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Liverpool Marine Biology Committee.

L.M.B.C. MEMOIRS
ON TYPICAL BRITISH MARINE PLANTS & ANIMALS
EDITED BY W. A. HERDMAN, D.Sc., F.R.S.

XV.
ANTEDON

BY

HERBERT CLIFTON CHADWICK,

*Curator of the Port Erin Biological Station and Honorary Lecturer in
Marine Biology in the University of Liverpool.*

(With 7 Plates)

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XV.

ANTEDON.

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EDITOR'S PREFACE.

THE Liverpool Marine Biology Committee was constituted in 1885, with the object of investigating the Fauna and Flora of the Irish Sea.

The dredging, trawling, and other collecting expeditions organised by the Committee have been carried on intermittently since that time, and a considerable amount of material, both published and unpublished, has been accumulated. Twenty Annual Reports of the Committee and five volumes dealing with the "Fauna and Flora" have been issued. At an early stage of the investigations it became evident that a Biological Station or Laboratory on the sea-shore nearer the usual collecting grounds than Liverpool would be a material assistance in the work. Consequently the Committee, in 1887, established the Puffin Island Biological Station on the North Coast of Anglesey, and later on, in 1892, moved to the more commodious and accessible Station at Port Erin in the centre of the rich collecting grounds of the south end of the Isle of Man. A new and larger Biological Station and Fish Hatchery, on a more convenient site, has now been erected, and was opened for work in July, 1902.

In these twenty years' experience of a Biological Station (five years at Puffin Island and fifteen at Port Erin), where College students and young amateurs form a large proportion of the workers, the want has been frequently felt of a series of detailed descriptions of the structure of certain common typical animals and plants, chosen as representatives of their groups, and dealt with by specialists. The same want has probably been felt in other similar institutions and in many College laboratories.

The objects of the Committee and of the workers at the Biological Station were at first chiefly faunistic and specigraphic. The work must necessarily be so when opening up a new district. Some of the workers have published papers on morphological points, or on embryology and observations on life-histories and habits; but the majority of the papers in the volumes on the "Fauna and Flora of Liverpool Bay" have been, as was intended from the first, occupied with the names and characteristics and distribution of the many different kinds of marine plants and animals in our district. And this faunistic work will still go on. It is far from finished, and the Committee hope in the future to add still further to the records of the Fauna and Flora. But the papers in the present series, started in 1899, are quite distinct from these previous publications in name, in treatment, and in purpose. They are called "L.M.B.C. Memoirs," each treats of one type, and they are issued separately as they are ready, and will be obtainable Memoir by Memoir as they appear, or later bound up in convenient volumes. It is hoped that such a series of special studies, written by those who are thoroughly familiar with the forms of which they treat, will be found of value by students of Biology in laboratories and in Marine Stations, and will be welcomed by many others working privately at Marine Natural History.

The forms selected are, as far as possible, common L.M.B.C. (Irish Sea) animals and plants of which no adequate account already exists in the text-books. Probably most of the specialists who have taken part in the L.M.B.C. work in the past will prepare accounts of one or more representatives of their groups. The following list shows those who have either performed or promised.

Memoirs from I. to XV. have now been published.

Pecten, by Mr. W. J. Dakin; Cancer, by Mr. Pearson; and Doris, by Sir C. Eliot, are now far advanced and ought to be out during 1907. It is hoped that Cucumaria, Buccinum, and the Oyster will follow soon.

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HALICHONDRIA and SYCON, A. Dendy.

In addition to these, other Memoirs will be arranged for, on suitable types, such as *Pagurus*, *Sagitta*, *Pontobdella*, a Cestode and a Pycnogonid.

As announced in the preface to ASCIDIA, a donation from Mr. F. H. Gossage, of Woolton, met the expense of preparing the plates in illustration of the first few Memoirs, and so enabled the Committee to commence the publication of the series sooner than would otherwise have been possible. Other donations received since from Mr. Gossage, Mrs. Holt, Sir John Brunner, and others, are regarded by the Committee as a welcome encouragement, and have been a great help in carrying on the work.

W. A. HERDMAN.

University of Liverpool,

June, 1907.

L.M.B.C. MEMOIRS.

No. XV. ANTEDON.

BY

HERBERT C. CHADWICK,

*Curator of the Port Erin Biological Station, Hon. Lecturer in Marine
Biology in the University of Liverpool.*

ANTEDON BIFIDA, Pennant (= *Comatula rosacea*, Linck, of Forbes and other authors), is the most familiar example of the Class CRINOIDEA found in British seas. Of the six species of the genus recognised as British, five appear to be confined to the deeper waters of our seas, but *A. bifida* has been recorded from depths of a few fathoms only at many points around our coasts. In the L.M.B.C. district it occurs in large numbers off Cemmaes Bay, North Anglesey, at a depth of 10 fathoms, and also off Bull Bay. It is abundant around the South end of the Isle of Man, and is often found clinging by means of its cirri to the wicker creels used by fishermen for the capture of lobsters and crabs. The fishermen state that specimens are always more numerous on the creels after stormy weather.

With abundant aeration and a moderate amount of light, Antedon may be kept under observation in tanks for months. It is not usually an active animal. By means of its cirri it clings tenaciously to stones, algæ, hydroids, &c., the arms being widely spread horizontally with the tips more or less flexed towards the disc (Pl. I., fig. 1). When disturbed it swims actively and with strikingly graceful movement, the two arms of each pair being invariably flexed and extended alternately (Pl. I.,

fig. 2). The colour of *Antedon* is very variable. Some specimens are of a deep reddish purple, uniformly distributed over both disc and arms, but the majority are clouded and spotted with rose, orange, and yellow tints. The colouring matter is highly soluble in fresh water, alcohol, and glycerine, but not in ether. Its properties in *Antedon bifida* and other species of the genus have been described by Moseley (1), Krukenberg (2), and MacMunn (3), to whose papers the reader is referred.*

EXTERNAL CHARACTERS.

Antedon is composed of a central disc and five pairs of long and flexible arms fringed with pinnules (Pl. I., fig. 2). The disc consists of a shallow cup or calyx, composed of a number of calcareous plates firmly articulated together, and a lenticular visceral mass, lodged within the cavity of the calyx, and containing the central parts of the ambulacral, nervous, and vascular systems in addition to the alimentary canal. A number of jointed appendages called cirri, each terminating in a claw, are attached to the sloping sides of the central plate of the calyx (Pl. I., fig. 3, *ci.*). The opposite face of the disc is the "tegmen calycis" (Pl. II., fig. 24, *tg. cl.*). Near its centre is the mouth (*mt.*), surrounded by five slightly elevated valvular folds (Pl. II., fig. 28, *v.f.*). The tegmen calycis is traversed by five ambulacral grooves, fringed with delicate tentacles (Pl. II., fig. 24, *amb. gr.*), which radiate from the mouth to the edge of the disc and there bifurcate to enter and traverse the entire length of the ten arms and all their pinnules except the first or proximal one (fig. 24). In one of the five interradial

* The black numerals in brackets refer to the list of references given at the end (p. 40).

portions into which the tegmen calycis is divided by the ambulacral grooves there is a conical projection, the anal funnel (Pl. II., fig. 24, *an. fl.*), at the apex of which the anus (*an.*) is situated. The margin of the anal aperture bears minute papillæ. With the aid of a good lens a number of minute pores may be detected in the tegmen calycis. These are the external apertures of the ciliated funnels of the water vascular system.

Orientation.—When *Antedon* is at rest with the mouth directed upwards and the anal interradius nearest to the observer, it is customary to call the opposite radius anterior. The four remaining radii are thus right anterior, right posterior, left posterior, and left anterior. In correspondence with this designation of the radii the interradii are called right anterior, right postero-lateral, posterior (or anal), left postero-lateral and left anterior respectively. To maintain this orientation when the animal is viewed from the aboral surface the posterior (anal) interradius must be turned away from the observer.

THE SKELETON.

The skeleton of the calyx is composed of a centro-dorsal plate (Pl. I., fig. 3; Pl. V., fig. 52; Pl. VI., fig. 59, *cent. dr.*), to the convex aboral surface of which the cirri are articulated; five radial plates (Pl. V., fig. 52; Pl. VI., fig. 59, *rd.*), which form a pentagon and rest upon the plane oral surface of the centro-dorsal; and five basal plates which are fused together to form a single plate, the rosette (Pl. I., figs 17 and 18; Pl. V., fig. 52; Pl. VI., fig. 59, *ros.*), which roofs over a bowl-shaped cavity in the centro-dorsal (Pl. I., fig. 19). To these must be added, as contributing to the support of the visceral mass, the two most proximal joints of the arms, called respectively the first and second primibrachials (Pl. I., fig. 3; Pl. V.,

fig. 52; Pl. VI., fig. 59, *pmb.* 1 and *pmb.* 2). The latter joint is axillary, and supports, in each radius, two long series of secundibrachials (Pl. I., fig. 3, *sec.*), which form the skeletons of the five pairs of arms, and to these the much shorter series of joints which support the pinnules are articulated.

Several specimens of *Antedon* with only eight arms have been observed by the writer, and one with twelve was described by Dendy (4). The eight-armed condition results from the absence of one of the radii, while the two extra arms of the twelve-armed specimen resulted from the bifurcation of two of the normal ones. In each of these the second secundibrachial became an axillary, similar to the second primibrachials, and of which each facet bore the long series of, in this case tertibrachial, joints forming the arms. In many species of *Antedon* one or both facets of the primibrachial axillary bear a series of two or three secundibrachial joints, the second or third of which is an axillary, and may in turn bear two or three tertibrachial joints, the second or third of which is also an axillary. In this way the large number of arms borne by many tropical species arise. All the skeletal plates are composed of more or less densely reticulate calcareous matter, to which the name "stereom" has been given. This reticulate structure may be seen in its simplest form in the skeletal plates of the larva (Pl. VI., figs. 66, 67, and 69), in which the reticulations are all in one plane, but in the much more massive plates of the adult they form a sort of sponge work, the meshes of which vary in shape and size even in the same plate.

The Centro-dorsal Plate.—The form of this plate (Pl. I., figs. 3 and 19) resembles that of a shallow bowl. It is of considerable thickness; and its outer margin, as well as that which bounds and slightly overhangs the

comparatively small cavity, is pentagonal, with rounded and slightly upturned angles (fig. 19). In the peripheral portion of the bottom of the cavity may be seen the inner ends of a number of minute canals, through which nerve cords pass to the cirri (Pl. V., fig. 52; Pl. VI., fig. 59). The central portion of the aboral face of the plate is flat or only slightly convex (Pl. I., fig. 20). The peripheral portion is wholly occupied by a number of sockets for the articulation of the cirri. Those which border the flattened central portion of the plate have a nearly circular outline, while the more peripheral ones become more or less angular, owing to close approximation. At the bottom of each socket there is a minute papilliform elevation, perforated in its centre by the external opening of one of the canals already mentioned. The oral face of the plate is nearly flat. Shallow grooves traverse it at the interradian angles from the periphery to the margin of the cavity, marking it out into five equal and radial segments (fig. 19).

The Cirri.—These vary in number from twenty to nearly forty. Each cirrus (Pl. I., fig. 3; Pl. III., fig. 38) is composed of from ten to eighteen calcareous joints, the terminal one being in the form of a claw, immovably articulated with the penultimate joint. The proximal and next succeeding joints are cylindrical and shorter than the remainder, which are compressed from side to side and slightly constricted about the middle of their length, the latter character becoming less marked, almost to disappearance, in the terminal joints. A minute canal, continuous with one of the canals of the centro-dorsal plate, traverses the whole series of joints and ends blindly in the terminal claw (fig. 38, *ax. cn.*). All the joints, except the penultimate and terminal ones, are united by elastic ligaments, and the interarticular spaces

between the joints are widest on the side nearest the vertical axis of the animal, towards which the whole cirrus is always more or less flexed.

