On the Anatomy of the Pedunculate Barnacle Lithotrya

H. Graham Cannon

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ON THE ANATOMY OF THE PEDUNCULATE BARNACLE
LITHOTRYA

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CONTENTS

1. INTRODUCTION

The genus *Lithotrya* G. B. Sowerby, 1822, comprises a group of pedunculate barnacles that have developed a rock- or shell-boring habit. Darwin dealt at considerable length with the genus in his Ray Society monograph in 1851, and since then only one new species has been described—*L. pacifica* Borradaile, 1900. In 1926, however, Seymour Sewell showed that, apart from one doubtful species, *L. rhodiopus* (Gray), all the others could be divided into two groups. One group of five, he suggested, constituted, in fact, a single species, *L. dorsalis* (Ellis). The other group of two I dealt with systematically in my report on the Great Barrier Reef Expedition collection (Cannon 1935) and came to the conclusion that they also represented a single species, *L. valentiana* (Gray).

The material on which this paper is based consists mainly of a few specimens of *L. valentiana*, collected and fixed in Bouin, which were very kindly given to me by Professor C. M. Yonge. I have also to thank Dr L. A. Borradaile for specimens of *L. dorsalis* collected by him in the Maldive Islands in 1900, and the Discovery Committee for specimens of various barnacles which I have used for comparison. In addition, I still have the official collection of the Great Barrier Reef Expedition, and a few of these have now been sectioned. I have been careful, however, not to section critical specimens of my detailed list (Cannon 1935, p. 5, table 1).

I decalcified all my specimens in Müller's fluid. Apart from this I used the same method of projection reconstruction from thick celloidin sections that I described in my monograph on *Gigantocypris* (Cannon 1940). All the drawings in this paper, unless otherwise stated, are made from such reconstructions, so that by reference to the working sheets it is possible to

refer any point in a figure to an actual section. Apart from celloidin sections I made the usual thin sections in paraffin, and among the stains which I found most useful were chlorazol black and Beyer brown (Cannon 1941).

2. Body shape and arrangement of plates

Lithotrya lives its post-larval life embedded in a hole, usually in coral rock, but more rarely in shell. The peduncle is attached to the side wall of the cylindrical hole, somewhere near its rounded internal end, while its capitular plates are on a level with the external opening. The cavity becomes deeper and broader throughout its length as the animal grows and the peduncular attachment moves down with the increasing depth of the burrow. How this excavation is brought about is still uncertain, but Darwin has written at great length on the matter (1851, p. 337).

In the species dealt with most fully in this paper, *L. valentiana* (Gray), the capitular plates of small specimens still show an elaborate sculpturing (Cannon 1935, text-figure 2), but as the animal grows, the plates become worn down, so that in older specimens they become flush with the surrounding rock surface. This exposes a section through the plates that shows very clearly their method of articulation (Cannon 1935, plate 1, figure 6*c*). In addition, this worn-down surface often becomes covered with a growth of encrusting organisms which may even include calcareous, tubicolous forms (Cannon 1935, text-figure 3).

Figure 1 is a sketch of a well-worn specimen from which the encrusting mat has been omitted. The head end of the animal is towards the lower left of the picture and is marked by a small, but complete, rostrum. At the opposite end of the animal (upper right) is the larger, but much worn, carina. Between the carina and rostrum on either side are two massive plates, the tergum and scutum.

3. Opening mechanism

Between the terga and scuta medially is the entrance to the mantle cavity in which lies the main body of the organism, and this slit-like entrance has to be widened each time the trunk with its cirriform appendages is thrust out in the typical feeding respiratory 'casting' movements of the cirripede. Now, the mechanism by which this opening takes place, as far as I am aware, has never been dealt with fully. All writers state merely that the limbs are cast out of the opening, but do not explain how the opening is enlarged to allow this to take place. Yet it is a complicated process, certainly in the pedunculate barnacles, for as Calman remarks (1909, p. 117), the only muscle attached to the valves of the shell is the adductor scutorum, and this muscle, since its opposite ends are attached to the two scutal plates, can only function in pulling the scuta closer together and so tending to close the mantle entrance.

In the absence of any direct musculature, the only other mechanism available is hydrostatic—that is, an enlargement or movement of one part of the body is brought about by the pressure of body fluids produced by muscular contraction in some other part. Now the stalks of all pedunculate barnacles that have been described show a circular and longitudinal muscle system in the body wall, and there is also in places a middle layer

of oblique fibres (figure 10). This system is used in bending and altering the length of the peduncle. But another important function is, I suggest, to force the blood by contraction from the peduncular into the capitular region. Thus, in the same way as the fingers of a glove can be distended and forced apart by blowing into the glove, so I conceive that this forcing of blood into the walls of the mantle cavity (which are in direct continuity with the peduncle) must cause them to become erect and open the entrance.
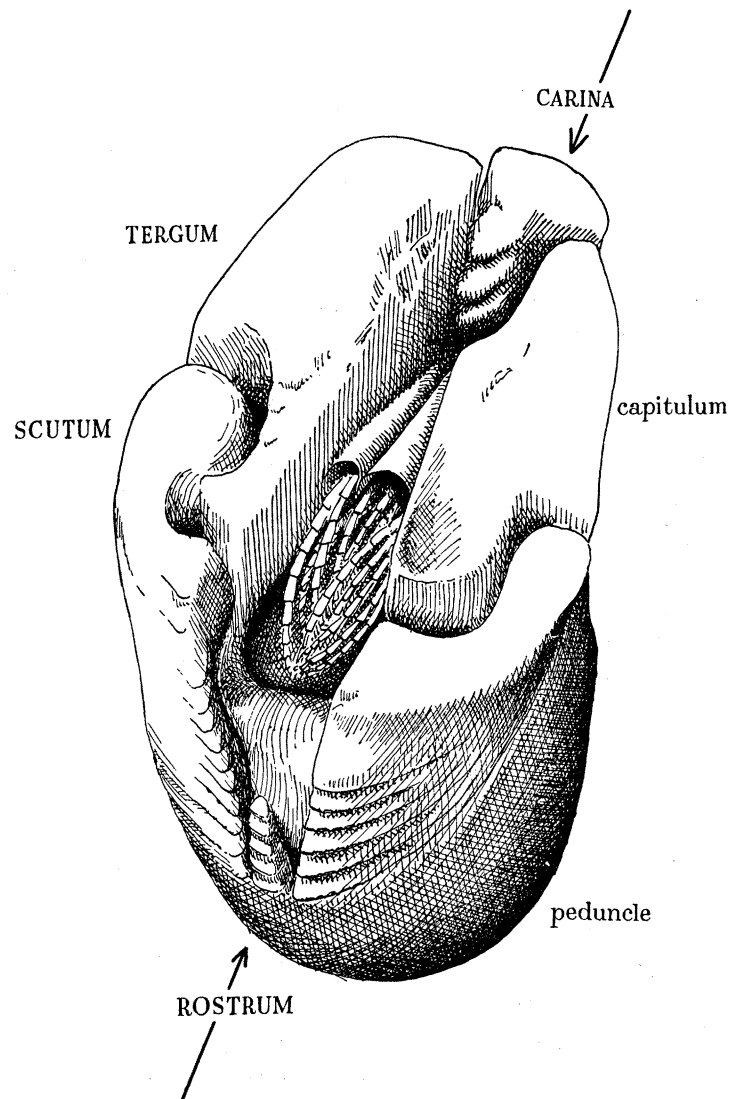

FIGURE 1. Free-hand sketch of specimen of *Lithotrya valentiana*, looking down obliquely on to the well-worn exposed surface of the capitulum. The arrows indicate the antero-posterior axis of the animal. The adductor muscle can be seen running across from one scutum to the other between the rostrum and the cirri. The velum is the folded membrane between the cirri and the carina.

This mechanism I believe holds for pedunculate barnacles as a rule. But the genus *Lithotrya* is an exception, for, as Darwin points out (1851, p. 33), it possesses a small muscle which is present in no other pedunculate cirripede (p. 338) and this muscle, from its attachment, must at least assist in opening up the valves. To understand this, the arrangement of the capitular plates must first be considered in more detail.

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The tergum and scutum which, as I have said, form on either side the wall of the mantle entrance, articulate with each other by an S-shaped joint (figure 1). This, incidentally, is much more marked in *L. valentiana* than it is in *L. dorsalis*. Now, it is obvious from the figure that if the terga can be moved away from each other they will carry the scuta with them. The tergum and scutum on either side will thus act like a single plate. That this is so is clear from the fact that the two plates are sometimes fused together across the S-shaped joint by tubes of encrusting forms (e.g. specimen 14, Great Barrier Reef collection, Cannon 1935, p. 5).

Darwin's muscle system consists of a band of fibres running parallel to the circular muscles of the peduncle, but joining the lower carinal margins of the terga with the carina, and, more important, with each other (figure 2a, b). There is thus a small but definite
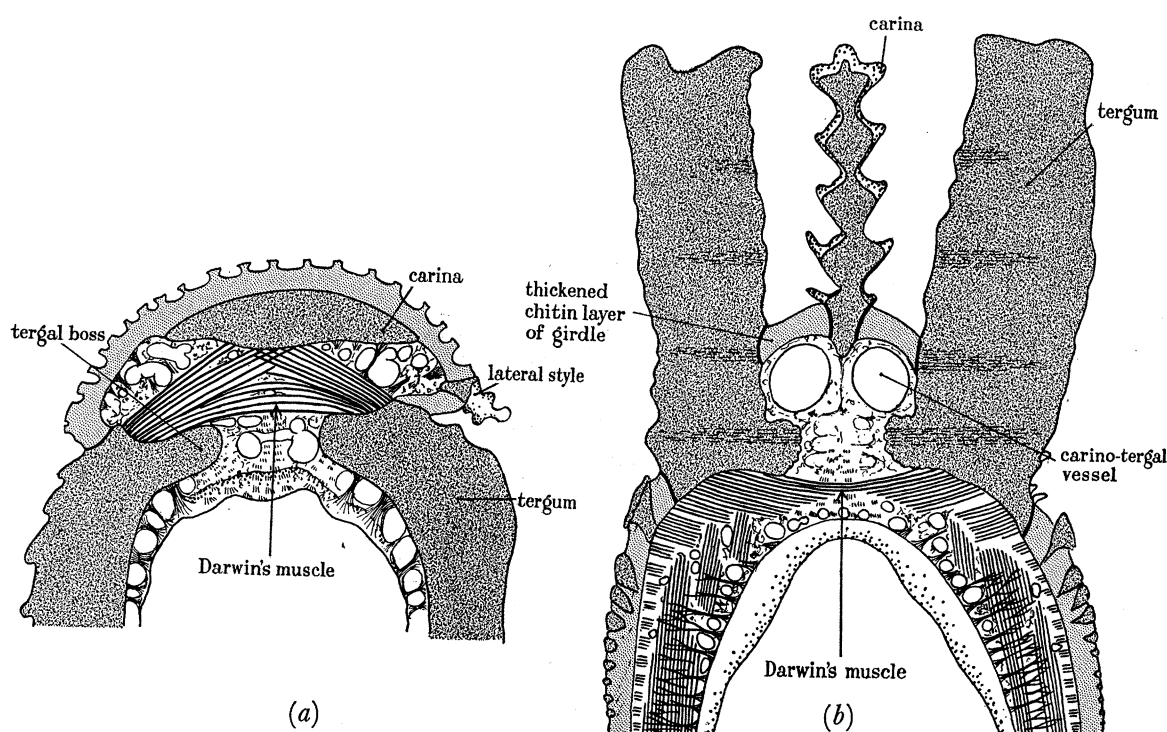

FIGURE 2. Sections showing Darwin's muscle (a) transverse to the peduncle and to the carina, (b) frontal to the peduncle and to the carina. The growth zones in the terga as revealed by polarized light are shown by light shading by horizontal lines. The pits in the outer body wall in (a) are those left after the complete disappearance of the peduncular scales on de-calcification. In (b) the scales have been drawn in as if they had not dissolved.

muscle running across from tergum to tergum in the same way as the adductor scutorum joins the two scuta. At first sight it looks as though such a muscle would function by pulling the terga together. But supposing these two plates were kept apart by some rigid fulcrum above the muscle, then the latter, while pulling the lower ends of the plates together, would at the same time pull outwards the upper parts. That this is what in fact occurs soon became evident from the study of sections transverse to the terga and longitudinal to the peduncle (figure 2b). A fulcrum occurs which is formed by the carina and a modification of the body wall.

The outer covering of the peduncle consists of a relatively thick, laminated chitin layer covered on the outside by a thin cuticular layer.* Towards the base of the peduncle the cuticle is modified in places as little star-shaped nodules (Darwin 1851, p. 337), each of which possesses a fine extension like a tail which runs through the chitin layer to the underlying ectoderm (figure 10). Passing up the peduncle these stars become slightly cup-like, and then as one continues these cups become larger and at the same time filled to overflowing with a deposit of crystalline calcareous matter. At the upper limit just below the capitular plate, the level that I have called the girdle (Cannon 1935, p. 9), the chitin layer is more than twice as thick as lower down the peduncle. But most of its thickness is occupied by the peduncular scales (figure 2*b*).

From the girdle, this thick chitin layer extends inwards between the capitular plates, and only after reaching the inner faces of the plates does it thin out as it emerges into the soft lips of the mantle opening. It thus forms a rigid framework, keeping the plates a definite distance apart from each other. It is very obvious in sections, for being unencumbered by peduncular scales it stains a uniform bright blue in Mallory.

Figure 2*a* represents a horizonal slice through the base of the capitulum and it shows Darwin's muscle in its entirety. There are the muscle strands running from tergum to tergum and also from the terga to the carina.The action of the latter must be partly to pull the base of the carina in a rostral direction, but from the wide angle between the muscle strands on either side it is clear that this forward movement must be very small. Its main action is clearly to assist the other muscles running direct from tergum to tergum in pulling the bases of the terga towards each other.

Figure 2*b* represents a slice at right-angles to 2*a*. Its plane is thus parallel to the length of the peduncle and is more or less transverse to the body. It cuts through the terga symmetrically and the teeth on the rostral edge of the carina. Darwin's muscle can be seen running across from the lower edge of one tergum to the other, and above them—about one-third of the way towards the upper edge of the tergum—is the rigid bridge holding apart the two terga. This consists laterally of the thickened chitin layer of the girdle, and, medially, of the carina itself. In the specimen figured it is obvious that if the muscles pull the lower edges of the terga a certain distance inwards, the upper edges will move outwards approximately twice this distance.

In *Lithotrya*, therefore, there is a muscular opening mechanism, and this will be antagonistic to the closing mechanism of the adductor scutorum. When Darwin's muscle pulls apart the terga, these plates, because of their peculiar articulation with the scuta, will cause the latter also to move apart. Conversely, when the adductor scutorum pulls the two scuta together, then again, and for the same reason, this will cause the two terga to move towards each other. The S-shaped joint is thus all-important. But it is not only that its shape gives a more intimate coupling between the two plates that is significant—the orientation of the S is also an essential factor. If the S, instead of being as shown in figure 1, occurred as the

* I have to thank Dr Ralph Dennell for an analysis of the body wall. He states that the inner laminated layer contains a relatively small amount of chitin, the remainder being protein associated with it. Overlying this protein chitin layer is the protein cuticle, showing no trace of chitin. Thomas (1944, p. 259) does not mention this double constitution of the chitin body wall—he merely states that the integument consists of a thick layer of chitin, presumably of uniform constitution, underlying a thin cuticle.
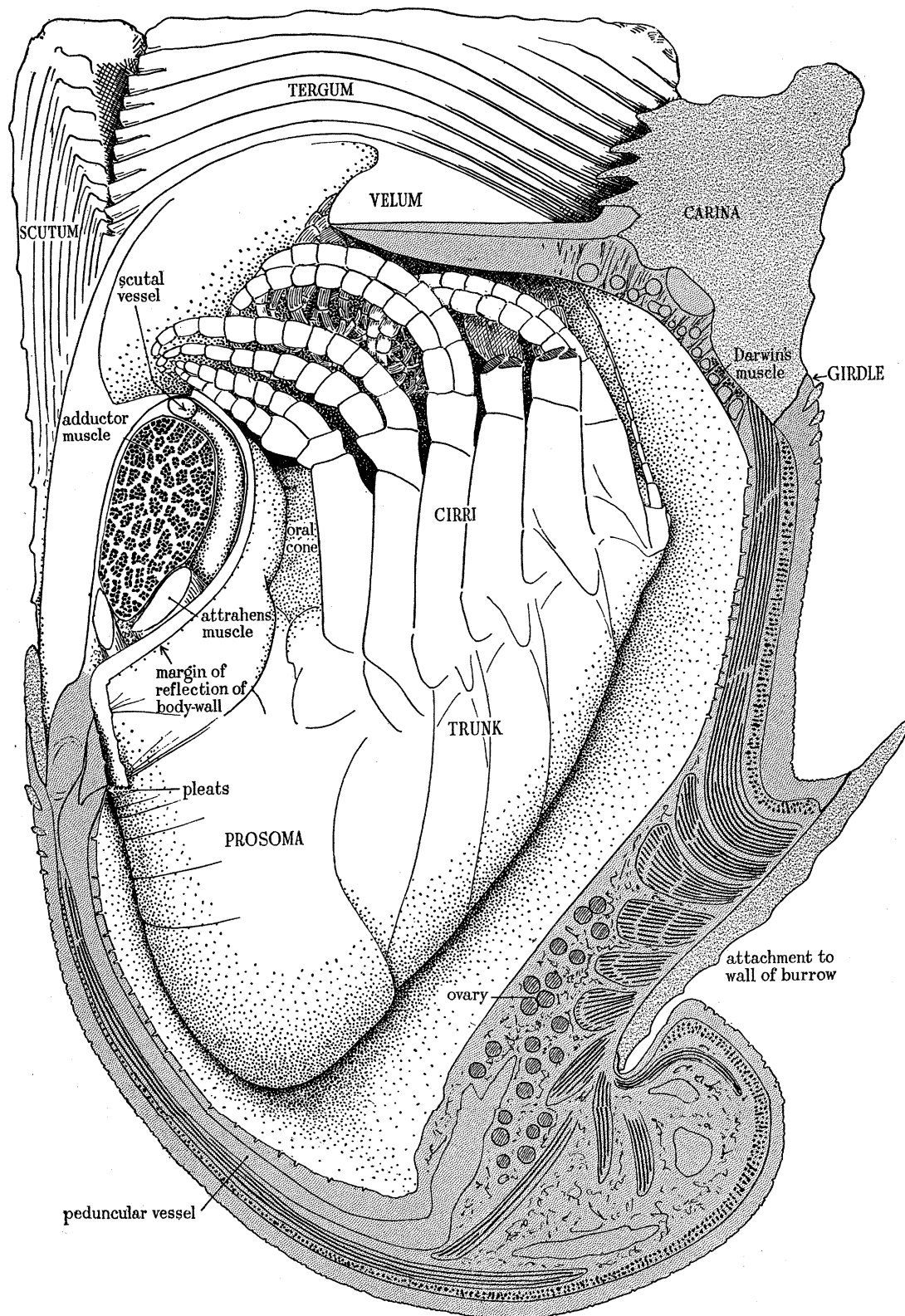
FIGURE 3. Reconstruction of whole animal in which the right half of capitulum and peduncle have been omitted. The figure represents the orientation of the animal, used in descriptions throughout the paper. Thus the ventral side is uppermost while the dorsal parts of the body are below.

mirror image, the whole mechanism would fail, for the coming together of the scuta would not drag with them the terga, and vice versa.

