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An octopus, *Ocythoe*, with a swimbladder and triple jets

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SUMMARY

A young female of the rarely seen pelagic octopod *Ocythoe tuberculata* (Rafinesque, 1814) (Argonautoidea) survived for two days in captivity. It possessed a swimbladder and controlled its buoyancy. When swimming, the dorso-lateral corners of the mantle aperture were converted into dirigible structures ('accessory funnels'), which jetted water from the upper chamber of the mantle cavity forwards, upwards, sideways or backwards. The dorsal sac or swimbladder lies on top of the visceral mass, has a duct into the mantle cavity, is supplied with a nerve and blood vessels and in immature specimens has thick gelatinous walls which contract peristaltically and contain spherical 'amoeboid' cells. The lumen is lined by a cuboidal epithelium 7 μm thick. In a ripe (2.2 kg) specimen the walls are less gelatinous and the lumen is large and permanently expanded (volume 110 ml). The living ocythoe was negatively buoyant when delivered to the laboratory and regained and lost buoyancy twice during captivity. On one occasion it was observed to release gas as it plunged to the bottom. The origin and nature of the gas is not known. Cephalopods have a variety of mechanisms for buoyancy control but *Ocythoe* appears to be the only species with a swimbladder. The structure is absent in the dwarf male. Probably it is derived embryologically from the shell Anlagen.

1. INTRODUCTION

Ocythoe tuberculata (Rafinesque, 1814) is a robust epipelagic octopod with a world-wide distribution (Roper & Sweeney 1975). In colour and in life-style it compares with some of the agile blue-fish of open waters. Verany (1847–51) believed that it roams the Mediterranean in the company of others of its kind ('espèce voyageuse que parcourt la Méditerranée en societé'); here it is preyed upon by swordfish and other top predators (Bello 1991; Carlini *et al.* 1992). It is only occasionally encountered in inshore waters, however, and being both elusive and unmarketable has been poorly studied. One of its adaptations to nektonic life is ovoviviparity.

The existence of a swimbladder in *Ocythoe* was briefly reported more than twenty years ago while reviewing the adaptive radiation of cephalopod buoyancy mechanisms (Packard 1972). It was noted that the swimbladder is fully developed only in females that are heavy with young. The original finding was based on one living specimen brought into the Naples Zoological Station and on old material from the same institute's conservation department. But no account of the organ has been published since.

In February 1990 a second live specimen brought into the Station revealed that this species has yet another adaptation for nektonic life: accessory dirigible jets high up on the side of the animal. This paper describes the accessory 'funnels' producing these jets, as well as the anatomy and functioning of the dorsal sac, or swimbladder (both names are used as the structure may be more than just a buoyancy organ).

The material we have available is based on the two fresh specimens and others in the British Museum of Natural History, National Museum of Scotland and Museum of Comparative Anatomy, Genoa. All specimens were females (table 1): the two living ones sub-adult. One of the specimens (III) and two further immature specimens (of 62 and 80 mm mantle length) have been examined by Dr M. Nixon and Professor J. Z. Young who have kindly lent us their sections and discussed the bladder. Their findings will be recorded in a forthcoming book (Nixon & Young 1996). A 'dwarf male' – which also leads a pelagic life in the tests of salps – has been sectioned, but no swimbladder was found. Histology was performed by Mrs K. Grant, Physiology Department, University Medical School, Edinburgh.

2. OBSERVATIONS ON THE LIVING ANIMAL

(*a*) *Behaviour in captivity: the question of buoyancy*

In view of the discoveries made on the first of the living specimens, the behaviour of the second, juvenile specimen acquired 27 years later, was watched to see if the animal appeared positively, negatively or neutrally buoyant (indicated below as (B^+), (B^-), or (B^0)). The following, summarized in figure 1, is from notes made at the time.

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Table 1. *Female* Ocythoe tuberculata *in this study first observed alive (captured in the Bay of Naples) or as preserved specimens from various sources*

(Sources of preserved specimens: SZ, Naples Zoological Station; RSM, Royal Scottish Museum, Edinburgh. All specimens originally from the Mediterranean. Masses in parentheses are of fixed specimens in Mediterranean seawater.)

		body mass (in seawater)/g	mantle (ML) or body (BL) length/mm	volume of sac(†) or lumen(*)/ml	dimensions of sac
I[b]	immature (SZ)	85		1*	
II[a]	immature (SZ 7/2/90)	160 (3.5)	115 (BL)	4.6†	
III[b]	immature	245	100 (ML) 118 (BL)		49 × 9 × 20 mm (25 mm at base)
IV[b]	immature (Genoa)	420 (9.5)	150 (ML)		
V[a]	immature (SZ 4/63)	700	185 (ML)	32†	145 × 12 × 36 mm (50 mm at base)
VI[b]	mature (SZ)	1600		42*	
VII[b]	ripe (SZ)	2200		110*	
VIII[b]	mature (RSM)	2000	172 (ML) 210 (BL)		

[a] Alive.
[b] Preserved specimen.

On arrival in the laboratory, the ocythoe – captured earlier that morning by local anchovy fishermen – was put in a large circular tank of running seawater (3 m diameter, 1 m deep) in the basement animal-holding facility of the Naples Zoological Station. (The basement was illuminated at night as well as in the day.)

(i) *First day*

1030 h. On being placed in the tank the ocythoe jetted straight to the bottom and stayed in a corner made by a brick (B^-). Later found swimming below the surface (B^0), colour orange-brown at sides and tips of arms, blue, changing to violet, above. *1230–1330 h.* Ocythoe found cruising at the surface with the top of the mantle just projecting above the water (B^+). On the approach of a photographer it begins to descend (figure 2*a*). Animal inspected in a net under water and rotated so as to free any air bubbles trapped in the mantle cavity. No bubbles found. On removal of the net, the ocythoe jetted straight downwards (funnel and mantle aperture facing upwards) and released two large bubbles of gas followed by three more. It then remained on the bottom (B^-). *1515 h.* Animal swimming in midwater (figure 2*b*) maintaining station in the water in the manner of a neutrally buoyant organism (B^0) such as a cuttlefish (i.e. without the back and forward or up and down movements seen in squids). The posture adopted by female *Ocythoe* in open water – with the arms held back over the mantle – is illustrated in figure 3.

Feeding. Dead anchovy proffered on a line to the dorsal arms reflected over the mantle: no response. Then presented in the midline just ahead of the ocythoe: released specific prey-capture action pattern: dorsal arms flung symmetrically and simultaneously forward from their reflected position along the mantle as if they had been tentacles. Photographed eating (figure 2*c*).

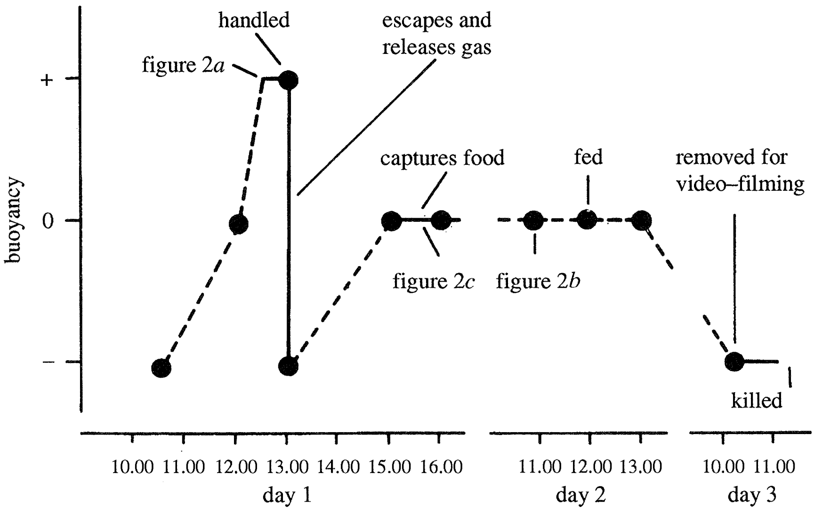

Figure 1. Estimated buoyancy condition (filled circles and solid line) and other behaviours of female *Ocythoe* (180 g body mass) during period of captivity (+, –, 0, positive, negative and neutrally buoyant respectively).

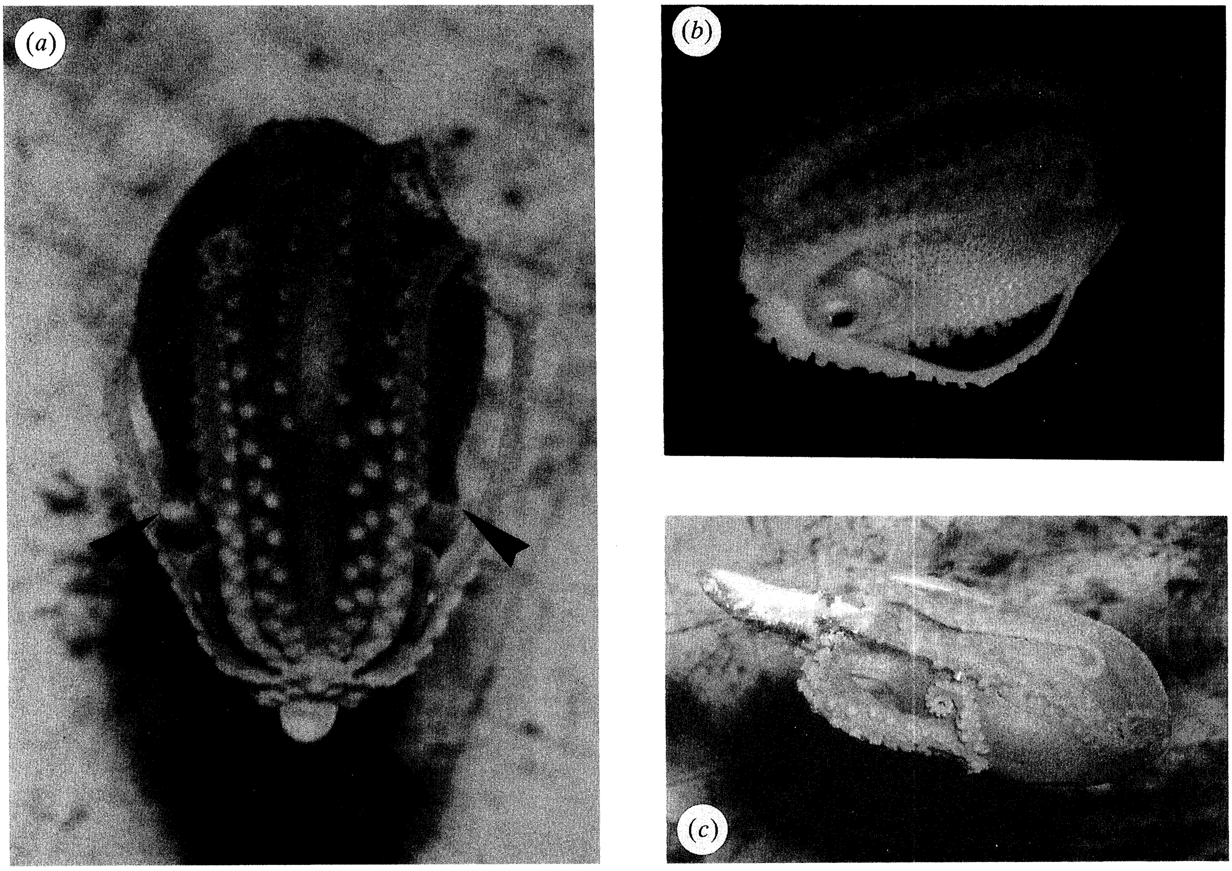

Figure 2. Captive *Ocythoe tuberculata* photographed from above. (*a*) All three jets are employed to descend from the surface. Note that both the accessory funnels (arrows) and the central funnel are directed upwards and that the insides of the funnels are illuminated by the electronic flash on the body of the camera. The animal is positively buoyant. (Photograph by Alfonso Toscano; 50 mm lens, scale given by floor-tiles: 10 cm × 10 cm.) (*b*) Neutrally buoyant ocythoe cruising in midwater (accessory jet is directed sideways). (*c*) Swimming at surface eating a fish.

