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FACTORS IN THE DISTRIBUTION OF FOSSIL CEPHALOPODS

Part 3: Experiments with exact models of certain shell types

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Abstract. This paper is a direct continuation of Reyment (1958) on experimental studies on cephalopod shells and Reyment (1970) on field observations on vertically oriented cephalopod shells in the fossil record. An analysis of recent literature on the postmortal distribution of cephalopod shells is followed by an account of the method of construction of the models used in the experiments. The technique of vacuum-moulding was used to reproduce the shape of the shell and the required increase in specific gravity was obtained, either by electroplating the model, or by coating it with a suitable lead-base paint. Experiments were made on some types of Palaeozoic nautiloids selected among the lituitids. These were found to float in seawater when empty. Three ceratitic forms were chosen upon which to base the construction of exact models of coiled shells of a general type. These coiled shells of varying degrees of inflation float relatively much higher in seawater than does a shell of *Nautilus pompilius* of the same size. It is suggested that the ammonoids contained much more liquid, relatively, in their chambers during life than does modern *Nautilus.*

Three models of extremely evolute cephalopod shells were constructed, which were made to differ with regard to the length of the body chamber; thus, one had a body chamber of three fourths of a whorl, one a body chamber of exactly one volution and one a body chamber of one and a half whorl. The first two shells float with a roughly horizontal orientation, whereas the last-mentioned floats vertically, providing the body chamber is completely full of water. This condition is unstable, and air readily enters the body chamber. As soon as this happens, the shell floats roughly horizontally. The horizontal orientation is the stable one for this shell type.

The behaviour of almost waterlogged shells was investigated for the ceratitid and evolute models. Various kinds of drag- and impingement marks made on the sediment by these shells when they are shifted by currents, are discussed and figured. The evolute shells orient themselves naturally at right angles to the direction of water-flow.

A simulatory study of the effects of putrefaction of the soft parts on the buoyancy of the shell was carried out.

A quantitative study of the growth of younger chambers of coiled nautiloid and ammonoid shells was made with the end in view of analysing the relationship between cameral capacity and size, and the possibility of "fingerprinting" individual cephalopods by means of their cameral growth patterns.

The multivariate statistical method of principal coordinates analysis was used in a comparative study of the relative buoyancy capabilities of 42 Jurassic and Cretaceous ammonite shells of various inflations and degrees of evolution, in order to produce a graded chart.

The study is concluded with notes on recent information on the distribution of *Nautilus* in the Pacific and Indian Oceans.

INTRODUCTION

This publication presents the third part of my studies on the necroplantkonic behaviour and postmortal fate of chambered cephalopod shells. The first part, issued in 1958 (hereinafter referred to as Part I), contains an account of a series of experiments based on the shells of two species of living *Nautilus* and some simple plastic models of nautiloids. It should be kept in mind that this study was not concerned with reconstructing the mode of life of some fossil species of shell-bearing

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* Part of this work was carried out while the author was a Visiting Professor at Syracuse University, New York State, U.S.A.

cephalopods; its aim was to elucidate the probable postmortal history of some types of chambered shells. In this respect, its goal could be claimed to be palaeoecological, without being palaeobiological.

The experimental work accounted for in Part I showed that the single most important factor amongst the interacting variables in deciding the postmortal buoyancy of a cephalopod shell is the length of its body chamber. The shape of the shell comes next in importance. Factors of lesser rank are: the thickness of the shell substance, the number of septa, and the effects of temperature and salinity. Intuitively, one might expect the thickness of the shell wall to be a first-rank factor. That this is seldom so is a reflection of the rigid bounds within which this variable is contained in that shell thickness does not differ greatly among the majority of cephalopods.

A highly compressed, involute shell with a large body chamber would sink postmortally, but it would remain upright on the seafloor, unless it should have happened to have sunk into deep water in which it would run the risk of implosion upon reaching some critical depth.

Special attention was paid in Part I to the hydrostatical properties of certain uncoiled types of cephalopod shells. The necroplanktonic behaviour of a stylized *Michelinoceras* and a stylized *Endoceras* was investigated by means of plastic models. It was found for the first-mentioned morphological type that, in order for it to have floated posthumously, the body chamber must have had to have been less than one half of the total length of the shell. For the latter type of shell, the body chamber must have been less than one fourth of the chambered length of the shell if it were to have floated after the loss of the soft parts.

The conclusions put forward in Part I were based mainly on laboratory experiments, and direct field evidence occupied a subordinate position. The second part of the present work appeared in 1970. It was concerned with the analysis of observations made over a period of 12 months, on vertically inbedded (I prefer this spelling to "imbedded" and "embedded") cephalopod shells. It was quite out of the question to publish an account of each occurrence I had seen and recorded since 1958, and I decided, therefore, to confine myself to the period 1968—1969. During this twelvemonth, I investigated occurrences of cephalopods in the Lower Ordovician of Jämtland (Sweden), the Middle Triassic (Hauptmuschelkalk) of Unterfranken (Germany), the Callovian of the Jurassic of Yorkshire and Brora (United Kingdom), and the Neocomian of the Cretaceous of the Iardomovacia Valley (Romania). This investigation showed that vertically oriented cephalopod shells are far from rare, a natural outcome of the fact that the postmortal history of a chambered cephalopod shell is correlated with its buoyancy potential.

The aim of this third part is to present the results of further experiments on more refined models than were used in Part I, to examine the possibility of using statistical methods in the analysis of shell shape and buoyancy potential and in the study of buoyancy adjustments in the immature shell, and to review recent work in the field, setting this in relationship to the reasoning used in my approach to the subject of cephalopod dispersal.

As in Part I, I have preferred the experimental approach, for I am convinced that the kind of problem represented here can only be solved by direct laboratory work; the role of speculation should be restricted to the planning of sound experimental procedures. As I shall demonstrate, mathematical analysis is a useful accessory, but it cannot lead to a yes-no decision on postmortal buoyancy properties other than in clearcut cases, sadly few in practice. Perhaps the main value of the mathematical study of shell-shape lies in its ability to range conches of different build into a "buoyancy continuum".

As the work with the present set of models progressed, it became apparent, that despite the range of shell types chosen for study, it was not going to be possible to develop a general hypothesis for the postmortal buoyancies of cephalopod shells. To do so would have necessitated the construction of a much greater number of models than has been possible within the framework of the study.

ACKNOWLEDGMENTS

An experimental investigation based on models must, needless to say, rely to a large extent on the exactness with which the models have been made. In this respect, I am greatly indebted to the laboratory engineer at Paleontologiska Institutionen, Mr. Eric I. Ståhl, who is a professional sculptor, clearly an essential qualification in a project of the present kind. Due to Ståhl's painstaking work, I believe that our models are close replicas of the cephalopod shells they are meant to portray. The photographical work and cinematography were carried out by Mr. Gustaf Andersson and the illustrations were prepared by Mrs. Dagmar Engström, both of Paleontologiska Institutionen. Mrs. Mary Koch, Heroy Geological Laboratory, Syracuse, typed the manuscript.

I am grateful to Professor Å. Sundborg and Associate Professor J. Norrman for permission to use the facilities of the Department of Physical Geography at Uppsala. Mr. C. F. Fowler, Honiara, Solomon Islands, greatly aided my project by carrying out a careful study of the distribution of stranded shells of *Nautilus pompilius* in the Solomon Islands and the Santa Cruz Islands.

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I wish to mention that I have greatly profited from discussions with Professor David Raup (Rochester, New York, U.S.A.) during his visit to Uppsala in May, 1972, and my colleague at Paleontologiska Institutionen, Dr. H. Mutvei. Professor James Brower, Syracuse University, read the manuscript and by his constructive criticism greatly improved its presentation.

The subject matter of this paper has been presented as a talk at the universities of Harvard (Mass.), Indiana (Bloomington), Princeton (N.J.), McMaster (Hamilton, Canada), Rochester and Syracuse (N.Y.). As a result of these talks, I have received useful advice from Professors Gerd Westermann, A. Fischer, D. Raup, D. Hatton, B. Kummel and S. J. Gould, and Dr. J. Chamberlain and Mr. R. Vicenzio. I wish to acknowledge this debt of gratitude.

REVIEW OF RECENT LITERATURE

This chapter contains an analytical review of the more pertinent literature on the postmortal history of chambered cephalopod shells that has appeared since the preparation of Part I, in which the literature up to 1959 was annotated. Studies on the interpretation of the behaviour of the living animal have not been included.

Seilacher (1963, p. 599) interpreted tracks in Solnhofen sediments as having been made by the venters of rolled, waterlogged perisphinctids. His interpretation of other tracks as the drag marks of partially waterlogged, upright perisphinctids may be correct in part. However, as I demonstrate experimentally, waterlogged but upright evolute shells of the perisphinctid type tend to orient themselves at right angles to the direction of the current. Certain aspects of this question are taken up experimentally in the present paper (p. 15). Seilacher (op. cit.), discussing thougtfully the secondary displacement of cephaloped shells, suggested that vertically inbedded shells may weather readily out of the host rock and then be spun along by currents, like hoops, as it were. I have not been able to duplicate this experimentally, neither with fossils nor plastic models. One of the interesting topics discussed in this publication is the quite large number of shells which Seilacher believes had originally a vertical orientation. (The high frequency of vertically inbedded shells in the Middle Triassic of Germany was documented in Part II.)

Geczy (1959) discussed the occurrence of vertical ammonite shells in the Hungarian Jurassic. Although he specifically proclaimed his acceptance of the general idea of necroplanktonic dispersal of chambered cephalopods, he dismissed this as being of slight regard for ammonites. This conclusion was not supported by experimental studies, nor by specific references to particular shell types.

Toriyama *et al.* (1965) reported on drifted *Nautilus pompilius* shells from the islands of Ko Phe

Tra and Ko Tarutao on the western coast of Thailand. Some of the shells they collected were very damaged. The finds on Ko Tarutao were made high up on the beach in the zone of fringing shrubs and grass, together with driftwood and shells of *Sepia.* It was concluded that these buoyant objects tend to be concentrated by storms along the maximum high-water mark.

Stranded *Nautilus pompilius* often occur in considerable numbers on the southern beaches of the island of Penang, off the northwestern coast of Malaya. While visiting Kuala Lumpur in 1964, I was shown a fine collection from Penang by Mr. Clive Jones, then of the Geological Survey of Malaya. Not one of the shells in this collection had escaped damage and all seemed to me to be smaller than any average *pompilius* I had seen previously. The damage to the Penang shells takes place during their passage over the fringing reefs of the island.

Kelling and Whitaker (1970) attributed marks in Palaeozoic sediments of Norway to transported orthoconic nautiloids rolling or impinging on firm mud bottoms. Their analysis of the tracks is very persuasive.

Seilacher's *Buchiceras* is next for consideration. This case is tending to become a palaeontological *cause célèbre.* Seilacher (1960), in a note, described and interpreted an oyster-encrusted specimen of *Buchiceras bilobatum* from the Upper Cretaceous of Peru. The oysters are attached to both sides of the shell. Seilacher believes that the encrustation took place during the life of the animal and that it could not have been a "bottom crawler", otherwise oysters could not have settled on the venter of the body chamber. Heptonstall (1970) re-interpreted this specimen on the basis of the information contained in Seilacher's note and used it for speculations on the mechanism of buoyancy control in *Buchiceras.* The general morphology of *Buchiceras bilobatum* is close to that of the most inflated of the three ceratitic models treated later, namely, that of *Acanthoceratites.* According to the results obtained in the present project, a necroplanktonic *Buchiceras* shell would hardly have had its buoyancy affected by the load of oysters involved in Seilacher's case, owing to the considerable buoyancy excess of many ammonoid shells in the postmortal state (Mutvei and Reyment, 1973). It seems most probable to me that the oysters on the *Buchiceras* shell did settle on it while it was freely floating, but not during the life of the animal. This, I think, is the most reasonable explanation, as anybody who has observed oyster-encrusted flotsam and jetsam in tropical lagoons and bays would be inclined to agree. This is not to say that epizoans could not have settled on living animals — serpulid tubes are sometimes found on the venters of inner whorls of *Nautilus* (e.g., specimen in the collection at McMaster University, Canada).

Teichert (1970) has recorded an oyster-encrusted, necroplanktonic shell of *Nautilus* and a further specimen encrusted with corals and bryozoans. In both cases, the epizoal growths are inside the body chamber. Cretaceous ammonite shells with oyster encrustations are not uncommon. I have figured a specimen of *Wrightoceras wallsi* (Reyment, 1955, pl. 24) with an oyster-encrusted body chamber. The ceratitid collection of the Department of Palaeontology, Uppsala, contains several specimens of *Ceratites* s. l. with encrustations of the pelecypod *Placunopsis,* and there is a large specimen of *Pachyvascoceras carteri* (Barber) with encrustations of *Exogyra olisiponensis* Sharpe. Vascoceratids are frequently oyster-encrusted. The occurrence of encrustations of *Placunopsis* on a specimen of *Ceratites semipartitus* (Montfort), reported on by Meischner (1968), seems to have had the same history as the oysters on the *Buchiceras.*

A statistical analysis of this placunopsid encrustation, by means of standard methods of the statistics of circular distributions (Reyment, 1971), suggests the following conclusions: 1) During the necroplanktonic phase in the history of the ammonoid shell, it was settled upon by several swarms of larvae of *Placunopsis ostracina*; 2) the shell probably stranded in a shallow pool and was again settled on by larvae of the pelecypod; 3) the conch finally toppled over onto its left flank to provide once again a settling surface for larvae of *Placunopsis.* An important link in the chain of argument developed by Meischner (*op. cit.*) is provided by his interpretation of the immediate postmoral phase of the ceratite animal. The carcass and shell are rightly considered to have been driven to the surface, but with the body chamber and defunct animal uppermost. It is, however, shown experimentally (p. 24) that this orientation is an hydrostatical impossibility.

Raup and Chamberlain (1967) revised Moseley's (1838) and Trueman's (1941) work on the determination of the volume of coiled cephalopod shells. Their modified form of Moseley's equation is:

$$V = \tfrac{2}{3}\pi \frac{KR}{lnW}(1 - W^{-3\theta/2\pi})$$

where K is the area of the whorl section (i.e., the area of the last generating curve), R is the radius to the centre of gravity (determined by balancing a templet of the whorl section), θ is the total angular growth in radians (= number of whorls times π), W is the whorl expansion rate, which is easily estimated by a simple quasi-regressional method (fitted by eye), applied to the semilogarithmic plot of the observations. Almost all of these variables require a considerable expenditure of time for their determination. The investigator may speed up the process by using photographs for determining K and W. This is a deterministic model and its limitations should be understood in relation to stochastic biological variation. From the point of view of studies on the postmortal dispersal of chambered cephalopod shells, the computer simulation of shell types is useful for providing natural bounds for ranges of models based on a particular shell type, thus allowing one to establish a kind of "safety mechanism" for avoiding impossible constructions.

Denton and Gilpin-Brown (1966) reported that about 80 % of the gas-space in the chambered portion of the shell of *Nautilus pompilius* is required to support the weight of the shell itself in seawater. It is only about the last ten chambers that contain liquid in measurable amounts and in progressively lesser quantities, from the youngest to the oldest of these chambers. The final chamber may only be completely liquid-filled when being formed, according to these authors. Experiments made on the strength of *Nautilus* shells showed them to be able to withstand pressures corresponding to those that occur at a depth of 600 m in the sea.

Writing on the subject of the siphuncle of *Nautilus pompilius,* Collins and Minton (1967) demonstrated experimentally the exceptional strength of the fresh siphuncular tube. My remarks in Part I on the fracturing of the siphuncle as being a means of admitting seawater into the cephalopod shell are therefore largely invalidated for fresh material.

Teichert (1970) reported on the necroplantkonic transport of shells of *Nautilus pompilius* into the Bay of Bengal, 3600 km from the nearest known habitat of this species. In the same note, he brought together some little-known published information on drifted shells, including a record of a floating shell, collected 250 km southwest of Ceylon, and another from north of Malagasy (in which region it now seems that a living population of *Nautilus* occurs (see p. 38)).

