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The Comparative Morphology of the Neck and Prothoracic Sclerites of the Order Coleoptera Treated from the Standpoint of Phylogeny

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THE COMPARATIVE MORPHOLOGY OF THE NECK AND PROTHORACIC SCLERITES OF THE ORDER COLEOPTERA TREATED FROM THE STANDPOINT OF PHYLOGENY

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INTRODUCTION

The comparative morphology and phylogeny of the order Coleoptera has been the subject of but few investigations, despite the fact that this is one of the largest orders of insects. Taxonomists have frequently carried on their work with but little regard to comparative morphology, and taxonomic keys frequently group together families of beetles that are entirely unrelated from a morphological standpoint. Studies in comparative morphology seek to arrange the families and series in a phylogenetic system so that the more primitive forms shall precede the more modified forms. Such studies are indispensable to the building of any thorough classification.

Phylogenetic systems were set up by Lameere in 1900 and 1903, Gangelbauer in 1903, Kolbe in 1901 and 1908, Handlirsch in 1906-1908, and Sharp in 1909. Handlirsch's voluminous work was based on fossil insects, while that of Kolbe was based on the theory that parts of the body proper, rather than its appendages, truly show the progressive modifications of the Coleoptera.

Other works on the comparative morphology of Coleoptera include Forbes' paper (1922) on the wing venation, Stickney's monograph (1923) on the head-capsule, Sharp and Muir's paper (1912) on the male genitalia, Tanner's paper (1927) on the female genitalia, Williams' paper (1938) on the mouth parts, and Holway's papers (1935, 1938) on the pretarsus.

The prothoracic sclerites of insects offer some of the most valuable evidence for tracing the evolution and relationships of the larger groups of insects, as well as the insects within a large order. Yet these structures have been studied by very few workers, the work of Crampton (1909, etc.,etc.) on the larger group being outstanding.

The order Coleoptera, which forms a rather aberrant group at the base of the holometabolous stem in evolution, has been strangely neglected. Since the prothoracic sclerites of this order differ somewhat from the typical condition, the interpretation of the parts has been completely misunderstood and homologies have never been established. In order to understand the relationships of the various parts to one another in the Coleoptera, it is necessary to start with more primitive types such as the Orthoptera, Plecoptera, etc., and observe the trends in these forms before attempting to interpret the trends exhibited by the Coleoptera. The present study of the prothoracic sclerites of representatives of most of the Coleopterous families has been made with the purpose of clarifying the interpretation of homologies and adding to the knowledge of the phylogenetic groupings of the families within this order.

The arrangement of the families in Blackwelder's Checklist of the Coleopterous Insects of Mexico, Central America, the West Indies, and South America has been followed. A representative of each family has been chosen for study. In the case of the Cantharidae, Cerambycidae, and Curculionidae, more than one species was selected to show the comparative morphology. Consideration of members of the various sub-families has ever been present and would undoubtedly have made comparisons much more complete, but due to the fact that suitable material was not available, the sub-families have not been included in this study. Several of the families have been omitted because they were either unobtainable or too minute to study with equipment available.

PREPARATION OF MATERIAL

With the exception of a few specimens which were preserved in alcohol and needed no special preparation, all of the specimens available were mounted on pins or paper points. The method of preparation worked out for the present study is outlined as follows: The specimen is dropped into a 10 percent solution of KOH and heated to near the boiling point for about half a minute and then removed and placed in a small amount of water in a watch glass. This heating time, which must necessarily be longer in the preparation of large and heavily sclerotized beetles, softens the body sufficiently to prevent breakage when the prothorax is separated from the rest of the body with the aid of dissecting needles and a binocular microscope. Care must be taken to retain the mesothoracic spiracle and cervical sclerites, if present, with the prothorax. The remaining parts of the body are thoroughly rinsed and placed in a labelled vial of 70 percent ethyl alcohol. The prothorax is then replaced in the KOH which is allowed to boil gently for from one to five minutes, depending on the hardness of the structures. The prothorax is then placed in distilled water for five minutes; then rinsed for two minutes in distilled water to which a few drops of 3 percent acetic acid have been added; and then removed to distilled water. After a five minute immersion in the water the specimen is placed in the properly labelled vial of 70 percent ethyl alcohol. Specimens are studied and dissected while immersed in water.

ILLUSTRATIONS

The illustrations, which form an important part of this study, are intended to serve two purposes. First, they illustrate the detailed prothoracic anatomy of representatives of the Coleopterous families (and precursor types); and second, they illustrate the variations within the order of each of the structures treated. The figures have all been drawn directly and later inked, and no attempt has been made to indicate the magnification attained, as this is probably of no importance to a knowledge of the morphology. All figures except that of Figure 10, which is a lateral view, are drawn from the ventral aspect with the right leg and basal piece removed. A supplementary ventral aspect drawing of the dissected-out left coxa and basal piece is placed beneath the drawing of the prothorax.

The figures in this study have been so arranged that Plate 1 consists of all of the figures utilized in the following section on Homologies. This method of placement makes it simpler to refer to the figures concerned. The remaining figures have been placed in a series starting with the most primitive beetles and ascending to the most highly evolved beetles. (The beetles on Plate 1 are not placed in the series, but their position in the series is indicated by reference in the text). The beetles at the extreme ends of the series are far more easily placed then intermediate forms whose structures have evolved at different rates. The author is fully cognizant of the fact that it is difficult to determine the phylogenetic relationship of a beetle which has evolved its structures at different rates, as well as the fact that the representative of each family studied is not always characteristic of the entire family, and for these reasons any series so arranged can only be tentative in character. However, such a series has been set up in this study with the hope that later studies including more representatives, or even family studies, will aid in the formation of a proper phylogenetic arrangement.

SPECIES STUDIED

Suborder ARCHOSTEMATA

Family		
Cupesidae	Cupes capitatus Fab.	Fig. 79

Suborder ADEPHAGA

Family		
Rhysodidae	Clinidium sculptile Newn.	Fig. 83
Cicindelidae	Omus dejeani Rche.	Fig. 82
Carabidae	Harpalus caliginosus Fab.	Fig. 12
Paussidae	undetermined Paussid	Fig. 85
Haliplidae	Peltodytes shermani Rbts.	Fig. 84
Dytiscidae	Acilius semisulcatus Aube	Fig. 81
Gyrinidae	Dineutes nigrior Rbts.	Fig. 80

Suborder POLYPHAGA
Series Haplogastra
Superfamily *Staphlinoidea*

Family		
Colonidae	Colon magnicolle Mann	Fig. 69
Leiodidae	Leiodes discolor Melsh.	Fig. 60
Scydmaenidae	Connophron fossiger Lec.	Fig. 67
Pselaphidae	Decarthron stigmosum Brend.	Fig. 29
Scaphidiidae	Scaphisoma convexum Say	Fig. 65
Silphidae	Silpha inaequalis Fab.	Fig. 42
Staphylinidae	Staphylinus maculosus Grav.	Fig. 41

Superfamily *Hydrophiloidea*

Family		
Hydrophilidae	Hydrophilus triangularis Say	Fig. 62

Superfamily *Histeroidea*

Family		
Histeridae	Hister obtusatus Harris	Fig. 44

Superfamily *Scarabaeoidea*

Family		
Passalidae	Passalus cornutus Fab.	Fig. 47
Lucanidae	Pseudolucanus capreolus L.	Fig. 46
Scarabaeidae	Phyllophaga fusca Froehlich	Fig. 45

Series Symphiogastra

Superfamily Dascilloidea

Family		
Dascillidae	Dascillus cervinaL.	Fig. 27
Cyphonidae	Cyphon concinnus Lec.	Fig. 26
Ptilodactylidae	Ptilodactyla serricollis Say	Fig. 28

Superfamily Byrrhoidea

Family		
Heteroceridae	Heterocerus near undatus	Fig. 39
Nosodendridae	Nosodendron unicolor Say	Fig. 24
Byrrhidae	Byrrhus cyclophorus Kby.	Fig. 25

Superfamily Dryopoidea

Family		
Elmidae	Stenelmis crenata Say	Fig. 49
Dryopidae	Dryops auriculatus Geoff.	Fig. 22
Psephenidae	Psephenus lecontei Lec.	Fig. 36

Superfamily Elateroidea

Family		
Cebrionidae	Cebrio bicolor Fab.	Fig. 35
Melasidae	Isorhips ruficornis Say	Fig. 37
Plastoceridae	Euthysanius lautus Lec.	Fig. 33
Elateridae	Aeolus dorsalis Say	Fig. 34
Trixagidae	Trixagus chevrolati Bonv.	Fig. 5
Rhipiceridae	Sandalus niger Knoch	Fig. 40
Buprestidae	Chalcophora virginiensis Drury	Fig. 32

Superfamily Cantharoidea

Family		
Lycidae	Eros aurora Hbst.	Fig. 14
Lampyridae	Lucidota corrusca L.	Fig. 13
Phengodidae	Phengodes plumosa Oliv.	Fig. 19
Cantharidae	Cantharis rotundicollis Say	Fig. 4
	Lycopolemius rouyeri Pic.	Fig. 6

Superfamily Cleroidea

Family		
Malachiidae	Malachius aeneus L.	Fig. 18
Dasytidae	Dasytes niger L.	Fig. 20
Cleridae	Enoclerus quadriguttatus Oliv.	Fig. 54
Temnochilidae	Tenebroides marginicollis Chev	Fig. 21
Dermestidae	Dermestes lardarius L.	Fig. 52

Superfamily Bostrychoidea

Family		
Bostrychidae	Xylobiops basillare Say	Fig. 68
Lyctidae	Lyctus linearis Goeze	Fig. 89
Ptinidae	Ptinus fur L.	Fig. 66
Anobiidae	Hadrobregmus carinatus Say	Fig. 31
Sphindidae	Eurysphindus hirtus Lec.	Fig. 30

Superfamily Lymexylonoidea

Family		
Lymexylonidae	Melittoma sp.	Fig. 15

Superfamily Nitiduloidea

Family		
Monotomidae	Monotoma americana Aube	Fig. 90
Nitidulidae	Osmosita colon L.	Fig. 76

Superfamily Cucujoidea

Family		
Cucujidae	Cucujus clavipes Fab.	Fig. 23
Languriidae	Aeropteryx gracilis Newm.	Fig. 78
Cryptophagidae	Antherophagus ochraceus Melsh.	Fig. 55
Phalacridae	Stilbus nitidus Melsh.	Fig. 58
Orthopteridae	Anthobium convexum Fauv.	Fig. 43
Byturidae	Byturus bakeri Bar.	Fig. 71
Anthicidae	Notoxus monodon Lec.	Fig. 87
Lathridiidae	Melanophthalma distinguenda Com.	Fig. 73

Superfamily Coccinelloidea

Family		
Endomychidae	Lychoperdina ferruginea Lec.	Fig. 63
Coccinellidae	Anatis quindecimpunctata Oliv.	Fig. 64
Erotylidae	Megalodacne fasciata Fab.	Fig. 38

Superfamily Colydioidea

Family		
Mycetophagidae	Typhaea fumata L.	Fig. 57
Colydiidae	Bothrideres geminatus Say	Fig. 48

Superfamily Mordelloidea

Family		
Mordellidae	Mordella scutellaris Fab.	Fig. 59

Superfamily Meloidea
Family

Rhipiphoridae	Macrosiagon limbatum Fab.	Fig. 86
Meloidae	Epicauta cinerea Fab.	Fig. 16

Superfamily Tenebrionoidea
Family

Oedemeridae	Nacerda melanura L.	Fig. 53
Cephaloidae	Cephaloon lepturides Newn.	Fig. 51
Pyrochroidae	Neopyrochroa flabellata	Fig. 17
Pythidae	Pytho niger Kby.	Fig. 50
Serroplalpidae	Melandrya striata Say	Fig. 61
Lagriidae	Anthromacra aenea Say	Fig. 88
Nilionidae	Nilio lanatum Germ.	Fig. 74
Monommidae	Hyporrhagus opuntiae Horn	Fig. 11
Alleculidae	Isomira quadristriata Couper	Fig. 77
Tenebrionidae	Tenebrio picipes Hbst.	Fig. 75

Superfamily Phytophagoidea
Family

Cerambycidae	Criocephalus agrestis Kby.	Fig. 7
	Saperda tridentata Oliv.	Fig. 8
	Oberea bimaculata Oliv.	Fig. 9
Chrysomelidae	Calligrapha sp.	Fig. 56
Bruchidae	Bruchus obtectus Say	Fig. 72
Anthribidae	Euparius marmoreus Oliv.	Fig. 94
Brenthidae	Eupsalis minuta Drury	Fig. 91
Scolytidae	Dentroctonus piceaperda Hopk.	Fig. 95
Proterhinidae	Proterhinus maurus Perkins	Fig. 96
Platypodidae	Platypus compositus Say	Fig. 70
Curculionidae	Lixus concavus Say	Fig. 92
	Cryptorhynchus lapathi L.	Fig. 93

Order Orthoptera
Family

Blattidae	Cryptocercus punctulatus	Fig. 1
Mantidae	Stagmomantis carolina	Fig. 2
Locustidae	Shistocerca americana	Fig. 10

Order Plecoptera
Family

	Taeniopteryx nivalis Fitch	Fig. 3

HOMOLOGIES

The order Coleoptera is broken down into two great groups, the POLYPHAGA and the ADEPHAGA (Blackwelder has a third suborder ARCHOSTEMATA made up of the family Cupesidae). That a difference in the prothoracic sclerites of the two groups exists has long been recognized by Coleopterists, but attempts to show their relationships have given no clear understanding of the matter.

In order better to understand the relationships of the various parts to one another in the Coleoptera, it is well to observe first the phylogenetic trends in more primitive forms and then the trends exhibited by the Coleoptera. The use of existing species to illustrate the stages of phylogenetic development is justified since what has been done by nature shows what is possible. Erroneous postulates and assumptions are thus avoided. It is obviously not implied that any primitive living form is actually ancestral to a living derived type. I have simply made use of the primitive conditions exhibited by certain forms which have not evolved as rapidly in regards to these conditions as certain derived types. This method of approach to the subject is commonly accepted by students of morphology.