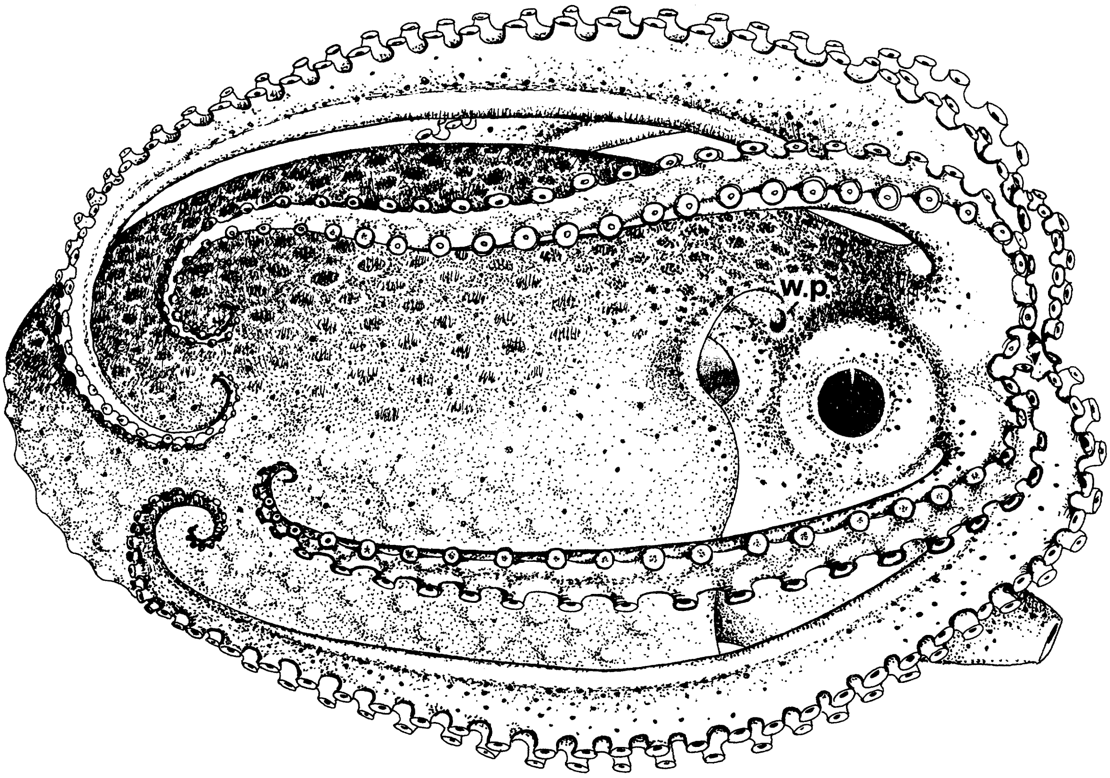

Figure 3. Trim of ocythoe in neutrally buoyant condition showing the laterally directed accessory funnel (see figure 2*b*) and the adjacent dorsal water pore (w.p.).

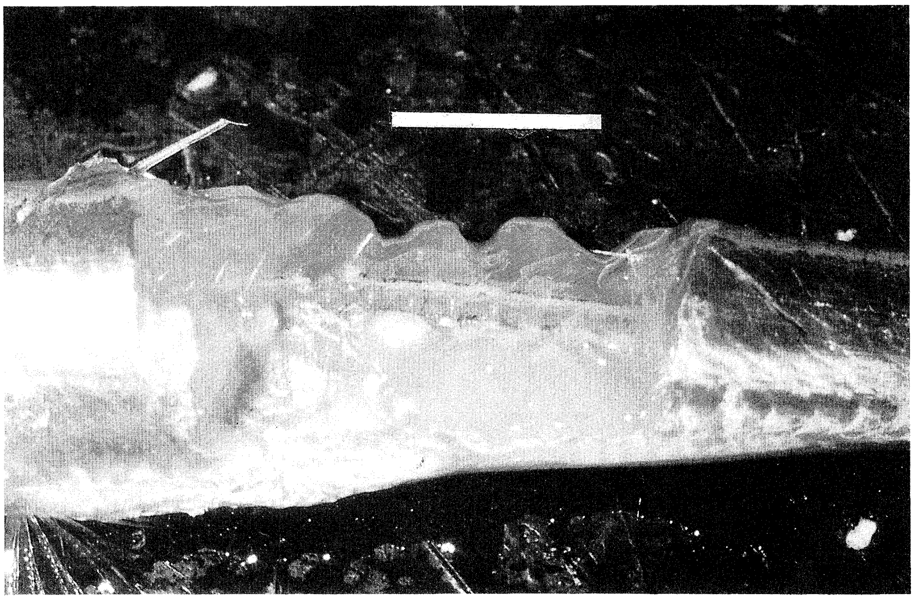

Figure 4. Half-eaten anchovy. Note the bite marks of the ocythoe. Scale bar 1 cm.

(ii) *Second day*

Ocythoe in fine condition. Midwater, horizontal posture as previous afternoon (B^0). Several attempts made to feed animal which does not respond; swims quietly away. Finally anchovy placed on arms near mouth, held there for three minutes while eating. (Three large bites of flesh removed from back of fish, figure 4). The mass of the fish (12 g) rotated the ocythoe into a slightly head-down posture.

(iii) *Third day*

Ocythoe found lying on the bottom partly on its side, apparently in difficulty, red in colour rather than blue and no longer with the arms gathered neatly over the mantle, and no longer buoyant (B^-). Removed for photography (figure 5) and filming.

(*b*) *Video-filming: use of jets and mantle aperture*

The brief video-film of the ocythoe in a 4 l bowl supplied with running seawater taken on the third day (two sessions of 2 min and 7 min), shows the central funnel (F) and accessory funnels (f_r and f_l) being used for swimming and breathing in four different combinations: (i) the animal lay on its left side; two strong jets of water directed through $F+f_r$, generated by contractions of the mantle, drove the animal onto its back; (ii) all funnels ($F+f_r+f_l$) deployed to drive

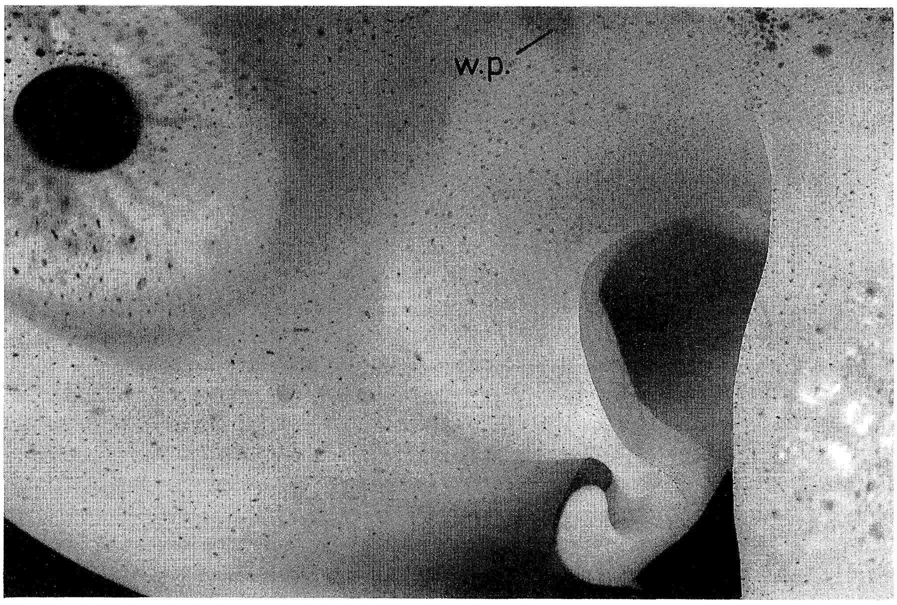

Figure 5. Lateral view (left) of the mantle aperture post mortem. The locking apparatus has been unlocked to show the inner rim of the accessory funnel; w.p., water pore. (Photograph touched up for clarity.)

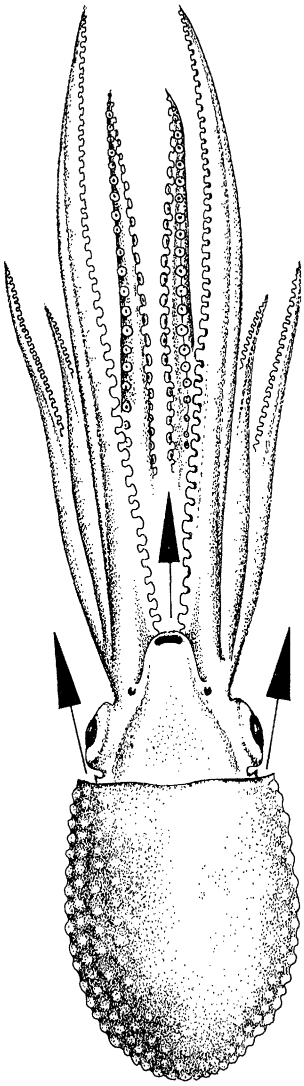

Figure 6. Drawing of an ocythoe seen from below to illustrate the use of triple jets (arrows) during an escape manoevre. The symmetrical lateral jets form a 'V', with the mantle at the apex, bisected by the central jet.

the animal backwards (this deployment is shown diagrammatically in figure 6); (iii) jetting with the midline funnel only (F); and (iv) animal on right side, low pressure pulses: water issuing partly from the midline funnel but mostly through the accessory funnel of the left side which rotates the exhalant jet until it points backwards ($(F)+f_1(180°)$).

The state of the inlet apertures of the mantle during these activities, and during respiration, varies in the folowing ways.

1. Prior to jetting, all inlets (lateral and ventral) open widely (figure 7*a*,*b*) by expansion of the mantle and complete adduction of the dorsal wings of the collar on either side (so that they lie against the visceral mass) and by raising the floor of the funnel into a shallow arch (letting water into the lower chamber). The ventral inlet (divided into two by the short midline septum which lies well forward in this species) is separated from the dorsal inlet by the locking apparatus on either side.

2. When manoevring with the accessory funnels see – (iv) above – inhalant water enters through the ventral intake only (by raising the floor of the back of the funnel) and the lateral apertures are closed off.

3. During quiet respiratory movements – seen in a final stretch of filming, just before sacrifice – the dorsal wings of the collar of the funnel perform paddle-like movements inside the mantle aperture creating an inhalant–exhalant current without any evident movement of other structures. (Similar movements of the funnel flaps without involvement of the mantle musculature, can be observed in cuttlefish: for instance the quiet respiration during light anaesthesia).

(*c*) *The dorsal sac*

After the animal was killed, the mantle lining covering the dorsal sac was removed. The duct was found to be patent and a few small bubbles of gas were seen in the lumen. They moved about inside when the sac was handled. Slow spontaneous waves of contraction were seen in the walls of the sac, and the jelly moved when the bladder was stimulated electrically.

3. FUNCTIONAL ANATOMY

(*a*) ***Subdivision of the mantle cavity***

Earlier authors (Verany 1847–51; Tryon 1876; Jatta 1896; Naef 1928; Sasaki 1929) do not mention the relatively enormous dorsal sac (figure 8). The sac can be seen bulging into the top of the mantle cavity in one of Jatta's drawings (figure 8 in his plate 19). Figures 8 and 10 in the same plate, and figure 450 in Naef (1928), also show the subdivisions of the mantle cavity but neither author mentions that the cavity is effectively divided off horizontally (figures 9 and 11) into an upper compression chamber, feeding the two lateral 'funnels', and a lower chamber feeding the true funnel (which opens far forward in the ventral midline below the mouth).

Figures 8 and 9 in the present paper show the upper chamber of the mantle cavity from the same angle as Jatta's drawing. The chamber is traversed by the lateral mantle adductors (posterior and anterior) and its floor is the funnel adductors.

The short posterior pair of adductors is attached to the sides of the visceral mass at the level of the systemic heart and just below the level at which the dorsal sac contacts the rest of the viscera.

