A Comparative Anatomical Study of the Alimentary Canal of Chrysomeloidea (Coleoptera: Polyphaga)

by

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A Comparative Anatomical Study of the Alimentary Canal of Chrysomeloidea (Coleoptera: Polyphaga) *

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ABSTRACT

This study comprises a detailed study of the alimentary canal of 1 Cerambycidae, 4 Bruchidae and 52 Chrysomelidae species. It was found that the size and distribution of the regenerative crypts of the mid gut, occurrence of the caeca and positions of the Malpighian tubes at their anterior and posterior insertions are of systematic importance at different taxonomic levels. Constitution of the anterior and posterior insertions of the Malpighian tubes was supposed to be evolved basically in three phyletic lines.

INTRODUCTION

The alimentary canal of the groups studied consists of a simple tube, sometimes with a few convolutions, which is probably a characteristic of phytophagous insects. The alimentary canal of these beetles is divisible into three main regions, both morphologically and embryologically; the fore gut or stomodeaum which is ectodermal in origin, mid gut or mesenteron which is endodermal in origin and hind gut or proctodaeum which is also ectodermal. For simplification only morphological correspondents of these terms (fore gut, mid gut and hind gut) are used here.

The fore gut consists of a narrow pharynx opening into the tubular oesophagus, which is narrow anteriorly but may be distended posteriorly to form a crop (absent in a number of species studied) and a proventriculus (absent in the most of the species studied). The mid gut forms usually the longest part of the gut, which is sometimes referred to the ventriculus or stomach. The hind gut.

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comprises the pyloric valve, ileum, colon and the rectum; the pylorus may not be distinct in some species. Posterior to the ileum the gut usually distends, then sharply narrows, tapering towards the anus. Both these parts were called rectum by the earlier authors, or the distended part as anterior rectum, the narrow part as posterior rectum whereas more recent authors referred only to the distended part as colon and to the narrow part as the rectum; the recent usage of these terminologies is adopted in this work.

As already remarked by previous authors [4,13,15 and others] there are basically 6 Malpighian tubes in most of the Cucujiformia, which are usually cryptonephric, so that they have become posteriorly attached into the walls of the colon. POLL [13] pointed out that in Chrysomeloidea both insertions tend to gather in two groups but the position of the insertions varies a great deal in different groups besides the structural modifications and reduction in number (reduced to 4 in some). The details of the alimentary canal and of Malpighian tubes will be separately discussed in each group.

MATERIAL AND METHODS

Materials: Most of the species studied were captured in the vicinity of Glasgow (Scotland) and numerous specimens were provided in dry and spirit collections of the Zoology Department of Glasgow University and in private spirit collection of Dr. R. A. Crowson. Orsodacne cerasi (L.) was sent by Dr. W. Wittmer from Switzerland and some Chrysomelidae specimens were presented by Dr. T. Sen Gupta from India. I collected Zeugophora flavicollis in Holland and Euspermophagus sericeus, Zabrotes subfasciatus, Criocerus asparagi, Clytra novempunctata, Chrysolina americana, Plagiodera versicolora, and Hispa testacea in Turkey.

Methods: For detailed examination of the alimentary canal, the specimens were preferred alive, because the spirit-preserved specimens often became brittle. However, where no alive specimen was available, preserved material was examined by softening it, preceding the dissection. The dissection procedure of the mounts were explained before [9]. The figures were drawn by free-hand to fully represent the fine details of the structures.
A COMPARATIVE ANATOMICAL STUDY

LIST OF SPECIES STUDIED

Cerambycidae: Rhagium bifasciatum F. (*).

Bruchidae: Acanthoscelides obtectus (Say) (*), Eusprmophagus sericeus (Geoffr.) (*), Zabrotes subfasciatus Boh., Caryedon serratus (01.) (*).

Chrysomelidae

Sagra: Sagra congoana Clav. (*).

Orsodacninae: Orsodacne cerasi (L.) (*).

Donaciinae: Donacia vulgaris Zschach. (*), Plateumaris discolor Panz. (*).

Criocerinae: Crioceris asparagi (L.) (*), Oulema melanopa (L.).

Megalopodinae: Zeugophora flavicollis (Mars.) (*).

Lamprosomatinae: Oomorphus concolor (Sturm.) (*).

Cryptocephalinae: Cryptocephalus rugicollis 01. (*), C. labiatus L., Brachycaulus ferrugineus Fairm.

Clytrinae: Clytra novempunctata 01. (*), Labidostomis taxicornis F.

Chrysomelinae: Phylocharis cyanicoris F. (*), Timarcha tenebriosa (F.) (*), Chrysolina americana L. (*), Ch. polita L. (*), Phytoecia pallidus (L.) (*), Phyloecia vulgatissima (L.) (*), Gastroidea viridula (Deg.) (*), Phaedon timidulus Germ. (*), Hydrothassa marginelle (L.) (*), Prasoeuris phellandrii (L.) (*), Plagiodya versicolora (Laich.) (*).

Halticinae: Derocrepis rufipes (L.) (*), Crepidodera transversa (Marsh.) (*), Chalcoidea fulvicornis (F.) (*), Mantura obtusata (Gyll.) (*), Haltica ericti All. (*), Sphaeroderma testaceum (F.) (*), Psylloides cuprea (Koch.) (*), Phyllectra undulata Kutsch. (*), Aphtona coerulea (Geoffr.) (*), Longitarsus melanocephalus (Deg.) (*), Chaetocnema concinna (Marsh.) (*), Apteropeda orbiculata (Marsh.) (*).

