



Evolution of cephalic feeding structures and the phylogeny of Arthropoda

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Abstract

Focusing on structural and functional changes during the evolution of Arthropoda, we based our approach on evidence provided by two major Cambrian lagerstätten yielding exceptional preservation: the Lower Cambrian Chengjiang lagerstätte, Yunnan Province, China, and the Lower to Upper Cambrian ‘Orsten’-type lagerstätten with their 3D-preserved fossils. We established a model of major steps in the evolution of the arthropod feeding system, with emphasis on the head region. Using fossils, we identify two major gaps in our knowledge about this evolutionary process to be filled in the future. One of them is how development progressed from the stem arthropod level toward that of Arthropoda s. str. The latter stage is known now from three Chengjiang taxa, which possess, besides other features, a head composed of only two segments, i.e. those bearing the compound eyes and the limb-shaped antennulae. The post-antennular trunk limbs are very simple and lack any feeding structures, spines or setae. With this, only the antennula could have been involved in food gathering. Another uncertainty concerns the transition from the Arthropoda s. str. level to that of the Euarthropoda. Euarthropoda embraces all those well-sclerotized arthropods with extant descendants, and its ground pattern includes a larger head tagma with four appendage-bearing segments and post-antennular limbs made of a rigid, but flat gnathobasic basipod carrying two rami. At this stage, feeding had become more elaborate than before, yet all post-antennular appendages remained serially designed. Crustacea changed their feeding system initially by modifying the anterior three cephalic appendages, and the mouth area and by developing a specific setation on various body parts. Subsequently, more appendages became involved within certain in-group taxa. Our model elucidates that changes of the functional system occurred at the macroscopic and the microscopic level. Although many allied features, such as the gut system or the appendage morphology, remained remarkably conservative over longer periods, feeding was most likely a significant driving force for evolutionary changes in the morphology of arthropods, particularly of the head region.

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1. Introduction

A major trigger of bilaterian evolution is evident in the progressive enhancement of mobility and feeding strategies. This was particularly achieved by the development

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of a subepidermal muscle system, a subepidermal nervous system and further specialisations of the sensory systems (e.g., eyes), as well as by specialisations of the internal anatomy such as the intestinal system. In the Arthropoda, in particular, regionalisation of the body, tagmatisation, played a significant role, specifically with regard to the formation of a head as the specific site of mouth, sense and feeding structures.

Based on evidence from two of the major Cambrian lagerstätten that provide exceptionally well-preserved fossils, thus once-lived morphologies, we investigate the structural and functional changes of the feeding system

in the evolutionary lineage of the Arthropoda. On the Chinese Yangtze Plate, Arthropoda have an extremely long fossil record right down to the lowermost Cambrian, as recorded in small shelly fauna components (e.g., Bengtson et al., 1986; Steiner et al., 2003) and trilobites (e.g., Steiner et al., 2001), and also trace fossils (e.g., Weber and Zhu, 2003; Zhu et al., 2004). Arthropoda are particularly well documented in the exceptionally preserved Chengjiang biota from the western edge of the Yangtze Plate in Yunnan province (e.g., Hou et al., 2004; Chen, 2004; examples in Fig. 1). A second exceptional source is the ‘Orsten’-type fossil

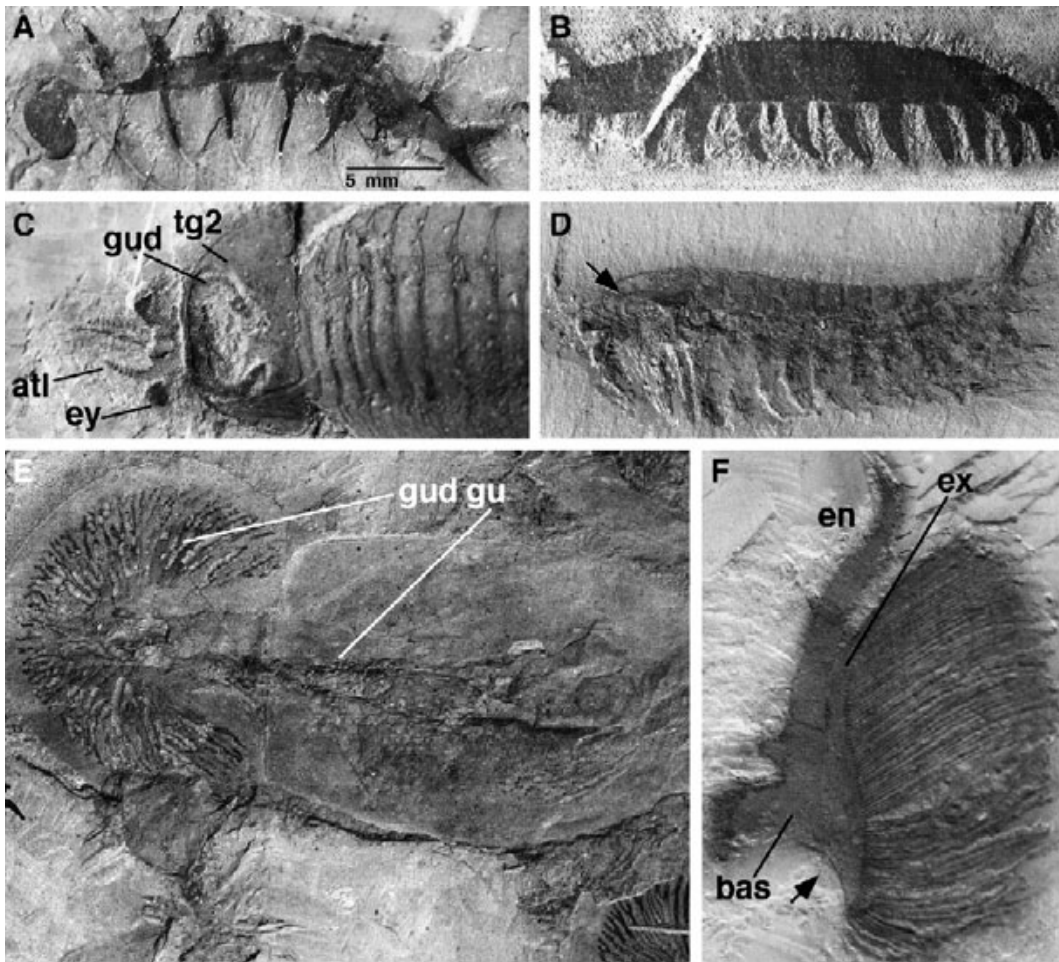


Fig. 1. Cambrian arthropods. A, C–F. Selection of Chengjiang arthropods. A. The lobopodian *Hallucigenia fortis* Hou and Bergström (1995) (photograph by Junyuan Chen, Nanjing, China). B. The Middle Cambrian *Aysheaia pedunculata* Walcott, 1911 (by permission from Conway Morris et al., 1982). C. Anterior body region of *Fuxianhuia protensa* Hou, 1987. Large second tergite prepared off medially, exposing the internal structures interpreted as gut diverticula (because of a cuticular layer underneath; cf. Waloszek et al., 2005). D. *Alalcomenaeus illecebrosus* Hou, 1987. Small individual displaying the gut bowing backwards within the head (arrow), toward the mouth at the rear of the hypostome. E. *Naraoia spinosa* Zhang & Hou, 1985; two specimens with well-preserved gut and cephalic gut diverticula; F. post-antennular limb of the naraoid *Misszhouia longicaudata* (Zhang and Hou, 1985) (Zhang & Hou 1985; Chen et al., 1997) with flat, medially spinose basipod, slender endopod and a slim exopod with fine spines or lamellae along its outer margin (see text). Arrow points to deep cavity originally filled with the missing arthrodistal membrane. All post-antennular limbs more or less identical. Abbreviations: atl=antennula; bas=basipod; en=endopod; ex=exopod; ey=eye; gu=gut; gud=gut diverticulum; tg=tergite.

assemblages (examples in Fig. 2), originally discovered in Sweden (overviews in Müller and Waloszek, 1985a, 1991a,b; Waloszek and Müller, 1992; recent compilations in Waloszek, 2003a,b). ‘Orsten’-type fossils are now known from the uppermost Lower Cambrian (Siveter et al., 2001, 2003) and Middle Cambrian (Waloszek et al., 1993; Müller et al., 1995) to the Upper Cambrian (see references above). Fossils with similar types of preservation have been found on several continents and in younger sediments (Canada, Europe, Russia, Australia, China; cf. Bottjer et al., 2002).

