XIX. The Croonian Lecture.—
Observations on the Locomotor System of Echinodermata.

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[Plates 79–85.]

PART I.—MORPHOLOGY.

§ 1. Ambulacral System.

1. Holothuria.—When a longitudinal incision is made through the perisome of a Holothurian (*Holothuria communis*) there is generally seen escaping, along with the branches of the respiratory tree and genital gland, a long sacculated tube filled with a fluid, and holding in suspension a large quantity of a brick-dust coloured pigment. This tube, which may be one-and-a-half times the length of the entire animal, and from one line to half-an-inch in diameter, is the polian vesicle (Plate 79, fig. 1, *a*). On following it upwards it is found to open freely into a wide circular canal (Plate 79, fig. 1, *b*) a short distance from the termination of the stone canal. From this circular canal five lozenge-shaped sinuses (Plate 79, fig. 1, *c*) project forwards, and from each of these two large oval sinuses (Plate 79, fig. 1, *d*) run forwards parallel with each other, the ten oval sinuses becoming continuous with the hollow stems of the tentacles (Plate 79, fig. 1, *e*). In a Holothurian 8 inches in length, exclusive of the tentacles, the lozenge-shaped sinuses, which may be designated the sinuses of the circular canal, measure a quarter of an inch from above downwards and a little more from side to side. From around the pointed upper ends of the canal sinuses the five longitudinal muscular bands take their origin.

When a solution of Berlin blue is injected into the polian vesicle, the circular canal and its sinuses, the oval sinuses and tentacles, the radial canals, pedicels and ampullæ are rapidly distended; but, unless the pressure be kept up for a considerable time, none of the coloured fluid penetrates into the stone canal, and either the vesicle, ring, or one of the sinuses gives way before it reaches the madreporic plate. If one of the radial canals be divided while the injection is being proceeded with, the coloured fluid at once escapes, and the tension within the polian vesicle, the circular canal, and the tentacles is diminished. If plaster of Paris be substituted for the solution of Berlin blue, a cast is readily obtained of the circular canal and its sinuses, but the plaster does not find its way either into the sinuses of the tentacles or into the radial canals.

When, however, a coloured solution of gelatine is forced into the polian vesicle, the tentacles and their sinuses, the radial canals, ampullæ, and pedicels are filled, as well as the circular canal and its sinuses. Examination of specimens injected with plaster of Paris and gelatine shows the circular canal to be a quarter of an inch in diameter, and to communicate freely both with the polian vesicle and with the lozenge-shaped sinuses springing from it. The specimens injected with a gelatine mass further show that each canal sinus opens into a cæcal tube, which runs forward internal to the sinuses of the tentacles as far as a wide circum-oral space (Plate 79, fig. 2, *a*). This space communicates by well-defined apertures (Plate 79, fig. 3, *b*), with that portion of the body cavity which lies between the sinuses and the œsophagus, and which is reached through the circular apertures between the sinuses of the circular canal (Plate 79, fig. 1, *f*).

Each canal sinus has three other apertures in its walls. It opens by a small round aperture into a radial canal. The radial canal, together with the longitudinal muscular band, runs up between two of the sinuses of the tentacles to reach the inner surface of the body wall, and gives off lateral branches which project outwards as pedicels and inwards at each side of the longitudinal muscle as long-pointed ampullæ (Plate 79, fig. 1, *g*). The two other apertures are in the form of minute slits, one at each side of the orifice of the radial canal, which lead into the adjacent tentacle-sinuses. Each of these tentacle-sinuses measures three-quarters of an inch in length, and a little over a quarter of an inch in diameter. When the tentacle into which the sinus opens is protruded, there is no constriction between the sinus and the tentacle; but when the tentacle is retracted, there is a well-marked annular constriction (Plate 79, fig. 1, *h*) at the junction of the sinus with the tentacle, which may aid in preventing the fluid that is driven into the sinus during retraction from again returning into and at once protruding the tentacle. If considerable pressure be applied to the polian vesicle when the tentacles are in a retracted state, this constriction disappears and the tentacles are distended, though not protruded. If the retractor muscles be divided while the polian vesicle is compressed, the tentacles become engorged and project forwards. On the other hand, when the pressure is removed from the vesicle and the divided retractors pulled backwards, the tentacles are approximated and, along with the group of sinuses and the anterior portion of the perisome, dragged backwards towards the centre of the body cavity. The eversion of the perisome and the protrusion of the tentacles are brought about chiefly by the shortening of the longitudinal muscular bands and the contraction of the polian vesicle; but the circular fibres of the body wall also assist by contracting immediately behind the group of sinuses, so as to act on them by direct pressure, and also indirectly by forcing the perivisceral fluid against them. The fully distended position of the tentacles represented in figure 3 is only reached when the fluid of the body cavity has been forced into the circum-oral space (Plate 79, fig. 2, *a*).

The amount of the body cavity fluid is constantly changing. At the entrance to the cloacal chamber a circular valve is seen alternately dilating and contracting, except when the aboral end of the Holothurian is forcibly retracted. When this valve dilates it lies in close contact with the walls of the cloaca (Plate 79, fig. 4) and allows water to enter for the respiratory tree. It remains open for a few seconds and then contracts so as to project beyond the aperture (Plate 79, fig. 5); when it begins to retract and dilate, water escapes from the cloaca. This alternate opening and closing takes place rhythmically, at a rate usually of six revolutions per minute. At the end of every seventh or eighth revolution the valve projects further than usual, and, while it is slowly dilating, a large stream of clear water is ejected. The escape of this stream occupies from 15 to 20 seconds. Occasionally along with the stream a quantity of sand and the remains of the food particles are carried out from the cloaca. When the tentacles are being protruded the rhythmic action of the valve goes on as before, but more water is taken in than escapes from the cloaca; on the other hand, retraction of the tentacles is preceded by an escape of a large stream of water, and while retraction is proceeding more water escapes than when the Holothurian is at rest with its tentacles projecting.

2. Echinus.—In *Echinus* (*E. sphæra* and *lividus*) two tubes spring from the under surface of the madreporic plate. The one (Plate 80, fig. 10, *a*) is dilated at its origin so as to include the greater portion of the plate (Plate 80, fig. 10, *b*), and ends in the so-called "heart" (Plate 80, fig. 10, *d*). The other (Plate 80, fig. 10, *c*) is small, deeply pigmented, and runs along a groove in the heart to open into a circular canal at the base of the lantern. From the under aspect of this circular canal the five radial ambulacral vessels (Plate 80, fig. 10, *i*) take their origin, and, after passing under the rotulæ and over the interalveolar muscles, they run along the inner surface of the ambulacral plates. The first series of pedicels (Plate 80, fig. 10, *j*) projects through the oral floor midway between the oral aperture and the margin of the shell. Their respective ampullæ (Plate 80, fig. 10, *k*) are long delicate tapering tubes which project upwards and outwards between the radial canals and the alveoli. The next four or five pairs of pedicels also pierce the oral floor. Their ampullæ are small rounded sacs, whereas the ampullæ of the first series of feet external to the auricles are slightly flattened and sometimes deeply constricted, whilst those beyond are in the form of flattened sacs lying at right angles to the radial canals (Plate 80, fig. 13, *a*).

Immediately within the oral margin of the shell, and alternating with the inner row of pedicels, are the five pairs of "tree-like organs." There is no evidence of the existence of these structures within the shell until a membrane (Plate 80, fig. 10, *m*), which extends from the apex of each tooth to the oral margin of the interambulacral plates and sides of the alveoli, is divided. If instead of dividing this membrane a fine glass canula be forced through it and a solution of Berlin blue introduced into the space between the membrane and the alveoli of the lantern, the fluid slowly diffuses upwards into, and greatly distends, the vesicles around the apices of the teeth (Plate 80, fig. 10, *n*). The fluid reaches these vesicles partly by passing directly upwards external to the alveoli, and partly by passing into the cavities of the alveoli and ascending through the circular sinus. When a solution of coloured gelatine, or what is better, plaster of Paris, is injected into the space above the tentacles, or into the vesicle around the soft apex of one of the teeth, a cast is readily obtained of the circular sinus and of the spaces communicating with it. A vertical section of the lantern of an urchin thus injected shows the wedge-shaped circular sinus (Plate 80, fig. 10, *e*) lying between the radius and rotula, communicating above with the vesicle around the tip of the tooth (Plate 80, fig. 10, *n*) and below with the cavity of the alveolus (Plate 80, fig. 10, *p*), through which the tooth passes, and by means of the latter cavity communicating indirectly with the large space lying above the "tree-like organs."

3. SPATANGUS.—In *Spatangus* (*S. purpureus*) the ambulacral circum-oral canal has no polian vesicles or sinuses developed in connexion with it. The ampullæ immediately around the oral aperture are tubular, and often measure a quarter of an inch in length. Those beyond on the under surface and round the equator are also tubular, but they are small and few in number. This is true of all the ampullæ of the anterior radial canal. The ampullæ which project inwards from the dorsal portions of the four remaining radial canals are, as in *Echinus*, transversely flattened sacs. Some of the pedicels have suckers, others are conical and devoid of suckers, while others again are flattened at their tips, or flattened and split up into segments.

4. SOLASTER.—When one of the arms of *Solaster papposa* is divided transversely an inch from the disc, and a coloured solution is introduced into the proximal portion of the radial canal, the ampullæ and pedicels at the base of the arm injected are at once distended. The solution next penetrates the circular canal, polian vesicles, ampullæ, and pedicels of the other arms; but unless a considerable pressure be continued for some time, none of the solution enters the madreporic canal. In one specimen, when the injection had been continued for five hours with the pressure bottle raised two feet above the level of the Star-fish, the solution had ascended two-thirds of the entire length of the stone canal, and two hours later it began to diffuse slowly through the madreporic plate. When a thin slice was removed from the surface of the plate, the solution was observed escaping from a small circumscribed area (Plate 80, fig. 12, *a*) situated between the centre and margin of the plate—an area corresponding in size and position with the termination of the stone canal on the inner surface.

Starting from the inner aspect of the madreporic plate the stone canal gradually increases in diameter, and passes obliquely over the accompanying sinus till it finally hooks round the sinus to open into the circular canal (Plate 80, fig. 11, *a*). Springing from this canal, which occupies a sinuous groove on the dorsal aspect of the inner ambulacral ossicles, and opposite each interradial space (with the exception of the space occupied by the stone canal) is a polian vesicle (Plate 80, fig. 11, *c*). Each vesicle consists of a tubular stem measuring from two lines to a quarter of an inch in length, and of a dilated portion which may be exceedingly small (Plate 80, fig. 11, *i*), or takes the form of a large oval sac (Plate 80, fig. 11, *d*). The size and form of the vesicles are largely determined by the amount of fluid in the pedicels, the vesicles diminishing when the feet are protruded, and enlarging when they are retracted.

The first series of ampullæ (Plate 80, fig. 11, *e*) are small semi-lunar sacs, which lie in close contact with each other opposite the origin of the polian vesicles, and between the ambulacral canal and the circular vessel. The other ampullæ (Plate 80, fig. 11, *f*) are spherical in form. In none of the injected specimens was there any evidence of a communication between the ambulacral vessels and the body cavity, or between the ambulacral and the blood (neural) vessels. There was, however, abundant evidence of communication between the latter and the exterior. When a canula was introduced into the outer end of the sinus, a coloured watery solution could be easily forced through the sinus into the circular blood-vessel (Plate 80, fig. 11, *h*), and from the circular vessel into the radial blood-vessels. But when the canula was introduced into the proximal end of the sinus, the solution rapidly rushed along the sinus and escaped freely through the madreporic plate—proving that the blood-vessels of *Solaster* communicate far more freely with the exterior than do the water vessels.

5. URASTER AND ASTROPECTEN.—The ambulacral system of the common Star-fish (*Uraster rubens*) differs from that of the Sun-star (*Solaster*) only in having no polian vesicles. *Astropecten* (*A. aurantiaca*), on the other hand, has polian vesicles ; but in it the pedicels have departed from the typical form. In *Holothuria* and *Echinus* the feet terminate in well-marked sucking discs (Plate 79, fig. 6), which have their margins frequently strengthened by a deposit of calcareous matter. All the pedicels of *Solaster* and *Uraster*, with the exception of a few at the tip of each arm, are also provided with suckers. Those at the tips of the arms are long and pointed, and when the Star-fish is moving they project forwards in the direction of advance, and appear to act the part of tentacles. In *Astropecten*, however, the feet are short and conical, and instead of ending in suckers they terminate in rounded points (Plate 79, fig. 7). But although suckers are absent, *Astropecten* is able slowly to ascend a vertical surface. We have repeatedly observed slight inversions of one side of the pedicels near their pointed tips when this Star-fish slowly ascended from the bottom of a glass aquarium ; hence we are inclined to believe that *Astropecten* has the power of converting a portion of the side of its pedicel into an imperfect sucker (Plate 79, fig. 8, *a*).

6. OPHIURA.—In the Brittle and Sand-stars, the ambulacral feet are morphologically similar to those of *Astropecten*, though shorter and more slender. Those near the disc further differ from the pedicels of *Astropecten* in being more pointed (Plate 79, fig. 9). The pedicels beyond the disc gradually diminish in size, and at the ends of the arms they are scarcely visible. All the feet are devoid of suckers, and no attempt is ever made to form even a temporary imperfect sucker by slightly inverting a portion of the side of the foot.

§ II. General Homologies.

The madreporic plate of a Holothurian is a pale, straw-coloured, hollow, conical, calcareous mass, lying on or near the circular canal. It may, however, be broken up into several portions; from each portion a canal originates, and the several canals generally unite to form a single stone canal. The stone canal, though sometimes straight, and hanging from the circular canal into the body cavity, is generally folded on itself, and in contact throughout the greater portion of its length with the circular canal. A small sinus, which sometimes exists around the stone canal, may correspond to the large sinus which lies in contact with the stone canal of *Solaster*.

In *Echinus* the madreporic plate is a modified genital plate, the stone canal is a delicate pigmented fibrous tube, lined with cells provided with long vibratile cilia. This tube springs from a limited area of the plate, and runs along the "heart" to open into the circular canal at the base of the lantern. The sinus, springing from the larger portion of the plate, contracts into a narrow tube, and then dilates and has developed in its walls a lobulated glandular-looking mass, which may act the part of an excretory organ in connexion with the vascular system.

In *Solaster, Uraster,* and *Astropecten,* the madreporic plate, though still placed on the dorsal aspect, has been removed from the genital and ocular plates by the appearance of antambulacral ossicles. A small calcareous stone canal and a wide membraneous sinus arise from the inner surface of the madreporic plate. The stone canal opens into a narrow circular canal; the sinus runs along under the stone canal, and, after diminishing considerably in size, opens into a circular blood-vessel. From this circular blood-vessel the radial (neural) vessels take their origin. A small glandular-looking mass, which lies in the floor of the sinus, may correspond to the glandular portion of the "heart" of *Echinus.* In *Ophiura* the madreporic canal springs from one of the interradial oral plates. Before opening into the circular canal it dilates into a vesicle.

The wide circular canal of the Holothurian corresponds to the circular canal at the base of the lantern of *Echinus,* and to the narrow canals of *Solaster, Uraster, Astropecten,* and *Ophiura.*

The long single polian vesicle of the Holothurian corresponds to the polian vesicles of *Solaster* and *Astropecten,* and to those of *Ophiura* when they are present. The lozenge-shaped sinuses of *Holothuria* have apparently nothing homologous to them in either the Sea-Urchins or the Star-fish; but the large oval sinuses of *Holothuria* may correspond to the sinuses lying over the rudimentary tentacles of *Echinus.* In *Holothuria* the radial canals take their origin from the sinuses of the circular canal; in all the other types mentioned the radial canals arise directly from the circular canal.

In *Holothuria* the ampullæ are long and pointed; in the Star-fish they are spherical; in *Echinus* the first series are conical, while the others within the auricles are rounded and those without the auricles are large transversely flattened sacs. In *Ophiura* the ampullæ are absent.

In *Holothuria* and *Echinus* the pedicels are provided with sucking discs, which are sometimes strengthened by a calcareous skeleton. In both, but especially in *Echinus*, they can be projected to a considerable distance beyond the surface. In *Spatangus* the feet are comparatively short, and although some have suckers, many are without them and end in simple rounded points, while others are either simply flattened at their apex, or flattened and split up into leaf-like segments. In *Solaster* and *Uraster* the feet are long, and terminate in large sucking discs, with the exception of a few at the end of each arm, which are pointed, and act as feelers. In *Astropecten* the feet are conical, devoid of suckers, and can only be projected about a quarter of an inch beyond the surface. In *Ophiura* the feet are even more pointed and shorter than those of *Astropecten*. Under the disc at the bases of the arms they are nearly as long as in *Astropecten;* but they gradually diminish in size from within outwards, until near the tips of the arms it is almost impossible to recognise them.

§ III. Nervous System of Echinus.

The internal nervous system of *Echinus* consists of five radial trunks, which may be traced from the ocular plates along the ambulacral areas external to the radial canals to the oral floor, where they bifurcate and unite with each other, so as to form a pentagonal nerve-ring. This ring lies between the œsophagus and the tips of the teeth which project from the lantern. Small branches leave the ring and supply the œsophagus, and lateral branches arise from the several trunks to escape with the pedicels through the apertures of the pore plates. Each trunk lies in a sinus (Plate 80, fig. 13, *c*) situated between the lining membrane of the shell (Plate 80, fig. 13, *d*) and the ambulacral radial canal (Plate 80, fig. 13, *e*); the lateral branches which accompany the first series of pedicels through the oral floor are large and deeply pigmented; the other branches within the auricles are small; those external to the auricles gradually increase in size until the equator is reached, and from the equator to the ocular plates they again diminish. At the equator the trunk is wider than at either pole, and it is often partially divided for some distance at each side of the equator by a deep longitudinal fissure. When the nerve trunk, after being stained with chloride of gold or with osmic acid, is removed from its sinus, it is seen to be enveloped by a thin fibrous sheath. This sheath contains numerous large pigment cells, and has scattered over it irregular masses of protoplasm which have been deposited from the fluid of the neural sinus.

When the sheath is removed the trunk is seen to consist of delicate fibres and of fusiform cells (Plate 80, fig. 14); the cells consist of a nucleus and a thin layer of protoplasm, which projects at each end and terminates in a nerve-fibre.

The lateral branches of the trunk escape along with, and are partly distributed to, the pedicels; the remainder breaks up into delicate filaments which radiate from the base of the pedicel under the surface epithelium (Plate 80, fig. 13, *l*). When one of the large branches already referred to as escaping with the inner row of pedicels is traced through the oral floor after sending a branch to the foot, it breaks up into delicate fibres, some of which run towards the bases of the adjacent spines and pedicellariæ, while others run inwards a short distance towards the oral aperture.

Either in connexion with, or anatomically independent of these filaments from the lateral branches of the nerve trunks, there is an external plexus lying almost immediately under the surface epithelium and extending from the shell to the spines and pedicellariæ. The fibres (Plate 80, fig. 15) of this plexus closely resemble those of the lateral branches of the trunk; but generally they are smaller in size and have a distinct connexion with nerve cells. The cells consist of an oval nucleus and of a layer of protoplasm, which is generally seen to project in two, or sometimes in three, directions—the several processes often uniting with similar processes from adjacent cells so as to form a fibro-cellular chain or network.

In preparations from portions of Echini treated with both chloride of gold and osmic acid, we have succeeded in tracing the plexus over the surface of the shell between the spines and pedicellariæ; and from the surface of the shell to the capsular muscles at the bases of the spines (Plate 80, fig. 16). Further, we repeatedly observed delicate fibres passing beyond the muscles, apparently to end under the epithelium over the surface of the spines (Plate 80, fig. 13, l').

In the case of the pedicellariæ, the plexus on reaching the stem runs along between the calcareous axis and the surface epithelium, to reach and extend over and between the muscular and connective tissue-fibres between the calcareous axis and the bases of the mandibles (Plate 80, fig. 13, l'', and fig. 18). The plexus, now in the form of exceedingly delicate fibres connecting small bipolar cells, reaches the special muscles of the mandibles. In several preparations, delicate fibres appeared to extend towards the sensitive epithelial pad (Plate 80, fig. 13, s) situated on the inner surface of each mandible, a short distance from the apex. Although this plexus is especially related to the muscular fibres—lying over and dipping in between them—it is also related to the surface epithelium, and delicate fibres often extend from it to end under or between the epithelial cells.

PART II.—PHYSIOLOGY.

§ I. Natural Movements.

It is desirable to begin this account of the physiology of the locomotor system, with a somewhat full account of the natural movements exhibited by the various species of Echinoderms which we have had the opportunity of observing. This is desirable, not only because it is necessary to study the natural movements before we can be in a position to appreciate the results of the following experiments, but also because these natural movements form in themselves a study of considerable interest.

1. Star-fishes.—(A) Taking the common Star-fish (*Uraster rubens*) as our start-

ing point, it is needless to dwell upon the well-known mechanism of the ambulacral system. The rate of crawling upon a flat horizontal surface is 2 inches per minute. The animal usually crawls in a determinate direction, and, while crawling, the ambulacral feet at the end of each ray are protruded forwards as feelers; this is particularly the case with the terminal feet on the ray, or rays, facing the direction of advance. When in the course of their advance these tentacular feet happen to come into contact with a solid body, the animal may either continue its direction of advance unchanged, or may deflect that direction towards the solid body. Thus, for instance, if, while the Star-fish is advancing along the floor of a tank, the tentacular feet at the end of one of its rays happen to touch a perpendicular side of the tank, the animal may either at once proceed to ascend this perpendicular side, or it may continue to progress along the floor—feeling the perpendicular side with the ends of its rays perhaps the whole way round the tank, and yet not choosing,* as it were, to ascend. What it is that determines the animal in some cases to ascend, and in other cases not, we were unable to ascertain.

