

'Orsten' arthropods – small in size but of great impact on biological and phylogenetic interpretations

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The first secondarily phosphatized cuticular remains in shells of phosphatocopine ostracodes etched from Upper Cambrian limestone nodules ('Orsten') were found in 1975. Since then, processing of more than one ton of rock material has yielded a variety of small arthropods, mainly crustaceans and crustacean-like forms. The exceptional three-dimensional preservation of the bodies, appendages and setation permits a study of the morphology of these animals, down to details less than one micrometre in size. A further advantage is the recovery of series of ontogenetic stages. This permits not only comparisons between the different forms but also monitoring morphogenetic changes of features. Detailed analysis of functional morphology and aspects of life habits (e.g. locomotion, feeding patterns, sensory structures) is also possible. Yet, abundance of phosphatic remains is low and quite uneven: while forms such as phosphatocopine ostracodes are now available in some thousands of specimens, other forms are still known only from single, very incomplete individuals.

One of the forms studied already in detail is *Agnostus pisiformis*. The calcitic shelly remains of larger specimens may be rock-forming. Ventral cuticular details could recently be described from the nine earliest developmental stages up to the first one with the definite segment number. Functional analysis led us to suggest that *Agnostus* could not have entirely opened its cage-like exoskeleton (made of head and tail shields plus two intermediate segments in the largest instars). Most likely it had floated around with slightly gaping shields, being slowly rowed along with the setiferous outer rami of its second

and third limbs. It seems as if the only structure available to gather food was its first antenna which had much less articles than that of trilobites and was equipped with long setae at its inner edge. All the ventral structures (e.g. limbs) were highly adapted to withdrawal and to fitting into the 'box' at complete closure (Fig. 1).

Among a number of arthropod larvae discovered, one type shows striking similarity to the earliest stages of modern pantopods, the only extant chelicerate taxon with early instars. With its huge cheliphores and frontoterminal mouth it may have been ectoparasitic, as are all living pantopods. This is the first record of true chelicerates as early as in Late Cambrian times. If a pair of small hooks are accepted to represent the rudiments of the first antennae it would confirm the assumption that this appendage had become reduced during the early evolution of Chelicerata (Fig. 2).

Other forms could be placed not only close to the Crustacea but clearly within particular sub-taxa (e.g. Skaracarida and Orstenocarida as maxillopod Crustacea, Fig. 3). Other animals are obviously closely allied to these, but structural differences have led us to place them as offshoots from the stem-lineage of the whole group (Fig. 4). These forms not only provide a valuable insight into the early evolutionary path leading toward the modern crustaceans, i.e. the crown group taxa, but they may also have a bearing on controversial aspects of arthropod morphology and phylogeny in general.

The morphology of the majority of forms indicates that they were members of benthic assemblages, possibly living on a flocculent bottom layer, in some cases also within it. Yet, despite

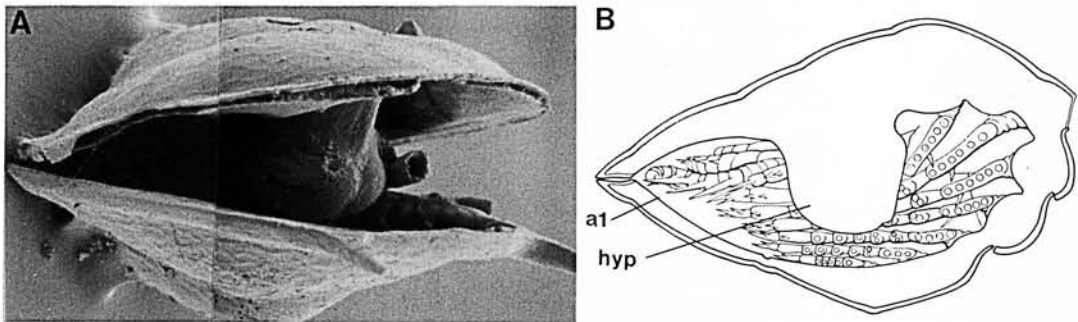


Fig. 1. *Agnostus pisiformis*. □ A. SEM-photograph of specimen from one of the earliest instars, with slightly gaping "shell" (shield length 360 µm); first antennae inserting at the sides of the hypostome as in Müller & Walossek 1987, Pl. 11:1, 17:2). □ B. Reconstructed sagittal cross-section of advanced instars in the "enrolled" position (a1 = 1st antenna; hyp = hypostome).

