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SOME FACTORS IN THE  
DISTRIBUTION OF FOSSIL  
CEPHALOPODS

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# 6. Some factors in the distribution of fossil cephalopods

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*Abstract.* The literature on the distribution of fossil cephalopoda is reviewed.

The experimental section shows the following factors to be important in the buoyancy of cephalopod shells: the shape of the shell and thickness of its walls and, if coiled, the nature of the coiling, the size and form of the body chamber, the properties of the septa and the siphuncle, and the influences of pressure, temperature and salinity.

The specific gravity of the aragonite in the shell material of living nautilus was determined to be 2.63 so that virtually no volume change occurs on recrystallization to calcite. Plastic models of some common shell types were made and subjected to simple buoyancy experiments. Straight shells with large siphuncles (endoceroid shells) float with the siphuncular side underneath; the effect of cameral deposits on the buoyancy of such shells is discussed. An endoceroid shell without cameral or siphonal deposits will not float if the length of the body chamber exceeds a quarter of the length of the chambered portion of the shell. If the body chamber is less than 8 % of the length of the chambered shell the shell floats with the tip lower than the oral end.

Straight shells with narrow siphuncles (orthoceroid shells) were found to be buoyant. Such a shell will not float if the length of the body chamber exceeds a half of the total length of the shell. Orthoceroid shells float vertically up and down (body chamber beneath), at an angle to the horizontal, or with the tip below the oral end of the shell, depending on the size of the body chamber. Supporting field evidence is discussed.

Lituitoid and baculitoid shells were nekroplanktonic as were probably some turrilitoid. Scaphitoid and hamitoid shells were less frequently nekroplanktonic.

Experiments on coiled cephalopod shells showed that air is displaced less readily through the siphuncular orifice of highly involute shells than from evolute shells. Exposure of Recent nautiloid shells to prolonged immersion in salt water leads to the formation of small holes in the wall at sites of imperfect shell secretion. The uplift on very compressed and highly depressed shells is not sufficient to cause them to float, although they poise in an upright position on the sea floor.

Experiments were made on the effect of the dimensions of the body chamber on buoyancy; it was ascertained that the body chamber is of prime importance in this respect and is the dominant factor in buoyancy. Some shells are ornamented with solid elements which weight the shell; hollow ornament assists uplift. Experiments show that evolute shells will strand in slightly deeper water than involute shells. X-ray investigations and thin section studies show that aragonitic shells usually have thicker shell material than the same species in calcitic preservation owing to loss of calcium carbonate by solution.

Ammonites usually possess more septa and whorls than coiled nautiloids at comparable radii. Ammonite septa are seldom situated at mathematically regular distances from each other. Observations on the direction of inflation of ammonite septa are presented. Entirely convex-outwards septa are shown to be rare amongst ammonites. External siphuncles when damaged permit readier access of water to the air chambers than centrally or dorsally situated. Good agreement was obtained between the disposition of experimentally waterlogged shells and the relationship between fine sedimentary material and crystalline calcite in fossil shells.

Sediment gained access to the air chambers through the siphuncle. The study of thin median sections discloses that the siphuncle is often missing in the last whorl and even in inner whorls, which is due to the effect of water pressure and waves.

Temperature, pressure and salinity are shown to have a great influence on nekroplanktonic shells. Temperature fluctuations tend to sink a floating shell as water successively replaces expelled air. Shells were probably distributed widely under water by the agencies of thermal and saline stratification. The examination of thin median sections of ammonites shows that the effect of pressure has been of considerable importance. Water was injected into the air chambers by rupturing the siphuncular sheath. Aptychi and cephalopod jaws are considered to have fallen to the bottom from the rotting carcasses of drifting ammonites, or to have been transported away from the shell by water action. This explains why ammonites and aptychi have a widely different distribution. The presence of an aptychus in a body chamber implies the absence of reworking after the burial of the ammonite.

Some actual field occurrences are reviewed in the light of the experimental results of the paper. The application of these to the interpretation of some marine environments is discussed. Evidence is presented to

show that the most common occurrences of fossil cephalopods are in coastal sediment. It is suggested that cephalopod shells should prove a useful tool in the identification of sedimentary environments and in the interpretation of aspects of paleoceanography and paleohydrology.

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### INTRODUCTORY REMARKS

Many workers have in the past been concerned with various problems connected with the distribution of fossil cephalopods. As is generally known ammonites, for example, are very often of exceptionally wide geographical distribution and it is in part to this fact that they owe their great value as index fossils. Most study on the subject of cephalopod distribution has been associated with attempts at reconstructing the mode

of life of the living animals. Some authors have tried to combine different shell forms with diverse activities and from these considerations drawn conclusions about ammonite shell shapes as environmental indicators.

All works on the subject available to the present writer disclose that the commonly adopted line of reasoning is based on how cephalopod animals can be thought to have lived. This type of argument is no doubt of value when employed for groups that have well-known, present-day representatives, but becomes less useful when applied to such a group as the fossil cephalopods whose only representatives alive today of the tetrabranchiate section are a few species of the genus *Nautilus*. Bearing in mind that this genus is very imperfectly known neozoologically it becomes apparent that theories based on our knowledge of it must be largely conjectural.

The present author feels that sight has been lost of the really fundamental problem; as far as geology is concerned it is what happened to the empty shell after the death and decay of the animal that is vital. For many fossil groups this factor is of lesser importance. In the following pages it will be shown that the peculiar structure of the cephalopod shell necessitates more involved reasoning to elucidate its ultimate fate.

## PREVIOUS OBSERVATIONS

In this chapter papers are reviewed that have a direct bearing on the subject in hand; where necessary for elucidation or elaboration of a particular point unpublished observations and information contributed by colleagues is included. In a few cases remarks on modern dibranchiate cephalopods are presented where it is thought that they are pertinent to extinct tetrabranchiate cephalopods.

The subject of fossil cephalopod distribution has been treated in varying degrees of detail by several authors. The following papers have come to the notice of the present writer; no doubt further observations occur in the literature and the discussion appearing below makes no claims to completeness.

The kernel of the problem centers around the possibility whether or not the empty cephalopod shell would have floated or sunk. As shown here, opinion is divided between these two possibilities, although by far the majority of paleontologists either directly or indirectly incline to the view that the shells of fossil cephalopods sank or stayed in place on the sea floor in the same fashion as gastropod shells. The minority subscribe to the opinion that the empty shells floated like those of *Spirula spirula*, whose shells drift widely with ocean currents and are washed up in great numbers along beaches far outside the area of living distribution. The chance of both occurring does not seem to have received much consideration.

LINDSTRÖM (1890, p. 4) in discussing the distribution of the Silurian cephalopods of Gotland noted the presence of considerable accumulations of ascoceratid and lituitid shells. He came to the conclusion that these "cephalopodan strata" were built up in shallow water, near to the shore, where they make up beds of up to 2 meters in thickness. After the soft parts had rotted away he considered that the shell floated unless too heavily weighted by organic deposits. He supposed that the shells drifted ashore in the same way as *Spirula* today. It is of interest to compare this observation with that of SCOTT (1940, p. 309) who reported that in early Paleozoic deposits cephalopods are often found associated with heavy-shelled benthonic animals, thus indicating relatively shallow water.

JAEKEL (1902) expressed the view that "*Orthoceras*" (the citation marks are mine) forms grew fast in the same way as conulariids are supposed to have done, and the cameral deposits assisted in anchoring the shell. He thought (1902, p. 8) that the forms with restricted apertures, such as *Phragmoceras*, *Tetrameroceras* and *Hexameroceras* lived like *Dentalium* and used the funnel solely as a respiratory organ. Belemnites were also considered to have been more or less sessile creatures. In discussing the theory of a torpedo-like mode of progression for orthoconic cephalopods JAEKEL (1902, p. 70) held forth that the presence of cameral deposits together with the fact that these cephalopods have thick shells would operate against such a means of movement. As he saw the facts the reasons for a sessile existence were very strong and almost all orthoconic nautiloids seen by him had broken tips or, if the tips were whole, they were scarred. In the discussion appended to JAEKEL's paper BRANCO (1902, p. 89) mentioned that if cephalopods really did live in the way postulated by JAEKEL then one would expect to find them preserved in this state. This remark was countered by JAEKEL who said that sandy beds are readily distorted, which would erase all signs of the living position. In the same discussion MENZEL (1902, p. 91) observed that at Hildesheim (northern Germany) large numbers of ammonites and belemnites in company with a few pelecypods occur in beds that he thought had been formed far from the coast where no indrifting of material could have taken place. In his opinion "pelagic ammonites" and belemnites sank after death. In connexion with JAEKEL's paper mention was made of CLARKE's (1900) observation concerning vertically bedded cephalopods in the New York area. TEICHERT (1933, p. 196) pointed out, however, that CLARKE found only cavities and that the rock concerned is a fresh-water sandstone. RUEDEMANN, who examined the locality, reported the cavities to have been formed by gas. The true position is, however, yet unresolved.

The following has a direct bearing on the question. Dr. R. COPE, Geological Survey of Nigeria, in a personal communication about an area mapped by him in Northern Ireland in 1953 mentioned that he had frequently come across orthoconic cephalopods vertically or obliquely

bedded in shale. In his opinion this took place owing to the heavy shells falling into the soft bottom sediment after the death of the animals. Unfortunately, none of the specimens (all preserved in the Geological Department of the University of Liverpool, England) is sufficiently well preserved to permit even generic determination.

WALTHER (1897, p. 258) clearly realized the importance of the problem here under review and made some very sharp-witted statements on the transport of ammonite shells. In this paper, he was struck by the apparently inexplicable complete lack of the remains of ammonite soft parts, particularly as impressions of the body are known of belemnites and other cephalopods. He was of the opinion that ammonite shells could float for at least some period of time before becoming sedimented (1897, p. 261). As WALTHER indicated on the same page this fact is one of the main features that make ammonites the excellent zonal fossils they are inasmuch as they occur in many types of facies; he also made the observation that the distribution of chambered cephalopod shells is independent of the mode of life of the animal. His points of view have received little acclamation from later workers, probably because they were backed by little tangible evidence. WALTHER (1897, p. 262) did not consider all ammonites to have been transported in this fashion and noted that some species have a very localized occurrence. This he thought to represent the area of distribution of the living species.

ROTHPLETZ (1909) published a stimulating paper on the mode of burial of the ammonites in the Solnhofen beds. This area seems to have been a long tidal coast with daily fluctuations in sea level. Many species of ammonites are found in these deposits but well preserved forms are rare. The fact that aptychi are so commonly present in the body chambers of Solnhofen ammonites suggests that the animals were buried together with their shells. Although most of the ammonites described by ROTHPLETZ were embedded in a horizontal position some vertically bedded shells also occur. ROTHPLETZ further observed (1909, p. 317) impressions of the venters of shells beside horizontally situated and often crushed shells. He considered that the shells first poised vertically, buoyed up by the shallow water, and then slowly sank over as the tide receded. Aspidoceratid shells are often found in a vertical position in which they were stably held by the ventral horns. It is noteworthy that these ammonites are not so frequently of compressed shape as the perisphinctids. The aspidoceratid shells are assumed to have been buried rather quickly as otherwise the effects of wind, weather and sea would have damaged the exposed portions. Certain calculations made by ROTHPLETZ also tend to support this viewpoint.

The photographs reproduced in ROTHPLETZ' paper seem to indicate that the majority of the perisphinctids were stranded at the turn of the tide; the ventral indentations were made at this juncture. A few shells were caught, however, in pools where they became vertically entombed.

The same thing tended to happen to inflated aspidoceratid shells. Consequently, the shells must have been able to float and the ammonites probably had their normal habitat near to the shore (at least during part of the year). Some living animals were almost certainly trapped by the tide at times, but most were dead. As is shown in the following sections there is a good chance that some of these dead creatures may have stayed poised in a hovering position a short period before putrefaction had advanced far (cf. pp. 134, 136, 159, this paper).

JOHN (1909) recorded that oysters are often found attached to ammonite shells in considerable number (1909, p. 9) (cf. p. 138, this paper). He thought that oyster larvae are able to fasten onto the shells of swimming cephalopods in the same way as certain other organisms are able to append themselves to ships. He considered, however, that the oysters, which for example grow on many Solnhofen plattenkalk perisphinctids and Lias ammonites from Boll and Holzmaden, grew onto the empty, drifting shells. As a basis for this opinion he quoted CHUN's report of nautilus shells overgrown with this and other organisms. The present author has yet to see such a specimen and there are none in the museums of Sydney, London and Stockholm. It seems likely that such overgrown shells are rare and are the product of special circumstances. SCHINDEWOLF (1934, pl. 2) recorded several ammonites with serpulid growths.

JOHN also recorded (via QUENSTEDT, 1909, p. 10 in JOHN) that certain inflated ammonites are found in a vertical position. According to JOHN, the mass occurrence of ammonites suggested to JAEKEL that these forms were bottom dwellers and had their habitat in the same place as where they occur as fossils. JOHN leaned to the view that such accumulations had been formed when dead shells were swept into bays and buried there. He criticized WALTHER's conception of ammonite distribution based on the idea that empty shells drifted until they become water-filled enough to sink, by quoting ORTMANN who is reported to have stated that in such a case the shells could only have been embedded after damage and sinking, which would be shown by the presence of calcitic fillings and crushing; as JOHN found the majority of shells to be undamaged he concluded that the ammonite was covered and held down by sediment before the body had rotted. He also observed (1909, p. 18) that as ammonites often occur together with belemnites it must be concluded that most sank and that floating shells were a rarity.

Although the main paper in which WALTHER published his ideas on cephalopod distribution was not available to the present writer the principal lines of argument employed may be gleaned from a discussion by SCUPIN (1912) on the mode of life of ammonites. WALTHER was impressed by the nekroplanktonic spreading of *Nautilus* and *Spirula*. He considered most ammonites to have been benthonic and to have lived in closely confined areas or ecologic niches. The empty shells were, however, borne far and wide by ocean currents and so distribution was independent of facies and depth.

In opposition to WALTHER's views SCUPIN cited KOSSMAT's observation that not all ammonite species are widely distributed and that in the Indian Cretaceous many European species are not found although they frequently have close relatives. In the present writer's opinion this fact may be explained in certain cases in the following manner. Firstly, many ammonite and nautiloid species (in particular, Mesozoic and Cenozoic nautiloids) have been founded on single specimens or, at the best, two; so that no idea is available concerning the range of variation of the "species". Secondly, the imperfection of the geological record must be taken into account; two almost similar faunas may consist of respectively slightly more advanced or retarded members in an evolutionary sequence or sequences. That is, geographically widely separated faunas may be chronologically different and the constituent species will thus show a certain amount of chronologic variation. This is more noticeable amongst the rapidly evolved cephalopods than amongst more conservative groups.

SCUPIN (1909, p. 352) did not entirely dismiss nekroplanktonic distribution as a factor and was of the opinion that it should always be considered a possibility when isolated foreign elements occur in a fauna. He also expressed the view that larval wandering assisted in the wide distribution of cephalopod genera (cf. HESSLAND, 1945).

DIENER (1912) published a philosophical discussion on the mode of existence and the distribution of fossil cephalopods. He believed that most ammonites are autochthonous and are found in the same place as that in which they lived; the passive transport of empty shells was considered to be of minor importance and the implications attached to this process by WALTHER were regarded as vastly exaggerated. DIENER could not believe that the animal rapidly rotted away and that the shells subsequently found their way up to the surface. He cited ROTHPLETZ' work on the Solnhofen plattenkalk in support of his reasoning (1912, p. 85). According to DIENER (1912, p. 86) the shell, weighted down by the body of the deceased animal, sank rapidly to the bottom where it became enveloped by sediment.

KESSLER (1923, p. 502) considered that after the death of the ammonite animal the shell sank and was entombed. TRUSHEIM (1934, p. 8) was of the opinion that the imprints of shells in the lithographic slates of southwestern Germany come from the rounded undersides of ammonites and that the animals were alive in the shells at the time, as no marks such as might have been made by the dragging soft parts of carcasses have yet been brought to attention. The present writer believes these shells may have been already empty when the impressions were made; the habitat of the live animals could have been in the vicinity of the strandline.

FREBOLD (1928, p. 25), in connexion with the study of an area in Spitzbergen, came to the conclusion that vertical changes in a fauna may be due to mechanical sorting of the shells by water, although this is generally put down to fluctuations in environment. Ebb and flood will cause sorting

of the fauna into species as objects of the same shape tend to become concentrated together under the influence of wave action. The factors of size, shape and weight will tend to bring about a zonal arrangement of the shells. This point of view, as far as cephalopod shells are concerned, seems to imply belief on FREBOLD's part in the non-buoyancy of empty shells and that they behave in much the same way as other mollusk shells. If all cephalopod shells be considered as floating objects then the effect of ebb and flood tides under the above-outlined conditions would only build up a concentration of stranded cephalopod shells along the furthest line of advance achieved by the flood tide. There would be virtually no sorting effect.

In a little-known paper on Recent Philippines mollusks TALAVARA & FAUSTINO (1931) made mention of some interesting facts about the biology of *Nautilus*. According to these workers, *N. pompilius* is distributed throughout the Polynesian Islands, particularly the New Hebrides, and the Fiji Group. In the Philippines the species is abundant off the southern coast of Negros, Tanon Strait, Bantayan, Gebu, Palaman, Cuyo, Basilan, Leyte, and Mindoro. It probably also occurs around the Lingayen Gulf, the Cagayan coast, Tayabas, Camarines Norte, and Mindanao. According to TALAVARA & FAUSTINO *N. pompilius* is a coral bottom dweller. It swims by jerks (1931, p. 344). It is often captured at depths of around 400—600 m in bamboo traps and these authors think it can thrive around depths slightly in excess of 600 m, but they advise, nevertheless, caution in evaluating reports of catches made in so-called deep-sea traps as most of these are set at depths of roughly 60 m (1931, p. 345). Dead shells are reported to be commonly found in great numbers along the beaches and in the shallows and the species is most common in Philippines waters during the summer months (cf. observations of TINBERGEN & VERWEY, 1945 on cephalopod migration; this paper). Another interesting observation is that the sense of smell of *Nautilus* appears to be keener than its sense of sight. Fijians catch the living animal in water from 4—6 m deep; they watch until a nautilus is seen to alight on a ledge or some other prominence and then carefully lower over it a specially constructed trap. See also IREDALE (1944, p. 298).

MILLER, DUNBAR, & CONDRA (1933, p. 12) expressed the opinion that the shells of dead nautiloids must have floated and drifted widely after the fleshy bodies had decayed and dropped out of them and so a geographically confined species can have drifted widely after death and thus achieved an impressive posthumous distribution.

KREJCI-GRAF (1932, 1935) published some notes on his observations concerning shells of the gastropod genus *Cerithium* in the Sormat of Wiesen, Burgenland (1932, p. 295) where these shells are found in sediment with their apices pointing downwards. Experiments show that watery sand will cause buoyant gastropods to float upwards and they may fasten in this position. Furthermore, he cast a number of shells into water and

saw that a few cerithiums floated with the pointed end downwards (cf. p. 124, this paper). All shells behaving in this manner were seen to have very narrow apertures while the shells that sank were sediment-filled, broken, or had very wide, ornate apertures. After blocking the apertures of several gastropods it was found that all floated, but *Natica* and *Nassa* had their apices directed upwards. Completely dry specimens of *Cerithium* with blocked apertures were found to adopt a horizontal floating position. Later experiments with other species of *Cerithium*, in which the apical angle was either greater or smaller, showed that as long as the aperture remained open these shells sank.

In a later work (1935, p. 42) an account was presented of the floating capabilities of empty mussel shells. The periostracum of *Corbicella manillensis* dissolves in gyttja in the same way as was noted by HECHT (1932) for *Mytilus edulis*; it loosens and may cover the edges of the shell and fasten them. These shells floated with the umbo directed upwards for at least a few hours and in one experiment a shell was noted to have floated throughout a whole night. Nauidids also floated, but not for more than half an hour. Thus, even the possibility of flotation for fossil pelecypods should be taken into account.

TEICHERT (1933) in connexion with his study of the actinoceroid cephalopods also put forward his views on the buoyancies of certain straight nautiloid shells in the living state. Some of his more important observations may be summarized as follows. He considered that even nautiloid shells with fairly wide siphuncles as well as cameral deposits should have floated. However, *Kochoceras* and *Selkirkoceras* (1933, p. 190) have such a very broad siphuncle that the small air chambers cannot reasonably be conceived to have been able to bear up the shell; cameral deposits would have further decreased the buoyancy. TEICHERT's results are considered in more detail in a later chapter (see p. 125).

TRUEMAN (1941, p. 340) in his theoretical treatment of the buoyancy of living ammonites made the observation that the uplift in this case must have been greatly influenced by the ratio of the body chamber to the chambered portion of the shell. This assumption is shown to be correct in the experimental section of the present paper.

SCOTT (1940), as already observed in the introduction, attempted to devise a bathymetrical zonation scheme based on the shape and ornament of ammonite shells, in itself a tacit statement of belief in the idea that ammonite shells did not float. In reference hereto (1940, p. 302) SCOTT wrote that the relatively prevalent opinion that the shells of dead ammonites floated widely over the oceans to become entombed in sediments far from the native haunts of the animal has been given an emphasis far in excess of its importance. He attacked the standpoint that the present distribution of the fossils gives only a poor idea of the apportionment of these forms when alive. The reports of WILLEY (1902) and ROGERS (1908) that shells of nautilus drift ashore at certain localities was con-

sidered by SCOTT to be ascribable to dispersal by natives who use the animal for food. Signs of attrition owing to weathering and transport are usually absent from cephalopod shells, which SCOTT took as indicative of the rarity of distribution by flotation. He mentioned that occurrences of battered shells are rare enough to incite special comment. SCOTT considered that where a large number of ammonite shells occur together they must be considered to be in situ. HAAS (1956, p. 197) used SCOTT's concepts in a review of the bathymetric conditions of certain Jurassic ammonites from Mt. Hermon, Syria.

JAWORSKI (1940, p. 1004) in criticism of SCOTT's paper pointed out that the uplift of the ammonite air chambers does not permit the assumption of a benthonic or nektobenthonic existence.

Not only the few surviving tetrabranchiate species are poorly known but also the habits of the modern dibranchiates. A very important paper by TINBERGEN & VERWEY (1945) contained numerous observations of weight in connexion with the determination of the distributional factors of fossil cephalopods. These authors made a study of *Loligo vulgaris* in the waters around Den Helder, Holland.

The species was found to occur commonly from April to August and to be otherwise rare. It reproduces regularly around Den Helder during this period. Many cephalopods are known to reproduce periodically and some species spawn longer in Mediterranean waters than they do in the North Sea, a fact which the authors think may be ascribable to the influence of temperature. The reproduction of *L. vulgaris* begins in the North Sea in conjunction with increasing daylight while the reverse is true for the Mediterranean. The first migratory day varies only slightly from year to year which would also seem to suggest a certain degree of dependency on temperature. The animals also tend to appear later in cold years than in warm. The investigations showed, however, that in actual fact temperature is of subordinate importance, whereas the time of the year (i. e. the length of the daylight period) is decisive. The number of squids arriving in the North Sea varies from year to year and the greatest numbers were found during exceptionally warm years.

*L. vulgaris* was found to be strongly bound to the coastal area. In June the squids come closer inshore than in April and May, on the one hand, and in July and August on the other. Winter catches were made in deeper water than summer catches. The tidal flat sea is only visited by the animals when the salt content exceeds 30.3 per mille. The parts of the coastal sea furthest from land are visited when the salt content is lower than normal (under 34 per mille) and the temperature fall small. Calamars seem to dislike unmixed North Sea water and to favor warmer areas and both of these characteristics tend to bind them to the coastal neighbourhood, where the salt content is lower and the temperature higher than further from the coast (spring and summer). Depth would seem to be a less decisive factor.

The common squid is found from the Mediterranean coasts to the Eastern Atlantic between  $21^{\circ}$  and  $59^{\circ}$  N; it does not disappear in the Mediterranean during the winter. Around the Portuguese coast the species is commoner during the winter than during the summer which TINBERGEN & VERWEY think may be due to migration. Observations made along the Dutch coast show the calamar to pass from south to north during the spring; this movement is more pronounced than the currents and is therefore active. The animals appear to overwinter in Portuguese waters.

According to TINBERGEN & VERWEY, LO BIANCO has observed that reproduction of Mediterranean squids continues for a longer period than elsewhere. Other cephalopods show a similar periodic reproduction but in the Mediterranean and elsewhere certain forms spawn throughout the year. *L. vulgaris* spawns immediately it enters the coastal region; it is also known that outside this area reproduction is virtually unknown to occur.

TINBERGEN & VERWEY pointed out that there seems to be a direct connexion between maturity and migration. One of the main migratory forces may be reproductive (*Laibzug*, 1945, p. 244). Migrational habits vary from species to species and *Loligo forbesi* STEENSTRUP is a migratory species in both the North Sea and the Mediterranean.

The above review suggests that the possibility of wide annual migrations and periods of near-shore habitation should be kept in mind by workers on fossil cephalopods.

Some squids, including the entire suborder Cirromorpha, live as deep-sea forms. Many octopods are too deep-sea species (EKMAN, 1953, p. 280).

Whilst on the subject of cephalopod migration it is in place to note the following. The migrational behaviour of the calamar may also be duplicated, at least partly, by tetrabranch cephalopods living today. As has already been indicated, TALAVARA & FAUSTINO observed for *Nautilus pompilius* that it appears periodically, there being a maximum during the summer months.

Summing up, it appears to the present writer that the following points ought to be taken into consideration in discussions of the distribution of fossil cephalopods, further to the nekroplanktonic distribution of empty shells:

(a) Some species, but not necessarily all those belonging to a genus, may have migrated seasonally. As seen from the above-presented account of the habits of the calamar this factor is also strongly influenced by the habitat of the species in question. Mediterranean calamars do not migrate whereas northern dwellers do. Much of the above work definitely argues against the concept that ammonites and fossil nautiloids were bound to ecologic niches and that fossil shells of these animals may be used as indicators of the nature and position of the niche. Even if it be assumed that all ammonites are autochthonous, the factor of normal seasonal migration must be taken into account.

