

The 'Alum Shale Window'—Contribution of 'Orsten' Arthropods to the Phylogeny of Crustacea

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Abstract

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Exceptional three-dimensional preservation of phosphatized Upper Cambrian arthropods of different groups from southern Sweden permits not only description of their morphology in full detail but also assumptions on functional morphology and life habits. Ontogenetic stages, in some cases in complete sequences, give additional information about habitual changes in the life cycle. Altogether this provides a wide data basis for phylogenetic considerations, particularly for the crustacean branch of the Arthropoda. Among the 'Orsten' fossils, a number could be recognized as representatives of crown-group crustacean taxa, such as the Skaracarida and *Bredocaris* as members of each of the two different lineages of Maxillopoda, or *Rehbachella* as a member of the Branchiopoda. Another set of forms shares some characters with the crown-group crustaceans but lacks a large number of others. These fossils, identified as representatives of the stem line of Crustacea, provide a hitherto unknown data set for the interpretation of morphological and functional changes in the evolution towards the crown-group of this taxon.

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General Remarks

In 1975, in the course of routine micropaleontological etching of Upper Cambrian bituminous limestones with 15% acetic acid, cuticular remains of bodily preserved arthropods were discovered among a large number of microfossils, such as conodonts, small horny brachiopods and elements of uncertain affinities (Müller 1985, 1990). Since then, processing of more than one ton of rock has yielded a variety of small arthropods, mainly crustaceans and similar forms (Müller & Walossek 1985a). In addition, completely preserved specimens of *Agnostus pisiformis* (Müller & Walossek 1987) as well as larvae of chelicerate (Müller & Walossek 1986b) and possible pentastomid affinities (Walossek & Müller in preparation) have been found. Because of the small size of the fossils, less than 2 mm, they can be studied in detail only with the scanning electron microscope (SEM). The material is extremely brittle, and already repeated exposure to evacuation of the chamber of the SEM can cause damage to the specimens.

Over many years extensive sorting of etched residues has yielded quite a large number of specimens. By far the most predominant are the ostracode-like Phosphatocopina, with more than 50,000 specimens at hand. They document extensive taxonomic diversity (Müller 1979a,b, 1982b). Other forms are much rarer. The Skaracarida, for example, are represented by about 100 specimens of each of two species now. *Bredocaris admirabilis* Müller, 1983, is known from about 100 individuals; *Rehbachella kinnekullensis* Müller, 1983, from about 130; and *Dala peilertae* Müller, 1983, from about 60. Rarer yet are *Hen-*

ningsmoenicaris scutula (Walossek & Müller 1990), with about 30 specimens; *Martinssonella elongata* Müller & Walossek, 1986, with 24 specimens at hand; and both *Goticaris longispinosa* Walossek & Müller, 1990, and *Cambropachycope clarksoni* Walossek & Müller, 1990, each with about 15 specimens. Of *Oelandocaris olandica* Müller, 1983, only a single specimen has been found so far (major references: Müller 1983; Müller & Walossek 1985b, 1986a, 1988; Walossek & Müller 1990).

Arthropods, and Crustacea in particular, can be easily distinguished from other organisms. The interrelationships of the arthropod groups, however, have not yet been satisfactorily clarified, and the origins of the major groups remain obscure. This uncertainty also has strongly affected discussions concerning the homology of various structures and associated terminology.

The 'Orsten' provides us with a large set of animals of different body plans that flourished more than 500 million years ago and permits comparisons vertically as well as horizontally. The exceptional preservation of the body and appendages, including all surface structures, such as setation and pores, permits a detailed study and reconstruction of the external morphology of these fossils at a level of resolution of fractions of a micron (e.g. bristles on setae). This presents a broad basis for constructional and functional analysis with respect to the reconstruction of the mode of life of each of these early arthropods. Also the presence of ontogenetic stages of various forms, in part even in sets, is a great benefit, because it provides an insight into the growth patterns with their specific morphological and functional changes during ontogeny.

Taphonomy and Ecology

The faunal associations recovered apparently came from a rather restricted benthic environment, presumably a soft bottom or flocculent layer. In this exceptional preservational 'window' representation of organisms seems to be limited to a specific size range, and it is possible that the composition of the associations has been biased by very selective preservation. *Agnostus*, for example, is known from more than a hundred specimens representing eight developmental stages (Müller & Walossek 1987), while remains of unquestioned trilobites, though their calcareous exoskeletal remains are abundant in the rock, have not yet been discovered in this type of preservation.

