THE WATER-VASCULAR SYSTEM IN LIVING AND FOSSIL ECHINODERMS

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ABSTRACT. All Recent echinoderms possess extensile tube-feet, and probably all extinct groups had them too. In the most primitive of the living groups, the Crinozoa, the tube-feet are extended by muscular contractions of the water-vascular canals that link together all tube-feet in the animal; most probably, all fossil crinozoans share this method. In the Asterozoa, as well as the agency of the canals, various accessory structures, such as bulbs and ampullae, also become involved. The Homalozoa appear to have most resembled the asterozoans in the operation of their tube-feet. In the Echinozoa, either the accessory ampullae assume the dominant role in tube-foot protractions or, as in aspidochirote holothuroids, protraction is brought about solely by retraction of adjacent tube-feet; some extinct groups could have adopted this method too. The evolution of the water-vascular system is discussed.

WHEN a series of hydraulic structures protrudes into the surrounding sea-water from an otherwise almost totally enclosed animal theca, they may be expected to assume considerable importance in the life of the animal possessing them. Such a situation occurs in the echinoderms, where tube-feet emerge from a rigid test to provide highly mobile, thin-walled, sometimes sucker-ended projections which may play a part in feeding, respiration, burrowing, reproduction, locomotion, and even excretion. They are very important effector organs to members of the phylum, and occur, so far as is known, in all living members; in fact, their presence is diagnostic for the phylum. They are connected together within the body by a series of canals constituting the water-vascular system, which is anatomically a part of the secondary body cavity or coelom. All parts of the system are fluid-filled, the fluid being virtually sea-water with a dense population of coelomocytes suspended in it, and sometimes migrating through its walls to other body cavities, and also out to the surrounding sea-water.

The function of the system is to generate, distribute, and control the hydrostatic pressure necessary for the operation of the tube-feet, but secondarily it may also serve other functions which make use of the fact that it carries a fluid of the body into close proximity with the surrounding sea-water; for instance, it may assist in gaseous exchange to the inner parts of the body and in removal of waste. A major problem with any hydraulic system is the recognition of changes in the head of water in which the animal is living (Nichols 1966), so that appropriate adaptations to the changing hydrostatic situation can be brought about. A part of the water-vascular system, the hydropore and its associated structures, is devoted to this aspect, and is a place where the water-vascular system opens to the surrounding sea-water.

The system is not wholly unique in the animal kingdom; though nothing precisely comparable occurs elsewhere, it is likely that the ancestry of the system lies in the lophophoral canal system in that group of animals generally referred to as the minor coelomate phyla (Nichols 1967*b*; Smith, Carthy, Chapman, Clark, and Nichols 1971), the canal system which creates and distributes fluid pressures associated with

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the protraction of the lophophoral tentacles. In most of these phyla the lumina of the lophophore tentacles are connected by a circum-oral coelomic canal, even in some cases with a hydropore-like opening to the exterior. Among comparable systems of this sort are, first the brachial canal system in brachiopods, which is a tubular part of the coelom concerned with maintaining turgor in the lophophoral filaments, and secondly, the mesocoelic cavity of pterobranch hemichordates, which maintains turgor in the tentacles and even has an opening to the exterior, though this is not to say that the opening has a similar function to the echinoderm hydropore.

The purpose of this paper is to review our knowledge of the mode of action of the water-vascular system in present-day echinoderms and see how far the structure and function of the system in fossil groups can be inferred from this.

THE STRUCTURE AND OPERATION OF THE ECHINODERM WATER-VASCULAR SYSTEM

There are three main parts to the system (text-fig. 1):

i. The *ring canal*, encircling the oesophagus, which may have accessory bulges and pouches off it.

ii. The *stone canal*, which originates at one point on the ring canal and leads to an opening to the exterior, usually called in modern forms the *madreporite*, because of its resemblance to madreporarian coral. Typically sieve-like in modern forms, it was more usually a single pore in early echinoderms, and hence is referred to as the *hydropore*, and this term will be used throughout to avoid confusion. The ring canal and stone canal, with the hydropore, may be thought of as the *central* parts of the system.

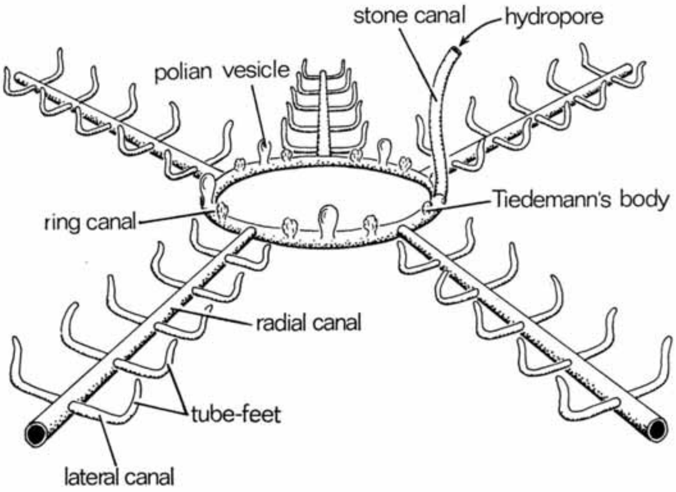
iii. The *peripheral system*, composed of radial canals and the tube-feet and their accessory structures. The radial canals, usually five or multiples of five, arise from the ring canal and pass centrifugally along each arm or other radial structure. They may be internal or external, and the tube-feet may either lead straight off them, or there may be lateral canals leading to the origin of the tube-feet. The radial and lateral canals may be variously modified with muscular or elastic tissues and with valves to assist in protraction of the tube-feet.

The mechanics of the system

The central parts of the system maintain a supply of coelomic fluid to each radial canal, as required. Some of the accessory structures which branch from the ring canal, such as the muscular, bag-like polian vesicles, which are present in some members of all groups except crinoids, appear to hold water-vascular fluid in reserve and under slight pressure until it is required by the animal; other accessory structures, such as Tiedemann's bodies, are cytopoietic, and manufacture some of the coelomocytes which float in the coelomic fluid and act in transport and excretion (Bargmann and Behrens 1964).

