Different Types of Cirral Activity of Barnacles

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DIFFERENT TYPES OF CIRRAL ACTIVITY OF BARNACLES

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[Plate 66]

CONTENTS

From direct observation and from cinematographic records five different types of cirral activity have been recognized in sessile barnacles. They are, arranged in increasing degree of muscular and cirral movement: (1) testing, in which the valves hardly open and the cirri are not protruded; (2) pumping, in which strong rhythmic movements of the operculum occur, but the cirri are protruded only slightly, and not extended; (3) normal beat, a development of pumping, but with the cirri fully extended and withdrawn in rhythm with the opercular movements; (4) fast beat, with less opercular movement, but strong and fast rhythmic cirral movements; (5) extension, in which the cirri are held outside the shell for varying periods without rhythmic movements.

Stalked barnacles show simpler cirral activity, without regular rhythmic movements.

The internal current which passes through the mantle cavity during normal beat and pumping in sessile species is considered to be primarily respiratory. The flow is shown to be sufficient for this purpose, and the energy expended in driving it through is calculated to be comparatively small. Further respiratory exchange of importance in fast beat and extension takes place via the larger cirri, which are distended and emptied of body fluids during cirral activity.

In laboratory experiments under various conditions the balanoids alone showed the full range of movements. The Chthamalidae showed less rhythmic activity and no fast beat, while the stalked barnacles relied mainly on extension. These differences limit the habitats available to the latter groups, as compared with the Balanidae.

Micro-feeding, with the smaller cirri used as a filter, can take place during pumping and normal beat, but is less efficient, to judge from rates of filtration, than captorial feeding on larger particles, when the larger cirri are employed. Fast beat is particularly well adapted to captorial feeding in still water, extension to captorial feeding in moving water. A wide range of food particles was found to be ingested, of sizes varying from a few microns to several millimetres; proteinaceous materials, such as planktonic animals and chopped lamellibranch muscle were most readily utilized, phytoplankton less so, while pure fats and starches passed unchanged through the gut.

The interrelationship of cirral movements, feeding, and respiratory exchange is traced through the possible course of evolution of cirripedes, to the culmination in the most highly developed group, the Balanidae.

Introduction

When we began work on the cirral activity of barnacles it might have been assumed from the published descriptions (e.g. Cole 1929, 1932; see also Darwin 1854) that the rhythmic casting out and withdrawing of the cirri was the only activity shown by the sessile (operculate) forms. It was soon discovered, however, that in most species any individual could display several types of activity (Southward 1955*c*), which differed not only in rate of beating but also in the degree of muscular activity developed in each beat and the resulting mechanism of feeding (Southward & Crisp 1959). It was obviously desirable to investigate further the various types of cirral activity before embarking on comparisons of rates of respiration or feeding between species.

We have now analyzed cirral activity in several species of the commoner British barnacles and have made occasional observations on many other species, including a few from the western shores of the Atlantic (table 1). We have been able to link up the presence of a through current in the mantle cavity of barnacles (Nilsson–Cantell 1921; Crisp & Southward 1956) and the possible occurrence of microphagy (Southward 1955*a*; Barnes 1959) with the more numerous descriptions of captorial feeding on large particles (Darwin 1854; Gruvel 1905; Batham 1945; Howard & Scott 1959; Barnes & Reese 1959). These observations, and those of other workers scattered in the literature, can now be brought together into some degree of order.

Methods

At room temperatures rhythmic beating of barnacle cirri occurs at too fast a rate to be seen clearly, and slight variations in the rhythm rule out the use of stroboscopic techniques. We have therefore had to employ cinematographic methods. The barnacles were first photographed in still water against a black background, with strong lights on either side, while the water currents set up by cirral movement were demonstrated by introducing streams of milk from above. It was found that, unlike suspensions of the usual inert particles employed for the purpose (carmine, clay, graphite, starch), milk streams were fully controllable at the start, remained suspended for some time, and when finally dispersed left very little opacity (Crisp & Southward 1956). Experiments with inert emulsions in place of milk proved as unsatisfactory as those with suspensions of particles. Milk has the possible disadvantage of providing a feeding stimulus, but, in general, little difference was noticed in beating if inert material was replaced by milk. However, unco-operative specimens could be made to beat by addition of fresh plankton, chopped lamellibranch muscle or, to a lesser degree, milk.

Some barnacles were photographed in a specially constructed tank that enabled a three-dimensional record to be obtained. Mirrors were placed in the tank so that the animal was seen simultaneously from the side, from the front and from above, the longer

Table 1. The species of barnacles examined, their habitat, and their cirral behaviour in the laboratory

	habitat	cirral activity				
		testing	pumping	normal beat	fast beat	extension
Thoracica						
Lepadomorpha						
Lepadidae						
Lepas anatifera L.	s	+	(+)	(+)	–	++
Trilasmidae						
Octolasmis mülleri (Coker)	s*	+	(+)	–	–	++
Verrucomorpha						
Verrucidae						
Verruca stroemia O. F. Müller	I, s; sh	+	(+)	(+)	–	++
Balanomorpha						
Balanidae						
Balanus amphitrite Darwin	I, s; sh, exp	+	+	++	++	+
B. tulipiformis Ellis	s	+	+		(see text)	
B. perforatus Bruguière	I; sh, exp	+	+	++	++	+
B. spongicola Brown	s, (I); (sh)	+	+	(insufficient material)		
B. eburneus Gould	I; sh	+	+	++	++	+
B. improvisus Darwin	I; sh	+	+	++	++	+
B. crenatus Bruguière	I, s; sh	+	+	++	++	+
B. balanus (L.)	I, s; sh	+	++	++	+	+
B. balanoides (L.)	I; sh, exp	+	+	++	+	+
B. hameri Ascanius	s	+	+	–	–	+
Acasta spongites (Poli)	s, (I)†	+	+	(insufficient material)		
Pyrgoma anglicum Leach	s‡	+	+	–	–	+
Tetraclita squamosa Bruguière	I; exp	+	+	+	?	++
Elminius modestus Darwin	I; sh	+	+	+	++	+
Chelonobia patula (Ranzani)	s§	+	+	(+)	–	++
Chthamalidae						
Chthamalus fragilis Darwin	I; exp	+	++	(+)	–	++
C. stellatus (Poli)	I; exp	+	++	(+)	–	++
Hexelasma hirsutum (Hoek)	d	+	(+)	–	–	+
Acrothoracica						
Apygophora						
Alcippidae						
Alcippe lampas Hancock	s‖	(+)	+	–	–	–

s	sublittoral	–	no activity of this type
I	intertidal	(+)	rare activity of this type
sh	sheltered shores	+	some activity of this type
exp	wave-beaten shores	++	much activity of this type
d	deep water		

* In branchial chamber of the crab *Callinectes*.
† In sponges.
‡ Embedded in *Caryophyllia*.
§ On carapace of crabs.
‖ In *Buccinum* shells inhabited by *Eupagurus*: cirri are not protruded.

path of the light rays in the mirror views being compensated by a proportionately longer travel in water (figure 1). The records from this tank proved useful in determining the simultaneous current 'flux' all round the animal.

Further observations, particularly on feeding, were made in a trough-like tank (Southward 1957) in which water currents could be set up by means of an enclosed paddle wheel. Opercular and thoracic movements have also been observed through a fenestra cut in the shell, but photographs have not yet been taken using this method.

The ciné records have been analyzed frame by frame. Many sequences were projected on to a drawing board and each frame drawn in outline on tracing paper to enable the movements of cirri, milk trails and food particles to be measured. At the normal repetition rates (16 to 64 frames per second) the coarser movements could be followed with ease on successive frames, but there was slight blurring of details on the smaller cirri and setae owing to the slow shutter speed of the ordinary 16 mm camera ($\frac{1}{40}$ to $\frac{1}{160}$ s). Apart from this difficulty there was no need to employ a high-speed camera, and the finer details are now being sought by coupling electronic flash equipment to the ciné camera (cf. Lester 1948; Jones 1952).

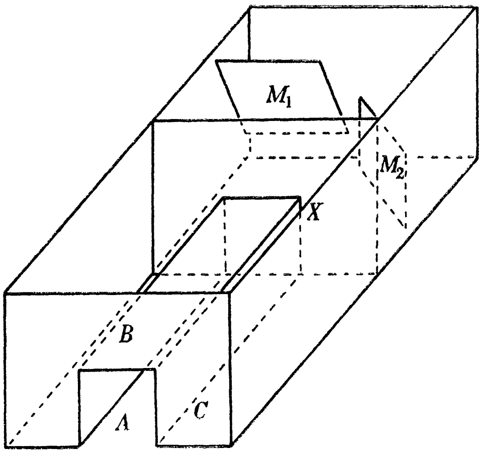


FIGURE 1. Isometric drawing of the tank used for photographing barnacles simultaneously from three aspects. *X*, position of animal; *A*, side view obtained here through tunnel under outer trough; *B*, view from above obtained here via mirror M_1; *C*, front view obtained here via mirror M_2. In the mirror views (*B*, *C*) the light rays have a longer path from animal to film; this is compensated by making them travel a greater distance in water compared with view *A*.

Throughout the work our greatest need was for a means of calculating the flow of water through the mantle cavity, since it is impossible to observe or measure this without damage to the animal. One of us (D.J.C.) has attempted to overcome this difficulty by the use of equations published by Schlichting (1933) and the observations of Andrade & Tsien (1937); the method is included as an appendix (p. 303).

THE TYPES OF ACTIVITY

It will help to shorten the following sections if we first describe the cirri and other organs involved in the movements.

The parts involved in cirral activity

The shell compartments of a typical sessile barnacle are shown diagrammatically in figure 2*A*. Usually the rostrum is considered anterior, the carina posterior, but from the normal position of the mouth and thorax these directions can also be regarded as ventral and dorsal, respectively. To avoid confusion, therefore, we have followed Darwin (1854) and made frequent use of the terms rostral and carinal instead. The mouth of the shell is closed by the operculum, which is attached well down inside the rim by a strong and flexible chitinous membrane (figure 2*C*). The four shell plates which make up the operculum are joined together in pairs to form two valves, which open along the rostro-carinal axis to allow communication of the shell cavity with the exterior. The edges of this opening are lined by thinly chitinized flaps of tissue, *F*, continuous with the lining of the shell or mantle cavity; they act as a seal or gasket when the valves are closed and tightly pressed together (Southward & Crisp 1961). The operculum is attached to the shell only by means of the opercular membrane, and is thus free to move in all directions. Movement upward is controlled by the springiness of the chitin and by turgescence of body fluid within the sinuses of the membrane (cf. Tait & Emmons 1925), and is restricted only by the amount of stretch permitted by the membrane and the degree of relaxation of the three pairs of

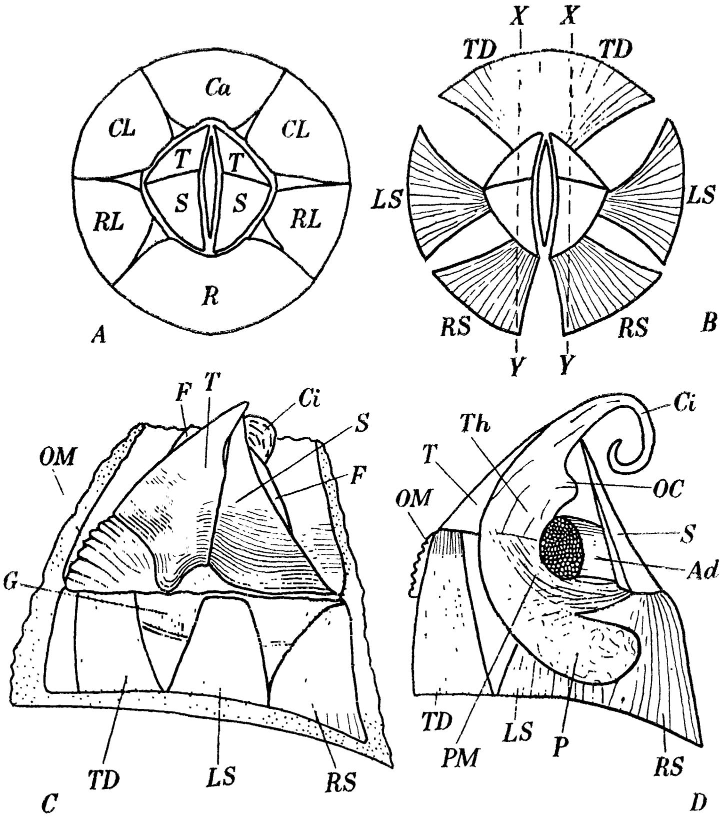


FIGURE 2. Explanation of the parts of a sessile barnacle involved in cirral activity. *A*, diagram of the shell compartments and operculum of a typical small balanoid, seen from above; *B*, the opercular muscles of *A*, after removal of compartments; *C*, side view of larger, thick-shelled balanoid (based on *Balanus perforatus* and *B. nubilus*), with shell sectioned in carino-rostral plane; *D*, as *C*, but with right-side half of operculum, muscles and small cirri removed. Details of cirri and thorax not drawn. (*A* and *B* approx. × 5; *C* and *D* approx. × $2\frac{1}{2}$.)

Ad, adductor muscle; *Ca*, carinal shell compartment; *Ci*, cirri; *CL*, carino-lateral shell compartment; *F*, tergo-scutal flaps; *G*, branchiae; *LS*, lateral scutal depressor muscle; *OM*, opercular membrane; *P*, prosoma; *PM*, prosoma muscles and attachment to operculum; *R*, rostrum; *RL*, rostro-lateral shell compartment; *RS*, rostral scutal depressor muscle; *S*, scutum; *T*, tergum; *TD*, tergal depressor muscle; *Th*, thorax; *X–Y* axes on which valves move (see text, p. 278).

depressor muscles *TD*, *LS*, *RS*. The latter bring about downward movement of the operculum, when the extent of the travel is limited by the opercular membrane, and also take part in rhythmic activity (figure 2*B*).

The depressor muscles run from the operculum to the base, between the shell and the mantle lining and are thus outside the mantle cavity proper. The rest of the barnacle body (prosoma and thorax), lies within the mantle cavity, and is attached by a large number of muscles to the rostral ends of the two scuta (figure 2*D*), which are themselves connected at the same position by the adductor muscle. This muscle is not comparable with the adductor muscle of lamellibranchs; it is used mainly in rhythmic movements of the valves during cirral activity (p. 278) and does not apparently play much part in holding the valves and operculum closed when the barnacle is out of water. The prosoma, which corresponds to the head plus a much enlarged first thoracic segment, carries the first pair of cirri. The other five pairs of cirri are borne on the remaining five segments of the thorax (figure 3*A*). The mouth and mouthparts are placed between the bases of the first and second cirri, on a projection (oral cone) which actually arises from the prosoma.

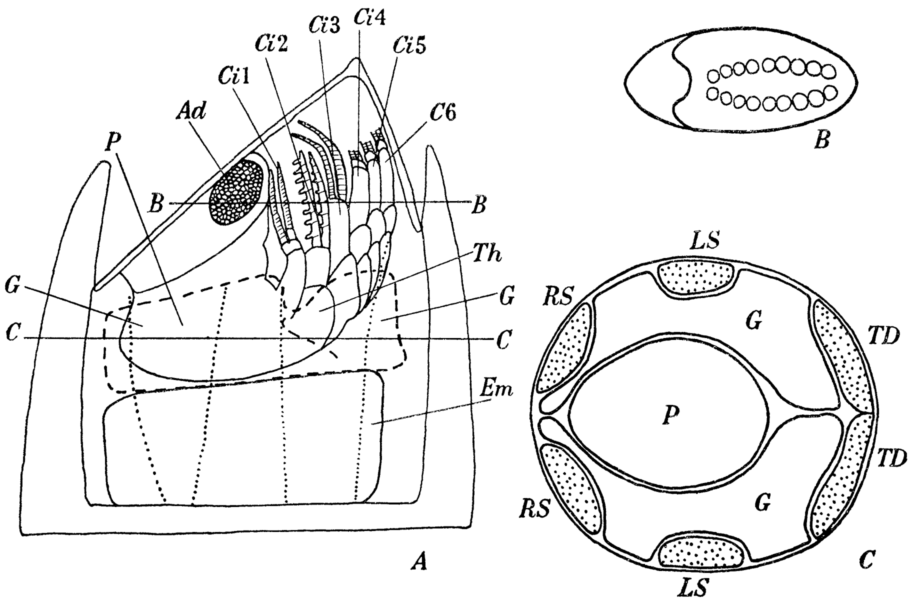


FIGURE 3. Diagram of large balanoid (based on *Balanus hameri*) to show arrangement of parts and spaces inside the shell. (Approx. × 2.) *A*, section of shell in carino-rostral plane, with depressor muscles and branchia of one side removed to display prosoma and thorax. The distal segments of the large cirri (4 to 6) are not drawn. *B*, horizontal section across line *B* to *B*; *C*, section across line *C* to *C*. *Em*, mass of developing eggs or larvae; *Ci* 1 to 6, individual cirri. For details of other lettering please refer to figure 2.

It is important to note that the pairs of cirri differ greatly in form and function. The first three in balanoids (two in chthamalids) are short and stout, and the twin rami of each cirrus are of different length. These small cirri can be accommodated inside the mantle cavity without being rolled up, are well supplied with sets of muscles acting on each segment, and can show a variety of movements. The other cirri (numbers 3 to 6 or 4 to 6) are longer and thinner, with rami equal or almost equal in length: the musculature of their bases resembles that of the smaller cirri, but the long rami possess only a pair of flexor muscles, which roll them up for withdrawal inside the mantle cavity. There is no doubt that the rami of the large cirri are extended by means of body fluid forced into them by contraction of muscles of the prosoma. The existence of such a mechanism was suggested by Cannon (1947) on anatomical grounds, for contrary to Darwin's views (1854) there are no extensor muscles to be found. Full extension of the large cirri cannot take place if the sinuses of the operculum or gills are damaged and the body fluids thus allowed to escape, whereas the thorax and smaller cirri still appear capable of a range of movements.

