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THE ECHINODERMS AS ABERRANT ARTHROPODS

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CONTENTS

PREFACE

Of all the larger animal groups there is none which has been the subject of such diversified opinion regarding its affinities and systematic position as the Echinodermata. Originally assumed to be related to the cœlenterates on account of their radial symmetry, the echinoderms were later placed near the flat-worms, the annelids and the chordates. At present they are regarded as representing a very distinct and isolated group, some considering them as allied to the chordates, while others emphasize their points of similarity with the annelids; most zoologists, however, are reluctant to commit themselves regarding their probable affinities.

For many years I have been convinced that the echinoderms are by no means such anomalous creatures as they appear to be, and that, in spite of their many and extraordinary peculiarities, they are undoubtedly closely allied to the crustaceans, and especially to the barnacles. In the following pages the reasons for this belief are given.

THE DOMINANT CHARACTERISTICS OF THE ECHINODERMS

The echinoderms are very anomalous forms, and their relationships to other animals are masked not only by a highly perfected radial symmetry, but also by a unique development of all the organs of the body. Their outstanding features are the presence of a vascular, a respiratory, and a superficial skeletal system, the last composed of articulated (calcareous) elements, the absence of gill clefts, and the sharp division of the body externally into (five radial) segments. In these features they agree only with the arthropods.

THE LARVÆ OF THE ECHINODERMS

The unique larvæ of the echinoderms, which are of very varied types, vermiform, bean-shaped with five ciliated rings and a long anterior tuft of cilia, auriculariæ, bipinnariæ, brachiolariæ, plutei, etc., and differ more or less widely among themselves in the details of their development, are always at first bilaterally symmetrical, which may be accepted as an indication that the echinoderms are derived from bilaterally symmetrical ancestors.

The larvæ do not grow directly into the adults, but the latter for the most part arise from new growth within the larval body, the structures peculiar to the larvæ being absorbed; in a few cases the development is direct.

There is little in the structure or in the development of the echinoderm larvæ which is comparable to the structure or to the development of the larvæ of any other animals, and it is evident that the extraordinary features exhibited by the adult echinoderms have been projected so far forward in the ontogeny as quite to destroy the value of the larvæ as phylogenetic indices.

THE CHANGE FROM MID-SOMATIC TO INTER-SOMATIC DEVELOPMENT IN THE CRINOIDS

Perhaps the most interesting feature connected with the morphology of the crinoids, and one which it is necessary especially to emphasize in order to understand the relationships between them and the other echinoderms, is the abrupt change in the regions of bodily growth and extension which takes place beginning with the formation of the arms. It is this sudden change from interradial to radial, or from mid-somatic to inter-somatic, development which occurs at the commencement of arm formation that has always proved the chief stumbling block in the way of a correct interpretation of these animals.

In the echinoderms the primary appendages, the teeth, the water pores, and the genital openings, and in the crinoids the primary nerve cords as well, are all interradial in position. There can be no doubt, therefore, that the dividing lines between the five half somites fall in the middle of the so-called radial areas, and in the echinoids and asteroids a sharp line of division is always maintained down the middle of the radial series of plates throughout life, while no such dividing line is found in the interradial regions.

In the young crinoids each of the somatic regions is completely walled in by two large superposed plates, a dorsal basal and a "ventral" oral; beneath the basals there are usually 3-5 small infrabasals alternating with them and corresponding with the oculars of the echinoids which, since they are entirely absent in large groups, and are usually more closely associated with the column than with the calyx, are probably to be interpreted as a dissociated columnal.

The young crinoid therefore has its body protected by ten large somatic shields, five dorsal and five ventral, the latter with the primitive appendage under the median line.

The arms first appear as evaginations in the intersomatic lines at the plane of separation between the dorsal and ventral plates. The evidence is that the skeleton of the arms is double, half being derived from the somite on either side; but whatever may be the ultimate genesis of their skeleton, the arms arise as linear and almost immediately biramous appendages taking their origin from the intersomatic planes.

From this point onward the development of the animal is entirely intersomatic; the peristome and its underlying nerve ring, the water tube ring about the mouth, the blood vascular ring, the genital cord, and the cœlomic cavities all send off radial branches which increase in length as the arm grows, while along either side of the peristomial extensions (ambulacral grooves) there is formed progressively a continuous series of reduplications (ambulacral lappets) of the little flaps with their associated tentacles, the latter in communication with the radial water tube, which surrounded the mouth in the "prebrachial" stage.

THE NERVOUS SYSTEM OF THE ECHINODERMS

In the chordates the central nervous system never becomes separated by mesodermal tissues from the tract of ectoderm from which it originated in the embryo. Sedgwick remarks that this is a feature of all echinoderms in so far as the ventral nervous system is concerned, and when this nervous system is removed from the surface the removal is effected by invagination.

