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On Phymosoma varians.

By

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With Plates I, II, III, IV.

The material which forms the basis of the following paper was collected and preserved by Mr. W. F. R. Weldon, of St. John's College, Cambridge, during a visit to the Bahamas. On his return to England Mr. Weldon commenced to work at Phymosoma, and made many microscopic sections and drawings. When, however, he received the appointment which he now holds at Plymouth he handed the whole material, together with his drawings, to me, with a request that I would complete the work thus interrupted. This statement will serve to show how much I am indebted to Mr. Weldon, both for material and for many of the drawings; but I have further to express my indebtedness to him for many suggestions and much help in completing the work he was unfortunately obliged to lay aside.

The observations here recorded were made on a species of Phymosoma (Ph. varians, Selenka) collected in the Bahama Islands.

This species was sufficiently common in the island of New Providence; but it occurred still more abundantly in the lagoon of the Bemini atoll. The specimens were obtained by breaking up soft masses of coral rock with a hammer. Pieces of rock which were completely covered at low water contained many more specimens than those which were left dry by the tide.

The species seems to be capable of much variation; and the descriptions hitherto published are incomplete in one or two important points. A detailed account of the external characters may therefore be not altogether useless.

External Characters and Ectoderm.

The length of fully extended specimens averages 50 mm., varying, however, from about 40 mm. to 55 mm. The greatest diameter of the trunk is from 4 mm. to 5 mm.; that of the introvert about 2 mm. The introvert is at least equal in length to the rest of the body.

The head (figs. 1 and 5) bears a crown of about eighteen tentacles, arranged in the form of a horseshoe, with the open ends directed backwards; the whole structure lying far back on the dorsal region of the head (fig. 1). The ends of the tentacular horseshoe are connected with the lower lip; which is a thick vascular crescent enclosing considerably more than three fourths of the circumference of the head (figs. 2 and 6). The mouth is a narrow crescentiform slit, extending between the dorsal margin of the lower lip and the convex surface of the crown of tentacles. These relations of tentacular crown, mouth, and lower lip are shown in the diagram (figs. 1 and 32). It will be seen that in this species the condition of the head presents a marked resemblance to that which obtains in Phoronis.

The tentacles themselves are short and simple, the surface directed towards the outer (convex) side of the lophophor being grooved, and the groove is ciliated; the opposite surface is covered with a deep brown pigmented epithelium (fig. 5).

The space included within the concavity of the lophophor (the representative of the præoral lobe) is covered with a wrinkled, pigmented skin. In its centre lies a deep depression, similar to that of Sipunculus, at the base of which lies the brain; while a sense-pit opens on to it on each side[1] (figs. 1 and 7).

The introvert is dividable into several regions. Immediately behind the head follows a narrow, perfectly smooth region, extending for about 2 mm. At the posterior edge of this region is attached a small but very extensile collar, its anterior margin being free (figs. 1 and 4.) Behind the attachment of the collar the introvert swells slightly, and there follows a region about 6 mm. in length, which bears about twenty rows of hooks. Then follows a region of variable length, bearing papillæ; and lastly a second region of hooks, which in our specimens bore from forty to between fifty and sixty rings. Among the hooks of the posterior region are many papillæ; and these in passing backwards get more and more conspicuous, at the expense of the rings of hooks. These papillæ also exhibit traces of a tendency to form rings round the base of the proboscis. The characters of the hooks have been well described by Selenka and by Keferstein:[2] it will be sufficient here to refer to description given by these authors, and to the drawing (fig. 21).

The papillæ on the introvert have the form shown in fig. 15; they are hemispherical or hemielliptical, being often higher than broad, each having a central opening surrounded by three or four plates of chitin, which often fuse into a single piece; and surrounding this central piece are numerous small rounded plates covering at least the upper half of each papilla.

The papillæ on the trunk (figs. 11, 14, and 16) have a somewhat different appearance, being larger and flatter, and having no marked central plate. They are also surrounded by a much pigmented ring. These trunk papillæ agree with the description given by Selenka, who, however, seems to have overlooked the difference between the papillæ in the two regions of the body. The papillæ are large and conspicuous at the two extremities of the trunk, where they are present on all sides;

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[1] Cf., Spengel, "Die Sipunculiden," 'Reisen im Archipel der Philippinen,' Bd. iv, 1883.

[2] Selenka, loc. cit., 'Keferstein, Zeit. für Wiss. Zool.,' Bd. xv, 1865.

in the middle of the body they are, however, almost entirely confined to the dorsal surface. These papillæ are shown in fig. 11.

The colour varies in different specimens. The ground colour is always yellowish-brown, with a peculiar iridescence, noticed by other observers: on this are patches of a black or deep brown pigment, which are generally so arranged as to form a few irregular rings in the middle of the introvert and smaller patches on the anterior dorsal part of the trunk. Individuals are, however, found in which the pigment is only very slightly developed; while in others the whole dorsal surface of the body is thickly mottled with dark patches.

The body wall is everywhere covered by an ectodermal epithelium, one cell thick. The characters of the cells presenting marked differences in different regions.

The ectoderm covering the lower lip and the outer grooved surface of the tentacles is columnar and covered with short thickly set cilia (figs. 4 and 8).

The præoral lobe, together with the inner surface of the tentacles, is covered by a layer of cubical cells, the outer half of each cell in this region being loaded with granules of a dark brown pigment (figs. 4, 7, and 8). These cells are not ciliated.

The epithelium covering the collar is formed of short cubical cells, which appear to become more flattened when this organ is extended (fig. 4).

On the remainder of the introvert the ectoderm secretes, except in the region of the hooks and papillæ, a clear homogeneous cuticle 0·02 mm. thick.

Each hook is secreted by a raised papilla, which projects into the cavity of the hook. The cells covering the papilla being large and cubical, provided with conspicuous spherical nuclei (fig. 21).

Behind each hook is a small organ, apparently sensory, which will be described below.

The ectoderm of the trunk consists of lamellar, dome-shaped cells, secreting a thick cuticle almost ·04 mm. in thickness (fig. 13). The outer surface of this cuticle is rough and granular; and it absorbs staining fluids with a certain readiness, while the main body remains in all the preparations quite unstained. The cuticular substance appears in the greater part of the body to be arranged in wavy columns, running more or less regularly at right angles to the surface of the body, and resting each on a single ectoderm cell (fig. 10). Each column exhibits a further tendency to a laminated structure, the layers composing it lying concentrically to the body of the animal.

A result of the peculiar shape of the ectoderm cells in the trunk-region is the formation beneath them of a series of small cavities, containing a coagulum. By a kind of lifting up of several cells from the adjacent muscles, these cavities communicate with one another and so attain a considerable size (fig. 10). They communicate with the cavities, to be presently described, which lie between the two layers of the papillæ (fig. 16).

The function of these channels is in all probability connected with the circulation of the nutrient fluids; but I have not succeeded in tracing a connection between these and any other of the cavities of the body. The analogy between these spaces and the dermal spaces of Sipunculus need hardly be pointed out. A surface view of the skin shows that the cuticle is broken up into a series of fusiform areas (fig. 11). These areas roughly correspond with the skin-papillæ, the lines limiting them being formed by thickened portions of cuticle. When the animal is in an expanded condition the areas become thicker and shorter.

The papillæ of the introvert and trunk are entirely ectodermal. Their external appearance has already been described; the arrangement seen in section is shown in figs. 14 and 16.

The cuticle seems, in the region round the base of each papilla, to contain irregular spaces, as if its inner and outer surfaces had been pulled apart, an appearance which may, of course, be due to the action of the knife used in cutting sections. On the papilla itself, the plates seen in surface views are visible as local thickenings of the cuticle, and are often loaded with a bright yellow-brown pigment.

The body of the papilla has the form of a double cup, as if it had been formed by the invagination of a spherical outgrowth of the general ectoderm. The outer layer of the cup is composed of flattened cells, which are continuous with those of the general ectoderm at the base of the papilla, and with those of the inner cup at its apex. The inner layer of the cup consists of large cells, loaded with granules of a bright yellow substance, so that the remains of their protoplasm are seen as slender strings of stained material, separating masses of the yellow formed material. This inner cup contains a small cavity, which communicates with the exterior by the pore at the apex of the papillæ. Between the two cups is a cavity, continuous with the subepidermal system of spaces above mentioned.

In the absence of a detailed knowledge of the habits of the living Phymosoma it would be rash to assign any function to these very curious organs, but it seems not improbable that the secretion they produce may assist in softening the coral rock in which the animals form long tubular passages.

General Anatomy.

The arrangement of the internal organs is shown in fig. 3 which represents a Phymosoma cut open longitudinally and the body wall turned back to expose the viscera. The introvert is invaginated to almost its full extent, the true anterior end of the body being at the point where the sense-pits lie.

The longitudinal and circular muscles of the skin have been omitted for the sake of clearness; a detailed description of them is given below.

The retractors of the introvert are four in number. They fuse round the first half of the œsophagus forming a muscular tube, and then separate into a dorsal and a ventral pair. The former are much the shorter pair; between them lies the dorsal blood-vessel, whilst the ventral pair have at their base the generative ridge and between them the nerve-cord. The spindle muscle supporting the alimentary canal is shown running up the axis of the intestinal coil. The œsophagus is anteriorly surrounded by the retractor muscles, but the posterior half is free and ends in the coiled intestine. The number of coils varies, usually there are about fifteen. The intestine forms a thicker tube than the œsophagus, it ends in the rectum which passes straight to the anus in the dorsal middle line.

The only part of the vascular system visible is the crumpled dorsal vessel.

The brain is indicated through the walls of the introvert, and close behind it, at the sides, two black spots, the sense-pits, are visible; the ventral nerve-cord is seen running down the body.

The nephridia or brown tubes are conspicuous objects, varying very much in size and shape in different individuals. Their external opening is at the anterior end and a little in front of the level of the anus. The opening is followed by a short neck which opens into the swollen portion or bladder which passes into the true secreting portion. The anterior half of the nephridia is attached to the body wall by muscle-fibres, the posterior is free (fig. 18).

The generative ridge runs across the body at the base of the ventral retractors (fig. 22). It is sometimes V-shaped, the ridges slanting backward in the middle ventral line.

The Muscular System.

The muscular system is composed throughout of fusiform fibres with simple pointed ends. Each fibre consists of an outer contractile and an inner granular portion, the outer portion being longitudinally striated. The elongated oval nucleus lies entirely within the inner layer, the nucleus and the contractile layer being easily stained, while the inner substance does not absorb staining fluids (figs. 13 and 21).

The fibres of the retractor muscles are much larger than those of the body wall, their diameter being at least twice as great.

The fibres of the general body wall are arranged in an external circular and an internal longitudinal layer, separated by an exceedingly delicate layer of oblique fibres. This latter can only be seen in surface views, as, owing to its extreme thinness, it is difficult to detect in sections.

The circular muscles commence behind the collar fold, where they form a series of rings round the introvert, one lying beneath each ring of hooks (fig. 1). Posteriorly to the hook-bearing region the circular fibres form a continuous sheath, which extends to the posterior end of the animal (fig. 22).

The longitudinal fibres form a complete sheath round the introvert, commencing anteriorly just behind the attachment of the collar. At the posterior extremity of the introvert these fibres separate into longitudinal bundles, generally about twenty-two in number, which run parallel with one another down the trunk. In passing backward these bundles gradually fuse with one another, and so become fewer and larger, till near the "tail" they form a series of projecting ridges, giving to a section of the body-cavity in this region a characteristic star-shaped appearance (fig. 13). At the posterior extremity of the body the bundles finally unite. The longitudinal bands occasionally give off side branches, which pass into the adjacent bands (fig. 22).

The retractor muscles of the proboscis arise by a common origin from a kind of dissepiment, stretching across the body at the level of the origin of the mantle fold, and just behind the skeletal tissue of the collar (fig. 9). Almost immediately after their origin they split into two bands, which pass backwards, one on each side of the œsophagus, for about half its length. Each lateral band then again divides into two branches, a shorter dorsal and a longer ventral branch, which run to the body wall, where they fuse with the adjacent bands of longitudinal fibres. The ventral bands, being longer than the dorsal, are attached to the body wall behind these, lying one on each side of the nerve-cord, and being connected by the generative ridge. The posterior ends of the retractor muscles are fan-shaped and split up into bundles of fibres, which pass into the adjacent longitudinal bundles.

A special muscle accompanies the nervous system on each side (fig. 29), and is described in connection with the nerve-cord. Its purpose is probably to regulate the movements of this important organ during the eversion or retraction of the introvert.

The spindle-muscle and the intrinsic muscles of the alimentary canal are described with the digestive organs, and the intrinsic muscles of nephridia with the account of these organs.

Except along the generative ridge, the body wall is lined by a layer of flat epithelial cells, which is never ciliated, in this respect differing from that of Sipunculus.

The Skeletal Tissue.

A curious form of tissue is found in the collar and the tentacular crown of Phymosoma. As it seems to subserve the purpose of supporting and stiffening the collar and tentacles, and as a support for the insertion of the retractor muscles, I propose to call it the skeletal tissue.

The cells composing this tissue are large rounded cells, which lie close to one another, but are not so crowded as to become hexagonal. The cell nucleus is large, and both it and the protoplasm of the cell stain deeply. Running across the cell, usually in a radial direction, are a small number of wavy lines.

This tissue forms a ring lying in the substance of the collar, which it seems to stiffen. The horseshoe-shaped blood-space lies internal to this tissue, which is thicker at some parts, and thus serves to break up the blood-space as indicated in figs. 4 and 6. It also sends extensions into the tentacles, a group of these skeletal cells being formed on both sides of the tentacular nerve in each section of the tentacle (fig. 17).

From the position of this skeletal ring in the collar it will be readily understood that it is just in front of the invaginable introvert, and consequently it affords a valuable hold for the insertion of the retractor muscles which are attached to this part of the body.

The Alimentary Canal.

The digestive tube may be divided into three parts: (1) the œsophagus, which extends from the mouth to the beginning of the coiled intestine; (2) the intestine which forms a close, fairly regular coil with from ten to sixteen turns; in its coiled state it is almost 10 mm. long; (3) the rectum, which is a straight tube passing from the anterior end of the coil to the anus.

In spirit specimens the whole of the alimentary canal is white in colour, and is usually full of fine sand. A spindle-muscle serves to support and keep in position the coiled intestine and rectum. This muscle arises from the extreme posterior end of the body wall, and passes forward along the axis of the coiled intestine and then parallel with the rectum, to be inserted into the body wall a little in front of the anus (fig. 3). It gives off during its course numerous fibres, which are inserted into the walls of the intestine and rectum. In addition to the spindle-muscle the intestine is held in position by a thin muscle, which arises from the ventral surface of the body and is inserted into the anterior end of the coil.

The position of the mouth has been described above. It is a crescentiform slit, lying between the lip and the convex side of the tentacular crown (fig. 6). It is lined with a continuation of the columnar ciliated cells which cover the inside of the lip and the ciliated grooves of the tentacles. The walls of the œsophagus are produced inwards into a series of from six to eight ridges, which reduce the lumen of the œsophagus to a star-shaped tube. The grooves between these ridges are continuous with the grooves on the outside of the tentacles (fig. 9). The whole is beset with short thick-set cilia. Surrounding the œsophagus are a few muscle-fibres arranged circularly. For about half its length this first part of the alimentary canal lies between the retractor muscles, which in this region of the body have been reduced to two bundles of fibres by the fusion of the anterior and posterior muscles of the left and right side respectively. These lateral bundles have fused with the œsophagus, a small amount of gelatinous connective-tissue containing branched cells being found between them and the circular muscles of the œsophagus. The dorsal blood-vessel lies between the lateral muscles in a groove, closely applied to the dorsal side of the œsophagus, and extending back almost to the beginning of the intestinal coil.

Owing to the presence of very fine sand in the intestine and the delicacy of the tube which made it impossible to satisfactorily wash the sand out, I had considerable difficulty in studying the histology of this part. The intestine is lined throughout by a layer of columnar epithelial cells, one cell thick. The nuclei of these cells are situated near the base. Outside this layer is a thin membrane in which muscle-fibres are sparsely scattered. I do not think the intestine is uniformly ciliated, but patches of cilia occur here and there. The arrangement of these ciliated patches I failed to make out. There is no groove with long cilia running the whole length of the animal, such as has been described by Keferstein in Sipunculus.

The lumen of the rectum is almost occluded by the presence of numerous folds projecting into it. These folds are covered with a number of columnar cells some of which are ciliated, but the majority are crowded with large vacuoles containing minute granules; these are devoid of cilia. The rectum has no cæca opening into it, such as are found in Sipunculus.

The external cuticle is folded into the anus for a little way, and the circular muscle-fibres of the body wall are thickened around the anus in this region, forming a very efficient sphincter. A number of radially arranged fibres also pass out all round the anus; these fibres are derived from the longitudinal muscles. Their action is obviously antagonistic to that of the sphincter.

The Vascular System.

There are two varieties of blood-corpuscle found in Phymosoma. The larger kind exist in great numbers in the body-cavity, together with the ripe generative products (fig. 30). They are oval, about ·02 mm long and two thirds as broad; their protoplasm is very clear and transparent, but the nucleus stains well and they have a very definite outline. The cœlomic fluid, in which these corpuscles float, bathes all the internal organs of the animal, and when the contraction of the posterior circular muscles forces the fluid forward it would serve to evert the introvert, which is withdrawn again by the retractor muscles.

The second variety of blood-corpuscle is much smaller than the first, being about half as long and as broad; the protoplasm is not so transparent and stains more readily. These corpuscles are contained in a close space which is usually called the vascular system. This space may best be described as consisting of three parts, all communicating with one another. The first of these is a horse-shoe shaped space (figs. 2 and 7) at the base of the tentacles. From this space there runs up into each tentacle a series of three vessels which anastomose freely with each other and communicate at the tip. As a rule sections of the tentacles show one vessel near the inner pigmented surface of the tentacle, just external to the tentacular nerve and two near the outer surface, one each side of the ciliated groove (fig. 17). The free ends of this horseshoe-shaped space at the base of the tentacles, near the dorsal middle line, are continuous with the ends of another horseshoe-shaped space which lies in the collar. This forms the second of the above-mentioned spaces. As the diagram (fig. 2) shows, it is very irregular in form, breaking up and anastomosing into a number of spaces. This communicates only with the inner smaller horseshoe, between the two is the crescentiform space in which the mouth opens. The third space—usually termed the dorsal blood-vessel—is a very extensile sac running along the dorsal middle line of the œsophagus between the right and left retractor muscles (figs. 2, 3, and 9). It usually extends about $\frac{1}{2}$ cm. behind the head, and it ends blindly behind. Anteriorly it opens in the middle ventral line into the smaller or tentacular horseshoe, and at the point of junction is a large sinus which surrounds about three quarters of the brain—in fact, all those parts which are not in contact with the epidermis (figs. 2, 4, and 8). The nervous matter is thus in close contact with the blood, being separated only by a thin layer of connective tissue, and the endothelium of the blood-space (fig. 27).

The walls of this third part or dorsal vessel are muscular, and in some specimens are much contracted and crumpled. This vessel appears to serve as a reservoir for the corpusculated fluid, and when it contracts and the fluid is forced forward, it would serve to evert the lip and extend the tentacles. The whole of this space is lined by flat epithelium. I have never seen cilia on the walls, and it is entirely closed.

THE NEPHRIDIA.

The nephridia or the renal organs are in the form of a single pair of "brown tubes," as in other Sipunculidæ. They lie on either side of the middle ventral line at some little distance from the nerve-cord. Their anterior extremities, near which are the external openings, being a little anterior to the level of the anus (fig. 3).

Each nephridium is about 1 cm. long, the length in preserved specimens varying according to the space of contraction of its muscular coat; by means of this muscular layer the whole organ has the power of shortening and dilating, and also of throwing itself into a number of curious curves.

At the anterior extremity is a dilated bladder, the diameter of which is from four to five times that of the posterior cellular portion of the organ. The internal opening is situated at the anterior extremity of the bladder and is provided dorsally with a prominent ciliated lip[1] (fig. 18). The external orifice is just

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[1] The existence of this opening is doubted by Selenka, 'Die Sipunculiden,' but it is sufficiently obvious in all the specimens. It was demonstrated in another species of Phymosoma by Dr. Spengel.

behind the internal, and opens also into the bladder. The opening to the exterior is surrounded by a thickened ring of connective tissue with muscle-fibres intermingling, the latter forming a sphincter. The walls of the passage are folded and lined with cubical epithelial cells. The communication between the internal opening and the bladder is effected by means of a short passage, the epithelium of which is ciliated. The walls of the bladder itself are formed of a single layer of cubical cells, a middle coat of irregularly arranged muscle-fibres, and an external investment of peritoneum. The relations of the bladder and its openings will be evident from the diagram, fig. 18. The walls of the bladder are very elastic, they contain many muscular fibres, and are lined with cubical epithelial cells.

The tubular portion of the kidney is a backward prolongation of the bladder, and is attached from the anterior half of its course to the body wall by a mesentery, its posterior half being free. The tube possesses anteriorly a simple lumen, which is broken up posteriorly by a number of septa, producing an appearance which reminds one of that presented by the interior of a frog's lung, the transition between the two regions is very gradual.

The epithelium lining the tubular portion of the kidney is generally one cell thick; it is produced internally into a series of long papillæ, which are separated from one another by a series of depressions (see figs. 19 and 20).

The cells forming the papillæ are extremely long, and are loaded with fine, yellowish granules. In specimens killed during the functional activity of the organ these papilla-cells are furnished at their inner extremities with a series of large thin-walled vesicles, which appear to be thrown off from time to time into the lumen of the kidney (fig. 20).

The granules, with which the kidney-cells are loaded, appear to decrease in number as the vesicles are approached; and it seems possible that the excretory products of the nephridial cells are stored up in the vesicles before being thrown, together with the vesicles themselves, into the nephridial tube. The whole process is very similar to what takes place in a mammary gland during the excretion of milk. Théel mentions that the excretory organs of Phascolion emitted yellow vesicles which resembled drops of oil when the living animal was disturbed.[1]

Between the papillæ lie a series of hemispherical depressions lined by a flattened epithelium, the cells of which are usually loaded at their base with the yellow granules above mentioned. These cells seem to develop into the high columnar cells described above.

The muscle-fibres form an irregular network outside the nephridial cells, lying chiefly at the bases of the papillæ. The hemispherical depressions seem to pass through the meshes of the muscular coat, and to lie in direct contact with the peritoneal investment of the organ (figs. 19 and 20), forming a series of projections visible on the external surface.

The peritoneal epithelium which surrounds the kidney is distinguishable from the nephridial cells by the greater ease with which it absorbs staining fluids, and by the absence of secretion granules. In the region of the hemispherical depressions the peritoneal cells frequently form thick masses several cells deep.

It is difficult to avoid the conclusion that the excretion products are passed through the peritoneal cells to the cells of the hemispherical cups, and thence to the cells of the papillæ, the internal opening of the nephridium having relation chiefly to its function as a generative duct.

The relative amount of the secreting epithelium to the cubical epithelium lining the bladder varies greatly; in one specimen even the area between the external opening and inner end of the internal opening was lined with the former cells, thus reducing the bladder to a very small structure.

The lumen of the nephridium contains nothing but the vesicles above described, together with ripe ova or spermatozoa. It is remarkable that the cœlomic corpuscles appear never to pass through the internal opening of the organ.

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[1] Théel, "Recherches sur le Phascolion strombi," 'Kongl. Svenska Vetenskaps-Akademiens Handlingar,' Bandet 14, No. 2.

The Nervous System and Sense-Organs.

The brain is a bilobed organ, continuous by its anterior face with the ectoderm of the invaginated præoral lobe, and surrounded elsewhere by a process of the lophophoral blood-vessel, from which it is separated, not only by the endothelium of the vessel, but also by a connective-tissue capsule (see figs. 2, 4, 8, and 27). The groove between the two lobes is deepest and widest on the anterior surface, where the substance of the brain is continuous with that of the præoral ectoderm.

In the brain, as in the ventral nerve-cord, the ganglion-cells are aggregated in the side nearest the skin; they are on the dorsal side of the animal in the brain, on the ventral in the nervous system.

As the figs. 24, 25, and 26 show, there is a cap of ganglion-cells covering the anterior, dorsal, and posterior surfaces of the brain. The ventral surface is not invaded by the ganglion-cells; but here the fibrous tissue, which makes up the rest of the brain, comes in contact with the thin connective capsule. It is this region of the brain which projects into the blood-sinus.

The majority of the ganglion-cells are small, with deeply stained nuclei, occupying about one half of the cell; they are either unipolar or bipolar. At the postero-dorsal angle of the brain, however, a certain number of giant ganglion-cells are found (fig. 27). These cells have a diameter of ·02 mm., at least four times that of the smaller cells; their nuclei are relatively smaller, and they are unipolar. I was unable to trace what becomes of the fibres given off from these giant-cells. No such giant-cells occur in any other part of the nervous system.

A pair of sense-organs, usually described as eyes, lie embedded in the substance of the brain.

Each of these sense-organs has the form of a long tube bent upon itself, so that one limb is nearly at right angles to the other. The outer limb, the lumen of which is narrow, opens on to the surface of the præoral lobe (figs. 1 and 25), the opening lies at the dorsal lateral angle of the brain, just dorsal to where the circumœsophageal nerve-commissure leaves the brain; the lumen of the inner limb dilates into a vesicular swelling in the substance of the brain (fig. 23); the whole tube has, therefore, nearly the shape of a retort, and lies entirely in the lateral part of the brain. The wall of the tube is everywhere formed by a layer of clear, nucleated cells. In the outer limb these cells form a fairly regular columnar epithelium one cell thick, which becomes less regular as the inner limb is approached. The cells bounding the inner limb are arranged irregularly, and they appear to send out processes from their peripheral extremities, which may be supposed to communicate with the processes of adjacent nerve-cells. The cells of the inner limb also secrete a deep black pigment, which lies in that portion of each cell which is turned towards the lumen of the tube. A clear coagulum sometimes lies in the cavity of this sense-pit. These organs are visible as two black spots at the level of the brain in the dissected animal (fig. 3).

No trace exists in this genus of the curious finger-like processes which project from the brain of Sipunculus into the body-cavity.

Three pairs of nerves are given off from the brain: (1) dorsally, a small pair supplying the skin of the præoral lobe—these lie nearest to the middle line (fig. 26); (2) ventrally, a nerve on each side, going to the corresponding area of the lophophor, and supplying a branch to each tentacle (fig. 24); (3) and posteriorly on each side arises a nerve which passes round the œsophagus, and joins its fellow of the opposite side to form the ventral cord (fig. 24). The lophophoral nerve arises between the point of origin of the nerve of the præoral lobe and the exit of the circumœsophageal commissures.

The ventral cord itself shows no trace either of a division into two halves, or of a segregation of its nerve-cells into ganglia. It runs along the ventral surface of the body as a perfectly uniform filament, terminating posteriorly without any ganglionic swelling such as that found in Sipunculus.

The fibres are on the dorsal, the cells on the ventral side of the cord.

Along each side of the nerve-cord runs a longitudinal band of muscle-fibres, the cord and its pair of muscles being together enclosed in a special peritoneal sheath. The space between the sheath and the cord is filled with a peculiar connective tissue (fig. 29), which has been regarded by some observers as clotted blood, the cord being said to lie in a blood-vessel. My preparations afford no evidence in support of this view; and I am strongly of opinion that the substance lying between the nerve-cord and its peritoneal investment is, as above stated, connective tissue.

By contraction of the muscles within the peritoneal sheath the nerve-cord may become crumpled, so that while the sheath is perfectly straight the cord within it presents the appearance shown in fig. 28.

The nerve-sheath is attached to the ventral body wall by a series of mesenteric cords, each of which contains, not only a prolongation of peritoneal epithelium, but also a central axis of connective tissue (figs. 28 and 29).

The peripheral nerves form, as in Sipunculus, a series of rings encircling the body, and lying between the circular and the longitudinal muscles. In the region of the introvert a nerve-ring lies beneath each ring of hooks, at the base of the circular muscle which supports them (figs. 1 and 2).

Each nerve-ring is connected with the ventral cord by a single short nerve, which runs from one to the other in the middle ventral line.

The lophophoral nerve runs along the base of the tentacles, one on each side of the lophophore. Each gives off a series of small nerves, one of which passes up the axis of each tentacle, lying immediately beneath the ciliated groove (figs. 2, 5, and 17).

In addition to the sense-pits on the brain there are a number of ectodermal structures on the introvert, which are probably sensory in function, and may well be described here. These bodies are arranged in circles parallel to the rows of hooks running round the introvert (fig. 21). One of these organs is shown in fig. 12; the ectoderm-cells have multiplied and increased in size, forming a small heap; some of these cells have then formed stiff processes, which project beyond the level of the skin. These processes are gathered up into a small brush by a chitinous ring which surrounds the base.

The hooks (fig. 21) are very closely packed in a series of ridges formed by the circular muscle-fibres of the introvert. The point is directed backward, while the row of sense-organs lies immediately behind them, embedded in the muscular cushion.

The Generative Organs.

Phymosoma varians is diœcious; in no case are ova and spermatozoa found in the body of the same individual.

The ovaries are formed by a fold of the peritoneal epithelium, elsewhere flat, which occurs at the base of the insertion of the long ventral pair of retractor muscles. This genital ridge extends beyond the inner edge of the muscle attachment across the ventral middle line lying between the nerve-cord and the skin; it does not extend beyond the outer or dorsal end of the muscle. The ridge is not quite continuous, but it is interrupted from time to time; its free border is also irregular, and this gives it a puckered or frilled appearance (fig. 22).

In transverse section—parallel to the long axis of the Phymosoma—the ovary is seen to be much thicker at its free border than at its base; the latter indeed is formed of but two layers of cells, thus giving the appearance of a simple fold of endothelium. These layers, however, thicken towards the free edge. Nearly all the cells have become ova, and are held together by a very scanty matrix. The organ is solid, and the ova dehisce from it into the body-cavity.

In the ovary the ova increase in size towards the thickened free edge, where the oldest are. Those found free in the body-cavity also differ somewhat in size, and undoubtedly grow whilst suspended in the perivisceral fluid; but there is a very marked difference in size between the largest ovarian ovum and the smallest floating one—a difference I am quite unable to account for.

The floating ova are oval in shape, the largest about 1 mm. long, with a thick zona radiata, in which the radial markings can only be detected with very high powers (fig. 30). This membrane stains deeply except its outermost layer, which does not absorb any staining fluid. The protoplasm is very granular, and stains well. The nucleus is very large, and sometimes reaches almost from one side of the cell to the other; it does not stain at all. No micropyle was to be seen.

The testis occupies in the male a position similar to that of the ovary in the female. The mother-cells of the spermatozoa separate from the testis before or whilst dividing. Whilst floating in the perivisceral fluid the nuclei of these cells commenced to divide, and the whole floats about as a multinucleated mass of protoplasm. The stages which most commonly occurred were those with eight or sixteen nuclei (fig. 8). The males were much rarer than the females, and none of them contained ripe spermatozoa.

SUMMARY.

The following is a brief summary of the more important points described in detail in the body of the paper.

(1) The head of Phymosoma is surrounded by a stiffened vascular horseshoe-shaped lip, the dorsal ends of which are continuous with the ends of a hippocrepian lophophor. The lophophor bears a crown of about eighteen tentacles—the number is always even. In the hollow of the lophophor lies the brain, which is continuous with the ectoderm of the præoral lobe. The inner surface of the tentacles and the ectoderm above the brain is crowded with dark brown pigment-granules, and the ectoderm of the præoral lobe is curiously wrinkled. Between the hippocrepian lophophor and the vascular lip is the crescentiform opening of the mouth.

(2) At some little distance behind the lip is a thin but very

extensile collar, which may be so extended as to entirely cover the head.

(3) The ectoderm consists of a single layer of cells. This secretes outside a cuticle of varying thickness. The ectodermal cells are vaulted, so that spaces are left in which a nutrient fluid might circulate between the circular muscles and the ectoderm. The ectoderm of the lower lip and of the outside of the tentacles is ciliated.

(4) The skin-glands are of two kinds; each is formed by the modification of ectoderm-cells, which results in the pushing in of certain of the cells to form a double cup. The inner layer of cells thus produced develops a number of granules, which are extruded through a median aperture. In one kind of skin-gland, those of the introvert, this aperture is surrounded by a chitinous ring, which is absent on those of the trunk.

(5) Rows of hooks set very closely together are found in the introvert; these are each secreted by a small multicellular papilla.

(6) A skeleton tissue is present in the lip and tentacles. This seems to stiffen these structures, and to form a firm hold for the attachment of the retractor muscles of the introvert.

(7) The nephridia or brown tubes consist of two parts, the bladder and the secreting part. The former opens both to the exterior and to the body-cavity, the latter opening being shaped like a flattened funnel and ciliated. The secreting part opens only into the bladder. Its walls are lined with a columnar epithelium, the cells composing which are crowded with granules. From time to time a vesicle or bubble crowded with these granules is formed at the free end of the cell, and ultimately breaks off into the lumen of the nephridium, and so passes out of the body. The only other structures found in the cavity of these organs besides these vesicles, were the ripening generative cells.

(8) The vascular system consists of a horseshoe-shaped plexus in the lower lip, a similar plexus in the lophophor which gives off branches into each tentacle, and a reservoir

lying dorsal to the œsophagus. This communicates with the lophophoral sinus in the dorsal middle line. Just at this point is a blood-sinus which surrounds all those parts of the brain which are not continuous with the ectoderm. This system of blood-vessels is closed. It contains numerous small oval corpuscles. In addition to these the cœlomic fluid contains a number of much larger corpuscles, as well as ova and sperm morulæ. The cœlom is lined by a flat epithelium which is not ciliated.

(9) The brain is a bilobed mass, partly connected with the ectoderm of the præoral lobe and partly surrounded by a blood-sinus. The relative position of the ganglion-cells and fibrous tissue is described above. There are a number of giant ganglion-cells arranged in the lateral and posterior parts of the brain.

(10) The brain gives off three pairs of nerves : (1) the first pair pass to supply the pigmented tissue of the præoral lobe; (2) the second pair run along the base of the lophophor, and send a branch into each tentacle; (3) the third pair pass round the œsophagus, and unite to form the ventral nerve-cord. This is supported by a strand of muscle in each side, and by numerous connective-tissue strands which pass to the body wall. It has no trace of a double structure, and no segmentally arranged nerve-ganglia. It gives off from time to time a median nerve, which soon splits, and each half runs round the body, these fuse together again in the dorsal middle line, thus forming a nerve-ring.

(11) The sense-organs consist of two pigmented pits in the brain, and of certain structures in the introvert. The former pits open on to the præoral lobe, and then pass into the brain at each side. Each pit is bent on itself, and expands slightly at its inner end. The cells lining the pit are crowded with black pigment. The sense-organs on the introvert lie in rows close behind the rows of hooks. Each consists of a number of ectodermal cells produced outwards into a stiff process. These processes are gathered up into a little brush by a chitinous ring which surrounds their base.

(12) The animals are diœcious. The generative organs are in the form of ridges at the base of the ventral retractors. The flat cœlomic epithelium is here modified to give rise to ova in the females and the sperm morulæ in the males.

Conclusions.

I do not propose to consider at any length the theoretical conclusions which might be drawn from the facts above indicated until I have worked out in detail other forms of the Gephyrea, which I hope to do in the immediate future. I should, however, like to say something in favour of maintaining the genus Phoronis in its old position—that is, as a form closely allied to the more normal Gephyrea inermia.

This relationship is most easily seen by comparing a view of the head of Phymosoma as seen from above with a view of Phoronis (figs. 31 and 32). In both genera the mouth is surrounded by a pair of vascular horseshoe-shaped ridges, one of which is dorsal and the other ventral : the sole point of difference lies in the fact that while in the one case the tentacles of the lophophor extend along both the ventral and the dorsal horseshoe, they are in the other case confined to the dorsal limb.

Again, the præoral lobe of Phoronis bears two large sensory pits, one on each side of the middle line; these are obviously comparable to the similar pits which open into the area in the concavity of the Gephyrean lophophor which I have spoken of as the præoral lobe. Further, the nervous system of Phymosoma, like that of Phoronis, is permanently connected with the epidermis.

I do not enlarge upon the resemblances in the position of the anus, and the lengthening of the ventral surface at the expense of the dorsal, or on the presence of two nephridia, as these points have been already emphasised by Lankester. But I would direct attention to two structures hitherto, I believe, undescribed in the Gephyrea, which in my opinion have homologues in Phoronis.

The first of these is the skeletal tissue; this, as the description above shows, agrees in position and function with the mesoblastic skeletal tissue which supports the tentacles of Phoronis as described by Caldwell. The second structure I wish to refer to is the thin membranous fold which I have above termed the collar. This seems to me to correspond very closely with the calyx or web which surrounds the base of the head in Phoronis.

The absence in the unarmed Gephyrea of mesenteric partitions in the post-oral body-cavity, similar to those which exist in Phoronis, may be accounted for by the twisting of the intestinal loop in the more normal genera. The radial muscles which extend from the visceral loop to the body wall are, in all probability, the remains of an ancestrally continuous mesentery.

It will be remembered that in Phoronis the body-cavity is divided into an anterior and a posterior division by a transverse septum passing from the body wall to the œsophagus, at the level of the nerve-ring. The former division includes the cavity of the præoral lobe and tentacles, the latter the rest of the body-cavity. I am disposed to think that a similar disposition of parts obtains in Phymosoma. The organ which is usually regarded as forming the blood-vessels in the Gephyrea occupies precisely the same position as the anterior body-cavity in Phoronis; it has, however, acquired a reservoir—the dorsal vessel—into which the fluid may pass when the head is retracted. As this involution is impossible in Phoronis no such reservoir has been developed. If this homology holds, there is nothing in the Gephyrea homologous with the true blood system of Phoronis. In connection with this it is perhaps worth noticing that the so-called vascular system in the Gephyrea gives off no vessels or capillaries, but simply consists of a number of intercommunicating spaces.

April, 1889.

The Morphological Laboratory,
Cambridge.

DESCRIPTION OF PLATES I, II, III, and IV,*

Illustrating Mr. Arthur E. Shipley's paper "On Phymosoma varians."

PLATE I.

Fig. 1.—A semi-diagrammatic view of the anterior end of Phymosoma varians. The introvert is everted and the tentacular crown expanded. The collar is not extended and lies at the base of the head. Only two rows of hooks are shown.

Fig. 2.—A semi-diagrammatic view of the closed vascular system and nervous system, showing their relation to the alimentary canal. The vascular system shows the three parts, the lophophoral, the lower lip, and the dorsal blood-vessel. The latter communicates with the lophophoral in the middle line, and just at this point the sinus round the brain is given off. The brain is relatively too small. The three main nerves are shown, and the circular nerves which run in the skin. The œsophagus is cut off abruptly in front in order to display the vascular ring.

Fig. 3.—View of a Ph. varians which has been opened along the median dorsal line. The introvert is retracted, the true anterior end of the body being where the eye-spots lie. Here and there patches of skin are seen which bear papillæ.

PLATE II.

Fig. 4.—A median longitudinal section through the head. The introvert is retracted, and the collar expanded until it encloses the whole head. The section is not quite in the middle line, or the lip on the dorsal surface would not be shown, cf. Fig. 6. The brain is cut through that part which is continuous with the ectoderm.

Fig. 5.—A transverse section through the tentacles: the introvert is retracted. The tentacles show the ciliated groove on the outer surface, the pigmented epithelium in the inner, and the vascular spaces and tentacular nerves.

Fig. 6.—A transverse section through the base of the lophophor and lower lip, just where the two fuse dorsally, the introvert is retracted. The skeletal tissue is shown in the lip, which is ciliated all round.

Fig. 7.—An oblique transverse section through the base of the lophophor, showing the blood-space; and in the centre some of the wrinkled pigmented tissue of the præoral lobe. The introvert is everted.

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[1] I am indebted to Mr. Weldon for the following figures:—Nos. 1, 7, 10, 12, 14, 15, 16, 20, 21, 23, and 27.

Fig. 8.—A transverse section through the head in the region of the brain, The introvert is everted. This specimen had its body wall pushed upwards inside the lower lip in the ventral side into a kind of hernia, this accounts for the swelling containing blood-corpuscles and sperm-morulæ. The brain is shown in its sinus, also the depressions in the tissue of præoral lobe leading to the sensory pits.

Fig. 9.—A transverse section through the œsophagus. The dorsal and ventral retractor of each side have fused into a common lateral muscle, which almost fills up the body-cavity. The lumen of the œsophagus is occluded by ciliated ridges.

Fig. 10.—A section through the ectoderm and cuticle. Below the ectoderm some fibres of the circular muscle may be seen. The ectoderm is vaulted leaving spaces which sometimes contain a coagulable fluid. The cuticle is traversed by numerous perpendicular lines, and the outer part only stains.

Fig. 11.—A surface view of the skin, showing the longitudinal and circular muscle-fibres, the skin papillæ, and the ridges formed by thickenings of the cuticle.

Fig. 12.—A section of one of the sense organs on the introvert, at the base of the ring of hooks.

Fig. 13.—A transverse section through the posterior end of the animal. The longitudinal muscles have fused together and reduced the lumen of the body-cavity to a star-shaped mass. The skin papillæ are very numerous in this region, and the cuticle unusually thick.

PLATE III.

Fig. 14.—Section taken through one of the skin papillæ of the trunk. It shows the opening to the exterior, and the small cavity in the cup composed of enormous cells crowded with spherules.

Fig. 15.—Surface view of the papillæ and hooks in the introvert. The chitinous plates round the orifice of these papillæ are shown.

Fig. 16.—An oblique section through a trunk papilla. This section shows the space between the two layers of the cup in communication with the sub-ectodermal spaces of the skin.

Fig. 17.—Transverse section of a tentacle. At the base of the ciliated groove the tentacular nerve lies. Three blood-spaces are seen, and between them certain skeletal cells. The inner epithelium is crowded with pigment grains.

Fig. 18.—A diagram showing the anatomy of the nephridium. The posterior blind diverticulum is the secreting part, the anterior thin-walled part is the bladder. The arrangement of the internal and external openings may also be seen.

Fig. 19.—An oblique section through the secreting part of the nephridium, under a low power. This shows the peritoneal epithelium, then a dark

layer of muscle-fibres and internally the secreting epithelium. The breaking up of the lumen into numerous side chambers is also shown in this figure.

Fig. 20.—A portion of the same under a high power. The secreting epithelium is seen crowded with granules; at their free edges these cells form vesicles, which break off and fall into the lumen.

Fig. 21.—A section through parts of several of the hooks on the introvert. The multicellular papillæ which secrete the hooks are shown. One of these sense organs at the base of the hooks is also shown cut tangentially.

Fig. 22.—A view of the base of the two ventral retractor muscles, showing the generative organ. The ventral nerve-cord lies between the muscles and dorsal to the generative ridge. The circular and longitudinal muscles are also shown, and the outline of the papillæ.

PLATE IV.

Fig. 23.—A section through the antero-dorsal corner of the brain, to show the blind end of the sense-pit. The cells lining the inner end of the pit are crowded with pigment. A few cells of the ectoderm of the præoral lobe are seen, and part of the blood sinus in which the brain lies.

Fig. 24.—An oblique section through the lateral part of the brain, showing the origin of the circumœsophageal commissure and of the lophophoral nerve. This figure and the three succeeding ones show the arrangement of the ganglion-cells, the giant cells, and nerve-fibres.

Fig. 25.—A section through the brain, transverse to its long axis, and nearer to the middle line than the preceding figure. It shows the fusion of the brain with the ectoderm of the præoral lobe, and the commencement of the præoral lobe nerve.

Fig. 26.—A section in a place parallel to the preceding, but still nearer to the median line, it shows the origin of the præoral lobe nerve.

Fig. 27.—A horizontal section through the posterior part of the brain at right angles to the preceding. This shows the histology of the giant-cells and their relative size.

Fig. 28.—A longitudinal median section of the ventral nerve-cord, showing the arrangement of the ganglion-cells and fibres, and the mesenteries which attach the cord to the ventral body wall.

Fig. 29.—A transverse section of the nerve-cord, showing a mesentery from the ventral body wall, the arrangement of ganglion-cells and nerve-fibres, the connective-tissue sheath, and the lateral muscles which run along each side of the nerve-cord.

Fig. 30.—An ovum and some of the cœlomic corpuscles. The ovum shows the granular protoplasm, the large nucleus, and the zona radiata.

Fig. 31.—A diagrammatic view of the head of Phoronis, seen from in ront.

Fig. 32.—A similar view of Phymosoma.

The Spinning Apparatus of Geometric Spiders.

By

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With Plate V.

The familiar circular snare constructed by the "geometric" spiders has always been an object of interest to naturalists, but it is remarkable how little has been known until lately of the highly complicated organs which compose the spinning apparatus of these animals.

Thanks mainly to the labours of Blackwell,[1] Emerton,[2] Bertkau,[3] and lastly Apstein, a tolerably complete knowledge has now been obtained of the structure and general arrangement of these organs.

Apstein's excellent paper,[4] recently published, contributes much that is new and valuable, and fairly represents our present knowledge of the subject. Recent researches, however, have led me to dissent from some of that author's conclusions as regards the functions of the various spinning glands, conclusions based upon evidence for the most part too indirect to be entirely satisfactory.

Before discussing this matter, some description of the

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[1] "On the Mammalæ of Spiders in Spinning," 'Trans. Linnean Soc. London,' 1839, vol. xviii, pt. ii.

[2] 'The Structure and Habits of Spiders,' Boston, Cassino & Co., 1883.

[3] "Cribellum und Calamistrum," 'Archiv für Naturgeschichte,' 1882, p. 316.

[4] "Bau und Function der Spinnendrusen der Araneida," 'Archiv für Naturgeschichte,' 1889, p. 29.

morphology of the organs in question will be necessary. The large garden spider, Epeira diademata, is taken as the most convenient type of the family, but the following remarks apply in the main to all its orb-weaving congeners.

External Spinning Organs.

These occupy a small round area on the under surface of the abdomen towards the posterior end, where, when at rest, they present a bluntly conical protuberance (figs. 1 and 2, *sp.*). If this area be examined under a low power, it is seen to be occupied mainly by four conical spinnerets, their bases forming a quadrilateral, and their apices meeting in the centre of the area (fig. 8). The narrow space which intervenes between the bases of the anterior (or inferior) spinnerets (*a*) is filled by a small tongue-like process (*t*). The wider gap separating the posterior (or superior) spinnerets (*p*) is occupied by a terminal projection of the abdomen (*z*) containing the anus. Each of these spinnerets is two-jointed, and furnished at its extremity with a multitude of hair-like tubes containing the ducts of the spinning glands.

They are possessed of a wonderful mobility, and can be widely separated, or energetically rubbed upon each other with a rotary motion at the will of the animal. Their separation discloses a third and smaller pair of spinnerets consisting of one joint only, and having their apices directed backwards and inwards, so as to lie immediately beneath the apices of the posterior spinnerets (fig. 10, *i*).

These again present a large number of glandular orifices. They will be referred to hereafter as the intermediate spinnerets. Thus we have, in all, three pairs of spinnerets capable of a great variety of movement, and bearing at their extremities, as will be presently seen, about 600 spinning tubes.

Internal Spinning Organs.

Apstein has shown that there are, in this group of spiders, five distinct kinds of glands, to which he assigns the names Ampullaceal, Aggregate, Tubuliform, Piriform, and

Acinate. The first three kinds are few in number and of large size, extending throughout the greater part of the abdomen. The piriform and acinate glands are minute and numerous, and are closely grouped together immediately above the spinnerets.

Their exact arrangement is important and may be summarised as follows:

There are two pairs of Ampullaceal glands (fig. 3) debouching on the anterior and intermediate spinnerets respectively on the inner side.

There are three pairs of Aggregate glands, their three outlets on each side being situate upon the inner surface of the posterior spinneret.

There are three pairs of Tubuliform glands, two opening on the inner side of the posterior spinnerets, and one upon the outer surface of the intermediate spinnerets.

The above glands are comparatively large, and their ducts terminate in distinct tubular prominences.

There are about 200 Piriform glands, all connected with the anterior spinnerets, where their ducts terminate in hair-like tubes.

Finally, there are about 400 Aciniform glands, each posterior and each intermediate spinneret bearing the hair-like terminations of about a hundred ducts.

Or thus, tabulating for one side only:

GLANDS.	ANT. SPINNERET.	INTERMEDIATE.	POSTERIOR.
Ampullaceal . .	1 on inner side	1 on inner side	...
Aggregate . .	...	...	3 on inner side.
Tubuliform . .	...	1 on outer side	2 on inner side.
Piriform . . ,	About 100	...	...
Aciniform . .	...	About 100	About 100.

The question naturally arises as to the different functions performed by glands apparently so distinct. Apstein attempts its solution by reasoning which is mainly indirect and, in my opinion, misleading. It occurred to me that the problem might be attacked in a more direct manner, and with this view the experiments to be now described were performed.

A spider of this group usually trails a line from its spinnerets while walking. With a little dexterity it can be quickly seized, and imprisoned in such a manner that the spinnerets from which the line is proceeding can be microscopically examined.

This may be best effected by means of a piece of wood about the size and shape of a microscope slide, with a narrow band of cloth attached by its end to one extremity. The cloth band is then held in front of the crawling animal, which may, with a little practice, be thus trapped between the cloth and the wood, so that the band passes beneath the cephalothorax, leaving the abdomen free for examination with the lately emitted line still attached.

The fourth pair of legs must be kept from interfering with the experiment by pins suitably adjusted. The spinnerets will now be in their quiescent position, and the precise origin of the threads therefore invisible. If, however, it be gently drawn forwards, i. e. towards the animal's head, certain facts with regard to it become at once clear. As, however, the phenomena differ at different times, we must take the various cases in succession.

In the simplest case (fig. 9) one of the anterior spinnerets will be pulled forward with the thread, which will be easily seen to consist of a single line emanating from one large tube.

More frequently (fig. 10) the line will be double issuing from similarly situated tubes on the inner sides of the two anterior spinnerets. This is probably the most usual case, and I have drawn out from a spider many yards of such a double line of silk, its origin being all the time plainly visible.

It is important to note that there is no adherence between the two lines, which remain perfectly distinct throughout their whole parallel course.

The spider will probably tire of having its silk thus drawn out—a process which it can only influence indirectly. Were its hind legs free it would seize the thread and break it. It sometimes contrives to do this by a rapid movement of its spinnerets, but occasionally it decides to strengthen the thread instead. The spinnerets are accordingly actively rubbed together, and a little flocculent mass of silk appears upon the line, which is thereafter seen to consist of four strands, two of finer calibre having made their appearance between the former lines (fig. 11). To see their origin the anterior spinnerets must be kept forward by a gentle strain on the thread, and the posterior spinnerets thrust aside with a needle. The new lines may then be traced to the intermediate spinnerets, and proceed from large spinning tubes on the inner side. Again, the four lines remain distinct and non-adherent.

Should the spider still resolve on strengthening the line a further rubbing together of the spinnerets occurs, and presently a large number of strands are seen to proceed from the numerous hair-like tubes on the anterior spinnerets (fig. 12). The four previous lines are still distinguishable by their greater thickness.

If after drawing out several inches of this compound line it be slightly slacked, a puff of air separates the strands, showing that, though contiguous, they are not adherent.

Lastly, upon rare occasions, the whole battery of tubes seems to be brought into play, the posterior spinnerets contributing their quota to the strengthening of the line. Thus the "trailing line," as I have called it, will be found at any moment to be constituted as indicated in one of the cases above described.

It appears, therefore, that such a line usually consists of either two or four non-adherent threads emanating from what Apstein has shown to be the origin of the Ampullaceal glands, and that it may on occasion be strenghened by contributions from the Piriform and Acinate glands opening upon the anterior and posterior spinnerets respectively.

It was next attempted to apply the same direct method to the observation of the animal when employed naturally in its various spinning operations. Here the difficulties experienced were considerable, but some results were obtained by the aid of a simple contrivance, consisting of a pair of compasses with the points fixed some two inches apart, and between them a narrow strip of cloth stretched.

A flat piece of wood was held behind the spider while at work, and between this and the strip of cloth the creature was suddenly trapped, the points of the compasses, which projected the eighth of an inch beyond the cloth, being buried in the wood on either side.

Flies were now placed in the various webs, and the spiders seized in the act of binding them up in the usual manner. The fly is held and rotated by means of the jaws, palps, and anterior legs, while the fourth pair of legs draw up from the spinners the bands of silk which are to enclose it. These silken bands were found to be constituted as shown in figs. 12 or 13. There seems no doubt, therefore, that the Aciniform and Piriform glands are mainly used in performing this operation.

The structure of the geometric snare was next investigated. This is a familiar object, and may be said to consist of—

(1) a sort of frame or scaffolding, to which are attached the distal ends of

(2) the radial lines ;

(3) the spiral line, extending from the periphery to near the centre.

(1) The thread of the framework was generally found to be composed as exhibited in fig. 11. When necessary the spider strengthened the line by repeating the journey, and laying it down a second time.

(2) The same line, or that of fig. 10, was also employed in constructing the radii of the snare.

Thus the framework and radii of the geometric web are supplied by the Ampullaceal glands.

(3) The spiral line requires a more detailed description.

A low power shows it to consist of bead-like viscid globules strung upon a thread with remarkable regularity, as shown in fig. 14 *d.*

It was until a few years ago supposed that these globules were separately deposited by the spider, whereas a uniform coating of viscid matter is given to the thread in the first instance, and its subsequent subdivision into globules is an entirely physical phenomenon. Boys[1] well describes the spider's action as follows:

"The spider draws these webs slowly, and at the same time pours upon them a liquid, and, still further to obtain the effect of launching a liquid cylinder into space, he pulls it out like the string of a bow, and lets it go with a jerk."

That this separation into globules is really a secondary phenomenon I have shown by taking upon a slide a portion of such a spiral immediately upon its completion. It readily stains with hæmatoxylin, and on microscopic examination shows the various stages indicated in fig. 14.

We have thus separately to consider the ground-line (Grundfaden, Apstein) and the viscid matter with which it is enveloped.

Apstein imagines the ground-line to be furnished by the Aciniform glands, and to be many-stranded.

I have not yet succeeded in tracing it with certainty to its origin, but have established the following facts with regard to it:

In the first place, it is not many-stranded, but double only.

When engaged upon this line the creature is so absorbed as to allow of pretty close examination with a hand-lens. I have at such times noticed that the posterior spinnerets are partly open, and that the line is, at first, distinctly double, fusing, by virtue of its viscid envelope, where grasped by the leg which draws it forth. Moreover, on staining and teasing the spiral line, the ground thread readily shows its double nature (fig. 15), but no amount of teasing breaks it up into further strands, as would surely be the case if such existed, for their separate

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[1] "Quartz Fibres," by C. V. Boys, F.R.S., 'Nature,' July 11, 1889.

existence as threads implies a degree of dryness inconsistent with complete fusion.

As far as I have been able to trace these lines they have appeared to emanate from the intermediate spinnerets. They are much more elastic, however, than the radial lines, and can therefore hardly proceed from the Ampullaceal orifices.

The only other paired orifices on the intermediate spinnerets are those of the Tubuliform glands. Now, an important function of these glands is undoubtedly, as Apstein remarks, the spinning of the egg cocoon, for they are always distended with yellow fluid in the female just before the deposition of ova, and comparatively inconspicuous after, while the cocoon consists of yellow silk.

If, however, they also furnish the ground-threads, this would help to explain their presence in the male spider, which has not hitherto been very easy to understand.

The objections to this view are, first, that cocoon silk is not especially elastic, and secondly, that I have not been able to find threads in the cocoon of the precise diameter of the ground-threads.

In spiders of the species under consideration the following thread-diameters were found to be fairly uniform:

Cocoon line	·006 mm.
Anterior Ampullaceal	·003 „
Ground-line of spiral	·0025 „
Intermediate Ampullaceal	·0016 „

The imperfect view I obtained of the origin of the ground-thread led me to think that though it proceeded from the intermediate organs, it had some subsequent relation to the posterior spinnerets.

It is possible, therefore, that Apstein is correct in supposing that the Aggregate glands, which debouch on the inner side of the posterior spinnerets, deposit the viscid matter above described.

The arguments hitherto adduced in support of this view are, first, the convenient arrangement of the Aggregate orifices for such a purpose, and secondly, the presence of these glands in such spiders—and such only—on whose threads the viscid matter has been observed. On dissecting out the various glands from a spider, isolating them on slides, and crushing them, I found that the contents of the Aggregate glands retained their viscidity the longest. Evidence was also sought from histological changes in the glands themselves before and after web-spinning, and though a much larger series of observations would be necessary to afford trustworthy results, alterations similar to those known to occur in active serous glands seemed to be taking place (figs. 19 and 20).

This would show that the Aggregate glands are used in spinning the web, in which case they must furnish the viscid matter, all the other structures being accounted for.

The unsafe nature of such indirect evidence is, however, freely admitted, but it may be pointed out that the certainty which now exists with regard to some of the glands gives greater probability of the true function being allotted to the remainder.

One other web structure remains to be briefly discussed. Foundation lines are attached to surrounding objects, and ordinary non-viscid lines are glued to one another by little patches of silk which we may call attachment discs (Haftscheibe, Apstein). The spider rubs its anterior spinnerets against a surface, emitting silk from the Piriform glands, and upon walking away a line is drawn out from the spinnerets.

I have been best able to study these structures in a small bottle in which a spider was obliging enough to deposit its eggs, fixing the cocoon in its place by a multitude of cross threads fixed to the sides of the bottle at their ends, and to one another where they intercrossed. Their appearance is given in figs. 16—18. It was this structure which led to the belief in the highly compound nature of the spider's line.

Summary.

1. Facts newly established.—A spider's line does not consist of many strands fused or woven together, but ordinarily of two or four distinct threads.

The framework and the radii of circular snares are supplied by the Ampullaceal glands.

The Acinate and Piriform glands are those mainly employed in binding up captured prey.

The "trailing line" consists primarily of Ampullaceal threads, sometimes strengthened by contributions from the Acinate and Piriform glands.

The ground-line of the spiral is double only, and the two strands are bound together merely by the viscid matter which envelops them.

2. Corroborative of Apstein.—The "attachment discs" are furnished by the Piriform glands.

The Tubuliform glands supply the silk for the egg-cocoon.

The viscid matter of the spiral is probably the product of the Aggregate glands.

Finally, the origin of the spiral ground-line is uncertain, but it may proceed from the Tubuliform orifices on the intermediate spinnerets.

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EXPLANATION OF PLATE V,

Illustrating Mr. Cecil Warburton's paper on "The Spinning Apparatus of Geometric Spiders."

Fig. 1.—Profile of Epeira diademata, sp. spinnerets.

Fig. 2.—Ventral aspect of the same species.

Fig. 3.—Ampullaceal gland.

Fig. 4.—Aggregate gland.

Fig. 5.—Tubuliform gland.

Fig. 6.—Piriform gland.

Fig. 7.—Acinate gland.

Fig. 8.—External spinning organs at rest. *a.* Anterior, *p.* Posterior spinnerets. *t.* Anterior tongue-like fold. *z.* Terminal fold of abdomen.

Figs. 9—13 show the composition of the "trailing-line" under various circumstances. *i.* Intermediate spinnerets.

Fig. 14.—Stages in the formation of the viscid globules. *d.* Shows the final arrangement.

Fig. 15.—Teased spiral line, showing that the "ground-line" is double.

Fig. 16.—"Attachment disc" (Haftscheibe, Apstein).

Fig. 17.—The same, more in profile.

Fig. 18.—Attachment disc, gluing together irregular strands which held an egg-cocoon in position.

Fig. 19.—Section (somewhat diagrammatic) of aggregate gland at rest.

Fig. 20.—Ditto of aggregate gland when the spider had just constructed its web. (The right half only of Figs. 19 and 20 is shaded.)

On the Structure and Functions of the Cerata or Dorsal Papillæ in some Nudibranchiate Mollusca.

By

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With Plates VI, VII, VIII, IX, and X.

Most of the Nudibranchiate Mollusca are provided with brightly coloured and sometimes elaborately branched projections from the sides and dorsal surface of the body. These include—

1. The Rhinophores, or dorsal tentacles.
2. The true Branchiæ.
3. The Cerata, or dorsal papillæ.

The rhinophores are a pair of tentacles placed near the anterior end of the body, on the dorsal surface of the head. They are undoubtedly sense-organs, and are supplied by large nerves arising from the cerebral ganglia. They are present in all the forms discussed in this paper.

The branchiæ, although they may possibly not be true ctenidia, are specialised organs of respiration. They are not present in all Nudibranchs.

The cerata, which were the special subject of my investigation, vary greatly in number, size, and arrangement in the different genera and species, and the characteristic appearance of the animals is in a great measure due to these structures. They are often termed dorsal papillæ, or branchial papillæ, or even branchiæ; and they have been supposed by many zoologists to be organs of respiration. They are not present in all Nudibranchs, but in many cases they are very large and conspicuous. They may be present along with true branchiæ. I find the cerata in the genera which I have examined to be of two kinds:

1. There are those which contain large diverticula of the liver, as in the case of the genera Eolis and Doto.

2. There are those which are essentially processes of the body-wall, and have no connection with the liver, as in the genera Tritonia, Ancula, and Dendronotus.

The term "cerata" may, as introduced by Lankester in his article "Mollusca,"[1] be employed for these processes in general, while those in the first category might be specially denoted as hepato-cerata, and those in the second as parieto-cerata. All the forms which I have examined are either distinctly hepato-cerata or are parieto-cerata. I have found no intermediate conditions. In regard to their morphological nature, if the fold of integument overhanging the foot in Doris is to be regarded not as a mantle edge, but as an epipodial ridge (see Lankester, loc. cit., p. 655), then the smooth or tuberculated dorso-lateral ridges in the genera Goniodoris, Polycera, and Idalia, the larger row of lateral tubercles of Ægires punctilucens, the lateral clavate processes of Triopa claviger, the palisade-like cerata of Ancula, the branched parieto-cerata of Tritonia and Dendronotus, and probably also the hepato-cerata of Doto, Eolis, Proctonotus, and all other forms, may be considered as epipodial papillæ—outgrowths from a more or less distinct epipodial ridge.

The six common British genera, Doris, Ancula, Tritonia, Dendronotus, Doto, and Eolis, show very different conditions of the cerata and other dorsal processes, and form an instructive series of types. The general anatomy of all these forms is well known, thanks chiefly to the labours of Alder and Hancock and of Rudolph Bergh, and many points in the detailed structure of particular organs have been worked out by Bergh, Vayssière, Trinchese, and others; but the method

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[1] 'Ency. Brit.,' ninth edition, vol. xvi, p. 655.

of serial sections, giving the exact histological relations of the different parts of the body, has apparently not up to now been made use of by any of these writers on the structure of the Nudibranchiata.

My specimens have been collected in the Liverpool Bay district, either in the neighbourhood of the Biological Station on Puffin Island, or at Hilbre Island, in the estuary of the Dee. They were generally killed with Kleinenberg's picric acid, hardened with graduated alcohols, stained in picro-carmine, embedded in paraffin, cut with the Cambridge "rocking" microtome, and mounted in Canada balsam. Some were soaked in gum, cut in the freezing microtome, and examined in water, in glycerine, and in Farrant's solution for comparison with the others. My laboratory assistant, Mr. J. A. Clubb, who is working along with me in the collection and identification of the Nudibranchs of the district for the Reports upon the Fauna of Liverpool Bay, has given me a great deal of assistance in preparing the specimens and cutting the sections.

Doris.

In Doris (Pl. VI, fig. 1) there is a pair of short stout laminated rhinophores on the head, and a clump of well-developed branchiæ near the posterior end of the dorsal surface of the body. There are no cerata or other dorsal processes. The branchiæ are in the form of a number (usually 6 to 12) of pinnate plumes arranged in a circle round the anus. In sections the branchiæ have the structure shown in fig. 2. The branches are subdivided and the surface is very irregular. The epithelium varies from nearly squamous to columnar, and there are large blood-lacunæ forming irregular spaces and passages and coming into close relation with the surface, being only separated from the ectoderm in some places by a very thin layer of structureless connective tissue.

Ancula.

In Ancula cristata (fig. 3) there are rhinophores, well-developed branchiæ, and large but simple unbranched cerata.

The rhinophores are large, and are placed in the usual position on the head. Each of them has its upper half strongly laminated or marked with parallel transverse ridges, while near the base of each two simple tapering branches arise, the one directed horizontally forwards and the other rather outwards to the side. There are three branchial plumes, which are placed in the centre of the dorsal surface. The largest one is median and anterior, and the other two form a pair placed a little further back: they are all much branched.

The cerata form a series of five erect, rod-like processes along each side of the back. They extend from the centre nearly halfway to each end of the body, and thus form a protecting palisade along the middle third of the back, at each side of the branchiæ.

In sections through the front of the head (fig. 4) it is seen that the branches of the rhinophore are, like the cerata further back, prolongations upwards of the body-wall composed of ordinary mesodermal tissue containing only the usual small blood-lacunæ. A few sections behind (fig. 5) we come upon the rhinophore proper, showing the broad lateral laminæ, while the stem contains a large bundle of nerve-fibres and, further up, a ganglionic mass of nerve-cells (fig. 5, *g*).

Some way further back in the body the cerata and branchiæ are seen in section. Fig. 6 shows in the centre the basal part of the first or median branchia cut near its anterior end. It contains a large blood-cavity. On each side is seen one of the cerata, that on the right having had several undulations near its middle. These cerata are seen from this and neighbouring sections to be direct continuations upwards of the ectoderm and mesoderm of the body-wall, and to contain no special structures beyond the epithelium and the connective and muscular tissues of the integument (fig. 6). There are many small blood-lacunæ in the mesoderm, but these are not more numerous nor larger than the corresponding spaces in the body-wall, and nothing approaching the structure of a branchia is seen.

Pl. VII, fig. 7, shows a section further back where the median branchia is cut through longitudinally about its central part, while the second pair of cerata are seen one on each side. This shows well the laminated structure of the branchia and the bundle of muscle-fibres branching through its interior. A few spaces are visible in the branchia, but they are comparatively small, and it is only under a higher magnification that the numerous lacunæ lying in the mesoderm close under the ectoderm, and containing blood-corpuscles (fig. 8), become visible. This is part of a vertical section; while fig. 9 shows part of a transverse section similarly magnified. These two figures show the deep infoldings of the surface of the branchia, and the former (fig. 8) exhibits well the change in the character of the ectoderm cells from place to place. The general arrangement and structure is the same as in the section of the branchia of Doris (fig. 2), and is very different from the structure of the cerata when similarly sectionised and magnified (see fig. 10). So that, although in sections such as are represented in figs. 7 and 11 the cerata and the branchiæ sometimes overlap and become displaced, small pieces of the one are always distinguishable by their structure from those of the other. The cerata (see figs. 6, 7, 10, and 11) have the ectoderm very thick, and the infolds are not nearly so deep or so close as those of the branchiæ. A layer of longitudinal muscle-fibres (fig. 10, *m*) lies under the ectoderm in the cerata, and there are only a few small lacunæ in the mesoderm.

Fig. 11 represents a section further back, in which parts of all three branchiæ and of two pairs of cerata are seen. The lateral branchiæ have their inner surfaces much more deeply folded than their outer surfaces, and this is especially the case near their bases. This is shown in fig. 12, a vertical section of the base of one of the lateral branchiæ, where the left side shows the outer surface next to the cerata, while the right side is the inner surface nearest to the middle line of the body. Some of the deepest infolds of the ectoderm are seen to end in little crypts where the ectoderm cells become suddenly large and are arranged in a radiating manner around the end of the infold so as to form a spherical clump (fig. 12, *gl*). These are probably glandular.

TRITONIA.

In Tritonia (e. g. Tritonia, or Candiella, plebeia) the body is long and low, nearly square in transverse section, and tapers rapidly to the posterior end (fig. 13). The rhinophores are large and complicated, having the base surrounded by a sheath and the terminal part divided up into a number of branches. There are no true branchiæ such as are present in Doris and in Ancula, but placed along each side of the dorsal surface is found a row of short branched cerata (fig. 13, *c*). These are seen in sections (figs. 14 and 15) to be merely processes of the body-wall containing no special structures and only a few small lacunæ, such as are present under the integument all over the body. In some transverse sections, where the sides of the body are much corrugated the irregular folds of the surface are almost as much branched as the cerata, and have very much the same appearance (see *k* in fig. 14).

It is clear then (1) that true branchiæ, such as those of Doris and Ancula, are not present in Tritonia plebeia; (2) that the cerata of the latter are merely processes of the body-wall like the cerata found along with branchiæ in Ancula; and (3) that although these cerata may become considerably branched (see fig. 15) they have not the structure of special respiratory organs.

DENDRONOTUS.

In Dendronotus arborescens there is practically the same condition as in Tritonia. Branchiæ are absent, but the rhinophores are large and complicated, and the branched cerata arranged along the sides of the back are so greatly developed as to form the most conspicuous part of the animal in the living condition (Pl. VIII, fig. 16). There are usually six pairs of these cerata, with occasional much smaller ones scattered between. In a specimen 4 cm. in length the largest pair of cerata may be 1 cm. in height, and have stems 3 mm. in diameter at the base. They branch repeatedly so as to form an arborescent structure.

The cerata of Dendronotus have been generally described as branchiæ, and have been universally supposed, until quite recently, to contain large digestive cæca or diverticula of the "liver." I regard them, however, as being merely excessive developments of the small cerata found in Tritonia, and as having no special branchial function; while last summer Mr. Clubb and I showed[1] that no digestive cæca penetrate into the cerata in Dendronotus. Such cæca were described and figured originally by Alder and Hancock,[2] and more recently by Dr. R. Bergh,[3] but these distinguished anatomists worked entirely, I believe, by means of fine dissections, and I can explain, I think, how it is that a deceptive appearance of hepatic diverticula is produced which has led to error when not corrected by the examination of serial sections.

The so-called liver is a very large organ lying underneath (ventral to) the ovo-testis. It consists of a posterior and right and left anterior lobes, as correctly described by Bergh. It gives off a few diverticula directed dorsally, but these do not reach to the bases of the cerata, but end blindly in the body-wall. In the specimens examined by Mr. Clubb and myself last summer we found such prolongations going towards the rhinophores and the two first pairs of cerata, and sometimes, but less definitely, towards the smaller succeeding cerata, but in no case, either in dissections or in sections, were they found to reach the base either of rhinophores or of cerata.

Dissections alone are apt to be misleading, as there are large blood sinuses (*a*) in the side walls of the body close to the liver and (*b*) extending up into the cerata, and these cavities join and open into the dorso-lateral veins close to where the hepatic diverticula terminate, so that it is easy to imagine a direct continuity between the slender end of the diverticulum and the blood sinus and so proceed to trace the supposed hepatic cæca onwards into the cerata. In serial sections, however, the pro-

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[1] 'Proc. Liverpool Biol. Soc.,' vol. iii, p. 228, 1889.

[2] 'Ray Soc. Monograph,' pt. ii.

[3] "Bijdragen tot de Dierkunde," 'Natura Artis Magistra,' Afl. xiii, viii, p. 25, Amsterdam, 1886.

longations of the liver can be followed with exactness until their terminations in the body-wall are found. In one case, for example, amongst our preparations the hepatic cæcum going towards the left rhinophore can be traced forwards through sixty-six sections, gradually narrowing until it ends blindly, the last section passing through its anterior wall. At this point it has not nearly reached the base of the rhinophore.

Dr. Bergh has figured[1] the cæcal extremities of the hepatic diverticula in the terminal branches of the cerata as seen in transparent preparations, and I freely admit that such appearances are sometimes to be seen and that they look superficially very like granular, dark-coloured liver cæca; moreover, when one of the cerata is cut off near its base from a living Dendronotus the cut surface sometimes (i. e. in darkly coloured individuals) shows an outer clearer zone, and then a dark chocolate-coloured ring which is very suggestive of the hepatic cæca, as seen in the cerata of some species of Eolis. Sections, however, show that in both such cases, the terminal twigs and the freshly cut stumps of the cerata, the appearance is due to branching masses of pigment-cells lying in the solid mesoderm, always a little way in from the surface and sometimes more densely aggregated around the blood sinuses. I found that a specimen killed and hardened rapidly, soaked in syrup and gum, and cut at once in the freezing microtome without staining, showed these pigment-cells much better than did the specimens carefully hardened and stained and embedded in paraffin. Pl. VIII, fig. 19, shows the arrangement of the pigment in such a fresh section: it is of a rich reddish-brown colour.

I believe, then, that the appearance of hepatic prolongations in the cerata, which have been described by various careful investigators, is due to the presence (1) of blood sinuses, and (2) of a good deal of dark pigment in the mesoderm, and that the hepatic cæca are not really prolonged into the cerata.

Dr. Bergh has lately suggested to me in conversation that possibly my results might be due to the cæca being contractile,

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[1] Loc. cit., pl. ii, figs. 21, 22.

and having been in some specimens retracted completely into the body; but that cannot have been the case, because, in the first place, it is difficult to understand how a system of cæca extending up into the terminal twigs could be completely withdrawn from a densely branched structure like the cerata; and, in the second place, some of my sections were made from specimens in which the cerata were suddenly cut off from the living animal with a pair of fine scissors, when fully expanded and healthy, in a dish of sea-water, and these showed the same structure when sectionised as did the other preserved specimens. I mention this, here, to show that this conceivable explanation of the absence of the cæca, which might occur to other readers, had been foreseen, and found not to be possible. The argument that as Dendronotus belongs to the group Kladohepatica it is very unlikely to be without hepatic cæca in its cerata is worthless, as Bergh has described an Eolid (Bornella excepta) which has absolutely no prolongations of the liver into the cerata.[1]

The large cerata of Dendronotus are, then, as we would expect from our previous examination of the smaller similar cerata of Tritonia, prolongations upwards of the mesoderm and ectoderm of the body-wall, and contain no special structures, such as are found in the cerata of Eolis and Doto.

The upper part of fig. 17 shows a longitudinal section of one of the cerata, and fig. 18 is a drawing of a transverse section. The ectoderm-cells throughout are of moderate size, of low columnar form, and are not differentiated in any part. The mesoderm, which has the same structure as that of the cerata of Ancula and Tritonia, is penetrated by large, irregular spaces, containing blood-corpuscles. These may be called the ceratal sinuses; they are near the centre of the mesoderm, and run in the main longitudinally (see fig. 17, *c.s.*); they occasionally branch, and they open into the numerous minute lacunæ which exist in the mesoderm here as elsewhere. Fig. 18 shows a transverse section where several branches of the ceratal sinus are present. In fig. 19 also several spaces containing blood-

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[1] See 'Report upon the "Challenger" Nudibranchiata,' p. 41.

corpuscles are seen. Fig. 20 shows a small portion of the mesoderm more highly magnified, to show the network of connective tissue and the small blood-lacunæ in the meshes.

At the bases of the cerata these large ceratal sinuses are continued into the body, and their communication can be traced in sections with the anterior and posterior dorso-lateral veins (fig. 17, *d. l. v.*), which open directly into the auricle. The junction between the ceratal sinus and the dorso-lateral vein is effected by means of a narrow transversely running branch, and from this point the ceratal sinus is continued ventrally through the mesoderm of the body-wall outside the "liver," and may be called the lateral sinus (fig. 17). It is with the upper part of these lateral sinuses that the prolongations from the liver come in some places into close proximity, and so may have given rise in dissections to the appearance of a direct continuity between the liver and the blood-spaces in the cerata.

The cerata contain also bands of muscle-fibres, mostly longitudinal in direction, nerves, pigmented connective tissue, forming branched masses and ramifying threads of a rich brownish colour, and finally masses of large distinctly nucleated cells, lying in meshes of fibrous connective tissue (see fig. 21). These occur chiefly in the smaller branches of the cerata, and are possibly mucus-secreting glands; they resemble the small groups of gland-cells seen under the ectoderm in the cerata of some species of Eolis (see fig. 37). The contrast in structure between transverse sections of the cerata of Dendronotus and of Eolis is seen by comparing figs. 18 and 34 or 35.

DOTO.

In the genus Doto there are no true branchiæ; the rhinophores are large with simple filiform distal ends, but having their bases surrounded by large funnel-shaped sheaths. The cerata form a row along each side of the back (fig. 22); they are very large and complicated, being swollen, tuberculated, usually brightly coloured, and forming the most conspicuous part of the body. They contain large branched hepatic diverticula, and are therefore hepato-cerata.

Transverse sections of Doto coronata show the relatively very large size of the hepato-cerata (fig. 23), and the manner in which they are occupied by numerous branches of the large hepatic cæca; ten or a dozen branches may often be found lying in one section. In fact, in this form, there is far more of the liver in the cerata than in the body proper. The median portion of the liver is rèduced to a small tube flattened dorso-ventrally, which lies along the under surface of the large ovo-testis (see figs. 23 and 27, *m. l.*), and gives off at intervals lateral branches, which run up the sides of the ovo-testis (figs. 25 and 26, *h. c.'*) to enter the cerata, and there expand into the large branched cæca. The difference, then, between this state of affairs, where the part of the liver in the body is little more than a duct leading from the hepato-cerata to the stomach, and that seen in Ancula, Tritonia, and Dendronotus, where the liver is wholly in the body, and the parieto-cerata are merely processes of the mesoderm and ectoderm of the integument, is very great, and affords sufficient ground, I think, for the separation of the cerata into two categories.

EOLIS.

For my present purpose it is convenient to use the term Eolis in its older, wide sense, as employed for example by Alder and Hancock, and as including the modern genera Facelina, Flabellina, Coryphella, Galvina, &c. In these forms we have much the same condition as in Doto. There are no true branchiæ, rhinophores are present, and there are also large coloured hepato-cerata arranged along the back (Pl. X, fig. 29), and constituting the most conspicuous part of the animal.

The hepatic diverticula in the cerata are either simple or not so much branched as in Doto, and are not cæcal, but communicate indirectly with the exterior at their apices. The hepato-cerata also contain at their apices cnidophorous sacs which open at the upper end to the external world, and at the lower into the extremity of the hepatic diverticulum.

This state of affairs was long ago pointed out by Alder and Hancock[1] as seen in transparent specimens, and it has more recently been demonstrated by Bergh in Phidiana Selencæ, Facelina Janii, Chlamylla borealis and Gonieolis typica; but the communication has often been denied or doubted, and Ray Lankester probably expressed the mental attitude of most zoologists towards the matter when he wrote in 1883 that the supposed communication of the hepatic cæca in the dorsal papillæ or cerata of some of the Ceratonota with the exterior by means of apertures in the apices of the papillæ "requires confirmation."[2] Last year Mr. Clubb and I described and figured[3] sections showing the exact manner in which the communication takes place in specimens of an Eolis from the Puffin Island Biological Station, and I now give some more detailed figures here (Pl. X, figs. 32, 36, and 37).

The upper end of each of the hepato-cerata is occupied by a sac containing a number of large cells (the cnidocysts) filled with cnida or thread-cells. This cnidophorous sac is evidently an invagination of the ectoderm, the cnidocysts being modified ectoderm cells (figs. 32, 36), and it communicates with the exterior by a small but perfectly distinct and clearly-defined aperture at its apex, through which the thread-cells are sometimes found protruding (fig. 36).

The size and shape of the cnidophorous sac varies in different species. Figs. 28A to 28C represent the upper ends of hepato-cerata from Facelina drummondi where the sac is greatly elongated, may become irregularly shaped, and overlap the upper end of the hepatic cæcum (fig. 30). The cnida are ovate or nearly spherical in shape (figs. 30, 38, and 39), with a small terminal projection, and the everted threads bear some large spines arranged in a spiral round the base (fig. 39), and smaller ones projecting alternately from opposite sides all the

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[1] 'Ray Soc. Monograph,' part iii.

[2] Article "Mollusca," 'Ency. Brit.,' ninth edition, vol. xvi, p. 659.

[3] 'Proc. Biol. Soc. Liverpool,' vol. iii, p. 233, and pl. xii.

way along. In (?) Cuthona nana (figs. 36, 37) the sac is short and rounded, and the cnida are much smaller than in the last species, but still spherical in form; while in Galvina picta (figs. 31, 32) the sac is more elongated, the cnidocysts are very distinct (fig. 40), and the cnida are narrow rod-like bodies (fig. 33).

The hepatic cæca occupying the greater part of the interior of the cerata (see figs. 34 and 35, which show transverse sections of two species) reach nearly or quite to the lower end of the cnidophorous sac, and communicate with it by means of a longer or shorter slender tube with thin walls strengthened by a few muscle-fibres. In Facelina drummondi (figs. 28 and 30) the connecting-tube is very long, and may be bent upon itself. In the small species of Eolis shown in figs. 36 and 37 (probably Cuthona nana) the cnidophorous sac is nearly spherical, and the connecting-tube is short and has a distinct muscular thickening, forming a sphincter around the small opening into the hepatic cæcum. This condition suggests that possibly in all cases the communication between the hepatic cæcum and the exterior through the cnidophorous sac may not be permanently open, but be kept closed when required by the contraction of the sphincter muscle.

Functions of the Cerata.

In regard to the functions of these various kinds of cerata in the Nudibranchiata, in the first place I do not think that in any case they are specially branchial. In Ancula, as I have shown above, there are parieto-cerata existing along with true branchiæ, and the two have a distinct structure, so that, although in sections pieces of the cerata and of the branchiæ may become displaced, they can be distinguished by their structure from one another. Then in Tritonia and in Dendronotus I have shown that the parieto-cerata agree in structure with those of Ancula, and not with the true branchiæ of Doris and Ancula. From a recent conversation with Dr. Bergh I learn that he regards the cerata as having a branchial function, and even in Ancula, where there are large true branchiæ present, he thinks that the cerata are supplementary respiratory organs. I am still of opinion, however, that, considering the relatively large size of the branchiæ and the perfection of their adaptation to their function and the absence of any such adaptation in the cerata, the action of the latter in effecting respiration must be so feeble, compared with the action of the branchiæ, that it may be neglected.

Dendronotus arborescens is the form in which it might be most readily supposed that the parieto-cerata have acquired, secondarily, a branchial function, but a close comparison of sections shows that these processes do not contain more blood-cavities than the general body-wall, and have not even so many small lacunæ close to the surface as some parts of the dorsal and lateral integument. Hence, although they may by their extended surface aid somewhat in respiration, still they cannot be regarded as in any way specialised branchiæ.

Then, again, in Eolis and Doto, although from their relatively very large size the hepato-cerata may be of some importance in respiration, it is merely as being an extension of the general integument, and not as being special respiratory organs. Nearly the whole of the space in the hepato-cerata in these two genera is occupied by the large hepatic cæca, and there are only a few small blood-lacunæ to be seen scattered here and there in sections. Specimens of both Eolis and Doto continue to live after being deprived of most of their cerata; so, both from their constitution and as the result of experiment, it may be inferred that these structures cannot be of primary importance as respiratory organs. One function, of course, of the cerata in these genera is to contain the greater part of the liver; and no doubt this has led to an increased size and some modification of structure. In Eolis, finally, the apices of the hepato-cerata accommodate the cnidophorous sacs, which act, doubtless, as important organs of offence.

But I believe that, in addition to these minor functions, the cerata of the Nudibranchiata are of primary importance in giving to the animals, by their varied shapes and colours, appearances which are in some cases protective and in others conspicuous and warning; and in this, it seems to me, we have an explanation of the extraordinary development and variety of these otherwise mysterious processes of the dorsal body-wall.

For several years past I have been paying some attention to the colours of Nudibranchs and their variations in connection with their habits and natural surroundings. In October, 1888, I described[1] a peculiarly coloured Doris (Archidoris) tuberculata which was especially well protected from observation, and since then I have found the same species repeatedly lying in hollows in the surface of large sponges, generally Halichondria panicea, and simulating the colours of its surroundings so closely as to be quite inconspicuous.[2] Giard has recently noticed this same point on the coast of Normandy, and has also recorded a few other cases of protective colouring amongst common Nudibranchs.[3]

The view which I have given above in regard to the primary function of the cerata occurred to me early last summer, when observing some of the Nudibranchs in their natural conditions on the shore at Puffin Island, and I have since brought the theory briefly before the notice of the Liverpool Biological Society and before Section D of the British Association at the recent Newcastle-on-Tyne meeting.[4] Since then Mr. Garstang has independently arrived at practically the same conclusions in regard to the function of the cerata from his observation of the colouring and habits of the Nudibranchs at Plymouth.

I shall now give a few instances from my own observations in support of my views.

Tritonia (or Candiella) plebeia is fairly abundant at Puffin Island and at Hilbre Island, near Liverpool, and is always found (so far as I have noticed) in these localities

[1] 'Proc. Biol. Soc. Liverpool,' vol. iii, p. 13.

[2] I see that Mr. Walter Garstang, in his recently published "Report upon the Nudibranchs of Plymouth Sound," has noticed this same instance of protective colouring. 'Journ. M. B. A.,' vol. i, No. 2, p. 174.

[3] 'Bulletin Scientifique de la France et de la Belgique,' t. xix, 1888, p. 492.

[4] See Abstract in forthcoming volume of Reports.

creeping over the surface of colonies of Alcyonium digitatum. The specimens of Tritonia plebeia are marked with many colours (none of them bright) including tints of yellow, brown, blue, grey, black, and opaque white; and when examined in a vessel by themselves considerable differences between individuals are noticed, but when in their natural condition on the Alcyonium colony they are nearly all equally inconspicuous. The colonies of Alcyonium differ considerably amongst themselves in tint, some being whiter, others greyer, and others yellower than the rest. Different parts of the same colony also vary in appearance on account of the different states of expansion of the polypes, and on account of irregularities of the surface and of adhering sand and mud, so that the varieties of colouring found in Tritonia plebeia do not render it conspicuous, but are suited to the varying conditions of the Alcyonium colonies. The small branched cerata along the back of the Tritonia aid the protective resemblance not only by contributing to the general colouring, but also by their similarity in appearance to the crown of tentacles of the partially expanded polypes. They are placed at just about the right distance apart, and have the necessary tufted appearance.

Then, again, Doto coronata when isolated is a very conspicuous and brightly coloured animal, but I find it at Hilbre Island invariably creeping on the under surfaces of ledges and stones on which are large colonies of the zoophyte Clava multicornis, and in that position the Doto is not readily seen. The gay appearance of this Nudibranch is mainly due to the large and brightly coloured cerata, and these agree so closely in their general effect with the upper ends of the zooids of Clava, covered with the numerous tentacles and the clusters of sporo-sacs, that when the Doto remains still it is hidden to a very remarkable extent.[1]

Dendronotus, again, with its large branched cerata and

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[1] Mr. Garstang tells me, in a letter just received (October), that at Plymouth the specimens of Doto are not so highly coloured, and are found upon Calyptoblasts, Clava being rare there.

its rich reddish-brown and yellow markings, is a handsome and most conspicuous object, but I have frequently found it amongst masses of brown and yellow zoophytes (coarser forms such as Sertularia abietina and Hydrallmania falcata) and on purplish-red seaweeds, where it was very completely protected from observation and I did not for several seconds recognise what I was looking at.[1]

Now, these are all cases where the colouring is protective, and I have no doubt there are many other similar instances to be found amongst the Nudibranchiata,[2] but the species of Eolis appear to belong to a different category. They are noted for the very brilliant hues of their cerata and they are always conspicuous, so far as I have noticed, even in their natural conditions.

Then, again, the species of Eolis are rarely found hiding in or on other animals; they are not shy, and they are active in their habits—altogether they seem rather to court observation than to shun it. When we remember that the species of Eolis are protected by the numerous stinging-cells in the cnidophorous sacs placed on the tips of all the cerata, and that they do not seem to be eaten by other animals, we have at once an explanation of their fearless habits and of their conspicuous appearance. The brilliant colours are in this case of a warning nature for the purpose of rendering the animal provided with the stinging cells noticeable and easily recognisable. It is, of course, important for the soft-bodied Nudibranch that it should be not only disagreeable to taste but also as conspicuous as possible, in order that it may not run the risk of being tried by voracious animals. An experimental snap from a fish might cause the death of the Nudibranch even though it was immediately rejected as food.

These, then, are the grounds upon which I base my view that the cerata from their structure cannot be important respira-

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[1] Professor Giard finds it at Wimereux amongst red seaweeds of the genus Callithamnion.

[2] Such as the interesting cases of Hermæa bifida and H. dendritica, described by Garstang, loc. cit., p. 191.

tory organs and that their chief function is by their varied shapes and colours to enable the animals to assume protective or warning appearances as may be found best suited to their surroundings and mode of life.

It is still necessary for the satisfactory establishment of this theory that I should have some more definite experimental grounds for my opinion that such forms as Doto and Dendronotus are edible, while Eolis is distasteful to (say) fishes, and I have lately arranged a series of experiments which will be conducted in the fish-tanks of the aquarium here, with the kind assistance of Mr. T. J. Moore, the curator of the Liverpool Museum. We have just commenced observations, and have got satisfactory results so far with eight species of shore fishes, but at this season it is almost impossible in this neighbourhood to get Nudibranchs in any quantity. As soon as more material can be obtained the experiments will be resumed, and I shall give a detailed account of the results when sufficient evidence has been accumulated.

Summary.

1. In Doris there are true branchiæ and no cerata. In Ancula both branchiæ and cerata are present. In Tritonia and Dendronotus there are cerata, but no true branchiæ. In Ancula, Tritonia, and Dendronotus the cerata, whether simple or branched, large or small, are merely processes of the body-wall (parieto-cerata) and contain no special organs or structures.

2. In Doto and Eolis there are no true branchiæ. The cerata (hepato-cerata) are large, and contain extensive hepatic diverticula.

3. In Eolis the hepato-cerata contain also cnidophorous sacs which communicate on the one hand with the distal end of the hepatic cæcum, and on the other with the exterior at the apex of the ceras.

4. Morphologically, all the forms of cerata are probably epipodial processes.

5. The large, elaborately branched parieto-cerata of Dendronotus are merely a further development of the small tufted parieto-cerata of Tritonia, and although they may on account of their extended surfaces have secondarily acquired to a certain extent a respiratory function, they cannot be regarded as specialised branchiæ.

6. The cerata, whether they are large branched parieto-cerata as in Dendronotus, or hepato-cerata containing the greater part of the liver as in Doto, or having cnidophorous sacs in addition as in Eolis, are not of primary importance either in respiration or in digestion, but give to the animals, by their varied shapes and colours, appearances which are in some cases protective and mimetic, and in others conspicuous and warning, as may be found best suited to their individual surroundings and mode of life.

EXPLANATION OF PLATES VI, VII, VIII, IX, X,

Illustrating Prof. W. A. Herdman's paper "On the Structure and Functions of the Cerata or Dorsal Papillæ in some Nudibranchiate Mollusca."

a. Artery. *ap.* Aperture of cnidophorous sac. *b. c.* Blood-corpuscles. *br.*, *br*^{1}., *br*^{2}. Branchiæ. *b. s.* Blood-space. *c.*, *c*^{1}., *c*^{2}. Cerata. *cn. s.* Cnidophorous sac. *c. t.* Connecting tube between hepatic cæcum and cnidophorous sac. *c. tis.* Connective tissue. *d. l. v.* Dorso-lateral vein. *ec.* Ectoderm. *ec'.* Invaginated ectoderm-cells (cnidocysts) which produce cnida. *ec''.* Young cnidocysts or cells of cnidophorous sac. *f.* Foot. *f. gl.* Foot-glands. *g.* Ganglion. *gl.* Gland-cells. *h. c.* Hepatic cæcum. *h. c'.* Narrow part of hepatic cæcum in the body of Doto. *j.* Junction of Cerata with body in Doto. *k.* Folds of the integument. *l.* Liver. *l. m.* Longitudinal muscles. *m.* Muscle-bands. *m'.* Longitudinal muscle-bands in body of Dendronotus. *m. l.* Median part of liver in body of Doto. *mes.* Mesodermal tissues. *n.*

Nerves. *o. t.* Ovo-testis. *p.* Pigment. *r. c.* Renal cavity. *rh.* Rhinophore *sph.* Sphincter muscle. *t. m.* Transverse muscles. *tn.* Oral tentacles.

			Diameters.
S. 1	= Swift's 1 in. obj., oc. 2	magnifying about	45
S. $\frac{1}{4}$	= ,, $\frac{1}{4}$,, ...	,, ,,	230
S. $\frac{1}{6}$	= ,, $\frac{1}{6}$,, ...	,, ,,	330
Z. $\frac{1}{12}$	= Zeiss's $\frac{1}{12}$,, (oil immersion), oc. 2 .	,, ,,	505
	,, ,, ,, oc. 4 .	,,	950 to 1363

Where not otherwise stated, the drawings were made from specimens hardened in Kleinenberg's picric acid and graduated alcohols, stained in picro-carmine, embedded in paraffin, and cut with the "rocking" microtome.

PLATE VI.

Fig. 1.—Outline of a Doris seen from the left side, showing the rhinophores (*rh.*) and the branchiæ (*br.*). About natural size.

Fig. 2.—Part of a longitudinal section through the branchia of Doris (Acanthodoris) pilosa. *b. s.* Large blood-space. S. $\frac{1}{6}$.

Fig. 3.—Outline of Ancula cristata seen from the right side, showing the rhinophores, the branchiæ, and the cerata (*c.*). × 3.

Fig. 4.—Upper part of a transverse section through the head of Ancula (middle of odontophore), showing the tentacle-like branches of the rhinophores (*rh.*) cut in longitudinal section. The mesoderm contains only a few small blood-spaces (*b. s.*). S. 1.

Fig. 5.—Transverse section through the front of the body of Ancula, showing the rhinophores cut longitudinally. *m.* Muscles. *n.* Nerves. *g.* Ganglion. S. 1.

Fig. 6.—Transverse section through Ancula at the anterior end of the median branchia (br^1.), showing the first pair of cerata (c^1.), and the large blood-space in the branchia (*b. s.*). S. 1.

PLATE VII.

Fig. 7.—Transverse section through Ancula in the middle of the median branchia, and first pair of cerata. S. 1.

Fig. 8.—Small part of median branchia in longitudinal section, showing the blood-spaces in the mesoderm. S. $\frac{1}{6}$.

Fig. 9.—Small part of same branchia in tranverse section. S. $\frac{1}{6}$.

Fig. 10.—Part of the outer edge of one of the cerata shown in Fig. 7, near base. S. $\frac{1}{6}$.

FIG. 11.—Transverse section of Ancula through the lateral paired branchiæ (br^2.) S. 1.

FIG. 12.—Vertical section of part of base of lateral branchia. S. $\frac{1}{6}$.

FIG. 13.—Tritonia (Candiella) plebeia, from right side. × 3.

FIG. 14.—Outline of transverse section of Tritonia plebeia through rhinophores, showing processes of the body-wall (*k.*). S. 1.

FIG. 15.—Outline of transverse section of Tritonia plebeia through middle of body, showing cerata. S. 1.

PLATE VIII.

FIG. 16.—Dendronotus arborescens from the left side. Natural size.

FIG. 17.—Transverse section of Dendronotus near the middle of the body, showing one of the second pair of cerata cut in longitudinal section (c^2.). The relative positions of the liver (*l.*), short hepatic cæcum (*h. c.*), ceratal blood-sinus (*c. s.*), and dorso-lateral veins (*d. l. v.*) are shown. S. 1 (reduced).

FIG. 18.—Transverse section of one of the third cerata of Dendronotus, showing the solid mesoderm (*mes.*) containing muscles (*m.*) and ceratal blood-sinuses (*c. s.*). S. $\frac{1}{4}$.

FIG. 19.—Transverse section near the base of one of the cerata cut off the living animal, rapidly hardened, cut in the freezing microtome, and examined unstained in water, to show the distribution of the dark-brown pigment. S. 1.

FIG. 20.—A small piece of the mesodermal tissue as seen in some sections of the cerata, to show the lacunæ containing blood-corpuscles. S. $\frac{1}{6}$.

FIG. 21.—A section near the top of one of the cerata, from a specimen killed with corrosive sublimate and glacial acetic acid, then hardened gradually with alcohols of different strengths, soaked in gum, cut with the freezing microtome, and stained with picro-carmine, to show the masses of gland-cells lying in meshes of connective tissue. S. $\frac{1}{6}$.

PLATE IX.

FIG. 22.—Outline of Doto coronata, from the left side. × 3.

FIG. 23.—Transverse section of Doto coronata through the posterior part of the body, showing the large cerata and their contained hepatic cæca (*h. c.*). S. 1.

FIG. 24.—Part of a similar transverse section more highly magnified, showing the junction of one of the cerata with the body. S. $\frac{1}{6}$.

FIG. 25.—Part of another similar section, showing the continuation of the hepatic cæcum (*h.* c^1.) into the body alongside the ovo-testis (*o. t.*). S. $\frac{1}{6}$.

Fig. 26.—Part of another similar section, showing the narrow continuation of the hepatic cæcum (*h. c*^{1}.) sinking into the body and moving to a more ventral position, so as to reach the median tube lying under the ovo-testis. S. $\frac{1}{6}$.

Fig. 27.—Part of another section, showing the median tubular part of the liver (*m. l.*) lying in the body below the ovo-testis (*o. t.*). S. $\frac{1}{6}$.

Fig. 28, a, b, c.—The extremities of three cerata of Eolis (Facelina) drummondi preserved in glycerine and then treated with potassic hydrate, and slightly squeezed to show the long recurved tube connecting the tip of the hepatic cæcum with the cnidophorous sac. S. 1.

PLATE X.

Fig. 29.—Eolis (Galvina) picta from the left side. × 6.

Fig. 30.—Part of the tip of one of the cerata of Eolis (Facelina) drummondi from Hilbre Island, preserved in glycerine and treated with potassic hydrate, showing the connecting tube (*c. t.*) between the cnidophorous sac (*cn. s.*) and the hepatic cæcum (*h. c.*). *sph.* Sphincter muscle. *ec.* Ectoderm, covered with fine cilia. *l. m.* and *t. m.* Longitudinal and transverse muscle-bands. S. $\frac{1}{6}$.

Fig. 31.—Transverse section near the tip of one of the cerata of Eolis (Galvina) picta, showing the cnidophorous sac (*cn. s.*) containing large invaginated ectoderm-cells (*ec'*.), in which are placed the cnida. S. $\frac{1}{6}$.

Fig. 32.—Longitudinal section through the tip of one of the cerata of Eolis (Galvina) picta, showing the ectoderm (*ec.*) turning in at the terminal aperture (*ap.*) to form the large cells or cnidocysts (*ec'*.) in the cnidophorous sac (*cn. s.*). S. $\frac{1}{6}$.

Fig. 33.—Three of the cnida of Eolis (Galvina) picta. Z. $\frac{1}{12}$.

Fig. 34.—Transverse section (with freezing microtome) of one of the cerata of Eolis (Acanthopsole) coronata from Puffin Island. *ec.* Ectoderm. *mes.* Connective tissue and muscle-fibres. *b. s.* Blood-spaces in the mesoderm. *h. c.* Hepatic cæcum. S. $\frac{1}{6}$.

Fig. 35.—Transverse section of one of the cerata of Eolis (Cuthona) nana (?), showing in addition to the hepatic cæcum (*h. c.*) groups of large gland-cells (*gl.*) embedded in the mesodermal tissues. S. $\frac{1}{4}$.

Fig. 36.—Longitudinal section through the tip of one of the cerata of Eolis (Cuthona) nana (?), showing the opening (*ap.*) of the cnidophorous sac (*cn. s.*) to the exterior, the continuation inwards of the ectoderm-cells (*ec.*) to form the cnidocysts (*ec'*.) which contain the cnida, the sphincter muscle (*sph.*) round the opening of the cnidophorous sac into the hepatic cæcum, and the clumps of gland-cells (*gl.*) lying in the mesodermal tissues. S. $\frac{1}{4}$.

FIG. 37.—A neighbouring section to the preceding one, showing the connecting tube (*c. t.*) between the cnidophorous sac and the hepatic cæcum, cut open in the greater part of its length, being only crossed by a few of the fibres of the sphincter muscle at its lower end. The other parts are before. S. $\frac{1}{4}$.

FIG. 38.—Group of cnida of Eolis (Facelina) drummondi in various positions ; the upper four are unexploded, the lower one has the thread everted. Z. $\frac{1}{12}$.

FIG. 39.—Cnida of Eolis (Facelina) drummondi more highly magnified (× about 1360), showing the arrangement of the spines on the basal part of the thread. Z. $\frac{1}{12}$, oc. 4, tube.

FIG. 40.—One of the large cells or cnidocysts (*ec'.*) from the cnidophorous sac of Eolis (Galvina) picta, in which the cnida are formed, showing the nucleus and nucleolus and the numerous elongated cnida embedded in the protoplasm. Two younger cells (*ec''.*) are seen at the base. Z. $\frac{1}{12}$.

Further Observations on the Histology of Striped Muscle.

By

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Late Platt Physiological Scholar in the Owens College.

With Plate XI.

In a recent paper published in this Journal[1] I gave the results of some researches on the histology of muscular fibre. The present paper is a record of my further investigations on this subject. These are somewhat incomplete owing to want of time to finish them satisfactorily, but several results have been obtained which I trust are worthy of publication.

In order to render the questions dealt with more intelligible the summary of results arrived at in the former paper is reproduced.

Summary of Former Paper.

1. In all muscles which have to perform rapid or frequent movements a certain portion of the muscle is differentiated to perform the function of contraction, and this portion takes on the form of a very regular and highly modified intracellular network.

2. This network, by its regular arrangement, gives rise to certain optical effects which cause the peculiar appearances of striped muscle.

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[1] "Observations on the Structure and Distribution of Striped and Unstriped Muscle in the Animal Kingdom, and a Theory of Muscular Contraction," 'Quart. Journ. Micr. Sci.,' 1887.

3. The contraction of the striped muscle-fibre is probably caused by the active contraction of the longitudinal fibrils of the intra-cellular network: the transverse networks appear to be passively elastic, and by their elastic rebound cause the muscle to rapidly resume its relaxed condition when the longitudinal fibrils have ceased to contract; they are possibly also paths for the nervous impulses.

4. In some cases where muscle has been hitherto described as striped, but gives no appearance of the network on treatment with the gold or other methods, the apparent striation is due to optical effects caused by a corrugated outline to the fibre.

5. In muscles which do not perform rapid movements, but where contraction is comparatively slow and peristaltic in nature, this peculiar network is not developed. In most if not all of the invertebrate unstriped muscle there does not appear to be an intra-cellular network present in any form; but in the vertebrate unstriped muscle a network is present in the form of longitudinal fibrils only; this possibly represents a form of network intermediate between the typical irregular intra-cellular network of other cells and the highly modified network of striped muscle.

6. The cardiac muscle-cells contain a network similar to that of ordinary striped muscle.

Discussion of the Views of Recent Observers.—Before commencing the subject-matter of this paper I propose to discuss the results arrived at by several recent observers concerning the structure of muscle-fibre, and also some of the criticisms which have lately appeared concerning the existence of an intra-cellular network in striped muscle.

The most important paper to discuss is that of Rollett.[1] He considers the muscle-fibre to consist of longitudinal fibrillæ grouped together into "muscle-columns," the cross-sections of which correspond to Cohnheim's areas. Filling up the spaces between the muscle-columns is the interfibrillar material or

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[1] 'Arch. f. mikr. Anat.,' 1888, pp. 233—265.

"sarcoplasma." Each muscle-column consists of alternating thick and thin segments; in the centre of each thin segment is a dark granule. The thick segments of the muscle-columns correspond to "Bowman's sarcous elements," and the dark granules in the centre of the thin segments correspond to "Krause's membrane" or the "transverse network" (fig. 13 and diagram B).

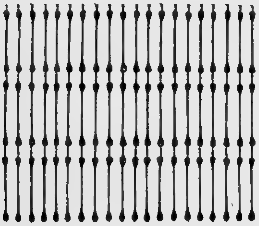

Diagram A (high focus).

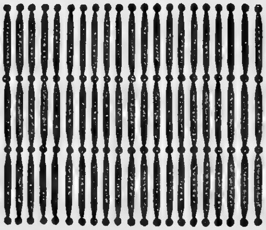

Diagram B (low focus).

The sarcoplasma is the part which is stained in gold preparations. In short, Rollett regards the appearance of gold preparations as due to the staining of the sarcoplasma, and considers this to be a honeycomb of interfibrillar material, and not a true intra-cellular network.

The latter portion of Rollett's paper is devoted to an elaborate criticism of the network view of the structure held by Melland, Van Gehuchten, Carnoy, and myself. He states that what we describe as the fibrils of the network are only transverse and longitudinal sections of the walls of the honeycomb or sarcoplasma ("Was beide Autoren an diesen als Faden beschreiben sind nur Quer- oder Längsschnitte der Wände des Wabenwerkes, welches das Sarcoplasma um die Muskelsäulchen bildet," p. 252).

He describes the appearances seen in fresh muscle-fibre as follows:—At low focus (diagram B) the muscle-columns appear dark and in a line with the granules, the sarcoplasma appearing light. At high focus (diagram A) the sarcoplasma appears dark, the muscle-columns light, and two rows of granules appear in a line with the sarcoplasma and alternating with the muscle-columns. He states that the dark lines drawn by Melland joining the dark granules are only parts of the optical longitudinal sections of the walls of the sarcoplasma and are only seen at high focus; and that they do not lie in a line with the dark granules, but alternate with them, the dark granules being only seen at low focus. The granules which appear at high focus he considers to be thickenings of the sarcoplasma.

The above diagrams, modified from Rollett's figures, will make these points clearer. Diagram B represents the appearance at low focus, and diagram A the appearance at high focus according to Rollett. In B the muscle-columns appear dark and the sarcoplasma light; in A the sarcoplasma dark and the muscle columns light.

In the same way he states that the rows of granules seen in gold preparations are thickenings of the sarcoplasma lying between the thin segments of the muscle-columns, and that the true row of granules which correspond to and are parts of the muscle-columns are only seen at low focus, and then do not lie in a line with the dark lines, but alternate with them.

He describes the same appearance at low and high focus in hardened muscle, and states that Melland and Van Gehuchten place the granules alternating with the muscle-columns, whereas they are really in a line with them.

In short, he concludes that a network does not exist, and that the appearances described by Melland, Van Gehuchten, and myself are due to errors in the interpretation of microscopic appearances and confusion of high and low focus ("Ich komme also zum Resultate dass ein Netzwerk im Sinne von Melland, Marshall, und Van Gehuchten und ein Enchyleme im Sinne des Letzteren in der quergestreiften Muskelfaser nicht existirt," p. 262).

In answer to this criticism I venture to make the following observations.

1. If the appearance of the network in fresh muscle is due to the optical appearance of the "sarcoplasma" at high focus, there must always be a double row of granules—one on each side of Krause's membrane. (I use this term for the sake of convenience, and take it to represent the row of dark

granules of Rollett's muscle-columns, and the row of granules of the transverse network of Melland, &c.).

2. If the granules seen at high focus in gold preparations are thickenings of the sarcoplasma stained by gold, there must again be a double row, one on each side of the true row of granules which are only seen on the low focus, and further, the former rows of granules must alternate with the latter. (Vide diagram A.) Although I have examined several hundred preparations of muscle-fibre, I have never seen two rows of granules in any gold or fresh preparation, nor have I seen any change in the position of the granules at high and low focus. The granules have always appeared to me to be in a line with, and connected with the longitudinal lines of, the network (or "sarcoplasma") at both high and low focus.

3. Rollett states that the "sarcoplasma" is a honeycomb, and that the appearance of the network is due to the optical sections of the walls of that honeycomb. If this is true, I do not understand why there is never any appearance of honeycomb structure in finely teased preparations, whereas isolated pieces of network are easily obtained. Moreover, one preparation obtained by Melland is, I think, almost conclusive in favour of a network (fig. 15).

4. According to Rollett, the "muscle-columns" are the essential parts of the fibre, and the "sarcoplasma" is simply interfibrillar material; we should therefore expect the latter to be least abundant in the most perfectly developed muscles. Now, in insects which possess the most powerful and most rapidly contracting muscles of all animals, the part stained by gold is more strongly marked than in other animals. This seems to point to the fact that it is the most essential part of the fibre and not interfibrillar material, and is therefore in favour of the network view.

5. Again, in developing muscle-fibre I have shown that the network is present but only demonstrated with difficulty; whereas if it were inert interfibrillar substance, one would expect it to be relatively more abundant in the embryonic fibre.

6. If, as I have attempted to show, the nerve-ending is

connected with the part of the fibre stained by gold, this again points to the latter being the essential portion of the fibre; while if Rollett's view is correct, we should expect the nerve-ending to be connected with the muscle-columns.

7. The apparent connection in some cases of the network with the intra-nuclear network of the muscle-corpuscles is in favour of the network view.

8. Lastly, the network view places the muscle-cell on a basis of comparison with other cells having intra-cellular networks, whereas all other views of the structure are at variance with such a comparison.

Dr. Klein[1] adopts Rollett's view in the new edition of his text-book, and states that "the reticulation described by Melland, Marshall, and others, is due to the coagulation of the sarcoplasma brought about by certain hardening reagents."

Dr. Michael Foster apparently holds the same view of the structure in the new edition of his book,[2] for he states that the muscle-substance is composed of longitudinal fibrillæ, embedded in interfibrillar substance which stains with gold, and hence appears as a network. He says, "The interfibrillar substance is relatively to the fibrillæ more abundant in the muscles of some animals than in those of others, being, for instance, very conspicuous in the muscles of insects, in which animals we should naturally expect the less differentiated material to be more plentiful than in the muscles of the more highly developed mammal."

Now, I think I am right in saying that the muscular system of insects is the most highly developed in the animal kingdom; certainly the muscles are far more powerful in comparison with the size of the animal than in mammals, and among insects are found the most rapid movements. It therefore appears to me that the fact of the meshwork being more conspicuous in the muscles of insects is strongly in favour of its being the active part of the pike, and not of the nature of interfibrillar substance.

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[1] 'Elements of Histology,' p. 76.

[2] 'Text-book of Physiology,' vol. i, p. 91.

I shall next give a *résumé* of the results of some recent observers who are in favour of the existence of a network.

Van Gehuchten[1] has described a network in striped muscle similar in most respects to that described by Melland, myself, and others, but differing in some details.

Carnoy[2] also adopts the network view, and remarks that "La cellule musculaire est une cellule ordinaire dont le réticulum s'est regularisé, et l'enchyleme chargé de myosine."

Haswell[3] has recently published an important paper on this subject. His observations were made on the gizzard of various species of Syllis, where he claims to have found very primitive forms of striped muscle. He divides striped muscle into simple and compound types, the simple type showing only transverse striation, not due to network; the compound both transverse and longitudinal. These two types correspond to what I have termed true and false striation; the characteristics of the compound or true striped muscle being as follows:

1. Each fibre consists of a bundle of fibrils.
2. Each fibre is composed of two alternating series of anisotropous and isotropous segments, the former of which are more easily stained than the latter.
3. Running across the fibre in the middle of each isotropous segment is the transverse network, or Krause's membrane.
4. Between the fibrils run the strands of the longitudinal network.
5. Each fibre is formed from a single cell, the nucleus of which divides and forms "a multinucleated protoplasmic body, by modification of whose protoplasm the muscle substance and networks are formed."

He states that in these animals the elements of the fibre are on a larger scale than in Vertebrates and Arthropods, and

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[1] "Etude sur la structure intime de la cellule musculaire Striée." Extrait de la Revue 'La Cellule,' t. ii, 2 fascicul. Louvain, Gand et Liege, 1886.

[2] 'La Biologie cellulaire,' 1884.

[3] 'Quart. Journ. Micr. Sci.,' 1889.

are hence favorable for the study of the structure of muscular fibre, which "seems to lead to that view of the structure of compound striated fibres advocated by Retzius, Bremer, Melland, C. F. Marshall, and others; the only point of importance in which there seems reason for dissenting from that view being with reference to the relation of the transverse networks to the fibrils." The chief differences between the network Haswell describes and that described by the above observers are these: (1) He states that the transverse networks are not only in the interspaces between the "fibrils," but partly also penetrate them. (2) The longituninal networks, though mostly longitudinal, have oblique strands and anastomoses. (3) The transverse networks sometimes appear as rows of spindle-shaped granular bodies, but in crushed specimens he says these are seen to consist of a close reticulum of delicate threads, the spindle bodies being condensed parts of it. (4) The distance between the transverse networks is much greater.

Haswell regards the "fibrils" as the contractile part, and not the network.

I shall refer to Haswell's observations again in the subsequent portions of this paper.

A. B. Macallum[1] has published some interesting observations dealing with striped muscle. He confirms the existence of the network of Retzius, Melland, and others, and considers it the contractile part of the fibre. He states that the muscle-nuclei are marked by furrows, sometimes transverse and sometimes longitudinal, and that these are probably caused by pressure of the trabeculæ of the network. He also states that in some nuclei there is an intra-nuclear network similar to that of the fibre itself.

It thus appears that the view of the existence of a true intra-cellular network in striped muscle-fibre has received much support, and has been confirmed by several recent observers; and that the view held by Rollett and others that it

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[1] "On the Nuclei of the Striated Muscle-fibre in Menobranchus," 'Quart. Journ. Micr. Sci.,' 1887.

is interfibrillar material has not sufficient evidence for it to be accepted. I shall therefore, in accordance with the results of Retzius, Bremer, Melland, Carnoy, Haswell, Macallum, and myself, assume that the former view represents the true structure of striped muscle.

The present paper deals with the following points:

1. The connection of the transverse networks with the muscle-corpuscles.
2. The development of the network.
3. The connection of the nerve-ending with the network.

Connection of Network with Muscle-corpuscles.

It was shown by Retzius[1] that the transverse portions of the muscle network were directly connected with the muscle-corpuscles. He states that the protoplasm of the muscle-corpuscle is produced into several processes from which finer processes arise forming the transverse networks. Retzius' results were obtained by a modification of gold staining. The fresh muscle-fibre was first placed in a 1 per cent. solution of formic acid for a few seconds, then in gold chloride $\frac{1}{5}$—$\frac{1}{2}$ per cent. for twenty-five minutes, then in formic acid 1 per cent., and exposed to light for 10—20 hours.

By a special method of staining I have been able to confirm Retzius' results, and have made specimens showing the undoubted connection of the transverse networks with the muscle-corpuscles.

Method of Preparation.—The method of staining I adopted is a modification of that employed by Mays for demonstrating nerve-endings in muscle. He uses the following solution:

Arsenic acid $\frac{1}{2}$ per cent..	20 parts.
Gold chloride 1 per cent . . .	4 ,,
Osmic acid 2 per cent.	1 ,,

This solution although it preserves the nerve-endings disintegrates the muscle-fibre. This I found was due to the arsenic

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[1] 'Zur Kenntniss der Quergestreiften Muskelfaser.' Biologische Untersuchungen, 1881.

acid. I therefore tried various strengths of acetic and formic acid in place of the arsenic, and found the best combination was the following:

Acetic acid 1 per cent.	20 parts.
Gold chloride 1 per cent. . . .	4 „
Osmic acid 1 per cent.	1 „

The muscle-fibre was placed in this solution for fifteen minutes, after previous immersion in acetic acid 1 per cent. for a few seconds; then in acetic acid 1 per cent. in a warm chamber for one or two hours.

1. Dytiscus.—Fresh muscle-fibre of Dytiscus stained by the above method shows the muscle-corpuscles in the form of one or more chains of nuclei in the substance of the fibre, the nuclei being surrounded by a small amount of undifferentiated protoplasm. The transverse networks are seen directly continuous with the nuclei. This is well shown in fig. 1. Fig. 2 shows a portion of fibre with two rows of muscle nuclei; the transverse networks are seen to be connected with both sets of nuclei in some places. Fig. 3 shows several isolated nuclei with the transverse processes attached to them.

Transverse views of the network and nuclei are more difficult to obtain. Fig. 4 shows a transverse view of an isolated nucleus, with part of the transverse network connected with it.

2. Dragon-fly.—The muscle-corpuscles of the muscle-fibre of the dragon-fly are situated peripherally, i. e. just under the sarcolemma, contrary to the general rule in insects.

In one preparation of this muscle I could trace the transverse networks into the muscle-corpuscles; and, moreover, the networks appeared to be distinctly connected with the intranuclear networks of the muscle-corpuscles (fig. 5).

3. Crayfish.—In a preparation of crayfish muscle prepared by Retzius' method I could apparently trace the connection of the muscle network with that of the muscle-corpuscle. In this case it was somewhat difficult to tell whether the effect was not due to the network lying over the muscle-corpuscle; but by careful focussing I think the connection could be made out (fig. 6).

These observations confirm Retzius' results, viz. that the transverse portions of the muscle network are directly connected with the muscle-corpuscles; and, furthermore, that the network is directly continuous with the intra-nuclear network of the corpuscles.

Development of the Network.

This I have studied in embryos of the trout and rat.

Trout.—In some gold preparations of embryo trout, taken from the ova, I found developing muscle-fibres in an early stage. These consisted of a portion of undifferentiated protoplasm containing the nucleus, and a portion already transversely striated. Under a comparatively high power the transversely striped portion showed darkly stained masses of an ellipsoidal shape arranged side by side, and causing the appearance of striation. Under a very high power ($\frac{1}{25}$ immersion) the network could be seen between these darkly stained masses, and in the same form in which it appears in the adult fibre. The dark masses appear to be some substance altered by the method of staining, and shrunken in the meshes of the network (figs. 7, 8 and 9). No connection was seen between the network and the nucleus.

In older fibres the network is more fully developed, but still no connection appears to exist between the nuclei and the network (fig. 10).

Rat.—In developing muscle-fibre from the embryo rat the fibres consist of an axial core of undifferentiated protoplasm containing the nuclei, and a peripheral part with developing network. Here, again, no connection was observed between the nuclei and the network.

It thus appears that—

1. The network appears at a very early stage.

2. It develops in its permanent form, and is not produced by the transformation of an irregular network into the adult type.

3. Each muscle-fibre is probably developed from a single cell, and is not formed by a coalescence of cells, either end to

end or laterally (as Calberla[1] states), because the fibres of trout muscle examined were evidently single cells, and had the network well developed. It is difficult to conceive that these become fitted together, either end to end or laterally, so that the network of one cell should exactly fit on to that of the next.

4. The network develops centripetally, and commences at the part of the cell farthest away from the nucleus; moreover, it does not appear to become connected with the nuclei till the fibre is fully developed.

Haswell,[2] from his observations on the muscle of the gizzard of Syllis, forms a view of the ontogeny of striped muscle which does not agree with that described above.

In the same organ, in various species of Syllis, he finds in one case bundles of non-striped fibres; in another, compound hollow striated fibres, consisting of bundles of fibrils similar to the above, and bound together by a single transverse network. In a third there are three transverse networks, and so on up to the fully developed type of striped muscle found in Vertebrates and Arthropods. He therefore regards each striped fibre as derived from a bundle of non-striped fibres. He thinks the transverse network probably the equivalent of a transverse line of nuclei of the unstriped fibres, which occupies a similar position.

If this is correct each striped fibre must be a multicellular structure, and the network intercellular, and not intra-cellular. However, in another part of his paper he speaks of each fibre being formed from a single cell, the nucleus of which divides and forms "a multinucleated protoplasmic body, by modification of whose protoplasm the muscle-substance and networks are formed."

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[1] 'Arch. f. mik. Anat.,' xi, 1875.

[2] Loc. cit.

Connection of Nerve-ending with Muscle Network.

Nerve-endings may be divided into two main types, the circumscribed and the diffused form. Between these types there are many intermediate forms, as shown by Kühne in his classical work on 'Nerve-Endings.'[1] The nerve-endings in the muscle of the snake form a good example of the circumscribed variety. Here we have a localised end-plate, compact and non-ramifying. This is also the common type in mammalian muscle. In Dytiscus, on the other hand, we find the diffuse form, which branches and ramifies nearly to the end of the fibre.

In each case the nerve-ending, when stained by any of the gold methods, is seen to consist of a slightly stained ramifying portion, with darkly stained irregular masses between the branches of the lighter stained portions. The lighter stained part appears to be continuous with the axis-cylinder of the nerve.

In attempting to demonstrate a connection between the nerve-ending and the muscle-network there is great difficulty, because the methods which best show the nerve-endings usually disintegrate the muscle-fibre and destroy the network. The best method of obtaining the nerve-endings is that employed by Mays,[2] and also, with modifications, by Kühne,[3] viz. the mixture of arsenic acid, gold chloride, and osmic acid mentioned in the first part of this paper. But this method usually destroys the network, owing to the action of the arsenic acid. Another difficulty arises from the fact that the connection, if it exists, must take place underneath the nerve-ending, and hence in the normal position of the parts it could hardly be seen.

Dytiscus.—In one preparation of Dytiscus muscle prepared by May's method I succeeded in finding a portion of fibre with the network still intact (fig. 11). A portion of the ramifying nerve-ending is seen crossing the fibre transversely; both the

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[1] "Untersuchungen über motorische Nervenendigung," 'Zeit. f. Biol.,' Bd. xxiii.

[2] 'Zeit. f. Biologie,' Bd. xx, 1884.

[3] Loc. cit.

fibre and nerve-ending are stretched out transversely more than in the normal state. The nerve-ending appears to have been broken off from the upper part of the network and tilted over to show its inner surface, which here appears to be connected with the longitudinal bars of the network. The upper border of the nerve-ending, in the position of the figure, I take to be the external surface next the sarcolemma, the lower border to be the internal surface; the outline of the latter seems to me to point strongly to the fact that it is really connected with the longitudinal bars of the network.

Crayfish.—In preparations of crayfish muscle there are frequently found what I may, for want of a better term, call "streaks" of slightly stained matter usually crossing the fibre transversely. In some preparations these are seen to be distinctly continuous with the nerve-fibre going to the muscle, and are hence presumably portions of the nerve-ending. They appear to correspond to the lighter stained part of the nerve-endings as usually seen.

In several specimens these streaks appeared to be connected with the longitudinal bars of the network, in the same way as in the specimen of Dytiscus muscle. Fig. 12 shows one of these streaks of nerve-ending connected with the network. The reason that these are so much stretched out appears to be on account of their connection with the network, which stretches them with it when it becomes stretched itself. In this figure the triangular deeply-stained bodies appear to represent the deeper stained part of the normal nerve-ending. They also appear to be continuous with the network at their apices.

Although the above results are imperfect, and not so conclusive as those discussed in the previous portions of this paper, nevertheless it appears to me that the nerve-ending is connected with the muscle-network, and apparently chiefly with the longitudinal fibrils of the network.

A recent paper by Macallum[1] on the termination of nerves in the liver of Menobranchus has an important relation

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[1] 'Quart. Journ. Micr. Sci.,' March, 1887.

to the above question. He states that he has traced the terminal fibrils of the nerves into direct connection with the intra-nuclear network of the hepatic cells, and the figures he gives seem to place this beyond doubt. This by analogy gives support to the view that the nerve-ending of muscle is connected with the network; and possibly this is the normal method of termination of nerves in connection with cells.

