ON TRACES OF ANCESTRAL RELATIONS IN THE STRUCTURE OF THE ASTEROIDEA. BY W. PERCY SLADEN, F.L.S., F.G.S.

[Plate XV.]

The Echinodermata constitute a sub-kingdom of animals in which the structure of the various divisions presents a number of highly remarkable points of affinity and difference. Indeed, so strikingly is this the case, that when typical or representative specimens are subjected for the first time to superficial examination by a person unacquainted with their internal anatomy, the principal groups would most probably be looked upon by him as perhaps the most diverse of creatures—popularly speaking—that it could be possible to link together. Five Classes of living Echinoderms are included in this category:—

- 1. The Crinoidea, which are familiarly known as 'Sea-Lilies.'
- 2. The Ophiuroidea or 'Brittle-Stars.'
- 3. The Asteroidea or 'Starfishes.'
- 4. The Echinoidea or 'Sea-Urchins.'
- 5. The Holothuroidea or 'Sea-Cucumbers,'

The present communication will deal with certain homologies that exist in the structure of the Asteroidea and Ophiuroidea, upon which deductions of considerable importance have been based. It will be desirable, however, to explain before proceeding further that although the word 'homologies' is employed in this instance as synonymous with 'traces of descent,' it is not the purpose of this paper to trench upon the subject of the phylogenetic development of the Echinodermata as a whole, but simply to confine the remarks to several points of evidence that indicate ancestral relations between the two groups in question.

Although we shall not directly press into our service palæontological evidence, I make bold to believe that the subject will not be without interest to Geologists;—first, from the circumstance that Asteroids and Ophiuroids are amongst the earliest representatives of the Echinodermata with which we are acquainted; and secondly, because the facts about to be enumerated encroach upon one of those border-lands that stand between neighbouring classes, and which from the very nature of their being, reflect to us some traces of the structure of ancestral forms that have long since passed away, or even of architypal phases with the actual persons of which we are altogether unacquainted.

It will not perhaps be unprofitable to describe briefly and in plain words for the benefit of those who may not be acquainted with this branch of Zoology, the general appearance and character of the two sets of animals of which we are about to treat.

The Asteroidea or Starfishes possess a more or less depressed body, which may vary in outline in every conceivable degree between a goniodiscoid or pentagonal form, and a deeply indented or truly stellate form. The shape is maintained by a more or less compact frame or meshwork of calcareous pieces, over which is stretched a coreaceous skin, and which, in the generality of cases, is beset with a number of projecting spinelets or prickles. mouth is situated in the centre of the under surface, and a deep furrow proceeds along each of the radii or 'arms,' as they are familiarly called. When the animal is alive and in health there may be seen protruding from either side of the median line of this furrow, a long continuous row of white pellucid sucker-feet, with which the starfish crawls along. This area of the ray has been named the ambulacrum or ambulacral area, and the tube feet, the 'ambulacral suckers.' On making a dissection of a starfish it will be found that the stomach not only occupies the central part of the animal, but also that a portion of it, as well as of the digestive organs and other viscera, is extended along the rays or arms.

Comparing now the Brittle Stars or Ophiuroidea, (which were so named from the long serpent-like arms they possess), we find a small depressed discoid body to which five or more long, worm-like, segmented appendages or rays are attached; the disk being closely tessellated with scale-like plates and the rays being covered with four longitudinal series of large symmetrical plates, of which the lateral ones bear spines. The mouth is situated in the centre of the under surface of the body-disk, but there are no ambulacral

furrows along the rays and no sucker feet, only a pair of small semi-retractile tentacles to each joint, which have little or nothing to do with locomotion; that function being performed by the specially-adapted, slender, flexible arms themselves. The internal anatomy presents still more striking differences, for the stomach is a simple sac confined entirely to the disk, and no prolongations of it in the form of digestive organs or other viscera are extended into the ray; the interior of the ray being occupied by a great number of vertebra-like joints: the whole arm forming a truly independent appendage to the disk, instead of being an actual lobe of the body as is the case in starfishes.

With this introduction we may now proceed to compare the special structure of what is generally regarded as a typical Asteroid with a typical Ophiuroid.