Mutvei and Reyment (1973) discussed the relationship between buoyancy and the structure and location of the siphuncle of the ammonoid shell. It was shown experimentally in this paper that if the mode of life of the ammonoid animal were analogous to that of *Nautilus*, the relatively more buoyant shell of most ammonoids would have needed to have had more liquid in its chambers than *Nautilus.* The structure of the siphuncle, and its location in the last chambers of the majority of coiled ammonoids, is such as to suggest that it may have been non-functional in these chambers. Many non-involute ammonoid shells, when empty, floated higher in the water than one would be led to expect from observations on living species of *Nautilus.* Mutvei and Reyment (*op. cit.*) came to the conclusion that ammonoids were on the average inferior to living *Nautilus* with respect to swimming ability, as indicated by a reconstruction of their anatomical features. Their siphuncular structure seems to indicate that they were fairly well suited to vertical movement and perhaps had a mode of life similar to that of *Spirula spirula.*

Vossmerbäumer (1972) interpreted occurrences of mainly *Germanonautilus* in the Muschelkalk of Mainfranken, relating his discussion of the necroplanktonic history of his material to the pertinent section of Part II. This study confirms the opinion expressed in Part II that the Muschelkalk was deposited in shallow water. He was also able to demonstrate that cases of redeposition of these nautiloids are not uncommon.

EXPERIMENTS WITH PLASTIC MODELS

a. Construction of the Models

Each of the models was based on an actual specimen with the exception of those of evolute morphological varieties of ammonite shells. Uncoiled shells were sliced along the median plane and the model constructed by building up a copy of each of the halves and then welding these together. The matrices of the ceratitic shells were made by dissecting the specimen, chamber by chamber, and preparing a mould of each of the walls as it was uncovered.

A plastic substance with a specific gravity of 1.3 was used for the models. The required weight increase for simulating aragonitic shell substance (Part I) was achieved either by copper-plating the plastic components of the model, or by coating these with a lead-base paint. Both procedures give equally good results, but the plated models are more costly.

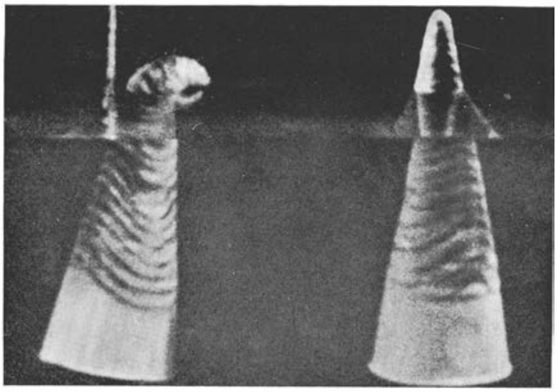

Fig. 1. Floating orientations of models of a straight nautiloid shell and a nautiloid shell with a curved initial portion. Taken from a frame of a 16 m film of an hydrostatic experiment in moderately fast-flowing water, hence the poor definition.

Fig. 2. Floating orientation of a model of a nautiloid shell with a strongly curved initial portion. Taken from a frame of a 16 m film of an hydrostatic experiment in fast-flowing water, hence the poor definition.

The replication of the nautiloid chamber walls caused no particular difficulty, but the walls did pose a problem for the ceratites. A certain simplification could be brought about for virtually identical but reduced sutures by the use of a mould-reduction technique, devised by Mr. Eric Ståhl. The plastic substance used for the final production can only be worked under heat and reduced pressure by the method of vacuum-moulding over plaster dies. This method gives the final product a "professional touch". It has the added advantage of permitting any number of duplicates of a model. Examples of models produced by this procedure are shown in Figs. 1, 2, 3 and 4.

Chamberlain (1969) has developed an ingenious computer method for producing models of a wide variety of cephalopod shells. The computer plotting apparatus contours planispiral surfaces of the cephalopod shell being investigated. The outputted contours are then used to produce plastic models of these surfaces, which may then be glued together. These are solid models, certainly, but there is no reason why the plastic slices should not be so cut as to allow the construction of hollow models. This direction remains to be explored, but it would seem to have excellent possibilities for future studies.

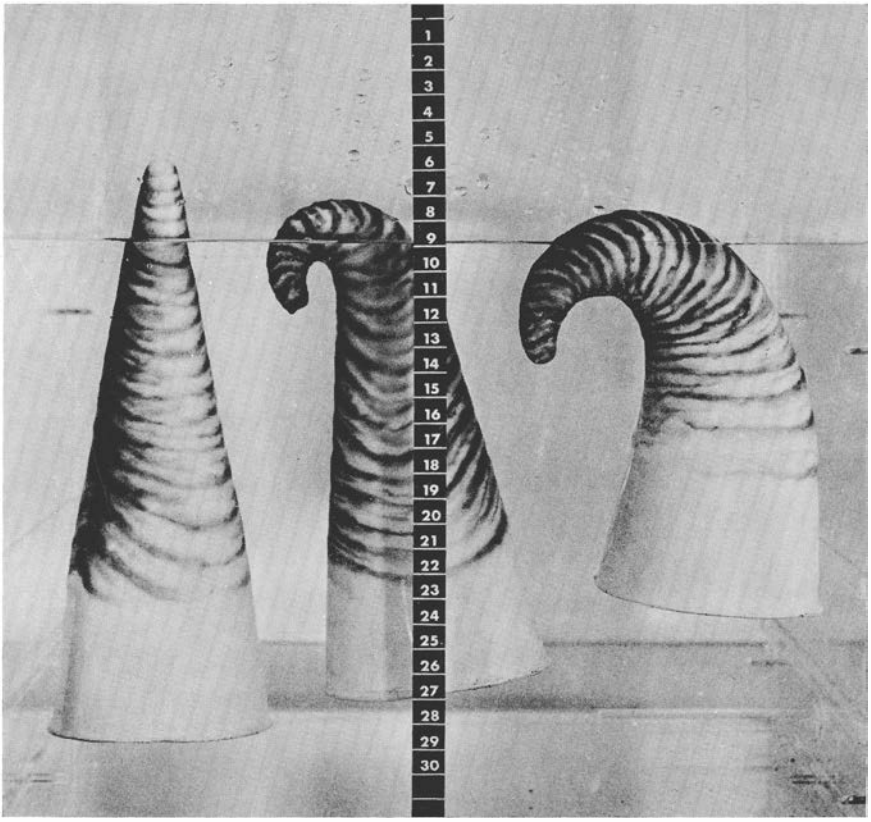

Fig. 3. Floating orientations of the models of *Ancistroceras* and the *Rhynchorthoceras* in undisturbed water. These models were made by the method of copper-plating the plastic form. Scale in cm.

b. Experimental Results

Straight and curved nautiloid shells

The shells were modelled on the following lituitid species: the straight shell on *Rhynchorthoceras beyrichi* Remelé, the curved shell on *Rhynchorthoceras* sp., and the shell with the curved initial portion on *Ancistroceras undatum* Boll. The method of weighting used here was that of copper-plating.

Fig. 1 shows the floating positions adopted by the straight nautiloid shell and the one with a curved initial part. The straight shell floats vertically (the body chamber is just less than 45 % of the total length of the shell). The other shell (the body chamber has the same length as the straight shell) floats at a slight angle to the vertical. Fig. 2 shows the floating position of a nautiloid shell with a more curved initial part; this is oriented at a slightly higher angle than the shell with a curved beginning. The length of the body chamber is the same as for the models depicted in Fig. 1.

The three models were used for flotational experiments in a flume, the results of which were photographed with a 16 mm movie camera. At all water speeds tried in a series of experiments, the three models remained stably in an upright orientation. An interesting point is that they "bounce" along; that is to say, they move with the current in an undulatory manner, bobbing over a range of about one fourth of the length of the shell. In shallow water, there are frequent impacts with the bottom sediment, which produces a typical, asymmetrical jab-mark (cf. Kelling and Whitaker, 1970).

Although I have not yet investigated the matter systematically, it looks as though each of the morphological categories used makes, on the average, a characteristic impingement mark in the sediment. The floating orientations adopted by two of the models in still water are shown in Fig. 3.

As was shown in Part I, the orthoconic type of shell tends to approach a vertical floating orientation, depending on the length of the body chamber. Deviations from straightness, as represented by two of the models used in the present study, displace the centre of gravity of the conch, thus causing it to take up an orientation deviating from the vertical.

The fact that the lituitid models float roughly vertically when empty leads one to the conclusion that, in life, the animals must have had about the same orientation. This conclusion seems inescapable, as there is no reason to believe that the body of the nautiloid animal was lighter than water. No kind of buoyancy adjustment I can think of, apportionment of water in the chambers, and the like, could induce the three kinds of shells to intake a horizontal floating position. This result has important implications for the interpretation of the probable mode of life of these lituitids. For reasons of stability, it seems to me to be out of the question for them to have been able to swim other than slowly in a horizontal direction. In order to attain the most favourable orientation of the shell, that is, the most streamlined orientation, the animal would have been forced to hold a quite improbable swimming speed. What alternative remains? I strongly suspect that the lituitids led some kind of browsing existence, with the main part of their feeding activities centred around such sources as could be readily obtained without recourse to pursuit; there is even a very reasonable possibility that these cephalopods were not predators.

The lituitids analyzed in the foregoing are almost in equilibrium with seawater when empty (Fig. 3). It is significant that they lack cameral deposits and calcifications of the siphuncle. It was, however, pointed out in Part I that endoceroids, with their relatively short body chambers, are, as a rule, provided with characteristic siphuncular calcifications in the older half of the conch. The experimental work reported on in Part I showed that the endoceroid type of shell, without allowance for the effects of the weight of the siphuncular fillings, floated at about 20°—30° to the horizontal. The addition of siphuncular deposits to the older part of the conch would have had the effect of bringing the animal, plus its hard parts, into a roughly horizontal position. It seems to be reasonably likely that the endoceroids could have been fairly active swimmers and that their mode of life resembled that of living *Nautilus.*

As I see things from the results of the experimental work, siphuncular deposits (and cameral deposits) offer a solution to the problem of altering the centre of gravity and the centre of buoyancy of a straight shell. Even very early in the history of the chambered cephalopods, the more optimal solution of achieving about the same result, by coiling, had evolved. I believe that this explains why coiled nautiloid shells almost always lack extra calcifications in the chambers and siphuncle.

The shell function of the heteromorphic ammonites, and particularly, the orthoconic *Baculites*, would seem to be more readily explicable in terms of the somewhat different hydrostatic properties of the ammonite shell and siphuncle (Mutvei and Reyment, 1973).

Models based on ceratites

The three models made for these experiments were based on individuals of the species *Ceratites (Acanthoceratites) spinosus* Philippi, *Ceratites nodosus* (von Buch) and *Discoceratites* sp. The lead-

Table 1. Buoyancy indices for some shells

Species	Index
Nautilus pompilius	13
Discoceratites sp.	28
Ceratites nodosus	35
Ceratites (Acanthoceratites) spinosus	45

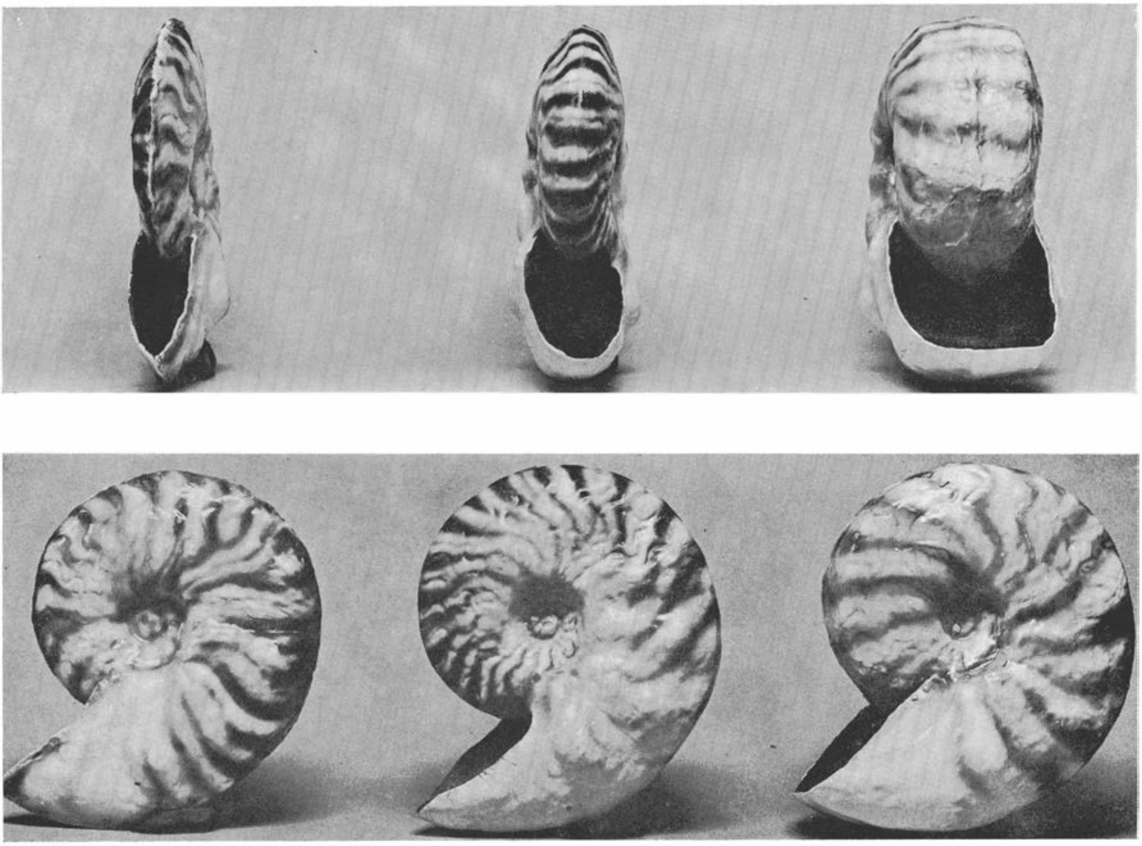

Fig. 4. The models of the ceratites. From left to right: *Discoceratites,* sp., *Ceratites nodosus* (von Buch), and *Ceratites* (*Acanthoceratites*) *spinosus* Philippi.

painting technique was used. Photographs of the models are shown in Fig. 4.

Flotational experiments: The principal object of these experiments was to see how great an increase in weight could be tolerated by the three ceratite models before they sank. A fresh shell of *Nautilus pompilius,* the function of which is now fairly well understood, was used as a standard of reference. It was found expedient to use a form of index comparing the buoyancies of the four conches. In this connexion, I define an arbitrary "buoyancy index" as the weight increase required to bring a shell to sink, divided by the weight of the shell in air, expressed as a percentage. This index for the ceratites and the *Nautilus* are shown in Table 1.

The striking thing brought out by the information in Table 1 is that the models of species of *Ceratites* seem to be more buoyant than the *Nautilus pompilius.*

An alternative kind of determination of critical load can be made by finding the weight of water required to be injected into the chambers in order for a shell to sink. Two such determinations are shown in Table 2. The difference between the

Table. 2. Buoyancy indices for two shells with flooded chambers

Species	Index
Discoceratites sp.	40
Ceratites nodosus	55

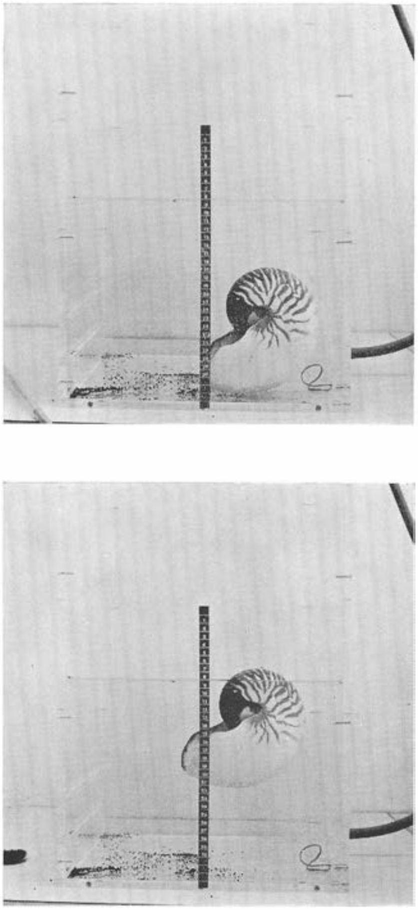

Fig. 5. Shell of *Nautilus pompilius* sunk by weighting the body chamber.

two sets of values for the two species tested are significant, but not greatly different. This difference is due to the loss of effective buoyancy caused by partial flooding of chambers. These simple experiments show quite clearly that the ammonoid shells investigated require appreciably more water in their chambers in order to be in equilibrium with water than does *Nautilus pompilius.* In this connexion, it should be noted that: 1) the ceratites are more evolute than *Nautilus*; 2) the whorl of the conch of *Nautilus* has a fairly low, ventrally compressed section, while the ceratites have more vaulted, spacious chambers, at least in the last, and decisive, whorl.

