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The problem of early bilaterian evolution

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The next year will be celebrative for 200 anniversary of Charles Darwin and 150 anniversary of his “The Origin of Species...” first publication. Two chapters of this seminal book he dedicated to the geological record. He wrote that “the number of intermediate varieties, which have formerly existed, be truly enormous” but emphasized “the extreme imperfection of the geological record” by which those varieties gone away.

Nowadays, such localities of extremely perfect preservation as Burgess Shale in Canada, Chengjiang in China, Sinsk in Russia, and Murero in Spain provide a “truly enormous” variety of intermediate forms, which represent the beginning of the metazoan evolution. The problem is in the understanding of their real nature. For instance, worm-like palaeoscolecidans are well-known during 130 years, but over a century they were affiliated to annelids. During the last two decades only, it has been proved that these creatures possessing terminal mouth and anus, inverting proboscis with pointed skalids, thick integument built of numerous plates, sensory trunk tubuli, and caudal hooks are probable ancestors of the Cephalorhyncha – a phylum which units some “primitive” worms such as priapulids and kinorhynchs.

It is necessary to note that cephalorhynchs are now accepted close relatives of arthropods and form together the Ecdysozoa clade, while annelids are affiliated with lophophorates and molluscs (the Lophotrochozoa clade). This new conception of the protostomian subdivision is well-grounded by molecular biology including analyses of small subunit rRNA sequences, Hox genes, Na-K ATPase α-subunit gene, and some tissue-specific markers (Aguinaldo et al., 1997; de Rosa et al., 1999; Haase et al., 2001; Anderson et al., 2004). Moreover, Cambrian localities yield a number of forms sharing morphological features with both the Cephalorhyncha and the Arthropoda. These are the Tardipolypoda and Anomalocaridida. Representatives of these groups possess commonly terminal mouth, proboscis, thick integument built of plates – the features typical of cephalorhynchs – but also walking and/or grasping appendages similar to those of arthropods. This set of close similarities has been used repeatedly to build an evolutionary tree of the Ecdysozoa (e.g., Dzik & Krumbeigel, 1989; Budd, 2001). All the authors build basically the same tree (cladogram) rooted within the cephalorhynchs and crowned by the euarthropods.

Despite an apparent logic of such an alignment of the Ecdysozoa, such cladograms are disproved by the absence of any evidence of development of appendages from sensor organs and of the origin of ventral mouth from a terminal opening in the arthropod embryogenesis. Vice versa, many animal clades display a multiple origin of limbless forms, accompanied by axial elongation, from limb-bearing ancestors (e.g., over 100 independent incidences among tetrapod lineages, Caldwell, 2003). Commonly such events related to the following advantages: more efficient locomotion, ability to utilize crevices and to burrow. These were actually the advantages of the stem-group cephalorhynch lifestyle. Consequently, those were the cephalorhynchs which derived from limb-bearing tardypodys through some semi-burrowing intermediates alike Cambrian Facivermis. The latter was a sedentary worm-like animal with lobopodian appendages surrounding terminal mouth and limbless plate-bearing trunk (Liu et al., 2006). Moreover, similarities in the developmental genetic underlying the formation of
insect and vertebrate appendages indicate that an ancient ancestor of tetrapods and arthropods (and, thus, other bilaterians) had primitive appendages, whose formation was under the control of a network of *Hox* genes (Tabin *et al.*, 1999). The fossil record shows that this was a real pattern.

This hypothesis is further supported by comparative embryology and morphology data showing that the ventral side of all bilaterans (excluding the Chordata) is derived from the blastoporal side while the mouth and anus are originated from the anterior and posterior ends of a slitlike blastopore and that bilaterian ancestors crawled on their oral (=ventral) surface (Malakhov, 2004). The hypothesis is also consistent with regulatory gene analysis indicating that early bilaterians indeed were holobenthic (Dunn *et al.*, 2007). A further extrapolation of this idea implies a bilaterian origin within slime molds – social amoebas which already obtained homeobox-containing gene regulating anterior-posterior patterning (Han & Firtel, 1998). Thus the common bilaterian ancestors were motile epibenthic animals which, probably, left some trace fossils in the sediments of 1.7 B.y. old (Rasmussen *et al.*, 2002).

**References**


