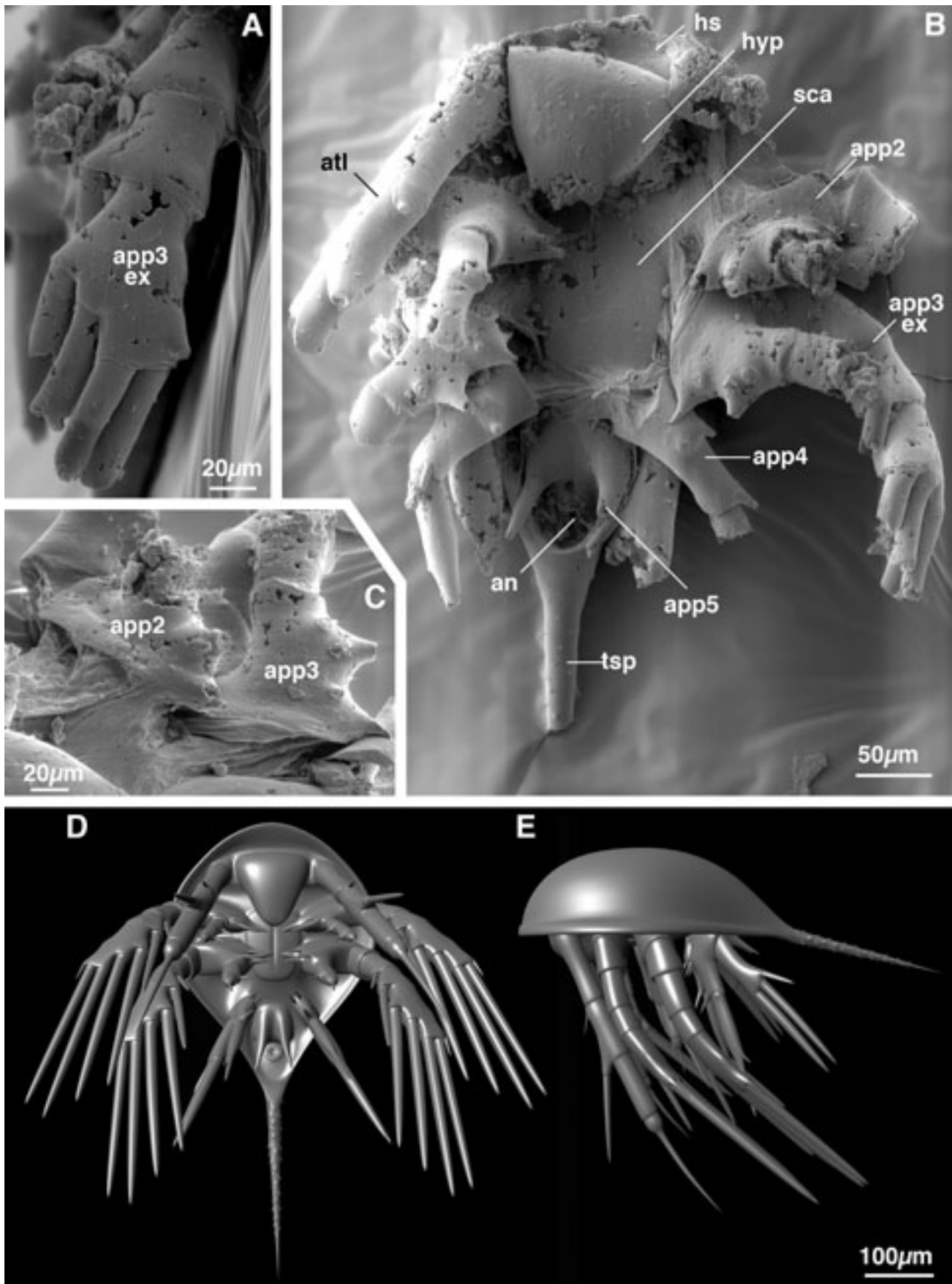


Figure 21 †*Sandtorpia vestrogothiensis* gen. et sp. nov.: (A–C) Holotype specimen UB W 340/SPEC 4144: (A) details of the exopod of the left third appendage; (B) ventral view displaying general organisation; (C) details of proximal aspects of second and third appendages. (D, E) 3D model based on the holotype specimen: (D) ventral view; (E) lateral view. Abbreviations: an=anus; app=appendage (2–5); atl=antennula; ex=exopod; hs=head shield; hyp=hypostome; sca=sclerotised area; tsp=terminal spine.

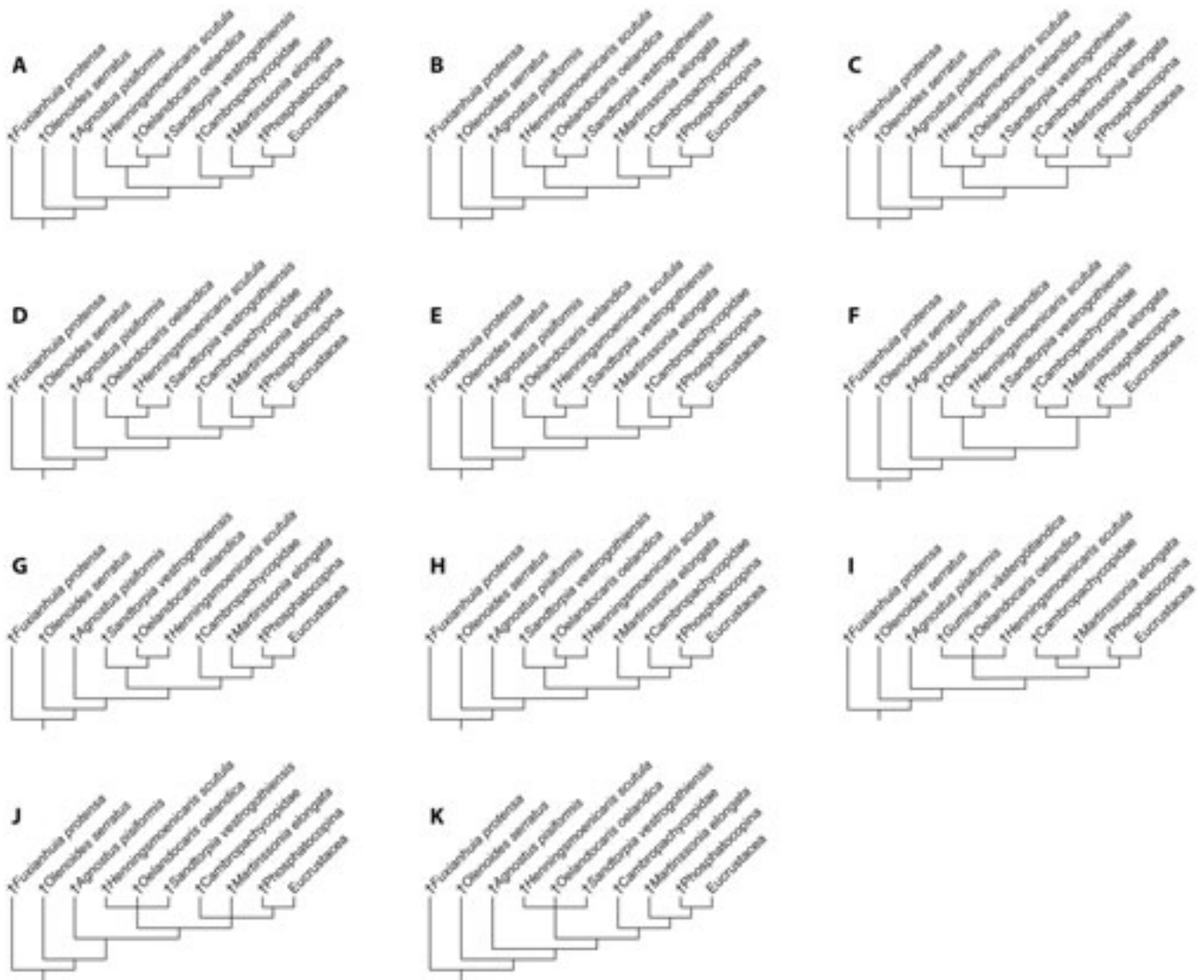


Figure 22 (A–I) Results of phylogenetic analysis, yielding nine cladograms of equal length produced by PAUP* based on the data matrix (Table 2). (J) One out of two cladograms produced by PHYLIP pars, which has the exact topology of the strict consensus tree based on the nine trees produced by PAUP*. (K) Second cladogram produced by PHYLIP pars. This is in fact one of the possible solutions of trichotomies unresolved in cladogram J, i.e. the strict consensus of the nine PAUP* cladograms. It is seen as the most comprehensible one and, therefore, favoured over the others (see text).

