

Phosphatocopina – ostracode-like sister group of Eucrustacea

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Abstract

The Phosphatocopina were long considered as the oldest, Cambrian, record of ostracode Crustacea. However, our detailed analysis of more than 2,500 specimens from the Upper Cambrian ‘Orsten’ of Sweden reveals that Phosphatocopina are neither Ostracoda nor Eucrustacea. The antenna and mandible of the phosphatocopines investigated consist of a prominent limb stem which carries a two-segmented endopod and multi-annulated exopod. This stem portion is now recognised as the fusion product of the coxa and basipod during ontogeny. Phosphatocopina share features, such as the coxa and basipod on antennae and mandibles, as well as ventral body structures such as the prominent pre-oral labrum and a single post-oral cephalic plate, the sternum (with paragnaths on the mandibular sternal portion), exclusively with the Eucrustacea. As a plesiomorphy, the ontogeny of Phosphatocopina starts with a ‘head larva’ with four pairs of limbs, a larva type found in the ground pattern of the Euarthropoda as well as the Crustacea. In contrast, eucrustacean ontogeny begins with a nauplius with three pairs of limbs, a ‘short-head larva’ or orthonauplius. Again, the post-mandibular limbs of phosphatocopines retain the plesiomorphic limb design of a basipod with a setiferous ‘proximal endite’, whereas Eucrustacea, including the Ostracoda, have their first post-mandibular limb differentiated into a ‘mouthpart’, the maxillula. Autapomorphies of Phosphatocopina include the small antennula with few terminal setae, a bivalved shield with interdorsum, and the fused coxa and basipod on antenna and mandible. We therefore consider the Phosphatocopina to be the sister group of the Eucrustacea. The respective phosphatocopine species of the Upper Cambrian of southern Sweden are restricted to a particular time zone and may be useful as stratigraphic markers.

Introduction

The taxon Phosphatocopina was established in 1964 by Klaus Müller, Bonn, on the basis of paired lateral shield valves from approximately 490 million-year-old Upper Cambrian ‘Orsten’ of Sweden. In the light of the ostracode-like shield Müller (1964) assigned the new taxon to the exclusively Cambrian Bradoriida. Bradoriida were traditionally considered to be the earliest representatives of Ostracoda and as a consequence Crustacea. More than 10 years later, Klaus Müller recovered from the same sites the exceptional finds of phosphatised bodies including appendages of various minute arthropods (e.g., Müller, 1979). The new

material, with soft parts three-dimensionally preserved, added significant new information relating to the early evolution of Crustacea (e.g., Müller, 1983; reviews in: Walossek, 1999, 2001; Walossek & Müller, 1998). Phosphatocopines were also amongst the material and they turned out to be the most abundant and species-rich component of the so-called ‘Orsten’ fauna. We have now at least 50,000 specimens from different species including various ontogenetic stages, plus isolated limbs and other body parts. Aside from one species with preserved soft parts described (Müller, 1982), detailed investigations of the body morphology of the Phosphatocopina ceased in 1979. Other finds of Phosphatocopina from all over the world, e.g.,

in Poland (Bednarczyk, 1979), England (Hinz, 1987; Siveter et al., 2001), Australia (Jones & McKenzie, 1980; Hinz-Schallreuter, 1993) and China (e.g. Huo & Shu, 1985; Tong, 1987; Zhao, 1989) confirm the scientific importance of this small group of crustaceans. This investigation carried out co-operatively with Klaus Müller, presents significant new information on the morphology, ontogeny and systematics of Phosphatocopina, some major aspects of which are presented here, and was funded as part of a German Science Foundation project. A detailed description of the morphology and ontogeny of all Upper Cambrian phosphatocopines from the 'Orsten' of Sweden plus a comprehensive phylogeny discussion has been done by Maas et al. (2003).

Principal questions regarding the Phosphatocopina are:

- Are Phosphatocopina monophyletic?
- What are their autapomorphies?
- What is the systematic position of Phosphatocopina?
- Are Phosphatocopina stratigraphically useful?

Terminology

To describe the morphology of phosphatocopines, we applied general crustacean terminology (Walossek, 1993; see Table 1 for a list of abbreviations used in the illustrations). The first appendage is called antennula, the second antenna and the third mandible. Since the post-mandibular appendages are serially similar, the term 'maxillula' for the first post-mandibular limb is misleading, so we used the neutral terms first post-mandibular limb, second post-mandibular limb and so on. We avoid the term protopod because it is related to a limb stem that consists of a coxa and a basipod. Instead, we use the neutral term 'limb stem' and refer to that part of the limb that is located proximal to the rami. We do not apply the term 'carapace' for the cephalothoracic shield of Phosphatocopina, as is still done in the literature (e.g. Hinz-Schallreuter, 1998; Williams & Siveter, 1998; Siveter et al., 2001) and frequently done for the shields of various other crustacean and even arthropod groups. Walossek (1993) suggested restricting the term

Table 1. Abbreviations used in the figures

Abbreviation	Structure
ant	Antenna
am	Arthrodistal membrane
asp	Anterior cardinal spine
atl	Antennula
avsp	Anteroventral spine
bas	Basis
cox	Coxa
dbl	Doublet
en	Endopod
ex	Exopod
hyp	Hypostome
id	Interdorsum
il	Inner lamella
lbr	Labrum
lst	Limb stem
lva	Left valve
md	Mandible
me	Median eye
pmX	Postantennular limb X
pe	Proximal endite
pgn	Paragnath
psp	Posterior cardinal spine
rva	Right valve
sh	Shield
ste	Sternum
stp	Sternitic plate

'carapace' to the situation in Crustacea when thoracomeres I–VII are included in the shield. This is the case in Euphausiacea and Decapoda, where the first seven thoracomeres (not eight as often claimed in the literature, e.g. Newman & Knight, 1984; Gruner, 1993) are incorporated into the shield (cf. Maas & Waloszek, 2001). We agree with Walossek (1993) in using the term carapace only for this special condition. All other crustacean shields can be recognised as either simple head shields retained from the ground pattern of Eucrustacea, including segments of antennula and three post-antennular limbs, or cephalothoracic shields with a different number of thoracomeres integrated. The term hypostome is used in the sense of general arthropod terminology (see, e.g., Müller & Walossek, 1987). Confusingly, some ostracode workers call the post-oral sternal

surface, the ‘lower lip’, the ‘hypostome’. In crustacean terminology the term sternum is used for this structure.

