THE COMPARATIVE INTERNAL LARVAL ANATOMY
OF SEVERAL GENERA OF SCARABAEIDAE

by

SUTHARM AREEKUL

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APPROVED:

[Blank]

Associate Professor of Entomology
In Charge of Major

[Blank]

Chairman of Department of Entomology

[Blank]

Chairman of School Graduate Committee

[Blank]

Dean of Graduate School

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THE COMPARATIVE INTERNAL LARVAL ANATOMY
OF SEVERAL GENERA OF SCARABAEIDAE

INTRODUCTION

Considerable work has been done on the internal larval anatomy of insects, especially for Hymenoptera, Diptera, and Lepidoptera. In the members of these orders both the digestive and nervous systems show very marked changes and specializations. In Coleoptera, on the other hand, little has been published concerning the differences of the internal larval anatomy. However, recent workers have demonstrated the value of the internal larval anatomy as a taxonomic tool and as an indicator of phylogenetic relationships. The work that has been done on the comparative internal larval anatomy of saw-flies is an example. In 1932 Yuasa (31, pp.120-132) stressed the intrinsic importance of the immature stage in a study of the phylogeny of saw-flies larvae, even though he recognized the danger of mistaking adaptive structures for phylogenetic indices. In 1955 Maxwell (21, pp.1-132) had considerable success in using the internal anatomy of saw-fly larvae for studying phylogenetic relationships. It is recognized that identification by external larval anatomy in the case of saw-flies is very difficult. However, the internal anatomy can be used in determining to genus and species as well as to family and subfamily. Probably we can expect that internal larval characters will be of value in other groups of
insects. If this is true, the significance of internal larval anatomy studies will be most valuable in studying phylogenetic relationships.

The larvae of four genera representing three subfamilies of the family Scarabaeidae were selected for this study. The family Scarabaeidae was chosen because it is considered to be the most primitive family of the superfamily Scarabaeoidea, and its phylogenetic arrangement is most interesting. In this paper the writer will describe and compare the digestive and nervous system of these larvae. Certain characters have been pointed out as possibly correlated with the phylogenetic scheme of this family as proposed by Leng (18, pp.248-264). The species used were Pleocoma crinita Linsley of the subfamily Pleocominae; Lichnanthe rathvoni Lec. of the subfamily Glaphyrinae; Polyphylla decemlineata Say and Dichelonyx lateralis Fall of the subfamily Melolonthinae.

The internal anatomy of different larval instars of each genus were also compared. Of the genus Pleocoma seven stages were compared and in the other genera, the second and third instars were studied. These several comparisons were made to determine which changes were associated within the species and which changes were associated with generic differences.
MATERIALS AND METHODS

Living and preserved larvae of different instars were obtained through Dr. P. O. Ritcher, Chairman, Department of Entomology, Oregon State College. Dissections were carried out under a dissecting microscope with magnification of \( \frac{1}{4} \) to 60 X. Injection with trypan blue in saline solution was useful in demonstrating the outline of digestive tracts and gastric caeca. For gross dissections, specimens were dissected and pinned out under 70% alcohol. Within a few hours such delicate structures as the ventriculus and gastric caeca became sufficiently hardened for dissection. For studying the movement of the gut, specimens dissected in 0.9 normal saline could be observed for at least half an hour. Nervous systems were studied by dropping 5-4 drops of Bouin's solution on the dissected specimens so as to distinguish the brain, ganglia, and nerves from other parts of body. A number of larvae were dissected for each category studied in order to learn the degree of variation within a category.

Both transverse and longitudinal serial sections were made for the digestive tracts of all the genera studied in order to compare such similarities and differences between genera, as the formation of muscles, epithelia or any other particular characters. Standard staining techniques were followed by fixing the material in Bouin's fluid, imbedding
in paraffin, sectioning, mounting, and staining with Harris's hematoxylin and Eosin.

THE INTERNAL ANATOMY OF FOUR GENERA OF SCARABAEID LARVAE

A. DIGESTIVE SYSTEM

THE DIVISIONS OF SCARABAEID ALIMENTARY CANALS

The alimentary canals of the larvae of the three subfamilies which were studied can be subdivided as follows:

1. Fore-gut
   a. Pharynx
   b. Oesophagus
   c. Crop and cardiac valve

2. Mid-gut
   a. Ventriculus
   b. Gastric caeca

3. Hind-gut
   a. Ileum, pyloric valve, and malpighian tubules
   b. Colon (anterior and posterior colon)
   c. Rectum

THE CHANGES OF DIGESTIVE TRACT DURING THE DEVELOPMENT OF DIFFERENT LARVAL INSTARS

Changes in the alimentary canal of Pleocoma larvae were observed for several instars. According to data furnished by Mr. Floyd Ellertson and Dr. P. O. Ritcher, head capsule measurements give a rough approximation of what instar is being observed. Five individuals were
examined for each of the capsule measurements for the two and ten day old larvae. Several were examined for each of the other instars.

**TABLE I**

**HEAD CAPSULE MEASUREMENTS OF PLEOCOMA SP. LARVAE OBSERVED AND THE APPROXIMATE INSTAR**

<table>
<thead>
<tr>
<th>Width of Head Capsule</th>
<th>Instar</th>
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<tr>
<td>2.2 MM</td>
<td>1</td>
</tr>
<tr>
<td>3.43 MM</td>
<td>4</td>
</tr>
<tr>
<td>5.00 MM</td>
<td>6</td>
</tr>
<tr>
<td>6.43 MM</td>
<td>8</td>
</tr>
<tr>
<td>7.14 MM</td>
<td>9 (last instar)</td>
</tr>
<tr>
<td>7.86 MM</td>
<td>10 (last instar)</td>
</tr>
<tr>
<td>8.30 MM</td>
<td>11 (last instar)</td>
</tr>
<tr>
<td>8.73 MM</td>
<td>11 (last instar)</td>
</tr>
</tbody>
</table>

The first instar was observed when the Pleocoma larvae were two and ten days old. The exact age of the others was unknown.

No major changes occurred in these larvae except in changes of the gut-length and the development of the gastric caeca. In the two and ten day old larvae of the first instar, the length of the fore- and mid-gut remained nearly the same (Figure 1). The hind-gut was a little longer than the other parts. Two sets of gastric caeca were developed at the anterior end of the mid-gut. The first set appears on the ventral side as swellings which are blind pouches. The second set is located just
posterior to the first set and appears as small annuli around the gut. In the fourth to the eighth instars of *Pleocoma* the fore- and hind-gut remain nearly of the same length while the mid-gut is about two times longer than the fore-gut (Figure 2). The first set of gastric caeca branches into five lobes covering the underside of the crop while the second set develops into small blind pouches (Figure 5). In the late instars, both sets of gastric caeca degenerate. At the same time the mid-gut shortens while the fore- and hind-gut elongate. At this time the fore- and hind-gut are nearly the same length while the mid-gut is only one-half as long (Figure 4). The elongation seems to occur at the posterior end of the fore-gut and anterior end of the hind-gut. The malpighian tubules move anteriorly to a point just posterior to the pyloric value. The adult stage has no gastric caeca.