Darwin's muscle in *Lithotrya* is simply a modification of the circular musculature of the peduncle at the capitular margin. This relationship is very evident from a study of sections transverse to the peduncle. It is also to be seen in the sagittal section shown in figure 3. But the most convincing evidence is that its nerve supply (see later, p. 132) is a small branch of a nerve which otherwise spreads over the peduncular musculature just below the girdle.

A very obvious structure in figure 2*a* is the knob or boss that occurs just above Darwin's muscle (figure 2*b*). At first sight, having discovered Darwin's muscle in sections, it appeared as though these bosses, by coming together with the middle line, formed the fulcrum about which the terga rocked. It soon became evident, however, that this was not so. For one thing, no section ever showed the bosses in contact. They were always separated by a zone occupied by connective tissue as in figure 2*b*, or by a peculiar ovoid, apparently closed vesicle, as in figure 3. When the latter occurs, it has a definite shape, but equally definitely it may be absent. There is a similar structure between the lower tips of the scuta where they are connected to the base of the rostrum, and these plates also carry small bosses in this region (figures 3 and 4).*

The constitution of the tergal bosses is as puzzling as their function. They are always irregular in outline, a fact noticed by Darwin (1851, p. 368), who describes them as roughened. The difficult point to explain arises from the method of growth of the capitular plates of *Lithotrya*. These grow by adding on new zones at their bases, and polarized light shows very clearly the manner by which new calcareous matter has been laid down (figure 2*b*). It will be seen that a zone of deposition passes right through a tergal boss. It can only be concluded from this that the boss is resorbed at each moult and then reformed lower down the plate. This fact would make it impossible for the bosses to act as a hinge during opening and closing of the valves. It would, however, account for the irregular outline of the boss.

4. The velum

The soft vascular lining of the mantle cavity extends upwards from the peduncle to end in the capitular region on a level with the lower margins of the capitular plates. Rostral to the carina, however, the lining projects forwards between the two terga as a shelf which thus forms a velum partly closing the mantle entrance (figures 1 and 3).

On either side of the carina the thickened chitin layer of the girdle, which I have already described, extends inwards at the base of the crevice between the carina and the terga. The two strips of chitin so formed meet in front of the carina and then extend to the edge of this velum, becoming thinner as they go (figure 3).

When the valves are closed, the velum is folded so that the right half touches the left, the actual fold pointing down the peduncle. When the valve opens slightly the two halves open like the arms of a V (figure 1), and if they open still farther the velum will become flattened out. Now, during this process the fixed points of the velum relative to the whole animal will be the places where it is attached to the valves at the upper ends of the two arms of the V.

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* Nussbaum mentions this structure in *Pollicipes* under the heading of 'Undefinbare Organe' (1890, p. 41), but figures it as a sense organ (plate 10, figure 8, *s.o.*).
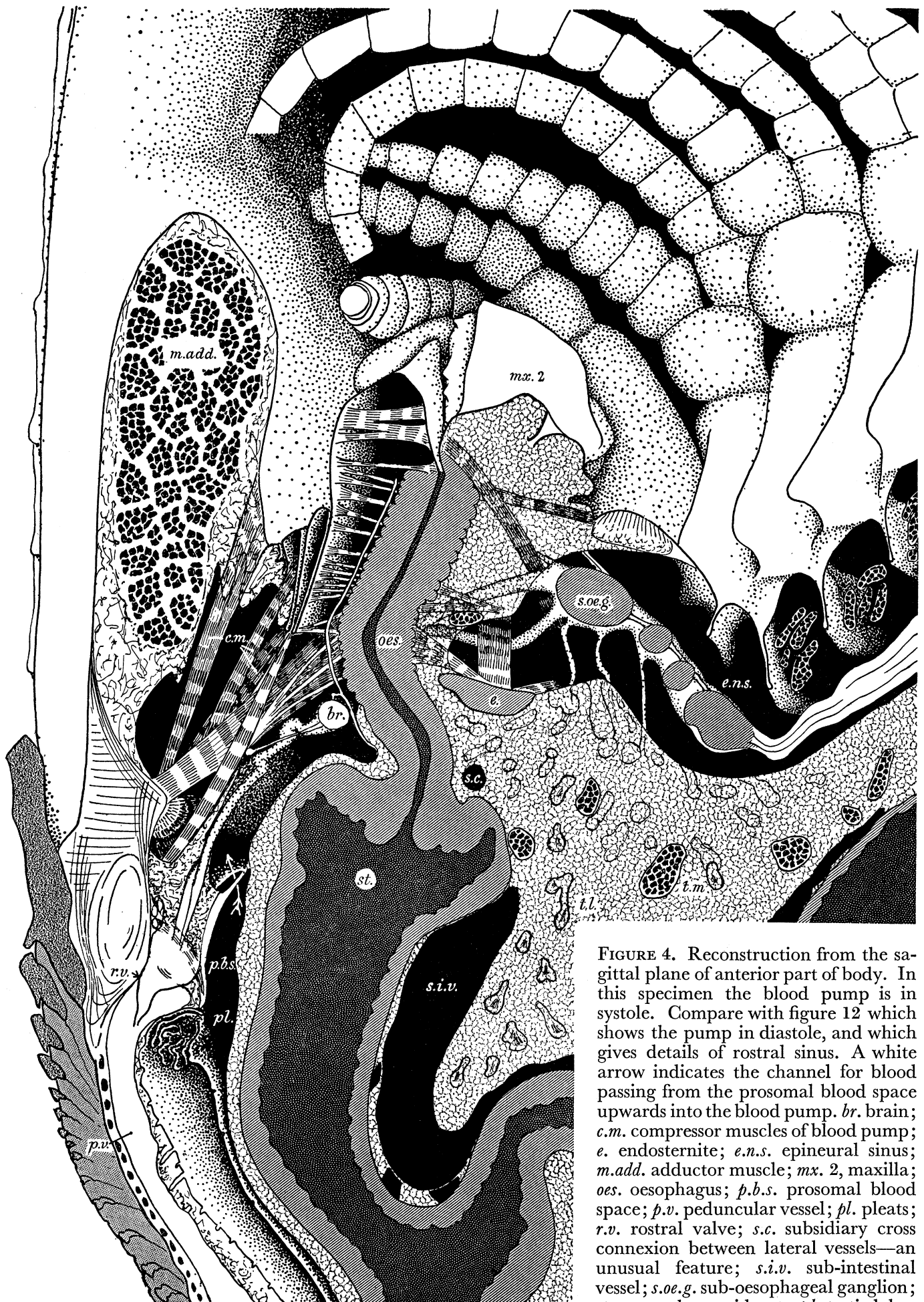
FIGURE 4. Reconstruction from the sagittal plane of anterior part of body. In this specimen the blood pump is in systole. Compare with figure 12 which shows the pump in diastole, and which gives details of rostral sinus. A white arrow indicates the channel for blood passing from the prosomal blood space upwards into the blood pump. *br.* brain; *c.m.* compressor muscles of blood pump; *e.* endosternite; *e.n.s.* epineural sinus; *m.add.* adductor muscle; *mx.* 2, maxilla; *oes.* oesophagus; *p.b.s.* prosomal blood space; *p.v.* peduncular vessel; *pl.* pleats; *r.v.* rostral valve; *s.c.* subsidiary cross connexion between lateral vessels—an unusual feature; *s.i.v.* sub-intestinal vessel; *s.oe.g.* sub-oesophageal ganglion; *st.* stomach or mid-gut; *t.l.* testis lobe; *t.m.* transverse muscle.

These represent a fixed level. The lower point of the V will be free to move, and as the valves open, this lower point will move up towards the level of the top of the arms. In other words, the velum flattens out as the valves open, and at the same time moves upwards away from the cavity of the mantle (figure 7 *a* and *b*). That is, it acts as a piston sucking on the cylindrical mantle cavity each time the valves open. Thus, as the cirri are cast out, a suction will be produced into the mantle cavity. Water, and hence suspended food, will, therefore, be drawn towards the mantle cavity. The action of the velum thus clearly forms an accessory feeding mechanism.

This very obvious structure is present in both *L. valentiana* and *L. dorsalis*, but I can find no mention of it in the literature, and it is a mystery how Darwin overlooked it. Also, I have found no trace of a comparable structure in any other barnacle.

5. Mechanical arrangement of body

In the following description, for the sake of convenience I shall consider always a specimen embedded in rock so that its burrow is vertical and the capitulum is uppermost. I shall use the terms ventral, dorsal and lateral in their strict morphological sense. Thus, in figure 3, the capitulum is above the peduncle and the ventral side of the body is uppermost. This is the orientation in which barnacles are usually compared in morphological textbooks. Actually, according to Stanley Gardiner (1903, p. 337), living specimens of *Lithotrya* hang downwards with their appendages just projecting out of their tubes when their entrances are covered by water.

The body inside the mantle is divided into two parts, which were named somewhat unfortunately by Darwin (1851, p. 6) as the prosoma and the thorax. The prosoma is described by Calman (1909, p. 113) as the cephalic region, while the thorax, which one is tempted to call the abdomen, carries the six pairs of cirriform limbs. I am convinced that the division between them is not an important morphological boundary such as, for example, the boundary between the thorax and abdomen in *Malacostraca*. It represents rather a functional boundary, for the constitution of the body wall differs in a functionally critical manner on the two sides of the boundary. Also, according to Darwin (1851, p. 39) the adductor muscle is included in the prosoma. This is most fortunate, as there is, in fact, a very sharp division both functionally and structurally between the hinder margin of the adductor muscle and the more posterior part of the prosoma (in Darwin's sense). In my description I shall use the term prosoma to exclude the adductor muscle, and I shall use the non-committal term 'trunk' instead of thorax.

The prosoma bears on its upper surface a helmet-shaped armature of rigid chitin (figures 4 and 5) which I call the oral cone. This whole structure is described and figured by Darwin as the mouth. According to more modern nomenclature it includes an anterior labrum which is fused round the sides of the oesophagus with the more posterior almost non-existent hypostome. The rigid helmet so formed bears laterally and posteriorly the mouthparts and at its apex the mouth.

The oral cone in a sense floats on the body. It is not joined by any articulating sclerite system either with the enclosing mantle or with the rest of the body. It is an isolated structure, and considering it as such it can be said to function as the skeletal framework for

FIGURE 5. Same reconstruction as figure 4, but from a parasagittal plane so chosen as to expose the main blood channel of the body. *a.d.l.m.* anterior group of dorsal longitudinal muscles; *a.v.* afferent vessel leading into cirrus; *c.c.* connecting blood channel between dorsal blood space of prosoma and cavity of blood pump (see figure 13); *d.b.s.* dorsal blood space of prosoma; *d.g.* digestive gland opening by minute duct on extreme right into stomach; *e.s.* end sac of maxillary gland; *h.g.* hind gut; *h.p.* hydraulic parenchyma of blood pump; *l.v.* lateral vessel; *m.add.* adductor muscle (m. adductor scutorum); *o.c.* oral cone; *s.i.v.* subintestinal vessel; *st.* stomach or mid-gut; *s.v.* scutal vessel; *v.l.m.* ventral longitudinal muscle; *v.s.* vesicula seminalis.
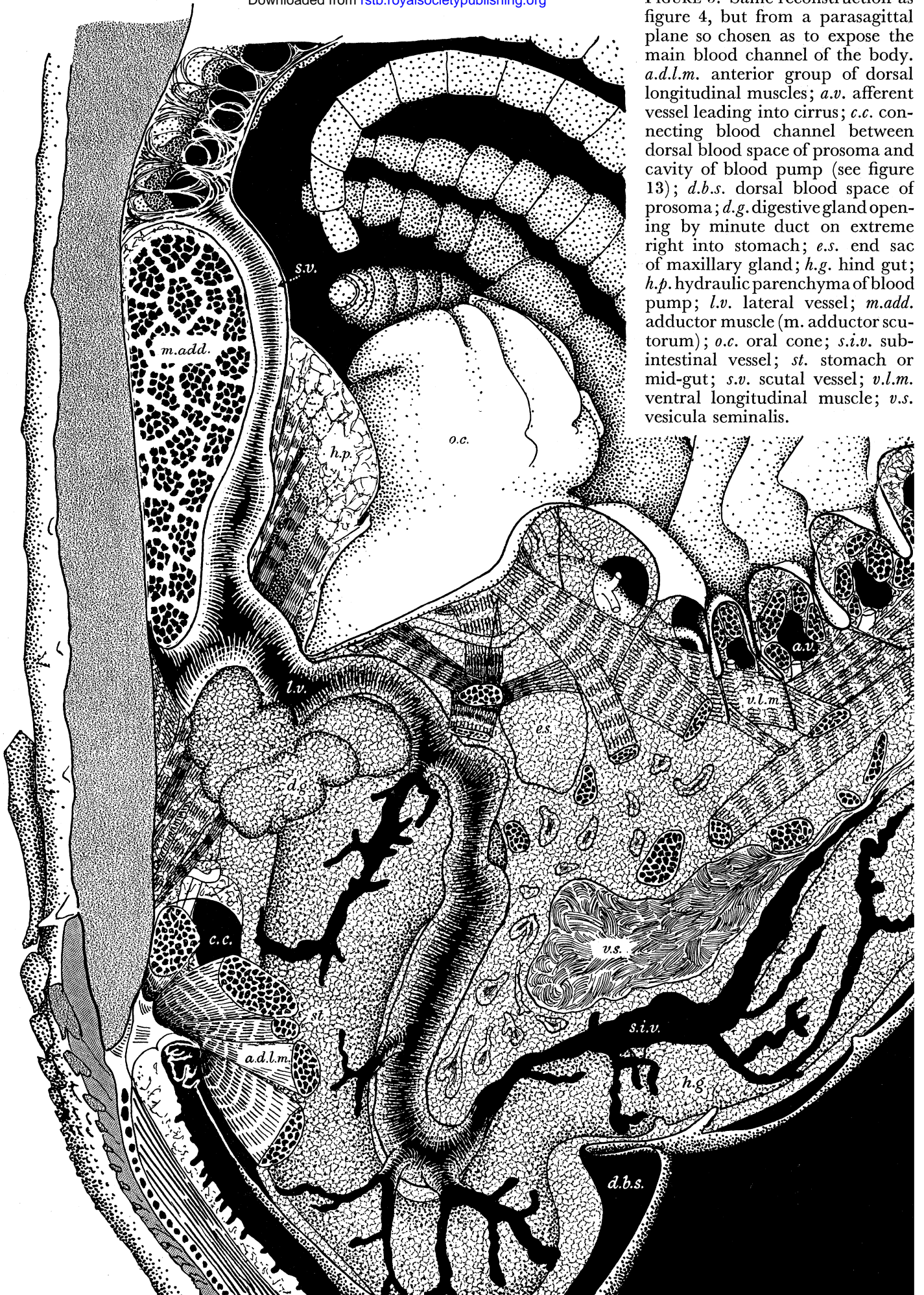
the muscles of the mouthparts. However, as I shall show, it also serves for the attachment of muscles which come into play when the body is protruded from the mantle cavity.

The lower, that is, the dorsal, wall of the prosoma is extremely thin and flexible and this softness extends up the sides to the base of the oral cone. Anteriorly and antero-laterally, it extends to the margin of reflexion below and behind the adductor muscle, where the outer surface of the main body is reflected to form the inner surface of the mantle (figure 3). At the median lowermost part of this margin the soft body wall is thrown into a series of folds which I call the pleats (figure 4). The function of these pleats I take to be without doubt to allow of the swinging out of the body from the mantle. When the body is protruded it rotates about an axis approximately through the adductor muscle, and to allow this to take place the pleats must unfold (figures 7 a and b).

In a preliminary survey of other forms, I find that in *Pollicipes* the conditions are as in *Lithotrya*. In *Conchoderma auritum* (L.) the pleats are replaced by one large intucked fold which functions in the same way. But in *Lepas* the pleats are absent. Instead, the body wall between the place where they would occur and the lowermost part of the prosoma consists of a continuous sheet of massive elastic fibres in the form of a net. In *Lithotrya*, therefore, in order that the body may be cast out, the dorsal wall unfolds, while in *Lepas* it attains the same result by being stretched.

At the opposite side of the prosoma from the pleats, between the anterior edge of the oral cone and the hinder surface of the adductor muscle, the body wall is also thrown into folds (figure 4), but, as I shall show later (p. 119), the purpose of this folding is quite different from that of the pleats.

In the trunk region, the dorsal, that is, lower body wall, is strongly chitinized, while the ventral, or upper, is flexible, and is thrown into a series of deep intersegmental folds (figure 4).

The tergum of each segment is a powerful sclerite, while the sternum is a narrow transverse strip of chitin. The arthrodial membranes between the sternal strips are extensive and form the deep folds along the mid-ventral line, while the terga articulate directly with each other. Each tergum is V-shaped. The apex of the V is in the mid-dorsal line and points forwards, while the arms of the V slope backwards and up the sides of the body towards the bases of the limbs. The apex of one tergum articulates closely with the inner angle of the tergum in front. The apex of the tergum of the second trunk segment, however, projects as the upper side of a fold into the prosoma (figures 5, 6 and 7 a). Between the arms of successive V's the lateral body wall is soft and flexible.

The foregoing description does not apply to the first pair of cirri. These always differ in their position relative to the trunk from the remaining five pairs, and corresponding to this a rigid tergum of this segment is missing. This constitution of the tergal system of the trunk has been figured very clearly by Darwin for *Coronula* (1854, plate 26, figure 8), but apparently has been overlooked by subsequent workers.

There is in the trunk region a series of ventral and dorsal longitudinal muscles as in all typical arthropods, the ventral series running on either side of the nerve cord, attaching intersegmentally to apodemal tendinous plates (figure 5).