Both lagerstätten provide different data sets (taxa) of early arthropods.

The Chengjiang biota contain, besides representatives from all major metazoan taxa, a wealth of arthropods from different evolutionary levels that display a stepwise

evolution from worm-like ancestors to euarthropods (Hou et al., 2004; Chen, 2004). The first set comprises stem-taxa referred to as lobopodians, xenusians or tardipolypods (example Dzik and Krumbiegel, 1989; Hou and Bergström, 1995; Monge-Najera, 1995; Chen and Zhou, 1997; Ramsköld and Chen, 1998; Bergström and Hou, 2001; Chen, 2004). These soft-cuticled stem arthropods, most of them several centimetres long, have a small mouth at their anterior end and a set of often hook-bearing soft limbs with tubular or slender conical form. A second set of larger animals, such as *Fuxianhuia protensa* Hou, 1987; *Chengjiangocaris longiformis* Hou and Bergström, 1991, and *Shankouia zhenghei* Chen, Wang, Maas and Waloszek in Waloszek et al. (2005) have been identified as early members of the Arthropoda s. str., which includes all well-sclerotized forms with equally

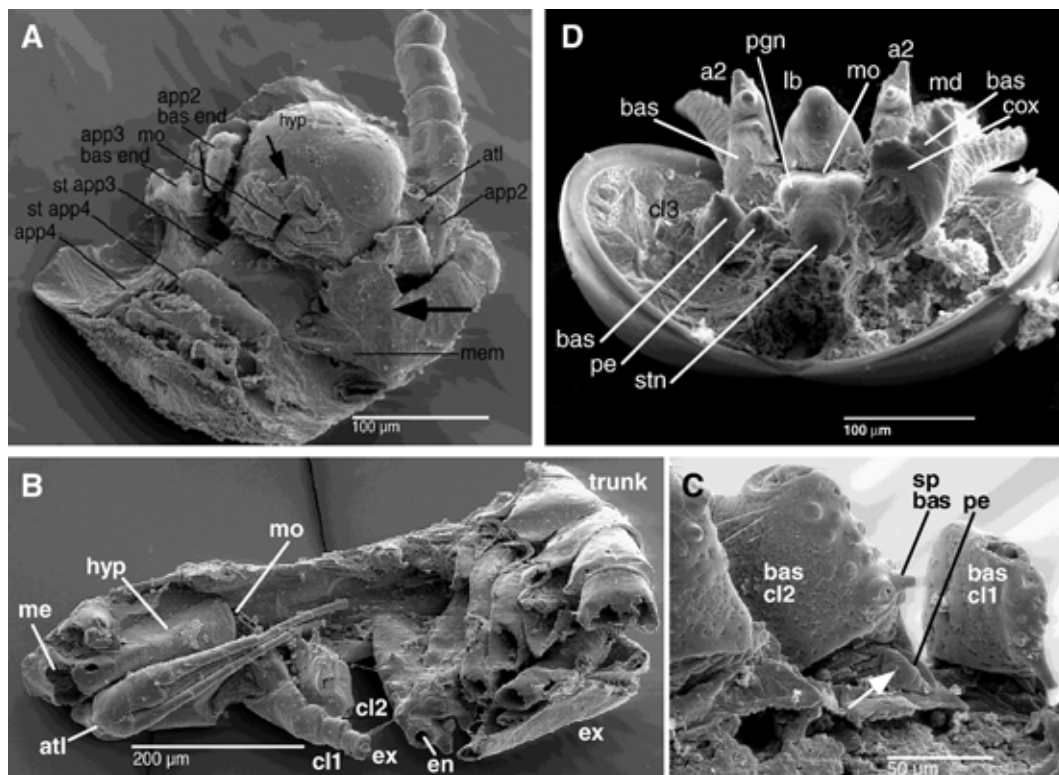


Fig. 2. Scanning electron micrographs of selected ‘Orsten’ arthropods. A. Young specimen of *Agnostus pisiformis* (UB 845, cf. Müller and Waloszek, 1987, pl. 12–5). Dorsal shield, trunk and distal parts of the appendages broken off permitting a view on the large hypostome and appendages arranged around the mouth (mo). Small arrow points to mouth membrane, the distal part of which presumed to be extruded into the labrum in labrophoran Crustacea (see panel D and text). Note the subtrapezoidal shape of the basipod with its oblique lateral edge, from which the exopod arises (large arrow). B, C. *Oelandocaris oelandica* Müller, 1983 (UB W 263; cf. Stein et al., 2005). B. Ventral view of a fragmentary specimen. C. Inner view of the proximal region of the second and third head appendages. A proximal endite is located only in the ample membrane of the third limb, bearing a small seta (arrow). Note the specific median armature of the basipods with spines and setae mostly broken off. D. Posteroventral view of a larva of the phosphatocopine *Hesslandona suecica* Maas et al. (2003) (UB W 140), from behind, toward the mouth, in the atrium oris below the labrum. Note the second antennae (a2) and mandibles flanking the labrum, the rigid sternum, the paragnaths and the ample membrane of the mandibular coxa suggesting large movements. Abbreviations other than in Fig. 1: app=appendage; cl=(post-antennular) cephalic limb; md=mandible; me=median eye; hyp=hypostome; lb=labrum; mem=arthrodial membrane; mo=mouth; pe=proximal endite; pgn=paragnath; sp bas=basipodal spine; st=sternite; stn=sternum.

sclerotized and jointed appendages (for characterisation of this taxon see Maas and Waloszek, 2001; Maas et al., 2004; Waloszek et al., 2005). A third, large set includes a number of euarthropods, such as anomalocaridids and ‘great-appendage’ arthropods (recently identified as stem chelicerates, see Chen et al., 2004) and a variety of animals with feeler-like antennula, such as trilobites and trilobite-like forms including naraoiids. Trilobites are much less represented in Chengjiang biota (4–5 species) than in the slightly younger Kaili fauna, also from China. The latter fauna contain far fewer soft-bodied taxa (cf. Zhao et al., 1999a,b). Other arthropods may well comprise representatives of the lineage between the earliest arthropods s. str. and Euarthropoda. Examples are *Canadaspis laevigata* (Hou and Bergström, 1991), *Ercaia minuscula* Chen et al. (2001), *Xandarella spectaculum* Hou and Bergström, 1991, *Cindarella eucalla* Chen, Ramsköld, Edgecombe and Zhou in Chen, Zhou, Zhu, and Yeh, 1996, *Primicaris larvaformis* Zhang, Han, Zhang, Liu and Shu, 2003, species of *Isoxys* Walcott, 1890, or the small bradoriids.

