

# The evolutionary history of crustacean segmentation: a fossil-based perspective

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**SUMMARY** The evolution of segmentation in Crustacea, that is, the formation of sclerotized and jointed body somites and arrangement of somites into tagmata, is viewed in light of historical traits and functional constraints. The set of Early to Late Cambrian ‘Orsten’ arthropods have informed our current views of crustacean evolution considerably. These three-dimensionally preserved fossils document ancient morphologies, as opposed to purely hypothetical models and, because of the unusual preservation of larval stages, provide us with unparalleled insight into the morphogenesis of body somites and their structural equipment. The variety of evolutionary levels represented in the ‘Orsten’ including lobopodians, tardigrades, and pentastomids also allows phylogenetic interpretations far beyond the Crustacea. The ‘Orsten’ evidence and data from representatives of the Lower Cambrian Chengjiang biota in southwestern China, including

phylogenetically earlier forms, form the major source of our morphology-based review of structural and functional developments that led toward the Crustacea. The principal strategy of arthropods is the simultaneous development of head somites, as expressed in a basal “head larva,” and a successive addition of postcephalic somites from a preterminal budding zone with progressive maturation of metameric structures. This can be recognized in the developmental patterns of extant and fossil representatives of several euarthropod taxa, particularly crustaceans, trilobites, and chelicerates (at least basally). The development of these taxa points to an early somite-poor and free-living hatching stage. Embryonic development to a late stage within an egg, as occurring in recent onychophorans and certain in-group euarthropods, is regarded as achieved several times convergently.

## INTRODUCTION

Segmentation is a characteristic feature of Arthropoda. Because of this, it has long been thought that the segmented (= metamerized) arthropods and annelids are closely related (Articulata hypothesis; see Ax 1999). Shared features of both taxa would have been obtained from a common ancestor, the stem species of Articulata. The system of serial body subdivisions in arthropods differs, however, in several ways from that of annelids. Annelid development starts with a spiral cleavage and deterministic development; both features are missing in arthropods. Annelids basally hatch as a trochophora larva, retained from the ground pattern of Trochozoa (Ax 1995); arthropods lack this character. In annelids, mesoteloblasts, the daughter cells of the so-called 4d cell, produce the mesoderm including the walls of the segmentally organized coelomic cavities. Coelomic cavities increase in number between the budding zone and the anterior part of the body by a process called “terminal addition.” Adult arthropods show no clear evidence of such a coelomic system, but it exists in the early embryology at least of onychophorans (Bartolomaeus and Ruhberg 1999).

Molecular and developmental biologists have recently challenged this traditional view of a sister-group relationship between arthropoda and annelida. Their alternative, the Ecdysozoa hypothesis (e.g., Aguinaldo et al. 1997; Schmidt-Rhaesa et al. 1998; Manuel et al. 2000; Valentine and Collins 2000; Zrzavý 2001; Almeida et al. 2003; Giribet 2003; Nielsen 2003; Mallatt et al. 2004), recognizes particular in-groups of nemathelminths as being related to arthropods instead. Major supporting arguments at the morphological level are the layered chitin-bearing cuticle (collagenous in annelids) and its regular molting (ecdysis; no molting in annelids). Characters such as the lack of a coelom, lack of a trochophora, lack of spiral cleavage, and lack of deterministic growth in arthropods could be explained as primary. Both hypotheses have certain advantages (for arguments in favor of the Articulata hypothesis see, e.g., Wägele et al. 1999; Wägele and Misof 2001; Scholtz 2002, 2003), but likewise also involve conflicts. We, therefore, feel that it is still too early to jump onto the Ecdysozoa “bandwagon.”

Accordingly, the problem of understanding segmentation of arthropods in an evolutionary context is not just only a problem of history within the arthropod lineage but also of

history dating back to phylogenetically earlier nodes. Attempts to understand segmentation have to face this. We have to search for traces of earliest developmental patterns in light of a clear topological and ontogenetic reference system and by application of different methodological and theoretical approaches. The ability to document phenotypic changes through time is one of the unique contributions of paleontology to evolutionary biology. Interpreting causal factors, however, remains a difficult task. We base our approach mainly on data obtained from two fossil sources. One is from Early to Late Cambrian ‘Orsten’-type arthropods (overviews in Müller and Walossek 1991; Waloszek 2003a, b). The other source is the fossils from the Early Cambrian Maotianshan shales in southwestern China (overviews in Chen 2004; Hou et al. 2004). For comprehensive comparisons we add examples from extant crustaceans.

‘Orsten’ animals, found on various continents, are preserved in an exceptional three-dimensional fashion. This was caused by secondary phosphatization of the cuticle shortly after death and the absence of any compaction (cf. Müller 1990; examples in Müller and Walossek 1985a, b, 1987, 1988; Walossek 1993; see also Roy and Fåhræus 1989; Walossek et al. 1993; Müller et al. 1995; Siveter et al. 2001, 2003 for examples of discoveries outside Sweden; general review in Tang 2002). Many of the ‘Orsten’ fossils are larvae or, at least, immature, and the fossilization window seems to be restricted to meiofauna, that is, to small-sized benthic to infaunal animals that had lived in or on a soft bottom environment. ‘Orsten’ fossils provide unique data about ontogenetic stages and morphogenesis of structures, extremely rare in the fossil record.

The fossils from the Chinese Lower Cambrian Maotianshan shales are preserved in a flattened fashion. Details, and particularly the topological context, are more difficult to obtain than in the ‘Orsten,’ not least as the original cuticle is not exactly replicated, hematite crusts from former bacterial activities giving a generalized “vision” of the former animal (Braun, personal communication 2004). Although delicate body parts and cuticles (e.g., sipunculids, see Huang et al. 2004) may also be represented, there is no record as yet of early larvae. On the other hand, the Maotianshan shale fossils exhibit an excitingly broad span of metazoan taxa, outranging that of any other Lower Paleozoic lagerstätte (summary in Chen 2004). The age of both Maotianshan shale and ‘Orsten’ datasets, according to be at about half a billion years is an excellent empirical data source for any hypothesis dealing with arthropod morphology, and also for developmental patterning and metazoan evolution in general. Because we are dealing with fossils, we have to restrict ourselves to morphological features. We do not dismiss anatomical, developmental, or molecular data, but focus on comparable data with both fossil and extant taxa.