Monophyly of Phosphatocopina

Phosphatocopina, more precisely all those taxa, for which we have soft parts, cover a wide range of different forms. Yet apart from the possession of a bivalved shield which superficially resembles that of ostracode crustaceans, all species share a number of features that occur only in this group.

Examples of characters occurring in the two traditional sub-units Hesslandonidae Müller, 1964 (including *Hesslandona* Müller, 1964, *Trapezilites* Hinz-Schallreuter, 1993, *Cyclotron* Rushton, 1969, and *Waldoria* Gründel, 1981) and Vestrogothiidae (Kozur, 1974) (including *Vestrogothia* Müller, 1964 and *Falites* Müller, 1964) and which support the monophyly of the Phosphatocopina are described in the following.

Antennulae

The antennulae (= ‘first antennae’) are located laterally on a large, case-like structure of trapezoid abaxial cross-section, the hypostome, which also houses median eyes located anteriorly (Fig. 1). The antennulae are very small compared to the entire body and consist of a few more or less irregular annuli and three terminal plus one or two subterminal setae. In fact, the antennulae are so small that they were overlooked in the earliest papers of Müller (1979) and the subsequent appendages were mislabelled accordingly. This resulted in confusion and misunderstanding with respect to concepts of crustacean evolution, since the first antennula is traditionally thought to be a uniramous appendage and the erroneously identified biramous antennula – actually the antenna – became integrated into the ground pattern of Crustacea. The bi- or triramous flagellate antennulae, present in various Crustacea (e.g., Malacostraca) are in fact secondary features and

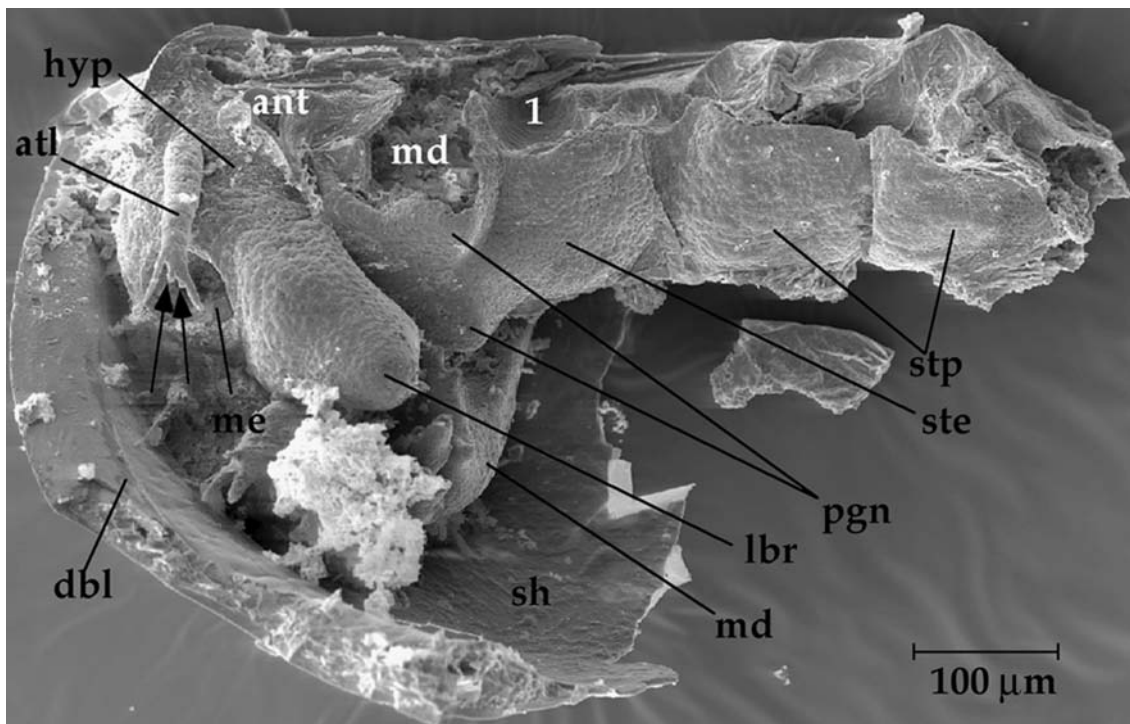


Figure 1. *Hesslandona unisulcata* Müller, 1982 (UB W 119). Left lateral view. Large part of shield missing, post-antennular limbs only indicated by their insertion areas (ant, md, 1), hind body not preserved. Arrows point to two antennular setae, broken basally.

as a consequence cannot characterise the ground pattern of either Crustacea or Eucrustacea.

Outgroups of Phosphatocopina, such as Eucrustacea and all known derivatives of the stem lineage of Eucrustacea (see Fig. 8) have relatively prominent antennulae with numerous segments and various setae well adapted for swimming and food gathering, which are an autapomorphy for Crustacea.

Coxa and basipod of antenna fused

In Upper Cambrian phosphatocopines the antennae ('second antennae') have a single prominent limb stem and two rami. However, the limb stem morphology is misleading. The antennae of a single recently discovered phosphatocopine specimen from the Lower Cambrian of England show a limb stem consisting of separate coxa and basipod (Siveter et al., 2001). In terms of character polarity, it is important to indicate that derivatives of the stem lineage of the Eucrustacea have no coxal portions at all, but merely a small, setae-bearing medial element underneath the basipod on all post-antennular appendages, termed the proximal endite by Walossek & Müller (1990). This discrete proximal endite is considered an autapomorphy of Crustacea (Fig. 8) by, e.g., Walossek (1999). This element is interpreted as the phylogenetically earlier stage of a coxa and is retained in all post-mandibular limbs of phosphatocopines (Fig. 2B) – which therefore have no coxae. The proximal endite of the antenna is never retained in any crustacean species but transformed into a coxa from the earliest stages of ontogeny onward.

In eucrustacean species, the coxa and basipod of the antenna and mandible are basically separate. It has therefore to be considered that the transformation of an antennal proximal endite to a coxa led to a two-segmented limb stem, such that we now consider the fusion of both portions as an autapomorphy in Upper Cambrian Phosphatocopina.