The work of Crampton (1926) on the neck and prothoracic sclerites throughout the orders of insects demonstrates the origin of the primitive beetles from ancestors related to living Mantids as well as other Orthoptera. His comparison of Orthoptera and Coleoptera shows the tendency for the pronotum to grow down over the pleural region to the base of the coxa, thus covering practically all of the pleural region but leaving visible the precoxal bridge extending to the sternal region, largely composed of the basisternum with which the furcasternum is closely associated. The coxal cavities are open behind (i.e. there is no postcoxal bridge connecting the sternal region with the pleuron) and this is apparently the primitive condition for the Coleoptera.

In the insects shown in Figs. 1, 2, and 3, certain significant structures are apparent. The pronotum (pn) tends to grow ventro-mesad to the precoxal bridges (pc), although in none of these specimens has it become firmly attached to the precoxal bridge (although nearly so in Fig. 3). (In Figs. 1 and 2 the pronotum actually covers more of the pleural region than shown by the figures, the author having retracted the pronotum for visibility of the pleural area.) The pleural area consists of upper and lower pleural regions that are closely associated with each other. Both upper and lower regions are made up of an episternum (eps) and epimeron (em) which join to form the pleural suture (ps) and resultant internal ridge or apodeme. The epimeron in both upper and lower pleural regions is small and tends to become reduced. The pleural suture of the lower pleural region forms a ventral process which is the pleural coxal process or major condyle in the articulation of the coxa (cx). Contiguous or closely associated with the anterior and mesal portion of the lower episternum is the trochantin (tn), the ventral tip of which forms the minor condyle for articulation of the coxa. The anterior edge of the upper episternum is joined to the precoxal bridge which in turn is contiguous with the basisternum (bs) in Figs. 2 and 3, and separate from the basisternum in Fig. 1. The furcasternum as shown by the furcal pits (fp) is small and weakly developed, the internal furcal arms (fa) extending to the pleural apodeme as shown in Fig. 3. The cervical sclerites (cvs) are large, and in the case of Figs. 1 and 2 consist of two pairs, while those in Fig. 3 seem to have become fused to form but one pair.

Thus we find the precursors of beetles presenting us with the following structures which we may use as landmarks in tracing the relationships of structures in the beetles: the pleural area is divided into an upper and lower region, each region consisting of an episternum and an epimeron joining to form the pleural suture and resultant internal ridge or apodeme; and anterior and mesal portion of the episternum of the lower pleural region is contiguous or closely associated with the trochantin, whose tip forms the minor condyle for articulation of the coxa; the pleural suture of the lower pleural region forms the pleural coxal process or major condyle for articulation of the coxa; the anterior edge of the upper episternum is contiguous with the precoxal bridge.

The following trends may also be noted: the pronotum tends to grow ventro-mesad to the base of the coxa and partially covers the pleural area, leaving the precoxal bridge visible; the furcasternum tends towards greater development; the cervical sclerites tend to become reduced in number; the epimeron is small in both upper and lower pleural regions and tends to become reduced.

In the primitive beetle shown in Fig. 4, the pronotum (pn) has indeed grown ventro-medad to join the precoxal bridge (pc). The sternal region consists of the median basisternum (bs) and a small furcasternum (fs). The pleural area is nearly covered by the overlapping pronotum, only the trochantin, part of the episternum, epimeron and pleural suture, and the pleural coxal process being visible. If the dissected out trochantin and contiguous pleural region are compared with the insect shown in Fig. 3, one sees that the basisternum, furcasternum, and precoxal bridge are fundamentally the same in each, although the pronotum has joined the precoxal bridges in Fig. 4. It is only in the pleural area that there appears to be a difference. The lower pleural region of Fig. 3 consists of an episternum (eps) and an epimeron (em) forming a pleural suture and pleural coxal process which articulates with the coxa (cx). Joined to the anterior edge of the episternum is the trochantin (tn), the ventral tip of which forms the minor condyle for articulation of the coxa. In Fig. 4 we observe a similar condition with an episternum and an epimeron joined to form a pleural suture, a similar ventral coxal process, and the trochantin joined to the anterior edge of the episternum. In Fig. 4, however, we find the anterior and dorsal portion of the pleural suture has invaginated to form a very deep internal ridge or apodeme. The combined structure consisting of the episternum, epimeron, pleural suture, and trochantin and bearing the two condyles is called the eutrochantin by Crampton. In Fig.

4, however, one finds no such structure as the upper pleural region found in Fig. 3, where the episternum and epimeron are joined at the pleural suture and the anterior edge of the episternum is joined to the precoxal bridge.

It thus becomes necessary to establish the proof of what has happened to the upper pleural region or to postulate as to its possible position. The alternatives appear to be that the upper pleural region has joined or fused with either the precoxal bridge, the overlapping pronotum, or the eutrochantin, or has disappeared completely and left no trace.

Again the use of living cases showing a primitive condition explains the position of the upper pleural region very logically. If one compares the beetle shown in Fig. 5 with the Plecopteron shown in Fig. 3, it should be apparent that the upper pleural region in beetles is joined to the precoxal bridge. In Fig. 5 the lower pleural region is made up of a lower episternum and epimeron with a pleural suture forming the pleural coxal process and a long apodeme with a broadly flared dorsal end. The trochantin is contiguous with the anterior and mesal portion of the episternum. This combined structure, or eutrochantin (etn) is similar to the structure of the lower pleural region and trochantin of Fig. 3. In Fig. 3 the upper pleural region is formed of an episternum (eps) and an epimeron (em) separated by the pleural suture (ps). The anterior edge of the episternum is contiguous with the precoxal bridge (pc), which in turn is joined to the basisternum (bs). In Fig. 5 the so-called precoxal bridge extends laterad and forms a broad process that extends caudad at the lateral margin. Near the posterior margin of this process is a well defined suture (ps) with a deep invagination. Comparing Fig. 5 with Fig. 3, one sees that the precoxal bridge in each case is the same. Contiguous posteriorly with the lateral margin of the precoxal bridge in each case is a medium sized area whose posterior margin is separated from the next area by a suture. This suture has been shown to be the upper pleural suture in Fig. 3. The origin of the parts in Fig. 5 seems perfectly clear. The upper pleural region of the Coleopteron has joined the precoxal bridge in what may be called the sterno-pleural region. It should also be noted that the suture in Fig. 5 is closely associated with the eutrochantin which lies entad of the suture. A similar close association is present between the upper and lower pleural regions in Fig. 3. Similar sutures have also been observed by the author in properly prepared specimens of the family Cebrionidae, although the sutures are very weak. In Fig. 4 the posterior edge of the pronotum-abutting precoxal bridge forms a short pointed arm that is attached to the eutrochantin. This condition, wherein the lateral margin of the precoxal bridge extends caudad as a slender arm which is closely associated with the eutrochantin, is apparent in many families of beetles, although the actual suture is not visible. In the case of most beetles the pleural suture of the sterno-pleural region is not visible and hence the upper pleural region is either rudimentary or completely fused with the precoxal bridge, and for this reason it is probably preferable to call the structure cephalad of the coxal cavity a precoxal bridge. Whatever the present condition of the precoxal bridge, it is apparent from morphological reasoning that the upper pleural region is joined to the precoxal bridge.

The author has studied some eighty families of Polyphagous beetles and in all of these families the above interpretations present a logical and morphological explanation of the prothoracic sclerites.

In the light of the discussion based on the tracing of certain landmarks, the interpretation of the prothoracic sclerites of the Polyphaga seems clear. The lower pleural region has joined the trochantin to form a eutrochantin with two articulating condyles and a pleural suture with resultant apodeme. The upper pleural region is joined to the precoxal bridge, or having done so, has become rudimentary or completely fused with the precoxal bridge. The overlapping pronotum, consequently, is made up of the pronotum alone.

Ferris (1935) has arrived at this interpretation of the eutrochantin as well as the conclusion that the pronotum is made up of pronotum alone. Since Ferris evidently does not recognize the presence of an upper pleural region, his interpretation seems to have been based on rather thin premises, although it is evident now that this is the correct interpretation.

The Adephagous beetles have as a morphological characteristic a more or less longitudinal suture (d, Fig. 12) which lies on the ventral side of the inflexed pronotum. In the case of a more cylindrical prothorax the suture may take on a curved appearance. Interpretations of the prothoracic sclerites of the Adephaga have resolved around this suture. The most commonly accepted interpretation has been that this suture is the noto-pleural suture demarking the ventral limits of the inflexed pronotum and the lateral margin of the fused pleural region or pleuron (p). This interpretation, although receiving almost universal acceptance, has not been arrived at by morphological methods.

If one first observes the eutrochantin (etn) in Fig. 4, one notes that the major and minor condyles are widely separated and the apodeme is of only moderate size with no particular modifications. One would expect the eutrochantin being a primitive type to have been so derived from its precursors. A comparison of the eutrochantin in Fig. 5 with that of Fig. 4 reveals that the major and minor condyles are nearer together and that the apodeme has invaginated to form a flaring horn-shaped structure at the dorsal end. In both Fig. 4 and Fig. 5 the trochantin is long and pointed. If one compares the eutrochantin of the Cerambycid shown in Fig. 7 with the eutrochantin shown in Fig. 5 one sees that in both cases the coxal condyles are present, although the tip of the trochantin in Fig. 7 has become noticeably broadened. A comparison of Fig. 8 with Fig. 7 shows a further development of the eutrochantin. In Fig. 8 the trochantinal tip has broadened anteriorly and the apodeme has shortened. In Fig. 9 the anteriorly broadened tip of the trochantin remains broad and the mesal edge tends to parallel the pleural suture. The suture between the episternum and epimeron has become weak or obliterated and the pleural coxal process has become a blunt condyle. The apodeme has become much reduced. A comparison of the coxae in the Cerambycids shown reveals a similar change, the coxa tending to become shorter and more globular with the reduction of the eutrochantin.

If we observe the Adephagous beetle shown in Fig. 12, we see that the structure at the base of the coxa is composed of two closely apposed articulating points. A comparison of this structure with those shown in Figs. 7, 8, and 9 indicates that the mesal articulating point is homologous with the trochantinal tip or minor condyle. Similarly, a comparison of these same figures shows the relative position of the lateral or basal articulating point in Fig. 12 to be the same as that developed in Fig. 9. In both Fig. 9 and Fig. 12 the pleural suture is much reduced and the pleural coxal process or major condyle has become very blunt and rounded. In Fig. 12, however, the apodeme is not present. The coxa in Fig. 12 has shortened even more and is nearly globular.

Observing a series made up of Figs. 7, 8, and 9 one sees that a line development is shown as the eutrochantin becomes reduced in size. The trochantinal tip broadens noticeably anteriorly; the apodeme tends to shorten and become much reduced; the minor and major condyles tend to become more closely apposed. We also observe that a simultaneous series made up of the coxae sets up another line of development in which the coxa tends to shorten and become more globular. Adding Fig. 12 to the series, one sees that the eutrochantin has developed even further, the apodeme having become totally absent or completely reduced. The minor and major coxal condyles for articulation of the coxa remain in the approximate position of those in Fig. 9. The coxa in Fig. 12 has become almost globular. Thus the structures in Fig. 12 remain the same or continue the trends shown by the Cerambycids.

If one observes a series of eutrochantins such as that above, as well as the simultaneous coxal series, it is evident that the Adephagous structure referred to as the eutrochantin by the author is in fact homologous with the eutrochantin found in the Polyphaga. The reduction of this structure in the Adephaga has been quite great, although two landmarks, the two articulating condyles, still persist. In certain Adephagous beetles, such as the Cicindelid _Omus_ _dejeani_ Rche., the eutrochantin has become further reduced by the reduction of the epimeron, placing the major coxal condyle at the posterior tip of the lateral margin. In many cases of the Adephaga a third condyle (ac, Fig. 12) is formed by a secondary growth of the sclerite (p) just laterad of the coxal cavity. Since it is known that one or more additional structures or condyles may develop for the articulation of the coxa, and may even become the major functional condyle, there seems to be no need to interpret this sort of secondary condyle as homologous with the major coxal condyle shown in Fig. 4, or the Cerambycids. To do so is to fail to take cognizance of the trends shown by a series of figures and to utterly disregard the presence of two articulating condyles on the eutrochantin. There is no reason to believe that the major condyle, homologous to the major condyle in Fig. 4, or even Fig. 3, has moved to another structure.

As was pointed out earlier in the discussion of trends based on Figs. 1, 2, and 3, and also in the work of Crampton, the pronotum tends to grow down over the pleural area to the precoxal bridge, or as has been shown in some cases, to the sterno-pleural region. We have seen that this takes place in the primitive beetle shown in Fig. 4, where the pronotum has grown down to meet the precoxal bridge but has not formed a postcoxal bridge. Since the tendency of the pronotum is to grow ventro-mesad, it is logical to expect the growth to continue posterior to the coxal cavity.

A comparison of the Cerambycid shown in Fig. 7 with the Cantharid shown in Fig. 4, shows that a pointed projection (px) of the inflexed pronotum has developed just posterior to the coxal cavity (cc), and a narrow arm of the furcasternum has joined a secondary growth of the postcoxal lobe (px). A comparison of the inflexed pronotum in Figs. 8 and 9 with that of Fig. 7 indicates a further ventro-mesad projection of the postcoxal lobes, the postcoxal lobes reaching to the prosternal lobe (psl). It is interesting to note that this development of the inflexed pronotum correlates well with the progressive development of the coxa and eutrochantin shown above. If one compares Fig. 12 with Fig. 9, it will be noted that a similar postcoxal projection of the lateral plate (p), although the projection does not extend as far mesally as does that in Fig. 9. The basisternum (bs) and furcasternum (fs) have developed about equally, although the Cerambycid prosternal lobe (psl) is long while that of this Adephaga is somewhat short and broad. The precoxal bridges (pc) of both are broad and joined to the inflexed pronotum in Fig. 9 and to the oblique anterior and mesal wall of the lateral plate (p) in Fig. 12. In each case the lateral edge of the precoxal bridge is extended posteriorly to form a pointed projection that may be the rudimentary upper pleural region mentioned above. In Fig. 12 the posterior portion of the lateral plate is marked by an indication of a suture at line (e).

We are thus reduced to the figures of two specimens, Fig. 9 and Fig. 12, that are very similar, although they have been interpreted very differently by Coleopterists. The presence of a longitudinal suture in Fig. 12 has made it appear incongruous to give the two types any relationship. It has been simpler to call the lateral plate (p) of the Adephagous beetle a pleural area or pleuron, disregarding all morphological tendencies and landmarks as well as the fact that the suture might be secondary.