The change in the length of the gut and the development of gastric caeca are probably adaptations for the feeding of the larvae. Sections of the alimentary canal showed no other changes except the number of the epithelial cells is tremendously increased. Active secretion seems to be great in the mid-gut and even greater in gastric caeca during the feeding stages. The epithelial cells are reduced and become degenerated in late instar larvae.
The alimentary canals of the second and the third instars of *Lichnanthe*, *Dichelonyx* and *Polyphylia* showed no differentiation.

DESCRIPTION AND COMPARISON - THE ALIMENTARY CANALS OF SCARABAEID LARVAE

The length of the alimentary canal of both adult and larvae scarabaeid insects is known to be correlated with their feeding habits. Becton (1, p.315) studied the digestive tract of adult *Phanaeus vindex* (Coprinae) which feed on dung and found that the tube is of great length, averaging a little less than eight times of the length of the body. Swingle (27, p.185) in studying the digestive tract of adult Japanese beetles (Popillia japonica: Rutelinae) which feed on fresh leaves, found that it is approximately twice as long as the body. Rapp (24, p.145) found the larval digestive tract of *Canthon pilularius* (Coprinae), which feed on dung to be about twice the length of the body. In the case of *Oryctes rhinoceros* (Dynastinae) it is only a little longer than the body in the third larval instar (8, p.24). In the alimentary canal of the larvae which were studied here, there are only minor differences in the length, ranging from 1.3 to 1.8 times the length of the body.
The fore-gut of most of the adult scarabaeid insects is very short when compared with other parts of the canal. This is shown in the cases of adult Phanaeus vindex (1, p.135), Popillia japonica (27, p.185). Fletcher (7, p.110) and Jones (15, p.95) found that in the adult of Phyllophaga gracilis and of Diplotaxis liberta, the fore-gut comprised about 12% and 10% of the total length respectively. This is also true in the larvae which were studied here. The fore-guts of Pleocoma, Lichnanthe, Dichelonyx and Polyphylla are about 25%, 12%, 10%, 10% respectively, of the total length of the body.

The fore-gut extends from the mouth in the head to the first or second thoracic segment. It is not highly specialized, and its major function probably is no more than transferring food from the mouth to the mid-gut. All the larvae which were studied had a narrow tube-like fore-gut (Figures 2, 11, 12, 13). Histologically the fore-gut shows no difference from that of a typical insect. The outer layer consists of very conspicuous and numerous circular muscles which surround the inner layer of less numerous longitudinal muscles. The epithelial cells have an indistinct basement membrane and usually follow the longitudinal folds of the membrane which lies on the inner surface of the circular and longitudinal muscles (Figures
23, 24, 25). The innermost cuticular layer is of chitin which is homologous with the cuticula of the body wall, and is known as the intima. This intima forms a rather thin, non-cellular, almost transparent layer which lines the entire fore-gut and is more or less thrown into longitudinal folds corresponding to the epithelial layer.

(a) PHARYNX

The initial region of the digestive tract just posterior to the mouth, the pharynx of scarabaeid larva, is evident as a short, slight dilation of the tract in the head. The external circular muscles and intima are thicker than other parts of the fore-gut (Figure 23). The intima may be covered with chitinous spines as found in Pleocoma and Dichelonyx larvae or the spines may be absent as in the cases of Lichnanthe and Polyphylla. These spines are also found in the adult stage of Phanaeus (1, p.316), Phyllophaga (7, p.111), Diplotaxis (15, p.96), Popillia (27, p.185). Spines, when present, usually protrude inwardly and caudally (Figure 42). The epithelial cells are cuboidal in shape and they line the numerous folds of the walls of the pharynx. Such folds cause the lumen to constrict at the posterior end where the oesophagus is found. The longitudinal muscles are not well developed except in the pharynx of Pleocoma.
(b) OESOPHAGUS

The oesophagus is marked by the constriction of the tube between the pharynx and dilated tube of the crop. No distinct division of this part can be drawn. In this portion the circular muscles and the innermost intima are thinner than in the pharynx region. The longitudinal muscles and the basement membrane are very weak. The longitudinal folds are well developed especially in Lichnanthe, so that the lumen is very narrow. These folds are formed by cuboidal epithelial cells and the intima. Spines are not found in this region.

(c) CROP

The crop is present as a slight dilation of the hinder portion of the oesophagus, but is different from that of many insects in that it is not large and conspicuous. It is also present in the larva of Oryctes rhinoceros (8, p.24). It is doubtful whether it functions as a food reservoir as true crops do. Histologically, the crop consists of very thin circular muscles and the intima. These form the thinnest part of the fore-gut (Figure 24). The internal longitudinal muscles are undeveloped. Some isolated strands of longitudinal muscles extending from the mid-gut insert at the distal end in the external circular muscles. The basement membrane is indistinct.
The epithelial cells are of a low cuboidal shape. Spines and other special structures are not found on the intima.

The stomodeal or cardiac valve is found at the junction of the fore- and mid-gut. This structure is formed by the slight extension of the fore-gut into the lumen of the ventriculus as folds. The valve is composed of the epithelium of the hypodermal cells and the intima of the fore-gut (Figures 43, 44, 45, 50). These cells become longer and longer in shape as they extend along the innermost side of the fold. Then they decrease in size where the projection of the fore-gut becomes folded back upon itself and passing forward unites with the mid-gut wall. The intima which is continuous around the valve disappears at the point where the fore- and mid-gut are united. No special structures such as proventricular teeth, pads or spines have been found in these larvae.

2 MID-GUT

(a) VENTRICULUS

The mid-gut is an elongate tube which is marked anteriorly by the cardiac valve, and posteriorly by the pyloric valve. This part is usually very long and is a rather large division of the digestive tract. Becton (1, p.316) found it 6.7 times as long as the body in adult Phanaeus. It comprises more than one-half of the total
length in adult *Phyllophaga* (7, p.110) and *Diplotaxis* (15, p.95). In larvae the length varies as follows: in *Pleocoma* it comprises about 50%, *Lichnanthe* 30%, *Polyphylla* about 30% and *Dichelonyx* 40% of the total length. It is a fairly straight tube, tapering slightly from the anterior to the posterior end and extending from about the first thoracic segment to the eighth abdominal segment.

Special structures may be found in the mid-gut of some scarabaeid insects. Crypts or papillae occur in the mid-gut of adult *Phanaeus* (1, p.316) and *Passalus* (19, p.18). Such structures are not found in the larvae which were studied here.

