Arthropod Systematics & Phylogeny 255
67 (2) 255–273
© Museum für Tierkunde Dresden, eISSN 1864-8312, 25.8.2009

Early Crustacean Evolution and the Appearance of Epipodites and Gills

Andreas Maas [1]*, Carolin Haug [1], Joachim T. Haug [1], Jørgen Olesen [2], Xiguang Zhang [3] & Dieter Waloszek [1]

[1] Biosystematic Documentation, University of Ulm, Helmholtzstrasse 20, 89081 Ulm, Germany [andreas.maas@uni-ulm.de]
[2] Natural History Museum of Denmark, Universitetsparken 15, 2100 København Ø, Denmark
[3] Key Laboratory for Palaeobiology, Yunnan University, Kunming 650091, PR China

* Corresponding author

Received 08.iv.2009, accepted 11.v.2009.
Published online at www.arthropod-systematics.de on 25.viii.2009.

> Abstract

Epipodites are structures on the outer edges of crustacean appendages serving as gills or for osmoregulation. Their evolutionary origin has been debated for a long time. Three major issues are of relevance: 1) the function of epipodites, 2) their development, and 3) the fossil record. While it has long been a problem to distinguish the gill and osmoregulatory functions of epipodites histologically, this has recently become possible based on ultrastructure. A respiratory function has particularly been claimed for the limbs or parts of limbs of early arthropod fossils. Not only rami and cuticular structures, but also entire appendages, have been referred to as "gills". Among living taxa, the opisthosomal limbs of limulids are called gills or gill limbs, although the numerous leaf-like gill structures occur only on the posterior side of the exopods. It has long been known that crustacean exopods do not serve a respiratory function, which is restricted to structures along the outer proximal edge of the limbs. Three-dimensionally preserved fossil crustaceans from the 'Orsten' have contributed much to our understanding of the evolution and phylogeny of Crustacea, in particular limb evolution. The recently discovered *Yicaris dianensis* from the Lower Cambrian demonstrates not only the presence but also the morphogenesis of three epipodites on all post-maxillulary appendages. *Yicaris dianensis* may therefore be a valuable model for understanding the evolutionary origin of epipodites, not least since comparative morphology demonstrates that epipodites show a large plasticity among living eucrustacean taxa and may not even be homologous. Epipodites are discussed here in the light of 1) other putative respiratory and osmoregulatory structures in other 'Orsten' taxa, 2) morphological and functional variations of epipodites in living eucrustaceans, and 3) the discovery of two new species of 'Orsten' eucrustaceans, also showing evidence of three epipodites. This contribution aims to provide a guide for further investigations on the evolution of crustacean epipodites.

> Key words

Arthropoda, Crustacea, limbs, exopod, epipodite, gill, osmoregulation, respiration, phylogeny, Orsten.

1. Introduction

1.1. Epipodites, respiration and osmoregulation

Epipodites are outgrowths that insert on the lateral edge of the limb base of various crustaceans. Such structures are generally also called "exites" (= "lateral outgrowths"; see Boxshall 2004). Epipodites can serve two functions: gas exchange and osmoregulation. The two functions are closely related to the morphology of the epithelium. Epithelia for respiration and osmoregulation occur widely within Metazoa, and they are situated on different parts of the body, so do not necessarily have the same evolutionary origin. For a long time the two functions could not be distinguished because of the technical limitations of light microscopy and silver staining techniques (e.g., Croghan 1958). Silver staining stains epithelia of both functions (cf. Rieder et al. 1984; Holliday et al. 1990), while the resolution of light microscopy is insufficient to detect the subtle differences in the epithelial cells

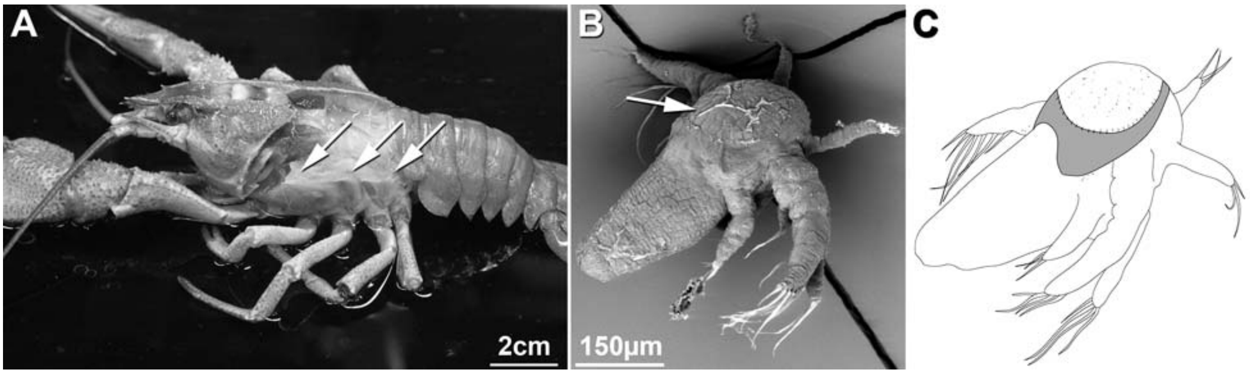

Fig. 1. Examples of respiratory and osmoregulatory organs in Crustacea. **A**: Gills of the crayfish *Astacus leptodactylus* (Eschscholtz, 1823) are epipodial outgrowths of the limb bases and outgrowths of the lateral body wall (arrows). **B**, **C**: Dorsal organ of the nauplius larva of the fairy shrimp *Artemia salina* Linnaeus, 1758. **B**: SEM micrograph of a specimen in dorsolateral view displaying the dorsal organ (arrow) located on the head shield. Note the distinct margin of the dorsal organ. **C**: Drawing of the same view as in B.

of respiratory and osmoregulatory surfaces. Transmission electron microscopy made it possible to recognize these differences, showing that the flat respiratory and osmoregulatory epithelia can be distinguished by the latter possessing cells with a folded basal surface and basal membrane, having many mitochondria in the cells (to provide energy), and containing active ion pumps (Rieder et al. 1984; Keyser 1990). This is why osmoregulatory epithelia are also called ion-transport epithelia.

Epipodites do not occur in any other euarthropod taxon except Crustacea. Even within the Crustacea it remains uncertain if epipodites are homologous. “Gill” is a term restricted to structures specifically involved in respiration, i.e. gas exchange (Wolvekamp & Waterman 1960). Gills occur in various arthropods but their homology among major lineages can be readily excluded. Arthropod gills may occur as lateral outgrowths of the proximal (limb stem) portions of appendages, in which case they are epipodites (e.g. in decapod crustaceans; Fig. 1A), or they may occur as parts of such outgrowths, e.g. feather-like outgrowths together with a club-shaped epipodite (only in decapod crustaceans; see, e.g., Boxshall 2004: fig. 5B). Arthropod gills may also occur on other parts of the limbs, e.g. as outgrowths on the exopods of opisthosomal limbs in Xiphosurida, or they occur on other positions of the body (on the lateral body wall close to limb insertions of various decapod crustaceans; cf. Fig. 1A), in which cases they should not be confused with epipodites. Gills not associated with legs also occur in the larvae of several insect taxa with fresh-water living young. These gills are mainly outgrowths of the body wall of the abdomen close to the anus, e.g. the independently evolved structures in mosquito or dragonfly larvae (e.g. Thorpe 1933; Watson 1966).

Gills of arthropods may also have an osmoregulatory function (for general reviews see Potts & Parry 1964; Mantel & Farmer 1983; see also Freire et al. 2008 for a recent review). However, osmoregulatory functions may also be performed by other structures. For example, the so-called ‘dorsal’ or ‘neck organ’, which is conspicuous in early larvae of various crustaceans, particularly branchiopods (Fig. 1B,C; Conte et al. 1972; Ewing et al. 1974), performs an osmoregulatory role. When this organ vanishes during ontogeny, its osmoregulatory function shifts to the epipodites (Croghan 1958).

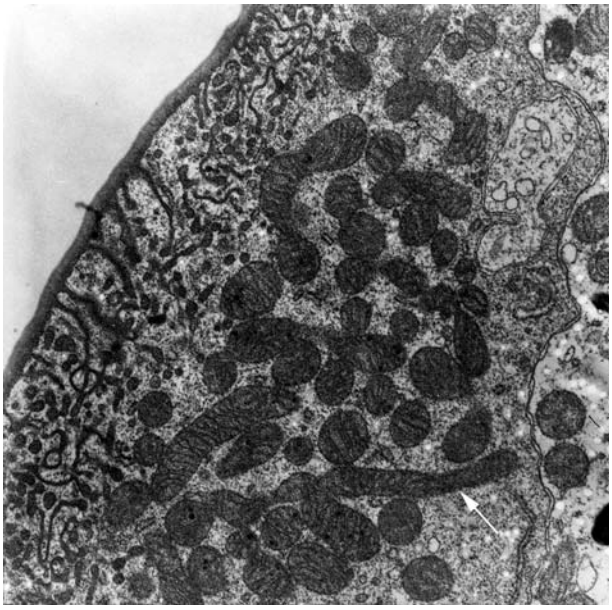

Fig. 2. Transmission-electron micrograph of the ostracod *Cyprideis torosa* (Jones, 1850). Cuticle on the left, basal lamina on the right. Note the many mitochondria (arrow) close to the basal lamina, which indicates active ion transport across the epithelium (image kindly provided by D. Keyser, Hamburg).

For a long time it was thought that the cuticle below the bivalved shields (known as the inner lamella) of crustaceans such as ostracods serves as a specific respiratory organ, a view dating back to Claus (1865) and accepted by subsequent authors, e.g. Hartmann

(1966–1975), but this has been rejected recently for some ostracods (Keyser 1990). Keyser (1990) demonstrated that the underlying tissue in podocopid ostracods is rather specifically developed for osmoregulation (Fig. 2). Herein we intend to trace the occurrence of epipodite structures within arthropods and provide particularly data on fossil forms. We also pay attention to morphogenetic data gained from fossil evidence to add to the current discussion on the origin of epipodites and their function.

1.2. Terminology

The terminology for limbs and limb parts and for structures associated with limbs has developed over almost 200 years, and inconsistent use of terms has long been a recurring theme (see Boxshall 2004 for an overview; see also Waloszek 2003a,b). The same holds true for the function of structures, which was sometimes merely assumed rather than empirically demonstrated. Historically, workers often uncritically applied definitions without questioning whether homology of putatively different structures could actually be supported. An example is *how trilobites got their gills*. In fact the outer ramus of a trilobite limb is the exopod, a feature retained from the ground pattern of Arthropoda in the strict sense (Waloszek et al. 2005). It received the term pre-epipodite originally by Störmer (1938) because of a morphological misunderstanding relating to the insertion of the ramus (Waloszek 2003b). Störmer, labelling the basipod of the trilobite limb a coxa, believed that the exopod would insert even below the coxa. Therefore he named the portion, on which the exopod inserts, unduely 'precoxa' and created the term 'pre-epipodite' accordingly (see also Walossek 1993). Based on this and assumptions made by earlier authors (e.g. Walcott 1881), Störmer inferred that the entire outer ramus represents a gill, in the same way as the epipodites on the thoracic limbs of decapod crustaceans function as gills.

Based on comparative morphological evidence within Crustacea, Walossek & Müller (1990) could demonstrate that the interpretation of the structure named pre-epipodite in trilobites was based on a multiple mismatch of various terms between taxa (see also Maas et al. 2003 for a detailed discussion of this issue). Another example of mismatching parts of appendages between taxa is Preuss (1957), who mislabelled endopod, exopod and endites of anostracan and phyllopod crustaceans: he mislabelled the epipodite of phyllopods as exopod. Since he found no musculature in the structure he labelled as exopod (because it actually was the epipodite), he concluded that phyllopods are quite different from anostracans because the exopod of the latter bears musculature. This mismatch led to the assumption of a multiple origin of the Branchiopoda (see Walossek 1993; Olesen 2007 for discussion). Terminology in this area can be rather imprecise and misleading. At least, a name alone cannot give us sufficient information. We also need some structural data to evaluate its nature confidently. The examples of trilobites and branchiopods remind us to be careful with terminology and definitions. Therefore we do not want to define epipodites here but rather try to carefully compare structures in terms of shape, function and developmental origins so as to be better able to pinpoint potential homologies between taxa. Applying a uniform homology-based terminology to the complex system of limbs, epipodites and gills is, in our view, of greatest importance. Yet, it requires some elucidation.