On the other hand, this preservational bias can provide evidence of a specific life habit of the adult organisms and/or their larval stages: preservation potential of small-sized components of the meiofauna which lived close to the zone of fossilization underneath the flocculent layer (life zone) appears to be much greater than that of free-swimmers. Accordingly, selective representation influenced by taphonomy effects also yields information of specific interest for studies of the origin and evolution of taxa (major reference: Müller & Walossek 1991, particularly fig. 5).

Heterogeneity

We interpret the heterogeneous 'Orsten' material as consisting of permanent and transitory components of meiofaunal associations. Examples of truly meiofaunal forms are *Bredocaris*, known from growth stages as well as the adult, and *Skaracarida*, of which only adults are known. Examples of forms from which only early larval stages are known and whose later stages most likely had lived mainly further off the bottom layer and are either not preserved or known only from empty exoskeletons include *Agnostus*, the Phosphatocopina, *Rehbachiella* and, possibly, *Martinsonia*. Preservational and environmental restriction to particular ontogenetic stages as well as life form types may be one of the major reasons for the apparent lack of morphological and taxonomical overlap between the 'Orsten' and the Burgess Shale associations. This lack of similarity is remarkable because the Burgess Shale faunal components have a world-wide distribution and are now known from more than 30 localities (cf. Conway Morris 1989).

Forms of Crustacean-like Appearance

Remarkably, those 'Orsten' taxa recognized as true crustaceans have been affiliated with only certain members of the 'entomostracan' clade, such as Branchiopoda and Maxillopoda (see below). Interestingly, the extant representatives of this set of crustaceans are in general small and only lightly sclerotized, and various forms are meiofaunal elements. This circumstance may give some clues as to the origin and evolutionary pathways of the members of this clade. On the other hand, it also may have a

bearing upon the absence of certain crustacean taxa, such as the Malacostraca and the Cephalocarida.

With the discovery of *Martinsonia* (Müller & Walossek 1986a) and three other forms with a mixture of crustacean and non-crustacean characters, while lacking various characters, considered as belonging to the derived ground plan of the Crustacea *s.str.* (crown group; cf. Walossek & Müller 1990), the present state of knowledge of the composition of the 'Orsten' fauna permits a new view of the constituent characters of Crustacea. With this, the analysis of these four forms demonstrates that our material of crustacean-like arthropods is by no means homogeneous but consists of two distinct clusters with obviously different evolutionary origins. Although heterogeneous within themselves, these clusters share at least two characters with one another:

(1) slender first antenna ('antennula') composed of a limited number of segments and functioning mainly for locomotion and feeding rather than being 'antenniform'; and

(2) a separate lobate endite arising from the inner proximal edge of the coxae of the subsequent limbs, which is termed 'proximal endite'.

These two characters are basically developed in all extant crustaceans but are clearly lacking in all other arthropods. Accordingly, they are considered as evolutionary innovations of the line leading to the Crustacea. On the other hand, a large set of characters at least basically present in 'Orsten' crustaceans (e.g. *Skara*, *Bredocaris*, *Rehbachiella*, *Dala*, *Walossekia*) as well as the extant crustacean taxa but not developed in *Martinsonia* and its three related forms mentioned above documents a large morphological and evolutionary gap between the two clusters. This set of features is considered to be part of the derived ground plan characters of Crustacea *s.str.* It includes:

(1) a fleshy 'labrum' (glandular organ) and 'atrium oris' (mouth funnel);

(2) a post-oral sternum with humped paragnaths, representing outgrowths of the mandibular sternite;

(3) division of the limb apparatus into a naupliar set of limbs—the two pairs of antennae and the mandible—and a posterior set;

(4) a 'proximal endite' which is enlarged into a coxal gnathobase in the mandible;

(5) the fourth limb being differentiated into a maxilla (first maxilla; 'mouthpart'); and in the trunk region

(6) a conical telson with articulate furcal paddles and the anus positioned at its truncated rear.

The nauplius, representing the most oligomeric arthropodan larval type with only the anterior three pairs of cephalic appendages ('partial-head' larva), also is considered as a derived feature of Crustacea *s.str.*, while *Martinsonia* and its related taxa have nauplius-like larvae but with a larger set of appendages, retained from the ground plan of Euarthropoda [first antennae and three pairs of functional limbs (= 'complete-head' larva); Walossek & Müller 1990, particularly their fig. 5].

An additional new character developed in the early evolution of Crustacea appears to be the flagelliform outer ramus (exopod) of the post-antennular limbs that are used basically for locomotion, mostly swimming. This

type of ramus with setation on the annuli facing the endopod clearly differs from that of the 'trilobitomorphs' (in the sense of Bergström 1980; see in particular Chen Jun-yuan *et al.* 1991, their fig. 6 of a *Naraoia* leg), where it is made up of lamellate spines. According to Bergström (personal communication 1990), this latter feature is shared by trilobites and all other forms recognized as 'trilobitomorphs' (in the sense of Bergström 1980). Also in *Agnostus* the setation is on the outer side, best recognizable in the second and third cephalic limbs.

