

A COMPARISON OF THE ANTERIOR ABDOMINAL
SEGMENTS OF SOME SCARABAEOID LARVAE

by

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A COMPARISON OF THE ANTERIOR ABDOMINAL
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INTRODUCTION

In the past writers have based their phylogenetic concepts of insects primarily on the morphology of the adults. Most all of our concepts of the subfamily relationships of the Scarabaeoidea are drawn from the adult beetles. To test the relationships that Leng (16, p. 248-265) proposed in his catalog on Scarabaeoidea the writer has explored the musculature of the anterior abdominal segments of several scarabaeoid larvae.

The musculature of insects is a subject that has received but little attention in the past. Perhaps this is not so much because of its lack of phylogenetic importance but because of the extremely laborious and minute dissections that such a study demands. A review of the literature shows that little work has been done on the musculature of the larvae of the Scarabaeoids. The present paper is the first attempt that has been made to compare the musculature of the anterior abdominal segments of several subfamilies of Scarabaeoid larvae to test the phylogeny suggested by Leng. In this study I am arranging my data on the basis of Leng. However, I will show in my discussion that the position of several of the subfamilies is questionable, particularly Glaphyrinae, Troginae, and Melolonthinae.

Hence, I am proposing a new arrangement of the subfamilies of the Scarabaeoidea.

The larvae of eight subfamilies representing two families of the superfamily Scarabaeoidea were selected for this study. In those eight subfamilies seven were chosen from family Scarabaeidae which is considered by Leng (16, p. 248-265) to be the most primitive family of the superfamily Scarabaeoidea. The species studied were Pleocoma crinita Linsley of the subfamily Pleocominae; Lichnanthe rathvoni Lec. of the subfamily Glaphyrinae; Trox sp. of the subfamily Troginae; Polyphylla decemlineata Say of the subfamily Melolonthinae; Plusiotis gloriosa Lec. of the subfamily Rutelinae; Dynastes tityus (L.) of the subfamily Dynastinae; Osmoderma eremicola Knoch of the subfamily Cetoniinae, and Sinodendron rugosum Mann of the subfamily Sinodendrinae, family Lucanidae. In addition, several other genera in most of these subfamilies were observed in order to compare the similarities of the patterns of the muscles in each subfamily.

LITERATURE REVIEW

I am reviewing here the more important papers on the abdominal musculature in insects of several orders. There are six papers on caterpillars, two on the honey bee, one

on mayflies, one on the housefly, three on dragonflies, two on cockroaches, and three on crickets. Also a partial study of the abdominal muscles in the principal orders is reviewed. I shall discuss these papers in chronological order.

The earliest and the classical description of a detailed dissection of insect musculature is that of Lyonet (1762) (12, p. 207-320) on the anatomy of the larva of the goat moth, Cossus ligniperda. Lyonet considered each muscle fiber as a separate muscle and by enumerating the fibers in the layers of the different segments and internal organs reckoned that there was the astounding number of four thousand and sixty-one muscles in a single larva.

A second investigation of the musculature of caterpillars was made by Newport (1839) (22, p. 853-998) on the larva of Sphinx ligustri. Newport preferred to describe each layer of fibers collectively as a muscle and thereby simplified the descriptions of the muscle system of insects.

As a comparative study with Lyonet's results, Lubbock (1858) (18, p. 173-191) investigated the arrangement of the muscles in the larvae of Pygaera bucephala and concluded that Lyonet was right in terming each fiber a muscle since the fibers do not vary in relative size or number, except in certain instances among the small muscles.

A brief description of the muscles of a typical abdominal segment of the bee was given by Carlet in 1884 (5, p. 758-759).

In 1884 Plateau (24, p. 1-94) discussed the respiratory mechanism in the relation to the arrangement of the abdominal segments and the disposition of the attached muscles.

In 1886 Miall and Denny (20, p. 1-224), in their textbook on the structure of the cockroach, Periplanata orientalis, included a description of the noteworthy muscles of the generalized regions, but no references were made to the smaller muscles. Following Newport's nomenclature, they defined a muscle as a sheet of fibers. All later investigators have followed Miall and Denny.

Peytoureau (1895)(23, p. 1-248) was the first to describe the musculature among the orthopteroid insects, both of the generalized segments and of the genitalia.

In 1905 Voss (30, p. 358-521), in an excellent paper, described the thoracic muscles of Gryllus domesticus in much detail. Included in the study is the musculature of the anterior abdominal segments.

In 1907 Durken (10, p. 435-550) studied the thoracic and abdominal musculature in the Ephemeridae. The homologies between the muscles in the thorax and abdomen were completely worked out.

In 1909 Berlese (2, p. 1-1004) in "Gli-Insetti" included in his chapter on musculature some original illustrations of the muscles controlling the female genitalia in Acridium lineola and Decticus albifrons, but drew no homologies between these and other muscles of the abdomen.

In 1914 Hewitt (13, p. 281-293) clearly described and figured the muscular system in the larvae of the houseflies Musca domestica Linn.

Further studies on the musculature of the Lepidoptera were made in 1914 by Forbes (11, p. 109-124) in the families Lasiocampidae, Noctuidae and Sphingidae. Up to this time, including the work of Lyonet, Lubbock and Berlese, five families had been studied by dissection; comparisons between these were made by Forbes.

In 1914 Boving (4, p. 55-61) studied the abdominal structure of certain campodeiform insects. The relation between the internal structure of the integument and the muscles was clearly described.

The musculature of the larva of the honey bee is outlined in 1915 by Nelson (21, p. 1-282) in connection with his embryological study.

In 1916 Craighead (6, p. 129-146) determined the muscles in the abdominal and thoracic areas of the cerambycid larvae.

In 1917 Tillyard (29, p. 1-396) included in his "The Biology of Dragonflies", a description of the principal abdominal muscles of the Odonata.

A study of the comparative morphology of the abdomen in the Odonata led Whedon in 1919 (31, p. 373-461) to examine the musculature of nymphs and imagoes in both Zygoptera and Anisoptera. Homologies were demonstrated between the muscles of the nymphs of various species, and also between those of the imagoes, but no comparisons were made between the nymph and the imago.

The musculature of Gryllus assimilis Fabr., the common American field cricket, was investigated in 1920 by Du Porte (9, p. 16-52) and he compared his results with the work of Voss. Du Porte gives a complete account of the body musculature in male and female, but without homologizing the specialized with the generalized muscles.

In 1958 Crome (7, p. 228-262) studied the morphology and anatomy of the dynastid larva, Oryctes nasicornis L., describing the general musculature without naming the individual muscles. For the abdominal musculature Crome separated the muscles into three main groups; the dorsal longitudinal muscles; the ventral longitudinal muscles and the dorso-ventral muscles. Also, he recognized three layers of muscles in the anterior abdominal segments, the inner

layer, the median layer and the outer layer. Crome described clearly the general morphology and anatomy of this larva.

The latest study on musculature was made in 1960 by Lewis (17, p. 387-397) on the Indian rat flea, Xenopsylla cheopis (Siphonaptera). Ford (12, p. 207-320) comments that, "Of the types investigated, the caterpillars have the most complicated musculature, the arrangements being associated in this case with the ambulatory function of the abdomen." Newport (22, p. 853-994) in working with the sternal and pleural regions of the caterpillar of Sphinx ligustri redescribed nineteen paired muscles arranged in ten layers. In the tergal musculature of lepidopterous muscles Forbes (11, p. 109-124) recognized six muscles.

Similarly associated with movement is the rather complex musculature of the larva of the housefly. In the full grown larva of Musca domestica, Hewitt (13, p. 281-293) described approximately eight pairs of muscles in a typical segment with an arrangement that dorsally and ventrally is mainly of two layers but laterally three- and four-layered.

The inactive larvae of the bee has a musculature that is much simplified, consisting of one unpaired and five pairs of muscles as described by Nelson (21, p. 1-282).

MATERIALS AND METHODS

Most of the larvae used were living specimens which were obtained through Dr. P. O. Ritcher, Chairman, Department of Entomology, Oregon State University. Preserved specimens were also used when there were no available living larvae. Even in well preserved larvae the muscles become detached especially in the pleural and ventral regions.

Dissections were carried out under a Cycloptic microscope with magnification of 10 to 40X.

Larvae were killed by dropping them into a 400 ml. beaker containing 200 ml. hot water and boiling the specimens for two to three minutes. This method proved to be the most useful for dissecting and made easy the brushing off the fat bodies. Also, fat bodies could be removed by dropping 7 to 8 drops of Lacto-phenol on the dissected specimens.

Specimens were dissected and pinned out under 70 per cent alcohol. Both lateral and ventral sagittal dissections were made. Mayer's Carmalum dye was used as staining material. This technique was very useful in demonstrating the outline of the muscles, and differentiating the fat bodies, nervous system and the tracheal system. The dissected specimen was stained with four or five drops of

Carmalum for ten to fifteen minutes and then was washed off with 70 per cent alcohol.

The most satisfactory method for a detailed study of musculature was as follows:

First the specimen was opened and pinned immediately after killing. At this time the muscles are still elastic so that the body can be carefully stretched until quite flat. Preservation in flattened condition was done by hardening with a solution of 70 per cent alcohol and 2 per cent formaldehyde.

THE DETERMINATION OF THE ANTERIOR ABDOMINAL SEGMENTS OF LARVAE

The terminology used here for the areas and demarcation lines of the anterior abdominal segments of the scarabaeoid larvae follows, for the most part, the work of Boving (4, p. 55-61) who studied the abdominal structures of certain campodeiform beetle larvae. I found his work in agreement with my work on scarabaeoid larvae.

I am using the Pleocominae as a prototype for defining the limitation and definition of the areas and lines. This subfamily is suitable for a prototype because it is the most generalized scarabaeidae larva that I have in my series. The two subfamilies, which may be more generalized than the Pleocominae, were not available.

The Intersegmental Costa

The segments of an insect larva are, as is well known, connected by a perpendicular intersegmental costa, which, along with the other lines and folds, is shown in figure 1. The intersegmental costa is divided medially into two parts. The superior costa terminates ventrad and laterad to the spiracle. The inferior costa terminates a short distance below the spiracle and opposite the termination of the superior costa. At the ends of each of these two costa there are small notches to which the muscles are attached; these are called the anterior costal notch (AN) and the posterior costal notch (PN) respectively. A third notch is found dorsad of the anterior costal notch; Böving called this notch the superior notch (SN). Finally there is a fourth notch at the end of the parascutal line slightly above the anterior costal notch; I am calling this notch the parascutal notch (PASCN).

The Lateral Zone

On the inside of the integument, between the two posterior costal notches is found a staff-like or uniformly carinated apodeme, which on the outside appears as a deep groove. This groove has been named the pleural suture (PL) by Doctor Hopkins. Above and parallel with the pleural

suture is found a similar groove which Doctor Boving called the anti-pleural suture (ANTI), which is sometimes more, sometimes less developed than the pleural suture. Also, the antipleural suture is somewhat shorter than the pleural and does not reach either of the margins of the segment. The band-like region between these two sutures I am calling the pleural lobe (PLL).

Determination of the Lines and Areas
Above and Below the Lateral Zone

Above the antipleural suture the abdominal segment is divided into the following areas: prescutum (PRSC), scutum (SC), scutellum (SCL) and spiracular area (SPA) (Plate 1, fig. 1).

The boundary line of the line between the scutellum of one segment and the prescutum of the following segment, I am calling the prescutal line (PRSC). The boundary line between the prescutum and scutum, I am calling the scutal line (SC), and the boundary line between the the scutum and scutellum, I am calling the scutellar line (SCL).

The spiracular area (SPA) is characterized by the presence of the spiracle and is limited above by the parascutal line (PASC) and below by the antipleural suture.

The boundary line between the parascutum and scutellum, I am calling the parascutellar line (PASCL).

The prescutum of the Pleocominae is divided into two parts. I am calling the anterior part the prescutum I (PRSC-I) and the posterior part the prescutum II (PRSC-II).

Areas Below the Lateral Zone

Below the pleural suture (Plate 1, fig. 1) the segment is separated into the following areas: the hypopleurite (HYPL) that is immediately below the pleural suture, and the sternum (ST) that is separated by the triangular parasternum (PAST) from the sternellum (STL). The line limiting the hypopleurite below, Doctor Boving has called the hypopleural line (HYPL). Below this line lies the parasternum (PAST). The line separating the parasternum from the sternum I am calling the parasternal line (PAST). The anterior region of the sternellum is defined by sternellar line (STL), separating the hypopleurite and the parasternum from the sternellum.

In the subfamily Pleocominae, the presternum is very difficult to delimit because it is not separated from the sternum. For this reason I am considering the presternum to be part of the sternum and am calling the entire area the sternum (ST) (Plate 1, fig. 1).

ANNOTATED CHECK LIST OF THE MUSCLES FOUND IN THE
ANTERIOR ABDOMINAL REGION OF SCARABAEOID LARVAE

The musculature of the anterior abdominal segments of the following subfamilies has been studied: Pleocominae, Glaphyrinae, Troginae, Melolonthinae, Rutelinae, Dynastinae, Cetoniinae and Sinodendrinae. In the following discussion, I will take up each subfamily separately discussing the musculature and the absence or presence of the muscles in each subfamily. The arrangement of the muscles in each of the first five anterior abdominal segments of the larva is essentially the same. Hence, I can use the third and fourth segments as representative of the anterior abdominal segments. I found that the muscles can be arranged into three major groups. Admittedly this division is somewhat arbitrary because of the complex interrelationships of all three groups, yet such a grouping simplifies discussion. These three groups are: the tergal muscles, the pleural muscles and the sternal muscles. Each group of muscles will be discussed separately.

The following symbols have been adopted for designating muscles. The prefix T indicates that the muscle is in the tergal region, P that it is the pleural region, and S that it is in the sternal region. Consecutive numbers are used for the muscles in each region in the following sequence: the intersegmental longitudinal muscles,

beginning with the most dorsal muscle as number 1, the intersegmental diagonal muscles and finally the intrasegmental muscles. The names of the muscles have been derived from the points of origin and insertion, the origin always being the first word. The two words are hyphenated whenever necessary.

In discussion I am indicating first the symbol of the muscle, then the name, and finally the position of the muscles.

TERGAL MUSCULATURE

The tergal muscles of the anterior abdominal segments of Scarabaeoid larvae separate into two main groups, the intersegmental tergal muscles, which are attached to adjacent segments, and the intrasegmental tergal muscles, which are attached within the segment. Each main group will be described separately for each subfamily.

Subfamily Pleocominae

This subfamily is used as a prototype for comparison with other subfamilies, because it is the most generalized of the subfamilies studied.

The Intersegmental Tergal Muscles

In the Pleocominae there are two intersegmental, tergal longitudinal muscles and three intersegmental, tergal diagonal muscles. These muscles are numbered from T-1 to T-5 and have the following positions.