(b) The habit of squids of at times, during favorable parts of the year, moving in close to the coastal area, but during the winter mainly migrating (a few squids are left behind in deeper water), is of considerable account for paleozoological work.

MILLER & YOUNGQUIST (1949, p. 199) published an account of a nautiloid coquina. Specimens of *Dolorthoceras sociale* (HALL) were found in direct association with a few representatives of *Endoceras*, *Spyroceras*, and *Beloitoceras*, as well as rare examples of small graptolites, bryozoa, brachiopods, gastropods, trilobites, etc. embedded in an argillaceous limestone with thin, intercalated shell beds. In some cases the orthoconic cephalopods are aligned with the long axes roughly parallel, but the arrangement is mostly heterogeneous (cf. p. 125, this paper, the Sâtatorp occurrence in Västergötland). An interesting point is that while most of the shells lie parallel to the bedding planes some are strongly inclined thereto (cf. p. 124, this paper). In many cases up to four individuals may be telescoped into each other. The described specimens are unusual in that the telescoping effect extends far beyond the living chamber and fractures the septa of the chambered portion of the shell.

MILLER & YOUNGQUIST then go on to say (1949, p. 200) that there is considerable evidence to indicate that the early Maqueoketa (the formation in question) waters were extremely shallow. The telescoping as well as fracturing of the cameral walls would seem to reflect the action of waves, and this point of view is further supported by the presence of fragmentary trilobite remains. The occurrence at Sâtatorp, described further on in this paper, is without telescoped specimens, which may be due to the cushioning effect of the calcareous ooze [cf. KUMMEL (1957, p. 459) on Lower Triassic ammonites].

A similar occurrence has been brought forward by BOHLIN (1949, p. 560), who observed some trilobites, brachiopods and other fossils in the Ordovician of Öland (Sweden) that transverse the bedding planes. In connexion herewith, BOHLIN mentioned an occurrence of fossils that cut the bedding of Lower Liassic sediments at Pinhay Bay, Devonshire. Here, limestone beds about 2 dm in thickness contain large, vertically orientated ammonites. BOHLIN suggested that this is due to the gas in the chambered portion of the shell holding it in a vertical position sufficiently long for the postulated rapid sedimentation to securely fasten it into position. He considered rapid sedimentation to have been a necessary prerequisite as the shells, which are quite well preserved, would in the case of slow sedimentation have been etched and attacked by burrowing organisms. As will become apparent from the later chapters of this paper, BOHLIN's interpretation of the reasons behind the vertical positions of the shells is essentially correct. A further point well worth mentioning is that the fossils of the surrounding shales (the ammonites occur in an alternating limestone-shale sequence) lie horizontally.

LANGE (1952) presented some interesting viewpoints on ammonite

distribution in connexion with his monograph of the Psilonotenschichten of Germany. He (1952, p. 66) considered the Lias of the area studied by him to be of shallow-water origin and gave a number of reasons to back his conclusions. The deposit consists of a sequence with sessile pelecypods, gastropods, brachiopods and some ammonites. This is overlain by a bed in which ammonites are so crowded that they touch. The peculiar grouping of the ammonite shells suggested to LANGE (1952, p. 70) that they either sank or drifted together. He drew the final conclusions that the ammonites lived around reefs, that all of them were contemporaneous, and that all suffered death in the same catastrophe. He considered this occurrence in the Fonsjoch area to represent a spawning ground. As far as the observation on the reefs is concerned it may here be mentioned that the reefs, stromatoporoid in particular, of the Gotland Silurian show evidence in support of LANGE's arguments (cf. pl. 1, figs. 5).

FLOWER (1955, p. 858) observed trails with shells of the genus *Orthonyboceras* at their ends and considered that these represent the dying movements of the cephalopod, which after death left the shell at the end of the trail. This theory assumes that the shells of this cephalopod did not float posthumously.

ARHELL (1949, p. 408) considered that the dead shells of ammonites when filled with water would have sunk to the bottom without injury arising from the effects of pressure. Further on in this paper (1949, p. 413) he drew attention to the amazingly comprehensive, world-wide distribution of Jurassic ammonites. The interested reader is referred to a number of informative papers quoted by ARHELL in his bibliography. In a later paper, ARHELL (1952, p. 15) discussed ammonite distribution in the Bathonian. The postulation is made that in part of the Bathonian, up to the Cornbrash, the frontier of primary ammonite habitation shifted south to the Mid-Cotswolds; it is probable that the scattered finds north of that represent wanderers or drifted shells, not autochthones. On the next page comes the interesting observation that ammonites in the Stonesfield shale are mingled with the bones of land animals and plants and may have drifted far from the south.

KOBAYASHI (1954) in a paper primarily concerned with the occurrence of an *Aturia* in the Miocene of Japan, discussed in some detail certain factors in the distribution of *N. pompilius*. He thought that the Japanese Tertiary nautiloids are of nektoplanktonic origin and were transported in much the same way as *Spirula* and *Nautilus* today. The pearly nautilus sometimes appears in Japanese waters and its line of travel follows the warm Kuroshio current from the Philippines. Studies on floating bottles indicate that a nautilus shell can arrive at Misaki from the Luzon Coast after having floated for a period of 2—3 months (cf. HESSLAND, 1945). It is significant that more than half of the Tertiary nautiloids of Japan have been found in embayment sediments. KOBAYASHI's conclusion (1954, p. 51) contained the statement that although it is difficult to arrive at

a precise evaluation of the subject it would seem that most of the Japanese Tertiary nautiloids are probably allochthonous infloats rather than autochthonous inhabitants of the localities where they were found. As a corollary to this conclusion the author under discussion pointed out that inasmuch as *Aturia yokoyamai* is associated commonly with "*Nautilus*" *japonicus* (the citation marks are mine — see KUMMEL, 1956) or *Neocymatoceras tsukushiensis* at some places it may be assumed that the animals lived at no great distance from where the fossil shells were picked up.

In a paper on fossil and Recent argonauts KOBAYASHI (1954, p. 27) thought it quite improbable for argonaut shells cast ashore to have been preserved owing to the fragile and coarsely crystalline shell. In his opinion only those that sank onto a quiet bottom could have been fossilized.

MILLER & FURNISH (1956, p. 327) mentioned that *Aturia lotzi* (BÖHM) was dredged up in 1938 from a depth of around 55 meters between Slangkap lighthouse and Cape Point, South Africa. They studied a collection consisting of 4 phosphatic internal molds associated with gastropods, pelecypods, and mammalian remains. The shells bear serpuloid worm tubes (cf. SCHINDEWOLF, 1934) even on exposed septa, which in MILLER'S & FURNISH'S opinion suggests that the pieces lay loose on the sea floor and became dissociated. Perusal of plate 26, fig. 4 of the paper discloses that the siphuncle of the species is relatively wide and, as is shown in a succeeding section of the present paper, this is a possible site of leakage. If, however, one assumes that all the shells drifted ashore, one is left with no other alternative than to postulate a Miocene or post-Miocene rise in sea level for the part of South Africa under survey of around 50—60 m.

In this connexion, namely, the possibility of the nautiloid shells under discussion having sunk away from the shore reference is here made to a previously unpublished personal communication from D. HALL of the Singapore Fisheries, dated July 12th, 1956. This letter was received in reply to a request of the present author concerning the distribution of shelled cephalopods in the area under the surveillance of the Singapore Fisheries. Mr. HALL reports that nautilus specimens are taken occasionally in the South China Sea. During 300 trawl hauls made there recently by the R. V. *Manibine* no living specimens were brought up and only three battered shells were collected. Thus, although nautilus shells usually drift widely we have here a record of three shells having sunk well out to sea. As is shown in the experimental section of this paper an empty pearly nautilus shell has excellent flotation properties and requires drastic treatment to bring it to sink.

The South African aturias discussed above may well have sunk in a like fashion, although it is noteworthy that four shells were found together, which is hardly to be expected in the case of drifting shells, bearing in mind the comparative rarity of Mesozoic and Tertiary nautiloids in the geological record.

According to STENZEL the genus *Nautilus* is known only from the southwestern Pacific and northwestern Australian waters. Contrary to popular conception its range is large (STENZEL, 1952, p. 18). Regarding other distributional data he noted that the species has been recorded from 315 fathoms, but most have been trapped in shallow water (cf. TALAVARA & FAUSTINO, 1931). Dead shells are known from Misaki (cf. KOBAYASHI, 1954), 1,800 mls from their habitat, also Lao Chao I., New South Wales, New Zealand, the Nicobar Islands and Sunday Islands. Further observations on the distribution of species of *Nautilus* have been made by ADAM (1934, p. 5) and STENZEL (1948, p. 84).

STENZEL (1948, p. 94) has also observed that at Tertiary localities where large numbers of other marine mollusks have been collected, and can be collected, usually only a few nautiloids are to be found. This is a true observation and holds good for most nautiloid shells belonging to post-Paleozoic genera. The reason is, as is shown in the succeeding chapters, that the empty shells float up to high level mark, whereas the shells of other marine mollusks tend on death to remain in situ and thus under water.

HESSLAND (1945, p. 34) in connection with the Recent distribution of *Mya arenaria* made a study of the time taken for the Gulf Stream to transport the larvae of this species to Europe and came to the conclusion that this was far in excess of the length of the pelagic stage of these. He pointed out (HESSLAND, 1945, p. 36) that large objects, such as derelict ships, may take many months to cover part of the distance; he concluded that on the basis of statements in the literature it can be calculated that the Gulf Stream could take more than two years to span the distance in question.

In a discussion of the distribution of certain baculitids PERRIN-SMITH (1901, p. 46) noted that his postulations concerning the geographic range might suggest suppositions for distribution surpassing those of other invertebrates, a thought which he dismissed as ludicrous, for to him the baculitids were not pelagic forms, but shore dwellers, and individual species were regarded by him as being no more widely distributed than the gastropods and pelecypods associated with them. The present investigation has, however, disclosed that *Baculites* and morphologically related forms must be considered as ideal nekroplanktonic types and have therefore a very wide distribution.

USHER (1952, p. 32) expressed himself at some length on the subject of the distribution of ammonite shells. These reflections indicate that this author considers the shells to have sunk immediately after the death of the animal. He thought that as the ammonites of the Nanaimo and Comox basins are found almost exclusively in thin-bedded, fine-grained, argillaceous often calcareous shales and are absent from coarser sandstones and conglomerates the latter type of sediment must have been repugnant to the animals. According to the ideas expressed in the present

paper their occurrence in the first type of sediment is normal, as this is representative of shallow-water sedimentation. USHER also expressed the opinion that the arenaceous sediments were deposited in water too shallow or too brackish for the well-being of the ammonites. He did not find ammonites in shaly beds showing evidence of shallow-water environmental conditions and considered the absence of pelecypods and gastropods in the ammonitiferous rocks to indicate deep-sea conditions. As noted in a foregoing paragraph on STENZEL's investigations the ammonite shells probably represent the high-water line. As is now generally known coarse sediment is no criterion of deposition in shoal water, nor is fine sediment always characteristic of deep-sea deposits. USHER (1952, p. 33) noted the possibility that the empty shells of his proposed bathyal ammonite types may have drifted into other waters but believed that the concentrations of shells observed by him and the lack of such damage as would be caused by abrasion indicate drifting to have been an unimportant distributional factor.

IMLAY (1955, p. 11) recorded the presence of ammonites and benthonic pelecypods in calcareous shales and noted this association to be the most common one in the area investigated. He also wrote that ammonites are rare in thick-bedded and ripple-marked sandstones, especially those containing *Ostrea* and *Mytilus* and drew the conclusion that ammonites must have favored those parts of the sea outside of the littoral zone with an abundance of bottom-dwelling mollusks. These ideas reveal a lack of belief in the spreading of ammonite shells by flotation; IMLAY considered that he had support for the bathyal and perhaps temperature control of ammonite distribution. Further on in the same paper (1955, p. 57, pt. II) he suggested deposition must have occurred along a steep slope fronting a major ocean, as evinced partly by the presence of the thin-shelled *Phylloceras*.

BRUUN (1955, p. 61) in discussing observations made on *Spirula* during the *Galathea* expedition wrote that the shells of this cephalopod are often the most abundant species amongst the strandline associations, "and if the sediment were fossilized, the *Spirula* shells would form the most characteristic fossil. These accumulations represent mixtures of oceanic and littoral species, which will constitute a puzzle to the future geologist".

HAAS (1949, p. 7) reported on acanthoceratid ammonites that occurred together with fossil wood, here and there charred. In evaluating the import of this observation he (1949, p. 32) wrote that empty shells of these relatively compressed forms may have been able to drift, but he could not think the distance was particularly great. Actually, this occurrence of charred wood and ammonite shells in the one deposit seems to the present author to be indicative of the shells having been cast up at the high-water mark together with pieces of drift wood in much the same manner as flotsam and jetsam is today cast up along beaches. In the Lower Liassic deposits of northwestern Skåne, Sweden, for example,

the present writer has frequently observed wood fragments in calcareous and arenaceous sediments that contain numerous pelecypods and occasional gastropods and ammonites (particularly the Katslösa area).

An analogy with the nekroplanktonic distribution of cephalopods may be found amongst another group of excellent zonal fossils, namely, the graptolites. BULMAN (1955, p. 17) considers that graptolitic shales represent conditions generally to be regarded as unfavorable to bottom life. According to him the graptolites owe their distinctively wide geographic distribution to the superficial drifting mode of life. Thus the dispersal of true graptolites was mainly dependent on ocean currents and drifting so that their paleogeographic distribution may be practically world wide. Nearly all families, most genera, and many species are cosmopolitan, and they are very useful in the working out of Paleozoic marine connexions. Although little work has been done on the subject using ammonites it is hoped that some of the points of view put forward in the present paper will prove helpful.

Recent analogies are to be found amongst other groups. EKMAN (1953, p. 20) pointed out that the ability of fish to make use of ocean currents is an important factor in their distribution. Porcupine fish (Diodontidae) are able to inflate themselves and drift passively on the surface of the sea.

For living animals EKMAN (1953, p. 21) wrote that under present geographical conditions active migration is only possible for those species able to endure the wide abyssal zone and this is out of the question for, for example, tropical shelf animals. Some of these species can, however, migrate passively as did the graptolites. Several have planktonic stages, but these are too short to account for wide dispersal. The majority were spread by drifting attached to seaweed or other floating material.

YOUNG (1957, p. 2) in discussing the problem of establishing lineages for Albian ammonoidea that are acceptable over the whole world assumed as one possible explanation that "generic and subgeneric" provinces must have been more sharply delineated than heretofore supposed. The observations accounted for in the present paper tend to discount such a possibility.

Finally, it is of interest to note that in 1957 a few shells of "*Argonauta tuberculosis*" floated ashore on east Otago beaches, New Zealand (personal communication from Dr. E. BATHAM, dated 21. 10. 57).

### *Summarising remarks*

To summarize this review on the distribution of fossil cephalopods the following may be said. As far as the writer has been able to ascertain no concise study has ever been made on the subject, although a good deal of conjecture occurs in the literature. Much of this is of slight use as many conclusions are based on outmoded views of sedimentology.

The migratory habits of living cephalopods provide further food for thought in the evaluation of stratigraphical and geological occurrences. Evidence for seasonal and monthly movements of some dibranchiates is now available and there seems every reason to believe, on the basis of such observations as have been made, that the few living tetrabranchiates behave in the same fashion.

One fact is clear, namely, that cephalopod occurrences, as opposed to those of other mollusks, give only rarely an idea of the original habitat of the animal.

## INTRODUCTORY REMARKS ON IMPORTANT FACTORS IN THE BUOYANCY OF CEPHALOPOD SHELLS

The following factors are of importance in the determination of the buoyancy of chambered cephalopod shells.

- a. The shape of the shell; i. e. whether the shell is straight, slightly bent, loosely coiled or tightly coiled, compressed or depressed, highly inflated, etc. Connected herewith are the influences on these shells on pressure, temperature, salinity and the thickness of the shell material.
- b. Size of the body chamber; this is probably the most important single factor.
- c. Number and thickness of the septa in the shell.
- d. Width of the siphuncular tube.

These factors have been experimentally determined or discussed from observations available in the literature, in the succeeding sections.

TEICHERT (1933) attempted a theoretical treatment of the subject for pure orthoceroids and TRUEMAN (1941) for ammonites. In the case of an ideal cephalopod of conic shape and without surface ornament and whose septa increase regularly in thickness it is possible to deduce, for example, the volume of the shell substance in relation to the entire volume of the shell. More complicated cases such as bent, ornamented nautiloids are less easy to work out and require many approximations; the most complicated cases represented by coiled cephalopods, particularly ammonites with constantly varying, irregular whorl sections and septal faces, make a mathematical approach to the problem a virtual impossibility. TRUEMAN (1941, p. 343) finally gave up the idea of finding a workable mathematical formula for calculating the volume of ammonite shells.

### THE SPECIFIC GRAVITY OF CEPHALOPOD SHELL MATERIAL

TEICHERT'S (1933) calculations show that the chambered part of an ideal orthoceroid cone will just sink when the volume of the calcareous material (specific gravity taken as 2.60) is a little less than 40 % of the

entire volume of the shell, i. e., including shell, septa, siphonal deposits and cameral deposits. Although the shells of nautiloids are now known definitely to be composed of aragonite (SWITZER & BOUCOT, 1955; REYMENT, 1956; REYMENT & ECKSTRAND, 1957) the specific gravity in the pure state of which is 2.93—2.95, specific gravity determinations on the shell material of *N. pompilius* and *N. umbilicatus* by A. HENRIQUES, K. FREDRIKSSON and the author have shown both to have a value of between 2.62 and 2.63, which can be put down to the porosity of the shell and the presence of light organic matter in it. Thus TEICHERT's approximate figure of 2.60 is actually very near the truth while TRUEMAN's figure of 2.95 (1941, p. 351) is too high. A specific gravity determination carried out on the aragonite shell of the Neocomian ammonite *Speetoniaceras versicolor* (TRAUTSCHOLD) by Fil. lic. K. FREDRIKSSON gave a value of 2.82—2.83. This higher figure is probably ascribable to loss of some of the horny organic matter. The septa of Recent nautilus shells were found to contain less light organic material than the outer shell so it is possible that they, as well as other structures inside the shell, had a specific weight approaching 2.93—2.95.

In the case of a hypothetic straight shell composed of pure, solid aragonite the maximum volume of calcareous material permissible is 35 % of the total shell volume. TEICHERT's calculations were made with the mode of existence of the living animal in mind. For dead orthocones the siphuncle, often quite wide, became filled with water, which further decreased the buoyancy of the shell. In most cases TEICHERT (1933, p. 189) calculated the volume taken up by the siphuncular tube to be approximately 11 % of the entire volume of the shell.

#### SHELL FORM AND THE BODY CHAMBER

A still more important factor in the posthumous buoyancy of chambered shells is the size of the body chamber. Thus an orthoceroid shell that was just buoyant in life would not have floated after the decay of the soft parts, owing to the increased deadweight caused by the empty living chamber [see TEICHERT (1933, p. 192) for a discussion of the importance of the body chamber in orthoceroid nautiloids]. The coiled cones of most ammonites and many nautiloids set a more involved problem. The whole chambered cone of the orthoceroid nautiloid possesses a buoyancy effect as it is entirely exposed to the water. For coiled cephalopod shells it is only the last whorl and the shape of the shell that decides the dimension of the buoyancy effect while the parts of the coiled cone contained within this form, together with all septa, the siphuncle and, in actual fact the body chamber, provide deadweight acting against this; at the same time they also diminish the effective air volume. Consequently, an involute shell with the same number of whorls as an evolute shell will have a lesser buoyancy effect than the latter, as far as the chambered part of

the shells is concerned. As the siphuncles of coiled cephalopods, particularly those of ammonites, are of small diameter the loss of buoyancy occasioned by these becoming water-filled is slight.

As the various shells of cephalopods are almost in equilibrium with water, either slightly lighter or slightly heavier, this explains the absence of cameral and siphuncular deposits in coiled shells. That is, the weight of extra deposits needed to just hold a straight nautiloid buoyant is represented in coiled nautiloids by the weight provided by the enveloped shell parts.

Generally, highly evolute shells contain a greater weight of shelly matter for the same volume but not all of this functions as deadweight as the exposed parts of the whorls contribute to the overall buoyancy of the shell. This may explain why evolute shells tend to have longer body chambers than involute.

The determination of the buoyancy of a coiled cephalopod by measurement and calculation is seriously hindered by the constant change in whorl section, variability in ornamental strength, and the fact that the "cone" varies in shape from species to species and specimen to specimen and also the difficulty in working out the total mass of the shell.

## EXPERIMENTAL OBSERVATIONS ON SOME SHELL TYPES

### GENERAL

For the purpose of ascertaining the behaviour of various shell types it was decided to approach the problem by making models of certain common types of cephalopod shells. It will be readily appreciated that all the experiments described in this chapter are of a simple nature and represent idealized conditions. It is hoped, however, that they will indicate possible lines of research.

Considerable time and trouble were expended in attempting to come over a suitable material which would not only permit preparation of models of the shells concerned, but would also result in a substance with much the same physical properties as the cephalopod shell. It was also considered desirable that the material should have roughly the same apparent specific gravity as aragonite in cephalopod shells, namely, 2.63. It was finally decided to use Vinagel 118, a product manufactured by VINATEX LTD., Surrey, England. This compound possesses the first of the two properties listed above, but unfortunately has a relative density of less than a half that required, namely, 1.23 (after hardening). All attempts to obtain a suitable plastic with a higher specific gravity were without success.

The problem was finally overcome by loading the semi-hardened plastic with a calculated quantity of very fine lead shot until the required weight-

volume relationship was reached. The models could then be made with the desired wall thickness corresponding to that of the shell under investigation, weighed after partial hardening, and then the calculated amount of lead material added. It should also be possible to mix red lead with the plastic and achieve the same effect. Vinagel 118 is a white material which can be readily modelled with the hands and which becomes more plastic after a short period of working. It can be molded into shapes and then moved without destroying form or detail. The mass hardens somewhat if left to stand after working. In order to gelatinize the model and obtain a fast form the object is warmed for 20 minutes in an oven at a temperature of 150—170° C. The final hard form is taken on after the model has cooled to room temperature. For some processes in the preparation of the models it was found necessary to employ an adhesive agent. Experiment showed that the most satisfactory material is a product of VINYL PRODUCTS LTD., namely, the polyvinyl acetate emulsions Vinamul N. 9800 and N. 9820. To increase the water resistivity of these materials, if an experiment involved lengthy exposure to water, it was found advantageous to add 0.5—1.0 % of a 30 % glyoxal solution to the emulsions.

In order to avoid the technical difficulty of making complete models, half shells were made; it was thus also possible to observe directly the water entering a shell. It was found that a nautilus shell cut exactly along the median line and covered on the opened side with a layer of celluloid floated with the same proportion of the shell above water as the whole shell. Therefore, in almost all cases this expedient was employed. It should, however, be mentioned that the half shell floated with a slight list to the unsectioned side.

All flotation experiments involving small models were carried out in a large 10 liter beaker in brine solution with a specific gravity of 1.026. For experiments involving the large *Rhynchothoceras* models an ordinary household bathtub was used.

There is, of course, no guarantee that the salt content of the oceans has always been the same as that today and it is well known that the salinity of modern oceans varies greatly.

## STRAIGHT AND SLIGHTLY CURVED SHELLS

### Endoceroid shell

Models were first made of the species *Endoceras duplex* (WAHL.) from the "Ortocerkalk" (Lower Ordovician) of Kinnekulle, Västergötland (G. I. 5869). This is a form with a relatively wide siphuncle of a type typical for endoceroids; this is, however, not excessively wide. As already indicated in the introductory remarks the weight of the shell was calculated assuming an apparent relative density for the shelly aragonite of

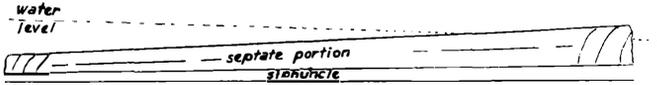


Fig. 1. Sketch illustrating the floating position adopted by a model of *Endoceras* without body chamber.

2.63, although there is no sure way of knowing whether or not this figure is too low. Measurements on the original specimen showed the outer wall of the shell to be 1.8 mm in thickness, the septa to be between 0.3 mm and 0.5 mm in thickness, and the wall of the siphuncle to be 0.5 mm in thickness. [These measurements are certainly too small; as indicated further on (p. 147) thickness determinations carried out on calcitically preserved shells suffer from inaccuracies occasioned by the loss of shell material through solution.]

The author wishes to point out that the observations described in the following are not to be taken as referring specifically to *E. duplex*. They refer primarily to the type of cephalopod shell represented by this species, namely, that possessing a wide siphuncle.

The first experiments were made on the shell without its body chamber. The shell was found to float with the water-filled siphuncle on the underside and with the last few air chambers just clear of the water and the smallest air chambers under water (see fig. 1). Similar observations were made by the writer on an occurrence brought to his attention by Prof. I. HESSLAND in the limestone quarry at Sätatorp, Västergötland (see p. 125).

The interiors of the air chambers were loaded with cameral deposits as the next stage in the experiment so as to represent an extreme case of this condition. It was found that the loss of buoyancy occasioned by water entering the open siphuncle was sufficient to cause the shell to sink. The siphuncle when made watertight was able to keep the shell just buoyant. A shell with a narrower siphuncle, and thus a larger volume of chambered shell, with the same percentage of cameral deposits would consequently not float.

The effect of adding a body chamber to the septate portion of the shell was then studied. The length of the body chamber was successively increased until the shell just sank. It was found that for a condition of equilibrium to be achieved the body chamber had to be 49 mm long to a length of the septate shell of 185 mm. That is, for this endoceroid cone the body chamber cannot exceed 26 % of the length of the chambered portion of the shell without causing the empty shell to sink. In fig. 2 the position adopted by the floating shell with a body chamber of almost maximum length is illustrated schematically. The shell then floated at an angle of about 45°; a slight increase in this length caused it to sink, which it did obliquely. Up to a length of the body chamber of 15 mm the shell still floated with the oral end higher than the adoral end, as in the case of the shell without body chamber.