Coxa and basipod of mandible fused

In the youngest stages of only one Upper Cambrian phosphatocopine, *Vestrogothia spinata* Müller, 1964, the mandibular coxa is separated from the

basipod (Fig. 2A), but it becomes partly fused with it later in ontogeny (Fig. 2C). During ontogeny, the basal part of the basipod merges with the distal coxal surface and as a result, the exopod appears to originate from the coxa, and the distal basipodal endite is compressed between the coxal rim and the proximal endopodal podomere. This situation is found in all other Upper Cambrian taxa from the beginning of ontogeny onward (Fig. 2B, C). In addition, the specimen from the Lower Cambrian of England shows – as do the young larvae of *Vestrogothia spinata* – a mandible with separate coxa and basipod (Siveter et al., 2001).

As stated above, the known derivatives of the stem lineage of the Eucrustacea have no coxae at all. Ontogenetically, a proximal endite of the mandible is found in the youngest instars of *Rehbachella kinnekullensis* Müller, 1983 from the Upper Cambrian 'Orsten' of Sweden (Walossek, 1993).

In eucrustacean species, the coxa and basipod of the mandible are always separated. It has therefore to be considered that the transformation of a mandibular proximal endite to a coxa also led to a two-segmented limb stem, from which we consider that the fusion of coxa and basipod in Upper Cambrian Phosphatocopina is an autapomorphy.

Endopods of all limbs with no more than three segments

All Upper Cambrian phosphatocopines have only two endopodal podomeres in the antennae and mandibles (Fig. 2B, C) and three in all post-mandibular limbs (Fig. 3). In the recently found phosphatocopine specimen from the Lower Cambrian of England (see above) the endopods of all post-antennular limbs including antenna and mandible have three segments (Siveter et al., 2001). There may be eucrustaceans with as few endopodal segments but in terms of ground patterns, Euarthropoda have seven endopodal podomeres and Crustacea have basically five. This reduction of endopodal podomeres from seven to five is considered as an autapomorphy of Crustacea (Walossek, 1999). This character is conservatively retained particularly in the thoracopods 1–8 of Malacostraca and in the Cephalocarida among the Entomostraca. It must

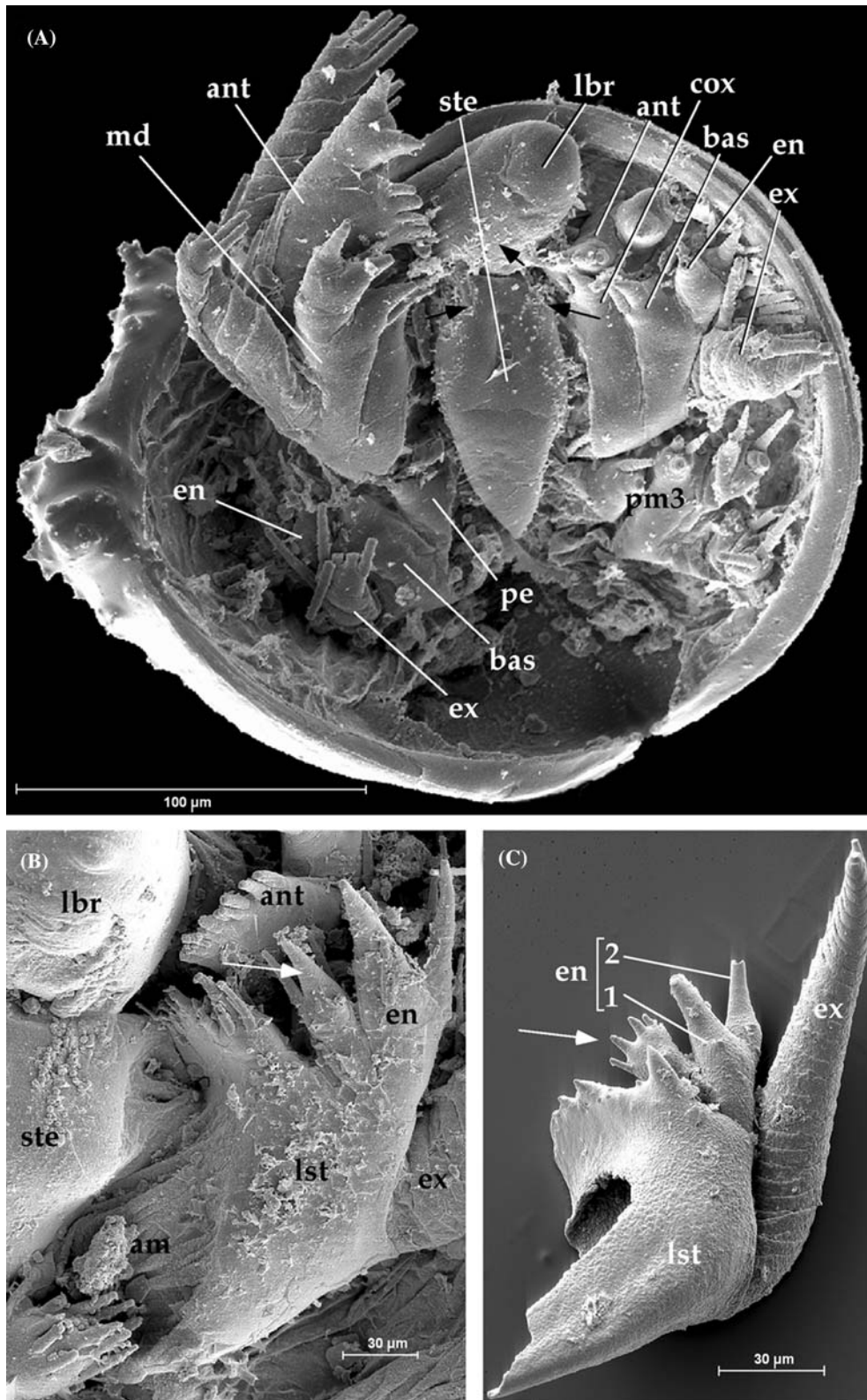


Figure 2. A–B: *Vestrogothia spinata* Müller, 1964. (A) Ventral view of an early larval stage, having the mandibular coxa (cx) and basipod (bas) separated (UB W 120). (B) Close-up view of the mandible of an advanced growth stage (UB W 247) with fused coxa and basipod forming an undivided limb stem (lst), the endite of the basipod (arrow) separated from the median edge of the coxa. The median extension of the basipod remains as an enditic protrusion. (C) Isolated phosphatocopine mandible of an advanced growth stage (UB W 106); the endite of the basipod seems to be a portion of the endopod (arrow), portions of the endopod (en) numbered, exopod (ex) preserved without setae.

therefore to be considered that in the ground pattern of Phosphatocopina, a reduction of endopodal segments from five to three occurred, probably due to the restricted space inside the

bivalved shield and/or to a change of function. In the later evolution of Phosphatocopina the endopods of antennae and mandibles were reduced to only two podomeres.

