FLOATING ORIENTATIONS OF CEPHALOPOD SHELL MODELS

by R. A. REYMENT

ABSTRACT. Accurately constructed models of ammonoid shells were used in experiments on floating orientations. These experiments show that inflated shells of the cadicone type float stably, with or without liquid in the final chambers. Highly compressed involute shells are unstable unless the last two chambers contain liquid. The highly evolute shell type, represented by *Dactylioceras*, floats on its side when empty and vertically when the last four chambers contain liquid.

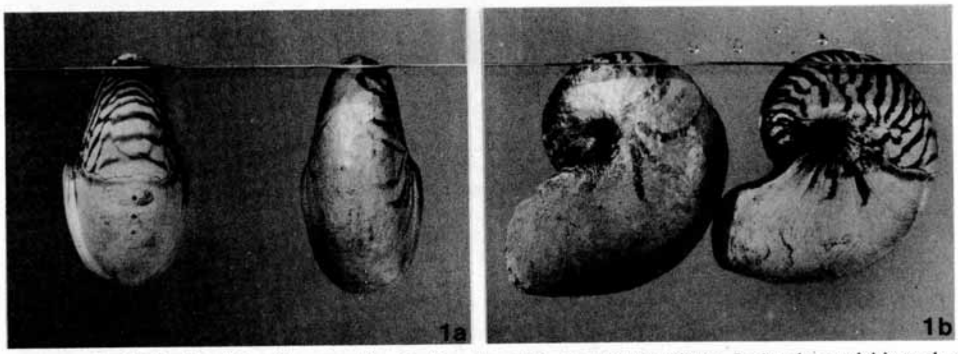
THE present note is a continuation of a series of studies by the writer on the nekroplanktic properties of cephalopod shells (Reyment 1958, 1968, 1970, 1973). The observations summarized here are based on the behaviour of four exact models of ammonoid species; namely, the early Turonian *Hoplitoides ingens* (von Koenen), *Paravascoceras hartti* (White), and *Pseudaspidoceras*? sp., and the Toarcian *Dactylioceras* sp. The first three forms were selected from Brazilian specimens in the Palaeontological Museum of Uppsala University; the *Dactylioceras* comes from the Jurassic of Great Britain.

In order to test the accuracy of the techniques used for making the models, as well as the structural assumptions involved, a model of *Nautilus pompilius* was made. Motion pictures were made of all experiments.

METHOD OF CONSTRUCTION OF THE MODELS

The models were made from actual specimens in the following manner. The ammonoids were dissected, and the component parts for the models prepared by means of a commercial vacuum-moulding apparatus. The technique of vacuum-moulding consists of quickly sucking a preheated sheet of plastic of suitable thickness around a plaster-of-Paris mould. Vacuum-moulding is a widely used method for making children's toys. The required specific gravity (here taken as 2·89) was obtained by copper-plating the plastic parts until the desired weight had been obtained.

Although the models were produced in as accurate a way as possible, it is difficult to be absolutely sure how close to the original shell a particular replicate may be. In order to test the reliability of the method of construction used, a shell of *N. pompilius* was made as a control. The resulting model is shown in text-figs. 1*a*–*b*, floating alongside a real shell of the pearly nautilus of about the same size.



TEXT-FIG. 1*a*–*b*. Model of *Nautilus pompilius* floating alongside an actual specimen. In 1*a*, the model is to the right, in 1*b* it is to the left.

[Palaeontology, Vol. 23, Part 4, 1980, pp. 931–936.]

The experiments were made on empty and weighted shells thereby simulating the effect of the animal in the body chamber. Salt water at a concentration of thirty-three parts per thousand was used.

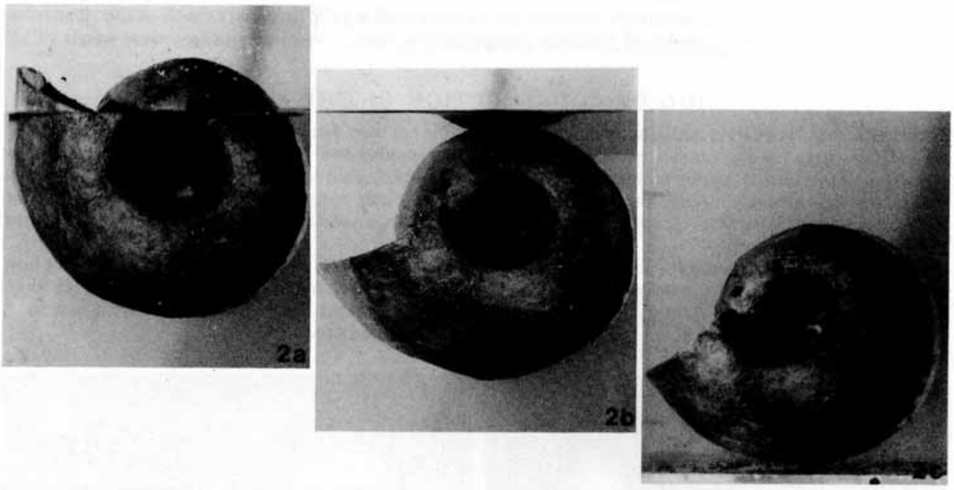
INFLATED SHELLS

Two kinds of moderately evolute, inflated shells, with square to broadly oval whorl sections, were made for studying the properties of this kind of ammonoid. Both were found to possess quite similar buoyancy properties.