But the only nervous system found in the echinoderms which in its details is at all comparable to the central nervous system of the other higher invertebrates is the so-called apical nervous system of the crinoids, which first forms relatively late in life, and which appears to arise in connection with the cœlomic epithelium.

It seems to me that this nervous system of the crinoids, which is possibly (though not by any means probably) represented by the so-called mesodermal nerve plexus in the starfishes, but which is quite unrepresented in the other echinoderms, affords the best indication of the probable affinities of these animals, and at the same time its high state of development suggests that the crinoids have departed less widely from the ancestral type than have the other classes.

In the developing crinoid the ectoderm of the surface of the body becomes more or less disintegrated, and its cells to a greater or lesser extent pass inward and intermingle with the cells of the underlying mesoderm so completely that they can in no way be distinguished from them, the body wall being formed of an ectoderm-mesoderm complex in which the cells of the two types cannot be differentiated.

On the inside of this body wall, apparently in connection with the cœlomic epithelium, the apical nervous system arises; but in view of the mixed nature of the component cells of this wall it seems not illogical to assume that this apical nervous system is in reality formed from cells which, originally ectodermal, have infiltrated through the underlying mesoderm and now appear as if they belong to the cœlomic epithelium. If this hypothesis can be accepted it is obvious that the apical nervous system of the crinoids is in no way comparable to the nervous system of the chordates, and as this is the only echinodermal nervous system comparable with the nervous system of other animals it naturally follows that no affinity with the chordates can be inferred from the nervous system of the other echinoderms.

In the crinoids the larvæ become attached by the ventral side of the anterior end, and the column is a development of the preoral lobe, arising therefore from the place where in the larvæ the anterior nerve mass, just in front of the mouth, is situated. The mouth moves from the ventral surface onto the left side and then migrates upward, away from the point of attachment, until it comes to lie at the pole opposite the latter, that is, at the posterior end near the anus.

The larval nerves disappear; but some time after the torsion of the animal is completed a new nerve mass forms in exactly the place that the preceding nerve mass occupied, now become the point just above the top of the column. It is thus natural to assume that the central mass of the apical nervous system in the adult crinoid, appearing in the region previously occupied by the anterior nerve mass of the larval crinoid, corresponds to it, and therefore that it represents the anterior nerve mass in other invertebrates. But as a result of the torsion which the animal has undergone the right cœlomic sac has become extended anteriorly and, following the enteric wall, has reached over onto the left side; from its anterior end it gives off five anteriorly directed diverticula which at a later stage become cut off and give rise to the chambered organ about which the central nerve mass forms a close and almost complete investment.

The central nerve mass gives off five stout cords which immediately branch, the two branches from each being connected by one or two commissures, and then joining the similar branches from the nerve trunks on either side to form the radial nerves of the division series and arms. In each segment of the arms and pinnules, the nerve cord gives off from a ganglionic swelling four branches, two dorsolateral and two ventrolateral. In addition to these nerve cords, which may be either single or double, and are in some types represented by two widely separated parallel cords, each cirrus in its central canal contains a prolongation from the chambered organ ensheathed in nerve fibers continuous with those of the central nervous mass, and five similar prolongations from the chambered organ and the central nerve mass extend downward into the stem.

THE ECHINODERM CŒLOME

Much has been made of the fact that in the echinoderms the cœlome is enterocœlic in origin, as in the Brachiopoda, Chætognatha, Chordata, and probably the Phoronida, while in the developing molluscs, annelids and arthropods the cœlome is not enterocœlic in origin.

Sedgwick notes that in all the chordates except the tunicates the cœlome in its first state in the embryo shows more or less marked traces of three divisions, the anterior or proboscis cœlome, which in the Vertebrata and Enteropneusta is single and in *Amphioxus* double; the collar or middle cœlome, which is always double, and the trunk cœlome, which is double and which in the Vertebrata and in *Amphioxus* becomes metamerically segmented. In the echinoderms there seem to be indications, at least, of a similar tripartite division;

there is the anterior cœlome, which is sometimes single (*Asterina*) and sometimes double (*Echinus*), the hydrocœle, which is probably fundamentally double, though in some cases (holothurians and crinoids) only one hydrocœle sac is formed, and the posterior cœlome, which is always paired. But in those chordates in which the enterocœlic origin of the cœlome is clearly presented these three divisions of it always come off from the enteron separately, while in the echinoderms the enteron at most gives off only one pair of cœlomic sacs; and whereas in the chordates the middle (collar) cœlome is never more closely associated with the anterior than with the posterior, in the echinoderms it is always closely associated with the anterior cœlome, being developed from it and remaining connected with it by the stone canal throughout life.

Whatever its origin the cœlome is clearly homologous in all these types so that the manner of its development may be considered as due to special mechanical or other limitations imposed by conditions in the early stages—size, form, amount of yolk, etc.—and not to phylogenetic causes.