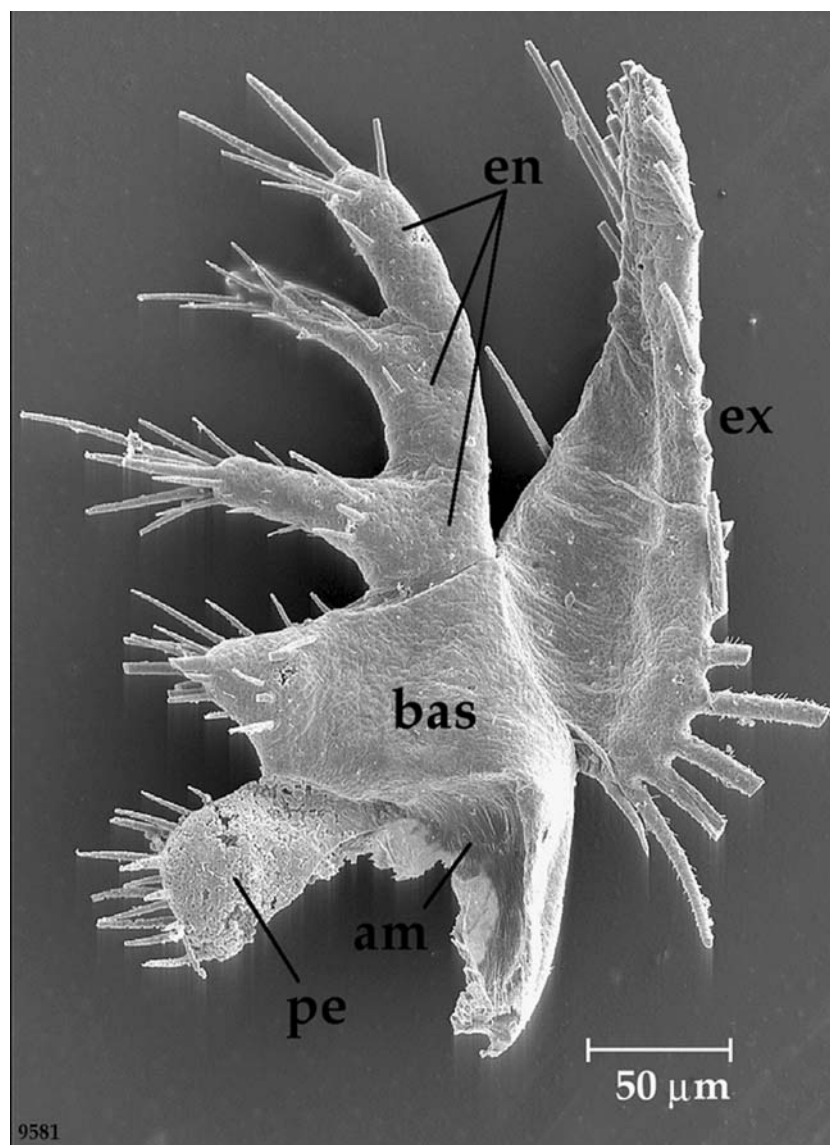


Figure 3. *Hesslandona unisulcata* Müller, 1982 (UB W 156). Isolated postmandibular limb of a late growth stage with all three endopodal portions (en) drawn out into long endites.

Uniquely shaped bivalved shield

Phosphatocopina have a uniquely shaped bivalved shield. However, a bivalved shield neither characterises the stem lineage of Crustacea nor the ground pattern of Eucrustacea. Additionally, that shield is quite different from the ostracode shield, e.g. in having the free margin of the valves curved inward to form a so-called doublure (Fig. 1 and 2B). The species of the Hesslandonidae have a plate termed the interdorsum between both valves, which is bordered by a pair of simple dorsal furrows (Fig. 4). The interdorsum may be drawn out antero- and postero-dorsally into cardinal spines (Fig. 4), which vary in length considerably. The species of the taxon Vestrogothiidae, partly species with both valves drawn out into antero-ventral spines, lack the interdorsum (Fig. 5). However,

they have small triangular plates anteriorly and posteriorly between the valves, which may be drawn out into a spine (Fig. 6). These plates may either be the remains of an original interdorsum from the ground pattern of Phosphatocopina or alternatively could represent an intermediate evolutionary stage of development of the interdorsum within the Phosphatocopina.

A shield adductor muscle, and thus an isthmus and muscle scars, as in ostracodes, are clearly absent in phosphatocopines and cannot be expected because the body is connected to the shield only along a very narrow area, approaching almost the width of the interdorsum.

Whether or not the interdorsum is in the ground pattern of the Phosphatocopina has considerable bearing on the systematic position of species within the two major lineages because presence