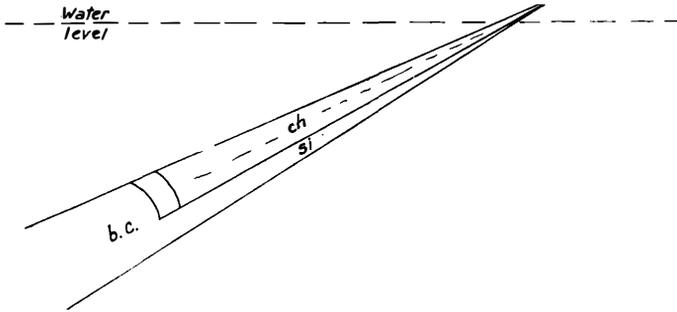


Fig. 2. Floating position adopted by an endoceroid shell with a body chamber of almost maximum length. The figure is not drawn to scale; ch = chambered portion of shell, si = siphuncle, b. c. = body chamber.

### Orthoceroid shell

The second type of straight nautiloid shell chosen was that represented by the shell of *Rhynchorthoceras oelandicum* REMELÉ from the Ordovician of Öland, a form with a considerably narrower siphuncle than that of *Endoceras duplex* (cf. REMELÉ, 1882, pl. 5, fig. 5). Whether or not *R. oelandicum* is synonymous with other species of the genus cannot be gone into here.

The siphuncle of the form in question is 2.5 mm wide where the diameter of the entire shell is 20.5 mm (REMELÉ, 1882, p. 134). It is slightly excentric. The following measurements were made on the shell of the specimen used as a base for the plastic model (N. B. the same reservations as to the shell thickness measurements of *Endoceras duplex* apply here also).

Thickness of shell wall = 1.2 mm, thickness of septa = 0.6 mm (aver.), thickness of siphuncular wall = 0.5 - 0.6 mm. One of the models used for experiments is depicted in pl. I, fig. 2. The shell without body chamber floated high out of the water and with the pointed end under water.

Fig. 3 illustrates diagrammatically the effect produced on this type of shell by increasing the size of the body chamber.

In these experiments it was found that water entered the narrow siphuncle with difficulty; when the siphuncle became full of water this had very little effect on the buoyancy of the shell, as opposed to the foregoing endoceroid type. In order for the shell to just sink, the body chamber had to have a length of slightly greater than 50 % of the total length of the shell and thus a length in excess of that of the chambered part of the shell. The approximate dimensions are shown in fig. 3 c. The length of the chambered section was 163 mm and the maximum length of body chamber 166 mm, with a maximum terminal width of 55 mm. In this condition the shell floated vertically with the body chamber directed downwards. Gradual reduction in the length of the body chamber eventually resulted in the shell passing over from a vertical position to

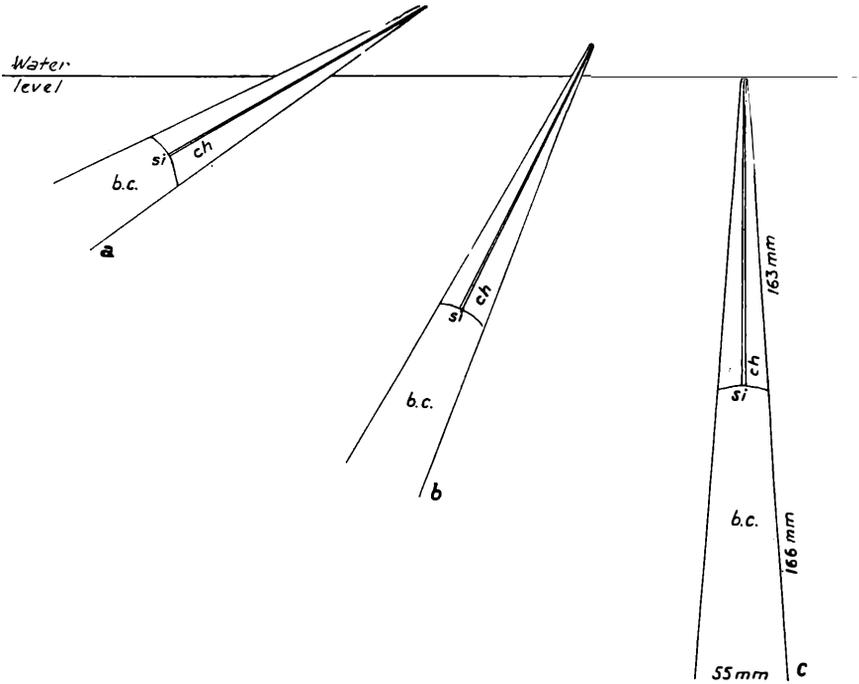


Fig. 3. The figure shows the effect of increased body chamber length on the floating position of the orthoceroid nautiloid; b. c. = body chamber, ch = air chambers, si = siphuncle.

a slightly inclined one and further reduction brought about the changes shown in figs. 3, a—b.

Further increase in the length of the body chamber beyond the equilibrium length caused the shell to sink but made no change in the vertical resting position taken up on the bottom of the containing vessel. It would require an entirely unreal increase in the length of the body chamber for the shell to topple over and lie horizontally on the bottom.

In the experiment here described the wall of the body chamber was not made thicker than that of the chambered section, apart from allowing for normal increase in thickness owing to growth. In nature, the body chamber tends to have thicker walls, coarser ornament, often lip-shaped processes at the end of the shell together with some sort of thickening of the edge. All of these factors would lessen the equilibrium ratio of the body chamber to the chambered portion.

It has been the writer's observation that by far the majority of finds of straight nautiloid shells (also other cephalopod shells) consist either of chambered shell without body chamber or isolated body chambers (with sometimes a few attached air chambers). This is in most cases to be ascribed to the floating position of these shells, for even if the body chamber were much smaller than in the equilibrium state outlined above, it would still hang lower than the chambered section. The body chamber

would have been exposed to damage as the drifting shell trailed along rocky bottoms and been readily broken off, entirely or partially. Once free of this encumbrance the chambered portion would have floated, boatlike, ashore leaving the other part to sink at the foot of the reef or cliff where damage occurred. In the case of a long, cliffy coast with no available opportunity for the lightened shells to strand, the attrition processes would continue until a sufficient number of air chambers became damaged to cause the shell to sink. This could also occur on the seaward side of a string of reefs. The author has collected stromatoporoids in the Silurian of Gotland (Hemse formation) which have grown around the broken shells of cephalopods damaged on the reefs in the manner just outlined (see pl. I, fig. 5). Stromatoporoids required an object of some sort around which to grow and which formed a nucleus or foundation for the larval organism; the broken shells of nautiloids around the reefs were evidently suitable and readily accessible. The specimen figured has encompassed the body chamber of a curved nautiloid.

A cross section through Paleozoic cephalopod literature indicates how certain sides of the above discussion occur in nature. But first a few remarks on the obvious difficulty of reconciling the vertical or inclined position of floating nekroplanktonic orthoceroids with the horizontal position of such shells as usually found in sediments. If we consider that the majority of cephalopod shells found in Paleozoic rocks were stranded along the high-water line, then no difficulty in interpretation is experienced. Drifting shells would eventually have been cast up on the shore and, in favorable cases, preserved. Not all deposits have this origin, however, and one would expect to find at least a few shells embedded in inclined positions, transversing the bedding planes. Reference has already been made in this paper to COPE's (p. 102) observations on an occurrence in Northern Ireland (Devil's Rock area) where vertically bedded orthoceroids have the tips pointing downwards. The present writer has observed a similar occurrence at Leskusänget in the Siljan area, Dalarna, Sweden (fig. 4), in an impure limestone containing numerous well preserved orthoceroids which lie for the most part parallel to the bedding planes. A few specimens were found to be at an angle thereto which may have its explanation in the possibility that the sediment represents a nearshore, shallow-water sediment with most of the shells lying flat along the strand line. Some, however, fastened slightly on the seaward side of this line. The inclined shells are orientated with the apex lower than the oral end.

Geometrically, straight cephalopod shells are cones and behave hydrostatically as such. It was mentioned in the foregoing section that endoceroid shells will float with the tip lower than the oral end if the body chamber is small or missing (no "endocone" structures in the siphuncle). An orthoceroid shell with its narrower siphuncle behaves even more like a solid right circular cone than an endoceroid shell, the broad siphuncular tube of which complicates its floating position.

## Section



Fig. 4. Diagrammatic representation illustrating the mode of occurrence of cephalopod shells in Lower Ordovician limestone at Leskusänget, Siljan district, Dalarna, Sweden.

The angle of depression of the apex of a floating cone depends on the size of the apical angle of the cone. The larger the apical angle of a straight cephalopod shell, the shorter becomes its length and the more important the buoyancy effect of the volume of the orally located air chambers. A short body chamber has little appreciable effect on the floating position of a shell of this type. The greater the length of the body chamber, the nearer to the horizontal position will the shell float. A length in excess of this equilibrium dimension will cause the shell to float with the tip higher than its oral end. The above is of particular value in connection with short forms with rapidly diverging sides.

TEICHERT (1933, p. 196) noted that species of the genus *Westonoceras* have peculiar shells and they could not possibly have floated in a horizontally stable position and he concluded that the apex must have been directed downwards. As already noted in the introductory section to the present paper, KREJCI-GRAF (1932, p. 295) reported the conical shells of certain *Cerithium* forms float with the apex pointing downwards. SCHMIDT (1930, p. 196) recorded straight nautiloid shells found with the apices pointing downwards, but could find no satisfactory explanation for these occurrences.

Many so-called straight nautiloids are actually slightly curved, bent or arched, if not along the entire shell, then at least in the neighbourhood of the apex (cf. MUTVEI, 1957, p. 228).

TEICHERT (1933, p. 194) suggested that in living cephalopod animals the larger the body chamber in relationship to the rest of the shell the higher the maximum buoyancy values must have been; the reverse holds true for the empty shell.

TEICHERT (1933, p. 195) also discussed another fairly common type of shell-weighting illustrated by the flat species of the genus *Gonioceras* in which the shell has numerous, closely spaced septa. The weighting effect is increased by the development of septal undulations.

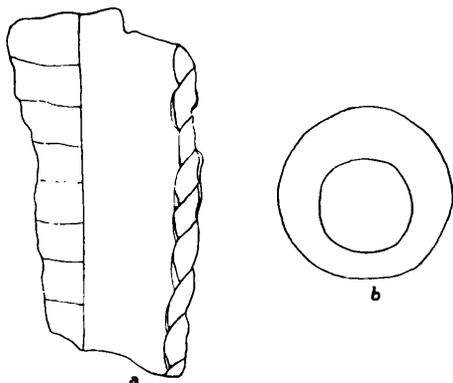


Fig. 5. Diagrammatic representation of *Endoceras megastomum* EICHWALD showing (a) the siphuncle in longitudinal section and its relationship to the camerae and (b) the siphuncle in cross section (after TEICHERT, 1930).

### Discussion of field evidence

TEICHERT (1930, p. 273) made an interesting observation on the Ordovician species *Endoceras megastomum* EICHWALD. In this species the siphuncle occupies somewhat more than one half of the shell diameter. The siphonal necks stretch from one septum to the next, which is typical of true *Endoceras*, according to HYATT. In the Lyckholm sequence of Estonia this cephalopod and *E. regulare* EICHWALD are the largest nautiloids. In the specimen figured by TEICHERT half the siphuncle is filled with calcite crystals and the rest with sediment. In TEICHERT's opinion, after the death of the animal the shell took up a balanced position with the siphuncle on the underside. As pointed out by TEICHERT, this sort of orientation has already been commented on by SAEMANN, BARRANDE, DEWITZ, ANDRÉE, WEPFER, and others who have also noted that the side of the shell opposite to the side containing the siphuncular tube is often missing. This was found to be so in some cases at Sâtatorp (see below) but is not common there. TEICHERT considered that owing to rapid burial the siphuncle was not completely filled so that a cavity remained in which calcium carbonate could later crystallize. The present investigation supports this explanation in all essential details. The empty shell sank, owing to the wide siphuncle, and with this structure downwards. More or less rapid sedimentation covered the shell and only succeeded in partially filling the siphuncular tube, after the loss of its soft parts. Later percolation of calcareous solutions filled the space with calcite crystals. Fig. 5 illustrates schematically these features (after TEICHERT, 1930).

A shallow limestone quarry in the "Platyuruskalk", Lower Ordovician, Sâtatorp, Kinnekulle, Västergötland, Sweden, gave ample opportunity for studying the type of occurrence just discussed. Here, numerous straight cephalopod shells are excellently exposed in the western face of

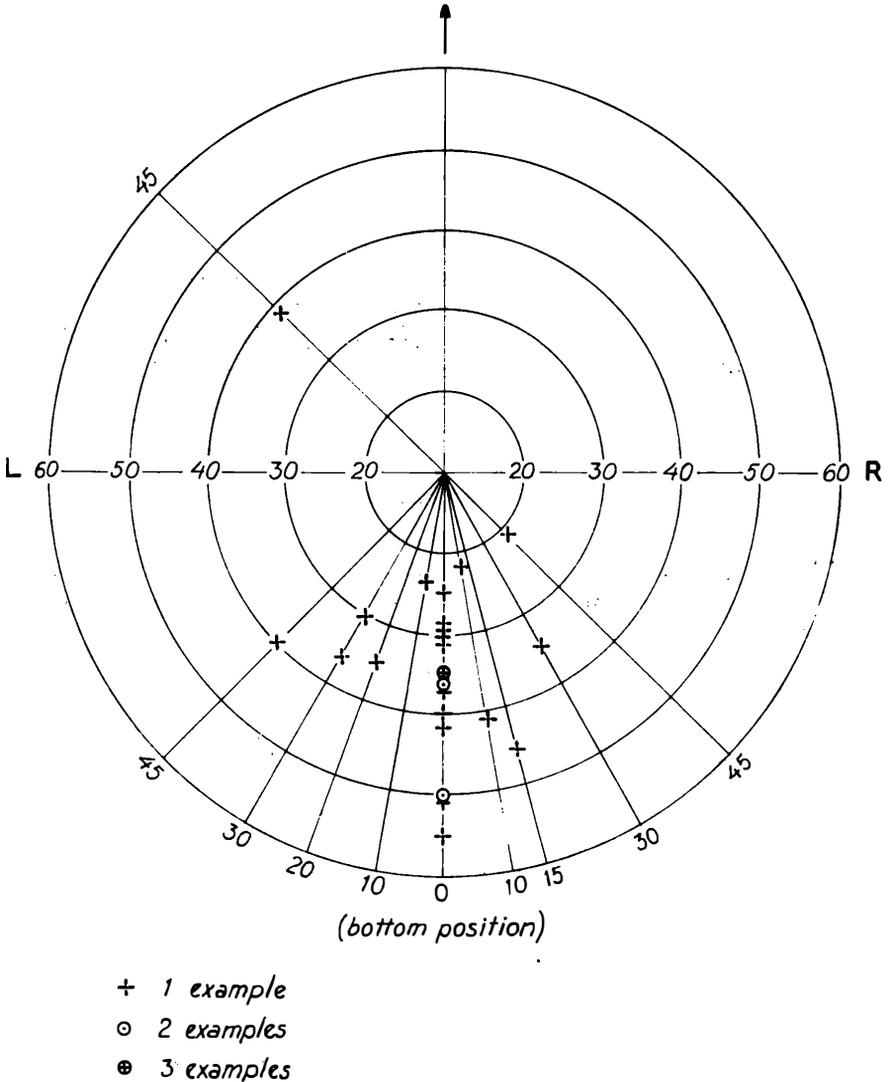


Fig. 6. Diagram illustrating the orientation of endoceroid shells exposed in the western wall of the quarry at Sätatorp, Västergötland. The numbers along the circumference of the largest circle indicate the angle of deviation of the siphuncle from the bottom position. The inner circles represent the percentage of the total shell diameter occupied by the siphuncular tube. L = left; R = right.

the quarry. It was found that although some nautiloid shells were orientated with the siphuncle on the upper side most of the shells had been buried with the siphuncle beneath. None of the nautiloids encountered had such a wide siphuncle as *Endoceras megastomum* and it would seem, judging from the field evidence, that the preferred orientation of the shells indicates them to have been stranded in calcareous ooze. Those forms with

the siphuncle directed upwards were probably turned over by intermittent waves breaking over the mud. Some shells lie in intermediate positions but these are inferior in number to shells orientated with the siphuncle on the netherside. The adjacent diagram presents measurements made on shells in a section of the quarry wall:

Of the 28 measurements made it will be seen from fig. 6 that only one is of a shell whose siphuncle is orientated in an upper position. More than half, that is 17 specimens, have the siphuncle directly beneath, while the remainder have the siphuncle orientated at small angles from this position. The shells occur at various depths throughout the limestone and it would seem that conditions were uniform during the deposition of the sediment.

Two main approximate orientations of the shells were observed, chiefly NE—SW (22 specimens), but also NNE—SSW (6 specimens). It was also found that in the majority of cases the shells are orientated with the adoral end directed northwards. Many shells are, however, oppositely situated. Nevertheless, it seems clear that an opportunity here presents itself for working out the prevalent directions of the main currents during the burial of these nautiloid shells.

The nautiloid described by TEICHERT (1930) most probably sank post-humously whereas in the case of the specimens observed by the present writer in Västergötland most of the evidence suggests that the shells stranded on a coastline fringed with calcareous ooze. It is not particularly easy to find a parallel amongst present-day sediments to the type of environment envisaged here, but a few examples are quoted in a later section of this paper (p. 166).

It is of interest to record here the find of a curved nautiloid in the Sätatorp limestone preserved in its floating position (pl. II, fig. 1). The shell appears to have been trapped in semifluid ooze in which it remained buoyed up until the sediment solidified. The apex points upwards.

### *Concluding discussion*

TEICHERT (1933, p. 166) presented an exhaustive account of camera deposits. Methods are given of distinguishing between primary and secondary cameral deposits and three types of these are separated (1933, p. 169). As shown in fig. 28 on p. 170 of TEICHERT's paper for *Actinoceras tenuifilum* (HALL) the primary deposits are marked by regularity and never occur along the siphonal wall, whereas secondary deposits do cover the siphuncular sheath. See also TEICHERT (1933, p. 182, text-fig. 33) for a reconstruction of the nature of intercameral deposits in an orthoceroid nautiloid ("*Orthoceras*" sp. nov.). Cameral deposits were often formed on only one side of the shell, which would seem to imply that one would expect to find this side underneath in sediment (TEICHERT, 1933, p. 183).

In this connexion it is of interest to record that MOJSISOVICS (1873) observed cameral deposits in Triassic nautiloids. A similar note has recently been made for Permian nautiloids by KEMP (1957, p. 591).

TRUEMAN (1941, p. 375) considered that orthoceroid straight Paleozoic nautiloids lived with the aperture more or less tipped downwards. In this connexion he criticized DUNBAR and BERRY for following RUEDEMANN who assumed, on the basis of certain color markings on some straight nautiloids, that the animals were benthonic and that the shells extended roughly horizontally. The preceding discussion in the present paper suggests, however, that both interpretations may be correct and that some straight nautiloids floated vertically, others in a horizontal position.

FLOWER (1955) in a paper on the subject of "saltation in nautiloid coiling" made some interesting notes. After discussing the floating position probably adopted by the shells (1955, p. 246) he remarked that many Ordovician endoceroids occur with body chambers of a length of around 30—40 cm while the chambered portion is in these forms about 3—4 m long (body chamber 10 % of chambered length). He considers that the cameral deposits held the shell in a horizontal position but a few shells with obviously excessive and heavy deposits were dominantly bottom dwellers. The observations of the present author favor the view that if one restricts oneself to those cases of siphuncular and intercameral deposits which without doubt may be taken to be of primary origin the shells are in all cases almost exactly balanced, being either slightly heavier or slightly lighter than water, assuming the siphuncle and body chamber free from water. In this case the benthonic mode of existence envisaged by FLOWER must be considered unlikely.

FLOWER (1955, p. 247) also noted that both the Plectronoceratidae and the Ellesmeroceratidae possess very closely spaced septa; he wrote "that if one considers the small space of the camerae it is doubtful whether the buoyant effect of the gas in these extremely shallow receptacles would have been sufficient to more than reduce the total weight of the shell to a slight degree". Buoyancy was attained by increasing the depth of the camerae, which both enlarged the gas space and decreased the weight of shell. These opinions accord with those of the present writer and it may be safely assumed that the majority of the ellesmeroceratids and plectronoceratids sank after the death of the animal. This can only be verified by direct experiment, however, and close field observations. Owing to the lack of the necessary material such investigations could not be undertaken in the present work.

Fig. 7 represents schematically the shell of a *Piloceras*, a genus with small air chambers, a large siphuncle, and a large body chamber. It is considered by the writer to have sunk posthumously.

SCHMIDT (1930, p. 195) considered "*Orthoceras*" to have been a nektonic type and to have swum with the shell held in a horizontal position. He also quite logically remarked that "eine Normallage des *Orthoceras*-

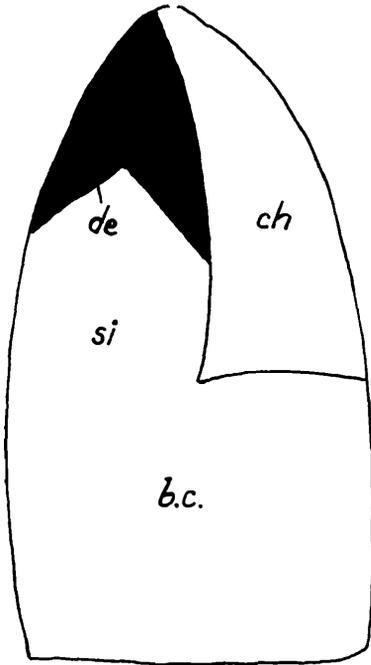


Fig. 7. Diagrammatic representation of *Piloceras*; b.c. = body chamber, ch = chambered part of shell, si = siphuncle, de = siphuncular deposits (after FLOWER, 1955).

Gehäuses mit der Spitze nach oben ist undenkbar, weil dann jeder Bewegungsantrieb an der Mündung zum Pendeln geführt hätte”.

#### HETEROMORPHIC SHELLS

For convenience this group is here considered to embrace straight or slightly curved Paleozoic nautiloids with coiled early chambers (“lituitoid” shells), turrilitoid shells, scaphitoid shells, baculitoid shells with a long, straight shaft and a few coiled initial chambers.

The body chamber of *Lituites lituus* MONTFORT is rare (NOETLING, 1882, p. 169). The examples known indicate, that it is relatively short compared to the septate part of the shell. This relationship is such as to suggest that the empty shell floated at a fairly acute angle to the horizontal.

Fig. 8 shows a longitudinal thin section through *Baculites teichertii* REYMENT consisting of a portion of the body chamber and 9 chambers. Owing to the state of preservation the siphuncle is lacking. No trace of primary cameral deposits could be found but in a few chambers secondary cameral deposits were recognized. A longitudinal section through a smaller fragment failed to disclose any cameral deposits. The pieces of siphuncular sheath found loose inside three of the chambers show that it had thin walls. The fragment of the shell preserved is fairly thick but

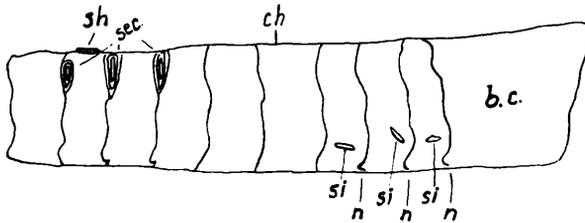


Fig. 8. Longitudinal section through the shell of *Baculites teichertii* REYMENT (G.I. C 1028). Observe the crowding of the last three air chambers; ch = air chambers, n = septal necks, b.c. = body chamber, sh = fragment of outer shell, sec = secondary cameral deposits, si = fragment of siphuncle. XI.

the septa are thin-walled. Other species of *Baculites* studied possess numerous fragments of the initial coiled portion of the shell. On the basis of the experiments on the orthoceroid type of shell it is here considered that baculitoid shells functioned as nekroplankton. The small body chamber of some species and the large, light air chambers suggest that the empty shell may have floated in an almost horizontal position.

The fragments of broken siphuncle in the last three chambers of the specimen depicted in fig. 7 suggest that wave action may have damaged the siphuncular tube, which would have permitted water to enter the chambers and assist in decreasing the buoyancy of the shell. The possibility of siphuncular damage is of lesser importance among straight Paleozoic nautiloids, which have thick siphuncular sheaths, which are often thicker than the septa. Ammonites have thin, narrow siphuncles that must have been quite susceptible to water damage. In a coming paper by the author (REYMENT, 1958, pl. 1, figs. 1, 2) specimens of *Baculites ovatus* SAY<sup>?</sup> are figured in the same rock fragment as fragments of *Inoceramus* [see also REESIDE (1927, pl. 7) for a similar figure] as well as coiled initial chambers. The shells of *Baculites* probably drifted ashore where they were broken up by wave action, the delicate coiled parts being easily snapped off.

TRUEMAN's investigation of some uncoiled ammonites (1941, p. 362) showed that for *Baculites ovatus* SAY there was a relationship of 1 : 0.7 (a rather high figure) for chambered part to body chamber, for *Scaphites nodosus* OWEN a relationship of 1 : 2, for *Crioceras duwali* LÉVEILLÉ 1 : 1.6 and for *C. mulsanti* (ASTIER) 1 : 2.5.

SMITH (1901, p. 40) in his paper on the coiled portions of *Baculites* wrote that the "young flocked together in quiet nooks". He was impressed by the mass occurrence of juvenile baculitid shells. WOLANSKY (1932, p. 7) observed that in the Pomeranian Cretaceous the baculitid shells are always found in a broken condition which she explained as being a result of sedimentation in turbulent water. SCHOELLER (1949, p. 234) thought that straight ammonites such as *Baculites*, *Rhabdoceras* and

*Bactrites* were probably passive pelagic forms. The nekroplanktonic behaviour of baculitoid and lituitoid shells may well have been similar.

### Other shells with spiralled first whorls

These types of shells are related to the foregoing but differ in having a more prolonged spiral portion and the body chamber is seldom merely straight, but shows considerable variation in shape. This group embraces, for example, scaphitoid shells and hamitoid shells.

