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# Testing the hydrodynamics and stability of ammonoids: empirical and simulation studies

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The coiled shells of ammonoids have classically been modelled in theoretical morphospaces with just a few variables. As dynamic accretionary structures, their shells preserve developmental trajectory as well as adult morphology. In traversing mass extinction events, the morphospace occupation of ammonoids was repeatedly reduced, but the clade often recolonized much of this morphospace in the wake of each mass extinction. The gross morphology of ammonoid shells was therefore subject to high levels of homoplasy and convergence. However, it is unclear what precise functions the ammonoid shells may have been optimized for, neither is it known what determined the bounds of their morphospace given that not all geometrically possible forms were realized. We demonstrate that the actualized occupation of Raupian morphospace can be predicted from numerical modelling, given the dual requirements for stability and manoeuvrability, both while stationary within the water column and while swimming. We test these theoretical predictions in two ways: firstly using 3D printed models in waterflow tank experiments, and secondly using computational fluid dynamic (CFD) approaches. All concur that ammonoids were not especially efficient or impressive swimmers. Spherocone forms maximized stability at the expense of manoeuvrability, while platycone and oxycone morphologies were better adapted for more rapid directional change rather than stability. We speculate that the former were optimized for stability within the water column, while the latter were adapted for moving dynamically around obstructions close to the bottom or for predation-avoidance manoeuvres.