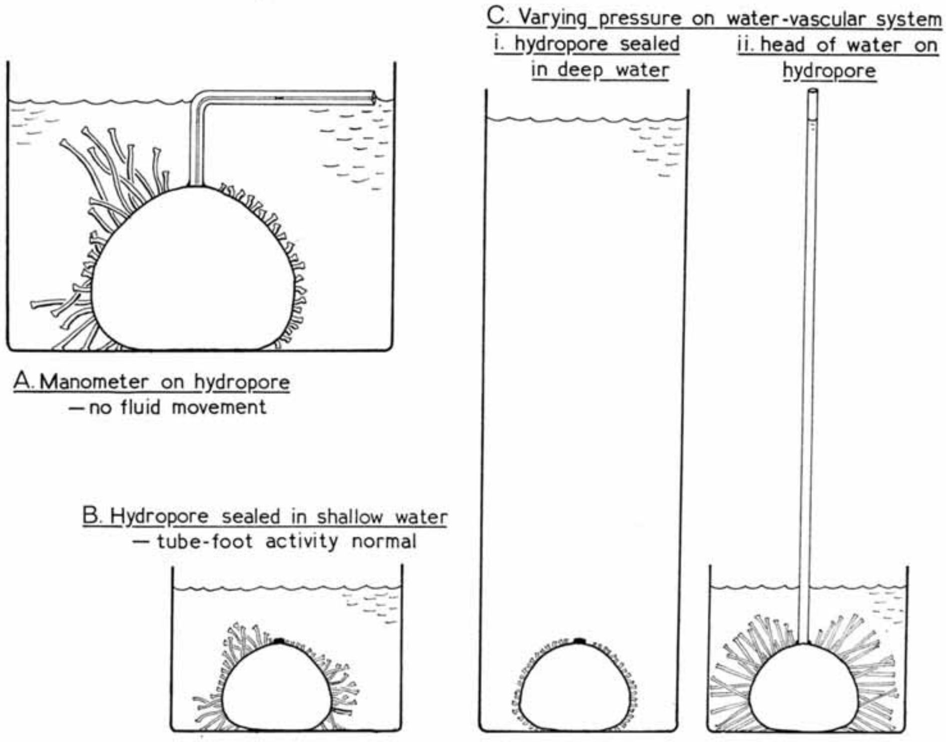
The fluid pressure needed to operate the tube-feet is most often generated mainly within the peripheral canals and to do this the canal walls are either muscular or elastic. In advanced echinoderms, however, various accessory structures, such as bulbs and ampullae, may assist the contractile canals in forcing out the tube-feet. On mechanical grounds, such a system requires a 'safety-valve' for the release of excess fluid when, say, all tube-feet contract together to cause an unusual increase in pressure within the test.

Conversely, when a tube-foot or canal is ruptured, as happens quite frequently in life, the system needs to replenish lost coelomic fluid with sea-water from its surrounding. One might expect that the hydropore acts in both these capacities, since it is the only opening to the exterior, and many writers have assumed this to be the case. But a series of experiments by Fechter (1965) and Buchanan (1969) has shown that this is not so: when an unusually high fluid pressure is generated within the animal, for whatever reason, the peristome and periproct first bulge outwards, and then fluid may escape from the anus; but no fluid has been observed to escape from the hydropore, as evidenced by a manometer sealed over it (text-fig. 2). Similarly, excision of tube-feet and even arm severance does not lead to an incursion of fluid into the hydropore. So neither replenishment of fluid nor the release of excess pressure appear to take place via the hydropore.



TEXT-FIG. 1. Diagram of a generalized echinoderm water-vascular system. The ring-canal, with its accessory vesicles and bodies, surrounds the first part of the gut. The radial canals lie on the oral side of the arms or brachioles, and the tube-feet, drawn here directed upwards, as in crinozoans and some echinozoans, form avenues to the food grooves.

One must therefore ask: what is the function of the hydropore? The obvious experiment of blocking it up and observing the result was first performed by Dakin (1923) who blocked the hydropore of echinoids with shellac and returned them to his shallow aquarium; their behaviour or capabilities did not appear to have been altered. Fechter (1965), however, plunged similarly-treated echinoids to the bottom of a *deep* aquarium, about 2 m below the water-surface (text-fig. 2, Ci). In this case, the echinoid was unable to protract its tube-feet normally. In the converse experiment, in which a head of water was sealed over the hydropore (text-fig. 2, Cii) so that a positive pressure was created within the water-vascular system relative to the surrounding sea-water, the tube-feet all extended to their maximum length and could not be retracted. A head of water of only 20 cm in the tube, Fechter reports, is sufficient to bring about tube-foot extension so that they protrude 'like taut tubes, incapable of executing lateral [pointing] movements' (my translation).



TEXT-FIG. 2. Fechter's (1965) experiments on the function of the hydropore in echinoids. A, With a manometer sealed over the hydropore openings and tube-feet in normal activity (left side), no movement of the mercury bubble in the capillary, indicating no fluid movement across the hydropore; similarly, if all tube-feet are induced to retract together (right side), there is still no fluid movement across the hydropore. B, If the hydropore is sealed and the animal returned to shallow water, there is no noticeable effect on tube-foot activity. C, i, If the hydropore is sealed and the echinoid is plunged into deep water, so that there is a positive ambient pressure on the water-vascular system, then the tube-feet are unable to protract normally. ii, In the converse situation, in which a head of water is sealed on to the hydropore, the tube-feet extend maximally, unable to retract.

I have been unable to repeat Fechter's results using a tube of water sealed over the hydropore, even with the level of water in the tube as much as 2 m higher than that of the surrounding water: the tube-feet of my experimental animals (*Psammechinus*) did not protrude like taut tubes. A possible explanation is that care was taken to ensure that the water tube surmounted only the hydropore, and did not overlap any of the gonopores.

If pressure is applied to the gonopore, then indeed the tube-feet do extend markedly, pressure presumably being transmitted from the gonad sac to the perivisceral coelom and thence to the water-vascular system.

One must be cautious in interpreting such experiments; one must remember that the animal will almost certainly never in its life experience a pressure situation like that in the 'water-tube' experiment. Nonetheless, experiments like these seem to indicate that however it works, and whatever protective devices, such as valves and sphincters, it may subsequently be shown to possess, the hydropore is concerned at least in part with pressure equalization, necessary when the head of water above the animal changes, as, for instance, in tidal rise and fall. For it to be effective, no fluid need pass across the hydropore: it suffices to be merely an opening, so that the dynamic fluid system operating the tube-feet is confluent with the external milieu.