Haswell's[1] observations are also interesting in connection with this question. He describes a ganglion-cell at the end of each fibre, and occupying the axis of the fibre. This sends out numerous branching processes, which penetrate between the fibrils. He states that the core of the fibre is occupied by granular protoplasmic material, through which runs a network of fine threads, "connected with the fine branches of the nerve-processes of the ganglion-cell, and with the network of the muscle substance." Special branches of nerve-processes also ramify on the surface of the fibre, and probably enter into connection with the transverse networks.

Hence both Macallum's and Haswell's observations lend support to the view that the network is connected with the nerve-ending.

Conclusion.

In reviewing the foregoing observations we are at once met by an apparent contradiction, viz. that in the young muscle-fibre the network does not appear to be connected with the nucleus, whereas the connection is definitely established (Retzius, Marshall) in the adult fibre. This at first sight is an absolute contradiction: for, on the one hand, it is difficult to conceive that processes originating as outgrowths from the nucleus could exactly hit off and fuse with the already formed network; on the other hand, it is almost equally inconceivable that the fibres should grow into the nucleus. This apparent contradiction can, I think, be to a great extent explained. Firstly, we must bear in mind that histological differentiation proceeds during its development from without inwards, i. e.

[1] Loc. cit.

centripetally; and that the special characters of the adult cell appear first and are most marked at the periphery, i. e. farthest from the nucleus. Examples of this rule are seen in the development of epidermic cells, dentine, cartilage, and bone. In bone and dentine the processes are not supposed to grow from the cells, but to be formed by the lengthening of connecting strands by deposit of new matter.

Secondly, the nerve-ending being on the surface of the fibre, and the network also appearing first on the surface, the connection between the two can be established from the first; whereas if the network grew out from the nuclei it could only be connected with the nerve-ending at a much later period. Hence the fibre would be useless till it was far advanced in development, because for the network to be of any use it must from the first be connected with the nerve-ending. For a new structure of any kind to be developed it must always have been of use from the first, either for its ultimate purpose or for some other. If the network grew out from the nuclei it could not be of use till it got to the nerve-ending, i. e. to the surface.

In considering this point we may imagine that the cell divides into "formed and unformed matter" (Beale), the formed matter being characteristic of the particular cell. In the case of the muscle-fibre the protoplasm divides into network and muscle-plasma all along, beginning at the periphery and gradually extending to the nucleus. We are here met by an apparent difficulty, for in the muscle-fibre the "formed matter" which is characteristic of the cell is the muscle-plasma, and not the network (which is presumed to be the contractile part). But the special feature of striped muscle is not the fact that it contracts, but the mode in which this is brought about, i. e. the rapidity; and this will be a matter of nutrition which will depend on the muscle-plasma. Therefore the special feature of striped muscle is probably the mode of nutrition of its specially contractile part, i. e. quick repair. The active network bathed in such a fluid is placed in a good position for such rapidity.

Summary.

1. The transverse portions of the network of the striped muscle-fibre are directly connected with the muscle-corpuscles.

2. The nerve-ending appears to be connected with the muscle-network, and chiefly with the longitudinal bars of the network.

3. The development of the network takes place at a very early stage in the development of the fibre, and the network develops from the first in its permanent form.

4. The network develops first at the surface, and grows centripetally. It does not appear to be connected with the muscle-corpuscles till the fibre is fully developed.

5. Each muscle-fibre appears to be developed from a single cell, and not by a coalescence of cells.

The investigations described in this paper were carried on in the Physiological Laboratory of Owens College during the winter of 1887. My thanks are due to the Council of the College for a special grant to enable me to carry on the research.

I must express my thanks to my brother Professor Milnes Marshall for many valuable suggestions in producing this paper, and for examining several of the preparations. I must also thank Professor Stirling for much assistance to me in my work.

DESCRIPTION OF PLATE XI,

Illustrating Mr. C. F. Marshall's paper, "Further Observations on the Histology of Striped Muscle."

[The main details were drawn under the camera in all the figures.]

Fig. 1.—Muscle-fibre of Dytiscus, showing transverse networks connected with muscle-corpuscles. The longitudinal bars of the network are omitted

for the sake of distinctness. $\frac{1}{5}$th obj. Acetic acid, osmic acid, and gold chloride.

Fig. 2.—Portion of another fibre, with transverse networks connected with two rows of muscle-corpuscles. $\frac{1}{10}$th immersion obj. Same method.

Fig. 3.—Three isolated muscle-corpuscles of Dytiscus muscle, with transverse networks attached. $\frac{1}{10}$th immersion obj. Same method.

Fig. 4.—Muscle-corpuscle of Dytiscus, with portion of transverse network connected with it. Transverse view. Gold preparation. $\frac{1}{10}$th immersion obj.

Fig. 5.—Muscle-fibre of dragon-fly, showing two muscle-corpuscles with their intra-nuclear network. Some of the transverse networks are seen to be connected with the intra-nuclear network of the upper corpuscle. $\frac{1}{10}$th immersion obj. Acetic acid, osmic acid, and gold chloride.

Fig. 6.—Muscle-corpuscle of crayfish, with portion of the muscle network apparently connected with its intra-nuclear network. $\frac{1}{10}$th immersion obj.

Figs. 7 and 8.—Developing muscle-fibres of trout, showing striation. *n.* Nucleus. $\frac{1}{10}$th immersion obj. Acetic acid 2 per cent., a few seconds; gold chloride 1 per cent., fifteen minutes; formic acid 25 per cent., thirty minutes in warm chamber.

Fig. 9.—Portion of the striated part of one of the above fibres, showing the network and the darkly stained bodies in its meshes. $\frac{1}{25}$th immersion obj.

Fig. 10.—More fully developed fibre of trout. *n.* Nucleus. $\frac{1}{10}$th immersion obj.

Fig. 11.—Muscle-fibre of Dytiscus, with a portion of nerve-ending apparently connected with the longitudinal bars of the network. $\frac{1}{10}$th imm. obj. Mays' method.

Fig. 12.—Muscle of crayfish, showing a "streak" of nerve-ending apparently connected with the longitudinal bars of the network. $\frac{1}{10}$th imm. obj. Retzius' method.

Figs. 13 and 14.—Diagrams comparing the view of Rollett and others with the network. In Fig. 13 the structure, according to Rollett, is marked in full lines, and the network marked in dotted lines. In Fig. 14 the thick segments of Rollett's muscle-columns are shown by dotted lines in the meshes of the network. *n.* Network. *s.* Muscle-columns. *g.* Granules.

Fig. 15.—Portion of muscle-fibre of Dytiscus, showing network very plainly. One of the transverse networks is split off, and some of the longitudinal bars are shown broken off. (Copied from Melland, loc. cit., fig. 6.)

[Note.—In figure 13 the lines connecting the thick parts of Rollett's muscle-columns should be much thicker. They represent the thin segments of the columns.]

On Chætobranchus, a New Genus of Oligochætous Chætopoda.

By

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With Plate XII.

Habitat.—I discovered this very remarkable worm in the mud from a pond (Anglo-Indian "tank") in Madras town. The mud had been placed in a bottle and allowed to stand, so that the Naids for which I was searching might come to the top. On examination I found projecting from the surface of the mud, among numerous individuals of Nais and Dero, several specimens of this worm. These at once attracted my attention on account of the branchial processes, which could be seen with the naked eye. The mud is of a very finely divided character and is brown in colour, and contains very little animal and hardly any vegetable life, and very little organic débris. I obtained a large quantity of it, and by the use of muslin sieves secured numerous specimens of Chætobranchus.

The worm does not secrete any glutinous material, and so make itself a mud tube; but, as I have been enabled to ascertain by keeping them in a small aquarium nearly filled with the mud, makes for itself long tracks in the mud—"burrows," they might be called; and each worm appears to reside in its own "burrow," at times projecting from the surface of the mud into the water, and at other times withdrawing itself completely into its "burrow." The mud is of such a character that unless disturbed in some way the "burrow" remains as a permanent structure. The mud can be dried in cakes, and when such a cake is broken across, the "burrows" are as obvious as they are in a lump of earth in which earthworms have lived.

Some of these mud-living Oligochæta secrete a glutinous substance, so that when they are removed and the loose particles washed away a tube of mud remains, while others secrete no such substance; and when these latter are removed and the loose mud washed away the worm remains quite unprotected. Chætobranchus belongs to the latter category.

External Characters—Branchial Processes—Setæ. —The worms vary in size, but when stretched out and crawling on a slide an average sized individual is about $1\frac{1}{2}$ inches to 2 inches in length, and about $\frac{1}{50}$ inch in breadth (fig. 9), and consists of about 130 segments. The anterior extremity is a little thinner than the rest of the worm, and the body wall in this region is slightly pigmented; the pigment is to a certain extent arranged in transverse bands on the dorsal surface, each band corresponding to a segment. There is no proboscis, and the eye-spots are absent.

The most remarkable and striking feature of the worm is the presence of dorso-laterally placed processes, of which there is a pair to each of the anterior segments, commencing with the second[1] segment. It is difficult to say how many pairs of these processes exist, as, after the ten to twelve most anteriorly placed pairs, they gradually diminish in size until they become mere warts on the surface of the worm, and in the posterior segments are entirely absent (fig. 1). I have counted about sixty to seventy pairs. In most of the individuals I have examined the five or six most anteriorly placed processes are a little shorter than those immediately following, but there is no

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[1] I have assumed that the first setigerous segment is the second segment of the body, the first segment of the body being the buccal segment with the prostomium. The nomenclature of the segments in earthworms is usually based upon this assumption, and it would be more convenient if a similar practice were always adopted with regard to other Oligochæta.

regularity about this, and I am inclined to believe that these get more or less injured in the "burrowing." The length of the processes relatively to the size of the body may be judged of from an examination of fig. 1.

These processes are obviously branchial in function. The structure of one of these branchial processes is shown in fig. 2. Each is virtually a hollow prolongation of the body wall; the cœlomic corpuscles may occasionally be seen pushed out into it. The epidermis is bounded externally by a distinctly visible cuticle, through which project very fine cilia—so fine that they might easily escape notice but for the commotion which they create among particles of mud in the water. At the extremity are a few stiff processes, doubtless sensory in function.

Into each of the longer processes (about the first fifty) runs a loop of the lateral vessel (see below, circulatory system).

Entirely contained within each process are all, in the case of the more anterior, or some in that of the more posterior, processes of the setæ belonging to the dorsal bundle; so that in the anterior portion (about thirty segments) of the worm no dorsal setæ project freely outside the body wall, while in the region immediately following (about thirty segments) two at least of the dorsal setæ do not freely project, while one seta of the dorsal bundle does so project, and in the remaining portion of the body all the setæ project.

There are no muscular structures in the branchial processes, which are kept fairly rigid, and are moved by the dorsal setæ, and thus serve the worm as locomotor organs.

The seta bundles are placed in four rows—two ventral rows and the two dorsal rows mentioned above. The dorsal seta bundles commence in the same segment as do the ventral seta bundles, i. e. the second body segment. Two kinds of setæ occur in the dorsal bundles: the one kind is the straight capillary seta shown in fig. 5; they vary in length; in the anterior segments they are very long. The seta drawn in fig. 5, if intended for one of the longest, should have been drawn double the length it is, to be on the same scale as the setæ drawn in figs. 6 and 7 *a*. The relation of these long capillary setæ to the branchial processes is described above. The other kind of seta occurring in the dosal bundle is always of the same length, and has a curved sickle-shaped free extremity (fig. 6). Such setæ do not occur in the more anterior bundles, and in passing backwards one comes across intermediate conditions between a short straight capillary seta and the sickle-shaped form figured. As a rule, there are two or three straight and two or three curved setæ in each bundle.

The ventral setæ are all "crotched-shaped;" in the most anterior segments the free extremity has the shape drawn in fig. 7 *b*; but this, in going backwards, soon passes into the shape shown in fig. 7 *a*. Each of these ventral setæ has a little swelling placed rather nearer to the free extremity than to the root. There are four to six setæ in each ventral bundle. All the setæ diminish rapidly in size as one approaches the posterior extremity, which presents therefore, as in Naids, the appearance of being a region of continued growth.

Viscera.—The alimentary canal presents no special feature of interest ; there is no enlargement corresponding to the so-called gizzard of many Naids.

The cœlom is, as in most Oligochæta, incompletely divided into a series of chambers by diaphragms placed between the segments.

The cœlomic corpuscles are rounded (fig. 8), and like those of Naids. They contain numerous olive-green granules, which look like droplets of fatty matter. They may be seen passing from segment to segment, and at times into the branchial processes.

The circulatory system consists of a dorsal and ventral vessel and a series of lateral vessels, a pair in each segment, which run from the dorsal to the ventral vessel, and in those segments provided with well-developed branchial processes loop out into the process (fig. 2).

The walls of the dorsal vessel are much pigmented, as in many Oligochæta, while those of the ventral vessel, and, as a rule, the lateral loops, are unpigmented.

The nephridia are not very clearly seen, but are undoubtedly present, a pair in each of the segments. In the middle region of the body they have exactly the same appearance as have the nephridia of Naids.

Asexual Reproduction.—Although I have examined a very large number of individuals I have found a few specimens only in the act of asexual reproduction, and this process appears to be more like one of simple fission, as opposed to gemmation, than it is in Naids and Chætogaster. In these latter forms a new region, a "budding zone," is produced between two existing segments; this divides into two portions: the anterior portion forms the new tail of the anterior daughter zooid, and the posterior portion forms a head for the posterior daughter zooid, while the previously existing segments[1] of the parent zooid undergo little or no change.

In Chætobranchus I cannot find any "budding zone." In the specimen which is drawn in fig. 10, for instance, I counted over 200 segments. The most anterior sixty segments bear recognisable branchial processes, which, as usual, get smaller as one passes backwards; then there are about thirty segments which bear no trace of processes; then about forty-five segments on which branchial processes can be counted, the anterior ones almost as large as those usually found in the head region, and the posterior ones becoming so small as to be unrecognisable; behind the last process-bearing segment I counted about sixty-five segments, the posterior ones very much crowded together, as though active growth were taking place in this region.

This individual would doubtless soon have divided into two zooids, the posterior one of which must form a head, consisting, at any rate, of a buccal segment and a prostomium. The remarkable feature in this process is the new growth which occurs in connection with so many segments of the parent zooid, viz. the development of the branchial processes in all those segments which bear them, and which subsequently form part of the posterior daughter zooid.

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[1] Semper, 'Arb. Zool. Zoot. Institut, Wurzburg,' Bd. iv, 1877–8.

I have found several individuals preparing in this way for fission, but never found any trace of a "budding zone." At some other time of year I shall, I hope, be able to make further observations with regard to this process, and also with regard to the generative organs. I have hitherto found no trace of generative organs. This is unfortunate, as it leaves the systematic position of the worm still open to some doubt.

Systematic Position.—This is without doubt the worm referred to by Semper as occurring along with Dero philippinensis.[1] In many details of its structure, as well as in the fact that it exhibits fissiparous reproduction, Chætobranchus resembles the Naidomorpha, and represents, I believe, a family closely allied to the Naidomorpha (Vejdovsky) and the Chætogastridæ (Vejdovsky). The most remarkable feature in its structure is, of course, the possession of branchial processes, and these processes are themselves remarkable in completely surrounding the whole or a portion of the dorsal seta bundle. With the exception of the contained setæ these branchial processes closely resemble in structure the long branchial processes found in the anal region of some species of the genus Dero.

The only other Oligochæte which possesses branchial processes is Alma nilotica; but, judging from Vejdovsky's remarks anent this form, it is very different from Chætobranchus.

Generic Description.—Chætobranchus, g. n.—Capillary setæ present. Each of the anterior segments, from the second segment backwards, bears a pair of dorso-laterally placed branchial processes, which entirely include some or all of the setæ in the dorsal bundle. Dorsal setæ commence in the same segment as do the ventral setæ, i. e. the second segment.

Chætobranchus Semperi, sp. n.—Fresh stagnant water, Madras town.

I have dedicated the species to Professor Semper, as the

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[1] 'Arb. Zool. Zoot. Institut, Wurzburg,' Bd. iv.

worm which he discovered in the Philippine Islands is undoubtedly either the same or a closely allied species.

It is impossible, in dealing with a single species such as this, to define the specific characters; the absence of eye-spots, the character of the setæ, the length of the branchial processes, the nature of the pigmentation, will probably serve, among other characters, to mark the species.

DESCRIPTION OF PLATE XII,

Illustrating Professor A. G. Bourne's paper "On Chætobranchus Semperi."

Fig. 1.—Lateral view of Chætobranchus; the branchial processes and dorsal and ventral setæ of one side only are drawn. *pr.* Prostomium. *m.* Mouth. *an.* Anus.

Fig. 2.—A single branchial process. *s.* Dorsal setæ. *a.* Afferent blood-vessel. *e.* Efferent blood-vessel.

Fig. 3.—A portion of the dorsal blood-vessel. *l.* A pair of lateral vessels.

Fig. 4.—A portion of the ventral blood-vessel. *l.* A pair of lateral vessels.

Fig. 5.—A capillary seta from a dorsal seta bundle.

Fig. 6.—A seta from a dorsal seta bundle, with a sickle-shaped free extremity.

Fig. 7.—*a.* A seta from a ventral seta bundle in the posterior region of the body. *b.* The free extremity of a similar seta from the anterior region of the body.

Fig. 8.—A cœlomic corpuscle.

Fig. 9.—Dorsal view of Chætobranchus. Natural size.

Fig. 10.—A "budding" individual of Chætobranchus. About twice the natural size.

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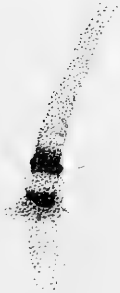
2.

3.



4.

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F. Huth, Lith^{r} Edin^{r}

The Presence of Ranvier's Constrictions in the Spinal Cord of Vertebrates.

By

Dr. William Townsend Porter,
of St. Louis.

With Plate XII, *bis.*

No question in the controversy over Ranvier's constrictions is more interesting than that of distribution. Torneaux and Le Goff[1] declared in 1875 that constrictions are present in the spinal cord. Their discovery remained almost unnoticed until Schiefferdecker,[2] not aware that he had been anticipated by the French observers, offered silver pictures as proof that the constrictions are not confined to the peripheral nerves. The statements of these authors have been contested. Boll[3] wrote against Torneaux and Le Goff; and Kölliker,[4] seeking to test the results of Schiefferdecker, worked over the same ground, but arrived at opposite results, and brought new arguments in favour of the old opinion.

It is of importance to have this question examined by many observers, for the presence of constrictions in the spinal cord

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[1] "Note sur les étranglements des tubes nerveux de la moelle épinière," 'Journal de l'Anatomie,' 1875.

[2] "Beiträge zur Kenntniss des Baues der Nervenfasern," 'Arch. f. mikr. Anat.,' Bd. xxx, 1887.

[3] "Ueber Zersetzungsbilder der markhaltigen Nervenfasern," 'Arch. f. Anat. u. Entwickelungsges.,' 1877.

[4] 'Handbuch des Gewebelehre des Menschen,' Leipzig, 1889, Bd. i, p. 154.

must influence our conceptions of the form and the purpose of these structures in the peripheral fibres.

In order to prove that constrictions are present in the central nervous system, it is necessary to demonstrate them in silver and in osmium preparations, in isolated fibres and in sections.

Silver Preparations—teased.—Small pieces of the white sustance of the spinal cord treated with silver-osmium solution give these results: the colour ranges from pale grey to deep black, according to the size of the piece, the strength and quantity of the osmic acid, the duration of its action, the distance of the fibre from the surface of the piece, and the thickness of the myelin. Beneath the outer darker parts of the fragment used is a portion whose pale grey colour and soft consistence show that the osmic acid has affected it but slightly. It is here that the silver crosses are seen at their best, for the silver solution readily penetrates the entire piece, and its deep brown impregnations contrast strongly with their grey surroundings. The teasing should not be too thorough; the nerves are easily broken at the constricted points, and even in the most careful preparations many will be found with the silvered constriction torn in two. In the grey fibre-groups are numerous axis-cylinders cross-striped with Frommann's lines, and sticking out in all directions from the edges of the group. Small granular silver masses, of a great variety of forms, may at first be taken for constriction stains; some of these are probably the remains of broken crosses, and others are precipitations between the fibres. The medullary sheath is poorly marked, often quite unrecognisable, and again only indicated here and there by faint lines, more or less parallel to the axis-cylinder. Well-shaped crosses are hard to find, but crosses whose sharpness of outline is somewhat blurred by the silver granules lying about them are common. A sceptical observer will sooner or later be convinced by finding an unmistakable cross in a fibre whose medullary sheath is still recognisable, and whose isolated position guards against deception. The lines of Frommann have in my preparations been seen to best advantage in the frog and the guinea-pig; but the crosses are larger and clearer in the spinal cord of the ox.

Osmium Preparations—teased.—Difficulties surround the demonstration of constrictions in teased preparations of central fibres treated with osmic acid alone. Only a small number of the fibres are properly "fixed." The absence of Schwann's sheath makes isolation difficult, and from the same cause by far the greater number of the constrictions are torn by the needles. We have no reason to suppose that the rule according to which the interval between any two constrictions is approximately directly proportional to the thickness of the fibre is any less true of central than of peripheral fibres. It is the larger central fibres which are most easily isolated, and their constrictions, if this rule holds good, must be widely separated. In the animals used by me it seemed impossible to isolate pieces long enough to show two constrictions. Only when the locus minoræ resistentiæ has escaped the teasing needles and the fibre is torn through the myelin can constrictions be found. If the teasing is not too thoroughly done, small groups of fibres, lying for the most part parallel, will be secured. It is near the edges of these groups that the constrictions are most likely to be found, because the outermost fibres protect the rest. In both rabbit and ox I have seen entirely isolated fibres with good constrictions.

Osmic Acid Preparations; Sections.—Longitudinal sections of central fibres are best made from the spinal cord of the ox. The part used by me was taken from the neighbourhood of the median fissure. For the detection of the constrictions sections of the average thickness of the fibres are most suitable. The constrictions are not so easily seen when the nerves are cut in the plane of the axis-cylinder. Only the outer fibres of a section should be used, because they are usually found lying with more space between each fibre than is the case elsewhere, and are better "fixed."

Many of the interruptions in the continuity of the nerves are of considerable width. They are so broad that one at once thinks of artificial separations or of places where fibres have been cut through as they rose above or sank below the plane of section. Examination with a high power shows that this is true of only a small number, and that the myelin at many of the other interruptions is plainly neither cut nor torn. The myelin has here the shape of a cylinder, ending in a truncated cone. When the fibre is seen a little obliquely, the observer looks into the end of this cone and sees that out from it comes a pale, ribbon-like or cylindrical structure, which runs a more or less wavy course until it enters another myelin sheath. It has the look of a constriction elongated by the process of preparation. A little search shows that the space which separates two medullary sheaths is often not greater than the breadth of the fibre, and in such cases appears large because the fibres are very broad. In these narrower interruptions the axis-cylinder is usually well shown. In a good section are interruptions not wider than half the breadth of the fibre. On either side is the cone-shaped ending of the medullary sheath; between the two, looking very small and colourless in contrast with the thick myelin, is the axis-cylinder—straight, of uniform calibre, and often faintly striped in a longitudinal direction. All the structures lie in parallel planes. The fibre is neither cut nor torn. It is a true constriction, and closely resembles, except that the sheath of Schwann is absent, the Key and Retzius[1] drawings of peripheral constrictions in man.

With a strong immersion system it is possible to see that most of the constrictions are crossed about the middle by a very fine line, which seems to lie closely upon the axis-cylinder, and sometimes appears as an indistinct ring. From the margins of this ring I have sometimes seen a line of equal fineness, passing on either side towards the medullary sheath. These delicate structures are just within the limits of visibility. They correspond to the lines found in silvered central fibres, and are probably portions of the ensheathing neuroglia. No sheath of Schwann is present. Long fusiform

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[1] 'Studien in der Anatomie des Nervensystems und des Bindegewebes,' Stockholm, 1876, ii, Bd. i, plate vii, figs. 11, 13, 14, 15.

nuclei sometimes lie against the myelin, but I have found no proof that these do not belong to the neuroglia. The myelin was not broken by the incisures of Schmidt and Lantermann.

The value of these results depends of course on the value of the method by which they were obtained. Well-founded objections have been brought against nitrate of silver. This reagent may be reduced in all parts of the nerve-fibre, and even between the individual fibres.[1] Combinations of various forms of impregnations give a great variety of pictures. In teased preparations, for reasons previously stated, the crosses are not often found isolated. These facts make deception easy, but do not lessen the force of the truth that unmistakable crosses are proof of the presence of Ranvier's constrictions. It may be said that the constrictions found in osmium preparations were artificially produced. Naturally, the only evidence which can be offered here is the testimony of accurate drawings.

The demonstration of the presence of constrictions in central fibres helps directly in the settlement of some vexed questions and is of indirect value with respect to many others.

Ranvier[2] advanced the opinion in his original memoir that the myelin is impervious to crystalloids, and that nitrate of silver enters the nerve at the constriction. This, he said, goes to show that nutritive fluids take the same route; and his explanation is accepted by most physiologists. There is, as Boveri insisted, no reason for supposing that the nutrition of medullated central fibres is different from that of medullated peripheral fibres. Boveri,[3] not finding the constrictions in the spinal cord, rejected Ranvier's hypothesis and substituted his own, which was that the constrictions served a purely mechanical end, permitting great freedom of motion, like a

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[1] I can confirm Kölliker's statement that stripings similar to Frommann's lines occur in silver preparations of small blood-vessels. Boll (l. c., p. 310) saw cross-striping in elastic fibres treated with nitrate of silver.

[2] "Recherches sur l'Histologie et la Physiologie des Nerfs,' 'Arch. de Physiologie,' iv, Mars, 1872, No. 2.

[3] "Beiträge zur Kenntniss der Nervenfasern," 'Abhandl. der math. physik. classe d. k. Bayer. Akad. der Wissensch.,' Bd. xv, 1886.

jointed chain, and removing the danger of injury from the sudden bendings to which many peripheral nerves are exposed. This can be accepted as one of the uses of peripheral constrictions, but the objection to Ranvier's explanation falls to the ground with the confirmation of Torneaux and Le Goff's discovery, and the constrictions may be looked upon as a food-way to the axis-cylinder.

Constrictions are present in the spinal cord; the sheath of Schwann is absent from the spinal cord; therefore the sheath of Schwann is not concerned in the formation of constrictions in central fibres, and is probably not an essential part of peripheral constrictions. We can safely reject the dictum of Hans Schultze:[1] The sheath of Schwann is "die formgebende Ursache der Ranvier'schen Markunterbrechungen," an idea prominent in many researches, and may look with suspicion on theories that find in Schwann's sheath an explanation of the structure of the constrictions.

Further inferences are very tempting. The central nerve-fibres are epiblastic, and lie in an epiblastic framework (Gerüst); no mesoblastic tissue ensheathes them (Gierke); in Palæmon squilla the medullated nerves have no connective-tissue sheath; therefore, the myelin of central fibres, like the axis-cylinder, is of epiblastic origin, and the medullary sheaths of peripheral nerves are probably formed from the axis-cylinder. If the myelin is formed from the protoplasm of the axis-cylinder, then the function of the sheath of Schwann is that of a simple connective-tissue envelope. The many theories of development and degeneration that affirm a generic relation between the sheath of Schwann and the medullary cylinder are incorrect; spinal nerves are developed and regenerated through their cells of origin, and changes in the nuclei of Schwann's sheath are not the cause of the growth or decay of the medullary substance. But the evidence in our possession does not warrant our going so far, for, although Gierke[3] de-

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[1] 'Axen-cylinder und Ganglionzelle,' p. 27.

[2] i. e. Axis-cylinder and medullary sheath.

[3] "Die Stützsubstanz des central Nervensystems,' 'Arch. f. mikr. Anat.,'

clares that no connective tissue surrounds the individual nerve-fibres in the spinal cord, yet it is by no means settled that the medullary sheath of central fibres is not mesoblastic. Blood-vessels enter the cord at a very early date in the life of the embryo,[1] and it is not certain that the mesoblastic tissue which forms and surrounds them is limited, as Gierke thinks, to the blood-vessels themselves. Joseph's[2] assertion that a continuous network penetrates and binds together axis-cylinder and medullary sheath in the peripheral nerves—a fact of much importance if true—has been denied by Retzius,[3] who found the network only in the axis-cylinder. The discovery of Retzius[4] that Palæmon squilla has medullated nerves which lack Schwann's sheath and are provided with oval nuclei lying between the medullary sheath and the axis-cylinder has not yet been confirmed. There are finally many who still deny the correctness of the views of His[5] regarding the formation of the central nervous system.

Such reflections are therefore merely suggestive, and are of use only as they emphasize the fact that a solution of many weighty problems is to be found through a sufficient explanation of the origin of myelin.

I take this opportunity to gratefully acknowledge the kindness of Professor Flemming, under whose direction this work was done at the Anatomical Institute in Kiel.

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xxv, 1885, p. 533 :—" Alle faserigen Elemente der Stützsubstanze Fortsätze von Gliazellen sind; andere Fäden, als elastische oder Bindegewebsfibrillen, sind durchaus zwischen den Nervenfasern nicht zu finden."

[1] His found blood-vessels in the cord between the fourth and fifth week. See "Zur Geschichte des Menschlichen Rückenmarkes und der Nervenwurzeln," 'Abhandl. der math. phys. Classe der Kgl. Sächs. Gesellsch. der Wissensch.,' 1886, xiii, No. 6.

[2] "Ueber einige Bestandtheile der peripherischen markhaltigen Nervenfaser," 'Sitzungsber. d. Berlin. Akad.,' Bd. ii, 1888, p. 1231.

[3] "Der Bau des Axencylinders der Nervenfasern," 'Verhandlung des Biol. Vereins in Stockholm,' Bd. i, Jan., 1889, No. 4.

[4] "Ueber myelinhaltige Nervenfasern bei Evertebraten," 'Verhandl. d. Biol. Ver.,' Stockholm, Bd. i, Dec., 1888, No. 3.

[5] "Every nerve-fibre is a process from its own nerve-cell; this is its genetic, nutritive, and functional centre." His, l. c. p. 513.

DESCRIPTION OF PLATE XII, *bis*,

Illustrating Dr. William Townsend Porter's paper, "The Presence of Ranvier's Constrictions in the Spinal Cord of Vertebrates."

Figs. 1, 2, 3, 4, 5.—White substance near median fissure. Ox. Osmic acid 2 per cent., nitrate of silver 1 per cent., each 1 part, two hours. Dilute solution of caustic potash, about five minutes. Teased in glycerine diluted about one third with distilled water. Leitz, $\frac{1}{16}$, ocular 3, draw-tube out.

Fig. 6.—Spinal Cord. Guinea-pig. Osmium-silver mixture as above, three hours. Teased in diluted glycerine. Leitz, $\frac{1}{16}$, oc. 3, d. t. out.

Fig. 7.—Medulla oblongata. Rabbit. Osmium-silver mixture, two hours. Picro-carmine, twenty-four hours. Teased in diluted glycerine. Leitz, $\frac{1}{16}$, oc. 1. Axis-cylinder shows three silver cross-stripes at constriction; the lines between the ends of the medullary cylinders represent the light reflex.

Fig. 8.—White substance near median fissure. Spinal cord. Ox. Osmic acid 2 per cent., twelve hours. Celloidine, cloves, balsam. Leitz, $\frac{1}{16}$, oc. 3, d. t. out. The section was cut the average thickness of the fibres.

Professor Bütschli's Experimental Imitation of Protoplasmic Movement.

Professor Bütschli, of Heidelberg, has recently made some extremely interesting observations upon a substance which simulates in a remarkable way the appearance and movements of the protoplasm of an Amœba, or of the plasmodium of Mycetozoa. He has been kind enough to send to me some oil in a suitable condition for use, with directions as to the exact details of the experiment. In my laboratory, by following his directions, the movements described by him have been observed in a satisfactory manner. In order to obtain the best results some experience and care is requisite, and probably they cannot always be obtained by a single experiment. The subject is so interesting, and so fitted for further investigation by all who have leisure and a taste for the study of the vital phenomena of the Protozoa and of living protoplasm in general, that I think it will be of advantage to readers of this Journal to have Professor Bütschli's directions, which he has permitted me to publish, placed in their hands.

E. Ray Lankester,
March, 1890.

Heidelberg, February 1st, 1890.

You have kindly asked me how I prepare the protoplasma-like drops which I have described. As you yourself feel greatly interested in this discovery, and presumably a like interest exists among other English biologists and microscopists, I hasten to satisfy your desire, and to explain somewhat more fully the methods which I have described in a previous publication.

As you well know already, I use in the preparation of these globules—showing protoplasma-like streaming—ordinary olive oil. My first experiments were made with a small quantity of olive oil which had been standing for a long time in my laboratory in a small bottle. By some happy chance this oil had just the right properties which are necessary for the success of the experiment, for not every sort of olive oil is suitable. As far as my experience goes, it tends to show that the ordinary oil cannot be directly used, because it is too thin, or is perhaps deficient in other qualities on which the success of the experiment depends. In order, therefore, to prepare a suitable oil, I proceed in the following manner :—A medium-sized watch-glass or flat dish is filled with a thin layer of common olive oil, and is placed on a water-bath or in a small cupboard, such as are used for embedding in paraffine, at a temperature of about 50° C. Under the influence of the higher temperature the oil gradually loses its yellow colour and becomes thicker. The great point now is to select the right moment at which the oil will have attained the proper degree of thickness and viscosity, as also the other properties which at present I am not able to define more exactly, but on which much of the success seems to depend. The exact moment can, however, only be found out by systematic trials. After the oil has been thickening for three or four days a trial should be made with a drop of it in the manner described below. Should the drop not become finely vesiculate, and exhibit little or no streaming, continue the heating process and experiment again on the following day. If the oil should have become too thick it will form good frothy drops, but will scarcely show any streaming. In this case mix it with a small quantity of ordinary olive oil, and thus render it more liquid. If it has become much too thick it will form a good froth, but the latter dissolves very rapidly in glycerine.

You see thus that the process to obtain the suitable oil is somewhat slow, but I do not at present know of any other method by which the result can be arrived at more quickly and surely.

To prepare the vesiculate drops I proceed in the following way :—In a small agate mortar I grind a small quantity of pure dry carbonate of potash (K_2CO_3) to a fine powder. I then breathe on to the salt till it becomes slightly moist, and with a glass rod add to it a drop of oil, mixing the two constituents to a thickish paste. The success of the experiment depends, however, more upon the nature of the oil than upon the proportions of oil and salt in this mixture. Then with a glass rod or a needle I place a few drops of the paste, about the size of a pin's head or smaller, on a cover-glass, the corners of which are supported by small pegs of soft paraffine. I then place on a slide a drop of water, and put the cover-glass over this in such a manner that the drops of the paste are immersed in the water, but are not much compressed, to which end the corners of the cover-glass have been supported by the paraffine. The preparation is then placed in a damp chamber, and remains there about twenty-four hours. The drops have now a milk-white and opaque appearance. The preparation is then well washed out with water by applying blotting-paper to one edge of the cover-glass, and supplying water at the other edge from a capillary tube.

If the drops have turned out well, they will begin almost immediately after this to move about rapidly, and change their shape continuously. The water under the cover-glass must now be displaced by glycerine, diluted with an equal bulk of water, and the drops will then exhibit a vigorous streaming and forward movement, becoming gradually quite transparent. The amœboid movements are generally more distinct if the drops are somewhat compressed. If the drops do not show the streaming movement you may succeed in producing it by tapping the cover-glass slightly, by applying gentle pressure, or sometimes by breaking up the drops. For it seems as if at times incrustations were formed on the surface of the drops, which prevent or impede the streaming movement, and which can, in part at least, be removed by the above-mentioned manipulations.

It is especially interesting to see how fast and beautifully the drops creep to and fro in water, or in half-diluted glycerine, even when they are not compressed. The streaming movement, on the other hand, is better seen if the drops are somewhat compressed, which may be done by inserting under the cover-glass a piece of a broken cover-glass of medium thickness, and then removing the paraffine pegs. Then draw away the liquid until the necessary pressure is obtained. This streaming movement is best demonstrated twenty-four hours after the addition of the glycerine, as the drops will then be thoroughly cleared and transparent. Further, it is interesting to note that a progression of the drops takes place in the direction in which the streaming moves.

As this forward movement is rather slow in compressed drops, it is necessary to use a micrometer ocular to satisfy oneself of the advance.

Unfortunately the oils which I have prepared since my first experiments do not move and stream so well or so rapidly as those I employed then. The movement and streaming show themselves much more markedly and distinctly if they are examined on a warmed stage at a temperature of 50° C. If you should be in a position at your demonstrations to conduct the experiment at this temperature, the phenomena will certainly be much more evident.

From the preceding description you will see that it will be necessary, to obtain good results, to gradually get hold of the methods, and you must not doubt the correctness of the phenomena which I have described if the first trials do not give the desired results.

At all events, you will have at first to make some experiments so as to obtain an insight into the conditions and sort of phenomena, but I do not doubt that you will succeed in observing the appearances and in demonstrating them to others, though perhaps in not so vigorous a degree as I might desire.

I have lately made some trials to render olive oil suitable for these experiments by heating it more rapidly. Although at present I have no entirely reliable results, it seems to me that by heating ordinary olive oil to 80°—90° C. for twelve or twenty-four hours, a suitable medium may be obtained.

Finally, I would like to remark that I am the last person to defend the view that these drops, exhibiting protoplasma-like movements, are directly comparable to protoplasm. Composed as they are of oil, their substance is entirely different from protoplasm. They may be, however, compared with the latter, in my opinion, firstly with regard to their structure, and secondly with regard to their movements. But as the latter depend on the former, we may assume that the amœboid movement of protoplasm itself depends on a corresponding physical constitution.

These drops, too, resemble organisms inasmuch as they continue for days to exhibit movements, due to internal causes, which depend on their chemical and physical structure. I do not believe that up to this time any substance has been artificially prepared which in these two points, viz. structure and movement, has so much resemblance to the most simple form of life as have these vesiculate drops. I hope, therefore, that my discovery will be a first step towards approaching the problem of life from the chemico-physical side, and towards passing from vague and general hypotheses of molecular constitution to the surer ground of concrete conceptions of a physical and chemical nature.

It is, however, a special satisfaction to me to hear that in your country, which has given rise to so many and so celebrated men in biological science, my investigations are followed with interest and sympathy.

With friendly greetings,
Yours sincerely,
O. Bütschli.

The Embryology of a Scorpion (Euscorpius italicus).

By

Malcolm Laurie, B.Sc.,
Falconer Fellow of Edinburgh University.

With Plates XIII—XVIII.

Since 1870 there has been no detailed work on the development of the Scorpion. As it seemed likely that with modern methods of section-cutting and the great advance which has been made of late years in the field of embryology, a renewed examination might yield interesting results, I have, at Professor Lankester's suggestion, examined and cut sections of a large number of embryos of Euscorpius italicus preserved for him by the Zoological Station at Naples. I have also examined a number of embryos of Scorpio (Buthus) fulvipes preserved and sent over from Madras by Professor Bourne. These, however, chiefly owing to the small amount of food-yolk, show such a great difference from E. italicus in their mode of development that it seems better to postpone the description of them to a future paper.

The Scorpion is interesting not only as being the lowest, and, as far as we know, the oldest type of air-breathing Arachnid, but also as being exceptional among Arthropods in that the whole development takes place within the body of the female—in the ovarian tubes. The only other instances of this with which I am acquainted are Phrynus, which is also viviparous, and Sphœrogyna ventricosa, one of the Acarina in which the young are born sexually mature.

I may fitly here express my thanks to Professor Ray Lankester not only for the suggestion that I should work at this interesting subject, and for the generous way in which he has provided me with material, but even more for his continual and invaluable assistance and advice while the work has been in progress.

HISTORICAL INTRODUCTION.

Johannes Müller[1] gave a short description, with five or six figures, of the development of Buthus. Owing to its brevity and the absence of any attempt to ascertain the internal arrangement, his paper is of little value except from an historical point of view.

Duvernoy[2] gives also only a few figures of Buthus and of another form, probably Euscorpius. He describes at some length a cord (baguette) which he says passes from the appendix of the follicle in Buthus to the mouth of the embryo, and which Müller had compared to an umbilical cord. I hope to be able in a future paper to give a detailed account of this and other curious points in the development of Buthus. The chief value of Duvernoy's paper was that he reconciled the contradictory descriptions of the ovary which had been given by Müller and Rathke.[3] While doing this he makes a rather serious mistake in describing the ovum of Buthus as occupying the whole of the diverticulum of the ovarian tube, instead of only a small space at the top.

The next writer on this subject is **Léon Dufour**,[4] who gives

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[1] Joh. Müller, "Beit. z. Anat. des Skorpions," 'Meckel's Arch. f. Anat. u. Phys.,' Bd. xiii, 1828.

[2] Duvernoy, "Fragments sur les organes de la génération de divers Animaux," 'Mém. de l'Acad. des Sci. de l'Institut,' t. xxiii.

[3] Rathke, "Zur Morphologie," 'Reisbemerkungen aus Taurien,' 1837, Riga, 4to.

[4] Dufour, "Hist. Anat. et Phys. de Scorpions," Mém. Presentés à l'Acad. des Sciences,' t. xiv, 1856.

an elaborate description with numerous figures of the anatomy of the adult. His description of the embryo is, however, very brief and his figures unsatisfactory.

Elias Metschnikoff[1] is the only writer who has treated of the development of the Scorpion with any degree of fulness. He gives a detailed account of the whole development, and his paper, which deals chiefly with the surface views and optical sections, contains a large amount of accurate and laborious observation. It is the classic on this subject, and up to 1886 no attempt was made to add to it or supersede it.

In 1886 **Kowalevsky** and **Schulgin**[2] published a short account of the development of Androctonus ornatus. Unfortunately their paper has no figures, which detracts much from its value. I find reason to differ from them on a few points, but it is quite possible that this may be due to our having worked on different genera.

The only other paper on this subject which I am acquainted with is by **G. H. Parker**,[3] who treats at some length of the development of the central and lateral eyes. I had worked at this point before the appearance of his paper, and on the whole agree with his conclusions. These are briefly that the lateral eyes are monostichous, being formed from the hypodermis without invagination. The median eyes, on the other hand, are formed by invagination, and are therefore three-layered, all the layers being derived from the hypodermis. The retina is the second layer, the third being reduced to a post-retinal membrane. The material at Mr. Parker's disposal did not enable him to go back to the commencement of the formation of the central eyes and their connection with the cerebral invaginations.

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[1] Metschnikoff, "Embryologie des Skorpions," 'Zeit. f. wiss. Zool.,' 1870.

[2] Kowalevsky and Schulgin, "Entwickelungsgeschichte des Skorpions," 'Biol. Centralblatt,' Bd. vi, 1886.

[3] Parker, "The Eyes in Scorpions," 'Bull. Mus. Comp. Zool., Harvard,' vol. xiii.

The Ovary and Ovarian Egg.

The ovary consists, as is well known, of three longitudinal tubes connected by transverse anastomoses, so as to form eight quadrilateral meshes. The oviducts arise from the lateral angles of the two foremost meshes and run forward to open together on the genital operculum. The ovary appears to be embedded in the liver, the chief mass of which lies dorsal to it; this is not really the case, for, though lobes of the liver pass through the meshes of the ovarian network they do not unite on its ventral side. Both the longitudinal and transverse tubes bear ova, which project from their outer surface as oval bodies each attached by a short pedicle and measuring when ripe about 1·2 mm. in length and ·83 mm. in breadth. Ova in all stages of development are present on the ovarian tubes at the same time, and there are in addition the corpora lutea (v. p. 111).

The microscopic structure of the ovarian tubes is shown in Pl. XIII, fig. 2. They are there seen to be formed of two layers surrounding an irregular lumen. The outer layer, *o. l.*, which is purely skeletal in function, consists of irregularly polygonal cells, with circular nuclei and strongly marked cell outlines. The contents of these cells are highly refractive. Towards the inside of this layer the cells become flattened so as to form a distinct, cellular, limiting layer. The inner layer, which surrounds the lumen of the tube, is formed of very long and thin columnar cells, with oval nuclei and clear, faintly granular protoplasm. The nuclei are for the most part confined to a central zone, leaving a large part of the outer and a smaller part of the inner ends of the cells clear. It is from this inner layer of cells that the ova and their follicles are formed; it is, in fact, the germinal epithelium.

The first sign of the formation of an ovum is that one of the cells of the inner layer of the ovarian tube begins to increase in size (fig. 1, *ov.*). It contains finely granular protoplasm, a large and distinct oval nucleus, and a darkly staining nucleolus. There is at first no sign of its presence on the outside of the ovarian tube. As it increases in size, however, it pushes its way, at the head of a column of cells, towards the outside. The outer layer of the ovarian tube becomes very thin, but remains as a membrane containing few, if any, nuclei (fig. 2, *fol′.*). By the time the ovum is about ·04 mm. in length (fig. 2) it has passed completely through the outer layer and is visible as a small protuberance on the surface of the ovary. It remains connected to the inner layer of the tube by a column of cells which is somewhat expanded over the base of the ovum. The nucleus has not increased in size in proportion to the growth of the cell.

The nuclei of the cells of the column which connects the ovum to the inner layer of the ovarian tube next arrange themselves so as to leave a clear space down the centre of the column (Pl. XIII, fig. 3, *mi.*). They also grow round the ovum so as to form a follicle (fig. 3, *fol.*) one cell thick. The cells of this follicle rapidly become flattened and their nuclei become smaller. The cells which remain clustered at the base of the ovum (fig. 3, *ger′.*) on the other hand increase in size, and shortly after the stage represented in fig. 3, which is a drawing of an ovum of about ·1 mm. in diameter, they begin to secrete the yolk of which the greater part of the ripe egg is composed. The outer layer of the ovarian tube can still be traced as a thin and apparently structureless membrane (fig. 3, *fol′.*) surrounding the egg outside the cellular follicle. The nucleus has increased in size and is now a distinct oval body with a round, granular nucleolus.

In fig. 4 is shown a longitudinal section of an egg of about ·4 mm. in length and ·28 mm. in breadth. A considerable quantity of yolk is now present in the form of spheres ranging in size from mere granules up to as much as ·025 mm. These spheres are clear, homogeneous, sharply defined bodies showing no internal structure except that there is, in the larger ones, a collection of granules at one point near the outside. Round the nucleus the yolk-spheres are small, and round the margin of the egg the protoplasm is coarsely granular, the rest of the space being filled up with the larger spheres.

The nucleus (fig. 4, *n.*), which retains its central position, is large (·05 mm.) but indistinct in outline and is probably breaking down as I have been unable to find any trace of it in eggs larger than that here figured. The nucleolus (fig. 4, *n′.*), which is situated towards one side of the nucleus, is also large, staining darkly with carmine and showing a very distinct circular outline. It often contains one large, clear, circular vesicle and a number of smaller ones.

The whole egg is surrounded by a distinct, rather thick vitelline membrane (fig. 4, *v. m.*). No trace of pores or any other structure was made out. Outside the vitelline membrane the egg is surrounded, except at the base, by the follicle in which the two layers (*fol.* and *fol′.*) of the ovarian tube can still be traced. The cells of the inner layer of the follicle are now flattened and small. The large yolk-forming cells at the base of the egg (*ger′.*) have increased in size and arranged themselves in a circle the centre of which is occupied by a prolongation of the ovarian tube (*mi.*). The egg is only separated from this prolongation of the lumen by the vitelline membrane. The spermatozoa are thus enabled to reach and fertilize the egg while it is still in its follicle.

Pl. XIII, fig. 5, shows the base of a ripe egg attached to the ovarian tube. The pedicle has become shortened and its lumen has increased very much in size. The yolk-forming cells have degenerated, their flattened nuclei (*ger′.*) being, however, still distinguishable, and the follicle has become much thinner owing to the growth of the egg. The egg itself is a mass of tightly compressed yolk-spheres, among which I have in vain sought for the nucleus. It is probable, however, that the nucleus and the greater part of the protoplasm migrate to the base of the egg as segmentation commences there.

The yolk (Pl. XIII, fig. 6) consists of spheres, ranging up to ·2 mm. in diameter. They are not homogeneous, but contain spherical or prismatic bodies, which stain darkly with borax carmine. These bodies are very large in the smaller yolk-spheres, which contain one, two, or more of them. In the larger spheres they are much more numerous and much smaller. Many of the spheres show round holes as if the darkly staining bodies had dropped out. It may be, however, that these cavities contained a fatty or oily substance, which has been dissolved out in the course of embedding and mounting.

The only structures remaining to be described in connection with the ovary are the **corpora lutea** mentioned above (fig. 7). These are irregularly shaped bodies of about ·12 mm. in diameter, showing a slight tendency to radiate structure, and containing a considerable number of nuclei, which are scattered about without any definite arrangement. They project from the surface of the ovarian tubes, and are evidently the collapsed remains of the follicles after the egg has passed out. I was confirmed in my idea that these were corpora lutea by their resemblance to the structures described by v. Siebold[1] in the ovary of Apus. They differ from these latter, however, in not containing fluid.

First Period.—Formation of Blastoderm.

The egg is fertilized in the follicle, from which it does not begin to pass out until the end of this period. It then passes into the ovarian tube in which it undergoes the rest of its development, the young when born being exactly like the parent in form. Kowalevsky and Schulgin[2] state that the egg in Androctonus is not fertilized until it has entirely left the follicle, and passed into the ovarian tube, or, as he calls it, uterus. I can hardly believe this to be the case, but it is quite possible that it leaves the follicle at an earlier stage in Androctonus than in Euscorpius.

Stage A.—I have not, unfortunately, been able to observe the processes of fertilization and the formation of the first segmentation-spheres. I should think it probable that the

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[1] v. Siebold, 'Beiträge zur Parthenogenesis der Arthropoden,' Leipzig, 1871, p. 191.

[2] Loc. cit., p. 526.

greater part of the protoplasm with the nucleus collects at the base of the egg. The youngest stage in my possession is shown in surface view in Pl. XIV, fig. 8, and in section in fig. 9. The blastoderm forms a circular patch about ·2 mm. in diameter, lying on the surface of the yolk at the end of the egg nearest to the micropyle, and consists of about twenty large cells, those in the centre measuring about ·03 mm. in diameter. In section (Pl. XIV, fig. 9) it is seen to be a single layer, the cells of which are about ·023 mm. thick in the centre. Round the margin the cells are wedge-shaped so that the blastoderm lies flush with the surface of the yolk. The cell-contents are coarsely granular, rather more so towards the lower side. The nuclei are large, round and granular with distinct outlines.

The yolk-spheres under the blastoderm appear to be breaking down. The blastoderm and yolk are closely surrounded by the structureless vitelline membrane (*v. m.*). This stage seems to be a little younger than that figured in Metschnikoff's paper in Pl. XIV, fig. 6.

Stage B.—In the next stage (Pl. XIV, fig. 10) the blastoderm is somewhat larger, measuring ·23 mm. in diameter. The blastoderm is now almost twice as thick (·045 mm.). Some of the cells are columnar, and occupy the whole depth of the blastoderm, but the majority have divided in a plane parallel to the surface, so that it is in places two or even three cells deep. The nuclei vary in shape, those in the columnar cells being oval.

Stage C.—In the next stage (Pl. XIV, fig. 11) the blastoderm, now ·3 mm. in diameter, is formed of an irregular mass of cells showing as yet no trace of arrangement into layers. The cells are comparatively small with well-marked outlines and large nuclei. Round the margin of the blastoderm the cells form a single layer on the surface of the yolk, but in the centre the blastoderm is five or six cells thick, and the cells push their way in between the yolk-spheres to which some of the cells attach themselves. These cells, which attach themselves to yolk-spheres, lose their definite outline and take, as far as I have been able to ascertain, no part in the further growth of the embryo. There is no doubt that these yolk-cells are derived from the blastoderm in this and the next stages, and do not arise in the yolk by any process of free cell-formation. Kowalevsky is also of this opinion. The yolk in the Scorpion's egg shows no sign of segmenting as does that of the Spider. The yolk of the Spider's egg seems[1] to represent the hypoblast, and takes an active part in the building up of the embryo; that of the Scorpion, on the other hand, remains throughout development an inert mass of food-material. This fundamental difference in the segmentation makes any comparison of the early stages of these two groups impossible, and would seem to point to an independent origin for their abundance of food-material. If the segmentation in Scorpions is a modification of the centrolecithal type, as would seem probable from the modes of segmentation in other groups of the Arachnida, it is a very extreme one, and almost all trace of its origin has been lost.

SECOND PERIOD.—Formation of the Three Layers and the Embryonic Membranes.

Stage D.—It is difficult to get good sections at this stage as the blastoderm is often humped up at the end of the egg and compressed by the ovarian tube into which it is beginning to pass. In one, and only one, series of sections I have seen what appeared to be a longitudinal groove in the blastoderm. This primitive groove is figured by Metschnikoff (Pl. XVII, figs. 2 and 3), but he may have been misled by the edges of the serous membrane which is growing up and might easily give the appearance of a groove in surface view. If the primitive groove exists, which I am inclined to doubt, as the appearance in my sections may have been due to shrinking, it is a very temporary structure. Towards the posterior end of the blastoderm the cells are proliferating and forming what I shall call the **primitive thickening**. From this primitive thickening is formed the mass of **hypoblast** which is found later on in the tail-segment.

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[1] Locy, "Observations on the Development of Agelina nævia," 'Bull. Mus., Harvard,' vol. xii.

It would seem to represent a modified invagination, and is comparable to the primitive streak in the chick. I was at first inclined to call this the primitive cumulus, but considering the fundamental differences between Scorpions and Spiders, and also the fact that, while Balfour[1] places what he calls the primitive cumulus at the posterior end of the embyro, Locy[2] gives the same name to a thickening at the anterior end, it seemed better to avoid a term which might suggest erroneous homologies.

A layer of cells (fig. 12, *pr. hy.*) is seen to be forming under the rest of the blastoderm, though not yet extending to its edges. This is well marked in the next stage, and forms the greater part of the **primitive hypoblast or hypomesoblast.** It would seem to be simply split off from the epiblast. I have seen no appearance of a "down-sinking" of cells to form the hypoblast, such as is described by Kowalevsky and Schulgin;[3] but, without the help of figures, it is not easy to be certain of their exact meaning. Whether this "down-sinking" is supposed to take place over the whole blastoderm or only at the primitive thickening is not clear from their description.

Round the edges of the blastoderm a single layer of large cells (fig. 12, *s. m'.*) is seen to be spreading a little way over the surface of the yolk. These **peripheral cells,** which are at present continuous with the epiblast, form later on the continuation of the **serous membrane.** This serous membrane, or outer layer of the amnion, is seen growing up as a single layer of cells from the edges of the blastoderm (Pl. XIV, fig. 12, *s. m.*). It spreads over the surface of the blastoderm from all sides, and its edges ultimately meet and fuse in the middle line. At this stage the edges have not yet come together, and the cells of the layer are still small and similar in appearance to those of the rest of the blastoderm.

The yolk is broken down to a considerable extent, and the

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[1] Balfour, "Notes on the Development of the Araneina," 'Quart. Journ. Micr. Sci.,' vol. xx, 1880.

[2] Locy, loc. cit.

[3] Loc. cit., p. 526.

cells in it (fig. 12, *y. c.*) are numerous. Their nuclei are very large and granular, and of irregular shapes. The cell-outlines have entirely vanished, the cells being swollen up by an enormous quantity of yolk-stuff. According to Kowalevsky and Schulgin these cells are capable of amœboid movements. Cells continue to be added from the under surface of the blastoderm to those already in the yolk up to the end of this stage. Their function—of breaking down the yolk—is carried on at a later period by the hypoblast.

Stage E.—In the next stage the blastoderm (Pl. XIV, fig. 13) has assumed an oval form, the thickened part or ventral plate measuring ·35 mm. in length and ·25 mm. in breadth, though the peripheral cells extend some way beyond this. I have not been able, either in surface view or section, to find any trace of the primitive groove, and imagine that, if ever present, it has filled up. The primitive thickening (fig. 14, *pr. t.*) is better developed than in the last stage, and the single layer of primitive hypoblast (figs. 14 and 15, *pr. hy.*) is now quite definite and extends a little way beyond the thick part of the blastoderm, and forms a layer (*hy'.*) of cells under the peripheral cells. These last (*s. m'.*) extend a good deal further than in the last stage. The serous membrane (*s. m.*) is now completed over the surface of the ventral plate.

Stage F.—In the next stage the embryo, of which fig. 16 shows a longitudinal section, consists of two somites—those which will afterwards bear the cheliceræ and chelæ—in addition to the head- and tail-segments. The head- and tail-segments are large, and a third somite is beginning to be formed from the tail. The first somite is smaller than the second, and not as yet very distinctly marked off from the head. It does not become fully separated from the head until a much later stage (eight somites). Except for this curious delay in the formation of the first, all the somites are formed and separated in regular succession from the tail-segment.

The epiblast has undergone little change since the last stage, except that it is somewhat thinner between the somites than in them. It is beginning to grow up at the edges over the surface of the ventral plate as a single layer of flat cells to form the inner embryonic membrane—the **amnion** proper (fig. 16, *am.*). This amnion never loses its connection with the epiblast as the serous membrane has now done, but remains attached to its edges and only extends round the egg as the epiblast extends.

The most important change in this stage is the formation of the **mesoblast** (*mes.*). This layer is formed under the whole ventral plate by a multiplication of the cells of the primitive hypoblast, from which it is in places not yet distinguishable. The mesoblast extends across the whole ventral plate from side to side, and is much thicker in the somites than between them.

The **serous membrane** (*s. m.*) has, as mentioned above, now lost all connection with the blastoderm, and is continued round about two thirds of the egg by the "peripheral cells," which are now beginning to separate from the egg and form a definite membrane. The cells of the serous membrane are becoming large and flat.

The **hypoblast** extends a little way beyond the ventral plate, forming a single layer of cells (*hy.*) in the periphery of the yolk immediately under the serous membrane.

By the time the embryo has reached a stage with three somites completely formed (Pl. XIV, fig. 17) most of the changes which were going on in the last stage are completed. The **amnion** has entirely closed over the embryo (fig. 18, *am.*), though its cells have not yet attained their characteristic form. The **mesoblast** (*mes.*) is entirely separated from the hypoblast, and remains henceforth a distinct and independent layer. The **hypoblast** (*hy.*) is now a single layer, extending under the whole ventral plate, except in the tail-segment, where it consists of a spherical mass. This hypoblastic mass in the tail-segment is the direct product of the primitive thickening. The hypoblast extends somewhat further round the egg than the other layers, as is diagrammatically shown in fig. 19.

The description given above of the mode of formation of the serous membrane and amnion differs very considerably from that of Kowalevsky and Schulgin. They describe it as a fold, the outer layer of which forms the serous membrane while the inner forms the amnion. This is probably the more primitive mode of origin for these structures, and the mode described above for E. italicus is probably derived from it either by a hastening of the formation of the serous membrane or a retardation of that of the amnion. I am unable to confirm their statement that mesoderm cells are present between the two layers.

THIRD PERIOD.—Up to the Formation of Nine Somites.

This period covers the rest of the time before the appendages begin to form. The egg has by this time entirely passed into the ovarian tube. It has also increased considerably in size, but I am unable to say whether this is due in any degree to absorption of fluid or whether it is entirely due to internal changes.

Stage G.—In the first stage belonging to this period which I have examined (Pl. XV, fig. 20) the embryo consists of nine somites. The first of these—that which will bear the cheliceræ, is much smaller than the others, and is seen in section to be not yet fully separated from the head. The second somite, which will bear the chelæ, is larger than those following it. The next four are the ambulatory, and the seventh will bear the genital operculum. A slight groove (*n. g.*) runs down the middle line of the body; this is chiefly due to the mesoblast having divided into two longitudinal bands (figs. 21 and 22, *mes.*).

The **epiblast** is moderately thick in the somites, and is beginning to grow as a single layer round the rest of the egg (fig. 21, *ep′.*), carrying the amnion with it. By this stage it has extended almost as far as has the hypoblast. The cells in the middle line show a more definite arrangement than the rest of the epiblast. This is preparatory to the formation of the neural groove. The cells of the **amnion** (*am.*) have developed their characteristic nuclei—spindle-shaped in section—and form a well-marked thin membrane lying close over the embryo.

The **mesoblast** (figs. 21 and 22, *mes.*) shows most important changes. As mentioned above, it has now separated into two longitudinal bands. This separation does not extend into the tail-segment (fig. 23, *mes.*), where the mesoblast remains as a solid mass of cells somewhat thinner in the middle line. The **cœlomic spaces** are now formed by a splitting of the mesoblast in the somites. They are best seen in the posterior somites (fig. 21, *cœ.*), where the mesoblast is thin and forms only a single layer on each side of the cœlomic space. Further forward (fig. 22) the mesoblast is thicker and the cœlomic space is not so well marked.

The **hypoblast** has undergone very little change. It is still visible in the tail as a solid mass (fig. 23, *hy. m.*), and spreads under the ventral plate and a little way beyond its margin as a single layer (figs. 21—23, *hy.*). The cells of this single layer have large oval nuclei which stain less darkly than those of the epi- and meso-blast. These nuclei are somewhat widely separated from each other, and the cells seem to contain a considerable amount of food-stuff.

The **serous membrane** (figs. 21—23, *s. m.*) is by this time quite separate from the egg all round. It has attained its final structure, the nuclei being enormously large (·05 mm.), flat, and at a considerable distance from each other. As far as my observations go I can confirm Blochmann's statement[1] that the nuclei of the serous membrane divide directly without forming any karyokinetic figures. As the serous membrane plays a purely passive part in the future development it will not be necessary to refer to it again.

Stage H.—In the next stage (Pl. XV, fig. 24), which is the last before the formation of the appendages, the embryo consists of nine somites. The first is very much smaller than the others, while on the second, which is the largest, a trace of the appendages is just visible. The first six somites are clearly distinguished from those further back, owing to their sloping backwards and outwards, while the posterior ones are at right angles to the axis of the embryo.

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[1] "Ueber direkte Kerntheilung in der Embryonalhülle der Skorpione," 'Morph. Jahrb.,' vol. x.

A distinct groove, the **neural groove** (*n. g.*), runs down the middle line and extends some distance into the head-segment. It is due to a thinning of the epiblast in the middle line (figs. 25 and 26, *n. g.*). The ventral nervous system is formed by a thickening of the epiblast along each side of this groove.

The **epiblast** now spreads as a single layer beyond the hypoblast (*ep'.*) and extends over nearly half the yolk, carrying the amnion with it. This is diagrammatically shown in fig. 27. In the head-segment (fig. 25) the epiblast is irregularly grooved and thickened. This is the commencement of the formation of the cerebral ganglion. In the thoracic somites (fig. 26) the epiblast is very thick and solid at the corners (*ap.*) where the appendages are about to appear. It is also somewhat solid just at each side of the neural groove (*n. th.*). This is the commencement of the thickening which will form the ventral nervous system.

The **mesoblast** is a thin layer in the head-segment (fig. 24, *mes.*), but shows the cœlomic space (*cœ.*) distinctly. This development of a head cœlom does not, of course, as Balfour has pointed out, necessarily indicate that the head-segment is equivalent to a body somite. In the body somites (fig. 26) the mesoblast is pretty thick and the cœlomic space is almost entirely closed up. The mesoblast does not extend across the middle line or beyond the limits of the ventral plate.

The **hypoblast** (figs. 25, 26, *hy.*) shows no change from the last stage but remains as a single layer, except in the tail-segment, where the hypoblastic mass is distinctly visible.

As the next stage shows the commencement of a large number of new structures, the ventral nervous system, the appendages, &c., it seems advisable to give a short summary of what has taken place so far.

First Period.

(1) The **blastoderm** commences as a single saucer-shaped layer of cells at one end of the egg (Stage A).

(2) These multiply and form a thick mass (Stages B, C).

Second Period.

(3) The **serous membrane** grows up from the edges of the blastoderm over its surface as a single layer of cells, and is continued round the yolk by the peripheral cells (Stages D—F).

(4) The **hypo-mesoblast** is formed partly as a single layer of cells split off from the under surface of the blastoderm and partly, at the tail end, as a thick mass, the primitive thickening, which probably represents an invagination. Before and up to this stage cells pass from the blastoderm into the yolk (Stage D).

(5) The **mesoblast** is formed as a layer several cells thick, extending right across the blastoderm. The **hypoblast** remains, after the formation of the mesoblast, as a single layer, except in the region of the primitive thickening, where it is a spherical mass (Stage E).

(6) The **amnion** is formed as a single layer of cells growing up from the edges of the epiblast, with which it retains its connection. The **serous membrane** has by this time lost all connection with the blastoderm, and spreads round the greater part of the yolk (Stage F).

The embryo by this time consists of three somites and the large head- and tail-segments. The somites are formed from the tail in regular succession.

Third Period.

(7) The **mesoblast** divides into two longitudinal bands, and **cœlomic spaces** are formed in the somites and in the head (Stage G).

(8) The **epiblast** and **amnion** begin to spread round the egg beyond the limits of the ventral plate (Stage G).

(9) The **neural groove** is formed by a thinning of the epiblast in the middle line (Stage H).

(10) The epiblast in the head-segment begins to thicken to form the **cerebral nervous system** (Stage H).

Fourth Period.—From the Formation of the Appendages to the Hatching of the Embryo.

Stage I.—The first stage of this third period shows—as mentioned above—the commencement of some of the most important structures. The embryo, of which a surface view is given in Pl. XV, fig. 28, now consists of twelve somites in addition to the head- and tail-segments. These somites are no longer separate thickenings as in the last stage, but have grown close up to one another, and are marked off by narrow grooves. The epiblast extends as a single layer all round the egg. The longitudinal neural groove is well marked and extends the whole length of the body with the exception of the tail-segment.

The first six somites bear appendages, i. e. the cheliceræ, chelæ, and four pairs of walking legs. These appendages are simple outgrowths, and are, with the exception of the first two pairs, of approximately equal size. The cheliceræ are much smaller, and the chelæ somewhat larger than the other appendages. The appendages are an outpushing of the epiblast and the outer layer of mesoblast or somatopleure (Pl. XVI, fig. 31). They are hollow, the spaces being prolongations of the cœlomic pouches. There is at this stage no sign of appendages on the somites behind those bearing the walking legs.

The embryo has a strong dorsal flexure so that the cephalic segment curves round the end of the egg. This is best seen in longitudinal section (Pl. XVI, fig. 29). The anterior margin of the cephalic segment is deeply cleft in the middle line, the segment being thus divided into two lobes. The lobes are in much the same state as in the last stage, and show no signs of the cerebral invagination from which a greater part of the brain is formed. In the middle line, and a very short way behind the bottom of the cleft, is a circular raised area with a pit in its centre (Pl. XV, fig. 28, *st.*). This pit is the stomodæum. It is seen in section in Pl. XVI, fig. 29, and is a simple inpushing of the epiblast.

The **ventral nervous system** consists of a pair of thickened bands of epiblast running the whole length of the body on each side of the neural groove (Pl. XV, fig. 28). The bands are cut up into blocks by the grooves which separate the somites. The epiblast is not evenly thickened, but the nuclei are arranged so as to present a wavy outline. This is characteristic of the formation of nerve-tissue in this animal, and was well seen in the cerebral lobes in the last stage (Pl. XV, fig. 25). The small ganglia of the cheliceral somite are well seen at this stage (fig. 28, *g.* I).

The **tail-segment**, from which the six caudal somites have yet to be formed, has begun to be pushed out (Pl. XVI, fig. 29). The epiblast in this region is very thick, and the cavity of the outpushing is lined by a thick layer of **hypoblast**, which is the "hypoblastic mass" of earlier stages (fig. 29, *hy. m.*).

Besides this mass in the tail-segment the hypoblast extends as a single layer round the whole egg (Pl. XVI, fig. 29, *hy.*). Along the ventral side the cells of this layer are close together, but towards the sides and back they become more scattered, and are to a great extent involved in the yolk. It is from the mass in the tail-segment that the **mesenteron** is chiefly formed. The hypoblast along the ventral surface also takes some part in its formation, but that round the sides and back is not involved, though it aids in the formation of the great digestive gland or liver.

The **mesoblastic bands** (Pl. XVI, fig. 31) are not yet united across the middle line. The **cœlomic spaces** (Pl. XVI, figs. 30 and 31) are well marked and quite separate for each segment. Those in the first six somites are prolonged into the appendages. The somatopleure is several cells thick; the splanchnopleure, on the contrary, consists of a single layer of cells. The mesoblast in the cephalic segment is thinner than in the body somites, and the cœlomic space is narrower.

Stage K (Pl. XVI, fig. 32).—The thoracic appendages have increased very much in size, and the cheliceræ and chelæ are both bifurcated at the extremity. A section through the base of one of the ambulatory appendages (Pl. XVI, fig. 33) shows a well-developed process extending inwards towards the middle line. This is undoubtedly the sternocoxal process, which is present on the second, third, and fourth appendages of the adult. Lankester[1] characterises the presence of this process as a very important point of resemblance between the thoracic appendages of Limulus and Scorpio. It is therefore interesting to find it at this early stage present on all four pairs of ambulatory appendages. A series of sections through the base of the fifth appendage, i. e. third ambulatory (Pl. XVI, fig. 34, *a*—*h*), shows the first stage of another structure characteristic of Limulus and the Arachnids—the coxal gland. This consists of a simple tube opening to the exterior at the base of the fifth appendage (fig. 34 *a*), and running forwards through the mesoblast to open in fig. 34 *h* into the cœlomic space. There can be no doubt that it is a nephridium. Gulland's researches[2] on the coxal gland in the young Limulus point to the same conclusion. I have been unable to find traces of nephridia in any other somites, unless, indeed, the genital tubes are partly nephridial. The six abdominal segments also bear appendages (Pl. XVI, figs. 32 and 35). These appear on surface view much more prominent than they really are owing to their white colour, which is due to the greater thickness of cells. In section (Pl. XVI, fig. 35) they are seen to project very slightly, and to be formed by a thickening of the epiblast and somatopleure, but with no definite outpushing such as there is in the thoracic appendages. The first pair of these appendages—the genital opercula—is very small, and concealed by the last pair of walking legs. The other five pairs—the pectines and four pairs of lung-books—are all of approximately equal size and structure. I have been unable to find the smallest trace of appendages on the somites behind these, i. e. somites 13—17, and do not believe they exist.

The cephalic segment is not so deeply cleft as in the last stage, and the mouth has shifted posteriorly so that now it lies between the bases of the cheliceræ. In the centre of each

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[1] 'Limulus an Arachnid,' p. 20.

[2] 'Quart. Journ. Micr. Sci.,' vol. xxv.

cephalic lobe is seen a dark spot (fig. 32, *ce. in.*). These spots are the cerebral invaginations. They begin in a somewhat earlier stage (Pl. XVI, fig. 36) as a pair of small inpushings. These extend rapidly backwards and meet in the middle line, their two lumens becoming continuous. This is seen in Pl. XVI, fig. 37 A—D, in which four transverse sections through this region are figured. Owing to the strong cephalic flexure in this stage the stomodæum (*st.*) is also shown in section. The cells, both at the sides of the cephalic lobes and throughout the greater part of the invaginations, are rapidly increasing in number to form the cerebral ganglia. Those in the centre of the cerebral lobes remain as a thin layer, and take no part in the brain formation. The cells also on the dorsal side in the middle, where the two invaginations have united (Pl. XVI, fig. 37 D, *oc.*), are more closely packed than the others, and take no part in the formation of the brain. They are the beginning of the retinal layer of the central eyes.

The ventral nervous system is in much the same condition histologically as it was in the last stage. The commencement of its separation from the hypodermis can, however, be seen (Pl. XVI, fig. 35) where the hypodermis is growing over it from each side as a thin layer.

The tail segment is now divided into six somites, and extends forward along the ventral surface of the body, reaching, at this stage, to the third abdominal somite. The epiblast is thickened on the ventral surface to form the nervous system. This is not shown in fig. 35, as the section passes between two thickenings. The cavity of the tail is occupied by a tubular extension of the hypoblast (fig. 35, *hy.*) surrounded by mesoblast. There is as yet no trace of the proctodæum.

The cœlomic spaces in the thoracic somites have not developed much. Those in the abdominal somites, however (Pl. XVI, fig. 35, *cœ.*), have extended enormously, and now reach round almost one third of the egg. The mesoblast, except in abdominal appendages, consists of two single layers of cells. In the tail the cœlomic spaces are not yet formed.

Stage L.—The embryo, of which fig. 38 (Pl. XVII) shows a surface view, has by this time made considerable progress in several important points. The thoracic appendages are slightly segmented (Pl. XVII, fig. 39, *ap.*), though this is not apparent in a surface view. The cheliceræ have moved in towards the middle line, and the mouth is now concealed between their bases. The chelæ are very large, and have their pincers well developed. The coxal gland, which opens at the base of the fifth pair of appendages, is no longer a straight tube, but has become bent on itself, so that a section through it (Pl. XVII, fig. 39, *cox.*) shows the tube cut in three places. It can still, however, be traced through a series of sections as a simple tube opening into the cœlom. The abdominal appendages have undergone great changes. The genital opercula are still simple thickenings of the epi- and meso-blast, but the pectines (Pl. XVII, fig. 40) have become folded in a direction parallel to the long axis of the body, i. e. transverse to their own axis. The most important change is, however, that of the four following abdominal appendages. These (Pl. XVII, fig. 41) are pushed in so as to form shallow cup-shaped cavities. The inpushing is on the posterior part of the appendage, and is directed slightly forwards. This is the commencement of the formation of the lung-book.

The cephalic segment, which is shown in Pl. XVII, fig. 38, extended in the same plane as the ventral surface of the embryo, is no longer so distinctly bilobed as in the last stage. The cerebral invaginations (Pl. XVII, figs. 42, *a* and *b*, and 43) are much shallower, and have entirely joined together, so that there is now only a single inpushing. This lies just in front of the cheliceræ (Pl. XVII, fig. 38). The brain is being formed from the sides of the inpushing, and shows a very characteristic structure. The mass of cells is more or less grouped round small circular clear spaces (fig. 43), which give to this part of the brain the appearance of being composed of a number of small vesicles. I have not succeeded in tracing the development of the nerve-fibres, which occupy the centre of the cerebral ganglion (fig. 43). This central portion appears at this stage perfectly transparent and empty.

The retina of the central eyes is still a thickening of the dorsal layer of the cerebral invagination (Pl. XVII, fig. 43, *rtn.*). It is visible in surface view (fig. 38, *oc.*) as a white spot on the margin of the invagination. The hypodermis immediately outside it is somewhat thickened, and will in this region form the vitreous layer (fig. 43, *vit.*).

The **ventral nervous system** is now completely separated from the hypodermis (figs. 40 and 41, *n. c.*). The cells are beginning to congregate together to form the ganglia, though the nerve-cord between the ganglia is still largely cellular. **Nerves** are seen growing out from the ganglia as thick cords of cells (fig. 40). The ganglia contain a clear space in their centre which later is occupied by a mass of fibres.

The tail (Pl. XVII, fig. 38) has now attained its full number of segments but the sting is not yet formed. The gut extends up almost the whole length of the tail. There is no sign yet of the formation of the proctodæum. The hypoblast in the rest of the body remains as a scattered layer of cells.

The **mesoblast** has now grown round the body as a double layer, with the cœlomic space between. In the middle line of the back, where the right and left folds of mesoblast meet, there is a somewhat irregular thickening in which both somatopleure and splanchnopleure seem to be involved. From this thickened band, which extends from close behind the brain to the beginning of the tail, the heart is formed. On the ventral side in the thoracic region the mesoblast of the outer layer is broken up into long strings of cells—the muscles—so that the cœlomic space can no longer be very definitely made out.

The **stomodæum** reaches as far as the back of the cerebral ganglion. This is the limit of its growth, and it remains a closed tube until, at a much later stage, the gut has grown forward and united with it.

Stage M.—The embryo (Pl. XVII, figs. 44 and 45) does not show very much change in surface view. The thoracic appendages are longer and distinctly segmented. They overlap across the middle line and conceal the pectines. The cheliceræ are further forward in relation to the mouth, which can now be seen lying between the bases of the chelæ.

The genital opercula begin to grow out from the body wall and the genital duct begins to be formed. This last (Pl. XVII, fig. 46) is developed in the mesoblast as a tubular portion of the cœlom, but does not open to the exterior up to the time of hatching. It may be nephridial in its nature, but this very late formation of the external aperture is not very favorable to such an hypothesis. The pectines are separated at their outer ends from the body wall. The inpushings for the lung-books are much deeper, and the cavity, which extends forwards from the opening, is divided up by lamellæ which grow down from its upper end (Pl. XVII, fig. 47). It is in close relation to a space in the mesoblast which contains blood-corpuscles.

The cephalic segment (Pl. XVII, fig. 45) is now rapidly approximating to its final shape. The cerebral ganglion, which is seen from the surface as a four-lobed white mass (fig. 45, *ce.*), has now lost all connection with the epiblast. The invagination remains, but its sides no longer give rise to nerve-tissue (Pl. XVII, figs. 48 and 49). The thickening for the central eye (figs. 48 and 49, *rtn.*) is more largely developed, and pigment is deposited in the ends of the cells furthest from the invagination. The eye is plainly visible as a double black spot on the surface. The upper edge of the invagination is growing down to close its orifice. The hypodermis lying immediately above it is clearly marked off from the rest as the vitreous layer (fig. 49, *vit.*). A considerable space still separates the retina from the vitreous layer.

The lateral eyes now appear for the first time as black spots on what Lankester terms the "optic area," *i. e.* the front margin of the head (Pl. XVII, fig. 45, *oc.*). Their development, as Parker[1] has shown, is strikingly different from that of the central eyes. Each eye, and in this species there are at first three, is formed (fig. 50) by a slightly cup-shaped thickening of the hypodermis. The nuclei of this thickened portion become larger, and pigment soon begins to be deposited at the

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[1] Loc. cit.

outer ends of the cells. Fig. 50 *a* shows a somewhat later stage, in which the cupping of the hypodermis has become flattened out. There is no invagination of any sort, and the eyes are, as Lankester and Bourne[1] described them, monostichous. The ventral nervous system has not undergone much development. It has sunk somewhat deeper and is separated from the hypodermis by the mesoblast.

The tail has now developed its terminal segment—the sting. The cavity of this last is partly occupied by the paired poison gland, apparently formed by inpushing of the hypodermis (Pl. XVIII, fig. 51, *p. gl.*). Each mass is connected to the superficial hypodermis by a short duct.

The gut extends down the whole length of the tail, and the proctodæum is present in the form of a solid mass of hypodermis cells blocking up its end (Pl. XVIII, fig. 51, *proct.*). The gut has also begun to grow forward (Pl. XVIII, figs. 52 and 53). In the last abdominal segment it is a complete tube surrounded by a thin layer of mesoblast (fig. 52, *int.*). It gives rise to two tubular outgrowths from its dorsal side, which are the Malpighian tubes (fig. 52, *mlph.*). These run first towards the back and then bend forward. There can be no doubt as to their hypoblastic origin in this form, as the proctodæum is not yet formed. They have been already shown to be outgrowths of the mesenteron in some Spiders by Loman,[2] and also in terrestrial Amphipoda by Spencer.[3] Further forward (Pl. XVIII, fig. 53, *int.*) the gut is simply a semi-cylindrical layer of hypoblast supported by a string of mesoblast and open to the yolk on its dorsal side. In the thorax it has not yet begun to form.

The mesoblast is broken up into strings and bands. The cœlom is still pretty distinct in the abdominal region (Pl. XVIII, fig. 53, *cœ.*), and the heart is a large thin-walled tube apparently connected with both somatopleure and splanchnopleure. As mentioned above, the genital tube is formed in the somatopleure in the seventh somite and is a portion of the cœlom.

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[1] 'Quart. Journ. Micr. Sci.,' vol. xxiii.

[2] 'Tijdschrift der nederl. Dierk. Vereen,' i.

[3] 'Quart. Journ. Micr. Sci.,' vol. xxv.

Stage M.—The changes from the last stage up to the time of hatching are not very numerous, though very important. The body attains a structure almost exactly like that of the adult, the appendages being segmented and the whole animal covered by a thin, structureless, highly refracting cuticle. The coxal gland still opens by a small aperture to the exterior at the base of the fifth appendage (Pl. XVIII, fig. 54). This aperture, which is lined for a short distance by the cuticle, leads to a straight duct (fig. 54) lined by cubical cells with round nuclei, which closely resemble the cells of the gland. The gland itself is distinguishable into medullary and cortical portions as described by Professor Lankester[1] in the adult. The tubules have distinct lumens surrounded by a cubical epithelium. The gland and its duct are surrounded by a thin capsule of flat mesoblast cells.

The genital tubes have pushed their way some distance between the lobes of the liver, but they are not yet connected by transverse tubes nor do they open to the exterior. The two layers of which the tube is composed in the adult (v. supra, p. 108) are not yet distinguishable. The pectines approximate very closely to their adult structure.

The ninth, tenth, eleventh, and twelfth appendages are also very similar to those in the adult (Pl. XVIII, fig. 55). The number of lamellæ is not so great, but their structure is very well shown. Each lamella is covered by a thin cuticle, and its cavity is in direct communication with a blood-sinus (fig. 55, *bl. s.*). The cells which form the lamellæ are very large, especially towards the base of the appendage. Towards the apex they become smaller, and finally pass into a mass of different cells from which more lamellæ are formed as the animal grows. The spaces between the lamellæ (fig. 55, *a. c'.*) are narrower and in communication with the exterior through the stigma.

The head is now completely formed, the mouth having shifted so as to lie behind the cheliceræ. The invagination which forms the central eyes has closed up. A stage immediately after its closure is shown in Pl. XVIII, fig. 56. Here the

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[1] 'Proc. Roy. Soc.,' vol. xxxiv, 1882–83.

lips of the invaginations have come together, but not fused. The posterior layer of the invagination is visible as a thin layer of cells (fig. 56, *rtn'.*), separated from the retina by a narrow space. The vitreous layer (*vit.*) is distinctly marked as a thickening of the hypodermis on the top of the head, the nuclei in that region being elongated, but there is still a small space separating it from the retina. By the time the embryo is hatched the eye (Pl. XVIII, fig. 57) has lost all connection with the hypodermis at the point where it was invaginated. The cells are long and deeply pigmented round their margins. The pigment is not equally abundant throughout the whole length of the cell, but five alternately more and less deeply pigmented zones can be distinguished (fig. 58). The base of the cells is most deeply pigmented, and their superficial ends come next. The nuclei of the retinal cells lie in zone 4, but I have been unable to find any trace of either rhabdomes or phaospheres. I have also not been able to trace any migration of mesoderm cells among the retinal cells. The posterior layer of the invagination can with difficulty be made out in depigmented sections owing to the flatness of its nuclei, and it is absolutely undistinguishable in sections from which the pigment has not been removed. This posterior layer forms the post-retinal membrane of the adult eye. The optic nerve is beginning to grow out from the cerebral ganglion, but has not yet come into connection with the eye. The hypodermis, immediately in front of the eye, is formed of a single layer of large transparent cells with faintly staining oval nuclei (Pl. XVIII, figs. 57 and 58, *vit.*). This vitreous layer is covered by a thin cuticle exactly like that which covers the rest of the surface of the body. The only sign of the formation of the lens is a slight cupping of the vitreous layer at one point (fig. 58). The hollow formed here is, however, not as yet filled up by any cuticular substance, but the cuticle passes straight over it. Round the area, where the lens will form the hypodermis is deeply pigmented. The cells are much smaller than those of the vitreous layer, and their nuclei are irregular in shape.

The cells of the lateral eyes (Pl. XVIII, fig. 59) are about the same size as those of the median ones. The pigment is not, however, arranged in definite zones, though it is more abundant at the base and at the outer ends of the cells than in the middle. There is a small third lateral eye present, and the hypodermis around and—the lateral eyes being so to to say on the edge of the head—below the eyes is all pigmented. I have been unable to find the nerve to these eyes and think it is probably not yet formed. The cuticle over the lateral eyes is not thickened to form the lens, and I have seen no sign of the peculiar mode of lens-formation described by Parker,[1] i. e. the ends of the perineural cells pushing in front of the retina. It is, of course, possible that this does not take place till later.

The brain and ventral cord have almost attained their adult structure. In the nerve-cord there is a string of cells in the middle line (Pl. XVIII, fig. 60) dorsal to the cords proper, which seems to represent the centre of the neural groove.

The tail is exactly similar to that of the adult, and is carried in the same way curved over the back. The **poison-glands** are fully formed and surrounded by muscles, but do not occupy so much of the terminal segment as in the adult. The proctodæum is lined by flat cells and has pushed its way almost to the base of the tail. The mesenteron is fully formed only in the hind segments of the body (Pl. XVIII, fig. 60). From the end of the stomodæum to where the last hepatic cæca join it the intestine (fig. 61) is surrounded by a definite cylindrical layer of mesoblast which is continuous with that surrounding the lobes of the liver, but the hypoblast cells lining this cylinder (fig. 61, *hy.*) are not yet definitely arranged. The nuclei are scattered about in groups for the most part near the outside, and the cells are drawn out into irregular more or less pyramidal form, the apex of the pyramid pointing towards the centre of the tube. There is no definite lumen, the space between the cells being filled up by small yolk-spheres (fig. 61, *yk.*).

The **liver-follicles** are much the same in structure as the

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[1] Loc. cit., p. 199.

intestine. They contain, however, a rather larger proportion of yolk. The scattered layer of hypoblast cells, which in the preceding stages surrounded the yolk, takes a large part in their formation. They open into the intestine in pairs by wide ducts.

The Malpighian tubes (Pl. XVIII, fig. 60, *mlph.*) have not undergone much development. They reach well forward in the body, and open into the intestine in the first caudal segment.

It is evident from the structure of the intestine that the young scorpion does not need food for some time after hatching. The large amount of yolk which still exists must last it for some weeks, or most probably till the next spring. If this is the case embryonic life practically lasts twelve months as the eggs are fertilized in May.

The outer layer of the mesoblast has now for the most part formed itself into muscles. The inner layer is very much complicated, being folded in so as to surround the gut and the lobes of the liver. The spaces between the lobes of the liver, which are undoubtedly the true cœlom, are filled up by a network of trabecular tissue (Pl. XVIII, fig. 60). The heart, pericardium, and blood-vessels are fully formed and contain a considerable number of large nucleated corpuscles.

Summary of the Changes during the Fourth Period.

(1) The thoracic appendages begin as simple outpushings of the body wall containing a portion of the cœlom (Stage I).

They rapidly increase in length and the cheliceræ and chelæ become bifid at their extremities. Sternocoxal processes are present on the third to sixth appendages (Stage K).

The cheliceræ, which were at first behind the mouth, gradually move forward relatively to it till they come to lie in front of it (Stage L).

(2) The coxal gland begins as a simple tube opening to the outside at the base of the fifth pair of appendages, and opening at the other end into the cœlom (Stage K). The tube soon becomes coiled, but the external opening persists until after hatching. It is undoubtely a nephridium.

(3) The **abdominal appendages** appear as thickenings of the epi- and meso-blast on the seventh to twelfth somites (Stage K). The first pair (genital opercula) does not develop further till a late stage (L).

The second pair (pectines) form a number of short longitudinal ridges on the surface of the abdomen (Stage K). They then separate from the body, the separation beginning at their outer ends (Stage M).

The third to sixth pairs (gill-books) begin to be pushed in (Stage L). The inpushing becomes deeper, and begins to be divided up (Stage M), and by the time the embryo is hatched they have attained their adult condition in every respect except size and number of lamellæ.

(4) The **cerebral ganglion and central eyes** begin as a pair of invaginations on the cephalic lobes. These invaginations meet in the middle (Stage K). The cerebral ganglion is formed from the sides of the invaginations, which rapidly become shallower and unite so as to open in the middle line. The dorsal surface of the invagination becomes thickened to form the retina of the central eyes (Stage L).

The brain becomes entirely separate from the hypodermis, the invagination remaining to form the eyes (Stage M). The invagination closes up and its lumen disappears. The cells of its lower layer form the post-retinal membrane. Those of the upper layer form the retina, and come in contact with the hypodermis on the top of the head, which is thickened in this region to form the vitreous layer. The retinal cells become deeply pigmented (Stage N).

(5) The **lateral eyes** form as cup-shaped thickenings of the hypodermis in the "optic area," the cells of which become pigmented. There is no invagination, and they consist of a single layer (Stage M).

(6) The **ventral nervous system** forms as a pair of thickened segmented bands, one on each side of the neural groove (Stage I). The nerve-cords sink down, a thin layer of hypodermis growing over them. There is at this time (Stage K) a distinct postoral pair of ganglia for the cheliceræ. The cells

become aggregated to form ganglia, and the cheliceral ganglia become fused with the cerebrum.

(7) The tail grows out, lying along the ventral surface of the abdomen. The poison-gland in its terminal segment is formed by a pair of invaginations of the epiblast.

(8) The hypoblast consists of an irregular layer under the whole embryo and a solid mass at the tail end (Stage I). As the tail grows the hypoblast grows into it as a tube reaching down to the last somite (Stage K).

The hypoblast forms the gut in the abdominal portion of the body, growing forward in a sling of mesoblast at first as a flat layer, which soon becomes bent round into a cylinder. The Malpighian tubes are formed as outgrowths from the mesenteron in the first post-abdominal somite (Stage M).

The gut does not reach forward to the stomodæum till shortly before hatching, and at this period the portion of it into which the liver-follicles open is not fully formed (Stage N).

(9) The stomodæum is formed early. It lies at first in front of the cheliceræ (Stage I), but soon shifts its position and comes to lie behind them. It extends inwards as far as the back of the brain.

(10) The proctodæum is formed much later than the stomodæum. It is at first a solid plug of cells (Stage M). As it increases in size it appears to replace the hypoblast in the last four somites.

(11) The mesoblast consists at first of a pair of segmented bands with a separate cœlomic space in each somite, and also one in the cephalic segment (Stage I). The cœlomic spaces soon unite, and the mesoblast bands join across the ventral surface. Somewhat later they extend round—the cœlomic space extending with them—and unite in the middle line on the dorsal surface (Stage L). From the thickened band where they have united on the dorsal surface the heart is formed. A portion of the cœlom in the seventh segment becomes separated off to form the genital tubes (Stage M). These do not open to the exterior. The outer layer of the mesoblast forms chiefly the

muscles of the body. The inner layer becomes folded so as to surround the liver and intestine, and the cœlomic space becomes partly filled up by trabecular tissue.

Conclusion.

The development cf this Scorpion, of which I have tried to give an outline above, is interesting in many points. It does not agree closely with any other Arachnid type as yet described, and I have for the present given up all attempts at comparison.

The development of the central and lateral eyes entirely bears out Lankester and Bourne's description of their structure. It is true that the central eyes are three-layered, but as the retina is the second layer from the surface—the third layer forming only a post-retinal membrane—they may be called diplostichous. The account given above of their development agrees in all essential respects with that of Parker, but, having a larger supply of embryos, I have been able to trace the earlier stages and the connection of the eyes with the cerebral invagination. Their mode of origin resembles very closely Locy's[1] description of the development of the eyes in Agelena nævia, the chief difference being that in Agelena the optic invaginations appear to have no connection with the formation of the brain. Locy does not, however, give a detailed description of the formation of the latter.

The description given above of the development of the lateral eyes also agrees pretty closely with that of Parker. In these, as in the central eyes, Lankester and Bourne's conclusions are confirmed, and Patten's[2] conclusions as to what the structure of the eyes must be in order to fit in with his theories are shown to be without foundation. The lateral eyes are monostichous, being simply somewhat specialised hypodermis cells.

The mode of formation of the ventral nervous system is exceptional among Invertebrates, resembling rather that of

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[1] 'Bull. Mus. Comp. Zool., Harvard,' vol. xii, p. 85.

[2] "Eyes of Molluscs and Arthropods," 'Mitth. Zool. Stat. Naples,' Bd. vi.

Chordata. The nerve-cord instead of peeling off from the superficial layer of epiblast sinks down bodily, and is covered by a layer of epiblast which grows over it from each side.

The development of the coxal gland leaves, I think, no room to doubt that it is a nephridium. That of the genital tubes is less conclusive, but I should think it probable that they are also, at least in part, nephridial.

The gill-books are undoubtedly appendages comparable to the abdominal appendages of Limulus. Whether they are really invaginated, i. e. whether the edge of each lamella in the Limulus appendage corresponds to the bottom of the fold between the lamellæ in the Scorpion's gill-book, or whether the whole appendage has become sunk in a hollow in the abdominal surface without being invaginated, it is difficult to say. Undoubtedly, the surface now exposed to the air has always been the external surface, but that would be the case with either of the above modes of derivation. Although the second alternative has the advantage that it is easy to see how the change could take place gradually, I am inclined to think the first is probably the true way in which they have arisen. One argument in its favour is that if the second alternative were correct one would expect the gill-book to commence as a distinct outgrowth, which would become sunk in a pit. Now, there is no such outgrowth in the formation of the gill-book. The first thing to appear on the thickened portion of the epiblast, from which the gill-book is formed, is a pit (Pl. XVII, fig. 41). The lamellæ do not begin to form till a later stage. Again, the abdominal appendages of Limulus are directed towards the tail as one would expect abdominal appendages to be. Now, if the appendage had sunk in without invagination, one would expect it to be still directed towards the tail unless there were some very good reason for its having changed its direction. If, on the contrary, it had become invaginated it would naturally be directed in the opposite direction towards the head, and this is what we find in the Scorpion. The inpushing is from the beginning towards the head, and the aperture opens towards the tail (Pl. XVII, fig. 47). I think it is quite conceivable that the changed conditions of development, due to terrestrial life, and the consequent pressure on the embryo, may have produced this change. A detailed account of the development of these appendages in Limulus may throw more light on the matter, but, unfortunately, though many authors have attacked the problem, a complete and satisfactory account of the development of Limulus is not yet in existence.

EXPLANATION OF PLATES XIII, XIV, XV, XVI, XVII, & XVIII,

Illustrating Mr. Malcolm Laurie's paper on "The Embryology of a Scorpion (Euscorpius italicus)."

Abbreviations.

a. c. Air-cavity in gill-book. *ac'.* Air-spaces between the lamellæ of gill-book. *ab. ap.* Abdominal appendage. *am.* Amnion. *am. c.* Amniotic cavity. *ap.* Appendage. *bl.* Blastoderm. *bl. s.* Blood-space. *bl. c.* Blood-corpuscle. *cau.* Caudal segment. *ce.* Cerebral ganglion. *ce. in.* Cerebral invagination. *ceph.* Cephalic segment. *cœ.* Cœlom. *cox.* Coxal gland. *cox. d.* Duct of coxal gland. *ep.* Epiblast. *ep'.* Extension of epiblast beyond ventral plate. *fol.* Follicle. *fol'.* Outer non-cellular layer of follicle. *g. I.* Ganglion of cheliceral somite. *ger.* Germinal epithelium or inner layer of ovarian tube. *ger'.* Yolk-forming cells derived from germinal epithelium. *ge. t.* Genital tube. *ht.* Heart. *hy.* Hypoblast. *hy'.* Extension of hypoblast beyond ventral plate. *hy. m.* Mass of hypoblast in caudal segment. *int.* Intestine. *l.* Gastric gland. *mes.* Mesoblast. *mi.* Prolongation of ovarian tube to egg. *mlph.* Malphigian tubes. *n. g.* Neural groove. *n. n'.* Nucleus, nucleolus. *n. c.* Nerve-cord. *n. gl.* Nerve-ganglion. *n. th.* Neural thickening. *oc.* Central eye. *oc'.* Lateral eye. *o. l.* Outer layer of ovarian tube. *ov.* Ovum. *p. gl.* Poison-gland. *pr. hy.* Primitive hypoblast (hypomesoblast). *proct.* Proctodæum. *pr. t.* Primitive thickening. *rtn.* Retina of central eye. *rtn'.* Third layer of central eye, post-retinal membrane. *s. m.* Serous membrane. *s. m'.* "Peripheral cells." *som. mes.* Somatic mesoblast. *spl. mes.* Splanchnic mesoblast. *st.* Stomodæum. *ste. p.* Sternocoxal process. *stg.*

Stigmata. *te.* Telson. *tr. mes.* Trabecular mesoblast occupying cœlom. *vit.* Vitreous layer of central eye. *y. c.* Cells in yolk. *yk.* Yolk. The somites are numbered I, II, III, &c.

PLATE XIII.

FIG. 1.—Transverse section of ovarian tube, showing the two layers; one cell of the inner layer enlarging to form an ovum. $\times \frac{220}{1}$.

FIG. 2.—Transverse section of ovum and ovarian tube. The egg has now pushed its way through the outer layer, and appears as a small protuberance on the ovarian tube. The follicle is beginning to form from the cells of the inner layer, which have accompanied the ovum. $\times \frac{220}{1}$.

FIG. 3.—Longitudinal section of ovum of ·1 mm. diameter, showing the two-layered follicle and the yolk-forming cells (*ger'.*). $\times \frac{220}{1}$.

FIG. 4.—Longitudinal section of egg of ·4 mm. in length, showing yolk-spheres, indefinite nucleus, and strongly marked nucleolus. The egg is surrounded by a vitelline membrane. The rest as in Fig. 3. $\times \frac{220}{1}$.

FIG. 5.—Section through the base of a ripe egg. $\times \frac{110}{1}$.

FIG. 6.—Yolk-spheres from ripe egg, showing the darkly stained spherical and prismatic bodies and the clear spaces. $\times \frac{110}{1}$.

FIG. 7.—Section through a corpus luteum and part of ovarian tube. $\times \frac{220}{1}$.

PLATE XIV.

FIG. 8.—Surface view of one-layered blastoderm. $\times \frac{30}{1}$.

FIG. 9.—Section through one-layered blastoderm, same stage as Fig. 8. $\times \frac{230}{1}$.

FIG. 10.—Section through blastoderm later than Fig. 9, showing the cells multiplying to form a mass at one pole of the egg. $\times \frac{220}{1}$.

FIG. 11.—Section through more advanced blastoderm. $\times \frac{220}{1}$.

FIG. 12.—Transverse section through blastoderm at time of formation of primitive hypoblast and serous membrane. The yolk and yolk-cells are drawn in detail in this figure to show the breaking down of the former. $\times \frac{220}{1}$.

FIG. 13.—Surface view of blastoderm now becoming oval. $\times \frac{30}{1}$.

FIG. 14.—Transverse section through posterior end of embryo figured in Fig. 13, showing serous membrane, primitive thickening, primitive hypoblast, and "peripheral cells." $\times \frac{220}{1}$.

FIG. 15.—Transverse section through anterior part of embryo about the same stage. $\times \frac{220}{1}$.

FIG. 16.—Longitudinal section through an embryo a little younger than Fig. 17, showing two somites with a third forming. The mesoblast is forming from the primitive hypoblast, the amnion is growing up from the

edges of the hypoblast, and the primitive thickening is well seen in the caudal segment. × $\frac{110}{1}$.

Fig. 17.—Surface view of embryo, with three somites fully formed. × $\frac{30}{1}$.

Fig. 18.—Transverse section through posterior end of Fig. 17, showing hypoblastic mass, mesoblast, &c. × $\frac{110}{1}$.

Fig. 19.—Diagrammatic representation of the relative extension of the various layers in an embryo of the stage of Fig. 17.

PLATE XV.

Fig. 20.—Surface view of an embryo with seven somites, drawn as if flattened out. *a—b* and *c—d* are the planes of the sections figured in Figs. 21 and 23. × $\frac{30}{1}$.

Fig. 21.—Transverse section through one of the posterior somites of an embryo with seven somites (*a—b* in Fig. 20), showing the three layers, epiblast thinning in centre, and mesoblast thin; amnion, serous membrane, and cœlomic spaces. × $\frac{110}{1}$.

Fig. 22.—Transverse section through one of the anterior somites of Fig. 20. × $\frac{110}{1}$.

Fig. 23.—Transverse section through tail-segment (*c—d*) of Fig. 20, showing the undivided mesoblast and the hypoblastic mass. × $\frac{110}{1}$.

Fig. 24.—Surface view of embryo of nine somites, drawn as if extended. × $\frac{30}{1}$.

Fig. 25.—Transverse section through head-segment of Fig. 24, showing epiblast thickening to form cerebral nervous system and spreading (*ep'.*), with the amnion beyond the ventral plate, neural groove, thin mesoblast, with small cœlomic space and hypoblast. × $\frac{110}{1}$.

Fig. 26.—Transverse section through one of the anterior somites of Fig. 24, showing the epiblast very solid where the appendage will develop (*ap.*) and form the neural thickening (*n. th.*) at each side of the neural groove. Mesoblast thick, and cœlom not very evident. × $\frac{110}{1}$.

Fig. 27.—Diagrammatic representation of the relative extension of the various layers in an embryo of the stage of Fig. 24.

Fig. 28.—Surface view of embryo at Stage I (ten somites) extended in a plane, showing appendages, cheliceral ganglion, stomodæum, &c. × $\frac{30}{1}$.

PLATE XVI.

Fig. 29.—Longitudinal section of Stage I in the middle line, showing dorsal flexure of the embryo, commencement of tail outgrowth, stomodæum, &c. × $\frac{50}{1}$.

Fig. 30.—Longitudinal section to one side of the middle line, showing the appendages and cœlomic spaces. × $\frac{50}{1}$.

Fig. 31.—Transverse section through the third somite of Stage I, showing the formation of the appendage, the neural thickening, &c. × $\frac{66}{1}$.

Fig. 32.—Surface view of embryo at Stage K, showing the cerebral invaginations, abdominal appendages, tail, &c. × $\frac{30}{1}$.

Fig. 33.—Transverse section through the base of a thoracic appendage, showing the sternocoxal process.

Fig. 34, *a*—*h*.—Series of sections through base of fifth appendage, showing the coxal gland.

Fig. 35.—Transverse section through one of the abdominal appendages and the tail, showing the appendage, the neural thickening beginning to separate from the epiblast, the gut forming in the tail, &c. × $\frac{75}{1}$

Fig. 36.—Transverse section through the cephalic segment of a somewhat earlier embryo, showing the beginning of the cerebral invagination. × $\frac{50}{1}$.

Fig. 37, a—d.—Sections through the head of an embryo of Stage K, showing the cerebral-optic invaginations. × $\frac{75}{1}$.

PLATE XVII.

Fig 38.—Surface view of an embryo of Stage L extended in a plane, showing the cerebral invagination, the central eyes, &c. × $\frac{30}{1}$.

Fig. 39.—Transverse section through the base of the fifth appendage, showing the coxal gland. × $\frac{75}{1}$.

Fig. 40.—Section through the pectines. × $\frac{75}{1}$.

Fig. 41.—Section through an abdominal appendage, showing the inpushing to form the gill-book. × $\frac{75}{1}$.

Fig. 42, *a*, *b*.—Transverse sections through the cerebro-optic invaginations. × $\frac{50}{1}$.

Fig. 43.—Longitudinal section through the cerebro-optic invaginations, showing the formation of the brain and the central eye. × $\frac{118}{1}$.

Fig. 44.—Surface view of an embryo of Stage M, from the ventral surface. × $\frac{30}{1}$.

Fig. 45.—Surface view of the dorsal side of the head of the same embryo, showing the central and lateral eyes. × $\frac{30}{1}$.

Fig. 46.—Section through the seventh somite, showing the formation of the genital tube from part of the cœlom. × $\frac{80}{1}$.

Fig. 47.—Longitudinal secion through a gill-book, showing the commencement of the formation of the lamellæ. × $\frac{111}{1}$.

Fig. 48.—Longitudinal section through the head end, showing the stomodæum and the cerebro-optic invagination from which the brain is now entirely separate. × $\frac{44}{1}$.

Fig. 49.—Transverse section through the same region. × $\frac{33}{1}$.

Fig. 50.—Longitudinal section through the lateral eye, showing its formation by a thickening of the hypodermis. $\times \frac{150}{1}$.

Fig. 50*a*.—Section through a somewhat older lateral eye in which the inpushing of the hypodermis has disappeared. $\times \frac{222}{1}$.

PLATE XVIII.

Fig. 51.—Longitudinal section through the tail end of Stage M, showing the poison-gland, proctodæum, intestine, &c. $\times \frac{33}{1}$.

Fig. 52.—Transverse section through the posterior end of the body, showing the intestine, with the Malpighian tubes, the heart, &c. $\times \frac{62}{1}$.

Fig. 53.—Transverse section a little further foward than Fig. 52, showing the intestine, which has not yet closed into a tube. $\times \frac{62}{1}$.

Fig. 54.—Section through the coxal gland of a newly-hatched scorpion, showing the opening to the exterior, &c. $\times \frac{75}{1}$.

Fig. 55.—Longitudinal section through a gill-book of a newly-hatched scorpion. $\times \frac{330}{1}$.

Fig. 56.—Longitudinal section through the central eye of an embryo a short time before hatching, showing the closure of the cerebro-optic invagination and the three layers of the eye. $\times \frac{89}{1}$.

Fig. 57.—Longitudinal somewhat oblique section through the central eyes of a newly-hatched scorpion. $\times \frac{222}{1}$.

Fig. 58.—A few cells of the same eye more highly magnified, and showing the inpushing in the vitreous layer.

Figs. 58, *a*, *b*, *c*.—Transverse sections through the same eye at different levels.

Fig. 59.—Section through the lateral eyes of a newly-hatched scorpion. $\times \frac{222}{1}$.

Fig. 60.—Transverse section through the posterior part of the body of a newly-hatched scorpion, showing the fully-formed intestine, the Malpighian tubes, the nerve-cord, and the trabecular tissue filling up the cœlomic space. $\times \frac{222}{1}$.

Fig. 61.—Transverse section through the intestine further forward, where it is not yet properly formed, showing the irregular hypoblast cells and yolk-spheres. $\times \frac{222}{1}$.

On the Morphology of the Compound Eyes of Arthropods.

By

S. Watase,
Fellow of the Johns Hopkins University.

With Plate XIX.

Prefatory Note.—The following extract and accompanying plate, from a memoir recently published in the 'Studies from the Biological Laboratory, Johns Hopkins University,' vol. iv, are here reproduced because it seems to me that they form a very important contribution to a subject which has been largely discussed in the pages of this journal, whilst they may not be readily accessible to European morphologists. In Mr. Watase's original paper a description and figures of the structure of the lateral eyes of Limulus, and of the compound eyes of other Arthropods, are given; but the diagrams in the plate now reproduced are sufficient to indicate the author's conclusions.

The distinctive feature about Mr. Watase's views is that he does not, as I did in my paper published conjointly with A. G. Bourne, on the "Eyes of Scorpio and Limulus," 'Quart. Journ. Micr. Sci.,' vol. xxiii, endeavour to derive the compound eye of Arthropods from a segregation of such diplostichous eyes as the central eyes of Arachnida; but, leaving these entirely aside, derives the commoner type of Arthropod compound eye from the monostichous lateral eyes of Limulus.

This seems to me to be a very happy suggestion. At the same time, I regret that the author has not, apparently, accepted the statements made by Bourne and myself as to the simple monostichous structure of the lateral eyes of Scorpions—nor investigated their structure for himself. Had he done so, he would have been able to assign even a clearer and simpler starting point for the "ommatidium" of the compound Arthropod eye than that afforded by the lateral eyes of Limulus, where the anomalous central ganglion-cell discovered by him, presents us with a complication. There is, I believe, no longer any doubt that a simple monostichous structure characterises the lateral eyes of Scorpions as originally shown by Bourne and myself. It is perhaps well to note that Grenacher was the first to describe the characteristic monostichous structure of the lateral eye of Limulus, on which Mr. Watase's theory is based.

Interesting matters for investigation and speculation are opened up by Mr. Watase's views. Such matters are the relation of the diplostichous monomeniscous central eyes of the Arachnida to compound or polymeniscous ommatidial eyes of Arthropoda generally. And especially interesting, it seems to me, would be the attempt to account for that incipient segregation of the retinal cells into groups united by a five-fluted rhabdom which we find in both the lateral and the central eyes of Scorpio.

March, 1890. E. RAY LANKESTER.

Balfour[1] has given a sketch of the possible evolution of a visual organ. He starts with a simple organism in which a spot on the surface of the body may become spontaneously pigmented and therefore become specially sensitive to light. The cuticular covering of the body may become thickened at this spot and act as an apparatus for condensing the light upon the pigmented spot lying beneath it. He further expresses his view elsewhere,[2] that the lens-like dioptric apparatus of the eye, formed either as a thickening of the cuticle or as a mass of cells, was at first formed simply to concentrate the light on the sensitive spot; the power to throw an image of external objects on the perceptive part of the eye was acquired gradually afterward.

The part which is played by pigment in the physiology of vision is considered a most obscure problem. I quote the following, clearly put forward by Foster,[3] as a physiological aspect of the question bearing upon the discussion at issue:

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[1] F. M. Balfour, "Address to the Department of Anatomy and Physiology, British Association, 1880," 'Nature,' vol. xxii, p. 417, 1880.

[2] 'Comparative Embryology,' vol. ii, chap. xvi, "Organs of Vision," p. 470.

[3] M. Foster, 'A Text Book of Physiology,' 4th edition, book iii, chap. ii, "Sight: the Photochemistry of Retina," pp. 515, 516.

"But in order that light may produce chemical effects (upon protoplasm), it must be absorbed; it must be spent in doing the chemical work. Accordingly, the first step towards the formation of an organ of vision is the differentiation of a portion of protoplasm into a pigment at once capable of absorbing light and sensitive to light—i.e. undergoing decomposition upon exposure to light. An organism, a portion of whose protoplasm had thus become differentiated into such a pigment, would be able to react towards light. The light falling on the organism would be in part absorbed by the pigment, and the rays thus absorbed would produce a chemical action and set free chemical substances which before were not present. We have only to suppose that the chemical substances are of such a nature as to act as a stimulus to the protoplasm of other parts of the organism (and we have manifold evidence of the exquisite sensitiveness of protoplasm in general to chemical stimuli), in order to see how rays of light falling on the organism might excite movements in it or modify movements which were being carried on, or might otherwise affect the organism in whole or part. Such considerations as the foregoing may be applied to even the complex organ of vision of the higher animals. If we suppose that the actual terminations of the optic nerve are surrounded by substances sensitive to light, then it becomes easy to imagine how light, falling on these sensitive substances, should set free chemical bodies possessed of the property of acting as stimuli to the actual nerve-endings, and thus give rise to visual impulses in the optic fibres."

Lubbock[1] advances essentially the same idea as Balfour's in his recent work on the subject, illustrated with some lucid diagrams. "In the simple forms," he says, "the whole surface is more or less sensitive. Suppose, however, some solid and opaque particles of pigment deposited in certain cells of the the skin. Their opacity would arrest and absorb the light, thus increasing its effect, while their solidity would enhance

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[1] 'On the Senses, Instinct, and Intelligence of Animals,' Inter. Sci. Series, vol. lxix, 1888.

the effect of external stimulus. A further step might be a depression in the skin at this point, which would serve somewhat to protect these differentiated and more sensitive cells, while the deeper this depression the greater would be the protection."

That such steps of gradual development of visual organs have actually taken place in some forms is quite probable. In Arthropods, it seems to me worthy of remark that the ommatidium of the lateral eye of Limulus makes the nearest approach to this primitive condition. It is nothing more and nothing less than a depression in the skin, with the thickened chitinous cuticle fitting in the open cavity, and acting as a lens to condense the light. The cells which form the sensory part of the structure are modified ectodermic cells, and, like the rest of the ectodermic cells lying on the surface of the body, secrete the chitinous cuticle on a part of their surface. Assuming the surface where the chitin is secreted to be the exterior, we may describe the ommatidium of the lateral eye of Limulus as a group of modified ectodermic cells aggregated around and beneath the funnel-shaped depression in the skin. A glance at the diagrams (Pl. XIX, figs. 1 and 2) will show this clearly. The sensory cells of the ommatidium come into direct contact with the conical lens, which is the thickened part of the general cuticle; or, to express this in the phraseology of Lankester and Bourne, the ommatidium in the lateral eye of Limulus is "epistatic." The cornea and crystalline cone as such have no separate existence in this stage.

Suppose such an ommatidium to become duplicated until a considerable number be formed, as we may safely imagine to have been the case, from the general tendency in the perfection of a visual organ. What will be the result? The first effect of such an increase in the number of ommatidia in a given area will be the lengthening of each unit in the direction of the ommatidial axis, and the cells (Pl. XIX, fig. 3, *V.*) which were situated directly on the outside of the retinulæ will travel over and above the sensory portion (*Rt.* and *G.*, fig. 3).

The distal ends of such (*V.*) which were thus pushed over will meet one another in the median or the "optic axis" of the ommatidium; further, they will continue to secrete chitin (fig. 3, *c. c.*) from their original chitin-secreting surfaces which are now median and axial. The chitin thus secreted will have an independent existence from the cornea, thus forming the rudiment of the crystalline cone, and the cells themselves will form the vitrellæ (figs. 3, 4, *V.*, &c.). Finally as the deepening still further goes on, the corneal lens (*C.*) and crystalline cone (*c. c.*) will be entirely separated, thus producing a condition somewhat similar to that which obtains in Serolis (figs. 5 and 6).

From this point onward, the three chitinous structures cornea, crystalline cone, and rhabdomere, undergo a different development in different Arthropods. In some the crystalline cone assumes a transparent semi-liquid state, while the whole cell becomes extremely elongated, forming the crystalline cone of certain crustacea (Pl. XIX, fig. 7); it may form a hard chitinous ball as in Serolis (Pl. XIX, fig. 6); or a cuneiform chitinous structure, as in Talochestia (Pl. XIX, fig. 9); or, finally, the whole cell may remain as a clear, transparent body, as in several insects, forming Grenacher's "aconous type" of the compound eye.

The forms assumed by the rhabdomeres in different Arthropods are equally diverse. The rhabdomere may exist as a plain cuticular covering over the non-pigmented part of the retinula, as in Limulus or in Serolis; it may become extremely elongated and narrow as in Musca or in Callinectes (Pl. XIX, fig. 8, *Rb.*); it may become transversely folded as in Cambarus (Pl. XIX, fig. 7, *Rb.*); these transverse folds may become still finer, showing the chitinous serrature along the axial edge of the retinula, as in Penæus and Homarus; or this transverse serrature may become extremely fine and regular, as in Squilla.

The cornea undergoes equally diverse modifications according as it is purely protective, or partly protective and partly dioptric in function. The range of variation is shown by the degrees of curvatures and by the varieties of its thickness. In several of the Decapod Crustacea which I have examined, as Penæus, Cambarus, Homarus, Callinectes, Gebia, &c., the curvatures of the individual cornea on both surfaces are very slight; it is biconvex in an extremely small degree. In Talorchestia both surfaces of the cornea are parallel. In Serolis, four species of which I have studied, all having well-developed compound eyes, there exists a considerable difference in different species in the nature of the cornea. In some the curvature on the proximal surface is very strong, and the whole structure is quite thick; while in others the cornea is rather thin, and a slight development of curvatures exists. This is interesting, showing that even within the group of nearly allied species there are considerable differences in this respect.

This fact is easy to understand when we remember the functional property of the cornea and the crystalline cone. As has been noticed already, the crystalline cone is always dioptric in function, while the cornea may be partly protective and partly dioptric, or wholly protective. When the cornea becomes partly dioptric, as in Serolis and in several other Arthropods, the dioptric function in an individual ommatidium comes to be performed by two structures, the crystalline cone and the corneal lens. When the two structures act together for the same end at the same time, it is easy to see how a certain trivial peculiarity of the one may induce a correlative modification of the other, and how a slight specific peculiarity may appear exaggerated in the thickness or in the degree of curvature of the corneal lenses in different species.

After so much has been said in regard to the unity of structure of the ommatidium in different Arthropods, one important point awaits our consideration, viz. the homology and fate of the central ganglion-cell found in the ommatidium of Limulus. Unless a great many forms of ommatidia in different Arthropods be compared, a discussion on this point appears to be unprofitable. The consideration which follows is therefore a purely provisional one.

There can be no question that the central ganglion-cell is an important factor in the ommatidium of Limulus, nor can we doubt the existence of a fundamental homology between the retinulæ of Limulus and those of all the other Arthropods which I have examined. With the exception of a few problematical bodies, such as the "hyaline cells" of Serolis, there are no structures in the ommatidia of most Arthropods which correspond to the central ganglion-cell of Limulus, in spite of the existence of a fundamental homology in the other elements of the ommatidium.

What has become of the central ganglionic element of the ommatidium? Was it lost in the course of the phylogenetic history of a more complex ommatidium? Or is it reasonable to suppose that some ommatidia came into existence without it from the beginning? Or, if it were lost at all, is there any evidence which makes this supposition probable?

The colourless ganglionic cell and the pigmented rod-bearing cells which surround the former I consider as the two primitive morphological factors in the unit of the sensory part of the Arthropod retina, somewhat in the same way as the circle of rods with a cone in the centre are the two essential factors in the neuro-epithelial layer of the human retina. In the absence of enough comparative data in Arthropods at present we have to dwell largely on the analogy suggested in the other groups of animals. Whatever be the views as to the fundamental homology of the ommatidium of Limulus to a structural unit of the sensory part of the human retina, a superficial resemblance of the one to the other is certainly very strong. The structural resemblance is paralleled by a physiological one. The place where the light acts in the visual end-organ of Arthropods and of man may alike be considered as consisting of a number of definite groups of cells, each group being a morphological and a physiological unit; or, in other words, the sensory part of the retinæ in both cases consists of a mosaic of several sensitive spots. The image formed on such a surface is therefore a mosaic one, whether in an Arthropod or in a Vertebrate.

Fundamental as this arrangement appears to be in the human retina, these two factors are liable to variation in their relative distribution in different Vertebrates. In fact, the variation takes place between the two extremes where the rods alone exist on one hand and where the cones alone constitute the essential part of the retina on the other. Thus, according to Schultze, "either form of percipient element (rod and cone) may be represented by the other" in the Vertebrate. This range of variability in the distribution of the cones and rods occurs even in a single group of Vertebrates, as in mammalia, showing that the variation in the distribution of the essential factors, even within a tolerably well circumscribed group of animals, is sometimes quite extensive. The group of Arthropods is a heterogeneous one, and I see no a priori objection to believing in the existence of a phenomenon analogous to what we find in Vertebrates, viz. that the two percipient elements represented by the central and the peripheral cells in the ommatidium of Limulus may be differently represented in different Arthropods.

There is no doubt whatever that the retinula cells are homologous throughout the Arthropods. In fact, in most Arthropods which I have examined no other elements but the retinulæ have any connection with the optic nerve-fibres, and they often undergo an enormous development and acquire most complicated structures, as in Homarus or in Penæus, giving rise to the much discussed "spindle."

But what has become of the central element which is so conspicuous in the ommatidium of Limulus, if the retinulæ in all Arthropods are homologous? I believe the central cell is fully functional, judging from its position and from its veritable connection with optic nerve-fibre in Limulus. What in other Arthropods strongly reminds one of this cell is the "hyaline cell" at the bottom of the ommatidial pit in Serolis and, according to Beddard, also in the Cymothoidæ. One important difference, however, exists between the "hyaline cell" of the Isopods and the central cell in the ommatidium of Limulus, viz. that, while in the latter the cell is connected with the optic nerve, the "hyaline cell" in the former has no connection with the central nervous system whatever. Hence the "hyaline cell" cannot be sensory, even if it be homologous with the central cell of Limulus, which it resembles in its general appearance and in its position. The number of "hyaline cells" in Serolis is always two, while its supposed homologue in Limulus is, as a general rule, only one. This fact does not offer any objection to my view of their homology when we bear in mind that other elements in different ommatidia, as vitrellæ and retinulæ, show a wide range of variation so far as their numbers are concerned, and yet they can be considered as perfectly homologous.

A further embryological and comparative knowledge in regard to the "hyaline cell" in Isopods is necessary for the determination of its exact homology. Meanwhile I would observe that if the central and the peripheral cells which we see in the ommatidium of Limulus may be taken as the two essential factors of the sensory element of the typical Arthropod retina, the case of Serolis may be taken as a loss of balance in the relative development of these two factors, the central cells having lost their sensory function and remaining as a sort of supporting mechanism. We can imagine this change in the function of the central cell as carried still further, and with the excessive development of the peripheral elements, the retinulæ, the central element may finally have disappeared.

All this is, however, a mere suggestion, and my interpretation of the nature of the Arthropod ommatidium in general does not lose its force even if this section of my views in regard to the fate and homology of the central cell or cells be proved untenable. It is quite possible that the ommatidia in which there is no element corresponding to the central cell of Limulus may have originated without it from the beginning. It seems, however, more natural to suppose that such an ommatidium had it originally and lost it later, observing that the simplest form of ommatidium possesses it in its fully functional, sensory form.

Finally, we have to consider the nature of the compound eye as a whole as presented in various types of Arthropods.

That a certain structure in the body of an animal may repeat itself and give rise to a secondary aggregate, or to a compound organ, is a well-known fact; the repetition of similarly constructed uriniferous tubules forms the essential part of a Vertebrate kidney, or the similar repetition of gill-filaments forms the respiratory organ of a Lamellibranch. Sundry other examples of this nature might be given, but the above two will suffice. Tracing, as I have attempted to do, the most complicated ommatidium into a simple, open, ectodermic pit, there is to my mind no difficulty in believing that the compound eye of the Arthropod is one of the most astonishing examples of the formation of an organ by the vegetative repetition of the similar structure. Thus, according to Lubbock, there are about 4000 facets in the compound eye of the house-fly (Musca), each facet corresponding to a single tubular invagination of the skin, the ommatidium. There are 4000 independent invaginations in the area in the head of the fly occupied by the compound eye; in the gad-fly (Œstrus), 7000; in the goat-moth (Cossus), 11,000; in the death's-head moth (Sphinx atropos), 12,000; in a butterfly (Papillio), 17,000; in a dragon-fly (Æschna), 20,000; in a small beetle (Mordella), as many as 25,000. On the other hand, the number of ommatidia seems to have reached its minimum in certain Copepods, as in Corycæus, where the whole visual organ seems to be represented by a single colossal ommatidium.

Certain forms of Collembola[1] seem to have a very small number of ommatidia; thus in Templetonia only one ommatidium exists on each side of the head; Orchesella has six on each side of the head; Tomocerus, Ipsoma,

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[1] Lubbock, 'Monograph of the Collembola and Thysanura,' the Ray Society, 1873, p. 57, pls. lv and lvi. Lubbock uses the term "ocellus" to designate a single element of the eye, which I here called an ommatidium. If the structure of this "ocellus" differs from the ommatidium of other Arthropods, it has, of course, nothing to do with the discussion at issue.

have seven; Degeeria, Lepidocyrtus, Smynthurus, and Papirius, eight. In the ants we observe a similar gradation in the number of ommatidia.