Radial Plates.—These plates (Pl. V., fig. 52; Pl. VI., figs. 56 and 59, *rd.*), closely adhering to each other by their lateral faces and together forming a well marked pentagon, are also adherent by their aboral faces (figs. 52 and 59) to the oral face of the centro-dorsal plate. Each radial plate is of triangular form. Its slightly truncated apex, forming the internal face of the plate (Pl. I., fig. 4), is turned towards the vertical axis of the animal, its base forms one of the sides of the radial pentagon, while its lateral faces are in close contact with its fellows on either side. The lateral faces are flat, and each presents a fairly large aperture in the angle formed by the aboral and internal faces (fig. 6). Two apertures of slightly larger size appear in the latter face, which is small and irregular (fig. 4). The external face (fig 5) presents an oval aperture in the middle of its width, and a well marked transverse ridge divides this face into upper and lower portions. The former is divided into two pairs of fossæ by an incomplete transverse ridge and the continuation of two converging ridges, which are more conspicuous on the oral face of the plate (fig. 7). The upper, deeper pair lodge the proximal ends of the powerful flexor muscles, while the lower, shallow pair afford attachment for the proximal ends of the inter-articular ligaments. The lower (aboral) portion of this face is occupied by a single fossa which lodges the proximal ends of an elastic extensor ligament. The oral face of the plate presents two curved ridges (fig. 7), the shorter ends of which approach each other along the median line and form the median edges of the pair of fossæ which lodge the flexor muscles. The apertures

on the external, internal, and lateral faces of the radial plates belong to a system of canals which radiate from the central funnel-like space enclosed by the five plates, and also form an annulus around it. These canals lodge the radial cords and commissures of the apical nervous system, and their courses will be more readily understood in relation to that system.

The Rosette.—This plate (Pl. I., figs. 17 and 18) assumes the form of a disc with a circular aperture in the centre, and a margin divided by deep clefts into ten radiating processes. Of the latter, five are triangular and lie in nearly the same horizontal plane as the disc (fig. 8); whilst the alternating five have nearly parallel margins, which are inflected in such a way as to form a shallow groove, the whole process being markedly reflected in the direction of the centro-dorsal plate. The exact form of the rosette can only be made out after dissociation from the radial pentagon by maceration in a solution of caustic potash. When in situ it almost completely shuts off the funnel-shaped cavity enclosed by the five radials from the cavity of the centro-dorsal plate, the circular aperture in its centre being the only communication (Pl. V., fig. 52; Pl. VI., fig. 59). The five triangular processes are interradiar, that is to say, they are directed towards the sutures between the radials; the alternating processes are radial, and abut upon the axial faces of the radials, from which also a number of irregular calcareous outgrowths pass to the oral face of the rosette (Pl. VI., fig. 59).

First Primibrachial Plates.—Each of these is an ellipsoid disc-like plate of moderate thickness (Pl. I., fig. 3, *pmb.* 1; figs. 8 and 9), having two nearly parallel faces, of which the inner, or axial, has much the larger area (fig. 8), and articulates with the outer, or

abaxial, face of the corresponding radial. The axial face is divided transversely by a well-marked ridge into two portions of unequal size. The larger portion is on the oral, or upper, side of the ridge, and is sub-divided by a median vertical and two oblique and less prominent ridges into two pairs of fossæ, of which the upper pair are the deeper. The smaller portion of the face is on the aboral, or lower, side of the ridge, and is wholly occupied by a broad and deep fossa. At the point of intersection of the transverse, vertical, and oblique ridges is the oval opening of a canal which traverses the plate from face to face. The smaller abaxial face (fig. 9) is of simpler character, and presents only one pair of fossæ, divided by a vertical ridge which passes round the opening of the above-mentioned canal, and at its upper, or oral, end is continuous with a slightly raised margin, which bounds the fossæ above. The oral margin of the plate presents a well-marked notch when viewed from this face.

Second Primibrachial Plates.—These plates resemble the radials in general form (Pl. I., fig. 3, *pmb.* 2; figs. 10 and 11). Each one presents a triangular figure when viewed from above or below, and has three articular faces. Of these, the axial closely resembles the abaxial face of the first primibrachial, with which it is articulated, having a single pair of lateral fossæ divided by a vertical ridge, which also passes round the transversely oval aperture of the axial canal. The surfaces of the lateral fossæ slope away slightly from the vertical ridge, so that when the latter is in close contact with the corresponding ridge of the first primibrachial the second primibrachial has a slight range of lateral movement upon the first. A median crest and a pair of divergent lamellæ project from the upper, or oral, margin of the axial face to form parts of the two oblique surfaces of articulation (fig. 11).

In general plan these latter correspond with the articular faces of the radials and first primibrachials, there being a strong transverse ridge that separates a deep fossa on its aboral side from two pairs of fossæ on its oral side (fig. 10). The divergent lamellæ described above form vertical dividing ridges between the latter. The radial canal, which has been seen above to traverse the first primibrachial, enters the second and immediately bifurcates, and the oval apertures of its two branches appear on the corresponding oblique articular faces at the point where the transverse ridge is joined by the vertical one.

Interradial Plates.—In some specimens of *Antedon* three or four small interradial plates are found in the interradii between the axillaries.

The Arms.—The arms (Pl. I., figs. 1, 2 and 3) are rather slender and taper gradually to extreme tenuity. Each arm is composed of a long series of joints or segments (figs. 3 and 21), placed end to end and bound together by muscular and ligamentous fibres (Pl. V., fig. 50). These segments are termed secundibrachials, and are of the same fundamental form throughout the length of the arm, each one being a short cylindrical rod, traversed by a minute axial canal (figs. 12 to 16, also fig. 21). The absolute length of the segments decreases very gradually from the base to the tip of the arm, those at the latter extremity being rather more than half the length of those at the former. The proportion of length to diameter presents considerable variation. Thus, at the proximal end of the arm the length of the first few segments is less than half their diameter; in the middle region their length is less than twice their diameter; while at the distal extremity of the arm the segments become more and more cylindrical in form, and their length is at least four times their diameter. Viewed from the aboral

surface the outer margins of the first secundibrachials (Pl. I., fig. 3) are seen to be considerably longer than the inner, so much so that the angle of about 80° at which their proximal articular faces incline towards each other is widened out to one of about 130° between their distal faces. The outer margin of the second joint also is longer than the inner, and presents a shallow socket divided by a transverse ridge, in which a minute perforation appears. To this socket the first (oral) pinnule is articulated (fig. 3). With certain exceptions to be presently described, the succeeding joints present a similar inequality in the length of their margins, but the longer margin is alternately outer and inner, and the pinnule borne by every such joint is articulated to it. Hence, when viewed from the dorsal surface, the joints present the appearance of triangles, the apices of which point alternately to one side and the other (fig. 3). In the middle and more distal parts of the arm the inequality of the margins becomes less and less marked; and while in the proximal portion of the arm the articular socket of the pinnule encroaches upon the distal articular socket of the segment (fig. 14), in the middle and distal portions it is more and more restricted to the lateral face (fig. 15). The articular faces of the great majority of the secundibrachial segments present very similar characteristics (figs. 12 to 16). A transverse ridge, pierced by the opening of the axial canal, crosses each more or less obliquely and separates a single deep fossa on its dorsal side from a pair of shallower ventro-lateral fossæ. A pair of radial lamellæ separates the latter from a second pair of fossæ, which are deeper, occupy the ventral portion of the articular face, and are themselves separated by a median and more or less vertical lamella. The single dorsal fossa lodges the elastic ligament which extends the arm; the

ventro-lateral ones lodge the inter-articular ligaments; while the ventral pair lodge the flexor muscles. Actual contact between the successive segments of the arm occurs only along the great transverse ridges. The distal articular face of the first secundibrachial and the proximal articular face of the second resemble the proximal face of the second primibrachial and the distal face of the first in having a vertical ridge separating a single pair of lateral fossæ.

Exceptions to this general rule are presented by the distal faces of certain segments and the proximal faces of the next succeeding ones, which are almost flat, and the articular and muscular fossæ are replaced by a series of slightly elevated ridges and alternating furrows, which radiate from the opening of the axial canal to the dorsal and lateral margins (Pl. I., fig. 16). Ligamentous fibres only (Pl. V., fig. 50) bind the two apposed faces together. To this close and immovable union of two segments, the direction of which is always at right angles to the axis of the arm, the name syzygy was given by Joh. Müller (Pl. I., fig. 3, *syz.*). Of the two segments concerned in the formation of a syzygy only the distal one (epizygal) bears a pinnule, the proximal (hypozygal) never has one. In *Antedon bifida* syzygies occur between joints 3 and 4, 9 and 10, 14 and 15, and then between every fourth and fifth or sixth and seventh. Syzygies appear to be points of least resistance, at which autotomy very frequently occurs.

A transverse interbrachial muscle runs from arm to arm of each pair, and its two ends are lodged in corresponding rounded fossæ excavated in the inner ends of the proximal faces of the first primibrachials (Pl. I., fig. 12).

The pinnules, like the arms, are composed of articulated segments, the diameter of which gradually

decreases from the base to the tip (Pl. I., fig. 3; Pl. II., fig. 24; Pl. III., figs. 32 and 33). The penultimate and terminal segments are armed with minute hooks (Pl. III., fig. 34). The axial canal which traverses the arm branches into all the pinnules and ends blindly in the terminal segment of each. The movements of the pinnules are effected by flexor muscles lodged in deep notches in the ventral margin of each articular face, and extensor fibres which pass from segment to segment on the dorsal margin. Ligamentous fibres only bind the proximal segment to the brachial segment that bears it. The pinnules borne by the second brachial segments are usually twice the length of the succeeding ones, and are distinguished as the oral pinnules (Pl. I., fig. 3; Pl. II., fig. 24; Pl. III., fig. 32). They have no tentacles and no ambulacral grooves, and during life are found more or less strongly flexed over the tegmen calycis (fig. 24). The next pair are quite short, but the succeeding pairs gradually increase in length until the middle portion of the arm is reached, beyond which the length decreases to its distal end or growing point. Dichotomous division occurs repeatedly at the latter, and one branch, on the right and left sides alternately, remains short and constitutes a pinnule. .

The external surface of the disc and arms is everywhere invested by a delicate cuticle, beneath which the cells of the ectoderm are distinguishable only in the ambulacral grooves, the inner faces of the oral and marginal tentacles, and upon the pinnular tentacles, where they form sensory papillæ.

In other parts, notably along the sides of the arms and the lateral and dorsal surfaces of the visceral mass, the most superficial cells beneath the cuticle have a more or less regular arrangement, but no sharp distinction can

be drawn between those of the ectoderm and those of the cutis, except in young specimens. Where the subjacent tissue is calcified, especially along the dorsal and dorso-lateral surfaces of the apical plates and the brachial segments, they become fusiform and still more regularly arranged, and the delicate filamentous processes into which their basal ends are divided are continuous with similar processes of many of the cells of the deeper layer (Pl. II., fig. 26).

MUSCLES AND LIGAMENTS.

