thin, pellucid, pale, with whitish rays and darker submarginal streaks; covered with a thin pale brown laminar periostracum; lunule and lozenge smooth, keeled; lateral teeth very thin. —Hab. China.

Very like *M. Helvacea*, but smaller and much more compressed.

V.—Prodromus of a Monograph of the Radiata and Echinodermata. By Louis Agassiz, D.M.*

HAVING had occasion for some years to examine a great number of Echinodermata, and having paid particular attention to their general organization, but more especially to the solid portions of their integument, which have been hitherto considered the most important of their external characteristics, I have felt induced by these circumstances, and others no less favourable to inquiries of this kind, to publish the following outline of a survey of the genera of this class as an introduction to a more general and critical work, in which I purpose hereafter to treat of all the species and their comparative anatomy.

The section of radiated animals to which the Echinodermata belong, should, in order to be characterised in a general manner, be reduced to three classes : the Polypi, the Acalephæ, and the Echinodermata. Intestinal worms, and a great part, if not the whole, of the Infusoria should be restored to the section of articulated animals. That I may not be compelled for a moment to lose sight of the main object of this paper, I think it advisable, as M. de Blainville has already proposed some of these changes, to refer for information as to the limitation of these classes to the article "Zoophytes" in the 'Dictionnaire des Sciences Naturelles,' though there are several points of detail on which he and I disagree.

The class of the Echinodermata confined within its natural limits should contain no more than the three genera *Holothuria*, *Echinus*, and *Asterias* of Linnæus, which have become the

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^{*} Translated from the extract in the 'Annales des Sciences Naturelles,' Mai 1837, taken from the 'Mémoires de la Société des Sciences Naturelles de Neufchâtel,' tome i.

types of as many families. It is therefore necessary to exclude from it the Sipunculi, &c., which constitute the second order of this class in the Animal Kingdom of Cuvier, and to place them amongst the Vermes. Thus reduced the class is characterised especially by the presence of retractile pedicles arranged in rows between the vertical segments of the integument of the body. On account of this peculiarity M. de Blainville has changed the name of Echinodermata, which is not really applicable to the Holothuria, into that of Cirrhodermata, although the nature and functions of these moveable organs, as well as their relations to the external integument, are too imperfectly known at present to justify him fully in giving them that name. The name of Radiated, borrowed from Lamarck, and restricted to the limits which science now assigns to this class, seems therefore entitled to a preference. It has the advantage of being simple, and that of involving no systematic idea.

The most general character commonly assigned to the Echinodermata is that all the parts of their bodies are disposed like radii about a common centre. This character they possess in common with the whole division of radiated animals. However, on closely examining this radiated disposition of the parts, it is observable that in different genera the rays are not always alike, and do not always tend to a centre of the same nature. My first care has been therefore to discover the general laws of configuration and organization in this class, and to determine the analogies which the different regions of the body bear to one another and to those of other animals, in order thus to obtain an appropriate terminology for their description. The regular radiated disposition of the parts in most of the Radiata renders it difficult to fix such a terminology. I thought it best therefore to begin with the study of the forms most remote from the star type, (in which an anterior and posterior, a superior and inferior, and consequently a right and a left region are naturally exhibited,) in order, if possible, by easy gradations to trace the same relations in the most regular and even in the spherical and star forms. If, for instance, we examine the disposition of the parts in the Spatangi, we see at once that the form of their body, more or less elongated, is a consequence of the mouth and the anus being placed towards