COBBAN (1951, p. 1) in his monograph of North American scaphitids noted that as these forms occur in different lithological units they are valuable for stratigraphic correlation. Their living chambers are partly unrolled (1951, p. 2) and make up from a half to three quarters of a whorl. In adult *Scaphites* the body chamber is almost wholly freed from the septate coil.

In fig. 9 schematic figures of some types of heteromorphic cephalopod shells are shown. Heteromorphic shells have frequently very large body chambers, apart from the baculitoid type of shell. Although no laboratory experiments were carried out on uncoiled shells it seems likely that many species of the types represented in text-fig. 9, figs. 5, 6, 7, probably sank posthumously. Those scaphitoid shells with the body chamber occupying three fourths of a whorl almost certainly sank when empty, depending mainly on the thickness of the shell, the dimensions of the body chamber, and on the strength of the ornament.

As far as can be ascertained, turrilitoid shells may have occupied an intermediate position. Field observations by the writer in Nigeria suggest rather persuasively that at least *Cirroceras* and some species of *Turrilites* drifted posthumously.

### COILED SHELLS

From the point of view of the investigation outlined in these pages this group makes up the most numerous and important category. It embraces most ammonite shells, almost all Mesozoic, and many Paleozoic nautiloids. For the present study the author united both involute and evolute morphologic types in this group.

### Experimental observations

Numerous attempts were made to produce plastic models of various types of coiled cephalopod shells in the same fashion as was done for straight cephalopods, but the technical difficulties were found to be greater than could be coped with by the resources at the author's disposal.

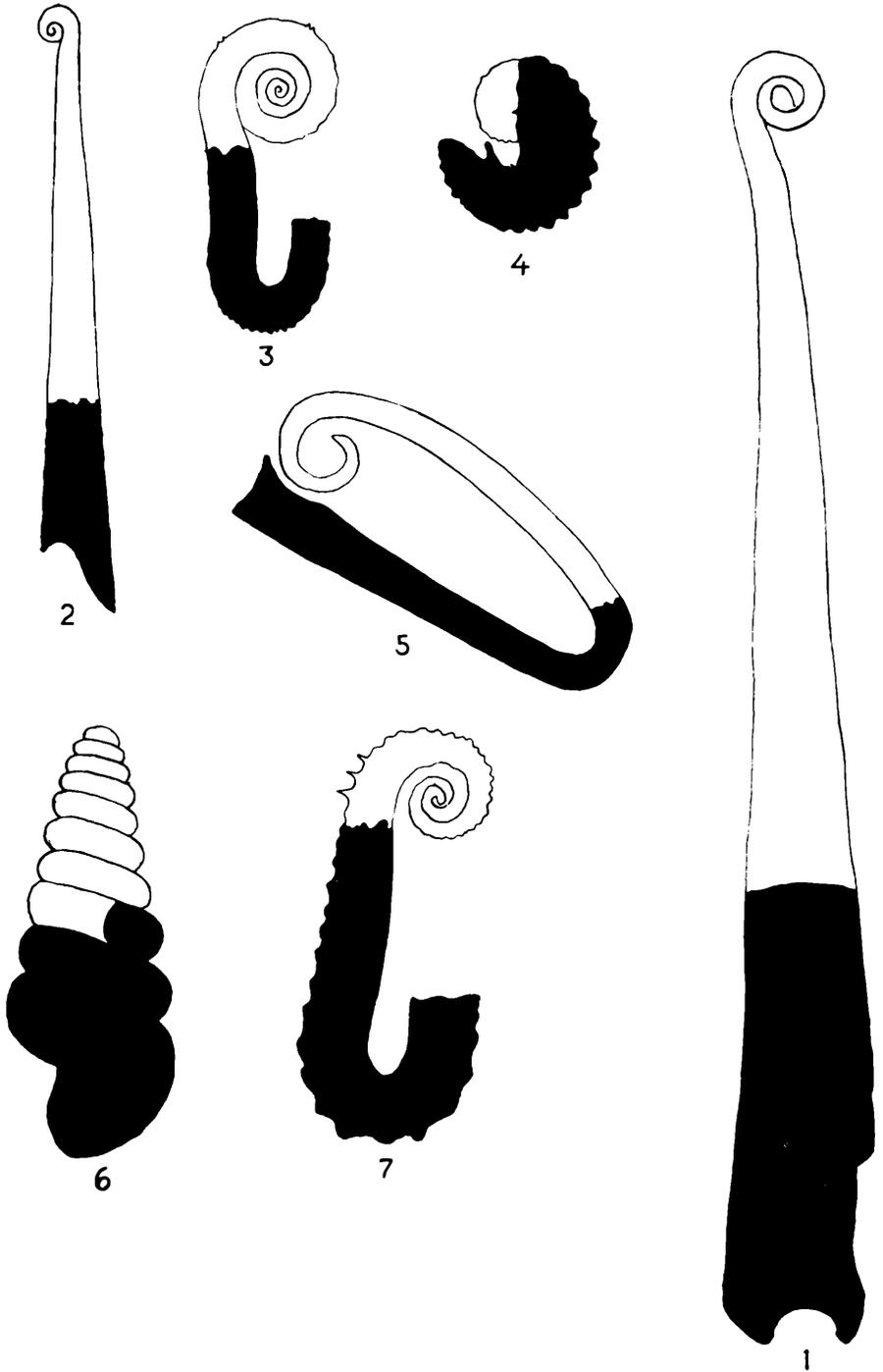


Fig. 9. Diagrammatic representations of uncoiled shells of, (1) *Lituus lituus* MONTFORT ( $X_1$ ) (after NOETLING, 1882, pl. 11, fig. 1); (2) *Baculites compressus* SAY ( $X_5$ ), showing the form of an entire juvenile shell; (3) *Macroscaphites*; (4) *Scaphites*; (5) *Lytocrioceras*; (6) *Turrillites*; (7) *Ancyloceras*. Figures 1—7 indicate the proportion of body chamber to chambered shell. Figures 5—6 adapted from TRUEMAN (1941) and figures 3, 4, 7, adapted from SCHOELLER (1949).

It is no doubt possible to produce such models in the same manner as wax reproductions of the details of fossil fish skulls, by serial sectioning and rebuilding the shells layer by layer. But after discussion with Dr. JARVIK of the National Museum, Stockholm, it was decided that the time and expense involved in producing models of cephalopods by this method was out of all proportion to their usefulness in the present study. It would take at least 6 months to make a model of a medium-sized ammonite by employing this method, according to Dr. JARVIK's calculations.

It was finally decided to base observations on two species of *Nautilus*, the involute *N. pompilius* (pl. III, fig. 3, a—b) and the moderately evolute *N. umbilicatus* (pl. III, fig. 2, a—b). A series of observations were made on both shells under various conditions after which the shell of *N. pompilius* was modified by slicing away parts and replacing these with the plastic material already mentioned in the foregoing. In this way the degree of inflation of the shell could be varied and different shell types produced. The specific gravity of the salt water used for the flotation experiments was kept at 1.026 and the specific gravity of the plastic material was adjusted to 2.63, the same as that of the shells of *N. umbilicatus* and *N. pompilius*, as determined in the laboratory. The X-ray analysis of the material forming both shells showed them to consist of aragonite (S. G. = 2.93) and the lower specific gravity is attributed to the presence of light-weight organic matter in the shell.

#### Floating position of *Spirula spirula*

Shells of this (uncoiled) species were found to float with the median plane horizontal to the surface of the water and with a considerable portion of the shell above waterline. All fossil shells of this type must have come to rest along beaches in the same way as living *Spirula*. The lack of a body chamber and the lightness of the shells means that they can float for a virtually unlimited period. It is of interest to note that the distribution of *Spirula* shells is much wider than that of the living animal and some have even been picked up on the coasts of England and Newfoundland. The young stages of *S. spirula* are found only at 1,000—1,750 m depth, the older forms up to 200 m, seldom 100 m. The shell material is aragonite (REYMENT & ECKSTRAND, 1957). See also IREDALE (1944, p. 298) and EKMAN (1953, p. 362).

#### Flotational experiments with *Nautilus pompilius*

A small shell of this species weighing 119 gm was placed in water and let float for 32 days without disturbance. At the end of this period the shell was again weighed and it was found that the weight had increased to 134 gm; 15 gm of water had thus been taken in. The coloring of that part of the shell that was under water during the whole period had faded considerably, whereas that part that had remained above water

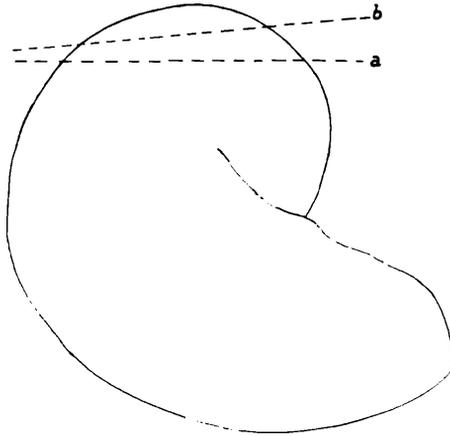


Fig. 10. Shell of *Nautilus pompilius*. a = water level at the outset of the experiment and, b = the level after 32 days ( $X\frac{1}{2}$ ).

retained the same brilliancy (cf. REYMENT, 1957 a). The black conchiolin part was found to have rotted partly away and two small holes had appeared in the shell wall. One of these passed right through the wall. In fig. 10 the level of the water on the shell is shown, (a) at the beginning of the experiment and (b) at its close. A considerable amount of agitation did not sink the shell.

The fact that small holes developed in the shell wall could provide a source of leakage. Another, larger shell was let float for several days in salt water which was kept aerated by means of an aquarium aerator; it also developed holes. Similar results were obtained with other shells. A possible explanation of the appearance of the holes may be that these may represent sites of deficient calcium carbonate secretion with a resultant higher percentage of light organic matter in the shell material. Such points of weakness would be readily breached by long exposure to water (for example, bacterial action and the softening effect of soaking).

#### Flotational experiments with *Nautilus umbilicatus*

The same sequence of events was applied to a shell of this species. The shell at first floated relatively higher than *N. pompilius* but quickly sank lower. Gentle agitation caused air to become displaced from the chambers and the shell eventually sank. As already pointed out the same procedure with different shells of *N. pompilius* did not cause them to sink.

The weight of the shell used in the above experiment prior to immersion was 212 gm and after sinking, 235 gm. The shell thus required 35 gm of salt water to sink it, a weight increase of 11 %. The sunken shell remained upright. (A *N. macromphalus* from New Caledonia containing the animal was sent me by Dr. F. McMICHAEL in Jan. 1958. It is still poised upright on the floor of its container after 75 years in 80% spirit).

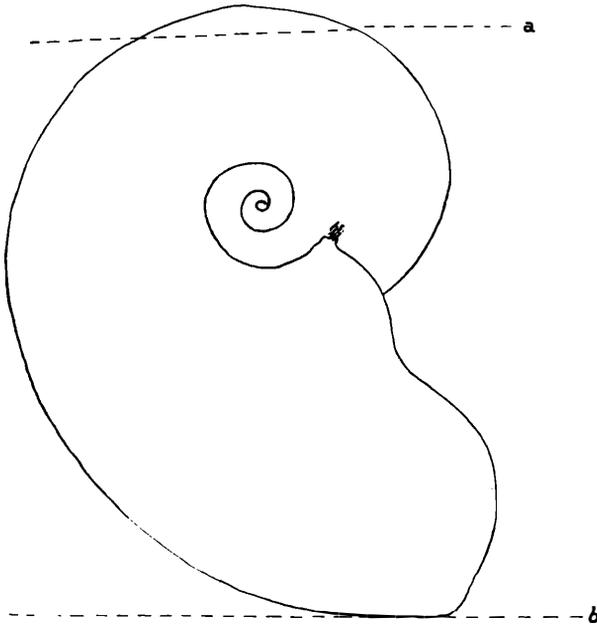


Fig. 11. *Nautilus umbilicatus*. Line "a" indicates the water level on the shell in undisturbed salt water. Line "b" represents the bottom of the containing vessel and illustrates the position of rest taken up by the shell after sinking ( $X\frac{1}{2}$ ).

It may be concluded that the more involute *N. pompilius* will be more widely distributed nekroplanktonically than *N. umbilicatus*.

The connecting rings of both species are fragile so the ease with which the second species was brought to sink may not be put down to the probability that its siphuncular sheath is more easily broken than that of *pompilius*. The correct explanation seems to be that the wider siphonal orifice of *N. umbilicatus* more readily lets in water and its open coiling leaves more chambers vulnerable to loss of air. The more involute *N. pompilius* has more entrapped air above the level of the septal necks and will thus not admit so much water. The relatively larger body chamber of *N. umbilicatus* is a further factor of importance. During the four days in which *N. umbilicatus* was left in salt water it developed a hole in the wall of the body chamber.

#### The effect of degree of inflation on the buoyancy of coiled shells

By successively slicing the flanks of a specimen of *N. pompilius* and building up the sides with plastic material of the same specific gravity as aragonite in cephalopod shells a series of models were produced which were used to establish the effect of variation in the degree of inflation of the shell on its buoyancy. In fig. 12 the behaviour of the various shell types is shown diagrammatically.

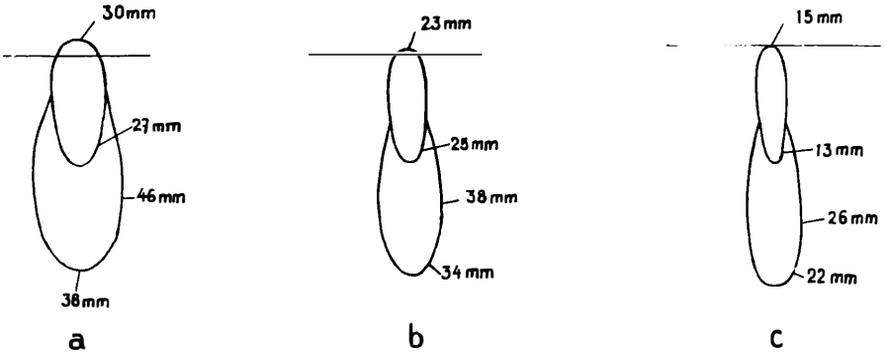


Fig. 12. Diagram illustrating the effect of inflation of the shell on the buoyancy of coiled cephalopods. The figures are drawn approximately to scale. All models have a diameter of 176 mm. The horizontal lines indicate the level of the water in the containing vessel.

The model represented in fig. 12 a is only a slight modification of the nautilus shell and it floated almost as efficiently as *N. pompilius*. The model shown in fig. 12 b is more compressed and was found to just keep afloat. The third type, illustrated in fig. 12 c, is still more compressed; it sank on immersion in salt water but remained upright on the bottom of the container. It may therefore be concluded that the transitional, just buoyant form is a shell shape somewhere between that of the models illustrated in figures 12 b and 12 c. As will be shown in a later chapter, the dimensions of the body chamber are of great importance in deciding the transitional form. The body chambers of the models here described were of the same length as that of *N. pompilius*, namely,  $15/36$  of the last whorl. A longer, more inflated body chamber would naturally permit more inflated chambered whorls and yet still cause the shell to sink. As already noted, the shells of chambered cephalopods are delicately poised and will either just float or just sink when empty. In life, the necessary adjustments were no doubt made by the animal [see TEICHERT (1933) and SCHMIDT (1930) for proposed mechanisms]. The experiment just described indicates that moderately inflated involute shells probably behaved in much the same way as *N. pompilius*, but more compressed forms may be expected to have sunk after the death of the animal. Highly compressed shells probably sank under all circumstances but the behaviour of intermediate shell types was probably conditioned by the dimensions of the body chamber.

The reason for this depends on the reduced air volume in relation to shell material in compressed forms. After a certain transitional volume the decrease in air space is greater than the associated decrease in mass of shell material. Although no experiments were carried out to verify the assumption, the same must hold true for highly depressed shells, so-called *cadicones*. Here again a certain air-volume/shell-weight ratio will

be exceeded in connexion with increasing depressedness of the whorls; strongly depressed shells may also be expected to have sunk posthumously.

The experimental observations accounted for above were made on shells with the same thickness as *N. pompilius* (wall thickness 1.20 mm—1.25 mm; septal thickness 0.70 mm—1.70 mm for the final whorl, inner whorls thinner). The thickness of the shell wall of *pompilius* is by no means constant, particularly that of the body chamber.

### Discussion

If it be so that compressed cephalopod shells did not float after the death of the animal but sank and became embedded in the bottom sediment we should expect to find some evidence of this. This is actually so and SCHWARZBACH (1934, p. 8) has described and figured an oppeliid with aptychi in its body chamber which he interprets as coming from cannibalistically eaten young; the aptychi are considered to represent the contents of the stomach (see also ARKELL, et al., 1957). The fact that such finds apparently are rare is almost certainly to be ascribed to the methods of collection of fossil material. If SCHWARZBACH's oppeliid, a very compressed form, had drifted widely after the death of the animal all the soft parts, including the stomach and its contents, would have been completely lost.

SCUPIN (1912, p. 366) questioned the possibility of flat, compressed forms with many septa of being able to rise and float after death. He wrote (1912, p. 355) that evolute, flat, compressed, disk-shaped forms are often locally bound. He pointed out correctly that an inflated shell is relatively more buoyant than a compressed one as the percentage of shell to space must be greater in the latter case. He also pointed out the greater weight occasioned by augmented septal complexity (SCUPIN, 1912, p. 356) and he realized that evolute shells contain more shell material than involute shells at comparable diameters.

### General remarks on non-buoyant shells

a. Very compressed shells. — Many of these forms may have inhabited the coastal zone and probably drifted ashore before the decay of the soft parts had proceeded far. Therefore, in such cases the flotation capabilities of a shell are of no importance; it is only when the shell was sufficiently free of the soft parts as to be able to behave independently that the results of the experiments outlined in this chapter and the next are applicable.

Among non-buoyant shells of the compressed type may be mentioned many *Oppelia* species, compressed desmoceratids, *Beloceras* species, many of the Triassic species figured by HYATT & SMITH (1905) and SMITH (1914) and many sphenodiscids, to quote a few examples.

b. Very depressed shells. — No experimental observations were made on this type of shell, but arguing on analogy with the compressed forms, very depressed shells may also be expected to have behaved similarly to them. Depressed involute shells were probably less buoyant than depressed evolute shells.

A few depressed shells of the type here considered to have been posthumous sinkers are, for example, some species of *Tulites*, *Pachyascoceras*, *Fagesia*, and *Cadoceras*.

Oyster growths on compressed and very depressed shells. — Many ammonite specimens conforming to these types are found encrusted with oyster shells (for example, see REYMENT, 1955, pl. 24, fig. 3). This suggests that the shells came to rest in an environment with sufficient water to sustain life for oysters.

## THE SIZE OF THE BODY CHAMBER

### Introductory remarks

The importance of the relative size of the body chamber of a cephalopod to the chambered portion was recognized by SCUPIN (1912, p. 357) and later TRUEMAN (1941). The latter worker found that in many cases the body chamber occupies from 2—3 times the bulk of the air chambers and in *Dactylioceras*, for example, the body chamber weighs approximately three times as much as the septal part — this calculation is only very approximate (TRUEMAN, 1941, p. 354). In comparison SCUPIN (1912) may be quoted; he assumed that a body chamber occupying one to one and a half whorls would leave less than half the volume of the shell for the chambered section. In the adjacent table, compiled partly from TRUEMAN (1941, p. 360) and PUTZER (1938, p. 479), ammonites are listed, whose body chambers exceed in length more than three quarters of a whorl. The lengths are expressed in degrees.

TRUEMAN (1941, p. 363) also made the interesting observation that, according to his calculations many living ammonites were of approximately the same density as seawater. He also considered that in many "normal" ammonites, as in nautilus, the length of the body chamber approximates to one third of the total length of the conical shell. Referring to species of the genus *Liparoceras*, such as *L. chelteniense* and *L. substriatum*, the body chambers are from 6 to 8 times as bulky as the air chambers and he concluded (1941, p. 365) that this genus was distinctly heavier than water. TRUEMAN was of the opinion that there seems to be a lack of transition forms between lipoceratids that may have been heavier than seawater and those that might be considered to have been lighter. In the Nigerian Upper Cretaceous complete transitions are known from shells that would have sunk posthumously to shells that would have floated. Particularly species of the genera *Bauchioceras* and *Gombeoceras* supply good examples.

*Dimensions of ammonite body chambers*

Name of species	diameter in mm	length of body chamber in degrees
<i>Schlotbeimia colubrata</i> (ZIETEN) . . . . .	174	270
<i>Libyoceras afikpoense</i> REYMENT . . . . .	140	290
<i>Benuites benueensis</i> REYMENT . . . . .	48	300
<i>Kamerunoceras jacobsoni</i> REYMENT . . . . .	110	330
<i>Chondroceras</i> sp. . . . .	45	360
<i>Schlotbeimia pseudomoreana</i> SPATH . . . . .	187	360
<i>Oxynoticeras simpsoni</i> (BEAN) . . . . .	225	360
<i>Echioceras notatum</i> TRUEMAN & WILLIAMS . . . . .	100	360
<i>Vermiceras conybeari</i> (SOWERBY) . . . . .	460	380
<i>Microderoceras birchi</i> (SOWERBY) . . . . .	254	390
<i>Psiloceras planorbe</i> (SOWERBY) . . . . .	?	390
<i>Deroceras</i> sp. . . . .	47	450
<i>Cruciloboceras cheltiense</i> SPATH . . . . .	84	450
<i>Paltechioceras? elicatum</i> BUCKMAN . . . . .	160	480
<i>Pleuromegalites forticostata</i> BUCKMAN . . . . .	160	480

The nature of the occurrences of these shells is in some cases such as to suggest that in life they inhabited the same shallow local basin of small extension and lived together in the same communities. After death the highly compressed forms sank near to the site around which they lived while the buoyant shells of the fauna drifted until they sank or became stranded. This posthumous process of differentiation according to buoyancy produces an entirely false picture of the faunal distribution during the life of the ammonites.

## Experimental observations

The following experiments were carried out in order to ascertain the effect of the size of the body chamber on the buoyancy of an involute shell. A shell of *Nautilus pompilius* was increased in length by extending the body chamber with plastic material so that the diameter of the shell was raised from 175 cm to 235 cm, slightly more than a quarter of a whorl. The effect of this increase was to cause the shell to float much lower down in the water. As soon as the final air chamber began to let in water the shell sank.

By increasing the length of the body chamber to almost two thirds of a whorl, a length was found that just brought the shell to sink. This is illustrated diagrammatically in fig. 14. It should be mentioned that one shell of *N. pompilius* with a diameter of 190 cm only required an overall increase in the diameter of 6 cm before it became heavier than water. The body chamber then occupied 48 % of the last whorl.

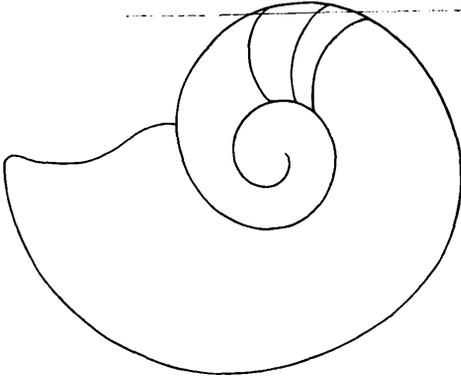


Fig. 13. Sketch illustrating a nautilus shell with increased body chamber length. The line indicates the water level on the shell.

In concluding these remarks it may be stated that the size of the body chamber of a cephalopod is probably the most important factor in the buoyancy of a shell. In life, the possession of a large body chamber probably permitted considerable latitude in buoyancy variations and may have been an asset to the animals; its net effect on the empty shell was nevertheless to decrease its buoyancy (see also the section on straight cephalopods for a discussion of the importance of the body chamber in these forms).

#### Apertural structures

Structures of influence on the buoyancy of an ammonite shell are the extensions of the apertural margin or peristome of the body chamber, the so-called "ears", which may be comparatively heavy in relation to the rest of the shell. In some forms these processes may be nearly a quarter of a whorl in length (ARKELL, 1957, p. 87). Ventral lappets may be developed and this structure in extreme cases will build rostra (for example, certain species of *Mortoniceras* have very solidly developed rostra). Some of these apertural structural types are illustrated in fig. 15.

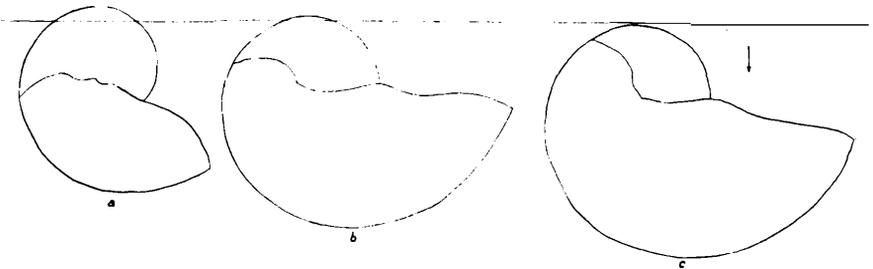


Fig. 14. Diagram showing the increase in the length of the body chamber of a specimen of *Nautilus pompilius* necessary to cause it to sink. In the case of figure c the shell would not float. Horizontal line = water level. Approximately  $X_{\frac{1}{3}}$ .