- T-1. The first tergal longitudinal muscle (Plate 2, fig. 3) originating on the prescutal line about one-third the distance from the dorsum, is inserted at the similar position on the prescutal line of the following segment.
- T-2. The second tergal longitudinal muscle (Plate 2, fig. 3) originating on the prescutal line at the superior notch and passing posteriorly and parallel with T-1, inserts on the prescutal line of the following segment.
- T-3. The first tergal diagonal muscle (Plate 2, fig. 3) originating on the prescutal line just below T-1, passes ventrad to its insertion on the prescutal line of the following segment, just above T-2.
- T-4. The second tergal diagonal muscle (Plate 2, fig. 4) originating on the prescutal line beneath the origin of T-1, passes dorsad to its insertion close to the dorsum on the prescutal line of the following segment.
- T-5. The third tergal diagonal muscle (Plate 2, fig. 4)

originating on the prescutal line at the superior notch, passes dorsad and parallel with T-4 to its insertion on the prescutal line of the following segment.

The Intrasegmental Tergal Muscles

There are one prescutal-scutal diagonal and three scutal-prescutal diagonal muscles. These are numbered from T-6 to T-9 and have the following positions.

- T-6. The prescutal-scutal muscle (Plate 2, fig. 4), originating on the prescutal line dorsad of the origin of T-4, passes dorsad to its insertion on the scutal line close to the dorsum.
- T-7. The first scutal-prescutal muscle (Plate 2, fig. 4), originating on the scutal line close to the dorsum, passes ventrad to the insertion on the prescutal line of the following segment beneath the insertion of T-1.
- T-8. The second scutal-prescutal muscle (Plate 2, fig. 4), originating on the middle portion of the scutal line, passes ventrad and parallel with T-7, to its insertion on the prescutal line of the following segment beneath the insertion of T-3.
- T-9. The third scutal-prescutal muscle (Plate 2, fig. 4), originating on the distal portion of the scutal line

close to the superior notch, passes ventrad to the insertion on the prescutal line at the superior notch of the following segment.

Subfamily Glaphyrinae

Leng (16, p. 248-265) placed the Glaphyrinae between the Pleocominae and the Troginae. I will show later that this position is untenable for the Glaphyrinae because it is an anomalous subfamily and does not fit very well into any phylogenetic scheme. Muscles in the Glaphyrinae (Plate 3, figs. 9 and 10) are somewhat narrower than those in the Pleocominae.

The Intersegmental Tergal Muscles

In the Glaphyrinae, muscle T-1, which is present in the Pleocominae, does not occur, while an intersegmental, tergal diagonal muscle, T-0, is present in the Glaphyrinae but not in the Pleocominae.

T-1. The first tergal longitudinal muscle does not occur in this subfamily.

T-2. and T-3. The second tergal longitudinal muscle and the first tergal diagonal muscle (Plate 3, fig. 9) are similar to those in the Pleocominae.

- T-4. The second tergal diagonal muscle (Plate 3, fig. 9) is present but it differs from the T-4 in the Pleocominae. In the Glaphyrinae T-4 separates into four to five fibrous muscles but the origin and insertion positions are similar to the position of T-4 in the Pleocominae.
- T-5. The third tergal diagonal muscle (Plate 3, fig. 9) has the same position as T-5 in the Pleocominae.
- T-0. The fourth tergal diagonal muscle (Plate 3, fig. 9) does not occur in the Pleocominae, but T-0 is present in the Glaphyrinae. This muscle passes ventrally and dorsad of the T-3, originating on the beginning of the prescutal line on segment 3 and inserting on segment 4 at the same level as its origin.

The Intrasegmental Tergal Muscles

The intrasegmental muscles of Glaphyrinae differ from Pleocominae in that muscles T-7 and T-9 are absent. Also five intrasegmental, tergal diagonal muscles, not present in Pleocominae, occur in the Glaphyrinae. These are a prescutal-scutellar muscle, a scutellar-prescutal muscle, a scutellar-parascutellar muscle and two scutal-scutellar muscles. These muscles are numbered from T-10 to T-14.

T-6. The prescutal-scutal muscle (Plate 3, fig. 10) is

composed of a series of eight separated fibers in the Glaphyrinae. In the Pleocominae this muscle is a narrow band while in the Glaphyrinae the separate fibers of T-6 have spread ventrad to cover half of the area of the prescutum.

- T-7. The first scutal-prescutal muscle does not appear in the Glaphyrinae.
- T-8. The second scutal-prescutal muscle (Plate 3, fig. 10) of Glaphyrinae, as with muscle T-6, is separated into individual fibers. In the Pleocominae this muscle is a narrow band while in the Glaphyrinae there are several fibers which are spread farther apart posteriorly than anteriorly, forming more or less a fan.
- T-9. The third scutal-prescutal muscle does not occur in the subfamily Glaphyrinae.
- T-10. The prescutal-scutellar muscle (Plate 3, fig. 10) occur in the Glaphyrinae but it is not present in the Pleocominae. Muscle T-10 consists of a band of diagonal muscles, passing dorsally from its origin on the prescutal line, to its insertion on the scutellar line, dorsad and beneath T-4, ventrad and above T-6. This muscle is composed of six fibers.
- T-11. The first scutellar-prescutal muscles (Plate 3, fig. 10), which appear for the first time in Glaphyrinae, are a group of fibrous muscles passing across the

scutellum, dorsad of T-8 and ventrad of the midtergal line. They originate on the scutellar line of segment 3, inserting on the prescutal line of segment 4.

T-12. The first scutal-scutellar muscles (Plate 3, fig. 10) are a group of fibrous muscles which pass across the scutum, the lower muscles overlapping T-8, the upper muscles being close to the dorsum. This group originates on the scutal line and passing dorsad, is inserted on the scutellar line.

T-13. The second scutal-scutellar fibrous muscles (Plate 3, fig. 10) pass from their origins on the distal portion of the scutal line to their insertions on the distal portion of the scutellar line, passing below T-12 and also cross the scutum.

T-14. The scutellar-parascutellar fibrous muscles (Plate 3, fig. 10) originate on the distal portion of the scutellar line at the same level as the insertion of T-13, inserting on the distal portion of the parascutellar line, passing diagonally across the parascutum.

Subfamily Troginae

Leng (16, p. 248-265) considered this subfamily as more specialized than the Glaphyrinae and less than the Melolonthinae.

The Intersegmental Tergal Muscles

This subfamily differs from the Pleocominae in not having T-1 and has an additional intersegmental, tergal diagonal muscle which is numbered T-0.

T-1. The first tergal longitudinal muscle does not appear in this subfamily.

T-2. and T-3. The second tergal longitudinal muscle and the first tergal diagonal muscle (Plate 2, fig. 6) are present but T-3 is a larger band when compared with T-3 in the Pleocominae.

T-4. and T-5. The second tergal diagonal muscle and the third tergal diagonal muscle (Plate 2, fig. 7) are also found in this subfamily but T-5 is much bigger than in the Pleocominae.

T-0. The fourth tergal diagonal muscle (Plate 2, fig. 6) occurs in this subfamily as in the Glaphyrinae. In the Troginae T-0 is closer to T-3 than in the Pleocominae. It splits into two branches at its own origin.

The Intrasegmental Tergal Muscles

The intrasegmental tergal muscles are different from those in the Pleocominae in not having muscle T-9 and having in addition four intrasegmental, tergal diagonal muscles. These are a prescutal-scutellar muscle, a scutal-parascutellar muscle and two scutellar-prescutal muscles. These muscles are numbered T-10, T-15, T-11 and T-16 respectively.

T-6, T-7 and T-8. The prescutal-scutal muscle, the scutal-prescutal muscle and the second scutal-prescutal muscle (Plate 2, figs. 7 and 8) appear in this subfamily to be similar to those in the Pleocominae.

T-9. The third scutal-prescutal muscle of the Pleocominae does not appear in the Troginae.

T-10 and T-11. The first prescutal-scutellar muscle and the first scutellar-prescutal muscle (Plate 2, fig. 7) appear in this subfamily as in the Glaphyrinae. They differ from those in the Glaphyrinae in that they do not form a group of fibrous muscles, but each muscle is composed of a single band. Both muscles are located in the upper portion of the tergum.

T-12, T-13 and T-14. The first scutal-scutellar, the second scutal-scutellar and the scutellar-parascutellar muscles do not occur in the Troginae.

- T-15. The scutal-parascutellar muscle (Plate 2, fig. 8) originates on the distal portion of the scutal line, passing dorsad to the insertion on the parascutellar line.
- T-16. The second scutellar-prescutal muscle (Plate 2, fig. 8) originates on the middle portion of the scutellar line, passing ventrad and parallel with T-8 and T-11, to its insertion on the prescutal line of the following segment. The lower portion of this muscle is underneath muscle T-8.

Subfamily Melolonthinae

Leng (16, p. 248-265) considered this subfamily as more specialized than either Pleocominae, Glaphyrinae or the Troginae.

The Intersegmental Tergal Muscles

The Melolonthinae differ from the Pleocominae in not having T-1 but have an additional muscle, T-0, that is not present in the latter.

- T-1. The first tergal longitudinal muscle is not present in the Melolonthinae.
- T-2. The second tergal longitudinal muscle (Plate 4, fig. 15) is similar to that in the Pleocominae.

- T-3. The first tergal diagonal muscle (Plate 4, fig. 15) in the Melolonthinae consists of two bands running parallel to each other and in the same position as that of T-3 in the Pleocominae. I am calling them T-3 and T-3a.
- T-4. and T-5. The second tergal diagonal muscle and the third tergal diagonal muscle (Plate 4, fig. 16) are similar to those in the Pleocominae. The only difference is that T-4 has migrated somewhat ventrad and is close to T-5.
- T-0. The fourth tergal diagonal muscle (Plate 4, fig. 15) is found in the Melolonthinae as well as in the Glaphyrinae and Troginae. In the Melolonthinae, T-0 has two bands, the dorsal band is smaller than the ventral. I am calling the bands T-0 and T-0a.

The Intrasegmental Tergal Muscles

The intrasegmental tergal muscles in the Melolonthinae differ from the Pleocominae in that T-9 is not present, but two intrasegmental, tergal diagonal muscles, one prescutal-scutellar and one scutellar-prescutal muscle (not present in the Pleocominae) occur in the Melolonthinae. These muscles are numbered T-10 and T-16.

T-6, T-7 and T-8. The prescutal-scutal muscle, the first scutal-prescutal muscle and the second scutal-

prescutal muscle (Plate 4, fig. 17) are similar to those of Pleocominae except T-7 migrates ventrad close to T-8 which splits into two branches at its origin.

T-9. The third scutal-prescutal muscle does not occur in the Melolonthinae.

T-10. The prescutal-scutellar muscle (Plate 4, fig. 16) occurs in this subfamily as well as in the Glaphyrinae and Troginae. This muscle is a single band in the Troginae but it is bigger in the Melolonthinae.

T-11, T-12, T-13, T-14 and T-15. The first scutellar-prescutal muscle, the first scutal-scutellar muscle, the scutellar-parascutellar muscle and the scutal-parascutellar muscle are not present in the Melolonthinae.

T-16. The scutellar-prescutal muscle (Plate 4, fig. 17) in the Melolonthinae is the same as T-16 in the Troginae.

Subfamily Rutelinae

Leng (16, p. 248-265) considered this subfamily as more specialized than the Melolonthinae.

The Intersegmental Tergal Muscles

The musculature of the intersegmental tergal muscles of the Rutelinae is similar to that of the Pleocominae except T-1 is not present in the former.

T-1. The first tergal longitudinal muscle is not present in this subfamily.

T-2. The second tergal longitudinal muscle (Plate 5, fig. 21) is similar to that in the Pleocominae.

T-3. The first tergal diagonal muscle (Plate 5, fig. 21) is present and is greatly expanded covering the entire tergum and joining with T-2 on the same point of the insertions. This muscle consists of numerous bands that are close together and are very hard to separate. They are similar to the longitudinal muscles in being slightly oblique.

T-4 and T-5. The second and third tergal diagonal muscles (Plate 5, fig. 22) are found similar to those in the Pleocominae. In the Rutelinae T-4 migrates ventrad close to T-5. These two muscles are very similar to those in the Melolonthinae.

T-0. The fourth tergal diagonal muscle (Plate 5, fig. 21) coalesces with T-3. I am considering it to be the dorsal part of T-3.

The Intrasegmental Tergal Muscles

The intrasegmental tergal muscles of the Rutelinae differ from the Pleocominae in T-9 being absent, and in addition, three intrasegmental tergal diagonal muscles appear that are not present in the Pleocominae. These are a prescutal-scutellar muscle, a scutal-scutellar muscle and a scutellar-prescutal muscle. These muscles are numbered T-10, T-12 and T-16.

T-6, T-7 and T-8. The prescutal-scutal muscle, the first scutal-prescutal muscle and the second scutal-prescutal muscle (Plate 5, Fig. 23) are present and closely resemble those in the Pleocominae, but the origin of T-7 has migrated ventrad and close to the origin of T-8.

T-9. The third scutal-prescutal muscle does not appear in the Rutelinae.

T-10. The first prescutal-scutellar muscle (Plate 5, fig. 22) is similar to those in the Glaphyrinae, Troginae and Melolonthinae but not to Pleocominae. This muscle closely resembles T-10 in the Melolonthinae.

T-11. The first scutal-prescutal muscle is not present in the Rutelinae.

T-12. The first scutal-scutellar muscle (Plate 5, fig. 24) is present in the Rutelinae as in the Glaphyrinae.

This muscle consists of a narrow band of muscles that passes ventrad from the origin on the scutal line to the insertion on the scutellar line on the upper portion of the tergum.

- T-13, T-14 and T-15. The second scutal-scutellar muscle, the scutellar-parascutellar muscle and the scutal-parascutellar muscle do not appear in this subfamily.
- T-16. The second scutellar-prescutal muscle (Plate 5, fig. 24) closely resembles those in the Troginae and Melolonthinae.

Subfamily Dynastinae

Leng (16, p. 248-265) considered the Dynastinae as more specialized than the Rutelinae.

The Intersegmental Tergal Muscles

The Dynastinae are similar to the Pleocominae in having the same numbers of the intersegmental tergal muscles. However, in the Dynastinae these muscles are more developed in having more bands.

- T-1. The first tergal longitudinal muscle (Plate 6, fig. 27) is a very broad muscle covering the upper two-thirds of the tergum. This muscle is marked by a series of 12-15 grooves that superficially divide the muscle into bands. These grooves are lines of

- weakness. When dissecting needles are used to tease the muscle apart, it separates along the lines.
- T-2. The second tergal longitudinal muscle (Plate 6, fig. 27) is found in a position similar to that for T-2 in the Pleocominae. In the Dynastinae T-2 consists of an inner and the outer layer. The inner layer overlaps the dorsad part of the outer layer.
- T-3. The first tergal diagonal muscle (Plate 6, fig. 27) has a groove that gives it the appearance of being composed of two bands. The upper portion of T-3 overlaps T-1 so that it appears to be a part of T-1.
- T-4 and T-5. The second tergal diagonal muscle and the third tergal diagonal muscle (Plate 6, fig. 28) are very similar to those in the Melolonthinae and Rutelinae.

