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On buoyancy and the lives of modern and fossil cephalopods

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[Plates 13–18]

For about 500 million years the cephalopods have been among the most successful of marine animals. Their evolution depended on the development of buoyant chambered shells, and the lives and behaviour of modern forms are also largely dependent on the particular solutions to the problem of buoyancy adopted.

There are striking similarities on the ways in which the shells of *Nautilus*, *Spirula* and *Sepia* are formed and used. These similarities, together with comparisons of the gross and fine structures of modern and fossil shells, give a firm base on which hypotheses about the lives of the fossil nautiloids, ammonoids and belemnoids can be made.

Although many modern squid are active and swim continuously to remain in mid-water, a very large number of oceanic squid have replaced the buoyant shells of the fossil cephalopods by tissues containing large amounts of ammonium. These 'ammoniacal' squid, although they are not readily caught in mid-water nets, are extremely numerous for they form the principal food of the approximately 1½ million sperm whales still living in the oceans of the world.

For about 500 million years the cephalopods have been among the most important animals in the seas. Their early success seems, in large measure, to have depended upon the development of buoyant chambered shells which could balance the weight in sea water of their living tissues. The earliest fossils universally agreed to be cephalopods are some rare nautiloids from the late Upper Cambrian. Their shells are usually small (< 1 cm long), straight or slightly curved cones. Towards the apex of such a cone there is a series of chambers and running through these chambers there is a closed tube, the siphuncle. The fine detail of the structure of the siphuncle has been studied in a similar though later fossil *Ruedemannoceras* by Flower & Teichert (1957). They have shown that where the siphuncular tube passes through a chamber it has one region which is calcareous and another, the chitinoid zone, which is not calcified. We shall see later that the functioning of the shells of modern cephalopods depends very much on the properties of the siphuncle and that porous regions through which exchanges of substances can take place between the chambers and the living tissues of the animal are necessary if the shell is to be used for buoyancy. Flower & Teichert's results show that this feature was present in the earliest known cephalopods.

Since the fossils of the early forms have often been found in association with

those of bottom-dwelling animals there has been some discussion as to whether the chambered shells of these animals were buoyant. We cannot resolve this problem but it should be said that the possession of neutral buoyancy can be very useful to animals which live and hunt immediately over the sea bottom. We shall see later how well the bottom-living cuttlefish *Sepia officinalis* can regulate its buoyancy and can note now that the squaloid sharks, which bring themselves extremely close to neutral buoyancy, are almost always caught on the sea bottom (Corner, Denton & Forster 1969).

The history of the cephalopods has been characterized by periods of explosive evolution followed by the extinction of large numbers of species (see, for example, Donovan 1964; Teichert 1967). Thus the ammonoids were almost extinguished in the Late Permian and the Late Trias and finally became extinct in the Late Cretaceous. Happily, although the nautiloids (now often divided into several major groups, e.g. by Teichert into the Orthoceratoidea, the Actinoceratoidea, the Endoceratoidea, the Bactritoidea and the Nautiloidea) were largely superseded first by the ammonoids and later by the coleoids, one genus, the famous *Nautilus*, remains alive. These 'fossil' animals are evidently fairly abundant since periodically large numbers of mature *Nautilus* shells are cast ashore on the beaches of the southwestern Pacific Ocean suggesting mass death after mating, a feature well known among modern cephalopods.

Two other types of living cephalopods have chambered shells, the small oceanic *Spirula* and the various species of the cuttlefish *Sepia*. These animals are the closest living relatives of the belemnoids. On figures 1 and 2 we show the animals and the shells of *Nautilus macromphalus*, *Spirula spirula* and *Sepia officinalis* side by side. They are very different in appearance. *Nautilus* lives inside its shell while the shells of *Spirula* and *Sepia* are totally enclosed in living tissues. It is the purpose of this lecture first to describe how these shells function, to bring out the similarities and differences between them, to discuss briefly the light these studies throw on the fossil forms and finally to describe a quite different solution to the problem of buoyancy which is used by very large numbers of modern oceanic squid. We shall base this discussion mainly on the properties of the *Nautilus* shell and adopt the nomenclature usually used by palaeontologists in describing the part of the siphuncular tube which is a continuation of the septum as the septal neck and the tube linking one septal neck to the next septum as the connecting ring.

THE CHAMBERED SHELLED CEPHALOPODS

The gas in the shells

The swimbladder of the fish is the most studied of all the organs used to give buoyancy. Typically it has a compliant wall and is filled with a gas at a pressure equal to the external pressure of the sea. The pressure of gas in the swimbladder of a deep-sea fish can sometimes be very great (several hundred atmospheres) and the composition of swimbladder gas varies greatly with the depth at which the

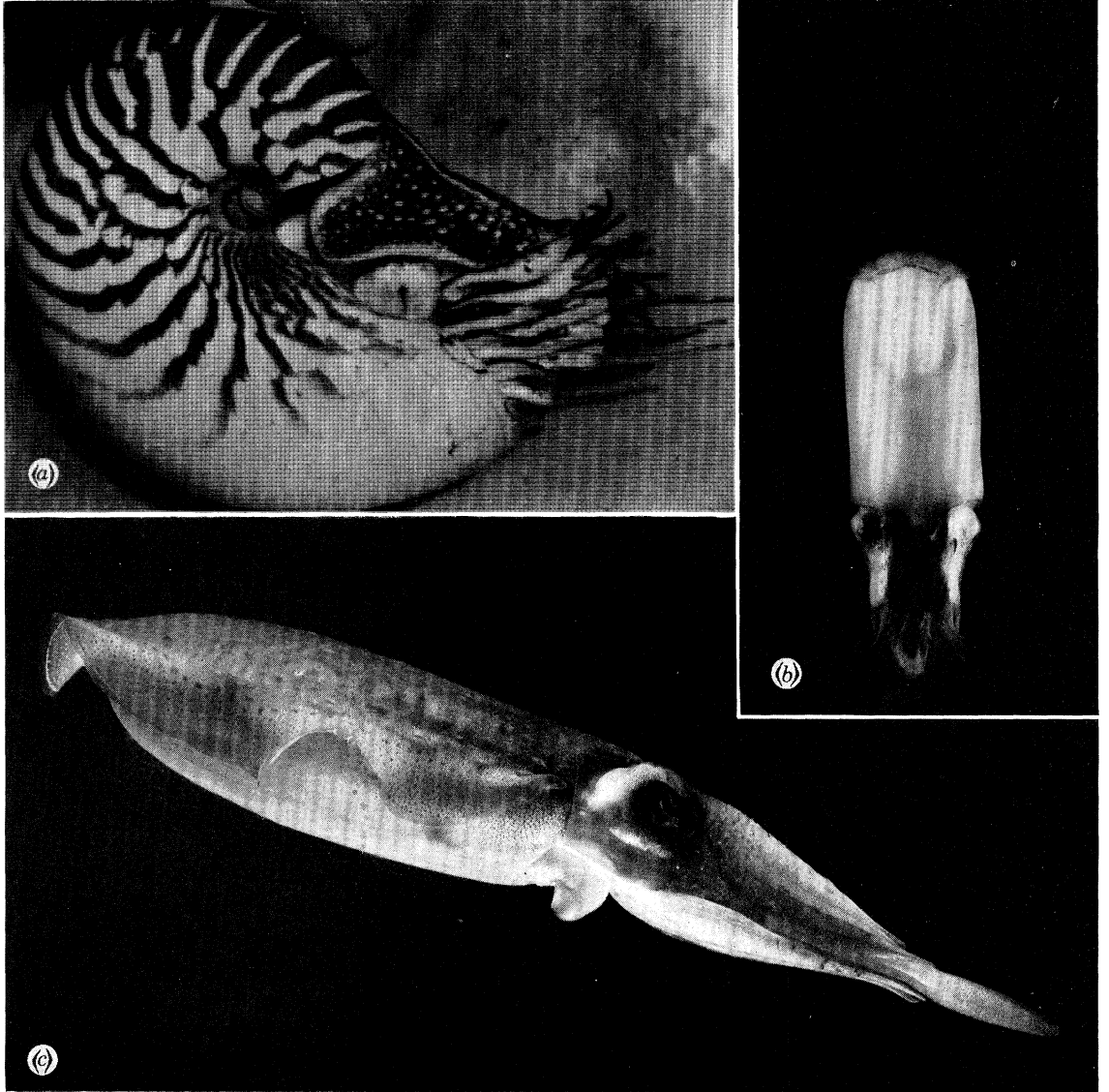
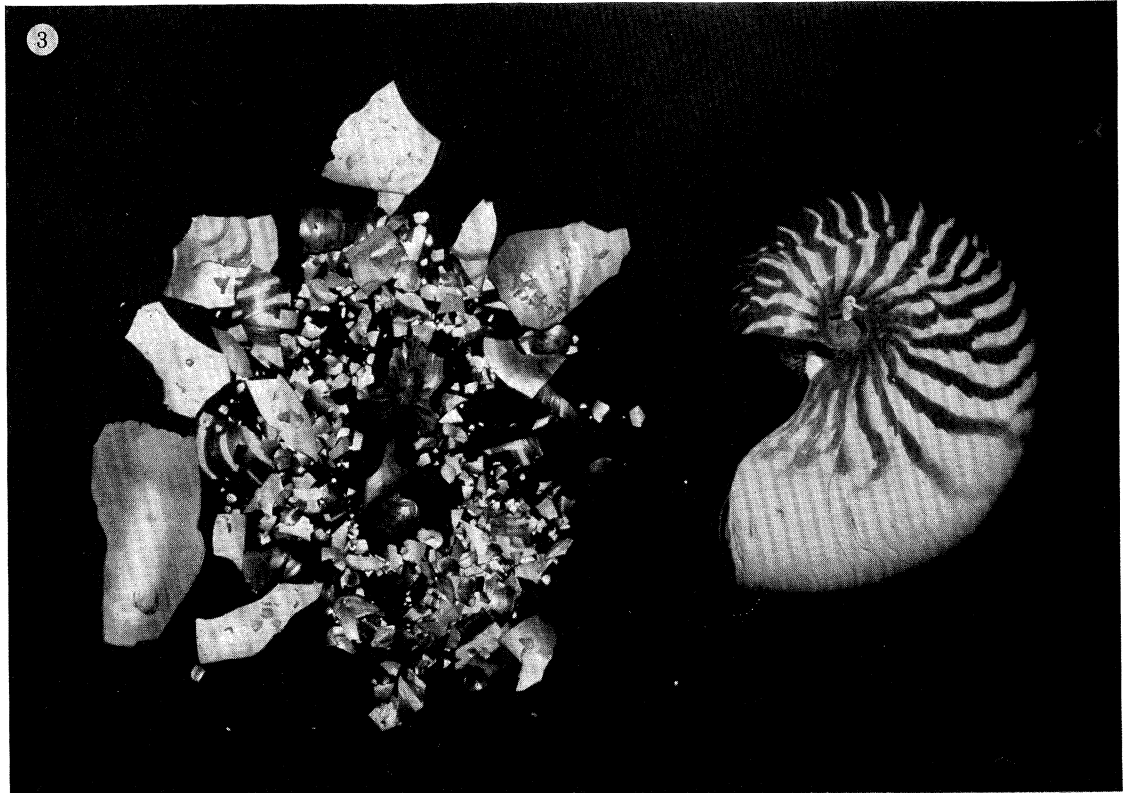
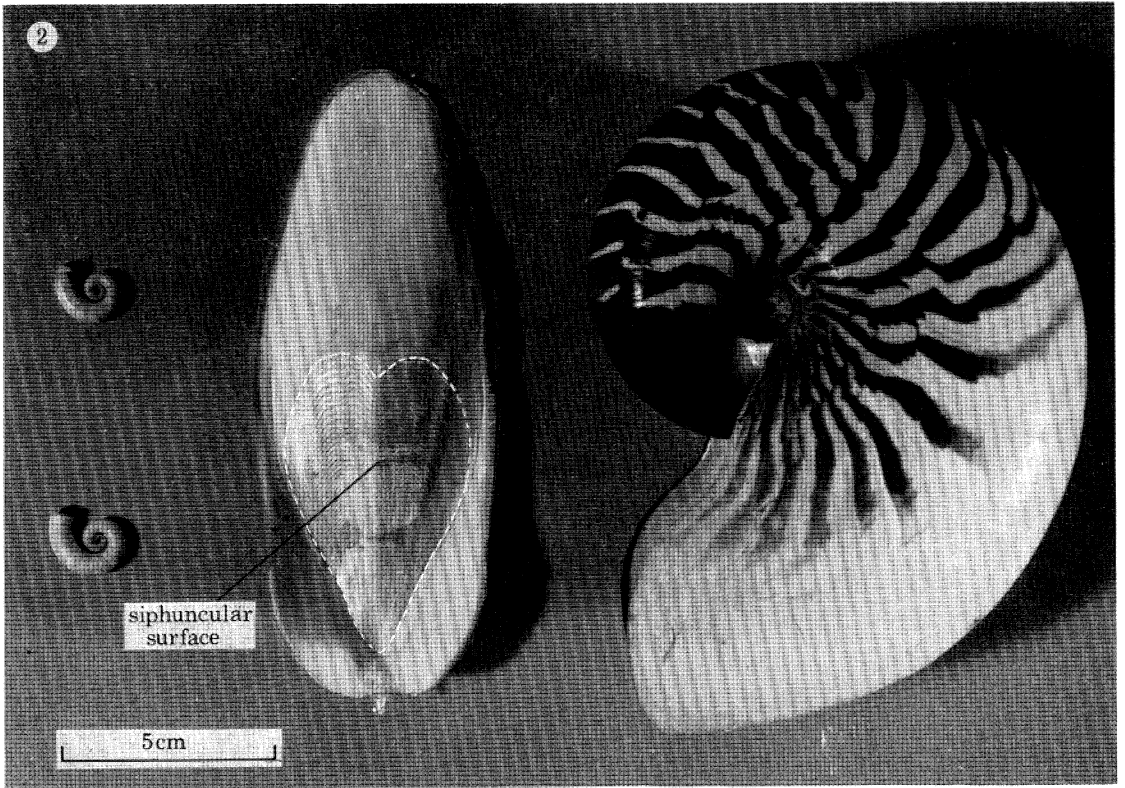


FIGURE 1. Photographs of living specimens of (a) *Nautilus macromphalus*; (b) *Spirula spirula*; and (c) *Sepia officinalis*. The magnifications are $\times 0.5$, $\times 0.6$, and $\times 1$, respectively. The photographs are by Dr J. B. Gilpin-Brown, Mr P. M. David and Mr D. Nicholson respectively.



FIGURES 2 and 3. For description see facing page.

fish lives. The swimbladders of fish living near the surface usually contain a gas mixture not very different from that of air, whilst the swimbladders of fish living deep in the sea contain mostly oxygen (Biot 1807; Scholander & Van Dam 1953).

The principal properties of the swimbladder were elucidated by a series of beautiful experiments by Armand Moreau (1876). He was followed by Paul Bert who hoped to make the physiology of the cuttlefish as well known as that of the frog. He worked very little on the shell or cuttlebone, but he did grind a shell under water and showed that the gas liberated was mainly N_2 with just a few per cent O_2 . He concluded that the cuttlebone probably functions in a similar way to the swimbladder (Bert 1867).

In these thoughts Paul Bert was preceded by no less a person than Robert Hooke who spoke of the *Nautilus* to the Royal Society on 2, 16 and 23 December, 1696 (see Derham 1726). He seems to have been the first to realize that the only connexion between animal and shell was through the siphuncle. This is a calcareous and chitinous tube through which a strand of living tissue passes through all the chambers of the shell. Its structure is shown on figure 12. He says of the siphuncle: 'This admirable structure seems to me not a mere *Lusus Naturae*, or a Form by Chance, to express, a Variety, but an Emanation of that infinite Wisdom, that appears in the Shapes and Structure of all other created Beings, which is to endow them with sufficient Abilities to perform those Actions, which are made necessary to their Well-being.' He thought, on the basis of early accounts of the *Nautilus* by Aristotle, Pliny, Oppian, Aelian and Bellonius, some of whose accounts may have referred to the Argonaut and not the Pearly Nautilus, that the animal must be able to fill and empty its shell of water. He writes: 'It was easy to conceive, how he could fill his Shell with Water, and so sink himself to the Bottom; but then how (when there, at such a Distance, from the Air) he could evacuate the Water, and fill the Cavities with Air, that was difficult to comprehend, especially being under so great a Pressure of Water: But if Nature had furnish'd him with a Faculty of producing an artificial Air, then the Riddle would quickly be unfolded. I found, therefore, that by Art it was feasible to produce such an artificial Air, and that it was endued with a very great Power of Expansion, so that it would not only make itself Room to expand, notwithstanding the incumbent Pressure of the Air on all Sides; but, if sealed up in strong Glasses, it would break out the Sides thereof, which might have as much Power of Expansion as might counterpoise, nay, out-power both the Pressure of the Air, and also the Water too, though

DESCRIPTION OF PLATE 14

FIGURE 2. The shells of: *Nautilus macromphalus* (right); this animal lives inside its shell. *Sepia officinalis* (centre); in this animal the siphuncle, which is a long thin tube passing through the shells of *Nautilus* and *Spirula*, is represented by the wide lined surface on the posterior ventral part of the shell. *Spirula spirula* (left); the shell lies inside the animal. It resists imploding pressures much better than do the shells of *Nautilus* and *Spirula*.

FIGURE 3. *Nautilus macromphalus*. The shell on the left has been exposed to a pressure only just sufficient to break it yet the shell is completely shattered.

100 Times greater than that of the Air.' He freely admits that although there was great probability in his conjecture he could not be positive about it and calls for *Nuntii ad Abyssum* to solve this and other problems. 'I have', he writes, 'heretofore produced some such Nuntii, for this or that particular Design, but when there may be an Opportunity of sending them, I shall be able to produce divers others, for other Purposes, if God spare my Life so long as to see the Seas again free from Rovers, and that the Study of Arts does succeed the Study of Arms.'

Unhappily Robert Hooke's hopes were not fulfilled in his lifetime but the Royal Society has since then helped many '*nuntii ad abyssum*' including the author of this paper.