Nussbaum has described the more posterior dorsal muscles as *longissimi* (1890, p. 26). Broch (1927, in Kükenthal, p. 514, figure 482) has copied Nussbaum's figure (1890, plate 5,

figure 1), but has incorrectly labelled it. He has labelled two sets of muscles, the dorsal of which he calls 'extensors' and the ventral the 'flexors'. Nussbaum, however, did not use these names. The dorsal he called the *longissimi*, but these must not be called 'extensors',
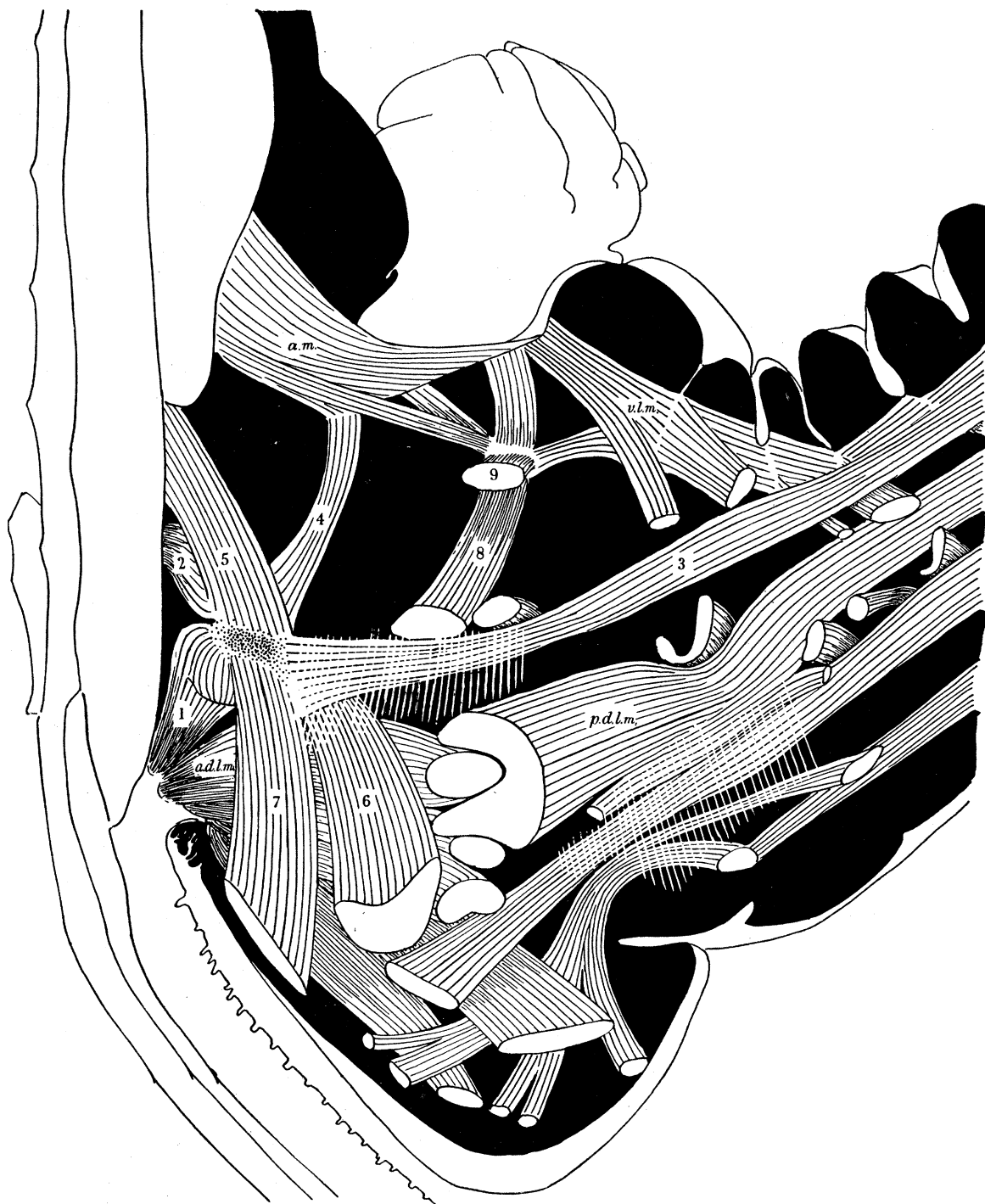
FIGURE 6. Diagram based on reconstruction of same specimen as shown in figures 4 and 5 to show muscular system of trunk region. The tendinous sheet in the lateral wall of the prosoma is dotted. The insertion muscles are indicated by close parallel white lines. *a.d.l.m.* anterior group of dorsal longitudinal muscles; *a.m.* attrahens muscle; *p.d.l.m.* posterior group of dorsal longitudinal muscles; *v.l.m.* ventral longitudinal muscles.

for Nussbaum states (1890, p. 26) that they shorten the body. The ventral are a series of limb muscles which Nussbaum called the *musculi attrahentes pedes*.

Apart from this iconographic error, to call these longitudinal muscles 'extensors' and 'flexors' would be correct only if the body segments articulated in a normal fashion. Thus, for example, in the abdomen of a crayfish there are dorsal extensors and ventral flexors, and these muscles act in the way that they do simply because the sclerite rings of each segment articulate with each other at the *sides* of the body; that is, at a level between the two sets of muscles. The muscles relative to the hinge joints pull in an opposite or antagonistic fashion. Now, in the barnacle, the articulation between one trunk segment and the next is peculiar in that it is not a pair of hinges, one on either side, but a single hinge in the mid-dorsal line. The two sets of muscles are therefore on the same side of the articulation. They pull in the same direction and hence cannot be antagonistic to each other, and thus must not be named 'extensors' and 'flexors'.

However, what is much more important is that it follows that the mechanism by which the body is moved about cannot depend on the ordinary muscle-skeleton relationship of an arthropod—a system of levers of which the joints form the fulcra. It must depend, according to my thesis, on a hydrostatic mechanism acting through turgor controlled mainly by the longitudinal series of muscles that have just been described.

I have already suggested that those pedunculate barnacles which possess no muscles for opening the valves of the mantle cavity use their blood system to distend and so enlarge this opening. An even more obvious case of hydrostatic action is in the extension of the cirriform appendages. Each cirrus is provided in its basis (protopodite) with a complete set of muscles to bring about controlled movements. But the multi-articulate rami possess only a flexor muscle—there is no extensor. Thus, as the cirri are coiled up during the withdrawal of the 'casting net' (Calman 1909, p. 114) into the mantle cavity, the coiling up is brought about by muscular activity. But as the net is cast out, this cannot be so; the cirri must be extended by being distended by blood (see later, p. 105).

In the cypridinid ostracod, *Doloria*, I suggested that the thin dorsal body wall of the trunk, with its criss-cross musculature, functions largely in moving body fluids (Cannon 1931, p. 448). In *Gigantocypris*, I extended this view and showed how the movement of the mouth and mouthparts towards the opening in the bivalve shell is brought about by a hydrostatic mechanism (Cannon 1940, p. 195). The movement of parts of the body of a barnacle, I consider, show a similar, but much greater differentiation of this power of hydrostatic control.

6. Mechanism of extrusion of body

The ventral longitudinal muscles of the trunk region occupy a typical position on either side of the nerve chain, forming, in fact, the walls of an epineural blood sinus (figures 4 and 5). They consist, on either side, of an inner series and a separate lateral constituent which I deal with later. The inner series is attached to the tendinous sheets which extend inwards from the deep intersegmental folds along the ventral body wall. From these same sheets oblique muscles extend posterodorsally. Anteriorly the inner series bifurcates into an upper muscle which attaches to the hinder lateral edge of the oral cone, and a lower muscle which runs to a small endosternite situated directly below the mouth and behind the oesophagus (figures 4 and 5).

VELUM

ventral
longitudinal
muscles

adductor
muscle

region of
blood pump

oral
cone

attrahens muscle

endosternite

pleats folded

anterior dorsal
longitudinal muscles

posterior
dorsal longitudinal
muscles

articulating terga
of trunk

dorsal body-wall
of prosoma
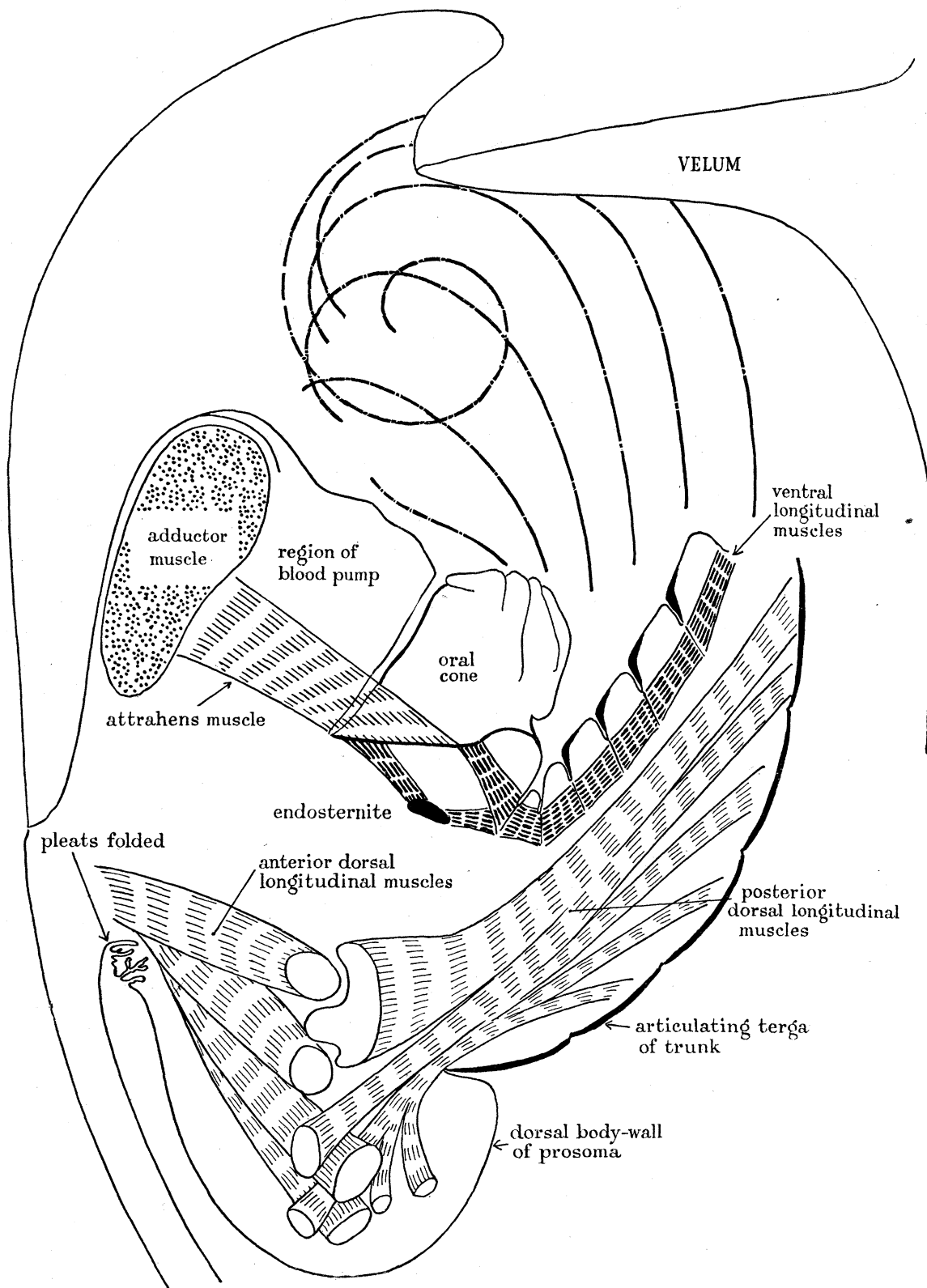
FIGURE 7 a

FIGURE 7. Diagrams to show action of muscles of trunk during the casting out of the body from the mantle cavity. The muscles which are contracting are heavily, and those which are relaxing lightly, shaded. (a) Body withdrawn into shell, limbs coiled up, and blood pump in diastole. (b) Body and limbs cast out and blood pump in systole.

VELUM

ventral
longitudinal
muscles

posterior
dorsal
longitudinal
muscles

oral
cone

adductor
muscle

← articulating terga
of trunk

endosternite

attrahens
muscle

dorsal body-wall
of prosoma

pleats
unfolded

anterior dorsal
longitudinal muscles

FIGURE 7 *b*

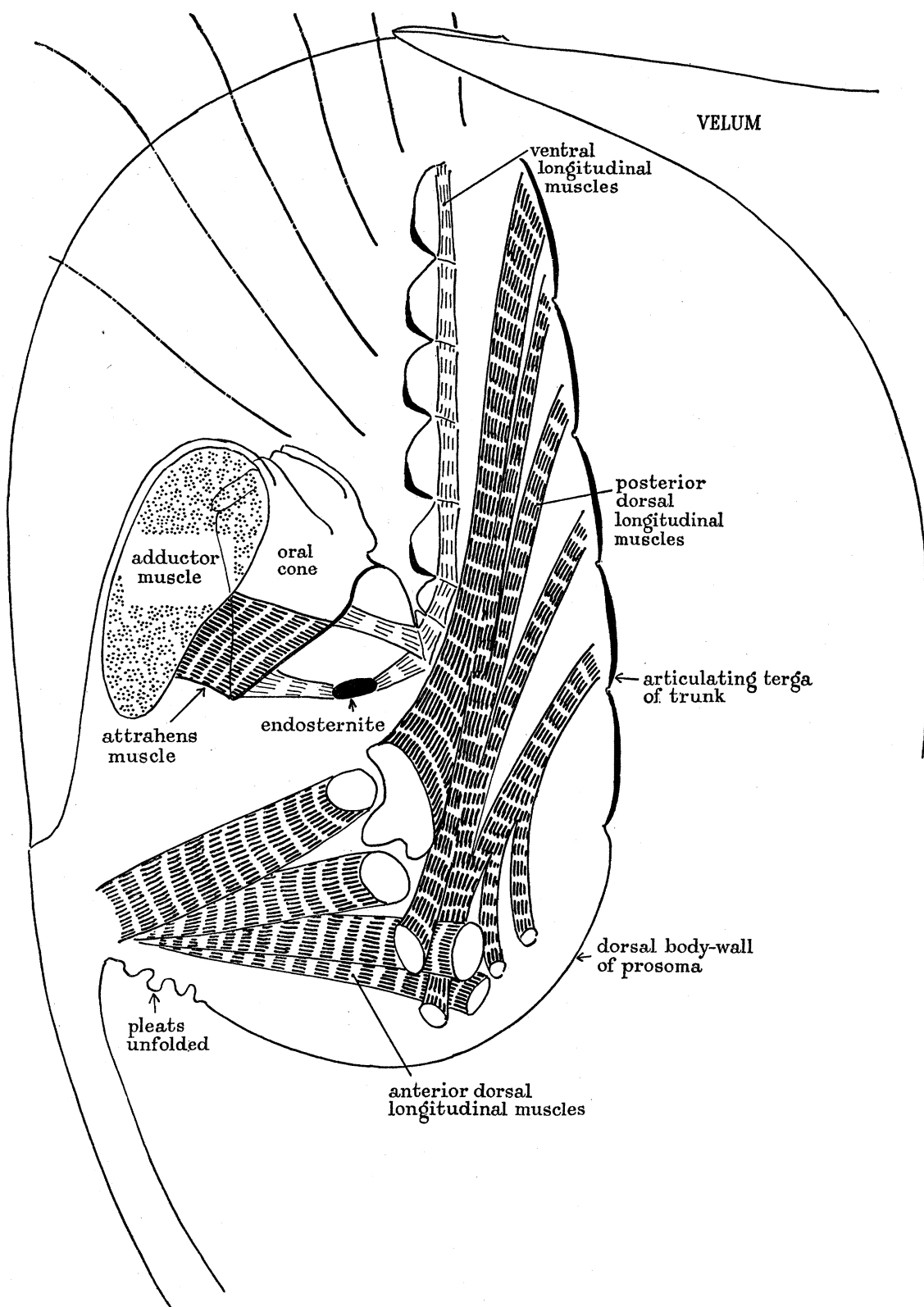From the front lateral edge of the oral cone a broad muscle continues forwards to attach to the hinder lower margin of the *adductor scutorum*, where this attaches to the scutal plate—Nussbaum's *m. attrahens* (1890, p. 22)*—and is joined by a narrow strip of muscle running forwards from the endosternite (figure 6). The inner series of longitudinal muscles is thus continuous, to the oral cone and thence to the scutal plates. Functionally, however, the
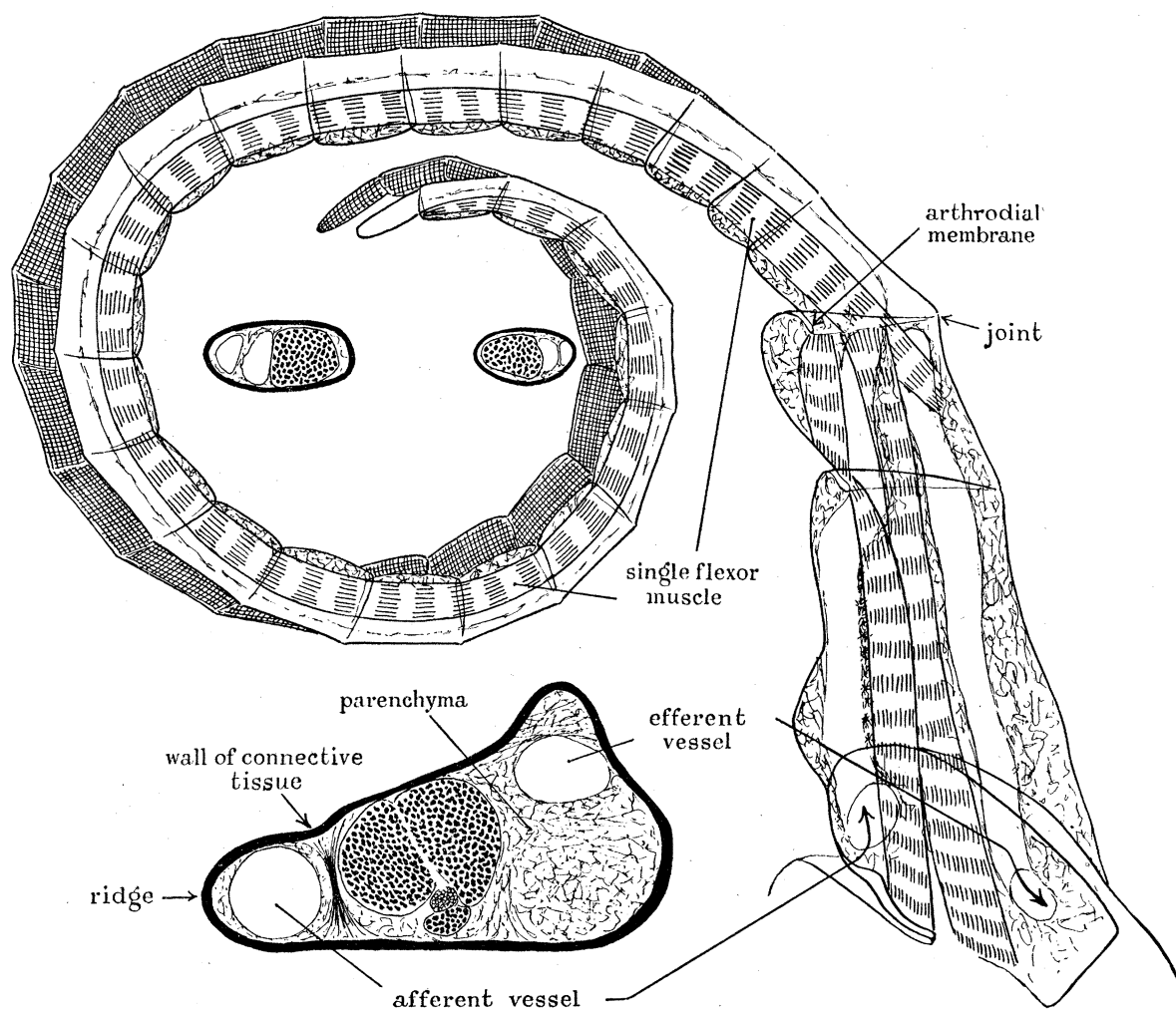

FIGURE 8. Reconstruction of cirrus to show musculature and blood vessels, together with sections through the limb at three different levels. Whole limb × 56. Sections × 108.

portion behind the oral cone must be considered quite separately from that in front. The former clearly is the effective mechanism for coiling up the body, while the latter brings the oral cone up towards the adductor muscle and so to the opening of the mantle. The two parts are thus in a sense antagonistic, for when the oral cone is protruded from the mantle, the trunk will not be coiled up but stretched out.

The inner ventral series behind the oral cone can thus be referred to as the flexor system of the trunk. It is the extensor system which is not evident. Extension of the trunk is

* It is impossible to say whether this muscle is the *attrahens primus* or *secundus*, as Nussbaum's figures do not agree (1890, plate 5, figures 1, 10). The insertion of his attrahens is also obscure, and he describes it as 'running from the neighbourhood of the *adductor scutorum* to the ventral edge (*Rande*)' of the body cavity. I shall refer to the muscle simply as the attrahens.

brought about, according to my views, by hydrostatic pressure controlled largely, but not entirely, by the dorsal longitudinal muscles, and only in this sense can they be referred to as the extensor system.