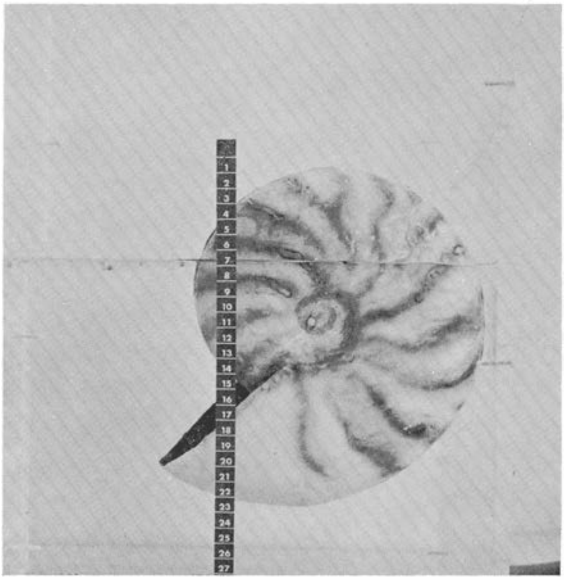

Fig. 6. Floating position adopted by the model of *Ceratites nodosus.*

A shell sunk by loading the body chamber is shown in Fig. 5. Fig. 6 shows the free floating position of the model of *Ceratites nodosus*, and Fig. 7 that for *Discoceratites* sp. The difference in relative buoyancy between the two shells is clearly apparent.

In order to be in hydrostatical equilibrium with seawater (i.e. to have zero buoyancy), the ceratite animal must have had a greater number of liquid-containing chambers than *Nautilus.* As shown by

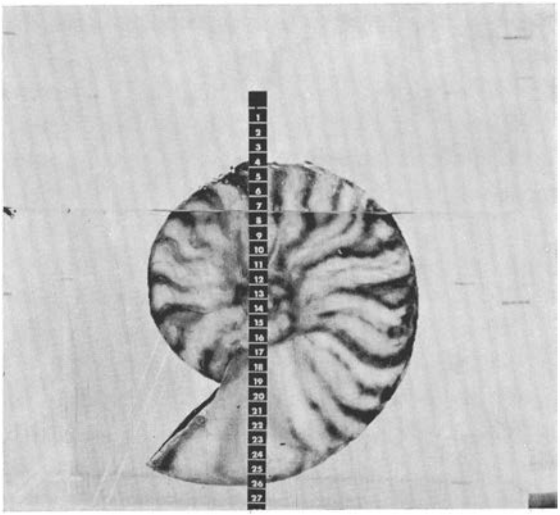

Fig. 7. The floating position adopted by the model of *Discoceratites* sp.

Mutvei and Reyment (1973), the structure of the ammonoid siphuncle and the buoyancy properties of the conch are such as to suggest that the animal would have been reasonably efficient in vertical motion but poorly adapted for horizontal translation. The reduced complexity of the ammonoid siphuncle may be interpreted as an adaptation to the needs arising from the presence of liquid in a relatively great number of chambers (Mutvei and Reyment, 1973).

It has been well documented that the cameral liquid in *Nautilus* in dissipated quickly on the death of the animal. None of the shells I opened during my stay in the South Pacific in 1967 contained liquid in any of the chambers, which accords with the observations of Bidder (1962) and Denton & Gilpin-Brown (1966), who also observed that dying animals find it difficult to maintain zero and negative buoyancy. The cameral liquid is therefore lost, in some yet unknown fashion, during the initial postmortal phase.

Models of highly evolute ammonoids

The work with the moderately evolute ceratitids indicated that coiling, in conjunction with the length of the body chamber, is of first-rank importance, not only for deciding the necroplanktonic fate of a shell, but also for reconstructing the probable mode of life followed by an individual.

Three schematized models of the extremely evolute kind of cephalopod shell were constructed, differing from each other in the length of the body chamber, allowing for a chambered length — body-chamber correlation of about a half (see below). The body chambers were made to occupy three quarters of a whorl, an entire whorl, and one-and-a-half whorls. No particular species was selected to provide the basis for any model, as it was considered more to the point to consider the properties of the highly evolute shell from a more general standpoint, this being, as it were, a kind of natural morphological limit. Shells of the type treated here are common in the Jurassic and Triassic. Two genera that come to mind are *Morphoceras* of the Middle Jurassic, certain species of *Dactylioceras* of the Lower Jurassic and some *Peroniceras* and *Texanites* of the Upper Cretaceous.

The length of the body chamber. Some of the classical literature on Jurassic ammonites was searched for information on the length of complete body chambers, based as far as possible on sections. Only figures and, or, descriptions supplying exact details on the termination of the sutured part of the shell and the presence of typical apertural structures were considered acceptable. Contrary perhaps to what one might expect, such information is seldom forthcoming. Many otherwise good examples, showing complete apertures, could not be used as the descriptions lacked information on the length of the body chamber. Reasonably reliable lengths for 62 species of evolute ammonites were extracted from the publications consulted; of these, only 33 species were provided with reliable details of the number of whorls making up the chambered part of the shell.

The results of the graphical analysis are given in Fig. 8. The histograms, Figs. 8 a and 8 c, indicate that the most "popular" length lies around 80—90 % of the final volution and that the distribution of body-chamber-length is right-skewed. Lengths of more than 1.3 volutions are rare. The scatter diagram, Fig. 8 b, and the correlation coefficient of the length of the body chamber and the number of whorls, show that variables are not strongly associated. There is naturally an overall tendency for longer body chambers to be correlated with the number of whorls; there is, however, considerable biological variation in the relationship. This calls for extreme caution in the use of deterministic (non-statistical) models for the analysis of shell growth.

It has been suggested (e.g. Trueman, 1941), that there is a hard-and-fast relationship between the length of the chambered part of the ammonoid shell and the length of the body chamber. The correlation coefficient of 0.35 obtained in the present study is low, and not indicative of absolute association between the variables. As only to be expected, it is significantly different from nought (it is significant at the 5 % level); in other words, there is a certain correlation between the two

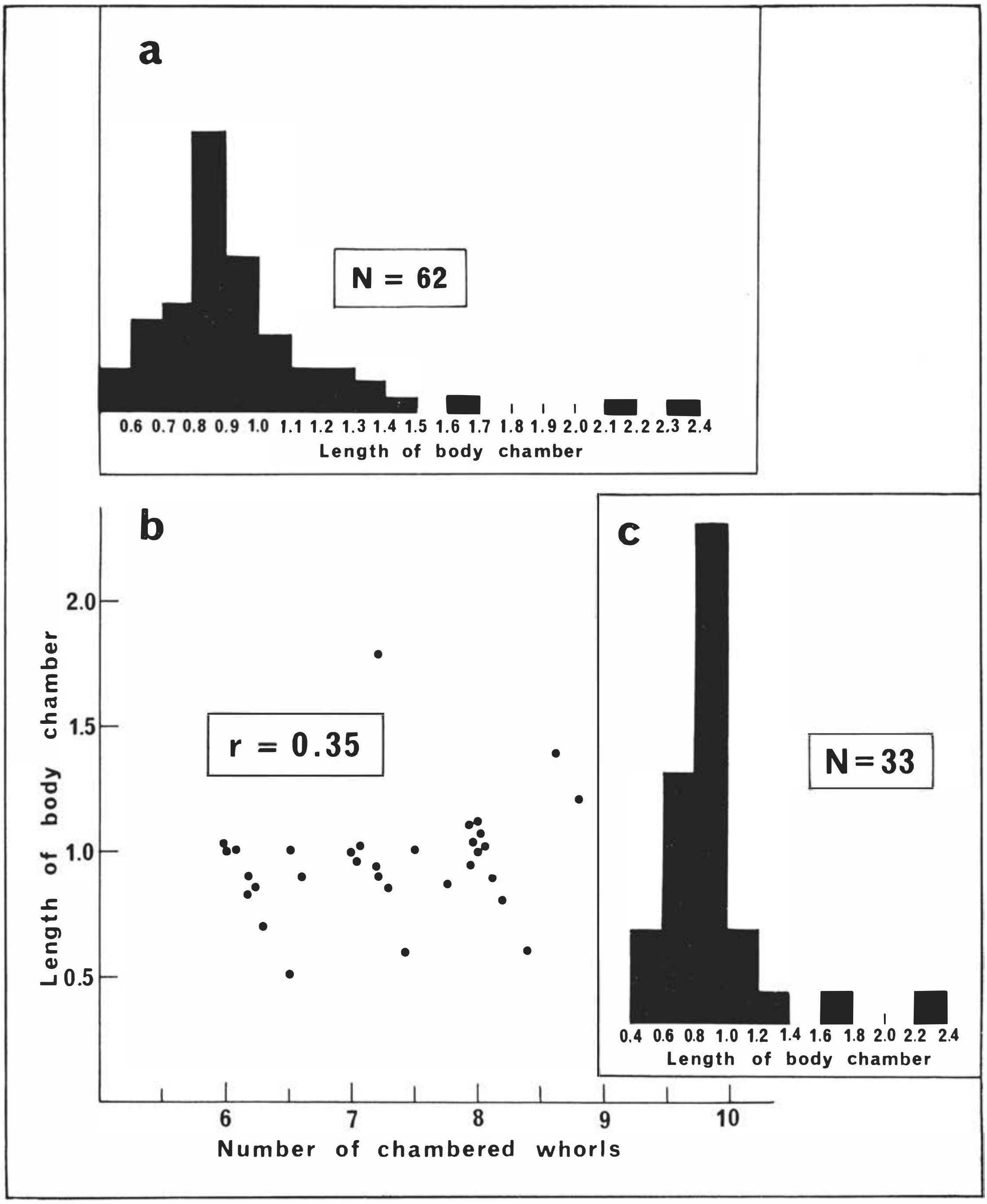

Fig. 8. Graphical analysis of the length of body chambers, measured on highly evolute shells of Jurassic ammonites: a) histogram of the proportion of the final whorl taken up by the body chamber; b) scatter diagram of the relationship between the length of the body chamber and the number of chambered whorls of the conch; c) histogram of the proportion of the final whorl occupied by the body chamber of the species analysed in graph b). The correlation coefficient for the length of the body chamber and the number of chambered whorls is shown.

variables, but there is considerable slack available for variation. The scatter diagram discloses an interesting trend in the material towards the formation of clusters or groups. Inspection of the diagram (Fig. 8 b) discloses that for each of the discernible groups, centred around a whorl number of between 6 and 7 volutions, the range of variation in the lengths of the body chambers is approximately the same, and their marginal distributions are approximately normal. The rather rigid framework of the logarithmic growth pattern does make for a restriction in the variability of some variables in ammonites. High correlations occur between many size parameters ($r > 0.85$), such as whorl dimensions, and coefficients of variation are often low ($V \approx 3$).

Several hypotheses for this relationship suggest themselves. One of these is particularly relevant to the evolute ammonites, namely, that they may have been adaptable to a range of niches, reflected in slight differences in the buoyancy, achieved by variation in the length of the body chamber. For example, an exceptionally long body chamber would be a reflection of a differing disposition of essential organs of the body. A second possibility is that different requirements for the function and efficiency of the hydrostatical apparatus of the animal might be mirrored in the size of the body chambers; a form aspiring to greater motility would have profited from having a shorter body chamber, allowing a more efficiently structured body as regards swimming ability.

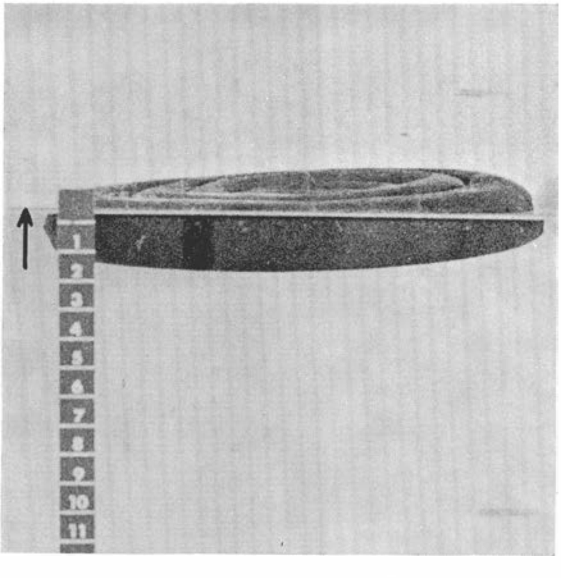

Fig. 9. The floating orientation of the model of the evolute shell with the body chamber occupying three fourths of the final whorl, seen in lateral aspect. Scale in cm. The body chamber will not retain more than about three quarters of its volume of water.

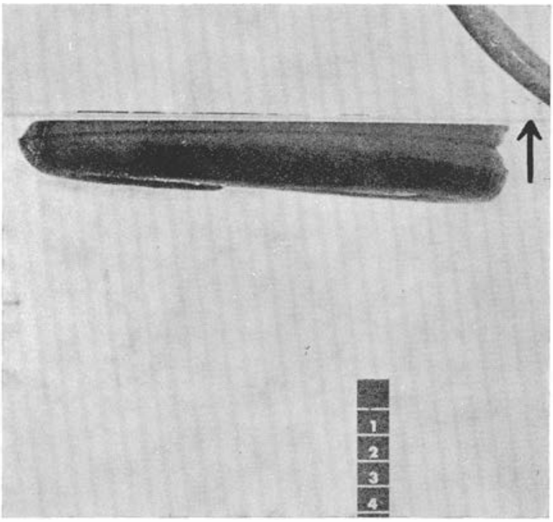

Fig. 10. Floating orientation of the model of the evolute shell with a body chamber of one complete whorl, viewed from the side. Scale in cm. The body chamber does not become completely water-filled.

The primary role of the shell of cephalopods was undoubtedly to bring about zero buoyancy, that is, a condition of weightlessness in water. The efficiency of such a relationship is clear. It follows that a shell-plus-animal-weight that cannot be brought to zero buoyancy is functionally unsound.

Flotational experiments with models of evolute shells

Body chamber three fourths of the final whorl: The model floats in an almost horizontal position, with about one third of the shell-breadth above water. The shell lists in a direction away from the aperture. Even if the body chamber is filled with water, air soon enters, owing to this free-floating orientation (Fig. 9).

Body chamber an entire whorl: The body chamber acts as a thickened rim on a hollow discoidal

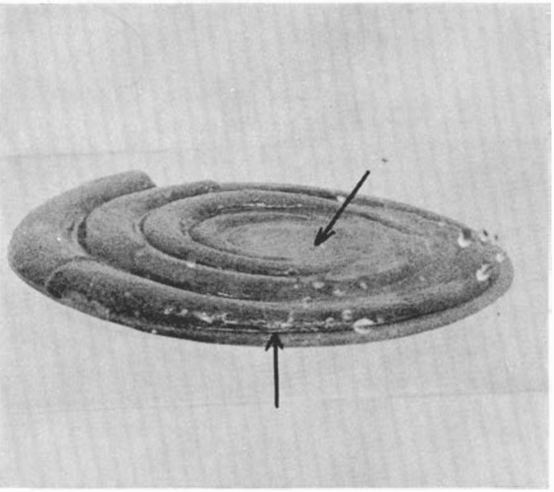

Fig. 11. Oblique view of the floating model shown in Fig. 10. The arrows denote the level of the water on the shell.

object. The model floats almost flat in the water, low, and slightly tilted, with one side awash (Figs. 10, 11, 12, 13). The lower edge lies opposite the aperture.

Body chamber of one-and-a-half whorl. The imbalance caused by the addition of a further half whorl brings about a marked change in the floating orientation adopted by the shell. With the body chamber completely water-filled, this model floats in a vertical position (Fig. 14), with about one tenth of the conch above water, analogously to the *Nautilus.* The body chamber, when entirely filled with water, has a different moment of inertia from the involute, *Nautilus*-type of shell, although the centre of gravity lies in roughly the same position. This has important effects on the floating stability of the shell. The vertical orientation is easily disturbed and air can readily become trapped in the body chamber. When this happens, the shell floats on its side, not unlike the first two models.

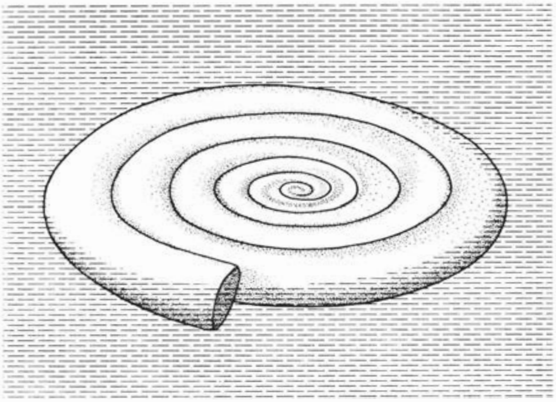

Fig. 12. Sketch of Fig. 11, illustrating schematically the orientation of the shell in relation to the surface of the water.

