The Activities of the Tube Feet of Asterias rubens L.

I. The Mechanics of Movement and of Posture

BY

J. E. SMITH

(Zoological Department, University of Cambridge)

With seven Text-figures

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I. INTRODUCTION

ASTERIAS RUBENS, under the normal circumstances of its life in tide pools and in the deeper waters of the continental shelf, displays a range of activities which include locomotion, the capture of food, and the maintenance of a posture in which the oral surface is kept in apposition to the substratum. These and other organismal activities require an harmonious integration of movement of the different parts and organs of the body, chief among which are the tube feet and the muscular walls of the arms. These integrated movements of widely separated systems contrast vividly with the strictly autonomous behaviour of the spines and pedicellariae situated on various parts of the lateral and dorsal surfaces of the arms and disk.

It is apparent from the work of Romanes and Ewart (1881), Preyer (1886), Demoor and Chapeaux (1891), Jennings (1907), Mangold (1908), and Diebschlag (1938), among other authorities, that the ability of the tube feet and myodermal wall of the arms to take part in organismal responses is dependent on an innervation which includes nervous connexion with the neurones and tracts of the radial nerve cord and circumoral nerve ring, and that the autonomous behaviour of the spines and pedicellariae is a consequence of their being innervated solely through the peripheral plexus of the dorsal sheath (i.e. the integument lateral to the tube feet). Some of the implications of peripheral and central innervation in terms of the integration of activity in starfishes have been discussed in a recent review (Smith, 1945). The present paper, on the kinematics of tube foot activity, is intended to serve as an introduction to a
more detailed examination of the mechanisms underlying nervous integration in the starfish as evidenced by an analysis of the circumstances of stimulation and innervation appropriate to the appearance of the reflexly and centrally controlled activities of the feet.

II. THE MOVEMENTS AND POSTURES OF THE FEET

The activities of a starfish podium comprise a number of readily recognizable movements and postures all of which originate in the contraction of smooth muscle fibres contained within the wall of the foot and of its annexant ampulla. Text-fig. 1, which illustrates schematically the arrangement and

**Text-fig. 1.** Diagram of a longitudinal section through a foot and ampulla of *A. rubens* showing the arrangement of the principal muscle systems.

distribution of the principal systems of fibres, shows two series of muscles, the vertically running circumferential fibres of the ampulla and the longitudinal retractor muscles of the column of the podium, which have long been recognized (Greeff, 1871). The figure includes, in addition, three muscle systems not previously figured, namely, the basal sheath of orienting fibres, the radial fibres of the terminal plate, and the levator fibres of the plate, while omitting, for reasons later to be given, the musculature of the sucker figured and described by Cuénot (1891) and Chadwick (1923).

The muscles are separated from the fluid-filled cavity of the foot and ampulla by a thin coelomic epithelium and are bounded externally by a layer of connective tissue, to the collagen fibres of which they are attached either along their entire length or at their extremities. When the muscles contract, they initiate movements of the foot either by pulling directly on its wall or by exerting pressure on the fluid contained within the virtually closed system of
III. Protraction and Retraction of the Foot

Only brief reference will be made to these movements as their kinematics have been discussed in some detail in a previous paper (Smith, 1946).

Protraction (Text-fig. 2A) is initiated by the contraction of the ampulla muscles whereby fluid is expelled through the neck of the ampulla into the cavity of the podium. The inner layer of the connective tissue sheath of the foot comprises circular fibres (Text-fig. 2A), which, being inextensible, resist the pressures exerted on the side walls of the foot by the contained fluid and prevent a lateral bulging of the column; the effective pressure of the fluid is exerted against the terminal plate and the foot protracts. During protraction the longitudinal fibres of the outer layer of the collagen sheath, which in sections of a retracted podium (Text-fig. 2D) are seen to be much convoluted, gradually straighten; though at the normal limit of protraction (Text-fig. 2C), determined in the first place by the fluid content of the ampulla, they are still somewhat folded. By pulling at the foot it is possible to extend it farther, but attempts to stretch it beyond about twice its normal protracted length invariably result in the rupture of the wall of the column. In view of the observed degree of folding of the longitudinal fibres at various extensions of the foot it...
seems reasonable to infer that amputation occurs at the point when the longitudinal fibres are fully tautened.