Histologically, the ventriculus of all insect larvae has similar structures. It consists of a layer of outer longitudinal muscles surrounding less developed, isolated circular muscle strands. Lining the inner surface of circular muscles is a layer of well developed epithelial cells (Figures 29, 43, 44, 45, 50). These cells are irregular, more or less columnar or cuboidal shape. The striated border can be seen at the distal end of epithelial cells, under the oil immersion lens. In some sections, however, this striated border is indistinct especially in the gut of *Lichnanthe* larvae. The epithelial cells usually contain very large and distinct nuclei.
Groups of small replacement cells with 3-4 very distinct nuclei in each group, have been found resting on the basement membrane at the base of the epithelium. Fletcher (7, p.113) stated that secretion of the mid-gut of adult *Phyllophaga gracilis* Burm. seemed to be of the holocrine type, where the entire contents of the cell burst out into the lumen of the intestine, after which the cell is replaced by new cells. Jones (15, p.97) also found this condition in the mid-gut of adult *Diplostaxis*. The type of secretion could not be determined from the sections obtained, but it is evidently holocrine in all the genera which were studied. The formation of new cells is accomplished by the division of cells within round, cellular aggregations of nidi, most of which have dropped below the epithelium while some lie among the strands of circular muscles (Figure 29). These replacement cells are nearly equal in size, and do not form the usual bud-like nidus. Nidi are not usually found among the cells of the epithelial layer in the mid-gut of *Pleocoma, Lichnanthe* and *Dichelonyx* larvae but on the other hand, the formation of them is common in *Polyphylla*.

A very thin structureless peritrophic membrane may be found surrounding the food within the mid-gut. Waterhouse and Day (28, p.285) stated that two types of peritrophic membrane occur; a single, uniform continuous structure and
a tube consisting of a series of concentric lamellae. A peritrophic membrane of the first type is found in the mid-gut of *Polyphylla* which is a very thick and distinct membrane. This is formed by a group of epithelial cells of the mid-gut located around the anterior end (Figure 44). The peritrophic membranes of *Fleccoma* and *Dichelonyx* are very thin and evidently of the second type because they are formed by the epithelial cells throughout the mid-gut (Figures 43, 45). A peritrophic membrane is not found in the canal of *Lichnanthe* larvae.

(b) GASTRIC CAECA

The diverticula of the mid-gut are known as gastric caeca. They consist of blind pouches varying in number and length and they may be found on different parts of the gut. Rapp (24, pp.145-147) in examining the internal anatomy of several specimens of scarabaeid larvae, found that the gastric caeca varied in number and shape with the species which he observed. According to Rapp, larvae of *Canthon pilularius* (Coprinae) contain no trace of gastric caeca. In *Phyllophaga* (Melolonthinae) he found one set of two gastric caeca at the anterior end of the ventriculus. Two genera in the subfamily Melolonthinae, *Dichelonyx* and *Phyllophaga* were similar as to gastric caeca both in number and location (Figure 13). In *Polyphylla* the number and
location are quite different; it contains three sets of gastric caeca (Figure 12). The first set consists of small lobes located around the anterior end of the ventriculus. In the second set are eight small blind pouches surrounding the middle part of the mid-gut. In the third set are two groups of large lobes located at the dorsal and ventral portion of the posterior end of the mid-gut. Two sets of gastric caeca were found in *Pleocoma* (Pleocominae); *Lichnanthe* (Glaphyrinae) and two sets have been reported for larvae of these two subfamilies: Rutelinae, *Pelidnota*; Dynastinae, *Dynastes, Ligyrodes* (24). In the case of *Pleocoma* larvae, both sets are located at the anterior end of the mid-gut (Figure 2). The first set is very large and branches into five lobes covering the underside of the crop. The second set consists of small blind pouches encircling the ventriculus just posterior to the first set. In the case of *Lichnanthe* the first and second sets are located at about one-fourth the distance from the anterior end and posterior end of the mid-gut respectively (Figure 11). Each set consists of eight small blind pouches of the same size bounding the gut. Three and four sets of gastric caeca were found by Rapp (24, p.147) in *Xyloryctes* (Dynastinae) and *Osmoderma* (Cetoniinae) respectively. These are located in a different position on the ventriculus. Thus, according to Rapp, in the scarabaeid larvae, the gastric caeca when present may number up to at least
four sets and may be located on any portion of the ventriculus.

The structures of gastric caeca do not differ from the ventriculus except that the number of epithelial cells seem to increase tremendously at times (Figure 30). Extension of the peritrophic membrane from the ventriculus into gastric caeca is found, but none of caeca's epithelial cells show the secretion of this membrane.

3 HIND-GUT

The hind-gut is marked anteriorly by the pyloric valve and posteriorly by the anus. It is a rather long tube when compared with the other parts of the gut. In *Pleocoma*, *Lichnanthe*, *Polyphylla*, and *Dichelonyx*, the hind-gut is about 25%, 60%, 50%, and slightly less than 50% of the total length respectively. Generally the hind-gut is differentiated into several parts. Usually it is located in the last three abdominal segments. The divisions of the hind-gut are: ileum, colon and rectum.

The hind-gut of scarabaeid larvae shows a similarity in the arrangement of tissue layers. The external circular muscles surround the isolated bundles of longitudinal muscles throughout the gut. Epithelial or hypodermal cells, which occur as a layer in the innerside of longitudinal muscles, are usually cuboidal in shape, and contain
very large nuclei. The basement membrane is well
developed. The non-cellular intima originates from the
point of division between the mid- and hind-gut and is
homologous with the cuticula of the body wall at the anus.
Numerous isolated strands of longitudinal muscle tissue are
scattered along the outside of the external circular muscle
layer. These muscle strands are quite prominent at the
anterior ileum, some parts of the colon and the rectum.

(a) ILEUM, PYLORIC VALVE AND MALPIGHIAN TUBULES

The initial portion of the hind-gut is the ileum. It
is a short and fairly narrow tube which gradually tapers to
the posterior end. The ileum is marked anteriorly on the
innerside by the pyloric valve. The valve is formed by a
group of high columnar epithelial cells of the hind-gut
(Figures 46, 47, 48, 51). These cells abruptly rise to
form a ring of greatly elongated cells which extend into
the lumen of the gut. The inner margin of the valve is
covered with a thick intima. Numerous thick folds of the
innerside of the gut can be observed in this region (Figure
33). No teeth or other special structures have been
observed. The circular muscles which bound the outside of
the ileum are well developed and are thicker toward the
posterior end. The longitudinal muscles on the other hand
are not well developed. They are present as isolated
strands and in the cases of Dichelonyx and Pleocoma these
muscles are found inserted between the folds of epithelial layer of the pyloric valve (Figures 46, 48). The walls formed by hypodermal cells of the ileum along with the thick intima are usually thrown into the longitudinal folds throughout the lumen. These folds cause the lumen to be narrower at the posterior end.