The fact that the longitudinal suture (d) in

Adephaga is well developed has led to the conclusion that it must be a primary suture and could not be a secondarily formed suture. However, if we observe the inflexed pronotum of the Cantharid shown in Fig. 6, we see that it is very closely related to the Cantharid shown in Fig. 4. The pronotum of Fig. 6 is slightly shorter and broader than that shown in Fig. 4, and the inflexed pronotum is consequently broader. In Fig. 6, however, a very pronounced transverse suture (a) extending from the coxal cavity to the lateral margin of the prothorax divides the inflexed pronotum into nearly equal anterior and posterior areas. Similar sutures, as well as shorter less developed sutures and sutures extending more obliquely from the coxal cavity, have been observed in other Cantharids. They are also to be found in the Anthribidae and Rhipiphoridae. Without the benefit of morphological study, one might conclude that this inflexed area is either the pronotum fused with the pleural region or the pleural region alone. To do so would be to interpret the suture as the pleural suture and the lateral plates as the episternum and epimeron, either alone or fused with the pronotum. It has been shown in the Polyphaga that this is not true, and that the inflexed area is made up of the pronotum alone. Thus the suture, although well developed and forming an internal ridge, must be purely secondary in formation. If we observe the pronotum of the common Orthopteron, Shistocerca americana, shown in Fig. 10 from the lateral aspect, we note three well developed sutures (s) which stretch ventrad from the median carina (c) and a smaller suture that is situated near the anterior margin of the down-flexed pronotum. In Orthoptera these sutures are referred to as sulci (s) and are generally believed to be secondarily developed. The sulci, like the suture shown in Fig. 6, were probably formed by the infolding of the pronotal wall which then pressed together to form the sutures and internal ridges for greater rigidity.

If we observe the inflexed pronotum of Fig. 5, we see an oblique groove (b) extending latero-caudad from the coxal cavity to the lateral carina (c). The fact that this groove is used for receiving the antenna while at rest is evidence of its secondary nature, and it can be seen that this may be one way in which a developing insect has formed a secondary suture in this region of the body. Although this groove is rather broad, it can be seen that, if the flat surfaces of the inflexed pronotum were placed together, the resulting suture would resemble that of Fig. 6, although somewhat differently situated. Likewise, if we observe Fig. 11, we see that the basisternum (bs), precoxal bridges (pc) with a posterior process or extension at the lateral margin, and postcoxal lobes (px) are quite similar to the same structures in Fig. 12. Line (x) in Fig. 11 is oblique as is line (y) of Fig. 12. In Fig. 11 we also observe a longitudinal groove (g) formed by the infolding of the inflexed pronotum. It can be seen that a growing together of the walls of this groove, with consequent bringing together of the closely apposed flat pronotal surfaces, would form a secondary suture. Since the longitudinal suture (d) in Fig. 12 is situated in the same relative position as the groove (g) in Fig. 11, it is entirely possible and probable that this suture in Fig. 12 was derived in this manner from an ancestor closely related to the Monommid in Fig. 11. It should be noted that the eutrochantin, coxa, and furcasternum in Fig. 11 have not evolved as rapidly as similar structures in Fig. 12, nor indeed as rapidly as its own pronotum, and since this type may be called a precursor to the Adephaga, it is, as might be expected, not as highly modified.

The suture on the flexed pronotum of Fig. 6 has been shown to have been secondarily formed, since it is homologous with no other true suture or landmark, and no one would doubt the secondary formation of the sutures or sulci shown in Fig. 10. The fact that these secondary sutures do occur in the insect prothorax in Figs. 6 and 10 shows that it is entirely possible for the longitudinal suture (d) in Fig. 12 to have been secondarily formed. Comparisons of the grooves in Figs. 5 and 11 with the sutures in Figs. 6 and 12 indicate that it is very probable that the longitudinal suture in Fig. 12 was formed secondarily. Thus the suture would secondarily cut off the pronotum, the cut off ventral portion following the trends of development already observed, viz., the ventro-mesad growth of the inflexed pronotum to meet the precoxal bridges and to project behind the coxal cavity to form postcoxal lobes.

As was shown earlier, the cervical sclerites tend to become reduced in derived types. In Figs. 7, 8, and 9 one sees that the cervical sclerites have been totally reduced, and no indication of their presence can be found. In Fig. 12 one sees that the cervical sclerites are also lacking. The condition of the cervical sclerites, along with the reduction of the eutrochantin and development of the furcasternum, indicates that the Cerambycids and

Adephaga are derived types having evolved to a considerable degree from the primitive type represented by Fig. 4.

Since the Adephagous beetles are definitely derived types, as their continual development of trends indicates, it is logical to expect that other structures have evolved along similar lines, although not necessarily at the same rate. The assumption that the longitudinal suture (d) on the ventral part of the Adephagous prothorax is a suture dividing the pleural area from the pronotum can be shown to be in direct contrast to all morphological trends.

It has been shown that the eutrochantin of the Adephaga, as illustrated by Fig. 12, is homologous with the eutrochantin shown in Fig. 4, or the lower pleural region plus trochantin in Fig. 3. Therefore, it is only the upper pleural region with which we must be concerned. From Figs. 1, 2, and 3, and in the work of Crampton it has been pointed out that the phylogenetic trend for the pronotum is to grow ventro-mesad to the precoxal bridge (or sternopleural region if present as such) and partly cover the pleural area. In Figs. 4, 5, 6, 7, 8, 9, and 11 we see that this trend has been followed, the pronotum meeting the precoxal bridge at line (x). In Fig. 12 there is complete agreement among workers that the pronotum does meet the the precoxal bridge at suture (x). However, the greater part of the precoxal bridge is met by the lateral plate (p) at suture (y). It has been observed that in Figs. 1, 2, and 3 the episternum (eps) of the upper pleural region is contiguous with the precoxal bridge (pc), and there is no indication of a suture between these two areas. In Fig. 5 one again sees that the upper episternum is contiguous with the precoxal bridge and there is no sutural division between the areas. If one assumes that the lateral plate consists of the episternum and epimeron, the episternum must join the precoxal bridge at suture (y). One could then assume the weak suture (e) to be the pleural suture dividing the episternum from the epimeron. It should be noted that in more modified Adephaga the postcoxal lobe or bridge (epimeron in this interpretation) has become more extensive and extends to the prosternal lobe or almost to the median line. To espouse the above interpretation of the lateral plate (p) as the pleural area and line (e) as the pleural suture one must base the idea on assumptions that directly oppose the trends exhibited by precursors of the Adephagous type. One must first assume that the pronotum overlaps and joins only a very small portion of the precoxal bridge. This is in direct contrast to the trend of the pronotum to overlap or meet the entire lateral portion of the precoxal bridge or sterno-pleural region. It must then be assumed that a suture is formed at the junction of the episternum and the precoxal bridge, although in all precursors this suture has never been indicated. One must further assume that the epimeron is a structure that may develop and enlarge, again a condition that is refuted by trends which tend to reduce the epimeron. If morphological reasoning based on trends and landmarks has any validity, as the author sincerely believes it has, the interpretation based on the assumptions above cannot be justified, and the suture (y) cannot be the division of episternum and precoxal bridge.

It might be proposed that the episternum is joined contiguously with the precoxal bridge mesad of the suture (y). With this proposal the author is in partial agreement, since it has been shown in the Polyphaga that this is the case. But an assumption that the episternum has joined the precoxal bridge and that suture (y) is the pleural suture is contradicted by the fact the entire lateral plate would then be the epimeron. To interpret suture (y) as the pleural suture is to disregard the trend wherein the epimeron is small and the tendency is towards reduction. Suture (y) cannot, therefore, be the pleural suture.

It should be noted that a suture extending from the anterior edge of the pronotum to the coxal cavity has been present in all beetles examined (except when obliterated by the fusion of pronotum and precoxal bridge), thus precluding the possibility that suture (y) might be secondarily formed. Since morphological methods have shown that suture (y) cannot be a suture separating the episternum from the precoxal bridge, and likewise, cannot be the pleural suture, there remains but one conclusion, viz., that suture (y) plus the short suture (x) in Fig. 12 is homologous with suture (x) in Fig. 11, and consequently the lateral plate can only be the inflexed pronotum, since suture (x) always separates the precoxal bridge from the inflexed pronotum. Likewise, the probability of the longitudinal suture (d) having been secondarily formed seems to be the actual case.

It must be concluded, therefore, that in the Adephaga the pronotum extends to the precoxal bridge and coxal cavity and is secondarily cut off by the longitudinal suture. Since it should be evident that the Adephaga are derived from ancestors somewhere along the Polyphagous development, the upper pleural region has apparently joined and fused with the precoxal bridge in the same manner as in the Polyphaga, no alternative evidence having been found in these derived types. The postcoxal lobes develop behind the coxal cavity in the same manner as shown in the Polyphaga. The structure at the base of the coxa is a eutrochantin consisting of trochantin and lower pleural region whose pleural suture and apodeme are reduced. The major functional coxal condyle may be found on the inflexed pronotum, but this is not homologous to the major coxal condyle found in less derived types.

This interpretation of the prothoracic sclerites of the Adephaga is in almost complete disagreement with the commonly accepted interpretation that the lateral plate (p) is the pleuron. Ferris (1935) concludes that this is the correct interpretation. As was pointed out above, Ferris does not recognize, or at least has not mentioned, the presence of an upper pleural region, although this structure is an important factor in the tracing of other structures. If one follows the trends and observes that the trochantin and lower pleural region are united, one will not be misled by the third condyle (ac Fig. 12) on the lateral plate. This condyle, although of major functional importance to the coxa, is not homologous with the major coxal condyle in Polyphagous beetles. However radical this interpretation may sound in comparison to the commonly accepted interpretation, this interpretation of the longitudinal suture as a secondary suture is very apparent from comparative morphology.

In view of the above discussion, we may summarize the findings on the prothoracic sclerites most briefly by stating that the Adephagous beetles have followed the same lines of development as those shown by the Polyphagous beetles. The Adephaga, however, have advanced further in certain directions.

The Polyphaga are characterized by the presence of a eutrochantin consisting of the trochantin and lower pleural region. The lower pleural suture forms an apodeme as well as the pleural coxal process or major condyle for articulation of the coxa. The upper pleural region is joined to the precoxal bridge, although it apparently has become rudimentary or completely fused with the precoxal bridge. The overlapping pronotum is made up of pronotum alone.

The Adephaga are characterized by a secondary longitudinal suture that cuts off the inflexed pronotum. The eutrochantin is small and reduced, the trochantinal tip is broad, and the apodeme is lacking. The major condyle is on this structure, although the major functional condyle may be on the inflexed pronotum. The upper pleural region has apparently joined the precoxal bridge in the same manner as shown by the Polyphaga. The overlapping pronotum is made up of pronotum alone.

GENERAL MORPHOLOGY

As a basis for discussion of the comparative morphology of the prothoracic sclerites of the Coleoptera, it is essential to choose a form exhibiting primitive characters. Since Crampton has indicated that Coleoptera were derived from ancestors related to Mantids as well as other Orthoptera in the common Protorthopteron-Protoblattoid stem, and Lampyroidea (Cantharoidea of Blackwelder) are the most primitive, a Lamyprid or Cantharid beetle should be a suitable form. Although specimens from either family would serve the purpose well, the author has selected the Lampyrid Lucidota corrusca Linn. (Fig. 13) as a basis for the discussion of morphology.

The pronotum (pn) consists of a single sclerite which is nearly semi-circular in outline. The lateral edges of the pronotum are folded ventrally to form thin flat discs, while the mesal dorsal region covering the head is convex. Ventrally the pronotum is inflexed to form two nearly parallel walls which serve to connect the pronotum with the prosternum.

The sternum of the prothorax includes a basisternum (bs), furcasternum and two precoxal bridges (pc).

The sternum is a narrow band which connects with the overlapping pronotum at line x (x). Mesally the basisternum (bs) is produced caudally a short distance to form the prosternal lobe which appears as an elevated portion of the posteriorly projecting arm of the basisternum. The precoxal bridges (pc) extend to the pronotal wall and include the greater part of the area cephalad of the coxal cavities. The furcasternum appears as a flat area at the base of the prosternal lobe and bears the internal furcal arms (fa) which project caudad and dorsad at an angle of 45 degrees from the basisternum. These projections serve as muscle attachments and help in the formation of the coxal cavities.

The precoxal bridges abut against the pronotum at line x. The posterior edge of the abutting precoxal bridges forms a short slender arm which is attached to the lower pleural region of the prothorax. This slender arm is possibly rudimentary evidence of the upper pleural region.

Imbedded in the cervix just cephalad of the sternum are two pairs of cervical sclerites (cvs). The anterior cervical sclerite of each pair is hinged posteriorly to the anterior margin of the smaller posterior cervical sclerite. The posterior margin of the posterior cervical sclerites is closely associated with the anterior margin of the sternum.

The pleural region of Lucidota corrusca is situated within the prothoracic cavity and is partially hidden from view. Thus it is called a hidden pleural region. In the case of this species, the episternum (eps) forms an arch in cross-section and is separated from the epimeron (em) by a strong pleural suture (ps). The epimeron folds over the episternum ventrally, the pleural suture extending dorsad in the form of an apodeme. Ventrally the pleural suture projects into the coxal cavity and forms the major coxal condyle in the articulation of the coxa. Contiguous with the anterior and mesal portion of the episternum is a long pointed extension called the trochantin (tn). The ventral tip of the trochantin acts as the minor condyle in the articulation of the coxa. This combined type of lower pleural region-trochantin is called the eutrochantin (etn) by Crampton. The coxa (cx) is cylindrical in shape and cut off diagonally at the base.

The mesothoracic spiracles (sp) lie imbedded in the membrane caudad of the coxal cavities.

In the following discussion of the comparative morphology of the prothoracic sclerites, the combined lower pleural region-trochantin is referred to as the eutrochantin. Since the mesothoracic spiracles are present in all of the species studied, and since they do not appear to present any significant changes of a comparative nature, they are included in the figures but are not mentioned in the discussion.