Or in a written form as proposed by Hennig (1965):

- †*Fuxianhuia protensa*
- NN (Euarthropoda *sensu* Waloszek *et al.* 2005) †*Olenoides serratus*
- MM
 - †*Agnostus pisiformis*
- OO (Crustacea s. l.=Crustacea *sensu* Waloszek & Müller 1990)
- PP (Oelandocarididae taxon nov.)
 - †*Oelandocaris oelandica*
 - †*Hemingsmoenicaris scutula*
 - †*Sandtorpia vestrogothiensis*
- QQ unnamed
 - †Cambropachycopidae *sensu* Waloszek & Müller 1990
- RR unnamed
 - †*Martinsonia elongata*
- SS (=Labrophora *sensu* Siveter, Waloszek & Williams, 2003)
 - †Phosphatocopina
- TT (Eucrystacea *sensu* Waloszek 1999).

5. Discussion

5.1. Discussion of the phylogenetic analysis

5.1.1. Non-alliance between †*Agnostus pisiformis* and †Trilobita. The fact that †*Agnostus pisiformis* (possibly the whole †Agnostina) and also polymeroid (non-agnostid) ‘trilobites’ resolve near Crustacea is, of course, a result of the low number of taxa involved in this analysis and the choice of †*Fuxianhuia protensa* as out-group. Crucial taxa for inferring euarthropod relationships like Chelicerata were not included in the present analysis, because it was seen as beyond the scope of the present work to judge overall euarthropod relationships. The position of †*Agnostus pisiformis* (possibly the whole †Agnostina) as a possible sister group to Crustacea has been proposed previously (Waloszek & Müller 1990; Shergold 1991; Stein *et al.* 2005) and is confirmed in the present analysis, based on the multi-annulation of head appendages two and three. Nevertheless, this does not exclude a close relationship of †Agnostina+Crustacea to †Trilobita (most features shared by polymeroid trilobites and †Agnostina are dorsal hard-part

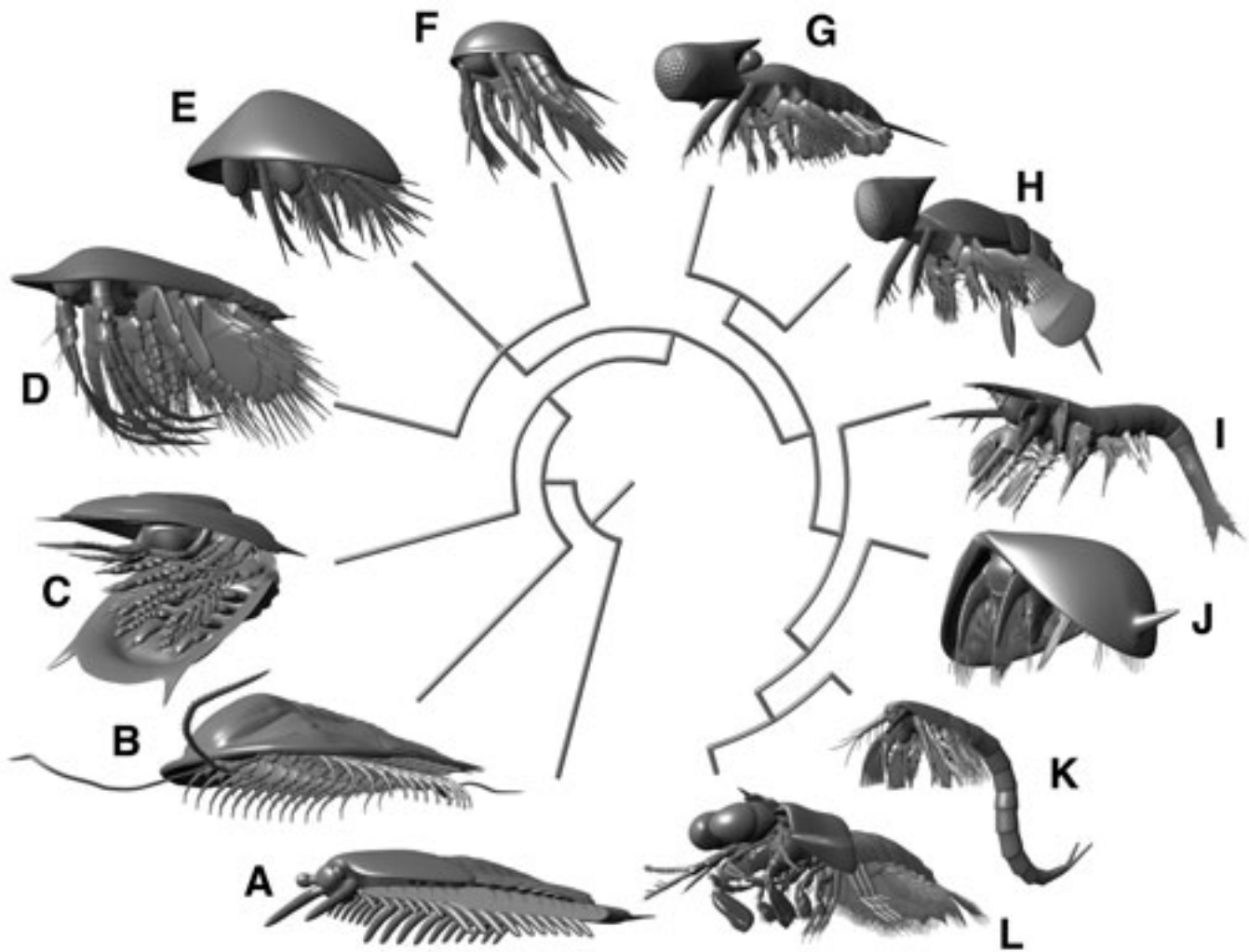


Figure 23 Display of the preferred most parsimonious cladogram as a ring phylogram. The †Cambropachycopidae are represented by two species. The Eucrustacea are represented by two species belonging to each of the two sub-taxa recognised by Maas *et al.* (2003), namely Malacostraca and Entomostraca. The 3D models of the following species are shown: (A) †*Fuxianhuia protensa* Hou, 1987 (reconstruction based on Hou & Bergström 1997 and Waloszek *et al.* 2005); (B) †*Olenoides serratus* (Rominger, 1887), a polymeroid trilobite (reconstruction based on Whittington 1975); (C) †*Agnostus pisiformis* (Wahlenberg, 1818) the only known member of †Agnostina with preserved soft part anatomy (reconstruction based on Müller & Waloszek 1987); (D) †*Oelandocaris oelandica* Müller, 1983 (reconstruction based on Stein *et al.* 2005, 2008); (E) †*Henningsmoenicaris scutula* (Waloszek & Müller, 1990) (reconstruction based on the present work); (F) †*Sandtorpia vestrogothiensis* gen. et sp. nov. (reconstruction based on the present work); (G) †*Goticaris longispinosa* Waloszek & Müller, 1990 (reconstruction based on Haug *et al.* 2009); (H) †*Cambropachycope clarksoni* Waloszek & Müller, 1990 (reconstruction based on Haug *et al.* 2009); (I) †*Martinsonia elongata* Müller & Waloszek, 1986 (reconstruction based on Müller & Waloszek 1986a); (J) †*Vestrogothia spinata* Müller, 1964, a basal member of †Phosphatocopina (reconstruction based on Maas *et al.* 2003, and unpublished data); (K) The maxillopod †*Skara anulata* Müller, 1983 as a member of Entomostraca (reconstruction based on Müller & Waloszek 1985); (L) The stomatopod †*Neogonodactylus bredini* (Manning, 1969), a member of Malacostraca (reconstruction based on Morgan & Goy 1987).

features that were not included in the present analysis, because of the high probability of homeomorphy, see above). One feature shared by polymeroid trilobites and †Agnostina (also †*Agnostus pisiformis*) is the mode of development. New thoracomeres appear at a terminal growth zone as in all arthropods, but are at first conjoined at least to the next anterior segment and may become free, i.e. jointed to it later in ontogeny. This special mode clearly differs from the developmental mode seen in most Crustacea. In the detailed sequence of the Cambrian branchiopod †*Rehbachella kimmekullensis* Müller, 1983 a new segment is demarcated off early, even before the appendages of this segment appear (Waloszek 1993). A similar mode of development can also be observed in other crustaceans, for example in the development of Mystacocarida, where the new tergites are present before the limbs appear (Olesen 2001). In

some Crustacea these mechanisms are hard to judge, as new segments become recognisable mainly because of their limbs at first and the whole posterior trunk end appears rather soft, therefore dorsal segment boundaries are disguised (e. g. Müller & Waloszek 1988).

