

INTERNAL ANATOMY OF EURYURUS ERYTHRO- PYGUS (BRANDT). (DIPLOPODA).*†

HUGH H. MILEY.

INTRODUCTION.

In a previous paper the writer (1927) reported the results of observations upon the development of the male gonopods, distribution and life history studies of *Euryurus erythropygus* (Brandt), a Polydesmid millipede, which lives on decaying wood.

A review of the anatomical literature on Diplopods revealed no information concerning the internal anatomy and physiology of *Euryurus*. Anatomical studies available were mainly on European forms, mostly of Germany, and with relatively little included on the *Polydesmidæ*. The literature on investigations concerning the digestion and embryology of the alimentary tracts of the Myriapoda, as well as some other studies, is rather meager. There exists no connected description of the Diplopods or Chilopods. The anatomical studies of Attems (1926), Randow (1924), Verhoeff (1910-1915), and (1926), in Bronn's "Tier-Reich," Effenberger (1909), Wernitzsch (1910) and Rossi (1901), (1902) are the most extensive and important for Diplopods. The best bibliographies were found in the references by Latzel (1884), Attems (1926) and in Bronn's "Tier-Reich" (1926).

The whole subject of arthropod histology during moulting and metamorphosis is rather obscure and there are often as many interpretations as there are investigators.

This paper deals with the internal anatomy of *Euryurus*, the histology of the mid-intestine during ecdysis and feeding condition, fauna found in the intestinal canal and especially with the body, leg and mandible musculature and the gross and histological anatomy of the digestive tract. A comparison with the anatomy of other *Polydesmidæ* and *Julidæ*, already studied, showed differences and similarities.

*Dissertation presented in partial fulfillment of the requirements for the Degree of Doctor of Philosophy in the Graduate School of The Ohio State University.

†Contribution No. 103 from the Department of Zoology and Entomology, Ohio State University.

Leidy (1851) first called attention to the extensive floral and faunal association within the ventriculus, the large intestine and rectum of *Spirobolus marginatus*, a millipede, which, like *Euryurus*, lives on decaying wood. His description of the alimentary tract will be included in the discussion of the tract of *Euryurus*.

In all specimens of *Euryurus* in which the intestinal tract was examined flora and fauna were found. The fauna found are as follows: Gregarines in the fore-intestine (genus and species not identified); *Nyctotherus velox*, a protozoan, in the hind-intestine and rectum.

The nematodes *Rhigonema infectum*, *Thelastoma attenuatum*, identified by N. A. Cobb, were found in the posterior part of the mid-intestine and the anterior portion of the hind-intestine. The malpighian tubules are located on a portion of a constricted area (Plate III, Fig. 4). As many as fifteen nematodes were found in a small area just preceding the constriction and as many as twenty-six in a small area following it.

Mites as ectoparasites were observed in a few cases.

A few investigators have studied the physiological relationship of many insects to organisms, but the writer has found nothing of a similar work on the Myriapoda.

MATERIAL AND TECHNIQUE.

The animals used were collected near Oxford, Ohio, although a few were found around the vicinity of Columbus and Lancaster, Ohio. Attention is called to a wider distribution of this organism than previously reported by the writer (1927). Many adults and especially a large number of moulting and non-moulting larvæ, of all stages, were found in their natural surroundings by the writer at Oxford, the latter part of August (1927). The millipedes are easily kept in the laboratory and breed in the somewhat artificial environment described by the writer (1927). An abundance of material was available for study, including adults and the seven larval stages.

Many difficulties have been encountered in these studies, both in gross dissections and histological technique. The feeding animals, especially adults and later larval stages, besides being small and flat have an extremely thick, hard and brittle chitinous exoskeleton and the underlying extremely delicate tissues adhere closely to the chitin. *Spirobolus margi-*

natus, a much larger, cylindrical millipede, is much easier to work with because of its size, shape and flexible chitinous body wall.

The internal anatomy described has been determined by careful gross dissections of feeding adults, moulting and non-moulting larvæ, using binocular microscope, and by serial transverse and longitudinal sections of entire animals. Serial longitudinal sections of all stages were prepared.

Material fixed in Carl's or Henning's or Gilson's fluids gave good results. Delafield's hematoxylin and eosin were used for ordinary studies and Heidenhain's iron hematoxylin for cytological work, with sections cut from 3 to 5 microns in thickness. Sudan III was used in testing for fat. Euparal, used instead of balsam, was also found valuable.

Photomicrographs of histological details have been taken and drawings made using a micro-projector drawing apparatus in vertical position.

INTERNAL ANATOMY.

THE ALIMENTARY CANAL.

Effenberger (1907), (1909), Verhoeff (1914), (1910-1915), Attems (1926) have made rather extensive observations on European *Polydesmidæ*. Effenberger (1909) compared *Polydesmus* with *Julus* studied by Krug (1906). The outstanding works on *Julidæ* are by Plateau (1876), Voges (1878), Visart (1894), Krug (1906), Verhoeff (1910-1915), Randow (1924). Randow (1924) made the most extensive comparisons regarding the morphology and physiology of the intestinal canals of *Julidæ*.

Leidy (1851) gives a short description of the alimentary tract using a slightly different terminology from that generally used at present. Considering, as with the insects, that the attachment of the Malpighian tubules is a landmark in marking off the hind-intestine from the mid-intestine, the proventriculus as used by Leidy consists of the fore-intestine and the mid-intestine, which includes the ventriculus or true stomach. In *Polydesmidæ* and *Julidæ* the hind-intestine commences with a ring fold shown as (RF) in Plate III, Figs. 4, 4-C. This ring fold is slightly anterior to the attachment of the Malpighian tubules.

The ventriculus according to Leidy is a part of the hind-intestine, since it is set off from the mid-intestine by the attachment of the Malpighian tubules and is lined with a chitinous intima. Leidy called the Malpighian tubules biliary tubes and the hind-intestine the large intestine.

The later writers on *Polydesmidæ* and *Julidæ* divided the tracts into three main divisions, namely, fore-, mid-, and hind-intestine.

The intestine of *Euryurus* shows some similarities with and some differences from similar studies on European *Polydesmidæ* and *Julidæ*.

THE GROSS ANATOMY OF THE ADULT CANAL OF *Euryurus*.

The alimentary canal of the adult *Euryurus* shows considerable specialization in form and structure. It extends in almost a straight line from mouth to anus and is very large and capacious in relation to the size of the animal, in accordance with the nature of the food. There is a general rule that in herbivorous insects the alimentary tract is longer or more capacious than in carnivorous insects. In the local Myriapoda, the digestive tract has, for the most part, a greater circumference in the Diplopods. Three chief divisions of the tract of *Euryurus* are readily recognized, the fore-intestine (stomodeum), the mid-intestine (mesenteron or ventriculus), and the hind-intestine (proctodeum). The general form of the external gross anatomy is shown in Plate III, Fig. 4, and of the internal gross Anatomy in Plate III, Fig. 4. The natural lengths of three portions of the photographed alimentary tract were as follows: fore-intestine = 5 mm.; mid-intestine to Malpighian tubules = 13 mm.; Malpighian tubules to anus = 16 mm.

The oesophagus is a comparatively short slender tube, lined with a chitinous intima, extending to about the fourth trunk segment. Here it enlarges and connects with the mid-intestine. Internally at this junction there is a projecting valve which is formed by a padded girdle composed of six cushions or elevations each of which has a ridge in the middle extending into a point. These points (P) are quite long and bend outward into the lumen. (Plate I, Fig. 3 and 4-C). There is a ring furrow in front of the girdle. As many as twelve long rods, attached anteriorly in the oesophagus, have been counted projecting into the mid-intestine. Two, curving to a common attachment in the oesophagus, were noticed in some specimens.

The mid-intestine is a rather long, capacious, straight tube and is ochreous yellow in color. It is almost uniform throughout in size and usually smooth, although some irregular folds were noticed. The intestine commences to decrease in diameter a short distance anterior to the entrance of the Malpighian tubules. Where this narrowing begins there is a noticeable internal thickening encircling the intestine. A gross internal examination reveals a ring fold or valve and a ring furrow. (RF) (Plate III, Fig. 4-C). This marks the commencement of hind-intestine and the Malpighian tubules enter the intestine a short distance posterior to the ring fold. For insects the attachment of the Malpighian tubules is considered as the landmark in setting off the hind-intestine from the mid-intestine. Verhoeff (1910-1915) states that the ring fold is absent in European *Polydesmidae*. The mid-intestine and its digestive epithelium terminate abruptly, being followed immediately by hind-intestinal epithelium. Sometimes there is a thickening of the muscle layers at this junction and it is spoken of as the pyloric valve in insects. In *Euryurus* there is considerable thickening of muscle layers posterior to the ring fold and which continues a short distance posteriorly. This, by Attems (1926), was called a closure valve (Verschlussklappe) in *Julida*. This portion Leidy called the ventriculus and it is short, cylindrical and much narrower and stronger than the mid-intestine. Upon its exterior surface it is smooth.