Galerucinae: Luperus longicornis (F.) (*), Phylobroctica quadrimalculata (L.) (*), Sermylassa halensis (L.), Galerucella nymphaeae (L.) (*), Lochmea suturalis (Thoms) (*).

Cassidinae: *Cassida flaveola* Thunb. (*), *C. rubiginosa* Muell. (*).

Hispinae: *Aproida balyi* Pasc. (*), *Hispa testacea* L. (*).

The species whose alimentary canal is figured in the text is indicated (*)

**RESULTS**

(i) **CERAMBYCIDAE**

The alimentary canals of *Prionus cararius*, *P. faber*, *Lamia textor*, *Aromia maschata*, *Cerambyx cerdo*, *Callidium violaceum* and *Leptura cordigera* Füssl. were figured by DUFOUR (4) and that of *Nupserha bicolor* Thoms. by DUTT (5). The gross morphology of the alimentary canal of *Prionus laticollis* (Drury) was described and figured by BENHAM (1) and a portion of the alimentary canal of *Cerambyx cerdo* L. by POLL (13). The alimentary canal of *Rhagium bifasciatum* was studied here (Fig. 1). From the illustrations and descriptions of the authors and myself it appears that all the species mentioned have a distinct crop, except *Lamia textor* and *Leptura hastata*. The mid gut of *P. laticollis* is short and has no regenerative crypts [1]. Except for *Cal. violaceum* and *N. bicolor*, the other cerambycids mentioned have some regenerative crypts. According to the figures of DUFOUR (4) *L. textor* has an unusually long, once or twice looped mid gut and *C. cerdo* has a kind of annulations on the mid gut. DUTT (5) figured at least 9 ceaca on the anterior margin of the mid gut of *N. bicolor*.

POLL (13), reviewing the previous literature on Cerambycidae, distinguished three groups of species according to the anterior openings of the Malpighian tubes and two groups of species according to the posterior insertions. STAMMER [15] figured only one generalised type for Cerambycidae. The Malpighian tubes of *R. bifasciatum* (Fig. 1) are grouped three by three at both insertions; posteriorly two Malpighian tubes of each group first join together than the third joins in some distance behind.
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(ii) BRUCHIDAE

There seemed to be no previous data on the alimentary canal of Bruchidae. The alimentary canals of namely 4 species, Acanthoscelides obtectus (Fig. 2), Euspermophagus sericeus (Fig. 3), Zabrates subfasciatus and Carya don serratus (Fig. 4) were studied in this work. The alimentary canals of these species show a similar structure, being a short tube with few convolutions. The fore gut consists of a narrow and comparatively long oesophagus and a small proventriculus, which contains internally 8 teleotised longitudinal ridges [14]. The mid gut is rather short and set with prominent crypts, which are dense in C. serratus but rather sparse in A. obtectus, E. sericeus and Z. subfasciatus. The hind gut is short, with only a single loop.

Four Malpighian tubes were found in Carya don (Fig. 4) and six in A. obtectus (Fig. 2), E. sericeus (Fig. 3) and Z. subfasciatus. Details of the anterior openings and posterior insertions of the Malpighian tubes of each species are shown in the respective figures 2, 3, and 4.

(iii) CHRYSOMELIDAE

There was no fresh material of Sagriinae available for this investigation. Dissections of a few dry specimens of Sagriinae, obtained from the collections of the Zoology Department of Glasgow, University revealed some features of the internal anatomy of this species. The alimentary canal of S. congoana (Fig. 5) is moderately long, consisting of a short oesophagus, without a distinct crop, a moderately long mid gut and an unusually long hind gut, even longer than the mid gut. The mid gut is entirely set with regenerative crypts, which are rather prominent, and moderately densely distributed.

The anterior openings of the Malpighian tubes are grouped and joined four and two; the four run into a short common duct before joining the gut; both groups open at the same level of the gut. Unfortunately, the posterior of the Malpighian tubes were not observed for sure but I had the impression from the fragmentary remains of the Malpighian tubes that they were grouped and
joined three by three on each side, one of the Malpighian tubes of each group being more posteriorly joined than the others (Fig. 5)  

**Orsodacninae:** To our knowledge there was no published data on the internal anatomy of this systematically important subfamily. The alimentary canal of *Orsodacne cerasi* (Fig. 6) has a very short and narrow oesophagus with a small crop. The mid gut is less than half as long as the hind gut and set with rather prominent regenerative crypts all over.

Anteriorly, the Malpighian tubes are grouped three by three and the 2 groups are approximated dorsally, the Malpighian tubes of each group being evenly spaced between each other. Posteriorly they are grouped and joined to each other at one point again three by three forming a common trunk on each side before inserting into the beginning of the colon (Fig. 6).

**Donaciinae:** The alimentary canals of *Donacia simplex* F. and *Plateumaris discolor* were figured by DUFOUR [4] and of *Donacia semicuprea* Panz by GOECKE [7] and of *D. semicuprea* and *D. crassipes* F. by STAMMER [17]. I also investigated the alimentary canal of *Donacia vulgaris* (Fig. 7) and *Plateumaris discolor* (Fig. 8). All these observations agree in showing that the alimentary canal of Donaciinae is a rather short tube consisting of a large and long oesophagus, a distinct crop, the mid gut at least half as long as the whole gut, and the hind gut in which ileum, colon and the rectum are hardly distinguishable. The mid gut is completely covered with rather prominent regenerative crypts. In Donacia these crypts are relatively longer than those of Plateumaris (cf. Figs. 7,8).