Three frames from a 16 mm motion picture film of an experiment with this model are shown in Figs. 15, 16, and 17. The results of this experiment are discussed in the next section. It is of interest here to note that Figs. 15 and 16 show the shell with the body chamber completely filled with water. Fig. 17 shows the shell floating on its side, borne by the water current, after air had entered the body chamber.

Implications of the buoyancy experiments. The implications of the buoyancy experiments for inter-

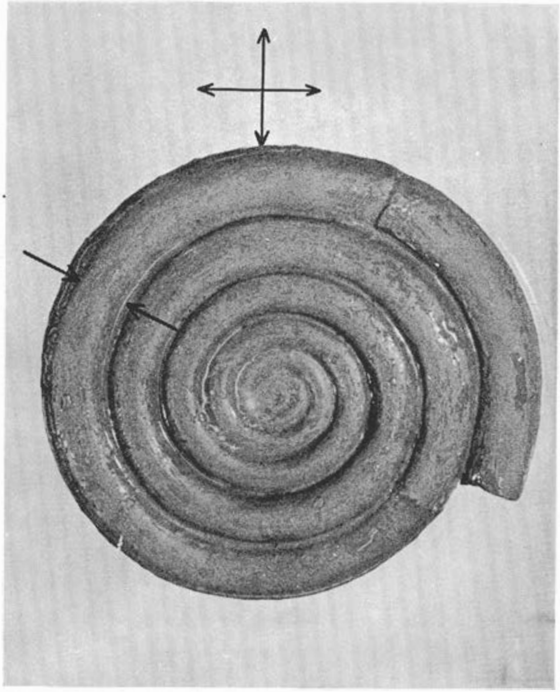

Fig. 13. The model shown in Fig. 10, seen from above. The two arrows on the last whorl mark the water level on the shell. Horizontal floating position.

preting the mode of life of evolute ammonoids and nautiloids are far-reaching. It is clear, that the weight of the animal itself would have been insufficient to bring the entire creature into a vertical position in the case of the models with body chambers in the class of approximately a half whorl, three quarters of a whorl, and one volution, let alone produce a buoyancy almost in equilibrium with water, unless several of the air chambers were filled with liquid. Inasmuch as the majority of evolute Jurassic ammonites considered fall within this category of shell-body-chamber association (Fig. 8), it seems reasonable to assume, that the mode of life of these forms was not a highly active one (Mutvei and Reyment, 1973). The shell is well adapted for vertical motion, but less well-suited for horizontal displacement.

The shell with the longest body chamber, a rare construction in nature, is almost in equilibrium with seawater. As pointed out by Mutvei and Reyment (1973), the shape of the animal must

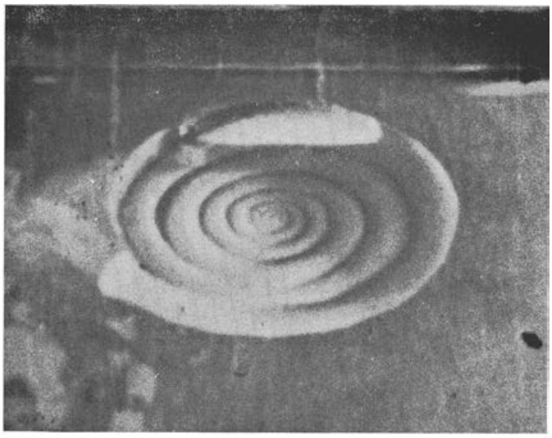

Fig. 15. Flotational experiment with the model of an evolute shell with a body chamber of one-and-a-half whorl. The natural orientation taken up by the shell in relation to the current is with the sagittal plane at right angles to the direction of flow. The body chamber is water-filled. Frame from a 16 mm film.

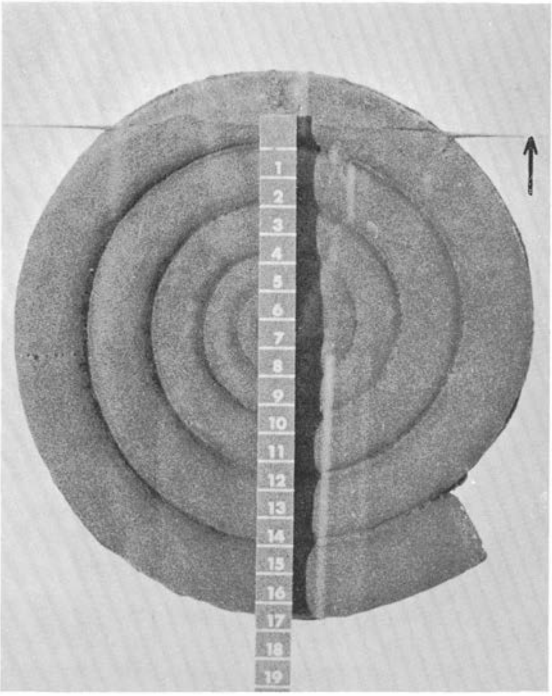

Fig. 14. The floating position adopted by the model of an evolute shell with a body chamber of one-and-a-half whorl, seen in lateral aspect. The arrow marks the surface of the water. Scale in cm.

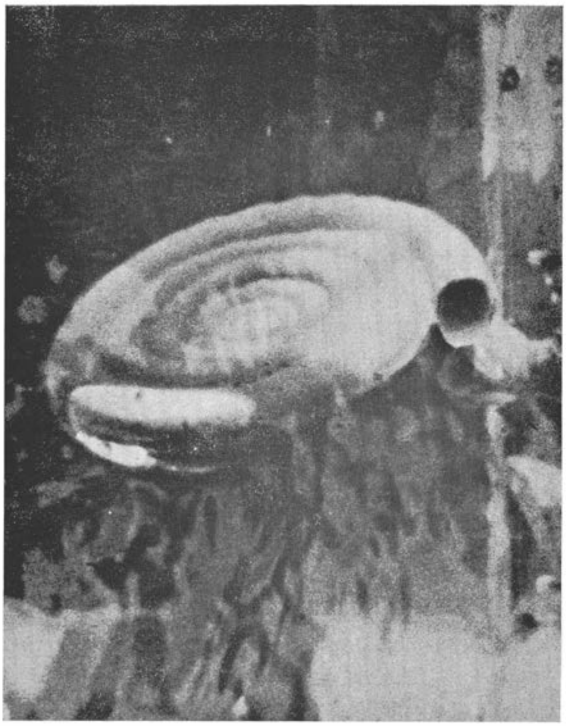

Fig. 16. A frame from the 16 mm film referred to under Fig. 15. The body chamber in this experiment was water-filled.

Fig. 17. Frame from another part of the film referred to under Fig. 15. With a water-filled body chamber, the floating position of the shell is unstable. It requires no more than a moderate level of wave activity for it to become unbalanced and for water to enter the body chamber. When this has happened, the shell floats at a slight angle to the horizontal, as illustrated in this figure.

have been almost "wormlike", with a body-build poorly suited for the muscular activity associated with swimming. However this may be, it seems clear that the more successful trend within highly evolute ammonites was towards body chambers of about three-fourths of a whorl in length.

Behaviour of the ammonoid shells in shallow-water currents

As part of the experimental programme with the models of ammonoids, their transportational behaviour in shallow water was studied. The shells were filmed as they were subjected to a variety of experimental conditions in a flume. One of the factors given special attention was the drag-marks made by the models in fine sand.

The ceratite models. Some of the more important results obtained with the ceratite models will now be reviewed. Fig. 18 shows drag-tracks made by almost waterlogged *Ceratites* and *Ceratites* (*Acanthoceratites*). The shells orient themselves both parallel to the stream (at 2.5 cm/sec), and at right angles to it. As soon as they strike a raised area, they work through it by the winnowing-out of sediment particles through the action of the current.

Owing to the greater resistance presented by it to the water current, the *Acanthoceratites* moved along the bottom more rapidly than the *Ceratites.* Marks made by all three shell types, including ventral impressions (the upper two arrows) and diagonal drag-marks (lower arrows), are depicted in Fig. 19.

The models, when in a state of slight "negative buoyancy", are occasionally lifted over short distances by the water current. This was seen to take place more readily for the *Acanthoceratites* than for the other models, owing to the greater surface

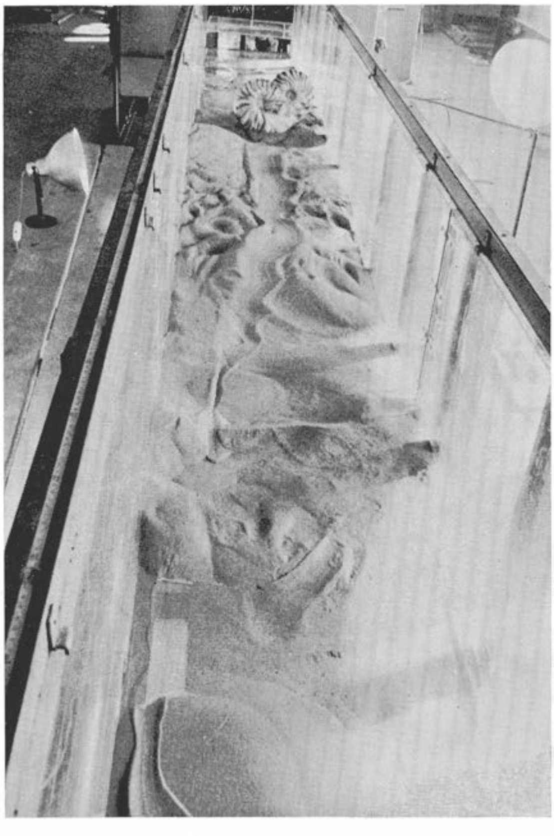

Fig. 18. Drag marks made by the ceratite models in a slow current. The deep track in the foreground was scoured by the venter of *C. nodosus* with the shell oriented parallel to the direction of the current. After travelling with this orientation for a short distance, the shell then swung around to a position at right angles to the current and produced the broad track visible as a continuation of the deep track.

it offers to the water. When the shells alight again on the sediment, they produce impact-marks or bounce-marks, if the shell takes off again immediately after impact. Examples of these marks are given in Fig. 20 for the *Acanthoceratites,* and Fig. 21 for the *Ceratites.*

The evolute models. As already pointed out, the two models with the shorter body chambers float almost flat in the water and the experiments with them only confirm what one would expect, namely, that they strand on the shore like floating boards.

The model with the body chamber of one-and-a-half whorl (body chamber entirely filled with water) floats as shown in Figs. 15 and 16, which are enlargements of two frames from a 16 mm movie film. The only transportational orientation adopted by this shell was the axis of coiling at right angles to the direction of the current. The figures indicate that there is a fair amount of oscillatory movement of the shell as it is transported by the current. The vertical orientation of this model is unstable, for at the first more violent oscillation, air enters the body chamber to cause the shell to take up an approximately horizontal floating orientation. Once this position has been obtained, there is little possibility for the body chamber to become entirely water-filled again. Fig. 17 illustrates the model after air had entered the body chamber.

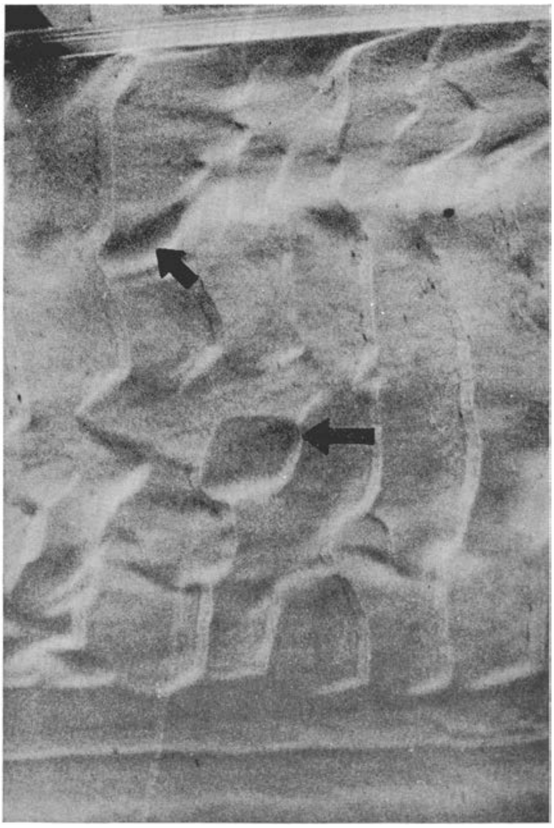

Fig. 20. Shells with a slight negative buoyancy are easily lifted and dumped on the bottom by a swift current. This gives the appearance of a bouncing motion to the shell. Characteristic marks are made by the venters of the shells. This picture shows bounce-marks (arrows) made by the model of *Acanthoceratites.*

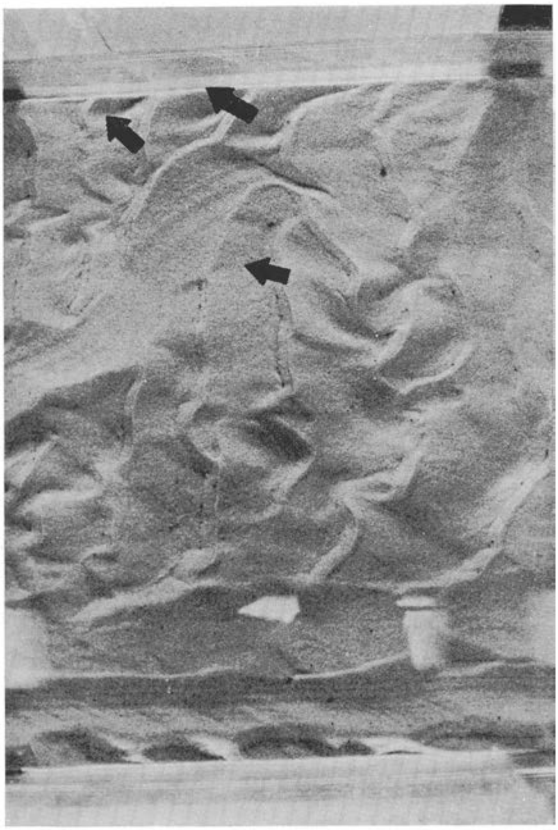

Fig. 19. Impressions made by the venter of the model of *Discoceratites* sp. (arrows in the upper part of the picture) and diagonal drag-marks made by the model of *Ceratites nodosus* (lower arrow). The track along the bottom margin of the picture also derives from *C. nodosus.*

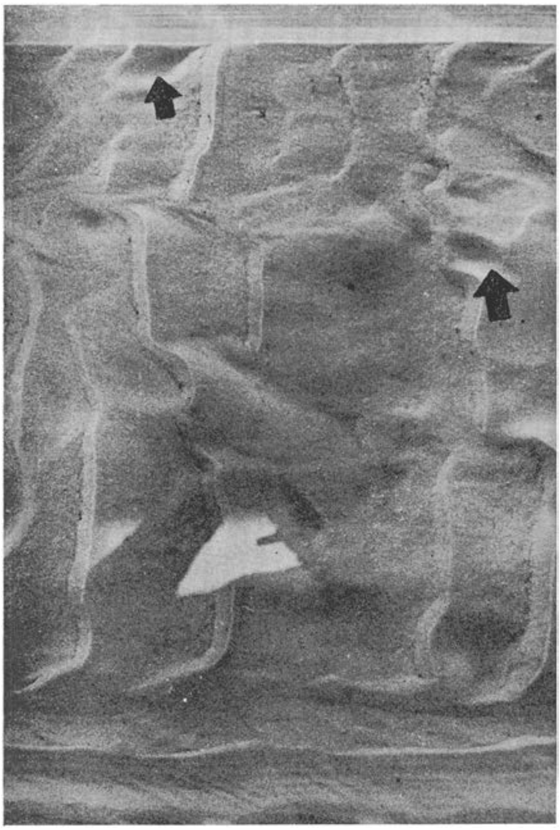

Fig. 21. Bounce marks (arrows) made by the model of *Ceratites nodosus* in a swift current (N.B. ripple shapes).

The results of these experiments on the behaviour of the serpenticonic type of shell to moving water show that: 1) the normal shell orientation is roughly horizontal to the surface of the water; 2) the concepts of these shells rolling along the bottom, or being rolled while floating in the water, as is sometimes postulated in the literature, lack foundation, partly because of the ease with which air enters the long body chamber of all forms, and partly because of the fact that the shell always orients itself with the plane of coiling at right angles to the direction of the current.