Withdrawal of the foot is brought about by the contraction of the muscles of the retractor sheath, fluid being expelled from the diminishing cavity of the foot into the ampulla, the muscles of which relax. So long as the conditions of retraction are comparable around the entire periphery of the sheath the foot retains its cylindrical form (Text-fig. 2b), but if there is differential contraction of the individual fibres, the foot bends towards the more contracted side (Text-fig. 2e). Localized bending movements of this kind are invariably exhibited by feet during their withdrawal from the substratum at the end of the backward step (Text-fig. 7, A4). In this instance the curvature arises as a result of the difference in length of the posterior and anterior faces of the podium (relative to the direction of the step): the former, being under greater tension at the moment of release, becomes concavely curved. As will later be shown, localized bending movements may also be evoked by unilateral stimulation of the foot column.

IV. ATTACHMENT AND DETACHMENT OF THE SUCKER

Mucus undoubtedly plays an important part in the adhesion of starfish podia to solid surfaces, but the principal adhesive force in feet possessing a terminal sucker is provided by suction (Paine, 1926). Niemiec (1885) and Preyer (1886) attributed the suction effect to the cupping of the centre of the disk with a consequent lowering of the pressure within the fluid of the suction cavity. Whereas there has been general agreement on this point there is less unanimity concerning the disposition and role of the muscle systems by which the suction mechanism is operated.

In 1891 Cuenot described and figured a system of radially arranged muscle-fibres within the sucker of the foot of A. rubens, distal to the terminal plate, and the view has been expressed (Sedgwick, 1927) that these muscles, by their contraction, cup the disk and fix the sucker. Notwithstanding Chadwick's (1923) confirmation of Cuenot's account, it is certain, however, that these radial fibres are not muscle but connective tissue. In sections stained with Heidenhain's iron-alum haematoxylin or with Delafield's haematoxylin and eosin, they may easily be mistaken for muscle, but when care is taken to differentiate myosin from collagen by the use of polychrome dyes such as Mallory's triple stain it is evident that muscle-fibres are absent from the disk and that the suction mechanism is operated by muscles wholly extrinsic to the sucker.

Text-figs. 3A and 3B show the principal systems of muscle-fibres and the disposition of the collagen connective tissue as seen in a median sagittal section of an Asterias foot, the material used being fixed in Heidenhain's 'Susa' mixture and stained in Mallory's triple stain. Although many of the fibres of the retractor musculature have a distal termination on the side wall of the podium, some of them (the levator muscles of the diaphragm) converge towards and are attached to the central area of the terminal plate of connective
tissue. The upper and lower limits of the plate are indicated in the figure by the broken white lines and it will be seen that the centre of the plate (the diaphragm) is very much thinner than is its margin. The latter forms a thickened rim continuous, proximally, with the cylindrical connective tissue sheath investing the cavity of the foot. Distally, it is drawn out into a series of vertical laminae which thrust into the substance of the sucker as a series of radially arranged wedges, the arrangement of which is well seen in transverse sections through the sucker (Text-fig. 5A). Along a considerable part of the free margin of each lamina, and over the distal surface of the centre of the terminal plate, the connective tissue is frayed out into numerous strands (Text-fig. 3B), the individual fibres of which interdigitate with, and are attached to, the ectodermal cells of the sucker. When the muscles which are inserted on the upper surface of the diaphragm contract they cause it to be invaginated into the hydrocoel. The doming of the plate is clearly seen in sections through fully retracted, but unattached, feet (Text-fig. 3B). In this instance the tensions developed in the contracting musculature and transmitted through the collagen fibres of the sucker have caused a slight inward and upward rotation of the two laminae and a perceptible reduction in the diameter of the suction disk. A drawing-in of the disk is not, however, to be observed in feet the suckers of which are in contact with the substratum at the time of contraction of the retractor musculature.

