# SHORT COMMUNICATIONS

# REMARKS ON MUTVEI AND REYMENT'S HYPOTHESIS REGARDING AMMONOID PHRAGMOCONES

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IN their recent discussion of buoyancy control and function of the siphuncle in ammonoids, Mutvei and Reyment (1973, p. 628) have concluded (for shells of the ceratitid type) that 'more than half of the chambers of the last whorl, and probably all the lower chambers of the second last whorl, must have been entirely filled with cameral liquid if the shell functioned hydrostatically'. The siphuncle is supposed to have functioned only in the chambers of lowermost position in the whorls where it was always fully submerged; the liquid completely filling the last half whorl would have prevented the weak terminal siphuncle from exploding under hydrostatic pressure. This would imply that my calculations of depth limits based on the strength of the ectosiphuncle (Westermann 1971) are inappropriate for the adult growth stage for which I inferred migration to shallower water.

Their evidence is (1) the positive buoyancy of several ceratitid models which (p. 625) 'would require weight increases of from 35% to 45% in order to sink' (this corresponds to 26–31% of the camerae filled with liquid, according to the equation $x:(1-x) = 0{\cdot}35$ to $0{\cdot}45$ where $x$ is the proportion of liquid, (2) the general thinning, often leading to non-preservation, of the siphuncle in the last half to one whorl as reported by earlier authors, (3) the slow growth in thickness of the siphuncular wall in ammonoids as opposed to nautiloids, and (4) the absence of the calcareous 'blotting-paper-lining' of *Nautilus*, which is believed to make extraction of liquid impossible in decoupled position.

Simple calculations of the volume increments in phragmocones comprising logarithmic spirals, however, invalidate this model. Linear dimensions increase with the logarithm of the angle of rotation and volume increases with the cube of linear dimensions, as confirmed by measurements on real shells. The ceratitid phragmocone has an expansion rate of about 2·2; with each whorl (360°) the volume will therefore increase at the rate of $2{\cdot}2^3$ so that the volume increment of the last whorl is $(2{\cdot}2^3-1):1 = 9{\cdot}6:1$. For one-half whorl (180°) the increment is $(2{\cdot}2^{\frac{3}{2}}-1):1 = 2{\cdot}3:1$. Therefore the last half whorl contains more than twice as much cameral volume as all previous camerae, i.e. 70% of the total; thus, liquid filling the last half whorl would reduce the uplift of the ceratitid phragmocone by 70%—not 26–31% as indicated by Mutvei and Reyment's experiments. The increment corresponding to their experimental data is only one-eighth to one-sixth whorl (45–60°), if all earlier

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chambers were empty. If high ontogenetic and/or infraspecific variation is assumed, with the expansion rate ranging from 2·0 to 2·4, the respective values for the half whorl increment would lie between 1·8:1 and 2·8:1. Consequently, the assumption of Mutvei and Reyment that more than the last half whorl and probably parts of the inner whorls, are filled with liquid is incompatible with their experimental data. Their model is internally inconsistent. I believe that, for reasons of economy of shell construction, the actual liquid contained in ammonoid phragmocones rarely exceeded 10–15% of the total volume (i.e. the one to three last camerae).

Furthermore, most recently Dr. R. Cowen (oral communication at the Palaeontological Association's 'Phylogeny of Mollusca' colloquium in London, April 1974) has proposed that decoupling of the connecting rings of the siphuncle from the cameral liquid, *not* immersion in it, was required. Cowen suggests that this would prevent significant passive liquid exchange resulting from pressure differentials during the relatively rapid vertical movement powered by the hyponome; while the osmotic liquid exchange would be for buoyancy adjustment and more persistent (e.g. diurnal) vertical movements requiring only relatively slow exchange of liquid. Thus he regards the surface transport of liquid along the cameral walls towards the ventro-marginal siphuncle in uppermost position as a built-in braking system.

## REFERENCES

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# REPLY TO WESTERMANN

MUTVEI: The osmotic regulation mechanism of the volumes of the cameral liquid in recent and fossil cephalopods has been reviewed by Denton (1974) who arrived at the conclusion that in ammonoids this mechanism cannot yet be interpreted in detail. This topic was only briefly touched on in our paper. The main stress was placed with the fact that in prosiphonate ammonoids, the formation of connecting rings has been delayed, which can only mean that several of the last-formed chambers must have been full of liquid. This condition is fundamentally different from that in all other fossil and recent shell-bearing cephalopods. According to Denton (1974), most recent squids are held neutrally buoyant by an ammonium compound in their tissues. It is significant here that the muscular tissue is greatly reduced and that these squids are not actively swimming animals. Their mode of life would appear to be similar to that of the ammonoids which had feebly developed retractor muscles and which for this and other reasons, discussed in our paper, do not seem to have been actively