Representatives of the Stem-lineage of Crustacea

Henningsmoenicaris, *Cambropachycope*, *Goticaris* and *Martinssonsonia* are considered as representatives of the early stem-lineage of Crustacea (Walossek & Müller 1990; for discussion of the stem-lineage concept see Ax 1985),

but they do not comprise a natural, i.e. monophyletic, group. Of these, two genera share a bulging forehead structure with the mouth opening at its rear, the 'hypostome', with *Agnostus* and the 'trilobitomorphs' (supposedly reduced in *Cambropachycopidae*). Other characters of these forms also are clearly symplesimorphic, i.e. retained from older phylogenetic levels, such as the number of head segments or the degree of differentiation of the limbs, or the position of the anus on the ventral side of the tail end, while others are autapomorphic—e.g. the peculiar probable eye of *Cambropachycopidae*.

Henningsmoenicaris. This form is known from several ontogenetic stages. The largest one, approximately 1 mm long, has a bowl-shaped shield, a tail with three tergite-bearing segments, and a flattened caudal spine covering the anus. During ontogeny stalked eyes developed at the inner rim of the shield duplicature anterolateral to the first antennae (Walossek & Müller 1990, their fig. 4B).

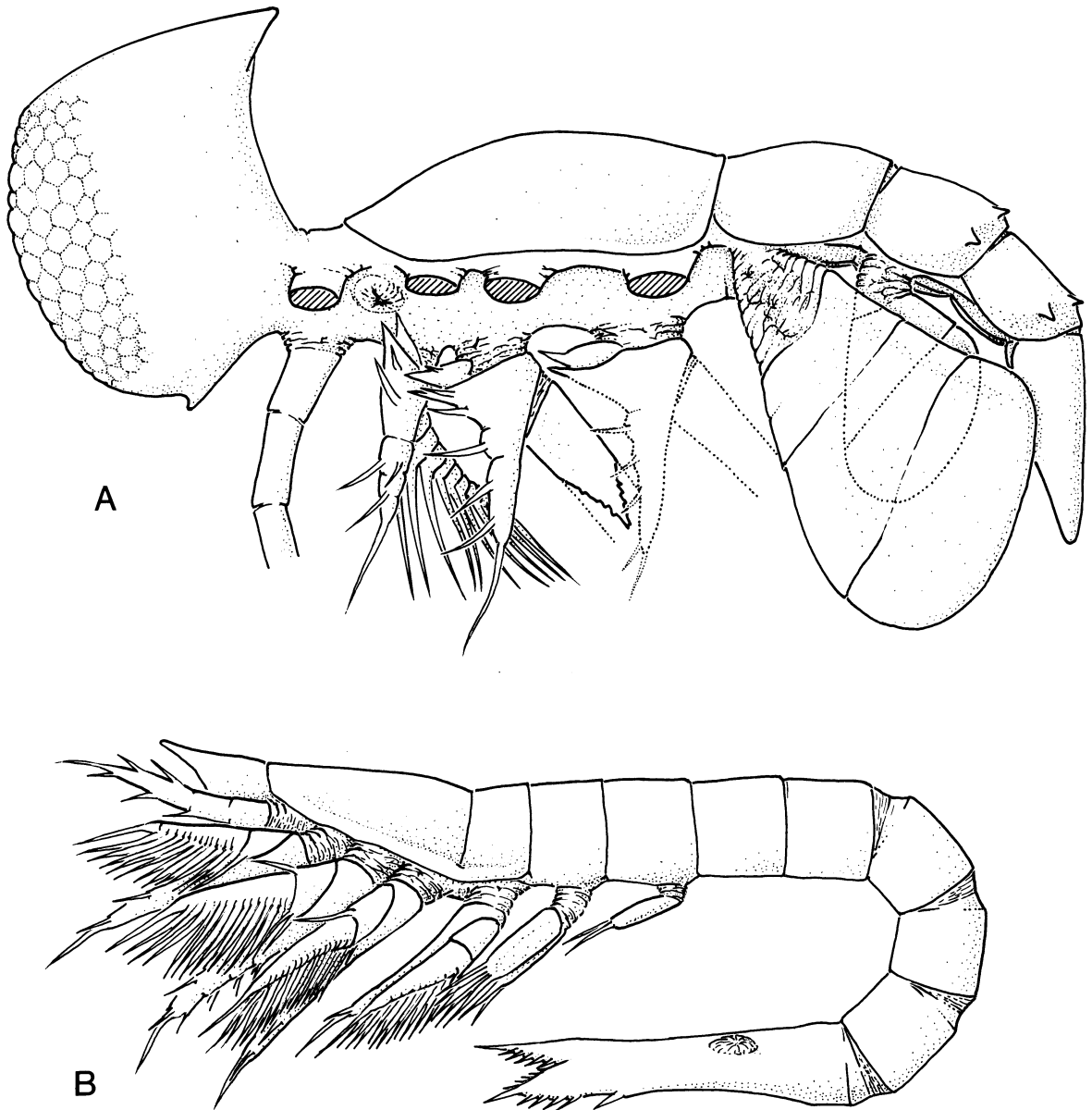


Fig. 1. Representatives of Upper Cambrian 'Orsten' stem-lineage crustaceans.—A. *Cambropachycope clarksoni* Walossek & Müller, 1990.—B. *Martinssonsonia elongata* Müller & Walossek, 1986 (for sizes of all forms see text).

Various features show remarkable resemblances to *Agnostus*. This is particularly true of the hypostome and the rigid limb corms (basipod) with a spinose inner rim, but which, in contrast, bear a 'proximal endite'. The first larval stage resembles that of *Martinssonina* but already has the characteristic 'hypostome' with a small triangular mouth at its rear (for correction of name see Walossek & Müller 1991).

Cambropachycopidae. In *Cambropachycope* and *Goticararis* the mouth opens freely on the ventral surface slightly anterior to the second pair of appendages; a humped hypostome is missing, presumably being reduced. Both forms share a large faceted lobe at the forehead, possibly a single compound eye. The head comprises only four limb-bearing segments. In *Cambropachycope*, which is about 1.8 mm long, the head bears a small shield with weakly developed margins, and the tail is composed of no more than three segments and a conical terminal portion (Fig. 1A). The anterior two trunk segments have large uniramous and paddle-shaped limbs. *Goticararis* is known from several ontogenetic stages. In all stages known the head and trunk are fused to form a barrel-shaped body which tapers into a long spine. The largest stage known is about 1.5 mm long and has four slender uniramous limbs on the trunk.