COMPARATIVE MORPHOLOGY

Suborder ARCHOSTEMATA

Family: Cupesidae

The pronotum (pn) of the Cupesid (Fig. 79) is rounded dorsally and flexed ventro-mesad at the lateral margins to meet the sternal region. The inflexed portion of the pronotum is secondarily cut off by the suture d (d) which extends latero-caudally from the suture x (x) and then caudad to the caudal and ventral margin of the pronotum. This cut-off protion (p) has a short lateral infolding or groove which lies within the body wall at line (d) and is best shown in the lower drawing of Fig. 79. This gives the anterior portion of line d the effect of a broad suture or groove. The precoxal bridges (pc) are broad and the posterior two-thirds of the entire sternal plate is somewhat elevated. Mesally the broad basisternum (bs) is produced caudally to form a long, broad prosternal lobe (psl). The furcasternum is almost completely concealed by the prosternal lobe. Small pointed areas bearing the furcal pits (fp) extend dorsad and outward from the prosternal lobe, and a secondary growth extends dorsad and slightly outward from the prosternal lobe and entad of the precoxal bridges to which it is joined. The furcal arms are very short. The eutrochantin (etn) is well sclerotized and consists of a broad trochantin which bears the minor condyle and the lower pleural region bearing the major condyle, although the epimeron appears to be completely reduced. The basal end of the eutrochantin is closely associated with the cut-off portion of the inflexed pronotum. There is no evidence of an apodeme. The coxa (cx) is very iregular in shape and articulates basally with a small process on the inflexed pronotum as well as with the two condyles of the eutrochantin. The cervical sclerites are lacking in this specimen.

A comparison of the prothoracic sclerites of this specimen with those of the generalized Lampyrid (Fig. 13) shows it to be a greatly evolved type. The presence of the secondarily formed longitudinal suture d, the reduced eutrochantin, and reduced cervical sclerites would seem to place this family with the suborder ADEPHAGA, although the furcasternum is not as highly developed in this family as it is in the Adephaga.

Suborder ADEPHAGA

Families studied: Rhysodidae; Cicindelidae; Carabidae; Paussidae; Haliplidae; Dytiscidae; Gyrinidae.

The prothorax in this suborder may take on a number of appearances, from the very broad and short outline of the Haliplid (Fig. 84), Dytiscid (Fig. 81), and Gyrinid (Fig. 80) to the rather long and narrow outline of the Rhysodid (Fig. 83). The pronotum (pn) may be rounded dorsally and laterally, giving the prothorax a cylindrical appearance, or may be flattened dorsally with sharply inflexed margins giving rise to a lateral carina (c) as in the Carabid (Fig. 12), Dytiscid, and Gyrinid. The pronotum is inflexed ventro-mesad in these representatives to join the precoxal bridges (pc) anteriorly and forms postcoxal lobes (px) or bridges just caudad of the coxal cavities. These postcoxal lobes (px) may be short as in the Dytiscid and Gyrinid or may extend to the prosternal lobe (psl) as in the Cicindelid (Fig. 82) and Rhysodid, or the two postcoxal lobes may even fuse mesally as in the Paussid (Fig. 85). In all cases the postcoxal lobes join the posterior outward extension of the furcasternum (fs). The most obvious condition present in this suborder, when compared with the generalized type, is the presence of the secondarily formed longitudinal suture (d) that cuts off the inflexed pronotum to form the plate (p). There may be indications of other sutures in the cut off portion of the inflexed pronotum such as the secondarily formed suture (e) in the Carabid and Cicindelid.

The precoxal bridges (pc) are slender in the Dytiscid and Gyrinid, and unlike those of the generalized Lampyrid, they are broader and shorter in the Rhysodid. Likewise the basisternum (bs) and its mesal posterior projection or prosternal lobe (psl) is considerably developed from the basisternum and prosternal lobe of the Lampyrid. The prosternal lobe (psl) may be long and narrow as in the Paussid, or may be of variable size up to the very broad and long prosternal lobe shown in the

Haliplid. The furcasternum (fs) also shows considerable development from the type exhibited by the generalized Lampyrid. In the Haliplid and Rhysodid the furcasternum is hidden from view by the prosternal lobe, while in the Carabid the furcasternum extends dorsad and outward from the prosternal lobe, being joined to the posterior edge of the precoxal bridges. The furcasternum in the Gyrinid forms a very extensive coxal pocket. In general, all of these forms have the furcasternum secondarily developed and fused anteriorly with the posterior edge of the precoxal bridges and posteriorly meeting the postcoxal lobes. The internal projections or furcal arms originate with the furcal pits (fp), which are more distantly apposed than those of the Lampyrid. The furcal arms (fa) may be long and slender as in the Gyrinid, or short and broad with secondary lateral projections as in the Dytiscid. The cervical sclerites are lacking in this group.

The eutrochantin (etn) in this group differs greatly from that exhibited by the Lampyrid beetle, although it has been shown that this type of eutrochantin (exhibited by the Adephaga) is homologous with the eutrochantin of the Lampyrid. Although indications of the pleural suture are generally present and the two articulating condyles are visible, the eutrochantin in this group must be considered as greatly modified when compared to the Lampyrid eutrochantin. In this group the epimeron is entirely or almost completely reduced, and the apodeme is completely lacking. The major and minor coxal condyles for the articulation of the coxa are present on this structure, although the major functional condyle (ac, Fig. 12) for articulation of the coxa appears to be a secondary process on the internal wall of the inflexed pronotum. The coxa (cx) in this group is well rounded and nearly globular in shape.

Despite the fact that there is a great diversity in the inflexed pronotum and sternal region, the fact that each representative has the secondarily formed longitudinal suture (d) present seems sufficient evidence that the members of this group are of common origin. The advanced development of the inflexed pronotum, cervical sclerites, and eutrochantin indicates that this group is rather highly developed and of much more recent origin than the generalized Lampyrid. As mentioned above, the Cupesid should probably be included in this group.

Suborder POLYPHAGA

The greater number of families of beetles occurs in this suborder and the variation from the most primitive to the most highly developed is very great. Undoubtedly, the most characteristic prothoracic difference between this suborder and that of the Adephaga (and Archostemata) is the absence of the secondarily formed longitudinal suture throughout the Polyphaga, although small secondary sutures are present and even deep infoldings of the inflexed pronotum are found.

Series HAPLOGASTRA

Superfamily Staphylinoidea

Families studied: Colonidae; Leiodidae; Scydmaenidae; Pselaphidae; Scaphidiidae; Silphidae; Staphylinidae.

When the members of this superfamily are compared with the generalized Lampyrid, it can be seen that all of the families represented show postcoxal lobes as well as a highly developed furcasternum. Comparison of other structures shows a greater diversity of change from the generalized type and these changes are not characteristic of the entire group.

The prothorax in this superfamily shows a variety of shapes and sizes. The pronotum (pn) may be rounded dorsally and laterally as shown by the Scydmaenid (Fig. 67) and Pselaphid (Fig. 29), or rounded dorsally and inflexed somewhat to form a lateral carina (c) as in the Colonid (Fig. 69), or even rounded dorsally and inflexed sharply to form thin, flat lateral discs as in the Silphid (Fig. 42). As was pointed out above, all of the families show the development of postcoxal lobes (px), although this development shows considerable diversity. In the Silphid and Pselaphid the postcoxal projections of the inflexed pronotum are very short. In the Staphylinid (Fig. 41) the projections are longer, although still but a third of the distance to the median-line, and in the Leiodiid (Fig. 60) the postcoxal lobes (px) overlap the furcasternum (fs) and reach nearly to the prosternal lobe (psl). In the Colonid, Scaphidiid (Fig. 65), and Scydmaenid the posterior mesad projections of the inflexed pronotum are short and are met by the greatly broadened furcasternum.

The precoxal bridges (pc) in this group are slender and not unlike those of the generalized type. Mesally the basisternum may or may not be produced caudally to form a prosternal lobe (psl). The prosternal lobe may be barely indicated, as in the Colonid, Scaphidiid, and Silphid, or long and narrow as in the Leiodiid and Pselaphid, or virtually not present at all as in the Staphylinid and Scydmaenid. The furcasternum (fs) has developed considerably from the small structure shown in the generalized type (Fig. 13). In the Silphid the furcasternum is produced a short distance caudad and laterad, while in the Staphylinid the furcasternum is produced laterally behind the precoxal bridges (pc) to which it is joined. In the Pselaphid the furcasternum is nearly as broad as the sternal region and extends nearly as far caudally as the prosternal lobe. In the Colonid, Leiodiid, Scydmaenid, and Scaphidiid the furcasternum is secondarily developed behind the precoxal bridges and the posterior-lateral edges are joined to the postcoxal lobes. In these four specimens the entire furcasternum is well developed and forms a concave pocket for the coxae. The furcal pits from which the furcal arms originate, are widely separated and, with the exception of the Colonid, are at the posterior-lateral margin of the furcasternum. The furcal arms (fa) are long and extend dorsad, although in the Pselaphid and Silphid they extend slightly caudad as well.

The cervical sclerites (cvs) of the generalized Lampyrid consist of two pairs. Among these representatives two pairs are to be found only in the Staphylinid. In the Silphid there appears to be one pair of large, fused cervical sclerites, while in the Scaphidiid and Leiodiid but one small pair is to be found. No cervical sclerites are present in the Colonid, Scydmaenid, and Pselaphid.

The eutrochantin (etn) throughout these representatives shows a similarity to that found in the generalized type. In general, the trochantin is not as slender as that found in the Lampyrid, and in the Scydmaenid and Scaphidiid the trochantin is much shorter. The pleural region is plainly visible. The Apodeme may be short and broad as in the Pselaphid or long and narrow as in the Scaphidiid, or the apodeme may take on a more or less bizarre anterior folding as in the Staphylinid. The coxae (cx) in this group are moderately long and somewhat cylindrical, the exception being the somewhat shortened coxae of the Colonid and Scydmaenid.

The two pairs of cervical sclerites, moderately developed postcoxal lobes, and weakly developed furcasternum show the Staphylinid to be the most primitive representative of this group. The Silphid is probably the nearest to the Staphylinid and is possibly followed by the Scaphidiid. Although certain structures may have developed considerably, the remaining representatives of the group are not too distantly related to the Staphylinid. The entire group is formed of representatives somewhat closely related to each other and is of somewhat more recent origin than the generalized type.

Superfamily Hydrophiloidea

Family: Hydrophilidae

The representative of this superfamily shows some characteristics as primitive as those shown by the generalized Lampyrid, while other characteristics show considerable development.

The pronotum (pn) of the Hydrophilid (Fig. 62) is broad and rounded dorsally and flexes ventro-mesad at the lateral margins to form a lateral carina (c) and long pointed postcoxal lobes (px). Posterior to the coxal cavities a secondary projection extends dorso-mesad from the postcoxal lobes to join the posterior margin of the furcasternum (fs). The precoxal bridges (pc) are slender and moderately long. The basisternum (bs) forms a rounded anterior lobe and a short elevated mesal ridge that extends slightly caudad as a prosternal lobe (psl). The furcasternum (fs) is about twice as broad as long and the posterio-lateral margins join the projections from the postcoxal lobes. The long, broad furcal arms (fa) originating with the furcal pits extend dorsad and slightly caudad. The cervical sclerites (cvs) consist of two pairs that extend from slight projections on the anterior-edges of the precoxal bridges. The eutrochantin (etn) consists of a long, well developed trochantin, pleural region, and an apodeme of moderate length that is broadly flared at the dorsal end. The eutrochantin is similar to that of the generalized type. The coxa is cylindrical in shape and has a long basal arm with which the major condyle of the eutrochantin articulates.

In this representative of the superfamily the eutrochantin and cervical sclerites are but slightly modified from those of the generalized type, while the development of the postcoxal lobes and furcasternum indicates considerable development from the generalized type. Despite these inconsistencies, it would seem that this form is of much later development than the generalized type and should be placed much later in a phylogenetic grouping.

Superfamily Histeroidea

Family: Histeridae

The pronotum (pn) in this representative (Fig. 44) is broad, the lateral margins inflexing sharply to form a lateral carina (c) and extending ventro-mesad to form pointed postcoxal lobes (px) reaching half the distance to the prosternal lobe (psl). In this specimen the dorsal portion of the pronotum is slightly rounded and secondarily developed into a lattice work of chitinized areas. The precoxal bridges (pc) are long and slender, while the basisternum (bs) forms a broad anterior lobe and mesally is produced caudally to form a long and somewhat broad prosternal lobe (psl). A short transverse suture (h) separates most of the anterior lobe from the basisternum proper. The furcasternum (fs) extends dorsad and outward from the prosternal lobe and joins the mesal posterior edges of the precoxal bridges. The furcasternum is quite broad and nearly meets the inflexed pronotum or postcoxal lobes (px). The furcal pits at the extreme posterior and lateral margins of the furcasternum give rise to the weakly sclerotized dorsad-extending furcal arms. The cervical sclerites (cvs) consist of two pairs, the posterior pair being very small. The eutrochantin (etn) shows considerable modification over that exhibited by the generalized Lampyrid, the anterior mesal portion of the episternum extending with the apodeme to form a convex structure that appears related to the eutrochantin of the Staphylinid (Fig. 41). The pleural suture lies at about a right angle to the long axis of the coxa. The coxa (cx) is cylindrical in shape and cut off diagonally at the base.

The condition of the cervical sclerites, inflexed pronotum, and development of the furcasternum indicates that this representative is considerably modified from the generalized type, and although the basisternum is more highly developed, the eutrochantin and other modifications indicate a rather close relationship of this group with the Staphylinid.

Superfamily Scarabaeoidea

Families studied: Passalidae; Lucanidae; Scarabaeidae.

The representatives of this superfamily show a marked dissimilarity to the structures of the generalized Lampyrid. In general, the prothorax is broader than long, the postcoxal lobes are long, and the eutrochantin is highly developed.

The pronotum (pn) in these representatives is rounded dorsally and flexed ventro-mesad at the lateral margins to form a blunt lateral carina (c). The inflexed pronotum of the Scarabaeid (Fig. 45) extends mesad half the width of the coxal cavity to meet the posterior portions of the precoxal bridges (pc). Just caudad of the coxal cavities the pronotum extends mesad to the prosternal lobe (psl). In the Scarabaeid the postcoxal lobes (px) taper mesally, but in the Passalid (Fig. 47) and Lucanid (Fig. 46) the postcoxal lobes are parallel sided.