Under these latter conditions (Text-fig. 4A) the levator fibres of the diaphragm exert a tension with a component (N) normal to its surface. The consequent tendency for the volume of the suction cavity to increase results in the pressure (p) within its contained fluid falling below the level of the pressure (P) acting on the outer wall of the foot. Suction will occur provided that the lateral wall of the cavity resists the tendency to collapse under the reduced pressure and provided also that the attached margin of the sucker does not
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slip inwards. It is, of course, evident, in view of the fact that suction does occur when the levator fibres pull on the terminal plate, that there is neither slipping of the foot nor a collapse of its wall, but the interest of the mechanism lies in the manner in which the properties and arrangement of the muscles and connective tissue ensure the rigidity of the wall during suction.

TEXT-FIG. 4. A. Diagram of a median sagittal section through the distal end of a tube foot of *A. rubens* showing the distribution and direction of the forces acting on the wall of the suction cavity during the attachment and detachment of the sucker. 

(p) is the pressure within the fluid of the suction cavity, (P) the pressure outside the foot. a. A part of the same section showing the orientation of the collagen fibres within the terminal plate and one of the radial laminae of the sucker. In both figures the connective tissue is shown in black. (a) the horizontally oriented fibres of the outer margin of the lamina; (b) the longitudinally oriented fibres terminating on the distal and inner edges of the lamina.

The tendency of the margin of the sucker to slip inwards is resisted by centrifugally acting frictional forces (F) and by the horizontally and centrifugally acting components of the forces (n). These latter forces are the tensions developed in the connective tissue laminae of the sucker as a result of the contraction of the retractor muscles N' N' inserted around the periphery of the terminal plate. The terminal plate and the laminae are composed of a network of collagen fibres which have the property of being inextensible when subjected to forces applied along their length. While (Text-fig. 4B) the proximal face of the terminal plate is made up of closely matted circumferential fibres—in effect the most distal of the circular fibres of the inner zone of the cylindrical sheath of the column—the wedge-shaped laminae are composed of fibres which have a predominantly longitudinal orientation. As will be seen from Text-fig. 4B, some of the fibres (a) curve outwards to form the thickened margin of the upper and outer surface of the lamina, but for the most part (b) they run downwards while turning all the while towards the midline of the foot. The result of this arrangement is that by far the greater number of the fibres converge on the distal and inner margins of the lamina, to be inserted at right angles to its surface. It is along a length of the lamina exactly corresponding to the line of normal insertion of the main series of fibres that the collagen tissue is frayed out into the branching strands which ultimately terminate between the cells comprising the wall of the adhesive disk and suction cavity. The inextensibility of the collagen fibres, their orientation normal to the wall of the cavity and disk, and the arborescent
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endings of the system collectively contribute to a mechanism that is admirably adapted for translating, with maximum effect, the tensions \( N' \) developed in the contracting muscles of the retractor sheath into forces \( N \) acting outwards from all parts of the lateral wall of the suction cavity. The rigidity of the wall of the cavity being thereby assured, the suction mechanism can operate on the principle of a piston (the central diaphragm of the terminal plate) tending to be drawn up within a rigid cylinder (the margin of the sucker).

Mucous prints left by the suction disk (Text-fig. 5c) show that, in addition to the main suction cavity, there are a number of subsidiary spaces functioning as secondary centres of negative pressure. As will later be shown (p. 8), they may in addition play an important part in effecting the detachment of the disk.

The primary condition of detachment of the sucker is that the forces tending to hold it to the substratum shall be opposed by greater forces acting in the opposite direction. Forces tending to pull the foot away from the substratum may be generated within the foot itself or be applied externally by the traction of the animal as a whole as, for example, during locomotion. As we have seen, however, the negative pressure of suction will hold against these traction
forces beyond the point of rupture of the column of the foot and of amputation of the podium. Before a foot can be withdrawn undamaged from the substratum its disk must first cease to act as a sucker.