1.3. Arthropod ground pattern and cuticle

Knowledge about the early evolution of arthropods and particularly of crustaceans has increased significantly in the last few years, especially regarding morphological character evolution (e.g., Maas & Waloszek 2001a; Waloszek 2003a,b; Maas et al. 2004; Waloszek et al. 2005, 2007; Scholtz & Edgecombe 2006; Mayer & Harzsch 2008). Accordingly we can use the emerging phylogenetic system as a basis for discussing ground-pattern conditions and for revealing what these evolved into within the diverging arthropod lineages. One of the main autapomorphies of arthropods in the wider sense (= Arthropoda s.l. sensu Maas et al. 2004; Aiolopoda sensu Hou & Bergström 2006) is that the epidermis (outer epithelium = ectoderm) secretes a cuticle composed of two major layers, a hydrophobous outer epicuticle and an inner procuticle, which contains chitin among other components (Cutler 1980). The cuticle may become rather rigid and thick, but irrespective of modifications, it must serve and allow numerous different functions: protection against penetration of substances, but at the same time allow transport of, e.g., oxygen into the body; limited permeability to water to maintain haemolymph concentration; sensing the surroundings; expelling gland products, and more. Also respiration has to function through the cuticle. Many of these necessities existed from the very beginning since all are crucial in a marine environment. Accordingly, these features are plesiomorphically retained in the diverging arthropod lineages. Remarkably, most papers on the arthropod cuticle consider only land animals like beetles or other insects (e.g. Gibbs et al. 2003; Vincent & Wegst 2004; Sun et al. 2008; Elias-Neto et al. 2009; Lin et al. 2009). Yet, these animals have a modified cuticle also containing wax to provide protection against water loss. In addition, the cuticle of some land-living insects, possibly also that of trilobites with their calcareous inclusion, is developed as an armature against enemies, not very likely an original duty of the cuticle. The first arthropods were soft "worms on legs" = lobopodians (Hou & Bergström 1995; Budd 1997; Maas et al. 2007). In fact arthropods started out having soft and thin cuticle as it is still seen in velvet worms (onychophorans) with their extremely thin cuticle. Furthermore, specific external respiratory organs cannot be assumed to be part of the arthropod ground pattern. Rather plesiomorphically both respiration and osmoregulation are likely to have occurred across the entire body surface with its originally thin and permeable cuticle.

2. Homology and occurrence of epipodites within Arthropoda

2.1. Eucrustacea[1]

Eucrustacea seem to be the only arthropod group, in which outgrowths at the outer edge of the limb stem portions occur. These outgrowths, candidates for being considered as epipodites, insert either on the coxa (if present), on the basipod or on the transition between coxa and basipod. Musculature occurs very rarely in these structures (Boxshall 2004). Epipodites in these taxa may function specifically in respiration and/or osmoregulation.

Surveying the diversity of eucrustaceans, epipodites occur in various taxa within the Malacostraca.

- **Leptostraca**: These have a single blade-like epipodite with a concave outer margin inserting laterally on the limb stem of each thoracopod (Fig. 3A,B; Itô 1988). Its function has not yet been studied.
- **Stomatopoda**: Mantis shrimps have single leaf-shaped respiratory epipodites on the proximal outer side of the first five thoracopods (Fig. 3E; Burnett & Hessler 1973) and bloom-like branched gills on the outer side of their pleopods. They arise from the antero-median edge of the exopod. In fact, stomatopods are the only malacostracan taxon having gills on the pleopods. Burnett & Hessler (1973) stated that these gills should not be termed epipodites because of their location on the pleopods, which, in our view, is not contradictory because also the pleopods are part of the original trunk-limb series.
- **Neocarida (= Thermosbaenacea + Peracarida)**: Within this taxon, the plesiomorphic condition in the ground pattern has been reconstructed as having single fine epipodites on the basipods of the thoracopods (Kobusch 1999; see also Richter & Scholtz 2001; Wirkner & Richter 2007a,b). During evolution within Peracarida, the epipodites seem to have become reduced in favour of a respiratory surface underneath the shield in the ground pattern of a monophyletic unit including the Mysida and Mancoida (Kobusch 1999). However, Lophogastrida have both a respiratory shield surface and respiratory epipodites (Wirkner & Richter 2007b). In Mysida and Mancoida only the first thoracopod retains its epipodite, but it is unclear if it has a respiratory function. Remarkably also the oostegites of Peracarida have been referred to as epipodites that appear laterally in early ontogeny and shift towards the median side during development (Claus 1885; Boxshall 2004). These are oriented medially and serve in brood care in Peracarida, one of the autapomorphies of this taxon.
- **Syncarida**: Epipodites occur on the thoracopods as two leaf-like structures e.g. in *Anaspides tasmaniae* (Fig. 3C,D; Boxshall 2004), or are club-shaped, as in bathynellids (e.g. Schminke 1980). In *A. tasmaniae*, epipodites and an exopod are lacking on thoracopod 8, while in thoracopod 7 the exopod is reduced to a club-shaped structure very similar to an epipodite (Fig. 3D).
- **Euphausiacea**: Their thoracopods carry a lobate gill with marginal filaments on the outer basipod rim (Alberti & Kils 1983). The gills increase in size from the first to the eighth thoracopod. In Euphausiida the eighth thoracopod consists almost exclusively of the limb stem and the prominent epipodite (Maas & Waloszek 2001b). It is most often named a gill, but its homology with the epipodites/gills of decapods is at best unclear.
- **Decapoda**: Within this group, several types of gills occur besides a single club-shaped epipodite, all of them being rather complicated (Suzuki et al. 2008). A reason may be that decapods have an elaborate circulatory system that also runs into the gill stems and branches. From crabs it is known that the proximal gills of the more posterior pereiopods serve for osmoregulation (Hebel et al. 1999). Function and homology of the club-shaped epipodite, however, are not known.

Homology between decapod gills (particularly those on the outer body sides = pleurobranchia) and the lobate or club-like epipodites with their simple form and epithelia must be treated as uncertain. However, based on the occurrence of at least one epipodite in almost all in-group malacostracans, the ground-pattern state of Malacostraca seems to have included at least one single epipodite on every trunk limb.

Epipodites are also present in a few taxa of the Entomostraca (see Waloszek 2003b for their monophyletic status), but their identification as such is often ambiguous:

---

[1] Sensu Walossek (1999); characterization in Waloszek (2003b).

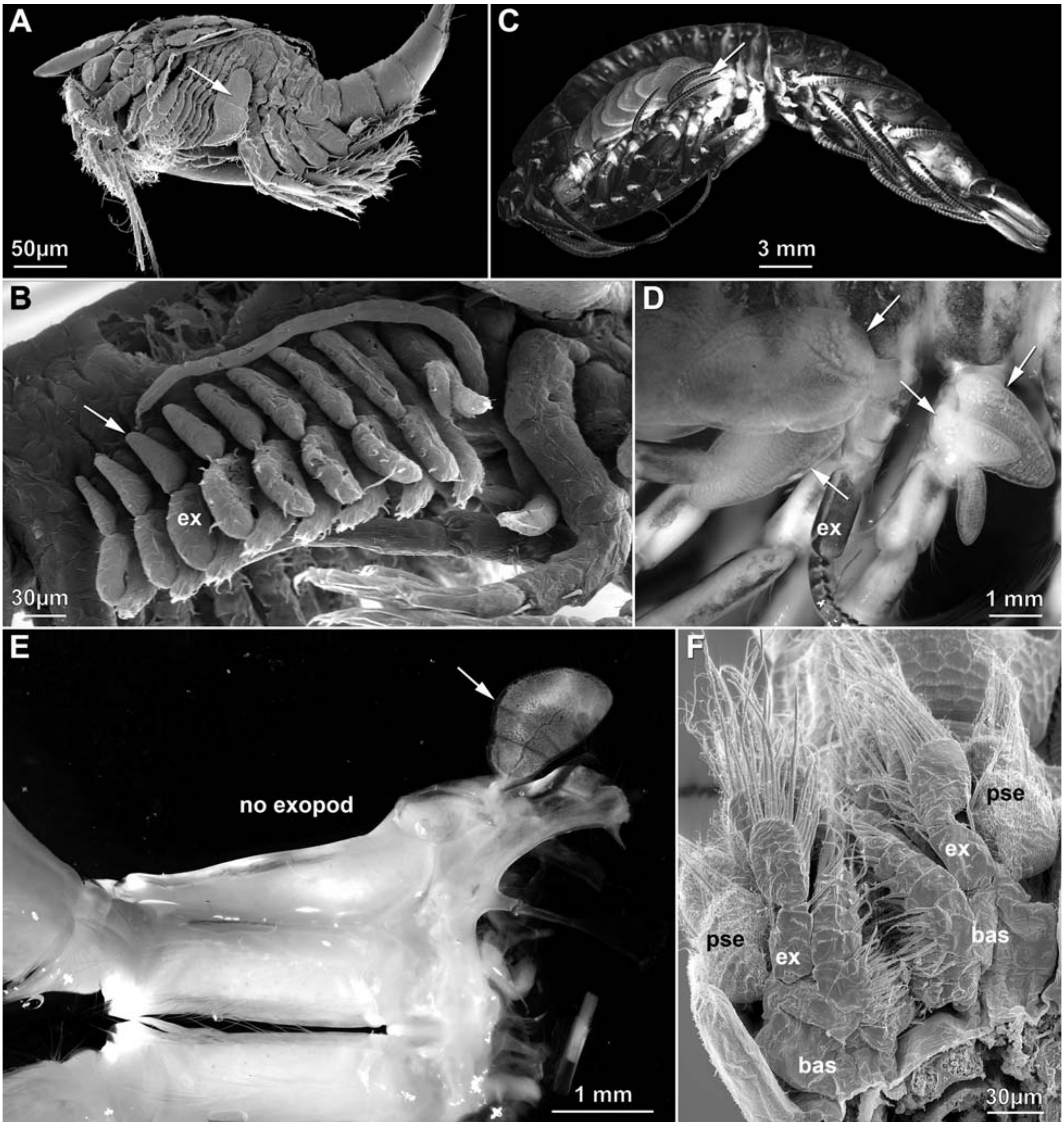

Fig. 3. Examples of epipodites within Eucrustacea (A–E: Malacostraca; F. Cephalocarida). **A**, **B**: SEM micrographs of leptostracans. **A**: Adult of *Nebalia brucei* Olesen, 1999; shield and anterior epipodites removed (from Olesen & Walossek 2000: fig. 9A; image flipped horizontally). The arrow points to the epipodite of the sixth thoracopod. **B**. Close-up of the trunk of a late embryonic *N. longicornis* Thomson, 1879 displaying the thoracopods with their club-shaped to triangular epipodites proximal to the similarly lobate to club-shaped exopods (ex) (from Olesen & Walossek 2000: fig. 5C; anterior to the right). **C**, **D**: Photographs of *Anaspides tasmaniae* Thomson, 1892 (Anaspidacea). **C**: Lateral view of adult specimen. **D**: Close-up of posterior part of thorax I of *A. tasmaniae* displaying thoracopods with a bilobed or paired epipodite. Thoracopod 7 has also a bilobed or paired epipodite and a reduced, hence club-shaped exopod (ex; thoracopod 8 has no exopod and epipodite). **E**: Thoracopod of a stomatopod (*Squilla* sp.). **F**: Mx2 of the cephalocarid *Lightiella moniotae* Jones, 1961. "Pseudepipodite" (pse) stems from the triangular proximal part of the exopod (ex) and has no contact to the basipod (bas) below. Arrows point to epipodites.

- ***Yicaris dianensis*** Zhang, Siveter, Waloszek & Maas, 2007, a recently described entomostracan with unclear in-group affinity (see Zhang et al. 2007) from the Lower Cambrian of China, has three epipodites positioned along the outer edge of the basipod of all postmaxillulary limbs (Zhang et al. 2007). The maxillula lacks epipodites but has two fine setae in the same position as the postmaxillulary epipodites (see below for a more detailed discussion of the epipodites of *Yicaris* and their significance).

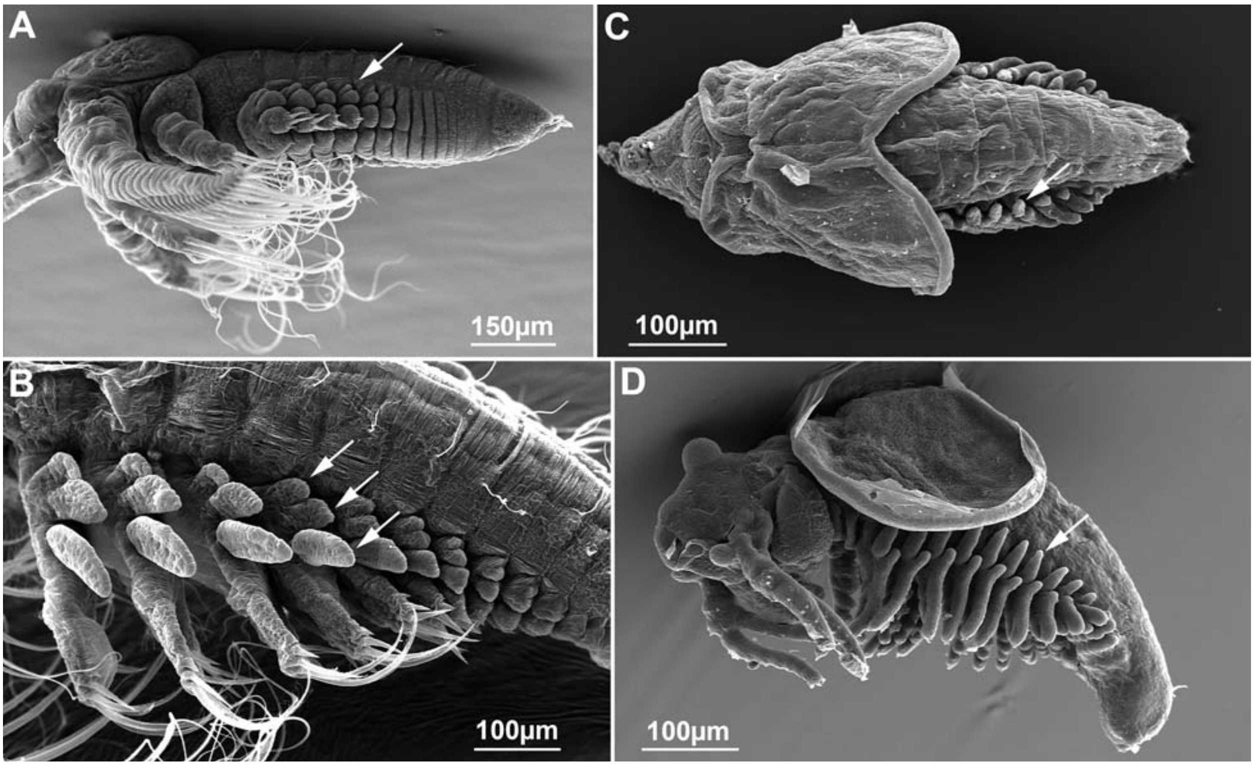

Fig. 4. SEM micrographs of different Branchiopoda. **A**: An early larval *Eubranchipus grubii* (Dybowski, 1860). Arrow points to the developing club-shaped to sub-triangular lobate epipodites. **B**: Lateral view of a later larval *Artemia salina* (Linnaeus, 1758), viewed slightly from the posterior. Epipodites of this stage grown out to flattened sub-quadratic to sub-triangular lobes (arrows). **C**, **D**: SEMs of a juvenile *Cyclestheria hislopi* (Baird, 1859). **C**: Dorsal view. Epipodites club-shaped view "from above" (arrow; see also Fig. 11B for comparison with the Cambrian *Yicaris dianensis*). Anterior epipodites appear more lobate. **D**: Lateral view (arrow as in C).