The dorsal longitudinal muscles are not simple, any more than are the ventral muscles, but a detailed description would not be significant to my argument. The relevant fact is that the dorsal series is divided into two distinct parts (figure 6), the anterior group— Nussbaum's *retractor corporis* (1890, p. 26) and Batham's 'mantle-body-wall muscles' (1945, p. 368, figure 17)—and the posterior group—Nussbaum's *longissimi* and Batham's 'lateral body-wall muscles'. The latter run from the terga of the hind end of the body downwards and forwards to end below the stomach on the dorso-lateral walls of the prosoma. From this latter region an equally massive group of muscles, the anterior group, runs upwards and forwards to converge on the peduncular wall just lateral to the pleats. There are thus attached to the soft lower side walls of the prosoma two sets of muscles, one running forwards and the other backwards, but both pulling upwards. When they contract they will pull the thin flexible prosomal wall inwards and so force fluid out of the prosoma into other parts of the body. It is this action which I maintain distends, and so extends, the trunk region (figures 7*a* and *b*). It is not so much that blood from the prosoma is forced into the trunk region, but it is the pressure put up in the prosoma as a result of this muscular activity which is transmitted to the whole trunk, and causes it to distend.

In this distension the dorsal skeleton of the trunk cannot elongate, for the tergal sclerites are firmly jointed together. On the ventral side, however, the sternal pieces are separated by the soft, folded, arthrodial membranes. Hence the trunk will elongate by the stretching out of its flexible ventral skeleton.

It is the same principle that underlies the extension of the cirri. In these multi-articulate appendages, each segment consists of a sclerite in the form of a laterally compressed cylinder which diminishes in size as one passes to the tip of the cirrus. These fit into each other, but the hinge by which one cylinder moves on the other is a single point on the morphologically posterior side of the cirrus. On the other side there is an arthrodial membrane which tucks into the more proximal cylinder when the cirrus is closed up (figure 8). Clearly if pressure from the haemocoele is put into the cirrus, the arthrodial membranes will open out, thereby allowing the cirrus to straighten out, and at the same time increasing its volume and so allowing the entry of blood (see later, p. 124).

However, the pressure produced by the contraction of the dorsal longitudinal muscles pulling on the prosomal wall will act in all directions. Not only will it act along the length of the body to elongate out, but laterally it will tend to blow out the trunk wherever the body wall is flexible. To counteract this there is a range of transverse muscles occurring down the trunk. I can find no previous record of them, but they appear very conspicuously in sections. Nussbaum (1890, p. 26) describes muscles which he names *transversalis primus* to *quintus*, but as they attach to a median tendinous apodeme they are probably limb muscles running more or less transversely. The muscles I am describing have no median attachment. They run uninterruptedly across the body. There appear to be two sets: one attaches to the arms of the V-shaped terga of the segments and thus alternate with the other set that attach rather to the soft flexible body wall between the segments (figures 4 to 6).

Their action is, I consider, to act as a safety system holding in the lateral walls of the trunk, which would otherwise bulge outwards when the body was extruded. By so doing they maintain the pressure in the trunk and so increase the effectiveness of the dorsal longitudinal series.

These soft flexible areas to which the transverse muscles are attached form a relatively small area of the trunk walls. In the prosoma, however, as I have described, the walls right up to the oral cone are extremely thin, and it is here that the compensatory muscles are seen in the most interesting form.

In the anterior lateral wall of the prosoma, directly underneath the point of attachment of the attrahens muscle to the scutal plate, is a tendinous sheet (figure 6), and to this is attached a whole series of muscles which must serve to hold in the flexible lateral prosomal walls. To give these muscles separate names could only lead to subsequent confusion; their homologies, and hence names, must wait until the anatomy of *Pollicipes* or some other more primitive form has been worked out. In the meantime, in order to discuss the functioning of this muscle system, I have numbered the muscles rather than named them.

Muscle 1 runs from the lateral sheet directly inwards and slightly downwards to attach alongside the pleats and just above the point of attachment of the anterior section of the dorsal longitudinal muscles. It is possible that it represents, in fact, the most ventral constituent of this series. Muscle 2 similarly extends inwards, but slightly upwards, to attach to the scutum. These two muscles clearly pull in the lateral prosomal walls directly.

Muscle 3 is the lateral constituent of the ventral longitudinal series. It runs the whole length of the trunk to attach to the body wall on either side of the anus. Its points of attachment anteriorly—the prosomal tendinous sheet—are clearly much wider apart than the hinder attachments. The muscles thus slope inwards as they pass backwards, and hence must exert an oblique inwards pull on the prosomal walls.

Muscle 4 also slopes inwards as it passes upwards to attach to the antero-lateral corner of the oral cone.

Muscles 1, 2, 3 and 4 thus form a four-pronged arrow-head of radiating muscles, which together must exert a strong force to resist any lateral distension of the prosomal walls. They are assisted in this action higher up by two muscles, numbers 8 and 9, both of which originate on the small endosternite. Muscle 9 runs directly transversely to the flexible skin just below the oral cone, while muscle 8 slopes downwards as it extends outwards and attaches to an area just posterior to the lateral tendinous plate. This last muscle must also therefore exert an upward pull on the prosoma, and so assist the dorso-longitudinal series of muscles.

The remaining muscles radiating from the lateral tendinous plates do not form a part of the safety system of transverse muscles. Muscles 6 and 7, like muscle 8, assist the dorsal longitudinal series in pulling upwards the lower wall of the prosoma. They, however, have little or no inward component. Muscle 6 originates on the lateral plate, closely median to muscle 3. It is a massive muscle and attaches to the body wall just anterior to the zone where the anterior and posterior series of dorsal longitudinal muscles intermingle in their attachments. Muscle 7 is a thin sliver of muscle in front of muscle 6 and lying directly

inside the ectoderm. The last muscle, muscle 5, which runs upwards to attach to the scutal plate just below the *adductor scutorum*, probably assists the attrahens muscle.

Associated with the muscle system I have just described, and with the prosomal body wall, there is a very striking system of elastic fibres which occur in some of the muscles but are completely absent in the others. Both muscles 8 and 9 are surrounded by a sheath of such fibres. These are very massive, staining brilliantly in eosin, and showing the typical anastomosis of elastic fibres. In addition, however, to forming a sheath, the fibres ramify through the muscle, especially in muscle 9. This can be seen very clearly in thick para-sagittal sections, where the remarkably homogeneous elastic fibres surround the muscle like a palisade, while others are scattered among the muscle fibres. Now while these fibres are so conspicuous in these two transversely acting muscles, there is no trace of them in any of the transverse muscles of the trunk.

Similarly, muscles 6 and 7 from their attachment must function in a similar manner, and yet muscle 7 is permeated by a plexus of fibres, while there are none in muscle 6.

In the body wall itself there are two bands of muscle which may be termed insertion muscles, as they commence and finish in the body wall and throughout their length are closely applied to the ectoderm. In this sense they closely resemble the circular muscles that I described in the trunk of *Gigantocypris* (Cannon 1940, p. 196), but whereas the latter are long muscles curving round through the quarter of a circle to follow the body wall, the muscles I am now describing are short, wide strips. One of them extends backwards from the lateral tendinous plate and the other occurs at the junction of the trunk with the prosoma. In both, the direction of the muscle fibres is pointing directly upwards towards the oral cone, so that on contraction they would pull up the lower prosomal wall. In both there is a network of elastic fibres which originate and terminate along with the muscle fibres.

What the function of this elastic fibre system can be is difficult to say with any certainty, but I suggest that it forms a safety system for the prosoma generally. From what I have described it is clear that fluid will be continuously forced in and out of the prosoma as the body is cast in and out of the valves. Later on I describe the circulatory process, and here again blood is regularly forced into this distensible region by muscles in other parts of the body, whether or not the body is actively 'casting'. The elastic fibre system I imagine is the safeguard which comes into play if the prosoma becomes overloaded with blood. In this case the muscles will become unduly stretched, but proportionately as this happens the plexus of elastic fibres will take the strain and so relieve the muscles.

I have summarized the mechanism of extension of the body in figure 7, and in order to simplify the diagram have omitted all the transversely acting muscles. On the left, the animal is coiled up inside the valves, and so the ventral longitudinal muscles are contracted, while the attrahens and dorsal longitudinal series are relaxed. On the right, the animal is projecting from the valves. The ventral longitudinal muscles are therefore relaxed, while the attrahens is contracted, and the whole series of dorsal longitudinal muscles are in a state of contraction.

These two diagrams are based on actual sagittal sections, so that the proportions of the body are correct. It will be seen from this that although the dorsal longitudinal muscles go into contraction during the casting out of the body, they do not shorten during the process. The posterior series remains approximately the same length but the anterior series

undoubtedly elongates. This contraction phase may be compared with the activity of the human *recti abdominales* during the later stages of bending the body backwards. As the trunk moves backward, the abdominal musculature must of necessity elongate and yet the muscles are in a state of contraction the whole time. There is an important difference, however. The *recti abdominales* are working against an extrinsic force—the force of gravity tending to pull the bent body downwards. In *Lithotrya* the force is intrinsic, produced by the muscles themselves.

7. Blood system

(a) Historical

Darwin's descriptions of nearly a century ago (1851, p. 46, and 1854, p. 87) of the blood system of cirripedes represents roughly our present state of knowledge of this very important system. He pointed out quite correctly that there is no heart, but added and emphasized that the circulation is largely lacunar, the body being permeated by vessels without any real walls. These statements have been repeated, I think without exception, by all sub-sequent workers on the problem.

A heart in an arthropod, to merit the name, must be a contractile vessel, but I consider that it would be wrong to call any contractile vessel a heart. The arthropod heart is homologous throughout the group, and therefore any structure called by this name must conform to a certain structural type and must also arise embryologically in the typical manner. In this sense the cirripede does not possess a heart, but as I shall show there is a structure which does force the blood around the body and this I have called the blood pump.

As regards circulation, while this is in part lacunar, definite blood vessels with well-defined walls are present much more than has hitherto been thought. Darwin (1851, p. 46) described a main blood vessel leading from the body down the rostral side of the peduncle which is now known as the rostral sinus. He described a valvular structure at the origin of this vessel which he correctly surmised prevents the regurgitation of blood from the peduncle into the body. All this has been accepted by subsequent workers, and the only addition has been made by Nussbaum (1890) who figures the valve accurately and describes a peculiar muscular structure by which the sinus can be completely blocked.

Darwin (1851, p. 46) added that there are two dorso-lateral channels in the anterior region of the body which are direct in continuity with the rostral sinus; and also that the blood from the rostral sinus, after passing down the peduncle and percolating among the tissues of the ovary, passes up again and re-enters the body near the sides of the adductor scutorum muscle. Both these statements are correct but as far as I can make out have been overlooked since Darwin's time.

Nussbaum (1890, p. 44) states that the heart and blood vessels of the cirripede are practically unknown and does not mention Darwin's account. He states

'The heart consists of two parts, ventricle and auricle, separated by a diaphragm bearing a valve which allows the passage of blood only from auricle to ventricle. From the ventricle various vessels lead to different parts of the body including one down the peduncle. At the origin of this peduncular vessel is a valve allowing the blood to pass from the body down the peduncle but not in the reverse direction.'

This surprisingly inaccurate statement is in contrast to the really accurate transverse section of the rostral valve which he figures, and of which I have already spoken. He calls a heart such, although, as he states, it has no muscular walls and is contracted and expanded by movements of neighbouring parts of the body. Worse still, his division of the heart into auricle and ventricle is not permissible morphologically; such a division is unknown in the Arthropoda. His auricle is the mid-dorsal space above the stomach wall, while the ventricle is the median rostral sinus. The valve between the two is the thin median strand of tissue running from the stomach wall to the hinder margin of the pleats (figure 12) together with the parenchymatous sheets that I mention later (p. 117 and figure 13).

Nussbaum's paper is very difficult to follow, but it seems that he considers a system of arteries as radiating from his ventricle, that is, the rostral sinus, up the cirri. Actually there is no such connexion and his cirrus vessels which he considers afferent are in fact efferent.

Nussbaum dealt with the musculature at great length. Unfortunately, it is usually impossible to follow his detailed descriptions. None of his figures of the musculature dissected out are labelled as to orientation, and as the muscles have been reflected on dissection, this is of critical importance. However, he states clearly (p. 21) that a series of muscles runs from the rostrum to the body surface which 'connects the oral cone to the heart'. This surface I take to be the soft flexible body wall between the oral cone and the adductor muscle. He states that these bring about the closure of the shell, or 'compress in various directions the loose tissue which lies between the oesophagus and the adductor scutorum'. His first suggested function is clearly impossible, but the second is correct. He did not, however, see the significance of these muscles, for they actually form the contractile part of what I describe later as the blood pump (p. 117).

Gruvel (1905, p. 392) quotes Nussbaum as regards the blood system and adds ideas of his own, but does not mention Darwin. He admits the existence of the rostral sinus but considers that from this space blood can either pass down the peduncle or laterally to irrigate the peripheral parts of the body. From the lateral spaces blood is said to pass to each cirrus. After passing up the cirrus it passes down and enters an epineural space. 'This ventral space extends forwards, around the oesophagus and then connects up to a big space around the adductor muscle and this last space is in direct communication with the rostral sinus.' I feel that this is entirely conjectural, for Gruvel does not give any descriptions or illustrations in support of his ideas. As I see it, he has the circulation entirely the wrong way round. One morphological mistake upsets his mechanism. The epineural sinus ends blindly in front and does not extend forwards around the oesophagus. Also it is *from* the epineural space into the cirri, and not the reverse, which, as I shall show later, represents the direction of blood flow. The big blood space which he describes around the adductor muscle does not, in fact, exist.

More recently Broch 1927 (in Kükenthal, p. 518) has published a short statement on the cirripede blood system. He adds nothing except a statement that in the 'more highly organised forms' blood collects in a ventral sinus on either side, which opens in the rostral sinus. He gives no evidence for this state of affairs, and I know of none.

Beyond stating that a cirripede does not possess a heart, Darwin (1851, p. 46) did not commit himself as to how the blood gets round the body. Most subsequent workers, however, state that the body movements are responsible for the circulation. Thus, Broch (1927, p. 518) says that the contraction of the rostral sinus is brought about by the general body movements. Gruvel (1905, p. 392) says the same, but adds significantly that the muscles responsible are chiefly 'abaisseurs et redresseurs'—presumably those muscles that are supposed to lift the body out of the mantle and those that pull it back again.

Now these views seem to me incorrect from two points. First, there is no need to assume that the rostral sinus itself contracts or is made to contract in order that the blood shall move round the body. All agree that the rostral sinus has no intrinsic musculature, and it

therefore becomes simply a tube leading from the body down the peduncle. There is no more reason in ascribing contraction to this sinus than to any other sinus or vessel that may be discovered. Secondly, if the rhythmical movements of the body are responsible for the circulation, then the movement of blood would cease when the valves were closed. Considering that many barnacles are capable of remaining closed for hours on end, it would appear very improbable that in such a group a blood system would evolve which would rely for its motive power on the normal rhythmical feeding and respiratory movements.

(b) General account

I have previously remarked that all authors following Darwin have stressed the lacunar nature of the cirripede blood system. The only vessel described with any certainty is the rostral sinus and even to this Gruvel (1905, p. 391) denies proper walls. In my study of *Lithotrya* I have found just the reverse. There is an organized circulatory system which is canalicular in the main. I am certain also from preliminary work on other barnacles— *Lepas, Pollicipes* and *Conchoderma*—that in all essentials the plan of the blood system is the same throughout the Pedunculata.

There are lacunae in spaces between muscles and there are special sinuses in which various organs lie. But, largely through the development of a parenchymatous connective tissue, the body cavity is partitioned into a series of blood channels rather than lacunae. In the ordinary thin sections that I have used for comparison with the thick celloidin slices, it certainly appears that there is nothing that can really be called a wall to these blood vessels; that is, no columnar or even squamous epithelium. But in the thick slices, especially where the vessel runs obliquely through the celloidin, a definite wall with a particular structure can be made out. It consists of a film supporting a mat of interlacing fibres without any apparent nuclei. Often there can be made out undoubted nerve fibres or even nerve cells, and a few elongated nuclei which may be epithelial, but there is no regular epithelium.

The simplest way of describing the circulatory system will be to start with the blood leaving the rostral sinus and follow it round the body. The rostral sinus, as its name implies, lies immediately internal to the rostrum. It opens through a rostral valve, into a long vessel, the 'canal pédonculaire' of Gruvel, which runs down the whole length of the peduncle.

To illustrate the structure of the rostral valve I have figured a series of thin sections 10μ thick which are taken transverse to the peduncle (figure 9). The number appearing below each section indicates the number of the section in a continuous series. Section 1 (top left) is at the peduncular, and 73 (bottom right) at the capitular end of the series. In all sections I have also indicated the oviducts and the antennulary peduncular nerves, as these are closely associated structurally with the rostral valve. Apart from these structures, in order to avoid confusion, I have omitted all other histological details.

Commencing at the top end of the series, section 73 is actually above what has been termed the rostral sinus. It cuts through the median blood space just anterior to the stomach and shows the median connective tissue strand which I have described (p. 109) as extending from the pleats to the stomach wall (figure 12). On the rostral side, that is, uppermost in the figure, is the semi-cylindrical wall which lower down becomes the rostral wall of the peduncular vessel. At this level, while the antennulary nerves continue to extend upwards,

the oviducts leave the line of the peduncular vessel and bend backwards to open on the first cirrus.
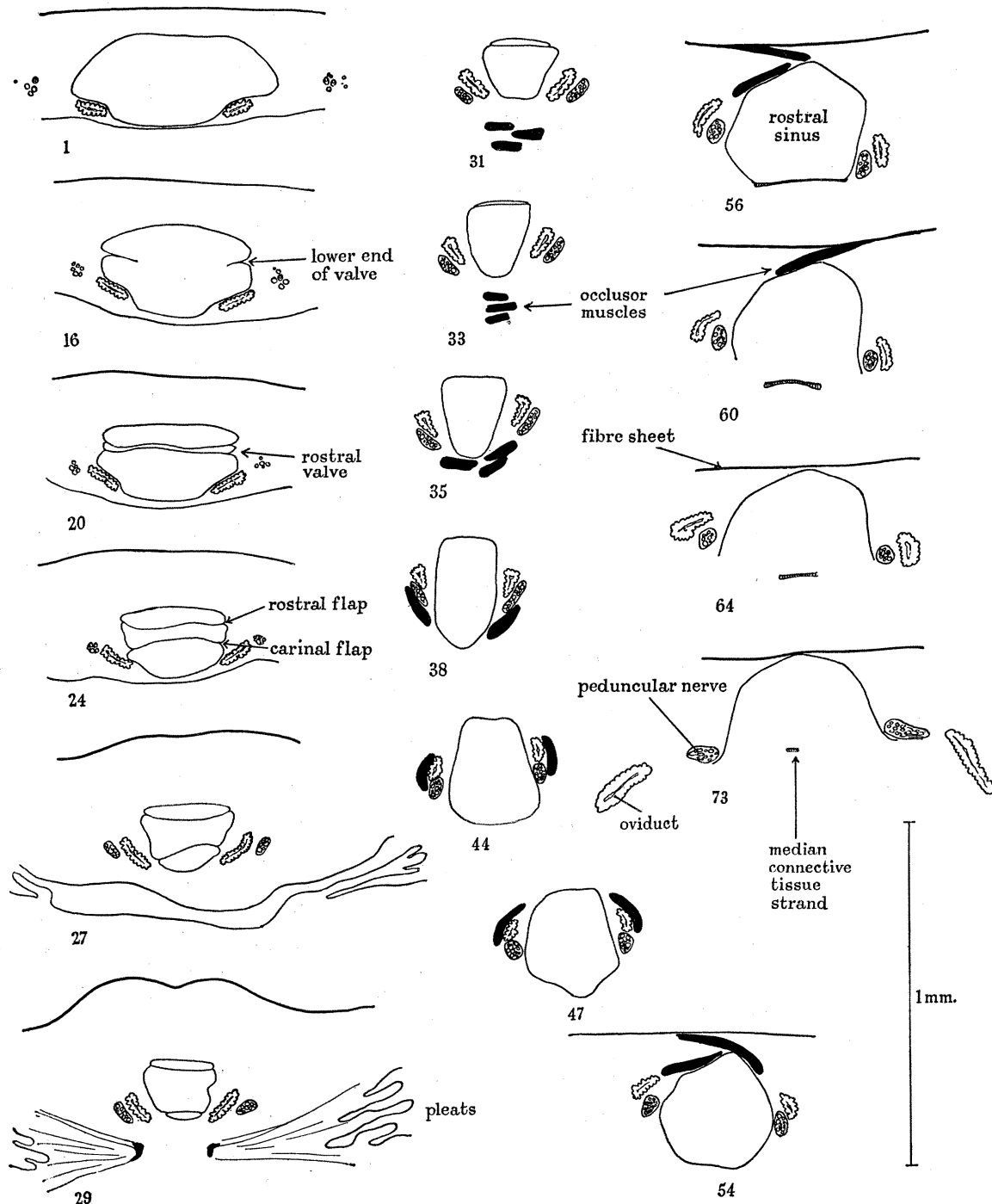

FIGURE 9. A series of projection drawings of thin sections cut transversely to the rostral sinus to show the constitution of the rostral valve and the arrangement of the occlusor muscles. × 108.