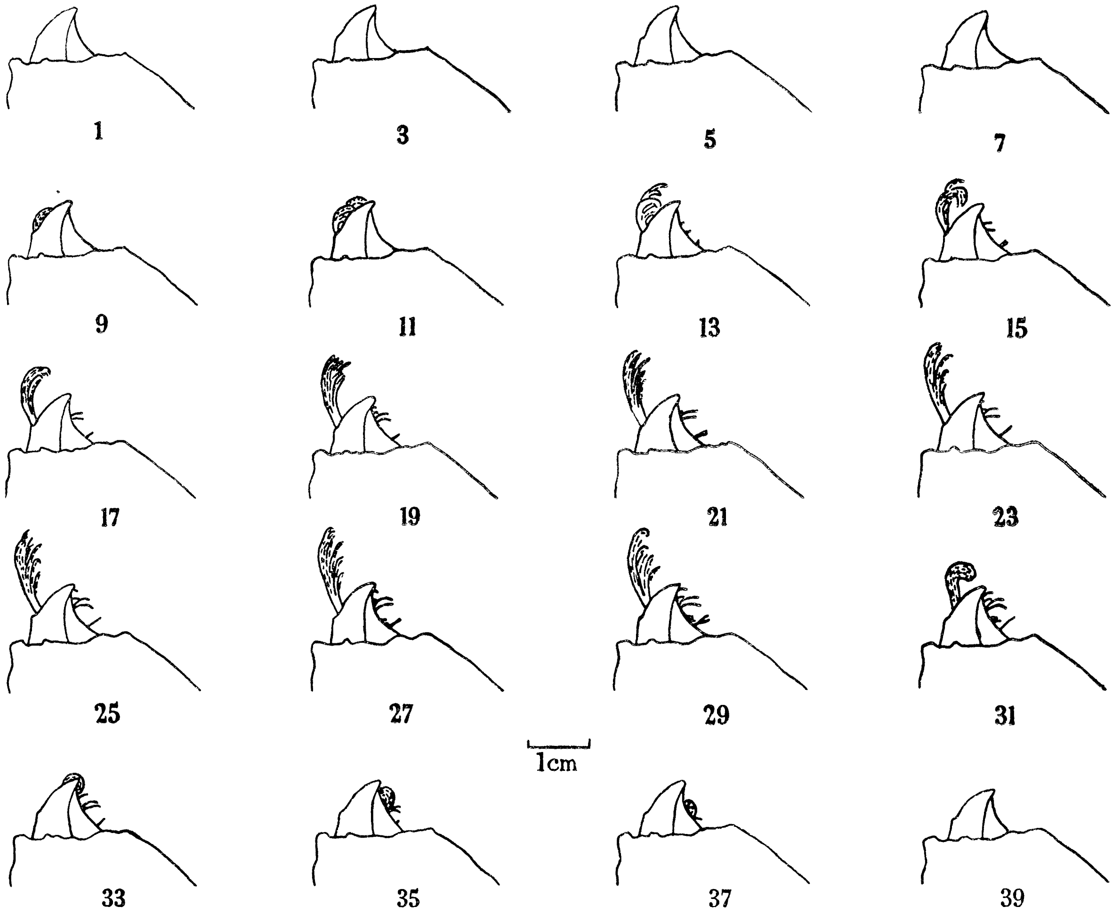


FIGURE 4. Normal beat in *Balanus balanus* seen in side view. Tracing of alternate frames from ciné record at 16/s.

Normal beat

When cirral activity of sessile barnacles is mentioned it is usually the rhythmic casting out and withdrawal of the cirral net that is implied, since this is the type of activity that is often seen under aquarium conditions. We therefore refer to such activity as 'normal' cirral beating although it is merely one of the series of types of activity. Since normal beat contains most of the elements that are found in the other activities, it is described first and then the others by reference to it.

As a preliminary to all types of activity, the operculum must be raised to allow room for movement of the thorax and cirri. This raising movement depends on relaxation of the depressor muscles: the tergal depressors relax greatly but the lateral and rostral scutal depressors relax only slightly. Thus the operculum rotates in a vertical plane towards the rostrum, as it rises under the influence of hydrostatic pressure in the membrane. The tip or beak of each tergum therefore can be seen to move away from the carina towards the centre of the shell opening. Normally, the operculum is not withdrawn below this level until all activity has ceased, as, for example, on closure after shock.

Normal cirral beating may be defined as the type of rhythmic behaviour in which the cirri are fully expanded and then withdrawn into the mantle cavity again without pause. A diagrammatic representation traced from the ciné record is shown in figure 4. The sequence of one beat appears to be as follows. The operculum is slightly raised by further relaxation of the rostral scutal and tergal depressor muscles. At the same time the adductor muscle relaxes and the lateral scutal depressors contract. As a result, the two halves of the operculum (valves) move outward about axes joining the tergal and rostral scutal depressors (*X* to *Y* in figure 2), thus widening the entrance to the mantle cavity. As the valves part the thorax and prosoma begin to move upward and towards the carina, exposing the cirri between the flaps lining the opening to the mantle cavity. The rami of the large cirri extend as they emerge from the mantle cavity, and are finally spread out and thrust back against the terga by an upward movement of the last three thoracic segments. This completes the opening phase of a beat. The closing phase is quicker, and the various movements overlap more closely. The extended large cirri are thrust forward towards the rostrum, and at the same time are rolled up by contraction of the flexor muscles. As the rolled-up cirri and other appendages are withdrawn inside the mantle cavity the operculum is lowered and the two valves brought together again.

In the opening phase the raising of the operculum and widening of the valves causes an enlargement of the space inside the mantle cavity, and water enters from outside. The space within the mantle cavity is reduced again during the closing phase and water is expelled. The time occupied by the various movements in a large specimen of *Balanus balanus* at 18 to 20° C is:

enlargement of mantle cavity	0·4 to 1·0 s	
extension of cirri	0·75 to 1·25 s	
withdrawal of cirri	0·5 to 1·0 s	overlapping, total 0·5 to 1·25 s
reduction of mantle cavity	0·4 to 0·74 s	

In *B. amphitrite*, which beats at a faster rate, the cirri take 0·31 to 0·43 s to expand at 20 °C and are withdrawn again in only 0·18 to 0·31 s. Similar differences in time of extension compared with withdrawal are found in most species. It is an obvious advantage in feeding and other activities if the recovery stroke is slower and gentler than the effective stroke, but an additional reason may be found in the mechanics of movement. As already noted, extension is caused by distension with body fluids which have to travel some distance, while contraction is brought about by the directly acting flexor muscles.

External water movements

It is easily seen how the fast forward sweep of the extended cirri at each beat imparts a greater momentum to the water than the gentle recovering stroke in which the cirri are rolled up for most of the time; this combination of movements produces a general drift of water over the barnacle from carina to rostrum. The exact path of this drift is best made out from three dimensional records of *B. balanus* (figure 5). In successive sequences shot in the special tank, the milk trails were placed far on one side, close to one side, down the centre-line (carino-rostral axis), and on the other side. The results from these shots have been combined to show the current 'flux' around the animal. As might be expected, the strongest flow was in the centre line, close to the cirri. A weaker flow, directed rostrally and slightly above the animal, was present behind the carina (and cirri) for a short distance. The forward flow was measurable only as far as the edge of the rostrum, and close to the surface of the latter was a weak counter-current forming part of the inflow to the mantle cavity (dotted arrow, figure 5). From either side of the barnacle and from behind the cirri there was considerable drift inwards to the cirri, but the records show that particles carried in this drift do not always touch the cirri and are thus not always captured.

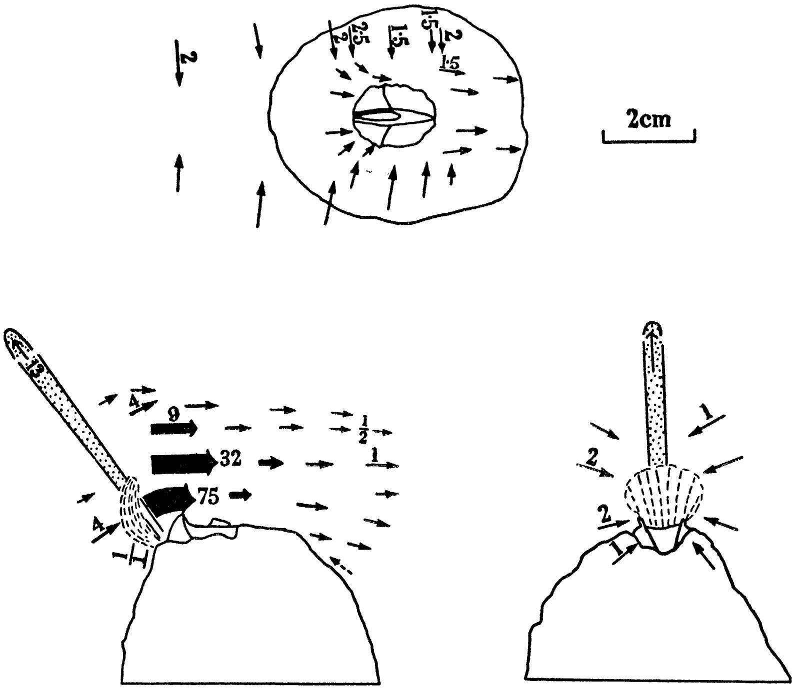


FIGURE 5. The external water movements set up during normal beating, derived from ciné record of *Balanus balanus* taken in the special tank (figure 1). The outgoing pulse from the internal flow is shown stippled. The figures over the arrows give the velocity in mm/s.

Other water movements detectable outside the shell are a consequence of internal currents.

Internal water movements

The occurrence of a through current in the mantle cavity of barnacles has already been noted. Details have been studied from ciné records of the ingoing current and the outgoing pulse, but the flow as a whole has been confirmed in most species by placing milk trails at the point of entry over the small cirri and mouth as the valves are being opened, and observing the jet of milky water at the exit between the thorax and terga when the valves come together again. Further evidence was obtained from specimens of *Elminius* growing on glass, which allowed the presence of milk in the mantle cavity to be seen, though not very clearly, through the basal membrane. In normal beat the inflow to the mantle cavity is slow and causes little or no disturbance to the main external drift over the barnacle. Inflow starts as the mantle cavity begins to expand, and takes place in front of the thorax on either side of the prosoma (figure 6). The position of the inflow appears to be controlled by the position of the thorax which is pressed back against the terga and thus water can enter the cavity only in front between the scutal plates. The ingoing flow passes over the smaller cirri which are spread out into a fan, and which apparently filter off small organisms (p. 297). The gentle character of the inflow may assist effective filtration and permit removal of oxygen from the water by the pair of gills situated in the mantle cavity just below the prosoma on either side (*G*, figure 3).

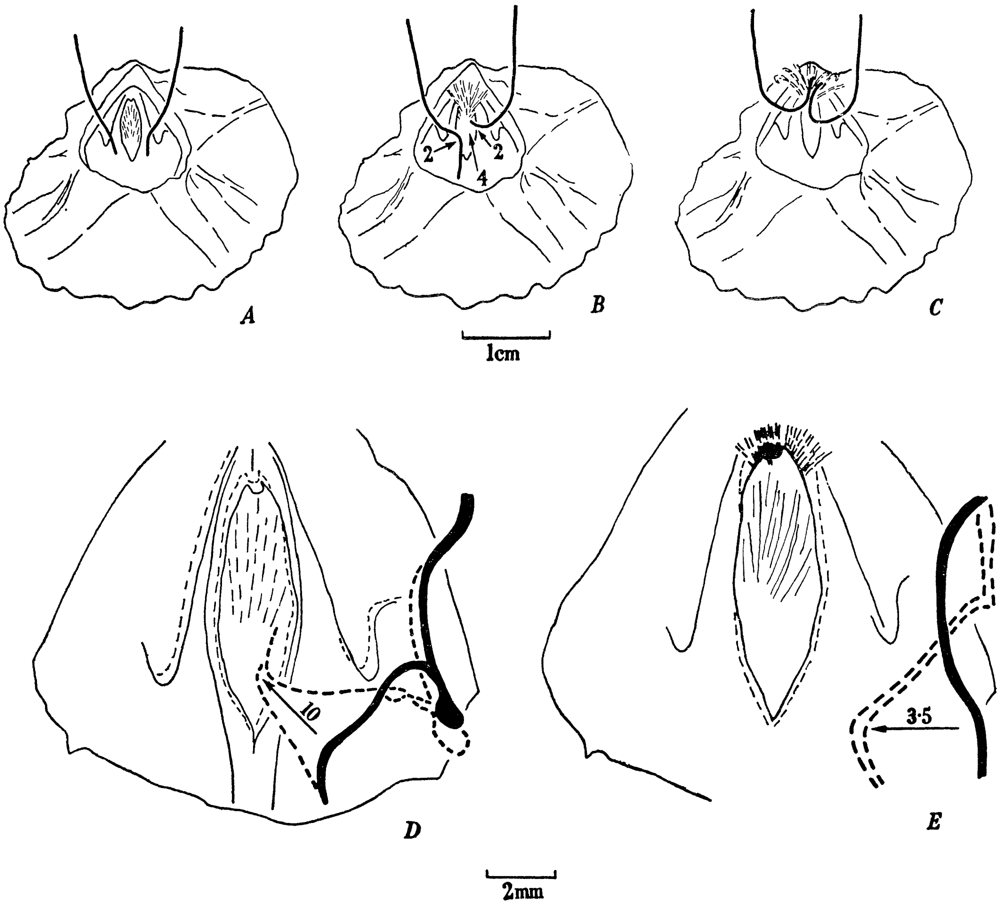


FIGURE 6. The inflow to the mantle cavity during normal beat in *Balanus balanus*. The rostrum was cemented down to the bottom of the tank and milk allowed to stream from above the carina. *A*, start of beat with two streams of milk (shown *black* here); *B*, the same with large cirri starting to unroll, showing velocity of inflow in mm per sec; *C*, cirri fully expanded, and milk streams drawn into the net; *D* and *E*, two closer views with only one stream of milk, showing the greater velocity near the mantle opening. Thin solid lines show position of operculum in the closed phase, thin broken lines the position in the open phase.

The transition from slow inflow to rapid outflow is very abrupt and there must be vigorous movement of the gills as the thorax and cirri move forward and downward. This rostral movement closes the ingoing aperture and opens the exhalant aperture ready for the outgoing pulse. It seems probable that additional blocking of the inlet takes place as the valves and operculum move, and the volume of the mantle space is thus reduced; the gills have the shape and position to act as simple flap valves operating by pressure to close the inhalant region. Sometimes, however, when closure is particularly abrupt, as in a shock response, water is ejected from between the scuta in front of the cirri.

The ciné records (figure 7) show that in normal beating there is a very slight ingress of water into the exhalant aperture at the start of the closing phase, but this is soon ejected again as the full thoracic and opercular movements force out the water in the mantle cavity. The exhalant pulse is at first very strong, but is reduced as the mantle cavity empties and a new cycle of beat commences. The following times were determined for *Balanus balanus* at approximately 20 °C:

inflow into mantle cavity	1·15 s
slight flow into exhalant canal as cirri begin to withdraw	0·125 to 0·375 s
strongest exhalant flow	0·094 s
exhalant flow continues until mantle cavity at closed position	0·375 s
operculum begins to rise again for next cycle	1·125 s later
further detectable flow at limits of exhalant envelope for	0·2 s

During the time of the true outflow of water in this sequence (0·375 s), the jet travelled about 35 to 40 mm upwards from the orifice. The bulk of the water which had passed through the mantle cavity was therefore shot well clear of the main external flow over the barnacle, and there was little chance that it could have contaminated the ingoing current to the mantle cavity.

It will be appreciated that the inertia of the jet results in a continued external pulse of fluid after the exhalant discharge has ceased and the passage between thorax and carina has closed. A slight change in direction of the jet axis is shown in the close-up sequences (figure 7, frames 66 to 84), where the milk trail can be seen bending forward as the thorax moves forward and downward and the opercular movements take place.

Pumping

The level of activity in pumping beat is lower than in normal beat. Typically, the operculum is raised slightly and the mantle cavity aperture widened as in normal beat, but the large cirral rami are not unrolled and thrust out; they move carinally with the thorax, and are sometimes protruded still rolled up at the top of the beat (figure 8). In closing, as the operculum is lowered and the mantle cavity reduced, the rolled up cirri and thorax move rostrally and downward. The phases may have a slightly different time sequence compared with normal beat since the opening movement takes longer:

species	*T* (°C)	enlargement of mantle space	reduction of mantle space
Balanus balanus	*ca.* 10	3 s (cirri 1 to 3 extended for last 1·5 s of this)	0·5 s
B. hameri	10	7·0 to 8·5 s (extension of small cirri for last 4 s)	1·5 to 2·2 s (up to first 1·5 s for withdrawal of small cirri)
B. balanoides	*ca.* 20	1·5 to 3·0 s	0·8 to 1·0 s

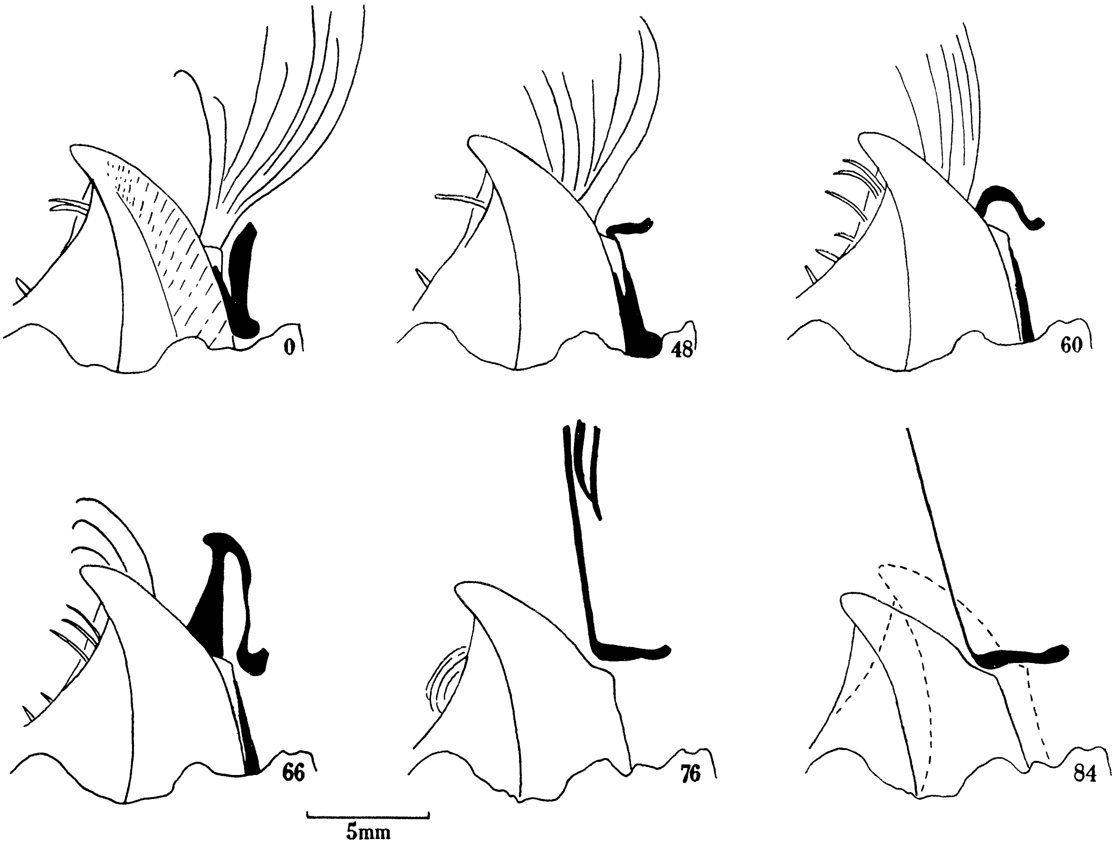


Figure 7. The exhalant current in *Balanus balanus*, with one milk trail placed close to the terga. The numbers give the frame numbers of the ciné sequence, taken at 64/s. On the last frame the position of the operculum at the top of the next beat is indicated by broken lines. Cirri shown only roughly.

