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The 'Orsten' window – a three-dimensionally preserved Upper Cambrian meiofauna and its contribution to our understanding of the evolution of Arthropoda

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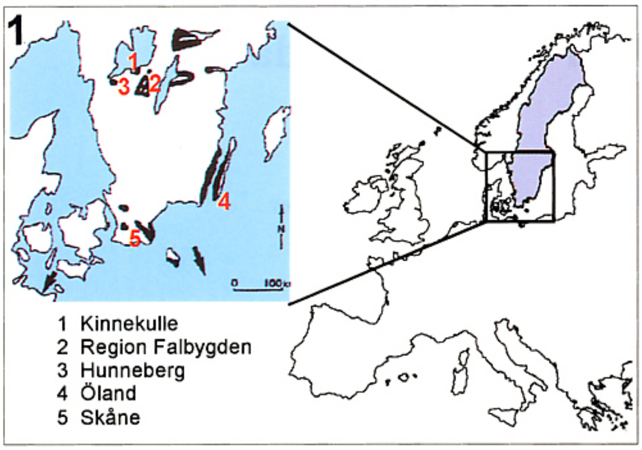
Abstract. 'Orsten'-type preservation, i. e., phosphatisation of cuticles without further diagenetic deformation, has yielded three-dimensional fossils at a scale of 0.1–2.0 mm. Such fossils, first described from Upper Cambrian limestone nodules found in Sweden, have been reported from several continents and from the early Cambrian (approx. 520 M. y. BP) to the early Cretaceous (approx. 100 M. y. BP). Fossils from Cambrian 'Orsten'-type lagerstatten are mainly representatives of different euarthropod groups and also of different evolutionary levels. This allowed the reconstruction of the early phylogeny particularly of Crustacea in great detail and the recovery of major evolutionary traits within this group, i. e., in the progressive modification of the locomotory and feeding apparatus of the head region. More recently, derivatives also of the early stem lineage toward the Euarthropoda have been discovered. These include apparently parasitic larvae of stem-lineage Pentastomida (tongue worms) today living in various tetrapods, a minute fossil related to the equally minute tardigrades (water bears), and fragments of a small tubular organism with segmental tubular limbs, interpreted as the first lobopodian in an 'Orsten'-type preservation. Lobopodians are worm-like derivatives of the earliest phase in the evolution of arthropods before the development of a sclerotic, segmented dorsal cuticle (arthrodized tergum) and similarly segmented limbs (arthropodia), hitherto known only from the Lower to Middle Cambrian. The presence of these "pre-euarthropods," which lack, or partly lack, characteristic features developed later in the arthropod evolutionary lineage, and the recent record of phosphatocopine Crustacea in the earliest Palaeozoic are regarded as a support for the view that the ancestry of Arthropoda lies much further back, possibly well in the late Pre-Cambrian. This does not support a "Cambrian explosion".

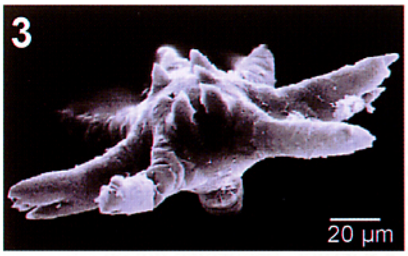
Key words: Arthropoda, Crustacea, evolution, 'Orsten', phosphatisation, phylogeny, stem-lineage Euarthropoda, three-dimensional preservation

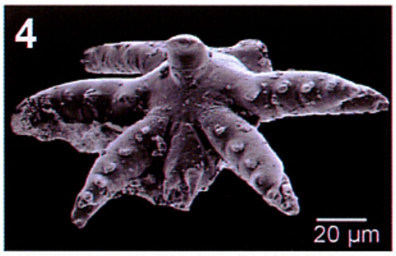
Introduction

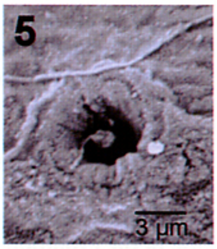
Arthropoda represent not only the most species-rich group of animals on Earth, but they were also among the first animals to be discovered in rocks that date from a few million years later than the transition from the Precambrian to the Cambrian. The discovery of Early to Middle Cambrian soft-bodied faunas, particularly from the Chinese Maotianshan Shales (also known as the Chengjiang fauna; e.g., Chen *et al.*, 1989a, 1991, 1992; Hou *et al.*, 1991) and the slightly younger faunal assemblages of the Burgess-Shale type (more than 40 localities worldwide; e.g., Conway Morris, 1994, 1998; Conway Morris and Whittington, 1979; Whittington, 1985) have made it clear that there were a large number of taxa belonging to different Metazoa groups around in the sea at that time. Among them were also various arthropods, but it turned out that the †Trilobita (in the present paper, the symbol †depicts extinct forms), although widely recorded due to their strongly calcified cuticle, neither formed the major animal group in the Cambrian nor did they represent primitive precursors of the modern arthropods, as is sometimes stated (e.g., Storch *et al.*, 2001).

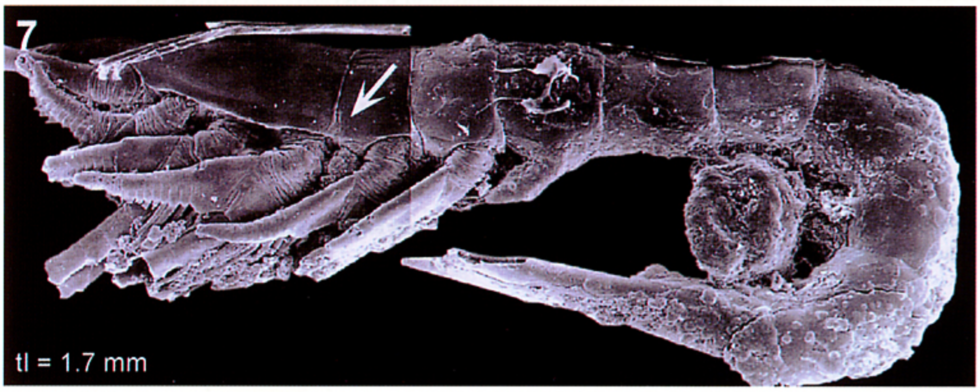
Indeed, other animals from early Cambrian soft-body faunas permit a much better view of the early evolutionary path of the Arthropoda toward their crown group, the Euarthropoda (sensu Walossek, 1999). Examples are the 'lobopodians', "segmented worms with tubular limbs" (e.g., Chen *et al.*, 1989a, b, 1994, 1995; Ramsköld, 1992a, b; Hou and Bergström, 1995, 1997; Ramsköld and Chen, 1998), the arthropod-like †*Fuxianhuia protensa* Hou, 1987, or †*Canadaspis perfecta* (Walcott, 1912). The latter two have apparently more of an arthropod design than these tubular forms, but “still” lack various features, which characterize the Euarthropoda. All these early animals were, until now, only known from flattened fossils. This limited the possibility to reconstruct their morphology and to interpret their evolutionary implications. Much confusion has

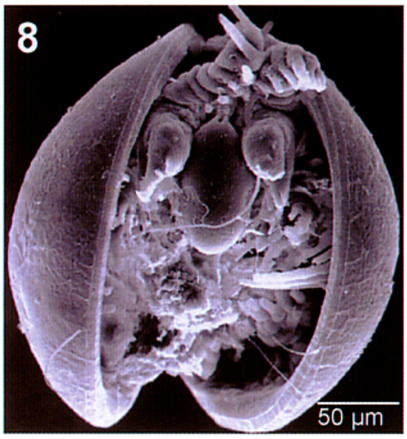


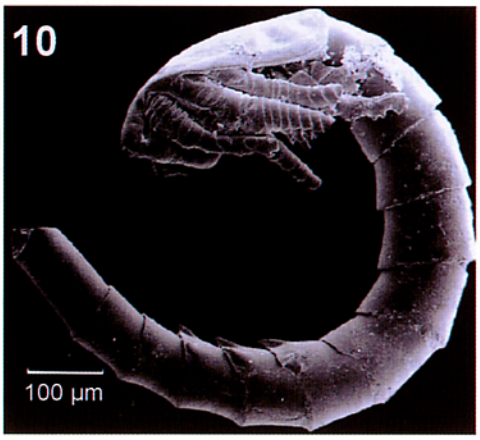












resulted from incomplete or fantasy-loaded reconstructions and descriptions, making some of these forms look rather monstrous and difficult to relate to any larger systematic units, while other forms were misplaced into particular living taxa to which they do not have any relationship. 'Or sten'-type fossils have been studied over the last 25 years and have lead to a more sound and firm understanding of the evolution of the Arthropoda ,The aim of this paper is to promote the 'Orsten' as a key reference system or tool box for solving many of the above stated problems.

