

# **New Data on *Kimberella*, the Vendian Mollusc-like Organism (White Sea Region, Russia): Paleocological and Evolutionary Implications**

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The late Precambrian *Kimberella quadrata* Glaessner et Wade, 1966, a member of the Ediacara faunal assemblage, was originally described from the Pound Quartzite of the Ediacara Hills, South Australia. First recognized as a problematic fossil, possibly belonging to the Siphonophora (Glaessner, in Glaessner and Daily, 1959), *Kimberella* was first reconstructed as a medusa of uncertain affinities (Glaessner and Wade, 1966). Known from only a few specimens, it was later interpreted as a pelagic cnidarian medusa, closely related to extant cubozoans or box jellies (Wade, 1972). Later authors reconstructed *Kimberella* as a form similar to extant chirodropid cubozoans or sea wasps (Glaessner, 1984; Jenkins 1984, 1992; Gehling, 1991). Thus, *Kimberella* has been cited as one of the best examples of a metazoan lineage crossing the Precambrian-Cambrian boundary with essentially little morphological change up to the present. It has been used as one of the most convincing

examples countering hypotheses that group all Vendian macrofossils into non-metazoan higher taxa (e.g. Seilacher, 1992). Acceptance of *Kimberella* as an essentially modern cubozoan also has fundamental paleoecological implications. Living chirodropids are fast-swimming predators with powerful venom, and *Kimberella* has so been reconstructed by some workers as a coelenterate predator (Jenkins 1992).

New fossil material from the Vendian has led to reinterpretation of *Kimberella* as a mollusc-like, triploblastic animal with a high dorsal, non-mineralized shell (Fedonkin and Waggoner, 1997). Over 700 new specimens of *Kimberella* have been recovered from the Vendian-aged siliciclastic rocks in the White Sea region of northern Russia during last few years. Significant fossil localities have been discovered in the valleys cut by rivers on the Onega Peninsula (the Suzma, Karakhta, and Solza rivers) and along Zimny Bereg (the Winter Coast) of the White Sea. Radiometric dating of zircons recovered from volcanic ash beds associated with *Kimberella*-bearing sediments give an age of 555 Ma for this taxon (Martin, *et al.*, 2000). All specimens are preserved on the soles of fine-grained sandstones. Several preservation styles of the soft body imprints of *Kimberella* have been observed. In addition to that, an imprint of a separate shell, feeding tracks, crawling trails, and escape structures of *Kimberella* are well documented. The study of this world's richest, collection of *Kimberella* firmly establishes the existence of a morphologically complex, heterotrophic invertebrate of triploblastic grade being part of late Neoproterozoic marine ecosystems. Taphonomic diversity allows observation of extremely fine details of the external morphology, internal anatomy as well as the modes of locomotion and feeding styles of *Kimberella*.

The high dorsal shell of *Kimberella* was covered with numerous protuberances and possessed a hood-like structure on the presumed anterior end. A limb-like outer zone had fine transverse wrinkles. The shell reached up to 15 cm in length, 5-7 cm in width, and was 3-4 cm high. It was stiff, yet flexible. It appears to have been non-mineralized in the early stages of growth but mineralized (presumably with aragonite) in later growth stages. Numerous large protuberances could be interpreted as the sclerites that may have dissolved after death of the organism, in particular due to anoxia caused by the decomposition of the body. *Kimberella's* elongated, bag-like body had an extensive foot with a lateral, delicate fringe. This broad foot could stretch out, expanding far beyond the shell. The complex

musculature of this peripheral foot was able to create a “running wave” used for locomotion (gliding over the floor), respiration, and likely ventilation of the mantle cavity. *Kimberella* had well developed dorsal-ventral musculature, arranged in a metameric (segmental) pattern and fine transverse ventral musculature. This musculature provided the source of locomotion by means of peristaltic contraction, both for movement over the surface of the sea floor and perhaps within the sediment when animals were occasionally buried by sand brought by changing currents or storms. Scratch marks arranged in fan-like patterns have been interpreted as feeding marks produced presumably by a retractable proboscis bearing terminal hook-like organs (Fedonkin, 2001). Other interpretations of these marks are also under consideration. Well preserved cascades of these fan-like scratch marks indicate that *Kimberella* moved backwards during the feeding process (or the feeding organ was situated in the rear end of the body!).

*Kimberella* appears to share many features with primitive molluscs, especially monoplacophorans. The metameric lobes that are preserved on some specimens are clearly the imprints of metameric, dorsoventral muscles, comparable to those in monoplacophorans and chitonids (metameric muscles occur also in the anterior body of some Caudofoveata).. The frilled fringe that is so remarkably preserved on almost all specimens seems to correspond with the fringe of ctenidia. However, when fully extended it certainly flattens, forming an extremely thin lamella. Clearly the folded arrangement occurs when the flange is partly retracted. It is quite possible that this flange was permanently folded when inside the shell where it would increase the respiratory surface without the need to extend much beyond the shell border. A true circulatory system must have been lacking in *Kimberella*, but instead it was rather a meshwork of lacunae as suggested by some specimens. Extension of respiratory folds well beyond the foot and shell may have been because *Kimberella* had not yet developed fringed ctenidia and the inefficient circulatory lacunae required a greater respiratory surface. Or in the absence of efficient predators, the respiratory surface did not need protection (the shell having basically the function of an insertion surface for metameric muscles and not an armour against carnivores). The fact that the ctenidia of monoplacophorans are structurally rather different from those of typical molluscs gives some support to the idea that ctenidia evolved in molluscs independently at least twice. The

presence of a true foot, quite possibly comparable in structure to that of the Monoplacophora, rather narrow and elongated, can be deduced from the trails left by the moving animals. Prominent circumpodial bands close to the base of the respiratory flange may be gonads, nervous tracts, or a very large blood lacuna – it is difficult at this point to be too precise.

*Kimberella* clearly establishes that mineralised shells, so common for most molluscs, were preceded (and that may be common for all shell-bearing phyla) by organic dorsal structures covered by or impregnated with microsclerites so common in later strata. True shells may have developed by fusion of microsclerites. This development occurring simultaneously in a number of phyla, assisted by the presence of specially developed areas of cuticle, could have become the periostracum of later animals.

Some implications of the molluscan nature of *Kimberella* require more attention. If we assume that *Kimberella* is a true mollusc, then this implies that it had a trochophora, a spiral segmentation and this, in turn, further implies that: a) the “Trochophorata” are really a monophyletic assemblage (discarding for the time being the argument by Nielsen (2001) about trochophora and pseudotrochophora) or b) trochophoras are merely polyphyletic “convergenents.” If we assume a) then most all the living phyla must have begun to differentiate well before *Kimberella*, that is, well before commonly assumed.

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