Absence of suction implies that the pressure within the fluid of the suction cavity has become equilibrated with the pressure acting on the outer wall of the disk. There appear to be two possible ways of effecting this change: (1) by allowing the outside sea-water to communicate with the fluid of the suction cavity, and (2) by the exertion of a pressure on the walls of the suction cavity equal to the negative pressure of suction.

It will be seen on examining a sucking disk prior to and at the moment of withdrawal of the foot from the substratum that; on occasions, the margin of attachment exhibits a slight wrinkling. One effect of this wrinkling will be to enlarge some of the subsidiary cavities of the suction disk and to permit of their communication one with another. If the water channels so formed lengthen sufficiently in a radial direction they will ultimately open both to the outside of the disk and into the central cavity and the disk will no longer be able to adhere by suction. The frequent detachment of the foot immediately after wrinkling has occurred appears to offer direct evidence of the actual operation of this mechanism.

It is, however, more usual for sucking disks to become detached without the occurrence of any previous wrinkling. In this event the walls of the suction cavity have presumably been subjected to forces tending to press them inwards and so to increase the pressure within the contained fluid. As will be seen by reference to Text-figs. 3 and 4A, there are no mechanisms by which an inwardly acting pressure can be exerted on the lateral walls of the cavity. These walls, solidly built and firmly attached at their base to the substratum, will not, moreover, yield to centrifugally acting forces such as will be developed when the pressure within the suction cavity rises. In the detachment, as in the attachment of the sucker, they therefore remain relatively immovable and rigid.

The central diaphragm of the terminal plate, forming the roof of the cavity, is, however, in different case. A thin circular disk with a slight convexity into the hydrocoel, it has attached to its upper surface a number of radially arranged muscle-fibres (Text-figs. 3A, 5B, radial muscle) which, originating on the inner margin of the thickened rim of the terminal plate, are inserted at the centre of the diaphragm. It will be evident that the whole relations of these radial muscles, their limitation to the one part of the wall of the suction cavity that is capable of being distorted, their radial arrangement, and their origin on a relatively immovable plate, are such as to ensure that, on contracting, they will exert forces acting tangentially to the surface of the diaphragm (Text-fig. 4A (T)) and so, by tending to depress the diaphragm, will cause a rise in pressure within the fluid of the suction cavity and the eventual cessation of suction.

The two methods of release from suction, by a wrinkling of the sucker and by the exertion of tangentially acting forces on the surface of the central
diaphragm of the terminal plate, are both brought about by the contraction of the radial muscles. Attachment of the sucker results from the contraction of the longitudinally oriented levator fibres of the diaphragm. Consequently these two systems of muscles are functionally antagonistic. Since, however, they may at times be in simultaneous contraction, as, for example, at the moment the sucker is pulled away from the substratum, they cannot be regarded as standing solely in the relation of reciprocally contracting and relaxing systems. It is interesting in this connexion to note, as will be shown in a later communication, that they are innervated through different systems of nerve arcs. There is accordingly no a priori reason why they should always act reciprocally.

V. Postural Pointing

These activities include all postures of the feet that can be said to be oriented in the sense that the podia, instead of hanging vertically downwards from the under surface of the arm, have their long axes directed obliquely to the surface. Postural pointing is exhibited during the various phases of the ambulatory step (Text-fig. 7B, 1-4), and in lateral pointing, in which latter movement the foot swings directly outwards from the mid-line of the arm.