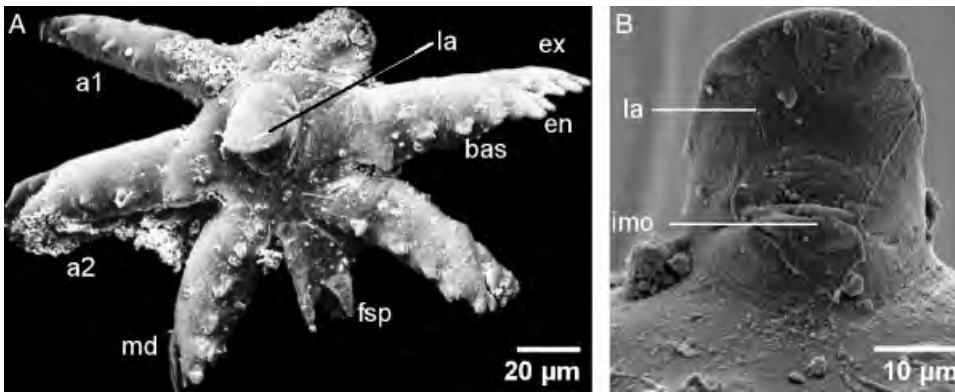
## POSTEMBRYONIC STAGES OF CRUSTACEANS/ARTHROPODS PRESERVED IN THE ‘ORSTEN’

The preservation of ontogenetic stages (e.g., Müller and Walossek 1986a) permits the documentation of changes of ventral body details ranging from the appendages to finest structural details such as pores or cuticular surface ornaments like setules on setae even smaller than 1  $\mu\text{m}$ . The detailed morphology observable in ‘Orsten’-type preservation also permits access to ecological aspects of locomotion, food gathering, and habitat preferences of different stages (e.g., Müller and Walossek 1991). Some of the preserved larvae can even be assigned to successive stages. Yet, their interpretation would have been impossible without a clear phylogenetic hypothesis as a backbone. This helped us sort the material and in recognizing that the earliest euarthropod larva possesses the segmental condition of the adult head (the “head larva” according to Walossek and Müller 1990, 1998a, b). In a broader perspective, we tried to investigate some major questions such as the following:

- Were the larval appendages and other structures functional at hatching?
- Were the larvae mobile and feeding?
- Are these larvae the earliest stages of a set of postembryonic instars for a particular species, and can they be interpreted in an evolutionary context?
- How do the larvae contribute to questions of terminal somite addition and maturation of the somites?
- Which came first, an embryo developing a yolk-rich egg or a mobile “larva” with just a few somites?

### ‘Orsten’ larvae, morphologies, and affinities

The smallest ‘Orsten’ larvae in the material are 100–130- $\mu\text{m}$  long (Fig. 1A). These so-called type-A larvae have an egg-shaped body, one uniramous and two biramous pairs of appendages, a labrum on the ventral side, an initial mouth as a slit behind it (Fig. 1B), and an initial anus at the rear of the rounded end between three stout spines. Some of these larvae are inflated and extremely well preserved. This, and their poor setation, are indicative of a nonfeeding life of this type, living only on internal yolk, which is similar to nonfeeding eucrustacean larvae. Type-A-larvae have no visible head shield (Müller and Walossek 1986a; see Walossek and Müller 1989 for a second, slightly larger type and Roy and Fåhræus 1989 for similar larvae from Newfoundland). Type-A larvae cannot be affiliated with the larger stages of any of the ‘Orsten’ arthropods. Yet, they bear functional appendages more differentiated than those of the earliest arthropod limbs (e.g., Waloszek et al. 2005). The number of limb-bearing segments, together with the labrum (Fig. 1B), exopods with inwardly pointing setae (Fig. 1A), and the set of tail spines is seen as evidence of their nature as true eucrustacean (ortho)nauplii.



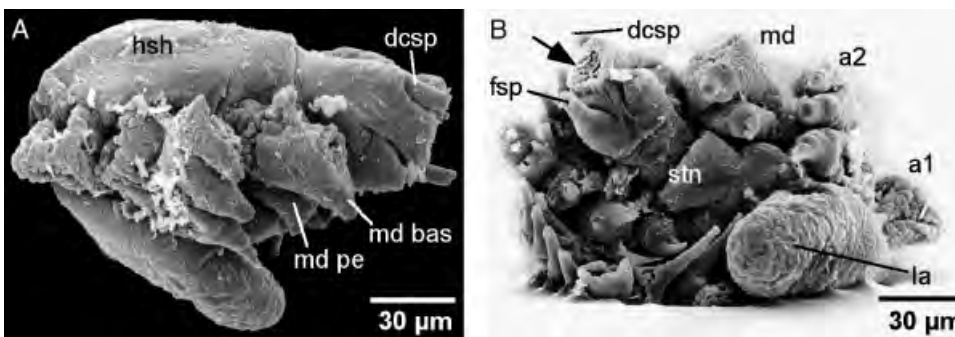
**Fig. 1.** SEM pictures of type-A larvae. (A) Ventral view of a complete specimen lacking left antennula (UB W122; Waloszek 2003b, Fig. 1.4, new figure). Note the tiny setae, often arranged in pairs. (B) Same specimen as in (A); detailed view of the posterior side of the labrum with the initial mouth. a1, first antenna or antennula; a2, (second) antenna; bas, basipod; en, endopod; ex, exopod; fsp, furcal spine; imo, initial mouth; la, labrum; md, mandible.

The small, 160-µm first instar of the branchiopod eucrustacean *Rehbachella kinnekullensis* Müller, 1983 (Waloszek 1993) also possesses only three appendages (Fig. 2, A and B). By contrast, these are well developed and bear a conspicuous setal armature (Fig. 2B) demonstrating their ability to serve as locomotion and feeding devices. Possession of a head shield (Fig. 2A), compound eyes, a prominent labrum covering the mouth recessed deeply in an atrium oris, and several other features make it a eucrustacean orthonauplius.

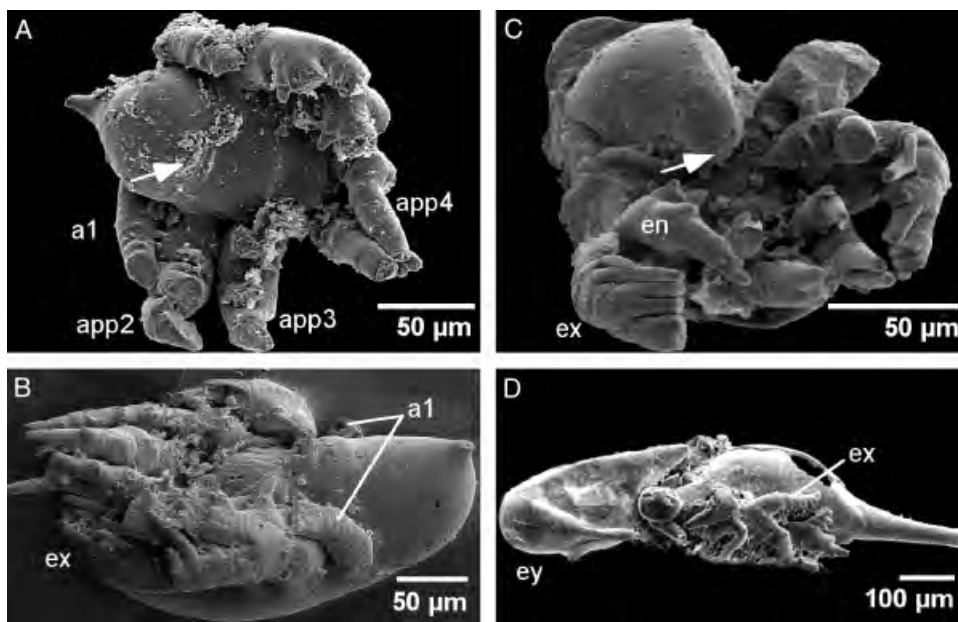
Other larvae in the ‘Orsten’ material could be allied with crustacean-like species that we interpret as derivatives of the early stem lineage of Eucrustacea. Such larvae (Fig. 3, A–D) have antennulae and three functional biramous limbs, thus representing head larvae. They share the lack of a labrum, they do not show a recessed mouth but a hypostome with a mouth at its rear (if developed), and they have no fine setulae on setae and the mouth area, as do orthonauplii (and those of phosphatocopine larvae). Differences between them concern the presence or absence of the mouth, hypostome, anus, and dorsal shield, indicative of an array of life styles for these larvae from nonfeeding (Fig. 3A) to fully free living and feeding (Fig. 3, B–D). For example, the egg- to spindle shaped first stage of *Martinsonia elongata* (Müller and Waloszek 1986b) (Fig. 3A) has no hypostome, mouth or anus. By the third stage (Fig. 3B) the hypostome (the antennular sternite, see Waloszek et al. 2005) appears as a shallow hump, likewise

