

THE INTERNAL ANATOMY OF *BATHYNOMUS GIGANTEUS*, WITH A DESCRIPTION OF THE SEXUALLY MATURE FORMS.

By R. E. LLOYD, M.B., B.Sc., Captain, I.M.S., formerly Surgeon Naturalist,
Marine Survey of India.

INTRODUCTION.

In the year 1878 the naturalists of the U. S. Survey Ship "Blake" obtained the first example of *Bathynomus giganteus*. This specimen, an immature male measuring 23 cms. in length and 10 cms. in breadth, was taken from 955 fathoms in the Carribean Sea. In the following year Milne Edwards (1) published a short account of it and defined the genus. It was not until 1902, however, that a full description of the external characters was published by Milne Edwards and Bouvier, in an admirable monograph (2). In the preparation of this work, the authors had at their disposal the original "Blake" specimen, and two examples of a new species, *B. döderleini*, from an unrecorded depth in Sagami Bay on the coast of Japan. The authors also refer to the capture of three immature female specimens, in the Laccadive Sea off the West Coast of India (3). The monograph contains a full historical summary on the subject of *Bathynomus*, in light of which further introductory remarks are superfluous.

The present memoir treats of *Bathynomus* chiefly in regard to features other than those described by M. Bouvier. The subject will be treated under the following headings:—

1. A description of the internal anatomy of the genus.
2. A description of the external characters of the sexually mature egg-bearing female and of the mature male.
3. On certain differences between the Indian and American forms of *Bathynomus*.
4. The occurrence and distribution of the species in Indian seas.
5. A few notes on the natural history of the genus.

I.—THE INTERNAL ANATOMY.

PRELIMINARY.

During the last two years, the R.I.M. Survey Ship "Investigator" has obtained four more specimens of *Bathynomus giganteus* from three widely separate stations;

so that, although these animals are very desirable as museum acquisitions, it seemed well to spare one of them for dissection. In anticipation of this, one specimen was treated in the following way: After making numerous small slits in the soft cuticle between the segments, and puncturing the eyes, the animal was deposited in 2 per cent. formalin solution for 48 hours; from this it was transferred to strong spirit. The dissection was performed six months later, when the tissues were found to be in such good condition that even histological detail could be made out with some satisfaction.

The example dissected was an immature female measuring 193 mm. in length and 89 mm. in breadth, to which standard all measurements of internal organs may be referred. The description is unfortunately incomplete. Before describing the internal organs of any animal, the dissector should examine several specimens. Doubtful points arise in a first dissection, which ought to be confirmed by subsequent examination of other specimens. Only those points which were clearly observed have been described here; the doubtful points have been left as gaps in the description. Besides this, certain special difficulties were met with in this case. On opening the carapace mid-dorsally, the most noticeable feature was a mass of eggs. These eggs were nearly of the mature size (scarcely less than 1 cm. in diameter); they did not seem to form part of well-defined ovaries, but lay above and between the other organs, being shaped irregularly to suit their surroundings. They were of a resinous colour, somewhat translucent and very hard, and were imbedded in a white, fatty material. This condition was probably brought about by the bursting of the limiting membrane of the ovaries, at the time when the animal was removed from the pressure of its native depths. Whatever the cause, yolk material of resinous appearance was found, even below the intestine and between the lobes of the hepatopancreas, and caused considerable trouble in elucidating the anatomy.

Let us pass, now, to a consideration of the previous work done on the internal anatomy of Isopods. Among the group several types have been described in this respect. The internal anatomy of land genera, such as *Armadillidium*, *Oniscus*, *Porcellio* and *Ligia* has been amply described by Lereboullet and other observers (4—9). *Asellus* has been fully treated by Sars and others (10, 11). Several of the smaller marine genera have been investigated (12, 13). These descriptions show that the different genera of smaller Isopods are, on the whole, similar in their soft parts. As to its internal anatomy, *Bathynomus* is found to differ from those genera in several important respects. Unfortunately, I have not been able to find descriptions of the internal organs of the *Cirolanidæ*, which might be expected to resemble *Bathynomus* more closely.

It would seem, however, that, merely owing to its size, *Bathynomus* must be different in certain respects from all smaller members of the group. Thus, consider for a moment, the structure of the hepatopancreas. In a small Isopod such as *Asellus*, this organ consists of two pairs of tubules extending almost the whole length of the intestine, and occupying to a great extent the space between that

organ and the body wall. These tubes are composed of few but large cells arranged in one layer. In *Asellus* there are only about ten rows of cells, in *Porcellio* there are not more than twelve. If this plan of organisation, which is shown in text-fig. 1,

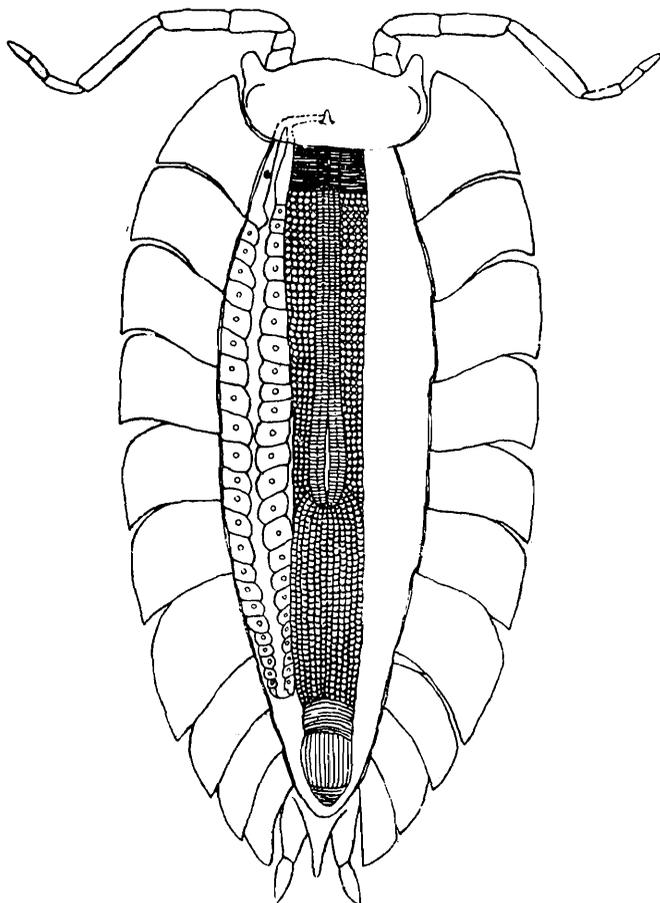


FIG. 1.

were to be exactly reproduced in an Isopod of 20 cms. in length, the individual cells of the tubules would be at least 5 mm. in length. We should not expect to find this. If, on the other hand, the cells of the tubules were increased in number but not in size, the lumen of the tubule would be of disproportionate dimensions. Such a cavernous organ could not well perform either of the functions of a hepatopancreas. We should expect, therefore, in *Bathynomus*, either that the tubules would be very largely increased in number, or that they would be replaced by compound glands of a racemose nature.