Hamilton (1922) alone of previous authors has considered the implications of these postures in terms of the muscular anatomy of the foot. He found that the distal part of the column of a starfish foot can be twisted without affecting the angle of orientation of the podium, and concluded from this that the orienting musculature must lie towards the base of the foot. One doubts whether it is possible to draw this conclusion from a repetition of Hamilton's experiment on the foot of A. rubens. The podium, if allowed to attach to a needle, can be twisted readily enough but its orientation, while so attached, is too much influenced by external forces for any assessment to be made of the freely developed angle of orientation. Moreover, as soon as the needle is removed, the foot withdraws and its former pointing attitude is lost.

The occurrence of a basal orienting musculature can, however, be justified on other grounds, in spite of the fact that it is not to be distinguished in sections of the foot as an anatomically distinct system of fibres. When longitudinal sections through a foot, killed and fixed in the pointing position, are examined (Text-fig. 6) it is seen that the side of the podium which makes an acute angle with the under surface of the arm is not curved but is wrinkled at its base. These circumstances suggest that pointing results from the unilateral contraction either of short fibres within the base of the foot or of the most proximal parts of the long fibres of the retractor sheath. The latter hypothesis leads to evident difficulties. It necessitates, for example, the supposition that, during the change from the retracted (Text-fig. 7, b1) to the protracted pointing position (b2), the basal part of each of the protagonistic fibres remains contracted at a constant length while its more distal portion undergoes extension. Or again, it requires that, during the backswing of the foot (Text-fig. 7, b2 to b3), the proximal parts of the protagonistic and
antagonistic fibres shall undergo reciprocal contraction and relaxation while maintaining a substantially unaltered length distally. While such sequences and combinations of accurately graded differential contractions within the limits of a single fibre, applying *mutatis mutandis* to all the fibres of the ring, are not beyond the bounds of possibility, it seems more reasonable to suppose, in view of all the circumstances, that the postural and retractor muscles not only function as, but are indeed, in actual fact, morphologically separate systems.

It must further be supposed, since the foot can be directed towards any point of the compass, that the orienting muscles, like the retractor fibres, comprise a cylindrical sheath which, in this instance, consists of short fibres encircling the base of the podium.

**VI. LOCOMOTORY STEPPING**

During locomotion all the ambulatory feet step in the line of advance of the starfish. The form of the locomotory step is shown in Text-fig. 7A. A retracted podium first orients with its tip thrust forward (A1). The foot then protracts and, when fully extended (A2), swings back through an angle of about 90° with the sucker pressed against, but not firmly attached to, the substratum. This pendulum-like movement has the effect of thrusting the base of the foot forward relative to the sucker, and the sum of the forward thrusts of all the stepping feet determines the movement of the animal as a whole. At the end of the backswing (A3) the sucker detaches and the foot is withdrawn. During the withdrawal movement the foot re-orientates so as again to point in the forward direction (A1).

The step is thus a cyclical activity, comprising a series of linked movements. Ideally it should consist of four movements—protraction, swing back, retraction, and swing forward—alternating with four transitory phases of static
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posture (Text-fig. 7, B1–B4). Each posture would be characterized by the static contraction of one member of each of the two opposing pairs of muscles engaged in the execution of the step, namely, the protractor–retractor series and the diametrically opposed protagonists and antagonists of the orienting ring, the four postures representing the four possible combinations of action of the two pairs of opposing muscles. These conditions are set out in Table I below, muscles in contraction being represented in the larger, and relaxed muscles in the smaller, type:

As the arrows in Table 1 indicate, each phase of static posture ends, and a new movement begins, with a reversal of the contraction–relaxation relationships of one of the two pairs of opposing muscles, the stepping cycle comprising, in its ideal form, a regular alternation of such changes, first one and then the other pair of muscles being affected.