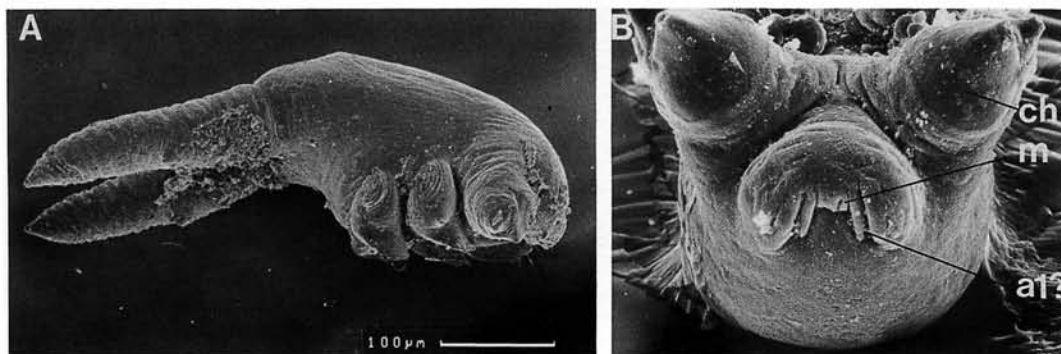


Fig. 2. Unnamed chelicerate larva with presumed affinities to Pantopoda. □ A. Lateral view (same specimen as in Müller & Walossek 1986b, fig. 8a). □ B. Anterior view (same authors, fig. 10; al? = probable 1st antenna, ch = chela, m = mouth).

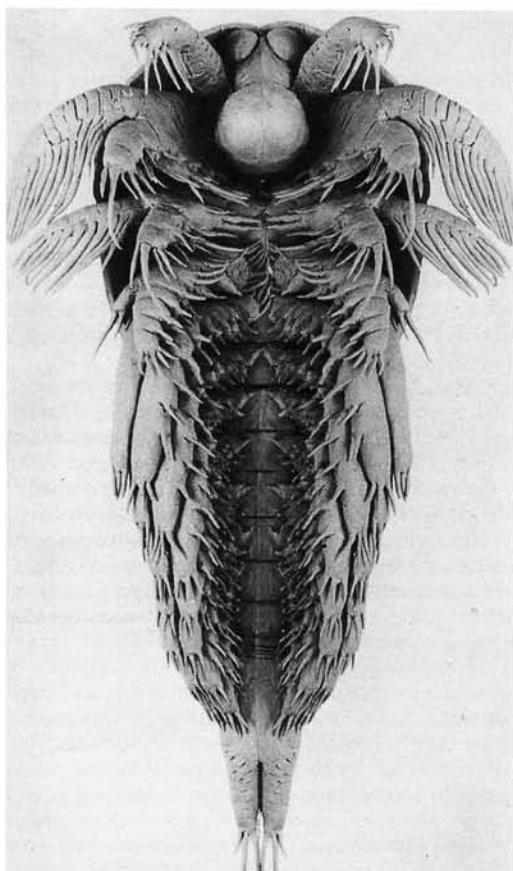


Fig. 3. *Bredocaris admirabilis* Müller, 1983. Ventral view of clay model (combined photographs of one side; total length of animal about 850 μ m; model 500X = 43 cm).

or because of this extraordinary kind of preservation, many new questions arise, for example: the restriction of size in the material (fragments with cuticular remains are always < 2 mm), the

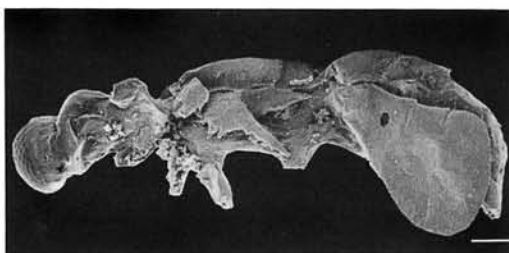


Fig. 4. *Cambropachycope clarksoni* Walossek & Müller, 1990, a stem-lineage crustacean from the Upper Cambrian "Orsten", with faceted eye (on the left) and paddle-shaped uniramous first trunk limb (on the right; scale bar: 100 μ m; from Walossek & Müller 1990, their Fig. 1A, but front turned to the left).

poor record of 'non-crustacean' arthropods, or the apparent distinctiveness between 'Orsten' forms and the Lower to Middle Cambrian arthropods of the Burgess Shale type faunas.