In these aquatic insects, the Malpighian tubes, unlike those of other Chrysomelidae, are not cryptonephric; they have no attachment to the hind gut. Their openings are arranged as in Sagriniae, the only difference is that the group of two are well separated from each other. Posteriorly the group of four Malpighian tubes form a pair of loops, by joining two by two at their apexes. The other two Malpighian tubes are completely free and modified, being swollen medially, probably to accommodate some bacterium-like intracellular micro-organisms, as found in Donacia species by STAMMER [16]. This arrangement of the Malpighian tubes was previously figured in *Donacia simplex* and *Plateumaris discolor* by DU-
FOUR [4] and stated to be similar in *D. eisenia* Hrbst. by POOL [13], in the species of *Donacia* and *Plateumaris* by STAMMER [15, 16] and in *D. semicuprea* by GEOECKE [7]. In the general arrangement of the Malpighian tubes there is no great difference between *Donacia* and *Plateumaris*. STAMMER [15, 16] figured the Malpighian tubes of *Plateumaris* somewhat differently, showing each of the Malpighian tubes of the group of two mentioned above, not ending freely but attaching to the middle of one of the loops; I was unable to trace this pattern in my specimens.

*Criocerinae*: DUFOUR [4] figured the alimentary canal of *Lilioceris mordigera* (L.) and DAVIDSON [2] studied the general anatomy and histology of *Crioceris asparagi* but failed to notice the regenerative crypts. The alimentary canal of *C. asparagi* and *Oulema melanopa* studied was seen to be basically similar (Fig. 9). The alimentary canals of these species consist of an oesophagus, a moderately large crop, a long mid gut entirely covered with regenerative crypts and a rather short hind gut.

The Malpighian tubes of *L. mordigera* [4], those of *C. asparagi* [2, 13, 15] and those of *C. asparagi* (Fig. 9) and *O. melanopa* studied here have a similar arrangement, as seen in Fig. 9. The group of two Malpighian tubes are shorter and thinner than the other four.

*Megalopodinae*: The alimentary canal of *Zeugophora flavicollis* (Fig. 10) is a moderately long tube. It has a very short and narrow oesophagus with a small crop as in Orsodacninae. The mid gut forms the largest part of the gut and it is devoid of the regenerative crypts.

The Malpighian tubes are grouped and joined three by three at one point anteriorly and they are as in Criocerinae posteriorly, so they form two common trunks at their openings to the end of the mid gut and at their insertions on the colon, see Fig. 10. This type of arrangement of the Malpighian tubes is known elsewhere in Chrysomeloidea only in some cerambycids [13].

*Lamprosomatinae*: The alimentary canal of *Ommorphous ovatovalis* (Fig. 11), the only European species representing this subfamily, exhibits some peculiar structures; it consists of an oesophagus,
a large asymmetric crop which connects with the mid gut via a narrow neck, a long and large mid gut and a short hind gut. A similar asymmetric crop was also found in its larva by KASAP and CROW SQN [10]. The regenerative crypts are rather small, short and moderately densely distributed all over the mid gut.

The Malpighian tubules of Oomorphus (Fig. 11) are grouped three by three at their anterior openings, one group on each side of the gut and the Malpighian tubes of each group are usually evenly spaced between each other. Posteriorly they are also grouped three by three, and joined to each other nearly at one point, though the third pair is slightly displaced towards the gut, thus forming a common duct to insert in the colon, as was also figured by STAMMER [15]. The Malpighian tubes are unusually thick, in their posterior ends before they join each other; this pattern was not observed in any other chrysomelid.

Cryptoccephalinae: The alimentary canals of Cryptoccephalus rugicollis (Fig. 12), C. lahitiatus and Brachycalus ferrugineus have a similar structure. A short pharynx is followed by a symmetrically distended oesophagus (= crop), which connects with the mid gut via a short neck region. In this subfamily distribution and size of the regenerative crypts present some special features as also seen in Clytrinae and higher Eumolpinae; the anterior three fifths and posterior one fifth of the mid gut have no crypts, although the anterior part has some sparsely distributed minute tubercles. It is the one fifth of the mid gut which is set with a few but unusually long crypts (Fig. 12); these crypts are in fact drawn into small tubules.

The Malpighian tubes are more or less evenly spaced at their anterior openings and joined each other posteriorly three by three, one pair being displaced towards the gut forming a common trunk on each side to insert in the colon laterally (Fig. 12). STAMMER [15] also figured the Malpighian tubes of Cryptoccephalus but with the anterior insertions grouped three by three as in Oomorphus (grouped and joined at one point), which does not agree with my findings.

Clytrinae: The alimentary canals of the species studied, Clytra novempunctata (Fig. 13) and Labidostomis taxicornis, in general
resemble that of the Cryptoccephalinae, particularly with the crop which is also large, symmetrical and connected with the mid gut via a short neck region and also with the tubular crypts limited to the four-fifth of the mid gut.