THE CRINOZOA

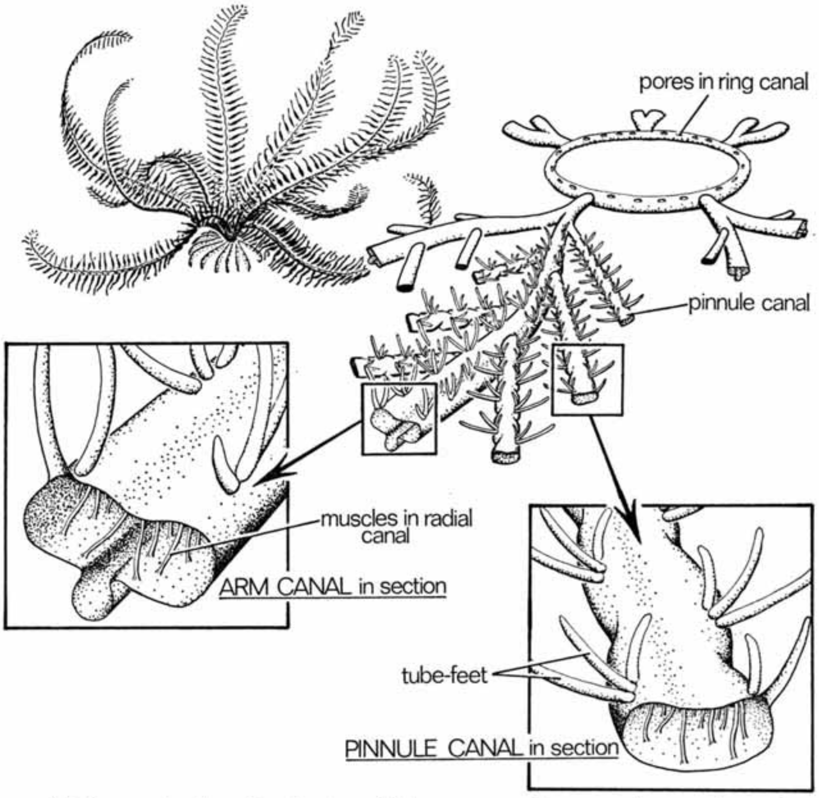
Tube-foot operation in a living crinoid

On many grounds, including the structure and operation of the water-vascular system, the Class Crinoidea is the most primitive living class of the echinoderms. An understanding of the mode of operation of the system in this class is therefore vital to a true understanding of the system in all other living classes. The modern crinoid on which most of the work on the system has been done is the British comatulid *Antedon*, an unstalked form from shallow water. The following account is based on this genus (Nichols 1960), though the system in other crinoids probably works in much the same way.

The 'central' part of the system consists solely of a ring vessel: there is no stone canal or hydropore as such. The central disc is not rigid, and it may well be that the adjustment to pressure change differs from that of rigid echinoderms. This may be why the hydropore as such is absent. Instead, the whole tegmen (the upper surface of the animals' disc) is perforated by tiny pores, and the whole of the ring canal is similarly perforated, like an irrigation pipe. Perhaps such a confluence of water-vascular fluid via perivisceral coelom to the outside water suffices the needs for pressure regulation. A comparable simplification of the hydropore may also be seen in some flexible-bodied holothuroids.

The peripheral part of the system consists of radial canals running along the upper (oral) side of each arm, of which there are ten in *Antedon*, with branches to each pinnule. The canals are flattened, not cylindrical. From both brachial and pinnular canals there arise the tube-feet, in groups of three. Each arm group has tube-feet of similar size, but in each pinnule group there is one long, one medium, and one short tube-foot: the long ones are held out laterally, and nearly touch their equivalents from the adjacent pinnule, the medium ones project dorso-laterally and the small ones project nearly vertically upwards on either side of the food groove, like a fence bordering a shallow ditch (text-fig. 3). Between each group of tube-feet the brachial or pinnular canal is constricted transversely, so that it forms a linear series of interconnecting compartments. Muscle fibres stretch across the actual lumen of the canal. Additionally, in the brachial canal there is a longitudinal gulley in the floor of the canal.

Protraction is brought about mainly if not entirely by generation of pressure produced by contraction of the muscles within the brachial and pinnular canals: there are no



TEXT-FIG. 3. Diagram to show the structure of the water-vascular system in a modern crinozoan, based on the British comatulid *Antedon*. A radial water-vascular canal, traversed by muscles, runs along the oral side of each of the ten arms and their alternating pinnules, giving off groups of tube-feet on either side of the food groove; the canals are constricted at intervals, prominently so in the pinnules. The arm canal, shown in section at lower left, has a ventral by-pass running along its length, to ensure a through-channel to more distal parts of the system; no such channel exists in the pinnule canal, shown in section at lower right.

accessory structures. Considering first the situation in each arm, the sequence of events as the canal muscles contract is probably this: first, the ventral gulley is closed off so that water-vascular fluid can still by-pass the region undergoing activity; then the transverse constrictions on either side of the tube-feet to be protracted are closed off; then finally, the volume of the compartment so formed is reduced, to drive fluid into the lumina of the tube-feet, extending them. In the pinnules, the situation is much the same, except that there is not the same problem of maintaining a by-pass for fluid to distal regions, so the ventral gulley is missing.

In both arms and pinnules the change in shape of the canal is brought about at the expense of cavities lying above and below, that is, the sub-neural and sub-tentacular canals. The walls separating the canals are thin yet tough, to permit flexibility without rupture. The walls of the tube-feet are muscular, to bring about both bending and retraction. By their movement the tube-feet can distribute a sticky mucous food net, collect it up again and pass it into the food groove, whence it is transported to the mouth. To bring about retraction, the longitudinal muscles of the tube-foot contract and the canal muscles relax, so that fluid from the tube-foot lumen is transferred back into the canal.

The water-vascular system in fossil crinozoans

In modern crinozoans, the tube-foot system is very extensive, and one presumes that the tube-feet subserve almost all the respiratory needs of the animal in addition to being the main feeding organs. Certainly no other special respiratory organs occur. This is not so in many extinct crinozoan groups, where more often than not there are additional respiratory devices, such as the dichopore and fistulipore systems of cystoids and some paracrinoids, the hydrospires of blastoids, the epispires of eocrinoids and the cataspires of parablastoids. Perhaps it is safe to infer from the presence of these other respiratory surfaces that the tube-foot systems of these extinct groups were not so extensive as that of today's crinoids. On the fossil evidence the system of brachioles and pinnules in some of these groups does not appear to have been very extensive, particularly in those forms which we regard as the more primitive members of the groups, in which the brachioles arise from facets very close to the mouth, often only two or three to an animal. But then in later forms of the same groups there is sometimes a trend to increase the number of brachioles, and they come to arise from a larger and larger part of the theca.

It does appear that the blastoids may have had a crinoid-like water-vascular system. Well-preserved specimens sometimes show a ring-like groove in the wall of the peristome which probably held a ring canal in life (Breimer and Macurda 1972) and this may have opened, in the crinoid manner, by a number of hydropores.

With the exception of the blastoids and most of the crinoids, all other crinozoan groups appear to have had a hydropore. Sometimes it becomes double, and in some cystoids, such as *Jaekelocystis* (Kesling 1967), it even has a sieve plate across it, as in the more advanced echinoderm groups. This suggests that in all these cases the central parts of the water-vascular system, that is, the ring vessel and associated organs, were internal, and in a few cases it is possible to see the pores through the theca by which the radial canals left the inside to travel up the outside of each arm or brachiole.