What reasons can we assign for this enormous multiplication of similarly constructed parts? What advantage follows from this arrangement? If the view of the nature of the compound eye which is put forward in the preceding pages be a true one, Müller's celebrated theory of mosaic vision is the only one that can account for the enormous multiplication of the similarly formed pits in the skin. The subject has been so fully discussed by Lubbock that I need not enter into details here. "According to his (Johannes Müller's) view, those rays of light only which pass directly through the crystalline cones, or are reflected from their sides, reach the corresponding nerve-fibre. The others fall on and are absorbed by the pigment which separates the different facets. Hence each cone receives light only from a very small portion of the field of vision, and the rays so received are collected into one spot of light. The larger and more convex, therefore, is the eye, the wider will be its field of vision; while the smaller and more numerous are the facets, the more distinct will the vision be. In fact, the picture perceived by the insects will be mosaic, in which the number of points will correspond with the number of facets."[1] The whole explanation of the problem seems to me to be contained in the passage above cited; and no further comment will be necessary more than a statement that the increase in the number of ommatidia is a decided advantage to their possessor. An eye like that of Limulus might by a slight change be converted into one of a more protuberant nature so as to command a wider field of vision, as we see in some species of Serolis or in some Trilobites; a slight change again might produce a protuberant ocular area mounted on an ophthalamic stalk, and accompanied by the accessory apparatus of vision, such as the socket for protection or the set of muscles to move the eye-stalk in different directions so as to command a

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[1] Lubbock, 'Senses, Instinct, and Intelligence,' p. 163.

still wider field of vision. In this connection I may refer to a series of diagrams (Pl. XIX, figs. 10–17). The black heavy layer represents the ectoderm, and the region in which the ectoderm is thrown into folds the area of the compound eye. The yellow-coloured layer outside represents the chitin, and the dotted line beneath the ectoderm the basement membrane.

In Limulus (fig. 10) the ectoderm is thrown into a series of shallow folds, which, when viewed from above, would be a group of shallow pits in the skin. Each pit is an ommatidium. In Serolis (fig. 11) the invagination of the skin is a little deeper than that of Limulus, and the whole ocular area is more prominent. Fig. 12 represents the condition of the ectodermal folding in Notonecta, and fig. 13 that of Agrion larva. Fig. 14 represents the eye of Branchipus, only a part of the stalk being shown in the figure. Fig. 15 represents the eye of Cambarus; fig. 16 that of Penæus; and fig. 17 that of Lucifer.

It must not be understood that the number of folds given in the diagrams have anything to do with the actual number of ommatidia that may exist in the actual specimens; no more than a morphological expression of the eye in a simplest possible form was intended. If one suppose a single invagination of the skin, say of fig. 15, to be divided into three strata and the cells in the bottom stratum to send out nerve-fibres, those in the middle to form the crystalline cone and those in the outermost to form the cornea (fig. 7), the interpretation of the diagram will be complete.

According to this view the compound eyes of Arthropods, either in the sessile or in the stalked form, are nothing more than a collection of ectoderm pits whose outer open ends face towards the sources of light, and whose inner ends are connected with the central nervous system by the optic nerve-fibres. The cells forming the walls of the pit arrange themselves into three strata, in most cases accompanied by three regional functional differentiations. Grenacher's classification of the compound eyes of insects into "acone," "pseudocone," and "eucone" types refer to the condition of the cells and their products in the middle stratum—the vitrellæ.

Morphologically, then, the compound eye of an Arthropod is strictly single-layered, although, as is evident, the present conception is entirely different from the monostichous theory maintained by some recent writers. From Limulus to Squilla we have a series of forms showing all degrees of modification in the general structure of the eye as well as the structure of its individual elements, and there is not here a single form which invalidates the view maintained in the present paper. Moreover, this view has the advantage of greatly simplifying our conception of these structures, reducing, as it does, all of them to one primitive structure, a depression in skin, in which several organs of ectodermal nature, often of a very complicated type, find their common morphological origin. And when thus the nature of the unit is reduced into a simple invagination of the skin, the formation of the compound eye appears to be but another instance of the well-known method in the formation of a morphological organ, namely, the vegetative repetition of a similar structure.

SUMMARY.

In studying the structure of the ommatidium of the compound eye of Serolis it has been found that it may be reduced to a simple ectodermic invagination of the skin. Extending my researches over several other Arthropods, of which Talorchestia, Cambarus, Homarus, and Callinectes were mentioned in the preceding pages, the same interpretation of the ommatidium may be applied without exception. This view of the ommatidium finds its strongest support in the fact that in Limulus the ommatidium is an open pit of the skin.

By supposing that the ommatidial pit of Limulus became deeper, and that this was accompanied by modifications in the structure and arrangement of the component cells, we can show the probability of our first supposition that the omma-

tidium of the compound eye of an Arthropod is an independent invagination of the skin. If this view is correct, the unit of the compound eye of an Arthropod is not, after all, so complex a structure as has been supposed by some; and the enormous increase in the number of ommatidia in a given area of the skin which results in the formation of the compound finds its parallel in the well-known method of the formation of the morphological organs, viz. the duplication of a simple unit.

DESCRIPTION OF PLATE XIX,

Illustrating Mr. Watase's paper on "The Morphology of the Compound Eyes of Arthropods."

Figs. 1—5.—Diagrams showing the probable evolution of the three-layered ommatidium from the single-layered surface depression in the skin by the gradual subsidence of the neuro-epithelial elements, *Rt.* and *G.*, Fig. 1. In Fig. 2 the ommatidium of Limulus is represented, which is considered a step further advanced from the condition shown in Fig. 1. The distal end of the retinula (*Rt.*) instead of being pointed toward the exterior as in Fig. 1, in Limulus points towards the median axis of the ommatidium. The chitinous substance being still secreted on the outside, a distinct body of chitin beneath the lens-cone (*C.*) is formed, the rhabdom (*Rb.*). In Fig. 3 this deepening is supposed to have gone still further, resulting in the formation of another independent chitinous body, the crystalline cone (*c. c.*). In Fig. 4 this deepening is considered to have advanced still further, the crystalline cone (*c. c.*) being entirely separated from the corneal lens (*C*) by a distinct stratum of cell, the corneagen (*cg.*). In Fig. 5 an ommatidium with three strata of cells, each secreting chitinous substance on the part of their surface, is formed. These three strata of cells are known as the corneagen (*cg.*), the vitrella (*V.*), and the retinula (*Rt.*). Three chitinous bodies secreted by each group of cells above mentioned are the cornea (*C.*), the crystalline cone (*c. c.*), and the rhabdomere (*Rb.*), respectively.

Fig. 6.—Serolis. Diagram of the ommatidium of Serolis. The general arrangement of cells in this is not very different from that shown in Fig. 5 The place of ganglion-cell in Fig. 5, *G.*, is taken by a pair (of which only one is shown in the diagram) of transparent "hyaline cells" (*H.*).

Fig. 7.—Cambarus. This is introduced in comparison with the hypothetical ommatidia.

Fig. 8.—Callinectes.

Fig. 9.—Talorchestia.

In the last three forms no element corresponding to the central ganglion cell of Limulus nor to the "hyaline cell" of Serolis can be found. The sensory element of the ommatidium is represented by the retinulæ (*Rt.*) only.

Fig. 10.—Limulus. Diagram of the compound eye of Limulus, the black, heavy line representing the ectoderm, and each depression in this layer corresponding to an ommatidium.

Fig. 11.—Serolis. In the same way as the above, the eye of Serolis may be represented by a series of folds.

Fig. 12.—Notonecta.

Fig. 13.—Agrion (larva).

Fig. 14.—Branchipus.

Fig. 15.—Cambarus.

Fig. 16.—Penæus.

Fig. 17.—Lucifer.

On the Structure of a Species of Earthworm belonging to the Genus Diachæta.

By

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With Plate XX.

I RECEIVED some time since, through the kindness of Mr. Windle, a number of examples of earthworms from the Bermudas. Some of these belonged to a species of Lumbricus, while others seemed to be referable to the genus Urochæta; under this generic name I described a year ago in 'Nature' the remarkable characteristics of the setæ of the hinder end of the body of the worm.

I believe now that the earthworms belong to Mr. Benham's genus Diachæta (5), though probably representing a new species of that genus, which is at present only known by Mr. Benham's account of the anatomy of Diachæta Thomasii.

I cannot, however, be certain about this, as Mr. Benham's description of this species is not complete, any more than is the description of the Bermuda form contained in the following pages.

The worms measure about four inches in length, are comparatively stout, particularly in the anterior region, comprising about the first ten segments, which is smooth and swollen.

So far as I can see, there is no prostomium, but the mouth opens terminally, as in D. Thomasii[1] and in Urochæta.

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[1] I have been as careful as possible in ascertaining this, because I find that I have made a mistake in stating that Thamnodrilus has a terminal mouth and no prostomium; Mr. Benham suggested the possibility of an error

There is some little difficulty in counting the anterior segments, for the reason that the first two or three appear to be retractile, as they are stated to be in Urochæta.

Moreover, the first two are very narrow (see Pl. XX, fig. 1), and although there is a distinct furrow separating them,[1] their total diameter is less than that of the IIIrd segment. From this point onwards, the only difficulty in mapping the segments accurately is caused by the fact that a number of the anterior segments of the body are entirely unprovided with setæ. In three specimens, which were particularly examined with regard to this point, the first five segments were entirely without setæ, so that the first setigerous segment is the 6th body-segment.

So far as I am aware, this is the only instance among the Oligochæta of so large a number of segments whose setæ have disappeared; in certain forms, such as Nais, the setæ of the first few anterior segments are considerably reduced in number by the disappearance of the dorsal bundles, while in Chætogaster there is apparently a number of segments without any setæ intercalated between the first and second setigerous segments.

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in my description, having discovered a long prostomium in an example of a worm which seems to be identical with my Thamnodrilus Gulielmi (**2**); on re-examining my specimens I find that a prostomium is present in that species, and that I actually figured it (**2**, woodcut, fig. 2, p. 157) in its retracted condition. The ornamented setæ are, moreover, not confined to the clitellum, but are found all over the body, though the ridges upon them are very much less marked, and quite escaped my attention. It is therefore evident that my Thamnodrilus is identical with Rhinodrilus. It is possible that Anteus does not generically differ from either of these forms.

[1] I am not at all prepared to state positively that there is really this division. In longitudinal sections the supposed division looked of no more importance than the division between the annuli of the succeeding segments; the brain is as usual placed between two segments, or rather near to the posterior boundary of the segment containing it. If this is reckoned the third, as in other earthworms, then the supposed two segments will be really only one; but then we shall have the apparently anomalous position of the testes and vas deferens funnels in the IXth and Xth, instead of in the Xth and XIth segments.

The setæ of this Diachæta are remarkable for three different reasons.

In the first place, they are irregularly disposed, and the irregularity commences, as in D. Thomasii, from the very first, and continues to the end of the body;[1] to the end of the xith segment the setæ are grouped in two lots on either side of the median ventral line, as shown in fig. 1, but their arrangement does not exactly agree in any two consecutive segments; further back there are four setæ separated from each other by considerable intervals, and two closely approximated on each side to form a pair; towards the tail end the paired arrangement is again lost, and the irregular disposition of the setæ is returned to. Fig. 8 illustrates this arrangement.

Another remarkable fact about the setæ of this species of Diachæta is that in the first three (setigerous) segments, at any rate, they are not situated along one line running parallel with the intersegmental furrow; they have a curiously alternate arrangement as seen in the figure (fig. 1), some being situated further forwards, others further back in the segment to which they belong; they form, in fact, almost a double row. It might, perhaps, be supposed that this appearance is due to the simple fact that I have confounded two segments and regarded them as one; and this supposition is strengthened by the fact that in two out of the three segments a faint groove divided the segment into two. Nevertheless, I regard this groove as the division between two annuli; it is frequently the case among earthworms that the anterior segments, when large, are marked by one or more annulations; moreover, in Segments vi and vii the setæ, although showing the curious arrangement referred to, are only eight in number. The ixth segment, on the other hand, in one of the three specimens, was certainly furnished with nine setæ; indeed, I actually counted eleven; but it is possible that two of these, being placed each very close

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[1] The irregularity in the arrangement of the setæ is much like what Schmarda (11) has described in his genus Pontoscolex.

beside another seta, may represent only setæ ready to replace the others; but as they were perfectly mature, and appeared to protrude from the body, it is at least equally possible that this segment was furnished with two pairs of setæ in addition to seven scattered setæ. I did not observe anywhere else more than eight setæ in the segment, though their arrangement in two ill-defined rings was very noticeable on several of the anterior segments. In Perichæta Houlleti I have occasionally seen a similar dislocation of the ring of setæ, but in no other forms, though I have not yet specially investigated the point. These various facts with regard to the setæ have some bearing upon, though of course I do not pretend that they entirely explain, an important question in Annelid morphology.

One of the most remarkable facts in the structure of this group is the varying position of the different organs in different genera and families. For example, in most earthworms the testes are in x, xi, and the ovaries in xiii; in Nais, on the other hand, the testes and ovaries are respectively developed in the vth and vith segments. Are we to consider in such cases that the testes of one form are perfectly homologous with the testes of another genus which are placed in a different segment? or are we rather to regard them as 'serially homologous,' believing that any and every segment can develop testes, which are actually developed here in one case and there in another? A third possible alternative is to consider that Nais and Lumbricus have been evolved along different lines from a common ancestor, in which there were at least six pairs of testes, occuping Segments v, vi, vii, viii, ix, x, xi. If either of these views were true, we might expect to meet with abnormal specimens with a larger number of testes; but this is not the case—such individuals have not been met with.[1] Connected with this view as to the reason for the

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[1] It is true that Lumbricus is often provided with what appear to be an additional rudimentary pair of ovaries in Segment xii. But this is hardly a case in point, inasmuch as the normal presence of the ovaries in Phreoryctes and Eudrilus seems to indidate, as do other considerations, that two ovaries

varying position of important organs, and apparently confirming it, is the observed fact that the growth of the worm—the addition of new segments—takes places at the tail end. It is common to find worms in which the last segment, or the last two or three, have no setæ at all, or fewer than the normal number, while the internal organs show a corresponding embryonic condition. In spite, however, of these facts, which are undoubtedly true so far as they go, another mode of formation of new segments occurs in earthworms. Fritz Müller (6), in describing the anatomy of Urochæta corethrura (termed by him Lumbricus corethrurus), called attention to the invariable presence, at a constant distance from the clitellum, of a group of segments evidently newly formed, for the reason that they were unprovided with setæ. Here, therefore, is an example of an intercalary growth of segments; but as it takes place in the least differentiated part of the body, it is perhaps to be regarded as being essentially different from the process of formation of new segments at the caudal end.

The structure of Diachæta appears to me to be suggestive in the light of the hypothesis of an intercalary growth of segments at the anterior end.

It has been mentioned that the first three segments are very much narrower than those which follow, and they can be apparently retracted into the buccal cavity; it may be, therefore, that they are in course of disappearance—the initial steps, i.e. the disappearance of the setæ and the reduction in size, having already occurred. The opposite interpretation is of course possible. But whatever may be the value of these facts, the arrangement of the setæ on the vith, viith and viiith segments (or vth, vith and viith) seems to be inexplicable except on the hypothesis of the intercalary production of new segments.

Throughout the body the setæ, although they are so far irregular in their arrangement that they do not correspond in position in successive segments, are nevertheless regular, in that

corresponding to the two testes on each side may be the original condition in the Oligochæta.

they are disposed along a line encircling the segment; in two individuals (the only ones examined from this point of view) this regularity in the first three setigerous segments was lost. The setæ of each segment were placed in two quite distinct lines, separated by a slight furrow. This abnormal state of affairs may perhaps seem capable of being explained by the simple theory that the supposed "segment" was in reality two segments. But in this case there should be sixteen setæ, whereas I counted them very carefully and only found a total of eight, except in one of the three segments of one individual; here there were eleven setæ, distributed fairly equally between the two annuli of the segment. On first noting these facts (which, as they occurred in three individuals selected at random, must surely be fairly constant) it appeared possible that there was in this earthworm just a trace left of a primitive condition, in which the setæ, like the nephridial pores, were scattered irregularly. There is, however, no evidence that the setæ have, like the nephridia, been derived from some unsegmented ancestor. If this be the case, there is no reason to suppose that the setæ were not disposed in a perfectly metameric fashion from the first.

It seems, therefore, that these facts, if they have any meaning, point to the conclusion that the scattering of the setæ is a preliminary to the formation of two segments out of one; it does not seem likely that the reverse interpretation—viz. the nearly complete fusion of two segments—is the right one. If this be allowed, we then have a means of understanding the varying position of certain important organs in allied genera.

The third point in which the setæ of Diachæta are remarkable is their very unusual degree of specialisation. Examples of the various setæ are illustrated in figs. 3—7, all carefully drawn to scale by the help of the camera lucida.

On the first few segments of the body the setæ are all of the form indicated in fig. 6: there is a long shaft ornamented with raised arches, like the setæ of Rhinodrilus, and the clitellar setæ of Urochæta; the distal end of the setæ is sharply curved; these setæ are found on about the first ten segments; after this they still occur, being sometimes (fig. 6*a*) of very large size, but are mingled with setæ (fig. 5) of the usual lumbricid pattern, and of which no special description is necessary; these setæ gradually come to be the only only ones present, and towards the end of the body their free extremities are much more hooked. Benham has remarked (5, p. 90) that in Diachæta Thomasii "the extremity is more strongly curved than in the ordinary setæ of Lumbricus."

At the tail end the setæ become enormously enlarged (figs. 3, 4); they are so large that their amber-yellow colour can be distinctly recognised by the unarmed eye, and their strongly recurved apices catch in the skin when the worm is held by the tail, and produce the impression of some sticky substance. In a recent number of 'Nature' I have referred to the probable use of these setæ, viz. to give the worm a stronger hold upon the ground when it is lying outside its burrow with only the tail concealed. These large hooked setæ, although all are larger than the setæ of the segments in the middle of the body, vary much in size, as will be seen from an inspection of figs. 3, 4. On the whole, they increase in size towards the end of the body. The last few segments have fewer setæ; their numbers in the last few segments of one individual were as follows—8, 7, 7, 7.

Though most earthworms are furnished with two kinds of setæ, I am not acquainted with any case which is quite comparable to the present. It is remarkable to find that the sculptured setæ of the anterior segments become less numerous upon the clitellum than they are in the segments in front of it, for the reason that the similar setæ of Urochæta and Rhinodrilus, two genera evidently allied to Diachæta, are either confined to or better developed upon the clitellum.

The clitellum occupies a large number of segments, perhaps as many as in D. Thomasii (5), but I am not able to state the exact number.

So much, then, for external characters, the description of which has occupied an unusual amount of space; this worm, however, possesses a more interesting exterior than is generally the case.

INTERNAL ANATOMY.

It appears from Mr. Benham's account of the internal segmentation of Diachæta that there is some difference between his species and mine in the segments occupied by the various organs. There are six strong intersegmental septa (fig. 9), the first bounding the vith segment posteriorly, and the last intervening between the xith and xiith segments; the position of these is the same as in D. Thomasii, but there is one more.

The spermatheca are situated a segment further back, the first (of the three pairs) being in Segment vii, behind instead of in front of the first thickened intersegmental septum. Benham mentions the presence of a single pair of long "tongue-shaped" sperm-sacs attached to the anterior wall of Segment xii. I find two pairs of sperm-sacs, both small, and confined to the xith and xiith segments respectively. The vas deferens funnels are in Segments x, xi; only one pair of these organs are mentioned by Benham, those occupying the xith segment. The testes are in the same segments, and occupy the usual position, i.e. they are attached to the front of the segment opposite to the funnels of the vasa deferentia.

§ Integument.

There are two points in the structure of the body wall which require notice. The first point is the absence of those peculiar structures in the epidermis which have been regarded as possibly abortive setæ; it is important to mention their absence in Diachæta, for the reason that they are present in Urochæta, which is in many other respects so closely allied to Diachæta.

In all the segments of the body, commencing with the vith (the first setigerous segment), the circular muscular layer is interrupted in the middle line, as shown in the figure (fig. 15); a number of muscular fibres of different appearance from those out of which the circular muscular layer is formed; they are of less diameter, and not composed of a bundle of closely united fibrils. These few fibres are shut off in a compartment which runs completely round the segment, and which is partially divided up by a fine network in the meshes of which lie the individual fibres. This peculiar specialisation was to be seen in the anterior segments of the body commencing with the VIth; it is possibly this which gives rise to the appearance of annulation already referred to as seen in the anterior segments.

§ Nephridia.

The nephridia do not seem to differ much from those of D. Thomasii. The first six segments are occupied by a large pair of nephridia, which differ much in minute structure from the "mucous glands" of Urochæta, although agreeing with them in being very much larger than the following nephridia; the apertures of these nephridia appear to be upon the IVth segment, and all the following segments are provided with a pair. The external apertures are placed very far forward in the segments, quite in the intersegmental furrow; they are furnished with the remarkable cup-like structure (fig. 14) at their external aperture, which has hitherto been only found in Urochæta; it seems to be clear that the structures are muscular, and perform the office of a sphincter; the muscular fibres are chiefly disposed in a radial direction, but outside is a thin layer of circularly disposed fibres, which, though fewer, are thicker than the radial fibres, and may be of equal strength.

§ Alimentary Tract.

There are two noticeable peculiarities about the alimentary canal of this earthworm: the first is the presence of a large thin-walled crop of equal diameter with the gizzard, into which it opens immediately; the gizzard itself is situated in the VIth ring, just in front of the first of the specially thickened intersegmental septa. The second peculiarity concerns the calciferous glands, or rather their equivalents; for, like Mr. Benham, I have been unable to find any calciferous glands like those of Urochæta. The œsophagus is a narrow tube with greatly vascularised walls, there being apparently a continuous blood sinus below the lining epithelium. Its inner wall is raised into numerous irregularly arranged folds; in the XIIth segment it suddenly increases in diameter, and exhibits a remarkable structure, which is illustrated in Pl. XX, figs. 9*gl.*, 10*ca.*, 11. The folds which are distinctive of the œsophagus become greatly increased in depth, and at the same time regularly arranged; each fold consists of two layers of epithelium, enclosing in the space between them a blood channel. The structure of this part of the gut, which occupies three segments, is not unlike that of the calciferous glands in Acanthodrilus (Beddard 3); its epithelium is not ciliated.

§ Vascular System.

The vascular system of this worm is distinguished by the enormous size of two pairs of "hearts," which unite the dorsal and ventral vessels in the xth and XIth segments. Both in dissection and longitudinal sections these vessels were seen to be gorged with blood. The interior of each vessel was distended with a coagulated mass of blood, which, however, did not consist of a uniform yellow-coloured clot; but, as shown in the accompanying figure (Pl. XX, fig. 13), contained scattered through the blood certain curious structures, concerning the nature of which I feel rather doubtful. The two pairs of hearts opened each by a relatively very narrow opening into the two longitudinal trunks. The orifice of communication was in each case guarded by a well-marked valve, which consists of a mass of elongated cells (see Pl. XX, figs. 12, 13), evidently a special growth of cells which line the blood-vessel throughout. It is interesting to note the valve between the heart and the dorsal vessel (fig. 13) projected into the former, while in the case of the communication between the heart and the ventral vessel (fig. 12) the valve projected into the ventral vessel, thus showing the course of the blood to be from the dorsal vessels through the hearts into the ventral vessel, as in Lumbricus.

§ Nervous System.

The position of the cerebral ganglia, as already mentioned, is somewhat anomalous. They lie close to the posterior boundary of a segment which, if the oviducts are to open on to the xivth, and the other organs of the reproductive system to be normally placed, must be regarded as the ivth, i.e. a segment further back than is usual. The cerebral ganglia give off two intertwined bundles of fibres to the pharynx, which represent the stomatogastric system, usually developed in earthworms. There are not many data regarding the minute structure of this stomatogastric system. In Megascolides Spencer describes and figures (12) this system, and expressly notes the absence of ganglionic corpuscles. In longitudinal sections of Diachæta, the presence of numerous ganglion-cells in the branches forming the stomatogastric system was quite obvious.

§ Testes, Sperm-sacs, and Vasa Deferentia.

In Diachæta Thomasii there are a pair of extraordinarily long sperm-sacs attached in front to the septum separating Segments xi, xii, and extending back through more than twenty segments. Similar sperm-sacs have been described in Urochæta (10), and, though much smaller, by myself in Typhæus (4). I find, however, in Diachæta two pairs of these organs in the xith and xiith segments (fig. 9, *vs*), not at all large, though containing abundant developing spermatozoa. It is possible that the single pair of sacs described by Benham may be the result of a fusion between two sacs on each side; but the matter requires further study, and, in the meantime, Benham only discovered one pair of vas deferens funnels. Two pairs of these organs were quite obvious in longitudinal sections, and, corresponding to them, two pairs of testes in the Diachæta investigated by myself. There is nothing in the structure of these organs that calls for particular remark.

§ Ovaries and Oviducts.

There is a single pair of ovaries in Segment XIII; the oviducts open into the same segment and on to the exterior on Segment XIV, on a line with and between the ventral setæ; aperture is distinct.

§ Spermathecæ.

There are three pairs of these organs in Segments VII, VIII, IX.

The first spermatheca, although lying in Segment VII, opens on to the exterior in Segment VI; its duct perforates the thickened intersegmental septum separating these two segments, and opens on to the exterior distinctly in front of the intersegmental groove. This fact appears to me to be of some little importance, and for the following reasons. Benham has mentioned that in D. Thomasii the spermatheca are in Segments VI, VII, VIII, i.e. a segment farther forward than in the present form; but the apertures are, according to Benham, placed posteriorly in each segment; accordingly, the present species, though differing in many particulars from D. Thomasii, and, among others, in the fact that the spermatheca are in VII, VIII, IX, instead of VI, VII, VIII, agrees in the important fact that the external aperture has remained in the same place, uninfluenced by the slight alteration of the segmentation; a very slight shifting in the attachment of the intersegmental septum, such as occurs in many worms—for example, in Hormogaster (Rosa, 9, 11)—would place the spermatheca entirely in the VIth segment.

I have myself pointed out an analogous change in the position of the spermatheca of Allolobophora complanata. In this case, therefore, it is clear that the spermathecæ of Diachæta are homologous in both species, and that their position is only apparently and not really changed.

It is clear from the above very brief account of the organization of Diachæta that, as Mr. Benham pointed out, it is closely allied to Urochæta.

But the two species of Diachæta differ from each other in most of their points of agreement with Urochæta. In both species there is no prostomium, and the setæ alternate in position from segment to segment as they do in Urochæta, though the alternation begins from the very first in Diachæta, and not until later in Urochæta; there are five strong septa commencing behind Segment VI, and three pairs of simple spermathecæ. Diachæta Thomasii agrees with Urochæta in having only a single pair of testes, sperm-sacs, and vasa deferentia.

Diachæta Windlei, as I desire to name my species, agrees with Urochæta in that the clitellum commences at Segment XV, and in the mass of muscles which surrounds the aperture of the nephridia.

In the following table the principal points of resemblance and difference between the three forms are shown:—

	UROCHÆTA.	DIACHÆTA THOMASII.	DIACHÆTA WINDLEI.
Setæ	Irregular in distribution after Segment X; *f*-shaped, with bifid extremity. Some of clitellar setæ ornamented with ridges	Irregular in distribution from the first. *f*-shaped, with pointed extremity. Clitellar setæ not different?	First five segments without setæ, irregular in distribution on remaining segments. Setæ highly specialised, there being three forms: (1) simple *f*-shaped, (2) ornamented setæ as in Urochæta, (3) large hooked setæ.
Epidermic glands between setæ	Present	Absent	Absent.
Prostomium	Absent	Absent	Absent.
Clitellum	XV (XVI)—XXII	XX—XXXIII	XV— ?
♂ pore	XIX/XX	XXII	?
Atria	Absent	Absent	Absent.
Testes	One pair in XI	One pair in XI ?	Two pairs in X, XI.
Vasa deferentia funnels	One pair in XI	One pair in XI	Two pairs in X, XI.
Sperm-sacs	One elongated pair extending from XII to XIV	One elongated pair extending from XII to XXXVIII	Two pairs (small) in XI, XII.
Spermathecæ	Simple sacs without diverticula in VII, VIII, IX (opening at anterior border of segment)	Simple sacs without diverticula in VI, VII, VIII (opening at posterior border of segment)	Simple sacs without diverticula in VII, VIII, IX (opening at posterior border of Segments VI, VII, VIII).
Nephridia	Anterior pair forming a branched "mucous gland" opening on Segment II. First pair of ordinary nephridia in Segment IV. External opening surrounded by a "sphincter"	Anterior pair forming a "mucous gland," not branched, opening on Segment III. Ordinary nephridia commence in Segment IV. No sphincter.	Anterior pair forming a "mucous gland," not branched, opening on Segment IV. Ordinary nephridia commence in following segment. Orifices guarded by a sphincter.
Posterior glands connected with nephridia	Present	Absent	Absent.
Alimentary tract	Three pairs of calciferous glands	No calciferous glands	No calciferous gland, but a portion of intestine (in Segments XII—XIV) with a similar structure.

It may perhaps be considered that the points of difference enumerated in the above Table are sufficient to distinguish generically all three forms; but I defer the discussion of this matter until something is known about the structure of other allied forms, which may occur in the West Indies. It is to be noted, however, that the species, which for the present I refer to the genus Diachæta, although much specialized in the shape of the setæ, and in the loss of the setæ of the anterior segments, connects in some ways (e.g. in the structure of the generative organs) the genus Urochæta with allied forms, such as Geoscolex.

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DESCRIPTION OF PLATE XX,

Illustrating Mr. Frank E. Beddard's paper "On the Structure of a Species of Earthworm belonging to the Genus Diachæta."

Diachæta Windlei.

Fig. 1.—Ventral view of anterior segments, to illustrate arrangement of setæ and their disappearance from the first five segments.

Fig. 2.—Front view of first segments, to show absence of prostomium.

Figs. 3 and 4.—Hooked setæ of posterior segments.

Fig. 5.—Setæ of middle segment.

Fig. 6.—Setæ of anterior segments. *a.* Seta of larger size.

Fig. 7.—Extremity of one of these setæ, more highly magnified to show ridges.

Fig. 8.—Tail end of body. *s.* Large hooked setæ. *m.* Muscles moving them. *l.* Last segment. *i.* Intersegmental groove.

Fig. 9.—Semi-diagrammatic longitudinal view. *c.* Brain. *nph.* Aperture of anterior nephridia. *g.* Gizzard. *sp.* Spermathecæ pore. *t.* Testes. *vs.* Sperm-sacs. *gl.* Calciferous gland. *v. d. f.* Funnels of vasa deferentia. *ov.* Ovary. *od.* Oviduct. The segments are numbered.

Fig. 10.—Longitudinal section through calciferous gland. *œ.* Œsophagus *s.* Septa. *ca.* Gland.

Fig. 11.—A portion of ditto more highly magnified. *p.* Peritoneal covering. *l, l.* Muscular layers. *bl.* Blood-space. *ep.* Epithelium.

Fig. 12.—Section through point of opening of heart into ventral vessel. *h.* Heart. *b.* Ventral vessel. *v.* Valve.

Fig. 13.—Similar section through opening of heart into dorsal vessel. *h.* Heart. *b.* Dorsal vessel. *v.* Valve. *a.* Fibrous matter contained in blood.

Fig. 14.—Sphincter (*sph.*) at aperture of nephridium (*np.*).

Fig. 15.—Section through body-wall in middle of Segment VII or VIII. *ep.* Epidermis. *tr.* Transverse muscles. *l.* Longitudinal muscles. *x.* A tract of transversely running fibres enclosed in a separate fibrous sheath.

Hekaterobranchus Shrubsolii. A New Genus[1] and Species of the Family Spionidæ.

By

Florence Buchanan,
Student of University College.

With Plates XXI and XXII.

THIS worm was found at Sheppey by the members of the University College Biological Society during an expedition made there in July, 1889. It appears to have been already known to naturalists living at Sheppey, but no one had tried to identify it. Not being able to find any published account of it, I believe it to be as yet undescribed, and have therefore, at Professor Lankester's kind suggestion, undertaken the examination and description of it.[2]

Occurrence.—The worm was always found associated with Haplobranchus (described by Dr. Bourne in the 'Quart. Journ. Micr. Sci.,' 1883), and occurs therefore in soft mud at the bottom of gullies, usually overlain by an inch or so of water. It is not so tenacious of life as Haplobranchus, and is hence not always to be found in mud containing Haplobranchus. Its

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[1] See, however, note at the end of this paper.

[2] I have been greatly helped in my investigations by the kindness of Mr. Shrubsole, of Sheerness, who has sent me up from time to time, as I required it, fresh material. I will take this opportunity of thanking him for the kind way in which he has allowed me to encroach upon his time and patience; for collecting and searching through mud to see that a particular animal, and that a very minute one, is present in it is no very easy nor interesting task.

other associates are Nais littoralis, Hemitubifex (Clitellio) ater, nematodes, and planarians. It is, however, more of a marine form than its associates, since, after heavy rain at low water, it is, Mr. Shrubsole informs me, seldom to be found, while the other forms of life may be still abundant. When present it can, as a rule, be recognised readily by its nematode-like movements and red colour, and the four tentacles waving on its head.

It is usually from about 6 to 10 mm. in length, the size varying according to the number of segments. It is, therefore, slightly larger than the Haplobranchus. It forms loosely coherent tubes by gathering up particles of mud round it, but inhabits each only for a very short time. It is more frequently to be found moving about in the mud.

Anatomy.—The number of segments varies. I have never counted more than forty-eight, and the greater number of specimens examined had between thirty and forty. The body is divided into regions which, as in other members of the family, are not so distinctly marked off from one another as in most sedentary annelids.

Cephalic Region.—The 1st or head-segment has a well-developed prostomium, on which are two well-marked pairs of eye-spots, one pair more dorsal and median than the other. In two out of the many specimens examined there were eight eye-spots, not, however, arranged as four pairs, but scattered and at very unequal distances apart. In another specimen there were five eye-spots, three on one side and two on the other. It is not unusual for the number of eyes to vary individually in marine annelids; it is, indeed, usual for the number to be greater in the larva than in the adult; and it would therefore seem that the eight-eyed condition is to be explained rather as a retention of a larval feature, than as due to the division of the four eyes normally found in the adult.

Behind the eye-spots, at the base of the prostomium, between it and the body of the 1st segment, are the cephalic tentacles, each containing a single contractile blindly-ending vessel (Pl. XXI, figs. 1 and 2, *t.*). They are richly ciliated all round, the cilia not being confined, as in most other members of the family, to a single longitudinal groove. The tentacles have an annulate appearance, due to slight surface ridges on which are the cilia, and to greenish-yellow streaks crossing the tentacles here and there. Between the ridges are short, stiff, tactile hairs. The contractile vessel (figs. 2 and 12) lies freely in the cavity of the tentacle which is part of the cœlom, and in which, in transparent specimens, cœlomic corpuscles can be seen. The tentacles are situated more laterally than in most members of the family: they are placed on either side of the mouth, and slightly above it. When the animal is at rest they are bent forwards in search of food, and infusorians may be seen carried down by their cilia to the mouth. When the animal is moving and tosses its head, the tentacles stand up more or less vertically; or, when it is moving in a definite direction, they are bent back over the dorsal surface, reaching back usually to the 3rd or 4th segment.

Behind these tentacles, which, for want of a better name, I have merely called "cephalic," and dorsad of them, situated on the body of the 1st segment, is a pair of organs with the characteristic structure of Spio branchiæ, although a great deal larger than these usually are (figs. 1 and 2, *br.*). They are about half as long again as the "cephalic" tentacles, and of a reddish-orange colour, due to the presence of an ascending and descending blood-vessel, forming together a simple loop in each. They are ciliated, but the cilia are shorter than they are on the "cephalic" tentacles, and they do not appear to be ciliated quite all round. The vessels, not being contractile, are not readily seen except in section (fig. 10). They run close to the epidermis, projecting into the cavity of the branchia which is a prolongation of the cœlom. The one vessel is rather larger in calibre than the other. Like the "cephalic" tentacles, they may either be carried erect, or bent back over the dorsal surface. Their length, also, varies much individually. Usually when bent back they would cover the first five segments; sometimes, however, they reach back over more than eight. At the base of each branchia are two or three short capillary chætæ (fig. 1, and fig. 12, *ntp*^{1}.)

On the same segment (the 1st), placed ventro-laterally, almost vertically below but a little behind each branchia (fig. 1), is another group of three or four rather longer capillary chætæ, behind and below each of which is a membranous lobe—the ventral "cirrus" of most authors, the neuropodial "lamina" of others.

The body of the first segment reaches further forward on the ventral than on the dorsal surface, and is there folded, forming a kind of ventral collar (figs. 1 and 3, *v. coll.*). This fold can be traced up laterally to the base of the branchiæ, which appear to be attached to it.

Thoracic and Abdominal Regions.—On all the other segments of the body there are, as on the first, two groups of chætæ on each side, but the chætæ are longer (when of the same kind) and more numerous than on the 1st segment. Their number varies in different individuals and in different segments of the same individual, but with no constancy. Five, six, and seven are usual numbers, but sometimes there are as many as nine in a group. Seeing that they may so very easily be knocked off, and that new ones may always be forming, not much importance can be attached to their exact number in different segments and in different individuals. In the dorsal groups throughout the whole length of the body the chætæ are capillary only (fig. 4, A.). In the ventral groups they are so also in the anterior region of the body; but from the 8th segment onwards there are, as well as these, also hooked or crotchet chætæ. We may, therefore, consider the thoracic region to extend as far as the 7th segment (inclusive), and the abdominal region to begin in the 8th. There are at first two or three crotchets to about four or three capillary chætæ. More posteriorly there are usually about five hooked chætæ to two capillary ones. Each crotchet (fig. 4, C.) is three-toothed at the extremity, the one tooth being larger and more prominent than the other two, so that in some views it alone is to be seen clearly (fig. 4, C.^{1}). The hooked extremity is surrounded by a membrane.

[1] The name "cirrus" would imply a homology with the cirrus of the

The chætæ all arise from sacs, each group from one sac, firmly implanted in the body-wall and projecting into the body-cavity, though the ventral sacs do not project so far as the dorsal. The wall of each sac is supplied by muscles, by means of which the sac can be moved in and out as a whole. Springing separately from the body-wall behind both dorsal and ventral chætæ-bundles slightly dorsad, of the dorsal ones and ventrad of the ventral ones, are the membranous lobes known either as "cirri" or "parapodial laminæ."[1] They can readily be seen in the first few segments, but then gradually grow smaller, and are not found in the posterior region of the body. It is difficult to determine exactly in which segment they cease to exist, and whether this is constant in all, since, to see them clearly, the animal must be living and moving, and it is then not easy to count them. When the animal is killed the lobes become, by the position taken up by the worm, very difficult to see and be certain of. The dorsal ones are much closer to one another, i. e. nearer to the median line, anteriorly than posteriorly, and in the 2nd segment (the first one in which they exist) they are so close together that they seem to form, or form part of, a collar, which is therefore dorsal, and quite distinct from the ventral collar of the 1st segment (figs. 1 and 12, *d. coll.*). There are very minute stiff hairs on all these lobes, resembling cilia, but without their movement. Such hairs are also found elsewhere on the cuticle of the body-wall.

Internal Anatomy.—The body-wall consists of—(1) An outer epidermic layer of cells, in parts more than one layer thick, with a fine cuticle (figs. 5, 6, 7, and 8, *epid.*). The epidermis is thicker on the ventral surface than elsewhere.

parapodium of an Errant annelid, e.g. Nereis or Phyllodoce; and it is difficult to say whether this homology exists without first deciding, by the comparison of a large number of forms, to which families of the Errantia the Spionidæ are most nearly allied, taking the Spionidæ to be, as they probably are, the living representatives (though probably degenerate) of the most primitive of the Sendentaria. A cirrus may vary so much both in form and position that we can see no reason why these membranous lobes in the Spionidæ should not represent cirri; but this, of course, does not alone in the least prove them to be true cirri.

Here and there in the epidermis, and occupying its whole thickness, are a few large coarsely granular cells with well-marked large nuclei and nucleoli, probably opening to the exterior, and secreting the material by which the animal holds the fragments together which compose its temporary tube. (2) The circular muscular layer (*c. m.*) is only very slightly developed, and can scarcely be seen except in longitudinal sections. It is best developed in the ventral region just over the nerve-cord (where there are no longitudinal ones), and can there be seen in transverse sections. (3) The longitudinal muscular layer, on the other hand, is very well developed, running in three bands, one dorsal and two ventral (figs. 5, 6, 7, and 8, *d. l. m.* and *v. l. m.*). Although a single band, the dorsal one is much more feebly developed in the median line than on either side. (4) Below this again is a delicate layer of cœlomic epithelium, forming the outer wall of cœlom, and only to be distinguished by a few nuclei scattered here and there on the extremities of the muscle-fibres (figs. 5, 6, 7, and 8, *c. ep.*).

Coming from and dividing the dorsal longitudinal muscles on either side, and stretching vertically downwards to be attached close to the thickened portion of the epidermis of the ventral surface on either side, are, in the anterior region of the body, i. e. from the 2nd to the 6th segments, very distinct dorso-ventral muscles (fig. 5, *d. v. m.*), dividing the cavity of each of these segments more or less completely into three longitudinal chambers.

Besides these there are in every segment muscles going from the ventral epidermic thickening on each side to the two setal sacs (*s. s. m.*), but these appear to be rather continuations of the circular than of the longitudinal layer. Both these and the dorso-ventral muscles are covered by a delicate layer of cœlomic epithelium.

Alimentary Canal.—The mouth is not terminal, but is overlapped by the prostomium (fig. 1, *m.*). The two "cephalic" tentacles, as already mentioned, arise just above it on either side. The pharynx extends through the first two segments (fig. 2). Its anterior part is evertible and richly ciliated. It is almost always extruded at once when the animal is first compressed by a cover slip (fig. 3, B. *ph.*). The pharynx narrows in the posterior part of the 2nd segment to form the œsophagus, which is continued through the next few segments. The canal then gets much wider, and begins to be constricted intersegmentally by the septa. The segment in which this change from œsophagus to intestine takes place varies with the size of the individual. Posteriorly, i.e. in the posterior third or fourth of the body (again varying according to the size of the individual), it narrows again, and this part especially is exceedingly contractile. The anus is terminal (fig. 2). From it cilia can be seen moving upwards towards the mouth, indicating thereby some anal respiration. In some specimens, but not in all, ciliated ridges could be seen in the intestine just in front of the anus (fig. 11), probably the same thing as the richly ciliated swelling found in the larvæ of allied forms. The alimentary canal is lined throughout by columnar epithelium, consisting of cells one layer deep, ciliated in the pharynx and œsophagus, and also in the hinder unconstricted part, of the intestine, but apparently not in the anterior constricted part, which occupies the greater length of the body. This epithelium is much folded in the anterior region, especially in the pharynx (fig. 5, *int. ep.*), not so much in the third and fourth segments, but again in the hinder œsophageal region. It is not folded, and the lumen of the canal is wide, in the anterior intestinal region (fig. 6); afterwards it again becomes folded to some extent (fig. 7). The cells forming the folds are longer and narrower than the others (figs. 5 and 7), but their nuclei, as in the other cells, are situated close to the peripheral wall, all the nuclei together forming a very regular circular layer.

Outside the epithelial layer is a very thin circular muscular layer, best seen in the anterior region of the body (fig. 5, *c.* m^2.), but not seen at all distinctly posteriorly, though its presence would seem to be indicated by the muscular contractions of the whole alimentary canal. There are no longitudinal muscles to be seen, and directly outside the circular muscle layer comes the cœlomic epithelium. Neither of these last two layers takes any share in the folds.

In one specimen which I had, which was evidently a young form with only about twenty segments, the alimentary canal was wide, and constricted intersegmentally in all the anterior segments of the body as far back as the 10th. Between the 10th and 11th segments was a deep permanent constriction, the canal continuing very narrow throughout the rest of the length of the body. This would seem to imply that the pharyngeal and œsophageal region of the alimentary canal developed late.[1] In this specimen there was green pigment all down the sides of the alimentary canal, not, as far as I could see, enclosed in any way. There were also no thoracic nephridia.

Like so many other Chætopods, this one has almost constantly present parasitic monocystes in its intestine, and these are often very numerous. They are broad at one extremity (apparently the anterior), and usually pointed at the other (fig. 13). The cortical substance forms a clear zone, wider at the anterior extremity. The medullary substance is coarsely granular, and in it, reaching to the posterior extremity, is usually a long narrow vacuole (*vac.*), which may sometimes be found bursting. Sometimes they have no vacuole, and such I at first mistook for eggs, until finding that they were in the alimentary canal and not in the cœlom. They may be seen moving backwards and forwards with the intestine, apparently incapable, while in the body at least, of any independent motion of their own. The nucleus (*n.*) is spherical and well marked, containing a nucleolus.

Vascular System.[2]—There is a contractile dorsal vessel

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[1] But it may be that the œsophagus is developed, but resembles the part of the intestine following it in being intersegmentally constricted, since this appears to be the case in the larva of what is probably a Spio or Nerine described by Leuckart in the 'Arch. f. Naturg.,' 21st Jahresg., 1855, p. 63, &c., and pl. ii, fig. 1. Here, however, I did not observe anything marking off the two regions of the alimentary canal from one another, as Leuckart describes in his larva.

[2] The whole arrangement of the vascular system is not easy to determine,

(figs. 2 and 12, *d. v.*) in the anterior region of the body, continued forwards into the prostomium. Just before it reaches the prostomium two vessels are given off, one to each branchia (*d. br. v.*). These run up the inner sides of the branchiæ, and return by vessels on the outer side (*v. br. v.*), which meet in the median line on the ventral surface in the posterior part of the first segment to form the ventral vessel (*v. v.*).[1] Before they meet each appears to give off or be joined by the single contractile vessel going to the "cephalic" tentacle (*t. v.*). The ventral vessel runs throughout the whole length of the body (figs. 2, 5, 6, 7, 8, *v. v.*), passes in the anal segment into a sinus (figs. 2, 7, 8, *sin.*) surrounding the intestine, and lying just outside the epithelium, probably between it and the circular muscular layer; or it may be that the circular muscular layer is really absent in this region, and that the sinus lying between the intestinal and the cœlomic epithelium of the alimentary canal has some contractile power of its own, as it has in other sedentary annelids, e. g. Spirographis,[2] where, however, muscular fibres are present as well. This sinus completely surrounds the intestine in the whole of its posterior non-constricted part, and is at first continued over part of the constricted part; then, however, a nucleated mass appears inside it on the median dorsal line of the wall of the intestine, and forms a longitudinal upstanding ridge. Part of the sinus closes in round this ridge, and becomes nipped off from the rest of the sinus (figs. 2 and 6, *d. s. v.*), and so is continued forwards

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and what is given in the text is only what appears to me—after the examination of numerous living specimens and series of sections—to be its probable distribution. When living the animal is too opaque, when dead the vessels are seldom in the same state of contraction or expansion in two individuals. The vascular system in the highest animals even is subject to individual variation, and it may be that there are really slight individual variations in its arrangement in worms, and in this amongst others.

[1] The direction in which the blood flows in the branchiæ cannot be determined, as the vessels cannot be seen in the living. It probably may flow in either direction, from the ventral to the dorsal at one time and from the dorsal to the ventral at another.

[2] Claparède, 1873, 'La Structure des Annélides sédentaires.'

on the intestine, the ridge inside it being separated from the intestinal epithelium by a very fine layer of cœlomic epithelium only. Some series of sections would seem at first sight to show that the ridge was in its posterior part directly continuous with the intestinal epithelium; but a more careful examination leads rather to the conclusion that it is formed by the tucking-in of the cœlomic epithelium which lies outside the sinus on either side. It lies, however, especially posteriorly, exceedingly close to the intestinal wall. Its significance (whether physiological or morphological) is as difficult to determine as that of the so-called "Herzkörper" or "cardiac body" of certain other Polychæts,[1] which it in all probability represents. No lumen is to be seen in it here throughout its course.

In the œsophageal region the nipped-off upper part of the sinus enclosing the longitudinal ridge (fig. 2) leaves the walls of the alimentary canal, and becomes the contractile dorsal vessel which runs upwards until it comes to lie just beneath the thin part of the body-wall in the dorsal median line, *i. e.* where the longitudinal muscle layer is only very feebly developed (fig. 5, *d. v.*). It is here surrounded by a well-developed circular muscular layer (*c. m′.*) to which its contractile power is due. The walls of all the other vessels and of the sinus appear to consist only of cœlomic epithelium. It is difficult to say what happens to the rest of the sinus (which is continued throughout the intestinal region) when the dorsal vessel finally leaves the wall of the alimentary canal in the œsophageal region. It certainly is not continued as a sinus, but whether it forms vessels or not is a difficult point to determine, since there are other very much coiled vessels in each segment of the œsophageal region. These coiled transverse or dorso-ventral vessels seem to me to connect the dorsal and ventral vessels (as shown diagrammatically in fig. 12), but it may be that they connect the ventral not with the dorsal, but with lateral vessels which are continuations forwards of the sinus, lying, for some part of their course at least, close to the dorsal vessel. The dorso-ventral vessels

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[1] See Cunningham, "Some Points in the Anatomy of Polychæta," this Journal, vol. xxviii, 1887.

all lie freely in the cœlom. They are represented in the first segment by the vessels going to the branchiæ. In the posterior region of the body, *i. e.* where there is the sinus, it is difficult to say whether transverse vessels are present or not. In some series of sections vessels may be seen here and there leaving the upper part of the remaining sinus where the dorsal vessel is just nipped off. More posteriorly, where the sinus is continuous all round the intestine, vessels may sometimes be seen running from the ventral vessel (fig. 8, *v. v.*). These do not appear to occur regularly in every segment, and they cannot be seen at all in some series of sections which show the other parts of the vascular system clearly. But it is difficult to say whether they are really not present, or whether they are merely contracted, and therefore not seen, or not recognised as blood-vessels. We should not, therefore, be justified in concluding that the sinus represents them, although this would seem not unlikely in the most posterior region where the sinus is complete. In other Polychæts where there is a sinus (*e. g.* Scalibregnia, Trophonria, Eumenia) transverse vessels running to it from the ventral vessel are long and well marked.[1]

The blood flows from behind forwards in the sinus and dorsal vessel, from in front backwards in the ventral vessel. It is probably aërated both at the anus and in the branchiæ on the head-segment, and also to some extent in the "cephalic" tentacles. It would be interesting to note whether all forms that have a sinus round the intestine have also other indications of an anal respiration. The blood is red, coloured probably by hæmoglobin. It contains, as far as I have seen, no corpuscles.

Cœlom and Nephridia.—The cœlom is partially divided into separate cavities by the septa, which are thin muscular partitions between the segments coated with cœlomic epithelium on either side. They move backwards and forwards with the intestine. There is a dorsal and ventral mesentery supporting the intestine (fig. 7), and thus dividing the cœlom longitudi-

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[1] See A. Wiren, 'Beiträge zür Anat. u. Hist. d. Anneliden. Königl. Sv. Vet. Akademiens Handlingar,' Bd. xxii, No. 1.

nally into two halves. Besides this there are in the anterior region the three longitudinal chambers separated from one another by the dorso-ventral muscles.

There are nephridia of two kinds. In the anterior (thoracic) region of the body there are at once seen in the living (fig. 1) two green tubes, one on either side of the alimentary canal. On further examination each is seen to be bent on itself, and cilia may be seen moving in it, especially well seen at the bend of the tube which is in the posterior part of the 6th segment. As far as I can make out from examination of the living and from sections, the opening to the exterior is between the second and third ventral bristle bundles, in the hinder part of the 2nd segment. By analogy we should expect the internal opening to be in the septum dividing the 1st from the 2nd segment. Whether this is so or not I am unable to say; I can trace the lumen of the internal limb in longitudinal sections up into the 2nd segment to the level of the second pair of bristle bundles, but it is difficult to trace further. It may be that the septum is temporarily bent back, so as to lie partly within the 2nd segment. In transverse sections the internal limb (fig. 5, *neph. i.*) is not at all easy to see and to trace, since it lies almost in the dorso-ventral muscles or is obscured by them. The external limb (fig. 5, *neph. e.*) lies below the internal one on either side of the ventral vessel, with it in the middle one of the three longitudinal cavities shut off by the dorso-ventral muscles. Both limbs consist of simple drain-pipe cells. These nephridia are probably excretory in function.[1]

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[1] Such thoracic nephridia in other sedentary annelids have been called "tubiparous glands" by Claparède and others; but it is more probable, as has been pointed out by Cosmovici, Soulier, and Brunotte (as quoted by Meyer in the 'Zool. Mith. v. Neapel' for 1888), that it is the unicellular glands of the epidermis, not the thoracic nephridia, which secrete the material for fixing together the particles of mud or sand of which the tube is formed, since worms from which the thoracic region of the body has been entirely removed can still form tubes, and since the tube does not begin to be formed until after the development of the unicellular glands. In favour of this view is the fact that, in forms most nearly allied to the one we are here considering, which are more tubicolous in habit, there are not these modified thoracic nephridia.

In the young specimens above mentioned (p. 182) these tubes were not to be seen, showing probably that they also develop late with the œsophagus.

The second kind of nephridium is found in the abdominal region of the body only of those individuals in which the gonads are developed, a single pair in each segment in which there are gonads. In such individuals they may be seen very distinctly in transverse section (fig. 8, *neph.*). They are very short, simple, uncoiled, ciliated tubes (fig. 14). But here, again, it is very difficult to say with absolute certainty whether they lead through a septum from one segment to the next, or whether they lie wholly in a segment.

In individuals in which there are no genital products present they are, if represented at all, at any rate functionless, and with no lumen. They serve, therefore, as genital ducts.

Genital Organs. — The sexes appear to be distinct, though I am not sure that I have seen any specimens with ova. As is usual in marine annelids, the generative products develop only at certain seasons of the year, and at other times the males and females are indistinguishable. In living specimens which I examined in the summer I thought I saw eggs, i. e. I saw bodies resembling eggs, but forget whether I distinctly saw them in the cœlom, or only inferred them to be there. They may, therefore, have been only parasites. Unfortunately, thinking that I was sure to get plenty more with eggs, I did not preserve or cut sections of any of them.

The sperm-mother cells are oval or spherical, with well-marked nuclei which may be seen dividing. Masses of them may be seen in the ripe male individual on either side of the intestine just above the nephridium, and attached to the cœlomic epithelium surrounding the sinus of the intestine in all the hinder abdominal segments (fig. 8, *test.*). Spermatozoa with long tails may also be seen. Together they occupy almost the whole cavity of the cœlom in the region where they are developed. In the one ripe male individual of which I was able to cut sections, which was a specimen with thirty-five segments altogether, the gonads (and consequently the nephridia) were present in the posterior twenty-two segments, i. e. from the fourteenth to thirty-fifth inclusive.

Nervous System.—There is a supra-œsophageal ganglion nearly filling the prostomium (fig. 2, *gng.*), and probably supplying the much-thickened epidermis of the anterior region of the prostomium, the eyes, and the anterior pair of tentacles.[1] From this a commissure goes down on either side to join the ventral nerve-chain, which runs throughout the whole length of the body as a double cord in the much-thickened epidermis of the ventral surface (figs. 5, 6, 7, and 8, *n. c.*). The two cords are distinct from one another, although very close together. There are no ganglionic swellings on them. Very minute giant-fibres ("neural canals," "fibres tubulaires," "neurochords") may be made out by careful staining in each cord on its dorsal and inner side. In sections stained with hæmatoxylin each appeared as a hollow tube, containing a shrunken homogeneous mass inside (figs. 5, 6, and 7). In other sections, stained with borax-carmine (fig. 8), the giant-fibres were more difficult to distinguish from the rest of the nerve-cord, the homogeneous mass not having shrunk away from its sheath. A similar position for these structures has been noted in the anterior region of Nerine foliosa, Sars, and in Scolecolepis vulgaris, Johnst., amongst the Spionidæ. In Prionospio there are also two neural canals, but these are inferior in position.[2] In forms belonging to other families the same position of the giant-fibre with regard to the nerve-cord is found, e. g.[3] Arenicola (Telethusidæ), Trophonia (Chlorhæmidæ), Sabellaria (Hermellidæ).

Affinities.—Hekaterobranchus I take to belong to the family Spionidæ on account of (1) the single pair of tentacles containing a single blindly-ending vessel; (2) the branchiæ, each containing an afferent and efferent vessel not connected with one another by capillaries; (3) the very superficial posi-

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[1] Jacobi, 'Polydoren d. Kieler Bucht,' 1883, p. 23.

[2] M'Intosh, "On the Structure of the Body-wall in the Spionidæ," 'Proc. Roy. Soc. Edin.,' vol. ix, pp. 123—129.

[3] See Cunningham, "Some Points in the Anatomy of the Polychæta," this Journal, vol. xxviii.

tion of the nerve-cord, the distinctness of the two cords from one another, and the absence of ganglionic swellings.

It differs from all other genera of the family Spionidæ in the possession of only one pair of dorsal branchiæ.[1] These are on the first or head-segment. They are found in this position as well as on the following segments in some species of some of the other genera (e. g. Spio fuliginosus,[2] Scolecolepis vulgaris, and Scolecolepis cirrata[3]). The single pair of branchiæ of Hekaterobranchus are much larger and more developed than are any of the numerous branchiæ of other Spionidæ. This reduction in number of the branchiæ, their increase in size, and their position on the head together seem to indicate that the worm once led a more sedentary life than it now does. Other facts leading to the same conclusion are—the presence of a ventral collar, the single pair of modified thoracic nephridia, the reduction of the parapodia, and, as in all other sedentary annelids, the possession of crotchet chætæ.

It is true that most genera of the family Spionidæ, with a much greater number of dorsal branchiæ, inhabit now much more distinct tubes than Hekaterobranchus. It would appear, therefore, either that they have not yet degenerated so far as Hekaterobranchus from the ancestral Spio, or that Hekaterobranchus has developed other modes of respiration which other Spionids have not, e. g. the anal respiration and that of the cephalic tentacles. For although in other genera the cephalic tentacles do serve as respiratory organs, they do so to a very slight extent only: they are ciliated only on one side, and they serve mainly as prehensile and tactile organs; whereas here they are ciliated all over, and probably

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[1] See, however, note at the end of this paper.

[2] Claparède, 'Ann. Chæt. du G. de Naples,' 1868, part ii, pl. xxiii, fig. 1. In the text (p. 63) Claparède says the branchiæ begin on the second segment; but this is evidently a slip, as, in his definition of the species (p. 62), he says, rightly enough, they begin on the first setigerous segment; and here, as in most, if not all the Spionidæ, the first segment is setigerous.

[3] Malmgren, 'Ann. Polych.,' 1867, pl. x, figs. 54 A and A′.

serve to a much greater extent for respiration, though retaining their other functions as well.

The ventral collar, usually taken as a characteristic of the family Serpulidæ, has not been actually mentioned as present in the Spionidæ. Judging, however, from a very incomplete and imperfect figure given with the Report on Annelids by Webster and Benedict in the 'Commissioner's Report of Fish and Fisheries for the United States' in the year 1881, there would appear to be a collar of the same sort in Streblospio Benedicti.[1]

Large modified thoracic nephridia are found in several families of sedentary annelids, e. g. the Terebellidæ, Hermellidæ, Serpulidæ, and Cirratulidæ, sometimes a single pair only, sometimes two or even three pairs, and sometimes, as in the Serpulidæ, one pair with a common opening to the exterior. They have not been described in other genera of the family Spionidæ.

The sinus round the intestine has also not, as far as I am aware, been described in other Spionids, but a vascular plexus occurs round the intestine in some forms, e. g. Nerine cirratulus.[2] A sinus is found in the Serpulidæ, Chætopteridæ, Ariciidæ, Terebellidæ, and in many of the Cirratulidæ amongst others, but cannot be regarded as of much classificatory importance.

The dorsal collar of the 2nd segment is not found in other Spionids,' nor in other families; but in some Spionids, e. g. Spiophanes Verrilli (described in the same paper by Webster and Benedict), there is a membranous ciliated dorsal ridge connecting the bases of the opposite so-called "cirri" on every segment from the 6th backwards, and this may be something of the same kind.

We see, therefore, that Hekaterobranchus has many characters in common with the Serpulidæ,[3] and I think there is good reason to regard it as the degenerate descendant of a form

[1] See note at the end of this paper.

[2] Claparède, 'Annélides sédentaires,' 1873.

[3] It also has many characters in common with the Cirratulidæ which oth Spionids have not. This family is notably closely allied to the Spionidæ, being probably an earlier and more primitive offshoot than the Serpulidæ.

from which the ancestors of the two families (Spionidæ and Serpulidæ) have been derived. It would appear to be nearest to the tribe Amphicoridæ of the family Serpulidæ.

In order to grant that Hekaterobranchus does thus connect the two families we must follow Meyer in his recent and very interesting paper on the homologies of the branchiæ of the Serpulidæ ('Mitth. Zool. St. v. Neapel,' vol. viii, 1888), and grant that the cephalic branchiæ of the Serpulidæ are developments of the cephalic tentacles of the Spionidæ. The branchiæ of the Serpulids have been clearly shown to be prostomial organs, both in development and in innervation. The tentacles of the Spionids are, according to Leuchart,[1] and Leuckart and Pagenstecher,[2] prostomial in origin. According to Jacobi ('Polydoren der kieler Bucht, Inaugural Dissertation zur Erlangung der Doctorwürde, 1883, pl. ii, fig. 27, p. 23) they are innervated from the prostomial ganglion. So far we should have no difficulty in deriving the complex branchiæ of Serpulids from the simple tentacles of Spionids. Were the simple remaining pair of dorsal branchiæ of Hekaterobranchus to disappear, still more work would be thrown on the cephalic tentacles; and an organ with these important functions (respiration, prehension, and tactile sensibility) localised in it would be subject to great variation, and would consequently develop rapidly. Thus we should find these organs first multiplying, but remaining simple as in Haplobranchus and Manayunkia,[3] then each becoming more complex and giving off secondary rays, as in Fabricia and Amphi-

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[1] 'Arch. f. Naturg.,' 21st yr., p. 63, &c., pl. ii. Leuckart says they develop on either side of the "Kopfhöcker" (? = prostomial crest), between it and the enlarged "upper lip." This "upper lip," he says, marks the boundary between the pro- and peri-stomium; and where the tentacles join it there is a group of long cilia on either side, probably representing the remains of the cephalotroch of the larva.

[2] 'Müller's Archiv,' 1858, pp. 610—613, pl. xxiii. Here it is said that the middle ciliated band of the larva separates the body into two halves, from the anterior of which the prostomium with the tentacles is formed, and from the posterior of which all the body-segments are formed.

[3] Leidy, 'Proc. Acad. Nat. Sci. Philadelphia,' pp. 204—212, pl. ix.

glena; and, finally, both primary and secondary rays multiplying greatly until we get the complex condition of other Serpulids (tribes Sabellidæ, Serpulidæ proper, and Eriographidæ); and in all these forms, even in the most elaborate, the same structures can be traced.

In Haplobranchus and Manayunkia there is a single pair of tentacles, with the same single blindly-ending contractile vessel running up them as in Hekaterobranchus and other Spionids.[1] The other tentacles, which I would regard as multiplications of this one, have not as yet the contractile vessel developed in them; but their cavity is, as I have been able to ascertain from sections of Haplobranchus, in continuity with that of the tentacle containing the blood-vessel some way above the base.

In Amphiglena and Fabricia all the branchial rays, and not a single pair only, have the contractile vessel in them. That they also still retain their tactile function is shown by the fact that each ray is non-ciliated, but provided with short, stiff, tactile hairs at its apex. In all the other Serpulids there is the same single contractile vessel ending blindly in each secondary ray.[2]

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[1] Bourne calls these "palps" in Haplobranchus, but says their homology is difficult to determine. They are certainly, as confirmed by sections, ventral in position. Leidy says that they are dorsal in position in Manayunkia, but apparently this has not been confirmed by sections. If there is this difference in position in what would at first sight (cf. the figures of Bourne and Leidy) appear so very evidently to be the same thing, it seems to me that it would go far towards showing that all the tentacles on the head of either form are developments (multiplications) of one, it being indifferent in which one the original characteristic contractile vessel develops.

[2] It will be seen from the above that if I accept Meyer's premises, I do not agree with him in his conclusions with regard to the relationships of the Serpulidæ inter se. That is to say, I do not regard the tribe Amphicoridæ, to which Haplobranchus, Manayunkia, Fabricia, and Amphiglena belong, as degenerate from higher existing tribes, but rather as primitive; i.e. I regard these forms as the descendants (degenerate undoubtedly in many ways) of a form more primitive than the ancestors of any of the other existing tribes. No doubt, as Meyer remarks, they once led a much more sedentary life than they now do; but it does not therefore necessarily follow that they are

Granting, therefore, that the cephalic tentacles of the Spionidæ are prostomial, there would seem to be little or no doubt of their homology with the branchiæ of the Serpulidæ. But may we grant this? The transverse section of Nerine given by Claparède in his 'Structure des Annélides sédentaires,' 1873, pl. xv, fig. 1, would seem directly to contradict Jacobi's figure and explanation already referred to. Setæ are never found on the prostomium; yet, according to Claparède, there are setæ at the base of the cephalic tentacles in Nerine cirratulus.[1] Also, according to Claparède ('Beobactungen ü. Anat. u. Entwickelungsgesch. wirbellöser Thiere,' 1863, p. 71), and Claparède and Mecznikow ('Zeitsch. f. w. Zool.', vol. xix, pp. 172 and 177), they develop not from the prostomium but from the peristomium. Claparède evidently never thought of these tentacles as being anything but peristomial, and a good many of the figures in his 'Ânnélides Chætopods du Golf de Naples (1868)' would seem to point to the fact. He very seldom, however, gives here a ventral or lateral view, and it is therefore very difficult to determine what is truly prostomial. From dorsal views only one is very apt to mistake the crest which is developed on the prostomium, but also sometimes on one or two of the segments as well, for the prostomium. Whether Claparède would have come to different conclusions had he had the question before him is of course impossible for us to say, but he is, as a rule, such an accurate observer that, without further examination of the same forms that he describes, we are not, I think, justified in concluding, as Meyer does, that this was a "Beobachtungsfehler." The point can only be decided by a renewed study of the development, and by further observations on the living in as many genera as are obtainable,[2] since in spirit specimens, even when

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degenerate from ancestors of now existing forms. Meyer's arguments are, in my opinion, insufficient to prove this.

[1] Unfortunately, in the only specimens of Nerine cirratulus I was able to procure for examination the tentacles had fallen off, and I was unable to confirm Claparède's observation.

[2] The forms described in the 'United States Fishery Reports' would no doubt prove of great interest if properly figured, but unfortunately the writers

the tentacles remain attached, it is very difficult to make out their point of attachment, though sections of well-preserved specimens would also be of value. Meyer appears to think that there is sufficient evidence of their prostomial nature, and he goes on to show that both they and the branchiæ of Serpulids probably represent the palps, not the so-called "prostomial tentacles" of the Errantia (e.g. Nereis and Polynoë).[1] He considers (pp. 614, 615) that there is a good deal of evidence that the tentacles of Spionids originate ventrally on either side of and slightly in front of the mouth, and only later move upwards more on to the dorsal surface. He regards the small quite anterior tentacles of Polydora antennata and others as representing the "prostomial tentacles" proper of the Errantia. He also quotes in support of his view Pruvot's observations on the nervous system of annelids, which led that observer to conclude that the branchiæ of Serpulids probably represent the palps of the Errantia.[2] Again, he shows that in the adults of some of the Spionidæ (e.g. Polydora antennata), Chætopteridæ (e.g. Telepsarus costarum and Phyllochætopserus), and Cirratulidæ (e. g. Heterocirrus frontifilis) the tentacles are much more ventrally placed than in others; and in some cases, as in Heterocirrus, they are situated quite ventrally in front of the mouth. In this view, if the prostomial nature of the tentacles may be granted, I entirely agree with him. He might also have given instances amongst the Errantia in which the palps are much higher up on the lateral surface than usual, e. g. Staurocephalus.[3] It may also be of some significance, though perhaps

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of the report have taken care to figure most of the forms without their characteristic tentacles, or else to figure the tentacles with some very limited portion of the head only.

[1] For definitions of the different tentacles on the head of polychæt worms see Bourne's paper on "Haplobranchus" above referred to, footnote to p. 169.

[2] 'Arch. de Zool. Expérimentale,' 2nd series, vol. iii, 1885, pp. 314, 322.

[3] Claparède, 'Ann. Chæt. du G. de Naples,' part i, pl. vii, fig. 2A. Compare also Bourne's description of the palps in the Polynoina ('Trans. Linnæan Soc.,' 1883, 2nd series, "Zoology," vol. ii, part vii, p. 351). He says, "The palps differ from all other tentacular structures in being muscular along their whole length. They are capable of great elongation and contraction. . . . . .

not much, that the ciliated groove of the tentacles of most Spionids is used in conveying food down to the mouth, the cilia being continuous with those of the mouth opening, which would make it the more probable that the tentacles were once outgrowths of the side of the mouth. According to this view, the name "palp" given to the most ventral pair of cephalic tentacles of Haplobranchus by Dr. Bourne might be retained, but extended so as to include the other tentacles as well. Dr. Bourne in his paper regards these other tentacles as peristomial, from a certain superficial resemblance they bore to the peristomial tentacles of Nereis, and he tries to show that the cephalic branchiæ of the Serpulidæ are peristomial; but, as Meyer has shown, there is no evidence of fusion of ganglia in the Serpulidæ as there is in the Nereidæ. When Dr. Bourne wrote his paper, however, he was unaware of the existence of Manayunkia, which was first described in the same year (1883), or he might have been led to different conclusions with regard to what he has called "peristomial tentacles."[1]

They originate [sections of Polynoë (Harmothoë) areolata] just where the prostomium joins the peristomial and buccal somites, although they appear to have more connection with the prostomium than with the other somites. Their nerve-supply appears to come from the supra-œsophageal ganglion." Such a description would need but little modification to serve for the tentacles of some of the Spionidæ (e.g. Polydora antennata) and Cirratulidæ (e.g. Heterocirrus frontifilis). Bourne does not mention a contractile blindly-ending vessel in them, but there is this in Staurocephalus. The chief difference is the absence of cilia on the palps of Polynoë.

[1] As regards the rest of Meyer's view, I should like to point out that in Hekaterobranchus the lateral parts of the collar are evidently not formed by the ventral cirri, since these are present quite independently as well on the 1st segment. The collar appears to be a mere folding of the ventral surface; if anything it could only be the dorsal cirrus which assists in forming it. I have especially looked for the "Wimper-organe" on the prostomium, which Meyer mentions (p. 639) as a feature which we might expect to find in the Spionidæ, but have been unable to find any trace of them. I may also mention in reply to Meyer's suggestion (vol. vii, p. 723) that there are probably thoracic nephridia with a single external duct in Haplobranchus, that in my sections of Haplobranchus I have been unable to find any trace of such an arrangement; and I even doubt whether what Bourne marks "gl" in his figure of Haplobranchus are to be regarded as nephridia at all. There is

SYSTEMATIC DESCRIPTION.

Family Spionidæ.

Hekaterobranchus,[1] gen. n.

Spio quadricornis, Lam., 'Anim. s. Vert.,' vol. v, p. 319.[2]

A single pair of dorsal branchiæ, situated on the 1st segment, and very large.

no trace whatever of a lumen in them, and consequently none of external or internal openings. In Haplobranchus there are the same pigmented organs of unknown function on the bases of the branchiæ, in some specimens at least, as are described and figured by Mecznikow in Fabricia ('Zeit. f. wiss. Zool.,' vol. xv, p. 331, and pl. xxiv, fig. 8). Can these represent the prostomial ciliated pits from which Meyer considers (vol. viii, pp. 629—634) the most anterior portion of the common median duct to the exterior of the modified thoracic nephridia of Serpulids is to be derived? They open separately to the exterior on either side beneath the collar. Mecznikow does not say whether the common aperture to the exterior of the pair of nephridia he describes in the 2nd segment is on the prostomium or not.

I will also mention that there is a sinus round the intestine in Haplobranchus, as Dr. Bourne suggests there may be. In the anterior region I cannot in my sections see the dorsal vessel he mentions. The alimentary canal nearly touches the body-wall dorsally. The cœlom, however, in this region is divided into distinct longitudinal cavities, four, or more anteriorly, two, on each side.

My sections would also seem to show that Haplobranchus has an evertible pharynx, which, when inverted, reaches back into the 2nd segment. But further investigation is needed.

[1] Ἑκατερος = each (singly) of two. The name is meant to imply that two kinds of branchial organs are present, and that there is one single pair of each kind.

[2] I have identified this form with the Spio quadricornis of Lamarck, because it with its four horn-like tentacles (tentacles proper and branchiæ) is exceedingly suggestive of the name—much more so than the animal—Spio crenaticornis figured by Montague, to which Lamarck refers. (Lamarck refers to it as "Diplotus hyalina" because Montague's figures are wrongly numbered, but according to the text the figures 6 and 7 of pl. xiv ('Trans. Linnæan Soc.,' xi) should be marked as Spio crenaticornis.) It is extremely probable that Lamarck saw Hekaterobranchus, and gave the name "Spio quadricornis" to it; and that he wrongly identified it with Spio crenaticornis, Montague, which was probably also not a Spio at all, but a Leucodore.

Cephalic tentacles not grooved, but ciliated all over.

Prostomium well developed, bearing four eyes.

1st segment prolonged forwards on the ventral surface to form a collar.

Pharynx evertible and richly ciliated.

A single pair of thoracic nephridia, opening to the exterior in the 2nd segment, reaching back into the 6th segment, and thence bending forwards again.

Giant-fibres minute, one in each nerve-cord near the upper and inner surface.

Dorsal "cirri" forming a sort of collar in the 2nd segment.

H. Shrubsolii, sp. n.

The following characters are probably of specific value.

Ventral crotchet chætæ begin in 8th segment, accompanied by a few capillary chætæ.

Shape of chætæ (fig. 4).

Sinus round intestine posteriorly.

Intra-vascular ridge in dorsal vessel.

Thoracic nephridia green.

Habitat.—The mouth of the Thames.[1]

POSTSCRIPT.

WHILST the foregoing paper was in the press I succeeded in obtaining Webster's original description of the genus Streblospio, which is in the 39th Annual Report of the Trustees of the New York State Museum of Natural History. Had I seen the full description of this genus earlier, I should have been loth to make a new genus for a form which may well be included in Webster's genus. But having seen a figure of the head of Streblospio, and this not even suggesting to me the identity of the genus I was studying with the one figured, I contented myself with merely mentioning (p. 190) what appeared to be one point of resemblance between the two

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[1] Mr. Shrubsole informs me that he has found both this form and Haplobranchus as far up as Gravesend on the south side of the river.

forms, and did not concern myself with hunting for the fuller description before sending my paper to the press.

From the description which I have now seen, it appears to me highly probable that Hekaterobranchus will have to be regarded, for the present at least, in virtue of its single pair of branchiæ placed on the head, its ventral collar, and its dorsal collar (equivalent to the so-called dorsal "pouch" of Webster), as a new species of the genus Streblospio, rather than as a distinct genus. There are, however, differences between the two forms, which might rank as generic differences were there a large number of forms with their common characteristics known. For instance, the "conical median papilla or cirrus" on the anterior margin of the first segment, the short conical dorsal cirri of the posterior segments succeeding and replacing the plate-like lobes of the anterior, the fact that the "proboscis is incomplete above" (though, as I have failed to grasp what this means, I cannot attach much importance to it), the absence of thoracic nephridia (unless the dark green colour observed in the first eight segments of a few specimens was due to their presence), are all features in Streblospio which might prevent the association of Hekaterobranchus with it as one genus. How much, or how little, importance is to be attached to these differences is difficult to say without comparing the two forms, or at least proper representations of them, side by side. The drawings published by Mr. Webster of his Streblospio are so fragmentary and rough that I cannot undertake to form a final opinion on the subject by their aid alone.

EXPLANATION OF PLATES XXI and XXII,

Illustrating Miss Florence Buchanan's paper on "Hekaterobranchus Shrubsolii, a new genus and species of the family Spionidæ."

Fig. 1.—Lateral surface view of the whole animal. *pro.* Prostomium. *m.* Mouth. *t.* Cephalic tentacles, with cilia and tactile hairs. *br.* Branchiæ. *v. c.* Ventral collar of 1st segment. *d. c.* Dorsal collar formed by the two "cirri" of the 2nd segment. *a.* Anus. The ventral crotchet chætæ are seen beginning in the 8th segment.

Fig. 1 a.—The same, natural size.

Fig. 2.—Semi-diagrammatic view of the left side of the animal from the inside, as would be seen were the animal cut in two by a longitudinal, vertical, nearly median section. The tentacle (*t.*) and branchiæ (*br.*) are supposed to have been cut separately. The digestive, vascular, nervous, and excretory systems are shown. *m.* Mouth. *ph.* Pharynx. *œs.* Œsophagus. *int.* Intestine (large, intersegmentally constricted part). *int′.* Intestine (narrow, non-constricted part). *a.* Anus. *d. v.* Dorsal vessel. *t. v.* Vessel of tentacle (its junction with the branchial vessel, which meets the ventral vessel, is seen in Fig. 12). *d. br. v.* Branchial vessel in connection with the dorsal vessel. *v. br. v.* Branchial vessel in connection with ventral vessel. *v. v.* Ventral vessel. *sin.* Sinus. *d. s. v.* Dorsal vessel nipped off from the rest of the sinus, but lying close to the wall of the intestine, containing the intravascular ridge. *n. c.* Nerve-cord. *gng.* Prostomial ganglion. *neph. e.* External limb of thoracic nephridium, opening to the exterior in the 2nd segment. *neph. i.* Internal limb of thoracic nephridium. *cœl.* Cœlom. *sept.* Septa. Longitudinal muscles would really be seen in such a view underlying the epidermis, but are omitted for the sake of clearness.

Fig. 3.—Ventral view of anterior extremity. A. Showing ventral collar (*v. coll.*), and prostomium lying beneath it. The collar is pushed forwards, and so covers the mouth. B. The pharynx (*ph.*) everted, hiding the prostomium.

Fig. 4.—Chætæ. A. Notopodial capillary chæta. B. Neuropodial capillary chæta. C. Neuropodial crotchet (side view). C′. The same (ventral view).

Fig. 5.—Transverse section through the thoracic region of a specimen in which no gonads were developed (stained with hæmatoxylin). *Epid.* Epidermis. *c. m.* Circular muscle layer of body-wall. *c. m*^{1}. Circular muscle layer of dorsal vessel (*d. v.*). *c. m*^{2}. Circular muscle layer of alimentary canal. *d. l. m.* Dorsal longitudinal muscles of body-wall. *v. l. m.* Ventral longitudinal muscles of body-wall. *c. ep.* Cœlomic epithelium. *cœl.* Cœlom. *int. ep.* Intestinal epithelium. *ntp.* Notopodial chætæ. *nrp.* Neuropodial

chætæ. c^{ntp}. Notopodial "cirrus." c^{nrp}. Neuropodial cirrus. (The right side of the section is behind the left.) *s. s. m.* Muscles going to setal sacs. *d. v. m.* Dorso-ventral muscles. *gl.* Gland-cell in epidermis. *neph. e.* External limb of thoracic nephridium. *neph. i.* Internal limb of thoracic nephridium. *vasc. r.* Intra-vascular ridge in *d. v.* dorsal vessel. *v. v.* Ventral vessel. *d. v. v.* Parts of dorso-ventral vessel. *n. c.* Nerve-cord. *g. f.* Giant-fibre.

Fig. 6.—Transverse section of the same worm through the anterior abdominal region. The section is taken just in front of a septum, and therefore the intestine does not occupy so much room in section as it otherwise would. The dorsal vessel (*d. s. v.*) is separated from the intestinal sinus; the intra-vascular ridge (*vasc. r.*) is very close to but distinct from the wall of the intestine. Other letters as in Fig. 5.

Fig. 7.—Transverse section of the same specimen through the posterior abdominal region, where the intestine is not constricted intersegmentally. *sin.* Sinus, complete all round the intestine. *mes.* Dorsal mesentery. mes'. Ventral mesentery. Other letters as in Fig. 5.

Fig. 8.—Transverse section through another specimen, in which the gonads are developed (stained with borax-carmine). *test.* Testes. *neph.* Nephridia, seen opening to the exterior on the left-hand side of the figure in *ext.* A parasite (*par.*) is seen in the intestine. The section is taken farther back than that represented in Fig. 6, and consequently the sinus shows no trace of the dorsal vessel. From the ventral vessel (*v. v.*) a branch is seen passing off on the right-hand side. Other letters as in Fig. 5.

Fig. 9.—Transverse section of cephalic tentacle. *epid.* Ciliated epidermis. *c. m.* Circular muscle layer. *l. m.* Longitudinal muscle layer. *c. ep.* Cœlomic epithelium. *cœl.* Cœlom (containing cœlomic corpuscles in the living). *t. v.* Vessel of tentacle.

Fig. 10.—Transverse section of branchia. *d. br. v.* Branchial vessel in connection with dorsal vessel. *v. br. v.* Branchial vessel in connection with ventral vessel. *cœl.* Cœlom. Other letters as in Fig. 9.

Fig. 11.—Dorsal view of the posterior extremity of the body of a specimen in which the ciliated ridges could be seen in the intestine (*int.*), just in front of the anus (*a.*).

Fig. 12.—Semi-diagrammatic dorsal view of the head to show the probable arrangement of vessels. *Pro.* Prostomium. ntp^1. Notopodial chætæ of 1st segment. nrp^1. Neuropodial chætæ of 1st segment (with "cirrus"). *d. c.* Dorsal collar (notopodial "cirri") of 2nd segment. *d. v.* Dorsal vessel. *d. br. v.* Branchial vessel in connection with dorsal vessel. *v. br. v.* Branchial vessel in connection with ventral vessel. *v. v.* Ventral vessel. *t. v.* Vessel of cephalic tentacle. *d. v. v.* Coiled dorso-ventral vessel.

Fig. 13.—Parasite from intestine (Monocystis hekaterobranchii). *vac.* Vacuole. *n.* Nucleus.

Fig. 14.—Abdominal nephridium. *ext.* Its external opening.

An Attempt to Classify Earthworms.

By

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The hard and fast line between Earthworms and Fresh-water worms, as indicated by Claparède's terms[1] "Terricolæ" and "Limicolæ," is gradually becoming less distinct; and as new knowledge in both these groups is acquired we are led to recognise that the plan adopted by Vejdovsky is the more natural one: although I believe that it is possible to arrange the various families into which he divides the Oligochæta into certain groups.

The anatomical characters which served Claparède as points of distinction between his two groups were drawn from the knowledge of Lumbricus alone. They were (1) the possession of two blood-vessels below the intestine, the subintestinal and subneural vessels; (2) the presence of nephridia in the genital somites; (3) the position of the clitellum behind the male apertures; and (4) the presence of a plexus of capillary blood-vessels on the nephridia. The investigations of Per-

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[1] Claparède, "Rech. sur les Oligochétes," 'Mém. de la Soc. de phys. et d'hist. nat. de Genève,' t. xvi, 1862.

rier,[1] and later of Beddard, Horst, Rosa, myself, and others, have shown that, of these four characters, only the last can be retained; and at the same time numerous points of agreement between "Limicolæ" and "Terricolæ" have been brought to light, especially by the help of microscopic research. For example, Beddard has pointed out the similarity between the genital organs of the earthworm Moniligaster and the water-worm Stylaria.

From his observations of the various specimens of earthworms in the Paris Museum, Perrier suggested a subdivision of the "Terricolæ" into four groups: (1) Anteclitellian; (2) Intraclitellian; (3) Postclitellian; and (4) Aclitellian.

Beddard and Horst have already shown that the second and third of these names cannot be always applied to all species of the same genus, one species being Intraclitellian, others Postclitellian; and A. G. Bourne[2] has described a species of Moniligaster, for which the fourth group was formed, in which a clitellum is present.

Vejdovsky,[3] in his beautiful monograph on the Oligochæta, divides the members of the group into seventeen families, each of equal value. These are—

Family 1. Aphanoneura.
2. Naidomorpha.
3. Chætogastridæ.
4. Discodrilidæ.
5. Enchytræidæ.
6. Tubificidæ.
7. Phreoryctidæ.
8. Lumbriculidæ.
9. Pontodrilidæ.
10. Criodrilidæ.
11. Lumbricidæ.
12. Eudrilidæ.

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[1] Perrier, "Rech. pour servir à l'hist. des Lombriciens terrestres," 'Nouv. arch. du Mus. d'hist. nat. de Paris,' t. viii, 1872.

[2] A. G. Bourne, 'Proc. Zool. Soc.,' 1886.

[3] Vejdovsky, 'Systeme und Morphologie der Oligochaeten,' Prag., 1884.

13. Acanthodrilidæ.
14. Perichætidæ.
15. Plutellidæ.
16. Pleurochætidæ.

? 17. Moniligastridæ.

He gives the characters of the first eleven of these families, but does not characterise the remaining six. As will be seen below, I shall split up some of his families, and unite others into one family.

Rosa[1] does this to some extent; but I have not taken quite the same lines as he has. He retains Claparède's "Terricolæ" for the members of the last nine families, and groups these into six families; and regards "Terricolæ" as of equal value to any of the first eight of Vejdovsky's families.

Vaillant, in the recently published volume 'Annèles' ('Suite à Buffon'), divides the Oligochæta into two groups:

(1) Naidina, including Vejdovsky's first three families;

(2) Lumbricina, including the remainder with the exception of Discodrilidæ.

But, as he only deals with the genera and species of earthworms known up to and including Perrier's memoir in 1872, his subdivisions are not of that value that we should expect in such a work.

I. Nomenclature of Certain Organs.

Before proceeding to the classification which I have to suggest, I will make a few remarks on the words and terms employed therein.

The setæ in a large number of worms are arranged, as in the common earthworm, in "twos." These are nearly always spoken of as "pairs" by writers on the subject; but this word seems to me to be ill-chosen: by "pair" we usually understand a right and a left organ of a bilaterally symmetrical animal. I suggest, therefore, the word "couple" to denote the

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[1] Rosa, "Nuova Classificazione dei Terricoli," Boll. d. Mus. Zool. ed Anat. Comp.,' tom. iii, 1882.

two setæ placed close to one another; and in place of the terms "dorsal" and "ventral" setæ I shall employ the words "outer" and "inner" in describing the couples in reference to their position relative to the ventral mid-line of the body. When the eight setæ become wider and wider apart it sometimes becomes advisable to speak of such setæ as being "separated."

The four setæ on each side may be termed, with Perrier,[1] 1, 2, 3, 4; the first being most ventrally placed, the fourth most dorsally.

The prostomium is frequently a lobe nearly as wide as the first somite of the body, and sometimes separated from it by a transverse groove; but very frequently grooves extend back into this first somite, one starting from each side of the prostomium, so that the prostomium appears as a narrow or broad lobe embedded in, or "dovetailed into," the first somite. Sometimes these lateral grooves stop after traversing the first somite for only a short distance; the prostomium is then only "partially dovetailed" into the first somite. If, as in Lumbricus agricola, Hoffmeister, the lateral grooves reach the intersegmental groove dividing the first from the second somite, the prostomium is said to be completely "dovetailed."

The first somite, that surrounding the mouth, is frequently called the "buccal segment or somite;" but, following the nomenclature used in works on Polychætes, I have adopted the word "peristomium" or "peristomial somite" in the following classification.

Most of the writers of the present day regard this as the first somite, and this is the view I shall take. It may be noted that Vaillant[2] retains Dugés' enumeration, and speaks of the first setigerous somite as the "first" somite.

In referring to the position of an aperture between two somites I use the form "x/xi," for example, meaning that such an aperture lies between Somites x and xi.

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[1] Perrier, "Sur un nouv. Gen. des Lombriciens terrestres," 'Arch. f. Zool. Exp. et Gen.,' t. ii, 1873.

[2] Vaillant, "Annèles," 'Suite à Buffon,' 1889.

The glandular modification of the epidermis indicated by the word "clitellum" is in many cases equally developed all round the body, as in Perichæta; this is indicated by using the word "cingulum," or speaking of the clitellum as "complete." In Lumbricus and many others the glandular modification does not extend across the ventral surface: this is a true "clitellum" in the strict sense of the word, or an "incomplete clitellum" using the word in its wider sense.

Intermediate conditions are sometimes met with, where, as in Acanthodrilus, the clitellum is "complete" in the anterior part of its extent, and "incomplete" over the last two or more somites. The lower edge of the incomplete clitellum is sometimes, as in Lumbricus and Rhinodrilus, further modified, presenting the appearance of a linear band, or group of glands over more or fewer somites. To these the name "tubercula pubertatis" has been applied by Eisen.

The external openings of the sperm-ducts are the "male or spermiducal pores;" those of the oviducts, "oviducal pores;" those of the spermathecæ, the "spermathecal pores." The first of these is frequently placed on a more or less prominent papilla, and in many worms other papillæ, median or paired, are present in their neighbourhood. These "copulatory papillæ" are probably of value for the diagnosis of species; but it is only recently that exact observations have been recorded as to the number and position of these papillæ in different worms, and as they appear to be fully developed only at the breeding season they are not of value for absolute identification. Of this nature are the depressed reddish papillæ in Somite XXVI in the common earthworm.

The setæ in certain somites are not unfrequently modified for the purpose of copulation: those in more or less immediate relation to the male pores are known as "penial setæ" (Lankester); whilst those which are found, for instance, in Acanthodrilus layardus and other species, in connection with the spermathecæ, have been distinguished by Horst as "copulatory setæ." These two terms are, to all intents and purposes, identical: so that I shall distinguish penial setæ in the neighbourhood of the prostates, or spermiducal pores as "male copulatory setæ," or "posterior penial setæ," and those in neighbourhood of spermathecæ, as "female copulatory," or "anterior penial setæ."

Certain terms in connection with the internal reproductive apparatus may require definition. The testes are usually present to the number of two pairs, and these are nearly always placed in Somites x and xi. The difficulty in counting the somites, or the delicacy and fragility of the septa, sometimes render it difficult to be certain of the true position of the testes, especially as in some worms the septa do not correspond exactly in position to the true limits of the somites; hence it may be that some, at any rate, of the exceptions are apparent rather than real. The ovaries likewise are nearly universally placed in the Somite xiii; the oviducts open externally on the Somite xiv.

The terms vesiculæ seminales, and seminal reservoirs, are conveniently replaced by "sperm-sacs" (i. e. the "testes" of the older authors). Similarly the rather clumsy term "receptaculum ovorum," which has been observed in several worms, may be replaced by "ovisac;" a word at the same time simpler than the original term, and also in agreement with "sperm-sac," both in nomenclature and in function.

I shall use the word "sperm-duct" for the more old-fashioned "vas deferens;" however, I shall retain "ciliated rosette" as a more convenient and shorter term than "funnel of the sperm-duct."

In many genera there is, attached to the sperm-duct near its external pore, a glandular diverticulum, which may be lobed as in Perichæta, or tubular and coiled as in Pontodrilus, and others. Most writers have referred to these structures as "prostates;" but Beddard has recently, in two papers ('Zool. Anz.,' No. 268, 1887, and 'Quart. Journ. Micr. Sci.,' xxix, p. 117), sought to establish an homology between these prostates and the " atrium," or enlarged part of the sperm-duct of Tubifex, into which the cement gland opens; and in his various papers on earthworm anatomy uses " atrium " to signify the prostate of authors, and by " prostate " refers to the peritoneal (? glandular) covering of the terminal portion or " atrium " of Moniligaster and Stylaria.

I will not, here, enter into a discussion of this subject; I shall, however, reject "atrium," and retain the older word "prostate" for these glands, which either pour their secretion into the sperm-duct, or open, independently, to the exterior.

This prostate is a hollow structure, the wall of which is formed of club-shaped cells similar to those found in the clitellum: sometimes, a layer of columnar epithelial cells intervenes between the clitellar cells and the lumen; sometimes the columnar cells are absent. A layer of muscles usually surrounds the clitellar cells; or the muscular layer may be confined to the proximal region of the prostate.

In many cases, as in Perichæta, Pontodrilus, Eudrilus, &c., the prostate opens into the sperm-duct, so that we only have one "male pore." In other genera, as in Acanthodrilus, Deinodrilus, &c., the prostates open to the exterior independently of the sperm-ducts: in these cases we must distinguish "spermiducal pores" from "prostate-pores."

The word "spermatheca" is retained, in preference to the " receptacula seminis " of other authors.

The glandular structures met with in Lumbricus, Perichæta, Brachydrilus, and others, and usually called "capsulogenous glands," are misnamed. As far as we know they have nothing to do with the formation of the capsule or cocoon, which is formed by the hardening of the secretion of the gland-cells of the clitellum; but they give rise to the albuminous fluid found in the cocoon, in which the ova and spermatozoa are deposited, and which serves as nourishment for the developing embryos. Vejdovsky suggests the word "albumen-glands" for these structures, a term which I retain.

The excretory system has quite recently had a new light thrown upon it by the researches of Beddard[1] and of Baldwin Spencer.[2]

Perrier, in 1872, noticed that the nephridia were replaced in Perichæta by small tufts of tubules; and a similar arrangement is found in many other worms.

Beddard[3] described a species of Acanthodrilus with eight "nephridia" per somite; these he more recently[4] discovered were not really large tubules, but eight groups of small tubules opening to the exterior by numerous apertures. Again, more recently he has shown us that in Perichæta armata there is a network of delicate tubules in addition to a pair of large nephridia in each somite; and this network of delicate tubules is provided with many external apertures, sometimes without internal funnels, rarely with them.

Baldwin Spencer, in his detailed description of Megascolides australis, demonstrates the transition between the large nephridia in the posterior part of the body and the delicate small tubules which line the inner surface of the body-wall in the anterior somites. Anteriorly there is a network of these delicate tubules, which have no internal funnels, but numerous external openings, the network being continuous somite to somite. About the middle of the body this network becomes confined to a band of small tubules round the somite, of which one tubule is larger than the rest. Further back this tubule increases in size, and ultimately attains a size almost equal to that of a nephridium in Lumbricus; moreover, this tube communicates with the cœlom by means of a funnel, but still retains a connection with the network of smaller tubules. Both Beddard and Spencer favour the idea of the development of a "nephridium" from such a network of tubules.

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[1] Beddard, 'Quart. Journ. Micr. Sci.,' vol. xxix, and see literature therein.

[2] Baldwin Spencer, "The Anatomy of Megascolides australis," 'Trans. Roy. Soc., Victoria,' vol. i, 1888.

[3] Beddard, 'Proc. Roy. Soc.,' 1885.

[4] Beddard, 'Quart. Journ. Micr. Sci.,' vol. xxviii.

The possession by earthworms either (1) of such a network or "tuft" of small tubules (a "plecto-nephric" condition), or (2) of a pair (rarely two pairs) of large "nephridia" (a "mega-nephric" condition), suggested to me the possibility of dividing the earthworms into two groups, according to conditions of the excretory system. This has formed the basis of the classification here put forward; but we are instantly met by the fact that some species of certain genera comprised in the first set—i. e. those with a network of small tubules—have apparently large "nephridia;" but is this really the case?

Both in Acanthodrilus and in Perichæta species have been originally described as having large nephridia; but a renewed and more careful microscopical examination has proved either that this large nephridium is accompanied by a network of tubules as in P. armata (Beddard), or that the supposed "nephridium" really consists of a mass or tuft of small tubules as in Ac. multiporus. So that when Fletcher states that several species of Cryptodrilus, a genus which is usually "plecto-nephric," have three pairs of large "nephridia" per somite, I think we are justified in assuming that these will turn out to belong to one or other of the above categories.[1] I may add that Fletcher's descriptions of numerous species are unaccompanied by figures, except in a few instances of external characters.

The genus Perionyx, formed by Perrier for the reception of a worm very similar to Perichæta, has always been closely associated with this latter genus, and I feel considerable hesitation in removing it from association with Perichæta; but it differs from the latter in possessing a pair of large nephridia in each somite unaccompanied by smaller tubules, as well as in some other small details. This I have ascertained by the examination of sections, and by mounting a portion of the body-wall, with nephridia, complete.

[1] Beddard has recently ('Quart. Journ. Micr. Sci.,' xxx, Feb.), described these new species of Acanthodrilus, in which only large nephridia are mentioned. Here again, I think, we may suspect that a network of small tubules is present in addition.

The nephridium here has all the appearance of that in the common earthworm.

For this reason I have separated it from its former allies; and although, at present, we know but few points of apparent difference between Perionyx and Perichæta, yet it may be possible to separate some of the species of the latter genus and place them in the former genus.

Assuming with Beddard and Baldwin Spencer that the excretory network is more primitive than paired nephridia, and regarding the perichætous condition as secondary, it is not impossible to conceive this condition making its appearance both in worms which still retain the network, and in those which have acquired the large nephridia; or perhaps Perionyx is a descendant from forms which had become perichætous whilst still retaining the network, but which have lost this latter character and retained the former.

The histological structure of the nephridia still remains to be worked out, although, thanks to Beddard and Spencer, we have a fair knowledge of the details in the case of the small tubules of the network in Acanthodrilus and Megascolides. These, like the larger nephridia, are made up of a series of "drain-pipe" cells—no doubt ciliated in some part of the tubule—which form the mass of the tubules; but this intracellular lumen becomes converted into an intercellular lumen near its external opening, and the wall is here frequently provided with muscle-fibres.

Of the exact arrangement of the convolutions of the more or less elongated tube of the nephridia of other forms we have little or no information. Gegenbaur's well-known figure of the nephridium of Lumbricus still remains the only accurate drawing of such a nephridium. The recent drawing given by Goehlich ('Schneider's Beiträge,' Bd. ii) is not quite accurate; and he is mistaken in thinking that the cilia are continuous from the funnel to the muscular duct. This is not the case; certain regions of the duct are provided with cilia, and others are deprived of them.

Goehlich's drawing of the funnel of the nephridium of Lumbricus is wrong; and in the various genera we find nephridia with more and with less complicated convolutions of the tubule; for instance, Microchæta and Moniligaster or Rhinodrilus. The character of the muscular region or "duct" also varies.

In many cases it is, as in Lumbricus, a mere continuation of the tube; in other cases the muscular region is, in proportion, very much larger, and the tube does not enter it at its extremity, but at some point along its side, so that the muscular region is produced as a "cæcum," or bladder; and to some extent the families are in part characterised by possessing either a simple "duct" or a "cæcum."

The family Eudrilidæ, for instance, all possess simple nephridia; the tube is comparatively short, and the duct simple and in many cases ill-marked. In the accompanying diagrams I have inserted the nephridia—so far as I have been able to obtain information on the point—in order to show, first, the presence or absence of a "cæcum;" and secondly, the somite in which the series commence.

In the family Rhinodrilidæ all the genera have cæcal prolongations of the nephridial duct, more or less marked. And frequently this cæcum is less developed in the most anterior than in the greater number of nephridia: for example, Urobenus and Microchæta; in the latter genus the muscular portion attains the greatest relative size, and the coiling of the tubule the greatest complexity to be found amongst earthworms. In Rhinodrilus the more anterior nephridia have a simple duct, those more posteriorly possess a cæcum.

Plutellus is noticeable for the alternation, from somite to somite of the position of the nephridiopore, which is placed in front of the second or the fourth seta on each side, counting from the most ventral seta.

Perionyx saltans, A. G. B., presents a somewhat similar condition, and according to Fletcher, certain species of Cryptodrilus;[1] but see above as to whether large nephridia are really present in this genus unaccompanied by a network.

Brachydrilus possesses four nephridia per somite, all alike.

In a large number of genera the anterior nephridia—both in those retaining a network and those with large nephridia—are more or less modified. For instance, Beddard was the first to show for Ac. dissimilis that a group of tubules on each side of the pharynx is connected, by means of a strong duct, with the buccal cavity; the same is the case with Dichogaster and Digaster—all genera in which the nephridia are in the form of a network elsewhere in the body.

In Megascolides, Baldwin Spencer has described and figured the presence of numerous nephridial tubules around the pharynx, which open separately into the cavity of the alimentary tract.

In other cases, e. g. Typhæus and Deinodrilus, the tubules of the network are much more abundant in the first two or three somites, but do not communicate with the cavity of the pharynx.

We are, therefore, entitled to consider that these anterior nephridia are used by the worm for some other purpose in addition to excretion: they are probably used for softening or otherwise acting on the food, either when the everted buccal region has seized the food, or previously to this. How the external aperture of a group of tubules has shifted from its position on the body-wall to the pharyngeal wall, and how at the same time, in some cases, the numerous apertures have united into a duct, we do not know. We can only form conjectures on the subject. The epiblast is known to grow in at the blastopore, so as to form the lining of the pharynx; and the shifting of the nephridiopores may perhaps be connected with this invagination.

I have used in my diagnoses of the genera the term "pepto-nephridium[2]" to indicate this modification of the

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[1] Beddard describes a similar alternation in Ac. rosæ and Ac. dissimilis.

[2] Πεπτω=I soften.

anterior nephridia for the purposes of alimentation, both for cases where they open into the digestive canal and where they merely open to the exterior, i. e. intra-buccal pepto-nephridia, and extra-buccal pepto-nephridia.

This modification of the anterior nephridia is also found in some of the families in which large nephridia have replaced the network. In the Geoscolecidæ, this is the case: and although in Geoscolex the first nephridium is not very greatly modified, it will be seen to be slightly different from the following ones; and in fact the coiled tubule is thicker, and is distinctly glandular in appearance. The following ones are somewhat similar. The point of entrance of the tubule into the duct gradually shifts towards the pore, so that the cæcum becomes more and more marked. But in the other two genera of the family, Diachæta and Urochæta, the first pair of nephridia are very different from the following ones, both in regard to their size and complexity, and are "pepto-nephridia." From a glance at the diagrams it will be seen that Diachæta presents an intermediate stage between the more simple condition in Geoscolex and the more complicated in Urochæta.

Rhinodrilus and Microchæta also present variations in their nephridia, not so markedly as in the last family, and not so pronounced in Microchæta as in Rhinodrilus, where the first pair of nephridia are much larger than the following ones, and lie underneath the pharynx.

In connection with the nephridia it is worthy of note that in Criodrilus and Pontodrilus they are entirely aborted in the first dozen or more somites. Is this connected with their aquatic habits? Is the absence of anterior nephridia analogous to the absence of salivary glands in fishes?

The position of the nephridiopore is not in all cases characteristic of genera, though this is usually the case.

The Alimentary Canal.

The regions that I have distinguished are—(1) buccal region, (2) pharynx, (3) œsophagus, (4) gizzard, (5) tubular intestine, (6) sacculated intestine.

The buccal region is always present, and is bounded posteriorly by the circumpharyngeal nerve-collar: this region is thinner-walled than the pharynx, and is eversible.

The pharynx occupies some two to four of the following somites: it is probable that the buccal region occupies always the first and second somites,[1] and the pharynx the third to fifth; but as there are no septa in this region the pharynx frequently appears more extensive than this: the thick muscular wall is confined nearly entirely to the dorsal surface.

The following region, up to the gizzard, is the œsophagus. As will be readily seen by a glance at the diagrams, this region is extremely variable in extent, according to the position of the gizzard, which may lie in Somite v or in Somite xvii, or, as in Moniligaster, still further back.

The presence of two or more gizzards is by no means uncommon, and this leads to a repetition of the œsophagus. How far the position of the gizzard is a generic characteristic it is impossible to say: descriptions of the alimentary tract are in most cases very brief, and it is well known that the gizzard rarely lies opposite to the somite to which it belongs; the septa are very frequently pushed backwards, so that the septum bounding a somite may, in the middle of the body, come to lie at the level of a somite some little way behind: in addition to this, the septa in the region of the gizzard are not unusually very thin, and easily broken; and it thus comes about that, whereas the positions of the various parts of the reproductive apparatus are carefully noted, the real situation of the gizzard has sometimes been less accurately observed. From the peculiar constancy in position of the parts of the generative organs, and the variability in the position of the gizzard, I believe it will repay future observers to turn their attention more particularly to

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[1] In the diagrams I have represented the buccal region as occupying the first somite only: so little positive information is available on this point, that I have not attempted to mark out the limits of the region accurately.

the latter organ. For instance, most species of Perichæta have the gizzard occupying three somites, viz. VIII, IX, X. Some species have been credited with a gizzard in Somite V or VI. I believe that the former is the typical position for Perichæta, and that a further examination of the forms with a forward position of the gizzard will lead to a separation of these species.

The absence of a gizzard in Criodrilus and Pontodrilus, in addition to the absence of the anterior nephridia, is a point worthy of note, both negative characters being, no doubt, connected with their habitat and characters of food.

The fixity of the ovary and testes in the thirteenth and tenth somites respectively—or, rather, their nearly constant position—gives us a fixed point or centre from which to count the variations in position of other organs. And I am greatly tempted, with Rosa, to regard the ovary as always in the thirteenth: notwithstanding the apparent exceptions—Microchæta and Brachydrilus, where they appear to be in Somite XII, the error may be due to fusion of two of the anterior somites to form a single "peristomium."[1] However this may be, the majority of earthworms possess an ovary in Somite XIII—this may be taken as a fixed point, and we may compare the position of other structures in regard to their greater or less distance from this point: thus the gizzard lies so many somites in front, or behind, in the various genera. This fact seems to indicate that the gizzard of Eudrilus in Somite VI is not homologous or homogenetic with the gizzard in Lumbricus in Somites XVII and XVIII; but that a similar modification of the wall of the gut has occurred in different somites in different worms.

The region following the gizzard, and before the typhlosole commences, is in Lumbricus very short, occupying only a

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[1] This is certainly the case in Microchæta beddardi, where small setæ can be detected in the apparent peristomium: and as this somite never carries setæ, we have here one somite occupying the position of two morphological somites. In M. rappi I can detect no setæ on the peristomium; the fusion is here complete.

couple of somites; but in those cases where the gizzard is far forwards there is a greater extent of intestine in which the typhlosole is absent, and in which the walls are not distinctly sacculated or nipped by the septa. This non-typhlosolar region is the "tubular intestine;" and on it, instead of in the œsophagus, are situated the calciferous or other diverticula of the gut in genera with an anteriorly situated gizzard.

The typhlosolar region appears to begin, in the majority of cases, somewhere about Somites XIV to XVI; but we have very scanty material for generalising on this point. Many of the diagrams of the canal are correct only so far as the position of the calciferous glands go. In the majority of cases authors confine themselves to the position of gizzard and glands, and rarely state where the typhlosolar or sacculated region commences.

Only a few cases is this typhlosole absent, e. g. Pontodrilus, Microscolex. It is sometimes a mere thin, compressed fold; or it is cylindrical, and nearly fills the cavity of the intestine. Rhinodrilus is peculiar—at any rate, no record of this has been published—in having its typhlosole, which is a mere fold, attached along a spiral line running round the intestine, instead of hanging down from the dorsal mid-line.

In a few cases—Perichæta, Urobenus, Hormogaster—the hinder part of the "tubular" region is distinctly pouched; not merely nipped by the successive septa, but with thick walls, giving rise to a number of paired pouches, the walls of which are probably more vascular than elsewhere. This thrusts the commencement of the sacculated or typhlosolar region backwards; and the point of union is marked by a pair (rarely more pairs in some sp. Perichæta) of blind cylindrical outgrowths or "intestinal cæca." These lie in Somite XXI in Hormogaster, in Somite XXVI in Perichæta and Urobenus. I may mention once more that some worms, referred to Perichæta, are deprived of these cæca; and I believe this negative character goes hand in hand with a forward position of the gizzard.

A more usual variety of diverticulum of the canal is that found in Lumbricus, and known as "calciferous glands," or "glandes de Morren." Here there are three apparent pouches on each side of the œsophagus, two pairs lying in Somite XI, and one pair in Somite XII. But of these, only the first pair actually communicates with the gut; the other two pairs are not pouches, but thickenings of the œsophageal wall, which is here hollowed out by a number of horizontal, antero-posteriorly directed cavities, which end blindly behind, and open into the first "pouch" in front. The horizontal lamellæ separating the chambers from one another contain blood-sinuses, and are lined by large cells which secrete $CaCO_3$; this escapes from the cells, or more probably the cells themselves break away, and find their way by means of the anterior pouch into the œsophagus.

We have little or no detail as to the "calciferous glands" in other worms; in some cases we do not even know whether they produce lime; but throughout I speak of them as "calciferous glands." They are very frequently absent, and when present are very variable in number and position.

In some cases "salivary glands" are said to be found amongst the muscles of the pharyngeal wall.

II. OUTLINES OF THE CLASSIFICATION.

The class OLIGOCHÆTA may be divided into two sub-classes, according to the presence or absence of asexual reproduction.

Sub-class I. NAIDOMORPHA.

Order 1. Naidina.

Families 1. Aphanoneura.
2. Naididæ.
3. Chætogastridæ.
[And the genus Ctenodrilus.]

Small worms of relatively few somites; blood uncoloured; male genital pores in front of Somite VII, or in this somite.

Asexual as well as sexual reproduction occurs. The anterior few somites of the body are frequently different from the following somites, e.g. in Naids and in Chætogaster the setæ have a different arrangement or form in the anterior somites ("cephalization" of Lankester); or the prostomium is pigmented and ciliated, as in Æolosoma and Ctenodrilus. Eye-spots are frequently present.

Sub-class II. LUMBRICOMORPHA.

Reproduction only by sexual process; no "cephalization;"[1] somites behind the peristomium all similar; and setæ are similar throughout the body, except in special regions, e.g. on clitellum.

Male genital pores behind Somite VII.

No eye-spots (? Helodrilus, Hoffmeister).

The various families included in this sub-class cannot really be separated by any very marked anatomical characters; but they may be divided roughly into—

Order 1. Microdrili (Lumbricomorpha minora);
2. Megadrili (Lumbricomorpha majora);

which correspond to "water-worms" and "earthworms" respectively. The only constant difference between these two groups is the absence in Order 1 of a capillary network of blood-vessels on the nephridium, and the presence of such blood-vessels on the nephridium in Order 2; and this is very likely due to the difference in size, and to the character of the medium in which the members of the two groups live.

Other characters which are usual to Order 1, and rarely present in Order 2, are as follows:

Small size, and thin, transparent body-wall.

Prostomium not separated from the peristomium by a groove.

Setæ always in four groups per somite, and usually more than two in each group: frequently the setæ are of two sorts

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[1] In a paper on a new species of Diachæta, a proof of which Professor Lankester has very kindly allowed me to see, Mr. Beddard states that no setæ are present on the first five somites.

in each somite, and may be capillary, uncinate, forked, or simple. The clitellum is always developed round the male pores, and generally occupies only two somites. There are no nephridia in the genital somites. There is no true gizzard, no typhlosole, no subneural vessel. [These last four negative characters, however, hold for some "earthworms."]

The characters nearly constant in Order 2, in which "earthworms" differ from water-worms, are—

Large size, varying from two inches (or less) to six feet; thick, pigmented, and opaque body-wall, though the pigment may be absent and the wall more or less transparent on the ventral surface.

Prostomium separated by a groove from the peristomium.

Setæ frequently not arranged in groups; when they are so arranged there are never more than two setæ in a group (? Echinodrilus, Vaillant). These setæ are nearly always simple, or the modification when present takes a different direction from that in Order 1.

The clitellum varies in position with regard to the male pores, and always occupies more than two somites (? certain species of Perichæta).

A gizzard is nearly always present, except in such cases as Criodrilus, Pontodrilus, Microscolex, and Photodrilus, where the character of the food renders it useless.[1]

With the exception of a few genera, nephridia occur in all somites after the third or fourth, including the genital somites.

Order 1 includes Vejdovsky's "families" Discodrilidæ, Enchytræidæ, Tubificidæ, Phreoryctidæ, and Lumbriculidæ.

Order 2 contains the remainder of his families, and these I will now proceed to group as follows:

Branch I. Plectonephrica.[2]

Excretory system in the form of numerous delicate tubules

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[1] In Pontodrilus there is a modification of the gut-wall which probably represents the gizzard.

[2] Πλεκτη = a net.

in each somite, uniting to form a network, with more or less numerous external apertures: a large "nephridium," with cœlomic funnel, may be present in addition to these tubules.

a. Setæ, eight per somite (rarely twelve), either in couples or separate.

1. Spermiducal pores on Somite XVII or XVIII; one pair of prostates in the same somite.

Family I. TYPHÆIDÆ.

Genera:—

1. Typhæus.
2. Megascolides.
3. Cryptodrilus.
4. Didymogaster.
5. Perissogaster.
6. Dichogaster.
7. Digaster.

2. Spermiducal pores on Somite XVIII; two pairs of prostates in Somites XVII and XIX.

Family II. ACANTHODRILIDÆ.

Genera:—

8. Acanthodrilus.
9. Trigaster.
10. Deinodrilus.

b. Setæ more than twelve, usually twenty to eighty per somite; arranged in a continuous or discontinuous circle.

Family III. PERICHÆTIDÆ.

Genus 11. Perichæta (including Megascolex).

Branch II. Meganephrica.[1]

Excretory network absent; replaced by a pair (rarely two pairs) of large nephridia in each somite.

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[1] Μεγας = large.

A. Prostates present.

a. Spermiducal pores intersegmental, and placed far forwards; sperm-duct traversing only one somite; clitellum on Somites X to XIII.

Family IV. MONILIGASTRIDÆ.

Genus 12. Moniligaster.

b. Spermiducal pores on Somite XVII or XVIII; clitellum occupying all or any of the Somites XIII to XVIII.

1. Eight setæ per somite, in couples or separate.

Family V. EUDRILIDÆ.

Genera :—
13. Eudrilus.
14. Teleudrilus.
15. Pontodrilus.
16. Photodrilus.
17. Microscolex.
18. Rhododrilus.
19. Plutellus.

2. More than eight setæ, usually thirty or more, per somite, arranged in a ring.

Family VI. PERIONYCIDÆ.

Genus 20. Perionyx.

B. No prostates present.

1. Spermiducal pores behind Somite XVIII, within the area covered by the clitellum.

a. One pair of sperm-sacs occupying several somites; eight setæ, separate or alternate in some part at least of the body.

Family VII. GEOSCOLECIDÆ.

Genera :—
21. Geoscolex.
22. Urochæta.
23. Diachæta.

b. Two or more pairs of sperm-sacs; setæ in couples, and exhibiting no tendency to alternate.

Family VIII. RHINODRILIDÆ.

Genera :—

24. Rhinodrilus.
25. Microchæta.
26. Urobenus.
27. Hormogaster.
28. Brachydrilus.

2. Spermiducal pores in front of Somite XVIII, anterior to the clitellum.

Family IX. LUMBRICIDÆ.

Genera :—

29. Lumbricus.
30. Allolobophora.
31. Criodrilus.
32. Allurus.

III. CHARACTERS OF THE FAMILIES AND GENERA IN EXTENSO.

Branch I. PLECTONEPHRICA.

The excretory system is in the form of a number of delicate tubules in each somite, more or less united to form a network, and having numerous external apertures in each somite. Added to this, there may be a pair of larger "nephridia," each possessing one external aperture and a funnel communicating with the cœlom.

a. The setæ are never more than eight (with the exception of one genus) per somite; and these may be arranged in couples, or are more or less separated from one another.

1. Spermiducal pores in Somite XVII or XVIII; only one pair of "prostates," which lies in the same somite as these pores.

Family I. TYPHÆIDÆ, mihi (= part Eudrilidæ, Rosa).

The clitellum, which is more feebly developed on the ventral than on the dorsal surface, begins on Somite XIII or

XIV, and includes from five to ten of the following somites. "Copulatory" papillæ are usually present in the neighbourhood of the spermiducal pores. The "prostates" are tubular and convoluted, or are lobed structures.

Genus 1. TYPHÆUS, Beddard, 1883.

Setæ in couples, all on the ventral surface.

Clitellum occupies Somites XIV to XVII.

The male pores are on Somite XVII, in line with the inner couple of setæ; sacs with penial setæ present. The "prostates" are convoluted tubes.

Sperm-sacs.—A single pair in Somite X, which may occupy more than one somite.

One pair of testes and ciliated rosettes in Somite X, enclosed in a median portion of the sperm-sac.

[Prostomium[1] nearly as broad as the peristomium, and not dovetailed into it.

A single pair of spermathecæ in Somite VIII; the aperture is placed in the anterior part of this somite.

Dorsal pores present.

A single pair of calciferous glands in Somite XII. The gizzard occupies Somites VI, VII; peculiar intestinal glands farther back.]

Species 1. T. orientalis, F. E. B., 1884; India.
2. T. gammii, F. E. B., 1888; India.

See Beddard, 'Ann. Mag. Nat. Hist.,' 5th ser., vol. xii, 1883; and 'Quart. Journ. Micr. Sci.,' vol. xxix, 1888.

Genus 2. MEGASCOLIDES, McCoy, 1878 (= Notoscolex, Fletcher, 1886).

Setæ in couples, all on the ventral surface.

Clitellum occupies Somites XIII to XXI (or XXIII), and though feebly developed, extends across the ventral surface.

The male pores are on Somite XVIII, on slight papillæ. No penial setæ.

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[1] The characters placed in square brackets are less easily observed, or are more subject to specific variation.

Sperm-sacs.—Four pairs in Somites XI, XII, XIII, XIV (in one species a less number has been described).

Prostates tubular, and very greatly coiled.

[Prostomium broad, not dovetailed into peristomium. Dorsal pores are present.

Testes and ciliated rosettes in Somites X, XI, free; the two sperm-ducts on each side are separate throughout their course, only uniting at their junction with the prostate.

Spermathecæ, with appendices, two pairs in Somites VIII and IX (or four pairs).

The nephridia are in form of network anteriorly, continuous from somite to somite, one tubule of which gradually enlarges till posteriorly there is a pair of large nephridia, together with a network of small tubules in each somite.

Gizzard in Somite V or VI; no œsophageal glands; no typhlosole.

Intestine dilated in Somites XII to XVIII.

Numerous intra-buccal pepto-nephridia are present.

The septa of anterior segments greatly thickened.]

Species 1. M. australis, McCoy, 1878; Australia.
2. M. camdenensis, Fletcher, 1886; Australia.
3. M. grandis, Fletcher, 1886; Australia.
4. M. tasmanicus, Fletcher, 1887; Australia.
5. M. tuberculatus, Fletcher, 1887; Australia.
6. M. mawarræ, Fletcher, 1887; Australia.
7. M. pygmæus, Fletcher, 1888; Australia (? genus).
8. M. illawarræ, Fletcher, 1888; Australia.

See Baldwin Spencer, 'Trans. Roy. Soc. Victoria,' vol. i, 1888; and Fletcher, 'Proc. Linn. Soc. N.S.W.,' vols. i and iii.

Genus 3. CRYPTODRILUS, Fletcher, 1886.

Setæ separate.

Clitellum on Somites XIII to XVII (or less), complete ventrally.

Male pores on Somite XVIII, not on papillæ; no penial setæ.

Prostates lobate, and sometimes extending beyond their proper somite.

Sperm-sacs.—Two pairs in Somites IX and XII.

[Prostomium small; dorsal pores present.

Testes and ciliated rosettes in Somites X and XI, free.

Spermathecæ with appendices, usually two pairs in Somites VIII and IX (rarely more).

Gizzard in Somite V or VII.

"Salivary glands" are present, but do not appear to open into the pharynx.

Intestinal calciferous glands occur in Somites IX or X to XIII.]

Species 1. C. rusticus, Fletcher, 1886; Australia.
2. C. saccarius, Fletcher, 1886; Australia.
3. C. fletcheri, F. E. B., 1887; Australia.
4. C. rubens, Fletcher, 1887; Australia.
5. C. mediterreus, Fletcher, 1887; Australia.
6. C. fastigatus, Fletcher, 1888; Australia.
7. C. unicus, Fletcher, 1888; Australia.
8. C. singularis, Fletcher, 1888; Australia.
9. C. canaliculatus, Fletcher, 1888; Australia.
10. C. manifestus, Fletcher, 1888; Australia.
11. C. mediocris, Fletcher, 1888; Australia.
12. C. tenuis, Fletcher, 1888; Australia.
13. C. illawarræ, Fletcher, 1888; Australia.
14. C. mudgeanus, Fletcher, 1888; Australia.
15. C. sloanei, Fletcher, 1888; Australia.
16. C. oxleyensis, Fletcher, 1888; Australia.
17. C. purpureus, Michaelsen, 1889; Australia.

See Fletcher, 'Proc. Linn. Soc., N.S.W.,' vols. i, ii, iv; Beddard, 'Proc. Zool. Soc.,' 1887; Michaelsen, 'Jahrb. d. hamburgischen wiss. Anstalten,' vi, 1889.

Genus 4. DIDYMOGASTER, Fletcher, 1886.

Setæ separate, nearly equidistant.

Clitellum feebly developed; occupies Somites XIV to XVIII.

Male pores on Somite XVIII, on papillæ.

Prostates flattened, equally bilobed.

Sperm-sacs.—Two pairs in Somites IX, XII.

[Prostomium small; dorsal pores present.

Spermathecæ, three pairs, greatly elongated, in Somites VII, VIII, IX; their apertures in IX, X, XI; not intersegmental in position.

Two gizzards in Somites VI, VII.

No accessory intestinal diverticula.

The intestine is dilated and very vascular in Somites X to XVI; the following region of the intestine is stated to be coiled like a corkscrew.

Anterior septa greatly thickened.

Dorsal vessel doubled in each somite.]

Species 1. D. sylvaticus, Fletcher; Australia.

See Fletcher, 'Proc. Linn. Soc. N.S.W.,' 2nd ser., vol. i, 1886.

Genus 5. PERISSOGASTER, Fletcher, 1887.

Setæ not in couples, but all close together on the ventral surface.

Clitellum on Somites (XIII) XIV to XVIII, complete ventrally except on last somite.

Male pores slit-like in Somite XVIII (?); penial setæ present.

Prostates unequally bilobed.

Sperm-sacs.—Two or four pairs in Somites IX, X, XI, XII. Testes and ciliated rosettes free, in Somites X, XI.

Three gizzards in Somites V, VI, VII.

[Prostomium wide; no dorsal pores.

Spermathecæ with appendices, two pairs, in Somites VIII; IX; apertures anterior, intersegmental.

Intestine with (?) calciferous glands in Somites IX to XIV; salivary glands present around pharynx.]

Species 1. P. excavatus, Fletcher, 1887; Australia.
2. P. nemoralis, Fletcher, 1888; Australia.
3. P. queenslandica, Fletcher, 1888; Australia.