‘Orsten’ arthropods were secondarily phosphatized, i.e. their cuticle was impregnated by calcium apatite, possibly shortly after death (Müller, 1990). Since this process affected also the thin top layer, the epicuticle, impregnation was most likely not associated with chitin. Even very delicate surface structures became preserved, such as membranes, pores, and fine setules or bristles on hairs, which are even smaller than 0.3 µm in diameter. Due to phosphatization, unless pieces are incompletely impregnated or broken off, all structures are preserved in place, i.e. they are retained in their original three-dimensional context or topology. This makes reconstructing the organisms much easier than in virtually any other type of fossilisation. Another extraordinary feature of the ‘Orsten’ is the fossilisation of ontogenetic stages (e.g., Müller and Walossek, 1985b), which allows monitoring of features during their morphogenesis. Changes in size and form can easily be recognized, and missing parts reconstructed from other instars (examples in Müller and Walossek, 1986a,b, 1987, 1988; Walossek, 1993; Waloszek and Dunlop, 2002; Maas et al., 2003). Also assumptions of functional and biological/palaeo-ecological aspects (e.g., Müller and Walossek, 1991b) can be made with a much higher degree of confidence than with most other fossil material (cf. the exceptional fossils from the Silurian Hereford lagerstätte, UK, preserved in volcanoclastic sediments; see Orr et al., 2000). These data can be further utilized for phylogenetic analyses and the reconstruction of evolutionary processes of structures and functional systems (see, e.g., Walossek and Müller, 1998a,b; Walossek, 1999; Waloszek, 2003a,b; Maas et al., 2003). The small size of the specimens restricts

finds to small-sized animals and ontogenetic stages. As yet not even fragments above a size of max. 2 mm are known. Notwithstanding, this ‘Orsten’ material permits a view into a different ecological window, the so-called meiofauna (for definition and overview see Higgins and Thiel, 1988). This assemblage of originally small and dwarfish animals occupies the interstitial, the sediment–water interface and the top layer of a soft-bottom regime (fluff layer), rarely preserved otherwise in the fossil record but obviously present in ecosystems throughout the Phanerozoic.

From these two different sources of evidence and based on our phylogenetic analyses, with regard to common occurrence and the parsimony principle, we established a model (Fig. 3) that visualizes the major evolutionary changes in the arthropod feeding system. During evolution, a large number of structures underwent changes or developed progressively: body parts, tagmata, were formed, appendages became modified and sensorial devices (eyes, sensilla etc.) or organ systems advanced, such as the nervous system, the intestinal, the excretory, the circulatory and the reproductive systems. Since an exhaustive review is beyond the scope of this paper, we focus mainly on the changes that affected the feeding system with particular emphasis on the head region. Indeed the cephalon, regardless of its size or segmental composition, seems to be that body region of an arthropod, if not of Bilateria in general, which is mostly concerned with feeding. This is particularly apparent when looking at Recent arthropods, and, evidently, arthropods spent much effort developing a vast number of different feeding types by modifying their cephalic limbs and associated structures. Accordingly, the changes along the appendage apparatus can even be regarded as the principle source of information when evaluating evolutionary aspects of feeding in Arthropoda. A large number of papers have addressed the question of the evolution of the arthropod head from different historical backgrounds, different data sets or points of view. Of these only the theoretical approach of Dewel et al. (1999) will be considered in more detail, as they have presented a model that was based largely also on Cambrian fossils.

2. Modelling the evolution of cephalic feeding in arthropods

2.1. The first phase in the evolution of arthropods

The systematic affinities within the Arthropoda have been controversial for decades. A supposed close relationship to the Annelida, however, was not questioned for a long time until recently, challenged in particular by

molecular studies (see Maas et al. this volume for a brief overview of the Articulata and Ecdysozoa hypotheses and references). This alternative interpretation suggests a closer alliance of arthropods with the cuticle bearing, also moulting but acoelomate cycloneuralian Nematelminthes. Regardless of this, the earliest arthropods in the wider sense may have appeared much as the Lower to Middle Cambrian lobopodians (Fig. 1A, B). These

centimetre-long ‘worms with legs’ reflect, in our view, the ground pattern design (see also Dzik and Krumbiegel, 1989), in particular in as much as they must have had a slim tubular body, a very thin cuticle, 6 to about 25 body segments, each with a pair of ventrolaterally extending, similarly unjointed appendages. Their head varied in form from being elongated or short conical shape, barrel form and bulb-like, in a number of laterally situated head