The connectives containing the anterior lateral adductors are twisted on themselves like a piece of drapery. They carry the pallial nerve to the stellate ganglion and join the wall of the mantle in a long insertion which continues back to the posterior adductor. Medially, the more membranous portion, twisted beneath the adductor, is also long and reaches more than half way back along the visceral mass at which point it is running at about 120° to the rest of the adductor. In fixed specimens it can easily be mistaken for another adductor (figure 8). Whether these membranous portions also contract is not known but they extend the attachment of the adductors along much of the capsule of the bladder. Anteriorly, they join the back of the head just inside the mantle

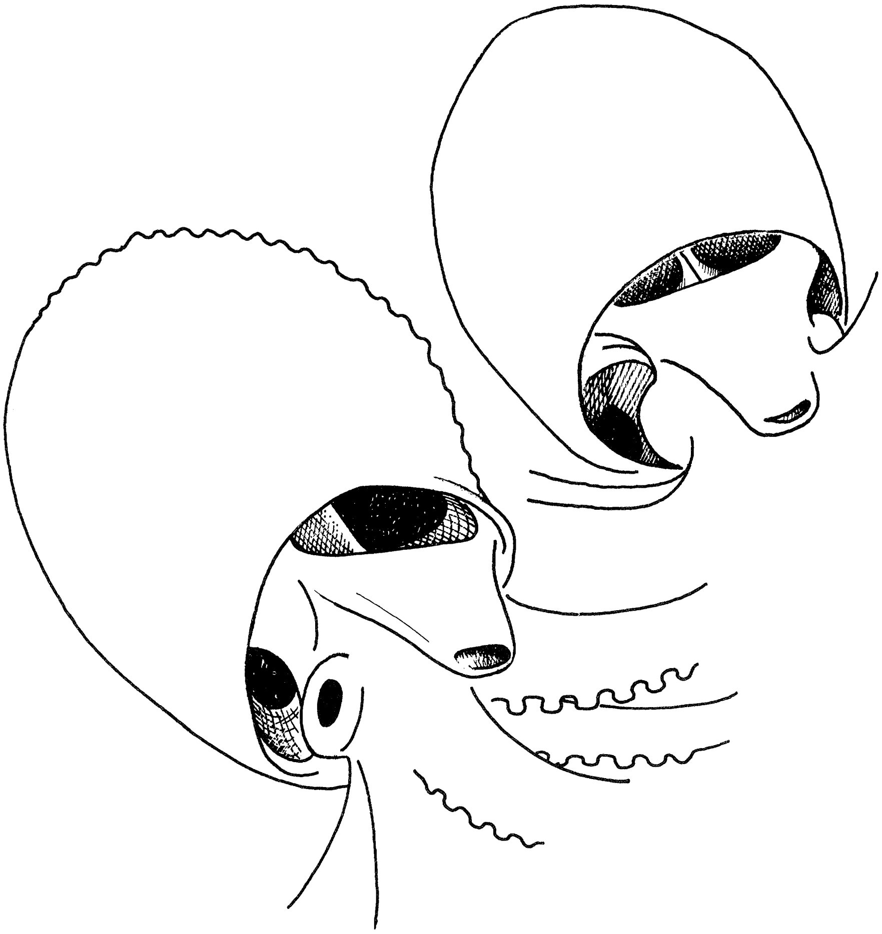

Figure 7. *Ocythoe* during an escape manoevre at the peak of the inhalant stroke drawn from frames of video-film. Note the short midline septum, funnel attached to mantle (at the level of the locking apparatus), mantle aperture wide open laterally and ventrally. Accessory funnels are suppressed.

aperture and close to the medial anterior adductor. The insertion fans out laterally and in front of the dorsal wings of the collar (which form the accessory funnels, see below) at the point where these attach to the roof of the mantle.

Well ventral to these structures, the upper chamber is closed off below by the wide funnel adductors, which are united across the midline and held tightly against the mantle muscle wall by the locking apparatus (figures 5, 9 and 11). As the adductors run backwards to their insertion near to the origin of the gills, the floor narrows leaving a triangular window between upper and lower chambers. This window is partly filled by the attenuated, decapod-like, gills (see figure 450 in Naef (1928)). All three adductors (retractors) converge posteriorly.

The back of the upper chamber is formed by the ovary and by the oviduct which grows to enormous size in the mature female as the young inside the oviduct develop to the free-living stage (figure 8). The front of the upper chamber ends far forward, dorsally and medial to the accessory funnels, in a dead space formed by two blind pockets (figure 9) (see below).

(*b*) *Accessory funnels*

The transient accessory funnels (figures 2, 3 and 5) are located in the upper corners of the mantle aperture, which extends particularly far dorsally in this species. Ventrally they are delimited by the locking apparatus. They can be directed forwards, sideways and backwards, rotating the exhalant stream of water through as much as 180°.

The lips of the accessory funnels are relatively thin and flexible. The outer lip is a modification of the outer edge of the mantle aperture and is slightly cut away. In other cephalopods, this part of the mantle – which we propose to call the lapel because, like the lapel on a coat, it is the part that turns outwards – has a separate musculature from the rest (Bone *et al.* 1982) consisting of longitudinal cholinergic muscle fibres, which allow the edge to curl outwards and thus hold the aperture open. In *Ocythoe* this property is enhanced. The inner lips are a modification of the dorsal-most part of the funnel flaps or collar, which also form the anterior wall of the upper chamber (see above). When everted and applied to the outer lip (lapel), they form the other three sides of the accessory funnel. They are responsible for opening and closing this dynamic structure and co-ordinate with the outer lip in directing the accessory jet. During the inhalant stroke of the escape reaction the accessory funnels completely disappear (figure 7).

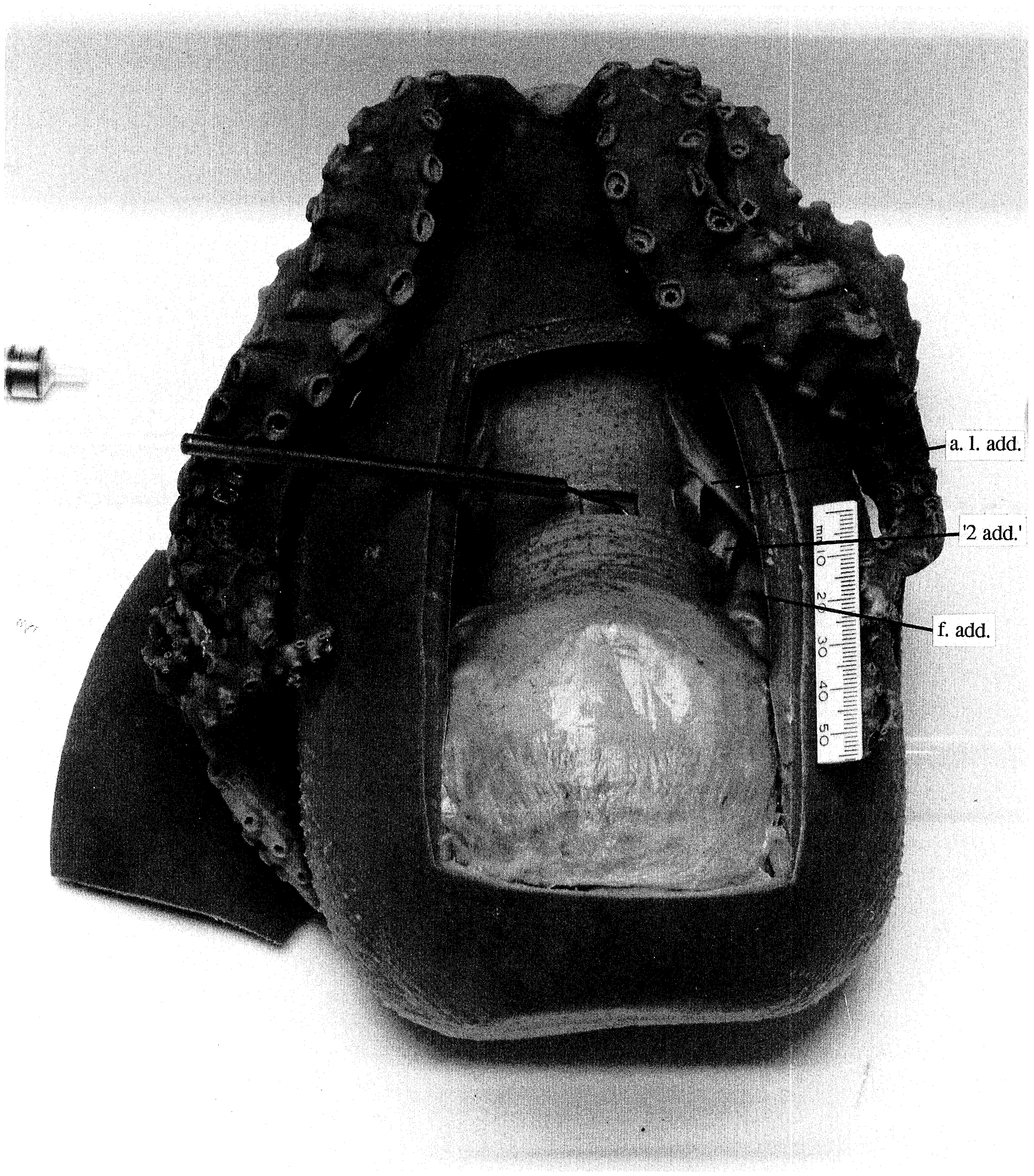

Figure 8. Ripe female *Ocythoe* (specimen VIII), photographed in air, with a large window cut out of the thick muscular roof of the mantle. The dorsal sac is seen through the upper (forward) half of this window. It is supported by the anterior lateral adductor (*a.l.add.*). Below, what appears to be a second adductor (*2.add.*), running diagonally to the first and inserting just behind the mantle aperture (not seen) is morphologically an extenson of the a.l.add. (see figure 9); *f.add.*, funnel adductor. A rectangular cut has been made in the roof of the sac, which is empty, to allow the tip of a seeker into the lumen. The lower (rear) half of the window is occupied by the greatly expanded oviduct, which is covered by a white membrane. (Ruler divisions, millimetres.) Copyright Trustees of the National Museums of Scotland.

(*c*) *The dorsal sac, or swimbladder*

(i) *General relations*

This large organ is a midline structure present in all the females studied. It lies on top of the visceral mass immediately above the digestive gland, the cephalic aorta and the oesophagus – which opens into a capacious crop – and is covered by the connective tissue capsule lining the mantle cavity. Posteriorly, it is attached to the roof of the mantle. Anteriorly, it touches the back of the head. A short duct situated at the right posterior corner of the organ (figure 10) leads from the lumen of the sac backwards and downwards into the mantle cavity. Its opening into the cavity is hidden beneath and behind the base of the right gill where it connects with the mantle wall.

(ii) *Detailed anatomy and histology*

The anatomy of the dorsal sac changes as the female grows. In the fresh, juvenile, specimens it is

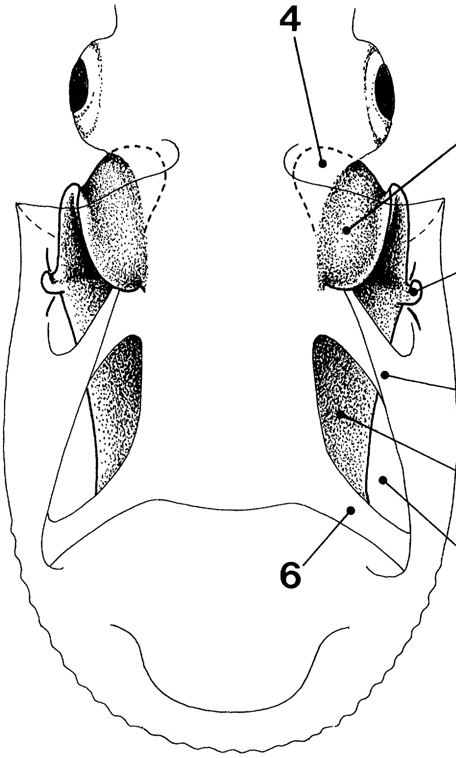

Figure 9. Semi-diagrammatic view of the upper chamber of the mantle cavity of immature *Ocythoe* during exhalation (seen from above and behind to compare with Plate 19, fig. 8 in Jatta (1896)). The structures closing the chamber in front and separating it from the lower chamber below are shaded. 1, Dorsal wings of the collar of the funnel which can transform themselves into accessory funnels; 2, the funnel adductors; 3, locking apparatus; 4, position of blind pockets (indicated by dashed line) (see text); 5 and 6, anterior and posterior lateral mantle adductors; 7, space occupied by the gills (not shown).

shaped like the human tongue: flatter than it is wide and twice as long as large (figure 12, inset). The dimensions of two of them, after being dissected away from the capsule) are given in table 1. The base (or root) of the tongue – and place of attachment to the mantle roof – is also its widest part. There are a few large extrategumental chromatophores on the outer surface both above and below the organ (see Discussion).