See Fletcher, 'Proc. Linn. Soc. N.S.W.,' 2nd ser., vols. ii, iii.

Genus 6. DICHOGASTER, Beddard, 1888.

Setæ in couples; ventral setæ absent in Somites XVII, XVIII, XIX.

Clitellum on Somites XIII to XX; more feebly developed ventrally.

Spermiducal pores on Somite XVII; no penial setæ.

Two pairs of prostate-pores on Somites XVIII, XIX.

Sperm-sacs.—Three pairs in Somites X, XI, XII, connected across the middle line both above and below the intestine. Testes and ciliated rosettes in Somites X and XI, enclosed in sperm-sacs.

Prostates tubular, slightly coiled, in Somite XVII.

Additional club-shaped prostates, two pairs in Somites XVIII and XIX, without connection with sperm-ducts.

Two gizzards, each occupying two Somites, VII, VIII, and IX, X.

[Dorsal pores are present. Only one pair of spermathecæ in Somite VIII; aperture near ventral mid-line.

Calciferous glands in XV, XVI, XVII.]

Species 1. D. damonis, F. E. B., 1888; Fiji.

See Beddard, 'Quart. Journ. Micr. Sci.,' xxix.

Genus 7. DIGASTER, E. P., 1872.

The setæ in four couples.

The clitellum on Somites XIV to XVII, complete ventrally, though not so well marked as on the dorsal surface.

The male pores on Somite XVIII (XVII, Perrier).

Penial setæ present.

Sperm-sacs in Somites IX, XII (or X, XI, Perrier).

Prostates lobulated.

Two gizzards in Somites V and VII.

In Somites V and VII nephridia in groups, forming "peptonephridia," the duct of which opens into the pharynx.

Nephridia tufted; though apparently, according to Fletcher, large ones are present in addition.

Dorsal pores are present.

Species 1. D. lumbricoides, E. P., 1872; New South Wales.
2. D. armifera, Fletcher, 1886; New South Wales.
3. D. perrieri, Fletcher, 1888; New South Wales.

See Perrier, 'Nouv. Arch. du Mus. d'Hist. Nat. Paris,' viii, 1872; Fletcher, 'Proc. Linn. Soc. N.S.W.,' 2nd ser., i and iii.

Remarks on the Typhæidæ.

The beautiful monograph on Megascolides australis by Professor Baldwin Spencer gives the details of the anatomy generally found in this group. Many of the genera are very closely allied, no doubt. Fletcher's descriptions of the various species are only verbal, and unaccompanied, except in his first paper, by any figures. For instance, the description given by him of Perissogaster and of Didymogaster rather lead me to think that the two genera should be included in one genus. In the former the prostates are said to be unequally lobed, i.e. the posterior lobe occupies two somites; in the latter the two lobes are equal. In Perissogaster, however, no dorsal pores are present; in Didymogaster they are present. In Didymogaster the spermathecal apertures are not intersegmental as is the case in Perissogaster and other germs. This seems to be the only point of real difference; for, as I have remarked, the number of gizzards cannot of itself furnish a generic character. Dichogaster differs from any other genera in possessing three pairs of prostates; the first pair being in connection with the sperm-ducts, the two hinder pairs being independent of them. Typhæus, again, is a well-marked genus, in possessing a single pair of sperm-sacs and testes.

In some species of Cryptodrilus, Fletcher and Beddard describe large nephridia in all somites, and nephridiopores which have an alternate or irregular arrangement with regard to setæ. It is very probable that a network will be found, in all cases, in addition to these large nephridia.

In one species, Cr. purpureus, there are five median spermathecæ, instead of two pairs usual to the genus.

2. Spermiducal pores on Somite XVIII; two pairs of tubular, more or less convoluted prostates, in Somites XVII and XIX, and opening to the exterior on these somites.

Family II. Acanthodrilidæ, Rosa (=partly L. postclitelliens, E. P. = partly Acanthodrilidæ, Claus, Vejdovsky).

Setæ, eight or twelve per somite, in couples or separate.

Clitellum occupies XIII or XIV to XIX, or fewer somites, or extends to Somite XL; either complete ventrally throughout or only anteriorly.

Spermiducal pores, one pair on Somite XVIII, in line with the inner setæ.

Prostate-pores on Somites XVII and XIX, in same line as spermiducal pores.

Genus 8. ACANTHODRILUS, E. P., 1872 (= Mandane, Kinberg, 1866).

Setæ eight, in couples or separate.

Clitellum usually occupies Somites XIII to XIX; sometimes one additional somite at each end, sometimes fewer; usually complete in anterior somites, but leaving a non-glandular ventral area on Somites XVII, XVIII.

Sperm-sacs.—Two pairs in Somites XI, XII.

Prostates usually accompanied by sacs containing special "penial" setæ.

[Prostomium more or less dovetailed into the peristomium. Dorsal pores are present.

Testes and ciliated rosettes in Somites X and XI.

Spermathecæ with appendices, and sometimes accompanied by sacs containing "anterior penial" setæ; apertures in a line with the inner couple of setæ.

Gizzard usually single, occupying two somites; rarely two separate gizzards in VI and VIII.

Pepto-nephridia are frequently present in the anterior somites. Calciferous glands present.

Dorsal vessel sometimes double.

Some species have been described as possessing large nephridia without a network of small tubules (see above).]

Species 1. A. obtusus, E. P., 1872; New Caledonia.
2. A. ungulatus, E. P., 1872; New Caledonia.
3. A. verticillatus, E. P., 1872; Madagascar.
4. A. kerguelenensis, E. R. L., 1879; Kerguelen.
5. A. capensis, F. E. B., 1884; Cape of Good Hope.
6. A. buttikoferi, Horst, 1884; Liberia.
7. A. schlegelii, Horst, 1884; Liberia.
8. A. layardi, F. E. B., 1886; New Caledonia. (Horst believes this species to be identical with A. ungulatus.)
9. A. novæ-zelandiæ, F. E. B., 1885; New Zealand.
10. A. multiporus, F. E. B., 1885; New Zealand.
11. A. dissimilis, F. E. B., 1885; New Zealand.
12. A. neglectus, F. E. B., 1887; New Zealand (? = dissimilis).
13. A. annectens, F. E. B., 1888; New Zealand.
14. A. beddardi, Horst, 1888; Liberia.
15. A. australis, Michaelsen, 1889; Australia.
16. A. georgianus, Michaelsen, 1889; South Georgia.
17. A. littoralis, Kinberg, 1866; Magellan.
18. A. scioanus, Rosa, 1888; Africa.
19. A. bovei, Rosa, 1889; Magellan.
20. A. antarcticus, F. E. B., 1889; New Zealand.
21. A. rosæ, F. E. B., 1889; New Zealand.
22. A. dalei, F. E. B., 1890; Falkland Isles.

For descriptions of this genus and its species see Perrier, 'Nouv. Arch. du Mus. d'Hist. Nat. de Paris,' viii, 1872; Beddard, 'Proc. Zool. Soc.,' 1885—1887; 'Quart. Journ. Micr. Sci.,' xxviii, xxix, and xxx; Horst, 'Notes from Leyden Museum,' ix, x; Michaelsen, 'Jahrb. d. hamburgischen wiss. Anstalten,' vi, 1889; Rosa, 'Ann. d. Mus. Civico d. Stor. Nat. di Genova,' ser. 2, vi, 1888, and vii, 1889.

Genus 9. TRIGASTER, Benham, 1886 (= Benhamia, Michaelsen, 1889).

Setæ in four couples, all on the ventral surface; individual setæ of each couple close together.

Clitellum occupies Somites XIV to XL; complete ventrally only on the first few somites.

Spermiducal pores in XVIII, and prostate-pores in XVII and XIX, in a large pit or fossa occupying the middle of the ventral surface of Somites XVII to XX, the margins of which are formed by two papillæ.

Sperm-sacs not observed.

Prostates as in Acanthodrilus. No penial setæ.

[Prostomium not dovetailed into peristomium. No dorsal pores are present.

Spermathecæ simple pear-shaped sacs without appendices, opening close to mid-line on ventral surface.

Three gizzards in Somites VII, VIII, and IX. No calciferous glands. Anterior masses of nephridial tubules in Somites IV, V, VI, grouped to form "pepto-nephridia."]

Species 1. T. lankesteri, W. B. B., 1886; St. Thomas, West Indies.

2. T. rosea, Michaelsen, 1889; West Africa.

See Benham, 'Quart. Journ. Micr. Sci.,' xxvii; Michaelsen, 'Jahrb. d. hamburgischen wiss. Anstalten,' vi, 1889.

Genus 10. DEINODRILUS, Beddard, 1888.

Setæ twelve per somite, nearly equidistant.

Clitellum complete ventrally; occupies only Somites XIV to XVI.

Spermiducal pores, prostate-pores, sperm-sacs, &c., as in Acanthodrilus.

[Prostomium dovetailed into peristomium.

Spermathecæ with three small globular appendices, two pairs in Somites VIII and IX.

A single gizzard occupies Somites VI, VII. No calciferous glands.

The dorsal vessel is double throughout its length, and is enclosed in a special cœlomic tube.]

Species 1. D. benhami, F. E. B.; New Zealand. See Beddard, 'Quart. Journ. Micr. Sci.,' xxix.

Doubtful Genus.

Neodrilus monocystis, F. E. B., New Zealand.

Founded on a single specimen, and differs from Acanthodrilus in possessing a single pair of prostates and a single pair of spermathecæ. It appears to me very doubtful whether this should be considered as a new genus, or whether the characters are merely some peculiar variations of Acanthodrilus.

Remarks on the Acanthodrilidæ.

The genus was originally characterised by the presence of two pairs of male pores; it is only recently that Beddard has shown that these pores belong to the prostates, and that the sperm-ducts open by a pair of pores on the eighteenth somite. The chief points of difference between Acanthodrilus and Trigaster lie in the fact that the male pores and atriopores in the latter genus are in a pit (in my original description I placed the atriopores in XVI, XVIII; I believe that this statement is wrong, and that the prostate-pores and spermiducal pores are placed as in Acanthodrilus), and in the absence of penial or copulatory setæ and the presence of three gizzards. When the genus was formed, the only worm with more than one gizzard (except Moniligaster) was Digaster. That the existence of three gizzards is not generic is now established by the formation of Michaelsen of a species, T. rosea, with only two gizzards.

Three species of Acanthodrilus are known with two gizzards—A. buttikoferi and A. beddardi of Horst; and A. scioanus, Rosa.

Horst also figures the prostate-pores in A. schlegelii as situated in a fossa.

But the great extent of the clitellum in Trigaster, together with the position of the spermathecal pores close to the ventral mid-line, and the general appearance of the worm, warrant the retention of the genus. I may mention here that frequently a mere description of the position of pores and organs, unaccompanied by figures, might lead to the association of two worms, an examination of which would leave a very different impression as to their relation.

The genus Deinodrilus is sufficiently interesting and peculiar in the possession of twelve setæ per somite; but this interest is greatly enhanced on comparison of the internal organs with those of Acanthodrilus on the one hand and of Perichæta on the other.

Some species of Acanthodrilus have large nephridia, the power of which alternate in position; but no statement is made as to whether these nephridia are accompanied by a network: I believe we may expect this to be the case. Many species have the dorsal vessel double to a greater or less extent.

b. **Setæ more than twelve (usually many more) in most of the somites, arranged in a ring, which is continuous all round, or interrupted dorsally and ventrally.**

Family III. Perichætidæ, Claus (= partly L. postclitelliens, E. P. = Perichætidæ + Pleurochætidæ, Vejdovsky).

Clitellum completely surrounding the body, obliterating entirely the intersegmental grooves, and extending over all or some of the Somites XIII—XVII.

Spermiducal apertures on Somite XVIII, on the ventral surface.

Oviducal apertures close together on Somite XIV.

Genus 11. PERICHÆTA, Schmarda, 1861 (includes Megascolex, Templeton, 1844; Pleurochæta, Beddard, 1883; and many of Kinberg's genera).

Setæ from twenty to eighty, or even 100 per somite, on a ridge (at least in spirit specimens), either in a continuous ring or interrupted by a greater or less gap in the dorsal or ventral mid-line, or both. Setæ usually small and of equal size, and generally equidistant, though in some species more or fewer of the more ventral ones are larger than the rest. On the clitellum the setæ are invisible.

Clitellum on Somites XIV to XVI or XVII, rarely only two or more than four; well defined, and altogether obliterating the intersegmental grooves.

Spermiducal pores in Somite XVIII, usually rather laterally placed.

Oviducal pores in Somite XIV very close together, or more usually single and median.

Penial setæ and various "copulatory papillæ" are frequently present.

Sperm-sacs, in Somites XI and XII, two pairs, rarely more, and sometimes connected by median sacs enclosing testes.

Prostates.—A pair in Somite XVIII, lobed or greatly subdivided, or even digitate; the duct after being joined by the sperm-duct is very muscular and probably protrusible; it may be called a "penial duct."

[Worm cylindrical; prostomium sometimes dovetailed into peristomium, sometimes not dovetailed.

Dorsal pores present.

Testes and ciliated rosettes in Somites X and XI, sometimes, at any rate, enclosed in the median portion of the sperm-sac.

Ovaries in Somite XIII.

Spermathecæ, usually only two pairs, in Somites VIII and IX, opening anteriorly; sometimes only one pair; sometimes more than two pairs. Usually with an appendix which varies in shape.

Gizzard occupies any position between Somites V and X.: usually occupying three Somites, VIII, IX, and X.

In most species a pair of tubular cæca in Somite XXVI are present.]

Species 1. P. houlleti, E. P., 1872; Calcutta (and Nice); Bahamas (F. E. B.); Manila (F. E. B.).

2. P. posthuma, Vaillant, 1869 = P. affinis, E. P., 1872; Cochin China; Java (Horst); Philippines (F. E. B.).

Species 3. P. robusta, E. P., 1872 = partly P. cingulata, Sch. and Vaillant; Mauritius, Manila, Nice, Bahamas.
4. P. aspergillum, E. P. 1872 (loc. ?); Bermuda (F. E. B.).
5. P. quadragenaria, E. P. 1872 = partly P. cingulata, Sch. and Vaillant; East Indies.
6. P. elongata, E. P., 1872; Peru (? indigenous).
7. P. indica, Horst, 1883; Sumatra; New Caledonia (F. E. B.).
8. P. sumatrana, Horst, 1883; Sumatra.
9. P. hasseltii, Horst, 1883; Sumatra.
10. P. sieboldii, Horst, 1883; Japan.
11. P. japonica, Horst, 1883; Japan.
12. P. musica, Horst, 1883; Java.
13. P. capensis, Horst, 1883; Cape of Good Hope.
14. P. annulata, Horst, 1883; Malay.
15. P. cœrulea, Templeton, 1844; Ceylon.
16. P. ceylonica, F. E. Beddard, 1885; Ceylon.
17. P. armata, F. E. Beddard, 1883; Calcutta; Burmah (Rosa); Nias, near Sumatra (Rosa).
18. P. horsti, F. E. Beddard, 1886; Manila.
19. P. newcombei, F. E. Beddard, 1887; Australia.
20. P. upoluensis, F. E. Beddard, 1887; Upolu, Pacific Isles.
21. P. lawsoni, A. G. Bourne, 1886; India.
22. P. bivaginata, A. G. Bourne, 1886; India.
23. P. gracilis, A. G. Bourne, 1886; India.
24. P. stuarti, A. G. Bourne, 1886; India.
25. P. burliarensis, A. G. Bourne, 1886; India.
26. P. hulikalensis, A. G. Bourne, 1886; India.
27. P. mirabilis, A. G. Bourne, 1886; India.
28. P. salettensis, A. G. Bourne, 1886; India.
29. P. australis, Fletcher, 1886; Australia.
30. P. coxii, Fletcher, 1886; Australia.
31. P. tenax, Fletcher, 1886; Australia.

Species 32. P. austrina, Fletcher, 1886; Australia.
33. P. barronensis, Fletcher, 1886; Australia.
34. P. darnleiensis, Fletcher, 1886; Australia.
35. P. gracilis, Fletcher, 1886; Australia.
36. P. peregrina, Fletcher, 1886; Australia.
37. P. queenslandica, Fletcher, 1886; Australia.
38. P. bakeri, Fletcher, 1887; Australia.
39. P. dorsalis, Fletcher, 1887; Australia.
40. P. canaliculata, Fletcher, 1887; Australia.
41. P. exigua, Fletcher, 1887; Australia.
42. P. fecunda, Fletcher, 1887; Australia.
43. P. hamiltoni, Fletcher, 1887; Australia.
44. P. monticolla, Fletcher, 1887; Australia.
45. P. raymondi, Fletcher, 1887; Australia.
46. P. stirlingi, Fletcher, 1887; Australia.
47. P. wilsoniana, Fletcher, 1887; Australia.
48. P. birmanica, Rosa, 1888; Burmah.
49. P. feæ, Rosa, 1888; Burmah.
50. P. modigliani, Rosa, 1887; Nias (Sumatra).
51. P. antarctica, Baird 1873; New Zealand.
52. P. intermedia, Beddard, 1889; New Zealand.
53. P. attenuata, Fletcher, 1888; Australia.
54. P. enormis, Fletcher, 1888; Australia.
55. P. dissimilis, Fletcher, 1888; Australia.
56. P. macleayi, Fletcher, 1888; Australia.

Doubtful Species.—Some of Perrier's, viz. P. bicincta, P. luzonica, P. cœrulea, P. biserialis, P. juliana. Schmarda's P. leucocycla, P. viridis, P. brachycycla, P. cingulata. Kinberg's genera, Amyntas, Nitocris, Pheretima, Rhodopis, Lampito.

See Perrier, 'Nouvelles Arch. du Mus. d'Hist. Nat. de Paris,' viii, 1872. Beddard, 'Ann. Mag. Nat. Hist.,' 5th ser., vol. xvii, 1886; 'Proc. Zool. Soc.,' 1886; 'Proc. Roy. Soc. Edin.,' xiv, 1887. Rosa, 'Ann. d. Mus. Civico d. Storia Nat. di Genova,' 2nd ser., vi, 1888, vol. vii, 1889; Fletcher, 'Proc. Linn. Soc. N.S.W.,' 2nd ser., vols. i, ii, iii; A. G. Bourne, 'Proc. Zool. Soc.,' 1886.

Remarks on the Perichætidæ.

Although some fifty species of this genus have been formed within the last few years (besides those which have been characterised only by their external anatomy, and which must be in many cases discarded), yet very frequently insufficient data have been given. On the whole it is a well-defined family, but the single genus may really be capable of subdivision.

I have already mentioned my reason for removing Perionyx from the family, a proceeding which may at first appear arbitrary.

The character of the prostomium and the presence or absence of the characteristic intestinal cæca, as well as the position of the gizzard, may prove to be of generic value. The observations on the excretory system are in most cases very superficial and incomplete, and frequently no mention is made as to whether in a particular species large "nephridia" or a small network of tubules is present. Where these observations have been carefully made the presence of a pair of large nephridia[1] appears to be associated with the absence of the intestinal cæca, a forward position of the gizzard in Somite v or vi, and with the existence of three pairs of spermathecæ. But there are too many apparent exceptions to generative on this point at present.

Amongst the more peculiar species may be mentioned P. indica, Horst, where some of the more ventral setæ are larger than the rest; P. hasseltii, Horst, in which the ventral setæ are more closely placed; P. stuarti, Bourne, with two pairs of male pores and two pairs of prostates. P. bakeri and P. intermedia have prostates resembling those of Acanthodrilus.

The number of setæ per somite, position of copulatory papillæ, extent of clitellum, number of spermathecæ and shape of appendix, and of the prostates, serve as the leading characters in which the species differ from one another.

The worms figured by Schmarda are only described so far

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[1] Probably accompanied by a network.

as their external anatomy is concerned, and cannot be recognised with certainty. Kinberg's genera must be relegated to oblivion.

Branch II. MEGANEPHRICA.

The excretory system is in the form of large, greatly coiled tubes unaccompanied by a network of small tubules. Each nephridium opening into the cœlom by a funnel: usually a pair in each somite, though the most anterior somites may be deprived of nephridia.

A. A prostate is present.

a. **Male pores intersegmental, immediately behind Somite X or XI; clitellum developed around this and the adjacent somites.**

Family IV. Moniligastridæ, Claus, Vejdovsky Rosa (= L. aclitelliens, E. P.).

Genus 12. MONILIGASTER, E. P., 1872.

Setæ in four couples.

Clitellum observed in only one species (M. sapphirinaoides, A. G. B.), where it occupies Somites X to XIII; it is ill-marked.

Male pores between Somites X/XI; or XI/XII.

Oviducal pore on Somite XII (or XIV).

Sperm-sacs, one pair occupying Somite XI (Horst), or IX and X (Beddard).

Ovisac in Somites XIV to XVI, or fewer somites.

Nephridiopores in a line with the outer couple of setæ.

Prostates small, or large and tubular.

Testes in Somite IX (Beddard).

Spermathecæ in Somite VIII or IX.

The nephridium has a long cæcal prolongation of the duct beyond the point at which the short slightly coiled tubule enters. There is apparently no modification of the anterior nephridia.

Gizzard moniliform, four-lobed, in all or some of the Somites XIII to XXII (sometimes there is an additional gizzard anteriorly).

Species 1. M. deshayesii, E. P., 1872; Ceylon.
2. M. barwelli, F. E. B., 1886; Manila.
3. M. houteni, Horst, 1887; Sumatra.
4. M. grandis, A. G. B., 1886; India.
5. M. uniquus, A. G. B., 1886; India.
6. M. sapphirinaoides, A. G. B., 1886; India.
7. M. robustus, A. G. B., 1886; India.
8. M. papillatus, A. G. B., 1886; India.
9. M. rubens, A. G. B., 1886; India.
10. M. minutus, A. G. B., 1886; India.

See Perrier, 'Nouv. Arch. du Mus. d'Hist. Nat. de Paris,' viii, 1872; Beddard, 'Ann. Mag. Nat. Hist.,' 1886; 'Zool. Anzieger,' 1887, No. 268, and 1889; 'Quart. Journ. Micr. Sci.,' vol. xxix, 1888; Horst, 'Notes from Leyden Mus.,' ix; Bourne, 'Proc. Zool. Soc.,' 1886.

Remarks on Moniligastridæ.

The three authors who have studied the internal anatomy of the genus Moniligaster differ from one another in their statements as to the position of the male pores and other organs.

Perrier, in his description of M. deshayesii, describes, as is well known, two pairs of male organs; the ducts of the first pair opening between Somites VII and VIII, those of the second pair between Somites X and XI. In connection with each of the first pair of ducts is a double gland (his "prostate"); and similarly there is a gland in connection with the other pair of ducts, which is fairly elongated (his "seminal vesicle").

Beddard's original description in 1886, as well as his more recent figures, shows considerable differences from this arrangement, apart from the question of numbering. He identifies Perrier's first pair of "testes" as spermathecæ; the "prostates" (which are not represented in M. barwelli) he suggests may be accessory sacs, which are so frequently found in connection with spermathecæ, whereas Horst identifies these "prostates" of Perrier as the true spermathecæ.

Horst's figures are much more like those of Perrier than are Beddard's; and were it not that the spermathecæ and sperm-sacs in M. houteni occur one somite behind those of M. deshayesii we might believe that he was dealing with the same species. In fact, we have here another example of the difficulty of accurately counting the somites in earthworms. Beddard has quite recently (October, 1889) altered his previous numbers for M. barwelli, owing to the discovery of a small setigerous somite following the peristomium, so that the male pores of M. barwelli are, as in M. deshayesii, between Somites X and XI. The spermathecal pores, too, which were previously given as between VI and VII, now agree with the pores of Perrier's "anterior sperm-ducts," in being placed between Somites VII and VIII.

The diagram accompanying this paper is taken from Horst's figure of M. houteni, and the position of the various organs differs somewhat from that in the other two species. As will be seen, the sperm-sacs are in Somite XI (and probably also the testes and funnels of the sperm-ducts which open externally between Somites XI and XII). The ovipore is in Somite XIV, and probably the ovary is in Somite XIII, these organs being therefore in the normal position. Here the prostate is a large structure, whilst in M. barwelli it is extremely small.

The spermatheca in Somite IX has a long duct opening anteriorly.

The "ovary" of Perrier's species is not the true gonad, but the "ovisac," or receptaculum ovorum, and recalls the way in which the ova push their way back through several somites in Microdrili. The ovary is unknown. Beddard has figured ('Quart. Journ. Micr. Sci.,' xxix, pl. xi) the oviduct with its funnel and external aperture; but the numbering here given is revised in the 'Zool. Anzeiger,' No. 318, where the external aperture is placed on Somite XII, and the funnel in Somite XI, so that in all probability the gonad is in Somite XI.

Prof. Bourne has given us a few facts about seven new species of the genus, chiefly as regards the position of the gizzard, but says nothing about the genital organs. The most interesting point in this connection, however, is his description of a clitellum in M. sapphirinaoides occupying Somites x—xiii, a structure previously denied to the genus.

The recorded absence of a clitellum is probably due to the fact that, as in the water-worms, this structure is only developed at the breeding season.

The anterior gizzard, which Perrier described, has not been recognised in the later species.

I believe Moniligaster to be more nearly related to the ancestors of earthworms than any other genus we know of, as I have pointed out in Part VI of this paper.

b. **Male pores on Somite xvii or xviii.**
Clitellum occupies all or any of the Somites xiii to xviii.

1. Eight setæ per somite, in couples or separate.

Family V. Eudrilidæ, Claus (=Lumbriciens intraclitelliens, E. P., in part=part of family Eudrilidæ, Vejdovsky, Rosa).

The eight setæ are in couples or separate; the clitellum, complete ventrally, extends over all or some of the Somites xiii to xvii.

The male pores are behind the clitellum, or just within its limits.

The prostate is simply tubular, convoluted, or lobed.

Spermathecæ usually with diverticulum.

Typhlosole absent.

The duct of the nephridium is not produced into a cæcum, nor is there any modification of the anterior nephridia.

Genus 13. Eudrilus, E. P., 1872.

Setæ in four couples.

Clitellum covers Somites (xiii) xiv to xviii.

Male pores large, on Somite xvii (from it the curved chitinous penis sometimes protrudes), in line with inner couple of setæ.

Female pores on Somite XIV, slit-like, large, dorsad of the inner couple of setæ.

Nephridiopores in line with outer setæ (or inner setæ in E. sylvicola, Beddard).

Generative Apparatus.—Three pairs of sperm-sacs in Somites X, XI, XII. Testes and ciliated rosettes in Somites X, XI, enclosed in median sperm-sacs. The two sperm-ducts of each side run separately to the prostate, which is much elongated, and occupies Somite XVII and following somites. This communicates with a "bursa copulatrix" in Somite XVII, into which also open two small glands. The bursa contains a curved chitinous penis.

There appear to be two pairs of ovaries (Beddard) in Somites XIII and XIV, enveloped in membranes which are continuous with the wall of the spermatheca. Into the neck of the latter there also opens an albumen gland. The "ovary" in Somite XIV is also an ovisac.

[The gizzard occupies Somite VI.

In Somites X, XI, there are ventral diverticula of the alimentary tube; in Somite XII, lateral calciferous diverticula.

The nephridium consists of a slightly coiled tubule, the terminal portion of which is only slightly dilated to form a duct.]

Species 1. E. decipiens, E. P., 1872; Antilles.
2. E. lacazii, E. P., 1872; Martinique.
3. E. peregrinus, E. P., 1872; Rio Janeiro, Surinam.
4. E. boyeri, F. E. B., 1886; New Caledonia.
5. E. sylvicola, F. E. B., 1887; British Guiana.

Note.—Horst believes that the first four of these are in reality the same species, and proposes to retain the name of E. decipiens for them.

See Perrier, 'Nouv. Arch. du Mus. d'Hist. Nat. de Paris,' viii, 1872; Beddard, 'Proc. Roy. Soc. Edin.,' xiii, 1885-6; 'Proc. Zool. Soc. Lond.,' 1886-7; 'Journ. Anat. and Phys.,' xxii, 1887; 'Zool. Anzeiger,' 1888, No. 293; 'Encycl. Brit.,' 9th edition, "Worms;" Horst, 'Notes from Leyden Museum,' ix; Beddard, 'Quart. Journ. Micr. Sci.,' xxx.

Genus 14. Teleudrilus, Rosa, 1888.

The eight setæ, in couples, are rather far apart.

The clitellum includes Somites xiv—xvii.

The male pore is median on Somite xix; the pair of oviducal pores between Somites xiv and xv; a median spermathecal pore between Somites xiii and xiv.

Nephridiopores in line with outer setæ.

The testes in Somites x and xi, enclosed in a sac-like continuations of the sperm-sacs, which lie in Somites xi and xii. The ciliated rosettes are in the latter somites.

The two prostates open into a median copulatory sac, communicating with the exterior and receiving another median sac.

The ovary is continuous with the wall of the ovisac, into which the funnel of the oviduct opens. There is a communication between the ovisac and the neck of the spermatheca on each side.

[The gizzard occupies Somites vi and vii (? also v); there is a pair of lobed calciferous diverticula in Somite xiii, and ventral diverticula in ix, x, xi.

Nephridia simple, as in Eudrilus.]

Species 1. T. raggazii, Rosa, 1888; Africa.

See Rosa, 'Ann. d. Mus. Civico del Storia Nat. d. Genova,' Series 2, vi, 1888.

Genus 15. Pontodrilus, E. P., 1881.

The eight setæ are separate.

The clitellum, which is complete, occupies Somites xiii to xvii.

The male pores in Somite xviii.

The prostate is tubular and convoluted.

Sperm-sacs.—Two pairs, in xi and xii. Testes and funnels in ix, x. Ovary and oviduct as usual.

The nephridia do not commence till Somite xv; the pores are in line with the second seta. The "duct" of the nephridium is feebly marked.

There is no gizzard, no typhlosole, no subneural vessel, no dorsal pores.

[Found on the sea-shore.

Two pairs of spermathecæ, which have small appendices in Somites VIII and IX, opening anteriorly.]

Species 1. P. littoralis, Grube, 1855; Villa-Franca.
2. P. marionis, E. P., 1874; Marseilles.

See Perrier, 'Arch. d. Zool. Exp. et Gen.,' ix, 1881.

Genus 16. PHOTODRILUS, Giard, 1887 (=Lumbricus phosphoreus, Dugés).

The eight setæ are separate. No. 1 seta is near the middle line.

Clitellum on Somites XIII to XVII.

The male pores on Somite XVIII. There are "penial" setæ in this somite, and anterior penial setæ in Somites XII and XIII.

Genital organs as in previous genus.

The nephridia commence in Somite XIV; the pores are in a line with the second seta.

There is no gizzard, no typhlosole, no subneural vessel.

[One pair of spermathecæ in Somite IX.

The prostomium does not encroach on the buccal somite. "Septal glands" in Somites v to IX, probably open dorsally.

Four œsophageal swellings in Somites x to XIII.

Small, transparent, rose-coloured worm, clitellum orange; phosphorescent.]

Species 1. P. phosphoreus, Dug., 1837; Europe.

See Giard, 'Comptes Rendus,' 1887; Rosa, 'Boll. Mus. Zool. ed Anat. Comp. Univ. Torino,' iii, 1888.

Genus 17. MICROSCOLEX, Rosa, 1887.

The setæ in four couples; those of outer couple further apart than those of the inner couple.

The clitellum, complete, covers Somites XIII to XVI (XVII).

The male pores are in Somite XVII.

Sperm-sacs, testes, ovaries, as in preceding genus.

The prostates lobate; penial setæ present.

The nephridia commence in Somite IV; nephridiopores in front of the third seta.

There is no gizzard, no typhlosole, no subneural vessel, nor dorsal pores.

[Small, transparent; white clitellum.

One pair of spermathecæ in Somite IX.]

Species 1. M. **modestus**, Rosa; Italy.

See Rosa, 'Boll. Mus. Zool. ed Anat. Comp. Univ. Torino,' ii, 1887, and iii, 1888.

Genus 18. RHODODRILUS, Beddard, 1889.

The setæ separate, in eight series.

The clitellum occupies Somites XIV to XVII.

The prostates are tubular; penial setæ present; the male ducts open independently of the prostates—all in Somite XVII.

The sperm-sacs in Somites XI, XII.

Prostomium incompletely dovetailed into the peristomium.

[Spermathecæ.—Four pairs, in VI, VII, VIII, IX; each with appendix.

A gizzard is present in Somite V.

No calciferous glands.

Nephridiopores in front of third seta.

Dorsal pores are present.]

Species 1. R. **minutus**, F. E. B.; New Zealand.

See Beddard, 'Proc. Zool. Soc.,' 1889.

Genus 19. PLUTELLUS, E. P., 1873.

Setæ eight, equidistant.

The clitellum covers Somites XIV to XVII, complete ventrally.

The male pores on Somite XVIII.

Oviducal pores on Somite X (?).

The nephridial pores in line alternately with setæ two and four except anterior four pairs, which open in front of third seta; nephridia simple, slightly coiled tubule, lying entirely within one somite (?).

The sperm-sacs in Somite XII.

Prostate tubular, convoluted.

[Spermathecæ.—Five pairs, in Somites V to IX; very small, with coiled diverticulum.

Ovary in Somite X (?).

Gizzard in Somite VI; œsophageal glands in Somites X, XI, XII.

The dorsal pores begin behind Somite VI. Lateral hearts in Somites X, XI, XII.]

Species 1. P. heteroporus, E. P.; Pennsylvania.

See Perrier, 'Arch. d. Zool. Exp. et Gen.,' ii, 1873.

Remarks on Eudrilidæ.

I have here united with the peculiar genera Eudrilus and Teleudrilus a number of other genera which are much more normal in the arrangement of their genital organs than are these two; for I think, with Rosa, that Eudrilus need not form a type of a separate family.

It is only lately that we have had a thorough description of the female genital organs of Eudrilus; and though from Perrier's descriptions, and the earlier ones of Beddard, it appeared as if we had to do with a very abnormal type, Beddard's more recent papers on the subject, and Rosa's description of Teleudrilus, remove some of the apparent peculiarities. But they both remain very different from other worms, in that the ovary is not freely dependent in the cœlom, but enclosed in a sac, the walls of which are continuous with those of the oviduct; a similar condition of things is present in Microchæta in regard to the testis. And no doubt both these cases are in reality similar to the enclosure of the testes and rosettes in a common sac in Lumbricus and other forms. Here, however, the portion of cœlom separated by the wall of the sperm-sac is very considerable, whereas in the case of the ovary of Eudrilus and the testis of Microchæta, this separated cœlomic space is smaller, and has appeared more peculiar than it really is. As above mentioned, Eudrilus possesses two pairs of ovaries according to Beddard, the posterior pair serving apparently as ovisacs.

Rosa has already pointed out the close relation between Pontodrilus, Photodrilus, and Microscolex. These three forms serve to show the invalidity of Claparède's characteristics of "Terricolæ." The absence of a gizzard is, no doubt, connected with the character of the food.

Plutellus is altogether a peculiar form; the only description we have of it is that by Perrier. The position of the oviducal pore and of the ovary is so abnormal that a renewed examination is desirable.

2. Setæ more than eight (30—40) per somite.

Family VI. Perionycidæ.

Genus 20. PERIONYX, E. P., 1872.

Setæ thirty to fifty per somite.

Prostomium dovetailed incompletely into peristomium.

Clitellum on Somites XIV—XVII or less, complete ventrally; intersegmental grooves not completely obliterated.

Male pores close together, in a depression on Somite XVIII.

Oviducal pore median, in Somite XIV.

Prostate flattened, rounded; its pore common with the spermiducal pore.

[Genital organs as in Perichæta, but without a median sperm-sac.

Gizzard in Somites VI and VII; no cæca or other diverticula of the canal.

Nephridia large, paired; the duct not provided with a cæcum; apertures irregularly arranged in some species, as in P. saltans.]

Species 1. P. excavatus, E. P., 1872; Cochin China, the Philippines, and Burmah.

2. P. McIntoshii, F. E. B., 1883; Burmah.

3. P. saltans, A. G. B., 1886; India.

See Perrier, 'Nouv. Arch. du Mus. d'Hist. Nat. de Paris, viii, 1872; Beddard, 'Ann. Mag. Nat. Hist.,' 5th Series, vol. xii, 1883; 'Proc. Zool. Soc.,' 1886; Bourne, 'Proc. Zool. Soc.,' 1886; Rosa, 'Ann. d. Mus. Civico d. Storia Nat. d. Genova,' vi, 1888.

Remarks on Perionycidæ.

In external characters Perionyx agrees exceedingly closely with Perichæta. In the former, however, the male pores are close together in a median pit, whereas in most species of Perichæta they are rather wide apart, and on papillæ. Again, the clitellum does not so completely obliterate the segments and the grooves in Perionyx (nor are its limits so distinctly defined) as in Perichæta. The absence of cæca, and of any other diverticula of the alimentary canal, and the presence of large nephridia, are characters said to be found in some species of Perichæta. The median position of the oviducal pore has certainly a striking resemblance to that of Perichæta. It may be possible to transfer those worms with large nephridia, with forward position of the gizzard, without cæca, and with closely approximated male pores, which are at present regarded as species of Perichæta, to the genus Perionyx.

At present only three species have been described: P. excavatus, E. P.; P. McIntoshii, F. E. B.; and P. saltans, A. G. B.—the last two very briefly.

B. There is no hollow prostate in connection with or in the region of the male pore.

1. The male apertures are behind Somite XVIII, within the area occupied by the clitellum.

***a.* Eight setæ, separate or even alternate in some part of the body. There is only one pair of sperm-sacs, which extend through several somites.**

Family VII. Geoscolecidæ, Rosa (=partly L. intraclitelliens, E. P.=partly Eudrilidæ, Claus, Vejdovsky=partly Geoscolecidæ, Rosa).

The eight setæ have a tendency to separate, or even to be arranged alternately in consecutive somites, either throughout the body or only posteriorly.

The clitellum commences behind Somite XIV usually, and extends over nine or more somites, intersegmental grooves not being obliterated.

The sperm-sacs are very long; there is but one pair of testes and rosettes; the genital pores are very small, and may be accompanied by glandular swellings.

A few of the anterior nephridia are larger than the following ones, and may even be collected into a mass forming a peptonephridium.

The typhlosole is a mere dependent fold.

Genus 21. GEOSCOLEX, Leuckart, 1841 (=Titanus, E. P., 1872).

The separation of the setæ occurs posteriorly, but no alternation seems to occur.

Clitellum is incomplete ventrally, and extends over Somites XV to XXIII.

Spermiducal pores are intersegmental between Somites XVIII and XIX, surrounded by an internal thickening of epidermis.

Oviducal pores are on Somite XIV.

Sperm-sacs extend from Somites XII to XX or XXV.

[Testes and ciliated funnels are in Somite XII.

No spermathecæ are known.

Gizzard is in Somite VII; calciferous glands in Somite XIII.

Nephridia commence in Somite IV; the pores are in front of the inner couple of setæ. The nephridium consists of a short, slightly and loosely coiled tubule, opening into a strongly developed duct, which is produced into a blind sac: this cæcum varies in its proportions in different parts of the body. The first nephridium is rather different from the following, as the coil of the tubule is larger and more compact; it serves probably as an extra-buccal pepto-nephridium. Both Leuckart and Perrier were unable to see the nephridiopores in front of the fourteenth somite, but nephridia are present although the pores are difficult to see.]

Species 1. G. maximus, Leuckart, 1841 (=T. brasiliensis, E. P., 1872), Brazil.
2. G. forguesii, E. P., 1881; La Plata.

See Leuckart, 'Zool. Bruchstücke,' Stuttgart, part ii, 1841; Perrier (Titanus), 'Nouv. Arch.,' &c., viii, 1872; and ibid., ix, 1881, foot-note, p. 235; Rosa, 'Boll. d. Mus. Zool. ed Anat. Comp. Univ. Torino,' iii, 1888.

Genus 22. Urochæta, E. P., 1872.

Setæ eight; anteriorly in couples, then they gradually become separate; and finally, alternate in consecutive somites.

Clitellum on Somites xiv to xxii, complete ventrally; intersegmental grooves not obliterated.

Spermiducal pores between Somites xx and xxi (on Somite xx, E. P.; between xix and xx, Rosa).

Nephridiopores in line with the 3rd seta.

Sperm-sacs, one pair, occupying Somites xiii to xv, or even more.

[Prostomium appears to be absent.

Penial setæ on Somites xix, xx, xxi, and xxii.

Testes and ciliated rosettes in Somite xii.

Three pairs of spermathecæ, in Somites vii, viii, ix (Rosa), vi, vii, viii (Beddard, Horst), or viii, ix, x (Perrier).

The nephridia, except the anterior pair, are simple, slightly coiled tubes, without any or only with very feebly developed duct.

The anterior nephridia are massed together to form "pepto-nephridia," the tubules of which open at one end into the cœlom by ciliated funnels, and at the other into a large duct which communicates with the exterior in front of Somite iii.

The gizzard occupies Somite vii; and there are three pairs of flask-shaped calciferous diverticula, in Somites viii, ix, x.

"Pyriform" sacs occur in posterior part of the body, on the ventral surface.]

(N.B.—The enumeration of the somites is given differently by the three authors who have described Urochæta. Rosa has pointed out that there is some reason to believe that Perrier counted a portion of the extended buccal region as the first somite; with the result that his first setigerous somite, instead of being the second, as in all other worms, is the third; hence it becomes necessary to subtract one, in some cases, from Perrier's numbers. Beddard has elucidated the position of the gonads by means of longitudinal sections—the only reliable means of deciding their position; and on this point I have followed him. The position of the external organs, and some of the internal structures, I have been able to decide for myself by an examination of some specimens kindly given to me by Mr. W. Sclater, who obtained them in Demerara.)

Species 1. U. corethrura, Fr. Muller, 1857; Brazil, Java, Martinique, Fernando Noronha, and Australia.

2. U. dubia, Horst; Sumatra.

See Perrier, 'Arch. de Zool. Exp. et Gen.,' iii, 1874; Beddard, 'Proc. Roy. Soc. Edin.,' 1887; 'Quart. Journ. Micr. Sci.,' xxix; Rosa, 'Ann. d. Mus. Civ.,' Genova, viii, 1889.

Genus 23. DIACHÆTA, Benham, 1886.

Setæ 8, separate, alternate from somite to somite throughout the body, except Seta 1, which always retains a linear arrangement.

Clitellum complete; covers Somites XX to XXXIII, intersegmental grooves distinct all round.

Spermiducal pores on Somite XXII; no penial setæ.

Sperm-sacs extend through Somites XII to XXXVIII.[1]

Nephridiopores in front of the outer setæ.

[No prostomium.

Testes (?) and ciliated rosettes in Somite XI.

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[1] In a paper by Beddard (a proof of which Prof. Lankester has kindly allowed me to see) on a new species of this genus, two pairs of sperm-sacs are described.

Spermathecæ.—Three pairs in Somites VI, VII, and VIII, opening at the posterior edge of the somites.

Gizzard in Somite VI; no accessory glands or cæca.

Septa in anterior somites strong as in the other two genera.

Nephridia large, the duct simple without a cæcum. Those of the first pair, which open externally in Somite III, are much larger than the rest; the coil of tubules compact, and having a glandular appearance. It no doubt serves as a "pepto-nephridium." I have not observed any funnel to this first nephridium.]

Species 1. D. thomasii, W. B. B., 1886; St. Thomas, W. Indies.

See Benham, 'Quart. Journ. Micr. Sci.,' xxvii.

Remarks on Geoscolecidæ.

I have divided Rosa's family of this name into two families, retaining his name to include three genera which agree closely with one another, especially in having a single pair of testes and sperm-sacs. But the structure of the nephridia do not here serve as a family character, since the cæcum of Geoscolex is not present in other two genera.

The position of the male pores is noticeably different from that in most other families, and resembles that in the Rhinodrilidæ.

The fact that Perrier's worm Titanus is identical with a worm described by Leuckart some thirty years before was apparently discovered by Rosa, who pointed out the curious agreement even in the words used by these two zoologists in their description of the worm.

b. **The eight setæ are in couples and exhibit no alternation in their arrangement. There are two or more pairs of sperm-sacs.**

Family VIII. Rhinodrilidæ, mihi (= partly L. intraclitelliens, E. P., partly Eudrilidæ, Claus, Vejdovsky, Rosa).

The eight setæ are in four couples, the individual setæ of each couple being close together.

The clitellum, incomplete ventrally, commences in front of Somite XVIII, and occupies ten or more somites.

The spermiducal pores are behind Somite XVIII (with the exception of Hormogaster), and are usually nearly in the middle of the clitellum.

There are two or more pairs of sperm-sacs, and two pairs of testes and rosettes.

The spermathecæ are either small, or if large are quite simple, without appendices.

The gizzard is in front of Somite X.

Nephridia are provided with a large duct, usually produced into a cæcum; nephridiopores are in a line with the outer couple of setæ (except in Hormogaster).

Genus 24. RHINODRILUS, E. P., 1872 (= Thamnodrilus, Beddard, 1887).

Prostomium is two or three times longer than the first somite [and can be withdrawn into the buccal cavity; at any rate, it is so in spirit specimens].

The setæ are ornamented near their distal ends with several rows of crescentic ridges, which are slightly more marked in the clitellar setæ.

The clitellum, which does not extend across the ventral surface, occupies seven or more somites, XV to XXV (XX—XXVI, Horst). Along its ventral boundary, on each side, is a glandular band—tubercula pubertatis—on Somites XX—XXV.

The spermiducal pore is intersegmental between XX and XXI (according to my own observation) (XIX/XX, E. P.).

The nephridiopores are in a line with the outer setæ.

Sperm-sacs are two pairs, in Somites XI, XII, with median sacs.

[Two pairs of testes and ciliated rosettes in Somites XI, XII.

Spermathecæ are long and club-shaped, in Somites VII, VIII, IX (Horst), or globular, in Somites V to VIII, in a species examined by myself.

The nephridium has only a short and slightly coiled tubule; the duct is produced into a cæcum. The anterior six or seven pairs of nephridia are larger than the following ones; and the duct is simple. The first pair, or extra-buccal pepto-nephridia, opening externally on Somite II, is particularly large, and lies below the œsophagus.

Gizzard in VII or VIII.

Typhlosole is a small fold, with a spiral line of origin.

Œsophageal glands, six or eight pairs, in the next following somites.

In addition to the dorsal vessel, there is a supra-intestinal trunk below it, from which two or three pairs of large "intestinal hearts" go to the sub-intestinal vessel.]

Species 1. R. paradoxus, E. P., 1872; Venezuela.
2. R. tenkatei, Horst, 1887; Surinam.
3. R. gulielmi, F. E. B., 1887; Brit. Guiana.
4. R. ecuadoriensis, W. B. B., 1889 (MS.); Ecuador.

See Perrier, 'Nouv. Arch. du Mus. d'Hist. Nat. de Paris,' viii, 1872; Beddard (Thamnodrilus), 'Proc. Zool. Soc.,' 1887; Horst, 'Notes from Leyden Museum,' ix.

Genus 25. MICROCHÆTA, F. E. B., 1885.

Setæ extremely small, in couples.

Clitellum occupies ten to twelve somites between X and XXV.

Spermiducal pore on Somite XIX or XX.

Oviducal pore between Somites XII and XIII.

Nephridiopores very large, in a line with outer setæ.

Sperm-sacs in Somites X and XI, each pair being connected by a median sac in Somites IX and X.

[Prostomium small. No dorsal pores.

Testes in Somites IX, X, in special sacs communicating with sperm-sacs.

Ovary in Somite XII.[1]

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[1] The peristomium in M. beddardi is provided with setæ, and is therefore homologous with the peristomium + the second somite of Lumbricus, hence the position of the ovary and other structures is typical, although dissection shows them one somite anterior to their real somites. In

Spermathecæ very minute and numerous, being from two to four pairs in all or some of the Somites XII to XV.

Nephridia very large, and of a peculiar form, each consisting of a greatly coiled tubule, arranged as a tuft, communicating with a large duct, which is produced into a great sac-like outgrowth. This cæcum is less developed in the anterior somites; and is most feebly marked in the first pair of nephridia.

Gizzard in Somite VI.

A single pair of œsophageal glands in Somite IX, or partly in VIII and partly in IX.

The dorsal vessel is doubled anteriorly and specially enlarged in Somite VIII.

Lateral hearts, VI—XI.]

Species 1. M. rappi, F. E. B., 1885; Cape of Good Hope.
2. M. beddardi, W. B. B., 1886; Natal.

See Beddard, 'Trans. Zool. Soc.,' xii, 1886; Benham, 'Quart. Journ. Micr. Sci.,' xxvi and xxvii.

Genus 26. UROBENUS, W. B. B., 1886.

Setæ in couples.

Clitellum occupies Somites XIV to XXV, incomplete ventrally.

Spermiducal pore on Somite XX.

Nephridiopores in a line with the outer setæ.

Sperm-sacs two pairs, of which one pair is in Somites XII and XIII, the second pair in Somite XIV.

Peculiar "pyriform sacs" occur in pairs on the ventral surface of the body-wall opening externally ventrad of the inner setæ, commencing in Somite X.

Testes and ciliated rosettes in Somites XII and XIII.

[Spermathecæ three pairs, in Somites VII, VIII, and IX.

Gizzard in Somite VIII.

Three pairs of flask-shaped calciferous glands in Somites IX, X, XI.

M. rappi I find no trace of setæ in the peristomium—the fusion is complete.

Intestinal pouches in Somites XVI to XXV.

A pair of tubular intestinal cæca in Somite XXVI resembling those of Perichæta.

All the nephridia have a large cæcum; the duct being very long in the first seven nephridia.]

Species 1. U. brasiliensis, W. B. B., 1886; Brazil.

See Benham, 'Quart. Journ. Micr. Sci.,' xxvii.

Genus 27. HORMOGASTER, Rosa, 1887.

Setæ in couples; those of the inner couple rather far apart.

Clitellum occupies Somites XV to XXV.

Tubercula pubertatis along the edge of the clitellum on Somites XVIII to XXIV.

Spermiducal pores between Somites XV and XVI.

Nephridiopores in line with Seta 2.

Sperm-sacs in Somites XI and XII.

Gizzards three, in Somites VI, VII, VIII.

[Globose intestinal cæca in Somite XXI, and smaller ones in following few somites.

Spermathecæ in Somites X, XI, XII.

Testes and rosettes in Somites X, XI.

Nephridial ducts provided with slight cæcal prolongations.]

Species 1. B. redii, Rosa, 1887; Italy.

See Rosa, 'Sulla Struttura dello Hormogaster Redii,' Torino, 1888.

Genus 28. BRACHYDRILUS, Benham, 1888.

Setæ very small, in four couples.

Clitellum occupies Somites XVI to XXI (though probably more).

Spermiducal pores in a deep fossa occupying Somite XVIII.

Two pairs of sperm-sacs, in Somites X, XI, enclosing the ciliated rosettes.

Large and muscular thickening of body-wall, through which the sperm-ducts pass to the exterior, occupies Somites XV to XX.

Spermathecæ small; two or three pairs on hinder margin of Somite XI.

Two pairs of nephridia in each somite, each a simple tubule without a distinct duct.

[Sixteen globular "albumen-glands" are present, as four sacs on each side of Somites X, XI.

Ovaries in Somite XII.[1]

The worm is very short in proportion to its width.]

See Benham, 'Zool. Anzeiger,' 1888, No. 271.

Remarks on Rhinodrilidæ.

I include in this family the remaining genera grouped by Rosa in his Geoscolecidæ; the two families together nearly correspond with Perrier's "intraclitellian worms."

The most aberrant form is Hormogaster, with its male pores far forwards, and nephridiopores in line with the inner couple of setæ. In these two points, showing a decided affinity to Lumbricus, and perhaps it belongs to the family Lumbricidæ.

Brachydrilus is of interest in possessing two pairs of large nephridia in each somite; evidently an intermediate condition between a network in which the tubules have become grouped, as in Cryptodrilus, into three masses on each side, and the ordinary condition of a pair of nephridia. It is quite conceivable that, as in Megascolides, one tubule becomes gradually larger, whilst at the same time the rest become fewer, in some other form two such tubules might increase in size, and so result in two pairs of nephridia per somite.

The testes and spermiducal pores have abnormal positions very usually in this family; for instance, in Microchæta testes and ovaries are placed one somite further forwards than is normally the case;[2] in Urobenus and Rhinodrilus the

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[1] The fusion between peristomium and first setigerous somite appears complete.

[2] See foot-note on p. 254.

funnels are further back, as I have ascertained by longitudinal sections, in addition to dissection.

2. Male pores in front of Somite XVIII, anterior to the clitellum.

Family IX. Lumbricidæ, Claus and Rosa (=L. anteclitelliens, E. P. = Lumbricidæ + Criodrilidæ, Vejdovsky).

The eight setæ are either in couples, the individual setæ being very close together; or they may gradually separate so as to give eight equidistant setæ per somite.

The clitellum, incomplete ventrally, usually commences behind Somite XX (in one case on Somite XV), and occupies from six to nine, sometimes more, somites.

The spermiducal pores are on Somite XV, or on an anterior somite.

There are three or four pairs of sperm-sacs in Somites IX to XII.

Testes and ciliated rosettes in Somites X, XI.

The oviducal pores are on Somite XIV.

Spermathecæ may be absent, or when present are nearly spherical sacs without diverticula.

Nephridiopores in a line with the inner couple of setæ.

Each nephridium is a greatly coiled tube, terminating in a large muscular duct without a cæcum.

The gizzard when present lies behind Somite X.

There are no pepto-nephridia.

Genus 29. LUMBRICUS, Eisen (= partly Lumbricus, Limnæus, &c.).

Prostomium dovetailed completely into the peristomium.

Setæ always in couples, the individual setæ of which are close together.

Clitellum occupies six or seven somites, commencing somewhere between Somites XXVI and XXXII.

Spermiducal pores on Somite XV.

Sperm-sacs three pairs, in Somites IX, XI, XII, connected across the middle line in Somites x, xi, by sacs enclosing the testes and ciliated rosettes.

Tubercula pubertatis, four on each side, forming a band along the ventral limit of the clitellum. These, and the spermathecæ are absent in L. eiseni.

[Colour reddish brown, iridescent.

Form cylindrical, more or less flattened posteriorly.

First dorsal pore may begin between Somites vii and viii, or posteriorly to this.

Anus terminal.

Spermathecæ.—Two pairs in Somites ix and x, opening posteriorly nearly in a line with the lateral setæ.

Spermatophores, in the breeding season, fixed to the body behind the genital pores.

Gizzard occupies Somites xvii and xviii.

Œsophageal calciferous glands xi and xii.]

Species 1. L. agricola, Hoffm., 1845; Europe, N. America (= L. terrestris, L., partly).
2. L. rubellus, Hoffm., 1845; Europe, Newfoundland.
3. L. castaneus, Sav., 1829; Europe, Newfoundland.
4. L. meliboeus, Rosa, 1884; Europe.
5. L. eiseni, Levinsen, 1883; Europe.
6. L. caucasicus, Kulagin, 1888; South Russia.

See Hoffmeister, 'Die bis jetzt bekannten Arten aus d. Fam. der Regenwürmer,' 1845; Eisen, 'Ofvers. af Kong. Vetensk. Akad. Förhandlungen,' 1870, 1873, &c.; Rosa, 'Il Lombricidi del Piemonte,' Torino, 1884, and later papers in 'Boll. Mus. Zool.,' Torino.

Genus 30. ALLOLOBOPHORA, Eisen (=Lumbricus, L., partly).

Prostomium only partially dovetailed into the peristomium.

Setæ either in four couples, or individual setæ more or less widely separated.

Clitellum occupies five to nine somites (rarely more), commencing somewhere between Somites xxvi and xxxii.

Spermiducal pores on Somite xv.

Sperm-sacs.—Four pairs, in Somites ix, x, xi, and xii, unconnected from side to side, so that the testes and ciliated rosettes lie freely in Somites x and xi.

Tubercula pubertatis are two or three pairs, sometimes in consecutive somites, sometimes on alternate somites (ten pairs in one species): rarely absent as in A. subrubicunda.

[Colour more varied than in Lumbricus; from deep sienna-brown to light transparent grey, sometimes green. First dorsal pore may begin as far forwards as Somite iv, or more posteriorly.

Spermathecæ usually two pairs (sometimes more, or they may be absent as in A. subrubicunda), opening either anteriorly or posteriorly, either near the lateral setæ or near the dorsal line.

Spermatophores fixed behind the genital pores.

Œsophageal pouches in Somite x, and calciferous glands in xi.

Gizzard as in Lumbricus.]

Species 1. A. chlorotica, Sav., 1832; Europe, N. America (= L. riparius, Hoffm., 1845).
2. A. fœtida, Sav., 1829; Europe, N. America, Australia (= L. olidus, Hoffm., 1845).
3. A. submontana, Vejd., 1875; Bohemia.
4. A. fraissei, Orley, 1881; Balearic Isles.
5. A. mediterranea, Orley, 1881; Balearic Isles.
6. A. nordenskjoldii, Eisen; Scandinavia, Siberia, Azores, Newfoundland.
7. A. subrubicunda, Eisen, 1873; South Siberia, Europe, Magellan.
8. A. tumida, Eisen, 1874; Denmark, N. America.
9. A. parva, Eisen, 1874; Denmark, N. America.
10. A. arborea, Eisen, 1874; Denmark.
11. A. dubiosa, Orley, 1881; Europe.

Species 12. A. norvegica, Eisen, 1873; Norway.
13. A. mucosa, Eisen, 1873; Europe, Siberia, N. America.
14. A. trapezoides, Dug., 1828; Europe.
15. A. turgida, Eisen, 1873; Europe, N. America, Australia.
16. A. longa, Uhde, 1885; Germany.
17. A. hispanica, Uhde, 1885; Spain.
18. A. profuga, Rosa, 1884; Italy.
19. A. transpadana, Rosa, 1884; Italy.
20. A. minima, Rosa, 1884; Italy.
21. A. constricta, Rosa, 1884; Italy.
22. A. alpina, Rosa, 1884; Italy.
23. A. veneta, Rosa, 1886; Italy, Portugal.
24. A. ninnii, Rosa, 1886; Italy.
25. A. tellinii, Rosa, 1888; Italy.
26. A. molleri, Rosa, 1889; Portugal.
27. A. orleyi, Horst, 1887; Hungary.
28. A. (Dendrobæna) rubida, Sav. 1832; Europe, Siberia, N. America (= L. octohedra, Sav., = A. boeckii, Eisen, 1870; = L. puter, Hoffm., 1845).
29. A. bagdonowi, Kulagin, 1888; Russia.
30. A. nassonowi, Kulagin, 1888; Russia.
31. A. celtica, Rosa, 1886; Brittany.
32. A. camplanata, Dug., 1828; Europe.
33. A. icterica, Sav., 1832; Europe.
34. A. gigas, Dug., 1828; Europe.

Genus 31. CRIODRILUS, Hoffmeister, 1845.

Prostomium not dovetailed into the peristomium.

Setæ in couples, which are so placed as to give the body a quadrangular outline in section.

Clitellum, ill-marked, extends from Somite XIV to about Somite XLV.

Spermiducal pores on Somite XV, on a large rounded papilla almost lateral in position.

No tubercula pubertatis.

[The worm is aquatic in habit; in colour, brownish green.

In the breeding season one or more "spermatophores" are found fixed to the body in the neighbourhood, and in front, of the genital pores.

Cocoons spindle-shaped, dark green.

The anus is dorsal.

Genital apparatus as in Allolobophora; the male duct passes through a glandular thickening of epidermis situated around the aperture.

No spermathecæ.

No gizzard and no œsophageal glands are present.

The typhlosole, frequently denied, is present.

The nephridia commence in Somite x (according to Collin, Zeit. Wiss. Zool.,' xlvi, 1888).]

Species 1. C. lacuum, Hoffm., 1845; Europe.

See Benham, 'Quart. Journ. Micr. Sci.,' xxvii; Orley, 'Quart. Journ. Micr. Sci.,' xxvii; Rosa, 'Sul Criodrilus lacuum,' Torino, 1887.

Genus 32. ALLURUS, Eisen (= L. tetraedrus, Dugés).

Prostomium partially dovetailed into the peristomium.

Setæ in four couples, latero-ventral and latero-dorsal in position.

Clitellum occupies Somites XXII to XXVII.

Spermiducal pores on Somite XIII, lateral in position.

Sperm-sacs as in Allolobophora; sperm-duct opens through a glandular thickening of epidermis as in Criodrilus.

[Body posteriorly quadrangular.

Spermathecæ minute sacs (visible only in sections) in Somite VIII; aperture not intersegmental, but close to the lateral setæ.

Gizzard in Somite XVII.

Small œsophageal glands in Somites X—XIV, not very distinct.

The nephridia commence in Somite IV.

First dorsal pore between Somites IV and V.]

Species 1. A. tetraedrus, Sav., 1832; Europe.
See Beddard, 'Quart. Journ. Micr. Sci.,' xxviii.

Remarks on Lumbricidæ.

Eisen was the first to subdivide the genus Lumbricus into two sub-genera, according to the relative amount of dovetailing of the prostomium into the peristomium. This is accompanied by certain other characters, which have been held sufficient to characterise genera in other cases. So that I retain his subdivisions Lumbricus and Allolobophora; but as his genus Dendrobæna is only distinguished from the latter genus in having all the setæ equidistant, and as all stages occurring in this separation are found in Allolobophora, I agree with Rosa that we ought not to recognise it.

The anatomy of Criodrilus, recently worked out by Rosa and myself, and again by Collin, is not very greatly different from that of Allolobophora. The most important points of difference are in the extent of the clitellum—which, till my discovery of it, had been denied, and in which Collin confirms me—and in the fact that this glandular modification of the epidermis commences in Somite xv; together with the absence of spermathecæ. This last character—which at first sight seems to mark it off from the rest of the family—serves in reality as a further link; for spermathecæ are absent in Lumbricus eiseni, Levinsen,[1] and in Allolobophora constricta, Rosa.[2] This negative character is, as Rosa has recently[3] pointed out, accompanied by another negative character, viz. the absence of tubercula pubertatis—structures almost limited to the family Lumbricidæ, as they have only been mentioned or figured in the species of Rhinodrilus, and in Hormogaster.

The spermatophores, so noticeable a feature in nearly every adult specimen of Criodrilus, are also known in many

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[1] Levinsen, 'Syst. geogr. oversigt over de nordiske annulata,' &c., Copenhagen, 1883.

[2] Rosa, 'Il Lumbricidi del Piemonte,' 1884.

[3] Rosa, 'Boll. Mus. Zool. ed Anat. Comp.,' Torino, vol. iv, November, 1889.

species of Lumbricus and Allolobophora; and unknown elsewhere.

Criodrilus, in fact, must be regarded as a degenerate Allolobophora, owing to its altered mode of life; its aquatic habit has no doubt a connection with the absence of a gizzard, and very likely with the absence of nephridia in the anterior somites, which may probably be used in ordinary earthworms as salivary glands—that is, for the purpose of moistening the food. At any rate, we find the same absence of anterior nephridia in another aquatic form, Pontodrilus; and the fact that in so many worms the anterior nephridia are specially large, or modified in some way (as in Urochæta, Diachæta, &c.), and even open into the pharynx instead of externally, bears me out in this idea.

In this connection it is interesting, though contradictory, to find that Allurus, which is also an aquatic form, but lives in the soil below the water, whilst Criodrilus lives actually in the water, has nephrida in the anterior somites.

Allurus has no true spermathecæ. Beddard describes a minute sac embedded in the body wall, and opening externally on the somite, but no spermatozoa were observed in it; and it may perhaps be either degenerate, or of the nature of an albumen ("capsulogenous") gland.

The species both of Lumbricus and Allolobophora are in a state of great confusion; even modern authors make two species out of one, or split up one into two. The list I have given is taken from Vejdovsky's 'System und Morphologie,' with additional species described since the date of his monograph.

Incertæ sedis.

HELODRILUS, Hoffmeister, 1845.

Setæ black, in couples.

Clitellum absent.

Spermiducal pores on Somite xv.

Gizzard present.

Pigment spots are present on peristomial somite, but are absent in young individuals.

ECHINODRILUS, Vaillant, 1869 (= L. multispinus, Grube, 1851).

Setæ four bundles of 5 in each somite.
Clitellum absent.
Spermiducal pores in Somite XII.

ANTEUS, E. P., 1872.

Setæ four couples.
Clitellum ill-defined, on Somites XV to XXIX.
Spermiducal pores unknown.
Sperm-sacs, two pairs, in Somites IX, X.
Gizzard, Somite VI.
Nephridia large; pores in line with outer setæ.
Anterior septa very thick.

Vaillant points out that in many respects Perrier's description agrees with that given by Beddard and myself for Microchæta rappi. Size: Anteus, 1·16 m. (i.e. 45 inches); Microchæta is 3 feet 6 inches to 6 feet.

The arrangement of setæ and indistinctness of the clitellum are also points of resemblance. To show the difficulty of deciding where the clitellum commences in Microchæta, it is noteworthy that whereas Beddard puts the extent of this structure as Somites X to XXX inclusive, I reckoned it as occupying Somites XIII to XXV.

Both Beddard and I were unable to recognise the spermiducal pore externally.

The annulation of the somites rendered it difficult to count them; thus Beddard figures the gizzard in Somite VII, whilst I found it to be in Somite VI. He states that the spermiducal pore is on Somite XVIII; I found it to be on XIX.

In both Anteus and Microchæta the anterior septa are especially thick and infundibuliform. Perrier places the last of these thick septa behind Somite IX; Beddard places it in Microchæta behind the eighth, and I found it behind the seventh. These discrepancies are no doubt due to the difficulty of counting the somites.

A nephridium of Anteus is figured by Perrier. He represents it as a long, narrow tube, equal in diameter throughout, and thrown into a number of curves. It ends in what he regards as the cœlomic funnel—"une sorte de houpe formée par une série de replis membraneux implantés sur sa portion terminale libre." This I take to be in reality a tuft of loops of the coiled tube, such as exists in the nephridium of Microchæta (see my paper, 'Quart. Journ. Micr. Sci.,' xxvi, pl. xvi, figs. 21, 25, 26). It is possible that the wide muscular duct there figured might in an ill-preserved specimen shrink, and have the appearance of such a duct as Perrier figures. Perrier states that behind the twentieth somite the nephridia are smaller and somewhat different from those anteriorly; such is also the case in Microchæta.

The fact that the spermathecæ in Microchæta are very small, and quite differently situated from what is the rule in other earthworms, might be suggested in explanation of their having been overlooked by Perrier.

In Microchæta the dorsal vessel becomes doubled in each of the Somites IV, V, VI, VII, and VIII, and in the last is very much thickened. In Anteus Perrier figures and describes it as ampullate and bent aside in Somites XII—XVII, and does not note any doubling.

It would be exceedingly interesting to investigate more fully the anatomy of Anteus, for its locality, Cayenne, in Brazil, is so far removed from the home of Microchæta in South Africa that it seems scarcely credible that the two are identical.

EISENIA, Vaillant, 1889 (= Tetragonurus, Eisen, 1874).

Prostomium does not dovetail into peristomium.
Setæ in couples.
Male pores in Somite XII.
No further details are given.

Species 1. E. pupa, Eisen, 1874; Canada, N. America.

See Eisen, 'Ofvers af. Kongl. Vetensk. Akad. Förhandl.,' 1874.

IV. Tabular Summary of Generic Characters.

I have here brought together the main characters of the various genera in a tabular form, the genera being arranged alphabetically. The information is, of course, condensed, and the terms employed are defined in the chapter dealing with nomenclature.

V. Index to Identification of Genera.

In addition to the following "tabular summary" it has occurred to me that it would be useful to zoologists examining earthworms to have the genera arranged in such a manner that identification to some extent may be rendered less difficult, as it is by no means an easy matter to distinguish many of the genera from one another, and I have found a table of this sort a great help to myself.

In order to add to its usefulness I have appended to each genus the page in this memoir in which will be found further details and references to papers on the genus.

IV.—TABULAR SUMMARY.

Name with Author.	Date	Setæ.	Clitellum.	Male Pore.	Prostomium.	Nephridia.	Nephridiopore. In line with—
1. Allolobophora, Eisen	1874	Sometimes in couples, or more or less separate	5, 6, 7, 8, 9 somites, beginng. between 26 and 32	15	Dovetailed incompletely into peristomium	Meganephric, simple	Inner couple
2. Acanthodrilus, E. P.	1872	4 couples, or 8 separate	13–19, complete anteriorly	18	Partially dovetailed into peristomium	Plectonephric	Numerous
3. Allurus, Eisen	1874	Couples, ventro-lateral and dorso-lateral	22–27	13	Partially dovetailed into peristomium	Commencing in 4, simple	Inner couple
4. Brachydrilus, W. B. B.	1888	Small, in 4 couples	16–21 [? more]	In a deep pit, 18	—	Two pairs, simple	Inner and outer couple
5. Criodrilus, Hoffm.	1845	Couples, ventro-lateral and dorso-lateral	Ill-marked, about 15–45	15	Large, not dovetailed into peristomium	Large, simple, commencing in 10	Inner couple
6. Cryptodrilus, Fletcher	1856	8, separate	13–17 complete, ventrally	18, no papillæ	Small, partially dovetailed into peristomium	Tufts, or 1 or 3 pairs, large tubes. Plect.	—
7. Deinodrilus, F. E. B.	1888	12 per somite, nearly equidistant	14, 15, 16 complete, ventrally	18	Dovetailed into peristomium	Plectonephric	—
8. Diachæta, W. B. B.	1886	8, separate, distant, alternate	20—33 complete, not developed intersegmentally	22	None	Large, simple	Outer couple
9. Dichogaster, F. E. B.	1888	4 couples, ventral and lateral	13–20, not well developed ventrally	17	—	Plectonephric	Numerous
10. Didymogaster, Fl.	1886	8, nearly equidistant	[13] 14–18, not greatly developed	18, on papillæ	Partially dovetailed	Plectonephric	—
11. Digaster, E. P.	1872	4 couples	14–17, complete ventrally	18 [17, E. P.]	Partially dovetailed	Plectonephric	—
12. Eudrilus, E. P.	1872	4 couples	[13] 14–18 complete	17	Partially dovetailed	Meganephric, simple	[Inner or] outer couple
13. Geoscolex, Leuckart	1841	4 couples, but separate posteriorly	15–23, incomplete ventrally	18/19	Broad	Meganephric; cæcal; commencing in 4	Inner couple
14. Hormogaster, Rosa	1887	Couples, those of inner couple far apart	15–25 incomplete	15/16	Not dovetailed	Meganephric; cæcal	Seta 2
15. Lumbricus, Linn.	1757	Always in couples	6 or 7 somites, commencing 26–32	15	Dovetailed completely into peristomium	Meganephric, simple	Inner couple
16. Megascolides, McCoy	1878	In couples, all ventral	13–21 complete, feebly marked	18, on papillæ	Broad, not dovetailed	Network anteriorly, network with large tubes posteriorly	Numerous
17. Microchæta, F. E. B.	1885	Very small, in couples	12 somites, incomplete, somewhere between 10–25	19 or 20	Small	Meganephric; cæcal	Outer couple
18. Microscolex, Rosa	1887	4 couples	13–16 (17) complete	17	Dovetailed into peristomium	Meganephric, simple	Third seta; begin in fourth somite

Ref. No.	Sperm-sacs.	Testes and Funnels.	Prostate.	Gizzard.	Remarks.
1.	4 pairs, 9, 10, 11, 12, unconnected across the middle line	10, 11, testes and ciliated rosettes free	None	17, 18	Tubercula pubertatis on some of the clitellar somites; œsophageal diverticula in Somites 10 and 11. Number of spermathecæ variable.
2.	11, 12	10, 11, free	2 pairs, convoluted 17, 19; penial setæ	8, 9	Diverticula behind gizzard; pepto-nephridia frequently present. Spermathecæ with appendages.
3.	4 pairs, 9, 10, 11, 12, no median sac	Free, 10, 11	None	17, one somite	Slight dilatation of œsophagus, 10–14.
4.	10, 11	10, 11	None	6	Spermathecæ, 1 or 2 pairs of small sacs in Somite 11. Albumen-glands, 10, 11; thickening of body-wall in Somites 15–20.
5.	4 pairs, 9, 10, 11, 12, no median sac	Free, 10, 11	None	None	No spermathecæ, body square, anus dorsal; aquatic.
6.	9 and 12	10, 11, free	Lobate; no penial setæ	5 [6 or 7]	Intestinal calciferous dilatations in Somites 9–13; usually several copulatory papillæ.
7.	11, 12	10, 11	2 pairs, 17, 19, convoluted	6, 7	Dorsal blood-vessel double throughout and enclosed in special cœlomic tube. Spermathecæ with appendices; no calciferous glands.
8.	1 pair, 12 to 38	11	None; no penial setæ	6	Extra-buccal pepto-nephridia; no diverticula.
9.	10, 11, 12, median sac and dorsal connections	10, 11	3 pairs, 17, 18, 19, tubular	Two, 7, 8, and 9, 10	Calciferous diverticula in 15, 16, 17; only 1 pair of spermathecæ in 8, near median line. No penial setæ.
10.	9, 12	10, 11	18, equally bilobed	Two, 6, 7	Intestine dilated in 10–16, spirally twisted; dorsal vessel doubled. Spermathecal apertures not intersegmental.
11.	10, 11 [9, 12, Fl.]	Funnels free	Lobulated; penial setæ	Two, 5, 7	—
12.	10, 11, and 12	10, 11, sperm-ducts separate	Elongated; chitinous penis in sac	6	Diverticula lateral and calciferous in 12, and ventral in 10, 11; no typhlosole; the genital apparatus is peculiar.
13.	1 pair, 12 to 25	12	None	7	Calciferous diverticula large, 13; typhlosole; no spermathecæ known.
14.	2 pairs, 11, 12	10, 11	None	Three, 6, 7, 8	Globose diverticula of intestine, 21; tubercula pubertatis on Somites 18–24.
15.	3 pairs, 9, 11, 12, with median sac	10, 11, enclosed in sac	None	17, 18	Calciferous diverticula 11, 12, and a pouch in 11, tubercula pubertatis.
16.	Racemose, 11, 12, 13, 14	10, 11, free	Tubular, much coiled; no penial setæ	5 or 6	No œsophageal diverticula, but intestinal dilations in all or any of Somites 12–18. Intra-buccal pepto-nephridia. No typhlosole.
17.	10, 11	9, 10, testes in special sacs	None	6	Pair of œsophageal diverticula in 9; nephridia very conspicuous. Spermathecæ numerous and inconspicuous.
18.	11, 12	10, 11, free	Lobed; penial setæ	None	One pair spermathecæ in 9; no typhlosole, no subneural vessel; small transparent worm.

IV.—TABULAR SUMMARY (*continued*).

Name with Author.	Date.	Setæ.	Clitellum.	Male Pore.	Prostomium.	Nephridia.	Nephridiopore. In line with—
19. Moniligaster, E. P.	1872	4 couples	10–13, ill-marked	Intersegmental, 10/11 or 11/12	—	Meganephric; cæcal	Outer couple
20. Perichæta, Schmarda	1861	20–100 on ridges, continuous or discontinuous	14, 15, 16 [or more], complete	18, latero-ventral	Sometimes dovetailed into peristomium	Plectonephric	Numerous
21. Perionyx, E. P.	1872	30 or more, continuous	14–17, complete ventrally	18, close together	Dovetailed partially	Meganephric, simple	Irregular on each side
22. Perissogaster, Fl.	1887	All close together on ventral surface	[13] 14–18, complete, except in the hinder part, 16, 17	18 [?]	Wide, dovetailed into peristomium	Plectonephric	—
23. Photodrilus, Giard	1887	8, separate, No. 1 near middle line	13–17 complete	18	Not dovetailed	Megan., simple, commence in Somite 14	Second seta
24. Plutellus, E. P.	1873	8, equidistant	14–17, complete ventrally	18	Dovetailed into peristomium	Entirely within one somite. Meganephric	Alternate, 2 and 4 setæ
25. Pontodrilus, E. P.	1881	8, separate	13–17 complete	18	—	Megan., simple, commence in 15	Second seta
26. Rhinodrilus, E. P.	1872	4 couples, ornamented	7 or more somites incomplete, 15–25=[20–27]	Intersegmental, 19/20 (20/21)	Elongated	Meganephric; cæcal; anterior 6 or 7 pairs very long	Outer couple
27. Rhododrilus, F. E. B.	1889	8, separate	14–17	17	Partially dovetailed into peristomium	Meganephric	Third seta
28. Teleudrilus, Rosa	1888	4 couples, though setæ are far apart	14–17 complete	Median, 19	—	Meganephric, simple	Outer couple
29. Trigaster, W. B. B.	1886	4 couples, all ventral	14–40 incomplete	18, in deep fossa	Broad, not dovetailed into peristomium	Plectonephric	—
30. Typhæus, F. E. B.	1883	4 couples, all ventral	14–17	17	Broad, not dovetailed	Plectonephric	—
31. Urobenus, W. B. B.	1886	In couples	14–25 incomplete	20	Distinct	Meganephric; cæcal	Outer couple
32. Urochæta, E. P.	1872	Anteriorly in couples; the 8 equidistant alternate posteriorly	14–22, not developed intersegmentally, complete ventrally	20/21 [20, E. P.]	None	Meganephric, simple	Third seta

Ref. No.	Sperm-sacs.	Testes and Funnels.	Prostate.	Gizzard.	Remarks.
19.	1 pair, occupying partly 9, partly 10	Testes 9	Tubular and long, or very small	Long, 13–22, or fewer somites	Ovisac occupies two or three somites, 14–16; a single pair of spermathecæ in 8 or 9.
20.	11, 12	10, 11	Lobed, or deeply incised	Usually 8, 9, 10, or any 2 segments between 5 and 8	Usually a pair of intestinal cæca in Somite 26, sometimes metamerically repeated; accessory glands anteriorly; spermathecæ with appendix.
21.	11, 12	10, 11	Flattened, slightly lobed	6, 7	No cæca, no accessory digestive glands, no copulatory papillæ; spermathecæ without appendix.
22.	9, 10, 11, 12	10, 11, free	Lobed, one lobe long and extends into 19; penial setæ	Three, 5, 6, 7	Intestinal calciferous (?) diverticula in 9–14.
23.	11, 12	Testes and ciliated rosettes 10, 11	Penial setæ	None	Septal glands in anterior somites appear to open near dorsal surface. No typhlosole; no subneural vessel.
24.	12 ?	?	Tubular, convoluted	6	Œsophageal diverticula, 10, 11, 12. The ovary in 10 [?]. Five pairs of spermathecæ in 5–9.
25.	11, 12	Testes free, and ciliated rosettes 10, 11	Convoluted, tubular	None	Lives on sea-shore. No typhlosole, nor subneural vessel.
26.	2 pairs, 11, 12	11, 12	None	7 or 8	Six or more pairs of diverticula in 9–14. Tubercula pubertatis, 20–25.
27.	11, 12	—	Tubular 17, independent aperture; penial setæ	5	No alimentary diverticula. Spermathecæ have appendices.
28.	2 pairs, 11, 12	10, 11 enclosed in a special sac, funnels 11, 12	Two prostates enter a median sac, which passes to exterior and also receives another sac	6, 7	Calciferous diverticula in 13. Dorsal vessel is doubled in anterior somites. Generative apparatus peculiar, and characteristic; median spermathecal pore, 13/14; and paired oviducal pore, 14/15.
29.	—	—	17, 19, tubular; convoluted; no penial setæ	Three, 7, 8, 9 [or two]	Pepto-nephridia are present. Spermathecæ simple.
30.	1 pair, 10, or occupying more than 1 somite	1 pair, 10 in median sperm-sac	Convoluted; penial setæ	6, 7	Calciferous diverticula in 12, and intestinal dilatations. One pair of spermathecæ in 8, opening anteriorly.
31.	2 pairs, 12, 13, 14	12, 13 free	None	8	Three pairs of calciferous diverticula, 9, 10, 11; intestinal cæca, 26; pyriform sacs opening externally, ventrad of inner setæ.
32.	1 pair, 13 to 15, or further	12	None; penial setæ	7	Three pairs of calciferous diverticula, 8, 9, 10. Pyriform sacs in posterior part of body on ventral surface. Extra-buccal pepto-nephridia.

V.—INDEX TO IDENTIFICATION OF GENERA.

Setæ per somite

- 16 to 80 or more, in a ring. Male pores
  - Far apart . . . . Perichæta (small tufts of nephridia), p. 233.
  - Very close together . Perionyx (large nephridia), p. 247.
- 12 . . . . Deinodrilus (clitellum XIV, XV, XVI), p. 231.
- 8
  - Alternate in consecutive somites.
    - Throughout the body . . Diachæta (male pore XXII), p. 251.
    - Only posteriorly . . . . Urochæta (male pore XX/XXI; clitellum XIV—XXII), p. 250.
  - In rows, not alternating. Male pores on Somites
    - X/XI or XI/XII . . . . Moniligaster, p. 238.
    - XIII . . . . Allurus, p. 262.
    - XV. Prostomium
      - Dovetailed completely into peristomium . Lumbricus, p. 258.
      - Dovetailed incompletely . . . . Allolobophora, p. 259.
      - Not dovetailed into peristomium . . . . Criodrilus, p. 261.
    - XV/XVI . . . . Hormogaster, p. 256.
    - XVII. Clitellum on Somites
      - XIV—XVII. Setæ
        - Separate; prostomium dovetailed into peristomium . . . . Rhododrilus, p. 245.
        - In couples; prostomium not dovetailed . . . .
          - One pair of sperm-sacs Typhæus, p. 223.
          - Two pairs of sperm-sacs Digaster, p. 227.
      - XIV—XVIII . . . Setæ in couples; prostomium dovetailed Eudrilus, p. 241.
      - XIII—XVII . . . Lobed prostates; one pair . . . . . Microscolex, p. 244.
      - XIII—XX . . . Tubular prostates; two pairs, XVIII, XIX Dichogaster, p. 227.
    - XVIII. Prostates
      - Two pairs, in Somites XVII and XIX. Male pores
        - In deep fossa . . . Trigaster, p. 231.
        - Not in a fossa . . . Acanthodrilus, p. 229.
      - One pair, in XVIII. Clitellum on Somites
        - XIII—XVII. Prostomium
          - Dovetailed into peristomium. Prostate
            - Convoluted Pontodrilus, p. 243.
            - Lobate . . Cryptodrilus, p. 224.
          - Not dovetailed . . . . Photodrilus, p. 244.
        - (XIII) XIV—XVII. Prostomium . . Dovetailed into peristomium; setæ separate Plutellus, p. 245.
        - XIV—XVIII. Prostomium
          - Dovetailed slightly into peristomium; setæ equidistant . . . . Didymogaster, p. 225.
          - Not dovetailed; setæ in couples. . . . . Perissogaster, p. 226.
        - XIII—XXI (or more) . . . . . Megascolides, p. 223.
      - None . . . . . Clitellum XVI—XXI . . . . . Brachydrilus, p. 256.
    - XVIII/XIX. Prostomium
      - Broad; setæ simple . . . . Geoscolex (clitellum XV—XXIII), p. 249.
      - Elongated, narrow; setæ ornamented . Rhinodrilus (clitellum XV—XXV; tubercula pubertatis), p. 253.
    - XIX
      - Paired; clitellum X—XXV . . . . . Microchæta, p. 254.
      - Median; clitellum XIV—XVII. . . . Teleudrilus, p. 243.
    - XX . . . . . . Clitellum XIV—XXV . . . . Urobenus, p. 255.

VI. Phylogeny.

I will now endeavour to trace the phylogeny of the group of earthworms, but owing to the scanty information as to their ontogeny, it is impossible to found anything like a true phylogenetic tree.

First of all it will be desirable to say a few words as to what may be considered "primitive characters," as two widely different families have been regarded as the more primitive, viz. Perichæta by Beddard, and Acanthodrilus by Rosa. I hope to be able to bring forward sufficient reason for denying to either of them an archaic condition.

The excretory system, the setæ, clitellum, prostate, and sperm-ducts may be taken as the more important characters.

The Excretory System.—The recent researches of Beddard and Spencer have resulted in the conclusion that the network of tubules is a more primitive state than the large nephridia; that, in fact, the latter have been derived in some way from the former.

In Megascolides the excretory system in the anterior region of the body consists in a network of delicate tubules, with numerous external apertures, but without cœlomic funnels. Further back, one of these tubules on each side increases in size, and the network diminishes in extent; whilst in the somites quite posteriorly there is on each side a large tubule, which possesses a cœlomic funnel, and which still retains its connection with the network. Spencer regards the anterior plectonephric condition as more primitive, and differs from Beddard in considering the nephridial funnels as new structures, and not as derivatives of the flame-cells of Platyhelmia. It is to be noticed that the modification begins in the posterior somites, whilst the anterior part of the body still retains a primitive condition.

Other instances of the co-existence of large nephridia with the network of tubules have already been given.

In Perichæta we have certainly a primitive condition, but more modified than in Megascolides, in that, at any rate in some species, the plectonephric tubules are provided with funnels, and in others co-exist with large nephridia.[1]

2. The Setæ.—Beddard considers the perichætous condition as antecedent to the octochætous. Now, I believe we have ample evidence that the reverse is the case. Firstly, it is a nearly universal character of the Chætopoda that the setæ are in two bundles on each side of each somite; in the Polychæta there are many setæ in each group, in the Oligochæta only a few, and in a very large number of cases only two. In the Archi-annelida setæ may be absent or only in one bundle on each side in each segment, but it is not unlikely that this group contains degenerate and not primitive forms.

In Perichæta itself it is very usual to find fewer setæ on the anterior somites than posteriorly. Unfortunately, as far as I am aware, we are not in possession of actual details as to the mode of development of the setæ in this genus. But if the modification of nephridia in Megascolides commences posteriorly and works forward, may we not assume that the same has happened in the case of the setæ of Perichæta or Perionyx? If this were so, we should expect to find just what is actually existent, fewer setæ anteriorly, i. e. less modification than posteriorly where greater modification has taken place.

In some of the species (P. attenuata and P. enormis) described by Fletcher ('Proc. Linn. Soc. N.S.W.,' vol. v, 1888) there are only eight setæ in four couples in the first few somites; then twelve in some of the following somites; and posteriorly they become more numerous. In P. dorsalis, only 16 at first, more posteriorly 30. In P. monticolla, only 16 per somite on first few rings, increasing to 27 about clitellar region, and behind to 50.

Again, in Urochæta and in Geoscolex the setæ are arranged

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[1] For a discussion of the subject see Baldwin Spencer's monograph on Megascolides, and Beddard's papers in 'Quart. Journ. Micr. Sci.,' xxviii and xxix.

normally—i.e. in couples—anteriorly, but become separated posteriorly, or even, in Urochæta, alternate from somite to somite. That is, according to my view, modification has commenced posteriorly, but has not affected the whole of the body; whilst in Diachæta this change has extended all along the worm.[1]

The perichætous condition, according to my view, has arisen firstly by the separation of the individual setæ, originally in couples, so as to produce eight equidistant setæ (as in species of Acanthodrilus, in Plutellus, and Allolobophora boeckii); and then intermediate setæ have appeared gradually filling up the spaces, leading on through Deinodrilus with twelve, to Perichæta with 20—100 per somite. I conceive this intercalation of setæ to be effected by the gradual increase in length of the accessory setæ ("soies de remplacement" of Perrier), which are very usually found, one to each of the functional setæ in many, perhaps in all earthworms. Supposing all the accessory setæ of a somite became thus fully developed contemporaneously with the existent setæ, we should get a doubling of the setæ, i.e. sixteen per somite. Each of these would, later on, have an accessory seta, and these might develop into functional setæ, and so on, till we get the perichætous condition.

Mr. Beddard would regard the penial setæ in special sacs, found in many earthworms, as vestigial representatives of a perichætous condition. I would regard them, however, as secondary and as developed from ordinary accessory setæ, which if carried to a greater extent would lead to a perichætous condition. If we look upon the perichætous condition, then, in this light, the removal of Perionyx from its associations with Perichæta merely indicates that the condition has been developed twice, and independently; and if we

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[1] In a new species, D. windlei, Beddard states that there are no setæ on the first five somites. Here the modification has gone further, and the setæ have disappeared altogether. Microchæta presents a somewhat similar case of disappearance of setæ and fusion of somites. This condition, of course, may have resulted also from a perichætous condition.

remember that the separation of the couples and that penial setæ are present in various genera and families, I think it is allowable to so regard it.

The Position of the Clitellum.—In the fresh-water worms (*Microdrili*) the clitellum is developed only during the breeding season, and around the somite carrying the male pore, or those immediately on each side of it. That is, the "intra-clitellian" condition is the more primitive.

Now, in *Moniligaster sapphirinaoides* the clitellum is on Somites x—xiii, and the male pores between Somites x and xi. The reason that it has not been observed in other species of this genus is very likely due to the fact that it is present only for a short period, during the actual breeding season.

When the male pores shifted backwards, as they have done in the rest of the earthworms, the clitellum probably accompanied them, giving rise to what Perrier called "lombriciens intra-clitelliens:" in some cases the extent of the clitellum is small, at other times it is great. But apparently in some cases—*Perichæta*, *Acanthodrilus*, &c.—whilst retaining its limited extent, it has not kept up its relative position, coming to lie in front of the male apertures; whilst in the family *Lumbricidæ* it is still further removed from its primitive position, and lies far behind the spermiducal pores.

The Sperm-ducts.—In the majority of the water-worms (except *Lumbriculidæ*) there is only *one* pair of sperm-ducts, and this I regard as the primitive condition—that is to say, when once the position of the genital glands had become fixed to definite somites, and the nephridia specialised for the purpose of conveying generative products to the exterior, there was only *one* pair serving as sperm-ducts, and *one* pair as oviducts; previously to this state of things of course we should get a less limited specialization; but from general considerations I believe *one pair*, and not two pairs (if so, why not three pairs or four pairs?), of sperm-ducts was the typical arrangement.

This condition is retained in Moniligaster, where, too, the ducts are limited in length, passing through only one septum, and have their external aperture more nearly in the position common to the majority of water-worms than in any other earthworm. The single pair of sperm-ducts (and testes) is retained in the family Geoscolecidæ, in which, too, we find the sperm-sacs occupying, as in Tubifex, several somites. In Typhæus, again, this primitive character is retained. The size of the ovisac in Moniligaster recalls the fact that the ova in water-worms after separation from the ovary push the septa back, and come to occupy several somites.

When a second pair of sperm-ducts appeared, each would have its separate external aperture; but (except in Perichæta stuarti, A. G. B.) the two pairs of apertures have disappeared; the two sperm-ducts become more or less fused together; and as in the case of setæ and nephridia this fusion commences posteriorly and gradually extends forwards. Thus in Acanthodrilus, and in Eudrilus and Megascolides, the two ducts remain separate till they join the prostate; in Microchæta they remain separate through several somites; finally, in Lumbricus and others, the two unite immediately behind the second rosette.

The Prostate.—In the majority of water-worms there is an enlargement of the sperm-duct near its pore, and this enlargement may have glandular walls; this condition is retained in Moniligaster barwelli. In the rest of the earthworms, when present, we have either (*a*) a diverticulum of the sperm-duct, (*b*) a single pair of sacs opening independently of the sperm-ducts, or (*c*) a couple of pairs of separate prostates. In all the prostatiferous earthworms except in Acanthodrilidæ we find either (*a*) or (*b*). Dichogaster has prostates of both varieties. No doubt the tubular prostates, as seen in these latter and in other genera, are more primitive than the branched prostates of Perichæta, the flattened condition seen in Cryptodrilus and Perionyx leading towards this.

Moniligaster barwelli is, in this matter, more primitive than the remainder of the earthworms, and closely resembles Stylaria in the condition of its prostate.

As I said above, we have practically no embryological data on which to found our theories as to "primitive" and "secondary" characters in the earthworms. But there is one organ on which we have definite information, and that is that the dorsal blood-vessel is in Criodrilus formed by the fusion of a double vessel. Now, in several earthworms we find this double condition of the vessel.

In Acanthodrilus multiporus and in Deinodrilus benhami there is a pair of dorsal vessels; in A. dissimilis this vessel is doubled in every somite, fusing at the septa: this condition is also present in the anterior somites of Microchæta rappi, and according to Beddard in Perichæta cœrulea (Pleurochæta moseleyi), and this seems to have been the chief reason, in addition to its plectonephric condition, for regarding Acanthodrilus as the more primitive genus.

In which worm are any of these organs retained in their most primitive condition? I think that Moniligaster supplies the answer in most points. The setæ, clitellum, sperm-ducts, and prostate are all in agreement with the above-formulated conditions. The gizzard, too, is very different from what we find in other worms; its walls appear to be much less muscular than is usually the case; it is less marked, extends through several somites, and recalls the enlarged intestine of water-worms, with its wall only slightly thicker than the preceding œsophagus.[1]

Thus, on the whole, I am inclined to regard Moniligaster as the most primitive living earthworm, or rather as approaching most nearly to their original ancestor. At the

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[1] I should add that the anterior gizzard mentioned by Perrier has not been found in any of the species recently described—seven by Bourne, one by Horst, one by Beddard; and it is probable that he mistook for gizzard a mere dilatation of œsophagus, as was the case in his description of Perionyx. Here he stated that the gizzard was in Somite XII; Rosa found here a swelling only, the true gizzard being in VII.

same time, in the condition of its excretory system and in the matter of the dorsal blood-vessel, Moniligaster is in a less primitive condition than many other worms, which, whilst advancing in respect of certain of their other organs, retain the primitive network of tubules more or less completely.

My idea as to the relation of the various families is as follows:—From some of the earlier "Limicolous" forms—Lumbricomorpha minora—the earthworms have been derived along two lines.[1] Along one branch (A) the more primitive plectonephric condition has been retained from some Platyhelminth ancestor of the whole Chætopoda. Along the other (B) this has been replaced by the meganephric condition more usually found in the group.

The Typhæidæ, having a single pair of prostates, stand at the end of the main branch of the first line (A); but from this line a branch has given rise to the Acanthodrilidæ, to which Dichogaster has some affinity.

The Perichætidæ appear to have arisen from the Typhæid stem—from some form with flattened prostates, by multiplication of setæ. Deinodrilus, having a dozen setæ, would not necessarily be related to the Perichætidæ, but might point to the possibility of the development of a perichætous condition in the family Acanthodrilidæ.

The branch (B) leads through Moniligaster to the Geoscolecidæ, which retain the single pair of testes, &c., and exhibit amongst the genera stages in the separation of the setæ, but which have lost the prostate, a primitive character of the group. Springing from this branch is another, leading, after the appearance of the second pair of testes, &c., through the Eudrilidæ to the Perionycidæ.

The loss of prostates and the extension of the clitellum gives us a new line leading to Rhinodrilidæ, which, through Hormogaster, presents some affinity to the Lumbricidæ.

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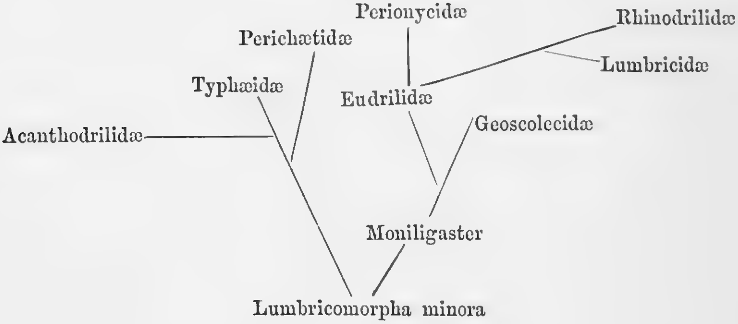
[1] It is quite possible, of course, that earthworms have not been derived from water-worms; the latter may have been developed from earthworms, but I think the evidence is in favour of the statement in the text.

Indeed, Hormogaster might perhaps be included in the latter family but for the existence of only two pairs of sperm-sacs.



I would here record my thanks to Professor Lankester for his help and advice on many points during the progress of this paper.

Postscript, April 30th.

While this paper was in the press, I received from Dr. Michaelsen his recently published memoir[1] describing two new species and six new genera from the neighbourhood of Zanzibar.

The two new species are Trigaster stuhlmanni and T. affinis, which are evidently very closely similar. He suggests, with good reason I think, the removal of Horst's species Acanthodrilus schlegelii, A. büttikoferi, and A. beddardi, as well as Rosa's A. scioanus, from the genus under which they have been placed in the present paper to my genus Trigaster (= Benhamia, Mich.), since the male pores are

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[1] "Beschreibung d. v. H. Dr. F. Stuhlmann im Mündungsgebiet des Sambesi gesammelten Terricolen," 'Jahrb. d. hamburg. wiss. Anstalten,' vii, 1890.

placed in a deep median fossa, and with the exception of T. schlegelii they each have two gizzards. It is to be regretted that the "law of priority" is so frequently disregarded. The name Trigaster, though losing its structural significance, has every right to be retained as a generic title. The new genera appear to belong to my family Eudrilidæ with one exception; but it is a pity that more figures, in illustration of the very curious arrangement of the genital system in some of these, have not been given. I have diagrammatised four of these genera.

1. Pygmæodrilus.

Setæ in four couples.

Clitellum complete, round Somites XIV, XV, XVI.

Male pores paired on Somite XVII.

Nephridiopores in front of the outer couples of setæ.

The male apparatus resembles that of Eudrilus, but the female system is not aberrant [for further characters see fig. 33].

Species.—P. quilimanensis; from Quilimane.

2. Eudriloides.

Setæ in four couples.

Clitellum complete, on Somites XIV to XVIII.

Male pore single, median, on Somite XVII.

Spermathecal pore single, median, between Somites XIII/XIV.

There is no direct communication between oviduct and spermatheca.

Penial setæ and dorsal pores are present.

The details given are insufficient to diagrammatise.

Species.—E. parvus and E. gypsatus.

3. Nemertodrilus.

Setæ in four couples.

Clitellum on Somites XIII to XVIII.

Male pores paired between Somites XVII/XVIII.

"Spermathecal" (?) pores paired on Somite XIII.

Ovipores on Somite XIV.

Nephridiopores in line with inner couples of setæ.

No penial setæ.

The septa, XIII/XIV and XII/XIII, are fused together except below the intestine, so that Somite XIII is almost obliterated.

There is a connection between the oviduct and "spermatheca" of each side; in fact, the so-called spermatheca appear to be a greatly elongated ovisac, which has, as Michaelsen suggests, taken on the function of spermatheca (see Polytoreutes). Apart from this the genus somewhat resembles Rhododrilus.

Species.—N. griseus.

4. Callidrilus.

Setæ in four couples.

Clitellum only developed ventrally on Somites XVII to XXI.

Male pores paired on Somite XVII.

Spermathecal pores numerous, between Somites XIII/XIV.

Ovipores on Somite XIV.

Nephridiopores in line with inner couple of setæ.

Numerous paired copulatory pits are present on Somites XI to XXIV.

Spermathecæ in the form of small sacs; a dozen in anterior of Somite XIV [cf. Brachydrilus].

Species.—C. scrobifer.

5. Polytoreutes.

Setæ separate, eight.

Clitellum on Somites XIII to XVIII.

Male pore median on Somite XVII.

"Spermathecal" pore median, single, on Somite XIX.

Ovipores paired on Somite XIV.

No penial setæ.

Each prostate is very long, and provided with two rows of small contiguous diverticula along its whole length. The two prostates unite on Somite XVII. The "spermatheca" is a median sac passing forwards from its pore in Somite XIX to

Somite XIV, where it divides into two short processes, one to each oviduct. In Somites XVI and XVIII there are long, paired, blind processes from the spermatheca. These remind one of the elongated ovisacs of the water-worms. This is the only form known with spermathecal aperture behind the male pore, and it appears to me to be doubtful whether this sac is homologous with the spermatheca of the ordinary type. Michaelsen makes no statement as to its contents. It may be, though he gives no grounds for this supposition, that the oviducts are in a state of degeneration, and that the "spermatheca" serves as an enlarged ovisac, in which perhaps the ova are fertilised and retained during development. In fact, the worm may be oviparous.

Species.—P. cœruleus.

6. Stuhlmannia.

Setæ four couples.

Clitellum on Somites XIV to XVII.

Male pore median in Somite XVII.

Spermathecal pore median, single, in Somite XIII.

Ovipores in Somite XIV.

Two long prostates extending from Somites XVII to XXIV, and uniting in XVII.

Median spermatheca; from its proximal end a pair of outgrowths surround the intestine and meet dorsally.

Oviducts communicate with the spermatheca.

These structures are so complicated, and so brief a description of them is given, that I have not attempted to construct a diagram.

Species.—S. variabilis.

Of these six genera, all but one—viz. Callidrilus—are probably referable to the family Eudrilidæ, mihi. The exception appears to belong to the family Rhinodrilidæ, mihi, although it presents one or two points in which it does not agree with my diagnosis of the family, e.g. position of male pore and of nephridiopores. Michaelsen gives no details as to the structure of what he called "prostate," and it may very likely be merely a thickening of the body-wall. If it be a prostate, then Callidrilus, like the rest, will belong to Eudrilidæ; but even here it will form an exception to the general characters of the family in the position of the clitellum, and in the character of the nephridia and spermathecæ.

The chief point in which Pygmæodrilus approaches Eudrilus is in the possession of elongated prostates, and of a penis within a "bursa." The muscular part of the sperm-duct very probably corresponds to a portion of the prostate of Eudrilus, in which the duct enters the prostate some distance along its length.

Polytoreutes and Stuhlmannia present so many abnormal characters that it is desirable that we should have more detail before deciding on their affinities. Apparently they are most nearly related to Teleudrilus.

VII. Explanation of Diagrams.

These diagrams, representing the genital, alimentary, and excretory systems of the genera recognised in the accompanying paper, have been constructed in most cases from drawings published by the various authors mentioned below, or, where no figures have been given, from the descriptions of the different worms. I have usually selected those species which have been most fully and most recently described, as types of the genera. It must be borne in mind that the accompanying figures are merely diagrams, and are not accurate copies from previous figures. I have arranged them in the same order as that in which the genera have been described in the body of the paper, and the numbering of the figures agrees with the numbering of the genera.

In every case the clitellum, if it occurs within the first twenty somites, is indicated by the thickened boundary of the diagram. In all cases the upper figure (*a*) represents genital system; the middle (*b*), alimentary and excretory systems; the lowermost figure (*c*), a few somites seen externally.

In the diagrams of the genital system the testes and ovaries are in black, the genital ducts in outline, the sperm-sacs and ovisacs are dotted; the spermathecæ are outlined; and the prostate and sac with penial setæ are also represented in outline.

In the alimentary canal, the extent of the buccal cavity as represented is not intended to indicate the actual extent, as we have no sufficient data for determining this point; hence the position of the commencement of pharynx is hypothetical; but its posterior limit is true in most cases, although in many genera this point is left vague in the drawings and descriptions of authors: the limit here assigned is, in these cases, deduced from analogy with better known genera. The gizzard is indicated by its thicker outline, and by the transverse line in front and behind it.

In the excretory system the black dots represent the funnels, the thicker line the "duct," and the narrow wavy line the coiled tube: there is no attempt to indicate the arrangement of this coil. In the "plectonephric" genera the short lines are intended to indicate the passage of the duct through the body-wall to the exterior. The external openings are shown in the lowermost diagram as small circles,[1] the setæ as short lines, and any genital apertures as black dots. In cases where the nephridiopores are not indicated their arrangement is not known.

The representation of the excretory system is purely conventional, especially in forms with "tufts" or network, and merely serves to indicate whether the genus is "plectonephric" or "meganephric," and in the latter case whether the duct is "simple" or "cæcal."

The modification of the anterior nephridia or excretory network to serve to moisten the food, and act as "pepto-nephridia," is indicated.

The diagrams represent the worms slit open along the middle line of the dorsal surface, and cut edges of the body-wall pinned aside.

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[1] Unfortunately the "process" has in many cases not reproduced the circle, so that the nephridiopores appear as small black dots. The index lines, too, are often not reproduced.

Family I.—TYPHÆIDÆ.

FIG. 1.—Typhæus. The drawings, both the alimentary and the genital systems, are taken from the descriptions and figures of T. gammii by Beddard, 'Quart. Journ. Micr. Sci.,' xxix, p. 111, and pl. xii.

In fig. 1 *a*, the small sac (PS.) in Somite XVII represents the special sac with penial setæ, the external aperture of which is shown in fig. 1 *c*, in front of the male pore on each side, which is indicated by the large black dot. PRO. is the prostate, which joins the sperm-duct before the latter opens externally. The outlined structures in Somite VIII are the spermathecæ.

In fig. 1 *b*, the gizzard is shown in Somite VII; the calciferous diverticula in Somite XII (Ca.). The sacculated intestine commences in Somite XVI. EPN. is the extra-buccal pepto-nephridial network, which is shown in thicker lines than the remaining network.

Fig. 1 *c*, represents Somites XVI, XVII, and XVIII seen externally, when flattened out; showing the arrangement of the setæ, the numerous nephridiopores (as small dots), the penial setæ in Somite XVII replacing the ordinary setæ; and behind these the large black dots indicate the male pores.

Distribution of the genus: India.

FIG. 2.—Megascolides. Modified from the drawings of M. australis, McCoy, given by Baldwin Spencer in 'Trans. Roy. Soc. Victoria,' vol. i, pl. i.

In fig. 2 *a*, the four pairs of lobed, dotted structures marked S., in Somites XI, XII, XIII, and XIV, represent the sperm-sacs. PRO. is the coiled prostate.

In fig. 2 *b*, the plectonephric condition is seen, the network in Somites I to IV communicates with the pharynx by small ducts, and forms an "intra-buccal pepto-nephridial network" (IPN.). G. is the gizzard in Somite V. In Somites XII to XVIII the pouched intestine is shown (PP.), the sacculated, non-typhlosolar intestine commencing in the next somite.

Fig. 2 *c*, represents Somites XVII, XVIII, and XIX externally, showing setæ, nephridiopores, and the male pores which are in XVIII.

Distribution of the genus: Australia.

FIG. 3.—Cryptodrilus. *a.* Genital system, modified from the figure of C. fletcheri, given by Beddard in 'Proc. Zool. Soc.,' 1887, p, 547. PRO., the prostate. *b.* Alimentary system, composed from Beddard's description of C. fletcheri in 'Proc. Zool. Soc.,' 1887, and from Fletcher's description of various species in 'Proc. Linn. Soc. N.S.W.'

The gizzard occupies two somites. CA. The first of the four calciferous diverticula on each side. The sacculated intestine commences in Somite XVI.

The plectonephridia are not continuous from somite to somite.

Fig. 2 *c*, represents any three somites behind the male pores, showing the setæ: the nephridiopores are probably numerous and irregular.

Distribution: Australia.

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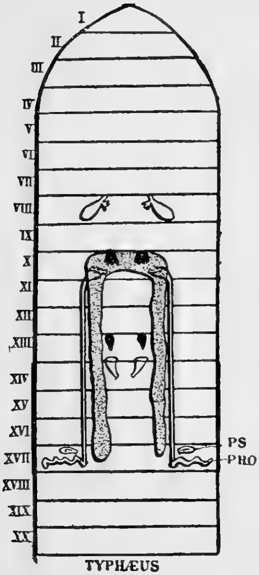
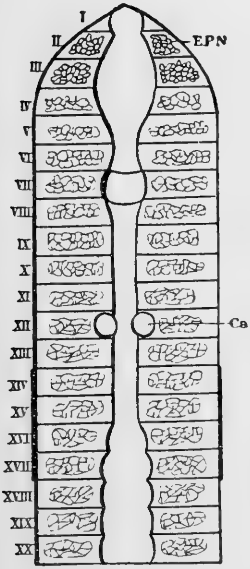


TYPHÆUS



TYPHÆUS

TYPHÆUS

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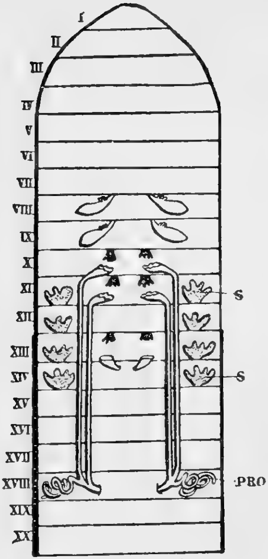
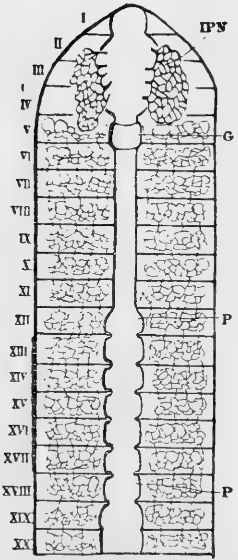


MEGASCOLIDES



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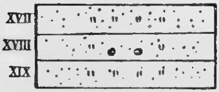

MEGASCOLIDES

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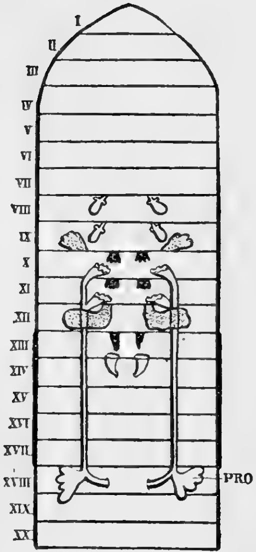
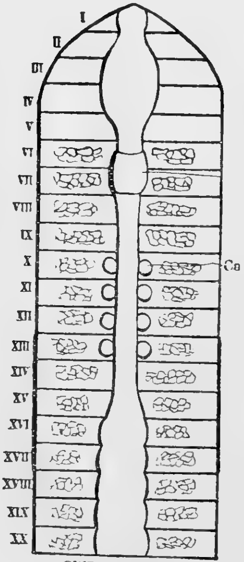


CRYPTODRILUS



CRYPTODRILUS

CRYPTODRILUS

FIG. 4.—Didymogaster. *a.* Genital system. The clitellum, XIV to XVIII. SP.[1], SP.[3], are the first and third spermathecæ. S. The digitate sperm-sac of Somite IX. PS. The sac of penial setæ; and PRO., the prostate. *b.* Alimentary system. G.[1], G.[2] The two gizzards lying in Somites VI and VII. Both diagrams modified from Fletcher's figures of D. sylvaticus in 'Proc. Linn. Soc. N.S.W.,' i (2nd ser.), 1886. *c.* represents three somites from any part of the body, and shows the arrangement of the setæ; the nephridiopores are probably, as in other plectonephric genera, numerous.

Distribution: Australia.

FIG. 5.—Perissogaster. *a.* Genital system. PS. Sac with penial setæ. PRO. The unequally lobed prostate. *b.* Alimentary system. G.[1], G.[2], G.[3] The three gizzards. D. The first dilatation of the intestine in Somite IX, followed by five others, all of which are doubtfully calciferous. S. The commencement of the sacculated intestine in Somite XV. *c.* shows the arrangement of the setæ. Constructed from the description given by Fletcher for P. excavatus in 'Proc. Linn. Soc. N.S.W.,' vol. ii, ser. 2, 1887.

Distribution: Australia.

FIG. 6.—Dichogaster. *a.* Genital system. PRO.[1] The first prostate, communicating with the sperm-duct. PRO.[2] and PRO.[3] The second and third prostates, which are independent of the sperm-duct. *b.* Alimentary system. C.[1], C.[2] The two gizzards, each occupying two somites. *Ca.* The first of the three calciferous diverticula on each side. S. The commencement of the sacculated intestine. IPN. The intra-buccal peptonephridium with its duct. *c.* represents the Somites XVI, XVII, and XVIII externally. The large black dots in XVII are the male pores, those in XVIII the prostate pores of this somite. In these two and in Somite XIX the inner couples of setæ are absent. Modified from the figures given by Beddard for D. damonis in 'Quart. Journ. Micr. Sci.,' xxix, pls. xxiii, xxiv.

Distribution: Fiji.

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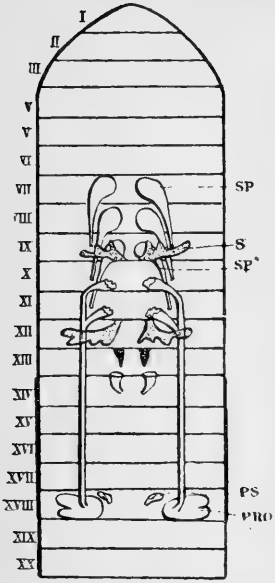

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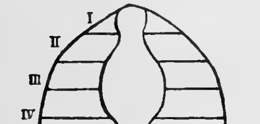

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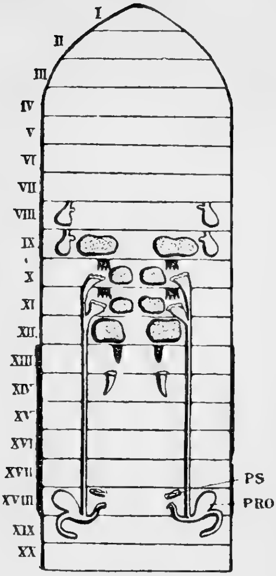

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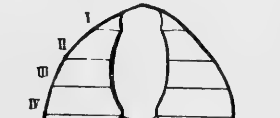

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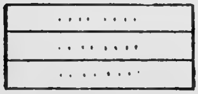

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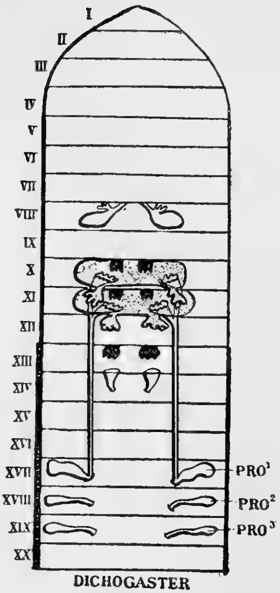

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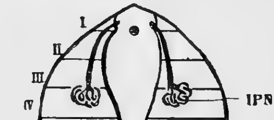

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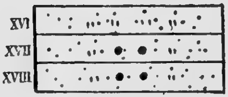

DICHOGASTER

FIG. 7.—Digaster. *a.* Genital system. PS.[1] The anterior sac with penial setæ. The posterior sac, which is described as lying in this somite, is omitted to prevent crowding. PRO. Prostate. *b.* Alimentary system. G.[1], G.[2] The two gizzards lying in Somites V and VII. The intra-buccal pepto-nephridia are indicated at IPN. *c.* The exterior of Somites XVII, XVIII, and XIX to show the setæ; male pores represented by black dots, and the openings of the two pairs of sacs with penial setæ, PS.[1], PS.[2], lying one in front of the other.

Modified from the figures of D. lumbricoides given by Perrier in 'Nouv. Arch. du Mus. d'Hist. Nat. de Paris,' viii, 1872, pl. ii; the modifications being in accordance with Fletcher's description of D. armifera in 'Proc. Linn. Soc. N.S.W.,' vol. i, p. 943.

Distribution: Australia.

Family II.—ACANTHODRILIDÆ.

FIG. 8.—Acanthodrilus. *a.* Genital system. Modified from Beddard's figure of A. dissimilis in 'Proc. Zool. Soc.,' 1887, p. 388, in accordance with his more recent observations in regard to the independent opening of sperm-duct and prostates. PS.[1], PS.[2] The sacs of penial setæ in Somites XVII and XVIII. PRO.[1], PRO.[2] The prostates in Somites XVII and XVIII. *b.* Alimentary system.

Modified from Beddard's figure of A. multiporus in 'Proc. Zool. Soc.,' 1885, pl. liii. *Ca.* The first pair of calciferous diverticula. S. Commencement of sacculated intestine in Somite XVI. IPN. Intra-buccal peptonephridia. The grouping of the nephridial network so as to form eight groups, six of which only are represented, is indicated in Somites XVI, et seq. See Beddard, 'Proc. Zool. Soc.,' 1885. The clitellum in A. dissimilis and A. multiporus commences in Somite XII. I have represented it as beginning at Somite XIII, which appears to be more usually the case. *c.* External view of two Somites, A, B, of A. multiporus, and others in which the eight setæ are separate. C, somite of A. novæ-zealandiæ, and other species in which the setæ are in couples.

Distribution: New Zealand, Australia, West Africa, New Caledonia, Kerguelen Island, the shores of Magellan Strait.

FIG. 9.—Trigaster. *a.* Genital system. SP. Spermathecæ. O. Ovary. PRO.[1], PRO.[2] The prostates. Sperm-ducts, sperm-sacs, and testes unknown.[1] *b.* Alimentary system. Slightly altered from my own figures of T. lankesteri in 'Quart. Journ. Micr. Sci.,' xxvii, pl. ix, after a renewed examination as to the position of some of the structures.

G.[1], G.[2], G.[3] The three gizzards. S. Commencement of sacculated intestine. The anterior nephridial network is more evident than that more posteriorly, but it is uncertain whether there is any communication with the pharynx. *c.* Three somites seen externally to show the arrangement of the setæ.

Distribution: St. Thomas, West Indies.

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[1] Michaelsen, however, has in his last paper described the testes and ciliated rosettes in Somites X and XI, and sperm-sacs in Somites XI and XII.

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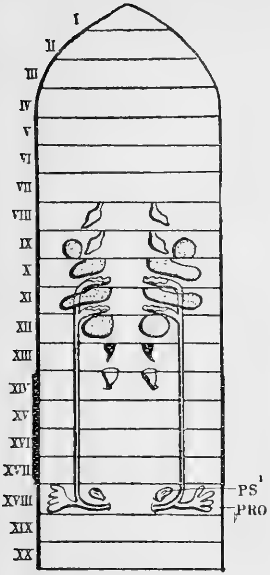

DIGASTER

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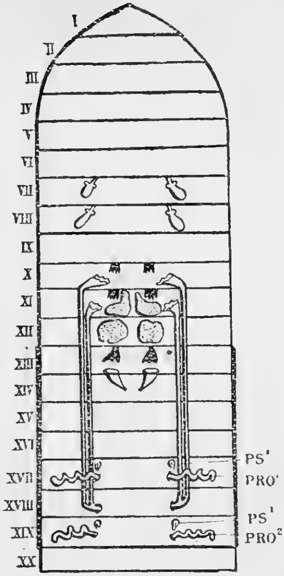

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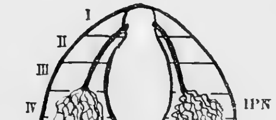

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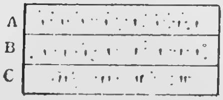

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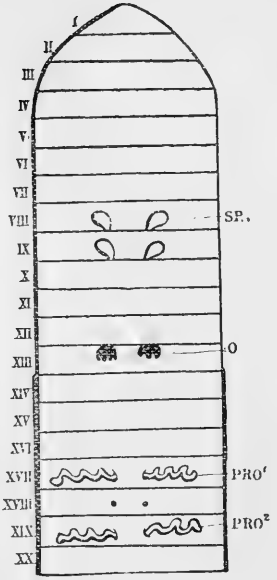

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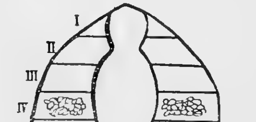

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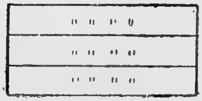

TRIGASTER

FIG. 10.—Deinodrilus. *a*. Genital system. SP. Anterior spermatheca. PRO.[1], PRO.[2] The two prostates of one side. *b*.[1] Alimentary system. G. Gizzard occupying two somites. EPN. The extra-buccal pepto-nephridia. A connection exists here and there between the nephridial network of neighbouring somites. Beddard says but little of the alimentary canal or the nephridia, but special groups (EPN.) of the latter occur in Somites II, III, and IV. *c*. Exterior of these somites, showing the characteristic twelve setæ and numerous nephridiopores. Constructed from Beddard's description of D. benhami in 'Quart. Journ. Micr. Sci.,' xxix, p. 105.

Distribution: New Zealand.

Family III.—PERICHÆTIDÆ.

FIG. 11.—Perichæta. *a*. Genital system. Modified from Rosa's figure of P. feæ in 'Ann. Mus. Civico d. Stor. Nat. di Genova,' vi, 1888, pl. iii. *b*. Alimentary system. G. Gizzard, occupying more or less of three somites. P. The first, and P.[1] the last, of the thirteen pouches. Nine somites are cut away, as they are merely a repetition of these pouches. C. The characteristic cylindrical cæcum of one side. [These are absent in some species.] S. The commencement of the sacculated, typhlosolar intestine. Composed partly from Perrier's and Rosa's description. The excretory system is taken from Beddard's figure of P. aspergillum in 'Quart. Journ. Micr. Sci.,' xxix, pl. xxiv. The black dots represent the funnels of the nephridial network. *c*. represents three somites from different regions of the body of P. monticolla, Fletcher, 'Proc. Linn. Soc. N.S.W.,' vol. ii. In Somite A, from anterior part of body, only sixteen setæ are present; in Somite B, from about Somite XV, there are thirty setæ, and posteriorly in Somite C fifty or more. This same variation in numbers occurs in other species. The nephridiopores (represented as small dots) are drawn from Beddard's description of P. aspergillum.

Distribution of the genus: India (with Ceylon), Malaya, Australia, and islands between the two continents.

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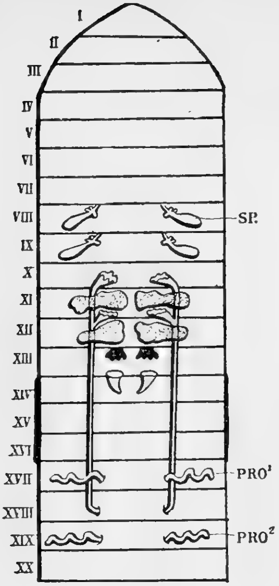
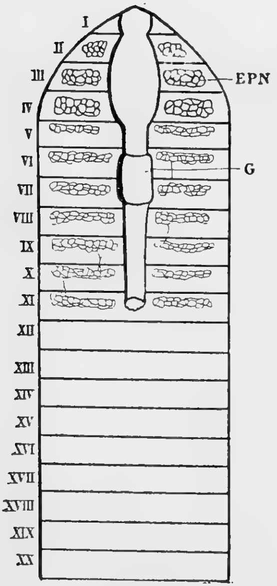
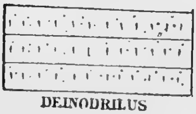


DEINODRILUS



DEINODRILUS



DEINODRILUS

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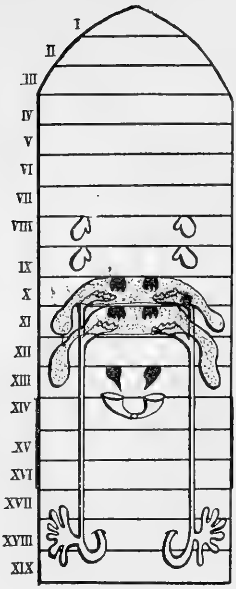
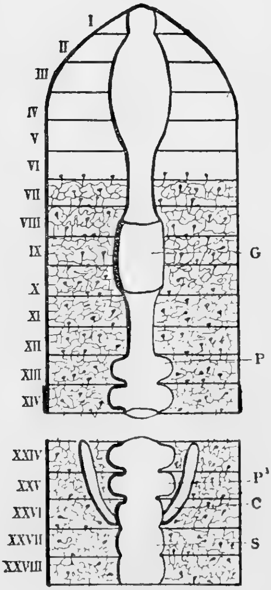


PERICHÆTA



PERICHÆTA

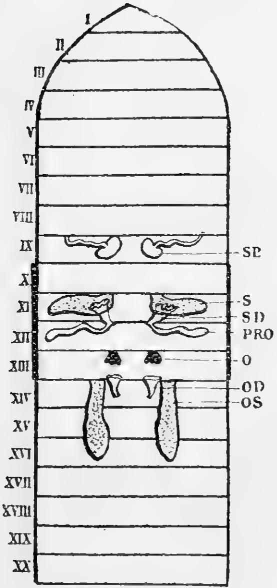
PERICHÆTA

Family IV.—MONILIGASTRIDÆ.