THE ALIMENTARY SYSTEM.

The alimentary canal, as in other Isopods, can be at once divided into three divisions,—the fore gut, mid gut, and hind gut. But whereas in the small Isopods the hind gut is of insignificant length and the mid gut composes at least three quar-

ters of the whole canal, in *Bathynomus* the length of the hind gut is greater than that of the fore and mid gut together. It will be seen later on that there is some doubt as to whether the three divisions of the gut are homologous in both cases.

The fore gut (pharynx).

In describing the buccal orifice, M. Bouvier mentions its cleft-like character and describes two projecting processes at the anterior and posterior ends of this aperture. The anterior of these is much the larger, but internal examination shows that it is continued into the roof of the pharynx for a short distance only, whereas the smaller posterior one becomes more prominent as it ascends into the pharynx. In a transverse section of the middle of the pharynx, this ridge is the only prominent feature; it comes to an end in the gizzard. The pharynx lies in a position half-way between the vertical and the horizontal. Its length is about 10 mm. In transverse section it measures 6 mm. in the longitudinal axis, 4 mm. in the transverse. It is lined

by a tough cuticle of a dark brown colour, which is folded in a somewhat irregular manner; the only definite fold being the trenchant ridge on the posterior or ventral side.

Fore gut (gizzard).

This is a complex organ, and although at first sight it seems to differ considerably from the same structure in the small Isopods, consideration shows that the component parts are homologous in the two cases. The gizzard is sharply marked off from both pharynx and mid gut. In form, it is an elongated, polygonal solid, measuring 19 mm. in length and 9 mm. in breadth. It lies almost entirely within the head. In the natural position, the posterior third of the gizzard cannot be seen from above, since the anterior end of the mid gut protrudes over it as a blind pouch. Below it rests on a skeletal plate, part of the internal skeleton of the head which will be described later on. The outward form of the gizzard is shown in figures 5 and 7, pl. xi. From whatever side the organ is examined, its wall exhibits deep grooves or furrows: these are the outward expressions of certain involutions of the gizzard wall, which have become thrust into the cavity.

On opening the gizzard, these involutions are seen to have almost abolished the cavity, which is reduced to a number of small crevices between them. The form and position of these involutions is best studied by examining the interior of the organ, after it has been divided by a longitudinal section in the middle line. Figure 8 shows the appearance of the inner surface of one half of the organ, after such a division. The most prominent features are two large ampullæ situated one in front of the other (*a.a.*, *p.a.*); the anterior of these is the smaller, but seems to be functionally the more important, as most of its outer or concave side gives attachment to a large muscle; whereas the larger and posterior one is an empty cavity (fig. 6), in the dead specimen, being lined merely by a thin layer of white fatty material.

In its posterior third, the roof of the gizzard is involuted along two oblique converging lines, the results of which are seen internally as two long, smooth processes, *u.v.p.*, projecting downwards and backwards, one on either side of the median plane and almost in contact with one another. The principal part of the opening from the gizzard to the mid gut lies between these two processes. They appear to have a valvular function, to prevent regurgitation from the mid gut. They contain a basis of fatty material and are covered with a smooth, thick cuticle. They are 7 mm. in length and have acutely pointed ends.

The floor of the gizzard also exhibits some important structures. In its posterior third, on either side of the middle line, is an elevated ridge with a falciform and trenchant margin; this is shaped posteriorly so as to act as a lower valvular process, *l.v.p.* In about the middle third of the floor of the gizzard is another somewhat similar pair of ridges; these are distinct from the others but overlap them slightly. They are very hard, especially on their median surfaces, which are in contact. The cuticle of these surfaces is yellow and shining in contrast with the rest of the lining of the organ, which is greyish white.

Besides these features there is, in the floor of the gizzard, a third pair of structures of greater importance; for they are the only part of the organ which shows a surface designed for the attrition of food. These are a pair of low ridges set transversely in the floor of the gizzard, at the junction of the anterior and middle thirds of its length. They lie beneath and in contact with, the anterior or muscular ampullæ, and are somewhat curved in accordance with the shape of those structures. These transverse ridges are the only structures in the gizzard which can properly receive the name of ossicles; they are covered with shining, yellow cuticle. The edge of either ridge is slightly and irregularly lobulated (fig. 6). The cuticle of the lower part of the muscular ampullæ, where in contact with these transverse ridges, is somewhat thickened and is of a dark colour. Food material is evidently subjected to a grinding process as it passes between these contiguous surfaces.

The mid gut.

The mid gut is plainly differentiated from the gizzard and from the hind gut, both by its outward form and by the structure of its walls. It is 55 mm. in length, and 15 mm. in breadth in the middle, where it is circular in cross section. It commences in front within the head, where it projects in pouch-like form over the hinder part of the gizzard: posteriorly it extends as far as the upper border of the fifth thoracic segment, at which level it opens into the hind gut. The opening of the mid gut into the hind gut is remarkable. In its general form the mid gut is spindle-shaped, for its diameter gradually becomes less posteriorly. In the last centimetre of its length it has the form of a slim cylindrical process, which is thrust into the hind gut, in precisely the same way as the cervix of a mammalian uterus is thrust into the vagina. The wall of the hind gut is so thin, that this process can be seen dimly outlined within the cavity of the hind gut, before that organ is opened (pl. x, fig. 1). A median section through the length of both mid gut and hind gut shows that the cavity of the mid gut is present though small in the anterior half of this cervix-like process, but is merely potential in the posterior half. Furthermore, the change from the open cavity to the potential one is sudden, and is accompanied by a complete change in the character of the epithelium (fig. 2).

The mid gut differs from both fore and hind gut in the much greater thickness of its walls, which is more than a millimetre. At least four-fifths of the thickness of the wall is composed of the internal epithelium, which is rugose and contorted to a remarkable extent. Examination of this corrugated epithelium shows that it is composed of ridges and furrows, which although very tortuous are in the main set longitudinally. Moreover, the summits of these ridges are crossed by lesser transverse grooves, dividing them irregularly into papillæ. In some parts of the organ the longitudinal arrangement is very plain, while in others the papillæ are more in evidence. The organ is not provided with a typhlosole.

The hind gut.

This is the longest division of the alimentary canal, its length being in all 90 mm. It extends from the upper part of the fourth thoracic segment to the anus,

which is situated on the lower surface of the telson close to its junction with the last abdominal segment. With the exception of the last fifteen millimetres of its length, the hind gut of the specimen examined was flattened horizontally to such an extent, that its upper and lower walls were in close contact throughout, and the lumen in transverse section appeared as a horizontal line. The breadth of this flattened organ was about 20 mm. in the anterior half, but it gradually became less behind. Near the telson it becomes much narrower; and about 15 millimetres from the anus the horizontal position of the linear lumen becomes vertical. Anteriorly, the wall of the hind gut is very thin and its mucous membrane is thrown into delicate folds arranged in a reticular manner: it becomes thicker behind, owing mainly to an increase in the longitudinal muscle fibres. Near the anus, where the lumen is vertical, it is lined by thick, smooth, yellow cuticle, the opposing surfaces of which are in close contact, so as to retain the intestinal contents.