POLL [13] stated that the Malpighian tubes of Clytrinae were evenly spaced out at their openings and posteriorly with three on each side being joined at one point forming a common trunk to attach to the colon as he figured only in Coptocephala scopolina L.; he did not name the species on which this generalisation was based. STAMMER [15] found both ends of the Malpighian tubes of Clytra, Gynandrophalma and Labidostomis grouped three by three, posteriorly one pair being somewhat displaced from the junction of others towards the gut forming a common trunk to attach to the hind gut. Findings of STAMMER appear to contradict the generalisation of POLL. I studied the Malpighian tubes of C. novempunctata (Fig. 13) and of L. taxicornis. The openings of the Malpighian tubes of C. novempunctata are as described by POLL, but posteriorly the attachments of them are as described by STAMMER. The openings of the Malpighian tubes of L. taxicornis are as in C. novempunctata but not posteriorly, being three on each side joined at one point forming a common trunk to attach to the hind gut as described by POLL. T’AN [19] figured the arrangements of the Malpighian tubes of Coptocephala pallens mandarinie Ws., closely resembling those of C. punctata, as figured here.

Chrysomelininae: The alimentary canals of the chrysomelines studied (Figs. 14-22) are fairly long tubes and in most of the species they consist of a short pharynx, a moderately long mid gut and the hind gut. Only in Timarcha tenebricosa (Fig. 14) the crop is not distinct and even the oesophagus is extremely reduced. In this subfamily, the presence and distribution of the regenerative crypts are very variable; (i) in Phytodecta pallidus (Fig. 22) they are absent, in Chrysolina americana (Fig. 16) and C. polita and (iii) in Phyllocharis cyanicorne (Fig. 15) they are moderately long and (iv) in Plagiodera versicolora (Fig. 21), Hydrothorax marginella (Fig. 20) and Prasocerus phellandri (Fig. 19) they are long and sparsely distributed (v) in Gastroidea viridula (Fig. 17), Phaedon tumidulus (Fig. 18) and Phyllopecta vugatissima they are big and mo-
derately long, sparsely distributed only on the anterior portions of the mid gut whereas they spread all over the mid gut of other species of Chrysomelinae studied. *T. tenebricosa* was previously studied by DUFOUR (4) and *Phaedon cochleariae* F. by HAMNETT (8) but these authors did not notice the presence of the regenerative crypts. From the figures of PAVLOVSKIY and TERAVSKIY (12) *Leptinotarsa decemlineata* Say seems to have the regenerative crypts like those of *Chrysolina* spp.

According to the anterior insertions of the Malpighian tubes the studied species of this subfamily may be divisible into two groups, although the posterior insertions of the Malpighian tubes are similarly arranged in the chrysomelines studied. The first group includes *Phyl. cyanicornis*, *C. americana*, *C. polita* and *Phyt. pallidus* whose Malpighian tubes are grouped four and two as seen Figs. 15, 16 and 22. Only on *Phyt. pallidus* the arrangement of the four Malpighian tubes is a little different that they open to the end of the mid gut not via a reservoir but close to each other and quite separately. The second group includes the rest of the species studied in this subfamily; the Malpighian tubes are grouped four and two again but the group of four Malpighian tubes are spread out more or less evenly (verticillate) around the end of the mid gut and the group of other two Malpighian tubes, which are thinner and shorter than the others, open separately more anteriorly among the crypts of the mid gut, therefore above the level of the other four Malpighian tubes. Only in *T. tenebricosa* of the other four Malpighian tubes. Only in *T. tenebricosa* the ventral two of the four Malpighian tubes are more or less approximated (Fig. 14). POLL [13] studying *Timarcha* and *Phytodecta* and STAMMER [15] studying *Phylloleptus*, *Chrysolina*, *Prasocuris*, *Phadeon* and *Chrysomela* (*Melasoma*), HAMNETT [8] studying *Phaedon cochleariae* F. and T’AN [19] studying *Chrysolina auriculata* Mann. figured the arrangement of the Malpighian tubes respectively similar of those groups described above, although STAMMER [15] ascribed *Chrysomela* (*Melasoma*) to a different (third) group on the basis of the group of two Malpighian tubes which in his figure seem to be a little longer than those of other genera of *Chrysomelinae* he studied. PAVLOVSKIY and TERAVSKIY [12] did
not show the exact arrangement of the Malpighian tubes of *Leptinotarsa decemlineata*. DUFOUR [4] was obviously mistaken in showing the Malpighian tubes of *T. tenebrosa*, posteriorly being joined to each other at one point.

**Halticinae**: The alimentary canal of Halticinae is scarcely studied; to our knowledge only WOODS [21] studied the Malpighian tubes of *Haltica birmanica* Say and T’AN [19] those of *Haltica cyanea* Weber. Of the halticines studied (i) *Chaetocnema concinna* (Fig. 31), *Apteropeda orbiculata* (Fig. 30), *Haltica ericeti* (Fig. 29), *Longitarus melanoecephalus, Aphthona coerules* (Fig. 28), *Crepidodera transversa* (Fig. 23), *Derocepis rufipes* and *Mantura optusata* (Fig. 25) have a distinct crop; in *C. transversa* and *A. orbiculata* it is rather small whereas in others nearly half as long as the mid gut, (ii) in *Sphaeroderma testaceum* (Fig. 26), *Phylloretae undulata, Chalcoes fulvicornis* (Fig. 24) and *Psyllodes cuprea* (Fig. 27), the oesophagus is separated from the mid gut by a slight constriction; the alimentary canal of this group has no distinct crop. In all the species studied the gut is a relatively short tube, usually lacking any convolutions. The mid gut has no crypts.