In the ripe full-grown preserved specimens (figures 8 and 11) the sac is a distended empty bladder 2–3 cm high occupied mostly by the lumen, the volume of which is about 5% of total body volume (see table 1). The floor is somewhat gelatinous. The roof is a 1–2 mm thick layer of connective tissue and muscle.

The muscle layer continues right round the bladder and in the immature specimens lies within the jelly of the walls and floor. It consists of a loose mesh of muscle fibres in which the bundles run at an oblique angle to each other. The muscle layer is relatively thicker and more compact in the dorsal sac of the adult than in the soft largely gelatinous structure of the juvenile.

In both the mature and immature specimens, the lumen occupies the full width of the bladder between muscle walls, but in the immature females it is collapsed dorso-ventrally. The lining of the lumen (figure 14*a*,*b*) is a regular cuboidal epithelium one-cell thick (6–8 μm). It is ciliated dorsally, and thrown into little pleats presumably formed when the lumen collapses. Unevenly distributed in the epithelial lining, mostly at its base, is a class of cells with a clear cytoplasm, subspherical outline and spherical darkly staining nuclei (P in figure 14*b*). Ventrally, where the epithelium is well separated from the muscle layers, these cells are directly in contact with the jelly.

The jelly, which is traversed by a network of nucleated fibres, contains numerous spherical 'amoeboid' cells (figure 14*a*,*c*) with granular cytoplasm and densely staining subspherical nuclei (sometimes two or more). Traces of jelly and occasional darkly staining 'amoebocytes' (figure 14*e*) are also found in the lumen. Similar cells occur in the trabecular spaces of the dermis (see Nixon & Young 1996).

On either side of the bladder of the immature (fresh) specimen runs a blood vessel, easily seen through the transparent walls of the sac, which branches repeatedly after its origin from the common swimbladder artery near the rear of the sac. These vessels have the structure typical of cephalopod arteries (figure 14*d*) (Schipp 1987), with parenchymatous strands leading off at right angles (figure 13, STR) and are associated with occasional nerves (figure 13, N). Other small arteries and venous spaces (figure 12) are distributed throughout the sac both in the muscular and the gelatinous regions. Pear-shaped cells with very little cytoplasm protrude from the parenchyma of these vessels into the lumen of the artery (figure 14*d*).

The short duct of the bladder leading into the mantle cavity is surrounded by the same muscle as the rest of the sac and is lined by an epithelium which appears to be continuous with the lining of the main lumen, but is here many cells thick and permeated by crypts (figure 14*f*, *g*, *h*).

The arterial blood supply of the sac and the vessels draining it are shown in figure 15. As the single small swim bladder artery branches from the right pallial artery immediately after it leaves the aorta at its junction with the large systemic heart, the dorsal sac is the first organ (apart from the gonads which have their own aorta) to receive oxygenated blood from the heart. This anatomical priority in blood supply arrangements is matched, on the venous side, by two vessels (v1 and v2) that drain one into the anterior vena cava and the other into the right vena cava by way of the right pallial vein. For further anatomical details and illustrations see Nixon & Young (1996).

There is no trace of the dorsal sac in the dwarf male *Ocythoe*. In an old specimen in the collection of the British Museum of Natural History, which was sectioned in the posterior half of the mantle, the only tissue that could possibly correspond to this structure is a fold of the mantle lining overlying the dorsal part of the viscera.

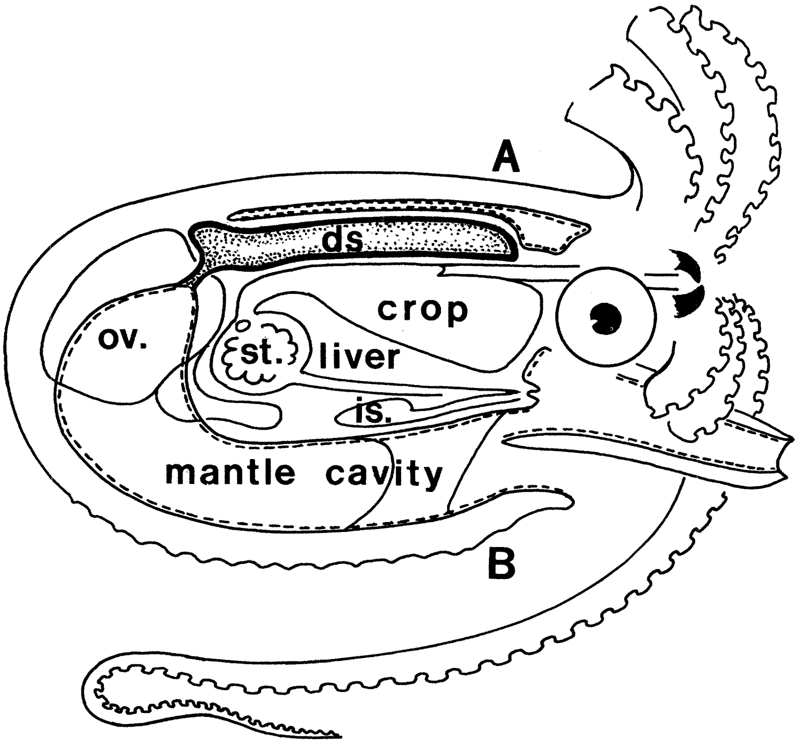

Figure 10. Relation of the dorsal sac (ds) to the rest of the visceral mass and position of the duct communicating with the right side of the mantle cavity. ov, ovary; st, stomach; is, ink sac. Lining of mantle cavity and central funnel indicated by dashed line. (A–B, level of section in figure 11).

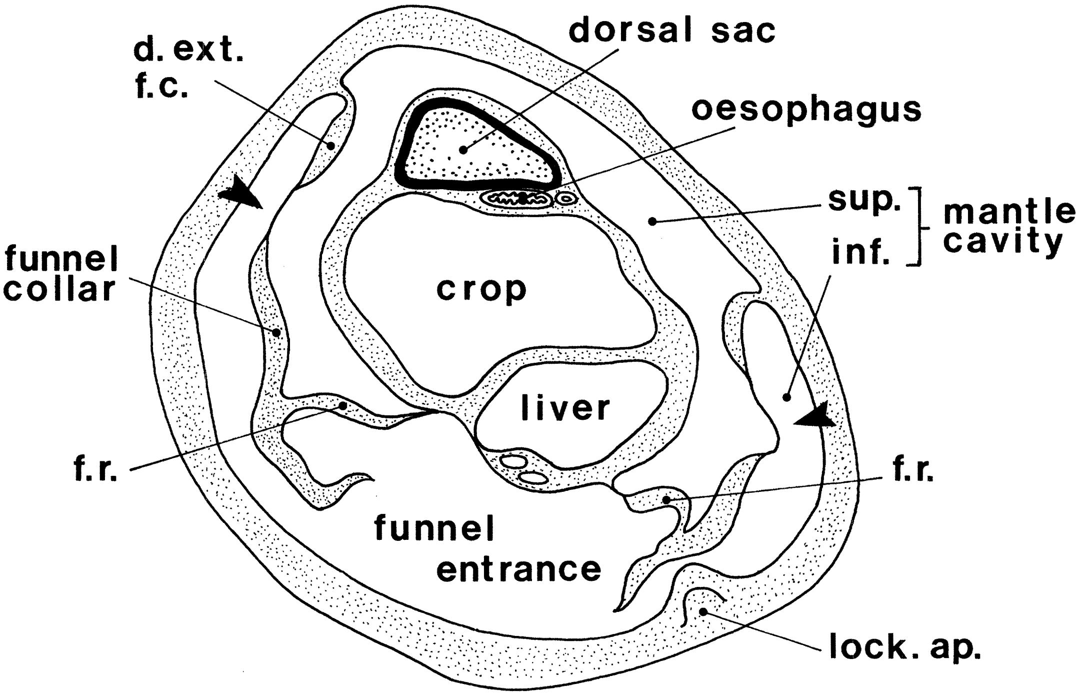

Figure 11. Transverse section through mantle of mature *Ocythoe* (specimen VI, distorted by fixation) taken at the level A–B in figure 10 to show the dorsal sac (lumen outlined in black) situated above the large crop. This is also the level of the 'accessory funnels' (arrows). Note that the funnel retractors (f.r.) are united across the midline and with the collar of the funnel, the upwards extensions (flaps) of which: (i) are attached dorsally to the roof of the mantle (d.ext.f.c.); (ii) divide the mantle cavity into upper (inner) and lower (outer) chambers (sup. and inf. mantle cavity); and (iii) form the innner lip of the accessory funnels.

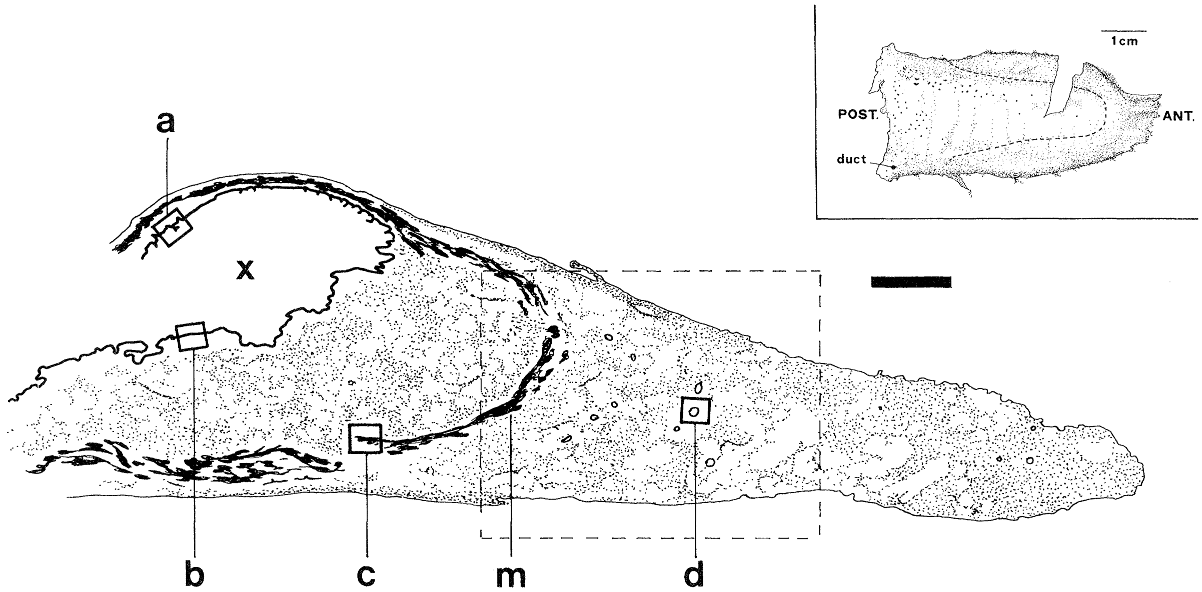

Figure 12. Transverse section (stained with haematoxylin and eosin) through part of the swimbladder of an immature *Ocythoe* drawn from low power photograph to show the extensive jelly (irregular stipple) and loose muscle coat (m) surrounding the lumen (x) of the bladder. Also shown, locations of the photographs of figures 13 (dashed line) and 14*a*–*d*. Scale bar 1 mm. (Inset: dorsal view of the bladder showing segment removed for sectioning.)

4. DISCUSSION AND CONCLUSIONS

(*a*) *Triple jets*

One of the early synonyms for *Ocythoe* is *Parasira* (Steenstrup 1860, p. 333) derived (according to Fischer 1889) from Para- (alongside) -seira (lock or closing apparatus). Evidently Steenstrup had in mind the stout laterally placed locking apparatus of the genus. It is a principal element in the subdivision of the mantle cavity and forms the bond that closes off the lateral 'funnels' below. Horizontal subdivision of the mantle cavity is a feature of cranchid squids (Clarke 1962) in which there remains only a foramen between upper and lower chambers.