General conclusions. The general conclusions arising from these experiments may be summarized in the following terms. Almost waterlogged shells, that is, shells with a slight negative buoyancy, may leave a scrape-mark characteristic of each morphological type. There are longitudinal dragmarks and transverse scrapes, the latter deriving from the rocking motion set up by the conch when passing over minor irregularities on the surface of the sediment, mainly ripple marks. Bounce marks are formed by shells almost in equilibrium with water when they impinge on the bottom. Other marks are formed when a shell swings broadside to the current. Some of the marks formed by dragging ceratitic shells are depicted in Fig. 22, a stereopair. It is worth noting that the sudden disappearance of a track is a result of the shell having been swept upwards by a surge of current. Finally, shells tending towards the cadiconic type (such as the *Ceratites (Acanthoceratites)* of the present account) are, when in a state of slight negative buoyancy, shifted more rapidly by currents than are sleeker shell types.

Simulation of the initial postmortal phase

Interest sometimes attaches to the fate of the newly defunct cephalopod. Some idea of what must be taken into account may be obtained by experiments on *Nautilus* shells, using some kind of simulated soft parts which may be made to behave in the same way as a decomposing body. My observations on dead *Nautilus*, made during a visit to the South Pacific in 1967, served as a guide-line for the experiments.

The body chamber of a shell of *Nautilus pompilius* was fitted with a soft, rubber bladder, the effects of putrefaction being simulated by inflating this. Figure 23 shows the first part of the experiment, with the shell raised slightly in the water. Fig. 24 shows an advanced phase of the experiment which was continued to simulate the theoretically interesting but practically unreal situation in which the carcass does not detach from the shell and continues to decompose and inflate. The possibility of a *Ceratites* shell having become waterlogged around this phase, as has been suggested by Meischner (1968), would appear to me to involve an hydrostatical impossibility. Water most easily gains access to the chambers of cephalopods through portions of the siphuncular tube, but as long as the body and shell have not parted company, this route is sealed by

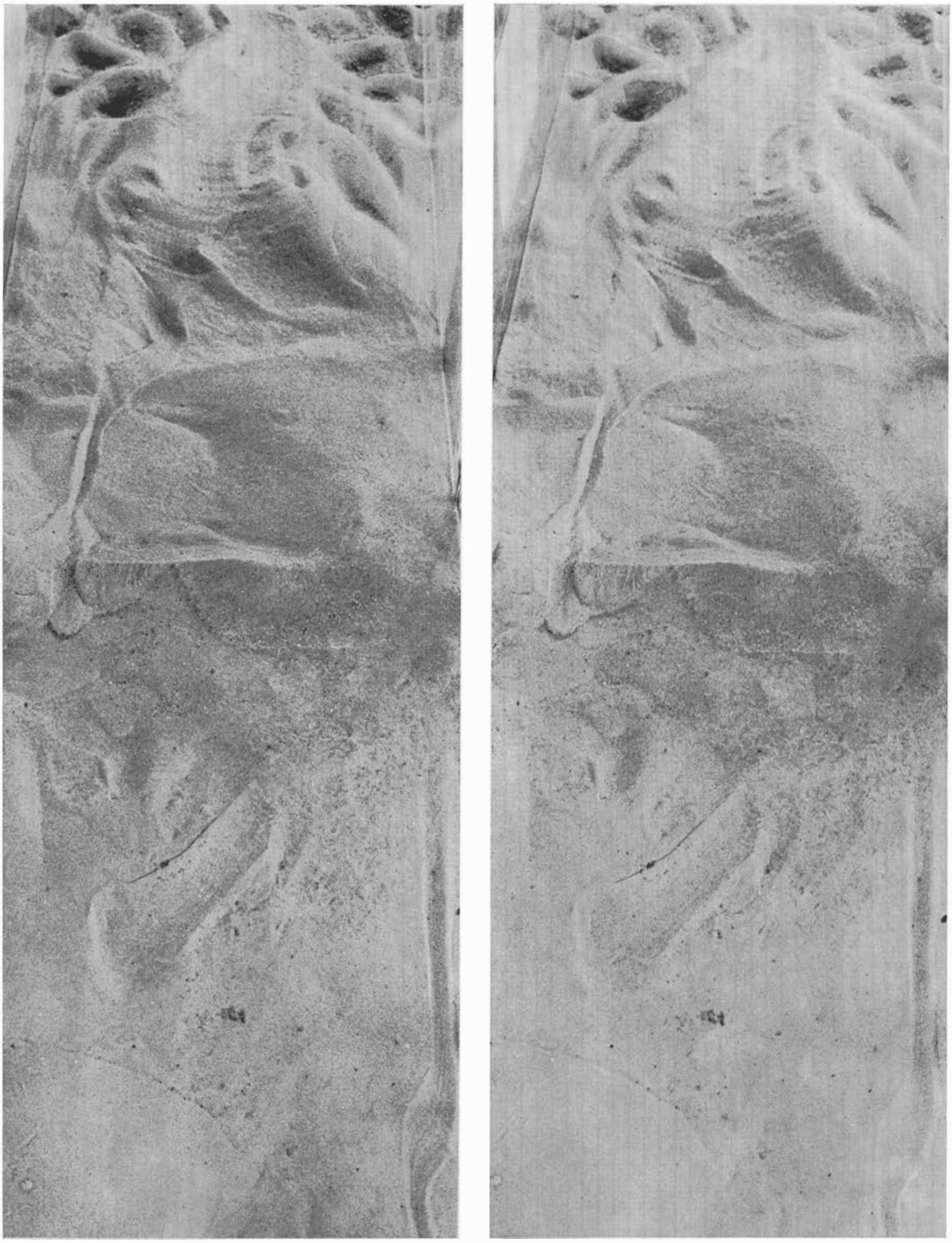

Fig. 22. Stereopair of drag-marks made by the models of *Ceratites nodosus* and *Discoceratites* sp. The picture displays bounce-marks, transverse keel-marks, scrape-marks resulting from shells moving transversely with a rocking motion, and a ripple mark, breached by a shell. In order to avoid diminishing the stereographic effect of the figure, the structures have not been marked.

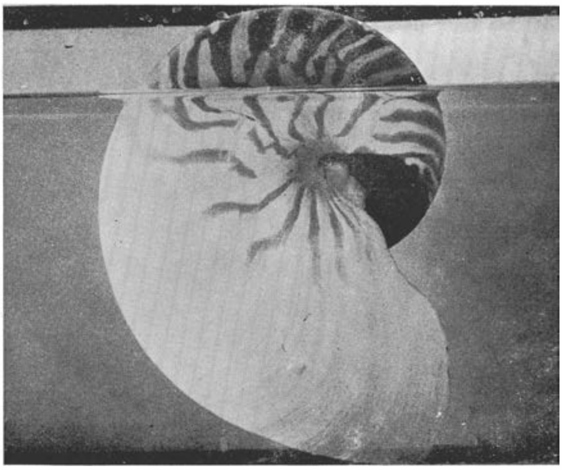

Fig. 23. Phase in an experiment for simulating the effects of putrefaction of the soft parts of *N. pompilius.* This figure illustrates an early stage.

the siphuncular cord. The alternative of water entering through the chambered part of the shell requires such extensive damage to have taken place, that the effects would be readily visible on fossils.

Analysis of the ontogeny of advanced chambers

One of the problems frequently brought up in the study of chambered cephalopods, but which has not been given treatment beyond qualitative discussion, concerns the regularity in the appearance of the cameral walls and the relationship between whorl radius and the distance between septa. This problem is clearly of importance for any study of the buoyancy of cephalopod shells and related ontogenetic adjustments. The theoretical model requires that there be a regular relationship in the distance between successive chambers. Thus, each new chamber is a little larger than the preceding one by some predictable amount. In quantitative terms, this would mean that virtually absolute correlation between the whorl radius and the distances between chambers must exist.

A few aspect of the problem are examined here for the advanced growth development of *Nautilus pompilius, Ceratites nodosus* and *Amaltheus margaritatus.*

The first question we shall consider is whether there is a close relationship between the distances between successive chambers and the size of the cephalopod shell. This may be gauged by the correlation coefficient between the radius of the shell to a cameral wall and the distance between two chambers at that site. The result of such an analysis for *Ceratites nodosus* is shown in Fig. 25. It will be seen that the correlation is relatively high and significant.

An intuitively useful way of graphically characterizing the growth pattern of an individual is by some method of internal comparison of the order of appearance of the chambers. One such way is by some kind of ordering technique, whereby the distances between cameral walls, always measured at the same site (here, the venter), are ordered into suitably chosen classes. An informative and handy way of examining the ordered data is by plotting the logarithm of the proportion $K(X)$ intervals longer than some cameral distance, X, against X. If the plotted points lie on a straight line, the growth sequence is random and accords with a kind of Poissonian process. This study can be suitably backed up by an analysis of the serial correlation coefficients of the succession of cameral intervals. Observed irregularities in cameral widths in the ceratites forming the bases

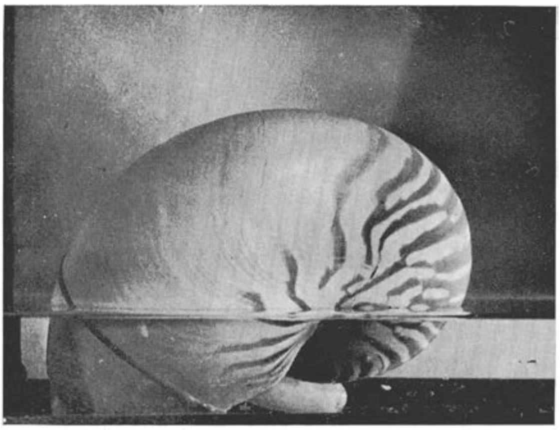

Fig. 24. Simulation of an advanced stage of putrefaction of the body of *N. pompilius.* A stranded shell is shown in an almost upright position as a result of the swollen body.

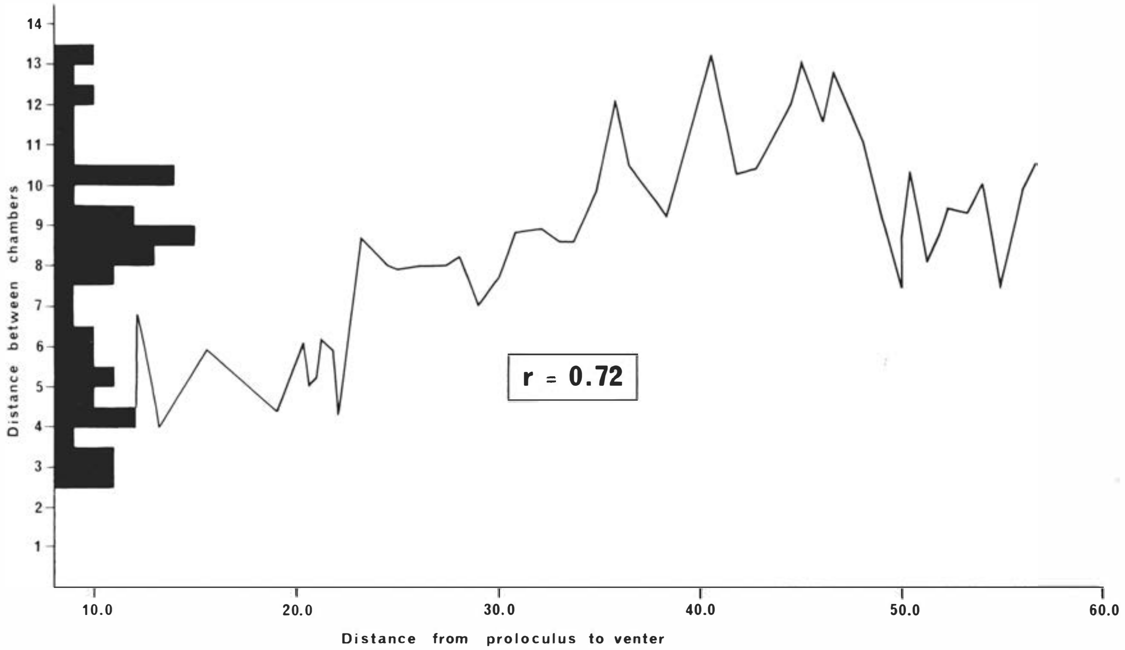

Fig. 25. Graphical illustration of the relationship between the distance between successive cameral walls and the distance from the proloculus to the venter of *Ceratites nodosus* for each chamber. The histogram displays the distribution of the distances between successive chambers.

of the models provided the impetus for this study.

Ceratites nodosus. Trend occurs in the succession of 56 cameral distances, which immediately indicates that the sequence is non-random. The trend is negative, which discloses that there is a gradual decrease in the rate of formation of the chambers. The graph of $\log_e K(X)$ is convex-upwards, with a rapid fall-off and almost vertical tail. The serial correlations between chambers are highly correlated up to and including a lag of 20. The correlation coefficients decrease regularly and successively as the lag is increased, a reasonable outcome of the trend already known to occur in the observations (Fig. 26). Biologically, this indicates that there is a serial relationship between the cameral distances and that this becomes more and more tenuous, the further apart the comparisons are made.

Amaltheus margaritatus. The plot of $\log_e K(X)$ (for 38 chambers) (Fig. 27) resembles that of *Ceratites nodosus*, but differs in the less rapid fall-off displayed by the tail. All of the serial correlation coefficients are highly correlated. The graph of the serial correlation coefficients shows a less regular descent than for *C. nodosus.*

Nautilus pompilius. In order to obtain a reasonable idea of the relationships at the level of the individual, four sectioned shells of *N. pompilius* were studied. The graphs of $\log_e K(X)$ and the serial correlation coefficients are shown in Figs. 28 to 31. Regarding firstly the plot of $\log_e K(X)$ against X, it will be seen that these agree closely. All plots begin with an almost flat portion and then descend with the same slope, to terminate with an almost vertical tail. These curves agree more closely with that of *C. nodosus* than with *A. margaritatus.* Moreover, although the shapes of the plots are close, there are definite individual differences, such as to tempt one to think in terms of using these for "fingerprinting". There

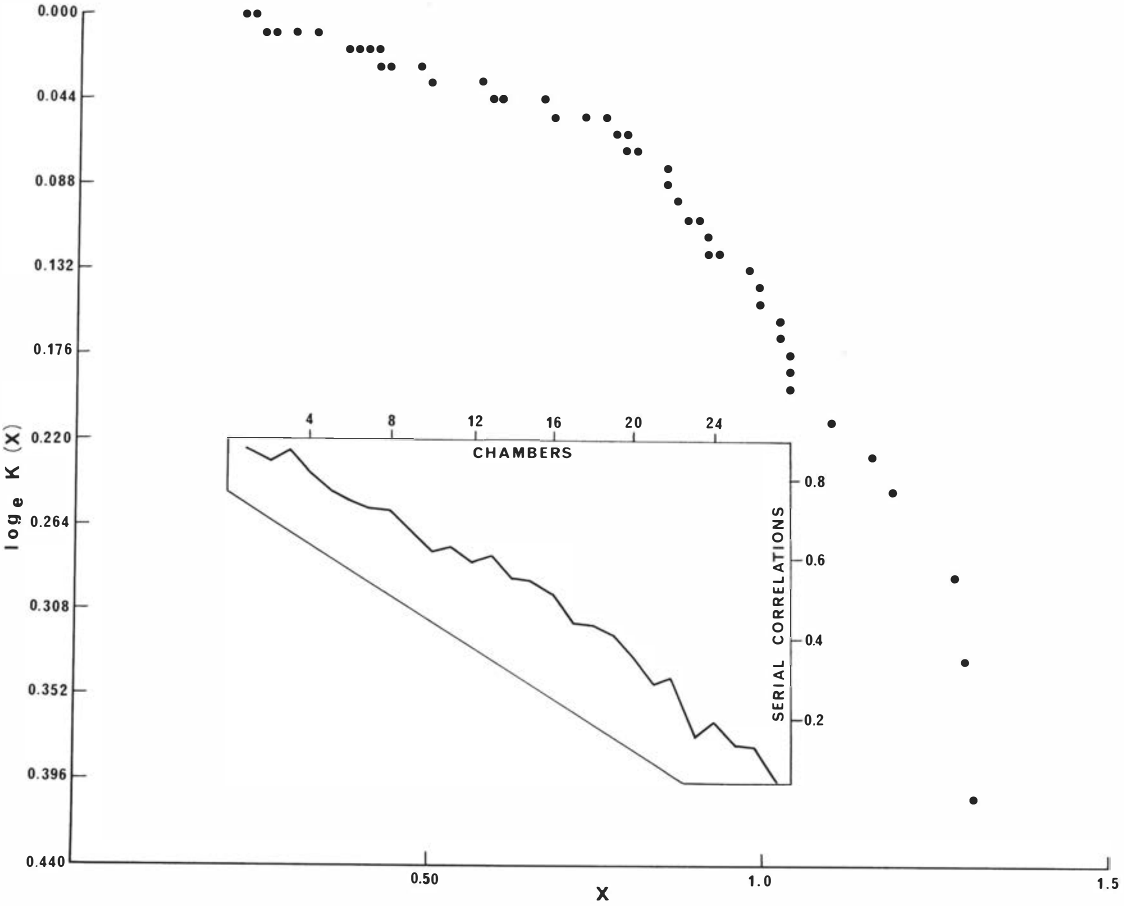

Fig. 26. The graph of $\log_e K(X)$ against X and the serial correlation coefficients for a specimen of *Ceratites nodosus* from Mainfranken, Germany.

would seem to be a distinct possibility of each species having a characteristic serial correlation pattern curve of $\log_e K(X)$, with allowance for individual variation.