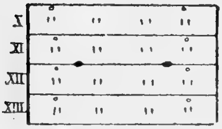
FIG. 12.—Moniligaster. *a.* The left upper figure, genital system. Modified from Horst's figure of M. houteni in 'Notes from the Leyden Museum,' ix, pl. i, fig. 1, in accordance with Beddard's more recent figures and descriptions ('Quart. Journ. Micr. Sci.,' xxix, pl. xii, fig. 12; and 'Zool. Anz.,' No. 318, 1889). SP. Spermatheca, with its long duct, in Somite IX. These are the "anterior testes" of Perrier. S. Sperm-sacs—Perrier's "posterior testes." SD. Sperm-duct and ciliated rosette. PRO. Prostate. O. Ovary. OD. Oviduct. OS. Ovisac. *b.* The right figure, alimentary system. Modified from Perrier's figure of M. deshayesii in 'Nouv. Arch. d. Mus. d'Hist. Nat.,' viii, 1872, in accordance with the more recent descriptions of Beddard, Horst, and Bourne, who have not observed Perrier's anterior gizzard. G. The characteristic elongated gizzard region. The nephridia are after Horst. CŒ. The cæcum of the nephridial duct. *c.* The left lower figure, the exterior of Somites X to XIII—the region of the clitellum, showing the setæ, nephridiopores, and male pores, which lie between Somites XI and XII.

Distribution: India, Ceylon, Sumatra.

12.



MONILIGASTER



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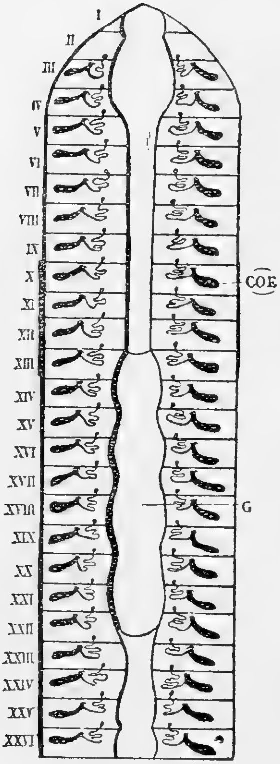

MONILIGASTER

Family V.—EUDRILIDÆ.

FIG. 13.—Eudrilus. *a.* Genital system. Modified from Beddard's figure of E. sylvicola in 'Proc. Zool. Soc.,' 1887, p. 381, in accordance with his subsequent descriptions and figures of the female apparatus, which are peculiarly arranged.

It will be seen that the ovary (o^1.) in Somite XIII is enclosed in a sac, the neck of which communicates with the true oviduct (OD.); into the latter also open an albumen-gland (GL.), a large spermatheca (SP.), and the ovisac ($o.^2$),[1] which functions also as a second ovary, and lies in Somite XIV. PRO. is the prostate, into which the sperm-ducts open about halfway along its length. X. is one of two glands communicating with B.C., the bursa copulatrix, which contains a chitinous penis: the bursa opens externally at P. in XVII, a dotted ring[2] indicating the male pore. *b.* Alimentary system. Modified from Perrier's figure of E. decipiens in 'Nouv. Arch. Mus. d'Hist. Nat.,' viii, 1872, pl. ii, fig. 26, in accordance with Horst's more recent description in 'Notes from the Leyden Museum,' ix. G. The gizzard. CA. Calciferous diverticula. Commencement of the sacculated intestine in Somite XV. The nephridia are original; they present no cæcum, but the duct is continuous with the tubule as in Lumbricus. *c.* External view of a normal somite of E. decipiens, showing (A) setæ and nephridiopores; (B) Somite XVII of the same species, showing the male pores—as black oval dots—occupying the position of the inner couples of setæ, which are absent; (C) is a normal somite of E. sylvicola, in which the nephridiopores are in line with the inner couple of setæ, instead of with the outer couple, as in other species.

Distribution: South America and New Caledonia.

FIG. 14.—Teleudrilus. *a.* Genital system. Notice the peculiar recurved ciliated rosettes; the median position of the male pore in Somite XIX (represented as a dotted semicircle P.) and spermathecal pore in Somite XVII is peculiar.

The female organs present some difference from the typical arrangement, analogous to that in Eudrilus in that there is a connection between the oviduct and spermatheca, but a less direct communication in that genus. O. Ovary. OD. Oviduct. OS. Ovisac.[3] SP. Spermatheca. B.C. Bursa copulatrix, opening externally at P in XIX. It is in communication with the sperm-ducts, prostates (PRO.), and a sac (S.), probably glandular. *b.* Alimentary system. After Rosa's figures of T. raggazii in 'Ann. Mus. Civ. d. Stor. Nat. di Genova,' vi, 1888, pl. ix. G. Gizzard. CA. Calciferous diverticula. S. The commencement of sacculated intestine. *c.* represents the exterior of Somites XVIII, XIX, and XX, showing setæ, nephridiopores, and median male pore in Somite XIX.

Distribution: Scioa, Africa.

FIG. 15.—Pontodrilus. *a.* Genital system. PRO. Prostate. SP. Spermatheca. *b.* Alimentary system. Note absence of gizzard. S. Sacculated but non-typhlosolar intestine. Note: the nephridia do not commence till Somite XV. *c.* shows the exterior of Somites XVI, XVII, and XVIII, with setæ, nephridiopores, and male pores. After Perrier's figures for P. marionis in 'Arch. de Zool. Expér. et Gén.,' ix, 1881.

Distribution: Europe (France).

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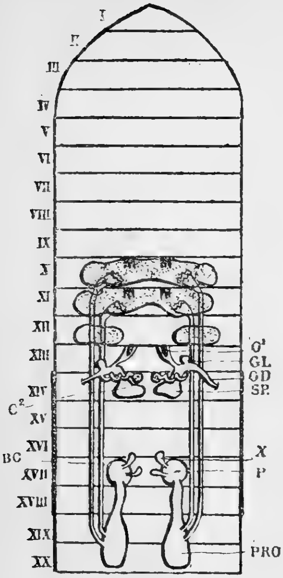
[1] The index line does not go quite far enough; it should extend to the small round sac at the end of the tortuous tube.

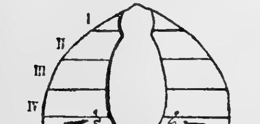
[2] This is very feebly indicated in the diagrams.

[3] The index line should extend to the round dotted area.

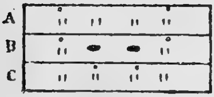
13.



EUDRILUS



EUDRILUS



EUDRILUS

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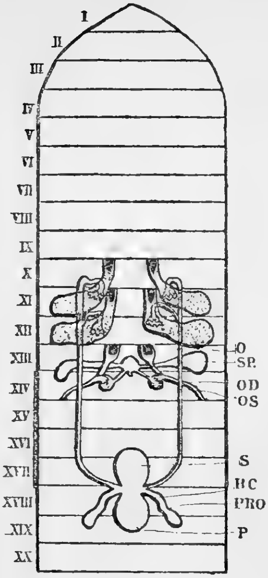
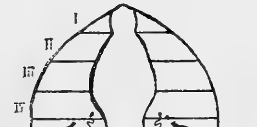


TELEUDRILUS



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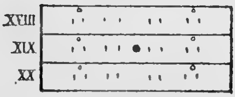

TELEUDRILUS

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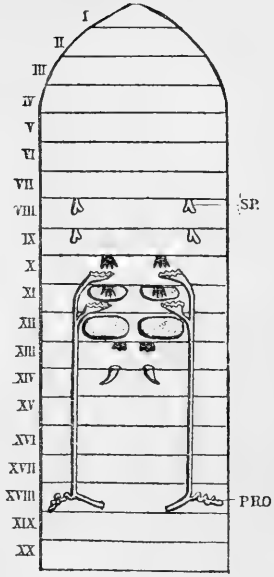
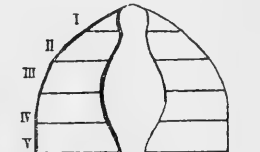
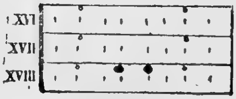


PONTODRILUS



PONTODRILUS



PONTODRILUS

Fig. 16.—Photodrilus. *a.* Genital system. sp. Spermatheca. pro. Prostate. *b.* Alimentary system. Both diagrams are constructed from the description given by Giard for P. phosphoreus in 'Comptes rendus,' 1887. Here the nephridia do not commence till Somite xiv. Their pores are between the outer and inner couple of setæ as shown in fig. *c.*

Distribution: Europe (France).

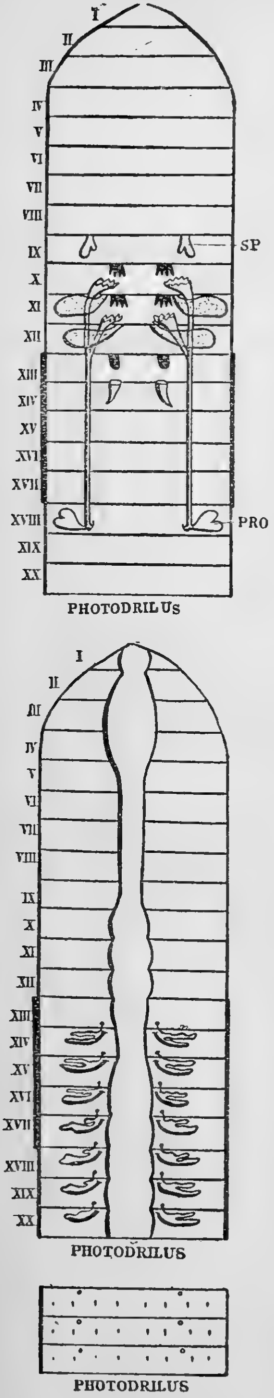
Fig. 17.—Microscolex. *a.* Genital system. pro. Prostate. ps. Sac with penial setæ. *b.* Alimentary system. Constructed from Rosa's descriptions of M. modestus in 'Boll. Mus. Zool. ed Anat. Comp. Torino,' ii and iii. Although closely allied to the two preceding genera, the nephridia, as usual, commence far forwards. *c.*, taken from Rosa's woodcut, represents Somites xvi, xvii, xviii. He does not state that the setæ are absent on this somite, but he does not figure them. The male pore is in line with the seta 1.

Distribution: Italy.

Fig. 18.—Rhododrilus. *a.* Genital system. sp. The first of the four spermathecæ on one side. pro. Prostate opening independently of the sperm-duct. *b.* Alimentary system. g. Gizzard. s. Commencement of sacculated intestine. *c.* Exterior of three somites. Diagrams constructed from Beddard's brief diagnosis of R. minutus in 'Proc. Zool. Soc.,' 1889, p. 381.

Distribution: New Zealand.

16.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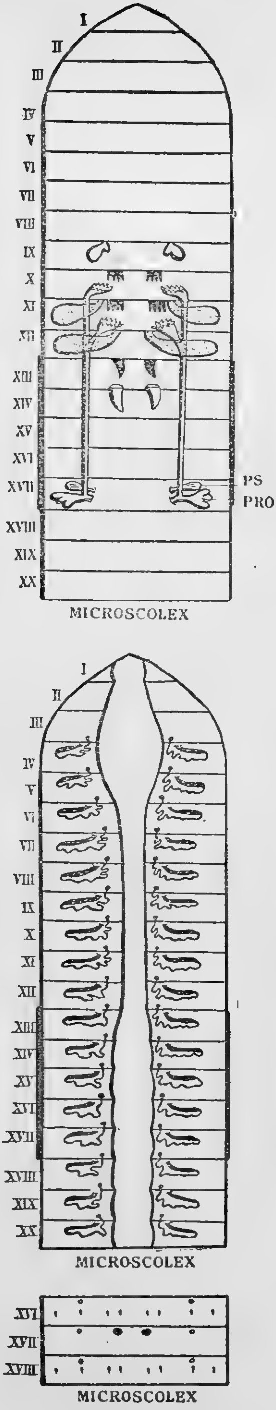
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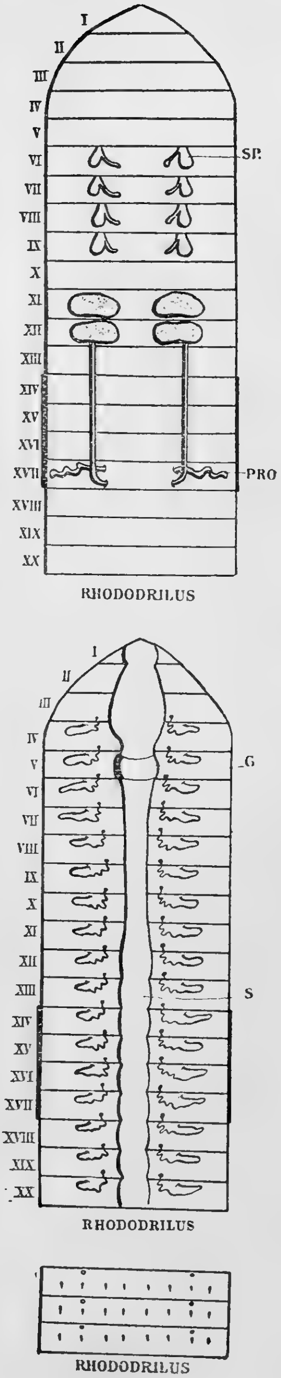
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Fig. 19.—Plutellus. *a.* Genital system. The position of the genital organs is very abnormal, and requires confirmation. s. The sperm-sacs in Somite XII. SP. The first of the five spermathecæ. PRO. Prostate. The sperm-funnels and ducts are unknown. O. Ovary in Somite X; and OD., the oviduct opening externally in Somite XI. *b.* Alimentary system. G. Gizzard. ca. Calciferous diverticula. s. Commencement of sacculated intestine. The nephridia are shown alternating in position, the first four pores being in line with the third seta, the rest alternating with second and fourth setæ. Moreover, the funnels are said to be in the same somite as the coiled tubule and external aperture. N.^{1} The first of the series of nephridia which open in line with the third seta. N.^{2} The first of the series which open in line with the fourth seta. N.^{3} The first of the series in line with second seta. *c.* An external view of Somite VI, to show spermathecal pore (black) in line with second seta, and nephridiopore (N^1) in line with third seta; of Somite XII, to show the normal arrangement in the even numbered somites; and of Somite XIII, to show normal arrangement of the odd numbered somites. Composed from Perrier's description of P. heteroporus in 'Arch. de Zool. Expér. et Gén.,' ii, 1873, p. 331.

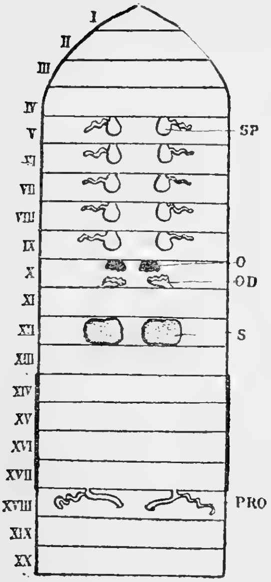
Distribution: Pennsylvania.

Family VI.—PERIONYCIDÆ.

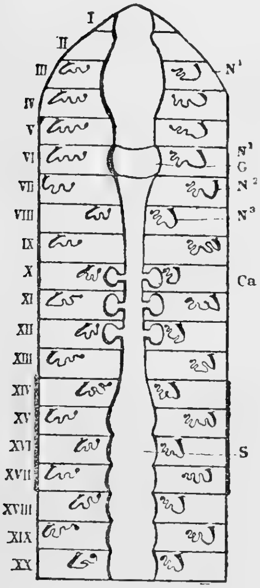
Fig. 20.—Perionyx. *a.* Genital system. O. Ovary. OD. Oviduct. PRO. Prostate. *b.* Alimentary system. G. Gizzard. s. Commencement of sacculated intestine. Modified from Perrier's figures of P. excavatus in 'Nouv. Arch. d. Mus. d'Hist. Nat.,' 1872, in accordance with Rosa's description of the same species in 'Ann. Mus. Civ. d. St. Nat. di Genova,' vi, 1888. *c.* External view of three somites, showing the numerous setæ and the paired nephridiopores.

Distribution: India, Burmah, Philippines.

19.



PLUTELLUS



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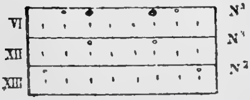

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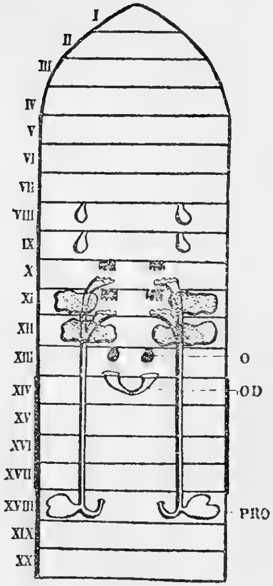
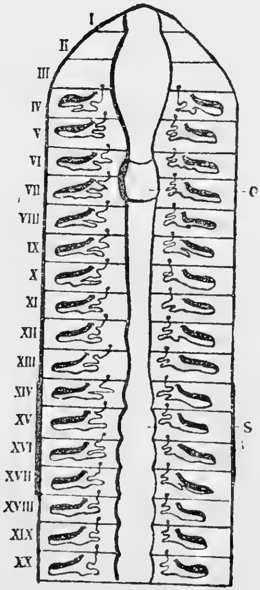
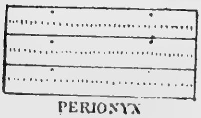


PERIONYX



PERIONYX



PERIONYX

Family VII.—GEOSCOLECIDÆ.

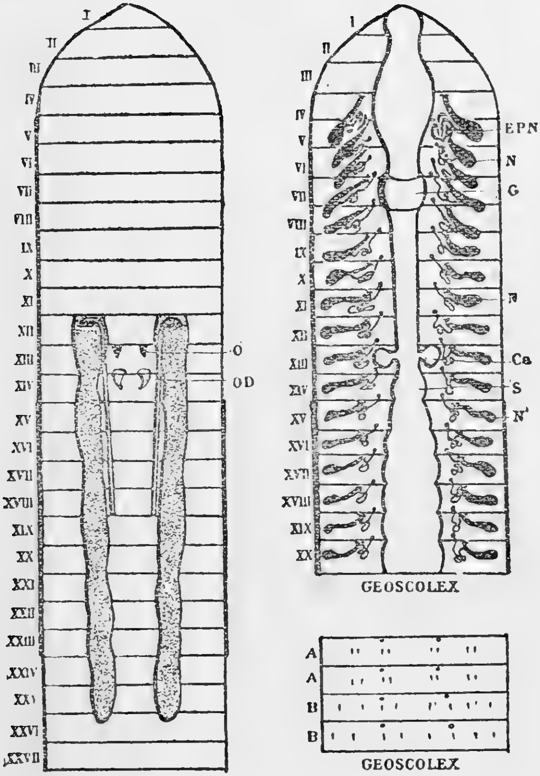
FIG. 21.—Geoscolex (Titanus). *a.* On the left genital system. O. Ovary. OD. Oviduct. No spermathecæ are known. Modified (in accordance with my own observations) from Perrier's figure of G. maximus, Leuckart (T. brasiliensis, E. P.), in Nouv. Arch. Mus. d'Hist. Nat.,' viii, 1872, pl. i, fig. 15. *b.* On the right alimentary system. G. Gizzard. ca. Calciferous diverticulum. S. Commencement of sacculated intestine. The first nephridium is slightly different from the rest, and forms an extra-buccal pepto-nephridium, EPN., the coiled tubule being more compact, and the cæcal part of the duct shorter. NN. The anterior nephridia, in which the tubule leaves the duct about halfway along its length. N.[1] The posterior nephridia, in which the tubule joins the cæcum near its external aperture. Composed from my own observations. *c.* Exterior of four somites: A.A. from the anterior part of the body, where the setæ are in couples; B.B. from the posterior region, where the setæ are separate.

Distribution: Brazil.

FIG. 22.—Urochæta. *a.* Genital system. Composed from Beddard's description in 'Quart. Journ. Micr. Sci.,' xxix, p. 246. SP. The first spermatheca. *b.* Alimentary system. G. Gizzard. ca. Calciferous gland. S. Commencement of the sacculated intestine. Composed from my own observations. The nephridia are modified from Perrier's figures of U. corethrura in 'Arch. Zool. Exp.,' iii, 1874. The first nephridium (EPN.) is much larger than the following ones, both the tubular portion and its duct being greatly developed; there are at least three funnels to this extra-buccal pepto-nephridium. *c.* View of four somites, namely, VI, XX, and two consecutive more posterior somites (PP.), in order to show the couples of setæ anteriorly, and the scattered and alternate arrangement of these posteriorly. In Somite XX, in which the spermiducal pore is situated but not shown, the ventralmost setæ (No. 1) are replaced by groups of larger penial setæ. After Beddard, 'Proc. Roy. Soc. Edinb.,' xiv, 1887, p. 162.

Distribution: South America and neighbouring islands also Australia, Sumatra.

21.

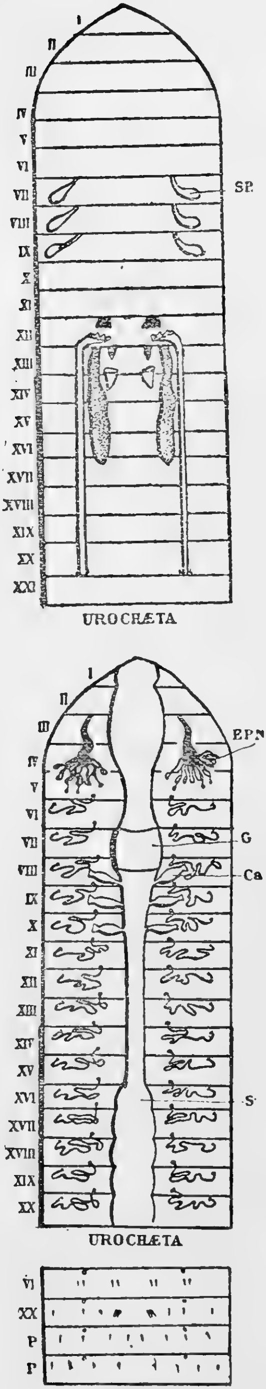


GEOSCOLEX

GEOSCOLEX

GEOSCOLEX

22.



UROCHÆTA

UROCHÆTA

UROCHÆTA

Fig. 23.—Diachæta. *a, b.* Genital and alimentary systems. sp. Spermatheca. g. Gizzard. s. Commencement of acculated intestine. Modified from my own figures in 'Quart. Journ. Micr. Sci.,' xxvii. n. The normal nephridia commence, as in Urochæta, immediately behind the extra-buccal pepto-nephridium (epn.). *c.* Somites xxi, xxii, xxiii, seen externally, showing the alternation of the setæ with exception of No. 1 on each side, the position of the nephridiopores (rings), and of the spermiducal pores, which are represented as black dots.

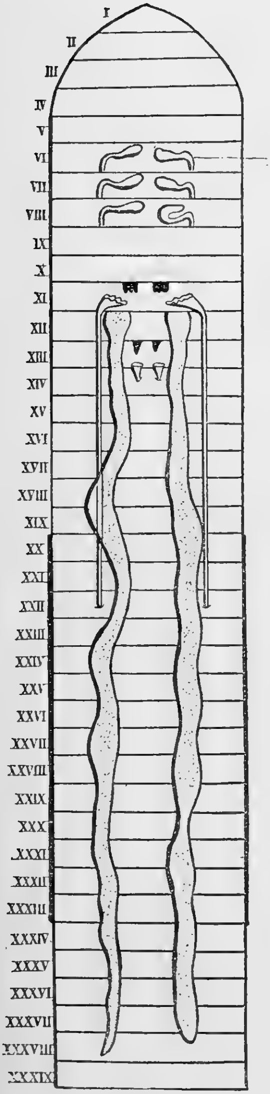
Distribution: St. Thomas, West Indies.

Family VIII.—Rhinodrilidæ.

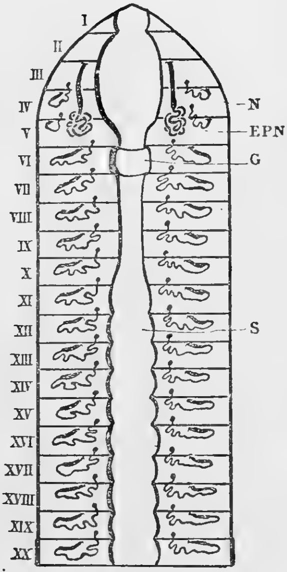
Fig. 24.—Rhinodrilus. *a, b.* Genital and alimentary systems and nephridia. Composed from my own observations on, and from Beddard's description of, R. (Thamnodrilus) gulielmus, 'Proc. Zool. Soc.,' 1887, p. 154. Following the greatly modified first or extra-buccal pepto-nephridium (epn.) are seven pairs of nephridia (n.) which differ from the more posterior ones (n.^{1}) in Somite x in having no cæcal prolongation of the duct. cœ. The cæcum of the posterior nephridia. sp. Spermathecæ. g. Gizzard. ca. The first calciferous diverticulum. s. Commencement of the sacculated intestine. *c.* External view of Somites xix, xx, and xxi, to show setæ, nephridiopores, and intersegmental spermiducal pores.

Distribution: North of South America.

23.



DIACHÆTA



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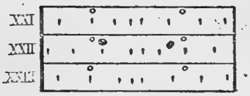
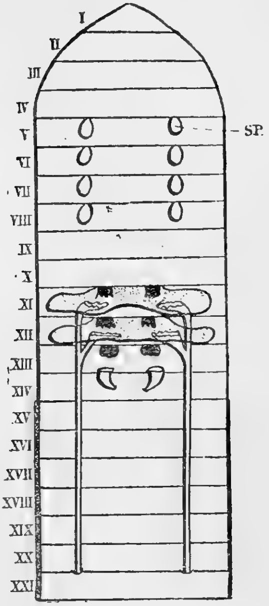
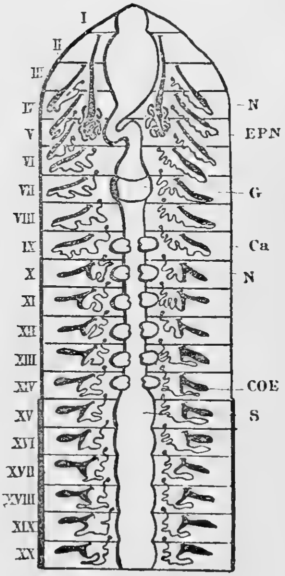


DIACHÆTA

24.



RHINODRILUS



RHINODRILUS

RHINODRILUS

Fig. 25.—Microchæta. *a, b.* Genital and alimentary systems and nephridia. Copied from my own figures of Microchæta rappi, 'Quart. Journ. Micr. Sci.,' xxvi, pl. xv. The cæcum of the nephridium is less marked in the anterior nephridia (N.). In the posterior nephridia (N.[1]), in Somite x, et seq., the cæcum (CŒ.) is very large. In *a*, O. is ovary; OD. oviduct; OS. ovisac; SP. the numerous small spermathecæ. As mentioned in the body of this paper, the peristomium in M. beddardi is provided with setæ, so that the ovaries and testes are morphologically in their normal position. In M. rappi, however, there is no trace of setæ in the peristomium, so that the gonads appear in one somite in advance of the normal position. In *b*, G. is the gizzard; ca. the calciferous diverticulum; S. the commencement of the sacculated intestine. In *c*, three normal somites are shown.

Distribution: Cape of Good Hope and Natal.

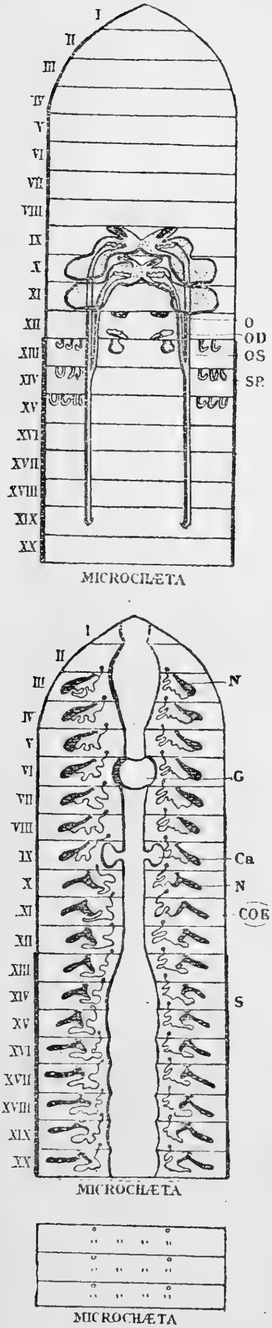
Fig. 26.—Urobenus. *a, b.* Genital and alimentary systems and nephridia. Copied from my own figures in 'Quart. Journ. Micr. Sci.,' xxvii, pl. viii. The anterior nephridia (N.N.) are larger than the following ones (N.[1]), and the cæcal portion (CÆ.) of the duct is less developed. In *a*, SP. marks the first spermatheca. In *b*, G. is the gizzard; ca. the first calciferous diverticulum; P. the first of the series of pouches of the intestines; P.[1] the last of the series,—the intermediate eight somites are removed; C. the peculiar cæcum in Somite XXVI, and S. the commencement of the sacculated intestine. *c* represents Somites XIX, XX, and XXI, to show the setæ, nephridiopores, and spermiducal pores.

Distribution: Brazil.

Fig. 27.—Hormogaster. *a, b.* Genital and alimentary systems and nephridia. Modified from Rosa's figures of H. redii in 'Sulla Struttura dello H. redii,' Torino, 1888. We have no information as to any variation of nephridia. SP. Spermatheca. OS. Ovisac. G.[1], G.[2], G.[3] The three gizzards. C. Globose cæcum in Somite XXI. Six somites are removed. *c* represents three ordinary somites.

Distribution: Italy.

25.

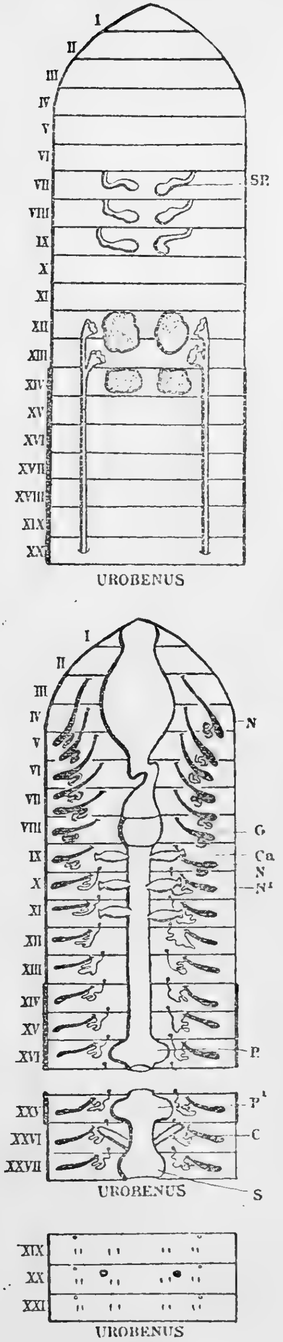


MICROCHÆTA

MICROCHÆTA

MICROCHÆTA

26.

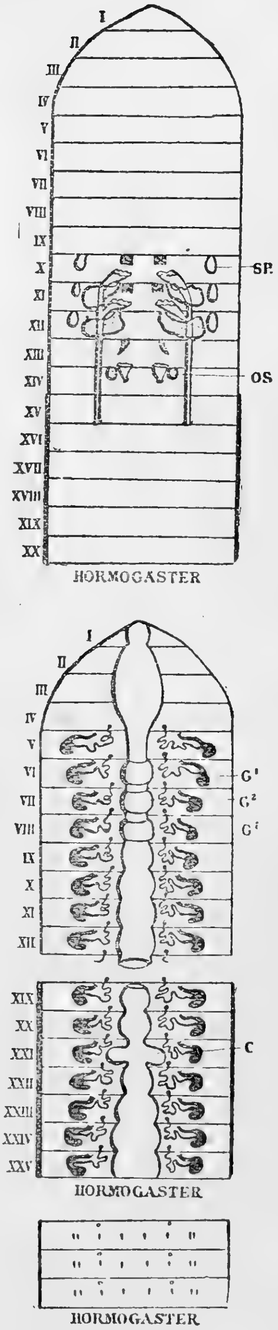


UROBENUS

UROBENUS

UROBENUS

27.



HORMOGASTER

HORMOGASTER

HORMOGASTER

Fig. 28.—Brachydrilus. *a, b.* Genital and alimentary systems. Original. See the description, 'Zool. Anzeig.,' 271, 1888. There are two pairs of nephridia which are very simple —IN. the inner nephridia; ON. the outer nephridia in every somite. In the Somites X and XI are four sacs on each side, which are not represented, as they lie underneath the sperm-sacs; these probably correspond to the "albumen-glands" of Lumbricus. I believe the same fusion of somites has gone on here as in Microchæta. In *a*, SP. is one of the small spermathecæ, which in position is abnormal. O. is the ovary. In *b*, G. is the gizzard. ca. Calciferous gland. S. Commencement of sacculated intestine. In *c*, the setæ and nephridiopores are shown.

Distribution: Unknown.

Family IX.—LUMBRICIDÆ.

Fig. 29.—Lumbricus. *a, b.* Genital and alimentary systems. Original. See Hering, 'Zeit. f. wiss. Zool.,' viii, 1856, pl. xviii; Lankester (alimentary canal), 'Quart. Journ. Micr. Sci.,' 1865–6. In *a*, SP. the first spermatheca of one side. OS. Ovisac. In *b*, G. is gizzard. PR. Proventriculus. S.[1] Commencement of sacculated intestine. ca. Calciferous glands, bilobed, one lobe in Somite XII, the other in Somite XI; these communicate with a pouch (CP.) which opens into the œsophagus in Somite XI. *c* shows the exterior of Somites XIV, XV, and XVI, with setæ, nephridiopores, oviducal pore in XIV, and spermiducal pore in XV (as black dots).

Distribution: Europe.

Fig. 30.—Allolobophora. *a.* Genital system. SP. Spermatheca: three pairs are shown, as is the case in A. chlorotica; in other species more, in others less than three pairs are present. OS. Ovisac. Modified from Bergh's figure of A. turgida, 'Zeit. f. wiss. Zool.,' xliv, pl. xxi. *b.* Alimentary canal. G. Gizzard. PR. Proventriculus. ca. Calciferous gland in Somite XI, opening into the pouch (CP.). Original. *c.* External view of a somite from three different species: A. of A. chlorotica; B. of A. subrubicunda; and C. of A. boeckii.[1]

Distribution: Europe.

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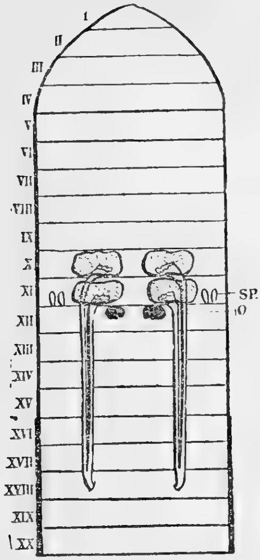
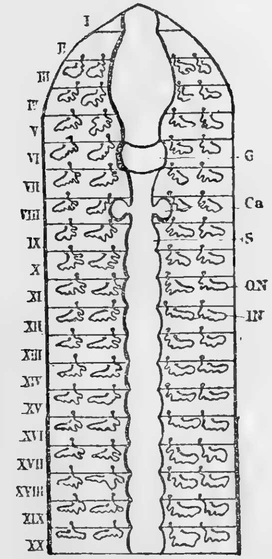
[1] The nephridipores are too feebly indicated.

28.



BRACHYDRILUS



BRACHYDRILUS

BRACHYDRILUS

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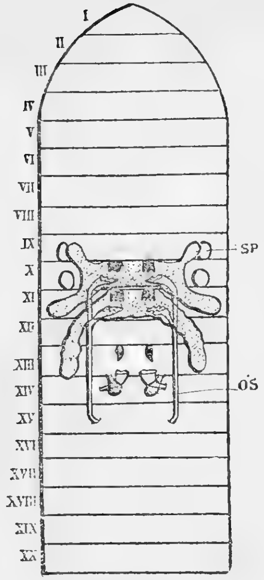
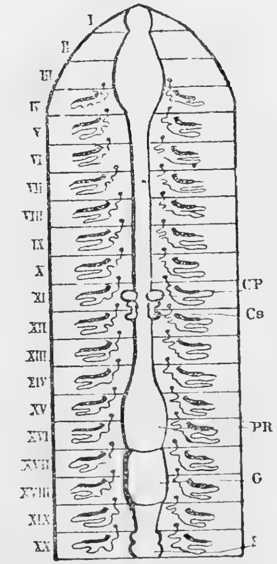
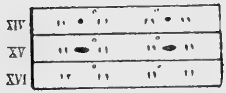


LUMBRICUS



LUMBRICUS



LUMBRICUS

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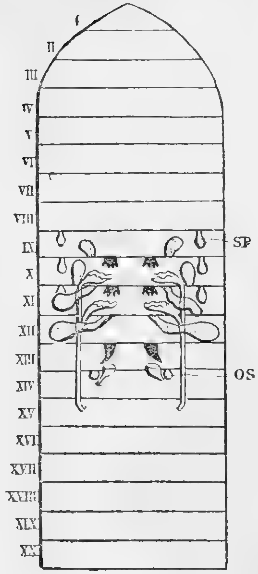
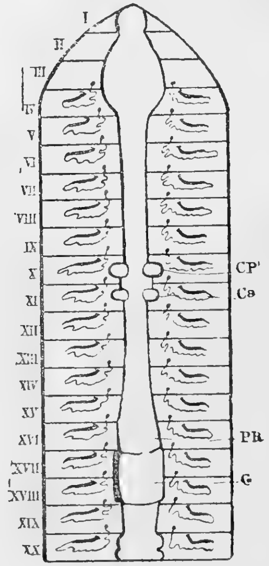
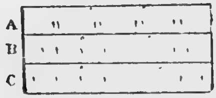


ALLOLOBOPHORA



ALLOLOBOPHORA



ALLOLOBOPHORA

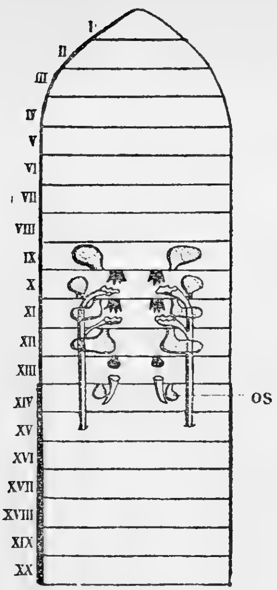
FIG. 31.—Criodrilus. *a, b.* Genital and alimentary systems. os. Ovisac. w. Thick-walled region of œsophagus. From my own figures, 'Quart. Journ. Micr. Sci.,' xxvii, pl. xxxviii. The nephridia, similar to those of Lumbricus, commence in Somite x.

Distribution: Europe.

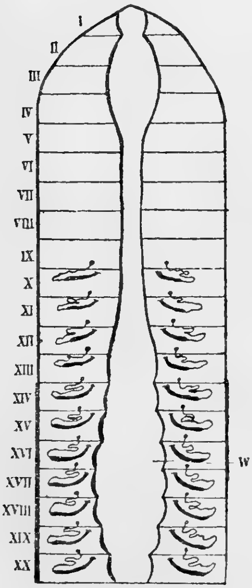
FIG. 32.—Allurus. *a.* Genital system. Modified from Beddard's figure, 'Quart. Journ. Micr. Sci.,' xxviii, pl. xxv, fig. 2. The small white circles (SP.) in Somite VIII represent certain microscopic spermathecæ according to Beddard, but no spermatozoa were found, and perhaps, from their abnormal position, they may be "albumen-glands." os. Ovisac. In *b*, G. Gizzard. s. Commencement of sacculated intestine. ca., ca. The first and last of the four calciferous glands. x. A pouch (? corresponds to the pouch [CP.] in Lumbricus). *b.* Alimentary system. Composed from Beddard's description, 'Quart. Journ. Micr. Sci.,' xxviii, p. 368.

Distribution: Europe.

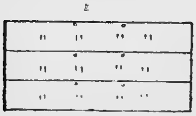
31.



CRIODRILUS

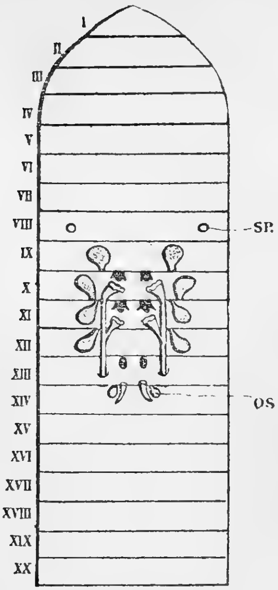


CRIODRILUS

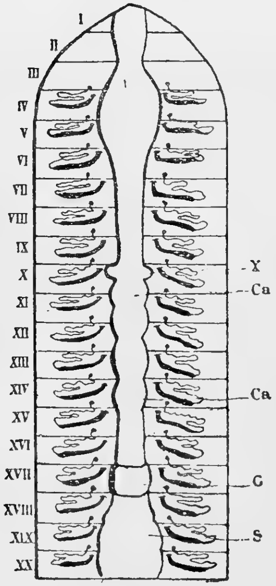


CRIODRILUS

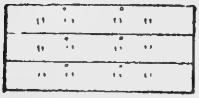
32.



ALLURUS



ALLURUS



ALLURUS

[The following figures are placed out of their proper place, as they have been constructed during the passage of the text through the press.]

FIG. 33.—Pygmœodrilus. *a.* Genital organs, partly from Michaelsen's figure of P. quilimanensis ['Jahrb. d. hamburgh wiss. Anstalten,' vii, 1890]. SP. Spermatheca, with its numerous diverticula. s. Sperm-sac. M. Muscular thickening of the sperm-duct. BC. Bursa copulatrix, which contains a penis. PRO. The lay prostate; the narrow portion is muscular, the distal region is glandular. *b.* Alimentary canal, from Michaelsen's description. ca. Calciferous diverticulum. There is some doubt experienced as to the existence of a gizzard. The nephridia are not described beyond the statement that there is a pair in each somite. *c.* Exterior of three somites, showing setæ in couples; the nephridiopores; and male pores in XVIIth Somite.

Distribution: Quilimane, near Zanzibar.

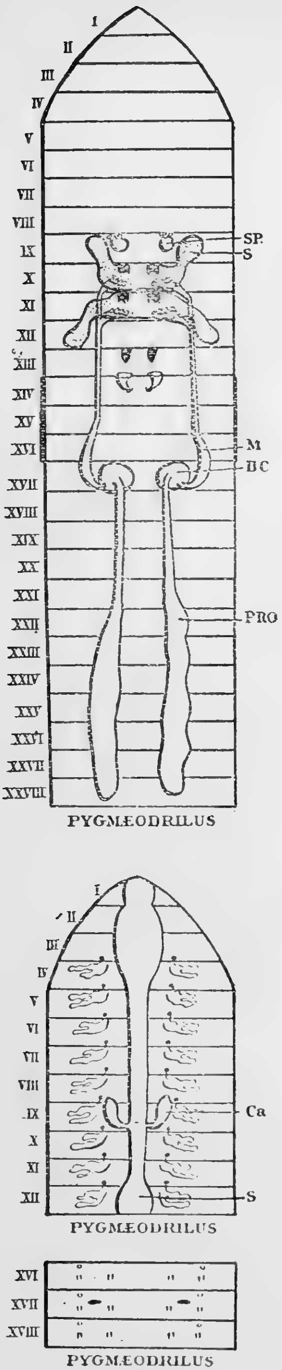
FIG. 34.—Nemertodrilus. *a.* Genital system, from Michaelsen's description of N. griseus in 'Jahrb. d. hamburg. wiss. Anstalten,' vii, 1890. s^1. Anterior sperm-sac. s^2. Greatly elongated posterior sperm-sac. os. Ovisac, which is prolonged backwards (os^1.) and is regarded by Michaelsen as "spermatheca." PRO. Prostate. *b.* Alimentary tract and nephridia, from Michaelsen's description. G. Gizzard. s. Commencement of sacculated intestine. No details as to nephridia are given, except that they are a pair to each somite, and have, apparently, a dilated "duct." *c.* Exterior of Somites XVI, XVII, and XVIII, to show the couple of setæ, nephridiopores, and male pores.

Distribution: Quilimane, Zanzibar.

FIG. 35.—Callidrilus. From Michaelsen's description of C. scrobifer, in 'Jahrb. d. hamburg. wiss. Anstalten,' vii, 1890. *a.* Genital system. s. $s.^4$ The first and fourth sperm-sacs. SP. The numerous, small spermathecæ. X. is a structure which Michaelsen identifies as a prostate. He states that it is small, and from the general anatomy of the worm I fancy that it may be merely a thickening of the body, such as is present in Brachydrilus. *b.* Alimentary and excretory system. M. A thickening, which is, according to Michaelsen, not muscular. It probably represents a gizzard. s. Commencement of sacculated intestine. The nephridia are merely said to be paired, and to be provided with a bladder, which I take to mean a "cæcal" outgrowth of the duct. *c.* Exterior of Somites XVI, XVII, and XVIII, to show couples of setæ, nephridiopores, and male pores. [*N.B.*—I believe this worm belongs to my family Rhinodrilidæ].

Distribution: Quilimane, Zanzibar.

33.



PYGMÆODRILUS

PYGMÆODRILUS

PYGMÆODRILUS

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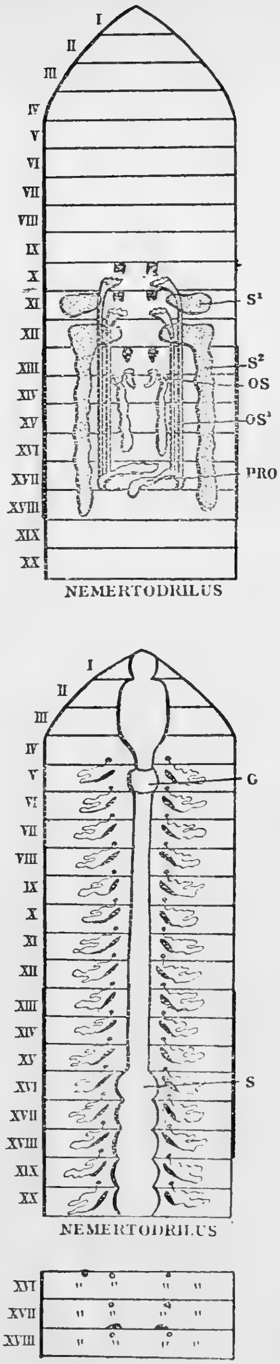
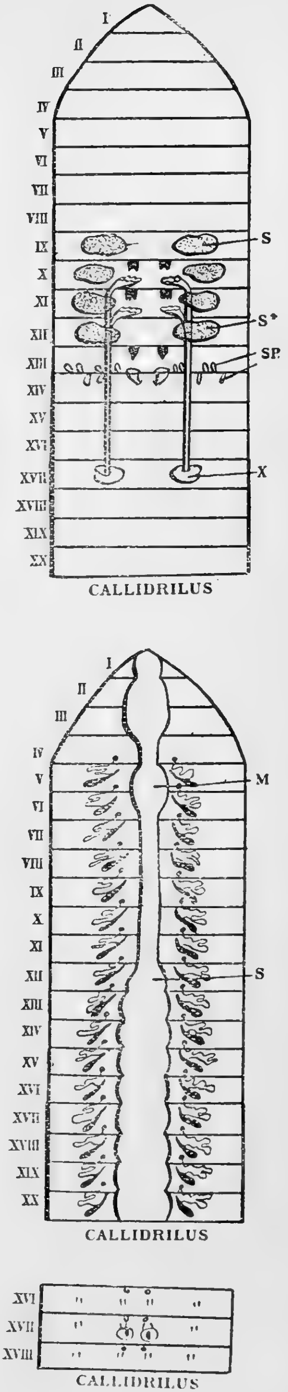


NEMERTODRILUS

NEMERTODRILUS

NEMERTODRILUS

35.



CALLIDRILUS

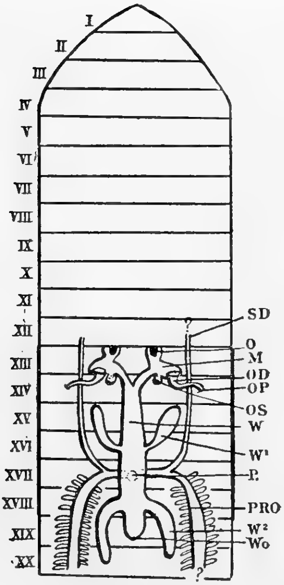
CALLIDRILUS

CALLIDRILUS

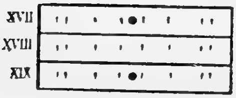
Fig. 36.—Polytoreutes. A very brief description, with a figure, is given by Michaelsen of the hinder portion of the genital system of P. cœruleus, in 'Jahrb. d. hamburg. wiss. Anstalten,' vii, 1890. No details are given of the alimentary system. *a.* Genital system. SD. Sperm-duct. O. Ovary. M. A large sac, into which open (OD.) the oviduct; the ovisac (OS.) and the so-called "spermathecæ" (W.). This has a unique position and shape; it is produced into lateral pouches (W.^{1}, W.^{2}), and opens externally by a median pore (WO.) in Somite XIX. The oviducal pore is shown at OP. The prostate (PRO.) is long, but how long Michaelsen does not say; and is beset with numerous secondary sacs. Its aperture is in front of that of the spermatheca on Somite XVII, and is represented by a dotted circle, and labelled P. *c.* Exterior of Somites XVII, XVIII, and XIX, to show the setæ and median genital pores; that of the spermatheca in XIX, and that of the ducts in XVII.

Distribution: Zanzibar.

36.



POLYTOREUTES



POLYTOREUTES

On the Origin of Vertebrates from Arachnids.[1]

By

William Patten, Ph.D.,
Professor of Biology in the University of North Dakota, Grand Forks.

With Plates XXIII and XXIV.

> "In the growth of each science, not only is correct observation needful for the formation of true theory, but true theory is needful as a preliminary to correct observation."—H. Spencer.

[2] The "Annelid theory," after fifteen years of dexterous modelling, is now as far as ever either from fitting the facts of Vertebrate structure, or from shedding any direct light on the great problem of the origin of Vertebrates. It certainly is not without significance that, of all those who with willing eyes and minds have grappled with the Annelid theory, not one has discovered a distinctively Annelid feature in Vertebrates: mesoblastic somites, nephridia, segmental appendages, and segmental sense-organs are found in nearly all segmented animals.

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[1] I include in the Arachnida the Spiders, Scorpions, Limulus, Trilobites, and Merostomata.

[2] Most of my observations on Acilius, Scorpio, and Limulus were made in the Lake Laboratory, Milwaukee, Wis. I am greatly indebted to the founder of that institution, Mr. E. P. Allis, for generously placing at my disposal the excellent facilities for research which his laboratory affords.

As a full description of my observations could not be published without considerable delay, it seemed advisable to present my theoretical conclusions first, at the same time giving a short account of those facts bearing directly on the subject-matter.

A few simple diagrams have been introduced to make the text more intelligible. These are throughout referred to as Figs. 1, 2, 3, &c. The reference to figures in the two plates is always indicated by the addition of the letters Pl. XXIII or Pl. XXIV.

In failing to add materially to what the anatomy and embryology of Vertebrates themselves can demonstrate, the Annelid theory not only is sterile, but is likely to remain so; because unspecialised segments being characteristic of Annelids, it cannot hope to elucidate that profound specialisation of the Vertebrate head which it is the goal of Vertebrate morphology to expound. Moreover, since Vertebrate morphology itself reflects as an ancestral image only the dim outlines of a segmented animal—but still not less a Vertebrate than any now living,—it is clear that the problem must be solved, if at all, by the discovery of some form in which the specialisation of the Vertebrate head is already foreshadowed.

Since of all Invertebrates, concentration and specialisation of head segments is greatest in the Arachnids, it is in these, on a priori grounds, that we should expect to find traces of the characteristic features of the Vertebrate head. Finding from time to time confirmation of this preconceived idea as the unexpected complexity of the Arachnid cephalothorax revealed itself, I now feel justified in formulating a theory that Vertebrates are derived from Arachnids.

I have presented the facts as they appear to me, and have hazarded an interpretation of them; not, however, without a lively sense of the difficulties of the task, certainly not without the conviction that I may have fallen into errors which greater experience and a better knowledge of the intricacies of Vertebrate anatomy might have avoided.

In the following preliminary sketch of the structure of Limulus, and especially of the Scorpion, I shall attempt to prove—(1) That in the Scorpion the cephalothoracic neuromeres, nerves, sense-organs, and mesoblastic somites present, in a general way, not only the same specialisation and the same numerical arrangement in groups, but also the same difference as a whole from the body-segments, as do the corresponding parts in the Vertebrate head; (2) that the Arachnid cartilaginous sternum represents the primordial cranium of Vertebrates; (3) that in the Trilobites and Merostomata the internal structure of the cephalothorax resembles in some respects that of Scorpio and Limulus; (4) that the remarkable fish-like Pterichthys and related forms, judging from their external structure, are closely related to the Merostomata, and serve to connect Arthropods with Vertebrates; and (5) that the embryology of Vertebrates in its main features can be reduced to the Arthropod type.

First let me state certain conclusions that have been reached concerning segmentation in Arthropods.

In Scolopendra each neuromere has four pairs of spinal nerves; the first two pairs in each neuromere are larger and darker, and probably contain more sensory fibres than the two following pairs.

Certain facts indicate that this condition is the ground plan of the nervous system in all Arthropods, and that the various modifications of it found in other Arthropods are produced by fusion of the nerves. The two sensory nerves tend to fuse with each other first; afterwards the two motor nerves; and finally the double motor and the double sensory nerves unite, thus producing, in different groups of Arthropods, neuromeres with four, three, two, and one pair of nerves.

In Scolopendra the neuromeres appear to be double; and, if what we have indicated above is true, it follows that in all Arthropods the neuromeres, and consequently the segments themselves, are double. In support of this view we mention the following facts:—(1) In all Arthropods carefully studied two cross commissures have been found in each neuromere. (2) In Acilius the median furrow between these cross commissures is similar to that between the successive neuromeres. (3) In Acilius, according to my observations, there are two pairs of tracheal invaginations in each segment: one pair, that which is always readily seen, is situated near the anterior edge of the segment; the other, which is very rudimentary and difficult to distinguish, is situated in the same line as the first, but near the posterior edge of the segment. (4) In all the insect embryos I have examined, and in almost all figures where the tracheal openings were represented, the stigmata were situated near the anterior edge of the segment. (5) The frequent presence in Arthropods, especially Crustacea, of bifurcated appendages; this condition is due, we may suppose, to the partial fusion of two originally distinct appendages. (6) The frequent occurrence of insect monsters having double pairs of legs. (7) According to Heathcote's important observations, the segments in Julus are certainly double, as shown by the duplication in each segment of the somites, cardiac ostia, arteries, neuromeres, tracheæ, and legs. (8) In Scorpio the neuromeres are distinctly double, each one being composed of a large anterior portion and a small posterior one. Large pit-like invaginations of the median furrow are found between the halves of the anterior portions, and faint indications of a second series of pits between the halves of the posterior portions (Pl. XXIV, fig. 3). But in Scorpio the most singular feature of all is that the parts of each abdominal neuromere finally separate, the posterior portions uniting with the anterior portion of the neuromere just behind it (Pl. XXIV, figs. 3 and 4, and Fig. 11, p. 348). This process may be followed with ease and perfect certainty in surface views.

All these facts point to the conclusion that the segments in all Arthropods are double, and are derived from those of diplopod-like ancestors.

If Vertebrates are derived from Arthropods, they are also, in all probability, composed of double segments. It may be worth mentioning in this connection that in many fishes the spinal nerves, and especially the cervical ones, split up into two, three, and sometimes four pairs of nerves for each neuromere.

I. The Grouping of the Cranial Neuromeres of Scorpio is a result of the varying union of the first thirteen neuromeres.

From the cephalic lobes three neuromeres arise which fuse completely to form the fore-brain of the adult (figs. 1—4, Pls. XXIII and XXIV, and Fig. 1, f. b., p. 321).

The first neuromere of the six thoracic segments pushes its

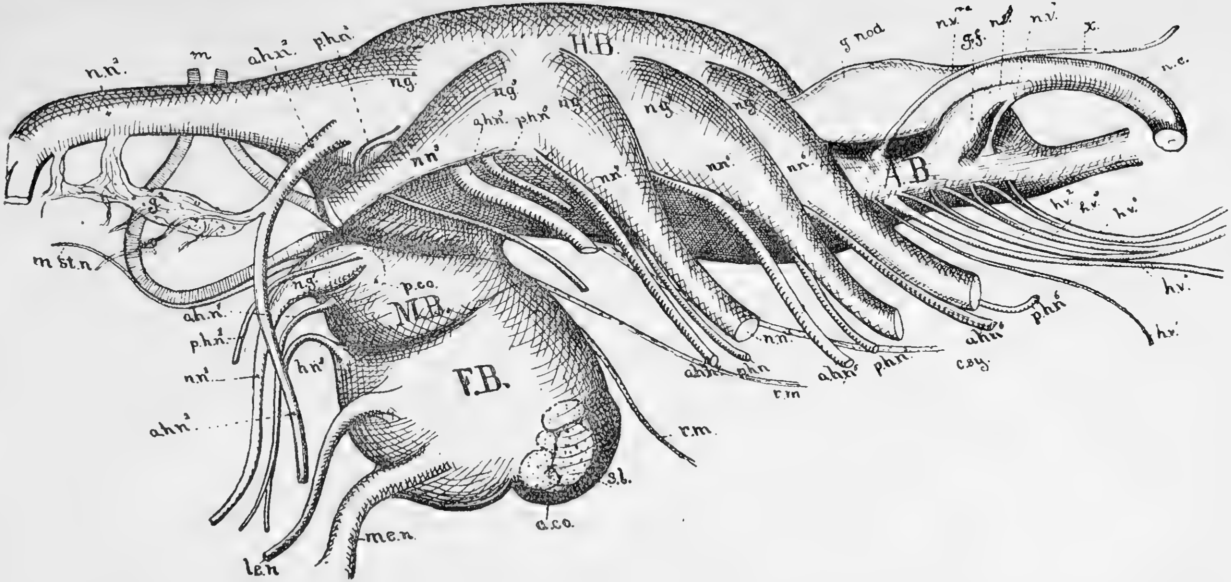

Fig. 1.—Brain of adult Scorpion, constructed by means of sections and dissections.—*A. B.* Accessory brain. *H. B.* Hind-brain. *M. B.* Mid-brain. *F. B.* Fore-brain. *a. co.* Anterior commissures. *a. h.* n^{1}–^{6}. Anterior hæmal nerves of the thoracic neuromeres. *c. sy.* Cranial sympathetic (?). g^{2}. Large ganglion derived from the segmental and coxal sense-organs, and giving off many branches to the scattered sense-organs in skin of chelæ. *g. f.* Ganglion fusiforme. *g. nod.* Ganglion nodosum, or g. striatum. *h.* n^{3}. A very delicate root, probably representing the hæmal nerve of the third fore-brain neuromere, partially fused with the hæmal nerve of the cheliceral segment. *h.* v'. and *h.* v''. The independent anterior and posterior nerves of the first vagus neuromere. *h.* v^{2}. and *h.* v^{3}. The four partially fused hæmal nerves of the second and third vagus neuromeres. *l. e. n.* Lateral eye nerve. *m.* Mouth. *m. e. n.* Median eye nerve. *m. st. n.* Median stomodæal or rostral nerve. *n. e.* Comb or pectinal nerve. *n.* g^{1}–^{6}. Neural ganglia at the base of the neural nerves. *n.* n^{1}–^{6}. Neural nerves of the thoracic segments. *h.* v^{1}–^{4}. Roots of the neural vagus nerves. *p. h.* n^{1}–^{6}. Posterior hæmal nerves of the thorax. *p. co.* Posterior brain commissure. *s. l.* Semilunar lobe, or first brain-segment. *r. m.* Retractor muscles to œsophagus.

way in front of the mouth, forming a sharply defined region, that I shall call the mid-brain (Fig. 1, M. B.).

The remaining five thoracic neuromeres are imperfectly fused; they constitute the hind-brain (H. B.). Finally, four very intimately fused abdominal neuromeres are added to the preceding ones, forming an accessory brain (A. B.).

A very similar grouping is found in Vertebrates. (1) As shown by the segmental character of the optic, pineal, and olfactory nerves, the fore-brain probably contains at least three completely fused neuromeres. (2) The mid-brain, as is now generally recognised, contains but a single neuromere, which, judging from the character of its nerves and somite, probably belonged originally to what Gegenbaur calls the six primitive head-segments, and which, just as in Arachnids, has subsequently become separated from them, forming an independent region. (3) The hind-brain is composed of five or six neuromeres, which Gegenbaur, omitting the fore and accessory brain, regards as the primitive brain; the large size of these neuromeres in Vertebrates, their incomplete fusion, and the distinct swellings at an early stage in this brain region, are facts to be expected on the Arachnid theory, for these features are also characteristic of the six thoracic neuromeres of Scorpio and Limulus. (4) According to Balfour and Van Wyhe, there is an accessory brain in Vertebrates composed of four body neuromeres, secondarily added to the head.

There is difference of opinion as to the exact number of neuromeres in each brain region of Vertebrates; but as the matter now stands it would not violate these views more than they do one another to assume that the grouping of cranial neuromeres in Vertebrates is exactly the same as in Scorpions.

II. Spinal Nerves.—In embryo Scorpions each neuromere, except those of the fore-brain, has three pairs of nerves; one pair is mainly motor, another mainly sensory, and the third is probably sympathetic.

In the abdominal region the nerves to each neuromere fuse to form the spinal nerves of the adult; but the distal and proximal ends of the primitive motor and sensory nerves remain unfused, forming for each spinal nerve two distinct branches and two roots. The abdominal sympathetic nerves are very small, and their relation to nerves of the adult has not been in all cases determined.

The sensory root of the adult spinal nerve arises near the neural surface of the neuromere. Besides the ordinary fibres, it contains an axial bundle of coarse and deeply stainable nerve-tubes, surrounding which is an elongated mass of small ganglion-cells (Fig. 2, *sp. g.*).

The motor root arises near the hæmal surface of the neuromere, and is distinguished by its light colour and by the absence of the dark nerve-tubes and ganglion-cells. A short distance from the neuromere the motor and sensory roots unite to form a single nerve, which, on reaching the sides of the body, divides into two branches, one extending backwards, the other laterally (Fig. 4).

The above features are not so clearly defined in the caudal segments.

Thus the abdominal spinal nerves of Scorpio resemble the spinal nerves of Vertebrates—(1) In their origin from two or more originally separate nerves; (2) in the failure of the distal and proximal ends of the nerves to unite; (3) in the motor and sensory roots arising respectively from the hæmal and neural surfaces of the nerve-cord; (4) in the presence of two kinds of nerve-tubes in the sensory root; (5) in the presence of a collection of ganglion-cells in the sensory root, between the nerve-cord and the point where the two roots unite; (6) in the origin, as will be shown later, of this ganglion from a specialised part of a dark lateral border of the ventral cords, comparable with the neural crest of Vertebrates.

III. THE THORACIC OR CRANIAL NERVES of Scorpio remain separate throughout life; hence they differ from the abdominal nerves in the same way that it is supposed some of the Vertebrate cranial nerves differ from the spinal ones.

Examined more closely, we find that of the three pairs of nerves to the first hind-brain neuromere, that supplying the chelæ is much the largest. We shall call it the neural or pedal nerve; it undoubtedly corresponds to the sensory roots of the abdominal segments, and agrees with them in being a mixed motor and sensory nerve, in containing two kinds of nerve-tubes, and in having at its base a ganglionic swelling that we shall call the neural ganglion (Figs. 1 and 3, *n. g.*). The latter is serially homologous with the spinal ganglia, as shown by its development from the neural crest; but it differs from them in being very much larger, in having the ganglion-cells arranged upon the surface of the nerve-root, and in being more intimately fused with the nerve-cord. In Limulus there are at the base of the pedal nerves similar swellings; they are here more clearly ganglia of pedal nerves, because they are more independent of the nerve-cord than in Scorpio (Fig. 10, *g.* n^4.).

In Scorpions about ready to hatch, a short distance beyond the neural ganglion is a purely sensory and richly ganglionated coxal nerve; it is distributed to a number of sense-organs on the median basal side of the legs; one of these organs is very much larger than the rest, and from it is split off a very large coxal ganglion (Fig. 3, *cx. g.* and *cx. n.*). Each of the sense-buds (*s. b.*) also gives rise to one or more ganglion-cells, which pass into the nerve that supplies the bud. There is a similar set of coxal sense-organs in the spiny mandible-like swellings in the coxal joints of Limulus.

The main nerve is continued beyond the coxal nerve into the chelæ. Near the base of the chelæ it expands into a ganglionic swelling, formed by an inward proliferation from a true segmental sense-organ (*s. s. o.*).

The exact fate of the coxal and segmental ganglia I have not been able to determine. The large coxal sense-organ seems to disappear, but the ganglion produced by it wanders inward, forming a swelling on the coxal nerve. The segmental sense-organ also disappears, and its ganglion probably unites with the coxal ganglion. At any rate in the adult, I find a large lateral ganglion united by several branches not only with the pedal and hæmal nerves of the chelæ, but also with the skin (Fig. 1, *g. r.*). I believe this ganglion is formed by the fusion of the segmental and coxal ganglia.

All the pedal nerves of the thorax are built on the above

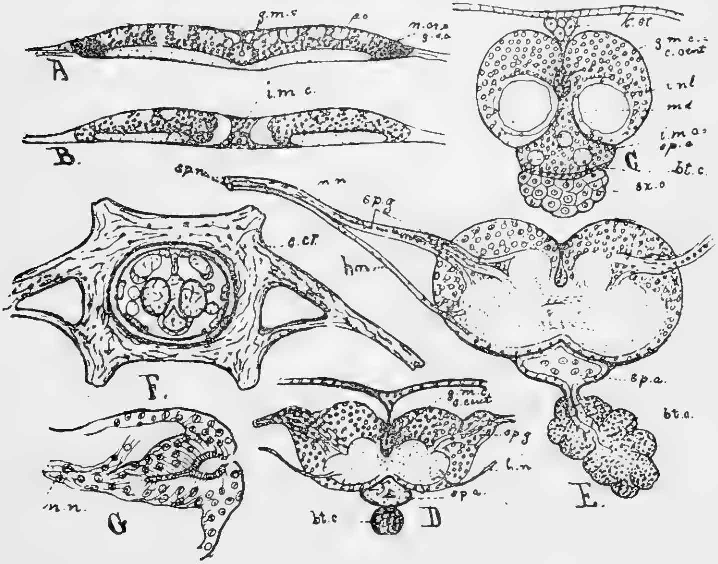

FIG. 2.—*A.* Section through the anterior portion of a neuromere of Scorpio in Stage E, fig. 3. *B.* Section, at same stage, through the posterior portion of a neuromere. *C.* Section of nerve-cord in anterior portion of abdomen of a Scorpion embryo, with pigment just appearing in the body-wall. *D.* Section through the third abdominal neuromere of embryo about ready to hatch. *E.* Section through first abdominal neuromere of adult. *F.* Section through the occipital ring of the endocranium or sternum of Scorpio. *G.* A segmental sense-organ of Stages F, G. *bt. c.* Botryoidal cord. *c. cr.* Cartilaginous endocranium. *c. cent.* = *g. m. c.* Imperfect canalis centralis formed by the ganglionic portion of the median furrow. *g. m. c.* Ganglionic portion of median furrow. *g. s. o.* One of the large marginal sense-organs that give rise to the spinal ganglia. *h. n.* Hæmal nerve. *i. m. c.* Interganglionic portion of median furrow, or "anlage" of spinal artery. *i. nl.* Inner neurilemma. *k. st.* Wedge-shaped cord, a remnant of the median furrow, out of which a branch to the spinal artery is formed. *n. cr.* Neural crest. *md.* Medulla. *n. n.* Neural nerve. *sp. a.* Spinal artery. *sp. g.* Spinal ganglion. *sp. n.* Spinal nerve. *sx. o.* Sexual organs.

plan, the only difference being that in the other segments the coxal sense-organs and consequently the coxal nerve are smaller, and there seems to be no lateral ganglion in the adult.

Two pairs of hæmal nerves arise from each of the six thoracic neuromeres; they are small and light coloured, and are probably entirely motor, supplying the innermost muscles, and probably some of the anterior viscera (Figs. 1 and 3, *a. h. n.* and *p. h. n.*).

Segmental Sense-organs and Ganglia.—One of the most important evidences of the Annelid origin of Vertebrates has been the similarity between the segmental sense-organs of fishes and Annelids. The value of this evidence has recently been destroyed, because it is now known, from the researches of Beard and Allis, that the lateral line-organs of fishes are formed by a backward growth of cranial sense-organs, and that their segmental arrangement is only secondarily acquired. Moreover, Beard's researches show such an unsuspected complication of cranial ganglia, sense-organs, and nerves, that it is difficult, if not impossible, to compare them with similar parts in the body. To say the least, his observations do not strengthen the Annelid theory, because the latter cannot explain this extraordinary difference between the cranial and spinal nerves, its aim and only hope being the reduction of the ancestral Vertebrate to a collection of like, not unlike metameres. We certainly do not have this difficulty with the Arachnid theory, because the distribution and history of the thoracic sense-organs, ganglia, and nerves of Scorpio and Limulus, resemble in a striking way those of the corresponding parts of Vertebrates. For example, in Scorpio (1) the pedal nerve, its neural and lateral ganglia, and its purely sensory branch, or coxal nerve, the coxal and the segmental sense-organs, and the anterior and posterior hæmal nerves,—all these features produce in each thoracic neuromere a complex condition similar to that found in a typical cranial neuromere of Vertebrates. (2) Omitting the fore and accessory brain, and using the cranial ganglia as guides, there are in the head of

Vertebrates six sets of sense-organs, or exactly the same number as in Scorpio and Limulus. In Vertebrates the ganglia, presumably derived from segmental sense-organs, are the ciliary, Gasserian, facial, auditory, and glossopharyngeal, and the first free vagus; or omitting the latter, and counting with some authors the facial ganglion as double, we would still arrive at the same conclusion. (3) In both Scorpio and Vertebrates these sense-organs give rise to "lateral ganglia." (4) In both cases neural ganglia are developed in the head, which are serially homologous with spinal ganglia. (5) In both cases the neural and the spinal ganglia develop from a special modification of the edge of the nerve-cords, the "neural crest." In Scorpio the crest consists of a row of large dark sense-organs extending the whole length of the nerve-cord (Pls. XXIII and XXIV, figs. 1—3, *nc.* = *sp. g.*; and text, Fig. 2, A and D, *nc.* and *sp. g.*; also text, Fig. 11, *sp. g.*). (6) The manner in which the coxal nerve unites with a coxal sense-organ and receives ganglion-cells from it, and the way it becomes connected by small branches

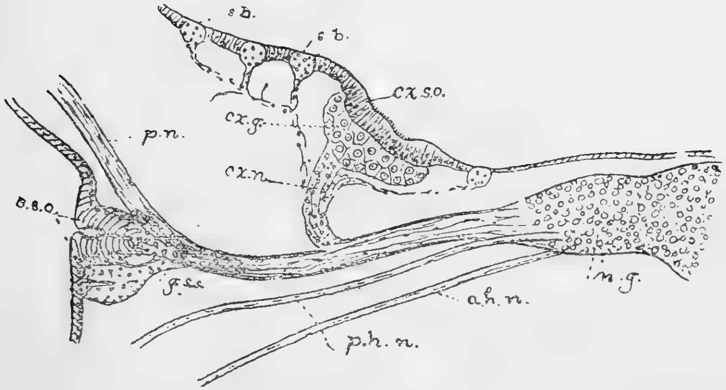

FIG. 3.—Semidiagrammatic section through the base of a leg and a thoracic neuromere of an embryo Scorpion.—*a. h. n.* Anterior hæmal nerve. *cx. s. o.* Coxal sense-organ. *g. s. s.* Ganglion-cells arising from segmental sense-organ. *n. g.* Large neural ganglion, serially homologous with spinal ganglia of abdomen. *p. h. n.* Posterior hæmal nerve. *p. n.* Pedal nerve. *s. b.* Sensory buds (comp. fig. 4, Pl. XXIV, *s. o''.*). *s. s. o.* Segmental sense-organs.

with innumerable sense-buds scattered over the skin of the legs and ventral surface of the body (Fig. 3, *s. b.*, p. 327, and Pl. XXIV, fig. 4) is comparable with the growth of the "supra-branchial" nerve of Vertebrates. (7) Moreover, although we have not determined with certainty the history of the ganglia arising from the segmental sense-organs of Scorpio, there is reason to suppose they represent the ganglia which, according to Van Wyhe, are connected with the ventral branch of cranial nerves. We should thus, in another way, arrive at and confirm the conclusion of Froriep, that the ventral root-ganglion is the most primitive; for in Scorpio and Limulus the segmental sense-organs and ganglia are undoubtedly more primitive than the coxal ones. Beard denies that there is any ganglion to the ventral root, so it is difficult to determine whether the coxal sense-organs or the segmental ones, or both, correspond to the supra-branchial sense-organs described by Beard; but for several reasons I am inclined to think they are the coxal sense-organs.

If we accept Beard's scheme of the cranial nerves, the enormous transitory sense-organs of Limulus would come in exactly the same place as the ear of Vertebrates—that is, reckoning three segments to the fore-brain, on the seventh cranial segment. It is also worth mentioning that the general appearance of the two organs at an early stage is very much alike.

The lateral cord of ganglion-cells and nerve-fibres of Limulus may be compared with the "ganglien-zellen-strang" described by Vejdovsky in the Oligochæta, and may be regarded as having the same morphological value as the lateral cord of the central nervous system. It is not improbable that the longitudinal nerves of the Vertebrate head, such as that, for instance, uniting the seventh and fifth nerves, are remnants of a lateral nerve-cord like that in Limulus.

IV. THE VAGUS NERVES of Scorpio, as I shall call them, or those arising from the accessory brain, are intermediate in character between the cranial and spinal nerves; at the same time they present remarkable features not found elsewhere.

The neural nerves to the four vagus neuromeres fuse completely to form the large pectinal nerve; but the neural ganglia at the base of the nerves retain to a certain extent their integrity, forming what I have called the ganglion nodosum or ganglion laminatum (owing to the remarkable concentric laminæ composing its medullary core), the ganglion fusiforme, and the ganglion minus (Fig. 1).

The hæmal nerves to the first vagus neuromere form two distinct pairs, as in the typical cranial segments (*h.* v^1. and *h.* v^2.). In each of the succeeding neuromeres the hæmal nerves have united with each other, forming three nerves with double roots; the latter decrease in length from the first pair to the third, passing gradually into a condition like that in the abdominal hæmal nerves.

A short distance from the brain all five hæmal nerves form a compact bundle extending backwards, some of the nerves passing through the hæmal wall of the cartilaginous cranium or sternum, others passing out of the neural canal. The second and third double nerves (v^2. and v^3., Fig. 4), some distance from the brain, fuse to form a single nerve supplying the first and second lung-books and the ventral surface of the body; on its way to these organs it passes over the ventral surface of the liver, to which it possibly gives branches. The anterior hæmal nerve of the first vagus neuromere (v^1.) runs close to the coxal gland, and, dividing into numerous branches, is lost on the surface of a thick peritoneum-like membrane. The posterior nerve (v^2.) extends along the arthrodeal membrane supplying numerous sense-organs in the skin of the sides and back of the abdomen. The fourth vagus (v^4.) supplies the skin and longitudinal muscles on the ventral surface of the abdomen.

A small nerve arises from the ventral surface of the accessory brain, and supplies the distal portion of the sexual ducts (Figs. 1 and 4, *x.*). I could find no way of ascertaining to what neuromere this nerve belongs.

Hence the term vagus is applicable to these nerves, for, owing, as we shall see, to the almost complete disappearance of their proper field of distribution, they have not only wandered into other segments, but to organs which they do not normally supply.

Little is certainly known about the vagus nerves of Vertebrates, but at present I see no serious objection to supposing they are derived from the vagus of Scorpions. The most important resemblance between these remarkable groups of nerves are the following:—(1) The vagus nerves in both Scorpions and Vertebrates extend backward (although the neuromeres to which they belong have been pushed forward), and supply muscles and internal organs to which the corresponding nerves of the other segments are not normally distributed. (2) This wandering of the nerves in both Vertebrates and Scorpio is probably due to the same cause, i. e. the great concentration of their neuromeres and the absence of their mesomeres; the result is that the nerves must also disappear or wander to other tissues. This point is an important one, because these conditions are not found in any other animals besides Vertebrates and Arthropods. (3) In the Scorpion the main vagus nerve is formed by the early and remarkably complete fusion of four neural nerves of an accessory brain. In Vertebrates the vagus is formed in the same way; but there is nothing to show whether these fused nerves, either in Scorpio or Vertebrates, represent neural nerves or only their sensory branches, or both. (4) The hæmal vagus nerves of Scorpio form a compact and isolated group of nerves evidently undergoing profound secondary changes; already they are partly fused with one another, and their roots have moved backward at the same time that the neural roots have moved forward. Since in Vertebrates there has probably been a similar movement in the vagus region (Gegenbaur), it is possible that in Petromyzon the four posterior vagus roots of the eight described by Ahlborn represent hæmal vagus roots which have moved backward along the medulla oblongata only a little more markedly than the hæmal vagus roots in Scorpio. A part or all of these hæmal nerves in both Scorpio and Petromyzon supply segmental respiratory organs. (5) One large nerve in the vagus group of both Scorpions and Vertebrates is conspicuous on account of its sensory nature and lateral position. (6) In Scorpio the neural vagus nerves supply a specially modified appendage called the comb. There is reason to suppose that originally the vagus of Vertebrates also supplied a specially modified appendage—the pectoral fin. The resemblance between these appendages will be considered later. (7) In Scorpion the neural roots of the vagus and their ganglia decrease in size from before backwards; this is remarkable, since we should naturally expect the third or comb root to be the largest. Van Wyhe has discovered a similar condition in the "anlage" of the vagus of Selachians. (8) The vagus nerves of Vertebrates and Scorpions are derived from four neuromeres not belonging originally to the brain, which are more intimately fused with one another than are those in front of or behind them, while the nerves themselves are the most complex and most modified nerves in the whole body. This condition is all the more extraordinary since, from their position, we should naturally expect these nerves and neuromeres to be intermediate in character between those of the head and trunk. Finally, (9) if we count three segments to the fore-brain, the vagus neuromeres in Scorpio and Vertebrates fall in exactly the same place in the series—that is, in the tenth to thirteenth segments inclusive. Nowhere else in the animal kingdom do we find four segments in the middle of the body with these extraordinary characters.

There are, of course, important differences between the vagus of Scorpio and that of the lowest Vertebrates; but we are content to show here that there are very decided resemblances between them, and that the differences are not greater than those found among the Vertebrates themselves. It is evident that a still further modification of the vagus of Scorpio, in the direction along which it has already advanced so far, would lead up naturally to the most primitive condition of the vagus in Vertebrates.

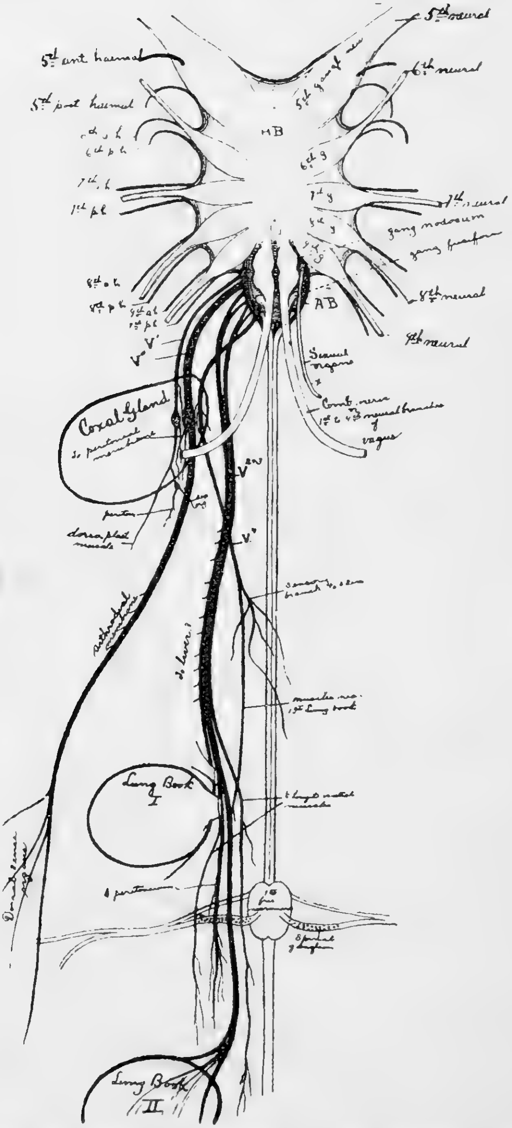

FIG. 4.—Brain and portion of nerve-cord of adult Scorpion, seen from the neural surface, constructed from sections and surface views.—*A. B.* Accessory brain. *H. B.* Fore-brain. V'. and V''. Hæmal nerves of first vagus neuromere. V^2. and V^3. Hæmal nerves of second and third vagus neuromeres. V^4. Hæmal nerves to fourth vagus neuromere.

V. THE FORE-BRAIN.—The structure of the fore-brain and its nerves of Scorpio and of Limulus cannot be fully understood without a knowledge of the development of the brain and optic ganglia of some forms like Acilius. Here the cephalic lobes consist, at a very early embryonic period, of three segments, each segment bearing two pairs of eyes, a pair of optic ganglia, and a segment of the brain. Each optic ganglion arises from a separate invagination on the median edge of the optic plate, just opposite the pair of eyes to which it belongs[1] (Fig. 9, A).

After carrying the ganglion inwards the invagination closes, leaving the ocelli in their original position on the outer surface of the optic plate (Fig. 5, *a*).

The cephalic lobes of Scorpio represent merely a modification of the Acilius type. In both cases the relative positions of the optic plate, optic ganglia, and segments of the brain are, at first, the same (Pls. XXIII, XXIV, figs. 1—4). According to my interpretation, the ganglionic invaginations of the first segment unite with each other across the median ventral line to form a deep transverse furrow (Fig. 5, A), the thickened walls of which are probably derived from the rudiments of that part of the optic plate, optic ganglia, and brain belonging to the first segment. It is possible that this furrow contains an unsegmented portion, comparable with the preoral lobe of Annelids; but this is a question which cannot be discussed here. No eyes are developed in this segment.

The second ganglionic invagination is at first like the corresponding one in Acilius, except that the optic plate is rudimentary and the eyes are not at first discernible. The invagination becomes so large that it involves the optic plate, which then forms the outer wall of a ganglionic sac (Fig. 5, *b*); the crescent-shaped openings to the invaginations, meantime, move backward and inward until they unite with each other over the median line, forming a single sac with a poste-

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[1] The optic ganglion to the convex eyes of Vespa, in which no larval ocelli are developed, arises in a similar manner on the median edge of the optic thickening. (See "Eyes of Vespa," Patten.)

rior median opening. Owing to its mode of formation the sac is at first very broad and bilobed, but it is rapidly reduced to the size of the future median eye. The lines *a* and *b* in Fig. 5, B, on the right, show the successive positions assumed by the lateral limb of the ganglionic invagination.

The outline of the cavity itself is only shown in this figure in the last two stages; in the earlier stage the cavity is shaded, in the later surrounded by a dotted line. At this period the outer wall of the sac is formed by the closely united and well-developed eyes (Fig. 6, C). It is evident that this sac is in no sense an optic vesicle, nor, strictly speaking, the cavity of a ganglionic invagination, although derived from one. I shall call it the optico-ganglionic vesicle.

Almost to the time of hatching it extends backwards a short distance as a rather thin-walled tube, opening outward by a narrow pore (Fig. 5, B, *n. p.*, and Fig. 6, F). By this time the optico-ganglionic vesicle is secondarily shut off from the brain; otherwise the pore would lead directly into the cerebral cavity.

The carrying of the originally lateral eyes toward the median line also affects the optic ganglia to this segment, folding them over the brain as shown in Fig. 5, B and *d*.

The ganglionic invagination of the third segment is in all respects like a typical ganglionic invagination in Acilius; it is deep and well defined, but does not involve the optic plate; hence the difference between the lateral and the median eyes of Scorpio. It is important to notice that while all the ganglionic invaginations of Scorpions are deeper and larger than those in Acilius, in both cases they decrease in size and depth from the first to the third.

Although the entire anterior portion of the fore-brain of Scorpio is practically invaginated, so that the brain and its epithelium form the floor of a great complicated sac, the brain itself takes no active part in the invagination. It is enclosed solely by the extension of the lateral ganglionic invaginations, and the consequent inward and backward growth of the optic plate and ganglia over the brain. This fact is of great theoretic importance, especially when compared with

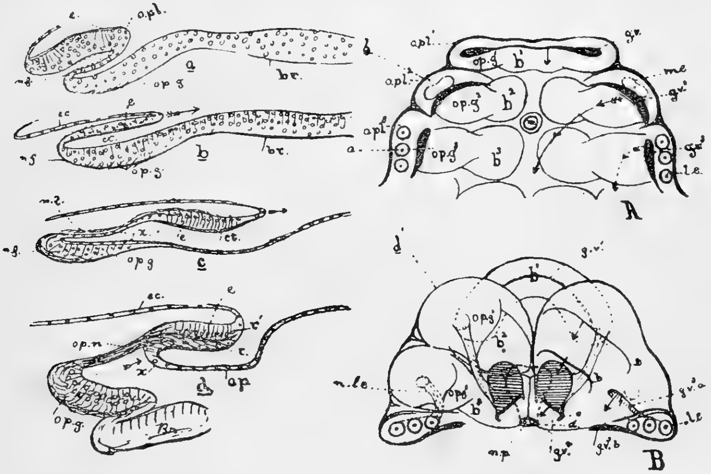

Fig. 5.—*A*. Plan of cephalic lobes of Scorpion at an early period; the arrows indicate the directions along which the lateral lip of the ganglionic pits advance. *B*. Semi-diagrammatic view of fore-brain of Scorpion in Stage F. The left side shows the position of the deeper portions; the right side, the superficial ones. The lines *a*, *b*, *c*, and *d* represent successive positions of the rim to the ganglionic pits. The shaded portion in front of *c* represents the area of the optico-ganglionic pockets about to unite; the dotted line back of *d*, the sac after the union has taken place; the lateral eye-plate, *l. e.*, represents the only part of the original cephalic lobes now on the surface. *A*. Section through cephalic lobes of Acilius, or through third brain-segment of Scorpio; compare *A*, *a*. *B*. Section through second segment of Scorpio, in direction *b*, *A*. *C*. Same at later period. *D*. Ditto, still later. *a*, *b*, and *d*. Direction of sections *a*, *b*, and *d*. b^{1-3}. Lobes of brain. *Br*. Brain. *c.p.* Capsule of eye. *ct.* Cuticula. *e*. Eye. *ec.* Ectoderm. $g. v^{1-3}$. Ganglionic pits. $g. v^{3}$., *a*, *b*. Successive positions of third pit. *l. e.* Lateral eyes. *m*. Mouth. *me*. Median eyes. *n. f.* Nerve-fibres. *n. l. e.* Nerve to lateral eyes. *n. p.* Neuropore. $op. g^{1-3}$. Optic ganglia. *op. n.* Optic nerve. $o. pl^{1-3}$. Optic plates. *r*. Primitive retina. *r'*. Secondary permanent retina.

what takes place in the ventral cord, where only a narrow median furrow, the only part lined by primitive ectoderm, is invaginated (see Fig. 9 and Fig. 2, C E).

The development of the cephalic lobes in Limulus represents a still greater modification of the Acilius type. There is a well-marked transverse furrow at the anterior end of the cephalic lobes, probably representing, as in Scorpio, the fused ganglionic pits of the first segment. Behind the furrow, on either edge of the cephalic lobe, is a small pore leading into a long narrow tube. The latter may be regarded as extremely deep optico-ganglionic invaginations; they correspond, in part at least, to the invaginations of the second segment of Scorpio. The position of the pits is the same in both cases; besides, just as in Scorpions, the mouths of the pits move toward the median ventral line, forming an unpaired pore leading into the cavity of the optic tubes. The latter have, meantime, united to form an unpaired tube with a swollen blind end from which the median eyes are finally developed (Fig. 7, B). The walls of the tube give rise to the optic nerve to the median eye, and the basal portion of it to the optic ganglia (Fig. 10, g^1. and g^2.).

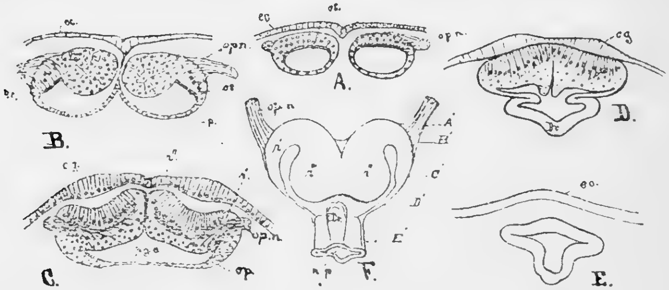

FIG. 6.—*F*. Median eye of Scorpion about ready to hatch, seen from above as a transparent object (compare Fig. 5, *B*). *A'*–*E'* indicate planes of sections *A*–*E*. *cg*. Corneagen. *cp*. Capsule. *ct*. Cuticula, on ends of primitive retinal cells. *Dr*. Diverticulum (?). *ec*. Ectoderm. *np*. Neuropore. *op. n*. Optic nerve. *pg. c*. and *r'*. Pigment-cells, derived from primitive retina. *p. r*. Primitive retina. *r'*. Ditto. *r''*. Secondary retina.

There is a third ganglionic invagination, much like the corresponding one in Scorpio, which gives rise to the optic ganglion of the lateral eyes (Fig. 7, *g*. v^3.). This ganglion, strictly speaking, does not belong to the lateral eyes, for they develop on the third thoracic segment, but to a small sense-organ lying on the outer edge of the invagination (Fig. 7, A, e^3.); consequently this sense-organ and not the lateral eye, is homologous with a lateral eye of Scorpio. In the larvæ it is connected by a nerve with the ganglion of the lateral eyes (Fig. 10, e^3.); it is there deeply pigmented, and connected with a branching plexus of pigment-cells. In this stage it has been seen and described as a mere pigment-spot (Brooks). In the adult this simple eye stands close to its fellow in the median line, in front of the mouth; the overlying cuticula is there clear and transparent, forming two rudimentary lenses. These facts establish beyond doubt the visual character of the organ and its serial homology with the other eyes.

Passing backward into the thorax, we find that each line of the ganglionic pits just described is continued into a segmentally deepened furrow extending the whole length of the thorax (Fig. 9, E, *l. f.*, and Fig. 16). On the lateral side of this furrow there is a thickened band of ectoderm, which in each thoracic segment contains a broad shallow depression, undoubtedly of a sensory nature. The sense-organ of the second or third thoracic segment (I could not determine with certainty which) gives rise to the lateral eye, *l. e.*; that in the fourth is very large, and has erroneously been supposed to give rise to the lateral eyes (Kingsley), or to represent a dorsal organ (Watase). It is a true sense-organ, and is connected by a nerve-bundle with the cord of ganglion-cells arising from the lateral furrow; it persists until the end of the first larval moult, and in this period is covered by a great disc-like thickening of the cuticula, which, judging from its shape and transparency, undoubtedly represents a rudimentary lens.

The nerve to the lateral eyes arises, like the lateral cord of ganglion-cells, from or near the lateral furrow, and may be regarded as a specialisation of that part of the cord extending from the third segment of the brain to the second or third segment of the thorax. It is accordingly unlike any other nerve of the body, resembling rather one of the lateral cords of the central nervous system; or it may be compared with the "Ganglien Zellenstrang" of Vejdovsky.

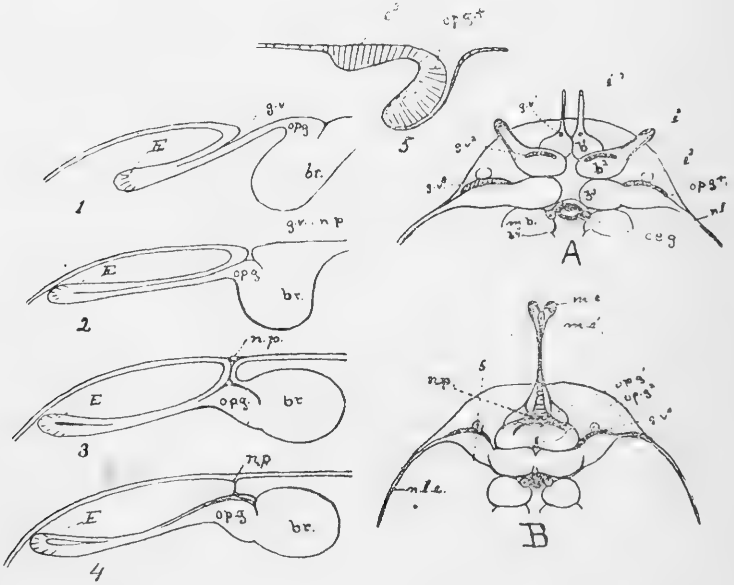

FIG. 7.—*A.* Diagram of fore-brain of Limulus embryo, constructed merely to show probable condition from which the parts in the older embryos are derived, and the relation of these parts to similar ones in fore-brain of Scorpion. *B.* Diagrammatic view of fore-brain at later stage, showing the union of ganglionic pits and eye-tubes. 1–4. Diagrammatic sections, showing origin of eye and unfolding of brain and optic ganglion. 5. Section through the third eye-plate and ganglionic invagination. *B*, 5 indicates direction of section. f^{1-3}. Lobes of fore-brain. *br.* Brain. e^{1-3}. Eyes of the three brain-segments. *g.* v^{1-3}. Ganglionic pits. *m. b.* Mid-brain, or fourth neuromere. *m. e.* Median eye of first segment. *m. e'.* Median eye of second segment. *n. l. e.* Nerve to lateral eye. *np.* Neuropore. *œ. g.* Ganglion to stomodeal nerves. *op.* g^{1-3}. Optic ganglia. *op. g.*+ Optic ganglion to lateral eye and to e^3.

The segmental thoracic sense-organs and the lateral furrow of Limulus, as shown by their position and mutual relations, are, respectively, serially homologous with the cephalic sense-organs or eyes and their ganglionic invagination; and the lateral cord of ganglion-cells may be regarded as a cord of segmental ganglia serially homologous with the optic ganglia.

Each segmental sense-organ of Limulus is represented in Scorpio by a pair of sense-organs at the base of each thoracic appendage (Pls. XXIII and XXIV).

If now we compare Acilius, Scorpio, Limulus, and Vertebrates, we shall find they present four distinct stages of one process of enclosing the fore-brain—that is, four stages in the extension of the ganglionic invaginations (see Fig. 9).

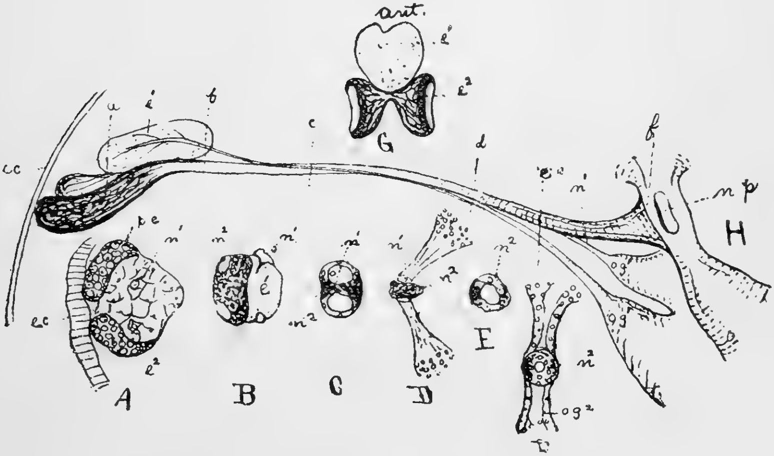

FIG. 8.—*H.* Semi-diagrammatic view of median eye of young Limulus larva, seen from the side (compare Woodcut 10). *A–F.* Section of the eye and its stalk at points *A–F.* *G.* Surface view of median eyes. *ant.* Anterior side of eye. e^1. Eye of first brain-segment. e^2. Eye of second brain-segment. *ec.* Ectoderm. n^1. Nerve to eyes of first segment. n^2. Nerve to eyes of second segment. *np.* Neuropore. $o. g^{1}–^{3}$. Optic ganglia.

In Acilius we have three distinct pairs of invaginations on the outer edge of the cephalic lobes. In Scorpio and Limulus the invaginations of the first two segments unite, forming a continuous, amnion-like fold, the free edge of which grows medianly and backward, infolding not only the optic ganglion, but the eyes and the anterior part of the brain.

The third ganglionic invagination of Scorpio and Limulus is not yet extensive enough to involve the adjacent eyes, but it is much deeper than in Acilius; and in Limulus it shows a tendency to repeat the condition found in the preceding segment, for the sense-organ on its lateral edge is finally carried toward the median ventral line, and just falls short of being invaginated with the ganglion. Hence it is evident that the next step in the extension of the ganglionic invagination would result in the union of the three pairs of invaginations, and the formation of a continuous fold which would finally grow over and enclose the entire fore-brain, which, with the median and lateral eyes and the optic ganglia, would form the walls of a single sac. The result would be a condition practically like that in Vertebrates. If, as in Scorpions, the appearance of the eyes was deferred until the infolding of the brain was completed, and if no secondary optic tubes were formed, as would naturally be the case if the eyes were degenerate, then the eyes would appear as thickenings of the outer wall of the brain-sac, as in Ascidians and Amphioxus. If there was a tendency to develop the eyes in long tubes as in Limulus, and the formation of the tubes postponed until after the brain was enclosed, the eye would appear at the end of a long tube produced apparently by an evagination of the outer wall of the brain-sac (pineal eye and lateral eye of most Vertebrates). On our hypothesis it is not surprising such variations should occur, for similar ones are found in Arthropods. For example, in Scorpions and Limulus the involved eyes do not appear, as such, until long after they have been carried inward, although they ought to appear much earlier if ontogeny gave a complete picture of phylogeny.

A careful examination of the diagrammatic figures will, I think, make clear what has preceded, and will, no doubt, suggest a number of other interesting comparisons which we have not space to consider here.

The Median Eyes of Arachnids and the Pineal Eye of Vertebrates.—If we have progressed so far on solid ground, it is evident that the pineal eye of Vertebrates must be derived from the median eye of Scorpio and Limulus. As we shall now show, the structure of the median eye of Limulus supports this conclusion. In Limulus the optic tubes of the median eye unite in such a way as to form a ⊥-tube, with the median pore at the junction of the arms and upright (compare Figs. 7 and 10). This condition is easily understood if we imagine that as each tube was bent toward the median line its mouth was gradually carried toward the distal end of the tube. The median pore represents not only the last trace of the coalesced ganglionic invaginations, but also the last point where the enclosed brain is attached to the surface ectoderm or communicates with the exterior. Nos. 1—4, Fig. 7, represent, in a diagrammatic way, the formation of the optic tube of the median eyes; at first they are apparently not connected with the brain at all, but later the invagination involves both the brain and optic ganglion. It is important to notice what a great variety of conditions might arise by slight variations of this process. The base of the ⊥-shaped optic tube soon splits, in a way not thoroughly understood, into three nerves: (1) a delicate anterior pair (Fig. 7, B, and Fig. 10, n'), which arise from the very anterior lobe of the brain and unite with the eye-stalk some distance in front of the neuropore; after joining the stalk they may be followed along its sides to the eyes (Fig. 8, *C.*, n'.); (2) a posterior impaired nerve (Fig. 10, n^2.), which for a long time is tubular at its base. Here it divides into two smaller arms (g^2.), which join the sides of the second brain-segment. Towards the eyes the tube is gradually converted into a small bundle of pigmented nerve-fibres (Fig. 8, n^2.). The structure of the median eye and its stalk is well shown by the series of cross sections in Fig. 8.

The eye-stalk extends through the anterior part of the body to the dorsal surface, and then expands into a bulb-like thickening. The outer wall of the bulb develops two groups of cells filled with black pigment; they give rise to the median eyes proper, and are supplied by the median pigmented nerve, n^2. The inner wall of the bulb is filled with white pigment granules, and forms an unpaired mass of cells below and a little in front of the eyes proper; it is supplied by the paired

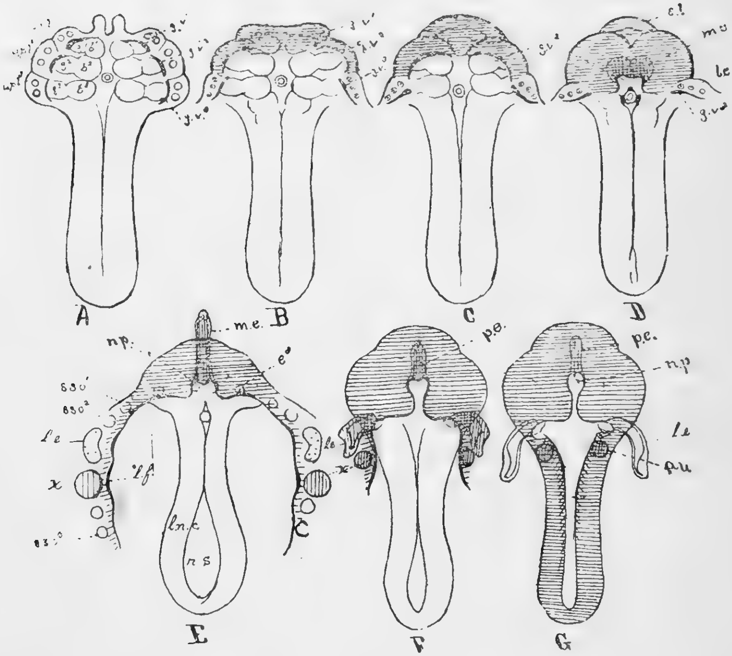

FIG. 9.—Diagrammatic views of Arthropod and Vertebrate embryos, to illustrate the stages in the infolding of the brain, optic ganglia, and eyes; the heavy black lines indicate the ganglionic pits, and the shaded portions the parts that are infolded.—*A.* Acilius. *B, C,* and *D.* Three stages in the development of Scorpio. *E.* Limulus. *F.* Hypothetical transitional form. *G.* Vertebrate. *au.* Ear. e^3. Eye on third segment of fore-brain of Limulus. $g.\ v^{1-3}$. Ganglionic invaginations. *l. e.* Lateral eye. *l. f.* Lateral furrow. *m. e.* Median eye. *np.* Neuropore. $o.\ pl^{1-3}$. Optic plate. $s.\ s.\ o^{1-6}$. Segmental sense-organs of thorax. χ and $s.\ s.\ o^4$. Very large ear-like sense-organ.

colourless nerves, n^1. Toward the late larval stages the white mass becomes constricted off as a solid diverticulum of the primitive bulb, and finally lies some distance from the surface as a cylindrical mass of cells filled with white pigment; in all stages the walls of the cells composing this body develop refractive rod-like thickenings, which resemble those in the superficial median eyes.

The extraordinary condition described above can be explained by supposing that two distinct pairs of segmental eyes are fused in the primitive eye-bulb; one pair belonging to the first, the other to the second brain-segment. Compare the diagrammatic figs. A and B, Fig. 7. In confirmation of this view it may be added—(1) at an early stage there are traces of two pairs of

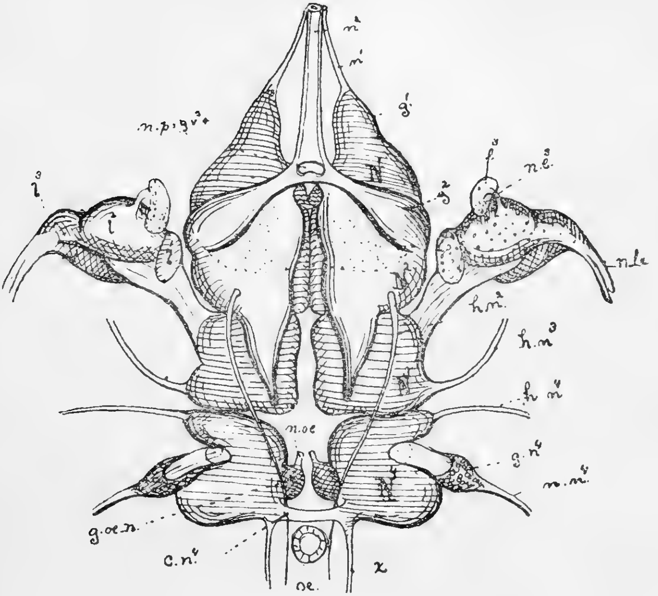

FIG. 10.—Fore- and mid-brain of young larva of Limulus (just hatched), seen from neural surface; constructed from sections and dissections.—*c. n*⁴. Posterior commissure of brain. *e.* Eye to third brain-segment. g^1–^{3}. Optic ganglia. *g. n*⁴. Spinal ganglion on fourth neural nerve. *g. œ. n.* Ganglion to stomodeal nerves. *h.* n^2–^{4}. Hæmal nerves to second, third, and fourth neuromeres. l^1–^{3}. Three ganglionic lobes to ganglion of lateral eyes. N^1–^{4}. First four neuromeres. *n. e.* Nerve to rudimentary eye of third segment. *n. l. e.* Nerve to lateral eyes. *n.* n^4. Neural nerve to fourth neuromere. *np.* and *g.* v^2. Neuropore. *n. œ.* Stomodeal nerves. *œ.* Œsophagus. *x.* Small nerve, extending backwards from posterior brain commissure.

ganglionic pits, one of which was small and disappeared quickly, so that its history could not be determined. (2) Although there are only three distinct nerves in the eye-stalk, they represent four completely fused nerves, for the colourless nerves are still clearly enough paired, while the median one was undoubtedly paired originally, as shown by the diverging arms terminating in paired ganglia. (3) The anterior pair of nerves arise from a distinct crescent-shaped brain-lobe (with small dark nuclei), which is undoubtedly homologous with a similar lobe in Scorpio, and which there represents the first brain-segment; the posterior pair arise from another lobe, which probably represents the second brain-segment. Thus the diverticulum of the median eye-bulb represents, in all probability, a pair of eyes belonging to the first brain-segment.

We will merely note in passing that in some Trilobites on the anterior portion of the glabellum are three eye-like spots, which may possibly represent the three fused ocelli of Limulus.

In comparing the median eye of Limulus with the pineal eye of Vertebrates the following points are important—(1) In both cases the eye is situated at the end of a long median tube. (2) In both cases the tube is apparently an evagination of the roof of the brain. (3) In both cases the position of the tube relative to the rest of the fore-brain is the same. (4) In both cases the manner in which the distal end of the tube grows forward away from its point of attachment is the same; the exception to this manner of growth in some Vertebrates is probably due to the subsequent enlargement of the cerebrum. (5) In Limulus the bulb-like swelling at the distal end of the tube, which gives rise to a pair of median eyes lying close beneath the ectoderm, may be compared with the terminal sac of the pineal eye-stalk. (6) The remarkable diverticulum of the under wall of this bulb, giving rise to a peculiar whitish body not connected with the surface ectoderm, but which contains undoubted retinal cells, may be compared with a very similar diverticulum in Vertebrates. (7) The proximal end of the eye-stalk in both Limulus and Hateria (Spencer) contains three distinct nerves, two anterior paired ones and a totally different unpaired one. (8) In both cases the unpaired nerve may at certain stages be a mere hollow tube, the wall of which is composed of ordinary columnar cells, showing no trace of nerve-structure. (9) In both cases the proximal end of the eye-tube may represent either the last point where the brain is connected with the ectoderm (Leydig), or the lips of a round, median opening or neuropore, leading into the cavity of the pineal eye or into the brain, or into both, according to the stage and method of development. (10) The manner in which, in Vertebrates, the fore-brain is enclosed and the median eye-tube formed represents a modification of a fundamentally similar process found in Limulus, and the Arachnids generally; and this fact is of the utmost importance on account of the peculiar and complicated nature of the process, and its total absence in other groups of animals.

The lateral eyes of Scorpion and Limulus are not involved by ganglionic infoldings so as to lie at the ends of brain-tubes, but, as shown above, the next step in the changes already accomplished would probably lead to that condition. Suppose a kidney-shaped eye, such as is usually present in and best adapted to forms like Limulus and other Merostomata, came to lie at the end of an optic tube; then a kidney-shaped retina would be produced with its concave edge directed hæmally, instead of in the opposite direction, as in Limulus, &c. As a kidney-shaped retina would no longer be required, it would naturally become circular; and, owing to the peculiar distribution of nerve-fibres, this would be most easily and economically accomplished by bringing the halves of the concave edge together, thus producing a choroid fissure, the direction and position of which would be like that in Vertebrates.

Now the ommateum of Limulus consists of circles of from fifteen to twenty retinal cells surrounding a single central one of a little different character (Watasi). If such an ommateum were converted into a true retina the arrangement of the cells would probably be retained, and we would have a retina like that in many Vertebrates. Again, the lateral eye of Limulus arises from the third or fourth thoracic segment, although its nerve and optic ganglia are united with the third brain-segment; if such an eye were involved by ganglionic invagination, it would lie at the end of a long backwardly directed tube, like that of the lateral eye of Vertebrates.

In other words, we can explain the most remarkable and characteristic features of the lateral eyes of Vertebrates, such as (1) the shape of the retina, (2) its histological structure, (3) the formation of the choroid fissure, (4) the backwardly directed eye-stalk (in marked contrast with the forwardly directed pineal eye), by supposing them to be derived from kidney-shaped thoracic eyes like those in Limulus, Trilobites, and Merostomata.

The proximal ends, at least, of the optic nerves of Scorpio and Limulus, are probably serially homologous with the pedal or neural nerves of the thorax; this is shown by their histological structure and by their position. For example, in Limulus both the second and third segments of the fore-brain (and possibly the third in Scorpio) are provided with segmentally arranged motor nerves exactly like the motor nerves of the post-oral segment; the optic nerves taking the place of, and resembling in structure, the pedal or neural ones of the thorax (Fig. 10).

In Limulus, one of the motor-like nerves of the fore-brain is connected with the skin about the upper lip; this fact, together with its position, suggests that it may represent an incipient olfactory nerve (Fig. 10, hn^2.).

VI. THE CRANIAL FLEXURE of Vertebrates has been explained by supposing that the fore-brain represents an invertebrate supra-œsophageal ganglion. But, judging from Kleinenberg's view and Beard's speculations, this theory must be abandoned, since the Annelid brain arises independently of the remaining central nervous system, while the Vertebrate fore-brain does not. It is therefore tacitly admitted that the Annelid theory cannot explain the cranial flexure, that extraordinary feature of the Vertebrate brain which has always been justly regarded as the strongest evidence in favour of the origin of Vertebrates from segmented animals. But if we still attach the same significance to the cranial flexure that many of the ablest zoologists have done in the past, then we exclude the Annelids from any direct genetic connection with the Vertebrates; at the same time we strengthen the Arachnid theory, because the Arachnid brain, not only in its flexure, but also in its primitive continuity with the nerve-cord, fulfils completely the condition demanded by a rational theory of the origin of Vertebrates.

There is another neural flexure of equal importance with that mentioned above; I shall call it the somatic flexure. At certain periods it is present in nearly all Arthropods as a ventral flexure of the tail, producing in such forms as Scorpio and others an S-shaped embryo. Now, in many mammalian embryos there is a strong flexure just behind the brain, the "cervical flexure" of His, and in many fish and amphibian embryos there is at one period a strong upward curve of the tail. In fact, the Vertebrate embryo is also somewhat S-shaped, a condition to be expected on the Arthropod theory, but otherwise inexplicable.

Beard attempts to explain how the distal portion of the hypophysis cerebri may represent an Annelid œsophagus, but he only succeeds in showing how the difficulties are thickening around the Annelid theory. He does not recognise that if there is no Annelid brain in Vertebrates there should be no cranial flexure, and no reason whatever for regarding the present Vertebrate mouth as secondary, or the hypophysis or any part of it as the remnant of a former œsophagus. Moreover, his view necessitates the assumption that the fore-brain represents a single segment, whereas its complex nature can hardly be doubted.

On the other hand, (1) the strong cranial flexure in Arachnids, (2) the primitive continuity of the fore-brain and ventral cord, (3) the absence of the mesoblastic somites in the fore-brain region, (4) its remarkable complex structure, as well as the development of its nerves and sense-organs,—all invite a detailed comparison of the œsophagus and fore-brain of Arachnids with the fore-brain and hypophysis of Vertebrates.

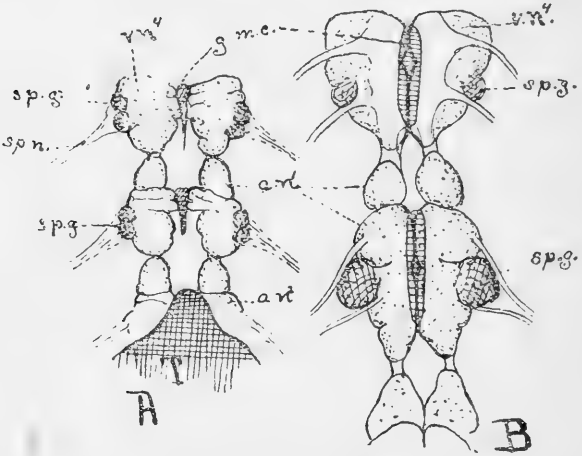

Fig. 11.—The fourth vagus and first abdominal neuromeres of Scorpion, seen from the neural surface.—*A.* Stage F. *B.* Stages G, H. By comparing with figs. 1–4 in the Plates we see how the parts of the primitive double neuromeres have recombined to form new ones. *a.* n^1–^{2}. First and second abdominal neuromeres. *g. m. c.* Ganglionic portion of median furrow. *sp. g.* Spinal ganglia. *sp. n.* Spinal nerve. *v.* n^4. Fourth vagus neuromere. *T.* Tail.

The arguments in favour of supposing that the infundibulum cerebri represents an Arachnid œsophagus with its nerves are much stronger, I believe, than those advanced by Beard in favour of his view. (1) Since in most Arachnids the œsophagus is very small, owing to their blood-sucking habits, and the canal for its passage through the brain is extremely small, the Arachnid theory can give some explanation of how and why the old mouth has disappeared. (2) In Limulus and Scorpio two large parallel nerves extend along the whole length of the sides of the œsophagus. Each nerve arises from a thickening, which persists for a long time, of the distal end of the œsophagus. As the latter increases in length, the thickening is carried inwards; when the process is once started we get between the inner and outer ends of the œsophagus all stages in the separation of the nerve from the ectoderm. The proximal ends of the nerves are united in the middle of the fourth neuromere, and then terminate in a pair of large ganglia. The latter arise not from the œsophageal walls, but from an invagination of the median surface ectoderm, and so close to the neuromere that there is no distinct boundary between them (Figs. 7 and 10, *g. œ.*, and Fig. 2, *sp. n.*). I will also add that the unpaired frontal ganglion of insects arises as an evagination of the œsophageal wall. Thus we would naturally expect that if the infundibulum represents an Arachnidan œsophagus, it would contain a large portion of nervous tissue, and be directly continuous, through the rudiments of the stomodeal ganglia, with the brain. (3) The dorsal organ of some Arthropods is derived from the embryonic membranes, and is finally invaginated into the yolk and absorbed. In some Crustacea a dorsal organ is retained throughout life, and is often used as a sucking or adhesive disc of attachment. If an animal attached itself by such an organ to the soft tissues of another, and if the inner portion of the disc were absorbed by the yolk, a way would be opened for the alimentary canal to communicate with the exterior by a new sucking mouth, which would lie in about the same place as the embryonic mouth of Vertebrates. In Dytiscus larvæ, where the points of the sickle-like mandibles are perforated and serve as mouths, the old one becomes temporarily closed and functionless.

In Scorpio I have found nothing like a dorsal organ, but in Limulus embryos there is a great mass of loosely connected cells near the anterior dorsal surface of the yolk, or about where the dorsal organ in other forms is present. In most of my sections this portion was cut out, so that I know little about it. It is not impossible that it represents a rudimentary dorsal organ, all the stages in the formation of embryonic membranes, &c., being omitted.

VII. THE MEDIAN FURROW (or Mittelstrang of Hatschek) AND THE NOTOCHORD.—The ventral nervous system of Arthropods consists of three longitudinal cords (five in Limulus), two lateral and one median. The latter, in its indifferentiated state, is represented by the so-called "sympathetic" or "median nerve."

In Acilius, between the ganglionic swellings of the lateral cords the median furrow is almost tubular and somewhat swollen, forming what may be regarded as the ganglia of the median nerve. In the abdomen the interganglionic portions of the median furrow give rise to the median nerve proper, which is therefore merely a longitudinal connective, comparable with those of the lateral cords.

In the thoracic region the interganglionic parts of the furrow produce great ectodermic thickenings (the furcæ), to which muscles are attached.

In Scorpio, the median furrow, in the centre of each neuromere forms a deep pit, the thick walls of which, epithelium and all, are converted into ganglion-cells (Pls. XXIII and XXIV, and Fig. 2, A, C, and E). By the crowding together of the thoracic neuromeres the pits in some places unite, forming a temporary central canal.

Between successive abdominal neuromeres the median furrow proliferates inwards, producing solid spindle-shaped clusters of cells, which grow forward and backward until they meet, forming beneath the nervous system a continuous longitudinal cord (Fig. 2, G, *i. m. c.*). Owing to its method of formation, the latter is for some time segmentally swollen. In embryos about to hatch, the cord is hollowed out, and forms the "spinal artery." The whole cord is sometimes filled with large vesicular cells with small nuclei (Fig. 2, C), and in half-grown specimens the wall of the artery may be extremely thick and hyaline (D). Thus the whole organ presents a striking resemblance to a Vertebrate notochord.

At the anterior end of the embryo, beneath the vagus neuromeres, the interganglionic part of the median furrow forms a great solid ball of tissue, composed of a confused mixture of coiled muscle-fibres and gland-like cells. As this remarkable body represents an isolated and specialised segment of the spinal artery, I have called it the merochord. In the adult it is a rather compact ball of tissue lying between the brain and the posterior portion of the cartilaginous sternum, or endocranium (Fig. 12, *mc.*).

In Lepidoptera (Cecropia) the "lemmatochord" is derived in part from the neurolemma of the persistent median nerve, and in part from the neurolemma of the lateral cords; but in some parts of the thorax of Cecropia the lemmatochord is entirely derived from the neurolemma of the median nerve, the nerve itself having disappeared. The median nerve in some cases runs in the centre of a spinal artery (S. Selvatico, 'Zool. Anz.,' Aug., 1887, p. 562).

These facts show that the median furrow is a much more important organ, morphologically, than has been supposed. It is certain that the interganglionic portions of the furrow, or at any rate something that cannot be distinguished morphologically from them, may give rise to an extraordinary variety of structures—to the furcæ (in the thorax of Acilius), the median nerve (in the abdomen), the lemmatochord, or at least a portion of it, in Lepidoptera, and to the spinal artery of Scorpio. Practically it makes little difference whether we regard the spinal artery of Scorpio as derived from the median nerve itself, its sheath, or a lemmatochord-like organ with traces of the median nerve in the centre. The important fact remains that, in a great many Arthropods there is a median cord, which in position and general character bears such an extraordinary resemblance to the notochord of Vertebrates, that the burden of proof lies with those who deny that the two cords are of the same nature. If it is urged that in Arthropods the median cord arises from the ectoderm while the notochord arises from the endoderm, we may safely answer that there is nothing in the embryology of Vertebrates to show to what germ layer the notochord belongs. It is never continuous with functional endoderm; there is no evidence that it ever exercised, itself, any alimentary functions; it is never connected in any way with an alimentary canal. Only a strong faith in enteric diverticula, and in the red, white, and blue gastrules of embryological treatises, can lead one to believe in the endodermic origin of the notochord. On the other hand, its growth at both ends from superficial cells, and the manner in which it is frequently wedged in between the nerve-cords, indicate its ectodermic origin.

Owing to the origin of the spinal artery of Scorpio from the interganglionic portions of the median furrow, temporary communications are formed between the central canal and the artery. The communications between the notochord and the neural canal of some Vertebrates (lizard, duck, &c.), may be of a similar nature.

The indefinite anterior termination of the notochord beneath the hind-brain, just behind the pituitary body, and its segmental swellings in this region, may be compared to the gradual disappearance of the spinal artery in the same region just behind the merochord, and to the segmental swellings of the artery between the successive neuromeres.

The "godets" of Moreau found in Amphioxus may be remnants of arterial branches; and the origin of the chorda cells from the sheath may be compared to the origin of blood-corpuscles from the wall of the spinal artery.

The fact that the notochord does not at first lie for its whole length in the ectoderm may be regarded as a secondary condition, all its very early phylogenetic stages being passed over hurriedly in the primitive streak, or growing-point.