The precoxal bridges (pc) are not noticeably broadened and together with the basisternum (bs) form a rather long plate. Mesally the basisternum (bs) is produced caudally to form a prosternal lobe (psl). The prosternal lobe in each of the families is long and moderately broad, being broadest in the Lucanid and narrowest in the Passalid. The furcasternum (fs) extends dorsad and outward from the prosternal lobe, and in the Scarabaeid the furcasternum extends laterad behind the precoxal bridges to which it is joined. The furcal pits, giving rise to the furcal arms, are situated somewhat further forward in the Lucanid and Passalid than the posteriorly situated furcal pits of the Scarabaeid. The furcal arms are short and extend more or less dorsad. The Scarabaeid, like the generalized Lampyrid, has two pairs of cervical sclerites (cvs), although the posterior pair is very small. The Lucanid and Passalid have but one pair of cervical sclerites, those of the Lucanid being long and curved, and those of the Passalid being short and broad.

As was mentioned above, the eutrochantin (etn) of these representatives is greatly modified from the type exhibited by the generalized Lampyrid. In these families the trochantin is well developed, nearly straight, and somewhat broad. The episternum and epimeron are plainly visible and the pleural suture approximates a 90 degree angle with the trochantin. The apodeme has grown anteriorly and mesally and joined the anterior edge of the trochantin and episternum, the resultant eutrochantin (etn) structure appearing as a well developed trochantin and lower pleural region adjoined anteriorly by a weakly sclerotized convex area (apodeme). The coxae are long and cylindrical in shape and cut off diagonally at the base.

The development of the postcoxal and prosternal lobes and eutrochantin seems to indicate a much later origin than the condition of the cervical sclerites shows.

The similarities of the coxae, cervical sclerites, prosternal lobes, postcoxal lobes, and eutrochantin indicate that this group is very closely related to the Histeridae, although possibly of a more recent origin.

Series SYMPHIOGASTRA

Superfamily Dascilloidea

Families studied: Dascillidae; Cyphonidae; Ptilodactylidae.

A comparison of the representatives of this superfamily with the generalized Lampyrid reveals variations in the development of the inflexed pronotum and precoxal bridges. The prosternal lobe, furcasternum, and eutrochantin appear to have achieved rather similar development within the superfamily.

The pronotum (pn) in these representatives is rounded dorsally and the lateral edges of the pronotum flex ventro-mesad to meet the precoxal bridges (pc). In the Cyphonid (Fig. 26) there is no postcoxal lobe present, a condition similar to that of the generalized type (Fig. 13). In the Dascillid (Fig. 27) there are short postcoxal lobes (px) with a mesad projection posterior to the coxal cavities, while in the Ptilodactylid (Fig. 28) the inflexed pronotum forms short rectangular projections (postcoxal lobes) whose anterior edges meet the posterior edge of the laterally broadened precoxal bridges (pc).

The precoxal bridges (pc) in the Cyphonid are slender, while in the Dascillid they are slightly broader, and in the Ptilodactylid the lateral portions of the precoxal bridges extend caudad a considerable distance and meet the postcoxal lobes. Mesally the basisternum (bs) in this group is produced caudally to form a moderately long prosternal lobe (psl) which is narrow and pointed in the Dascillid and slightly broader in the other two representatives. The furcasternum (fs) in all three families is moderately developed when compared to the generalized type and extends dorsad and outward from the prosternal lobe to join the posterior edge of the precoxal bridges anteriorly. The furcasternum is largest in the Cyphonid. The furcal pits are situated near the posterior and lateral margins of the furcasternum, although slightly further forward in the Cyphonid, and the furcal arms (fa) are short and extend dorsad and slightly caudad. The cervical sclerites (cvs) consist of but one pair of long sclerites. These sclerites are straight in the Dascillid and Ptilodactylid and somewhat curved anteriorly in the Cyphonid. Thus the cervical sclerites have apparently fused to form but one pair in contrast to the two pairs exhibited by the generalized Lampyrid.

The eutrochantin (etn) in these three representatives appears to be quite similar to that of the generalized type, although the trochantin in this group is somewhat shortened and the apodeme is slightly flared at the dorsal end. The coxae (cx) are somewhat cylindrical in shape and cut off diagonally at the base.

The similar condition of the cervical sclerites, eutrochantin, coxae, and prosternal lobes in this superfamily makes the group appear to be closely related. The differences in the inflexed pronotum, postcoxal bridges, and furcasternum are not great and emphasize the close relationship of the group. This superfamily is obviously of more recent origin that the generalized type, but the group is not far advanced.

Superfamily Byrrhoidea

Families studied: Heteroceridae; Nosodendridae;
Byrrhidae.

A comparison of this superfamily with the generalized type indicates that only in the inflexed pronotum is there a close group similarity to the generalized type. Other differences within this group are considerable.

The pronotum (pn) is rounded dorsally and flexed ventro-mesad to meet the precoxal bridges (pc) and form slight mesad projections or postcoxal lobes (px) posterior to the coxal cavities in the Heterocerid (Fig. 39) and Nosodendried (Fig. 24) and no projection in the Byrrhid (Fig. 25). The ventro-mesad projection of the pronotum shows but a slight modification over that of the generalized Lampyrid (Fig. 13).

The sternal region exhibits considerable differences. The precoxal bridges (pc) are broad in the Heterocerid, of moderate width in the Byrrhid, and rather slender in the Nosodendrid. Mesally the basisternum (bs) is produced caudally to form a long narrow prosternal lobe (psl) in the Heterocerid, a broader pointed prosternal lobe in the Nosodendrid, and a short, broad, well-rounded prosternal lobe in the Byrrhid. The furcasternum (fs) extends dorsad from the prosternal lobe and is developed far laterad behind the precoxal bridges to which it is joined in the Nosodendrid and Byrrhid, and only slightly laterad behind the precoxal bridges in the Heterocerid. The furcal pits are situated at the posterior and lateral margins of the furcasternum. In the Heterocerid the furcal arms (fa) are long and slender and extend dorso-caudad, while in the Nosodendrid and Byrrhid the furcal arms are short and broad and extend nearly dorsad. The cervical sclerites (cvs) of the Byrrhid consist of two pairs of partially fused sclerites, while the cervical sclerites of the Heterocerid and Nosodendrid consist of but one pair.

The eutrochantin (etn) consists of a broad trochantin in these three representatives, and in the case of the Nosodendrid and Byrrhid, a well formed pleural region and apodeme that flares at the dorsal end. In the Heterocerid and pleural region of the eutrochantin is poorly defined and the apodeme extends laterad and cephalad. The coxae (cx) are more or less long and cylindrical in shape and cut off diagonally at the base.

It would seem from an intraseries comparison of these representatives based on the sclerites of the prothorax that the Nosodendrid and Byrrhid are closely related, while the sclerites of the sternal region as well as the eutrochantin seem to indicate that the Heterocerid may be related more closely to some other group like the Staphylinoidea, although the inflexed pronotum differs greatly from this group.

Superfamily Dryopoidea

Families studied: Elmidae; Dryopidae; Psephenidae.

When the representatives of this superfamily are compared with the generalized Lampyrid, the greatest changes are found in the sternal region and the eutrochantin, although the cervical sclerites and the inflexed pronotum show changes as well.

In these representatives the pronotum (pn) is rounded dorsally and flexed ventro-mesad at the lateral margins to join the precoxal bridges (pc). In the Elmid (Fig. 49) there is no indication of a postcoxal lobe formed by the inflexed pronotum, while in the Dryopid (Fig. 22) there are short postcoxal lobes (px), and in the Psephenid (Fig. 36) there are sizable postcoxal lobes.

The precoxal bridges (pc) of the Elmid and Dryopid are broad, while those of the Psephenid are of only moderate width, and the lateral portions extend far caudally. Mesally the basisternum is produced caudally to form a short, broad prosternal lobe (psl) in the Elmid, a longer, narrower prosternal lobe in the Dryopid, and a longer and more slender prosternal lobe in the Psephenid. The furcasternum (fs) in these beetles extends dorsad and outward from the prosternal lobe, and in the case of the Elmid the short furcasternum is situated caudad of the precoxal bridges to which it is joined. In the Dryopid the furcasternum is not associated with as much of the posterior edge of the precoxal bridges, while the long furcasternum of the Psephenid is joined anteriorly to much of the precoxal bridges and is broad posteriorly as well. The short furcal arms extend somewhat dorsad from the furcal pits. The cervical sclerites (cvs) are lacking in the Elmid, and but one pair is present in the Dryopid and Psephenid.

The eutrochantin (etn) in these families, although showing a resemblance to the generalized type, shows a distal broadening of the trochantin, especially noticeable in the Elmid. The pleural suture is visible and the apodeme is rather short and flared at the dorsal end. The coxae (cx) are more or less cylindrical, and in the case of the Elmid and Psephenid somewhat shortened.

In this group we find the Elmid without postcoxal lobes or cervical sclerites, while the other two representatives have postcoxal lobes and one pair of cervical sclerites. It is difficult to give an accurate placing of such specimens since certain structures have evolved at different rates. It would appear, however, that the Elmid and Dryopid are more closely related and the Psephenid is more related to some other group, such as the next superfamily, Elateroidea.

Superfamily Elateroidea

Families studied: Cebrionidae; Melasidae; Plastoceridae; Trixagidae; Rhipiceridae; Buprestidae.

In general, the representatives of this superfamily exhibit broadened precoxal bridges and a basisternum that has been produced caudally to form a strong prosternal lobe. These conditions contrast with the slender precoxal bridges and short prosternal lobe of the generalized Lamyrid (Fig. 13).

The pronotum (pn) in these forms is rounded dorsally and flexed ventro-mesad at the lateral margins, forming a more or less sharp lateral carina (c) in the Elaterid (Fig. 34), Trixagid (Fig. 5), and Buprestid (Fig. 32) and rounding laterally in the other forms. In all of the representatives the pronotum projects mesally posterior to the coxal cavities to form short postcoxal lobes (px). In the Plastocerid (Fig. 33) and Elaterid the postcoxal lobes are secondarily marked off by a weak suture (e). The posterior portions of the inflexed pronotum in the Trixagid are marked off by a deep groove (b) extending obliquely laterad from the coxal cavities to the lateral carina. The antennae rest within these grooves.

The sternal region shows a marked development when compared with the generalized type. In the Melasid (Fig. 37), Plastocerid, Elaterid, and Buprestid, and the precoxal bridges (pc) are broad and mesally the basisternum (bs) is produced caudally to form a long prosternal lobe (psl). In the Cebrionid (Fig. 35) and Trixagid the precoxal bridges are of moderate width and the lateral portions of the precoxal bridges extend caudad. In the Trixagid this posterior extension bears a suture (ps) which has been shown above to be the pleural suture of the upper pleural region, while in the Cebrionid a similar but weak suture is visible with proper preparation of the specimen. Mesally the basisternum of the Cebrionid and Trixagid is produced caudally to form a very long and slender prosternal lobe in the former and a long, broad lobe in the latter. In the Rhipicerid (Fig. 40) the precoxal bridges and basisternum with short prosternal lobe are similar to the same structures in the generalized type, although the furcasternum (fs) of the Rhipicerid is more modified than that of the generalized Lampyrid. The furcasternum (fs) extends dorsad and laterad from the prosternal lobe and extends behind the posterior edges of the precoxal bridges with which it is joined. Short, narrow arms extend laterad from the Melasid furcasternum to the postcoxal lobes. In general, the furcal arms arising from the furcal pits are short and extend more or less dorsad. With the exception of the Melasid which possesses but one long pair of cervical sclerites, the cervical sclerites (cvs) in this group consist of the two primitive pairs found in the generalized Lampyrid.

The eutrochantin (etn) in this group shows numerous modifications. In general, the pleural region, including the pleural suture and major coxal condyle, is similar to the generalized type. The trochantin in all of these families is shorter than that of the generalized type, the one exception being the Rhipicerid which exhibits a long, stout trochantin. The apodeme in the Rhipicerid is bluntly rounded, whereas in the other representatives a flaring dorsal end is present. In the Melasid the apodeme is long and slender with a flared structure at the dorsal end. The coxae (cx) appear somewhat cylindrical in shape, although shorter than that of the generalized type.

This group of beetles shows several primitive structures, such as two pairs of cervical sclerites, short postcoxal lobes, and a weak furcasternum, and in the Trixagid and Cebrionid sterno-pleural structures are present which show little change from Orthopteroid forms. A study of the prothoracic sclerites indicates that, with the possible exception of the Rhipicerid and Melasid, these representatives are rather closely related and not of much later origin than the generalized type. The Melasid and Rhipicerid, although not very closely related to this superfamily, should still be placed somewhere near this group.

Superfamily Cantharoidea

Families studied: Lycidae; Lampyridae; Phengodidae; Cantharidae.

Since this superfamily includes the generalized Lampyrid, it is natural to find many similarities within this group, especially since the representatives seem fairly well grouped phylogenetically.

The pronotum (pn) in these representatives is more or less rounded dorsally and the lateral margins flex ventro-mesad to form thin flat lateral discs in the generalized Lampyrid (Fig. 13) and the Phengodid (Fig. 19), while in the Lycid (Fig. 14) and Cantharids (Figs. 4 & 6) the pronotum flexes ventro-mesad to form a more or less sharp lateral carina (c) although no flat lateral discs are formed. In none of these specimens is a postcoxal lobe present. In the Cantharid (Fig. 6) a secondarily formed transverse suture (a) is present on the inflexed pronotum.

The precoxal bridges (pc) are similar to those of the generalized type and mesally the basisternum (bs) in only the Lampyrid extends caudally a short distance to form a short prosternal lobe (psl). In the remaining representatives a definite prosternal lobe is not present. The furcasternum (fs) in this superfamily is but weakly developed. In the Phengodid the furcasternum is broadest and probably the most highly developed. The furcal arms (fa), originating from the furcal pits at the posterior corners of the furcasternum, are moderately long and slender and extend dorsad and slightly laterad or caudad. With the exception of the Phengodid which has but one pair, the members of this superfamily possess two pairs of cervical sclerites (cvs).

The eutrochantin (etn) in this group is closely related to that of the generalized Lampyrid, although that of the Phengodid appears slightly more evolved. In the other representatives an open pit shows wherein the sclerites invaginated to form the apodeme. The coxae (cx) are moderately long and cylindrical in shape and diagonally cut off at the base, although those of the Lycid are somewhat shorter.

A comparative study of the prothoracic sclerites of this superfamily indicates that, with the exception of the Phengodid, these representatives, showing similar pronotal, sternal, and eutrochantinal development, are very closely related and make up the most primitive group of beetles (although other families might be included here as well). The reduction of the cervical sclerites and development of the furcasternum and eutrochantin seem to indicate a slightly more advanced position for the Phengodid.