The malpighian tubules typically arise from the anterior end of the hind-gut according to Snodgrass (26, p.378). In the case of scarabaeid larvae this does not hold true in all genera. In the adult Phanaeus Becton (1, p.316) found four malpighian tubules attached separately to the canal; two were anterior to the pyloric valve and two were posterior to the valve. This is also true for Polyphylla larvae. Two of the tubules are located separately at the dorso-lateral side just posterior to the proctodeal valve, while the other two are located closely together and have the same opening at the ventral side of the gut just anterior to the valve (Figures 12, 19). In the case of Dichelonyx larva, four malpighian tubules are found rising separately on the gut, just anterior to the pyloric valve. In contrast, with Dichelonyx, Lichnanthe larva the four malpighian tubules are attached just posterior to the valve. Pleocoma larvae, on the other hand, have four malpighian tubules opening separately at about one-fourth of the total distance from the anterior end of the ileum (Figure 2). The location of the malpighian
tubules changes in the different stages of Pleocoma larvae and of the adults as mentioned above. Four malpighian tubules are also found in Phanaeus (1, p. 316), Diplotaxis (15, p. 95), Popillia (27, p. 190), and Oryctes (8, p. 27).

Each malpighian tubule is a single, unbranched tube and throughout is the same diameter. The malpighian tubules of the larvae studied here are of the type described by Roeder (25, p. 391) as being found principally among the Coleoptera and Lepidoptera. The tubes are extended anteriorly and turn back to posteriorly. The distal ends of the tubes are attached to the rectal structure. Actually, they lie on the surface of the rectum and are held in place by an enveloping membrane. In all the larvae studied, the tip of all tubules was attached at the same point on the rectum.

The malpighian tubules consist of a layer of columnar epithelial cells surrounded by thin circular muscles (Figures 38, 39). These cells contain quite large and distinct nuclei. The number of cells which were seen in cross section vary within the tube and in different insects. In Pleocoma, Lichnanthe, Dichelonyx and Polyphylla, 7 to 15, 3 to 6, 4 to 9, 6 to 8 cells were found respectively. The striated border can be seen at the distal end of the epithelial cells. However, in some sections this striated border is indistinct. The intima
layer is absent. On the outside, the malpighian tubules are bounded by a narrow layer of connective tissue.

(b) COLON

The colon of scarabaeid larvae constitutes the most outstanding part of the alimentary canal. It is usually divided into an anterior and a posterior colon, which are folded under the ileum. The colon may differ in shape and structure in different genera. Generally the anterior colon is a very large thin-walled sac. This is found in *Polyphylla* (Figure 12), *Dichelonyx* (Figure 13), *Oryctes* (8, p.28) and *Popillia* (27, p.190). Histologically the epithelial cells are of a broad cuboidal shape, and scattered on a very distinct basement membrane (Figure 36). The outer circular muscle layer is thin but well developed. The longitudinal muscles are not well developed and only an occasional strand is found. Some strands of longitudinal muscles extend across the upper surface of the gut from the ileum and the posterior colon. These muscles probably aid in the contraction of the colon. The intima is very thin and distinct.

The anterior colon of *Lichnanthe* larva is different in shape and structure from above. It forms a rather long tube with irregular transverse folds appearing inside (Figure 11). The folds are caused by the layer of
epithelial cells pulling inward toward the lumen. Other structures such as circular muscles, longitudinal muscles and intima do not exhibit any differences from other scarabaeid larvae.

The anterior colon of *Pleocoma* is nearly spherical in shape (Figure 2). It differs from other genera in that the external circular muscles are very thick, with six distinct strands of longitudinal muscles forming a layer with distinct basement membrane. This layer forms numerous folds inside the gut (Figure 34).

The posterior colon of *Dichelonyx* and *Polyphylla* is a narrow sac. It differs from the anterior colon in that the circular muscles are very thick in this region. Numerous folds are found in the epithelial layer and the intima is very thick and distinct. In the case of *Lichnanthe* and *Pleocoma*, the posterior colon is a very narrow tube. Thus, the throwing inward of the epithelial layer and the thick intima causes the lumen to be very narrow. The circular muscles are much thicker than those of the anterior part. The longitudinal muscles are not well developed in *Lichnanthe* but in *Pleocoma* longitudinal muscles are found inserted between the lobes of epithelial layer. The basement membrane is very distinct in all genera.
(c) RECTUM

Externally the rectum is a narrow sac resulting from the dilation of the posterior end of the alimentary canal (Figures 2, 11, 12, 13). The circular muscles are well developed, but are weak in some parts, especially in the middle part (Figure 41). The epithelial layer is slightly folded. It consists of regular cuboidal cells with very distinct nuclei. The longitudinal muscles are few and inconspicuous. A small number of isolated groups of muscles comparable to those in the posterior colon are present. The chitinous intima is very thick. The basement membrane is very distinct. Generally the structures of rectum of larvae which were studied did not differ.

B. NERVOUS SYSTEM

THE DIVISIONS OF NERVOUS SYSTEM

The nervous system of scarabaeid larvae, as in most insects, can be conveniently divided into the following divisions:

1. The "brain" proper or supra-oesophageal (supra-stomodeal) ganglion and stomodeal or stomogastric nervous system.

2. The ventral ganglionic chain, which is composed of:

a. The suboesophageal (substomodeal) ganglion.
b. The thoracic ganglia.
c. The abdominal ganglia.
d. The peripheral nerves.
Several instars of *Pleocoma* were observed. The head capsule measurements have already been presented in Table 1. The nervous system of these larvae consists of the brain; the stomodeal nervous system which is composed of a frontal ganglion, a hypocerebral ganglion, a pair of oesophageal ganglia; a sub-oesophageal ganglion; three thoracic ganglia and eight abdominal ganglia. No major changes are found during the development of the instars studied, the nerves and ganglia remaining the same in number throughout the larval stages. Only minor changes, such as shortening of connectives and an anterior movement of posterior ganglia can be observed. The abdominal ganglia became more and more elliptical as the larvae grow older and become somewhat reduced in size.

The shortening of the nerve cord during the growth of the larva brings about a change in position of the ganglia. The brain, the sub-oesophageal, thoracic and the first abdominal ganglia remain in the same position in all larval stages, while the position of the abdominal ganglia changes in different instars. Thus, in the two and ten day old first instar larva, ganglia two to six are located in abdominal segments one to five respectively, while ganglia seven and eight are found in the abdominal segment six.
In the fourth instar, ganglia two to seven are located in segments one to five and only the last one remains in the segment six (Figure 52).

Beyond the fourth instar, only a very slight change in position of the nervous system occurred. Ganglia two and three are in the first abdominal segment, ganglia four to six lie in abdominal segments two to four, and the last two ganglia remain in the segment five (Figure 53).

In both male and female adults, the first abdominal ganglion becomes fused with the third and second thoracic ganglia and moves anteriorly into the first thoracic segment. The chain of the remaining five abdominal ganglia begins in the second thoracic and ends in the first abdominal segment. Since the last abdominal ganglion of the adults contains five pairs of lateral nerves rather than the three found in larvae, this ganglion is probably formed by the fusion of the last three abdominal ganglia of larval stages (Figure 54).

No changes of the nervous system were found in the second and third instars of Lichnanthe, Polyphylla and Dichelonyx larvae.