Hepatopancreas.

In *Bathynomus* this organ is quite different from that of other Isopods, so far as they are known. It consists of three pairs of elongated glandular organs (pl. x, fig. 1) or six separate lobes, each of a simple racemose type. In the spirit specimen, they can be distinguished at once from the other contents of the thorax by their reddish brown colour. The six lobes are situated alongside of the mid gut. They are of about the same size; each, measuring 40 mm. in length and 7 mm. in thickness, extends from the posterior part of the first segment to the lower border of the third. The outer surface of each lobe is covered with small granulations, the outward expressions of the short tubules of which the organ is composed. From near the anterior end of the highest pair, small ducts are given off which open into the mid gut close to its union with the gizzard. The lowest pair lie wholly beneath the mid gut in close contact with one another, and are therefore not shown in the figure. The ducts of the middle and lower lobes were not traced, owing to difficulties arising from the presence of yoke material. They probably open by separate ducts into the mid gut, in the same way as the ducts of the highest pair of lobes.

The salivary glands.

Situated on either side of the pharynx are two small bodies of soft, friable consistency. On microscopical examination these bodies are seen to be racemose glands. When examined in section, they show at first sight a remarkable resemblance to the salivary gland or pancreas of a vertebrate animal. These organs, which are shown in pl. xi, fig. 2, measure about 4 mm. in length and 2 mm. in breadth. Beneath them is the cuticle, between the mouth and the base of the mandible: in front, they are in contact with a dilator muscle of the pharynx *d.p.*: internally, they touch the side wall of the pharynx at its lowest part. The duct or ducts of these organs were not traced; though it may be stated, that in all probability they do not open into the pharynx, for the following reason: Before the gland of one side was dissected it was gently separated from the pharynx, while light was transmitted through the cuticle from

below. This examination, which gave a negative result, must have disclosed any small duct passing between the gland and the pharynx, if existent. The opening of these glands is probably among folds of the cuticle on either side of the mouth. The general appearance of a section of one of these organs is shown in the photograph (pl. xii, fig. 6). The lumen of the tubules composing the organ is lined by a delicate chitinous intima. Salivary glands have been previously described in Isopods (7, 18).

Homologies of the alimentary system.

Although, at first sight, the gizzard of *Bathynomus* appears considerably different from those of the smaller Isopods, consideration shows that this difference is more apparent than real. A conspicuous feature of the gizzard of such genera as *Asellus* and *Armadillidium* is a pair of large ampullæ, which project into the cavity of the organ in its anterior part. The ampullæ of the gizzard of *Asellus* seem to be homologous with the anterior ampullæ in *Bathynomus*, for in both cases the principal muscle of the gizzard is attached to the concave side of these structures. The posterior or large ampullæ of *Bathynomus* are not represented in the smaller genera. The principal pair of ossicles in the gizzard of *Asellus* lie in the fore part of the floor of that structure and together form a V-shaped figure. These seem to be represented in *Bathynomus* by the transverse ossicles, which lie, one on either side, beneath the muscular ampullæ. The transition from the arrangement of these structures in *Asellus* to that in *Bathynomus*, by the widening out of the limbs of the V until they are both in one transverse line, is easy to imagine.

In the case of the mid gut and hind gut, the homologies between *Bathynomus* and its smaller allies are less clear. As shown in text-fig. 1, which is copied from Murlin (8), the mid gut of *Oniscus* is relatively of great length, comprising by far the greater part of the whole alimentary canal. This condition is also found in *Asellus* and other small Isopods so far as they are known. In *Bathynomus* the relative size of the divisions of the alimentary canal contrasts with this, for in this genus the hind gut is greater than the combined length of the first two divisions. As shown in the text-figure, the extensive mid gut of *Oniscus* is not of the same structure throughout its whole length. There is a typhlosole in its anterior part. Posterior to this the mid gut shows a curious arrangement of its cells, described by Murlin in the following words:—

“Another striking feature of the epithelium (of the mid gut) is the rectangular arrangement of the cells in longitudinal and transverse rows. One exception occurs at the posterior end of the typhlosole, at which point the longitudinal rows converge, so as to form, as Schönichen says, ‘parallel parabolas, making a picture in optical section not unlike a longitudinal section through a vegetative point’ ” (see text-fig. 1). Again, in speaking of the muscular coat of the mid gut, he says, “The muscular coat has been fully described by Ide and Schönichen. It consists of two layers, an outer longitudinal and an inner circular. Over the anterior portion of the mid gut (*i.e.*, as far back as the typhlosole extends) the outer is imposed upon the inner; posterior to this both layers thin out so that the fibres are quite widely

separated from one another, each one running in the groove between adjacent rows of cells."

Thus we see that in *Oniscus* there is a considerable difference between the anterior and posterior parts of the mid gut. This differentiation of the mid gut into two parts, and the parabolic arrangement of the cells in the posterior half, may be regarded as foreshadowing the organisation of the intestine in *Bathynomus*. In other words, it is probable that the organs herein described as the mid and hind gut of *Bathynomus*, which are completely different in the structure of their walls and are as separate from one another, both in degree and kind of separation, as the uterus and vagina of a mammal are separate, are together homologous with the extensive mid gut of the smaller Isopods; for we can see at least in some small Isopods such as *Oniscus* a distinct indication of division of the mid gut into two parts.

Minute Structure of the Hepatopancreas.

In the structure of this organ the genus differs remarkably from all other Isopods so far as they are known. As previously mentioned, this difference in the structure of the organ seems to be a necessary result of the large size of its possessor.

A transverse section of one of the six lobes shows that it is composed of a number of short tubules, radiating from the central axis of the organ. Some of these tubules are simple, and lie in a straight line between the centre and periphery of the organ, others branch dichotomously and are somewhat contorted. Figure 1 (pl. xii), which is a photograph of a thick unstained section cleared and mounted in balsam, shows the character of these tubules. On referring to this figure it will be seen that the separate tubules are clearly defined by a blotched, wavy, dark line, which is due to the presence of certain peculiar contents of the cells composing the tubules. In proximity to the nucleus of each cell are numerous yellow granules, which in the aggregate form a dark brown mass. The united presence of these granules has marked out the limits of the tubules; while the protoplasm and nuclei, being unstained, have been rendered almost invisible by the medium in which the section is mounted. Figures 1 and 3 show clearly that the hepatopancreas of *Bathynomus* is a racemose gland of primitive type.

Figure 2 is a photograph of a thin stained section, cut transversely through a single component tubule. It is not unlike a transverse section of one of the four simple unbranched tubes which compose the hepatopancreas of a small Isopod. It is composed of about twenty rows of large conical cells the apices of which protrude into the lumen. Towards the base of each cell is a large oval nucleus measuring as much as .05 mm. Grouped round this nucleus is a mass of coarse granules, which take the stain with such avidity that they appear almost black in sections stained with hæmatoxylin. These are the granules which, unstained, have a yellowish brown colour. Towards the apex of the cells the protoplasm shows large circular vacuoles, from which their contents have been dissolved. In the reticulum between the vacuoles fine granules can be seen.