- **Branchiopoda**: Epipodites are common structures in branchiopods, but their number and shape is taxon-dependent (e.g. Olesen 1999, 2004). Anostracans have 1–2 leaf-shaped epipodites proximally and a sac-like epipodite distally on the basipod (Fig. 4A,B), the latter of which functions in respiration, while the proximal one(s) function(s) in osmoregulation (Holliday et al. 1990). Phyllopods have only one epipodite, which is rather large and club-shaped (Fig. 4C,D) and which has an osmoregulatory rather than a respiratory function (Kikuchi 1983).
- **Sister taxon to Eubranchiopoda**: In *Rehbachiella kinnekullensis* Müller, 1983, of which no adults are known, Walossek (1993) could not find any evidence for epipodites. However, it cannot be excluded that such structures developed later during the post-larval phase and therefore have not been found.
- **Maxillopoda**: Fossil representatives, such as *Bredocaris admirabilis* Müller, 1983, *Skara anulata* Müller, 1983, *S. minuta* Müller & Walossek, 1985, *S. hunanensis* Liu & Dong, 2007, and *Dala peilertae* Müller, 1983 (Müller 1983; Müller & Walossek 1985, 1988; Liu & Dong 2007), have no structures that could represent epipodites. This also holds true for *Walossekia quinquespinosa* Müller, 1983, another 'Orsten' eucrustacean not yet described in detail. For Recent maxillopods Boxshall (2004) interprets two outgrowths on the limb base of the maxillula of copepods as epipodites, while the succeeding limbs lack any epipodite-like structures – if one ignores a seta on the outer side of the limb stem of the maxilla (Huys & Boxshall 1991). Epipodites or gill structures have not been described for mystacocarids, branchiurans, and thecostracans (tantulocarids, facetotectans, ascothoracids and cirripedes).
- **Ostracoda**: Species of this taxon that may belong to the Maxillopoda seem to have epipodites as leaf-shaped outgrowths on the maxilla. A single seta inserting laterally on the limb stem of the maxillula has been interpreted as a vestigial epipodite (Boxshall 1997). The so-called branchial plate of the maxillula of podocope ostracods, possibly serving as water-current producer and originally interpreted as epipodite (Cohen et al. 1998) is now regarded as the modified exopod (Horne et al. 2002; Boxshall 2004).
- **Cephalocarida**: This group has serially similar post-maxillulary appendages, so no specifically modified second maxilla. These limbs have no outgrowths on the lateral surface of their basipod. However, a type of outgrowth, not present in any other crustacean

taxon, is located on a triangular basal portion of the exopod (Fig. 3F) that has been termed pseud-epipodite (Sanders 1963) or epipodite (Hessler 1992; Ax 1999). This structure is equipped with musculature internally (Hessler 1964) and is interpreted as a part of the exopod rather than as an epipodite (Walossek 1993; Boxshall 2007). It serves, together with the main part of the exopod, for closing the sucking chambers laterally to control the water currents that leave the individual chambers between the limbs – a function unknown from epipodites. Its dense cover with fine hairs also argues against it being an epipodite.

- **Remipedia**: Species of this taxon do not have any outgrowths on the lateral sides of any of their limbs.

2.2. Arthropods other than Eucrustacea

Arthropoda s.l. sensu Maas et al. (2004) comprise the most likely paraphyletic lobopodians and the monophyletic Onychophora, Tardigrada – all having uniramous appendages – and Arthropoda s.str. (Maas et al. 2004; for detailed characterization and internal relationships see Waloszek et al. 2005, 2007). Onychophora autapomorphically possess tracheae, specific respiratory organs for living on land. Tardigrada do not have any discrete respiratory organs. Three fossil species of the Lower Cambrian Chengjiang fauna, the stem euarthropods *Fuxianhuia protensa* Hou, 1987, *Chengjiangocaris longiformis* Hou & Bergström, 1991 and *Shankouia zhenghei* Chen, Waloszek, Maas & Wang in Waloszek, Chen, Maas & Wang, 2005 (Fig. 5A,B) provide some details of the morphology and structural design in the ground pattern of Arthropoda s.str. (= *F. protensa*, *C. longiformis*, *S. zhenghei* + Euarthropoda; see Waloszek et al. 2005).

- **Stem-euarthropods**: Their dorsal cuticle was subdivided in the long axis of the animal into sclerotized tergites connected by membranous portions (the head shield is an enlarged single tergite; see Waloszek et al. 2005). Each tergite was subdivided abaxially into a central raised area and two outwardly pointing tergopleurae, which had free anterior, lateral and posterior margins to allow dorso-ventral flexure of the animal. From what is known, it appears that the ventral surface was soft and continuous, hence ventral segmental subdivision was not as elaborate as dorsally. Each segment bore a pair of limbs, but the cuticle between the left and right limb of a pair might not have been strongly sclerotized – the so-called sternites may have evolved significantly later. The trunk limbs behind the antennula, the single cephalic limb, were composed of a multi-annulated corm and a flap-shaped outer ramus (Fig. 6A). A rigid basipod that carried the rami was not formed initially. Form and position imply that the outer ramus was the early exopod, accordingly an autapomorphic element present at least in the ground pattern of Arthropoda s.str. The exopod may have mainly served for locomotion and/or steering. Specific respiratory organs were apparently not developed, although the animals could reach up to more than 8 cm in size (all three species known, i.e. *F. protensa*, *C. longiformis*, *S. zhenghei*). Accordingly the entire (ventral) body surface may have served in respiration and osmoregulation.

The major novelties (autapomorphies) of Euarthropoda are the formation of a larger head tagma now including four appendage-bearing segments, and formation of a rigid basal limb portion, the basipod, which carries the endopod and exopod (Waloszek et al. 2005, 2007). The basipod may have evolved by fusion of several proximal articles of the original limb corm, as exemplified by *F. protensa* or *S. zhenghei* (Waloszek et al. 2005). The medio-distally arising endopod may be simply the remaining distal part of the original limb corm. The leaf-like exopod now bears many setae around its outer margin and inserts on the sloping outer edge of the basipod. In parallel and to counteract the rigidity of the basipod, an ample arthrodial membrane developed to guarantee flexibility at the base of the appendage. Regarding respiration or osmoregulation, no morphological structures seem to have existed in stem euarthropods and the ground pattern of Euarthropoda specifically serving these functions. Among euarthropods different structures evolved to aid respiration if necessary because of large body size and/or active, oxygen-consuming life habits.

- **Trilobita** and the rest of the euarthropods known only from fossils, including taxa such as naraoiids, had no limb-associated gill structures (Suzuki & Bergström 2008). The limb consisted of those elements named for the euarthropod ground pattern (Fig. 6B). The sometimes lamella-like appearance of the exopods of some fossil species (see, e.g., Hou & Bergström 1997) cannot be interpreted as indicating a gill function (Suzuki & Bergström 2008). Their flat appearance may well be just preservational. Since cuticular structures are hollow, they would flatten considerably during diagenetic compression. Accordingly, a series of densely located setae would likely appear similar to lamellae. Instead Suzuki & Bergström (2008) identified the soft surface ventrally underneath the tergopleurae as specifically adapted for respiration purposes.
- **Chilopoda**, **Progoneata** (diplopods, symphylans, pauropods) and **Hexapoda** all lack limb-based gills or epipodites at all stages of their development. Even if one wishes to follow the ideas by some authors that wings could have originated from gills originally present on the thoracic appendages (e.g. Kukalová-Peck 1983; Averof & Cohen 1997; Damen et al. 2002), one still has to explain the lack of epipodites on all

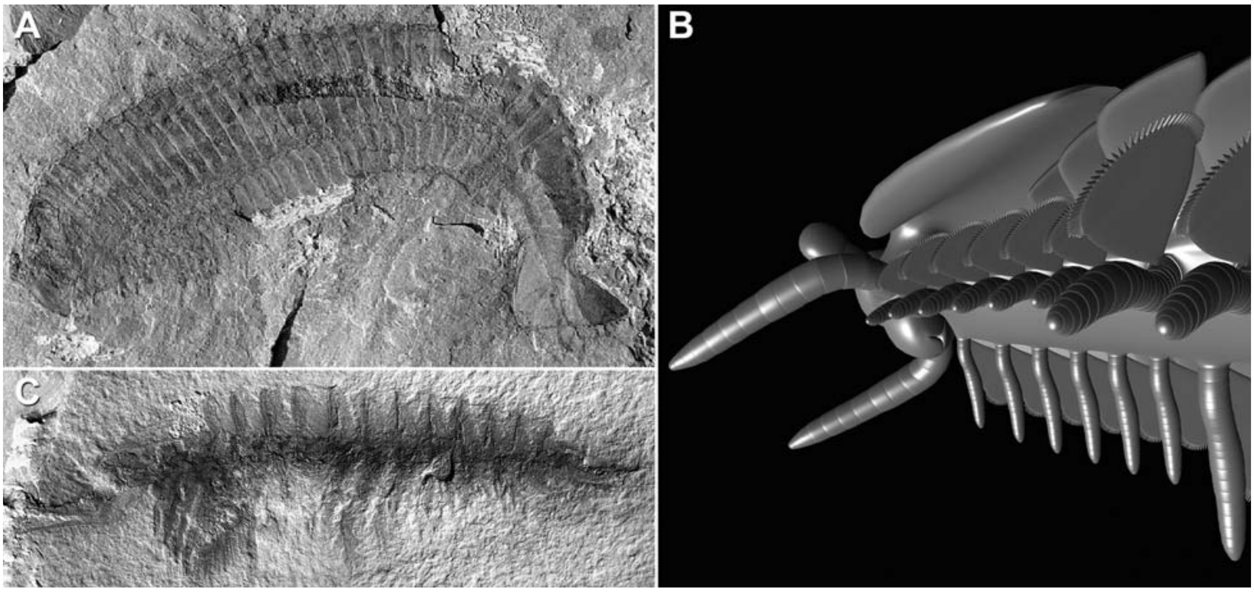

Fig. 5. Examples of Lower Cambrian arthropods from the Chengjiang biota. **A**, **B**: *Shankouia zhenghei* Chen, Waloszek, Maas & Wang in Waloszek, Chen, Maas & Wang, 2005. **A**: Holotype in lateral view, total length 61 mm (from Waloszek et al. 2005: fig. 1A; kindly provided by Chen Junyuan, Nanjing). **B**: 3D reconstruction in ventrolateral view. Limbs comprise a long, multiannulated rod and a flap that inserts latero-proximally (exact insertion on limb rod unknown, see also Fig. 6A). **C**: Stem chelicerate *Leanchoilia illecebrosa* (Hou, 1987) in lateral view, total length 29 mm (kindly provided by Yu Liu, Ulm).

legs in primarily wingless insects (see also Hovmöller et al. 2002; Boxshall 2004; see Hasenfuss 2002, 2008 for support of the alternative paranota hypothesis of wing origin; see Béthoux & Briggs 2008 for scrutiny of further surmised basal leg appendages in fossil Hexapoda reported in various papers by J. Kukalová-Peck). Since Boxshall (2004) discussed this issue in detail, concluding that epipodites and wings do not have a common evolutionary origin, we do not want to go into more detail here. It does not contribute to the main focus of this paper either. Species of these taxa have a tracheal system for respiration on land. Whether this has evolved once (e.g. Ax 1999) or several times (e.g. Kraus 1998) is not relevant here (discussion in Klass & Kristensen 2001).