The Intrasegmental Tergal Muscles

The intrasegmental muscles of the Dynastinae differ from the Pleocominae in that T-7 and T-9 are absent. There are three intrasegmental tergal diagonal muscles, which are not present in the Pleocominae. There are the prescutal-scutellar muscle, the scutal-scutellar muscle and the scutellar-prescutal muscle. These muscles are numbered T-10, T-12 and T-16.

- T-6. The prescutal-scutal muscle (Plate 6, fig. 28) consists of many fibers. The lower part of this muscle expands underneath T-10.
- T-7. The first scutal-prescutal muscle does not appear in the Dynastinae.
- T-8. The second scutal-prescutal muscle (Plate 6, fig. 29) is found similar to that in the Pleocominae.
- T-9. The third scutal-prescutal muscle does not appear in this subfamily.
- T-10. The first prescutal-scutellar muscle (Plate 6, fig. 28) is similar to this muscle in other subfamilies that are mentioned previously except T-10 does not appear in the Pleocominae. This muscle is very much the same as in the Melolonthinae and the Rutelinae.
- T-11. The first scutellar-prescutal muscle does not appear in the Dynastinae.
- T-12. The first scutal-scutellar muscle (Plate 6, fig. 29) is similar to that in the Rutelinae.
- T-13, T-14 and T-15. The second scutal-scutellar muscle, the scutellar-parascutellar muscle and the scutal-parascutellar muscle do not appear in the Dynastinae.
- T-16. The second scutellar-prescutal muscle (Plate 6, figs. 29 and 30) is present as a group of separated small fibers. The origins and insertions are located in

the positions similar to T-16 in the subfamily Troginae, Melolonthinae and Rutelinae. I am identifying this muscle from its origin and insertion and not from its appearance.

Subfamily Cetoniinae

Leng (16, p. 248-265) considered the Cetoniinae as the most specialized group of the family Scarabaeidae.

The Intersegmental Tergal Muscles

This subfamily differs from Pleocominae in not having muscle T-1. The muscles in the Cetoniinae differ from those in the Pleocominae in having additional bands.

T-1. The first tergal longitudinal muscle does not appear in the Cetoniinae.

T-2. The second tergal longitudinal muscle (Plate 7, fig. 33) consists of an upper band and a lower band. The upper band is very close to the lower part of T-3. The lower band is overlapped by the insertion of P-2. This muscle is very similar to that in the Dynastinae in having the two bands.

T-3. The first tergal diagonal muscle (Plate 7, fig. 33) almost covers the entire tergum. This muscle consists of sixteen to twenty small bands that are very close

together, forming a single band. This muscle also looks very much like a longitudinal muscle because it is only slightly oblique in position.

T-4 and T-5. The second and the third tergal diagonal muscles of Cetoniinae (Plate 7, fig. 34) are similar in form to those in the Melolonthinae, Rutelinae and Dynastinae. T-4 and T-5 are not close to each other and there is an additional intrasegmental diagonal muscle (T-17) between the muscles T-4 and T-5.

T-0. The fourth tergal diagonal muscle (Plate 7, fig. 33) joins with T-3. It appears to be the dorsad part of T-3. I am including it with T-3.

The Intrasegmental Tergal Muscles

The intrasegmental tergal muscles of the Cetoniinae differ from the Pleocominae in T-7 and T-9 being absent. Also there are eight intersegmental, tergal diagonal muscles that are not present in the Pleocominae. These muscles are: a scutal-scutellar muscle, two prescutal-scutellar muscles, three scutellar-prescutal muscles and two tergal short muscles. They are numbered T-10, T-11, T-12, T-16, T-17, T-18, T-19 and T-20.

T-6. The prescutal-scutal muscle (Plate 7, fig. 34) is similar to that of the Dynastinae.

T-7. The first scutal-prescutal muscle does not appear in

the Cetoniinae.

- T-8. The second scutal-prescutal muscle (Plate 7, fig. 35) is similar to T-8 in the Pleocominae but it is a somewhat larger muscle.
- T-9. The third scutal-prescutal muscle does not appear in the Cetoniinae.
- T-10. The first prescutal-scutellar muscle (Plate 7, fig. 34) is similar to those of other subfamilies studied except the Pleocominae.
- T-11 and T-12. The first scutellar-prescutal muscle and the first scutal-scutellar muscle (Plate 7, fig. 35) are similar to those of the Glaphyrinae. These muscles consist of many fibers, each muscle covering the upper portion of the scutellum and scutum.
- T-13, T-14 and T-15. The second scutal-scutellar muscle, the scutellar-parascutellar muscle and the scutal-parascutellar muscle do not appear in the Cetoniinae.
- T-16. The second scutellar-prescutal muscle of the Cetoniinae (Plate 7, fig. 35) is similar to that in the Dynastinae.
- T-17. The second prescutal-scutellar muscles (Plate 7, fig. 35), which are diagonal muscles appearing first in the Cetoniinae are a group of fibrous muscles, passing dorsad and parallel with T-4 and T-5. They originate on the prescutal line dorsad of the superior

notch and insert on the scutellar line.

T-18. The third scutellar-prescutal muscles (Plate 7, fig. 35), appearing for the first time in the Cetoniinae, are also a group of fibrous muscles, that originate on the scutellar line at the posterior of the insertion of muscle T-17, passing almost parallel with the mid-tergal line to its insertion on the prescutal line of the following segment.

T-19 and T-20. The tergal short muscles (Plate 7, fig. 36) are the intrafolded muscles that run within the scutum and scutellum beneath muscles T-11 and T-12. These muscles originate medially on the skin of the scutum and scutellum and insert on the scutellar and prescutal line of the following segment respectively.

Subfamily Sinodendrinae

Leng (16, p. 248-265) assigned this subfamily to the family Lucanidae, a family more specialized than the Scarabaeidae but also in the superfamily Scarabaeoidea.

In the Sinodendrinae, the tergal folds, found on the anterior abdominal segments of Scarabaeidae larvae, are not present. The scutal and scutellar lines are probably represented by the line formed by the attachment of the muscles to the body wall.

The Intersegmental Tergal Muscles

The larvae of Sinodendrinae differ from the Pleocominae in not having muscles T-3, T-4 and T-5. Also T-1 and T-2 differ from those in the Pleocominae.

T-1. The first tergal longitudinal muscle (Plate 3, fig. 12) consists of six fibers and it is in a position similar to that of T-1 in the Pleocominae. The origins and the insertions of the fibers of this muscle migrate posteriorly from the prescutal line to attach on the skin.

T-2. The second tergal longitudinal muscle (Plate 3, fig. 12) is composed of fibers. The origin and insertion are in a position similar to that of T-2 in other subfamilies. There are five fibers, two on the dorsum and three just below the former.

Other muscles of the intersegmental tergal muscles do not appear in the Sinodendrinae.

The Intrasegmental Tergal Muscles

None of the muscles in this subfamily are similar to those in the Scarabaeidae. Two groups of fibrous muscles, the scutal-prescutal muscles are numbered T-21, and the scutellar-prescutal muscles are numbered T-22. They have the following positions:

T-21. The scutal-prescutal muscle (Plate 3, fig. 13) apparently has become separated into a series of many individual fibrous muscles which originate in a row at one-third the distance of the posterior of the prescutal line. I presume the line formed by the origin of these fibrous muscles represents the position of an obsolete scutal line. The muscle, speaking of the series of fibrous muscles collectively as a muscle, runs parallel and dorsad to its insertion on the prescutal line of the following segment.

This muscle, again speaking collectively, covers two-thirds of the posterior portion of the tergum.

T-22. The scutellar-prescutal muscle (Plate 3, fig. 13) is similar to T-21. It also consists of a series of separated fibrous muscles which originate along the possible position of a scutellar line which is two-thirds of the distance from the anterior margin of the segment. The scutellar line is not visible but the origins of each fibrous muscle are along the straight line where this line is present in the larvae of the Scarabaeidae. For this reason I am assuming that the insertion marks the position of the scutellar line which has disappeared. The muscles run parallel and ventrad to the insertion on the prescutal line of the following segment. This

muscle, speaking collectively, covers one-third of the posterior portion of the tergum.

PLEURAL MUSCULATURE

The pleural muscles of the Scarabaeoid larvae can be separated into three main groups: the intersegmental pleural muscles, the intrasegmental pleural muscles and the spiracular muscles.

Subfamily Pleocominae

The Pleocominae are also used as a prototype in the discussion of the pleural musculature.

The Intersegmental Pleural Muscles

There are two intersegmental, pleural longitudinal muscles that are numbered P-1 and P-5, and four intersegmental, pleural diagonal muscles are numbered P-2, P-4, P-7 and P-8. These muscles have the following positions:

P-1. The first pleural longitudinal muscle (Plate 2, fig. 3) originates on the posterior notch at the end of the inferior costa or sternal line and is inserted at a similar position on the posterior notch of the following segment.

P-5. The second pleural longitudinal muscle (Plate 2, fig. 4) originates on the anterior notch of one

segment and is inserted at the same position on the anterior notch of the following segment.

- P-2. The sterno-tergal diagonal muscle (Plate 2, fig. 3) originates on the posterior notch of one segment and is inserted on the anterior part of the superior notch of the following segment.
- P-4. The pleuro-tergal diagonal muscle (Plate 2, fig. 4) originates on the anterior notch of one segment and passes dorsad to its insertion on the posterior notch of the following segment beneath the insertion of P-2.
- P-7. The pleuro-sternal diagonal muscle (Plate 2, fig. 4) originates on the anterior notch of one segment and passes ventrad to its insertion on the posterior notch of the following segment.
- P-8. The tergo-sternal diagonal muscle (Plate 2, fig. 4) originates on the superior costa ventrad of the superior notch of one segment and passes ventrad to its insertion on the posterior notch of the following segment beneath the insertion of P-7.

The Intrasegmental Pleural Muscles

There are three intrasegmental pleural muscles in the Pleocominae, two pleural vertical muscles and an intrasegmental pleural diagonal muscle. These muscles are

numbered P-3, P-6 and P-9 and have the following position:

- P-3. The tergo-sternal vertical muscle (Plate 2, fig. 3) originates on the superior notch beneath the insertion of P-2 and passes ventrad to its insertion on the posterior notch of the same segment.
- P-6. The tergo-pleural diagonal muscle (Plate 2, fig. 4) originates on the end of the scutal line of one segment and passes ventrad to its insertion on the anterior notch of the following segment beneath the insertion of P-5.
- P-9. The pleuro-sternal vertical muscle (Plate 2, fig. 4) originates on the anterior notch and passes ventrad to its insertion on the posterior notch of the same segment.

The Spiracular Muscles

The spiracular muscles are a group of short muscles located close to the spiracular area. There are six muscles altogether in the Pleocominae which are numbered from one to six.

1. The parasternal-parascutal notch muscle (Plate 2, fig. 5) originating on the parasternal line near the posterior notch, passes dorsad to its insertion on the parascutal notch.
2. The parasternal-anterior notch muscle (Plate 2,

- fig. 5) originating on the parasternal line ventrad of the origin of the parasternal-parascutal notch muscle, and passes dorsad to its insertion on the anterior notch.
3. The antipleural-hypopleural muscle (Plate 2, fig. 5) originating on the antipleural suture close to the parascutal notch, passes ventrad to its insertion on the hypopleural line.
 4. The antipleural-sternellar muscle (Plate 2, fig. 5) originating on the antipleural suture dorsad of the origin of the antipleural-hypopleural muscle, passes ventrad to its insertion on the beginning of the sternellar line.
 5. The anterior-pleural muscle (Plate 2, fig. 5) originating on the anterior notch of one segment, passes ventrad to its insertion on the pleural suture near the posterior notch of the following segment.
 6. The parascutal-pleural muscle (Plate 2, fig. 5) originating on the parascutal notch, passes ventrad to its insertion on the middle portion of the pleural suture.

Subfamily Glaphyrinae

The Intersegmental Pleural Muscles

The subfamily Glaphyrinae differs from the Pleocominae

in not having muscle P-1. There is only one intersegmental, pleural longitudinal muscle, which is numbered P-5; four intersegmental, pleural diagonal muscles are numbered P-2, P-4, P-7 and P-8. These comparisons of the muscles of Pleocominae and Glaphyrinae can be made:

- P-5. The second pleural longitudinal muscle (Plate 3, fig. 9) is similar to that in the Pleocominae.
- P-2. The sterno-pleural diagonal muscle (Plate 3, fig. 9) is V-shape, the origin being on the posterior notch as in the Pleocominae. The anterior arm of the V, P-2b, has shifted its insertion to the scutellar line and becomes an intrasegmental muscle. The broader posterior arm of the V remains in the original position as in the Pleocominae. The distal end of P-2 subdivides into two smaller muscles.
- P-4. The pleuro-tergal diagonal muscle (Plate 3, fig. 10) differs from that in the Pleocominae at the insertion. The insertion of this muscle in the Glaphyrinae has shifted dorsad to become inserted on the middle portion of the prescutal line of the following segment.
- P-7 and P-8. The pleuro-sternal diagonal and the tergo-sternal diagonal muscle (Plate 3, fig. 10) are similar to those in the Pleocominae.

The Intrasegmental Pleural Muscles

The intrasegmental pleural muscles of the Glaphyrinae are the same as in the Pleocominae. There are two pleural vertical and a pleural diagonal muscles which are numbered P-3, P-6 and P-9.

P-3. The tergo-sternal vertical muscle (Plate 3, fig. 9) is enlarged on the origin and gradually narrows toward the insertion and becomes fan-shaped. The origin of this muscle is above the insertion of P-2 while in the Pleocominae it is beneath the insertion of P-2.

P-6. The tergo-pleural diagonal muscle (Plate 3, fig. 10) differs from that in the Pleocominae since in the Glaphyrinae the origin of P-6 has shifted dorsad.

P-9. The pleuro-sternal vertical muscle (Plate 3, fig. 10) is similar to that in the Pleocominae.

The Spiracular Muscles

There are six spiracular muscles altogether but these differ somewhat from those in the Pleocominae; they have the following positions:

1. and 2. The parasternal-parascutal notch muscles (Plate 3, fig. 11) are paired, originating on the parasternal line near the posterior notch and pass dorsad to

their insertion on the parascutal notch. These two muscles are homologous to the parasternal-parascutal notch muscle in the group of spiracular muscles of the Pleocominae.

3. and 4. The parascutal-pleural muscles (Plate 3, fig. 11) are paired, originating at the beginning of the parascutal line and passing ventrad to their insertions on the pleural suture.
5. The pleural-sternellar muscle (Plate 3, fig. 11) originating on the pleural lobe anteriorly to the anterior notch of the following segment, passes ventrad to its insertion on the beginning of the sternellar line.
6. The parascutal-pleural muscle (Plate 3, Fig. 11) originating on the parascutal notch, passes ventrad to its insertion on the central part of the pleural suture. This muscle is homologous to the parascutal-pleural muscle in the Pleocominae.