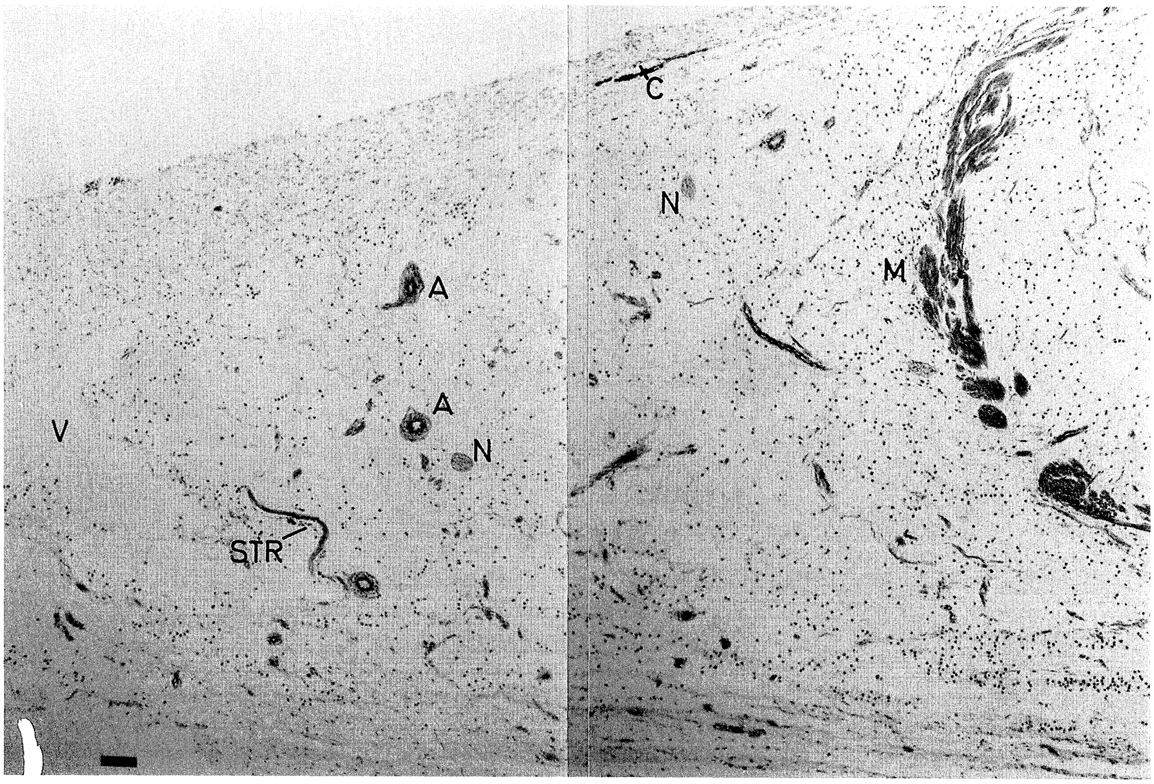

Figure 13. Gelatinous part of dorsal sac. M, muscle coat; A, blood vessel associated with strands of tissue (STR); C, chromatophore; N, nerve; V, ?venous spaces. 'Amoebocytes' are scattered throughtout the jelly.

The chief interest of the accessory funnels is their role in the control of swimming. They are capable of a variety of subtle movements and orientations that direct the pressure pulse during expiration. But they are not permanent structures, so the question arises how it is that these subtle movements are hydromechanically possible. The flaps forming the accessory funnels are very flexible, but they are attached to the muscular mantle above and below (at the locking apparatus) as well as anteriorly to the head, which largely limits their freedom of movement to the fore and aft direction. When seen from the side, the funnels seem to be standing upon the blind pockets at the front end of the upper chamber (see figure 3). Evidently the resistance against which the lips of the accessory funnels operate and direct the jet is supplied partly by the turgour of the blind pockets, swollen with water under pressure from the muscular mantle, and partly by the exhalant stream of water itself. This helps to explain the complex subdivisions of the mantle cavity noted above.

Figure 2*a* shows how all three funnels contribute to locomotion in this species. Since octopods such as *Octopus vulgaris*, have no fin or horizontal hydrofoil surface created by the arms, they are unstable in the rolling and the pitching planes when they swim. (For instance, *Octopus* released in midwater swims to the bottom with an erratic and sometimes looping course). Female *Ocythoe* also has no fin and its arms do not spread out flat as in *Tremoctopus* or some members of the genus *Octopus*. As in other octopods, the stream of water exiting from its central (true) funnel well forward of the centre of gravity, acts as a rudder in swimming and controls yawing. At the same time the lateral jets located above and forward of its centre of gravity enable *Ocythoe* to convert inherent instability in the rolling and pitching planes into manoevrability.

One may reasonably ask how does an inlet aperture become converted into outlet? Octopuses provide an answer. Although this aspect of the hydrodynamics of respiration and locomotion have been poorly studied, in *Octopus* too the mantle aperture can serve both as inlet and outlet. For instance, during hyperventilation (Trueman & Packard 1968) the free edges of the collar, the funnel flaps, are held against the visceral mass and at each expiration water and the tips of the gills exit freely through the mantle aperture. During normal ventilation in *Octopus*, the build up of pressure in the mantle cavity forces the collar against the mantle edge closing off the inlet aperture in the manner of a flap valve so that water exits only through the 'proper' funnel. But as pressure increases, for instance during jetting, the flaps of the valve balloon outwards and sometimes the seal breaks and water escapes through the inlet. It would require a small structural and functional modification to break this seal in a regulated way.

(*b*) *The dorsal sac or swimbladder*

(i) *Questions of homology*

It is puzzling – and somewhat embarassing – that this organ was never described in any of the classical accounts of *Ocythoe*. The species is known by local fishermen round the Bay of Naples as 'purpe-seccia senza scorcia' (Lo Bianco 1909) – i.e. 'cuttlefish–octopus without a shell' – to distinguish it from that other argonautid, *Argonauta*, sometimes seen swimming at the surface, and this mode of life is itself reason for expecting some kind of hydrostat in the female. Perhaps it was simply missed by the earlier authors, and we are left – *vice* Naef – asking with what organ or structure in other cephalopods is the dorsal sac homologous? It is too highly modified to be considered a shell and it does not lie in the mantle wall but on top of the viscera.

And what of the jelly? Jatta (1896) recounts that the Nice and Genovese fishermen believe that *Ocythoe* possesses a gelatinous shell which it throws off when about to be captured, but dismisses this as 'certainly fruit of the lively imagination of fisherfolk'.

Nevertheless there is an intriguing possibility that the dorsal sac may be homologous with the ancestral cephalopod shell, itself a buoyancy structure. In *Ocythoe* and *Argonauta* the hard shell vestiges are absent. In other incirrate octopods these remnants of the original proostracum are embedded in the mantle wall at the base of the posterior mantle retractors: i.e. at the level where in *Ocythoe*, the dorsal sac abuts on the muscular mantle wall. During ontogeny the sac increases in relative size by growing forwards from its base at the back of the mantle cavity. Other evidence comes from the curious distribution of extrategumental chromatophores. Extrategumental chromatophores are common in the mantle lining covering the visceral mass of octopods. In *Ocythoe*, they are not confined to the dorsal covering of the bladder, but are also present on its undersurface where it contacts the rest of the visceral mass: as if the bladder were originally part of the mantle which has intruded onto the viscera.

Direct evidence for such an origin comes from the comparative embryology of Naef (1928*a*). Although he did not have access to fully developed embryos of *Ocythoe tuberculata*, he followed the shell Anlagen – the rudiments still exist in octopods – from stages VII to XII. They consist of three parts: the shell sac, the shell pore and the shell epithelium. The latter is of considerable girth and reminiscent of decapods. Unusually, it lies directly on top of the yolk and not on the muscular mantle rudiment which circumscribes the opening of the shell sac. He writes that in *Ocythoe* 'the shell is so to speak doubly represented'. (The figures accompanying the text are the last in the final plate of Naef's last cephalopod publication.)

The bladder should not necessarily be equated with the hard parts of the ancestral shell. The dorsal sac could be the shell sac. Professor J. Z. Young (personal communication) has suggested that the vascularized jelly may be homologous with the siphuncle: the soft tissue whose activity controls the volume of gas in the phragmocone of all cephalopod shells.

(ii) *Functional considerations*

Functional grounds for interpreting the sac as a swimbladder include its position, size, structure and

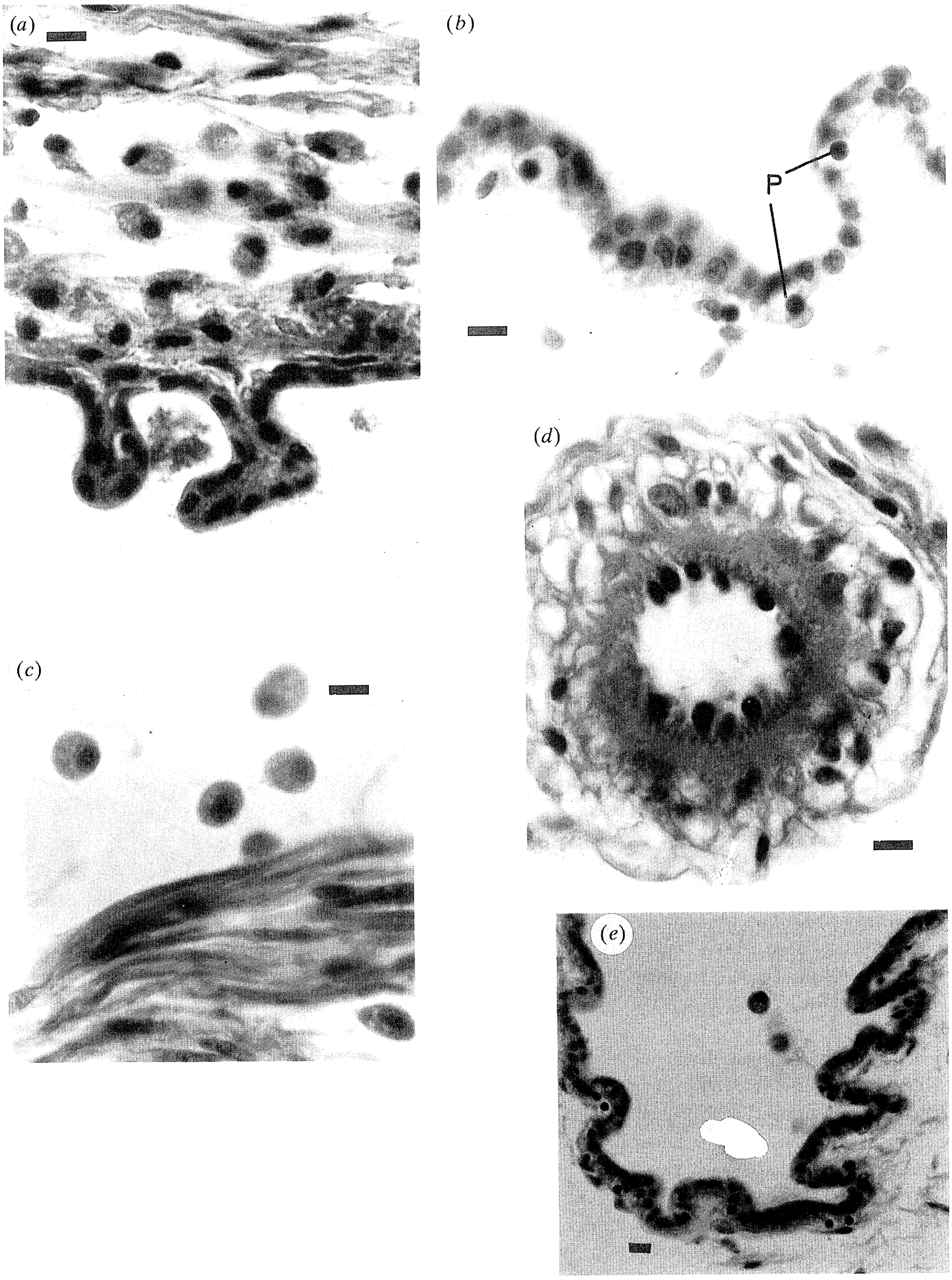

Figure 14. Roof (*a*) and floor (*b*) of the bladder. The lining of the lumen is a single-celled epithelium which is closely associated with 'amoebocytes' (P) having clear cytoplasm and round nuclei. (*c*) Spherical and subspherical (amoeboid) cells with darkly staining cytoplasm (similar cells in (*a*)) lying loose in the jelly (muscle fibre bundle below). (*d*) Typical blood vessel with parenchymatous walls. (*e*) Two 'amoebocytes' and jelly in the lumen of the same bladder. (Scale bars 10 μm.) (*f–h*) Haematoxylin and eosin section of the swimbladder duct; M, muscle coat; X, lumen which extends into crypts (CR) and contains traces of jelly, seen at higher power in (*g*) and (*h*). Scale bar 100 μm.

the posture and behaviour of the animal. It occupies the same position in the middle of the body as does the cuttlebone of the cuttlefish (figure 10): i.e. the centre of mass, directly above the centre of gravity when the animal is swimming with antero-posterior axis horizontal (as in figures 2*b* and 3), is in the hydrodynamically preferred place for a buoyancy tank, combining both stability and manoevrability (Denton & Gilpin-Brown 1966). In full-grown specimens it is two-fifths, and in the smaller specimens is one-quarter, of the length of the body from mouth to tip of mantle.