The diagram given on Plate XV., Fig. 1, represents a transverse cut through one of the rays of a starfish. The section of the ambulacral furrow may be recognised on the lower margin, and it is now seen that this furrow is bounded, or indeed formed, by a calcareous arch, (marked a). This, however, is not a portion of a solid continuous roof or groove, as might naturally be supposed from such a drawing, but simply represents the end view of a pair of thin lamelliform plates: the length of the ray being built up of a great number of such pairs of plates placed end to end the whole way along. These plates are known as the 'ambulacral plates,' and between each neighbouring pair, a pair of the ambulacral suckerfeet take their passage, (Fig. 1, t.). The manner in which these organs are worked is very interesting, and takes effect in the following way:-On the upper surface of the disk-portion of a starfish a small round body may be seen, intersected by a number of fissures and resembling in miniature a brain- or madrepore coral. Through this sea-water passes freely, and traverses a filtering tube until it reaches a vein that encircles the mouth; branches are given off from this oral vessel opposite each ray and proceed along the median line of the furrow; small transverse veins being given off from this main trunk between each pair of

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ambulacral plates, and these open into the upper bag-like portion of the sucker feet,—which latter may be described as simple sacs, having very extensile and strongly muscular walls. It will thus be seen that the whole system of vessels is filled with fluid; and this is known as the 'water-vascular system.' (Coloured blue in the diagram.) When the starfish wishes to extend its sucker, muscular pressure is exerted upon the bag-like portion of the sac: this causes the contained water, and with it the tentacle-foot, to be squeezed forwards in consequence of the contraction of the reservoir-bag. When it is necessary to retract the foot, the reverse of this process takes place. Returning to the section,—at the outer extremity of each ambulacral ossicle is a small plate (Fig. 1, b.), and the series of these form the margins of the furrow. They are called 'adambulacral' plates, and usually carry spines. The sides of the ray are occupied by the lateral or marginal plates (Fig. 1, l.), which may be two in number or many; and the upper portion by the dorsal plates, which are usually arranged in a more or less regular meshwork, and bear clustered spinelets or 'paxille' (Fig. 1, p.) The internal cavity is extensive, and in it are disposed the digestive cæca previously mentioned. The main radial nerve-cord is situated superficially to the water-vascular vessel, and its position is indicated in the diagram in red.

It will not be necessary for the present purpose to go more minutely into the anatomy of the Starfish, we will therefore proceed to compare a similar section made through the ray of an Ophiuran, which is given in Fig. 2. Here it will be observed that the outer walls are formed by four large plates, and what we see in the diagram are the ends of these plates which constitute the annuloid segments of the ray; the whole space within, excepting only a very small cleft above and below, being occupied by the extensions of a large calcareous disk, marked a., (Plate XV., Fig. 2), presenting various articulatory prominences and depressions, and which, when the upper arm-plate (Fig. 2, c.) is removed, will be seen to be the extremity of a vertebra-like joint, which articulates with a similar body that occupies the neighbouring segment. On

examining one of the segments on the under side, after the under arm-plate (Fig. 2, d.) has been removed, it will be seen that the ambulacral tentacles are situated in a pair of quite small pits, excavated, as it were, out of the joint itself. The size of these cavities limiting, as a matter of necessity, the capability of the retraction of the tentacle to such an extent that they can never be entirely drawn in. The vessel of the water-vascular system is situated in the angle of the inferior notch, and the nervous system is placed external to this. (These systems being coloured blue and red respectively.) The internal axis of each joint is attached to that of the neighbouring segment by very largely developed muscular bands.

It now remains to point out the homologies that exist between the structures just passed in review.

If one of the axial joints from the ray of an Ophiuran be carefully examined, it will be seen that this vertebra-like body is in reality formed of two pieces ankylosed together along the median line. (The plate marked a in Fig. 2 being one half.) These two plates are in fact the greatly developed and modified representatives of the ambulacral plates of the Asteroid (Fig. 1, a.). The side arm plates (Fig. 2, b.) are the homologues of the adambulacral plates (Fig. 1, b.); whilst the dorsal or upper arm-plates of the Ophiuroid (Fig. 2, c.) stand in the place of the dorsal and lateral plates of the Asteroid (Fig. 1, l, p.). One other plate yet remains to be mentioned (Fig. 2, d.), and it is perhaps the most interesting of all, because entirely wanting in the diagram of the starfish. In the latter the ambulacral furrow, with its contained water-vascular and nervous systems, is quite open and uncovered; in the Ophiuran, on the other hand, it is enclosed entirely by the ventral or under arm-plate (Fig. 2, d.). To account for such a discrepency would be a difficult task, if light were not thrown upon the subject by the embryology of Asteroids; and we owe the discovery to Mr. Alex. Agassiz* that a similar calcareous plating is present along the furrow of a starfish when in a very early phase of growth. This formation, however, becomes so modified during the process of development, that all

^{*} Mem. Mus. Comp. Zool. Harvard, vol. v., pt. 1.

traces have entirely disappeared long before the adult stage is arrived at.

It will be unnecessary for me to point out to those acquainted with the general principles of Biology, the significance and extreme importance of this fact; and it will suffice to say for the present occasion, that this devolves upon a law in embryology—that the phases in the individual development of a complex organism represent, in a more or less epitomised manner, the conspicuous characters of the stages passed through during the course of phylogenetic development, or in other words, symbolise the race-history of the animals to which they belong.