Perhaps owing to the large size of its constituent cells the hepatopancreas of the

smaller Isopods has attracted the attention of several histologists (7, 8, 14-17). All agree that two kinds of cells are apparent in the walls of these tubular organs, a large sort which projects into the lumen and a small sort which does not; but the majority of observers hold that the smaller kind is merely the young stage of the larger. The smaller cells, when examined in the fresh condition, always show a dense mass of spherical yellow granules surrounding the nuclei. These granules are generally spoken of as zymogen: in some circumstances and in a somewhat capricious manner they readily take up stain. Their behaviour to reagents is given in detail by Murlin. There can be little doubt that the granules, which are shown aggregated in figure 1, more detailed in figure 2, are of a similar nature.

Examination of the hepatopancreas of *Bathynomus* therefore shows, that whereas the gross structure of this racemose organ is quite different from that of the simple tubular glands of smaller Isopods, there is a close similarity in cell detail between the two. In another respect there is a similarity and a difference. The hepatopancreas of *Bathynomus* has, deep in its substance, well-developed strands of muscle fibres; these strands lie between the radial tubules; they must be homologous with the bands of muscle fibres, present in the smaller Isopods, which take a spiral course and give to the organ its characteristic twist.

Minute Structure of the Alimentary Canal.

The text-figs. 2—4 represent sections of the several parts of the alimentary canal. Each of them was drawn, magnified to the same degree, by means of the camera lucida; hence the proportional thickness of the organs is accurately shown in the figures.

The wall of the gizzard is only about .15 mm. in thickness throughout most of its extent; more than half of the thickness is due to an outer layer of fibrous material, which does not stain readily, and closely resembles in its histological detail the cornea of a mammal. The inner part of the wall is composed of an epithelial layer in which round nuclei, situated at regular intervals but not separated by cell outlines, are a conspicuous feature. This endothelial layer supports a cuticular "intima" which varies much in thickness throughout the gizzard. Between the outermost layer and the endothelium is a narrow, fibrous-looking layer which stains deeply, the exact histological character of which was not understood; it is separated from the epithelium by a narrow homogeneous layer which appears to be a "basement membrane" for the endothelium.

The structure of the mid gut is now to be considered. As mentioned before, the endothelium is relatively of great thickness and is convoluted to a remarkable extent. The convolutions take the form of alternate ridges and furrows, the axes of which are somewhat irregular in position, but are, on the whole, set longitudinally. The whole thickness of the wall is about 1 millimetre: about $\frac{9}{10}$ ths of this is composed of the endothelium, while the remaining $\frac{1}{10}$ th is made up of a few inner circular and outer longitudinal muscle-fibres. The fissures between the ridges extend nearly as far as the muscular layer. Each ridge is composed of a thick outer layer of

translucent cuticle which plainly shows parallel lines of growth. The inner part of each ridge is composed of two layers of large nucleated cells between which capillary blood vessels are often to be seen.

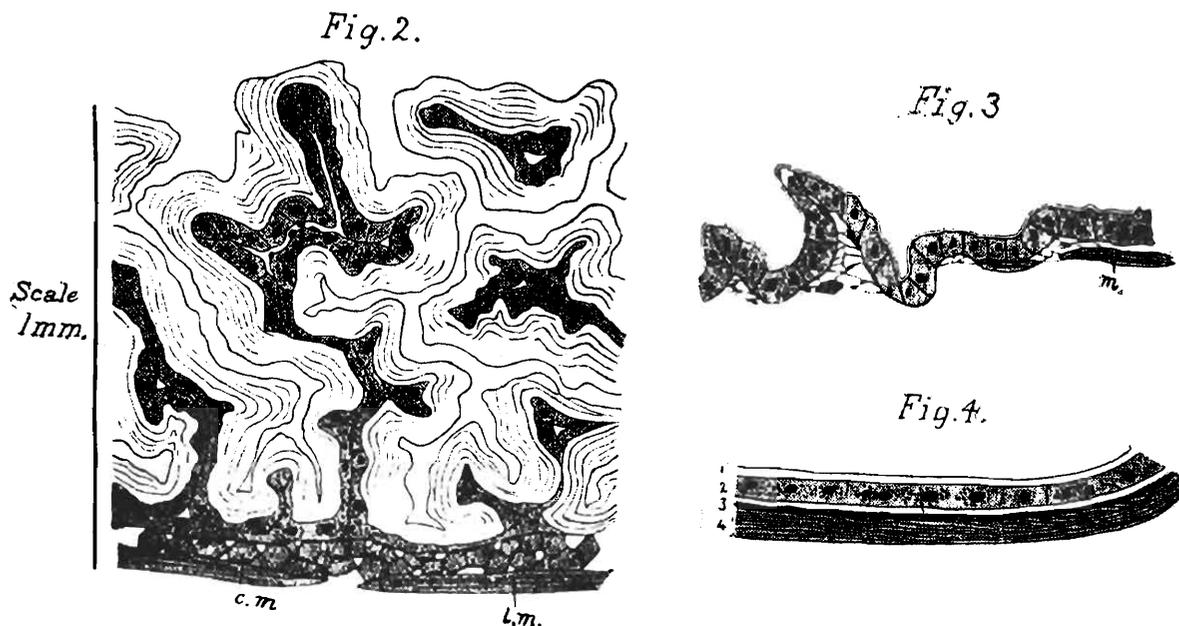


FIG. 2.—Section of the wall of the mid gut, $\times 60$: *c.m.* = circular muscle fibres; *l.m.* = longitudinal muscle fibres. The cuticular intima is very thick and shows lines of growth.

FIG. 3.—Section of the wall of the hind gut, $\times 60$.

FIG. 4.—The gizzard wall: 1 = the cuticular intima; 2 = the endothelium; 3 = homogeneous layer or "basement membrane" (the representation of this layer is somewhat exaggerated); 4 = the outer fibrous coat.

The anterior part of the hind gut is remarkably thin; so thin, that its coherence must be largely due to the cuticular intima, a slender wavy layer formed upon the endothelium. External to the endothelium are a few muscle fibres; these are much more plentiful posteriorly, where they are arranged longitudinally for the most part.

THE VASCULAR SYSTEM.

Owing to their friable nature in the preserved specimen, it was found impossible to trace the blood vessels to any extent. The large heart and its principal arteries, however, afforded material for a partial description (pl. x, fig. 1). The heart is 5 cms. in length and 1 cm. in its greatest breadth. It lies upon, and in close contact with, the hind gut, and occupies the last thoracic and the five abdominal segments. For descriptive purposes it may be divided into anterior and posterior halves. The anterior half, which is roughly oval in transverse section, gives off eleven vessels: one median artery from its anterior end, and five pairs of lateral ones. The posterior half of the heart, from which no vessels are given off, forms in transverse section a quadrilateral figure, somewhat greater in height than in breadth.