- **Stem euchelicerates**, some of them being also named ‘great-appendage’ arthropods (see Chen et al. 2004, cf. Cotton & Braddy 2004), had, most likely, no “gills” or epipodites originally. At least nothing has been described to suggest a gill function. Their serially similar postantennular appendages (exemplified by *Leanchoilia illecebrosa* (Hou, 1987); Fig. 5C) comprised a proximal portion, the basipod, on which the endopod inserts mediodistally and the exopod laterally on an outer sloping edge of the basipod (Fig. 6C), a condition retained from the euarthropod ground pattern (Chen et al. 2004; Waloszek et al. 2005).
- **Euchelicerata** is the only taxon apart from Crustacea in which specific limb-associated structures serving for gas exchange are present. In Xiphosurida these occur as a large number of fine blades on the posterior side of the exopods of some of the opisthosomal limbs (Suzuki et al. 2008). It must be stressed that these gill blades are only part of the exopod; the exopod itself and the limb itself should not be named a gill. Structures found in eurypterids are interpreted as gills similar to those in xiphosurans (Manning & Dunlop 1995; Dunlop 1998). The euchelicerate *Offacolus kingi* Sutton, Briggs, Siveter, Siveter & Orr, 2002 from the Silurian Herefordshire lagerstätte, reconstructed in three dimensions (Sutton et al. 2002), had exopods on its prosomal and opisthosomal legs, but additional structures have been referred to as gills similar to those of extant xiphosurans. The flabellum inserting on the outer edge of the basipod of the last walking limb of xiphosurans has repeatedly been interpreted as an epipodite (e.g. Mittmann & Scholtz 2001 based on gene expression data). However, Boxshall (2004) gave additional evidence for the interpretation of the flabellum as a remnant of the exopod (see also Dunlop & Braddy 2001).

It is a long-standing idea that the exopodal blades, such as those in xiphosurans, should have become transformed into a meshwork of trabeculi forming the book lungs of Arachnida (Lankester 1881; Dunlop 1998), a transformation that has been accepted as an arachnid autapomorphy (Ax 1999; see also Scholtz & Kamenz 2006 for a recent review). This event should have been paralleled by a backward orientation of the according limbs and their partial and eventually complete fusion with the body cuticle.

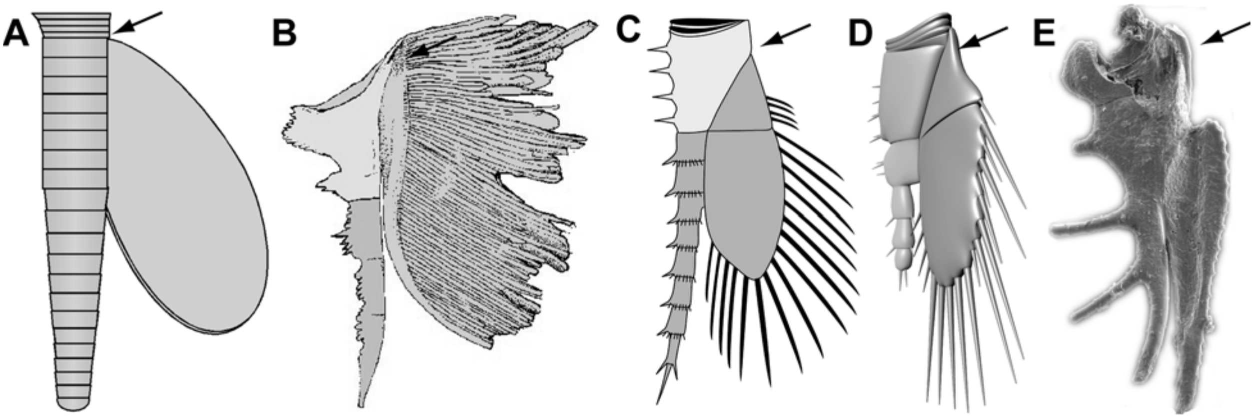

Fig. 6. Isolated trunk limbs of extinct arthropods. Arrows point to the outer proximal edge of the limbs, which does not possess any outgrowths. **A**: *Shankouia zhenghei* Chen, Waloszek, Maas & Wang in Waloszek, Chen, Maas & Wang, 2005, drawing. Note the main stem of the limb developed as a multi-annulated rod, while other limbs (B–E) have a prominent proximal portion, the basipod. **B**: *Misszhouia longicaudata* (Zhang & Hou, 1985), drawing. **C**: *Leanchoilia illecebrosa* (Hou, 1987), drawing (kindly provided by Yu Liu, Ulm). **D**: *Oelandocaris oelandica* Müller, 1983, 3D reconstruction. **E**: *Hesslandona unisulcata* Müller, 1982; SEM micrograph of UB W 125 (from Waloszek 2003a, image flipped horizontally for better comparisons). Images not to scale.

- **Non-labrophoran crustaceans**. These include exclusively Cambrian species from the Swedish 'Orsten' type of preservation, e.g. *Martinssonia elongata* Müller & Walossek, 1986, *Henningsmoenicaris scutula* (Walossek & Müller, 1990), and *Oelandocaris oelandica* Müller, 1983 (see Stein et al. 2008; Haug et al. in press). As is plesiomorphic for Euarthropoda, the trunk limbs consist of a basipod with endopod and exopod inserting medio-distally resp. laterally (Fig. 6D). No other structures occur. All other Crustacea can be named Labrophora (see Maas et al. 2003) and include the two sister taxa Phosphatocopina and Eucrustacea, the crustacean crown group.
- **Phosphatocopina**. This taxon comprising about 30 species of bivalved Crustacea is regarded as the sister taxon of the Eucrustacea (Maas et al. 2003). Phosphatocopines lack, on any of their limbs, structures that could be interpreted as an epipodite or are specifically suitable for respiration or osmoregulation. Their second and more posterior postmandibular limbs are serially similar, i.e. they lack the modification of the first postmandibular limb to a maxillula, and consist of a basipod carrying an endopod and exopod and a movable setose endite underneath the basipod, the proximal endite (Fig. 6E).

We can summarize that epipodites occur exclusively in eucrustaceans and are restricted to postmandibular limbs. Their occurrence on maxillulae is uncertain, and generally their occurrence is systematically sporadic. If the setae mentioned above for *Y. dianensis* and ostracods on the maxillulae are vestiges of epipodites (as Boxshall 2004 suggested for ostracods), then these structures became reduced very early in eucrustacean evolution. Comparison of the structures surveyed here that could putatively be epipodites within Crustacea implies that at least some of them could be homologous and indeed be named epipodites. We can further state, based on physical conditions for gas exchange in tissues, that gas exchange may occur over the entire surface of the animal (as is the case in earthworms as a common example for cutaneous respiration), but that the leaf-shaped exopods as present in stem chelicerates (e.g. *Leanchoilia illecebrosa* Hou, 1987; Figs. 5C, 6C) and stem euarthropods (e.g. *Shankouia zhenghei*; Figs. 5A,B, 6A), may have had a too small surface to represent an area large enough for a specific gas-exchange function (see also Suzuki & Bergström 2008), although they contributed to that function as any other body surface.

There is no reason or evidence to name any specific body part a gill in these given example taxa of non-eucrustacean arthropods. Likewise it is critical not to mismatch exopods with epipodites: limbs that possess epipodites almost always have exopods, too. The problem of assigning a specific function to limbs or limb parts according to a morphological interpretation alone for trilobites has been mentioned above. This mismatch was recognized long ago (Cisne 1973, 1974, 1975; Schram 1978) but has been continuously upheld in the literature, leading Suzuki & Bergström (2008) to clarify the matter. This teaches us to be very careful in interpreting structures too superficially. In all, we regard "gill" as a functional term and do not wish to have it mismatched with structural terms. These must be clearly named because they may – often – be not homologous.

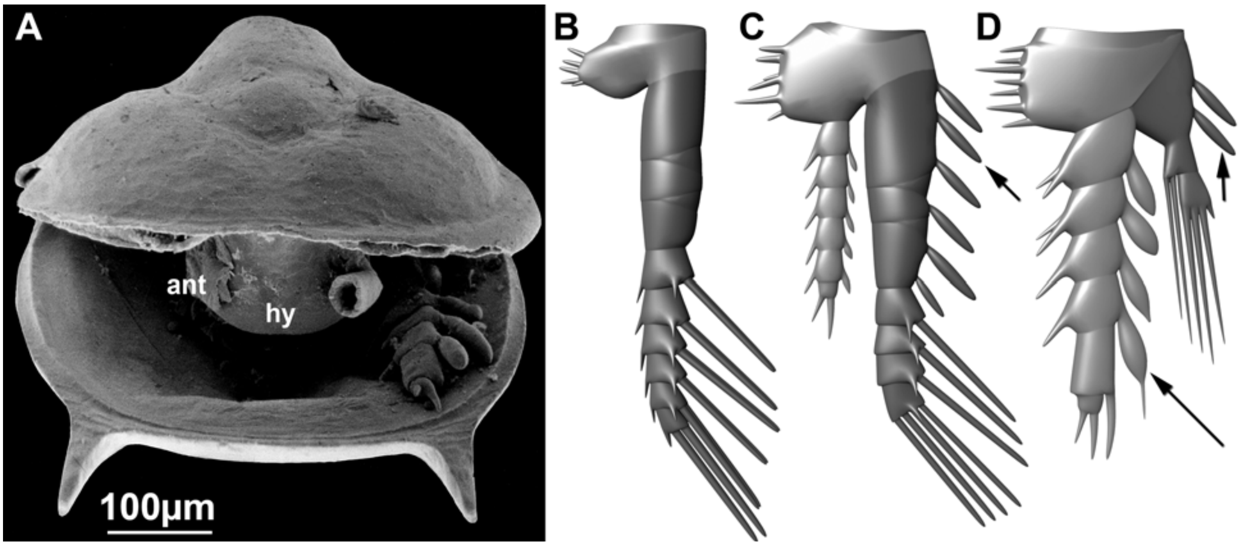

Fig. 7. *Agnostus pisiformis* (Wahlenberg, 1818). **A**: SEM micrograph of an instar at meraspid stage 1b, viewed from the anterior onto the slightly gaping head (up) and tail shields (underneath) and the spherical hypostome (hy) "hanging down" from the head shield (UB 838; see MÜLLER & WALOSSEK 1987, cf. their pls. 12:5, 14:1,2, 16:1). Antennulae broken off (ant), only the more posterior limbs preserved in full pointing out of the "shell". **B–D**: Reconstructions of post-antennular head limbs. **B**: Second cephalic appendage ("antenna" in Eucrustacea). **C**: Third cephalic appendage ("mandible" in Eucrustacea). **D**: Fourth cephalic appendage ("maxillula" in Eucrustacea). A longer arrow points to the club-shaped structures on the outer distal edge of the proximal endopodal portions, shorter arrows to the soft setae on the lateral edge of the proximal part of the exopods in C and D. Images not to scale.

2.3. Origin of epipodites

The origin of epipodites has long been discussed (e.g. HANSEN 1925; SIEWING 1957; BURNETT & HESSLER 1973; LAUTERBACH 1979; WALOSSEK 1993; BOXSHALL 2007) with respect to:

- the distribution of such structures among various taxa in a phylogenetic context;
- their morphological nature and morphogenesis;
- the unclear early evolution of Crustacea;
- the fossil record of such fragile structures and their function.

Among these, our main focus is on the fossil evidence of epipodites and on the morphogenesis if data is available, which significantly helps in the understanding of evolutionary processes (e.g. manuscript submitted by J.T. Haug and coworkers). This is made particularly possible when investigating the Cambrian three-dimensionally preserved 'Orsten'-type arthropod fossils, which include preservation of many life stages. Accordingly, one is able, as in extant animals, to follow a structure not only along a limb or along a limb series of an individual, but also along the ontogenetic sequence. Many taxa of the tiny 'Orsten'-type arthropods studied so far develop via long series of larval or immature stages. Possibly the best example is the branchiopod *Rehbachiella kinnekullensis* Müller, 1983 (WALOSSEK 1993) with 30 successive stages, which starts from the 170 µm long nauplius stage up to a stage with thirteen pairs of thoracopods and about 1,700 µm in length. A larval series in the fossil record provides not only information on the available stages, but also provides data on the process of development. Although information of the adult might be missing in many cases, the phylogenetic signal provided by a series of larvae is much larger than by the adult alone (manuscript submitted by J.T. Haug and coworkers).