Although Robert Hooke's conjectures on the production of 'artificial air' under pressure by animals have been amply confirmed in fishes, high pressures of gases have never been found in the shells of cephalopods. When holes have been made under sea water in the shells of these animals after they have been hauled up from depth, sea water always entered the shells. This showed that the pressures of gas within their chambers were sub-atmospheric. There were no signs that gas had escaped from these shells into other tissues and it was shown in *Sepia* that the shell does not contain a gas particularly soluble in water. Estimates of the maximum pressures of gas within the shells of *Nautilus*, *Sepia* and *Spirula* showed that no matter from what depth the animal had been hauled these pressures were always around 0.8 to 0.9 atm. As these animals grow they add new chambers to their shells, the numbers of such chambers in mature animals being approximately 32 for *Nautilus macromphalus*, 27 for *Spirula spirula* and 120 for *Sepia officinalis*. It is convenient in discussions of physiology to number the chambers from that most recently formed backwards in time. The pressure of gas in the most recently formed chambers of specimens of *Nautilus* and *Sepia* which are still growing are shown on figure 4 and qualitative experiments on *Spirula* show that the pattern of pressures is exactly the same in this animal too. The pressure of gas is very low in the chamber recently formed and rises progressively in succeeding older chambers to attain a pressure of about 0.83 atm in *Sepia* and about 0.9 atm in *Nautilus* (Denton & Gilpin-Brown 1961*a, c*, 1966; Denton, Gilpin-Brown & Howarth 1967; Bidder 1962). Analyses of gas by Scholander's method for *Sepia* and by mass spectrometer for *Nautilus* show (figure 5) that the gases within the chambers of *Nautilus* and *Sepia* are principally N₂ (including Ar) and a little O₂. In the older chambers of the shells of both animals, the partial pressures of N₂, O₂, Ar and CO₂ are close to the partial pressures expected for their tissues. In *Nautilus*, which was studied in more detail, the attainment of equilibrium was about twice as fast for Ar and O₂ than for N₂. Much the simplest explanation of these results is that the gases present in the tissues simply diffuse into spaces created by some other force.

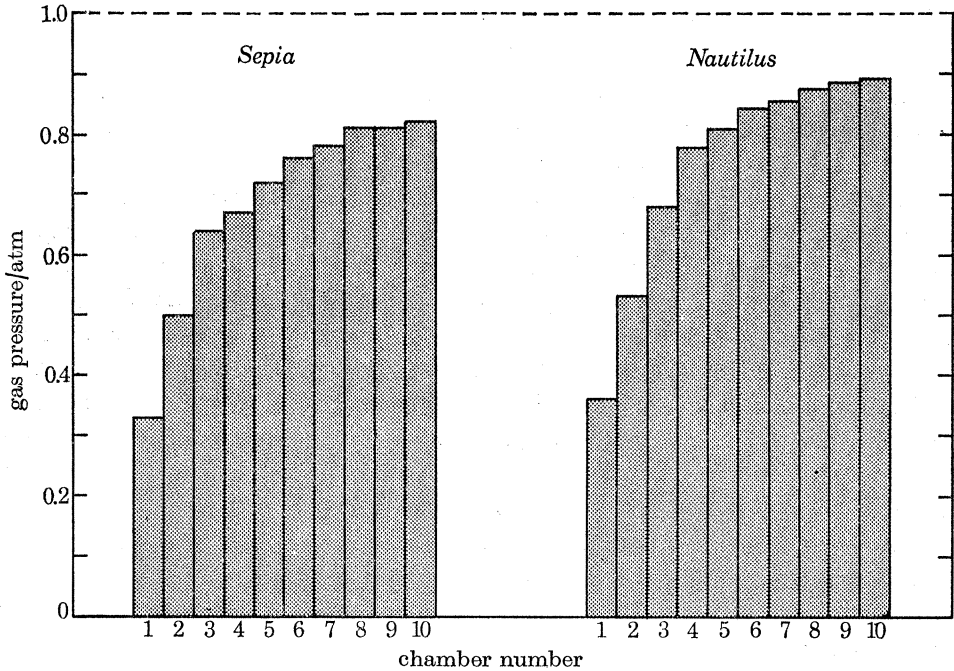


FIGURE 4. Typical patterns of pressures found in successive chambers of the shells of *Sepia* and *Nautilus* for animals which are still laying down new chambers. The chambers are numbered backwards in time, number 1 being the one most recently formed. When the animals are actively growing, *Sepia* (off Plymouth) lays down chambers at the rate of two or three per week while *Nautilus* lays down chambers at the rate of one every few weeks.

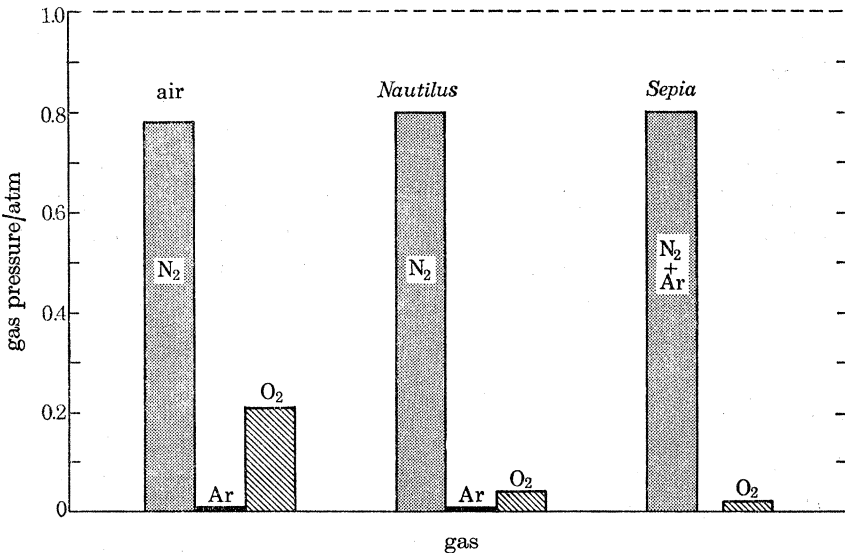


FIGURE 5. The partial pressures of individual gases in air, at atmospheric pressure, and in the older chambers (e.g. those numbered 10 in figure 4) of *Nautilus* and *Sepia*. The animals in life are exposed to hydrostatic pressures very much greater than atmospheric pressure.

The strength of the shells

If, as the above observations show, the maximum pressure of gas within these shells is less than atmospheric then, if the shells are not to implode, their walls must be strong enough to withstand the hydrostatic pressure of the sea down to the maximum depths at which the animals live. *Sepia* is known to live in coastal waters and to descend only to about 150 m. Its shells, either isolated and wrapped in a polythene sheet, or within dead or anaesthetized animals, implode at pressures of around 20 atm (this corresponds to the shell imploding at about 200 m depth). The maximum depth to which *Nautilus* descends is not accurately known and may vary a little between the various species. One *Nautilus* was caught by the *Challenger* in a dredge fishing down to 570 m, but since the net was not a closing net this might have been caught at a lesser depth. Dean's (1901) figure of 450 to 700 m is suspect since it refers to an area only charted to depths of 200 m, but Griffin (1900) certainly believed that the 66 specimens of *N. pompilius* of the Menage Collection were trapped between 360 and 540 m, although he gives no precise details in support of these figures. The strength of the external shell of *Nautilus* with the opening of the siphuncle sealed has been shown to be sufficient to withstand 60 to 70 atm (Denton & Gilpin-Brown 1966; Raup & Takahashi 1966). When the shell of *Nautilus* does implode it is shattered completely (figure 3, plate 14) and there could be little chance of an animal living within such a shell surviving a catastrophe of this kind if it descended too deeply. At first sight the connecting ring of the siphuncular tube appears to be by far the most fragile part of the *Nautilus* shell for it can be easily pierced or torn with fine forceps, but thin tubes, like the siphuncular tube, do not need to have a very high tensile strength to withstand exploding pressures. Denton & Gilpin-Brown have calculated that the 'horny' layer of the connecting ring (see figures 11 and 12) which is clearly the only strong part of the connecting ring, would need to have a tensile strength of 5 kgf/mm² to withstand a pressure difference between siphuncle and chamber of 60 atm. This is not a particularly high figure for a natural material. Richards (1951) gives a tensile strength of 36 kgf/mm² for dry silk and up to 58 kgf/mm² for chitin. The best direct test of the strength of the siphuncular tube has been given by Collins & Minton (1967). They found that the siphuncle of *Nautilus* could withstand a pressure of 45 atm but they could not determine the upper limit of its strength.

The distinguished Danish zoologist Anton Bruun, who did not have the benefit of opening and closing nets, estimated by analysing the catch in nets fished down to various depths that *Spirula* lived down to 1750 m (176 atm) (Bruun 1943, 1955). He also tested the strength of *Spirula* shells which had been cast ashore and found that the strongest of these withstood pressures of only 65 atm. This discrepancy led him to believe that, in life, the shells must contain gas under pressure. More recent work has made this assumption unnecessary. On a plentiful supply of material caught off the Canary Islands Clarke (1970) has shown that the maximum

depth at which *Spirula* is found is about 1200 m (121 atm) and Denton & Gilpin-Brown (1971) who measured the implosion pressures of shells of *Spirula* within recently dead or anaesthetized animals found values between 136 and 201 atm (mean value 170 atm).

It seems therefore that the shells of *Nautilus*, *Spirula* and *Sepia* are all sufficiently strong to withstand the full pressure of the sea down to the depths at which these animals live. We may notice that these three shells differ greatly in the pressures which they can withstand yet the margins of safety between strength of shell and the maximum pressure which they encounter in life are very similar (figure 6). The relatively low margins of safety, i.e. between 1.3 and 1.4, are not very surprising: animals, like aeroplanes, are not generally designed with large mechanical safety factors.

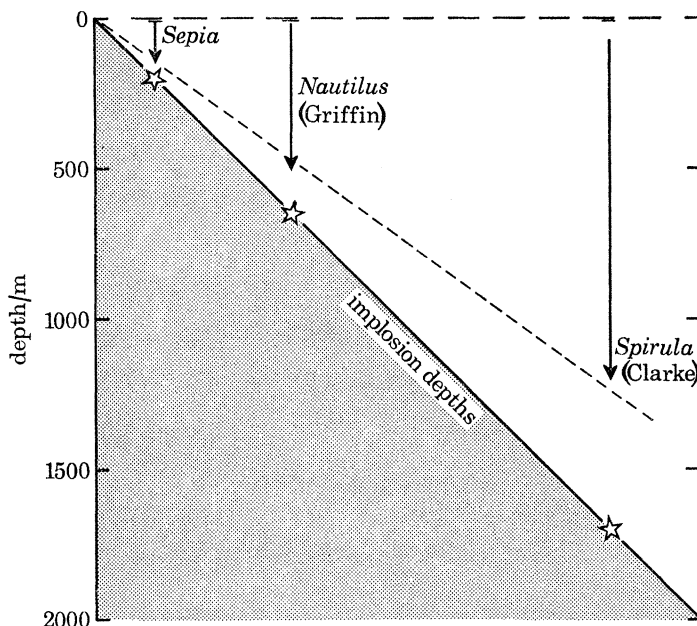


FIGURE 6. The relation between strength of shell and depth range for the three types of modern chambered-shelled cephalopods. The safety factor, i.e. pressure of implosion of shell, divided by the maximum pressure to which the animal is exposed in life is about 1.3 for all three species. The gas pressure within the shell is always less than atmospheric. The depth ranges are shown by the heavy lines ending in downward pointing arrows, the implosion pressures are shown by stars.

The formation of a new chamber

Following Robert Hooke, authors have generally assumed that, like the man-made submarine, spaces in the buoyant chambers were formed by the expulsion of liquid by gas under pressure. It has therefore been conjectured, and is still supposed by some workers, that a space is formed by the active secretion of a gas under pressure and that this space is subsequently sealed off by the building of

a new septal wall. There is no evidence at all to support this view. The processes of formation of a new chamber have been followed in *Sepia*, *Nautilus* and *Spirula* (Denton & Gilpin-Brown 1961c, 1966, 1971). In all three species a chamber when first formed is full of liquid (figure 7, plate 15). In *Nautilus* and *Spirula* it has, moreover, been shown that this liquid is very close to being isosmotic with sea water and hence with the blood. In *Sepia* and *Spirula*, since the shells are internal, these liquids must be body fluids. In *Nautilus* it is possible to imagine that the animal would form a liquid-filled space by allowing sea water to pass around the body into the terminal part of the living chamber, but it has been shown that although this fluid is isosmotic with sea water, it differs in composition from sea water and is a body fluid. The demonstration that the pressure of gas in a new chamber is always markedly subatmospheric makes it extremely unlikely that the liquid would be pumped out of a chamber until its new septal wall was sufficiently strong to withstand the pressure of the sea around the animal. Very many growing *Sepia* have been examined by Denton & Gilpin-Brown. They never saw any sign of a gas space below the shell in the region where new chambers are formed. One *Nautilus* studied was clearly in the process of forming a new chamber for the new septum sealing off the last-formed chamber from the living tissues was only about one-third of its final thickness (i.e. that expected from septa already fully formed).

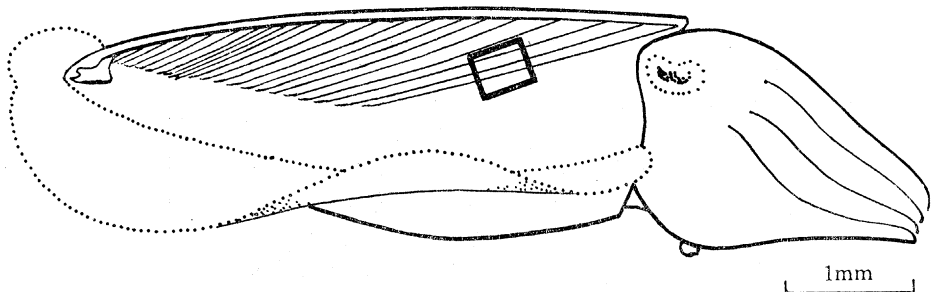


FIGURE 7A.

DESCRIPTION OF FIGURE 7

FIGURE 7. (A, B) *Sepia officinalis*. The diagram (figure 7A) shows the cuttlebone in section within the animal and on it the region shown on plate 15 is indicated by a small black rectangle on the lower surface of the cuttlebone. The photograph on plate 15 is of part of a cuttlebone sawn into two along its mid-ventral line. The illumination was such that liquid within the chambers appears bright. The chamber being formed is full of liquid as is the one most recently finished, i.e. the lowest complete chamber. (C) *Spirula spirula*: (a) A very small specimen of *Spirula*; the shell can be seen through the animal's tissues; the mantle length of this animal was about 3 mm. (b) A shell dissected from an animal like that shown in (a); the largest and most newly formed chamber is full of liquid. The next chamber to be formed has hardly been begun; the two oldest chambers contain little or no liquid. (c) A shell in which the first tiny bubble of gas is appearing within the most newly formed chamber; the cylindrical walls of the next chamber to be formed are relatively longer than in (b). (d) A large fraction of the liquid has been pumped from the most newly formed chamber; the cylindrical walls of the next chamber to be formed are relatively longer than in (c).

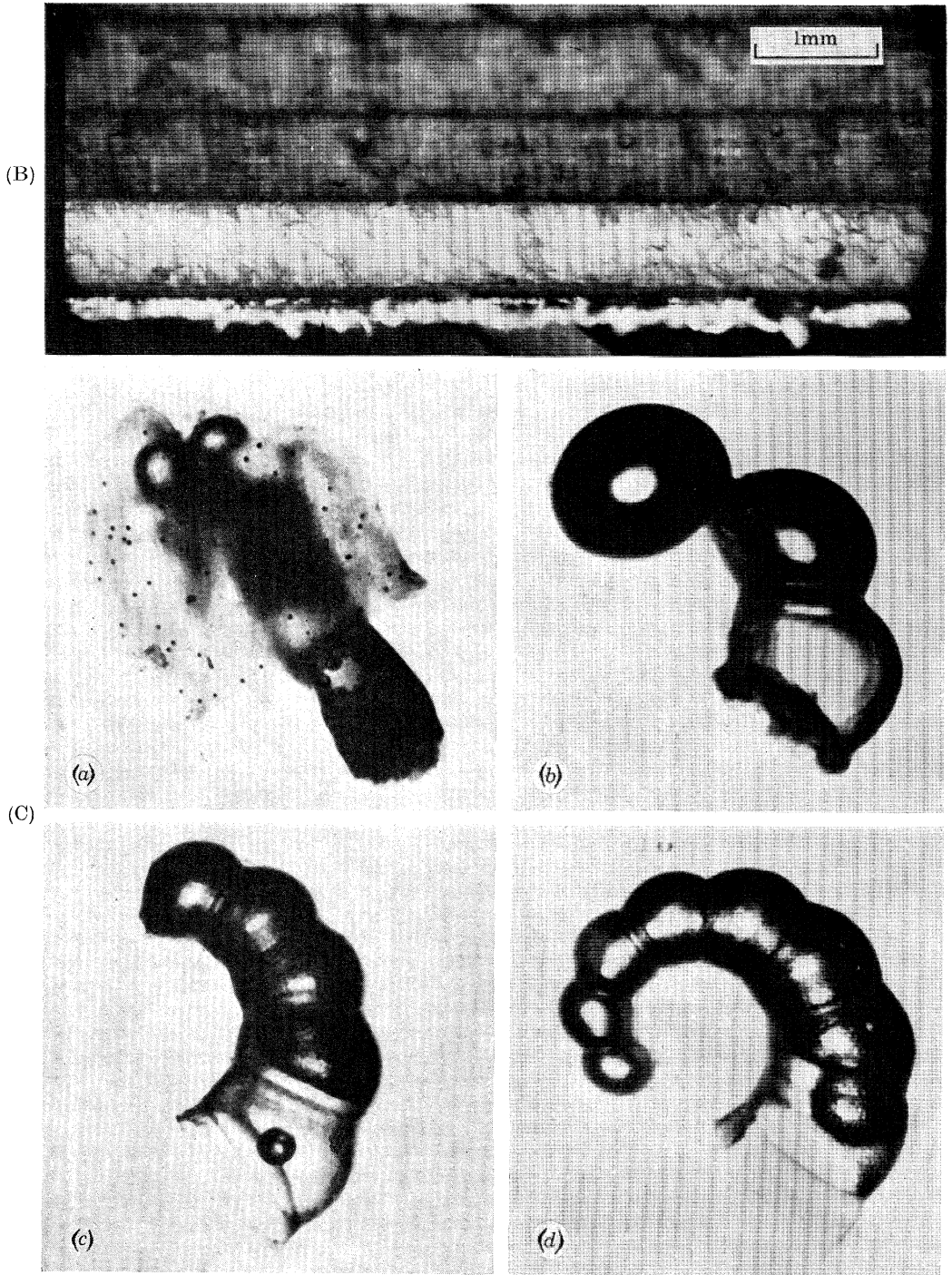


FIGURE 7 B, C.