the Y-shaped mouth within a pliable membrane and the anus appear. The first larva of *Henningsmoenicaris scutula* (Waloszek and Müller 1990) is similarly egg-shaped, but the hypostome, Y-shaped mouth, anus, and setae are developed already by the smallest, possibly first stage (Fig. 3C). The much larger larva of *Goticaris longispinosa* Waloszek and Müller (1990) is sack shaped and possesses a huge uniform eye and a long caudal spine. Mouth and anus are present (hypostome lacking in this species, as in *Cambropachycyope clarksoni* Waloszek and Müller 1990). Further growth seems to be gradual in all these taxa by somite addition in front of the ventral preterminal anus (unpublished data).

Phosphatocopina are considered to be the sister taxon of the Eucrustacea together comprising the Labrophora, named after their characteristic labrum at the rear of the hypostome (cf. Siveter et al. 2003; see also Maas et al. 2003; Maas and Waloszek 2005). The specialties of Phosphatocopina are the short body enclosed in a bivalved (cephalothoracic) shield (largest shield approximately 5-mm long), tiny antennulae, and maximally three-segmented endopods on their biramous limbs. The first known, approximately 130-µm long, larval stage is already enclosed within the shield and, therefore, a “head larva,” that is, having antennulae plus three biramous limbs (the orthonauplius is an autapomorphy of Eucrustacea). Besides this, the first phosphatocopine larva (Fig. 4A) shares several features with the eucrustacean nauplius, which



**Fig. 2.** Orthonauplius of *Rehbachella kinnekullensis* Müller, 1983 (UB W3; from Waloszek 1993, pl. 1:1, 4). (A) Lateral view, limbs broken off distally. (B) Same specimen in ventral view. Arrow marks the anus. Abbreviations other than those than in Fig. 1: dcsp, dorsocaudal spine; hsh, head shield; md bas, basipod of mandible; md pe, proximal endite of mandible; stn, sternum.



**Fig. 3.** Larvae of stem-lineage Crustacea. Arrows point to mouth area. (A) First larva of *Martinsonia elongata* (UB W129), approximately 190- $\mu$ m long, lacking hypostome, mouth and anus (new figure). (B) Third larva of *M. elongata*, 390- $\mu$ m long, with a minute swelling identified as the initial hypostome and the pliable mouth membrane at its rear (UB 757; new figure, compare with *Agnostus pisiformis* Fig. 11A; cf. Müller and Walossek 1986b, Figs. 11E and 12, C and D). Front and tail extend in a short spine. (C) Egg-shaped first larva of *Henningsmoenicaris scutula* (UB W130), 200- $\mu$ m long, with a huge hypostome bearing the mouth at its rear (new figure). (D) Youngest larva of *Goticaris longispinosa* having a sac-like body extended into a long spine

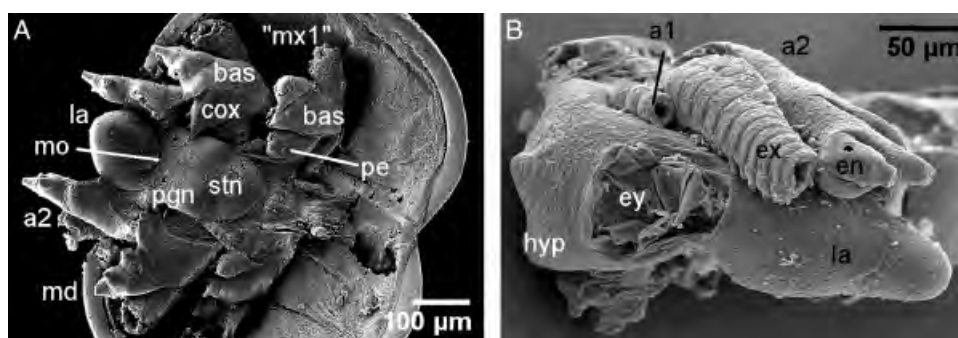
(UB 98; larva 300- $\mu$ m long; from Walossek and Müller 1990, Fig. 3, A and B; new figure). Abbreviations other than those in Figs. 1 and 2: app, appendage; ey, eye.

are lacking in the stem-lineage larvae (and their later stages) noted above: the huge labrum as a fleshy outgrowth above the recessed mouth (Fig. 4, A and B, a sternum (fusion product of the sternites of mandibular and first postmandibular somites) with paragnaths (on mandibular part; Fig. 4A), the (second) antennae and mandibles bearing a coxal element proximal to the basipod (Fig. 4A), and fine setulae on labrum, sternum, paragnaths, and setae. The hypostome remains plesiomorphically present in front of the labrum (but this is true also for eucrustaceans). The fourth pair of functional limbs behind the mandibles is designed in the fashion of the limbs of the stem-lineage taxa, that is, it has a small setiferous endite, the “proximal endite,” medially below its basipod (Fig. 4A). As this fourth cephalic limb and all more posterior limbs are

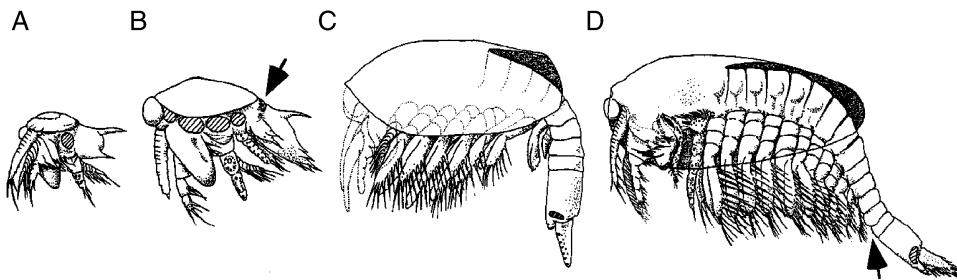
serially similar, the differentiation of the fourth limb into the maxillulae does not occur at the labrophoran level, but is a further autapomorphy of the Eucrustacea.