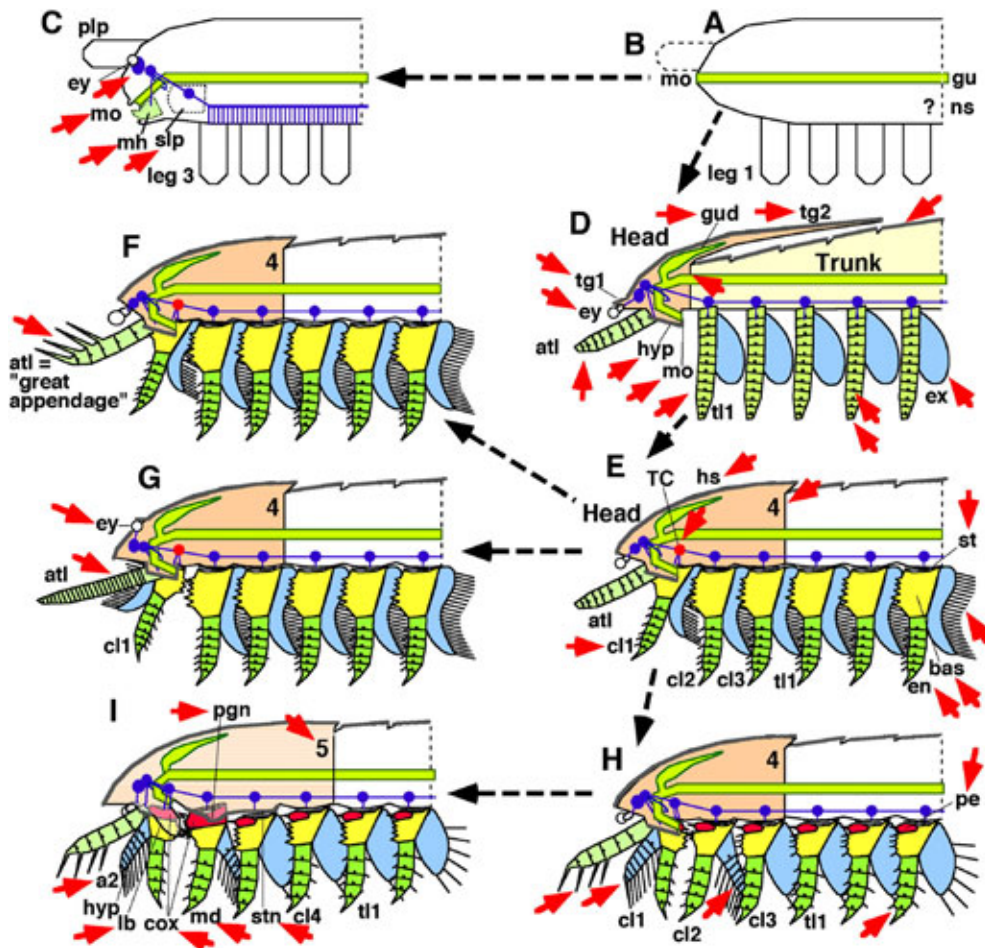


Fig. 3. Hypothesized evolution of the anterior body region along the arthropod lineage (drawn as sagittal sections). External features obtained from Recent and fossil taxa, but simplified (only example taxa included); internal structures also simplified, restricted to gut and nervous systems. Arrows point to newly achieved features (see text). A, B. Cambrian Chengjiang and Burgess-Shale lobopodians exemplifying the earliest level, having a frontal mouth, simple gut system, either lacking (A) or having special antero-laterally directed first limbs, and serial, tubular, uniramous appendages (B). C. Model of an extant onychophoran (nervous system according to Eriksson and Budd, 2001). D. Arthropoda s. str. level, as reconstructed from three Chengjiang taxa (see text and Waloszek et al., 2005). E. Hypothesized euarthropod stem species; uncertainty exists so far only about the anterior movement of the tritocerebral segment and size of its sternite. F. Chelicerate stem-lineage level, four limb-bearing head segments retained (Chen et al., 2004), as exemplified by Cambrian Chengjiang and Burgess-Shale representatives having a “great appendage” (precursor of the chelicerae, see Chen et al., 2004) with a four spines bearing claw, such as *Jianfengia multisegmentalis* Hou, 1987. G. Trilobites having multi-annulated/segmented antennae and dorsally positioned eyes; compound eyes dorsally located. H. Representative of the crustacean stem lineage, drawn as a mixture of the ‘Orsten’ taxa *Martinssonella elongata* Müller and Waloszek (1986a, b) (lacking eyes and with a small shield) and *Henningsmoenicaris scutula* Waloszek and Müller (1990) (with stalked eyes and large shield; see also *Oelandocaris oelandica* Müller, 1983 in Stein et al. (2005), having only 1 proximal endite at the third appendage). I. Labrophoran level, exemplified by the ‘Orsten’ Phosphatocopina (cf. Maas et al., 2003). Abbreviations other than in Fig. 1: a2=antenna; cox=coxa; leg=limb; mh=mouth hook; ns=nervous system; plp=palp; slp=slime papilla; TC=tritocerebrum; tl=thoracic limb.

appendages and in having one to two pairs of head appendages to absence of these. Despite the fact that some authors claimed the presence of head sensory structures (including eyes) and a head shield, no reliable sensory structures have been found yet in the head region. The trunk is tubular in form, supported, in some cases, by pairs of ventrolaterally extending limbs. The limb in basal forms most likely bore a pair of terminal claws, which are pointed and curved posteriorly in most of the limbs except the last pair of limbs, which is pointed anteriorly. The last pair of limbs is located, in most if not all cases, at or near to the terminal end of the trunk.

Trunk and limbs are both walled by a delicate cuticle, which often is finely annulated. In addition to these annulations, the trunk may be ornamented with hard, or possibly mineralized sclerites, which lie dorsal to the limbs. The sclerites varied in form between species. They may be spine-like, plate-like and triangular, dome-like with a spine-like extension on top, or dome-shaped with holes. Since the last pair of limbs is located at or near to the terminal end of the body, it is possible to determine the anterior–posterior orientation, although some authors still confuse this orientation of some lobopodians. To the six Chengjiang biota taxa, namely *Cardiodictyon catenulum* Hou, Ramsköld and Bergström, 1991, *Hallucigenia fortis* Hou and Bergström (1995) (Fig. 1A), *Luolishania longicruris* Hou and Chen, 1989, *Microdictyon sinicum* Chen, Hou and Lu, 1989, *Onychodictyon ferox* Hou, Ramsköld and Bergström, 1991 and *Paucipodia inermis* Chen, Zhou and Ramsköld, 1995 (see, e.g., Ramsköld, 1992a; Chen, 2004) have to be added *Xenusion auerswaldae* Pompeckji, 1927 from German erratic boulders (only one more specimen discovered subsequently: Schallreuter, 1985) and the Middle Cambrian taxa *Aysheaia pedunculata* Walcott, 1911 (see, e.g., Whittington, 1978) and *Hallucigenia sparsa* (Walcott, 1911) (see, e.g., Ramsköld, 1992b). There are two further species that possibly belong to this set or may be slightly more advanced: *Kerygmachela kierkegaardii* Budd, 1993 and *Pambdelurion whittingtoni* Budd and Peel, 1998 from the Upper Lower Cambrian Sirius Passet of Greenland (Budd, 1993, 1998; Budd and Peel, 1998). They could not be studied by us in detail, and hence are not yet included in this present study.

Based on evidence from the Cambrian lobopodians, that of Recent onychophorans and tardigrades, including anatomical features, and that of better sclerotized arthropods, we suggest that the ground pattern of Arthropoda should have included at least the following characters:

- an undifferentiated head, only one or two segments incorporated (even number of appendages uncertain),

bearing a fronto-terminal mouth (Fig. 3A referring to animals lacking special anterior appendage-like outgrowths, Fig. 3B referring to animals with one special fronto-lateral appendage-like outgrowth) — status uncertain;

- a simple open circulatory system with a dorsal heart and segmental ostia — autapomorphy;
- a simple, tubular and straight gut with a terminal anus, possibly having midgut diverticula — gut plesiomorphic, diverticula unclear;
- a simple brain consisting possibly of no more than a circum-oral or pre-oral ganglial mass, no sensory organs — status depends on the phylogeny hypothesis, thus left as uncertain.

A circum-oral so-called stomodeal nervous system as present in extant cycloneuralians may be present also in the arthropod ground pattern, but this must remain uncertain due to contradictory interpretations (e.g., Dewel et al., 1999; Eriksson and Budd, 2001). It may well be that a long slender head without head appendages, as exemplified by *Paucipodia* and *Microdictyon*, represents the original condition from which the head became more sophisticated with the rise of one or two pairs of new head appendages and possibly related neuromere(s). In the absence of better data, it remains similarly difficult to estimate whether the lateral, palp-like appendages of *A. pedunculata* (indicated by Fig. 3B) and *K. kierkegaardii* were innervated by post- or pre-oral neuromeres.

If the two head appendages in seemingly more advanced lobopodians are homologous to the stalked eyes and the first appendages of the Arthropoda s. str. (see below), their neuromeres, equivalent to the so-called protocerebrum and deutocerebrum, respectively, should still have a nerve connection behind the gut, the post-oral commissure, as this is true for Chelicerata within Euarthropoda (Mittmann and Scholtz, 2003). Feeding must have been rather simple; possibly the animals ingested food by sucking in particles or softer material but even scavenging would not be impossible. Some lobopodians were preserved in close contact with medusa-like forms (Chen et al., 1995; Chen and Zhou, 1997; Chen, 2004; cf. Dzik et al., 1997). Chen and Zhou (1997) and Chen (2004) have interpreted this as an indication of an ectoparasitic life on or in such organisms, probably feeding on body fluids by sucking. Alternatively, these animals may have simply benefited from food brought in by currents produced by the host organisms (food stealing=kleptoparasitism, as observable in various extant mutualistic associations, e.g., Martinez and Bachmann, 1997).

Long pathways led from lobopodian-like arthropod ancestors to two different extant lineages, e.g., the terrestrial predatory velvet worms, Onychophora (Fig. 3C) and the microscopic eight-legged water bears, Tardigrada (which cannot be covered here). The cephalic morphology of Onychophora appears quite advanced relative to that of Cambrian tardipolypods in several aspects, e.g., in that the mouth is oriented somewhat downwards, the head region is slightly swollen and bears three pairs of outgrowths: the palps or antennae antero-dorsally – with eyes close to their bases –, a pair of lateral short outgrowths, the slime papillae, on which glands open that produce a secretion for capturing prey, and a pair of chitinous hooks inside the mouth for mashing food (incorrectly called ‘mandibles’). The two latter structures can be regarded as highly modified limbs, recognizable in their ontogenetic development from limb anlagen (cf. Pflugfelder, 1948). Besides many further specialisations not mentioned here, it is noteworthy that the gut is very simple (plesiomorphic), while changes affected the nervous system. One may even speak of a brain in Onychophora, but the situation is controversial. According to a tentative interpretation by Harzsch (pers. communication 2004), the brain includes three neuromeres: the protocerebral part innervating the eyes, the deutocerebral innervating the slime papillae, and one to innervate the mouth hooks. The fourth ganglion by this interpretation would innervate the first pair of walking legs (see Eriksson and Budd, 2001; Eriksson et al., 2003 for a different interpretation).