DESCRIPTION AND COMPARISON: THE NERVOUS SYSTEM OF SEVERAL GENERA OF SCARABAEID LARVAE

The most important differences in the nervous system are exhibited in the ventral cord of many species of
Coleoptera. Brandt (4), after studying many species of beetles, both adults and larvae, concluded that the most generalized type of nervous system, in addition to the supra- and infra-oesophageal centres, consists of three thoracic ganglia and eight abdominal ganglia. *Dictyopterus* is an example. Reduction in the number of abdominal ganglia, accompanied by a similar specialization of the thoracic centres, may be traced through a number of genera of Coleoptera. Thus, there are two, three, four, five, six, and seven abdominal ganglia in *Coccinella, Cassida, Donacia, Silpha, Cicindela* and *Lampyris* respectively. Also in a number of other Coleoptera, all in the family scarabaeidae, the second and third thoracic ganglia are closely united together as in *Melolontha, Phyllopertha, Cetonia*. The center thus formed also includes the fused ganglia of the abdominal chain. *Serica* and *Rhizotrogus* are recognized as the most specialized. In these genera all thoracic and abdominal ganglia unite to form a single complex nervous center in the thorax. In *Rhizotrogus*, the sub-oesophageal ganglion also coalesces.

Larvae of the various subfamilies of Scarabaeidae which the writer has observed also show various types of the nervous systems. *Pleocoma* represents the most primitive type, *Polyphylia* the highest type, while *Dichelonyx* and *Lichnanthe* represent intermediate types.
1 THE BRAIN, ITS NERVES AND THE STOMODEAL NERVOUS SYSTEM

The brain of scarabaeid larvae is composed of a pair of large simple lobes located in the cephalic region. The compact pear-shaped white masses of the brain show no distinct divisions. The location of divisions can be determined by only the location of the principal nerves. In the four genera studied the nervus opticus, nervus antennalis, nervus lateralis, frontal ganglion connective and labral nerve are present.

The stomodeal nervous system consists of a frontal ganglion, a hypocerebral ganglion, a pair of oesophageal ganglia and a pair of stomachic ganglia. These ganglia are well developed in Pleocoma and Dichelonyx larvae. The hypocerebral ganglion is degenerated in the nervous system of Polyphylla and all the ganglia, except the frontal ganglia, are undeveloped in Lichnanthe larva (Figures 53, 56, 57, 59).

2 THE VENTRAL GANGLIONIC CHAIN

(a) THE SUB-OE SOPHAGEAL GANGLION

The sub-oesophageal ganglion is large and located in the cephalic region. It is joined with the brain by a pair of circumoesophageal connectives. The peripheral nerves of this ganglion innervate the mandibles, the hypopharynx,
the maxillae, and the labium. The shape of the ganglion is usually flat and nearly circular. In the more specialized forms, as stated above, this ganglion is fused with the thoracic ganglion. Thus Polyphylla is an example of this type (Figure 56). In the other three genera, this ganglion remains separate and is joined with other ganglia by a pair of connectives.

(b) THE THORACIC GANGLIA

In the most generalized form, the thoracic ganglia are three in number and are joined together with other ganglia by a pair of connectives. They are usually nearly spherical in shape and are a little larger than the abdominal ganglia. The shortening of the connective causes the ganglia to move anteriorly which can be traced in the genera which were studied. In Pleocoma larvae the thoracic ganglia with rather long connectives are located in thoracic segments 1, 2, 3 respectively (Figure 53). In Lichnanthe and Dichelonyx larvae the thoracic ganglia with rather short connectives are found in thoracic segment 1 and 2 (Figures 57, 59). In Polyphylla on the other hand, the connectives are absent. Here the thoracic ganglia are fused with the sub-oesophageal ganglion. The resulting ganglion is located in between the cephalic region and the first thoracic segment (Figure 56).
(c) THE ABDOMINAL GANGLIA

In the most primitive forms there are eight abdominal ganglia which are equal in size except the last one. This latter ganglion is slightly larger than the others. Similar to the thoracic ganglia, these ganglia have rather long connectives and form the long chain of the ventral nerve cord in the more generalized form. Thus in Pleocoma larva, eight abdominal ganglia are joined together by a long pair of connectives and are located in the region between the third thoracic segment and the fifth abdominal segment (Figure 53). On the other hand, the eight abdominal ganglia of Lichnanthe, as well as of Dichelonyx are joined by a very short pair of connectives. In Lichnanthe larva, the first three ganglia are located in the second thoracic segment. The third thoracic segment contains four ganglia and only one ganglion is in the first abdominal segment (Figure 57). In Dichelonyx larva the first two ganglia are located in the second, and the next three are in the third thoracic segment. The last three ganglia remain in the first abdominal segment (Figure 59). The abdominal ganglionic chain of Polyphylla shows a very specialized form. All the ganglia are fused into a short narrow mass forming a ganglion located in the first thoracic segment. The slight constrictions of this ganglion and the peripheral nerves show that probably six
ganglia of the abdominal ganglionic chain have fused together (Figure 56). The last ganglion probably results from the fusion of three ganglia during the early development stage.

(d) **PERIPHERAL NERVES OF THE VENTRAL NERVE CORD**

In studying the peripheral nerves of the ventral nerve cord of several genera, it is found that each thoracic ganglion contains two pairs of lateral nerves and each abdominal ganglion except the last one, has one pair. Three pairs of peripheral nerves are present on the last abdominal ganglion. These nerves usually arise from the lateral side of the ganglia except in the *Polyphylla* larva where it is found on the dorso-lateral sides. Each thoracic or abdominal segment is innervated by peripheral nerves from the respective thoracic or abdominal ganglia. Only the last abdominal ganglion is found to supply the last three abdominal segments (Figure 52).

It should be noted here that the peripheral nerves supply the same segments in which they were originally located, although there has been a slight shortening of the nerve cord, a condensation of ganglia, and a loss of connectives as found in *Pleocoma* and *Polyphylla* larvae (Figures 52, 55).
Observations were made on the nervous system of some other scarabaoid larvae. In *Geotrupes blackburni* (Geotrupinae), the brain is rather peculiar in shape and the sub-oesophageal ganglion is very distinctly located in the cephalic region. The ventral nerve ganglia are joined together by a long pair of connectives. A thoracic ganglion is located in each of the three thoracic segments. The eight abdominal ganglia are found beginning in the third thoracic and ending in the second abdominal segment. The seventh and eighth abdominal ganglia are nearly fused together (Figure 58). In the genus *Trox* of the subfamily Troginae, the writer has found that the central nerve cord resembles that of *Pleocoma*, except in *Trox* the number of abdominal ganglia are reduced to six. In *Pelidnota punctata* (Rutelinae), the central nerve cord is very specialized and similar to *Polyphylla* larva. Other genera which were observed to be of this type are *Xyloryctes* (Dynastinae) and *Osmoderma* (Cetoniinae).

*Oryctes rhinoceros* (Dynastinae) according to Gressitt (8, p.29) probably has the most specialized nervous system of the scarabaeidae. The larva has only a pro- and a meso-thoracic ganglion. The meso-thoracic ganglion is partially fused with the common meta-thoracic abdominal ganglion, so that this fused ganglion appears to have
12 pairs of peripheral nerves in the third larval instar. In the adult stage all of these ganglia fuse with the sub-oesophageal ganglion to become one large lobe.