On opening the abdominal carapace, a large empty space was seen on both sides of the posterior half of the heart. These spaces were thought to represent the pericardial cavity, the walls of which were so friable that they could not be defined by dissection. Before any manipulation was performed it was noticed that these cavities communicated directly with the heart by means of two patent apertures. These apertures were oval in shape, and of the same size and appearance in every respect. They appeared to be natural features of the heart's structure, for the fibres composing the heart wall diverged to form them. These openings have the appearance of being "ostia," but some little doubt was felt as to their nature, for they were by no means symmetrical in their position on either side. The one on the right side was situated on the highest part of the side wall of the heart, while the other was situated much further forward and at a lower level on the left side wall of the organ.

There is little doubt but that these openings are ostia, but the asymmetry of their position is so unusual that until this can be confirmed in other specimens, one cannot be quite certain as to their nature.

The posterior end of the heart is somewhat dilated and comes to an abrupt termination behind, where it touches the upper border of the telson. The large arteries were traced only so far as they are shown in pl. x, fig. 1.

This description, incomplete though it is, will perhaps suffice to show that the vascular system of *Bathynomus* is not unlike that of the other Isopods. The abdominal position of the heart and the presence of eleven main arteries are well known features in the anatomy of other Isopods. The fact that the eleven arteries in *Bathynomus* are all given off from the anterior half of the heart, the posterior half being free from them and being perforated by ostia, seems unusual among Isopods. In *Asellus*, *Porcellio*, *Ligidium* and other genera, the five pairs of arteries spring from the heart at equal intervals along its whole length, while the ostia are situated in a corresponding way. The heart of *Anceas maxillaris* has been figured by Dohrn (18); this organ shows four ostia which are not arranged in symmetrical pairs, but are distributed irregularly on the surface of that organ. This is a parallel instance to the supposed arrangement of the ostia in *Bathynomus*.

THE NERVOUS SYSTEM.

After removal of the alimentary organs, most of the central nervous system is displayed (pl. xi, fig. 4). From this figure it will be seen that a portion of the ventral nerve cord is hidden from view by the union of the sternal alar plates, the posterior borders of which form a wide notch. A large ganglion lies in this notch; it is connected with the cerebral ganglia by two stout commissures which lie in close contact beneath the alar plates, but diverge behind the pharynx to surround that organ. The commissures were without visible ganglionic enlargements, hence the large ganglion in the notch of the alar plates was at first considered to be the sub-oesophageal ganglion (*s.o.g.*, figs. 2, 4). Since, however, this ganglion did not seem to supply the muscles of the cephalic appendages, which were supplied by small filaments from the commissures anterior to the ganglion, some doubt was felt as

to its nature. The ganglion and commissures were, consequently, removed, stained and mounted *in toto*. On examination under the microscope, it was at once apparent that those parts of the commissures which lay in contact beneath the alar plates contained groups of nerve cells. There were four pairs of these ganglionic groups in this situation, corresponding to the four post-oral appendages of the cephalon. Each pair of these cell groups was connected across the middle line by nerve fibres, and from each group an external nerve was given off (text-fig. 8, 1-4).

The ganglion indicated by the letters *s.o.g.* (fig. 4) is, therefore, in all probability the first thoracic ganglion. Like the other thoracic ganglion it gives off two pairs of lateral nerves which supply, in this case, the chief flexor muscle of the trunk close to its attachment to the cephalon (see fig. 1).

Consequently, the ganglion indicated by the letters *g.t. 7* is the first of four abdominal ganglia. The position of the ganglia in relation to their respective segments is by no means regular.

Each cerebral ganglion shows division into two lobes; the anterior of these gives off the optic nerve and from its lower surface a small nerve to the first antenna; the posterior lobe gives off a nerve to the second antenna.

THE INTERNAL SKELETON OF THE HEAD.

On account of its size, *Bathynomus* is a good type in which to observe the internal skeleton of the head, a structure not very well known among Isopods. This part of the skeleton has been previously studied in the smaller Isopods, by examining the decapitated head under the microscope, after treatment with caustic potash. It was first described by Schöbl, in the genus *Haplophthalmus*, who named it the "kieferzungengerüst" (19). Sars has figured a similar apparatus in the case of *Asellus*.

In *Bathynomus* this apparatus consists of two pairs of wing-like plates composed of rigid chitinous material, which are attached to the inner aspect of the cephalon, and project into its interior. They serve for the attachment of muscles. One pair is developed from the dorsal or tergal part of the cephalic shell, and the other from the ventral or sternal part. These plates will, therefore, be referred to as the sternal and tergal alæ. The sternal alæ are firmly united with, and probably derived from, a stout skeletal bar, which is seen externally on the lower aspect of the head separating the maxilliped from the second maxilla. (This bar can be seen in pl. iv, fig. 9, of Bouvier's monograph.) Within the head the sternal alæ of opposite sides meet in the middle line, and are firmly united by tough fibrous material. By their union, a plate-like structure is formed, upon which the gizzard rests.

For descriptive purposes, this chitinous plate may be divided into anterior and posterior portions, which are separated by a groove; both portions consisting of right and left halves united by fibrous material in the middle line. The anterior portion occupies a position not far removed from the horizontal, but each half inclines slightly upwards on either side. The upper surface of this part of the plate gives attachment to muscles which are inserted into the anterior ampullæ of the gizzard. The border which limits the plate in front is widely V-shaped, and embraces the œsophagus. The

limbs of the V are continued forward, on either side of the œsophagus as two chitinous rods, each of which passes over the optic nerve and the nerve to the second antenna of the same side, and, after becoming fan shaped, joins the inner surface of the carapace along an oblique line close above the fossa of the first antenna. This line of junction is clearly indicated externally by a faint groove which is distinct in the largest specimens; immediately around this groove, the minute pits elsewhere present on the carapace, are wanting, and the carapace has a lighter colour. This feature is shown in pl. iii, fig. 2, of Bouvier's monograph as a somewhat curved linear area of a lighter tint situated 2 or 3 mm. above the antennary fossæ.

The posterior portions of the sternal alæ plates are shaped somewhat like the wings of a butterfly, and occupy a position half-way between the vertical and the horizontal. Each is composed of two laminæ of chitin, between which is a certain amount of fatty material. Their lower or outer surfaces give attachment to muscle fibres, which are inserted into the first and second maxillæ and the maxilliped.

Let us pass now to a consideration of the tergal alæ. These are a pair of rigid chitinous structures, the principal function of which is to give attachment to the powerful mandibular muscles: arising on either hand from the roof and side walls of the cephalon, they occupy a position half-way between the vertical and horizontal; so that they present nearly the same appearance when viewed from above, as from behind. The upper or posterior surface of each of these is smooth and convex, the lower or anterior surface is concave and forms the posterior limit of a large fossa. This fossa is covered by the lateral part of the dorsum of the cephalon; it is bounded externally by the side wall of the same including the eye, internally it is limited by the chitinous rods which lie on either side of the œsophagus. The space limited by these boundaries measures 23 by 12 mm. in its greatest length and breadth, and is wholly occupied by the powerful mandibular muscle, part of the fibres of which are in close proximity to the inner side of the eye.