Water movement during pumping

Both the flow of water into the mantle cavity, and the exhalant pulse seem identical with those observed during normal beat (figures 9 and 10). The velocity of the jet is comparable with normal beat, and the envelope reaches similar heights above the animal. In most individuals observed the outgoing pulse was not truly vertical, and set up a slight drift of water around the shell, usually towards the rostrum, but sometimes directed carinally as in figure 10. This drift did not exceed 1 mm/s, which is much less than the comparable flow found in normal beat.

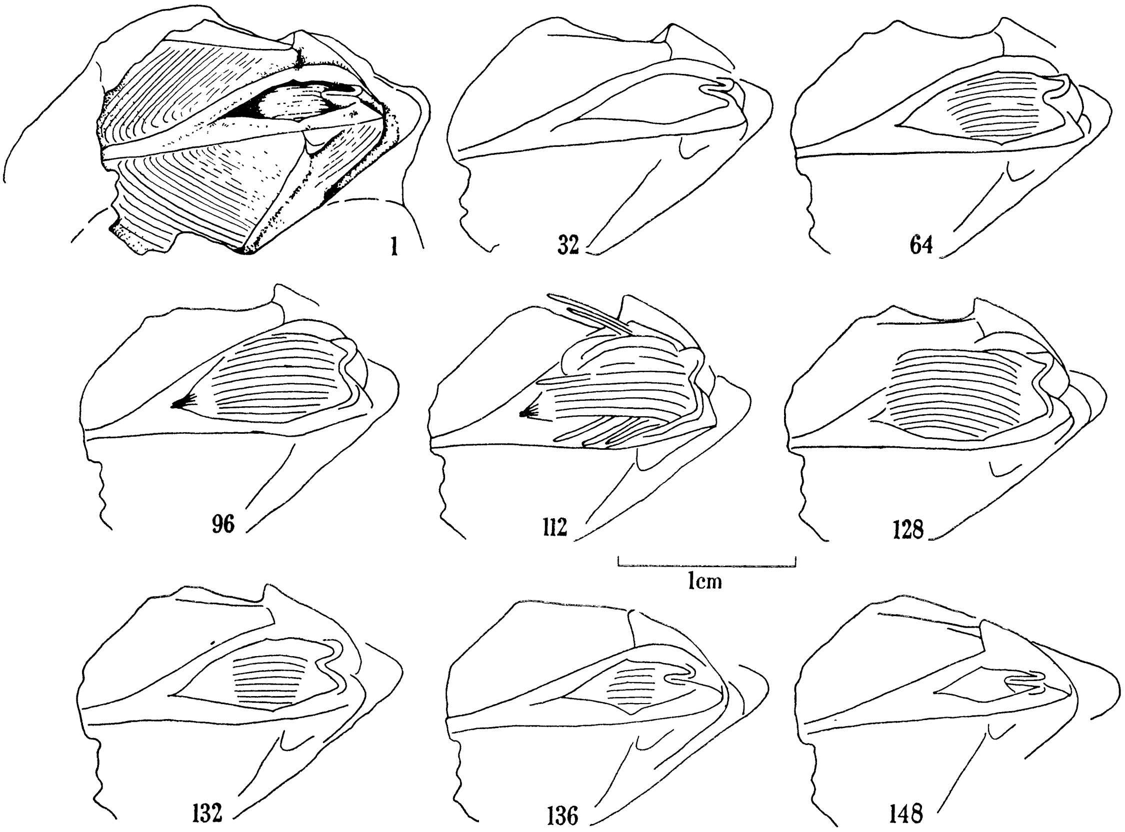


FIGURE 8. Pumping in *Balanus hameri*, seen from above and to one side. The numbers refer to ciné frames at 16/s.

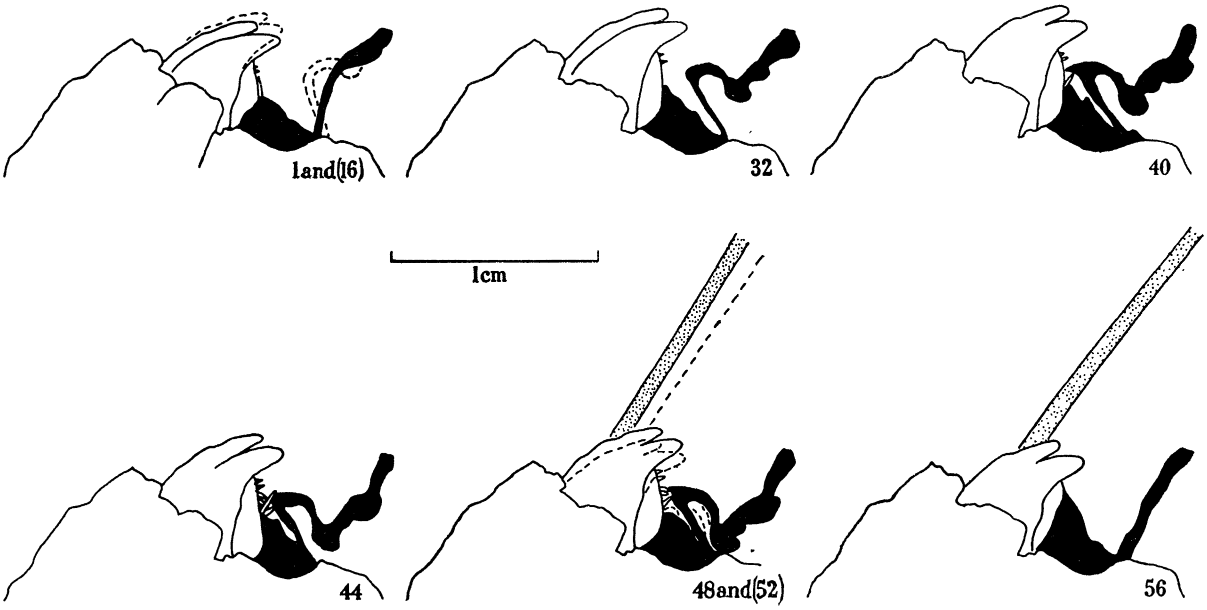


FIGURE 9. Side view of pumping in *Balanus balanus* with one milk trail, showing inflow (black) and exhalant pulse (stippled). The numbers refer to ciné frames at 16/s, those in parentheses to the positions indicated by broken lines.

Testing

A much lower level of activity than is displayed in pumping is often found in specimens kept in the laboratory. Seen from above, the distance between the flaps lining the opening to the mantle cavity widens slightly, and is then contracted again: corresponding carinal and rostral movements of the thorax may be glimpsed through the opening (figures 16 and 17, plate 66). There is a well-marked groove across the middle of each flap, and the flaps part first at this point as the aperture between the valves is widened. Thus water first enters the mantle cavity in the region of the grooves. Frequently one or two cirral rami are protruded slightly, and it seems probable that the function of this activity is to test the condition and movement of the outside water.

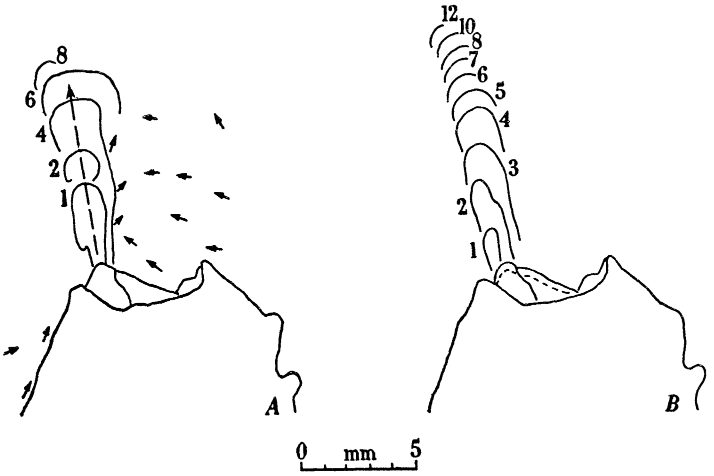


FIGURE 10. Side view of *Balanus balanoides* showing: *A*, the exhalant pulse and the external water flow during pumping; *B*, the outgoing pulse on complete closure of the operculum (position after closing indicated by broken lines). The numbers refer to ciné frames at 16/s.

Milk trails prove that water enters the mantle cavity on widening of the aperture, and leaves again on closing, but it is not possible to see if there is also a through current or if the water is simply puffed in and out. This type of activity most often occurs under

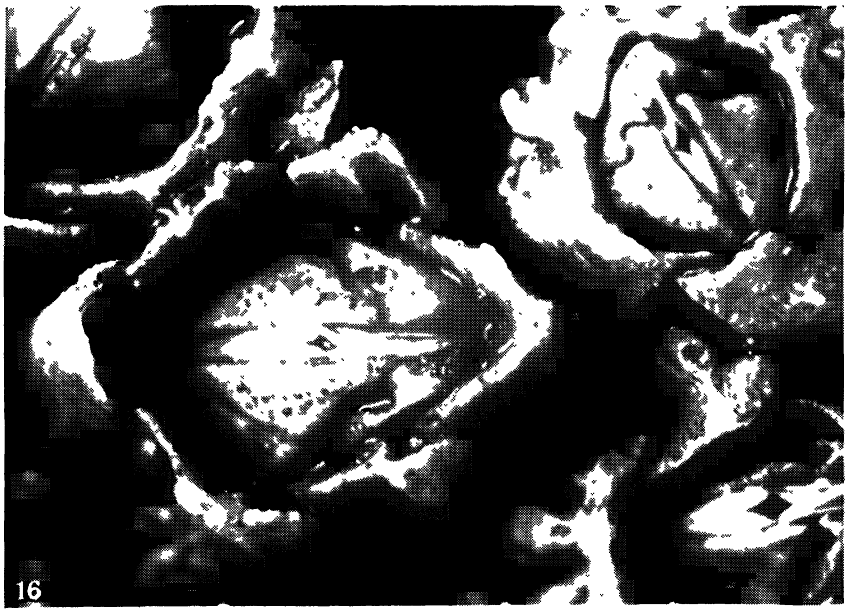
DESCRIPTION OF PLATE 66

FIGURE 16. Specimens of *Balanus balanoides* seen from above, showing testing activity while out of the water but still wet. (Approx. × 7.)

FIGURE 17. *Balanus crenatus* seen from above while under water. The specimen on the left shows the closing phase of pumping, that on the right testing activity. (Approx. × 7.)

FIGURES 18 to 21. Enlarged ciné sequence of *Hexelasma hirsutum* showing behaviour to a current of water flowing from the right. The rostrum is at the right-hand bottom corner, and in the untwisted position the cirral net would face the camera at a slight angle. In the first view (18) the net is partly twisted away from the current, and in the last (21) has been swung round to face the current. Interval between frames approx. 2 s. (Approx. × 2.)

FIGURES 22 to 25. Enlarged ciné sequence (successive frames at 16/s) of *Balanus hameri* showing captorial feeding by extension. The cirri are twisted to the left to face the current. A piece of lamellibranch muscle carried in the current is seen causing first a reaction from the cirral rami touched (figure 23), then complete withdrawal of the net. (Approx. × 2.)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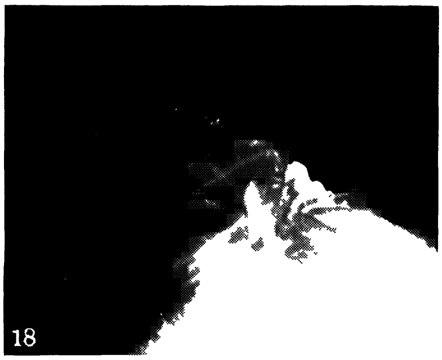
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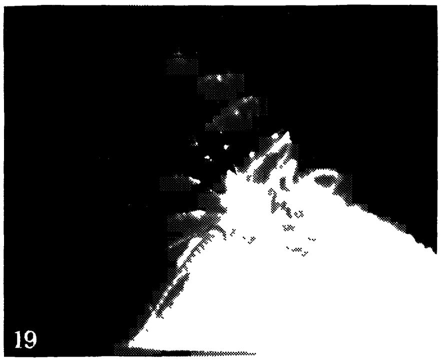
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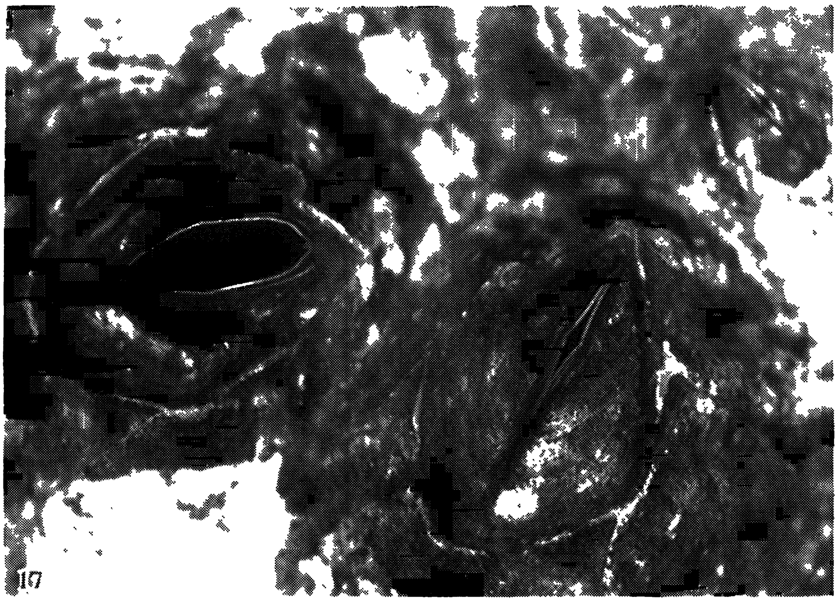
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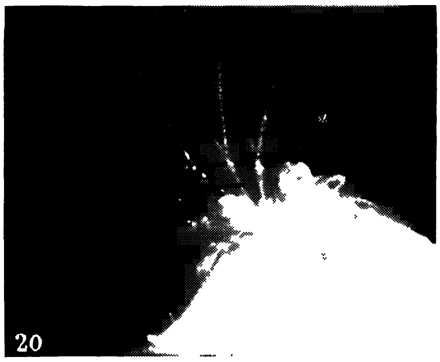
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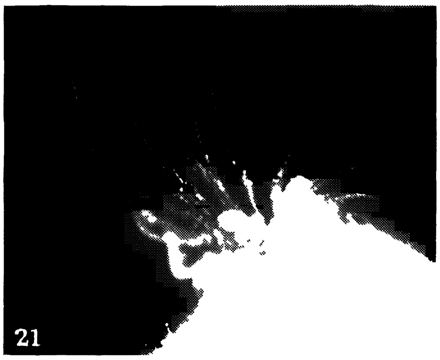
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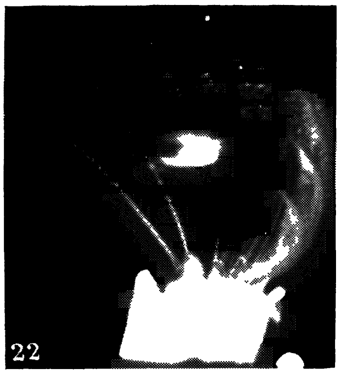
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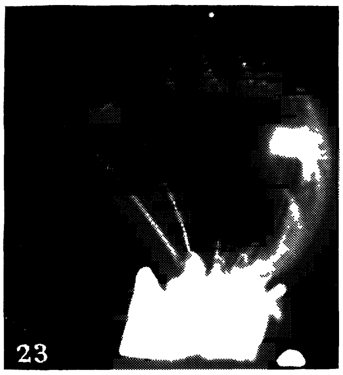
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seemingly unfavourable conditions and is frequently a precursor of full beating. Similar movements without the protrusion of cirri may be observed in barnacles out of water in a damp atmosphere (figure 16, plate 66; see p. 301).

Fast beat

In fast beat the movements are not only faster, but differ from those of normal beat in the absence of any noticeable exhalant pulse. To the eye it seems that the cirri remain outside the mantle cavity, and are then simply waved to and fro.

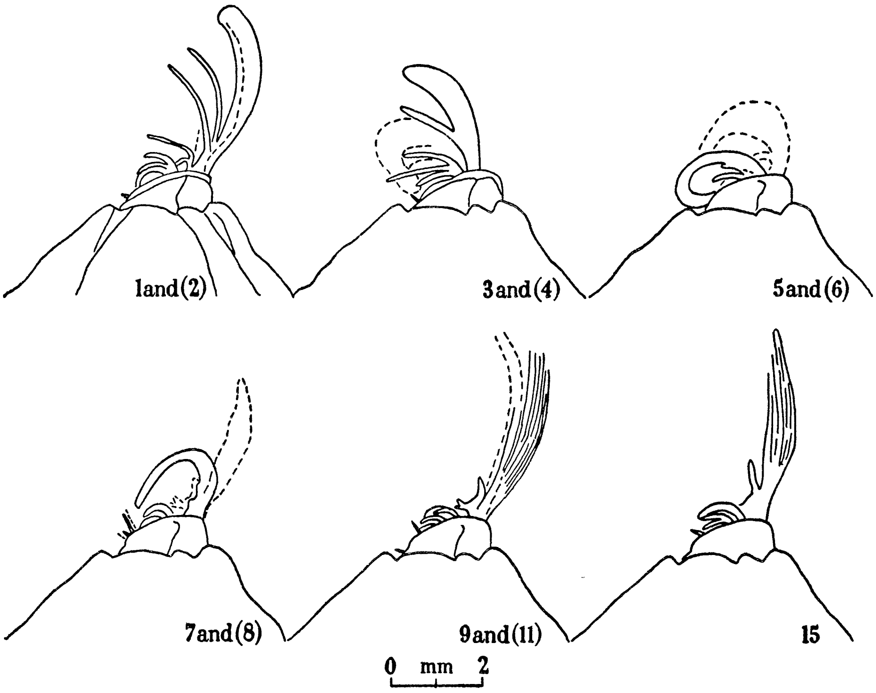

Figure 11. Fast beat, with slight extension, in *Balanus balanoides*, seen from the side, with large cirri indicated only roughly. Numbers refer to ciné frames at 16/s, those in parentheses to positions shown by broken lines.