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Origin and early evolution of rugose corals

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The general knowledge of Vendian and pre-Ordovician Cnidaria, and likewise of the earliest rugose and tabulate corals, has increased considerably during the last 30 years. Nevertheless, the origin of both rugose and tabulate corals is still rather obscure.

The earliest rugose corals discovered to date are the Early Caradocian lambelasmatic taxa with monacanthine septa. These are *Lambeophyllum* reported from the Chazyan of North America but more reliably known from Blackriveran, *Hillophyllum* reported from the Gisbornian (middle Lower Caradoc) of Australia and *Primitophyllum* from the Idavere, Jöhvi and Keila Beds (upper Lower Caradoc) of Estonia and the Leningrad area in USSR (for references, see Neuman 1984). The earliest rugose coral discovered in Scandinavia until now is a poorly preserved *Primitophyllum*-like specimen from the upper Dalby Limestone in Jämtland, Sweden. The lambelasmatic corals slightly predate the earliest streptelasmatic and stauriid corals (with fibro-lamellar septa), which appear in the Blackriveran in North America (the earliest genera are *Streptelasma*, resp. *Paleophyllum* and *Favistina*).

The origin of rugose corals has been eagerly discussed for more than 100 years by a great number of authors (see Scrutton 1979 and Neuman 1984 for references). Most seriously evaluated ancestors of the rugose corals are: (1) a Vendian or Cambrian cnidarian such as *Cothonion* Jell & Jell 1976, (2) a tabulate coral, or (3) a sea anemone which developed the ability to secrete a skeleton. Considering the first possibility, the morphological differences between *Cothonion* and the rugose corals indicate that this genus (sensu Scrutton 1979) could be "an early skeleton-evolving side branch to the main line of rugosan descent". Tabulate corals have been widely discussed as possible ancestors for the Rugosa, especially by Russian specialists,

and the genera *Aulopora* and *Lichenaria* have been most seriously considered. I agree with Scrutton (1979) that it is unlikely that a colonial form, such as a tabulate coral, could be an ancestor for all rugose corals, both colonial and solitary.

Detailed studies have convinced me that all rugose corals represent a monophyletic group. No clear intermediates between Rugosa, Tabulata and Scleractinia have ever been found (Hill 1960). Tabulate corals predate both rugose corals and scleractinian corals.

The oldest scleractiniamorph coral found until now was reported by Scrutton & Clarkson (1989) from Upper Ordovician strata of Scotland. It is most probable that all these groups with a presumed ectodermal skeleton had developed separately from sea anemone ancestors. It can also be considered that the first rugose coral was a *Primitophyllum*-like solitary form with a funnel-shaped corallite lacking tabulae or dissepiments, and having very short monacanthine septa.

Lambelasmatic rugose corals with monacanthine septa are dominant in the Caradoc and lower Ashgill. Streptelasmatic corals are sparsely represented in the Caradoc, but undergo rapid diversification in the Ashgill. Stauriid corals appear sparsely already in the Blackriveran (e.g., *Paleophyllum* and *Favistina*), but show low diversity throughout the Ordovician, and become very common in the Silurian. The first genuine tryplasmatic coral, with rhabdanthine or holacanthine septa and lamellar sclerenchyme, have been reported from the Middle Ashgill of Australia and from the Upper Ashgill elsewhere.

Rugose corals with dissepiments of lonsdaleoid type first appear in the late Middle Ordovician with the genus *Estonielasma* (with monacanthine septa) and in the Upper Ordovician with the genus *Paliphyllum* (with fibro-lamellar septa). Globose dissepiments appear first with