VIII. THE BOTRYOIDAL CORD.—Beneath the spinal artery of Scorpio lies a remarkable rod-like body which I shall call the botryoidal cord. It develops as a forward growth from a great primitive-streak-like group of cells, in much the same way the notochord of Vertebrates does. The primitive streak itself is at first situated at the posterior end of the body, but when the tail fold arises it lies just at the junction of the tail with the posterior end of the abdomen; the primitive streak then seems to produce tissue in both directions. At first it is short and massive, but it finally extends forwards (partly, perhaps, by an actual forward growth, but mainly owing to its being left behind by the backward growth of the posterior end of the body) the whole length of the abdomen as a rather large cylindrical cord; the latter, about the time of hatching, splits into two parts, an outer one composed of a thin layer of small dark nuclei, representing the "anlage" of the botryoidal cord, and an inner one composed of large polygonal cells, representing the anlage of the sexual organs (Fig. 2, c).

The anlage of the botryoidal cord soon develops, at irregular intervals, spindle-shaped enlargements, each intermediate portion being reduced to a delicate hyaline fibre. The spindles, eight to ten in number, become attached to the wall of the spinal artery, and in most cases an imperfect communication is established between the cavity of the artery and the interior of the spindle (Fig. 2, E, also *d. bt. c.*).

In the adult the spindles are composed of botryoidal masses of fibroid tissue densely packed with small, deeply stained nuclei. The organ is, perhaps, a gland for the production of blood-corpuscles.

If the spinal artery of Scorpio represents a notochord, then the botryoidal cord probably represents the "subchordal rod."

IX. THE CARTILAGINOUS STERNUM AND THE PRIMORDIAL CRANIUM.—A characteristic organ of the Arachnida is the cartilaginous sternum or "endocranium." In Scorpio (and in Limulus it is about the same) it is a broad, lyre-shaped bit of fibroid cartilage, with forwardly directed arms, lying beneath the hind-brain (Fig. 12). Its posterior portion is more massive, and completely surrounds the posterior portion of the brain, forming a kind of occipital cartilaginous ring (Fig. 2, F). It develops from the mesoderm as a membranous diaphragm underlying the thoracic neuromeres. In size, shape, position, structure, and manner of development—in fact, in every particular except its chemical composition, the endocranium of Scorpio corresponds with the primordial cranium of Vertebrates.

There are in primitive fishes no head-muscles sufficiently powerful to account for the development of the primordial

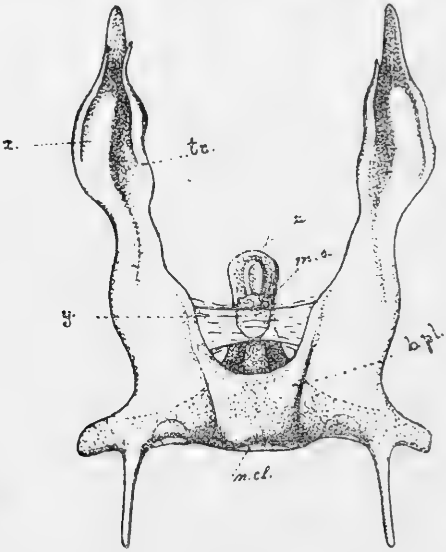

Fig. 12.—The endocranium or cartilaginous sternum of Scorpion, seen from the hæmal surface. The figure has been constructed entirely by carefully plotting a complete series of transverse sections, only the purely cartilaginous parts being drawn.—*b. pl.* Basal plate, forming a thick floor to the central canal. *m. c.* Merochord, an hypophysis-like segment of the spinal artery. *n. cl.* Neural canal or passage through the occipital ring for the nerve-cords (compare section of this region in Fig. 2, *F*). *tr.* Trabecula. *z.* Thickened portion of trabeculæ χ. Thick bar of cartilage extending forwards from the neural surface of the occipital ring, and forming an imperfect roof to the endocranium. *y.* Membrane for support of merochord.

cranium. As the cranial segments were very early immoveably united, the cranium could not have served for the attachment of muscles moving the segments on each other for purposes of locomotion as the vertebral column does in the body. In fact, we can best account for the primordial cranium of Vertebrates by supposing that it has been evolved independently of the spinal column, serving originally for the attachment of powerful muscles of locomotor visceral arches or Arachnoid appendages.

The nature of the trabeculæ, the occipital ring, the diaphragm-like membrane, the absence of segmentation, and the relation of the primordial cranium to the vertebræ are obscure points which the anatomy and embryology of the Vertebrate head failed to elucidate, but which the Arachnid theory resolves into the comparatively simple question as to the origin of the cartilaginous sternum. Vertebrate embryology, it seems, told all there was to tell: the fault was not in the answer, but in the interpretation; or rather, in the conviction that if ontogeny did not show what was expected, it was due to the imperfections of the ontogenetic record, not of the expectations.

X. Gill-slits and Gill-arches.—In Scorpio there are coils of mesoderm (?) cells in the coxal portion of each pair of thoracic appendages (Pls. XXIII, XXIV, figs. 1—3). All these cell-coils disappear except that in the fifth coxa, which develops into the adult nephridium-like coxal gland; hence each of these coils probably represents a rudimentary nephridium.

An ectodermic invagination, which appears on the outer side of the base of the fifth pair of legs, gives rise to the outlet of the gland. There are similar invaginations at the bases of the other appendages; but they give rise to chitin-lined tubes, which serve for the support of muscles. The chitinised tubes are comparable with the three or four pairs of tracheal invaginations which in insects give rise to the tentorium. Since in Acilius some of the abdominal tracheæ at first communicate with the cavities of the mesoblastic somites, it is probable that all the tracheæ represent the ectodermic portions of nephridia. I regard the lung-books of Scorpio and the chitin-lined tubes described above as belonging to the same category, for after careful study I have found nothing to indicate that they arise as modifications of rudimentary abdominal appendages.

If we suppose that all the thoracic and vagus appendages are reduced, by parasitism or a variety of other causes, to transverse ridges (like the pectens, for example, Pl. XXIV, figs. 3 and 4; or like the thoracic and abdominal appendages of Limulus), and the segmental tubes enlarged to great transverse respiratory slits, like those in the abdomen of Scorpio, then we should have a condition much like that of the gill-slits and gill-arches of Vertebrates. Such an Arthropod appendage would resemble a gill-arch (1) in being supplied with a neural nerve; (2) in containing an artery following the nerve first mentioned; (3) in possessing a great sense-organ, from which a ganglion to the neural nerve arises; (4) in the origin of its muscles from a diverticulum of a mesoblastic somite; (5) they would agree approximately in number with true gill-arches; (6) they would agree with gill-arches in their serial physiological differentiation, for in both cases the anterior pairs are of great size, forked, and serve as mouth parts, the posterior ones being associated with respiratory organs, and showing a tendency to degenerate.

Segmental respiratory sacs or tubes are eminently characteristic of Arthropods; and, as they are probably derived from the outlets of nephridia, they represent just the kind of respiratory organs required, according to Dohrn's theory, in ancestral Vertebrates.

In Scorpio the wandering backward of vagus nerves to abdominal lung-books is important, and shows that we may not, without other evidence, assume that in Vertebrates the true gill-arches agree in number with or belong to the same segment as the nerves that supply them. Accepting Van Wyhe's views as to the structure of the Vertebrate head, we offer the following tentative conclusions:—(1) The chelæ and first, or perhaps first and second, walking legs of Scorpio correspond to the mandibular and hyoid arches. (2) The remaining two or three pairs of thoracic appendages and somites are not present in Vertebrates. (3) The rudimentary vagus appendages of Scorpions and the corresponding somites, except the muscles extending to the pectoral or pectinal arches, have in Vertebrates disappeared. (4) The true gill-arches represent the tissue between segmental respiratory organs or lung-books, and not modified appendages; consequently they differ from the true appendages, like the mandibular and hyoid arches, in not containing somatic diverticula (Van Wyhe). (5) The cheliceræ are represented in Vertebrates by adhesive pre-oral papillæ; this is not so improbable as at first might appear, for in many Crustacea the first antennæ, which are probably homologous with the cheliceræ, aided by the secretion of a sticky substance, serve as sucker-like organs of attachment.

XI. Muscles.—Since longitudinal muscles serve to move the segments on one another, the complete fusion of the first thirteen segments to form the cephalothorax is, without doubt, the cause of the disappearance of the dorsal and ventral longitudinal muscles of Scorpio.

In the Vertebrate head the dorsal and ventral longitudinal muscles are also absent; therefore we conclude that in the ancestral Vertebrates the segments were immoveably united to form a hard outer skeleton like the thoracic shield of Arthropods; the partial union of soft, flexible parts, as in an Annelid thorax, would not explain the absence of these muscles. As longitudinal muscles, when present, are very large, we can thus account, in a measure, for the great difference between the development of the head and trunk somites of Vertebrates and Arachnids.

A more detailed comparison shows further that, (1) in both Scorpio and Vertebrates, there is very little mesoblastic tissue, and no distinct somite at all in the fore-brain. It is even possible that all the original fore-brain mesoblast has disappeared, that which is now present being derived from a forward growth from the post-oral segments. (2) The mid- and hind-brain region in both Vertebrates and Arachnids contains six mesoblastic somites, from which diverticula are formed leading into the appendages (gill-arches), and giving rise to muscles passing from these appendages to the cartilaginous cranium. (3) In the accessory brain region of Scorpions and in the vagus region of Vertebrates the mesoblastic somites disappear completely with the exception of a few longitudinal muscles passing from the occipital region of the cranium to the pectoral (= pectinal) arch.

It is important to observe that in Arthropods, according as the anterior portion of the body becomes more specialised, the appearance of segmentation in those regions is retarded. For example, in insects, segmentation appears in the cephalic lobes and in the region of the mandibles and first maxillæ later than in the rest of the body; being the exact reverse of what we should expect, since the anterior part of the body is the oldest. It is the same with the cephalic lobes of Scorpio. In Limulus the fourth, fifth, and sixth (?) thoracic segments appear first; the third, second, and first later, and those of the fore-brain last of all.

In view of these facts it is probable that in Vertebrates what has been taken for an intercalation of new head-segments is really a retarded segmentation.

Eye Muscles.—In Scorpio, and probably in most Arachnids, there is a small number of muscles which belong neither to the system of leg muscles nor to the longitudinal ones. They are dorso-ventral, and in Scorpio the largest one is attached to the hæmal wall of the head on either side of, and close to, the median eyes. Although I have not been able to follow the development of these muscles, it is almost certain they develop from the first two or three thoracic somites. No such muscles are found in the posterior part of the thorax. They thus agree to some extent with the Vertebrate eye muscles, for the latter arise, as Van Wyhe has shown, independently of the eye from the first three somites, and belong neither to the primitive gill-arches nor to the longitudinal muscles.

XII. Pectoral Fins.—There are four completely fused segments in the vagus region of Scorpions, the comb belonging to the third. As there is no external evidence of this condition in the adult, we must, in attempting to determine the homologies of the appendages in such forms as Merostomata, be guided in the main by comparison with those related forms whose internal anatomy is better known.

If the metastomum of Pterygotus is homologous with the similarly-named organs of scorpions, it must be derived from the first two abdominal segments. If, as its position indicates, it arises in front of the swimming legs, the latter would belong to the third abdominal segment, and would, therefore, be homologous with the pectines of Scorpio. If this be so, then the four pairs of appendages in front of the oars would correspond in number and uniformity of structure with the four pairs of walking legs of Scorpio; consequently the great chelate appendages would be homologous, as indicated by their structure and function with the chelæ of Scorpions. The small size of the four appendages of Pterygotus and the large size of the anterior ones is not difficult to understand, because if a Scorpion-like animal should gradually adopt the habit of swimming on its back by means of its comb or any oar-like appendage, the walking appendages would naturally decrease in size, while the grasping ones would not be so readily affected by such a change. There should be in Pterygotus, according to the above view, a pair of cheliceræ in front of the chelæ; but, as in all Arachnids these appendages are very small, it is not strange there is no trace of them in the fossil forms under consideration.

XIII. Arachnid Features of Pterichthys.—We have been impressed with the way certain fossil fishes, such as Pterichthys and allied forms, resemble the Merostomata,[1]

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[1] That this external resemblance is real may be shown by the fact that those most familiar with the subject, and the ones best able to judge, were also greatly impressed by the same fact.

The "genialer" Hugh Miller, the discoverer of Pterichthys, says ('Old Red Sandstone,' p. 50), in comparing a Tribolite with Cephalaspis, "The fish and the Crustaceans are wonderfully alike. . . . . They exhibit the points at which the plated fish is linked to the shelled Crustacean."

Also Sir Roderick Murchison, when first shown specimens of Pterichthys, wrote regarding them that, "if not fishes, they more clearly approach to Crustaceans than to any other class." Again, "They [Cephalaspis and Pterichthys] especially as regards size, shape of the body, the hard outer

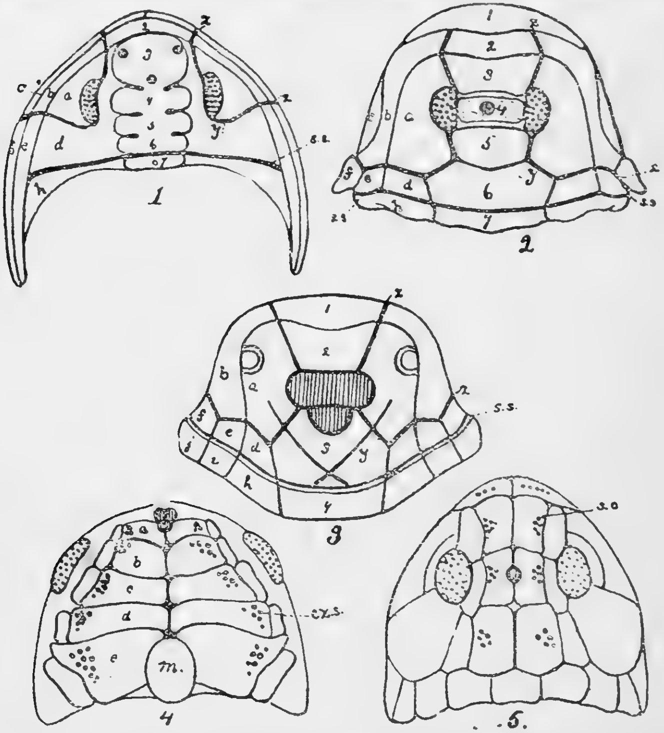

Fig. 13.—(1) Ocular or hæmal surface of the cephalic shield of a Trilobite. (2) Same of Pterichthys. (3) Same of Bothriolepis. These figures are intended to show the similarity in the arrangement of the cranial plates, and of the cervical and facial sutures. (4) Diagram of the neural surface of a merostomatous Arachnid, showing paired arrangement of coxal plates, and the eyes passing from the hæmal to the neural surface. (5) Hæmal surface of a Vertebrate head.—*m.* Metastomum. *s. s.* Cervical suture. *x.y.z.* Facial suture. *cx. s.* Coxal sense-organs. *s. o.* Sense-organs.

skeleton and its peculiar sculpturing, its concentration at the

form the connecting links between Crustaceans and fishes." Agassiz himself was at first in doubt as to whether Pterichthys was a fish or Crustacean.

To show still further the doubtful position of some of these primitive fishes, it may be stated that recently a distinguished palæontologist advanced the opinion that forms like Bothriolepis were Ascidians!

head end to form a compact cephalothoracic shield or cranial buckler—the post-cranial segments being in some cases probably soft and disconnected,—the shape of the swimming appendages, and the probable method of locomotion. And, moreover, since the concrescence of vagus segments and their union with the true thorax is shown in the adult Scorpion and also in Trilobites and Merostomata by the cervical suture, and since a similar suture is seen in Pterichthys and Bothriolepis, we may infer that the last two forms also possess vagus segments, and that their swimming appendages are homologous with the combs of Scorpio and with the swimming legs of Pterygotus. But as Pterichthys is also fish-like, its swimming appendages are probably homologous with pectoral fins, and consequently the combs of Scorpio are also homologous with pectoral fins.

In support of this view we may add (1) that the fundamental structure of the pectens of Scorpio and the pectoral fins of embryo Selacians is the same, for the framework of both consists of a longitudinal bar, attached by its median end to the body, which gives off at right angles a series of rays. (2) In Scorpio the pectens, which develop differently from any other Arthropod appendages, first appear as an enormously long transverse ridge, divided into a series of small lobes (Pl. XXIV, fig. 4). The important point is that the lateral end is gradually separated more and more from the body, until finally the whole appendage is only supported by a slender stalk at its neural extremity. This method of development agrees with the well-known development of the pectoral fins of Selacians, and the result is a long basal bar attached at one end only, and which may thus be swung forwards or backwards as on a pivot, or even rotated on its long axis. (3) They probably belong to the same segments, i.e. to the vagus. That the pectoral fins arose very far forward is certain; their probable origin from the vagus region is shown by the fact that in Protopterus (Wiedersheim) they receive nerves from the vagus, and also by the fact that the remarkable longitudinal muscles uniting the pectoral arch with the cranium are derived from the vagus mesomeres. (4) They show the same backward migration. (5) They are associated with transverse cartilaginous bars or pectoral arches, to which are attached longitudinal muscles arising from the cartilaginous cranium. The transverse bar in Scorpions is quite small, owing to the tactile function of the pectens; but in the gigantic Merostomata the muscles to their oar-like appendages must have been enormous, and the cartilaginous bar for their support not a bit inferior in size to the pectoral arch of Vertebrates.

The hæmal surface of the cephalothoracic shield of Trilobites is divided into a number of distinct plates, which resemble in shape and arrangement those on the cephalic bucklers of Pterichthys and Bothriolepis (Fig. 13, 1—3).

The most important resemblances are shown—(1) In the size and general shape of the shields. (2) In the posterior line or row of small plates, which form a cervical suture, and which indicate the presence of vagus segments. (3) In the great semicircular sutures extending parallel with the edge of the shield around the front and sides. (4) In the roughly triangular ocular plates, with the eyes on their median edges. (5) In the facial suture, *z. z.* (6) In the median row of plates or lobes in which the median eyes are situated. If the reader is not impressed with the resemblances above indicated, I am sure a careful comparison will convince him that the resemblance is at least much greater than that between the ocular surface of Bothriolepis and Pterichthys and that of a true Vertebrate.

Now let us compare the neural surface of Pterichthys, or the neural surface of a true fish, with the neural surface of Scorpions and Merostomata, and we shall see that in all these cases the median cranial plates are arranged in pairs, terminating in a posterior unpaired plate (Fig. 13, Nos. 4 and 5). If these facts mean anything, they show that whenever distinct plates are developed in the cephalothoracic shield of Arachnids and lower Vertebrates the hæmal surface will contain an unpaired median row, and the neural surface a paired median row, terminating posteriorly with an unpaired plate or metastomum.

As in all true Vertebrates, the eyes are found on the same side as the paired cranial plate, we may conclude that the real break between Arthropods and Vertebrates is made by the transference of the eyes to the neural surface. Since their eyes are situated on the hæmal surface, we may conclude that Pterichthys and Bothriolepis, &c., are nearer related to the Arachnids than to the Vertebrates. The position of the eyes undoubtedly depends largely on the position in swimming. In Pterygotus, for example, where locomotion was probably largely effected by swimming on the hæmal surface, the eyes have already become lateral—a position very unusual in Arachnids. This change is readily explained, since the original position of the eyes in the embryo of all Arthropods is neural; moreover, this history of Arthropod eyes shows conclusively that they can assume any position the method of locomotion may demand.

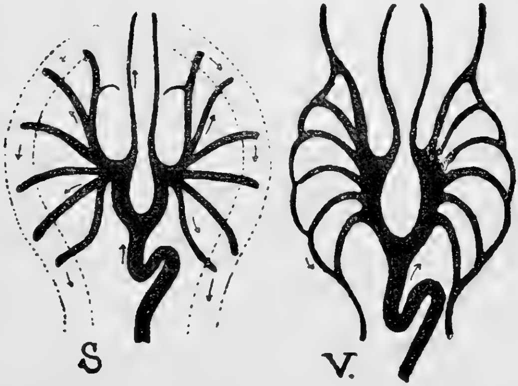

FIG. 14.—Diagram of the circulation (*S*) in the thorax of an Arachnid, and (*V*) in the head of a Vertebrate.

The above view of the Vertebrate cranium explains why the cephalic bucklers of many primitive fossil fishes are frequently divided into distinct dorsal and ventral shields, and also why the abocular or neural surface is so imperfectly preserved.

It follows from what has preceded, that in Vertebrates and Arachnids, those surfaces of the head bearing a median row of paired plates and those bearing a median row of unpaired plates are homologous. This conclusion is supported by the position of the nervous system, and also by the relation these plates bear to ganglionic sense-organs. For example, each of the median cranial plates of Vertebrates contains a primary group of sense-organs supplied by a ganglionated "ramus dorsalis;" they therefore agree perfectly in this respect with the coxal plates, each of which also contains a group of coxal sense-organs, supplied by a nerve which, on other grounds, we concluded was homologous with a "ramus dorsalis." Thus, since the coxal plates of Arachnids and the paired cranial plates of Vertebrates are homologous and segmentally arranged, the old Goethe-Oken theory of the bony cranium appears in a new light.

I trust in all that has preceded I have succeeded in showing that there are important resemblances between the cephalothorax of Arachnids and the head of Vertebrates. There are other resemblances of a more general character, a few of which we shall merely mention here:—(1) The division into cephalothorax, body, and tail. (2) The tadpole-like larva of Vertebrates, with its enormous head, and small body and tail, is explicable on the Arachnid theory. (3) The Trilobites probably swam, if at all, on their backs; and it is still more probable that the Merostomata, from their shape and the position of their oar-like appendages, swam in the same way. The larvæ of Limulus, according to my own observations, always swim on their backs. Thus the way is prepared for the manner of locomotion in fishes. (4) The development of the Arthropod heart from the concrescence of paired mesodermic folds is like that in some Vertebrates; and the aortic, arch-like blood-vessels in the appendages may be compared to the branchial arteries (Fig. 14, 5.) (5) Moreover, the enormous liver of Arachnids, (6) the blood, (7) the histological structure of the nervous system, and the manner of nerve terminations, (8) the minute structure of the muscles, and (9) the development of the ova and spermatozoa, all supply us with abundant evidence of the great morphological and histological specialisation of the Arachnids, and their structural similarity to Vertebrates.

There is another point which deserves more than passing notice. In insects the sexual organs are developed (Acilius) from the wall of one, or at most two, mesoblastic somites, and are carried by the growth of these organs to the hæmal surface; the adult organs are never reticulated. In Scorpio (and Limulus ?) it is just the reverse; the sexual organs arise as a median longitudinal band of cells underlying the nervous system, and extending the whole length of the primitive abdomen—that is, over at least seven segments; moreover, in the adult the sexual organs are remarkable for their reticulation. In the adult Scorpion the sexual gland is neural in position, and is composed of three longitudinal tubes united by transverse ones. Now in Protopterus the testis has exactly the same arrangement of longitudinal and transverse bars as in Scorpio, the only difference being the position of the outlets and the small size of the median longitudinal tube. In other words, it is a most significant fact, when viewed in connection with all that has preceded, that the sexual organs of Scorpio and Limulus, in their exceptional position, structure, and development, should resemble in these very features the sexual organs of primitive Vertebrates.

XIV. Embryology.—Kleinenberg's admirable observations on the development of Lopadorhynchus afford the first secure foundation for the interpretation of the embryology of the higher segmented animals. They teach us not only exactly what the gastrula of a segmented animal is, but also what it is not. As long as such forms show no trace of concrescence, of cœlomic diverticula, or of any connection between an undoubted gastrula and an undoubted "primitive streak," we must, in order to explain the facts of Arthropod and Vertebrate embryology, follow other paths than those laid down by the concrescence theory, the cœlom theory, or any other theory that regards the "primitive streak" and "blastopore" as remnants of a gastrula—unless, indeed, we expect to prove that the Vertebrates out-Cœlenterate the Cœlenterates. The absence of an Annelid pre-oral lobe, and the formation of the head by the pushing forwards of three post-oral body segments, show that the Arthropod head and body are comparable only with the post-oral portion of the Annelid. The Arthropod body represents an outgrowth from the trochosphere, but the trochosphere itself, the Cœlenterate stage, has disappeared. Hence there is no such thing as a gastrula in Arthropods, and, strictly speaking, no germ layers. The germ-layer theory requires, as one of its ablest expounders, Balfour, explicitly states, that the entire ectoderm, mesoderm, and endoderm be derived directly from the primitive layers. Now in Lopadorhynchus it is certain that the greater part of the mesoderm arises from the ectoderm at the growing tip of the tail, and has nothing to do with primitive mesoderm. In Arthropods the mesoderm and also part of the endoderm may arise in an exactly similar manner. Besides, mesoderm may arise (Acilius) at a late embryonic period from a great variety of places, just as ganglionic cells are formed from the general surface of the body wherever a new sense-organ is formed. Hence it is highly probable that all the endoderm, except possibly a small portion at the inner end of the œsophagus, and the mesoderm have arisen independently of, and have finally supplanted, the primitive layers; just as in Arthropods the pre-oral lobe and brain of Annelids have been replaced by other organs.

If we suppose that the body of segmented animals represents, not the elongated body of a Cœlenterate, but only one of its tentacles, we can explain why a segmented animal always grows at one end only—something the concrescence and other theories cannot do; we can also explain why the Annelid and molluscous body is a lateral outgrowth from the subumbrella; and this supposition would be in perfect harmony with the position and history of the "Prototroch" nerve, as described by Kleinenberg. Moreover, the imperfect division of Cœlenterate tentacles into joints provided with lateral processes may be regarded as a forerunner of metameric segmentation (Fig. 15).

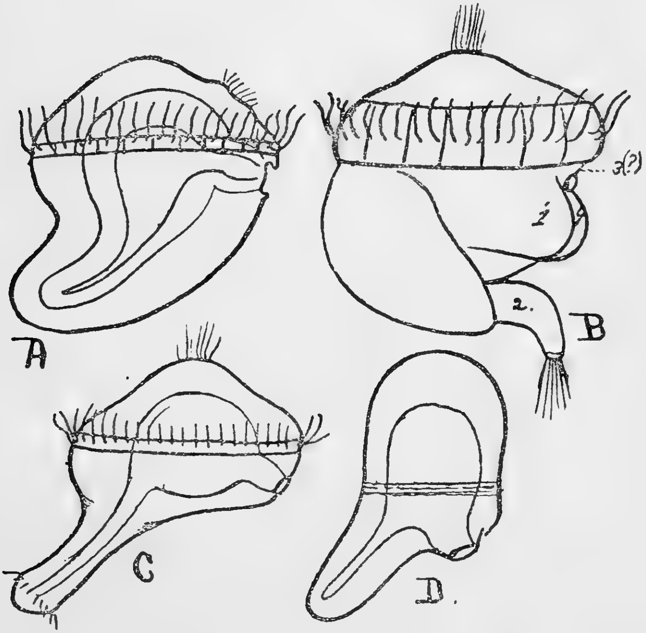

Fig. 15.—Diagram of an Annelid (*A*), Mollusc (*B*), primitive Annelid (*C*), and Cœlenterate (*D*) larva.

To show, further, that a reasonable explanation of some of the salient points in the embryology of segmented animals may be given on the above view, without resorting to impossible gastrulas, I suggest the following. Since in Cœlenterates mesoderm cells are constantly forming from the ectoderm, it is probable that their growing tentacles contain at least some mesoderm and endoderm cells not derived from the primitive layers. If such a tentacle were transformed into the body of a segmented animal, its elongation and the formation of the layers in the embryos would naturally take place by the rapid division of large terminal cells like those found in all rapidly elongating organs of both plants and animals, and, indeed, just as it probably takes place in the Cœlenterate tentacle itself; moreover, there would be no necessity for regarding these terminal cells or teloblasts as any part of a gastrula. Bearing in mind the above conclusions, it is evident that two surface teloblasts or mesoblasts multiplying by tangential and radial division would produce two long mesoblastic bands lying beneath the ectoderm, as in most Annelids. Many surface teloblasts dividing by radial division alone would produce a band of mesoderm lying its whole length on the surface. Then, if tangential division began, a longitudinal cord of cells would be either proliferated or invaginated inwards; if this median cord divided into two lateral ones, which then became segmented, we should have the essential features in the development of the mesoblastic bands of many insects. The important point is that the segmented mesodermic bands of insects have been produced in exactly the same way as those of Annelids, except that the tangential division of the teloblast and of its products is slightly postponed. That the median furrow of insects is merely an ontogenetic adaptation is sufficiently evident from the fact that it may be present or absent in closely related forms. When it is absent the resemblance of the mesoblastic bands and their growth, to those of Annelids is more evident.

In Doryphora, Acilius, Musca, and others, the great mass of terminal proliferating cells also gives rise to two cords of endoderm extending forward, one on either side of the median line. In some insects the median furrow produced by the invagination of mesoderm tends to close from before backwards, leaving a terminal pore, the anterior wall of which continues to proliferate endoderm and mesoderm : in this case the mesodermic bands would appear to grow forwards from the anterior median wall of the pore, while the endodermic bands would appear to arise from its anterior lateral walls.

Ordinarily the mesodermic bands become segmented while the endoderm is yet only two narrow bands (Fig. 16, c), but later the endodermic bands begin to spread out ventrally and dorsally to enclose the yolk. Suppose the segmentation of the mesoderm is retarded and the extension of the endoderm accelerated, we might then have a continuous sheet of mesoderm and endoderm, apparently a forward continuation of the anterior wall of the terminal pore or telopore (Fig. 16, D and F). Suppose the hæmal edges of the mesodermic bands unite before the mesoderm is separated from the endoderm, we should have a condition like that in Amphioxus, where the endoderm and mesoderm form a sac opening outward posteriorly by the telopore (Fig. 16, E and H). All the so-called gastrulas and blastopores of Arthropods and Vertebrates can be explained on the same principle. Accepting

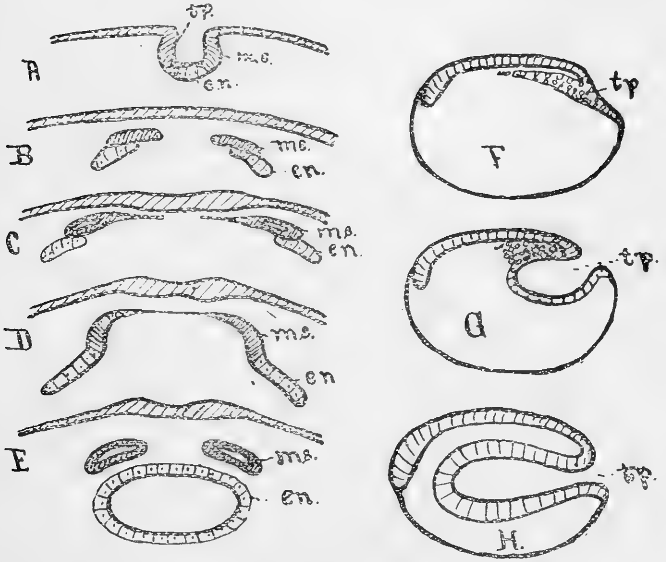

Fig. 16.—Diagrams to illustrate the formation of germ layers.—*A.* Cross section of the posterior end of telopore of an insect just before it closes. *B.* Section a little in front of the last, showing the cords of mesoderm and endoderm. *C.* One still farther forward. *D.* Section through an embryo in which it is supposed mesoderm and endoderm form a continuous layer. *E.* Section of an embryo in which it is supposed the lateral endodermic bands have grown completely round the yolk before the mesoderm became segmented and separated from the endoderm. *F*, *G*, *H.* Three longitudinal sections, showing successive stages in the formation of a telopore by the invagination of teloblasts. *F.* Insect. *G.* Crustacean, Astacus. *H.* Amphioxus.

the above view, it is plain that no invagination at the posterior end of a segmented embryo can be justly regarded as a gastrula; and conversely, in all segmented animals the gastrula or any remnant of it must lie at the very anterior end of the body. The conclusion is obvious that no trace of a gastrula, any more than of Annelid pre-oral lobes, is to be found in Vertebrates and the higher Arthropods.

Just as in the blastosphere the invagination of endoderm to form a true gastrula is the ontogenetic way of repeating what was originally a mere local proliferation, so in the segmented animals the invagination of endoderm and mesoderm to form a telopore is an ontogenetic modification of a cluster of proliferating cells or teloblasts. The telopore and the gastrula are thus to a certain extent analogous, but in no wise homologous. The formation of the telopore is complicated by the increase in length, and by the presence of both mesoderm and endoderm; but we have, I believe, in Arthropods and Vertebrates a complete history of its various phases.

It is a fact of great importance that in Vertebrates and Arthropods the functional endoderm exists at one time as two longitudinal lateral bands—a condition, as far as I know, not found in Annelids.

The importance of yolk in modifying development has been greatly exaggerated. If its presence obscures the primary characters, it is extremely probable that in animals normally having large eggs its absence would result in a still farther modification, not in a reversion to the simpler condition. Such has been the case, I believe, in Amphioxus, where the simplicity in development is apparent, not real. In fact, the cœlom theory proves too much, for it cannot explain why Amphioxus in the development of its body-cavity falls little short of being a typical Cœlenterate, while the Annelids themselves do not in this respect show the slightest trace of Cœlenterate characters.

In Cymothoa the multiplication of the teloblasts goes on with great regularity (Fig. 17). This condition is undoubtedly a mere modification of that found in most insects. But it is incredible that these teloblasts can have anything to do with a gastrula. There is no segmentation of a continuous sheet of mesoderm, but each somite arises from the repeated division of a single row of eight cells. Each somite consists of two lateral parts arising from the six lateral mesoblasts, and a median one arising from the two median mesoblasts.

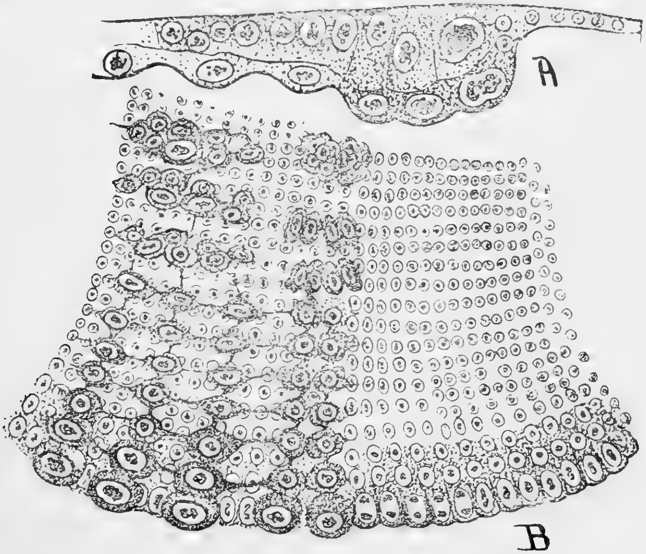

Fig. 17.—Formation of layers in Cymothoa.—*A.* Median longitudinal section of posterior end of germ band. *B.* Posterior end of embryo, seen from below; the rows of inner layer cells are not represented on the right. The last row of ectodermic teloblasts often divides simultaneously along its whole length.

I long ago pointed out that in Phryganids the neural furrow is developed in the anterior portion of the germ band before the terminal pore has disappeared, and that its posterior end extends into the terminal pore. I then stated, and still maintain, that an incipient neurentric canal is thus formed, similar to that in Vertebrates.

But there are certain structures in Arthropods which may represent remnants of gastrulas. For example, if the mouth and œsophagus of Arthropods is primitive—and there is no reason to suppose it is secondarily acquired,—then we must look for primitive endoderm at its inner end. I have figured in "Eyes of Acilius," at the very anterior end of the embryo, a great sac of endoderm cells which probably arise by invagination, although the process was not directly observed. The sac, which soon opens outward by the œsophagus, afterwards becomes solid, and finally is converted into two longitudinal bands, one on either side, extending backwards towards the middle of the body, where they become continuous with similar bands extending forwards from the posterior end of the embryo.

There are several other cases where great vesicular cells appear at the inner end of the œsophagus, and they probably are of a similar nature to those just described.

In Limulus there is a great lump of endoderm-like cells at the inner end of the œsophagus; they grow fainter, and are quickly absorbed without forming either yolk-cells or any part of the definite endoderm.

These endoderm-cells are the only structure in Arthropods which I can see any reason for regarding as remnants of a gastrula. This evidence consists solely in their position at the inner end of the œsophagus, and their speedy absorption in Limulus, and possibly other Arthropods. But even this evidence is of no great weight, since in Doryphora—according to Wheeler, whose preparations I have had the privilege of examining—a great mass of cells arising from the posterior end of the body is absorbed in very much the same manner as the œsophageal ones in Limulus.

The history of the layers in Scorpio and Limulus is complicated, and I have not yet obtained satisfactory results; much of the endoderm and mesoderm is produced from the cluster of cells at the posterior end of the body, but there are no such distinct endodermic bands as in insects. It is probable that some of the endoderm, and perhaps mesoderm, is split off from the blastodisc before the germ-band is formed.

In surface views of the germ-band of Scorpio, we see in the median line at the posterior end of the body a great thickening, from which cells grow forward and laterally. From the median portions of the band of tissue thus formed arise the sexual organs and the botryoidal cord, and from the more lateral portion the mesoblast and endoderm.

In Limulus there is, at the posterior end of the embryo, a short, but distinct slit-like invagination, which, in surface views and in sections, is exactly like the primitive streak of many birds and reptiles (Fig. 18, B and D).

The lateral edges of the wedge-shaped mass of cells produced by this invagination spread out on either side between the yolk and the ectoderm to form poorly defined mesodermic bands. At irregular intervals, but principally near the primitive streak, great masses of cells wander inwards from the inner layer cells, and are scattered throughout the yolk.

Moreover, in a number of different places great masses of mesoderm and endoderm cells may be proliferated inwards from the ectoderm of the ventral plate, in a manner very similar to what occurs in the primitive streak; the proliferating points differ from the primitive streak in being nearly transverse instead of longitudinal, and in not being accompanied by any overlying depression of the ectoderm[1] (Fig. 18, A χ, χ). These facts prove conclusively, I think, that the formation of mesoderm and endoderm in the ventral plate of Limulus does not follow any method which can possibly be regarded, in the concrescence theory or any other, as a modification of a gastrula. I have examined a great many embryos, and have never seen any traces of a median furrow connecting the mouth and anus such as is described by Kingsley, and

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[1] It is possible that in some places at least these proliferating points may be cross sections of the somites, which are much curved at the posterior end of the body. I have seen indications in young scorpion embryos that some somites are formed by a distinct transverse proliferation of the ectoderm.

which he regards as the remnants of a medianly coalesced gastrula. According to my observations, the mouth, the primitive streak, anus, and the neural canal, are totally independent organs, and appear at widely different stages.

Out of a large number of embryos, a few are provided at the posterior end with an enormous depression, either circular, oval, or pyramidal in outline, at the bottom of which, or on its anterior wall, lies the primitive streak. It is not accompanied by any special modification in the development of the

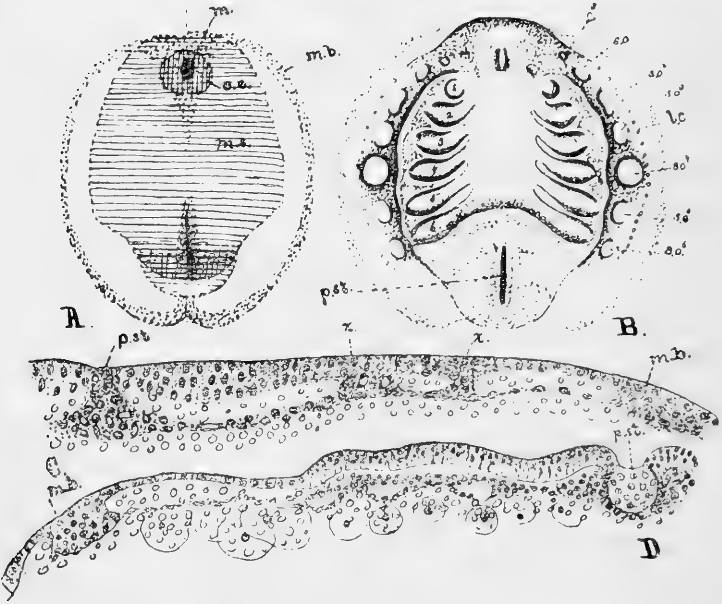

FIG. 18.—*A.* Diagram to show distribution of mesoderm and endoderm in young embryo of Limulus. *m. b.* Peripheral zone of mesoderm (?). *m. s.* Mesoderm underlying the ventral plate. *o. e.* Mass of transient endoderm at inner end of œsophagus. *B.* Slightly diagrammatic view of Limulus embryo. *C.* Cross section of same through primitive streak. *D.* Ditto, a little older stage than *C.* *l. e.* Lateral eyes. *m. b.* Mesodermic (?) bands. *m. s.* Mesoderm. *s.* o^{1-6}. Thoracic sense-organs. *p. s.* Primitive streak. χ. Masses of cells passing inward from the ectoderm.

germ layers, and it certainly is not a gastrula, although in surface views it is suggestive of such an organ.[1]

In Limulus there is a remarkable ring of mesoderm cells extending completely around the embryo. It may be seen in surface views as two dark bands diverging from the region behind the primitive streak, and uniting with each other in the neighbourhood of the œsophagus (Fig. 18, A). In sections the bands appear as two clusters of oval cells, formed by an inner proliferation of the ectoderm (Fig. 18, C and D, *m. b.*). They are soon freed from the overlying ectoderm, and finally, after increasing enormously in size, meet each other along the median dorsal surface. By the time the bands are well formed the cells are oval, and contain an enormously long, brilliantly refractive filament, which is either wound or bent back and forth a great many times. The small remaining space in the cell is filled with a watery fluid, and a small, laterally placed nucleus. Some of the cells become elongated, and the coiled fibres give rise to the striæ of the longitudinal dorsal muscles. Some of the cells appear to degenerate and disappear. The resemblance of this ring, at an early stage, to the "Keimwall" of Vertebrate embryos need not be enlarged upon here. I have not with certainty found anything similar in Scorpions.

The following expresses what I conceive to be the most natural arrangement of the segmented animals :—

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[1] This condition is probably produced by some peculiarity in the division of the cells of the posterior end of the body. All foldings of cellular membrane are due, I believe, to local variations in cell division. Wherever a cell layer tends to increase in thickness by tangential division a simple thickening will be produced. But if the cells thus produced at the same time multiply by radial division, the inner surface of the membrane will be larger than the outer, and the whole membrane curved or warped. The direction of curvature will depend entirely on the relative rapidity of division at certain points. All foldings may then be regarded as the expression of certain methods of cell-growth, and may not have themselves any morphological significance.

Vertebrata

Urochorda Cephalochorda

SIPHONEURA

Central nervous system tubular.

Eyes on neural surface. Retinas to both median and lateral eyes, inverted.

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Ichthyoida . { Cephalaspis, Pterichthys, Pteraspis, Bothriolepis, &c.

Arachnida Merostomata { Limulus, Eurypterus

Trilobites

PELTACEPHALA.

Head shield-shaped. Eyes on hæmal surface.

SYNCEPHALA.

Divided into Head, Body, and Tail.

Head-segments 9—13; in four groups; first three head-segments devoid of appendages. Terminal segments more or less fused to form a urostyle. Eyes median and lateral. Median eyes 2—4, in a common sac or tube; retinas inverted.

Insecta Crustacea

Myriapoda

PSEUDOCEPHALA.

Brain segmented; originally post-oral.

Annelida

ENCEPHALA.

Brain unsegmented; pre-oral.

SEGMENTATA

CŒLENTERATA **ECHINODERMATA ?**

PROTOZOA

EXPLANATION OF PLATES XXIII and XXIV.

Illustrating Mr. William Patten's paper "On the Origin of Vertebrates from Arachnids."

a. n. Abdominal neuromeres. *br.* Brain. *c. g.* Coxal glands or nephridia. *ch.* Chelæ. *chl.* Chelicerœ. *c. s.* o^6. Indicated position of coxal sense-organs. *e. s.* Outline of optico-ganglionic sac. *f. b.* = *s. l.* Frontal or semilunar lobe. *g. m. c.* Ganglionic portion of median furrow. *g.* v^{1-3}. Ganglionic invagination. *i. m. e.* Interganglionic portion of median furrow. *l.* b^{1-4}. Lung-books. *l. e.* Lateral eyes. *m.* Mouth. *m. e.* Median eye. *mxl.* Maxillaria. *n.ph.* Nephridia. *n. c.* = *sp. g.* Neural crest or spinal ganglion "Anlage." *op.* g^{1-3}. Optic ganglia. *op.* p^{1-3}. Optic plates. p^{1-4}. Walking legs. *s. l.* Semilunar lobe. *s.* o^1. Sense-organs near joints of legs. *s.* o^2. Scattered sense-organs. *sp. n.* Spinal nerve. *s. s. o.* Segmental sense-organs. *st. n.* Anlage of stomodæal nerves. *t.* n^{2-6}. Thoracic neuromeres. *v.* n^{1-4}. Vagus neuromeres. *v.* p^{1-4}. Vagus appendages.

PLATE XXIII.

FIG. 1.—Stage B: surface view of embryo Scorpion removed from the yolk. Observe the forward position of the mouth, and the absence of nervous or other tissue immediately in front of it; the absence of abdominal appendages; the post-oral position of the chelicerœ; the divergence of the abdominal nerve-cords; the segmental sense-organs, *s. s. o.*; the absence of the eyes, and of the rudimentary optic plate; the innumerable sense-organs from which the nervous system arises; the large sense-organs, *n. c.* = *sp. g.*, which later form an incipient "neural crest," and from which the spinal ganglia develop; the "anlage" of the optic ganglia, *op. g.*, and of the brain, *bc.*, which is not yet segmented. (Obj., oc. 2.)

FIG. 2.—Stage C: surface view of detached embryo of Scorpion, showing the three brain-segments; the beginning of the second and third ganglionic invagination, *g.* v^2. and *g.* v^3.; the paired median sense-organ-like invagination in the brain region, those opposite the fourth neuromere giving rise to the ganglia of the stomodæal nerves; the continuity of the paired pits with the median furrow; the great frontal lobe, *f. b.*, produced by the invagination of the first brain metamere, and possibly made up in part of an Annelid pre-oral lobe (?); the large optic ganglion of the second and third brain metameres, *op.* g^2. and *op.* g^3.; the nephridia-like cell-coils in the basal portion of each

pair of thoracic legs; the double-lobed neuromeres; the four pairs of rudimentary vagus appendages, *v.* p^{1-4}.; and the bundle of nerve-fibres lying in the skin from which the spinal nerves are developed, *sp. n.*

PLATE XXIV.

FIG. 3.—Stage E: surface view of detached embryo of the Scorpion. The left side of the head is represented as an opaque object, and shows the growth of the optic ganglia over the brain-segment, and the advance of the lateral lips of the ganglionic invagination over the optic ganglia. The right side is represented as transparent; the dotted line, *e. s.*, shows the form of the sac, the outer wall of which is formed by the eye; the frontal, now nearly semilunar lobe, *s. l.*, lies beneath the brain and optic ganglia, *op.* g^2. and *op.* g^3. We also see the position of the coxal sense-organs indicated at *c. s.* o^6., although I have not been able to detect them in surface views; the appendage-like maxillaria, *mxl.*, in the third and fourth thoracic segments; the double neuromeres, the anterior portion of each containing in the median line a very distinct pit-like invagination of the median furrow, *g. m. c.*; the posterior portion, a very small and indistinct one, the interganglionic portion of the median furrow, *i. m. c.*; the four lung-books, *l.* b^{1-4}., the first one belonging to the last vagus segment, the rudimentary appendage of which has disappeared. I have found no evidence that it is infolded to form the lung-book, the development of this lung-book being the same as the following segments where no appendages are ever present.

FIG. 4.—Stage F: surface view of a detached embryo of Scorpion, showing the almost complete union of the two optico-ganglionic sacs; the lateral eye-plates, *l. e.*; the numerous sensory buds, *s.* o^1., scattered over the surface of the segmental sense-organs, *s. s. o.* There are also usually one or more quite large sense-organs on the basal joints of the appendages, *s.* o^1. The first three vagus neuromeres have completely fused with one another, but the fourth is still quite independent.

N.B.—The Scorpion referred to in the present memoir is probably Buthus carolinianus.

On the Origin of Vertebrates from a Crustacean-like Ancestor.

By

W. H. Gaskell, M.D., F.R.S.

With Plates XXV, XXVI, XXVII, XXVIII.

CHAP. I.—THE EVIDENCE GIVEN BY THE CENTRAL NERVOUS SYSTEM AND PINEAL EYES OF THE AMMOCŒTES OF PETROMYZON PLANERI.

IN a former paper (1) I have described how my investigations into the Vertebrate nervous system have led me to the conclusion that that system is composed of nervous material grouped around a central tube which was originally the alimentary canal of the Invertebrate from which the Vertebrate arose; and in a second paper (2) I have suggested that the physiology and anatomy of the Vertebrate nervous system both fit in best with the assumption that the Invertebrate ancestor was of the Crustacean[1] type. In both papers I have promised to point out the confirmation of this theory which is afforded by the study of the lowest Vertebrate nervous system, viz. the Ammocœtes form of Petromyzon. This promise I propose now to redeem, and in order to bring out as prominently as possible the theory which I hold to be true I will discuss the nervous system of the Ammocœtes in terms of the Crustacean;

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[1] By Crustacean I include such a form as Limulus, without intending to pronounce any opinion on the question whether Limulus is an Arachnid or a Crustacean; it would, perhaps, be better to use the term proto-Crustacean, meaning thereby a form from which both Crustaceans and Arachnids may have been derived.

in other words, I will take separately the prominent features of the alimentary canal and central nervous system of a Crustacean-like animal, and point out how each one exists in the nervous system of the Ammocœtes.

Before commencing the study of the special nervous system treated of in this paper I will briefly recapitulate the general arguments which I have put forward in my previous papers.

The central nervous system of all Vertebrates consists of two parts—(1) a nervous portion, and (2) a non-nervous epithelial portion, which is in part free from admixture with nervous elements, and partly helps to form the supporting tissue of the nervous elements. This non-nervous part of the central nervous system forms a canal around which the nervous material is grouped, in the same manner as the nervous system of the Crustacean is grouped around the alimentary canal. This similarity of grouping is not merely anatomical, but is also physiological; the functions of the supra-œsophageal ganglia of the infra-œsophageal and of the ventral chain correspond to the functions of those parts of the Vertebrate central nervous system which are situated in the same anatomical position, with respect to the non-nervous tube, as the corresponding ganglia of the Crustacean with respect to the alimentary canal.

The natural conclusion to draw from this striking coincidence is that this non-nervous tube of the Vertebrate central nervous system is the altered alimentary canal of the Crustacean ancestor of the Vertebrate.

If this conclusion is right, then not only should the evidence upon which it is based come out more clearly when the lowest Vertebrate nervous system is examined, but also fresh evidence of Crustacean characteristics may reasonably be expected to be found in such nervous system. We should expect, in fact, to find a nearer approach to the Crustacean type than in the higher Vertebrates.

We should expect, therefore, to find that the vestiges of the mouth, œsophagus, and cephalic stomach were more conspicuous than in the higher forms; that such an ancestral characteristic as the pineal eye was easily recognisable and of a Crustacean type, and that the proportion of nervous material to non-nervous approached nearer to the proportion found in the Crustacean than in the higher Vertebrates.

In addition, we should expect to find the vestiges of other Crustacean organs which are connected with the alimentary canal, especially that large and important organ the so-called liver; and, indeed, seeing that the so-called liver represents the whole of the digestive glandular apparatus of the alimentary canal of the Crustacean, the cephalic stomach and straight intestine being simple epithelial structures for the purpose respectively of holding food, perhaps also of absorbing it, and of passing out the indigestible residue, it follows that any theory which compares the simple epithelial non-nervous tube of the central nervous system of the Vertebrate with the non-glandular epithelial stomach and intestine of a Crustacean is imperfect, unless some explanation is given of the fate of the large glandular liver which must have existed in the cephalic region of the ancestor of the Vertebrate if that ancestor was formed after the Crustacean type.

Conversely, the theory which I have put forward is immensely strengthened if the examination of the lowest type of Vertebrate brain brings to light the vestiges of a large glandular organ, which bears the same anatomical relation to the ventricular cavity of the brain as the so-called liver bears to the cephalic stomach of the Crustacean.

I have chosen the Ammocœtes stage of Petromyzon as the subject of investigation because it undoubtedly represents a very primitive form among living Vertebrates, and also because it is easy to obtain in large quantities at different ages, and will live well in the laboratory: all my specimens were obtained by me at Hind Head, in Surrey—the first batch, to the number of about forty, in the beginning of September of 1888; and the second batch, amounting to 100, at the end of October, 1889. They were all Ammocœtes of Petromyzon Planeri, and varied in size from 25 mm. in length up to full-grown specimens of 130 mm. or more.

Those which I brought with me to Cambridge in 1888 were kept alive in a small basin containing sand and weed from their native stream, the water in which was renewed occasionally. They lived in this way perfectly well, and some of them are still living; as far as I can see they have not grown at all, or made the slightest attempt at transformation. The others, which I have obtained lately, are kept in a large tank with sand and weed in it.

The method of observation which I have mainly relied on is that of serial sections, the whole head of the animal having been embedded in paraffin, or else the brain dissected out and then embedded. For hardening and staining I have used various methods; the whole head has been placed either in osmic acid 1 per cent. solution, or else in Perenyi's fluid and then alcohol, with subsequent staining in boro-picro-carmine or picro-carmine and eosin: I have also stained on the slide with aniline colours and with hæmatoxylin.

As a rule the sections are cut through the whole head and mounted in order. By this means it is certain that all the structures within the cranial cavity will be fixed on the slide in their right position; but, on the other hand, there are in many specimens hard parts in the region of the basilar plate which turn the edge of the razor and tear through the neighbouring soft tissues; also so large a section is apt to be crumpled when cut into ribbons by the Rocking microtome. I have succeeded in getting over the folding of the sections by a method which I have now used for some years past, but have never as yet published; it consists simply in floating the series of sections on the surface of warm water and then transferring them to the slide, which has been previously coated over with albumen and glycerine. By this means the sections are flattened; they are then dried by pressure between blotting-paper, the wax is melted, removed by xylol, and the series of sections mounted in Canada balsam.

The figures in Pls. XXV, XXVI, XXVII, XXVIII, are, for the most part, drawn by myself, and by Mr. Wilson, of the Scientific Instrument Company. I am indebted to Mr.

Durham and Mr. Grünbaum for making me photographs of various specimens, which have been of great assistance in making the drawings; to Mr. Shipley for making the series of drawings in Pl. XXVI, figs. 13*a*—13*e*; to Mr. Hardy and Mr. Shore for assistance in the preparation and staining of material; and to Dr. Hunter for valuable advice in connection with the formation of pigment. To all these gentlemen I beg here to offer my sincere thanks.

The description of the brain of the adult Petromyzon as given by Ahlborn (3) is so thorough and so excellent, that it is hardly necessary for me to re-describe the arrangement of its different parts, especially as the brain of the Ammocœtes resembles very closely that of the adult form; the main difference being, as Ahlborn has pointed out, that the internal cavities are more roomy, and that the optic lobes are not so fully developed. I shall, therefore, refer my reader to his descriptions and illustrations, and only give such illustrations from my own specimens as seem to me necessary to make clear the arguments brought forward in this paper.

In Pl. xiii of Ahlborn's paper (3) drawings are given of the brain from different points of view: as, however, he has removed the choroid plexuses in all his drawings I have thought it best to give a drawing of the dorsal aspect of the brain as it appears in the fresh condition when the brain-case is removed. The specimen from which fig. 1, Pl. XXV, was taken measured 120 mm. in length, and the brain was carefully dissected out under a dissecting lens, and then the drawing was made. The greater portion of the dorsal surface is taken up with the transparent folds of the choroid plexuses ii and iii; the folds of these two plexuses meet, as described by Ahlborn, over a deep fissure, which indicates the position of the band of fibres constituting the cerebellum. In front of the folds of the choroid plexus ii are seen, in the middle line, the large r. gangl. habenulæ, and the white opaque pineal eye with the masses of the cerebral hemispheres on each side. On the ventral side (see Ahlborn) the brain is divided by a marked constriction into a pre-chordal and an epi-chordal portion. The epichordal portion terminates in a projecting prominence, termed by Fritsch the conus post-commissuralis, and recognised by Ahlborn as the region of the ganglion interpedunculare. The ventral appearance of the brain is shown in Pl. xiii, fig. 6, of Ahlborn's paper (3) after removal of the hypophysis and saccus vasculosus. If the brain is carefully dissected out so as to leave the saccus vasculosus intact, and then examined in the fresh state, it is seen that the projection formed by the infundibular region, and also that of the conus post-commissuralis, stand out most prominently from the rest of the nervous material owing to their peculiar appearance: instead of appearing white and opaque like the rest of the nervous matter, they look like transparent jelly-like masses imposed upon the opaque white mass of the rest of the brain; so transparent is the material here that the brain-cavity shows through, as can be imagined from the inspection of Ahlborn's fig. 6.

Further, the brain lies in a mass of glandular-looking material composed of cells, and characterised by the amount of pigment which ramifies between the cells. This tissue clings largely to the brain when it is dissected out, so that the surface of the brain presents an appearance as in Pl. XXV, fig. 1. This thick glandular material is arranged in a definite manner on the surface of the brain; it forms a bilateral pigmented cellular organ, which may be looked upon as forming two lobes symmetrically placed on each side of the ventral constriction which marks the separation between the epi- and pre-chordal portions of the brain. From here, as starting-point, the tissue spreads in a fan-shaped fashion over the lateral portions of the epichordal brain, never reaching the mid-line dorsally, but stopping short at the choroid plexus iii. In the prechordal portion it passes towards the dorsal surface, round the infundibular projection, up to the choroid plexus ii, and surrounds the pineal eye and cerebral hemispheres, so as to fill up the brain-cavity anteriorly to the nervous system. In most of the sections I have shown the arrangement and structure of this tissue.

Sect. 1.—The Cephalic Stomach.

The brain of the Ammocœtes, then, differs markedly in external appearance from that of higher Vertebrates; and one of its most striking peculiarities consists in the fact that nearly the whole of its dorsal surface is composed of membranous folds, and not of nervous material. The large amount of surface which these folds represent is manifest upon inspection of the external appearance of the brain, and is clearly visible in transverse sections such as are represented by figs. 2, 3, 9, Pl. XXV. These membranous folds form the choroid plexuses ii and iii of Ahlborn, and may be looked upon as a folded crumpled globular bag which stretches from the commencement of the fourth ventricle to the posterior commissure and ganglion habenulæ; this folded bag has been constricted into two parts, which form the roofs of two cavities, viz. the fourth ventricle and the cavity of the mesencephalon, by the presence of a narrow constricting band formed by the fourth nerve and the incipient cerebellum (see also Ahlborn). This bag, if unfolded, would, in accordance with the view put forward in my previous papers, form the main part of the large globular cephalic stomach of the Crustacean-like ancestor; it is only possible to imagine its expansion on the dorsal side, for ventrally the epithelial walls of this bag form the lining membrane of the ventral nervous masses of the brain, and in the epichordal portion of the brain at all events the internal surfaces of the most ventral portion are brought close together by the pressure of the two lateral nervous masses, thus forming the raphe (see p. 394). In other words, the infra-œsophageal and upper ganglia of the ventral chain, which, on my theory, form the epichordal portion of the brain, have by their growth nipped and compressed the ventral surface of the cephalic stomach which was lying dorsal to them.

Lying on the anterior part of the cephalic stomach we see, in the position of the supra-œsophageal ganglia (see fig. 1, Pl. XXV), the nervous masses known as the cerebral and olfactory lobes, optic thalami, ganglia habenulæ, together with the pineal eye. These nervous masses have enclosed the walls of the stomach in this region to such an extent that only a small portion of its surface remains free, and is not utilised for the purpose of lining the cavities of the brain in this region. Its anterior rounded extremity forms the lamina terminalis, *l. t.*, the surface of which continued backwards up to the ganglia habenulæ is slightly folded, and spans the space between the two optic thalami forming the choroid plexus i of Ahlborn. Passing round to the ventral surface, the stomach wall forms a bulging known as the recessus chiasmaticus. Laterally it forms the lining of the optic thalami, and is compressed by the growth of the nervous matter of the cerebral and olfactory lobes so as to form the diverticula called by Ahlborn the lateral ventricles (fig. 6, Pl. XXV; also Ahlborn's fig. 37, Pl. xv). The appearance presented by a longitudinal vertical section in the middle line through the brain of an Ammocœtes is given by Ahlborn in fig. 41, Pl. xvi; and if the choroid plexuses were dilated we should have an appearance somewhat as in the diagram on Pl. XXVIII, fig. 29, where the red line represents the contour of the cephalic stomach of such an animal as Limulus, and the yellow line represents the modifications of contour which have occurred by the growth and compression of nervous material in the case of the Ammocœtes. In fact, it is perfectly clear that in this primitive form of Vertebrate the non-nervous epithelial bag which was originally the cephalic stomach of the Crustacean-like ancestor of the Vertebrate is more conspicuous and stands out more prominently with respect to the nervous system than in the higher Vertebrates; in other words, the relation between the size of the nervous system and of the cephalic stomach approaches to that which occurs in the Crustacean as we descend from the highest to the lowest Vertebrates.

Sect. 2.—The Mouth and Œsophagus.

Again, we see in this animal more clearly than in any other Vertebrate the remains of the old Crustacean œsophagus. From the central cavity a broad passage (the infundibulum) exists on the ventral side leading into the saccus vasculosus or saccus infundibuli, the thin walls of which come to the surface of the brain on the ventral side. The bag of the saccus vasculosus is limited in front by the optic chiasma, which separates it from the recessus chiasmaticus; its cavity is continuous backwards into that of a well-defined tube which lies in the middle line and extends nearly up to the large ventral fissure which separates the prechordal and epichordal portions of the brain. This tube is apparently called by W. Müller (**5**) the processus infundibuli; it is called by Ahlborn (**3**) the thick-walled lobus infundibuli; and is compared by him with the unpaired lobus infundibuli of the Amphibia. It is figured *L. i.* in his drawings, and is shown in transverse section in figs. 27 and 28, Pl. xiv. The walls of this tube are composed of ependyma continuous with that of the central cavities of the brain, and as it approaches its termination its lumen becomes occluded by the coming together of its walls. Near its termination it is in very many cases found to be lying outside the brain, being separated from the nervous matter by lines of pigment continuous with the pigmented tissue around the brain. The appearance which it then presents is given in fig. 3, Pl. XXV, which is a section through a carmine preparation of the brain of a specimen which had just undergone transformation. In fig. 2 I give another section from the same series a few sections nearer the infundibulum, to show the commencing separation of this tube from the brain-substance. In fig. 2 the section has cut the last portion of the right ganglion habenulæ, and the notochord is not yet involved in the section; it corresponds very nearly with fig. 27, Pl. xiv, of Ahlborn. In fig. 3 the notochord has just made its appearance, and the section passes through the posterior commissure; it corresponds so closely with Ahlborn's fig. 26 that the very next sections contain the two large nerve-cells pictured by Ahlborn in that figure. The comparison of his figure and mine shows that he had really before him the closed end of this tube, but he has misinterpreted its meaning and labelled it *M. B.*, or Meynert's bundle.

In his description (p. 285) of this figure he says, speaking of Meynert's bundles, " Dicht über der Haubeneinschnürung [i.e. the large ventral fissure which separates the pre-chordal and epichordal portions of the brain] lösen sich die Bündel auf; ein grosser Theil der Fasern fährt pinselförmig gegen die Mediane aus einander und bildet hier einen asymmetrischen, eigenthümlich hellen und äusserst feinkörnigen Körper, welcher der Haubeneinschnürung direct aufgesetzt ist."

This description expresses very well the appearance of the termination of this occluded tube as it appears in my specimens, with the exception that I have not noticed any appearance of asymmetry in the peculiar transparent termination of this tube. The meaning of this tube is to my mind perfectly plain; we see here more clearly than in any other Vertebrate that a median tube formed of ependyma, continuous with that of the central cavity of the brain, is lying freely on the surface of the brain in the exact position where the œsophagus ought to be found if the central cavity of the brain is the cavity of the cephalic stomach of a Crustacean-like ancestor. This tube, to my mind, cannot be called lobus infundibuli; it is not homologous with the paired lobi infundibuli of other fishes: it is the same in position and in meaning as the median tube which I have described (1) in the tuber cinereum of the sheep; it corresponds with the median prolongation from the saccus vasculosus which I have described in the brain of the dog-fish, where this same tube exists in addition to the paired lobi infundibuli. The difference in its apparent position in the dog-fish and in the lamprey is due simply to the more extensive cranial flexure which has taken place in the former animal.

In fact, the paired diverticula from the canal of the infundibulum which form the cavities of the lobi infundibuli open into the infundibular canal between the saccus vasculosus and the third ventricle; while the so-called lobus infundibuli of the lamprey, and I presume also of the Amphibian, is a posterior median prolongation from the saccus vasculosus itself, exactly as is found also in the dog-fish, in the sheep, &c.

We see, then, in the lowest Vertebrate, the presence not only of the cephalic stomach, but also of the mouth and œsophagus, is much more clearly visible than in the higher forms. Another point worthy of note is the shape of the cavity of this median tube; it is always either round or compressed into a horizontal slit, never into a vertical slit; showing that the pressure to which it has been subjected by the growth of the nervous system is not lateral, but is in the dorso-ventral direction, as would naturally follow if the œsophagus of such a form as Limulus were compressed by the growth of the infra-œsophageal ganglia under which it lies.

Embryologically, this tube and its termination form the anterior neuropore, which, as Ahlborn (**4**, p. 333) has pointed out, must be looked for in the neighbourhood of the hypophysis rather than of the epiphysis.

Sect. 3.—The Relation of the Infra-œsophageal and Thoracic Ganglia to the Walls of the Cephalic Stomach.

If the choroid plexuses are the free dorsal walls of the cephalic stomach thrown into folds, it follows that the continuation of the tissue of the choroid plexuses which lines the cavities of the brain must be the ventral portion of the stomach walls. Also the nervous masses which lie on the outer side of the lining epithelium, and form the grey and white matter of the brain, must, on the same theory, be composed of elements arranged in the same way, and of the same intimate structure as the nerve-masses which form the supra-œsophageal, infra-œsophageal, and thoracic ganglia of the Crustacean-like ancestor. Such appears to me to be undoubtedly the case; and although I must wait for the proof of the complete homology of the different parts in the two nervous systems until the completion of this series of papers, yet it is well worth while to point out how strikingly the microscopic appearance of the brain of the Ammocœtes bears out the theory. I will first deal with the epichordal portion of the brain, i.e. with the relations of the infra œsophageal and thoracic ganglia to the stomach walls;

and then in a subsequent section treat of the supra-œsophageal ganglia.

The intimate structure of the brain has been described so fully and well by Ahlborn (3) that it is unnecessary for me to treat of the different parts, section by section, as he has done. I will therefore confine myself to the description of general features as much as possible.

In the whole of the epichordal portion the white and grey substances form two well-defined layers, the former being compact, dense, and fibrous, while the latter is loose, transparent, and composed mainly of cellular elements. Further, the grey matter is itself divided into two very distinct layers in all Ammocœtes which are at all fully grown. The innermost of these two layers is formed by the columnar cells which constitute the lining epithelium of the central cavities; they are separated in the most marked way from the cells of the outermost layer of the grey matter, not only by difference of structure, but also by a distinct band of tissue, which presents an appearance as of a limiting membrane. In sections stained with hæmatoxylin the line of separation between the columnar cells with their dark-staining oval nuclei, and the cells of grey matter with round nuclei which stain less darkly, is very well shown. In fig. 4 I give a section through the commencement of the fourth ventricle, and in fig. 5 a magnified representation of a part of the same section. In fig. 7 I give a magnified section through a portion of the cerebral hemispheres. In both figures we see how clearly the lining layer of columnar cells forms a distinct membrane, which is marked off from the rest of the grey matter by a clear space. This clear space separates the oval nuclei of the lining epithelial cells from the neighbouring mass of cells with round nuclei which form the greater portion of the grey matter; it looks as though the walls of the cells of the internal membrane were distended with some transparent substance. The nature of the contents of these cells is shown by treatment with osmic acid. I have cut a continuous series through the brain of Ammocœtes at different ages after the whole head of the animal has been treated with osmic acid (1 per cent.). The result of such treatment is most striking, as is seen in figs. 6, 11, Pl. XXV, and figs. 12, 13, Pl. XXVI.

We see in all cases that the white matter of the brain stains of a greyish colour, and that the cells and cell nuclei of the grey matter stain also of a greyish colour, their contour being much less well defined than with carmine or hæmatoxylin preparations. The tissue of the cellular layer is less dense than that of the white substance, and, being different also in character, it stands out most conspicuously from the darker coloured white-fibred layer. Further—and this is what is so striking—the whole of this cellular layer is sprinkled over with intensely black fatty granules, which in the younger stages are seen to be more especially congregated in the neighbourhood of the lumen, as represented in figs. 13*a*—13*e*, Pl. XXVI.

These fat-granules are confined to the grey matter; and if a very few black dots are to be seen in the white matter, they are invariably found to indicate the position of one of the nuclei similar to those found in the grey matter. At a later stage, when the Ammocœte is near the time of its transformation, the lumen of the brain-cavity is found to be marked out in the most extraordinary way by this layer of black fat-granules, which now form a dense black lining to the central canal, marking out not only that part of the cavity which is patent, but also the line of closure, wherever the original cavity has become closed by its walls coming into contact. The general appearance is shown in fig. 11, Pl. XXV, which represents a section, through the fourth ventricle, of an Ammocœte which was near the time of transformation. Examination with a higher power (fig. 12, Pl. XXVI) shows that only the cell layers near the lumen are crowded with this dense mass of fat-globules, and that a very distinct limiting line of tissue separates the layer of fat-globules from the deeper lying cells of the grey matter. In among the radially arranged cells of this deeper layer fat-globules are seen scattered about here and there up to the edge of the white-fibred tissue of the medulla.

A comparison of the osmic specimens with those stained by hæmatoxylin shows that the main portion of the fat-globules are situated in the position of the clear space which is so conspicuous in the latter specimens ; in other words, the epithelial layer of the central nervous system, which is, upon my theory, formed by the columnar epithelium of the original stomach, is clearly differentiated from the rest of the grey matter at a certain stage in the development of the Ammocœtes by its cells becoming distended with fat, so that a marked limiting line between these cells and those of the grey matter is brought prominently into view.

This accumulation of fat is due, in my opinion, to fatty degeneration of the old stomach walls, rather than to the absorption of fatty particles, such as yolk-granules, which, I understand, have been found in connection with the central canal of the nervous system in the embryos of various Vertebrates. I have come to this conclusion from the consideration of the following facts. In the first place, these globules which stain so black with osmic acid are really of a fatty nature, because they dissolve away when the slide is placed in turpentine over a water-bath for some time. In the second place, they are due to degenerative changes, and not to absorption of yolk-particles, because they increase in number as the animal grows ; in the youngest specimens which I possess—about 23 mm. long—the globules of fat are sparse and scattered about in the neighbourhood of the lumen, as shown in figs. 13*a*—*e*, Pl. XXVI ; while in the nearly full-grown Ammocœtes osmic specimens show the dense black line of fat at the base of the columnar epithelial cells which is so conspicuous in figs. 6, 8, 11, Pl. XXV. Also I have made an osmic preparation of one of the Ammocœtes (70 mm. long) which had been kept alive in the laboratory over a year without having increased in size. In this specimen the layer of fat-globules is not only present, but also the fatty change is much more marked than in fresh-caught specimens of the same size.

Further, the changes which take place in the cells of the lining epithelium as the animal grows into its adult form are of such a kind as to confirm the view that we are dealing here with true degenerative changes. We find, in the first place, evidence that the formation of the substantia centralis gelatinosa is partly due to the transformation of the cylindrical cells which line the central cavities. In the second place, we find that, in those parts where the lining surfaces come into contact, a process of stitching together of the two surfaces takes place, so as to form a seam, or raphe, as it is called by anatomists. This fusion of the two layers of cylindrical cells so as to form a seam is largely due to the fatty degeneration and breaking down of the cells.

(1) The Formation of the Substantia Centralis Gelatinosa.—In the adult Petromyzon, Ahlborn describes (**3**, p. 247) the changes which take place in the grey substance as we pass from the spinal cord to the medulla oblongata "as consisting in part of an extraordinary increase in the so-called connective tissue or non-nervous elements, so that these, embedded in a thick tangle of the finest fibres, now form a broad zone around the lining epithelium and spread laterally in between the ganglionic elements of the grey substance. They form the greater and compact central part of the grey substance, on the outside of which the ganglion-cells are imposed as a peripheral cortex."

In the adult condition, then, we find that the cellular portion of the grey substance is separated from the lining epithelial layer by a space which is composed of a complicated mass of the finest fibrils, some of which form supporting structures, others are probably nervous. The appearance of a basement membrane to the columnar epithelial cells has disappeared, and these latter cells themselves have altered very much in appearance; they can no longer be called columnar epithelium, for, as Rohon (**6**) has described and figured, and as is seen in fig. 10, Pl. XXV, the basal part of the cell is drawn into a long-tailed process, which is lost in the fibrillar tissue of the substantia centralis gelatinosa; the protoplasm of the cell is very scanty, so that the nucleus fills up the greater part of the body of the cell, and the nuclei themselves are no longer so closely packed together as in the younger stages, so that the appearance of carmine preparations of the brain in the animal after transformation is as is represented in figs. 9, 10, Pl. XXV. This transformation of a columnar cell into a tailed cell which forms part of the supporting tissue in, at all events, the substantia centralis gelatinosa, the shrinking of the cell body, and the disappearance of a marked limiting layer at the base of the columnar epithelial cells, are due mainly to the fatty degeneration already described; so, also, I imagine that the lining cells themselves are no longer so crowded together, because some of them have shrunk to such an extent that they no longer form properly developed cells, but present rather the appearance of strands and shreds of tissue.

In so far, then, as the columnar cells of the old stomach wall assist in forming supporting tissue for the nervous elements of the brain, I am not prepared to say more than that they assist in forming the supporting tissue of the substantia centralis gelatinosa by their elongation into long-tailed processes in consequence of a process of fatty degeneration which they have undergone.

(2) The Formation of the Raphe.—Further, the result of this breaking down of protoplasm into fat brings about not only the formation of a lining epithelium with long processes directed into the nervous matter, but also causes a raggedness in that part of the cells which is turned towards the lumen, so that wherever the cavity is closed by the coming together of its walls, as is the case in the medulla oblongata, the original lumen is bridged over by a ragged reticulum, the interlacement of the fibres of which tend to permanently close the lumen; in other words, owing to the degenerative changes going on, the walls of the original cavity become, so to say, stitched together in the middle line, and in this way the raphe, which is so characteristic of the epichordal portion of the brain, is formed.

It is especially instructive to notice that throughout the medulla oblongata the closed tube which forms the raphe, and the limits of which are clearly marked out by the layers of blackened fat-cells, extends close to the ventral surface, so that the nerve-matter with its groups of ganglion-cells giving origin to the segmental cranial nerves is situated on each side of, and ventrally to, the original large bag; in other words, a small ventral portion of the cephalic stomach has been nipped in this region by the growth of the two laterally situated masses formed by the upper ganglia of the ventral chain. By this lateral compression the original cavity has become first converted into a vertical slit, and then by the fatty degeneration of its cell-walls into an interlacement of fibres, known in anatomy by the name of the raphe.

This formation of a raphe or seam by the lateral compression of two nerve-masses can be followed up to the infundibulum; in other words, not only the upper ganglia of the ventral chain, but also the infra-œsophageal ganglia, have compressed a small ventral portion of the cephalic stomach, thus forming the raphe of the aqueduct. In this region, however (fig. 3, Pl. XXV, r. aq.), the raphe no longer extends to the ventral surface of the brain, but, on the contrary, the ventral surface is occupied by a tube, the sides of which have been compressed as already mentioned, not so as to form a vertical slit, but, on the contrary, so as to form a horizontal slit. In other words, the growth dorsalwards of the bilateral infra-œsophageal mass has nipped and compressed a ventral fold of the cephalic stomach, with the result of forming a vertical slit, which ultimately becomes the raphe of the aqueduct; and at the same time the increase in size of the whole infra-œsophageal nervous mass has compressed (as already explained) the œsophagus which lies between it and the wall of the cranial cavity, with the natural result of causing the lumen of the œsophageal tube to take the form of a horizontal and not a vertical slit. Also we see that the presence and position of the horizontally compressed œsophagus in the infundibular projection is the reason why the raphe comes to the ventral surface in the middle line only in the epichordal portion of the brain.

The appearance, then, of an interlacement of fibres in the ventral middle line of the epichordal portion of the brain of all Vertebrates, which is known by the name of the raphe, is due to the breaking down of the two apposed layers of cylindrical epithelial cells which originally lined the central cavity in this position. Doubtless the closeness of the apposition of these cells by which the lumen was obliterated was due very largely at first to the interlacement of the cilia with which these cells are provided, and not simply to commencing degenerative changes.

With respect to the question whether the lining cells of the cavities of the central nervous system are ciliated or not, the literature of the subject shows that a considerable discrepancy of opinion exists. In a recent paper from Johns Hopkins University, Wightman (**8**) gives a list of observers for and against the occurrence of cilia in this region, and concludes from his own experiments that cilia are undoubtedly present in the ventricles of the frog. As to Petromyzon, Ahlborn (**3**, p. 249), speaking of the transition of the central canal of the cord into the cavity of the fourth ventricle, says that "the epithelium of the central canal, where it passes into the ependyma of the brain-cavities, undergoes a considerable elongation of its cells; the cilia are conspicuous to the view, and one can easily recognise a long oval nucleus in the body of the cell, as well as a tailed prolongation which passes deep into the brain substance." Rohon (**6**) figures isolated cells of P. marinus with cilia attached; and Owsjannikow (**7**) describes the epithelium in the neighbourhood of the optic thalami as composed of cells, each of which bears a single cilium.

My preparations, especially those stained with osmic acid, present appearances as of ragged, irregular projections protruding into the lumen of the cavity; in some places these appeared to resemble a close-set fringe of cilia, in others they presented single projections or a loose sort of network. Such appearances might be caused by a breaking down of the edge of the cells turned towards the lumen, or they might be due to a ciliated edge, the cilia of which were more or less matted together and cut at different angles, as well as mixed up with the shreds of the coagulum of the albuminous fluid which the central cavities contain.

Mr. Hardy kindly undertook to make specimens for the express purpose of solving this question, and found conclusively that cilia are present in the cells lining the brain-cavities, and also on those of the choroid plexuses. The brain-cavities were opened, and a small portion of the lining epithelium, as well as of the choroid plexuses, examined in normal saline solution in the living condition; in various places the action of the cilia upon small fatty particles and even red blood-corpuscles was very clearly visible. Other portions were taken, washed out with normal saline solution, and exposed to the action of osmic vapour; sections then showed clearly a fringe of short cilia standing out from the lining epithelial cells.

So far, in considering the relations between the cephalic stomach and the infra-œsophageal and thoracic ganglia, I have dealt mainly with the changes of the stomach wall in consequence of its altered function, and have merely incidentally mentioned that the compression of a ventral fold of the stomach by which the raphe is formed was due to the growth of the nervous masses of the fused infra-œsophageal and thoracic ganglia; I will now shortly consider the structure of that portion of the brain of the Ammocœtes which I look upon as formed by these ganglia: at the same time I feel that I cannot, as yet, compare the structure of the two nervous systems in such minute detail as I feel convinced further investigation will enable me to do. I desire at present merely to point out that there is nothing in the structure and arrangement of the nervous elements in the epichordal portion of the brain which is inconsistent with the supposition that we have here the fused infra-œsophageal and thoracic ganglia of the Crustacean-like ancestor.

The structure of the Arthropod nervous system may be described as consisting of nervous elements, held together by a framework of supporting tissue, the nervous elements consisting of—(1) nerve-fibres which connect the different ganglia together and form the outgoing nerves; (2) groups of large pear-shaped ganglion-cells, some of which have relation to the outgoing metameric nerves; (3) masses of closely packed small cells which are presumably nervous in nature; and (4) a peculiar mass of fine nerve-fibrils, known by the name of the reticulated substance, or "Punctsubstanz." These two latter elements increase in amount as we approach the supra-œsophageal ganglia. Corresponding to these separate elements we find in the epichordal portion of the brain of the Ammocœtes externally—(1) the white substance composed of nerve-fibres; internally the grey substance composed of (2) groups of large ganglion-cells, which are partly the nuclei of the segmental cranial nerves, and partly are connected with the large Müllerian fibres; (3) a thick layer of closely packed small cells in which the groups of larger cells are embedded (see figs. 12, 14, Pl. XXVI). These small cells are arranged like clusters of berries, and are called therefore by Ahlborn "beerenförmige Zellen;" their numbers increase enormously, as he points out, when the spinal cord passes into the medulla oblongata. (4) Internally, of all in the adult condition, a thick layer of very fine fibrils, interlacing in all directions, which forms the substantia centralis gelatinosa, and which, as already mentioned, increases markedly as we pass from the spinal cord into the medulla oblongata.

If, as I believe, these four structures are the same as in the nervous system of the Crustacean, then it follows that the supporting tissue of the Ammocœtes' brain is derived from the supporting tissue of the Crustacean nervous system mainly, and only to the slight extent already mentioned, from the modification of the walls of the old stomach. In the substantia centralis gelatinosa we have, on the view put forward, the meeting-place of so many different structures; here we must find the remains of the connective-tissue elements surrounding the stomach, and those which surround the nervous system; here are the modified extremities of the columnar stomach-cells as already mentioned; here also is that whorl of fine fibrils partly nervous (corresponding to Gerlach's plexus), partly supporting, known by the name of the reticulated substance, or "Punctsubstanz;" and it is very suggestive to read Ahlborn's description of the relation between the masses of small berry-like cells, and the reticulated tissue of the subepithelial spongiosa. Speaking of the grouping of the small cells in the central grey matter, he says (**3**, p. 253) they can be observed especially well about the middle of the aquæduct where they are not mixed up with cells of other kinds, and where they are arranged in regular rows, hanging together like the berries on a grape-vine. He goes on to say, "Die Spitzen der Zellen sind nach aussen gewandt, und die feinen daraus hervorziehenden Fädchen treten in die zwischen den Reihen befindlichen engen Zwischenräume, wo sie sich mit Fortsätzen aus der benachbarten Zellreihe zu vereinigen scheinen. Querschnitte (Osmium) Zeigen daher an dieser Stelle Bilder, als seien die kleinen Zellen wie die Beeren einer Traube mit einander verbunden. Die Traubenspindel ist hier jedoch meist kein einfacher Faden oder ein glattes, gleichsam durch die Komposition der Beerenstich entstandenes feines Bündelchen, sondern sie zeigt die Eigenschaften der peripherischen Neuroglia (oder der subepithelialen Spongiosa), mit welcher sie unmittelbar zusammenhängt; nur an besonders günstigen Stellen kann man beobachten, dass sich aus den Zellfortsätzen zunächst ein feiner Faden bildet, der dann in ventraler Richtung gegen die Spongiosa zieht und sich in derselben aufzulösen scheint."

Seeing, then, that the whorl of fine fibrils which form the substantia gelatinosa centralis (or sub-epithelial spongiosa) is known to consist, in the higher Vertebrates, largely of Gerlach's plexus of fine nerve-fibrils, Ahlborn's description is wonderfully like a description of the relation between the small cells supposed to be nervous, and the reticulated tissue (Punctsubstanz) of the nervous system of an Arthropod.

SECT. 4.—The Relation of the Ventral Ganglia to the Walls of the Intestine.

In the region of the spinal cord where, according to my theory, the nervous matter of the ventral chain of ganglia has surrounded the straight intestine of the Crustacean-like animal from which the Vertebrates arose, we find a decided difference of structure from what occurs in the higher parts of the central nervous system. Here the central grey matter is very much subordinated to the surrounding white matter. The white matter is remarkably free from any scattered nuclei in it, and contains a large number of giant nerve-fibres which run longitudinally. The grey matter contains but little of the spongy reticulated substance, and very few of the small nerve-cells with circular nuclei as compared with the higher parts of the central nervous system.

It is significant, in connection with the meaning which I ascribe to these small nerve-cells, to find that Ahlborn, after criticising the view ascribed to Freud, that fibres of the posterior roots are in connection with certain large cells, speaks as follows (**3**, p. 242): "Dagegen glaube ich nicht mehr bezweifeln zu dürfen, dass die dorsalen Nervenwurzeln wenigstens zum Theil thatsächlich ihren Ursprung in den 'kleineren Zellen' Reissner's nehmen." In addition to these small nerve-cells, Reissner (**9**) describes two groups of large cells—(1) an inner group situated bilaterally close to the central canal on the dorsal side, and (2) an outer group situated near the extremity of the elongated band of grey matter. This latter group is recognised by Ahlborn and others as corresponding to anterior horn-cells. The inner group were the "Hinterzellen," supposed to be connected with the fibres of the posterior roots. Ahlborn, however, can find no trace of such connection, and he cannot say what their connections are; all he finds on sagittal sections are (**3**, p. 242) "kurze, starke, nach vorn (nasalwärts) gerichtete Zellfortsätze und eben solche feinere, die sich sehr schnell in rein dorso-ventraler Richtung (nach oben) auflösten."

In addition to these three kinds of cells, which are all nervous, a fourth kind is found which are recognised by all observers as non-nervous. These cells are described by Ahlborn as lying thickly crowded near the central canal, and diffused over the whole of the grey matter. He then goes on to say

(**3**, p. 244), "Sehr auffallend ist ihre grosse Ahnlichkeit mit den Epithelzellen des centralkanals die sich von ihnen nur durch die oberflächliche Lage unterscheiden." Although he looks upon it as highly probable that they are derived directly from the epithelium surrounding the central canal, he considers that the proof must be left to embryological investigation.

Shipley (**10**) does not deal with this point. Scott (**11**, p. 274), however, describes how the shape of the spinal cord is at first like that of other Vertebrates with a large central canal, and how a portion of the canal closes up when the cord by its elongation forms its well-known flattened ribbon-like shape. He does not, however, attempt to trace the fate of the cells of this closed-off portion. In connection with this paper of Scott I may mention that he still holds to the belief that the epithelium of the central canal is formed by the epidermic layer of epiblast passing down into the nervous layer, notwithstanding the criticism of Shipley. Naturally, as far as I am concerned, Scott's explanation of the appearances presented by his sections is entirely in accord with my theory, that this epithelium lining represents the original intestinal wall. Although these observations of Scott require extension, they make it possible, if not probable, that the diminution of the central canal gives rise to the formation of groups of outlying elements, derived from its epithelial walls in a similar manner to that noticed by Corning (**12**), who describes the substantia gelatinosa Rolando as formed by a lateral and nipped-off fold of the original embryonic tube. A still further piece of evidence in favour of considering these cells to be derived from the epithelium of the central canal, i.e. from the walls of the old intestine, is afforded by osmic specimens, which show the presence of fat-globules in the epithelial cells of the central canal, and the extension of those fat-globules in two lateral lines, corresponding exactly to the position of these non-nervous cells.

Here, then, if anywhere, we find a tissue corresponding to the myelospongium of His (**13**), and it is possible that in the spinal cord a system of supporting elements derived from the walls of the old intestine, as I have suggested in my former papers, may be formed after the fashion described by His. At the same time I agree with Ahlborn that we cannot look upon the epithelial layer of the central canal as many-layered until the origin of these small cells has been demonstrated embryologically. Certainly, as far as can be judged from His's (**14**, fig. 30) figure of a section of the cord of a larva of Petromyzon fluviatilis 6 mm. long, the epithelial layer at that age is only one cell thick, and also from his figure and description there is no sign of any supporting tissue elements (myelospongium) outside the layer of epithelium, but only of nervous elements, so that any formation of supporting structures from this epithelium layer must take place at a later stage than in an Ammocœtes of **6** mm. long. In Scott's description of the closure of the canal his figures are drawn from larvæ of 7 mm. in length and upwards.

Sect. 5.—The Cephalic Liver and its Duct.

We have already noticed how clearly the fatty degeneration of the columnar epithelium cells which line the cavities of the brain enables us to trace out the original limits of those cavities even when the lumen has been closed by the approximation of their walls, as in the formation of the raphe. In the same way any diverticula from the main cavity will be disclosed by the black staining of the fat-globules in its walls, even if its lumen has entirely disappeared.

In the medulla oblongata the vertical slit which forms the raphe comes close to the surface on the ventral side (figs. 13*a*, 14, Pl. XXVI); on the other hand, in the region of the aqueduct, as seen in fig. 3, Pl. XXV, the raphe is short, and only extends a short distance on the ventral side. Now the series of sections show that the most ventral portion of the fold which forms the raphe ceases abruptly at the projection of the conus post-commissuralis, its termination coinciding with the position of the so-called ganglion interpedunculare.

Sections through this region show indications of a separation of the raphe into two parts—a ventral one which terminates in the conus post-commissuralis, and a dorsal one which continues without interruption as the raphe of the aqueduct. The appearance (fig. 11, Pl. XXV) is as though the ventral part was formed from a separate small tube lying in the middle line ventrally, while the dorsal part was formed by the compression of the ventral portion of the large cephalic stomach as already mentioned. In some cases the separation of this ventral tube from the rest of the raphe is much more conspicuous than in others, and in one instance it was remarkably evident.

In figs. 13*a*—13*e*, Pl. XXVI, I give a selection out of the series of sections, to show the formation of this tube. The Ammocœtes from which these sections were cut was by no means fully grown ; its length was not measured, but judging from the size of the sections I should estimate it somewhere about 40 mm. in length. The sections are all through the epichordal portion of the brain, and, as is seen by the diminishing size of the notochord, are numbered in the headwards direction.

In the first section of the series, fig. 13*a*, the raphe of the epichordal portion of the brain is seen to extend close to the ventral surface, and we see from the shape of the section the commencement of a constriction on each side of the external surface of the white matter; this constriction marks the beginning of the separation from the rest of the brain of that portion of nervous matter which forms the ventral projection known as the conus post-commissuralis.

In the succeeding sections we see how this indentation becomes deeper and deeper, until at last, as in figs. 13*d*, 13*e*, this projecting mass is entirely separated from the rest of the brain by the strongly pigmented tissue which surrounds the brain, and marks out most clearly the extent of the lateral indentations. Further, the sections show clearly that this portion, which is thus cut off, contains the continuation of the ventral portion of the raphe in the shape of a tube whose walls are marked out with the usual fat-globules, and whose lumen has disappeared in consequence of the closure of its walls by the lateral compression of the nervous material.

On the one hand, then, this particular specimen shows what is only indicated in others, that the remarkable ventral projection known by the name of the conus post-commissuralis is due to the growth of nervous material around a ventral median tube, which arises from the cephalic stomach near its pyloric orifice; on the other hand, it shows that the closure of this tube has taken place in such a manner as to form a vertical slit by the compression of the nervous material on each side, just as in the case of the formation of the raphe, and that the tube comes to the surface of the brain in a very similar manner to the tube which forms the old œsophagus already described in a former section. In both cases the structure of the actual end of the tube is a reticulum filled with transparent material, so that in the fresh condition the end of the conus post-commissuralis and the infundibular projection are so transparent as to allow the central cavity to be dimly seen through their walls.

The nervous material immediately around the raphe is similar to that surrounding the ependyma, and is composed therefore mainly of the small berry-like cells already spoken of; some of these cells continue onwards around the ependyma of this ventral tube or duct, as it may be called, and so in combination with the broken-down epithelium of the duct walls gives rise to the structure known as the ganglion interpedunculare. The connection of the ganglion interpedunculare with the cells of the central grey matter is noticed by Ahlborn, who says (3, p. 254) "es ist nicht zu bezweifeln, dass die Zellen des Ganglion interpedunculare thatsächlich aus dem centralen Bodengrau hervorgegangen sind."

We see, then, that the extraordinary shape of the brain on the ventral side, with its two projections in front of and behind the large ventral constriction, is due to the presence in the middle line of two tubes, both of which pass from the central cavity to the surface: the one tube, compressed to form a horizontal slit, leads out of the third ventricle, i. e. out of the anterior end of the cephalic stomach, and is directed tailwards, terminating at the commencement of the notochord; this forms the remnant of the original œsophagus. The other tube, compressed to form a vertical slit, leads out of the fourth ventricle, i. e. out of the pyloric end of the cephalic stomach, and is directed headwards, terminating also near the commencement of the notochord. This latter tube is in my opinion the remnant of a single median duct of the cephalic liver, which in the Crustacean ancestor opened into the pyloric end of the stomach on the ventral side. In the diagram already referred to (Pl. XXVIII, fig. 29) I have indicated how the liver-duct and œsophagus from the Crustacean cephalic stomach would form the projections known as the conus post-commissuralis and the infundibular projections. If this interpretation is true, we ought to find evidence of the vestiges of the large cephalic liver in connection with the termination of this duct.

In the description of the external surface of the brain I have already described how the brain is covered over with a glandular-looking organ containing a large amount of pigment arranged in irregular clumps and lines, and I have described also the general arrangement of this tissue on the brain surface. It forms what is called by Ahlborn the "arachnoidale Füllgewebe," and is looked upon by him and other observers, e. g. Sagemehl (**15**), as a peculiar kind of connective tissue somewhat allied to fat tissue.

Peculiar the tissue undoubtedly is, but that it bears the slightest resemblance to any form of connective tissue, whether fat-bearing or otherwise, I entirely deny. It presents the exact appearance of a compact mass of large gland-cells belonging to some such organ as a liver, each cell containing a central nucleus surrounded by the remains of the protoplasmic cell-contents. These cells are pressed closely to each other in all directions, so as to form a bilaterally symmetrical organ as described on p. 384, the glandular nature of which is in my opinion fairly evident. The arrangement of the cells is seen in fig. 16, Pl. XXVI, which represents a magnified portion of an osmic preparation from the series represented in figs.

6, 8, Pl. XXV, and *20a—20d*, Pl. XXVII. The body of each cell contains a homogeneous semi-fluid substance, which stains but slightly with osmic acid. In the centre of this is seen in some cells an irregular brownish mass, in others a more clearly defined large round nucleus, surrounded with some of the same irregular brown granular-looking débris. In other cells nothing is seen but the clear slightly-staining fluid. These appearances evidently mean that the cells composing this substance have so much thickness that some sections pass through the nucleus; others through the scanty granular strands of material surrounding the nucleus, which represent the remains of the protoplasm of the cell; and others still nearer the edge of the cell, where nothing but clear fluid is to be found. The same appearances are seen in whatever direction the section is made, showing that these cells are solid polygonal bodies pressed together in all directions, without any sign of being in connection with specially arranged connective-tissue elements either in one direction or the other. Again, that they have no connection with adipose tissue is evident, for in the first place they do not stain like fat. A small fat-globule may be seen here and there, but that is all. All the deep blackness seen in the osmic preparations is due to the presence of pigment in between the cells. In the second place, the nucleus lies in its natural position in the centre of the cell, and the semi-fluid contents lie simply in between the meshes of the degenerated-looking protoplasmic material which surrounds the nucleus and spreads thence towards the periphery. Again, staining with hæmatoxylin or carmine gives appearances as drawn in fig. 15, Pl. XXVI. Here, again, we see that the nucleus stains but poorly, and the staining material in the cell consists of a broken-down network which starts from the nucleus and forms scanty strands which pass towards the periphery. In fact, the structure and massing of this "arachnoidale Füllgewebe" is precisely what one would expect if it represented the degenerated remains of the cephalic liver of the Crustacean-like ancestor of the Ammocœtes.

I have already described its general arrangement on the surface of the brain, and I will now briefly point out how the examination of sections still more clearly defines the limits of this tissue.

A series of sections, both transverse and horizontal, through the whole brain show that it forms two lateral masses which do not spread dorsally beyond the choroid plexuses, so that the latter, with the blood space surrounding them, are pressed against the roof of the cranial cavity; anteriorly at the termination of the choroid plexus ii it reaches to the dorsal roof, and fills the spaces round the pineal eye and ganglion habenulæ, as seen in figs. 20*a*—20*d*, Pl. XXVII, spreading over and in front of the cerebral lobes, even to the space between the two olfactory nerves, as in fig. 6, Pl. XXV. On the ventral side it does not exist in the infundibular region, for here the pituitary body and the infundibular projection come into close contact with the floor of the cranial cavity. In the region of the medulla oblongata it is at first very scanty on the ventral side, but thickens as the termination of the conus post-commissuralis is reached, until at last in the region of the large ventral commissure it attains a considerable thickness, so that here, and here only on the ventral side is there anything in the nature of a starting-point, from which it spreads so as to form two symmetrically placed bilateral organs; at the junction of the medulla and the cord the cells pass round to the dorsal side, but here (fig. 4, Pl. XXV) they are no longer compact and thick, but isolated and scattered. We are here clearly on the fringe of the compact organ, isolated cells from which are found far down the spinal canal.

At the termination of the conus post-commissuralis, in the deep ventral fissure where alone anything approaching to a hilus is to be found, we see, as in fig. 13*e*, Pl. XXVI, how the lines of pigment in between these large cells are massed together; and we see how the termination of the tube which I have spoken of as the liver-duct is lost in among this pigment mass at the very place where it ought to come to the surface if the cells of this so-called arachnoidal tissue are in reality the cells of the so-called liver of the Crustacean-like ancestor, and this duct is the liver-duct opening into the pyloric end of the cephalic stomach. Further, as I have mentioned in my paper in 'Brain' (2), it is absolutely necessary to explain why so large a portion of the cavity of the brain-case is occupied with this peculiar tissue in the lowest Vertebrates only. The one explanation which is offered, as far as I know, is no explanation at all, viz. that the fat-tissue fills up the space between brain and cranial walls in order to support and steady a brain which is too small for its case. The natural rejoinder to this is, according to modern views of evolution, why is the brain too small for its case? and why also is not the spinal cord also supported by the same kind of tissue?—for here, as well as in the brain, we find the cavity in which the cord lies is very much larger than the cord itself; and yet, apart from a few large cells, the only solid structures which are found in the space around the cord are irregular strands of connective tissue, as seen in fig. 19, Pl. XXVII, formed, according to Ahlborn, of elastic fibres and "Schleimzellen."

In accordance with evolutionary ideas, the natural answer to this question is that this peculiar tissue, which is different from any other, the cells of which appear degenerated, which contains lines of pigment between its cells, which is found only in the lowest Vertebrates, and is gradually pushed out of existence in the higher classes as the brain increases in size, fills up the space around the brain because it represents some pre-existing organ which was of importance to the animal from which the Vertebrate sprang. Such an organ is clearly the cephalic liver of the Crustacean-like ancestor—a conclusion which is in perfect harmony with not only the rest of the arguments in this paper, but also with those which I hope to bring forward in the series of papers following this one. As to the tissue round the spinal cord, it is natural that the cells of the liver should not be found in any great quantity there, and it is possible that the loose connective tissue which is there found is the remnant of the connective and muscular tissues which originally were situated in the neighbourhood of the intestine, along the length of the body of the Crustacean.

One of the most striking characteristics of this degenerated liver-tissue is the presence of so much pigment in between its cells and lining the surface of the brain. What, then, is the meaning of this pigment?

SECT. 6.—The Formation of Pigment.

The almost universal source of pigment in the Vertebrate kingdom is the colouring matter of the blood; we must, therefore, look especially to the destruction of red blood-corpuscles in order to account for the presence of pigment in the majority of instances.

Recently a paper has appeared by Hunter (**16**), who has been occupied for a long time in the investigation of the nature of the destruction of the red blood-corpuscles. He concludes that pigment is formed from the hæmoglobin of the blood-corpuscles in two distinct ways, called by him respectively Active and Passive destruction, and defined as follows:

Active destruction is that form of disintegration of the red blood-corpuscles where the hæmoglobin is liberated and escapes into the plasma; it is the change in the blood-corpuscles which is caused by the action of water, various salts, &c. The chief evidences of this active destruction are—(1) the formation of bile-pigments by the liver, to which organ the hæmoglobin thus set free is mainly carried; (2) to a secondary and altogether subsidiary extent in health, the formation of blood-pigment.

The chief characters of this blood-pigment are the small uniform size and spherical shape of its individual particles. The size of the red corpuscles have no influence on the size of the pigment particles resulting from active destruction. It is the same in mammals as in birds or amphibians. The pigment is formed from free hæmoglobin.

Passive destruction of the blood-corpuscles, on the other hand, is a slow and gradual decay of the red blood-corpuscles. The hæmoglobin remains in the corpuscle to the last, and becomes gradually converted into a globule of inert blood-pigment.

It is the mode of death of the red corpuscles which would occur were the blood subjected to no other changes than those involved in carrying on its respiratory functions. This change can be best studied in extravasated blood.

The chief evidence of passive destruction is the presence of pigment, and in health the chief organs in which this evidence is to be found are the spleen and bone marrow. The chief characters of this pigment are the large and varying size of the pigment particles and their irregular shape. The larger the red corpuscles of the animal the larger are the pigment particles which result from their passive destruction. He attaches special importance to this difference in the character of the pigment in the two varieties of blood destruction. From it alone he is able to say in any particular case whether the pigment has been formed in situ from red corpuscles, or from free hæmoglobin carried thither in solution. When once formed this blood-pigment is remarkably resistent to the action of reagents. It can be recognised long after the death of the original blood-corpuscles. Hence the amount of pigment found in the organs specified affords a most reliable indication as to the amount of passive destruction that has occurred.

Active destruction depends on certain changes in the blood, most marked during digestion, and occurring chiefly within the blood of the portal system. The spleen, however, is par excellence the seat of active blood destruction. Active destruction in this organ is specially favoured by certain structural features, viz. (1) slowness of circulation, (2) closeness of relation of the cells of the pulp to the blood flowing through it, (3) capacity for accommodating large and varying quantities of blood.

The same features favour also the seizure of red corpuscles in process of becoming effete by slow and gradual decay. The spleen is thus also the great seat of passive destruction, and is hence the chief seat of pigment accumulation resulting from this process. Next to the spleen the red bone marrow is the most important seat of passive destruction, the structural features here being closely similar to those in the spleen.

The observations of Hunter, then, point to the conclusion that in health wherever the blood tends to stagnate the conditions are most favorable for passive destruction, and therefore for the accumulation of pigment. As he shows, all active cells in immediate relation to the stagnating blood play a part in converting the hæmoglobin of the original blood-corpuscles into blood-pigment. Around extravasated blood it is the cells of leucocytes and of connective-tissue nature which carry on this process ; in the spleen and bone marrow the still more active splenic and marrow cells.

The same conditions as are present chiefly in the spleen and red bone marrow in the case of the higher Vertebrates occur freely in different parts of the body in the Ammocœtes owing to the peculiarities of its circulation, for the characteristic of the vascular system of the Ammocœtes, especially before transformation, is the abundance of large blood spaces in different parts of the body. These blood spaces have been somewhat strangely described as lymph spaces containing red blood-corpuscles. In them, as in the spleen pulp, the blood circulates slowly and with difficulty. In addition, important and extensive changes in the arrangement of various parts of the body take place during metamorphosis. In fact, all the conditions necessary for passive blood destruction are present in the most pronounced manner.

The examination of the Ammocœtes by dissection and sections shows that masses of pigment are found in very definite arrangements in many different regions of the body. Apart from such places as the eye and the skin, we find pigment most markedly in connection with the branchiæ and with the pronephros. In both these cases the pigment is found in close connection with the vascular arrangements. Thus the tubules of the pronephros of the Ammocœtes are enclosed in a large lacunar blood space, the walls and septa of which are strongly pigmented. In the branchial regions masses of pigment are found forming a coarse network, the meshes of which are full of blood-corpuscles, so that the pigment here, just as in the pronephros, is situated in the walls of the vascular system. The heart itself and the large aorta springing from it are absolutely free from pigment. It is the walls of the large venous spaces, where the blood flow is slow, that are so markedly pigmented.

Further, in the Ammocœtes, especially near the time of transformation, we find evidence of changes going on in the red blood-corpuscles, remarkably like those which Hunter distinguishes as passive destruction. Here and there, in the neighbourhood of the layers of pigment which have been already formed, especially in the region of the upper branchiæ, we see red corpuscles, the nucleus of which does not present the usual finely granular appearance, but, on the contrary, is more or less hidden by large strongly refracting globules of a yellowish-brown tint: in cases where these globules are numerous the blood-corpuscle appears to carry upon its surface an irregular-shaped mass of dark brown, almost black pigment, which presents the same appearance as the thinner, more translucent portions of the neighbouring pigment masses. Such appearances point strongly to the conclusion that the pigment in the branchiæ and other places is due to the accumulation in these places of blood-corpuscles which have undergone passive destruction similar to the formation of pigment in the spleen.

This conclusion is rendered certain by the examination of individuals in which metamorphosis has been delayed. In September, 1888, I brought with me from Hind Head, in Surrey, a large number of Ammocœtes of different sizes, varying in length from about 25 to 130 mm. These were placed in a basin containing sand and weed, brought from the stream in which they were living, and the water in the basin was renewed occasionally. A considerable number of these were killed soon after their arrival at Cambridge; about twenty, however, were left alive, and have continued to live in the sand up to the present time, October, 1889, i.e. more than a year after they were caught. They show no sign of transformation, and have apparently not grown in length, some being still as small as 28 mm., others from 40 to 70 mm. I have made series of sections of these Ammocœtes through different regions of the body, the animal having been stained and prepared for section-cutting as a whole, so that all parts of it had undergone the same preliminary treatment. These sections show that the heart and large blood-vessels in connection with it are full of blood-corpuscles of normal character, amidst which it requires careful search to find a single pigment-bearing corpuscle; while, on the other hand, the blood spaces of the branchiæ, especially the upper ones, are so loaded with corpuscles bearing masses of pigment of all shapes and sizes as to give the appearance of an injection of a pigmented mass into the branchial vessels.

In fig. 18 I have drawn a group of corpuscles as they appeared in a section of one of the upper branchial blood spaces. *a* and *b* are normal blood-corpuscles ; in the others the nucleus is more or less concealed by the dark-yellow brown irregular clumps of pigment: the colour is not shown in the figure.

These pigmented blood-corpuscles are found lying singly or massed together, especially in the upper branchial vascular spaces, often in close contiguity to the pigmented walls of these spaces ; and it is frequently difficult to decide whether a mass of pigment belongs to a blood-corpuscle or to the pigmented walls.

Further, the comparison of these sections with those of a fresh-caught Ammocœtes of the same size shows that the former is much more pigmented than the latter, and that the increase of pigment is due to the accumulation of pigment in those places where pigment is always found, viz. in the blood spaces of the branchiæ, and other places where stagnation is liable to occur. The result, then, of preventing metamorphosis by placing the animal in a condition of impaired nutrition—a condition which, according to Hunter, is the one most favorable to passive blood destruction in health—is to increase largely the passive destruction of the red blood-corpuscles in those places where the blood is liable to stagnate, and concurrently to increase the deposition of pigment in those places. This thickening of the pigmented walls and septa of the blood spaces naturally must lead to a diminution of their size, and so to a quickening of the current through them, and consequent diminution of the tendency to stagnation. In addition to this possible cause of narrowing of the bed of the stream another factor in all probability comes into play, viz. the formation of fibrous tissue around and amidst the pigment masses. The presence of pigment in the walls and trabeculæ of the blood spaces is due to the circumstance already noted, that all active cells seize on inert pigment with which they are brought into relation. If, as may sometimes happen, there is entire stagnation of a mass of these effete blood-corpuscles, then the changes in this mass will correspond in all respects to those met with in the organisation of a thrombus, viz. the penetration and final replacement of the blood mass by cells of connective-tissue nature; the subsequent contraction of this newly formed tissue, just as in the formation of a cicatrix would convert the original space which contained the blood-corpuscles into a strand of pigmented connective tissue.

The process which is going on seems to me to be somewhat as follows:—The effete blood-corpuscles heavy with pigment do not circulate with the general circulating normal blood-corpuscles, for the heart and ventral aorta are free from them. They remain stranded in those parts where the current is slow, and where, owing to the absence of fine capillary channels, eddies and back currents must take place. In such places they are apt to congregate and remain stationary against the walls and septa of these spaces, thus forming a thrombus of dead pigment-bearing corpuscles. By the growth and spreading inwards of the connective tissue of the walls and septa this thrombus becomes part and parcel of the walls against which it is formed, in the same way as a thrombus becomes organised in any other Vertebrate. With this organisation constriction occurs, so that the original blood space is narrowed or obliterated, and at the same time its walls become more and more full of pigment-granules. These pigment-granules are partly taken up by the cells of the connective tissue, but many are doubtless lying free in the interspaces of the fibrous bundles between the time of the death of the blood-corpuscles which contain them, and their absorption into the cells of the connective tissue. Ultimately the formation of regularly arranged pigmented connective tissue is complete, and in the adult animal the circulation has become so modified that such marked stagnation no longer occurs.

In the whole life of the animal, as far as I have had an opportunity of judging at present, the time when most pigment is accumulated in the walls of the blood spaces of the branchial and other regions is just before the time of transformation. In the embryo, as shown by Shipley's specimens, very little pigment is to be found. In the adult, again, the pigment in the internal regions is much less apparent than in the full-grown Ammocœtes; and indeed it seems to me probable that not only are the pigment-granules arranged in an orderly manner in the connective-tissue cells after the metamorphosis of the animal, but also that a considerable proportion is got rid of, perhaps after the fashion described by Eisig (**17**), by excretion into the skin.

This process of the formation of pigment, as I have imagined it to be taking place in the Ammocœtes, is in strict harmony with what is known to occur in the liver of the frog, and in pathological cases of cirrhosis of liver accompanied by pigmentation. Thus Hunter describes the occurrence of cirrhosis in the liver of a rabbit as a result of the presence of pigment. In one experiment he found a form of perilobular cirrhosis, some of the lobules being entirely replaced by small-celled connective tissue. In each case the seat of formation of this tissue corresponded with the presence of larger or smaller heaps of pigment. In a case of cirrhosis in man he found similar appearances, and also in the liver of pigeons. The large size of the red corpuscles in birds renders their arrest within the capillaries of the liver very easy after they have undergone passive destruction, and become converted into rigid pigment masses. Wherever they become arrested a proliferation of the cells of the capillary walls takes place, and the small clumps soon become surrounded by a small-celled growth of connective-tissue cells. He concludes that in all such cases the pigment is in the position of a foreign body, and acts as a mild irritant to the surrounding connective-tissue cells, with the result of increased proliferation and increased fibrous-tissue formation.

I conclude, then, that in the Ammocœtes the formation of pigment which is so characteristic of this animal is due to the large amount of spleen-like tissue in this animal in the spaces of which passive destruction of blood-corpuscles occurs, with the result of the deposition of pigment in the walls of these spaces, and the diminution in the size of the spaces themselves. Conversely I conclude that lines and irregular masses of pigment in any locality indicate the existence of former spleen-like tissue—in other words, are evidence of the position of obliterated lacunar blood spaces.

If we now revert to our original question—what is the meaning of the pigment found so markedly in among the degenerate cells surrounding the brain ? the answer would be : These lines and collections of pigment are the remains of the blood channels which supplied the cells of the old cephalic liver with blood. With the loss of function of this organ these blood channels have become filled more or less with pigment-bearing corpuscles, thus obliterating the greater part of the original vascular space, certain blood-vessels only being left in the tissue itself, as shown in fig. 2, Pl. XXV (*b. v.*). The remnant of the blood space surrounding this tissue is still to be seen in the shape of the so-called venous sinus found both on the dorsal and ventral sides of the brain. The dorsal sinus is figured in figs. 9, 14, and is a large blood space which surrounds the choroidal plexus, and separates the two lateral masses of arachnoidal tissue from each other. The pigment in between the folds of the choroidal plexus (figs. 9, 14), which Ahlborn considers to represent included arachnoidal tissue, is, to my mind, much more probably due to the passive destruction of the blood-corpuscles of this sinus ; and the vessel described by him in the extremity of the pigmented folds is the remnant of the original blood space. This sinus itself is perhaps homologous with the longitudinal sinus of the higher Vertebrates.

On the ventral side, in the region of the medulla oblongata, the obliteration of the original blood space by the deposition of pigment has also left a blood sinus which may be divided into two, one on each side of the middle line, as shown in fig. 14. These sinuses are perhaps homologous with the cavernous sinuses of the higher Vertebrates.

Such I imagine to be the history of the pigment in the tissue around the brain; and this view is confirmed by its appearance in those Ammocœtes which have been kept over a year in the laboratory. As already mentioned, the accumulation of large irregularly shaped pigment masses in the branchial regions, in close connection with the occurrence of a great number of pigment-bearing corpuscles, is a most striking result of such confinement. Precisely the same kind of increase of pigment is apparent in the pigmented tissue around the brain, as is seen in fig. 17, Pl. XXVI.

The length of the Ammocœtes from which fig. 17 is taken was 28 mm.; it had remained in the laboratory from the end of September, 1888, until October, 1889, and I doubt whether it had increased in size at all. The increase of pigment in connection with the branchia was very marked, and the pigmented tissue around the brain had undergone most marked modifications. In fig. 17 I have drawn a part of one of the sections through the epichordal region of the brain, and the difference between it and the appearance it would have presented in a fresh-caught Ammocœtes of the same size is most striking; instead of closely packed liver-cells with lines of pigment in between, we see that the cells have disappeared, leaving only irregular-shaped clumps and shreds here and there, while the pigment lines have become large irregular clumps on a coarse network of connective tissue. Close against some of these masses of pigment are seen blood-corpuscles (*a*) lying in the ventral sinus, which bear masses of pigment round their nuclei; and the pigment in some of them is indistinguishable from projections of the pigment masses themselves.

It is, then, clear that an increase of the pigment between the cells of the arachnoidal tissue just as the increase of the pigment in the branchial region, can be produced by a process of malnutrition which causes at the same time extensive passive degeneration of the red blood-corpuscles; and the evidence here is just as striking as in the branchial region, that this increase of the pigment is due directly to the presence of pigment-bearing corpuscles. The natural conclusion is that the pigment which is normally found in this situation is also due to the passive destruction of blood-corpuscles, and that therefore these lines of pigment represent closed-up vascular spaces in between the cells.

If, then, these cells represent the cells of the old cephalic liver of the Crustacean-like ancestor, a straightforward explanation of the pigment between them, and of the formation of the dorsal and ventral sinuses, is afforded by the supposition that the whole represents the blood spaces and blood channels by which the liver-cells were originally supplied with blood.

The interpretation of the pigment found in other places, such as that in connection with the branchiæ, upon the hypothesis that such pigment denotes the locality of previously existing lacunar blood spaces, will be dealt with in the next chapter, where I shall consider the formation of the present alimentary canal.

Sect. 7.—The Relation of the Supra-œsophageal Ganglia to the Walls of the Cephalic Stomach.

Upon the supposition that the Ammocœtes is derived directly from a Crustacean-like ancestor, we ought to find that the supra-œsophageal ganglia are situated in front of the œsophagus, close against the anterior rounded termination of the cephalic stomach on each side of the middle line; and these supra-œsophageal ganglia ought to form—(1) olfactory lobes giving origin to olfactory nerves, (2) cerebral hemispheres giving origin to no outgoing nerves, and (3) an optic portion which gives origin to the optic ganglia and nerves of eyes of an Arthropodan type. Further, seeing that the nervous matter in the infra-œsophageal region has in the course of its growth become closely united with the walls of the cephalic stomach, and has compressed and folded those walls in various ways in different regions, it is reasonable to suppose that here also the elements of the supra-œsophageal ganglia will be found in close connection with the walls of the anterior termination of the cephalic stomach, and will also surround diverticula produced by the compressing growth.

The mere inspection of the dorsal view of the brain of the Ammocœtes (fig. 1) almost compels us to recognise the supra-œsophageal ganglia in the separate masses of nervous matter which are situated in front of the folds of the choroid plexuses, and form the cerebral and olfactory lobes connected by means of the optic thalami with the ganglia habenulæ, which in their turn are connected with the pineal eyes.

Here, also, we find, as in the lower regions of the brain, that the walls of the cavity are partly free from the invasion of nervous matter, and partly form the lining epithelium of the nervous masses which are lying outside them. Thus, as already mentioned, we can trace the free anterior wall of the cephalic stomach in the middle line in front of the choroid plexus ii as forming the recessus infrapinealis (Ahlborn), then the choroid plexus i which bridges over the space between the two optic thalami (Hirnschlitz), continuing onwards as the lamina terminalis to reach the ventral side of the brain, where it forms a bulging known by the name of the recessus chiasmaticus.

On each side of the lamina terminalis lie the simple olfactory lobes and cerebral hemispheres of the Ammocœtes. They have grown round the anterior wall of the cephalic stomach, so as to include two diverticula called by Ahlborn the lateral ventricles of the brain. In fig. 6, Pl. XXV, I give a section through an osmic preparation of the brain of an Ammocœtes 100 mm. long. The section is a horizontal one, and is one of a consecutive series through the whole brain. It shows the olfactory nerves passing from the olfactory lobes, and the lateral ventricles of Ahlborn connected by the ventriculus communis, which is bounded in front by the lamina terminalis, and is continuous behind with the third ventricle. Again, we see that here also in those parts of the walls of the cephalic stomach which form the lining epithelium of these anterior ventricular cavities the same marked fatty degeneration of the cells has taken place as already mentioned in the region of the infra-œsophageal ganglia.

This figure is much the same as fig. 1, Pl. II, in Edinger's paper (**18**) on the "Comparative Anatomy of the Brain," in which he shows that the simple cerebrum of Ammocœtes corresponds to the olfactory lobes and corpus striatum of the higher Vertebrates. In this most instructive paper he points out that the cortical grey matter of the brain does not appear until we reach the reptiles. In fishes, as in Ammocœtes, the cerebral hemispheres consist simply of an olfactory part, and the basal ganglion or corpus striatum, with the grey matter inside and the white matter outside. The peripheral cortex of grey matter is only formed much later in phylogenetic development. The connecting commissure between the two basal ganglia is described by Ahlborn as the anterior commissure, and it is recognised as such by Edinger through the whole ascending series of Vertebrata. If, then, the olfactory lobes and basal ganglia are the cerebral portion of the supra-œsophageal ganglia, then the anterior commissure is the commissure which originally connected together the corresponding parts of the supra-œsophageal ganglia; and as evidence of its antiquity we see that it is stated to be the earliest formed of all the commissures of the brain.

Further, we see that these two nervous masses which form the brain proper and the olfactory lobes are not only in the position of the supra-œsophageal ganglia with respect to the walls of the cephalic stomach, but also are in connection with a special optic portion which is also supra-œsophageal in situation, and gives origin to eyes of a strictly Arthropodan type.

Lying between and dorsal to the two cerebral lobes we see in fig. 1 the large rounded right ganglion habenulæ; much less conspicuous is the smaller left ganglion habenulæ. These two masses of nervous matter are connected, as Ahlborn has shown, with each other by a band of fibres forming the commissura tenuissima, and with the cerebral lobes by strands of peculiarly coloured fibres which he calls the tænia thalami, represented in fig. 8, Pl. XXV, by *t. th.* That part of the nervous system connecting together the cerebral lobes and the ganglia habenulæ is recognised by Ahlborn as the optic thalami (~~*tho*~~. in fig. 8)./ op. t.

SECT. 8.—The Median Eyes and their Optic Ganglia.

In close connection with the ganglia habenulæ are the structures known as the dorsal and ventral pineal eyes. Of these the dorsal eye is the large and conspicuous intensely white object which is seen in front of the right ganglion habenulæ; and the descriptions which have been given of the pineal eye refer in the majority of instances to this eye, and not to the much more insignificant ventral eye. Before entering upon a criticism of the statements which have been already published respecting the pineal eye, I will describe the appearances presented by my sections which have forced me to the conclusion that this eye is, as I have already stated in my paper in 'Brain' (2), an Invertebrate eye of the Crustacean or Arachnidian type.

I have cut sections through a large number of heads of Ammocœtes of sizes varying from 25 to over 100 mm. These sections have been cut either transversely to the long axis of the animal or horizontally in the direction of that axis, and I have found that the transverse sections do not cut the eye in the direction of its optic axis, but that the horizontal sections give a much nearer approximation to sections parallel to the true median plane of the eye, so that we must imagine the eye has been bent forwards so that its optic axis is directed somewhat forwards as well as upwards. Also by compression the eye has been distorted out of shape sufficiently to prevent any plane of section accurately passing through the median plane of both eye and nerve. In figs. 20*a*—*d*, Pl. XXVII, I give selections only of a series of horizontal sections through the pineal eye of a full-grown Ammocœtes, the whole head of which was placed in osmic acid soon after it was caught.

These sections show very clearly the arrangement of the pigment in the eye, the shape and position of the eye, the course and relations of its nerve, and the manner in which its supposed central cavity is filled up with masses of definite protoplasmic material.

1. The Pigment Layer and Nerve-end Cells.—With respect to the pigment, we see that Wiedersheim (**19**) and Ahlborn (**3**) describe the eye as containing, in all cases, intensely white pigment, while Beard (**20**) asserts that in all his specimens of the eyes of Ammocœtes pigment was not present except in three sections which were given to him and came from another locality; in these specimens the pigment was black, not white. He concludes, therefore, that pigment is only rarely present in the eyes of Ammocœtes Planeri, that the white pigment of Ahlborn and Wiedersheim if it is present is dissolved away in the process of preparation; and he claims to have discovered the presence of black pigment.

By the careful study of the pineal eye I am able to absolutely clear up these apparent discrepancies of fact, and to show that Ahlborn is entirely right in his interpretation, while Beard has misinterpreted what he saw. The eye of every Ammocœtes, without exception, presents an intensely white appearance, due to the presence of white pigment as described by Ahlborn; never in one single instance have I seen a specimen free from this glistening white substance. At first, specimen after specimen which I cut presented on section lines and markings of apparently black pigment without exception, so that I was utterly unable to understand Beard's assertion that the eye in Ammocœtes was only rarely pigmented; at the same time it was difficult to understand how such a white, glistening little mass could be so full of what was apparently intensely black pigment. Afterwards I began to find that some of my preparations were entirely free from pigment, and looking through the whole series which I possessed, it was immediately evident that all those which were killed with osmic, and had then been mounted after passing through the series of alcohols in the ordinary way, were full of pigment, as in fig. 20, Pl. XXVII; while all those which contained no pigment had been killed in Perenyi's fluid or in picric acid, and then stained with various staining reagents. Clearly the pigment had been removed during the preparation of the specimens in these latter cases; and doubtless one agent in its removal is the nitric acid, which is so important a constituent of the Perenyi's fluid. I have dissected out the eye and placed it in Perenyi's fluid, and watched how the white pigment was dissolved away. Ahlborn says that these white granules are composed of calcium phosphate, and are the same as the brain-sand found in the pineal body of man and the higher Vertebrates. Ahlborn also lays stress on the absolute untransparency of these particles.