In contrast to this, the development of †*Henningsmoenicaris scutula* includes two stages where new segments appear and are conjoined at first to the next anterior segment. Therefore the term pygidium can be applied to this structure (see above). The mode of development with new segments being at first conjoined to the next anterior segment is therefore not exclusive to †Trilobita and †Agnostina. This mode of development may well be a shared feature of †Trilobita+(†Agnostina+Crustacea) and lost in later branchings of Crustacea. A closer relationship of †Trilobita to mandibulates than to chelicerates

has already been proposed by earlier publications (Scholtz & Edgecombe 2005, 2006; Waloszek *et al.* 2005; Hughes *et al.* 2008).

However we cannot exclude that the mode of development of †*H. scutula* is autapomorphic for this species, as it is not known in detail for other closely related taxa. Furthermore this developmental mode may also characterise a much larger phylogenetic group, as pygidia are also known for a number of other taxa, such as †*Retifacies abnormalis* Hou, Chen & Lu, 1989 from the Chinese Chengjiang Lagerstätte (Hou & Bergström 1997) or †*Buenaspis forteyi* Budd, 1999 from the Sirius Passet fauna (Budd 1999). The difficulties in judging this in all details is of course that a fused terminal shield, fulfilling the definition of a pygidium, is also present in Xiphosura, but shows a different developmental pattern when compared to that in †*Trilobita*, †*Agnostina* and †*H. scutula*. Therefore, they have to be identified as convergent; there is a functional necessity for such a structure during enrolment (for Xiphosurans see Racheboeuf *et al.* 2002). Thus the detailed development of these pygidia has to be re-investigated carefully in the future.

5.1.2. Monophyly of Crustacea s. l. One of the autapomorphies that characterises Crustacea s. l. as a monophylum is the presence of a proximal endite on the third appendage. The distribution of this character on our cladogram would demand parallel appearance of proximal endites in †*H. scutula* and †Cambropachycopidae+(†*M. elongata*+Labrophora) or a loss of these in †*O. oelandica*. An ontogenetic explanation is therefore preferred for the absence of proximal endites on other limbs in †*O. oelandica*, i.e. that more proximal endites might appear in later ontogenetic stages of †*O. oelandica*. Thus, the presence of proximal endites on all post-antennular limbs in the adults is also an autapomorphy of Crustacea. The computer-based analysis also results in a head with four post-antennular segments as part of the ground pattern of this node. This would require a loss of this character in †Cambropachycopidae. As there are no known examples of such a loss of head segments, without any traces of a former inclusion on the secondarily free segments, this is judged to be unlikely. Cases where subdivisions of the head appear to still show differences compared to trunk segments include the shield of the *Onychura* within the Branchiopoda, which is derived only from the segments of the maxillae (Walossek 1993), or from the propeltidium in various chelicerate taxa (e.g. Dunlop & Alberti 2007 for discussion of the origin of the propeltidium and references therein). It is concluded that the head in the ground pattern of Crustacea s. l. comprises three post-antennular segments, and the inclusion of additional segments occurred independently.

5.1.3. Monophyly of †Oelandocarididae taxon nov. The †Oelandocarididae are composed of three taxa, namely †*Oelandocaris oelandica*, †*Henningsmoenicaris scutula* and †*Sandtorpia vestrogothiensis*, which form an unresolved trichotomy in our phylogeny. All three taxa have large antennulae with at least one strong seta to the anterior. The strong seta present in †*H. scutula* and †*S. vestrogothiensis* seems to correspond to the anterior two outgrowths of †*O. oelandica* especially when looking at the larval specimen of †*O. oelandica* (Stein *et al.* 2008). This orientation of the setation is not present in any other taxon and, therefore, is considered an autapomorphy of †Oelandocarididae. Another autapomorphy of †Oelandocarididae is the pattern of setation on the exopod of the third appendage, with three setae on the terminal article and two setae on the penultimate article in younger stages (although this relies on the interpretation of the terminal article of the exopods of †*S. vestrogothiensis* being a product of fusion, or non-separation of the ultimate and the penultimate

article). In general the terminal portion with three setae and the penultimate portion are interpreted as fusions of portions with a single seta, as it is indicated by the ornamentation in UB 130 (Fig. 6E). As †*Agnostus pisiformis* and the †Cambropachycopidae both have a head comprising three post-antennular segments, the inclusion of the fourth post-antennular segment into the head is also interpreted as an autapomorphy of †Oelandocarididae.

Other autapomorphies of †Oelandocarididae are equivocal since older stages of †*S. vestrogothiensis* are not known. Thus, it can only be postulated that further autapomorphies are the setation pattern of the exopod of the second appendage (comparable to that of the third appendage) and the extension of the proximal exopod parts of the post-mandibular limbs into the basal arthrodial membrane, resulting in a laterally not closed basipod.

Since all three animals show such a comparable morphology, it is concluded that the life habits of all three species are similar. †*O. oelandica* has been interpreted as an active swimmer with a metachronal beat, using mainly the large antennulae for sweeping in food particles (Stein *et al.* 2005, 2008). The well-developed and highly movable eyes might indicate that †*H. scutula* has chosen special food items, at least in later developmental stages. The general life habits with the antennula dominating the sweeping of food particles is, of course, coupled to the functional morphology of the antennula but, with this, can serve as another autapomorphy of the †Oelandocarididae.

5.1.4. Monophyly of †Cambropachycopidae+(†*M. elongata*+Labrophora). This monophylum is based on the following autapomorphies: (i) the exopod of the fourth limb is multi-annulated and the proximal endites or their derivatives on the second and third limbs are present in early ontogenetic stages; (ii) the early presence of the proximal endites is easily identified in all taxa, although it is more difficult to verify in †Phosphatocopina; (iii) their coxa, the derivative of the proximal endite, becomes fused to the basipod during ontogeny (Maas *et al.* 2003); (iv) the multi-annulation of the exopod of the fourth appendage is more problematical, as it is not present in Eucrustacea; and (v) in Entomostraca, when present, the exopod of this limb is paddle-shaped. Therefore, we have to assume a modification of this character, from multi-annulation back to paddle-shaped, at least in Entomostraca, maybe already for Eucrustacea. But the derived in-group-phosphatocopine †*Hesslandona unisulcata* Müller, 1982 demonstrates through its ontogeny the transition from a multi-annulated exopod with median setation to a paddle-shaped exopod with latero-distal setation on their post-mandibular limbs (Maas *et al.* 2003). As for most of the derivatives of the early branching of Crustacea and †Phosphatocopina, which show the multi-annulated exopods on third post-antennular and in parts on fourth post-antennular appendage and are just known from relatively early developmental stages, it cannot be excluded that the mode seen in †*H. unisulcata* is a plesiomorphic trait of a very basal node. Thus, the modification of multi-annulation on this limb in Eucrustacea or Entomostraca is considered to be plausible, as it might just rely on a shift of timing in development.

5.1.5. Monophyly of †*M. elongata*+Labrophora. The monophyly of this taxon is based on the following two autapomorphies: the fifth limb-bearing segment is incorporated into the head, and the exopod of the fifth limb is multi-annulated. For the latter autapomorphy, the same arguments as for the exopod of the fourth limb apply. The inclusion of the fifth appendage-bearing segment is recognised as an autapomorphy, although it relies on the assumption that

a kinetic joint within the head shield of †*M. elongata* evolved secondarily.