When a Star-fish ascends the perpendicular side of a tank or bell-jar till it reaches the surface of the water, it very frequently performs a number of peculiar movements, which we may call acrobatic (see Plate 81, fig. 19). On reaching the surface of the water, the animal does not wish to leave its native element, and neither does it wish again to descend into the levels from which it has just ascended. It therefore begins to crawl to one side or the other, and while crawling it every now and then throws back its uppermost ray, or rays, to feel for any solid support that may happen to be within reach. The distance to which the rays may thus be thrown back is remarkable; for the animal may hold on with its two lower rays alone, or even with the end of a single ray, and throw back the whole of the other rays with the central disc into a

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* It may be as well to explain that in using such words as these, we do not, in the present paper, attach to them any psychological signification; they are used as merely metaphorical terms which serve most briefly, and therefore most conveniently, to express the resultants of those systems of physiological stimuli, the composing members of which we were not able to observe. When one Star-fish appears to choose to ascend the side of a tank, while another Star-fish, under apparently precisely similar circumstances as to stimulation, seems to prefer walking along the floor, we can only suppose that the circumstances of stimulation, although apparently similar, are not really so, and therefore that the difference in the result is due to some difference in the stimulation. Of course it may be objected to this that the same remark applies to cases in which the psychological element unquestionably enters—choice on its physiological side being merely the resultant of some unobservable system of stimuli. But without here entering on the whole question of the relation between body and mind, it is enough to point out that the only evidence we can have of a physiological determination presenting a psychological side, is by observing that the organism which exhibits the determination is capable of altering it on future occasions, if the determination first made is found by individual experience to be injurious. In other words, the power of learning by individual experience is the only unequivocal evidence we can possess of the presence, in any animal, of a psychological element; and as we have observed no such evidence in the case of any of the Echinoderms, we desire it to be understood that we consider all their movements to be of the so-called "reflex" kind.

horizontal position—the ambulacral surface of the rays which are thrown back being then of course turned up, so as to face the surface of the water. If the rays succeed in finding a solid body, they will perhaps—though not necessarily—fasten upon it, and when their hold is secure, the rays which hitherto held the animal to the side of the tank relax their suckers, so that the Star-fish swings from its old to its new surface of attachment. The activity and coordination which the rays manifest in executing these various acrobatic movements is surprising, and give to the animal an almost intelligent appearance.

If a Star-fish is turned over on its dorsal surface upon the flat floor of a tank, it almost immediately begins to right itself. Its method of doing so (see Plate 81, fig. 20) is to twist round the tip of one or more of its rays (*a*), until the ambulacral feet there situated are able to get a firm hold of the floor of the tank; then by a successive and similar action of the ambulacral feet further back in the series, the whole end of the ray is twisted round (*b*), so that the ambulacral surface of the end is applied flat against the flat surface of the tank (*c*). The manœuvre continuing, the semi-turn or spiral travels progressively all the way down the ray. Usually two or three adjacent rays perform this manœuvre simultaneously; but if—as is sometimes the case—two opposite rays begin to do so at first, one of them soon ceases to continue the manœuvre, and one or both of the rays adjacent to the other takes it up instead. The spirals of all these rays being turned in the same direction (see *a*, *b*, *c*), the result is, when they have proceeded sufficiently far down the rays, to drag over the disc and the remaining rays (*d*, *e*), which abandon their hold of the bottom of the tank, so as not to offer any resistance to the lifting action of the other rays; the animal, therefore, turns a complete somersault—the disc and inactive rays being thrown over the active ones with considerable rapidity. The whole movement—from the first twisting round of the tips of the active rays to the final turning over of the whole animal—does not usually occupy more than about half a minute. It will be seen that this whole movement implies no small amount of co-ordination, and it is therefore of interest to consider it in this connexion. As a general rule, the rays are from the first co-ordinated to effect the righting movement in the direction in which it is finally to take place—the rays which are to be the active ones alone twisting over, and so twisting that all their spirals turn in the same direction. This, however, although usually, is by no means invariably the case; for at the commencement of the righting movement different rays may act in antagonistic ways—twisting their spirals in opposite directions, and doubling their ends under, without reference to the direction in which the somersault is eventually to be turned. But in all cases a definite plan, so to speak, is very soon made—the opposition rays, as previously stated, leaving go their hold, the antagonistic spirals of adjacent rays being unwound or reversed, while any antagonistic doublings are straightened out; so that the whole righting movement in fresh specimens never, at the most, occupies more than a minute.

(B.) SUN-STARS (*Solaster*).—All the remarks which have been made on the natural movements of the common Star-fish, are equally applicable to the Sun-stars. When placed on the dorsal surface, however, their righting movements are conducted on a slightly different plan. Owing to the disc being here so large in proportion to the length of the rays, it would be useless in the latter to endeavour to turn over the former by twisting themselves into spirals. They therefore adopt a device which in the common Star-fish is sometimes made accessory to that of twisting the rays, and which is also shown in Plate 81, fig. 20;* they double under the ends of a number of adjacent rays, laying hold of the floor of the tank with their ambulacral feet as the doubling progressively advances up the length of the ray. When this doubling has advanced up a considerable length of a number of adjacent rays, the ambulacral feet upon these rays obtain a sufficient purchase to drag over the whole of the large disc in a manner otherwise similar to that which has just been described in the case of the common Star-fish.

(C.) Astropecten aurantiacus.—The ordinary locomotor movements of this species are highly peculiar. The form of the animal very much resembles that of the common Star-fish, although its disc is proportionally larger, and the whole animal smaller. Its ambulacral feet are pointed tubes, rather less than a quarter of an inch long, and, as before stated, unprovided with any sucker at the tip. When the animal is not walking, these feet are nevertheless in a constant state of movement, and their movements are then of a peculiar writhing, almost vermiform character—twisting about in various directions, and frequently coiling round each other. When fully protruded, however, they are perfectly straight and stiff. Their protrusion—whether complete or partial—takes place with great suddenness, and at all times—whether the animal is stationary or not—a number of feet are being protruded, while a number of others are as continually being retracted. The feet usually remain extended for a considerable though indeterminate time (quarter to half a minute), and then very suddenly again collapse. These movements of protrusion and retraction are so sudden that the eye is unable to follow them, and as they are always taking place over a large number of feet at the same time, the appearance presented by the whole series is that of a continual flick-flacking. The erection of the feet takes place obliquely from the median line of the ray, and the collapse takes place laterally—the feet therefore falling over upon the sides of the ray. The animals, as previously observed, can crawl up perpendicular surfaces in the manner previously described; but, owing probably to the absence of any differentiated structures in the form of sucking discs, they soon tire—never succeeding in crawling more than a few inches up the side of a tank before they drop off.

The ordinary locomotor movements of this species are, as we have said, highly

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* This figure has been drawn so as to show both these devices. Very often the common Star-fish does not double under the ends of the rays at all, as represented in the figure; but depends entirely on the spiral rotation of the rays for the execution of its righting manœuvre—the dorsal aspect of the active rays being therefore not raised from the floor of the tank as represented.

peculiar, and they may best be studied by taking the animal out of the water, placing it upon a dry flat surface, and watching the movements of its feet by placing the eye on a level with them. It may then be observed that the mode of locomotion is as follows:—The animal points all the feet of all the rays in the direction of advance, and then simultaneously distends them with fluid; they thus become so many pillars of support, which raise the animal as high above the flat surface as their own perpendicular length. The fluid is then suddenly withdrawn, and the Star-fish falls forward flat with a jerk. This manœuvre being again and again repeated at intervals of about a quarter of a minute, the animal progresses in a uniform direction at the rate of about an inch per minute. It is particularly noteworthy that, in this mode of progression, all the feet of all the rays are co-ordinated in their action for determining one definite direction of advance—those in the ray facing that direction acting forwards, or centrifugally, those in the hinder rays backwards, or centripetally, and those in the lateral rays sideways.

When the animal is walking along a flat horizontal surface in water, its mode of progression appears to be the same as it is on a dry surface, only the motion of the feet is now so rapid that there is a considerable difficulty in following it with the eye. It appears, however, as if the feet, besides being used as walking-poles in the manner just described, are also used to sweep backwards along the floor of the tank, and so to assist in propelling the animal forwards after the manner of cilia. Therefore, while walking in water, this Star-fish is kept stilt-high above the surface on which it is walking, by some of its feet, while others of its feet are engaged in these sweeping movements.

The result of all these movements is to produce a kind of locomotion which would seem more suited to a Centipede than to a Star-fish, and the suggestion that it is so is borne in upon the mind all the more forcibly by the surprising rate at which the animal is thus enabled to move. For while an ordinary Star-fish only crawls at the rate of 2 or 3 inches per minute, *Astropecten* can crawl, or perhaps more correctly run, at the rate of between 1 and 2 feet per minute.

When placed upon their backs, the righting movement of these Star-fish are performed by raising the disc from the floor of the tank, till the animal rests only on the tips of its five rays (Plate 81, fig. 21). Two rays—for instance, 4 and 5—are then bent under the disc, while 2 and 3 are raised on a level with the disc. The disc becoming tilted in the direction of 4 and 5, 2 and 3 are now thrown over the disc, and assist by their weight in revolving the whole system upon an axis situated at about the level A, A. This mode of executing the righting manœuvre is somewhat similar to that which occurs in the Sun-stars, only in this case the disc is raised entirely from the floor of the tank, and the whole movement is performed without any aid from the ambulacral feet; the latter, however, are kept in active motion during the whole of the righting movement. Sometimes only one arm, instead of two, is used as the fulcrum over which the disc and the other arms are thrown. In all cases the righting is effected with much more energy than in the case of any of the species previously mentioned.

(D.) BRITTLE-STARS. (*Ophiuridæ*).—In these Star-fish the ambulacral feet have been reduced to rudiments, which, however, are exceedingly active—their mode of protusion and retraction being precisely similar to that which has just been described in the case of *Astropecten*. Indeed, their activity is even greater in the case of the Brittle-stars; but as they are very short, and not provided with suckers, it does not appear that they are of any use in assisting locomotion. The Brittle-stars, however, are much the most actively locomotive of all the Star-fish; and the reason is that, having discarded the method of crawling by the ambulacral system, which is common to nearly all the other Echinoderms, they have adopted instead a completely new, and a much more effectual method. As the family name of the group implies, the muscular system of the rays is very perfectly developed, enabling these long and snake-like appendages to perform with energy and quickness a great variety of snake-like writhings. As the movement of all the arms is co-ordinated, the animal is able by these writhings to shuffle itself along flat horizontal surfaces at a considerable speed. But when it desires to move still more rapidly, it adopts another plan. If the animal is advancing in the direction of the arrow (Plate 82, fig. 22), one of its rays, 1, is pointed straight in that direction; the two adjacent rays, 2 and 3, are thrown forwards as far as possible, and then, by a strong contraction downwards upon the floor of the tank, these two rays partly elevate the disc, and, while keeping the disc so elevated, throw themselves violently backwards into the form of crescents, as represented in 2′ and 3′. The result of this movement is to propel the animal forwards —ray 1 being pushed into the position 1′, while rays 4 and 5 are dragged along into the positions 4′ and 5′. As soon as the rays 2 and 3 have assumed the position 2′ and 3′, they are again, without an instant's delay, protruded straight, to be again as instantly thrown into the form of the curves 2′ and 3′. Thus the animal advances by a series of leaps or bounds, which vary between 1½ and 2 inches in length, and which follow one another with so much rapidity, that a lively Brittle-star can easily travel at the rate of 6 feet per minute. While thus travelling, the ray, 1, is usually kept straight pointed and partly uplifted—doubtless in order to act as a feeler; but sometimes the animal varies its method of progression, so as to use two pairs of arms for the propelling movements, and in this case the remaining arm is, of course, dragged behind, and so rendered useless as a feeler. The Star-fish is able to use any pair, or pairs, of its arms as propellers indifferently, and in all cases it so uses them by resting their outer, or distal, thirds upon the tank floor, and at each leap raising their remaining two-thirds, together with the anterior part of the disc, off the floor; at the end of each leap, however, the whole animal (except, perhaps, the elevated feeler-ray) lies flat upon the floor.

Brittle-stars, when placed upon their backs, adopt the same method of righting themselves as has already been described in the case of *Astropecten*. They are, however, even more energetic in executing their righting movements—raising their discs high above the tank floor upon their long arms, and completing their movements in a few seconds. So vigorous are these Star-fish, that they are able to execute this manœuvre even upon a dry table, although the weight to be overcome is so much greater in air than in water.

It may be added that these Star-fish are not able to ascend perpendicular surfaces, owing to the rudimentary condition of their ambulacral apparatus.

2. ECHINI.—In striking contrast to the rapid locomotion of the Echinoderms last considered, stands the slow locomotion of the *Echinus*, which along a horizontal surface takes place at the rate of only 6 inches per minute, and up a perpendicular surface at the rate of 1 inch in 4 minutes. Looking to the slowness of this rate of locomotion, it must strike us as a curious fact that there is, perhaps, no animal which can properly be said to approach the *Echinus* in respect of the number and elaboration of special mechanisms subservient to the function of locomotion. Careful observation has satisfied us that these special mechanisms are four in number, and each of these displays an immense amount of elaboration. We may best consider these four mechanisms by taking them separately.

(A.) *Ambulacral feet, or pedicels.*—This system is both structurally and functionally closely similar to the homologous and analogous system in Star-fishes. In the *Echinus*, however, it is of more use than in the Star-fish as a system of anchors and feelers. The form of the *Echinus* being globular, while that of the Star-fish is flat, it follows that the animal is more exposed to the displacing influence of currents, because offering a larger surface for their action. Consequently, a need arises for a more secure system of attaching the animal to the surfaces over which it may be crawling, and this need is supplied by the ambulacral feet acting more the part of anchors than they do in the Star-fish. Thus it is that in forcibly removing an *Echinus* from whatever surface it may be adhering to, a much greater resistance is encountered than one finds in the case of Star-fish, and—especially if a little time is given to the animal after a first alarm to establish a firmer hold—the suckers stick so tightly that a certain number allow themselves to be torn from the organism rather than leave go their attachments—these suckers being therefore left behind, fastened upon the surface to which they were adhering. Under similar circumstances a Star-fish will never thus leave its suckers behind. Indeed, a Star-fish does not seem to fear abandoning itself to the mercy of currents; for, as we shall subsequently see, a very small amount of provocation will induce it to abandon its hold of a perpendicular surface spontaneously, in order to effect its escape by falling through the water. An *Echinus*, on the other hand, always seems, as it were, nervously anxious about its anchorage—in all its movements its first concern appearing to be to have its steadiness amply secured by a sufficient number of suckers, and this even in the perfectly still water of a tank.

The other function of the pedicels which is peculiar to the *Echinus*, viz., that of feelers, also no doubt arises from the shape of the animal; for while in the Star-fish the pedicels are confined to the ventral surface of a flat-shaped organism, in the *Echinus* they are protruded from all sides of a globe. That they are habitually used as feelers is evident from watching their movements. For instance, when an *Echinus* is crawling along a flat horizontal surface, the rows of pedicels facing the direction of advance are more strongly protruded than those of the other rows; although none of the pedicels from some distance below the equator are in use for walking, in the rows mentioned they are extended to their fullest length, in order to feel for any object which the animal may possibly be approaching. On the other rows only a single pedicel here and there is thus fully extended; such, however, no doubt also act as feelers, to warn the *Echinus* of the approach of any object from behind or from the sides. When a perpendicular surface is reached, the animal may either ascend it or crawl along for an indefinite distance, feeling it all the way with its pedicels. It may here be added that when an *Echinus* starts walking, it generally keeps pretty persistently in one direction of advance. If it be partly rotated by the hand, or other external means, it does not continue in the same direction, but continues its own movements as before; so that, for instance, if it has been turned half round, it will proceed in a direction opposite to that in which it had been proceeding before its rotation. When fresh specimens are at rest, a certain small percentage of feet are used as anchors. The others are strongly protruded on all sides as feelers; but in specimens not quite fresh, nearly all the feet not in use as anchors are retracted, with only one here and there protruded as a feeler.

When an *Echinus* is inverted upon its ab-oral pole, its shape renders execution of the righting manœuvre a much more difficult matter than is the case in the analogous position of a Star-fish; for while a Star-fish is provided with flat, flexible, and muscular rays, composing a small and light mass in relation to the motive power, an *Echinus* is a rigid, non-muscular, and globular mass, whose only motive power available for conducting the evolution is that which is supplied by relatively feeble pedicels. It is therefore scarcely surprising that unless the specimens chosen for these observations are perfectly fresh, they are unable to right themselves at all; they remain permanently inverted till they die. But if the specimens are fresh, they sooner or later invariably succeed in righting themselves, and their method of doing so is always the same. Two, or perhaps three, adjacent rows of pedicels are selected out of the five, as the rows which are to accomplish the task (Plate 82, fig. 23). As many feet upon the rows as can reach the floor of the tank are protruded downwards and fastened firmly upon the floor; their combined action serves to tilt the globe slightly over in this direction—the anchoring feet on the other, or opposite, rows meanwhile releasing their hold of the tank floor to admit of this tilting (Plate 82, fig. 24). The effect of the tilting is to allow the next feet in the active ambulacral rows to touch the floor of the tank, and when they have established their hold, they assist in increasing the tilt; then the next feet in the series lay hold, and so on, till the globe slowly but steadily rises upon its equator (Plate 83, fig. 25). The difficulty of raising such a heavy mass into this position by means of the slender motive power available can be at once appreciated on witnessing the performance, so that one is surprised, notwithstanding the co-ordination displayed by all the suckers, that they are able to accomplish the work assigned to them. That the process is in truth a very laborious one is manifest, not only from the extreme slowness with which it takes place, but also because in the case of not perfectly strong specimens complete failure may attend the efforts to reach the position of resting on the equator—the *Echinus* after rearing up a certain height, becoming exhausted and again falling back upon its ab-oral pole. Moreover in some cases it is interesting to observe that when the equator position has been reached with difficulty, the *Echinus,* as it were, gives itself a breathing-space before beginning the movement of descent—drawing in all its pedicels save those which hold it securely in the position to which it has attained, and remaining in a state of absolute quiescence for a prolonged time. It then suddenly begins to protrude all its feet again, and to continue its manœuvre. At any time during such a period of rest, a stimulus of any kind will immediately determine a re-commencement of the manœuvre.

It will be perceived that as soon as the position just described has been attained, gravity, which had hitherto been acting in opposition to the righting movement, now begins to favour that movement. It might, therefore, be anticipated that the *Echinus* would now simply let go all its attachments, and allow itself to roll over into its natural position. But an *Echinus* will never let go its attachments without some urgent reason; and in this case it lets itself down almost as slowly as it raised itself up. So gently, indeed, is the downward movement effected, that an observer can scarcely tell the precise moment at which the righting is concluded. Therefore, in the downward movement, the feet, which at the earlier part of the manœuvre were employed successively in rearing the globe upon its equator, are now employed successively in preventing its too rapid descent (Plate 83, fig. 26).

Several interesting questions arise with reference to these righting movements of *Echinus.* First of all we are inclined to ask what it is that determines the choice of the rows of feet which are delegated to effect the movements. As the animal has a geometrical form of perfect symmetry, we might suppose that when it is placed upon its pole, all the five rows of feet would act in antagonism to one another; for there seems nothing more to determine either the action or the inaction of one row rather than another. The answer to this question is not very clear. First of all it occurred to us that, although the form of the animal presents a geometrical symmetry, the anatomy of the animal is not symmetrical, and therefore that some of the feet-rows might be functionally prepotent over the others. But on observing a great number of specimens, we satisfied ourselves that among different individuals any homologous rows of feet might be used indiscriminately—*i.e.*, taking the madreporic plate as the point of reference, we found that in different individuals rotation might take place in any direction with reference to that plate indifferently. On the other hand, individual specimens would sometimes manifest a marked tendency to rotate in one direction, *i.e.*, they would repeatedly choose the same feet-rows wherewith to execute their righting movements. In these individual specimens, therefore, the probability is that the feet-rows thus selected were selected because of some slight accidental prepotency or superiority over the others; and thus the explanation in all cases doubtless is that, although the physiological conditions are pretty nicely balanced, they are not so nicely balanced as to leave positively nothing to determine which rows of feet shall be used.

Another question of still more interest is that as to the prompting cause of all these laborious movements. Is it that the animal has some dim consciousness of discomfort, owing to a disturbance of a nascent sense of gravity? Or is the whole series of movements purely mechanical, and determined only by the fact that the feet in the feet-rows are all arranged serially, and therefore when feet A, B, and C have established a firm hold and thereby tilted the globe over a certain distance, opportunity is afforded for D, E, and F to establish a hold, and so on? This question had better, for the present, be deferred.