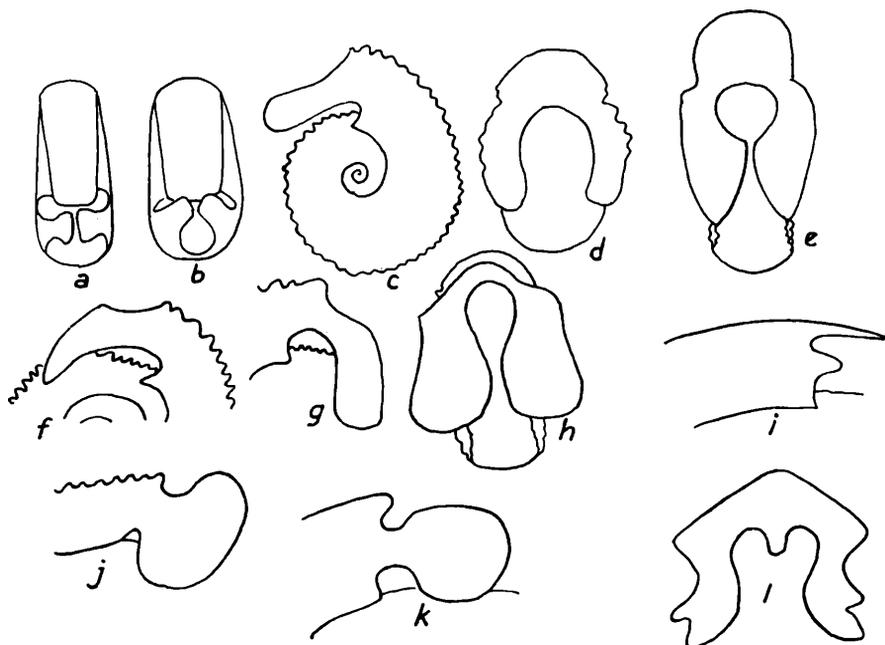


Fig. 15. Some types of apertural appendages found on ammonite body chambers: a, *Morphoceras* sp.; b, *Stephanoceras* sp.; c, *Otoites contractus* (SOWERBY) (after WESTERMANN, 1954, p. 82, fig. 11); e—f, *Normannites (Normannites) orbigny multicostatus* WESTERMANN (after WESTERMANN, 1954, p. 131, fig. 35); g—h, *Itinsaites itinsae* MCLEARN (after WESTERMANN, 1954, p. 250, fig. 103); i, *Harpoceras* sp.; j, *Grossouvria* sp.; k—l, *Strenoceras* sp.

#### MODE OF SETTLING OF THE SHELLS OF *NAUTILUS POMPILIUS* AND *NAUTILUS UMBILICATUS*

In order to gain an approximate conception of the minimum depth of water required for these two shells to take up their resting positions, water from a large container was slowly drained and the behaviour of the shells noted. In the first case a partially waterlogged shell of *N. pompilius* was employed and in the second case an almost waterlogged shell of *N. umbilicatus*. The purposes behind these experiments was to see at what depth of water these shells would strand and if they could lie at rest and still be surrounded by water, a factor of no mean importance in connexion with the entombment of the shells in sediment. It is obvious that in nature many more forces are to be reckoned with than those taken into account in the here discussed laboratory experiment. The effect of tidal movements would be for the flood-tide to carry the shells well up onto the strand and for them to become anchored by their body chambers during the period of ebb-tide. Swashing will also tend to anchor floating shells in the same manner; storms represent special conditions for which many factors must be brought into review.

The present study showed the most fragile part of *Nautilus* species is the body chamber. Loss of part of the body chamber will permit the

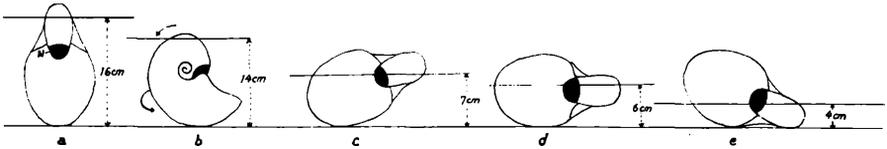


Fig. 16. Sketches showing the way in which the shell of *Nautilus umbilicatus* settles. The upper line represents the level of the water and the lower line the bottom of the container. Figure not drawn to scale. The arrows in figure b indicate the direction of the settling movements.

remaining shell to stay buoyant despite far-reaching damage to the air chambers. This may explain why so many ammonite shells are found without the body chamber.

The way in which the shell of *Nautilus umbilicatus* settles is indicated in fig. 16. In fig. a the shell (diameter 18 cm) is shown supported by a column of water 16 cm deep. At a depth of 14 cm the shell began to tip backwards and sideways. At a depth of 7 cm (fig. c) the shell was inclined at an angle of roughly  $45^\circ$ . At a depth of 6 cm (fig. d) the shape of the shell hindered settling movements so that it temporarily fastened at an angle of  $30-40^\circ$ . There was no further movement until a depth of 4 cm (fig. e) when the shell suddenly fell a short distance. It had then achieved its final resting position. This and the following experiment were carried out on a smooth, hard bottom. Various sedimentary bottoms may be expected to yield slightly different results. At a depth of 5 cm the shell was observed to be very susceptible to swirling movements and swang easily around the point of contact with the bottom. On a soft bottom this would assist in burrowing the shell into the sediment. This was later verified practically under actual sea conditions for some types of sediment. See also ROTHPLETZ (1909, fig. 158) and ARKELL (1957, p. 122).

The shell of *N. pompilius* (diameter 19 cm), which has more rounded contours than the species just discussed, remained in a vertical position until around a depth of 12 cm when it began to settle sideways (fig. b). It did not finally come to rest until the water had fallen to a depth of 1.5 cm. It was not as susceptible to swirling motion as *N. umbilicatus*.

From the above it may be concluded that the type of shell represented by *N. umbilicatus* will reach a stable resting position in deeper water than the type of shell represented by *N. pompilius*.

#### EXPERIMENTS ON THE STRANDING OF RECENT NAUTILUS SHELLS

The observations accounted for below were made on shells of *Nautilus pompilius* and *N. umbilicatus* at the following three places; Stora Värtan, an inlet of the Gulf of Bothnia, some 15 km north-east of Stockholm, Öresund, 7 km south of Hålsingborg, and in the tidal flat area of the Ho Bugt, Esbjerg, Denmark. The observations were carried out in order

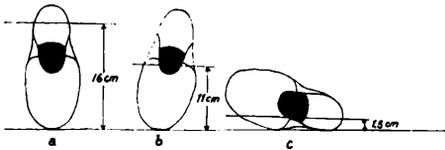


Fig. 17. Sketches showing the manner in which the shell of *Nautilus pompilius* settles. The upper horizontal line represents the water level and the lower horizontal line indicates the bottom of the containing vessel. Not to scale.

to ascertain the exact way in which coiled cephalopod shells drift ashore, a subject which has received no treatment in the literature.

During the first series of experiments in Stora Värtan the sea conditions were very mild with a light northeasterly breeze driving towards the shore. The waves were never more than 15 cm in height where they rolled suddenly forwards after breaking. The shells drifted with a slight pendulatory motion ashore, this movement being stronger for *N. umbilicatus*. Although they also rotated during drifting they moved mostly with the median plane in the direction of motion. Even very feeble waves were sufficient to cause the shells to continue shoreward movement over a sandy bottom and they did not strand in a vertical position (see pl. V, figs. 1—4). The shells finally came to rest in a position very near to that obtained experimentally by the writer (cf. figs. 16, 17 and pl. V, figs. 6, 7; pl. VI, figs. 3—6). Consequently, on a sandy bottom both shells finally stranded close to the strandline and in a horizontal position. The requirements necessary for a chambered cephalopod shell to come to rest in a vertical position would then have to be millpond conditions with a complete absence of wave motion (see pl. VI, fig. 2).

The pendulatory motion of the shells caused them to scoop sand and small stones into the body chamber when they first made contact with the bottom sediment. When the experiments were repeated at a locality with relatively loose (but not sticky) argillaceous shore sediment it was found that the shells tend in some cases to fasten when they began to scrape over the bottom.

Where wave action is more vigorous the shells may become buried in the shore sand owing to the scouring action of swashing water (pl. IV, fig. 1—5). The second series of experiments in Öresund were chiefly concentrated on this problem. It is here of interest to note that MENARD & BOUCOT (1951, p. 147, fig. 4) were able to demonstrate experimentally in the laboratory that terebratuloid brachiopods will become buried in sand because of scour by moving water; it was found by these authors that shells will not move over sand if the current is more readily able to shift sand. In this case a scour forms around the shell which tends to be buried therein by moving sand. On the whole, cephalopod shells would be harder to move for the currents than the brachiopod shells studied by MENARD & BOUCOT, even bringing into consideration the low effective density of the former. The present writer found the body chamber of cephalopods to assist scour burial. It should be pointed out, however, that buried objects frequently become exposed again when the scouring currents change intensity or direction.

Observations made in the Danish wadden sea (Ho Bugt) indicated that the shells fasten very soon after having come into contact with the newly deposited, adhesive wadden mud at some distance from the shore during the ebb period, where they, under favorable conditions, could become entombed. During the flood tide floating objects are carried up to the highwater level where some strand. Freshly deposited wadden mud forms a soft but coherent mass that is not readily scraped into the body chamber of a drifting cephalopod. Sandy sediment is, however, readily scooped up by the stranding shell (for example, pl. VI, fig. 5). The figures reproduced in pls. 5, 6 indicate various aspects of the stranding of cephalopod shells.

Vertically embedded shells are sometimes found in sediments. From the above it becomes clear that in the cases discussed, shells would have little chance of remaining in a vertical position. Vertical entombment of shells may occur if the effective density of the shell in question is greater than the density of water or if a partially water-filled shell is able to stay upright long enough on the bottom to become cemented into position in the sediment. All shell types studied in the experiments outlined in the present paper were found to remain upright on the bottom of the containing vessel after sinking. Under conditions of rapid sedimentation, or where the shell was heavy enough to sink well into the bottom slime, it could have become vertically embedded. Under less rapid conditions of sedimentation the shell would have eventually keeled over, after having filled with water. Actually quite a number of ammonite shells are found covered with encrusting oysters, which would seem to suggest a relative long period of submergence prior to complete burial (cf. pp. 104, 138).

The conclusion may be drawn that drifting cephalopod shells would have had an equal opportunity of stranding in any kind of coastline sediment. That they are so rare in sandy sediment is probably a reflection of the facts that shells are less likely to remain undamaged in coarse sediment and that such sediment permits readier loss of the shell material owing to the dissolving action of percolating solutions than does finer, less pervious sediment.

It is of interest to note that the undersides of ammonite body chambers may often show evidence of damage such as would be caused by movement to and fro over very coarse material [for example, the specimen of *Coilopoceras vandersluisi* figured by the writer (REYMENT, 1957, pl. 10, fig. 1, a—b)].

A large fragment of the body chamber and part of the second last whorl of *Craspedites* aff. *okensis* NIKITIN (*non* D'ORBIGNY) (pl. I, fig. 6, a—b; G. I. C 1004) has a belemnite in the body chamber. This ammonite species is very compressed, although relatively evolute, and is considered by the writer to have sunk after the death of the animal. It seems that it fell to the sea floor amongst the remains of belemnites but was sufficiently buoyant to remain upright. Slight water movements were enough to cause the belemnite rostrum to be scraped into the body chamber, which it probably effectively anchored.

## THICKNESS OF THE SHELL MATERIAL

The thickness of the shell of a cephalopod is important in connexion with calculations of its buoyancy. The subject is less complicated for smooth shells than for ornamented shells; it may be almost impossible to foresee the effect of any particular sculptural type on the buoyancy. Although the ornament of many fossil cephalopods is principally hollow, we know of a number of cases in which the tubercles, ribs and other features of the sculpture are solid and thus leave little or no traces on the steinkern; for example, *Sagenites (Trachysagenites) herbichi* MOJSISOVICS, whose tubercles show up only in the shell material but not on the steinkern. The figures of this species given by HYATT & SMITH (1905, p. 39, pl. 26, figs. 1—2; pl. 27, figs. 1—4; pl. 28, figs. 1—18) indicate that the tubercles are strong and must have provided a considerable load.

Studies of ornamental details in thin section by the author indicated that although these are often hollow, they are in most cases thicker than the non-ornamented parts of the test. In order to illustrate this point the following Cretaceous species may be taken as examples:

Species	Remarks
<i>Mammites mutabilis</i> REYMENT . . . . .	Tubercles thicker toward crests and at point of fusion with wall.
<i>Mammites dixeyi</i> REYMENT . . . . .	Same as above.
<i>Kameruniceras eschii</i> (SOLGER) . . . . .	Hollow tubercles that thicken toward crest; less solid than tubercles of <i>Mammites</i> .
<i>Barroisiceras</i> sp. indet. . . . .	Perfectly hollow tubercles.
<i>Speonticeras versicolor</i> (TRAUTSCHOLD) . . . . .	Ribs composed of thicker shell than rest.

It is clear that a shell with solid or semisolid sculptural elements will be weighed down by these, whereas a shell with unthickened tubercles and ribs will have a greater air volume and consequently a somewhat greater buoyancy. SCUPIN (1912, p. 358) did not consider ornamental features to play an important role in questions of buoyancy as he was convinced that all ornament is quite hollow, arguing on analogy with his conception of the shell of the argonaut. The ribs of *Argonauta argo* are certainly hollow, but the tubercles are only partially so, besides which they are fairly strong (see p. 149). DIENER (1912, p. 73) expressed similar opinions to those of SCUPIN on the subject of the thickness of the ornament of ammonite shells.

Observations on the thickness of the shell material in some ammonites. — In all cases cited in the following table the shell material consists of the original unaltered aragonite as proved by x-ray determinations (cf. REYMENT & ECKSTRAND, 1957).

Species	Shell radius (mm)	Shell thickness (mm)	Venter	Septa
<i>Libycoceras afikepoense</i> REYMENT (G. I. C. 1003) . . .	54	1.6		0.6
	35	1.3		
<i>Subcraspedites kascchpuricus</i> (TRAUTSCHOLD) (G. I. C. 1013)	20	0.3		
		0.4		
<i>Speetonicerias versicolor</i> (TRAUTSCHOLD) (S. M. F. 12157)		2.2	2.6	1.6
			2.3	
» » » (S. M. F. 12158)	56	1.7	1.6	1.7
» » » (G. I. C. 1011) .		2.0		
		2.9		2.1
<i>Baculites compressus</i> SAY (S. M. F. 9138) (body chamber)		1.7		
<i>Macrocephalites</i> sp. (G. I. C. 1002) . . . . .	36	0.3		0.3
<i>Placenticerias whitfieldi</i> HYATT (S. M. F. 9105) . . . . .	55	0.8		0.6
<i>Craspedites</i> aff. <i>okensis</i> NIKITIN non D'ORBIGNY (G. I. C. 1004) . . . . .	47	1.3		
		1.4		
» » (G. I. C. 1005) . . . . .	62	1.3		
<i>Craspedites subditus</i> PAVLOW (G. I. C. 1008) . . . . .	12	0.2		0.15

The measurements on the shell thickness were made with a KRÖPLIN dial micrometer (schnelltaster) with an accuracy of 0.025 mm (range 0—10 mm).

Several observations on the thickness of ammonite shells are available in the literature, but there is no way of knowing whether these were made on aragonitic shell material. For example, SPATH (1950, p. 83) noted in connexion with his investigations of thin sections of ammonites that the Pinacoceratidae were difficult to study owing to the thinness of the shells. As noted elsewhere in this paper (p. 147), the recrystallized calcitic shell is usually thinner than the original aragonitic shell so care should be exercised in using measurements on calcitically preserved specimens.

TRUEMAN (1941, p. 350) noted that in many cases the shell may be about 3—4 mm thick and *Chalcedoniceras* was found by him to attain 9 mm. Comparing these thicknesses with those given by the present author in the above table it will be seen that such figures are very great indeed and these shells, unless greatly inflated, can hardly be expected to have floated. TRUEMAN also carried out some rough estimations of the volume occupied by the shelly material in some ammonite shells, a procedure for which no accurate method suggests itself to the present writer. These approximations indicated that the shell volume of *Promicroceras* is one twelfth of the total volume. TRUEMAN indicated one of the serious hindrances to shell volume determinations is provided by the fact that in almost all cases the dorsal side of the shell secretes variable extra quantities of substance which is difficult to ascertain, even by breaking back the shell and determining the volumes of the fragments obtained

(see TRUEMAN, 1941, p. 352). Excluding the volume of the siphuncular material and that of the septa (which is by no means insignificant; see further on in this paper), TRUEMAN (1941, p. 352) obtained the following approximate values for the volumes of the shell walls for some ammonite species:

<i>Dactyloceras</i>	= 9 % of the total volume.
<i>Liparoceras</i>	= from 1.5 % to 3 % of the total volume — apparently a very thin-shelled form.
<i>Ludwigia</i>	= 7 % of the total volume.
<i>Asteroceras smithi</i>	= 12 % of the total volume.

TEICHERT (1933, p. 120) observed that in actinoceroid nautiloids the siphonal wall is thinner than the septa, and that the latter are usually more than three times as thick as the former. He also pointed out that the material forming the siphuncle may not be the same as that in the septa. For ammonites we know this material to be calcium phosphate (GRANDJEAN, 1910; REYMENT, 1956).

MILLER & COLLINSON (1950, p. 673) observed in connexion with their description of the nautiloid species *Tylosidoceras unicum* that it is marked by the very thick test which in the ventral region is 5 mm thick and which becomes even thicker on the sides.

#### DIFFERENCES IN THE SHELL THICKNESS OF ARAGONITIC AND CALCITIC SPECIMENS

Observations were made on unaltered aragonitic shells and the same species in calcitic preservation.

As a good example may be taken the Maestrichtian (Upper Cretaceous) species *Libyoceras afikepoense* REYMENT, which was available in large quantities both in aragonitic preservation in friable clay shale, and in calcitic preservation in limestone and marl. Thin sections of the calcitic specimens disclosed thin septa (about 0.3 mm) and a wall thickness of 0.9 mm (ventral). At a comparable radius aragonitic shells have a septal thickness of 0.6 mm and a ventral thickness of 1.5—1.7 mm. These measurements indicate that the shell thickness of an aragonitic shell may be double that of the same species in the altered state. The explanation is probably that water in the chambers dissolved part of the aragonite which was later recrystallized as, for example, encrusting calcite crystals.

As a consequence, remarks concerning the thinness of ammonite septa ought to be treated with caution unless the nature of the preservation also is stated. TRUEMAN'S (1941) calculations on the volumes of ammonite shells suffer from the serious defect that his investigations were carried out on calcitic shells with the result that his figures for the weight of the shell material are too low. There is, unfortunately, no way of knowing how much of a shell has been dissolved during diagenesis so that attempts

to arrive at a satisfactory method of calculating the volume and weight of a calcitized shell are doomed to failure; at best only rough approximations would be possible. Moreover, there is so little difference in weight between a buoyant nautilus shell and one that will just sink that such approximations exceed the necessary degree of accuracy.

Studies on the shell structure of fossil cephalopods in calcitic preservation should take into consideration the loss of detail caused through the recrystallization of the calcium carbonate making up the shell and the fact that a quantity of the shell surface has been lost through solution.

TRUEMAN (1941) was inclined to believe that the shells of ammonites may have been composed of calcite and not aragonite as none of the numerous thin sections studied by him gave evidence of the destruction of structure such as would be expected to have been brought about by the volume change on recrystallization, bearing in mind that the specific gravity of pure aragonite is 2.93—2.95 and that of pure calcite is 2.71. Determinations by A. HENRIQUES, K. FREDRIKSSON and the author on the specific gravity of the shell material in *Nautilus pompilius* and *N. umbilicatus* gave a figure of 2.63—2.65, which shows that the volume occupied by the aragonite in shelly material is greater than that, that would be occupied by pure aragonite, owing to the chitinous material present. Therefore, the recrystallization of aragonite to calcite and expulsion of the horny matter would be accompanied by a negligible change in volume.

#### EXPERIMENT ON THE EFFECT OF TUBERCLES ON THE BUOYANCY

The experiment described below concerns the effect of tubercles on the buoyancy of a moderately inflated, involute shell.

The final whorl of a specimen of *Nautilus pompilius* was loaded with three rows of partially hollow tubercles glued onto each flank (see fig. 18) thus making the shell trituberculate. Twenty such tubercles weighed 6.7 gm (approx. 5 % of the weight of the shell). Owing to technical difficulties it was not found possible to produce regular tubercles; in general, however, they had thicker crests than sides. The shell floated awash in still water but the first loss of air caused by agitation of the water brought the shell to sink. The conclusion drawn here is that a moderately strongly ornamented trituberculate shell of the same shape as *N. pompilius* will be unlikely to stay afloat for a long period. In the above experiment only the last whorl was made tuberculate. Considering the added weight provided by the presence of tubercles on the inner whorls and, for example, ribs and a solid keel it will be appreciated that the same effect would be attained with weaker ornament.

The experiment was repeated with a much larger shell weighing 175 gm. The tubercles were made less solid than in the preceding case and the weight of the inner, concealed tubercles roughly calculated and com-

pensated for. It required a total mass of 47 gm (27 % of the weight of the shell) of these tubercles to cause the shell to sink, no water being permitted to enter the air chambers. These thin-walled tubercles had clearly contributed to the buoyancy effect of the shell. The wall thickness of the specimen used in the experiment, as far as could be determined, was between 1.1 and 2.0 mm. Before making a determination of an ornamented form it should be ascertained if the ammonite possesses a hohlkiel, and hohlknoten, besides ribs (cf. HÖLDER, 1952, p. 29).

In conclusion it may be stated that strongly ornamented, tuberculate shells and some less strongly ornamented tuberculate shells will not float if the ornamental elements are solid or partly solid.

In this connexion reference has often been made in the literature to the shell of the argonaut in which the tubercles and ribs are supposed to be only very slightly thickened in relation to the interspaces. The author made the following measurements on a moderate-sized, almost complete shell in his possession, which shows these statements to be exaggerated:

Thickness of flank = 0.4 mm

thickness of ribbing on flanks = 0.3—0.4 mm

thickness of ventrolateral tubercles = 1.1 mm—1.4 mm

thickness of the umbilicolateral area = 1.8—2.8 mm

The argonaut shell is unchambered and floats almost awash if undisturbed. X-ray determinations on the shell of this cephalopod show it to be composed entirely of calcite (REYMENT & ECKSTRAND, 1957).

HÖLDER (1952) published some observations on hohlkiel ammonites. This type of structure occurs widely amongst certain Jurassic ammonites and has also been noted by the present writer in Cretaceous species, for example, *Glebosoceras glebosum* REYMENT. HÖLDER (1952, p. 19) found that *Lioceras*, *Dumortieria*, *Ludwigia*, and *Hildoceras* possess entire keels whereas *Hammatoceras* and *Harpoceras* have hollow keels. A hohlkiel may appear in various growth stages, but as far as is known, it does not continue much onto the body chamber. Some hohlkiels may have the space between the siphuncle and the keel filled with shelly material, which would

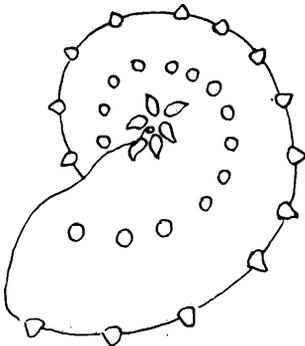


Fig. 18. Sketch showing the appearance of the model used to investigate the importance of ornament on the buoyancy of an inflated, involute shell. Not drawn to scale.

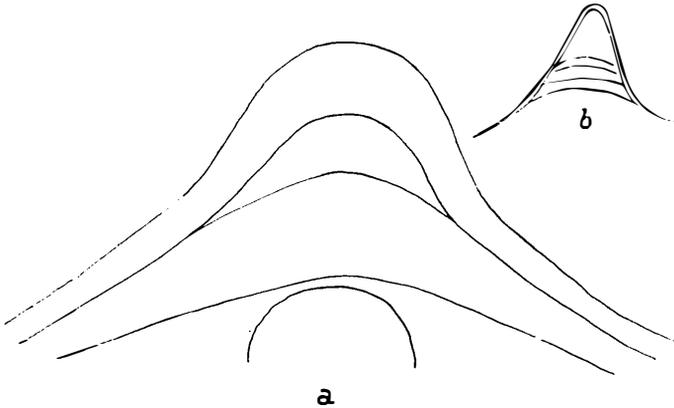


Fig. 19. Two figures indicating the nature of the hohlkiel; a, *Oxynoticeras*, b, *Stephanoceras* (after HÖLDER, 1952).

be an added tax on the buoyancy of a shell. HÖLDER (1952, p. 35) has also observed that the ribs of ammonites often represent places of thickening.

#### THE INFLUENCE OF THE SEPTA ON BUOYANCY

The number of septa possessed by those modern shelled cephalopoda on which figures are available are:

*Nautilus pompilius* LINNÉ 33—38

*N. macromphalus* SOWERBY 27—28

*N. umbilicatus* LAMARCK 32

This information was obtained from STENZEL (1952, p. 13).

In all cases investigated by the present author, fully grown ammonites have many more septa than coiled nautiloids at comparable diameters. In the following discussion a review is first presented of notes in the literature on ammonoid septa and, secondly, some experiments and observations on thin sections made by the author are accounted for.

We are indebted to BÖHMERS (1936) for the first large-scale study on ammonite septa, although BRANCO (1879, 1880), PFAFF (1911) and SWINERTON & TRUEMAN (1918) also made important contributions. GRANDJEAN (1910) published notes on ammonite septa but was primarily concerned with the nature of the siphuncle.

BÖHMERS' investigations of Permian ammonites indicated that the siphuncles of these are only rarely preserved; in one hundred thin sections studied he found only four specimens with preserved siphuncular sheaths. For *Pronorites timorensis* HANIEL (1936, fig. 4) he reported the first two proseptra to be concave outwards and also that these are thicker than other septa. Similar observations were made for other species. He wrote

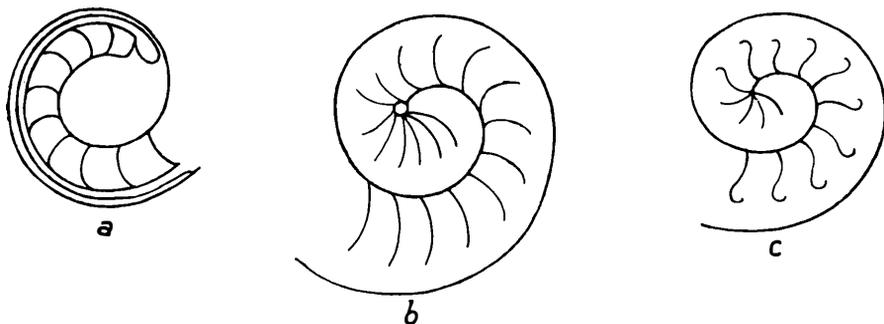


Fig. 20.