Martinssonina. This form has the most crustacean-like appearance of the cluster, particularly in regard to its trunk, which ends in a long bifurcate portion (Fig. 1B). It is known from five different developmental stages, three egg- to spindle-shaped larval stages with four pairs of functional appendages (Müller & Walossek 1986b, their fig. 2), and two stages with a segmented trunk, only the anterior two of them bearing limbs. It remains unclear, however, whether the largest stage (about 1.5 mm long and with five pairs of head appendages) is an adult or still immature, not least because the posterior trunk limb appears still rudimentary (for additional details see Walossek & Müller 1990).

'Crown-group' Crustaceans

A second cluster includes Skaracarida, Orstenocarida, and *Rehbachella*, which have been studied in detail. On the basis of synapomorphies all three can definitely be recognized as representatives of specific crown-group taxa of the Crustacea. In addition, *Dala* and *Walossekia* most likely belong to this set, but still have to be studied in detail.

Skaracarida. The Skaracarida embraces two species of small crustaceans, about 1.2 and 0.7 mm in length, which have only one pair of trunk limbs specialized as maxillipeds and a long worm-shaped trunk made of 11 ring-shaped segments (Müller 1983; Müller & Walossek 1985b; Fig. 2). Younger stages have not been encountered. Reconstruction of the Skaracarida as representatives of the Maxillopoda has been based primarily on the tagmosis and a variety of structural similarities with Mystacocarida

and Copepoda, particularly in the possession of the maxilliped, which is missing in the thecostracan lineage of Maxillopoda (here basically an ordinary trunk limb). This assignment gained further support from the body plan of *Bredocaris* (see below) and a new description and reinterpretation of the tagmosis of Tantulocarida (cf. Huys 1991), extant forms recently recognized as maxillopods presumably of the thecostracan core (Boxshall & Huys 1989).

Additional support comes from the unique subdivision of the corms of the postmandibular limbs of the Skaracarida, particularly the first maxilla. On this limb the 'proximal endite' differs from the basic plan, found in the stem-lineage derivatives, and is transformed into a distinct corm segment, resembling the second antenna and mandible. The basipod has three setiferous endites medially and, moreover, is split into two to three portions (fig. 5 and plates 8:1, 5, 7 in Müller & Walossek 1985b; portions are re-interpreted, the coxa is restricted to the proximal corm portion, a feature recognizable only on posterior surface, fig. 5C). A similar arrangement occurs in the mystacocarids (e.g. fig. 2D of Hessler & Sanders 1966 for *Derocheilocaris typica*) and copepods (e.g. fig. 18 of Boxshall 1985 for *Euaugaptilus* sp.). Consequently, in addition to the maxilliped, this may be a further synapomorphic character of the proposed members of the 'copepodan lineage' among the Maxillopoda.