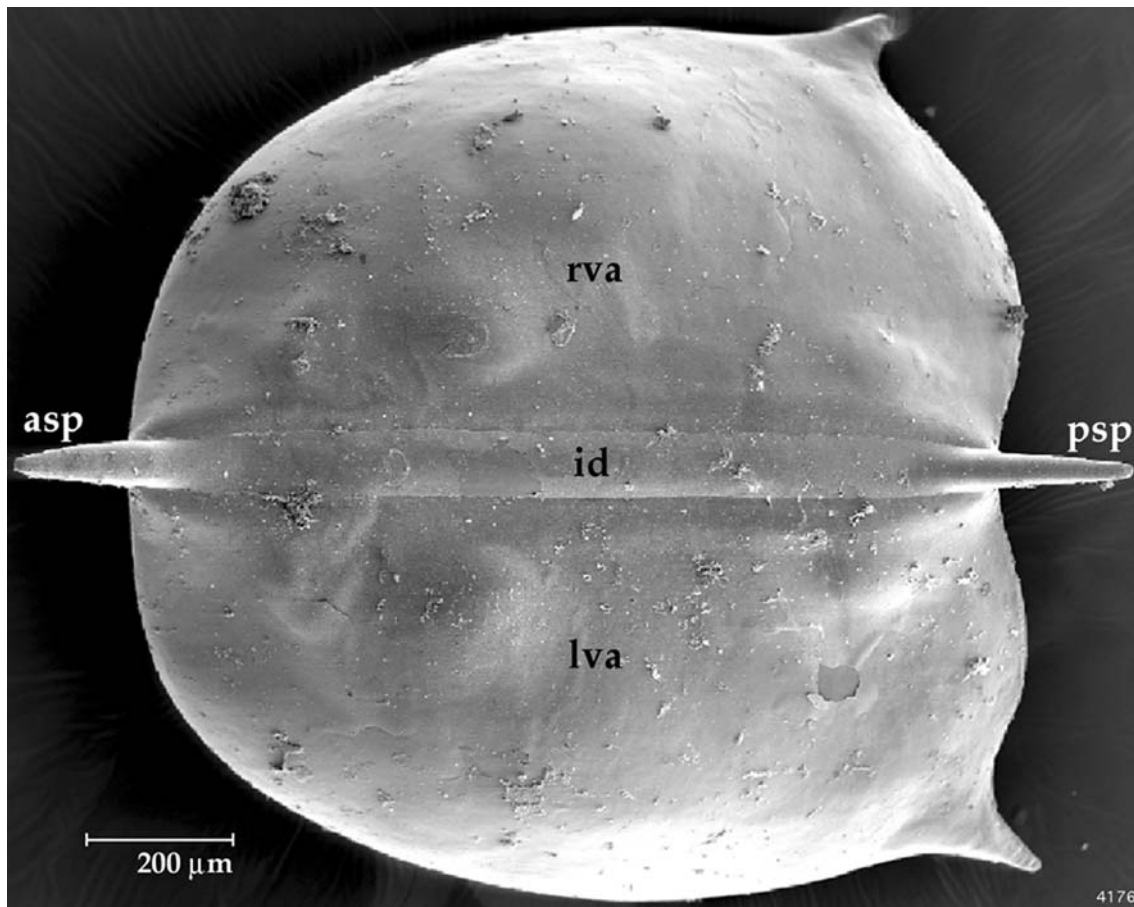


Figure 4. *Hesslandona ventrospinata* Gründel, 1981 (UB W 187). Dorsal view of shield showing both valves (lva, rva) separated from each other by a complete dorsal plate, the interdorsum (id).

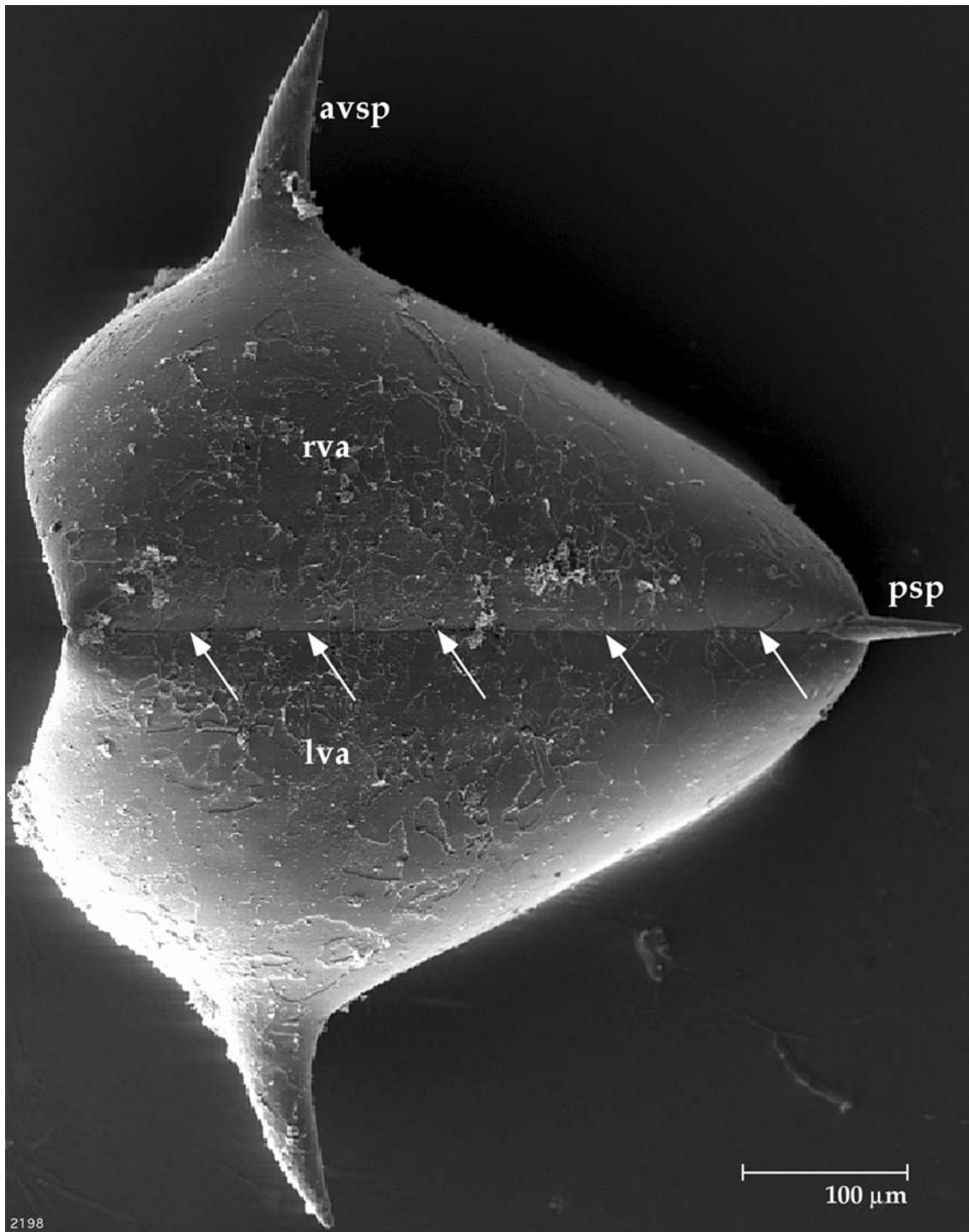


Figure 5. *Vestrogothia spinata* Müller, 1964 (UB W 121). Dorsal view of shield showing both valves (lva, rva) separated only by a complete dorsal furrow (arrows); this species shows small plates antero- and postero-dorsally, the posterior one drawn out into a cardinal spine (see Fig. 6).