The serial correlation coefficients of the four *Nautilus* diminish in the same fashion. All are positive and almost all are significantly different from nought. This is a reflection of the fact that the growth periods for successive chambers show trend. All plots display an initial decrease, then an increase, to form a "hump", after which there is a regular, concave-downwards fall-off. There is, thus, a general similarity with the pattern of the two ammonoids, as is to be expected. The graph of the serial correlation coefficients for *A. margaritatus* (Fig. 27) shows a less regular decrease than *Ceratites* and *Nautilus* and, although the general

Table 3. Coefficients of variation for cameral distances

Species	Number of chambers	V
Ceratites nodosus	56	0.39
Amaltheus margaritatus	38	0.38
Nautilus pompilius A	33	0.62
Nautilus pompilius B	38	0.60
Nautilus pompilius C	37	0.60
Nautilus pompilius D	34	0.60

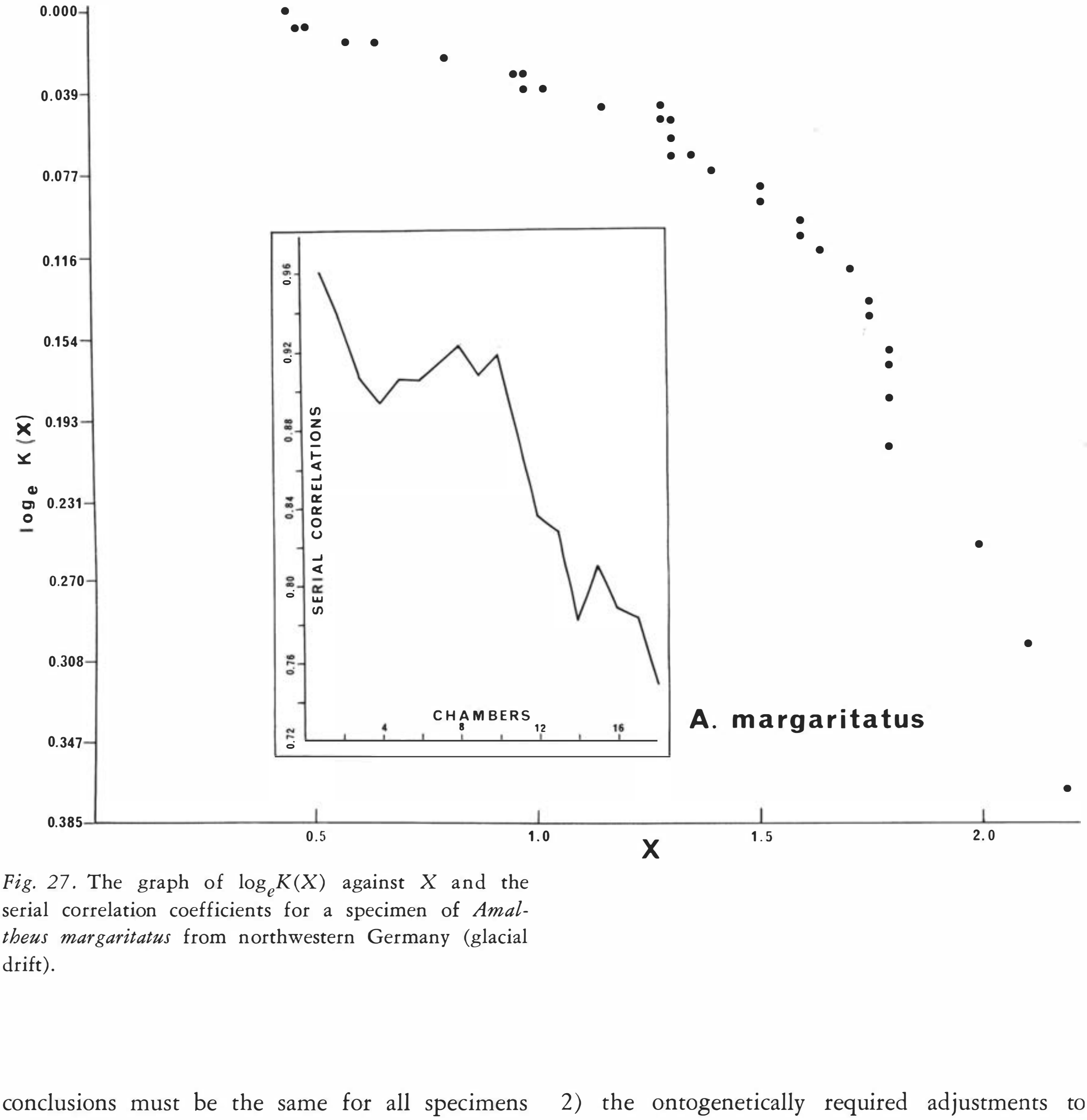

Fig. 27. The graph of $\log_e K(X)$ against X and the serial correlation coefficients for a specimen of *Amaltheus margaritatus* from northwestern Germany (glacial drift).

conclusions must be the same for all specimens analyzed, there is clearly less regularity in the growth of the *Amaltheus.*

Comparison of the coefficients of variation for the material (Table 3) shows that the ammonites lie around 0.38—0.39 and those for the four specimens of the pearly nautilus lie around 0.60—0.62.

Summarizing Remarks. In summary, I think one is entitled to venture the opinion that the overall growth relationships of the forms studied are similar, which is a natural outcome of the fact that: 1) the whorls have the same geometric plan; 2) the ontogenetically required adjustments to buoyancy will result in approximately the same cameral progression. The analysis also shows that there may be a species-related pattern of the chambers as well as individual "fingerprints".

QUANTITATIVE APPRAISAL OF THE BUOYANCY POTENTIAL OF A SHELL

The most ideal means of reaching a decision on the buoyancy properties of a particular shell is by making an exact model of it, and then observing the hydrostatical behaviour of this model in salt

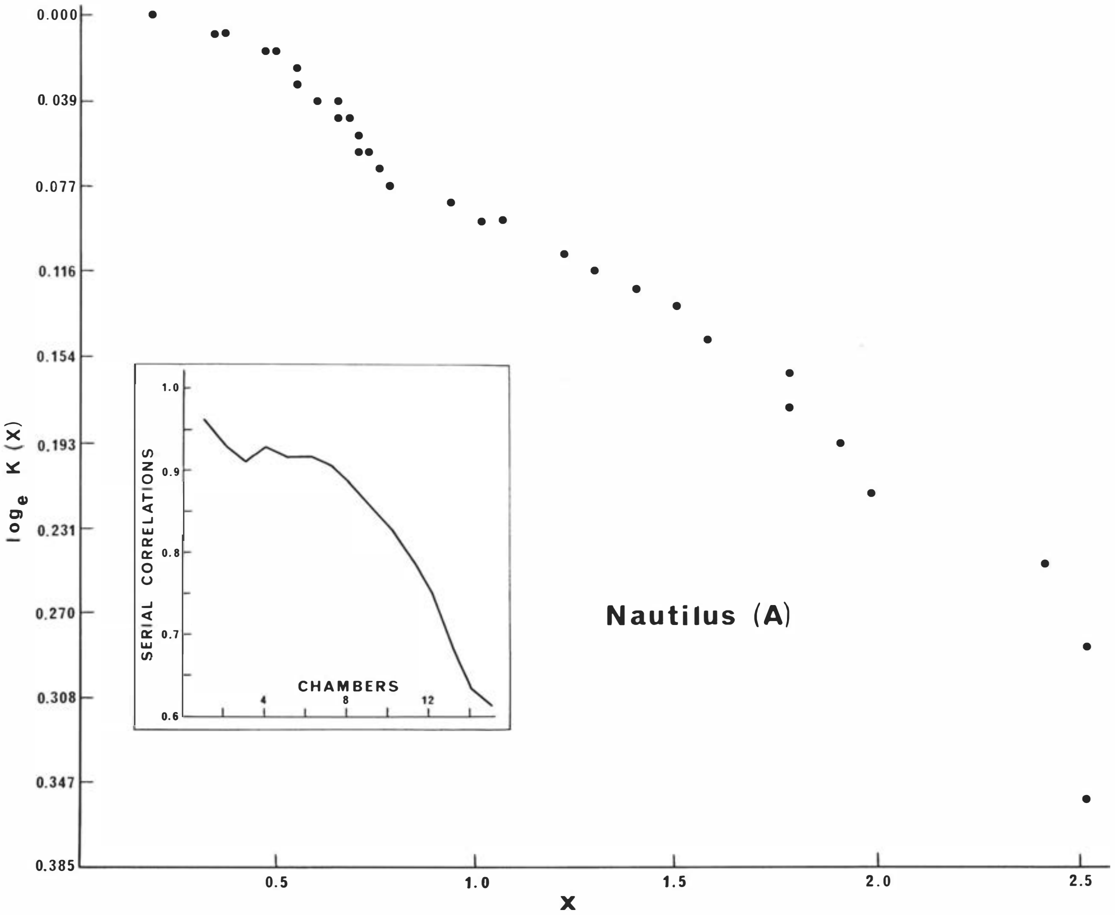

Fig. 28. Plots of the serial correlation coefficients and of $\log_e K(X)$ against X for specimen A of the pearly nautilus. Specimens A—D from Riksmuseet, Stockholm by courtesy of Dr. H. Mutvei and the Trustees.

water. This is what was done for the ceratitids of this paper. It is expensive to make exact scale models and this line of approach is normally only feasible for special problems.

A less costly way of obtaining a concept of the hydrostatical properties of a shell is by recourse to some kind of mathematical procedure, able to provide a criterion for decisions on relative buoyancy potentials.

The ideal method would clearly be one that calculated the exact volume of the chambered portion of the shell and the uplift on it and contrasted these results with the dead-weight of the body chamber and the total weight of shell substance.

The literature contains several solutions to the problem of determining the volume of an idealized cephalopod shell, starting with Mosely (1838), and there is no doubt that a reasonable appraisal of the buoyancy of a shell is possible by utilizing the properties of the logarithmic spiral. An approximate means of attacking the problem is by avoiding a direct estimation of the volume of some shell type and instead choosing variables

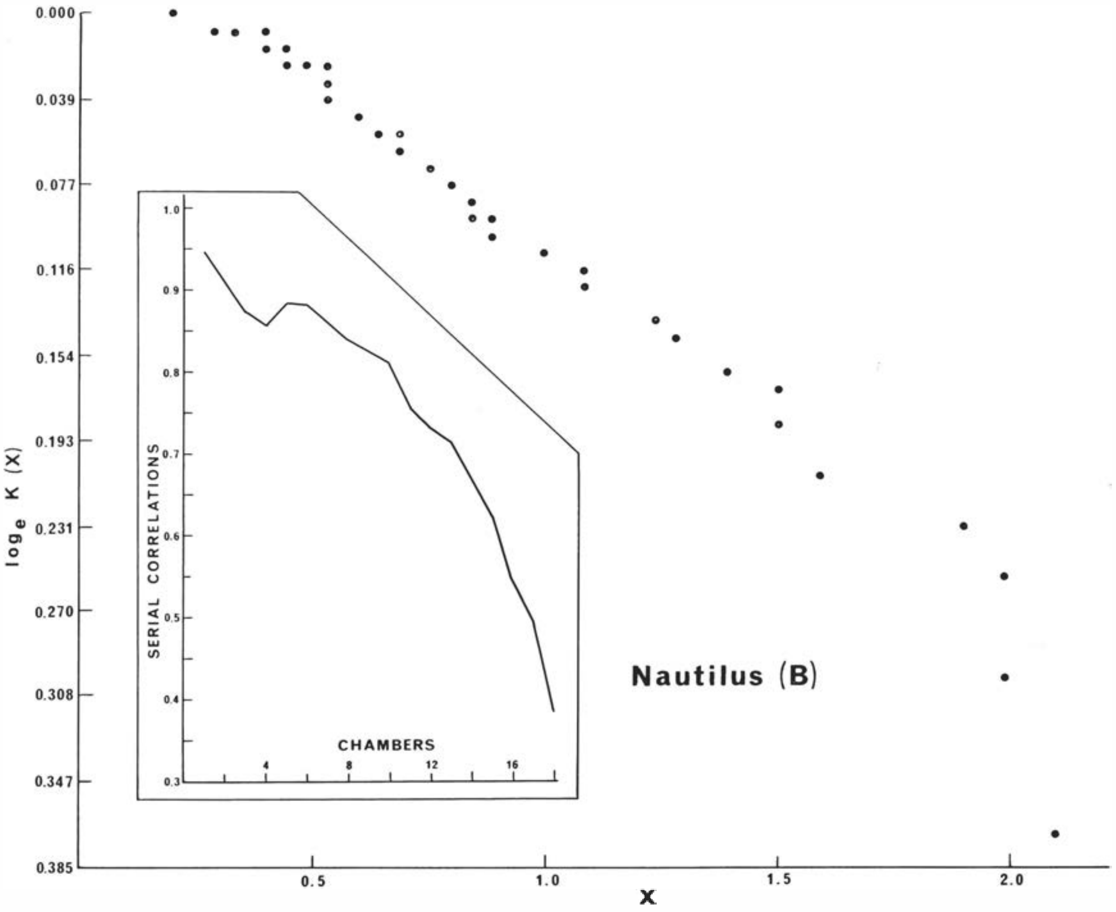

Fig. 29. Plots of the serial correlation coefficients and of $\log_e K(X)$ against X for specimen B of the pearly nautilus.

that are correlated with the massiveness, volume and the degree of evolution of the conch, and a variable for including the exact length of the body chamber. Providing all shells are measured in the same manner, these data will yield a reasonably consistent basis for comparison of shell shapes, if analyzed with a suitable statistical model.

This type of problem is certainly not new to palaeontology and there are several ways of going about it. The most widely employed method still is what may be termed "inverted factor analysis", to borrow an expression from M. S. Bartlett (1965). (In actual fact, the so-called factor analysis of biological and geological literature is really principal components analysis.)

The problem to be solved may be represented in the following fashion. Consider a space of n dimensions, the value of n being determined by the number of p-variate individuals in the sample. Interest will be directed towards finding natural groupings of the n individuals within the confines of the p variables measured on them. The obvious starting point is to calculate some kind of measure of association between the individuals. The most commonly used measure in statistical work

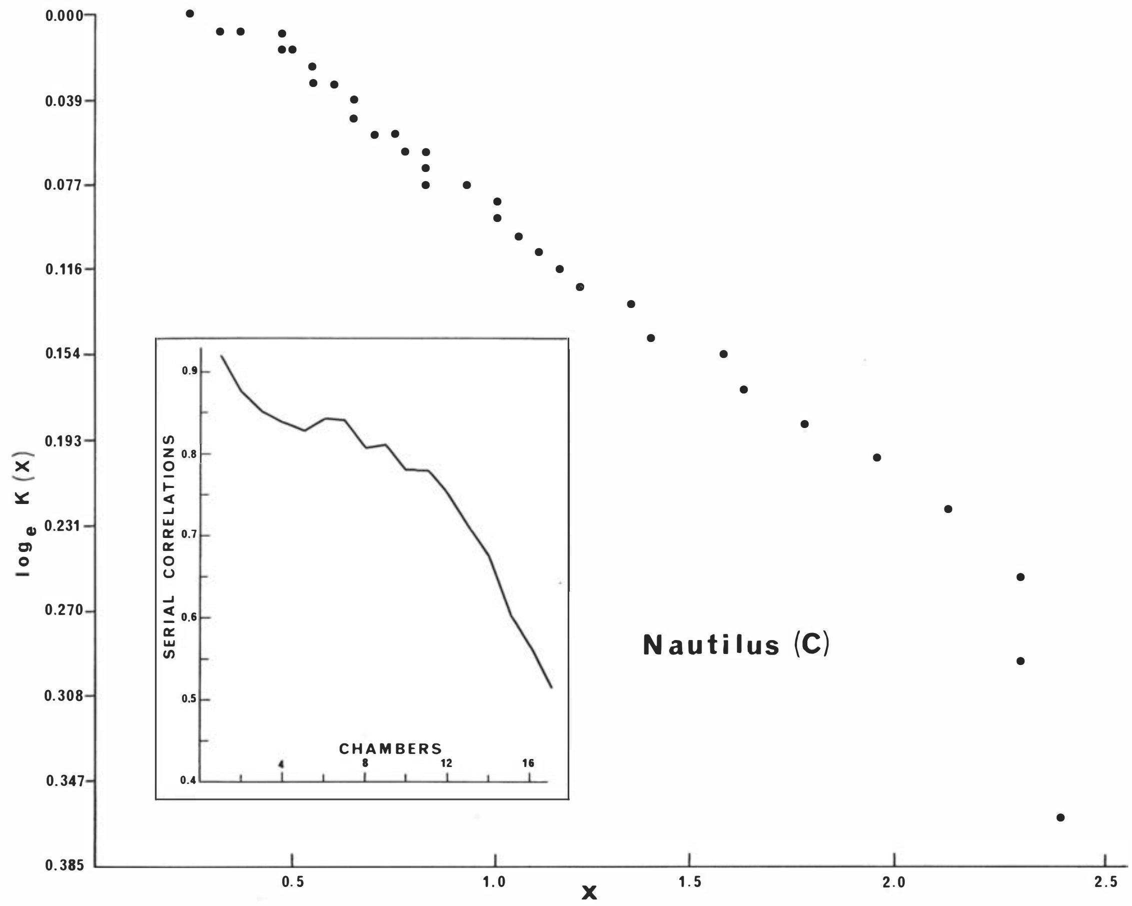

Fig. 30. Plots of the serial correlation coefficients and $\log_e K(X)$ against X for specimen C of the pearly nautilus.

is the Pearsonian correlation coefficient, but this applies only to the common, "normal" situation in which points in a p-variate space are correlated and upon each of which, n observations are available, the reverse of the foregoing.