The Malpighian tubes of all the halticines mentioned above are grouped four and two at their anterior openings, the group of four form a duct before opening and the group of two open side by side and a little anterior to the former group. Posteriorly, each of the two Malpighian tubes, which are shorter and thinner, joins a pair of the longer ones some distance behind the junction of that pair (only in *Apt. orbiculata* this distance is very small) thus forming a common trunk to attach to the colon (Figs. 23–31). The same arrangement of the Malpighian tubes was also figured in different species of *Haltica* as cited above, respectively by WOODS [21], STAMMER [15] and T’AN [19].

**Galerucinae**: The general structure of the alimentary canal of Galerucinae resembles that of Halticinae, except that in Galerucinae the gut is longer with more convolutions (Figs. 32–34) and all the species studied have more or less a distinct crop. The alimentary canals of *Luperus longicorns* (Fig. 32), *Phyllobrotica quadrimaculata* (Fig. 33), *Sermylissa halensis, Galerucella nympheae* (Fig. 34) and *Lochnaena saturalis* are as illustrated.
ying Galeruea tanaceti L., Khatib [11] studying Galerucella birmanica (Jacoby) found the gut structure as described above.

The Malpighian tubes of L. longicornis (Fig. 32), P. quadrimaculata (Fig. 33), S. halensis, G. nymphaeae (Fig. 34) and L. suturalis are arranged as in Halticiniae. The Malpighian tubes of Galeruca tanaceti L. were similarly figured by Dufour [4], those of Galeruca, Galerucella, Lochmaea by Stammer [15], of Aulacophora femoralis chinensis Weise by Tan [19] and of Galerucello birmanica by Khatib [11].

Eumolpinae: In the eumolpine species studied, the length of the alimentary canal varies in different species, but all have a fairly large crop, a long mid gut partially set with regenerative crypts and with enteric caeca, and a moderately long hind gut. The crop connects with the mid gut via a short, narrow and rather musculated neck region, which is a simple contractile tube, but in Spilopryra sumptuosa and Macroloeca vitatta this neck region is highly specialised in having an oesophageal valve directed into the crop and a special armature directed into the mid gut. This special armature probably represents a kind of modified proventriculus and it has eight well-sclerotized radial arms (Figs. 37, 38). The enteric caeca are bottle-shaped structures (Figs. 35–45), opening to the anterior margin of the mid gut via a narrow duct. The number of these caeca varies in the species studied, e.g. 12 in Abirus rubripes, 14 in Scelodonta indica, 10 in Trictona sp. and 18–20 in Chrysochus cobaltinus. Only in Sp. sumptuosa (Figs. 35–36) (not studied in M. vitata) are many structurally similar caeca also present on the anterior portion of the mid gut; this species, as indicated by its gut content, appears to feed on some woody plant material which probably needs symbiotic organisms to be digested. Stammer [17] recorded 15–20 symbiotic caeca in Bromius obscurus L. harbouring some intracellular and intercellular organisms. The small and not prominent regenerative crypts are moderately densely distributed on the posterior mid gut in Sp. sumptuosa. In the species studied (Figs. 39–42), except for Sp. sumptuosa, the regenerative crypts of the posterior or the intermediate mid gut are tubular as in Cryptoccephalinae and Clytrinae and those on the medio-anterior part of the mid gut are still small and not distinct. As seen in the
relevant figures 39-42, some regions of the mid gut do not possess any regenerative crypts, e.g. the posterior end of the mid gut of *A. rubriipes*, the intermediate part and very posterior end of the mid gut of *Trielia sp.* (Fig. 42), etc. The general structure of the alimentary canal of *B. obscurus* was figured by STAMMER [17]; it very much resembles that of *S. indica* (Fig. 40).

On the basis of our present knowledge, the enoplipine species studied can be divided into three groups according to the arrangement of the Malpighian tubes: (i) in *Sp. sumptuosa* (Fig. 38), *A. rubriipes* (Fig. 39) and possibly in *Trielia sp.* (Fig. 42) (the posterior insertions of the Malpighian tubes of this genus are not known to me), the Malpighian tubes are grouped, three by three, at both ends, their anterior insertions are separate and lateral to the mid gut; and posteriorly each group join each other at one point to form a common duct to attach to the colon. (ii) in *Pseudopimera andressi* (Fig. 41) the anterior insertions of the Malpighian tubes are grouped two, two and two (or two) and posteriorly, they are arranged as in group (i), (iii) in *S. indica* (Fig. 40) according to STAMMER [17] in *B. obscurus* and according to TAN [19] in *Paraplectos parryi* Baly and *Basilepta fulvipes* Motsch., the openings of the Malpighian tubes are verticillate while they are posteriorly divided three by three on each side, with one on each side joined posteriorly to the other two to form a common trunk to attach to the colon. The two latter joining Malpighian tubes differ from the others only in being a little shorter.