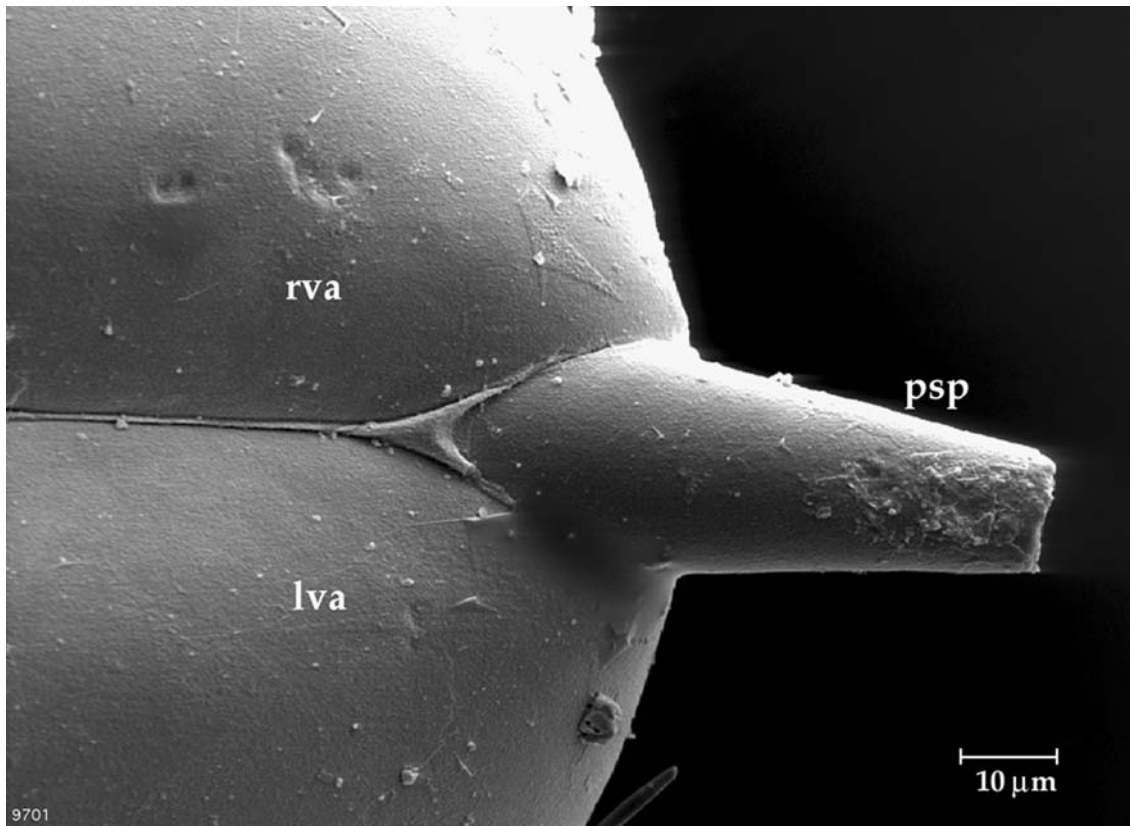


Figure 6. *Vestrogothia spinata* Müller, 1964 (UB W 245). Dorsal view of postero-dorsal area of shield showing the posterior plate drawn out into a cardinal spine (psp).

and absence of an interdorsum has been traditionally understood as significant. This might be true, but the order of appearance in phosphatocopine evolution is still certain.

Relationships of Phosphatocopina

Phosphatocopina share several characters with the Eucrustacea, the taxon including all crustacean taxa with extant derivatives. Examples of these characters, not found in any derivative of the earlier stem lineage of crustaceans or in the ground pattern of Euarthropoda, points to a common ancestry of both taxa. They are discussed in the following.

Antenna and mandible with coxa and basipod

Both antenna and mandible of Phosphatocopina have a limb stem consisting of a coxa and basipod (Fig. 2, see above). This is in contrast to all

posterior limbs that do not have a coxa. Eucrustacea also have antennae and mandibles with a subdivision of a limb stem in a coxa and basipod. The plesiomorphic condition is hypothesised as having been a basipod with a small setiferous proximal endite medially underneath as it is also in all post-mandibular limbs of Phosphatocopina (Fig. 2B) in the ground pattern of Crustacea or only a basipod in the ground pattern of Euarthropoda.

Labrum with hairs, sensilla and pores overlapping the oral area

In Phosphatocopina the labrum overlaps the oral area (Fig. 1). The labrum is an organ housing glands and carrying pores, sensilla and fine hairs posteriorly (Figs 2A and 7). It is seen as an outgrowth of the rear end of the more sclerotised hypostome; the hypostome is already present in