Cadicone shell

The species *P. hartti* (White) is a typical cadicone, with whorls in adults appreciably wider than they are high (depressed whorl section). The specimen on which the model was based has a diameter of 20 cm. The following observations were made on the model and simulated ammonoid animal.

1. All chambers empty: the shell floats with 20% of it above the water, measured in terms of the diameter at right angles to the water surface. The aperture faces upwards (text-fig. 2*a*).
2. Three chambers liquid-filled: the shell is just in contact with the water surface but does not break it (text-fig. 2*b*). The aperture is lower than for the orientation shown in text-fig. 2*a*.
3. Fourth chamber quarter-filled: the shell sinks to the bottom. The resting position taken up by the cadicone is shown in text-fig. 2*c*.



TEXT-FIG. 2. *Paravascoceras hartti* (White), Early Turonian (Cretaceous). *a*, floating orientation of empty shell. *b*, floating orientation with the last three chambers liquid-filled. *c*, with some liquid in the fourth last chamber, the shell sinks, showing resting position of the model. Weight of 'animal' added to model (uplift compensated).

A highly ornamented evolute shell

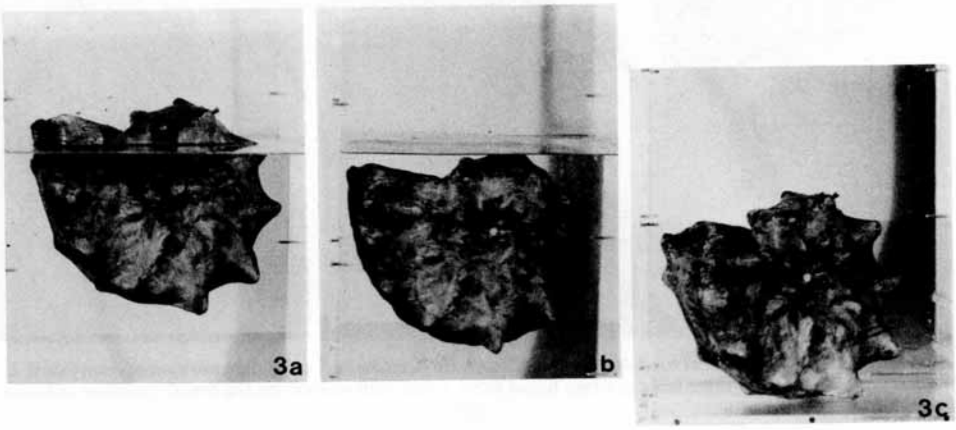
The form here determined as *Pseudaspidoceras*? sp. has a diameter of 32 cm. Its whorl section is square to rectangular and the prominent tubercles are hollow and open to the chambers. The question of whether tubercles are hollow, open or floored, or solid, is of consequence in buoyancy studies. The ammonoid animal was not simulated in the experiment recorded below.

1. The empty shell: this model floats with 26% of the shell above water; the aperture faces upwards (text-fig. 3*a*).

2. Three chambers liquid-filled: a small part of the shell remains above water; the aperture is still directed upwards.

3. Four chambers liquid-filled: the shell is just buoyant; the aperture is now lower than that shown in text-fig. 3*a*. The orientation for this stage of the experiment is shown in text-fig. 3*b*.

4. Fifth last chamber quarter-filled: this slight increase brings about an immediate loss of buoyancy. Prior to this, the shell floated with the body chamber directed upwards (text-fig. 3*c*).



TEXT-FIG. 3, *Pseudaspidoceras*? sp., Early Turonian (Cretaceous). *a*, floating orientation of empty shell. *b*, floating orientation with last four chambers filled. *c*, loss of buoyancy occurs when a small amount of liquid is added to the fifth last chamber.

COMPRESSED INVOLUTE SHELL

The oxynote variety of shell

This was studied by means of a model of *H. ingens* (von Koenen), based on a very large specimen with a diameter of 49 cm. The ammonoid animal was not simulated in the experiment recorded below.

1. Floating position of the empty shell: this is unstable and the shell floats at an angle to the water surface, with 17% of the shell above water (text-fig. 4*a*).