5.1.6. Monophyly of Labrophora. Maas *et al.* (2003) and Siveter *et al.* (2003) discussed the monophyly of Labrophora in detail. Some of the autapomorphies therein identified, namely the fused sternum with paragnaths and the labrum, as well as the presence of coxae on the second and third appendage, have been included in the present analysis and, indeed, turn out to be autapomorphic for Labrophora. As new data indicate, a sternum with paragnaths might be also present in insects (Wolff & Scholtz 2006). Insects (or even Tracheata) might therefore indeed be an ingroup taxon of Labrophora. This will be evaluated in a future larger-scaled analysis.

5.1.7. More characters for future analyses. Many characters have not yet been considered because of the small scale of the analysis, but may be important for future large-scale analyses. One such character complex concerns the eyes. Several 'Orsten' species show eye structures, some of them very specialised as in the †Cambropachycopidae (Haug *et al.* 2009), but there are also quite simple 'bubbles' as in †*Bredocaris admirabilis* Müller, 1983 (Müller & Walossek 1988), †*Rehbachella kimmekullensis* (Walossek 1993) or †*Yicaris dianensis* (Zhang *et al.* 2007). A possibly different type of eye structures is also present in †*Agnostus pisiformis* (Müller & Walossek 1987). The eyes of †*H. scutula* seem to be very special in possessing a heavily sclerotised area in the eye stalk, but also two ample membranous areas proximal and distal to it. The detailed morphogenesis of this structure in such an ancient animal has never been documented before. Thus, even Cambrian crustaceans show a large variety of differentiated eyes, and eyes should, therefore, be included in future phylogenetic analyses.

Another character of interest displayed by †*H. scutula* is the presence of setae on the latero-proximal area of the appendages that appear to be soft. †*H. scutula* shows these structures only on the third appendage and probably also on the second appendage. In †*A. pisiformis* comparable structures are present also on more posterior limbs (Müller & Walossek 1987). Furthermore, in the eucrustacean †*Y. dianensis*, epipodites are derived from soft setal sockets on the lateral side of the basipod (Zhang *et al.* 2007; Maas *et al.* 2009). Thus, the question arises whether these structures are homologues.

5.1.8. Other 'Orsten' stem-lineage derivatives. †*Cambrocaris baltica* was described by Walossek & Szaniawski (1991) as a stem-lineage derivative of Crustacea. In the original paper the species was described as having coxae on the first and second post-antennular appendages and thus possibly being more closely related to Eucrustacea (with new data we should say Labrophora) than the other stem-lineage derivatives. In later publications, Walossek and co-workers withdrew partly from this view and included †*C. baltica* in a polytomy with the other stem-lineage derivatives (e.g. Maas *et al.* 2003; Walossek 2003a, b; Stein *et al.* 2005). This was because the holotype is glued on its dorsal side, and the lateral aspects of the appendages are more or less concealed. The species was not included in the present analyses because it has relatively few recognisable characters for an 'Orsten' species. First, it is known only from a single, and already advanced (i.e. late) developmental stage, and thus, in contrast to the single specimen of †*S. vestrogothiensis*, lacks any developmental information. The exopod is known only from the second appendage and is plesiomorphically multi-annulated. The low number of annuli casts doubt on any assignment close to Labrophora. The state of the exopods of the third and fourth post-antennular appendage remains unknown. Even the exact number of head segments is unclear. Thus, the species clearly displays features of Crustacea s. l., namely the multi-annulated exopod with

exclusively median setation and the presence of proximal endites, but a more precise assignment seems to be impossible due to the lack of characters.

Another 'Orsten' fossil that might be a derivative of the stem lineage of Crustacea is the so-termed C-type larva. Müller & Walossek (1986b) have stated that it might be 'a phylogenetically older larval type than the nauplius'. Although the whole morphology looks rather specialised and the appendages lack proximal endites, the multi-annulated exopods with exclusively median setation on appendages two to four might indicate a sister group-relationship of the C-type larva to †Cambropachycopidae+(†*Martinssonella elongata*+Labrophora). The animal would have 'already' gained the multi-annulated exopod of the fourth appendage, but 'not yet' gained the presence of the proximal endites in early developmental stages. The C-type larva will be included in a future large-scale analysis to support or reject the given assumption.

5.2. Heterochrony as a driving force in evolution

5.2.1. Difficulties with the concept of heterochrony. There are three major difficulties in understanding and applying the concepts of heterochrony. The first is the idea of a global heterochronic event, i.e. one that affects the whole organism, being the rule. In fact there are almost no examples for this kind of heterochrony. In most cases we are dealing with local heterochrony, i.e. where only certain structures of an organism are affected.

Fortey & Theron (1994) discuss the origin of naraoiids and agnostids through paedomorphic events from a trilobitic ancestor. They stated that the mode of heterochrony that led to the naraoiids was hypermorphosis. As hypermorphosis is a peramorphic event, it should result in a 'more mature' morphology not in a larval, paedomorphic one. This confusion seems to be the result of which part of the animal was affected by the heterochronic event. Fortey & Theron further state that the pygidium gains more and more segments during evolution.

Here, Fortey & Theron (1994) have confused peramorphosis and paedomorphosis. The pygidium does not gain (from the anterior – it develops new segments from the posterior of course) more segments during ontogeny but releases thoracic segments. Therefore, the pygidium as a whole was not affected by the heterochronic event, but only the individual thoracic segments. The thoracic segments are retained in a larval state, being conjoined with more posterior segments instead of being freely articulated, therefore this morphology is neotenic. The heterochronic effect that led to the naraoiids (if this scenario is correct) is in fact neoteny and not hypermorphosis. This example demonstrates that even if one is aware of the details it is not easy to deal with the concepts of heterochrony.

The second difficulty arises over the differentiation of the six subtypes of heterochrony. There is a clear difference between peramorphosis and paedomorphosis, but the three subtypes of each kind of heterochrony, e.g. neoteny and progenesis, may not always be clearly differentiable, or a combination of two or more subtypes might appear (see below).

The third difficulty arises in detecting heterochrony, as its definition is based on differences when compared to the ancestor of the studied taxon. But we probably do not have fossilised direct ancestors, only derivatives of a common ancestor.

Thus, when trying to detect heterochronic events one has to deal with all three difficulties. The first two are simply a matter of awareness, while the ancestor problem can be solved by applying the methods of phylogenetic systematics, as discussed below.

5.2.2. Phylogenetic systematics and the concept of heterochrony. When applying the concept of phylogenetic systematics *sensu* Hennig (1965) and *sensu* Ax (1985b), one is able to reconstruct a likely ground pattern for each node, i.e. the stem species on the phylogram. The general power of this approach has been repeatedly shown. The reconstructed ground pattern can be compared to the next node below in the tree. For example, the presence or conditions of structures of the adult of one ground pattern can simply be compared with that of larvae in the ground pattern of the deeper ancestral node. If a structure that characterises the immaturity of the ancestral node is present in the adult of the node of interest, a paedomorphic event must have occurred in the direct stem-lineage of the species.

Thus, applying phylogenetic systematics avoids the problem of not having an ancestor through comparing ground patterns. But this demands a phylogenetic analysis in advance. Heterochrony can, therefore, only be confidently detected *a posteriori*. This is the logical consequence when we think of two species. The adult of species A looks like a larva of species B. We cannot be sure whether B is peramorphic or A is paedomorphic without knowing the relationships, the ground patterns and the direction of evolution in advance. This problem has already been addressed in part by other authors, e.g. Rasmköld (1988), who demands an out-group comparison for establishing polarity, when dealing with heterochrony.

In conclusion, for detecting heterochronic events it is necessary to have a detailed knowledge of the structures we are dealing with. These are usually three-dimensional bodies. Furthermore, it is essential to know the ontogenetic fate of the structures of the species studied, i.e. four-dimensional reconstructions of all species in focus. Thirdly, there has to be a robust phylogeny to detect heterochronic events. This can be interpreted as a change of four-dimensional structures over time and therefore as a quasi five-dimensional reconstruction (change over time (evolution) of change over time (ontogeny) of a three-dimensional structure).