Coming down the series, the median connective tissue strand spreads out laterally—sections 64 and 60—to become the hinder wall of the now complete rostral sinus at section 56. The oviduct and antennulary nerve have come to lie close against the lateral wall of the sinus.

Just outside the rostral wall of the sinus there is a very marked, apparently powerful sheet of fibres which stretch across from the hinder surface of one scutum to the other. I cannot see any positive indication that it is a muscular sheet, but lower down it becomes continuous with the circular muscles of the peduncle, and also, what is more significant, at the level of section 60 it gives rise to a peculiar muscle which runs from it to the wall of the rostral sinus.

In section 60 the muscle arises from the left side of the animal (right side of the figure), while in section 56 a corresponding muscle arises from the opposite side and crosses the path of the first muscle. Following these muscles through the middle column of the figure, it can be seen that the muscles, after crossing over, extend round the outside of the rostral sinus and finally come back to the side from which they originated. In their encirclement of the sinus they pass to the outside of the oviducts and antennulary nerves—sections 47, 44 and 38. In section 35 the muscle on the right side of the figure is divided into two so that the other muscle can pass through it—section 33. The muscles terminate in massive connective tissue masses which run laterally among the pleats—section 29.

The muscles are thus in the form of two letter U's, each lying on its side but pointing in opposite directions, and in such a way that the semicircular bases of the U's overlap to form a complete circle. Included in this circle is the rostral sinus centrally, with the oviducts and antennulary nerves running close against its sides. It is obvious that contraction of these muscles will simply close the rostral sinus, and so I refer to these muscles as the occlusor muscles. Their real significance, however, is not at first apparent, and this I deal with later (p. 125).

Nussbaum (1890) was the first to mention them, but he gave no figure. He merely stated (p. 45) that they are 'crossing circular muscles'. As Gruvel (1905, p. 392) correctly points out, they are not strictly circular muscles. If they were, the system would simply be a sphincter. They are rather two loops of muscle which, pulling from opposite sides, will squeeze the rostral sinus and obliterate its cavity. The only similar case known to me occurs in the blood vessels of the Oligochaete, *Lumbricus variegatus* Müll. Here, according to Haffner (1928, p. 22), the dorsal blood vessel is slung periodically in a U-shaped muscle running from the body wall, while at the same time it is included in a circular muscle running around the gut. It can thus be squeezed, not laterally as in the barnacle, but from above and below.

Between sections 35 and 33 a flap of tissue originates from the rostral wall of the sinus, while between 31 and 29 a corresponding flap—the carinal flap—arises from the opposite side of the vessel. These two flaps projecting downwards approach each other until between sections 20 and 16 they come into contact and end. Together they form the rostral valve (figures 12, 3 and 4). In *Pollicipes*, according to Nussbaum's figures (1890), the valve has the same constitution, but in *Lepas* and in *Conchoderma auritum* a preliminary study shows that only the rostral flap of the valve is present.

The flaps have a simple squamous epithelial constitution and show no fibrous basis. They thus differ markedly from the walls of the vessels where the fibres form a continuous sheet, and epithelial nuclei are difficult to see with any certainty. In a specimen stained with borax carmine and then with chlorazol black, the walls of the vessels are black from the contained fibres, while the flap of the valve shows bright red nuclei unobscured by the black.

I describe later a scutal valve (p. 114). This has only a single flap which shows the same epithelial constitution and also a conspicuous thickened margin with more numerous nuclei.

In *Lithotrya* the peduncular vessel does not give off branches until it reaches the ovaries at the bottom of the peduncle. Here it splits up into numerous vessels, some of which can be traced to individual oocytes. The main vessel continues up the carinal side of the peduncle and divides into smaller branches which finally disappear about the level of the attachment of the peduncle to the wall of the burrow, by opening into spaces between cells of the parenchymatous connective tissue.
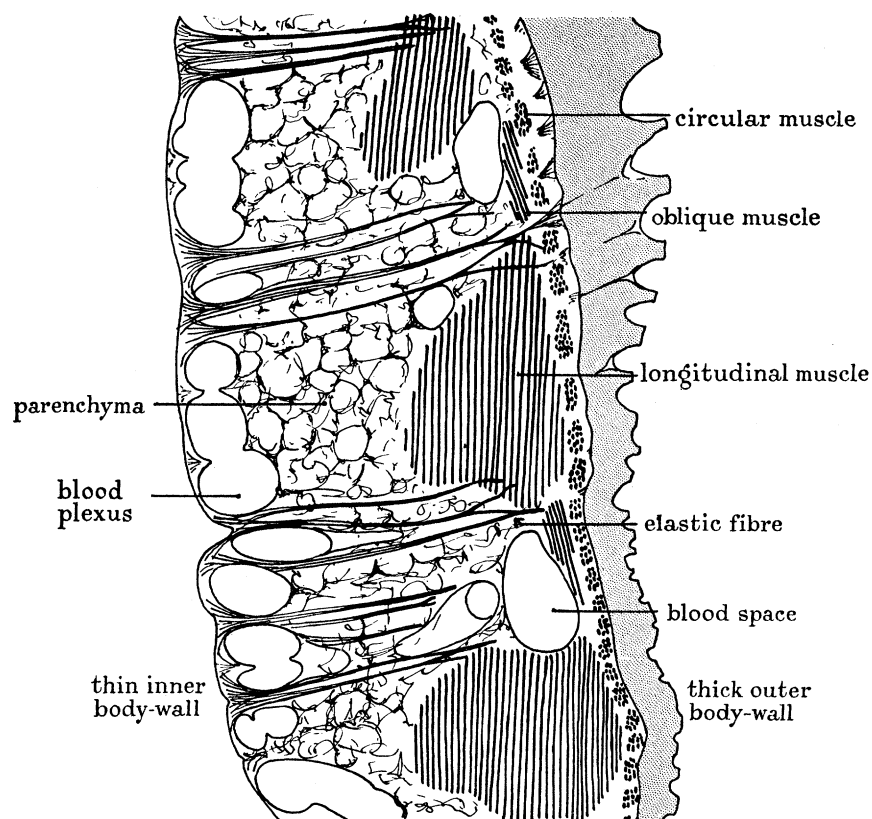

FIGURE 10. Section through peduncular wall cut parallel to the long axis of the peduncle, to show its constitution. × 56.

The constitution of the walls of the peduncle has been described briefly by Gruvel (1905, p. 377 and figure 371). The three layers of muscle are placed on the outside immediately underneath the ectoderm, and these muscles are apparently entirely unstriated. The circular and oblique muscles are often very difficult to distinguish apart. The inner portions of the body wall are mainly filled with the parenchyma and its contained blood spaces. The latter, however, do ramify to a certain extent towards the outer surface among the muscles (figure 10).

The inner surface of the peduncular wall is covered by an extremely thin cuticular layer in contrast with the outer layer of ectoderm which is invested by the thick chitin-cuticle layer which I have previously mentioned (see p. 93). The two layers are joined by parallel rows of groups of conspicuous connective tissue cells. The latter are massive and have all

the appearance of elastic fibres of vertebrates. That is, they appear homogeneous in substance and anastomose markedly. They show the same staining reactions as the elastic fibres which I have already described as ramifying among the muscle fibres of the lateral prosomal compressors (p. 107). At their inner and outer ends they divide up into numerous fine strands which radiate and appear to pass right through the ectoderm cells. The inner surface of the peduncle is thus scored by a series of oblique ridges, the furrows between the ridges indicating where the inner ectoderm is being held by these elastic fibres.

The plexus of blood vessels extends up the inner surface of the peduncle, and on the carinal side the vessels gather themselves together into paired main vessels which enter the capitulum at the carino-tergal angle. On either side a large vessel extends inwards immediately below the thickened chitin strut which forms the hinge about which the terga oscillate (p. 93). From their position they may be named the carino-tergal vessels (figure 2b).

The two vessels now continue in a rostral direction and break up again into a plexus. This joins across from side to side at the base of the velum, that is, just anterior to the tergal bosses, but does not penetrate the velum itself (figure 3). It extends on either side lining the body wall covering the inner faces of the terga and scuta to the level of the adductor scutorum. Here, at the uppermost point of the area of attachment of the muscle to the scuta, the plexus once again joins up on either side into a main vessel, which now enters the body and which may be referred to as the scutal vessel (figures 3 and 5).

The scutal vessels extend down the hinder surface of the adductor scutorum, closely fitting into the angle formed by the muscle and the scutum to which it is attached. A little more than half-way down is the upper limit of the attachment of the attrahens muscle (see p. 104). At this point the scutal vessel continues as a vessel lying medial to the attrahens muscle, but still closely adhering to the margin of the adductor scutorum. From this point, for a reason which I explain shortly, the vessel must have another name, and I am calling it simply the lateral vessel.

The scutal vessel at its upper limit sends a branch down the rostral side of the adductor muscle which peters out in the connective tissue between the muscle and the rostrum. Similarly, the lateral vessel on reaching the lower limit of the adductor sends a branch upwards (figures 5 and 11) which also dwindles and disappears. The adductor muscle is thus almost completely encircled at the margin of its attachment to the scuta by large blood vessels in the form of a reversed C.

At the level of the top of the attrahens muscle there is a watch-pocket valve, allowing the blood to pass from the scutal vessel into the lateral but not vice versa. There is a valve, in fact, which controls the passage of blood back from the capitulum, and hence peduncle, into the body. This in itself would not necessitate a different name for the two parts of the apparently single vessel above and below the valve. But in the preliminary study of *Conchoderma auritum* I have found that the lateral vessel consists of the sheath of the attrahens muscle, or, to put it another way, the lateral vessel contains the attrahens muscle. The valve occurs just where the scutal vessel enters the muscle sheath. In this form, therefore, the two parts of the blood channel are very different in shape and constitution and naturally require separate names. It was the discovery of this valve in *Conchoderma* that made me look for such a structure in a homologous position in *Lithotrya*.

The excessively thin membrane forming the flap of the valve in *Lithotrya* slopes downwards, outwards and slightly posteriorly. In a series of thick sections transverse to the peduncle, on passing downwards towards the body, the scutal vessel appears to taper to a point, but as it does so the lateral vessel commences medially alongside it from a blind ending and enlarges to become wider than the scutal vessel above. The point to which the scutal vessel narrows is actually a minute slit and forms the entrance through the valve into the lateral vessel (figure 11).
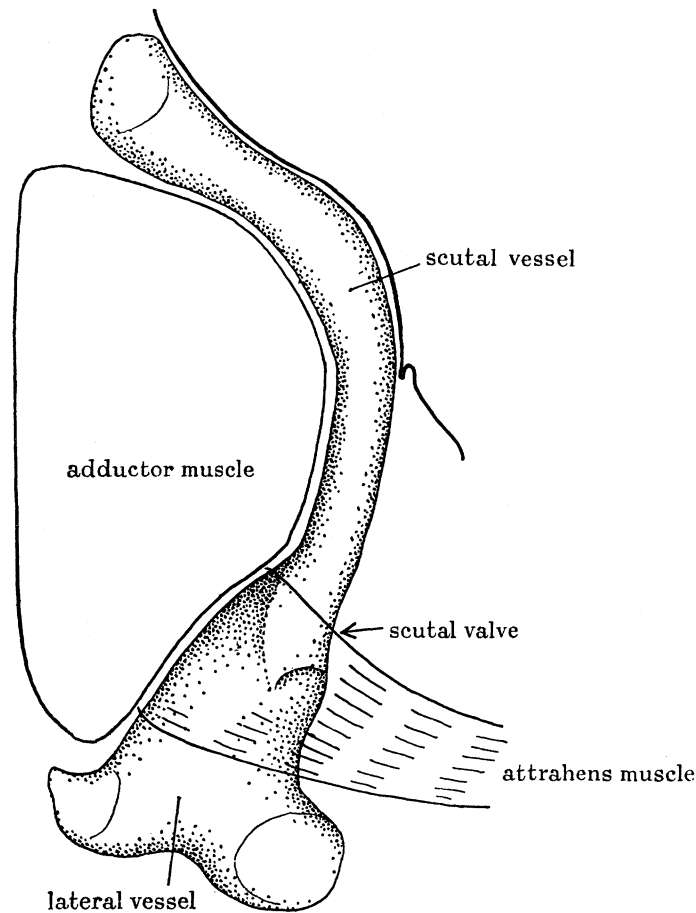

FIGURE 11. Reconstruction of scutal and lateral vessels to show position of scutal valve. × 46.

The lateral vessels now give off branches to the gastric glands and then extend backwards to enter the parenchyma which closely invests the whole of the gut beyond the oesophagus. The two vessels extend on either side of the latter to join on its hinder surface. The single median vessel so formed runs in the form of a loop along the mid-ventral line of the gut and can thus be called the subintestinal vessel.* It gives off branches throughout the whole of its length which can be traced ramifying over the surface of the gut. All these branches, like the main vessel itself, dwindle in size and finally disappear between the cells of the gut parenchyma (figure 5).

This parenchymatous tissue is very difficult to illustrate except by photograph. It

* In the specimen reconstructed in figures 4 and 5 the two lateral vessels made a subsidiary cross-connexion just below the endosternite before the main fusion lower down.

resembles the central tissue of an ordinary herbaceous stem. It is not possible to see canaliculi or even crevices between the individual polyhedral cells in the sections I have used. Embedded in it are all the numerous lobes of the testes and the massive vesiculae seminales. The terminal testis lobes appear to be surrounded by small blood sinuses which form the ends of branches from the subintestinal vessel.

The parenchyma, in addition to covering the gut with a relatively thick layer, extends on either side upwards, that is, ventrally to the ventral longitudinal muscles which it engulfs, and then to the base of the cirri, where it becomes continuous with the parenchyma of these limbs. There is formed in this way a median ventral cavity in which lies the ventral nerve cord and which therefore can be called the epineural sinus. Posteriorly this narrows down with the narrowing trunk, becoming almost fully occupied by the bundle of nerves to the cirri; anteriorly, it is blocked by a transverse wall formed by the large bladder-like ducts of the maxillary segmental excretory organs and the connective tissue filling the oral cone. The gut parenchyma merges into this oral cone tissue and also extends as far forwards as the gastric glands.

Opening into the epineural sinus there can be seen short vessels from the parenchyma mostly situated along the mid-ventral line (figure 4). These vessels sometimes branch but do not appear to taper much; rather they end in a globular cavity of the same diameter as the vessel. I have never traced a direct connexion between the terminal vessels of the subintestinal vessel and these vessels opening into the epineural sinus, but I presume that the blood percolates through the parenchyma in the same way as I suggested for the blood passing through the gut parenchyma of a cypridinid ostracod (Cannon 1931) (see later, p. 121).

Opening from the epineural space are vessels entering the cirri, which can be referred to as the afferent system (figure 5). One vessel enters each trunk limb and runs up the inner edge of the two-jointed basis of the limb. Then at the distal end of the latter, it crosses over towards the outer edge and divides into two vessels which run up the middle of each ramus close against the outside of the solitary flexor muscle (figure 8). These vessels form the only exits from the epineural space with the exception of a posterior opening which leads into a blind vessel running the length of the penis and another very small vessel which leads anteriorly into the connective tissue of the oral cone among which it breaks up and disappears.

The efferent system running from the cirri consists of a vessel running down the outer convex side of each ramus. At the distal end of the basis the two vessels unite into a single vessel on the outer side of the limb. This then enters the trunk and continues down its sides as a definite tubular vessel running through a mass of connective tissue. At the level of the ventral longitudinal muscles it gives off a branch which extends medially to ramify and disappear among the parenchyma occupying the spaces between these muscles. Only when it reaches the dorso-lateral region of the trunk does it open into a sinus which runs forward into the lower part of the prosoma. This represents the body cavity in which the dorsal longitudinal muscles lie and the sinus in fact follows the course of these muscles. The sinuses on either side do not join across underneath the dorsal side of the gut in the hinder part of the trunk, as the gut parenchyma extends medially as far as the body wall and so forms a barrier. In the prosomal region, however, the parenchyma only stretches to the mid-dorsal

body wall in separate strands or pillars and so the sinuses become confluent and form simply a dorsal blood space (figure 12).

The dorsal prosomal blood space extends upwards between the pleats and the anterior stomach wall into the median space which is the cavity of what I have called the blood pump (figure 12).

At the entrance to this space there is the median connective tissue strand which runs from a point just above the pleats upwards and backwards to attach to the wall of the stomach at its widest part (see pp. 109 and 110). Its point of origin marks the hinder, lower, median point of the entrance to the rostral valve. What the function of this strand can be I do not know, unless it is another safety valve to prevent over-distension in this region. It is this structure that Nussbaum (1890, p. 44, and plate 10, figure 8) describes as a valve between the two haemocoelic spaces that he so incorrectly calls auricle and ventricle. Even if it were part of a valve, there is nothing to show in what direction the valve would be effective.

The blood pump consists of that part of the body I have already mentioned as occurring between the anterior edge of the oral cone and the posterior surface of the adductor muscle. Its upper body wall is soft and flexible and is thrown into transverse folds. When the pump is in systole, as in figure 4, the folds are marked and deep, while in diastole the distension smooths out the surface as in figure 12. If the hinder surface—that is, the surface abutting against the front of the oral cone—is followed laterally, it is seen to curve forwards to the margin of attachment of the body to the capitular walls, and this margin closely follows the hinder surface of the scutal vessel (figure 3). The pulling inwards of this body wall, that is, the beat of the blood pump, is brought about by a series of muscles which run upwards from the lower corners of the scutal plates in the rostral region, to attach directly to it. They are symmetrically arranged on either side of the median plane, and so on either side of the actual cavity of the pump. Similar muscles have been figured for *Pollicipes* by Nussbaum. He has, however, given names to each separate muscle (1890, plate 5, figure 1), names such as *adductor capitis* and *levator capitis* which suggest that the separate muscles function in different ways. This is certainly not the case. From their common point of origin on the rigid skeletal plates and the fact that they all end on the soft flexible outer wall of the blood pump they can only function in one way, as simple compressors, pulling in this wall.

Inside the wall is a thick lining of very delicate, large-celled parenchymatous tissue which is continuous anteriorly with the parenchyma surrounding and permeating the adductor scutorum. This tissue does not fill the blood pump, but leaves a median space free and it is this space that is continuous with the dorsal prosomal blood space that I have just described. In addition, however, as can be seen from figures 4 and 12, it is continuous through the rostral valve with the peduncular vessel.