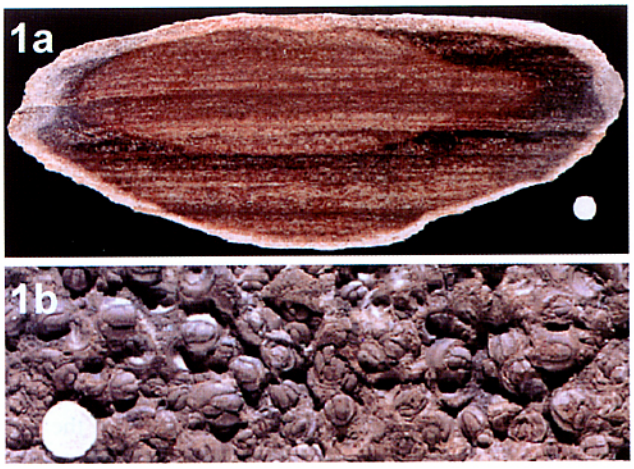
'Orsten' preservation and contribution of 'Orsten' fossils to systematic and evolutionary interpretations

Knowledge of the early evolution of the Arthropoda, particularly the Crustacea, and their morphology, ontogeny and life habits, has increased significantly due to evidence raised by the so-called 'Orsten'-type fossils. These almost 500 million years old fossils were discovered in the mid-seventies in Upper Cambrian limestones in southern Sweden (mainly Västergötland and the Isle of Öland, see Figure 1.1) by Professor Klaus J. Müller from Bonn, Germany (see e.g., Müller, 1979, 1982, 1983). 'Orsten' is now understood as an expression for an exceptional type of preservation and/or type of *Konservat-Lagerstätten* rather than referring to a specific geographical location or time interval. 'Orsten' may also be used as the equivalent of the discoveries of arthropods made in Sweden and therefore as a synonym for the particular animal group preserved. 'Orsten'-type preservation is a secondary phosphatisation (fluoritic apatite) of the outer part of the animal's cuticle, which became impregnated apparently soon after the death of the animal. Later the carcasses became enclosed in a limestone matrix forming nodules (cf. Seilacher, 2001 for a hypothesis for this special type of nodule formation) within shales (Figures 1.2, 2.1a, b). This prevented diagenetic deformation, with the exception of wrinkling or shrinking effects, resulting in three-dimensional, mostly hollow, fossils. These can be etched from their surrounding rock matrix using weak acetic acid. 'Orsten'-type preservation is rather rare and seems to have affected mainly arthropods. Fragments and complete specimens never exceed a size larger than 2 mm, with a minimum of 0.1 mm. This small size makes 'Orsten' fossils particularly suitable for research using scanning electron microscopy (SEM). Many of the fossils represent larval stages, which could sometimes be encountered in sequential sets (examples in Figure 1.3, 1.4, 1.8). Another advantage of 'Orsten'-type preservation over other preservation types is that such fossils retain all their cuticular details, such as minute pores (Figure 1.5), hairs and bristles on the limbs (Figure 1.6) or eyes (Figure 1.9) in their original topology. Thus, they can be investigated almost as though they were living forms (example references for 'Orsten fossils': Müller, 1982, 1983; Müller and Walossek, 1985, 1986a, b, 1987, 1988; Walossek and Müller, 1990, 1994; Walossek, 1993; Walossek *et al.,* 1994; Waloszek and Dunlop, 2002).

The name of these nodules, *orsten,* comes from a local Swedish name, possibly originating from "orne sten" (= pig stone), referring to the early usage of such stones to cure pigs (not, as we formerly thought, to its characteristic smell of rotten eggs when cracked or processed because of their high content of organic matter). 'Orsten' nodules and the surrounding alum shales (Figure 1.2) contain many remains of calcitic (Figure 2.1b) and silicified macro- and microfossils ranging from brachiopods and trilobites (some being minute and very spinose, see Clarkson and Ahlberg, 2002) to sponge spicules, so-called Small Shelly faunal elements (SSF; 'small shelly fossils'), other problematic taxa, and many, most likely primarily phosphatic conodonts (see e.g., Müller and Hinz, 1991). Here we restrict the term 'Orsten' to three-dimensionally preserved secondarily phosphatized, soft-bodied fossils, not including the 'Small Shelly Fossils'.

Three-dimensional phosphatic preservation was first reported by Bate (1972) in ostracode crustaceans associated

← **Figure 1.** 'Orsten' in Southern Sweden and its animals. **1.** Main localities of 'Orsten' in southern Sweden (numbered, arrows point to discoveries outside Sweden). **2.** Quarry near Falbygden, Västergötland, showing exposed alum shales enclosing 'Orsten' nodules (arrowed); shales topped unconformably by Ordovician limestones (from Walossek, 1999). **3–10.** Examples of SEM pictures of 'Orsten' arthropods and morphological details. **3, 4.** 'Type-A' larvae; body length approx. 100 µm. **3.** UB 793, ST 1416 (Müller and Walossek, 1986b, figs. 1 (m–o), 3 (b, e), 4 (f); Walossek and Müller, 1989, fig. 3A; Walossek *et al.*, 1993, fig. 1D). **4.** UB W 122, ST 2860 (Maas and Waloszek, 2001, fig. 2A). **5.** Pore of 1–2 µm in diameter on the shield surface of †*Agnostus pisiformis* (head and tail shields of this species are highly abundant in the rock, see Fig. 2.1b; UB 878, ST 4948; Müller and Walossek, 1987, pl. 32:8). **6.** Fourth head limb, maxillula, of the maxillopod eucrustacean †*Bredocaris admirabilis* Müller, 1983 (body length of presumed adult 0.85 mm; UB 640, ST 1417 (Müller and Walossek, 1988, pl. 4:8)). **7.** Advanced instar stage of stem-lineage crustacean †*Martinssonia elongata* Müller and Walossek, 1986 (length 1.5 mm; UB 104, ST 6702, Walossek and Müller, 1990, fig. 6); arrow points to border behind the fourth limb-bearing head segment (= maxillulary segment); apparently cephalization had not advanced to include the 5th = maxillary segment in this phase of crustacean evolution. **8.** Earliest larva of the bivalve phosphatocopine †*Vestrogothia spinata* Müller, 1964 (shield length 170 µm, UB 632, ST 982 (Müller 1979, fig. 38A, B). **9.** Forehead region of †*Hesslandona unisulcata* Müller, 1982 with eye-bearing hypostome flanked by minute antennulae (UB 659, ST 2206 (Müller, 1982, pl. 2, fig. 2a, b; Maas *et al.*, 2003, pl. 3A)). **10.** lateral view of the eucrustacean †*Skara anulata* Müller, 1983, a species lacking post-maxillipedal thoracopods (slim shape is typical for meiofaunal crustaceans; body length approx. 1.2 mm, from Müller and Walossek, 1985; for systematic relationships within Maxillopoda see Walossek and Müller, 1998; UB W 123, ST 4215, Maas and Waloszek, 2001, fig. 2B).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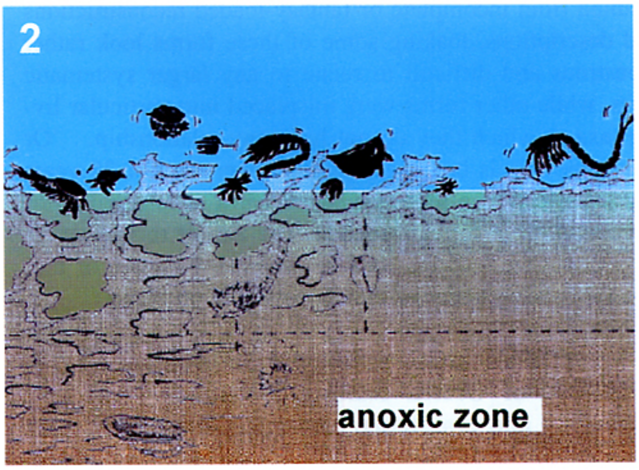
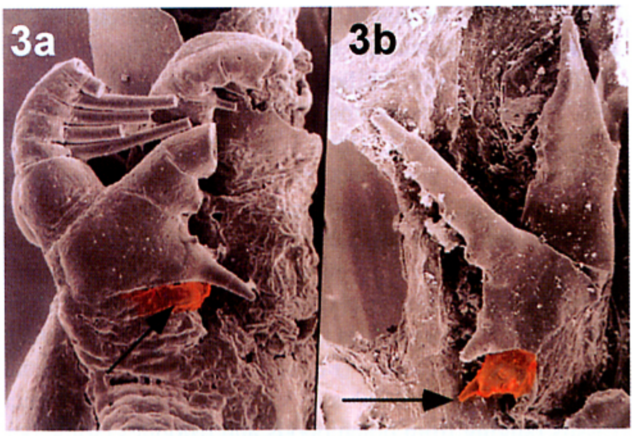

2
anoxic zone


3a
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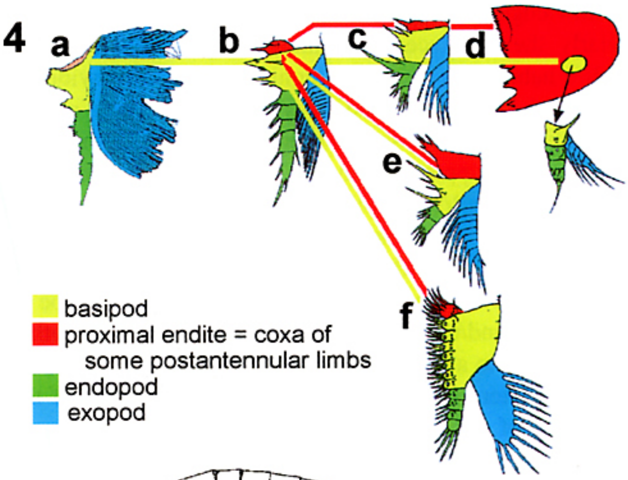
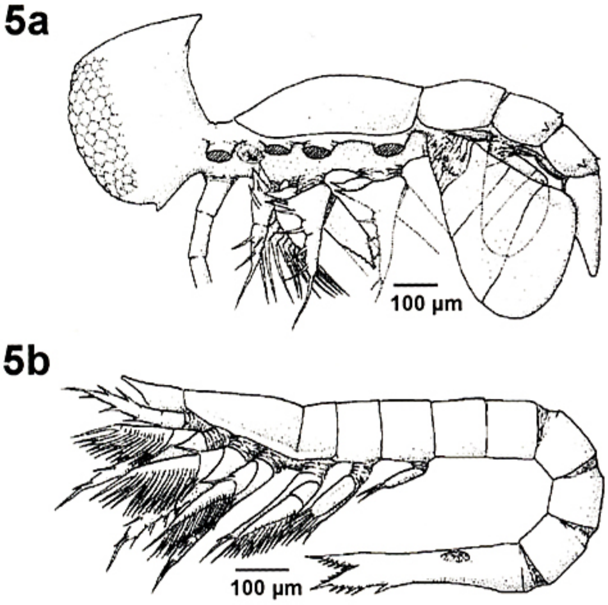
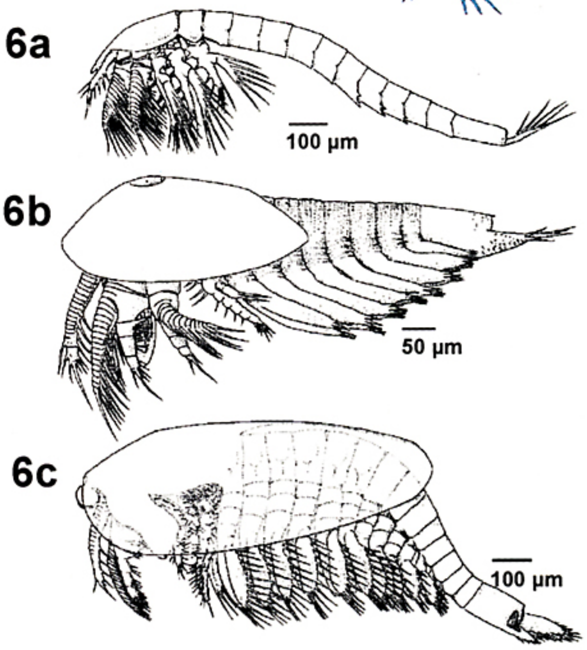