### Larval sequence of *R. kinnekullensis* as a reference model for crustacean and arthropod ontogeny

The long series of larvae reconstructed for *R. kinnekullensis* permits a detailed view of the development of metamerization (process of somite formation) and of the structural differentiation of all metameric details, particularly of the appendages (Walossek 1993). Accordingly, it can serve as a useful tool for



**Fig. 4.** Larval Phosphatocopina. (A) Early larva of *Hesslandona suecica* Maas et al. (2003), viewed from postero-ventral (UB W 140; about 280  $\mu$ m; from Maas et al. (2003) their Fig. 59B). (B) Anterior view of hypostome and labrum of an advanced stage of *Hesslandona* sp. (UB W 131). Abbreviations other than those in Figs. 1–3: cox, coxa; hyp, hypostome; mo, mouth; “mx1”, first postmandibular limb = “maxillula” of eucrustaceans; pe, proximal endite; pgn, paragnaths.



**Fig. 5.** Examples of the larval series of the 'Orsten' branchiopod eucrustacean *Rehbachella kinnekullensis* Müller, 1983. (A) Stage 1, orthonauplius. (B) Stage 4, meta-nauplius 3 (last naupliar stage; segment of maxilla still free from shield, arrowed). (C) Stage 20, Ts8 with eight trunk somites. (D) Stage 30 Ts13 with 13 trunk somites, last lacking limbs, and posterior two limbs as buds (from Walossek 1995).

wide-ranging comparisons of morphology and morphogenesis within Crustacea and Arthropoda in general.

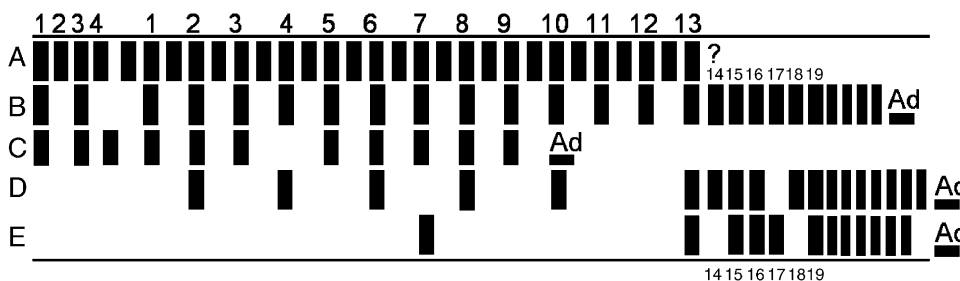
The (ortho)nauplius of *R. kinnekullensis* has segmented and setiferous antennulae involved in the sweep-net feeding and locomotory mechanism. The (second) antenna and mandible (Fig. 2, A and B) have a limb stem subdivided into a coxa and a basipod, both armed with strong spines medially, a feature retained from the Labrophora level. These features—the well-developed armature with setae and spines, all with secondary setulae, and the protruding compound eyes at the front of the short head shield covering the three limb-bearing somites—point to a free-living and feeding mode of life of this larva type. The postmandibular trunk of the first larval stage is just a short bud with a dorso-caudal spine above the anus and ventro-caudal buds of the furcal rami—no different from a modern copepod or cirripede nauplius (see also the type-A larva above). A preterminal budding zone is not expressed externally at this stage.

The known larval cycle of *R. kinnekullensis* comprises a series of 30 successive stages, mostly documented by actual specimens (Walossek 1993). The described sequence ends at a stage with 13 trunk somites, 12 of which bear limbs. The posterior limbs are rather short and less developed than the anterior ones. Fragmentary specimens that have much larger limbs than those known from the largest complete specimens are present in the material. This suggests that ontogeny proceeded further, possibly in a third phase similar to that of

anostracan branchiopods, in which the abdomen appears and further differentiations occur.

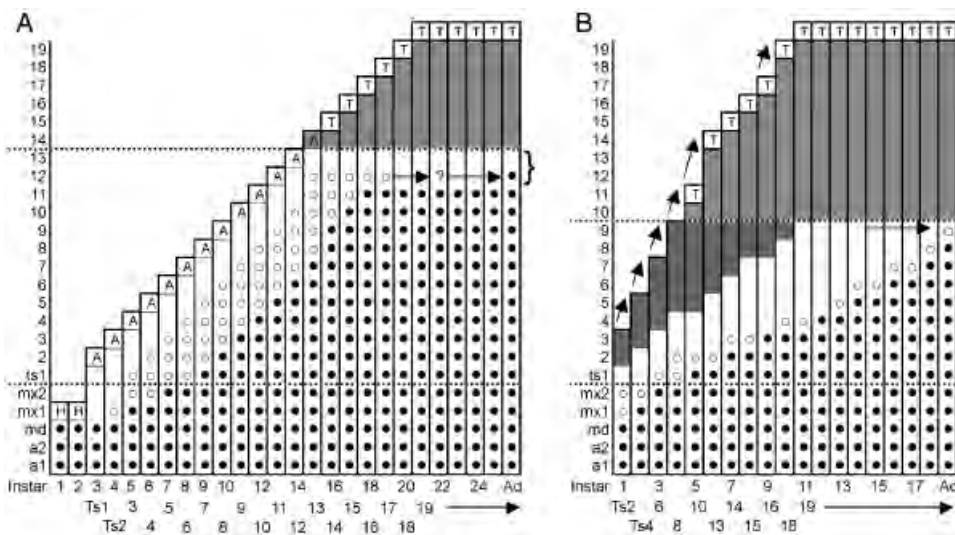
The sequence until trunk segment stage 13 can be differentiated into two principal phases. The first comprises four instars. During this phase the two maxillae appear in a pattern which matches that of Recent eucrustaceans: The subconical bud of the hind body carries a pair of strong furcal spines latero-caudally and a median dorso-caudal spine terminally, with the anus between them. The maxillula appears as a seta on the hind body, and by the next stage it is a bifid bud. Stage 4 has the bifid buds of the maxillae, whereas the maxillulae are armed with median spines (cf. Walossek 1993, Fig. 5, B–D). During this phase, no clear segments are budded off from the trunk bud.

During the second phase the trunk somites develop (Figs. 6 and 7). Remarkably, each trunk somite develops in two steps, that is, most likely in two molts. In the first step, the somite is only partly released, visible as a dorsal incision that partly delineates the tergite. Limbs appear at the second step, when the formation of the somite is completed, and the tergite is clearly developed. This two-step acquisition of trunk somites continues until 13 somites are formed—a phase with 26 stages altogether. The last somites are almost ring shaped and have no clearly defined tergites. A transverse dorsal furrow delineates the incipient somites. During this second phase, 12 trunk limbs appeared progressively, and each limb achieved a filter-limb morphotype with more than 200 setae [developed?] in



**Fig. 6.** Ontogenetic patterns of *Rehbachella kinnekullensis* (A) compared with that of the anostracan branchiopod *Artemia salina* (B), the harpacticoid copepod *Drescheriella glacialis* (C), and the two cephalocarids *Hutchinsoniella macracantha* (D) and *Lightiella incisa* (E) figure modified from Walossek 1993, see also for original sources of data from other

crustaceans). Line 1 (left numbers 1–4), larvae only having head somites, line 1 (right numbers 1–13 and 14–19), number of thoracomeres developed; lines 2–5 (black rectangles), instar present of respective species having corresponding numbers of thoracomeres developed. Question mark, a later instar of *R. kinnekullensis* than that having 13 thoracic somites is not known because of preservational aspects. Ad, adult.