The theories of principal components analysis and factor analysis were constructed around the p-space case. Hence, if one attempts to apply these methods to the n-space situation, one is "inverting" the model. Statisticians have frequently pointed out that a mathematical justification for this inversion in relation to n-space is lacking. Not only is the theory violated, but such a fundamental matter as the validity of the correlation matrix may be transgressed. Gower (1966) summarized the mathematical reasons for avoiding an inverted analysis of this kind. He then proceeded to develop a statistically sound theory and technique, his method of Principal Coordinates. I do not propose here to delve into the intricacies of this method; some biological applications are given in Blackith and Reyment (1971). Suffice it to say that the same kind of numerical analysis is done to a matrix of associations as in principal components, namely, the extraction of its latent roots and vectors, but only after this matrix has been

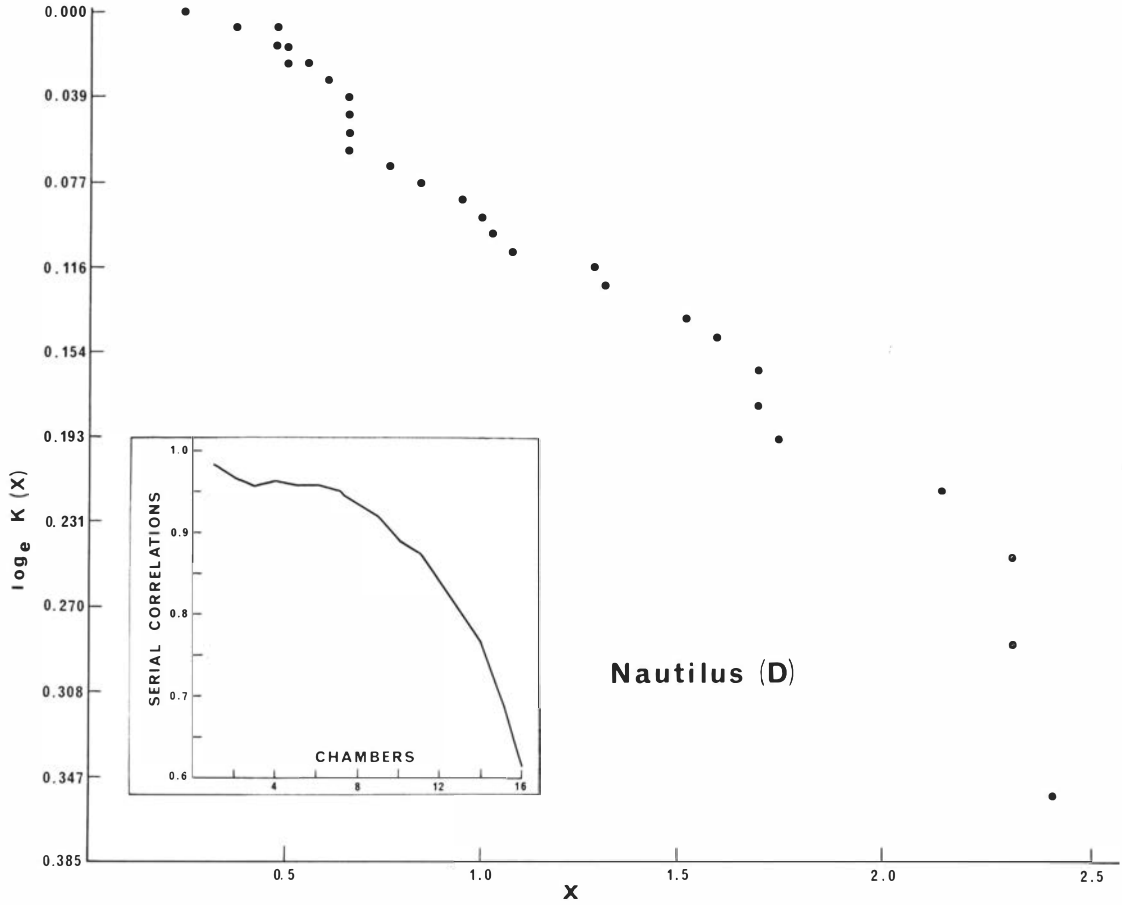

Fig. 31. Plots of the serial correlation coefficients and of $\log_e K(X)$ against X for specimen D of the pearly nautilus.

subjected to a transformation procedure. Consequently, the method extracts a set of coordinates from a transformed matrix of associations, each pair of coordinates representing one individual. The bivariate plot of these points will disclose the presence of groupings in the data such that individuals with like properties will lie together, while individuals completely disalike will be as far apart as possible.

The literature on Mesozoic ammonoids was searched for suitable data for analysis. Some 40 representative morphological categories were selected for study. It turned out to be surprisingly difficult to obtain complete sets of observations, as few authors seem to think it worthwhile to supply information on the body chamber.

The plot of the coordinate pairs for the ammonoid species listed in Table 4 is shown in Fig. 32. There is a clear breakdown of the data into groups, each of which can be related to the morphological characteristics of the shells. These characteristics can in turn be connected with the inferred buoyancy properties of the shell types. Remarkable agreement with the experimental results for the restricted number of shells already discussed is to be seen in the dia-

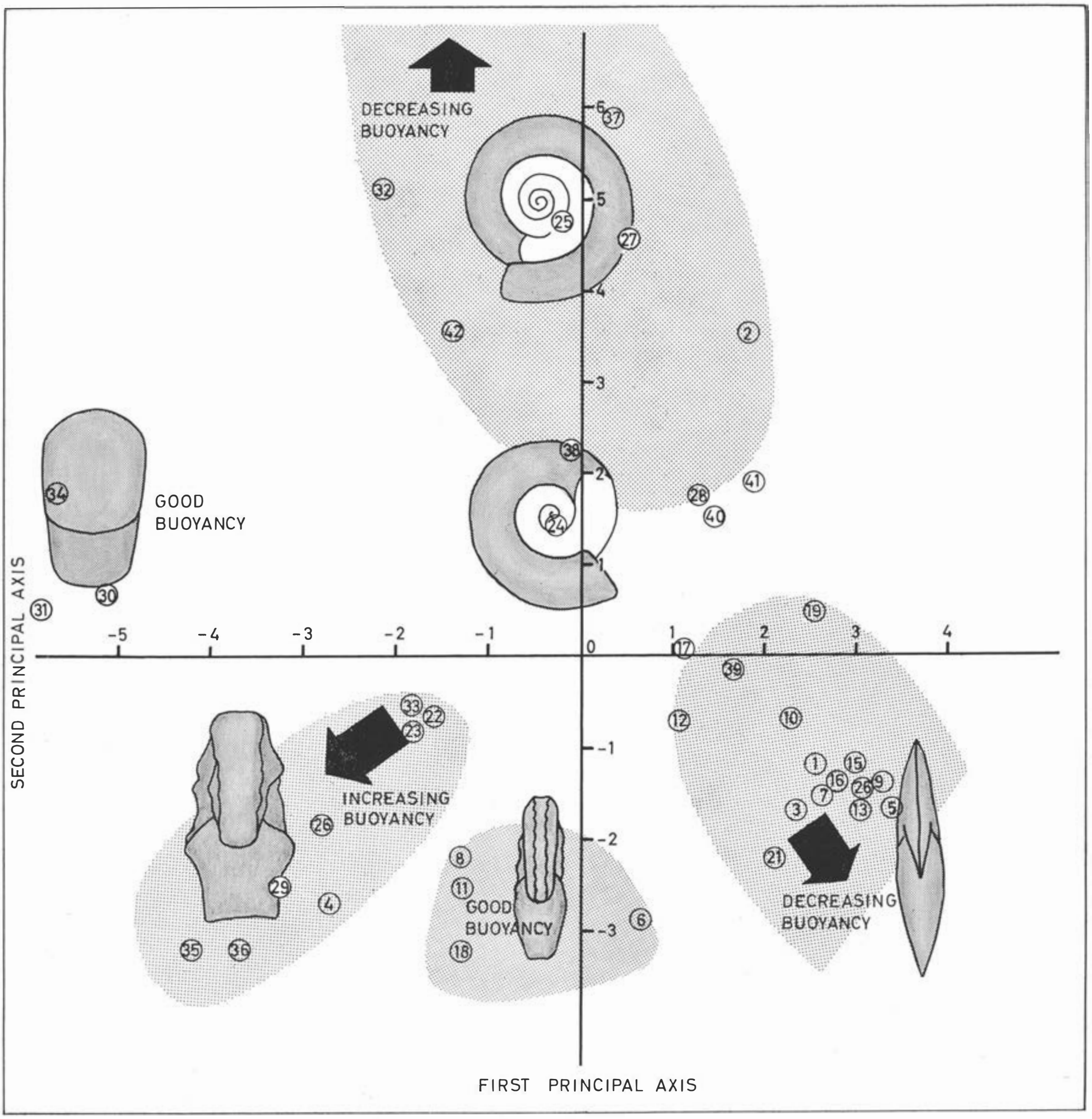

Fig. 32. Plot of the results of the principal coordinates analysis (cf. Gower, 1966) of 42 ammonoid shells of various inflations and different umbilical widths. The main bounding shell types are shown and the clusters interpreted in relation to the probable relative buoyancy properties of the main groups. The *X* and *Y* axes are dimensionless. The key for the numbers is given in Table 4.

gram. The clusters tend, in the right-hand half of the plot, to pass towards decreased buoyancy in an outward direction. Cadicones are located to the extreme left of the figure. The lower, left-hand quadrant contains forms displaying a tendency towards increased buoyancy in an outward direction. In general, the trend in buoyancy is towards better necroplanktonic floating properties diagonally towards the lower left-hand corner of the figure.

Table 4. List of ammonoid species used for the preparation of Fig. 32

Number in figure	Name of species
1	*Meekoceras gracilitate*
2	*Echioceras raricostatoides*
3	*Placenticeras lenticulare*
4	*Buchiceras subplanum*
5	*Sphenodiscus pleuriseptus*
6	*Metoicoceras whitei*
7	*Knemiceras attenuatum*
8	*Knemiceras gabbi*
9	*Engonoceras subjectum*
10	*Neolobites vibrayanus*
11	*Stantonoceras guadalupe*
12	*Placenticeras sancarlosense*
13	*Placenticeras intercalare*
14	*Kamerunoceras eschi*
15	*Hoplitoides ingens*
16	*Hoplitoides gibbosulus*
17	*Proplanulites koenigi*
18	*Frechiella subcarinata*
19	*Amaltheus depressus*
20	*Agassiceras simpsoni*
21	*Libycoceras afikpoense*
22	*Pseudaspidoceras crassicostatum*
23	*Nigericeras costatum*
24	*Arieticeras nitiscens*
25	*Peronoceras verticosum*
26	*Phlycticeras hyperbolicum*
27	*Eoderoceras impavidum*
28	*Ovaticeras pseudovatum*
29	*Pachyceras rugosum*
30	*Normannites formosus*
31	*Labyrinthoceras perexpansum*
32	*Skirroceras macrum*
33	*Cardioceras sagittum*
34	*Tulites tula*
35	*'Morrisites' fornicatus*
36	*Cadoceras sublaeve*
37	*Paltechioceras elicitum*
38	*Reineckeites duplex*
39	*Brasilia platys*
40	*Durotrigensia parkinsoni*
41	*Saxoceras grammicum*
42	*Emileia contrahens*

The analysis was made on the five variables: diameter, maximum inflation, length of the body chamber, ventral inflation, and the umbilical width. The variables were reduced to the same scale for all specimens.

OBSERVATIONS ON THE DITRIBUTION OF LIVING NAUTILUS

General Comments

Owing to the exceptional importance attaching to the pearly nautilus for studies on necroplanktonic distribution, it is essential that a close watch be kept on reports of discoveries of drifted shells and living animals. In this section, some recent information on these topics is summarized.

I have already referred to Teichert's (1970) note on the distribution of *Nautilus* in the Bay of Bengal, some 3600 km from the nearest known occurrence of living animals of the genus. The comprehensive report of Stenzel in the nautiloid section of the *Treatise on Invertebrate Paleontology* was reviewed and discussed in Part I.

I have Dr. Anna Bidder to thank for a useful extract of her notes on the records of the United States Museum of Natural History, Washington, on finds of *Nautilus* in their collection. An item of interest, pertinent to the present discussion, is the relatively large number of records of specimens with epizoal encrustations from beaches in the Pacific. This information is summarized in Table 5.

Dr. Bidder informs me that she has no records of living *Nautilus* in the area around the Marshall Islands, and the occurrences listed in Table 5 must be long-way drifts. The presence of encrustations and the damage to the shells would seem to be evidence of this. Serpulids manage to settle on

Table 5. Records of *Nautilus* shells from the Marshall Islands with epizoal encrustations

U. S. Nat. Mus. Catalogue No.	Locality	Nature of epizoans	State of shell
N. pompilius			
6149719	Ujelang Atoll	oysters	broken
586297	Bock I.	coral	broken
607349	Migenkar I., Ujal Atoll	oysters	worn
N. scrobiculatus			
614480	Elizabeth Atoll	coral and oysters	broken

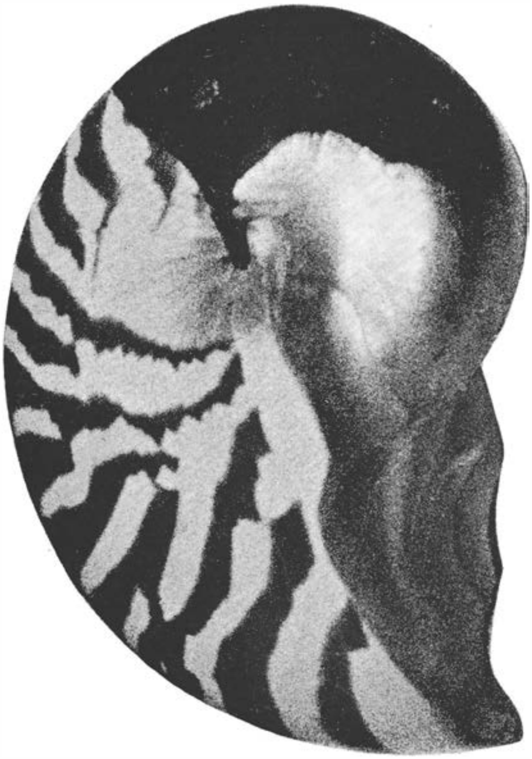

Fig. 33. Specimen of *Nautilus pompilius* taken up out of the water near Suva, in September, 1967. The specimen has lost all of its body chamber. There are no sharp edges to the fractures, indicating that the shell had floated for a long time before being found.

juvenile *Nautilus.* A specimen in Dr. G. Westermann's collection (McMaster University, Hamilton, Canada) shows, in section, a serpulid encrustation on an inner whorl.