5.2.3. Applying the concepts of heterochrony in phylogenetic systematics to basal branches of Crustacea. (Fig. 24) Comparing the ground patterns of various nodes with their immediate ancestral nodes in the current tree reveals several peramorphic events that affect the limb base of the appendage homologous to the second and third appendages (Fig. 20).

Comparing the ground patterns of the taxon (†Agnostina+Crustacea s. l.) with that of Crustacea s. l. reveals that the older stages in Crustacea s. l. show a 'more mature' morphology. Younger stages show the same organisation of the proximal limb parts with a simple basipod. In the older stages, however, an additional structure, the proximal endite, appears. This can be interpreted, just by referring to heterochrony, as an additional stage of development terminally added to the ontogeny of the proximal limb stem. Adding an additional stage or prolongation of a development is termed hypermorphosis, but as the limbs are not larger than those of the stem species of (†Agnostina+Crustacea s. l.) a pre-displacement must also have occurred within the direct stem lineage of Crustacea s. l.

†Cambropachycopidae+(†*M. elongata*+Labrophora) show proximal endites already in the euarthropod head larva, which is not the case in the ground pattern of Crustacea s. l. Therefore, the occurrence of a pre-displacement in the direct stem lineage of †Cambropachycopidae+(†*M. elongata*+Labrophora) is concluded.

In Labrophora the proximal endite is enlarged to form a laterally closed ring, the coxae. In the branchiopod †*Rehbachella kinnekullensis*, the proximal endite of the mandible in the first larval stage is still a laterally 'open' proximal endite, only becoming an enclosed coxa in later developmental

stages. Thus, the enclosed coxa is interpreted as a new terminally added developmental stage. Therefore, it is again concluded that we have the combined occurrence of hypermorphosis and pre-displacement in the direct stem lineage of Labrophora.

Although three peramorphic events characterise early evolution, it is important to point out that the idea of a tendency or a trend towards more mature adults has to be rejected in advance. This idea results in a bias produced by the special arrangement of the phylogram. But the positions of two branches at a single node are interchangeable, and evolution is not 'aim-oriented'.

6. Conclusions and outlook

The ontogeny of †*Henningsmoenicaris scutula* displays interesting features, such as the morphogenesis of the limbs and especially that of the stalked eyes, from sessile eyes in a 500 million year-old animal. This is the first report of a fossil exhibiting such a delicate developmental pattern of the compound eyes.

†Oelandocarididae taxon nov. is recognised as the sister taxon of †Cambropachycopidae+(†*Martinsonia elongata*+Labrophora), while †*Agnostus pisiformis* (possibly the whole †Agnostina) may possibly represent the sister taxon of the Crustacea. †*H. scutula*, as a derivative of an early branch of Crustacea, shows a developmental pattern that may reflect the pygidial development of †Agnostina and †Trilobita and therefore points to a close relationship between †Agnostina+Crustacea s. l. and †Trilobita, although this developmental pattern may characterise an even larger taxon. Heterochrony can be detected by comparing ground patterns of successive nodes. Three peramorphic events can be determined along the evolutionary lineage towards Crustacea on the limb stems of at least the first and second post antennular appendages. In the direct stem lineage of Crustacea s. l., hypermorphosis and pre-displacement are inferred. In the direct stem-lineage of †Cambropachycopidae+(†*M. elongata*+Labrophora), pre-displacement can be established. And in the direct stem-lineage of Labrophora, both hypermorphosis and pre-displacement have been identified.

7. Acknowledgements

We thank the Central Unit for Electron Microscopy of the University of Ulm for providing technical help with the SEM, especially for the 90°-tilting device. We furthermore thank all people involved in the projects making useful software available for free, in our case especially the people involved in Combine ZM, Gimp, Inkscape, and Blender. We are very grateful to Euan Clarkson, Edinburgh, for significantly and extensively improving the manuscript linguistically. We thank Greg Edgecombe, London and two other anonymous reviewers for further improving this manuscript. Parts of this work were funded by the Priority Programme 'Deep Metazoan Phylogeny' SPP 1174 of the German Research Foundation. JTH is currently funded by the DFG under the project number Wa-754/15-1.

8. Supplementary material

The original diagnosis for †*Henningsmoenicaris scutula* (after Walossek & Müller 1990) and its phylogenetic analysis is published as Supplementary Material with the on-line version of this paper. This is hosted by the Cambridge Journals Online service and can be viewed at <http://journals.cambridge.org/trc>

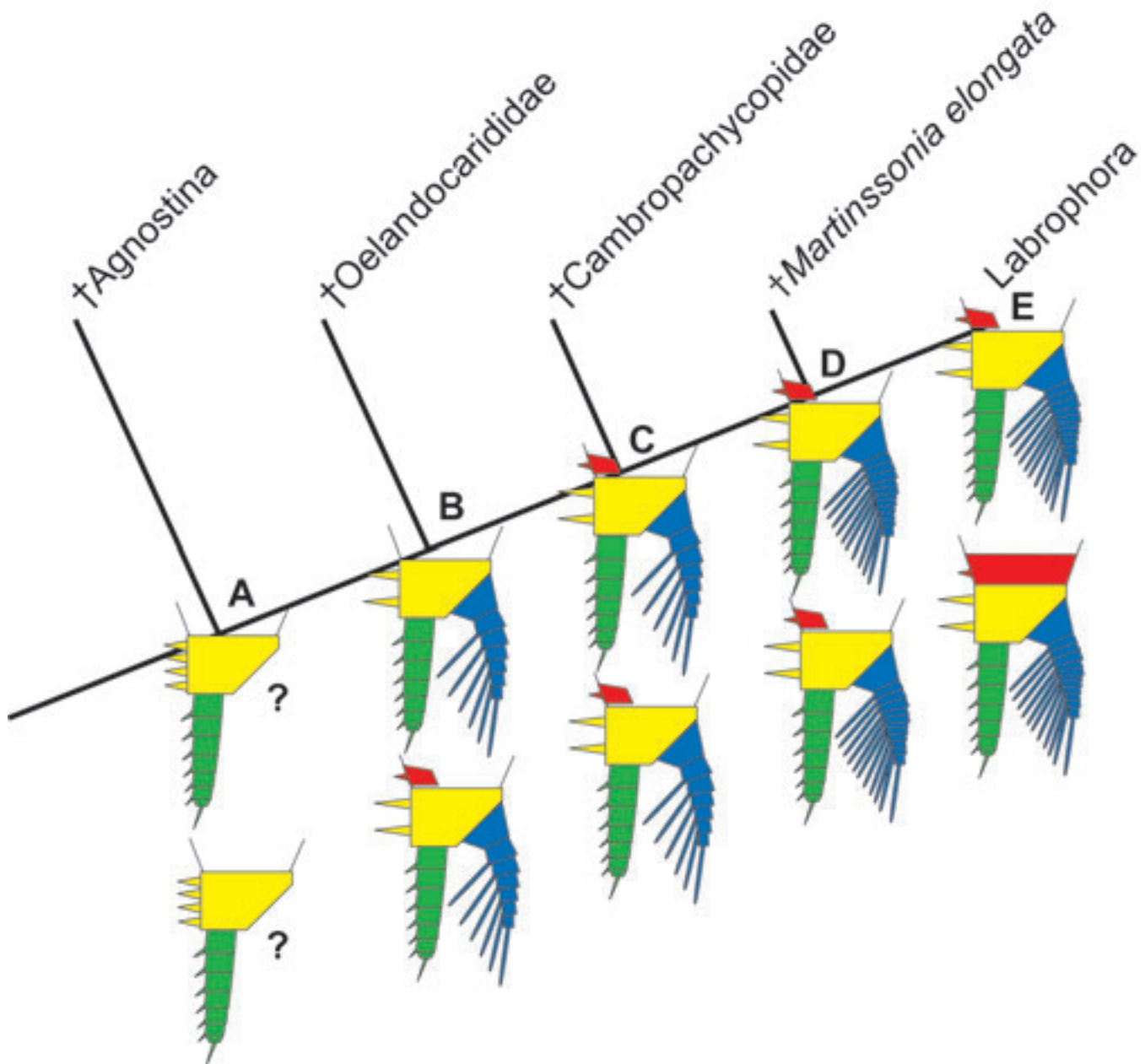


Figure 24 Reconstruction of the ground pattern conditions of the appendage of the third limb-bearing segment in early (upper row) and late (lower row) developmental stages: (A) stem species of †*Agnostus pisiformis*+Crustacea s. l.; (B) stem species of Crustacea s. l.; (C) stem species of Cambropachycopidae+(†*Martinssonella elongata*+Labrophora); (D) stem species of †*Martinssonella elongata*+Labrophora; (E) stem species of Labrophora. Three peramorphic events can be identified. From A to B a new developmental stage appears characterised by the appearance of a new structure, the proximal endite. The development is ‘prolonged’ (hypermorphosis), i.e. a new condition is terminally added although the appendage does not become larger and we could, thus, assume pre-displacement additionally. From B to C this stage is transferred to an earlier developmental stage (pre-displacement). The evolutionary event from D to E is, again hypermorphosis: the proximal endite closes laterally to a ring, the coxa. Again the appendage does not become larger so, consequently, additional pre-displacement is assumed.