Internally, as with the oesophagus, a series of longitudinal folds were noticed in the chitinous intima, and long rods, resembling those found in the oesophagus, were observed in this region.

Verhoeff (1910-1915) has discussed the hind-intestine of certain European *Polydesmidæ*, comparing them with the *Julidæ*. Krug (1906) divided the hind-intestine of *Julidæ* into three sections. Verhoeff divided the hind-intestine of *Julidæ* into five sections, namely, a urine chamber, fold chamber, wrinkled chamber, pre-anal constriction and rectum. The long main chamber of the hind-intestine of *Polydesmidæ*, he compared to the fold chamber and wrinkled chamber of *Julidæ*. Randow (1924) found five sections but he called the first "*Verschlussklappe*" or closure valve.

In *Euryurus* the hind-intestine is narrow for a short distance posterior to where the Malpighian tubules enter it. It widens rather abruptly and continues about the same size to the pre-anal constriction, and again widens into the rectum. The hind-intestine is stronger than the mid-intestine and externally presents some irregularities such as indentations and slight folds, and is dark brown in color, for the most part. Internally a urine chamber, a fold chamber, a pre-anal constriction and a rectum are present. However, these sections vary in many respects from those of European *Polydesmidæ* and *Julidæ* observed by others. At the ring fold there are numerous longitudinal elevations and depressions. Larger longitudinal folds are seen in the narrow region and these continue to the fold chamber which in *Euryurus* is characterized by numerous small, dark brown papilla-like structures which have not been described in the literature reviewed. The pre-anal constriction presents a chitinous intima with longitudinal folds.

The writer (1927) named the mouth parts and described some aspects of the external anatomy of *Euryurus*.

THE HISTOLOGICAL STRUCTURE OF THE FORE-INTESTINE.

Oesophagus.—A pharynx is not referred to in the literature reviewed but Effenberger (1909), Verhoeff (1910-1915), Attems (1926) describe the fore-intestine as being hexagonal in shape behind the mouth opening. This is true for *Euryurus* but further posteriorly a cross section presents a different picture.

The fore-intestine for its entire length has a heavy chitinous lining continuous with that of the body wall. This chitinous cuticula is of uniform thickness but the epithelium and muscles vary some in the different regions. Near the mouth opening the epithelium consists of a definite, thin layer of small irregular cells. Further posterior the epithelium gradually thickens to the region characterized by a series of usually six longitudinal folds (Plate I, Fig. 1 and Plate II, Fig. 1).

The primary intima is well developed. The secondary intima underneath is almost transparent.

The epithelium consists of irregular elongate cells, whose nuclei located near the bases contain deep staining chromatin material. A basement membrane is present. (Plate I, Fig. 2.)

The longitudinal muscles start near the mouth and are most numerous at those points where the epithelium invaginates. They do not

all run directly longitudinally, but some intervene, so that cross-sections of this region show some of them running in an oblique fashion. All sections prepared show that the space between the epithelium and the circular muscle layer is not completely filled by these longitudinal muscles. Tracheoles were present, scattered among the longitudinal muscle fibers and what Effenberger (1909) and Krug (1906) called a homogeneous connective tissue. No connective tissue cells were observed in *Euryurus* as Krug (1906) reports for *Julus*.

The circular muscles form a layer outside the longitudinal muscles. This layer varies somewhat in thickness and completely surrounds the tract. Striations are easily observed here as well as in muscle of other portions of the tract except in the mid-intestine. Visart (1895) concluded from his studies on other forms that all the muscle in the intestine is striated. Randow (1924) seems to have the same opinion in regard to Julidæ.

Oesophageal Valve.—The fold of tissue composing this valve lies in the transition from the fore-intestine to the mid-intestine. (Plate I, Fig. 3). The gross appearance has been previously described by the writer. Effenberger (1909) merely mentions the presence of a valve in *Polydesmus*. Intima, epithelium, basement membrane, longitudinal and circular muscle fibers are present. The main structure of the fold is similar to that of the oesophagus.

The intima ends at (A) on the posterior surface of the fold which marks the limits of the fore-intestine.

The epithelium of the anterior face of the oesophageal valve continues much the same as in the oesophagus until just before reaching the tip of the fold. Here the cells gradually elongate until the end of the fore-intestine is reached. The epithelial cells of the mid-intestine are cuboidal at the annulus where they commence. A short distance back they are higher and rod-shaped. The basement membrane is continuous from the fore-intestine to the mid-intestine.

The longitudinal muscles of the fore-intestine end near the base of the fold. On the posterior surface of the fold the inner longitudinal muscles of the mid-intestine commence. They are fewer in number and smaller than those of the fore-intestine.

The circular muscles of the fore-intestine end near the annulus on the posterior surface of the oesophageal valve. The circular muscles of the mid-intestine appear soon after the inner and outer longitudinal muscles of the mid-intestine begin. They form a continuous layer.

THE MID-INTESTINE.

The mid-intestine or ventriculus is an elongated tube and is almost of uniform size. (Plate I, Figs. 4, 5). Its lumen is considerably larger than that of the oesophagus and is without folds. The histology of this portion of feeding animals varies in some respects from that of moulting forms so will be described separately.

A. Feeding Condition.

Cross sections of tracts of feeding animals showed the condition indicated in Plate I, Figs. 4, 5 and Plate II, Fig. 2. Towards the

lumen the epithelial cells are covered by a rod-like fringe. (CSB). This extends from behind the oesophageal valve at the anterior end of the mid-intestine to within the hind-intestine. Many times one observes a separation of the fringe but in many places it remains in position. The rods do not stain with eosin.

A membrane analogous to the peritrophic membrane of insects is present in *Euryurus* but the cuticula is distinct and separate. In the insects the usual explanation given is that this process of formation continues indefinitely and the peritrophic membrane shrinks around the food in the lumen of the intestine, while new membranes are repeatedly being formed by the discharging epithelial cells.

The epithelium is composed of a single layer of small cylindrical cells which appear like a fringe of very small rather uniform rods located on a tunica propria or basement membrane.

Some of the cells are larger towards the lumen. The growing cells push themselves between the old cells. Mucous cells as found by Balbiani (1890) in *Cryptops* were not observed in *Euryurus* nor did Randow (1924) find them in *Julidæ*.

Secretion is holocrine, that is, the entire cell contents are discharged into the lumen of the gut.

The cells, in *Euryurus* have comparatively large nuclei, nucleoli, chromatin lumps and contain much granulated secretion. The cell membranes in thin sections are usually very distinct. On the distal borders of the cells a thin homogeneous, non-alveolar edge is found under the rod-like fringe.

The tunica propria or basement membrane is a smooth or slightly waved lamella. It cannot be easily differentiated from the layers of circular muscle which follow.

Outside the two circular muscle layers is found a layer of cells which Plateau (1876) and Visart (1895) called adipose tissue in the forms they studied. Rossi (1902) and Leger and Duboscq (1904) are against this opinion. Krug (1906) called it "Drusenschicht" or glandular layer and Randow (1924) prefers the more general names "Hüllschicht" or "Leberschicht" designated by Verhoeff (1910-1915) as the function of this layer is in many respects that of a liver. Fixing with osmic acid in a number of cases has not shown it to be a fat network. Sudan III proves the presence of fat in some cases.

This, in *Euryurus*, is a single layer (H) which is found over the entire mid-intestine. The cells are of various sizes. Its structure is compact just as Krug (1906) and Randow (1924) observed in *Julidæ* but Verhoeff (1910-1915) described it as being loose. The nuclei are spherical and show chromatin lumps in connection with the nuclear membrane and nucleoli. Frequently open spaces were observed where presumably xylol had dissolved the fat.

Yellow granules of various shapes are very characteristic in the covering layer.

The writer observed an increase of granules after specimens of *Euryurus* were starved for some weeks. Possibly the granules were excretory material but tests for uric acid and guanin were negative as were tests for albumen and stored iron.

No such layer, in a similar position, is found in insects.

In *Euryurus*, what is thought to be internal small longitudinal muscles surrounded by clear spaces are present at regular intervals in the portion of the network near the layer of circular muscle.