On careful examination of slow motion and electronic flash synchronized sequences the differences from normal beat appear less marked. Although the operculum remains almost fully raised and the aperture continues wide open between beats, there is a further slight raising and widening as the cirral net moves carinally and the large rami are unrolled (figure 11). In the closing phase of a fast beat slight reduction of the mantle space occurs as the cirri and thorax sweep rostrally, as evidenced by very slight traces of an exhalant puff that have occasionally been seen on the ciné records. At the end of the closing phase of fast beat the larger cirral rami remain just outside the mantle cavity, though they are rolled down to the level of the smaller cirri.

The lack of full withdrawal of the larger cirri is partly responsible for the greater frequency of fast beat. Typical sequences at 20 °C are:

species	cirri unroll and move carinally	cirri swept rostrally and rolled up
Balanus balanoides	0·25 to 0·31 s	0·25 to 0·31 s
B. amphitrite	0·25 to 0·31 s	0·19 to 0·25 s
Elminius modestus	0·12 to 0·16 s	0·12 to 0·16 s

Thus the forward and recovery phases seem to be of nearly equal duration in contrast with other types of beat (table 2).

TABLE 2. COMPARISON OF ACTIVITY OF *BALANUS BALANOIDES* (APPROXIMATELY AT 20 °C). PERCENTAGE OF TOTAL TIME FOR ONE BEAT OCCUPIED BY THE OPENING AND CLOSING PHASES

	pumping	normal beat	fast beat
opening phase	65 to 75	65 to 70	50
closing phase	25 to 35	30 to 35	50

Water movements

The external currents set up during fast beat are, as might be expected, very strong, and cannot be called a drift. The flow is detectable much farther away than in normally beating specimens, up to a distance equal to three times the diameter of the shell in rapidly beating small *Elminius* (figure 12). The strength of the external flow must be partly due to the more rapid series of beats, but the forward stroke may also be more powerful than in normal beating, since the cirri and thorax are extended farther out of the mantle cavity.

Any internal water movements occurring during fast beat are masked by the external flow. It is, however, obvious from the movements of the operculum that some water must enter the mantle cavity and slight signs of exhalant pulse could be detected in some of the ciné sequences in which large amounts of milk were used.

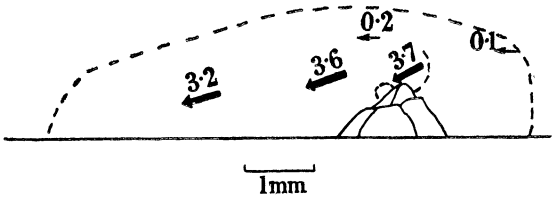

FIGURE 12. The external water movements during fast beat, as recorded with small *Elminius modestus*. The broken line shows the area of water in movement; the arrows give the speed in mm/s. The approximate position of the large cirri at the top and bottom of a beat is indicated.

Extension

In the type of activity that we have termed extension there is no regular beating of the cirri. Instead they are unrolled and thrust out as in normal or fast beat, and are then kept extended for periods varying from only a few milliseconds to several seconds, before being withdrawn again. The degree of extension response shown by a specimen may reflect its previous habitat (see p. 292; Southward 1955*c*), but in the laboratory it is also related to the immediate environment. The briefest response may be found in otherwise normally or fast-beating specimens when milk trails or plankton organisms are added. Extension is most regularly shown in most species under the stimulus of a water current, and there is usually an increase in the time the cirri are held open as the current velocity increases. In *Balanus balanoides* the following sequences were observed at 15 to 18 °C:

speed of current (cm/s)	cirri unrolling	cirri extended	cirri being rolled up
nil	0·25 s	nil	0·25 s
5	0·375 s	0·188 s	0·375 s
12	0·25 s	1·3 to 1·8 s	0·25 s
20 to 25	0·25 s	from 0·125 to 0·875 s in 10 sequences	0·375 s

At the higher velocities (above 20 cm/s) it was obvious the animal had difficulty holding the cirral net against the force of the current. At times the net was whipped away from the vertical almost like an umbrella blown inside out in the wind: at other times the animal appeared to dodge the full force by turning the net edge on to the flow; at yet other times the cirri became entangled in one another and movements became irregular. These reasons explain why at the highest velocity the cirri were held extended for a shorter time than at intermediate velocities.

At the slower current speeds the movements of the large cirri can be analyzed in more detail from the ciné sequences. It can be seen that the rami unroll and open out into a fan which is at first held momentarily in the most extreme position right back against the terga and carina. The net is then brought forward slightly (about $\frac{1}{2}$ mm in *B. balanoides* of 7 mm basal diameter), where it remains extended in the current. In this position the whole net may be rotated from side to side on its axis, like a seeking radar antenna, and if the current is not parallel with the fore and aft line (rostro-carinal axis) of the barnacle the net may remain twisted to one side so that it is set at right angles to the flow (figures 18 to 21, plate 66). The cirral net can be turned through a large angle (nearly 180° in most species) if the direction of the current is reversed and made to flow from the carinal aspect, but in this reversed position it is very subject to difficulties at high current velocities. At low current speeds the frequency of beat may be greater in the reversed than in the normal position, as the cirri appear to show the extension response less readily when the current is directed from behind the cirral net than in the normal position facing the current (see table 3).

TABLE 3. EFFECT OF SOME ENVIRONMENTAL FACTORS ON RATE OF BEATING OF BARNACLES

	rate of beating per 10 s					
	B. crenatus			*B. balanoides*		
A at 14 to 15 °C	rate	s.d.	s.e.	rate	s.d.	s.e.
no stimulus	10·4	±2·4	±1·0	4·4	±0·8	±0·2
water current	4·9	±2·6	±1·2	3·9	±0·3	±0·1
water current and food	7·2	±0·7	±0·3	6·0	±1·0	±0·4

B at 17 °C		*E. modestus*
no stimulus		21·5
water towards cirral net		
	1 cm/s	16
	2–3 cm/s	6·6
water away from cirral net		
	1 cm/s	26
	4 cm/s	9·6*

* Cirral net reversed while extended.

Other movements

There are several other types of behaviour involving cirral or opercular movements.

Shock closing

Full lowering of the operculum is usually caused by some outside shock, such as vibration or touch, or the well-known shading response caused by a reduction in the amount of light falling on the shell. This complete closure is brought about by sudden contraction of all the depressor muscles, and the resulting reduction in volume of the mantle cavity may be shown as a puff of water all along the aperture, from both inhalant and exhalant canals.

Rocking

The rocking movements of the operculum described by Tait & Emmons (1925) for *B. nubilis* can be seen in other large balanoids, especially those with beaked terga, such as *B. perforatus* and *B. balanus*; the reaction is most often produced by further irritation after the animal has closed. The whole operculum is raised quickly, but with the valves tightly closed, and by contraction of one or more of the depressor muscles the whole is rocked from side to side, or swept round in a circular path with the terga held against the inner edge of the shell compartments. Tait & Emmons (1925) suggested that the rocking movements were adapted for the prevention or removal of encrusting growths from the inner edges of the compartments surrounding the operculum. It is obviously necessary that these parts and the adjacent part of the terga should be clean enough to permit vertical movement of the operculum. Their normal pristine condition may be contrasted with the scutal surfaces, which are often overgrown by various plants and animals (as in figure 17, plate 66). In *Chelonobia patula*, which has reduced terga and scuta, this activity is not possible; and young individuals of the same species can be found growing above the operculum in the angles formed by the inner edges of the shell compartments.

Cross-fertilization

Although it was not noted by Gruvel (1893), nor by Barnes & Barnes (1956) in their corresponding account of copulation in *Balanus balanoides*, two different types of cirral activity are displayed by the partners. Individuals acting as males make a few normal beats after opening and then pass into extension: when the body is fully extended the penis is unrolled and directed towards a specimen acting as female (cf. Southward 1955*b*). Barnacles 'inviting' insemination do not extend the large cirri fully, but show slow pumping activity and may stop for a while in the open phase of a pumping beat. On completion of insemination the 'male' withdraws its penis into the normal position between the last pair of cirri and resumes beating. The 'female' usually closes completely, expelling surplus semen, and displays rocking movements, which in this case appear to be associated with oviposition inside the mantle cavity.*

It is obvious that the penis is erected by distension with body fluids forced into it although movement during, and withdrawal after, copulation are directly muscular. Since erection appears never to take place until the large cirri have been fully distended, it represents further penetration by body fluids from the prosoma.

Emission of nauplii

It was recorded by Barnes & Barnes (1956) that newly hatched nauplii were emitted in a jet of water from the carinal end of the aperture. Our observations show that this jet is the normal exhalant puff found to a greater or lesser degree in all types of cirral activity, rendered more obvious by the clouds of larvae carried within it. Occasionally the nauplii

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* Clegg, D. J., M.Sc. Thesis, Univ. Coll. N. Wales, 1956.

appear during normal beat, but more generally they are emitted during pumping, when the energy can be concentrated on producing a powerful jet. In fact, the puffs may sometimes be more vigorous and spaced at longer intervals than usual. It is an obvious advantage in dispersal to have the larvae carried as far as possible above the area swept by the cirri of neighbouring barnacles, so eliminating any possibility of capture before their own activity carries them upwards to the light. When barnacles which are liberating nauplii are kept in small dishes of water, especially in the dark, they will readily devour their own larvae (Crisp & Patel 1960).

Movements in the pedunculate barnacles

So far we have been describing the types of cirral activity exclusively from examples among the sessile species. To what extent do the stalked barnacles show the same behaviour? In table 1 will be found a summary of our observations on a few pendunculate forms, while Barnes & Reese (1960) have described some of the reactions of *Pollicipes*. It must be remembered that cirral activity in stalked species does not involve any opercular movements, but on the other hand the chitinous peduncle can show a range of independent vertical and horizontal movements. However, in all the activities of stalked barnacles the movements of prosoma and thorax appear similar to those of sessile species. They differ only in the opening of the valves by tension of the chitinous membranes after the adductor muscle has been relaxed, rather than by a positive muscular or hydraulic mechanism for which there is apparently no provision (but cf. Cannon 1947). The rami of the larger cirri are extended hydraulically.

Rhythmic movements are comparatively rare in pendunculate barnacles. There can be no regular circulation of water through the mantle cavity, though weak currents can be demonstrated by use of streams of milk, and no maintained movements of water externally. In general their behaviour is simpler and less interesting than that of sessile species.

THE CURRENT IN THE MANTLE CAVITY

It is worth analyzing in more detail the through current of water in the mantle cavity. This circulation is present to a greater or lesser degree in most species, and is more characteristic of cirripedes as a whole than so-called normal beating, which is not shown by all. To determine the function of the mantle current we must make some estimate of the volume of water passing, and of its velocity, but such measurements cannot be made directly, and must be deduced from the part of the flow outside the mantle cavity. For this purpose the exhalant pulse is more useful than the diffuse and gentle inflow.

In operculate species the exhalant pulse issues from the canal formed between the dorsal side of the forward moving thorax and the mantle cavity lining where the two terga are joined together (figure 7). The canal appears to be almost lunular in cross-section but has had to be regarded as circular for purposes of calculating the flow from the ciné records. As recorded on the film, the exhalant pulse takes the form of an envelope, the outer boundary of which is made up of milk particles which were originally part of a milk stream placed in and near to the opening of the canal. As the water shoots out of the mantle space its momentum is transferred to the adjacent fluid, which is thereby set in motion and carried with it (figure 13). As a result, the issuing stream of water broadens out and slows down after it passes through the exhalant opening into the surrounding fluid. The volume of water contained in the envelope may, therefore, be much greater than the actual volume ejected by the animal. The treatment employed to avoid this error is summarized in the appendix (p. 303), and the calculated volumes and velocities for selected sequences are given in table 7, p. 305.

During the exhalant pulse, the calculated pressure of water in the mantle cavity of both *Balanus balanus* and *B. balanoides* is of the order of 1 cm of water. The flow is about 0·1 ml./s in the larger *B. balanus*, and 0·013 ml./s in the smaller *B. balanoides*. In *B. balanus* the exhalant current lasts for about 0·5 s and occurs once every 2 s: hence the total water circulated during a beat is about 50 mm^3 or about 100 ml./h. The energy necessarily dissipated by *B. balanus* in pumping the water through its mantle space amounts to about 2·5 ergs/s over a long period. These figures are all very rough estimations because of the large errors that may have been introduced by the irregular shape of the jet aperture and other unavoidable approximations. However, they are of use in considering the function of the through current.

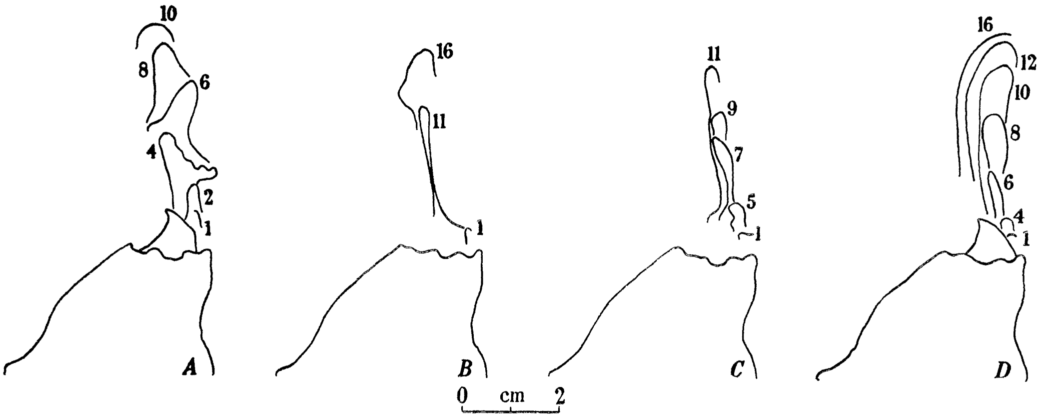

FIGURE 13. The positions of the exhalant envelope found in four different sequences of *Balanus balanus*. These sequences were used to calculate the velocity and volume of the flow (table 7, appendix). Numbers refer to ciné frames at 16/s.

Function of the flow

Darwin (1854) assumed that the structures he termed branchiae were in fact used for respiratory exchange, as indeed their structure indicates, and that the mantle water flow, which he assumed was simply puffed in and out ('may be compared to the heaving of a man's chest'), was required to bathe these structures. We have shown that the flow of water takes place predominantly in one direction. The resultant more or less continuous replenishment of water is the more efficient condition for gills, as distinct from lungs in which rapid micro-diffusion is possible. Nevertheless, it is impossible to prove that the internal flow is required entirely for, or always needed in, respiration. Certainly, as the water passes through the mantle cavity it must bathe the branchial surfaces, but it might be argued that any respiratory function of the branchiae could be subordinate to their functioning as flap valves to control the water flow. In fact, some respiratory exchange must take place via the larger cirri, which are alternately distended and emptied of body fluid during beating, especially during the very energetic fast beat, when the water flow through the mantle cavity is reduced. However, at lower levels of activity the cirri are not protruded and the internal flow must then provide the only respiratory mechanism available.

We can show that the internal flow during pumping and normal beat is sufficient for the purposes of respiration. The volume of water going through at each beat is not large compared with the volume of the whole animal and shell: *B. balanus* of shell volume approximately 3 cm^3 has a calculated flow of 50 mm^3 per beat. The shell volume is, of course, much larger than the free water-filled space of the mantle cavity, which, to judge from dissections and sections, appears very small in comparison with the total volume of thorax, prosoma, ovary, gills, depressor muscles and mantle linings (figure 3). Unfortunately we have no reliable figures of oxygen consumption of *B. balanus* and *B. balanoides* under the conditions of the current flow experiments, at *ca*. 20 °C. The latter species, at 15 °C, gave values of 0·2 to 1·6 ml. O_2 (g wet wt)$^{-1}$ h^{-1} under continuous stirring designed to stimulate normal beat or higher levels of activity. Borsuk & Kreps (1929) at Murmansk found values of 2 mm^3/min for a group of thirty-two *B. balanoides* in air at an unstated, but probably low, temperature: if we allow a tissue weight of 0·1g per individual, a reasonable value for English specimens, this gives a possible rate of 0·04 ml. (g wet tissue)$^{-1}$ h^{-1} out of water. In water of normal salinity at 6 °C, Kreps (1929) found that the related species *B. crenatus* (which has a higher rate of beating) consumed 1·2 ml. oxygen per twenty-two specimens in 5 h; if again we use a tissue weight of 0·1 g per individual, this value becomes 0·11 ml. (g wet tissue)$^{-1}$ h^{-1}. Barnes & Barnes (1959) observed only the oxygen consumption of the excised thorax and prosoma, which is useless for present purposes. However, working at temperatures near those of our experiments on current flow, Costlow (1958) found the oxygen consumption of the subtropical species *B. amphitrite* to vary from 0·05 to 0·2 ml. (g wet wt)$^{-1}$ h^{-1}.

From all these observations, and taking into account differences of size and temperature, we might reasonably estimate a value of the order of 0·1 ml. (g wet tissue)$^{-1}$ h^{-1} for purely pumping activity in *B. balanoides* at 20 °C. If we assume a tissue weight of 0·1 g, an individual would require 0·01 ml. oxygen per hour. The oxygen available in the calculated volume of 10 ml. water pumped per hour is approximately 0·05 ml., which should be quite adequate. The energy expended in producing the internal flow is relatively small. In the aerobic oxidation of glucose, 1 ml. of oxygen could theoretically yield 3·43 cal, equivalent to $14{\cdot}4 \times 10^7$ ergs. Assuming a muscular efficiency of 20% (Hill 1939) the energy produced by 0·01 ml. oxygen might be about 3×10^5 ergs, which is very much more than the energy necessarily expended (1×10^3 ergs/h) in pumping 10 ml. water per hour (E_0, table 7).