I have now described a passage for blood right round the body and it remains to discuss the mechanism by which the circulation is maintained.

8. MECHANISM OF CIRCULATION

To explain how the blood is forced around the canalicular system just described, I shall assume merely that the muscles of the blood pump contract periodically, whether regularly

FIGURE 12. Reconstruction from the sagittal plane of blood pump and rostral sinus. In this specimen the pump is in diastole. Compare figure 4 in which the pump is in systole. *br.* brain; *c.b.p.* cavity of blood pump; *c.m.* compressor muscles of blood pump; *h.p.* hydraulic parenchyma; *oes.* oesophagus; *o.m.* occlusor muscles surrounding rostral valve; *p.v.* peduncular vessel; *st.* stomach.

or not is of no consequence. This I consider a legitimate assumption, and it is supported by the two figures 4 and 12. Both show sagittal sections through the blood pump and it so happened that in one specimen (figure 4) the blood pump muscles were contracted when the animal was fixed, while in the other they were relaxed. I shall consider first the simpler case, when the animal is at rest with its body withdrawn into the mantle cavity, and the capitular plates closed.

(a) *Animal at rest.* The effect of the contraction of the blood pump muscles can only be appreciated by a proper understanding of the parenchymatous tissue immediately inside the walls. This parenchyma, which may be referred to as the hydraulic parenchyma, is full of fluid, but the fluid is locked up in the individual cells. It cannot escape and, being fluid, it is incompressible. Hence, when the walls are pulled in, the hydraulic parenchyma is pressed inwards on to whatever free fluid there is in the pump, and, to relieve the high pressure so produced, the free fluid must be forced out of the pump.

This mechanism of the blood pump I deduce entirely from anatomy. I have never observed a contraction, and I doubt whether the mechanism could be tested experimentally. Such experiments, however, were they possible, I should consider redundant. There is no more doubt about the method of action of this muscular system than there is about the action of any muscle attached to the bones of a vertebrate which may happen to be revealed in a dissection. I am emphasizing this point as the whole of my subsequent argument depends upon the acceptance of this interpretation of structure.

The free fluid in the pump consists of the blood in the median blood space and also the blood in the lateral vessels which run through the lateral margins of the pump. The latter I shall consider later (p. 120). The former has two possible channels for exit: down through the rostral valve into the long peduncular vessel, or, more posteriorly, into the dorsal prosomal space. That it does in fact take the former route is shown by the existence of the valve itself. Since the days when Harvey first demonstrated the function of valves in blood vessels, anatomists have taken the existence of a valve in a blood vessel as proof that blood moves through the valve in one direction, that direction being determined by the arrangement of the flap or flaps of the valve. The paired flaps of the rostral valve of *Lithotrya* are so arranged that the blood can pass between them down into the peduncle, but not in the reverse direction. I therefore take it from this fact alone that the blood, squeezed out of the blood pump, does pass down the peduncle.

However, from the anatomy I have described, it is clear that there is no structural hindrance to the blood passing out of the blood pump into the prosoma (figures 4 and 12, and see also later, p. 121). There is no valve such as described by Nussbaum (1890, p. 44). I must therefore demonstrate the existence of some means by which this passage of blood is prevented. I believe it is brought about by high pressure produced in the prosoma by the contraction of those muscles, some transverse and some dorso-ventral, which I have described in the prosomal and trunk regions (p. 105). I showed that these muscles formed a regulatory system controlling the internal body pressure which varies every time the limbs are cast out. We are now considering the case when the limbs are not being cast out, but this does not affect the possible activity of this group of muscles. In fact, it simplifies matters, for they will be unhindered in their activity. They will simply contract sufficiently to produce a higher pressure in the prosoma, and hence in the blood pump—

for these spaces are directly continuous—than occurs in the peduncular vessel. In this case, the valve will open and allow blood to pass through.

On the peduncular side of the valve there is morphological evidence that the pressure is always relatively low. The peduncular vessel itself is long and wide and shows no sign of narrowing throughout its length. Its total volume will be considerable, and more than that, it ultimately opens at the base of the peduncle into a voluminous network of canalicular spaces lining the inner wall of the peduncle. Now, since the single peduncular vessel is opening out into others of much greater total volume, it is clear that the blood pressure in it will tend to be low. Pressure certainly can be put up in this system by the contraction of the circular muscles of the peduncle. But the effect of such contraction must be taken up largely by the elastic inner wall of the peduncle, as I shall describe presently. It is difficult to imagine that any high pressure could be produced in this way in the peduncular vessel itself.

The peduncular network can be considered as one system covering the whole lining of the peduncle up to the carinal region and across the capitulum to the scutal vessels. Throughout its extent, the vessels intermingle with the very numerous pillars of elastic tissue (figure 10). This tissue I consider functions in preventing any stagnation of the blood in its passage through the peduncle. Blood is continually arriving from the body down the peduncular vessel, and this enters the network at the lower end of the peduncle. Blood will thus accumulate, and as it does so it will distend the blood vessels. It will push inwards the soft, flexible, inner lining of the peduncular wall. But this inner wall is held by the elastic tissue, and hence when a certain state of distension is reached, the elastic tissue will react and pull on this lining. This, in turn, will press on the blood vessels and so tend to move on the contained blood. The peduncular elastic tissue system of *Lithotrya* can thus be looked upon as a diffuse accessory circulatory mechanism.

While this elastic tissue is of such importance in *Lithotrya*, another means of preventing the stagnation of blood at the base of the peduncle must obtain in a form such as *Lepas*. Here, where the stalk may be more than a foot in length, the peduncular vessel runs the whole length without diminishing in diameter. Hence it is probable that in this form also it does not give off any branches until the attachment of the peduncle is reached. The peduncle, however, is solid and not a hollow cylinder, as in *Lithotrya*. Probably in *Lepas* the powerful circulatory muscle system, certainly in the lower parts of the peduncle, is used largely to force the blood through the mass of connective tissue which forms the central core of the peduncle up again towards the capitulum.

The blood in *Lithotrya* has only one exit from the peduncular network and that is via the paired scutal valves into the lateral vessels. Blood will probably pass through these valves at a steady pressure. The varying pressures which must occur in the peduncular vessel as the blood pump contracts will be damped down, probably completely, by the time the blood has passed through the peduncular network, and the whole pressure will be maintained by the stretched elastic fibres of the peduncular wall.

The lateral vessels, at their commencement, run along the lateral wall of the blood pump (see p. 119). More exactly, they can be considered as lying just inside the lateral margin of the pump, embedded in the hydraulic parenchyma. Obviously, then, when the blood pump muscles contract, the blood in the lateral vessels will be forced out in the same way

as the centrally placed blood space is emptied. This blood cannot pass upwards owing to the disposition of the scutal valves. It must, therefore, be forced downwards into the sub-intestinal vessel and so into the gut parenchyma. This means that the blood does not percolate into the gut parenchyma at a steady pressure, but that it is forcibly injected into the tissue by the blood pump. The pressure at which this takes place must be considerable, for from transverse sections it looks as though the lateral vessels would be completely occluded every time the blood pump contracted.

This second effect of the blood pump is important because of the condition I have described for *Conchoderma auritum*. Here the lateral vessel immediately below the scutal valve forms the sheath of the attrahens muscle. Hence, by contracting this muscle, blood will be injected into the gut parenchyma with very considerable force indeed.

That the blood forced into the blood parenchyma does in fact pass right through it, I take to be established on morphological evidence alone. The existence of the scutal valve and the arrangements of its flap, show conclusively that blood must pass into the lateral vessel. If blood passes into a vessel, except in the case of erectile tissue (see later, p. 125), it is obvious that it must also have a way out. Now, since the lateral vessel divides up and appears to end blindly among the gut parenchyma cells it follows that this parenchyma must be in fact permeable to the blood.

How the blood actually passes through the parenchyma it is impossible to say. One thing that is certain is that there is no capillary system joining the ends of the branches of the subintestinal vessel with the small vessels that open into the epineural sinus (see p. 116). As I have just stated, the ventral gut vessel simply ends among the parenchyma cells, and the openings from the parenchyma commence among these same cells. What happens in between can only be deduced morphologically. If material were more abundant it might be possible to inject from the lateral or scutal vessel and force an injection mass through to the epineural sinus. I can only say from the appearance of sections of this tissue —both thin sections and thick slices—that it looks as though the blood oozes through the interstitial crevices between adjacent cells.

The steady stream of blood passing through the epineural space will pass into the cirri and then back again into the dorsal trunk region by the route I have already described, and so back to the blood pump. I do not think there is anything of particular interest to note as long as the animal remains at rest within the capitulum.

(*b*) *Animal actively 'casting'*. When the animal commences its casting movement the first thing that must happen is the opening of the mantle. The effect of this on the blood vessels of the capitulum it will be convenient to deal with later (p. 123). It is the effect on the circulation in the body and blood pump that I am now going to describe. For this purpose I assume therefore that the mantle valves are open or are in the process of opening. The first activity in the body will be the contraction of the dorsal longitudinal series of muscles. According to my explanation this contraction will continue so long as the body is being swung out of the mantle cavity. However, right at the very beginning of this movement, directly the muscles commence to contract, blood will be forced out of the prosoma. Some will pass into the trunk, but some also will pass into the blood pump cavity. Therefore we can deduce that at the commencement of casting, the blood pump will be distended with blood.

On the other hand, the main swinging out of the body is the work of the attrahens muscle, and one of the first effects of the contraction of this muscle will be to pull the oral cone forwards and press it on to the adductor scutorum. Not only will it bring the cone up against this muscle, but will press it into the latter (figure 7). In fact, from the arrangement and size of the various parts of the body I do not think it possible for the body to be extruded without this taking place. The adductor scutorum during this phase will be relaxed and therefore soft, and so will offer little resistance to such a process. Now, the main result of this will be that as long as the body is being thrown out, the region between the oral cone and the adductor muscle will be squeezed out of existence, and in this region is the blood pump. Thus, one piece of morphological evidence—the arrangement of the dorsal longitudinal muscles—suggests that the blood pump will be filled, while another, the disposition of the attrahens muscle, indicates that it will be emptied at the beginning of the casting movement. What actually happens can, I think, be deduced from the fact that in a barnacle, when casting commences, it is not the body that is extruded first of all, but the cirri. Now the cirri are extruded by being distended, and this distension is an erection brought about by the contraction of the dorsal longitudinal series. We can conclude, therefore, that at the commencement of each cast of the body the dorsal muscles contract first and so distend, not only the cirri, but the blood pump. Only later does the attrahens muscle contract, and, since the contraction of the attrahens muscles tends to bring about the emptying of the blood pump, I think it legitimate to deduce that the blood pump muscles will contract at the same time as the attrahens.

I have previously mentioned (p. 119) that there is nothing structural that can be interpreted as a valve between the prosoma and the rostral sinus and hence blood pump. In figure 13 I have drawn a reconstruction of this region. It represents a slice through *Lithotrya* approximately transverse to the peduncle at the level of the entrance to the peduncular vessel. From this figure it will be seen that the median strand connecting the stomach with the pleats, towards the lower part of the slice, spreads out laterally into two parenchymatous sheets. These curve backwards, run alongside, and merge into some of the lower anterior longitudinal muscles. Towards the upper part of the slice it similarly spreads out into quite independent sheets which, however, curve forwards and merge into anterior longitudinal muscles higher up in the series. Now it is possible that when the dorsal longitudinal muscles are in contraction this brings together these sheets and that in this way they form a barrier cutting off the rostral sinus above from the prosomal space below. If so, then when the animal is actively casting, a valve would occur diverting the blood from the blood pump into the peduncular vessel. I merely describe this as something which looks possible from the structure, and even probable, but I have no direct evidence for it. If a specimen were obtained which had been fixed instantaneously with the body cast out of the mantle, then the arrangement of the parenchymatous sheets would show whether they did in fact close the opening into the prosoma and act as a barrier. Unfortunately however, in all well-fixed specimens the body is withdrawn into the mantle.

The histological constitution of these sheets is interesting. They are undoubtedly parenchymatous, arising in continuity with the main gut parenchyma and the parenchyma running along the dorsal muscles. But the cells are so stretched out that the sheets look at first sight to be of a typical squamous epithelial constitution.

The passage of blood down the peduncular vessel and through the peduncular network will not differ when the animal is casting from when it is at rest. When it returns to the capitular plexus then I think there is a difference. In all barnacles other than *Lithotrya* I pointed out (p. 91) that the valves of the mantle must be opened solely as a result of the contraction of the peduncular muscles—more particularly of the circular muscles—this producing an erection of the capitulum by distending its blood vessels. In *Lithotrya*, in addition, a special muscle (Darwin's muscle) which is probably a specialized part of
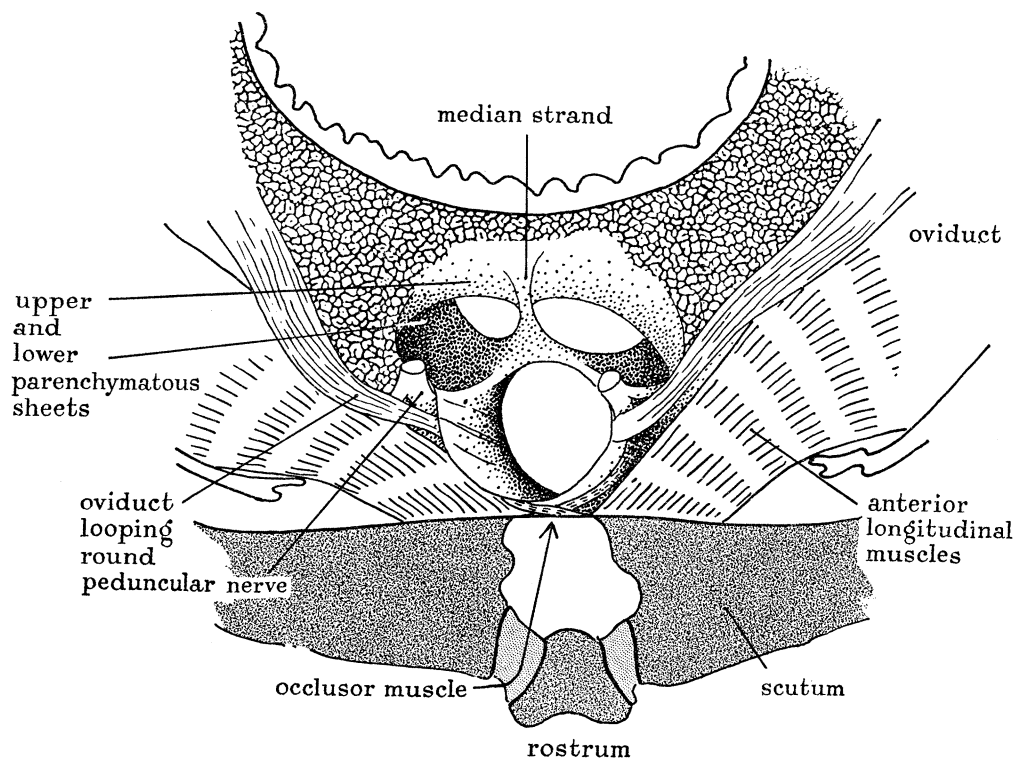

FIGURE 13. Reconstruction from a series transverse to the rostral sinus to show the connexion of cavity of blood pump with (*a*) the dorsal blood space of the prosoma (above and divided by median strand) and (*b*) the rostral sinus (below). The slice is being viewed from the cavity of the blood pump. The cut surface of the gut parenchyma is represented by a fine network.

the circular muscles, assists by directly pulling apart the tergal plates. From this we can assume that at each opening of the mantle the mantle vessels which include the scutal vessels will be distended with blood. Now if the scutal vessels are being blown out with blood, naturally blood will escape from them as fast as possible through the scutal valves into the lateral vessels. I showed previously (p. 120) that since the lateral vessels run through the sides of the blood pump it follows that they will be forcibly emptied at each contraction of the pump. It now follows that at each cast of the body, not merely will the lateral vessels be emptied, but that they will be distended with blood just before the blood pump contracts, and forces their contents into the gut parenchyma.

During rhythmical casting activity, therefore, blood will arrive periodically through the gut parenchyma into the epineural sinus in relatively large amounts, and from here will pass into the cirri.

The cirri themselves, I think, form an accessory circulating mechanism as long as they are being periodically cast out. I have already explained (p. 105) how it is that these appendages are extruded by blood forced into them and that this blood comes from the epineural sinus. In figure 8 I have drawn a reconstruction of the last cirrus in a fully retracted position and it is possible by measuring and comparing the inner and outer edges of this profile to obtain some idea of the increase of volume of the cirrus when it is straightened out. The outer margin remains the same length whether the limb is extended or retracted. The inner margin becomes equal in length to the outer only when the limb is fully extended. In the specimen I have figured the inner margin is just about one-fifth shorter than the outer. This means that the volume of the cirrus will increase by one-tenth when it is extended.

Now on extension or contraction of the limb it will, of course, be the contained blood which will be increased or diminished, for the volume of the muscle and the parenchyma will remain the same whether it is contracted or relaxed. Thus considering one of the rami of the limb and omitting for the sake of simplicity the basis of the limb, it will be seen from the transverse sections that the blood vessels form just about one-third or say three-tenths of the appendage. Thus blood to the extent of one-tenth of the whole volume of the limb has to pass into blood vessels occupying three-tenths of the limb, and so at each cast one-third of its contained blood must pass into and out of the limb.

Each multi-articulate ramus can thus be looked upon as a pump, sucking in blood on extension and forcing it out on being withdrawn. Considering that there are twenty-four of these rami on the six pairs of cirri they must collectively form an efficient pumping system. I have, however, merely shown that they act as pumps sucking blood in and forcing it out. They will only be effective in the circulation if there is a means of ensuring a one-way passage of blood through their vessels. I have not found any actual valves in the limbs of the nature of the scutal or rostral valves, but I do not think this is necessary. On the one side of the limbs is the epineural sinus constantly fed from the gut parenchyma, with blood which can only escape up the afferent vessels of the cirri. On the other are the lateral blood spaces which are constantly being emptied into the dorsal blood space and so to the blood pump. Clearly then there must be high pressure on the afferent side and low pressure on the efferent, and this in itself is sufficient to ensure a passage in one direction through the cirri. However, even if the pressure on both sides of the cirrus were the same, there is, I think, in the basis of the limb, a beautiful adaptation which, though not structurally a valve of the usual type, must in fact act as one when the limbs are being cast. In transverse sections (figure 8) it will be seen that the afferent vessel occupies the whole of a cavity of a ridge on the inner edge of the basal joint, and is separated from the muscle and the parenchyma by a very definite wall of connective tissue. On the other hand, the efferent vessel is embedded in a mass of parenchyma. Now on full extension of the limb, both vessels will be full of blood. On contraction of the limb, the muscle throughout its length will shorten and hence become broader. In the joints of the basis this broadening of the muscle will press laterally and tend to compress the blood vessels. But the afferent vessel is protected by its screen of connective tissue and so the whole of the pressure will be concentrated through the hydraulic parenchyma on to the efferent vessel. Now the contained blood has two ways out, either by the cirrus or into the body. Passing up the

cirrus would be passing into a much smaller vessel, while into the body means opening into a large space. Clearly then, on the coiling up of the limb, the blood will pass into the dorso-lateral body space and the efferent vessel itself become either occluded or at least very much diminished. Therefore, at the commencement of the extension of the limb, the connection between the epineural space and the limb will be fully open, while that between the limb and the lateral body space will be closed. Thus, even supposing that the pressure were the same on both sides of the limb, the blood would be forced into the afferent side rather than the efferent side on extension.

