



The Swimming Ammonite: How Computed Tomography can Address Questions of Functional Morphology

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The external shell of the ammonite is a readily recognized and iconic fossil yet the function of this structure remain contested. The shell is divided into the phragmocone, comprised of a series of mostly gas filled chambers separated by septa, and the body chamber where the animal would have resided. Quantitative studies of the functional morphology of the shell have relied on geometric simplifications and mathematical models which limit accuracy and invite controversy. Past work has used simplified models which showed adult ammonites as negatively buoyant and were the basis for arguments of a benthic mode of life for adult ammonites. Many palaeobiologists however argue ammonites lived in the water column, if this is true then the shell must possess neutral/positive buoyancy to allow the animal to live in the water column without expending energy to stay afloat. Using exceptionally preserved hollow ammonite fossils and the shells of modern cephalopods: the external shell of *Nautilus pompilius* and the internal shell of *Spirula spirula*, we employ micro-CT, nano-CT and synchrotron x-ray tomography techniques to construct 3D models that are used to evaluate the buoyant properties of the cephalopod phragmocone. This method is applied to the Nautilus to evaluate the accuracy of the method and demonstrates the utility of CT data in volumetric analyses. The phragmocone of a hatchling *Spirula* seems to be capable of supporting the body in the water column with a single chamber, however difficulties in estimating the volume of the soft body create divergent developments of the buoyant properties through ontogeny. Further investigation of the hatchling ammonite *Cadoceras* show that it was capable of achieving neutral/positive buoyancy provided the phragmocone possess three or more chambers. Using this technique we are able to reconstruct the ability of the Nautilus and *Spirula* to maintain a position in the water column by exploiting the buoyancy of the phragmocone. This method has strong potential to address the controversial life-habits of adult ammonites through the study of the buoyant properties of the phragmocone and the structural properties of the shell. The implications for palaeobiology are clear, however the understanding of ammonite life-habits is also important for utilization as archives for palaeoenvironmental/geochemical data.