External groups of longitudinal muscle were observed outside and attached to the network.

The intestine of *Euryurus* is surrounded by numerous fine tracheoles. The tracheoles frequently pierce the network as is indicated by small, spherical bodies with clear spaces observed in sections.

B. Moulting Condition.

The condition of the mid-intestine of a specimen in the seventh larval stage which had just shed its exoskeleton is shown in Plate II, Fig. 3. This condition has been observed only in moulting or just moulted specimens of all seven stages of *Euryurus* sectioned. Gross dissections and microscopic sections of many specimens have disclosed no such condition in the tracts of feeding animals. The bodies labelled (DC) have been grossly dissected from moulting specimens. The bodies apparently not containing nuclei but concentric optical rings were not green in color but in view of the possibility that they might be algæ or fungi, cultures were tried, using plain agar agar and nutrient agar media and filtered lake water to which had been added decaying wood and heated to boiling. After many attempts these bodies were not successfully cultured. That some of the bodies are slightly phagocytic has been shown by experiments, using India ink and carmine, as they ingested small droplets of the ink or carmine. That the condition is not seasonal has been shown by sections of animals made during summer, fall, winter and spring.

The preceding observations seem to indicate that the condition is connected with the process of moulting and its associated phenomena. It is apparent that if this be true the process is very intricate. At any rate many questions concerning it are yet unsolved.

The bodies (DC) may be digestive cells given off from the old epithelium of the mid-intestine. It appears also that there has been a regeneration of the entire mid-intestine epithelium and that an old epithelial ring (AE) lies inside the outer tube. The cells have been observed multiplying amitotically in the inner ring.

In serial cross sections a pocket begins ventrally and anteriorly. (Plate I, Fig. 15-A). This is outside the circle of a tomodeal epithelium. Followed posteriorly, the pocket widens, and soon the stomodeal wall is interrupted ventrally (Plate I, Fig. 15-B). Continued posteriorly, the discontinuous stomodeal ring shrinks dorsally, and a crescent of other epithelium expands dorsally, until finally the former disappears and the entire tube is composed of the epithelium continued backward from the outer wall of the original pocket. (Plate I, Fig. 15-C).

This can only mean that the pocket is the anterior end of the ventricular lumen outside the lower lip of a short pre-ventricular fold between stomodeum and mesenteron, or ventriculus. The same structure occurs in insects; the pre-ventricular fold may be a mere rim at the anterior orifice of the stomach, or a long funnel-like tube. In

Euryurus it is very short, and the opening slopes from above forward and downward.

Verhoeff (1910-1915) in his eighth number of "Die Diplopoden Deutschlands" described his observations and those of vom Rath (1890) briefly in regard to the relations of the intestinal tract to moulting and above all to the characteristic phenomena which he designated as "leucocyte flood." His statements are mainly relative to *Iulidæ*, while *Polydesmus* and *Craspedosoma* are only briefly treated. Most of his material regarding *Polydesmus* is in a special article (1914) devoted to the transformation of the mid-intestine in *Polydesmus* during the moulting periods. A series of *Polydesmus monticolus vallicolus* Verh. larvæ in stages of moulting were observed and differences from conditions in *Iulidæ* were recorded and a few physiological factors considered.

Verhoeff stated that his theories concerning mid-intestinal histolysis show many loop-holes, which, he commented, is not surprising as it has never been observed before and is a very intricate process. It is true that many questions are yet unsolved. Verhoeff claims that the spheres are not digestive droplets because they are much larger and often nucleated and have the same appearance as leucocytes.

Randow (1924) in his studies upon epithelial regeneration did not include observations during moulting. In *Julus* he states that the renewal of epithelium takes place through "Blastemzellen" found over the entire mid-intestine as previously mentioned.

Randow and Verhoeff are the only workers who have made observations upon the epithelial regeneration in *Iulidæ*. Randow objects to Verhoeff calling the epithelial cells leucocytes, a name which he thinks should be reserved for bodies in blood and body cavity fluids. Otherwise he is in agreement with Verhoeff's observations of regeneration during the non-moulting condition.

Hundreds of sections through the mid-intestine of just moulted specimens of *Euryurus* showed the condition as shown in Plate II, Fig. 3. There were two layers of epithelial cells and in between large numbers of spherical bodies of various sizes and some in clumps. They show concentric optical rings but apparently no nuclei. If present nuclei are not clearly defined. The cells of the outer epithelium are regular and key-like in arrangement. Cylindrical cells lie next to and near this layer. The epithelial layer lying in the lumen is in a stage of degeneration and has lost its cellular nature. Verhoeff called this the yellow layer. The dissolution of this layer and cells forming by amitosis have been observed. Spherical cells have always been observed in and outside the old layer. They are smallest inside where dividing and gradually are larger outside. The cells seem to be secretion globules of some kind that function in separating off the old epithelium and in bringing about its digestion or dissolution. Of course, small droplets may be formed during its disintegration.

In criticizing vom Rath's work Verhoeff assumes that if every epithelial cell divides to form an old and a new layer then the leucocytes must be in the inner layer. He says this is not the case because most of the leucocytes are found between the two layers, therefore regeneration as in the insects is not possible in Diplopods.

In *Euryurus* the bodies are formed in the inner layer by amitosis during and after the time when old epithelium becomes separated and thus are located in and between the two layers. They are largest between the layers. No sections have shown that the entire thickness of the mid-intestinal wall is thrown off, in *Euryurus*, and a new layer regenerated from primary leucocytes during moulting, as Verhoeff appears to claim is the case in *Polydesmidæ* and *Iulidæ*. Possibly Verhoeff's supposed leucocytes are similar to the small cells budded off in *Euryurus* from the epithelium and the latter is regenerated from primitive epithelial cells, and not from primary leucocytes. In *Euryurus*, digestive cells are rapidly used up during digestion and consequently during the feeding condition are being replaced from time to time from primitive epithelial cells. Verhoeff (1914) in his work on *Polydesmus* observed mid-intestinal transformations and found cells in all stages of development between the compressed and tongue-formed cells. It seems that he has made wrong interpretations in a number of cases. His observations are in favor of epithelium being replaced by primitive epithelial cells.

In *Euryurus* there is an exceedingly large formation of the bodies in animals which have just shed their old exoskeleton and the new chitin is still as soft as rubber. These animals are easily sectioned or dissected.

Sections showed that the spheres are not tremendously abundant until the animals are ready to shed their old skin. The spheres are of various sizes, without clearly defined nuclei if present at all. Most of them are single but many are in clusters.

Shortly after the old exoskeleton is shed the recently moulted specimen starts consuming it unless disturbed. In some cases all of the old chitin is consumed. When the first exoskeletal piece is swallowed there starts a new period of important changes in the mid-intestine.

In *Euryurus* during a part of the moulting period the mid-intestine is closed in front and behind. This reopens when ecdysis is complete, but is an obstruction to the first piece of exoskeleton. This obstruction is overcome more readily as the new mid-intestinal cuticula is formed, which separates it from the new epithelium. The exoskeletal pieces pass through the oesophagus and, in the mid-intestine, push the loosened container posteriorly.

In a specimen of *Euryurus* which had eaten about one-half of its old exoskeleton, this container was pushed back to the rear half of the mid-intestine.

Verhoeff has made similar observations in *Iulidæ* and *Polydesmus*. He describes what he calls a white body and a yellow body with a yellow layer which corresponds probably to the old epithelium judging from his criticism of vom Rath's work. The yellow body described by Verhoeff in "Die Diplopoden Deutschlands" Fig. 44, page 603 corresponds to the central portion of the lumen inside the old epithelial ring in *Euryurus*, and the white body that space between the cuticula and the old epithelium. This latter space is filled, in *Euryurus*, with spherical bodies of various sizes.

Verhoeff (1914) described, in the diminishing white body, leucocytes

varying much in shape and position, with larger nucleated ones between smaller non-nucleated ones.

The yellow body is described by Verhoeff as being composed of numberless leucocytes and full of fluid. In *Euryurus* very few bodies were usually observed in the central part of the lumen inside the old epithelial layer. The largest spheres were in large masses outside the inner layer. Smaller ones were scattered or in rows through the epithelium and dividing by amitosis inside cells, indicating their functioning in its dissolution and digestion. Perhaps true digestive cells from (H) shown in Plate II, Fig. 3 digest some or all the bodies formed from the inner layer.

The epithelium of *Euryurus* soon after ecdysis assumes a typical feeding condition, as the cells are elongated and over them collect numerous round, small digestive globules which Verhoeff says are fore-runners of the new primary leucocytes from which the epithelium is formed.

