

INVESTIGATOR SICARIUS, A GEPHYREAN WORM
HITHERTO UNDESCRIBED, THE TYPE
OF A NEW ORDER.

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Specimens of the animal for which the name *Investigator sicarius* is proposed have been taken on two occasions by the R.I.M.S. "Investigator." The first occasion was in 1900 at station No. 268, 7° 36' N. 78° E., in the Gulf of Manaar, where eight specimens were obtained at a depth of 595 fathoms from a bottom of green mud and sand. The second occasion was in 1908 at station No. 378, 19° 32' N. 92° 41' E. off Arakan at a depth of 250 fathoms on a bottom of soft green mud. Only one specimen was obtained at the latter station.

On being examined during the summer of 1908 in Calcutta the specimens from station No. 268 were found to be well preserved for examination of the exterior but to be so hardened by age and alcohol as to be useless for study by sections. The specimen from station No. 378, however, which, after being fixed with mercury and passed through absolute alcohol was preserved in cedar-wood oil, was in excellent condition for this purpose and a complete series of sections was obtained.

INVESTIGATOR SICARIUS, gen. nov., sp. nov. (Plate xxi.)

GENERAL APPEARANCE. (Pl. xxi, fig. 1.)

The body divides itself naturally into trunk, neck and head. The trunk is sausage-shaped, narrowing in front fairly abruptly to the neck which is approximately one-and-a-half times the length of the trunk and bears the globular head. There are no tentacles. The mouth is slit-like, situated on a diamond-shaped area of tough-looking skin. At the margin of this area is a circle of minute black dots, and behind it the head carries several circles of simple short spicules.

The skin of the neck and body is regularly covered with glassy chitinous spines, needle-shaped on the anterior portion of the neck, broadly lanceolate on the trunk (pl. xxi, fig. 2). (In fig. 1 the artist has represented the spines as not covering the whole of the body. This is due to their translucency which causes them to be visible only at certain angles.)

The hinder end of the body is formed by a hardened, flatly conical shield separated from the rest of the body by a shallow groove. The spines at the edge of the

shield are long and spike-like (pl. xxi, fig. 3), projecting outward, while on the surface of the shield they converge on the aperture which occupies the centre.

This aperture leads into a spherical cavity which contains a gill (pl. xxi, fig. 4). This latter organ consists of an oval mass divided into two bilaterally symmetrical halves, each built up of lamellæ which lie in the transverse plane of the animal. The gill of course recalls the caudal branchiæ of *Priapulidæ*. In *Priapulidæ*, however, the structure lies ventral to the anus, while in *Investigator* it is dorsal to it.

The anus curiously enough opens into this respiratory chamber on its ventral surface not far from the external opening.

In regard to colour, the head of the animal is pink, the body and neck olive-green with an added silvery sheen caused by the spines.

MEASUREMENTS.

Trunk length	12—13 mm.
„ max. diameter	5 „
Neck length	18—19 „
Head	4 „

These measurements are from preserved specimens.

SKIN AND BODY-WALL. (Pl. xxi, fig. 5.)

The ectoderm is represented by a protoplasmic layer which does not show cell outlines. Nuclei are scattered freely throughout it. The spicules and spines give the appearance of having been simply thrust into this layer. A few nuclei are aggregated around their bases, but there is no definite formative sheath.

Under the ectoderm a thin layer of circular muscular fibres is to be found throughout the entire length, and in the neck in addition to this a layer of longitudinal muscles occurs divided into four bands—two dorsal and two ventral.

The head corresponds physiologically to the “introvert” of other Gephyreans. The skin is smooth, and numerous bundles of muscle fibres arising from the wall of the pharynx and anterior portion of foregut are inserted on its cœlomic surface and can doubtless easily introvert this portion of the body, although none of the specimens before me show this condition.

The retractor muscles receive an extraordinarily rich nerve supply from the two lateral nerve cords. Large nerves run out to them and in several places form ganglia among the interlacing muscle fibres.

THE BODY-CAVITY.

The body-cavity extends continuously from the head to the shield, surrounding the alimentary canal. The liver, nephridia, gonads and splanchnic blood-vessels also lie within it.

The space is apparently completely lined by endothelium, a parietal layer on the body-wall, a visceral layer covering the organs above mentioned. This endothelium

differs in no way from that found in other coelomate worms. In situations where it is reflected on itself at a fairly acute angle, as at the junction of the coronal partition and the body-wall, the endothelial cells are somewhat heaped up and less flattened, and they closely resemble the free cells of the body-cavity, in fact it seems clear that the cells of the latter are derived from the endothelium. These free cells have a clear protoplasm which does not stain, a sharp round outline and an intensely staining nucleus. They are identical with those found in the dorsal blood-vessel.

The body-cavity is divided throughout the entire length of the neck and trunk by a fibrous and endothelial partition, lying in the coronal plane of the animal (pl. xxi, figs. 5, 6, 7). This partition does not extend into the head. Of the two divisions into which it divides the body-cavity, the dorsal is by far the largest and contains all the viscera,—alimentary canal, liver, nephridia, testis, and the main dorsal blood-vessel. In the region of the neck some of the sacculi of the foregut pass through the partition and project into the ventral division; the ventro-lateral nerve cords also project into it in this region, but with these two exceptions it is empty.