THE WATER VASCULAR SYSTEM

The most extraordinary structure of the echinoderm body is the water vascular system. This arises as a narrow dorsolateral outgrowth from a portion of the cœlome which unites with an ectodermic infolding on the anterior aboral surface. From this develop the stone canal and the madreporites. The ectodermic opening places the hydrocœle in communication with the exterior, so that the organ has often been compared, in whole or in part, to an annelid excretory organ or nephridium.

But Professor Patten has pointed out that it is much more like one of the typical excretory organs of the arthropods (shell gland, green gland, coxal gland) which consist of thin walled cœlomic sacs with a thick walled tubular outgrowth of varying length united to a short duct infolded from the ectoderm.

The five primary tentacles or tube feet of the echinoderm larva according to Professor Patten represent five modified thoracic appendages; an outgrowth of the underlying somite grows into each appendage in typical arthropod fashion, but instead of breaking up into separate muscles for the appendage it remains permanently in the form of a membranous diverticulum of the hydrocœle and becomes the distal end of a radiating water vascular canal. Only the distal end of the original appendage separates from the body as the primary tentacle; the remainder of the appendage, however long it may eventually become, may be regarded as lying in the surface ectoderm, developing on either side as it increases in length paired cirri which become the double row of tube feet for each arm into each of which a prolongation of the water vascular canal extends.

Primarily, then, each of the five primitive thoracic appendages, one from each of the five half metameres of which the echinoderm body is composed, contains a tube of nephridial intent leading into a canal opening to the exterior by a pore. The anterior and posterior ends of the series of half metameres join, and the excretory canal becomes a ring canal from which grow out five long radial canals giving off branches to the tentacles or tube feet as these are formed.

The excretory function of the water vascular system of the echinoderms is reduced to a minimum if, indeed, it can be said to exist at all. Its action is chiefly that of an hydraulic system whereby power originating in a great number of weak and dissociated muscle fibers scattered along and within the water tubes and their branches is unified and transmitted to the hollow tube feet, tentacles, and other appendages, while at the same time the constant inflow and outflow of water through the madreporic openings, especially when these communicate with the body cavity as they do in the gill-less crinoids, undoubtedly serve to a greater or lesser extent the purpose of respiration.

THE ECHINODERM VASCULAR SYSTEM

The vascular system, which is especially well developed in the holothurians and echinoids, is formed of a peculiarly modified connective tissue in which the fibers are sparse and which contains intercommunicating spaces without an epithelial lining. The fluid in these spaces does not appear to undergo any definite movement. Typically there is a circumoral tract with radial prolongations which lie between the radial water vessel and the radial nerve cord, an annular aboral tract in which the generative rachis is embedded and which sends off extensions to the genital organs, and in holothurians and echinoids a considerable development in the mesentery and on the gut wall.

In the barnacles no heart is ever present, and the lacunar channels in which the blood circulates are for the most part ill defined.

THE ECHINODERM SKELETON

MacBride and others have remarked that the presence of calcified skeletal tissue in the mesoderm of the body wall is a character found in the echinoderms and vertebrates only among cœlomate animals. It does not seem to me that this can be considered as any indication of affinity between these groups.

Many vertebrates have uncalcified mesodermal skeletons, and others have only partially calcified skeletons. The uncalcified skeleton of the notochord resembles in structure the parenchyma of the solid tentacles of certain cœlenterates, and is quite different from anything found in the echinoderms. Calcareous deposits of greater or lesser extent occur in the mesoderm of barnacles, brachiopods, rotifers and cestodes, as well as in the mesoglœa of sponges, and the calcareous skeletal structures of some cœlenterates are mesodermal in origin.

In certain of the early cystideans the skeleton appears to have been wholly or chiefly chitinous, and their surface exactly resembles that of the phyllopod and other crustaceans preserved in the same rocks. It is not improbable, therefore, that the calcareous exoskeleton of the echinoderms of the present seas developed from a chitinous body covering through an exoskeleton composed of chitin with an increasingly greater amount of inorganic matter such as we see today in most of the larger crustaceans.

In the developing crinoid the ectoderm of the surface of the body more or less completely disintegrates and its component cells largely pass inward and intermingle with the cells of the underlying mesoderm, so that in the crinoid the outermost layer of the body is almost as much mesodermal as it is ectodermal. This being the case, no matter what its phylogenetic relationships and tendencies are, the formation of an ectodermal skeleton has now become impossible as there is no continuous ectoderm from which to form it. A calcareous mesodermal skeleton appears, the first rudiments of which are formed in the deeper layers but soon move to a more superficial position enclosing the body in a calcareous investment formed of large and definite plates. Just before the appearance of the arms there are, in addition to the columnals, 13-15 thin cribriform films lying just below the surface and fitted edge to edge, including 3-5 infrabasals, 5 basals alternating with them, and 5 orals superposed upon the latter.