the two extremities, and that besides four ambulacral and four interambulacral series symmetrically placed in pairs on each side of a plain, which, if continued from the mouth to the anus, would divide the animal into two equal parts, there is an odd series of each kind. The odd ambulacral series, above the mouth, must certainly be the anterior series, while, in the posterior part of the body, it is the odd interambulacral series that occupies the middle of the disc. It is also a remarkable fact, that in these animals the anus is always placed amongst the plates of the latter odd series. In the Spatangi we have therefore an anterior region indicated by the odd ambulacral series, and a posterior region indicated by the odd interambulacral series. On the two sides of the animal the series of plates are disposed in symmetrical pairs, so that on the left and on the right there are two pairs of ambulacral and two of interambulacral series. The first or anterior pair, which is contiguous to the odd ambulacral series, is a pair of interambulacral series, immediately behind which there are placed, first a pair of ambulacrals, next a second pair of interambulacrals, and finally a second pair of ambulacrals, which includes the odd interambulacrals, posterior and middle. Notwithstanding this radiated and at the same time symmetrical arrangement, the series of plates not being of equal breadth throughout their height, the Spatangi have, between the mouth and the anus, a disc formed by the greater or less dilatation of the posterior interambulacral series, on which they creep, and which is, in fact, the lower side of the animal; while its upper side is the region towards which all the series converge above the disc.

As to the *Clypeastres*, the *Galerites*, the *Neucleolites*, &c., which have the mouth in the centre and the anus marginal or submarginal, it is still easy to judge of the position of their parts, because the position of the posterior interambulacral series being given by that of the anus, there can be no difficulty in determining the symmetrical relations of the other series, both the odd and the even. There are even some differences observable in the form of the plates and the ambulacra of the several pairs; and the bilateral parity which these animals still retain is rendered perceptible by this circumstance.

At first sight it may seem more difficult to discover any

traces of this bilateral symmetry in the Echini and the Asteria, whether simple or ramified, and consequently to determine the antero-posterior diameter in animals whose mouth is perfectly central, and the anus, when there is one, is likewise situated in the central but upper part of the body. Nevertheless, even in this case, nothing is easier than to determine the relations which all the radiated parts bear to the longitudinal axis of the animal. It is true that all their rays so closely resemble each other in their external aspect, that it might seem of little or no consequence whether we observe in their generic arrangement those traces of bilateral symmetry which are so clearly visible in the Spatangi. But if we take into account the differences of structure in some plates of the several series, we shall be convinced that the same symmetrical parity is preserved here also, though under the appearance of a completely radiated disposition. We observe in fact on the upper part of the disc of the Echinodermata, especially in the Echini, the Cidarites, &c., in that region where the series of plates constituting the testa become convergent, some plates of a peculiar form, which are called oviducal and interoviducal, and communicate with the ovaria and the aquiferous system. These plates may serve as infallible guides in determining the regions of the body. The largest of them (generally to the number of five) alternate with the ambulacral series, so that they make two pairs and an odd one. The anterior pair is thus placed on the sides of the odd anterior ambulacrum; the second pair between the anterior and the posterior pair of ambulacra; and the fifth or odd plate, which is not always to be found in them, is situated between the two posterior ambulacra, that is to say, towards the anus or posterior part of the body. The structure of this fifth plate is of a peculiar porous kind analogous to that of the madreporiform body of the Asteriæ, and is found in the Echini also, but under a different form. In those which have but four oviducals, the plate which presents this peculiarity of structure is that which is wanting, and its place is then indicated by a depression or even a lacuna. Therefore, however regular the position of these plates in the Cidarites and circular Echini may be, we can, nevertheless, always determine the posterior extremity of their body by the odd plate, which Ann. Nat. Hist. Vol. 1.- No. 1. March 1838. D

is also generally a little larger than the others : and in the oblong Echinodermata, should they have the mouth masked (which is often the case in the fossil species), the posterior end of the body may still be ascertained by the circumstance that an odd oviducal plate does not present itself between two of the ambulacra; for in this case, that these are always the two posterior ambulacra is evident from the position of the anus in those in which it is visible. We may therefore say that the direction of the anterior ambulacrum is always opposite to the odd oviducal plate, which is always placed towards the anus.

The analogy observable between the structure of the madreporiform body of the Asteriæ, and that of the odd oviducal plate of the Echini, is in these animals an important point of resemblance, which may help to guide us in determining the position of the parts in the first of these families, and enable us to discover in that also a bilateral arrangement. In fact, one of the five rays of the common Asteriæ is opposite to the madreporiform body, and must therefore be considered as the anterior ray, while the four others are placed in pairs on both sides of the longitudinal axis. The case is the same with the Solasteriæ, except that the number of rays arranged in pairs is greater, and that sometimes the odd rays are wanting.