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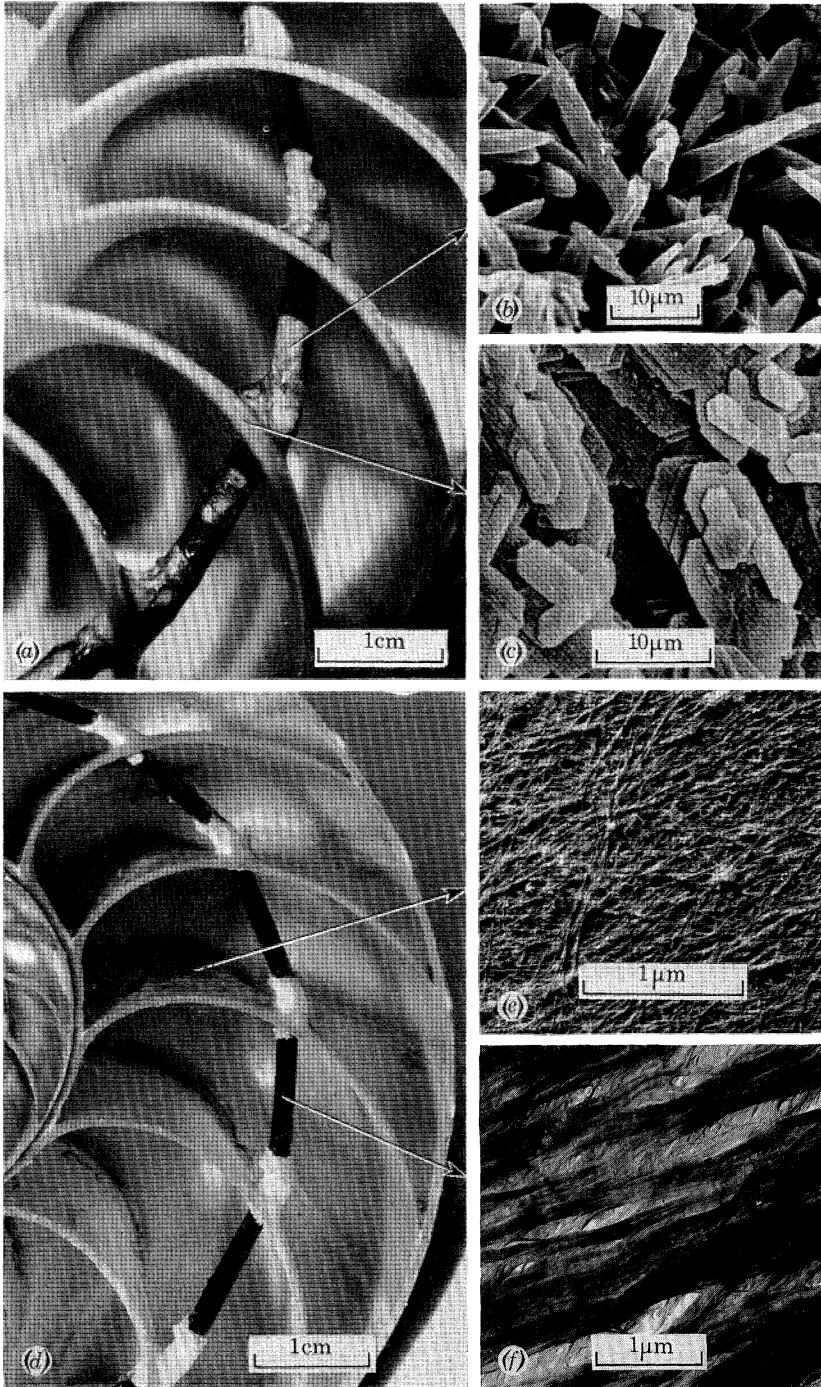


FIGURE 11. For description see facing page.

This incomplete chamber was completely full of liquid. In small specimens of *Spirula* the shell can clearly be seen through the body wall and again when a new chamber is being formed a clear liquid is secreted into the space which this chamber is to occupy. It is this liquid which is sealed off from the animal by a new septal wall.

The permeable parts of the shells

In *Sepia*, *Spirula* and *Nautilus* the only parts of the shell permeable to liquids are in the siphuncular regions. In *Nautilus*, entry of liquid into a shell from which the living tissues have been removed can be prevented by sealing the opening from the living chamber to the siphuncle. In *Sepia* liquids have been observed entering or leaving the intact shell only through the siphuncular surface. In *Spirula* liquids could only pass between the inside of the chambers and the space occupied by the living tissues through the small areas shown as porous in figure 8. Collins & Minton (1967) have made a quantitative measurement of the permeability of the siphuncle of *Nautilus* to liquid. They found that for a difference in pressure of 20 atm between the inside of the siphuncle and the chambers (the living tissues having been removed) the rate of flow of liquid was such as to completely fill the chambers in 2 h. They also gave further support to the idea that gases only arrive in the chambers by diffusion by showing that gas, as bubbles, could not pass through the siphuncular wall even under 10 atm pressure difference between the tube and chambers.

Liquid as ballast in the shells

Robert Hooke, from the accounts of earlier authors, some of which probably referred to the paper *Nautilus* and not the pearly *Nautilus*, believed that the latter animal could use changes in buoyancy to rise and sink in the sea and to alter its posture. He writes 'It is wonderful to consider, by what a plain and easy Contrivance the All-wise Creator has endowed him with sufficient Faculties to perform the same, with very little or no Fatigue at all, but to be carry'd in his

DESCRIPTION OF PLATE 16

FIGURE 11. (a) Shell of *Nautilus* which has been sawn into two parts to display the relation of the siphuncular tube to the buoyant chambers. The external walls of the shell, the septa and the septal necks contain nacreous layers which are impermeable to liquids and gases. The outer surface of the siphuncular tube, i.e. the surface facing into the chambers, is covered with a porous chalky layer. (b) Scanning electron micrograph showing the fine structure of the porous chalky tube. (After Mutvei 1972.) (c) Scanning electron micrograph showing the fine structure of a nacreous layer. (After Mutvei 1972.) (d) Similar to (a) but the chalky layer covering the connecting ring has been scraped away to display the 'horny' tube. This tube is porous but strong being made of concentric conchiolin sheets. (e) Electron micrograph showing the unorientated felting of microfibrils of the wetttable pellicle, or periostracum, which covers the external surface of the siphuncular tube and the convex sides of the septa. (After Gregoire 1962.) (f) Electron micrograph showing the fine structure of the strong conchiolin sheets which make up the horny layer of the connecting ring.

Chariot, or rather Ship, from Place to Place, as he has Occasion to change his Residence' and 'I conceive, that when this Cavity (the chambered part of the shell) is fill'd with Water, the whole Bulk becomes heavier than the Water, and so must sink to the Bottom of the Sea: But when the Cavity is fill'd with Air, then

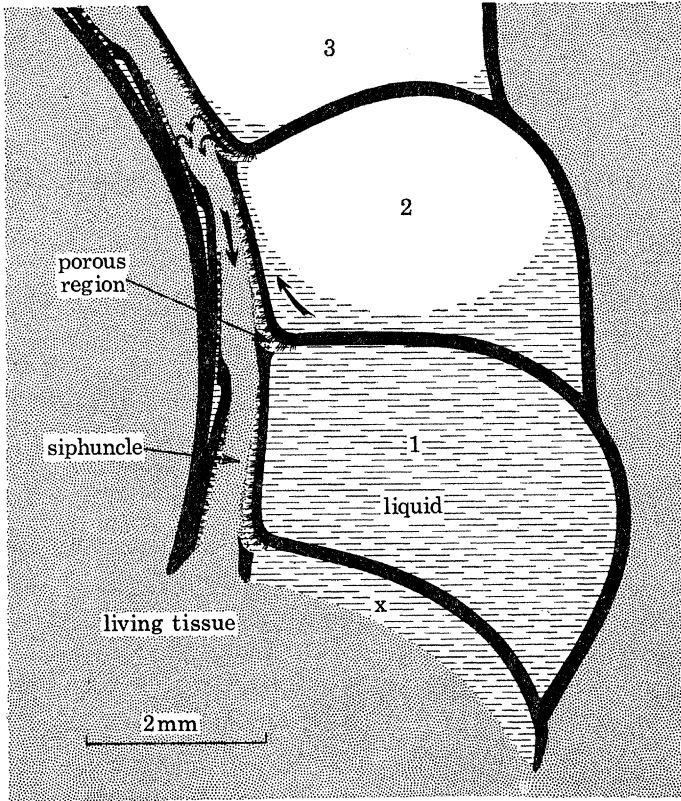


FIGURE 8. *Spirula spirula*. Diagram showing the relation of liquid within the chambers to the porous regions through which liquid must pass to leave the chambers. The animal is beginning to make a new chamber by creating a liquid-filled space (x). Chamber 1 is that most recently fully formed; it is still full of liquid.

the Whole will be boyant, and lighter than the Water, and so rise to the Top, and float on its Surface: These powers it would have had, supposing the Cavity of the Shell had had no other but the first or greatest Diaphragm, the rest had been one entire Cavity: But this would not have disposed the Shell to all those Motions, it is to perform, into the most convenient Postures; for that Posture, that is fittest for its rising, would not be so for its sinking, nor for its sailing, nor possibly for its Progression at the Bottom, (if such a Motion it does perform, as to me it seems rational enough to suppose) for that every one of them will need a different Posture. We find, therefore, this Cavity all subdivided by internal Diaphragms or Partitions, into a great Number of distinct Cells, (I have found 40 in some Shells)

and every one of these penetrated by this Gut or *Ductus*, so that by Means thereof, I conceive, the Animal has a Power to fill or empty each of those Cavities with Water, as shall suffice to poise and trim the Posture of his Vessel, or Shell, fittest for that Navigation or Voyage he is to make; or if he be to rise, then he can empty those Cavities of Water, or fill them with Air which lie toward that Side, that part the Shell, that best penetrate the Water: If he be to descend, he can fill those with Water, and empty the opposite; if to sail on the Top, he can evacuate those Cavities that will trim his Shell fit to sail with the Mount of it upwards, that he may there expand his Sails and use his Rudders; and if to move at the Bottom, he can fill those, and empty the opposite, so as the Mouth may be downwards, to respect the Ground or Bottom over which he passes, so to discover his proper Nutriment or other Convenience, and to descend to it when he finds it.'

Other authors, e.g. Trueman (1941), have considered that the shells of cephalopods contained no liquid.

Our observations and those of Dr Anna Bidder (1962) show that the shells of *Nautilus*, *Spirula* and *Sepia* all contain some liquid in life.

The pattern of liquid in *Nautilus* found by Denton & Gilpin-Brown (1966) is very simple. The chambers contain diminishing amounts of liquid from the newest chambers to the older chambers, most of the chambers containing very little liquid indeed.

Figure 9 shows that although specimens of freshly caught *Nautilus* contain varying amounts of liquid this is always sufficient to bring the animal plus its shell close to neutral buoyancy. It is not certain whether or not *Nautilus* can adjust its buoyancy quickly. From their observations on living animals in aquaria Bidder (1962) and Cousteau & Diolé (1973) thought that they probably can adjust their buoyancy to suit their activities.

A number of living specimens of *Spirula* were weighed in air and in sea water aboard R.R.S. *Discovery*: they were all slightly positively buoyant and there were no significant differences between those caught in the daytime and at night, although this animal is known to migrate downwards in the daytime and upwards at night. This gives no support to the idea that changes in buoyancy are used to enable *Spirula* to rise and fall in the sea but it does seem unlikely that *Spirula* is always positively buoyant. It may well be that a little liquid is pumped out of the shell into the circulation when the animal is hauled to the surface of the sea and the pressure on the animal is greatly reduced.

The distribution of liquid among the various chambers of the shells of *Spirula* differs between small and large animals. In small animals only the most newly formed chambers contain liquid; in older animals the newest and the oldest chambers both contain liquid.

We have the most complete information on the role of liquid within the shell for *Sepia officinalis*. The usual pattern of liquid distribution in this animal is such that, apart from the chambers very recently formed, the newest chambers contain little or no liquid while the oldest chambers are almost full of liquid (figure 10c).

Since the older chambers lie towards the animal's stern when they are filled with gas their buoyancy tips the animal's tail upwards and prevents it from adopting its normal swimming position. We have also very clear evidence that *Sepia* can actively change its buoyancy by increasing or decreasing the amount of liquid within its shell. Thus Denton & Gilpin-Brown (1961*b*) showed that *Sepia* can be

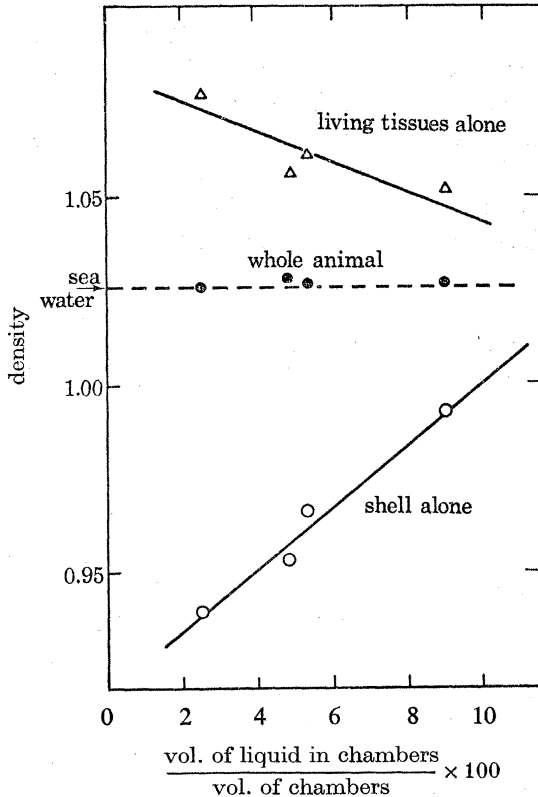


FIGURE 9. Results obtained on four specimens of *Nautilus macromphalus* soon after capture. The lower points (○) are for the shells alone, the variations in density are almost entirely due to differences in the liquid contents of the shells. (A shell with relatively more liquid has a smaller gas-filled space in its chambers and so it is more dense.) The upper points (Δ) give densities of the living tissues alone (animals removed from their shells). These densities vary a good deal from one animal to another. The central points (●) give densities of whole animals (living tissues + shells). These densities are all very close to that of sea water. This figure shows that, by varying the liquid content of the shell, *Nautilus* brings the density of the whole animal (living tissues + shell) close to that of sea water even when there are considerable differences between animals in the densities (and/or amounts) of living tissue. (After Denton & Gilpin-Brown 1966.)

induced to pump liquid out of its shell, and so become more buoyant, by keeping the animal in complete darkness. After several days in the dark specimens of *Sepia* are often found floating at the surface of their tank, being so buoyant that they cannot maintain themselves below the surface for more than a few seconds. If these very buoyant animals are then kept in the light, they increase the volume

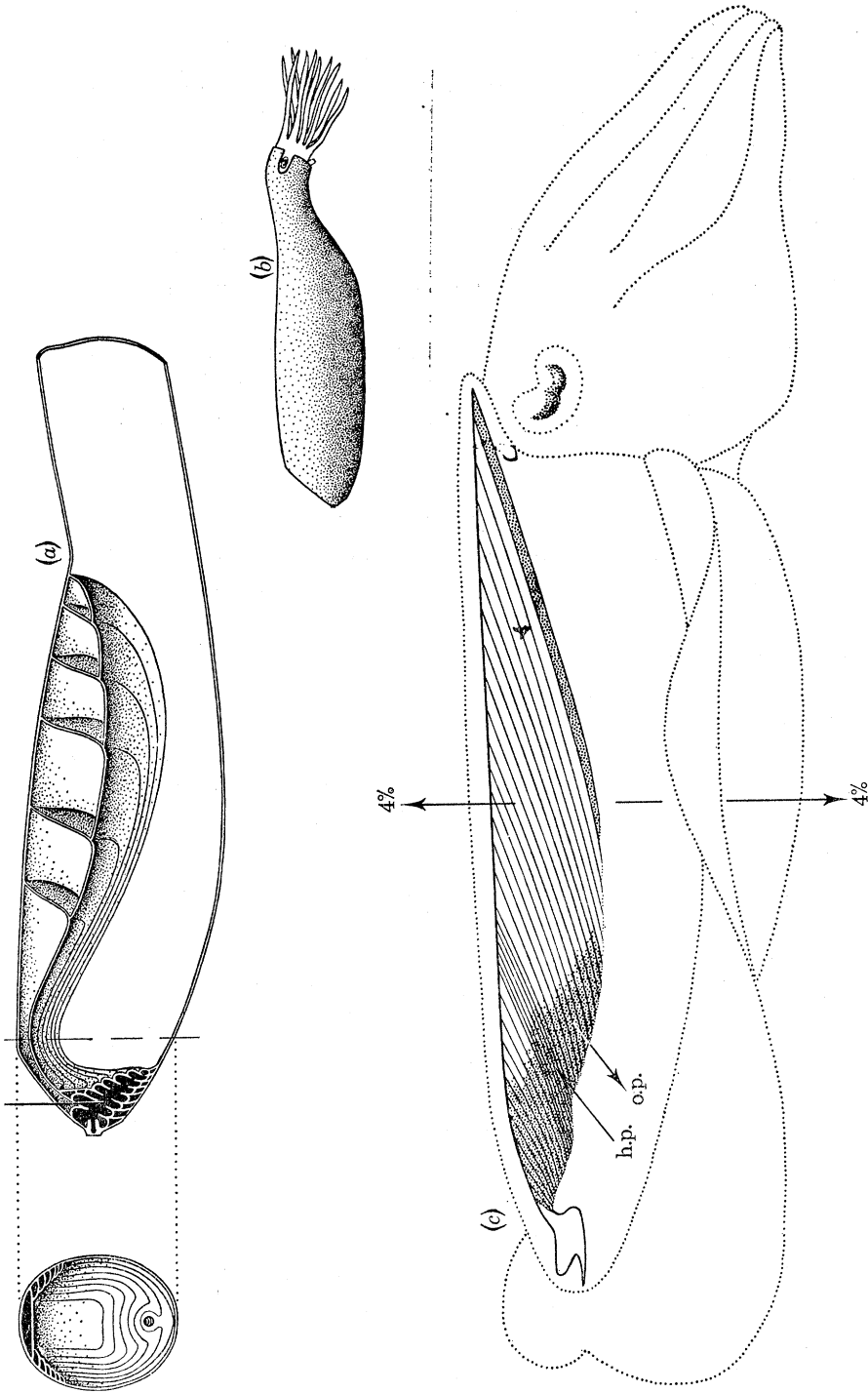


FIGURE 10. (a) *Ascoceras* (an animal of a family which flourished in the Ordovician and Silurian periods). Only the shell is shown, on the left in cross-section, on the right in a perspective diagram of the left half of the shell. The chambers are linked to the siphuncle only by thin tubes running on the upper part of the shell. The animal lived within this shell. (After Furnish & Glenister 1964.) (b) Diagram of an animal like *Ascoceras* within its shell. The form of the head and tentacles is based on our knowledge of living cephalopods. (After Furnish & Glenister 1964.) (c) *Sepia officinalis*. The shell is shown in section and a typical distribution of liquid within the shell is shown by the stipple. The chambers are, in fact, more numerous than this diagram indicates and consequently are thinner in relation to their lengths. The oldest and most posterior chambers are almost full of liquid. If they were filled with gas, this would tip the tail of the animal upwards. The hydrostatic pressure of the sea (h.p.) is balanced by an osmotic pressure (o.p.) between the cuttlebone liquid immediately under the siphuncular region and the blood. In sea water the cuttlebone gives a net lift of about 4% of the animal's weight in air and so balances the excess weight in sea water of the rest of the animal.

of liquid within their shells, become denser than sea water, and so can rest on the bottom. A feature in the regulation of buoyancy of *Sepia* is that it seems to be affected by the condition of the animal. Healthy animals can rest easily at the bottoms of their tanks while animals in poor condition usually pump liquid out of their shells often to such an extent that they float at the surface in an incapable fashion. The observations of Denton & Gilpin-Brown do not support, however, the idea that *Sepia* uses changes in buoyancy for locomotion in the sea but rather that it uses such changes to become approximately neutrally buoyant when it hunts over the sea bottom, and denser than sea water when it is resting on the sea bed.