Now although this skeleton is mesodermal and calcareous, the relations between it and the enclosed body of the animal are entirely different from the relations between the vertebrate skeleton and the body organs, being on the contrary quite like the relations between the chitinous or more or less calcified skeleton of the arthropods and their enclosed body. The crinoid skeleton is a superficial (though not external) skeleton enclosing the body and giving off articulated appendages; it therefore resembles the skeleton of the arthropods more closely than it does that of any other animals. The fact that it is mesodermal and calcareous seems to me to be, in view of its development in every way like an ectodermal chitinous exoskeleton, and especially in view of the fact that it lies outside of the ventral nervous system which runs along or just within its inner surface, of purely secondary significance.

Crinoids are undoubtedly descended from animals with an articulated exoskeleton, and their articulated superficial skeleton is calcareous instead of chitinous as would be expected solely because of the disintegration of their ectoderm in the young stages.

In the arthropods we find in the sessile barnacles the beginnings of a transition from a chitinous exoskeleton to a calcareous mesodermal superficial skeleton, and from the conditions in these animals it is not difficult to supply the connection between the crustacean and the crinoid skeleton.

AUTOTOMY IN THE CRINOIDS

The crinoids with more than ten arms increase the number of their arms by breaking off the larval arms at the base, the stump forming an axillary from which two or more arms arise. This is primarily due to the inability of the brachial skeleton, a rigid calcareous investment of the dorsal and dorsolateral portions of the arm, to keep pace with the other brachial structures in development, and is therefore distantly comparable to the moulting so characteristic of the arthropods.

THE APPENDAGES OF THE CRINOIDS

The appendages in the crinoids are of two kinds. From the base, and always in connection with the chambered organ and the central nerve mass of the apical nervous system, arise uniserial jointed appendages ending in a strong hook. These are especially developed in crinoids unprovided with a stem, and serve both as tactile organs and for attachment. In their position as anterior organs and in their function as tactile and grasping organs, as well as in their uniserial structure, they recall the antennæ of the barnacles.

About the ventral surface there are five long arms typically forking at the base, thus representing biramous ventrolateral appendages and calling to mind the biramous thoracic appendages of the barnacles.

There can be no question of any direct homology between the cirri of crinoids and the antennæ of barnacles, or between the thoracic appendages of barnacles and the arms of crinoids, but both sets of organs have the same functions and the same location in each group, and are constructed on a similar plan, so that it is not impossible to regard them as parallel manifestations of the same ancestral appendicular plan, a plan not occurring in the animal kingdom outside of the arthropods and crinoids.

CHARACTERS OF A HYPOTHETICAL CRINOID WITH MID-SOMATIC DEVELOPMENT ONLY

Let us imagine a crinoid with entirely mid-somatic development and with entire instead of half somites, that is, with bilateral instead of radial symmetry. We would have a body composed of five broad somites each covered with a broad arched plate (tergum) to the edge of which is articulated a flap (oral, corresponding to a pleuron); within this would be the radial (epimeron) at the inner edge of which arises a biramous appendage. A body with five terga and five pairs of biramous appendages with their bases covered by pleura from which they are separated by epimera would certainly be considered as crustacean in character, and if it were attached by the head end, with the mouth upward, it would unhesitatingly be pronounced a barnacle, its deficiencies and anomalies of organization being ascribed to degeneration.

THE CRINOIDS AND THE BARNACLES

The crinoid develops from a highly anomalous larva, with a so-called vestibule suggesting a partial development of a bivalved covering, which attaches itself by the anterior end like the cypris larva of a barnacle and turns a half somersault bringing its mouth upward and opposite the point of attachment, also like a barnacle; so far its development equally well suggests that of a polyzoan from a cyphonautes larva; but in its further growth it develops a superficial skeleton as does an arthropod of a sort already seen in rudimentary form in the barnacles, with the chief nerve cords, which are highly developed and arthropod-like, running over or just within its internal surface as in the arthropods, and uniramous anterior (oriented from the central nerve mass) and biramous ventrolateral appendages, both sets of which have functions similar to those of the corresponding appendages in the barnacles.

Thus in spite of the utter dissimilarity in the details the broader features of the structure of the crinoids and the barnacles as well as of their development are seen to be similar, or at least comparable, or perhaps it should be said that there is less divergence between crinoids and barnacles than there is between crinoids and any other organisms.

THE CRINOIDS AND THE ABERRANT BARNACLES

The crinoids represent a derivative from a branch of the same arthropod stock that gave rise to the barnacles, but they have gone much further; half of each of the five segments of which the body is composed fails to develop so that the body is composed of five half segments joined in a circle with the central organ of the ventral nervous system at one pole and the mouth, which has moved posteriorly and come to lie near the anus, at the other; the development of the body structures after early youth suddenly becomes entirely inter-somatic instead of mid-somatic; the peristomal region becomes enormously enlarged and extended, resulting in the formation of a sort of lophophore; and the appendages have been suppressed, or at least appear in a very modified form late in life. Certain hereditary tendencies show themselves after the animal has, so to speak, recovered from the profound ontogenetic shock resulting from the loss of half its body, in the appearance of articulated uniserial tactile and grasping organs at the neural pole (the original anterior end) and of articulated biramous appendages used for food gathering or for locomotion along the ventrolateral border.