Also it should be mentioned that in the genus Ceruchus of the family Lucanidae, the ventral nerve cord is of the same type as in Pleocoma. This type is also found in Passalus larvae (Passalidae) which were studied by Cody and Gray (6, p.508). In adult Passalus, the central nerve cord is very much different from the larval cord. The meso- and meta-thoracic ganglia which are fused with the abdominal ganglia, are located in the second thoracic segment while the pro-thoracic ganglion is separated in the first segment.

DISCUSSION

Beginning with the most primitive and placing the most specialized family last, Leng (18, pp.248-265) arranged the Scarabaeoidea phylogenetically as: Scarabaeidae, Trogidae, Lucanidae and Passalidae.

The primitive family Scarabaeidae contains many subfamilies. Beginning with the most generalized the important subfamilies have the following phylogenetic arrangement according to Leng: Corprinae, Geotrupinae, Pleocominae, Glaphyrinae, Troginae, Melolonthinae, Rutelinae, Dynastinae, and Cetoniinae.
These phylogenetic concepts have been further tested by studying the digestive tract and the nervous system of the larva of one species from each of the following subfamilies: Pleocominae; Glaphyrinae; Melolonthinae.

Recently Maxwell (21, pp.102-115) has shown that the salivary glands and the malpighian tubules have the greatest phylogenetic significance in the sawfly larvae. Also, she believes these characters to be of phylogenetic significance, but not of the same magnitude: variation in gut proportions, size and structure of the crop, differences in cuticular covering, variations in the epithelial lining of the gut, presence and absence of spines in the gut, number of the gastric caeca, and the structure of the individual malpighian tubules. It is possible that these characters may prove to be of phylogenetic significance in the Scarabaeidae.

The length of the gut in scarabaeid insects varies from one genus to another. Many workers consider the length of the gut as being subjected to the adaptation for feeding. Dung feeding insects such as Canthon, usually have a relatively longer digestive tract than fresh tissue feeding insects. Also there is some evidence that the length of the canal is correlated with the development of gastric caeca. The longer the alimentary canal, the more the gastric caeca are reduced and degenerated. This reaches the ultimate in Canthon larvae which have no gastric caeca.
and the alimentary canal is twice as long as the body. *Dichelonyx* has one set of well developed gastric caeca and a gut that is 1.5 times the length of the body. *Lichnanthe* has two sets of undeveloped gastric caeca and the canal is about 1.8 of the body's length, while *Pleocoms* has two well developed caeca and the canal is only 1.3 times longer than the body. Thus the feeding habits of scarabaeid larvae seem to have much influence in the development of the gut and gastric caeca.

Changes in the number of gastric caeca and changes in the length of the alimentary canal during the development of larval stages was found only in *Pleocoma*. The length of the fore-, mid-, and hind-gut and the development of gastric caeca are different between the first and the fourth instar and between the eighth and ninth instar. The changes are caused by the tremendous increase of the epithelial cells in the mid-gut and gastric caeca from the first instar to fourth to eighth instars. These early instars are considered by the writer to be the active feeding stage and at this time active secretion would be needed. The reduction of these cells causes the shortening of the mid-gut and degeneration of the gastric caeca, which occurs about the ninth instar. The author suggests that the degeneration of the gastric caeca indicates either a cessation of feeding or indicates a change in feeding habits. These changes do not occur in the other genera
studied. Both adaptive and phylogenetic features are to be found in the alimentary canal. For this reason phylogenetic interpretations must be made very carefully. However, there are features of the alimentary canal which seem to be definitely phylogenetic indicators.

Scarabaeid larvae possess a very short fore-gut and a rather long mid-gut. The hind-gut may be short or long depending on the species. The alimentary canal of the larvae studied did not differ greatly either in form or in histological structure. These differences were found: presence or absence of spines in the fore-gut; changes in the shape of the stomodeal valve; the presence or absence of the peritrophic membrane; the number, shape, and location of the gastric caeca; the structure and location of the malpighian tubules; the changes in form and structure of the colon; and the musculature of some parts of the gut.

The intima of the pharynx of Pleocoma, and Dichelonyx has a vestiture of retrose spines but such spines are absent in Polyphylla and Lichnanthe. These spines are also found in adult of many genera, such as Phanaeus, Phyllophaga, Diplotaxis, Popillia, etc. The peritrophic membrane of the mid-gut of Polyphylla forms a single, uniform continuous structure while in Pleocoma and Dichelonyx the peritrophic membrane forms a series of concentric lamellae. The membrane is absent in Lichnanthe. The shape of the stomodeal valves depends upon the shape of the lobes.
functioning as valves. In *Pleocoma* there are three large lobes, in *Polyphylla* six large lobes, in *Dichelonyx* numerous lobes. There is a thick ring in *Lichnanthe* (Figures 10, 14, 16, 18). The histological structure is similar in these genera. In the musculature there were such differences as the insertion of longitudinal muscles on the proctodeal valve of *Pleocoma* and *Dichelonyx*, while the muscles were absent in *Polyphylla* and *Lichnanthe*. These differences apparently have no significance phylogenetically, since they may occur in any subfamily.

The number of malpighian tubules in the larvae of many subfamilies of Scarabaeidae is the same. Even though their structures are the same, the location of the tubules differs from one subfamily to the other. The malpighian tubules occur on any portion of the mid- and hind-gut. They were found on the middle and posterior end of the mid-gut in *Osmoderma* (24, p.145) and *Dichelonyx* respectively. They may occur both anteriorly and posteriorly on the proctodeal valve as in *Polyphylla* or they may be found only on the posterior portion of the valve as in *Lichnanthe* and *Pleocoma*. Although the histological structures did not differ, yet the number of cells did. In cross sections of *Pleocoma* malpighian tubules, the walls were seven to fifteen epithelial cells thick, while in *Lichnanthe* there are only three to six cells.
The colon shows a diversity in shape and in its structures. In the primitive *Pleocoma* larvae there are two divisions of the colon as in the other genera, but both divisions consist of very thick circular muscles, which are crossed with six isolated strands of longitudinal muscles. A very thick intima is present. In *Lichnanthe* a long broad tube is formed anteriorly and narrow tube posteriorly. The distinct structures are the very weak circular muscles, the indistinct intima of the anterior colon and the very strong circular muscles and the conspicuous intima of the posterior colon. Also in *Dichelonyx*, *Polyphylla*, *Oryctes* (8, p.28), *Popillia* (26, p.190) and many other genera, the large sac-like anterior colon and the narrow posterior colon are characteristic of the genera. The distinct characters of the anterior colon, like as of *Lichnanthe*, are the weak circular muscles and the inconspicuous intima, but the epithelial cells are broad and irregularly scattered which is different from the epithelial layer in the colon of *Lichnanthe* or *Pleocoma*. The structures of the posterior colon do not differ from the other genera.