- a. *Megaphyllites jarbas* (MUNSTER). Triassic. Observe the concave-forwards septa. After BRANCO (1880, pl. 9, fig. 5) ( $X_{30}$ ).
- b. *Anarcestes lateseptatus* (BEYRICH). Middle Devonian. Note the pear-shaped proloculus, the concave-outwards septa and the external location of the siphuncle. After BÖHMERS (1936, p. 97) ( $X_{\frac{1}{2}}$ ).
- c. *Agoniatites* sp. Devonian. Observe the concave-outwards septa, the backwards-directed septal necks and the external siphuncle. After BÖHMERS (1936, p. 97) ( $X_{\frac{1}{2}}$ ).

(BÖHMERS, 1936, p. 18) that the septa of all the genera treated in his paper have strongly concave-forwards septa and that a primitive nautiloid stage, such as is found in many Devonian goniatites (for example, *Anarcestes* and *Agoniatites* have concave-forwards septa — see fig. 20, b—c) was seen only among prosepata. He also noted that the septa of Permian ammonoidea are thicker in the middle. Typical for pronoritid Permian ammonites (BÖHMERS, 1936, p. 20) is that the septal necks (apart from the prosepata) are still directed backwards, as in nautiloids. All other groups of Permian ammonoids have forward-directed septal necks.

In discussing various features of the pronoritid goniatites BÖHMERS expressed the view that the higher whorl section would accommodate more gas than other Carboniferous and Permian forms and this, coupled with their lense shape, would have greatly aided them in diving (BÖHMERS, 1936, p. 23). His observation concerning the completely round proloculus of pronoritids, that Triassic and Cretaceous ammonites have elliptical proloculi, is not borne out entirely by the present author's observations on Jurassic and Cretaceous ammonites in which he has observed that spherical proloculi are of common occurrence. Adrianitid forms have backwards-directed septal necks in the first whorl but these soon pass over to forwards-directed. S-shaped septa are of common appearance in these ammonites. BÖHMERS (1936, p. 114), on the basis of SCHMIDT's (1930) preseptal gas theory, connected concave-forwards septa with poor diving ability.

VOORTHUYSEN (1940) continued this line of investigation with a study on Triassic ammonites. He figured a thin, median section of *Halorites macer* VON MOJSISOVICS (1940, p. 25) which shows a number of concave-

forwards septa in the first whorl. The septa of trochitids are mostly concave forwards in the primary volution, but the concavity is sometimes so feebly developed that the septa are almost straight. One may, however, speak of "nautiloid" inner whorls for this group. In the second whorl the septa are straight or slightly convex outwards (VOORTHUYSEN, 1940, p. 52).

The species *Gonionotites waldthauseniae* WELTER (VOORTHUYSEN: 1940, p. 38, fig. 10) has concave-outwards septa in the fifth whorl inasmuch as the middle parts of the septa are concave forwards. It may here be mentioned that this condition is often to be seen amongst Upper Cretaceous (Turonian) ammonites, for example, the genus *Glebosoceras* (fig. 21 a). VOORTHUYSEN (1940, p. 53) also found that the septal density per whorl is uneven in different specimens of the same species. This observation has been verified by the present author's work on Jurassic and Cretaceous ammonoidea. The distances between neighboring septa are frequently uneven and there is no mathematical regularity in septal location. Very common amongst coiled cephalopods is the crowding of the last septa which, in ammonites, may take place throughout the entire last whorl. This crowding is irregular (cf. VOORTHUYSEN, 1940, p. 54).

In summing up his observations on the orientation of the septa VOORTHUYSEN (1940, pp. 130, 133) noted that those of Devonian goniatites are mostly concave forwards, whereas those of Carboniferous and Permian goniatites are mostly convex forwards. See also SCHINDEWOLF (1939).

There is thus some documentation available as regards the structure of the septa of Triassic and Permian ammonoidea thanks to the researches of BÖHMERS and VOORTHUYSEN as well as SPATH (1950). The same cannot be said of Jurassic and Cretaceous ammonites. In order to allow discussion of these a few thin, median sections of species, chosen at random, were made.

A summary of the most important results of this investigation in respect of the septa is given below.

#### DIRECTION OF INFLATION OF THE SEPTA

A rather surprising observation was that many Jurassic and Cretaceous ammonites have concave-outwards septa (i. e. "nautiloid" inflation) at advanced growth stages. The concave-outwards septa may appear irregularly (cf. fig. 21, b, d), they may be confined to the first formed whorls, or a large concave-outwards zone may occupy the major portion of a septum with convex-outwards wall contacts [for example, *Hildoceras bifrons* (BRUGUIÈRE), *Glebosoceras glebosum* REYMENT — fig. 21 a]. Many ammonites have the septal face divided into two concave-forwards zones with a convex-forwards median ridge between them. In median section this septal ridge shows up convex forwards, but sections cut on either side of it will be concave forwards (cf. fig. 21, b—g). Still more complicated septal faces are common, for example, species of *Placentoceras* (pl. I, fig. 7).

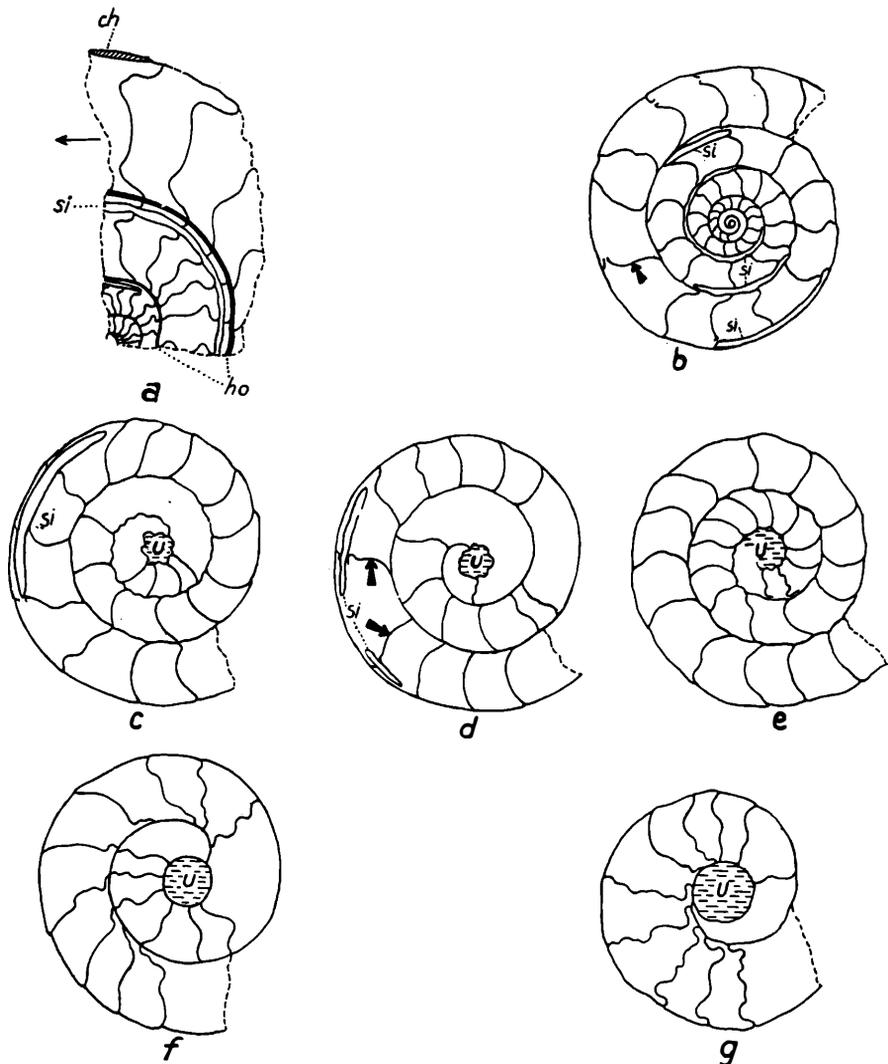


Fig. 21.

- a. *Glebosoceras glebosum* REYMENT. Turonian, Cretaceous. Median section. Channel after siphuncle = ch (hohlkiel ammonite), ho = hohlkiel. Note the concave-outwards centers of the septa. The specimen sectioned is the inner whorls of a much larger ammonite. G. I. C 1031 ( $X_1$ ).
  - b. *Pachynascoceras costatum* REYMENT. Lower Turonian, Cretaceous. Median section. Observe the concave-outwards septum with septal necks (arrow). G. I. C 1029 ( $X_7$ ).
  - c. Same specimen. Section cut 2 mm from the median plane. Part of the eccentric siphuncle appears in this section (si); here the septa are convex outwards, also in part of the innermost whorl preserved ( $X_{\frac{1}{2}}$ ).
  - d. Same specimen. Section cut at 4.5 mm from the median plane. The arrows indicate concave-outwards septa with septal necks ( $X_3$ ).
  - e. Same specimen. Section cut at 6 mm from the median plane. All the septa are now concave outwards ( $X_1$ ).
  - f. Same specimen. Section cut at 10 mm from the median plane ( $X_{\frac{1}{2}}$ ).
  - g. Same specimen. Section cut at 14 mm from the median plane. Observe the increased degree of crenulation of the septa ( $X_{\frac{1}{2}}$ ).
- u = umbilicus. si = siphuncle.

## Experiments with ammonitic septa

The flotation experiments described earlier on were made on nautilus shells, which have concave-forwards septa and the siphuncle located in the center of the septal face. In order to ascertain the possible effect on the buoyancy of an externally situated siphuncle and convex-outwards septa, nautilus shells were modified in the manner outlined below.

1. The primitive ammonite shell. — With this type of shell is meant those primitive forms with all the septa still concave forwards, but with the siphuncle in an external position (fig. 22). The septal openings of a shell of *Nautilus pompilius* were blocked (a shell sliced in two along the median plane was used) and a new set of holes drilled along the ventral margin to simulate the course of the siphuncle. It was assumed that the fragile siphuncular sheath had been damaged and water was free to enter. The external position of the siphuncle let more water into the shell, under relatively tranquil conditions, than the centrally located siphuncle of nautiloids. It was possible to bring the shell to sink by means of violent agitation. The model just sank when the equivalent of two and three quarter chambers became filled with water. The accompanying figure (fig. 22) indicates the minimum volume of water required in the air chambers, as shown by observation, to sink the shell.

A median section of *Mammites mutabilis* REYMENT (fig. 23) disclosed a disposition of coarsely crystalline calcite to fine sediment that is closely comparable to the disposition of air to water illustrated in fig. 22. In this figure the positions of the air bubbles in the chambers are those they took up when the shell came to rest, vertically, on the bottom of the experimental vessel. It seems therefore likely that the specimen of *Mammites mutabilis* sank in a similar manner and remained upright in the bottom sediment until it hardened. The coarsely crystalline calcite represents the air bubbles, that were later filled with percolating calcareous solutions and the fine sediment represents the liquid that was introduced into the air chambers contemporaneously with sinking.

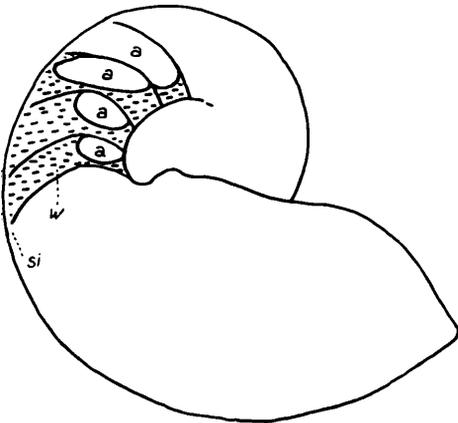


Fig. 22. Diagram illustrating the model of a "primitive" ammonite used in the experiments described in the text; si, position of the "siphuncle"; a, air bubbles; w, water. The figure shows the minimum volume of water required in the air chambers to cause the shell to sink.  $\times \frac{1}{2}$ .

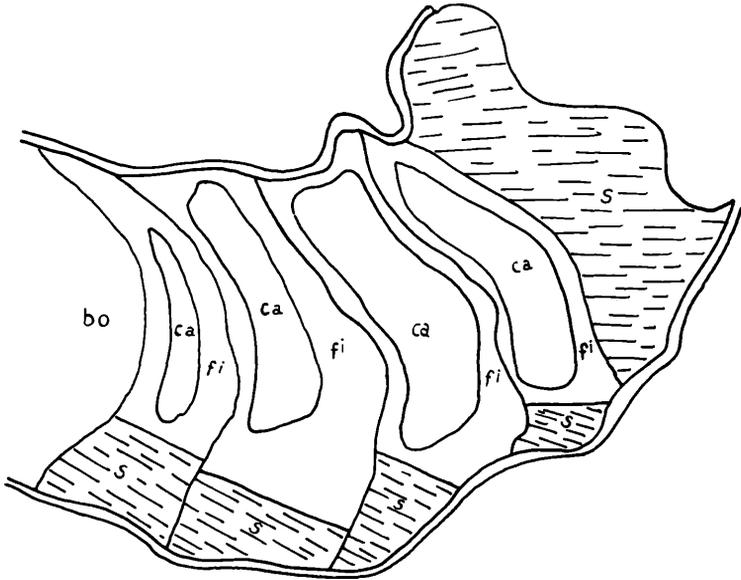


Fig. 23. *Mammites mutabilis* REYMENT. Lower Turonian, Cretaceous. Longitudinal section made 1.5 mm from the median plane; s = matter of fine-sedimentary origin; fi = fibrous calcitic cameral deposits; ca = coarsely crystalline calcitic deposits; bo = body chamber. Note the concentration of fine-grained, dark material in the lower parts of the chambers. X<sub>3</sub>.

2. The normal ammonite shell.—For the purpose of this experiment the last few chambers of a shell of *N. pompilius* were carefully removed and replaced with plastic chambers of the same thickness and density. “Siphuncular openings” were drilled through the septa, close to the ventral join. The resultant shell type was found to float somewhat higher out of the water than the same shell with convex-inwards septa and this is due to the increase in volume of the chambered part of the shell caused by the reversed orientation of the last septum. It was found that the second last chamber took in more water than the last chamber. The shell could not be sunk by agitation.

By removing every second septum and thus greatly increasing the capacity of the air chambers it was found that the shell could be more readily sunk. Therefore, coiled cephalopods with large air chambers sank quickly irrespective of other factors, owing to the considerable loss of buoyancy occasioned by water entering only a few chambers.

#### SEPTAL DENSITY

Ammonites generally have a much larger number of septa per whorl than do coiled nautiloids at comparable diameters. Furthermore, in the last whorl of almost all ammonites crowding of septa occurs. Both of these factors serve to lower the buoyancy of a shell. Irregular septal

spacing is one of the reasons why it is not possible to estimate by calculation the weight of an ammonite shell.

The table appearing below gives the total number of septa counted in some of the sectioned ammonites.

Name of species	Number of septa counted	Number of whorls	Diameter in mm	Remarks
<i>Amaltheus margaritatus</i> (DE MONTFORT) G. I. C 1019 . . . . .	102	6	115	incomplete
<i>Benuites spinosus</i> REYMENT G. I. C 1024 . . . . .	55?	6	28	»
<i>Craspedites</i> ( <i>Subcraspedites</i> ) <i>kaschpuricus</i> (TRAUTSCHOLD) G. I. C 1022 . . . . .	90?	8	42	complete
<i>Gombeoceras gongilense</i> WOODS G. I. C 1025 . . . . .	70	5	111	incomplete
<i>Harpoceras radians</i> (SCHLOTHEIM) G. I. 5327 . . . . .	50	6	70	complete
<i>Hildoceras bifrons</i> (BRUGUIÈRE) G. I. C 1020 . . . . .	60	7	105	incomplete
<i>Hoplitoides gibbosulus</i> (VON KOENEN) G. I. C 1032 . . . . .	60	6	53	»
<i>Pachyascoceras costatum</i> REYMENT G. I. C 1029 . . . . .	65	6	75	»
<i>Pachyascoceras proprium</i> REYMENT G. I. C 1026 . . . . .	50?	5	47	»
<i>Pseudoisotia</i> ( <i>Wrightoceras</i> ) <i>wallsi</i> (REYMENT) G. I. C 1033 . . . . .	90	6	75	»

All specimens listed in the above table are preserved as calcite.

#### SEPTAL SHAPE AND THICKNESS

As already indicated in a previous chapter many remarks in the literature concerning the extreme thinness of cephalopod septa are exaggerated owing to the loss of shell material during recrystallization and diagenesis of the enveloping sediment. For example, aragonitic shells of *Libyoceras afikpoense* REYMENT have a septal thickness of 0.6 mm at a diameter of 60 mm, whereas calcitic shells have a septal thickness of only 0.3 mm at the same diameter.

The ammonite species *Speetonicerias versicolor* (TRAUTSCHOLD) has a shell that in aragonitic preservation is distinguished by the robustness of not only the wall but also the septa (see REYMENT, 1956). The septa of the penultimate whorl are up to 1.8 mm thick and those of the last whorl can attain a thickness of 2.1 mm (see pl. VII).

The crenulations of the ammonite septum also serve to augment the overall weight of the shell. In *Speetonicerias versicolor* the septal complexities cause a weight increase for each septum of at least half the weight of the simple septum.

#### SHELL BUOYANCY AND THE SIPHUNCLE

Straight Paleozoic nautiloids with their broad siphuncles of stout construction behaved differently from almost all ammonites and from some

coiled nautiloids. The wider the siphuncle the lesser will be the posthumous buoyancy of the shell, after the loss of the soft parts. Nekroplanktonic nautiloid shells would also not have sunk so readily through loss of air through a damaged siphuncle. The less robust ammonite siphuncles on the other hand (and coiled nautiloids of the same type as modern species of the genus *Nautilus*) would have been readily damaged and thus have been an easy entry point for water.

Experiments showed that an externally located siphuncle, when fractured, has a tendency to let in more water than a centrally or dorsally situated siphuncle. Ammonite shells might therefore be expected to have sunk more quickly than coiled nautiloid shells.

The study of the thin sections of ammonites, already commented upon in the foregoing chapter, showed the presence of fine sediment in the body chambers of some specimens and of the same material also in chambers well inside the shell; the siphuncle was also found to be filled with this fine-grained sediment. This indicates that the material was forced in through the siphuncular sheath, which was ruptured in several places where it let in the liquid into the air chambers. Mud-filled last chambers adjacent to the body chamber usually lack the siphuncular sheath (see also the chapter on pressure, p. 160).

TRUEMAN (1920, p. 27) noted that the siphuncle was missing in the last 12 air chambers before the body chamber of *Harpoceras exaratum* and in a specimen of *Oxynoticeras oxynotum* investigated by him the entire last whorl, i. e. 25 chambers, were without the siphuncular sheath. He also observed (1920, p. 28) that the body chamber frequently contains material of muddy origin while the air chambers are filled with calcite crystals. As has been noted by the present writer those chambers in which the siphuncle is missing often are filled with sedimentary material, which seems to indicate leakage through the septal orifices. This impression was also gained by TRUEMAN. Some specimens studied by him (TRUEMAN, 1920, p. 29) suggested that the fleshy siphuncle decayed after the death of the animal and let the unsupported parts of the sheath hang or slip.

TRUEMAN (1920, p. 30) put forward two explanations for the non-existence of the siphuncular envelope in the last chambers of ammonites, neither of which do justice to his excellent observations. These theories are, that either old age was accompanied by decreased powers of phosphatic secretion, or that the lack of a siphuncle in the last chambers may have been a normal feature of growth manifested at all stages in the development of an ammonite. Sections of juvenile ammonites seem to bear out the latter hypothesis, according to TRUEMAN. The most obvious explanation of the missing siphuncular sheath was, however, overlooked, namely, damage by water action. In fact, TRUEMAN'S observations agree in all respects with the views put forward in the present paper.

## THE EFFECT OF TEMPERATURE ON SOME FLOATING SHELLS

Shells of *Nautilus pompilius* and *N. umbilicatus* were let float in warm water (about 35° C) which was allowed to cool slowly overnight (minimum temperature 14° C). It was found that *N. pompilius* had taken in a lot of water but still floated. *N. umbilicatus* was almost waterlogged and floated awash. The partly waterlogged shell of *N. umbilicatus* was again subjected to the same procedure, although this time with a smaller temperature difference. After a period of about ten minutes, during which the temperature of the water sank 3° C, the shell went to the bottom. It remained there in an upright position.

Interesting current effects were noted. After the shell had sunk, artificial currents were produced by mechanical stirring and by creating a temperature gradient. The shell, which rested almost in equilibrium in somewhat more than a meter of water, could be brought to skim rapidly over the bottom of the vessel. Once clear of the bottom the shell tended to hover and only slowly sank again. The conclusion may then be drawn that recently sunken shells are greatly at the mercy of submarine currents.

Thermal stratification in modern oceans is well known and studied. Shells sinking in a layer of one temperature would continue to sink until reaching colder water where they could remain buoyed up for a period of time until sinking to a further, and perhaps colder, stratum. Consequently, the possibilities of submarine dispersal of shells after sinking from the surface are potentially great.

Floating shells may be spread in one direction by surface water currents while semi-sunken shells of the same species may be borne in the opposite direction by reaction currents at depth. As a corollary hereto may be mentioned that the relative rarity of the shells of *N. umbilicatus* around the shores of recent beaches in relationship to those of *N. pompilius* may be due to the lesser seaworthiness of its shells and not to any real scarcity of the species. On a loose, sandy bottom the shell of *N. umbilicatus* tends to fasten owing to the presence of inscraped sand in the body chamber. Even a relatively insignificant quantity of sand was sufficient to anchor and stabilize the shell; in such cases it required quite a strong current to move the shell at all. No quantitative observations were made.

Temperature fluctuations tend thus to sink a floating shell. Warm water drives out air and cold water replaces this air when the temperature sinks. Admittedly the temperature differences used in the above experiment are probably difficult to duplicate in nature, but the overall effect of changes in temperature will be to replace successively air by water. This presupposes that the siphuncle in at least the last few chambers is damaged (see p. 156). It was found that the nautilus siphuncle is readily injured even by slight wave motion; the usually more fragile ammonite siphuncle must have been still more susceptible to injury. That this

seems to have been the case is supported by VOORTHUYSEN's (1940), SPATH's (1950), TRUEMAN's (1920) and the present writer's observations in connexion with the fact that the siphuncular sheath is frequently missing in the last chambers of ammonite shells.

### THE ROLE OF SALINITY IN POSTHUMOUS DISPERSAL

The effects of salinity and of temperature are much the same, as is indicated by the following experiment.

A shell of *Nautilus pompilius* was reduced in buoyancy so that it just sank in slightly saline water. A large glass vessel was then filled with a layer of slightly saline water at the top and water of normal average sea salinity at the bottom. The waterlogged shell was then placed in the upper layer. It sank slowly until it met the junction between the two liquids. Here it floated stably with a relatively large portion above the salinity boundary. A photograph of the experiment is reproduced in pl. III, fig. 1. The implications of this experiment are illuminated by the following discussion.

The Baltic Sea today is a sea with very low salinity and has a fauna atypical of a modern marine environment. Modern cephalopods are unable to live in its waters owing to the deficient salt content (cf. EKMAN, 1953, p. 119). It is conceivable that similar seas may have existed in the past and that cephalopod shells may have been swept into them by currents. In the case of the Baltic Sea the currents flow through Öresund so that the lighter, less saline water streams from the Baltic Sea towards the North Sea and heavier, more salt, North Sea water flows into the Baltic Sea underneath this layer. It is, however, hindered to a considerable degree by submarine ridges running across the sound, which leads to the development of large scale, slowly rotating swirls and the deposition of stagnation sediment. Such conditions during the Mesozoic could have led to cephalopod shells occurring together with brackish water faunas in a rock sequence not of typical marine origin. Some shells would also sink in the swirls and become entombed in stagnation sediment. EKMAN (1953, p. 105) noted that the salinity boundaries in Öresund are quite sharp.

Obviously only a relative few cephalopod shells could enter such a body of water as the Baltic Sea under the conditions outlined above, namely, those sufficiently waterlogged to sink on meeting the less dense fresh water, but still sufficiently buoyant to float in the saline medium; i. e. they could be borne in along the salinity boundary. As a consequence hereof the scattered occurrence of cephalopod shells in a formation or sequence of sediments ought to be treated with caution, as they need not necessarily be a definite criterion of a normal marine sedimentary environment.

## THE INFLUENCE OF PRESSURE ON CEPHALOPOD SHELLS

If it be assumed that all shelled cephalopods in life inhabited near-coastal waters and lived at no very great depth then the effect of pressure on the dead shell may be considered to have had little real significance. If it be assumed, however, that some cephalopods also inhabited greater depths then the effects of pressure can have been important. ARKELL (1957, p. 120) pointed out that the pressure exerted by sea water amounts to about one ton to the square inch at 1,800 meters, so that at even half this depth the shells of fossil cephalopods would have been crushed, this observation being based on the small and probably strong shell of *Spirula spirula*. ARKELL suggested that the elaboration of the sutural pattern could possibly aid in withstanding the effects of pressure.

The possibility remains for such species as may have inhabited considerable depths that on the death of the animal water would eventually have been forced under pressure past the muscular contacts of the decomposing animal with the wall of the shell and into the air chambers by, in the first place, destroying the thin and fragile siphuncular tube; examination of fossil shells shows evidence in support of this postulation.

## EVIDENCE IN FOSSIL SHELLS OF THE EFFECTS OF PRESSURE

Thin sections of ammonites cut in the median plane often disclose that the siphuncular sheath may be missing not only in the last few chambers before the body chamber, but also in the first chambers after the proloculus and even in various intermediary chambers. As has been indicated in the foregoing, the siphuncular sheath in the air chambers nearest the body chamber may be damaged by wave action during floating, but this does not explain ruptures in the tube in the inner whorls; it seems probable that these have been caused by water forced in through the siphuncular tube under pressure. Where the tube was not able to withstand the pressure it has been broken and the air chamber at this site filled with fluid. Amongst the examples observed by the writer in the study of the thin median sections the following may be mentioned.