Superfamily Cleroidea

Families studied: Malachiidae; Dastydidae; Cleridae;
Temnochilidae; Dermestidae.

When the representatives of this superfamily are compared with the generalized Lampyrid, it is evident that the changes in structures are not great, the pronotum showing considerable inflexing and postcoxal lobes in only the Dermestid. The furcasternum is but moderately developed and the cervical sclerites are not far from the primitive condition of the generalized type.

With the exception of the Temnochilid (Fig. 21) which forms flat lateral discs, the pronotum (pn) is rounded dorsally and flexed ventro-mesad at the lateral edges. The inflexed pronotum forms short postcoxal lobes (px) in the Clerid (Fig. 54) and longer postcoxal lobes in the Dermestid (Fig. 52). In the other representatives there is barely an indication of postcoxal projections of the inflexed pronotum.

The sternal region is composed of slender precoxal bridges and basisternum which are little different from those of the generalized Lampyrid. In the Clerid the lateral edges of the precoxal bridges are greatly broadened anteriorly and caudally. Mesally the basisternum (bs) is produced caudally to form a moderately long prosternal lobe (psl). In the Malachiid (Fig. 18), Dasytid (Fig. 20), and Dermestid the prosternal lobe is short and pointed, while in the Temnochilid the prosternal lobe is about twice as long as broad. The furcasternum (fs) in these representatives is longer and broader than that of the generalized type. In the Clerid and Dermestid the furcasternum extends dorsad and outward from the prosternal lobe and is joined anteriorly to the posterior edge of the precoxal bridges and posteriorly to the postcoxal lobes by long slender arms. In the Dasytid and Temnochilid the furcasternum extends dorsad and laterad from the prosternal lobe and is joined anteriorly to the posterior margin of the precoxal bridges. In the Malachiid the furcasternum projects dorso-cauded from the short prosternal lobe as well as laterally behind the precoxal bridges with which it is joined. The furcal arms (fa) are short and slender and extend dorsad and slightly laterad from the furcal pits. The cervical sclerites (cvs) in the Dasytid, Temnochilid, and Dermestid consist of two pairs, while the Malachiid and Clerid possess but one pair of cervical sclerites.

Although the trochantin is generally shorter and broader, the eutrochantin (etn) of the representatives of this superfamily is similar to that of the generalized type. The apodeme is of varying lengths but generally is broadly flared at the dorsal end. The apodeme is shortest in the Clerid and longest in the Dermestid. The coxae (cx) are more or less cylindrical in shape and diagonally cut off at the basal end as are those of the generalized type.

A comparison of the prothoracic sclerites of these representatives of the superfamily indicates a rather close phylogenetic relationship, although the somewhat greater development of the inflexed pronotum and furcasternum might place the Clerid and Dermestid in a group with a slightly more recent origin. It appears, however, that this superfamily is not of much more recent origin than the generalized type when the prothoracic sclerites are studied.

Superfamily Bostrychoidea

Families studied: Bostrychidae; Lyctidae; Ptinidae; Anobiidae; Sphindidae.

A comparison of the representatives of this superfamily with the generalized Lampyrid shows some representatives to be greatly modified and others to be only slightly modified, and a comparison of the representatives within the superfamily shows them to be inconsistently grouped from a phylogenetic standpoint.

The pronotum (pn) is rounded dorsally in these representatives and the pronotum continues rounding ventro-mesally to meet the precoxal bridges (pc) in the Bostrychid (Fig. 68), Lyctid (Fig. 89), and Anobiid (Fig. 31). In the Ptinid (Fig. 66) and Sphindid (Fig. 30) the lateral edges of the pronotum inflex sharply to form a lateral carina (c) and then flex ventro-mesad to meet the precoxal bridges.

With the exception of the Lyctid whose postcoxal projections of the inflexed pronotum form postcoxal lobes (px) or bridges reaching to the prosternal lobe (psl), these forms exhibit moderate-sized postcoxal lobes. In the Lyctid beetle the pronotum has fused with the anterior two-thirds of the lateral edge of the precoxal bridges (pc).

A comparison of the sternal region again shows the Lyctid to be at variance with the other representatives of this group as well as the generalized type, since it has broad precoxal bridges (pc) and the basisternum (bs) is produced caudally to form a long, lobed prosternal lobe (psl), while the other representatives of the group and the generalized type have slender precoxal bridges and short prosternal lobes. The lateral margin of the precoxal bridges of the Anobiid forms a flat, raised circular disc which extends ventrad at a 90 degree angle to the precoxal bridge. A strong prosternal lobe is also developed in the Sphindid, while the Anobiid has a short, broad prosternal lobe. The Bostrychid and Ptinid have a very small, pointed prosternal lobe. The furcasternum (fs) is broad in all of the representatives, being least developed in the Anobiid and Sphindid where the furcasternum does not extend to the inflexed postcoxal lobes. The furcasternum extends dorsad and outward from the prosternal lobe and anteriorly joins the posterior edge of the precoxal bridges in these families. In the Bostrychid the furcasternum extends far caudally as well as anteriorly joining the precoxal bridges and forms a large, concave coxal pocket. A large concave pocket is also formed by the greatly developed furcasternum of the Lyctid. The Sphindid is the only representative of the superfamily retaining cervical sclerites (cvs) and these have been reduced to but one pair in contrast to the two pairs exhibited by the generalized Lampyrid.

The eutrochantin (etn) is well developed when compared with the generalized type. With the exception of the Bostrychid whose trochantin is moderately long and the apodeme short, the trochantin is these forms is short and the apodeme is long and slender. The dorsal end of the apodeme is rather broad in the Sphindid and but slightly broadened in the other representatives. The coxae (cx) are more or less cylindrical in shape.

A comparative prothoracic study of this superfamily indicates a close relationship between the Ptinid, Anobiid, and Sphindid, while the extensive development of the furcasternum in the Bostrychid would seem to place it in a more advanced position. The partial fusion of the pronotum and precoxal bridges, well developed postcoxal lobes, well developed precoxal bridges and prosternal lobe, and extensive furcasternum indicate the Lyctid to be of much more recent origin than the rest of this superfamily.

Superfamily Lymexylonoidea

Family: Lymexylonidae.

The prothorax of this representative (Fig. 15) is given a cylindrical appearance by the rounding of the pronotum dorsally and laterally. The pronotum (pn) like that of the generalized Lampyrid forms no postcoxal lobes. The precoxal bridges (pc) are broader than those of the generalized type and the mesal, caudal projection of the basisternum (bs) forms a short but broader prosternal lobe (psl) than the generalized type. The furcasternum (fs) lies entad of this broad prosternal lobe and curves dorsad and laterad posterior to the mesal portions of the precoxal bridges to which it is joined. The furcal pits are more distantly apposed than those of the generalized type and the furcal arms extend dorsad and slightly cephalad. The eutrochantin (etn) has a much shorter and broader trochantin than that exhibited by the generalized type and the apodeme is shorter. The coxa (cx) is long and somewhat cylindrical in shape. This representative retains the primitive cervical sclerite (cvs) condition of the generalized Lampyrid.

Although the eutrochantin of the Lymexylonid differs considerably from that of the generalized type, the similarities found in the pronotum, sternal region, and cervical sclerites, indicate a not too distant relationship between this representative and the generalized Lampyrid.

Superfamily Nitiduloidea

Families studied: Monotommidae; Nitidulidae.

This superfamily of three families is represented here by but two families. A comparison of these two representatives with the generalized Coleopteron (Fig. 13) indicates that they are considerably developed forms.

The pronotum (pn) of both representatives is rounded dorsally, and that of the Monotommid (Fig. 90) forms a serrated lateral carina (c) and flexes ventro-mesad to fuse with the precoxal bridges (pc) anteriorly and meet the prosternal lobes (psl) posteriorly, while that of the

Nitidulid (Fig. 76) inflexes to form flat, lateral discs and flexes ventro-mesad to the precoxal bridges anteriorly and to the prosternal lobe posteriorly. Thus, both specimens have long postcoxal lobes (px) in contrast to the open coxal cavities of the Lampyrid.

The precoxal bridges (pc) are somewhat broader than those of the generalized type, and mesally the basisternum (bs) is projected caudally to form a long, broad prosternal lobe (psl). The furcasternum of the Monotommid lies entad of the prosternal lobe and is not as extensively developed as the broad furcasternum (fs) of the Nitidulid which forms a concave pocket for the coxa. The furcal arms extend dorsad from the furcal pits. In contrast to the two pairs of cervical sclerites (cvs) found in the Lampyrid, the Nitidulid has but one pair and the Monotommid has none.

The eutrochantin (etn) in these beetles is similar to that found in the generalized type, although the trochantin is slightly broader and the apodeme is shorter in the Nitidulid. The coxae are moderately long and cylindrical and are more or less cut off diagonally at the base.

Although fusion of the pronotum and precoxal bridges has taken place in the Monotommid and the furcasternum is more highly developed and the cervical sclerites less reduced in the Nitidulid, these representatives are somewhat closely related through postcoxal and other similarities. This group, however, may possibly belong with some other well advanced larger group.

Superfamily Cucujoidea

Families studied: Cucujidae; Languriidae; Cryptophagidae; Palacridae; Orthopteridae; Byturidae; Anthicidae; Lathridiidae.

The many variations to be found in the inflexed pronotum, basisternum, precoxal bridges, furcasternum, eutrochantin, and cervical sclerites shows this superfamily to be a somewhat incongruous group of beetles from a phylogenetic standpoint.

The pronotum (pn) in this group is more or less rounded dorsally, being but slightly rounded in the Cucujid (Fig. 23) and Orthoperid (Fig. 43) and greatly rounded in the Anthicid (Fig. 87). The pronotum is rounded at the lateral margins and flexed ventro-mesad in all of the representatives except the Phalacrid (Fig. 58), Byturid (Fig. 71), and Orthoperid where a lateral carina (c) and small flat lateral discs are formed by the inflexed pronotum. In the Cucujid a blunt serrated carina is formed at the lateral margins. The pronotum meets the precoxal bridges (pc) (fusing with the precoxal bridges in the Anthicid) and projects mesally posterior to the coxal cavities to form short postcoxal lobes (px) in the Cryptophagid (Fig. 55) and Phalacrid, postcoxal lobes extending half the distance to the prosternal lobe (psl) in the Cucujid and Orthoperid, and postcoxal lobes extending to or nearly to the prosternal lobe in the Languriid (Fig. 78), Byturid, Anthicid, and Lathridiid (Fig. 73). These conditions are in contrast to the open coxal cavities of the generalized Lampyrid. The pronotum of the Anthicid is secondarily projected cephalad to form a long hollow lobe which covers the head.

The sternal region shows similar differences within this group, wherein the precoxal bridges (pc) are broad in the Cucujid and Languriid, slender in the Phalacrid, Byturid, and Anthicid, and of moderate width in the Cryptophagid, Orthoperid, and Lathridiid. As mentioned above, the precoxal bridges and pronotum of the Anthicid are fused. Mesally the basisternum (bs) in these representatives is produced caudally to form a prosternal lobe (psl) which in the Orthoperid and Anthicid is slender and pointed, while in the Phalacrid, Byturid, and Lathridiid it is long and broadened posteriorly, and in the Cucujid, Languriid, and Cryptophagid it is long and broad. Likewise, the furcasternum (fs) may be but slightly more developed than the generalized type as in the Cucujid and Orthoperid, or broadly developed to join the postcoxal lobes (px) as in the remaining specimens. The furcal arms are short and extend more or less dorsad from the furcal pits. Only the Cucujid, Orthoperid, and Byturid exhibit cervical sclerites (cvs). In the Cucujid it appears that three pairs of sclerites are present, although it is possible that one pair may be secondarily marked off to give this impression. The Orthoperid and Byturid possess but one pair of cervical sclerites each.

The eutrochantin (etn) shows few congruities within this superfamily. In the Cucujid and Orthoperid the trochantin is broad, and in the Lathridiid it is long and slender, while in the remaining forms it is shorter and generally broader than that of the generalized Lampyrid. The Cucujid and Languriid exhibit well developed apodemes that flare broadly at the dorsal end, while in the Byturid and Anthicid the apodeme is well developed and the dorsal end is but slightly broadened. In the remaining representatives, with the exception of the Orthoperid, the apodeme is weakly developed and small. The pleural suture in the Orthoperid is situated nearly at a right angle to the trochantin and the apodeme extends latero-cephalad. The coxae (cx) in this superfamily are slightly elongate and more or less cylindrical in shape with a basal projection for articulation with the eutrochantin.

A comparative study of the prothoracic sclerites of this superfamily indicates that it is not a closely intrarelated group. It would appear from the cervical sclerites, postcoxal lobes, and furcasternal development that the Cucujid and Orthoperid are closely related and followed phylogenetically by the Cryptophagid, Phalacrid, and Byturid. Of still more recent origin are the Languriid, Anthicid, and Lathridiid. However, a comparison of the eutrochantin structures indicates different positions for the Cucujid and Orthoperid as well as separation of the Lathridiid from the Languriid and Anthicid, and the fusion of the precoxal bridges and pronotum may place the Anthicid in a group of even more recent origin.

Superfamily Coccinelloidea

Families studied: Endomychidae; Coccinellidae;
Erotylidae.

A comparison of the representatives of this superfamily with the generalized Lampyrid shows that certain characters may remain primitive in one specimen while others are greatly developed, and in another specimen the primitive characters of the first may be greatly developed while the developed characters of the first remain primitive.

The pronotum (pn) of these representatives is rounded dorsally and flexed ventro-mesad at the lateral margins to meet the precoxal bridges (pc) anteriorly and to project mesally posterior to the coxal cavities to form short postcoxal lobes (px) in the Endomychid (Fig. 63), longer postcoxal lobes extending half the distance to the prosternal lobe (psl) in the Coccinellid (Fig. 64), and postcoxal lobes reaching to the prosternal lobe in the Erotylid (Fig. 38). In the Endomychid a pair of invaginations (h) is formed near the posterior margin of the pronotum on the dorsal side and another pair is similarly formed on the ventral portions of the inflexed pronotum. The invaginations on the inflexed pronotum are moderately long and are possibly an indication of the suture (d) found in the Adephagous beetles.