Rapp (24, p.147) reported that the gastric caeca of scarabaeid larvae differ in number, shape, and location. This is also true for all larvae which were studied here. Large lobes are found in *Pleocoma*, *Polyphylla* while small blind pouches are found in *Dichelonyx*, *Lichnanthe*. The location of the gastric caeca on the mid-gut differ with
Only one set is found in *Dichelonyx*, two sets in *Pleocoma* and *Lichnanthe* and three sets in *Polyphylla* larvae.

The differences in the number and the development of the gastric caeca in *Dichelonyx* (Melolonthinae), and *Polyphylla* (Melolonthinae) are interesting. While the gastric caeca display adaptations in regard to the type of food eaten by the individual, yet a phylogenetic trend can also be traced. Thus, in the most generalized form there are no gastric caeca, but as the degree of specialization increases, the number of gastric caeca increase. This may be traced through a number of genera. The larvae of *Canthon* (Coprinae), which is considered the most primitive of the Scarabaeidae, have no gastric caeca. The larvae of *Phyllophaga* (Melolonthinae), *Pelidnota* (Rutelinae), *Xyloryctes* (Dynastinae), and *Osmoderma* (Cetoniinae), possess one, two, three, and four sets of gastric caeca respectively.

The number of gastric caeca indicates that *Polyphylla* should be removed from the subfamily Melolonthinae and placed in a higher family. In *Phyllophaga* (Melolonthinae), Rapp (24, p.145) found on the anterior end only of the mid-gut, two blind pouch-like gastric caeca. The writer has found similar gastric caeca in *Dichelonyx* larvae which also belong to the Melolonthinae. On the other hand, *Polyphylla* has three sets of well developed gastric caeca.
The value of the nervous system as a phylogenetic indicator is more clear cut than the alimentary canal. Brandt (4) recognized that the most important differences in the nervous system in Coleoptera larvae are found in the ventral cord. In the most generalized type of a nervous system there are three separate units, the sub-oesophagus, the three thoracic ganglia and the eight abdominal ganglia. Both the units and their component parts are connected by a pair of connectives. In the more specialized form, the abdominal ganglia become fused so that the number of individual ganglia is reduced. Also the thoracic ganglia are subject to fusion. Likewise the sub-oesophageal ganglion becomes a compact mass. The nervous system of Pleocoma larva is an example of the most generalized form in the Scarabaeidae. The nervous system of Lichnanthe and Dichelonyx is also of the generalized type, but here the connectives are shorter than in Pleocoma. On the other hand, in Polyphylla, all the ganglia, including the sub-oesophageal ganglion, are fused into a compact mass.

Thus, both the digestive tract and the nervous system of Polyphylla larva are of the specialized type while other species in the subfamily Melolonthinae are of the generalized type. Furthermore, the Polyphylla type of a nervous system is found in larvae of the higher specialized subfamilies, Pelidnota (Rutelinae), Xyloryctes (Dynastinae) and Osmoderma (Cetoniinae) are examples.
The number of ganglia which fuse into a compact mass probably can be determined by the number and location of peripheral nerves. In the various scarabaeid larvae which were observed, each thoracic ganglion contains two pairs of peripheral nerves; each abdominal ganglion contains one, except the posterior ganglion contains three. Although there has been a condensation of the ganglia and an anterior migration of the entire cord, the peripheral nerves still supply the same segments in which they were originally located. Also, they still arise from the ganglia and ganglionic mass in their same relative position. However, on studying Corydalis larvae, Hammar (10, p.120) was unable to number the fusing ganglia. He believed that an investigation of the embryological conditions was the only way to settle this problem.

There seem to be few changes in the nervous system during development of larval stages in scarabaeid insects. There is only a slight anterior movement of posterior ganglia by shortening of the connectives in Pleocoma and no changes occur in other genera which were studied here. There is considerable change from the larval to the adult nervous system. In Pleocoma the abdominal ganglia are reduced from eight in the larvae to six in the adults. The meso- and meta-thoracic ganglia are partially fused with the first abdominal ganglion in the adult but not in the
larva. Oryctes cornutus (6, p.513), Oryctes rhinoceros (8, p.31) are other examples.

Since the family Passalidae is considered to be more specialized than the family Scarabaeidae, an interesting comparison can be made. The nervous system of the larva of *Passalus* as figured by Cody and Gray (6, p.519) resembles *Pleocoma* very closely. However, the nervous system of the adult *Passalus* (6, p.521) is very specialized and closely resembles *Oryctes* (8, p.31). On the other hand *Oryctes*, which is considered to be closely related to *Passalus*, contains a very specialized type of nervous system in both larvae and adults. Thus *Passalus* does not exhibit its specialized form of the nervous system in the larval stage but only in the adult stage. Possibly this genus is the most primitive type of the family Passalidae. The generalized type of a nervous system is also found in the larva of *Coruchus* the family Lucanidae as observed by the writer.

**SUMMARY**

The digestive and nervous systems of larvae four genera including several instars of *Pleocoma* (Pleocominae), *Lichnanthe* (Glaphyrinae), *Dichelonyx* (Melolonthinae), and *Polyphylla* are described and compared. The results of this investigation can be briefly summarized as follows:

1. There are not many changes in the alimentary canal during the development of larval stages. The only changes
are in the length of the mid-gut and in the development of gastric caeca. These changes are accomplished by the development and degeneration of epithelial cells of the mid-gut. In *Pleocoma* larvae these changes occur between the first and the fourth instars and between the eighth and the ninth instars. Such changes do not occur between the second and the third instar of other genera.

2. Only minor changes of the nervous system, such as a slight anterior movement of posterior ganglia and the shortening of connectives, occur during the development of these larval stages.

3. The alimentary canal of the larvae of all the genera studied is not much different both in form and in divisions. These differences were noted in the digestive tract between genera:

Spines were present or absent in the fore-gut; the shape of the stomodeal valves; the presence, absence, and the formation of peritrophic membrane; the number, form and location of gastric caeca; the location and structure of malpighian tubules; the form and structures of the colon and the musculature in some particular part of the gut such as at the region of the pyloric valve.

4. The most important differences in the nervous system in these larvae are exhibited in the ventral nerve cord. In the most generalized system there are three
separate units: a sub-oesophageal ganglion, three thoracic ganglia and eight abdominal ganglia. These are joined together by a long pair of connectives in *Pleocoma* larvae which are considered to be the most generalized of the Scarabaeidae studied. The shortening of the connectives without the fusion of these ganglia in *Lichnanthe* and *Dichelonyx* is considered only as a step toward the more specialized forms. The fusion of all ganglia into a long compact mass, as found in *Polyphylla*, is considered to be the most specialized type.

5. Because the adaptive structures for feeding influence the shape and form of the digestive tracts of scarabaeid larvae, many structures of the alimentary canal are not of phylogenetic significance. There are however some evidences that the gastric caeca and the ventral nerve cord are important as phylogenetic indices.