This recent work shows therefore that although liquid is moved in and out of the shells of modern cephalopods in a less dramatic way than Robert Hooke imagined, yet liquid is used within all these shells as a ballast to regulate both density and posture.

The mechanism of pumping salts and water

The processes of emptying liquid from a newly formed chamber have been best studied in *Spirula* (figure 7b, plate 15). Here it has been shown that the osmotic concentration falls from that of sea water to about one-fifth sea water before the first bubble appears. Evidently most of the solutes are pumped out of the liquid within the chamber before water begins to leave the chamber. In *Sepia* it has been shown that the greater the pressure under which an animal has been living the lower is the osmotic concentration of the liquid within the cuttlebone. There is a good agreement of hydrostatic pressure differences between the gas inside the cuttlebone and the external pressure (which will tend to push liquid into the gas spaces of the cuttlebone) and osmotic pressure differences between the blood and the liquid within the cuttlebone immediately under the siphuncular surface. This strongly suggests that osmotic forces are used to control the flow of liquid into or out of the cuttlebone (Denton, Gilpin-Brown & Howarth 1961; Denton & Gilpin-Brown, unpublished observations referred to later in this paper).

The epithelia, which must do the work required to move liquid from the chambers of the shells, have been studied in both *Sepia* and *Nautilus* (see figure 12). They are about 100 μm thick and resemble other secretory epithelia. Their cells, which are packed with mitochondria, are closely joined on one surface. This surface is covered with microvilli whilst the other surface is folded to form canaliculi.

The fine structure of the shell of Nautilus in relation to its function

Recently with light, electron and scanning electron microscopes, excellent studies have been made of the various structures in the shell of *Nautilus* (Mutvei 1972; Gregoire 1962; Erben, Flajs & Siehl 1969; Wise 1969, 1970). Some of the results of these studies have been summarized by Mutvei.

The shell of *Nautilus* is made of two principal materials, aragonite crystals and conchiolin (a chitin-like substance or substances), but the dispositions and pro-

portions of these substances are varied in a very interesting way from one region of the shell to another. The main strength of the shell wall and of the septa and septal necks lies in their nacreous layers. These consist of conchiolin layers between whose interspaces tabular nacreous crystals composed of globular aragonite crystals are tightly packed (figure 11*a, c*, plate 16). These parts of the shell are impermeable to liquids and gases. The permeable part of the *Nautilus* siphuncular tube is the connecting 'ring' (a tube in *Nautilus*) which joins one septal neck to the next. Internally this consists of a horny tube made of many concentric conchiolin membranes composed of comparatively coarse fibres (figure 11*f*, plate 16). At the end proximal to the living chamber these membranes originate deep within, and are firmly anchored to, the nacreous layers of the septal neck and Mutvei has noted that the structural relation between the horny tube and the septal neck is analogous to that between the ligament and calcified valves in the lamellibranch shell. Distally from the living chamber the horny tube is joined to an annular calcified thickening of the next septal neck. The horny layer is undoubtedly the one which sustains the hydrostatic pressure of the sea which tends to explode the siphuncle into the chambers. External to the horny layer and surrounding the connecting ring and the septal neck is a 'chalky' layer formed almost entirely of irregularly arranged aragonite crystals (figure 11*b*, plate 16). This is the layer which Mutvei calls a spherulitic-prismatic layer. It is permeable to liquid and, when it is dry, acts like a wick quickly drawing water placed at its lower end upwards. Material like the chalky layer is also found in the lower external corners of the chambers. The external concave side of the chambers, i.e. the sides facing towards the living chamber, are covered with a porous layer, the semi-prismatic layer consisting of scattered crystals individually resembling those of the nacreous layer without being tightly packed. The whole of the inside walls of the chambers including the external surfaces of the siphuncle (i.e. the surfaces facing into the chambers) are covered with a thin conchiolin membrane (figure 11*e*, plate 16). This membrane and the semi-prismatic layer have the property of making the inside walls of the chambers wettable.

For *Nautilus* plausible functions can be assigned to these various structures. We know that most of the liquid within a newly formed chamber is removed relatively quickly yet, for the animal in its usual and very stable swimming posture, when about a half the liquid in a newly formed chamber has been removed the remaining liquid lies below the septal neck and is no longer in direct contact with the porous part of the siphuncular tube (figure 12). The chalky tube surrounding the connecting ring and the septal neck and the porous and wettable internal surfaces of the chamber will, however, still allow liquid to be drawn upwards to the permeable part of the siphuncular tube and so allow the pumping of liquid to continue and the chamber to be more completely emptied. At this time the main body of liquid within the chambers can only very slowly influence the relation between the liquid contained in the calcareous and horny siphuncular tubes (this has a volume of only one-thousandth that of the whole chamber) and

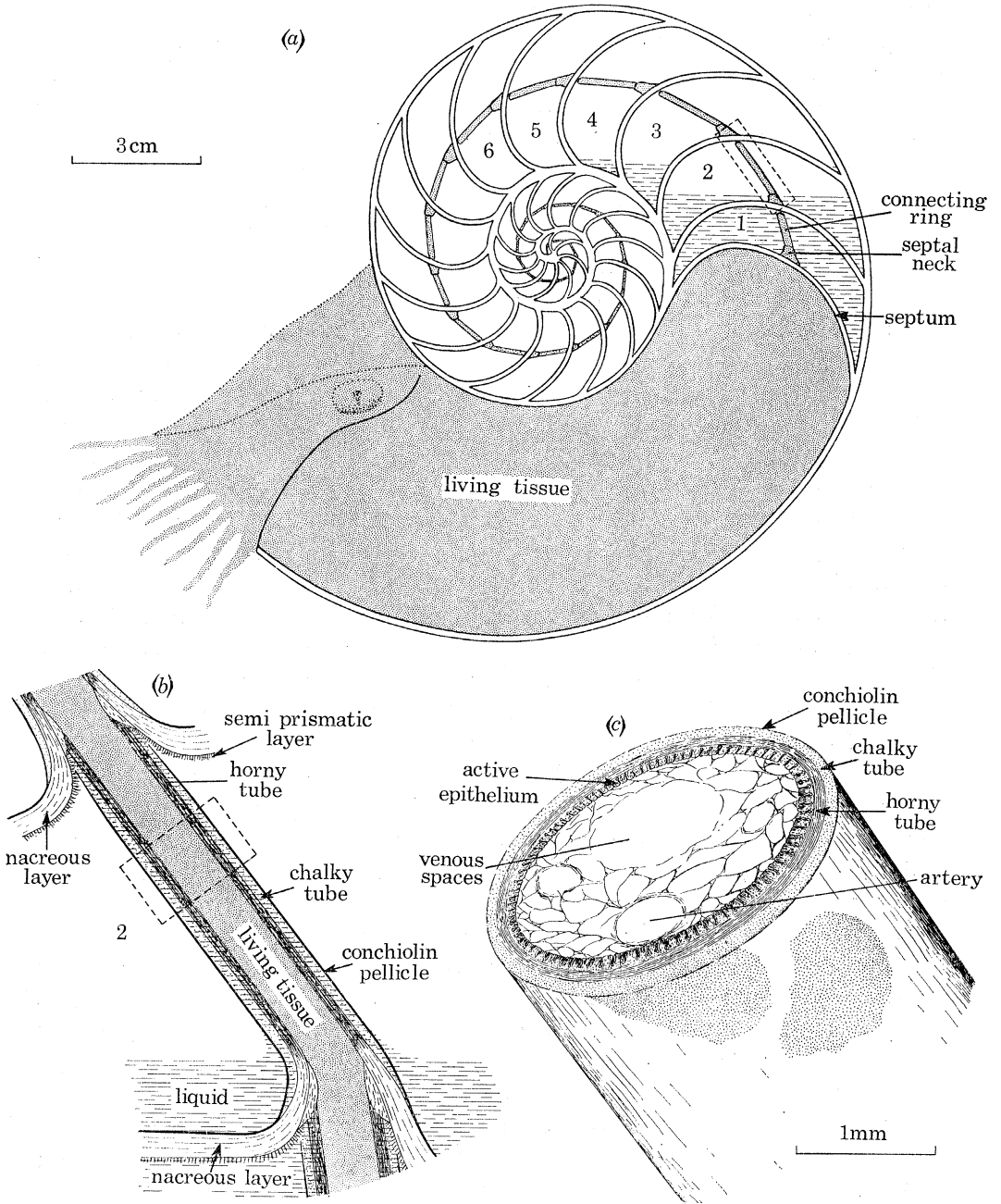


FIGURE 12. For description see facing page.

the active pumping epithelium. The composition of the main body of chamber liquid does not decide whether liquid passes either into or out of a chamber. Very likely in *Nautilus* as well as *Sepia* change of depth will involve a change in the equilibrium concentrations of salts on the low pressure side of the siphuncular wall. The virtual 'decoupling' of the main body of liquid within a chamber from that small fraction which is concerned in the pumping process means that when an animal changes depth only small amounts of salts or liquids have to be exchanged across the siphuncular wall to preserve near neutral buoyancy. Provided that a change of depth is not of very long duration, very little osmotic work will have to be done to prevent liquid moving either into or out of the chambers. We shall see later that a decoupling system of this kind is certainly effective in *Sepia*.

Structure and function in some other shells

Spirula and *Sepia*

In *Spirula* (figures 7*b*, plate 15, and figure 8) the porous part through which liquids can be exchanged between the living tissues and the insides of the chambers is restricted to a very small region of the siphuncular tube in the upper part of the chamber. In this animal there is no porous horny tube and the nacreous septal neck extends across the whole width of the chamber. A porous chalky tube, corresponding to the semi-prismatic layer in *Nautilus*, lines the septal neck and provides a connexion between liquid inside the chamber and the active epithelium of the siphuncle. Again we see that the siphuncle is a strong structure and that in the resting position the great bulk of liquid inside a chamber appears to be virtually decoupled from the region through which liquids leave the chamber. We have, however, to remember that *Spirula* is a small mobile animal and has been seen swimming head upwards.

With respect to its buoyancy *Sepia* has been more completely studied than any other cephalopod and E. J. Denton & J. B. Gilpin-Brown (unpublished observations) have worked on cuttlefish freshly caught at sea and on animals kept under

FIGURE 12. (a) Section of *Nautilus* showing position of animal within its shell. The living tissues pass in the siphuncular tube through all the chambers. The septal necks are impermeable to liquids. The connecting rings are permeable. (b) Detail of the part of (a) which is marked by a rectangle on the 2nd newest chamber showing (1) the nacreous layer which provides the main strength of the shell walls and the septa; (2) the horny conchiolin tube which is firmly anchored in the nacreous layer from which it arises and which provides the main strength of the siphuncle; (3) the 'chalky' porous tube (the spherulitic-prismatic layer); this holds some liquid and acts as a wick drawing liquid from the lower parts of the chamber to the porous region of the siphuncle; (4) the porous semi-prismatic layer; (5) the conchiolin pellicle which lines the internal walls of the chamber and the external wall of the siphuncle. (c) Perspective drawing of the section of the siphuncle marked by a rectangle on (b) with the living tissues of the siphuncle in place. Immediately inside the strong 'horny' tube lies the siphuncular epithelium which actively pumps liquid from the chambers of the shell. The centre of the siphuncle is filled by an artery and venous spaces.

various pressure in a special tank in the laboratory. The chambers of the cuttlebone become very thin as they approach the siphuncular region and they are, moreover, subdivided by conchiolin partitions and contain many pillars. We should expect therefore that the slowness of diffusion of salts along the chamber would make equilibration between the liquid inside the cuttlebone and that deeper within the chambers a slow process (Denton, Gilpin-Brown & Howarth 1961). Recent work in which the cuttlebone liquid was sampled at different depths within single chambers has confirmed this view. It was shown, for example, that when a cuttlefish is placed under an increased pressure it is several days before this change in pressure is reflected by a corresponding change in osmolarity of the liquid deep in the chamber while the liquid immediately inside the siphuncular surface becomes more hypotonic very quickly.

Some fossil animals

Many beautiful studies by palaeontologists have shown a bewildering variety in the form and fine structure of the shell and siphuncular tube which existed in the fossil cephalopods (see, for example, Flower 1964; Teichert 1964). It is very natural to assume, with Robert Hooke, that special features of shells were not 'lusus naturae or forms by chance to express varieties' but represented significant adaptations for particular functions. It is often not at all easy to think what these functions might have been but, although the modern work on living animals is very far from allowing us to understand all the structures which have been discovered it can sometimes give us considerable help. The experiments on modern cephalopods described above suggest for the fossil forms: (1) that a chamber being emptied or filled with liquid would always have had some region of its wall permeable to liquid. Studies on well-preserved fossil cephalopod shells show that they had such permeable regions and that these were always in the siphuncular tubes. These permeable regions did not all have exactly the same structure but this could hardly be expected in this great variety of animals. The three modern forms, *Nautilus*, *Spirula* and *Sepia*, are very different from one another in their siphuncular regions; (2) that the shell would be strong enough to withstand the maximum pressures to which the animal would be exposed in life but that the margin of safety would not be very large. This would mean that the depth ranges of fossil animals could be determined from the strengths of their shells. Westermann (1971) has examined the fossil shells of a number of ammonoids. He points out that the nature and properties of the siphuncular tube usually give a simpler indication of the strength of an ammonoid shell than do the main shell walls and septa which are often of a very complicated shape. He finds that the estimates of depth ranges indicated by his studies on siphuncles are compatible with previous estimates based on ecological evidence. In particular he found that the *Lytocerataceae* and *Phylloceratidae* almost certainly resembled present day *Nautilus* in depth range while the adults of the *Ammonitina* could generally not withstand the pressure at more than 100 m depth; (3) that newly formed chambers would

always contain liquid; (4) that liquid within the chambers of the shell would be used as a ballast regulating certainly the density and very likely the posture of the animal. Heptonstall (1970) has shown, for a number of ammonoids, that if the living tissues filled the living chambers of their shells and had densities like the tissues of modern cephalopods then they certainly all would have needed to have appreciable quantities of liquid within their shells to be brought close to neutral buoyancy, and (5) that shells of dead animals would often float to the surface and then be cast ashore even if their possessors, like *Spirula*, lived always at considerable depth. Collins & Minton (1967) have shown that the *Nautilus* shell will, if the tissues of the animal including the siphuncle are removed, quickly fill with liquid and become denser than sea water when placed under pressure in liquid. This would not, however, be true for an animal which died with its soft tissues in place. Denton & Gilpin-Brown (1971) have shown that while the chambers of the *Spirula* shell, from which the siphuncle has been removed, quickly fill with liquid when placed under pressure, this is not the case for an animal which has just died and in which the tissues remain in position. Evidence that a fossil shell floated and was cast ashore does not therefore allow us to conclude that the animal died in shallow waters.

We have also seen that in all three modern forms, *Nautilus*, *Spirula* and *Sepia*, in their normal swimming position, the relation of the liquid within the newly formed chambers to the permeable part of the siphuncular tube is such that the bulk of liquid can be almost 'decoupled' from the siphuncular epithelium. This arrangement certainly existed in very many fossil cephalopods and many of the nautiloids closely resembled modern *Nautilus*. As an interesting example of effective decoupling we show on figure 13, plate 17, part of the siphuncular tube of the endoceratoid *Dideroceras wahlenbergi* (or *Proterovaginoceras*). In this animal the septal necks were very long and each are extended into the siphuncular tube where it passed through the next oldest chamber. The only permeable regions of the wall of a chamber would in this animal be confined to the small region between the septal necks. In this it would be very like modern *Spirula*. Not all the fossil animals were like the modern ones in this respect. We can perhaps illustrate this and other problems in the interpretation of the structure of fossil cephalopods best by giving well studied examples.

The Ascoceratida (Orthoceratoidea)

In these animals the juvenile and mature animals had a very different relation between the position of the living tissues and the shell. The young animal had a straight conical shell whose siphuncle, like that of *Nautilus*, passed through the central parts of the chambers. The mature animal had an inflated shell which extended over the dorsal part of the living chamber; its chambers resembled those of the modern *Sepia* in being linked to the siphuncle only by long thin tubes (see figure 10*a*). In some way which is not known these animals lost the earlier formed part of the shell. Kerr (1931) has noted, however, that the gastropod

genus *Caecum* which periodically walls off the apex of its shell with a septum sheds the apical part of its shell so that this possibility is one that might have been expected of the cephalopods.

Promicroceras (Ammonoidea)

The siphuncle of this animal, unlike that of modern *Nautilus*, was ventrally placed within the chambers of the shell and so ran just inside the outermost walls of the chambers. According to Mutvei (1967), who has studied extremely well-preserved material, the siphuncular tube completely lacked an external chalky layer and consisted only of concentric conchiolin membranes. These membranes form a tube which clearly served the same function as the horny tube of *Nautilus* in being both permeable and strong but these two structures are not apparently homologous. Although the conchiolin membranes of the ammonoid are not continuous with the septal necks they are rigidly attached to annular calcareous deposits within the septal necks and again have a design which would allow them to sustain exploding pressures. The strength of the siphuncle in ammonoids is moreover often increased by their being held firmly against the chamber wall with bands of conchiolin (Westermann 1971).

The disposition and fine structure of the chambers and siphuncle in this animal are entirely consistent with the view that the shell functions in essentially the same way as that of the modern animals and that liquid was moved out of the chambers against the pressure of the sea through the siphuncle. Beyond saying this, it is difficult to be certain of anything. The absence of a permeable layer coupling the liquid in inaccessible parts of the chambers to the siphuncle means that the relation between liquid within the chambers and the siphuncle must have varied very greatly with the position of the chamber on the whorls of the shell. In chambers lying laterally or on the lower parts of the shell, liquid within the shells would have ready access to the siphuncle. In chambers lying on the upper parts of the whorls the liquid and siphuncle would be held apart. We do not know for certain the posture or the constancy of the posture in which the ammonoids swam, partly because we do not know which of the chambers of their shells contained liquid and which ones were empty. If, as seems likely, the position of a newly formed chamber in the Ammonoidea was usually the lower side of the shell then the relation between liquid and siphuncle would evidently be no problem in the pumping out of a new chamber.