(B.) *Spines.*—(C.) *Lantern.*—It is, of course, well known that the spines of the *Echinus* are used in locomotion; but hitherto their action does not seem to have been carefully observed, and we are not aware that the part played by the lantern has ever been observed at all. Observations on these points may best be made by taking the animal out of the water, and placing it upon a table; it will then soon begin to walk in some definite direction—*i.e.*, in a straight line—and in doing so the only organs used for the purposes of locomotion are the spines and the lantern, the ambulacral feet under these circumstances not being protruded at all. The rate of locomotion is very slow, viz., about 1 inch per minute; but it is continuous, takes place, as already observed, in a definite direction, and is accomplished by means of a number of highly co-ordinated movements. The latter are as follows:—

The whole dental apparatus, or lantern, admits of being protruded and retracted; when protruded, the sharp and polished point which is composed by the mutual contact of the five teeth, stands out below the ventral surface of the animal; when retracted, this point is drawn within the body cavity of the animal. The movements of protrusion and retraction are perfectly rythmical, at the rate of three or four revolutions per minute. When the lantern is drawn back to its fullest extent, it is tilted to one side, in such a way that the teeth point towards the direction of advance. The lantern is then brought down and protruded till the teeth rest upon the table; some of the spines have meanwhile been rotating on their ball and socket-joints, in such a way that their points are in a position on the table to push the animal towards the direction in which the teeth are pointing. This push being communicated by the spines while the teeth are held firmly down, the result is to raise the whole animal upon the point of its teeth, and to let it fall again upon the other side of the teeth; the point of the teeth is thus used as a fulcrum, over which the animal is made to move by the co-ordinated action of its spines. Of course, when it has completed this movement, the teeth are pointing away from the direction of advance—the whole lantern having been, as it were, left behind by the movement of the shell over it as a pivot, and therefore sloping away from the direction of advance at the same angle as that with which it had previously sloped towards it. The lantern is now again retracted, and during its retraction, partly rotated upon its horizontal axis, so that by the time it is again protruded, its vertical axis is again pointing towards the direction of advance. And so the manœuvre is repeated over and over again—the *Echinus* advancing by a succession of jerks as it repeatedly tumbles over its teeth. As already stated, the movements of the lantern are rythmical, and therefore the jerks take place at regular intervals. It is important, however, to observe that although the lantern is thus used to assist the spines in locomotion, it is doubtful whether such is the full explanation of the lantern's movements. For, on the one hand, it is certain that these movements are not necessary, but only accessory to locomotion; and, on the other hand, they continue to take place under circumstances where they can be of no use in locomotion. Thus we have observed that young specimens of *Echinus* do not use their lanterns for locomotion, as older specimens always do. Probably the older, and therefore larger specimens, use their lanterns more than the younger and smaller ones, on account of having to move so much heavier a mass. Also, the relatively greater length of the spines in the smaller specimens makes it much more difficult for the lantern to touch the table. This view is confirmed by the fact that, on cutting the spines of young specimens shorter, these small *Echini* begin to use their lanterns after the manner of larger specimens. But, be this as it may, the fact that in young specimens the lanterns rarely touch the table is proof that the spines are here alone sufficient to produce locomotion. Again, as before observed, these peculiar movements of the lantern take place under circumstances where they can be of no use in producing locomotion. Thus, for instance, they take place in young specimens in the same way as in old, although, as just stated, the lanterns in this case do not touch the table at all. And again, if an *Echinus* be placed on its aboral pole, the lantern at once begins its rhythmical movements, and continues them as long as the animal remains in that position. In this case there is added to the movements already described another perfectly rhythmical movement, which consists in closing and opening the teeth—the time of complete closure corresponding with that of greatest protusion, and the time of fullest opening with that of greatest retraction. It appears, therefore, that these rhythmical movements of the lantern, although undoubtedly of use in assisting locomotion in some cases, may possibly have some other function to perform in the economy of the animal. Whether this is so or not, there seems to be some intimate connexion between these movements of the lantern and the movements of the spines; for when one stops the other stops, and when one begins the other begins. The movements of the lantern may best be studied by taking away the top of the *Echinus* shell, and looking down upon the lantern from above; it may then be seen exhibiting its rhythmical movements, which when thus viewed forcibly remind one of the rolling of a ship at sea. The complex muscular system of the lantern seems to us mainly subservient to the execution of these movements, and yet —so far as we could detect—they are utterly useless for any purpose other than that of assisting locomotion.

(D.) *Pedicellariæ.*—A good deal of speculation has been expended on the probable function of these organs. Prolonged observation has satisfied us that they have a function which has not hitherto been suspected, viz., that of assisting locomotion. A full account of our observations on these structures, however, had better be reserved for the next section of this paper.

3. SPATANGUS.—This animal crawls about somewhat slower than *Echinus*, keeping its very long spines partly erect to act as feelers. It does not appear able to climb perpendicular surfaces. When placed upon its back, it has more difficulty in righting itself than any of the Echinoderms that we have observed; for, on account of its having such flat poles and such short ambulacral feet, it is, when inverted, placed at even a greater disadvantage than is *Echinus*. Therefore, many specimens—especially large specimens—are never able, when inverted on a hard flat surface, to right themselves at all; smaller specimens, however, are able to do so after an expenditure of much time and energy. Their method of doing so is quite different from that of *Echinus*. Indeed, looking to the shape of *Spatangus* and to the character of its pedicels, the method of righting adopted by *Echinus* would be here clearly impossible. This animal, therefore, rights itself entirely by the action of the only organs which are available for the purpose, viz., its long and mobile spines. The long spines are not very many in number; but as their strength and co-ordination is surprising, they enable the animal, by a series of pushings and proppings, eventually to turn itself completely over from one of its flattened surfaces to the other. In doing this it usually, but not invariably, turns over upon its broad end. When the long spines are removed, the animal, of course, is no longer able to right itself.

4. HOLOTHURIANS.—Very little has to be said on these sluggish members of the Echinoderm group. They crawl slowly, and indulge in prolonged periods of quiescence. They are, however, able to climb perpendicular surfaces.

From this account of the natural movements exhibited by the several groups of Echinodermata here considered, it may be observed that we have presented to our view an interesting series of graduated modifications. At one end of this series we have *Echinus* and *Spatangus* with their rays all united into a box-like rigid shell. At the other end of the series we have the Brittle-stars with their muscular rays, highly mobile, and indeed snake-like in their well co-ordinated movements. Midway in the series we have the Sea-cucumber and common Star-fish, where the body is flexible and mobile, though not so much so as in the Brittle-stars. Now, the interesting point to observe is, that in correlation with this graduated difference in the function of the rays, we have a correspondingly graduated difference in the development of the ambulacral system. In *Echinus* and *Spatangus* this system is seen in its most elaborate and efficient form—in *Echinus* the pedicels, spines, and pedicellariæ being more highly developed and useful than in any of the other groups, except *Spatangus*, where the spines are even more so. In the common Star-fish, Sun-stars, and Sea-cucumbers, the ambulacral feet are still the most important organs of locomotion, although even here we begin to see that the development of the general muscular system has begun to tell upon that of these specially locomotor organs. Again, in *Astropecten* the still greater development of the general muscular system has told still further upon that of the ambulacral feet, the terminal suckers having become aborted. Lastly, the Brittle-stars have altogether discarded the use of their ambulacral feet in favour of the much more efficient organs of locomotion supplied by their muscular rays; and not only the terminal suckers of these feet, but even the whole of the feet themselves, have dwindled into useless rudiments.

§ II. STIMULATION.

1. GENERAL FACTS OF STIMULATION.—All the Echinoderms we have observed respond to all kinds of stimulation. The period of latency varies considerably in different species, and in different parts of the same animal. In the Holothurians it is remarkably long, and from the seat of stimulation there very frequently starts a wave of strong contraction, which passes with extreme slowness throughout the length of the animal in the form of a deep constriction. Similar waves frequently occur spontaneously.

All the Echinoderms seek to escape from injury. Thus, for instance, if a Star-fish or *Echinus* is advancing continuously in one direction, and if it be pricked or cut in any part of an excitable surface facing the direction of advance, the animal immediately reverses that direction; or, if it be taken out of the water and a drop of some irritating fluid be placed on any part of the external surface, the animal will endeavour to move away from the source of irritation; whether placed upon a dry table or returned to the water, the Echinoderm will at once strike off in a perfectly straight line from the source of irritation, and for a long time will travel much more rapidly than usual. When two points of the surface are thus irritated, the direction of advance is usually the diagonal between them. When a greater number of points are irritated, the direction of advance becomes uncertain, but if any, even short, interval of time is allowed to elapse between the application of successive stimuli to different parts of the surface, the direction of advance will be in a straight line from the stimulus applied latest. When a Star-fish is fastened upon a perpendicular surface, and any part of its body is irritated, as, *e.g.*, by a nip with the forceps, the animal, if a Sun-star, will actively run away from the irritation. If, however, the latter be followed up and repeated, the Star-fish seems to make up its mind to escape in a still more expeditious manner, for it immediately lets go its hold with all its suckers, and falls to the bottom of the water. A common Star-fish will generally resort to this method when first irritated, without waiting for a repetition of the stimulus. An *Echinus,* on the other hand, will not drop off a perpendicular surface unless compelled to do so by serious irritation; it crawls away as quickly as possible, and sometimes rotates upon its axis in a manner afterwards to be described, whereby, without leaving go its hold of the perpendicular surface, it is able to alter its position rapidly. But of all the Echinoderms the most curious to observe in this connexion are the Brittle-stars, for these may be made to leap about in any number of directions with much activity, by gently stimulating different parts of their bodies successively. When any part of the dorsal surface of any Star-fish is irritated, not unfrequently one of the arms is doubled over and touches the seat of irritation, as if to endeavour to brush away the offending body.

That the external surface of a Star-fish should prove itself to be excitable is what we should perhaps expect *à priori,* although we might not expect to find so high a degree of co-ordination manifested by the nervous system as is implied by its responses to the cutaneous excitations above mentioned. But that the external surface of an *Echinus* or *Spatangus* should be so highly excitable as it is, we should scarcely have anticipated—particularly before our observation of the external nervous plexus; for at first sight it would seem that the numberless long and mobile feet—to say nothing of the spines—would be sufficient to convey all the information that the animal requires concerning the external world, without its exterior requiring to be rendered sensitive over its whole surface. Yet we find, so far is this from being the case, that the external surface cannot be touched with a needle's point at any part without the whole animal being affected thereby. We have already described the nervous plexus whereby this general sensitiveness of the external surface is secured. We must now enter pretty fully into the functions of this plexus as revealed by sundry experiments on the multitudinous and wonderful system of organs which, either directly or indirectly, depend upon this plexus for their innervation.

These organs are the ambulacral feet, the spines, and the pedicellariæ. That all these organs are in nervous connexion with the external plexus is proved by the fact that when any part of the external surface is touched, however gently, all the feet, spines, and pedicellariæ within reach of that point, and even far beyond, immediately approximate and close in upon the point, so holding fast to the needle, or whatever other body may be used as the instrument of stimulation. This simultaneous movement of such a little forest of prehensile organs is a singularly beautiful spectacle to witness. In executing it, the pedicellariæ are much the most active, the spines somewhat slower, and the ambulacral feet very much slower. If the object with which the external surface is touched be itself small enough, or presents edges narrow enough, to admit of the forceps on the pedicellariæ establishing a hold upon it, it is seen to be immediately seized by some of these organs, and held there till the spines and ambulacral feet come up to assist; but if the object is too large, or does not present any surfaces which the pedicellariæ are able to catch—such, for instance, as the point of a pencil—the spines alone are able to hold it with wonderful firmness by forcing their tips against it on all sides.

The area thus affected by an ordinary stimulation, such as that supplied by a touch with a needle, measures in a longitudinal direction about half an inch. The extent of the area affected in a tranverse or latitudinal direction depends upon the point stimulated with reference to the ambulacral feet. Midway in an interambulacral area the influence extends as far as the double rows of feet on either side; the feet, however, of the inner, or nearer rows, moving more decidedly than those of the outer, or further, rows. The spines are rarely affected beyond the area named by a stimulus of mere contact, but in the case of the pedicellariæ the irradiation of the stimulating influence may proceed further, sometimes extending as far as the second double row of feet, or ambulacral area, on either side; the certainty and activity of their movements, however, rapidly diminish with their distance from the seat of stimulation. At and near the seat of stimulation, *i.e.*, within the area first named, the certainty and activity of their movements are very great, and the period of latency very short; in other words, immediately any solid body touches any part of the external surface of an *Echinus*, it is surrounded by all the pedicellariæ in the neighbourhood, while even those which are too far away to touch the object will, perhaps for the long distance round which we have named, bend towards it.

2. PHYSIOLOGY OF THE PEDICELLARIÆ.—And here we have the proof of the function of the pedicellariæ. In climbing perpendicular or inclined surfaces of rock, covered with waving sea-weeds, it must be of no small advantage to an *Echinus* to be provided on all sides with a multitude of forceps, all mounted on movable stalks, which instantaneously bring their grasping forceps to bear upon and to seize a passing frond. The frond being thus arrested, the spines come to the assistance of the pedicellariæ, and both together hold the *Echinus* to the support furnished by the sea-weed. Moreover the sea-weed is thus held steady till the ambulacral feet have time also to establish their hold upon it with their sucking discs. That the grasping and arresting of fronds of sea-weed in this way for the purposes of locomotion constitute an important function of the pedicellariæ, may at once be rendered evident experimentally by drawing a piece of sea-weed over the surface of a healthy *Echinus* in the water. The moment the sea-weed touches the surface of the animal, it is seen and felt to be seized by a number of these little grasping organs, and—unless torn away by a greater force than is likely to occur in currents below the surface of the sea—it is held steady till the ambulacral suckers have time to establish their attachments upon it. Thus there is no doubt that the pedicellariæ are able efficiently to perform the function which we regard as their chief function. We so regard this function, not merely because it is the one that we observe these organs chiefly to perform, but also because we find that their whole physiology is adapted to its performance. Thus their multitudinous number and ubiquitous situation all over the external surface of the animal, is suggestive of their being adapted to catch something which may come upon them from any side,

and which may have strings and edges so fine as to admit of being enclosed by the forceps. Again, the instantaneous activity with which they all close round and seize a moving body of a size that admits of their seizing it, is suggestive of the objects which they are adapted to seize being objects which rapidly brush over the surface of the shell, and therefore objects which, if they are to be seized at all, must be seized instantaneously. Lastly, we find, on experimenting upon pedicellariæ whether *in situ* or when separated from the *Echinus*, that the clasping action of the forceps is precisely adapted to the function which we are considering; for not only is the force exerted by the forceps during their contraction of an astonishing amount for the size of the organ (the serrated mandibles of the trident pedicellariæ holding on with a tenacity that can only have reference to some objects liable to be dragged away from their grasp), but it is very suggestive that this wonderfully tenacious hold is spontaneously relaxed after a minute or two. That is to say, the pedicellariæ tightly fix the object which they have caught for a time sufficient to enable the ambulacral suckers to establish their connexions with it, and then they spontaneously leave go; their grasp is not only so exceedingly powerful while it lasts, but it is as a rule timed to suit the requirements of the pedicels.*

On the whole, therefore, we can entertain but little doubt concerning the main function at least of the trident pedicellariæ in the *Echinus*. But criticism will, of course, immediately object that in other Echinoderms these organs are too small or too few to be of any use in assisting locomotion in the way just described. The only answer to this objection is, that in ascertaining the function of any organ it is safest to study the activities of that organ in its most developed, or least degenerated, form. We could not, for instance, ever ascertain the function of the spines in any of the Echinodermata, if we were to consider these structures only in the Star-fishes and Holothurians, and if the pedicellariæ seem to be so small in Star-fish as not to appear capable of performing the function here assigned to them in *Echinus*, the explanation probably is that, as in the analogous cases of the spines, changed habits of life on the part of the animals have caused these inherited appendages to dwindle from disuse. Thus, for instance, Brittle-stars never climb sea-weed-covered-rocks at all, and those Star-fish which do so have their ambulacral feet restricted to the ventral surface; it would therefore be useless for these animals to have well-developed pedicellariæ, adapted to hold sea-weeds steady in the manner which may be of so much use to the globular *Echinus*, who throws out on all sides feet feeling for attachments. Therefore, whether the pedicellariæ of these other Echinoderms perform any function that yet remains to be detected, or whether they are mere rudiments now useless, we think

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* When pedicellariæ are detached from the *Echinus*, however, it is frequently observable that their grasp becomes, as it were, spasmodic, and endures for an indefinite time. For instance, it is not unusual to see a pedicellaria, which has been torn from its root while clutching a pedicel, carried about holding on to the pedicel for a very long time. But this spasmodic or continuous grasp of the organ when severed we have not observed to occur when the organ is *in situ*.

that the presence of such organs in these other Echinodermata raises no real difficulty in the way of accepting the proof which we have rendered of their observed functions as they occur in their most efficient forms.

Concerning the physiology of the pedicellariæ little further remains to be said under the present section. It may be stated, however, that the mandibles, which are constantly swaying about upon their contractile stalks as if in search for something to catch, will snap at an object only if it touches the inner surface of one or more of the expanded mandibles. Moreover, in the larger pedicellariæ, a certain part of the inner surface of the mandibles is much more sensitive to contact than is the rest of that surface; this part is a little pad about one-third of the way down the mandible (Plate 80, fig. 13, *s*); a delicate touch with a hair upon this part of any of the three mandibles is certain to determine an immediate closure of all the three. It is obvious that there is an advantage in the sensitive area, or zone, being placed thus low enough down in the length of the mandibles to ensure that the whole apparatus will not close upon an object till the latter is far enough within the grasp of the mechanism to give this mechanism the best possible hold. If, for instance, the tips of the mandibles were the most sensitive parts, or even if their whole inner surfaces were uniformly sensitive, the apparatus would be constantly closing upon objects when these merely brushed past their tips, and therefore closing prematurely for the purpose of grasping. But, as it is, the apparatus is admirably adapted to waiting for the best possible chance of getting a secure hold, and then snapping upon the object with all the quickness and tenacity of a spring-trap.

Another point worth mentioning is that if, after closure, any one or more of the mandibles be gently stroked on its outer surface near the base, all the mandibles are by this stimulation usually, though not invariably, induced again to expand. This is the only part of the whole organ the stimulation of which thus exerts an inhibitory influence on the contractile mechanism. If there is any functional purpose served by this relaxing influence of stimulating this particular part of the apparatus, we think it can only be as follows. When a portion of sea-weed brushes this particular part, it must be well below the tips of the mandibles, and therefore in a position where it, or some over-lying portion, may soon pass between the mandibles, if the latter are open; hence when touched in this place the mandibles, if closed, open to receive the sea-weed, should any part of it come within their cavity.

3. PHYSIOLOGY OF THE SPINES.—We must next consider stimulation with reference to the spines. It has already been said that these organs co-operate with the pedicellariæ in grasping any instrument of stimulation, and this proves that for a certain area round any seat of stimulation the spines admit of co-ordinated action. Further experiments prove that there is no limit to the area within which co-ordinated action of the spines may take place; but that all the spines of the organism may work together to the attainment of some common end. Thus it has already been stated in a previous part of this paper that a *Spatangus*, when placed upon its back, is able to right itself by

the co-ordinated action of its spines alone; and also that an *Echinus*, when taken out of the water and placed upon a table, will walk in a determinate direction by the same means. The very complete co-ordination of the spines implied by these facts is, however, rendered still more conspicuous by experiments in stimulation; for if, while an *Echinus* is walking on the table in the manner just alluded to, a scrape with a scalpel, a drop of spirit, a lighted match, or any other severe stimulus be applied at some one part of the animal's exterior, the spines all over the surface begin to take on an active bristling movement, and the direction of advance is immediately changed into a straight line of escape from the source of injury. And, were it necessary, other experiments could be detailed to show that the multitudinous spines of an *Echinus* are as closely co-ordinated in their action as so many limbs. To this account of the physiology of the spines it may be added that the nervous plexus overlying the tubercles on which they are mounted is more sensitive to stimulation than any other part of the external plexus. This is shown by the fact that, if the tubercle is stimulated by enclosing the spine in the tube of a pipette, and pressing the tubercle with the glass edges of the latter, more activity and a greater extent of irradiation of the stimulus among the spines and pedicellariæ is observed, than when any other part of the surface is similarly stimulated.

4. DETAILED FACTS OF STIMULATION.—At the commencement of this section it has already been stated, as a general fact, that when two points of the surface of an Echinoderm are irritated, the direction of advance which results from their joint influence is usually the diagonal between the two; also that, "when a greater number of points are irritated, the direction of advance becomes uncertain;" and lastly, that "if any, even short interval of time is allowed to elapse between the application of successive stimuli to different parts of the surface, the direction of advance will be in a straight line away from the stimulus applied latest." The following more detailed observations on this subject may here be worth recording.

Echini actively crawling in water along the floor of a tank were the subjects of the experiments, which are thus recorded in our notes :—

"1. Cut off tips of spines facing direction of advance—no effect.

"2. Cut off tips of protruded feet facing direction of advance—all the rest of the row retracted, animal stopped for some minutes, and then proceeded in the same direction as before.

"3. Plucked out some pedicellariæ facing direction of advance—no effect.

"4. Scraped with a needle small portion of the surface facing direction of advance —animal immediately stopped and reversed its direction.

Injuries 1, 2, 3, and 4, were inflicted on the equator.

"5. Scraped equator with a scalpel on two points opposite to each other—animal crawled at right angles to the line of injury.

"6. Scraped similarly at the aboral pole—no effect; there was no reason why injury here should determine escape in one direction rather than in another.

"7. Scraped similarly near pole, and half-way between pole and equator—little or no effect.

"8. Scraped in rapid succession five equatorial injuries, one on each of the five interambulacral spaces—*Echinus* crawled actively in one determinate direction; the equal and equidistant injuries all round the animal neutralized each other.

"9. Scraped a band of uniform width all the way round the equator—same result as in 8.

"10. Band of injury in 9 widened on the side facing direction of advance—no effect. Still further widened—slight change of direction, and, after a little time, persistent crawling away from widest part of injured zone.

Repeated experiment on other specimens, scraping round whole equator and simultaneously making one part of the zone of injury wider than the rest—same result; the animal crawled away from the *greatest amount* of injury.

"11. Scraped on base side of equator facing direction of advance—immediate reversal of that direction.

"12. After a few minutes similarly scraped opposite side—direction of advance immediately reversed to original one.

"13. Similarly scraped midway between the two previous injuries—direction of advance became oblique between the two first injuries, with a considerable simultaneous rotation upon the vertical axis of the animal.

"14. Similarly scraped a number of places on all aspects of the animal indiscriminately—direction of advance became uncertain and discontinuous, with a strong tendency to rotation upon vertical axis."

5. PHYSIOLOGY OF THE PEDICELS.—Taking here the Star-fish as a type of the Echinodermata, the results of our experiments on this head, and so far as stimulation is concerned, are as follows. When a drop of acid, or other severe stimulation is applied to any part of a row of protruded pedicels, that whole row is immediately retracted, the pedicels retracting successively from the seat of irritation—so that if the latter be in the middle point of the series, two series of retractions are started, proceeding in opposite directions simultaneously; the rate at which they travel is rather slow. This process of retraction, however, although so complete within the ray irritated, does not extend to the other rays. But if the stimulus be applied to the centre of the disc, upon the oral surface of the animal, all the feet in all the rays are more or less retracted—the process of retraction radiating serially from the centre of stimulation. The influence of the stimulus, however, diminishes perceptibly with the distance from the centre; thus, if weak acid be used as the irritant, it is only the feet near the bases of the rays that are retracted; and even if very strong acid be so used, it is only the feet as far as one-half or two-thirds of the way up the rays that are fully retracted—the remainder only having their activity impaired, while those near the tip may not be affected at all. If the drop of acid be placed on the dorsal, instead of the ventral

surface of the disc, the effect on the feet is found to be just the converse; that is, the stimulus here applied greatly increases the activity of the feet. Further experiments show that this effect is produced by a stimulus applied anywhere over the dorsal aspect of the animal; so that, for instance, if a drop of acid be placed on the skin, at the edge of a ray, and therefore just external to the row of ambulacral feet, the latter will be stimulated into increased activity; whereas, if the drop of acid had been placed a very small distance past the edge of the ray, so as to touch some of the feet themselves, then the whole row would have been drawn in. We have here rather an interesting case of antagonism, which is particularly well marked in *Astropecten*, on account of the active writhing movements which the feet exhibit when stimulated by an irritant placed on the dorsal surface of the animal. It may be added that in this antagonism the inhibitory function is the stronger; for when the feet are in active motion, owing to an irritant acting on the dorsal surface, they may be reduced to immediate quiescence—*i.e.*, retracted—by placing another irritant on the ventral surface of the disc. Similarly, if retraction has been produced by placing the irritant on the ventral surface of the disc, activity cannot be again induced by placing another drop of the irritant on the dorsal surface.

