BIOMECHANICS AS A TEST OF FUNCTIONAL PLAUSIBILITY: TESTING THE ADAPTIVE VALUE OF TERMINAL-COUNTDOWN HETEROMORPHY IN CRETACEOUS AMMONOIDS

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'Terminal countdown' heteromorphy (Seilacher and Gunji 1993), in which the onset of the new mode of growth signals the imminent end of skeletal accretion, is common among Cretaceous ammonoids. Most often represented in ammonoids by a shaft-and-hook-shaped body chamber, this strategy combines determinate growth with the development of novel form. The terminal countdown, like any determinate-growth strategy, can be viewed as a trade-off between continued growth and specialized adult form (with which further growth is incompatible). In theory, the adult morphology should be distinctly optimized to the adult life mode in order to make the trade-off evolutionarily 'worthwhile' (Klinger 1981; Seilacher and Gunji 1993).

But what is the adult life mode to which this morphology is apparently so specialized? Several hypotheses have been advanced over the past century for the function of this shaft-and-hook morphology, centering recently around arguments of hydrostatic stability. Kakabadzé and Sharikadzé (1993) and Monks and Young (1998) propose that the shaft-and-hook body chamber hydrostatically *destabilized* the shell, allowing the nektobenthic heteromorph ammonoid multiple stable orientations. Here I present results of buoyancy-based biomechanical and analytical tests of this hypothesis.

These authors propose two mechanisms by which attitude might be actively controlled during life. Kakabadzé and Sharikadzé (1993) grant ammonoids the ability to control the placement of fluid and gas in the phragmocone, while Monks and Young (1998) allow for mobility of a small ammonoid soft body within the body chamber. These authors find that their mechanisms afford the heteromorph ammonoid up to 110° of attitude lability. Among these models' flawed assumptions is the placement of the (animal+shell)'s center of mass at the center of mass of the soft body. Using life-size models, I show that the buoyancy contributions of soft body and shell material are of the same order of magnitude. Thus the spatial distribution of shell material must be taken into account in buoyancy/attitude calculations. Along similar lines, the distribution of gas and liquid in the phragmocone is found to have little effect on attitude for most morphologies. However, a small, dense, mobile soft body might provide sufficient change of attitude to allow contact with the benthos, especially considering the added weight of the aptychus.

Biomechanics can be the key to testing functional hypotheses. By ruling out the mechanical plausibility of even end-member morphodynamic effects, we can explicitly test functional hypotheses of adaptation. Thanks to the constraint of neutral buoyancy, ammonoids provide strong tests of functional hypotheses for accretionary morphologies. Future work on biostratinomy, ontogeny, geochemistry, and epibiosis will clarify the relationship of T-C heteromorphy to alternate hypotheses of life mode. The adaptive function of heteromorphy in Cretaceous terminal-countdown forms remains equivocal, but certainly less open to debate.