So beyond making somewhat vague assertions about the extent of the water-vascular system in fossil crinozoans, we cannot go far in interpreting details of its structure, because, as in modern crinoids, most of the peripheral parts of the system probably lay away from the ossicles and left no fossilizable impression. But the crinozoan system, as interpreted from living forms, sets the scene for an understanding of the evolution of the system in the other, more advanced, echinoderm groups.

THE ASTEROZOA

From the viewpoint of the state of the water-vascular system, the next evolutionary grade after the Crinozoa is seen in the Asterozoa, at least so far as echinoderm groups with living members are concerned. When this Class first appears in the Ordovician, with forms like *Chinianaster*, the system is remarkably crinoid-like, though there are important differences (Fell 1963*a*, *b*). Of course, there is in the Asterozoa a radical change in the posture of the body, in that the mouth now faces downwards. Some crinoids, such as *Edriocrinus*, may well have foreshadowed this reversal of their normal feeding posture by turning mouth-downwards, to feed from the sea-bottom, rather than from suspended matter in the water. But in asterozoans the 'mouth downwards' posture is the rule, and has been accompanied by a corresponding change in the uses to which the tube-feet are put, so they must be constructed so as to adhere to, or burrow into, the sea-bottom while still usually also playing a part in feeding.

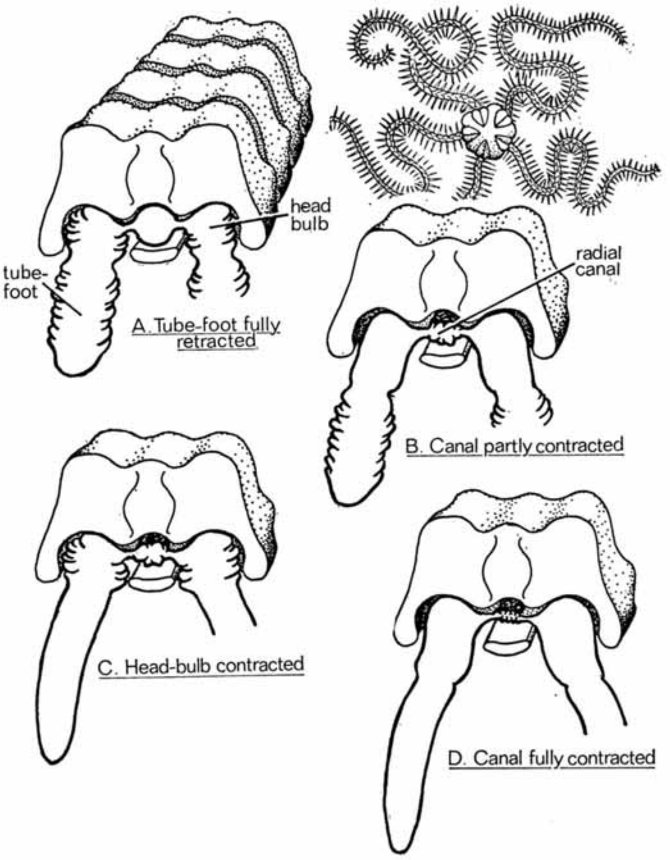
In asterozoans, the main structures for operating the tube-feet are still the canals, but there is a new departure, in that the canals are aided by special extra organs, such as bulbs and ampullae, one to each tube-foot, so that the strength and extent of protraction of the tube-feet can be increased.

Somewhat similar to crinoids in the general design of the water-vascular system, and the least sophisticated of the asterozoans are the ophiuroids. Though exhibiting a wide variety of habitat, more often than not the ophiuroid arm is used to capture food, either from the water or from the film on the sea-bottom. The tube-feet, single rather than grouped, very often create, spread, then gather up a mucous food net, and, like crinoids, they are highly active when the animal is feeding. What follows is a generalized picture, based on several different British ophiuroids (Buchanan and Woodley 1963; Woodley 1967).

While the radial canal running up each arm contributes to the build-up of hydrostatic pressure for tube-foot operation, as in crinoids, it does so by virtue of the elasticity of its walls, not by inherent musculature. A further difference from crinoids is that the canal leading out to each tube-foot is expanded into a muscular bulb (text-fig. 4), and it is this that apparently provides the principal muscular power for tube-foot extension, though one must not disregard the possible contribution made by other tube-feet when contracting (see below, p. 532). Just as the crinoid canal has muscular constrictions to confine the increase of hydrostatic pressure in the canal to where it is required, so the ophiuroid lateral canal has a muscle-operated valve on the proximal side of the bulb, so that any increase in water pressure within the bulb can be directed into the lumen of the tube-foot rather than dissipated down the canal. The tube-feet are, of course, themselves muscular for retraction. But the lumen of the extended tube-foot holds more fluid than does that of the head-bulb, so the excess fluid must escape down the lateral canal to the neighbouring part of the radial canal, which expands against the elasticity of its walls to accommodate this fluid. Additional elastic-walled reservoirs arise from the dorsal side of the radial canals in some ophiuroids, to help store additional water-vascular fluid. For fluid to escape from the tube-foot and its head-bulb, the tube-foot valve must be endowed with its own musculature so that it can open against a pressure on the distal side.

The sequence of events in ophiuroid tube-foot protraction (text-fig. 4) is probably this:

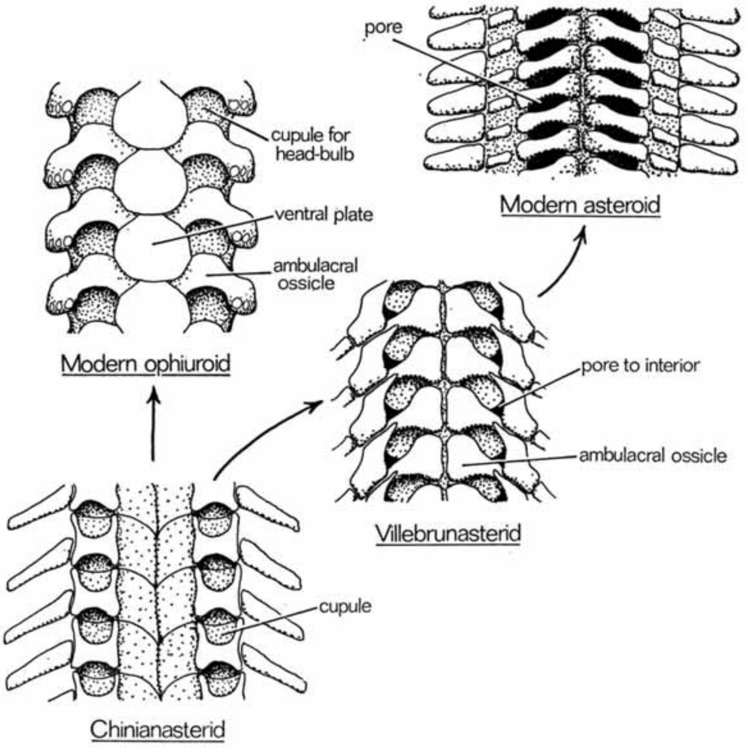
1. The radial canal partly contracts by elasticity, while the head-bulb relaxes, allowing the tube-foot to extend slightly.
2. The valve shuts and the head-bulb contracts, further forcing out the tube-foot.