The reason Verhoeff gives for the disintegration of the white body is that the larger leucocytes ingest the smaller ones and at the end of this process the yellow body tube is pushed into the lower intestine.

The old epithelial cells (yellow layer of Verhoeff) seem to serve as nourishment for the new cells in *Euryurus*. These new cells start to form and function shortly before the shedding of the exoskeleton judging from numerous slides and dissections showing the spheres or secretion globules in abundance at this time and in greater quantities after the shedding and eating of the old chitin.

In a specimen of *Euryurus* which had almost totally ingested its exoskeleton the front part of the mid-intestine did not contain pieces of the exoskeleton in the cuticular tube. The epithelial cells were rod or tongue shaped and cells in various stages of development were found between them.

In Plate II, Fig. 3, the epithelial cells are very compact. At this stage after the ingesting of the exoskeleton the cells were less compact.

There were fewer of the cells formed from the inner layer in the lower half of the mid-intestine. The anterior two-thirds of the hind-intestine contained a number of exoskeletal pieces. Gregarines were found in the hind-intestine during this period. Before moulting they are found in the mid-intestine. Some parasites may thus be eliminated during moulting.

THE TRANSITION FROM THE MID-INTESTINE TO THE HIND-INTESTINE AND A DISCUSSION OF THE HIND-INTESTINE.

The hind-intestine is set aside from the mid-intestine by a fold of tissue (RF) which may be compared with the pyloric valve of insects. Possibly it is not a true valve in the sense that it closes the tract at this point but it is a fold of tissue marking the transition from the mid-intestine to the hind-intestine. (Plate I, Fig. 6 and Plate III, Fig. 4 and 4-C).

Sections from several different specimens showed the form of the folds to vary to some extent, but the general form is shown in Plate I, Fig. 6.

The transition from the rod-shaped epithelial cells of the mid-intestine to the epithelium of the hind-intestine is shown. The epithelium of the latter soon becomes lower. The chitinous intima first appeared at the beginning of the anterior face of the fold. Numerous small longitudinal folds and depressions were noticeable over the fold but posteriorly these were much larger. The epithelial cells are elongate and rather regular. In some sections considerable striated longitudinal muscle was evident, and fibers of longitudinal muscle extend into the fold. The cuticular striated border extends from behind the fore-intestine for a certain distance into the hind-intestine.

Verhoeff (1910-1915) designated a second cuticula which he called "Einsatzrohr." He shows no drawing of it. Nothing similar has been observed in *Euryurus* nor by Randow (1924) in *Julidæ* or Effenberger (1909) in *Polydesmus*.

Both primary and secondary intimas are clearly evident. No spines were observed on the primary intima.

The epithelium is continuous from the mid-intestine to the hind-intestine. The digestive epithelial cells cease, as one might expect, at the point of the beginning of the fold or the valve and the point where the intima of the hind-intestine begins. At the beginning of the fold the epithelium was distinctly different from that of the mid-intestine. The cells were elongate and rather regular. The basement membrane appeared to be continuous from the mid-intestine to the hind-intestine. The circular muscles appear to be continuous from the mid-intestine to the hind-intestine. They are more numerous in the hind-intestine. With the beginning of the fold there appears a heavy set of longitudinal muscles in contrast to the scattered outer longitudinal muscles of the mid-intestine.

There is just one set of longitudinal muscles in the hind-intestine. They are thicker in the region of the valve and not a thin continuous layer from the mid-intestine to the hind-intestine. Posterior to the fold the longitudinal muscles were evident as a thin incomplete layer.

The histological structure of the region a little anterior to the entrance of the Malpighian tubules is shown in Plate I, Fig. 7. Both primary and secondary intimas are present. The former is much thicker than the latter and is almost transparent and has spines projecting posteriorly for a short stretch of the canal. The groove in which each Malpighian tubule has its outlet has been previously described for *Polydesmidæ* and *Julidæ*. This groove (UC) just anterior to the entrances of the Malpighian tubules is shown for *Euryurus* in the same figure. It varies from previous descriptions for either *Polydesmidæ* or *Julidæ*.

The epithelial cells appear as elongate areas which remain almost clear and with some vacuole-like spaces after staining with Harris's haemotoxylin and eosin. The basement membrane is clearly evident and the nuclei are near it.

The circular muscles are confined to an area between the epithelium and the incomplete layer of longitudinal muscles. The circular muscle layer becomes gradually thicker.

The sphincter-like constriction, a condition observed a short distance

posterior to the entrance of the Malpighian tubules is shown in Plate I, Figs. 9 and 10 and Plate II, Fig. 5. The details of structure can best be seen in Plate I, Fig. 10. The epithelial cells are smaller than in the preceding region. Small spherical light spaces or tracheoles surrounded by darkly stained outer borders were observed, indicate as (TR). A primary intima and a basement membrane were observed. The layer of circular muscles is thick and external to it are somewhat scattered longitudinal muscles.

Nothing was found comparable to the intestinal valve in the intestinal tracts of insects. A longitudinal section through a portion of the hind-intestine characterized by minute dark brown papillæ-like structures or folds (FC) is shown in Plate I, Fig. 15. A cross section is shown in Plate I, Fig. 11. Thin primary and secondary intimas appear to be present. The epithelial cells are somewhat elongated and regular and many are characterized by lightly stained areas. The circular muscle layer is much thinner and a few scattered longitudinal muscles are present.

The fold chamber narrows and the pre-anal constriction (PAC) is the next region observed. Randow (1924) described six longitudinal folds and smaller folds in between for *Julidæ*. The epithelium is lower in a region posterior to the fold chamber (FC) and gradually increases in height in the pre-anal constriction and continues to the rectum.

In *Euryurus* the pre-anal constriction is characterized by an increase in the number of the circular and longitudinal muscle layers.

Rectum.—The intima of the rectum has folds as shown in Plate I, Fig. 12. These almost close the lumen of the gut. From Plate I, Fig. 3, its detailed structure can be deduced. The intima is distinct and slightly roughened but no spines were observed. The epithelial cells are elongate and rather regular, in comparison with low cells described in *Julidæ*. Longitudinal muscles extend to near the rectum. Circular muscles only are found in the region of the rectum.

MALPIGHIAN TUBULES.

Two long and thread-like Malpighian tubules are present, attached to the alimentary canal slightly posterior to the point of transition from the mid- to the hind-intestine. The tubes pass cephalad, one on either side of the intestine, and are characterized by convolutions. They end blindly in the body cavity, attached to tracheæ. The blind ends are smaller than those attached.

Histologically, it was found that the intima is thin and irregular. (Plate I, Fig. 7). The epithelium consists of rod-shaped cells with darkly stained nuclei which make up the greater part of the wall. A basement membrane is present and muscular layers absent.

STUDIES ON INTERNAL ANATOMY IN ADDITION TO THOSE ON THE ALIMENTARY CANAL.

Glands.

The glands of *Polydesmus* have been studied by Effenberger (1909), Verhoeff (1910-1915) and Attems (1926).

Those of *Iulus* have been studied by Plateau (1878), Silvestri (1902), Rossi (1902), Krug (1906), Wernitzsch (1910), Verhoeff (1910-1915) and Attems (1926).

Effenberger (1909) has a good review of the literature on glands of *Iulidæ*. He reported many similarities between the glands of *Iulidæ* and *Polydesmus complanatus*.

The pair of tubular glands of *Euryurus* have the outlets of the ducts the same as in *Iulus* and *Polydesmus* but the glands show a different structure than previously described. (Plate II, Fig. 8). Effenberger (1909) in his Figure 9, on page 569 shows the gnathochilarium with the ducts of the tubular glands. The ducts run between the stipites gnathochilarii and the lamella linguales or according to vom Rath, using Latzel's terminology, between the mala gnathochilarii and the lobi linguales.

Three "traubigen Drusen" or grape-like glands were observed in *Euryurus*. Two have been reported for *Iulus* and *Polydesmus*, namely front and hind salivary glands. In *Iulus* and *Polydesmus* the lower pair of salivary glands are united to form a single glandular mass with the duct outlet between mandible and hypopharynx. In *Euryurus* they (SG) are separated and lie on each side of the oesophagus. (Plate II, Figs. 7 and 8). These are similar in *Craspedosoma* described by Wernitzsch (1910).

Plateau (1878), Rossi (1902) mistook the glands for fat bodies. Also Bruntz (1904) is mistaken regarding the true nature of the lower salivary glands as he associates them with the tubular glands.