2.2. The second phase in the evolution of arthropods

From this level, the evolutionary path led to those animals that were more firmly sclerotized and share a large number of features to be included in a taxon Arthropoda s. str. (Figs. 1C, 3D, 5A; see Maas et al., 2004; Waloszek et al., 2005). Examples of the characteristic/apomorphic features of this monophylum are:

- a pair of compound eyes with eye stalks, arising ventrally and anteriorly from a separate body segment with a short tergite;
- a pair of segmented and pivot-jointed, limb-shaped antennulae with limited number of articles (possibly 15) inserting ventrally on the second body segment;
- second body segment with a large, uniform tergite that expands laterally and caudally to cover the first 4–6 (short and narrow) trunk tergites freely;
- equipment of the post-antennular (trunk) metamers with sclerotized abaxial cuticular bars, tergites, with lateral extensions, tergopleurae; tergites connected by softer membranous cuticular areas (arthrodized condition);
- a softer ventral area of each segment bearing one pair of biramous limbs consisting of a multisegmented rod (segments connected by pivot joints) and a flap-shaped outgrowth laterally, the exopod (arthropodized condition; Fig. 4A, G);
- trunk ending in an elongated, conical end piece (telson or pygidium).

F. protensa (Fig. 1C), *S. zhenghei* and *C. longiformis* from the Chengjiang fauna exemplify this evolutionary level (cf. Maas et al., 2004; Chen, 2004; Waloszek et al., 2005 refer them as proarthropods, i.e. fossil representatives of the first evolutionary step of arthrodization). It is not very likely that all features mentioned developed in a single speciation event but evolved more gradually and stepwise. This leaves an apparent morphological gap between the shape of the tardipolypod-like ancestors and that of Arthropoda s. str.

The significant path to arthrodized and arthropodized animals was accompanied by various changes in the feeding and locomotory habits of these. The most significant modification may have been the posterior bend of the oesophagus leading to a backwards orientation of the mouth opening behind a sclerotic plate, hypostome. In this phase of arthropod evolution only one pair of appendages is morphologically differentiated from all others, the antennulae. This term is preferred here instead of “antennae” since the limb pair concerned here is homologous to the first antennae or antennulae of Crustacea. These appendages were stout, comprise possibly no more than 15 segments and were held in anteriorly directed posture (Waloszek et al., 2005). Apparently, they were the only food-gathering structures of the anterior body region, because all trunk limbs have neither median enditic protrusions nor any armature with setae or spines for food gathering and manipulation. Yet, this must have been necessary to some degree due to the mentioned posterior orientation of the mouth (Fig. 1D). The hypostome was possibly the sternite of the antennular segment, serving as an attachment structure of the appendage musculature, as is still recognizable in Recent ostracod Crustacea (Schulz 1976). The foregut, therefore, made a loop into the head and then backwards to continue into the trunk (Fig. 3D). Sucking without use of some kind of grasping elements appears unlikely. *F. protensa* shows a pair of large sac-like structures in the short head region (Fig. 1C) within the widely expanded (“hypertrophied”) second tergite that looks like a head shield. Waloszek

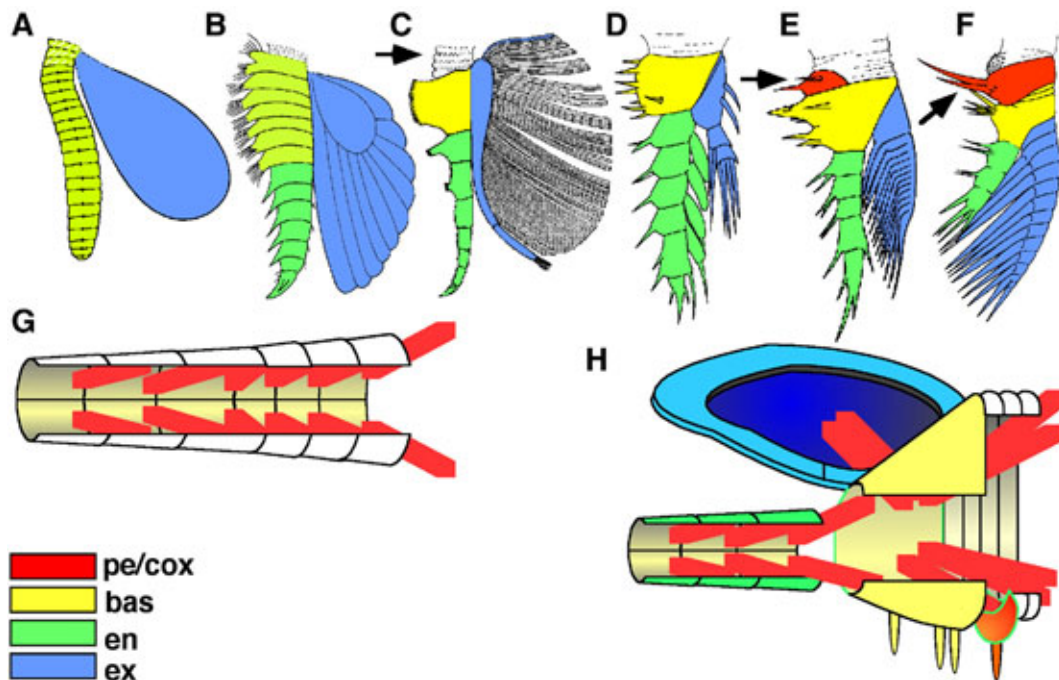


Fig. 4. Hypothesis of limb evolution in Arthropoda s. str. (images not to scale, see also Waloszek, 1993, 1999; Hou and Bergström, 1998). A. Ground-pattern level, exemplified by the limbs of *F. protensa*, *Shankouia zhenghei* and *Chengjiangocaris longiformis*, all from the Lower Cambrian of China (from Hou and Bergström, 1998; see also Fig. 3D). B. The lower to Middle Cambrian *Canadaspis* sp., a candidate taxon of the lineage from taxa like *Fuxianhuia* and allied to the Euarthropoda (from Briggs, 1978). C. Euarthropoda level, exemplified by a naraoiid limb from the Chengjiang fauna (from Hou and Bergström, 1997; see also Fig. 3E, F and G); arrow points to pliable arthrodistal membrane. D. Trunk limb of the Upper Cambrian 'Orsten' euarthropod *Agnostus pisiformis*, traditionally regarded as minute trilobite, but the anterior two post-antennular limbs are different and all three possibly acted in locomotion and food intake rather than the posterior limbs (from Müller and Waloszek, 1987). E. Ground-pattern level of Crustacea, exemplified by the 'Orsten' form *Martinsonia elongata* Müller and Waloszek (1986a, b); arrow points to the newly developed 'proximal endite' (from Müller and Waloszek, 1986a; see also Fig. 3H). F. Labrophoran/eucrustacean level, exemplified by the second antenna of the 'Orsten' maxillopod *Skara anulata* Müller and Waloszek (1985a, b). Arrow points to coxal element below basipod (from Müller and Waloszek, 1985b; see also Fig. 3I). G. Supposed musculature within limb rod of ground-pattern Arthropoda s. str. H. Supposed musculature within limb of ground-pattern Euarthropoda.

et al. (2005) suggest that this structure represents a pair of sac-like gut diverticula. Such gut diverticula are well known from numerous fossil and extant arthropods, such as from the Burgess-Shale arthropod *Burgessia bella* Walcott, 1911, Lower to Middle Cambrian naraoiids, or branchiopod crustaceans (Fig. 1E; see also Vannier and Chen, 2002; Hou et al., 2004, listing various living examples such as branchiuran Crustacea and xiphosuran Euchelicerata). Outgroup comparisons with onychophorans and tardigrades imply that this structure must have developed much earlier in the arthropod stem lineage, hence would be plesiomorphic to Arthropoda s. str.