Subfamily Troginae

The Intersegmental Pleural Muscles

The subfamily Troginae differs from the Pleocominae in not having P-1. There is only one intersegmental, pleural longitudinal muscle, which is numbered P-5. There

are four intersegmental, pleural diagonal muscles which are numbered P-2, P-4, P-7 and P-8.

- P-5. The second pleural longitudinal muscle of the Troginae (Plate 2, fig. 7) is similar to that in the Pleocominae.
- P-2. The sterno-tergal diagonal muscle of the Troginae (Plate 2, fig. 6) differs from that in Pleocominae in having a ring-band at the middle portion on the muscle, which is a dark area in the muscle but there is no differentiation in the muscle fibers in this area.
- P-4.¹ The pleural-tergal diagonal muscle (Plate 2, fig. 7) is much smaller than that in the Pleocominae and the insertion also shifts dorsad to insert on the prescutal line of the following segment, ventrad of the insertion of T-5.
- P-7 and P-8. The pleuro-sternal diagonal muscle and the tergo-sternal diagonal muscle (Plate 2, fig. 7) are similar to those in the Pleocominae.

The Intrasegmental Pleural Muscles

The Troginae also have the same intrasegmental pleural muscles as in the Pleocominae. These are two pleural

¹P-4 is always running parallel with T-5 in every sub-family studied in this investigation.

vertical and a pleural diagonal muscles. They are numbered P-3, P-6 and P-9.

P-3. The tergo-sternal vertical muscle (Plate 2, fig. 6) is somewhat smaller than that in the Pleocominae. The origin of the muscle is above the insertion of P-2; this is the same as found in other subfamilies except in the Pleocominae.

P-6. The tergo-pleural diagonal muscle (Plate 2, fig. 7) differs from that in the Pleocominae in that the origin shifts dorsad.

P-9. The pleuro-sternal vertical muscle (Plate 2, fig. 7) is similar to that in the Pleocominae.

The Spiracular Muscles

There are six muscles altogether but these differ from the Pleocominae as follows:

1. The superior-posterior notch muscle (Plate 2, fig. 8) originating on the superior notch and passing ventrad to its insertion on the posterior notch.
2. and 3. The parasternal-antipleural muscles (Plate 2, fig. 8) are paired muscles which run parallel from their origins at the beginning of the parasternal line to their insertions on the middle portion of the antipleural suture.

4. The parasternal-parascutal notch muscle (Plate 2, fig. 8) originating on the parasternal line, passes dorsad to its insertion on the parascutal notch.
5. and 6. The antipleural-pleural muscles (Plate 2, fig. 8) are paired muscles which run parallel from their origins on the antipleural suture to their insertions on the middle portion of the pleural suture.

Subfamily Melolonthinae

The Intersegmental Pleural Muscles

In the subfamily Melolonthinae there are two intersegmental, pleural longitudinal muscles numbered P-1 and P-5; four intersegmental, pleural diagonal muscles numbered P-2, P-4, P-7 and P-8. These differ from the muscles in the Pleocominae in having added two muscles in P-2, which are numbered P-2a and P-2b. Also, other differences are discussed below:

- P-1. The first pleural longitudinal muscle (Plate 4, fig. 15) is present in the Melolonthinae and is larger than that in Pleocominae. This muscle expands ventrad to cover a part of the sternal region of the segment.
- P-5. The second pleural longitudinal muscle (Plate 4,

fig. 16) is similar to that in the Pleocominae.

P-2. The sterno-tergal diagonal muscle (Plate 4, figs. 15 and 16) is V-shaped, the origin being on the posterior notch as in the Pleocominae. The anterior arm of the V, P-2b, has shifted its insertion to the scutellar line and becomes an intrasegment muscle. Beneath the posterior arm of the V, P-2, is another muscle, P-2a. This muscle has the same point of origin as the muscles P-2 and P-2b, and has an insertion in common with P-5 at the anterior notch of the following segment.

P-4. The pleuro-tergal diagonal muscle of the Melolonthinae (Plate 4, fig. 16) is somewhat different from the Pleocominae. At its insertion the pleuro-tergal diagonal muscle shifts dorsad to its insertion on the middle portion of the prescutal line of the following segment.

P-7 and P-8. The pleuro-sternal diagonal and the tergo-sternal diagonal muscles (Plate 4, fig. 17) are similar to those in the Pleocominae.

The Intrasegmental Pleural Muscles

The Melolonthinae also have the same intrasegmental pleural muscles as the Pleocominae. There are two pleural vertical muscles and a pleural diagonal muscle, numbered

P-3, P-6 and P-9. These differ from the muscles of Pleocominae in having one muscle added to P-6, which is numbered P-6a. Other differences are discussed below:

P-3. The tergo-sternal vertical muscle of Melolonthinae (Plate 4, fig. 15) is present and very similar to that in the Pleocominae except the origin of this muscle overlaps the insertion of P-2.

P-6. The tergo-pleural diagonal muscle (Plate 4, fig. 17) is present. There is an additional small narrow muscle that runs above P-6, its origin and insertion being common with P-6. I am calling this muscle P-6a.

P-9. The pleuro-sternal vertical muscle (Plate 4, fig. 17) is similar to that in the Pleocominae.

The Spiracular Muscles

In the Melolonthinae there are only four spiracular muscles. These have the following positions:

1. The parasternal-antipleural muscle (Plate 4, fig. 18) originating at the beginning of the parasternal line, passes dorsad to its insertion on the antipleural suture.
2. The parasternal-parascutal muscle (Plate 4, fig. 18) originating on the parasternal line near the posterior notch, passes dorsad to its insertion on the

parascutal notch.

3. The parascutal-pleural muscle (Plate 4, fig. 18) originating on the parascutal notch beneath the insertion of the parasternal-parascutal muscle, passes ventrad to its insertion on the middle portion of the pleural suture.
4. The antipleural-pleural muscle (Plate 4, fig. 18) originating on the antipleural suture, passes ventrad to its insertion on the pleural suture near the posterior notch of the following segment.

Subfamily Rutelinae

The Intersegmental Pleural Muscles

In the Rutelinae there are two intersegmental, pleural longitudinal muscles that are numbered P-1 and P-5 and four intersegmental, pleural diagonal muscles that are numbered P-2, P-4, P-7 and P-8. The muscles of the Rutelinae differ from the Pleocominae in having added two muscles to P-2; these are numbered P-2a and P-2b. Other differences are discussed below:

P-1 and P-5. The first and the second pleural longitudinal muscles of the Rutelinae (Plate 5, figs. 21 and 22) are present and are similar to those in the Pleocominae.

- P-2. The sterno-tergal diagonal muscle (Plate 5, figs. 21 and 22) appears to be a Y-shaped muscle, forking at the ring-band. However, beneath the second fork of the Y is another muscle, P-2a, that lies beneath P-2. This muscle also separates at the ring-band and has an insertion in common with P-5 at the anterior notch of the following segment. This muscle, P-2a, cannot be seen without lifting P-2. The first fork of the Y, P-2b, has its origin in common with P-2, and its insertion on the scutellar line.
- P-4. The pleuro-tergal diagonal muscle (Plate 5, fig. 22) is gradually broader from its origin to its insertion and the insertion is shifted dorsad to insert on the half portion of the prescutal line of the following segment.
- P-7 and P-8. The pleuro-sternal diagonal and the tergo-sternal diagonal muscle of the Rutelinae (Plate 5, fig. 23) are similar to those in the Pleocominae.

The Intrasegmental Pleural Muscles

There are two intrasegmental, pleural vertical muscles and a pleural diagonal muscle in the Rutelinae which are numbered P-3, P-6 and P-9. These muscles differ from those in the Pleocominae in having a muscle added to P-6,

which I am calling P-6a. There are other differences which I shall discuss below:

P-3. The tergo-sternal vertical muscle of the Rutelinae (Plate 5, fig. 21) is present and is similar to that of the Pleocominae except the origin of P-3 overlaps the insertion of P-2.

P-6. The tergo-pleural diagonal muscle (Plate 5, fig. 23) is present and also there is another smaller muscle running above with the same origin and insertion; I am calling this additional muscle P-6a. The P-6a in this subfamily is also present in the Melolonthinae but here it is a bigger band.

P-9. The pleuro-sternal vertical muscle of the Rutelinae (Plate 5, fig. 23) is similar to that in the Pleocominae.

The Spiracular Muscles

In the Rutelinae there are also four spiracular muscles that are similar to those in the Melolonthinae. They have the following positions:

1. The parasternal-antipleural muscle of the Rutelinae (Plate 5, fig. 24) originating on the origin of the parasternal line and passing dorsad to its insertion on the antipleural suture.

2. The parasternal-parascutal notch muscle (Plate 5, fig. 24) originating on the parasternal line, overlapping the origin of the parasternal-antipleural muscle, passes dorsad to its insertion on the parascutal notch.
3. The parascutal-pleural muscle (Plate 5, fig. 24) originating on the parascutal line near the parascutal notch, passes ventrad and beneath the parasternal-parascutal notch muscle to its insertion on the middle portion of the pleural suture.
4. The antipleural-pleural muscle (Plate 5, fig. 24) originating on the antipleural suture, passes ventrad to its insertion on the pleural suture near the posterior notch of the following segment.

Subfamily Dynastinae

The Intersegmental Pleural Muscles

The two intersegmental, pleural longitudinal muscles are numbered P-1 and P-5; the four intersegmental, pleural diagonal muscles are numbered P-2, P-4, P-7 and P-8. The P-1 muscle of the Dynastinae consists of two bands while in the Pleocominae there is only one band. In the Dynastinae, I am numbering the two bands P-1 and P-1a; P-2 has two more strands than in the Pleocominae. These are numbered

P-2, P-2a and P-2b. Other differences between Dynastinae and Pleocominae will be discussed as each muscle is described.

P-1. The first pleural longitudinal muscle (Plate 6, fig. 27) separates into two muscles at the origin but remains close together. I am calling the dorsad one P-1 and the ventrad P-1a.

P-5. The second pleural longitudinal muscle (Plate 6, fig. 29) is similar to that in the Pleocominae.

P-2. The sterno-tergal diagonal muscle (Plate 6, figs. 27 and 28) appears much the same as that in the Rutelinae (see P-2 in the Rutelinae).

P-4. The pleuro-tergal diagonal muscle (Plate 6, fig. 28) is the same as in the Rutelinae (see P-4 in the Rutelinae).

P-7 and P-8. The pleuro-sternal diagonal muscle and the tergo-sternal diagonal muscle (Plate 6, fig. 29) are similar to those in the Pleocominae.

The Intrasegmental Pleural Muscles

There are two pleural vertical muscles and a pleural diagonal muscle that are numbered P-3, P-6 and P-9. These three muscles differ from those in the Pleocominae in P-6 having one additional muscle, which I am calling P-6a. Other differences will be mentioned in the description.

- P-3. The tergo-sternal vertical muscle (Plate 6, fig. 27) is similar to the same muscle in the Pleocominae except the origin overlaps the insertion of P-2.
- P-6. The tergo-pleural diagonal muscle (Plate 6, fig. 29) is the same as in the Rutelinae (see P-6 in the Rutelinae).
- P-9. The pleuro-sternal vertical muscle (Plate 6, fig. 29) is a very short muscle because in this subfamily the anterior notch is very close to the posterior notch.

The Spiracular Muscles

There are four spiracular muscles in the Rutelinae.

1. The parasternal-antipleural muscle (Plate 6, fig. 30) is the same as in the Rutelinae.
2. The parasternal-parascutal muscle (Plate 6, fig. 30) originating on the parasternal line overlaps the origin of the parasternal-antipleural muscle, passes dorsad to its insertion on the parascutal line near the parascutal notch.
3. The parascutal-pleural muscle (Plate 6, fig. 30) originating on the parascutal line near the superior notch, passes ventrad and beneath the parasternal-parascutal muscle to its insertion on the middle portion of the pleural suture.

4. The antipleural-sternellar muscle (Plate 6, fig. 30) originating on the antipleural suture, passes ventrad to its insertion on the sternellar line near the posterior notch of the following segment.

Subfamily Cetoniinae

The Intersegmental Pleural Muscles

In the Cetoniinae two intersegmental, pleural longitudinal muscles are numbered P-1 and P-5; the four intersegmental, pleural diagonal muscles are numbered P-2, P-4, P-7 and P-8. Most of the muscles in this subfamily are similar to those in the Dynastinae, except P-1 has only one fan-shaped band that is similar to P-1 in the Rutelinae (Plate 7, figs. 33, 34 and 35).

The Intrasegmental Pleural Muscles

The two intrasegmental, pleural vertical muscles and a pair of pleural diagonal muscles are numbered P-3, P-6, P-6a and P-9. Most of the muscles are similar to those in the Dynastinae (Plate 7, figs. 33, 34 and 35).

The Spiracular Muscles

There are four spiracular muscles but two of them are paired muscles and have the following positions:

1. The parascutal-pleural muscle (Plate 7, fig. 36) originating on the parascutal line near the superior notch, passes ventrad to its insertion on the anterior portion of the pleural suture.
2. The parasternal-parascutal muscle (Plate 7, fig. 36) is a paired muscle which coalesces with a large band of muscle that originates on the parasternal line and passes dorsad to its insertion on the parascutal line close to the parascutal notch.
3. The parascutal-sternellar muscle (Plate 7, fig. 36) originating on the posterior portion of the parascutal line, passes ventrad to its insertion on the beginning of the sternellar line.
4. The spiracular-pleural muscle (Plate 7, fig. 36) is also a paired muscle that coalesces, forming a big band. It originates on the body wall close to the posterior part of the spiracle and passes ventrad to its insertion on the posterior portion of the pleural suture.

Subfamily Sinodendrinae

In the subfamily Sinodendrinae the pleural muscles are as unique as the tergal muscles. Most of the muscles are large with many strings coalesced and most of them are fan-shaped. I am considering such muscles as a highly

specialized character.

The Intersegmental Pleural Muscles

In the Sinodendrinae the lines and areas bound by them are more obscure than in those subfamilies which have been mentioned previously. Fortunately the patterns of the muscles can be homologized with those in other subfamilies, probably making it possible to locate the lines and areas by the origins and insertions of the muscles.

The two intersegmental, pleural longitudinal muscles are numbered P-1 and P-5; the four intersegmental, pleural diagonal muscles are numbered P-2, P-4, P-7 and P-8. The big difference between Sinodendrinae and Scarabaeidae is in the muscle P-8. In the Sinodendrinae, muscle P-8 is separated into two branches, the added branch shifting its origin dorsad to the attachment on the skin of the scutellum; I am calling this added branch P-8a. Other differences will be mentioned in the descriptions below:

P-1. The first pleural longitudinal muscle of the Sinodendrinae (Plate 3, fig. 12) is similar to that in the Pleocominae, but there is a triangular space between the origin and insertion, which does not appear in the Scarabaeidae.

P-5. The second pleural longitudinal muscle (Plate 3, fig. 13) is a thin band muscle, which consists of

about five strings of muscles joined in the same plane.