Megateuthis gigantea (Belemnoidea)

This animal, which has also been recently studied by Mutvei (1971), had a siphuncle which passed through the chambers of the shell close to its ventral surface and it is thought to have swum usually in the same posture as the modern *Sepia* or *Loligo* for, at the apex of its shell, it had a typical belemnoid calcareous guard which would counterbalance the weight in sea water of the living tissues which were mostly anteriorly placed. There could have been no need for a chalky

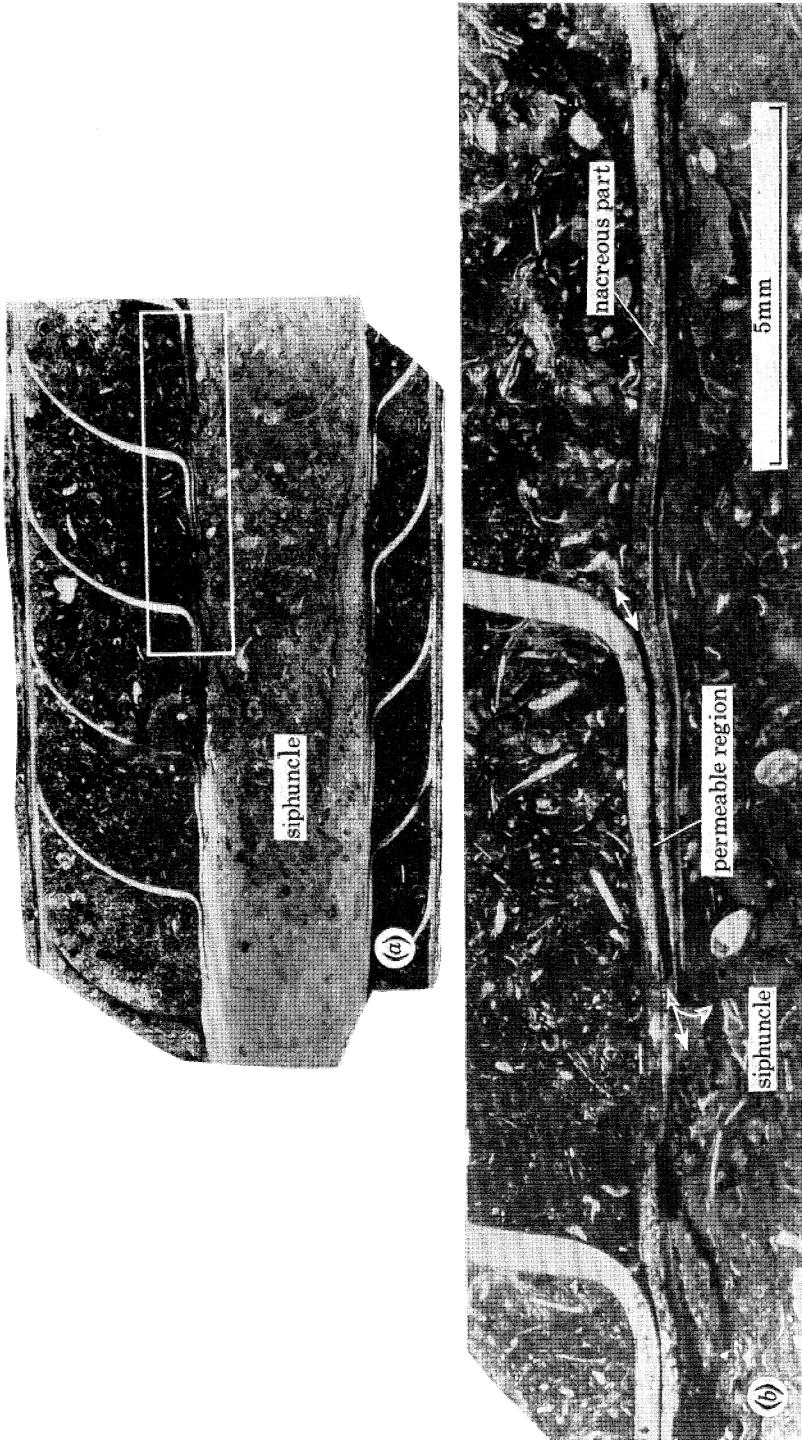


FIGURE 13. *Dideroceras wahlenbergi* (Foord) or *Protovaginoceras*, a fossil endoceratoid. (a) A longitudinal section showing some chambers with the siphuncle running through them. The septal necks are very long and only a small region could have been permeable to liquids. (b) Part of (a) enlarged. The part which was almost certainly the only permeable region is marked. (Sections and photographs made by Dr R. H. Flower (Flower 1964).)

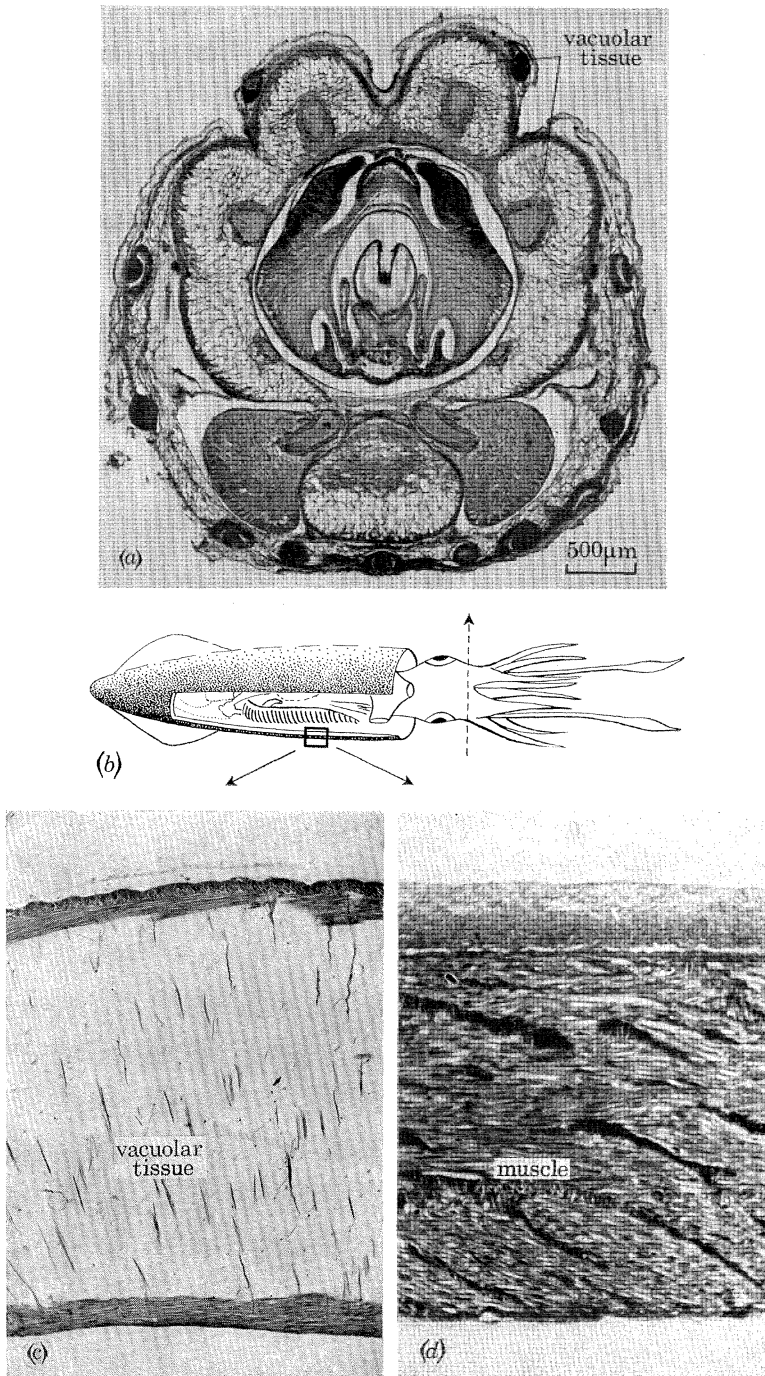


FIGURE 14. (a) A histological section through the buccal region of *Histiotteuthis* sp. made by Professor J. Z. Young. This animal has large amounts of ammonium in its body and the vacuolar tissues which hold the ammonium can be seen in its arms. (b) A generalized diagram of a squid. The positions of the sections (a) through the base of the arms and (c) and (d) of part of the mantle are shown. (c) and (d) Comparison of cross-sections of mantle of (d) *Sepia*, which uses a chambered shell for buoyancy, with that of (c) *Octopoteuthis* which has large amounts of ammonium in its tissues. In *Octopoteuthis* the musculature is very reduced and the major part of the tissue consists of the vacuoles which contain the liquid very rich in ammonium which give the tissue its positive buoyancy.

layer outside the siphuncular tube to conduct liquid to the pumping epithelium and no such layer is found. The connecting ring had a structure which shows it to have been both permeable and strong but it had, however, two unusual features: (1) the horny tubes which correspond to those found in *Nautilus* extended through two chambers so that within each chamber the connecting ring possessed two concentric horny tubes; (2) sandwiched between these horny tubes was a layer of aragonite crystals (like those of semi-prismatic layers in the shells of *Spirula* and *Nautilus*) which, from its structure, must also have been freely permeable to liquids. No simple reason for this rather complicated structure is known but it does seem that it would form a connexion for liquid movements between one chamber and its neighbours.

AMMONIACAL SQUID

In coastal waters, apart from the Sepiids, the common cephalopods, e.g. *Loligo* and *Octopus*, are muscular animals appreciably denser than sea water and so are the squid such as *Ommastrephes* and *Onychoteuthis* (the flying squid) which are commonly seen close to the surface of the sea from oceanographic ships. Until recently it seemed that, while the possession of neutral buoyancy must have been an essential step in the success of the early cephalopods, the later evolution of the squid and fish which could swim quickly and efficiently had given these animals such advantages that neutral buoyancy, even in the mid-waters, had become the exception rather than the rule. It now appears that this is not so and that enormous numbers of modern oceanic squid are neutrally buoyant. Most of these animals do not depend on chambered shells for buoyancy but on the possession of large volumes of body fluids which are isosmotic with sea water but contain largely ammonium chloride instead of sodium chloride.

The squid on which this phenomenon was first discovered belong to the family Cranchidae (Denton, Gilpin-Brown & Shaw 1969). The buoyant organ of a cranchid squid is an enormously enlarged coelomic cavity of volume almost two-thirds that of the animal's total volume. This cavity is filled with a liquid which has a specific gravity of between 1.010 and 1.012 while the sea water in which the animal lives has a specific gravity of about 1.026. The coelomic liquids of *Helicocranchia pfefferi*, *Verrilliteuthis hyperborea*, *Galiteuthis armata*, *Taonius megalops* and *Cranchia scabra* have all been analysed. The freezing-point depressions of these liquids are close to that of sea water. They contain very large concentrations of the ammonium ion, this ion being the principal cation while chloride is the principal anion, both ions being in concentrations of about 0.5 M (mol l^{-1}). The low relative densities of these liquids can be entirely accounted for by their composition in salts for an artificial solution mimicking them in ionic concentrations had a relative density of 1.011. These liquids are, for body fluids, very acid having pH's of around 5.

Since other families of squid do not have large coelomic cavities it seemed at first that the Cranchidae were a special case but we now know that the use of ammonium for buoyancy is by no means confined to this family. The accumulation

of strongly ammoniacal liquids, isosmotic to sea water, is certainly the principal buoyancy mechanism in the families Histiotteuthidae, Chiroteuthidae and Octopoteuthidae (Clarke, Denton & Gilpin-Brown 1969) and is almost certainly used by other families of squid. Dr Anna Bidder tells me that New Zealand fishermen who tried to use pieces of the giant squid *Architeuthis* for bait found they were useless for this purpose since they always floated upwards and, with Dr Clarke and Dr Gilpin-Brown, I have recently shown that pieces of mantle and arm contain very large (around 300 mM) concentrations of ammonium. Dr M. R. Clarke has also shown that large quantities of ammonia vapour were given off when sodium hydroxide was added to a piece of mantle of *Ancistrocheirus* of the family Enopteuthidae. Thus of the 25 families of squid in the world at least six use ammonium for buoyancy and Dr Malcolm Clarke tells me that of the other families which have not been tested for ammonium at least five are likely to be ammoniacal.

On figure 14, plate 18, we compare sections of mantle from *Sepia*, a muscular cephalopod which does not use ammonium for buoyancy, and *Octopoteuthis* which has ammonium in high concentrations in some of its tissues. The mantle of *Octopoteuthis* shows the vacuolar tissue which is characteristic of the buoyant tissues of the Octopoteuthidae, Chiroteuthidae and Histiotteuthidae. How very extensive the vacuolar tissue can be in such animals is illustrated by many histological sections made by Professor J. Z. Young and his colleagues, one of which is shown on figure 14*a*.

With Dr J. B. Gilpin-Brown and Professor P. G. Wright (unpublished work) I have shown that the nerves of such squid very quickly cease to conduct action potentials when placed in a liquid containing high concentrations of ammonium and that their blood contains ammonium in concentrations of only a few millimoles per litre. The ammonium in their bodies is therefore not distributed generally through their bodies but confined to the special tissues. Its retention in these tissues, as in the coelomic cavity, is almost certainly associated with the high acidity of the ammoniacal tissues (see Denton *et al.* 1969).

We might emphasize that the amount of ammonium which these animals contain is very large indeed. Squid normally excrete ammonia as the end product of their protein metabolism and we have concluded, assuming (1) that the squid eat only protein; (2) that ammonia is the only end product of protein metabolism; and (3) that they have a gross growth efficiency of one-third, that they have to store for buoyancy about 40% of all the ammonia produced during their lives to account for the quantity which they possess. The 'ammoniacal' system of buoyancy is evidently not one which could be used for rapid changes in buoyancy.

The distribution of buoyant tissues varies greatly from one species to another and so affects the postures of the animals. Thus in *Histiotteuthis* the ammonium is distributed throughout the body in such a way that very small forces enable it to adopt any attitude, while in the adult *Chiroteuthis* most of the buoyancy is contained in the enlarged 4th arms and this animal naturally rests with these arms pointing upwards.

The abundance of ammoniacal squid

We know very little about the lives or numbers of the larger animals which live in the deep ocean. The nets which are usually used for research on the mid-waters are small relative to commercial otter trawls and research ships can only tow these nets slowly. It is the common experience of those working on deep-living oceanic animals that the larger the net used the larger are the animals caught often even within one species of animal. The almost universal presumption is, therefore, that although the catches of the small slow planktonic animals by nets can give a good measure of their abundance, the numbers of the larger and more active animals are very much greater than net catches suggest. One very strong support for this presumption is that some animals which are not very commonly caught or never caught in mid-water nets are major foodstuffs for some large predatory cetaceans and fish. Thus the sperm whale lives very largely on squid species which are never or relatively rarely caught by research ships.

Recently Dr Malcolm Clarke (private communication) has made a detailed study of the stomach contents of sperm whales which had been caught at a number of whaling stations. He has also estimated the food intake of sperm whales in three ways: (1) by extrapolation from the food known to be eaten by other cetaceans in captivity (Sergeant 1969); (2) from oxygen consumption, computed from the number of breaths per day and the volume of the lungs. He made the reasonable assumptions that the ratio of tidal volume to lung volume and O₂ utilization are approximately the same for the sperm whale and for the cetaceans studied by Irving, Scholander & Grinnel (1941) and Ridgeway, Scronce & Kanwisher (1969); (3) by extrapolating curves of metabolism against mass obtained on smaller animals (Benedict 1938).

These estimates are in reasonably good agreement with one another. They give respectively 3.5, 2.3 and 1.9% for the fraction of its own body mass which the sperm whale would have to eat per day if its food was as nutritious as coastal squid.

Now the sperm whale is an animal of economic importance and the stocks of sperm whales in the world have been carefully studied by the International Whaling Commission. Dr R. Gambell (private communication), who has played a major role in these studies tells me that there are probably approximately 1¼ million sperm whales in the world and that their combined mass would be about 11 million metric tons (tonnes). Of these whales the exploitable stocks of larger animals is a much smaller number being about 400 000 in the southern hemisphere.

By bringing this data together Clarke has been able to give estimates of the world catch of squid by sperm whales and these turn out to be astonishingly large.

If we take the lowest of Clarke's values for the food intake of a sperm whale, i.e. 1.9% of its own mass per day in food like coastal squid we find that the sperm whale needs about seven times its own mass of such food per year. The food eaten by sperm whales is, however, on the average less nutritious than coastal squid.

Clarke found that sperm whales caught at whaling stations at Durban (South Africa), Donkergat (South Africa), Albany (Western Australia) and in the Antarctic had all been living almost entirely on squid and that the fractions by mass of ammoniacal squid in their diets were 75, 59, 53 and 78 % respectively. These ammoniacal squid are relatively poor as a source of energy. They are not very muscular (figure 14, plate 18), consisting largely of a solution of ammonium chloride and two specimens analysed by Clarke *et al.* (1969) contained relatively little protein. This means that sperm whales probably have on the average to eat not 7 but 14 or more times their own mass per year. We find therefore that the total mass of squid eaten by sperm whales in the world is probably over 150 million tonnes a year and that the mass of ammoniacal squid eaten is probably over 100 million tonnes per year. Even if we confine our calculations to the exploitable stock of sperm whales in the southern hemisphere, i.e. the whales studied by Clarke, we find a corresponding figure of about 76 million tonnes per year.

These masses refer of course only to that fraction of the ammoniacal squid which are caught by sperm whales. The stock on which the sperm whales prey must be several times larger. A total mass of several hundred million tonnes is a large one for a group of animals even on a world scale. Thus the mass of fish, including squid, caught by all the fishing fleets of the world is about 60 million tonnes (Gulland 1971) and the total mass of ammoniacal squid is probably comparable to that of all the humans in the world taken together. Yet these squid are animals which might from the catches in nets be thought relatively rare.

Buoyancy and the evolution of cephalopods

The two buoyancy mechanisms described here both depend on relatively small adaptations of features found in other molluscs.

Kerr (1931) pointed out that among the gastropods there are cases in which the visceral hump becomes withdrawn from the apical part of the shell, perhaps following the shrinkage of the gonad during the breeding season. In such animals the mantle surface, which has lost contact with the inner surface of the shell, sometimes continues its shell-forming activities and forms a 'septum' walling off the empty part of the shell. This process may be repeated several times so that the apical part of the shell cavity becomes divided into a series of chambers and in *Euomphalus* there are often several internal septa which are concave like those of *Nautilus*. In an animal living in shallow water, e.g. in the English Channel, the pumping of salts out of a chamber which would cause water to be drawn out of the chamber by osmotic forces requires nothing remarkable of the pumping mechanism. It is known that the giant nerve axon of the squid *Loligo* can pump sodium ions out of itself against gradients greater than 10:1 (Hodgkin 1964) and a pump which could work against gradients much less than this would allow the siphuncular epithelium of the cuttlefish to pump liquid from its shell at a greater depth than that at which this animal lives.

Ammonia is an end product of protein metabolism in squid, and *Sepia*, which

does not rely on the accumulation of ammonia for buoyancy produces an acid urine in which ammonia, largely in the form of ammonium, is accumulated to concentrations of over 100 mM. The system of control apart, it seems a relatively small step to evolve the buoyancy mechanism of the 'ammoniacal' squid.