9. The occlusor muscles

It now only remains to discuss the function of the peculiar muscles that I have termed the occlusor muscles (p. 112). Obviously by their contraction these muscles can control the size of the entrance to the peduncular vessel, and hence the rate of flow of blood into this vessel. It is quite likely that they function in this way normally. Unless, however, they close the vessel completely, their effect is only temporary. As long as they are open, then whether the animal is casting or not, any high pressure in the body will simply force blood out through the rostral valve and blood will continue to pass out until the pressure in the body has fallen to the same level as that in the peduncular vessel. This is no hindrance in the ordinary casting activity of the body, for the body is normally held out of the shell for a short time only. It is possible, however, for a barnacle, certainly *Lepas*, occasionally to hold its cirri extended out of the body for a considerable time without moving. This is especially the case in moribund specimens. Further, in *Pollicipes spinosus* (Quoy & Gaimard), according to Miss Batham (1945, p. 361), the normal habit of the animal is not the typical rhythmical casting action that one associates with a barnacle, but a deliberate out-thrusting of the cirri which may remain continuously expanded for some considerable time. Moreover, in the ordinary life of the animal, during copulation, all barnacles must remain partially extruded for a considerable time. During this process the individual acting as a male extrudes the very large penis for a considerable distance and inserts it into the mantle cavity of the female. Now the penis, like the cirri, has only a retractor muscle. It can therefore be extended only by erection. Unlike the cirri, however, it has only one blood vessel. Blood forced into the penis from the epineural sinus can thus only escape by being withdrawn again through the same passage. I deduce, therefore, that during copulation, the occlusor muscles must first be contracted. This closes the only exit from the body, but still allows the passage of blood from the capitulum into the body through the scutal valves. Contraction of any of the body muscles which I have described as putting up the blood pressure will now tend to erect both the cirri and the penis. The cirri may be retained within the mantle by the contraction of their muscles. Whether this happens or not, if the muscle of the penis relaxes the latter will be erected and so can pass out of the valves. The degree of erection can now be increased by further blood being pumped into the body through the scutal valves. The erection will remain so long as the occlusor muscles are contracted. In fact, there is no other way for the penis to be withdrawn into the valves than the opening again of the occlusor muscles, for there is no other escape route for blood from the body once it has passed in through the scutal valves.

In all fixed specimens the penis lies along the mid-ventral line between the bases of the cirri. It follows from what I have suggested above that, during the normal rhythmical casting activity, the muscle of the penis must always be contracted to prevent its erection along with the cirri.

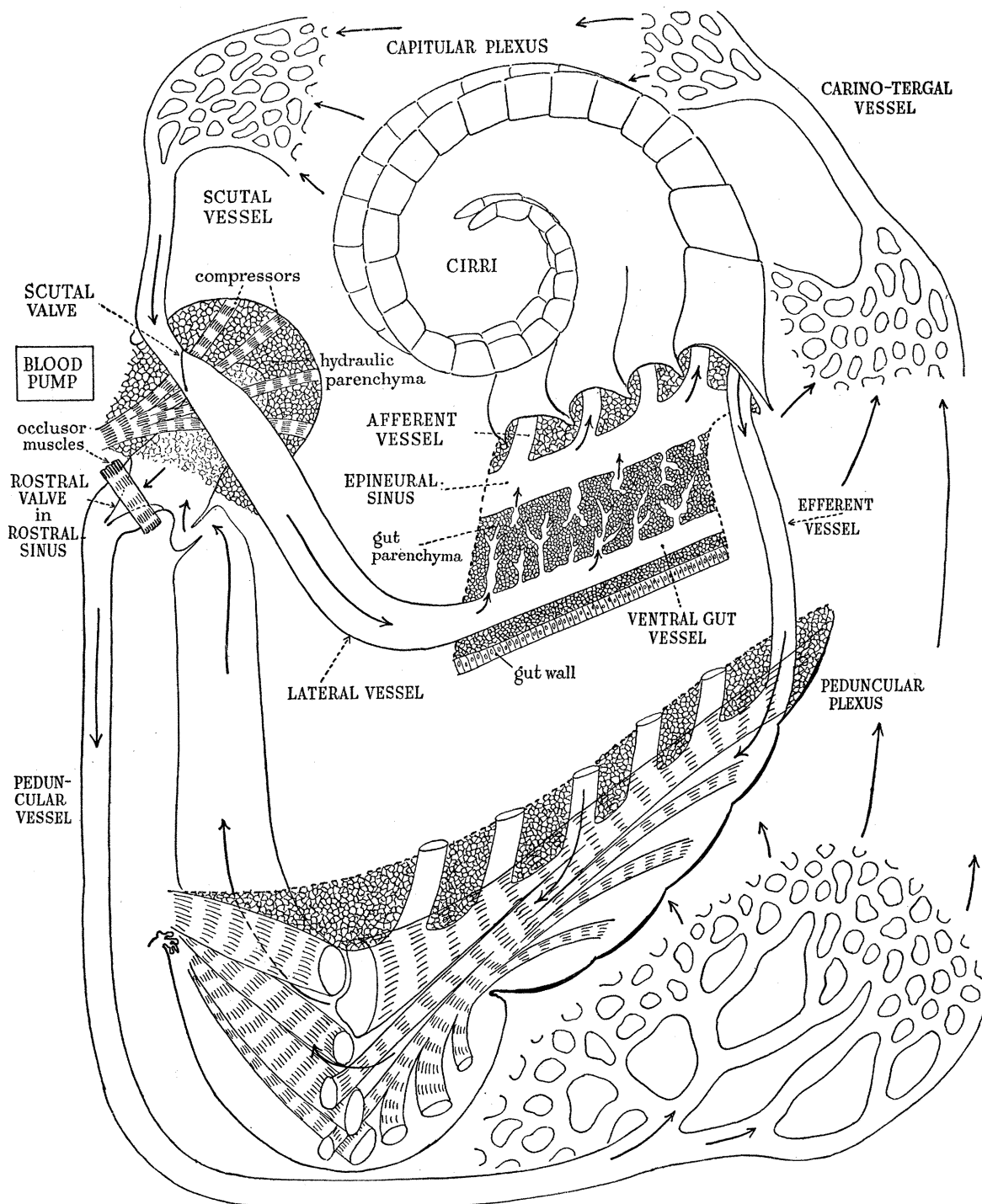A plan of the complete circulatory system is shown in figure 14.

FIGURE 14. Diagram summarizing the blood circulation of *Lithotrya.*

10. Nervous system

Little satisfactory work has been done on the nervous system of barnacles, especially as regards the pedunculate forms. Darwin gives only a meagre and semi-diagrammatic figure of the nervous system of *Lepas fascicularis* Ellis & Solander. The best account occurs in an obscure paper by Brandt (1871). He describes and figures the nervous system of *Lepas anatifera* L. Unfortunately, in the early part of this paper there occurs the statement that the whole of the nervous system occurs *underneath* the digestive system, and for this reason the paper has been lightly treated by subsequent workers such as Nussbaum, or practically ignored as by Gruvel. The actual words used are 'Das Gehirn, welches am Ende des ersten Körperdrittels gelegen ist, befindet sich ebenso wie die Ganglien der Bauchkette unter den Verdauungsorganen,...' (1871, p. 333). Later, however, in the same paragraph, referring to the commissures between brain and sub-oesophageal ganglion, he states that they encircle the oesophagus: 'Diese beiden eben genannten Commissuren umfassen ringförmig den *oesophagus* und entsprechen also vollkommen dem Schlundringe der übrigen Arthropoden' (p. 334). It is clear, therefore, that when he states that the nervous system is underneath the gut, he refers to a relatively unimportant topographical position rather than a morphological relationship.

In addition to Brandt's work, there is a general account given by Gruvel (1905, p. 402). This is not of much value as it commences with the form *Alcippe*, described even by Gruvel as one of the most degraded types, and then after dealing cursorily with the operculate barnacles, deals briefly with the pedunculate forms. It adds little, if anything, to Brandt's description.

Lastly, Sewell (1926, p. 321) has described the nervous system of *Lithotrya nicobarica* Reinhardt, and it is with this work, together with that of Brandt, that I have mainly dealt.

All previous work has been based on actual dissections. The following account is entirely the result of reconstructions from thick sections.

The number of distinct ganglia in the ventral chain is dealt with by Sewell, who states (p. 324) that 'the arrangement of the various ganglia...seems to provide a diagnostic feature between the various genera of the Family Lepadidae'. I do not think, however, that this is so. In the specimen figured in figures 4 and 5, there are quite definitely only four post-oesophageal ganglia, a condition said by Darwin (1851, p. 46) and recently by Batham (1945, p. 371) to exist in *Pollicipes*. On the other hand, the specimen on which figure 12 was based shows that the last ganglion is double; that is, it shows the condition described by Koehler (1889, p. 202) for the same genus. In the latter specimen, the sections are deeply stained with Mallory, and a very conspicuous sheet of connective tissue staining an intense blue is seen to cover the whole pale purplish ventral chain. This penetrates the chain at three places as a tubular sheath (figures 4 and 15), indicating the divisions between the first four ganglia. In addition, however, a solid band of connective tissue runs through the last ganglionic mass, indicating its double nature. Just as clearly as this is shown in this specimen, so in the other specimen (figures 4 and 5) there is no such band of tissue, and hence no such indication of a double constitution.

Across the top of the openings indicating the division between the ganglia, there run small median connective nerves (figures 4 and 15). These have been figured for *Lepas* by Gruvel (1905, p. 408, figure 399), but he does not mention Brandt's earlier account where each connective is referred to as the 'nervus sympathicus' (1871, p. 335, figure 1, Taf. xv).

From the sections it is clear that there are six paired nerves running to the cirri together with a seventh which goes to the penis and the caudal appendages, as will be seen from figure 15. While the first three pairs appear to arise from distinct ganglia the last four pairs emerge from the last ganglionic mass, a state of affairs described by Nussbaum (1890, p. 38) for *Pollicipes*.

From the ventral surface of the sub-oesophageal ganglion there arises a group of four paired nerves. The last three pairs serve the mouth parts, the mandibles, maxillules, and maxillae (figures 14 and 15). The first pair represents the visceral system. Sewell states (1926, p. 323) that there are three pairs of nerves instead of four, and that they arise from the dorsal surface. His figure (text-figure 18), however, shows them on the ventral surface.

The visceral system shows the same plan as that of an ostracod such as I described in *Doloria* and *Gigantocypris* (1931, 1940). The visceral nerves run forwards around the oeso-phagus to form a labral loop, at the anterior middle point of which is a small ganglionic swelling containing two or three neurones. From this labral ganglion a nerve passes dorsally down the oesophagus to the region of the supra-oesophageal ganglia or brain. Here it sends a connective forwards which joins the nervous system between the two halves of the brain and then continues down the oesophagus towards the stomach. Throughout the length of this labral connective, together with the labral loop itself, branches are given off which pass in between the circular muscles of the oesophagus and terminate on these same muscles (figure 16).

A slight difference from the ostracod plan is that the visceral nerves are joined behind the oesophagus as well as in front. This posterior connexion bears a small ganglion, the posterior oesophageal ganglion of one or two neurones, at its middle point (figure 15). Also paired nerves run from the labral loop down the postero-lateral sides of the oesophagus and may be cross-connected. They can be seen very clearly to enervate the dilator muscles of the oesophagus. I did not figure such a compact nerve in *Gigantocypris*, but there is in this form a plexus of nerve cells at the hinder surface of the oesophagus which I illustrated by photograph (1940, plate 41, figure 4). These also run to the dilator musculature.

From the most anterior part of the nerve ring, that is, between the right and left supra-oesophageal ganglia, and just dorsal to the point where the labral connective makes its junction, there arise three nerves—one median and two lateral (figures 15 and 16). The latter are stouter than the middle nerve and run directly forwards to end in an ovoid ganglion, referred to by Sewell (1926, p. 323) as the optic ganglion. Sewell states that he was unable to trace the nerves forward from the ganglia to the eye, which according to Gruvel (1905, p. 408) is a single mass, presumably median. I agree with Sewell. There is no trace of a median pigmented eye, and the nerves appear to end at the ganglia. Each so-called ganglion contains two large conspicuous cells, a fact which although he does not mention it, it is clear from his text-figure 18 that Sewell also observed.

The small median nerve runs forward on a sheet of tissue but in a tortuous manner, and not straight forward as do the lateral nerves. In its twistings it gives off various branches, until at the edge of the sheet there occurs a distinct, but small, ovoid structure also con-taining two relatively large cells. This does not appear to represent the end of the nerve as it continues its ramifications after the swelling has been reached (figure 15).

I suggest that of these three nerves the two lateral represent the lateral constituent of the tripartite nauplius eye. The median represents the median constituent, together with the frontal nerve, such as occurs in ostracods.
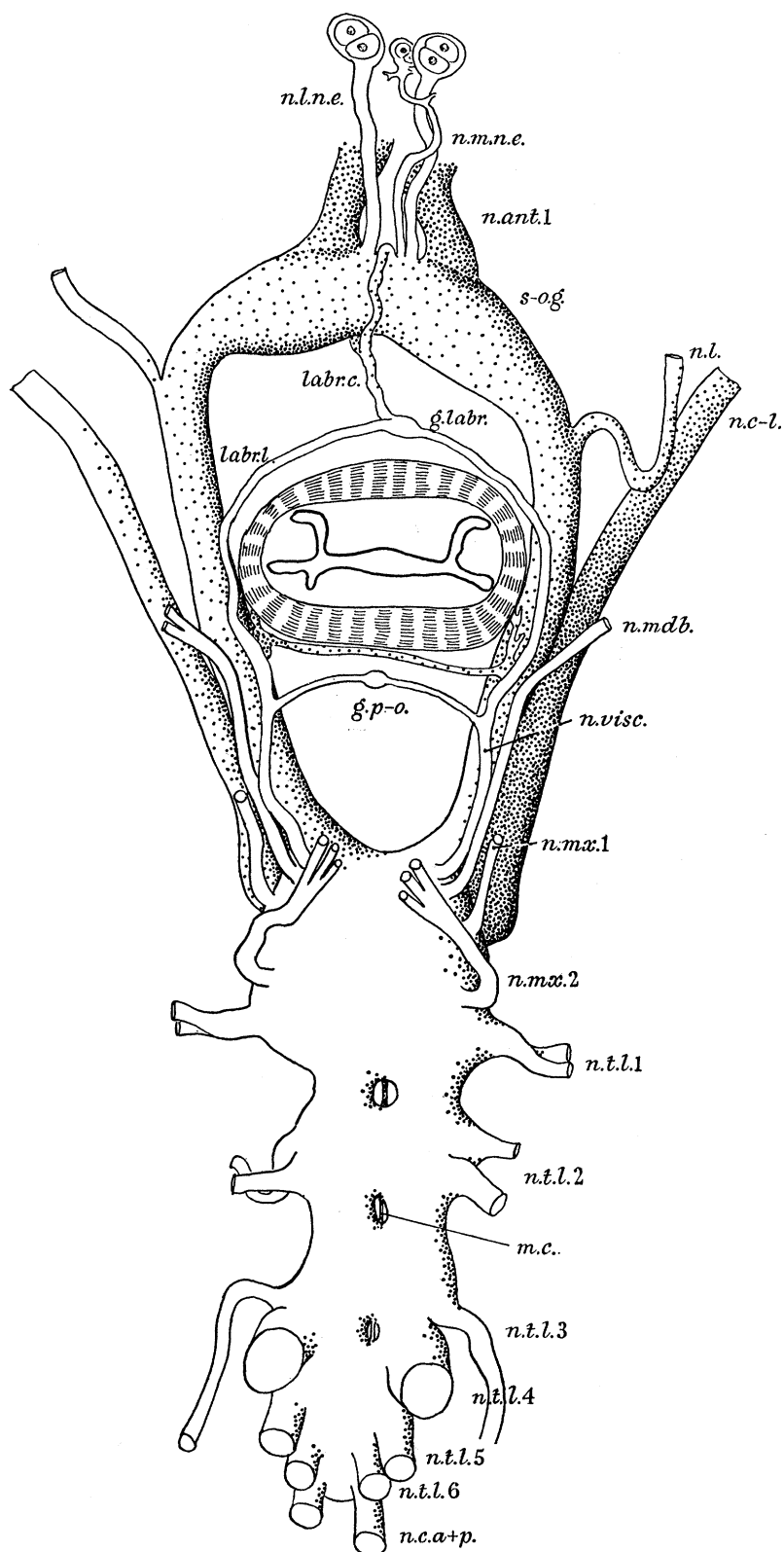
FIGURE 15. Reconstruction of nervous system seen from the ventral side. *g.labr.* labral ganglion; *g.p.-o.* post-oesophageal ganglion; *labr.c.* labral connective; *labr.l.* labral loop; *m.c.* median connective; *n.ant.* 1, antennulary nerve; *n.c.a.* + *p.* nerve to caudal appendage and penis; *n.c.-l.* corono-lateral nerve; *n.l.* lateral nerve; *n.l.n.e.* nerve to lateral constituent of nauplius eye; *n.m.n.e.* nerve to median constituent of nauplius eye; *n.mdb.* mandibular nerve; *n.mx.*1, maxillulary nerve; *n.mx.*2, maxillary nerve; *n.t.l.*1–6, nerves to cirri 1–6; *n.visc.* visceral nerves; *s.-o.g.* supra-oesophageal ganglion.
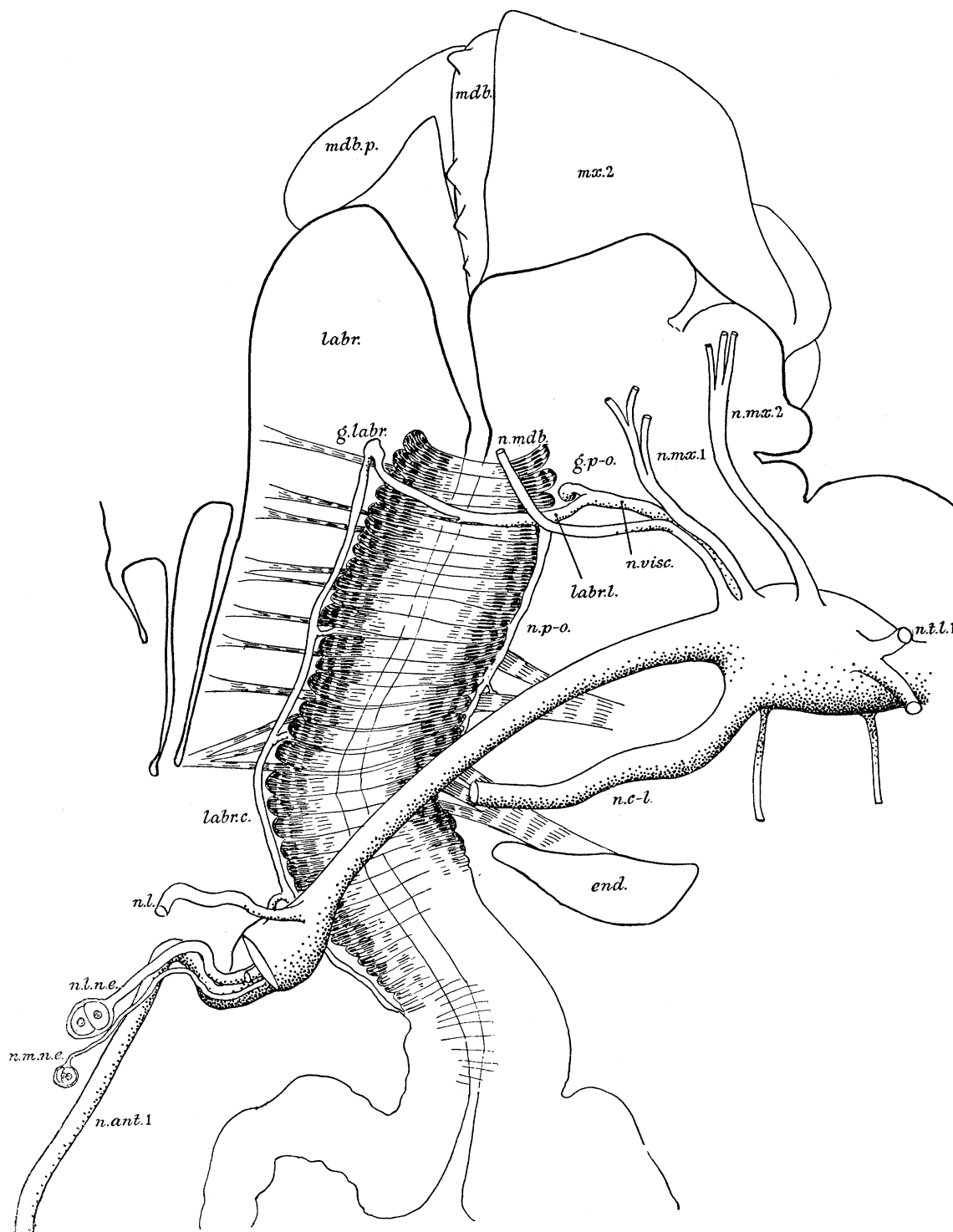
FIGURE 16. Reconstruction of anterior part of nervous system from the side to show the visceral system. *end.* endosternite; *g.labr.* labral ganglion; *g.p.-o.* post-oesophageal ganglion; *labr.* labrum; *labr.c.* labral connective; *labr.l.* labral loop; *mdb.* mandible; *mdb.p.* mandibular palp; *mx.*2. maxilla; *n.ant.*1, antennulary nerve; *n.c.-l.* corono-lateral nerve; *n.l.* lateral nerve; *n.l.n.e.* nerve to lateral constituent of nauplius eye; *n.m.n.e.* nerve to median constituent of nauplius eye; *n.mdb.* mandibular nerve; *n.mx.*1, maxillulary nerve; *n.mx.*2, maxillary nerve; *n.p.-o.* post-oesophageal nerve; *n.t.l.*1, nerve to 1st cirrus; *n.visc.* visceral nerve.