4
a
b
c
d
e
f
basipod
proximal endite = coxa of some postantennular limbs
endopod
exopod


5a
100 µm
5b
100 µm


6a
100 µm
6b
50 µm
6c
100 µm

with fish carcasses from the Lower Cretaceous. In all, the record of secondarily phosphatized fossils, reported by the 'Orsten' research group and by other researchers, now extends worldwide-with records from Sweden, Poland, Russia, Australia, Canada, Great Britain, and Brazil-and ranges in age from the early Cambrian (approximately 515 M. y. BP) to the early Cretaceous (approximately 100 M. y. BP; see overviews in Müller and Walossek, 1991; Walossek, 1999). The recent finds of 3D-preserved phosphatic embryos and eggs extend the age and range of animal groups even more (see, e.g., Zhang and Pratt, 1994; Pratt and Zhang, 1995; Bengtson and Zhao, 1997; Kouchinsky *et al.,* 1999; Zhao and Bengtson, 1999).

Particular features of 'Orsten' animals indicate that much of the assemblages found so far can be interpreted as a small-sized so-called meiofauna, i. e. a fauna of very small animals that lived in a special microenvironment similar to today's flocculent bottom layer in aquatic regimes (Müller and Walossek, 1991). In this substratum, sufficient nutrients permitted a flourishing, small-scale habitat, while the environment was probably oxygen-deficient due to the high degree of degraded organic matter. This might be the reason that such rocks generally contain a considerable amount of bitumen and sulphur. The interpretation of the 'Orsten' fauna as an example of meiofaunal life in the Cambrian sea is significant because this is the first and only fossil record of this type of fauna, with a gap of almost 500 million years to Recent analogues. Today, and presumably also in the past, meiofaunal animals live predominantly on detrital matter which was available *en masse* on the sea floor due to a continuous supply from the water column as in modern oceans (e.g., Rice *et al.,* 1986; Vetter, 1994, 1995). Therefore, many of the meiofaunal components can be viewed as decomposers or detritivores, the all-important first components in the nutrient web. Other meiofaunal forms may also live between sand grains (absent in the 'Orsten' facies) and even in the groundwater. Minute aquatic animals, such as the meiofaunal forms, are also special in being adapted to a regime in which water is highly viscous ("sticky", like life in honey). Thus they cannot necessarily be viewed as solely ancient or solely secondarily miniaturised, but have to be evaluated carefully, representative by representative.

In all, there are two major sources available now that have yielded exceptional preservation of soft-body morphologies: the 'classic' flattened fossils of the Maotianshan Shale faunas discovered in the area near the city of Kunming in southwestern China and those of the Burgess Shale lagerstatten (first discoveries in Canada, but more known subsequently from localities worldwide), and the 3D-preserved ones of the 'Orsten'-type fossil lagerstatten. The principle scientific superiority of material from the latter is in its three-dimensionality, preservation of the finest surface details and in the preservation of various, and even successive, ontogenetic stages. This has not only permitted the reconstruction of the early phylogeny of, for example, the Crustacea, but has also permitted the recognition of morphogenetic changes in developmental sequences, and the major evolutionary strategies and important key features leading to modern crustaceans. These are most apparent in the progressive change of limb design and the modification of the locomotory and feeding system, especially affecting the head region of the particular taxa (e.g., Walossek, 1993; Waloszek, 2003; Walossek and Müller, 1997, 1998).

Evolution of euarthropod and crustacean appendages in light of 'Orsten' fossil evidence

Studies of the 3D 'Orsten' fossils permit the evaluation of traditional and more recent hypotheses of arthropod/euarthropod phylogeny on the basis of real organisms. They also provide a valuable toolbox for: A) the recognition of details in flattened fossils; B) the reconstruction of their morphology and life habits, and C) the discussion of ground patterns of taxa in question.

← **Figure 2.** 'Orsten' and its animals continued. **1** 'Orsten' nodule (**a**) cut to show internal horizontal banding of the rock and (**b**) nodule surface with masses of agnostid shells below (white dot = 5 mm; from Walossek, 1999). **2.** Supposed life zone of meiofaunal 'Orsten' arthropods ("fluff layer"), †*Skara anulata* on the right side is about 1.2 mm long; †*Bredocaris admirabilis* Müller, 1983 on the left was 0.85 mm long only. Fossilisation occurred in the anoxic layer below the life zone (modified from Müller and Walossek, 1991). **3.** SEM image of the 'proximal endite' of (a) the 'Orsten' stem-lineage crustaceans †*Goticaris longispinosa* Walossek and Müller, 1990; UB W 124, ST 3571, and (b) †*Cambropachycope clarksoni* Walossek & Müller, 1990 (UB 96, ST 1839 (Walossek and Müller, 1990, fig. 1A, B-specimen figured but different view). **4.** The 'proximal endite' and the reconstruction of the evolution of arthropod limbs toward the eucrustacean level (modified from Walossek, 1993): **4a.** Naraoiid leg (redrawn from Hou and Bergström, 1997) to exemplify an euarthropod limb. **4b.** Post-antennal limb of the stem-lineage crustacean †*Martinssonia elongata.* **4c, 4e.** Larval mandible (**c**) and 2nd antenna (**e**) of extant Eucrustacea exemplified by the limbs of a barnacle metanauplius (Eucrustacea, Entomostraca, Cirripedia). **4d.** Developed mandible, exemplified by that of a late larva of the Upper Cambrian 'Orsten' branchiopod eucrustacean †*Rehbachiella kinnekullensis* Müller, 1983; coxa large, medially drawn out into flat obliquely oriented gnathic edge; distal part = palp lost in the adult stage of Entomostraca (ground-pattern feature). **4f.** Thoracic limb of entomostracan Eucrustacea, exemplified by that of †*Rehbachiella kinnekullensis,* having retained the 'proximal endite' (plesiomorphic), but having enlarged the basipod (apomorphic) bearing several setiferous endites medially. **5, 6.** Reconstructions of selected 'Orsten' crustaceans, some representing forms of the early crustacean evolutionary lineage and others being already members of particular groups within Eucrustacea. **5a.** †*Cambropachycope clarksoni.* **5b.** †*Martinssonia elongata.* **6a.** †*Skara anulata.* **6b.** †*Bredocaris admirabilis.* **6c.** †*Rehbachiella kinnekullensis* (from Walossek and Müller, 1998).

Broader comparison including all 'Orsten' and other fossil and Recent arthropods suggests, for example, that post-antennal limbs of crown-group Arthropoda, Euarthropoda were basically composed of a single sclerotized, antero-posteriorly flattened limb stem portion - and neither two nor three. This basic portion, the basipod carries only two rami. The 7-segmented endopod arises from the medio-dorsal edge of the basipod and the leaf-shaped exopod rests on the sloping outer edge of the basipod (in this sense: Figure 2.4a).

Recognition of this design has been founded on the pioneering work on limb design of Burgess-Shale (e.g., Cisne, 1975; Whittington, 1980) and Maotianshan-Shale arthropods (e.g., Hou and Bergström, 1997), and many early fossil euarthropods, such as trilobites, naraoiids and less well-known taxa have been shown to have had such limbs (examples in Hou and Bergström, 1997).

Euarthropoda is recognized here as a monophylum, embracing at least the fossil † Trilobita and all major living arthropod groups, such as the Chelicerata, the Crustacea, and the Atelocerata/Tracheata ("myriapods" and hexapods). Ground-pattern characters (not exclusively autapomorphies) are: A) a cephalon with one pair of antennae plus three pairs of biramous limbs (not four as often claimed; presumed autapomorphy); B) antennulae attachted to a hypostome with the mouth at its rear (plesiomorphy); C) a head covered by a uniform shield (no matter what size, plesiomorphy); D) a well-segmented, limb-bearing post-cephalic trunk with dorsal tergites and ventral sternites (plesiomorphy), and E) post-antennular limbs all comprising a basipod and two rami (see also Figure 5, state discussed below, possibly plesiomorphic to the crown group).

