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EARLY SHELL ONTOGENY IN BACTRITOIDS AND ALLIED TAXA : COMPARATIVE MORPHOLOGY, SHELL WALL ULTRASTRUCTURE, AND PHYLOGENETIC IMPLICATION

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Early ontogeny appears to be important for phylogeny, but in many groups of fossil cephalopods the initial part of the shell is not known. This paper is based on SEM studies of exceptionally well preserved juvenile shells of bactritoids, orthoceroids and ammonoids from the Upper Carboniferous-Lower Permian of the Southern Ural Mountains. In addition, the shell wall ultrastructure of initial portions of the shell of different taxa of Mesozoic ammonoids and coleoids was examined and compared with that in bactritoids.

Bactritoids are characterised by a marginal siphuncle. However, they initially have a submarginal siphuncle that migrates to the ventral position in the first 2 or 3 chambers. The protoconch is globular or egg-shaped with a boss-like primordial dome on the apex, oftern marked by a ring of modified ornament. There is no cicatrix on the apex of the protoconch. The shell wall is prismatic. The nacreous layer first appears immediately before the primary constriction near the fourth or fifth septum and soon becomes the dominant layer with a subordinate outer prismatic layer. There is no primary varix. The ornament of the initial portion of the shell, if it is present, disappears immediately before the primary constriction. The constriction, with the appearance of the nacreous layer and disappearance of ornament, is thought to represent the end of the embryonic shell, as in the ammonoids (Doguzhaeva, 1996a-c).

In orthocerids, with central siphuncle, the protoconch is cup-shaped and shows a cicatrix. A nacreous layer appears in the shell wall a short distance from the apex. The primary varix is absent. The cicatrix is known to be present in *Nautilus* (Arnold, 1988), orthocerids (Ristedt, 1971; Blind, 1988) and actinocerids (Ristedt, 1971; Doguzhaeva & al., 1996, 1998).

In respect of early shell ontogeny the bactritoids, ammonoids, belemnoids and spirulids stand apart from orthocerids, actinocerids and nautilids. The features which separate them are : 1) a protoconch that is larger than the next chamber, usually separated from the phragmocone, lacking a cicatrix and a nacreous layer (the first branch); on the contrary the protoconch is cap-shaped, sometimes smaller than the next chamber and possesses a cicatrix, nacreous layer appears at very early ontogenetic stage near the apex (the second group).

The bactritoids are distinguishable from ammonoids by lack of a primary varix and an interruption in the shell wall near the primary constriction; prominent features of all ammonoid groups. The bactritoids are thus considered as a separate taxon of the same rank as the ammonoids. However the data do not disprove the origin of ammonoids from the bactritoids but rather confirm it. The latter is also true for the phylogenetic relationship of the bactritoids and coleoids. In respect of shell wall ultrastructure there are no obstacle to believing that the bactritoids were the ancestors of the coleoids.

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Artikel/Article: Early shell ontogeny in bactritoids and allied taxa: Comparative morphology, shell wall ultrastructure, and phylogenetic implication 32