If we use the same estimate of oxygen consumption for *B. balanus*, 0·1 ml. (g tissue wt)$^{-1}$ h^{-1}, the results are similar, but not quite so convincing. At approximately 2 g wet weight of tissue for large specimens, the required water flow at 20 °C would be at least 37 ml./h, compared with the calculated value of 100 ml./h from the experiments. However, the energy available from the water flow, assuming that the animal can usefully extract over one-third of the available oxygen, is still much greater ($2{\cdot}9 \times 10^7$ ergs) than that dissipated in pumping the water (9×10^3 ergs/h).

The two species under consideration are not normally subjected to temperatures as high as 20 °C while under water in their natural habitat (Southward 1955*b*, 1957). At lower temperatures the balance sheet for flow versus consumption would be more favourable, and the water would contain more oxygen at saturation point. Normally, therefore, it seems that these species should be able to satisfy their respiratory requirements without extending the cirri. At higher levels of activity than pumping it is possible that respiratory exchange via the large cirri is necessary to supplement the uptake within the mantle space.

Relation of cirral activity to the environment

The type of activity shown by a particular barnacle can usually be related to the habitat from which it came, or in which the species as a whole lives, but there are also some basic differences in behaviour between the members of the different families and orders of barnacles. This is clearly brought out by comparing all the species we have been able to investigate (table 1) in systematic order and according to the habitat and type of cirral activity most frequently shown after collection.

Balanidae

Fast beat is found only in the Balanidae, and though it is not shown by all species, this group as a whole possesses the greatest versatility of cirral behaviour. To this we may relate their occurrence in a wide variety of habitats, from the intertidal zone to deep water, and their success under different degrees of water movement and wave action. As shown experimentally with *B. balanoides* (Southward 1955*c*), normal cirral beating is generally associated with a habitat showing a variable degree of water movement (but not excessive wave action). Fast beating seems more often shown by specimens from habitats where natural water movement is slight or intermittent, and where it would be an advantage to increase the volume of water filtered by the cirri for food. The greater respiratory burden caused by cirral activity will be compensated if the cirri can act as accessory branchiae, especially since the hydraulic mechanism of the cirri will increase the circulation of body fluids between them and the rest of the body. Although there is an inverse relationship between the amount of water movement in the habitat and the number of specimens showing fast beating (Southward 1955*c*), under experimental conditions it is often possible to stimulate individuals to beat faster by subjecting them to short bursts of fast current. It seems probable that this response may occur in nature in habitats where water movement is intermittent, such as in sheltered sites at the higher tidal levels. In the predominantly sublittoral species of Balanidae fast beating has been recorded only in *B. balanus*, which is indeed sometimes found at the lowest levels on the shore.

In deep-water habitats water movement may be essential to barnacles not only to carry sufficient food to them, but also to prevent sedimentation or silting up of the hard substrata they require. For this reason they cannot occur in places without water movement, and fast beating would be of little advantage. Instead, the extension response is developed where a steady movement of water enables the animal to satisfy most of its respiratory and nutritional requirements by passively holding out the cirri. In some of the larger balanoids from entirely sublittoral habitats, we have not been able to show even normal beating. For example, *B. hameri*, kept in still water or in water moving at a moderate velocity of about 10 cm/s, shows only pumping movements, and the cirri are fully extended only when the animal is placed in a massive flow of high velocity. A group of animals at Port Erin in June 1959 extended the cirri almost at once when water was passing at a calculated speed of 106 cm/s, though the response was sometimes hindered by the force of the current. The same animals after remaining in a tank for several hours without shock produced the full extension response within a few minutes of the start of a current of 62 cm/s, and later after longer periods of quiescence responded to water flowing at 38 cm/s. The minimum speed at which the response was ever observed was 22 cm/s.

Similar observations were made the following winter at Menai Bridge, where specimens kept several weeks without food had a threshold for cirral extension of the order of 25 to 30 cm/s. All the specimens of *B. hameri* used in these experiments came from depths of about 20 fm. off the south end of the Isle of Man, where they occur in a restricted area in association with *Modiolus* (Jones 1951). The surface tidal currents over these grounds approach 2 knots (1000 cm/s) and, although velocity on the sea bed will probably be much less, we can safely assume that the animals are subject to water currents with a velocity at least equal to those used experimentally. In no other way could the barnacle obtain sufficient food. We can, in fact, assume that fast currents are necessary to the species as a whole and thus explain its sporadic distribution.

A few observations were also made on equally large specimens of *Balanus tulipiformis*, which appear to have similar requirements to those of *B. hameri*. It was not possible at the time to subject them to currents greater than the normal flow in aquarium tanks, and only pumping was seen. However, Mr G. R. Forster, who collected the specimens by diving off Santander, had the good fortune to see the cirri extended in the aquarium tanks at night (cf. Mori 1958).

One other balanoid examined, *Pyrgoma anglicum*, extends the cirri in apparently still water. It occurs only on the solitary coral *Caryophyllia smithi*, with which it seems to have a commensal relationship, and its habits may be modified for this association. However, it is worth noting that *Pyrgoma* is normally orientated on the edge of the coral disk so that the extended cirri face inwards (and sometimes upwards, when just below the edge of the disk) and may thus be stimulated by the gentle outwardly directed ciliary currents which are found on the disk of this species and other Actinozoa (Yonge 1928). Certain species of Acrothoracica which also live among corals can extend their cirri outside the mantle cavity, unlike *Alcippe*, the species included in table 1. According to Utinomi (1957) these forms behave much like *Pyrgoma*, and can apparently show normal beat and extension.

The extension response is not so commonly observed in the Balanidae as in some other groups, but it can generally be evoked both in nature and in the laboratory by the stimulus of steady currents of water.

Chthamalidae

With one or two exceptions, the Chthamalidae are largely an intertidal group of barnacles, yet their habits differ markedly from those of the Balanidae, which are also predominantly intertidal. The typical shore species, *Chthamalus stellatus*, rarely shows rhythmic activity other than pumping. Although normal beating has been seen in the laboratory, it is usual for pumping to be converted directly to extension when the specimens are subjected to a current of water. On the shore, the extension response can be obtained even when the animal is exposed to the air by squirting water on it from a pipette (Crisp 1950). This species, and most of the other members of the genus, are more restricted in habitat than typical intertidal Balanidae; their need for some degree of wave action is obviously related to their cirral behaviour, for in the absence of normal beating a considerable degree of water movement will be necessary to ensure efficient feeding by passive extension of the cirral net. The same argument applies to the species of *Tetraclita*, which are aberrant members of the Balanidae. They are typically found in similar habitats and usually show extension in preference to normal beating: Mori (1958) found that *Tetraclita* also responds to water dashed over it, even when out of the sea.

The relative infrequency of normal beating among Chthamalidae is not due entirely to the wave-beaten intertidal habitat of the majority of species. In *Hexelasma hirsutum*, one of the few deep-sea members of the group, normal beating was not found and pumping activity was also very slight. The usual activity shown in the laboratory under the influence of water movement was extension, which could, however, be stimulated by much lower water velocities than required by *Balanus hameri* of similar size (a minimum of 4 cm/s compared with 22 cm/s). *Hexelasma* must presumably be limited to habitats where the water movement is of at least the same velocity as that used experimentally (Southward 1957; Southward & Southward 1958).

Stalked barnacles

The intertidal forms such as *Pollicipes* are restricted to very wave-beaten sites, while the free floating, epizoic, and related forms will be constantly stimulated by water movement. It is not surprising therefore that extension is the commonest activity in this group and that most species have cirri that are less sensitive to shock than those of other barnacles.

Sensitivity of cirri

Further differences related to habitat and systematic position can be found in the degree of sensitivity of the cirri to mechanical stimulation and shock. The Balanidae are generally the most sensitive, and will withdraw the cirri and close the opercular valves if the shell is lightly touched or if the cirri comes into abrupt contact with a large object, even of food material. *Elminius*, *Balanus balanoides* and *B. crenatus* will close even when a jet of water impinges on them (e.g. from a pipette), and may remain closed for some time. The exceptions in this group are *Tetraclita* and the forms found attached to other animals. *Chelonobia patula* can be fed, very gently, with small pieces of *Mytilus* muscle, which it will grasp with the net without showing a shock reaction if a stream of water is simultaneously entering the cirral net. *Coronula* is even less sensitive, and, according to Connell (private communication), prodding the opercular membrane with a blunt object will produce further extension of the cirri of *C. diadema*. The Lepadidae are generally rather insensitive and can readily be fed with large pieces of *Mytilus* muscle. *Scalpellum*, found in deeper water, may be exceptional among the stalked barnacles; large specimens from the English Channel were quite sensitive to shock and were difficult to observe fully.

In general, it can be said that the cirri of oceanic, intertidal, and especially surf-living forms are less sensitive to contact than those of barnacles living on sheltered shores or in deeper water.

Cirral activity and feeding

Details of the feeding processes in barnacles have not yet been worked out fully, but some deductions can be made from our observations and from a knowledge of the mechanism of the different types of cirral activity. Two methods of feeding are found: captorial feeding and microphagy. There is probably no hard and fast line between them, and both processes can sometimes occur together.

Captorial feeding

Captorial feeding on large particles can occur during normal beat, fast beat and extension. Feeding by extension of the cirri, rather than by beating, seems to be the rule in the Lepadidae. Our observations and those of Patel (1959) on *Lepas anatifera* agree with those of Howard & Scott (1959), confirmed by Barnes & Reese (1959, 1960) on *Pollicipes polymerus*. In this method of feeding, in both stalked barnacles and sessile species, the cirral net is held widely open and withdrawn only at intervals. In the stalked species (e.g. *Lepas* and *Pollicipes*) the net may be extended in still water, and single rami can convey to the mouth food particles trapped on the setae. In sessile forms which habitually feed by extension (*Balanus hameri* and *Hexelasma*) the cirri are extended only in moving water, and the whole net is withdrawn when touched by a food particle (figures 22 to 25, plate 66). If only a few cirral rami are stimulated these may begin to roll up slightly in advance of the rest of the net.

There is little difference between feeding by rhythmic beating and feeding by extension; in many species we found that there was a range of intermediate conditions varying according to the amount of food present and the degree of water movement. For example, in one experiment specimens of *Balanus balanoides* and *B. crenatus* were showing normal beat in still water. A flow of water slowed down the rate of beating by stimulating them to hold the cirri extended for a very short time at the top of each beat. When fresh plankton was added to the flowing water the rate of beating increased again, probably because the cirri had to be withdrawn more often to deal with the food captured (table 3, p. 287).

A full sequence of the capture of a particle is shown diagrammatically in figure 14. There was first a slight shock reaction involving only the cirral rami touched by the particle, then a pause during which the whole net moved slightly forward; finally the whole group of large cirri was rolled up, with the rami carrying the particle slightly in advance of the others. When the cirri were unrolled again the particle was no longer visible, having been cleaned off by the smaller cirri. The cleaning process, by which particles held by the large cirri are eventually conveyed to the mouth, is well seen in some slow-motion sequences of *B. balanus*. Unfortunately we cannot reproduce these here owing to slight blurring of some of the parts on individual ciné frames, which does not, however, prevent details being made out by very slow projection of the film: figure 15 shows a similar sequence at normal speed of 16 frames/s. It appears that cleaning of the large cirri takes place as they begin to unroll for the next beat. Each pair of rami, or two pairs of rami together, starting with the most posterior (sixth) are drawn upwards and towards the carina through the comb setae on the rami of the third cirri (frames 1 to 6, figure 15). After the last pair of large cirri have been cleaned the third cirri are bent down and inwards to the mantle cavity (7 to 10) and then outwards again (10 to 12), themselves

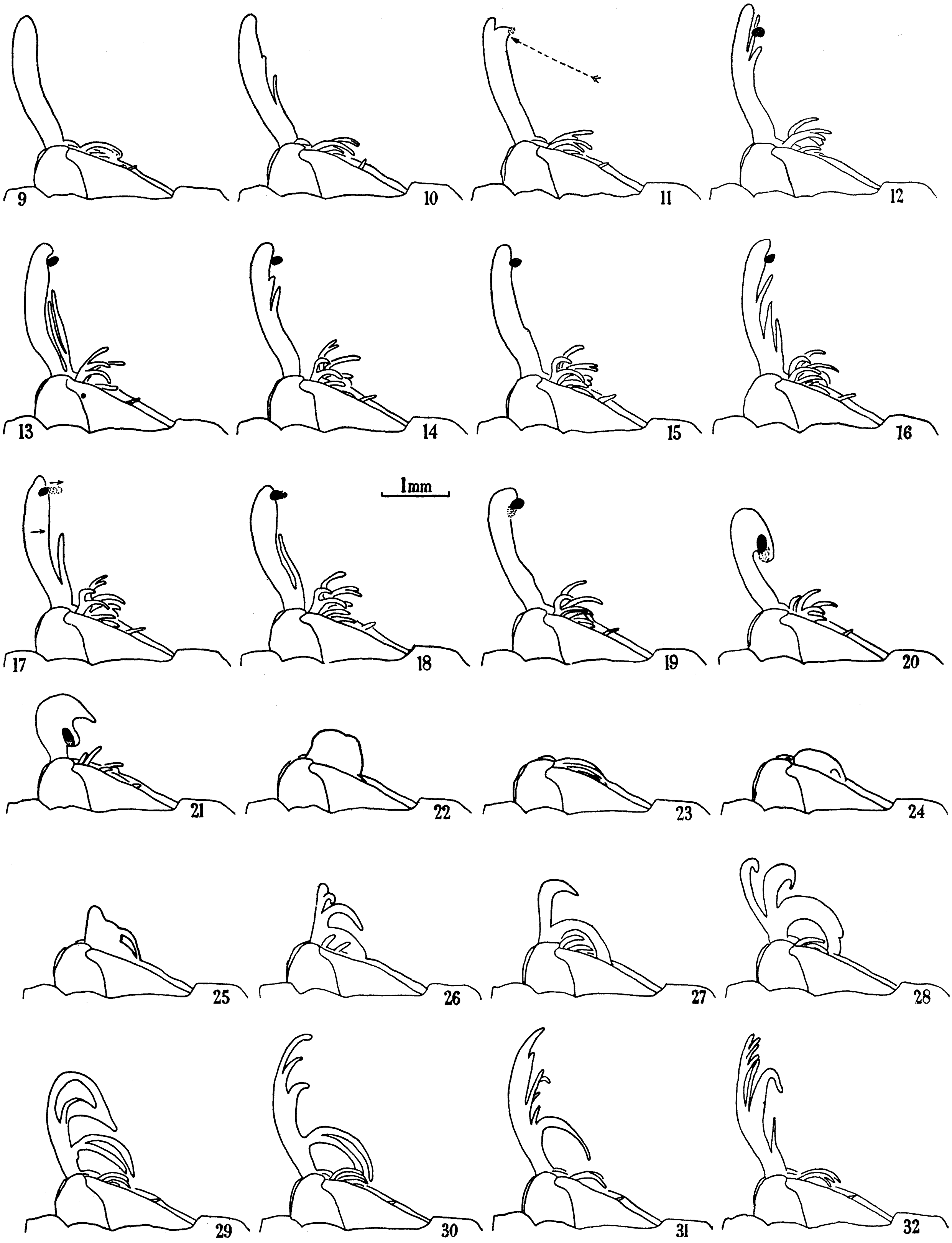

Figure 14. Fast beat in *Balanus balanoides* subjected to a current of water coming from the right, showing the capture of a particle, its transfer to the mouth, and the cleaning of the large cirri. Numbers refer to ciné frames at 16/s. On some frames the particle was moving while the shutter was open: the blurred image is shown by dotted lines and by the broken arrow on frame 11.

being cleaned by the setae of the second pair of cirri, the rami of which can sometimes be seen extending upward and brushing over the third cirri (12 to 14). The second cirri themselves appear to be cleaned by the upper ramus of the first cirri, and thence the food is passed to the mouth, but this part of the process remains to be worked out clearly, and cannot be made out in the sequence used to construct figure 15.

The lower rami of the first pair of cirri are held parallel together at the rostral end of the aperture to the mantle cavity where they can be seen to reject unwanted matter. The rejected material includes recently captured particles, which are presumed to have been tasted and rejected either by the smaller cirri or the mouth parts. All movements of the small cirri are very rapid compared with the rate of beating, and appear under visual observation as a series of shuffling movements.

In addition to the selection at or near the mouth, some selection also occurs, at least in balanoid species, on the cirral net. Such selection is very easy to see during experiments with water currents in a recirculating trough, where there is an unavoidable degree of aeration of the water, and contamination by dust and other particles, particularly cellulose fibres. In species in which cirral extension is the rule, and which can hold the cirri extended for several minutes at a time (e.g. *B. hameri*) air bubbles and fibres gradually accumulate on the extended cirri. Bubbles evoke little or no reaction compared with plankton animals or chopped lamellibranch muscle; they cause only slight bending of the ramus touched, and are not wiped off on to the smaller cirri. Instead the extended cirral net is rotated on its axis through 90 to 180°, and the current is allowed to sweep away the accumulation of inert material. A similar reaction was observed in *B. hameri* fed to repletion in a suspension of barnacle larvae: the unwanted nauplii caught by the cirral net were likewise allowed to be removed by the current after reversal of the net.

This selection reaction has also been seen in specimens of *B. balanoides* and *Hexelasma* in which the cirral net was being held extended in a current of water. It is possibly a general response of sessile forms, and may be contrasted with the apparent unselectiveness of the stalked form *Pollicipes*, as reported by Barnes & Reese (1959). Barnes (1959) now states that selection *can* occur on the cirral net of *Pollicipes* but that the response is due entirely to mechanical stimulation caused by the struggling of the prey.

Micro-feeding

Particles that are too small to be retained by the setae of the larger cirri are, nevertheless, captured and ingested by barnacles (Southward 1955*a*; Barnes 1959). Examination of faecal pellets from freshly collected specimens confirms that barnacles normally eat a wide range of organisms and particles from several millimetres down to a few microns in diameter. Micro-feeding seems to depend on the fine comb-setae of the smaller cirri (1 to 2 or 1 to 3) which apparently filter the ingoing flow of water into the mantle cavity; it should thus occur both during pumping and normal beating activities, in the latter at the same time as captorial feeding.