The flexor muscles of the arms and pinnules (Pl. V., figs. 50 and 52, *flx. m.*) consist of large bundles of parallel fibres which have a strong affinity for aniline stains, especially hæmatoxylin. Each fibre has a minute oval nucleus, and is of uniform diameter throughout its length (Pl. III., fig. 36), but it is thicker along one edge than the other, and thus presents a wedge-shaped figure in transverse section. The ends of these fibres are sharply defined. The extensor fibres are of extreme fineness and have less affinity for stains (Pl. III., fig. 35; Pl. V., fig. 50). In longitudinal sections they frequently possess a more or less wavy appearance. Their ends are split up into a variable number of fibrillæ, each of which may be traced into continuity with the cells of the stroma which forms the organic basis of the adjoining ossicles. The nuclei are smaller and rather more rounded than those of the flexor fibres. The fibres which form the interarticular ligaments are not distinguishable from the extensor fibres, and the interarticular fibres of the cirri are of similar character.

SACCU LI.

The sacculi (Pl. II., figs. 24 and 28; Pl. III., figs. 32, 33, 34, and 40; Pl. IV., figs. 41 and 47; Pl. V., fig. 52; Pl. VII., figs. 61, 62, 66, 67, 69, and 71, *sac.*) are minute globular or ovate sacs, which occur in great numbers immediately below the external epithelium at the edges of the ambulacral grooves of the disc, arms, and pinnules, and occasionally in small numbers in the wall of the intestine and mesenteries. Along the grooves of the disc they may form a double or even a triple row, and are especially numerous on the outer sides of the proximal ends of the brachial grooves, on the periphery of the disc (fig. 24). Along the arms and pinnules they form a single row, and alternate regularly with the triad groups of tentacles. Each sacculus consists of a delicate limiting membrane of connective tissue, lodged in the mesoderm and having no permanent aperture (Pl. III., fig. 40). The included space is almost invariably densely crowded with groups of refractive spherules, consisting of an albuminous substance, which are colourless during life, but turn yellow or red after death, owing to absorption of the very soluble pigment of the integument. They have a strong affinity for stains.

These spherules are the product of nucleated cells of pyriform shape (fig. 40, *a*), which clothe the inner face of the lower wall of the sacculus, and are apparently of mesodermal origin. The spherules make their appearance in processes of the cells which grow upwards and finally become attached in the form of filaments to the upper wall of the sacculus. The spherule-containing portion eventually separates from the base of the cell and lies free in the sacculus. Sacculi have been successively regarded as calcigenous glands, mucous glands, excretory

glands, symbiotic algæ, and accumulations of reserve material to be used in the regeneration of injured arms or pinnules. The value of the last view is somewhat vitiated by the fact that sacculi do not occur in the allied genus *Actinometra*, in the injured arms and pinnules of which regeneration goes on quite as actively as in those of *Antedon*. The present writer is inclined to regard the function of the sacculi as excretory.

DIGESTIVE SYSTEM.

The aperture of the mouth does not occupy the centre of the disc, but is more or less displaced in the direction of the anterior radius (Pl. II., fig. 24, *mt.h.*). It opens into a gradually widening œsophagus, which runs obliquely in the direction of the right posterior radius, and there expands into a large sacculated intestine (Pl. II., fig. 23, *int.*). This, descending towards the aboral face of the visceral mass, and gradually narrowing, makes a complete coil around the vertical axis of the disc in the direction of the hands of a clock. On re-entering the posterior inter-radius it ascends the anal funnel and opens to the exterior through the anal aperture. In addition to numerous short diverticula which open into the intestine in the first third of its course (fig. 23), there are two long ones with finely-branched extremities, which open upon its inner border in the neighbourhood of the left anterior radius (fig. 23, *div.*). The alimentary canal is of almost uniform structure throughout. It consists of an epithelium of fusiform, ciliated cells interspersed, in the œsophagus, with caliciform cells (Pl. II., fig. 25), and, throughout its length, with very minute rounded cells, especially between the basal ends of the fusiform cells. A layer of nerve fibres, continuous with the sub-epithelial nerve ring, underlies the œsophageal epithelium and

gradually thins out as the œsophagus passes into the intestine, in the walls of which it is difficult to trace.

The epithelium and subjacent nerve layer rest upon a delicate basement membrane of connective tissue, which is, however, enormously thickened in the rectal portion of the intestine (Pl. II., fig. 27, *en. ts.*). Thin but definite layers of muscular fibre form sphincters around the œsophagus and rectum (figs. 25 and 27, *sph. fb.*), but the musculature is elsewhere feebly developed and less definite.

The anal funnel has been observed to contract rhythmically, doubtless in connection with the ejection of water and excreta. The food of *Antedon* consists of diatoms, radiolarians, foraminifera, and other small organisms, which are captured by the tentacle-fringed arms and pinnules and swept down the ambulacral grooves to the mouth by the action of the cilia which line them.

THE BLOOD-VASCULAR OR LACUNAR SYSTEM.

This system is highly characteristic of the majority of the Echinoderma, and consists, in *Antedon*, of a number of lacunar spaces, bounded by walls of connective tissue scarcely distinguishable from that which forms the numerous strands and trabeculæ of the body cavity (Pl. V., fig. 52). These lacunæ traverse the body cavity in all directions, and are generally recognisable in sections by their albuminoid contents, which are coagulated by the fixing reagents and may even stain faintly. As will be presently seen, some of the lacunæ simulate true vessels by the assumption of a tubular form and considerable thickening of their walls. The largest and most easily recognisable lacuna is one to which the name 'circumoral blood-vascular

ring' has been given by various authors. It depends into the body-cavity from a point just below the circum-oral water vessel (Pl. IV., fig. 47; Pl. V., fig. 52, *c.o.bl.r.*), and appears to attain its greatest development in the inter-radii, especially the anal and right posterior ones. Its wall consists of a thin sheet of connective tissue containing rounded nuclei, and its form in sections depends largely upon the quantity of coagulable fluid contained at the moment of fixation. Generally speaking, however, it may be said to expand gradually and irregularly from its point of attachment to the wall of the œsophagus to its periphery. Here it becomes much more sacculated; and the nuclei are not only more numerous but assume in some parts a definite arrangement.

At one point in its circumference the lacunar walls become thickened, very irregular, and confluent, so as to form a roughly lenticular mass of connective tissue traversed by numerous interlacing tubules. This is the 'spongy organ' (Pl. V., fig. 51). Its tubules are in direct communication with a number of thick-walled trunks (Pl. IV., fig. 45), some of which run directly from the spongy organ to the oral end of the axial organ, and, branching and anastomosing, form a sort of vascular envelope thereon (Pl. V., fig. 52). Others run on alongside the axial organ towards the aboral face of the visceral mass, and there branch and assume more irregular forms upon the internal border of the intestinal coil. Other similar trunks issue from the blood-vascular ring to be distributed around the intestine and in the body cavity, and others to ramify in the substance of the tegmen calycis. Lastly, there is an annular lacuna which lies outside the periphery of the blood-vascular ring and is in communication therewith (Pl. V., fig. 52, *gen.bl.lc.*). From it a thin-walled tubular branch arises in each radius

to furnish the genital lacunæ of the arms (Pl. IV., fig. 41, *gen. le.*).

Corpuscles.—Under the term “corpuscles sanguins,” Cuénot (5) has described three kinds of amœboid cells which occur in the various tissues and cœlomic fluid of *Antedon*: (1) amœbocytes with short pseudopodia; (2) amœbocytes of extremely elongated form which are often found migrating in the tissues, but which ultimately become filled with rod-like bodies which have a special affinity for safranine, when the cell assumes a rounded form; (3) very slightly amœboid cells crowded with granules which are golden yellow in the living animal. These are the “oil cells” of Wyville Thomson, and they often occur in numbers amongst the cells of the ectoderm, as well as in the stroma of the skeletal plates. The rounded cells described above as occurring amongst the fusiform cells of the intestinal epithelium may possibly belong to the first of these groups.

THE CŒLOM.

In *Antedon*, as in other Crinoidea, the cavity of the cœlom is not a clear space like that of the Echinoidea and Holothuroidea, but is traversed in all directions by trabeculæ of connective tissue lined by cœlomic endothelium. The cavity is further partitioned by lamellæ of connective tissue which lie parallel to the body-wall into two well-defined but intercommunicating sub-cavities—the peripheral, or subtegumentary, and the peri-intestinal. The latter encloses the intestine, which coils around a central clear space which nearly coincides with the vertical axis of the disc, and is known as the axial sinus (Pl. V., fig. 52, *ax. si.*). The upper, or oral, end of this sinus communicates directly with the subtentacular canals of the arms (fig. 52; Pl. III., fig. 29; Pl. IV., fig. 41, *s.te.ca.*).

The peripheral cavity in like manner communicates with the dorsal or cœliac canals of the same (figs. 29, 41, and 52, *cœ.ca.*). These canals are, therefore, the cœlomic cavities of the arms, and are lined by cœlomic endothelium (fig. 41, *cœ.en.*). They traverse the arms and pinnules to their extremities, and communicate with each other at various points by minute openings in the horizontal and vertical septa which bound them. When viewed in a transverse section of an arm (fig. 29), the dorsal or cœliac canal (*cœ.ca.*) appears as a sub-triangular space, bounded dorso-laterally by the flexor muscles and ventrally by a horizontal septum. The latter forms also the dorsal boundary of the subtentacular canals, two quadrant-shaped spaces (*s.te.ca.*) separated by a vertical septum, which, however, disappears before the canals enter the disc. Immediately below the point where the vertical septum merges into the horizontal there is a small rounded or lenticular space, the genital lacuna (fig. 41, *gen.lc.*), which encloses the genital cord or rachis.

Ciliated Pits.—In the median sagittal line of the dorsal wall of the cœliac canal of the pinnules, and immediately above the nerve cord, there are groups of two to six bowl-shaped depressions with slightly raised margins, and lined by modified cells of the cœlomic endothelium (Pl. III., fig. 37, *cil.pt.*). The cells which line the bottom of the depression are flattened and non-ciliated, while those which line the sides are columnar and ciliated. The action of the cilia doubtless serves to promote currents in the cœlomic fluid, and on this account the ciliated pits of *Antedon* have been compared with the ciliated funnels of the Synaptidæ and the ciliated bands in the brachial cavities of the Ophiuroidea. Should this be their only function their comparative rarity in the cœliac canals of the arms is remarkable. Their linear

arrangement, in close proximity to the dorsal nerve cord, is probably not without significance, though no nervous connection between the two has been traced.

THE CHAMBERED ORGAN.

This organ (Pl. V., fig. 52; Pl. VI., figs. 54, 55, 57, 59, *ch. or.*) is a division of the cœlom, and is lodged for the most part in the cavity of the centro-dorsal plate. It consists of five radially situated chambers of roughly equal size, lined by cœlomic endothelium, and completely enveloped on all sides by the central capsule of the apical or aboral nervous system (fig. 57). In the vertical axis, from which the connective tissue septa which divide the chambers spring, there is a column-like prolongation of the axial organ (Pl. V., fig. 52; Pl. VI., fig. 59) which penetrates the central capsule and gradually tapers off in the substance of the centro-dorsal. Tubular extensions of the radial chambers, known as cirrus vessels (figs. 52 and 59, *ci. v.*), enclosed in corresponding extensions of the central capsule, called cirrus cords (*ci. cd.*), and divided throughout by a horizontal septum (figs. 58 and 59) traverse the thickness of the centro-dorsal and the axial canals which have been described above as running through all but the terminal joints of the cirri. The horizontal septa cross the chambers, some to be inserted in the vertical axis (Pl. VI., fig. 59), while others do not reach it. They thus appear in sagittal and tangential sections to divide the aboral ends of the radial chambers into a number of super-imposed spaces. On the other hand, the septa are not continued to the extreme ends of the cirrus canals, so that a circulation of the cœlomic fluid therein is possible.