The third "traubige Druse" present in *Euryurus* is the "vordere Speicheldruse" or "Kopfdruse," or head gland, as it may be called due to its position and has been described in *Iulus* and *Polydesmus*. It lies in the head over and in front of the brain, which is above the mouth opening. The ducts have their outlets about in the mid line of the dorsal part of the mouth.

Rectal glands or "Afterdruse" in females and "Saftdrusen" or odoriferous glands are described for *Polydesmus* by Effenberger (1909). They are essentially the same in *Euryurus*. The distribution of the repugnatorial pores was described by the writer (1927).

Musculature.

1. *Body*.—The body musculature of *Euryurus* appears to be rather simple. Muscles in the right half of a body segment are shown in Plate III, Fig. 6. In each double segment three paired sets of muscle are found, namely, two dorsolateral, longitudinal bands (DMCL) from the intercostal ridge (AC) of one segment to that of the next; a pair of lateral muscles on each side (LMCL); and a pair of slender ventral muscles (VMCL).

2. *Leg*.—The segments have been numbered I to VII. (Plate III, Fig. 7). They correspond with the segments of the insect and chilopod leg, as given in a paper (p. 93) by Snodgrass (1927). The number holds almost without exception (i.e., the number of segments with muscles) in all the Arthropod groups, but the nature of the articulations and the musculature differs.

Insects, Chilopods, and Diplopods lack a levator of the dactylopodite, or claw. Crustacea and Arachnids have both levator and depressor muscles of the dactylopodite, or claw-bearing segment. The musculature of the left leg of *Euryurus*, as determined from an anterior view, is as follows:

- | | |
|-------------------------------|--------------------------------------|
| A. Promotor of I (Coxa). | H. Levator of IV. |
| B. Remotor of I. | I. Depressor of IV. |
| C. Levator of II. | J. Levator of V (posterior). |
| D. Anterior depressor of II. | K. Depressor of V (anterior). |
| E. Posterior depressor of II. | L. Depressor of VI. |
| F. Levator of III. | M. Depressor of VII (dactylopodite). |
| G. Depressor of III. | |

3. *Mandible*.—This is complicated and difficult to study in *Euryurus*. The large local millipede *Spirobolus marginatus* was also studied because it is much easier to work with, due to its size and flexible body wall. Snodgrass has studied a large *Julid* from Siam. Thus, comparisons of the mandibular musculature of three forms have been made. It is believed that this musculature is essentially the same. Plate III, Fig. 5, is a drawing of the outer view of the left mandible of *Euryurus*. Figure 5-A is a dorsal view of the left mandible of a large *Julid* from Siam (after Snodgrass).

The mandible (MD) consists of two basal plates inserted into the head wall, and a distal, movable functional mandible. The basal plates have three muscles: (1) a large dumb-bell shaped muscle arising in the hollow of the basal plates on each side and continuous through the head by a thick, median transverse tendon. This muscle is lacking in Chilopods and insects but is characteristic of the more generalized Crustacea, including *Apus*. From the first basal plate a large muscle (2) goes to the bar at the sides of the mouth (suspensorium of hypopharynx). This muscle, according to Snodgrass, is present at least in *Machilis* and some Orthoptera. The third muscle (3) is a retractor, or promoter, of basal plate arising on the back of the head. The movable part of the mandible has a small adductor (4), in figure 5-A, going to the basal plate, and a large adductor (5) to the posterior dorsal wall of the head. Abductor muscles were not found and the mechanism by which the mandibles are opened is not known. The mandibular muscles appear to comprise crustacean and insect muscles and no account of them has been found.

The Nervous System.

The previous workers on this system in Diplopods are Newport (1843), Rossi (1901), Verhoeff (1910-1915) and Attems (1926).

The central nervous system of *Euryurus* consists of a brain or cerebral ganglion, suboesophageal ganglion and a ventral nerve cord with ganglia and nerves.

The brain of *Euryurus* consists of two main lobes separated by a slightly constricted area. (Plate III, Fig. 3). In the side view diagram, of course, this area does not show.

Antennal nerves are present. Optic nerves are absent, there being externally no organs of vision. The cerebral ganglia are connected to the sub-oesophageal ganglion (SG) by a circum-oesophageal con-

nection (CC). A single pair of legs is found on the first, third, and fourth segments of all the stages, and the second trunk segment lacks limbs in every case in *Euryurus*. A single ganglion (G) and two pairs of nerves (LN), (DLN) were found in the above-mentioned trunk segments.

The fifth trunk segment, as shown in the diagram, and all the succeeding trunk segments except the anal segment have two pairs of limbs. The gonopods of the male are modified from the eighth pair of legs on the seventh body segment. Two ganglia and three pairs of principal nerves were found in these segments. One pair of nerves runs dorsally, and the other two pairs run ventrally, each supplying a pair of legs.

The nerve cord is double and separated by more or less distinct strands with ganglionic swellings in each segment, which are connected by cross commissures.

In their following course both strands fuse to a greater or lesser extent into an uneven branch which is surrounded by the perineural sinus. (PNS) shown in Plate II, Fig. 7. The dorsal part of the branch is surrounded by the supraneural septum, its sides by the slanting muscles of the leg and ventrally by epithelium. The development of the supraneural septum has not been observed yet. The nerve cord rests upon a network of fat cells, part of which later are located between the epithelium and nerve cord when the cord is separate from the epithelium. Upon the ventral surface of the supraneural septum are found phagocytic organs (Bruntz 1906) and upon the dorsal are nephrocytes.

Rossi (1901) states that the ventral nerve cord of *Julus terrestris* is without ganglia, commissures and connections. He describes four pairs of nerves for each movable segment.

Newport (1843) describes in detail and illustrates in his Plate XI, Fig. 6, the central nervous system of *Polydesmus complanatus*. He states that the ganglia of the first two pairs of legs have united with the first suboesophageal ganglion. In *Euryurus* this was not the case as a single ganglion and two pairs of nerves were found in the first, third and fourth trunk segments.

Otherwise conditions in *Euryurus* are comparable to those described for *Polydesmus*.

The Tracheal System.

Many investigations have been made on the tracheal system in Diplopods. Rossi (1902) gives a detailed historical review of previous work. Wernitzsch (1910) adds additional references up to the time of his observations. He compares the tracheal system of *Craspedosoma* with that of other Diplopods (*Heteroporatia*, *Glomeris*, *Polydesmus*, *Iulus* . . .). More recent work is as follows: Verhoeff (1910-1915), Attems (1926).

Wernitzsch (1910) states that the tracheal system of Diplopods is of especial importance because it connects primitive conditions as found in *Peripatus* with the more complicated conditions in Chilopods and insects. The very fine unbranched tracheæ originating out of the tracheal pockets are similar to those of *Peripatus* and the tracheal

pockets are homologous to the ectoderm tube of *Peripatus* (Ziegler 1907). In many Diplopods, for example *Glomeris*, the trachea are similar to those of insects (Voges 1878).

The tracheal system of *Polydesmidæ* is considered in brief by Attems (1927) and in greater detail by Effenberger (1907) and Verhoeff (1910-1915). Verhoeff disagrees in certain points with Effenberger.

The writer has not worked out the complete tracheal system of *Euryurus*, nor checked contradictory points, however, a few observations follow, all of which are similar, in general, to those of others made on different *Polydesmidæ*. An adult *Euryurus* has twenty trunk segments. One tracheal system consists of a stigma, tracheal pouch and tracheæ and tracheoles. Stigmata were not found in the nineteenth and anal segments nor in the first, second and third segments.

One large tracheal bundle leaves a large tracheal pocket on each side of the anterior part of the sternite of the fourth segment. Each large bundle goes to the side of the head. A smaller bundle leaves each side of the anterior pocket of the fifth sternite. These latter bundles run anteriorly under the larger bundles and converge towards the mid-line of the head. Thus these bundles run anteriorly and supply the anterior segments and the head region.

In *Polydesmus* and *Craspedosoma* two pairs of longitudinal bundles run to the head region.

All investigators except Visart (1894) state that the tracheæ never bifurcate nor anastomose. Visart erroneously mentions and illustrates some tracheæ branching in the intestine of *Julus*.

The Reproductive Systems.

1. *Female*.—On the dorsal wall of the ovarian sack in *Euryurus*, running parallel on either side of the mid-line are the ovaries (EB). (Plate III, Fig. 1-A). These ovaries are covered with numerous developing ova (DO) and are enveloped by a single very delicate, transparent covering. This covering or ovarian sack has the form of a tube pressed together in a dorso-ventral direction and is located ventral to the intestinal tract and dorsal to the nerve cord.