Crinoids, like barnacles, are sessile, pedunculated, attached by hook-like processes, or unattached.

The strong probability that the arthropod stock which by profound modifications gave rise to the barnacles also gave rise to the crinoids is indicated not only by the asymmetry in the Verrucidæ, in which the operculum consists of the scutum and tergum of one side only, those of the other side being fused to form one half of the wall which is completed, on the side of the movable opercular plates, by the greatly developed and displaced rostrum and carina, but also by the anomalous parasitic forms which have developed among the former in which the aberrant features are so fundamental that they have been thrust forward into the ontogeny so far as to modify profoundly the form and structure of the nauplius. These forms also show that the occurrence of complicated ramifying roots, so highly developed in some crinoids, is an inherent possibility in the barnacles.

A combination of the asymmetry of the Verrucidæ (inherent also in very many other crustaceans, and especially noticeable in the Paguridæ and Bopyridæ) carried to its logical conclusion in the complete atrophy of one side, with the modifications of the body seen in *Sphærothylacus* or *Sarcotaces* in a less extreme form, the roots of the Rhizocephala, and a skeleton formed after the manner of the plates in the shell of the Operculata, furnishes all the elements needed for recombination to form the crinoid. It may be well to call attention to the fact that outside the Cirripedia there is no group in which all the morphological peculiarities exhibited in the crinoids coëxist—indeed they are not to be found in all the rest of the animal kingdom together.

In this connection it may be worth while to review the salient features of the more important of the aberrant barnacles.

The Rhizocephala are exclusively parasitic barnacles, the most degenerate of all parasites; in the adult stage they are distinguished from normal barnacles by the entire absence of all traces of segmentation and of appendages, and at all stages they lack an alimentary canal; every trace of arthropod organization has disappeared. Nearly all of them occur on decapod crustaceans.

The body has the form of a simple sac, or may be divided into numerous similar sacs, attached by a short peduncle from which root-like processes ramify throughout the body of the host; these absorptive roots appear to be absent in the aberrant genus *Duplorbis*. The body proper is completely enveloped by the mantle which usually has a narrow aperture capable of being closed by a sphincter muscle; in *Sylon* the opening is double, and in *Thompsonia, Clistosaccus* and *Duplorbis* the mantle cavity is completely closed.

The mantle commonly is attached to the visceral mass by a narrow mesentery near which on either side are the paired (more rarely unpaired) openings of the male and female genital organs. In the different genera the external form varies considerably, and with it the position of the mesentery and of the genital apertures.

Thompsonia, the most aberrant and highly specialized of all the parasitic barnacles, consists of nothing but a diffuse system of branching and sometimes anastomozing mycelium-like roots continuous throughout the body of the host and all arising from a single original larva; the peripheral division of the root system passes out into the walking legs, abdominal swimmerets and tail fans and there gives rise to numerous (up to more than 500) small sacs consisting of a thin mantle without muscles and containing only an ovary, without generative ducts, testis or nerve ganglion. During development the visceral mass disintegrates so that at the time of hatching the mantle contains a great number of cypris larvæ ready to emerge. The escape of the larvæ is contemporaneous with, or soon followed by, a moult of the host. The empty shells of the external sacs are carried away with the cast skin, and the terminal swellings of the root system emerge as a new crop of external sacs.

In *Peltogaster* the body has an elongated sausage shape, with the mantle opening at one end, and is attached by the peduncle about the middle of its length. The mesentery is longitudinal on the proximal side (next the peduncle).

In *Sacculina* the whole body is flattened in the plane of the mesentery and has assumed a secondary and superficial bilateral symmetry about a plane at right angles to this and coinciding with the median plane of the host. In other genera, such as *Lernæodiscus* and *Triangulus,* the symmetry becomes still more complicated.

In *Clistosaccus* and in *Sylon* the genital organs are unpaired.

The peduncle perforates the integument of the host and gives off on the inside the absorption roots which, in the case of *Sacculina*, penetrate into all the organs of the host with the exception of the gills and heart, and extend to the terminal segments of the legs and into the antennules and eye stalks. In *Duplorbis,* in which the root system appears to be absent, the peduncle is hollow, its cavity communicating with the closed mantle cavity and opening at the other end into the body cavity (hæmocœle) of the host.

Apart from a single nervous ganglion (absent in *Thompsonia*) which lies close to the mesentery near the female genital openings, the only organs present are those of the generative system.

Sphærothylacus is parasitic on a simple ascidian (*Polycarpa*), living attached by ramifying roots to the inner wall of the branchial sac. The globular body is enclosed in a mantle which has a small opening. There are no appendages, but there is a complete alimentary canal with mouth and anus, the latter near the mantle opening.