The small cirri are usually held spread out into a rosette covering the ingoing aperture to the mantle cavity during the opening phase of a beat, and present a veritable forest of bristles when viewed close-up from the front. The spaces between individual bristles may be as small as 1 or 2 μ and should thus be capable of retaining the small flagellates and bacteria which have been shown to be ingested. The collected material is apparently cleaned off the small cirri while the larger cirri are still held open: two or three shuffling movements can be made out, the sets of cirri brushing against one another in a manner similar to that already described for the cleaning of the larger cirri. These shuffling

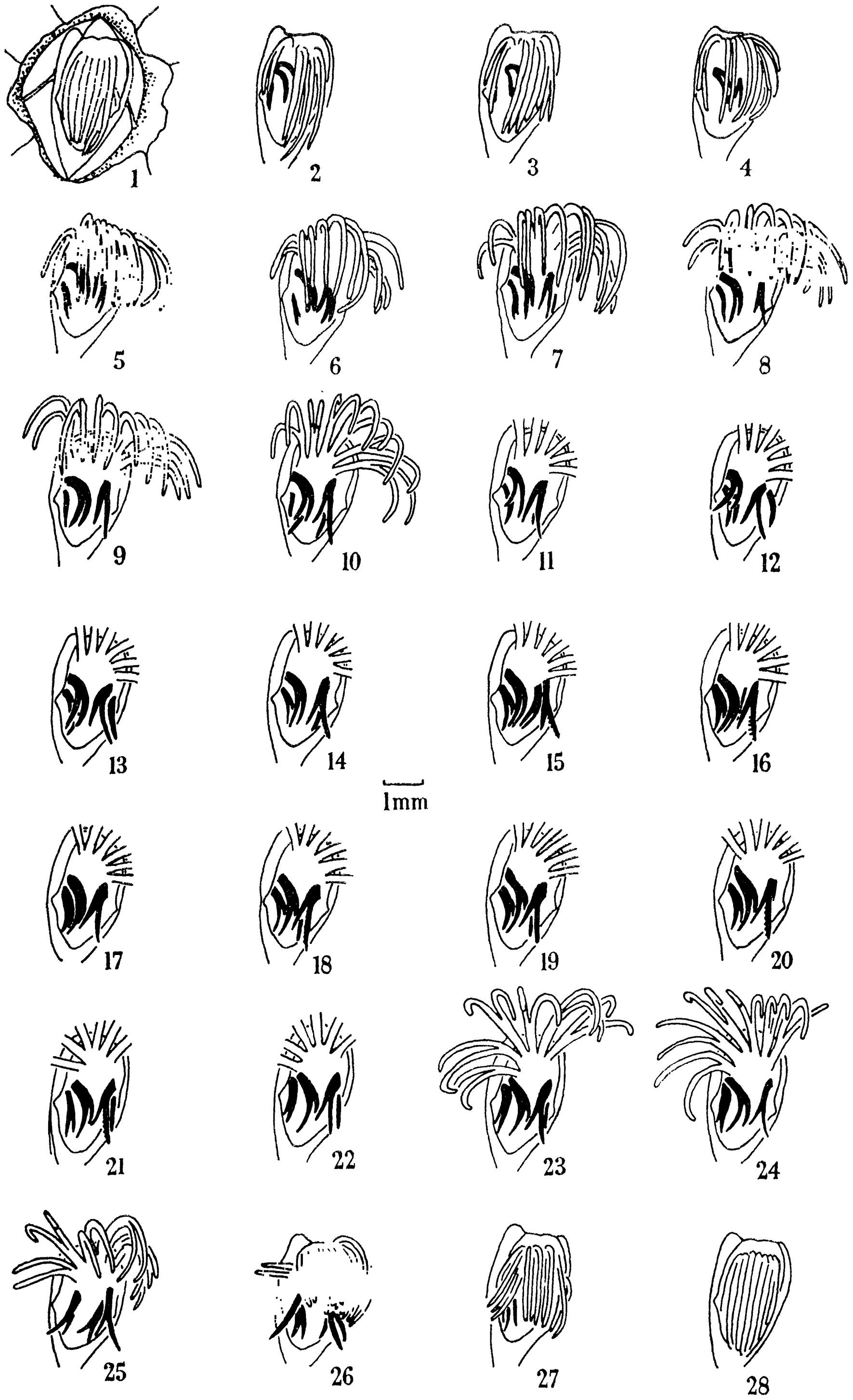

FIGURE 15. Normal beat, with slight extension, in *Balanus balanoides* viewed from above. The cleaning movements of the second and third pairs of cirri (shown black) can be seen while the large cirri are extended. Refer to text (p. 295) for full details.

movements can be clearly seen in film sequences of pumping in the presence of milk trails, and give the impression that the animal is actively 'tasting' the stream of milk, whereas it is, of course, merely collecting the particles of milk partly clotted by contact with sea water (figure 9). The milk is definitely ingested, but, as with other unnatural foods employed in experiments (see below), it reappears apparently little changed in the faecal pellets.

Rate of feeding and nutrition

Experiments were carried out to determine the efficiency of feeding on food particles of various sizes by placing one or more barnacles in vessels of water containing food and counting the number of organisms left unconsumed after varying periods of time both in still water and in water actively stirred. From these data we calculated the filtration rates (table 4). The amount of water filtered in captorial feeding of large particles was of the same order in three species studied, though *Elminius*, being the smallest, showed the greatest relative efficiency. It can also be seen from the experiments on *Balanus balanoides* that stirring the water, which caused extension of the cirri and increased the proportion of time spent feeding, also greatly improved feeding efficiency by increasing the relative movement of nutrient particles entering the cirral net. The amount of water passing the cirral net was, however, very much greater than the filtration rates, and many of the food particles escaped or failed to be dealt with rapidly enough by the mouth parts.

Table 4. Rate of feeding of barnacles on various food organisms

barnacle	temperature (°C)	duration of experiment (h)	size and nature of food particles	speed of stirring (cm/s)	mean no. of food organisms per ml.	maximum rate of filtration (ml./h)	mean rate of filtration (ml./h) individual
Balanus perforatus	15	2½	*Artemia* nauplii 750–1000 μ	7·5	32	15·0	8·7
	15	3	*Peridinium* sp. 30 μ	7·5	$2{\cdot}8\times10^{3}$	9·45	8·8
		6	*Peridinium* sp. 30 μ	7·5	$2{\cdot}4\times10^{3}$	7·30	3·4
		22½	*Peridinium* sp. 30 μ	7·5	$2{\cdot}5\times10^{3}$	4·82	2·0
	15	6½	*Gymnodinium* sp. 9–12 μ	7·5	$4{\cdot}1\times10^{3}$	3·3	3·0
B. balanoides	14	19	*Balanus* nauplii 300 μ	2 to 3	4·5	—	10·0
		19	*Balanus* nauplii 300 μ	nil	1·65	—	0·9
		19	*Phaeodactylum* 25 μ	2 to 3	320×10^{3}	—	$<$ 0·5
Elminius modestus	14	19	*Balanus* nauplii 300 μ	2 to 3	5·0	—	11·4

The size of food organisms is clearly important. A diameter of 30 μ is at the limit for retention by the cirral net and *Peridinium* was not captured as efficiently as the larger organisms. *Phaeodactylum*, which is long and narrow, was not appreciably removed at all by *Balanus balanoides* and may have been rejected by the animal.

The rate of feeding, measured as volumes filtered in unit time, showed considerable variation, but less than was shown by the actual rate of consumption of food particles. As can be seen from table 5, the rate of consumption of *Elminius* larvae was roughly proportional to the concentration at which they were given. At the higher concentrations, however, some of the larvae given as food, though captured, were not eaten but were rejected damaged into the water where they were later found to be dead. At the end of the feeding experiment with *Artemia* (table 4) all remaining uningested nauplii were found to be dead or damaged. Although halfway through the experiment the number available was still as high as 50% of that at the start, the apparent rate of filtration declined to one-fifth of the maximum. This behaviour suggests that at abnormally high concentrations of food either the oral feeding mechanism becomes saturated and is unable to deal with the amounts captured by the cirral net, or else there is a rejection of part of the food captured when the gut is full. The obvious solution—to stop cirral activity—is not available to the animal since other functions than feeding are involved.

TABLE 5. FEEDING OF *BALANUS BALANOIDES*. SPECIMENS OF 8 TO 11 MM DIAMETER FED ON *ELMINIUS* LARVAE AT 18 °C

range of concentration used per ml.	larvae consumed per hour (mean)	mean filtration rate (ml./h)	maximum filtration rate observed (ml./h)
10 to 16	160	13·5	24
1 to 2	20	25·2	40
0·65	13	21	25

TABLE 6. NUTRITION OF *ELMINIUS MODESTUS*

Specimens kept at 15 to 17 °C in the laboratory during the winter (1 to 29 February 1956).

group	% casting rate before expt.*	food	water stirred or not	% casting rate after expt.	cirral activity	faecal pellets	gut appearance on dissection	ovarian† index after expt.
1‡	79	nil	–	138	+	brown (own nauplii)	yellow	0·4
2	79	nil	+	75	–	none	yellow	0·6
3	65	fresh plankton	+	312	+ +	many, red, with crustacean remains, etc.	red-brown	3·7
4	87	ground chalk, later powdered carmine	+	105	+	few, with chalk and carmine particles	yellow or pink	0·9
5	65	potato starch	+	132	–	few, with starch grains	brown	0·6
6	77	fat (tristearin) stained red	+	119	–	few, pink, with undigested fat	pink	1·3
7	80	*Chlorella* and *Phaeodactylum*	+	161	+	few, green, with algal cells undigested	red-brown	0·7
8	85	chopped muscle (lamellibranch)	+	199	+ +	many, grey-brown	full of muscle tissue	2·4
9	77	nil, and at 12 to 13 °C	–	34	–	none	empty	0·5

* In still water at 12 to 13 °C, 11 to 31 January 1956.
† Mean of all specimens rated in arbitrary groups (0 = none, to 3 = well developed, and 4 = fertilized).
‡ Shed nauplii.

The response shown to an abundance of animal food contrasts with the behaviour of the same barnacles with cultures of *Peridinium*, a dinoflagellate with a thick cell wall (table 4). During a long series of experiments the plants were still being ingested in large numbers, and faecal pellets containing relatively undamaged plant cells were produced continuously on this diet. Such feeding may be compared with the well-known overgrazing activity of copepods in dense phytoplankton. In fact, with all substrates we found that there was a rough correlation between the quantity of food given and the rate of passage through the gut, although relatively smaller numbers of faecal pellets were produced on animal food. When feeding experiments ended, defaecation practically ceased, but those pellets that were produced showed a much better degree of digestion of the food given just before the experiment ceased.

Further observations were made on *Elminius* by feeding groups of individuals on various foods for a period of a month and estimating the uptake and nutritional value from (*a*) the disappearance of food particles, the appearance of the gut and the production of faecal pellets; (*b*) the rate of ecdysis (which has been shown by Crisp & Patel (1960) to increase with feeding); (*c*) the cirral activity of the barnacles; (*d*) the development of ovaries as measured by an arbitrary index. It can be seen from table 6 that these criteria were all in good accord with each other, indicating that raw plankton and chopped muscle (both consisting mainly of protein) were the most readily accepted and best foods. Some of the nanoplankton was taken up by micro-feeding, but this was inferior as a means of nutrition to captorial feeding. Potato starch, tri-stearin and the inert particles were all ingested to a very limited extent, defaecated in a more or less undigested state, and were of little value as food. The barnacles were more active when particles of high nutritional value were present in the water (cf. table 3).

Conclusions

The various forms of cirral activity we have described can now be linked with observations made by previous workers. Darwin (1854) noted that in air, both *Balanus balanoides* and *Chthamalus stellatus* kept the valves slightly open, with a bubble of air inside the mantle cavity, so that the orifice was in fact closed by a thin layer of water with air beneath. This was confirmed by Monterosso (1928) who found that such aerial respiration could continue for some time, but that as the animal dried out the aperture was closed, and only opened from time to time when 'respiratory movements' were observed. These descriptions correspond to what we have described as testing activity. From general observation it is apparent that a large proportion of the barnacles on a shore are slightly open when out of the water, and that the clicking noises produced when walking over the animals (see Darwin 1854, p. 64) are caused by closure from the testing position. It seems probable that some of the specimens of *B. balanoides* used by Barnes & Barnes (1958) to test the action of inorganic ions on the opening response to wetting were showing a testing response, and thus already partly open before the experiments began.

The next level of activity, which we have called pumping, has not been fully described before. Darwin (1854) noted the in and out movement of water but it is not clear whether his description refers to pumping or normal beat. Apart from this the only records are those of Barnes & Barnes (1956), who noticed the exhalant pulse of pumping activity when watching discharge of nauplii from the mantle space, and of Daniel (1953), who measured the opercular movements during pumping.

Normal beating, as already remarked, is the most common activity under aquarium conditions and has been the subject of experimental study, but fast beat has not previously been recognized. The differences between normal beat and fast beat are not at first obvious and can be analyzed fully only from cinematographic records. The phenomenon of extension also remained unnoticed in operculate barnacles until recently (Crisp 1950), but has been described in detail for the pedunculate species, in which it is often the commonest type of cirral activity (Batham 1945; Howard & Scott 1959; Barnes & Reese 1959, 1960).

All these forms of cirral activity can now be united into a series, with the same underlying mechanical principles. The movements of operculum and large cirri depend on antagonism between hydrostatic forces and direct muscular tension, a phenomenon deduced by Cannon (1947) from the anatomy of the pedunculate species *Lithotrya*, and probably very common throughout the Arthropoda (Parry & Brown 1959). There are two phases in all types of cirral activity: the fast phase of contraction, in which the valves move by direct action of the depressors and the adductor, and (if extended) the large cirri are rolled up by their flexor muscles; and the slow recovery phase in which most of the depressor muscles (not the laterals) and the adductor relax, the operculum is raised by hydrostatic pressure, and in some types of activity, the large cirri distended by body fluids forced into them. The opening and closing movements of the valves, however, depend on direct muscular antagonism between the adductor and the paired lateral scutal depressor muscles.

We can only deduce the nature of the hydrostatic mechanism: presumably body fluids draining from the lacunae of the opercular membrane and cirri enter the spongy tissues of the prosoma during the contraction phase and the muscles of the prosoma relax to allow this: the same muscles, mostly superficial, are presumably the hydraulic pump that forces the fluid into the operculum, cirri and possibly the gills, during the recovery phase. The series of types of cirral activity involves increasing action of the hydraulic and muscular mechanisms. At the lowest level, in testing, the depressors remain contracted and little fluid is permitted to flow into the opercular membrane: the slight rhythmic movements that do take place are mostly due to direct muscular action. In pumping, the depressors are more relaxed and undergo more pronounced rhythmic movements, while the prosoma muscles increase their tension to produce the opercular movement. With normal beat further prosomal muscular action is required to cause distension of the cirri at the same time as the other rhythmic movements take place. The tergal and rostral scutal depressor muscles and the adductor remain more or less continuously relaxed during fast beat, and the prosoma muscles must be under constant tension to maintain pressure in the opercular membrane. The operculum no longer moves appreciably, and a faster rhythm is possible in the cirri. In extension the same depressor muscles and the adductor muscle are also fully relaxed; the flexors of the cirral net just begin to contract, causing a slight forward movement of the net, but the contraction phase is then inhibited so that the flexors are kept just balanced against the hydrostatic force. When particles touch the cirral net the contraction phase sets in.

We have shown how the different levels of activity place a different emphasis on function. The lower levels, testing and pumping, appear to be respiratory or for micro-feeding; and the higher levels, fast beat and extension, are mainly feeding reactions in which the cirri may also serve as accessory respiratory organs.

The Balanidae alone seem to be capable of the full range of cirral activities; they are the most successful group occupying the greatest diversity of habitat and were considered by Darwin to be the most highly evolved. At the other extreme the Lepadidae seem restricted to habitats where there is water flow or wave action because they can feed only by extension. They differ from the operculates in the greater independence of movement of each cirrus, reflected in the more primitive separation of the thoracic ganglia.

We may suppose that the primitive free-swimming cirripede began to fasten itself to objects by its antennae. The antennae of males of other entomostracan groups are often modified as clasping organs for copulation, and it is possible to envisage the antennae being further adapted to anchor the animal in a current of water. Once fixed by the antennae, a slight forward roll would enable the more posterior appendages to be held against the current, and so allow the legs to grasp particles. The head and sense organs would then be far removed from important stimuli, and so might be expected to degenerate, while the mouth would tend to migrate closer to the base of the legs to facilitate transfer of food. Thus, the essential form of the stalked barnacles might be evolved, with passive extension of the cirral net, but independent action of each appendage, as appears to be the primitive condition.

In the sessile cirripedes the body developed a more complete protective covering of calcareous plates, which must have led inevitably to the development of gills and a mechanism to drive a current of water through the mantle space. The natural pulsation of the prosoma, caused by the ebb and flow of body fluids, was no doubt present in the most primitive forms and would therefore have been available as a source of energy to move fluids through the mantle space. The structures surrounding the mantle cavity could easily be modified, as in present sessile forms, to ensure that water entered at one place and was forced out at another. Given the need for as large a pulse of water as possible, it would be an obvious advantage if the cirri were to move in concert and if their movements coincided with those of other hydraulically controlled organs, notably the opercular membrane, so as to cause the maximum possible volume change in the mantle space at each pulse. In this way the feeding and respiratory movements of the cirral apparatus and operculum probably became connected. In the Chthamalidae these functions are still not usually separable, except when the animal reverts to the primitive extension reaction with the valves and prosoma motionless for long periods. The Balanidae, however, show a further development in the greater degree of separation of feeding from respiration during the fast beat. This enables them to feed more efficiently in still water and so to extend their range to a wider variety of habitats, while still retaining the ability to feed by extension of the cirri in flowing water.

APPENDIX

In order to obtain an approximate estimate of the water exchange, we have used Schlichting's (1933) treatment of a narrow jet of fluid of circular cross-section passing into a liquid of the same composition. The flow in this case is obviously radially symmetrical about the axis of the jet. Schlichting's equations give the velocity components u, along, and v, perpendicular to the axis of a circular jet at any point x, y, where x is the distance of the point measured along the axis of the jet from its source, and y is the radial distance of the point from the axis of the jet. J is the momentum per second crossing the plane perpendicular to the jet, ρ is the density and ν the kinematic viscosity of the medium. Then

$$u = \frac{3}{8\pi}\frac{K}{\nu x}\left(1+\frac{\epsilon^2}{4}\right)^{-2}, \tag{1}$$

$$v = \frac{1}{4}\sqrt{\frac{3K}{\pi}}\frac{1}{x}\frac{\epsilon(1-\epsilon^2/4)}{(1+\epsilon^2/4)^2}, \tag{2}$$

where $$\epsilon = \frac{1}{4}\sqrt{\frac{3K}{\pi}}\frac{1}{\nu}\frac{y}{x}, \quad K = \frac{J}{\rho}.$$

This equation was checked by Andrade & Tsien (1937) and found to agree with observations for a jet of radius approximately 0·5 mm.