When the eggs are mature, they become separated from the ovaries. The ovarian sac becomes much distended and gradually the ova reach the oviduct. The mutual ovarian sac terminates in a single oviduct (O) which soon bifurcates. Each oviduct branch curves laterally, posteriorly and internally (Plate III, Fig. 1-B) and connects with a vulva.

The vulvæ are attached to the second pair of legs. (Plate III, Fig. 1-B). Each vulva is composed of the opening of an oviduct, glands, and muscles. The vulvæ usually, unless the animals are copulating or ovipositing, lie in depressions surrounded by the sternite. The proximal end of each oviduct is situated on the bottom of a vulva and enters a chamber which opens to the outside. When the vulvæ are everted, the proximal end is outermost, which is most advantageous for oviposition and copulation.

The bursa makes up most of a vulva and is located behind the opening of the oviduct. The simplest operculum (OE) is in front of

the oviduct opening. The bursa is composed of a smooth, more or less depressed zone which is called "Cimier" by French writers. It appears similar to the valves of a mussel. The middle part of the "Cimier" is depressed trough-like and forms a seminal receptacle. By older authors (Fabre, vom Rath . . .) this was mistaken for a gland. In the front part of the receptacle are real glands which were previously overlooked. According to Fabre, *Polydesmus* has no seminal receptacle but Effenberger disagrees. The front rims of the valves and the posterior rims of the operculum, between which lies the oviduct opening, are connected by chitin clasps.

The vulvæ have the form of a compressed sphere and the valves and the operculum have bristles. The bristles on the valves are found on the side towards the median crest. Strong "teeth" are present. The seminal receptacle has the form of a coiled blind sac (SR). On the distal end it is bubble-shaped. Attems (1926) mentioned its lumen being filled with numberless spermatozoa in *Polydesmus*. The bottom channel piece (Kehlstuck) is to a lesser or greater extent loose from the valves. Attems (1926) described the large double-lobed bursa glands found in the front end of the receptacle and smaller gland masses, the glands of the Kehlstuck and vulvular glands.

2. *Male*.—The reproductive system of the male is formed of two long tubes united frequently with cross connections (TC) which makes it resemble a ladder. (Plate III, Fig. 2-A). The vasa deferentia start in the seventh segment and run forward with regular anastomoses to the paired openings (VD) found on projections located on the coxal joints of the second pair of legs. (Plate III, Fig. 2-B).

Fabre (1855) reported for *Polydesmus complanatus* that transverse connections disappear at about the seventh segment. Effenberger (1909) describes the vasa deferentia starting in the seventh segment and running anteriorly to the fourth segment and uniting. They go united for a short distance, then separate in the lower section of the third segment and each branch goes to its outlet in the coxal joint of the second pair of legs.

The second pair of legs is attached to the third trunk segment. The vulvæ of the female are found in a somewhat similar position attached near the base of the second pair of legs. The "ladder" commences in the next to last segment and the tubes open on projections as previously mentioned. The number of cross connections has varied some in specimens studied. Twenty-seven are shown in Plate III, Fig. 2-A. Fabre observed sometimes 13, sometimes 14. In *Euryurus*, the testicular follicles (T) usually appear in the seventh or eighth trunk segment and continue to the next to the last segment.

Effenberger states that for *Polydesmus* the spermatozoa are small, round and not free moving cells.

The seventh segment is the important one in copulation. Its first pair of legs are transformed (described by the writer, 1927) into gonopods.

Effenberger (1909) states that the internal branch of the gonopods of *Polydesmus* contains a bubble which must be filled with spermatozoa before copulation. Fabre (1855) has described in detail the filling of

the bubbles with spermatozoa. He states that before copulation the male lifts up the upper part of the body and coils S-formed, so that the third trunk segment approximates the seventh. He also observed a sperm droplet come out of each opening of the vasa deferentia and taken up by the chitin brushes which are found on the internal branches. He further states that there is no doubt that the droplets reach the bubbles through the opening (seminal receptacle) in the middle of the hair fringe.

Many male specimens of *Euryurus* have been observed coiling S-formed but the sperm droplets have not been observed coming out of the openings of the vasa deferentia and being taken up by the gonopods.

Circulatory System.

This is not as well known in the Diplopods as in the Chilopods. Rossi (1902) reviews the work on Chilopods and Diplopods in a historical note. There are a number of contradictory points in regard to the intimate structure of the heart. Rossi recorded his observations concerning several contradictory points. The most recent work is by Verhoeff (1910-1915) and Attems (1926).

The heart (HT) of *Euryurus* lies between the dorsal epithelium and the intestine. (Plate II, Fig. 7). Its walls from outside to inside are composed of circular muscle strands, a structureless cuticle or intima, adventitious cells, and a pericardial membrane. The heart appears wave-like in longitudinal sections. Its posterior end is blind while anteriorly it opens in a short aorta. In each double segment there are two ostia, two transverse vessels with short open branches, having their outlets ventral in contractile canals. These canals are lacunæ bordered dorsally by the wall of the perineural sinus and ventrally have their own walls consisting of transverse muscle fibers.

Newport (1843), in regard to ostia, does not decide whether he is dealing with simple openings or with terminations of delicate veins. He is inclined towards the latter opinion. No venous system was observed in *Euryurus* nor did Rossi find one in *Julus*.

The research upon which this report is based was carried on chiefly at The Ohio State University during a period of two years, (1925-1927). Some observations were made at the Franz Theodore Stone Laboratory, Put-in-Bay, Ohio, during the summers of 1926 and 1927; and at the Detroit College of Medicine and Surgery, Detroit, Michigan, (1927-1930).

The writer wishes to acknowledge his indebtedness to Doctors Raymond C. Osburn, C. H. Kennedy and R. A. Knouff, of the Ohio State University; S. R. Williams, of Miami University, for valuable suggestions and criticisms; R. A. Hefner, of Miami University, for additional material; R. E. Snodgrass, of the U. S. Bureau of Entomology, for examining material and other help; N. A. Cobb, of the U. S. Department

of Agriculture, for identifying nematodes; and to various members of the staff of the Detroit College of Medicine and Surgery for their hearty co-operation in the completion of this work.

LITERATURE.