In the hind region of the neck and the front of the trunk, before the liver appears to occupy the greater portion of the body-cavity, there are in addition to the coronal diaphragm two pairs of dorso-lateral longitudinal partitions running from the body-wall to the main dorsal blood-vessel and the gut (pl. xxi, fig. 6). It has not been possible to trace any communication between the body-cavity and either the exterior or the cavities of the testis or nephridia.

In regard to the nature of the body-cavity, the question arises is it coelom or not? Without the aid of embryology it may not be possible to give a very definite answer to this question. The main argument against its coelomic nature would be the fact that the cavity of the gonad does not communicate with it, but it seems to be fairly generally admitted that the body-cavity of Priapulids is a coelom from which a special part has been shut off to form part of the lumen of the reproductive tube. Now the Priapuloidea are the group to which *Investigator* is most closely allied, and the same interpretation might therefore be very reasonably applied to *Investigator*. But again the presence of the same type of free cells in both blood-vessels and body-cavity might suggest that the cavity was hæmocœlic, but lymph cells are known to pass freely into the blood stream (as, for instance, by the thoracic duct of Mammalia), so that no importance can be attributed to the distribution of these cells.

The fact that the nephridia project freely into the cavity is in favour of regarding it as coelom. Altogether the balance of evidence seems to be in favour of this view, and there is certainly as much reason to suppose that it is coelomic in *Investigator* as in the Priapuloidea.

THE ALIMENTARY SYSTEM.

The alimentary canal, extending from the slit-like mouth at the anterior extremity to the anus opening into the gill-chamber underlying the shield, can be divided into pharynx, foregut and hindgut.

The pharynx lies in the region of the head. Its walls are composed of tall columnar epithelium and it is chiefly remarkable for the peculiar poison fang which is situated in its ventral wall. It can doubtless be everted by the same muscles which presumably also introvert the head.

The poison fang (text-figs. 1—3). The base of this organ is attached to the external surface of the pharynx by muscles, the point projecting freely into the pharyngeal cavity and being directed away from the mouth. It is constructed of two cartilaginous bars (text-figs. 1—3, *cart.*) which diverge somewhat at the base, but near

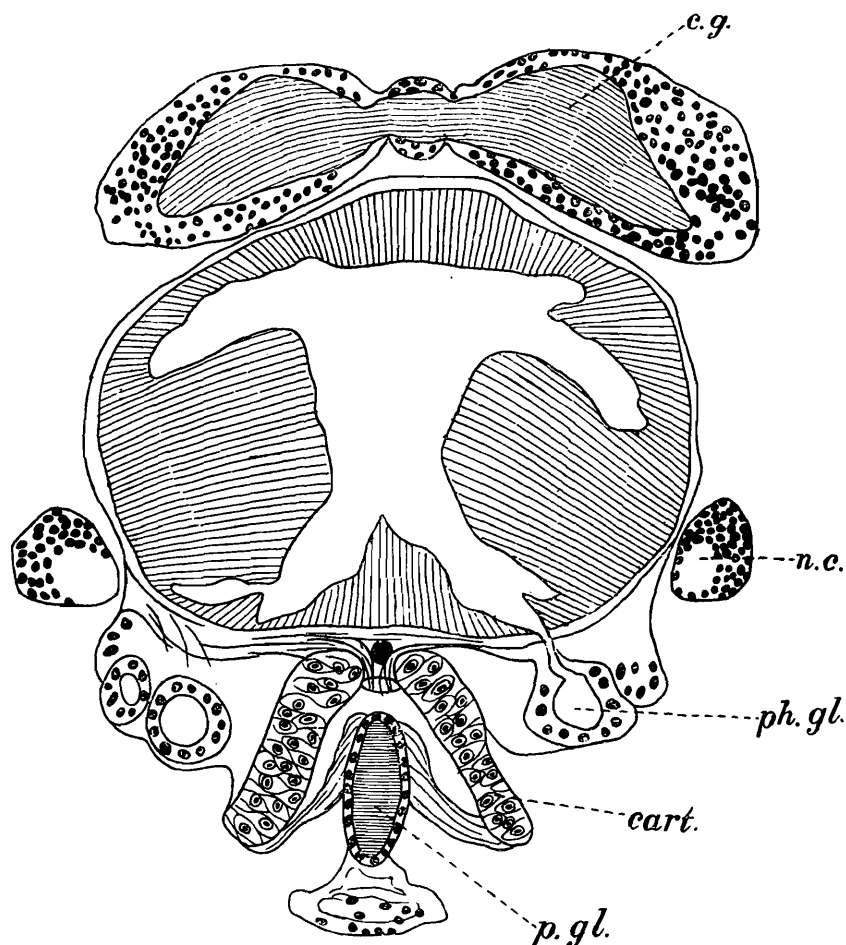


FIG. 1.—Transverse section through the pharynx, to show the cerebral ganglia, lateral nerve cords and poison fang, $\times 140$: *cart.* = cartilage; *c.g.* = cerebral ganglion; *n.c.* = lateral nerve cord; *p.gl.* = poison gland; *ph.gl.* = pharyngeal gland.

the point come together to form a hollow tube. This tube, which is the exposed portion of the tooth, is covered by a sharp-pointed chitinous cap, the analogue of the enamel of the mammalian tooth (text-figs. 2 and 3, *chit.*). A tubular gland with a wall composed of a single layer of flat cubical epithelium lies between the cartilaginous bars and opens close to the point of the tooth (text-figs. 2 and 3, *gl.ap.*). The aperture is armed with two sharp cutting edges (text-fig. 2, *c.e.*) which must inflict an exceedingly nasty wound. The specific name of the animal is given in recognition of the dagger-like character of this organ.