6. LUMINOUS STIMULATION.—The only other observations we have to detail under the present section are those relating to the influence of light. We have found unequivocal evidence of the Star-fish (with the exception of the Brittle-stars) and the *Echini* manifesting a strong disposition to crawl towards, and to remain in, the light. Thus if a large tank be completely darkened, except at one end where a narrow slit of light is admitted, and if a number of Star-fish and *Echini* be scattered over the floor of the tank, in a few hours the whole number, with the exception of perhaps a few per cent., will be found congregated in the narrow slit of light. The source we used was diffused daylight, which was admitted through two sheets of glass, so that the thermal rays might be considered practically excluded. The *intensity* of the light which the Echinoderms are able to perceive may be very feeble indeed; for in our first experiments we boarded up the face of the tank with ordinary pine-wood, in order to exclude the light over all parts of the tank except at one narrow slit between two of the boards. On taking down the boards we found indeed the majority of the specimens in or near the slit of light; but we also found a number of other specimens gathering all the way along the glass face of the tank that was immediately behind the pine-boards. On repeating the experiment with blackened boards, this was never found to be the case; so there can be no doubt that in the first experiments the animals were attracted by the faint glimmer of the white boards, as illuminated by the very small amount of light scattered from the narrow slit through a tank all the other sides of which were black slate. Indeed, towards the end of the tank, where some of the specimens were found, so feeble must have been the intensity of this glimmer, that we doubt whether even human eyes could have descried it very distinctly. Owing to the prisms at our command not having sufficient dispersive power for the experiments, and

not wishing to rely on the uncertain method of employing coloured glass, we were unable to ascertain how the Echinoderms might be affected by different rays.

On removing with a pointed scalpel the eye-spots from a number of Star-fishes and Echini without otherwise injuring the animals, the latter no longer crawled towards the light, even though this were admitted to the tank in abundance; but they crawled promiscuously in all directions. On the other hand, if only one of the five eye-spots were left intact, the animals crawled toward the light as before.

§ III. SECTION.

1. STAR-FISH.—Single rays detached from the organism crawl as fast and in as determinate a direction as do the entire animals. They also crawl towards the light, up perpendicular surfaces, and sometimes away from injuries; but they do not invariably, or even generally, seek to escape from the latter, as is so certain to be the case with entire animals. Lastly, when inverted, separated rays right themselves as quickly as do the unmutilated organisms.

Removing the tip of a severed ray does not impair any of these movements, except, of course, the crawling towards light, which it completely destroys. Dividing the nerve in any part of its length has the effect, whether or not the ray is detached from the animal, of completely destroying all physiological continuity between the pedicels on either side of the line of division. Thus, for instance, if the nerve be cut across half-way up its length, the row of pedicels is at once physiologically bisected, one-half of the row becoming as independent of the other half as it would were the whole ray divided into two parts; that is to say, the distal half of the row may crawl while the proximal half is retracted, or *vice-versâ*, and if a drop of acid be placed on either half, the serial contraction of the pedicels in that half stops abruptly at the line of nerve-division. As a result of this complete physiological severance, when a detached ray so mutilated is inverted, it experiences much greater difficulty in righting itself than it does before the nerve is divided. The line of nerve-injury lies flat upon the floor of the tank, while the central and distal portions of the ray—*i.e.*, the portions on either side of that line—assume various movements and shapes. The central portion is particularly apt to take on the form of an arch, in which the central end of the severed ray and the line of nerve-section constitute the points of support (tetanus ?) (Plate 83, fig. 27), or the central end may from the first show paralysis, from which it never recovers. The distal end, on the other hand, usually continues active, twisting about in various directions, and eventually fastening its tip upon the floor of the tank to begin the spiral movement of righting itself (Plate 83, fig. 27). This movement then continues as far as the line of nerve-injury, where it invariably stops (Plate 83, fig. 27). The central portion may then be dragged over into the normal position, or may remain permanently inverted, according to the strength of pull exerted by the distal portion; as a rule, it does not itself assist in the righting movement, although its feet usually continue protruded and mobile.

The above observations have reference to the common Star-fish, but they apply equally to other Star-fishes, except that in *Astropecten* single detached rays are not able to right themselves when inverted (owing to the feet not being used by this species for this purpose, and to the other rays being absent), and that after division of the nerve in a ray of this species, the feet of the proximal portion usually manifest more activity than those of the distal. The destruction, however, of physiological continuity between the two portions is as complete as in the case of the common Star-fish. Single detached rays of Brittle-stars are able when inverted to right themselves; they wriggle round by means of their snake-like movements, and do not require, as is the case with the less active rays of *Astropecten*, the assistance of adjacent rays to effect the manœuvre. On the whole, then, it may be said, as a general statement, that in all the species of Star-fish which we have observed, the effect of a transverse section of the nerve in a ray is that of completely destroying physiological continuity between the pedicels on either side of the section.

The only other experiments in nerve-section to which the simple anatomy of a Star-fish exposes itself is that of dividing the nerve-ring in the disc; or, which is virtually the same thing, while leaving this intact, dividing all the nerves where they pass from it into the rays. In specimens mutilated by severing the nerves at the base of each of the five rays, or by dividing the nerve-ring between each ray, the animal loses all power of co-ordination among its rays. When a common Star-fish is so mutilated it does not crawl in the same determinate manner as an unmutilated animal, but, if it moves at all, it moves slowly and in various directions. When inverted, the power of effecting the righting manœuvre is seen to be gravely impaired, although eventually it is always accomplished. There is a marked tendency, as compared with unmutilated specimens, to a promiscuous distribution of spirals and doublings, so that instead of a definite plan of the manœuvre being formed from the first, as is usually the case with unmutilated specimens, such a plan is never formed at all; among the five rays there is a continual change of unco-ordinated movements, so that the righting seems to be eventually effected by a mere accidental prepotency of some of the righting movements over others. Appended is a sketch of such unco-ordinated movement, taken from a specimen which for more than an hour had been twisting its rays in various directions (Plate 84, fig. 28). Another sketch is appended to show a form of bending which specimens mutilated as described are very apt to manifest, especially just after the operation. When placed upon their dorsal surface they turn up all their rays with a peculiar and exactly similar curve in each, which gives to the animal a somewhat tulip-like form (Plate 84, fig. 29). This form is never assumed by unmutilated specimens, and in mutilated ones, although it may last for a long time, it is never permanent. In detached rays this peculiar curve is also frequently exhibited; but if the nerve of such a ray is divided at any point in its length, the curve is restricted to the distal portion of the ray; it stops abruptly at the line of nerve-section. When entire Star-fish are mutilated by a section of each nerve-trunk half-way up each ray, and the animal is then placed upon its back, the tetanic contraction of the muscles in the rays before mentioned as occurring under this form of section in detached rays, has the effect, when now occurring in all the rays, of elevating the disc from the floor of the tank. This opisthotonous-like spasm is not, however, permanent; and the distal ends of the rays forming adhesions to the floor of the tank, the animal eventually rights itself, though much more slowly than unmutilated specimens. After it has righted itself, although it twists about the distal portions of the rays, it does not begin to crawl for a long time, and when it does so, it crawls in a slow and indeterminate manner. Star-fish so mutilated, however, can ascend perpendicular surfaces.

The loss of co-ordination between the rays caused by division of the nerve-ring in the disc is rendered most conspicuous in Brittle-stars, from the circumstance that in locomotion and in righting so much here depends upon co-ordinated muscular contraction of the rays. Thus, for instance, when a Brittle-star has its nerve-ring severed between each ray, an interesting series of events follows. First, there is a long period of profound shock—spontaneity, and even irritability, being almost suspended, and the rays appearing to be rigid, as if in tetanic spasm. After a time, feeble spontaneity returns—the animal, however, not moving in any determinate direction. Irritability also returns, but only for the rays immediately irritated, stimulation of one ray causing active writhing movements in that ray, but not affecting, or only feebly affecting, the other rays. The animal, therefore, is quite unable to escape from the source of irritation, the aimless movements of the rays now forming a very marked contrast to the instantaneous and vigorous leaping movements of escape which are manifested by unmutilated specimens. Moreover, unmutilated specimens will vigorously leap away, not only from stimulation of the rays, but also from that of the disc; but those with their nerve-ring cut make no attempts to escape, even from the most violent stimulation of the disc. In other words, the disc is entirely severed from all physiological connexion with the rays.

If the nerve-ring be divided at two points, one on either side of a ray, that ray becomes physiologically separated from the rest of the organism. If the two nerve-divisions are so placed as to include two adjacent rays—*i.e.*, if one cut is on one side of a ray and the other on the further side of an adjacent ray—then these two rays remain in physiological continuity with one another, although they suffer physiological separation from the other three. When a Brittle-star is completely divided into two portions, one portion having two arms and the other three, both portions begin actively to turn over on their backs, again upon their faces, again upon their backs, and so on alternately for an indefinite number of times. These movements arise from the rays, under the influence of stimulation caused by the section, seeking to perform their natural movements of leaping, which however end, on account of the weight of the other rays being absent, in turning themselves over. An entire Brittle-star when placed on its back after division of its nerve-ring is not able to right itself, owing to the destruction of co-ordination among its rays. *Astropecten*, under similar circumstances, at first bends its rays about in various ways, with a preponderant disposition to the tulip form, and keeps its ambulacral feet in active movement. But after half an hour, or an hour, the feet generally become retracted and the rays nearly motionless—the animal, like a Brittle-star, remaining permanently on its back. In this, as in other species, the effect of dividing the nerve-ring on either side of a ray is that of destroying its physiological connexion with the rest of the animal, the feet in that ray, although still remaining feebly active, no longer taking part in any co-ordinated movement—that ray, therefore, being merely dragged along by the others.

Under this division it only remains further to be said, that section of the nerve-ring in the disc, or the nerve-trunks of the rays, although as we have seen so completely destroying physiological continuity in the rows of ambulacral feet and muscular system of the animal, does not destroy physiological continuity in the external nerve plexus; for however much the nerve-ring and nerve-trunks may be injured, stimulation of the dorsal surface of the animal throws all the ambulacral feet and all the muscular system of the rays into active movement. This fact proves that the ambulacral feet and the muscles are all held in nervous connexion with one another by the external plexus, without reference to the integrity of the main nerve-trunks.

2. ECHINI.—(A.) *Section of external surface of shell.*—If a cork-borer be applied to the external surface of the shell of an *Echinus*, and rotated there till the calcareous substance of the shell is reached, and therefore a continuous circular section of the overlying tissues effected, it is invariably found that the spines and pedicellariæ within the circular area are physiologically separated from the contiguous spines and pedicellariæ, as regards local reflex excitability. That is to say, if any part of this circular area be stimulated, all the spines and pedicellariæ within that area immediately respond to the stimulation in the ordinary way; while none of the spines or pedicellariæ surrounding the area are affected. Similarly, if any part of the shell external to the circumscribed area be stimulated, the spines and pedicellariæ within the area are not affected. These facts prove that the function which is manifested by these appendages, of localising and gathering round a seat of stimulation, is exclusively dependent upon the external nerve plexus. It is needless to add that in this experiment it does not signify of what size or shape or by what means the physiological island is made, so long as the destruction of the nervous plexus by a closed curve of injury is rendered complete. In order to ascertain whether, in the case of an unclosed curve of injury, any irradiation of a stimulus would take place round the ends of the curve, we made sundry kinds of section. It is, however, needless to describe these, for they all showed that, after injury of a part of the plexus, there is no irradiation of the stimulus round the ends of the injury. Thus, for instance, if a short straight line of injury be made, by drawing the point of a scalpel over the shell, say along the equator of the animal, and if a stimulus be afterwards applied on either side of that line, even quite close to one of its ends, no effect will be exerted on the spines or

pedicellariæ on the other side of the line. This complete inability of a stimulus to escape round the ends of an injury, forms a marked contrast to the almost unlimited degree in which such escape takes place in the more primitive nervous plexus of the Medusæ.

Although the nervous connexions on which the spines and pedicellariæ depend for their function of localising and closing round a seat of stimulation are thus shown to be completely destroyed by injury of the external plexus, other nervous connexions, upon which another function of the spines depends, are not in the smallest degree impaired by such injury. The other function to which we allude is that which brings about the general co-ordinated action of all the spines for the purposes of locomotion. That this function is not impaired by injury of the external plexus is proved by the fact that, if the area within a closed line of injury on the surface of the shell be strongly irritated, all the spines over the whole surface begin to manifest their peculiar bristling movements, and by this co-ordinated action rapidly move the animal in a straight line of escape from the source of irritation; the injury to the external plexus, although completely separating the spines enclosed by it from their neighbouring spines as regards what may be called their local function of seizing the instrument of stimulation, nevertheless leaves them in undisturbed connexion with all the other spines in the organism as regards what may be called their universal function of locomotion.

(B.) Evidently, therefore, this more universal function must depend upon some other set of nervous connexions; and experiment shows that these are distributed over all the *internal* surface of the shell. Our mode of experimenting was to divide the animal into two hemispheres, remove all the internal organs of both hemispheres (these operations producing no impairment of any of the functions of the pedicels, spines, or pedicellariæ), and then paint with strong acid the inside of the shell—completely washing out the acid after about a quarter of a minute's exposure. The results of a number of experiments conducted on this method may be thus epitomised:—

The effect of painting the back or inside of the shell with strong acid (*e.g.*, pure HCl) is that of at first strongly stimulating the spines into bristling movements, and soon afterwards reducing them to a state of quiescence, in which they lie more or less flat, and in a peculiarly confused manner, that closely resembles the appearance of corn when "laid" by the wind. The spines have now entirely lost both their spontaneity and their power of responding to a stimulus applied on the external surface of the shell—*i.e.*, their local reflex excitability, or power of closing in upon a source of irritation. These effects may be produced over the whole external surface of the shell, by painting the whole of the internal surface; but if any part of the internal surface be left unpainted, the corresponding part of the external surface remains uninjured. Conversely, if all the internal surface be left unpainted except in certain lines or patches, it will only be corresponding lines and patches on the external surface that suffer injury. It makes no difference whether these lines or patches be painted in the course of the ambulacral feet, or anywhere in the inter-ambulacral spaces.

The above remarks, which have reference to the spines, apply equally to the pedicellariæ, except that their spontaneity and reflex irritability are not destroyed, but only impaired.

Some hours after the operation it usually happens that the spontaneity and reflex irritability of the spines return, though in a feeble degree, and also those of the pedicellariæ, in a more marked degree. This applies especially to the reflex irritability of the pedicellariæ; for while their spontaneity does not return in full degree, their reflex irritability does—or almost in full degree.

These experiments, therefore, seem to point to the conclusions—1st, that the general co-ordination of the spines is dependent on the integrity of an internal nerve-plexus, which, however, we have not been able to detect histologically; 2nd, that the hypothetical internal plexus is everywhere in intimate connexion with the external;* and 3rd, that complete destruction of the former, while profoundly influencing the functions of the latter, nevertheless does not wholly destroy them.

In order that a more clear conception may be rendered of the experiments on which these conclusions are based, we shall here quote from our notes one complete observation:—

"*Echinus* was divided into two hemispheres.

"After evisceration one hemisphere was painted over whole of internal surface with HNO_3. (A.)

"The other was painted down one row of ambulacral plates, and also down the inter-ambulacral plates at another part of internal shell. (B.)

"In (A.) the spines were 'laid'; spontaneity and reflex irritability almost totally destroyed.

"In (B.) similar effects observed above painted areas—unpainted areas unimpaired.

"Three hours after, no considerable recovery where painted; unpainted areas as active as before."

One further point, brought out by further experiments, may here be most conveniently mentioned; it is that a specially great influence, or shock, seems to be exerted on the external plexus by injury of the hypothetical internal plexus *along the lines of the ambulacral pores.* The following observations will serve to show this:—

"Another specimen was divided into two hemispheres. In one hemisphere two adjacent ambulacral rows were thoroughly scraped on internal surface of shell, and

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* It is remarkable that painting a portion of the internal surface of the shell should have the effect of injuring the spines and pedicellariæ of the *corresponding* portion of the external surface; for the fact seems to show that there must everywhere be intimate nervous connexions passing through the calcarious substance of the shell. So far, however, we have not been able to detect histological evidence of such connexions.

then well rubbed with sandpaper and brickdust.* The spines along these lines were laid in a very marked way, while spontaneity and reflex irritability, not only along them, *but also in the inter-ambulacral spaces between them*, were completely destroyed. The rest of the hemisphere was normally active.

" Ten minutes after operation the laid spines became more erect, and reflex irritability partly returned.

" Twenty minutes after operation pedicellariæ nearly completely recovered spontaneity and reflex irritability; spines still very imperfectly so.

" Two hours after operation both spines and pedicellariæ of the inter-ambulacral area *completely recovered in all respects*."

(C.) If an *Echinus* is divided into two hemispheres by an incision carried from pole to pole through any meridian, the two hemispheres will live for days, crawling about in the same manner as entire animals; if their ocular plates are not injured, they seek the light, and when inverted they right themselves. The same observations apply to smaller segments, and even to single detached rows of ambulacral feet. The latter are, of course, analogous to the single detached rays of a Star-fish, so far as the system of ambulacral feet is concerned; but looking to the more complicated apparatus of locomotion (spines and pedicellariæ), as well as to the rigid consistence and awkward shape of the segment—standing erect, instead of lying flat—the appearance presented by such a segment in locomotion is much more curious, if not surprising, than that presented by the analogous part of a Star-fish under similar circumstances. It is still more surprising that such a fifth-part segment of an *Echinus* will, when propped up on its ab-oral pole (Plate 84, fig. 30), right itself (Plate 84, fig. 31) after the manner of larger segments or entire animals. They, however, experience more difficulty in doing so, and very often, or indeed generally, fail to complete the manœuvre.

(D.) We are now again face to face with a question already propounded in § II., viz.: Is the action of the ambulacral feet in executing these righting movements of a merely serial kind, or does it depend upon nervous co-ordination? We have found this question very difficult of solution, and in the end have arrived at the conclusion that both principles are combined—the action of the feet being serial, but also assisted by nervous co-ordination. The experiments which lead us to this conclusion are as follows:—

If an unmutilated *Echinus* be suspended by a thread in an inverted position halfway up the side of a tank, in such a way that the ambulacral feet on one side of the ab-oral pole are alone able to reach the perpendicular wall, these feet as quickly as they can establish their attachments to that wall; the thread being then removed,

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* This method of destroying the hypothetical plexus was here adopted in preference to the method of painting with acid, in order to avoid a possible source of fallacy in some of the acid passing through the perforations of the shell, and so finding its way over the external surface. All our experiments with acid were on other specimens controlled by similar experiments conducted on this method.

the *Echinus* is left sticking to the side of the tank in an inverted position by means of the ab-oral ends of two adjacent feet-rows (Plate 85, fig. 32). Under these circumstances, as we should expect from the previous experiments, the animal sets about righting itself as quickly as possible. Now, if the righting action of the feet were entirely and only of a serial character, the righting would require to be performed by rearing the animal upwards; the effect of foot after foot in the same rows being applied in succession to the side of the tank, would require to be that of rotating the globular shell against the side of the tank towards the surface of the water, and therefore against the action of gravity. This is sometimes done, which proves that the energy required to perform the feat is not more than a healthy *Echinus* can expend. But much more frequently the *Echinus* adopts another device, and the only one by which it is possible for him to attain his purpose without the labour of rotating upwards: he rotates laterally and downwards in the form of a spiral. Thus, let us call the five feet-rows, 1, 2, 3, 4, and 5 (Plate 85, figs. 33 and 34), and suppose that rows 1 and 2 are in use near their ab-oral ends in holding the animal inverted against the perpendicular side of a tank. The downward spiral rotation would then be effected by gradually releasing the outer feet in row 1, and simultaneously attaching the outer feet in row 2 (*i.e.*, those nearest to row 3, and furthest from row 1), as far as possible to the outer side of that row. The effect of this is to make the globe roll far enough to that side to enable the inner feet of row 3 (*i.e.*, those nearest to row 2), when fully protruded, to touch the side of the tank. They establish their adhesions, and the residue of feet in row 1, now leaving go their hold, these new adhesions serve to roll the globe still further round in the same direction of lateral rotation, and so the process proceeds from row to row; but the globe does not merely roll along in a horizontal direction, or at the same level in the water, for each new row that comes into action takes care, so to speak, that the feet which it employs shall be those which are as far below the level of the feet in the row last employed as their length when fully protruded (*i.e.*, their power of touching the tank) renders possible. The rotation of the globe thus becomes a double one, lateral and downwards, till the animal assumes its normal position with its oral pole against the perpendicular tank wall. So considerable is the rotation in the downward direction, that the normal position is generally attained before one complete lateral, or equatorial, rotation is completed.

The result of this experiment, therefore, implies that the righting movements are due to something more than the merely successive action of the series of feet to which the work of righting the animal may happen to be given. The same conclusion is pointed to by the results of the following experiment.