2. Three chambers liquid-filled: a small fraction of the shell remains above water; the aperture of the body chamber is lower than for the empty shell (text-fig. 4*b*).

3. Four chambers liquid-filled: the shell sinks when four chambers are entirely full of liquid, and the resting position adopted is shown in text-fig. 4*c*.

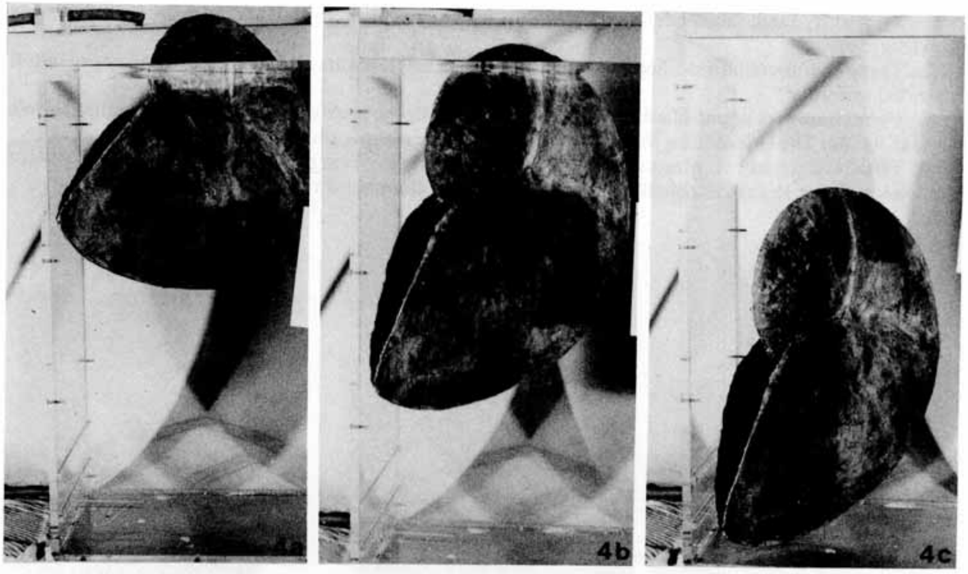
SERPENTICONE SHELL

The highly evolute shell

This type was investigated by a model of a specimen of *Dactylioceras* sp. with a diameter of 23 cm. The weight of the ammonoid animal was allowed for in the experiment described below (text-figs. 5*c*–*f*).

1. The floating position of an empty shell is illustrated in text-fig. 5*a*.

2. Three chambers liquid-filled: the shell just breaks the surface of the water but remains horizontally oriented (text-fig. 5*b*).



TEXT-FIG. 4. *Hoplitoides ingens* (von Loenen), Early Turonian (Cretaceous). *a*, floating position of empty shell. *b*, floating orientation with three last chambers liquid-filled. *c*, the shell sinks when the fourth chamber contains liquid.

3. Last four chambers liquid-filled: there is an abrupt change in orientation, and the shell becomes vertical. It floats upright and is reasonably stable; this is presumably the living position of the dactylioceratid animal. About 6% of the shell remains above water.

4. Last four and a half chambers liquid-filled: the shell does not break the surface of the water and sinks gradually to the bottom if struck sharply (text-fig. 5*c*).

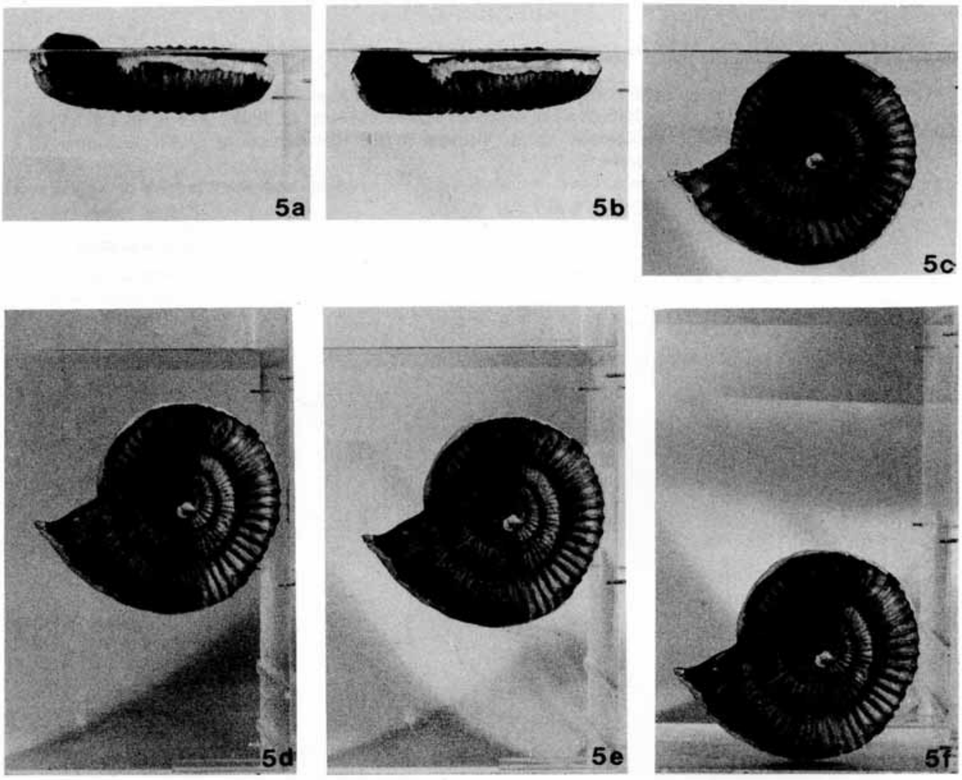
5. If held at the depth indicated in text-fig. 5*d*, the shell rises slowly to the surface.