**Fig. 7.** Ontogenetic patterns of *Artemia salina* (A) and the extant cephalocarid *Hutchinsoniella macracantha* (B) modified from Walossek 1993). Filled circles, developed and functional appendages; hollow circles, initial appendages; dashed lines, boundary between cephalon and thorax, and thorax and abdomen. Abbreviations for last body portion: A, undivided hind body; H, undivided larval hind body; T, telson, missing or incomplete delineation indicated by dotted line; ? with arrows in A, unclear when limb develops. Arrows indicate "jumps" in somite addition. Arrow pointing to last circle of adult *H. macracantha*: loss of mandibular pulp during final molt. Bright gray area marks the

abdomen, dark gray area in B marks hind body region of *H. macracantha*, which may include thoracic as well as abdominal segments. Abbreviations other than those in Figs. 1–6: mx2, second postmandibular limb = maxilla; ts, trunk segment; Ts, trunk segment stage.

eight half-steps (four segments in eight molts). The latest instar is estimated to be about 1.7-mm long, but the final size might have been considerably greater.

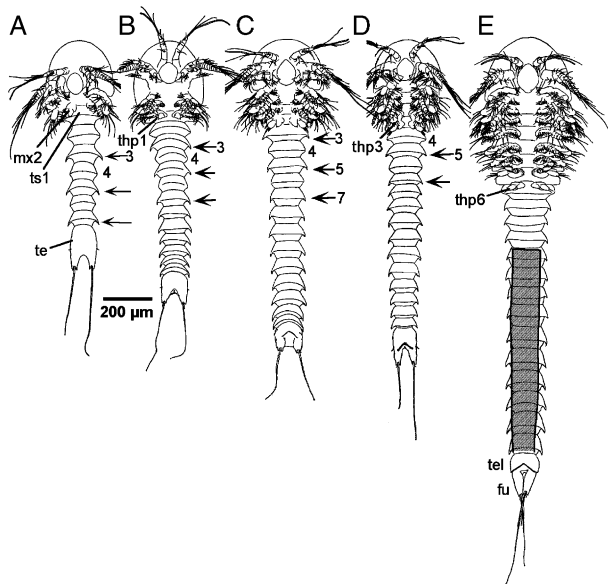
This strictly constrained development matches the anamorphic development of several extant entomostracan taxa, but none of them has such a regular and gradual sequence. No significant delay or any sequential interruption during the larval development of *R. kinnekullensis* seems to occur, and the change from phase one to the second phase is also minor. With this, the complete sequence is a good model for any kind of anamorphic development that starts with an early somite-poor but locomoting and feeding larva. Again, it can be taken as a reference pattern for comparisons of developmental patterning in all fossil and extant crustacean taxa, possibly even giving additional information on ontogeny of Arthropoda in general.

Comparing the ontogeny of phosphatocopines and stem-lineage crustaceans with that of *R. kinnekullensis*, it is evident that the eucrustacean nauplius, exemplified by the *Rehbachella nauplius*, cannot be more plesiomorphic than the larvae of phosphatocopines and particularly than those of the stem-lineage taxa of Labrophora/Crustacea (cf. Fig. 3). In fact, all major features of the phosphatocopine larvae are also developed in the eucrustacean nauplius (e.g., labrum and coxae on a2 and md), only that the latter has fewer limbs (Maas et al. 2003), but are clearly lacking in the head larvae of the labrophoran stem taxa. The most parsimonious explanation is to regard this as derived and to interpret the orthonauplius as an advanced larval type. Moreover, the subsequent growth series of *R. kinnekullensis* and Eucrustacea do not bypass a stage with four limb-bearing somites and fully functional limbs: the

maxillula appears first as a seta or bud only. Consequently, the orthonauplius, sometimes regarded as retained from older evolutionary branchings (Lauterbach 1983; Dahms 2000), is not a result of just a simple shift of hatching to an earlier time in the phase of development, but is a highly derived and shortened larva (Walossek and Müller 1990, 1998a; Walossek 1993, 1999; Maas et al. 2003).

Two extant eucrustacean taxa show a very gradual anamorphic development comparable with *R. kinnekullensis*: the anostracans and the copepods. Anostracans, like species of *Artemia salina* Linné, 1758, show a reduction of two early stages and some delay in limb development of postmandibular limbs (Fig. 6B); in copepods like *Drescheriella glacialis* Dahms and Dieckmann, 1987, most early stages are retained (Fig. 6C). Thorax development in *A. salina* includes exactly 13 stages, whereas there are 26 ( $= 2 \times 13$ ) in *R. kinnekullensis* because of doubling of somite formation (Fig. 6A). Subsequently, there are more stages in *A. salina*, revealing a third, postlarval differentiation phase in which the six abdominal segments form, the naupliar limbs are re-modeled, and the genital segments (thoracomeres 12 and 13) develop their characteristic sexual features (missing in *R. kinnekullensis* because of preservation). As there is no larval sequence in which thoracomeres formation occurs in two steps, as in *R. kinnekullensis*, neither in extant nor in fossil arthropods, it may well be that such is the autapomorphy of this fossil species.

Another extant eucrustacean taxon that has gained much attention in the past is the blind Cephalocarida. Often considered basal, their larval development seems to be highly specialized, but, although cephalocarids occupy a central focus for crustacean phylogeny, no more than three papers so



**Fig. 8.** Larval development of *Lightiella incisa* Gooding (1963) (modified from Sanders and Hessler 1964). Arrows and numbers in (A–D) mark trunk somites. (A) Stage 1, with seven trunk somites. Abdominal somites marked by a gray bar in (E). (B) Stage 2 with 13 trunk somites. (C) Stage 3 with 15 trunk somites. (D) Stage 5 with 17 trunk somites. (E) Stage 10 with 19 trunk somites (final number). Abbreviations other than those in Figs. 1–7: fu, furca; te, trunk end; tel, telson.

far have dealt with their ontogeny (Fig. 8; Gooding 1963; Sanders 1963; Sanders and Hessler 1964).