9. References

- Ax, P. 1984. *Das Phylogenetische System*. Stuttgart: Gustav Fischer.
- Ax, P. 1985a. Stem Species and the Stem Lineage Concept. *Cladistics* 1 (3), 279–87.
- Ax, P. 1985b. Die stammesgeschichtliche Ordnung in der Natur. *Akademie der Wissenschaften und der Literatur von Mainz, Abhandlungen der Mathematisch-Naturwissenschaftlichen Klasse, Jahrgang 1985* 4, 1–31.
- Ax, P. 1999. *Das System der Metazoa II. Ein Lehrbuch der phylogenetischen Systematik*. 1. Auflage, 1–384. Stuttgart: Gustav Fischer.
- Boxshall, G. A. 2007. Crustacean classification: on-going controversies and unresolved problems. In Zhang, Z.-Q. & Shear, W. A. (eds) *Linnaeus Tercentenary: Progress in Invertebrate Taxonomy*. *Zootaxa* 1668, 313–25.
- Brünnich, M. T. 1772. *Zoologiae fundamenta praelectionibus academicis accomodata*. Grunde i Dyrelaeren: Hafniae et Lipsiae. 254 pp.
- Budd, G. E. 1999. A nektaspid arthropod from the Early Cambrian Sirius Passet Fauna, with a description of retrodeformation based on functional morphology. *Palaeontology* 42 (1), 99–122.
- Campbell, N. 1998. *Biologie*. German Editor Jürgen Markl. Heidelberg, Berlin, Oxford: Spektrum Akademischer Verlag. 1440 pp.
- Chen J.-y., Vannier, J. & Huang D.-y. 2001. The origin of crustaceans: new evidence from the Early Cambrian of China. *Proceedings of the Royal Society of London B* 268, 2181–7.
- Dahms, H.-U. 2000. Phylogenetic implications of the crustacean nauplius. *Hydrobiologia* 417, 91–9.