A number of vigorous *Echini* were thoroughly shaved with a scalpel over the whole half of one hemisphere—*i.e.*, the half from the equator to the oral pole. They were then inverted on their ab-oral poles. The object of the experiment was to see what the Echini which were thus deprived of the lower half of three feet-rows would do when, in executing their righting manœuvres, they attained to the equatorial position and then found no feet wherewith to continue the manœuvre. The result of this experiment was first of all to show us that the *Echini* invariably chose the unmutilated feet-rows wherewith to right themselves. Probably this is to be explained, either by the general principle to which the escape from injury is due,—viz., that injury inflicted on one side of an Echinoderm stimulates into increased activity the locomotor organs of the opposite side,—or by the consideration that destruction of the lower half of a row very probably induces some degree of shock in the remaining half, and so leaves the corresponding parts of the unmutilated rows prepotent over the mutilated one. Be this as it may, however, we found that the difficulty was easily overcome by tilting the animal over upon its mutilated feet-rows sufficiently far to prevent the unmutilated rows from reaching the floor of the tank. When held steadily in this position for a short time, the mutilated rows established their adhesions, and the *Echinus* was then left to itself. Under these circumstances an *Echinus* will always continue the manœuvre along the mutilated feet-rows with which it was begun, till the globe reaches the position of resting upon its equator, and therefore arrives at the line where the shaved area commences. The animal then remains for hours in this position, with a gradual but continuous motion backwards, which appears to be due to the successive slipping of the spines—these organs in the righting movements being always used as props for the ambulacral feet to pull against while rearing the globe to its equatorial position, and in performing this function on a slate floor the spines are liable often to slip. The only other motion exhibited by *Echini* thus situated is that of a slow rolling movement, now to one side and now to another, according to the prepotency of the pull exerted by this or that row of ambulacral feet. Things continue in this way until the slow backward movement happens to bring the animal against some side of the tank, when the uninjured rows of ambulacral feet immediately adhere to the surface and rotate the animal upwards or horizontally, until it attains the normal position. But if care be taken to prevent contact with any side of the tank, the mutilated *Echinus* will remain propped on its equator for days; it never adopts the simple expedient of reversing the action of its mutilated feet-rows, so as to bring the globe again upon its ab-oral pole and get its unmutilated feet-rows into action. At first sight, therefore, this result seems to point to the conclusion that the righting movements are of a merely serial kind; it seems to indicate that the feet are only able to act in one direction, from ab-oral to oral pole, and that there is not sufficient central co-ordination to induce them to act in the opposite direction, when it is found to be useless, from the interruption of the series, to continue the manœuvre in the ordinary direction. But a little closer thought will show that this conclusion is not justified by the facts. For even if we assume that the righting movements of the feet are entirely due to some central co-ordinating influence, it does not follow, when the execution of these movements is interrupted by the highly artificial means of shaving off one-half the feet-rows, that the central co-ordinating apparatus should be adapted to meet so unnatural a state of things.

Suppose, for instance, that it is an incipient sense of gravity that determines this central apparatus to work the feet-rows serially, in order to rotate the animal into its normal position; it does not follow that, under any circumstances, the stimulus supplied by this sense of gravity should induce the central apparatus to *reverse* the action of the feet-rows; for to do this would, under any circumstances, be to act in opposition to the stimulus supposed. Only if we were to imagine that the central apparatus, if present, must possess a true psychological element capable of sufficient intelligence to reflect that by temporarily acting in opposition to the sense of gravity the peculiar exigencies of the situation might be overcome—only then could we fairly argue that the result of these experiments shows the righting movements of the feet to be purely serial, or wholly independent of nervous co-ordination. As a matter of physiology, therefore, the only question which in the present connexion we have to consider is this —is the mechanism of the ambulacral feet so constructed as to insure that their serial action shall always take place in the same direction? For if it can be shown that their serial action may take place indifferently in either direction, it would follow that the persistency with which the shaved *Echini* continued reared upon their equators is the expression of some stimulus (such as a sense of gravity) continuously acting upon some central apparatus, and so impelling the latter to a continuous, though fruitless, endeavour at co-ordinating the absent feet. If the righting movements were wholly independent of any such central apparatus, and due only to the serial action of the feet, we should expect that (supposing the feet to be able to act serially in either direction) when the equator position had been attained in shaved specimens, it would not be maintained. For if there were no constant stimulus emanating from any co-ordinating centre persistently trying to induce the absent feet to continue the serial action in the same direction, we should expect, if serial action can take place in either direction, that after a time it should begin to take place in the opposite direction; upon the supposition that the feet may act serially in either direction, there is no more reason why a shaved *Echinus* should remain permanently reared upon its equator than there is that it should remain permanently inverted upon its pole, and therefore the fact that in the latter position the feet set about an immediate rotation of the animal, while in the former and quite as unnatural position they hold the animal in persistent stasis—this fact tends to show that the righting movements of the feet are something more than serial. The question, therefore, that we set ourselves to determine was, whether the serial action of the feet invariably takes place in the direction of ab-oral to oral pole, or may likewise take place in the opposite direction. We found that it may take place in the opposite direction, as the following observations prove. We have seen a shaved specimen, which after remaining for several hours on its equator was accidentally rolled over into its normal position, forthwith begin to rear itself upon its uninjured feet-rows. Executing this what we may call an inverted righting movement with activity, the *Echinus* was speedily reared into the equatorial position on the opposite side to that from which it had just fallen—and in order to do this, it is needless to say, the feet of the uninjured rows had to be used serially in the direction opposite to that in which they are required to act when executing the ordinary righting manœuvre. We may wonder what the stimulus can have been which induced this *Echinus* spontaneously to rise upon its equator; but it is of interest in this connexion to add that, so soon as the equator position had been attained, and so soon therefore as any further action of the uninjured feet-rows in the same direction would have begun to get the animal into a position of ever-increasing difficulty as regards subsequent righting, so soon did the serial action in this direction cease, became reversed, and so again brought the animal gently into its normal position.

We have also seen wholly uninjured specimens when reaching the surface of the water by crawling up the sides of a tank, spontaneously rear themselves upon their equators and remain in that position for several minutes; but we have never observed a case of such rotation carried further than the equatorial line. The fact, however, that such rotation from oral to ab-oral pole can take place over half the whole length of a pair of feet-rows, proves that the feet may act serially in either direction. The same thing is further proved by the fact that single detached rays of Star-fish sometimes crawl backwards, and that in entire Star-fish the rays opposite to the direction of advance work their ambulacral feet centripetally, while those on the rays facing that direction work centrifugally.

Lastly, as proof that the ambulacral feet of *Echinus* are under the control of some centralising apparatus when executing the righting manœuvre, we may state one other fact. When the righting manœuvre is nearly completed by the rows engaged in executing it, the lower feet in the other rows become strongly protruded and curved downwards, in anticipation of shortly coming into contact with the floor of the tank when the righting manœuvre shall have been completed (see Plate 83, fig. 26). This fact tends to show that all the ambulacral feet of the animal are, like all the spines, held in mutual communication with one another by some centralising mechanism.

Such, then, is the evidence we have to adduce for the purpose of showing that the action of the ambulacral feet is not entirely or only of a serial kind, but is, in part at all events, dependent upon some centralising influence by which all the feet, like all the spines, are rendered capable of truly co-ordinated action. We have next to adduce our evidence to show that the action of the ambulacral feet, although as we have seen in some measure, is not exclusively dependent on this centralising influence.

(E.) In order to show this we must first narrate the experiments whereby we succeeded in ascertaining the central apparatus, on the integrity of which both the feet and the spines depend for their co-ordination. Having obtained the definite evidence of co-ordination which has now been fully detailed, we of course sought to localise the centre to which this co-ordination is due; and in searching for this centre our thoughts naturally turned to the only part of the nervous system where we could reasonably expect to find it. This part is the central nerve-ring, and, as we had anticipated, experiment revealed unmistakable evidence of this being the centre of which we were in search.

If a circular incision be made all the way round the lantern of an *Echinus*, at a sufficient distance from the lantern to insure that the connexions of the nerve-ring with the rest of the organism shall be severed, the following results are produced :—

1. *Pedicels.*—Spontaneity impaired, though not destroyed. They are protruded, but not in such numbers or with so much activity as in the unmutilated animal; they, however, form their adhesions in the ordinary manner whenever they come into contact with a solid surface, and therefore their function of anchoring the *Echinus* securely remains unimpaired. They also still continue able to crawl, but they do so feebly and no longer in a determinate direction; the animal therefore advances slowly and in a very uncertain manner, frequently changing its direction of advance, and manifesting a marked tendency to rotate upon its own axis, either without moving from one spot or gyrating round and round some one or more centres in a wholly aimless way. The animals, however, are still able to climb perpendicular surfaces, though in a most uncertain manner. When stimulated strongly the activity of the animal is increased, but its power of escaping from the source of injury is completely destroyed; it crawls indifferently in any direction—as likely as not *towards* the source of injury—rotates upon its axis, and after crawling some distance in one direction may very likely reverse that direction, and so return to the place from which it started. All these movements, standing in such marked contrast to those exhibited by unmutilated specimens under similar circumstances, prove that the co-ordination of the ambulacral feet has been destroyed. On the other hand, the fact that they continue able to act *at all* proves that their activity is not *wholly* dependent upon the nerve-centre; all that the destruction of this centre entails is the destruction of their power of *co-ordinated* action.

When perfectly fresh and vigorous specimens are inverted, a proportion of about three to four remain permanently inverted till they die. As this is never the case with perfectly fresh and vigorous specimens when unmutilated, there can be no question that destruction of the nerve-centre exerts a profound influence on the action of the ambulacral feet upon which the execution of the righting manœuvre depends. On the other hand, the fact that a certain proportion of individuals continue able to execute this manœuvre after destruction of the nerve-centre—although they never do so without much difficulty and great expenditure of time—proves that the integrity of this centre is not absolutely essential to the execution of this manœuvre. Therefore, as experiment has failed to reveal to us any other general nerve-centre in the animal, and as even a segment of the animal containing but a single row of feet is in many cases able to perform this manœuvre, we conclude, as previously stated, that the action of the feet in performing these righting movements is partly of a serial character, although, for reasons mentioned in the two previous paragraphs, we further conclude that in the unmutilated animal these movements are largely assisted by the co-ordinating influence that emanates from the nervous centre.

2. *Pedicellariæ.*—No effect whatever is produced upon these organs by destruction of the nerve-ring.

3. *Spines.*—These organs, on the other hand, are profoundly affected—not, indeed, as regards their spontaneity and the function which they share with the pedicellariæ of closing round any instrument of stimulation, but as regards their other two more general functions. That the particular or local function which they share with the pedicellariæ should not be impaired by destruction of the general nerve-centre is no more than we might expect from those experiments detailed in previous parts of this paper, which proved that this function is performed exclusively by the numberless local nerve-centres (cells) of the external plexus. Thus, for instance, it will be remembered that when a small piece is cut out of the shell of an *Echinus* or *Spatangus,* and the internal surface of that piece painted with acid, its spines and pedicellariæ, although severed from any possible nervous connexion save those of the external plexus, will continue to perform their function of localising a seat of stimulation.

As regards, then, the more general function of the spines, we have first to consider what we may term their general reflex irritability—*i.e.,* their power of active bristling response all over the animal when any part of its surface is strongly stimulated, as by burning. Immediately after the operation of removing the nerve-centre this function is found to be in abeyance, or nearly so—strong stimulation of one part of the animal not being followed by any response of the spines in other parts. This effect, however, completely passes off within several hours after the operation, and is therefore to be attributed to shock. The fact, however, that the influence of shock is thus revealed in temporarily suspending this general nervous communication among the spines, proves that this general communication, unlike the more special one which they share with the pedicellariæ, is itself in communication with the central nervous ring. Further, the experiments detailed in a previous part of this paper prove that the medium of communication is in this case the hypothetical *internal* nervous plexus, as in the case just mentioned the medium of communication has been proved to be the *external* nervous plexus. And as the effect of the operation in question is only transitory—after recovery from shock the spines being as responsive as ever to severe stimulation—we must conclude that the general communication between the spines is maintained by the direct conductility of the supposed internal plexus, and is not of the nature of a reflex in which the nerve-ring is concerned as a general centre. The only effect of removing this nerve-ring is temporarily to paralyse, through shock, the supposed internal plexus with which the ring is connected.

Lastly, the effect of removing the nerve-ring is that of completely and permanently destroying the general co-ordination of the spines; that is to say, after this operation these organs are never again of any use to the *Echinus* for the purpose of locomotion. When the animal is placed upon a table and a lighted spirit lamp held against one side, although all the spines will manifest their active bristling movements, they will not co-operate to move the animal away from the source of irritation, as is so invariably the case with unmutilated specimens. Removal of the nerve-ring has entirely destroyed the general co-ordination of the spines.

GENERAL SUMMARY.

I. Morphology.

In *Holothuria* the polian vesicle opens freely into a wide circular canal a short distance from the termination of the stone canal. From this circular canal five lozenge-shaped sinuses project forwards, and from each of these two large oval sinuses run forwards parallel with each other—the ten oval sinuses becoming continuous with the hollow stems of the tentacles. Injection of the polian vesicle shows that it forms one continuous tube system with the circular canal and its sinuses, oval sinuses and tentacles, pedicels and ampullæ. Unless the pressure is kept up for a considerable time there is no penetration of the injected fluid into the stone canal, and either the ring, vesicle, or sinuses, give way before the fluid reaches the madreporic plate. Specimens injected with a gelatine mass show that each canal sinus opens into a cæcal tube, which runs forwards internal to the sinuses of the tentacles as far as a wide circum-oral space. This space communicates by well-defined apertures with that portion of the body cavity which lies between the sinuses and the œsophagus, and which is reached through the circular apertures between the sinuses of the circular canal. Each canal sinus has three other apertures in its walls. It opens by a small round aperture into a radial canal, and the two other apertures occur as minute slits, one at each side of the orifice of the radial canal, leading into the adjacent tentacle sinuses. When the tentacle into which the sinus opens is protruded, there is no constriction between the sinus and the tentacle; but when the tentacle is retracted, there is a well-marked constriction at the junction of the sinus with the tentacle. The eversion of the perisome and the protrusion of the tentacles are effected chiefly by the shortening of the polian vesicle and the constriction of the longitudinal muscular bands, which run from the inner surface of the body-wall between each two adjacent tentacle-sinuses; but the circular fibres of the body-wall also assist in the process by contracting immediately behind the group of sinuses, so as to act on them by direct pressure, and also indirectly by forcing the body fluid against them.

The amount of the body-cavity fluid is constantly changing. At the entrance to cloacal chamber there is a circular valve which is constantly dilating and contracting, except when the aboral end of the animal is forcibly retracted. When open, this valve allows water to pass into the respiratory tree; when it begins to retract, water escapes from the cloaca. This alternate opening and closing takes place with perfect rhythm, at a rate of about six revolutions per minute. At the end of every seventh or eighth revolution a large stream of clear water is ejected, which sometimes contains sand and the remains of food particles. When the tentacles are being protruded more water is taken in at the cloaca than escapes ; on the other hand, retraction of the tentacles is preceded by an escape of a large stream of water.

In *Echinus* two tubes spring from the under surface of the madreporic plate. The one is dilated at its origin so as to include the greater portion of the plate, and ends in the so-called heart ; the other is small, deeply pigmented, and runs along a groove in the heart to open into a circular canal at the base of the lantern. From the under aspect of this circular canal the five radial ambulacral vessels take their origin. Immediately within the oral margin of the shell and alternating with the inner row of pedicels, are the five pair of "tree-like organs." If a fine glass canula be forced through the membrane which extends from the apex of each tooth to the oral margin of the inter-ambulacral plates and sides of the alveoli, coloured fluids may be injected into the space between the membrane and the alveoli of the lantern; the fluid then slowly diffuses upwards into the vesicles around the apices of the teeth. It reaches these vesicles partly by passing directly upwards external to the alveoli, and partly by passing into the cavities of the alveoli and ascending through the circular sinus.

In *Spatangus* the ambulacral circum-oral canal has no polian vesicles or sinuses developed in connexion with it. Some of the pedicels have suckers, others are conical and devoid of them, while others again are flattened at their tips, and sometimes split up into segments.

If one of the arms of *Solaster papposa* is divided transversely and a coloured fluid is introduced into the open end of the radial canal, the ampullæ and pedicels of the injected arm are at once distended. The fluid next penetrates the circular canal, polian vesicles, ampullæ and pedicels of the other arms; but unless considerable pressure be kept up for some time, none of the solution enters the madreporic canal. If, however, the pressure is maintained for several hours with a column of fluid 2 feet high, the fluid ascends through the stone canal and diffuses slowly through the madreporic plate. When a thin slice is then shaved off the plate, the fluid is observed escaping from a small circumscribed area situated between the centre and the margin of the plate, and corresponding in size and position with the termination of the stone canal on the inner surface. The stone canal gradually increasing in diameter as it passes inwards from the madreporic plate, runs obliquely over its accompanying sinus, till it finally hooks round this sinus to open into the circular canal. Springing from this canal and opposite to each inter-radial space (with the exception of the space occupied by the stone canal) is a polian vesicle. The size and form of these vesicles are largely determined by the amount of fluid in the pedicels. In none of the injected specimens was there any evidence of a communication between the ambulacral vessels and the body cavity, or between the ambulacral and the blood (neural) vessels. There was, however, abundant evidence of communication between the latter and the exterior. When a canula was introduced into the outer end of the sinus, a coloured solution could be easily forced through the sinus into the circular blood-vessel, and from this into the radial blood-vessels. But when the canula was introduced into the proximal end of the sinus, the solution rapidly rushed along the sinus and escaped through the madreporic plate—proving that the blood-vessels of *Solaster* communicate far more freely with the exterior than do the water-vessels.

The ambulacral system of the common Star-fish only differs from that of the Sun-star in having no polian vesicles. *Astropecten*, on the other hand, has polian vesicles; but in it the pedicels have departed from the usual form in being short, conical, and unprovided with terminal suckers. In *Ophiura* the pedicels are morphologically similar to those of *Astropecten*, though shorter and more slender. They diminish in size as they proceed outwards, and at the ends of the arms are scarcely visible.

II. PHYSIOLOGY.

1. *Natural movements.*—The ordinary crawling movements of *Astropecten aurantiacus* are peculiar, the ambulacral feet acting the part of walking poles and cilia combined. Brittle-stars progress by using two opposite arms upon the floor of the tank, with a sort of leap, and can thus travel at the rate of 6 feet per minute. The ordinary progression of *Echinus* and *Spatangus* is assisted by the co-ordinated action of the spines, and when placed upon a flat surface out of the water the animal advances by means of its spines alone. In *Echinus* the lantern and pedicellariæ are also used to assist in locomotion.

All the Echinodermata that we have observed are able, when placed upon their dorsal surfaces on the floor of a tank, to recover their normal position on their oral surface. The common Star-fish does so by twisting the ends of two or more of its rays round, so as to bring its terminal suckers into action upon the floor of the tank, and then, by a successive and similar action of the suckers further back in the series, the whole ray is progressively twisted round, so that its ambulacral surface is applied flat against the floor. The rays which perform this action twist their semi-spirals in the same direction, and by their concerted action serve to drag the disc and the remaining rays over themselves as a fulcrum. Other species of Star-fish, which have not their ambulacral suckers sufficiently developed to act in this way, execute their righting movements by doubling under two or three of their adjacent rays, and turning a somersault over them, as in the previous case. *Echinus* rights itself when placed on its ab-oral pole, by the successive action of two or three adjacent rows of suckers—so gradually rising from ab-oral pole to equator, and then as gradually falling from equator to oral pole. *Spatangus* executes a similar manœuvre entirely by the successive pushing and propping action of its longer spines.

2. *Stimulation.*—All the Echinoderms that we have observed seek to escape from injury in a direct line from the source of stimulation. If two points of the surface are stimulated, the direction of escape is the diagonal between them. When several points all round the animal are simultaneously stimulated, the direction of advance

becomes uncertain, with a marked tendency to rotation upon the vertical axis. If a short interval of time be allowed to elapse between the application of two successive stimuli, the direction of advance will be in a straight line from the stimulus applied latest. If a circular band of injury be quickly made all the way round the equator of *Echinus,* the animal crawls away from the broadest part of the band—*i.e.*, from the *greatest amount* of injury.

The external nerve-plexus supplies innervation to three sets of organs—the pedicels, the spines, and the pedicellariæ; for when any part of the external surface of *Echinus* is touched, all the pedicels, spines, and pedicellariæ within reach of the point that is touched immediately approximate and close in upon the point, so holding fast to whatever body may be used as the instrument of stimulation. In executing this combined movement the pedicellariæ are the most active, the spines somewhat slower, and the pedicels very much slower. If the shape of the stimulating body admits of it, the forceps of the pedicellariæ seize the body and hold it till the spines and pedicels come up to assist.

And here we have proof of the function of the pedicellariæ. In climbing perpendicular or inclined surfaces of rock covered with waving sea-weeds, it must be no small advantage to an *Echinus* to be provided on all sides with a multitude of forceps adapted, as described, to the instantaneous grasping and arresting of a passing frond. For in this way not only is an immediate hold obtained, but a moving piece of seaweed is held steady, till the pedicels have time to establish a further and more permanent hold upon it with their sucking discs. That this is the chief function of the pedicellariæ is indicated by the facts that, 1st, if a piece of sea-weed is drawn over the surface of an *Echinus,* this function may clearly be seen to be performed; 2nd, that the wonderfully tenacious grasp of the forceps is timed as to its duration with an apparent reference to the requirements of the pedicels, for after lasting about two minutes (which is about the time required for the suckers to bend over and fix themselves to the object held by the pedicellariæ if such should be a suitable one) this wonderfully tenacious grasp is spontaneously released; and 3rd, that the most excitable part of the trident pedicellariæ is the inner surface of the mandibles, about a third of the way down their serrated edges—*i.e.*, the part which a moving body cannot touch without being well within the grasp of the forceps. When the forceps are closed, they may generally be made immediately to expand by gently stroking the external surface of their bases.

With regard to stimulation of the spines, if severe irritation be applied to any part of the external or internal surface of an *Echinus,* the spines all over the animal take on an active bristling movement. The tubercles at the bases of the spines are the most irritable points on the external surface.

With regard to stimulation of the pedicels, if an irritant be applied to any part of a row, all the pedicels in that row retract in succession from the seat of stimulation, but the influence does not extend to other rows. A contrary effect is produced by applying an irritant to any part of the external nerve-plexus, all the pedicels being then stimulated into increased activity. Of these antagonistic influences the former, or inhibitory one, is the stronger; for if they are both in operation at the same time, the pedicels are retracted.