- P-2. The sterno-tergal diagonal muscle (Plate 3, fig. 12) is a single large band with its insertion under the origin of P-3. This muscle is also somewhat fan-shaped being wider at the insertion.
- P-4. The pleuro-tergal diagonal muscle (Plate 3, fig. 13) consists of two string muscles forming one small band.
- P-7. The pleuro-sternal diagonal muscle (Plate 3, fig. 13) is present and is similar to that in the Pleocominae.
- P-8. The tergo-sternal diagonal muscle from the insertion point (Plate 3, fig. 13) separates into two muscles. I am calling this added muscle P-8a. The three muscles, P-7, P-8 and P-8a unite to form a fan-like muscle.

The Intrasegmental Pleural Muscles

The one intrasegmental, pleural vertical muscle and the one pleural diagonal muscle are numbered P-3 and P-6. In the subfamily Sinodendrinae P-9 does not appear and neither does P-6a.

- P-3. The tergo-sternal vertical muscle (Plate 3, fig. 12) is a large fan-shaped muscle. (This larger muscle may replace P-9 since they are the same type of

vertical muscle).

- P-6. The tergo-pleural diagonal muscle (Plate 3, fig. 13) is a thin muscle consisting of many string muscles joined together in the same plane. The muscle P-6a does not appear in this subfamily.

The Spiracular Muscles

There are five big spiracular muscles in the Sinodendrinae that have the following positions:

1. The first parascutal-pleural muscle (Plate 3, fig. 14) originating on the parascutal line, passes ventrad to its insertion on the anterior portion of the pleural suture.
2. The parasternal-parascutal muscle (Plate 3, fig. 14) originating on the parasternal line, passes dorsad to its insertion on the parascutal line near the parascutal notch.
3. The second parascutal-pleural muscle (Plate 3, fig. 14) originating on the middle portion of the parascutal line, passes ventrad to its insertion on the middle portion of the pleural suture.
4. The third parascutal-pleural muscle (Plate 3, fig. 14) originating on the posterior portion of the parascutal line near the parascutal notch, passes ventrad to its insertion on the posterior portion

of the pleural suture.

5. The hypopleural-anterior notch muscle (Plate 3, fig. 14) originating on the hypopleural line, passes dorsad to its insertion on the anterior notch of the following segment.

STERNAL MUSCULATURE

The sternal muscles of the Scarabaeoid larvae can be separated into two main groups as with the tergal muscles; the intersegmental sternal muscles and the intrasegmental sternal muscles.

Subfamily Pleocominae

In the subfamily Pleocominae, the prototype, there are five sternal muscles. These muscles are arranged in three layers.

The Intersegmental Sternal Muscles

- The four intersegmental, sternal diagonal muscles are numbered from S-1 to S-4 and have the following positions:
- S-1. The first sternal diagonal muscle (Plate 2, fig. 3) originates on the beginning of the sternal line, passing dorsad to its insertion on the middle portion of the sternal line of the following segment.
 - S-2. The second sternal diagonal muscle (Plate 2, fig. 3)

originates on the sternal line dorsad of the origin of S-1, passing dorsad to its insertion on the distal portion of the sternal line of the following segment.

S-3. The third sternal diagonal muscle (Plate 2, fig. 4) originates on the initial portion of the sternal line, passing ventrad and beneath S-1 to its insertion on the initial portion of the sternal line of the following segment.

S-4. The fourth sternal diagonal muscle (Plate 2, fig. 4) originates on the distal portion of the sternal line, passing ventrad and beneath S-2 to its insertion on the sternal line dorsad of the insertion of S-3.

The Intrasegmental Sternal Muscles

The only intrasegmental, sternal diagonal muscle in the Pleocominae is numbered S-5 and has the following position:

S-5. The parasternal-sternellar muscle (Plate 2, fig. 5) originates on the middle portion of the parasternal line and passes dorsad to its insertion on the distal portion of the sternellar line near the posterior notch of the following segment.

Subfamily Glaphyrinae

The subfamily Glaphyrinae differs from the Pleocominae in having six sternal muscles rather than five. They are numbered S-1, S-2, S-3, S-4, S-6 and S-7. The muscle S-5 does not appear in this subfamily.

The Intersegmental Sternal Muscles

There are four intersegmental, sternal diagonal muscles which are numbered from S-1 to S-4.

S-1. The first sternal diagonal muscle (Plate 3, fig. 9) is broader than S-1 in the Pleocominae, covering two-thirds of the sternal region.

S-2. The second sternal diagonal muscle (Plate 3, fig. 9) is similar to that in the Pleocominae but it is narrower.

S-3 and S-4. The third and fourth sternal diagonal muscles (Plate 3, fig. 10) together form a large band that covers the entire sternal region beneath S-1 and S-2.

The Intrasegmental Sternal Muscles

Glaphyrinae has two additional intrasegmental, sternal diagonal muscles which are not present in the Pleocominae. They are numbered S-6 and S-7 and have the following positions:

- S-6. The parasternal-presternal muscle (Plate 3, fig. 11) originates on the beginning of the parasternal line and passes dorsad to its insertion on the middle portion of the presternal line (sternal line in the Pleocominae) of the following segment.
- S-7. The sternellar-presternal muscle (Plate 3, fig. 11) originates on the middle portion of the sternellar line and passes dorsad to its insertion on the presternal line of the following segment.

Subfamily Troginae

In the subfamily Troginae, there are five sternal muscles as in the Pleocominae.

The Intersegmental Sternal Muscles

The four intersegmental, sternal diagonal muscles are numbered S-1, S-2, S-3 and S-4. They differ from the Pleocominae in S-1 and S-2 joining together, and covering the entire sternal region. Also muscles S-3 and S-4, join together, covering the entire sternal region beneath S-1 and S-2. (Plate 2, figs. 6 and 7).

The Intrasegmental Sternal Muscles

There is only one intrasegmental, sternal diagonal muscle; it is numbered S-6.

- S-6. The parasternal-presternal muscle of the Troginae (Plate 2, fig. 8) differs from S-6 in the Glaphyrinae in that it has migrated dorsad but the origin and the insertion are still in the same positions.

Subfamily Melolonthinae

In the Melolonthinae, the sternal muscles are different from those in the Pleocominae both in being separated into several bands and in joining to become one big single band. There are four intersegmental, diagonal muscles, one intrasegmental diagonal muscle and one intersegment, sternal longitudinal muscle that are not present in the Pleocominae.

The Intersegmental Sternal Muscles

The four intersegmental, sternal diagonal muscles are numbered from S-1 to S-4; an intersegmental, sternal longitudinal muscle is numbered S-8. These muscles have the following positions:

- S-1. The first sternal diagonal muscle of the Melolonthinae (Plate 4, fig. 16) separates into two bands which I am calling S-1 and S-1a. These bands are in the same position as S-1 in the Pleocominae.
- S-2. The second sternal diagonal muscle (Plate 4, fig. 16) also separates into two bands which I am calling

S-2 and S-2a. These bands are also in a position similar to S-2 in the Pleocominae.

S-3 and S-4. The third and the fourth sternal diagonal muscles (Plate 4, fig. 17) join together into one single band, covering the entire sternal region.

S-8. The second sternal longitudinal muscle (Plate 4, fig. 18) originating on the sternal line near the posterior notch, passes horizontally to its insertion at a similar position on the following segment. This muscle is a rather large band and covers about one-third of the sternal area.

The Intrasegmental Sternal Muscles

S-5. The parasternal-sternellar muscle (Plate 4, fig. 18) is similar to that in the Pleocominae.

Subfamily Rutelinae

The sternal muscles of the Rutelinae differ from those in the Pleocominae in the joining of muscles into a large band and each muscle is larger than in the other subfamilies.

The Intersegmental Sternal Muscles

The four intersegmental, sternal diagonal muscles of the Rutelinae form two large bands. These are numbered S-1

to S-4; an additional muscle, not in the Pleocominae, an intersegmental, sternal longitudinal muscle I am numbering S-0, and the second sternal longitudinal muscle S-8.

S-0. The first sternal longitudinal muscle of the Rutelinae (Plate 5, fig. 21) is an additional muscle not present in the Pleocominae. It originates on the sternal line ventrad of P-1 and covers the entire inner sternal area to its insertion at the same level on the following segment.

S-1 and S-2. The first and the second sternal diagonal muscles (Plate 5, fig. 22) join together in a single band and cover the entire sternal area beneath the S-0.

S-3 and S-4. The third and the fourth sternal diagonal muscles (Plate 5, fig. 23) also join together into a single band and cover the entire sternal area beneath the S-1 and S-2.

S-8. The second sternal longitudinal muscle (Plate 5, fig. 24) is similar to that in the Melolonthinae.

The Intrasegmental Sternal Muscles

There are two parasternal-sternellar muscles with their insertions close together. I am numbering them S-5 and S-5a. These two muscles have the same positions as S-5 in the Pleocominae.

Subfamily Dynastinae

The sternal muscles of the Dynastinae are somewhat similar to those in the Rutelinae.

The Intersegmental Sternal Muscles

There are four intersegmental, sternal diagonal muscles numbered S-1 to S-4, S-1 and S-2 joining together; two intersegmental, sternal longitudinal muscles are numbered S-0 and S-8.

S-0. The first sternal longitudinal muscle (Plate 6, fig. 27) is similar to the S-0 in the Rutelinae, except in the Dynastinae only the lower half portion of the inner sternal area is covered.

S-1 and S-2. The first and the second sternal diagonal muscles (Plate 6, fig. 28) join together as in the Rutelinae.

S-3. The third sternal diagonal muscle (Plate 6, fig. 29) is larger than that of the Pleocominae; it does not join with S-4 as in the Glaphyrinae, Troginae, Melolonthinae or Rutelinae. It also differs from the Pleocominae in expanding dorsad to overlap a part of the S-4 insertion.

S-4. The fourth sternal diagonal muscle (Plate 6, fig. 29) is similar to that in the Pleocominae.

S-8. The second sternal longitudinal muscle (Plate 6, fig. 30) is similar to that in the Melolonthinae and Rutelinae.

The Intrasegmental Sternal Muscle

In the Dynastinae, there is only one intrasegmental, sternal diagonal muscle which is the parasternal-sternellar muscle, S-5. This muscle is similar to that in the Pleocominae.

Subfamily Cetoniinae

The sternal muscles of the Dynastinae are similar to the subfamily Cetoniinae in having the same numbers of muscles except S-1 and S-2 do not join as they do in the Dynastinae. This is peculiar, since the Cetoniinae is considered the most specialized subfamily of Scarabaeidae. The patterns of the sternal muscles are similar to the Pleocominae. For example S-1, S-2, S-3 and S-4 are separated. Also S-5 is present. The presence of S-0 and S-8 is similar to the Dynastinae.

The Intersegmental Sternal Muscles

The Cetoniinae have four intersegmental, sternal diagonal muscles numbered S-1 to S-4 and two intersegmental, sternal longitudinal muscles numbered S-0 and S-8.

- S-0. The first sternal longitudinal muscle (Plate 7, fig. 33) is similar to the S-0 in the Dynastinae.
- S-1. The first sternal diagonal muscle (Plate 7, fig. 34) is similar to that in the Pleocominae but is a larger band which covers half of the sternal area.
- S-2. The second sternal diagonal muscle (Plate 7, fig. 34) is similar to that in the Pleocominae.
- S-3. The third sternal diagonal muscle (Plate 7, fig. 35) is very similar to that in the Dynastinae.
- S-4. The fourth sternal diagonal muscle (Plate 7, fig. 35) is very similar to that in the Pleocominae and is also similar to that in the Dynastinae.
- S-8. The second sternal longitudinal muscle (Plate 7, fig. 36) is similar to those in the Melolonthinae, Rutelinae and also Dynastinae.

The Intrasegmental Sternal Muscle

In the Cetoniinae, there is only one intrasegmental, sternal diagonal muscle which is the parasternal-sternal-lar muscle, S-5. This muscle is similar to that in the Pleocominae but it is a larger band.

Subfamily Sinodendrinae

The sternal musculature of the Sinodendrinae, which is considered by Leng as the most specialized form of the

Scarabaeoidea, is quite similar to the sternal musculature of the Pleocominae. The latter is considered as a very generalized subfamily. The Sinodendrinae differ but little from the Pleocominae except there is one more intersegmental, sternal diagonal muscle, which I am calling the hypopleural-posterior notch muscle, S-9.

S-1, S-2, S-3, S-4 and S-5 (Plate 3, figs. 12, 13 and 14) are present and are similar to those in the Pleocominae.

S-9. The hypopleural-posterior notch muscle (Plate 3, fig. 14) is a intrasegmental, diagonal muscle which originates on the hypopleural line and passes dorsad to its insertion on the posterior notch of the following segment. It is not present in the Pleocominae.

DISCUSSION

Phylogeny Based on Musculature

The data on the musculature of the anterior abdominal segments of larvae belonging to eight subfamilies of Scarabaeoidea show that there is considerable variability between subfamilies. Also, as I will show later in this paper, the musculature within a subfamily appears to be relatively stable. In order to reach conclusions regarding the phylogenetic relationships of the several subfamilies of the Scarabaeoidea I am making a number of assumptions.

My plates and figures show that there are several types of muscles in scarabaeoid larvae. Also, it seems evident that these various types probably represent varying degrees of specialization. My discussion will begin with the most generalized muscles and proceed up the scale to the most specialized muscle.

I am postulating that the evolution of the muscles of scarabaeoid larvae has proceeded along at least two paths. The most generalized muscle known to me is the strap-like band muscle which is common particularly in the Pleocominae, and in the pleural muscles of some of the other subfamilies. In the course of specializing this strap-like band increased in size until it was two to

four times wider than the original muscle. An example of such a wide muscle is muscle T-3 in the Troginae, Plate 2, fig. 6. After attaining its maximum width, the next step was the breaking up of the muscle into a series of narrow individual bands that are spaced equidistant apart and occupy the position of the original broad muscle. An example of such a muscle is illustrated in Plate 3, figs. 9, 10, 12 and 13 for the Glaphyrinae and Sinodendrinae.

The second path of evolution also begins with the strap-like band which increases in width at the point of insertion but not at the point of origin; thus the muscle becomes fan-shaped. The next step may go in several directions. The fan-shaped muscle may separate longitudinally, one section migrating to a new point of insertion, thus forming a V-shape. The fan-shaped muscle is illustrated by muscle P-1 in Plate 7, fig. 33, for the Cetoniinae, the V-shape muscle in Plate 4, fig. 15.

Later one or both arms of the V may become Y-shaped apically, one arm of the Y migrating to a new point of insertion. The Y usually forms just above the ring band (see Troginae, muscle P-2). Sometimes both arms of the Y redivide, one arm of each migrating to a new insertion. The Y-shaped muscles are illustrated in Plate 5, fig. 9 for the Glaphyrinae. Also, sometimes a trident rather than a Y is formed as shown on Plate 3, fig. 13 of the muscles P-7,

P-8 and P-8a, for the subfamily Sinodendrinae.

The separation of the Y may go in two directions. The muscle may split longitudinally, one arm of the Y remaining on the original insertion and the other migrating. Also the muscle may separate transversely so that the Y is formed, with each arm inserted on the different positions. An example is found in the subfamily Rutelinae, Plate 5, figs. 21 and 22 of the muscles P-2 and P-2a.