- Dohle, W. 2001. Are the insects terrestrial crustaceans? A discussion of some new facts and arguments and the proposal of the proper name 'Tetraconata' for the monophyletic unit Crustacea+Hexapoda. *Annales de la Société Entomologique de France* (N.S.) **37** (1–2), 85–103.
- Donoghue, P. C. J. 2005. Saving the stem group – a contradiction in terms? *Paleobiology* **31** (4), 553–8.
- Dunlop, J. A. & Alberti, G. 2007. The affinities of mites and ticks: a review. *Journal of Zoological Systematics and Evolutionary Research* **46** (1), 1–18.
- Edgecombe, G. D. & Chatterton, B. D. E. 1987. Heterochrony in the Silurian radiation of encrinurine trilobites. *Lethaia* **20**, 337–51.
- Fanenbruck, M., Harzsch, S. & Wägele, J. W. 2004. The brain of the Remipedia (Crustacea) and an alternative hypothesis on their phylogenetic relationships. *Proceedings of the National Academy of Sciences USA* **101** (11), 3868–73.
- Fortey, R. A. & Theron, J. N. 1994. A new Ordovician arthropod, *Soomaspis*, and the agnostid problem. *Palaeontology* **37** (4), 841–61.
- Freeman, S. & Herron, J. C. 2004. *Evolutionary Analysis*, 3rd edn. Upper Saddle River, New Jersey: Pearson Education. 802 pp.
- Fryer, G. 1999. Cambrian animals: evolutionary curiosities or the crucible of creation? *Hydrobiologia* **403**, 1–11.
- Futuyma, D. J. 1998. *Evolutionary Biology*, 3rd edn. Sunderland, Massachusetts: Sinauer Associates. 763 pp.
- Glenner, H., Thomsen, P. F., Hebsgaard, M. B., Sørensen, M. V. & Willerslev, E. 2006. The origin of insects. *Science* **314**, 1883–4.
- Haug, J. T., Maas, A., Waloszek, D., Haug, C. & Liu, Y. 2007. 4D reconstruction of *Henningsmoenicaris scutula* and early crustacean evolution. *The Palaeontology Newsletter* **66**, Abstract 75.
- Haug, J. T., Maas, A. & Waloszek, D. 2009. Ontogeny of two Cambrian stem crustaceans, †*Goticaris longispinosa* and †*Cambropachycyope clarksoni*. *Palaeontographica A* **289**, 1–43.
- Hennig, W. 1965. Phylogenetic systematics. *Annual Review of Entomology* **10**, 97–116.
- Høeg, J. T. 1992. The phylogenetic position of the Rhizocephala: are they truly barnacles? *Acta Zoologica (Stockholm)* **73** (5), 323–6.
- Hou, Xian-Guang 1987. Three new large arthropods from the Lower Cambrian Chengjiang, Eastern Yunnan. *Acta Palaeontologica Sinica* **26** (3), 272–85.
- Hou, X.-G., Chen, J.-Y. & Lu, H. 1989. Early Cambrian new arthropods from Chengjiang, Yunnan. *Acta Palaeontologica Sinica* **28** (1), 53–68.
- Hou, X.-G., Siveter, Da. J., Williams, M., Walossek, D. & Bergström, J. 1996. Appendages of the arthropod *Kunmingella* from the early Cambrian of China: its bearing on the systematic position of the Bradoriida and the fossil record of the Ostracoda. *Philosophical Transactions of the Royal Society of London B* **351**, 1131–45.
- Hou, X.-G. & Bergström, J. 1997. Arthropods of the Lower Cambrian Chengjiang fauna, southwest China. *Fossils and Strata* **45**, 1–116.
- Hughes, N. C., Minelli, A. & Fusco, G. 2006. The ontogeny of trilobite segmentation. A comparative approach. *Palaeobiology* **32** (4), 602–27.
- Hughes, N. C., Haug, J. T. & Waloszek, D. 2008. Basal euarthropod development: a fossil-based perspective. In Minelli, A. & Fusco, G. (eds) *Evolving pathways, keynotes in evolutionary developmental biology*, 281–98. Cambridge: Cambridge University Press.
- Humphries, J. C. 2002. Homology characters and continuous variables. In MacLeod, N. & Forey, P. L. (eds) *Morphology, Shape and Phylogeny. Systematics Association Special Volume Series* **64**, 8–26. London & New York: Oxford University Press.
- Hwang, U. W., Friedrich, M., Tautz, D., Park, C. J. & Kim, W. 2001. Mitochondrial protein phylogeny joins myriapods with chelicerates. *Nature* **413**, 154–7.
- Kraus, O. 2001. 'Myriapoda' and the ancestry of the Hexapoda. *Annales de la Société Entomologique de France* (N.S.) **37** (1/2), 105–27.
- Kull, U. 2007. *Evolution in Stichworten*. Berlin & Stuttgart: Gebrüder Bornträger Verlagsbuchhandlung. 402 pp.
- Maas, A., Waloszek, D. & Müller, K. J. 2003. Morphology, ontogeny and phylogeny of the Phosphatocopina (Crustacea) from the Upper Cambrian 'Orsten' of Sweden. *Fossils & Strata* **49**, 1–238.
- Maas, A., Braun, A., Dong Xiping, Donoghue, P. C. J., Müller, K. J., Olempska, E., Repetski, J. E., Siveter, D. J., Stein, M. & Waloszek, D. 2006. The 'Orsten' – more than a Cambrian Konservat-Lagerstätte yielding exceptional preservation. *Palaeoworld* **15**, 266–82.
- Maas, A., Haug, C., Haug, J. T., Olesen, J., Zhang, X. & Waloszek, D. 2009. Early Crustacean Evolution and the Appearance of Epipodites and Gills. *Arthropod Systematics & Phylogeny* **67** (2), 255–73.
- Maas, A. & Waloszek, D. 2001. Larval development of *Euphausia superba* Dana, 1852 and a phylogenetic analysis of the Euphausiacea. *Hydrobiologia* **448**, 143–69.
- Maas, A. & Waloszek, D. 2005. Phosphatocopina – ostracode-like sister group of Eucrustacea. *Hydrobiologia* **538**, 139–52.
- Manning, R. B. 1969. *Stomatopod Crustacea from the Western Atlantic. Studies in Tropical Oceanography* **8**, Contribution no. 991. Miami, Florida: Institute of Marine Sciences, University of Miami. 380 pp.
- McNamara, K. J. 1978. Pedomorphosis in Scottish olenellid trilobites. *Palaeontology* **21**, 635–55.
- McNamara, K. J. 1981. The role of pedomorphosis in the evolution of Cambrian trilobites. *U.S. Geological Survey Open-File Report* **81** (743), 126–9.
- McNamara, K. J. 1983. Progenesis in trilobites. *Special Papers in Palaeontology* **30**, 59–68.
- McNamara, K. J. 1986. The role of heterochrony in the evolution of Cambrian trilobites. *Biological Reviews* **6**, 121–56.
- Morgan, S. G. & Goy, J. W. 1987. Reproduction and larval development of the mantis shrimp *Gonodactylus bredini* (Crustacea: Stomatopoda) maintained in the laboratory. *Journal of Crustacean Biology* **7** (4), 595–618.
- Moura, G. & Christoffersen, M. L. 1996. The system of the mandibulate arthropods: Tracheata and Remipedia as sister groups, 'Crustacea' non-monophyletic. *Journal of Comparative Biology* **1** (3/4), 95–113.
- Müller, K. J. 1964. Ostracoda (Bradoriina) mit phosphatischen Gehäusen aus dem Oberkambrium von Schweden. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **121** (1), 1–46.
- Müller, K. J. 1982. *Hesslandona unisulcata* sp. nov. with phosphatised appendages from Upper Cambrian 'Orsten' of Sweden. In Bate, R. H., Robinson, E. & Sheppard, L. M. (eds) *Fossil and Recent Ostracods*, 276–304. Chichester: Ellis Horwood.
- Müller, K. J. 1983. Crustacea with preserved soft parts from the Upper Cambrian of Sweden. *Lethaia* **16** (2), 93–109.
- Müller, K. J. 1985. Exceptional preservation in calcareous nodules. *Philosophical Transactions of the Royal Society of London B* **311**, 67–73.
- Müller, K. J. 1990. Upper Cambrian 'Orsten'. In Briggs, D. E. G. & Crowther, P. R. (eds) *Palaeobiology – A Synthesis*, 274–7. Boston: Blackwell Scientific Publications.
- Müller, K. J. & Walossek, D. 1985. Skaracarida, a new order of Crustacea from the Upper Cambrian of Västergötland, Sweden. *Fossils and Strata* **17**, 1–65.
- Müller, K. J. & Walossek, D. 1986a. *Martinsonia elongata* gen. et. sp. n., a crustacean-like euarthropod from the Upper Cambrian 'Orsten' of Sweden. *Zoologica Scripta* **15**, 73–92.
- Müller, K. J. & Walossek, D. 1986b. Arthropod larvae from the Upper Cambrian of Sweden. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **77**, 157–79.
- Müller, K. J. & Walossek, D. 1987. Morphology, ontogeny, and life habit of *Agnostus pisiformis* from the Upper Cambrian of Sweden. *Fossils and Strata* **19**, 1–124.
- Müller, K. J. & Walossek, D. 1988. External morphology and larval development of the Upper Cambrian maxillopod *Bredocaris admirabilis*. *Fossils & Strata* **23**, 1–70.
- Müller, K. J. & Walossek, D. 1991. Ein Blick durch das <Orsten>-Fenster in die Arthropodenwelt vor 500 Millionen Jahren. *Verhandlungen der Deutschen Zoologischen Gesellschaft* **84**, 281–94.
- Newman, W. A. 2005. Origin of the Ostracoda and their maxillopodan and hexapodan affinities. *Hydrobiologia* **538**, 1–21.
- Nielsen, C., Haszprunnar, G., Ruthensteiner, B. & Wanninger, A. 2007. Early development of the aplacophoran mollusc *Chaetoderma*. *Acta Zoologica* **88**, 231–47.
- Olesen, J. 2001. External morphology and larval development of *Derocheilocaris remanei* Delamare-Deboutteville & Chappuis, 1951 (Crustacea, Mystacocarida), with a comparison of crustacean segment and tagmosis patterns. *Biologiske Skrifter udgivet af Det Kongelige Danske Videnskabernes Selskab* **53**, 1–59.
- Olesen, J. 2004. On the ontogeny of the Branchiopoda (Crustacea): contribution of development to phylogeny and classification. In Scholtz, G. (ed.) *Evolutionary developmental biology of Crustacea. Crustacean Issues* **15**, 217–69. Boca Raton, Florida: CRC Press.
- Olesen, J. 2007. Monophyly and phylogeny of Branchiopoda, with focus on morphology and homologies of branchiopod phyllopodous limbs. *Journal of Crustacean Biology* **27** (2), 165–83.
- Patterson, C. & Rosen, D. E. 1977. Review of ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. *Bulletin of the American Museum of Natural History* **158** (2), 85–172.