The siphuncle of a specimen of *Gombeoceras gongilense* (WOODS) (fig. 24) was observed to be missing in those chambers that were found to contain fine-grained, brownish sediment, but to be present in those with linings of fibrous calcite and kernels of coarsely crystalline calcite. All the chambers of the first two and a half whorls contain the brownish sediment and the siphuncular tube, throughout its entire preserved length, is filled with the same substance. It would seem that the fine-grained material gained access to the air chambers in the manner outlined above, namely, by bursting through the thin siphuncular wall at various places. This implies that the shell was under water and at a depth sufficient to cause

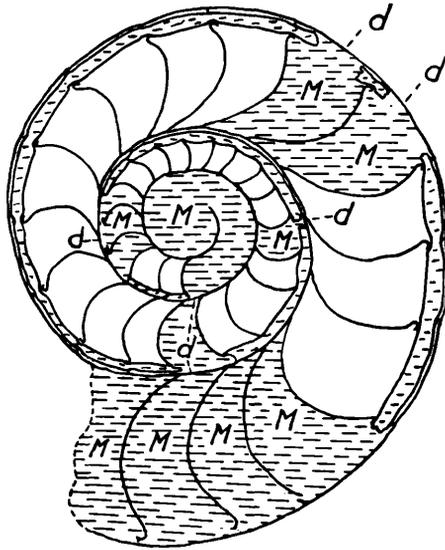


Fig. 24. *Gombeoceras gongilense* (WOODS). Lower Turonian, Cretaceous. Median section showing chambers and siphuncular tube filled with fine-grained sediment (M) and damage to the siphuncular sheath (d). The siphuncle contains sediment throughout its entire preserved length. The delicate septal necks are uninjured. G. I. C 1025 ( $\times\frac{1}{4}$ ).

a pressure great enough to rupture the siphuncle. The crystalline calcareous material was introduced into the unfilled air chambers at a later date by solutions percolating through the containing sediment. Some of these cameral fillings remind of crystal growths in vugs and have formed very slowly.

A specimen of *Libyoceras afikpoense* REYMENT, G. I. C 1035, was observed to have the body chamber and chambers of the last whorl filled with fine-grained material which may have been forced in under pressure. The inner whorls are mainly filled with crystalline calcite.

Similar observations were made for some other species studied in thin median section among which may be mentioned *Amaltheus margaritatus* (DE MONTFORT) and *Craspedites (Subcraspedites) kaschpuricus* (TRAUTSCHOLD).

## THE DISTRIBUTION OF APTYCHI

The problem of the distribution of aptychi is one that has often been discussed in geological literature, but hitherto no really universally satisfactory explanation seems to have been devised (cf. SCOTT, 1940, p. 300). The present investigation favors the following explanation. The aptychi fell here and there to the sea floor from drifting, decomposing ammonite carcasses. Consequently, the majority of ammonite shells are found without aptychi and usually far from sediments containing them. Those few cases

in which aptychi are found in the body chambers of ammonites may represent burial in quiet conditions, wherever they may have occurred. The presence of the aptychus in intimate association with the shell is good evidence that reworking did not occur after the entombment of the ammonite, at least during the lithification of the sediment.

Opinions on the subject in hand have been expressed by WAAGEN (1870), NEUMAYR (1875), TRAUTH (1930), WESTERMANN (1954) and ARKELL et al. (1957).

WAAGEN (1870, p. 192) noted that in the München Museum there were, at the time of his writing, about 100 specimens of ammonites with aptychi. Five of these have the aptychus at the end of the body chamber and all the others have it inside the body chamber. MILLER, FURNISH, & SCHINDEWOLF (1957, p. 14) gave an explanation for aptychus concentrations based on the supposed greater resistibility of the substance in aptychi over that of ammonite shells; this seems to be a less likely interpretation than that offered by the writer above. A second explanation given by these authors (1957, p. 22) in the same work agrees, however, generally with the ideas of the present writer.

Aptychi may occur in considerable concentrations, which fact reflects the possibility of water transport of them. TRUSHEIM (1931, p. 159) examined bottom samples from Blaue Balje in the wadden between Wangeroog and Minsener Oldoog; he found that almost no other material of organic origin occurred in the sediment than the calcareous opercula of the snail *Bithynia tentaculata*. His observations led him to conclude that the gastropod shells were concentrated at one place and the opercula at another by mechanical sorting. This idea can also be successfully applied to non-buoyant ammonite shells and aptychi; to a certain extent it is also applicable to buoyant ammonite shells trapped in very shallow water where they were not free of the sediment and were subjected to strong water action. As already noted in a previous chapter FREBOLD (1928, p. 25) has pointed out the possibility of the concentration of shells of the same shape by water action and the late Prof. G. SÄVE-SÖDERBERG has called attention to the fact that vertebrate bones of the same shape may occur concentrated together (communicated by Prof. I. HESSLAND).

## THE DISTRIBUTION OF CEPHALOPOD JAWS

The jaws of Recent species of the genus *Nautilus* are calcified and particularly the upper one may fossilize, although these appear to be rarer than the shells (STENZEL, 1952, p. 3). Just as aptychi fell from drifting ammonite carcasses cephalopod jaws also fell from the dead animals. This would give them a distribution quite different from that of the shells. The distribution of sharks' teeth on the ocean floor at the present day offers support to the above interpretations (see EKMAN, 1953, p. 273).

## APPLICATION OF RESULTS

## DISCUSSION OF SELECTED FIELD OCCURRENCES

In the following the results achieved in the experimental work are applied to a few selected field occurrences in Nigeria and Sweden of which the writer has first-hand experience.

a. The Hålsingborg area, southern Sweden. — The main ammonite occurrence in this area is in a calcareous clay of shore character where Lower Liassic species are fairly frequently found.

However, at Hittarp, in a sequence with the hallmarks of a terrestrial origin, a coarse, gravelly sandstone that contains abundant plant remains has yielded a single, well preserved arietitid. This rock is probably of back-beach origin. The drifting ammonite shell could have been cast far inland by a storm.

Observations of this kind are to be made in the backshore marsh environment of wadden coasts where purely marine animal remains occur in the marsh sediment, whence they have been cast up by storms.

b. The Makurdi area, central Nigeria. — The Lower Turonian ammonite fauna of Makurdi is composed of forms that, as far as can be judged from their shell shapes, sank after the death of the animals.

The fauna consists of species of *Hoplitoides* (highly compressed to moderately compressed), *Benueites* (compressed), *Kamerunoceras* [strongly ornamented (solid elements), evolute], *Mammites* (very coarsely ornamented with semi-solid elements).

The fossils occur in a dark, pure limestone about 3 m in thickness and are associated with pectinid pelecypods such as *Lima* (*Plagiostoma*) *pseudoboernesii* RIEDEL, *Camptonectes*, isognomonids, plicatulids and ostreids. All the forms belong to the type here considered to have sunk post-humously, except possibly the *Mammites*. Examination of thin median sections of this species and also *Benueites* indicates, however, extensive damage to the siphuncle as well as the presence of considerable quantities of fine-grained sedimentary matter in the chambers, suggesting water damage. The body chamber of *M. mutabilis* is at least two thirds of a whorl in length and that of the species of *Benueites* at least one whorl in length.

c. The Afikpo area, southeastern Nigeria. — A thin bed of limestone has yielded a very rich fauna of gastropods and pelecypods as well as specimens of *Libyoceras afikpoense* REYMENT in great abundance. Less common are specimens of a highly compressed species of *Sphenodiscus*. It is suggested that the occurrence represents in situ deposition of sunken shells. The body chamber of *L. afikpoense* takes up at least two thirds of a whorl and the shell wall is relatively thick, particularly on the body chamber. Elsewhere in the Afikpo area *L. afikpoense* is common in black shales in aragonitic preservation. The frequency of

color traces on the shells of specimens of this species in this preservation gives further weight to the interpretation favoring rapid interment of the shells. The color is confined to the outer layers of the shell (REYMENT, 1957); if the shells had lain for any considerable period exposed on a beach to weathering then the coloring would have been lost (REYMENT, 1957). The numerous, thick septa of *Libycoceras* would also assist in weighting down the shell.

#### RECONSTRUCTION OF THE ENVIRONMENT OF DEPOSITION OF THE HOST SEDIMENT

Attempts have been made in the past to employ the ammonite shell as an indicator of environment (see, for example, SCOTT, 1940), but as the factors behind the distribution of chambered shells were not well understood the results have, for the most part, been poor, so much so in fact that the ammonite shell as an environmental indicator has fallen into ill repute (cf. REYMENT, 1955 b).

It is hoped that the study presented here will offer some possibility of permitting the use of fossil cephalopods in studies on past environments and it is thought that further work along the present lines ought to place them in the forefront of paleogeographic indicators.

In general, then, it may be stated that an abundant association of inflated cephalopod shells of one or a number of species occurring together in a formation could indicate an ancient strandline. The occurrence of compressed shells solely in a bed suggests conditions of deposition away from the shore. The same remark also applies to very depressed shells. Mixtures of floater and sinker shells occur often in the geologic record. Such mixtures could have been brought about where the ammonites inhabited a confined, partly cut off shallow body of water; there was little possibility for empty shells to drift away from the inhabited area and thus to become differentiated from the sinkers.

Another possibility concerns entombment in strand sediment. When both compressed and inflated forms lived in the immediate shore zone, at least during part of the year, both types would have been thrown up by the waves.

Dr. C. TEICHERT in a personal communication dated 14.3.56 has kindly drawn the author's attention to an association of *Beloceras* and *Manticoceras* in the Devonian of northwestern Australia that fits in with the above.

According to WESTERMANN (1954, p. 36) HOFFMANN reports that in the German Lower Lias the round-mouthed, coarsely-ribbed *Echioceras* (*Gogaticeras*) is bound to coastal areas while the flat, smooth-shelled *Oxy-noticeras* is found in the middle part of the basin. This is here interpreted as showing that the first-named type drifted ashore nekroplanktonically while the second ammonite sank to the bottom immediately after death.

The migratory habits shown by modern dibranchiates, if applicable to tetrabranchiates, would also constitute an important distributional factor (cf. p. 106).

#### FOSSILIZATION POSSIBILITIES OF NEKROPLANKTONIC SHELLS

The question still remains to be answered that if certain cephalopod shells drifted posthumously how did so many become interred and fossilized. It could be expected that highly compressed and depressed forms should be poorly distributed and inflated shells widely spread. In the following section an attempt is made to supply an answer to some of the problems connected herewith.

#### The wadden (tidal flat) environment

In this section the tidal environment as typified by the North Sea waddens is taken into consideration. The conclusions are also generally applicable to shells stranding on non-tidal beaches.

*Wattenschlick*, a sort of mud formed in the intertidal zone, consists mainly of soft, slimy sediment, but in places contains admixed sand. The muddy material is deposited near to the highwater line generally and the sandier material nearer to the low-water line. There is also a sand boundary with the strandside. By far the greatest wattenschlick concentrations occur around the sites of emptying of terrestrial watercourses. Up to three meters of sediment may be deposited annually (HÄNTZSCHEL, 1939, p. 195). Therefore, ammonite shells stranding in a tideland would, under favorable circumstances, have become entombed in argillaceous sediment (pl. VI, figs. 5, 6). This may partly explain the comparative rarity of cephalopod shells in sandy sediment. It is of interest to observe that some varieties of wattenschlick are particularly soft and black and contain much water; solid objects have been shown to sink readily in it and stranded shells have consequently a reasonable chance of becoming preserved in such sediment. *Wattenschlick* is, however, a name that covers a large variety of tidal muds and the present writer has seen sediments of this class that would be less favorable for the preservation of shells.

Tidal flats are usually flanked by marshes. When the marshes are flooded much of the sediment being carried by the water is dropped which results in a laminated deposit relatively rich in clay. Marshes may pass gradually into the adjacent wadden flats but more often are cut off by low cliffs. When the surface of the tidal flat has been raised sufficiently for marsh plants to begin to grow the rate of vertical increase may rise, owing to the effective trapping capabilities of the plants for sediment. This condition would seem to offer greater chances of preservation, under favorable circumstances, to indrifted cephalopod shells than those given by merely stranding at the highwater line.

HAAS (1949) in Wyoming and the present author in Nigeria and Skåne, Sweden, have observed ammonites together with much plant material and this may indicate burial in the marsh environment of shells carried over at high tide during a storm. Consequently, the presence of cephalopod shells in a sediment does not offer indisputable evidence of the purely marine character of the rock as marshes clearly constitute a transitional environment. In the Stonesfield shale, England, ammonites occur together with terrestrial fossils (ARKELL, 1952, p. 16).

SCHÄFER (1956, p. 234) made the important point that complete vertebrate skeletons are found embedded in the wadden sediment but do not occur in open-sea sediment. In the land-distant sea the carcass will first sink but the putrefactive gases bring it up to the surface again and, if it does not have the opportunity of drifting ashore, the skeleton will be strewn in pieces over the ocean floor. The only chance for a complete skeleton to be preserved in the sediment of the sea floor is when the recently dead carcass sinks into poorly aerated water. These observations are directly applicable to ammonites inasmuch as if an ammonite dying on the high sea sank into poorly aerated water it would have a chance of being preserved in the sediment, even if the shell could float when empty.

Ammonite fragments, particularly concentrations of isolated body chambers, are sometimes common, as in the Upper Albian of Abakaliki, eastern Nigeria. These accumulations are a type of *schill* (shell concentrations in wadden sediment) and where such occur, it may be taken that the sediment was formed in shallow, turbulent water.

Tideland shell beds may consist of a single species, as already noted in connexion with the subject of concentration by wave action. VAN STRAATEN (1954, p. 21) noted that shell accumulations occurring in large channels tend to contain more diversified assemblages than those in small channels.

A word on the importance of bacteria in this environment is also in place. The pronounced effects of bacterial activity in the wadden area (VAN STRAATEN, 1954, p. 34) may explain why impressions of the soft parts of ammonites, even with the aptychus more or less in situ, are not found. VAN STRAATEN's investigations have brought to light the fact that the disintegration of the remains of larger animals is only in a slight degree ascribable to chemical influences and the effects of wave action and is in the main due to scavengers and bacterial decomposition.

### Preservation in carbonate rocks

Most fossil cephalopods are found in limestones and marls. If the majority of cephalopod shells drifted posthumously and finally stranded on beaches it may well be asked how could cephalopods so frequently become preserved in calcareous sediment. It is now proposed to examine several possibilities.

Part of the Great Bahama Bank offers an example of a large scale calcareous deposit at present under formation (NEWELL & RIGBY, 1957). This deposit is almost 100,000 square kilometers in extent. The abundant marginal reefs, shoals and cays of this area would provide excellent stranding places for drifting cephalopod shells. Intertidal lime-mud flats also occur; the mud consists of aragonitic ooze, an ideal substance for the ensnaring of stranding shells.

In the collection of ammonites studied it was found that a number of the fossils from northeastern Nigeria contain oolitic calcareous material mixed with finer-grained, calcareous, muddy sediment in their body chambers as well as in several of the air chambers. NEWELL & RIGBY (1957, p. 53) observed that oolitic sand is an important sediment in the marginal areas of the Bahamian platforms. NEWELL & RIGBY pointed out that the oolites form in agitated water. The Nigerian occurrence might therefore suggest that the shells were swept into quiet water together with already formed oolite material where they both were embedded in calcareous mud.

Another possibility is offered by the calcareous sediment known as *beachrock*. Outcrops of beachrock occur along the barrier islands west of the Florida coast and at shallow depths offshore in the area (GOULD & STEWART, 1955). Most exposures are situated a slight distance from the shore, ranging from low tide to a depth of about 4 m (1955, p. 7). The beachrock varies in color from mottled black and grey to white and consists often of broken shell fragments cemented firmly with calcium carbonate (aragonite). Locally, beachrock may contain well rounded phosphorite pebbles, bone fragments and quartz grains. The formation of this rock is confined to the intertidal zone (GINSBURG, 1953) and offers a good chance for the rapid entombment of cephalopod shells. There does not seem to be any reason to assume that beachrock did not form in past ages, in fact, it seems to have been common (cf. GOULD & STEWART, 1955). Beachrock is most commonly found along beaches that are normally protected but which receive storm wave action. The outbuilding of such beaches during storms will produce a deposit that is not disturbed by normal wave action (GINSBURG, 1953).

Cephalopod shells are often found in conjunction with reef limestones (for example, Silurian of Gotland; Devonian of northwestern Australia) and it has often been assumed that the animals in life had their habitat in the immediate neighborhood of the reef (cf. JUX, 1957, p. 61). In a personal communication dated August 12th, 1957, Dr. J. S. HYND of the Fisheries Laboratory, Thursday Island, Australia, kindly informed me that while *Nautilus* shells are common around the Barrier Reef islands living specimens are exceedingly rare in the area. Furthermore, argonaut shells are exceptionally rare. Dr. HYND has never seen a living *Nautilus* during his 9 years in Barrier Reef waters and only half a dozen argonaut shells. This suggests to the present writer that modern shelled cephalopods,

at least, live outside of the immediate reef environment but their shells drift and become trapped there posthumously. That argonaut shells are so scarce would seem to be a reflection of the fact that they readily sink, being unchambered (cf. p. 115).

Dredging operations reported on by GOULD & STEWART (1955, p. 8) indicate that in continental terrace sediments the most commonly collected limestone varieties are soft, marly limestone, sandy limestone, dense, fine-grained limestone, and phosphatic conglomeratic limestone and that these were obtained only from the inner part of the terrace, which ranges in depth from 4 m to 55 m. These workers concluded that the sea floor shoreward of the 55 m contour is made up largely of limestone.

ROTHPLETZ (1909, p. 311) interpreted the Solnhofen beds in Germany as being near-shore deposits. Here ammonites and ammonite impressions occur in the limestone variety, *plattenkalk*, which would agree with the most modern studies on the deposition of calcareous mud in wadden flats. ROTHPLETZ' paper has already been discussed in a foregoing chapter and needs no further comment here apart from the observation recorded that the ventral impressions of ammonites occur in such a manner as to indicate that the shell touched down gently on the calcareous mud while the tide was ebbing and was held fast by its slimy consistence; it then gradually fell over onto its side (cf. pp. 142, 143, figs. 16, 17, this paper; also pls. V, VI). The presence of aptychi in some shells also suggests that at least some of the ammonites were embedded with their soft parts at least partly in the shell and that there was no reworking of the sediment.

#### THE OCCURRENCE OF AMMONITES IN CONCRETIONS

Ammonites are sometimes found in concretions. By analyzing these occurrences it should be possible to arrive at a conception of what happened to the ammonite shell in these cases after the death of the animal.

WEEKS (1957) discussed the origin of carbonate concretions in certain shales of Colombia. Most of these concretions consist of calcium carbonate, some are argillaceous and some are siliceous. Ammonites are the commonest forms occurring in the concretions, which also often contain droplets of oil.

In this connexion may be mentioned that when the present writer was describing a collection of ammonites from the Coniacian of Colombia (REYMENT, 1958) recently he came across a specimen of *Forresteria* that contained much live oil. Most of the other ammonites in the collection are oil-stained (BARRINGTON-BROWN collection, Sedgwick Museum, Cambridge). The *Forresteria* shell was probably a sinker and a likely explanation of the oil droplets in this and the specimens referred to by WEEKS is that it is derived from the rotting carcasses of the ammonite animals that were entombed in stagnation sediment in which complete putrefaction of the soft parts could not take place.

According to WEEKS the carbonate concretions are usually associated with "stagnant water shale", marl, or argillaceous limestone facies. Inasmuch as the surrounding shale layers follow the contours of the concretions WEEKS thinks that the concretions were formed soon after deposition of the organic kernel. As the fish bodies occurring have not been flattened, early lithification would seem to have taken place with the building of the surrounding carbonate concretion before advanced decomposition or compression of the carcass could occur. The environment seems to have been deficient in oxygen with an accumulation of carbon dioxide with a pH too low to permit carbonate precipitation. The alkalinity caused by the decaying animal matter was sufficient to raise the pH enough to precipitate carbonate and then to form the concretions.

Similar types of concretions have been collected by the present writer in the Eha Amufu area of Eastern Nigeria where the Maestrichtian species *Libycoceras afikpoense* REYMENT occurs widely in an excellent state of preservation. Gastropods also occur in the same type of preservation. In the Abakaliki area of southeastern Nigeria numerous mortoniceratids have been found in similar conditions. The Eha Amufu area is without doubt of near-shore (but not strandline) origin and the Abakaliki area does not either seem to have been of more than shallow-water origin.

Thanks to the kindness of Mr. L. G. WEEKS further information was forthcoming on the nature of the Colombian ammonite occurrences (letter dated April 23rd, 1957 and letter from J. NUGENT, Standard Oil Co., dated April 3rd, 1957). The genera listed range throughout the Cretaceous from Aptian, or somewhat older, up to Turonian. The strongly compressed or depressed types are *Fagesia*, *Neolobites*, the remaining genera listed are all of the buoyant variety. Without having had an opportunity of examining the ammonites in question it is not possible to be sure of the accuracy of the generic determinations, but outgoing from the cited list it would seem that the assemblages mainly indicate shell types that may be reasonably expected to have been floaters. If, however, WEEKS' explanation of the formation of the concretions be correct then the dead fish and ammonites must have fallen directly into such an anaerobic environment as envisaged by SCHÄFER (1956) and accordingly did not putrefy. This would also explain the presence of inflated nautilus shells in offshore sediment, particularly as the forming concretions would tend to hold down the shell.

To the present writer there seems to be a considerable likelihood that the concretions formed in quite shallow water. Great depth is no criterion of anaerobic conditions; the Mindanao Trough is known to be well aerated at the bottom (8,000 meters depth).

APPLICATION OF CEPHALOPOD SHELLS TO THE STUDY OF ANCIENT  
COASTLINES AND CURRENTS

Once the buoyancy of a cephalopod shell has been established it should be possible to employ it for certain paleogeographical problems, particularly if forms of the same shape category occur together in large numbers.

## Paleoflumenology

The first definite concept of the possibility of using fossil cephalopod shells for tracing oceanic currents of the past was put forward by KOBAYASHI (1954). Study of Nigerian Cretaceous cephalopods has indicated to the present author that future work along the lines used by KOBAYASHI in connection with the widely spread species *Cirroceras hornbyense* (WHITEAVES), *Turrilites scheuchzerianus* BOSCH and *T. costatus* LAMARCK, for example, might lead to a positive result. It should at least prove possible to establish the trends of the main oceanic currents during a particular period of time. As a corollary hereto may be added the possibility of using cephalopod shells as an auxiliary in working out the disposition of the principal land masses during such periods.

KOBAYASHI has further pointed out (1954, p. 46) that floating shells have widely different travel times from each other. A floating shell being borne by an ocean current has its track complicated by counter currents, tidal influences and winds. The present author's experiments with nautilus shells indicate that the wind factor may often be of greater importance than weak sea currents, though its effect is usually limited to relatively short periods of time. The course of a floating body indicates, however, the trend of the principal prevailing current. The problem is nevertheless complicated. HESSLAND (1945, p. 34) calculated the time taken for objects to be carried by the Gulf Stream to Europe in connexion with his study of the distribution of *Mya arenaria*.

As EKMAN (1953, p. 318) so ably indicated, the faculty of floating which planktonic organisms and nekroplankton possess includes the possibility of unhindered transport. Some of the most important barriers for shelf animals, the open spaces of the oceans, thus, for example, in the case of floating cephalopod shells, are without effect. As all oceans are connected by ocean currents a barrier of land masses need not necessarily obstruct dispersal.

There is the possibility that certain of the shelled cephalopods in life may have been restricted by oceanic barriers, but after death the empty shells were transported over these barriers. Consequently the posthumous distribution of such species is far greater than that of the living.

## SUMMARY OF CONCLUSIONS

1. The subject of fossil cephalopod distribution has only been touched on casually by most previous authors concerned with the question. Papers by ROTHPLETZ (1909) on the Solnhofen ammonites, WALTHER (1897) and SCUPIN (1912) on theoretical discussions of the distribution of cephalopod shells, TALAVARO & FAUSTINO (1931) on living *Nautilus*, TEICHERT (1933) on actinoceroid cephalopods, TRUEMAN (1940) on attempts at calculating the buoyancy of ammonite shells, TINBERGEN's & VERWEY's studies of the migratory habits of recent dibranchiates, and KOBAYASHI's work on nekroplanktonic dispersal supply valuable information.

2. The present investigation shows that important factors in the buoyancy of a chambered cephalopod shell are. —

- a. The shape of the shell and the thickness of the shell material.
- b. The form of the body chamber; this is the most important single factor and it also decides the mode of settling of a stranding shell.
- c. The number of septa in the shell and their shape.
- d. The dimensions of the siphuncle.
- e. The effects of temperature, salinity and water pressure.

3. Plastic models of some common types of cephalopod shells were used for simple buoyancy experiments. The specific gravity chosen for the plastic material was 2.63, which was found to be that of the shell material in living *Nautilus* shells; the presence of organic matter of low specific gravity causes the low density (S. G. of pure aragonite = 2.93). A Lower Neocomian ammonite had a specific gravity of the shell of 2.82.

4. Endoceroid shells float with the siphuncle beneath. The body chamber of this type of shell cannot exceed a quarter of the length of the chambered part if the empty shell is to float. With a body chamber of almost maximum length the shell floats at an angle of about 45°. Therefore with a body chamber of maximum length such a shell sinks at an angle to the horizontal. With a very short body chamber (about 8 % of the chambered length) the shell floats with the oral end higher than the tip, which is then under water. The smaller the siphuncle the greater is the amount of cameral deposits that could be tolerated by an empty buoyant shell.

5. For an orthoceroid shell (narrow siphuncle; width in experimental model = 2.5 mm) to remain afloat the body chamber must be less than half the total length of the shell. With a body chamber of almost maximum size the shell floats in a vertical position. Reduction in the length of the body chamber leads to a floating position where the shell floats horizontally and finally a position with the tip lower than the oral end of the shell. Evidence supplied by field occurrences in support of the laboratory investigations is discussed.

6. Lituroid shells floated at an angle to the vertical; baculitoid shells

with their narrow siphuncles, relatively short body chambers in some species, but voluminous air chambers floated almost horizontally. The fragile structure of the baculitid siphuncle constituted, however, a weak point and when damaged would have permitted water to enter. Many scaphitoid and hamitoid shells may have sunk; these types of shells usually have large body chambers. Turrilitoid shells may have occupied an intermediate position.