Larval development of the Cephalocarida has been regarded as strictly anamorphic, but rather shows considerable deviation from the pattern of extant anostracans (Fig. 7A) and copepods (Fig. 7; Walossek 1993). It begins with a fairly advanced stage compared with the orthonauplius: The first larva of *Hutchinsoniella macracantha* Sanders, 1963 has already two thoracic somites (Figs. 6D and 7B), that of *Lightiella incisa* Gooding, 1963 has even seven (Figs. 6E and 8). *H. macracantha* adds two trunk somites at one molt until the thorax is terminated (Figs. 6D and 7B), not only a single somite, as in copepods or *A. salina*. In fact, *L. incisa* needs only two molts to reach the level of 13 trunk somites, the final number of thoracomeres in anostracans. Thus, somite addition in cephalocarids occurs in “jumps” (indicated by arrows in Fig. 7B). Similar “jumping” in somite addition also occurs in other crustacean taxa (e.g., decapod malacostracans), but in quite different ways (see Walossek 1993 for example in his Fig. 43 and his Table 4, pp. 84–86). One interpretation might be an independent abbreviation of ontogeny in such a way that original larval instars were skipped in order to reach the adult phase more rapidly and with fewer molts.

Two more features of the ontogeny of cephalocarids are noteworthy. One is that after having budded off 13 trunk

somites, development becomes very gradual, and only then (Fig. 6, D and E). Yet, addition and development of limbs remains extremely delayed: When the terminal addition is finished, still only three thorax limbs are fully developed (TS19, Fig. 7B). The last pair of limbs (the egg carriers) does not even appear before the final molt to the adult.

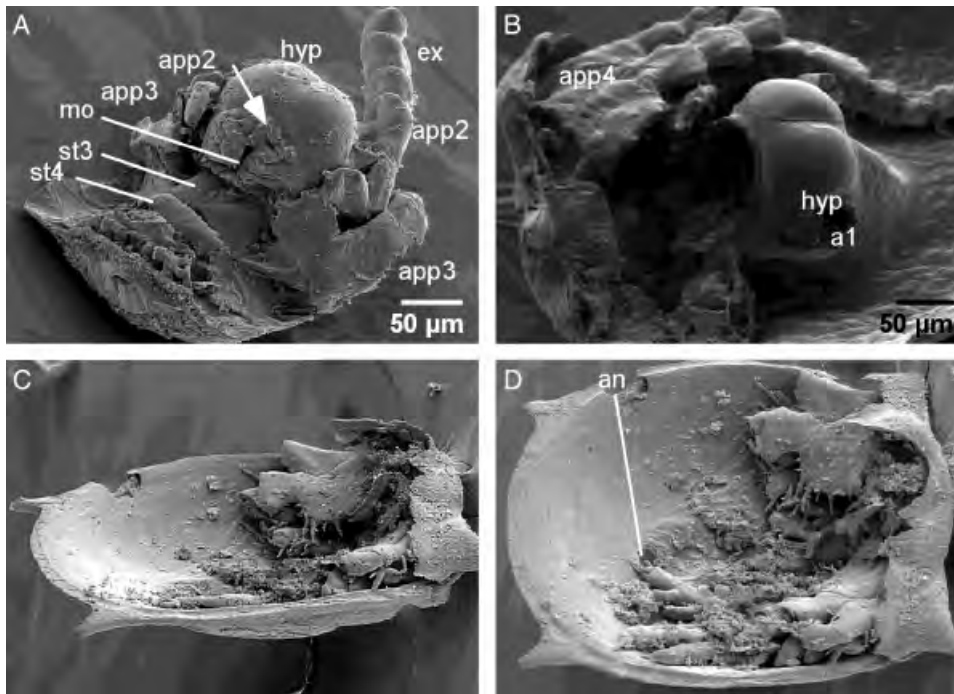
The other feature is, at least to our knowledge, unknown from any other crustaceans: At least in anostracans and also in copepods, the abdominal somites appear after all thoracomeres and their limbs are formed (Fig. 7A). However, it seems that in cephalocarids the long abdomen and thorax form in parallel. Abdominal somites are ring shaped (with lateral spines in *Lightiella*), whereas thoracomeres have tergites with pleurotergites, so displaying the plesiomorphic shape. As can be seen in *Lightiella* (Fig. 8), progressively rings are added (segments numbered), whereas far anteriorly thoracomeres, and, later, limbs, are formed (dark-gray zone in Fig. 7B). It may be possible that the patterning is caused by a differential activity of the underlying control genes, as hypothesized by Hughes (2003a), but at present we cannot explain this phenomenon of a transformation of segments from an apomorphic “abdominal shape” into a plesiomorphic “thorax shape”; this should be investigated further.

## A VIEW OF OTHER EUARTHROPODA

The smallest larvae of derivatives of the crustacean stem lineage, as known from the ‘Orsten’ taxa *M. elongata*, *H. scutula*, *G. longispinosa*, and *C. clarksoni*, are all “head larvae,” and their trunk is an undivided hump. Feeding structures are missing in the early larva of *M. elongata* (no mouth or anus, which develop later during ontogeny, cf. Müller and Walossek 1986b), but are present in larvae of the other three forms. Trunk development of these taxa is still under investigation.

## Ontogeny of *Agnostus pisiformis*

The most abundant component of the ‘Orsten’ and leading fossil of zone 1 of the former Upper Cambrian in Scandinavia is *A. pisiformis* Wahlenberg, 1818. *A. pisiformis* is a small arthropod having a head and tail shield of approximately 5 mm in length and two interposed tergites as an adult. The shields of adults are calcified and rock forming. Agnostids together with eodiscids, another taxon of small segment-poor euarthropods, are traditionally assigned to the Trilobita, but Stein et al. (2005) have pointed out some striking similarities with particular derivatives of the crustacean stem lineage mentioned above. Consequently, agnostids may have derived from the early crustacean lineage (as already tentatively



**Fig. 9.** SEM pictures of larval *Agnostus pisiformis* (Wahlenberg, 1818) (specimens illustrated in Müller and Walossek 1987; new pictures). (A) View of median part of the ventral head surface of first instar (UB 845). (B) Anteroventral view of cephalic shield with hypostome of second instar (UB 840). (C and D) Originally enrolled specimen, second instar, most of cephalic shield removed (UB 859). (C) Lateroventral view of thoracic shield. (D) Ventral view. Abbreviations other than those in Figs. 1–8: an, anus; st, sternite.