TEXT-FIG. 4. Diagram to show the probable sequence of events taking place in tube-foot protraction in a generalized ophiuroid, after Woodley (1967). A, Part of the arm, showing a short series of ambulacral ossicles ('vertebrae') and, superimposed in section, the radial canal and a pair of tube-feet, retracted. B, The first part of the protraction cycle, in which the muscles of the head-bulb relax, while the radial canal partly contracts by elasticity; the tube-foot partly extends. C, The head-bulb muscles contract, forcing fluid from the head-bulb into the tube-foot lumen. D, The muscles of the head-bulb relax, allowing further elastic contraction of the radial canal, so that the tube-foot extends to its maximum.

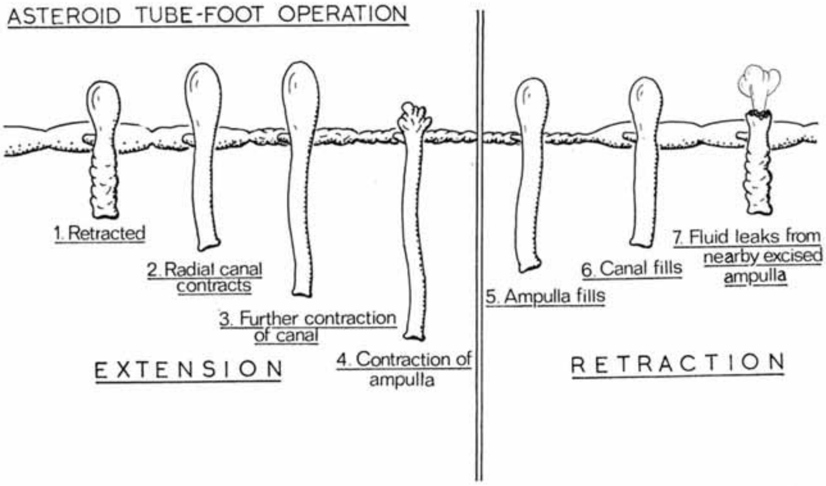
3. The valve opens and the head-bulb relaxes and the radial canal fully contracts by elasticity, to produce maximum tube-foot protraction.

So apart from the possible involvement of neighbouring tube-feet in the protractive process, the principal muscular component is the head-bulb, and this is anchored proximally in a concavity in the underside of the arm plates. A similar concavity is found in some of the earliest asterozoans to occur in the fossil record, such as *Chinianaster*, which is regarded by some (e.g. Fell 1963*a*, *b*; Ubaghs 1967; Nichols 1969) as lying close to the point where the ophiuroids and asteroids diverged. In the subsequent lines from this early fossil, while the ophiuroids appear to have retained the chinianasterid condition of the water-vascular system, the asteroids adopted a different method of creating protractive pressures: they evolved accessor ampullae within the body cavity of the arm, the presence of which is shown in the fossils by pores between the arm plates carrying canals to these structures in life. The probable course of evolution from *Chinianaster* through such forms as *Villebrunaster* to the modern asteroids can be traced with some confidence (text-fig. 5), and shows the gradual reduction in the size of the ambulacral plates from the ophiuroid-like 'vertebrae' to the delicate bridal arch of ambulacral plates of modern asteroids (Fell 1963*a*).



TEXT-FIG. 5. A possible phyletic diagram of the major stages in the evolution of the peripheral water-vascular system of the Asterozoa. In each case a short section of the ambulacrum is shown in ventral view. The somasteroid *Chinianaster* is seen as lying close to the common stem from which both modern ophiuroids (top left) and modern asteroids (top right) have arisen.

The acquisition of ampullae did not, however, relieve the radial canals from participating in tube-foot protraction: the canal is highly muscular in modern starfishes and can distend to receive fluid from retracting feet, and contract to distribute it (Nichols 1969; Blackman 1971). The valve guarding the tube-foot/ampulla system is, as in ophiuroids, muscle-operated, and can both shut and open against pressures on either side of it. Like the head-bulb of the ophiuroid tube-foot, the cavity of the ampulla is of very much smaller volume than the lumen of the fully extended tube-foot, so excess fluid must be able to escape down the radial canal and perhaps assist in the protraction of other tube-feet nearby, or at least be accommodated by the radial canal for future use. So a tube-foot and its ampulla are not necessarily antagonistic in activity, as was previously thought. One can check this directly by cutting a window in the dorsal integument of a starfish using a miniature circular saw, or other fast cutting tool that renders minimum damage to the basi-epithelial nerve plexus. Very often, this can be done without introducing excessive stimulation to the tube-feet, so one can watch them under near-normal activity, and can 'match up' a tube-foot and its ampulla during the stepping cycle (text-fig. 6). Usually a tube-foot will begin to extend unaccompanied by a contraction of its ampulla—in fact, its ampulla may also expand during this phase. The ampulla, if it takes part at all, contracts to provide about the last half of tube-foot extension. When the foot retracts, its ampulla usually takes up the first portion of the

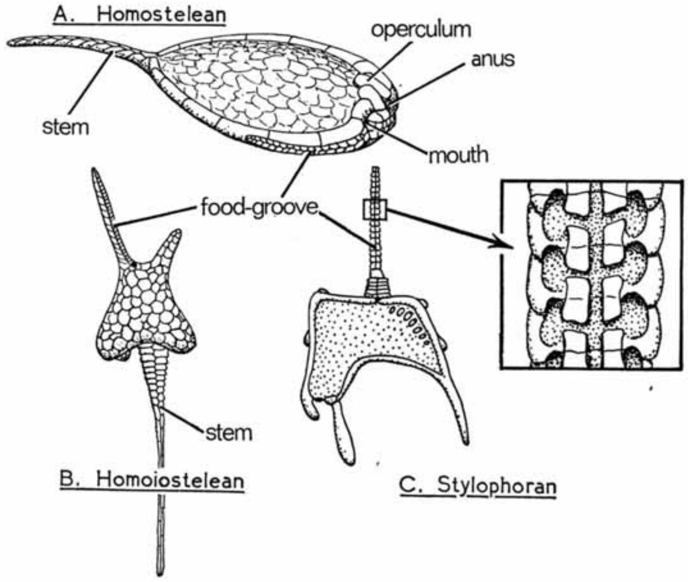


TEXT-FIG. 6. Diagram of tube-foot operation in modern asteroids. When the tube-foot is retracted (1), the ampulla and adjacent part of the radial canal are expanded. The first part of protraction (2) usually involves the contraction of only the appropriate section of the radial canal, and this continues (3) until the tube-foot is extended to between half and three-quarters of its maximum length. The final stage for maximum contraction is brought about by contraction of the ampulla (4). On retraction, the ampulla usually fills first (5), then the canal (6), and fluid may also pass to other parts of the system, which can be detected by leaks in the nearby parts (7).

fluid to be displaced, and so it expands. Then the valve presumably opens, against pressure, and releases further fluid back into the rest of the system.