Fortunately this jet is of the same order of cross-section as the exhalant canal in the specimens of *Balanus balanus* observed. We may therefore use Schlichting's equation and Andrade & Tsien's observations to obtain an approximate estimate of the volume of water emitted, and also of the energy dissipated at each puff. It is necessary to assume that these equations, which are strictly valid for steady laminar flow, can also be applied to obtain an approximate analysis of intermittent non-turbulent flow of fairly short duration.

It will be seen from an inspection of equation (1) that along the axis of the jet (where $y = 0$) the velocity u will be maximal and equal to

$$u_{\text{max.}} = \frac{3K}{8\pi\nu}\frac{1}{x}. \tag{3}$$

If we consider the movement dx in time dt of a particle of water flowing in the jet at point x, equation (3) becomes

$$u_{\text{max.}} = \frac{dx}{dt} = \frac{3K}{8\pi\nu}\frac{1}{x}.$$

The solution of this equation is $$x^2 = ct, \tag{4}$$

where t is the time interval which has elapsed since the particle passed the source and c a constant equal to $3K/4\pi\nu$. Hence from (4) a graph connecting x^2 and t should yield a straight line of slope c.

Hence $$K = \tfrac{4}{3}\pi\nu c.$$

c may be found from the slope $\Delta(x^2)/\Delta t$ from data plotted from cinematographic records and ν has the approximate value of 0·01 for water.

The value of K so obtained then enables the quantity emitted, the energy dissipated and the pressure behind the jet to be calculated.

The quantity of water emitted per second, Q, assuming the jet profile to be square headed, is given by the relation

$$Q = \sqrt{(K\pi)}\,a. \tag{5}$$

(The result is only slightly different for a parabolic velocity profile.)

The total quantity emitted $= \int_0^T Q\,dt$, where T = time of duration of the jet.

The rate of dissipation of energy in the jet is given by

$$E_0 = \frac{1}{2\sqrt{\pi}} K^{\frac{3}{2}} a^{-1}, \tag{6}$$

where a = radius of cross-section of the jet.

The pressure behind the jet at the orifice can be found from Andrade & Tsien's data connecting the momentum crossing the plane normal to the jet, J ($= k\rho$) with the pressure P. Assuming that Andrade & Tsien measured P not in absolute units but in centimetres head of water (their units are not quoted) the relation is approximately

$$J = 1{\cdot}41 p^{\frac{3}{2}}.$$

Since the density of water $\rho \simeq 1$ we have

$$p = 0{\cdot}79 K^{\frac{2}{3}} \text{ cm of water,}$$

or

$$P = 770 K^{\frac{2}{3}} \text{ dynes/cm}^2. \tag{7}$$

For an aperture of different radius the relation

$$P = \beta K^{\frac{2}{3}} \tag{8}$$

may be different if β is a function of the radius a.

To investigate the dependence of pressure on the radius, the method of dimensional analysis was employed. In simple inertial flow through an aperture the flow Q varies as $P^{\frac{1}{2}}$ and $P = \alpha K$ where α has dimensions ρ/a^2.

In simple viscous (Pouseille) flow in a tube of given shape (i.e. the length is assumed to be proportional to the radius), Q varies as P, and $P = \gamma K^{\frac{1}{2}}$ where γ has dimensions η/a^2.

The system studied here is intermediate between purely inertial and purely viscous flow, since Q varies as $P^{\frac{3}{4}}$ and $P = \beta K^{\frac{2}{3}}$.

Assuming β to be a function only of radius (a), Newtonian viscosity (η) and density (ρ) we find that

$$\beta \propto \eta^{\frac{2}{3}} \rho^{\frac{1}{3}} a^{-2}.$$

Hence β will vary as a^{-2}, and, since η and ρ are constant, we may rewrite equation (8) as

$$P = \phi a^{-2} K^{\frac{2}{3}}. \tag{9}$$

Substituting $a = 0{\cdot}455$, we have

either

$$P = 159 K^{\frac{2}{3}} a^{-2},$$

or $p = 0{\cdot}164 K^{\frac{2}{3}} a^{-2}$ according to the units employed for pressure.

This equation may be used to calculate the pressure for apertures of any radius.

Table 7 gives the values of K, Q, E_0 and p obtained by plotting x^2 against t from measurements on four jets of *Balanus balanus* and from two jets of *B. balanoides* and applying the above equations.

Table 7. Calculation of flow rate out of mantle cavity

species	run	$\frac{d(x^2)}{dt}$	radius of aperture (cm)	K	Q (ml./s)	E_0 (ergs/s)	p (cm)
Balanus balanus	1	37·5	0·05	1·56	0·11	11·0	1·07
	2	38·0	0·05	1·58	0·111	11·2	1·08
	3	32·0	0·05	1·33	0·102	8·65	0·96
	4	25·5	0·05	1·06	0·091	6·35	0·82
B. balanoides	1	2·25	0·025	0·094	0·0136	0·325	0·64
	2	1·90	0·025	0·080	0·0125	0·256	0·58