The foregut (pl. xxi, fig. 5) extends throughout the neck, lying in the dorsal division of the coelom. Its structure offers nothing worthy of remark.

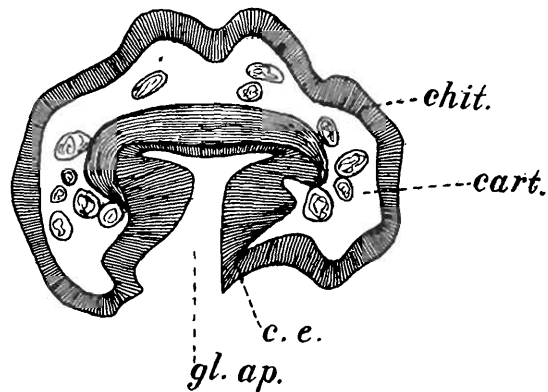


FIG. 2.—Transverse section through the tip of the poison fang showing the opening of the poison gland, $\times 700$: *cart.* = cartilage; *c. e.* = cutting edge; *chit.* = chitinous cap; *gl. ap.* = aperture of poison gland.

At the junction of neck and body a large blind sac grows out from the ventral wall of the canal and this outgrowth marks the division of the hind- from the fore-gut. The hindgut (pl. xxi, fig. 7) is a narrow cylindrical tube which does not appear

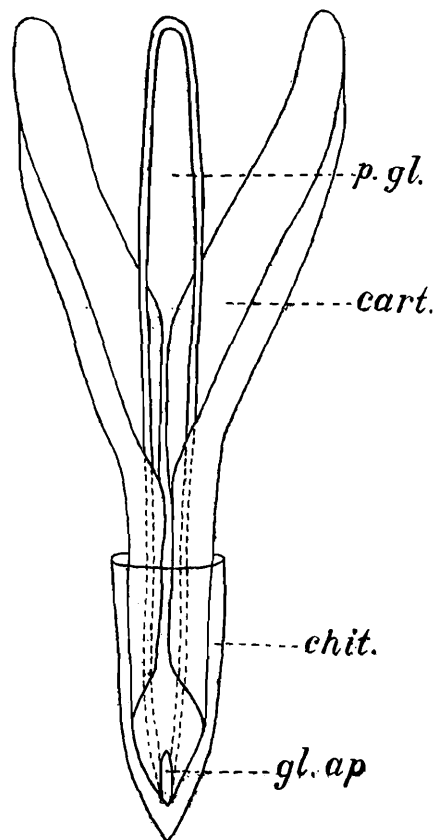


FIG. 3.—Diagrammatic reconstruction of the poison fang: *cart.* = cartilage; *chit.* = chitinous cap; *gl. ap.* = aperture of poison gland; *p. gl.* = poison gland.

to possess digestive or absorptive powers, since its contents consist of a series of oval faecal pellets. It lies in the dorsal line to the right of the dorsal blood-vessel and testis. On reaching the gill-chamber it bends towards the ventral surface (pl. xxi, fig. 9) and opens into that chamber in the mid-ventral line.

The blind sac (pl. xxi, fig. 7, *l.*) which arises at the junction of fore- and hindgut is a large hollow organ with thin sacculated walls which occupies the greater portion of the coelomic space in the body. Like the rest of the alimentary system it lies dorsal to the coronal diaphragm which it presses down until it is almost in contact with the ventral segment of the body-wall. Histologically its chief elements are large irregular epithelial cells with coarsely granular protoplasm. Its contents, in addition to cells of various types, consist mainly of masses of golden or black pigment granules. It doubtless fulfils the digestive and excretory functions of a liver.

THE VASCULAR AND RESPIRATORY SYSTEMS.

A large blood-vessel runs along the mid-dorsal line of the gut in the region of the neck (pl. xxi, fig. 6). On reaching the commencement of the trunk a number of small vessels are given off and form a plexus over the wall of the gut. It is here that the anterior end of the reproductive organ is situated and here the dorsal blood-vessel leaves the alimentary canal and continues its course backward in the dorsal wall of the reproductive organ (pl. xxi, fig. 7). On reaching the anterior margin of the gill-chamber both blood-vessel and gonad leave the mid-dorsal line of the animal and pass towards the root of the gill.