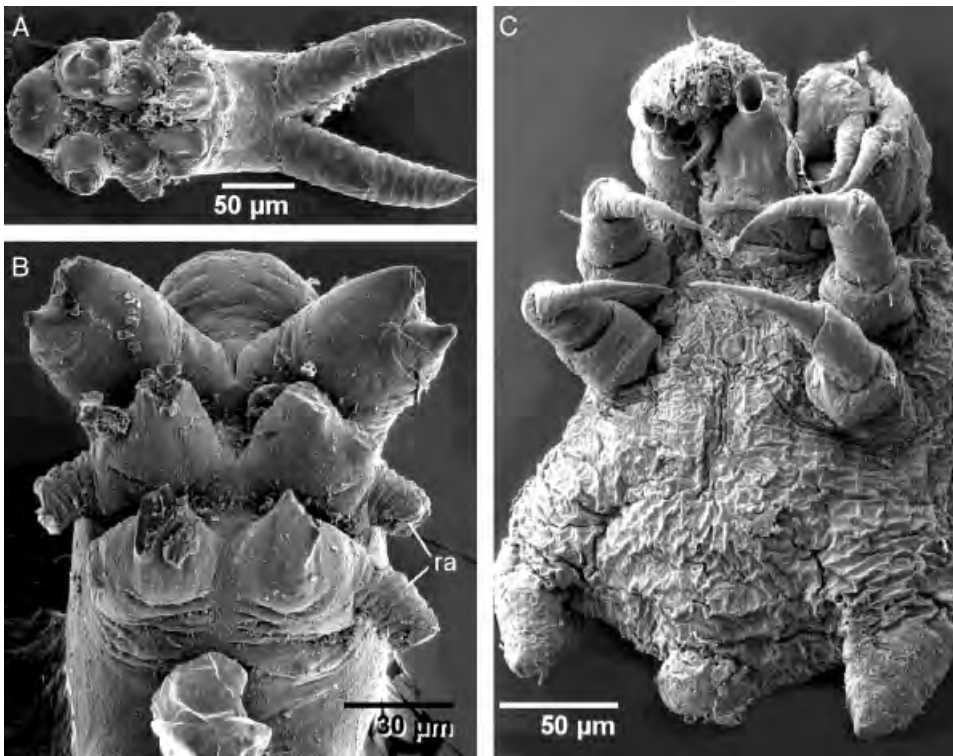
assumed by Walossek and Müller 1990), whereas eodiscids may well be miniature trilobites.

Postembryonic development of *A. pisiformis* starts with a larva approximately 300  $\mu\text{m}$  in length and already having a trunk shield as large as the head shield (Müller and Walossek 1987). Its head is composed of the same number of somites as the adult head, that is, it comprises the eye somite (inferred to be present although there are no eyes in this form), the antennular somite (the region of the huge hypostome with the antennulae attached laterally, Fig. 9, A and B) and three more limb-bearing somites. Buds of two to three limbs on the trunk (Müller and Walossek 1987) indicate that this first larva of *A. pisiformis* represents advanced stage and not a “head larva,” the basal type of euarthropod larva. Apparently, these first larvae were able to feed and move actively. In fact, no substantial morphological changes occur subsequently in ontogeny, except a slight somite increase (two somites), dorsal separation of the anterior two trunk somites and a progressive differentiation of the developing trunk limbs. In particular, the head does not change significantly. Only five trunk limbs occur until the first so-called holaspis stage (shield size 1 mm), as defined by the final number of externally visible tergites, that is, two in all agnostids, between head and tail shields. As segmentation is terminated here, the formation of these tergites is a phenomenon of differentiation, not a phenomenon of terminal addition. Until this first holaspis, each trunk limb matures progressively from a bud into a large flat limb with a final number of seven endopodal segments and long banana-

shaped outgrowths on most of the endopodal podomeres (Fig. 9, C and D; Müller and Walossek 1987). Furthermore, sternitic bars connecting the limbs appear one by one, indicating the correlation with increasing segmentation; elsewhere the ventral cuticle of the trunk is smooth and continuous (Fig. 9, C and D). Adults are not known to have limbs.

### Ontogeny of chelicerates

Within the crown group of Chelicerata, early larvae are known only from pycnogonids and xiphosurans. The so-called protonymph larvae of extant pycnogonids (crown group = pantopods) have three pairs of appendages: chelicerata, now known to be homologous to the antennula of other arthropods (cf. Mittmann and Scholtz 2003; see also Vilpoux and Waloszek 2003; Chen et al. 2004; see Waloszek et al. 2005 for the terms antennula vs. antenna for the first head appendage in Arthropoda s. str.), and two pairs of uniramous legs. The ‘Orsten’ material has yielded the geologically oldest pycnogonid larva, *Cambropycnogon klausmuelleri* Waloszek and Dunlop (2002) (Fig. 10, A and B; e.g., Waloszek and Dunlop 2002; Vilpoux and Waloszek 2003). This larva can be compared directly with extant pantopod protonymphs and differs mainly from them in a pair of rod-shaped caudal outgrowths (Fig. 10, A and B), but which are similar to the developing legs of postprotonymphal pantopod larvae (compare with *Nymphonella tapetis* Ohshima, 1927 (Korschelt and



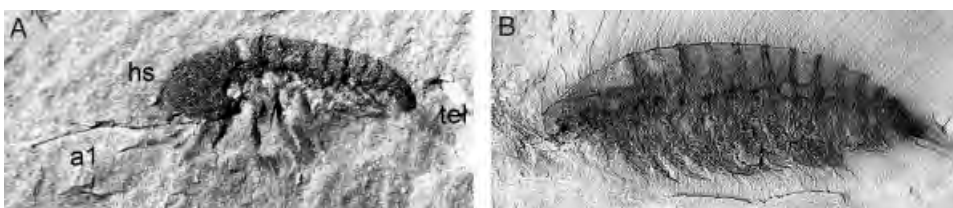
**Fig. 10.** SEM pictures of fossil and extant early pycnogonid larvae. (A, B) *Cambropycnogon klausmuelleri* Waloszek and Dunlop (2002). (A) Ventral view of complete specimen with caudal rami (UB 803; from Waloszek and Dunlop 2002). (B) Ventral view, detail of anterior region with large chelicera and the two posterior limbs with gnathobasic limb bases and thin annulated rami laterally (ra; UB 802; from Waloszek and Dunlop 2002). (C) *Pycnogonum littorale* (Ström, 1762), ventral view of stage 2, with initial fourth pair of legs (courtesy: Kathia Vilpoux, Ulm).

Heider 1936) or *Pycnogonum littorale* Ström, 1762 (Vilpoux and Waloszek 2003); see Fig. 10C).

As the adult head of pantopods (the so-called cephalosoma) bears the chelicerae (= antennulae) plus three pairs of legs basically, which represents the number of cephalic segments of the euarthropod head, the protonymph is less segmented than the basal euarthropod “head larva.” There are two possible phylogenetic interpretations: (1) The character state of the pantopod protonymph situation (only the antennular and two more limb-bearing somites) is plesiomorphic. If so, the chelicerates may not have reached the “final” head segmentation level early during ontogeny but developed it progressively (Vilpoux and Waloszek 2003). Consequently, terminal addition of somites first had to fill the head and then the trunk. (2) Chelicerates, or pycnogonids/pantopods, depending on where the feature arose, achieved a “short-head” larva convergently with the Eucrustacea, and subsequently

added somites first to the adult cephalosoma. We favor this second interpretation.

Further back phylogenetically, there are relatively few reports of smaller and less segmented stages (e.g., from some of the Burgess-shale arthropods); some descriptions may even be based on young stages rather than on adults. Species assigned to the so-called “great-appendage” arthropods, derivatives of the stem lineage of Chelicerata (Chen et al. 2004), may be an exception. For example, the substantial material of the several centimeter long Chinese Lower Cambrian *Alalcomenaeus illecebrosus* Hou, 1987, includes smaller specimens (Fig. 11A) with about seven to nine trunk somites, whereas the largest has 13 (own yet unpublished observations; Fig. 11B; see also Briggs and Collins 1999 for the Middle Cambrian *A. cambricus* Simonetta, 1970). It may well be that the lack of even smaller specimens is because of preservational bias.