THE HOMALOZOANS

This, the only subphylum of the echinoderms (on Ubagh's (1967) classification) with no living representative, has a water-vascular system that most resembles that of the asterozoans, apparently, so it is appropriate to consider it here. Formerly called 'carpoids' or 'heterosteles', its members have irregular symmetry and flexible theca. Gas exchange, apart from that taking place across the tube-feet, was probably anal, as in some of today's holothuroids, the flexible theca aiding this. Three classes are generally recognized, each of which has members with a typical crinozoan-like food groove (text-fig. 7), with cover-plates, which, distally at least, could most probably be opened to allow protraction of tube-feet. The arrangement of food grooves in the three classes is as follows:



TEXT-FIG. 7. Diagrams of the ambulacra in the Homalozoa. A, A homostelean, such as *Trochocystites*, in which there are food grooves in the plates of the margin. B, A homoiostelean, such as *Dendrocystoides*, in which the food groove is borne on a single projecting arm. C, A stylophoran, such as *Cothurnocystis*, in which the food groove is also on a single arm; an enlarged view of part of this arm shows an ophiuroid-like arrangement of ambulacral ossicles.

1. Homostelea—grooves round the front of the theca leading to the mouth.

2. Homoiostelea—single feeding arm, with groove down one side, on the side opposite the stem.

3. Stylophora—single feeding arm, with groove down one side, from one side of the boot-shaped theca.

It is in the Stylophora that we know the ambulacral structure best (text-fig. 7, c). The medial groove, which probably contained a radial nerve and radial water-vascular canal, has side-branches from it leading to lateral depressions, in very much the same arrangement as in early asterozoans (compare text-figs. 5 and 7, c), and one can assume that here too the cupules marked the site of tube-foot origin, probably with head-bulbs operating in much the same way as those in today's ophiuroids (see p. 526 above). Each cupule is joined to its ipsilateral neighbour by a short groove, which may have held lateral ambulacral nerves, as in modern asteroids (Nichols 1967*a*).

THE ECHINOZOANS

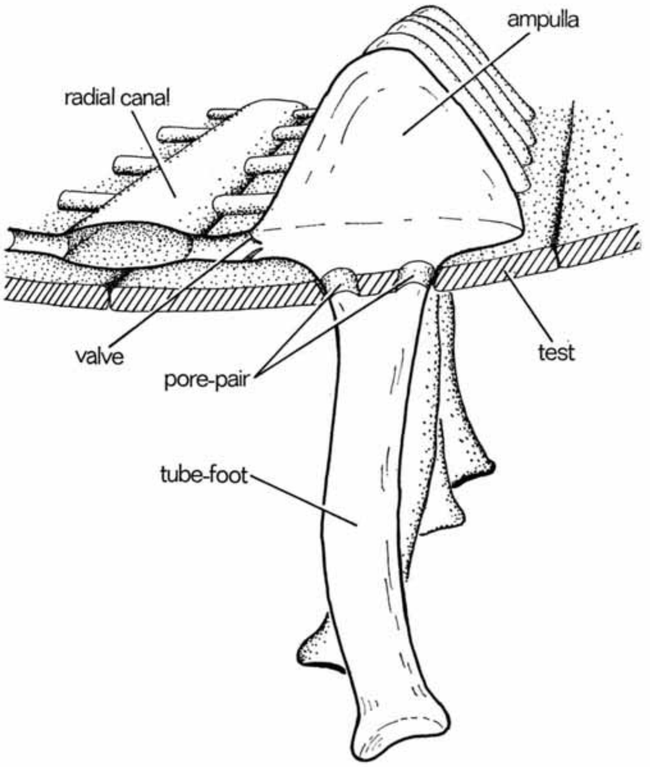
Echinoids and holothuroids

Here, as in asterozoans, tube-foot operation is usually assisted by accessory ampullae, though it appears that some echinozoans have delegated the task of protraction almost solely to the ampullae: here, it seems that the radial and lateral canals take only a minor part in pressure generation. Modern echinoids, for instance, usually have very flat ampullae (text-fig. 8), set close together, and there is hardly any distance of radial canal between the origins of successive branches to the tube-feet which might be concerned with the development of pressure, though the canal as a whole can expand to receive excess water-vascular fluid, say, when all tube-feet in a segment of one ambulacrum retract at the same time.

In other modern echinozoans, such as some holothuroids, the specialization in the protractive process has been in another direction, namely, to make no use of contractile canals and ampullae, but rely solely on the retraction of neighbouring tube-feet.

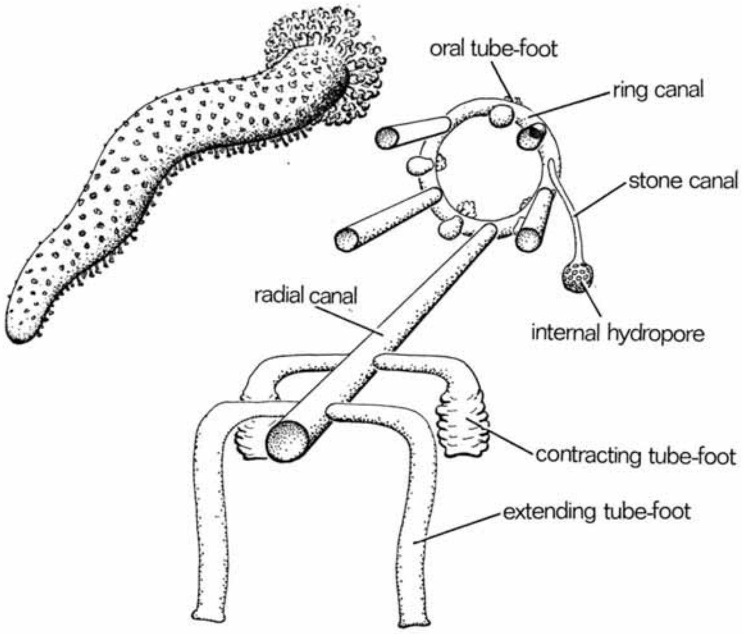
One interesting aspect of the evolution of the echinoid water-vascular system which emerges from a study of the fossil record (see, for instance, Kier 1965) is that early echinoids had the radial canal enclosed within the calcite of the ambulacral plates, whereas with the passing of time the canal was freed from this enclosure and came to lie against the inside surface of the plates, that is, within the body cavity. In view of what we know about the participation of the canal in primitive echinoderms, one wonders whether this 'emancipation' of the canal might not have allowed its greater participation in the protractive process, unrestricted by enclosure within a calcite tube. The question arises, however: why did the canal become enclosed in the first place, if this group arose, as seems likely, from a primitive group with external canals? Possibly with the increased importance of the ampullae in the protractive process the protection of the canal within the plates assumed a selective advantage, and this advantage was maintained when the canal 'broke through' to the interior of the theca, added to which it could again participate in protraction.