6. If held at the depth indicated in text-fig. 5*e*, the shell sinks slowly. In both stages (5) and (6) the shell contains the same amount of liquid. A motion picture is available of this part of the experiment. Careful frame-by-frame study shows that the serpenticone type of shell, as represented by *Dactylioceras*, reacts sluggishly to movement when in a state of buoyancy equilibrium. On the other hand, it appears to be as stable as, for example, the cadicone with respect to its vertical orientation.

7. Resting position of the model on the bottom of the tank (text-fig. 5*f*).

CONCLUDING REMARKS

The suite of experiments briefly reported here indicates the variability in stability shown by various kinds of ammonoid shell. The most stable of the types studied is represented by shells with depressed whorl sections; next, are shells with a sub-quadrate whorl section and a moderate degree of evolution. A highly compressed and involute shell form, such as possessed by many species of *Hoplitoides*, does not float in a vertical position when empty. The same observation applies for highly evolute, serpenticone shells of dactylioceratid type, which when empty float in a horizontal position. Serpenticones, when normally weighted with cameral liquid, appear remarkably sluggish when forces are applied to them.



TEXT-FIG. 5. *Dactylioceras* sp. Toarcian (Jurassic). *a*, horizontal floating position of the empty shell. *b*, with the last three chambers liquid-filled, the shell just breaks the surface, remaining horizontally oriented. *c*, with the last four and a half chambers liquid-filled the shell is in hydrostatic equilibrium. *d*, held at 6 cm below the surface of the water, the shell floats to the surface. *e*, held at 7·5 cm below the surface of the water, the shell sinks slowly to the bottom. *f*, the resting position of *Dactylioceras* on the bottom of the tank.

In an earlier study (Reyment 1973), the effect of varying the length of the body chamber on the floating orientation of empty shells was the main topic of interest. In the present paper the body chamber was allowed to remain a constant length, the experiments being directed towards studying the relationships between the amount of liquid in the last chambers of the final whorl and the floating orientation of the shells.

Compared with Reyment (1958, 1973) and Mutvei and Reyment (1973), the work here summarized gives answers to several questions which could not be treated with the cruder models used in the earlier investigations.

Acknowledgements. Very special thanks are due to Mr. Bertil Annell for his interest and skill in making the ammonoid models. The entire method for producing them was worked out by him in consultation with Mr. Eric Ståhl. Mr. Annell also actively assisted with the experiments. My thanks also to Mr. Gustav Andersson, who photographed the experiments, including the cinematography. All the above are at Uppsala University.

REFERENCES

MUTVEI, H. and REYMENT, R. A. 1973. Buoyancy control and siphuncle function in ammonoids. *Palaeontology*, **16**, 623-636.

REYMENT, R. A. 1958. Factors in the distribution of fossil cephalopods. *Stockh. Contr. Geol.* **1**, 97-184.

—— 1968. Orthoconic nautiloids as indicators of shoreline surface currents. *J. Sedim. Petrol.* **38**, 1387-1389.

—— 1970. Vertically inbedded cephalopod shells. Factors in the distribution of fossil cephalopods, **2.** *Palaeogeogr. Palaeoclimat. Palaeoecol.* **7**, 103-111.

—— 1973. Factors in the distribution of fossil cephalopods, 3. Experiments with exact models of certain shell types. *Bull. Geol. Instn. Univ. Uppsala*, N.S. **4**, 7-41.

R. A. REYMENT

Paleontologiska Institutionen
Uppsala Universitet
Box 558
S751 22 Uppsala
Sweden

Typescript received 13 September 1979
Revised typescript received 5 January 1980