

phosphate, resulting in unprecedented preservation of the cuticle and three-dimensional fossilization. These fossils are today found in anthracitic limestone nodules primarily in southern Sweden, and together constitute the *orsten* fauna, by far the clearest glimpse we have ever had into marine arthropod life of the Upper Cambrian.

As might be expected, the discovery of three-dimensionally preserved arthropods from Upper Cambrian deposits has yielded numerous surprises. For the Crustacea, these have included the first record from the Upper Cambrian of the class Maxillopoda [if maxillopods are indeed a natural monophyletic grouping, which is far from resolved despite Walossek's feelings on this (e.g. see Abele et al., 1992; Boxshall, 1992 and Wilson, 1992, all in *Acta Zoologica*, 73: 271–392)] with recognition of two new orders (the Skaracarida and Orstenocarida) and, with the present volume, the first record of a true branchiopod from the Upper Cambrian. Equally surprising to me is that, to my knowledge, none of the major western science journals (e.g. *Science*, *Nature*) has carried a word about these incredible finds, even though numerous articles on arthropod phylogeny have appeared among these journals, but based on far fewer data and much more speculation.

The detailed study of the *orsten* arthropods is a classic case of the right persons being in the right place at the right time. In the hands of any paleontologist, these fossils would have formed the basis of an important series of papers; they are in anyone's hands a major find. In the hands of Klaus J. Müller and Dieter Walossek, the animals themselves seem to come to life, and all arthropodologists are the happy beneficiaries. Details of the *orsten* arthropods have appeared in numerous specialized publications, the largest of which are the systematic monographs, a series of meticulously prepared treatments beginning in the early 1980s and published in the journal *Fossils and Strata*. The present volume, the first of the monographs authored by Walossek alone, is the fourth, and is by far the largest and most detailed.

Walossek's study on *Rehbachella* is in some ways his crowning achievement. The paper chronicles the life history and morphology of these

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Sometime around 500 million years ago, minute marine arthropods living on or near a flocculent sediment/water interface were preserved in an unusual manner. Although details of the taphonomic process are not clearly understood, it appears that rather soon after death, the integument of these creatures was impregnated by

minute crustaceans through 30 (!) molt stages, at which time the largest is still less than 2.0 mm long. The volume is divided into several sections, beginning with a brief and informative review of the paleoecological conditions that might have facilitated this very size-biased mode of preservation. The approximately 130 specimens are then described as belonging to one of two slightly different morphological series, with the differences interpreted as intraspecific variability. The series begins with a functional nauplius and proceeds through a well documented, completely anamorphic development until the oldest known stage (at 1.7 mm, and still immature) is reached. A rather lengthy discussion of the presumed life history of the species is presented, followed by a 10-page section on functional morphology of *Rehbachielliella* and crustacean nauplii in general. Finally the significance of the fossils is presented in a 63-page Discussion section, which, because of its size and because there is some redundancy with earlier sections, I found slightly unwieldy. The text is graced throughout with a large series of beautifully detailed line drawings, depicting the various morphological stages, features unique to each stage, detailed comparative graphs of crustacean developmental sequences, comparisons of limb morphology and depictions of presumed function. Walossek argues convincingly for inclusion of *Rehbachielliella* among the Branchiopoda, based primarily on an apomorphic suite of characters that constitute the branchiopod postnaupliar feeding apparatus. He also demonstrates that the second maxilla was not, at least in *Rehbachielliella*, modified as a feeding appendage. This carries with it the very important phylogenetic implication that modification of five appendages into the crustacean head has occurred not once but independently several times, and therefore was not part of the Crustacea ground pattern.

The text is followed by 34 plates of scanning electron micrographs of the highest caliber, with their legends appearing on the facing page. Careful consideration has been given to selection of each photograph, so that all important morphological features are shown, and these details have been carefully incorporated into the reconstruc-

tions of various stages in the text figures. The result is an almost unbelievable treat: readers are given a three dimensional view of an Upper Cambrian branchiopod crustacean.

The sheer size of the volume, and the fact that some ideas are presented in more than one section, is something of a drawback. For example, comments on morphology and phylogeny can be found at various points throughout the 63-page Discussion, and it is sometimes difficult to locate a particular piece of information. Because of the extensive and highly detailed text figures and plates, the list of abbreviations occupies a full page, unfortunately inserted at the very end of the paper (p. 202). This makes comprehension of the figures somewhat difficult, as the reader must constantly flip to the back.

The section in the Discussion on phylogeny is the most exciting, and yet to me the most troubling as well. The excitement comes from the workman-like presentation of competing ideas about where *Rehbachielliella* belongs. Each major grouping of the Crustacea is considered in turn, with discussions of relevant shared synapomorphic features that characterize it and of features that set it apart from *Rehbachielliella*. The inevitable conclusion reached is that we are indeed looking at a member of the class Branchiopoda, a realization of tremendous importance to students of branchiopod and crustacean phylogeny. The trouble comes from what appear (to me) to be a slightly uneven treatment of characters, and an almost dogmatic discussion of where *Rehbachielliella* belongs in phylogeny. Despite what looks like (and is) an enormous amount of data based on unprecedented fossil details, Walossek chooses to construct a phylogeny (fig. 41) based on only 8 characters (or character sets in some cases), many of which seem weak or controversial. He first unites all branchiopods with the class Maxillopoda on the basis of a shared "neck organ" (his character set 1). Little mention is made of the fact that many Malacostraca, including virtually all decapod larvae and the syncarids (e.g. Lake et al., 1974, *Z. Zellforsch.*, 147: 335–351), possess a similar feature. It is true that its function does not appear to be the same (it is an osmoregulatory device in branchiopods and syncarids, and of