Thus, whatever may be the external form of the Echinodermata, whether they are oblong like the *Spatangi*, and have the mouth and the anus placed towards two marginal extremities of the body opposite to each other, or are completely of the star form, circular, or even spherical, with the mouth and anus placed opposite to each other as the two poles of their spheres, it is still easy to observe in them a bilateral arrangement, and to determine which is the anterior and which the posterior region, as well as to see how all the parts are disposed in pairs on the two sides of the animal.

M. de Blainville has already observed the relations existing between the arrangement of the plates in the testa of the *Echini* and in that of the starfish, but has not formed a complete or precise idea of the connexion of those parts. He is perfectly right in giving the name of *ambulacral plates* to those which form the grooving of the inferior side of the rays, and that of *interambulacral* to those which are placed on their sides. In

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order however to complete the analogy, the starfish must be represented as if swelled; then its back answers to the dorsal summit of the Echini, whence the ambulacra radiate even to the mouth, by passing in the starfishes through the extremities of the rays. We have thus, as in the Chypeastres and the Spatangi, two sorts of ambulacra, one at the upper and the other at the lower part of the animal. So far the analogy is complete; but in order to be justified in saying that the lateral plates of the rays are analogous to the interambulacral plates of the Echini, we must not consider the upper and lower plate of each side of a ray as forming a whole, though M. de Blainville seems to admit this; but we must conceive the upper lateral plate of a ray as if soldered to the corresponding upper part of the next ray; and the lower lateral plates are to be viewed in the same manner, by always supposing the two sides of the rays which bound the channel between two neighbouring rays to be united. It is in these interambulacral plates that the large thorns of certain starfishes are found, and these thorns are analogous to the spines of the large mammellæ to be seen in interambulacral plates of the Echini. In the starfishes there are also secondary spines surrounding the principal spines in greater or less regularity.

Besides the five oviducal plates, we observe at the summit of the *Echini* five other smaller plates, situated at the extremity of the ambulacra with which they are connected, and likewise perforated at one point, but all of the same structure as the larger. Mr. Gray has given them the name of *interoviducal plates*.

As to the membranous tubes issuing from the holes of the ambulacra, it is proper to remark that they do not in any way contribute to *locomotion*. It is rather amusing to trace the history of their advancement to the honours of this function. As they are placed, in the *Echini*, in bands, more or less narrow, between the large mammellated plates which bear the spines, the old naturalists, fancying that they bore some resemblance to the alleys or walks in a park, gave them the name of *ambulacra*, without describing with greater precision their nature and destined use. More recently the idea attached to the word ambulacra was extended to the organ which is placed amongst them, and has been, since then, most erroneously considered as a locomotive organ. How, in fact, could these small tentacula, with all their softness of texture, situated as they generally are in that part of the body which is never brought into contact with the ground when the animal moves, and overhung (*debordés*) by calcareous solid spines,—how, I ask, could these flexible tubes be used as organs of motion? It is an undeniable fact, and I have often observed it myself, that it is with their spines the *Echini* move themselves, seize their prey and bring it to their mouths, by turning the rays of their lower edge in different directions. But the correction of an error respecting the functions of the ambulacral tubes does not solve the problem relating to their nature and use. This problem we are yet unable to solve, as we know nothing more respecting them than that they are connected with the aquiferous system.

The position of the anus, in the true Echini, between the oviducal and interoviducal plates and those additional plates which surround the orifice at the dorsal summit, where the ambulacra terminate, has suggested the notion of a relation of dependence between the ambulacra and the posterior orifice of the alimentary canal. But this is far from being a correct notion; for the ambulacra, which have been often represented as extending from the anus to the mouth, invariably converge towards the upper part of the disc, where they appear in the form of a rosette more or less distinct, while the position of the anus varies considerably. It is not even median and superior except in the Echini properly so called and in the Cidarites. In all the other Echinodermata, in which it exists, it is situated between the two series of plates which form the posterior interambulacral space and diverge more or less from each other at its issue. In this case, which is the more frequent of the two, the anus has no direct communication with the ambulacral spaces.