6. The gastric caeca and the ventral cord of *Pleocoma, Lichnanthe, Dichelonyx* are of the generalized type which is in agreement with the phylogenetic concept of authors in arranging subfamilies. On the other hand *Polyphylla* (*Melolonthinae*) is more highly specialized. For this reason *Polyphylla* should not be in the more generalized subfamily *Melolonthinae*.

7. However, more extensive studies are needed for determining which characters are of the most phylogenetic significance in the scarabaeid larvae.
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PLATE I

Figure 1. *Pleocoma* sp., the alimentary canal of the first instar.

Figure 2. *Pleocoma* sp., the alimentary canal of the fourth instar.

Figure 3. *Pleocoma* sp., the alimentary canal of the late instar with reduced gastric caeca.

Figure 4. *Pleocoma* sp., the alimentary canal of the late instar without gastric caeca.

Figure 5. *Pleocoma* sp., two sets of gastric caeca of the first instar.

Figure 6. *Pleocoma* sp., two sets of gastric caeca of the fourth instar.

Figure 7. *Pleocoma* sp., two sets of gastric caeca of the eighth to eleventh instars.

Figure 8. *Pleocoma* sp., two sets of gastric caeca of the late instar.

Figure 9. *Pleocoma* sp., the view of pyloric valve.

Figure 10. *Pleocoma* sp., the view of stomodeal valve.

AN, anus; CL, colon; CR, crop; GAS, gastric caeca; IL, ileum; LM, longitudinal muscles; MAL, malpighian tubule; MT, mouth; OE, oesophagus; PHY, pharynx; PV, pyloric valve; REC, rectum; SV, stomodeal valve; VENT, ventriculus.
Figure 11. *Lichnanthe* larva, alimentary canal.

Figure 12. *Polyphylla* larva, alimentary canal.

Figure 13. *Dichelonyx* larva, alimentary canal.

Figure 14. *Lichnanthe* larva, stomodeal valve.

Figure 15. *Lichnanthe* larva, pyloric valve.

Figure 16. *Dichelonyx* larva, stomodeal valve.

Figure 17. *Dichelonyx* larva, pyloric valve.

Figure 18. *Polyphylla* larva, stomodeal valve.

Figure 19. *Polyphylla* larva, pyloric valve.

Figure 20. *Polyphylla* larva, the alimentary canal and nerve cord, diagrammatic.

Figure 21. *Lichnanthe* larva, the alimentary canal and nerve cord, diagrammatic.

Figure 22. *Pleocoma* larva, the alimentary canal and nerve cord, diagrammatic.

ACL, anterior colon; AN, anus; BR, brain; CL, colon; CR, crop; GAS, gastric caeca; IL, ileum; LM, longitudinal muscles; MAL, malpighian tubule; OE, oesophagus; PCL, posterior colon; PHY, pharynx; PV, pyloric valve; REC, rectum; SV, stomodeal valve; VC, ventral nerve cord; VENT, ventriculus.
PLATE 3

Figure 23. Polyphylla larva, cross section of pharynx.
Figure 24. Pleocoma larva, cross section of crop.
Figure 25. Dichelonyx larva, cross section through region of stomodeal valve.
Figure 26. Pleocoma larva, cross section through region of stomodeal valve.
Figure 27. Polyphylla larva, cross section through region of stomodeal valve.
Figure 28. Lichnanthe larva, cross section through region of stomodeal valve.
Figure 29. Polyphylla larva, cross section of a portion of ventriculus.
Figure 30. Dichelonyx larva, cross section of a portion of gastric caeca.
Figure 31. Polyphylla larva, cross section of a portion of pyloric valve.
Figure 32. Lichnanthe larva, cross section of ileum.
Figure 33. Pleocoma larva, cross section of ileum.
Figure 34. Pleocoma larva, cross section of anterior colon.
Figure 35. Lichnanthe larva, cross section of a portion of anterior colon.
Figure 36. Polyphylla larva, cross section of a portion of anterior colon.
Figure 37. Polyphylla larva, cross section of a portion of posterior colon.
Figure 38. Dichelonyx larva, cross section of malpighian tubule.
Figure 39. Pleocoma larva, cross section of malpighian tubule.
Figure 40. *Pleocoma* larva, cross section of posterior colon.

Figure 41. *Polyphylla* larva, cross section of a portion of rectum.

Figure 42. *Pleocoma* larva, longitudinal section of larval pharynx.

BM, basement membrane; CM, circular muscles; EP, epithelial cells; IN, intima; J, junction of fore- and mid-gut; LM, longitudinal muscles; LUM, lumen; NU, nucleus; O, malpighian tubule orifice; PHY, pharynx; PM, peritrophic membrane; RG, regenerative cells; S, spines; SB, striated border; SV, stomodeal valve; TRA, trachea.
Figure 43. *Pleccoma* sp., longitudinal section of larval stomodeal valve.

Figure 44. *Polyphylla* sp., longitudinal section of larval stomodeal valve.

Figure 45. *Dichelonyx* sp., longitudinal section of larval stomodeal valve.

Figure 46. *Pleccoma* larva, longitudinal section of the mid- and hind-gut junction.

Figure 47. *Polyphylla* larva, longitudinal section of the mid- and hind-gut junction.

Figure 48. *Dichelonyx* larva, longitudinal section of the mid- and hind-gut junction.

Figure 49. *Lichnanthe* larva, section of proctodeal pyloric valve.

Figure 50. *Lichnanthe* sp., longitudinal section of larval stomodeal valve.

Figure 51. *Lichnanthe* sp., longitudinal section of the mid- and hind-gut junction of larva.

BM, basement membrane; CM, circular muscles; CR, crop; EP, epithelial cells; GAS, gastric caeca; IN, intima; J, junction of fore- and mid-gut; L, junction of mid-and hind-gut; LM, longitudinal muscles; MAL, malpighian tubule; PM, peritrophic membrane; PV, pyloric valve; RG, regenerative cells; SV, stomodeal valve; TRA, trachea; VENT, ventriculus.
Ventral nervous system and brain of scarabaeid insect.

Figure 52. *Pleocoma* sp., fourth larval stage.

Figure 53. *Pleocoma* sp., late instar.

Figure 54. *Pleocoma* sp., adult stage.

Figure 55. *Polyphylla* sp., larval stage.

Figure 56. *Polyphylla* sp., larval stage, showing the brain, the ventral and stomodeal nervous system.

Figure 57. *Lichnanthe* sp., larval stage.

Figure 58. *Geotrupes blackburni*, larval stage.

Figure 59. *Dichelonyx* sp., larval stage.

A, abdominal segment; ATN, nervus antennalis; BR, brain; FG, frontal ganglion; H, head; HG, hypocerebral ganglion; LN, nervus lateralis; OG, oesophageal ganglion; ON, nervus opticus; SC, sub-oesophageal commissure; SO, sub-oesophageal ganglion; T, thoracic segment.

I, prothoracic ganglion; II, mesothoracic ganglion; III, metathoracic ganglion; 1-8 abdominal ganglia.