A good example of a Cambrian euarthropod having structures possibly functionally equivalent to epipodites is *Agnostus pisiformis* (Fig. 7A). This tiny euarthropod has a large head and tail shield that can be closed to encapsulate the entire body and appendages (Fig. 7A); most likely these animals spent most of the time in the closed position. This is in analogy to the bivalved head shields of e.g. ostracods that enclose the body from the sides. *A. pisiformis*, traditionally regarded as a miniaturised eyeless trilobite (e.g. FORTEY & THERON 1994), may rather be closely related to Crustacea, an interpretation founded on the ventral body morphology, and particularly on the specialization of the anterior three cephalic appendages that serve for food intake and locomotion, i.e. the antennula, the "antenna" and "mandible" (Fig. 7B,C; antennula not illustrated), as they also do in the crustacean evolutionary lineage (e.g. WALOSSEK & MÜLLER 1990; STEIN et al. 2005, 2008). In the context of putative respiratory or osmoregulatory structures, it is of relevance that all limbs from the segmental homologue of the mandible onwards (that lacks an endopod; Fig. 7B) bear club-shaped structures on the outer distal edges of the endopodal portions (Fig. 7C,D). The large size

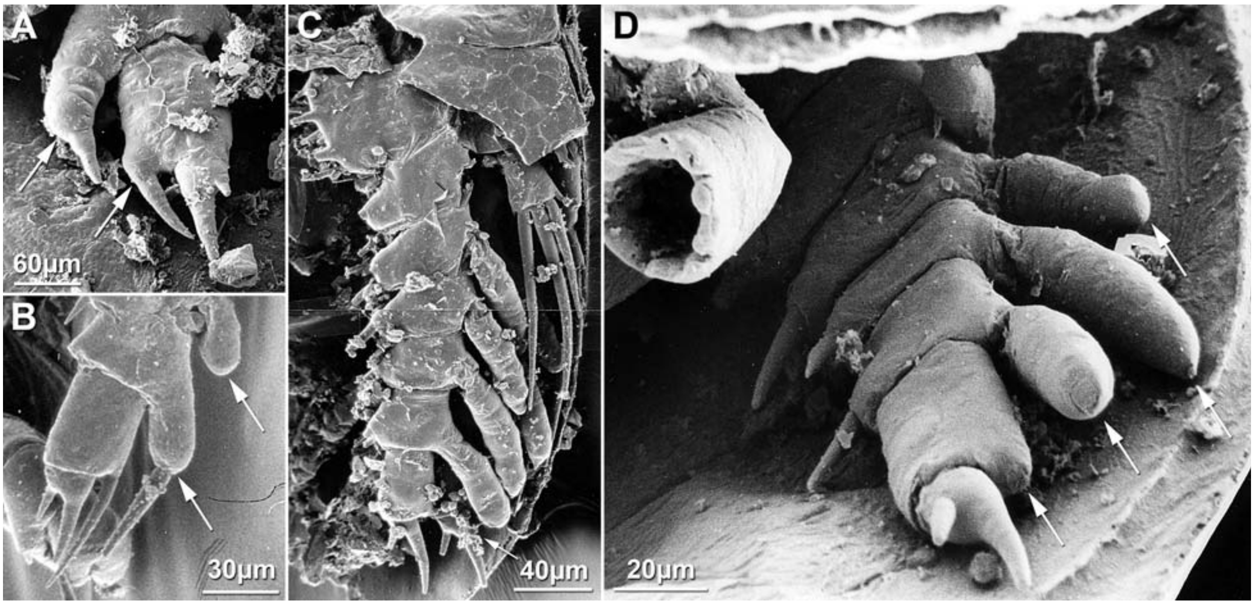

Fig. 8. SEM micrographs of details of *Agnostus pisiformis* (Wahlenberg, 1818). **A**: Distal part of endopod of fourth trunk limb of a meraspid stage 2c (UB 830; from Müller & Walossek 1987: pl. 26:7; see also their pls. 7:5–7, 22:3, 25:1–4, 26:10,11). Note the setal tip of the well developed club and the swelling of the basis of the penultimate seta (arrows). **B**: Distal end of the endopod of a trunk appendage of an instar at meraspid stage 1b (UB 852; from Müller & Walossek 1987: pl. 25:5, see also their pls. 16:2, 17:9, 19:3, 20:1,5, 26:8,9). Note the clubs on the distal portions (arrows), with one of these bearing a prominent seta at its tip. **C**: First trunk limb of a meraspid stage 2a (UB 863; from Müller & Walossek 1987: pl. 24:1, see also their pls. 24:2–4, 26:4–6). Note the penultimate swollen seta (arrow) and the lack of setae on other clubs. **D**: Endopod possibly of fifth appendage (= first trunk appendage) of a meraspid stage 1b, UB 838 (from Müller & Walossek 1987: pl. 23:2, see also their pls. 11:1, 12:2, 17:2, 29:2, 31:9) with well-developed clubs on the outer distal edge of podomeres 2–5 (arrows); terminal setae absent from the clubs of podomeres 2–4, seta broken off on club of podomere 5.

of the endopods and, likewise, large size of the clubs, but very small exopods in the last head limb (Fig. 7D) and the serially similar trunk limbs, suggest that the club-like structures possibly had some respiratory or osmoregulatory function in the animal's "life in a nutshell". If this interpretation was correct, *A. pisiformis* would be the only euarthropod taxon to bear such structures on the endopod. Hence, these club-shaped structures would have a function similar to gills of other arthropods, but would be non-homologous to these. The term 'gill' may be appropriate from a functional perspective, while 'epipodite' is not.

The endopodal clubs in *A. pisiformis*, irrespective of their non-homologous position, may serve in providing a better understanding of the possible original morphogenesis of the epipodial structures on the outer side of the basipods of crustacean limbs. The endopodal clubs of *A. pisiformis* grow out from the outer distal edges of each of the endopodal podomeres (Müller & Walossek 1987). In most cases, this edge is slightly humped and forms the socket of a robust seta or spine (Fig. 8A). Development of the club begins with a swelling of the setal base (Fig. 8B) and continues with the progressive elongation of the swelling into a club- to rod-shaped structure with a rounded to slightly pointed distal end (Fig. 8C,D). Initially, the original seta is retained at the tip of the swelling (Fig. 8A,B), but then becomes reduced (Fig. 8C) or even finally disappears (Fig. 8D). The cuticle of the clubs was rather soft, as can be deduced from the different specimens displaying the clubs in various states of preservation (compare Fig. 8A and C). Already Müller & Walossek (1987) have speculated that these clubs may have contributed to the respiration of the animal, but they concluded, in accordance with our explanations, that they may not necessarily have been specific respiratory organs, but rather that gas exchange may have occurred passively on their enlarged surface as it has happened on the entire body surface. Regardless of their position, the clubs present a good model for the possible morphogenesis of such lobate structures from original setal sockets.

Another feature of *A. pisiformis* are the fine, plumose setae at the outer edge of the proximal portions of the exopod of the last two head limbs and the trunk limbs (Figs. 7C,D, 9A,B). These setae appear to be very soft relative to the seemingly firm exopodal terminal setae. Moreover they are adorned with opposing rows of fine setules from proximal to distal. Morphological changes during ontogeny are not apparent. Müller & Walossek (1987) assumed that these setae may have played a role in producing water currents for the possibly respiratory body surface including the club-shaped structures discussed above, but it is difficult to assume

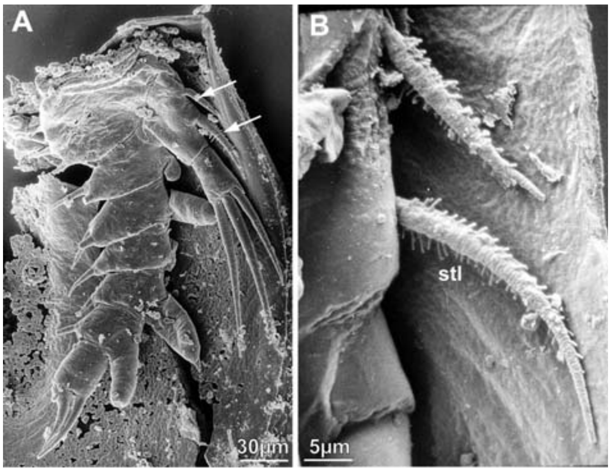

Fig. 9. SEM micrographs of *Agnostus pisiformis* (Wahlenberg, 1818) displaying soft setae at the outer edge of the proximal portions of the exopod of post-antennular limbs (arrows). **A**: First trunk limb of a meraspid stage 1c (UB 853; from Müller & Walossek 1987: pl. 23:5 [image flipped horizontally], see also their pls. 16:3, 17:6, 18:4, 20:3, 21:5, 23:4). Note that also the proximal endopodal podomere bears a short club. **B**: Close-up of exopodal setae of third head limb of a meraspid stage 1b (UB 858; from Müller & Walossek 1987: pl. 21:4, see also their pls. 17:7, 20:2). Abbreviation: stl = setules on the setae.

an active motion of these setae. In any way the small surface of these setae precludes them from playing an active role in the respiratory process. It is doubted that they were possible precursors of the epipodial structures occurring in eucrustaceans, in particular because they occur on the exopod and not on the limb stem in *A. pisiformis*.

The main fossil evidence for epipodites within Eucrustacea is *Yicaris dianensis* (Zhang et al. 2007; Fig. 10B–F). This species, preserved in three dimensions from Lower Cambrian rocks from China, has three outgrowths on the outer edge of its postmaxillulary limb bases that fulfil a number of criteria for being interpreted as epipodites. Although lacking in the Cambrian branchiopod *R. kinnekullensis* (Fig. 10A), the epipodites of *Y. dianensis* are located in the same position and appear in the same number as in certain anostracan eucrustaceans (Fig. 10B–G; Møller et al. 2004). Epipodites of *Y. dianensis* are lobe-shaped to trapezoidal flat structures that may carry a seta at their edge (Fig. 10C). Ontogenetically they first appear as setae or pointed swellings. Morphogenesis of the epipodites of *Y. dianensis* can be traced in three ways, i.e. along the limb, along the series of limbs, and during ontogeny (Fig. 10D–F). According to this information, the bases or sockets of the setae swell (Fig. 10F) and grow out into the lobe-shaped structures still carrying the setae at their tips (compare Fig. 10D and F). Consequently, the swelling structures that are becoming epipodites are not themselves the setae. Until this point the process is similar to that of the clubs of *A. pisiformis*. Thereafter, the lobes of *Y. dianensis* become progressively more flattened and achieve their triangular or sub-quadratic shape with a tiny seta still located on one of the edges (Figs. 10C, 11A). Most likely these setae disappear during later ontogeny, which is, however, not known for *Y. dianensis*. In particular, the comparison between the epipodites of *Y. dianensis* and certain anostracan branchiopods reveals that epipodite structures of the two taxa are strikingly similar in shape, and they are also similar with respect to their insertion position on the limb (Fig. 10F,G; compare Figs. 11B and 4C). As in *Y. dianensis*, the epipodites in anostracans develop on the outer edge of the limb bases as initially three tube- or club-shaped structures (Fig. 10G, cf. Fig. 4A) that grow out into the three lobate to sub-quadratic epipodites of the adults (some species only two) (see also Fig. 4A,B). One difference to *Y. dianensis* is the lack of setae in any stage, which might be explained by heterochrony (discussion of heterochronic effects in crustacean evolution in manuscript submitted by J.T. Haug and coworkers). Two epipodites are developed in various other eucrustaceans including malacostracan taxa. Many of these epipodites are lobate or even club-shaped (Fig. 4C,D) much as in *A. pisiformis*, which again highlights the possibility of using fossil evidence for comparisons. Other epipodites become progressively more flattened and subtriangular during ontogeny, which is exactly what is seen in *Y. dianensis* (cf. Figs. 4B, 10C).

Until now only *Y. dianensis* among fossils in an 'Orsten'-type of preservation carries putative epipodial structures. Their nature as epipodites was questioned by Boxshall (2007) who, based on information given by Zhang et al. (2007) particularly questioned the development of epipodites from setae. However, as we have pointed out above, the according structures in *Y. dianensis* do not grow out from setae (as Zhang et al. 2007 could be understood) but from pointed humps or sockets that carry setae (Fig. 10F). This explains the retention of setae on ontogenetically advanced epipodites, and Boxshall (2007) did concede that epipodites also of recent eucrustaceans may carry setae, as do the oostegites of peracarids. An idea to how the loss of setae of the epipodites of *Y. dianensis* may occur ontogenetically, and may have occurred evolutionarily, can be gleaned from the development of the endopodal clubs of *A. pisiformis*, where the setae become reduced or even disappear during development (see above). We agree with Boxshall (2007) that the pseudepipodite of Cephalocarida is most likely not related to any epipodite (as Zhang et al. 2007 proposed), but rather is an outgrowth of the proximal exopodal portion autapomorphic to Cephalocarida. Boxshall (2007) argued that we need "precise anatomical definitions of the different exites to make meaningful, homology-based comparisons". We think that we pre-