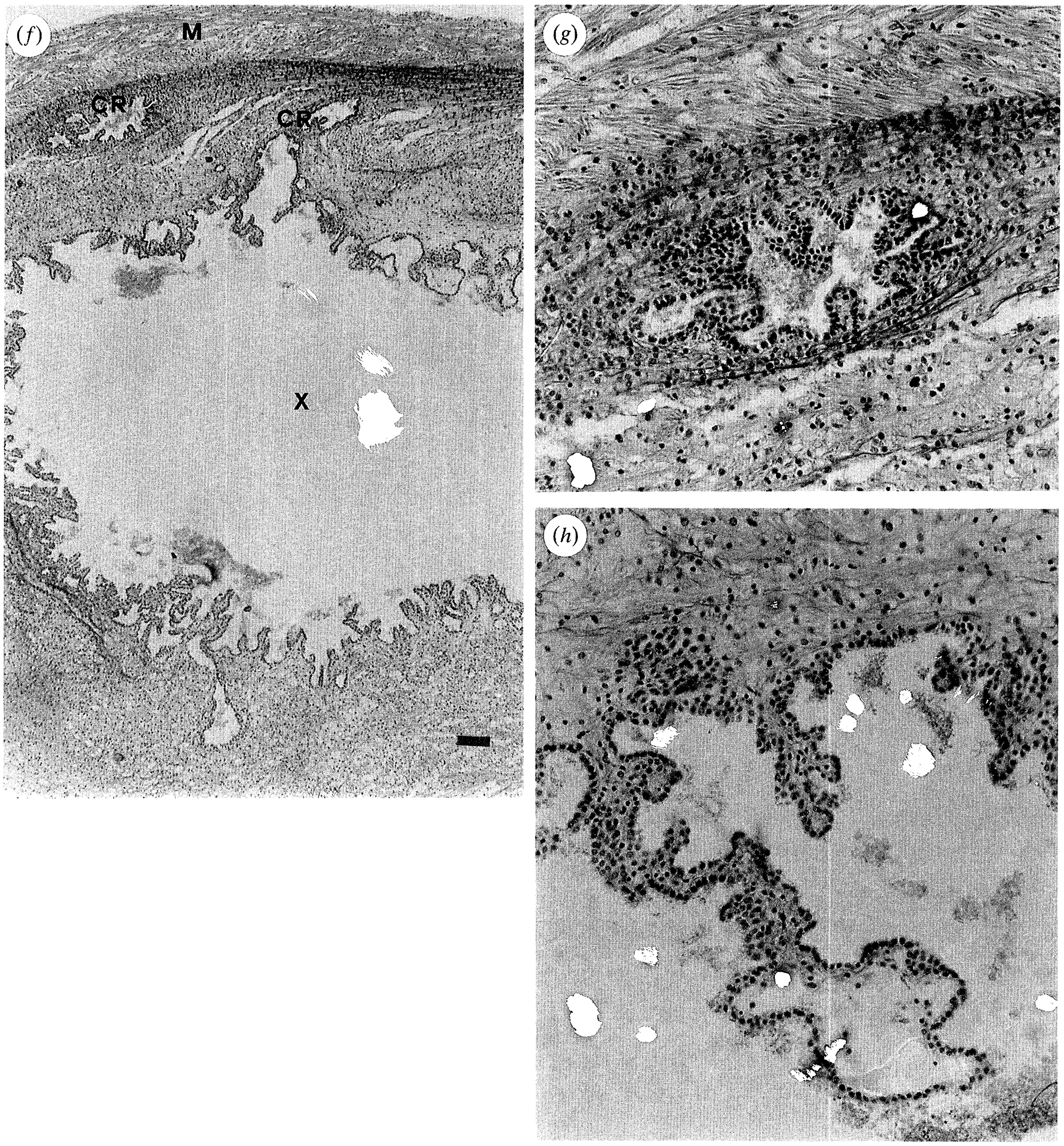

Figure 14. *Continued*

The expanded lumen of the organ in the adult (see table 1) is approximately 5% of the volume of the whole body: i.e. similar to the volume of the gas space of the cuttlebone of *Sepia* (Denton & Gilpin-Brown 1961) and adequate for achieving neutral buoyancy. It is difficult to estimate the potential lift provided by the bladder of the immature specimens because it was nearly empty and the lumen collapsed when dissected. The jelly itself does not float. The muscular coat, and the peristalsis observed in the fresh swimbladder, could have been the means for venting the gas. The duct into the mantle cavity (and thus to the outside world) recalls the physostomatous condition of some fish bladders.

The ocythoe replenished the gas at least twice within a period of 5 h during the course of the first day (figure 1). We do not know the nature and origin of this gas. Nixon & Young (1996) suggest that this species may be able to take air, trapped in the mantle cavity, into the sac since another argonautid uses air for floatation: trapped in the top of the shell in the case of *Argonauta*. It is more likely that it is secreted into the bladder through the thin epithelial lining from dissolved gases carried to the bladder in the blood, or from stores of oxygen or nitrogen (or some other gas) in the tissues. The cells responsible for transporting and storing the gas in their granular cytoplasm could be the many spherical 'amoebocytes' dispersed in the jelly. They have somewhat elongated nuclei containing figures that are more densely staining than the rest (figure 14*c*). The cells with completely clear cytoplasm and non-spherical outline found in or near the internal lining of the sac (figures 14*a*,*b*) could be these same 'amoebocytes' which have released their contents and are now empty (outer membrane partly collapsed, and nucleus rounded up).

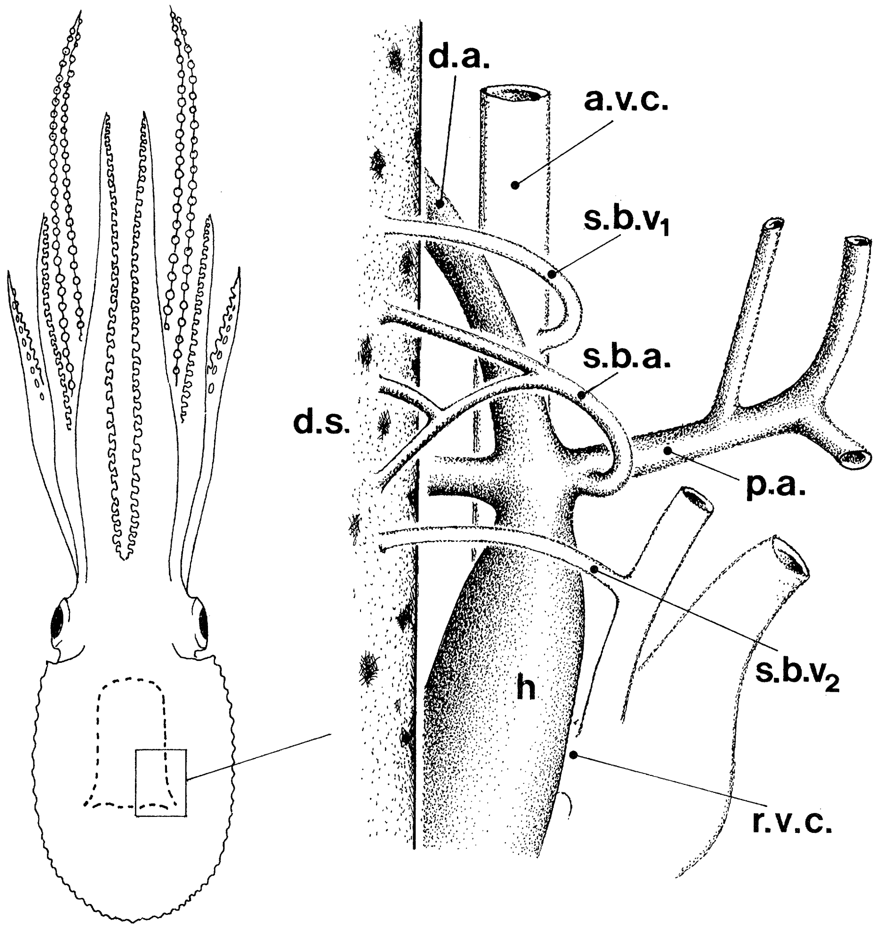

Figure 15. Swimbladder blood supply viewed from above. Left, bladder, dashed line, in situ. Right, the organ has been reflected to show the vessels entering its ventral surface. s.b.a., Swimbladder artery; p.a., pallial artery; *s.b.v.1* and *s.b.v.2*, anterior and posterior swimbladder veins draining into the anterior and right venae cavae (a.v.c. and r.v.c.); d.a., dorsal aorta; h, systemic heart.

We have not found any gas gland or rete of blood vessels which might be responsible for transporting the gas, but in the transverse sections across the bladders of the fresh specimens there are several small arteries (or profiles of the same artery cut several times) that have branched from the artery coming from the heart and run longitudinally one above another in the gelatinous walls. These small vessels have some thin strands of tissue running off at right angles and there are many 'amoebocytes' in this region of the jelly. In the sea, the volume of gas in the bladder will change whenever the ocythoe descends, unless more is secreted, or when it ascends, unless the gas is resorbed or vented. Our captive specimen vented gas as it swam to the bottom after being handled near the surface, and subsequently regained neutral buoyancy. If this behaviour is a normal part of an escape response then it suggests that control of the volume of the gas – and of buoyancy – are also a normal part of the physiology of this animal.

However, there may be strict limits on the frequency of such changes in the natural environment. When the ocythoe was sacrificed on the morning of the third day, after being found lying on the bottom and in poor condition, the bladder was empty. Yet the animal had fed and had appeared in good condition the evening before, swimming in midwater and enjoying an abundant supply of seawater. One is left with the impression that loss of gas itself hastened its demise.

Our specimen was not alone in dying after two days. Lo Bianco (1909) states that in some years several female *Ocythoe* were collected in the Bay of Naples during the spring months, but when put in the aquarium of the Zoological Station they lived only 'un paio di giorni'. *Argonauta*, which is also short-lived in the aquarium, nevertheless survives for up to a week. In its case the difficulties are that it is unable to release the hold of the suckers when they come into contact with the glass (Young 1960).

If this paper helps to stimulate further research into this elusive octopus it will have achieved its object. To capture and analyse the gas in the bladder will be almost as valuable as capturing the animal.

We are indebted to Marion Nixon for all her help, and to Kay Grant for histology. J. Z. Young, F.R.S. has contributed generously from his experience to all the episodes in this story. We also thank the Invertebrate Zoology Department of the British Museum of Natural History for the loan of specimens, David Heppel, National

Museums of Scotland, Flegra Bentivegna, Graham Ferguson, Professor Moriscalco and Alfonso Toscano.