Star-fish (with the exception of Brittle-stars) and *Echini* crawl towards, and remain in, the light; but when their eye-spots are removed they no longer do so. When their eye-spots are left intact they can distinguish light of very feeble intensity.

3. *Section* (A.).—*Star-fish.*—Single rays detached from the organism crawl as fast and in as determinate a direction as do entire animals. They also crawl towards light, away from injuries, up perpendicular surfaces, and when inverted right themselves. Dividing the ray-nerve in any part of its length has the effect of destroying all physiological continuity between the pedicels on either side of the division. Severing the nerve at the origin of each ray, or severing the nerve-ring between each ray, has the effect of totally destroying all co-ordination among the rays; therefore the animal can no longer crawl away from injuries, and when inverted it forms no definite plan for righting itself—each ray acting for itself without reference to the others, there is, as a result, a promiscuous distribution of spirals and doublings, which as often as not are acting in antagonism to one another. This division of the nerves usually induces, for some time after the operation, more or less tetanic-like rigidity of the rays. The operation, however, although so completely destroying physiological continuity in the rows of pedicels and muscular system of the rays, does not destroy, or perceptibly impair, physiological continuity in the external nerve-plexus; for however much the nerve-ring and nerve-trunks may be injured, stimulation of the dorsal surface of the animal throws all the pedicels and muscular system of the rays into active movement. This fact proves that the pedicels and muscles are all held in nervous connexion with one another by the external plexus, without reference to the integrity of the main trunks.

(B.) *Echini.*—If a cork-borer be rotated against the external surface of an *Echinus* till the calcareous substance of the shell is reached, and therefore a continuous circular section of the overlying tissues effected, the spines and pedicellariæ within the circular area are physiologically separated from those without it, as regards their local reflex irritability. That is to say, if any part of this circular area is stimulated, all the spines and pedicellariæ within that area immediately respond to the stimulation in the ordinary way, while none of the spines or pedicellariæ surrounding the area are affected, and conversely. Therefore we conclude that the function of the spines and pedicellariæ of localising and gathering round a seat of stimulation, is exclusively dependent upon the external nervous plexus. If the line of injury is not a closed curve, so as not to produce a physiological island, the stimulating influence will radiate in straight lines from its source, but will not irradiate round the ends of the curve or line of injury.

Although the nervous connexions on which the spines and pedicellariæ depend for their function of localising and closing round a seat of stimulation are thus shown to be completely destroyed by injury of the external plexus, other nervous connexions, upon which another function of the spines depends, are not in the smallest degree impaired by such injury. This other function is that which brings about the general co-ordinated action of all the spines for the purposes of locomotion. That this function is not impaired by injury of the external plexus is proved by severely stimulating an area within a closed line of injury on the surface of the shell; all the spines over the whole surface of the animal then manifest their bristling movements, and by their co-ordinated action move the animal in a straight line of escape from the source of irritation.

We have, therefore, to distinguish between what may be called the local reflex function of the spines, which they show in common with the pedicellariæ and which is exclusively dependent upon the external plexus, and what we may call the universal reflex function of the spines, which consists in their general co-ordinated action for the purposes of locomotion, and which is wholly independent of the external plexus. Apparently, therefore, this more universal function must depend upon some other set of nervous connexions (which, however, we have not been able to detect histologically), and experiment shows that these, if present, are distributed over all the *internal* surface of the shell. For if the internal surface be painted with acid, or scoured out with emery paper and brick-dust, the spines and pedicellariæ, after a short period of increased activity or bristling, become perfectly quiescent, lie flat, and lose both their spontaneity and irritability. After a few hours, however, the spontaneity and irritability of the spines return, though in a feeble degree, and also those of the pedicellariæ in a more marked degree. These effects take place over the whole external surface of the shell, if the whole of the internal surface be painted with acid or scoured with brick-dust; but if any part of the external surface be left unpainted or unscoured, the corresponding part of the external surface remains uninjured. From these experiments we conclude:—1st, that the general co-ordination of the spines is wholly dependent on the integrity of the hypothetical internal plexus; 2nd, that the hypothetical internal plexus is everywhere in intimate connexion with the external, apparently through the calcareous substance of the shell; and 3rd, that complete destruction of the former, while profoundly influencing through shock the functions of the latter, nevertheless does not wholly destroy them.

Echini may be divided into pieces, and the pedicels, spines, and pedicellariæ upon these pieces will continue to exhibit their functions of local reflex irritability, however small the pieces may be. If an entire double row of pedicels be divided out as a segment, and then placed upon its ab-oral end, it may rear itself up on its oral end by the successive action of its pedicels, and then proceed to crawl about the floor of the tank. We have therefore to meet the question:—Is the action of the ambulacral feet in executing these righting movements of a merely serial kind—A, B, and C, first securing their hold of the tank floor, owing to the stimulus supplied by contact, and then by their traction tilting over the globe, till D, E, and F, are able to touch the floor, and so on; or does the righting action depend upon nervous co-ordination? We conclude that both principles are combined—the action of the pedicels being serial, but also assisted by nervous co-ordination. This conclusion is sustained, not only by the movements of an unmutilated *Echinus* when suspended by a thread against the wall of a tank, but also by the experiment of shaving off the spines and pedicels over one half of one hemisphere—*i.e.*, the half from the equator to the oral pole. When then inverted and forced to use their mutilated pedicel-rows, the *Echini* reared themselves upon their equators, and then, having no more pedicels wherewith to continue the manœuvre, came to rest. This rest was permanent—the animal remaining, if accidents were excluded, upon its equator till it died. The question, then, here seems to resolve itself simply into this:—Is the mechanism of the pedicels so constructed as to ensure that their serial action shall always take place in the same direction; for if it can be shown that their serial action may take place indifferently in either direction, it would follow that the persistency with which the partly-shaved *Echini* continue reared upon their equators, is the expression of some stimulus (such as a sense of gravity) continuously acting upon some central apparatus, and impelling the latter to a continuous, though fruitless, endeavour to co-ordinate the absent pedicels. If the pedicels are able to act serially in either direction, there is no more reason why a partly-shaved *Echinus* should remain permanently reared upon its equator, than that it should remain permanently inverted upon its pole; and therefore the fact that in the latter position the pedicels set about an immediate rotation of the animal, while in the former and quite as unnatural position they hold the animal in persistent stasis—this fact tends to show that the righting movements of the pedicels are something more than serial. Thus the whole question as between the two hypotheses amounts to whether the pedicels are able to act serially from oral to ab-oral pole. Observation has shown us that they are so, for we have seen *Echini* spontaneously rear themselves from their normal position on the oral pole, to the position of resting upon their equators. Further, as additional evidence that the righting movements are at least assisted by some centralizing influence, is the fact that when the evolution is nearly completed by the pedicel-rows engaged in executing it, the lower pedicels in the other rows become strongly protruded and curved downwards, in anticipation of shortly coming into contact with the floor of the tank.

But, on the other hand, there is evidence to show that the action of the pedicels in executing this manœuvre, although as we have seen in some measure, is not exclusively dependent upon this centralizing influence. We found that the centre from which this influence proceeds is the nerve-ring that surrounds the lantern. For when this is removed, the following results are produced: the pedicels have their spontaneity impaired, though not destroyed—the animal still continuing to crawl, but only feebly, and no longer in a determinate manner, frequently changing its direction of advance, and showing a marked tendency to rotate upon its vertical axis. Moreover, the

Echinus is now no longer able to escape from injury, but when stimulated crawls indifferently in any direction. Thus, removal of the nerve-centre seriously impairs the activity of the pedicels, and totally destroys their co-ordination. Yet when specimens so mutilated are inverted, one out of every four specimens is able to right itself. This, however, is only done with great difficulty and after a long time, so that, under these circumstances, the execution of this manœuvre seems to be just barely possible. Still the fact of its being possible at all proves that the integrity of the nerve-centre is not absolutely essential to its performance. Therefore, as experiment has failed to reveal to us any other general nerve-centre in the animal, and as even a segment of the animal containing only a single row of pedicels is in many cases able to perform this manœuvre, we conclude, as already stated, that the action of the pedicels is partly of a serial character, though largely assisted by the co-ordinating influence that emanates from the nerve-centre.

The effect of this operation upon the spines and pedicellariæ still remains to be considered. No effect at all is produced upon the pedicellariæ; but upon the spines a profound influence is seen to be exercised. Their spontaneity, indeed, remains unimpaired, as does also the function which they share with the pedicellariæ of closing round any instrument of stimulation; likewise their power of responsive bristling all over the animal when any part of the animal is severely stimulated continues to be manifested as before, although for an hour or two after the operation this power is suspended by shock. But the general *co-ordination* of the spines is totally and permanently destroyed; for if the animal be placed upon a table and a spirit lamp flame held against one side, although the spines will manifest their bristling movements (if the period of shock has been allowed to pass away), they will no longer co-operate to remove the animal from the source of irritation. These facts prove, 1st, that the general co-ordination of the spines is wholly dependent upon the nerve-centre; 2nd, that the spontaneity and local reflex irritability are wholly independent of that centre—they depend entirely upon the external nerve-plexus; and 3rd, that the universal nervous connexions revealed in the bristling movements of the spines, and which as shown by previously narrated experiments depend upon the hypothetical *internal* nerve-plexus, are themselves in nervous connexion with the nerve-centre. For only thus can we explain the long period of shock which removal of this centre entails upon the functions of this supposed internal plexus. Nevertheless, the fact that these functions are eventually resumed in the general bristling of the spines, proves that this general communication between the spines is maintained by the direct conductibility of the supposed internal plexus, and is not of the nature of a reflex in which the nerve-ring is concerned as a general centre for the responsive, as distinguished from the co-ordinated, action of the spines.

LITERATURE.

For a general account of the literature on the morphology of the Echinoderms up to 1872 reference had best be made to BAUDELOT in 'Archives de Zoologie Exp. et Gen.,' t. i., pp. 176–216.

The observer who first detected the nervous ring in *Echinus* was VAN BENEDEN, who published his description in 'L'Echo du Monde Savant' in 1835. A more detailed description was afterwards given by KROHN in MÜLLER'S 'Archives' in 1841, which was followed by the well-known investigations of VALENTIN*, L. and A. AGASSIZ†, J. MÜLLER‡, HOFFMANN§, and LOVÉN‖. More recently still a valuable paper has been published by FREDERICQ¶, of the existence of which we were not aware until our own paper had been written. As we now find that some of our results have been anticipated by this author, we shall here devote a few paragraphs to epitomising all the more important features of his work.

FREDERICQ found that the pentagonal nerve-ring of *Echinus* and its five radial nerves are all contained in as many sheaths or tubes of membrane, which are mesentery-like expansions of the lining membrane of the shell. These enveloping tubes send out lateral branches which contain the lateral nervous offshoots; the latter pass out of the ambulacral pores in company with the pedicels which they serve to enervate, a delicate nerve running along the whole length of each pedicel to terminate at its distal end in a tactile organ.

FREDERICQ considers it probable that in their passage through the ambulacral pores the nerves also send branches to the spines and pedicellariæ; these branches, however, he failed to detect. The radial or ambulacral nerve-trunks terminate in the ocular plates. The latter, however, show no histological evidence of supporting any structure resembling an ocular apparatus; and FREDERICQ could obtain no physiological evidence of sensibility either to solar or to artificial light. He does not state clearly what his experiments in this connexion were, and so we infer that they cannot have been the same as ours. He regards the pigment spot as a "fiction."

The nerve-ring sends off, in addition to the ambulacral trunks, the nerve-cords to the intestine. In the ring and trunks there is no differentiation into ganglia and fibres, but the whole is in structure uniform and in function central. The brown colour is due to elongated and irregular cells having conspicuous nuclei filled with pigment, and supposed to betoken connective tissue. The nervous tracts are them-

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[*] 'Anatomie du genre *Echinus*,' 1841.

[†] 'Bulletin of the Museum of Comp. Zool.,' in vols. i., ii., and iii., "Revision of the *Echini*;" and 'American Naturalist,' vol. vii., pp. 398–406.

[‡] 'Abhandl. der Konigl. Akad. der Wissens. zu Berlin,' 1853, and MÜLLER'S 'Archiv.,' 1853, p. 175, and 1850, p. 127.

[§] 'Nederländisches 'Archiv. für Zool.,' i., 1871, p. 54.

[‖] 'Anns. and Mag. Nat. Hist.,' 1872, p. 28, and 'Études sur les Èchinoïdées,' 1875.

[¶] 'Arch. de Zool. Exp.,' t. v., pp. 429–440.

selves composed of two distinct layers—an external and an internal, each of which presents a uniform structure of cells and fibres.

In a division of his paper devoted to an account of physiological experiments, FREDERICQ records several observations which are identical with some of those recorded in the corresponding division of the present paper. Thus, he tried the effect of severing the five ambulacral trunks, and found, as we found, that, while the operation did not entail paralysis of the pedicels, it did entail complete destruction of co-ordination between their five rows. He also observed the righting movements of inverted *Echini*, and experimented on the effect upon these movements of severing the nerve-ring. Here, however, his results are not quite in accordance with ours, for he says that in no case does an *Echinus* when so mutilated succeed in righting itself; whereas we found, as before stated, that out of twelve perfectly fresh specimens so mutilated three were able to right themselves. We are quite sure that our results in this connexion are trustworthy; for, as these results were contrary to our expectations, we took the precaution of altogether removing the lanterns from a number of perfectly fresh specimens, and found, as previously, that a proportion of one in four continued able to right themselves.

Lastly, FREDERICQ observed the local reflex action of the spines and pedicellariæ, and also the insulating effect upon this action of a closed line of section. He inferred from these observations the presence of an external plexus, but was unable to detect its presence histologically.

We may now conclude this account of previous literature with a discussion of previous theories as to the function of the pedicellariæ.

In stating our opinion as to what we consider their main function, it seems desirable briefly to consider the functions which have been ascribed to these organs by previous observers. Professor OWEN supposes, or supposed ('Comp. Anat. of Inverts,' p. 203), that their work in the economy of the animal is that of removing parasitic growths from the shell; and somewhat allied to this view is that of Professor A. AGASSIZ, who regards the function of these appendages to be that of "scavengers." He says: "If we watch a Sea Urchin after he has been feeding, we shall learn at least one of the offices which this singular organ performs in the general economy of the animal. That part of the food which he ejects passes out of the anus—an opening on the summit of the body in the small area where the zones of which the shell is composed converge. The rejected particles, thrown out in the shape of pellets, are received on their little feeler-like forceps, and they are passed from one to the other down the side of the body till they are dropped off into the water. Nothing is more curious and entertaining than to watch the neatness and accuracy with which this process is performed. One may see the rejected bits of food passing rapidly along the lines upon which the pedicellariæ occur in greatest numbers, as if they were so many little roads for the carrying away of the refuse matter. Nor do the forks cease from their labour till the surface of the animal is completely clean and free from any foreign substance. Were it not for the pedicellariæ the fæces thus rejected would be entangled among the tentacles and spines, and remain stranded there till the motion of the water washed it away. . . . These curious little organs have other offices besides this very laudable and useful one of scavengers: they occur over the whole body, while they pass the excrements only along certain given lines. They are especially numerous about the mouth, where they are much shorter and more compact. The muscular sheath below the head is quite short, the tripartite head resting directly upon the lines of the base. On watching the movements of the pedicellariæ we find that they are extremely active, opening and shutting their forks unceasingly, reaching forward in every possible direction, the flexibility of the sheath enabling them to sweep in all the corners and recesses between the spines; and occasionally they are rewarded by catching hold of some unfortunate little crustacean, worm, or mollusca which has become entangled among the spines. They do not seem to pass their prey to the mouth—at least, I have never succeeded in seeing Sea Urchins pass the food thus caught—but merely threw it off from the surface like any other refuse matter. Their mode of eating, also —a sort of browsing, by means of their sharp teeth, along the surface of the rocks— does not favour the idea of using the pedicellariæ as feelers."*

From this account we gather that Professor AGASSIZ regards the main function of the pedicellariæ to be that of removing excrement, although they may also act the part of general cleansers to remove any other undesirable substance—whether parasitic or otherwise—from the general surface. This view has recently been confirmed by Mr. W. O. SLADEN, who says, in the course of an interesting paper,† "Mr. ALEXANDER AGASSIZ was, I believe, the first, who by actual observation assigned the true function to any of these organs. Unfortunately, Mr. AGASSIZ leaves the matter without saying which of the forms of this appendage was the agent employed. I also have seen the same operation performed; and it was always the *pedicellariæ tridentes* that came into use for the purpose; indeed, the most superficial examination would suggest that these alone could be employed for such a service, neither the *pedicellariæ globiformes* nor the *pedicellariæ triphyllæ* having valves capable of grasping so large a body as the ejected pellets in question. On the other hand, the jaws of the *pedicellariæ tridentes* are admirably fitted for the purpose; and that this is the chief use of that form of pedicellariæ there seems but little doubt."

Now, restricting our consideration in the first instance to this form of pedicellaria, it seems *à priori* improbable that so elaborate and peculiar a structure should have been developed for the purpose supposed. To sustain the supposition, it would at least require to be shown that the excrement of *Echinus* is so difficult of removal that were it not for the action of these pedicellariæ it would remain on the ab-oral pole of the animal in an amount, or for a time, that might be injurious. Yet we can confidently say that such is not the case. The dung-pellets are *generally* removed by the action

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* 'American Naturalist,' vol. xii., pp. 399–400, 1873.

† 'Annals and Magazine of Nat. Hist.,' Aug., 1880, p. 101, *et seq.*

of the *spines*, without assistance from any of the pedicellariæ. Being of a nearly spherical shape and somewhat firm consistence, their tendency is to roll down the sides of the globular animal, and to facilitate this movement the spines in their course diverge as soon as contact takes place—the pellet being thus allowed to pass between the spines with very little delay, and when brought up by other spines or stalks of pedicellariæ lower down in the series, these similarly diverge, and so on, till the pellet arrives at the equator of the animal, when it drops perpendicularly off the shell. We have watched the process over and over again, and have been so struck with the methodical action of the spines concerned in it that we find it impossible to entertain any doubt on the question whether they are alone sufficient to perform the process, or require any considerable assistance from the pedicellariæ. The assistance which the latter organs furnish in this process is only occasional, and seldom seems to be urgently required; it appears to us clearly but an accessory, if not an accidental function, for the performance of which the development of these organs cannot have been necessitated. And, direct observation apart, this view would seem to be rendered sufficiently obvious by the fact that these pedicellariæ are not restricted to the upper hemisphere of the animal, but occur also below the equatorial line, where they can never have a chance of seizing a dung-pellet at all.

Direct observation again apart, the homologies of the pedicellariæ would alone suggest that their function is probably subservient to locomotion. The valuable paper of Professor AGASSIZ already quoted derives its value from the clear demonstration which it supplies that the pedicellariæ are modified spines, and therefore the most obvious view would seem to be that they have been modified for the purpose of acquiring special proficiency as grasping organs of locomotion, over and above that which is presented by the unmodified or stilt-like spine.

On the whole, then, we believe that at least the *pedicellariæ tridentes* are not only homologous with, but analogous to, the spines; and therefore we demur to the statement of Professor AGASSIZ when he says, "the same reasoning will readily suggest to the student of Echinoderms the homology of the so-called claws of Ophiurians and of the anchors of Holothurians which, *although used for such totally different functions*, being a sort of prehensile organ for locomotion along the ground, are in reality only in their turn modified spines, or different forms of pedicellariæ." There can be no question about the homology, and our observations have satisfied us that there can be as little question about the analogy. The opinion, therefore, which we have here italicised and which refers to the pedicellariæ of *Echinus*, we think requires amendment; for observation has shown us that these organs here perform the same kind of functions as those which Professor AGASSIZ recognises the homologous organs to perform in Ophiurians and Holothurians, where—as he says, in words which follow the above quotation—"the pedicellariæ hooks and anchors perform the part of organs of prehension and locomotion at the same time."

Thus far we have been considering the case of the *pedicellariæ tridentes*. The other forms, having such much smaller grasping organs, might at first appear to be of no use in grasping sea-weeds. That they are not of so much use in this respect as the *tridentes* is rendered obvious by experiment; and therefore we do not doubt that these pedicellariæ are proportionally of more service than the *tridentes* as general cleansers. We cannot say that we have ourselves observed any actual evidence of such being the case; but the interesting experiments of Mr. SLADEN (which were not published till our observations had been completed) leads him to "offer it as a suggestion" that "the ciliary epithelium is altogether insufficient" to keep the general surface clean, and that "the duty devolves upon the *pedicellariæ globiferæ*, the following being the manner in which the work is performed:—

"When the tactile cushion of the pedicellariæ comes into contact with a tangible object of foreign matter, the valves close and a discharge of mucus takes place* wherewith the obnoxious object is covered. When the hold of the jaws is again relaxed, the irritating substance remains entangled in a cloud of the glairy exudation, ready to be easily disengaged from the surface of the animal by a few movements of the neighbouring spines, and is finally carried off by the ordinary currents of the water in which the *Echinus* lives.

"A similar process may be observed with the greatest ease to be carried out by *Astropecten;* and this I have been able to verify many times by placing a specimen of the common *A. aurantiacus* in a large flat vessel, convenient for observation, and when covered with sea-water sprinkled some fine sand and mud over its dorsal area. In the course of a short time most of this will have been carried away by the action of the paxillæ and by the lateral papillated grooves, whilst such particles as have resisted this operation will be found enveloped in a glairy pellicle, which is gradually and by very slight motion drawn into a narrow band extending over the median line of each ray. This is then disengaged from the surface entirely, and is finally cast off by the slightest movement the Star-fish may make."

POSTSCRIPT.

[Received December 2, 1881.]

Since this paper was sent in there has been a note published by MM. GEDDES et BEDDARD in 'Comptes Rendus' (tom. xcii., pp. 308–10) on the histology of the muscular tissues of Echinoderms. According to the observations of these authors the conflicting views of previous observers on the question whether the muscular fibres of Echinoderms are striated or unstriated, admit of being reconciled by the fact that the same muscle fibres are sometimes unstriated and at other times appear to be striated.