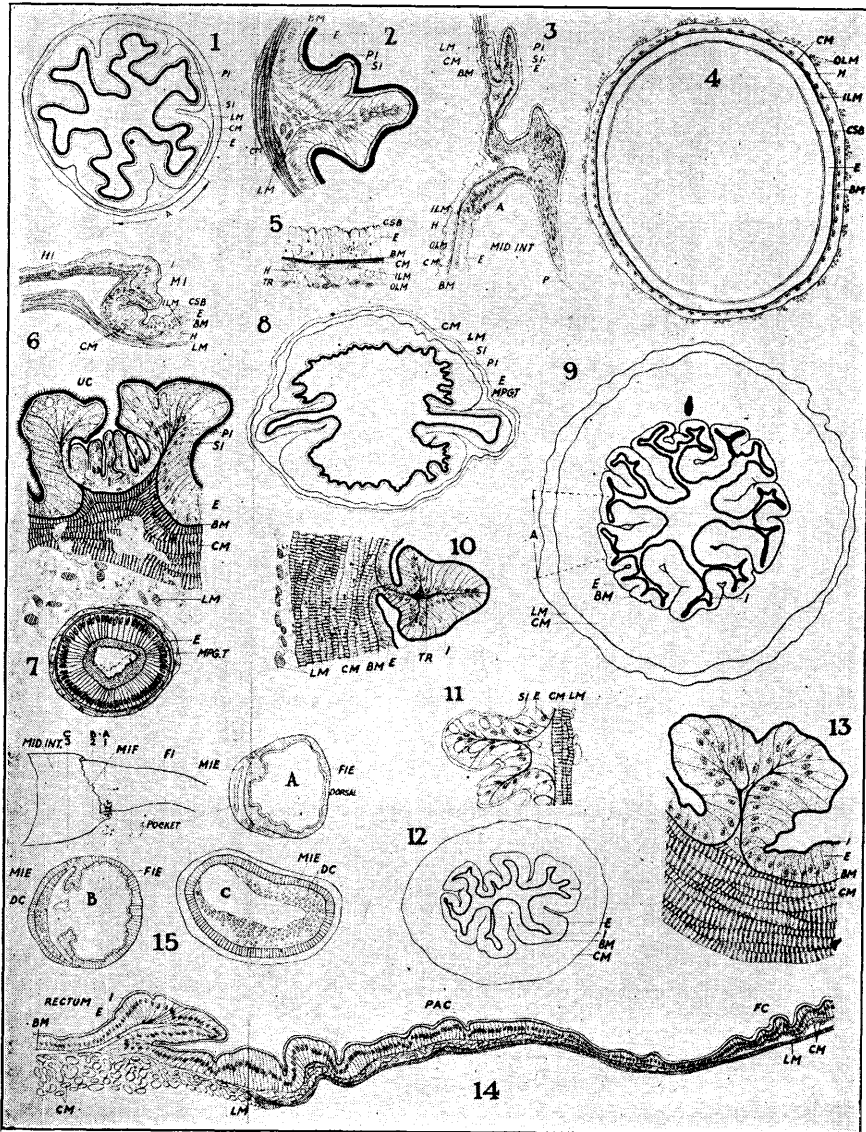
- Newport, G.** (1841). On the Organs of Reproduction, and the Development of the Myriapoda. First Series. Philosoph. Transact. Royal Society London, pp. 99-130.
- Newport G.** (1843). On the Structure, Relations and Development of the Nervous and Circulatory Systems, and on the Existence of a Complete Circulation of the Blood in Vessels, in Myriapoda and Macrourous Arachnida—First Series. V. 133. Philosoph. Transact. Royal Society London, pp. 243-302.
- Leidy, J.** (1851). A Flora and Fauna within Living Animals. Smithsonian Contributions to Knowledge. V, Art. 2, pp. 5-57.
- Leidy, J.** (1851). Communication sur les parasites des Iules. Proc. Ac. Philadelphia, V. 4.
- Fabre, M.** (1855). Recherches sur L'Anatomie des Organes Reproducteurs et sur le Developpement des Myriapodes. Annales des Sciences Naturelles. III, Ser. 4, pp. 257-316.
- Plateau, F.** (1876). Recherches sur les phenomenes de la digestion et sur la structure de l'appareil digestif chez les Myriapodes de Belgique. Mem. Acad. royale Sciences. . . . Belgique Bd. 42, 3 pls., pp. 1-94.
- Voges, E.** (1878). Zur Morphologie u. Anat. der Iuliden. 1. Das Tracheensystem von Glomeris. Zool. Anzeiger Nr. 16.
- Balbani, E. G.** (1890). Etudes anatomiques et histologiques sur le Tube Digestif des Cryptops. Arch. F. exper. (2) viii, pp. 1-82.
- Rath, O. vom.** (1890). Uber die Fortpflanzung der Diplopoden. Ber. d. Nat. Gesellsch. Freiburg. V Heft 1, 28 S. 1 Taf.
- Visart, J.** (1895). Sull 'intima struttura del tubo digerenta dei Miriapodi (Chilognati). Bollettino della Societa Natur. Napoli. Bd. 8, 2 pls., pp. 62-81.
- Verhoeff, K. W.** (1901). Uber d. Nautungsvorgang der Diplopoden. Nova Acta deutsch. Akad. Naturf. Halle, LXXVII, N. 6, 1 Taf., pp. 469-484.
- Rossi, Giovanni.** (1901). Sul sistema nervoso sottointestinale dei Miriapodi. Nota preliminare. . . . Atti della Reale Accad. dei Lincei. Rendiconti, Vol. X, 10 Semestre, Series V, pp. 319-324.
- Rossi, Giovanni.** (1902). Sulla orgnizzazione dei Miriapodi. Ricerche fatte nel Labor. di Anat. normale d. R. Univers. di Roma ed in altri Laborator. biolog., vol. IX, Fasc. 1: 2 Taf., 10 Fig. i. Test. pp. 5-88.
- Rossi, Giovanni.** (1902). Sull 'apparecchio digerente dell' Julus communis. Bull. Soc. Ent. Ital. Bd. 34, Pl. 1, pp. 1-9.
- Silvestri, F.** (1902). Note preliminari sulla morfol. dei Diplop. e Chil. Rivista di Patologia vegetale, Vol. X, pp. 179-184.
- Leger, L. et O. Duboscq.** (1902). Sur le regeneration epitheliale dans l'intestin moyen de quelques arthropodes. Arch. de Zool. exper. Bd. X, pp. 36-42. (Concerning Crustaces Decapodes; Chilopods; Insects.)
- Leger, L. et Duboscq, O.** (1904). Nouvelles recherches sur les Gregarines et l'epithelium intestinal des Tracheates. Arch. Protistenk. IV, Pl. 2, 11 Figs. pp. 335-383.
- Bruntz, L.** (1904). Contribution a l'Etude de l'excretion chez les Arthropodes. Arch. de Biol., T. XX, Pl. VII a IX, pp. 217-425. Diplopodes, pp. 310-324.
- Folsom, J. W. and Welles, M. U.** (1906). Epithelial Degeneration, Regeneration and Secretion in the mid-intestine of Collembola. Univ. of Illinois. Univ. Studies. Vol. II, No. 2.

- Krug, H.** (1906). Beiträge zur Anatomie der Gattung *Iulus*. Jenaische Zeitschr. f. Naturw., Bd. XLII. Hierzu Tafel XXIX-XXXL und 8 Figuren im Text. pp. 485-522.
- Effenberger, W.** (1907). Die Tracheen bei *Polydesmus*. Zoolog. Anzeiger. Bd. 31. Nr. 24, pp. 782-786.
- Effenberger, W.** (1909). Beiträge zur Kenntnis der Gattung *Polydesmus*. Jenaische Zeitschr. Naturwissensch. Bd. 44. 4 Taf., pp. 527-536.
- Verhoeff, K. W.** (1910-1915). Die Diplopoden Deutschlands. Eine allgemeine Einführung in die Kenntnis der Diplopoden—Systematik, der Organisation, Entwicklung, Biologie, Geographie. C. F. Winter'sche Verlagshandlung, Leipzig. 8 Lieferungen, 640 S., 25 Taf.
- Wernitzsch, W.** (1910). Beiträge zur Kenntnis von *Craspedosoma simile* und des Tracheensystems der Diplopoden Jenaische Zeitschr. f. Naturw. Bd. XLVI, N. F. 39, pp. 225-284.
- Verhoeff, K. W.** (1914). Die Verwandlungen des Mitteldarms von *Polydesmus* während der Hautungsperiode. Zoolog. Anzeiger. Bd. 44, pp. 517-526.
- Randow, Erich.** (1924). Zur Morphologie und Physiologie des Darmkanals der Juliden. Zeitschr. wiss. Zoologie. Bd. 122, pp. 534-582.
- Attems, Carl G.** (1926). Handbuch der Zoologie. Erste Lieferung, Bogen 1 bis 8. Progoneata, Chilopoda, Insecta. Zweite Lieferung, Bogen 9 bis 15. Berlin und Leipzig.
- Bronn, H. G.** (1926). Klassen und Ordaungen des Tier Reichs. Zweite Buch. Diplopoda Bearbeitet von Dr. K. W. Verhoeff. Leipzig.
- Miley, Hugh H.** (1927). Development of the Male Gonopods and Life History Studies of a *Polydesmid* Millipede. Ohio Jour. Science, XXVII, No. 1, pp. 25-43.
- Snodgrass, R. E.** (1927). Morphology and Meehanism of the Insect Thorax Smithsonian Miscellaneous collections. Vol. 80, No. 1, pp. 1-108.

EXPLANATION OF PLATE I.

(Drawings).