THE AXIAL ORGAN.

This organ, variously known as "dorsal organ," "glandular organ," and "genital stolon," has already been seen in connection with the chambered organ (Pl. V., fig. 52; Pl. VI., fig. 59, *ax. or.*). That portion which forms the axis of the latter consists of a comparatively slender cord, traversed by a few tubules lined with epithelium (fig. 59), which finally merge into one in the direction of the centro-dorsal (Pl. VI., figs. 54, 55, and 57, *ax. or.*). In the opposite direction the organ passes through the central foramen of the rosette plate, ascends alongside the axial sinus of the cœlom towards the mouth, and, in the adult animal, ends in a rounded extremity some little distance below the tegmen calycis, in the right anterior radius. This portion of the organ consists of a complex mass of tubules lined with cylindrical epithelium (Pl. IV., fig. 46), and enclosed in a stroma of connective tissue. As already stated above, a part of the lacunar system is in close relation with the axial organ; but the cord-like extensions of its free (oral) end which have been described as passing into the arms of the pentacrinoid larva, there to form the genital rachids, do not persist in the adult. A departure from the structural condition just described appears to be associated with the breeding season. The lumina of the tubules open into one another much more freely than at other times (Pl. IV., fig. 44), and the epithelial cells which line them break away from the basement membrane and become amœboid. Various stages of this process may be seen in serial sections of one and the same organ.

THE WATER VASCULAR SYSTEM.

This system consists of a circum-oral vessel and five radial vessels which spring therefrom and bifurcate at the base of the corresponding pairs of arms to traverse them and their pinnules to their extremities. In addition to these structures there are numerous water tubes which depend from and open into the circum-oral vessel, and still more numerous ciliated funnels which penetrate the tegmen calycis and open into the body cavity.

The circum-oral vessel surrounds the mouth at the base of the oral tentacles (Pl. IV., fig. 47; Pl. V. fig. 52, *c.o.w.v.*). In common with all other parts of the system, it is lined with endothelium, the cells of which are here rounded, non-ciliated, and have a central nucleus which stains faintly (Pl. IV., fig. 47, *cœ.en.*). Longitudinal muscle fibres form a thin but well-defined band upon the side of the vessel nearest to the œsophagus (fig. 47, *l.m.f.*).

Tentacular branches are given off directly to the five interradial groups of oral tentacles, and at these points the lumen of the vessel is traversed by little groups of isolated muscle fibres (*i.m.f.*). Similar groups occur at the points of origin of the radial vessels. The course of the latter coincides exactly with that of the ambulacral grooves of the disc, of the arms, and of the pinnules. A lacuna-like space, the sub-neural sinus (Pl. IV., fig. 41, *s.n.s.*), separates the vessel (Pl. III., fig. 29; Pl. IV., fig. 41; Pl. V., fig. 52, *r.w.v.*) from the sub-epithelial nerve band.

In traversing the arms the radial vessels follow a slightly zigzag course, and give off, at each of the angles, a lateral branch to a corresponding pinnule. Lateral branches are given off also, which, after a short course at right angles to the axis of the arm or pinnule (Pl. III.,

fig. 29; Pl. IV., fig. 41, *tn. vs.*) divide into three to form the cavities of the triad groups of tentacles which spring from a common point in the centre of the lappets which form the margins of the ambulacral groove. Tentacles and tentacular vessels are wanting in the oral pinnules. In its main features the histological structure of these tentacles agrees with that of the oral ones (Pl. IV., fig. 47, *or. tn.*). Passing from within outwards there is (1) an endothelium of rounded cells (*cœ. en.*) lining the lumen of the tentacle and resting upon (2) a thin but well-defined layer of longitudinally disposed muscular fibres (*l.m.f.*) with which the epithelial cells are said to be connected; (3) a layer of connective tissue, scarcely recognisable in the pinnular tentacles; (4) fibrils from the sub-epithelial nerve band (*sb. nv. f.*) (on the inner face of the tentacle only); (5) the external epithelium (ectoderm=*ect.*). In the case of the pinnular tentacles, however, the cells of the external epithelium are grouped together to form stiff projecting sensory papillæ (Pl. III., figs. 30 and 31, *sn. pp.*).

The water-tubes (stone canals of authors), to the number of about thirty in each interradius, open into the circum-oral vessel along its lower side (Pl. IV., fig. 47; Pl. V., fig. 52, *w.t.*). The slightly expanded free ends of the tubes depend and open into the peripheral portion of the cœlom. Their lumina are lined by columnar cells which are ciliated and have large oval nuclei which stain deeply (fig. 47). The ciliated funnels (Pl. II., fig. 22; Pl. V., fig. 52, *cl. fn.*) are scattered all over the tegmen calycis to its extreme edge between the bases of the arms, and are especially numerous along the borders of the ambulacral grooves. Their slightly raised external apertures, the water pores, are visible under a good hand lens. Passing from without inwards the diameter of the

funnel gradually narrows (fig. 22), then widens again to form a median dilatation. Here the columnar cells of the epithelium with which the funnel is lined bear long cilia which, in sections, are invariably directed towards the body cavity. Beyond the dilatation the cells lose their cilia and gradually thin out, until, as the lumen of the funnel gradually narrows, they are replaced by those of the coelomic endothelium. Occasionally two adjacent funnels unite before opening into the body cavity.

The water-vascular system of *Antedon* and its allies differs functionally from that of the great majority of Echinoderma in having no locomotor rôle. The function of the delicate tentacles which fringe the ambulacral grooves is probably respiratory; and, as will be seen later on, in the description of the nervous system, they are highly sensory. The ciliated funnels and water-tubes probably discharge the same function as the madreporites and water-tubes (stone canals) of the majority of other Echinoderma; but while, in the Echinoidea, Ophiuroidea, and Asteroidea the surrounding water passes directly through the madreporite and water-tube into the water vessels, in *Antedon* it must first enter the body-cavity before passing through the numerous water-tubes into the circum-oral water vessel.

THE NERVOUS SYSTEMS.

There are apparently three well-marked nervous systems in *Antedon*, known respectively as the Superficial Oral, the Deeper Oral, and the Apical or Aboral. The first of these consists of a nerve ring encircling the oral aperture (Pl. IV., fig. 47; Pl. V., fig. 52, *c.o.nv.r.*) in close proximity to the circum-oral water vessel, and radial nerves (Pl. III. fig. 29; Pl. IV., fig. 41; Pl. V., fig. 52, *amb.nv.*) which radiate from the ring and traverse the

arms and pinnules to their extremities. The ambulacral grooves are lined with an epithelium composed of fusiform ciliated cells (Pl. IV., figs. 42 and 43), beneath which there is a well-marked band of longitudinally disposed nerve fibres (*amb. nv.*), from which the inner faces of the marginal tentacles are innervated (fig. 41). The band is thickest in the median line of the groove and thins out gradually towards the sides thereof. The filiform basal ends of many of the overlying epithelial cells penetrate the nerve band to the basement membrane upon which it rests (figs. 42 and 43). Scattered between the epithelial cells, just above the nerve band, are many bipolar and tri-polar cells, which are not improbably in continuity with the epithelial cells and nerve fibres, and similar cells occur in small numbers in the nerve band itself. A layer of nerve fibres extends from the circum-oral ring for some distance along the alimentary canal (Pl. IV., fig. 47; Pl. V., fig. 52, *sb. nv. f.*), but is not readily traceable beyond the œsophagus.

The Deeper Oral system is situated, like the foregoing, on the oral side of the disc and of the arms, but is sub-epithelial in position, and consists of a circum-œsophageal ring with cords radiating from it (Pl. V., fig. 52), lodged in the connective tissue of the tegmen calycis and of the ventral faces of the arms. The circum-œsophageal ring (*d. o. nv. r.*) is of irregular thickness, and is not always readily traceable throughout a series of sagittal sections of the disc. Of the nerve cords which radiate from the ring Cuénot has described five principal pairs, which are said to run one on either side of the five ambulacral grooves of the tegmen calycis and from thence traverse the arms in the same relative position. The present writer has found the tracing of these nerves a matter of very considerable difficulty. In individual

sections of the arms in which a nerve appears in the position indicated by Cuénot it may be seen to give off twigs to the ambulacral tentacles and to others which run towards the dorsal face of the arm (Pl. III., fig. 29, *lt. nr. c.*) where they are said to unite with similar twigs from the brachial cords of the apical system. Moreover, it has not been shown how the single pair of nerve cords which are said to run alongside the ambulacral grooves of the tegmen calycis divide at the point of origin of each pair of arms, so as to furnish a lateral nerve cord to their inner faces. Nerves from the circum-œsophageal ring are traceable to the oral tentacles (Pl. V., fig. 52), and two cords traverse the anal interradius to innervate the anal funnel. Similar nerves occur in the other interradii, and their branches appear to anastomose, thus forming a subtegumentary plexus. From the latter, nerve twigs go to innervate the bands and trabeculæ of connective tissue in the body cavity. It is highly probable that this subepithelial system is in continuity with the superficial system as well as with the apical system.

The Apical system consists of a cup-shaped structure, the central capsule, from which stout nerve cords proceed and eventually unite in pairs to form the apical or dorsal nerve cords of the arms (Pl. V., figs. 48, 49, and 52; Pl. VI., figs. 54, 55, 56, 57, and 59, *cen. cap.*). The central capsule is lodged in the concavity of the centro-dorsal plate, to the walls of which it is closely applied, and its oral or ventral face is covered by the rosette plate (Pl. VI., fig. 59). Its thick walls form a close investment around the chambered organ; and, as has been already stated above, the cirrus vessels which radiate from the chambers are also invested by tubular extensions of the capsule which form the so-called cirrus cords (figs. 52 and 59).

From the margin of the oral face of the capsule arise five interradially situated and diverging pairs of cord-like extensions of the capsule (Pl. V., figs. 48 and 49). Trending towards the oral face of the disc, and entering the substance of the radial plates through the apertures seen in fig. 4, Pl. I., these cords unite to form five radial nerves, the left cord of one interradial pair uniting with the right one of the pair next to it. Just beyond the points of junction of the cords the five radial nerves are connected together by a pentagonal commissure (Pl. V., figs. 48 and 49; Pl. VI., fig. 56, *pnt. com.*) lodged in a canal of corresponding shape which traverses the five radials, in the lateral faces of which its openings may be seen (Pl. I., fig. 6). Beyond the commissure the radial nerve cords pass out of the radial plates into the axial canals of the first primibrachials, and from thence into the second primibrachials or axillaries. On entering the latter each nerve divides into right and left branches (Pl. VI., fig. 53), which pass outwards through the corresponding oblique facets of the plate to form the axial cords of the arms. The two branches are connected together just beyond their point of origin, and while still within the axillary plate, by a transverse commissure (*tr. com.*) and a chiasma (*chi.*), the latter occupying the triangular space bounded by the former and the diverging cords. Passing outwards from the Axillary plate, each branch enters the arm of its own side to become the brachial nerve cord of the apical system (*br. nr. c.*). Traversing the whole length of the arm through the axial canal which perforates all the calcareous joints, the cord gives off alternately right and left branches to the pinnules, and these arise from double roots (Pl. VI., fig. 60, *d. r. pn. br.*). Further, the cord gives off in each joint two pairs of nerves (Pl. III., fig. 29) which are considered to be

principally sensory. One pair arise from the oro-lateral (ventral) border of the cord (*vn. nv.*), and furnish principal branches to the interarticular muscles, numerous twigs which end in sensory cells of the external epithelium, and branches which are said to unite with similar ones from the lateral brachial cords of the deeper oral system. The other pair arise from the dorso-lateral border of the cord (*dr. nv.*), and the numerous branches divide again and again until, as exceedingly fine twigs, they end like some of those of the oral pair, in continuity with the sensory cells of the external epithelium. In longitudinal sections of the arms (Pl. V., fig. 50) the brachial nerve cord (*br. nv. c.*) presents a sort of nodal enlargement between every two joints, those between which a syzygy occurs excepted. These are the points of origin of nerves which are distributed to the interbrachial muscles and ligaments, and which are exceedingly difficult to trace.