This re-organisation of the early head region formed a major part in the model and discussion also of Dewel et al. (1999), though with a somewhat different focus than in our paper. Considering own studies of the tardigrade nervous system (Dewel and Dewel, 1996), Dewel et al.

(1999) put much emphasis on the circum-stomodaeal nerve complex. They also based their model on the two mentioned, poorly known Sirius Passet animals and on the assumption of a very basal systematic position of *Anomalocaris* Whiteaves, 1892 and related taxa within arthropods. Recently, Anomalocarididae sensu Hou and Bergström (1998) have been identified to be representatives of the cheliceratan stem lineage, thus are clearly Euarthropoda (Chen et al., 2004). Chen et al. (2004) also excluded the enigmatic *Opabinia* Walcott, 1912 (see Bergström, 1986) and the two Sirius Passet lobopod-like taxa from the Anomalocarididae. Considering this, the similarities between Dewel et al.'s and our model are less obvious. Particularly the movement of the mouth into a posteriorly pointing position and appearance of a hypostome occur much earlier in their model due to the assumption of a further limb-bearing segment between antennae and tritocerebral segment (possibly

influenced by the jaws of onychophorans) than the development of dorsal sclerotisation and other features characteristic of Arthropoda s. str. (Waloszek et al., 2005). Our model excludes the problematic taxa, and hence leaves the gap between the tardipolypods and the Arthropoda s. str. until better evidence is available. It is obvious that metameric sclerotisation of the cuticle along the body, development of a head region covered by a shield-like structure, compound eyes, and appendages with interconnecting pivot joints, as present in the stem species of Arthropoda s. str. (Fig. 3D), were important prerequisites for the morphology of the arthropod crown group, Euarthropoda.

2.3. The third phase in the evolution of arthropods

In the third phase of arthropod evolution, i.e. the euarthropod stage, the head comprises no less than the segments of the compound eyes, the antennulae and three more posterior biramous limbs. The dorsal shield covering this tagma is attached to all these segments — regardless of its size and extension to any side (Figs. 3E and 5B–F). The free trunk segments retain the plesiomorphic division into a domed middle part (rhachis region of the trunk) and the lateral tergopleurae (trilobitoid design). All post-antennal limbs in the ground pattern of Euarthropoda were subequal. They were composed of a flat but rigid, spine-bearing basipod that extended mediodistally into the endopod and carried the flap-shaped exopod laterally on its sloping margin (cf. Figs. 1F, 2A, 3E, 4C–F). The exopod flap bore numerous lamellae or setae marginally. Setae were apparently missing in *F. protensa* and allied taxa named above, but it may be possible that they evolved before the Euarthropoda level (plesiomorphies in its ground pattern). The enhanced rigidity of the limb stem portion enabled a more efficient musculature to operate the limbs in terms of locomotion and food intake, most likely coupled processes (compare Fig. 4G and H). Sustaining movement and flexibility of the sclerotized limbs requires extensive basal limb–body joint membranes. Possibly new to Euarthropoda is also the strong excavation in the basipod for the membrane and the abaxial position of the spindle-shaped insertion areas. These changes, which not necessarily developed in the stem species of Euarthropoda, but progressively, imply several significant changes also in the feeding and locomotory system. Most of the post-antennular limbs must have been involved in locomotion and food transport and manipulation simultaneously, implying that no food intake was possible without locomotion at this stage. Consequently, food must have approached

the backwardly pointing mouth from behind — thus, the ventral food path was ‘invented’. The exopods could have been used for different functions in the locomotion and food gathering process, but there is no hint that they, or their setae, acted as gills. This presumption, often considered for trilobites (Bergström, 1969; Bruton and Haas, 1999), is purely speculative, and to term the whole exopod as a gill is even less substantiated.

The compound eyes were located antero-ventrally on the anterior of the sclerotic hypostome. The coverage of the eyes by the anterior head-shield margin may have induced further modifications of the eyes. The development of more efficient eye structures facilitated life as prey and predator (see Parker, 2003). The development of functional body regions, the tagmatisation, may be an old evolutionary trait, and “already” *F. protensa* had a long limb-less caudal trunk region, in contrast to *S. zhenghei*, which bore only a very short limb-less caudal trunk piece (Chen, 2004; Waloszek et al., 2005). Releasing the antennulae from their primary function as grasping and food-gathering organs may have induced their use for sensation, such as in trilobites and allied taxa. Yet, at least two major euarthropod taxa retained the antennulae for grasping or locomotory purposes: the Chelicerata (Fig. 3F) developed this feature even further by shortening this appendage and by formation of a distal claw with rigid spines, the so-called chelicera (further tagmotic changes occurred within the crown group, see Waloszek and Dunlop, 2002; Vilpoux and Waloszek, 2003; Chen et al., 2004), and the Crustacea, which used their antennulae basically for sweeping in food together with the metachronous beat of their head appendages (cf. discussion in Waloszek, 1993; Stein et al., 2005). This is still seen today, best in the nauplius larvae with their long antennular setae (swimming devices), but also later larvae of several eucrustaceans.

Euarthropoda changed their head also in another respect, which seems to have drawn little attention as yet. The third body segment — the original first trunk segment of Arthropoda s. str. (Fig. 3D) — is a clear segment with an appendage similar to those of all posterior segments (Figs. 3E and 5B–F). This should have been taken over into the ground pattern of Euarthropoda, but we have still not identified this on a fossil. We only know that the third segment, i.e. the second limb-bearing one, is post-oral in the Chelicerata, retaining its equipment with organs and well-developed and functional limbs (often named pedipalps due to their specialisations with reference to certain Recent arachnid taxa). The ganglion of this segment, tritocerebrum, is well separated from the deutocerebral neuromere. Cisne