In a normal, active echinoderm, usually only about half its tube-feet are protracted at any one time (Fechter 1965; Blackman 1971) the other half being retracted. This period of retraction may be necessary to permit the mucous glands of the tube-foot sucker to recharge. What is interesting, from the viewpoint of tube-foot mechanics, however, is that usually as one tube-foot withdraws, another nearby extends, and, as mentioned above, it seems probable that the contraction of the one may be assisting in the protraction of the other. Some holothuroids demonstrate this principle well: while some, such as the British dendrochirote *Pawsonia* (= *Cucumaria*), have accessory ampullae, others, such as the British aspidochirote *Holothuria*, have no visible internal structures which might play the major part in protraction, such as ampullae or muscular or elastic canals. But it is a fact that whenever a tube-foot of *Holothuria* is extended, a neighbouring one is being withdrawn (text-fig. 9). A prerequisite for this system to work is, of course, that there must be a muscle-operated valve at the origin of each tube-foot, and such a structure is indeed present.



TEXT-FIG. 8. Diagram of the peripheral water-vascular system in the Echinoidea. The ampullae take the major part in protraction, and since the tube-foot and its ampulla are an important agency in gas exchange, circulation of water-vascular fluid is assisted by having the ambulacral pore subdivided, the circulating currents passing through each in opposite directions. A valve can isolate a tube-foot and its ampulla from the rest of the system.

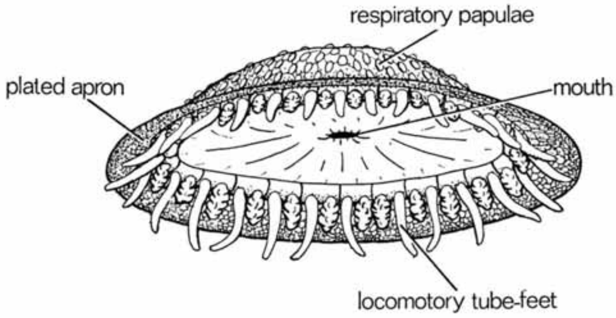
The implication of this principle, used to such good effect by *Holothuria* and clearly of importance to other groups too, is that it is not necessary for an echinoderm to show evidence of contractile structures in the water-vascular system to possess, or have possessed, highly extensile tube-feet. This principle is particularly pertinent to one group of echinozoans, the cyclocystoids, which are entirely extinct.



TEXT-FIG. 9. Diagram of tube-foot operation in an aspidochirote holothuroid, based on *Holothuria*. The 'central' parts of the system are shown, and the origins of the five radial canals; the ventral radial canal is drawn with two pairs of tube-feet. Tube-foot extension is brought about by retraction of neighbouring tube-feet, the process being controlled by valves at the head of each tube-foot and by the tube-foot retractor muscles. The hydropore is internal, because the body is flexible, and therefore transmits changes in external hydrostatic pressure to the coelomic fluid.

The cyclocystoids

This is one of the most fascinating and controversial of the extinct echinozoan groups. Its members are disc-like fossils (text-fig. 10) with an outer ring of hefty ossicles each bearing two (rarely one or three) large pores which are confluent by canals with the interior of the theca. Outside the ring is a skirt of small plates. There is an upper (aboral) and lower (oral) integument, with loose-fitting plates, within the ring. What is generally regarded as the upper surface has pores between the plates which most likely bore papula-like structures, that is, external blisters of the integument which have a lumen continuous with the perivisceral body coelom, but unconnected with the water-vascular system. On the inner face of the upper integument is a series of grooves radiating from the centre of the theca and passing beneath the pores between the plates. These are thought by some workers all to have contained elements of the water-vascular system, and therefore the soft structures protruding from the pores would have been tube-feet. But it seems more likely that the grooves merely directed the coelomic ciliary currents to the region of each papula, as an aid to respiratory efficiency, though some may have held radial canals leading towards the periphery. As for the large pores in the submarginal ring of plates, it seems highly probable that they gave rise to large tube-feet for locomotion, and the skirt of small plates would then have acted to protect both these tube-feet, and the downward-directed mouth in the centre of the undersurface.



TEXT-FIG. 10. One interpretation of *Cyclocystoides* (Camb.). In this attempt, the plates within the submarginal ring are seen as the aboral surface, bearing respiratory papulae from pores between the plates. The large pores in the submarginal plates are interpreted as bearing downwardly directed tube-feet in life, the retraction of one aiding the extension of its neighbour.

Other interpretations of this fossil have been given (see, for instance, Sieverts-Doreck 1951, Kesling 1967; Durham, *in* Nichols 1969; Henderson and Shergold 1971). Some think that the large tube-feet could not have been locomotory, because they would have required large ampullae. But suppose they operated in the manner of modern holothuroids, the retraction of one foot providing the main hydraulic pressure for the protraction of its neighbour: the tube-feet are, after all, often in pairs, and this is particularly well shown in those specimens which are well enough preserved for an accurate count to be made. Such a mechanism could explain the functional link between the two tube-feet arising from one submarginal plate. But it must be emphasized that this is only another possible interpretation of this fossil: until it is better known, it cannot be said definitely which orientation is correct.

Ophiocistioids, camptostromatoids, and lepidocystoids

Some interpretations of the little-known ophiocistioids (see, for instance, Ubaghs 1966; Fell and Pawson 1966) have it that the flexible, plated structures arising from the under-surface of the theca were heavy, plated, permanently retracted tube-feet. By comparison with other echinoderms this seems very strange, since nowhere else in the phylum are tube-feet so cumbersome or irretractible. Unfortunately, the morphology of these large, plated structures is imperfectly known, so one cannot be sure what they are; the fact that they were almost certainly hollow does indeed suggest that they are tube-feet, but the possibility of their being brachioles must not be ruled out. One could perhaps point to the camptostromatoids and lepidocystoids as echinoderms with similar plated structures arising, as in ophiocistioids, in five columns radiating from the mouth, and in these groups the structures are normally regarded as brachioles. Certainly, in *Lepidocystis*, in which the structure of these projections is better known, there does appear to be a food groove down one side (Durham 1967*a*), and maybe further finds in the other two groups will clarify the structure of these projections in them.

