Swimming abilities of ammonites and limitations

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With 5 figures and 3 tables

Abstract: Using some typical ammonites from the Posidonia shales, the aperture orientation, the ideal direction of propulsive thrust, the stability and the buoyancy of the living animals and of the empty shells were investigated as a function of the body chamber length. The emerging limitations indicate that ammonites were hardly suited for a nectonic mode of life. Only in case of favourable conditions empty shells could ascend to the surface and drift.

Introduction

Based on the famous paper of TRUEMAN (1941) who was the first to estimate and calculate the swimming abilities of ammonites, several papers have been published in recent years dealing with the aperture orientation, stability and buoyancy of ammonites. RAUP (1967) attempted to deduce the functional factors governing the coiling geometry of ammonoids. MUTVEI & REYMENT (1973) investigated the swimming abilities of some ammonites by means of mock-ups. EBEL (1983) calculated weight and buoyancy of some Jurassic forms. Using the equations given by RAUP & CHAMBERLAIN (1967), SAUNDERS & SHAPIRO (1986) evaluated the aperture orientation, stability and buoyancy of some Namurian ammonoids, assuming a nectonic or pelagic mode of life. Based on the results of computer calculations and on morphologic aspects, SWAN & SAUNDERS (1987) classified ammonoids of the Lower Carboniferous in several groups of which the members of which are interpreted as nectonic, pelagic or benthic.

In the following further results of computer-based calculations on some Liassic ammonites will be reported. On the basis of the author's assumption that ammonites were benthic animals the interpretation of the results will emphasize the limitations for a nectonic or pelagic mode of life of ammonites.

Assumptions and computer model

To be able to swim horizontally an ectocochleate cephalopod must fulfil several requirements, namely
- its weight must not exceed its buoyancy,
- the orientation of its aperture must be favourable,
- it must have sufficient stability.

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It is well known that the present-day Nautilus fulfils these requirements. At least during growth the animal's density is less than sea water (Ward 1979), which requires an additional amount of cameral water to compensate for the excess buoyancy.

For the investigation of the swimming qualities of ammonites the computer program, that was developed for the calculation of neutral buoyancy (Ebel 1983), has been modified. The modified program requires the following input data:

- K - spiral constant
- $a_2/a_1$ - ratio of outer radius to inner radius
- $V_w/W_h$ - ratio of ventral width to whorl height
- beta - flank angle
- sculpture factor - factor which takes into account the increase of shell weight by ribs or shell corrugation ($1.0 < \text{factor} < 1.5$)

Densities: sea water = 1.026 gr/cm$^3$, tissue = 1.056 gr/cm$^3$, shell = 2.59 gr/cm$^3$.

Since the sculpture factor can only be roughly estimated certain inaccuracies are inevitable. The spiral constant corresponds in a way to the expansion rate $W$ defined by Raup (1967) and $a_2/a_1$ corresponds to Raup's $D$. The cross section, Raup's $S$, is defined by $a_2/a_1$, $V_w/W_h$ and by beta. For further details of the computer program refer to Ebel (1983). A listing of the AMMONITE program may be obtained from the author on request.

The computer program calculates:
- weight and buoyancy
- the centres of gravity and buoyancy
- the relative stability
- the aperture orientation
- the ideal thrust direction.

The orientation of the aperture follows from the condition that the centres of gravity and buoyancy of a swimming or floating shell must be located on a vertical line. The angle of aperture represents its inclination relative to a horizontal line. The ideal direction of thrust is defined by a line connecting the ventral part of the aperture and the centre of gravity. A movement without pitching can be realized only by holding strictly to this direction. The angle of the thrust direction is compared also to the horizontal direction.

The stability of a shell is expressed by its tendency to return to its initial position following a displacement by a disturbance, i.e. by a propulsive thrust that does not pass through the centre of gravity exactly. As a criterion for the stability, the distance between the centres of gravity and buoyancy was chosen, relative to the maximum diameter of the shell. Since the numerical values of the stability are generally rather small the stability is expressed as a percentage of the diameter as shown in Fig. 2.

The calculations have been carried out using four typical ammonites of the Toarcian, namely Lytoceras siemensi (Denckmann), Dactylioceras commune (Sowerby), Harpoceras elegantulum (Young & Bird), Hildoceras bifrons (Brugière), as well as Nautilus pompilius (Linne) in order to find a standard of comparison. The input data for the computer program have been determined using various illustrations of Schlegelmilch (1976).

Tab. 1. Input data.

<table>
<thead>
<tr>
<th>Shell Type</th>
<th>K</th>
<th>$a_2/a_1$</th>
<th>$V_w/W_h$</th>
<th>Beta</th>
<th>Sculpt.-factor</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Nautilus pompilius</em></td>
<td>0.20</td>
<td>0.05</td>
<td>0.625</td>
<td>5.8</td>
<td>1.50</td>
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<tr>
<td><em>Lytoceras siemensi</em></td>
<td>0.16</td>
<td>0.39</td>
<td>0.65</td>
<td>0.0</td>
<td>1.05</td>
</tr>
<tr>
<td><em>Hildoceras bifrons</em></td>
<td>0.1</td>
<td>0.55</td>
<td>0.70</td>
<td>5.0</td>
<td>1.05</td>
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<tr>
<td><em>Dactylioceras commune</em></td>
<td>0.085</td>
<td>0.633</td>
<td>1.00</td>
<td>0.0</td>
<td>1.10</td>
</tr>
<tr>
<td><em>Harpoceras elegantulum</em></td>
<td>0.11</td>
<td>0.33</td>
<td>0.15</td>
<td>6.0</td>
<td>1.05</td>
</tr>
</tbody>
</table>