AS THE WHORL TURNS: ROTATION MECHANISMS OF TORTICONE AMMONOIDS

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The peculiar high-spired coils of torticone ammonoid shells present distinct challenges, and advantages, for the potential locomotion of these extinct cephalopods. Ecological consequences for this shell shape are particularly relevant to re-creations of Cretaceous habitats, due to the abundance, diversity, and cosmopolitan distribution of Turrilitidae ammonites of the middle Cenomanian. We examine motility interpretations for generalized torticone shapes through hydrostatics analysis, computational fluid dynamics simulations, and fluid chamber experiments.

We produced a variety of three-dimensional models of helically-coiled shells (simplified coils, and mimics of *Mariella brazoensis*) for analysis of predicted buoyancy and mass distribution. Conches with a variety of coil dimensions should have maintained a horizontally-oriented soft body during adulthood, with the high spire (and empty shell chambers) oriented upwards. *M. brazoensis*, specifically, could have maintained neutral buoyancy throughout ontogeny. This upright posture of the spire would allow the animal's water jet to direct away from the rotational axis at a variety of angles, each resulting in different combinations of translation, lift, rotation, or rocking. Computational fluid dynamics simulations do not illustrate likely scenarios for rapid lateral motion.

Finally, physical experiments in fluid demonstrate the shell's potential to acquire substantial rotation without direct jet action. Models 3D printed to execute buoyancy differences (computed to equal estimations of jet thrust) suggest that torticones may rotate as they rise or

sink through water. Model shape, size, and density each influence the relationship between rotation and vertical motion. Ultimately, a mix of jet techniques could alter the shell's default proclivities to rise, sink, spin, translate, and rock. Overall, we interpret that turrilitid ammonites could have gained substantial ecological advantage from their high-spired helical shells: stately rotation – whether it occur during lateral motion, or while rising or sinking through the water column – would provide steady access to detritus or macroplankton to the hungry cephalopod at minimal added metabolic cost.