**Cassidinae:** STAMMER [17] figured the alimentary canals of *Cassida viridis* L. and *C. nebulosa* L. In this work the alimentary canals of *Cassida flavicollis* (Fig. 43) and *C. rubiginosa* (Fig. 44) were studied. These species have a similar gut structure, a rather large crop and some regenerative crypts on the mid gut are always present. The regenerative crypts are usually not prominent and moderately dense, distributed only on the anterior half of the mid gut in the species studied but they were shown all over the mid gut in the species figured by STAMMER (17). A distinct feature seen in Cassidinae is the presence of some enteric ceca as in *Eupholpinae* and some *Hispanioidea*. These ceca are attached to the anterior margin of the mid gut, each with a short duct as figured in *C.*
flaveola (Fig. 43) and C. rubiginosa (Fig. 44). In these species two pair of caeca were found, a pair to be on each side. STAMMER [17] recorded four caeca in C. viridis, C. hemisphaerica Hrbst., two caeca in C. vibex L., C. rubiginosa and C. nobilis L. but no caeca in C. nebulosa L. and C. flaveola. There seems to be some disagreement between our observations and STAMMER's about the presence and number of these structures in C. rubiginosa and C. flaveola. These structures are also present in larvae and contain some bacterium-like micro-organisms like those of adults [16]. The variability in the presence and the number of them in adults suggest that they are primarily larval organs and not fully functional in adults. Therefore, they are liable to be reduced or lost in some species or even some time during the life-span of a species, probably after breeding season, having accomplished the transmission of the micro-organisms to the next generation of the insect. The Malpighian tubes of these species (Figs. 43-44) are similarly arranged to those of Criocerinae. But the arrangement of their anterior openings vary among the species; STAMMER [17] figured the Malpighian tubes of C. viridis and C. nebulosa being grouped three by three laterad to the end of the mid gut; each group being evenly spaced between each other, as in some other chrysomelids e.g. Oomorphus (Fig. 11). In C. rubiginosa anteriorly they are grouped three by three dorsally and more or less evenly spaced between each other. The two mid dorsal ones are differentiated in being shorter and thinner than the others. However, posteriorly they are grouped three by three, the shorter Malpighian tubes, one on each side, being more posteriorly joined to the others. In C. flaveola, strangely enough, three different types of the arrangement of the Malpighian tubes were observed in three specimens (2 females and 1 male) as shown in Fig. 43, which are grouped in four and two; three, one and two; and two, two and two. These various arrangements of the anterior insertions of the Malpighian tubes may suggest (i) these may be individual differences (ii) the anterior insertions of the Malpighian tubes may differ in different age groups (iii) the anterior openings of the Malpighian tubes are less stable than the posterior insertions as also seen in Oomorphus concolor.

Hispinae: TAYLOR [20] figured very diagrammatically the alimentary canal of Promecotheca reichsi Baly, showing a very simp-
le and short alimentary canal and apparently without crypts on the mid gut. He figured two pairs of enteric caeca. The alimentary canals of Aproida balyi (fig. 45) and Hispa testacea (fig. 46) were found to be a moderately long tube consisting of a pharynx, an oesophagus, a crop which is about half as long as the mid gut, a mid gut and the hind gut. In H. testacea the mid gut is relatively short and has no crypt whereas the mid gut of A. balyi is longer and entirely covered with rather prominent and moderately densely distributed regenerative crypts. A. balyi also has two pairs of enteric caeca as found in P. reichei by TAYLOR [20]; such caeca were not found in H. testacea.

Anteriorly the Malpighian tubes of P. reichei were shown by TAYLOR to open separately in two groups of three, one each side. A similar arrangement was found in A. balyi (Fig. 45) but in H. testacea (Fig. 46) they are differently grouped, four opening ventrally and two dorsally; the ones on the ventral side join two by two forming 2 ducts to open into the beginning of the hind gut. The dorsal two Malpighian tubes are also joined each other before opening. Such an arrangement of the Malpighian tubes in H. testacea seems to be of rather specialised type, not previously reported in Chrysomelidae. The posterior insertions of the Malpighian tubes of A. balyi and of H. testacea are as seen in Cassidinæ, Criocerinæ and others. In P. reichei the Malpighian tubes were figured by TAYLOR [20] as ending freely in the body cavity; it is very likely that he may have mistaken in his observations, because except for the aquatic donaciins, no other chrysomelines are known with free Malpighian tubes.

**SYSTEMATIC CONCLUSIONS**

The alimentary canal is rather short in some Cerambycidae, Bruchidae, Orsodacninae, Donacinae, Megalopodinae, Scolodonta (Eumolpinae), in some Chrysomelinae (e.g. Phyllodecta, Plagiode-ra), in the rest of the subfamilies it is rather long and has convolutions involving the mid and hind gut. In all the groups investigated the mid gut apparently forms the longest part of the gut. On the other hand, Saga has the longest hind gut among the genera studied.
The crop is absent only in Lamia textor [4], Bruchidae, Sagrinae and some Halticinae. It is largely developed in Camptosomatidae, Eumolpinae and Chrysomelinae. In Camptosomatidae the crop is posteriorly distended abruptly and turned out to be a balloon-like pouch and connected to the mid gut via a very short neck area. In other groups, the crop is slender or slightly wider than the mid gut. It is assymmetrical only in Gomphus.

The proventriculus is present only in Bruchidae, Spilopyra and Macrolema, in which it is rather modified.