The position of the dental apparatus, and particularly of the teeth themselves, with respect to the rays of the body, is an object which I would recommend to naturalists as well worthy of their attention; for at present I myself am unable to solve all the difficulties connected with the comparison of the different modifications of the dental system in the several genera of

Echinodermata. I shall therefore merely remark, in general, that the teeth alternate with the ambulacral spaces and are placed directly opposite to the middle of the interambulacral spaces, between the two series of plates which compose these, and to which they are attached by means of a very complicated apparatus. The structure of this apparatus, which is different in different genera, I shall describe as soon as my researches respecting it are more complete. As the teeth correspond to the interambulacral spaces, it is obvious enough that there must be an odd one. It is this odd tooth that is found behind on the antero-posterior axis itself. Its motion is directed forwards from the hinder part. The four other teeth are in pairs, and move laterally from right to left and from left to right in contrary directions on both sides of the mouth. Their motion may therefore be compared with that of the maxillæ of articulated animals, while the odd tooth may be considered as bearing some analogy to the lower lip of some of these. The space between the teeth and the lower orifice of the testa is covered with small moveable plates similar to those which surround the anus.

It is scarcely necessary to observe that the determination of these points must be of the utmost importance in examining the situation of the intestines and their mutual relations. Unfortunately, the state of the specimens which I had intended for dissection, did not allow me to investigate thoroughly all those points which I had wished to decide; and when I was dissecting some fresh specimens at the sea-side, I was not yet aware that it was possible to determine so precisely and positively the relation of the different regions of the body of these animals. I am therefore now obliged to postpone all further detail until I have completed this part of my labour. The facts which I have just stated appeared to me sufficiently remarkable to warrant their separate publication without an immediate review of the whole organization of this class. As to the manner in which I have designated the several regions of the Echinodermata, it may be objected that, most of these animals having the mouth beneath the disc, the side on which it is found cannot be considered as the anterior region of the body. But this denomination is no less correct on that ac-

count; and that the position of the animal in walking or swimming is not sufficient to guide us with reference to this point is evident from the case of the Mollusca and certain insects which swim on the back. Moreover, the anus of the Echinodermata is placed on the upper side, a situation different from that of the same organ in other animals. I feel therefore sufficiently warranted in considering the mouth as the principal point of departure and as determining the anterior part of the body. Do we not, in fact, see it placed in the fore part of the Holothuria, which by habitually moving on the same side approximates to the Vermes, and in the pedunculated starfishes, which, though fixed to the ground, uniformly put the mouth forward in balancing themselves on their stems? If, nevertheless, it were deemed advisable to adopt a different nomenclature, and to call that side on which the mouth is placed the lower side, that would make no change in the relations already pointed out: that which I call the upper would then become the forepart, that which I call the hind part would become the upper part, and the lower would become the hind part.

As I know not that anything has been yet published respecting the growth of the Echinodermata, I am the more inclined to think that the few observations which I have collected on this subject will be found interesting, at the same time that they will show the Echinodermata, whatever be their form, to be all subject to the same mode of development. The only known fact bearing on this point is, that the Echini and the starfishes consist of fewer pieces when they are young than at a more advanced age. It does not appear even that that there is any positive limit to their growth, though the several species habitually exhibit a sort of middle size which is proper to themselves, and from which the extremes are not very far removed. It is in the Echini more than any others, and especially in the Cidarites, that we find it most easy to decide on the exactness of this indication, although several authors appear to have sometimes forgotten it, particularly when their object has been to establish new species. But we have been told by no one where and how the new plates grow, and in what manner they are developed. In order clearly to comprehend the mode in which the Echinodermata grow, we