Orstenocarida. *Bredocaris* is known from six ontogenetic stages (Müller & Walossek 1988). The earliest is a larva with the typical naupliar set of three pairs of appendages and the anlagen of the first maxilla on the hind body. The latter limb is developed at the second stage. During subsequent development (next four stages) the second maxilla and four trunk limbs appear on the trunk but remain as anlagen. The final stage, about 0.85 mm long, is recognized as the adult particularly because of the simultaneous development of the functional second maxilla, the four trunk limbs, and three additional ones (Fig. 3).

This special mode of ontogeny, with delay of limb development in the naupliar/metanaupliar stages and simultaneous appearance of the subsequent limbs, characterizes only specific members of the 'thecostracan lineage' among the Maxillopoda, the Thecostraca *s.str.* Hence, it is recognized as a synapomorphy linking *Bredocaris* with this unit, embracing the Ascothoracida, Facetotecta and Cirripedia. Moreover, the change from the naupliar to the subsequent larval stage or phase—e.g. the 'cypris' in barnacles—is clearly not correlated in its segment number as well as its degree of appendage development with that of Copepoda (termed 'copepodid' phase there; Walossek *in press*).

With regard to the design of the late instars of the supposed relatives, the effacement of segmentation in the thorax, abdomen and the trunk limbs as well as non-articulation of the furcal rami of *Bredocaris* are considered indicators of a special mode of life of the fossil, possibly at or below the sediment-water interface, and not as larval features.

Bredocaris has seven well-developed thoracopods, which agrees with the basic number of the Maxillopoda,

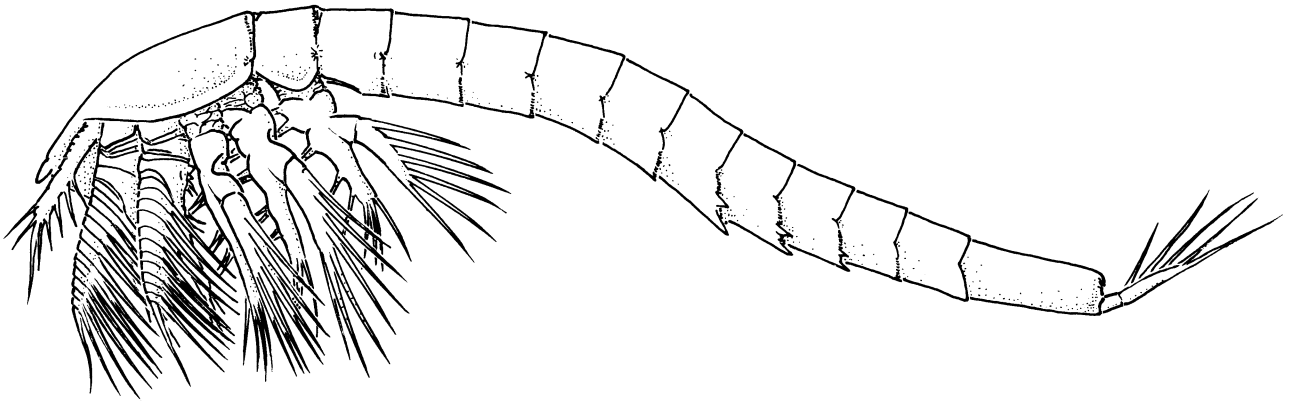


Fig. 2. *Skara anulata* Müller, 1983; note the corrected number of trunk segments (11 plus telson; see Müller & Walossek 1985, their fig. 3); furcal rami reconstructed from a newly discovered specimen (two-segmented rather than three-segmented).