The line of attachment of the tergal alæ to the carapace is of interest. The upper surface of the cephalon of *Bathynomus*, and some other Isopods such as the *Cirolanidæ*, shows two deep grooves on either side not far from its posterior edge. These grooves are usually considered to have resulted from the union of the first thoracic segment with the fifth cephalic; a union which, from the presence of the maxilliped among the appendages of the cephalon, we know to have occurred. These grooves are continued downwards on the side wall of the cephalon and end below in a deep pit, placed to the outer side of the interval between the mandible and first maxilla. This pit, which is seen in fig. 3, is also clearly shown in pl. iv, fig. 9, of Bouvier's monograph. Internal examination of the head shows that the tergal alæ arise in their whole length from these grooves, and they appear as though formed by invagination of the cuticle along their line. If these grooves indicate the union of the fifth cephalic with the first thoracic segment, we should expect them to end below in the interval between the second maxilla and the maxilliped.

The internal skeleton of the fore part of the head shows some interesting features.

The cerebral ganglia give off on either side three large nerves,—the optic nerve and nerves to the first and second antennæ. The last two nerves leave the cranium through two gaps in the cuticle, which are separated by a stout skeletal bar. The gap for the first or antennular nerve, which lies above and slightly to the inner side of the other, is nearly circular and measures about 2 mm. in diameter; it is surrounded by an elevated ridge of skeletal material which projects into the cavity of the head. This ridge is scarcely less than 2 mm. in height and nearly as much in thickness; it is continuous with the bar which separates the two gaps. The ridges which surround the antennular gaps on either side are united across the middle line by a short ridge of equal thickness and height. This transverse ridge lying as it does, a conspicuous feature, directly between the antennular gaps, must be considered as the first cephalic sternite. It is firmly based upon the internal side of the frontal lamina.

M. Bouvier speaks of the frontal lamina as the “segment antennulaire,” while the clypeus he refers to as the “segment antennaire.” This view receives support from the fact that the transverse ridge, which from its position must be regarded as the first sternite, is firmly fused with the frontal lamina. On the other hand, attention must be drawn to a deep groove separating the frontal lamina, and with it the clypeus, from the rest of the head. This groove, which is shown in fig. 3, commences above as the posterior limit of the frontal lamina, passes down in front of both antennular and antennary gaps, to end below between the antennary tubercle and a second smaller tubercle (*a.t.*, *t.*). The ending of this groove between the two tubercles is shown in Bouvier’s fig. 9 (pl. iv); the antennary tubercle is indicated by the letter *a*, the other to the inner side being unlettered.

The antennary gap, which is much larger than the antennular, measures about 5 mm. in diameter and is bounded below by a strong skeletal bar, continued externally into a ridge forming the anterior border of the mandibular gap.

THE STRUCTURE OF THE EYES.

In the position and size of its eyes, *Bathynomus* is remarkable among Isopods. According to Bouvier there are nearly three thousand corneal facets in each eye.

The internal structure of the eye was studied by means of sections, both vertical and tangential to the surface (pl. xii). The cuticular cornea, which comprises more than half of the total thickness of the eye, is made up of about thirty closely applied layers. These layers together show in vertical section a uniform wavy appearance; the centre of depression of each wave lying over the centre of each perceptive element or ommatidium. The outermost layer of the cornea differs from the others; it is denser, takes the stain with greater avidity, and is continued as an uninterrupted sheet over the whole external surface of the eye.

Between the cornea and the perceptive part of the eye is a well-developed homogeneous layer, which in its intimate structure much resembles the cornea, but is separated from that organ by a narrow cellular layer,—the corneagen.

The perceptive part of the eye consists of a number of ellipsoidal bodies composed of translucent yellow material; these are the vitrellæ or lenses, each of

which is composed of two separate halves. This separation of the vitrellæ into two halves can be seen, with some difficulty, in nearly all sections of those structures, both longitudinal and transverse. The separation is shown in the photograph (fig. 5), in which one of the lenses seen in transverse section is ill developed, and shows the division very clearly. Each vitrella is separated from its neighbours by a thick layer of pigmented protoplasm, which appears to be continuous below with the pigmented retinula cells. This pigmented material not only lies between the vitrellæ but spreads out above them, covering the peripheral part of their upper ends, so that only the axial part of each can transmit light. Vertical sections which pass through the central axis of the lenses show that the lower ends of these organs are almost in contact with a continuous pigmented layer, which forms the innermost limit of the perceptive part of the eye (fig. 4).

Rhabdomeres appear to be altogether absent. Careful examination of many sections failed to disclose them; though it is possible that there are small rudiments of these structures among the densely pigmented retinula-cells.

Around the lower or inner ends of the vitrellæ are grouped some four or five (the number was not definitely determined) densely pigmented cells. These are the retinula-cells. They are prolonged at their lower ends into pigmented filaments, which, after a short twisted or spiral course, pass into and make up a continuous pigmented substratum, lying beneath the lenses and forming the innermost limit of the perceptive part of the eye. One of these pigmented filaments, which were seen on many occasions in vertical sections, is shown in the photograph (fig. 4). In the pigmented substratum these filaments doubtless communicate directly or indirectly with the fibres of the optic nerve. The optic nerve becomes flattened out as it approaches the eye; it passes on to the inner side of that structure and spreads out in a fan-shaped form.

THEORETICAL CONSIDERATIONS.

The large vitrellæ, which are remarkably clear and translucent, the well-developed black pigment, which not only separates these lenses but spreads out and covers them peripherally like an iris, and the well-developed pigmented terminations of the retinula-cells, all point to the conclusion that the eye of *Bathynomus* is a useful light-perceiving organ. This fact lends support to "the theory of abyssal light," for *Bathynomus* is essentially a deep-water form which does not seem to be a recent emigrant from shallow waters.

The absence of a rhabdom does not seem to be of much significance, for this organ cannot be considered an essential part of the eye of an Isopod. Thus, among those species which have been examined, the rhabdom varies very much in its degree of development. Beddard (20, 21) found that in *Arcturus furcatus*, a deep-sea species, the rhabdom was hardly less than the vitrella in size, while in *Serrolis scythei* the rhabdom was considerably smaller than the vitrella. Again in a third case Beddard says, "Bullar has not figured or described more than a clear point at the summit of each cell of the retinula in *Cymothoa*, which he regards as the equivalent of a rhabdome." The presence or absence of a rhabdom has, therefore, no relation to the range

of depth of the species. In *Arcturus*, a deep-sea form, it is large, in *Cymothoa*, a shallow-water genus, it is very small, while in *Bathynomus*, essentially a deep-sea genus, it is probably absent altogether.

The broad homogeneous layer between the corneagen and the ends of the vitrellæ was plainly seen in all vertical sections, and is shown in the photograph (fig. 4). It seems to be peculiar to the genus *Bathynomus*. The corneagen seems to have secreted corneal material on its inner side to a certain extent, as well as on its outer side.

OTHER SENSE ORGANS.