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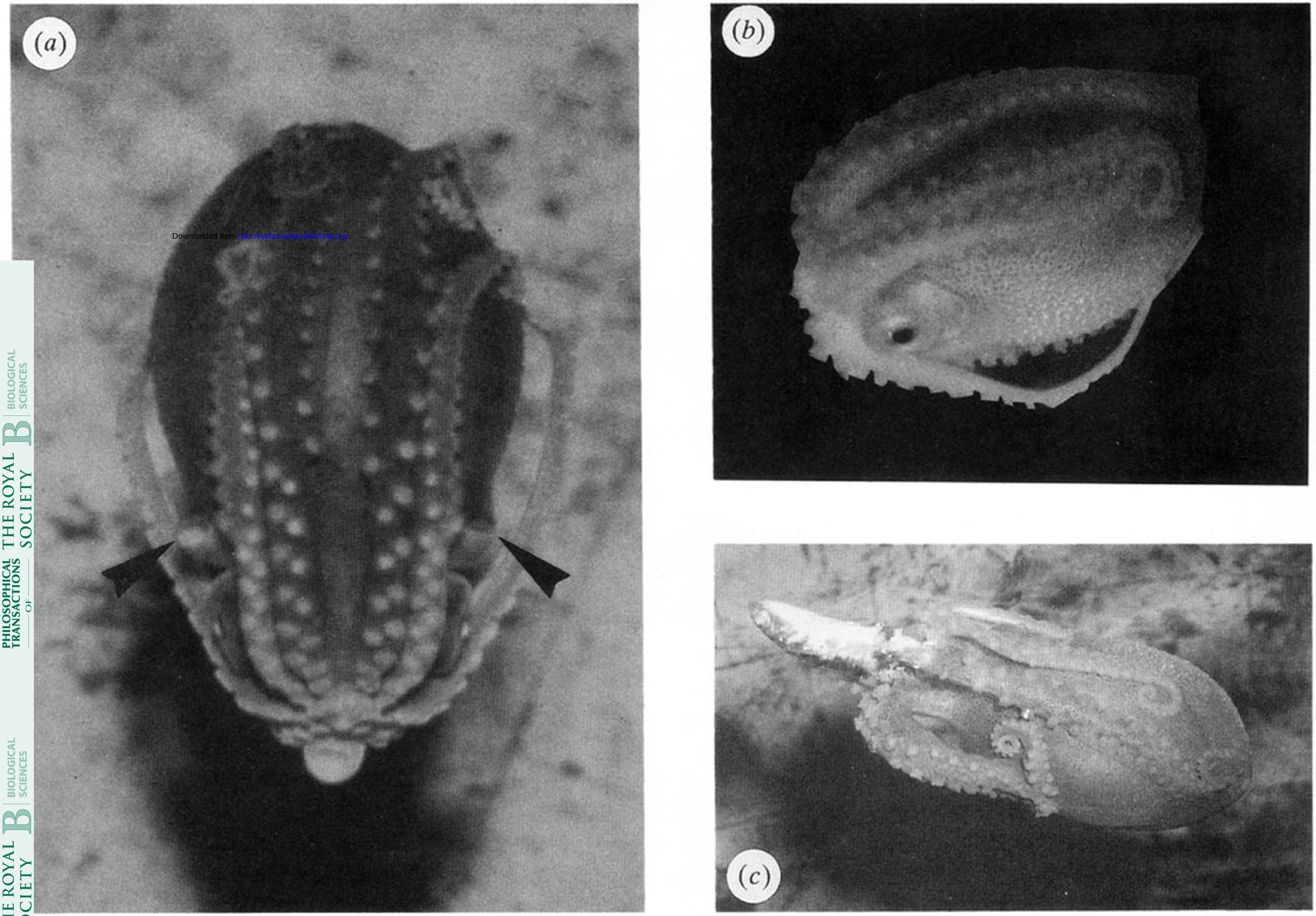


Figure 2. Captive *Ocythoe tuberculata* photographed from above. (*a*) All three jets are employed to descend from the surface. Note that both the accessory funnels (arrows) and the central funnel are directed upwards and that the insides of the funnels are illuminated by the electronic flash on the body of the camera. The animal is positively buoyant. (Photograph by Alfonso Toscano; 50 mm lens, scale given by floor-tiles: 10 cm × 10 cm.) (*b*) Neutrally buoyant ocythoe cruising in midwater (accessory jet is directed sideways). (*c*) Swimming at surface eating a fish.

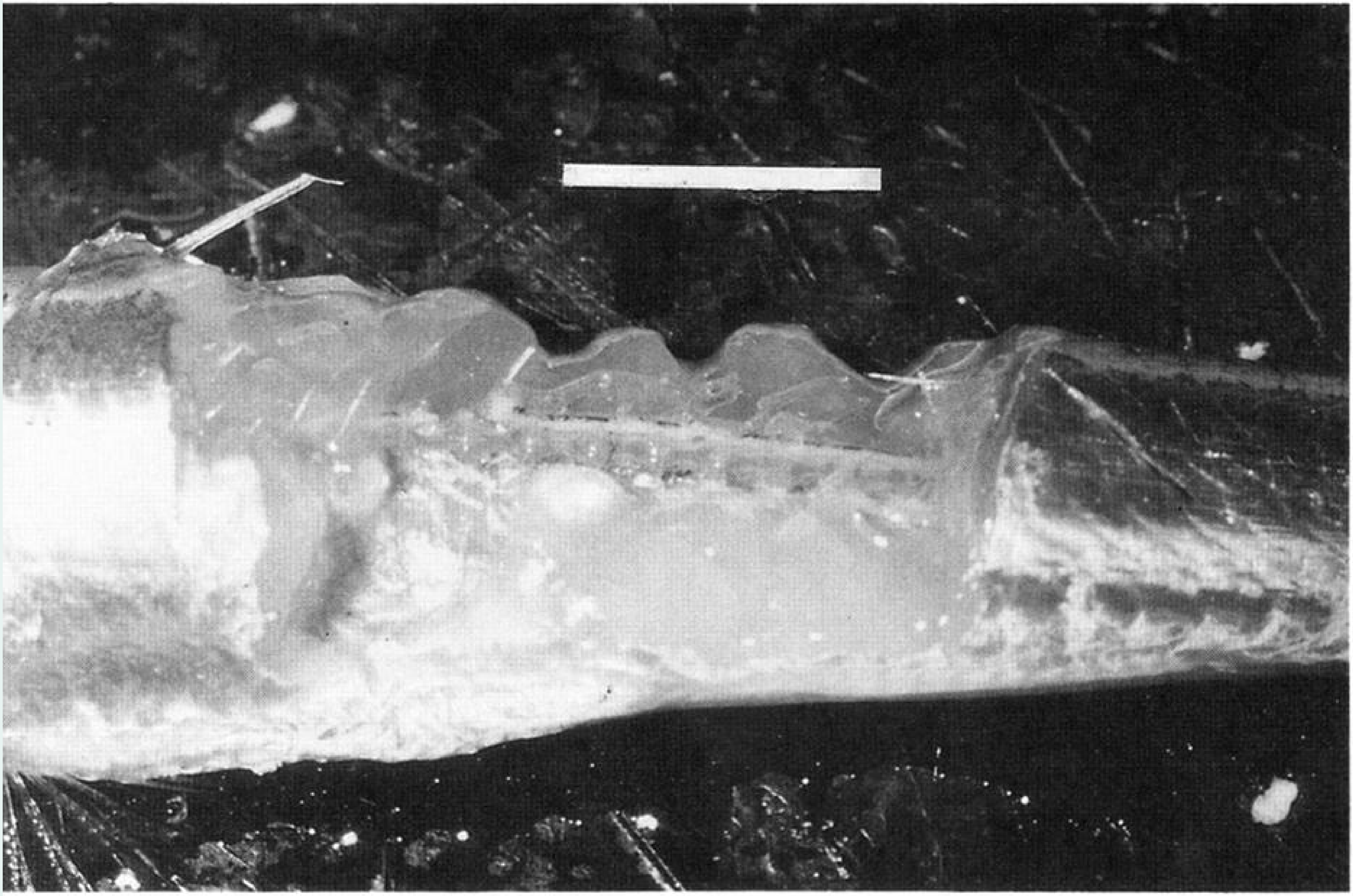
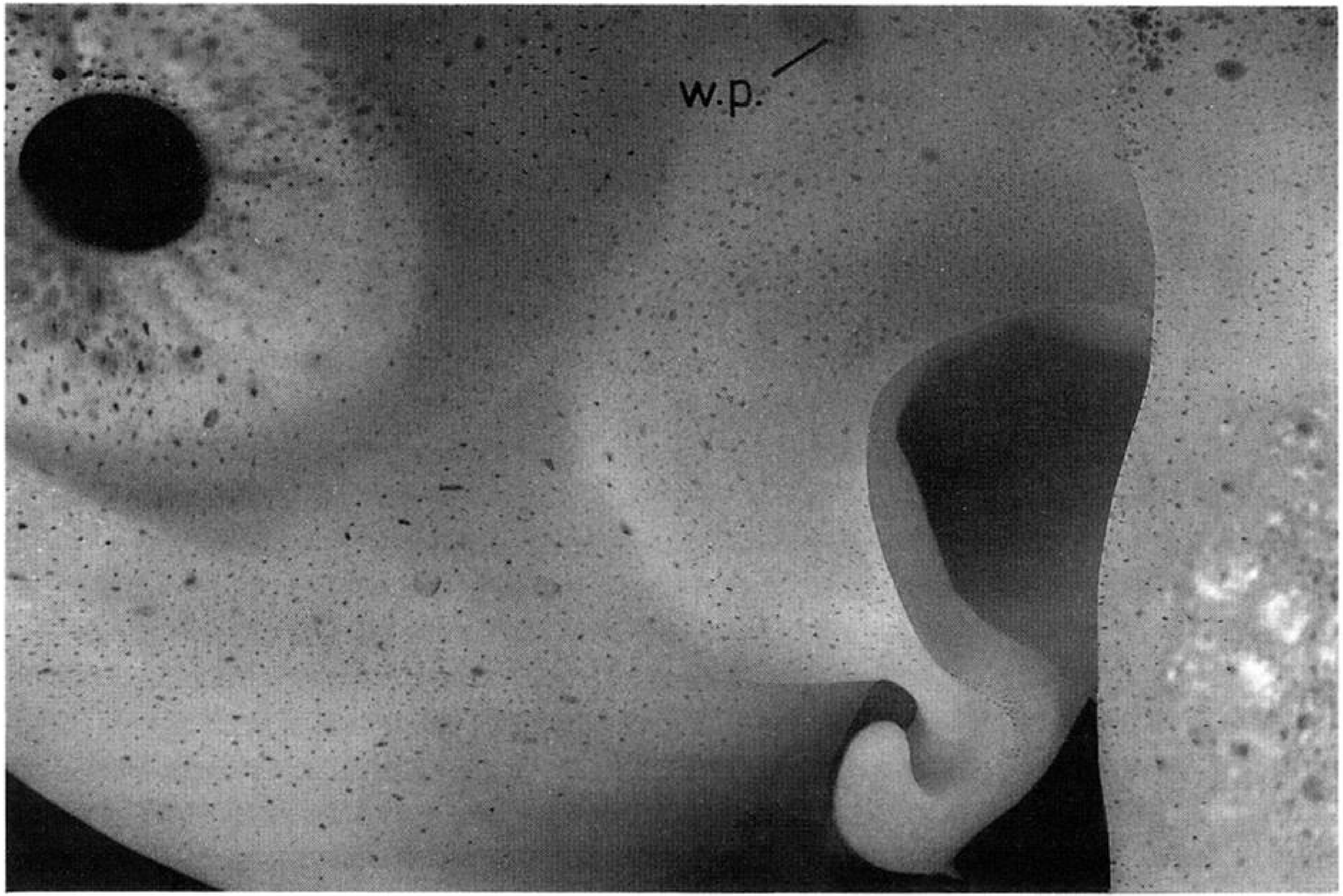
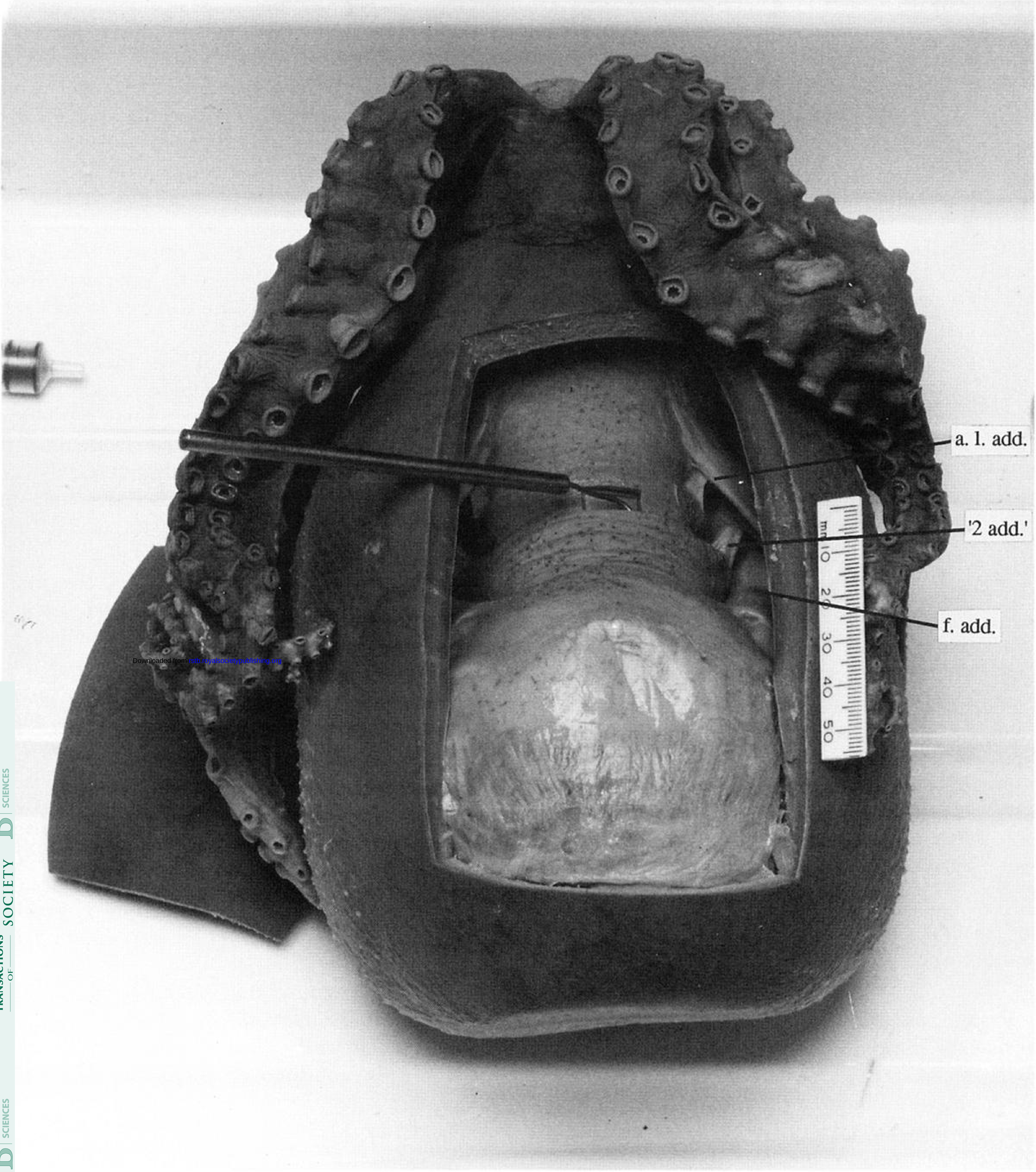