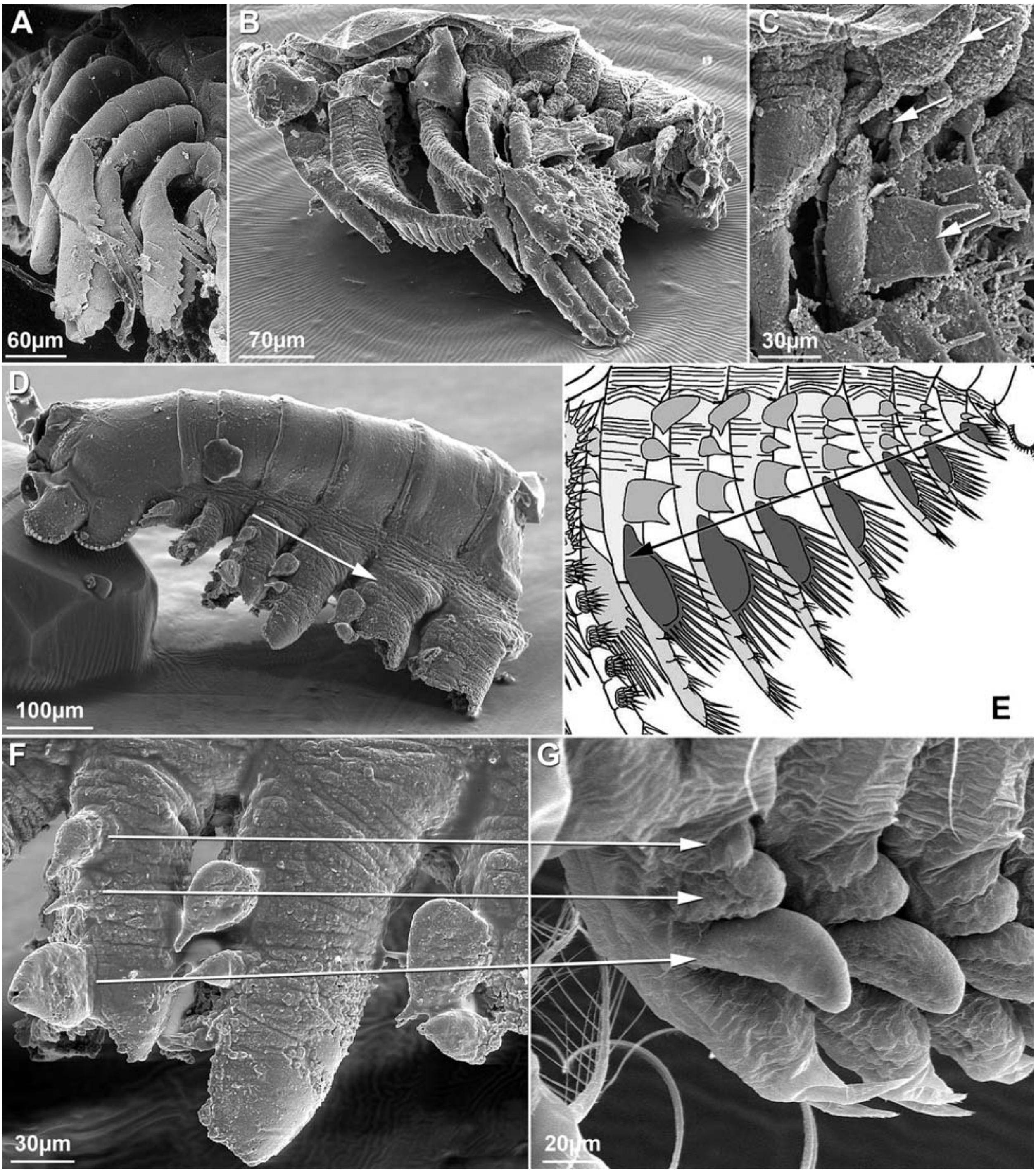

Fig. 10. Comparison of epipodites between larvae of the Cambrian branchiopod *Rehbachiella kinnekullensis* Müller, 1983 (A), the Lower Cambrian eucrustacean *Yicaris dianensis* Zhang, Siveter, Waloszek & Maas, 2007 (B–F), and the extant branchiopod *Eubranchipus grubii* (Dybowski, 1860) (G). **A**: Postero-lateral view of specimen UB 87 representing the latest stage known (cf. Walossek 1993: pl. 29:4,5), **B**: Head and anterior trunk in lateral view displaying the position of the epipodites on the limbs. **C**: Close-up of (B) of a few limbs bearing three epipodites as lobate outgrowths (arrows). Note that the two proximal epipodites are setae with a swollen basis, while the distal epipodite is lobe-shaped, with the distal seta being broken off in this specimen. **D**, **E**: Display of the developmental state of the epipodites along the limb series (arrows). **D**: Trunk fragment with epipodites. **E**: Reconstruction of the limb series. **F**, **G**: Comparison of the epipodites of *Y. dianensis* and *E. grubii* with epipodites in most likely homologous positions (arrows). Anterior to the right in (F), anterior to the left in (G).

dominantly need detailed data on the relationships within Eucrustacea, on ground patterns of its in-group taxa and comprehensive information on the character evolution for Crustacea. Reciprocal illumination between the various steps of work is required, after which appropriate terminology may be decided upon. This has already been done for the early phase of crustacean evolution (e.g. Maas et al. 2003; Waloszek

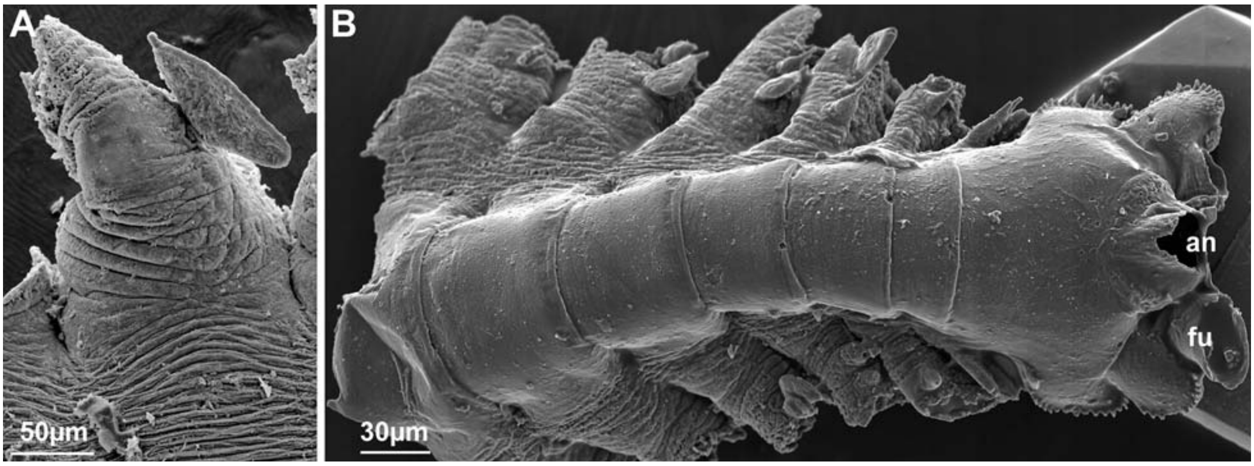

Fig. 11. SEM micrographs of *Yicaris dianensis* Zhang, Siveter, Waloszek & Maas, 2007. **A**: Close-up of a trunk limb from lateral displaying the triangular, proximal-most epipodite. **B**: Dorsal view of a trunk fragment with slightly stretched out limbs displaying the epipodites (compare with the same view of a Recent diplostracan in Fig. 4C). Abbreviations: an = anus; fu = furca.

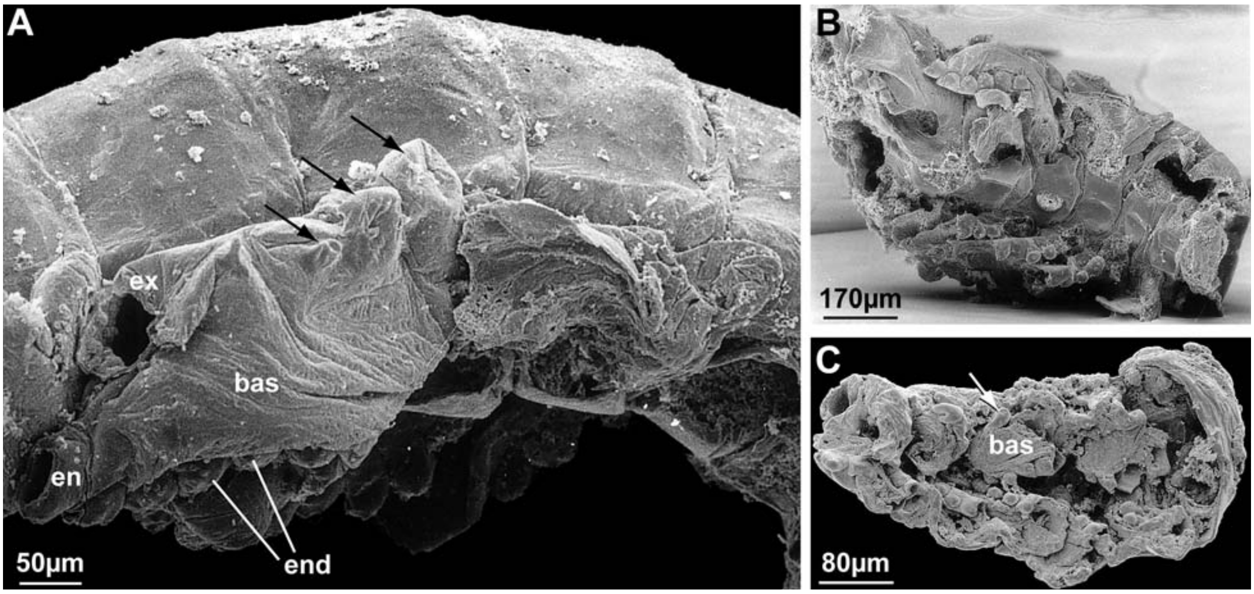

Fig. 12. SEM micrographs of fragmentary specimens from the Cambrian 'Orsten' of Sweden representing most likely two new species of Entomostraca. **A**, **B**: Species I, UB W 418. **A**: Lateral view. The club-shaped epipodites insert on the outer edge of the basipod (arrows). **B**: Ventral view of the same specimen showing the ample sternitic region behind the trunk limbs. Note the enditic protrusions of the inner edge of the preserved basipods. **C**: Species II, UB W 419, in ventral view (one epipodite marked by an arrow). Abbreviations: bas = basipod; en = endopod; end = endites on the inner edge of the basipod; ex = exopod.

2003b; Stein et al. 2008; Haug et al. in press), but this is seemingly an epipodite-less evolutionary phase. In this work we maintain the interpretation of epipodites in *Y. dianensis* and various recent eucrustaceans as being homologous as already suggested by Zhang et al. (2007). But this study also allows room for other explanations of some of the difficult to interpret material of the Swedish 'Orsten' fauna.

In addition to *Y. dianensis* there is further evidence for the presence of epipodites on other Cambrian Eucrustacea from the Swedish 'Orsten' material. Two fragmentary specimens, most likely representing two different species, exhibit three epipodite structures on the outer surfaces of their trunk limbs (Fig. 12A–C). Although the formal description of the species, here informally named "Species I" and "Species II" in open nomenclature, has to be postponed until more material is available to substantiate the species status, some relevant characters can be discussed here already. The two specimens have trunk limbs comprising a prominent basipod and two rami. The basipod is medially divided into a set of setiferous endites, which is only characteristic for the post-maxillulary limbs of entomostracan Eucrustacea (e.g. Waloszek 2003a,b; Zhang et al. 2007). Laterally on the basipod, between the basal arthrodial membrane and the exopod insertion, up to three (Fig. 12A) lobate or club-shaped outgrowths arise. These structures are interpreted as epipodites since they appear in the same number, shape, and positions as in *Y. dianensis*.

3. Phylogenetic interpretations, conclusions, uncertainties, and outlook

3.1. Phylogenetic interpretations and conclusions

Hessler (1992) interpreted the epipodites as a common structure of the Cephalocarida, Branchiopoda and Malacostraca and united these in his taxon Thoracopoda, a concept that was put forward by Ax (1999). We have already discussed that the "epipodite" of Cephalocarida is part of the exopod and would not support the view of Hessler (1992) anymore. Boxshall (2004), in his review of arthropod limb evolution, concluded that epipodites did not belong to the eucrustacean ground pattern although he confirmed that, at least, branchiopod and malacostracan epipodites are homologous, a view also supported by Richter (2002).

However, distribution of epipodites within eucrustacean taxa, including new evidence from Cambrian taxa, indicates that epipodites were part of the eucrustacean ground pattern. This assumption has been stated already in the past (Siewing 1960), but was mainly based on the misinterpretation of structures in fossil arthropods (Walossek 1993; see also above). Consequently, structures of maxillopods, such as certain ostracods, that were discussed above as possible epipodites (see also Boxshall 2004) can confidently be interpreted as epipodites or, at least, epipodite remnants. This does not necessarily imply the same function as for epipodites in other taxa. Fossil evidence, brought up by *Y. dianensis* and the two new forms (*Species I* and *Species II*), supports the presence of three epipodites on the outer edge of the basipods of Entomostraca, as they are also present in certain anostracan branchiopods. These epipodites may be club-shaped, lobate, or flattened. The study of the morphogenesis and diversification of the epipodites in *Y. dianensis* was made possible through 1) comparing epipodite morphology of different limbs, 2) comparing epipodite morphology on a single limb, 3) and establishing their ontogenetic development. In this manner *Y. dianensis* can serve as a useful model for the origin of epipodites within crustaceans, showing many similarities to Recent Crustacea such as anostracan branchiopods. Three epipodites never occur in Malacostraca, where one epipodite per thoracopod is most widespread although also two occur. Two different conditions present in Entomostraca and Malacostraca respectively prevent from specifying the number of epipodites in the ground pattern of Eucrustacea.

In summary, data provided by Cambrian fossil eucrustaceans such as *Y. dianensis* and two new species awaiting formal description, and the occurrence of epipodites in various living eucrustacean taxa help to enlighten the evolutionary origin of epipodites:

- Epipodites are basipod-associated (lateral) structures inserting on the outer edge of the basipod;
- Epipodites originated from out-growing humps;
- Subsequent growth leads to either a leaf shape or club shape;
- Epipodites may grow out at the position of a setal socket, thus carrying this seta marginally, or reducing it eventually;
- The common occurrence of leaf-shaped, basipod-associated epipodites in malacostracan and entomostracan taxa points to their presence (at least) in the ground pattern of Eucrustacea;
- Epipodites may function as gills, but gills may not necessarily be epipodites;
- Gill structures or epipodites functioning as gills occur in large-sized eucrustaceans, especially malacostracans;
- Three epipodites inserted laterally on postmaxillulary limbs in the ground pattern of Entomostraca, retained at least in the fossil *Y. dianensis* and in the Branchiopoda;
- Possibly one or two epipodites inserted laterally on postmaxillulary limbs in the ground pattern of Malacostraca.