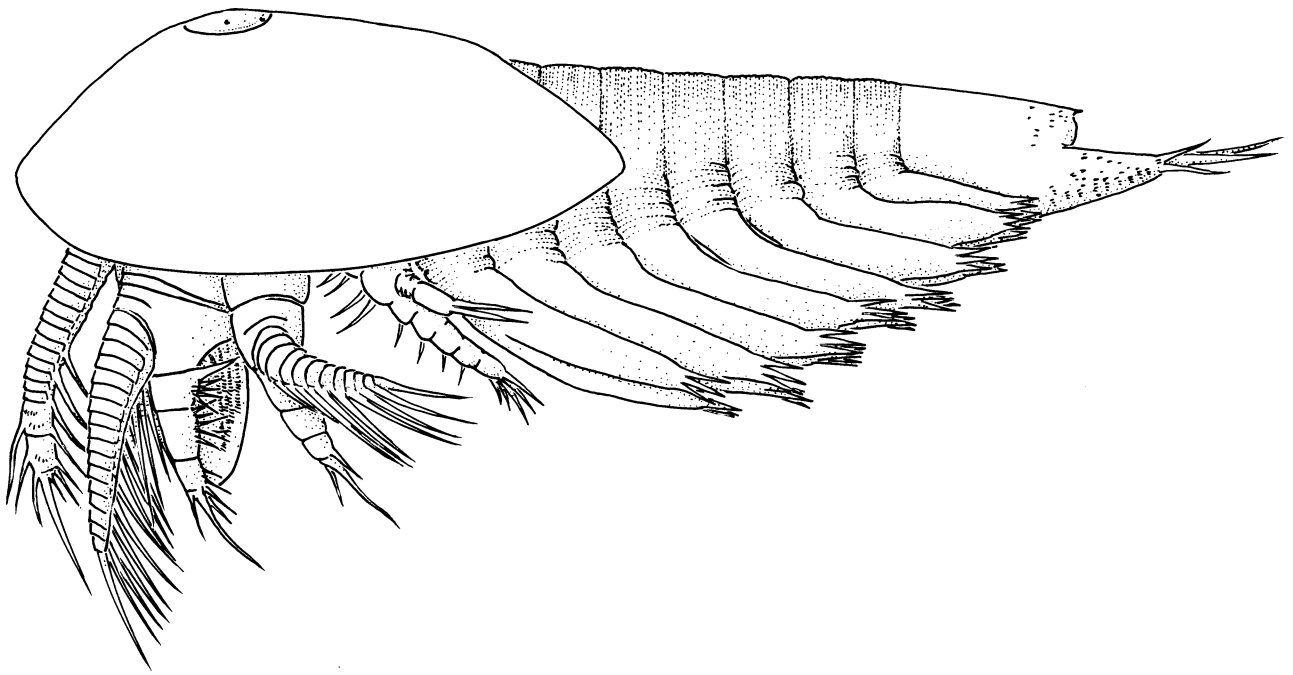


Fig. 3. *Bredocaris admirabilis* Müller, 1983; adult.

as predicted by Grygier (1983) and Newman (1983). In several aspects *Bredocaris* gives an insight into the basic body plan of this crustacean group, such as its compound eyes, simple head-shield, and similarities of the second maxilla to a trunk limb. Again, the seventh trunk limb is a typical biramous thoracopod, while in all other maxillopods this limb, when developed, has been modified into reproductive aids in the males, apparently by parallel evolution. Retention of naupliar locomotory and feeding structures (particularly the mandible with a palp consisting of basipod and both rami) that operated in parallel with the posterior set of limbs gives further support to the supposed pedomorphic origin of this taxon (see also Newman 1983).

Phosphatocopina. The bivalved phosphatocopines are the most abundant and widespread arthropods with preserved cuticular details in the 'Orsten' (Müller 1979a,b,

1982b). The distinctiveness of the taxa of this group, as documented in different appendage morphology as well as shield shapes, reflects their high diversification in the environment. The presence of a large labrum, a sternum with humped paragnaths, and a second antenna and mandible, which are clearly different from the posterior set of limbs, indicate their closeness to the crown-group level, while set off clearly from the level of the cluster of early stem-lineage derivatives. On the other hand, all known forms have very small first antennae, and there is, for example, no differentiation among the postmandibular appendages. A detailed study of this taxonomically diverse group is under way.

Rehbachella. For *Rehbachella* an ontogenetic sequence of as many as 30 stages has been established (Walossek in press). It begins with a true nauplius and, in contrast to *Bredocaris*, is strictly anamorphic in both limb appearance

and development. It ends in the material at an instar with 13 trunk segments and 12 pairs of trunk limbs, of which the posterior ones are still undeveloped. This indicates that the known largest stage, about 1.7 mm in total length, was still immature and the sequence is still incompletely known (Fig. 4).

The assumption that *Rehbachella* is a representative of the Branchiopoda rests mainly on the shared complex of structures associated with the postnaupliar locomotory and feeding apparatus that is adapted for filtration. This apparatus develops gradually, while the naupliar features are modified or eventually reduced (in further contrast to *Bredocaris*). Principal characters of this apparatus include the posteriorly directed lobate endites on the limb combs with special filtratory setation and a deep ventral sternitic food groove, as well as phyllopodous limbs with sucking chambers to generate the required feeding currents. Other crustaceans also may have developed filter apparatus, but these are structurally as well as functionally different. The phyllocarid malacostracans, for example, have neither the basipodal endites nor the sternitic food groove of the Branchiopoda and *Rehbachella*, and their setation is differently arranged. Since the phyllocarid apparatus cannot have originated from the branchiopod type (cf. Cannon 1927), it is recognized as a derived branchiopodan ground plan character (Walossek in press).