In addition to the modification of the shape of the muscle, there are other steps that seem to lead to specialization in the evolution of the musculature. The migration of the muscle from the original position found in the Pleocominae to a second position in a higher subfamily, is considered as a specializing process. Also, some of the muscles in the Pleocominae have disappeared in some of the other subfamilies. Likewise, muscles not in the Pleocominae are found in the higher subfamilies. They represent muscles in addition to the ones already present in the Pleocominae.

The highest type of specialization is in the Sinodendrinae. Here the broad muscle has become separated into narrow individual muscles, all being inserted equidistant apart in a straight line on the body wall. The line formed by the insertion of the muscles is in the same

position as the scutal or scutellar line as found in the Pleocominae (Plate 1, fig. 1). This is illustrated in Plate 3, figs. 12 and 13, for the Sinodendrinae.

In evaluating the phylogenetic position of the several subfamilies I have set up these values for each type of specialization. One muscle may exhibit two or three types of specialization. For this reason there are more specialized characters than there are muscles.

G--This symbol is given to the strap-like band muscle common in the Pleocominae. This is the most generalized type encountered in these studies.

S--This symbol is given to the muscles that are two to four times broader than the strap-like band. These muscles probably represent an intermediate stage in specialization.

SS--This symbol is given to the fan-shaped, V- and Y-shaped muscles. These muscles also represent an intermediate stage that is higher than that of the S-muscles.

SSS--This symbol is used for the narrow muscles placed equidistant apart and inserted along a straight line on the body wall. This is the climax stage of specialization.

The several subfamilies have been arranged after Leng

and each muscle is designated in a column. Then the value of specialization for each muscle for each subfamily is indicated in the respective columns. Tables 2-4, in the Appendix, present the data for the tergal, pleural and sternal muscles, respectively.

Tables 5, 6, and 7, in the Appendix, which are derived from Tables 2, 3 and 4, tabulate the number of generalized and specialized characters for each subfamily. These data are used to determine the per cent of the specialized characters in the tergal, pleural, and sternal regions. After obtaining the percentages, the subfamilies have been ranked according to the per cent of specialized characters found in each subfamily.

When the three regions are considered separately, Tables 5 to 7, the Pleocominae is the only subfamily that does not shift its position. The other subfamilies shift in rank with the region where the muscles are found. The shifting in rank is believed to be the result of the more or less artificial zoning of the body into three regions. Actually the muscles are not as neatly confined to one zone as I have indicated. Hence, a more reliable picture is obtained when the three groups of muscles are combined as I have done in Table 8.

In Table 1, Leng's phylogenetic arrangement is compared with the arrangement resulting from studies of the

muscles in the anterior abdominal region of the larvae of the several subfamilies:

Table 1. Comparison of Leng's arrangement of the Scarabaeoidea with the arrangement proposed by the writer.

Leng	The writer
Pleocominae	Pleocominae
Glaphyrinae	--
Troginae	Melolonthinae
Melolonthinae	Troginae
Rutelinae	Rutelinae
Dynastinae	Dynastinae
Cetoniinae	Cetoniinae
--	Glaphyrinae
Sinodendrinae	Sinodendrinae

The phylogenetic arrangement based on the generalized and specialized condition of the larvae of Scarabaeoidea results in several shifts from Leng's arrangement. The Rutelinae, Dynastinae, Cetoniinae, and Sinodendrinae remain in the same relative positions. The major change is the shift of the Glaphyrinae from its position next to the Pleocominae to the most specialized subfamily in the Scarabaeidae. Also, the Troginae and Melolonthinae shift

places in this arrangement.

Phylogeny and the Environment

Perhaps my hypothesis of the phylogenetic relationships of the Scarabaeoidea might be questioned because of the possibility of environment having an effect on the musculature of the larvae. However, my observations indicate that the environment does not seem to have any major effect on the muscles.

To test the hypothesis that environment affects the musculature, I have arranged the subfamilies on the basis of the activity of the larvae. I consider very active larvae as representing a generalized condition, and sluggish larvae as representing a specialized condition. On this basis the subfamilies would be arranged as follows: Pleocominae, Melolonthinae, Rutelinae, Dynastinae, Glaphyrinae, Troginae, Cetoniinae and Sinodendrinae. Furthermore, within the same subfamily there are considerable differences in the habitat and in the activity of the larvae.

I consider the musculature patterns of Osmoderma eremicola Knoch, which dwells in dead wood, and of Cotinus texanus Casey, which lives in the soil, to be fundamentally the same. The muscle bands of the inner layer of eremicola (Plate 7, fig. 33) are very close together, but still are

separate. In texanus the same muscle bands are spaced farther apart so that superficially they appear to be different. Some of the bands of texanus apparently are beginning to divide. Also, the muscles of the inner layer of both species are slightly oblique in position rather than longitudinal. The three outer layers of muscles of both species are similar in position and in appearance.

The patterns of the anterior abdominal segments of the scarabaeoid larvae seem to be unchanged within the subfamily. Other species within the other subfamilies have been dissected. While the habitats were different, I found no major change in their musculature patterns.

The Dorsal Folds in the Scarabaeoid Larvae

In examining scarabaeoid larvae the observer is struck by the presence of successive folds, particularly on the dorsal surface. The question arises, how many folds are there in one segment of the body? A study of the anterior abdominal musculature enabled me to determine the fundamental number of folds present.

Some larvae seem to have four folds in each anterior abdominal segment, the Pleocominae being an example. These folds are known as the prescutum, scutum, scutellum and post-scutellum. Three-fold larvae have also been found in other subfamilies; in these cases the post-scutellum is

not present.

By closely examining the attachment of the muscles of the larvae, I found that an anterior abdominal segment of scarabaeoid larvae has only three true folds; prescutum, scutum and scutellum.

Larvae in the subfamily Pleocominae are peculiar in that each of them has four folds in a segment. I consider the prescutum as composed of two folds, prescutum I and prescutum II. The reason for considering the first two folds of the Pleocominae as a prescutum is based upon the musculature. In each subfamily, the muscle P-6 originates from the sternal end of the scutal line, which is the border line separating the prescutal from the scutal area. In the Pleocominae, P-6 originates from the sternal end of the second line of the anterior abdominal segment. I, therefore, consider this second line as the scutal line and the anterior area of the scutal line should then be the prescutum. Also I consider the first line on the anterior abdominal segments of each segment of the Pleocominae as an unimportant line because there is no muscle attachment to this line. The fact that muscles are attached to the second line on the tergum of the Pleocominae is also a reason for considering the second line as a scutal line. For these reasons the Pleocominae, the most generalized subfamily in these studies, has only three important folds,

the same as the other subfamilies in the Scarabaeoidea.

SUMMARY

The anterior abdominal segments of the following eight subfamilies, Pleocominae, Melolonthinae, Troginae, Rutelinae, Dynastinae, Cetoniinae, Glaphyrinae, and Sinodendrinae of the Scarabaeoidea are described and compared. The results of this investigation can be briefly summarized as follows:

1. In scarabaeoid larvae there are no major changes in the areas and lines of the anterior abdominal segments. There are three tergal folds: prescutum, scutum, and scutellum; and two sternal folds: sternum and sternellum.

2. There is a minor change in the Pleocominae, which exhibits two secondary folds in the prescutum.

3. The terminology for the areas and lines of the anterior abdominal segments follows, for the most part, the work of Dr. A. G. Boving.

4. There are differences in the musculature system between the subfamilies studied. The writer found that tergal musculature exhibited more variations than either pleural or sternal musculature.

5. The naming of muscle involves the letters T, P and S which represent the tergal, pleural, and sternal

muscles, respectively. Combined with these letters are the numbers, starting from 0, to designate each individual muscle.

6. A comparative study is made of the origin and insertion of the muscles between the subfamilies. As a result of this all inclusive study, the following muscles are found in each region: on the tergum twenty-three muscles are found and numbered from T-0 to T-22; the pleurum contains nine muscles, numbered from P-1 to P-9, and a group of spiracular muscles (numbering from 1 to 6), which varies from four to six in number; and ten sternal muscles numbering from S-0 to S-9.

7. By using the generalized and specialized characters of the anterior abdominal musculature, the writer proposes to arrange the Scarabaeoidea phylogenetically as follows: Pleocominae, Melolonthinae, Troginae, Rutelinae, Dynastinae, Cetoniinae, Glaphyrinae and Sinodendrinae.

8. The writer finds that within any one subfamily, there appears to be no major change in muscle pattern of the anterior abdominal segments.

9. More extensive studies are needed for determining which characters are of the most phylogenetic significance in scarabaeoid larvae.

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APPENDIX

Table 2. The tergal muscles.

Subfam- ilies	Intersegmental						Intrasegmental Muscles																	
	T- 1	T- 2	T- 3	T- 4	T- 5	T- 6	T- 6	T- 7	T- 8	T- 9	T- 10	T- 11	T- 12	T- 13	T- 14	T- 15	T- 16	T- 17	T- 18	T- 19	T- 20	T- 21	T- 22	
Pleoco- minae	G	G	G	G	G	-	G	G	G	S	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Glaphy- rinae	-	S	S	SS	S	S	SS	-	SS	-	SS	SS	SS	SS	SS	-	-	-	-	-	-	-	-	-
Trog- inae	-	G	S	G	S	S	G	G	G	-	G	G	-	-	-	SS	S	-	-	-	-	-	-	-
Melolon- thinae	-	G	S	G	G	S	G	G	S	-	G	-	-	-	-	-	S	-	-	-	-	-	-	-
Rute- linae	-	G	S	S	G	-	G	S	G	-	G	-	SS	-	-	-	S	-	-	-	-	-	-	-
Dynas- tinae	S	S	S	S	G	-	S	-	G	-	G	-	SS	-	-	-	SS	-	-	-	-	-	-	-
Cetoni- inae	-	S	S	S	G	-	S	-	S	-	G	SS	SS	-	-	-	SS	SS	SS	SSS	SSS	-	-	-
Sinoden- drinae	SSS	SSS	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	SSS	SSS

Table 3. The pleural muscles.

Subfam- ilies	Intersegmental						Intra- segmental			Spirac- ular muscles
	P-1	P-2	P-4	P-5	P-7	P-8	P-3	P-6	P-9	
Pleoco- minae	G	G	G	G	G	G	G	G	G	G
Glaphy- rinae	-	S	S	-	G	G	S	S	G	G
Trog- inae	-	S	G	G	G	G	S	S	G	G
Melolon- thinae	G	S	G	G	G	G	S	S	G	S
Rute- linae	G	SS	S	G	G	G	S	S	G	S
Dynas- tinae	S	SS	S	G	G	G	S	S	S	S
Cetoni- inae	SS	SS	S	G	G	G	S	S	S	S
Sinoden- drinae	G	SS	S	S	G	SS	SS	S	-	SS

Table 4. The sternal muscles

Subfam- ilies	Intersegmental muscles						Intrasegmental muscles			
	S-1	S-2	S-3	S-4	S-8	S-0	S-5	S-6	S-7	S-9
Pleoco- minae	G	G	G	G	-	-	G	-	-	-
Glaphy- rinae	G	S	S	S	-	-	-	S	SS	-
Trog- inae	S	S	S	S	-	-	-	S	-	-
Melolon- thinae	S	S	S	S	S	-	G	-	-	-
Rute- linae	S	S	S	S	S	S	S	-	-	-
Dynas- tinae	S	S	S	G	S	S	G	-	-	-
Cetoni- inae	S	G	S	G	S	S	G	-	-	-
Sinoden- drinae	S	S	G	G	-	-	S	-	-	SS

Table 5. Number of generalized and specialized characters and the per cent specialized of the tergal muscles.

Subfamilies	Total generalized characters	Total specialized characters	Per cent of specialized characters
Pleocominae	8	1	11.1
Melolonthinae	6	4	40
Troginae	7	6	46.2
Rutelinae	5	6	55.5
Dynastinae	3	9	75
Cetoniinae	2	21	91.3
Glaphyrinae	-	20	100
Sinodendrinae	-	12	100

Table 6. Number of generalized and specialized characters and the per cent specialized of the pleural muscles.

Subfamilies	Total generalized characters	Total specialized characters	Per cent of specialized characters
Pleocominae	10	-	0
Troginae	6	3	33.3
Melolonthinae	6	4	40
Glaphyrinae	4	4	50
Rutelinae	5	6	55.5
Dynastinae	3	8	72.7
Cetoniinae	3	8	72.7
Sinodendrinae	2	11	84.6

Table 7. Number of generalized and specialized characters and the per cent specialized of the sternal muscles.

Subfamilies	Total generalized characters	Total specialized characters	Per cent of specialized characters
Pleocominae	5	-	0
Cetoniinae	3	4	57.2
Dynastinae	2	5	71.4
Sinodendrinae	2	5	71.4
Melolonthinae	1	5	83.3
Glaphyrinae	1	6	85.7
Troginae	-	5	100
Rutelinae	-	7	100

Table 8. The total number of characters and the per cent specialized.

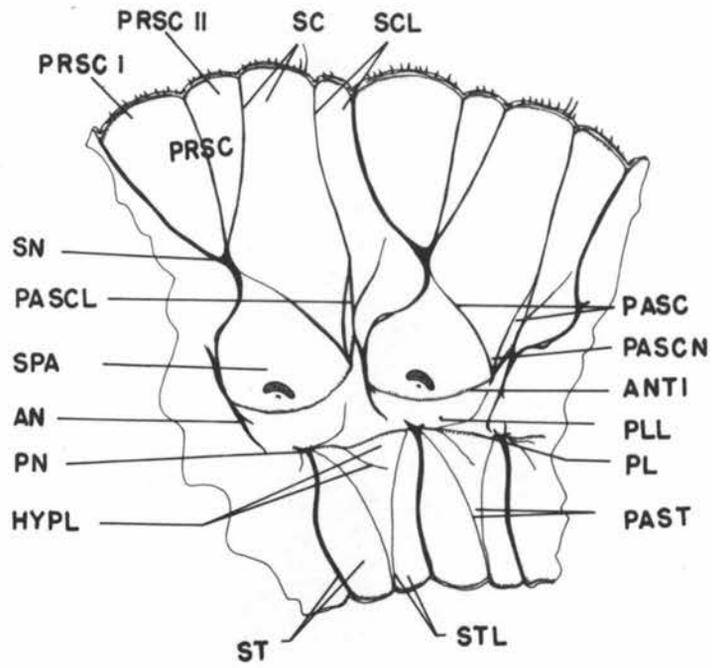
Subfamilies	Total number of characters	Per cent specialized characters
Pleocominae	24	3.7
Melolonthinae	26	54.4
Troginae	27	59.6
Rutelinae	29	70.3
Dynastinae	30	73.1
Cetoniinae	40	73.8
Glaphyrinae	45	78.6
Sinodendrinae	32	85.3

EXPLANATION OF PLATE I

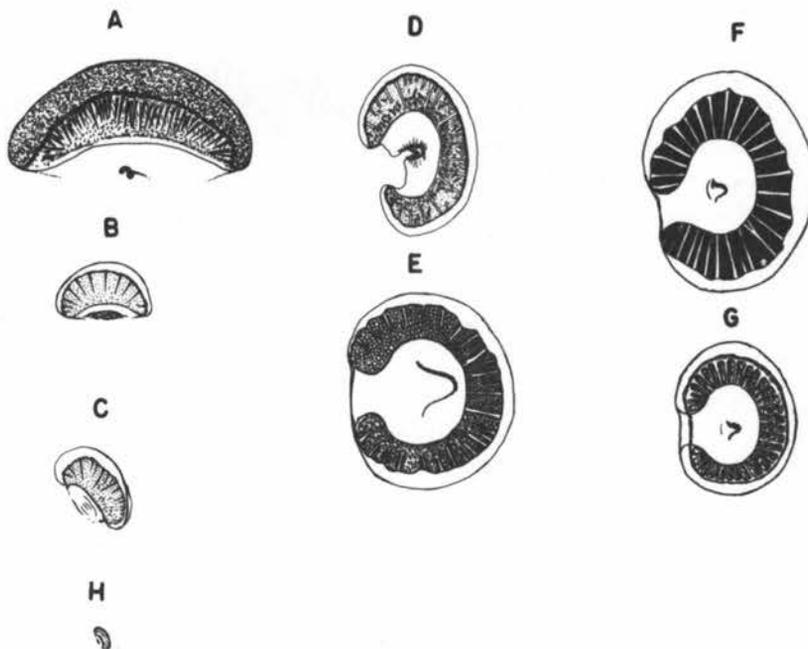
- Fig. 1. The interior integument of the third and fourth abdominal segments of the subfamily Pleocominae.
- Fig. 2. The interior views of the anterior abdominal spiracles: A. The Pleocominae, B. The Glaphyrinae, C. The Troginae, D. The Melolonthinae, E. The Rutelinae, F. The Dynastinae, G. The Cetoniinae and H. The Sinodendrinae.