In histological structure the central capsule and its radial cords are practically uniform. They consist of extremely delicate fibrils, with numbers of very minute ganglion cells intercalated between them. In the more apical portion of the central capsule the fibrils have no definite arrangement, but in the walls of its oral aspect they are disposed for the most part concentrically around the chambered organ (fig. 55). In the radial cords the nerve fibrils do not form one homogeneous bundle, but are bound together to form strands which are definite in position and direction. Thus, the chiasma (Pl. VI., fig. 53, *chi.*) is formed by two strands which run along the outer lateral borders of the undivided cord, and from thence cross over, one under the other, to be merged into similar strands which run along the inner borders of the two branches and, by the union of their proximal ends, form

the commissure. Transverse sections of the brachial nerve cords (Pl. III., fig. 39) show that their fibrils form five definite strands. Two of these run along the oral aspect of the cord and are in contact in the middle line; while the remaining three traverse its dorsal face, one being median and the other two lateral. Both the lateral strands contribute fibrils to the pinnular branches. The organic reticulum which forms the bases of the skeletal parts is a definite investing layer around the capsule and the cords.

Very little is known of the functions of the superficial oral and deeper oral nervous systems. The sub-epithelial bands which underlie the ambulacral grooves so closely resemble, in histological structure and relation to the ambulacral epithelium, the sub-epithelial bands of the Asteroidea, which are undoubtedly nerves, that there can be little doubt of their nervous character; but the experiments of Carpenter (6), Milnes Marshall (7), and Jickeli (8) show that neither the superficial oral nor the deeper oral system plays more than a very subordinate part in sensation and movement. In all probability the former is concerned with the ambulacral epithelium and the highly sensitive tentacles bordering the ambulacral grooves, structures with which the system is in close anatomical relation. The experiments cited above show that the apical system is the principal one. That the central capsule is a centre from which the complex co-ordinated movements of swimming and righting are controlled is shown by the fact that when this organ is entirely removed the movements cease; on the other hand, evisceration, with consequent removal of the circum-oral ring of the ambulacral system, has no effect whatever upon them. The commissure lodged in the pentagonal canal of the radial plates co-ordinates the movements of

the whole number of arms, as is shown by the partial or complete failure of co-ordination when the commissure is injured or wholly destroyed; while the commissure and chiasma which connect the bifurcating nerve cords in the second primibrachial in like manner co-ordinate the movements of each pair. The brachial cords are the paths along which afferent and efferent impulses travel to and from the central capsule. If the cord only be severed at any one point of an arm, leaving the ambulacral nerve band intact, even the severest irritation applied to the distal portion of the arm beyond the injury fails to excite any response in the disc and the remaining uninjured arms. Irritation applied to the cut end of the cord in the proximal part of the arm causes immediate and strong flexion of that and all the uninjured arms, while irritation applied to the cord in the distal part of the arm causes similar movements in that part of the arm alone.

THE GENITAL ORGANS.

The genital organs, testes and ovaries, are specialised portions of a system of sterile cords which radiate from the disc and traverse the arms and pinnules. In a transverse section of an arm (Pl. IV., fig. 41) there may be seen in the horizontal partition which divides the cœliac from the subtentacular canals another rounded cœlomic space, lined like its neighbours with endothelium (*gen. le.*). This is the genital lacuna or sinus. It encloses another tube, the genital strand or rachis (*gen. ra.*), which is suspended to its walls by slender filaments of connective tissue. At first a solid cord, the rachis eventually becomes a hollow tube lined with germinal epithelium. In its course along the arm it supplies a branch to each pinnule with the exception of the first. In the pinnules

the branches widen out enormously to form ovate cavities, the gonads (Pl. VI., fig. 61, *tes.*; fig. 62, *ov.*), which equal in length five or six of the pinnular joints, and, at the period of sexual maturity, are filled with spermatozoa, or ova, derived from the germinal epithelium.

The testes are invested by a delicate layer of connective tissue in which there are oblique muscular fibres; on the inner side this layer is thrown into many projecting folds, which greatly augment the surface upon which the spermatoblasts are developed. The mature spermatozoon has a conical head and a middle piece to which the tail is attached. Many of the germinal cells which line the ovaries remain small and form a follicular investment around the developing ova (fig. 62, *fol. c.*).

The course of the genital sinuses and the included genital strands in the disc is very difficult to trace. The sinuses almost certainly open into the circum-œsophageal plexus, but, in the adult animal at least, the genital rachids are not traceable into continuity with the oral end of the axial organ, from which they are said to arise in the larva. A sexually mature *Antedon* may be easily recognised by its swollen pinnules, to which the extruded ova, which are fertilised externally, adhere in little groups for four or five days, and until the embryo within has developed the rudiments of its skeleton. The gonads of the more proximal pinnules appear to be the first to ripen. The eggs probably escape from the ovaries by rupture of their walls at one or more points of least resistance, while the spermatozoa are discharged through a small funnel-like projection upon one or both sides of the gonad (fig. 61). Sexual maturity occurs in the months of May and June around the Isle of Man, but the time differs a little according to geographical position. According to Cuénot, it occurs in March and April in the

Mediterranean, and from the end of May to the end of June at Trieste.

Segmentation of the egg results in the formation of a spherical embryo, which consists of a single layer of cells enclosing a cavity filled with gelatinous matter. This is a cœloblastula. Immediately after the completion of this initial stage, a depression, due to invagination of the wall of the cœloblastula, appears at one pole, and the invaginating portion soon becomes bilaminar. The slit-like aperture of the invagination is the blastopore. The embryo is now a gastrula. The cells of the inner layer of the invagination migrate into the gelatinous matter to form mesenchyme (Pl. VI., fig. 63, *mes.*). The external surface of the embryo is covered with cilia, the action of which causes it to rotate within the egg membrane. Presently the blastopore closes completely, and the archenteron becomes a closed vesicle. A circular furrow now appears in its walls and, gradually deepening, eventually separates the archenteric cavity into two distinct vesicles, of which the anterior is slightly the larger (fig. 63). The latter gives rise to the intestine and the hydrocœl, while from the posterior vesicle the cœlom and the chambered organ are derived. The posterior vesicle elongates transversely; and concurrently, the anterior one is produced into horn-like dorsal and ventral extensions (fig. 64, *me. hy. vs.*), which grow around it until they touch, but do not communicate. The two ends of the posterior vesicle now enlarge, while the median portion, encircled by the horns of the anterior vesicle, becomes more tubular. The embryo is now bilaterally symmetrical, and begins to assume an oval form. A ventral outgrowth from the anterior vesicle now forms the rudiment of the hydrocœl (*ru. hy.*), and the vesicle itself becomes the intestine. The enlarged ends of

the posterior vesicle continue to increase in size, and by the eventual disappearance of the median connecting portion, become right and left enterocœlic sacs. About the fourth day the embryo assumes a still more elongated form, and at its anterior end a tuft of long cilia appears. This is borne by a thickened and slightly depressed area of the ectoderm known as the neural plate, in the deeper layers of which the rudiments of the larval nervous system appear. Close behind the neural plate, on the antero-ventral face of the embryo, is a slight depression, the adhesive pit, by means of which the free swimming larva eventually attaches itself. The right enterocœlic sac invades the segmentation cavity and spreads dorsally forwards and over the intestine. The left sac enlarges in the opposite direction and surrounds the posterior border of the intestine. The rudiment of the hydrocœl is now separated from the intestine, but remains for a short time in open communication with a small outgrowth from its anterior wall, the parietal sinus. The intestine undergoes changes of shape and becomes a vesicle. The rudiments of the skeletal system now make their appearance in the form of five oral plates, five basals, from three to five infrabasals, and about eleven segments of the stalk (fig. 65, *jt. sk.*). Externally the embryo is encircled by five ciliated bands (*cl. r.*), and there is a depression in the ventral ectoderm, known as the vestibule (*vs.*), the significance of which will appear later. At this stage the embryo is hatched out and becomes a free-swimming larva, with the tuft of long cilia directed forwards. Between the third and fourth ciliated rings there is a minute aperture, the primary water pore. During the free swimming stage the larval nervous system attains its highest development, and the adhesive pit enlarges and becomes glandular. The vestibule becomes tubular, owing

to the fusion of its lateral edges in the median line, a small anterior aperture being retained. The intestine assumes the form of a hollow plate, and the hydrocœl lies in its ventrally directed cavity (fig. 65). The rudiments of the chambered organ now appear as five tubular outgrowths from the right enterocœl vesicle; and the skeletal joints of the stalk, which are at first horse-shoe shaped, surround them. The hydrocœl vesicle separates from the parietal sinus and assumes a horse-shoe shape. Five outgrowths of its wall appear, each of which eventually gives rise to three primary tentacles, while the primary water tube (stone canal) appears at the blind end of the left limb of the vesicle. The parietal sinus takes up a new position in front of the hydrocœl and finally communicates with the exterior through the hydropore. Soon after the larva attaches itself the ciliated rings and tuft and the neural plate disappear. The vestibular aperture disappears and the vestibule itself takes up a new position at the posterior end of the larva, and by the assumption of a pentagonal form, determines the radiate structure of the adult. It is accompanied in its movements by the hydrocœl, so that the two structures maintain their relative positions. Communication between the hydrocœl vesicle and the parietal sinus is re-established by the water tube, which breaks through into the former. Concurrently with these changes a store of nutritive material is accumulated within the intestinal vesicle by numerous cells which become detached from its wall and finally completely fill it. A funnel-like depression of the floor of the vestibule passes through the hydrocœl ring and forms the œsophagus. A corresponding process of the intestinal vesicle eventually fuses with it. The left cœlomic sac becomes the oral cœlom, and the right sac the aboral or apical cœlom.

The axial organ arises as an epithelial thickening upon one of the primary mesenteries—the longitudinal accessory—formed by the approximation of the cœlomic sacs. Concurrently with the shifting of the vestibule to the posterior end of the larva a re-arrangement of the skeletal plates takes place.

The five orals (Pl. VII., fig. 66, *or. p.*) form a pyramid on the roof of the vestibule, while the five basals (*bas. p.*) form a similar but inverted pyramid in the body wall of the calyx. The plates forming both pyramids are inter-radial in position. Around the uppermost joints of the stalk there are from three to five small infrabasals, which are said to eventually fuse with the centro-dorsal. During subsequent development of the larva the definitive mouth is formed by perforation of the vestibule, and radial grooves soon divide the vestibular roof into five interradianal valves, in each of which lies an oral plate. Between these the five groups of primary tentacles and five primary sacculi make their appearance (fig. 66). The superficial oral nervous system appears as a multilaminar ring of ectoderm, the deeper cells of which give rise to the nerve tissue. The anus, in the formation of which the ectoderm takes no part, breaks through in the posterior interradianal, in which also the primary ciliated funnel (hydropore) appears (fig. 68, *hyp.*) The chambered organ is now shut off from the aboral cœlom, and the axial organ becomes an independent strand of cells, at first solid, but subsequently hollow. The horse-shoe-shaped hydrocœl (fig. 68, *hyd. r.*) becomes completely closed and forms the circum-oral water vessel. Four new ciliated funnels and four water tubes (stone canals) make their appearance, so that there is one of each in all five interradiani. The larva now consists of a well-marked stalk, composed of from eight to ten cylindrical joints, and a more or less expanded

calyx, supported, as we have already seen, by the circlelets of basal and oral plates. The lowest joint of the stem (figs. 66, 67, and 69) assumes a discoid or lobate form, so as to afford firm attachment to the substratum upon which the larva has fixed itself, whilst the highest is also somewhat expanded as a support for the calyx. In the latter the basal and oral plates are now fully developed.