- Peng, S., Babcock, L. E., Robison, R. A., Lin, H., Rees, M. N. & Saltzman, M. R. 2004. Global standard stratotype section and point (GSSP) of the Furongian Series and Paibian Stage (Cambrian). *Lethaia* **37**, 365–79.
- Pisani, D., Poling, L. L., Lyons-Weiler, M. & Hedges, S. B. 2004. The colonization of land by animals: molecular phylogeny and divergence times among arthropods. *BMC Biology* **2**, 1. doi:10.1186/1741-7007-2-1
- Pleijel, F. 1995. On character coding for phylogeny reconstruction. *Cladistics* **11**, 309–15.
- Racheboeuf, P. R., Vannier, J. & Anderson, L. I. 2002. A new three-dimensionally preserved xiphosuran chelicerate from the Montceau-Les-Mines lagerstätte (Carboniferous, France). *Palaeontology* **45** (1), 125–47.
- Ramsköld, L. 1988. Heterochrony in Silurian phacopid trilobites as suggested by the ontogeny of *Acemaspis*. *Lethaia* **21**, 307–18.
- Ramsköld, L., Chen, Junyuan, Edgecombe, G. D. & Zhou, Guiqing 1997. *Cindarella* and the arachnate clade Xandarellida (Arthropoda, Early Cambrian) from China. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **88**, 19–38.
- Regier, J. C., Shultz, J. W., Ganley, A. R., Hussey, A., Shi, D., Ball, B., Zwick, A., Stajich, J. E., Cummings, M. P., Martin, J. W. & Cunningham, C. W. 2008. Resolving arthropod phylogeny: exploring phylogenetic signal within 41 kb of protein-coding nuclear gene sequence. *Systematic Biology* **57** (6), 920–38.
- Rominger, C. 1887. Description of primordial fossils from Mt. Stephens, N. W. Territory of Canada. *Proceedings of the Academy of Natural Sciences at Philadelphia* **1887**, 12–19.
- Schallreuter, R. E. L. 1964. Neue Ostracoden der Überfamilie Hollinacea. *Berichte der Geologischen Gesellschaft in der Deutschen Demokratischen Republik Sonderheft* **2**, 87–93.
- Scholtz, G. & Edgecombe, G. D. 2005. Heads, Hox and the phylogenetic position of trilobites. In Koenemann, S. & Jenner, R. (eds) *Crustacea and arthropod relationships, Crustacean Issues* **16**, 139–65. Boca Raton, Florida: CRC Press.
- Scholtz, G. & Edgecombe, G. D. 2006. The evolution of arthropod heads: reconciling morphological, developmental and palaeontological evidence. *Development, Genes and Evolution* **216**, 395–415.
- Schram, F. R. & Hof, C. H. J. 1998. Fossils and the interrelationships of major crustacean groups. In Edgecombe, G. D. (ed.) *Arthropod Fossils and Phylogeny*, 233–302. New York: Columbia University Press.
- Schram, F. R. & Koenemann, S. 2004. Are the crustaceans monophyletic? In Cracraft, J. & Donoghue, M. J. (eds) *Assembling the Tree of Life*, 319–29. New York: Oxford University Press.
- Shergold, J. H. 1991. Protaspid and early meraspid growth stages of the eodiscid trilobite *Pagetia ocellata* Jell, and their implications for classification. *Alcheringa* **15**, 65–86.
- Siebold, von, C. T. E. & Stannius, H. F. 1845. *Lehrbuch der vergleichenden Anatomie. Erster Theil. Wirbellose Thiere*. Berlin: Veit & Co.
- Simonetta, A. M. & Della Cave, L. 1981. An essay in the comparative and evolutionary morphology of Palaeozoic arthropods. In *Origine dei Grandi Phyla dei Metazoi, Atti dei Convegni Lincei* **49**, 389–439. Rome: Accademia Nazionale dei Lincei.
- Siveter, Da. J., Waloszek, D. & Williams, M. 2003. An early Cambrian phosphatocopid crustacean with three-dimensionally preserved soft parts from Shropshire, England. *Special Papers in Palaeontology* **70**, 9–30.
- Siveter, De. J., Sutton, M. D., Briggs, D. E. G. & Siveter, Da. J. 2007a. A new probable stem lineage crustacean with three-dimensionally preserved soft parts from the Herefordshire (Silurian) Lagerstätte, UK. *Proceedings of the Royal Society B* **274**, 2099–107.
- Stein, M., Waloszek, D. & Maas, A. 2005. *Oelandocaris oelandica* and its significance to resolving the stem lineage of Crustacea. In Koenemann, S. & Vonck, R. (eds) *Crustacea and Arthropod Relationships. Crustacean Issues* **16**, 55–71. Boca Raton, Florida: CRC Press.
- Stein, M., Haug, J. T., Waloszek, D. & Maas, A. 2008. The stem crustacean *Oelandocaris oelandica* re-visited. *Acta Palaeontologica Polonica* **53** (3), 461–84.
- Strausfeld, N. J., Strausfeld, C. M., Stowe, S., Rowell, D. & Loesel, R. 2006. The organization and evolutionary implications of neuropils and their neurons in the brain of the onychophoran *Euperipatoides rowelli*. *Arthropod Structure & Development* **35**, 169–96.
- Wägele, J.-W. 2000. *Grundlagen der Phylogenetischen Systematik*. München: Verlag Dr. Friedrich Pfeil. 315 pp.
- Wahlenberg, G. 1818. Petrificata Telluris Svecanae, *Nova Acta Regiae Scientiarum Upsaliensis* **8**, 1–116.
- Walossek, D. 1993. The Upper Cambrian *Rehbachella* and the phylogeny of Branchiopoda and Crustacea. *Fossils and Strata* **32**, 1–202.
- Walossek, D. 1999. On the Cambrian diversity of Crustacea. In Schram, F. R. & von Vaupel Klein, J. C. (eds) *Crustaceans and the Biodiversity Crisis, Proceedings of the Fourth International Crustacean Congress, Amsterdam, The Netherlands, July 20–24, 1998* **1**, 3–27. Leiden, The Netherlands: Brill Academic Publishers.
- Walossek, D. & Müller, K. J. 1990. Upper Cambrian stem-lineage crustaceans and their bearing on the monophyletic origin of Crustacea and the position of *Agnostus*. *Lethaia* **23**, 409–27.
- Walossek, D. & Müller, K. J. 1991. *Lethaia* Forum: *Henningsmoenicaris* n. gen. for *Henningsmoenia* Walossek & Müller – correction of a name. *Lethaia* **24** (2), 138.
- Walossek, D. & Müller, K. J. 1992. The ‘Alum Shale Window’ – Contribution of ‘Orsten’ Arthropods to the Phylogeny of Crustacea. *Acta Zoologica* **73** (5), 305–12.
- Walossek, D. & Müller, K. J. 1998a. Chapter 5: Early arthropod phylogeny in the light of the Cambrian ‘Orsten’ fossils. In Edgecombe, G. D. (ed.) *Arthropod Fossils and Phylogeny*, 185–231. New York: Columbia University Press.
- Walossek, D. & Müller, K. J. 1998b. 12. Cambrian ‘Orsten’-type arthropods and the phylogeny of Crustacea. In Fortey, R. A. & Thomas, R. H. (eds) *Arthropod Relationships, Systematics Association Special Volume Series* **55**, 139–53. London: Chapman & Hall.
- Walossek, D. & Szaniawski, H. 1991. *Cambrocaris baltica* n. gen. n. sp., a possible stem-lineage crustacean from the Upper Cambrian of Poland. *Lethaia* **24** (4), 363–78.
- Waloszek, D. 2003a. Cambrian ‘Orsten’-type Arthropods and the Phylogeny of Crustacea. In Legakis, A., Sfenthourakis, S., Polymeni, R. & Thessalou-Legaki, M. (eds) *The New Panorama of Animal Evolution, Proceedings of the 18th International Congress of Zoology*, 66–84. Sofia & Moscow: Pensoft Publishers.
- Waloszek, D. 2003b. The ‘Orsten’ Window – A three-dimensionally preserved Upper Cambrian Meiofauna and its contribution to our understanding of the evolution of Arthropoda. *Paleontological Research* **7** (1), 71–88.
- Waloszek, D., Chen, J., Maas, A. & Wang, X. 2005. Early Cambrian arthropods – new insights into arthropod head and structural evolution. *Arthropod Structure & Development* **34**, 189–205.
- Waloszek, D., Maas, A., Chen, J.-Y. & Stein, M. 2007. Evolution of cephalic feeding structures and the phylogeny of Arthropoda. *Palaeogeography, Palaeoclimatology, Palaeoecology* **254**, 273–87.
- Waloszek, D. & Maas, A. 2005. The evolutionary history of crustacean segmentation: a fossil-based perspective. *Evolution and Development* **7**, 515–27.
- Wanninger, A. & Haszprunnar, G. 2002. Muscle development in *Antalis entalis* (Mollusca, Scaphopoda) and its significance for scaphopod relationships. *Journal of Morphology* **254**, 53–64.
- Webster, M. & Zelditch, M. L. 2005. Evolutionary modifications of ontogeny: heterochrony and beyond. *Paleobiology* **31** (3), 354–72.
- Wehner, R. & Gehring, W. 1995. *Zoologie*, 23rd edn. Stuttgart & New York: Thieme. 861 pp.
- Whittington, H. B. 1975. Trilobites with appendages from the Middle Cambrian, Burgess Shale, Columbia. *Fossils and Strata* **4**, 97–136.
- Wills, M. A. 1998. A phylogeny of recent and fossil Crustacea derived from morphological characters. In Fortey, R. A. & Thomas, R. H. (eds) *Arthropod Relationships, Systematics Association Special Volume Series* **55**, 189–209 London: Chapman & Hall.
- Wolff, C. & Scholtz, G. 2006. Cell lineage analysis of the mandibular segment of the amphipod *Orchestia cavimana* reveals that the crustacean paragnaths are sternal outgrowths and not limbs. *Frontiers in Zoology* **3**, 19.
- Wollesen, T., Wanninger, A. & Klussmann-Kolb, A. 2007. Neurogenesis of cephalic sensory organs of *Aplysia californica*. *Cell Tissue Research* **330**, 361–79.
- Zhang, X.-G., Siveter, Da. J., Waloszek, D. & Maas, A. 2007. An epipodite-bearing crown-group crustacean from the Lower Cambrian. *Nature* **449**, 595–9.