3.2. Uncertainties and outlook

Although the exciting find of the Cambrian eucrustacean *Y. dianensis* made us reflect on the evolutionary origin of epipodites and stimulated us to consider additional ideas, it also exposed open questions that still need to be considered. For example it remains unclear how the different shapes of epipodites in adults of many Crustacea developed. The morphogenesis of epipodites as a swelling of a setal base, as in *Y. dianensis*, might be understood as one, maybe even the original, possibility. Such a morphogenesis of epipodites is not known for recent Crustacea, which may be explained by overprinting of the original traces such that they are not recognizable anymore. Another open question is whether epipodites originally also occurred on the maxillula or only on more posterior limbs. Since the maxillula is a specialized "mouth part", autapomorphic for the eucrustacean ground pattern (Maas et al. 2003; Waloszek 2003a,b), it might well be that this limb never possessed epipodites – again, the two setae in just the corresponding position in *Y. dianensis* (Zhang et al. 2007) and similar setae in copepod maxillulae may lead to the opposite conclusion. If we assume the presence of epipodites in the eucrustacean ground pattern, we need to explain the lack of epipodites in various in-group taxa, e.g. in maxillopods, but also in *R. kinnekullensis* among branchiopods. For some of these taxa one may argue that miniaturisation was a factor in the evolution of these animals, e.g. in copepods or mystacocarids, possibly also the thecostracan lineage. Another possible explanation, at least for *R. kinnekullensis*, is that epipodites occur in development later than the stages known of this species (Walossek 1993).

As discussed above, epipodites, if present, may occur in numbers of 1–3 per limb in extant eucrustacean taxa. Their design ranges from being branched filaments to having a club-, lobe- or leaf-like shape. Yet, it has never been tested until now whether this combination of characters provides a phylogenetic signal for phylogeny analyses. Lack of epipodites in all the "stem crustaceans" known from the 'Orsten' is remarkable, but we have to be aware that, in this case, we only know immature stages of the relevant species, which in some cases are nevertheless rather advanced. Yet, we cannot simply presume lack of epipodites also in adult forms. Lack of epipodites also holds for the exclusively Cambrian phosphatocopines, the sister taxon of Eucrustacea. The largest phosphatocopine instars known also lack such structures (cf. Maas et al. 2003). At least this suggests that epipodites may be exclusive to, i.e. an autapomorphy of Eucrustacea. This is also supported by the lack of any epipodite-like structures in tracheates. The function of the ancestral epipodites is another unresolved problem. Respiratory and osmoregulatory functions might have evolved independently. Two structures to be kept in mind are the endopodal clubs and the soft setae of the Cambrian euarthropod *A. pisiformis*, the nature of which remains unknown. While the endopod structures may serve as a model to understand the development of outgrowths, they are clearly not homologous to the basipodal epipodites of eucrustaceans. With regard to the basipodal and exopodal setae, we need to provide more evidence before discussing these as evolutionary precursors of eucrustacean epipodites. Yet, on the other hand, one cannot simply exclude items without clear arguments *pro* or *contra*, and if the structures in question are not precursors of something else, one has likewise to demonstrate that there is no phylogenetic connection between the two structures.

4. Acknowledgments

We wish to thank Stefan Richter, Christian Wirkner, Ole Sten Møller and their team for organizing the meeting "Advances in Crustacean Phylogeny" in October 2008 in Rostock and for the opportunity to one of the authors (DW) to present a talk. This presentation formed the basis for our contribution. Furthermore, we are indebted to various colleagues, which discussed matters with us and which kindly provided suggestions. Particularly thanks to Dietmar Keyser, Hamburg, and Junyuan Chen, Nanjing, for their kind permission of using images of their collections. SEM images were taken at the Central Facility for Electron Microscopy of the University of Ulm and at the Natural History Museum of Denmark, Copenhagen. Part of the work in Copenhagen was supported by a grant from the European Commission's (FP 6) Integrated Infrastructure Initiative programme SYNTHESYS (DK-TAF 2171). Ronald Jenner, London, and two anonymous reviewers kindly improved the language and gave helpful suggestions. We also like to thank the editor of Arthropod Systematics and Phylogeny, Klaus-Dieter Klass, Dresden, for his editorial work and constructive criticism. Specimens illustrated with a UB repository number are stored in the collection of the Steinmann Institute for Palaeontology at the University of Bonn, Germany.

5. Referencens

Alberti, G. & U. Kils 1983. Light- and electron-microscopical studies on the anatomy and function on the gills of krill (Euphausiacea, Crustacea). – Polar Biology **1**: 233–242.

Averof, M. & S.M. Cohen 1997. Evolutionary origin of insect wings from ancestral gills. – Nature **385**: 627–630.

Ax, P. 1999. Das System der Metazoa II. – Gustav Fischer, Stuttgart. 384 pp. [also published in English as "Multicellular Animals II", Springer, Heidelberg, 2000].

Béthoux, O. & D.E.G. Briggs 2008. How *Gerarus* lost its head: stem-group Orthoptera and Paraneoptera revisited. – Systematic Entomology **33**: 529–547.

Boxshall, G.A. 1997. Comparative limb morphology in major crustacean groups: the coxa-basis joint in postmandibular limbs. Pp. 156–167 *in*: R.A. Fortey & R.H. Thomas (eds.), Arthropod Relationships; Systematics Association Special Volume 55. – London, Chapman & Hall.

Boxshall, G.A. 2004. The evolution of arthropod limbs. – Biological Reviews **79**: 253–300.

Boxshall, G.A. 2007. Crustacean classification: on-going controversies and unresolved problems. – Zootaxa **1668**: 313–325.

Budd, G.E. 1997. Stem group arthropods from the Lower Cambrian Sirius Passet fauna of North Greenland. Pp. 125–138 *in*: R.A. Fortey & R.H. Thomas (eds.), Arthropod Relationships; Systematics Association Special Volume 55. – London, Chapman & Hall.

Burnett, B.R. & R.R. Hessler 1973. Thoracic epipodites in the Stomatopoda (Crustacea): a phylogenetic consideration. – Journal of Zoology **169**: 381–392.

CHEN, J.-Y., D. WALOSZEK & A. MAAS 2004. A new "great appendage" arthropod from the Lower Cambrian of China and the phylogeny of Chelicerata. – Lethaia **37**(1): 3–20.

CISNE, J.S. 1973. Life history of an Ordovician trilobite. – Ecology **54**: 135–142.

CISNE, J.S. 1974. Trilobites and the origin of arthropods. – Science **186**: 13–18.

CISNE, J.S. 1975. The anatomy of *Triarthrus* and the relationships of the Trilobita. – Fossils and Strata **4**: 45–64.

CLAUS, C. 1865. Über die Organisation der Cypridinen. – Zeitschrift für Wissenschaftliche Zoologie **15**: 143–154.

CLAUS, C. 1885. Neue Beiträge zur Morphologie der Crustaceen. Arbeiten aus dem Zoologischen Instituten der Universität Wien und der Zoologischen Station in Trieste **6**: 1–108.

COHEN, A.C., J.W. MARTIN & L.S. KORNICKER 1998. Homology of Holocene ostracode biramous appendages with those of other crustaceans: the protopod, epipod, exopod and endopod. – Lethaia **31**: 251–265.

CONTE, F.P., S.R. HOOTMAN & P.J. HARRIS 1972. Neck organ of *Artemia salina* nauplii. A larval salt gland. – Journal of Comparative Physiology **80**: 239–246.

COTTON, T.J. & S.J. BRADDY 2004. The phylogeny of arachnomorph arthropods and the origin of Chelicerata. – Transactions of the Royal Society of Edinburgh, Earth Sciences **94**: 169–193.

CROGHAN, P.C. 1958. The mechanism of osmotic regulation in *Artemia salina* (L.): the physiology of the branchiae. – Journal of Experimental Biology **35**: 234–242.

CUTLER, B. 1980. Arthropod cuticle features and arthropod monophyly. – Cellular and Molecular Life Science **36**: 953–972.

DAMEN, W., T. SARIDAKI & M. AVEROF 2002. Diverse adaptations of an ancestral gill: a common evolutionary origin for wings, breathing organs, and spinnerets. – Current Biology **12**: 1711–1716.

DUNLOP, J.A. 1998. The origin of the tetrapulmonate book lungs and their significance for chelicerate phylogeny. Pp. 9–16 *in*: P.A. SELDEN (ed.), Proceedings of the 17th European Colloquium of Arachnology, Edinburgh.

DUNLOP, J.A. & S.J. BRADDY 2001. Scorpions and their sister-group relationships. Pp. 1–24 *in*: V. FET & P.A. SELDEN (eds.), Scorpions 2001. In Memoriam Gary A. Polis. – British Arachnological Society, Burnham Beeches, Bucks.

ELIAS-NETO, M., M.P.M. SOARES & M.M.G. BITONDI 2009. Changes in integument structure during the imaginal molt of the honey bee. – Apidologie **40**(1): 29–39.

EWING, R.D., G.L. PETERSON & F.P. CONTE 1974. Larval salt gland of *Artemia salina* nauplii. Effects of inhibitors on survival at various salinities. – Journal of Comparative Physiology **80**: 247–254.

FORTEY, R.A. & J.N. THERON 1994. A new Ordovician arthropod, *Soomaspis*, and the agnostid problem. – Palaeontology **37**: 841–861.

FREIRE, C.A., H. ONKEN & J.C. MCNAMARA 2008. A structure-function analysis of ion transport in crustacean gills and excretory organs. – Comparative Biochemistry and Physiology, Part A: Molecular & Integrative Physiology **151**(3): 272–304.

GIBBS, A.G., F. FUKUZATO & L.M. MATZKIN 2003. Evolution of water conservation mechanisms in *Drosophila*. – Journal of Experimental Biology **206**(7): 1183–1192.

HANSEN, H.J. 1925. On the comparative morphology of the appendages in the Arthropoda. A. Crustacea. Pp. 1–176 *in*: H.J. HANSEN (ed.), Studies on Arthropoda II. – Gyldendalske Boghandel, Kopenhagen.

HARTMANN, G. 1966–1975. Ostracoda. Pp. 1–786 *in*: H.G. BRONN (ed.), Dr. H.G. Bronns Klassen und Ordnungen des Tierreichs, 5. Band, I. Abteilung, 1.–4. Lieferung. – Akademische Verlagsgesellschaft Geest & Portig KG, Leipzig.

HASENFUSS, I. 2002. A possible evolutionary pathway to insect flight starting from lepismatid organization. – Journal of Zoological Systematics and Evolutionary Research **40**: 65–81.

HASENFUSS, I. 2008. The evolutionary pathway to insect flight – a tentative reconstruction. – Arthropod Systematics & Phylogeny **66**(1): 19–35.

HAUG, J.T., A. MAAS & D. WALOSZEK in press. Ontogeny of two Cambrian stem crustaceans, †*Goticaris longispinosa* and †*Cambropachycope clarksoni*. – Palaeontographica.

HEBEL, D.K., M.B. JONES, R.M. MOATE & M.H. DEPLEDGE 1999. Differing sensitivities of respiratory and osmoregulatory gill tissue of *Carcinus maenas* (Crustacea: Decapoda) to water-borne copper. – Marine Biology **133**: 675–681.

HESSLER, R.R. 1964. The Cephalocarida. Comparative skeletomusculature. – Memoirs of the Connecticut Academy of Arts & Sciences **16**: 1–97.

HESSLER, R.R. 1992. Reflections on the phylogenetic position of the Cephalocarida. – Acta Zoologica **73**(5): 315–316.

HOLLIDAY, C.W., D.B. ROYE & R.D. ROER 1990. Salinity-induced changes in branchial Na+/K+-ATPase activity and transepithelial potential difference in the brine shrimp *Artemia salina*. – Journal of Experimental Biology **151**: 279–296.

HORNE, D.J., A. COHEN & K. MARTENS 2002. Taxonomy, Morphology and Biology of Quaternary and Living Ostracoda. Pp. 5–36 *in*: J.A. HOLMES & A.R. CHIVAS (eds.), The Ostracoda: Applications in Quaternary Research; Geophysical Monograph 131. – American Geophysical Union.

HOU, X.-G. & J. BERGSTRÖM 1995. Cambrian lobopodians – ancestors of extant onychophorans? – Zoological Journal of the Linnean Society **114**: 3–19.

HOU, X.-G. & J. BERGSTRÖM 1997. Arthropods of the Lower Cambrian Chengjiang fauna, southwest China. – Fossils and Strata **45**: 1–116.

HOU, X.-G. & J. BERGSTRÖM 2006. Dinocaridids: anomalous arthropods or arthropod-like worms? Pp. 139–158 *in*: J. RONG, Z. FANG, Z. ZHOU, R. ZHAN, X. WANG & X. YUAN (eds.), Originations, Radiations and Biodiversity Changes – Evidences from the Chinese Fossil Record. – Science Press, Beijing [in Chinese; extended abstract in English on pp. 847–850].

HOVMÖLLER, R., T. PAPE & M. KÄLLERSJÖ 2002. The Palaeoptera problem: basal pterygote phylogeny inferred from 18S and 28S rDNA sequences. – Cladistics **18**: 313–323.

Huys, R. & G.A. Boxshall 1991. Copepod Evolution. – The Ray Society, London. 468 pp.

Itô, T. 1988. Location of the epipod on the thoracic limbs in *Nebalia bipes* (Crustacea: Leptostraca). – Annual Reports of the Seto Marine Biological Laboratory **2**: 36–39.

Keyser, D. 1990. Morphological changes and function of the inner lamella layer of podocopid Ostracoda. Pp. 401–410 *in*: R. Whatley & C. Maybury (eds.), Ostracoda and Global Events. – British Micropaleontological Society Publications, Chapman and Hall, London.

Kikuchi, S. 1983. The fine structure of the gill epithelium of a fresh-water flea, *Daphnia magna* (Crustacea: Phyllopoda) and changes associated with acclimation to various salinities. – Cell and Tissue Research **229**: 253–268.