The outward appearance of the gill has been described above. From the point of view of minute anatomy it consists of lamellæ of folded columnar epithelium with a basis of very fine connective tissue and blood-vessels (pl. xxi, fig. 9). The stalk of course consists also of connective tissue and blood-vessels. The vessels are doubtless continuous with the main dorsal vessel which we have traced to the base of the stalk. The surface of the respiratory chamber is clothed with cubical epithelium which near the outlet is also thrown into respiratory laminae similar to those of the gill proper. At the anterior extremity of the gill-cavity several muscular bands pass from it to the body-wall. These probably act by causing rhythmic expansions of the cavity, by changing the water in it and so assisting respiration.

The corpuscles found in the blood-vessels are identical with those of the coelom. They do not occur in large numbers.

NERVOUS SYSTEM.

The nervous system consists of a pair of closely connected large dorsal ganglia in the head and a pair of ventro-lateral nerve cords running throughout the entire length of the body.

The dorsal ganglia (text-fig. 1) present no unusual features. They consist of a fibrillar core and a richly cellular cortex. Sensory nerve filaments pass to them from the diamond-shaped area of skin around the mouth, which is apparently a specialized sensory patch.

The lateral nerve cords issue one from each dorsal ganglion. In the head they are closely apposed to the wall of the pharynx (text-fig. 1). The only ventral communication between them consists of a single fine commissure in this region.

In the neck (pl. xxi, fig. 5) they lie on the ventral side of the coronal diaphragm in the angle formed by this structure and the body-wall. This is also their situation in the region of the trunk (pl. xxi, figs. 6, 7, 9). Throughout the greater part of their course they are separated ventrally by $\frac{1}{8}$ th of the circumference of the body, dorsally of course by $\frac{5}{8}$ ths.

At the level of the anus they curve inward and toward the dorsum over the nephridia and gain the cœlomic surface of the respiratory chamber, lying at about the junction of the ventral and the two lateral quadrants of that organ (pl. xxi, fig. 9, *r.c.n.*). In this situation they run forward to the anterior extremity of the respiratory chamber and here join in a broad commissural band (pl. xxi, fig. 8).

It should be noted that throughout this part of their course, although they are actually in front of the anus, they are morphologically posterior to it, since the respiratory chamber is an introverted postanal portion of the body. More particularly still it should be noted that the commissure connecting the two cords lies dorsal as well as posterior to the anus. This subject will be further discussed below.

The situation of the lateral nerves relatively to the body-wall is worth notice. They lie throughout their course internal to the muscular layers and just external to the cœlomic epithelium. Compare this condition with that in *Priapulius* and *Halicryptus*. Of the latter two Scharff [6] writes 'the nervous system lies entirely in the ectoderm and 'all previous observers state that the nervous system lies immediately under the hypodermis, between it and the annular muscles. In reality, however, it is placed within the hypodermis, the ganglionic cells being simply modified hypodermic cells and the fibrils their processes.' *Investigator* has evidently advanced considerably in the evolution of its nervous system beyond the members of these two genera, its nearest allies.

REPRODUCTIVE SYSTEM.

The only specimen which was suitable for minute examination proved to be a male.

The single testis (pl. xxi, fig. 7) consists of an elongated cellular mass running for the whole length of the trunk in the dorsal line, to the left of the alimentary canal. It is contained within a membranous endothelial tube which is presumably a compartment of the cœlom. At its anterior end the walls of this tube are in continuity with the walls of the dorsal blood-vessel and of the vessels of the alimentary plexus, and throughout its course the dorsal blood-vessel runs in its dorsal wall.

On reaching the level of the anterior extremity of the respiratory chamber it curves inward to the axial line of the body, towards the base of the gill-stalk (pl. xxi, fig. 8). At this point unfortunately my series of sections is slightly torn and it has not been possible to clearly demonstrate an opening from the testicular tube into the respiratory cavity. It seems almost certain, however, from the course taken by the organ that its contents escape to the exterior through this cavity.

In regard to the structure of the organ itself. For almost its entire length the tube is imperfectly divided into a right and left half by a thin membranous partition springing in places from the dorsal in places from the ventral wall. The cells on the surface of this partition are the parent cells of the spermatozoa. The latter consist of apparently naked nuclei of the shape of a peg-top. From the pointed end a small flagellum projects. They stain very intensely with hæmatoxylin. They are found in very large numbers, completely filling the cavity of the gonocœl.

NEPHRIDIA. (Pl. xxi, fig. 9.)

The nephridia are a pair of branching tubes which open by a single pore at the edge of the shield in the mid-ventral line and extend forward in the cœlom for $\frac{1}{8}$ th of the body-length, one on each side of the mid-line. Each tube divides into three branches. They lie in the dorsal cœlomic compartment, between the gill-chamber and the hindgut dorsally, and the liver ventrally. A communication with the cœlom has not been found.

Histologically they are made up of a columnar epithelium, the cells of which exhibit large vacuoles at their free margin. The vacuolated portion of the cell breaks off into the lumen of the nephridium. This state of affairs is practically identical with that described by Shipley in *Phymosoma varians* [10].

SYSTEMATIC POSITION.