7. *Nautilus pompilius* and *N. umbilicatus* were used for experimental observations on the buoyancy of coiled shells. By modifying the degree of inflation of the shell of *N. pompilius* by slicing away the flanks and rebuilding them with plastic material it was possible to study the effect of variations in compression on buoyancy. Quite a number of compressed and very depressed ammonite shells seem to fall into the category of posthumous sinkers. The degree of evolution was determined to have a direct bearing on the buoyancy of a shell. Highly involute shells were found to be more seaworthy than evolute shells. In compressed and very depressed shells the relationship between the volume of air in the chambers and the weight of the shell material is not constant as the loss of weight brought about by the reduction of the surface area of the septa does not offset the loss of buoyancy caused by reduction in the air volume. Minima will be encountered in both directions, towards increasing depressedness and increasing compressedness, where the shell is no longer buoyant. A decrease in shell inflation below a certain degree in a shell with a body chamber of two fifths of a whorl was found by experiment to cause it to sink; it stood, however, upright on the bottom of the containing vessel.

8. The body chamber is one of the principal buoyancy factors. Experiment shows that a nautilus shell with a body chamber occupying two thirds of the last whorl will not float (ammonite body chambers frequently exceed three quarters of a whorl). Apertural structures (ears, lappets) where present have an adverse effect on the buoyancy.

9. Holes develop at sites of imperfect shell secretion in the shell wall of *Nautilus* specimens if they are left exposed to the effects of water for longer periods. The colors on the submersed part of the shell fade. The preservation of the aragonite shell of cephalopods, as well as the coloring, is favored by an argillaceous, lime-free medium. A calcium-carbonate-rich medium is unfavorable.

10. Thin section studies show some shells to have solid ornament; the majority have hollow sculpture with thickened crests. Experiments prove that solid and thick ornament diminishes buoyancy and hollow ornament aids uplift. Strongly ornamented, tuberculated shells and moderately strongly tuberculated shells with partially solid elements will not float. Aragonite shells usually have thicker shell material than the same species in calcitic preservation, owing to loss of calcium carbonate by solution.

11. Evolute shells take up a stable settling position in deeper water than involute shells; this is important in connexion with the preservation possibilities of these shell types.

12. Ammonite shells usually have a greater number of septa and whorls than coiled nautiloids. In ammonites the septa are frequently placed irregularly at mathematically unpredictable intervals from each other. This constitutes one of the serious difficulties met with in attempts at deriving a workable formula for expressing the weight of a shell. Complicated septal folding is an important factor in the weight of a shell. The conventional idea of uniformly convex-outwards ammonite septa does not always apply. Many ammonites have a convex-outwards median ridge with concave-outwards zones on either side. More complicated patterns of concave-outwards zones occur commonly. The distribution of water in the chambers of upright, sunken shells used in the experiments shows a striking similarity with the relationship between fine sediment and crystalline calcite in the air chambers nearest the body chamber of some coiled, fossil cephalopods. The fine-sedimentary material represents the watery substance that was injected into the air chambers under pressure and the crystalline calcite the later fillings of the remaining air spaces. Coiled cephalopods with large air chambers (and therefore few septa) sank more quickly than forms of the same size but with more chambers per whorl, owing to the loss of buoyancy caused when only a few chambers became waterfilled.

13. Experiments show that externally located, damaged siphuncles let in water rather more readily than centrally situated, damaged siphuncles. The thickness of the siphuncle in uncoiled and straight nautiloids is the most important feature as it was not readily fractured and thus effectively corked the chambers. The ammonite siphuncle was fragile and readily ruptured by water action. The study of thin median sections shows the siphuncle frequently to be missing or damaged, not only in the last whorl, but also in inner whorls. A damaged siphuncle let sedimentary material into those chambers in which rupturing had occurred.

14. The buoyancy of cephalopod shells is very susceptible to the temperature factor; temperature fluctuations tend to sink a floating shell as warm water expels air and cold water replaces the lost air when the temperature sinks. Recently sunken shells are readily transported by submarine currents. Experiments show the salinity factor to be important. The submarine dispersal of recently sunken shells is thought to be an important distributional medium. An almost waterlogged shell drifting inshore into an estuarine environment, or any place where the relative density of the seawater is lowered, would have sunk. A shell that will no longer float at the surface can be dispersed at depth by floating on a salinity boundary if it encounters saltier water. Drifting cephalopod shells could invade a non-marine environment, or environment such as the Baltic Sea and in particular the Gulf of Bothnia, where conditions of salinity today are such as to prohibit the existence of cephalopods. Therefore, cephalopod shells in a sediment need not definitely be taken as proof of an exclusively marine origin.

15. The commonly found condition in fossil cephalopod shells in which the siphuncular sheath is missing in some air chambers is believed in some cases to be due to the effect of waves (only damaged in the chambers nearest the body chamber) and in others to be ascribable to the effect of water pressure at depth (damaged well inside the shell). The nature of the fine sediment found inside these chambers suggests that injection often took place in bottom lutitic sediments.

16. The different distribution of ammonite shells and aptychi is thought to be due to the latter having fallen from drifting carcasses. Such aptychi indicate conditions of deposition for the enclosing sediment away from the strandline. Where aptychi occur in concentrations mechanical sorting in a tidal flat or other coastal environment is to be suspected. Those cases in which aptychi are found in intimate association with the shell may be taken to indicate quiet conditions of sedimentation and immediate burial for buoyant shells and perhaps sedimentation in deeper water for non-buoyant shells.

17. Review of some field occurrences of which the writer has first-hand knowledge indicates good possibilities of the application of the theoretical results of the investigation.

18. According to the experimental results obtained, most floaters were deposited in the strand zone and therefore occur in sediment of near-shore origin. This agrees well with the fossil occurrences. Analysis of cephalopod assemblages should facilitate the determination of environments of sedimentation.

19. The potential use of cephalopod shells in assisting the solution of paleogeographic problems, such as directions of principal ocean currents, disposition of main landmasses, delineation of ancient shorelines, would seem to be great.

20. Apart from the considerations presented in the foregoing pages there is still a factor that ought not to be overlooked. Many cephalopods must have been killed for food; as a result some of the shells would have been damaged and have sunk at the site of the disaster. In such cases floaters could have been preserved away from the immediate strand zone.

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Received Nov. 28, 1957

## PLATES

## EXPLANATION OF THE PLATES

Unless otherwise stated all the photographs were taken by L. KUTNAR of the Geological Department. None of the pictures has been retouched.

### PLATE I

- Fig. 1. Plastic model of an endoceroid type of shell used in the experiments ( $\times 1/4$ ) (photograph by the author).
- Fig. 2. Plastic model of the type of straight nautiloid shell typified by a narrow siphuncle ( $\times 1/6$ ) (photograph by the author).
- Fig. 3. Orientation of nautiloid shells in Lower Ordovician limestone at Sätatorp, Västergötland, Sweden. The photograph is taken from above. Observe that all the tips point in roughly the same direction.
- Fig. 4. Two transversely sectioned nautiloid shells exposed in the wall of the limestone quarry at Sätatorp, Västergötland, Sweden. The right hand specimen has the siphuncle netherly located, the left hand one has the siphuncle situated to the right of the bottom position ( $\times 1/2$ ).
- Fig. 5. Netherside of a stromatoporoid from the Hemse formation (Silurian) of Gotland, Sweden showing the innerside of the strongly ornamented body chamber of a curved nautiloid forming the "foundation" ( $\times 1/4$ ) (photograph by the author).
- Fig. 6, a—b. Specimen of *Craspedites* showing the presence of a belemnite in the body chamber. Neocomian, Polivna, U. S. S. R. ( $\times 2/3$ ).
- Fig. 7. *Placenticas whitfieldi* HYATT showing the nature of the septal face with the interplay of concave-forwards and convex-forwards septal orientation. Maestrichtian, Fort Pierre group, Alberta, Canada; aragonitic preservation ( $\times 2/3$ ).

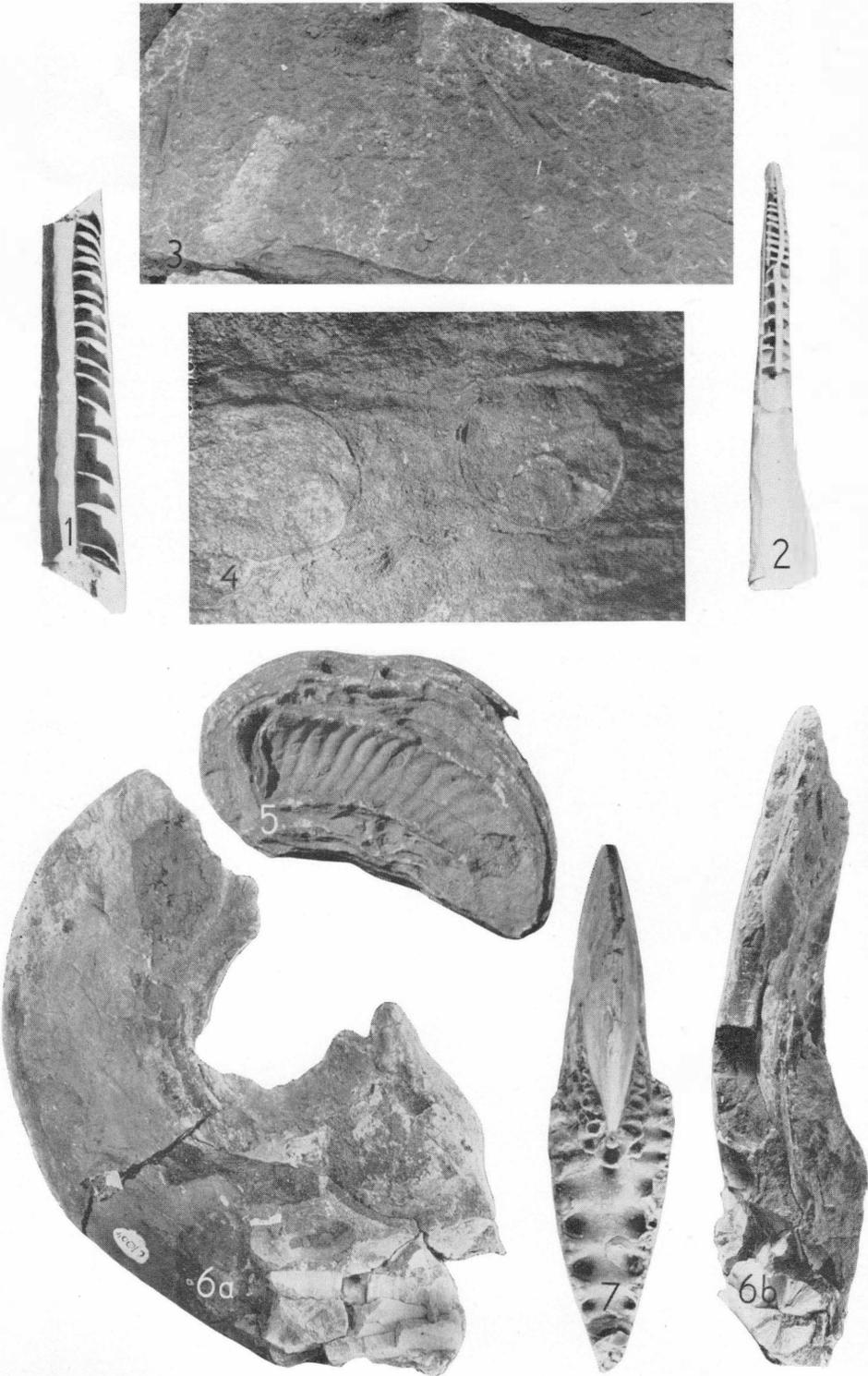


PLATE II

- Fig. 1. A vertically orientated, longitudinal section of a curved nautiloid with the body chamber preserved. The empty shell has drifted into calcareous ooze and become petrified in its floating position. Quarry wall, Lower Ordovician, Sätatorp, Västergötland, Sweden ( $\times 1$ ).
- Fig. 2. Median longitudinal section of a nautiloid shell exposed in the wall of the quarry at Sätatorp, Västergötland; observe the netherly located siphuncle. The arrow indicates the bottom of the shell ( $\times 1$ ).



PLATE III

- Fig. 1. Shell of *Nautilus pompilius* floating between salt and fresh water. The shell was partially waterlogged so that it sank in fresh water but was found to be quite buoyant in salt water (of S. G. 1.026). The two arrows demark the transitional zone of mixing of the two liquids. The photograph was taken 3 days after immersion of the shell.
- Fig. 2, a—b. *Nautilus umbilicatus* LAMARCK; one of the shells used in the experiments ( $\times 1/6$ ).
- Fig. 3, a—b. *Nautilus pompilius* LINNÉ; one of the shells used in the experiments ( $\times 1/6$ ).

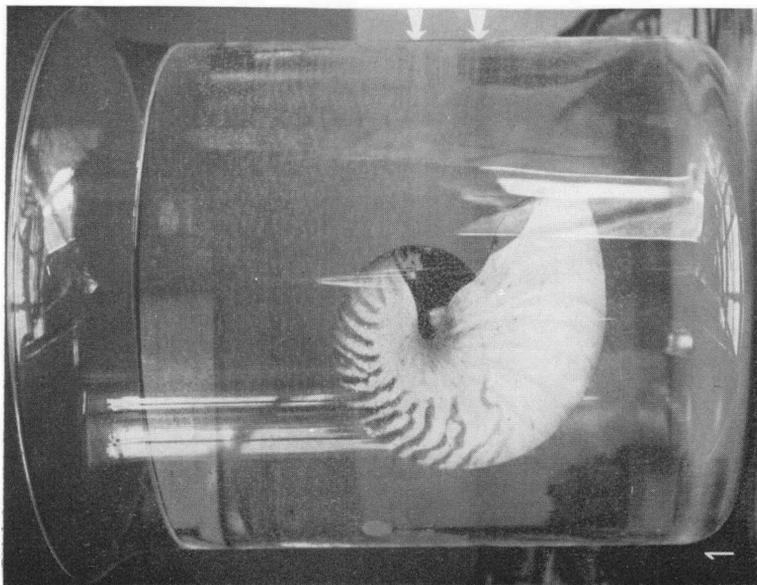
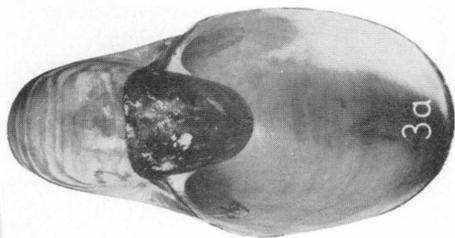
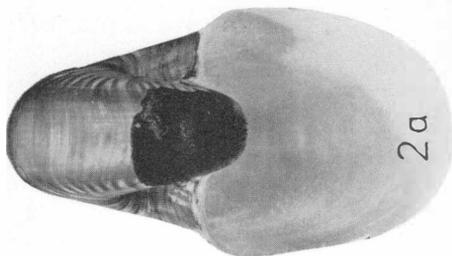
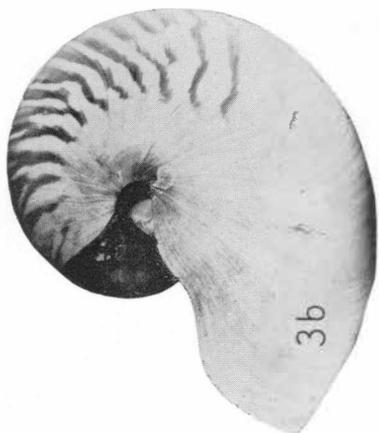


PLATE IV

(All photographs by the author)

- Fig. 1. Wave breaking around and shoving shorewards a stranding shell; the body chamber is already about a fourth filled with sediment.
- Fig. 2. The next stage in the initial burial of the shell which now rests at an angle. The body chamber is more than half filled with sediment. The nautilus is beyond the reach of most waves so that *standwirbelströmungen* (HESSLAND, 1943, p. 74) have little chance to develop. Instead, the tips of the waves scour out the sediment beneath the shell, which facilitates burial.
- Fig. 3. The backward burial movement has proceeded still further. The body chamber is almost completely full of sediment. Note the deep scour furrows.
- Figs. 4—5. Views of stranding shells. Note the almost constant orientation with respect to the scour streamlets formed by the withdrawing waves (exceptions are of fairly frequent occurrence). The arrows in these two figures indicate the furrowlets made by the withdrawing water, and its direction.

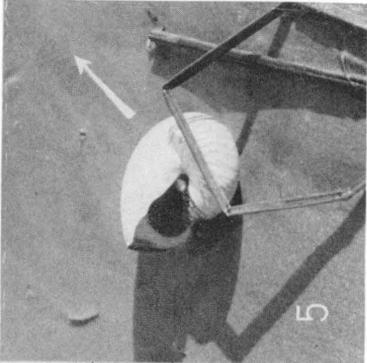


PLATE V

(All photographs by the author except fig. 6, which was taken by A. GROTH)

Experiments on the mode of stranding of nautilus shells

*Nautilus umbilicatus*

- Fig. 1. Freely floating shell seen from above.
- Fig. 2. Shell just in contact with a sandy bottom.
- Fig. 3. Shell beginning to topple sideways after having been washed further inshore by gentler wavelets than shown in fig. 2.
- Fig. 4. More advanced stage of toppling.
- Fig. 5. Shell almost at rest but still being jolted further ashore by the waves; observe the swirl ripples around the shell caused by its sawing motion.
- Figs. 6—7. Two aspects of stranded shells; note the presence of sediment in the body chamber of fig. 7. Fig. 6 shows a shell that was washed over a low sand ridge by an unusually strong wave, after having stranded. The drag of the withdrawing water tends to orientate the stranding shells with the body chamber on the seaward side and with the aperture facing inshore (cf. pl. IV, figs. 4—5).

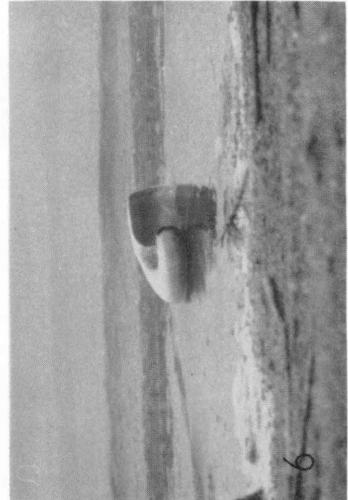
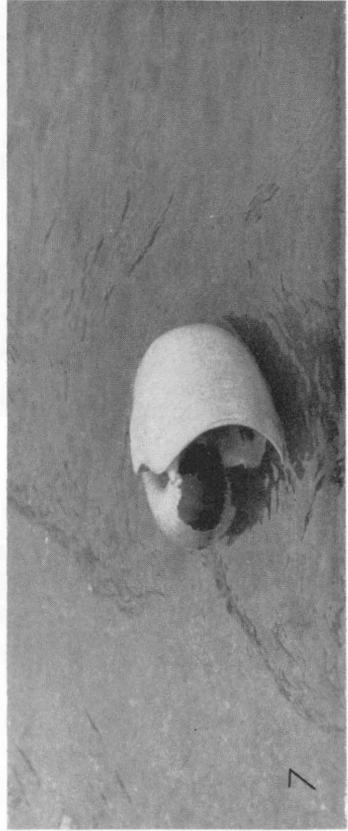
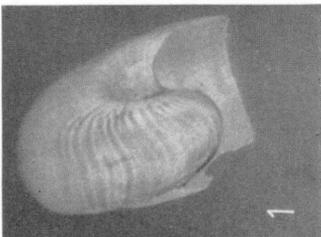
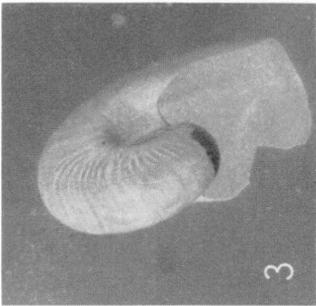
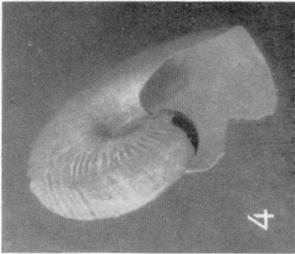
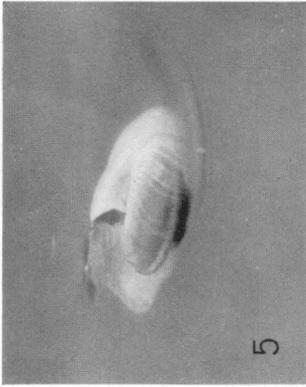


PLATE VI

(All photographs by the author except fig. 2, which was taken by A. GROTH)

Experiments on the mode of stranding of nautilus shells

*Nautilus pompilius*

- Fig. 1. Freely floating shell seen from above.
- Fig. 2. Shell in contact with the bottom but still vertical; there is more than a third of it above water (the arrows indicate the level of the water).
- Fig. 3. Shell almost stranded but still being moved by wavelets.
- Fig. 4. Stranded shell partly embedded; observe the presence of sediment in the body chamber.
- Fig. 5. Shell stranded by the ebbing tide in a ripple-lined tidal channel aligned parallel to the shore.
- Fig. 6. Shell stranded by the ebbing tide in wattenschlick about 50 m offshore; the body chamber contains some of this sediment. The arrows show the courses of receding water streamlets around the shell; H = washed out furrows around the shell.

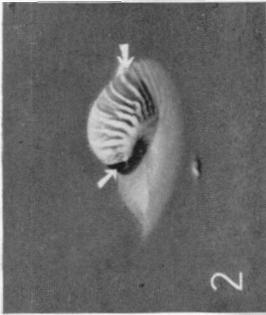
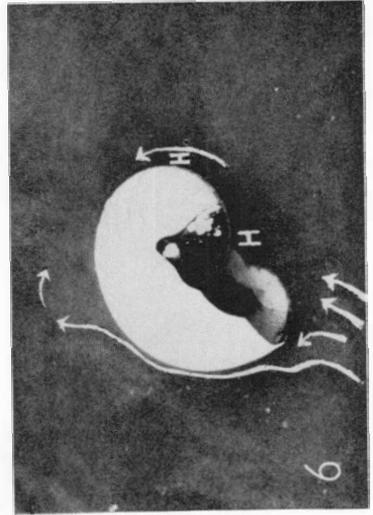
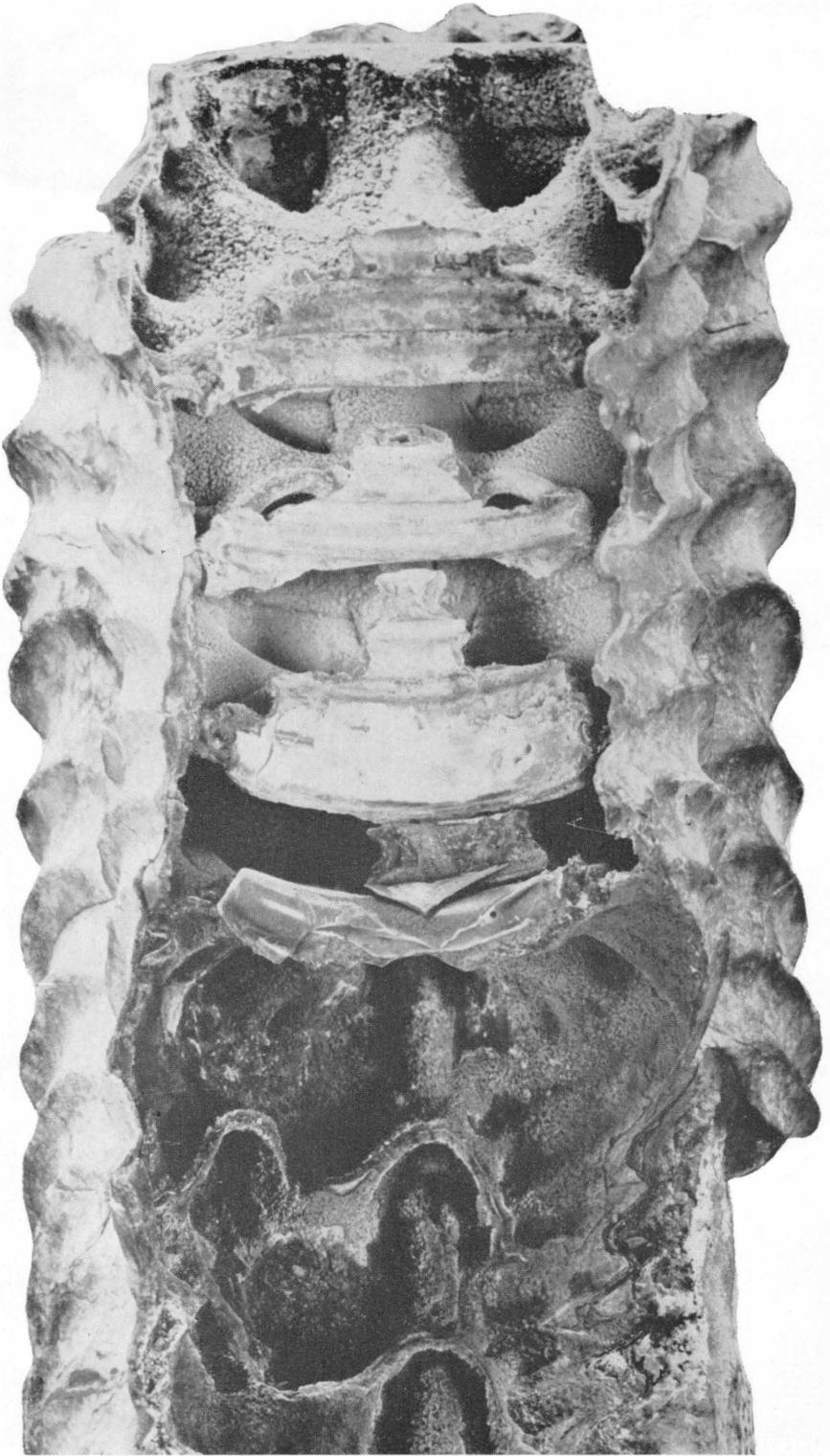


PLATE VII

*Speetoniceras versicolor* (TRAUTSCHOLD). Lower Neocomian, Polivna, U. S. S. R. View of the second last whorl with the body chamber whorl behind. The interiors of three completely preserved chambers are shown after dissection of the floor. Note the varying curvature of the septa and their thickness, the thickness of the shell walls and the thickness of the siphuncular walls. The shell material is composed of aragonite ( $\times 3/2$ ).



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