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The bolbozoids and early colonization of pelagic niches by crustaceans

V. Perrier (1), J. Vannier (1) and D.J. Siveter (2)

(1) Université Claude-Bernard Lyon 1, UFR Sciences de la Terre, UMR 5125 PEPS, Bâtiment Géode, 2 rue Raphäel Dubois, 69622 Villeurbanne, France, (2) University of Leicester, Department of Geology, Bennett Building, University Road, Leicester LE1 7RH, UK (vincent.perrier@univ-lyon1.fr / Fax: +33 (0)4 72448382)

The colonization of pelagic environments most probably started early in the evolution of animal life. Fossil evidence from Early Cambrian rocks suggest that ctenophores, medusoid organisms, chaetognaths (Vannier *et al.* 2007) and arthropods were among the pioneer colonizers of non-benthic niches. However, it was not a unique event and successive invasions and faunal replacements took place throughout the Palaeozoic (Vannier *et al.* 2003). Post-Cambrian benthic-to-pelagic ecological shift is exemplified here by bolbozoid ostracods, a group of small marine crustaceans that is assumed to have become pelagic in the Silurian (Siveter *et al.* 1991).

Silurian bolbozoids are atypical myodocopid ostracods, usually much larger (up to 2 cm long) than the average Lower Palaeozoic ostracods. They show a great numerical abundance and a relatively high diversity in late Silurian rocks throughout Europe. They are characterized by a pair of prominent bulb in the anterior part of the carapace, the muscle scars and various types of strong external ornament. Some species such as *Parabolbozoe bohemica* or *Bolbozoe anomala* have a wide palaeogeographical distribution across major oceanic barriers. This widespread distribution added to the facies where they were deposited (black shales), their recurrent pelagic faunal associates, and several morphological features of functional significance (rostrum and caudal process) suggest that bolbozoids were members of pelagic communities, which confirms previous interpretations.

Although mainly preserved in shales, bolbozoids and other myodocopids also occur in nodules preserved typically as clusters of closed carapaces occasionally associated with the remains of cephalopods, eurypterids and phyllocarids. These faunal associations probably preserved *in situ* question the autecology of bolbozoids. They suggest that bolbozoids had a possible scavenging behaviour and possibly fed on carrions of larger animals deposited on the bottom. This hypothesis is supported by similar cases in the fossil record (e.g. Wilkinson *et al*. 2004) and by the scavenging behaviour of numerous Recent myodocopid ostracods (Vannier *et al*. 1998). If this assumption is correct then, bolbozoids and their myodocopid associates were capable of epibenthic incursions and should not be considered as pelagic organisms *sensu stricto* (i.e. living permanently off-bottom).

The anterodorsal bulb of bolbozoids was an unornamented and virtually hemispherical structure and may have housed well-developed visual organs (e.g. compound lateral eye) and the basal part of the swimming antenna. The rostral complex of bolbozoids is identical to that of Recent swimming myodocopes. This important morphological feature of functional importance indicate that Silurian myodocopes such as bolbozoids and associated forms were swimmers that used their second antennae (A2) for locomotion through the water column in the same way as do the Recent myodocopids. The pores present on the carapace of *Parabolbozoe bohemica* and *P. armoricana* are interpreted as possible bioluminescent organs such as those known in Recent pelagic ostracodes.

In conclusion, bolbozoids ostracods were swimmers, living preferentially above dysoxic bottom (possible hyperbenthic niches), had scavenging habits and were possibly adapted to dim-light environments (eye hypertrophy, bioluminescence).