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must steadily keep in view the general disposition of the solid pieces which form their integument. In the Echini these are plates, of larger or smaller dimensions, arranged in vertical zones which diverge from the mouth towards the periphery of the body, and thence seem to converge towards the superior centre. In the starfishes they are plates, the smallest of which are placed at the top of the rays, and the largest at the centre of the channel by which the rays are separated. We mark however three distinct types in the form of these animals: some tubular (the Holothuria), some spheroidal (the Echini), and others of the starform (the Asteriae); but these types may be reduced to two, inasmuch as the tubular form may be considered an elongated spheroid; yet further, these two types may be reduced to the same plane of organization, since the large growth of the plates in the summits of a spheroid combined with the contraction of the interradial planes would produce a starfish; while, vice versá, the increase of the interradial planes and the reduction of the central plates in the starfish would produce a spheroid. Nor is this a mere hypothesis; we shall see hereafter that the essential difference between the Echini and the Asteriæ consists in the different modes of their growing. As to the disposition of the plates, there are in the Echini twenty series of them, forming ten zones, five of which are perforated and five not perforated. The five zones or double series of perforated plates are called the ambulacral, and the others the interambulacral series. In the starfishes the series formed by the solid plates are less regular and vary in number: however, in those starfishes that have large plates at the edges of the rays, we see that these plates correspond with the interambulacral series of the Echini, while each ray has a complete ambulacral series which extends from the mouth along the extremity of the ray to the superior centre, and the middle of which, at the extremity of the ray, is consequently narrower than the ends : in the Echini, on the contrary, each series is broadest in the middle and narrowest at the extremities. If we now attentively examine an Echinus of the middle size (among those of its own species), we shall find, especially in the genera Cidaris and Echinus, that the plates of the several series are not so strongly attached to each other

at the dorsal summit, and that the spines which they bear in this region are less fully developed. If, carrying the examination still further, we remove the spines, we shall then observe that amongst the oviducal and interoviducal plates and the interambulacral plates that bear spines there are some less fully developed, irregular in form, wanting even the mamellæ and the spines, and taking their place among the mammellated plates only in proportion as they gradually attain to a larger size. The new plates are at first very small, and may be compared to points of ossification which at first grow simultaneously in all directions, though their lower side completes its formation sooner than the upper, and the upper side is sometimes yet incomplete, even when an incipient mammella is observable in the middle of it. In the region of the body where this increase takes place, the membrane which unites all the plates and spreads itself over their surface, forming an articular capsule about the base of the spines, is softer and more spongy than it is in the inferior part where the plates are consolidated and immoveable. It is in fact this spongy mass that deposits the calcareous matter of which the plates are composed : and the spines shoot out in the centre almost in the same manner as the horns of a stag. They do not become moveable until they have attained a certain stage of development, and there is a period in their growth after which their size does not increase. Those however which drop off accidentally are replaced by others, formed, as those had been, by the tumefaction of the membrane which covers the plates. We may always observe in a single specimen of the Cidaris all the gradations of increase, from that of the plates which have completed their growth and bear spines several inches long, down to the smallest points of ossification of the plates yet unfurnished with spines. These facts I have ascertained by examining several individual specimens which exhibited all the intermediate stages of development through which the pieces in question must pass : and indeed, when we have no direct means of observing the growth of an animal in one individual, the only resource left us is to compare a great number of individuals representing a complete series of all the stages through which the species to which they belong has to pass before their

growth is completed. The only difference between this process and the *direct* observation of any development is, that in the one case we observe in one and the same individual that succession of changes, which in the other we trace through a series, as complete as possible, of several individuals. Such is the course that I have taken with respect to the Echinodermata. The young Echini have a small number of plates in each of their vertical series; they appear to be slowly increased in size by the deposition of calcareous matter at their circumference until those which surround the mouth have completed their growth and are entirely consolidated. The superior plates continuing to grow, increase, from the top downwards, the periphery of the body, which remains depressed so long as the inferior are the only plates consolidated ; but in proportion as a greater number of plates become immoveable, and as there is formed, in the upper region, a greater number of plates reaching down to the circumference of the spheroid, the testa becomes rounded and finally assumes a spherical form. It is to this cause that we are to ascribe the differences of contour exhibited by the Echini at different ages. In some species there are found individuals presenting even a pyramidal shape, and this takes place when there is still formed a great number of plates subsequently to the consolidation of those occupying the greater diameter of the animal's body. These facts sufficiently explain the gradual growth of beings which approximate more or less nearly to the spherical form, and show how carefully we should guard against the introduction of nominal species in consequence of a mere difference of form resulting from age only.