Sometimes a pre-antennal segment and an acron have been mentioned as the anteriormost part of the (eu)arthropod original head, but this has not been clarified yet. The acron seems to be an assumption coupled with the hypothesis of annelid relationships of Arthropoda. This assumption is now subject to serious debate in the light of a new hypothesis, the Ecdysozoa hypothesis, which suggests nemathelminth relationships of the Arthropoda - and with this convergent evolution of segmentation etc. (see, e.g., Aguinaldo *et al.,* 1997; Schmidt-Rhaesa *et al.,* 1998; Valentine and Collins, 2000). In the light of some fossils from the Lower Chengjiang faunas having an extra tergite in front of their shield and bearing the eyes, such as †*Fuxianhuia protensa* Hou, 1987 (see Hou and Bergström, 1997), it becomes more and more evident that a pre-antennal ocular segment did indeed exist. Also the design of euarthropod post-antennular limbs, basipod and two rami, might have been achieved earlier in its stem lineage, as does the character 'head composition'. In fact, in evolutionary terms, the endopod (inner ramus) has to be regarded as the retained distal portion of a formerly uniformly multiarticulated limb. Such a design, having "just" a long rod made of short articles connected by pivot joints really exists in the limb of the Lower Cambrian Chengjiang fossil †*Fuxianhuia protensa*, on this and other reasons being regarded as an early stem-lineage representative of Euarthropoda (Walossek, 1999, see also Hou and Bergström, 1997). We hypothesize that the basipod eventually emerged as a product of fusion of several, possibly 6-7, of the proximal articles of such an early multi-annulated limb (Waloszek, 2003). Consequently, †*Fuxianhuia* could not have possessed a basipod and also no body-limb joint, because such a structure is closely allied to the formation of a rigid basal limb portion. The same limb design characterizes another Chengjiang form, †*Chengjiangocaris longiformis* Hou and Bergström, 1991, and a third form will be described in the near future (Chen *et al.,* in preparation).

The outer ramus, exopod, of †*Fuxianhuia* and †*Chengjiangocaris* was a simple flap lacking marginal setation. Marginal exopodal setation, as known from, e.g., trilobites and naraoiids (flat lamellae) and other euarthropods-like crustaceans (round setae), seems to have developed later in the stem lineage toward the crown group, possibly in line with a positioning of the exopod on the sloping outer edge of the basipod (e.g., Walossek, 1993, fig. 54; Walossek and Müller, 1997). According to Hou and Bergström (1997, fig. 89) the exopod flap of the Lower to Middle Cambrian †*Canadaspis*, another form having a multisegmented limb rod rather than a basipod plus endopod, had only ridges on its surface but without marginal setae or lamellae. Since the 14-segmented limbs of †*Canadaspis* are subdivided into a proximal set of articles with a median tuft of setae and a distal set of seven simpler articles, this form provides an interesting intermediate design between the much lobopodium-like, multi-annulated limb of †*Fuxianhuia* and †*Chengjiangocaris* and that of Euarthropoda having a basipod continuing into the endopod medio-distally (†*Canadaspis* was originally assigned by Briggs, 1978 to the phyllocarid Malacostraca, but it clearly lacks all characters of this crustacean group; see, e.g., Walossek, 1993 and Hou and Bergström, 1997, for a new reconstruction). Free movability of the exopod flap via internal muscles may even have occurred later within the crown group, possibly even convergently in the various euarthropod lineages. Clearly, there was never an equality of the two original rami in morphological as well as in evolutionary terms of appearance and development.

Problems in the understanding of the morphology and evolution of arthropod/euarthropod limbs arose mainly from two traditional directions of views. One is that all sclerotic limb stems or all proximal-most limb portions were equally named 'coxa', regardless of their origin and homology, also affecting the terminology of the rami (see below). The studies of the 'Orsten' fossils suggest how-ever that these proximal portions are not necessarily homologous between the euarthropod taxa and along the series of limbs (see e.g., Walossek and Müller, 1990, 1997), or their homology has not yet been clearly demonstrated. The second problem is caused by wrong assumptions of either an original two-division or three-division of the limb stem of Euarthropoda.

While fossil euarthropod taxa like trilobites and naraoiids and extant Chelicerata have clearly only a single limb stem, subdivisions may indeed occur on several but not all limbs of the series in various extant eucrustaceans. This requires a closer, more differentiated view on these features. The, in our view, wrong idea that the stem of all post-antennular limbs in the ground pattern of Euarthropoda consisted of three portions-"precoxa" "coxa" and "basis" rather than only one seems to originate from more than one misinterpretation: A) One is the misidentification of the body-limb joint membrane as a separate stem segment, termed "pre-coxa" (e.g., Hansen, 1925), because this membrane may be quite prominent in several crustaceans, typically in the locomotory limbs (second antennae; thoracopods) of certain entomostracans. An example is the parasitic fish lice, Branchiura, in which the basal joint membrane may be quite large and of annulated appearance (personal observations). B) Another is Størmer's (1939) misinterpretation of the slightly extended outer part of the limb base of trilobites carrying the exopod as a separate limb portion, also called "pre-coxa". This led him to further misidentify the exopod as a "pre-coxal exite", "pre-epipod". Since the proximal-most portion was uniformly named "coxa" in those days, both distal rami, endopod and exopod, were consequently misidentified by Størmer as arising from the coxa and not from the basipod, hence being not homologous to the crustacean condition, in which the basipod carries the rami. Therefore, Størmer used the terms "telopodite" and "pre-epipod" respectively for the rami instead to stress this "difference". Since an epipod was thought to have a gill function (crustacean epipods may serve as a gill but are also osmoregulatory organs), all trilobites (and other early arthropods) were, as a further circular reasoning, considered as having gill-bearing limbs subsequently.

It was Cisne (1975) who demonstrated clearly that the trilobite limb stem was undivided and bore the two rami. Subsequent workers on Cambrian euarthropods confirmed this observation (e.g., Whittington, 1980 for †*Olenoides serratus*; Müller and Walossek, 1987 for †*Agnostus pisiformis*). D) Lastly Kaestner (1967, fig. 661) mislabelled in his textbook on arthropods the coxa-basipod joint membrane of a copepod as the coxa, thus, mislabelling the coxal gnathobase as the "pre-coxa" (the distal portion, basipod, carrying the rami remained correctly labelled). Regrettably, these basal misunderstandings continued to be carried deep into modern analyses of arthropod limb segmentation, instead of making reference to the clear fossil evidence.

In an attempt to standardize terminology, Walossek and Müller (1990) proposed the use of the term "***basipod***" for the single basal structure of a euarthropod limb carrying the two rami endopod and exopod (basis = "carrier of the rami" instead of coxa). This was mainly because if one retains the term 'coxa', it was exactly this traditional procedure that led to the above described confusion, which resulted in a presumed nonhomology of limb rami and limb portions respectively.

To avoid this, the term basipod was proposed because it can act as a valuable reference structure. Not only can the insertion of the rami be easily recognized in 'Orsten' fossils even when the limbs are broken, but also on flattened fossils such as Chengjiang and Burgess Shale arthropods. In this view, Euarthropoda never had coxae originally on their post-antennal limbs, and coxae are not a feature in the ground pattern of this taxon or can be used to validate its monophyly. Again, the single basal structure of the trilobite, naraoiid and chelicerate limb is the basipod, representing the plesiomorphic state by likely retention of this design from earlier levels (e.g., Walossek and Müller, 1998a, fig. 12.9 for a xiphosuran opisthosomal limb).

We propose to restrict the use of the term coxa only for particular structures developed in the stem lineage of Crustacea-not replacing but co-occurring with the phylogenetically older basipod. In fact, in a set of 'Orsten' fossils (Figure 1.7 showing †*Martinssonia elongata*, reconstruction in Figure 2.5b; see also Figures 2.3a, b, 2.4b and 3 for †Phosphatocopina; phylogram in Figure 5.1) we observed a small setiferous and most likely separately movable cuticular protrusion, the '***proximal endite***', at the inner proximal edge of the basipod (carrying the two rami and in shape matching exactly the design mentioned above), so "swimming" within the ample basal joint membrane. Development of this 'proximal endite' was probably not a simple event but affected also other modifications, such as a split-off of limb-stem based musculature to operate the proximal endite for individual food manipulation toward the mouth. We consider the appearance of this proximal endite as a key feature of Crustacea and a significant autapomorphy to validate its monophyly (not the features mentioned in current textbooks, which refer to features developed later and only in particular in-groups). Subsequently this proximal endite underwent, like many other features, considerable modifications, although several modern eucrustacean groups retained much of its original design in at least their set of post-cephalic limbs (Figures 1.6, 2.4f, 2.6b, c).