As will be seen in fig. 66, the oral plates usually stand almost erect, thus exposing the underlying oral apparatus, but they can be closed down upon it. Five pairs of tentacles make their appearance between the groups of three primary ones (fig. 68, *se. ten.*), making twenty-five in all; and whereas at first the five tentacles in each radius are connected by a common tentacle canal arising from the circum-oral water vessel, they eventually arise separately from the latter. Another circlelet of plates, the radials, now make their appearance in the spaces left between the contiguous angles of the basal and oral plates (fig. 67, 69, and 70, *rd.*). As their name implies, they are radial in position. A small asymmetrical plate, the anal, also appears between two of the radials, and on a level with them, but this undergoes resorption at a later period. The next plates to appear are the first primibrachials, which, supported by the radials, project upwards and slightly outwards between the orals (fig. 67, *pmb.* 1). These are soon followed by the second primibrachials or axillaries (*pmb.* 2), upon the distal extremities of which the first pair of secundibrachials (*sec.* 1) appear in due course. Eventually the basal plates fuse to form the rosette, which covers in the chambered organ and central capsule. By the outward growth of the arms and the consequent enlargement of the circumference of the tegmen calycis, the oral plates are left upon the oral

surface, and at a later period undergo resorption. When fully developed the larval stalk consists of about twenty joints, of which the two or three uppermost are short and disc-like (fig. 69). The first whorl of cirri, numbering five, is developed, interradi ally, upon the under surface of the uppermost joint, which ultimately fuses with the centro-dorsal. The members of the next formed whorl alternate in position with the first, and to these a third whorl is generally added before the young *Antedon* detaches itself from its stalk and becomes free. The first pinnules are formed before the larva detaches itself from its stalk, and when each of the arms consists of about twelve secundibrachial joints. A bifurcation now presents itself at the growing extremity of the arm, one ramus of which grows more rapidly than the other, and in a line continuous with that of the axis of the arm. The shorter ramus diverges at an acute angle and becomes the primary pinnule. With the exception of the second secundibrachial, upon which an oral pinnule early appears, the first formed and more proximal joints of the arm do not bear pinnules until the larva become free.

The larva is capable of considerable movement. Its stalk can be bent from side to side or thrown into a short spiral, while the arms are repeatedly extended and flexed with considerable vivacity. Detachment of the young *Antedon* from its stalk is not an accidental circumstance, resulting merely from atrophy of the upper joints of the latter. It is preceded by the appearance, at a point immediately below the centro-dorsal plate, of a narrow band of fine fibrils which run parallel to the axis of the stalk, and unite two layers of very minute cells. The plane of rupture passes between these two layers. Detachment does not take place until the cirri are sufficiently developed to enable the animal to attach itself

to surrounding objects, such as *Laminaria*, *Delesseria*, Hydroids and Polyzoa.

REGENERATION.

Antedon has long been known to possess considerable power of regeneration. The visceral mass may often be detached with great ease, and, as shown by Dendy (9), may be completely regenerated in the course of a few weeks. Specimens are occasionally found (10) only partially eviscerated, and the original visceral mass remains, more or less displaced, but with a new one developed in the normal position. Przibram (11) found that the visceral mass could be transplanted with success from one individual to another. Regeneration and transplantation cannot occur, however, in the absence of the apical nervous system. Regeneration of the arms is of very frequent occurrence, and not uncommonly results in monstrosity. Perrier (12) has fully discussed regeneration of the arms.

PARASITES.

Antedon bifida is the host of a number of parasites and commensals, of which the best known are two species of Myzostomidæ, *Myzostoma glabrum* and *M. cirriferum*. The former is found fixed in the neighbourhood of the mouth in specimens from the Mediterranean and the Adriatic, and the latter occurs in large numbers on the disc and arms of specimens from the same localities as well as from various parts of the British coasts, including the Isle of Man. A small Gastropod, *Stylina comatulicola*, is not uncommonly found attached by means of its proboscis to the anal funnel or to the cirri of specimens from the Mediterranean. Several Copepoda, including *Collocheres gracilicauda*, Brady, have been found attached to

the surface of the disc of specimens from various localities, and other Crustacean parasites have been found sunk in the tissues or inhabiting the alimentary canal. A pear-shaped holotrichous Infusorian is frequently abundant in the alimentary canal of specimens collected off the Isle of Man and in the neighbourhood of Roscoff, and a peritrichous form, *Hemispeiropsis antedonis* infests the surface of the body of Mediterranean specimens.

METHODS.

Antedon may be killed rapidly and with the arms fully extended by immersion in fresh water. Corrosive-acetic mixture is a good fixative, but the writer's best results were obtained by the use of corrosive-acetic mixture 3 vols. and 10 per cent. solution of formalin 1 vol. For sectioning, specimens which have died with the arms fully extended laterally should be selected, so that the primibrachials and proximal secundibrachials may be as nearly as possible in the same plane as the radials. After fixation, the specimens should be well washed in several changes of 70 per cent. alcohol. Decalcification may be effected by the addition of 3 per cent. of strong nitric acid to 97 e.c. of 70 per cent. alcohol; and the specimens, especially if large, should remain in this for at least twenty-four hours after bubbles of gas have ceased to escape from them. All trace of the nitric acid should then be removed by liberal washing in 70 per cent. to 90 per cent. alcohol. For staining sections the writer has used Heidenhain's iron hæm-alum method with excellent results, and methyl-blue-eosin is also good.

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DESCRIPTION OF THE PLATES.

LIST OF REFERENCE LETTERS.

- amb. ep.* = Ambulacral epithelium.
amb. gr. = Ambulacral groove.
amb. nv. = Ambulacral nerve.
an. = Anus.
an. fl. = Anal funnel.
arc. = Archenteron.
ax. cn. = Axial canal.
ax. or. = Axial organ.
ax. si. = Axial sinus.
bas. = Basal plate.
bl. lc. = Blood lacuna.
br. nv. c. = Brachial nerve cord.
cal. cl. = Caliciform cell.
cen. cap. = Central capsule.
chi. = Chiasma of radial cords.
ch. or. = Chambered organ.
ci. = Cirrus.
ci. cd. = Cirrus cord.
cil. pt. = Ciliated pit.
ci. v. = Cirrus vessel.
cl. fn. = Ciliated funnels.
cl. r. = Ciliated ring.
ent. dr. = Centro-dorsal plate.
cn. ts. = Connective tissue.
c. o. bl. r. = Circum-oral blood vessel.
cœ. ca. = Cœliac canal.
cœ. en. = Cœlomic endothelium.
cog. = Coagulum.
c. o. nv. r. = Circum-oral superficial nerve ring.
c. o. w. v. = Circum-oral water vessel.
ct. = Cuticle.
cv. p. = Covering plate.
d. o. nv. = Nerves of deeper oral system.
d. o. nv. r. = Circum-œsophageal deeper nerve ring.
dr. nv. = Dorsal nerves from brachial cord.
d. r. pn. br. = Double root of pinnular branch of brachial cord.
cct. = Ectoderm.
ep. = Epithelium.
ex. ch. or. = Extension of chambered organ.
ex. lig. = Extensor ligaments.
flx. m. = Flexor muscles.
gen. bl. lc. = Genital blood lacuna.
gen. ra. = Genital rachis.
hyd. = Hydrocœl.
hyd. r. = Hydrocœl ring.
hyp. = Hydropore.
i. m. f. = Isolated muscular fibres.
int. = Intestine.
int. ep. = Intestinal epithelium.
int. lig. = Interarticular ligaments.
jt. pn. = Calcareous joint of pinnule.
jt. sk. = Calcareous stalk joint.
l. cœ. = Left cœlom.
l. m. f. = Longitudinal muscular fibres.
lt. nv. c. = Lateral cord of deeper oral nervous system.
me. hy. vs. = Mesentero-hydrocœl vesicle.
mes. = Mesenchyme.
mth. = Mouth.
nv. l. = Nerve layer.
or. = Oral plate.
or. pn. = Oral pinnule.

<i>or. tn.</i> = Oral tentacle.	<i>sec. 1.</i> = First secundibrachial.
<i>ov.</i> = Ova.	<i>s. te. ca.</i> = Sub-tentacular canal.
<i>ovr.</i> = Ovary.	<i>sc. ten.</i> = Secondary tentacle.
<i>pd.</i> = Pedal plate.	<i>sn. pp.</i> = Sensory papilla.
<i>pmb. 1.</i> = First primibrachial.	<i>s. n. s.</i> = Sub-neural sinus.
<i>pmb. 2.</i> = Second primibrachial.	<i>sph. fb.</i> = Fibres of sphincter
<i>pn.</i> = Pinnule.	muscle in transverse section.
<i>pnt. com.</i> = Pentagonal com-	<i>sp. or.</i> = Spongy organ.
missure.	<i>st.</i> = Stomach of larva.
<i>pr. ten.</i> = Primary tentacles.	<i>syz.</i> = Syzygy.
<i>r. cæ.</i> = Right cœlom.	<i>ten.</i> = Tentacle.
<i>rad. nv.</i> = Radial cords of apical	<i>tes.</i> = Testis.
nervous system.	<i>ty. cl.</i> = Tegmen calycis.
<i>rd.</i> = Radial plate.	<i>tn. vs.</i> = Tentacular vessel.
<i>ros.</i> = Rosette plate.	<i>tr. com.</i> = Transverse commissure
<i>ru. hy.</i> = Rudiment of hydrocœl.	of radial cords.
<i>r. w. v.</i> = Radial water vessel.	<i>v. f.</i> = Valvular fold.
<i>sac.</i> = Sacculus.	<i>vn. nv.</i> = Ventral nerves from
<i>sb. e. nv. f.</i> = Sub-epithelial nerve	brachial cord.
fibres.	<i>w. t.</i> = Water tube.

PLATE I.

- Fig. 1. *Antedon bifida*, showing the attitude assumed by the animal when at rest. Natural size.
- Fig. 2. *Antedon bifida*, showing the disposition of the arms in swimming. Natural size.
- Fig. 3. *Antedon bifida*, viewed from the aboral surface. The cirri were removed from two-thirds of the periphery of the centro-dorsal to show the bases of the arms. $\times 5$.
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- Fig. 5. Abaxial (outer) face of a radial plate. $\times 8$.
- Fig. 6. Lateral face of a radial plate. $\times 8$.
- Fig. 7. Oral face of a radial plate. $\times 8$.
- Fig. 8. Axial face of a first primibrachial. $\times 8$.

- Fig. 9. Abaxial face of a first primibrachial. $\times 8$.
 Fig. 10. Lateral face of a second primibrachial axillary). $\times 8$.
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 Fig. 13. Proximal face of a secundibrachial joint from the base of an arm. $\times 8$.
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PLATE II.

- Fig. 22. Portion of a vertical section of the tegmen calycis, showing two ciliated funnels. $\times 320$.
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- Fig. 25. Longitudinal section of the lower portion of the œsophagus. $\times 320$.
 Fig. 26. Section of the ectoderm of the dorsal face of an arm. $\times 400$.
 Fig. 27. Portion of a longitudinal section of the anal funnel. $\times 320$.
 Fig. 28. The central portion of fig. 24. $\times 12$.