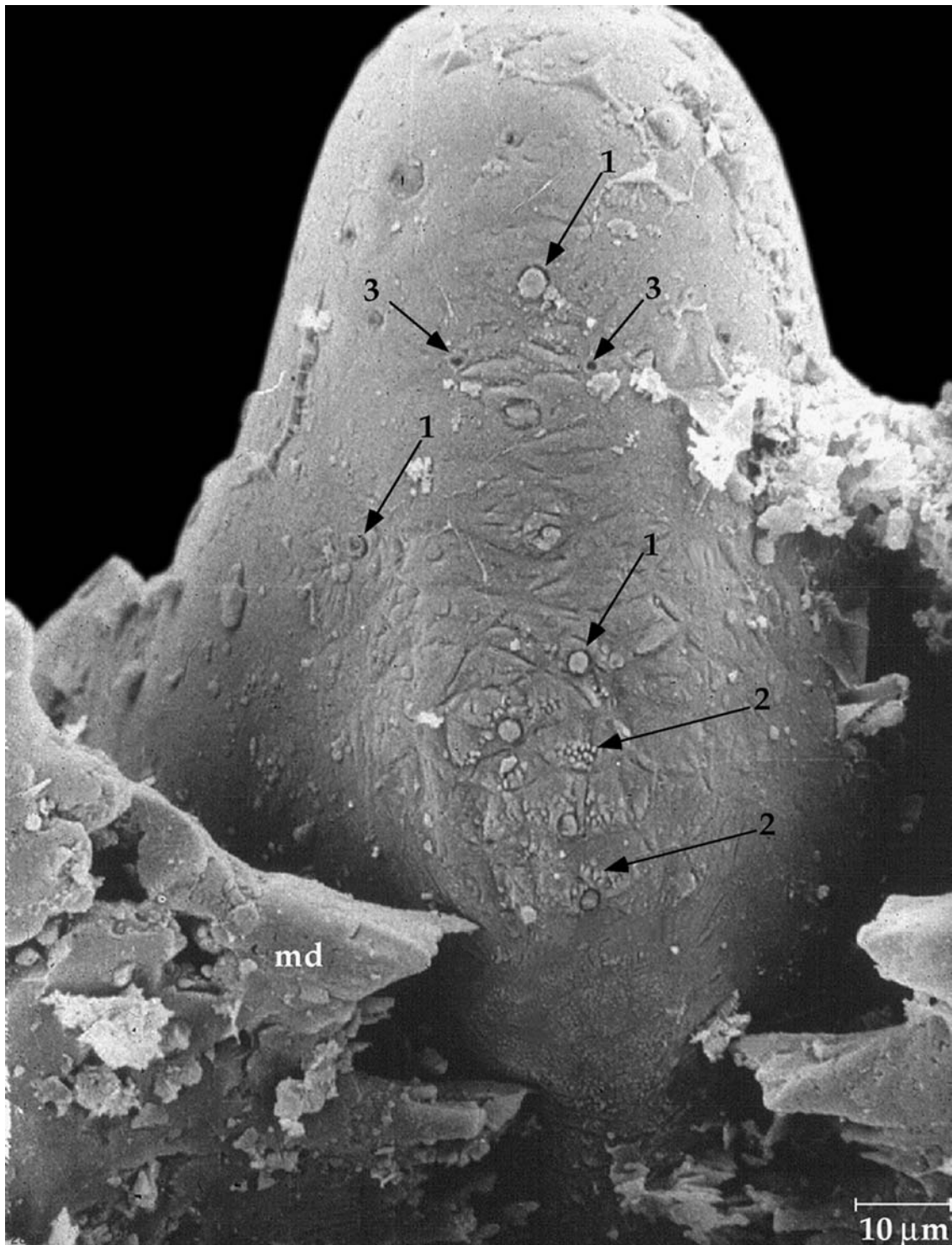


Figure 7. *Hesslandona unisulcata* Müller, 1982 (UB W 146). Labrum from the posterior; note sensilla (arrows 1), groups of fine hairs (arrows 2) and pores (arrows 3), possibly of slime glands.

the euarthropodan ground pattern. In Eucrusea, there is also a labrum overlapping the oral area. It also shows pores, sensilla and fine hairs posteriorly.

Sternum with paragnaths and hairs

In Phosphatocopina and Eucrusea, the post-oral sternites are fused into a single sternal plate, the sternum. On the mandibular part of the sternum there is a pair of humps termed the paragnaths (Figs 1 and 2A, B). The sternum including the paragnaths is furnished with fine hairs (Fig. 2A). The derivatives of the crustacean stem lineage have separated head sternites, retained from the ground pattern of Euarthropoda.

Plesiomorphies of Phosphatocopina

Phosphatocopina show a set of plesiomorphic characters retained from earlier evolutionary levels as described in the following.

Head larva as first ontogenetic stage

The first ontogenetic stage of Phosphatocopina is a so-called head larva having antennulae plus three pairs of functional limbs. This larval type is retained from the ground pattern of Euarthropoda (Walossek, 1999). Its size in Phosphatocopina is about 120 to 200 μm in shield length, depending on the species.

Post-mandibular limbs serially similar

The post-mandibular limbs of Phosphatocopina are similar to each other and consist of a basipod with a setiferous proximal endite medio-proximally and two rami, as in the ground pattern of Crustacea (new is the three-segmented endopod, see above).

Monophyly of Eucrusea

Eucrusea, comprising all crustacean taxa with extant derivatives, are clearly set apart from any other crustaceans and can be considered as monophyletic with autapomorphies, as described in the following.

Orthonauplius as first ontogenetic stage

The first ontogenetic stage of Eucrusea is the nauplius, also termed the short-head larva. The nauplius, or better the orthonauplius, has only antennulae, antennae, and mandibles. The entire locomotory and feeding apparatus of the nauplius is as described above for the head larva of the Phosphatocopina in having a labrum and sternum with paragnaths, hairs, specific appendage setation, and antenna and mandible with coxa and basipod. Therefore such an orthonauplius could not have been developed earlier in the evolution of Crustacea, i.e., it cannot be the most plesiomorphic larva type within the Euarthropoda (Lauterbach, 1988).

First post-mandibular limb as maxillula

The first post-mandibular limb of all Eucrusea is significantly different from succeeding ones. It is modified into a mouthpart that is strongly involved in the feeding process and is called maxillula or first maxilla.

The second post-mandibular limb in the ground pattern of Eucrusea is serially similar to the succeeding limbs, therefore a maxilla (or second maxilla) is not part of the ground pattern of the Eucrusea.

Phylogenetic conclusions

In summary, there are several autapomorphies of Phosphatocopina that validate their monophyletic status. Again, the Eucrusea, including all crustacean taxa with extant derivatives also share a set of autapomorphies that validate their monophyletic status. Both share characters, which set them clearly apart from the derivatives of the eucrusean stem lineage, considered as synapomorphies thus. Phosphatocopina nicely fill the morphological and evolutionary gap between the derivatives of the eucrusean stem lineage and the Eucrusea. Therefore, Phosphatocopina are recognised as the sister taxon of the Eucrusea (Fig. 8; see also Walossek, 1999). In consequence, Phosphatocopina can no longer be treated as early representatives of in-group eucruseans and, thus, can neither be treated as ancient Ostracoda