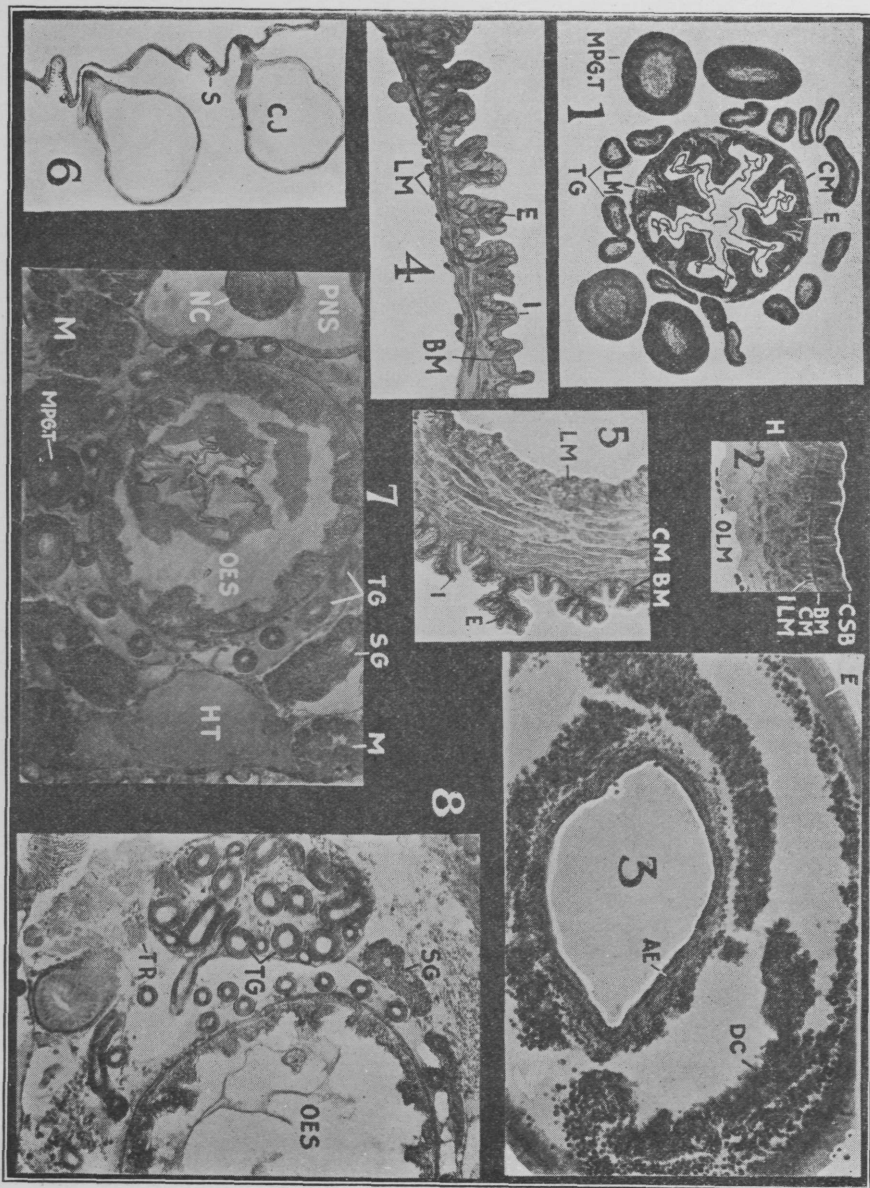
- Fig. 1. Cross-section of oesophagus. PI.—Primary intima; SI.—Secondary intima. LM.—Longitudinal muscle. CM.—Circular muscle. E.—Epithelium. Magnification=413X.
- Fig. 2. Section "A" of Fig. 1 enlarged. BM.—Basement Membrane. Magnification=825X.
- Fig. 3. Longitudinal section through oesophageal valve. Mid. Int.—Mid-intestine. I. L. M.—Inner longitudinal muscle. O. L. M.—Outer longitudinal muscle. H.—Cover layer. A.—Annulus. P.—Process.
- Fig. 4. Cross-section of mid-intestine of feeding animal. C. S. B.—Cuticular striated border.
- Fig. 5. Section of Fig. 4 enlarged. T. R.—Tracheole. Magnification=825X.
- Fig. 6. Longitudinal section through ring fold. H. I.—Hind-intestine. M. I.—Mid-intestine.
- Fig. 7. Cross-section of intestine, shortly anterior to entrance of Malpighian tubules. U. C.—Urine chamber. Mpg. T.—Malpighian tubule. Magnification=825X.
- Fig. 8. Cross-section through intestine where Malpighian tubules enter.
- Fig. 9. Cross-section of constricted region just posterior to the entrance of Malpighian tubules. Magnification=413X.
- Fig. 10. Section "A" of Fig. 9 enlarged. Magnification=825X.
- Fig. 11. Cross-section through fold chamber. Magnification=825X.
- Fig. 12. Cross-section through rectum.
- Fig. 13. Section of Fig. 12 enlarged. Magnification=825X.
- Fig. 14. Longitudinal section through fold chamber, preanal constriction and rectum. F. C.—Fold chamber. P. A. C.—Pre-anal constriction.



EXPLANATION OF PLATE II.

(Photographs).

- Fig. 1. Cross-section of oesophagus.
- Fig. 2. Cross-section of mid-intestine of feeding animal.
- Fig. 3. Cross-section of mid-intestine of moulting animal. D. C.—Cells formed in AE. A. E.—Old epithelium.
- Fig. 4. Cross-section through fold chamber.
- Fig. 5. Cross-section of constricted region just posterior to the entrance of Malpighian tubules.
- Fig. 6. Longitudinal section through stigma and coxal joints of a segment with two pairs of legs. S.—Stigma. C. J.—Coxal joints.
- Fig. 7. Cross-section through body in region of oesophagus to show relation of parts. OES.—Oesophagus. T. G.—Tubular glands. S. G.—Salivary glands. M.—Muscle. H. T.—Heart. N. C.—Nerve cord. P. N. S.—Perineural sinus.
- Fig. 8. Cross-section through another portion of oesophagus, tubular gland, tracheal bundle, etc.



EXPLANATION OF PLATE III.

(Drawings and Photographs).

- Fig. 1. Ventral view of adult female *Euryurus*.
 Fig. 1-A. Female reproductive system.
 Fig. 1-B. Second pair of legs with vulvæ and oviducts.
 Fig. 2. Ventral view of adult male *Euryurus*.
 Fig. 2-A. Male reproductive system.
 Fig. 2-B. Second pair of legs and openings of vasa deferentia of male.
 Fig. 3. Diagram showing side view of nervous system in head region and from segments 1-5, inclusive.
 Fig. 4. Dorsal view of adult alimentary tract.
 Fig. 4-A. Lower lip or gnathochilarium. (Labeled after Effenberger).
 Fig. 4-B. Anal segment with anal plates and anal scale.
 Fig. 4-C. View of portions of the inner wall of the intestine.
 Fig. 5. Outer view of left mandible.
 Fig. 5-A. Dorsal view of right mandible of a *Julid* from Siam. (After Snodgrass).
 Fig. 6. Muscles in right half of body segment.
 Fig. 7. Anterior view of left leg.

DETAILS IN FIG. 5.

- 1, Transverse adductor of basal mandibular plates. 2, Muscle from hypopharyngeal support to anterior basal plate of mandible (ventral to 1 in Figure 5-A). 3, Muscle from dorsal edge of mandibular plate to posterior rim of head. 4, Small adductor from mandible to mandibular plate. (Not seen in *Euryurus*). 5, Adductor of mandible arising on posterior dorsal wall of head.
 ABP, Anterior basal plate of mandible. PBP, Posterior basal plate of mandible.

ABBREVIATIONS USED IN THE FIGURES—PLATE III.

- | | |
|--|---|
| SR—Seminal receptacle. | R—Rectum. |
| OE—Operculum. | LL—Lamellæ linguales. |
| OVD—Oviduct. | STG—Stipes gnathochilarii (Stammteil). |
| EB or OB—Ovary. | ME—Mala exterior (ausere Lade). |
| DO—Developing ova. | MAI—Mala interior (innere Lade). |
| V—Vulvæ. | AC—Antecostal ridge. |
| L—Second pair of legs. | DMCL—Dorso-lateral longitudinal bands. |
| VD—Openings of vasa deferentia. | LMCL—Lateral muscles. |
| TC—Transverse connections. | VMCL—Ventral muscles. |
| T—Testicular follicles. | MD—Mandible. |
| MG—Male gonopods. | I-VII—Divisions of leg. |
| OES—Oesophagus. | A—Promotor of I (coxa). |
| N—Nerves. | B—Remotor of I. |
| B—Cerebral ganglia. | C—Levator of II. |
| CC—Circumeosophageal connectives. | D—Anterior depressor of II. |
| SG—Sub-oesophageal ganglion. | E—Posterior depressor of II. |
| LN—Lateral nerve. | F—Levator of III. |
| G—Ganglion in Fig. 3. | G—Depressor of III. |
| NC—Nerve cord. | H—Levator of IV. |
| DLN—Dorsal lateral nerve. | I—Depressor of IV. |
| DG—Double ganglion in double segment. | J—Levator of V (posterior). |
| RM—Mid-intestine. | K—Depressor of V (anterior). |
| G—Glands in Fig. 4. | L—Depressor of VI. |
| MPGT—Malpighian tubule. | M—Depressor of VII (dactylopodite). |
| RF—Pyloric valve. | |
| UC—Urinary chamber. | |
| WC—Fold or wrinkled chamber. | |
| PC—Pre-anal constriction. | |