Despite their basic simplicity these two mechanisms have played a decisive role in the successful evolution of the cephalopods. Packard (1972) has made a fascinating study of the convergence and limits of convergence of cephalopods and fish. He argues strongly that the convergence, e.g. of the form of the eyes, has been due not merely to similar demands of the marine environment but to dynamic interactions between the cephalopods and the vertebrates. The combination of an efficient locomotion, based on jet propulsion, and near neutral buoyancy, based on the chambered shell, permitted the success of the Palaeozoic cephalopods, then the highest animals in the sea. The great virtues of their shells were that they provided protection and gave neutral buoyancy in a way which allowed vertical migrations to be made without disturbance of buoyancy and at little metabolic cost. Their limitations were that they were often cumbersome and that they were limited in the lower depths to which they could be safely taken without mechanical disaster. Thus a *Nautilus macromphalus* with living tissues weighing 300 g in air needs a shell weighing about 200 g in air to allow it to descend to only 500 m depth and no less than 80% of the space within this shell is needed to buoy up the material of the shell itself. Clearly the greater part of the volume of the oceans, i.e. the part below say 600 m, would be inaccessible even to relatively small chambered shelled cephalopods like *Nautilus*. Before the competition from the fishes became very severe the cephalopods could, however, dominate the rich upper layers of the seas and oceans. Packard argues that buoyancy control gave the cephalopods their main advantage during the Late Palaeozoic and throughout much of the Mesozoic and that when the vertebrates invaded the adaptive zone of the cephalopods the latter had to 'move' in the direction of the vertebrate design or be confined into 'peripheral' habitats such as the deeper waters of the oceans. Clearly the evolution of the mechanism whereby ammonium could be used for buoyancy played a major role in allowing the cephalopods to colonize very extensively the deep oceans which, after all, constitute the largest living space in the world.

An abundance of life in the deep oceans ought not perhaps to surprise us, Robert Hooke write on this subject 'However, I think, that such Objections as most will be apt to make, that Animals and Vegetables cannot be rationally supposed to live and grow under so great a Pressure, so great a Cold, and at so great a Distance from the Air, as many Parts at the Bottom of very deep Seas are liable and subject to; I say, I think that these Objections may be easily answer'd, by shewing that they all proceed from wrong Notions that Men have entertain'd, from the small Experience they have had of the Effects, and Powers, and Methods of Nature, and a few Trials will easily convince them of the Erroneousness of them. We have had Instances enough of the Fallaciousness of

such immature and hasty Conclusions. The Torrid and Frigid Zones were once concluded uninhabitable; and to assert *Antipodes* was thought atheistical, heretical, and damnable; but Time has discover'd the Falsity and Narrowness of those hasty Conclusions.'

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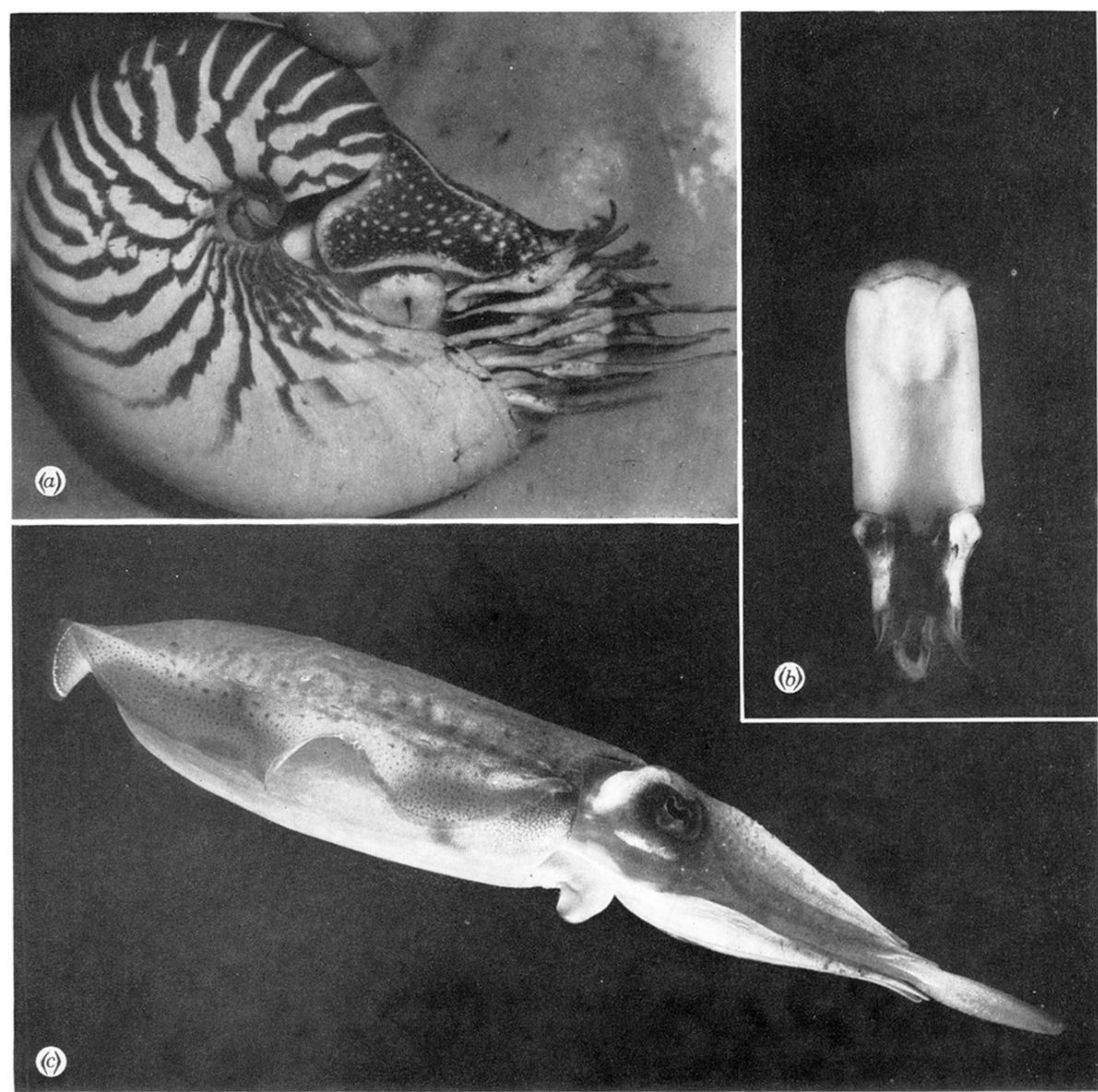
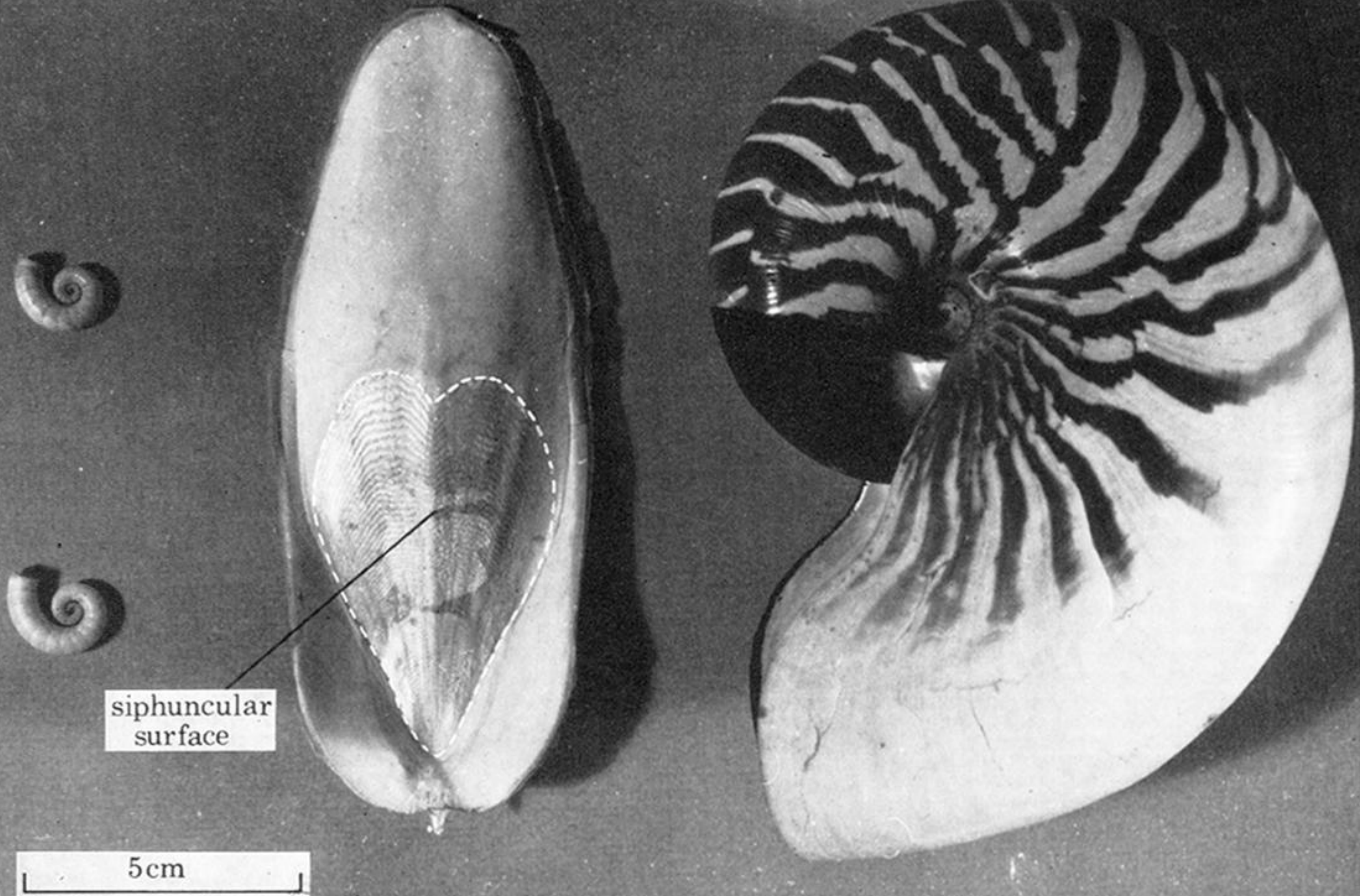
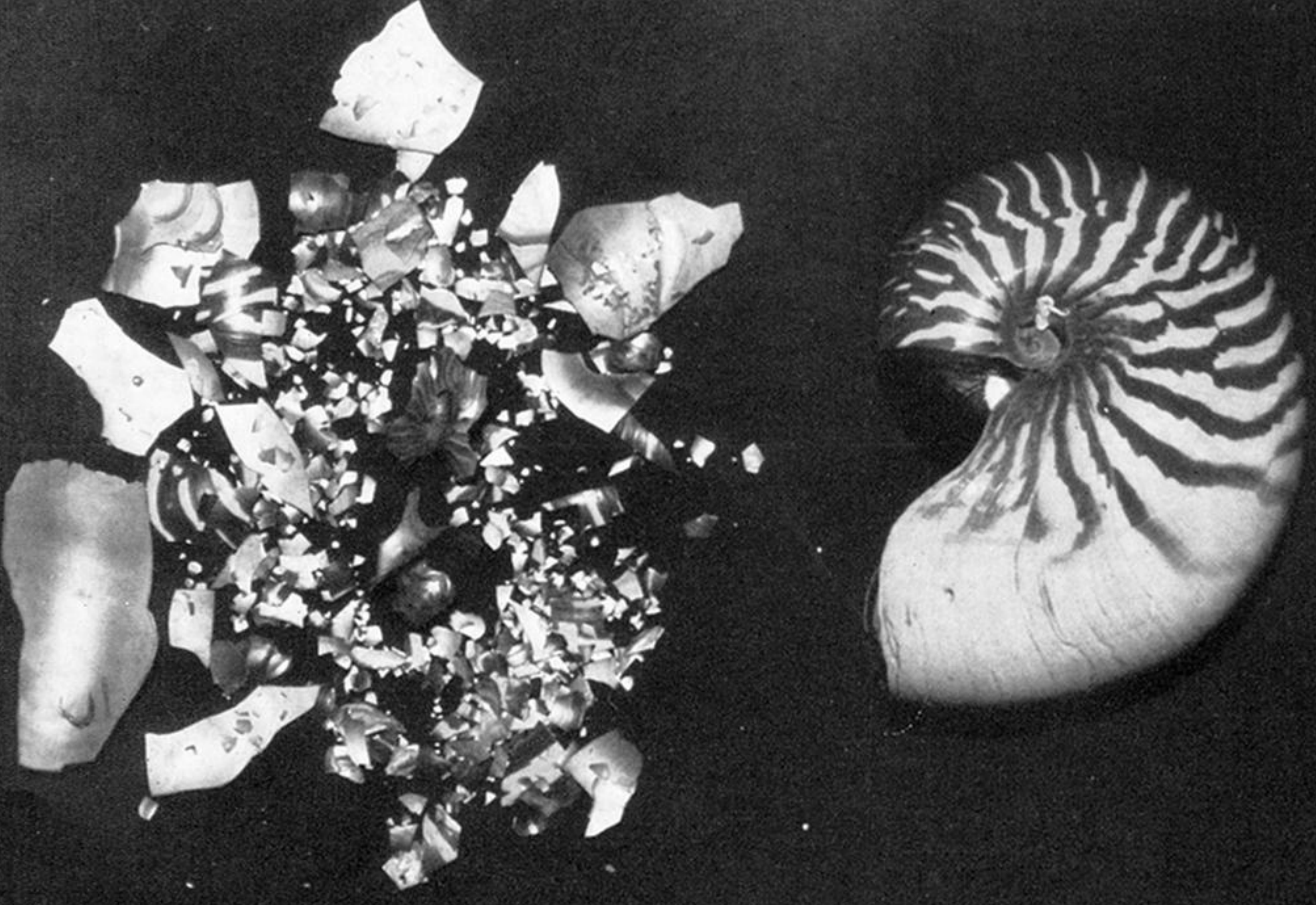


FIGURE 1. Photographs of living specimens of (a) *Nautilus macromphalus*; (b) *Spirula spirula*; and (c) *Sepia officinalis*. The magnifications are $\times 0.5$, $\times 0.6$, and $\times 1$, respectively. The photographs are by Dr J. B. Gilpin-Brown, Mr P. M. David and Mr D. Nicholson respectively.

2

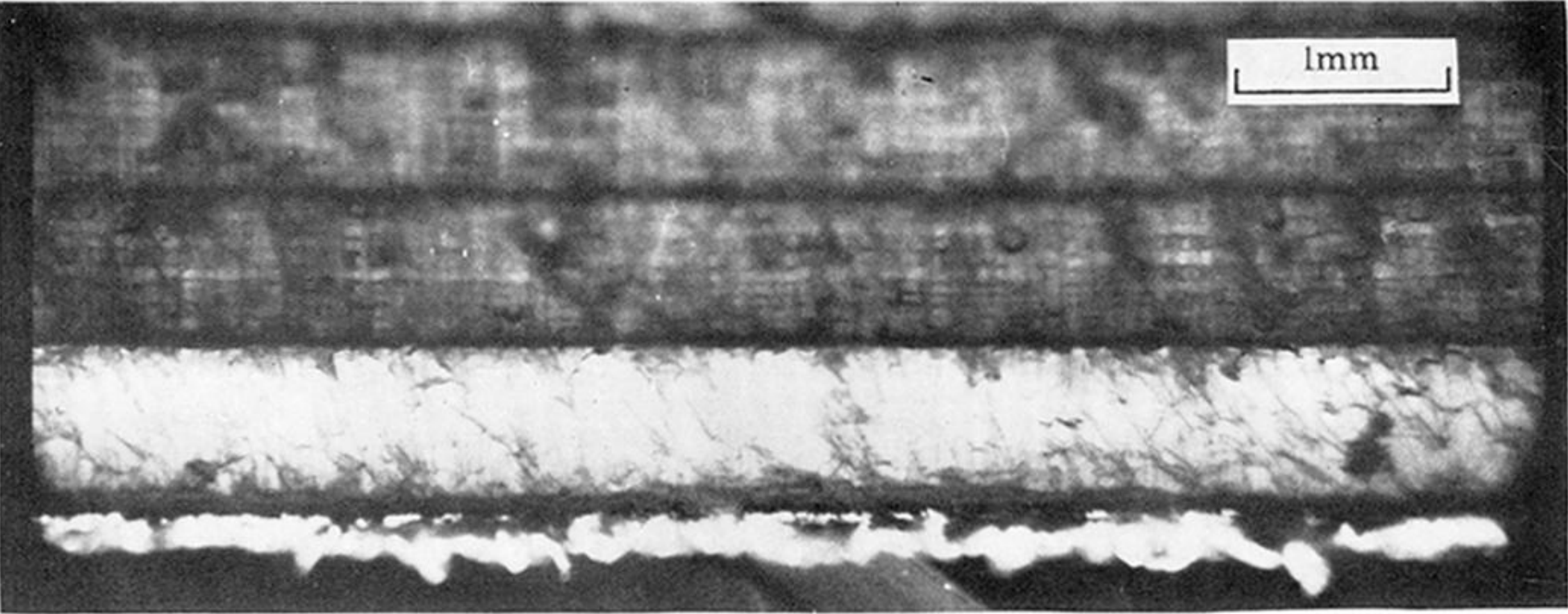


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FIGURES 2 and 3. For description see facing page.