**Fig. 11.** Lower Cambrian Maotianshan Shale arthropods (courtesy: Chen Junyuan, Nanjing). (A and B) *Alalcomenaeus illecebrosus*. (A) Small specimen with 9–10 trunk somites, approximately 8-mm long. (B) Larger specimen with 13 trunk somites, approximately 20-mm long.

## IMMATURE STAGES FROM OTHER EARLY ARTHROPODS

Although rather beyond the scope of our paper, we shall briefly review the report of developmental stages of other euarthropods and members of other levels. The largest record is available for trilobites. These well-sclerotized and calcified euarthropods show a very regular increase of trunk segmentation (e.g., Whittington 1957; Clarkson et al. 1997). Trilobites have a substantial set of stages starting with a so-called protaspis, with four limb-bearing head somites and a short shield, possibly antennulae, and three more pairs of head limbs, and a short trunk bud (e.g., Størmer 1941; Palmer 1957; Whittington 1957; Evitt 1961; Hu 1979; Speyer and Chatterton 1989; Clarkson and Zhang 1991; Shergold 1991; Berard et al. 1999; see also Hughes 2003a, b). The report of a so-called phaselus larva having only three limb-bearing somites by Fortey and Morris (1978) is doubtful. Early somite-poor stages have not yet been described for any other fossil euarthropod taxa.

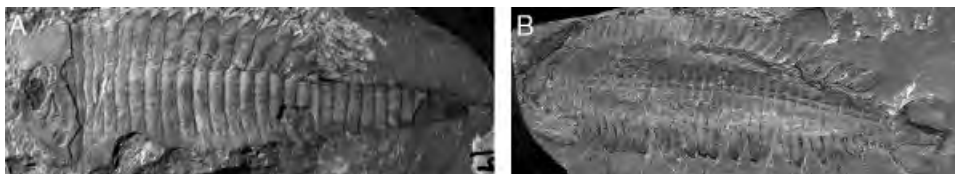
Those animals that have an arthrodized and arthropodized morphology have recently been included in the monophyletic taxon Arthropoda s. str. (Maas et al. 2004; Waloszek et al. 2005). The earliest members of these are, in our view, *Fuxianhuia protensa* Hou, 1987 (Fig. 12A), *Chengjiangocaris longiformis* Hou and Bergström, 1991, and a new Lower Cambrian Maotianshan Shale taxon *Shankouia zhenghei* Chen, Wang, Waloszek and Maas in Waloszek et al. (2005) (Fig. 12B; Chen 2004). All three forms are characterized by a set of features shared exclusively (synapomorphically) with euarthropods (e.g., sclerotized cuticle with tripartite tergites, compound eyes, segmented antennulae, biramous post-antennular limbs, pivot joints), but possess a head including only the ocular (pre-antennular) somite and one appendage-bearing somite, the antennular somite. The postantennular limbs consist of simple setae-less multi-segmented limb rods—showing no proximal rigid basipod portion—plus a flat exopodal flap. They clearly mark off an evolutionary step between the soft-cuticled Cambrian “lobopodian taxa,” onychophorans, and tardigrades (and, in our view also the pentastomids, see Waloszek and Müller 1994; Almeida and Christoffersen 1999; Maas and Waloszek 2001 contrasting, e.g., Lavrov et al. 2004) and the Euarthropoda embracing the

chelicerates, chilopods, progoneates, hexapods, and crustaceans plus a large number of allied fossil taxa (e.g., trilobites, naraoiids, etc.). There seems to be some size variation in *F. protensa*, but young have not been reported so far from this species, neither from *C. longiformis*. Of *S. zhenghei* we have found few smaller and less segmented specimens, but none with less than 25 trunk somites, so no data are available that help to illuminate the early developmental phase of Arthropoda s. str. from a fossil perspective.

The earliest phase of arthropod evolution is represented by onychophorans, tardigrades, possibly the pentastomids, and the so-called Lower to Middle Cambrian lobopodians. Briefly touching on this, nothing is known from the ontogeny of lobopodians as yet, which range in length from a few millimeters to approximately 8 cm. One of them, *Paucipodia inermis* Chen, Zhou and Ramsköld (1994), has significantly fewer limbs than all other species (Chen et al. 1994), but it is among the largest species, so is unlikely to be a juvenile of any of the others (Chen et al. 1994; see Chen 2004; Hou et al. 2004 for a general overview of Maotianshan shale lobopodians). Extant onychophorans have a so-called superficial cleavage and an embryonic development with hatching young that resemble miniature adults (Storch and Ruhberg 1993). Tardigrades may have a larva with three pairs of leg-bearing somites or hatch with the final number of four somites (Maas and Waloszek 2001; Kristensen personal communication, 2004). Pentastomids hatch with the adult number of two cephalic leg-bearing somites and three in the trunk in front of a caudal portion, which could be confirmed by fossils from the Upper Cambrian ‘Orsten’ (cf. Waloszek and Müller 1994 for further references).

## CONCLUSIONS

In light of the data from extant and especially those from fossil species, we favor the interpretation that a free-living and feeding early (head) larva with few somites represents the plesiomorphic state at least for Euarthropoda, including Chelicerata. Accordingly, the alternative, germ-band development (Scholtz 1998, 2000) is considered as apomorphic and must have evolved convergently numerous times likely because of different egg-protection strategies. Therefore, the answer to



**Fig. 12.** Two early members of Arthropoda s. str. B. *Fuxianhuia protensa* Hou, 1987 (about 12-cm long). Dorsal view (courtesy: Chen Junyuan, Nanjing, China). (A) *Shankouia zhenghei* Chen, Waloszek, Wang & Maas in Waloszek, Chen, Maas & Wang, 2005 (about 6-cm long). Dorsal view (from Waloszek et al. 2005).

the question as to whether larval appendages and other structures were functional from the beginning of ontogeny is “Yes.” The same would apply to locomotory and feeding abilities. Investigations of several of the fossil arthropods from the Maotianshan shale biota and especially of the arthropods from ‘Orsten’ type of preservation demonstrate that the early evolution of the arthropod head toward the euarthropod head was characterized by addition of somites ending in a larva that hatches with the complete head segments (eye segment, antennular segment, and three segments with limbs; “head larva”) formed already in the embryo phase. The terminal addition starts then with the formation of trunk somites paralleled by a successive specialization of more and more limbs for food intake and manipulation in the postembryonic = larval phase.

Basally the trunk grows from the posterior towards the anterior as new cell material appears at the posterior end of the larvae, regardless of whether development is embryonic or larval. Somites of the trunk may be delayed in structural maturation, but not in their strict sequential appearance. Modification of this condition has produced the bulk of variations seen in the ontogeny of modern crustaceans, the most deviant being development completed in the egg (e.g., in nebalicean Malacostraca). The addition of functional limbs may thus have become very different, and limbs from posterior body parts might be functional when more anterior ones may still be buds or even missing (e.g., in decapod mysids; an example of tergite differentiation in the middle of the body is *A. pisiformis*). This depends obviously on the functional necessities of the larva and its life style.

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