A short distance behind the brain, on either side, a nerve arises from the circumoesophageal commissure. It is figured by Brandt (1871, Taf. xv, figures 1, 2) and labelled without a name as running to the wall of the capitulum. It runs forwards and has been termed the 'lateral nerve' by Sewell (1926, p. 323). From the dorso-lateral surface of the sub-oesophageal ganglia, there arise the large paired nerves which have been termed by Sewell, Brandt, and others, the 'adductor nerves'. On dissecting out the nervous system it is understandable that these nerves have been so named, because they run forwards directly to the adductor muscle. My sections, however, have shown that, just before reaching the muscle, the nerve turns abruptly and runs up alongside its hinder margin, and then turns again, this time carinal-wards, to spread round the capitulum. Only a minute branch, excessively difficult to see, connects with the adductor muscle. The name I am proposing for the nerve is the 'corono-lateral', for it divides into the main branch I have just described, extending round the base of the capitulum like a crown, and a lateral branch which runs down closely parallel to the lateral nerve (figure 17).

The antennular nerves (= peduncular nerves of Brandt and Sewell) arise from the brain on either side of the nerves to the lateral constituents of the nauplius eye and run directly downwards to the rostral sinus, where they pass immediately inside the occlusor muscles (figure 9). Just before reaching this structure they each give off a lateral branch which, looping under the oviduct, is joined by the lateral nerve and the lateral branch of the corono-lateral.* The combined nerve then extends upwards to the surface of the peduncle on either side of the rostrum and spreads around the middle and upper regions of the peduncle (figure 17). I have named it the 'upper peduncular nerve'.

The antennular nerves, after giving off the lateral branch, are in close contact with the oviducts and extend with these structures through the occlusor muscle ring (figures 13 and 17). The nerves soon leave the oviduct (figure 9) and spread laterally to supply the lower parts of the peduncle. I have therefore called this nerve the 'lower peduncular nerve'.

One of the most interesting points about this nervous system is the absence of a nerve of any size to the adductor muscle—a muscle far and away the largest in the body. I have had to exaggerate the size of the nerve supply in figure 17. The nerve is, in fact, no larger than one of the minute nerves which can be traced from the visceral system to the small dilator muscles of the oesophagus. It consists of only two or three fibres at the most. It clearly cannot be a normal motor supply. A motor nerve such as those that supply the solitary muscle of the cirri (figures 5 and 17) or the nerves which run to the large swimming muscles of a cypridinid ostracod (Cannon, 1931) are large and massive structures. It would look, therefore, as though the adductor muscle in *Lithotrya* is without a motor nerve control, that is, it is an independent effector system.

The hypothesis that I am putting forward is that the adductor muscle is stimulated to contract by being stretched. This is brought about according to my explanation by the contraction of all the peduncular musculature. This forces apart the scuta and so stretches the muscle joining them. When the muscle is stretched beyond a certain point it tends to contract and does so in the ordinary rhythmical casting out of the cirri on the relaxation of the peduncular muscles.

* The junction between these two nerves is shown by Batham in her lateral reconstruction of *Pollicipes* (1945, plate 51, figure 10). She, however, does not figure any nerves spreading round the capitulum and also like other authors she figures what I have called the corono-lateral nerve as entering the adductor muscle.

At the same time, however, as the peduncular muscles contract, I have maintained that Darwin's muscle also contracts (see p. 123), and actively pulls apart the terga. In agreement with this view is the fact that the coronal nerve can be traced with complete certainty to terminate on Darwin's muscle.
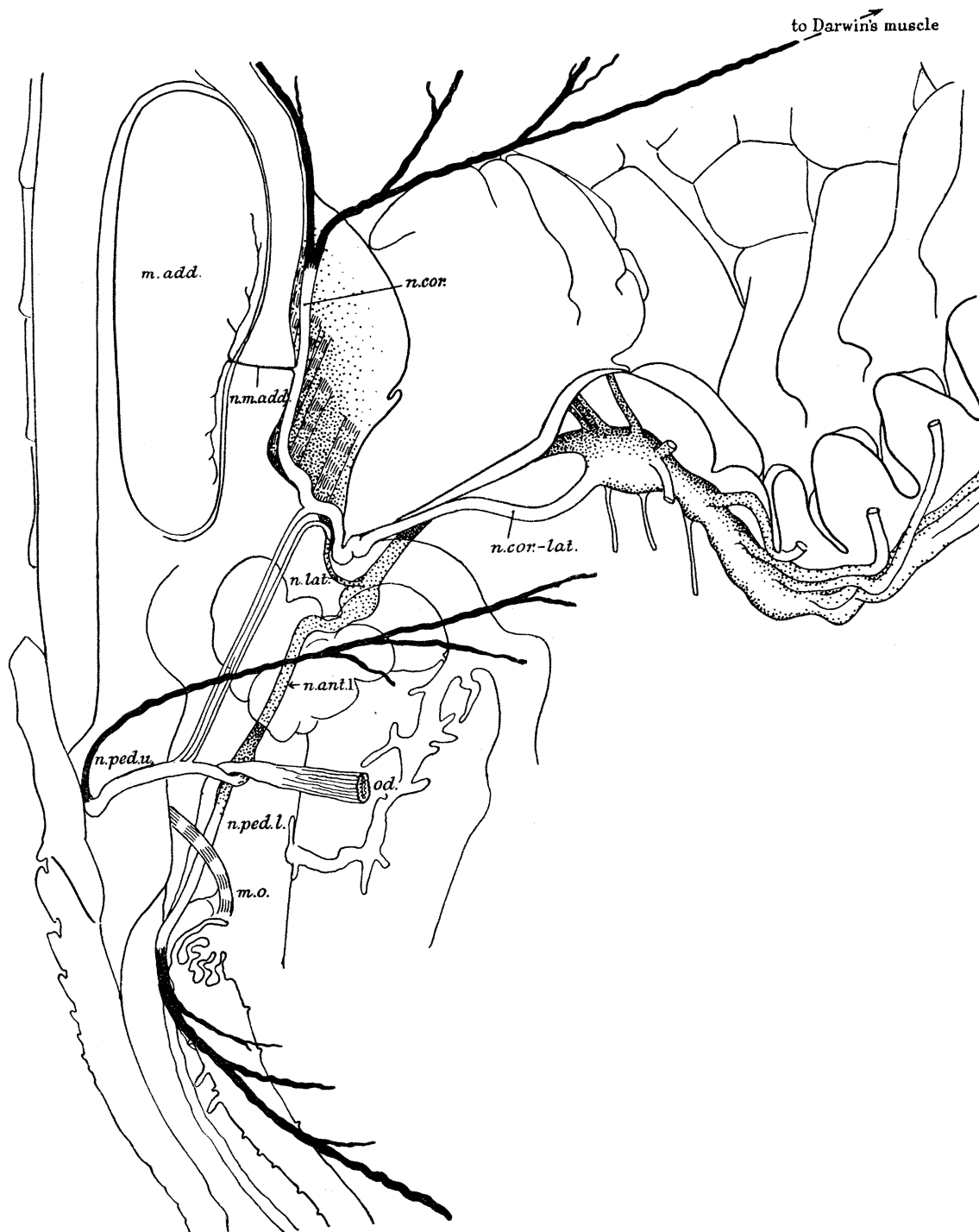

FIGURE 17. Reconstruction of the same specimen as shown in figures 4, 5, and 6, to show the nerve supply to the peduncular wall and to Darwin's muscle and the absence of any major nerve to the adductor muscle. *m.add.* adductor muscle; *m.o.* occlusor muscle; *n.ant.*1, antennulary nerve; *n.cor.* coronal nerve; *n.cor.-lat.* corono-lateral nerve; *n.lat.* lateral nerve; *n.m.add.* nerve strand to adductor muscle; *n.ped.l.* lower peduncular nerve; *n.ped.u.* upper peduncular nerve; *od.* oviduct.

11. Summary

In the following summary it is assumed that the orientation of the animal is such that the ventral side is uppermost and the anterior end of the animal to the left (figure 3).

The right and left series of calcareous plates supporting the mantle can be moved apart from each other, thus opening up the mantle cavity and allowing the extrusion of the main body, by a small muscle which runs across from the lower edge of one tergum to a corresponding point on the other, and which according to Darwin is peculiar to the genus *Lithotrya* (figures 1 to 3).

This action is made possible (1) by the very thick chitin layer of the outer covering of the upper limit of the peduncle which extends inwards between the terga and forms a fulcrum about which they can oscillate (figures 2 and 3), together with (2) the interlocking of the terga with the scuta (figure 1).

In addition, the opening of the entrance to the mantle is brought about by a hydrostatic mechanism in which blood is forced from the peduncular into the capitular region, thus erecting the walls of the mantle cavity. This results from the contraction of the circular, longitudinal and oblique muscles of the peduncle (figure 10).

The lining of the mantle cavity projects forwards as a folded membrane, the velum, extending from one tergum to the other. By the rhythmical unfolding and folding of this sheet during the 'casting' action of the trunk limbs, the suction of water into the mantle cavity must be increased so that the velum forms an accessory feeding mechanism (figures 1 and 3).

The two scuta are joined by a powerful adductor muscle (figures 1, 3, 4, 5, 7, 11 and 12).

The hinder margins of the adductor muscle mark the line of reflection of the body wall to form the inner lining of the mantle cavity (figure 3).

Underneath the adductor muscle where the body wall is reflected into the lining of the peduncle, it is thrown into a series of folds—the pleats—which are unfolded each time the body is cast out of the shell (figures 3, 4, 5, 6 and 7).

The body behind the adductor muscle consists of two functionally distinct parts, the anterior prosoma and the posterior trunk. Darwin used the term prosoma to include the adductor muscle and referred to the trunk as the thorax (figure 3).

The mouth parts articulate upon the oral cone, a rigid helmet-shaped structure which floats on the upper surface of the prosoma and is not connected by any articulating system with the remaining skeleton of the body (figures 5 and 7).

The body wall of the prosoma is entirely thin and flexible, containing no sclerites (figures 3 and 7).

The body wall of the trunk consists of a system of segmental articulating sclerite rings. The articulations, however, are not, as is usual, paired hinges along the side of the body between the terga and sterna, but are single hinges along the mid-dorsal line. Thus, the terga of the trunk articulate directly with each other. The sterna, on the other hand, are separated by extensive arthrodial membranes and are in consequence merely narrow chitinous struts across the ventral body wall between the cirri (figures 7a and b).

As a consequence of the isolation of the trunk skeleton from the adductor muscle, and the capitular skeleton to which the latter is attached, it follows that the movement of the body

cannot be actuated by the ordinary muscle-skeleton mechanism of an arthropod. It is controlled, according to the hypothesis put forward here, by a hydrostatic mechanism, in which the various parts of the body are moved by being distended with blood. The varying degree of turgidity necessary to bring about these movements of body fluid are brought about largely by the activities of the dorsal longitudinal series of muscles.

The dorsal longitudinal muscle consists of two distinct groups: an anterior group running backwards from the lowermost angles of the scuta and a posterior group running forwards from the terga of the trunk, but both running downwards to attach to the soft flexible dome forming the lower surface of the prosoma. As a result of this arrangement, contraction of these muscles will pull the lower wall of the prosoma upwards into the body. This will result in some body fluid being forced out of the prosoma but mainly will put up the pressure in the prosoma. This high pressure will be transmitted directly to the trunk and will cause it to distend. This distension will lead to extension owing to the presence of the extensive arthrodial membranes along the mid-ventral body wall (figures 7a and b).

The hydrostatic power of the dorsal longitudinal muscles is greatly increased by a series of transverse muscles down the trunk together with a group of muscles attached to the lateral walls of the prosoma, all of which must tend to prevent lateral distension of the body when the pressure in the prosoma is increased (figure 6).

Over-distension in a lateral direction is further guarded against, (a) by a very marked system of massive elastic fibres which in some cases form sheaths around the transverse muscle and in others ramify through the substance of the muscles; and (b) by sheets of muscle—the insertion muscles— which commence and terminate in the lateral body wall of the prosoma and run close inside the ectoderm (figure 6).

Retraction of the body results from relaxation of the dorsal longitudinal series together with contraction of the ventral longitudinal series. At the same time a muscle rising from the scuta to the base of the oral cone—the attrahens—acts in an antagonistic manner to the ventral series (figures 6 and 7).

The blood system is canalicular in the main. There are blood spaces in which organs lie, but largely through the development of a parenchymatous tissue the body is permeated by a series of blood vessels rather than lacunae (figures 5, 8 and 10).

There is no heart in an Arthropod sense but there is a structure between the oral cone and the adductor muscle which by its contraction forces the blood around the body. This is the blood pump (figures 4 and 12).

The upper wall of the blood pump is extremely thin and flexible. Immediately inside the wall is a thick layer of parenchyma which leaves a median blood space. Attached to the thin upper wall is a series of muscles—the compressors—which run downwards to converge on to the two lower corners of the scuta on either side of the rostrum. Contraction of these muscles must pull inwards the upper wall which will press the parenchyma inwards and so squeeze the blood out of the median blood space (figures 4 and 12).

The cavity of the blood pump is continuous with the dorsal blood space of the trunk but also with the rostral sinus—a median blood space which forms the entrance to the peduncular vessel—a long blood vessel extending down the length of the peduncle (figure 13).

That the blood leaving the blood pump enters the rostral sinus is shown by the presence of the rostral valve, the existence of which was first indicated by Darwin. This is a double

watch-pocket valve which allows blood to pass down into the peduncle but not in the reverse direction (figures 4, 9 and 12).

The peduncular vessel breaks up at the base of the peduncle into a plexus of vessels which ramify over the inner lining to the peduncle (figure 10).

The thin inner lining of the peduncular wall is connected to the outer rigid covering by a series of massive elastic fibres which will come into action if the plexus becomes over-distended with blood. The elastic fibre system thus prevents stagnation of blood in the peduncular wall and can be looked upon as an accessory circulatory structure (figure 10).

The plexus concentrates into two main vessels on either side of the carina where these enter the capitulum and after breaking up once more into a capitular plexus join up once again into a pair of scutal vessels. These run down the hinder margins of attachment of the adductor muscle and enter the body (figure 5).

About half-way down the adductor muscle, just at the tip of the attachment of the attrahens muscle, the scutal vessel becomes the lateral vessel, the junction of the two being marked by a single watch-pocket valve, the scutal valve, which allows blood to pass from the capitulum into the body, but not in the reverse direction (figures 3 and 11).

The lateral vessels extend into a mass of parenchymatous tissue which clothes the gut and after joining behind the oesophagus run along the gut as the sub-intestinal vessel. This gives off branches along the whole of its length, which like the main vessel itself dwindle in size and finally disappear between the cells of the parenchyma (figures 4 and 5).

The presence of the valve at the commencement of the lateral vessel shows that blood must be forced out of this vessel and through the gut parenchyma. Opening from the parenchyma there are numerous small vessels which all drain into a median epineural sinus (figure 4).

The only exits from the epineural sinus are a series of afferent vessels which run up the cirri and penis (figure 5).

After passing up the cirrus the blood passes down an efferent vessel into a blood sinus along the dorso-lateral part of the trunk (figures 8, 14).

The cirri possess only retractor muscles, extension being brought about by distension with blood. On extension, owing to the method of articulation of the ring-shaped sclerites of the numerous segments, the volume of the cirrus increases considerably. On retraction, therefore, of the cirri, blood is forced out of the limbs. Thus during 'casting' activity of the body the cirri act as accessory circulatory structures (figure 8).

Blood from the dorso-lateral body space passes directly into the cavity of the blood pump. It passes through no valve and it is argued that it is the higher pressure of blood in the trunk region which directs the blood back again into the blood pump.

The circulation just described is possible whether the animal is actively casting or whether it is at rest with the valves closed: the only difference is that in the latter case the circulation will not be helped by the action of the cirri as accessory blood pumps.

The rostral sinus just above the rostral valve is encircled by a double loop of muscles— the occlusor muscles—by which the only escape of blood from the body can be completely blocked (figures 4, 9, 12, 13 and 14).

It is suggested that this muscle is used in extension of the penis. By contracting it and at the same time contracting the peduncular muscles, blood will be forced past the scutal

valves into the body which will thus become distended. The penis will consequently become elongated by blood passing into it up its single vessel from the hinder end of the epineural sinus. It will only retract on releasing the high pressure by the opening of the occlusor muscle, for there is no efferent vessel from the penis.

The circulatory system is summarized in figure 14.

In the nervous system the ventral chain contains four or five ganglia, the last ganglion sometimes showing a double constitution but at other times appearing single (figures 4 and 15).

A well-developed visceral system based on the same plan as that of a cypridinid ostracod is present. This is largely associated with the musculature of the oesophagus.

A group of three nerves leaves the anterior face of the brain and run to ganglion-like structures each containing a pair of large cells. It is suggested that these represent the three constituents of the nauplius eye. The median of the three nerves probably also represents the frontal nerve (figures 15 and 16).

The large nerve—the corono-lateral—leaving the sub-oesophagal ganglion laterally, which has previously been described as the nerve to the adductor muscle, supplies the upper musculature of the mantle and its main stem ends in Darwin's muscle. It is connected to the adductor muscle by a minute strand of one or two fibres only and it is suggested that this muscle is, in fact, an independent effector organ (figure 17).

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