(B)



(C)

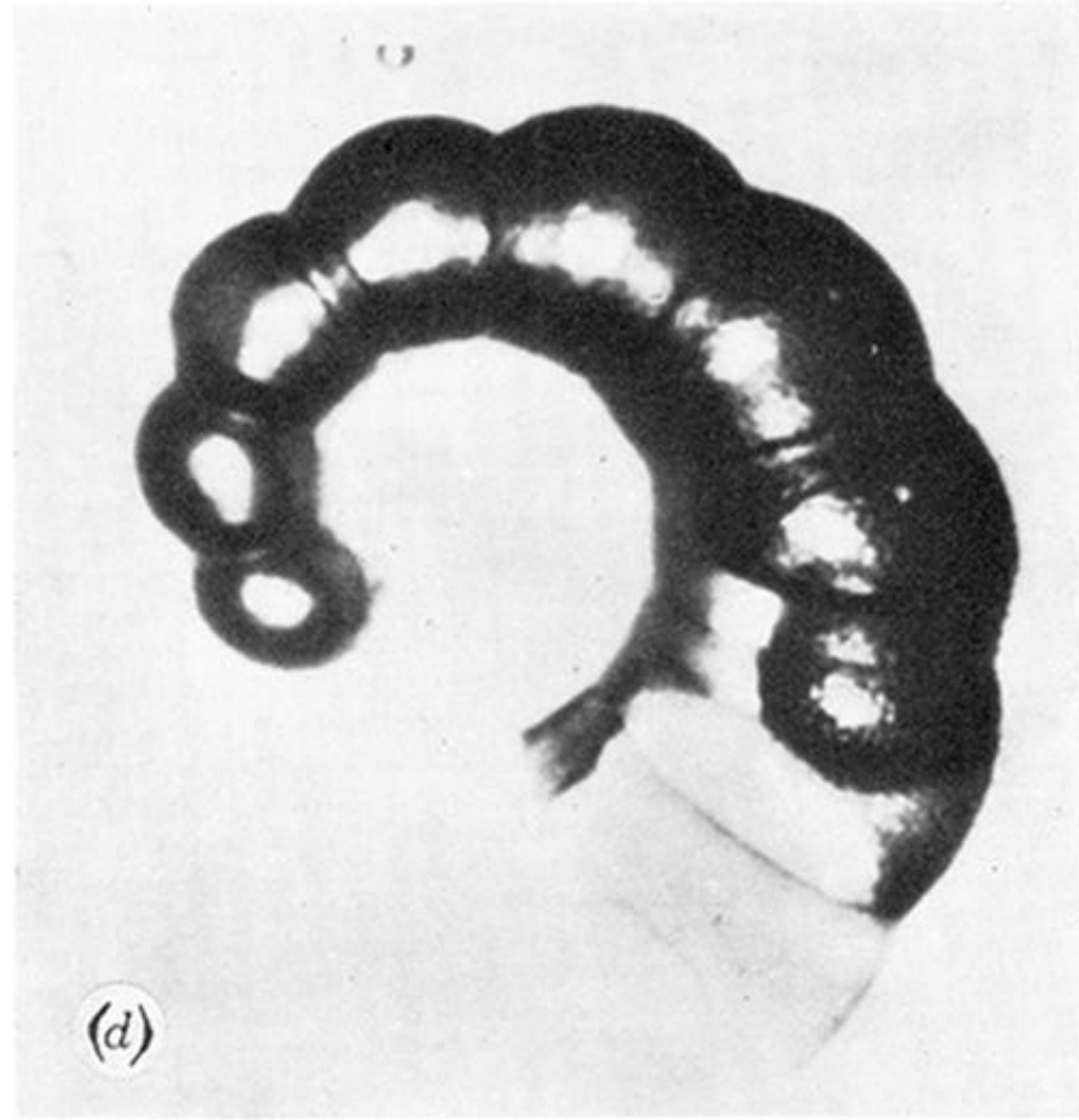
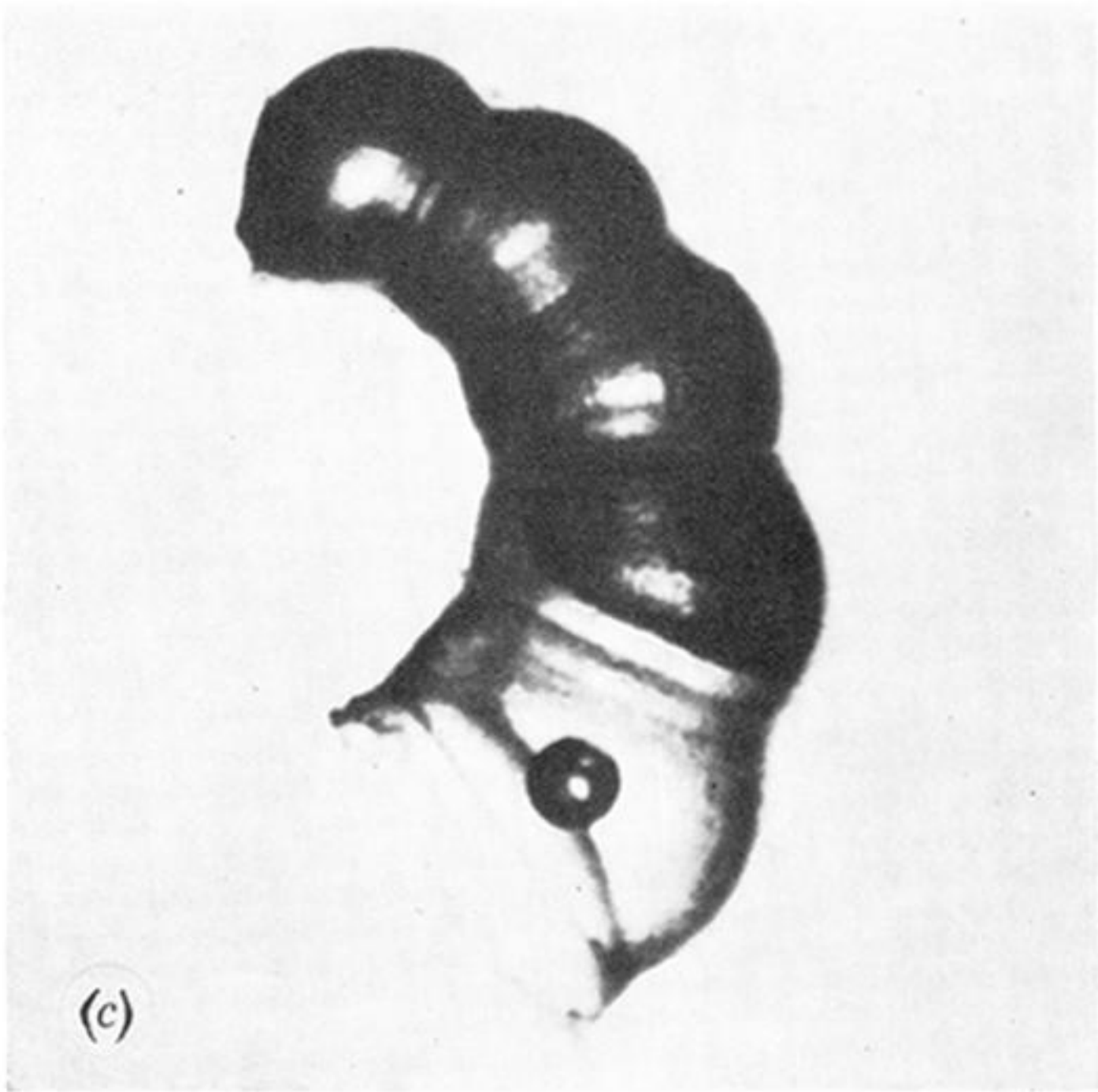
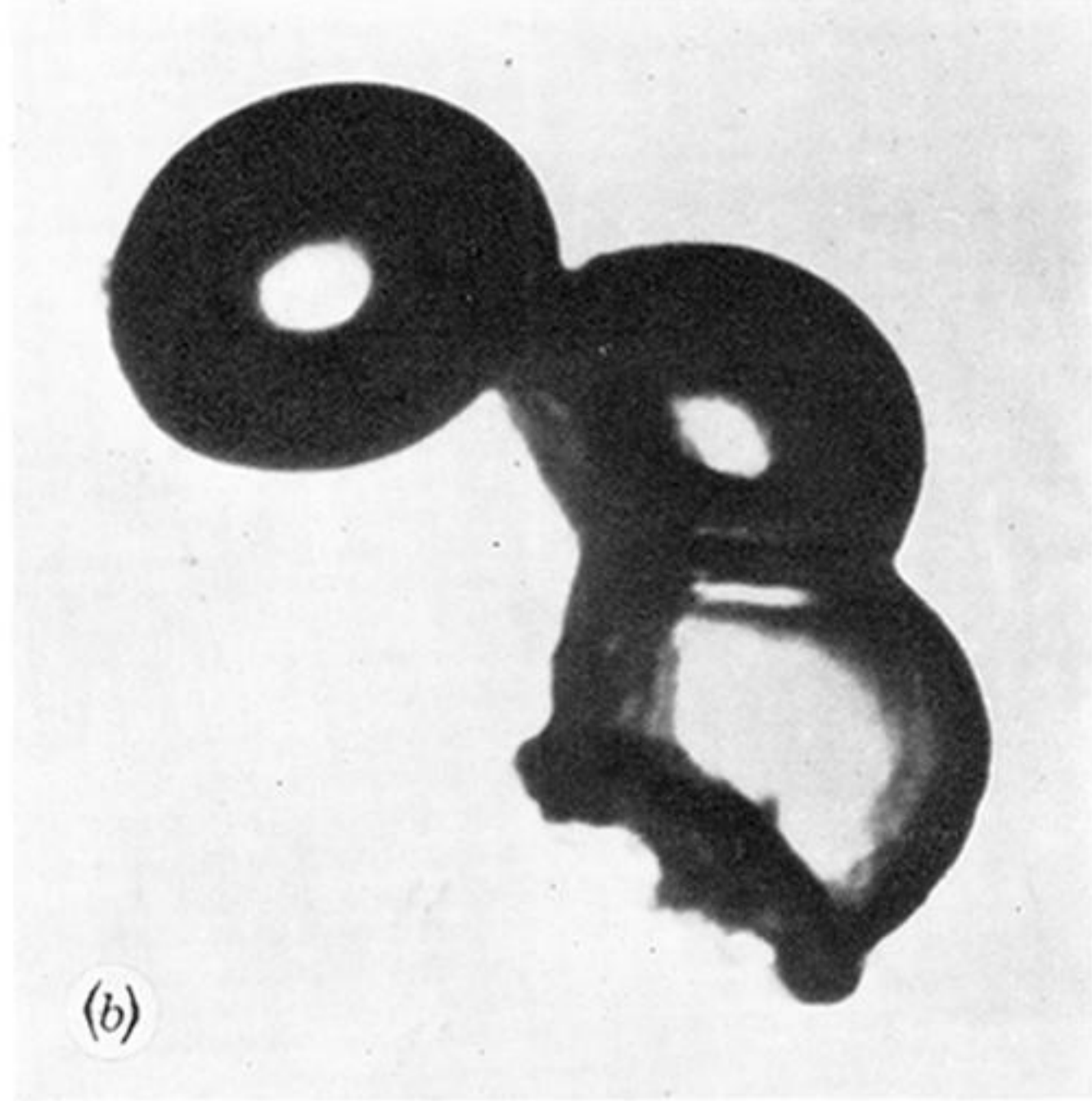


FIGURE 7 B, C.