unknown but possibly sensory function in decapods), and therefore homology is uncertain. But this uncertainty is even greater in the case of the Maxillopoda where no extant species has such an organ as described by Walossek, and where those that have what is *perhaps* a modified version of it do not use it for osmoregulation. Only one fossil maxillopod (*Bredocaris*) has such an organ (Müller and Wallosek 1988, *Fossils and Strata*, 23: 1–70), which looks to me less like the organ of *Rehbachella* than Walossek's text indicates (e.g. it lacks the cuticular ring that is one of the characterizing features Walossek lists on p. 108). Walossek is certainly aware of the presence of this organ in some malacostracans—he mentions it on p. 110—but ignores it in his table 5 and phylogeny (fig. 41), and therefore leaves the impression that it is indeed a uniquely shared feature of the maxillopod and branchiopod lines. It may be, but it may not, and readers deserve to know this. Another character, proposed to unite *Rehbachella* with the Lipostraca and “Euanostraca,” seems equally weak. A decrease in the relative size of the “neck organ” from larvae to adult (“reduction of the naupliar neck organ during ontogeny,” character set 5) is seen in virtually all branchiopod taxa, and is even evident in Walossek's figures (e.g. figs. 44, 45). It is true that the function of the organ in the anostracan line is probably lost by the adult stage, but we know very little about function in the adult of the other branchiopod taxa. Again, a less dogmatic tone, alerting the reader to possible pitfalls, would have made the text seem less subjective. At times, characters are employed that appear in larval stages only. For example, the “cephalic shield” of anostracans is treated as a major synapomorphy of *Rehbachella* and Anostraca, even though in anostracans this shield is found only in early larval stages (and I am slightly uncomfortable equating this with the carapace of *Rehbachella*). Thus, Walossek is employing a character expressed only in early larvae in one lineage. Yet elsewhere, larval characters apparently are dismissed. The fact that the adult anostracan naupliar eye is basically tripartite (as opposed to quadrapartite in other extant branchiopods) is used as additional evidence for separation of the

anostracans (pp. 72, 107). But according to Dahl (1959, *Qt. J. Microsc. Sci.*, 100: 445–462), notostracans, too, have a tripartite naupliar eye as larvae. Occasional erroneous statements are found (which are to some degree unavoidable, in that much of the discussion is based on a vast amount of earlier literature, not all details of which could be confirmed in a morphological study of one fossil species). Examples are in several statements meant to characterize various “phyllopod” groups [e.g. stating (p. 79) that all spinicaudatans have claspers on the male first and second thoracopod, or that compound eyes are always fused in the laevicaudates, or that laevicaudates bear furcal rami], and some statements supposedly uniting the conchostracans and cladocerans: “development of claspers at least on the first thoracopods” (p. 73), and “internalization” of the compound eyes, which is inferred to be a shared character exhibited by extant cladocerans (p. 71). The cladoceran compound eye may have originally possessed such a pore leading to the outside (as in the Notostraca and both conchostracan lineages), but there is no indication of it now. Thus, the discussion is a mixture of accurate statements based on first hand knowledge, and (fewer) erroneous statements taken from the literature; but the reader will have a hard time knowing which is which. Finally, I was surprised to see evidence of unfamiliarity with taxonomic rules in some places. For example, if the Conchostraca and Cladocera are united, then the oldest available name would seem to be Gerstaecker's (post 1868) “Diplostraca,” whereas Walossek employs “Onychura,” presumably sensu Eriksson (1934), for this grouping. Similarly, the taxonomic authority and date are not given for Euanostraca or Phyllopoda (although Walossek's definition is quite clear), which is particularly unfortunate in light of the many different assemblages that have been united under the latter name (see Fryer, 1987, *Zool. J. Linn. Soc.*, 91: 357–383).

None of these criticisms invalidates the proposed phylogeny. Indeed, he is probably correct. But the reader is left with the impression that the phylogeny (fig. 41) has been made rather than found, using characters selected to support pre-

conceived ideas. Also, I do wish that in several places he might have "softened" the text, to impress upon the reader that even in the face of these exquisite fossils, there is much we do not know. Some of the more dogmatic statements could have been modified to reflect this state of uncertainty, without loss of meaning, and conveying a more open minded treatment. These objections are all minor, and are at most an unfortunate tarnish on an otherwise sterling product.

Some of the above minor criticisms reflect my own personal disagreements with Walossek's interpretation of morphological features and with his phylogeny, and I recognize that this is not the place to argue methodologies or points of view. The real value of this work is not so much the phylogeny, but the beautiful baseline morphological information presented, which will undoubtedly lead to further speculation concerning crustacean evolution. Without question, this paper is a classic and will have to be seriously considered in any future discussion of the evolution of branchiopods or indeed the entire Crustacea.

The price, at US \$48, is an absolute steal (compare what it would cost to gather together virtually every historical reference on branchiopod phylogeny, whether based on fossil material or not; not to mention the *Rehbachella* information itself). No laboratory with an interest in crustacean or arthropod phylogeny should be without this volume.

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