The two known species of *Sarcotaces* live embedded in the muscles of fish; an alimentary canal is said to be present, and there are no roots.

In the Ascothoracica, all of which are parasitic in Zoantharia or in echinoderms, the mantle may have a bivalved form (*Synagoga* and *Petrarca*), or it may form a capacious sac (*Laura*) much larger than the body with which it is connected by a narrow neck and having only a small opening to the exterior. In *Dendrogaster* the mantle is still more developed and is produced into branched lobes. In *Laura* the mantle is covered with stellate papillæ penetrating the tissues of the host and presumably absorptive. In all cases the mantle contains ramifications of the enteric diverticula and portions of the gonads. In *Laura* the body is divided into six " thoracic " and three limbless " abdominal " somites, and ends in a caudal furca. In *Petrarca* and in *Dendrogaster* the body is unsegmented.

In these three genera a pair of preoral appendages is present and, except in *Laura,* are armed with hooked spines suggesting that they are organs of fixation. They are inserted, at least in *Laura,* at the sides of the buccal region, and are more or less enveloped by the mantle.

The cement glands appear to be absent, and the mouth parts are more or less reduced, but appear to be adapted for piercing.

The thoracic appendages are biramous and articulated only in *Synagoga.* In *Laura* they are uniramous and indistinctly segmented, and the first pair are long and slender. In *Petrarca* they are still further reduced, and in *Dendrogaster* they are represented only by some indistinct papillæ.

In all three genera the gut ends blindly, and the hepatic diverticula, which are large, extend into the mantle. The nervous system is reduced. An eye is said to be present in *Synagoga.* In *Laura* the oviducts open at the base of the first pair of cirri.

The larva of *Laura* is a nauplius lacking the frontolateral horns; in *Dendrogaster* the larva hatches as a peculiar cypris with only five pairs of biramous thoracic limbs.

In the Apoda the curious *Proteolepas bivincta* is elongated and maggot-like, with no trace of a mantle nor of appendages other than a pair of adhering antennules. The mouth parts, borne on the first " segment," seem to be adapted for piercing and sucking. The alimentary canal is greatly reduced; according to Darwin only the œsophagus is present, and there is no trace of stomach, rectum or anus.

THE CRINOIDS AND THE STARFISHES

In the crinoids during their development the mouth moves from the ventral surface onto the left side, indenting the left hydrocœle and the left posterior cœlome, and continues its migration until it comes to lie at the posterior end beside the anus. When it has reached this point the hydrocœle ring closes. As a result of this movement the right posterior cœlome has also shifted and come to lie on the aboral (originally anterior) side of the gut and the preoral lobe of the larva becomes enclosed by the rows of skeletal elements (apical plates) which are developed outside the right posterior cœlome in all echinoderms except holothurians; these plates are first laid down in a horse-shoe shaped ring which later closes, as does the hydrocœle, to form a complete ring.

In the asteroids the closure of this curved row of plates is effected far from the point of origin of the preoral lobe on the right or right dorsal side of the larval body; in the crinoids it is effected at the anterior end of the larval (posterior pole of the adult) body and encloses the preoral lobe just as the hydrocœle does in asteroids.

The larvæ of both crinoids and asteroids attach themselves by the preoral lobe; but whereas in the crinoids the preoral lobe is quite free of the circumoral vessel and arises from the apical or aboral surface of the adult, in the asteroids the preoral lobe is encircled by the water vascular ring and its withered vestige springs from the oral surface of the adult disc.

In the asteroids the mouth has shifted from the ventral surface onto the left side of the body, but has gone no further. Since the preoral lobe disappears as an appendage from the oral surface within the hydrocœle ring it is evident that the apical nervous system of the crinoids, which appears to be intimately connected with the preoral lobe, must be represented by a ventral nervous system in the asteroids.

In the crinoids the circumoral nerve ring and its extensions beneath the ciliated ambulacral grooves of the disc, arms and pinnules is associated only with the latter and with the ventral surface of the tentacles. In the asteroids the similarly situated ectodermal nervous tracts are in connection with a diffuse ectoneural plexus found throughout the ectoderm and at the mouth with an endoneural plexus which is the central portion of the so-called endodermal nervous system. The deep oral nervous system, consisting of a double cord in each radius just within the radial nerve thickening of the ectoneural system and centering in a more or less complete ring about the mouth, said to be exclusively motor in function, possibly corresponds to the deep oral system of the crinoids which consists of paired cords, one on either side of the water tube; but the latter is connected with the apical nervous system and the former is not. The apical nervous system of the asteroids, motor in function, consists of a cord in the mid-radial line of each arm and appears to develop from the dorsal peritoneum with which it remains in continuity. It differs from that of the crinoids in being radial (intersomatic) instead of interradial (mid-somatic) in position, in consisting of single cords instead of paired cords with commissures, and in lacking a well developed central organ. From its lack of any relation to the preoral lobe and its general indefiniteness of structure it is difficult to see how it can be in any way homologous with the apical nervous system of the crinoids. It is probably a special feature peculiar to asteroids.