PLATE III.

- Fig. 29. Transverse section of an arm. $\times 40$.
 Fig. 30. A pinnular tentacle, in optical section. $\times 300$.
 Fig. 31. Transverse section of pinnular tentacle. $\times 300$.
 Fig. 32. An oral pinnule. $\times 12$.
 Fig. 33. An ordinary pinnule, with ovary containing nearly ripe eggs. $\times 25$.
 Fig. 34. Distal end of a pinnule from the distal end of an arm. $\times 177$.
 Fig. 35. Fibres of extensor ligaments. $\times 400$.
 Fig. 36. Fibres of flexor muscle. $\times 400$.
 Fig. 37. Portion of longitudinal section of a pinnule, showing three ciliated pits. $\times 320$.
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PLATE IV.

- Fig. 41. Ventral portion of a transverse section of an arm. $\times 110$.
 Fig. 42. Transverse section of ambulacral epithelium and the sub-epithelial nerve band. $\times 650$.

- Fig. 43. Longitudinal section of ambulacral epithelium and the sub-epithelial nerve band. $\times 650$.
- Fig. 44. Portions of two transverse sections of the axial organ. $\times 320$.
- Fig. 45. Transverse sections of a group of tubular blood lacunæ. $\times 180$.
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PLATE V.

- Fig. 48. Side view of central capsule and pentagonal commissure of the apical nervous system, reconstructed from serial sections. $\times 20$.
- Fig. 49. Aboral view of central capsule and pentagonal commissure of the apical nervous system, reconstructed from serial sections. $\times 20$.
The cirrus cords are not represented in this figure.
- Fig. 50. Sagittal section of an arm. $\times 40$. The structures on the ventral side of the cœliac canal are not represented.
- Fig. 51. The "spongy organ," as seen in a horizontal section of the disc. $\times 122$.
- Fig. 52. Diagram of a sagittal section of the disc, partly after Ludwig.

PLATE VI.

- Fig. 53. Horizontal section of a radial nerve cord at the point of bifurcation to form the brachial cords, showing the commissure and chiasma. $\times 55$.
- Fig. 54. Horizontal section of the central capsule and the chambered organ, at about the level of the line * in fig. 59. $\times 40$.

- Fig. 55. Horizontal section of the central capsule and the chambered organ, at about the level of the line *** in fig. 59. $\times 40$.
- Fig. 56. Horizontal section of the pentagonal commissure, at about the level of the line † in fig. 59. $\times 40$.
- Fig. 57. Horizontal section of the central capsule and the chambered organ, at about the level of the line ** in fig. 59. $\times 40$.
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PLATE VII.

- Fig. 61. Horizontal longitudinal section of a pinnule, with a ripe testis showing the lateral papilliform projection through which the spermatozoa would eventually escape. $\times 56$.
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- Fig. 63. Horizontal longitudinal section of an embryo, fifty-seven hours old. After Seeliger, from Lang.
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- Fig. 67. An older attached larva, showing the radial plates interposed between the basals and orals, and supporting the two primibrachials in each of the radii. $\times 40$.
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- Fig. 71. Portion of one of the arms of the specimen represented in fig. 70, showing the "covering" plates.



Fig. 1. Nat. Size

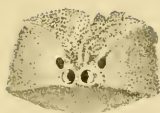


Fig. 4. x 8

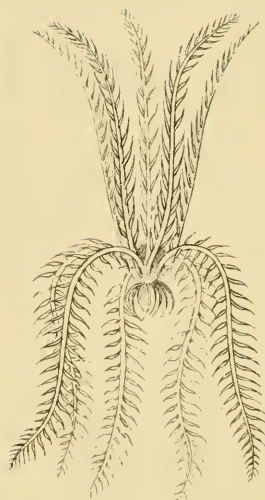


Fig. 2. Nat. Size

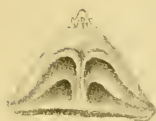


Fig. 7. x 8



Fig. 8. x 8



Fig. 5. x 8



Fig. 6. x 8



Fig. 9. x 8



Fig. 10. x 8



Fig. 11. x 8

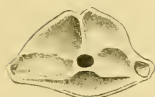


Fig. 12. x 8

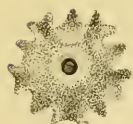


Fig. 17. x 12



Fig. 18. x 12



Fig. 14. x 8



Fig. 15. x 8



Fig. 13. x 8



Fig. 16. x 8

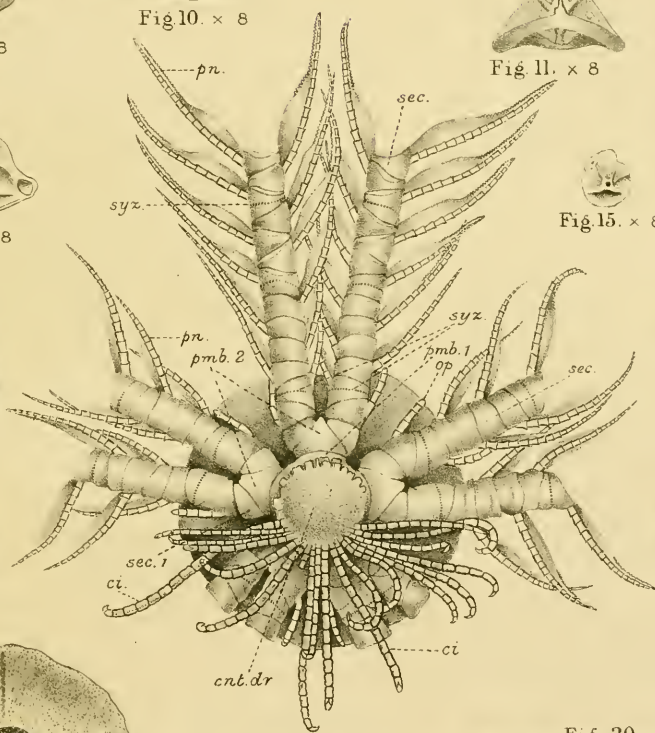


Fig. 3. x 5



Fig. 21.

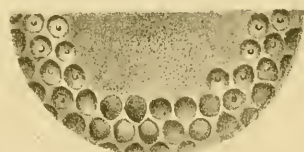


Fig. 20. x 10

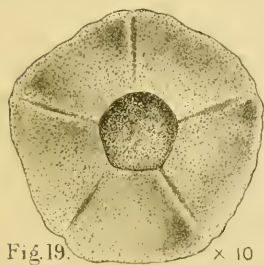


Fig. 19. x 10

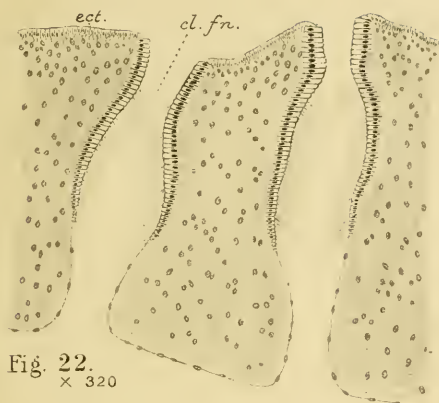


Fig. 22.
x 320

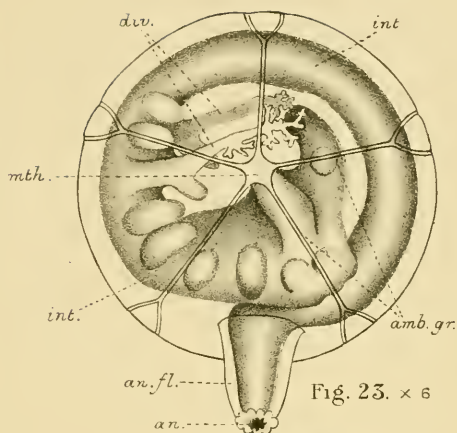


Fig. 23. x 6

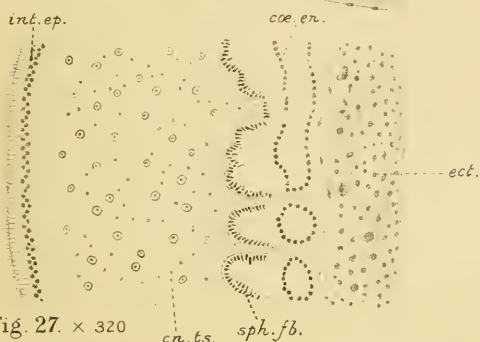


Fig. 27. x 320

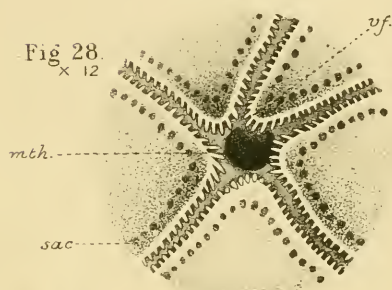


Fig. 28.
x 12

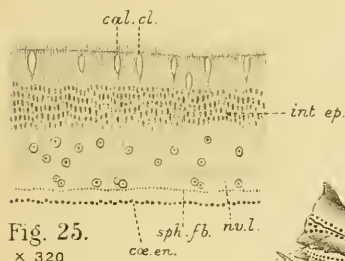


Fig. 25.
x 320

amb. gr.

Fig. 24.
x 6

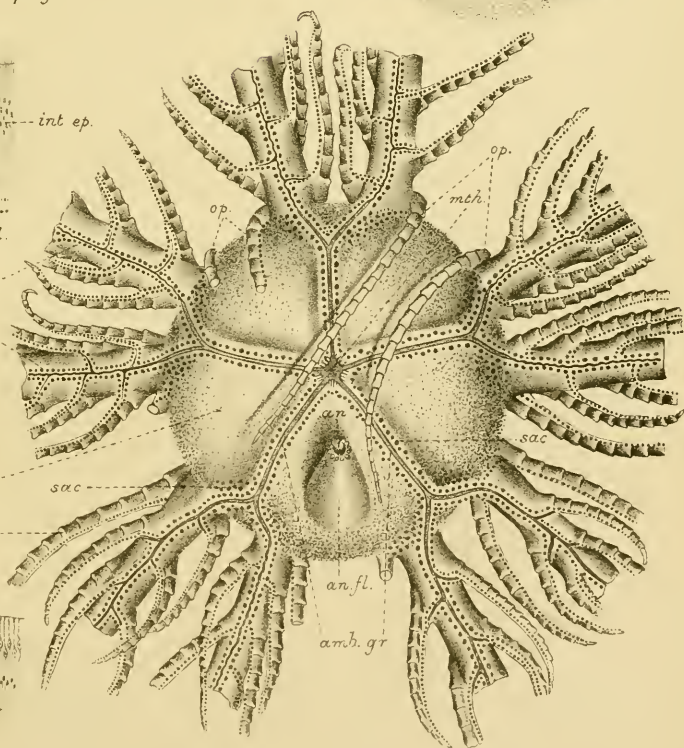
tg. cl.

sac.

op.

Fig. 26.
x 400

cl.