Hansen (23) has described from an Indian specimen in the Copenhagen Museum a small sense organ situated in the mid dorsal line of the cephalon close to its posterior border.

All specimens available in this Museum show the same organ as figured by that author.

II.—THE MATURE SEXUAL FORMS.

A mature female specimen was obtained from a depth of 195 fathoms in the Bay of Bengal (pl. ix). This measures 202 mm. in length and 93 mm. in breadth. It possesses a large brood-pouch containing twenty-six undeveloped eggs. The brood-pouch is composed of five pairs of oöstegites attached to the bases of the first five pairs of thoracic legs. Those on the third and fourth legs are the largest, measuring as much as 7 cm. in length and 4 cm. in breadth. Each oöstegite is composed of thin parchment-like material; with the exception of the last pair they all possess two longitudinal parallel ridges, each oöstegite having the appearance of a leaf with two midribs. At right angles to these ridges, between them and the margin, is a finer venation. The first pair of oöstegites are peculiar. On the upper surface of each is a very prominent ridge, which fits into the groove separating the maxilliped from the thorax, so that the part of the leaf placed in front of the ridge is closely applied to the under side of the head, while the part behind the ridge belongs to the brood-pouch and closes that cavity in front. Furthermore, from the inner end of this prominent ridge is a curved appendage measuring about 7 mm. in length, which in the undisturbed condition, touches its fellow of the opposite side (text-fig. 5). During life these appendages probably interlock and keep closed the front part of the brood-pouch. The fifth pair of oöstegites are considerably smaller than the others, each possesses one inconspicuous mid-rib: to the inner side of their points of attachment are the generative apertures, semilunar in shape and measuring 7 mm. in length (pl. x, fig. 6).

The maxilliped of the mature female differs in two respects from that of the immature form (text-figs. 6 and 7). Attached to the outer border of the basal joint of this appendage there is, in the mature female, a thin plate measuring 11 by 7 mm. This plate, which is in the position of an epipodite, resembles an oöstegite in its crinkled parchment-like appearance: it differs from those structures, however, in having a hairy margin. As it is only found in the mature oöstegite-bearing female, it may be regarded as having been produced in co-ordination with the oöstegites. Its occurrence lends support to the view that those structures have been derived from epipodites.

Of equal importance is the fact that among Isopods, the Cirolanidæ alone show similar rudimentary oöstegites on the maxilliped (22). Bouvier and Hansen (23) have shown in how many other ways *Bathynomus* resembles the Cirolanidæ.

The maxilliped of the mature female further differs in possessing a curious process arising from the inner side of its basal joint. This process, which is 7 mm. in length, is composed of soft cuticle fringed with hairs. A rudiment of such a process can be seen in the immature female but not in the male.

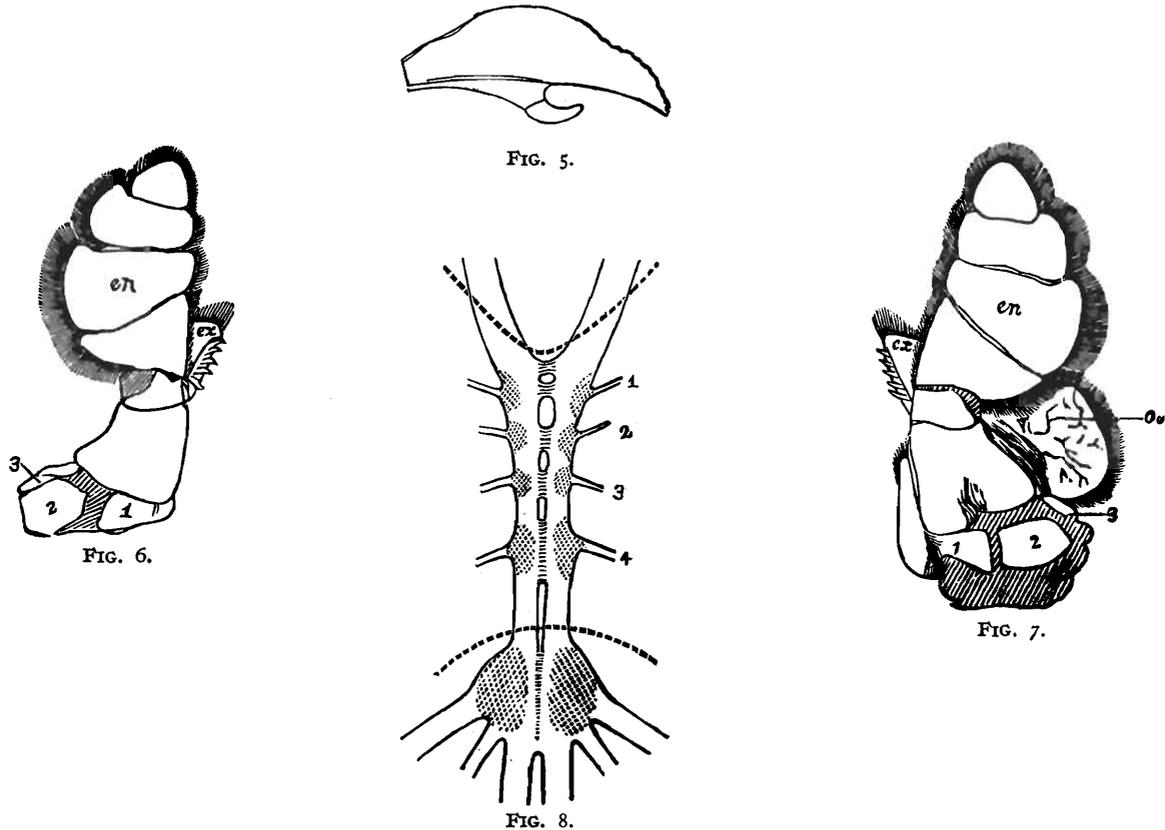


FIG. 5.—The oöstegite of the 1st thoracic leg (right) viewed from behind, showing the curved appendage.

FIG. 6.—Right maxilliped of an immature female.

FIG. 7.—Left maxilliped of a mature female: *en.* = endopodite; *ex.* = exopodite; 1, 2, 3 = the three basal plates; *oo.* = the oöstegite.

FIG. 8.—The subskeletal portion of the cephalic nervous system, $\times 6$. The thick dotted lines indicate the position of the superimposed skeletal plate. The groups of dots represent nerve cells. The largest pair of ganglia at the lowest part of the figure is the 1st thoracic ganglion (erroneously lettered *s.o.g.* in plate xi).

The thoracic sternites of the mature female differ remarkably from those of the immature female and of the mature and immature males. In the thoracic region of the latter the skeletal sternites are not continuous across the middle line. An examination of the thorax of an immature female or any male shows that there are in each

segment two pairs of tongue-shaped plates of hard chitin, easily distinguishable from the soft leathery cuticle of the lower surface of the thorax. These plates articulate externally with the base of the movable epimera. The members of each pair are separated by a narrow V-shaped area of soft cuticle; while they are both separated from the corresponding pair of the opposite side by the median area of soft cuticle about 2 cms. in breadth.