The apical nervous system of the crinoids, from which the whole animal with the exception of the peristomal region and its extensions is innervated, is absent in the asteroids, or rather it has become merged into the circumoral structures and their derivatives.

It has been shown that the crinoids before the development of the arms are encased in plates developed over the somatic divisions, but that beginning with the appearance of the arms the development becomes wholly intersomatic or radial. In the asteroids the development is radial from the first appearance of the plates, the interradial (mid-somatic) body covering seen in the young crinoids not appearing at all.

In the crinoids there are at first no plates belonging to the ventral surface, the basals being dorsal and the orals ventrolateral, but the latter become ventral plates after the formation of the arms, which themselves are composed of a series of dorsal ossicles carrying extensions from the ventral structures on their ventral surface. In the asteroids the plates at their first appearance represent those of the crinoids after the formation of the arms as far as their bifurcation, minus the orals. There is a central plate, corresponding to the infrabasals in the crinoids; about this are five basals, corresponding to the five basals of the crinoids; beyond and alternating with these are five terminals, corresponding to the radials of the crinoids, but always single and showing no indications of a primarily paired condition as the crinoid radials do. On the opposite (ventral) surface are five pairs of plates, one pair in each radial division, corresponding to the first two post-radial plates in the crinoids, but side by side instead of tandem.

Thus whereas the extensions of the crinoid body—the arms—are just on the border between the dorsal and ventral surfaces and are composed dorsally of dorsal ossicles and ventrally of extensions of ventral structures, in the asteroids the dorsoventral edge of the body has moved dorsally so that the dividing line between the dorsal and ventral surfaces falls between the radials and the succeeding plates, and the whole ventral surface is encased in plates which are represented in the crinoids on the dorsal surface only.

The asteroids therefore differ from the crinoids in the temporary attachment of the larvæ; in the relatively slight alteration in the position of the mouth; in lacking the apical nervous system, which has either completely disappeared or has become transformed into a ventral nervous system centering in a ring or rings about the mouth; in omitting the early mid-somatic development, the development of the body being inter-somatic from the first; and in having moved the border between the ventral and dorsal surfaces dorsally so that all the post-radial plates now lie on the ventral surface, the arms being formed by an extension of the body in the plane dividing the crinoid radials from the plates succeeding.

THE SEA-URCHINS AND THE BRITTLE-STARS

The echinoids and ophiurans differ still more widely from the crinoid type. Their larvæ, except in special cases, are extraordinarily developed plutei which have no attached stage at all, and are characterized by the small size of the preoral lobe, by the great development of the post-anal portion of the body, and by the possession of a special larval skeleton supporting the arms which is later resorbed.

Whereas the asteroids differ from the crinoids in transferring the post-radial plates from the dorsal to the ventral surface and thereby forming a ventral skeleton of primarily dorsal elements, the echinoids have gone further and have eliminated the dorsal surface altogether except for a ring of plates about the periproctal region and the small area within it, the globular body being composed of plates representing the ventral plates of the asteroids. The perfection of an entirely new type of compact radially symmetrical body from the crinoid through the asteroid, simulating the compact radially symmetrical cœlenterate body, has furnished a starting point for new development, and bilateral symmetry, superposed upon the perfected radial symmetry, has reappeared and in some cases (as in *Pourtalesia*) has been carried to an extreme.

The ophiurans are phylogenetically parallel to the echinoids, but their line of specialization is entirely different. In them the relation of the dorsal to the ventral surface has remained as in the asteroids, but the radial (intersomatic) extensions of the body have become narrowed and consolidated into highly efficient jointed appendages from which all non-essential structures have been eliminated.

THE FEEDING HABITS OF THE ECHINODERMS AND THE CRUSTACEANS

Corresponding with the progressive specialization in their structure it is interesting to note a progressive specialization in the feeding habits of the echinoderms. The crinoids are plankton feeders, like the barnacles. The starfishes are largely carnivorous, feeding especially upon molluscs, but some swallow mud out of which they digest the organic matter. The echinoids feed upon vegetable matter or upon organic detritus, and many are mud or sand swallowers. The ophiurans feed largely upon detritus or swallow mud, but many are ectoparasitic upon cœlenterates and crinoids from which they steal the food in or on its way to the stomach.

Thus along with the widening of the gap between the structure of the true barnacles and that of the echinoderms there is a similar divergence in their feeding habits; from plankton feeders they become simply scavengers and parasites.

The recent crustaceans as a whole show exactly the same line of specialization from the phyllopod, which feeds on minute organisms, to the decapod, which feeds largely on carrion or detritus, or is ectoparasitic on cœlenterates or on crinoids, and this development of the feeding habit, with the emphasis on the scavenging activities, is characteristic of these two groups alone.