There does not appear to be any reasonable objection to the claims of *Investigator sicarius* to the name Gephyrean. The general shape of the body, the existence of an introvert, the character of the spines, the absence of segmentation, the presence of a large cœlom, and the single pair of nephridia are strong proofs. The only fact which would count against this contention is the absence of the ventral nerve cord and the fact that its place is taken by two ventro-lateral cords. But although this must be regarded as a highly important character, it is probably in this case a fairly late modification and certainly not above ordinal value. If it were an early modification and above ordinal value the resemblances to the Gephyreans detailed above could hardly be so marked. It is not of such importance as in the case of, *e.g.*, the Nemertines.

Within the Phylum, *Investigator* most closely approaches the Priapuloida. The anus and the nephridial pore are situated close to the posterior end of the body. The only important difference is the difference in the nervous system.

The following addition to the Phylum Gephyrea is therefore proposed:—

Order INVESTIGATOROIDEA.

Gephyrea with anterior terminal mouth and posterior sub-terminal anus, with a nervous system consisting of dorsal cerebral ganglia and two lateral nerve cords.

Genus INVESTIGATOR, gen. nov.

It seems prudent to leave the definition of the genus until the discovery of other species and to proceed without further delay to the definition of—

Investigator sicarius, sp. nov.

Body divided into trunk, neck and head. Trunk sausage-shaped, narrowing fairly abruptly to the neck which is approximately one-and-a-half times the length of the trunk. Head globular, introvertible. No tentacles. Mouth slit-like, situated on a diamond-shaped area of specialized skin. Posterior to this area the head bears several circles of simple spicules. The skin of the neck and trunk is uniformly covered with glassy chitinous spines, needle-shaped on the anterior portion of the neck, broadly lanceolate on the trunk. The hind end of the body is formed by a flatly conical shield. The spines at the edge of the shield are long and spike-like, projecting outward, on the surface of the shield they converge on an aperture in the centre. This aperture leads into a gill-chamber containing a bilaterally divided gill. The anus opens on the ventral wall of this chamber. Nephridia two, opening at the edge of the shield.

Colour.—Head pink, neck and trunk olive-green with a silvery sheen due to the spines.

Measurements.

Trunk length	12—13 mm.
,, max. diameter	5 ,,
Neck length	18—19 ,,
Head ,,	4 ,,

Habitat.—Bay of Bengal and Indian Ocean, at a depth of 250—600 fathoms, on a muddy bottom.

SOME CONSIDERATIONS OF COMPARATIVE MORPHOLOGY.

1. Relationship of the post-anal region of *Investigator* to the similar region of *Priapulidæ*. By the post-anal region in *Investigator* is to be understood that portion of the respiratory chamber lying in front of the anus, and the gill. The respiratory chamber from its opening to the base of the gill-stalk is formed by an invagination of the body-wall and thus clearly all that lies actually in front of the anus is morphologically posterior to it. Now if in imagination this chamber be again everted so that it projects behind the anus as a conical tail with the gill at the tip, we get a structure bearing a very striking resemblance to the post-anal region of *Priapulids*. It is hollow, the cavity continuous with the cœlom. On its surface are projections of respiratory lamellæ. The gill is merely an exaggerated respiratory papilla. So far the resemblance is very striking, but, as has been pointed out above, the post-anal region of *Investigator* lies dorsal to the anus, that of the *Priapulidæ* ventral to it.

The question then arises can two organs placed in such antagonistic morphological situations be homologous or not? We shall content ourselves with stating the problem.

2. The nervous system, consisting of cerebral ganglia and two lateral nerve cords, consists of two bilaterally symmetrical halves. These two halves are joined together (*i*) in the head dorsally by the large commissures of the cerebral ganglia; (*ii*) behind the anus again dorsally by a broad important commissure rich in nerve cells; (*iii*) in the head ventrally by a fine commissure resembling a single nerve destitute of nerve cells.

Proceeding to make the condition diagrammatic, we get a picture of an animal with mouth and anus surrounded by a nervous loop lying dorsal to the alimentary canal. Now if we assume that the blastopore of the gastrula is the origin of both mouth and anus and that the primitive nervous system of the gastrula consists of a ring around the blastopore, we could easily derive *Investigator* from such a gastrula, and the only difference between our subject and an Invertebrate with a ventral nerve cord would be that the sides of the nerve ring had not, in *Investigator*, fused beneath the alimentary canal, which is formed by the coalition of the sides of the elongated blastopore.

The most important lesson to be derived from the anatomy of *Investigator* appears to be this, that in two closely allied groups such as the Priapuloidea and Investigatoroidea a marked difference can exist in the anatomy of the peripheral nervous system (regarding the dorsal cerebral ganglia as 'central' and all else as 'peripheral'), and that changes in the position of the main longitudinal nerve trunks in coelomates may not be so difficult of accomplishment as has been thought hitherto.

LIST OF SOME PAPERS BEARING ON THE SUBJECT.

1. Andrews, E. A. "Reproductive Organs of *Phascolosoma Gouldii*," *Zool. Anzeiger*, xii, p. 140 (1889).
2. Selenka, E. *Report Voyage H.M.S. "Challenger," Zoology*, vol. xiii, Gephyrea (1885).
3. Ehlers, E. "Ueber die Gattung *Priapulus*," *Zeits. für wiss. Zool.*, xi, p. 205.
4. Ehlers, E. "Ueber *Halicryptus spinulosus*," *Zeits. für wiss. Zool.*, xi, p. 401.
5. Koren, J., and Danielssen, D. C. *Fauna littoralis Norvegiæ*, Bergen, 1877.
6. Scharff, R. "On the Skin and Nervous system of *Priapulus* and *Halicryptus*," *Quart. Journ. Micros. Soc.*, 1885, p. 193.
7. Schauinsland, H. "Die Excretions- und Geschlechtsorgane der Priapuliden," *Zool. Anzeiger*, ix, p. 574 (1886).