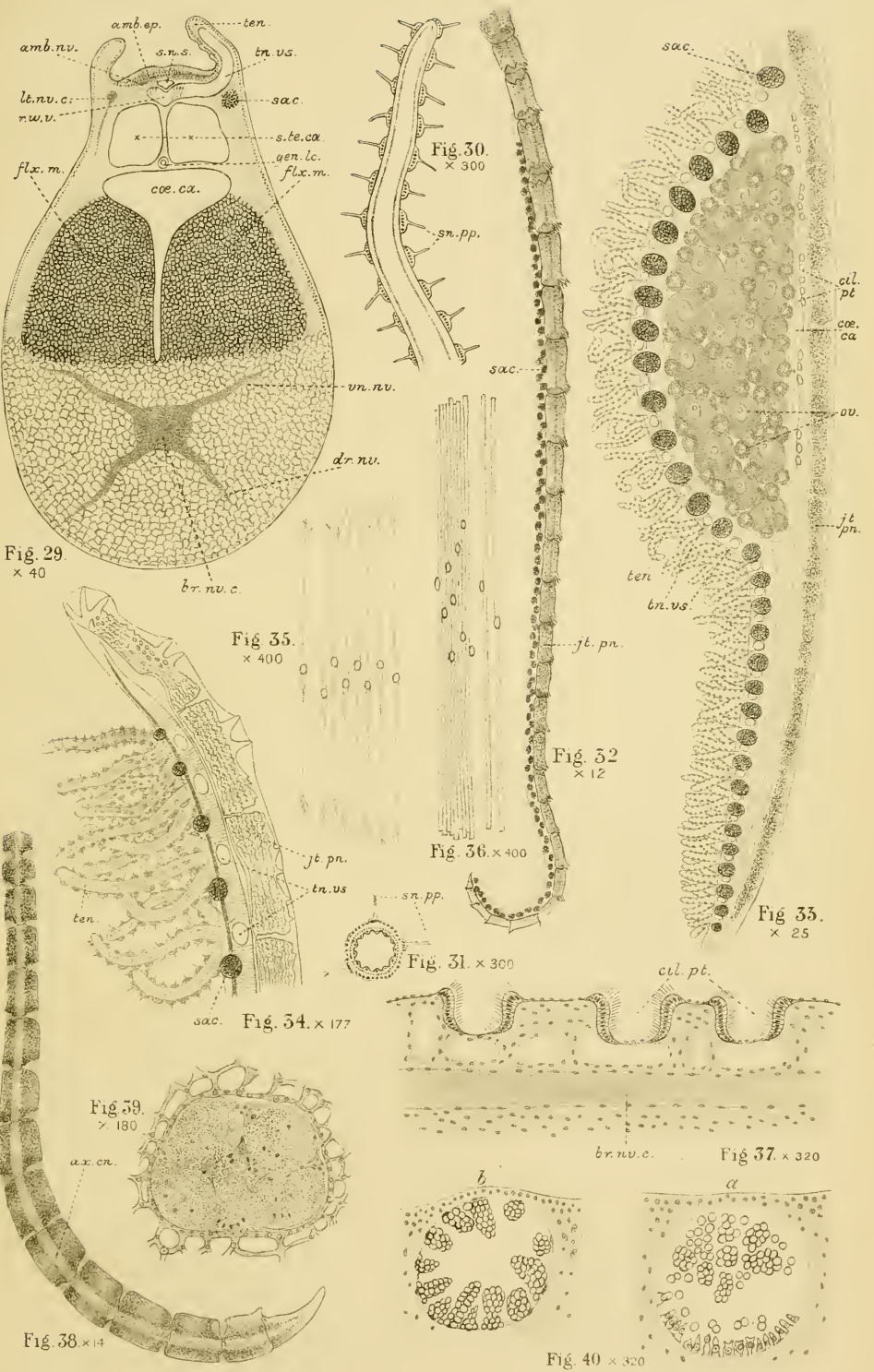


Fig. 47. $\times 180$

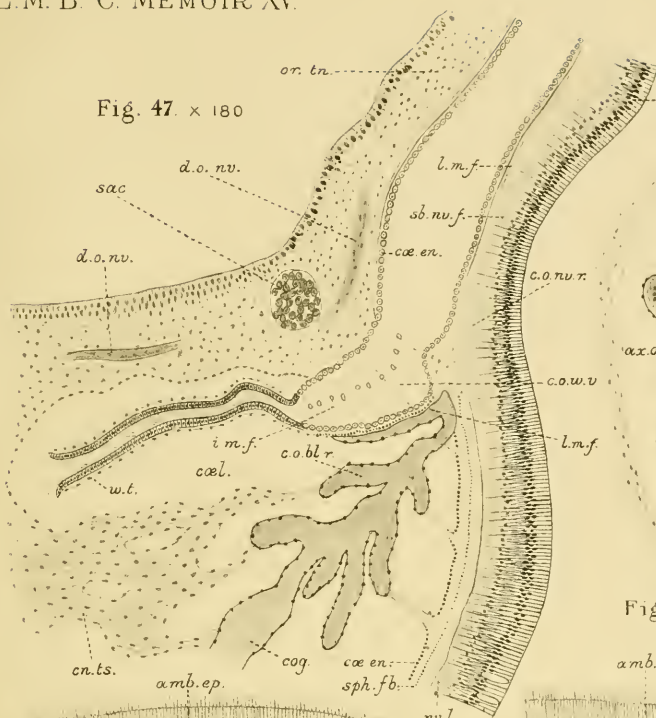


Fig. 46.
 $\times 180$

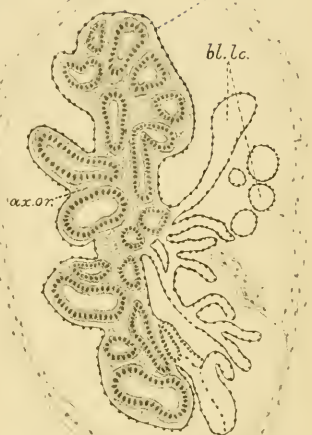


Fig. 43. $\times 650$

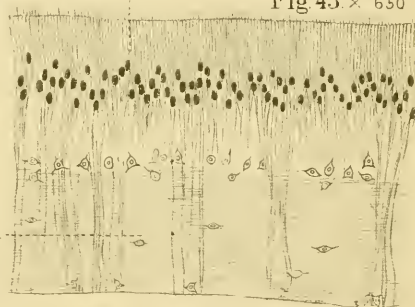


Fig. 42.
 $\times 650$

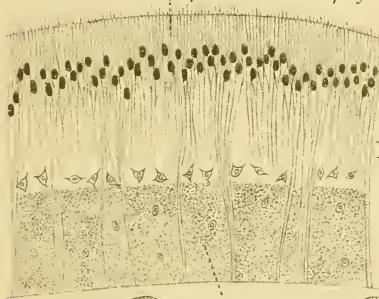


Fig. 41.
 $\times 110$

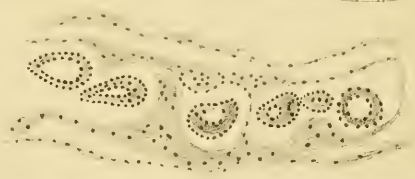
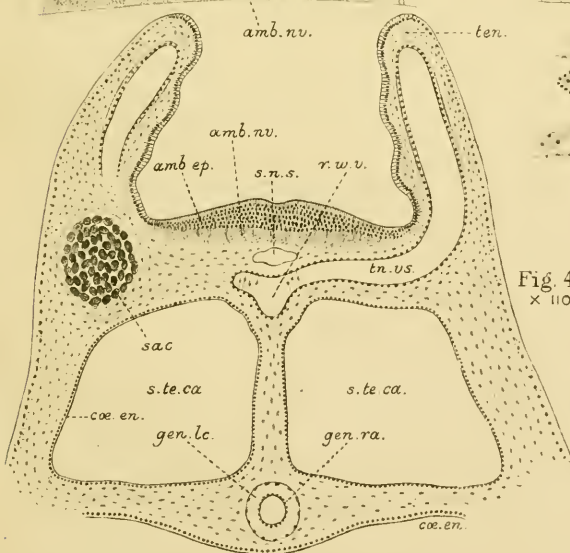


Fig. 45. $\times 180$



Fig. 44. $\times 320$



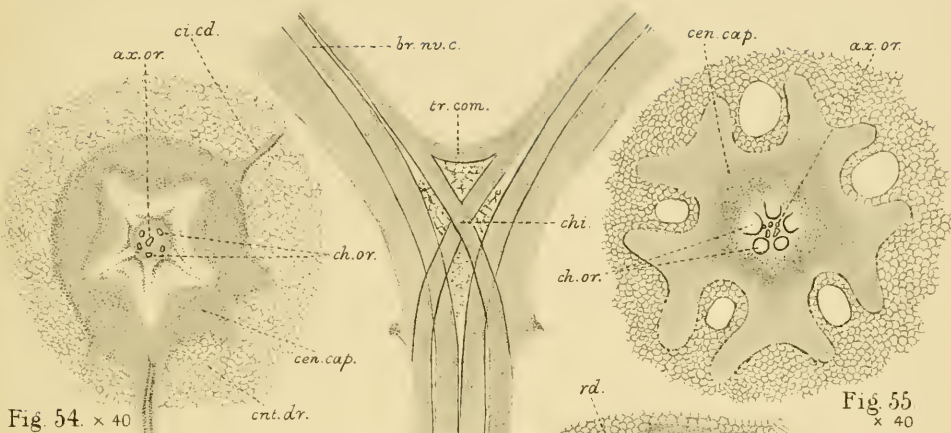


Fig. 53. $\times 55$

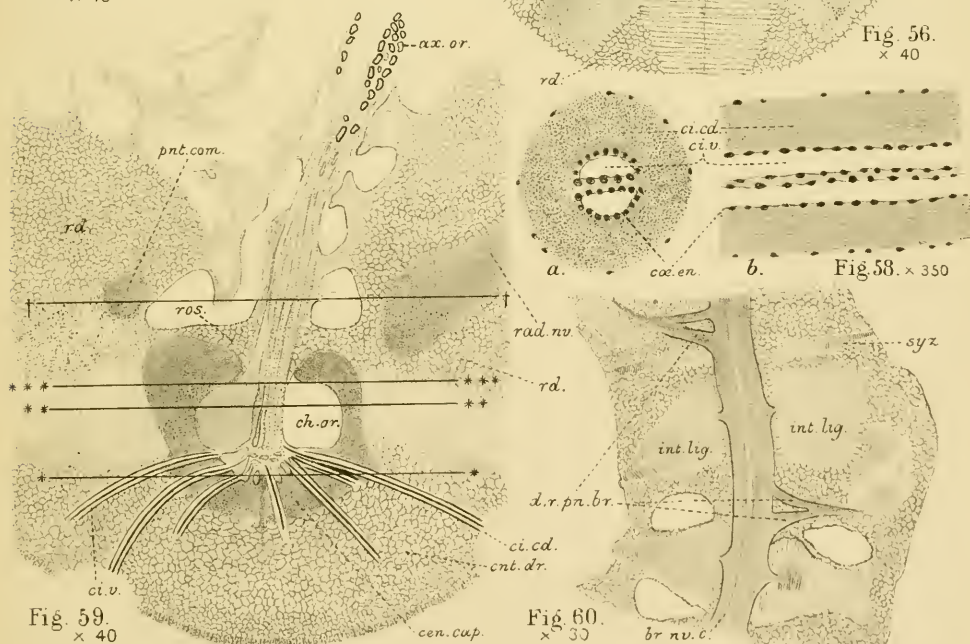
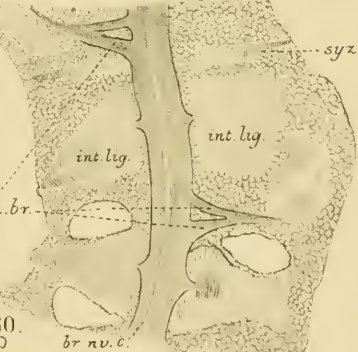
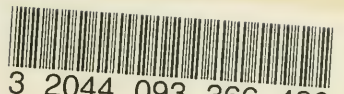


Fig. 60. $\times 30$





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