In the gravid female the ventral surface of the thorax is deeply concave; thereby the capacity of the marsupium is increased. On examining this surface, tongue-shaped plates similar to those found in the other forms are seen, but where these are in contact with the epimera the pairs are themselves united. From their union a thin band of hard skeletal material arises, which is continuous across the mid ventral line with its fellow of the opposite side. Thus in the mature female alone there are complete skeletal sternites in the thoracic region. These sternites are very conspicuous owing to their white colour and hard consistency. In the mid ventral line they each form a V-shaped figure (pl. x, fig. 6). They are present from the second to the sixth segment.

THE EGGS.

The eggs of *Bathynomus* are large spheres of a pale yellow colour, measuring as much as 11 mm. in diameter. This is probably the largest recorded crustacean egg. The brood-pouch, which contained twenty-six of these eggs, also contained eight empty egg-shells probably from a former brood. The eggs seemed to be quite undeveloped, being entirely made up of liquid yolk material enclosed in a thick parchment-like shell.

THE MATURE MALE.

A mature male form measuring 270 mm. by 118 mm. was obtained off Ceylon. This, although the largest recorded individual of the species, is not much larger than the American specimen, but it differs from that in being provided with copulatory stylets in the usual position attached to the endopodites of the 2nd pleopods. This appendage does not differ, except in minor details, from that of *B. döderleini*, already portrayed by Bouvier.

III.—ON CERTAIN DIFFERENCES BETWEEN THE INDIAN AND AMERICAN FORMS OF *BATHYNOMUS GIGANTEUS*.

Figure 4 (pl. x) was drawn by Babu Mondul, draughtsman to the Marine Survey. The work of this artist is usually so accurate, that I was surprised to find his rendering of the basal plates differed somewhat from Bouvier's figure of the same structures. In order to be quite clear on this point, I excised the membranous attachment of one of the pleopods and after clearing with caustic potash, drew it enlarged, with the camera lucida. As can be seen from the resulting figure 3, there are five separate plates in this situation, four on the anterior side and one on the posterior; whereas Bouvier's figure shows only two plates on the anterior side. Subsequent examination of all available specimens showed that five separate plates were

invariably present (numbered 1—5, pl. x, fig. 3). It will be seen from this figure that the small oval plate indicated by the number 2 is in the position of the muscle-attached "fossette" of the American specimen (*f.s.*, pl. vi, fig. 1, of Bouvier's monograph). The larger plate, 5, which is entirely on the posterior or hidden surface but articulates with the prominent fourth plate, is not represented at all in the figures of the American specimen.

M. Bouvier's work is such that we can eliminate the possibility of error in his rendering of the structures in question. We must conclude, therefore, that the Indian form of *Bathynomus* differs from the American in this respect. That these structures are prone to vary is shown by comparing the same author's figures of the American specimen with that of the Japanese species, *B. döderleini*.

IV.—THE DISTRIBUTION OF *BATHYNOMUS GIGANTEUS* IN INDIAN SEAS.

Nine specimens of this large Isopod have been taken by the "Investigator" from six separate stations. The following is a list of the stations from which they were obtained:—

- I. Station 105, Lat. 15° 2' N., Long. 72° 34' E., Laccadive sea, in 740 fathoms. Three immature female specimens were obtained, measuring 160, 195 and 200 mm., respectively. These were recorded by Wood-Mason and Alcock (3).
- II. Station 145, Lat. 15° 5' N., Long. 72° 38' 10" E., from the Laccadive sea, in 692 fathoms. "One small specimen" was obtained. The length and sex were not recorded, and the specimen has passed out of the Indian Museum. The naturalist's notes at the time of its capture record the fact that Station 145 was carefully chosen as close as possible to the previously successful Station 105, with the special intention of obtaining more specimens of *Bathynomus*. Exceptional good fortune must have attended the successful second attempt.
- III. Station 256, Lat. 9° 32' N., Long. 80° 59' 30" E., off north-east coast of Ceylon, in 594—225 fathoms (a very steep sea bottom). One large mature male with copulatory stylets: this is the largest recorded specimen; it measures 270 mm. by 118 mm.
It was referred to by Alcock in "A Naturalist in Indian Seas," page 271.
- IV. Station 358, Lat. 15° 55' 30" N., Long. 52° 38' 30" E., off south coast of Arabia, in 585 fathoms. Two specimens; an immature male measuring 55 by 130 mm., and an immature female measuring 83 by 184 mm. previously recorded by the author (24).
- V. Station 371, Lat. 12° 18' 46" N., Long. 74° 5' 29" E., Laccadive sea off west coast of Madras, in 580—540 fathoms. An immature female measuring 193 by 89 mm.

- VI. Station 373, Lat. $15^{\circ} 59' 10''$ N., Long. $93^{\circ} 39' 45''$ E., Bay of Bengal, off Pegu coast of Burma, in 195 fathoms. One mature female measuring 202 by 93 mm., with brood-pouch and twenty-six eggs.

These records show that *Bathynomus* is not uncommon in Indian seas, that it is widely distributed on both sides of the peninsula, but seems to be specially common in that part of the Arabian sea which lies between the Laccadive islands and the west coast of India and is spoken of as the Laccadive sea.

They show, further, that sexually mature individuals are uncommon in comparison with immature forms, some of the immature being nearly as large as the mature. The mature male is larger than the mature female.

V.—OBSERVATIONS ON THE NATURAL HISTORY OF *BATHYNOMUS*.

Most of the specimens obtained by the "Investigator" have shown a certain amount of life when taken out of the trawl, but they are not usually active. The mature female, however, which was taken from the comparatively small depth of 194 fathoms, was, owing to this reason perhaps, much more active and strongly resisted our attempts to view the contents of its brood-pouch. It lived in a tub of sea water for about two hours, during which time it continued to perform, at regular intervals, a sweeping movement of all its pleopods. When this movement was not taking place the pleopods were held closely applied to the under side of the abdomen; after intervals which varied between 7 and 10 seconds, all these appendages were quickly swept downwards and forwards, and as quickly returned to their former position. This movement is obviously to produce aëration of the blood in the peculiar branchial tufts. One may suppose from the fact that this movement was continued under such abnormal conditions that it was an involuntary one, akin to the movement of a scapognathite of a prawn, which, as is well known, will continue to move long after the animal has been removed from the water.

Of the five Indian specimens of *Bathynomus* examined all have carried a small barnacle attached to their pleopods. Two species appear to occur in this position, one of which, described recently by Annandale (25) as *Dichelaspis bathynomi*, has never been found apart from these large Isopods, while the other, which may be a variety of *Dichelaspis oclusa*, has also been found on the shallow-water Crustacea *Thenus orientalis*.

On plate xii is a photograph of the living specimen; the hinder part of the body is somewhat raised to allow the sweeping movement of the pleopods. The first pleopod of the right side was damaged and hung down.

My thanks are due to Dr. J. H. Ashworth of the University of Edinburgh for kindly supervising the reproduction of plates ix—xi of this Memoir.

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