Clearly, then, all the eyes are pigmented, and it is equally clear that there is no black pigment; it is always white. Beard's observations of the presence of black pigment are due to a want of care on his part; what he figures as black is in reality white, as he will see at once if he will look at his specimens with reflected light instead of transmitted light. The white shining particles of pigment are so opaque that they appear, when the section is viewed by transmitted light, quite black, as in figs. 20*a*—*d*. If now the sub-stage be darkened, and a ray of light from a condenser be thrown on the section so as to view it as an opaque object, the only part of the section which is visible are these pigment particles, and they shine and glitter as white particles on the uniform blackness of the rest of the section. Very curious is it to follow, in this way, the changes of the distribution of the pigment in a series of sections through the eye, and to see how, as we pass from section to section, the compact group of brilliant white crystalline-looking particles flashes suddenly into view from out of the uniform blackness.

We see, then, that the pigment which Beard considered to be black is really white, and that this white pigment is always present, but is easily dissolved out by reagents such as nitric acid.

As to the arrangement of the pigment, the nature and symmetry of its arrangement are seen much better in horizontal than in transverse sections. In fig. 22, Pl. XXVIII, which is a magnified portion of fig. 20*b*, Pl. XXVII, we see how the pigment is arranged in definite, somewhat conical masses, which terminate at a very distinct limiting edge, and are curved round towards the middle line in certain parts of the eye in a very striking and characteristic manner.

In the specimens where the pigment has been removed we see that the pigment region is made up of a number of lines arranged radially in the same manner as the lines of pigment; at the base of these lines numbers of nuclei are seen, which follow in their arrangement the shape of the pigmented region. These nuclei are of two kinds, large and small; the large ones are situated at the base of the lines, while the smaller ones are scattered about in between the large ones, and extend to the edge of the eye (figs. 26, 27, Pl. XXVIII). In the interior of the eye the limit of the pigment layer is still seen, and no nuclei occur between this limit and the row of basal nuclei. We may look upon this radial appearance as due to the presence of elongated cells, the nuclei of which are situated at the base, and form the more or less regular row of large nuclei seen in all the specimens. The appearance is exactly what one would expect in an eye which is no longer functional if these large nuclei belonged to the nerve-end cells of an Arthropodan eye, as described by Lankester and Bourne (**21**), Grenacher (**22**), and other observers. The pigment also corresponds in position to that always described in connection with the layer of nerve-end cells.

As to the smaller nuclei, it is possible that they belong to intrusive connective-tissue cells, as described by Lankester and Bourne (**21**) in the median eye of Limulus.

2. The Termination of the Nerve-end Cells with their Attached Rhabdites.—The pigmented layer which forms the posterior wall of the eye is separated from the anterior non-pigmented layer by a central cavity, which according to Beard (**20**), following the suggestion of Spencer (**23**), contains

nothing except the coagulated remnants of an albuminous fluid. In none of my specimens, whether cut horizontally or transversely, is there any sign of such a central cavity as figured by Beard; in all cases this space is filled with the remains of what is clearly a tissue possessing a well-defined structure. In the older Ammocœtes the substance of this tissue is very apt to be fissured irregularly (as in fig. 20, Pl. XXVII), or else to be vacuolated, the spaces so formed being of different sizes and somewhat circular in outline.

In all cases, however, square-shaped blocks and clumps of tissue, in which there is no sign of nuclei, are seen lying between the pigmented posterior part of the eye and the anterior non-pigmented part; and it is significant, as showing how this vacuolated appearance has misled Beard, that the younger the animal the more regular and compact is the arrangement of these square-shaped masses of tissue. According to Shipley (**10**), the eye at its commencement possesses no sign of an internal cavity, but presents an appearance of a regular solid mass of cells; this statement is denied by Owsjannikow (**7**), who says that the anterior and posterior walls come so close together at an early stage of development as to almost obliterate the appearance of a central cavity. Everything seems to me to point to the conclusion that the appearance of a large central cavity is brought about by the partial degeneration of elements which originally filled it, and that their remains have given rise to the impression held by Spencer and Beard, that a large cavity exists which is filled with a coagulated albuminous fluid.

In addition, it may be remarked that it is perfectly easy to see the appearance presented by the coagulated albuminous fluids within an eye by simply looking at sections of the lateral eyes of the same animal; the appearance presented resembles that of a blood-clot, and is totally dissimilar to the square-shaped masses of protoplasmic-looking material seen in the cavity of the pineal eye.

The examination of these square-shaped masses by a high power in osmic preparations, especially in the neighbourhood of the pigment layer, reveals an extraordinary sight; scattered about over the whole field of view of the microscope are seen rod-like bodies, some crescent-shaped, some nearly straight, some shaped like a hook, others like an elongated S, all apparently attached to the edge of one or other of these square or oblong-shaped masses, and differentiated from them by their greater refracting power. They lie in connection with the bodies to which they are attached at different angles to each other, but occasionally a number of them appear to be regularly arranged in respect to the pigment layer. In this case they present very closely the appearance given in fig. 25, Pl. XXVIII, which is taken from Grenacher (**22**), and represents the pigment free ends of the nerve-end cells of an eye of an Acilius larva with their attached rhabdites; in other cases the appearance is very like that represented in fig. 24, Pl. XXVIII, which is a reproduction of Lankester and Bourne's (**21**) picture of a section through the nerve-end cells and rhabdomes of a Euscorpius eye.

In fig. 22, Pl. XXVIII, I give an accurate copy of a magnified portion of the section in fig. 20 *c*, Pl. XXVII.

These bodies, then, which appear on section somewhat square or conical, according to the direction in which they happen to be cut, with their rod-like, highly refractile attached pieces, are by no means mere coagulated albumen, but, on the contrary, are the terminal parts of the nerve-end cells, with the rhabdites attached to them, which project freely beyond the pigment layer, and form the layer of rods as pictured and described in de Graaf's original paper (**24**) on the pineal eye of Anguis. The arrangement of the pigment of the nerve-end cells, and of the rods, calls to mind very forcibly the figures of the larval eye of Dytiscus and Hydrophilus as figured in Grenacher (**22**) and Patten (**25**). In specimens stained by hæmatoxylin no such distinct appearance of rod-like bodies can be seen; but here we find, in between the square or polygonal cell-like masses, lines and strands of substance which stain very much darker than the rest of the tissues of the eye, and in this respect resemble cuticular structures.

The most anterior part of the substance which fills up the central cavity is composed of masses which are less definite in shape than those near the pigment layer, and are free or nearly free from any appearance of possessing cuticular rods; they often closely resemble fig. 23, Pl. XXVIII, which is taken from the paper of Lankester and Bourne (**21**), and represents a transverse section of a clump of nerve-end cells from the eye of Euscorpius beyond the region of rods. When stained with picro-boro-carmine it is seen (fig. 24, Pl. XXVIII) that the middle portion of these polygonal masses stains reddish, while the edges stain yellow.

3. The Cells of the Hypodermal or Vitreous Layer.—The anterior part of the eye is free from pigment, and is composed, as is seen in hæmatoxylin or carmine specimens (figs. 26, 27), of an inner layer of nuclei which are frequently arranged in a wavy line. These nuclei are continous laterally with the nuclei at the base of the layer of nerve-end cells. From this nucleated layer strands of tissue, free from nuclei, pass to the anterior edge of the eye.

In the horizontal longitudinal sections it is seen (figs. 26, 27) that these strands are confined to the middle of the eye; on each side of them the nuclear layer reaches the periphery; so that if we consider these strands to represent long cylindrical cells, as described by Beard (**20**, p. 62), then the anterior wall may be described as consisting of long cylindrical cells, which are flanked on each side by shorter cells of a similar kind. The nuclei at the base of these cylindrical cells are not all alike. We see, in the first place, large nuclei resembling the large nuclei belonging to the nerve-end cells; these are the nuclei of the long cylindrical cells. We see also smaller nuclei in among these larger ones, which look like nuclei of intrusive connective tissue, or may, perhaps, form a distinct layer of cells, situated between the cells of the anterior wall and the terminations of the nerve-end cells already referred to. The appearance presented is drawn as accurately as possible by Mr. Wilson, of the Scientific Instrument Company, in fig. 27, Pl. XXVIII, from a specimen stained with picro-boro-carmine.

It shows between the layer of square-shaped, non-nucleated masses (*r*), which I consider to be the terminations of the nerve-end cells, and the layer of large nuclei (*v*) of the anterior wall, a more or less definite layer of small cells with distinct nuclei (*o.w.*).

In the diagram (fig. 28, Pl. XXVIII) I have depicted the different elements which I see in my sections as they would appear if the eye were restored; and without making any positive statement upon the meaning of the smaller nuclei in the anterior wall, whether they are connective-tissue elements, or form a distinct layer as figured by Patten (**26**), it seems to me clear that the large nuclei belong to the hypodermal layer of cells known by the name of the vitreous layer in the Arthropod type of eye.

According to the views of Patten (**26**, p. 165), the "ground plan of all the variations in the eyes of both Molluscs and Arthropods is a three-layered eye consisting of an invaginated optic vesicle, the inner wall of which becomes the retina, and an overlying layer of hypodermis, the corneagen."

According to this view the pineal eye would consist as in the diagram of the following layers:

1. (*R*) The inner or posterior wall of the optic vesicle or retina, composed of the large nerve-end cells with their associated pigment.
2. (*oc.*) The cavity of the optic vesicle, containing the terminations of the nerve-end cells with their attached rhabdites.
3. (*ow.*) The outer or anterior wall of the optic cavity, composed of a thin layer of small cells.
4. (*v*) The overlying layer of hypodermis or corneagen.

If, on the other hand, the small cell-elements be looked upon as intrusive connective tissue, as described by Lankester and Bourne (**21**) in the central eye of Limulus, then the pineal eye would be described as consisting of a retina with nerve-end cells associated with pigment and bearing rhabdites near their terminations, and in front of the retina the vitreous layer of large hypodermal cells, so that the eye would be included in the group of diplostichous eyes as defined by these authors.

In either case, whether Patten's or Lankester and Bourne's description be accepted as the more correct, the type of eye is clearly that of an Arthropod, and indeed of an ancient form, for the arrangement of the nerve-end cells, the shape of the internal cavity, the position and simplicity of the rhabdites, all point to larval characteristics, and therefore to an ancient type.

So far no mention has been made of any lens. One of the characteristics of the Arthropod eye is the cuticular lens. In the pineal eye of the Ammocœtes no observer has been able up to this time to clearly point to any lens-like structure in that eye. I entirely agree with Beard that the anterior wall of the eye does not represent a lens. In my opinion, as just mentioned, it does represent the corneagen. Where, then, is the lens?

4. The Cuticular Lens.—Upon the supposition that we are dealing here with an eye of an Arthropodan type, it follows that the lens must have been cuticular in structure, and simply a local modification of the general cuticular covering of the front part of the body.

In all the horizontal sections through the eye it is very plainly visible that the anterior wall of the eye is closely pressed against the tissue which forms the wall of the cranial cavity at this spot; and in many cases it is very striking to see how (as is represented in fig. 26, Pl. XXVIII) the anterior wall of the brain-case in this one place dips inwards, and is thickened so as to form a projecting knob which is closely attached to the pineal eye. The closeness of this attachment is seen when the brain and eye are dissected out under a dissecting lens. I have prepared many specimens in this way, and have found that with care it is easy to cut away and remove the brain-case with the overlying skin, and yet leave the eye in position and in connection with the brain. In every case the eye then appears as a white opaque round mass, in the centre of which anteriorly the surface is not flat, but is hollowed out to form a distinct manifest cup. The hollow of this cup was filled with the projecting knob of the cranial wall, which was therefore removed with the rest of that wall, and indeed can in some cases be plainly seen under a dissecting lens as a slight projection on the inner surface of the portion of the wall which has been removed. In Ahlborn's fig. 5, Pl. xiii (**3**), this hollow appearance is perhaps represented.

In horizontal sections the manner in which the eye is attached to the brain-case is clearly visible, and in some cases, as in fig. 26, Pl. XXVIII, the projecting knob of the tissue of the brain-case into the pineal eye so as to form its most anterior wall is very conspicuous. We see how the tissue of the cranial wall is thickened at this one spot, and dips down to meet the pineal eye which is lying beneath it. We see how easy it is to understand that the removal of the brain-case must leave a shallow depression in the anterior surface of the eye. Further, the structure of this tissue is very peculiar. When dissecting it out it feels more like cutting through cartilage than through fibrous tissue. Upon section it presents a curiously homogeneous appearance, with an evident tendency to split into fibrous-looking laminæ. It is remarkably free from any sign of nuclei in it, and is very apt to contain fine globules of yellowish refractile substance, somewhat like those which appear also in the sheath of the notochord and other places. It stains very deeply with hæmatoxylin, similarly to the bodies in the eye already mentioned, just as the cuticular lens and rhabdites of the eye in Arthropoda are known to stain deeply with hæmatoxylin.

In its reaction to staining fluids and in its general appearance it resembles that curious laminated layer of tissue which lies just below the epithelium layer of the skin in the Ammocœtes.

If, then, as I believe, this thickened portion of the tissue of the cranial wall represents the position of the cuticular lens of the pineal eye, it follows that the brain-case itself is partly a modified portion of the integument of the Crustacean-like ancestor—a conclusion which is entirely in harmony with my theory, and which will be considered by me when I come to treat of the manner in which the skeletal tissues of the Vertebrates have arisen.

5. The Optic Nerve and Optic Ganglion.—From the

eye itself arises the nerve, which is most beautifully shown in the series from which figs. 20*a*—*d* are taken. It is seen to be a delicate thin nerve, which is not mixed up with any other structures, and passes freely from the eye to the large ganglion habenulæ. It is clearly not hollow, and at the same time is filled with something which does not look like nerve-fibres, but more like somewhat elongated cells closely packed end to end. The only place where there is any appearance of a cavity is where the central cavity is prolonged in the direction of the place of entrance of the nerve. This contains the remains of nerve-end cells and rhabdites, just as the rest of the central cavity.

The shape of the central cavity is given in Ahlborn's fig. 44 (**3**), which represents a sagittal section through the eye. Its shape is due to the arrangement of the structural elements of the eye, and resembles the picture of the eye of the larva of Hydrophilus given in Patten's paper (**25**). Horizontal sections show that the axis of the cavity has been twisted upwards in the dorsal direction at the end where the nerve enters, so that the shape of the cavity may be likened to a cornucopia, the bent part of the stalk of which lies in the dorso-ventral plane. As the result of this distortion all the most dorsal of a series of horizontal sections must cut through the central cavity twice, first through the expanded mouth of the cornucopia, then through the stalk end, and in these sections the entrance of the nerve must be shown (see figs. 20*a*, 20*b*, Pl. XXVII); then in the middle sections one cavity will be shown consisting of a section through the expanded mouth and commencing stalk of the cornucopia (fig. 20*c*, Pl. XXVII), and finally on the ventral side of the middle section one cavity only will be shown, viz. the cavity of the expanded mouth of the cornucopia (fig. 20*d*, Pl. XXVII).

In this way the appearances seen on section receive a simple explanation, and in all probability the small circular cavity depicted by Owsjannikow in figs. 7, 8, and 9 of his paper (**7**) is due to the direction of his sections in a precisely similar manner.

Tracing the nerve in the series of sections, it is easy to see how it at first lies free in among the liver-cells until it reaches the left-hand side of the rounded mass of the right ganglion habenulæ. It then passes along the whole length of this ganglion, lying close against the side of it, successive sections showing that it is becoming less and less superficial, until near the posterior end of the right ganglion habenulæ it is lying between the left and right ganglia. It then, still passing deeper and deeper, curves round the posterior border of the right ganglion habenulæ just in front of the commissura posterior. From this point it is not easy to trace it further. All the latter part of its course it has been shifting its direction so as to become more and more vertical, and at this point it appears to me to pass straight downwards into the substance of the right ganglion habenulæ.

Ahlborn (3, p. 232) describes the thread-like portion of the epiphysis as a white hair-like thread, which passes from the upper snow-white vesicle (pineal eye) to terminate a little in front of the posterior commissure. He describes it as lying closely over the left ganglion habenulæ, and speaks of it as having undergone an unequal obliteration, so that its proximal part has disappeared to such an extent that "die umhüllenden Piablätter meist vollständig kollabirt sind." This description he illustrates with fig. 44, Pl. xvi, which is a sagittal section through the dorsal eye and the left ganglion habenulæ. Now in this very picture it is clear that the nerve has been cut by the section at the spot where he supposes this obliteration of its proximal part to commence, so that in reality the proximal part of the nerve is not in his section at all; the reason being, as already described, that it clings close to the side of the right ganglion habenulæ, and would therefore be found in the sections to the right of the one he has figured.

As is figured in my sections, the nerve lies free in among the cells of the arachnoid tissue, and passes along the face of the right ganglion habenulæ to its posterior border without any sign of connection with either the optic thalamus or the left ganglion habenulæ.

I have come, then, to the conclusion that the nerve is in connection with the right ganglion habenulæ, and originally passed straight to the surface from the posterior part of that ganglion. By the shifting forward of the eye and brain wall the nerve also was bent forward until it became almost horizontal in position. That such a shifting of position actually took place is nearly certain from the observations of Scott (**11**), who describes how the eye which was originally behind the ganglion habenulæ has shifted forwards during the development of the young animal. Ahlborn also mentions the same shifting of position.

Further, in the eyes of the Arthropoda the optic nerve passes into the optic ganglion, which is a well-defined structure separate from the rest of the supra-œsophageal ganglia. The optic ganglion is composed of a cortical layer of small nerve-cells closely packed together, and an internal medullary portion composed of nerve-fibres which form, according to Patten (**26**), the medullary stalk of the optic ganglion by which it is connected with the brain, and form also the medulla of the ganglion itself, which bears special relations to the eye belonging to that optic ganglion.

In my opinion the right ganglion habenulæ is the optic ganglion of the dorsal pineal eye. It is composed of an internal medullary portion of nerve-fibres, and a cortical portion of small nerve-cells closely packed together of the same kind as the berry-like cells of the grey matter of the brain, resembling therefore the cells of the optic ganglion as given by Patten (**25**). If I am right in my belief that the nerve of the pineal eye can be followed into the right ganglion habenulæ, it appears to me to lose itself in the central medullary mass of fibres. In the innermost portion of the ganglion the medullary part is the main portion From it are formed the large Meynert's bundle which is traceable to the ventral side of the brain in the neighbourhood of the large ventral fissure, also fibres which connect together the two ganglia habenulæ forming the commissura tenuissima of Ahlborn (which perhaps becomes the commissura mollis of human anatomy). A third set of fibres which arise from it are the conspicuous strands which pass by way of the optic thalami to the cerebral lobes. These latter form the medullary stalk of the optic ganglion, the optic thalamus being that part of the supra-œsophageal ganglion which connects together the brain proper and the optic ganglion. It is worthy of notice that all these strands of fibres do not stain like good nerve-fibres, but take on a peculiar tint with various staining reagents as pointed out by Ahlborn. Further, we see, from the series of horizontal sections that in the more superficial sections in which the left ganglion habenulæ is only slightly or not at all involved, the internal medullary part is divided into two portions, of which the one is composed of the more superficial fibres of the commissura tenuissima and tænia thalami, while the other forms the medulla of the ganglion habenulæ itself. In fig. 27, Pl. XXVIII, I give one of a series of horizontal sections through the pineal eye and ganglion habenulæ of an Ammocœtes 66 mm. long, which was stained whole in boro-picro-carmine. The peculiar shape of the arrangement of the nerve-fibres which form the medulla of the ganglion with respect to the nerve-cells is shown in the figure.

In every respect, then, it appears to me the right ganglion habenulæ proves itself to be the optic ganglion of the dorsal pineal eye.

6. The Left or Ventral Eye.—There is, however, a left ganglion habenulæ and a left Meynert's bundle, very much smaller than the right; if this also is an optic ganglion the eye belonging to it ought to be visible, though we should expect to find it more degenerated, and its structure less easy to define than the dorsal eye connected with such a vigorous optic ganglion as is represented by the right ganglion habenulæ. This second eye is the epiphysis iii of Ahlborn, i. e. the lower vesicle which he describes as possessing a structure similar to that of the upper vesicle, or epiphysis ii, which is now recognised as the pineal eye.[1] In this cavity, however, Ahlborn finds the remains of

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[1] He has evidently made a mistake in supposing that the lower vesicle communicates with the upper; all my sections show clearly that they are two separate structures.

strands of tissue similar to what he has noticed in the cavity of the dorsal eye. A description of it is given in Owsjannikow's paper (7), and he gives it the name of ventral eye, in contradistinction to the larger, more perfect organ which is the dorsal eye. This second eye is not only perfectly plain in all my sections, especially the horizontal ones, but it is clearly, as Ahlborn has pointed out, connected in a peculiar way with the left ganglion habenulæ: it is built up of similar elements to the dorsal eye, except that it is never pigmented, as far as I have seen, and it is not connected with the cuticular walls of the brain-case. As yet I have not distinguished any rhabdites in it, and the terminations of its nerve-end cells have broken down to such an extent as to give the whole organ the appearance of a tube in connection with the left ganglion habenulæ.

Owsjannikow (7) describes its posterior retinal wall as being connected by means of nerve-fibres with a group of nerve-cells, to which he gives the name of the ganglion of the eye. This group of nerve-cells seen in fig. 21, Pl. XXVII (ghl_3.), with the strands of fibres which proceed from them towards the long nerve-end cells of this eye, is called by Ahlborn the "Zirbelpolster," and is recognised by him as a part of the left ganglion habenulæ (ghl_3. in his figures). This outlying part of the left ganglion habenulæ is united with the rest of that ganglion (ghl_1. of Ahlborn) by a nervous stalk (ghl_2. of Ahlborn), which according to Ahlborn is short in Ammocœtes, but longer in the adult Petromyzon; this connection can be easily followed in a series of transverse sections; it cannot be shown in any one horizontal section, and therefore is not visible in fig. 21. In Ammocœtes it is so thick that undoubtedly Ahlborn's ghl_1. and ghl_3. are simply parts of the same left ganglion habenulæ.

Ahlborn further describes how a fold of pia mater entirely separates this outlying part of the left ganglion habenulæ from the lower vesicle, i.e. from the ventral eye, except at one place where the continuity of the membrane is broken by the passage of a bundle of fibres connecting the two structures. My sections show clearly the same appearances as those of Ahlborn, and in fig. 21 we see how the fold of pia mater is interrupted by the passage of the fibres (*f.*) from ghl_3. to the ventral pineal eye (pn_2.). I feel, therefore, inclined to look upon the group of cells (ghl_3.) which form the ganglion of Owsjannikow, and the cortex of the "Zirbel-polster" of Ahlborn, as the cortical layer of cells of the optic ganglion of the ventral eye, while the nerve-fibres (*f.*) which pass from them into the eye itself form the medulla and nerve of that eye; the main part (ghl_1.) of the left ganglion habenulæ being formed of the cortical cells and medullary fibres which connect this optic ganglion with its neighbour, and with the supra- and infra-œsophageal ganglia.

We see, then, that the original Crustacean-like ancestor had a pair of median eyes each with its optic ganglion, and its connections with both supra- and infra-œsophageal ganglia; the right eye of the two remained functional longer than the left, with the result of producing in the lamprey the noteworthy asymmetery of the ganglia habenulæ, and of the two Meynert's bundles.

I have no doubt but that further observation in the light of the facts narrated in this paper will suffice to prove that the pineal eye of lizards, &c., is also of the same kind as in the Ammocœtes; throughout the mistake of previous observers, with the exception of Ahlborn, has been to rely too much upon sections cut in the wrong direction, and to omit the most important contents of the eye, under the delusion that they were a coagulated albuminous fluid, and therefore due to the method of preparation, and not essential elements in the eye.

Sect.—9. The Structure of the Supra- and Infra-œsophageal Ganglia.

So close, indeed, is the comparison of the central nervous system of the Ammocœtes with that of an Arthropod, that I feel sure further investigation will bring out a complete coincidence, not only in the topographical arrangement of the several parts, but also in histological structure. Such an investigation is now being conducted in the Cambridge Physiological

Laboratory under my direction, and I will at present only draw attention to one or two points. In the first place, we see that the nerve-cells of the central nervous system of such an animal as a crayfish vary in size, being divisible into giant-cells, large cells, and small cells ; so also in the Ammocœtes we find the same three classes of cells. In the Ammocœtes the giant-cells are connected with the large Müllerian fibres which constitute a system of longitudinal paths in the nervous system itself; the large cells give origin to the series of segmental spinal and cranial nerves ; and the small cells form the closely set masses of "beerenförmigen" cells which constitute the chief part of the spongy portion of the grey matter in the upper portions of the central nervous system.

In the crayfish the large cells are in connection with the outgoing segmental nerves; the small cells form closely set masses of cells which bear a strong resemblance to the cells of the spongy portion of the grey matter, and are connected with the reticulated substance (Punctsubstanz) rather than directly with outgoing nerves. Ahlborn's description of the arrangement in the Petromyzon of these small cells, in rows like bunches of grapes on a stalk, and the appearance of them as I myself have seen them, is strikingly illustrated in Patten's fig. 7, on the plate illustrating his paper (**25**) on the development of the eyes of Vespa, &c. Whether the giant-cells in the Arthropod nervous system resemble those in the Ammocœtes, and are connected with a system of longitudinal fibres in the central nervous chain itself, I do not as yet know, although I think it very probable that such will be found to be the case.

Again, the similarity in the extent of this small-celled group is very striking. In the spinal cord of the Ammocœtes, and indeed of all Vertebrates, the small cells of the grey matter are but few, and confined mainly to the region of the posterior horn ; when, however, we reach the higher regions of the central nervous system we see how greatly this particular class of cell increases in number, forming the main feature of the grey substance ; we see how masses of these cells are grouped round the diverticula of the central canal in the region of the cerebral and olfactory lobes; how the commencing optic lobes are formed of a great lateral bank of these cells, spreading dorsally on each side of the aqueduct of Sylvius; and how, too, the commencing cerebellum is largely formed of an increase of these same kind of cells; further, we see, as already mentioned, how the cortex of the large ganglion habenulæ is formed of similar cells, arranged in a strikingly similar manner to those of the optic ganglion of an Arthropod.

Similarly, in the Crustacean the most striking difference between the higher parts of the nervous system—the supra-œsophageal and infra-œsophageal ganglia — and the lower ganglia of the ventral chain is the great increase of these small-celled masses, which are in connection with the reticulated substance (Punctsubstanz), and do not possess well-defined axis cylinder processes as in the case of the large pear-shaped nerve-cells.

In fact, the central nervous system of the Ammocœtes, and therefore of all other Vertebrates, is the direct descendant of the Arthropod nervous system in all respects; and it is for this reason, and not because similarity of function requires similarity of structure, as suggested by Bellonci (27), that the remarkable resemblance exists between the structure and connections of the olfactory lobes in the Vertebrates and in the higher Arthropods which he has pointed out in his paper (27), in the 'Archives Italiennes de Biologie.' In his conclusions he says: "La structure et les rapports des lobes olfactifs présentent chez les arthropods supérieurs et les Vertébrés le même plan fondamental. Dans les uns comme dans les autres les fibres olfactives et les fibres de connexion des lobes olfactifs se résolvent en un fin réticule, qui, se groupant par places, forme ce que j'ai nommé le glomérule olfactif." In the Ammocœtes the olfactory glomeruli resemble exactly in appearance, and in their reaction to staining with osmic, the reticulated substance (Punctsubstanz) of the Arthropod nervous system; here more clearly than anywhere else in the Vertebrates, we see the characteristic appearance of this peculiar Invertebrate tissue. I will not, however, dwell further here upon the question of the olfactory nerves, as I shall deal with them and the rest of the cranial nerves in my next paper.

Although I have dealt with the nervous system, I have purposely omitted the consideration of the pituitary body because it does not in reality belong to the central nervous system; it represents, in my opinion, the Crustacean green glands, and will be considered when I come to deal with the formation of the Vertebrate skeletal tissues, and of the excretory organs.

In the next chapter I propose to point out how the present alimentary canal arose; and as it is perhaps advisable to make a preliminary communication in this paper, I will say now that the view, the truth of which I intend to discuss, is as follows:

1. The alimentary canal is formed by the prolongation of a respiratory chamber.
2. The respiratory chamber contains the gill-bearing legs of the Crustacean-like ancestor, which are still present in the Ammocœtes as the bars bearing branchiæ, and still retain their Invertebrate type of muscles.
3. The first pair of such appendages do not bear branchiæ; they form the so-called velum, and are simply the foremost pair of legs of the Crustacean-like ancestor.
4. The segmental cranial nerves are the nerves which arise from the infra-œsophageal and thoracic ganglia, and supply the foremost appendages up to and inclusive of the gill-bearing legs.
5. The first two cranial nerves are the nerves of special sense arising from the supra-œsophageal ganglia.

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EXPLANATION OF PLATES XXV, XXVI, XXVII, XXVIII,

Illustrating Mr. W. H. Gaskell's paper "On the Origin of Vertebrates from a Crustacean-like Ancestor."

Examination of Reference Letters.

b. v. Blood-vessel. *b. s.* Blood-sinus. *cb.* Cerebellum. *cer.* Cerebral and olfactory lobes (supra-œsophageal ganglia). ch_1, ch_2, ch_3. Choroid plexuses (free walls of cephalic stomach). *com. ten.* Commissura tenuissima. *cr.* Cranial wall. *g. h. r.* Right ganglion habenulæ (right optic ganglion). *g. h. l.* Left ganglion habenulæ (left optic ganglion). *l.* Arachnoidal tissue (cephalic liver). *l. e.* Lens of pineal eye. *l. d.* Ganglion interpedunculare (duct of cephalic liver). *l. i.* Lobus infundibuli (old œsophagus). *l. t.* Lamina terminalis (anterior end of cephalic stomach). *M. b. r.* Right Meynert's bundle. *M. b. l.* Left Meynert's bundle. *med.* Medulla of pineal eye. *M. f.* Müllerian fibres. *n.* Nerve of pineal eye. *nc.* Notochord. *n. g.* Nerve-cells of grey matter. *o. c.* Central cavity of optic vesicle. *ol.* Olfactory nerve. *op. th.* Optic thalamus. *o. w.* Anterior wall of optic vesicle. pn_1. Dorsal pineal eye. pn_2. Ventral pineal eye. *p. com.* Post-commissure. *R.* Retina of pineal eye (layer of nerve-end cells). *r.* Layer of rhabdites. *ra.* Raphe. *r. aq.* Raphe of aqueduct. *st.* Lining epithelium of central cavity of brain (epithelium of stomach wall). *tr.* Trabeculæ. *t. th.* tænia thalami. *v.* Vitreous layer or corneagen. *V. aq.* Ventricle of aqueduct. *V. c.* Ventriculus communis. *V. lat.* Lateral ventricle. V_3. Third ventricle. V_4. Fourth ventricle.

FIG. 1.—Dorsal view of brain of Ammocœtes.

FIG. 2.—Transverse section through the infundibular region of the brain of an Ammocœtes, immediately after its metamorphosis. Picro-carmine and eosine preparation. The section cuts through the very commencement of the right ganglion habenulæ.

FIG. 3.—From the same series as Fig. 2. The section cuts through the posterior commissure and the very commencement of the notochord. Figs. 2 and 3 correspond closely to Ahlborn's Figs. 27 and 26 respectively.

FIG. 4.—Transverse section through the commencement of the formation of the fourth ventricle. Hæmatoxylin preparation.

FIG. 5.—Magnified drawing of the ventral portion of one side of the nerve-substance of the cord in Fig. 4.

FIG. 6.—Horizontal section through the brain of a full-grown Ammocœtes. Osmic preparation.

FIG. 7.—Magnified drawing of the part of the brain marked × in Fig. 6, taken from a hæmatoxylin preparation of the brain of a full-grown Ammocœtes.

FIG. 8.—From the same series as Fig. 6, to show the optic thalamus, third ventricle, ventricle of the aqueduct, and the fourth ventricle.

FIG. 9.—From same series as Fig. 2 and Fig. 3, to show substantia centralis gelatinosa and arrangement of groups of nerve-cells in the epichordal portions of the brain.

FIG. 10.—Magnified drawing of a portion of Fig. 9.

FIG. 11.—Transverse section through the conus post-commissuralis of nearly full-grown Ammocœtes. Osmic preparation. To show how the limits of the lumen are marked out by fat-globules.

FIG. 12.—From the same series as Fig. 11. Magnified drawing of the grey matter of the epichordal part of the brain, to show the formation of the raphe and the limiting line of the layer of fat-globules.

FIG. 13 *a, b, c, d, e.*—Selections out of a series of transverse sections through the region of the conus post-commissuralis, to show the presence of an occluded ventral duct in that region. Osmic preparation of the head of a half-grown Ammocœtes.

Fig. 14.—Transverse section through the region of the cerebellum, to show the arrangement of the cells of the arachnoidal tissue and the ventral and dorsal blood-sinuses. Boro-picro-carmine preparation.

Fig. 15.—Magnified drawing of the cells of the arachnoidal tissue. Carmine preparation.

Fig. 16.—Cells of arachnoidal tissue. Osmic preparation from the same series as Fig. 20.

Fig. 17.—Transverse section through the epichordal portion of the brain, to show the increase of the pigment round the brain. Carmine preparation of Ammocœtes 28 mm. in length which had been kept alive in the laboratory for a year. *a.* Pigment bearing blood-corpuscles in the ventral sinus.

Fig. 18.—Magnified drawing of red blood-corpuscles, to show formation of pigment in them. *a.* Normal blood-corpuscle. *b.* Commencing pigment formation round the nucleus.

Fig. 19.—Transverse section through the spinal cord of a full-grown Ammocœtes.

Fig. 20 *a, b, c, d.*—From the same series as Fig. 6 and Fig. 8, to show the relation of the dorsal pineal eye and its nerve to the surrounding tissue, and also the shape of the cavity of the eye. *en.* Place of entrance of nerve. *c. nas.* Nasal cartilage.

Fig. 21.—Horizontal section through the ventral pineal eye of a full-grown Ammocœtes. Boro-picro-carmine preparation. ghl_1. Main portion of left ganglion habenulæ. ghl_3. Optic portion of left ganglion habenulæ. *pi.* Fold of pia mater which separates the ventral eye from the left ganglion habenulæ, and is perforated by the bundle of fibres (*f.*) in one place.

Fig. 22.—Magnified drawing of a portion of the pineal eye represented in Figs. 20*a—d.* The drawing is taken from the section immediately following 20*b* as we pass in the direction of 20*c*, to show the nature of the contents of the central cavity, and the arrangement of the lines of pigment.

Fig. 23.—Ends of the nerve-end cells of a lateral eye of Euscorpius. From Lankester and Bourne, fig. 5.

Fig. 24.—Section across the nerve-end cells of a lateral eye of Euscorpius, showing the cuticular rods. From Lankester and Bourne, fig. 6.

Fig. 25.—Termination of nerve-end cells bearing rhabdites of an Acilius larva. From Grenacher.

Fig. 26.—Horizontal section through the dorsal pineal eye of a full-grown Ammocœtes, to show the relation of the eye to the walls of the cranial cavity. Carmine preparation. *nas.* Nasal cavity.

Fig. 27.—From same series as Fig. 21, to show the structure of the dorsal pineal eye and of the right ganglion habenulæ. The dotted lines represent

the course of the nerve as seen in the whole series of sections. The part of nerve shaded was the only part visible in this particular section.

Fig. 28.—Diagram of the pineal eye of Ammocœtes as restored, to show its Arthropod characteristics. For the sake of clearness most of the pigment surrounding the nerve-end cells is not shown in the diagram, but its limits only are indicated by the lines of black dots.

Fig. 29.—Diagram to show the transformation of the walls of the Crustacean cephalic stomach into the lining epithelium of the cavities of the brain of Ammocœtes. *Red* represents the contour of the cephalic stomach. *Yellow*, the contour of the lining epithelium of the cavities in the brain of Ammocœtes if the choroid plexuses were unfolded [cf. Ahlborn (3), fig. 41, Pl. xvi]. *Black* indicates the position of the principal nervous structures in relation to the Crustacean cephalic stomach, and to the brain-cavities respectively.

The Development of the Atrial Chamber of Amphioxus.

By

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and

Arthur Willey,
Student of University College.

With Plates XXIX, XXX, XXXI, XXXII.

Last year one of us (Mr. Willey) collected during the months of May, July, and August many hundreds of embryos and larvæ of Amphioxus in Sicily.

The material so obtained has been worked out in the laboratory of University College. The period of the development, to which we determined first of all to give attention, was that before which Hatschek's well-known work stops short. Series of sections were prepared in order to ascertain the mode in which the atrial chamber takes its origin and the subsequent history of the gill-slits, viz. as to how the slits on the left side of the pharynx originate. The relation of the larval to the adult mouth and the details of the curious process of movement of the mouth from a unilateral to a median position were included in the scope of our inquiries.

Amphioxus occurs in great numbers in a comparatively small lake, or pantano, which is situated behind, and separated from the sea by, the village of Faro, near Messina. It is connected with the Straits of Messina by a narrow canal, some two or three hundred yards in length.

The bottom of the pantano, in contrast to that of the Straits, consists of foul mud; and it may be mentioned in this connection, as stated by Professor Kleinenberg,[1] that Amphioxus is only occasionally met with in the Straits, and is entirely absent from another larger pantano which lies behind the neighbouring village of Ganzirri, and is joined by a short canal to the one at Faro.

The embryos float on the surface, and are to be had by dredging on the surface at sunrise; but the readiest method of obtaining them in quantity is to take the adults in glasses and allow them to spawn there, if they will. Spawning takes place about an hour after sundown.

The ova, if fertilised, must be very carefully distributed among several glasses containing clean, but unfiltered, water from the pantano. If the water is filtered, or if sea-water is employed, or if too many ova are placed in one glass, they will certainly either die or develop abnormally.

The first outward and visible sign of fertilisation is the separation from the egg-cell of the yolk-membrane (Dottermembran).

Most, if not all, of the ova obtained were discharged through the atriopore.

If Kowalevsky[2] had not seen them issuing from the mouth, it would not have been supposed that they could pass into the pharynx in opposition to the constant outflow of water between the gill-bars.

Segmentation always commences at dusk—between the

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[1] I desire to express my sincere thanks to Professor Kleinenberg, of Messina, for his kindness and for the invaluable assistance which he gave to Mr. Willey in accomplishing the object of the latter's visit to Sicily. I have also to thank the Government Grant Committee of the Royal Society for the funds which enabled me to obtain Mr. Willey's services in this inquiry.—E. R. L.

[2] "Entwick. des Amph. lanc." ('Mém. Acad. Impér. des Sciences de St. Pétersbourg,' series vii, vol. xvi, 1866).

hours of seven and eight—and goes on very rapidly through the night.

The early stages have been so fully described by Hatschek[1] that it will only be necessary to refer to them in the briefest manner.

At 8 p.m. segmentation commences; at 11 p.m. invagination commences; at 1 a.m. the gastrula is complete; at 3 a.m. the gastrula begins to revolve by cilia within the yolk-membrane; and at 5 a.m. two pairs of myocœlomic pouches have been formed, and the embryo ruptures the egg-membrane and becomes free-swimming.

During the first day the embryo grows in length and adds several pairs of somites. By about eight o'clock on the second morning—that is, thirty-six hours after the commencement of segmentation—the embryo has acquired a mouth on the left side of the body, and a gill-slit, which arises at first in the median ventral line, and subsequently comes to lie on the right side of the body.

The anus is formed soon after the appearance of the mouth and first gill-slit.

The embryonic period is now at an end, and the larval period begins. As Hatschek states, the only way of obtaining the larval stages is by pelagic fishing. This consists in dredging at depths varying from fifteen to twenty fathoms. At this depth the Amphioxus larvæ float in the midst of countless thousands of Sagitta larvæ.

A long, but not yet clearly ascertained interval (probably about a fortnight) elapses between the formation of the first and second gill-clefts.

In the period during which it is free-swimming the larva acquires from twelve to fifteen consecutive unpaired gill-slits, each one arising in the mid-ventral line, and then growing in such a manner as to lie on the right side of the body. This applies to the anterior two-thirds of the pharynx, but it is not quite clear yet as to whether the last two or three median slits ever move up to the right side. Meanwhile, longitudinal

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[1] Claus's 'Arbeiten,' 1881.

ridges, which are subsequently concerned in the formation of the atrium, have appeared (see Fig. 6). In this stage the larva rests habitually on one side at the bottom of the vessel in which it is kept, and does not bury itself in sand or mud.

At the time of the completion of the atrium, which occurs at the close of the larval period, some remarkable changes in the relative position of parts of the body in the anterior region take place, by which the mouth becomes median, and the gill-slits are arranged in two series, a right and a left. The larva emerges from this critical phase in its development as a symmetrical animal, but the details of the process of "symmetrisation"—the strongly marked character of which justifies the use of an otherwise undesirable term—are still rather obscure. The larva, now really a young Amphioxus, with atrium and paired gill-slits, ceases to lead a pelagic life, and takes to the sand, where it passes the rest of its life. In this condition it does not rest on one side on the sand, but buries itself upright tail downwards with the oral hood alone projecting from the sand (Willey obs.). Hence in the adult condition there are not one-sided relations of the Amphioxus to its environment.

Spawning occurs at least from April to September inclusive. The best month, however, in which to obtain the embryos is June, while all the larval stages, up to the passage into the adult form, are to be found during July and August.

Previous View as to the Formation of the Atrium.

The hitherto accepted method of formation of the atrial chamber of Amphioxus is that described by Kowalevsky,[1] and more fully by Rolph.[2]

Kowalevsky says that after a certain number of gill-slits have been formed, two longitudinal folds appear on opposite sides of the body, which grow round and meet, and finally fuse together in the median ventral line, leaving a wide aperture at one end—the atriopore. His figures, two of which

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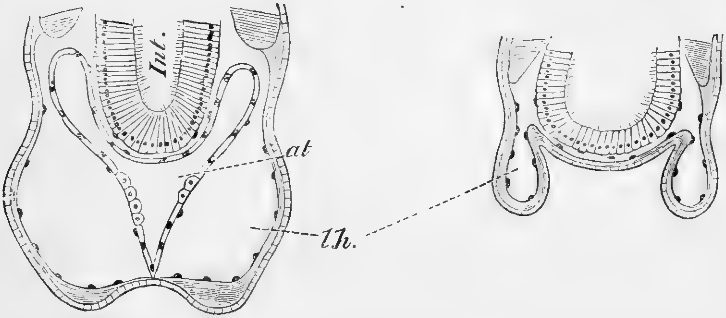
[1] 'Archiv für Mikrosk. Anat.,' vol. xiii, 1877.

[2] 'Morphol. Jahrbuch,' vol. ii, 1876.

are here reproduced (Figs. 1 and 2), bear this description out,

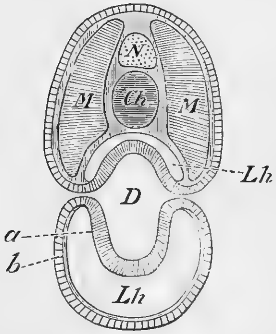
Fig. 1. Fig. 2.



Copy of Kowalevsky's figures of transverse sections through a larva of Amphioxus with fully formed atrium. Fig. 1 represents a section taken between pharynx and atriopore; and Fig. 2, one taken just behind the atriopore of the same larva. *Int.* Intestine. *at.* Atrium. *l.h.* Cœlom.

more or less, while Rolph's schematic figures bear it out entirely. The latter are reproduced in Figs. 3, 4, and 5.

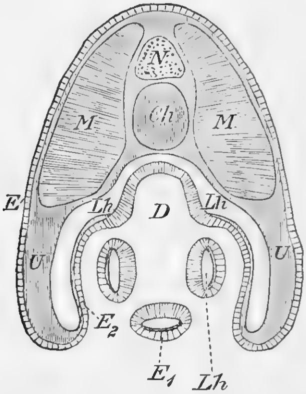
Fig. 3.



Copy of Rolph's theoretical section through the pharyngeal region of a larva before the formation of the so-called epipleural folds. *N*. Nerve-cord. *M.* Muscles. *D.* Intestine. *b.* Epidermis. *Ch.* Notochord. *Lh.* Cœlom. *a.* Intestinal epithelium.

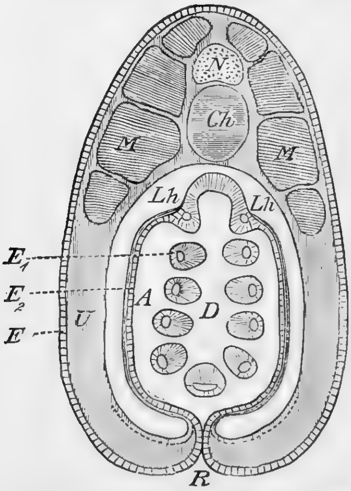
The most serious error in Kowalevsky's view lies in the fact that he makes the space in the lateral outgrowths continuous with the body-cavity, and consequently calls it "Leibeshöhle," or cœlom.

Fig. 4.



Copy of Rolph's theoretical section through an older larva, showing the commencing longitudinal downgrowths. *E.* Epidermis. E_1. Visceral epithelium of the (future) atrial cavity. E_2. Parietal epithelium of same. *U.* Subcutaneous tissue. Other letters as in Fig. 3.

Fig. 5.



Copy of Rolph's theoretical section, showing the meeting together of the "epipleura" in the ventral middle line. *A.* Atrium. *R.* Raphe. Other letters as in Figs. 3 and 4.

There is no evidence that this space is an offshoot of the original myocœlomic pouches: it arises apparently as an intercellular space in the midst of the connective tissue; in fact, it would seem to belong to that category of spaces to which the term "pseudocœl" has been applied. If this should prove to be its history it would stand in contrast to the spaces in connection with the dorsal and ventral fins, which have been shown by Hatschek to be derived directly from the myocœlomic pouches.

Rolph's figures (Figs. 3, 4, 5) do not profess to be more than diagrams. They show the epipleur originating as a depending ridge on each side of the pharynx (Fig. 4). Into this ridge the cœlom is extended. The epipleura meet finally in the middle line below the pharynx according to this theory (Fig. 5). It is no doubt true that the scheme of growth thus sketched by Rolph, and based upon Kowalevsky's erroneous figures, would account satisfactorily for the condition of the atrial chamber and its epipleural walls, as observed in the adult. It also gives a basis for the suggestion made by Kowalevsky that the epipleura are comparable to the opercula of Teleostean fish.

We shall now give an account of our recent observations.

Formation of the Atrial Chamber as now determined.

The first indication of the commencing formation of the atrial chamber is to be found in larvæ with nine or ten gill-slits on the right side. Behind the region of the pharynx we find that the mid-line of the body has become marked with a narrow groove, so that in section it is bifid (Fig. 6). The short upstanding ridges which limit the groove are the metapleura of the adult. Though at first solid, the connective tissue within the ridge soon becomes hollowed and forms a lymph-space, which we have not traced into connection with the cœlom. These ridges can be traced from about the middle of the larva's body forward towards the pharyngeal region, where they diverge considerably from one another (Pl. XXX, figs. A, B, C).

That belonging to the animal's left side keeps a more or less median position, and can be traced (though but small in elevation) when twelve gill-slits are present as a ridge situated at the lower or ventral margin of the gill-slits, and dying out in the anterior region of the pharynx (Pl. XXIX, fig. 6). The right-hand ridge, or metapleur, takes a course to the right of the gill-slits (which, it will be remembered, are on the right side of the body), and overhangs the upper limit of the slits to

Fig. 6. Fig. 7.

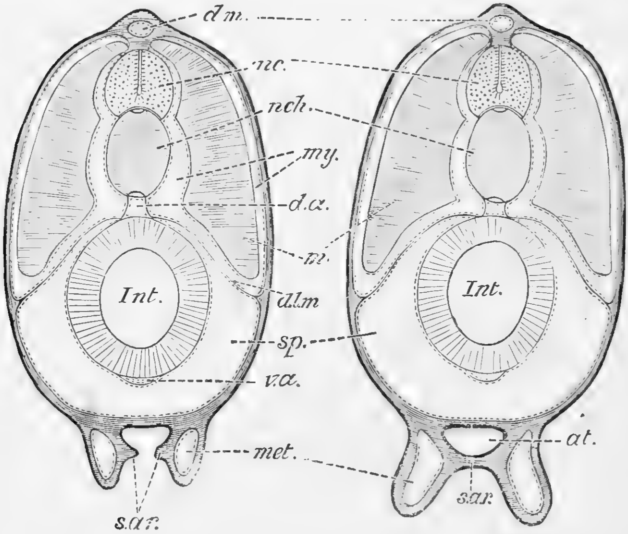


Fig. 6.—Transverse section through a larva with eleven or twelve unpaired gill-slits, showing the minute sub-atrial ridges. *d.m.* Dorsal division of myocœl in which the fin-ray will lie when it is developed. *nc.* Nerve-cord. *nch.* Notochord. *m.* Muscle-plate. *my.* Cavity of myocœl. *d.a.* Dorsal aorta. *Int.* Intestine. *d.l.m.* Double-layered membrane separating the myocœl from the splanchnocœl. *sp.* Primitive splanchnocœl. *v.a.* Ventral vessel. *met.* Metapleur. *s.a.r.* Sub-atrial ridges.

Fig. 7.—Transverse section through a slightly older larva. The sub-atrial ridges (*s.a.r.*) have fused for a short distance between atriopore and pharynx; but in the pharyngeal region the atrium is unclosed, and consequently the gill-slits still open directly to the exterior. *at.* Atrium.

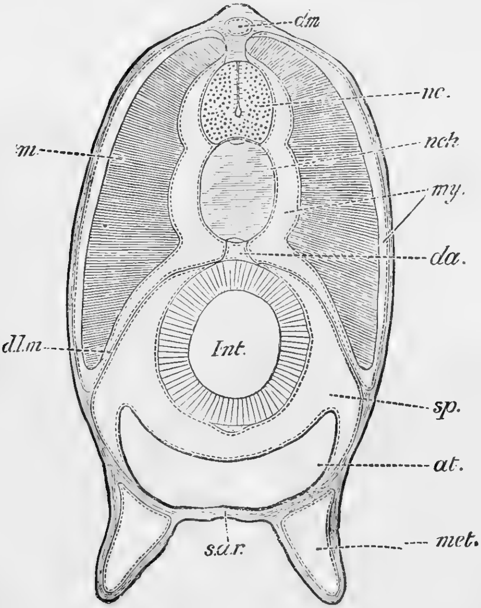
a small extent. It dies out in front of the first gill-slit, where it bends towards the middle line.

The atrium is formed by a small horizontal growth (*s.a.r.* in Fig. 6), which starts from the inner face of each metapleur and floors in the deeper half of the groove or area between the two metapleura (Fig. 7, *at.*).

These horizontal growths may be called the sub-atrial folds.

They are at first extremely small, and the atrial space floored in is a mere canal. Later the width of the atrial space increases greatly, and the sub-atrial folds consequently widen also, becoming that pleated expansible floor of the atrial chamber, with its transverse muscular layer, which all observers of Amphioxus know so well (Fig. 9, *s.a.r.*).

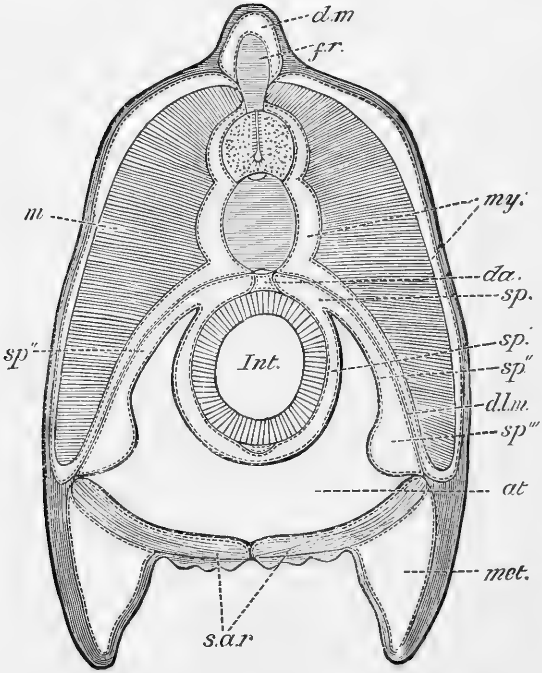
Fig. 8.



Transverse section through an advanced larva with fully-closed atrium. The latter has begun to encroach on the cœlom (splanchnocœl) (*sp.*). Letters as in Figs. 6 and 7.

The atrial groove becomes floored in first in the region of the atriopore. The growth of the sub-atrial folds extends gradually forwards, and the closure proceeds along one side (the right) of

Fig. 9.



Transverse section through an adult Amphioxus. The atrium has grown up so as to divide the primitive splanchnocœl into two portions—an inner or splanchnic, and an outer or pleural, portion (*sp'*. and *sp''*.). *sp*. The portion of the primitive splanchnocœl which is not so affected by the atrium, and which persists as the dorsal cœlom. *sp''*. Pleural cœlom. *sp'''*. Its perigonadial dilatation. *f.r.* Fin-ray. Other letters as in preceding figures.

the pharynx. The whole atrium thus formed is a very small tube-like space. The closure by means of the small horizontal sub-atrial outgrowths in the region of the large gill-slits is somewhat difficult to explain. The small left metapleur actually moves in course of growth from the mid-line, and rises on to the right side somewhat (Pls. XXX and XXXI, figs. 6, 7, 14, and 14A, *l. met.*). At the same time the much larger right metapleur is deepened, and overhangs the slits. Then the little horizontal junction is effected, and we get actually a nearly tubular atrium receiving the openings of successive gill-slits. With subsequent growth the narrow atrial tube widens and pushes itself right and left, so as to encroach on the space hitherto occupied by the cœlom, and finally it extends so far dorsalwards as nearly to surround the alimentary canal (see Figs. 8 and 9).

The evidence of this history, in the form of careful drawings of various sections, at various stages in the closure of the atrium, together with drawings of whole larvæ in two stages of development, is given in the plates (Pls. XXIX, XXX, XXXI, and XXXII) accompanying this paper. It is important to point out that the mode of formation of the atrium as a narrow groove, which closes and sinks (as it were) into the body of the Amphioxus, is really different in important respects from the enclosure of a space by downgrowth of large folds, though ultimately no doubt the two contrasted modes of formation come to the same thing so far as the more obvious morphological relations are concerned. The mode of formation which really occurs in Amphioxus is readily harmonised with the existence of the post-atrioporal extension of the atrium which gradually tapers to a fine cæcal canal. It also gives us an essentially different view of the region called "epipleur" by Lankester, and generally so designated, from that which Rolph's theory necessitated. That portion of the epipleur into which the myotomes of the body-wall extend is seen now to be no downgrowth, no extension or fold. It is the original unchanged body-wall which bounds the sides of the animal's body in front of the atriopore, just as much as it does behind. The only new growth in the atrial region which takes part in the limitation of the surface is the subatrial growth formed by the two little horizontal folds which floor in the atrium when it is a mere canal. These in the adult are represented by the region of longitudinally pleated ventral wall between the two metapleura.

The formation of the atrium as a narrow groove which closes, sinks into, and expands within the body of Amphioxus, is much more readily comparable to what is known of the formation of the atrial chamber in the Ascidians than is the Kowalevsky-Rolph scheme. In the Ascidian a pair of in-pushings are formed, each with a circular orifice of invagination; they expand within the body, fuse with one another to form one cavity, and one of the circular orifices disappears. In Amphioxus we have a single in-pushing with a longitudinal orifice of invagination, which closes as the invagination forms, excepting at its hindermost border, and then expands to a greatly increased volume.

The comparison of the so-called epipleura of Amphioxus with the opercula of fishes has only a remote morphological basis, and probably no genetic relationship exists between these two structures. On the other hand, it is very probable that whilst the median fin-rays and fin including the ventral fin with its double rays represent the median fins of fishes—the metapleura represent morphologically the primitively continuous lateral fins. The duplication of the fin-rays in the median ventral series of adult Amphioxus appears to be only a complete carrying out of a tendency to bifid structure which is found in the young dorsal fin-ray (see Lankester—Amphioxus, 'Quart. Journ. Micr. Sci.,' vol. xxix, Pl. XXXVI, B, fig. 11); and though in both dorsal and ventral median fins the fin-ray lymph-space is single, yet the floor of this space has a bilateral origin according to Hatschek.

* * *

The figures which are given in Pl. XXIX represent two stages of the larvæ of Amphioxus, an earlier with three gill-slits and the rudiment of a fourth (figs. 1, 2, 3), and a later with twelve gill-slits and the rudiments of two more (figs. 4, 5, 6).

Though the older larva is considerably larger than the younger, the two are, for the sake of comparison, represented of the same size.

Each larva is illustrated by three views: one a surface-view of the left side complete, one a surface-view of the right side of the anterior end, and one a deep focus of the anterior end.

The drawings were made from carefully preserved specimens (killed with corrosive sublimate), stained with carmine and mounted in balsam. They are diagrammatic in the sense that they represent the results of observation rather than an actual view as obtained by one focussing.

The most striking feature in both larvæ is the large mouth on the left side. In the younger larva the form of the tail, with its peculiar larval fin-rays, is noteworthy. In many respects this larval tail-fin recalls that of young Teleostean fishes. It is also closely similar to that of some Ascidian tadpoles (e. g. Styela). The small number and large size of the myotomes (indicated by numbers in the drawings) in the anterior region of the body are also remarkable. No evidence could be obtained by us of the intercalation of new myotomes, nor of the multiplication of anterior myotomes by division.

The new myotomes appear to form exclusively at the caudal extremity.

In the larger larva the full number of adult myotomes has been attained, and the larval tail-fin has become greatly modified, giving place to the mesoblastic expansion which forms the tail-fin of the adult.

When we remember that in the adult the oral sphincter lies in the vertical line of the apex of the tenth myotome, it is not a little astonishing to note the position of that myotome relatively to the alimentary canal in the younger larva, and even in that which has attained the full complement of myotomes. The independence of the metamerism of the body-wall from that of the gill-slits and alimentary canal is thus very sharply indicated.

In the cephalic region of both the older and the younger larva we see two remarkable larval structures, which lie in front of the mouth—the one in front of the buccal cavity, and the other within its area. These are the præoral pit and the club-shaped gland. They have been figured by Hatschek, who has described the præoral pit as consisting of a ciliated depression and a short glandular tube, and has traced to this structure the thickened ciliated epithelium which is found on the inner face of the oral hood of the adult forming there—the so-called "Räder-organ."

Hatschek, in his important memoir in the 'Arbeiten a. d. Zool. Institute d. Univ. Wien,' vol. iv, 1881, does not figure any larva later than one with a single gill-slit. In one of the wall-plates of Leuckart and Nitsche, however, received by us during the progress of this work, there are a number of figures of later stages, which have to some extent assisted us in arriving at an understanding of the later unillustrated note by Hatschek ('Zoolog. Anzeiger,' 1884, p. 517). None of the published figures exactly coincide with our younger larva as to age, and our later larva is even less closely represented in the diagrams above mentioned, so that the figures we are able to publish are new, and will probably be of service to naturalists. The club-shaped gland, though figured by Hatschek and earlier observers, has not been described. It is remarkable for its early development (observed by Hatschek), and for the fact that it seems to entirely disappear in the adult without leaving any trace. The gland is a sac with a large lumen. It lies obliquely on the right wall of the buccal cavity, and, bending round below, tapers to a narrow canal as it rises on the left wall of the buccal cavity, where it opens just below and external to the margin of the mouth. In the younger of the two larvæ figured the club-shaped gland has no internal opening; it ends blindly just below the notochord. But in the later stage (drawn in figs. 4, 5, 6) the gland has acquired an opening into the cavity of the mouth. This orifice is placed at the opposite end of the glandular sac to its external opening (Pl. XXIX, fig. 5; and Pl. XXX, fig. 5, *int. a.*, and fig. 2, *ext. a.*).

By the side of and anterior to the club-shaped gland is a tract of modified epithelium of the buccal cavity of about twice the breadth of the gland itself, and divided by a median clearer space into two parallel tracts. This strangely-placed group of cells has sometimes the appearance in published drawings of larvæ—of being a shadow cast by the gland, or in some cases looks like a duplication of it. It can be traced in the section drawn in fig. 2, Pl. XXX, where it is marked *me*.

In the deep-focus drawings, Pl. XXIX, figs. 2 and 5, another tubular structure is figured, which is also seen in the transverse sections (Pl. XXX, figs. 2 and 3, *neph.*, and fig. 4, *neph. a.*; and Pl. XXXI, fig. 13, *neph.*). This, so far as we can judge from the drawings given in Leuckart and Nitsche's diagram, is the structure which Hatschek has described as a nephridium in the 'Zoolog. Anzeiger,' 1884, p. 517, without a figure. In the condition in which we have observed this structure (viz. in larvæ ranging from the stage with three gill-slits up to closure of the atrial cavity) there does not seem to be any special reason for regarding it as a nephridium. We should prefer to call it the subchordal tube. It appears to end blindly anteriorly, and to open into the buccal cavity near the recurved extremity of the glandular tract which accompanies the club-shaped gland. The tube lies below, and to the left of, the notochord.

The drawings of the larger larva (Pl. XXIX, figs. 4 and 6) show some interesting features as to the disposition of the gill-slits and the metapleura. In this larva the atrial tube has formed from behind (the atriopore) forwards as far as the hindermost still very small gill-slits (*gs.* 9). It is a remarkable fact that all the gill-slits up to this stage originate in the median ventral line. This is true of the first and of all that follow up to the fourteenth, and possibly some few more. It is, however, not true of the formation of new gill-slits after the right and the left lateral series of gill-slits have become established. The figures in our plate show that, whilst gill-slit No. 1 occupies an entirely lateral area on the animal's right side—not reaching below to the median line —this position is gradually receded from by the hinder slits, which from No. 6 onwards are seen to encroach more and more on the left side. When we remember that gill-slit No. 1 as well as all that follow it originated in the median line, it is clear that the anterior slits must undergo a translation in growth which moves them up the right side. Now, if we look at the slits following No. 6, it appears as though a translation of these hinder slits were in progress, tending to bring them into position on the left side when fully formed. We do not, however, consider it likely that such a movement of the hinder slits to the animal's left side takes place, but believe that they also in due time move up firstly to the right side, alongside of those in front of them. We have found it impossible with our present material to trace the immediately subsequent history (subsequent to the stage drawn in figs. 4 and 6) of the gill-slits. We are of opinion that Kowalevsky's very definite statement and figures given in the 'Mémoires de l'Acad. Imp. de St. Pétersbourg,' 7th series, vol. xvi, No. 12, 1866, must be accepted. According to that account, after some dozen gill-slits have taken up their position on the animal's right side—having moved into that position from the median line—a new and startling change occurs. The whole series moves downwards across the median line and up the left side of the pharynx, so that the primitive right-side gill-slits become the left-side series; and in the meanwhile a new series corresponding in number make their appearance not one by one, but all together, in the right side of the pharynx, occupying, as it were, the position deserted by the rotated primitive series. This movement of growth appears to be a general one affecting the whole pharynx, for, simultaneously with the translation of the primitive gill-slits from right to left, the great larval mouth moves from its extraordinary position on the animal's left side, and, becoming relatively very much smaller, takes up its permanent position as an anterior median orifice whilst its hood and tentacles appear. We have not, we regret to say, at present been able to study any larvæ in which these remarkable changes are in progress. We have, however, many larvæ in which they are completed. It is noteworthy that these larvæ are scarcely, if at all, larger than that of Pl. XXIX, fig. 6; and yet they have the mouth reduced in size and nearly median in position, the anterior closure of the atrium completed, and a symmetrically placed right and left series of gill-slits.

We have taken steps to obtain the critical stages in the living condition during the present summer, and propose to ascertain whether the second row of gill-slits originates by any kind of fission from the first. If not, it is a curious fact that the morphologically median plane of the pharynx of the young larva becomes the left side of the adult, whilst the relations of the mouth to median plane, in adult and larva respectively, are even more curiously divergent. It is probable enough that in these differences the larva does not present the more archaic condition, but an adaptational arrangement. We do not at present know what are the conditions of life which render its excessive asymmetry advantageous to the larva.

The closure of the atrium by the growth of the little horizontal sub-atrial ridges from the median face of each metapleur is shown in the sections of various larvæ given in Pls. XXX, XXXI, XXXII.

In the drawings, figs. 4 and 6 of Pl. XXIX, we can trace the two metapleura in the still unenclosed region of the pharynx. The right-side metapleur is seen to have its free edge somewhat high on the animal's side, whilst the left metapleur in the perforated pharyngeal region is almost coincident with the median ventral line. (The reference line in fig. 4, Pl. XXIX, lettered "edge of left metapleur," has been by oversight carried up to the right metapleur. It should stop at the ventral line.) The right metapleur is larger and deeper than the left, which is barely traceable as a thickening of connective tissue, when its fellow of the opposite side is large and provided already with the characteristic lymph-space (see fig. 7, *r. met.* and *l. met.*, Pl. XXX).

The figures A, B, C, in Pl. XXX, represent diagrammatically three stages in the closure of the atrial tube, showing in A the metapleurs or metapleural ridges without any horizontal sub-atrial floor; in B the formation of this floor in the hinder region, where there are no gill-slits; and in C its continued formation so as to enclose the perforations of the pharynx. It must be pointed out that the sections are complicated and rendered a little difficult of interpretation at first, by the fact that the margins of the gill-slits are irregularly curved and folded, so that they cross the plane of section, and (as in fig. 7, Pl. XXX) the slit itself becomes divided in the section by a part of the projecting margin. A further modification in appearances is due to the greater or less opening of the gill-slits, which can be varied by muscular action during the life of the animal. The atrial tube or cavity is also found to vary in size and dimensions as soon as it is formed, owing to the varying extension or contraction of its muscular floor formed by the union of the sub-atrial ridges (compare fig. 12, Pl. XXX, and figs. 18 and 20, Pl. XXXII). As was pointed out by one of us in the case of adult Amphioxus distended with genital products (see Lankester, 'Quart. Journ. Micr. Sci.,' vol. xxix, Pl. XXXV, fig. 4), so here in the larva the atrium can be distended to such an extent as to practically obliterate the metapleural ridges and their lymphatic canals, which reappear when the distension ceases.

The description of the individual figures seriatim will be found, it is hoped, sufficiently explanatory of points which have not been specially mentioned in the general body of the memoir.

EXPLANATION OF PLATES XXIX—XXXII,

Illustrating Professor Lankester's and Mr. Willey's memoir on the "Development of the Atrial Chamber of Amphioxus."

PLATE XXIX.

FIGS. 1 and 2.—Right and left surface-views of larva, with four gill-slits. Length 1·496 mm.

FIG. 3.—Head of latter, seen with a deeper focus. Club-shaped gland open to exterior only.

FIGS. 4 and 5.—Right and left surface-views of larva, with fourteen gill-slits. Length 3·485 mm.

N.B.—In Fig. 4 the reference line belonging to the words "edge of left metapleur" has been carried too far, and touches the right metapleur. It should stop at the ventral line of the larva.

FIG. 6.—Head of latter, seen with a deeper focus. Club-shaped gland, open at both lower and upper extremities, externally and internally respectively.

PLATES XXX, XXXI, AND XXXII.

The *italics* in Plates XXX, XXXI, and XXXII have the significance given below.

ant. at. Anterior opening of atrium. *at.* Atrium. *at. p.* Atriopore. *br. e.* Modified intestinal epithelium bordering the gill-slits. *d. a.* Dorsal artery. *d. l. m.* Double-layered membrane, separating myocœl from splanchnocœl. *d. m.* Dorsal division of myocœl in connection with dorsal fin. *d. w.* Dorsal wall of atrium. *ext. a.* External aperture of club-shaped gland. *g. s.* Gill-slit. *Int.* Intestine. *Int. a.* Internal aperture of club-shaped gland. *kd.* Club-shaped gland. *l. a.* Left dorsal artery (unpaired). *l. m.* Lower lip of mouth. *l. met.* Left metapleur. *m.* Mouth. *m. e.* Modified epithelium on wall of mouth-cavity. *mus.* Muscle-plates. *my.* Primary myocœl. *my'.* Secondary upgrowth of myocœl, between the muscle-plates and notochord and nerve-cord. *n. c.* Nerve-cord. *nch.* Notochord. *neph.* Nephridium of Hatschek. *neph. a.* Opening of so-called nephridium into mouth-cavity. *o. h.* Commencing oral hood. *r. d.* Right embryonic diverticulum from the intestine. *r. c.* So-called "renal" cells of W. Müller. *r. met.* Right metapleur. *s. a. r.* Sub-atrial ridges or floor. *s. o.* Sense-organ (part of præoral pit). *som.* Somatopleur. *sp.* Splanchnocœl. *sp. p.* Splanchnopleur. *v. a.* Ventral vessel. *w. o.* Ciliated organ (of præoral pit).

General Remarks.

The intestinal epithelium is ciliated throughout. The epithelium bordering the gill-slits is much modified, being divided up into innumerable small cells, the cell-divisions between which cannot be seen under ordinary circumstances.

The nerve-cord consists of a nucleated portion surrounding the central canal and a peripheral fibrous portion.

Nuclei are to be seen in the notochord, and in the superior and inferior canals of the notochord.

There are nuclei in the muscle-plates, but, as Hatschek points out, there is no epithelium on the outer wall of the muscle-plates. The nuclei on the inner wall are sufficiently scanty.

The sense-organ and ciliated organ of the præoral pit are derived together from the left anterior diverticulum of the archenteron of the embryo, while the right diverticulum becomes simply the space occupying the anterior end of the body. It is included in Fig. 1, but not in Fig. 13.

A reference to the drawings of the whole animal in Pl. XXIX will show approximately through what regions the sections have been taken.

Figs. A, B, C.—Three diagrams of larvæ, seen from ventral aspect, to illustrate the origin and relation of the metapleural ridges to one another, and the gradual closure of the atrium from behind forwards.

Fig. A. No atrium.

Fig. B. Atrium behind pharynx.

Fig. C. First two gill-slits open to exterior, all the rest now open into the atrium.

Fig. 1.—Transverse section through the region of the ciliated organ and sense-organ of the præoral pit, just in front of the opening of the latter into the former. The anterior commencement of the splanchnocœl, and the posterior portion of the right embryonic diverticulum are shown. The epithelium of the præoral pit is of hypoblastic origin (Hatschek). This larva had twelve gill-slits, and no closed atrium. Preparation: osmic acid, borax car., followed by Meyer's carmine.

Fig. 2.—Transverse section through the commencement of the mouth-opening, showing the external aperture of the club-shaped or tubular gland. It also passes through the tract of modified epithelium. The very thin piece of epithelium, two thirds of the way up, is the cause of the clear space or line which gives a double appearance to the tract. The thickening of the right metapleur is tending to the right side. This larva had eleven slits. Preparation: sublimate and acetic; hæmatoxylin.

Figs. 3 and 4.—Portions of sections through another larva of same age, and prepared in same way as the last, taken just posterior to the region represented in Fig. 2, to show the opening of the nephridium of Hatschek into the mouth-cavity. Notice that the nephridium lies immediately below the left dorsal artery.

N.B.—In the larva there are not two dorsal arteries—right and left—in the pharyngeal region, as there are in the adult; but only one, and that on the left side of the notochord.

Fig. 5.—Section through first gill-slit of same larva, showing the club-shaped gland opening into the mouth-cavity at its upper extremity. The ventral vessel lies on the right wall of the intestine in the pharyngeal region. No cavity yet in the right metapleur.

Fig. 6.—Section through same larva as Fig. 1 (twelve gill-slits), through the same region as preceding, to be compared with Fig. 5 (with eleven gill-slits) where the mouth is half shut. In this case the mouth is wide open, and the appearance of the section is considerably altered owing to the expansion of the ventral portion of the cœlom. The right metapleur is more advanced, but still has no cavity in this region.

Fig. 7.—Section through the sixth gill-slit of the same larva. The double appearance of the slit is due to a fold in the wall of the slit. The right metapleur has a cavity here. The left metapleur has commenced as a thickening.

Fig. 8.—Section through twelfth and last gill-slit of same larva. The metapleural folds are nearly equal. There is a very small cavity in the right and none in the left fold.

Fig. 9.—Section through the post-pharyngeal region of a larva preserved with osmic acid vapour, rather older than Fig. 8, but with no part of the atrium floored in. The various divisions of the myocœl will be understood by a reference to Hatschek's figures, reproduced in Professor Lankester's paper in this Journal, vol. xxix, Pl. XXXVIa, figs. 6 and 7.

Fig. 10.—Section through the twelfth (last but one) slit of a larva of the age of that represented in Pl. XXIX, fig. 4. Preparation: concentrated sublimate; borax carmine.

Fig. 11.—Section through the post-pharyngeal region of the same larva (cf. Fig. 9), showing the fusion of the sub-atrial ridges. The character of the latter as ridges on the inner faces of the metapleura is not so well seen here as in other sections.

Fig. 12.—Section through the same region of another larva of the same age, showing the method of fusion of the sub-atrial ridges as described in the letterpress. Preparation: osmic acid and picro-carmine.

Fig. 13.—Section through the compound sense-organ (= præoral pit) of a larva in which all the gill-slits, except the first two, opened into a floored-in

atrium. It shows the sense-organ (*s. o.*) opening into the ciliated organ (*w. o.*), and the latter opening widely to the exterior. It also shows the independent origin of the oral hood (*o. h.*). Preparation: concentrated sublimate; borax carmine.

Fig. 14.—Section through the anterior opening of the atrium, in the same larva. It shows very well the position of the atrium anteriorly on the right side, also the sub-atrial ridges. Note the relatively huge size of the right metapleur, and the almost entire absence of any indication of the left metapleur; thus showing that the sub-atrial ridges are distinct structures from, and only secondarily dependent on, the metapleural folds; and that the latter serve a function (probably vascular) other than that of merely contributing to the formation of the atrium. This section is between the second and third gill-slits. The second slit opens to the exterior, the third opens into the atrium. The large cells at the bottom of the right metapleur are still in the epidermis; whereas, in fig. 7, Pl. XXX, they have migrated inwards.

Fig. 14 *a*.—Section through the same larva as the preceding, two or three sections farther back, showing a gill-slit (the third) opening into the laterally placed atrium.

Fig. 15.—Section between the tenth and eleventh slits of the same larva, showing an older condition of the atrium than that represented in Figs. 11 and 12, with "renal" cells on the dorsal wall. Note also the large size of the metapleura.

Fig. 16.—Section through the post-pharyngeal region of the same larva, showing a still more advanced condition of the atrium. The gelatinous subcutaneous tissue has disappeared from the dorsal wall of the atrium, leaving a thin double membrane, consisting of cœlomic and atrial epithelium (= somatopleur).

Fig. 17.—Section through the atriopore of same larva.

Fig. 18.—Section through the last gill-slit but two of a larva with the atrium floored in over three slits, showing expansion of atrium and temporary obliteration of metapleural spaces. Preparation: osmic acid and picrocarmine.

Figs. 19 and 20.—Sections through a larva in which the atrium had closed over two slits (the fourteenth and fifteenth), showing a narrow condition of the atrium in front (Fig. 19), followed by a more expanded condition behind (Fig. 20).

On the Structure of a New Genus of Oligochæta (Deodrilus), and on the Presence of Anal Nephridia in Acanthodrilus.

By

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With Plates XXXIII and XXXIIIa.

I. On the Structure of a New Genus of Oligochæta.

The present paper is based upon the study of only a single example of the worm. It was collected some years ago by Prof. Moseley in Ceylon, and was kindly entrusted to me for description by Prof. W. Hatchett Jackson.

The specimen measures thirteen inches in length by nearly half an inch in diameter at the broadest part (at the end of the 8th or 9th segment). Its intermediate characters lead me to suggest the generic name Deodrilus; the specific name I propose to associate with Mr. Jackson.

§ External Characters.

The prostomium is entirely absent, as it is in some other genera allied to the present.

The first or peristomial segment is traversed by longitudinally running grooves, which give it a characteristic appearance, often seen in worms when there is, as in this genus, no prostomium.[1]

The three following segments are of about equal antero-posterior diameter, though increasing rapidly in their breadth from side to side.

[1] Cf., for example, Beddard (1).

The 5th segment is the first which shows the commencing formation of annuli. A slight furrow crossing this segment partially divides it into two rings; the setæ are implanted just in front of this furrow.

The 6th ring is similar to the fifth, only that it is slightly longer.

The 7th ring is broader still, and is divided by two furrows into three annuli, the setæ being conspicuous upon the middle one of the three.

The 8th to the 14th segments are very broad, and each is divided by four furrows into five annuli, of which the middle one carries the setæ.

The 14th segment, though of equal diameter to those preceding it, has only three furrows; but there is an indication of the fourth.

The 15th and 16th have three annuli each.

After this point I cannot give accurate details, as the ridges which carry the male generative pores have introduced alterations into the annuli of the neighbouring segments.

Clitellum.—I am unable to map exactly the boundaries of the clitellum, as it did not appear to be fully developed.

On dissection, only two segments (15 and 16) showed a very marked difference in the structure of the body-wall from the others; here the deep yellow colour was very apparent, and was fully as well developed on the ventral as on the dorsal side.

The genital orifices, as already stated, are borne on two longitudinally running ridges, coinciding in position with the ventral series of setæ on each side.

These ridges, particularly in the immediate neighbourhood of the male pores, had a very glandular appearance. It is quite possible that the clitellum when fully developed extends as far as these ridges do.

In that case it may be stated provisionally that the clitellum extends over four segments (viz. 15—18).

It will be noted, however, that the clitellum differs in its anterior and posterior regions. The first two segments are entirely invaded by glandular substance, while the three posterior segments will in all probability be found to have a median area upon which there is no great modification of the epidermis. This area is of course bounded laterally by the genital ridges. It seems, therefore, that the clitellum of Deodrilus is constituted upon the same plan as that of Acanthodrilus.

Dr. Rosa has made some use, in his scheme of classification of earthworms, of the form of clitellum, which he terms saddle-shaped ("clitello a sello"), or complete ("cingulo completo"), admitting that Acanthodrilus offers an intermediate condition.

The fact is that it is not possible to classify the various modifications of the clitellum in this way.

There is a considerable series of gradations which renders it impossible to make a fixed demarcation between the different forms of clitellum. To commence at one extreme, we have species of Lumbricus and Allolobophora with a distinctively saddle-shaped clitellum: in these forms the glandular modified epidermis is only to be found on the dorsal and lateral regions of the clitellum; ventrally there is a wide space of equal diameter throughout, which has no trace of glandular tissue.

In such a form as Rhinodrilus Gulielmi the clitellum is divisible into two regions: in the last six segments of which it is composed the glandular substance is arranged quite as in Lumbricus; but in the first four the ventral area is encroached upon by the glandular tissue, though it is not completely invaded.

In Urochæta the clitellum is constituted in a way quite resembling that of Rhinodrilus, but the anterior bare ventral space appears if anything to be somewhat narrower.

In Deodrilus (which, as will be shown later, has points of affinity with Rhinodrilus) the anterior part of the clitellum is completely developed—extends all round the body—but the greater part is still only laterally developed.

Acanthodrilus has a clitellum in which the anterior portion is at least as great as, and may be greater than, the hinder portion, which still retains its saddle-shaped character.

Finally, we have such a form as Perionyx, in which the six or seven segments of the clitellum are completely occupied by the modified epidermis.[1]

Hence it appears to me to be inadvisable to use the characters of the clitellum to help in associating together, as Rosa has done, his families Lumbricidæ and Geoscolecidæ. The structure of Deodrilus shows that this cannot be done; and there are, among the Geoscolecidæ of Rosa, intermediate conditions leading to Deodrilus.

Genital Papillæ.—Most earthworms are furnished with genital papillæ, which are often very characteristic of the species in which they are found.

Deodrilus is not an exception to this rule, and has two sets of genital papillæ.

The first set consists of a single pair of large flattened papillæ, which are fused together to form a dumb-bell shaped area extremely conspicuous. The outer convex border on each side reaches to the level of the inner setæ of the outer pair.

The papillæ (see Pl. XXXIII, fig. 12, *p*) are situated between the 11th and 12th segments; they occupy the last annulus of the former segment and the first two annuli of the latter: the furrows dividing the annuli and the two segments from each other can be seen as faint lines traversing the papillæ. The furrow separating the last annulus of Segment 11 from the penultimate forms the anterior boundary of the papillæ, while its posterior boundary is formed by the furrow separating the second from the third annulus of Segment 12. The second set of genital papillæ are very much less conspicuous; they are to be found near the male genital pores, and no doubt correspond to the tubercula pubertatis: in front of each of the male orifices are two papillæ—one in front of the other; and behind each is a single papilla. So far as I can ascertain, they belong to Segments 17, 18, and 19; but, as I have already said, it is difficult to be certain about the limits of the segments in this region of the body.

Setæ.—The setæ are entirely restricted to the ventral surface of the body, where they are implanted in pairs.

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[1] I do not for the present consider how far the form of the clitellum may be influenced by the position of the generative pores.

On the 8th segment I found that the distance separating the two ventral pairs from one another was $2\frac{1}{2}$ mm.; the lateral pairs were separated by a dorsal area measuring 14 mm. The shape of the setæ is very remarkable, and is illustrated in fig. 18. Their general outline is similar to that of the setæ of other earthworms, but instead of terminating in a hooked extremity they present a truncated appearance, which will be understood by a reference to the figure cited. It occurred to me, when first observing the setæ attached to fragments of stripped-off cuticle, that they might be of the normal form, but with their extremities broken off. It frequently happens, as a result of rough usage, that the majority of the setæ, or at any rate a large number, are broken off short; but it is evident that that is not what has happened in the present case. The free extremity of the setæ showed no signs of having undergone any fracture; and, moreover, the shape of the freely projecting extremity is not such as would be produced by a fracture, or wear and tear.

The setæ illustrated in fig. 18 are drawn as seen on a lateral view; *a* and *b* represent the free extremities of such setæ more highly magnified.

Another peculiarity in the structure of the setæ is the fact that their distal region, i.e. that part which lies external to the slight swelling in the middle of the setæ, is ornamented by minute pointed processes.

The description just given, and the figures which illustrate it, refer to setæ from the first ten segments or so; but I have ascertained that the setæ in the posterior segments are absolutely identical in size and structure with those from the anterior segments.

The first five segments of the body are entirely deprived of setæ; a microscopic examination of these segments did not enable me to find any trace of the presence of setæ.

The disappearance of the setæ from the first few segments of Deodrilus, and of the species of Diachæta which I described recently in this Journal (1), is a remarkable fact. No other instances are at present known among earthworms, though possibly Microchæta Rappi may prove to be one; at any rate, it is excessively difficult to recognise the setæ upon the first few segments; I have not myself been able to find them at all. They are, however, figured by Benham (**11**, pl. xv, fig. 1); but he makes no definite statement as to their presence on the first two or three segments. Leaving Microchæta aside, the absence of setæ on the anterior segments is correlated with the entire absence of a prostomium. Not a vestige of this structure could be recognised in either of the two forms mentioned. This correlation, however, is not universal, for Urochæta has no prostomium, and yet the setæ are visible, as usual, from Segment 2 onwards. It is furthermore noticeable that in Diachæta Windlei the anterior non-setigerous segments show another modification in the presence of the specialised bundle of transversely running muscular fibres, which I have figured and described as occurring in the segments beginning with the 6th.

In most earthworms the first or peristomial segment is so far unlike the rest that it is grooved longitudinally, and that its epidermis is not clearly distinguishable into two classes of cells, or at least is not so clearly distinguishable as is the epidermis of the following segments. Sometimes this modification appears to affect the 2nd as well as the 1st segment.

In connection with this modification the varying position of the prostomium may be pointed out. Sometimes the prostomium is attached to the anterior border of Segment 1; in other species it encroaches upon this segment, and finally it often completely divides the 1st segment, and reaches the anterior border of the 2nd.

Earthworms, in moving along, use the mouth as a kind of sucker, even protruding a portion of the buccal cavity; this is remarkably the case with Perichæta indica (**3**), which everts what appears to be the whole of the buccal cavity at each movement. Conversely, there is often a temporary withdrawal of the peristomial segment into the mouth-cavity. These two phenomena appear to have led to the different enumeration of the segments of Urochæta adopted by Perrier

(13), Horst (12), and Rosa (10). As the latter has pointed out, Perrier appears to have described a specimen in which the buccal cavity was partly everted; while Horst, in stating that the mucous gland opened on to the first segment of the body, was deceived by the introversion of the peristomial segment.

Among the half-dozen series of longitudinal sections of Urochæta corethrura which I possess there is one in which the 1st and a portion of the 2nd segment are introverted, and the mucous gland appears, therefore, to open into the buccal cavity; in fact, it actually does open into a temporary extension of the buccal cavity.

It is, in my opinion, possible to believe that a temporary introversion, such as that to which I have just referred, may become permanent. In this case what will happen are two events of importance. In the first place the body will be shortened by one segment; in the second place the "mucous gland" will come to open into the anterior section of the alimentary tract.

As to the second point, I may call attention to the remarkable condition of the anterior nephridia in Acanthodrilus multiporus (4). In that worm the anterior segments are occupied by a mass of glandular tubes, clearly of nephridial nature, on each side of the pharynx. Each mass communicates with a long duct, which opens into the buccal cavity. It seems impossible to doubt that the nephridial masses of this Acanthodrilus originally opened on to the exterior, and that their connection with the buccal cavity is only secondary. That this "secondary" connection may be really the original point of opening, masked by the partial or entire introversion of the 1st segment, is surely not incredible.

With regard to the first point, the possible shortening of the body in this way involves really no serious difficulty, though it seems, of course, rather ridiculous to gravely assert that a worm becomes shorter by swallowing its own head. The structure of the epidermis of the 1st segment is more like that of the buccal cavity than it is like that of the succeeding segments.

These remarks, however, apply more particularly to such worms as Diachæta and Deodrilus, in which there is no prostomium, and in which, therefore, such an inversion will cause no external change of importance.

In worms which have a prostomium this structure may be prolonged backwards, so as to commence as an outgrowth of the 2nd segment; if, in such a case, the peristomial segment were permanently invaginated the prostomium would be left attached to the 1st segment of the body, i. e. in the more usual position; on the other hand, a permanent eversion of the commencement of the buccal cavity in a worm in which the prostomium arises from the anterior margin of the peristomial segment would lead to the apparent prolongation of the prostomium back to the 2nd segment.

§ Reproductive Organs.

I have not found the testes nor the ovaries and oviducts. Two pairs of sperm-sacs were to be seen attached to the anterior wall of the 10th and 11th segments; these organs are racemose in form, as in so many genera.

The vas deferens funnels appear also to be limited to a single pair, which open into the 11th segment.

The atrium, or prostate gland, is a compact flattened body on each side of the body connected by a short muscular duct with the male pore; it lies in the 18th segment. The atrium appears to be branched, and to resemble the same organ in Perichæta.

Connected also with the male reproductive apertures is on either side a thin-walled sac filled with penial setæ. Two of these setæ are shown in figs. 15, 16; it will be seen from an inspection of those figures that the form of the two setæ selected for illustration differs very considerably. In one the distal extremity is covered with numerous minute points like those which cover the distal half of the ordinary seta. In the other seta these points are entirely absent, and fine wavy lines are found on the distal part of the seta, ceasing, however, some little way in front of the extremity.

I call particular attention to the fact that two such different forms of penial setæ are met with in the same individual, inasmuch as these setæ have been made use of by myself and others as specific characters. I may recall the fact that in Acanthodrilus Georgianus (5) there is an analogous dimorphism of the penial setæ.

§ The Intersegmental Septa.

As is so constantly the case among earthworms, certain of the intersegmental septa are specially thickened, as well as connected with each other and with the parietes by muscular bands.

In the present species the septa between Segments 6 and 13 are thus strengthened, there being, therefore, seven. As in other cases, these septa are very concave forwards, the middle region lying much behind the peripheral attached margin; the septa present, therefore, have the appearance of a series of cups, each fitting within the one which follows it.

§ Alimentary Canal.

The gizzard lies in Segment 6 (cf. fig. 14).

The œsophagus extends as far back as Segment 18; it does not, however, abruptly widen into the intestine, which only commences (fig. 13) in the 20th segment.

In Segments 15, 16, and 17 are three pairs of calciferous glands. As shown in the figure (fig. 13), each of these glands is divided into two by a transverse furrow.

§ Nephridia.

The worm was not in a sufficiently good state of preservation to allow of any observations upon the minute structure of the nephridia.

So far as could be ascertained by dissection, the nephridia throughout the body appear to be of the "diffuse" type.

Lying alongside of the pharynx on each side was a conspicuous glandular body, which is doubtless similar to the salivary gland of Acanthodrilus multiporus, and to the "mucous" gland of Urochæta, Diachæta, &c.

§ Affinities of Deodrilus.

The question of the systematic position of this Annelid necessitates some review of recent attempts to classify the group. As, however, I intend to publish an attempt at the classification of these Annelids with a criticism of existing schemes, I shall make my references as brief as possible.

Deodrilus evidently belongs to the "Intraclitellian" group of Perrier (**13**) ; but as Perrier's scheme—undoubtedly a great advance upon what had gone before—is not now generally accepted, I shall not urge any reasons why Deodrilus does not fall in with that classificatory attempt.

The most recent schemes are those of Rosa (**9**) and Vaillant (**14**).[1] Rosa has divided earthworms into six families—Lumbricidæ, Geoscolecidæ, ? Moniligastridæ, Acanthodrilidæ, Eudrilidæ, Perichætidæ.

It is only with the second and fifth of these families that Deodrilus can have any connection.

These families are defined by Rosa as follows.

GEOSCOLECIDÆ.

(1) Male pores within the clitellum between the dorsal and ventral setæ, occupying segments or intersegmental grooves which are very variable.

(2) Clitellum generally saddle-shaped; length and position variable.

(3) Setæ eight per segment, in pairs or singly, or diversely arranged in the anterior and posterior segments.

(4) Copulatory setæ longer than the others and of a different form.

(5) Gizzard (or gizzards) placed anteriorly.

(6) Sperm-sacs one or two pairs.

(7) No prostates or penial setæ.

[1] Since writing the above I have received through the kindness of the author Mr. Benham's "An Attempt to Classify Earthworms," 'Quart. Journ. Micr. Sci.,' vol. xxxi, pp. 201—315.

EUDRILIDÆ.[1]

(1) Male pores one pair, on Segment 17 or 18, within or behind the clitellum, corresponding to the ventral setæ.

(2) Clitellum complete, occupying generally Segments 13 (14) – 16 (18) = 3—6.

(3) Setæ eight, paired or singly, but always parallel.

(5) Gizzard (or gizzards[2]) anterior in position.

(6) Sperm-sacs generally two pairs.

(7) Prostate and penial setæ present.

The only characters, therefore, which are decisive are (1), (2), and (7).

Deodrilus agrees with the Eudrilidæ in (1) and (7), and it is intermediate between the two in (2).

But there are other facts in its structure which signify that it combines the characteristics of genera which have been included in the Geoscolecidæ and in the Eudrilidæ. The absence of a prostomium is characteristic of certain genera of Geoscolecidæ—Urochæta and Diachæta. It is true that Typhæus, which Rosa refers to the Eudrilidæ, has no prostomium;[3] but it must be remembered that this genus agrees with Urochæta, Geoscolex, and Diachæta in having a single pair of long tongue-shaped sperm-sacs, and only a single pair of sperm-ducts.

In the absence of setæ from the first few segments Deodrilus resembles a species of Diachæta, of which a description has appeared in a recent number of this Journal (1).

Typhæus appears to have no setæ upon the first two segments, but, as stated in my paper upon that worm (6), I am not absolutely certain of the fact.

The presence of ornamented setæ affines Deodrilus to Rhinodrilus; nothing of the kind is met with in any of Rosa's Eudrilidæ.

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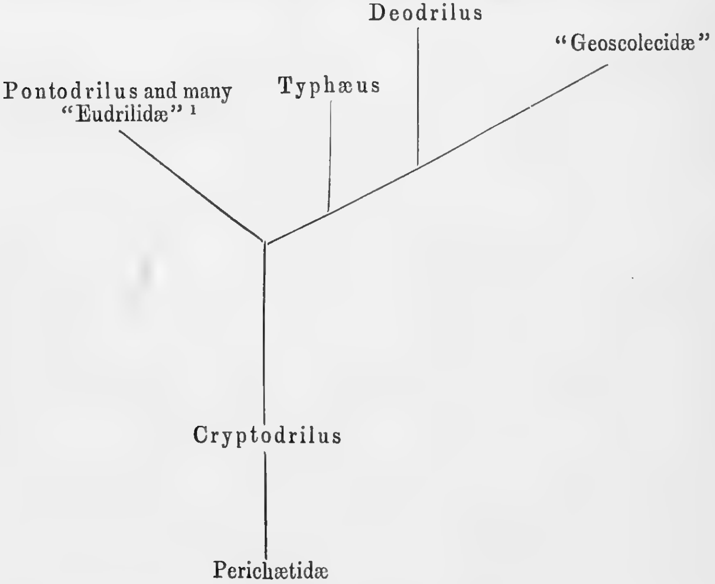
[1] I may remark that *Eudrilus* itself does not agree with this definition in all characters.

[2] I add "gizzards" myself, so as to include Perissogaster, &c.

[3] Loc. cit., p. 111. This statement requires confirmation, since Bourne has lately described a prostomium in Typhæus Masoni.

The diffuse nephridial system has not yet been met with in any of the Geoscolecidæ; in this particular, therefore, as in the presence of prostates and penial setæ, Deodrilus resembles certain genera (e. g. Cryptodrilus) of the Eudrilidæ. Finally, the absence of diverticula to the spermathecæ brings Deodrilus into relations with the Geoscolecidæ. It seems to me that the relationship of Deodrilus to some other forms is best expressed by the following diagram:



Genus—Deodrilus.

Setæ arranged in pairs upon the ventral surface, peculiar in shape, and ornamented. Absent upon the first four segments.

Prostomium absent.

Clitellum occupying Segments 15—18 (or thereabouts), complete anteriorly, saddle-shaped posteriorly.

Gizzard in Segment 6.

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[1] I do not for the present particularise the exact limits which I apply to these families.

Sperm-sacs, two pairs, in 10, 11, racemose.

Nephridia diffuse, a mass of tubules in the neighbourhood of the pharynx aggregated into a compact gland.

Atria lobate, each with a sac of penial setæ opening on to Segment 18.

Species—D. Jacksoni.[1]

Large worm, measuring 13 inches.

Copulatory papillæ forming a dumb-bell shaped area between Segments 11 and 12.

Penial setæ of two kinds, one ornamented by minute protuberances, the other transversely striate.

Two pairs of spermathecæ, without diverticula, in Segments 8 and 9 (see fig. 19).

II. Anal Nephridia in Acanthodrilus.

I have already (7) described some of the anatomical and histological characters of the nephridia in Acanthodrilus; their organs are in some species (e. g. in A. multiporus) represented by irregular tufts, which are furnished with numerous funnels, and numerous external orifices in each segment.

I have now to describe a connection of the nephridia with the terminal region of the intestine, which occurs in a species referable, I believe, to my Acanthodrilus multiporus.

The material I owe to the kindness of Mr. W. W. Smith, of Ashburton, New Zealand.

In fig. 1 of Pl. XXXIII, is represented half of a portion of the posterior end of the body of one of these worms, comprising about thirty segments. The body was divided by a cut at right angles to the dorso-ventral axis; the intestinal canal is laid open, and the typhlosole is seen to occupy the dorsal line of the intestine. The figure is twice the size of nature.

The typhlosole ends abruptly about an inch in front of the anus; a faint streak is, however, recognisable, extending for perhaps a quarter of an inch beyond the end of the typhlosole.

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[1] Named after Mr. W. Hatchett Jackson.

The part of the alimentary tract lying behind the typhlosole is thus sharply marked off, and the distinction between it and the terminal section is possibly an important one; I should be inclined to regard the "rectum" as being proctodæum. The diameter of the rectum, as shown in the figure, gradually narrows to the anus; its walls are marked by longitudinally running furrows.

In transverse sections the gut is seen to be lined by an epithelium of tall columnar cells, broader towards their extremities and narrower at their attachment. The folds observable (fig. 5) in such sections are, of course, due to the longitudinally running furrows. Outside the epithelium is a circular coat of muscular fibres, and outside this again longitudinal fibres; these latter do not form at all a thick layer, and they are partly interspersed among the meshes of a peculiar form of connective tissue which extends beyond them, and forms the outermost wall of the intestine. This connective-tissue layer is also found beneath the epithelium; in parts it consists of a meshwork of fine fibres with nuclei present, chiefly at the nodal points; in other parts the meshwork becomes very wide, and the tissue presents the appearance of a fenestrated membrane; the fenestræ are, relatively speaking, small, and the tissue lying between them is somewhat gelatinous in appearance, with fine fibrils passing through it (fig. 3); nuclei are present, which are frequently attached closely to the fenestræ, bulging out into these latter as depicted in fig. 3.

At the extreme end of the body these layers are not so conspicuous, owing to the crowding together of the last two or three of the intersegmental septa, and the continuity of these with the intestine.

The cœlomic space, on the ventral side of the body at any rate, is almost filled with the nephridia, which form two principal masses, one on each side of the nerve-cord. In a single section several funnels can be seen connected with the nephridia, and their ducts can be observed to perforate the body-walls, and to open on to the exterior by many pores.

In such sections the outer connective-tissue coat of the intestine may be observed to include numerous tubules cut across in various directions (fig. 5, *n*), indicating therefore a somewhat tortuous course; these tubules appear, in sections taken between two successive septa, to have no relation whatever with the nephridial tufts that have been already mentioned as occupying the cœlom. And yet they are clearly nephridial in their nature.

Fig. 5 represents a slightly magnified section through a portion of the intestine, showing the general appearance of these tubes.

Fig. 4 is a portion of the same more highly magnified, and drawn with the help of the camera lucida.

From this drawing it may be seen that the structure of the tubes is precisely that of the nephridia, although they are for the most part considerably wider. Their walls are granular, with large nuclei interspersed here and there, showing the lumen of the tube to be intra-cellular.

In the section figured a smaller tubule is seen to project into the lumen of the larger tubule, and another small tubule seen in transverse section lies entirely within the larger tubule.

This telescoping of one tube within another at once recalls the peculiar structure of the leech's nephridium, made known by the investigations of Bourne (**15**) and others. The difference is that in the leech the inner tube is closely invested by the outer, while in the earthworm there is a wide space between the two.

These nephridial tubes, which appear to be so curiously cut off from the general nephridial system, are in reality not so cut off. A series of sections shows that they become continuous with the general nephridial network at the septa; at any rate their branches pass along the septa, and can be traced into the nephridial tufts: these branches are of the same calibre as those of the general nephridial system.

Traced in the other direction, these nephridial tubes may be followed through the lining epithelium of the gut, into the lumen, which they open.

The wide tubes with an intra-cellular lumen become gradually crowded with nuclei,[1] though the boundaries between the individual cells are not to be discerned in my preparations; the lumen, however, is here clearly intercellular, the individual cells being apparently more or less cubical in form. The nuclei are quite similar to those of the portion of the nephridium with an intra-cellular lumen. The tube then bends up towards the epithelium of the gut, and its lumen becomes much contracted, owing to the great increase in the size of the cells which form its walls. In this region of the nephridium the cells are quite indistinguishable from those which form the lining membrane of the rectum.

It seems, therefore, probable that the diverticula of the intestine were developed as diverticula, and that the nephridia afterwards acquired a connection with them, just as the external portion of nephridia opening on to the surface of the body is developed from a separate epiblastic involution.[2]

In the absence of embryological data, I cannot do more than regard as highly probable the suggestion made above concerning the morphological nature of the rectum. The rectum is much more likely to be proctodæum than hypoblastic in origin. If this is not the case, then the facts recorded in this paper have an obvious bearing upon Lang's views (**17**) of the hypoblastic origin of the nephridia. I should, however, prefer for the present to consider the terminal section of the gut, into which the nephridia open, to be epiblastic in origin.

So far as I am aware, there has been no description of nephridia connected with the rectum in any other Chætopod.

The nearest group in which anything of the kind occurs is the Gephyrea; in Bonellia, and other forms belonging to the

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[1] Such a fact as this appears to me to show that the morphological distinction which some have attempted to draw between nephridia with intra-cellular lumen and intercellular lumen, e. g. between those of Oligochæta and Polychæta, cannot be maintained.

[2] Bergh (**16**) has, however, denied that this is the case in Criodrilus; according to him the nephridium is entirely mesoblastic, and bores its way to the exterior.

Gephyrea Chætifera, we have the branched "respiratory trees," whose structure appears to show that they are nephridial in nature; even in Sipunculus, two rudimentary diverticula attached to the intestine close to the anus may be homologous structures. It is true that some observers, such as Greef and Spengel, have denied that the anal glands of the Gephyrea are to be compared to nephridia; but the view of the former was based, partly at least, upon a misunderstanding of these organs.

There is no regularity that I could detect in the position of the apertures of these tubes; sometimes two could be observed quite close together, at other times an interval separated two adjacent apertures. One point of importance with regard to the position of the apertures is their limitation to three segments; whether the most anterior of these three segments marks the commencement of the proctodæum or not I am unable to say. Behind the last of the three segments in which they occur the limitations of the individual segments were obscured; they begin, therefore, in the last properly developed segment. It is well known that earthworms increase in length by the formation of new segments at the posterior end of the body; it is possible that, as the body increases in length, more of these proctodæal nephridia are developed.[1] In fig. 6 is illustrated the greater part of a single nephridial tube; but it by no means always happens that a tube has so long a course without branching. Very often I have noticed such a tube to divide into two shortly before its opening.

It has been already mentioned that the nephridia which open into the proctodæum communicate with the general nephridial system only at the septa. As may be seen in suitable sections, the surfaces of the septa are covered by innumerable tubes, which anastomose in every direction to form most complicated networks. I have never yet been able to show by a satisfactory preparation the actual form of the network in Perichæta or Acanthodrilus, or in any other form where a network must exist. Spencer (**18**) has figured

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[1] In another specimen I found these nephridia opening into the gut, in the last seven segments at least.

the network of Megascolides, but in quite a diagrammatic way. I think, however, that the figure which I now give (fig. 7) of the network in Acanthodrilus is sufficient to convince anyone of the reality of its existence. Usually the network exhibited the characters shown in that figure; that is to say, the individuality of the several tubes was quite distinct in spite of their anastomoses in every direction and at such frequent intervals. Very often, however, the network exhibited the appearance shown in fig. 2; here it will be observed that the tubes are in very close approximation, so much so that the mass formed by their fusion presents the appearance of an irregular system of lacunæ enclosed within a definite wall. This character, it is perhaps worth remarking, belongs to the nephridia of several invertebrate groups.

In describing the nephridia of Acanthodrilus I stated that the tufts of successive segments were isolated from one another; this is, however, as shown in fig. 9, not always the case. In that figure, which represents a longitudinal section, it will be seen that the nephridia which pass up the septa do not always open at once into the lumen of the gut, but apparently become connected with nephridial tubes derived from other segments, and course along the walls of the gut; a communication is thus established between the nephridial networks of a number of segments. In fig. 8 is illustrated a portion of one of the septa which is invaded by the nephridial tubes on their way to the intestinal walls: it will be seen that in such places hardly any traces are left of the muscles of the septum; the septum appears to be entirely built up of a mass of frequently anastomosing nephridial tubes.

I have not yet examined a large series of earthworms with diffuse nephridia, with a view of finding out whether anal nephridia are present in other species. I believe, however, that they are not present in A. antarcticus—a near relative of A. multiporus.

It is of importance to find undoubted nephridia in a comparatively low type of Chætopod opening into the anal section of the intestine. Such a discovery strengthens the current opinion that the respiratory trees of Bonellia are really of nephridial nature.

A remarkable fact about these nephridia in Acanthodrilus is the swollen terminal portion, which is lined by cells, and which has the characters (fig. 10) of a diverticulum of the gut. I have distinguished between the terminal section, which opens into the intestine and is lined with an epithelium, identical, so far as I can see, with the epithelium of the intestine, and the next section, the cells of which are rather different. If the nephridial tubes connecting this with the general nephridial system were to disappear, we should have the gut furnished with a series of tubular outgrowths ending bluntly. This is exactly what we meet with in the Tracheata, and even in some Crustacea—the Malpighian tubes; these structures have been compared with nephridia, particularly with the anal nephridia of the Gephyrea. It appears that the Malpighian tubes of Arthropods are formed by outgrowths of the proctodæum,[1] though in the Amphipods Spencer is inclined to regard them as appendages of the mid-gut. It is at least possible that we may trace the Malpighian tubes of Arthropods to these gut diverticula. Seeing how widely spread the Malpighian tubes are among Arthropods, it is not unreasonable to seek for their homologues in lower groups; and the Chætopods are the nearest group to which we can trace the Arthropods. It is true that Peripatus, which appears to stand somewhere near the base of the Tracheate series, has no Malpighian tubes; this seems to imply a great break between the anal nephridia of worms and the Malpighian tubes. It must be remembered, however, that Peripatus is furnished with paired nephridia, which structures are wanting in the Tracheata. Hence, there might possibly be no need for the extra nephridia opening into the extremity of the gut; the ordinary nephridia being absent

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[1] Recently Mr. Wheeler (19) has shown that in Doryphora decemlineata the Malpighian tubes, when first formed, open on to the exterior; they are subsequently drawn in along with the proctodæal invagination of the ectoderm.

in the Tracheata, they have been functionally replaced by the somewhat metamorphosed equivalent of the anal nephridia.

It must be admitted, however, that more facts are required before the above remarks can be considered as anything more than a suggestion.

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DESCRIPTION OF PLATES XXXIII AND XXXIIIA,

Illustrating Mr. Frank E. Beddard's paper "On the Structure of a New Genus of Oligochæta (Deodrilus), and on the Presence of Anal Nephridia in Acanthodrilus."

Figs. 1—11.—Acanthodrilus multiporus and nephridia.

Fig. 1. Dorsal half of the posterior twenty or thirty segments of Acanthodrilus multiporus, enlarged to twice the natural size.

Fig. 2. Part of a network of nephridia. The fusion of the tubules is so complete as to produce the impression of a system of lacunar spaces.

Fig. 3. Connective tissue from outer coat of rectum. *n.* Nuclei. *v.* Spaces.

Fig. 4. A portion of connective-tissue sheath of rectum, with contained nephridial tubes. *m.* Muscular fibres. *v.* Spaces. *bl.* Blood-vessels. *n.* Small tubule apparently contained in a larger one.

Fig. 5. Part of a transverse section through rectum. *ep.* Lining epithelium. *n.* Nephridial tubules in connective-tissue sheath.

Fig. 6. Part of Fig. 5, more highly magnified to illustrate structure of different regions of anal nephridia, *N.*, *N'n.*

Fig. 7. Network of tubules lying in and upon septum. *a.* Muscular fibre. *n.* Walls of nephridium.

Fig. 8. Mass of tubules passing up septa, the relations of which are shown in Fig. 9. *bl.* Blood-vessels. *a, b, c, d.* Nephridial tubes.

Fig. 9. Longitudinal section through a portion of rectal wall. *o.* Orifice of anal nephridium. *sp.* Intersegmental septum.

Fig. 10. Section through point quite close to opening of nephridium into rectum. *N.* Nephridium. *E.* Epithelium of rectum continuous with nephridium.

Fig. 11. Diagrammatic transverse section of a portion of posterior extremity of body, to show relations of anal nephridia. *n.* Their rectal orifices. *o.* External orifices. *f.* Funnels.

FIGS. 12—14.—Deodrilus.

Fig. 12. Ventral view of anterior segments. VI. Sixth segment, the first setigerous segment. *p.* Genital papilla between Segments 11/12. *cli.* Clitellum. ♂ sperm-duct orifice on 18th segment.

Fig. 13. Dissection of a portion of the body, to show the position and appearance of the calciferous glands, *ca.* *d.* Dorsal vessel. *œ.* Œsophagus.

Fig. 14. Diagrammatic longitudinal section, to show position of various parts of the alimentary tract. *g.* Gizzard. *ca.* Calciferous glands. The roman numerals refer to the segments.

PLATE XXXIIIA.

Deodrilus.

Figs. 15, 16. Penial seta, with chitinous sheath.

Fig. 17. One of the pairs of hearts (*h.*), with their connection with the dorsal (*d.*) and ventral (*v.*) vessel. *œs.* Œsophagus.

Fig. 18. Setæ of body.

Fig. 19. Two segments dissected to show spermatheca ($Sp.^1$, $Sp.^2$). *n.* Nerve-cord. *v.* Ventral blood-vessel. *l.* Lateral blood-vessel. *o.* Orifice of spermatheca. *m.* Intersegmental septum.

Excretory Tubules in Amphioxus lanceolatus.

By

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With Plates XXXIV and XXXV.

In the spring of last year, through the kind permission of the British Association for the Advancement of Science, I had the privilege of occupying the table which the Association supports at the Zoological Station in Naples. By the admirable arrangements made at this station I was able to have a constant and unlimited supply of living specimens of Amphioxus lanceolatus, and thought this a good opportunity to undertake some experiments with a view to ascertaining whether the curious patches of modified epithelial cells on the ventral wall of the atrium of Amphioxus had any excretory function, as Johannes Müller (1) had held probable; and whether also the atrio-cœlomic funnels first described by Professor Ray Lankester (2) in 187~~4~~5, and again more recently (3), had any such function.

Feeding experiments were made with Indian ink, carmine, and Bismarck brown, the carmine alone leading to good results, as the Indian ink is not able to be distinguished in the pigmented cells of the atrial cavity; and the Bismarck brown, though colouring the excreting cells very readily and deeply, penetrated also into many other cells.

Carmine is only very slightly soluble in sea water, but when well ground up in a mortar it remains suspended in granules sufficiently small to be taken up by the intestinal cells of the

Amphioxus. I found it most expedient to leave the Amphioxi in water thickly clouded with carmine, through which a constant current of air was passed. As a further precaution I changed the whole of the water every day, adding fresh carmine as before. In this way I was able to keep the Amphioxi for weeks together, and they seemed to remain as healthy as those kept in running water. The current of air which was passed through the water had the secondary but useful action of preventing the carmine granules from settling down, and this ensured a constant inhalation by the Amphioxi of carmine-laden water. Such a current seems to have no irritating action on these animals. I have been able by the aid of a syringe to pass sea water very highly charged with carmine through individuals, which were at the time in quite clear water, without their seeming to notice it, certainly without their closing their mouth for an instant, which they do immediately anything obnoxious to them is brought into their neighbourhood.

After a day or two the Amphioxi will have taken up a considerable amount of carmine in its very finest granules into the cells of the intestine, and their fæces are made up almost entirely of the coarser granules which could not be incepted by the cells.

From the intestinal epithelium the carmine is passed into the intestinal blood-vessels, which seem charged with corpuscles (lymph-cells ?).

Amphioxi which are kept longer still in carmine take up a considerable amount of it into their vascular system, so that I was enabled to follow out some of the blood-vessels, which are otherwise very difficult to make out.

The intestinal vessels join anteriorly to form a single vessel (Pfortader of Müller [1]; Darmvene of Schneider [4]), which, as Professor Lankester rightly states, is continued into the endostylar or cardiac subpharyngeal trunk, though Müller asserted that it ended at the commencement of the cæcum.

In each gill bar, whether primary or secondary (tongue bar), there are two blood-vessels, one running on the inner side of the bar, and communicating, as is seen from fig. 4, with the dorsal aorta. This vessel then separates either entirely into two parallel trunks, or is only constricted medianly, so that we find one vessel running below the median inner epithelial band, and the other one on the inner face of the chitinoid rod, as figured by Professor Lankester. In the case of the secondary or tongue bars carmine is found also within the hollow of the chitinoid rod, so that I think Schneider's conception of this space as a blood-vessel connected with the one running along the inner surface of the rod is probably correct. A very small vessel seems to run on the outer edge of the chitinoid rod. It would seem to be connected with the blood-vessel running beneath the excreting tubule in fig. 1, and being like those in the suspensory folds connected with the excretory function of the atrial epithelium. The two dorsal aortæ are either connected at intervals by very fine vessels, or else each gives off branches which run beneath the epithelium of the dorsal groove of the pharynx.

Besides these branches of the aortæ I was able to confirm Schneider's statement that branches are given off to the muscles of the body, passing up by the side of the notochord, and other branches to the inner face of the body-wall. These latter branches run beneath the cœlomic epithelium, and more ventrally beneath the atrial epithelium; they connect the dorsal aorta with a longitudinal vessel described by Müller as running on the inner body-wall above the gonads.

Indeed, the whole inner surface of the atrium seems very well supplied with blood-vessels running beneath the atrial epithelium, and in the case of these modified epithelial cells, described by Müller as possibly renal organs, diverticula are formed by the blood-vessel between the cells (fig. 6).

Along the inner lamella of cutis, too, of the ventral atrial wall I found a considerable amount of carmine in what I conclude must be a blood-vessel or a vascular space. I have not here given a general account of the vascular system of Amphioxus, but have confirmed statements by various observers, statements which Professor Lankester in his last memoir has cited as wanting confirmation. I feel sure, however, that much that is new might be made out by careful investigation of Amphioxi fed with carmine as above described.

The cœlomic cavities were singularly free of carmine, so that it would seem as if the vascular system were more distinctly separated from the cœlomic system than has hitherto been supposed.

In the metapleural lymph-spaces, however, I constantly came across cells containing carmine, though not to any very considerable extent.

My object, however, being to trace the carmine to the excretory organs, I found it best to examine specimens in which the carmine was already disappearing from the vascular system. After a week or a fortnight Amphioxi kept in the carmine-containing water would have assumed a quite definite pink coloration, and I then transferred them into a tank with running water, where they gradually became paler. Amphioxi thus treated gave the best results for the purposes I had in view.

As already mentioned, the patches of modified epithelial cells on the ventral wall of the atrium have a very definite blood-supply, of the nature of a subepithelial blood-space with short blood-vessels running up between the cells (fig. 6), and when the vessels were well coloured I found also carmine granules in these cells. In many cases they were not readily distinguished on account of the deep-coloured granules contained in the cells, and only in specimens which were very slightly pigmented could these carmine granules be unmistakably seen. This pigmentation of the atrial epithelium prevented my ascertaining whether excretion takes place to any great extent over its entire surface, or whether it is confined to the specialised portion described by Müller. It was this same circumstance which prevented me from obtaining any positive results from examination of the atrio-cœlomic funnels described by Professor Lankester. They are applied, as shown in Professor Lankester's drawings, to the wall of the dorso-pharyngeal cœlom, along which wall, as I have stated before, we find well-marked blood-vessels. This fact lends further support to the very justifiable view that they may have an excretory function.

A further set of modified atrial epithelial cells are those which cover the outer portion of the gill bars. These are columnar in shape, with a large nucleus near the base, and generally a considerable amount of granules at the opposite end. Definite pigment granules are found only in one or two cells where the epithelium of the alimentary tract borders on the atrial epithelium.

In the specimens fed with carmine the atrial epithelial cells of the secondary or tongue bars all showed carmine granules. In the primary bars I was unable to distinguish any carmine. This fact is, I think, to be explained by the circumstance that in the secondary bars the blood-vessel, which I described as running along the outside of the chitinoid rod, lies immediately beneath the atrial epithelium, while in the primary bars of course it lies beneath the cœlomic epithelium, and only very fine ramifications, if any, would pass round to the atrial epithelium.

On staining sections, and also in feeding living individuals with Bismarck brown, the same fact will be observed, the atrial epithelium covering the secondary bars becoming much more intensely stained than the similar epithelium of the primary bars. I made use of this colouring matter on the recommendation of Dr. Paul Mayer, of the Zoological Station at Naples, who invariably used it to colour excreting cells, chiefly in Crustacea.

Similar to the atrial epithelium of these gill bars behaves the epithelium of the dorsalward extension of the atrium lining the so-called suspensory or pharyngo-pleural folds. The cells of this portion of the epithelium are even larger than those of the gill bars in many parts, and stain deeply in their more granular portion with Bismarck brown.

That so large an amount of the atrial epithelium should be excretory does not seem strange or improbable to me, as Dr. Eisig, in experimenting with Capitellidæ, found these worms to excrete over the greater portion of their epithelial structures.

But the excretion of this atrial surface is not comparable in quantity, at least in the excretion of carmine, with the amount excreted by some small tubules which have hitherto remained unnoticed, but become very evident in the specimens fed with carmine. The course of one of these tubules is figured in the drawings of the successive sections (figs. 1 to 5). They lie on the outer side of the topmost of the pharyngo-pleural folds which connects the uppermost primary bar with the lateral ridge, from which all the gill bars start. Along this ridge we find a continuous chitinoid rod, which is connected in turn with each rod of the series of bars. These tubules occur thus serially, the last one being in connection with the last primary bar, and lying therefore much more ventrally than the foremost ones. They seem to project into the cœlomic cavity, but at the same time are covered with the thin cœlomic epithelium which lines that cavity.

In fig. 1 the tubule is cut longitudinally, and on its inner side will be seen a blood-vessel which is a branch from the dorsal aorta, and passes over the longitudinal chitinoid rod of the lateral ridge to join the aortic trunk. This branch of the aorta is seen passing upwards in figs. 3, 4, and 7. It is from this branch, too, that the blood-supply to the pharyngo-pleural folds and the vessel along the outer edge of the chitinoid rod of the gill bar is derived.

From the subsequent sections it will be seen that the tubule runs upwards and backwards, and then bending downwards opens (figs. 4 and 8) into the upward extension of the atrium at the highest point, which the latter reaches between the pharyngo-pleural folds. The opening is always placed at the origin of a secondary gill bar, and is just the place at which an excreting organ might profitably open to ensure its excreta being carried away. The chief difficulty with regard to the making out of these points was the obtaining of a suitable stain which would not hide the carmine granules. Carmine and hæmatoxylin proved quite unsuitable, and after trying most varied aniline colours, I finally adopted a colouring agent recommended me by Dr. Hugo Eisig, of the Naples Zoological Station, which answered the purpose better than any other stain. This was a solution of picric acid in turpentine, which has the advantage that after mounting the sections they need not be passed through weak alcoholic solutions. Though this stain, however, shows up the carmine well, it does not stain the nucleus or cell-wall differentially, so that in making the drawings I had to fill up most of the details from specimens stained with different colours, such as Bismarck brown, carmine, or hæmatoxylin. In sections coloured in this way I was able to make out these excreting tubules, but in the case of Amphioxus a very large number of individuals must be used to determine any point definitely, owing to the different appearance almost every individual presents, due to differences of contraction of the gill bars, distention by the genital products, and shrinkage during the killing, hardening, and embedding.

I have thus not been able to settle clearly whether these tubules just described have any internal opening to the cœlom, a point which is of very great interest. Still, to be true nephridial tubules they need not retain permanently a communication with the cœlom, and they may subsequently be found to possess such continuity at some stage in their development.

They may, on the other hand, be simply upward extensions of the atrium, though to this view I should not be very ready to give my support, owing to their bend downwards and their relation to the blood-vessel, which in all parts of its course seems to run outside the atrial and inside the cœlomic epithelium.

The cells, too, are devoid of one marked characteristic of the atrial epithelium, namely, the pigmentation, though this might be due to specialisation.

If these tubules are cœlomic in origin they would come very near true nephridial structures. Indeed, they would be very typical segmental organs devoid of any connecting duct, and their only difference from the most primitive form of nephridia would be the fact that they had become closed off from the remaining portion of the cœlom. Yet even this I do not consider quite settled, as the tubules in many instances seem very imperfectly closed off at their lower end, but I could not satisfy myself that this was not due to faulty preparation. Still there seemed to be no definite nephridial funnel, so that I must await further proof to consider them as closed off from the cœlom.

They are in this particular similar to the atrio-cœlomic funnels described by Professor Lankester, but that they are homologous structures with these belonging to a series of primitively equal dorsalward extensions of the atrium I am not inclined to believe, as the excreting tubules I have just described occur regularly in connection with the secondary gill bars of the region in which the atrio-cœlomic funnels have their opening. If the excreting tubules are simply extensions of the atrium, they must be looked upon as analogous to and not homologous with the atrio-cœlomic funnels.

Before concluding I should like to express my thanks for help and suggestions I received during my work to my teacher, Professor E. Ray Lankester, and to Dr. Paul Mayer and Dr. Hugo Eisig, of the Zoological Station at Naples.

April, 1890.

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2. E. Ray Lankester.—"Some New Points in the Anatomy of Amphioxus lanceolatus," 'Quart. Journ. Micr. Sci.,' vol. xv, 1875.
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EXPLANATION OF PLATES XXXIV & XXXV,

Illustrating Mr. F. Ernest Weiss's paper on the "Excretory Tubules in Amphioxus lanceolatus."

PLATE XXXIV.

Fig. 1.—Portion of a section through the pharyngeal region of Amphioxus, showing the right dorso-pharyngeal cœlom and an excretory tubule cut longitudinally. A blood-vessel coloured by the carmine runs on the inside of the tubule.

Fig. 2.—The next section, showing the beginning of the upward bending of the tubule. In these and the following sections some carmine is seen in the dorsal aorta.

Fig. 3.—This section shows the origin of the blood-vessel lying beneath the subexcretory tubule in Fig. 1 from the dorsal aorta. The atrial epithelium of the secondary gill bar also shows excreted carmine, though to a slighter extent than the tubule.

Fig. 4 shows the opening of the excretory tubule into the upward extension of the atrium at the commencement of the secondary gill bar. It shows also the branching from the dorsal aorta of the blood-vessel of the secondary gill bar, and of the blood-vessel to the excretory tubule.

In Figs. 3 and 4 can be seen the communication between the cœlomic cavity of the primary gill bar and the dorso-pharyngeal cœlom.

PLATE XXXV.

Fig. 5 shows the portion of the excretory tubule behind its opening into the atrium.

Fig. 6 shows the thickened patches of atrial epithelium in the hind region of the atrium described by Johannes Müller. Their cells contain excreted carmine granules. Below them is a blood-filled sinus, or possibly a network of closed vessels, with processes running up into the thickened portions.

Figs. 7 and 8 show an excretory tubule on the left side of the pharyngeal region, and the opening of the tubule at the origin of the secondary gill bar.

Studies in Mammalian Embryology.

II.—The Development of the Germinal Layers of Sorex vulgaris.

By

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With Plates XXXVI—XLII.

Introduction.

Of all embryological problems those concerning the gastrulation process of the Amniota and the formation of their mesoblast and notochord may certainly be said to be at the present moment one of the most burning questions; not only because of the number of important investigations that have of late years been directed towards their solution, nor of the high authority of the names of many of those who have been engaged in these investigations, but more especially because of the very conflicting results and conclusions to which these different researches have conducted their authors.