From the above-mentioned circumstance we reason that there was a time in the history of Asteroids when under arm-plates were possessed, and when in fact these Echinoderms were conformed to that plan of arrangement which we now associate with the Ophiuroidea only.

The homologies of parts just enumerated may be further pursued if we study the comparative anatomy of the mouth-armature of the two groups, and this investigation will at the same time furnish a proof of the correctness of the foregoing assertions. Such a circumstance is not difficult to understand when it is borne in mind that the mouth-parts are formed by the concrescence and modification of certain of the ray elements; and secondly, that representative elements, or in other words, homologous parts go to the formation of similar portions of the dental apparatus in both groups. As the discussion of this question in detail would absorb far more space than the present occasion would allow, I shall not extend my remarks further in that direction, having simply mentioned the fact as an evidence of the close affinity that may be traced between these apparently widely separated forms.

There is yet another point in the structure of the Asteroidea which ought not to be passed over when critically discussing the race-history of the group; and it is also an embryological observation for which we are indebted to Mr. Alex. Agassiz*; although I

^{*} Proceed. Am. Acad. Arts and Sci., April, 1863.

am not aware that that naturalist has availed himself of the deductions which necessarily follow. When describing the Starfish it may be remembered that I drew attention to the presence of a peculiar madreporiform body, situated between the margin and the centre, on the upper or dorsal surface of the disk, and which formed the orifice of the water-vascular system. In the Ophiuroidea the position is altogether different, the orifice being found on the ventral or under surface and occupying one of the plates that surround the mouth. Now in this very striking difference there lies—although it may seem strange at first thought—a highly important point of evidence in support of the argument which this paper maintains.

In an early stage of the development of an Asteroid, shortly after the young starfish larva has emerged from its brachiolaria phase, the plate that bears the punctures of the water-vascular system, and which eventually becomes the madreporite, is situated on the under side, and close adjoining the plates that form the margin of the mouth. In other words, we have again presented to us in the larval Asteroid, the precise arrangement of parts that occurs in the Ophiuroidea when in the mature form; and from this we are led to infer from our present knowledge of the laws of embryology, that the Asteroidea have in the course of the history of their race, passed through a stage which is now represented—in a more or less modified style, it may be—by the present Ophiuroidea.

Notwithstanding the existence of these resemblances in structure, it has always been held that the Asteroidea and Ophiuroidea were separated by a wide gulf of difference, over which no known echinoderm presented sufficiently modified characters to form a bridge, and which would serve as an index of their closer ancestral alliance. Recently, however, there has been discovered a remarkable organism of most abnormal form, undoubtedly intermediate between the two groups, and which passes unquestionably very much further over the borderland that lies between them than any other star fish or brittle-star with which we have hitherto been acquainted.

Space will not permit me to enter further into the description of this curious organism, than to say that it appears to present the 282

general character of ophiuran structure, arranged and modified according to the plan of asteroid organization, and in this manner to reflect as it were, a primitive stage of the race-history of the classes which we are discussing. There exists, however in the anatomy of Astrophiura—for such is the name under which I have described* this aberrant genus—a feature that bears so strikingly upon the subject with which we are dealing, that it will be found not unworthy of attention whilst we touch upon it very briefly.

The diagram given in Fig. 3, represents a section through one of the radii. On comparing this with those which we have previously been considering, it will be seen we have here a sort of compromise between the characters of both. In a modified form there is the internal skeleton belonging to the Ophiuroidea, together with the presence of the peritoneal cavity which is found in Asteroidea. The radial axis however is extremely aborted, and the disk-like processes, which in the Ophiuroidea extend from side to side across the section of the ray, are here reduced to diminutive ear-shaped processes of the most insignificant description. (Fig. 3, a.)

Furthermore, there exists a supplementary plate in Astrophiura (Fig. 3, e.), and upon this especial interest devolves. It consists of a large, broad, thin plate, that joins up to the aborted disk-processes of the axis and forms a partition reaching up to the inner surface of the abactinal wall of the test, constituting in fact the divisional septum, or wall of a compartment, for an ambulacral tentacle. No equivalent for this accessory plate can be pointed to in the section of the typical Ophiuroid, and search has to be made amongst the Asteroidea before any homologous structure is met with. In the more ancient forms of that group, such e.g. as the Astropectinidæ and Linckiadæ, a small supplementary plate occurs, which forms a connective or intermediate piece, filling in the angle formed by the ambulacral and ventro-lateral plates. (Fig. 1, e.) These are what I consider to be the homologues of the supplementary plates or ambulacral septa just mentioned in Astro-

^{*} Proceed. Roy. Soc., vol. xxvii, p. 456. Ann. and Mag. Nat. Hist., ser. 5 vol. iv, p. 401, pl. xx.

phiura. If this view be correct, the main interest will centre in the fact that we have here the representation of a stage in the genetic development of the Asteroidea, all traces of which have passed away in the course of the evolution of the more advanced forms of the group.