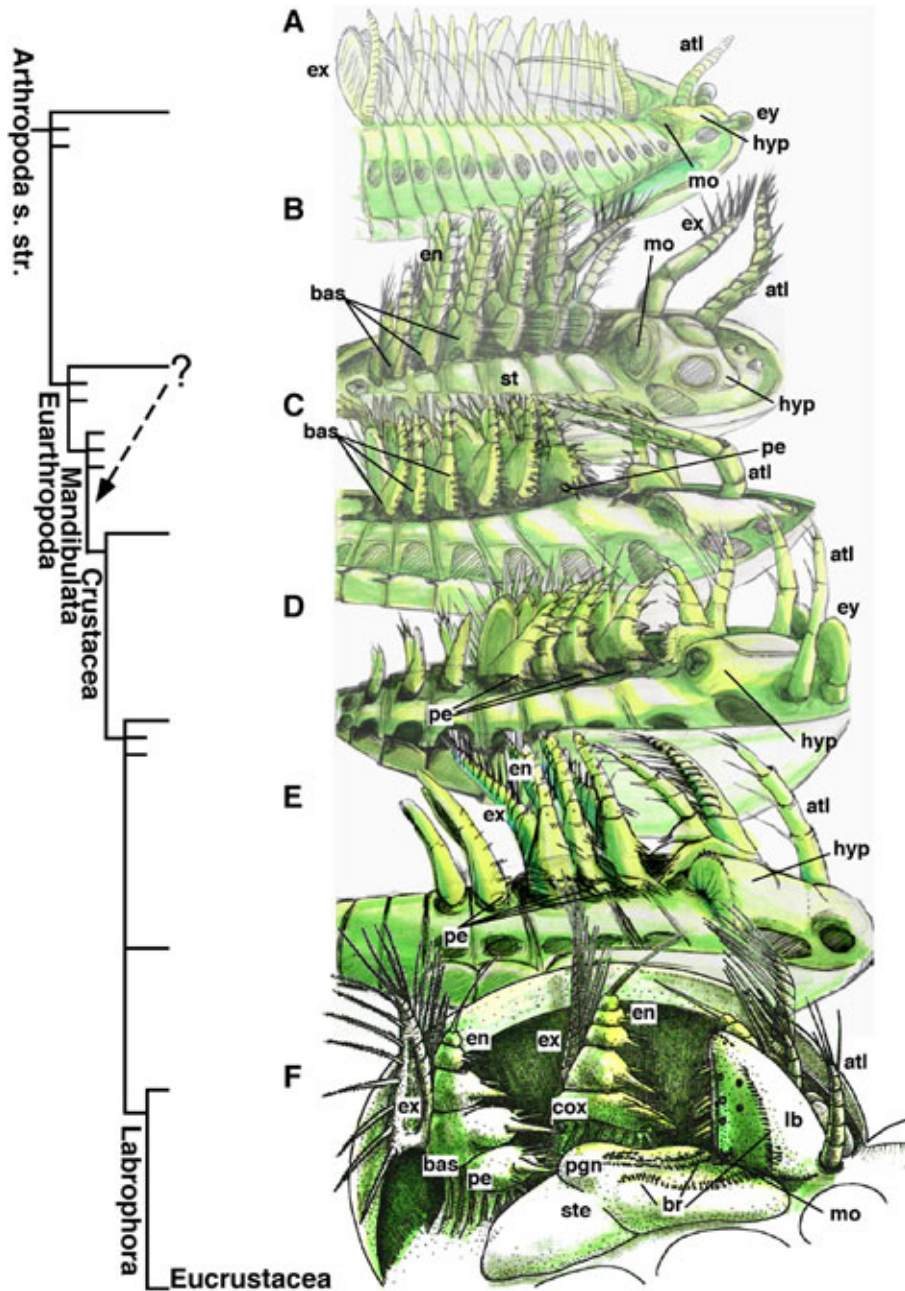


Fig. 5. Sketches of the cephalic feeding and locomotory systems of Cambrian Arthropoda, as if viewed from ventrolateral into the median body area (left limb series omitted). A. System as developed in Arthropoda s. str., based on the Chengjiang animals *F. protensa*, *Chengjiangocaris longiformis*, and *Shankouia zhenghei* (see also Fig. 2D). B–F. Systems within Euarthropoda, based on ‘Orsten’ animals: B. *Agnostus pisiformis* representing the euarthropod feeding system (see also Fig. 2E). C–E. Stem representatives of the Crustacea, with C, *Oelandocaris oelandica*, D, *Henningsmoenicaris scutula* Walossek and Müller (1990), and E, *Martinsonia elongata* (see also Fig. 2H). F. Labrophora level, exemplified by a phosphatocopine (young stage; see also Fig. 2I). Abbreviations other than in previous figures: br=bristle.

(1975) showed for the Ordovician trilobite *Triarthrus eatoni* (Hall, 1847) that the first post-antennular limbs are next to the mouth at the rear of the hypostome, pointing posteriorly with their basipod (which he termed

coxa). This situation can be observed also, e.g., in the Cambrian naraoiids, animals with long, multisegmented antennulae (e.g., Hou et al., 2004). The position of the first post-antennular limbs at the rear of the hypostome

also holds true for *Agnostus pisiformis* (Fig. 2A) and crustaceans (Fig. 2B).

Remarkably, neither in *A. pisiformis* nor in any of the adult labrophoran crustaceans (example in Fig. 2D) can a separate sternite be detected that can be referred to the tritocerebral segment (that of the second appendages). The only exceptions we are currently aware of are the orthonauplii of the branchiopod eucrustacean *Rehbachchiella kinnekullensis* (cf. Walossek, 1993) from the Upper Cambrian ‘Orsten’ and the extant copepod *Eudiptomus gracilis* (Mayer unpublished diploma work, University of Ulm 2002), both showing this separate sternite. A separate sternite may also be present in the holaspis of the Ordovician trilobite of the taxon *Placoparia* Hawle and Corda, 1847 (Whittington, 1993) but limited quality of the material renders the composition of the head of *Placoparia* species controversial (Edgecombe and Ramsköld, 1999). The result of this remarkable reduction/shortening of the tritocerebral or first post-antennular segment is that antennulae and the antennae are attached to the hypostome, one more anteriorly (at the anterior wings of the hypostome) and one more posteriorly (at the posterior wings; see also Schulz 1976 who studied the ostracod hypostome–labrum complex). The outer edge of the subtriangular insertion area of this limb is located further anterior and lateral (schematized in Fig. 5F).

Likewise, the second appendage-bearing, or antennal segment, as it is named in crustacean terminology, became squeezed in between the segments in front and behind, virtually losing its segmental identity as depicted in Fig. 3F and G. It seems, therefore, clear to us that further Cambrian taxa should be identified in the future showing that particular primordial state from which Chelicerata and the stem species of all taxa with squeezed third segment arose. This uncertainty (because it is still to be hypothesized) is enhanced in Fig. 3E by stippled lines to either of the subsequent taxa. At present, there is little evidence for the assumption that trilobites are derived from the evolutionary lineage of the Crustacea (or mandibulates).

The strong reduction in size of the third cephalic segment had several consequences. A more speculative one is that the nervous system found innervation contact to the hypostome and labrum in the labrophoran Crustacea. Yet it remained conservative in that the neuromere did not move much anteriorly relative to the oesophagus, and it also retained its post-oral commissure throughout. Although still part of textbook descriptions, neither arthropods nor euarthropods nor chelicerates nor crustaceans have a brain composed of proto-, deuto- and tritocerebrum; the tritocerebrum

being separated from the frontal ganglial mass (Waloszek and Müller, 1998a and references therein; see also Dewel et al., 1999). This innervation into the labrum may have been one of the reasons for misunderstandings of that body region as modified appendages, in particular in tracheates where the referent appendages appear only in the embryo and disappear completely (=intercalary segment; cf. Haas et al., 2001). This loss might even be induced by the fate of the segment. In crustaceans, the second antenna is also not an antenna in its literal sense originally, but a limb and becomes an important tool for any purposes. It is only reduced in highly aberrant taxa such as notostracan branchiopods (cf. Walossek, 1993). Operation of the second head limb in a backwards and forwards manner, stuffing food back to the rest of limbs or preventing food loss alongside the hypostome by its slim basipod is a clear change induced at the euarthropod level. Yet, this limb and all subsequent limbs retained their design, and this seems to hold for most of the Cambrian euarthropods discovered so far.