The precoxal bridges (pc) are slightly broader than those of the generalized Lampyrid and mesally the broader basisternum is produced caudally to form the prosternal lobe (psl). Near the posterior margin of the precoxal bridges of the Endomychid are long sutures which are evidently secondary in nature, although conceivably they could be homologous with the upper pleural suture (ps) found in the Trixagid (Fig. 5). (However, the position and length of these sutures makes the latter interpretation appear improbable.) In the Endomychid the prosternal lobe is narrow and pointed, and in the Coccinellid it is broader, while in the Erotylid the prosternal lobe is very broad and the caudal end is bi-lobed. The furcasternum (fs) of the Erotylid is barely visible and extends dorsad and laterad from the prosternal lobe and is joined anteriorly to a small portion of the posterior edge of the precoxal bridges. In both the Endomychid and Coccinellid the furcasternum is broad and joins a larger portion of the posterior edge of the precoxal bridges as well as meeting the postcoxal lobes posterio-laterally. The furcal arms extending dorsad from the furcal pits are short and slightly forked at the dorsal end. The Erotylid retains the two pairs of cervical sclerites (cvs) found in the generalized Lampyrid, while the Endomychid and Coccinellid possess but one pair of cervical sclerites each.

The eutrochantin (etn) of the Endomychid and Coccinellid is somewhat similar to that of the generalized type, although the apodeme of the Endomychid is smaller. In the Erotylid the trochantin is very short, although the apodeme is well developed. The coxae (cx) are long and cylindrical as in the generalized type, although that of the Endomychid is somewhat shorter and has a basal projection for articulation of the eutrochantin.

A comparative study of the pronotum, sternal region, cervical sclerites, and furcasternum, as well as the eutrochantin, indicates a rather close relationship between the Endomychid and Coccinellid. The strong development of the prosternal lobe and postcoxal lobes, as well as the development of the eutrochantin, seems to indicate a more recent origin for the Erotylid despite the primitive condition of the cervical sclerites.

Superfamily Colydoidea

Families studied: Mycetophagidae; Colydiidae;
Discolomidae.

A comparison of these three representatives with the generalized Lampyrid, or even of the three representatives themselves, shows considerable diversity in the prothoracic sclerites.

The pronotum (pn) in the Mycetophagid (Fig. 57) is rounded dorsally with sharply inflexed lateral margins forming a lateral carina (c), while the pronotum of the Colydiid (Fig. 48) is rounded dorsally and laterally so that no lateral carina is formed. The inflexed pronotum forms short, round postcoxal lobes (px) in the Colydiid and slightly longer postcoxal lobes which meet the furcasternum in the Mycetophagid.

The precoxal bridges (pc) of the Mycetophagid are slightly broader than those of the generalized type, but are only half as broad as those of the Colydiid. In the Mycetophagid the basisternum (bs) is produced caudally to form a long, rounded prosternal lobe (psl), while in the Colydiid the basisternum is produced caudally to form a prosternal lobe twice as broad as long. The furcasternum (fs) of the Mycetophagid extends dorsad and laterad from the prosternal lobe and is joined to the posterior margin of the precoxal bridges anteriorly and to the postcoxal lobes posteriorly. The furcasternum of the Colydiid lies entad of the broad prosternal lobe and extends nearly dorsad and slightly laterad anteriorly to join a small portion of the posterior margin of the precoxal bridges. The short, broad furcal arms extend cephalo-dorsad from the furcal pits. The Mycetophagid and Colydiid have one pair of greatly reduced cervical sclerites (cvs) each.

The eutrochantin (etn) in this group has the two articulating condyles more closely apposed than those of the generalized type, and the trochantin is slightly broader. The apodeme of the Colydiid eutrochantin is very short, while that of the Mycetophagid is longer and somewhat flared at the dorsal end. The coxae (cx) are shorter than those of the generalized type, and in the case of the Colydiid are nearly globular except for the extension at the basal end with which the eutrochantin articulates.

A comparison of the prothoracic sclerites of the representatives of this superfamily indicates that they are poorly grouped from a phylogenetic standpoint. The differences found in the sternal region and eutrochantin seem to outweigh the similarities of the cervical sclerites and postcoxal lobes and thus indicate that the Mycetophagid and Colydiid are not closely related.

Superfamily Mordelloidea

Family: Mordellidae

This superfamily is represented by but one family. The pronotum (pn) of the Mordellid (Fig. 59) is well rounded dorsally with sharply inflexed lateral margins. The inflexed pronotum overlaps and meets the laterally broadened precoxal bridges (pc) to form an oblique suture (x) and extends mesad posterior to the coxal cavities to form broad postcoxal lobes (px) that join the furcasternum (fs). The precoxal bridges (pc) are very slender and the lateral edges broaden greatly anteriorly. Mesally the basisternum (bs) is produced caudally to form a long, slender prosternal lobe (psl). The closely associated furcasternum (fs) extends dorsad and laterad from the prosternal lobe and anteriorly joins most of the posterior margin of the precoxal bridges and posteriorly meets the postcoxal lobes. The furcal arms extending dorsad from the furcal pits are long and form a short fork at the dorsal end. The cervical sclerites (cvs) consist of two pairs, but, unlike the cervical sclerites of the generalized type which lie end to end, the anterior and posterior cervical sclerites are situated parallel to each other, although the posterior sclerite (outer in this case) is but half as long as the anterior cervical sclerite. The eutrochahtin (etn) of the Mordellid differs from that of the generalized type in that the articulating condyles are more closely apposed and the trochantin is much broader and shorter. The apodeme is well developed. The coxa (cx) is very similar to that of the generalized Lampyrid.

The two pairs of cervical sclerites and slender precoxal bridges are primitive characters that are overshadowed by the greatly developed prosternal lobe, greatly developed furcasternum, postcoxal lobes, and modified eutrochantin. This group should be placed considerably later phylogenetically than the generalized type.

Superfamily <u>Meloidea</u>

Families studied: Rhipiphoridae; Meloidae.

A comparison of the two representatives of this superfamily with the generalized Lampyrid reveals one representative to be strikingly similar in many structures to the generalized type, whereas the other representative is greatly modified.

The pronotum (pn) of the Meloid (Fig. 16) is rounded dorsally and flexed ventro-mesad a short distance to meet the precoxal bridges (pc) anteriorly and form a very short postcoxal projection posteriorly. The pronotum of the Rhipiphorid (Fig. 86) is greatly rounded dorsally and laterally and continues its flexing ventro-mesally where it fuses with the precoxal bridges anteriorly and forms long pointed postcoxal lobes (px) posterior to the coxal cavities. The inflexed pronotum is marked by a weak transverse suture (a) which extends from the coxal cavity to the lateral margin.

The precoxal bridges (pc) of both specimens are but slightly broader than those of the generalized type, and mesally the basisternum (bs) is produced caudally only in the Rhipiphorid where a short, pointed prosternal lobe (psl) is formed. There is no visible prosternal lobe in the Meloid. The furcasternum (fs) in the Meloid is slightly more developed than that of the Lampyrid and adjoins a portion of the posterior margin of the precoxal bridges, while in the Rhipiphorid the furcasternum is well developed and adjoins the precoxal bridges as well as the postcoxal lobes. The short, slender furcal arms extend dorso-laterad from the furcal pits. The Meloid has one pair of large cervical sclerites (cvs), whereas the Rhipiphorid lacks such sclerites.

The eutrochantin (etn) of the Meloid has a shorter but broader trochantin and a shorter apodeme than does the eutrochantin of the generalized type, while the eutrochantin of the Rhipiphorid has a very short trochantin and the entire eutrochantin is much reduced. The coxae (cx) of both representatives are long and cylindrical in shape and that of the Meloid is diagonally cut off at the base.

The reduction of the cervical sclerites to one large pair (apparently fused), weak postcoxal development, weak furcasternum, and but slightly modified eutrochantin found in the Meloid indicates a rather close relationship with the generalized Lampyrid. The complete reduction of the cervical sclerites, fusion of the pronotum and precoxal bridges, greatly developed furcasternum, developed postcoxal lobes, and modification of the eutrochantin indicates the Rhipiphorid to be a greatly modified form and of much more recent origin than the Meloid or generalized Lampyrid.

Superfamily Tenebrionoidea

Families studied: Oedmeridae; Cephaloidae; Pyrochroidae; Pythidae; Serropalpidae; Lagriidae; Nilionidae; Monommidae; Alleculidae; Tenebrionidae.

A comparison of the representatives of this superfamily with the generalized Lampyrid (Fig. 13) shows a great diversity in the structures with which we are concerned. With the exception of the Nilionid (Fig. 74) whose prothorax is approximately twice as broad as long, the general prothoracic shape is not very diversified.

In all of the representatives except the Nilionid, the pronotum (pn) is rounded dorsally and flexed ventromesad to meet the precoxal bridges (pc) anteriorly and extend mesally posterior to the coxal cavities to form postcoxal lobes (px) of varying lengths. The Nilionid differs in that its pronotum is rounded dorsally and sharply inflexed laterally to form thin, flat, lateral discs and lateral carinas (c). In the Lagriid (Fig. 88) the pronotum meets and fuses with the precoxal bridges. In the Pyrochroid (Fig. 17) and Pythid (Fig. 50) the inflexed pronotum forms a very slight indication of a postcoxal lobe. In the Oedmerid (Fig. 53), Cepaloid (Fig. 51), and Monommid (Fig. 11) the postcoxal lobes (px) are very short, while in the Serropalpid (Fig. 61) the postcoxal lobes extend half the distance to the prosternal lobe (psl), and in the Lagriid, Nilionid, Alleculid (Fig. 77), and Tenebrionid (Fig. 75) the postcoxal lobes are well developed and extend to, or nearly to, the prosternal lobe. In the Monommid a long, broad, deep infolding or groove (g) extends the length of the inflexed pronotum on each side. As was mentioned above, these grooves are possibly the precursors to the longitudinal sutures (d) found in the Adephagous beetles.

The precoxal bridges (pc) in most of these representatives are of more or less the same width, although in the Nilionid the precoxal bridges are slender and broadened at the lateral edges. In the Cephaloid, Pyrochroid, and Serropalpid the basisternum (bs) is produced caudally a very short distance and the prosternal lobe (psl) is merely indicated, while in the Oedmerid and Pythid the basisternum is produced caudally a longer distance and a pointed prosternal lobe is formed. The Lagriid, Nilionid, Monommid, Alleculid, and Tenebrionid all have the basisternum produced caudad to form well developed prosternal lobes. It is interesting to note that the development of prosternal lobes in this latter group has evidently paralleled the development of the postcoxal lobes. The furcasternum in the Pyrochroid and Pythid is small and in the Oedmerid is slightly larger with narrow arms extending laterad to the inflexed pronotum. The furcasternum in the Monommid extends dorsad and laterad posterior to the precoxal bridges but no connection is present between the furcasternum and postcoxal lobes. In the Cephaloid and Serropalpid the furcasternum is more broadly developed and joins the postcoxal lobes, while in Lagriid, Nilionid, Alleculid, and Tenebrionid the furcasternum is well developed, extending to and joining the posterior edge of the precoxal bridges anteriorly and the postcoxal lobes posteriorly. In general, the furcal arms (fa) arising from the furcal pits (fp) extend dorsad, although they may extend slightly laterad or cephalad as well. Two pairs of cervical sclerites (cvs) are present in the Oedmerid, Cephaloid, and Pyrochroid, while one long pair of cervical sclerites is present in the Serropalpid. Cervical sclerites are lacking in the remaining six representatives.

The eutrochantin (etn) in this group shows considerable variations of the component structures. In the Cephaloid, Pyrochroid, Pythid, and Serropalpid the trochantin is considerably broader than that of the generalized type, and in the Cephaloid the articulating condyles are more closely apposed. In the Oedmerid, Lagriid, Monommid, Alleculid, and Tenebrionid the trochantin is more or less long and pointed, those of the Monommid and Tenebrionid being very similar to that of the generalized Lampyrid. In the Nilionid the trochantin appears to be quite short but not noticeably broadened, the broad area apparently being the episternum. The apodeme is generally well developed, although that of the Oedmerid is shortest and narrowest and that of the Serropalpid has a very broad flaring at the dorsal end. In the Lagriid and Nilionid the apodeme broadens only slightly at the dorsal end. The coxae (cx), in general, are more or less long and cylindrical in shape and cut off diagonally at the base, although that of the Serropalpid is shorter and somewhat globular with a basal extension for articulation of the eutrochantin.

A consideration of the cervical sclerites, postcoxal lobes, furcasternum, and prosternal lobe in this superfamily indicates that phylogenetically the Pyrochroid is the most primitive and is followed by the Cephaloid, Oedmerid, and Serropalpid. The Pythid seems to have developed the furcasternum and postcoxal lobes slowly, although the cervical sclerites are far from the primitive state, and probably this form is somewhere between the above representatives and a group made up of the Lagriid, Nilionid, Monommid, Alleculid, and Tenebrionid. Consideration of the development of the eutrochantin probably places some of the above specimens in other groupings phylogenetically.

Superfamily Phytophagoidea

Families studied: Cerambycidae; Chrysomelidae; Bruchidae; Anthribidae; Brenthidae; Proterhinidae; Curculionidae; Platypodidae; Scolytidae.

A comparison of the representatives of this superfamily with the generalized Lampyrid shows the group to consist of highly modified members. The pronotum has inflexed to form post coxal bridges or lobes; the furcasternum is well developed; the prosternal lobe is well developed; the precoxal bridges have fused with the pronotum in many representatives; the cervical sclerites are lacking; and the eutrochantin is greatly modified.

The pronotum (pn) in all of these representatives is rounded dorsally and at the lateral margins continues rounding and flexes ventro-mesad to meet or fuse with the precoxal bridges (pc) anteriorly and form postcoxal lobes (px) or bridges posteriorly. In the Anthribid (Fig. 94), Proterhinid (Fig. 96), Curculionid (Fig. 92 & 93), Platypodid (Fig. 70), and Scolytid (Fig. 95) the pronotum has fused with the precoxal bridges, while in the Cerambycid (Fig. 8) and Brenthid (Fig. 91) there is a partial fusion of the pronotum and precoxal bridges. In the Cerambycid (Fig. 7) and Chrysomelid (Fig. 56) the postcoxal lobes (px) extend half the distance behind the coxal cavities to the prosternal lobe (psl). In the Cerambycids (Figs. 8 & 9) and the Bruchid (Fig. 72) the postcoxal lobes extend to, or nearly to, the prosternal lobe, while in the remaining forms of this group the postcoxal lobes meet mesally and may fuse as in the Anthribid, Proterhinid, Curculionid (Fig. 93), Platypodid, and Scolytid, or form a short suture as in the Curculionid (Fig. 92) and Brenthid. In the Anthribid a transverse suture (a) on the inflexed pronotum extends from the coxal cavities to the lateral margins of the prothorax.