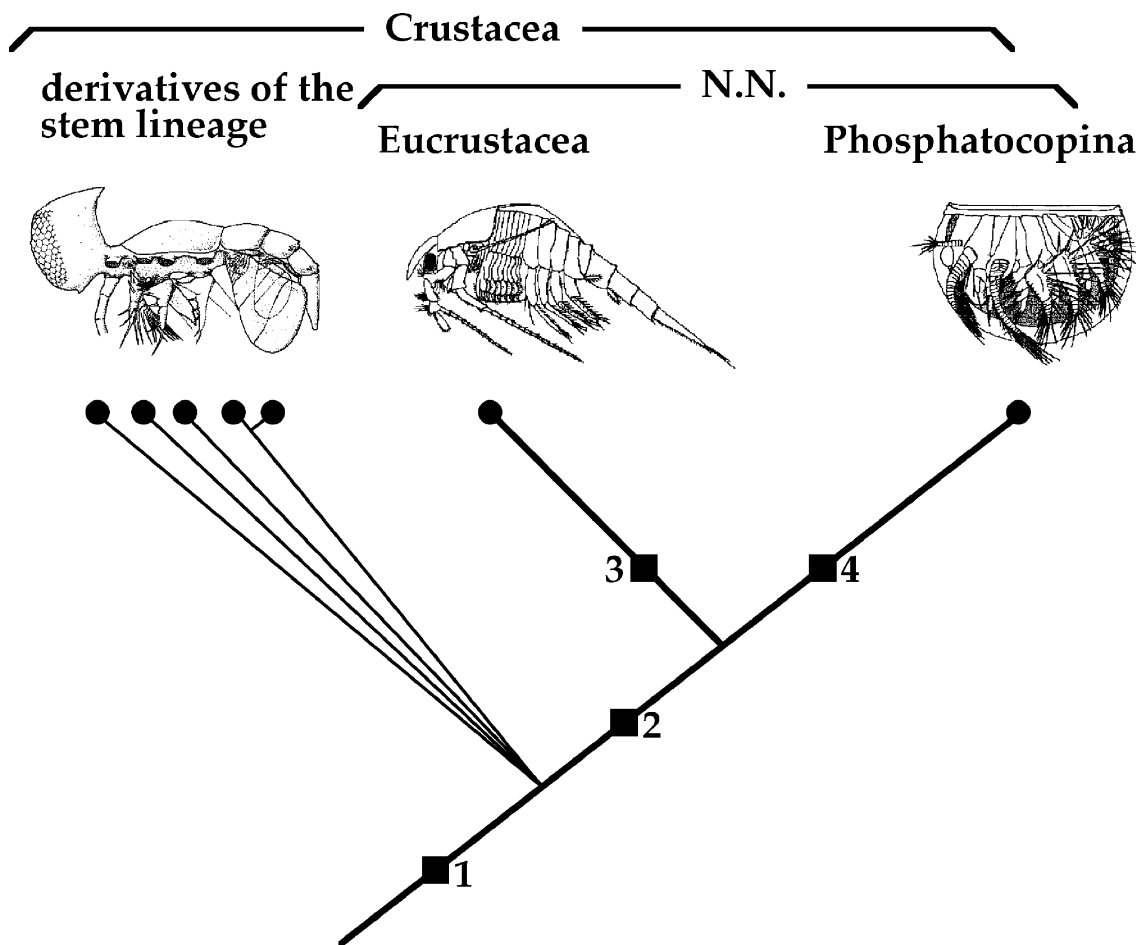


Figure 8. Relationships within Crustacea (see Walossek, 1999; Maas et al., 2003). Numbered black squares refer to respective autapomorphies. (1) Autapomorphies of Crustacea: postantennular limbs with a proximal endite medially underneath the basis; endopods of all postantennular limbs with five podomeres. (2) Autapomorphies of N.N. (=Phosphatocopina + Eucrustacea): antenna and mandible both with a protopod having a coxa and basis; labrum with lateral hairs and sensilla and pores posteriorly, overhanging mouth area; post-antennular sternites fused to a single sternal plate, the sternum, with fine hairs on its anterior part, humps on the mandibular part of the sternum (paragnaths). (3) Autapomorphies of Eucrustacea: orthonauplius as first ontogenetic stage; first post-mandibular limb modified into a maxillula. (4) Autapomorphies of Phosphatocopina: short antennulae with few terminal setae; coxa and basis of antenna and mandible fused to a single limb stem; endopods of all limbs with no more than three portions; specifically shaped bivalved shield. Known derivatives of the stem lineage of Eucrustacea are: *Martinsonia elongata* Müller & Walossek, 1986, *Cambropachycope clarksoni* Walossek & Müller, 1990, *Goticaris longispinosa* Walossek & Müller, 1990, *Henningsmoenicaris scutula* (Walossek & Müller, 1990) and *Cambrocaris baltica* Walossek & Szaniawski, 1991 (see Walossek & Müller, 1998, Walossek, 1999; for more information).

nor as Cambrian evidence of Ostracoda (e.g. Hinz-Schallreuter, 1998; McKenzie et al., 1999).

Stratigraphy

The stratigraphy of the Upper Cambrian of southern Sweden is well investigated since even

the nineteenth century (e.g. Wallerius, 1895; Westergård, 1947, 1953; Clarkson et al., 1998). The Upper Cambrian is subdivided into six zones, from which zones 1, 2 and 5 yield phosphatocopine material. The species described so far are restricted to a particular biozone (Table 2).

This suggests that Phosphatocopina may be useful for stratigraphic considerations in ways that

Table 2. Species of Phosphatocopina described from the Upper Cambrian 'Orsten' of Sweden with reference to the chronostratigraphical zone with which they are associated

Species	Zone
<i>Hesslandona necopina</i> Müller, 1964	1
<i>Hesslandona kinnekullensis</i> Müller, 1964	1
<i>Hesslandona unisulcata</i> Müller, 1982	1
<i>Waldoria</i> n. sp. 1 sensu Gründel & Buchholz, 1981	1
<i>Hesslandona</i> n. sp. a sensu Müller, 1964	2
<i>Trapezilites minimus</i> Kummerow, 1934	2
<i>Vestrogothia granulata</i> Müller, 1964	2
<i>Vestrogothia bratteforsa</i> Müller, 1964	2
<i>Falites fala</i> Müller, 1964	5
<i>Falites cycloides</i> Müller, 1964	5
<i>Falites angustiduplicata</i> Müller, 1964	5
<i>Vestrogothia spinata</i> Müller, 1964	5
<i>Vestrogothia hastata</i> Müller, 1964	5

have not yet been realised. Additional finds of some of the species named in Table 2 in other places in the same zones confirm this view. Rushton (1978) found *Hesslandona unisulcata* – he assigned his material to *Falites fala* (see Williams & Siveter, 1998) – from Zone 1 of the Nuneaton district, Warwickshire, UK. A species of *Waldoria*, described by Gründel & Buchholz (1981) from Zone 1 of the Upper Cambrian of Northern Germany in open taxonomy, is also among our material in Zone 1 of southern Sweden. Other species of Phosphatocopina from other places of the world have not yet been investigated in this respect.

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