AN, anterior notch; ANTI, antipleural suture;
PASCL, parascutellar line; PASCN, parascutal notch; PASC, parascutal line; PN, posterior notch;
PL, pleural suture; PLL, pleural lobe; PAST, parasternum; HYPL, hypopleurite or hypopleural line; PRSC, prescutum or prescutal line; PRSC I, prescutum I; PRSC II, prescutum II; SC, scutum; SCL, scutellum; SN, superior notch; SPA, spiracular area; ST, sternum or sternal line; STL, sternellum or sternellar line.

PLATE I



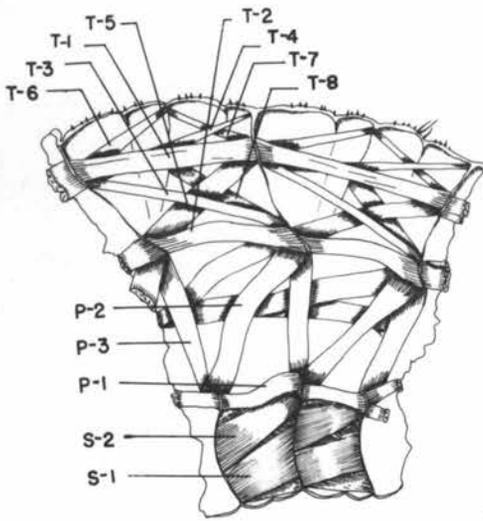
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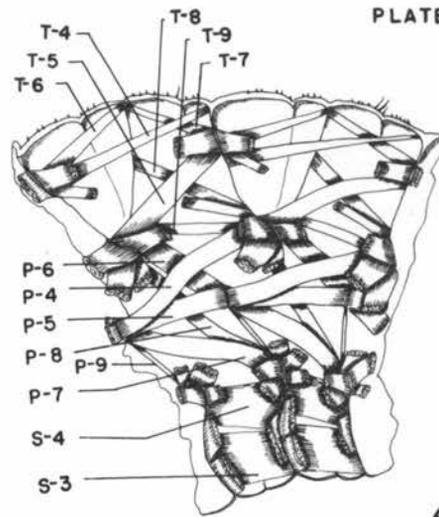
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EXPLANATION OF PLATE II

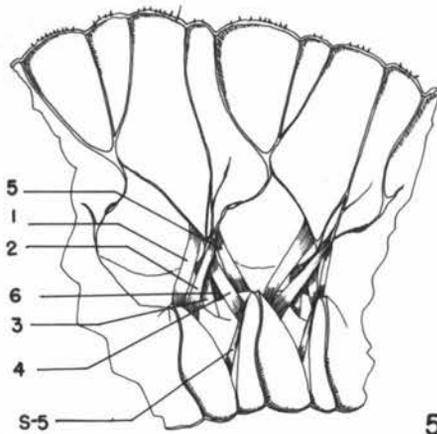
- Fig. 3. First sagittal dissection of the third and fourth abdominal segments of the subfamily Pleocominae.
- Fig. 4. Second sagittal dissection of the third and fourth abdominal segments of the subfamily Pleocominae.
- Fig. 5. Third sagittal dissection of the third and fourth abdominal segments of the subfamily Pleocominae.
- Fig. 6. First sagittal dissection of the third and fourth abdominal segments of the subfamily Troginae.
- Fig. 7. Second sagittal dissection of the third and fourth abdominal segments of the subfamily Troginae.
- Fig. 8. Third sagittal dissection of the third and fourth abdominal segments of the subfamily Troginae.



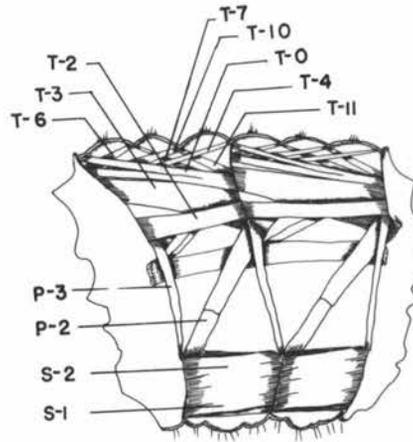
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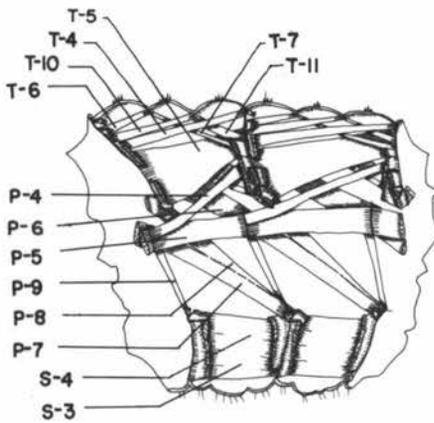
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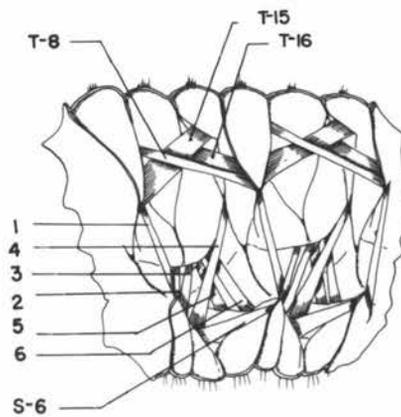
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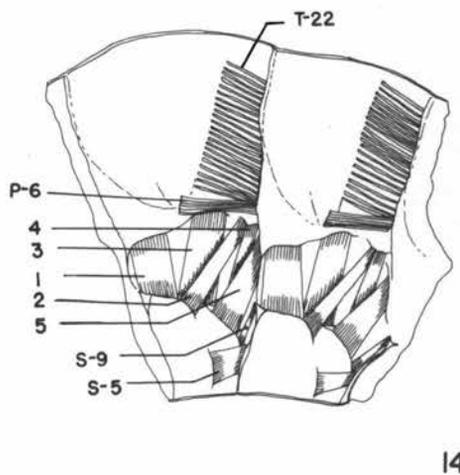
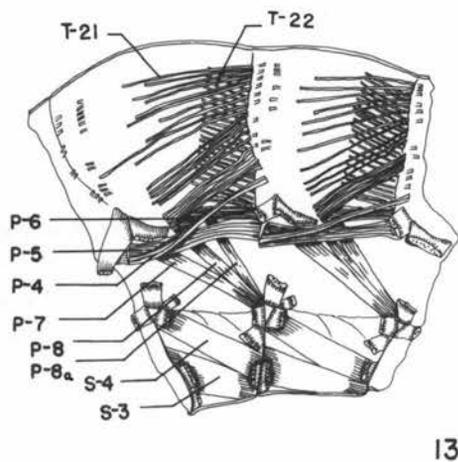
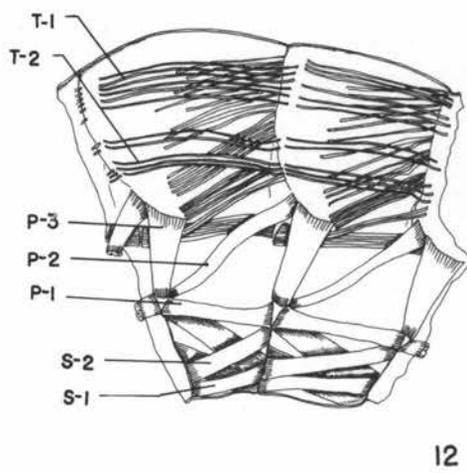
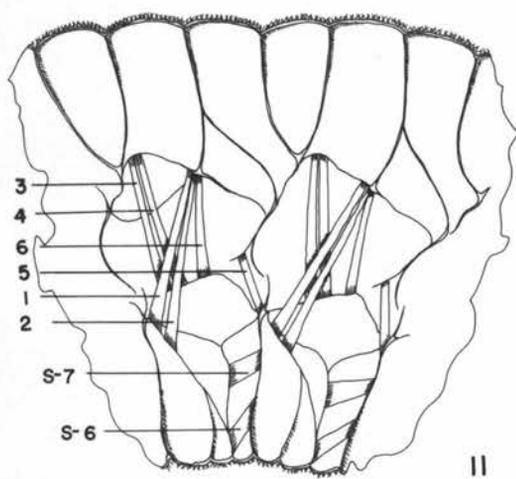
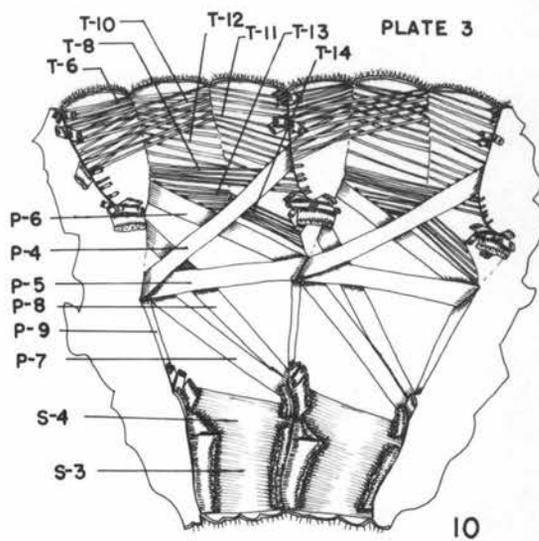
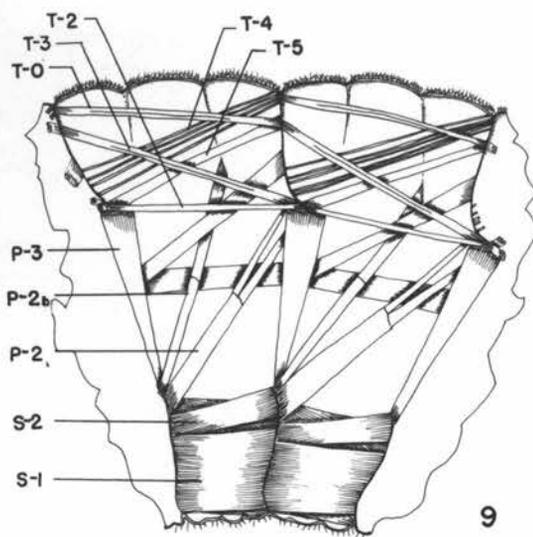
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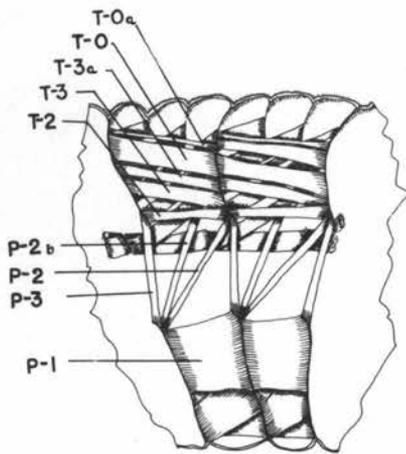
EXPLANATION OF PLATE III

- Fig. 9. First sagittal dissection of the third and fourth abdominal segments of the subfamily Glaphyrinae.
- Fig. 10. Second sagittal dissection of the third and fourth abdominal segments of the subfamily Glaphyrinae.
- Fig. 11. Third sagittal dissection of the third and fourth abdominal segments of the subfamily Glaphyrinae.
- Fig. 12. First sagittal dissection of the third and fourth abdominal segments of the subfamily Sinodendrinae.
- Fig. 13. Second sagittal dissection of the third and fourth abdominal segments of the subfamily Sinodendrinae.
- Fig. 14. Third sagittal dissection of the third and fourth abdominal segments of the subfamily Sinodendrinae.

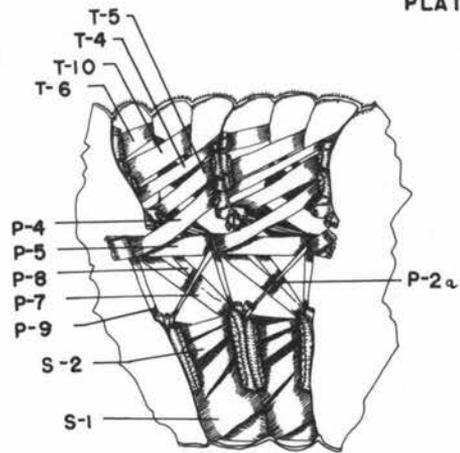


EXPLANATION OF PLATE IV

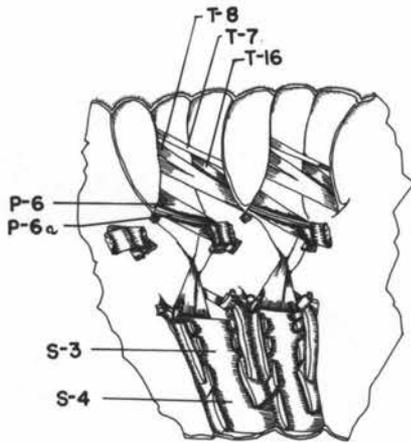
- Fig. 15. First sagittal dissection of the third and fourth abdominal segments of the subfamily Melolonthinae.
- Fig. 16. Second sagittal dissection of the third and fourth abdominal segments of the subfamily Melolonthinae.
- Fig. 17. Third sagittal dissection of the third and fourth abdominal segments of the subfamily Melolonthinae.
- Fig. 18. Fourth sagittal dissection of the third and fourth abdominal segments of the subfamily Melolonthinae.
- Fig. 19. The interior integument of the third and fourth abdominal segments of the subfamily Melolonthinae.
- Fig. 20. The interior integument of the third and fourth abdominal segments of the subfamily Troginae.