The basipod can serve, therefore, as a significant reference for the homologisation of the rami, while the proximal

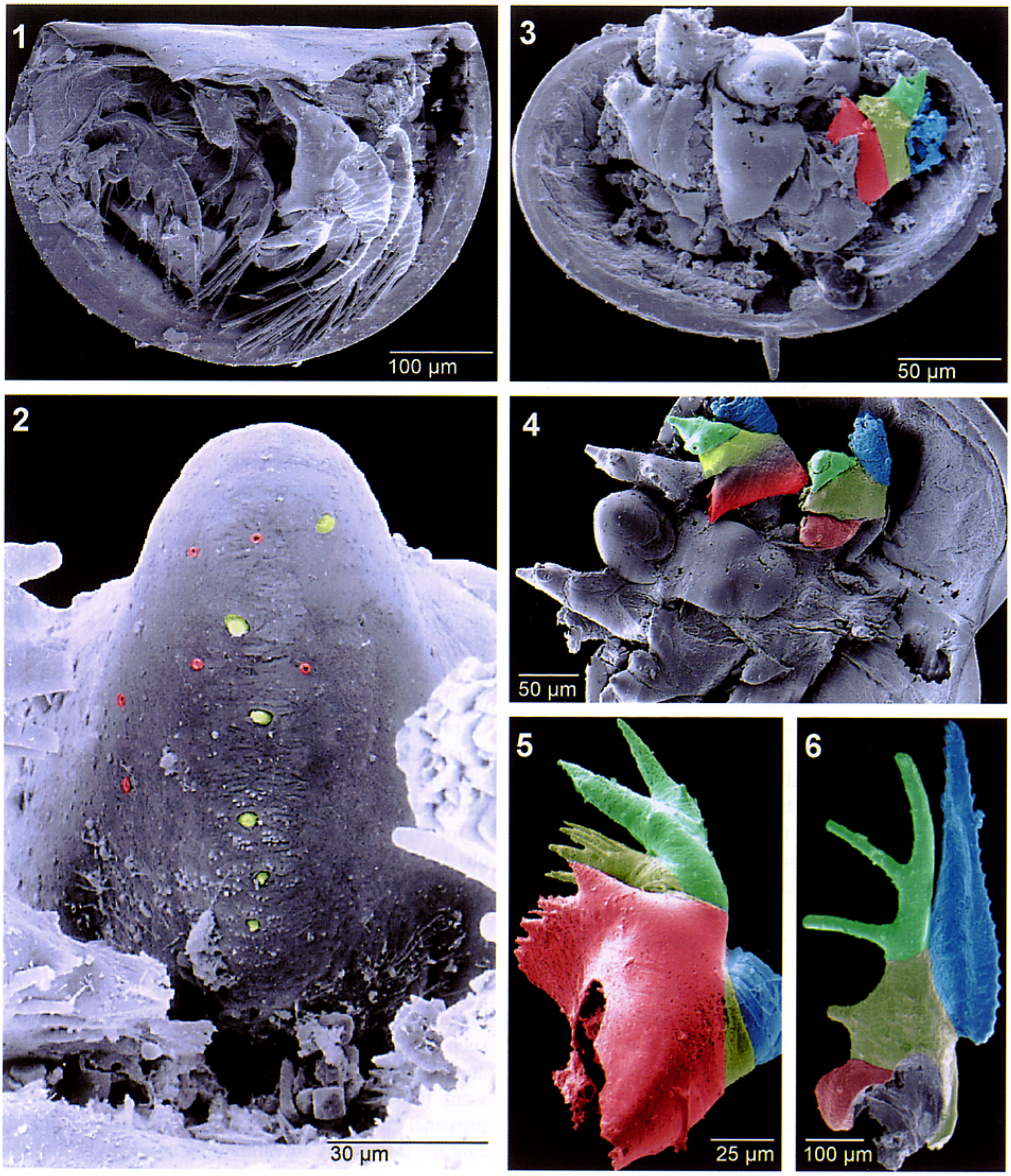


Figure 3. SEM images of †Phosphatocopina, sister group to Eucrustacea. **1**. Overview of complete specimen with right shield half opened to view the limbs (UB 658, ST 2197 (Müller, 1982, fig. 1a–d). **2**. Young larva (with four developed limbs) having coxa and basipod of the mandible separated (UB W 249, ST 1407 (Maas *et al*., 2003, pl. 45A, B). **3**. Labrum with slime pores and possible chemoreceptors (UB W 146, ST 2898; Maas and Waloszek, 2003, fig. 7; Maas *et al*., 2003, pl. 3G). **4**. Slightly later stage than (2) with coxa and basipod partially fused (UB W 140, ST 2627: †*Hesslandona suecica* Maas, Waloszek and Müller, 2003; Maas *et al*., 2003, fig. 59B). **5**. Large isolated mandible, which has a huge gnathobasic stem portion representing the product of fusion of the coxa and basipod; distal part of the basipod still present but squeezed between the endopod and syncoxa (UB W 139, ST 9176; Maas *et al*., 2003, fig. 59C). **6**. Isolated post-mandibular limb of †*Hesslandona unisulcata* Müller, 1982, showing the proximal endite and the prominent basipod. Endopod three-segmented, each podomere being drawn out, exopod paddle-shaped (UB W 125, ST 9219; for details and species assignments see Maas *et al*., 2003).

endite served to characterize particular 'Orsten' taxa as crustaceans. Lack or presence of particular features known from crown-group members, Eucrustacea, again, led to identify some of the 'Orsten' forms as derivatives of the early stem-lineage toward the Eucrustacea, while others could be identified on the possession of characteristic features as members already of certain in-group eucrustaceans (see below).

The exceptional preservation also of larval stages and comparative studies of Recent eucrustaceans, permitted following up the fate of the proximal endite during morphogenesis. In particular, study of the ontogeny of the 'Orsten' branchiopod eucrustacean †*Rehbachiella kinnekullensis* demonstrated that the proximal sclerotic portion of the two anterior post-antennal limbs, the 2nd antennae and mandibles, originates from the proximal endite and enlarges, by progressive sclerotization to finally form a ring surrounding the limb stem (Walossek, 1993). In its final stage of development it forms a separate limb stem portion proximal to the basipod (Walossek, 1999; Figure 2.4c–e). Recently it could also be shown that at least in living" copepods the mandibular coxa starts indeed "still" at a stage when it is only a small lobe medio-proximally below the basipod, growing out progressively into the characteristic coxa with its medially elongated grinding edge (gnathite) (Mayer, 2002 unpublished diploma thesis). This structure is understood here as the true '**coxa**', as such appearing clearly later within the evolutionary lineage of Crustacea, namely in the †Phosphatocopina and in the Eucrustacea, and only on two limbs at first. These coxal structures clearly developed from the proximal endite. Remarkably, all posterior limbs of †Phosphatocopina are of the plesiomorphic design having a large basipod with the proximal endite and the two rami (see below).

Careful examination of limb structures reveals indeed that other "*coxae*" or structures termed as such may not be homologous to the proximal endite, but rather originate from different structures: A) A better sclerotization of the original basal joint membrane of limbs may result in a "coxa-like appearance" of the membrane area, as it occurs in the four thoracopods of certain Branchiura (personal observations, NHM London 2003). Yet this can be easily differentiated from a true coxa. B) In several eucrustacean taxa the limb stem of more posterior limbs is clearly subdivided into two portions. While entomostracan eucrustaceans had basically no more coxal elements on postmandibular limbs, Malacostraca have coxal structures on both so-called maxillae and on the first eight thoracopods (not on the pleopods; e.g., Walossek, 1999, Waloszek, 2003). The homology of these coxal portions with the proximal endite has still to be demonstrated (cf. Boxshall pers. communication 2003). C) Within entomostracans, particular taxa also developed subdivided limb stems, but at least for the predatory notostracans among the branchiopod Eucrustacea it is clear that this is a secondary subdivision of the basipod, which became bent inward for prey capture and food manipulation (see Walossek, 1993). For copepods, ostracodes and other forms subdivision of the basipod appears likely, caused by functional needs (locomotion), but ontogeny studies and the reconstruction of the evolutionary path have still to clarify the origin of the two portions either from a single stem or from other structures.

Yet, it remains certain that all eucrustaceans have below their basipod either a proximal endite or a coxa, but never the two structures together because of their structural connection. The occurrence of proximal endites at the inner proximal edge of the basipod in a eucrustacean group is, therefore, regarded as its plesiomorphic retention from the ground pattern of the Crustacea. In either case, our hypothesis, which is based on 'Orsten' forms as well as other fossils and on extant material, clarifies or outlines several points: A) *Coxae* are not serially homologous in Eucrustacea because they developed in particular limbs at different evolutionary levels and not in one set. B) Stem-lineage representatives of Eucrustacea did not yet have coxae on any limbs, only proximal endites, hence Crustacea had no coxae in their ground pattern. C) Coxa and basipod are not structural homologues because coxae may develop from one median setae-bearing endite below the basipod, while the basipod originated from 6–7 articles of the basically multiarticulated limbs in the stem lineage toward the Euarthropoda. This is why the original structure cannot retain the name coxa or be alternatively named 'protopod'. The conflict is thus caused by the nonhomology.

In summary, from the design obtained from euarthropod ancestors - a uniform limb basis/basipod carrying two rami (Figure 2.4a) –, each limb or group of limbs developed along its own evolutionary pathway, not even necessarily in groups of similar limbs. Therefore, one has to carefully study each limb separately and must not oversimplify or over-generalise limb design. Proposals of generalizing "ur-legs" for a taxon in question (such as Schram and Koenemann, 2001) are little helpful approaches. In fact, early in the evolution of the Crustacea there were simply no coxae-and no mandibles in the strict sense respectively. Crustacea evolved coxal portions proximal to the basipod only on certain appendages and later in their evolutionary lineage and *not* on all post-antennal limbs. The common occurrence of so-called coxal structures on the legs of insects, chilopods and progoneates ("myriapods") seems to contrast with the situation outlined here for the crustaceans and requires a sound explanation by advocates particularly of a malacostracan-insect relationship - possibly these were as much basipods, as could be identified for chelicerates and fossil euarthropods.