The enteric ceca are present in anterior margin of the mid gut of Nupserha bicolor (Cerambycidae) [5] and of Eumolpinae, Cassidinae and Hispinae except Hispa. In this context, it should be noted that the females of these species, except for Nupserha, also have vaginal pouches attached to the common oviduct; they contain and transmit the symbionts (17, 18). In Sagra these vaginal pouches are present although there are no ceca attached to the mid gut of adults. However, it may be still possible that these ceca have been present in their larva and have been lost in adults, as it is the case in some other wood-feeding beetles, e.g. some Cerambycidae [18]. On the other hand, Spilopyra has similar symbiotic ceca all over the anterior part of the mid gut of adults as well as those in the anterior margin of the mid gut. It is noteworthy that it is the presence of these symbiotic ceca, at least the ones in the anterior margin of the mid gut, being the only positive character to link Spilopyra (probably the other primitive eumolpines as well) with the higher ones.

The regenerative crypts on the mid gut is present in most of the species studied, except in some Cerambycidae [1, 4, 5], Megalopodinae, Halticinae, Galerucinae, Phytodecta (Chrysomelinae) and Hispa (Hispinae). Their density and distribution vary between, even within, the subfamilies of Chrysomelidae. Broadly speaking, in Chrysomelinae they are rather prominent and densely distributed on the mid gut of Euapoden subfamilies (when present), whereas in other groups generally reduced, localised or somewhat specialised in structure e.g. they are small and absent in some parts of the mid gut of Chrysomelinae while in Cryptocephalinae, Cleytrinae and higher Eumolpinae they are localised in the mid paste-
rior part of the mid gut and drawn into small tubules; these are the only crypts occurring in Cryptocoelainae and Clytrinae but in higher Eumolpini smaller anterior ones may also occur.

Only higher Camptosomata (Chlamisinae, Cryptocoelainae, and Clytrinae) have rectal sclerites, which were partly considered by KASAP and GROWSON [10]. These sclerites characterise the camptosomatan gut and may be adaptive features for the manipulation of the faeces used to build the egg-case for the basis of their larval cases. There are no rectal sclerites in Lamprosomati- 
nae [3, my observation]. There are only two ventral sclerites in Chlamisinae [3], two dorsal and two ventral sclerites in Cryptocoelainae [8, 6 and my observation] and three dorsal two ventral sclerites in Clytrinae [3, 6 and my observation].

The arrangement of the Malphighian tubes varies in different groups. The usual and primitive number of the Malphighian tubes is six, but only in Caryedon are there only four. They are crypto- nphridic, except in Donaciinae, in which two out of six Malphighian tubes are modified to short symbiont-containing structures.

According to the anterior opening of the Malphighian tubethree main series may be recognised leading to eleven major types and a special type; these are diagrammatically shown in Fig. 47. The series are as follows: (i) the ones grouped three by three, (ii) the ones grouped four and two, (iii) the ones with three Malphighian tubes opening into each of two ducts. Phylogenetic relations of these groups are very difficult to interpret and to decide whether the verticillate positionnig or the grouping of the Malphighian tubes either in three and three or in four and two is the primitive case. As pointed out before there are some gradations between grouping three by three and being verticillate as in Cassida and Osmorphus. POLL [13] suggested that the arrangement of the Malphighian tubes anteriorly being evenly spaced and posteriorly being grouped three by three is the primitive condition. However, a possible suggestion was made as indicated by the arrows in Fig. 47, and the types were considered below as in line with this suggestion. They are as follows:
A) Both ends grouped three by three and inserted to the gut directly and separately, seen in some anonymous Cerambycidae according to POLL [13] (Fig. 47-A).

B) Both ends grouped three by three; anteriorly the Malpighian tubes of each group being evenly spaced between each other and posteriorly being joined each other at one point forming a common trunk to attach to the colon, seen in some Cerambycidae [13], Orsodacne (Orsodacninae), Spilopyra, Abirus and Pseudopio- mer (Eumolpinae) and Oomarphus (Lamprosomatinae) (Fig. 47-B).

C) Grouped three and three at both ends; anterior openings as above groups, in posterior attachments one Malpighian tube on each side being more posteriorly joined to the common duct to attach to the colon, seen in Sceledonota, Bromius, Corynodes (Eumolpinae), Aprodia, Promecotheca (Hispinae) and some Cassida spp. (Cassidinae) (Fig. 57-C).

D) Anteriorly evenly spaced, posteriorly like type (C), seen in Acanthoscelides (Bruchidae), some Cassida spp., Cryptocephalinae and Clytrinae species, except for Labidostomis (Fig. 57-D).

E) Four Malpighian tubes with their openings evenly spaced, the other two a little differentiated being thinner and shorter, others with their openings closely approximated and displaced anteriorly in their opening into the mid gut, and posteriorly as in types (C) and (D), seen in Euspermophagus, Zabrates (Bruchidae) and some chrysomelines (Fig. 52-E).

F) Similar to type (E) but with the two differentiated Malpighian tubes lost so that there are only four Malpighian tubes, posteriorly grouped and joined two by two, seen in Caryedon serratus only (Bruchidae) (Fig. 47-F).

G) Anteriorly grouped four and two, the former group joining in a small duct and the latter being shorter, thinner and closely approximated; posterior attachments as in types (C), (D) and (E), seen in Sagra (Sagrinae) (Fig. 47-G).

H) Very much like type (G), the only difference being that the differentiated group of two tubules are less closely approximated as in Criocerinae studied and in Phyllocharis, Chrysolina and Phytophaga (Chrysomelinae); the anterior insertions of the
group of four Malpighian tubes in *Phytodecta* do not form a real duct, their openings being separate but very close (Fig. 52-H).