PROFESSOR PATTEN'S INTERPRETATION OF THE AFFINITIES OF THE ECHINODERMS

Although I arrived at the conclusion that the echinoderms and the arthropods are in reality closely related more than ten years ago and in a short paper published in April, 1910, that conclusion is readily to be inferred, Professor William Patten was the first to attempt to explain the relationships of the echinoderms to the arthropods in detail. His reasoning is so entirely different from mine that it is worth while to repeat his arguments here.

He says: "The echinoderms are notable for their contrasts and contradictions. Their outward appearance and their pronounced radial structure distinguish them from all other animals, and at first sight suggest a very primitive organization similar to that of the cœlenterates. On the other hand they display a high degree of histological and anatomical specialization that is in marked contrast with their low grade of organic efficiency. They begin their early embryonic development with a bilaterally symmetrical body and with clear indications of metamerism, only to change it in the later stages for one that is radially symmetrical and in which all outward traces of metamerism have disappeared. After a short free-swimming larval existence they attach themselves, neural side down, by means of larval appendages and a cephalic outgrowth; they then turn neural side up and remain so attached for life; or in some cases they give up their sessile existence and again become free, moving slowly about, neural side down. There are, therefore, three chief characteristics of the echinoderms that demand our first consideration: (1) The early bilateral symmetry and metamerism; (2) the sessile life and mode of attachment by cephalic outgrowths; and (3) the asymmetry. There appears to be but one explanation for these remarkable conditions, which is as follows: The early development of bilateral symmetry and metamerism in the echinoderms, and the presence of a telocele and telopore in place of the more primitive gastrula and blastopore, clearly indicate that they had their origin in bilaterally symmetrical animals of the acraniate type that had already acquired a considerable degree of complexity. These ancestral forms probably belonged to the cirriped group, for before the latent asymmetry becomes effective the young echinoderm larva resembles a cirriped in its form, mode of attachment, and subsequent metamorphosis more than it does any other animal. The radiate structure of the later stages was due to a persistent local defect, or to the absence of a definite part of the embryonic formative material, which in turn created a condition of unstable equilibrium, the result of which is that the whole side, following the path of least resistence, bends toward the defective area, forming an arch that increases in curvature until an approximate equilibrium is again attained by the union of the two ends to form a circle. The original half metameres and segmental organs are then arranged in radiating lines, thus creating a new radiate type and a new set of internal conditions that dominate the future growth of the organism. If we assume that a strongly marked asymmetry, such as that which occurs so frequently as an abnormality in *Xiphosura,* or even as a normal character in the Bopyridæ and Paguridæ, was a fixed feature of the hypothetical ancestral cirripeds and was capable of a successful organic adjustment, we shall have a perfectly simple and natural explanation of the origin and structure of the echinoderms.

"The young asteroid larva is said to attach itself voluntarily at first, and for a short time only; later it becomes permanently attached, head first and neural side down, in the same remarkable manner as a young cirriped, both the cephalic appendages (which are thick walled and muscular, with a long basal portion and a short terminal knob studded with small adhesive papillæ, greatly resembling the minute adhesive antennæ of the cirripeds and parasitic crustaceans) and the adhesive disc taking part in the process. The young crinoid larva attaches itself wholly by means of the cephalic disc, as the adhesive appendages appear to be absent. Its first position is with the neural or oral surface down, as in the cypris stage of the cirriped. The disc then elongates, forming a slender cephalic stalk or peduncle, and the larva turns a somersault, bringing its neural side uppermost. Meanwhile the vestibule, or peribranchial chamber, which at first is small and temporarily closed, enlarges, then ruptures, and the five appendages project from the cup-like head in typical cirriped fashion. In certain of the representatives of the recent echinoderms, such as the asteroids, the fixed stage is temporary, while in certain others, such as the echinoids and holothurians, it appears to be omitted altogether and the young echinoderm, after its metamorphosis, again acquires a limited power of locomotion. But in most primitive echinoderms, such as the stalked crinoids, blastoids and cystideans, a permanent attachment by an elongated cephalic stalk, in typical cirriped fashion, was the almost invariable rule, and no doubt represented the primitive condition for the whole class. When an echinoderm does become free it acquires only a very limited power of locomotion and of coordinated movement. Its characteristic lack of efficiency in this respect is due not so much to its simple structure as to the fact that its freedom was gained at a late period in the phylogeny of a very ancient group in which sessile inaction was the prevailing condition. It is often assumed that a sessile or parasitic mode of life is the initial cause of degeneration. The various anatomical peculiarities common to the copepods, cirripeds and acraniates do not bear out this conclusion. The fact that in these diverse subphyla we see the same shifting of cephalic appendages to the hæmal side, the same cephalic outgrowths, and the same degeneration of the neuro-muscular organs, indicates that there are certain initial defects or peculiarities of germinal material common to the whole group, and that these are the underlying cause of defective organization, the defective organization being in every case of such a nature that a sessile or parasitic or vegetative mode of life is the only one possible."