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* Mr. SLADEN is here describing the functions of pedicellariæ globiferæ in a particular species of *Echinus* (*Sphorechinus granularis*) where such a discharge was found by him to be very copious.

Further, since this paper was sent in, our attention has been drawn by Dr. P. M. DUNCAN, and also by Professor LOVÉN himself, to an important paragraph in the work of the latter already referred to ('Études sur les Échinoïdées,' page 8). This paragraph, which had previously escaped our notice, is as follows :—

"Chacun des cinq grands troncs nerveux qui naissent des angles du collier, et qui parcourent la face interne des ambulacres, le long de leur suture médiane, fournit dans chaque plaque un ou deux nerfs, qui se dirigent chacun vers le pore tentaculaire correspondant. Conjointement avec le vaisseau aquifère du tentacule, le nerf s'y enfonce, pour reparaître sur la face externe au dehors de la couche calcaire du test. Sur ce trajet il doit fournir des filets nerveux au tentacule et au sphéricle, bien qu'on ne soit pas parvenu à en démontrer l'existence. Mais, comme ou peut le voir chez la Brissopsis lyrifera, et le plus distinctement sur la troisième plaque du bivium avoisinant le sternum et plus dépourvue de radioles que le autres, le nerf, en sortant du pore tentaculaire sur la face externe du test, se ramifie en un grand nombre du filets, lesquels, après avoir traversé la plaque diagonalement, se distribuent aux aires interradiales en formant des entrelacements serrés et riches en cellules ganglionnaires. On conçoit que, tous les rameaux du tronc nerveux se divisant de cette manière, il y aura, répandu à la surface du corps, un système nerveux périphérique extrêmement développé, fournissant des nerfs aux radioles, aux pedicellaires, aux clavules des fascoiles, et, en général, à toutes les parties externes. La figure donnée en représente une très petite partie dessinée à un fort grossissement."

It only remains to add that during the past autumn we have continued the research, and have been successful in obtaining full histological demonstration of the internal nervous plexus of *Echinus*. This plexus is therefore now no longer "hypothetical;" and in a subsequent paper its character, distribution, and mode of communicating with the external plexus will be fully described, together with some further physiological experiments.

G. J. R.,
J. C. E.

December 1, 1881.

DESCRIPTION OF THE FIGURES.

PLATES 79–85.

Fig. 1. Ambulacral system of *Holothuria*.
  a. Polian vesicle.
  b. Ambulacral circular canal.
  c. Circular canal sinus. Small circle at apex indicates position of opening into a radial canal (*k*) ; at each side the opening into a tentacle sinus (*d*) is indicated.
  e. Trunk of tentacle.

f. Aperture between sinuses which leads into space around œsophagus. This space communicates with circumoral sinus (Plate 79, fig. 2, *a*).
g. Ampulla.
h. Circle indicating constriction between oval sinus and retracted tentacle.
i. Madreporic plate.
k. Radial canal giving off two lateral branches, each branch gives rise to an ampulla (*g*) and a pedicel (*n*).
l. Longitudinal muscular band.
m. Retractor muscle.

Fig. 2. Section through anterior portion of *Holothuria*.
a. Circumoral sinus.
b. Circular ambulacral canal.
c. Sinus of circular canal.
d. Sinus of tentacle.
e. Aperture through which circumoral sinus communicates with space around œsophagus.
f. Cæcal prolongation from sinus of circular canal.
h. Fibres stretching inwards from sinuses and circular canal to œsophagus.
m. Retractor muscle.

Fig. 3. *Holothuria* with tentacles fully distended.
c. Circumoral sinus.
b. Aperture through which sinus communicates with space around œsophagus.
a. Cæcal end of prolongation from sinus of circular canal.
d. Aperture of cloacal chamber.

Fig. 4. Section of cloaca in *Holothuria;* valve open and retracted.

Fig. 5. Section of cloaca in *Holothuria;* valve closed and projected.

Fig. 6. Partially retracted pedicel of *Echinus* showing sucking disc.

Fig. 7. Section of partially retracted pedicel of *Astropecten*.

Fig. 8. Section of pedicel of *Astropecten* slightly retracted at one side (*a*) so as to act as a sucker.

Fig. 9. Section of pedicel of *Ophiura*.

Fig. 10. Section through lantern of *Echinus*.
a. Sinus under madreporic plate (*b*).
c. Madreporic canal.
d. "Heart."
f. Radius.
g. Rotula.
h. Circular muscle.
i. Radial canal.
j One of the inner series of pedicels with a tubular ampulla (*k*).

l. "Tree-like organ."
m. Membranous wall of large space above "tree-like organ."
n. Sinus around tip of tooth
o. Tooth lying in space (*p*) between the alveoli.
q. Edge of alveolus.
r. Interalveolar muscle.
s. Auricle.
t. Radial nerve.

Fig. 11. Ambulacral system—*Solaster*.
a. Madreporic canal.
b. Inner end (*g*) outer end of sinus leading to circular neural vessel (*h*) from which radial neural vessels (*l*) arise.
c,*d*. Polian vesicles.
f. Ampullæ.
m. Oral aperture.
n. Madreporic plate.

Fig. 12. Madreporic plate enlarged, showing space (*a*) through which fluid escapes from madreporic canal.

Fig. 13. Scheme showing portions of ambulacral and nervous systems of *Echinus*.
a. Ampullæ.
b. Radial nerve.
c. Neural radial sinus.
d. Lining membrane of shell.
e. Radial ambulacral canal.
f. Lateral branch of radial canal.
g. Pedicel.
h. Spine.
i. Pedicellaria.
k. Layer of fibres external to shell.
l. Subepidermic nerve-plexus.
l'. Plexus extending over base of spine.
l''. Plexus extending over pedicellaria towards base of mandibles.
m. Epidermis.
n. Lateral branch from nerve-trunk.
o. Continuation of lateral branch alongside of pedicel.
p. Portion of lateral branch which probably communicates with external plexus.
r. Ambulacral plate.

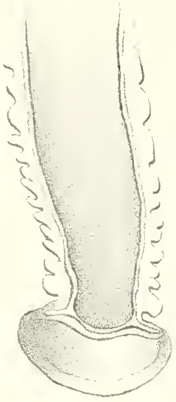
Fig. 14. Fibres and cells of nerve-trunk.

Fig. 15. External plexus partially covered by epidermis lying over muscular and connective tissue-fibres.

Fig. 16. Nerve-cells lying amongst muscular fibres at base of spine.
Fig. 17. Nerve-fibres lying between epidermis and calcareous stem of pedicellaria.
Fig. 18. Plexus lying over muscular fibres near base of mandibles of pedicellaria.
Fig. 19. Natural co-ordinated movements of common Star-fish.
Fig. 20. Natural righting movements of common Star-fish.
Fig. 21. Natural righting movements of *Astropecten.*
Fig. 22. Natural locomotor movements of *Ophiura.*
Figs. 23–26. Natural righting movements of *Echinus.*
Fig. 27. Righting movements of severed ray of common Star-fish after bisection of radial nerve.
Fig. 28. The unco-ördinated movements of inverted Star-fish after section of the five radial nerves.
Fig. 29. Tulip-shape assumed by the same.
Figs. 30, 31. Righting movements of segments of *Echinus.*
Figs. 32–34. Righting movements of *Echinus* on a vertical surface.

Fig. 1.

Fig. 6.



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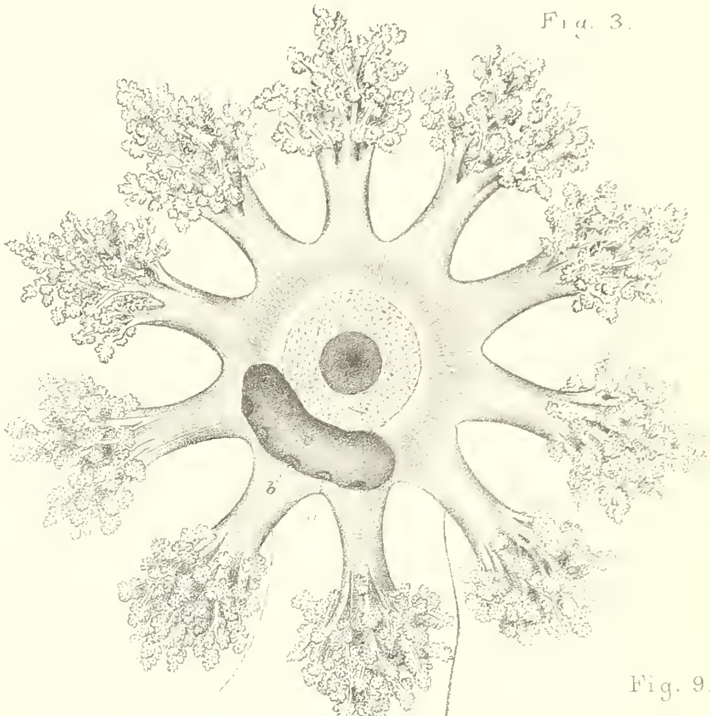

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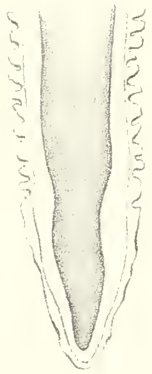

Fig. 9.

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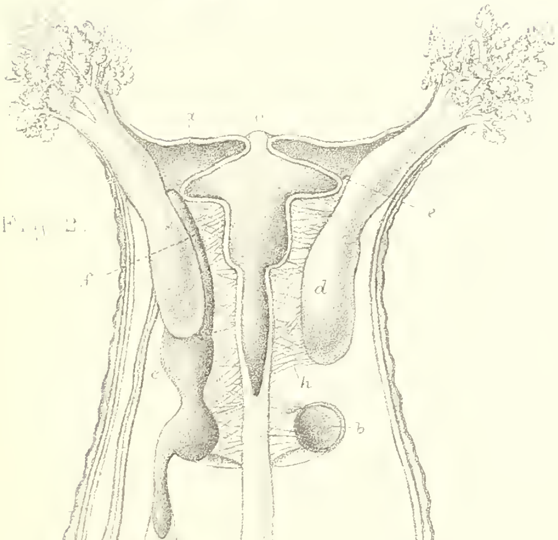

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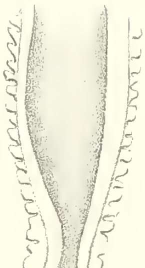

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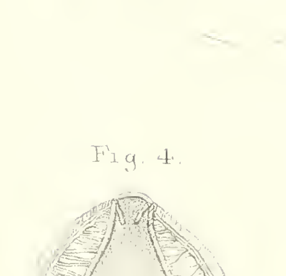

Fig. 5.

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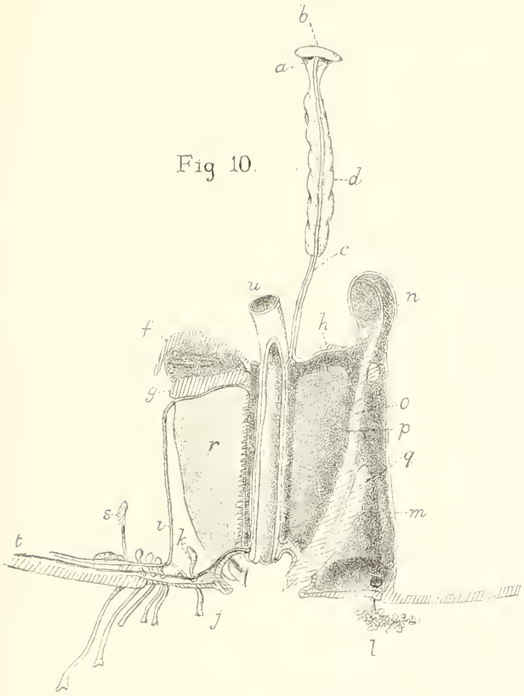
Fig 10.



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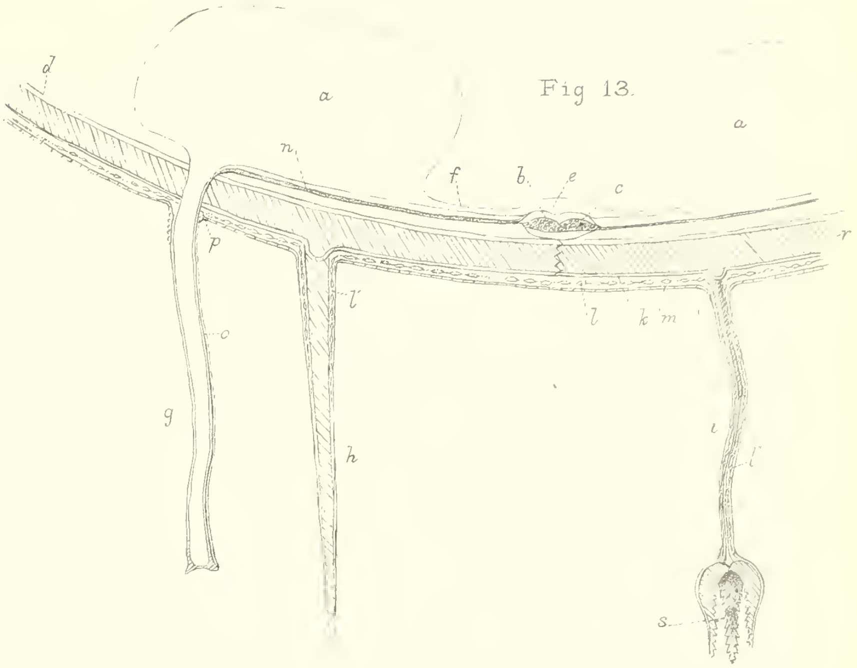

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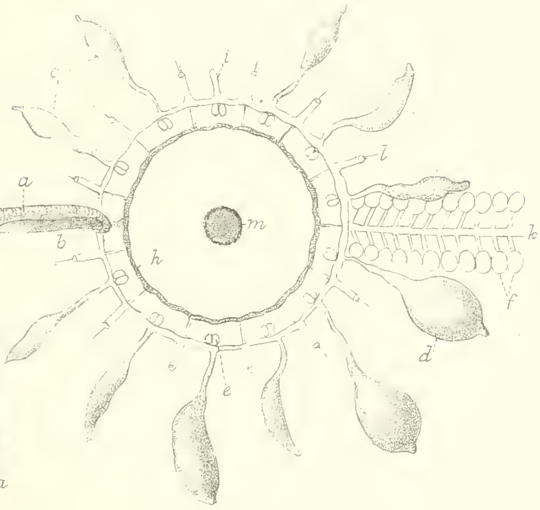

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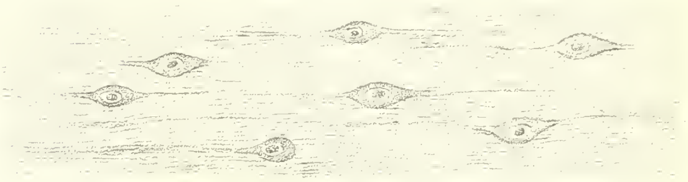

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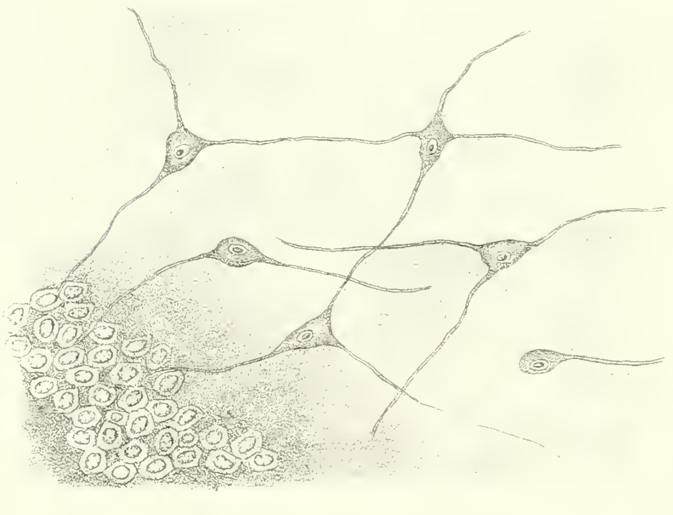

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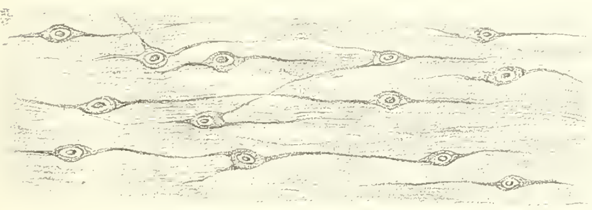

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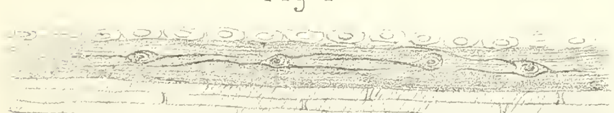

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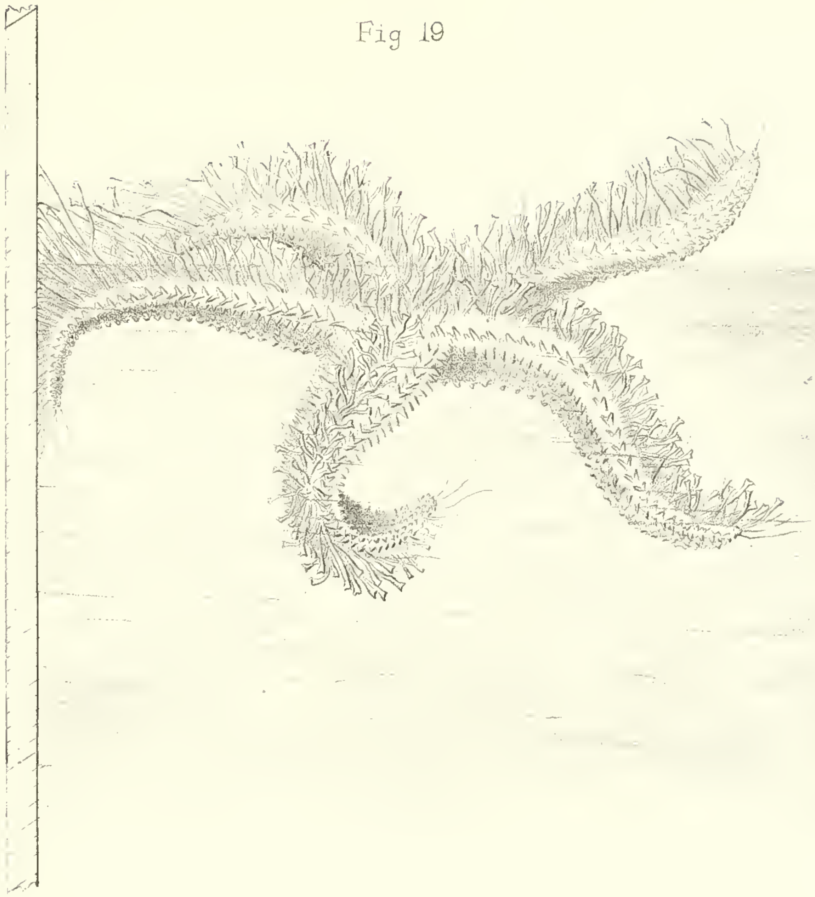
Fig 19



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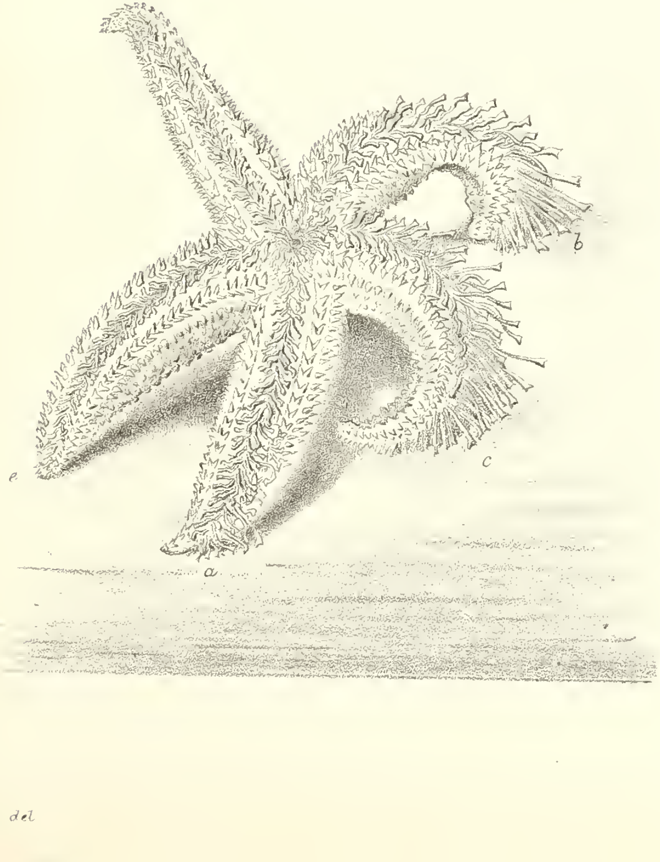

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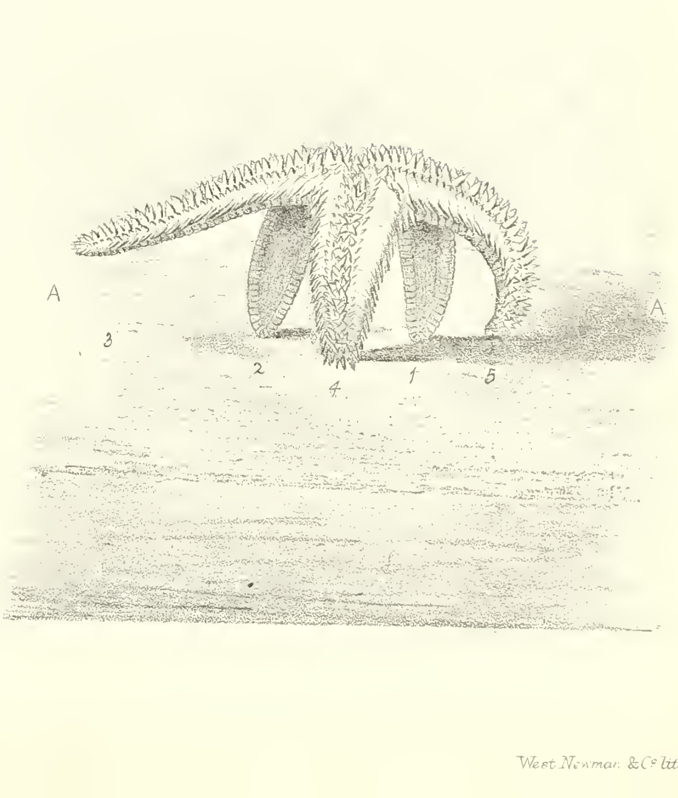