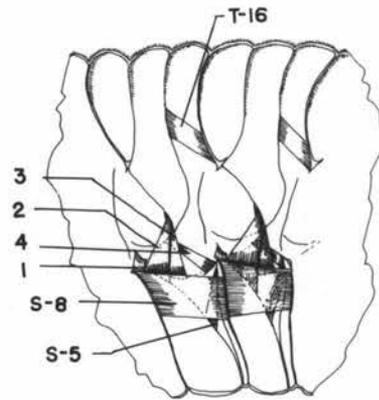
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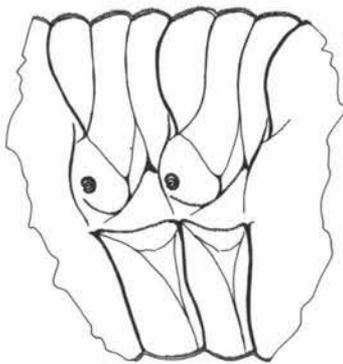
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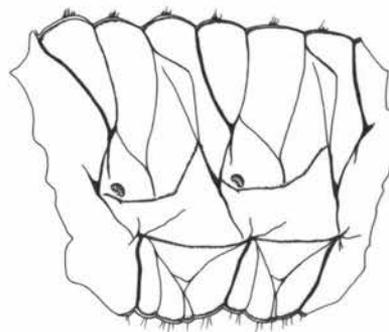
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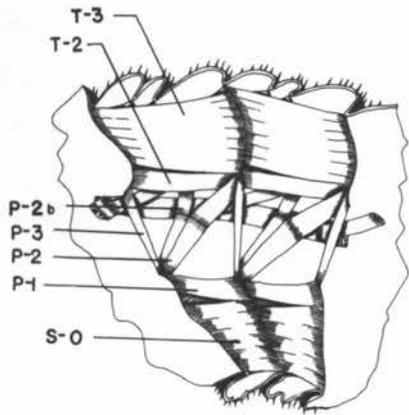
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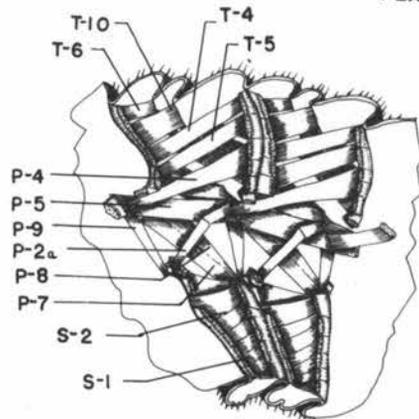
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EXPLANATION OF PLATE V

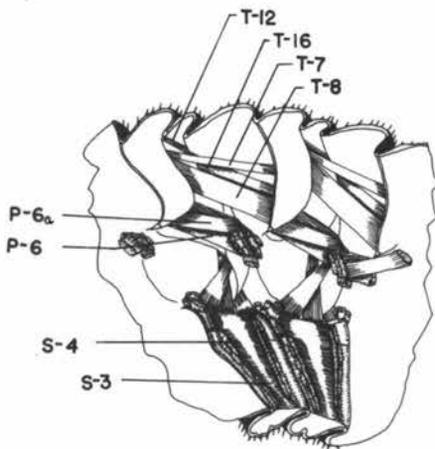
- Fig. 21. First sagittal dissection of the third and fourth abdominal segments of the subfamily Rutelinae.
- Fig. 22. Second sagittal dissection of the third and fourth abdominal segments of the subfamily Rutelinae.
- Fig. 23. Third sagittal dissection of the third and fourth abdominal segments of the subfamily Rutelinae.
- Fig. 24. Fourth sagittal dissection of the third and fourth abdominal segments of the subfamily Rutelinae.
- Fig. 25. The interior integument of the third and fourth abdominal segments of the subfamily Rutelinae.
- Fig. 26. The interior integument of the third and fourth abdominal segments of the subfamily Glaphyrinae.



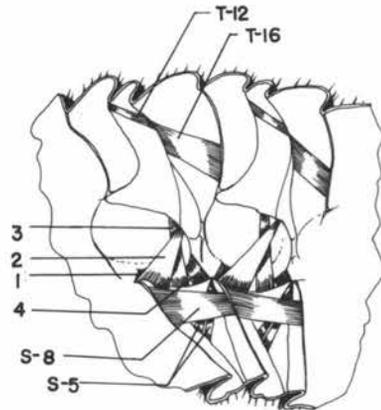
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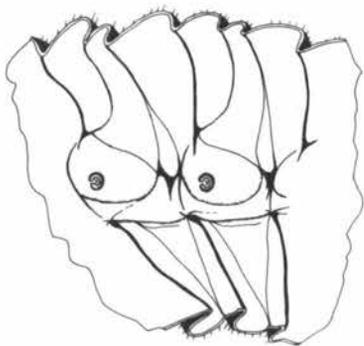
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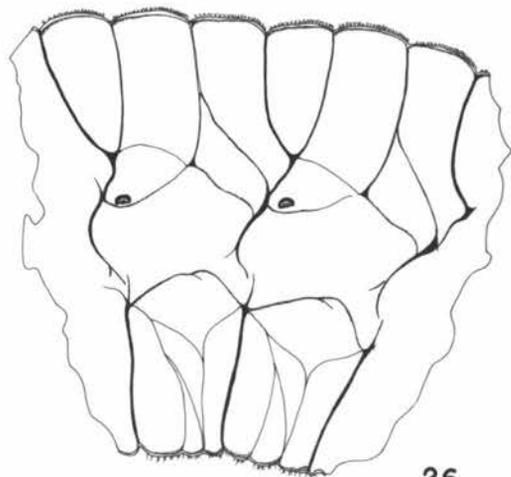
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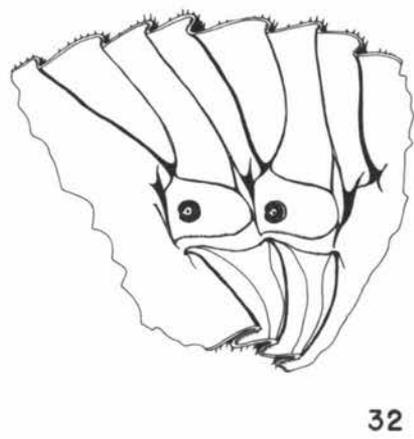
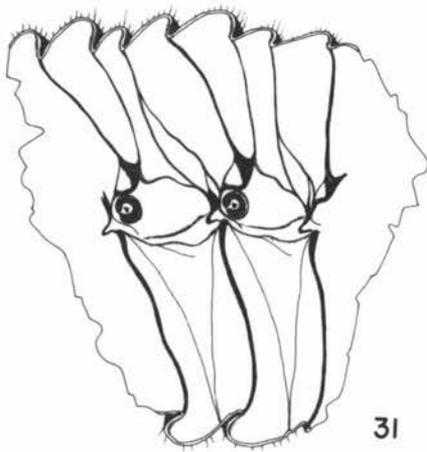
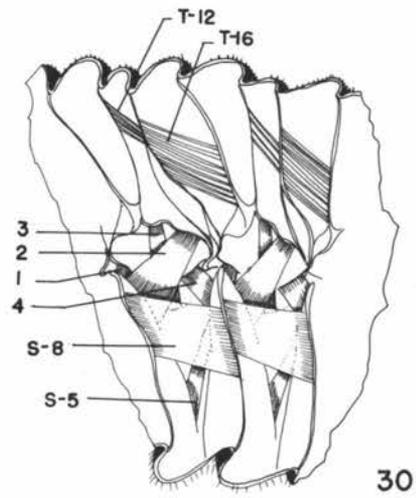
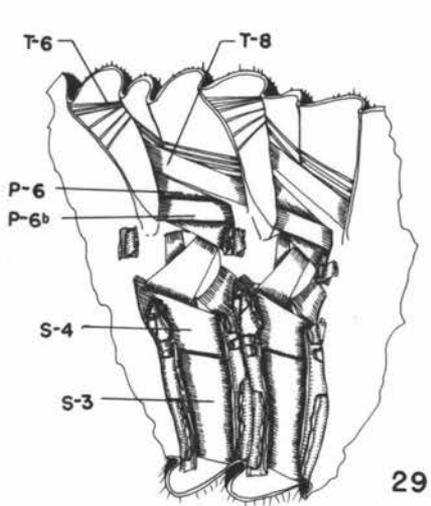
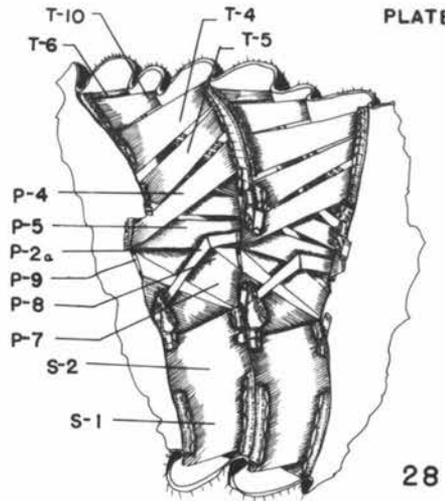
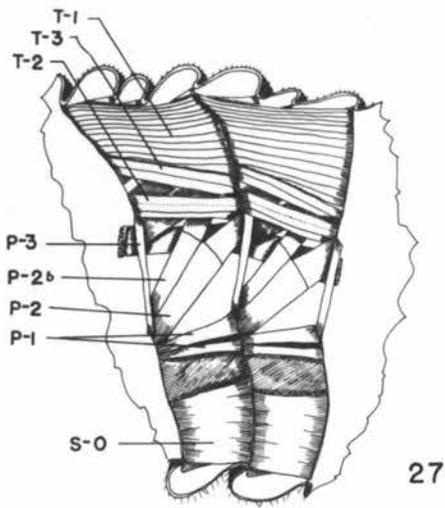
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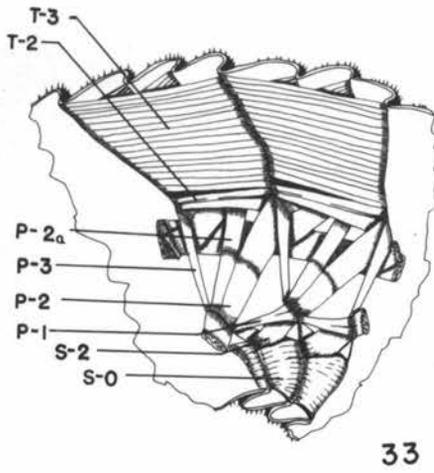
EXPLANATION OF PLATE VI

- Fig. 27. First sagittal dissection of the third and fourth abdominal segments of the subfamily Dynastinae.
- Fig. 28. Second sagittal dissection of the third and fourth abdominal segments of the subfamily Dynastinae.
- Fig. 29. Third sagittal dissection of the third and fourth abdominal segments of the subfamily Dyastinae.
- Fig. 30. Fourth sagittal dissection of the third and fourth abdominal segments of the subfamily Dynastinae.
- Fig. 31. The interior integument of the third and fourth abdominal segments of the subfamily Dynastinae.
- Fig. 32. The interior integument of the third and fourth abdominal segments of the subfamily Cetoniinae.

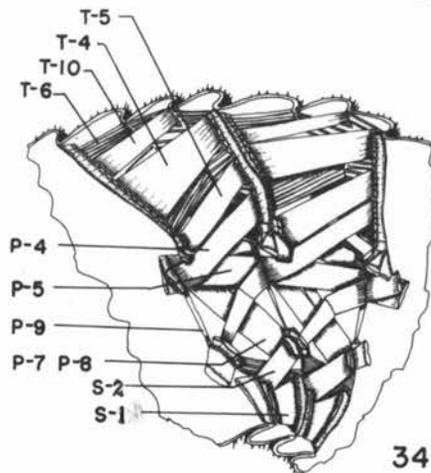


EXPLANATION OF PLATE VII

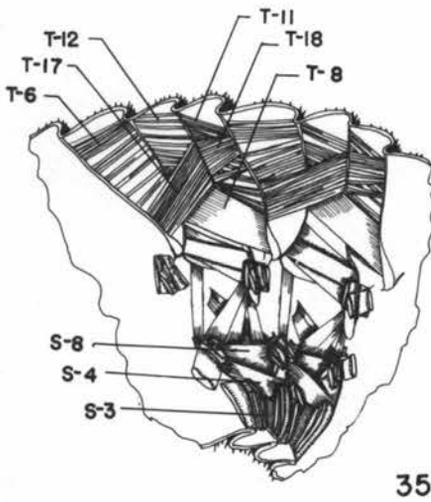
- Fig. 33. First sagittal dissection of the third and fourth abdominal segments of the subfamily Cetoniinae.
- Fig. 34. Second sagittal dissection of the third and fourth abdominal segments of the subfamily Cetoniinae.
- Fig. 35. Third sagittal dissection of the third and fourth abdominal segments of the subfamily Cetoniinae.
- Fig. 36. Fourth sagittal dissection of the third and fourth abdominal segments of the subfamily Cetoniinae.
- Fig. 37. First dissection of sternal longitudinal view of the subfamily Fleocominae.
- Fig. 38. First dissection of sternal longitudinal view of the subfamily Sinodendrinae.



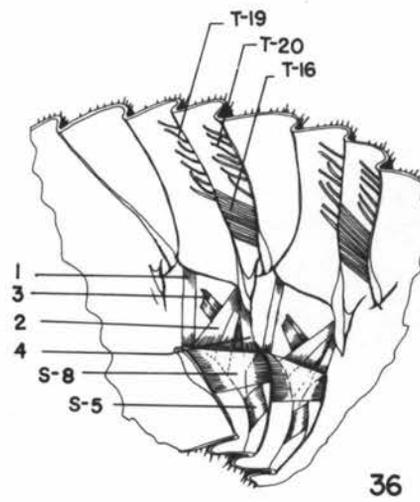
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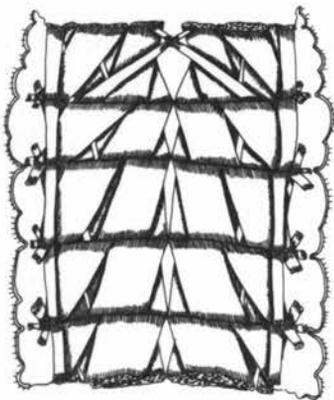
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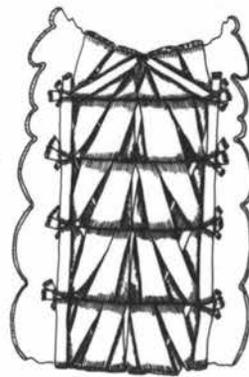
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