I) Not cryptonephridic, anterior insertions grouped as in type (H) the only difference being that the group of two are modified to form symbiont-containing structures, seen in Donaciinae only (Fig. 47-I).

j) Anteriorly and posteriorly rather similar to type (H) but in this type anteriorly the group of two Malpighian tubes are closely approximated and they are moved more anterioirly in relation to the others, posteriorly like types (H), (G) etc., seen in all Halticiniae and Galerucinae studied (Fig. 47-J).

K) Anteriorly grouped and joined three by three forming a short duct on each side opening to the end of the mid gut, posteriorly like types (C), (D), etc., seen in some Cerambycidae [1, 13] and *Zeugophora* (Megalopodinae) (Fig. 47-K).

L) Specialised case, seen in *Hispa* (Hispinae) only, as described in the text (Fig. 52-L).

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EXPLANATION OF FIGURE OF LETTERING

- **c**, crop
- **cae**, enteric caecum
- **cl**, colon
- **cm**, cryptonephridic, Malpighian tubes
- **cr**, crypt
- **fg**, fore gut
- **fm**, free Malpighian tubes
- **hg**, hind gut
- **mg**, mid gut
- **o**, oesophagus
- **ovl**, oesophageal valve
- **pv**, proventriculus
- **rc**, rectum
Figs. 1–10. Alimentary canal:

(1) Rhagium bifasciatum; (2) Acanthoscelides obtectus; (3) Euspermophagus sericatus, anterior insertion of the Malpighian tubes enlarged in cross section; (4) Caryedon serratus, anterior insertions of the Malpighian tubes enlarged in cross section; (5) Sagra congoana; (6) Oreodacna cerasi; (7) Donacia vulgaris A- general structure, B- anterior insertions of the Malpighian tubes enlarged; (8) Plateumaris discolor A- general structure, B- anterior insertion of the Malpighian tubes enlarged; (9) Criocerus asparagi; (10) Zêu- gophora flavicollis.
Figs. 11–22. Alimentary canal:

(11) Oomorphus concolor, two different arrangements of anterior insertions of the Malpighian tubes enlarged; (12) Cryptochorus rugicollis, anterior insertions of the Malpighian tubes enlarged; (13) Clyra nucempunctata, anterior insertions of the Malpighian tubes enlarged cross section; (14) Tympana tenebricosa, anterior insertions of the Malpighian tubes enlarged in cross section; (15) Phyllocharis cyanicornis; (16) Chrysolina americana; (17) Castoroides viridula; (18) Phaedon tumidulus; (19) Prasocerus phyllaphoros; (20) Hydrothessa marginella; A- general structure, B- anterior insertions of the Malpighian tubes enlarged in cross section; (21) Plagiodera versicolora; (22) Phytodecta pallidus, A- general structure, B- anterior insertions of the Malpighian tubes are enlarged.
Figs. 23–36. Alimentary Canal:

(23) Crepidodera transversa; (24) Chalcides fulvicornis; (25) Mantura obtusata; (28) Aphthona coerulea; (29) Halica ericeti; (30) Asteropeda orbiculata; (31) Chaetocnema concinna; (32) Luperus longicornis; (33) Phyllobrotica quadrimaculata; (34) Galerucella nymphaeae; (35, 36) Spiropyra sumptuosa, (35 A) general structure with the anterior insertions of the Malpighian tubes enlarged, (35 B) internal view of a part of the mid gut wall, (36) general view of the gut in situ.
Figs. 37-46. Alimentary canal:

(37, 38) *Macrolema vitata*, (37) proventriculus, (38) longitudinal section of gut at the junction of the crop and mid gut; (39) *Abirus rubripes*; (40) *Sceletenta indica*; (41) *Pseudopionera androceci*; (42) *Tricliena* sp. anterior insertion of Malpighian tubes enlarged in cross section; (43) *Cassida flavescens*, three different arrangements of anterior insertions of Malpighian tubes enlarged in cross section; (44) *Cassida rubiginosa*, A- general structure, B- anterior insertions of Malpighian tubes enlarged; (45) *Aprosida baliyi*, anterior insertion of Malpighian tubes enlarged in cross section; (46) *Hispa testacea*, A- general structure, B- anterior insertions of Malpighian tubes enlarged in dorsal view, C- anterior insertions of Malpighian tubes enlarged in ventral view.
Phyletic interpretation of anterior and posterior insertions of the Malpighian tubules in the species studied, for details see the text.
ÖZET

Bu çalışma, 1 Cerambycidae, 4 Bruchidae ve 52 Chrysomelidae türünün sindirim ve boşaltım sistemi üzerinde yapılan kararlıştırmaları bir anatomi incelenmiştir. Orta barsak üzerindeki rejeneryasyon papillerlerin büyüklüğü ve dağdırma, cafea saatinin ve Malpighi borularının son barsağa açılış ve rektuma tutuşan uçlarını kısımı, açıktı ve farklı taksonomik düzeylerde sistematiğin önem taşıdığı bulunmuştur. Malpighi borularının son barsağa açıldığı ve rektuma tutunduğu bölgelerdeki gruplaşma düzeninin başlıca üç evrimsel doğrudan geliştigi düşünülmüştür.

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