The actual locomotory step departs from the idealized cycle in certain particulars. As has already been noted, the phase of posteriorly oriented protraction (Text-fig. 7, B4) is omitted: the foot in passing directly from phase 3 to phase 1 combines the movements of withdrawal and of anterior orientation.
**Table I. Static phases of the 'ideal' step**

<table>
<thead>
<tr>
<th>Phase</th>
<th>Anteriorly oriented retraction</th>
<th>Anteriorly oriented protraction</th>
<th>Posteriorly oriented protraction</th>
<th>Posteriorly oriented retraction</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bi</td>
<td>Anterior Postural M.</td>
<td>Posterior postural m.</td>
<td>Retractor foot.</td>
<td>Protractor foot.</td>
</tr>
<tr>
<td>B3</td>
<td>Anterior postural m.</td>
<td>Posterior Postural M.</td>
<td>Retractor foot.</td>
<td>Retractor Foot.</td>
</tr>
<tr>
<td>B4</td>
<td>Anterior postural m.</td>
<td>Posterior Postural M.</td>
<td>Retractor foot.</td>
<td>Retractor foot.</td>
</tr>
</tbody>
</table>

**Swing back** Withdrawal (Effective step) B3-4

**Swing forward** B4-1

**In the actual step.**

- Tendency for protraction to be delayed.
- Marked tendency for swing back to be delayed.
- Withdrawal and swing forward occur simultaneously. Phase B4 omitted.

* The phases of static posture B1-B4 correspond to B1-B4 of Text-fig. 7. Movements are represented by their initial and terminal postures, e.g. B1-B2.
Evidently, at this time, two sets of muscles—the retractor muscles of the foot and the anterior postural muscles—are in simultaneous contraction. Secondly, the smooth rhythm of the step is liable to become dislocated. There is a tendency for the foot to remain poised, often for some seconds, either in the position of anteriorly oriented retraction (A1), or (more frequently) of anteriorly oriented protraction (A2), the podium hesitating either to begin its movement of protraction or to initiate the backswing. These three modifications of the idealized cycle are explicable on the assumption that in each of the two series of opposing muscles one member of each pair is more readily excited to contract than is its partner. Thus, in the protractor–retractor series, the foot muscles are more readily excited than are those of the ampulla while, in the orienting ring, the anterior fibres respond more readily than their posterior antagonists. Some implications of these events will be discussed in a later paper when the nervous mechanisms underlying stepping activity are examined.

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SUMMARY

1. An account is given of the muscular anatomy of the foot and ampulla of *Asterias rubens*. An intrinsic musculature of the sucker figured by Cuenot (1891) and Chadwick (1923) is shown not to be present; on the other hand, postural muscles responsible for orientating the podium, levator fibres which ‘cup’ the sucker, and radial fibres which flatten it are described and figured for the first time.

2. The role of the different muscle systems, the collagen connective tissue, and the fluid of the hydrocoel in protracting and retracting the foot, and in effecting the attachment and detachment of the sucker, is discussed.

3. Evidence is presented to show that postural pointing of the foot is brought about by the contraction of a ring of muscles encircling the base of the podium. The orienting muscles are functionally, but not anatomically, distinct from the longitudinal fibres of the retractor sheath.

4. The ambulatory step is shown to comprise a series of linked phases of static posture and of movement. Each phase is characterized by the contraction of one member of each of the two opposing pairs of muscles engaged in the development of the step. The two pairs of muscles are (1) the anterior and posterior orienting fibres, and (2) the protractors and retractors of the foot. In its ideal form the step comprises four phases of static posture alternating with four movements. Each movement is ushered in by a reversal of the contraction–relaxation relationships of one of the two pairs of opposing muscle systems. Four such changes are possible and they occur in a sequence that ensures the orderly succession of the four movements of protraction, swing
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back, retraction, and swing forward, of which movements the idealized stepping cycle is composed.

5. The actual locomotory step departs from the ideal form in two respects: (1) it is liable to become disrupted by a delay in the initiation of the protrusion or of the backswing movement, and (2) withdrawal of the podium occurs simultaneously with its re-orientation in the forward direction. It is pointed out that these variations are explicable on the assumption that, in the two series of opposing muscle pairs, the retractor fibres are more readily excited to contract than are their antagonists, and the anterior postural muscles than the posterior postural fibres.

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