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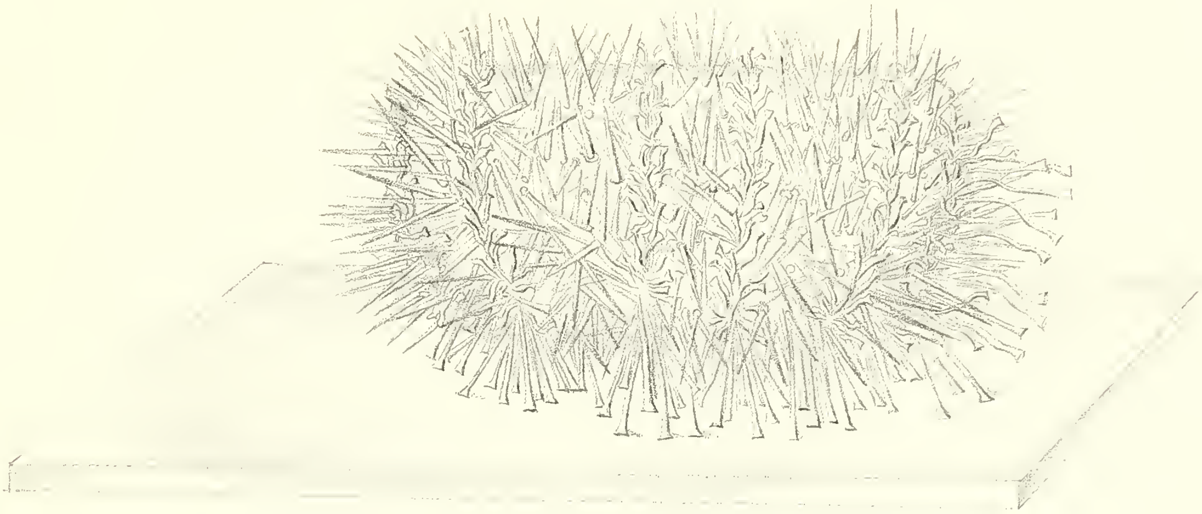

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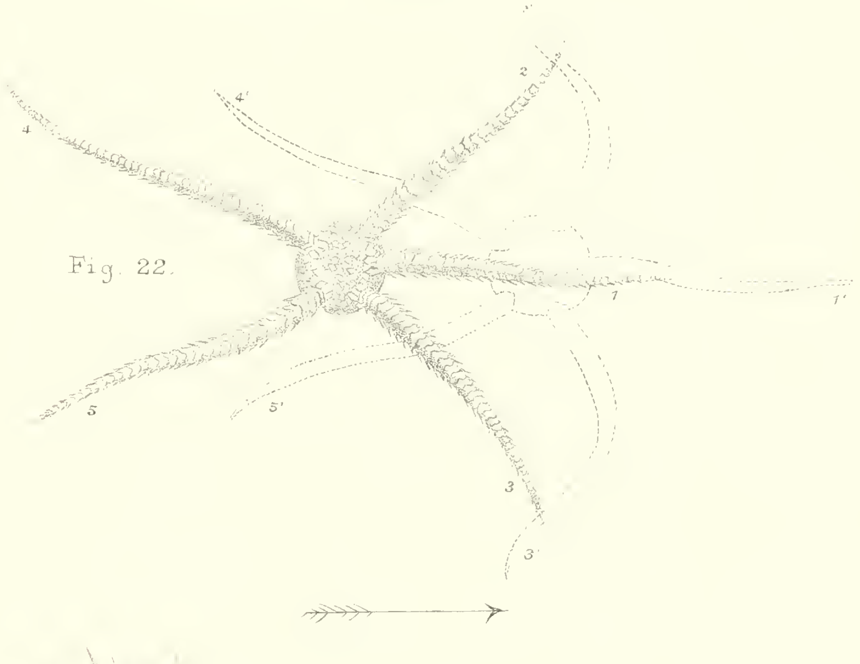

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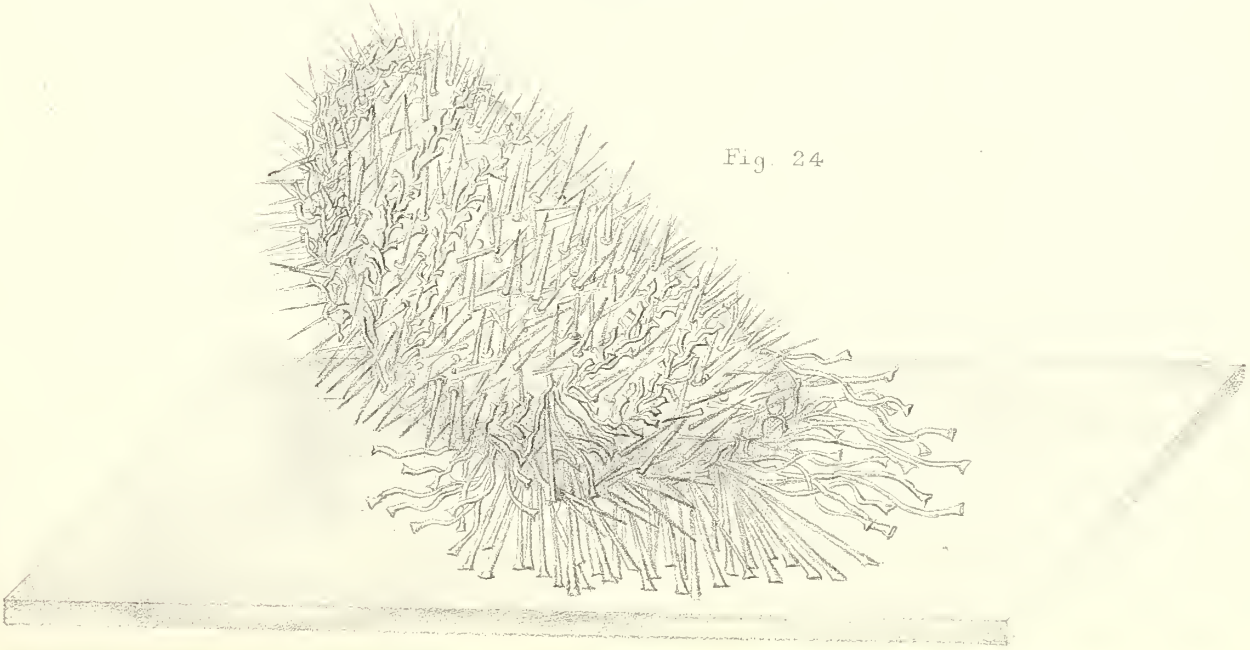

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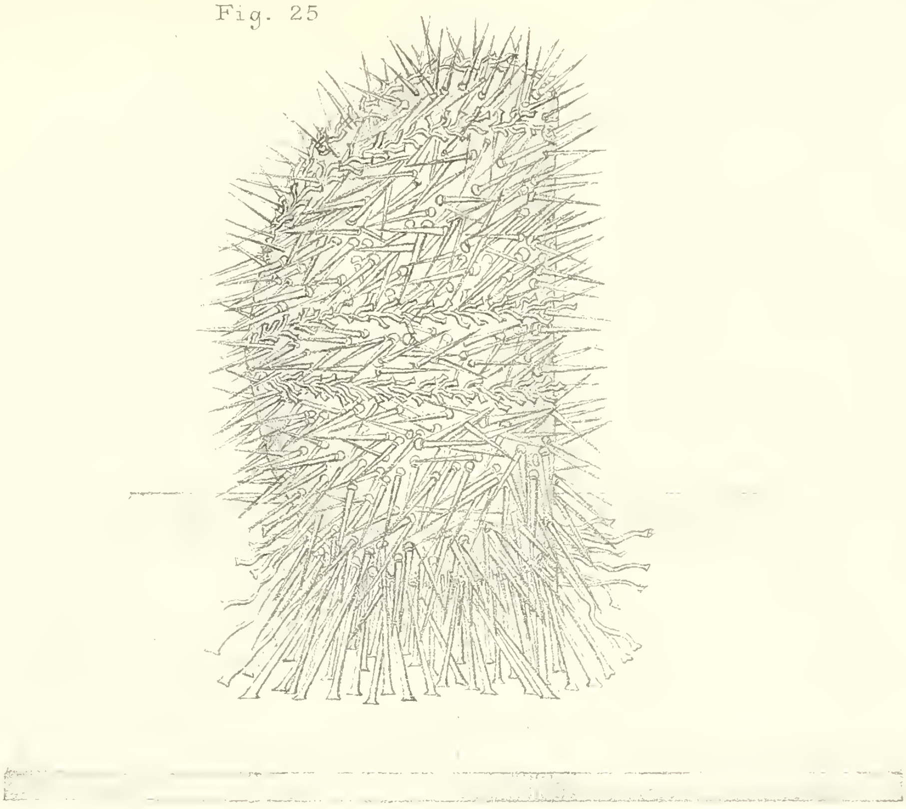
Fig. 25



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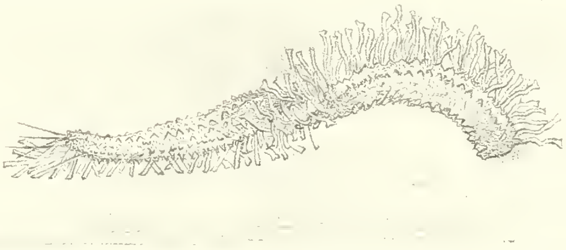

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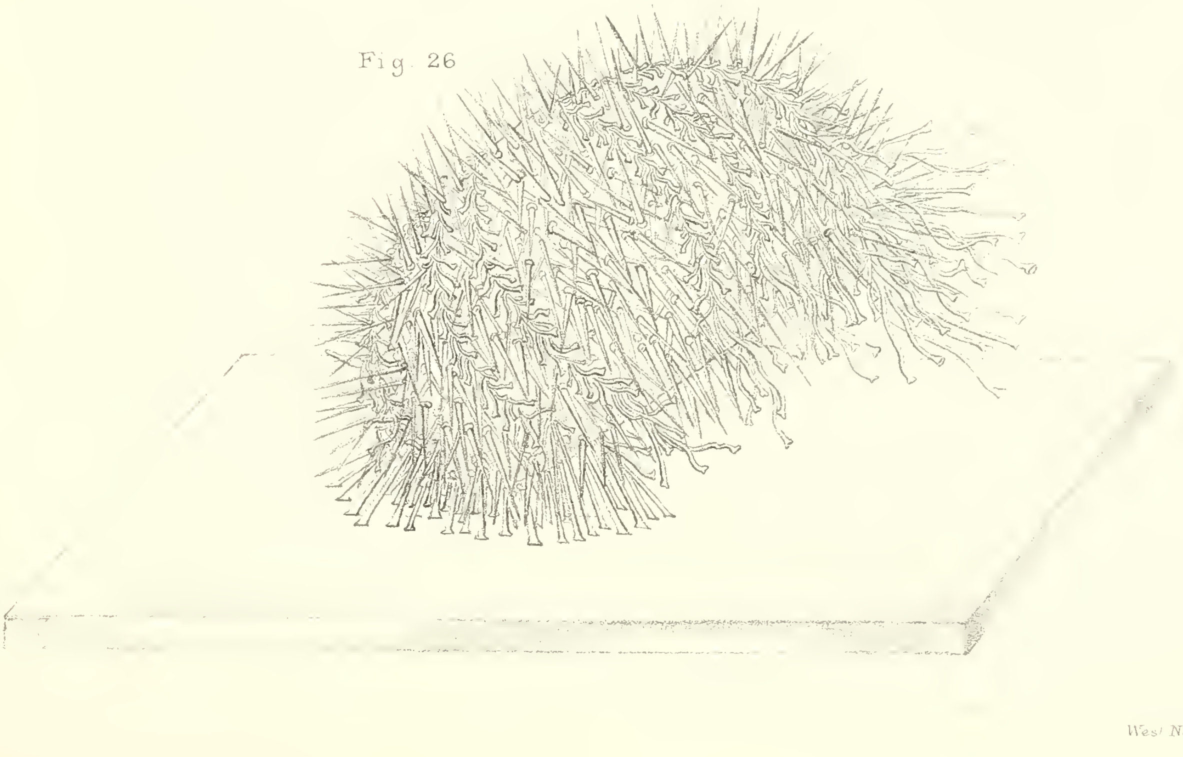

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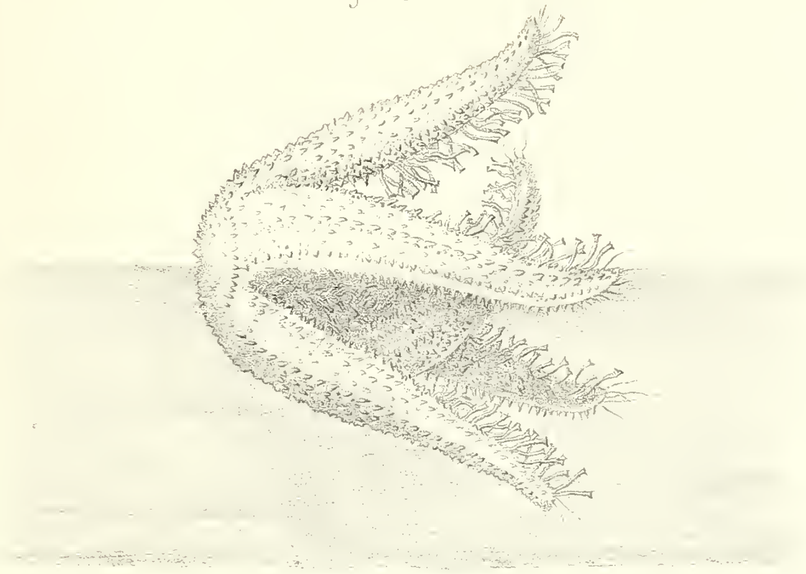

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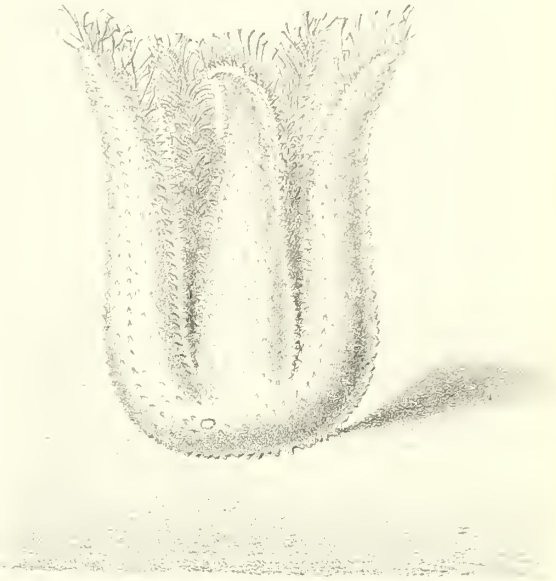

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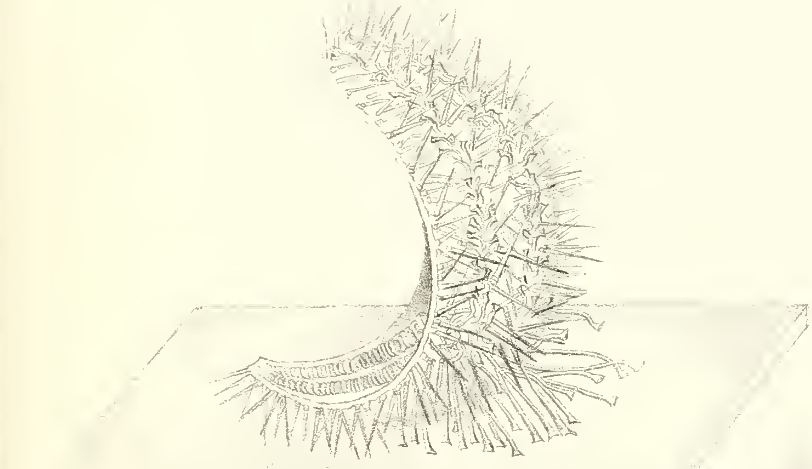

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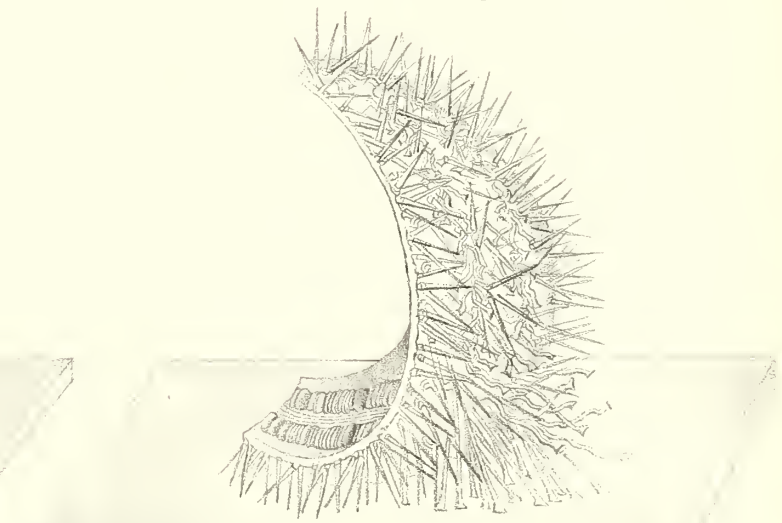

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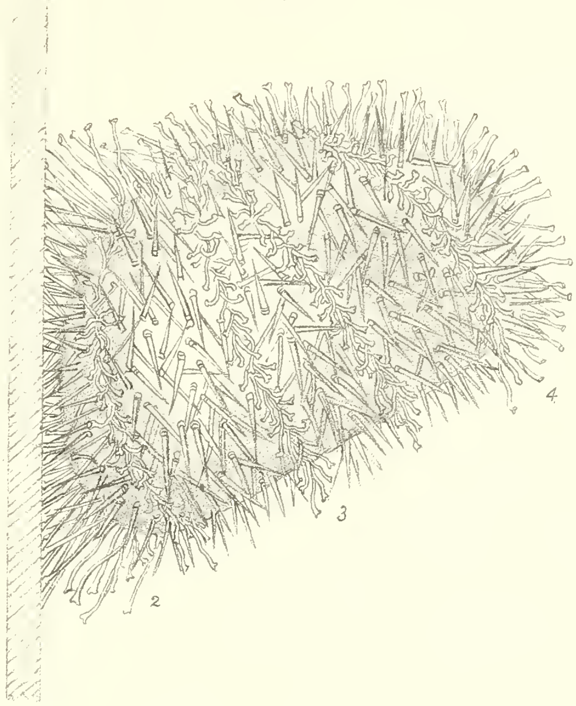

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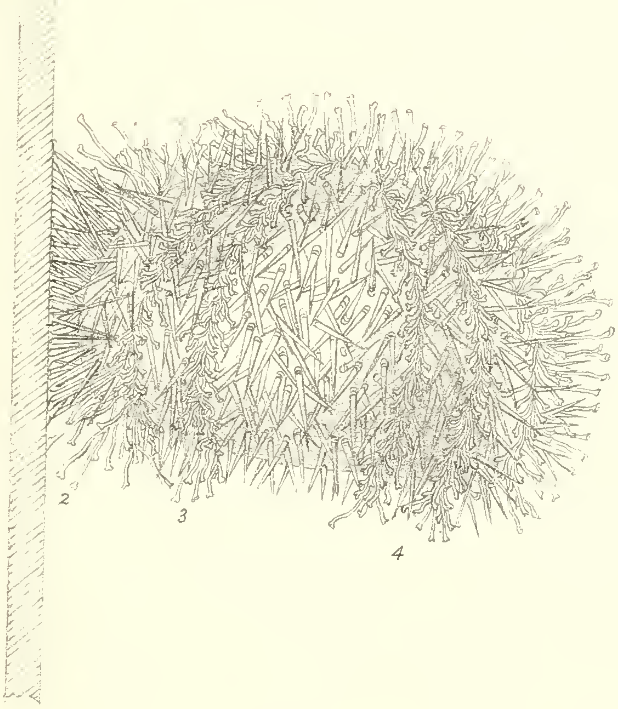

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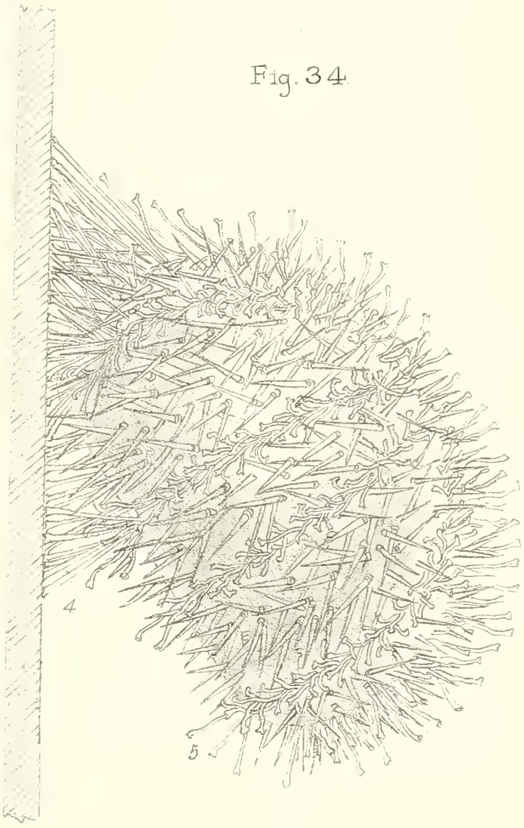

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