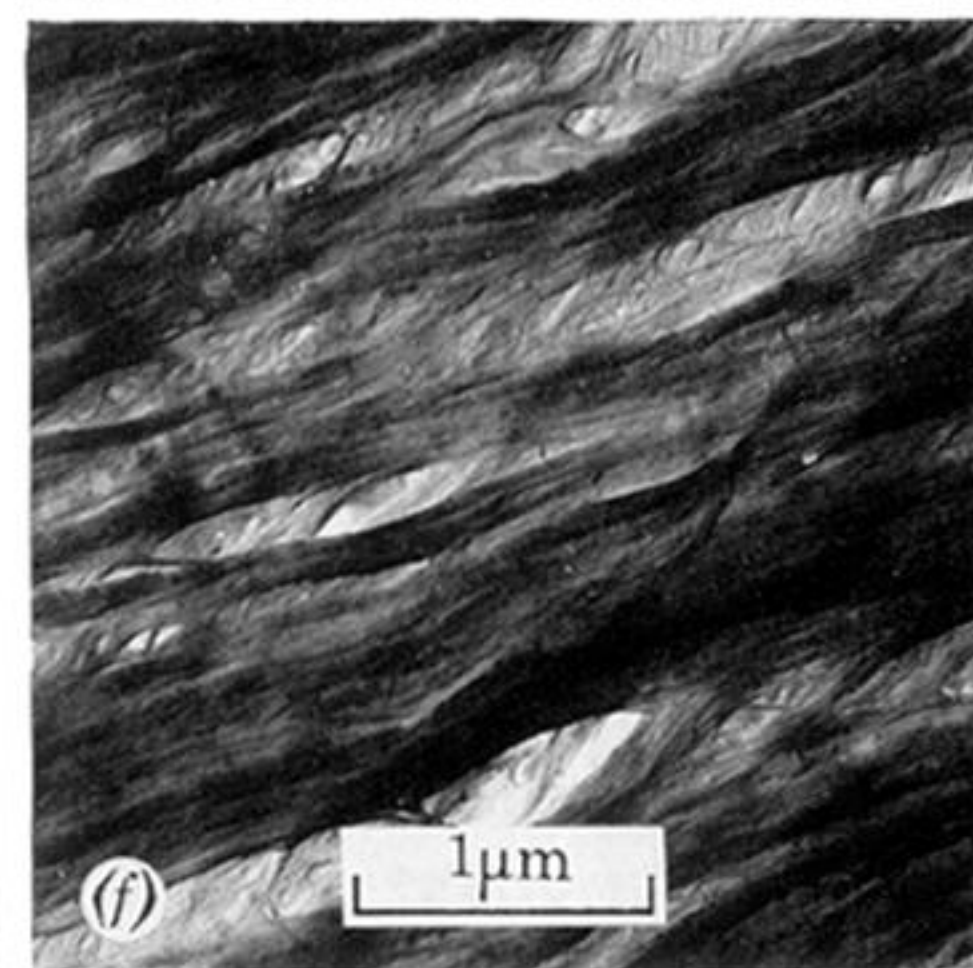
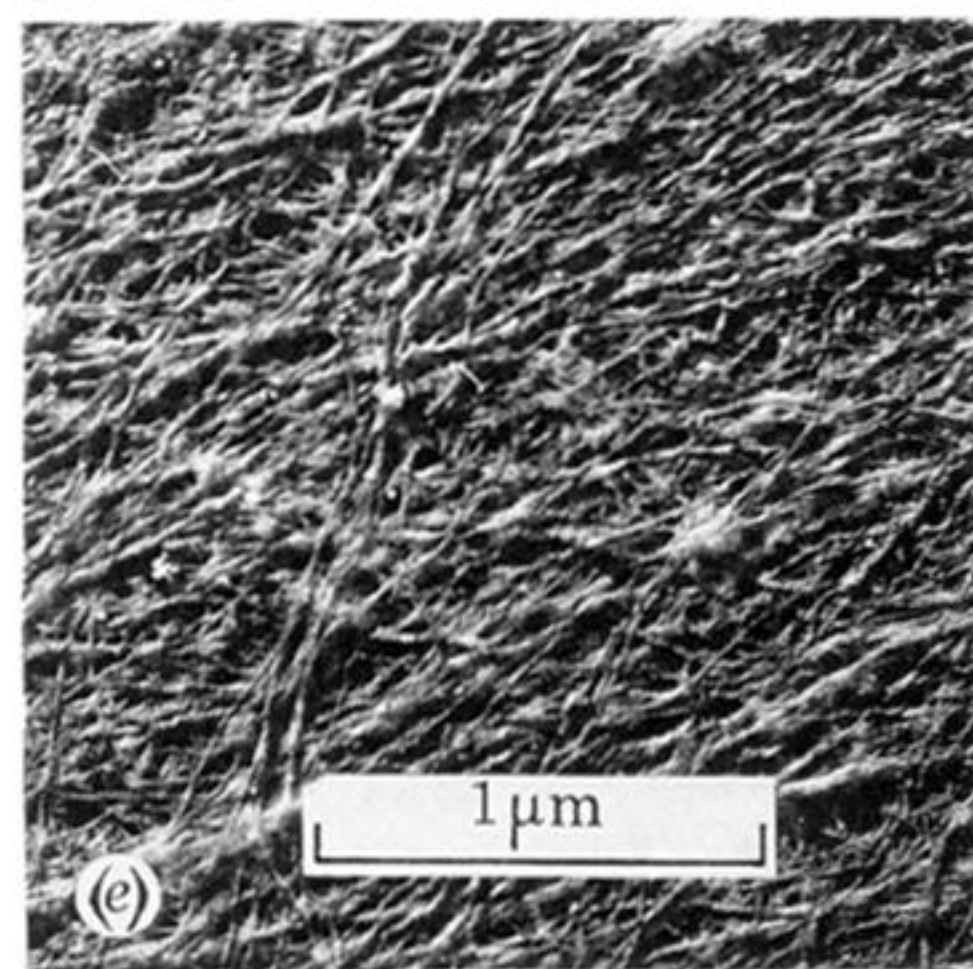
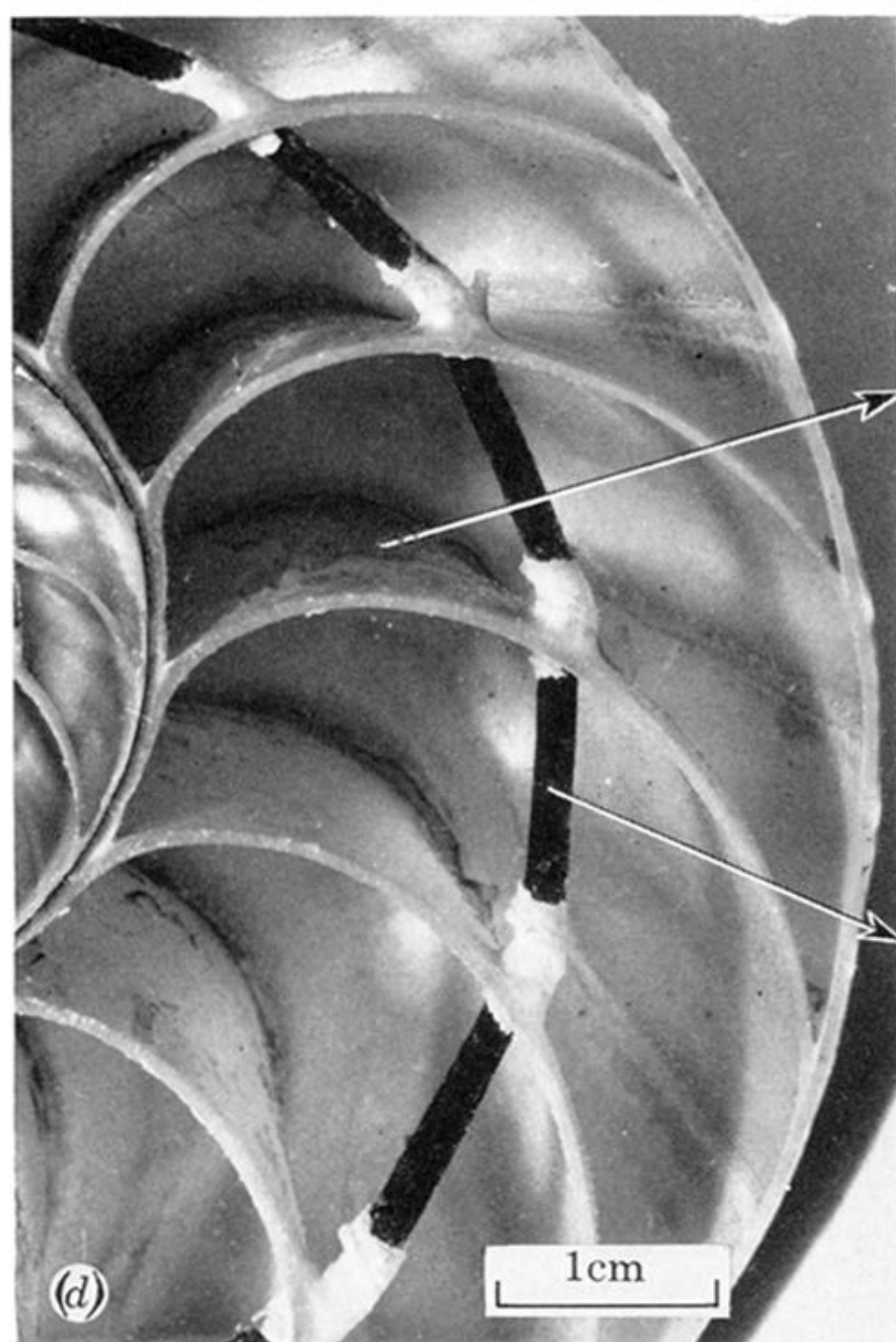
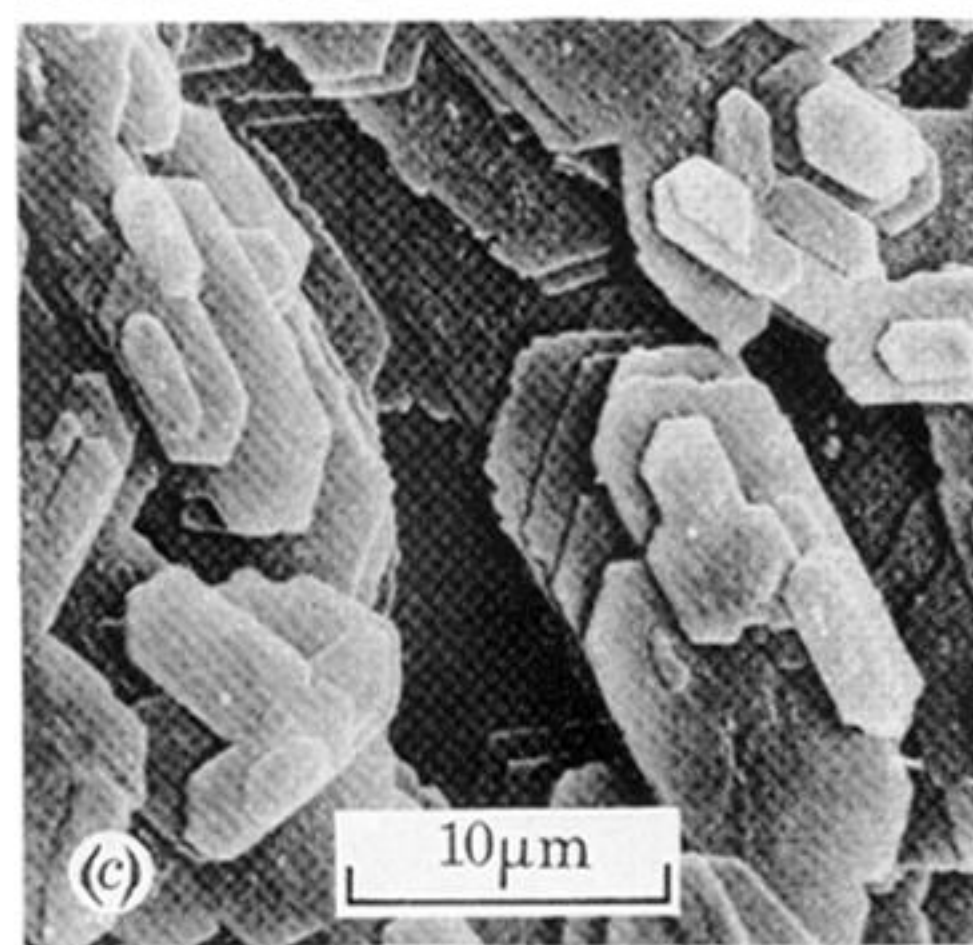
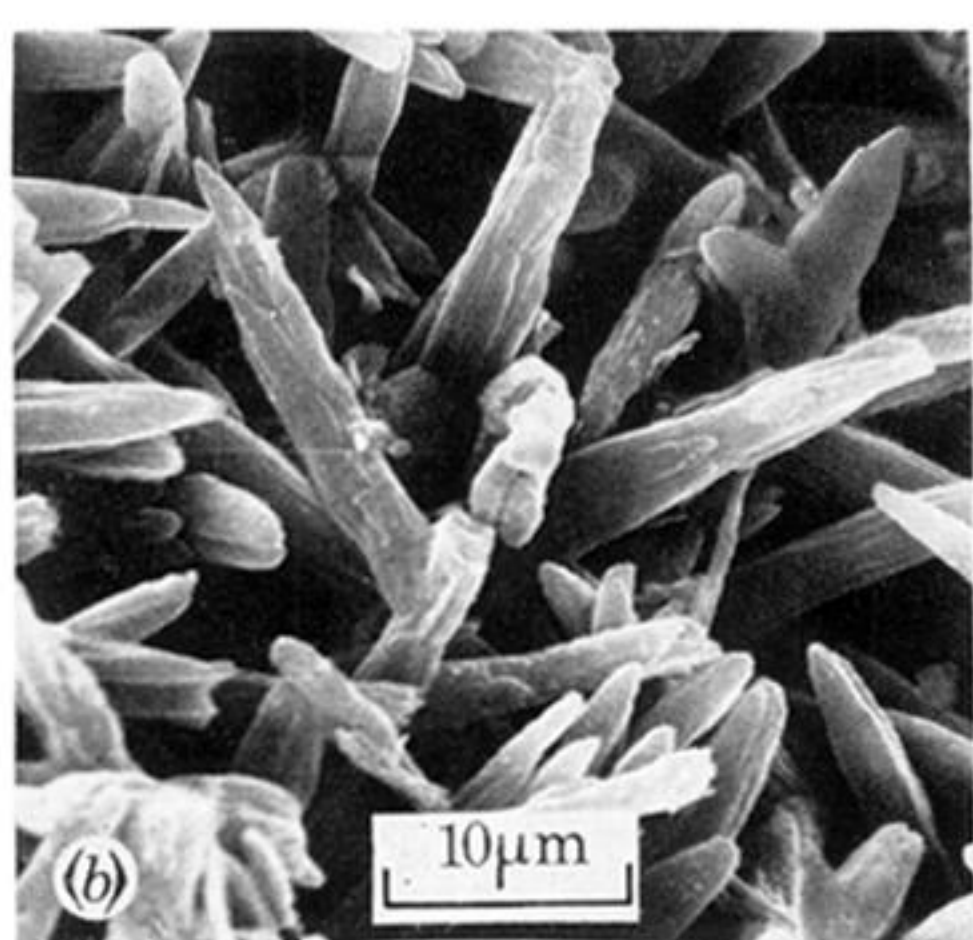
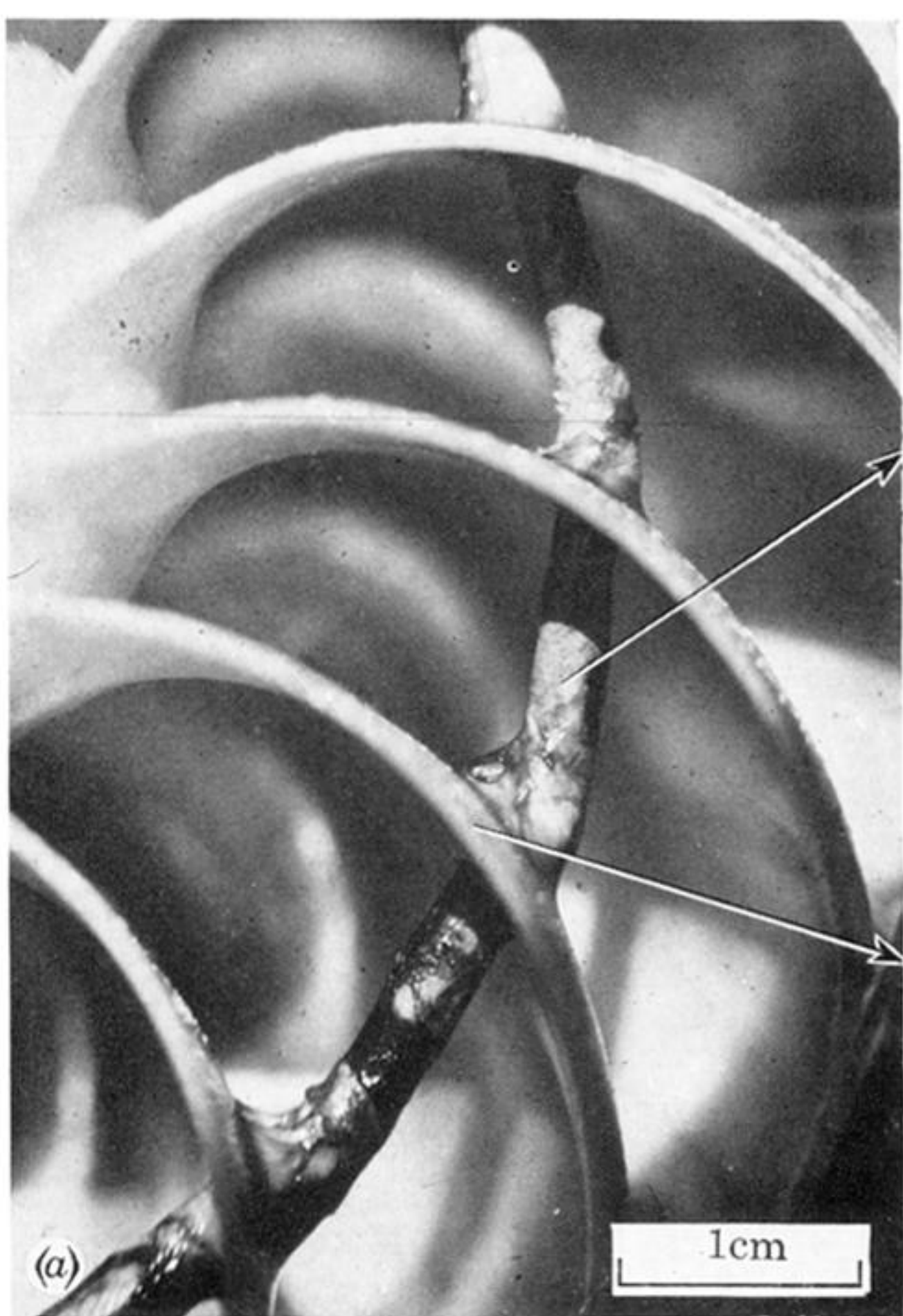


FIGURE 11. For description see facing page.

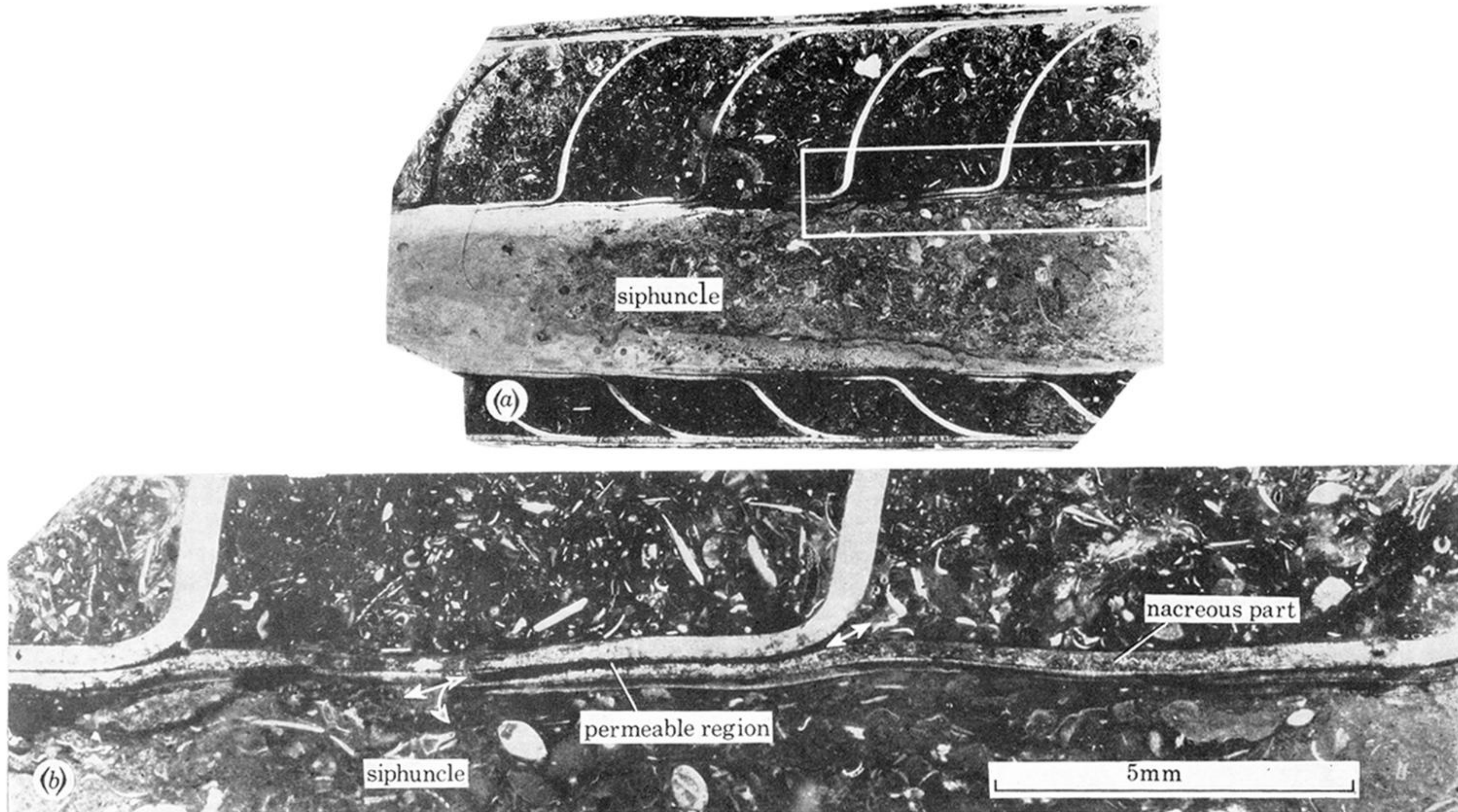


FIGURE 13. *Dideroceras wahlenbergi* (Foord) or *Protovaginoceras*, a fossil endoceratoid. (a) A longitudinal section showing some chambers with the siphuncle running through them. The septal necks are very long and only a small region could have been permeable to liquids. (b) Part of (a) enlarged. The part which was almost certainly the only permeable region is marked. (Sections and photographs made by Dr R. H. Flower (Flower 1964).)

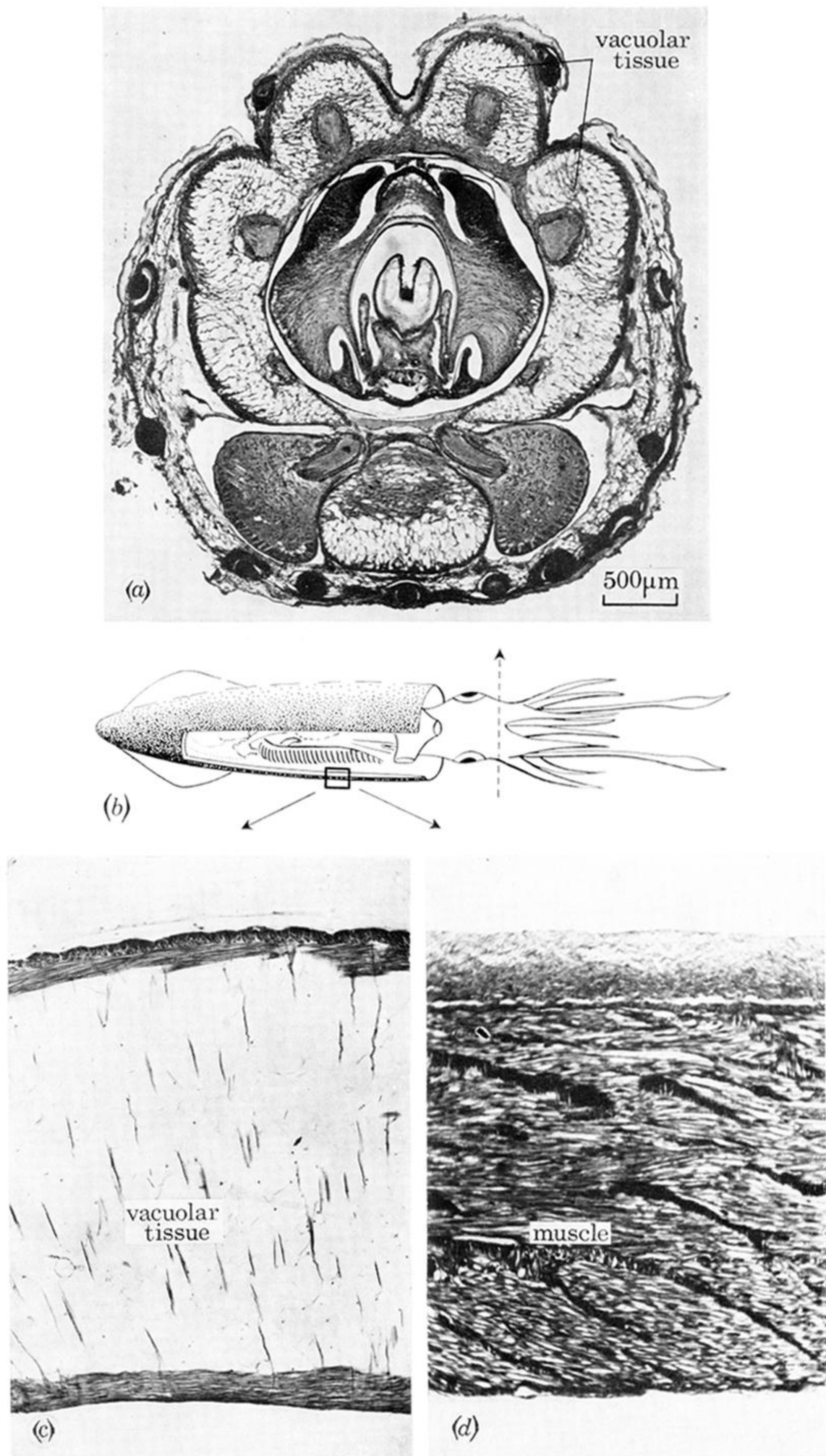


FIGURE 14. (a) A histological section through the buccal region of *Histiotteuthis* sp. made by Professor J. Z. Young. This animal has large amounts of ammonium in its body and the vacuolar tissues which hold the ammonium can be seen in its arms. (b) A generalized diagram of a squid. The positions of the sections (a) through the base of the arms and (c) and (d) of part of the mantle are shown. (c) and (d) Comparison of cross-sections of mantle of (d) *Sepia*, which uses a chambered shell for buoyancy, with that of (c) *Octopoteuthis* which has large amounts of ammonium in its tissues. In *Octopoteuthis* the musculature is very reduced and the major part of the tissue consists of the vacuoles which contain the liquid very rich in ammonium which give the tissue its positive buoyancy.