Using 'Orsten' evidence to unravel phylogeny of Crustacea

Crustacea seem to have played a major role in the late Cambrian bottom-living meiofaunal assemblages. Special 'Orsten' forms, the most abundant components in the material, †Phosphatocopina, even look strikingly similar to a group of small bivalve extant crustaceans, the Ostracoda. Initially affiliated with this crustacean group, the †Phosphatocopina were collected as more than 50,000 individuals, while from other 'Orsten' forms only a few or even only single fragments have been discovered, a number of them still to be described. On closer inspection, based especially on details of limb morphology, larval development and other details of the ventral morphology, recognisable due to this exceptional soft-part preservation, †Phosphatoc opina and several other crustacean-like forms could be distinguished as representatives of different evolutionary levels in the stem lineage to the modern Crustacea, the crown group, Eucrustacea (cf. Walossek and Müller, 1990; Walossek, 1999). Some apparently lack characters known from crown-group members, while others possess crown-group features and even specific features of particular in-group taxa (examples in Figure 2.5, 2.6; two example SEMs in Figure 1.7, 1.10; overviews in Walossek and Müller, 1997, 1998; Walossek, 1999; Waloszek, 2003). Our recently completed work on the †Phosphatocopina Müller, 1964 (first papers on their soft parts were by Müller, 1979, 1982) has helped us to recognize that †Phosphatocopina (Figures 1.8, 1.9, and 3; see Maas and Waloszek, in press; Maas *et al.,* 2003) and Eucrustacea (Figure 5.1) are clearly set off from the taxa of the early crustacean lineage. †Phosphatocopina and Eucrustacea share, synapomorphically, a characteristic, complex feeding system in the head portion of the body, which is not present in any of the derivatives of the crustacean stem lineage or other arthropods. This set of shared features = autapomorphies of the stem species of Labrophora (cf. Siveter *et al.*, 2003) - includes: A) a labrum as a large, bulged, soft organ in front and above the mouth opening enclosing slime glands and with chemoreceptors at its posterior side (Figures 1.9, 1.10 3.2–3.4); B) a sternum as the product of the fusion of formerly separate post-oral sternites (ventral body plates; Figure 3.2, 3.4); C) paragnath humps on the mandibular sternal portion (Figure 2.4); D) fine hairs on the labrum, sternum and setae on all limbs associated with the feeding process around the mouth; E) the development of the proximal endite of the antenna (antenna 2) and mandible into a rigid coxa (and only on these 2 limbs).

All these new features demonstrate a remarkable change in the locomotory, and particularly the feeding system in the evolution of Crustacea (see Walossek, 1999, fig. 8). This major morphological difference from the level in the earlier stem lineage to the labrophoran level has to be taken into account when discussing a possible origin of Insecta or Atelocerata / Tracheata from Crustacea or any in-group taxon, or better from a level "before" or "after" this change, which is usually neglected. Again, filtration holds neither as an ancestral mode of feeding for Crustacea, nor for Arthropoda - there are simply no structures developed for this very special mode of nutrient intake (e.g., Waloszek, 2003). With the discovery of this big change and the formulation of the sister-group relationship of †Phosphatocopina and Eucrustacea, it also becomes clear that the eucrustacean nauplius larva with its three pairs of limbs of a design as described above is a larval type which could have developed only after the development of these special feeding and locomotory structures in the common ancestor of Labrophora and not before (Walossek and Müller, 1990, 1997; Walossek, 1999; Waloszek, 2003). Therefore, the nauplius ('short-head larva' after Walossek and Müller, 1990) must be regarded as an advanced larva and not as the "most primitive" type of an arthropod larva. Indeed, the Upper Cambrian "stem lineage derivatives" from the 'Orsten' assemblages and also the †Phosphatocopina retained the phylogenetically older larval type, which embraces the complete head segmentation of the euarthropod ground pattern, i.e., having four pairs of functional limbs and thus representing a "head larva" (sensu Walossek and Müller, 1990, 1997; see also Siveter *et al.,* 2001 for the earliest record of such a larva). Thus, †Phosphatocopina retained: A) the phylogenetically older larva (Figures 1.8, 3.2) and B) the unspecialised post-mandibular set of limbs (Figure 3.6). On the other hand, †Phosphatocopina have various diagnostic characters (autapomorphies), such as large anterior eyes (Figure 1.9), a reduced antennula, and a bivalved shield from the earliest larva onward. Additionally, they developed a strange fusion of the antennal and mandibular coxa and basipod in the mandible during ontogeny and evolution (Figures 3.2, 4, 5). Monophyly of the Eucrustacea is based on their modification of the fourth head limb, the maxillula (= first maxilla), into a feeding device (mouthpart) and the development of the nauplius as a shortened larva relative to its precursor (relationship hypothesis in Figure 5.1; for autapomorphies of Entomostraca and Malacostraca see e.g., Walossek, 1999; Waloszek, 2003).

Inside Eucrustacea, two major evolutionary paths occurred leading to large-scale differences in locomotory and feeding habits of the groups involved. Malacostraca, having coxae and basipods on both maxillae and on their first eight thoracopods, both portions shortened in favour of the elongation of the plesiomorphically 5-segmented endopod to a slim structure. Subsequently, food manipulation was progressively shifted to the "mouthparts only". Entomostraca, on the other hand, retained the proximal endite on all post-mandibular limbs but enlarged the basipod instead, which acquired several setae-bearing endites medially, with internal muscles leading to them (Hessler, 1964 for Cephalocarida; see Walossek, 1999; Waloszek, 2003; Figure 2.4f). Here food manipulation was mainly a matter of the postmandibular limbs, the maxillae and thoracopods.

New 'Orsten' fossils add to knowledge of early evolutionary lineage of Arthropoda toward Euarthropoda

One of the great discoveries of the Burgess Shale and Chengjiang were worm-shaped, tubular forms with similarly tubular limbs, the so-called lobopodians (see, e.g., Whittington, 1978; Chen *et al.,* 1989a, b, 1994, 1995; Ramsköld, 1992a, b; Hou and Bergström, 1995). Lobopodians resemble extant so-called velvet worms, Onychophora lacking the firmly sclerotized cuticle of "true" arthropods with their distinctively subdivided skeleton and equally subdivided limbs. Relationships between lobopodians and extant Onychophora have long been assumed (e.g., Hou and Bergström, 1995) and found further support by more recent studies (e.g., Ramsköld and Chen, 1998), also with regards to the positioning of Onychophora in the stem lineage of Arthropoda (e.g., Ballard *et al.,* 1992; Schmidt-Rhaesa *et al.,* 1998; Eriksson and Budd, 2001). This group of organisms is even more interesting because it also contributes to the ongoing debate about the long-held view of an arthropod-annelid relationship (Articulata hypothesis) versus a nemathelminth-arthropod relationship (Ecdysozoa hypothesis). It is beyond the scope of this paper to review this interesting aspect, but again it becomes apparent that early fossils can play a major role in the investigation of systematic relationships and tests of hypotheses by real organisms.

The continuous investigations of the 'Orsten' material initially focused on crustaceans and crustacean-like forms, but also yielded forms of the early evolutionary lineage of the Arthropoda. Among these are exceptionally well preserved larval stages of Upper Cambrian stem-lineage representatives of the parasitic tongue worms or Pentastomida (Walossek and Müller, 1994; Walossek *et al.,* 1994) and a Middle Cambrian representative of the minute water bears, Tardigrada (Müller *et al.,* 1995). To this we can add a tiny Upper Cambrian representative of the lobopodians (Maas and Waloszek, 2001). These taxa are considered to have branched off before the evolutionary level of well-sclerotized forms, such as †*Fuxianhuia*, †*Chengjiangocaris*, †*Canadaspis*, and euarthropods because they all lack, such as a dorsal subdivision of the tergum into tergites, a cephalon covered by a dorsal shield or the biramous limbs, or only partially possess features developed in the latter taxa (Figure 5.2).

The relationships between Tardigrada, Onychophora and Pentastomida, sometimes referred to as "prot-arthropods" (e.g., Pflugfelder, 1980), are still difficult to assess. Adult Pentastomida are parasites that live exclusively in the respiratory tract including the mouth region and noses of land-living, mostly carnivorous amniote tetrapods, ranging from turtles, snakes and lizards to crocodiles, birds and mammals. Pentastomida feed on blood, mucus or lymph fluid. The larvae of Pentastomida hatch from the eggs, pass through the gut of their host and migrate through their host's body to live in different organs and finally, depending on their life cycles, in the lung system of their definitive host. The body of the larvae usually comprises a thicker anterior part with the small mouth fronto-ventrally and two pairs of hook-like limbs and a thinner tail piece carrying little papillae or hooks caudally (examples in Figure 4.1a, b). Upper Cambrian 'Orsten'-type fossils from Sweden and similar ones from Newfoundland (Walossek and Müller, 1994; Walossek *et al.*, 1994) – there are no others between the Cambrian and Recent – range from young stages of a size between 210 and 730 µm (Figure 4.2) to slightly longer and apparently older stages, found by Andres (1989) on the Isle of Öland, Sweden, possibly in slightly younger sediments. All fossil larvae also have a thicker anterior body and a thinner posterior part, like the extant early pentastomid larvae. Some have a mouth fronto-ventrally, as in the extant pentastomid larvae, and all have two pairs of large, claw-like limbs. As in the Recent *Reighardia sternae* (Diesing, 1864), one form has a pair of outgrowths fronto-lateral to the mouth, and the fine caudal papillae are also present in both Recent and fossil larvae (Figure 4.2). Other detailed similarities between fossil and extant larvae concern the limb design: Both have special pores on the proximal two of the three segments on both pairs of limbs. These pores were first discovered in the fossils and subsequently also in extant forms. In contrast to extant pentastomid larva, the fossils (but not all forms) may possess up to two pairs of rudimentary limbs on the tail part. This and a few more differences led to the interpretation of the fossil larvae as ontogenetic stages of derivatives of the stem lineage to the crown group of Pentastomida, the Eupentastomida, which includes all extant taxa.