8. Schauinsland, H. "Zur Anatomie der Priapuliden," *Zool. Anzeiger*, x, p. 171 (1887).
9. Selenka, E. "Monograph of Gephyrea," *Semper Reisen im Archipel der Philippinen*.
10. Shipley, A. E. "Phymosoma varians," *Proc. Roy. Soc.*, 1890, p. 122.
11. Shipley, A. E. "Phymosoma Weldonii," *Quart. Journ. Micros. Soc.*, 1891, p. 111.
12. Sluiter, C. Ph. "Gephyrea of Siboga Expedition," *Siboga Reports*.

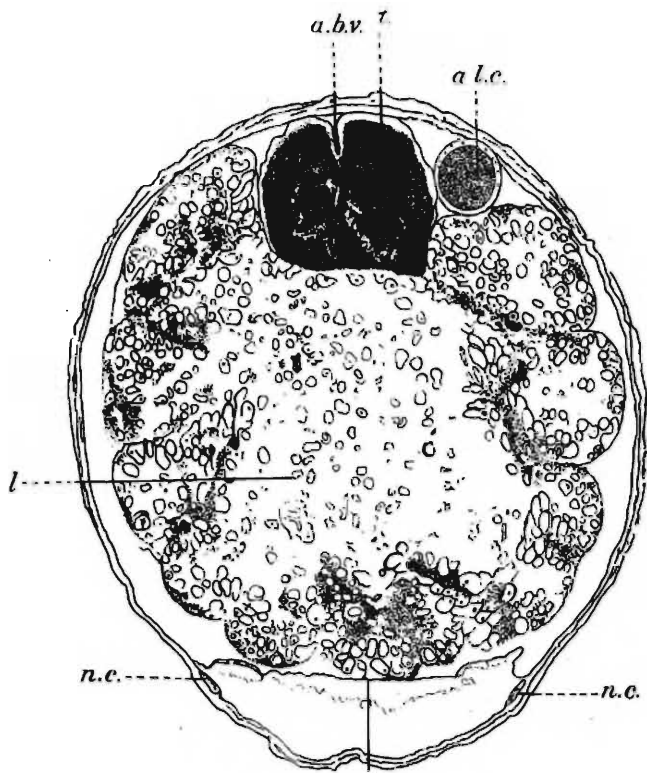
The reports on the Gephyrea of the "Belgica" and "Valdivia" expeditions have not yet appeared.



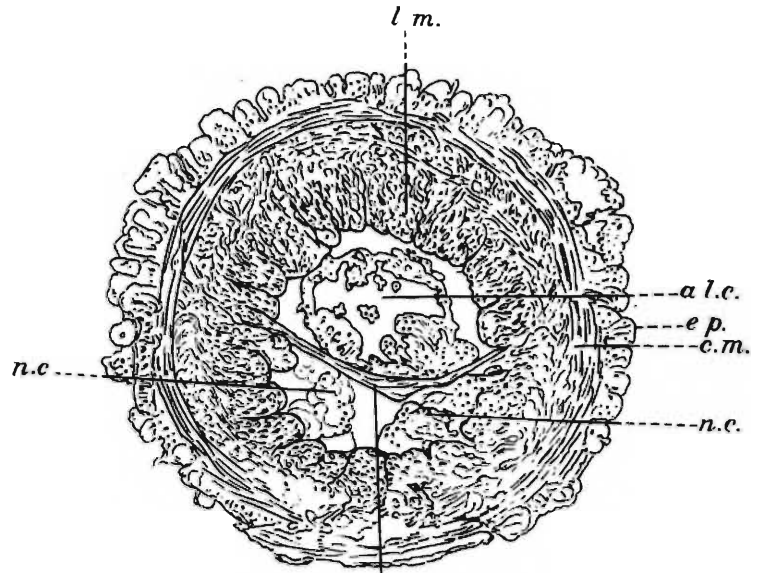
EXPLANATION OF PLATE XXI.

- FIG. 1. *Investigator sicarius*, × 6.
- „ 2. Spine from trunk, highly magnified.
- „ 3. Spine from edge of shield, highly magnified.
- „ 4. The gill and gill-chamber. The shield has been split in two longitudinally in the sagittal plane. The cut surface of one half is represented, showing one half of the gill lying in the gill-chamber, × 10.
- „ 5. Transverse section through the neck, to show structure of body-wall, the division of the coelom by the coronal diaphragm and the position of the lateral nerve cords, × 80.
- „ 6. Transverse section through the commencement of the trunk. Shows the coelom at its greatest extension with four septa in addition to the coronal diaphragm, × 60.
- „ 7. Transverse section through trunk, × 35.
- „ 8. Transverse section through hind end of the trunk at the level of the anterior wall of the respiratory chamber, to show the union of the lateral nerve cords in the posterior nerve commissure dorsal to the alimentary canal, × 37: *siph.* is a siphon-like outgrowth of the hind-gut. The section of the alimentary canal in the dorsal region of the figure is an oblique longitudinal section.
- The longitudinal nerves are too minute in this section to appear in the drawing.
- „ 9. Transverse section through the shield, × 55.

