REGULATION OF COILING IN PLANISPIRAL AMMONITES, INFERRED FROM CASES OF INFESTATION IN VIVO BY EPIZOANS

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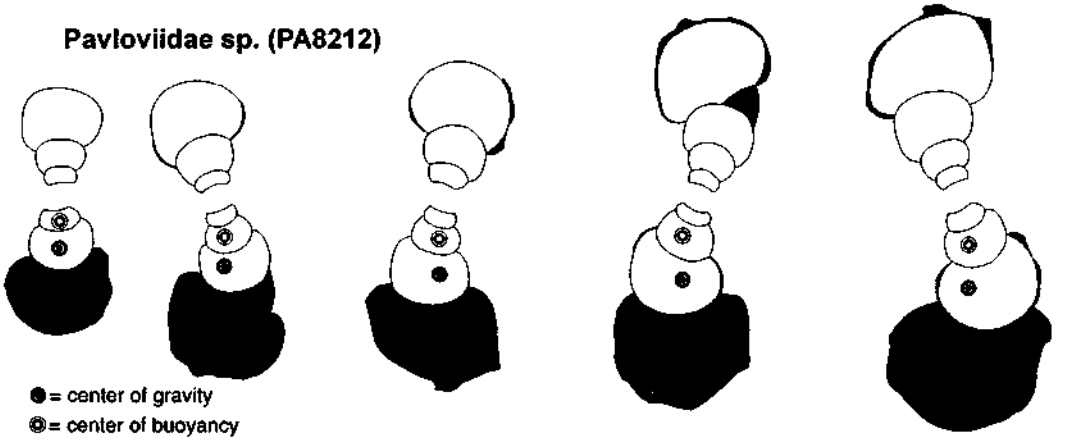
In morphology, abnormalities can be considered as natural experiments which may aid in unravelling morphogenetic processes. This is of special interest in fossils, in which experimentation is not possible. Rare instances of planispiral Jurassic ammonites which were infested by epizoans during life show abnormalities in their coiling pattern, which may decipher the rules followed by ammonites during coiling.

When epizoans settled near or at the venter of the ammonite, the subsequently grown whorl partially went over and surrounded the epizoan in following the shortest path. The whorl then deviated from the previous symmetry plane and this caused the centres of gravity and, to a lesser extent, of buoyancy, to deviate accordingly. The ammonite now floated with the regularly coiled part of the shell inclined opposite to the deviated whorl (scheme, centre left). Since the animal kept the aperture forming a permanent angle with the vertical, during later growth the whorl crossed the venter of the previous whorl and passed on the other side periodically when trying to coil in a new plane (scheme, centre to right views). The scheme shows successive



sections at 90° of an ammonite before (left) and after infestation on its left side. Epizoans which were placed ventrally caused the subsequently grown whorl to detach from and re-attach to the previous whorl. The reconstruction of apertural orientations (taking ribs as old apertures) during all this process indicates that this parameter remained constant and is consistent with a free-floating life style. Two ammonites coiled trochospirally due to epizoans which settled on one side and which caused the shell to be permanently inclined. In order to keep the apertural orientation constant, the whorl remained displaced permanently towards the side opposite to the epizoan. This caused a slight trochospiral coiling.

In summary, planispiral ammonites needed two basic inputs to regulate their coiling geometry: (1) a constant apertural orientation during growth and (2) a permanent attachment to the previous whorl. Therefore, they were mainly based on equilibrium buoyancy.