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Contents

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Ammonite maneuverability — a new look at the function of shell geometry

Within the classic functional model, ammonites have been considered as rather rapid nectonic swimmers. In this case streamlining would be important, because it reduces the waste of propulsive energy. This model has the advantage that it relates shell form to ecology in a very simple way. On the other hand several observations make it questionable whether streamlining ever became effective in ammonites. As CHAMBERLAIN (1976) found, the drag coefficient varies between 0.1 (for oxycones) and 0.7 (for widely umbilicate forms), which "is more than an order of magnitude greater than drag coefficients of rapid-swimming fish and squids". LEHMANN (1975) also concluded that "comparison with recent coleoids and with *Nautilus* suggests, . . . , that most ammonoids were poor swimmers". He supports this view with the respiration problems resulting from the comparatively low capability of haemacyanins to absorb oxygen. Summarizing these arguments (Fig. 1), the ectocochliates appear physiologically well separated from known rapidly swimming squids and fishes.

Furthermore, from a study of jet propulsion in *Nautilus*, CHAMBERLAIN (1980) concludes that "*Nautilus*" seems to be much more weakly powered

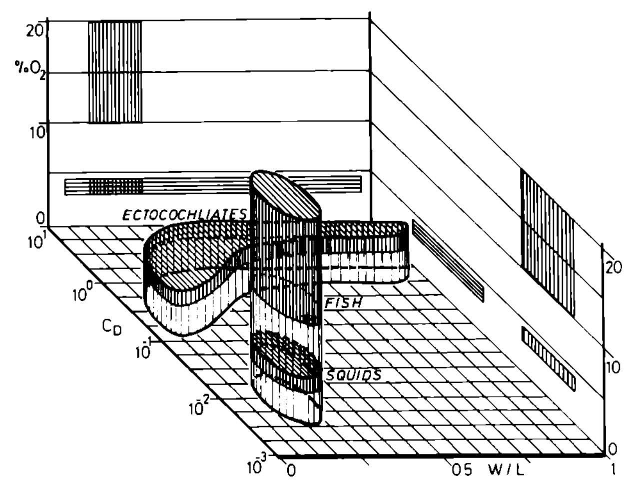

Fig. 1. Swimming capability of ectocochleates, squids and fishes in the three-dimensional space of drag coefficient (C_D), oxygen absorption capability of the blood (% O_2) and width-length ratio of the body (W/L). Data from CHAMBERLAIN (1975) and LEHMANN (1975).

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and inefficient than the others. Estimates of swimming speed in fossil ectocochliate cephalopods, . . . , suggest most were slower than *Nautilus.*"

Nevertheless, general experience and the analysis of anomalies (BAYER, 1970) give us the feeling that some relation must exist between ectocochliate shell geometry and locomotion, though not necessarily via streamlining. Rapid directional changes, rather than speed, may become important in certain environments. This is the case with most fishes living in bioherms and similar environments. As a consequence, they are laterally compressed to increase directional control. This aspect may be fruitfully applied to the locomotional function of ammonite shell geometry.

If a tangential propulsion force is applied to a globular shell, it will start to rotate around its center of gravity, but without much changing its course, while the course will immediately be affected in a discoid shell. But for this function extreme flattening to a cardboard-like disk would not be advantageous either, even if it could be constructed. It follows from the theory of airfoils, which relates shell form to hydromechanics (PRANTL & TIETJENS, 1934), that a streamlined profile is important not only for speed of a swimming apparatus, but also for its maneuverability, which depends on the force resulting from speed, direction of movement and the

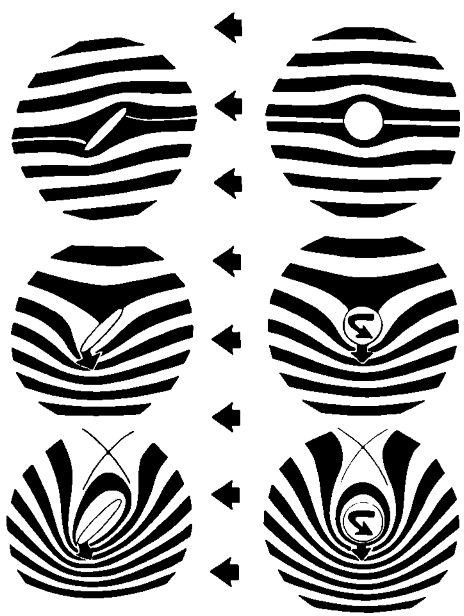

Fig. 2. Idealized conformable streamlines (computed) for a globular and an oxycone shell swimming from left to right. Superimposed circulation around the profile shows the resulting lift (heavy arrow) which positively influences the maneuverability of the oxycone shell.

additional steering impulse. In terms of hydromechanics, this additional force can be described as an asymmetrical lift that results from a circular motion of potential, superimposed on a symmetric flow (Fig. 2). The circular motion of the fluid builds up during the first instance of flow around the disk; in the ammonite case it can be related to the angular jet propulsion used for steering.

If we assume that maneuverability, rather than fast swimming, is the main factor, physiological and hydrodynamical constraints do not invalidate the functional significance of ammonite shell geometry. Furthermore, this view allows us to integrate into the model minor morphological features, such as sculpture, apophyses, and keels. Certain types of keels, for instance, may have functioned as trailing edges separating fluid layers of different velocities. Similarly, apophyses could have supplied an elongated support for the hyponome and thus have improved directional control.

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J. REITNER & T. ENGESER

Phylogenetic trends in phragmocone-bearing coleoids (Belemnomorpha)

Classification

Traditionally coleoids comprise all endocochlean cephalopods. The classification of fossil coleoids is difficult because of their lack of distinctive features and their low fossilization potential. Three groups (supraorders), however, can be easily distinguished: phragmocone-bearing coleoids (Belemnomorpha), Sepiomorpha and coleoids without phragmocone (Teuthomorpha). JELETZKY (1966) classified the orders of Belemnomorpha according to the proostraca. DONOVAN (1977) tried to use the arm-crown and