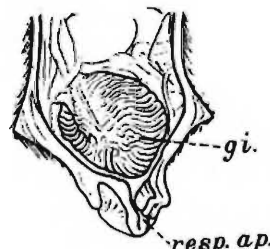
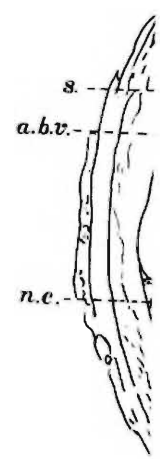
REFERENCE LETTERS.—*a.b.v.* = dorsal blood-vessel; *al.c.* = alimentary canal; *cart.* = cartilage; *c.e.* = cutting edge; *c.g.* = cerebral ganglion; *chit.* = chitinous cap; *c.m.* = circular muscle; *coel.c.* = coelomic corpuscles; *cor.d.* = coronal diaphragm; *ep.* = epidermis; *gi.* = gill; *gl.ap.* = aperture of poison gland; *l.* = liver; *l.m.* = longitudinal muscle; *n.c.* = lateral nerve cord; *neph.* = nephridium; *p.gl.* = poison gland; *ph.gl.* = pharyngeal gland; *p.n.c.* = posterior nerve commissure; *r.c.n.* = recurrent portions of lateral nerves on the respiratory chamber; *resp.ap.* = aperture of respiratory chamber; *resp.c.* = wall of respiratory chamber; *resp.cav.* = respiratory cavity; *resp.lam.* = respiratory laminae of gill-chamber; *s.* = septum; *t.* = testis.



cor. d.
7. x 35.



5. x 80.



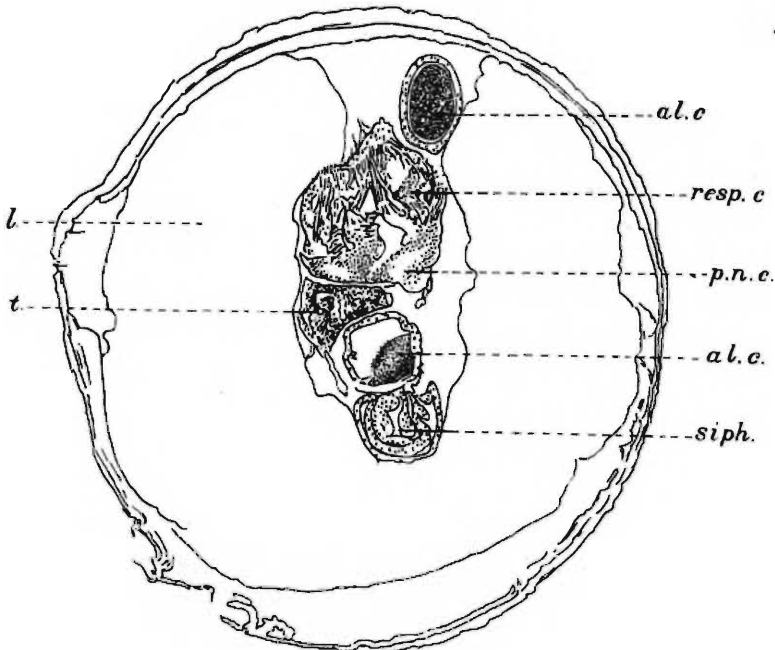
4. x 10.



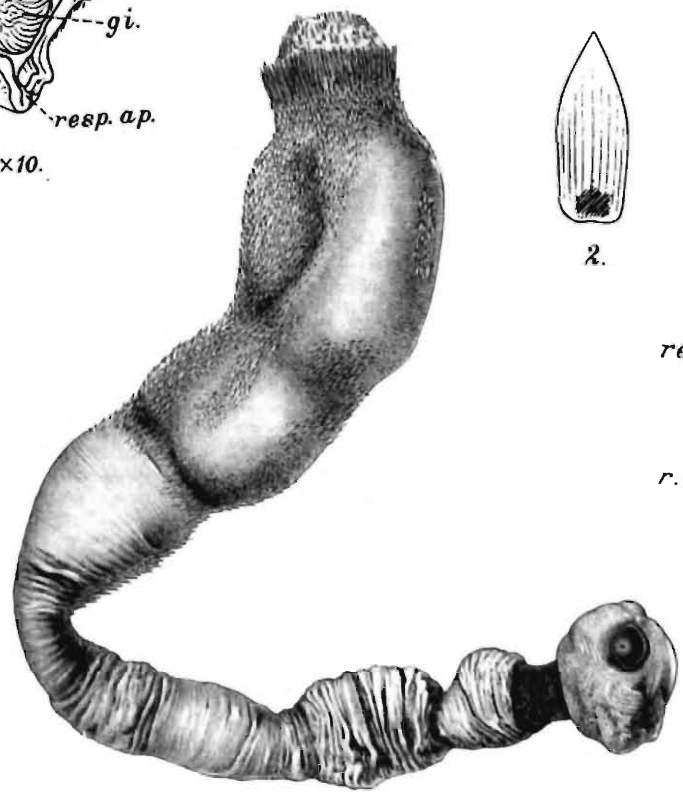
3.