Tetrapoda may not have existed in the Cambrian, but the various derivatives of its ancestral lineage were already abundant. This can be derived not only from the diverse conodonts, now known to be early craniate chordates, but also from exceptional finds of soft-bodied forms from the important Maotianshan-Shale / Chengjiang and Burgess-Shale faunas (example: †*Haikouella lanceolata* Chen, Huang and Li, 1999; see Chen *et al.*, 1999). Therefore the morphology of a pentastomid might not just reflect reduction of the body morphology according to parasitism, but just depicts ancestral design with regard to euarthropod

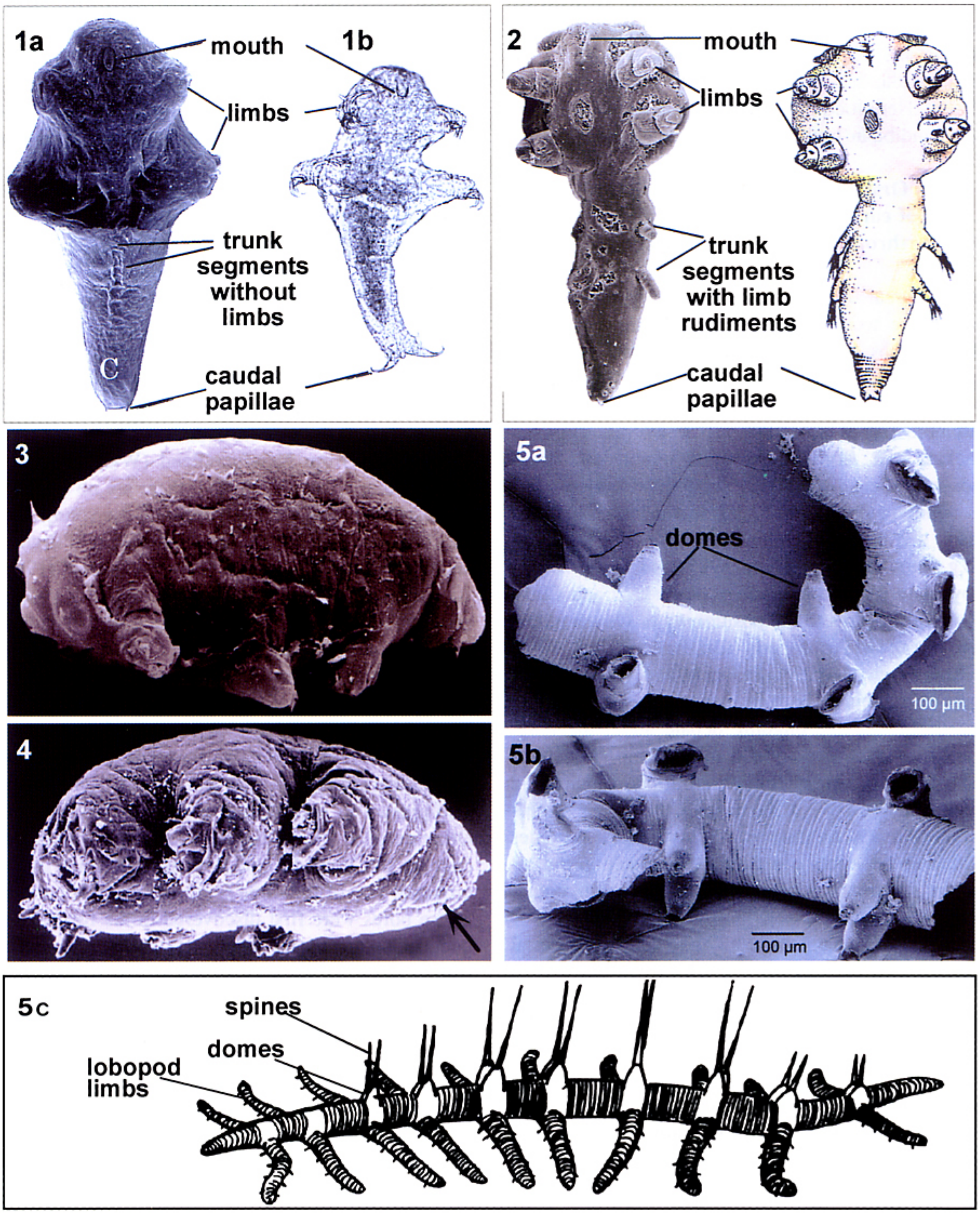


Figure 4. Selection of SEM images of 'Orsten' stem-lineage representatives of Euarthropoda and living counterparts. **1**. Recent pentastomid larvae for comparison; **a**) larva of *Reighardia sternae* and **b**) *Sebekia* sp.; from Walossek and Müller, 1994). **2**. Upper Cambrian 'Orsten' pentastomid larva *Boeckelericambria pelturae* Walossek and Müller, 1994; length approx. 450 µm (UB W 116; Walossek & Müller 1994, fig. 13a–h; picture fits to 13b). **3**. *Tetrakentron synaptae* Cuénot, 1892, a marine ectoparasitic arthrotardigrade (kindly provided by R. M. Kristensen, Copenhagen). **4**. Middle Cambrian 'Orsten' tardigrade, still unnamed; possibly not adult (arrow points to possibly developing fourth limb); body length approx. 350 µm (MU 1573, ST 9890 (Müller *et al*., 1995, fig. 2A, B different views; Maas and Waloszek, 2001, fig. 8C–E, D). **5**. Yet unnamed Upper Cambrian 'Orsten' lobopodian with tubular legs and associated dome-like outgrows dorsally, which bore a possibly large spine distally (diameter of body approx. 150–200 µm; UB W 126, ST 4157; Maas and Waloszek, 2001, fig. 12, but different view); **5a**. lateral view of largest fragment, **5b**. almost dorsal view; **5c**. first preliminary reconstruction.

characters, and also adaptation for parasitism already in the Upper Cambrian. In fact parasitism must not necessarily be accompanied by a reduction of features, and indeed extant Pentastomida still have a well-developed arthropod-type cuticle with no adaptations to the internalised mode of life in a host-lungs and the mouth or nose cavities are, in any case, in a way external.

The lack of arthrodisation of the body of the Pentastomida, the segmental state of their head, their nervous system and the oligomeric segmental state achieved already at hatching is in striking contrast to the euarthropod level of organisation. This renders close relationships with the ectoparasitic Branchiura, an in-group taxon of maxillopodan Crustacea, as it has been suggested by Wingstrand (1972) on the basis of a striking similarity in sperm morphology and by Abele *et al.* (1989) on the basis of 18s rDNA data, very unlikely (Walossek and Müller, 1994, 1998; Walossek *et al.*, 1994). It would also require numerous character reversals and/or convergences along the evolutionary lineage of crustaceans. We rather consider the Pentastomida as possibly the most recent offshoot in the euarthropod stem lineage due to their possession of articulated limbs with pivoted joints (Maas and Waloszek, 2001). Pentastomid limbs would, accordingly, be intermediate between a tubular lobopodian limb of lobopodians and Onychophora, possibly also the tardigrade limb, and the multi-segmented limbs of, e.g., †*Fuxianhuia* and †*Chengjiangocaris*.

The Tardigrada seem to comprise an even earlier branch on the arthropod lineage than the Pentastomida. They do not have the well-articulated and pivot-jointed limbs of the latter group, while it remains problematical whether Tardigrada "already" possess an arthrodized cuticle, i.e., a segmental or metameric thickening and thinning of the cuticle. The earliest ever discovered representative of the Tardigrada, found in the Middle Cambrian rocks of the Siberian platform (Figure 4.4; Müller *et al.*, 1995) shows only little arthrodisation. Some Recent forms may have a plated surface, but this may be a convergent cuticular development to provide some stability. The four specimens of the Cambrian fossil are between 250 and 350 μm long. With a barrel-like shape, they look much like living tardigrades, particularly when compared with marine ectoparasitic species (example: Figure 4.3). Besides size and general shape there are several detailed similarities between the fossil and living tardigrades, such as in the design of the cuticle with a peculiar substructure, called pillars, or the fronto-ventral mouth surrounded by fine vela and sensorial structures that correspond to the clavae and cirri of living forms. The sister-group relationship of the Cambrian fossil form to the crown group of Tardigrada including all living forms is apparent from its segmentation starting with only three pairs of limbs and thus demonstrating plesiomorphic anameric ontogeny, while in their groundpattern state extant tardigrades hatch with the final number of four limbs. Anlagen of the fourth pair of limbs may be developed in one of the four fossil specimens to hand (arrowed in Figure 4.4).

Like the Tardigrada, the Onychophora also have claws on the distal ends of their limbs. A possible, but uncertain, view is that the paired claws are a synapomorphy of both groups. Their classificatory grouping into a taxon † Lobopodia had been proposed long before the discovery of the Chengjiang taxa and was not based on a clear phylogenetic character analysis (Snodgrass, 1938). The taxa have a varying number of claws, not only in pairs. It remains difficult to judge if this set of taxa represents a monophyletic unit that branched off early in the stem lineage toward the Euarthropoda or if it is simply a grade (a paraphyletic assemblage of taxa with shared plesiomorphies). This progressively enlarging group of exclusively Lower to Middle Cambrian mostly centimetre-long fossils includes famous Burgess Shale fossils such as †*Aysheaia pedunculata* Walcott, 1911 (redescribed in detail by Whittington, 1978) and †*Hallucigenia sparsa* Conway-Morris, 1977, Chengjiang biota forms like †*Microdictyon sinicum* (Chen, Hou and Lu, 1989) and a species from German drift boulders, †*Xenusion auerswaldae* Pompeckij, 1927. Head and tail ends remain poorly understood and various reinterpretations change them around. Some authors have even added eyes, antennae-like structures or "barbles" that may also occur on the body and the limbs. The body between the insertion points of the limbs is variably finely annulated, as are the limbs and lobopodia, which insert ventrally. Other characteristic feature of several lobopodians are paired sclerotic plates above the limb insertions (Hou and Bergström, 1995) and dorsal spines of different lengths dorsal to a limb pair and arising from sockets.