It would be interesting to trace the development of these animals *ab ovo*. But no naturalist has yet observed the state of the *Echini* on their first issuing from the egg. As to the spines, it is evident, especially in the *Cidarites*, that those surrounding the mouth are the first that attain their full growth, while the largest are those in the upper tier of the disc; and those which have not yet completed their growth are found around the oviducal plates on the outside. The correctness of these observations will be demonstrated by comparing the differences of development exhibited in this region by the spines

that stand nearest to each other. We should be mistaken however as to the growth of the Echinodermata, did we think that there is a generic connexion between the plates, on account of their forming vertical series from the mouth to the summit of the disc. It has been already remarked that the plates of each space are alternately a little more elevated than each other, but no attention has been paid to the manner in which the plates of all the spaces succeed each other in the same Echinus; and yet, if we consider it closely, we shall see that the new plates are developed in spiral lines, passing, without interruption, from one series to another through all the spaces from the circumference of the mouth to the dorsal summit, so that those which rest on each other in a vertical line do not make their appearance in immediate succession. It appears to me well worthy of remark, that in these animals, holding so low a rank among organized beings, we should find the succession of the solid parts composing their integument so strikingly analogous to the arrangement of the leaves around the stems of plants ;--an arrangement, the laws of which have been recently discovered by M. Schimper, and explained, so far as regards the Coniferæ, in a memoir of M. Braun on the arrangement of the scales of their cones.

The small plates surrounding the mouth and those around the anus are arranged in a peculiar manner; they are easily moved, and thus facilitate the deglutition of the food and the voiding of the excrements. In general the testa of the *Echini* is not so immoveable as one who had not observed them in a fresh state might be led to suppose. All the plates forming the upper part of the disc are often set in motion: sometimes they sink, sometimes they rise, and, in the oblong species, the longitudinal diameter is often extended beyond its ordinary length. The great mobility of the spines, the variety of their movements, and the manner in which they help the animal to seize its food, have been already noticed.

The growth of the starfishes and the *Crinoïdes* will appear to be carried on by a process exactly the same, as soon as it is agreed that an ambulacral space of an *Echinus* answers to an ambulacral surface of a starfish, and that an interambulacral space of the former answers to the large marginal pieces of two contiguous rays in the latter: for the pieces exhibiting its growth are formed in the angles of the rays on the upper and lower surface of the body, and, becoming larger and larger, elongate the rays and drive the extremities of them to a greater distance; so that the number of the plates continually increases and cannot be considered as a specific characteristic. The growth of the summit in the *Asteriæ* and of the stem in the *Crinoïdes*, as well as that of the moveable pieces of the mouth, is also independent of the rays in these animals, and accompanied by a peculiar position of their parts, as in the *Echini*. Hence it is easy to conceive how a body of the star kind may grow larger and still retain its form.

The study of the organization of the Echinodermata has led me to introduce in their classification and in the defining of their genera some changes, which I shall also exhibit in a synoptical table. I found that the characters deduced from the combination of the plates and the arrangement of the ambulacra formed groups more natural and better defined than those deduced from the position of the mouth and the anus.

The class of the Echinodermata is divided into three orders: the *Stellerides*, the *Echinides*, and the *Fistulides*, which resemble in the degree of their organization the three classes of the Radiata. The *Stellerides* answer to the class of the Polypi; the *Echinides* to that of the Acalephæ, which connect the section of the Radiata with the Mollusca; while the *Fistulides*, as the culminating point of this division, represent the section of the articulated animals, and more especially the Vermes.

As to the genera established in this class, I found that the characters deduced from the combination of the plates and the disposition of the ambulacra formed groups more natural and better defined than those deduced from the situation of the mouth and the anus. My observations on this subject I shall publish in a monographic paper (accompanied with plates), for which I have already collected most of the necessary materials.

[To be continued.]



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