In August—September, 1967, I had the opportunity of visiting some of the areas within the region of distribution of *Nautilus* in the Pacific. The observations presented here are largely an outcome of this visit, and also from some information obtained in 1964, during a visit to Malaya, from Mr. Clive Jones, then of the Geological Survey of Malaya. He had in his possession at that time a collection of shells of *N. pompilius* collected by him from the southern shore of the island of Penang. Here, they are carried in by the breakers, over the reefs, usually suffering damage in the process. This occurrence ties up with that recorded by Toriyama *et al.* (1965). There is every reason to believe that there is a population of *pompilius* living at present off the coast of western Malaya.

Thanks to the assistance of the Fisheries Division of the Department of Agriculture of Fiji, at Suva, I was able to undertake several trips in the seas around Viti Levu, the largest of the islands of Fiji. The opinion I gained from this work, and from discussions with Fijian fisherman and others, is that the areal extent of living *Nautilus* around Fiji is patchy. For example, occurrences of living individuals are known from Nelewa Bay, northeastern Vanua Levu, Nukulau, Viti Levu, and around Nakasaleku, Kadavu; stranded shells are most common on the beaches near these areas. Floating shells are not uncommonly taken up out of the water by fisherman. The specimen figured in Fig. 33 has lost all of its body chamber. This, and other shells, fished out of the sea during my visit lacked cameral liquid.

Indirect evidence of the restricted distribution of *Nautilus* in the Fijian area is provided by Cooper's (1966) report of rain-induced mortality off northern Viti Levu — this exhaustive account contains not a single reference to a specimen of the pearly nautilus among the myriads of dead stenohaline organisms found after the storm.

Mr. L. T. Caparros, a schoolmaster in the Philippines, has informed me that he has seen shells of *N. pompilius* floating in Lamon Bay and in the sea outside the bay. Stranded shells occur on the beaches of islands off Lamon Bay and in the intertidal zone of the bay and these islands. He has not seen encrusting organisms on the shells, nor are there any on the shells of the collection he has kindly presented to the museum of the Palaeontological Institute, Uppsala, all of which were collected in the spray zone of Alabat I. He has seen that hermit crabs are common inhabitants of shells of the pearly nautilus.

Thanks to the energetic cooperation of Mr. C. F. Fowler, it has been possible to compile the information displayed in Fig. 34, showing sites at which stranded or drifting shells of *Nautilus* have been collected around the Solomon Islands within recent time. The area shown in this figure lies

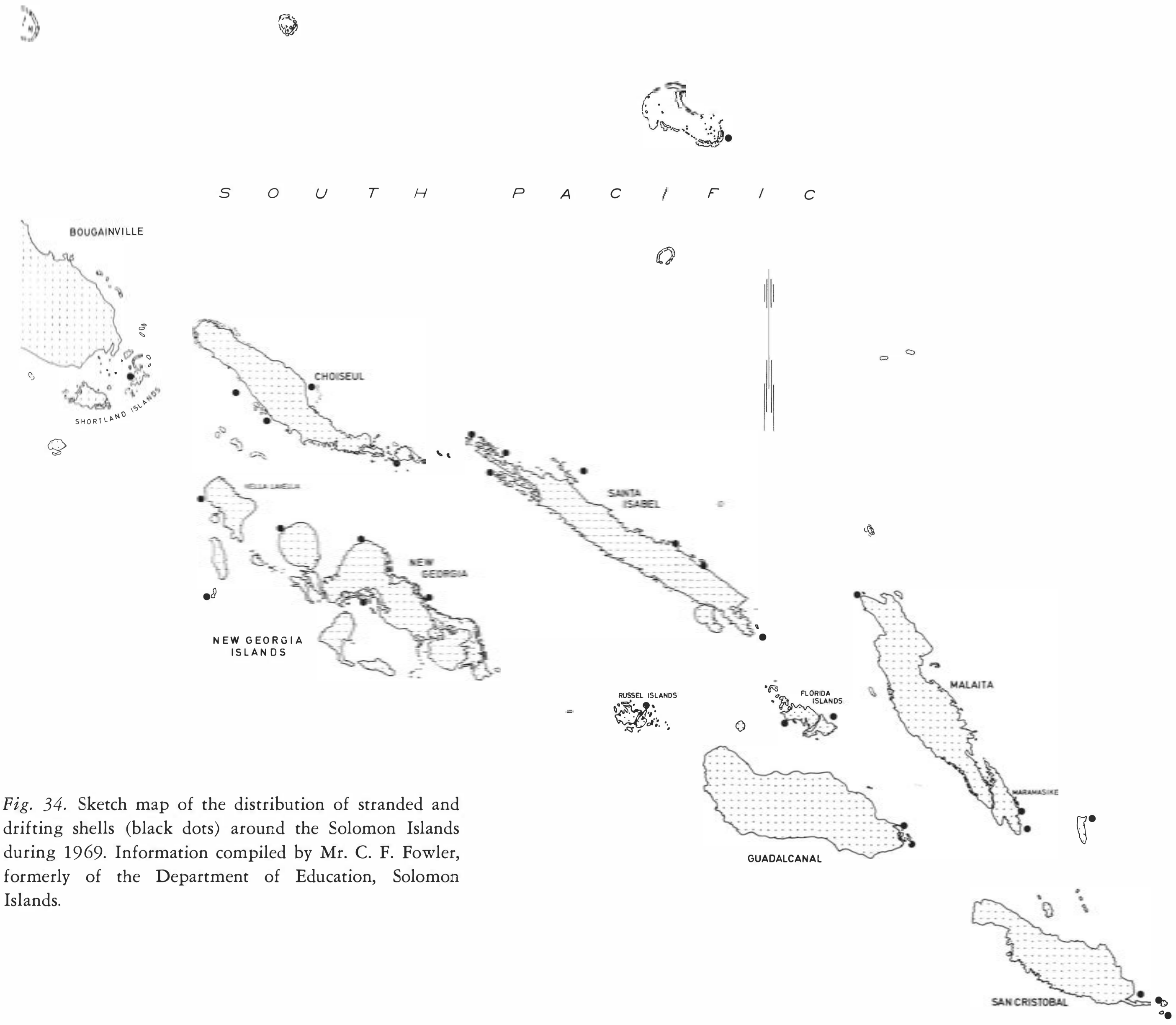

Fig. 34. Sketch map of the distribution of stranded and drifting shells (black dots) around the Solomon Islands during 1969. Information compiled by Mr. C. F. Fowler, formerly of the Department of Education, Solomon Islands.

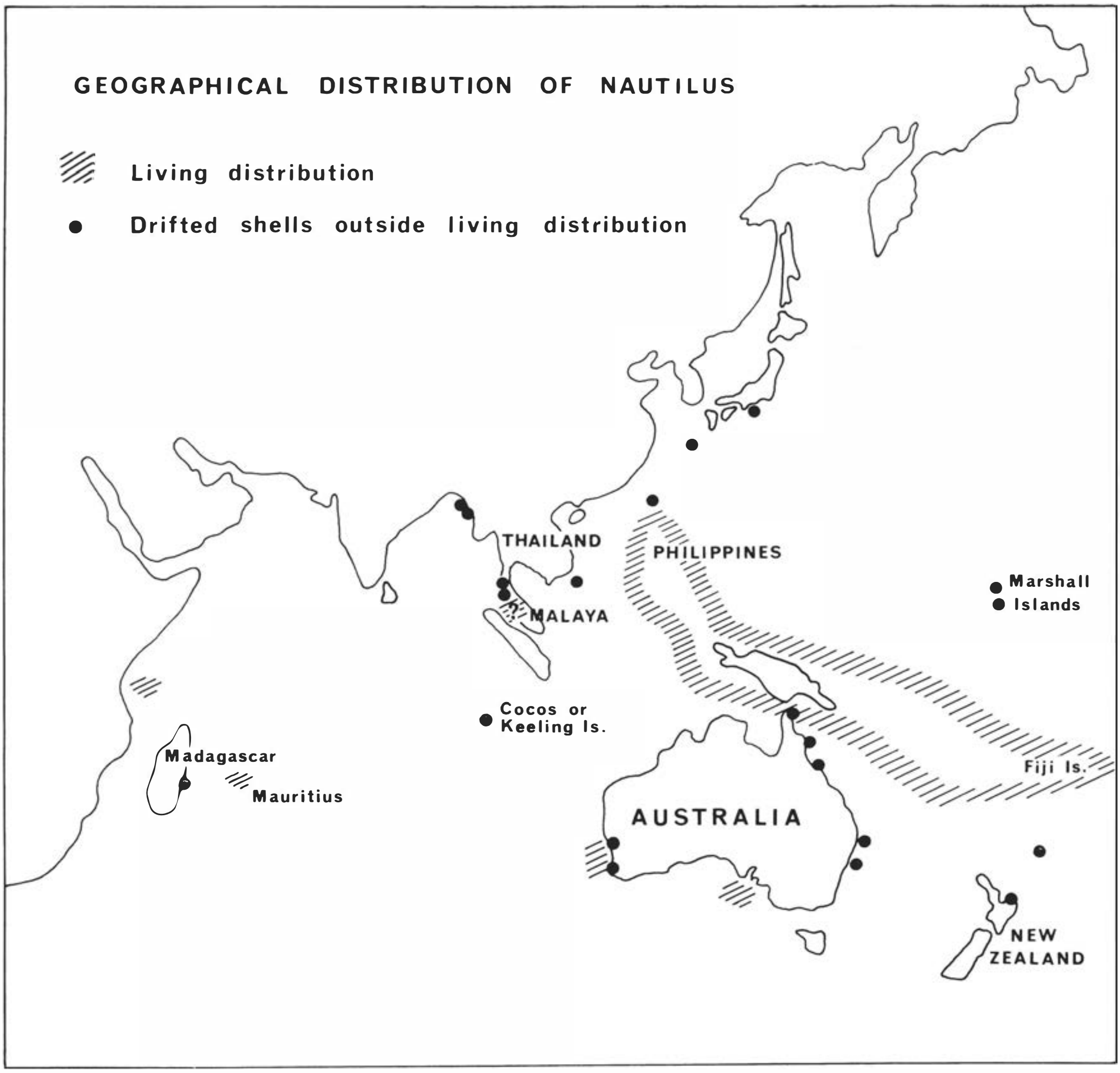

Fig. 35. Sketch map, based on Stenzel (1964), and subsequent publications, and my own observations, indicating the distribution of living species of the genus *Nautilus* and the locations of drifted shells outside of the area of this distribution. The geographical details of the South Pacific island areas have not been given.

well within the distributional range of living *Nautilus* (cf. Fig. 35).

For the Santa Cruz Islands, Mr Fowler found that shells strand around the atolls.

The pattern of distribution of shells for the Solomon Islands (Fig. 34) seems to show a tendency towards grouping of the finds of the eastern islands to their eastern extremities. This might be a reflection of the current directions prevailing in the area, but it could also be fortuitous, a product of how easy access is to the beaches.

The overall picture yielded by Fig. 34 is that *Nautilus* is fairly continuously spread throughout the coastal waters of the Solomon Islands and that the drifts have not been transported far before stranding (cf. comments under next heading). As far as I have been able to ascertain, the necroplanktonic distribution of *Nautilus pompilius* in the Solomon Islands tends to be more continuous than in the Fiji Islands.

Notes on the Distribution of Living Nautilus

Fig. 35 was prepared using data from the map published by Stenzel in Moore *et al.* (1964, p. K90), unpublished information supplied by Dr. Anna Bidder, Cambridge, Teichert (1970), Toriyama *et al.* (1965) and my own notes and observations. I am deeply indebted to Dr. Bidder for her help.

Dr. Bidder has informed me (letter dated 5 .12. 1967) that she now has evidence of living *Nautilus* from Mauritius and Zanzibar; this greatly extends the known distribution of modern representatives of the genus. It is therefore no longer correct to say that *Nautilus* is restricted to the southern Pacific Ocean. This also allows a more rational interpretation of drifts in the Indian Ocean.

I have difficulty in holding with Stenzel's supposition that the distribution of the genus may be continuous. As far as my personal experience may be taken as a guide, the distribution of *Nautilus* tends to be patchy, over part of the area of occurrence at least, and it seems to me that the more likely situation is that there are a number of communities, spread over the southwestern Pacific and Indian Oceans. The new information on the presence of living *Nautilus* in the western Indian Ocean helps to dispel some of the uncertainties and anomalies in the dispersal of dead shells in this region and the apparent conflicting nature of reports of drifts in relation to known oceanic currents.

REFLECTIONS ON FUNCTIONAL MORPHOLOGY AND MODE OF LIFE OF SHELLED CEPHALOPODS

Aspects of this topic were considered in Part I, although the aim of that study was not directed towards an analysis of questions of the functional morphology of the shelled cephalopods.

The present, and another (Mutvei and Reyment, 1973) study have shown that for many cases, the two themes, postmortal fate and functional morphology overlap.

A good deal of conjecture has resulted over the last 140 years on the reason why many ammonites possess highly frilled sutural zones of contact with the shell wall. The posthumous work of Schindewolf (1972) is largely concerned with an analysis of some of the literature known to him on the subject, and, in particular, a reappraisal of the celebrated paper of Pfaff (1911). Outgoing from a renewed consideration of the "anomalous" clymenids, Schindewolf sought an intuitive solution of the function of the dorsally located siphuncle of this group in relation to buoyancy control, and then went on to extend his line of argument to all other shelled cephalopods. The main point arising out of his discussion of the clymenids is that only a short part of the siphuncle in each chamber could have participated in the transfer of cameral fluid during buoyancy adjustments, owing to the excessive length of the septal necks. Consequently, in spite of the fact that the cameral liquid was in effective contact with the siphuncle in all but the last one or two chambers of the majority of species, the process of transferring the liquid back and forth would have been inefficient. This could have placed the clymenids at a disadvantage in relation to goniatites with short septal necks and a more efficient means of buoyancy control.

The results of the experiments made on exact models of certain ammonoids and palaeoanatomical considerations (this paper, and Mutvei and Reyment, 1973), suggest that ammonoids may have been more fitted to motion in a vertical direction. The palaeoanatomy of the ammonoids indicates that they cannot have been as good at swimming as the pearly nautilus, which in turn, is inferior to non-shelled cephalopods.

As many have surmised, the septal fluting may represent an adaptation towards strengthening the ammonoid shell, the walls of which tend to be thinner than is the general rule in nautiloids. This would tend to be most strongly developed in those forms that were faced with the need to adjust rapidly to great differences in pressure, perhaps diurnal vertical movements correlated with the daily migrations of some kind of phytoplankton. I think that there is now reason to believe that some ammonoids fed on plankton, or other organisms upon which they could browse, as the evidence yielded by the functional anatomy of these cephalopods seems to be little in favour of their having been able to pursue their prey actively.

With Schindewolf (1972), I agree that the development of the suture of shelled cephalopods must have been an outcome of the "hereditary programme", at least, as regards the basic outlines. I think, however, that one would expect the details of the ammonoid suture to be subjected to normal stochastic variation and to yield to selection pressure. After all, palaeontology abounds with examples of this, such as the shift in the relative average dimensions of the anterior and posterior limbs of Liassic steneosaur crocodiles in relation to the geosaurs and modern crocodiles, and the way in which ornamental changes appear, stochastically, in ostracods and other arthropods. I am therefore sceptical of methods of heuristic argument, based solely on "reasoning", in situations which only can be resolved by experimental work.

Indirect support for the possibility that the minor details of the suture line might have reacted even fairly rapidly to selection pressure is offered by ammonoids definitely known to have inhabited a shallow environment and for which adaptations of the shell to withstand water pressure would have been largely redundant. There are many such examples known, and I shall here confine myself to a discussion of a single group, the vascoceratids of the Lower Turonian of northern and West Africa, of which I have detailed knowledge. These ammonites are well known to have lived in a very shallow sea, usually less than 10 m in depth. During the Lower Turonian, northwestern Africa was covered by an epeiric sea, stretching from Nigeria in the south to Algeria and Tunisia in the north, in which vascoceratids occurred abundantly.

Vascoceratids have what has sometimes been called a "degenerate" suture, apparently a reduction from the acanthoceratid type of the Cenomanian. The vascoceratid suture could possibly have evolved as a response to life in a shallow environment in which the factor of shell robustness in relation to wave action was at a premium. The relaxation of selection pressure in one direction, but its tightening in the other, and the redundancy of the role of septal complication as a strengthening device, could have led to a simplification (i.e. "degeneration") of the suture line. In general, the conchs of the Saharan vascoceratids tend to be more robust than is usual in ammonites, which is a further point in favour of their adaptation to the epicontinental environment.

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