The edriosteroids and helicoplacoids

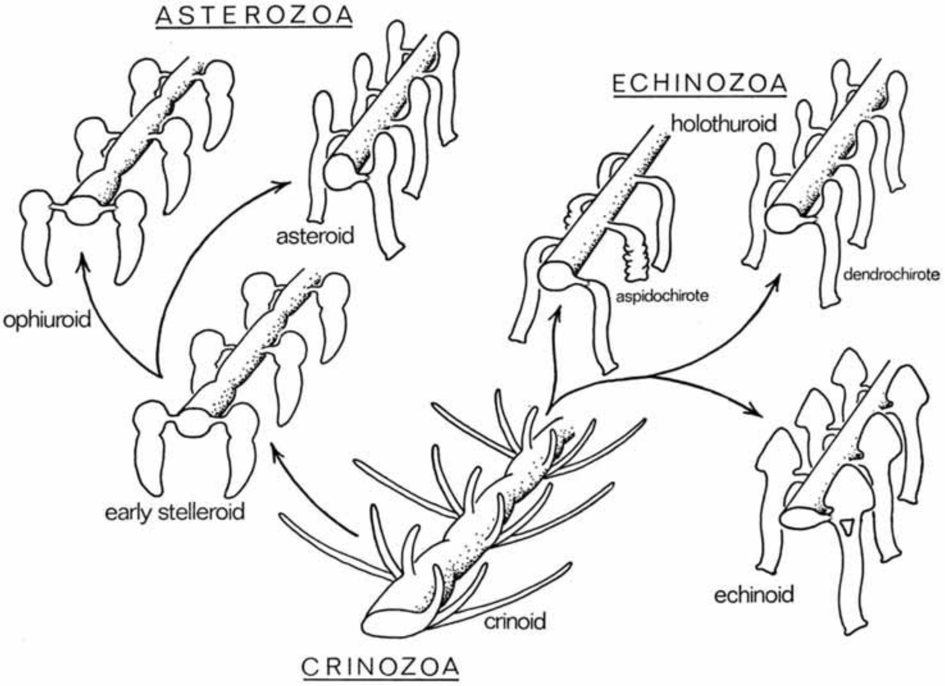
The most interesting fossil echinozoans are those that were on the scene apparently long before the first echinoids and holothuroids appeared. These are the stalked or flattened edrioasteroids (Regnéll 1966) and the spirally plated helicoplacoids (Durham and Caster 1963). Both these groups first occur in the lowest Cambrian rocks (Durham 1967*c*), and in both groups some members at least show evidence of pores between the ambulacral plates, indicating that a water-vascular system was present very early in the history of the group. In the edrioasteroids it is possible to say with fair certainty that the peripheral water-vascular system was external, because in some there is a pattern of external grooves in each ambulacrum which most probably cradled the radial water-vascular canal. There are also pores between the ambulacral plates through which canals probably passed to ampullae within the body. But not all edrioasteroids show either the external radial grooves or the interplate pores. Perhaps these edrioasteroids lacked a water-vascular system altogether, and relied on external ciliary currents for feeding; or perhaps the external parts of the water-vascular system were, like modern crinoids, contained in the soft tissues lying well away from the ambulacral ossicles, and not requiring the use of accessory ampullae.

Among the helicoplacoids, *Waucobella* (Durham 1967*b*) is a genus that shows ambulacral structures particularly well. The column of ambulacral pores is single, and there is no evidence of external or internal grooves which might have held a water-vascular canal, so it is not possible yet to say whether the system was internal or external. The helicoplacoids probably adopted an upright posture in a depression in the slit, and could untwist to extend for feeding, and twist up again to retreat. In twisting and untwisting they could open and close the plates covering the ambulacra and also could open up a spiral series of channels in the interambulacral areas of the animal's outer surface. Though tube-feet were almost certainly present, as evidenced by the pores in the ambulacra, it seems possible, as Durham (1967*b*) has said, that they were for respiration only, since in most helicoplacoids the ambulacral system is ridiculously short to cater for the feeding requirements of the animal. Perhaps food collected all over the animal's exterior, was passed to the mouth at the upper pole, along the interambulacral channels.

SUMMARY AND CONCLUSIONS

Only in the living classes of echinoderms have we direct evidence for the structure and operation of the water-vascular system. So, using the living forms as a basis, the evolutionary trends in the elaboration of the water-vascular system may be summarized as follows (see also text-fig. 11):

1. The most primitive situation is seen in the crinozoans, in which the radial canal itself is the sole pressure generator.



TEXT-FIG. 11. Summary diagram of the various kinds of peripheral water-vascular system seen in the three extant sub-phyla of echinoderms; the suggested evolutionary lines are based on the configuration of this system only.

2. In ophiuroids the lateral canal to each tube-foot plays a part.
3. In asteroids the radial and lateral canals are the main pressure generators, but assisted by ampullae to increase the effective extent of tube-foot protraction.
4. In echinoids and some holothuroids, independently, the greater part of pressure generation is performed by ampullae.
5. In other holothuroids it is other tube-feet which create the necessary pressure.

On this framework can be hung an interpretation of the system in some extinct forms:

6. Most extinct crinozoans, such as blastoids, cystoids, eocrinoids, paracrinoids, parablastoids and edrioblastoids, probably had structures very similar to those of living crinoids, with radial canals supplying the main protractive force.

7. The homalozoans may well have adopted an ophiuroid-like system, using head-bulbs.

8. The helicoplacoids possibly had a single column of tube-feet worked on the echinoid principle.

9. The edrioasteroids probably used canals and ampullae in an asteroid-like manner.

10. The cyclocystoids may have used the retraction of one tube-foot to protract another, as in some modern holothuroids.

The history of higher invertebrate animals is largely a story of elaboration of the coelom. The original function of the secondary body cavity, which is the function retained for it by the great majority of invertebrates, is to transfer pressure changes from one place to another, chiefly in connexion with the extension of soft structures. The echinoderms have retained this function too, but not for the whole coelom: the main part of the coelom is enclosed within a more or less rigid skeletal capsule, and is not involved in pressure-changes, except passively; but the water-vascular system represents a part of it which does involve the primitive function, in that it creates and controls the pressure changes which operate a vitally important set of soft parts, the tube-feet.

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