Figure 4. Half-eaten anchovy. Note the bite marks of the ocythoe. Scale bar 1 cm.

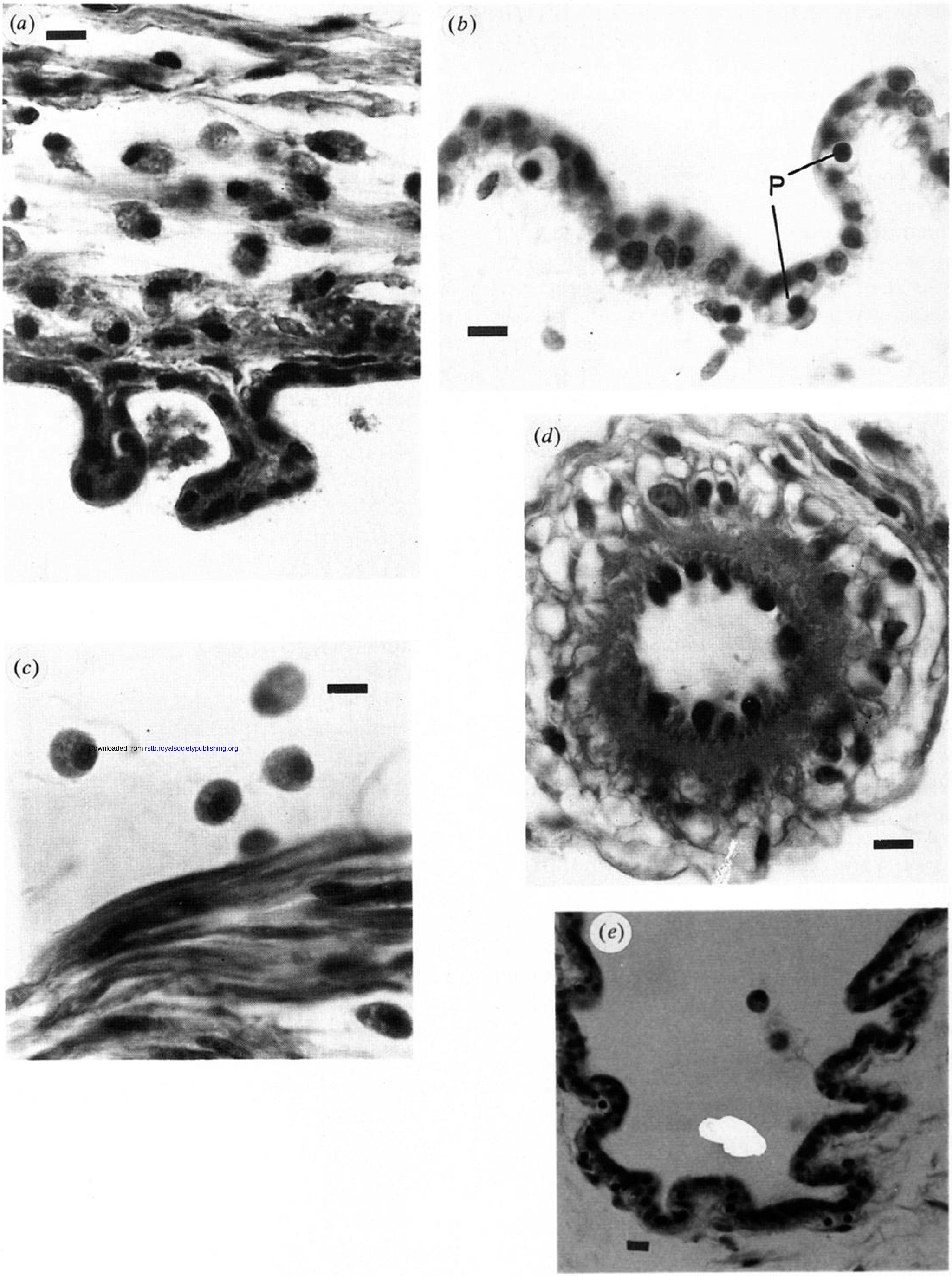


gure 5. Lateral view (left) of the mantle aperture post mortem. The locking apparatus has been unlocked to show the inner rim of the accessory funnel; w.p., water pore. (Photograph touched up for clarity.)



gure 8. Ripe female *Ocythoe* (specimen VIII), photographed in air, with a large window cut out of the thick mus-lar roof of the mantle. The dorsal sac is seen through the upper (forward) half of this window. It is supported by e anterior lateral adductor (*a.l.add.*). Below, what appears to be a second adductor (*2.add.*), running diagonally the first and inserting just behind the mantle aperture (not seen) is morphologically an extenson of the a.l.add. e figure 9); *f.add.*, funnel adductor. A rectangular cut has been made in the roof of the sac, which is empty, to ow the tip of a seeker into the lumen. The lower (rear) half of the window is occupied by the greatly expanded iduct, which is covered by a white membrane. (Ruler divisions, millimetres.) Copyright Trustees of the National useums of Scotland.

gure 13. Gelatinous part of dorsal sac. M, muscle coat; A, blood vessel associated with strands of tissue (STR); C, chromatophore; N, nerve; V, ?venous spaces. 'Amoebocytes' are scattered throughtout the jelly.



gure 14. Roof (*a*) and floor (*b*) of the bladder. The lining of the lumen is a single-celled epithelium which is osely associated with 'amoebocytes' (P) having clear cytoplasm and round nuclei. (*c*) Spherical and subspheri-l (amoeboid) cells with darkly staining cytoplasm (similar cells in (*a*)) lying loose in the jelly (muscle fibre ndle below). (*d*) Typical blood vessel with parenchymatous walls. (*e*) Two 'amoebocytes' and jelly in the men of the same bladder. (Scale bars 10 µm.) (*f–h*) Haematoxylin and eosin section of the swimbladder duct; , muscle coat; X, lumen which extends into crypts (CR) and contains traces of jelly, seen at higher power in) and (*h*). Scale bar 100 µm.

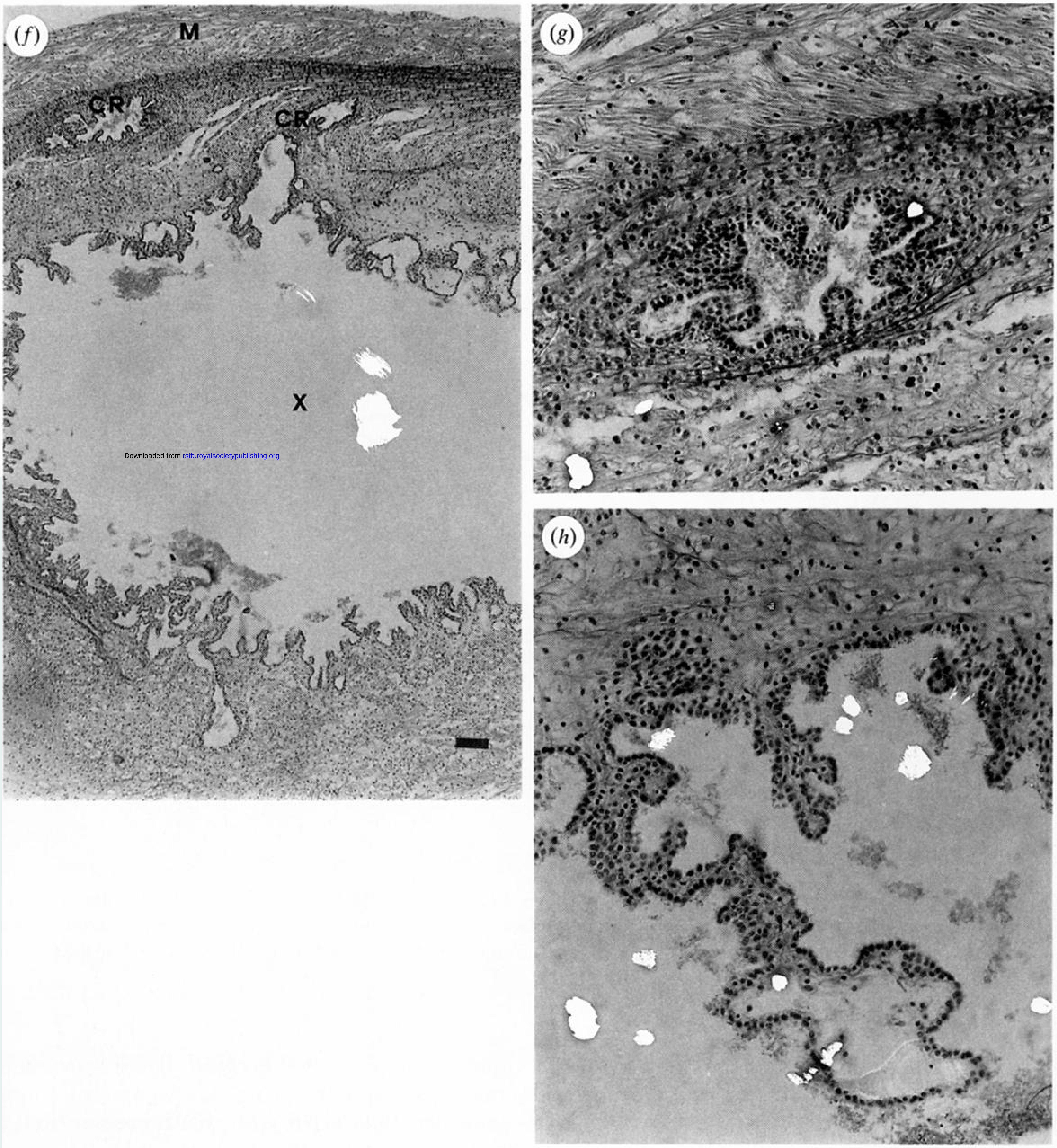


Figure 14. *Continued*