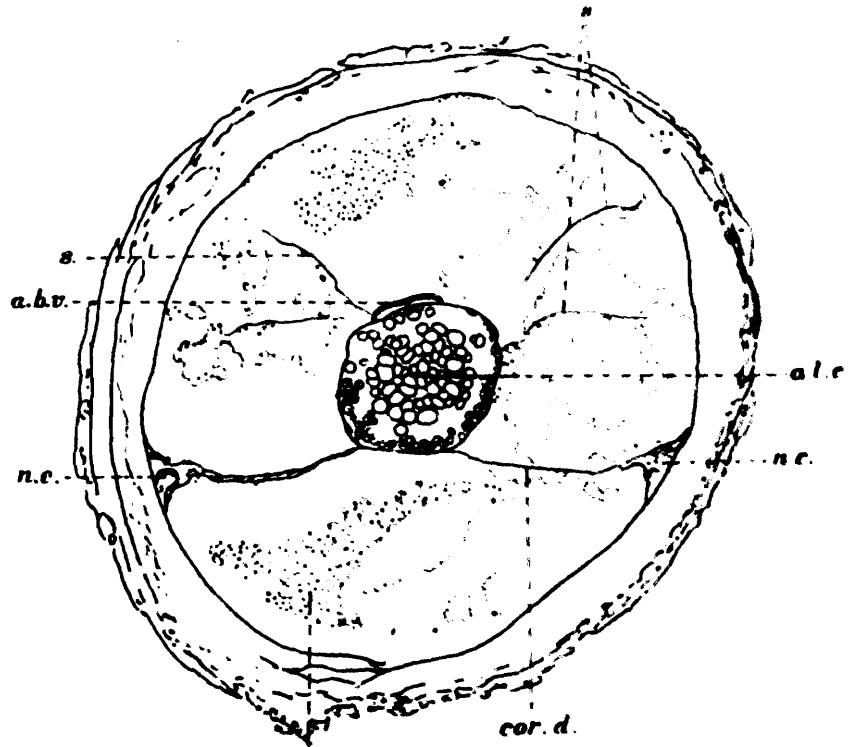
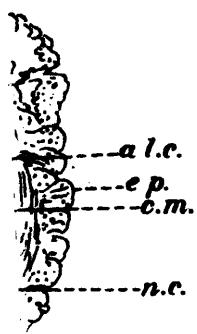
2.



8. x 37.



1. x 6.

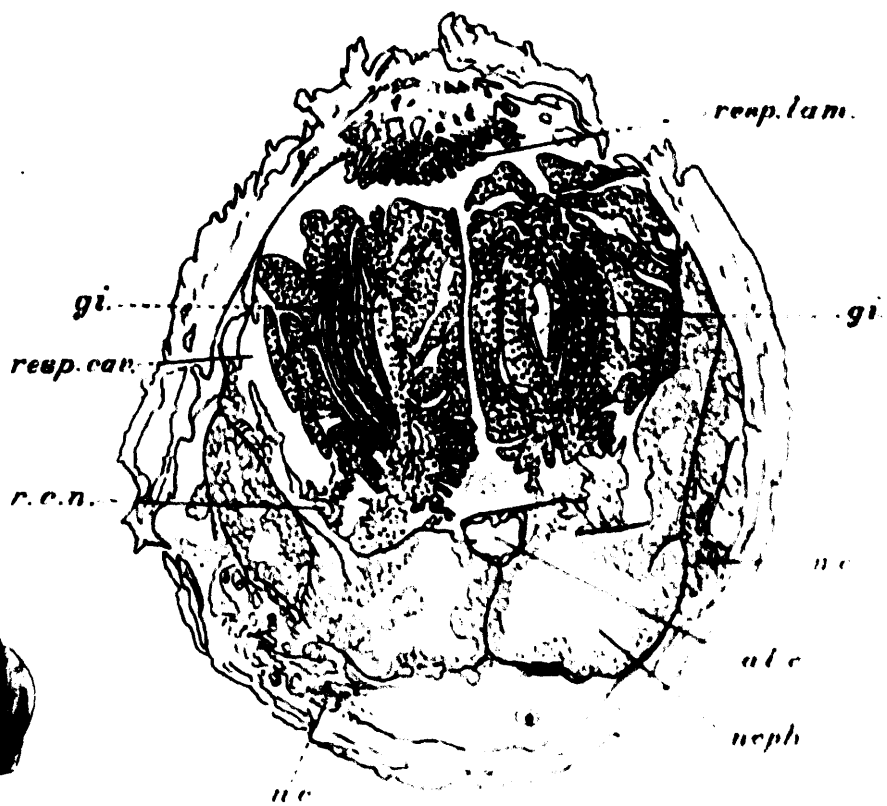


coel. c. 6. x 60.

3.



2.



9. 55