With the definite assignment of a fossil such as *Rehbachella* an extensive morphological data set becomes available for comparative morphological and phylogenetic analysis of a taxon and its relatives (cf. Schlee 1981, pp. 27, 28). This holds for both synapomorphies of the members as well as for apparent plesiomorphies of the fossil. For example, the trunk limb-shaped second maxilla of *Rehbachella*, also known from *Bredocaris*, the extant Cephalocarida and, most likely, the Lower Devonian *Lepidocaris rhyniensis* (Schram 1986, Walossek in press) strengthens the hypothesis that this limb did not evolve its distinctive form as a 'maxilla' and mouthpart before the branching of the distinctive crown-group taxa.

Again, morphological transformations, often reductions, become apparent with the knowledge of the basic plan seen in the fossil (e.g. head-shield, antennae, maxillae). Apparent synapomorphies thus may turn out to be simply homoplasies resulting from reduction. An example is the convergent modification and reduction of the two pairs of antennae within the different branchiopodan taxa, now known to be also clearly segmented in the Upper Triassic to Lower Jurassic Kazacharthra [up to 15 annuli, according to McKenzie *et al.* 1991, their fig. 12), the presumed sister taxon of the Notostraca (Walossek in press).

The long anamorphic larval sequence of *Rehbachella* permitted the monitoring of the morphogenetic changes of various features. It also has been used to compare ontogenetic sequences of other crustaceans through correlation of the segmentation pattern, which aided the recognition of general rules as well as special trends of all major crustacean lineages (Walossek in press). Hence the ontogeny shows up as an important additional character for phylogenetic analysis.

Perspectives

Part of the faunal associations on hand still have to be fully described. This includes mainly the phosphatocopines, *Dala*, *Walossekia*, and *Oelandocaris*, as well as a number of rare and still unnamed forms. There are also new larvae which cannot be assigned to any larger forms and fragments of hitherto unknown larger animals. Description of larvae with remarkable resemblances to the extant parasitic Pentastomida is under way. The collecting techniques established for the 'Orsten' have not yet been extensively applied to other deposits. The prospects for discovery of similarly well-preserved material in comparable lithologies from other areas and ages are, however, quite promising. Showings along this line have been produced already, for example, in the Lower

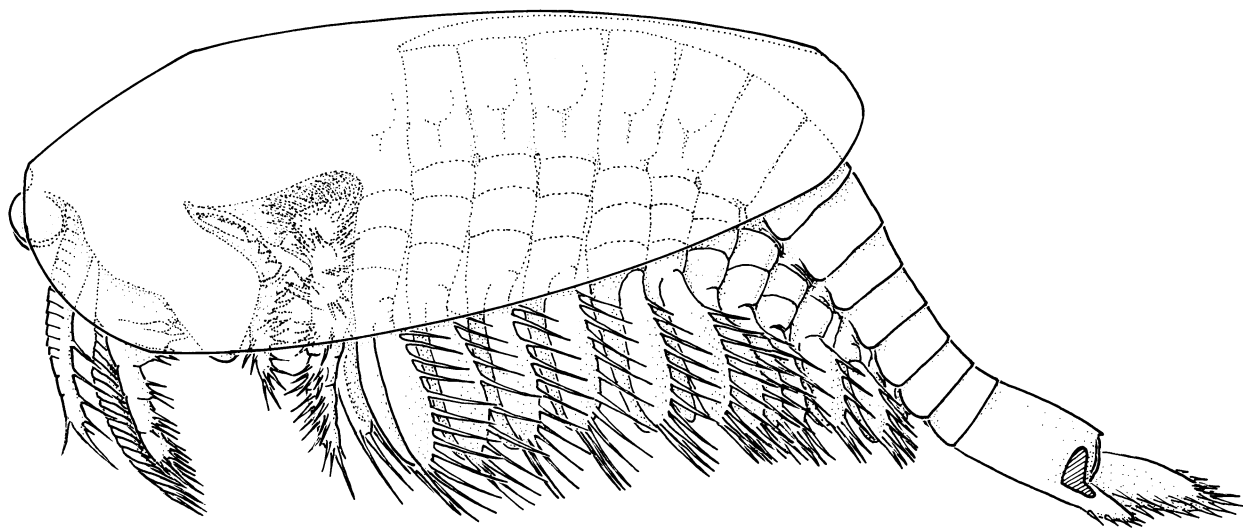


Fig. 4. *Rehbachella kinnekullensis* Müller, 1983; latest larval stage on hand, with 13 trunk segments, which 12 bear limbs of; posterior limbs still rudimentary.