Klass, K.-D. & N.P. Kristensen 2001. The ground plan and affinities of hexapods: recent progress and open problems. – Annales de la Société Entomologique de France **37**: 265–581.

Kobusch, W. 1999. The phylogeny of Peracarida (Crustacea, Malacostraca). Morphological investigations of the peracaridan foreguts, their phylogenetic implications, and an analysis of peracaridan characters. Vol. 1+2. – Cuvillier, Göttingen. 277 pp. + 76 figs.

Kraus, O. 1998. Phylogenetic relationships between higher taxa of tracheate arthropods. Pp. 295–303 *in*: R.A. Fortey & R.H. Thomas (eds.), Arthropod Relationships; Systematics Association Special Volume 55. – London, Chapman & Hall.

Kukalová-Peck, J. 1983. Origin of the insect wing and wing articulation from the arthropodan leg. – Canadian Journal of Zoology **61**: 1618–1669.

Lankester, E.R. 1881. *Limulus*, an arachnid. – Quarternary Journal of Microscopical Sciences **21**: 504–548.

Lauterbach, K.-E. 1979. Über die mutmaßliche Herkunft der Epipodite der Crustacea. – Zoologischer Anzeiger **202**(1/2): 33–50.

Lin, H.-T., A.L. Dorfmann & B.A. Trimmer 2009. Soft-cuticle biomechanics: A constitutive model of anisotropy for caterpillar integument. – Journal of Theoretical Biology **256**(3): 447–457.

Liu, J.-N. & X.-P. Dong 2007. *Skara hunanensis* a new species of Skaracarida (Crustacea) from Upper Cambrian (Furongian) of Hunan, South China. – Progress in Natural Science **17**(8): 934 – 942.

Maas, A. & D. Waloszek 2001a. Cambrian derivatives of the early arthropod stem lineage, pentastomids, tardigrades and lobopodians – an "Orsten" perspective. – Zoologischer Anzeiger **240**: 451–459.

Maas, A. & D. Waloszek 2001b. Larval development of *Euphausia superba* Dana, 1852 and a phylogenetic analysis of the Euphausiacea. – Hydrobiologia **448**: 143–169.

Maas, A., D. Waloszek & K.J. Müller 2003. Morphology, ontogeny and phylogeny of the Phosphatocopina (Crustacea) from the Upper Cambrian 'Orsten' of Sweden. – Fossils & Strata **49**: 1–238.

Maas, A., D. Waloszek, J.-Y. Chen, A. Braun, X.-Q. Wang & D.-Y. Huang 2004. Phylogeny and life habits of early arthropods – predation in the Early Cambrian sea. – Progress in Natural Science **14**: 158–166.

Maas, A., G. Mayer, R.M. Kristensen & D. Waloszek 2007. A Cambrian micro-lobopodian and the evolution of arthropod locomotion and reproduction. – Chinese Science Bulletin **53**: 3385–3392.

Manning, P.L. & J.A. Dunlop 1995. The respiratory organs of eurypterids. – Palaeontology **38**(2): 287–298.

Mantel, L.H. & L.L. Farmer 1983. Osmotic and ionic regulation. Pp. 53–161 *in*: L.H. Mantel (ed.), The Biology of Crustacea. Internal Anatomy and Physiological Regulation, vol. 5. – Academic Press, New York.

Mayer, G. & S. Harzsch 2008. Distribution of serotonin in the trunk of *Metaperipatus blainvillei* (Onychophora, Peripatopsidae): implications for the evolution of the nervous system in Arthropoda. – The Journal of Comparative Neurology **507**: 1196–1208.

Mittmann, B. & G. Scholtz 2001. Distal-less expression in embryos of *Limulus polyphemus* (Chelicerata, Xiphosura) and *Lepisma saccharina* (Insecta, Zygentoma) suggests a role in development of mechanoreceptors, chemoreceptors, and the CNS. – Development, Genes and Evolution **211**: 232–243.

Møller, O.S., J. Olesen & J.T. Høeg 2004. Study on the larval development of *Eubranchipus grubii* (Crustacea, Branchiopoda, Anostraca), with notes on the basal phylogeny of the Branchiopoda. – Zoomorphology **123**: 107–123.

Müller, K.J. 1983. Crustacea with preserved soft parts from the Upper Cambrian of Sweden. – Lethaia **16**(2): 93–109.

Müller, K.J. & D. Walossek 1985. Skaracarida, a new order of Crustacea from the Upper Cambrian of Västergötland, Sweden. – Fossils & Strata **17**: 1–65.

Müller, K.J. & D. Walossek 1987. Morphology, ontogeny and life habit of *Agnostus pisiformis* from the Upper Cambrian of Sweden. – Fossils & Strata **19**: 1–124.

Müller, K.J. & D. Walossek 1988. External morphology and larval development of the Upper Cambrian maxillopod *Bredocaris admirabilis*. – Fossils & Strata **23**: 1–70.

Olesen, J. 1999. Larval and post-larval development of the branchiopod clam shrimp *Cyclestheria hislopi* (Baird, 1859) (Crustacea, Branchiopoda, Conchostraca, Spinicaudata). – Acta Zoologica **80**: 163–184.

Olesen, J. 2004. On the ontogeny of the Branchiopoda (Crustacea): contribution of development to phylogeny and classification. Pp. 217–269 *in*: G. Scholtz (ed.), Evolutionary Developmental Biology of Crustacea; Crustacean Issues 15. – CRC Press, Boca Raton.

Olesen, J. 2007. Monophyly and phylogeny of Branchiopoda, with focus on morphology and homologies of branchiopod phyllopodous limbs. – Journal of Crustacean Biology **27**: 165–183.

Olesen, J. & D. Walossek 2000. Limb ontogeny and trunk segmentation in *Nebalia* species (Crustacea, Malacostraca, Leptostraca). – Zoomorphology **120**: 47–64.

Potts, W.T.W. & G. Parry 1964. Osmotic and Ionic Regulation in Animals. – Pergamon Press, Oxford. 423 pp.

Preuss, G. 1957. Die Muskulatur der Gliedmaßen von Phyllopoden und Anostraken. – Mitteilungen aus dem Zoologischen Museum Berlin **33**(1): 221–256.

Richter, S. 2002. The Tetraconata concept: hexapod-crustacean relationships and the phylogeny of Crustacea. – Organisms, Diversity and Evolution **2**: 217–237.

Richter, S. & G. Scholtz 2001. Phylogenetic analysis of the Malacostraca (Crustacea). – Journal of Zoological Systematic and Evolutionary Research **39**: 113–136.

Rieder, N., P. Abaffi, A. Hauf, M. Lindel & H. Weishäupl 1984. Funktionsmorphologische Untersuchungen an den Conchostracen *Leptestheria dahalacensis* und *Limnadia lenticularis* (Crustacea, Phyllopoda, Conchostraca). – Zoologische Beiträge, Neue Folge **28**(3): 417–444.

Sanders, H.L. 1963. The Cephalocarida. Functional morphology, larval development, comparative external anatomy. – Memoirs of the Connecticut Academy of Arts & Sciences **15**: 1–80.

Schminke, H.K. 1980. *Agnathobathynella ecclesi* gen. n., sp. n. aus Malawi und die Formenvielfalt der Familie Bathynellidae (Crustacea, Bathynellacea). – Bijdragen tot de Dierkunde **50**(1): 145–154.

Scholtz, G. & G.D. Edgecombe 2006. The evolution of arthropod heads: reconciling morphological, developmental and palaeontological evidence. – Development, Genes & Evolution **216**: 395–415.

Scholtz, G. & K. Kamenz 2006. The book lungs of Scorpiones and Tetrapulmonata (Chelicerata, Arachnida): Evidence for homology and a single terrestrialisation event of a common arachnid ancestor. – Zoology **109**: 2–13.

Schram, F.R. 1978. Arthropods: a convergent phenomenon. – Fieldiana **39**(4): 1–108.

Siewing, R. 1957. Untersuchungen zur Morphologie der Malacostraca (Crustacea). – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere **75**: 39–176.

Siewing, R. 1960. Neuere Ergebnisse der Verwandtschaftsforschung bei den Crustaceen. – Wissenschaftliche Zeitschrift der Universität Rostock, Mathematisch-Naturwissenschaftliche Reihe **9**(3): 343–358.

Stein, M., D. Waloszek & A. Maas 2005. *Oelandocaris oelandica* and its significance to resolving the stemlineage of Crustacea. Pp. 55–71 *in*: S. Koenemann & R. Vonck (eds.), Crustacea and Arthropod Relationships; Crustacean Issues 16. – CRC Press, Boca Raton.

Stein, M., D. Waloszek, A. Maas, J.T. Haug. & K.J. Müller 2008. *Oelandocaris oelandica* revisited. – Acta Palaeontologica Polonica **53**(3): 462–484.

Størmer, L. 1938. Studies on trilobite morphology. Part I. The thoracic appendages and their phylogenetic significance. – Norsk Geologisk Tidsskrift **19**(2–3): 143–273.

Sun, J.-Y., J. Tong & Y.-H. Ma 2008. Nanomechanical behaviours of cuticle of three kinds of beetle. – Journal of Bionic Engineering **5**: 152–157.

Sutton, M.D., D.E.G. Briggs, D.J. Siveter, D.J. Siveter & P.J. Orr 2002. The arthropod *Offacolus kingi* (Chelicerata) from the Silurian of Herefordshire, England: computer based morphological reconstructions and phylogenetic affinites. – Proceedings of the Royal Society of London B **269**: 1195–1203.

Suzuki, Y. & J. Bergström 2008. Respiration in trilobites: a reevaluation. – GFF **130**: 211–229.

Suzuki, Y., A. Kondo & J. Bergström 2008. Morphological requirements in limulid and decapod gills: a case study in deducing the function of exopod lamellae. – Acta Paleontologica Polonica **53**: 275–283.

Thorpe, W.H. 1933. Tracheal and blood gills in aquatic insect larvae. – Nature **131**: 549–550.

Vincent, J.F.V. & U.G.K. Wegst 2004. Design and mechanical properties of insect cuticle. – Arthropod Structure & Development **33**(3): 187–199.

Walcott, C.D. 1881. The trilobite: New and old evidence relating to its organization. – Bulletin of the Museum of Comparative Zoology **8**: 191–224.

Walossek, D. 1993. The Upper Cambrian *Rehbachiella* and the phylogeny of Branchiopoda and Crustacea. – Fossils & Strata **32**: 1–202.

Walossek, D. 1999. On the Cambrian diversity of Crustacea. Pp. 3–27 *in*: F.R. Schram & J.C. von Vaupel Klein (eds.), Crustaceans and the Biodiversity Crisis. Proceedings of the Fourth International Crustacean Congress, Amsterdam, The Netherlands, July 20–24, 1998, vol. 1. – Brill Academic Publishers, Leiden.

Waloszek, D. 2003a. The 'Orsten' Window – a three-dimensionally preserved Upper Cambrian meiofauna and its contribution to our understanding of the evolution of Arthropoda. – Paleontological Research **7**: 71–88.

Waloszek, D. 2003b. Cambrian 'Orsten'-type preserved arthropods and the phylogeny of Crustacea. Pp. 66–84 *in*: A. Legakis, S. Sfenthourakis, R. Polymeni & M. Thessalou-Legaki (eds.), The New Panorama of Animal Evolution; Proceedings of the 18th International Congress on Zoology Athens 2000. – Pensoft, Sofia.

Waloszek, D., J.-Y. Chen, A. Maas & X.-Q. Wang 2005. Early Cambrian arthropods – new insights into arthropod head and structural evolution. – Arthropod Structure & Development **34**: 189–205.

Waloszek, D., A. Maas, J.-Y. Chen & M. Stein 2007. Evolution of cephalic feeding structures and the phylogeny of Arthropoda. – Palaeogeography, Palaeoclimatology, Palaeoecology **254**: 273–287.

Walossek, D. & K.J. Müller 1990. Upper Cambrian stem-lineage crustaceans and their bearing upon the monophyletic origin of Crustacea and the position of *Agnostus*. – Lethaia **23**: 409–427.

Watson, J.A.L. 1966. The structure and function of the gill tufts in larval Amphipterygidae (Odonata: Zygoptera). – Journal of Morphology **120**: 9–21.

Wirkner, C.S. & S. Richter 2007a. Comparative analysis of the circulatory system in Amphipoda (Malacostraca, Crustacea). – Acta Zoologica **88**: 159–171.

Wirkner, C.S. & S. Richter 2007b. The circulatory system in Mysidacea – implications for the phylogenetic position of Lophogastrida and Mysida (Malacostraca, Crustacea). – Journal of Morphology **268**: 311–328.

Wolvekamp, H.P. & T.H. Waterman 1960. Respiration. Pp. 35–100 *in*: T.H. Waterman (ed.), The Physiology of the Crustacea. I. Metabolism and Growth. – Academic Press, New York.

Zhang, X.-G., D.J. Siveter, D. Waloszek & A. Maas 2007. An epipodite-bearing crown-group crustacean from the Lower Cambrian. – Nature **449**: 595–598.

ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: Arthropod Systematics and Phylogeny

Jahr/Year: 2009

Band/Volume: 67

Autor(en)/Author(s): Maas Andreas, Haug Carolin, Haug Joachim T., Olesen Jorgen, Zhang Xiguang, Waloszek Dieter

Artikel/Article: Early Crustacean Evolution and the Appearance of Epipodites and Gills 255-273