In conclusion,—the details of structure which have been brought forward require but very few words in the way of summing up. The facts speak for themselves, and, if we take a common sense view of things, the conclusion seems inevitable that the homologies now adduced indicate the existence of an ancestral relationship between the two groups in question; nay more, they point to a common origin or start-point of descent. From our present knowledge it would be difficult, it is true, to demonstrate definitely the actual line by which the Asteroidea have descended from Ophiuroidea, such as those at present known to us, but I submit that this much may be predicated with but little hesitation, -that both Asteroidea and Ophiuroidea are the descendents, (along collateral lines of development), from a more remote and common Ophiuroid-like ancestral stock, but with the actual form of which we are at present altogether ignorant, and of the probable structure of which we are only able to surmise.

Bold though such a statement may seem to some, I feel confident that biologists will grant that the nature of the evidence is such as to remove this conclusion from the region of mere vague speculation, and to place it upon the basis of warrantable generalisation.

EXPLANATION OF PLATE XV.

Fig. 1.—Section through the ray of an Asteroid (Astropecten), at the junction of two segments. Magnified and partly diagrammatic.

a. Ambulacral plate.

b. Adambulacral plate. This plate bears the 'ambulacral' spines, which have been omitted from the diagram for the sake of clearness.

e. Supplementary girder-like plate.

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- Lateral plates. These plates usually bear spines, which have been emitted from the diagram.
- v. Paxillæ of the dorsal area.
- t. Ambulacral tentacle or sucker-foot.
- Fig. 2.—Section through the ray of an Ophiuroid (Ophiarachna), at the junction of two segments. Magnified and partly diagrammatic.
 - a. Disk of the axial skeleton of the segment.
 - b. Side arm-plate. This plate bears the arm-spines, which have been omitted from the diagram for the sake of clearness.
 - c. Upper arm-plate.
 - d. Under arm-plate.
 - t. Ambulacral tentacle.
- Fig. 3.—Section through the ray of Astrophiura, at the junction of two segments. Magnified.

Same letters as above.

In each of the figures homologous parts are marked with the same letters.

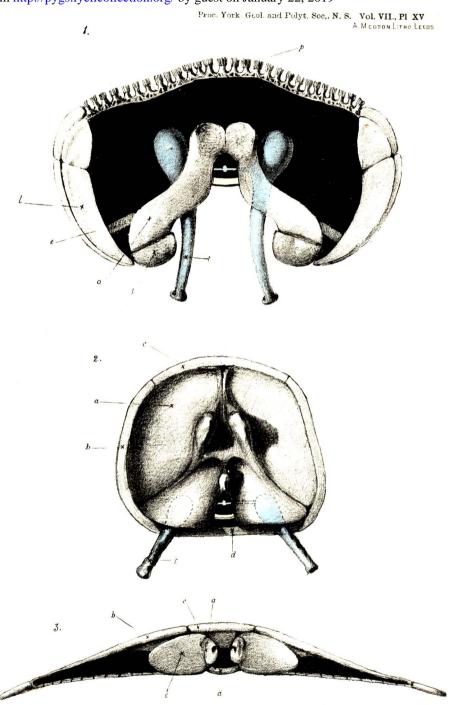
The Water-vascular system is coloured blue, and the position of the Nervous system is indicated in red.

ON THE GEOLOGY OF THE DISTRICT OF AROUND MIDDLES-BOROUGH. BY W. Y. VEITCH. (ABSTRACT.)

This Paper was of the utmost service to the members who attended the meeting at Middlesborough, and contains a clear account of the Geology; with remarks on the Flora of the District. There is however not sufficient new matter to render its publication necessary.

THE town rests upon an estuarine deposit consisting of clay, sand and gravel, with patches of a peaty nature distributed in low-lying places, containing much vegetable remains, large trunks of oak, a few antlers of the red deer, and numerous shells of the Scrobicularia piperita.

A staple going 27ft. below low-water mark, at the new gas tank, revealed nothing but layers of soft blue clay mixed with vegetable matter, and a loamy mixture of silt clay and vegetable matter. Below this is the new red sandstone containing enormous deposits of salt, upwards of 100ft. in thickness, at a depth of about 400 yds. At high water the low-lying places referred to are saturated subterraneously with water, which again disappears with the receding tide.



Henry Sykes, Del.

ASTEROID AND OPHIUROID STRUCTURE.