Remarkably, at one tenth of the size of the Lower to Middle Cambrian lobopodians, the fossil material from the Upper Cambrian 'Orsten' has also yielded a few fragments of similar worm-shaped forms (Figure 4.5, 4.6), introduced by Maas and Waloszek (2001) as the first lobopodian of that period, the first in an 'Orsten'-type of preservation and the youngest record of its kind. The 'Orsten' lobopodian shares with the Lower to Middle Cambrian lobopodians not only the annulated segmental limbs but also the segmental paired dorsal outgrowths on the finely annulated tubular body, which has a diameter of about 100 to 120 μm. The specimens provide significant new data for this group owing to their fine preservation of cuticular details, even though they are incomplete. At least the Upper Cambrian representative shows a reticulated, possibly cellular surface microstructure that resembles the onychophoran cuticular condition rather than that of later evolutionary levels (Waloszek, unpublished). It is, as expressed by Budd

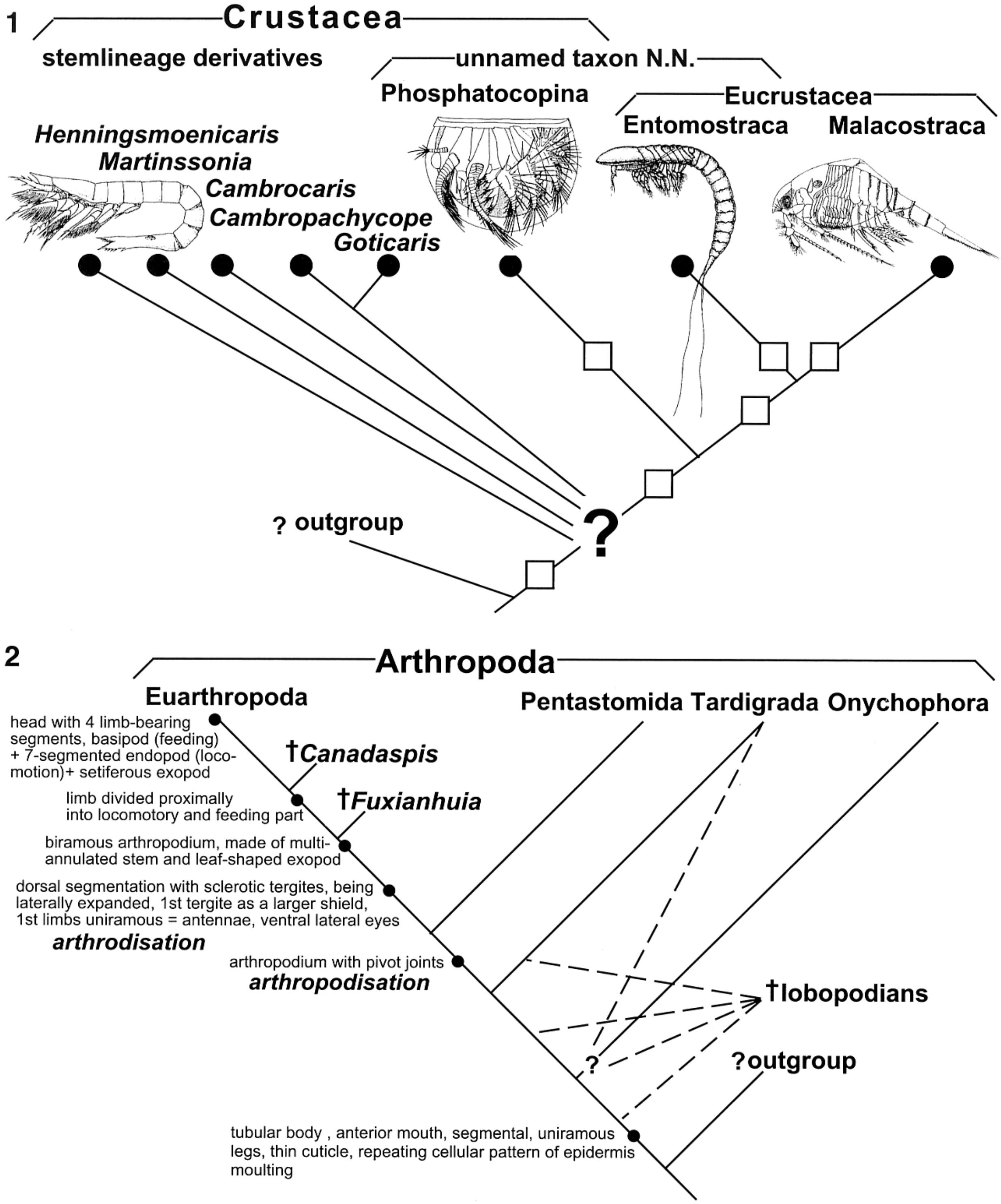


Figure 5. Phylogenetic hypotheses. **1**. Proposed relationships within Crustacea (modified from Walossek, 1999). Question mark indicates unresolved situation in the stem lineage of Labrophora (for sets of autapomorphies see Walossek, 1999; Waloszek, 2003; for features of †Phosphatocopina see Maas *et al.*, 2003). All stem-lineage taxa herein coexisted in the Upper Cambrian 'Orsten' with members of eucrustacean taxa; phosphatocopine record extends now down to the Lower Cambrian (Siveter *et al.*, 2001, 2003). **2**. Reconstruction of the early phylogeny of Arthropoda, with several groups branching off from the stem lineage leading to the monophylum Euarthropoda; major evolutionary innovations added; position of 'lobopodes' uncertain, as well as the relationship between tardigrades and onychophorans; outgroup uncertain (see text) (modified from Maas and Waloszek, 2001, characters discussed there).

(1996, 1997) more likely that lobopodians are a grade and not a taxon, and some of the forms with a frontal mouth and no associated sensorial frontal appendages may represent the earliest derivatives of the evolutionary lineage of the Arthropoda, while others may be stem-lineage onychophoran, and some may also be related to tardigrades - but nonetheless all having branched off prior to the Pentastomida.

All three described "proto-arthropod" taxa lack, or partly lack, characteristic features known from forms belonging to the later evolutionary lineage of the Arthropoda. A further gap exists also between forms like †*Fuxianhuia* or †*Canadaspis* and those taxa that can be assigned to the Euarthropoda (*sensu* Walossek, 1999), as is evidenced particularly in the formation of a head comprising an antennal segment plus three more segments with biramous limbs. None of the limbs of the mentioned taxa have an undivided limb stem, basipod, nor a distinctive endopod, and only the clearly arthrodized forms have paddle-shaped exopods. Therefore, *arthrodisation*, the segmentally repeated sclerotisations of the cuticle along the body proper, eventually leading to tagmotic events, and *arthropodization* repeated sclerotisations of the cuticle of limbs into arthropodia with pivot joints, subsequently developed into a stem and rami, are important but independent processes in the evolution of the Arthropoda (preliminary hypothesis of arthropod phylogeny in Figure 5.2, based on Maas and Waloszek, 2001).

Conclusions

The record of exceptionally preserved Cambrian fossils is still fragmentary and limited to a few lagerstatten having yielded assemblages of so-called Small Shelly Faunas, of the Chengjiang and Burgess Shale, and of the 'Orsten' type. We predict that hunting for fossils of these types, especially for fossils in the 'Orsten' type of three-dimensional preservation, holds the most promise for improving our still incomplete knowledge of the early phylogeny of Arthropoda and Crustacea, and the phylogeny of Metazoa in general. Not unexpectedly, the still poorly recognized "Orsten data base" presented here has led to interpretations that contrast traditional views considerably. Yet, our interpretations are based on animals, which are not hypothetical or paper models, but which had lived successfully in the Cambrian. They were real entities that can be documented by SEM. 'Orsten'-type fossils add to our understanding of the early evolution of particularly the arthropods because: A) They provide us with more detailed structural information from fossils than any other preservation type was ever able to do. B) They permit biological interpretations of life habits and the biology of these forms at a higher degree of confidence than fossil material in any other preservation. C) 'Orsten' yields preservation of ontogenetic stages, sometimes even in sets. This provides exciting and important additional information for phylogenetic interpretations. The access of character formation and morphogenetic changes during growth is extremely informative for the understanding of the evolution of structures and complex systems. Thus – more than any hypothetical or molecular-based concepts can ever do – fossils like the 'Orsten'-type ones can demonstrate how life evolved in the early marine realm.

'Orsten'-type preservation, first discovered in Upper Cambrian limestone nodules from Sweden has subsequently been found also at localities from older and younger strata. And it is no longer restricted "just to Crustacea". The discovery of muscles (Andres, 1989) indicates the possibility of preserving even internal details and demonstrates that we have only reached the edge of the potential of this extraordinary data source. It is apparent that more discoveries and effort will yield exciting further information to complete our picture of the early Palaeozoic world. It seems that Crustacea, abundant in the Upper Cambrian, played a lesser role in pre-Upper Cambrian faunal assemblages. Yet there is a confirmed early Cambrian record of Crustacea based on a recently described, 3D-preserved larval phosphatocopine from England (Siveter *et al.*, 2001, in press). This implies, according to the methodological approach of Phylogenetic Systematics (cf. Hennig, 1950; Ax, 1995) that also its sister taxon Eucrustacea existed in the Early Cambrian. Crustacea must, therefore, have evolved earlier than this, and it is proposed that the stem species of Crustacea existed between the late Precambrian and the earliest Cambrian. So, in line with the Lower Cambrian record of "pre"-euarthropods, all prior branchings of animal groups further down the arthropod and metazoan ancestral lineages should have occurred earlier, making speculations about a so-called 'Cambrian explosion' completely unnecessary (see also Walossek, 1999; Siveter *et al.*, 2001). Likewise their soft-body design also renders an "biomineralisation event" as a larger-scale trigger in the evolution of Metazoa equally unlikely.

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