If I venture to add new fuel to this fire it is only because I am not without hopes that the manner in which the facts present themselves in the as yet uninvestigated species of primitive Mammalia (Insectivora) which have been the object of my own researches may serve to reconcile varied and opposite interpretations to which the rabbit (Kölliker, van Beneden, Rabl, a. o.), the guinea-pig (Carius, Keibel, Strahl), the cat (Fleischmann), the opossum (Selenka), the bat (van Beneden), the mole (Lieberkühn, Heape), and the sheep (Bonnet) have led those respective authors.

Before entering upon a description of the embryological data, such as we notice them in the shrew, a short summary of the principal points upon which the above-named authors agree, and of those upon which they differ, may serve to clear the ground, to refresh the memory, and to facilitate the interpretation of the phenomena which are here brought to bear upon the points in contest.

In this brief summary I will aim at the utmost conciseness, referring the reader who wishes to make a full study of the intricate subject to the original treatises, of which I will give a list in an appendix to this article.

Omnium consensu, the primitive streak and the primitive groove are looked upon in the light in which Balfour first taught us to see them, i. e. as the region that corresponds to the blastopore of Amphioxus, of the Cyclostomata, and of the Amphibia.

The lips of the blastopore are stretched, and of the circular opening a longitudinal groove (Primitiv-rinne) is the representative, which may henceforth be designated, with Bonnet and Fleischmann, as the gastrula-groove.

The gastrula ridge (Gastrula-leiste, Fleischmann) is a very adequate name for the tissue which proliferates inwards from the epiblast in this region. This proliferating ridge was hitherto designated as the primitive streak.

From its cell-strata mesoblastic tissue spreads between the two primary germinal layers.

The inevitable consequence of our comparison with lower types is that we have to look upon this median streak of tissue that has proliferated inwards — although it undeniably originates out of the epiblast — as essentially a formation of hypoblastic material (Urentoderm, Kupffer, Bonnet, a. o.).[1]

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[1] This allows of considerable simplification of one point, about which much unnecessary controversy has been going on, viz. in how far the mesoblast of the Amniota is partly of epiblastic, partly of hypoblastic origin. As soon as the gastrula ridge is looked upon as representing archaic hypoblast, the question as above formulated can advantageously be allowed to drop.

The chief questions about which the numerous authors above cited disagree are—

1. In what relation stands this archaic hypoblast of the gastrula ridge to the remaining hypoblast of the didermic blastocyst, which forms a closed layer, and in most mammals even a closed sac beneath it?

2. Is the production of mesoblast restricted to the tissue of the gastrula ridge, or does the hypoblast proper take part in such production?

3. Does the notochord originate solely out of a median forward growth (Kopffortsatz) of the gastrula ridge (in which a central canal may arise to a smaller or greater extent), which pushes forwards between the primary layers, and which finally fuses with the hypoblast (Einschaltungsstadien, Keibel), after which this notochordal tissue again separates from the hypoblast .(Ausschaltungsstadien, id.), which then coalesces below it to form the dorsal wall of the gut?

4. Or does a flat portion of the lower layer of the didermic blastocyst participate in the formation of the anterior region of the notochord in addition to this median rod of tissue (Kopffortsatz) which has grown forwards out of the gastrula ridge?

5. Do both these median structures, which we shall henceforth designate as the protochordal wedge (median anterior prolongation of the gastrula ridge, often enclosing a protochordal canal or rudiments of it) and as the protochordal plate (developed in situ as part of the hypoblast), take part in the formation of lateral paired plates of mesoblast?

6. Does the gastrula ridge and its anterior prolongation (the protochordal wedge), together with the longitudinal cavity therein contained, represent the whole hypoblast and the archenteric cavity of Amphioxus, so that the inner layer of the didermic blastocyst is not the homologue of one of the germinal layers, but simply a yolk-membrane (paraderm, Kupffer; lecitophor, van Beneden), peculiar to the Amniota?

It will be clear from the enumeration of these points of disagreement that a satisfactory solution of the question of gastrulation and mesoblastogenesis in the Amniota is still a desideratum. More than one of the points formally exclude each other (e. g. 6 and 4). Still, it is impossible to arrange them in two or more groups into which the different investigators could be respectively brought together. To prove this it may be sufficient to say—restricting ourselves for the present to researches on mammalian embryology—that point 2 is now answered in the affirmative, as far as its first proposition goes, by Kölliker (**18**, **19**), van Beneden (**3**), and Fleischmann (**8**); in the negative (i. e. affirmative as far as its second proposition goes) by Heape (**9**), Bonnet (**5**), and myself (**14**).

Point 3 is affirmatively answered by Carius (**7**), Keibel (**17**), and van Beneden.

Point 4 by Heape and Bonnet, against whom Keibel argues at great length.

Point 5 is very diversely answered, certain authors, as Strahl, considering the paired lateral plates of mesoblast alongside of the median notochord to be lateral forward outgrowths of the posterior mesoblast in the region of the gastrula ridge, whereas others (amongst whom Rabl indulges in more general and comparative speculation) consider these plates as lateral wing-like growths of the median streak of tissue.

On point 6 van Beneden has committed himself to very far-reaching speculations, which are viewed with favour and adopted by Rabl (**24**), doubted by Bonnet (**5**, II) and myself (**15**), combated by Keibel (**17**).

This being a very general outline of some of the chief points in contest, I do not think it desirable to enter at any greater length into historical retrospects, or to go into more detail concerning the argumentation of the different authors. Many of the papers contain careful comparisons of the results therein brought forward with those of the other authors; many are ballasted by polemical remarks directed against the authors of such researches as would appear to lead to divergent conclusions.

As my object is in the first place a rearrangement of the known and published facts, for which we are indebted to those different authors, and professes to be an attempt (based on independent observations) towards harmonious interpretation, rather than a contribution towards polemics and criticism, I am all the more inclined to refrain from further "weighing of evidence."

And so now a full description of the chief points which I have noticed in the early developmental stages of the shrew may here follow.

CHAP. I.—EARLY DEVELOPMENTAL STAGES OF SOREX VULGARIS.

1. The Blastula and the Didermic Blastocyst.

The earliest ovum of which I possess transverse sections is in a stage just following upon the phase of the well-known rabbit's ovum, which was described and figured by van Beneden, and has since passed into every text-book of embryology as a specimen of the earliest mammalian blastocyst.

There is a very distinct zona pellucida, internally clothed by a layer of flattened cells, of which I count six to eight in the largest circumference, and at one spot there is an agglomeration of larger and more bulky cells of somewhat different size. The first-named layer is the trophoblast (vide Hubrecht, "The Placentation of Erinaceus," 'Quart. Journ. of Micr. Sci.,' vol. xxx, p. 298). The accumulation of cells contains the material for the embryonic epiblast and for the hypoblast (figs. 5—7). Counting the nuclei in this and the remaining sections, the embryo here figured is found to consist of from fifty to sixty cells. A cavity which is clearly marked though not yet over-spacious extends beneath the polar thickening. It is, properly speaking, the segmentation cavity; after the development of the cœnogenetic hypoblast the greater part of it is enclosed by hypoblast-cells, and becomes the cavity of the yolk-sac. The trophoblast forms its outer wall, the thick zona is again outside this. The embryos here described were found freely suspended in the lumen of the uterus, without any attachment to or enclosure by the uterine wall, as was described for the hedgehog (**16**).

Of the stages following upon the one here noticed numerous specimens are at my disposal, and as long as the blastocyst remains in the monodermic, and even in the didermic stage, it is either quite free in the lumen, or it shows the very first signs of bulging out, and adhering with its outer layer against the uterine epithelium. However, it has first to undergo a considerable increase in size, and during this growth there is at first an evident stretching of the existing cells, much more than an active subdivision and increase in number. Simultaneously with the stretching of the widening blastocyst the zona pellucida diminishes in thickness (figs. 6—11, 22—24). In the last phases of the didermic stage, just before the first traces of a mesoblast and of a gastrula ridge appear, the zona has reached its limit of tenuity (fig. 26). After that it disappears, and the definite attachment of the trophoblast to the uterine tissue is brought about.

In the preserved specimens which I examined, this increase in bulk of the blastocyst, coupled with the decrease in thickness of the zona, causes the blastocyst to lose its spherical shape, and to fall into folds of very varied form and dimension (figs. 8—12, 22—27). This folding—which is no doubt an artefact, as we may suppose the blastocysts to be spherical and elastic in life—is only counteracted when the trophoblast begins to adhere against the uterine walls (fig. 12). The blastocyst is then seen to reassume, in sections of uteri that were preserved in toto, its spherical aspect. For our appreciation of the developmental processes that go on in the trophoblast and in the inner cell-mass—which might also be designated as the embryonic knob—these folds are but of very little consequence, and do not interfere with an accurate interpretation of the phenomena.

To prove that indeed the increase in size of the blastocyst to its double diameter (i. e. an increase in bulk of eight times the original cubic span, and a surface increase of one to four) is more a phenomenon of stretching than of cell-division, we have only to count the number of cells that now compose the blastocyst, which we find at about fifty-six for the trophoblast, twenty-six for the embryonic knob; whereas these numbers were in the earliest phase thirty-six and nineteen for one and thirty and seventeen for another embryo.

In the sections of other embryos of about the same size the embryonic knob has the appearance of being more bulky (figs. 10 and 11, Pl. XXXVI). In the one case it, however, contains twenty-two, in the other twenty-three cells; the apparent discrepancy is thus evidently occasioned by obliquity of the section plane. Another somewhat older embryo, which immediately precedes the stage in which the hypoblast is going to separate from the inner cell-mass, shows a further increase in the trophoblast, with a stationary number of inner embryonic cells. The stage alluded to (fig. 9) contains twenty-two cells in its embryonic knob; the trophoblast is formed by eighty cells, and as yet no coating of hypoblast-cells is detected in any part of this blastocyst.

In the following stage the hypoblast-cells are seen to spread through the blastocyst, and at the same time the embryonic knob is more flattened, and projects somewhat less into the central cavity (figs. 22—24). There can be no doubt that these large hypoblast-cells which gradually form a continuous layer clothing the trophoblast, and which then constitute with it the didermic blastocyst, take their origin from the embryonic knob. The cells of the latter are less flattened and more bulky, the nuclei larger than those of the trophoblast; and by the latter peculiarity it is easy, even before the hypoblast-cells form a continuous layer, to distinguish them from the trophoblast-cells against which they are being applied (fig. 23).

With regard to the embryonic knob, two questions are not without a certain importance: (1) Is there an indication that the trophoblastic cell layer stretches above the embryonic knob, or does it merge into this all along the border of the latter?

The significance of this question will be understood when we bear in mind that in the rabbit (Rauber, a. o.), in the mole (Heape), in the hedgehog (Hubrecht), perhaps also in the bat and in other mammals, either isolated cells (Deckzellen) or a continuous layer of cells are present outside of the layer that is going to become the embryonic epiblast. These outer layer cells in some cases disappear or fuse with the embryonic epiblast (rabbit); in others they are separated more fully from it in later developmental stages (hedgehog).

In the shrew similar cells have been found by me; they do not, however, form a continuous nor a substantial layer, as in the mole and hedgehog. They are detected in the didermic stage, and figured on Pl. XXXVII, fig. 26, *tr′*. Their presence here can hardly leave a doubt that also in the earlier stages the trophoblast-cells with their smaller nuclei stretch above the embryonic knob. If we keep in mind that the nuclei of the trophoblast are in the beginning very wide apart, we cannot wonder that in sections through the earliest embryonic knob the outer trophoblastic covering cannot always be indubitably traced.

Certain of the sections figured give, however, indications that also in this earlier stage the embryonic knob may be said to be situated (figs. 6, 7, and 10) within the trophoblastic layer, and still to be continuous with it at the border. The latter connection distinctly prevails later on (figs. 28—31, &c.), when the sparse "Deckzellen" have wholly disappeared.

(2) Is the difference in size of certain cells composing the embryonic knob which is noticed in one of the specimens of the earliest phase (although I have not as yet specially mentioned it) a distinction by which at that early age the mother-cells of the later epiblast-cells and of the later hypoblast-cells are distinguished? Or is it an individual and fortuitous occurrence peculiar to one of those early specimens? (fig. 5).

I cannot definitely answer the question, but will merely call attention to it, remarking at the same time that in the two other specimens of the same age (figs. 6 and 7), as well as in those that follow (figs. 8—11), I could not recognise any difference in size between the cells composing the embryonic knob;

so that, even if the question were to be answered in the affirmative, we should have to add that the possibility of distinguishing potential epiblast- from potential hypoblast-cells is only limited to that very early stage.

When once hypoblast-cells have begun to emigrate from the embryonic knob towards the periphery of the blastocyst a stage is soon reached in which, in the region of the embryonic knob, an outer layer—more than one cell thick—of epiblast can be distinguished from a subjacent stratum, of which the cells have assumed a more flattened aspect (fig. 24), and are continuous with the hypoblast-cells beyond the embryonic knob. From this moment onwards we shall do well to drop the term of embryonic knob, and to call the thickened circular or oval patch of embryonic epiblast, in accordance with the name chosen by Bonnet and other authors, the embryonic shield. This is thus a purely epiblastic structure, whereas the embryonic knob contained both epiblastic and hypoblastic elements.

As the blastocyst gradually enlarges, and the zona still further attenuates, the embryonic shield increases both in size and in thickness (figs. 12 and 25; 26 and 31). The hypoblast now forms a complete and closed sac, clothing the entire inner surface of the trophoblast. This completion of the hypoblast into a closed and independent sac (nowhere coalescent or fused with the epiblast) is thus attained before the first trace of the origin of a middle layer has become apparent. The actual diameter of the blastocyst is now about 0·8 to 1 mm. Reconstructions of the entire surface of the embryonic shield out of a continuous series of sections show that in this stage the shield is hardly ever quite circular, but has generally an unmistakable oblong, sometimes an ovoid, shape, the thinner end of which corresponds to what will afterwards be the anterior, the thicker to the posterior end of the embryo.[1]

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[1] In some specimens (fig. 21) it is the anterior end that is the broader. Even in the later stages of Pl. XXXVIII the oblong shield is sometimes wider posteriorly, though generally anteriorly. At the same time it must not be forgotten that the surface views of figs. 16—21, 32—35, 62—64, and 79—81 were not drawn from the fresh specimens, but are careful recon-

A most remarkable fact, to which I must now call attention, is this, that it is not in the posterior region of the epiblastic shield that the formation of the middle layer and its earliest representatives—notochord and lateral mesoblast plates—is first inaugurated. IT IS IN THE HYPOBLAST that the first differentiation occurs which ultimately leads to the formation of the above-mentioned structures. In the dozen or more of embryos of this stage which are in my possession I invariably find that the hypoblast undergoes an important modification always in the selfsame spot, i. e. just below the anterior end of the embryonic shield. Here the hypoblast, which from the beginning was never more than one cell thick, thickens over an area which soon counts some five or six dozen of cells. It is not at the outset a splitting process, but the cells simply become thicker and more massive (fig. 30), and lose their flattened fusiform shape, whereas the nuclei become much more closely packed.

In fig. 20 the hypoblast-nuclei underlying the epiblastic shield are drawn in situ. This will give a general appreciation of the phenomenon, and at the same time prevent that the dark patches in figs. 18—21 and 32—35, by which the region here mentioned is indicated, should be regarded as very sharply separated from the rest of the hypoblast.

This patch of modified hypoblast-cells has at the beginning an oval shape, with the long axis perpendicular to that of the embryonic shield. Part of this patch will develop into the anterior portion of the notochord; for this reason I will call it the protochordal plate.

In the stages immediately consecutive upon this it retains its isolated position in the rest of the hypoblast; but now an increase in thickness is noted by the cells dividing in a plane

structions from an unbroken series of sections. If the plane of section is not quite perpendicular to that of the embryonic shield, the reconstruction will not exactly correspond to the shape of the latter, but rather to its projection on another plane. Still, with due allowance for similar small deviations, the figures here given may be said to give an accurate representation of the developmental phases of the embryonic shield.

parallel to the hypoblast, so that the protochordal plate becomes—at least the central part of it—more than one cell thick (figs. 28, 40, and 41).

While this process is going on, the gastrula ridge has, however, made its appearance in the posterior part of the embryonic shield, and its shape, extension, superficial groove, mode of development and of production of a peripheral sheet of mesoblast correspond to what has so often been described for other mammals. Still I will enter into a few details concerning these processes, yet not without once more insisting on the important fact that the formation of a protochordal plate has preceded the appearance of the very first indications of a gastrula ridge (primitive streak).

2. The Development of the Mesoblast.

Towards the origin and further development of the middle layer in Sorex vulgaris three distinct sources contribute.

It is only for a short period that they and the mesoblast which they produce remain distinct. Soon the mesoblast becomes a confluent plate of cells, more than one cell thick, stretching further and further between the two primary layers, and separated in the median axis of the embryo by the notochord or by the tissues that give rise to it. There is every reason to suppose that after a short time the process by which mesoblast originates from the three different sources above mentioned ceases, and that from this period onward the growth of the mesoblast is due to self-division of pre-existent mesoblast-cells. It follows from this that only by examination of certain favorable early stages we can obtain reliable data concerning the actual origin of the mesoblast.

The three sources above alluded to are—

(1) The protochordal plate noticed on p. 508.

(2) The gastrula ridge and its median prolongation forwards, which advances between epi- and hypo-blast, and which I have proposed to designate by the name of the protochordal wedge (Kopffortsatz, auct.).

(3) An annular zone of hypoblast situated just outside the

limits of the embryonic shield, and thus enclosing—but at the outset independent from—the protochordal plate.

This annular zone makes its first appearance when the gastrula ridge has already passed through its first stages of development. Its formation is thus a later phenomenon of differentiation in the hypoblast than was that of the protochordal plate.

Still it is of the same order, being essentially in the first instance a thickening and approximation of a number of hypoblast-cells that are contained in the annular zone below, but just outside the border of the epiblastic shield. This change in the hypoblast-cells appears to take place almost simultaneously.

Embryo 73*f* (fig. 32) was taken from the same uterus and preserved in the same way as the embryos 73*a*, *b*, and *d* (figs. 33—35). In it there was not yet a trace of the zone here alluded to, and also in other respects this embryo is somewhat behind the others in development. In the three others the closed ring can be discerned which is formed of the hypoblast-cells here alluded to; the formation of the ring may hence be concluded to take place rather suddenly.

There will be some difficulty in giving a concise description of the origin of the mesoblast from the three different sources here stated, because of the very early tendency of their products to become mixed up into one continuous layer. Only at the very earliest stages is the distinction a clear one. And so it is more especially these which will have to be described somewhat more fully. The embryos No. 73, above alluded to, are for this purpose all the more valuable, as they differ in development just enough to elucidate the actual course of the phenomena we are here investigating.

It must here be remarked that there is an apparent disadvantage in the fact that some of the sections are neither strictly transverse nor strictly longitudinal. This could not always be attained, since it had become obvious that the best way of cutting the blastocyst was to imbed it in situ in the uterus, even though in the early stages there is no strict concordance between the long axis of the uterus and that of the embryo. Still it was soon found that this disadvantage was imaginary; that, the series being complete, entire accuracy of reconstruction could be obtained, and that, more careful perusal and comparison being necessary under these circumstances, certain points came to light which otherwise might have remained unnoticed, whereas certain other points are much less evident in either transverse or longitudinal section series than in oblique ones.

The utmost care was bestowed on the surface views, which have been traced by means of direct reconstruction (in a given plane of projection) of the camera lucida drawings that were made of the actual sections. And so we commence our description with what occurs in the anterior source of mesoblast—the protochordal plate.

This plate of thickened hypoblast in embryo 73*f* (fig. 32) can hardly be said already to contribute to the formation of independent cells between hypoblast and epiblast (figs. 40 and 41). But in 73*b* (fig. 33) it does thus contribute. In the centre its original character as a thickened patch of hypoblast is retained, and even more marked by still more considerable local proliferation (figs. 53 and 54). At the borders of this patch fusiform cells are seen (in sections not here figured) to radiate from it, and to spread between the two primary layers in a direction more or less perpendicular to the long axis of the embryonic shield.

Thus the first trace of lateral wings of cells (that have originally a decidedly fusiform "mesenchymatic" aspect) developing from the protochordal plate becomes marked.

In embryo 73*d* (fig. 34) the mesoblast-cells in this anterior region have already attained a more considerable numerical development (figs. 43 and 44), it being at the same time very worthy of note that they do not to any extent spread backwards, i. e. in the direction of the front end of the gastrula ridge.

In the following stage, represented by the embryos No. 45 (figs. 62—64), the mesoblast is already one continuous plate. But in the anterior region of the embryonic shield we easily recognise (though I have not, as in figs. 31—34, marked this by a darker shading) our protochordal plate, broader and more massive, and laterally merging into plates of mesoblast (figs. 66, 67, 70, and 71). The cells of this mesoblast have no longer a fusiform aspect, but are more rounded and similar to the mesoblast-cells in the middle and posterior regions of the embryonic shield. A comparison of fig. 66 with 67, and of 70 with 71, will show that in 67 and 71 it is more difficult to distinguish between protochordal plate-cells, mesoblast-cells, and hypoblast-cells than in 66 and 70, although these latter sections are situated further forwards. It is in this stage that the protochordal plate may be said to have reached its maximal extension. In the following stage (embryos 42, figs. 79—81) it is hardly more than one or two cells thick; the mesoblast has become much more distinctly separate from it. In still later stages the protochordal plate-cells are fairly on the way of becoming indistinguishable for a time from the adjoining enteric hypoblast. With this they extend as a continuous plate (only one cell thick) below the medullary groove or canal, and only later the front portion of the notochord folds off, this being the last phase in the developmental phenomena of what we have called the protochordal plate. This has been figured by Heape for the mole, and is not further entered upon in this paper.

It is important to distinguish this primary excalation of notochordal tissue in the anterior protochordal plate region from the secondary excalation which takes place further backwards in the region where the protochordal wedge has first fused with the enteric hypoblast. This latter phenomenon has been described by other authors (**7**, **24**, **29**).

Passing to the second source of mesoblast-cells, the gastrula ridge, we find it to be indeed a very considerable contributor to the increase of the middle layer.

We have already noticed that it appears after the protochordal plate has become very distinctly differentiated.

When the gastrula ridge for the first time becomes apparent (embryo 73*f*, figs. 32 and 37—39) we notice a fusion which then obtains between hypoblast-cells (that have hitherto been subjacent to but independent from the epiblastic shield) and a posterior swollen knob of this epiblastic shield. This fusion is at the early stage so superficial that it is as yet easy to distinguish between the proliferated epiblastic cells of the gastrula ridge and the flattened hypoblast-cells that adhere to them (figs. 37 and 38). Moreover, the fusion at first only affects half a dozen hypoblast-cells. Certain important data should here be borne in mind as following from stage 73*f*, viz. (*a*) that the first gastrula-ridge proliferation arises at the posterior end of the epiblastic shield, and not anywhere towards its middle; (*b*) that the first indication of a forward growth (protochordal wedge) of this proliferation (fig. 39, *p. w.*) is unmistakably present; (*c*) that the epiblast in front of the gastrula ridge is henceforth quite distinct from that which belongs to the ridge; (*d*) that a perforation of the epiblast in the anterior end of the gastrula ridge can be faintly noticed (figs. 38 and 39*p*), it being very questionable whether it actually opens out at both ends. Also later on the traces of a lumen (canal) in the protochordal wedge (Kopffortsatz) are so sporadic (figs. 50, 69, 73, 78, 79, 81, 85, 86, 90) that I would not venture to apply the diagram which Heape has given for the mole's neurenteric canal without restriction to the shrew.

The point where this fusion between the originally independent sheets of epiblast and hypoblast first comes about is no doubt the spot that also passes by the name of Hensen's knob. Forward from it there is a growth that gives rise to notochord (pro parte) and gastral mesoblast (Rabl); posteriorly we find the region of the peristomal mesoblast. Such peristomal mesoblast is as yet absent in the embryo 73 *f*; to its formation the further backward growth of the proliferation is preliminary. The gastrula ridge gradually stretches backwards. Posteriorly it again dilates into a caudal swelling (Schwanzknoten, Endwulst; figs. 34, 35, 56, 59, 62, 63). There is here a very sudden passage from the epiblast of the embryonic shield, which is involved in the formation of this caudal swelling of the gastrula ridge into the epiblast outside of the embryonic shield (cf. fig. 56 and fig. 59).

The gastrula ridge gives rise to mesoblast in a way that was often described for other mammals and Sauropsida. Cells, evidently in direct connection with the superficial epiblast, proliferate so as to shove in between the primary layers as the lateral plates of peristomal mesoblast. At the posterior end of the gastrula ridge which, as above remarked, is so sharply defined in longitudinal sections, mesoblast is similarly seen to proliferate backwards in the direction of the long axis of the embryonic shield, so that the sheet of peristomal mesoblast had better not be compared to two lateral sheets fusing together posteriorly,[1] but to a fan-like extension of a cell layer proceeding from a linear source of proliferation, the gastrula ridge. It should be noted that the posterior and superficial portion of this proliferating sheet is in all my preparations marked by a somewhat different histological aspect, distinguishing the component cells from the subjacent strata of mesoblast. For this I refer to the figs. 56—60, and 83, 87, 91, but do not wish for the present to enter upon speculations concerning the eventual significance of this histological distinction (cf. p. 549).

That the peristomal mesoblast can indeed be compared to a fan that is opened to its maximum width, can be noticed in figs. 33—35 of stage 73 *a, b,* and *d.* The dotted line marks off the outer edge of mesoblast; it is more or less circular, with the gastrula ridge for a radius.[2]

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[1] In similar sense Kölliker expresses himself for the rabbit when he says ('Festschrift Würzburg,' Bd. i, 1882, p. 34): "Angesicht gewisser neuerer Erfahrungen über die Entstehung des Mesoderms aus paarigen Anlagen betone ich dass beim Kaninchen Axenplatte und Mesoderm bei ihrem ersten Auftreten eine zusammenhängende Lage darstellen und dass auch das Mesoderm bei seinem Weiterwucheren wenigstens nach der einen hinteren Seite eine unpaare Bildung darstelt."

[2] It must be observed that in these figures no dotted line is used to indicate the boundary of the less sharply defined mesoblast that originates from the protochordal plate, whereas the dotted line of figs. 62—64 and 79—81 does include such mesoblast, which has then become fused both with the gastrula-ridge mesoblast of figs. 33—35 and with the peripheral mesoblast that originates out of the annular hypoblastic zone.

Still I must now introduce a new factor into our considerations, viz. that not all the mesoblast-cells enclosed within the circle here indicated have arisen from the proliferation along the gastrula ridge just described, but that many of them can be seen to take their origin from what I have termed the third source from which mesoblast arises, viz. the annular ring of hypoblast round and outside the edge of the embryonic shield (figs. 33—35, 53—55, *hy. az.*). Figures are given on Pl. XXXIX (figs. 57—61) in which the participation of this hypoblastic zone towards the formation of mesoblast is put beyond all doubt. They are taken from three different embryos, and in all of them the plane according to which the nuclei divide, as indicated by the well-preserved karyolytic figures, is such as to leave no doubt that in each of these cases a cell divisioh was just on the point of taking place, one of the cells of which was going to number amongst the mesoblast-cells, whereas the other was going to remain in the underlying layer of hypoblast.

That, moreover, this latter layer also increases by multiplication of its cells can be demonstrated in these same preparations; for such an increase the plane of the nuclear division is, however, seen to be not coincident with that of the hypoblast, but, on the contrary, perpendicular to it.

Fig. 58 gives the most strongly marked karyolytic stage; fig. 59, *x*, a stage in which the nuclei have just regenerated after division. This latter figure would offer no convincing proof of the process here advocated; it is, however, a welcome corroboration of what is noticed in earlier phases in the other figures. The reconstructions on Pl. XXXVIII allow us to point at the exact spots, when seen from above, where the karyolytic stages of the foregoing figures are situated. We can then see that it is not only the posterior, but also the lateral parts of the annular ring that thus contribute to the formation of mesoblast-cells.

Also in the anterior portions of the hypoblastic ring, the participation of its constituent cells towards the formation of mesoblast can be proved by karyolytic figures. It would, however, seem that the process is most active in the region posterior to the gastrula ridge. Even after mesoblast has been derived from it, the annular zone of hypoblast has a different aspect from the circular patch of hypoblast which it encloses, as a glance at fig. 68, Pl. XL, will reveal.

There can hardly be a doubt that the annular zone of mesoblast-formation here described is homologous with the annular mesoblast which Bonnet has described and figured in the early developmental phases of the sheep.

Whereas the embryos 73 have allowed us to analyse the first origin of the mesoblast, the embryos 45 reveal a further step in the development of the middle germinal layer, which is very instructive. As far as the protochordal plate is concerned, we have already above (p. 512) noticed in what respect its features are changed when compared with stage 73. It is not less important to observe that the forward growth from the front end of the gastrula ridge which is often indicated as the "Kopffortsatz" of the gastrula ridge, but which has here been designated as the protochordal wedge, has evidently, during its forward growth, carried forward with it the wings of mesoblast. In stage 73 the protochordal wedge was as yet only in its very first phases, and the phenomenon here alluded to not yet very distinct. In the embryos 45 (figs. 68, 72—74) lateral plates of mesoblast are seen to be confluent with the median thickened string of tissue, the protochordal wedge. The latter fuses with the hypoblastic protochordal plate, thus constituting a continuous band of tissue, from which in the further stages the notochord will develop. At the same time the mesoblastic wings of protochordal wedge and gastrula ridge fuse with the lateral mesoblast that has sprung from the protochordal plate, and thus one continuous sheet is formed, which in the reconstructed surface views of Pl. XL, figs. 62—64, is again indicated by a dotted line. This dotted line marks off the outer boundary line of the sheet of mesoblast; it is again seen to be more or less circular, though, as we have seen, it is not simply the increase of the mesoblast within the circle of figs. 33—35 that has given rise to it, but also the anterior mesoblast connected with and originating from the protochordal plate, and that from the annular zone of hypoblast.

Thus the region bounded by the dotted line in stages 45 and 42 (figs. 62—64, and 79—81) contains mesoblast that has arisen from the three distinct sources above indicated. Histologically the mesoblast offers no salient points by which, from this stage onward, this different mode of origin could rigorously be detected. Still it deserves special attention, that in the oblique sections through the stage 42 (figs. 79—81) the difference between protochordal-plate-mesoblast, protochordal-wedge-mesoblast, and gastrula-ridge-mesoblast could yet be distinguished with some precision. Fig. 87 is the most striking example of this, and at the same time teaches us (as do also the figs. 84, 89, and 90) that the protochordal-wedge-mesoblast gives ample evidence of being from the beginning a double plate of cells.

The circular patch of hypoblast enclosed by the annular ring was yet more distinct in the embryos 73 than it is in the embryos 45. As far as it underlies the gastrula ridge and protochordal wedge it undergoes a retrogressive metamorphosis, and can no longer be distinguished as a separate layer.

It will be of better aid towards the comprehension of the description above given to compare figs. 66 to 78, which represent sections through stage 45, with those of Pl. XXXIX, than to enter into any further detailed statements. The preparations have been very carefully reproduced in the figures that were first sketched with the camera, and for criticism of the views here advanced the original preparations are at the disposal of such investigators as should wish to convince themselves by personal inquiry.

The passage from stage 45 to stage 42 is a more gradual one than was that from 73 to 45. The mesoblast covers a wider area. Protochordal plate and wedge now definitely constitute an axial strip of tissue, from which the notochord will take its origin when it has become isolated out of the enteric hypoblast, with which it is as yet continuous. The mesoblast, which was originally in direct lateral continuity with these two, is more distinctly, though not as yet entirely, separated from them along this axial line, the two lateral plates of mesoblast being, however, continuous with each other, both in front of the protochordal plate and behind the embryonic shield.

Moreover, the extra-embryonic cœlom has become apparent in the stage 42 all along a curved line, just behind the embryonic shield (figs. 79, 80, 83, 87, 91, *cœl.*). The cavity is widest and most spacious just behind the gastrula ridge, in the region where the development of the amnion will begin, and where the allantois will make its appearance. In front this cœlom is not yet continued into the mesoblast underlying the epiblastic shield. In one of the embryos 42 (see figs. 80 and 88) I find, however, two small spaces symmetrically situated in this mesoblast. I have as yet no definite suggestion to make, although presumably these two spaces may be looked upon as the first indications of the pericardial cavity. The further exposition of these phenomena and the participation of the protochordal plate in the formation of the wall of the fore-gut and pharyngeal membrane (primitive Rachenhaut, Carius), as well as in that of the heart, I wish to reserve for a future publication.

CHAP. II.—THEORETICAL CONSIDERATIONS ON THE GASTRULATION OF THE MAMMALIA.

In the preceding chapter a detailed description has been given of the mode of development of epiblast, hypoblast, and mesoblast in the shrew. We have seen that the last-named germinal layer has a multiple origin, and that the exact data concerning this latter fact can only be gathered from a study of certain particular developmental stages which are rapidly passed through. After this the mesoblast continues as a separate layer to increase in extension without revealing anything about its primary origin or the multiple foci of its formation. The notochord, the mesoblastic somites, and the lateral plates of mesoblast are the representatives of the middle layer in these later phases; whereas the formative foci of the earlier stages just alluded to are—(*a*) the gastrula ridge with its forward prolongation—the protochordal wedge; (*b*) the protochordal plate; (*c*) the peripheral annular zone of thickened hypoblast.

As late as 1889 a very careful investigator of the development of mesoblast in the Mammalia (R. Bonnet, in 'Archiv f. Anat. u. Phys.,' Anat. Abth., 1889) has written about this last-named peripheral zone (l. c., p. 60): "Was die entoblastogene Entstehung des peripheren Mesenchyms anlangt, so gebe ich von vornherein gerne zu, dass diese Frage mit zu den schwierigsten Aufgaben der Embryologie gehört;" and about the connection between protochordal wedge and protochordal plate (l. c., p. 84) as follows:—"Was die ganze, der definitiven Abschnürung der Chorda vorausgehende Canalisirung und Einlagerung des Kopffortsatzes in den Entoblast bedeutet ist, mir wenigstens, zur Stunde noch absolut unklar." Rabl expresses himself in a similar sense when in the same year (1889) he writes (**24**, p. 140) concerning the Mammalia, "Die von mir bisher untersuchten Stadien lassen eine Zurückführung auf einander und eine klare Darlegung der Mesodermentwickelung noch nicht möglich erscheinen."

The latest author who has grappled with the problem of mammalian gastrulation is Keibel ('Archiv f. Anatomie u. Physiologie,' 1889, Anat. Abth.), who in the conclusion of his essay writes: "Ferner hat die Arbeit gezeigt dass die bis jetzt aufgestellten Theorien der Gastrulation für das Säugethierei nicht durchzuführen sind und dass dies insbesondere auch von den neuesten Versuchen auf diesem Gebiete, von den Theorien von Rabl und van Beneden, gilt. Leider ist der Autor [Keibel] nicht im Stande diesem Verlangen [nach einer Neuordnung des wieder auf einen Haufen zusammengeworfenen Thatsachenmaterials] nachzukommen."

Under these circumstances a renewed attempt to deduce general conclusions from the facts now known to us will certainly not be looked upon as superfluous—general conclusions in which it is sought to correlate the phenomena of gastrulation, mesoblast-formation, and chordatogenesis, as we find them in Mammalia, with what we notice in the anamniotic Amphibia, Cyclostomata, and Amphioxus.

It appears to me that the principle of precocious segregation, which plays such an important part in ontogeny, will serve to explain many of the riddles of which even such an acute and eminently painstaking observer as Bonnet complains. In our case this principle must be applied to part of the hypoblast.

I assume—and we actually observe the fact in the opossum (**27**), the mole (**9**), the hedgehog (**15**), the shrew, the rabbit (**1**, **19**), the bat (**2**, **3**)—that in the monodermic stage of the blastocyst certain cells forming part of its wall separate from this and arrange themselves into a layer, which either at a very early (hedgehog) or at a later stage (rabbit) forms a closed sac inside of the outer layer.[1] A didermic stage of the blastocyst is thus inaugurated before the actual process of gastrulation has set in. It seems to me that we have here an eminent example of precocious segregation, the determining cause of which I will discuss later on (pp. 529—533).

As I have supposed that only a portion of the hypoblast has partaken in this precocious segregation, another portion of it can be expected to arise in a more palingenetic fashion.[2] This we actually notice in the gastrula ridge, and I have already above (p. 500) referred to the results of Balfour, Rabl,

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[1] Van Beneden has pretended that in the rabbit the hypoblast remains absent at the pole of the blastocyst opposite the embryo. Hensen, on the contrary, has figured (l. c., pl. viii, fig. 18) hypoblast-cells at the incriminated spot in an early didermic stage. Keibel (l. c., pl. xxiv, fig. 46*a*) again agrees with van Beneden, at least for the early stages.

[2] In the 'Anatomischer Anzeiger,' Band iii, 1888, p. 911, I have already hinted at the probability of the existence of two separate phases in which the process of gastrulation of the Mammalia has become subdivided. Keibel has taken up this suggestion in his essay above referred to ('Archiv für Anat. u. Phys.,' 1889, Anat. Abth.), but has not worked it out any further, which is for the first time done in this paper. Keibel's paper contains a severe but well-founded criticism of van Beneden's theory of the blastophore and lecithophore.

Bonnet, Fleischmann, a. o., who all agree in looking upon this as the homologue of the blastopore, and who must consequently regard the tissue which from here proliferates inwards as in the first instance hypoblast.[1]

If for a moment we leave out of consideration the participation of the coalescing lips of the blastopore in the formation of mesoblast, then the first question that presents itself to us is this: How does the palingenetic hypoblast arising in the region of the gastrula ridge reunite with the precociously segregated portion of the hypoblast which is already spread out below it as a closed sac, at all events as a continuous layer? If we suppose that instead of the solid gastrula ridge and the shallow gastrula groove of mammals an ingrowth along the lips of a wide-open circular or elongated blastopore could be noticed, even then the direct fusion of this palingenetic hypoblast with that which had been cenogenetically developed as a closed sac could not come about, and could not give rise to an arrangement resembling the gastrula of Amphioxus or of the Amphibia unless a circular patch of the cenogenetic hypoblastic tissue were to disappear by which—on the supposition here made—the palingenetic archenteron would be shut off from the cenogenetic cavity of the umbilical sac. Only after disappearance of the cell layers separating them the two cavities combined would correspond to that of the archenteron of Amphioxus.

And yet not strictly because of the additional space which the increase of food-yolk in the Hypotheria and Prototheria (Huxley), as represented by the fluid contents of the umbilical sac in the Eutheria, has called forth within the hypoblastic dominions.

We find an analogy to this circular patch of tissue separating as a thin cell layer the two cavities just mentioned in the membranes by which mouth and anus are primarily closed in early developmental stages. These membranes undergo a

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[1] Possibly it is the presence of a continuous sheet of hypoblast below the gastrula ridge which has hitherto been so much in the way of the recognition of the real sequence in the phenomena.

process of resorption; they leave no trace, and they can certainly not be looked upon as palingenetic structures having phylogenetic significance!

In the same way I am inclined to look upon a definite rounded patch of hypoblast below the embryonic shield and gastrula ridge as of cenogenetic significance, and I will now point out certain morphological, histological, and developmental peculiarities which substantiate this view, at least for certain mammals, viz. the shrew here described and the sheep (Bonnet). The patch to which I allude forms part of the space which is enclosed inside the annular ring of modified hypoblast, with the anterior part of which the protochordal plate (which arises independently of it) afterwards fuses (see p. 515). In figs. 33—35 the extension of the oblong patch here alluded to is distinctly marked.[1] In the sections the hypoblast-cells of this region are seen to be uncommonly flat, the nuclei very wide apart.

It is with these cells that the lower layer of the gastrula ridge fuses; it is here that the so-called connection between epiblast, mesoblast, and hypoblast comes about (cf. fig. 38), a connection which in Mammalia is undoubtedly secondary. If my view is correct the connection is one between primary (or palingenetic) and secondary (or cenogenetic) hypoblast, and we can well understand on this hypothesis that the fusion becomes so intimate that soon it is impossible to notice any boundary line. Actual resorption of the flattened patch of secondary hypoblast by the much more massive, bulky, and active cells of the primary hypoblast (gastrula ridge) may, for aught I know, take place. At all events, I have not noticed the slightest fact in support of what Heape has brought forward for the mole, and Lieberkühn and Hensen for other mammals, that at the point of fusion between gastrula ridge and underlying hypoblast (it is the anterior, not the posterior region

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[1] Bonnet figures early stages of the sheep's blastocyst ('Archiv. f. Anat. u. Phys.,' 1884, Anat. Abth., pl. ix, figs. 8, 14, 15, 36, and 38). The light space in the centre of his annular "Mesoblast-hof" corresponds to the region which is figured for the shrew, and which is here alluded to.

of the gastrula ridge that is here understood !) the latter takes any part in the production of new cell material for the gastrula ridge or the mesoblast. Karyokinesis of the nuclei forming part of this thin stratum of hypoblast in a plane coinciding with it was never noticed by me, and I am here in entire accordance with Bonnet.[1] However, if we carefully consider the wording of Heape's conclusions ('Quart. Journ. Micr. Sci.,' 1883, p. 47), we find that he writes, "Immediately below the primitive groove there is no layer of hypoblast to be distinguished, and here mesoblast is produced from hypoblast-cells (sic). Laterally all three layers are distinct, but in the middle line they may be said to combine with one another, and in this region, therefore, the middle layer is formed from both epiblast and hypoblast."

This proves that he deduces the participation of the underlying hypoblast in the front region of the primitive streak, towards the formation of mesoblast, not from any karyolytic indication, but from the mere fact that the distinction of the three layers being in this region no longer possible, a participation of both the primary ones in the formation of the third one cannot be strictly denied.

Since then the progress made in the study of karyokinesis has rendered us more careful, but at the same time more decided. So that I hold that I may safely deny any active proliferation, in the sense here alluded to, of the hypoblastic layer that first underlies and afterwards fuses with the front end of the gastrula ridge (primitive streak); and may, on the contrary, assume that a process of resorption of this patch of tissue is more in accordance with what we observe in sections. This resorption also applies to the short stretch of hypoblast underlying the protochordal wedge (see figs. 49, 55, 68, 74,

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[1] Bonnet writes (l. c., 1889, p. 41), "Dafür, dass dem Knoten oder der Gastrulaleiste vom Entoblast her durch Theilung oder Ausschaltung der Entoblast-Zellen Zuwachs geliefert werde, finde ich, auch nach erneuter Revision meiner Schnittserien, ebensowenig Anhaltspunkte wie v. Kölliker beim Kaninchen. Die mühsame Controle . . . . . ergab stets dass die Theilungsebene senkrecht auf der Entoblastfläche stand."

78), and I have no doubt that this small strip of tissue has actually been eliminated, when once the protochordal wedge has become fused with the protochordal plate, and when the mesoblast extends as a continuous sheet (though of multiple origin) between epiblast and hypoblast. The gastrula ridge and its forward prolongation—both of them palingenetic hypoblast—thus contribute material to the formation of the dorsal wall of the intestine, in a region where the underlying cenogenetic hypoblast-cells soon become indistinguishable—a fact in which nearly all observers concur, although they may offer different interpretations.

When this phenomenon is accomplished the effects of the precocious segregation above sketched have been eliminated, and comparison with lower vertebrates is much easier. Those portions of hypoblast that are enclosed inside the annular "Mesoblast-hof," and that have not been sacrificed to the fusion here alluded to, are in their turn utilised in the formation of the dorsal enteric wall: they lose their flattened aspect of the early stages, and become indistinguishable from the rest.

The fusion between palingenetic and cenogenetic hypoblast having thus finally come about, we can commence our comparison of the lowest vertebrates and of the mammals with respect to the further processes.

To begin with the notochord, we may say that its formation out of a continuons strip of mediodorsal hypoblast is also met with in mammals, but that here the strip has been divided into an anterior and a posterior portion, the former (protochordal plate) belonging to the group of hypoblast-cells that have undergone cenogenetic displacement, the latter (protochordal wedge) forming part of the palingenetic hypoblast and actually growing forwards from the blastopore, and connected with the epiblast in the front wall of the neurenteric canal, as we see in Amphioxus. The mesoblast in Amphioxus arises to the right and left of this strip of protochordal hypoblast in the form of separate diverticula, the walls of which are directly continuous with it.

In such mammals as the shrew, notwithstanding the very considerable cenogenetic changes, we find mesoblast to arise from and be connected with the selfsame strips of tissue from which we have seen the notochord to originate.

Both the protochordal plate and the protochordal wedge give rise to lateral wings of mesoblast, which posteriorly pass into the mesoblast that is segregated from the coalesced lips of the blastopore along the gastrula ridge. The duplicity in the origin of the notochord, here ascribed to precocious segregation of a portion of the hypoblast, very naturally also applies to the mesoblast that originates in the corresponding regions. At the same time it appears equally natural that when the fusion of the two protonotochordal halves has come about, the two pairs of mesoblast wings should also reunite.

Direct comparison between Amphioxus and Mammalia is less easy when we come to consider the mesoblast that arises from the gastrula ridge and that which takes its origin from the peripheral hypoblast. When the embryo folds off from the yolk-sac this latter hypoblast constitutes the greater part of the wall of the gut (Darmentoblast). As far as we can judge from Hatschek's and Kowalevsky's observations, nearly all the mesoblast of Amphioxus is derived from the archenteric diverticula above alluded to. Hatschek further mentions and figures two larger polar cells of mesoblast at the hind end of the embryo, right and left of the blastopore, but we only learn in very general terms that they participate in the formation of mesoblast for the caudal region (l. c., p. 35).[1]

Here, however, the Cyclostomata and the Amphibia furnish us with data that are valuable for the explanation of the phenomena in the Mammalia.

To Calberla, Scott (**25a**), Nuel (**22**), and Shipley (**28**) we are indebted for the facts as they present themselves in Cyclostomata; to Scott and Osborn (**25**), O. Hertwig (**12**), O. Schultze (**26**), and many others to those which are noticed in Amphibia. Still there is divergence of opinion amongst these authors on

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[1] "Wir werden sehen dass diese Zellen die stets den hinteren Körperpol bezeichnen bei der Bildung des Mesoderms den hinteren Abschluss desselben bilden."

some important points. One of these has more particular bearing on the question which we are here considering. It is—does the hypoblast (constituted in these groups of much more bulky cells than the epiblast) contribute towards the formation of mesoblast in the ventral and caudal regions by actual delamination from the surface?

Nuel, Scott and Osborn answer in the affirmative; Shipley and O. Hertwig in the negative. As the latter, however, very distinctly admit and figure a participation of hypoblast-cells towards the formation of mesoblast in the immediate vicinity of the blastopore the question is more one of quantity than of quality. Whether new cells are added from the hypoblast to the mesoblast along circles of increasing radius, or whether this increasing radius of the mesoblast is due to growth of the free edge of the mesoblast, which was primarily derived from hypoblastic cell matter, is in itself a phenomenon which may be modified either one way or the other by more or less precocity of the segregation process.[1]

The importance of the phenomenon lies in the fact that a special secondary portion of mesoblast (peristomales Mesoblast, Rabl) originating from the hypoblast can also be traced in the Amphibia, and that this portion must be homologous to that which in Amphioxus is derived from the (similarly hypoblastic) terminal "pole-cells of the mesoblast." We have seen above that the anterior part of the mesoblast in front of the blastopore (gastrales mesoblast, Rabl), as it originates in Amphibia, allows of very close comparison with the similarly situated mesoblastic diverticula of Amphioxus, a comparison which was firmly established by the most valuable investigations of O. Hertwig.

Turning to the Mammalia, we have seen that the comparison of the medio-dorsal mesoblast-wings (gastrales meso-

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[1] Osc. Schultze regards the phenomena as they present themselves in Amphibia in a very different light from Hertwig's. I will not here enter upon the points of dispute between them, but merely remark that the figures in both his papers would allow of an interpretation of the formation of ventral and posterior mesoblast in the sense of Scott (for Cyclostomata), and of Scott and Osborn (for Amphibia).

blast, Rabl) with the similar formations in Amphibia is easy enough.

And as for the so-called peristomal mesoblast, we shall have to look for that in the first place in the immediate vicinity along the sides and at the posterior end (Endwulst) of the gastrula ridge. The identification of the lateral wings of mesoblast that spring from the gastrula ridge with the Amphibian peristomal mesoblast has already been effectuated by Rabl himself. Still it appears to me that the woodcut which he gives on p. 173 of his essay (**24**) is not complete, but ought to show a posterior loop connecting the two parallel dotted lines, thereby expressing that from the gastrula-ridge mesoblast does not originate in the shape of two separated halves which afterwards coalesce posteriorly, but that the plate of mesoblast could better be compared to a fan which was brought to its maximum of expansion (see above, p. 514). It is the extension backwards of this continuous mesoblast plate that can of course be directly compared to what takes place in Amphibia. For the shrew, I have above demonstrated that at the posterior end of the gastrula ridge new cells are added to this plate of mesoblast, which directly spring from the underlying hypoblast belonging to the modified annular zone. This phenomenon is again comparable to what was noticed in Amphibia concerning the participation of a certain number of yolk-cells towards the formation of the peristomal mesoblast. I have also noticed above that laterally numerous indications were found of the actual participation of hypoblast-cells to a similar end; whereas for the sheep, Bonnet contends that to a no less considerable extent the hypoblast participates in the formation of peripheral mesoblast along the whole extension of an annular region slightly larger than the embryonic shield. To this annular zone, which I have above alluded to more fully, he has given the name of "Mesoblast-hof." I have above described an exactly similar ring of tissue in the shrew, which is at all events peculiarly modified peripheral hypoblast, even if we cannot fix for the present the exact extent to which either the whole or only a part of it actually produces mesoblast-cells by karyolytic cell-division. This latter point, however, is, as we shall see, to a certain extent secondary, in the same way as we have judged it secondary, whether in Amphibia mesoblast was produced from a larger or from a smaller extent of surface belonging to the hypoblast-cells that will finally constitute the lower and posterior wall of the larval intestine.

The difficulty that remains is this: is there any possibility of comparing that hemispheral surface belonging to the lower and posterior portion of the larval amphibian hypoblast with the annular zone observed in mammals? I think this comparison will offer no difficulties if for a moment we were to suppose the larval amphibian when it was in the stage of fig. 92 to increase by the addition of food-yolk. It might then be expected to expand ventrally, the actual cells which were afterwards to partake in the formation of the ventral wall of the gut being pushed aside, whereas at the same time a further inferior expansion of both epiblast and hypoblast furnished a sac in which this increased yolk might be expected to find its place. Of the state of things here described I have given an outline sketch in fig. 93, to the details of which I will presently return. It requires no straining of the imagination to picture to ourselves fig. 93 here alluded to still further expanding into a spherical sac, on the top of which the future embryonic tissue was flattened out, and we then immediately see that an annular zone of hypoblast would thus make its appearance (fig. 95) underlying the free borders of the embryonic epiblast, and contributing, when once the folding off of the embryo might have set in, towards the formation of the ventral and posterior wall of the gut. This assumption of a very considerable increase of food-yolk indeed serves to explain the change of shape and size, the origin of a vascular area on the yolk-sac, &c.

We have reason to expect that between the Amphibia and the Hypotheria a phylogenetic link has once existed in which actual food-yolk formed a very considerable addition to the early blastocyst. The case of the Ornithodelphia is most important in this respect. There is little or no food-yolk in the Didelphia, none in the Monodelphia; and the very large size (when compared to the embryonic area) to which the blastocyst of the higher Mammalia increases has generally been looked upon as a repetition, called forth by heredity, of these ancestral lecithophorous arrangements. To me it has always appeared that this explanation is rather strained. A yolk-sac without yolk would be an encumbrance to a mammal that completed its development inside the maternal genital ducts, and would long since have been reduced or even eliminated by natural selection—unless under the changed circumstances a new and important function has come to be fulfilled by it, which is of equally vital importance to the continuation of the species.

This has, I hold, been the case in Mammalia. When the nutritive contents of the yolk-sac were no longer of primary importance, and a considerable reduction in size of the blastocyst might have gone hand in hand with the change from mesoblastic to holoblastic segmentation, this was not effectuated because another factor came into play.

The vascular area which heredity called forth on the surface of the yolk-sac, and by the aid of which the nutritive contents of that sac were elaborated and absorbed, must have rendered eminent service for the establishment of a different mode of nutrition as soon as the embryo underwent a considerable part of its development inside the maternal generative ducts. The beautiful figures which Selenka has given for the opossum (**27**) demonstrate this most forcibly, and the temporary abdication of the allantois in this particular case is also most instructive. Now, for a satisfactory working of the new arrangement it is undoubtedly of the utmost importance that the surface of the area vasculosa should be stretched to its maximum extent, and at the same time should be elastic against pressure tending to throw it into folds. The change required would thus be the substitution of liquid contents, serving the purpose just alluded to, instead of the nutritive contents characteristic of the Hypotherian ancestors. With the absorption and retention of this liquid, under a certain pressure, the outer layer of cells of the mammalian embryo—the trophoblast—has no doubt been specially entrusted. For this purpose it is undeniably the most favorably situated.

It is certainly significant that in all Mammalia it forms a closed sac at the very earliest period after segmentation of the ovum has commenced. More significant yet is the fact which I have noticed in Sorex that a considerable increase in size of the early blastocyst is brought about (cf. figs. 5 and 6 with figs. 8—11) without any adequate increase of the number of cells composing it. This is the actual demonstration of the fact that the increase in size is due to an increased tension, which, in the case of the spherical blastocyst, can only be brought about by the accumulation of liquid contents that are under a higher pressure inside the blastocyst than is the surrounding medium. This in its turn has to be ascribed to inherent properties of the protoplasm of the trophoblast-cells—properties which may either be of a more secretive or of a more osmotic nature, as will some day have to be more carefully determined. The actual high elasticity of a mammalian blastocyst has often been observed and been commented upon.

The utility of this arrangement has probably contributed more towards the retention of what I would call the pseudo-meroblastic condition of the blastocysts of the higher Mammalia than has the hereditary tendency towards the production of this condition. Moreover, other factors came into play to increase the significance of this elastic and spacious blastocyst. It offers a very safe lodging for the developing head of the embryo, which already in Reptilia is seen to be enclosed in a proamnion that bends downwards into the yolk. Such a protection is all the more effective for the mammalian embryos that are no longer protected by a hard shell, but enclosed in moveable and contractile maternal tissue.[1]

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[1] Another reason which might apparently be given for the elasticity and the increase in bulk of the mammalian blastocyst has here been intentionally left in the background, viz. the reason that thereby the walls of the uterus are bulged out, in consequence of which nutritory facilities are obtained. I am not inclined to attach any value to this argument, which appears to me to be

The different size which the blastocyst of the same degree of development attains in different mammals (extremes being represented e. g. by the rabbit on one side and by the hedgehog on the other) may partly be influenced by the more or less favorable conditions of nutrition under which the vascular area finds itself placed. In a former publication ('Quart. Journ. Micr. Sci.,' 1889) I have described these as particularly favorable in the case of the hedgehog. In short, I have here touched upon several points which have all contributed to an important change in the function and also in the development of the outer wall of the early blastocyst. Now this change will, I presume, have been equally momentous for the development of the inner layer of the didermic blastocyst—the hypoblast.

And there can hardly be a doubt that the earliest function of the trophoblast, as above hypothetically described, can certainly be rendered more effectual if at the same time the hypoblast follows suit, and constitutes at the earliest possible moment an inner lining to the trophoblastic sac.

The area vasculosa spreads out between these two membranous cell layers. The danger of a slight defect in a monodermic expanded blastocyst might be reduced by 50 per cent. if the blastocyst is not monodermic, but didermic. The latter consideration may still further help us to understand a peculiarity in the gastrulation of the Mammalia, as compared to that of the Reptilia (lizards [Weldon, Strahl, Hoffmann]; tortoises [Kupffer, Mitsukuri and Ishikawa], a. o.). The palingenetic phenomenon of infolding at the lip of the blastopore, which in the latter is so clear and considerable, and so intimately linked with the formation of a neurenteric canal, is ever so much more obscured in mammals. Now, if the elastic tension of the mammalian blastocyst is a distinctive characteristic which has developed in the way that has been above hypothetically sketched, then we can very well understand that an open-mouthed blastopore has come to be more or less oblite-

too mechanical. Selection will probably not have operated in such a direct way, and the swellings of the maternal tissues are parallel to the increase in size of the ovum; they are certainly not occasioned by it (cf. fig. 12).

rated and retarded. Supposing for a moment the palingenetic phenomena in the region of the primitive streak were to follow the type of the Reptilia, a wide-open blastopore ensuing, and now this palingenetic hypoblast to fuse with the pre-existent cenogenetic hypoblast underlying it, and to turn into a gastrula in the way that was indicated above (p. 521), the fatal effect would inevitably be that the fluid contents would escape, and that the blastocyst would collapse. A first safeguard against this danger is the fact that the hypoblast is a closed sac; a second that the canal in the protochordal wedge—a palingenetic remnant of the posterior medio-dorsal region of the archenteron—is (1) often absent, and that (2) when present it is exceedingly fine, capillary resistance thus counteracting the tendency of the enclosed fluid to escape by that canal.

Moreover the canal is, firstly, very much bent forwards under nearly right angles to the radius of the blastosphere, which is another physical impediment towards the escape of fluid; secondly, only in later stages, when the so-called "intercalation" in the hypoblast has come about, it is in a more or less extensive communication with the cavity of the yolk-sac; thirdly, the attachment of the blastocyst within the uterine cavity has by that time become more definite, and thereby the pressure above the germinal area more or less equal to that inside the blastocyst.[1]

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[1] There is a figure in Selenka's treatise on the Opossum (**27**, pl. xviii, fig. 3) which at first sight would seem to go dead against the hypothesis here developed, because it shows a small pore in a blastocyst at an early though already considerably expanded stage. It should be noted—1. That the possible escape of fluid contents may in this case be most effectually counteracted by the thick albuminiferous layer enveloping the blastocyst. 2. That in other similar stages (l. c., figs. 4 and 10) there is no trace of a similar opening. So that I think my suggestion also holds good for the opossum. The phenomenon of stretching of the blastocyst wall, without increase in the number of cells, is very marked in Selenka's figures (cf. l. c., pl. xviii, figs. 2 and 3).

A stage directly comparable to the one just noticed is figured by Keibel (**17**, 1889, pl. xxiv, figs. 46*b* and 47) for the rabbit, and by Heape (**9**, pl. viii, fig. 31) for the mole. In both cases it cannot be said to be an actual perforation. In all the three cases it is in the region just behind the embryonic shield

At all events, these various considerations allow us to catch a glimpse—however hypothetical—of the causes that may have brought about the necessity of the precocious segregation of part of the hypoblast in mammals. And we can very well understand that once the double closed sac having been constituted, the further processes should again offer close analogies to what is observed in Sauropsida. The precocious segregation has not necessarily had any altering influence on the hereditary tendencies of the different portions of the hypoblast from which mesoblast originates. As might be expected, the palingenetic phenomena are more closely comparable; the cenogenetic changes do not, however, in any way escape the possibility of comparative analysis.

I will now attempt to further elucidate the argumentation contained in the foregoing pages by the discussion of four diagrams given on Pl. XLII.

Fig. 92 is a diagram of a developmental stage in either Cyclostomata or Amphibia after the infolding has commenced, and when from the medio-dorsal wall of the archenteron both the notochord and the lateral plates of gastral mesoblast have developed, whereas at the lower lip of the blastopore peristomal mesoblast is originating. If for a moment we give no attention to the different colours in this diagram, nor to the fact that the solid mass of hypoblastic yolk-cells is here only represented by a few polygonal outlines, we know that the continuation of the process just commenced leads both in

that the incriminated spot is found. Judging from Selenka's figures, it would seem to be the starting-point from whence the inwandering of cenogenetic hypoblast commences, and he on purpose applies the name blastopore both to it and to a yet earlier stage in which he noticed an actual displacement inwards (l. c., pl. xvii, fig. 8). It is all the more suggestive that this spot is at all events in the immediate vicinity of what will become the first trace of the gastrula ridge, i. e. of the point of origin of the palingenetic hypoblast appearing so much later, when the cenogenetic is already a closed sac.

That in Sorex the case lies somewhat differently, and that here no corresponding thinner spot is noticed, must no doubt be ascribed to the thickness of the epiblastic embryonic shield, which is comparatively considerable even in the very earliest stages.

Triton and Petromyzon—(1) to a further excavation of an archenteric cavity in the direction which in this figure is marked by five blue dots; and (2) to the simultaneous growth of notochord and paired mesoblast plates (gastrales mesoblast, Rabl) in that advancing anterior region.

It was above noticed that authors do not agree as to the extent of mesoblastic cell material yet produced by delamination from the hemispheric lower surface of the hypoblastic cell-mass, nor does it matter for the argumentation here put forward. Still I notice this point because by-and-bye we will have to reconsider this possibility, and will then have to picture to ourselves the hemispheric surface here alluded to, which in this diagram has received a uniform blue tint, and forms the lower layer of the hypoblastic tissue.

Recapitulating, we thus find that in this figure the round dots, both the white and the blue, are meant to designate the zone where notochord and gastral mesoblast originate; the white stripes, the zone where the peristomal mesoblast arises; and part of the uniform blue hemispherical region, the zone of what I will designate as the peripheral mesoblast.

The passage from this stage to one in which the yolk has very considerably increased, as is the case in Sauropsida embryos, has already been described by Rabl; his figure of a diagrammatic longitudinal section is reproduced with a very slight modification and without colours in fig. 94. The blastopore, the anterior lip of which is at the same time the anterior surface of the neurenteric duct, is easily identified in both figures. In front of this anterior lip (i. e. to the left in Rabl's figure) is the embryonic region; to the right is the region of the primitive streak, where the lips of the blastopore may be said to coalesce. The regions indicated by white dots and by white stripes in fig. 92 (notochord and peristomal mesoblast) are here indicated by the letters *pw.* and *pst.*; below them is a sheet of cells, the hypoblast, which is always distinct, although its significance has lately been differently interpreted (paraderm, Kupffer; lecithophore, van Beneden), and which I have here somewhat more distinctly indicated than is done in Rabl's original figure. We can identify this layer with the light blue layer overcapping the yolk-cells in fig. 92.

In how far also in Sauropsida regions might be distinguished that could be identified with protochordal plate and protochordal wedge in a stricter sense, and in how far an annular mesoblast-producing zone of hypoblast can also here be distinguished, are questions that will have to be reinvestigated very fully. We have not as yet enough data for any definite or exhaustive answer.[1] The chief point is that there is no difficulty in comparing the diagrammatic stage (fig. 92), which we start from in attempting to interpret the gastrulation of the Mammalia, with the diagrams for the Sauropsida which Rabl has given. This is all the more important because with respect to the Mammalia, this author, while acknowledging the insufficiency of the data at his disposal, yet inclines the other way, and has expressed himself in favour of van Beneden's views, which I must dissent from.

In Sauropsida (1) the great bulk of the yolk; (2) the participation of the upper layers in the phenomenon of retarded cleavage (Nachfurchung), by which new cell-material is added to the embryonic tissues; and (3) the simultaneous appearance (at least in the chick) of hypoblast and mesoblast, are phenomena which obscure the early points in contest by which the formation and homology of the layers can be judged.

In discussing the Mammalia, where, on the contrary, a well-defined didermic stage is indisputably present, we can therefore not derive much benefit from the diagram that applies to the Sauropsida, and we shall have to fall back upon another hypothetical intermediate stage. However, before doing this, the diagram here given of the phenomena as we actually find them in the Mammalia must first be more closely looked at. It is fig. 95 which represents a diagrammatic longitudinal section of a mammalian blastocyst (Sorex, Talpa, Ovis),

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[1] Figs. 53, 56, and 60 in Duval's 'Atlas d'Embryologie' (1889) are very suggestive as far as the protochordal plate is concerned; but I will refrain from any further discussion at present.

when the formation of the notochord and mesoblast has definitely commenced; *n. p.* is the front end of the gastrula ridge, and marks the dorsal lip of the blastopore. When a neurenteric duct is present it is here that its dorsal opening is situated. The epiblast of the embryonic shield is dark black, which in the pre-blastoporian region (*e.*) is applied as a uniform tint, in the region of the gastrula ridge interrupted by horizontal white stripes.

From the front end of the gastrula ridge a forward growth inserts itself between epiblast and hypoblast; it is our protochordal wedge (Kopffortsatz, auct.), and is here marked by a black band with round white dots.

The lateral border of the epiblastic embryonic shield is indicated in semi-perspective by a black boundary line, its general surface by a light grey tint, which also marks the trophoblast that forms the outer wall of the blastocyst.

Turning to the hypoblast, we find it represented by a blue tint clothing the inner surface of the blastocyst, forming a continuous layer beneath the embryonic shield. Phenomena of fusion between the blue hypoblastic lining of the blastocyst and the palingenetic hypoblast of which the protochordal wedge and the gastrula ridge consist, are in this phase already apparent, but not marked in the diagram. A blue semi-perspective annular band (*hy. az.*) indicates the annular region of the hypoblast that was fully described above, and that takes part in the formation of mesoblast. A thickened patch of hypoblast, enclosed within the anterior border of this ring (our protochordal plate), is represented in this longitudinal section by a blue band marked by darker blue round dots and contiguous to the black band of the protochordal wedge.[1]

The mammalian diagram having thus been explained in its general outlines, we shall have to consider how we can bridge the considerable gulf that separates it from the diagram 92 of the lower Ichthyopsida from which we have started in our

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[1] For better interpretation of the diagrammatic section, comparison with the figs. 33—35, 62 and 64, in which the blastocyst is seen from above, will be useful.

attempts at harmonious interpretation of the gastrulation phenomena in the Amniota.

A hypothetical intermediate stage may serve this purpose. It is given in the diagram of fig. 93. It may be derived from fig. 92 by supposing the ventral wall of this latter stage to bulge out into a more capacious reservoir for the retention either of nutritive yolk or of elastic fluid contents, as was already noted above (p. 528). If this process of development takes place at the ventral pole of the spherical blastocyst, then the ventral hemispherical cap of hypoblast of fig. 92 which in the Cyclostomata and Amphibia gives rise to the lateral and ventral walls of the intestine, will open out in trumpet fashion, as indicated in fig. 93. The additional sac-like reservoir will be a medio-ventral appendage to this intestine, and the hemispherical zone will have become annular, as is indicated in semi-perspective in fig. 93.

The regions which in fig. 92 were marked by the dark blue dots will retain their position, and so will the layer *hy'*. that temporarily forms the floor of the archenteric cavity of invagination. It should be borne in mind that also in Amphibia and Sauropsida this floor is only a temporary one, that it dwindles away as the so-called Dotterpropf is being resorbed, and that it is then finally replaced by the definite floor of the intestine which has developed out of the hypoblast-cells that ab origine occupied the lower surface of the hemispherical cap (= the annular zone of fig. 93).

If the transitory character of this layer *hy'*., which is indisputable in the lower Ichthyopsida, is retained in the hypothetical stage of fig. 93 and further in the mammalian (and sauropsidan) development, we shall have to look for it just below the protochordal wedge and the front end of the gastrula ridge, these being the coinciding regions that are stretched out above it. Now in Mammalia such a portion of hypoblast does exist, and coalesces with the cells of gastrula-ridge and protochordal wedge. Centrifugally it merges into those hypoblastic surfaces which actively contribute to the formation of what will ultimately be the lateral and ventral wall of the intestine. So in this respect the comparison of fig. 92 with fig. 95 holds good. It also does this if we compare the lower hemispherical hypoblastic surface of fig. 92, which we find back in the diagram of fig. 95 as a flat annular band of hypoblast. This shape it must necessarily have taken if we suppose the transitional phase of fig. 93 to have yet further become bulged out, so that finally, as was already discussed on p. 528, the formative blastoderm became spread out flat on the upper surface of a much larger spherical blastocyst, as is indicated in fig. 95.

The identity of the regions marked by the blue and white dots and by the thin white stripes in the figures is, moreover, self-evident.

And so now we have to turn to our hypothesis of precocious segregation of part of the hypoblast, and see how it can be applied to the diagrams here given. For this I have made use of the different colours, and will first discuss the mammalian diagram. The epiblast, whether of the embryonic shield or of the trophoblast, is black or grey. So is the palingenetic hypoblast, which arises in the gastrula ridge and extends forwards as the protochordal wedge. The blue sphere is the closed sac of cenogenetic hypoblast, the constituent cells of which have wandered inwards before the actual gastrulation process commences. On this cenogenetic hypoblast certain modified portions—the protochordal plate and the annular ring—appear before the definite fusion between the palingenetic and cenogenetic elements has been accomplished.

Those portions of the amphibian hypoblastic cell-mass, which I consider to be homologous to the mammalian cenogenetic hypoblast, are in fig. 92 artificially distinguished from the remaining part of the hypoblastic invagination by a similar blue colour. The way in which I picture to myself that from stage 92 the mammalian stage 95 has been arrived at was fully discussed above. I have here only to add that in all these diagrams a prominent part is allowed to the hypoblast in the formation of the notochord. This is indicated by the dark blue dots in the dorso-median region contiguous with the protochordal wedge. Suppose for a moment that the confirmatory results to which Bonnet, Heape and myself have arrived in respect to this question had not been obtained, but that in all mammals it was only the protochordal wedge from which the notochord developed, as Carius, v. Beneden and others will have it for the guinea-pig, rabbit, bat, a. o.; even then the hypothesis that has here been developed would to me seem more acceptable than van Beneden's hypothesis of the blastophore and lecithophore. It would at any rate not have to undergo any important modification.

Should future researches bring to light that indeed the formation of notochord and mesoblast in different mammals takes place according to divergent modes, as would appear to follow from the researches here cited, even then the theory of mammalian gastrulation here developed would remain applicable, whereas that of van Beneden collapses as soon as a definite participation of cenogenetic hypoblast (his lecithophore) in the formation of these tissues has been demonstrated. And this is now the case at any rate for the sheep and for the shrew.

As, moreover, van Beneden has to deny direct homology between the mammalian inner layer and the hypoblast of Amphioxus, whereas in my hypothesis these two remain perfectly comparable and homologous germinal layers, I think the latter hypothesis will also have a priori grounds in its favour. At all events, the supporters of van Beneden's view will have to bring Bonnet's and my own results in accordance with their own hypothetical solution. I myself do not see my way to effect this.

CHAP. III.—POINTS OF COMPARISON IN EARLIER INVESTIGATIONS BY OTHER AUTHORS.

I have not in the preceding pages very fully and repeatedly referred to the literature of the subject. Whenever references were indispensable they have been inserted. Still a large amount of embryological research which runs along parallel lines remains unnoticed. From this I have extracted such points as seem to have special bearing on the subject here treated, either as directly confirming or as in apparent contradiction to what has above been described for Sorex.

1. The Protochordal Plate of Rabbit and Cavia.

Carius' dissertation (p. 26) purposely refrains from deciding whether in the rabbit there might not possibly be a participation of the entoblast towards the formation of anterior portions of the notochord. A comparison of his fig. 8 with our figs. 44, 67, 70, and 71 undoubtedly suggests the presumption of their homology, i. e. of the presence also in the rabbit of a distinct hypoblastic protochordal plate which certainly is less distinct at the outset in the rabbit than we have found it in the shrew. In that case we shall also be allowed to institute more direct comparisons between the figures which he gives of the changes in the blind fore-gut with what is found in the shrew, but has not been entered upon in this paper.

Concerning Cavia Carius is much more emphatic in denying any participation of hypoblast in the formation of the notochord. Here, too, a renewed comparison with what the shrew has taught us will allow us to decide whether the protochordal plate is perhaps so much reduced that it most naturally escapes detection, or whether it is wholly absent, the protochordal wedge supplying the whole of the notochord. At all events, the extreme inversion of the layers, as we find it in Cavia, must necessarily induce us not to look upon Cavia as a fit representative of the normal mammalian development.

Keibel's publication (17) concerning the formation of the notochord is posterior to that of Carius, and on p. 27 of the reprint of his article he holds himself justified to exclude for the rabbit any participation of the hypoblast towards the formation of the notochord. He recognises that at the foremost extremity the decision in the sense he advocates is rendered extremely difficult. He has noticed a hypoblastic thickening in this anterior region, but only holds it to be of significance for the formation of the primitive "Rachenhaut" (pharyngeal membrane), whereas a direct comparison with the shrew's protochordal plate and with the chorda-entoblast which Bonnet describes and figures in the sheep would perhaps lead to different results. That Keibel feels all the importance of the contradiction between his own views and those of Bonnet (which are so fully supported by the facts observed in the shrew) may be concluded from the following passage which I translate from p. 345 of his article. He says, "I will not here further refer to Bonnet's doctrine of the mesoblast derived from the entoblast. Nothing like it is found either in the rabbit or in the guinea-pig, and even Bonnet's own figures have not convinced me. . . . Bonnet's observations are, at all events, not available in support of Rabl's or van Beneden's hypothesis. If they were confirmed this would mean a further difficult complication of our problem, and for this reason I believe I may be relieved from further entering upon Bonnet's data."

If we refer to van Beneden's early article on the rabbit's development ('Archives de Biologie,' vol. i, 1880), we find that he confounds for the earlier stage (VI) epiblast and mesoblast (pl. vi, fig. 2), regarding the trophoblast (Rauber's Deckzellen) as the definite epiblast. This confusion has been refuted by Lieberkühn, and seems to have since been recognised as such by the author, who on the same plate (figs. 11—13) gives correct interpretations of the three layers in a later stage (IX), a stage of which he definitely affirms that there was as yet no trace of Hensen's node (i. e. of the gastrula ridge). These three figures should be somewhat more carefully considered by us. They show that mesoblast is present in the rabbit before there is any trace of the gastrula ridge. This van Beneden emphatically states on p. 220, sub. 13. This mesoblast appears in crescent shape in the posterior region of the embryonic shield. Van Beneden does not mention how he has made out that this was indeed the posterior region, nor does his surface view in fig. 5, pl. vi (l. c.), throw any light on this question. I presume that he may have thus concluded on a priori grounds, and feel inclined to suggest that the region where sections 12 and 13 were taken was actually the anterior region of the embryonic shield. In that case the crescent-shaped mesoblast might be interpreted as mesoblast derived from a hypoblastic protochordal plate (not further mentioned, however, by van Beneden), and its presence before the appearance of any trace of the gastrula ridge would be very well in harmony with facts which we have observed in the shrew. However, it is only tentatively that I advance this proposition, which only renewed researches of very numerous early stages of the rabbit's blastocyst can bring to a definite test.

That the veteran leader in embryology, von Kölliker, retains theoretical objections against any participation of the hypoblast towards the formation of mesoblast is well known, as also that these views are all the more emphatically brought forward in his later publication. He has experienced the gratifying sensation that van Beneden, who in the publication above cited (p. 142) most vehemently attacked Kölliker's interpretations in terms which Kölliker resented, though he referred to them very magnanimously ('Die Entwickelung der Keimblätter des Kaninchens, Historische Vorbemerkungen,' p. 5, Festschrift Würzburg, 1882), has since turned over an entirely new leaf. In his latest, though as yet only preliminary communications on the rabbit and the bat ('Tageblatt der Naturforschervers.,' Berlin, 1886, and 'Anat. Anzeiger, iii, 1887) van Beneden not only wholly accepts Kölliker's views, but draws very full and far-going conclusions from them. As such we may consider his theory of the gastrulation of the Mammalia, their blastophore and lecithophore.

If we consider the plate by which Kölliker's essay just cited is illustrated, we find in the surface views a crescentic "vorderer Randbogen." This seems to correspond with van Beneden's crescentic mesoblast above alluded to. In the text (p. 9) Kölliker compares these stages with those of van

Beneden, and being apparently also doubtful whether van Beneden's definition of what is the anterior and posterior region of the embryonic shield was accurate, he places a ? behind the word "anterior" with which he indicated this border region, and which I am inclined to homologise with the region of the protochordal plate in stages 52 and 73 of the shrew.

Moreover, comparing Kölliker's pl. i, fig. 1, on which an embryonic shield is figured which very strongly resembles our fig. 32, pl. c, of the shrew's stage 73*f*, we in the first place notice the presence of the first trace of the gastrula ridge at the lower border of the embryonic shield. It seems improbable that from here the primitive streak should grow forwards as Kölliker interprets it. Fig. 3 would no doubt seem to militate in favour of such an interpretation, but then we must not forget that it is not drawn on the same scale of enlargement. Were we to draw it on the same scale as fig. 1 the embryonic region in front of the gastrula ridge would be of about equal size to that of fig. 1, and we might look upon the gastrula ridge as having arisen by a backward extension of the original posterior proliferation *hw.* of fig. 1, together with a general growth of the epiblastic shield much in the same way as we have been led to interpret the phenomena in the shrew.

A comparison of Kölliker's figs. 4 and 5 with our figs. 33—53 of embryos 73, *a, b, d,* and of his figs. 7, 8, with our figs. 62—64 of embryos 45, and figs. 79—81 of embryos 42, will also prove instructive. It must be borne in mind that Kölliker's drawings are made from surface views, whereas mine are reconstructions, and as such—though somewhat less reliable as far as the outline goes—more exact where they indicate histological differences. Kölliker himself says (l. c., p. 23), "I have made no special study of the differentiation of the cells of the germinal layers, nor of the karyokinetic processes in them." We further notice that in Kölliker's fig. 29 there is a central portion of flattened hypoblast, right and left of which a histological modification is apparent, which offers points of comparison with the modification by which the annular zone (*hy. ar.*, figs. 53, 54, 68) of the shrew is characterised. Moreover, fig. 47 of Kölliker raises the doubt whether also in the rabbit certain points of the hypoblast might not finally be detected, where its participation in the formation of mesoblast could not be as decidedly demonstrated as it has been done by Bonnet for the sheep and by myself for the shrew.

It does seem that the rabbit is in this respect a very recalcitrant subject, if we notice how also Rabl ("Theorie des Mesoderms," 'Morphol.-Jahrbuch,' 1889, p. 113, pl. ix) confirms the views as advocated by Kölliker. From Rabl's essay I will notice certain details which should be compared with what I have above advanced for the shrew. Rabl states that in an early stage of the rabbit's blastocyst the two layers are at first in no way directly connected, which corresponds with what was observed in the shrew.

Contrary to what we have noticed in Sorex, he states (l. c., p. 144) that in the rabbit this mutual independence of the two layers is maintained even after the gastrula ridge and protochordal wedge of the rabbit have made their appearance, and the formation of the mesoblast is already considerably advanced. Somewhat later, however (l. c., p. 149, pl. ix, fig. 9), the fusion of the three layers in the region of Hensen's knob comes about, although as yet to no considerable extent.

As to Rabl's figures (l. c., pl. ix, figs. 5—9), I must again invite comparison with what was figured for the shrew on Pl. XL, figs. 66—78. These figures do not exclude the possibility of seeing in the anterior part of his "Chordaplatte" a portion homologous to our hypoblastic protochordal plate, although, of course, Rabl's text goes the other way, and he wishes to interpret them as confirmative evidence for van Beneden's gastrulation hypothesis.

2. The Protochordal Plate, Protochordal Wedge, and Annular Zone of Modified Hypoblast in other Mammals, according to Bonnet, van Beneden, Selenka, Fleischmann, a. o.

In Bonnet's description of the developmental phenomena of the sheep very numerous points of coincidence with what has here been described for the shrew have already been repeatedly pointed out. Bonnet emphatically insists on the participation of an anterior (ab origine hypoblastic) chorda-entoblast towards the formation of notochord and mesoblast, in which further backwards the "Kopffortsatz" (our protochordal wedge) and gastrula ridge participate. His statements are all the more valuable as in his later paper (l. c., 1889) he recognises (p. 75) that the different results at which other authors have arrived have led him to most careful and repeated reperusal of his series of sections, and have changed his mind in this sense, that in a former publication (l. c., 1884) he gave too prominent a place to the anterior hypoblastic plate in the formation of the notochord. He is now willing to accord a much more considerable part to the "Kopffortsatz," of which he had formerly underrated the length; but he holds on as strongly as ever to the participation of a purely hypoblastic anterior portion. It will be best to quote his own words, which are nearly verbally applicable to the shrew. He says (l. c., 1889, p. 84):

"The definite formation of the notochord is only brought about when the gutter-like or flat 'Kopffortsatz' that has become intercalated in the entoblast is again pinched off longitudinally; only now we may, rigidly speaking, apply the terms 'notochord' and 'notochordal lumen,' in so far as by this latter name one would wish to designate remains of the folded-off enteric cavity in the segregated notochord. In the genesis of the notochord we must thus very strictly keep apart the originally solid but subsequently canalised Kopffortsatz, its ventral fusion by which it opens and becomes gutter- or plate-shaped, and intimately connected with the enteric hypoblast. Posteriorly the 'Kopffortsatz' passes into the gastrula ridge, anteriorly into the 'chorda-entoblast' without any strict boundary; all this together represents the material from which the notochord will originate. But only when the chorda-entoblast and the intercalated 'Kopffortsatz' (intercalated in the hypoblast) have again become pinched off—only then the definite notochord has originated. It is only the chorda-entoblast at the cranial extremity and the gastrula ridge contribution at the caudal extremity which, as follows from this description, is directly converted into notochord. By further differentiations in gastrula ridge and terminal knob the notochord extends further backwards; by further processes of growth in the split-off chorda-entoblast it extends further forwards."

The points of comparison between shrew and sheep will be self-evident for whomsoever compares certain figures from Bonnet's earlier paper (' Arch. f. Anat. u. Physiol.,' 1884, Anat. Abth., pls. ix—xi) with those here given for the shrew,[1] more especially—

Bonnet's fig. 30 . . .	with our figs. 45, 46
„ „ 31, 32 . . .	„ „ 43, 44
„ „ 29 . . .	„ „ 48
„ „ 28 . . .	„ „ 49, 50
„ „ 27 . . .	„ „ 51
„ „ 53, 54 . . .	„ „ 70, 71
„ „ 57, 58 . . .	„ „ 69, 78
„ „ 59, 60 . . .	„ „ 74, 76

Finally I may draw attention to a fact which I am inclined to attach importance to, viz. that Bonnet describes and figures in the anterior portion of the sheep's protochordal plate numerous downward proliferations of this hypoblastic tissue,

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[1] I hardly think Bonnet is justified in expressing doubt (p. 66, l. c., 1889) as to whether the median, anterior thickening of the hypoblast, noticed in early stages in front of the Kopffortsatz, stands in any relation to the formation of the notochord. I must acknowledge that I cannot succeed in connecting this statement with Bonnet's description of his "chorda-entoblast," which somewhat later occupies the same position (our protochordal plate), and which would naturally be looked upon as a further thickening of the region already similarly recognisable in the earlier stages.

protruding into the cavity of the fore-gut and marked *sp* (Entoblast sprossen) in his figs. 53 and 54. It is with these figures that I am inclined to compare the woodcuts which van Beneden has given on pp. 712 and 713 of vol. iii of the 'Anatomischer Anzeiger,' for Vespertilio murinus. In these he figures cellular matter (marked B on p. 713), which at the foremost extremity of these early embryos is meant by him to stand for the bottom of the "Chorda-kanal," i. e. belonging to the forward growth from the node of Hensen, which we have termed the protochordal wedge (Kopffortsatz, v. Beneden, a. o.).

In this forward growth the "Chorda-kanal" makes its appearance, and as the Kopffortsatz is intercalated in the hypoblast, the "canal" fuses (beginning in the middle, and from thence both backwards and forwards) with the lumen of the yolk-sac. This intercalating process can be noticed, according to van Beneden, even under the originating prosencephalon. It is with respect to this point that I must again refer to what I have noticed above when discussing Carius' and Keibel's description of the formation of "Kopffortsatz" and notochord in Cavia and rabbit.

Here, too, a very rigid inquiry will have to test the facts as stated by van Beneden. The possibility of a pre-existent hypoblastic protochordal plate must be rigorously excluded experimentally before we are justified in giving up the possibility that to a certain extent, however much reduced, there might be coincidence between the mammals which Bonnet, Heape, and myself have investigated, and those which have served for van Beneden's, Carius', Keibel's, a. o. researches. As stated above, the woodcuts furnish a starting-point for such comparison, which, however, I only bring forward in the very tentative manner here explained.

In the opossum the earliest developmental phenomena of the notochord were studied by Selenka, and although in his text ('Das Opossum,' p. 152) he declares himself an adherent of Kölliker's theoretical views, his figures certainly admit of a different interpretation, which if verified would bring the facts in the opossum on a level with Bonnet's and my own results in placental mammals.

Thus on Selenka's fig. 2, pl. xxi, the front end of the notochord in its very first stages is figured. A thin layer with nuclei beneath it should be erased in this figure, as we are told on p. 151 of the text. When this erasion has been brought about, the figure very strongly suggests the identity of the massive plate of 7—10 thick entodermal cells, with the protochordal plate of our figs. 66 and 67. It seems to me hardly possible here to adopt van Beneden's or Carius' views, and look upon this portion as the widened anterior part—intercalated in the hypoblast—of the "Kopffortsatz." The front end of the latter is perhaps situated in Selenka's fig. 4 (or 3). If we now consult his surface view (fig. 1, pl. xxi), we see that just in the level of section fig. 4 the notochord is very considerably constricted. Later researches will have to make out whether the two regions, anterior and posterior to this spot, may be identified respectively as protochordal plate and protochordal wedge. Of the very earliest phases of the gastrula ridge Selenka does not give any figures, nor do his figs. 8—11, pl. xviii, furnish material for a profitable comparison with those very earliest stages in Sorex.

A very emphatic opponent to some of Bonnet's views, particularly those which refer to the formation of an annular zone of hypoblast, from which mesoblast (on purpose I do not follow Bonnet in the use of the term mesenchyme) is originated, is found in Fleischmann, who has more especially occupied himself with the development of Carnivora. As we have been able to show that in the shrew Bonnet's results are fully substantiated, and to bring forward additional evidence in karyolitic figures which are not figured by Bonnet, we necessarily find ourselves in conflict with Fleischmann. This author ('Unters. über einh. Raubthiere,' 1889, p. 17) does acknowledge the possibility that in this respect fundamental differences between the Carnivora and the mammals which Bonnet and myself have studied exist. Still his a priori argumentation against the existence of an annular peripheral mesoblast, directly deriving from hypoblast-cells, is very sweeping.

Another detail in Fleischmann's paper (p. 11) to which I will direct attention concerns a difference which he has noticed in the staining properties of splanchnic and of somatic mesoblast-cells in the region of the primitive streak. A similar phenomenon in the cat was observed by Strahl ('Arch. f. Anat. u. Phys.,' Anat. Abth., 1886, p. 160) for the rabbit, and has been referred to above by myself (p. 514), and figured on Pl. XLI, figs. 83 and 91. Certain preparations (a. o., figs. 56 and 59) would lead me to believe that there is a more direct connection between this portion of the somatic mesoblast and the superficial layers of the gastrula ridge. Whether the phenomenon has a higher theoretical significance can for the present not be answered; attention should, however, be directed towards it. In Selenka's sections of the opossum a somewhat similar phenomenon—not, however, noticed in the text as being marked by different staining properties—is figured on Pl. XXI, fig. 7, *sm.* and *splm.*

One other point in Fleischmann's paper should be reflected upon, viz. whether his fig. 10, pl. i, in which three layers are figured in a section just in front of the medullary plate, and in which the hypoblast is uncommonly thick and proliferating, might not after all be interpreted as belonging to a region homologous to that of the protochordal plate in the shrew, or of Bonnet's chorda-entoblast.

3. Sundry Observations by Different Authors in Support of the Hypothesis of Precocious Segregation of Part of the Hypoblast in Mammals.

The views here brought forward with respect to the gastrulation of the Mammalia, which have been fully discussed above, receive independent corroboration from certain facts already passingly alluded to, which were noticed by other observers and by myself in other mammals. I wish to insist somewhat more fully on these observations.

In the opossum, Selenka (l. c., p. 114) describes and figures a very early blastula stage in which one or a few cells get separated from the outer blastula wall, wander into the archicoel (segmentation cavity), and form the starting-point for the development of the hypoblastic sac. In the beginning (Selenka's figs. 3, 8, and 11, pl. xvii; 2, 3, and 4, pl. xviii) these rapidly multiplying cells adhere to the outer blastula wall in a spot which Selenka calls the blastopore. When the formation of the hypoblastic sac is completed there is a stage in the development of the opossum's didermic blastocyst when the two layers are no longer thus primarily connected, but are separate though contiguous spherical sacs, the hypoblast consisting of flattened, the epiblast of more massive cells (Selenka's figs. 2, 3, 6, pl. xix).

Only in a further stage—immediately following on the foregoing—the palingenetic hypoblast (gastrula ridge and protochordal wedge) makes its appearance; the fusion which in consequence of this is established between epiblast and hypoblast stands in no direct relation to the earlier connection above alluded to, and which is noticed in the blastula stage.

There can thus be no doubt that the wall of the monodermic blastocyst of the opossum produces cell-material, which arranges itself into a second closed sac inside the primary one. The spot from whence this cell production emanates is distinct and circumscribed, it disappears without leaving any trace when the didermic blastocyst is fully established. Shortly afterwards there appears in about the same region of the outer layer a renewed cell proliferation which leads to the formation of the gastrula ridge.

The latter is what I have proposed to call the palingenetic, the former the cenogenetic hypoblast. In the opossum the clearness of the phenomenon leaves nothing to be desired. It is not a priori necessary that the spot from whence the cenogenetic hypoblast originates should be the same as that where afterwards the palingenetic blastopore (gastrula ridge, primitive streak) makes its appearance. That it appears to do so more or less in the opossum is nevertheless in favour of the hypothesis of precocious segregation here brought forward.

It remains doubtful whether it will be desirable to designate the first-named spot as Selenka does by the name of "blastopore." An additional adjective will render good service, and the name "cenogenetic blastopore" might recommend itself.

Of the eight embryos in this stage which Selenka has examined, five show this cenogenetic blastopore as a closed proliferative spot; in three of them small openings (Zellenlücken) were noticed[1] in the wall of the blastocyst, which soon closed up. In the hedgehog I have myself described ('Anat. Anzeiger,' iii, pp. 511 and 907; 'Quart. Journ. Micr. Sci.,' 1889, p. 286) a monodermic blastocyst, with hypoblast-cells adhering to the wall at a spot which I think we are justified in comparing to the opossum's cenogenetic blastopore. The comparison of still earlier stages of the hedgehog is as yet a desideratum in order to definitely sanction this comparison. Here, too, the faint trace of the spot where the cenogenetic hypoblast probably originates out of the wall of the monodermic blastocyst is obliterated; here, too, a didermic stage follows with the two layers separate; and here, too, the connection between epi- and hypoblast which results from the formation of the palingenetic blastopore is only a third phase in this developmental process.

For the mole we have Heape's observations, according to which (l. c., pl. ix, figs. 17—27) the hypoblast arises much in the same way as we have noticed in the shrew. It is hardly possible to indicate a spot from whence the cenogenetic hypoblast can more particularly be seen to take its origin. And the perforation which Heape indicates in his fig. 31 would seem to me not to be homologous to the spot above noticed

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[1] Selenka's figures of the blastocysts, in this and the following stages, are drawn on very varied magnifying scales. This should be borne in mind in comparing his figures with each other. It is apt to create some confusion, from which in this paper I have endeavoured to keep clear by adhering very strictly to the use of very few and always identical scales of enlargement for the different figures.

for the opossum, nor for that observed by Keibel in the rabbit, and to which I will refer lower down, but rather to the less markedly perforated hinder region of the embryonic shield of Sorex figured in Pl. XXXVIII, fig. 39. It should be especially kept in mind that Heape's fig. 31 has been preceded by another stage (his figs. 10 and 30), in which the hypoblast was already completed and an independent closed sac inside the epiblastic vesicle, so that their fusion and the perforation represented in fig. 31 are no doubt already a secondary connection, as is the fusion of the figs. 37 and 38 of Sorex. This early perforation before the protochordal wedge has as yet very far advanced is no doubt a peculiar feature which should be submitted to repeated observation, but it is in no way an obstacle to the theoretic views here given concerning the fusion of a palingenetic and cenogenetic hypoblast. Moreover another difference between Talpa and Sorex runs parallel to it, viz. the greater distinctness and width of the neurenteric perforation (see about this p. 532).

Finally, an observation of Keibel in the rabbit deserves more particular consideration with respect to this matter. He represents (17) in his section, figs. 46*a*, 46*b*, and 47, a stage which very nearly approaches what Selenka figures in the opossum. Keibel draws attention to this correspondence, as also to that between these stages and that of the mole according to Heape. I have above given my reasons for which in this latter respect I am inclined to differ from his interpretation; but I think we are fully justified in looking upon the spot BP in Keibel's figures as the true cenogenetic blastopore of the rabbit, homologous to that of the opossum.

From Keibel's text I gather with satisfaction, as I have already had occasion to notice above (p. 520, foot-note), that he is not adverse to the view which I first put forward two years ago, and have more fully advocated in this paper, viz. that the formation of the mammalian hypoblast (i. e. the phenomenon of gastrulation) is accomplished in two stages separated by a short interval. I cannot, however, acquiesce to his suggestion (l. c., p. 376) that in the first of these two phases the enteric hypoblast (Götte's enteroderm) is formed, whereas in the second the formation of notochord and mesoderm is accomplished. I have shown in the foregoing pages that the hypoblast which belongs to the first phase (cenogenetic hypoblast) has undoubtedly its share in the formation of both notochord and mesoblast, and I have at the same time attempted more definitely to determine the exact amount of this share, and also that of the palingenetic hypoblast.

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EXPLANATION OF PLATES XXXVI—XLII,

Illustrating Prof. A. A. W. Hubrecht's paper "Studies in Mammalian Embryology. II.—The Development of the Germinal Layers of Sorex vulgaris."

PLATE XXXVI.

Figs. 1—4.—(The numbers in brackets refer to the catalogue number of the uterus from which the embryos were taken.) Four uteri of Sorex containing the earliest embryonic stages that were investigated. The swellings visible in 16 are not caused by the enclosed embryos, but are the last visible remnants of a preceding pregnancy, and mark the areæ of placentation in their latest retrogressive phase.

These figures are given in natural size. The unpaired median portion is the vaginal part in which embryos are never found.

Figs. 5—7.—Transverse sections of three young blastocysts of No. 16. *Z.* Zona pellucida. *Tr.* Trophoblast. *E.* The inner cell-mass which will give rise to epiblast and hypoblast of the embryo.

In Fig. 5 there is a difference in size between certain cells of the inner mass, which was not noticed in Figs. 6 and 7. In all there is sufficient evidence of trophoblast-cells between the inner mass and the zona pellucida. The total number of cells constituting these blastocysts varies from fifty to sixty. The figures were drawn (as are all the other figures of sections on this plate) with Zeiss' apochr., oc. 4, obj. 4.

Fig. 5.—Mus. Utr. Cat. n°· Sorex 16 *a* and *b*, 3 *r*. 9 *s*.[1]
Fig. 6.— „ „ 16 *cg*, 2 *r*. 14 *s*.
Fig. 7.— „ „ 16 *cg*, 2 *r*. 14 *s*.

Fig. 8.—Section through an embryo of No. 44. Lettering as in the preceding figures. There is an artificial bulging in on one side of the blastocyst, which was absent in other embryos of the same age, and which must undoubtedly be ascribed to the thinning out of the zona simultaneously with the increase in size of the blastocyst. It must be ascribed to the reagents used in hardening the tissues.

It will be seen from the subsequent figures on this and the following plates that this phenomenon is very much on the increase as the size still further augments, and is only counteracted when once the blastocyst has become attached to the walls of the uterus (see Fig. 12).

Mus. Utr. Cat. n°· Sorex 44 *a*, *b*, 4 *r*. 11 *s*.

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[1] See this Journal, vol. xxx, p. 393.

Fig. 9.—A similar section through an embryo of No. 105, the zona being much folded.

Mus. Utr. Cat. n$^{o.}$ Sorex 105, 2 *r.* 6 *s.*

Figs. 10 and 11.—Section through two other blastocysts belonging to No. 110. Lettering as in the foregoing.

Mus. Utr. Cat. n$^{o.}$ 5, Sorex 110, 2 *r.* 8 and 10 *s.*

PLATE XXXVII.

Fig. 12.—An early blastocyst of Sorex in situ in the expanded portion of the uterine lumen. The section is transverse to the axis of the uterus. A small swelling was externally visible (see Fig. 20, which represents the same uterus, natural size, as drawn from the spirit specimen). *u. e.* The uterine epithelium. *bl.* Cavity of the blastocyst, already adhering by a small portion of its walls against the surfaces of the mucosa. The embryonic shield is seen to occupy the topmost surface, and to be turned towards the anti-mesometrical concavity of the uterine swelling. In this stage the hypoblast forms already a completely closed sac, constituting the inner layer of the didermic vesicular blastocyst.

Figs. 13—15.—Three outline sketches in natural size of the uteri (spirit specimens) from which the embryos were taken, of which sections are figured on this plate.

Cat. n$^{os.}$ 2, 65, 52.

Figs. 16—21.—Surface views of the embryonic area reconstructed from the series of sections through the early stages that were obtained from the uteri of the preceding figures.

These surface views, and similarly all those that are represented on the following plates, were obtained from camera lucida outlines that had been drawn with Zeiss' apochromatic objective 16 mm., oc. 4. They are thus about sixty-two times enlarged.

The outline given is not that of the blastocyst, but of the embryonic shield on the top of it.

The cross arrows indicate the exact extent and direction of the sections that are figured on this plate; the small numbers beside the arrows refer to the figure which represents the section.

In Figs. 18, 19, and 21 a distinct protochordal plate was present in the hypoblast; its outline, as underlying the anterior part of the embryonic shield, is indicated by a grey space.

In Fig. 20 all the nuclei that are present in the hypoblast below the epiblastic shield have been figured. It is here seen how they are much more closely packed at the anterior end, i. e. in the region which has here been termed the protochordal plate.

Fig. 22.—Transverse section of a blastocyst (cf. Fig. 16) in which the hypoblast is just being formed by cells detaching themselves from the polar thickening (cf. Figs. 10 and 11), which has become more flattened.

The zona is much thinner and more considerably folded.

Lettering and magnifying scale as in Figs. 5—11.

Mus. Utr. Cat. n$^{o.}$ Sorex 122, 2, 1 *r.* 11 *s.*

Fig. 23.—Part of the folded zona with trophoblast- and hypoblast-cells of a similar embryo. The hypoblastic nuclei, *hy.*, are distinctly larger sized than those of the trophoblast, *tr.*

Mus. Utr. Cat. n$^{o.}$ Sorex 122, 2, 1 *r.* 17 *s.*

Fig. 24.—The embryonic shield of another blastocyst in the same stage. Distinct flattened hypoblast-cells are present below the epiblastic shield, *E.*

Mus. Utr. Cat. n$^{o.}$ Sorex 122, 2 *r.* 7 *s.*

Fig. 25.—Blastocyst of a later stage, having become didermic in its whole extent. At the spots *tr''.* the trophoblast is thickened preliminary to the attachment of the blastocyst to the uterine mucosa (Zeiss' apochr., oc. 4, obj. 16).

Mus. Utr. Cat. n$^{o.}$ Sorex 2^a, 1 *r.* 30 *s.*

Fig. 26.—The epiblastic shield of the same embryo (cf. Fig. 17) more considerably enlarged (Zeiss' apochr., obj. 4, oc. 4). The zona, *z.*, has become extremely attenuated. *tr'.* Trophoblast-cells above the epiblastic embryonic shield (cf. Figs. 5 and 7). In later phases these have entirely disappeared.

Mus. Utr. Cat. n$^{o.}$ Sorex 2^a, 1 *r.* 29 *s.*

Fig. 27.—The modified trophoblastic zone, *tr''.*, of Fig. 25, more considerably enlarged (Zeiss' apochr., oc. 4, obj. 4).

Mus. Utr. Cat. n$^{o.}$ Sorex 2^a, 1 *r.* 30 *s.*

Figs. 28 and 29.—Two sections through another didermic blastocyst, of which the former passes through the hypoblastic protochordal plate, *pp.* (cf. Fig. 18).

Mus. Utr. Cat. n$^{o.}$ Sorex 52 *i*, 4 *r.* 11 *s.*
,, ,, ,, 4 *r.* 3 *s.*

Figs. 30 and 31.—Two sections through yet another didermic blastocyst (cf. Fig. 19). The protochordal plate is cut along its longest diameter.

Mus. Utr. Cat. n$^{o.}$ Sorex 52 *e*, 3 *r.* 26 *s.*
,, ,, ,, 4 *r.* 8 *s.*

PLATE XXXVIII.

Figs. 32—35.—The embryonic shield of four blastocysts that were taken from the same mother (Cat. n°· 73). These tracings were obtained by the reconstruction of the details of structure in the different regions of the embryonic shield from the unbroken series of sections. The epiblastic shield is marked by a dark outline. The annular ring of modified hypoblast has a uniform grey tint, and so has the protochordal plate, which was also already indicated on the foregoing plate.

The gastrula-ridge makes its first appearance in Fig. 32; in the other figures it is much farther advanced, and traces of a gastrula-groove are found. The regions right and left of the gastrula-ridge, as well as behind it, contain the continuous plate of mesoblast, of which the outer boundary is indicated by a dotted line. The arrows have reference to the different sections as figured on this and the next plates; the numbers attached to them are the same as the respective numbers of the figures in which those sections are represented. If the sections do not extend through the whole length of the embryonic region, the arrows are correspondingly shortened.

In Fig. 34 the front part of the annular ring of modified hypoblast is omitted, because this portion being bent in the plane of the section could not allow its outlines to be rigorously traced in the reconstruction process.

In Fig. 32, although obtained from the same uterus, no annular zone of modified hypoblast was as yet present. This zone may consequently be said to appear as a simultaneous modification of the region in question.

Figs. 36—39.—Four sections through the posterior region and first origin of the gastrula-ridge of the embryonic shield of Fig. 32. In four sections, two of which are figured, there is adhesion between the proliferating epiblast (palingenetic hypoblast) and the subjacent layer of flat cells (cœnogenetic hypoblast). At the front end of the incipient gastrula-ridge there are faint traces of a perforation indicated by *p.* in Figs. 38 and 39. *pw.* Cell-mass in front of this: incipient protochordal wedge (cf. Figs. 46—48, and 55, *pw.*, of slightly older stages). *gr.* Proliferating cell-mass behind it: incipient gastrula-ridge.

Fig. 36.—Mus. Utr. Cat. n°· Sorex 73*f*, 2 *r*. 15 *s*.
Fig. 37.— „ „ „ 17 *s*.
Fig. 38.— „ „ „ 19 *s*.
Fig. 39.— „ „ „ 20 *s*.

Figs. 40 and 41.—Two sections through the anterior region of the embryonic shield of Fig. 32. *pp.* The hypoblastic protochordal plate, already more than one cell thick.

Fig. 40.—Mus. Utr. Cat. n°· Sorex 73*f*, 2 *r*. 19 *s*.
Fig. 41.— „ „ „ „ 21 *s*.

PLATE XXXIX.

Fig. 42.—The uterus (Cat. n°· Sorex 73) from which the blastocysts of this and the foregoing plate were taken. Natural size; drawn from the spirit specimen.

Figs. 43—52.—Ten sections (Zeiss' apochr., oc. 4, obj. 4) through different regions of the embryonic shield of Fig. 34. The exact situation and extent of the sections are marked in that figure by numbered arrows.

The protochordal plate, *pp.*, is cut in Figs. 43 and 44, and is giving origin to mesoblast-cells.

Mus. Utr. Cat. n°· Sorex 73 *d*, 2 *r*. 19 *s*.
„ „ „ „ 22 *s*.

In Figs. 45 and 46 there is as yet no mesoblast laterally. The median cells, *pw.*, belong to the foremost extension of the protochordal wedge, which is not yet confluent with the protochordal plate. A thickened keel of epiblast is present in the median line.

Mus. Utr. Cat. n°· Sorex 73 *d*, 2 *r*. 30 *s*.
„ „ „ 3 *r*. 1 *s*.

In Fig. 47 the protochordal wedge, *pw.*, is connected with lateral mesoblast plates; the mesoblast is also present in the annular zone of modified hypoblast, *hy. az.*

Mus. Utr. Cat. n°· Sorex 73 *d*, 3 *r*. 4 *s*.

In Figs. 48—50 the unfolding of the lips of the palingenetic blastopore (front end of the gastrula-ridge) is especially distinct and expressed even in the position of the cells.

In Fig. 50 a faint trace of a partial perforation is observed in the median line.

Fig. 48.—Mus. Utr. Cat. n°· 73 *d*, 3 *r*. 6 *s*.
Fig. 49.— „ „ „ 7 *s*.
Fig. 50.— „ „ „ 8 *s*.

Figs. 51 and 52 are sections further backwards through the gastrula-ridge and its lateral plates of mesoblast.

Mus. Utr. Cat. n°· 73 *d*, 3 *r*. 15 *s*.
„ „ „ 25 *s*.

Figs. 53—55.—Three sections through the whole extent of embryonic shield and annular zone of modified hypoblast (*hy. az.*) of the blastocyst of Fig. 33 (Zeiss' apochr., oc. 4, obj. 8). *pp.* Protochordal plate. *E.* Epiblastic shield. *hy.* Unmodified flattened hypoblast both inside and outside the ring above mentioned. *tr.* Trophoblast. *pw.* Protochordal wedge. *gr.* Gastrula-ridge.

Fig. 53.—Mus. Utr. Cat. n°· Sorex 73 b^2, 2 *r*. 20 *s*.
Fig. 54.— „ „ „ „ 14 *s*.
Fig. 55.— „ „ „ 1 *r*. 19 *s*.

Fig. 56.—Section through the posterior knob of the gastrula-ridge with

the mesoblast stretching backwards. The future somatic mesoblast-cells (also in Figs. 57—60) are distinguished by their more flattened shape and stronger absorption of staining reagents.

Mus. Utr. Cat. n°· Sorex 75 b^2, 1 *r*. 14, 15 *s*.

Figs. 57 and 58.—Two sections through mesoblast that has originated partly from the gastrula-ridge, partly from the annular zone of hypoblast; karyolytic figures determining the details of the latter process are very distinct.

Fig. 57.—Mus. Utr. Cat. n°· Sorex 73 b^1, 4 *r*. 21 *s*.
Fig. 58.— ,, ,, ,, 17 *s*.

Figs. 59—61.—Three sections through other blastocysts in which further confirmation of these karyolytic processes is distinct.

In Fig. 59, *x* indicates a spot where the dividing nuclei have just separated and rearranged themselves.

Fig. 59.—Mus. Utr. Cat. n°· Sorex 73 a^1, 3 *r*. 23 *s*.
Fig. 60.— ,, ,, ,, 18 *s*.
Fig. 61.— ,, ,, 73 *c*, 3 *r*. 13 *s*.

(This latter section belongs to a series of which no surface reconstruction is given.)

PLATE XL.

Figs. 62—64.—Three surface views (obtained by reconstruction from an unbroken series of sections drawn with camera) of three embryos from the same uterus (No. 45). The mesoblast, of which the outer boundary is indicated by a dotted line, stretches some distance beyond the epiblastic shield. It is in this stage already a continuous plate, only interrupted in the median line below the epiblastic shield by the gastrula-ridge (*gr.*), the protochordal wedge (*pw.*), and the protochordal plate (*pp.*).

The arrows indicate the exact situations, and also the extent of the sections figured under the corresponding numbers.

Fig. 65.—The uterus, No. 45, natural size, drawn from the spirit specimen.

Figs. 66—68.—Three sections through the embryonic region of Fig. 62. *pp.* Protochordal plate. *pw.* Protochordal wedge. *hy. az.* Remnants as yet fairly distinct of the annular zone of modified hypoblast of Figs. 33—35.

Fig. 66.—Mus. Utr. Cat. n°· Sorex 45 *c*, 4 *r*. 5 *s*.
Fig. 67.— ,, ,, ,, 2 *s*.
Fig. 68.— ,, ,, ,, 3 *r*. 18 *s*.

Fig. 69.—An oblique section through another embryonic shield of the same stage. Letters as above. *C.* Rudiment of a canal in the protochordal wedge.

Mus. Utr. Cat. n°· Sorex 45 *e*, 4 *r*. 10 *s*.

Figs. 70—77.—Eight sections through part of the embryonic shield of Fig. 63. Lettering as above.

Fig. 70.—Mus. Utr. Cat. n°· Sorex 45 *b*, 2 *r.* $\frac{18}{20}$ *s.*
Fig. 71.— ,, ,, ,, 25 *s.*
Fig. 72.— ,, ,, ,, 3 *r.* 3 *s.*
Fig. 73.— ,, ,, ,, 5 *s.*
Fig. 74.— ,, ,, ,, 7 *s.*
Fig. 75.— ,, ,, ,, 9 *s.*
Fig. 76.— ,, ,, ,, 11 *s.*
Fig. 77.— ,, ,, ,, 17 *s.*

Fig. 78.—Part of a section through an embryonic shield not here figured. Here, again, there is an unmistakable rudiment (*c.*) of a canal in the protochordal wedge.

Mus. Utr. Cat. n°· Sorex 45 *a*, 4 *r.* 22 *s.*

PLATE XLI.

Figs. 79—81.—Three surface views of three embryos from the same uterus (No. 42). They were obtained in the same way as those of the foregoing plates. *pp.*, *pw.*, *gr.* as in Figs. 62—64. *Cœl.* Regions of the cœlom. (*per.*: in Fig. 80 first indication of pericardial cœlom, in transverse sections in Fig. 88.)

Fig. 82.—The uterus, No. 42, drawn from the spirit specimens (natural size).

Figs. 83—87.—Five sections through the embryonic shield of Fig. 79. The sections are oblique, i. e. asymmetrical. This brings out all the more clearly (especially in Fig. 87) the slight but still marked differences between the mesoblast that more particularly belongs to the protochordal plate (*mes. pp.*), that which is continuous with the protochordal wedge (*mes. pw.*), and that which belongs to the region of the gastrula-ridge (*mes. gr.*). Lettering as before. *gr.* and *gg.* The front end of gastrula-ridge and gastrula-groove as seen in oblique sections. (In Figs. 85 and 86, and also in Fig. 90, there are rudiments of a protochordal canal inside the protochordal wedge.)

Fig. 83.—Mus. Utr. Cat. n°· Sorex 42 *c*, 3 *r.* 6 *d.*
Fig. 84.— ,, ,, ,, 10 *d.*
Fig. 85.— ,, ,, ,, 12 *d.*
Fig. 86.— ,, ,, ,, 13 *d.*
Fig. 87.— ,, ,, ,, 18 *d.*

Figs. 88 and 91.—Two sections as indicated in Fig. 80.

Fig. 88.—Mus. Utr. Cat. n°· Sorex 42 *e*, 3 *r.* 6 *s.*
Fig. 91.— ,, ,, ,, 19 *s.*

Figs. 89 and 90.—Idem for Fig. 81. Lettering as above.

Fig. 89.—Mus. Utr. Cat. n°· Sorex 42 *b*, 4 *r.* 27 *s.*
Fig. 90.— ,, ,, ,, 22 *s.*

PLATE XLII.

Figs. 92—95.—Four diagrammatical figures to illustrate certain theoretical speculations developed in the text (p. 533).

Fig. 92.—An amphibian or cyclostomatous gastrula-stage.

Fig. 93.—A hypothetical transition between the foregoing and the mammalian diagram, fig. 95 (partial perspective).

Fig. 94.—A sauropsidan gastrula-stage (copied with very slight modifications from Rabl).

Fig. 95.—A mammalian stage corresponding to the phase which is also represented in the surface views 62—64 (partial perspective). Grey and black: trophoblast, embryonic epiblast. Black with white dots: palingenetic hypoblast of the protochordal wedge. Black with parallel stripes: palingenetic hypoblast of gastrula-ridge. Blue: cœnogenetic hypoblast with protochordal plate (*pp.*) and modified annular zone (*hy. az.*).

In Figs. 92 and 93 the distinction between palingenetic and cœnogenetic hypoblast is not actually existent, but arbitrarily introduced in order to elucidate the facts as presented by 95.

Terminations of Nerves in the Nuclei of the Epithelial Cells of Tortoise-shell.

By

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With Plate XLIII.

The land tortoise (Testudo græca), so commonly imported into England from the south of Europe, appears to be a very sluggish animal. This is not really the case, and its movements on a hot summer day are the reverse of phlegmatic. In this condition its carapace is sensitive to the slightest impact. If the carapace or plastron be very gently tapped, the nearest leg is alone withdrawn, a heavier tap causing a withdrawal of its whole body. We have here, therefore, a structure which is a true sensitive surface, and like the soft skin of a frog or of a man, it is brought into relationship with the central nervous system. Like the soft skin of other animals it may be mapped out into areas, from which the nerve-fibres passing to the spinal cord are all especially connected with outgoing motor nerves, so that the definite reflex movements of limbs as already described may come about.

The above experiment naturally suggested that the sensory nerves passed right through the thick bone of the carapace and plastron, and ended near the outer surface, either in the epithelial tissue of the tortoise-shell itself or in the layer of connective tissue which unites it to the subjacent bone.

After removal of a scute of tortoise-shell the connective tissue outside the bone was found, in confirmation of this surmise, to contain sensory nerve-fibres, for the application of acetic acid, or of an interrupted galvanic stimulus, caused definite reflex defensive movements, similar to those which follow the application of acid to the frog's skin.

Inasmuch, therefore, as sensory nerves evidently end quite superficially, it became an interesting question to determine their exact mode of termination in the curiously modified tissues of the carapace. Portions of the carapace, generally taken from the region of the costal plates, were softened in chromic acid and nitric acid fluid, frozen, and cut with a thick-bladed razor. In this way one can obtain fairly thin sections even of the tough tortoise-shell. The sections were treated in various ways, with a view of demonstrating nerves or nerve terminations, and in no case was I able to discover any nervous structure in the tortoise-shell itself.

In the subjacent connective-tissue layer, however, were bodies which I, at first sight, thought were end organs (Pl. XLIII, fig. 1). They turned out to be the transverse sections of curiously modified nerve-fibres. These nerve-fibres are easily distinguished from the blood-vessels (which in this situation are devoid of a muscular coat) by their solid appearance (fig. 2), strong connective-tissue covering, and by their occasional transverse section, which is very characteristic in appearance.

Fig. 1 represents, in transverse section, two of these fibres bound together by a common sheath of connective tissue (H). Each fibre consists of an external layer of concentrically arranged connective tissue, consisting of laminæ of colloid granular material with intervening connective-tissue corpuscles (M). Within this is a colloid-looking core (K), devoid of nuclei, and also staining pink with picro-carmine.

In the centre of the core is generally to be found a small spot, probably an axis-cylinder, somewhat differentiated from the rest of the core (G).

No trace of medullary matter is to be found in connection with any of these nerves, nor are ordinary medullated fibres to be found in this region; and one is forced to conclude that owing to their peculiar situation—perhaps on account of the pressure of the hard scutes placed immediately above them—the medullated nerves are replaced by axis-cylinders, enclosed and protected by the sheaths of modified connective tissue just described.

These modified nerve-fibres can be traced back a little way into the bone, and no doubt ultimately pass into the ordinary medullated nerves found so plentifully on the inner surface of the carapace. Under the scutes they freely branch, becoming smaller and smaller, and ultimately terminate in the lower epithelial cells of the tortoise-shell. We have, therefore, medullated fibres passing from the central nervous system to the bone of the carapace and plastron, these then pass into the medullary nerve-fibres seen under the scutes, from which, as we shall presently see, fine terminal naked axis-cylinders run into the scutes.

The final intra-epidermic termination of the nerves was never seen in any of the sections, for the softening of the tissue previously to its cutting prevented their subsequent demonstration by staining agents. The nerve endings may, however, be demonstrated by another very simple method.

The scutes from a recently killed tortoise are removed in pieces with a sharp scalpel, care being taken to keep attached to their under surfaces as much as possible of the subjacent connective tissue; and it will be found advisable before doing so to remove as much as possible of the dense outer part of the scute. In this way one can obtain thin and fairly transparent pieces of tissue, consisting of the lower layers of the tortoise-shell and the tissue connected with it. These are placed in absolute alcohol 2 parts, and distilled water 1 part, and after twelve hours are thoroughly steeped in distilled water until every trace of alcohol is removed. The tissues are then placed in a solution of hæmatoxylin until they are sufficiently stained; they may then be mounted in balsam, the connective tissue or deeper layer being above the epithelium and next the cover-glass.

Hæmatoxylin Solution.

A. $\begin{cases}\text{Ammonia alum, 3 grammes;}\\ \text{Distilled water, 100 c.c.}\end{cases}$ B. $\begin{cases}\text{Pure hæmatoxylin, 3 grammes;}\\ \text{Absolute alcohol, 16 c.c.}\end{cases}$

Mix A and B, keep in diffuse daylight for two weeks, and dilute with 20 volumes of distilled water.

On looking down into the connective tissue with a power of three or four hundred diameters, the modified nerve-fibres are seen branching in all directions. On deeper focussing the lower cells of the epithelium are seen from below. Their outlines are in most situations fairly well seen, and their nuclei should be stained with the hæmatoxylin.

In these preparations the nuclei frequently shrink within the nuclear cavities, appearing as dark blue granular masses (B, fig. 4); but in most cases they fill the nuclear cavity, and their chromatin filaments can clearly be made out. The greater number of cells are devoid of any nerves, but here and there nerve-fibres may be seen branching again and again in the connective tissue, and sending their finest ramifications to the nuclei of the epidermic cells. These are what appear to be definite sensitive spots where alone the nerves terminate. These spots are of variable size, so small as to correspond to a space occupied by only a dozen cells, or so large as to occupy two or three fields of the microscope. I should say that some twenty or thirty of these "spots" might be found on one square inch of a costal scute. Between these spots the epithelium presents, as already observed, nothing very remarkable, but within the spot the appearance is very striking.

The non-medullated fibres deeply stained with the logwood divide again and again, sending, in many cases, hundreds of fibres to the epithelial cells. Fig. 3 represents a sector of one of these spots carefully drawn from a specimen. At the circumference (B) the fibres terminate in only a few of the epithelial cells, but towards the centre all or nearly all of the cells receive fibres. The outlines of the cells are not well marked, the fibres at first sight appearing to terminate in little round blue masses, which are in reality the nuclei of the cells.

In fig. 4 a very small portion at the outer part of a sensitive spot is more highly amplified. At the upper part of the figure the epithelium outside the spot is seen. Below this the terminations of the nerves can readily be made out. They certainly pass into the nuclear cavity. Whether they end in little flat plates within the nuclear cavity and closely applied to the outside of the nucleus, or whether they are prolonged into the chromatin of the nucleus, I should not like dogmatically to state. I am inclined to believe in the latter view, and think it probable that they are continued into true nuclear substance. The appearances seen at E E E, fig. 4, are probably due to shrinkage as a result of treatment with alcohol; but in C C, fig. 4, the nuclear cavity is completely filled by the nucleus, all the chromatin substance having apparently gone to form the knob or cup at the end of the nerve, leaving the rest of the nucleus almost devoid of granular matter, and very faintly tinted by the hæmatoxylin.

The nerves end in the cells of the rete alone, for it is impossible to trace them beyond the deeper layer of the epithelium. This is what might be expected, for in the adult tortoise-shell the rete consists of one, two, or perhaps three layers of nucleated rounded cells, and above these, with hardly any transitional tissue, there are the dense laminæ of the horny layer, made up of flattened keratinised scales with unstainable nuclei.

It follows from the foregoing remarks that the scutes of the tortoise, in spite of their hard, dense nature, form a very typical epidermic sensory covering for the animal. As in the soft skin of mammals, the nerves end in localised sensitive spots in the epidermis, and before penetrating this tissue they form a horizontal plexus in the upper part of the connective tissue.

The final terminations of nerves in epithelium has received much attention from histologists, who have studied this subject perhaps most fully in the tadpole's tail.

In some situations the nerves appear to run entirely between the cells—indeed, this appears to be generally the case (Ranvier, **1**; Klein, **2**; Eberth, **3**; Leboucq, **4**). They either end in a simple plexus, or terminate in very small knobs or plates, which, judging from the drawings and preparations I have seen, are for the most part much smaller than the chromatin knobs of the tortoise.

But some authors have traced nerves into the epithelial cells themselves, where they appear to end in little knobs embedded in the cell protoplasm, *near* but never *in* the nucleus. Thus Pfitzner (5), working with the Amphibia, finds this to be the case; and more recently Macallum (6) describes nerves terminating both between and within the epidermic cells of the tadpole's tail.

In the tortoise-shell the nerves certainly pass right into the nuclear cavity, within which the only structures deeply stained by hæmatoxylin are the club- or cup-shaped masses into which the nerves pass. A very remarkable fact is the ease with which these preparations are obtained. I have made over twenty, and in all cases good demonstrations were obtained. I have tried several gold methods, but they were vastly inferior to the logwood, and, as usual, chiefly characterised by want of uniformity in the results obtained. In other situations the non-medullated nerves of the tortoise do not stain at all readily with logwood.

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DESCRIPTION OF PLATE XLIII,

Illustrating Dr. John Berry Haycraft's paper on "Terminations of Nerves in the Nuclei of the Epithelial Cells of Tortoise-shell."

FIG. 1.—Section through the lower part of the tortoise-shell, the subjacent connective tissue, and part of the bone of a costal plate. *A.* Lower laminæ of horny layer of tortoise-shell. *B.* Cells of rete, with big nuclei and deep ridges passing into subjacent connective tissue. (*c*) Process—profile view of a ridge—of connective tissue running into epithelial cell. *D.* Pigment-cell in tissue around nerve-fibres. *H.* Sheath common to two nerve-fibres. *m.* Outer covering of granular modified connective tissue. *K.* Inner part of nerve-sheath, consisting of granular non-nucleated connective tissue. *G.* Spot in centre, probably an axis-cylinder. *E.* Bone.

FIG. 2.—Longitudinal view of a nerve considerably smaller than the one represented in transverse section (Fig. 1).

FIG. 3.—Part of a sensitive spot; the tortoise-shell is viewed from below. × 250. *A.* Centre of spot. Branching nerve-fibres seen ending in nuclei of epithelium. Border of cells not seen because of low power used. *B.* At periphery of spot, where most of the epithelial cells are unconnected with nerve-fibres.

FIG. 4.—Part of the same highly magnified. × 800. *A.* Nucleus outside sensory spot. It contains chromatin filaments. *B.* Nucleus that has shrunk within nuclear cavity. *c c.* Nerve-fibre passes into nuclear cavity, and apparently ending in the chromatin of the cell, the rest of the nuclear cavity being filled with clear, almost colourless material. E E E. Nothing is to be seen inside the nuclear cavity except the knobs terminating the nerves. The rest of the nucleus has probably shrunk around this. *H.* Towards centre of spot the outlines of the epithelial cells are very indistinct.

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