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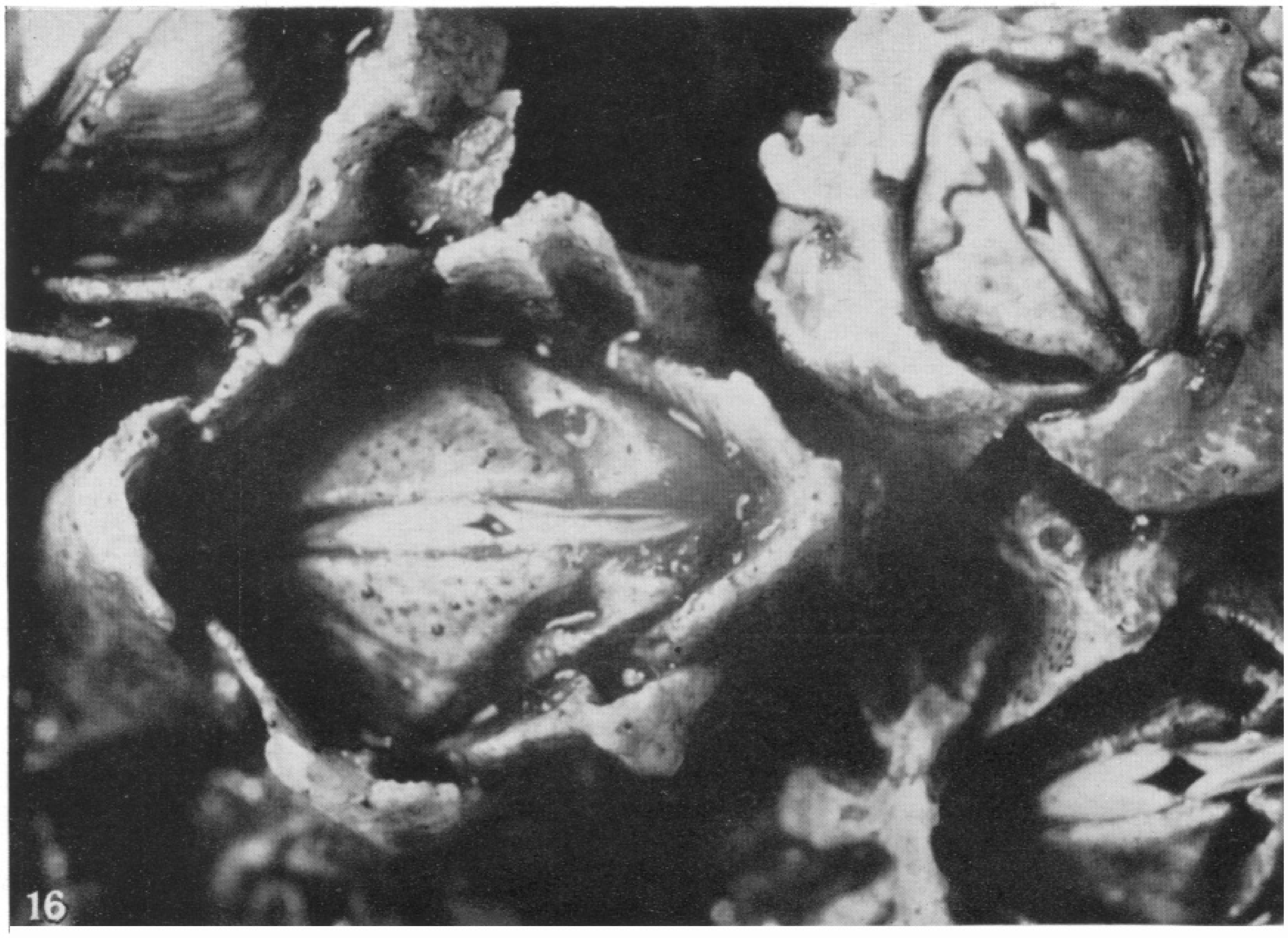
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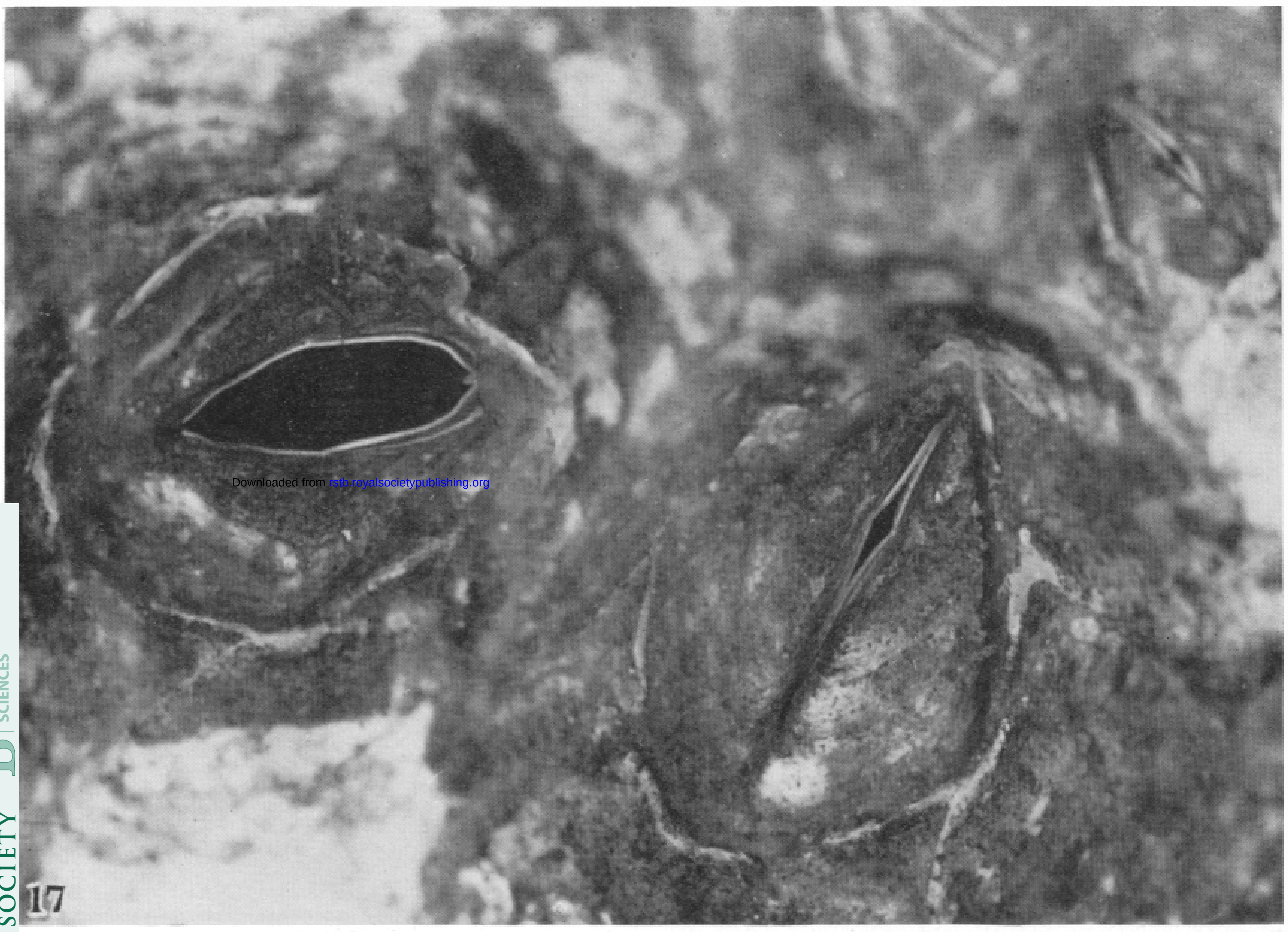
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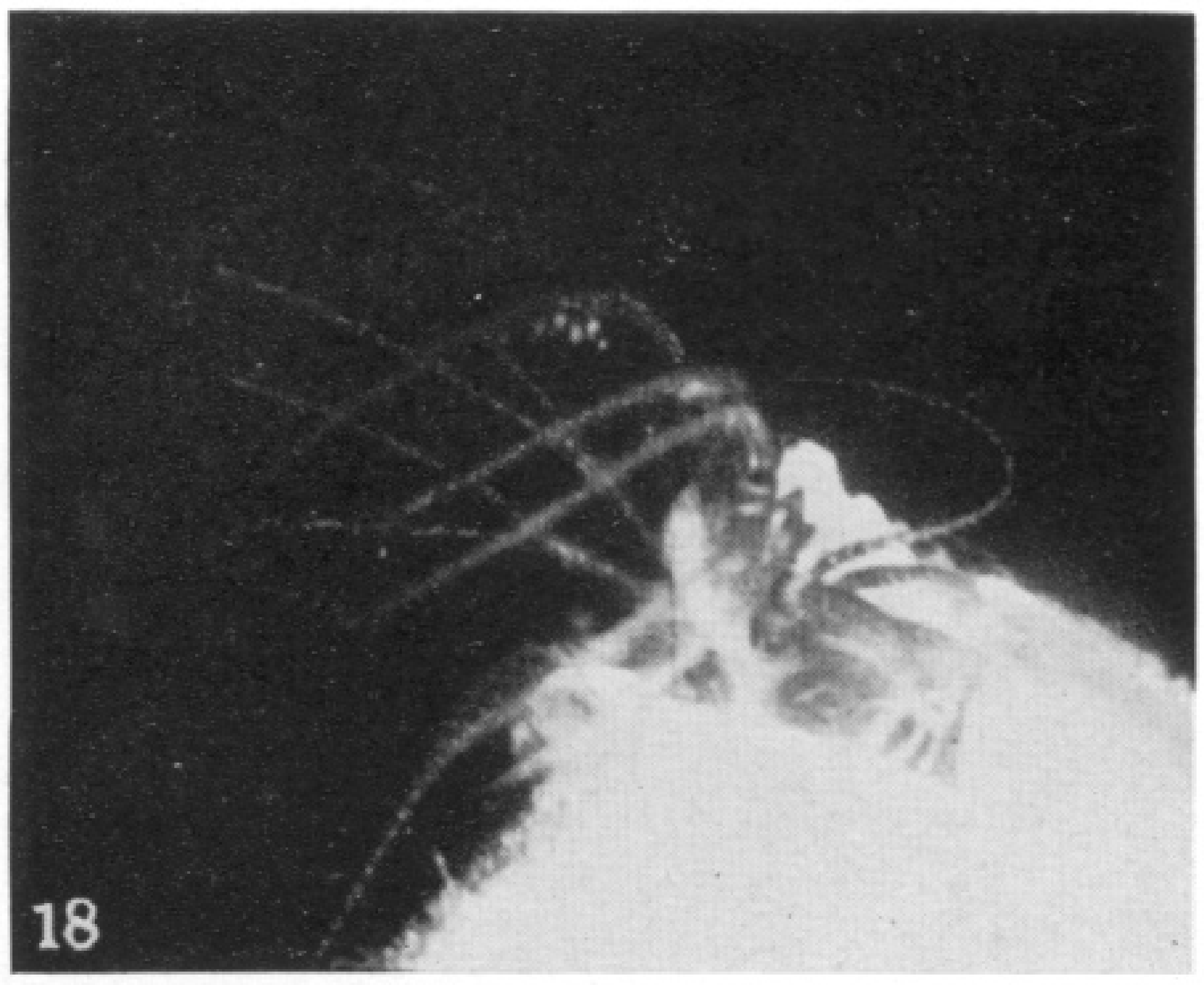
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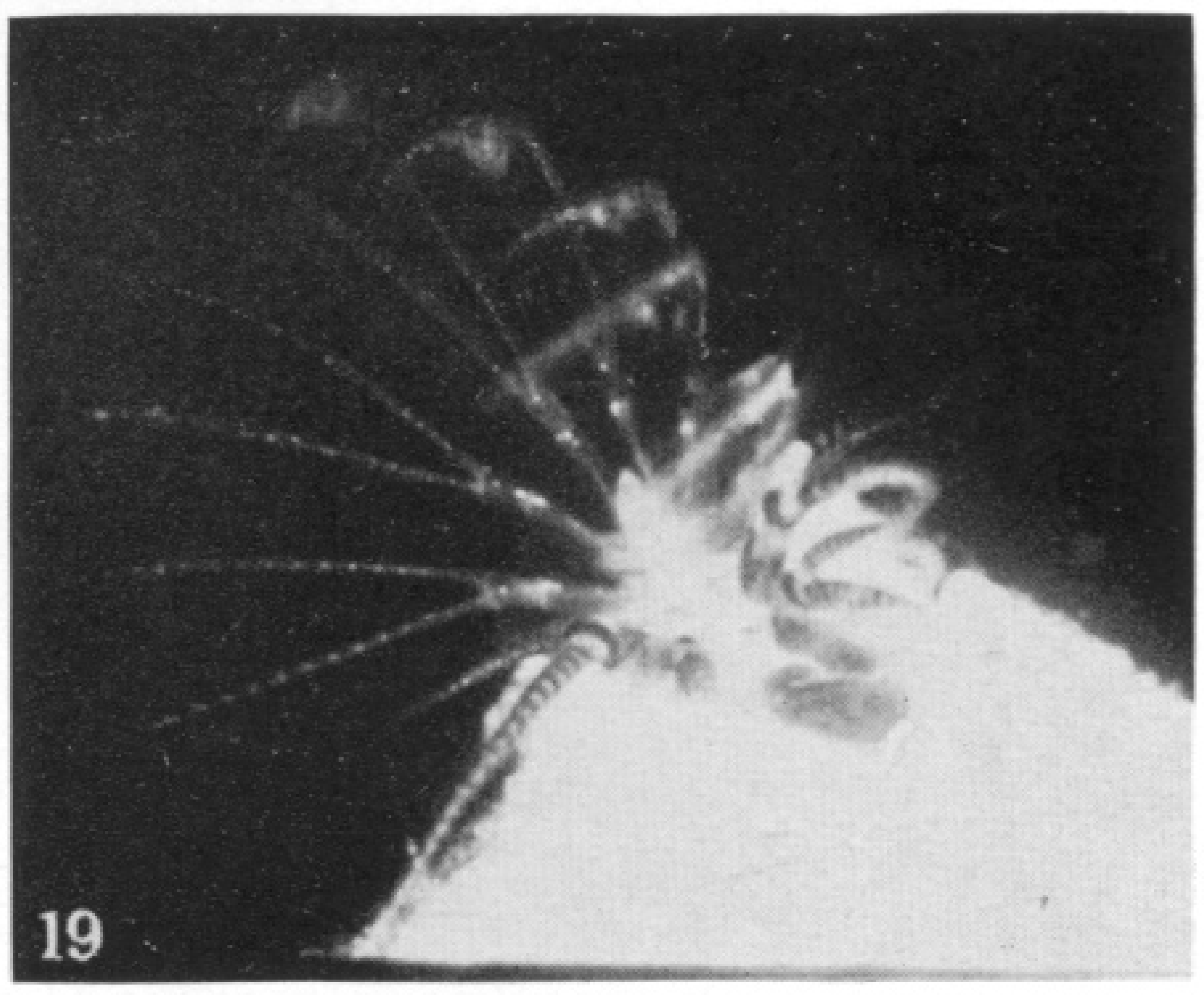
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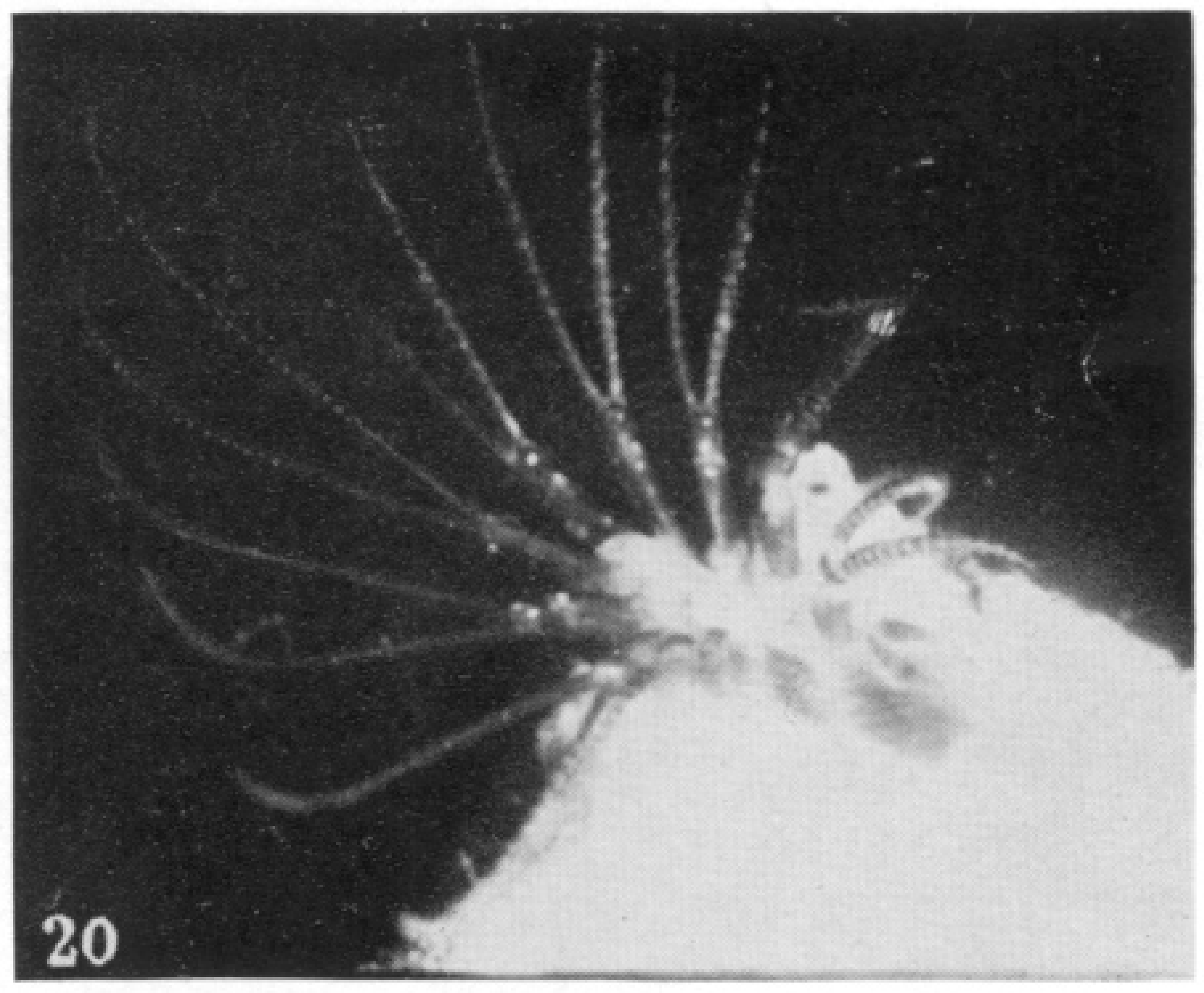
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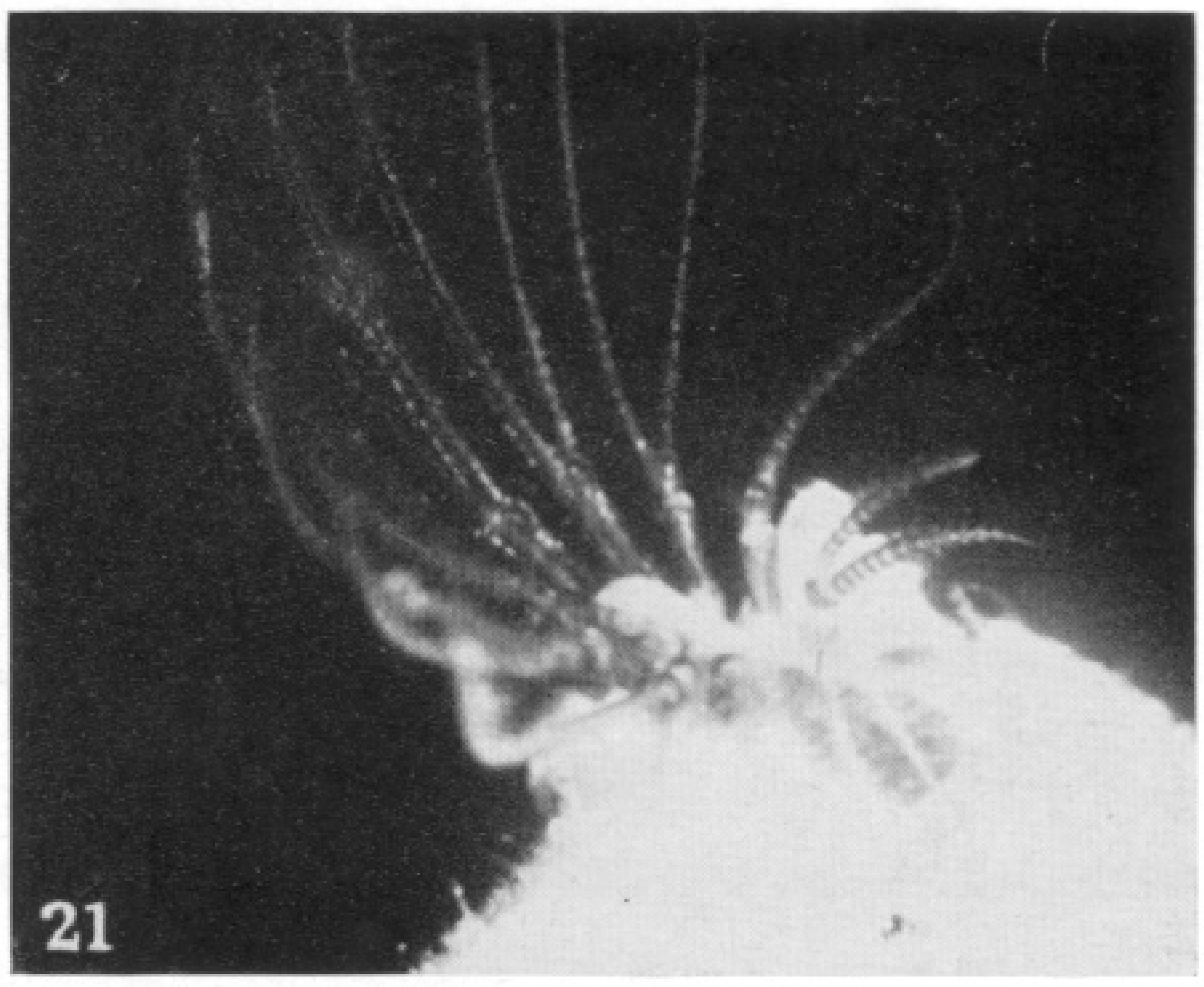
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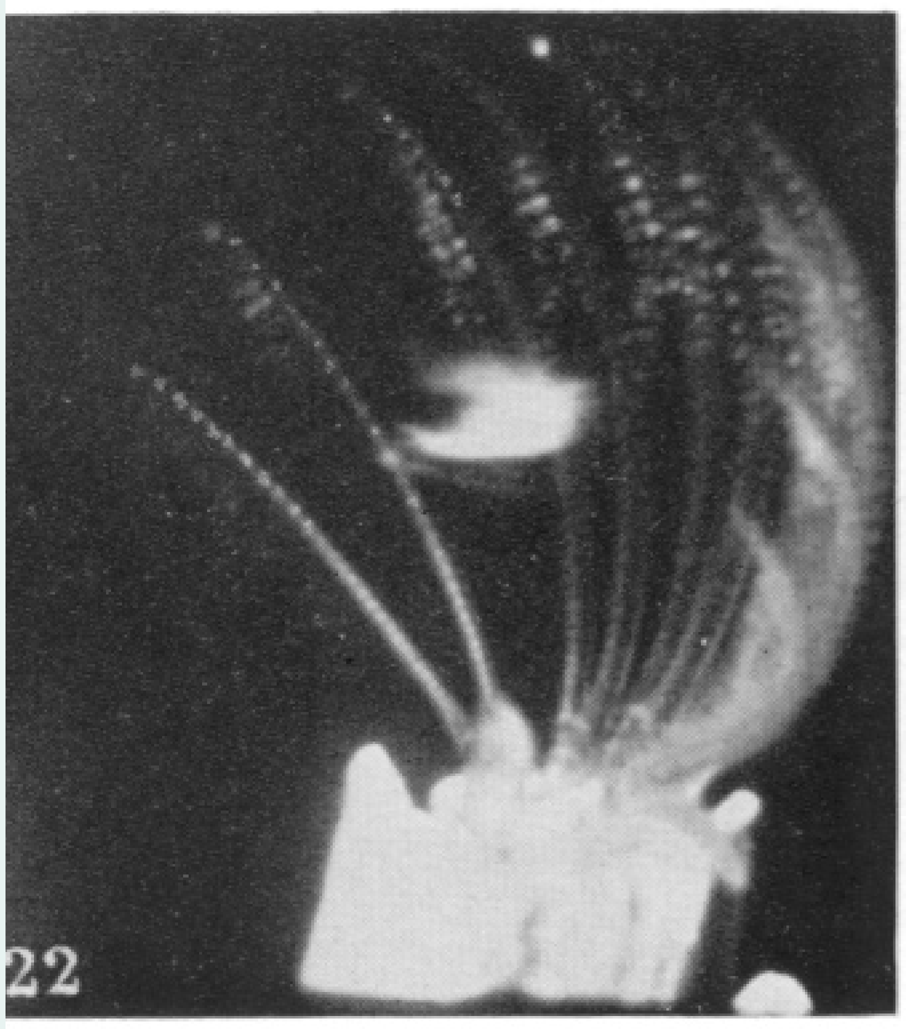
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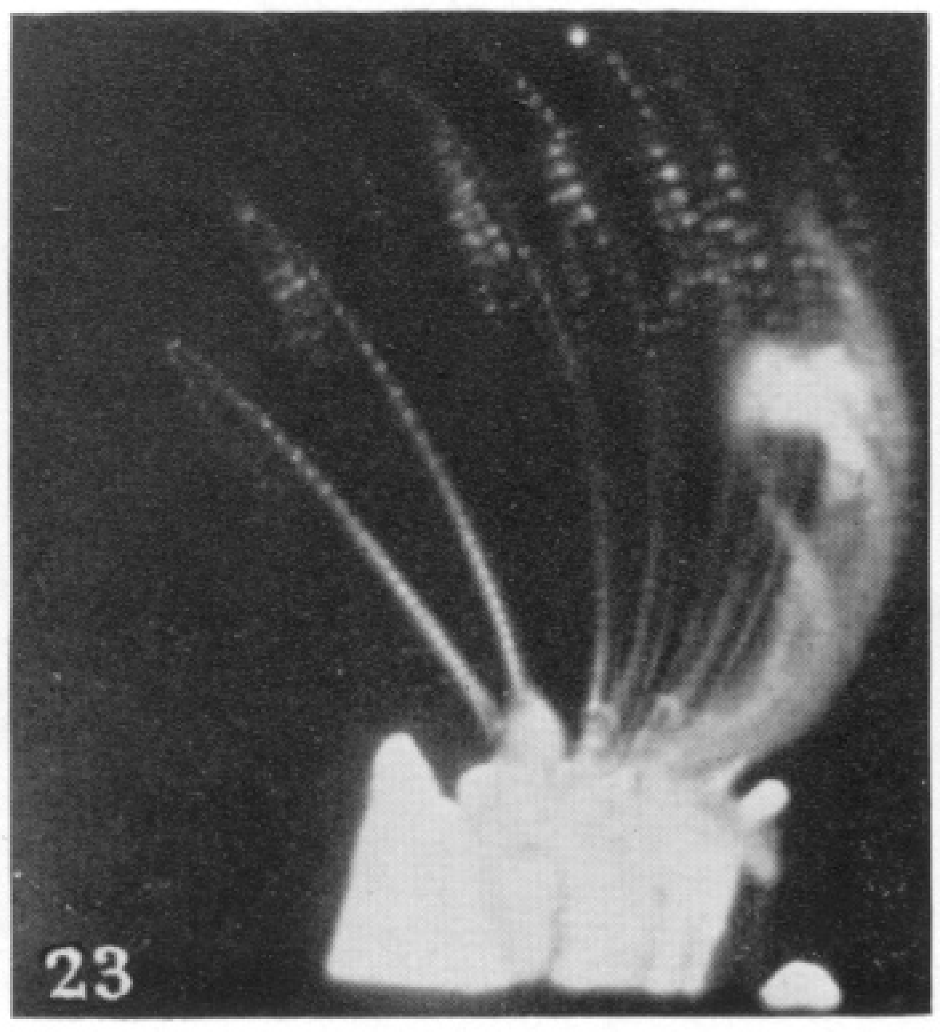
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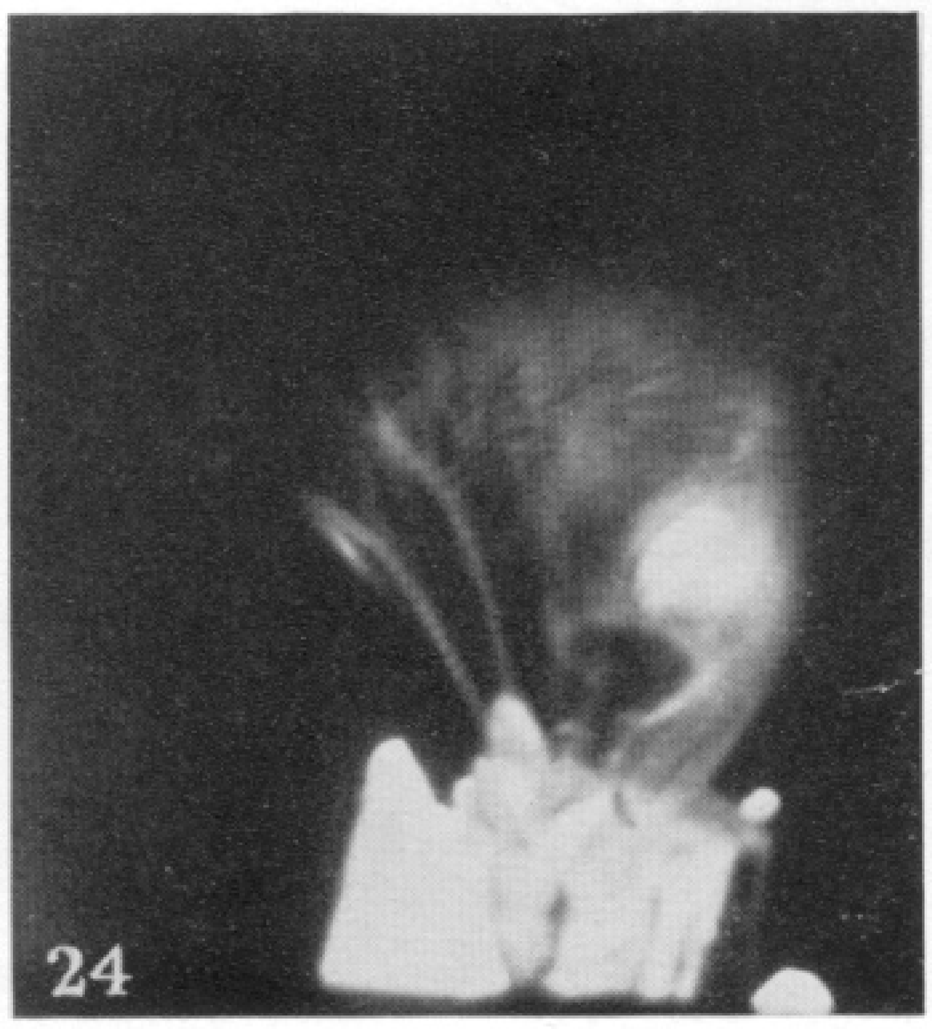
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