2.4. The crustacean lineage and its modifications of cephalic feeding

The crustacean lineage is an example of a significant deviation from this fairly conservative feeding and locomotion system developed in the Euarthropoda and retained in the other euarthropods basically, at least at a gross scale. Therefore, we add a short excursion into this taxon here, which has not been undoubtedly recorded from the Lower and Middle Cambrian two-dimensionally preserved fossil faunas. *Canadaspis perfecta*, already mentioned as a candidate for the stem lineage toward Euarthropoda, has erroneously been assigned to Crustacea (e.g., Briggs, 1978, 1992; see Dahl, 1984; Walossek, 1993 for corrections). The small bivalved bradoriids with species of *Kunmingella* Huo, 1956 as the only taxon with soft parts (e.g., Hou et al., 1996) show, despite differing statements (Shu et al., 1999), not a single feature of the autapomorphies of Crustacea (listed by Walossek and Müller, 1990; emended in Walossek, 1999; Maas et al., 2003; Waloszek, 2003a,b). Chen (2004) has interpreted the bradoriids as representatives of the euarthropod stem lineage. The recent study of another stem-lineage crustacean by Stein et al. (2005) showed that crustacean evolution is correlated with a specific change in limb morphology; such a creature having crustacean limbs has not yet been found in the Chengjiang biota. *E. minuscula* Chen et al. (2001) has been described as a putative maxillopod crustacean (Chen et al., 2001). The authors admit that all post-

antennular limbs are serially identical, hence affiliation with Eucrustacea is impossible and even an assignment of this species within Arthropoda s. str. remains unclear (one of the authors, JC, prefers to assign *E. minuscula* as a stem-lineage crustacean, see [Chen, 2004](#)).

One of the novelties in the ground pattern of Crustacea is a separately movable and setated endite, ‘proximal endite’ nested within the ample joint membrane medially below the basipod of the post-antennular limbs. This feature is exemplified by, e.g., *Martinssonina elongata* ([Fig. 3E](#)). *Oelandocaris oelandica* Müller, 1983 possesses this proximal endite only on the third limb pair, the mandible ([Figs. 2B, C and 5C](#); see also [Stein et al., 2005](#)). The ‘proximal endite’ ([Figs. 2C, 3H, 4E](#)) may have served to transport food on the ventral surface of the body towards the mouth, independently from limb movements. This endite is considered as a phylogenetic precursor of another limb portion developed in the Crustacea. This structure, the coxa, did not evolve earlier than in the stem species of the Labrophora and only on the second and third post-antennular limbs, from this stage on named the antenna and mandible ([Figs. 3I and 4F](#); see [Siveter et al., 2003](#)). The Cambrian Phosphatocopina exemplifies this stage. Phosphatocopines are the most abundant component of the ‘Orsten’ faunal assemblage in the Upper Cambrian of Sweden ([Fig. 2D](#); see also [Maas et al., 2003](#); [Maas and Waloszek, 2005](#)), and their post-antennular limbs retain the ‘proximal endite’ and are serially designed. The coxa of antenna and particularly the mandible retains much of its ‘proximal-endite’ shape with regard to the setal and spine pattern, but is a large, sclerotized limb portion. It is medially extended into a shovel-like gnathobase, the inner margin of which is armed with teeth or spines. Other coxal structures do not appear on more posterior limbs at this stage. Such coxae occur in the different eucrustacean lineages and on particular limbs or in series. Their absence in the post-antennular limbs of the tiny Cephalocarida (see [Sanders 1963](#)) implies that coxae on post-antennular limbs evolved convergently within particular eucrustacean in-group taxa. In further consequence, coxae do not characterise any other earlier level in arthropod evolution, and the limb base of other euarthropods like trilobites or chelicerates is the basipod retained from the ground pattern of Euarthropoda and should be termed accordingly (see, e.g., [Waloszek and Müller, 1990](#); [Waloszek, 1993, 1999](#); [Waloszek, 2003a,b](#)).

The evolutionary change from the coxa-less state to the possession of two coxa-bearing limbs in the ground pattern of the Labrophora accords well with the development of several additional features in the cephalic feeding system. One important feature is the labrum ([Figs. 2D](#)

and [3I](#)) most likely derived from the distal part of the mouth membrane. Besides openings of glands located within the labrum and used to slime in food, as known from extant crustaceans, the labrum bears sensilla and bristles at its flanks and expands above the mouth at the rear of the hypostome and can be withdrawn within a funnel-shaped area, the atrium oris. Another novelty is the sternum as a plate-like product of fusion of the antennal/mandibular and first post-antennular sternites. Also the sternum is covered with fine hairs or denticles. Moreover, the mandibular portion of the sternum bears a pair of humps adorned with bristles, the paragnaths ([Figs. 2D and 3I](#)), which may facilitate gliding of the mandibular coxae into the atrium oris. This complex cephalic feeding system characterises the labrophoran crustaceans (=Phosphatocopina, exemplified by several taxa in the ‘Orsten’ material, +Eucrustacea, exemplified by more ‘Orsten’ crustaceans, such as *Bredocaris admirabilis* Müller, 1983, *Dala peilertae* Müller, 1983, *R. kinnekullensis* Müller, 1983, the Skaracarida [Müller and Waloszek, 1985a,b](#), and *Waloszekia quinquespinosa* Müller, 1983). It involves the anterior three appendages and all the mentioned associated structures in the vicinity of the mouth and permit an effective mode of feeding and utilization of a diet most likely different from that in preceding evolutionary lineages (possibly a sweep-net feeding mode). The cephalic feeding system of the labrophoran ground pattern is also observable in labrophoran larvae. The first larva of the Phosphatocopina, although a head larva with four limb-bearing segments and thus plesiomorphically retained from the euarthropod ground pattern ([Waloszek, 2003b](#)), shows all characteristic features of the cephalic feeding system described above (cf. [Maas et al., 2003](#)). The same holds true for the nauplius of eucrustaceans, a larva with only three limb-bearing segments. Therefore, the nauplius is in any case a phylogenetically advanced larva ([Maas et al., 2003](#)). The nauplius and a specialised third post-antennular limb (maxillula) represent autapomorphies in the ground pattern of Eucrustacea. Plesiomorphically, the so-called maxilla is subequal to the succeeding limbs, a specialisation of this limb occurs several times independently within the Eucrustacea ([Maas et al., 2003](#); [Waloszek, 2003a](#)).

3. Concluding remarks

The initially soft-cuticle worm-shaped body of stem-lineage arthropods bore segmental, similarly soft appendages and had a rather undifferentiated head region. The original situation may be that the head had a small mouth situated at the anterior end. This level is

exemplified by soft-cuticle lobopodians from several Cambrian biotas (representative from the ‘Orsten’ currently under study). Structural modifications from the sclerotized (arthrodized) and arthropodized level onwards (=Arthropoda s. str.) affected mainly the anterior body part, the head. Initial changes include the formation of large compound eyes, grasping antennulae, and a posterior curving of the oesophagus with the mouth opening posteriorly behind a ventral sclerotic plate, the hypostome. Several Chengjiang animals document this phase. Subsequent morphological changes concern the inclusion of progressively more segments into the head, further specialisation of the post-antennal head appendages for grasping food and for food manipulation, and the development of specific outgrowths in the form of spines, setae, fine spinules and sensilla (something to be investigated in more detail in the future). A brief outlook into the crustacean lineage, which is particularly documented in the Cambrian ‘Orsten’, demonstrates significant changes not only at the macroscopic but also at the microscopic level. These include delicate changes of external (fine hairs or bristles, pores etc.) and internal details (e.g., glands within the labrum), functional modifications (use of all three anterior appendages), and splitting of functions along as well as between limbs of a series (multi-function vs. uni-function). Another output of our investigations of Cambrian fossils as representing ‘once lived morphologies’ compared with extant taxa was that the segment of the second head appendage, the second antenna of Crustacea, became significantly shortened and squeezed in between the first and third limb segments. This segment even lost its ventral sternite, and the limbs became attached, instead, to the posterior edge (wings in trilobite terminology) of the antennular sternite, which we refer to as the hypostome. It may be that this change of attachment and arrangement of the second appendages had severe consequences also for other anatomical features (e.g., nerves, muscles) of the antennal segment. And this may have initiated the eventual loss of its appendages in the myriapods and hexapods (named intercalary segment there).

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