Cambrian at Comley, Shropshire, U.K. (Hinze 1987), in the Middle Cambrian of western Queensland (Walossek *et al.* in press), in the Upper Cambrian of Poland (Walossek & Szaniawski 1991), in the Lower Ordovician of the isle of Öland, Sweden (Andres 1989) as well as Canada (Roy & Fähræus 1989), and in the upper Devonian of the Carnic Alps, Italy (Müller 1982a).

Conclusions

Detailed knowledge of the morphology and larval cycles of the heterogeneous 'Orsten' arthropod assemblages provides a large set of basic information for the reconstruction of the early evolution and development of life strategies particularly of Crustacea and associated forms. This is relevant to the evaluation of the status of characters in phylogenetic analyses. The discovery of a number of crustacean-like fossils with a character set clearly distinctive from that of the true crustaceans resulted in their identification as representatives of the stem-lineage of the Crustacea and recognition of constituent characters of the ground plan of Crustacea, in general, as well as of its crown-group.

Important in this respect is the possibility in such exceptionally preserved fossils of recognizing transformations of characters accompanied by changes in functional requirements which may be disguised or even lost in the evolution of their extant relatives (for the transformations of characters see also Willmann 1989). Dahl (1956) has pointed to the possible evolutionary change of crustacean ancestors toward a more swimming mode of life and, hence, different feeding strategies. An example is the fate of the 'proximal endite', with modifications of retention of its primordial shape on different appendages within the crown-group crustaceans (Walossek & Müller 1990). Its transformation into a distinct coxa on particular limbs is reflected in the larval development of various extant crustaceans, most clearly in the second antenna and mandible, but also in the first maxilla of Cephalocarida (Sanders 1963, his fig. 17). The transformation of the outer ramus of postantennular limbs may be another example.

With regard to the discussion of the validity of 'Mandibulata', we have restricted our argument to the line leading to Crustacea which is well documented in our material. The anatomical, physiological and biochemical data shared between Crustacea and Tracheata cannot be denied; however, many of them have not been clearly established as synapomorphies and their significance is moot. Morphological evidence for the close affinity of the Crustacea and Tracheata remains weak. It is not enough simply to postulate that the many characters of the Tracheata that differentiate them from the Crustacea evolved by reduction from the crustacean condition.

Establishment of evolutionary innovations, apomorphies, in the stem line of Crustacea, indicative of a significant change in the mode of life and recognizable in the stem-group crustaceans, as well as the recognition of their subsequent fate in the different crown-group lineages in the true crustaceans from the 'Orsten', will surely facili-

tate detailed evaluation of the interrelationships of these groups.

It may be possible that the branching point of the tracheates and crustaceans *s.str.* occurred at a specific level of the stepwise transformation of a particular feature. For example, the homologous position of the third head appendage in itself is simply a plesiomorphic character. The question if the tracheate mandible is the coxal portion of this limb, i.e. originating from the 'proximal endite' (= synapomorphy of the members of the 'Mandibulata'), or a basipod outgrowth, i.e. homologous to the original limb corm (plesiomorphic) remains to be answered. In the first instance, the basipod, rami, and their musculature would have been lost in the tracheates, while in the second instance only the rami and their muscles were reduced. Further investigations should be undertaken to determine if the coxal and basipodal muscle systems are or are not congruent, evidence that would point toward an answer to this question.

If synapomorphies between tracheates and crustaceans could be established, this would simply indicate that the Upper Cambrian stem-lineage forms are also members of the 'mandibulate' stem-lineage. The interpretation of phylogenetic interrelationships of the true crustaceans in the 'Orsten' would not be affected, because they belong to specific taxa within this group. The large morphological 'gap' between the true crustaceans and the stem-group forms reflects major evolutionary change in the crustacean lineages after their separation. On the other hand, the recognized set of derived features of Crustacea *s.str.*, in our sense, still contains characters of both tracheate and crustacean ground plans, among which the apomorphies of either group may be sorted out. Until this is demonstrated we prefer to restrict ourselves to features that we can identify.

Our analysis made it possible to recognize a new form from the Upper Cambrian of Poland as another representative of the stem-lineage of Crustacea (Walossek & Szaniawski 1991). Increasing information enforced by the knowledge of the 'Orsten' Crustacea will direct the search for critical characters and facilitate understanding of differently preserved fossils, particularly those of crustacean-like appearance.

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