With the exception of the Brenthid and possibly the Proterhinid, the precoxal bridges (pc) are but moderately broad. In the Brenthid these structures are very broad. Mesally the basisternum (bs) in all of these forms is produced caudally to form a well developed prosternal lobe (psl), although in the Bruchid the prosternal lobe is narrow and in the Curculionid (Fig. 92) and Platypodid the prosternal lobe is short (although probably secondarily reduced). In the Anthribid, Brenthid, Proterhinid, Curculionid (Fig. 93), and Scolytid the prosternal lobe is met caudally by a cephalad-jutting extension of a sclerite associated with the mesally joined or fused postcoxal lobes. In the Brenthid there is a Y-shaped suture separating the postcoxal lobes mesally as well as separating the postcoxal lobes from the mesal, pentagonal sclerite just cephalad of this suture. This pentagonal sclerite in turn is separated from the prosternal lobe by a suture. In the Curculionid (Fig. 92) one sees a similar suture separating the postcoxal lobes and mesal sclerite, but there is a large depressed area of the furcasternum separating this mesal sclerite from the short prosternal lobe. It would appear that this mesal sclerite is a part of the furcasternum that has developed a strong plate, and this plate later fuses with the postcoxal bridges and joins the prosternal lobe as in the Proterhinid, Anthribid, Scolytid, and Curculionid (Fig. 93). As was pointed out above, the furcasternum (fs) is well developed, being considerably developed in the Cerambycids and greatly developed in the forms possessing postcoxal lobes that meet or fuse mesally. The furcasternum of the Chrysomelid, however, is weakly sclerotized and less extensive in area than the other representatives of the superfamily. The furcal arms in this group are short and extend more or less dorsad from the furcal pits (fp). As mentioned above, cervical sclerites are lacking in this superfamily.

The eutrochantin (etn) in this group is a structure of considerable diversity. As was shown above under the homologies, the eutrochantin in the Cerambycids tends to become broadened anteriorly and the articulating condyles more closely apposed, while the apodeme becomes shorter. In the Chrysomelid, Bruchid, Anthribid, Platypodid, and Scolytid the trochantin is short and the articulating condyles are closely apposed, while the apodeme is generally long and narrow (although the apodeme may take on a broad flaring structure at the dorsal end as in the Anthribid). In the Brenthid, Proterhinid, and Curculionid the trochantin has not shortened as much as those above but the apodeme extends anteriorly as well as dorsally. This type of eutrochantin is somewhat similar to those found in the Lucanid-Passalid-Scarabaeid group. The coxae (cx) in this group are more or less cylindrical, although somewhat shorter than that of the generalized type in the Cerambycids, Chrysomelid, Bruchid, and Anthribid, and more or less globular in the Brenthid, Proterhinid, Curculionids, Platypodid, and Scolytid (although these globular coxae do have an extension on the basal end with which the eutrochantin articulates).

A prothoracic study of this group indicates that the Cerambycids, Chrysomelid, and Bruchid are the most primitive. The remaining representatives represent the greatest morphological development of not only this group, but of all Coleoptera, and form a group which includes the most highly developed beetles.

PHYLOGENETIC ASPECTS

In order to interpret the relationships of beetles from their prothoracic structures, it is necessary first to observe trends of development in these structures. Crampton has shown that the Cantharoidea are apparently the most primitive beetles and the author has given the general prothoracic morphology of the Lampyrid, Lucidota corrusca above, This beetle has the following primitive conditions or structures: the pronotum has grown ventromesad to the base of the coxae and partially covers the pleural region, leaving the precoxal bridges visible; the coxal cavities are open behind (i.e. no postcoxal lobes); the furcasternum is small; the eutrochantin consists of a long slender trochantin and lower pleural region whose suture forms a coxal condyle and an internal ridge or apodeme; and the cervical sclerites consist of two pairs. From observations during this study the following trends have been noted: the pronotum continues growing ventromesad behind the coxal cavities to form postcoxal lobes or bridges that may even fuse mesally; the furcasternum tends towards greater development; the eutrochantin tends to develop by shortening the trochantin, although the eutrochantin development appears very variable; the cervical sclerites tend to become reduced in number; and mesally the basisternum tends to extend caudally to form a prosternal lobe.

From a study of precursor types it is evident that the Cantharoidea are the most primitive beetles. Likewise, if one observes beetles such as the Curculionids (Fig. 92 & 93), Scolytid (Fig. 95), and Proterhinid (Fig. 96), it should be evident that these are the most evolved types of beetles, since each of the above trends has reached its limit as follows: the pronotum extends behind the coxal cavities to form postcoxal lobes or bridges that meet or fuse mesally; the furcasternum is well developed and forms an extensive coxal pocket; the cervical sclerites are totally reduced; a strong prosternal lobe which meets the fused postcoxal bridges (or, having so developed, is secondarily reduced by the outer plate of the furcasternum) has developed; the eutrochantin persists but is variable.

Thus, while it is simple enough to interpret the Cantharoidea as the most primitive beetles and families such as the Curculionidae, Scolytidae, and Proterhinidae as the beetles of most recent origin, the task of interpreting intermediate families or groups is far more difficult. It is difficult from this brief study to decide on which trend or trends of development the most importance should be placed. A series based on the development of postcoxal lobes would be entirely uncorrelated in parts with a series based on the development of the furcasternum, and a series based on the development of the furcasternum would be far from agreement with a series based on the reduction of the cervical sclerites. Furthermore, this study includes for the most part of but one representative of each family, and one has only to observe the Cerambycids shown in Figs. 7, 8, & 9 to see the variability of the postcoxal lobes within one family. Blackwelder (1936) has shown the great diversity in prothoracic structures in his work on the family Staphylinidae. An attempt to place the families of beetles in their correct phylogenetic positions can only follow extensive work including the use of all subfamilies and genera, and the arrangement reached by the author, who has used so few specimens in this study, can only be considered as very tentative and subject to numerous changes.

Attempts to arrange the families in a linear series based on one structure emphasizes the important fact that the various families of Coleoptera (and apparently sub-families and genera within a family) have developed along many lines. Thus, certain lines may develop the postcoxal lobes while the cervical sclerites remain primitive, and another line may develop the prosternal lobe much more rapidly than the postcoxal lobes, while still another line may develop the furcasternum much more rapidly than other structures. The present tentative arrangement follows several possible lines. The author, in attempting to average the degree of development, has placed primary importance on the development of the postcoxal lobes and furcasternum and secondary importance to the development of the prosternal lobe and reduction of the cervical sclerites. Third in importance, and greatly overwieghed by the above conditions, is the development of the eutrochantin, which at best appears to be somewhat variable. The author has arranged the following groups and families within the groups in a phylogenetic sequence based on the above premises. Since in some cases certain structures may develop very rapidly, the groups may appear to be out of place, but as indicated above, this arrangement is entirely tentative and is subject to numerous changes.

Group I

Cantharidae, Lampyridae, Lycidae, Lymexylonidae, Meloidae, Pyrochroidae, Malachiidae, Phengodidae.

This group, which includes the Cantharoidea, is made up of the most primitive types of beetles, all of which are characterized by: the absence of postcoxal lobes, weakly developed furcasternum, short prosternal lobe (if present), primitive type of eutrochantin, and the presence of cervical sclerites. The author considers the Cantharids (Figs. 4 & 6) and Lycid (Fig. 14) to be the most primitive, although the Lampyrid (Fig. 13) is also very primitive. In these three forms the pronotal downflexing may be considered identical, as is also the condition of the cervical sclerites. The furcasternum in Figs. 4, 6, & 14 appears to be slightly more developed than the furcasternum of Fig. 13. The eutrochantin of Figs. 4 & 14, however, retains the pit wherein the infolding of sclerites forms the apodeme, and because of this condition the author has placed the Cantharids and Lycid as the most primitive. The Lampyrid is very close and is probably from the same ancestors as those of the Cantharids and Lycid. Following the above families are the Lymexylonid (Fig. 15) and Meloid (Fig. 16), both showing a further development of the furcasternum. Although the furcasternum of the Meloid has not developed as much as that of the Lymexylonid, an indication of postcoxal lobes and reduction of the cervical sclerites to one pair seems to indicate a slightly less primitive condition for the Meloid. The remaining three families of this group have the furcasternum moderately developed, that of the Phengodid (Fig. 19) having the greatest development and being placed last in this group. The presence of two pairs of cervical sclerites in the Pyrochroid (Fig. 17) seems to indicate a slightly more primitive origin than the otherwise similar Malachiid (Fig. 18) which has but one pair. Despite the fact that these are all primitive forms, the development of certain trends shows some forms to be slightly more advanced than the more primitive forms of this group.

Group II

Dasytidae, Temnochilidae, Dryopidae, Cucujidae, Nosodendridae, Byrrhidae, Cyphonidae, Dascillidae, Ptilodactylidae, Pselaphidae, Sphindidae, Anobiidae.

The furcasternum in all the representatives of this group is moderately developed, but in no case does it reach the postcoxal lobes which are only present in the later members of this group. The cervical sclerites of the group are variable, from the two pairs of the most primitive forms to their absence in the more recent forms. In this line of development the prosternal lobe tends to develop early.

The Dasytidae (Fig. 20) is apparently the most primitive and is very similar to the Pyrochroid (Fig. 17) of Group I, the prosternal lobe of the Dasytid being slightly longer than that of the Pyrochroid, and it is possible that this line of development originated from ancestors closely related to the Pyrochroid mentioned above. In all later members of this group the prosternal lobe is well developed, the furcasternum tends to develop, and the cervical sclerites tend to reduce in number. The Temnochilid (Fig. 21) with two pairs of cervical sclerites and slightly more developed furcasternum follows the Dasytid, while the Dryopid (Fig. 22) with less developed furcasternum, longer prosternal lobe, and reduced cervical sclerites follows the Temnochilid. The Cucujid (Fig. 23), which appears to have three pairs of cervical sclerites, is very similar to the Dryopid which it follows, having the postcoxal lobes more developed.

The Nosodendrid (Fig. 24) probably has its ancestors among Dasytid-like beetles and has developed the furcasternum and reduced the cervical sclerites. The prosternal lobe is also more developed than that of the Dasytid. The broad prosternal lobe and developed furcasternum of the Byrrhid (Fig. 25) shows a development from Dasytid-like ancestors and in this case the two pairs of cervical sclerites have been retained. The Cyphonid (Fig. 26) has also developed from Dasytid-like ancestors and the large cervical sclerites indicate a reduction in number. The Dascillid (Fig. 27) is placed in this position because the postcoxal lobes have formed a secondary projection (although the small furcasternum would indicate an earlier position). The Ptilodactylid (Fig. 28) has developed the prosternal lobe as well as the postcoxal lobe and furcasternum and evidently follows the Dascillid and precedes the Pselaphid (Fig. 29) which has greatly developed the furcasternum and lost the cervical sclerites. Despite the fact that one pair of cervical sclerites persists, the great development of the postcoxal lobes, furcasternum, and prosternal lobe places the Sphindid (Fig. 30) late in this line of development. The aberrant Anobiid (Fig. 31), having a very broad prosternal lobe and moderately developed postcoxal lobes, is latest in this group. The loss of cervical sclerites also indicates a more recent origin, although this family is difficult to place and may actually be far from this group.

Group III

Buprestidae, Plastoceridae, Elateridae, Trixagidae, Cebrionidae, Psephenidae, Melasidae, Erotylidae, Heteroceridae.

This group consists of members that have well developed prosternal lobes. The more primitive members have but a moderately developed furcasternum and two pairs of cervical sclerites. It appears that this line of development has arisen from Cucujid-like ancestors, although the postcoxal lobes in the primitive member (Fig. 32) of this group have not developed as much as have those of the Cucujid (Fig. 23).

The Buprestid (Fig. 32) is the most primitive member of this group and is followed by the Plastocerid (Fig. 33) which has a slightly more developed furcasternum as well as short postcoxal lobes. The Elaterid (Fig. 34) shows a further development of the postcoxal lobes and the furcasternum, although not entirely visible, is about the same as that of its predecessor, the Plastocerid. The Trixagid (Fig. 5), which follows, has developed the postcoxal lobes slightly further mesad and this family is followed by the Cebrionid (Fig. 35), which shows considerable development of the furcasternum. All of the above mentioned members of the group are also linked together by the presence of two pairs of cervical sclerites, and the eutrochantin of each is also quite similar. The Psephenid (Fig. 36) which follows the Cebrionid is very similar, the postcoxal lobes and furcasternum being but slightly more developed. This family, however, has lost one pair of cervical sclerites, while the eutrochantin shows somewhat more primitive features than its predecessors. The Melasid (Fig. 37) shows a further development of the furcasternum, short, narrow arms extending to the postcoxal lobes which have not developed further. The long eutrochantinal apodeme in this specimen, however, may indicate that this family is out of place. The Erotylid (Fig. 38) has developed the postcoxal lobes and furcasternum, while the cervical sclerites remain primitive. This family has been placed here since the postcoxal lobes show considerable development, although here again this specimen may have been misplaced. The Heterocerid (Fig. 39), which follows the above specimen, seems to be somewhat out of order, but is included in this group since the prosternal lobe is so well developed. This family evidently comes from an ancestor similar to that of the primitive Buprestid of the group, although the development seems to differ. The development of the eutrochantin indicates a somewhat in-between placement of this specimen with this and the following group.

Group IV

Rhipiceridae, Staphylinidae, Silphidae, Orthoperidae, Histeridae, Scarabaeidae, Lucanidae, Passalidae.

The Rhipicerid (Fig. 40), which is the most primitive member of this line of development, is possibly derived from ancestors related to the Meloid (Fig. 16), although in the Rhipicerid the cervical sclerites are not reduced in number. The eutrochantin consists of a broad trochantin, pleural region and short, broad apodeme. In this line of development the eutrochantinal apodeme tends to grow cephalad as well as latero-dorsad.

The Staphylinid (Fig. 41), which follows the Rhipicerid, has developed longer postcoxal lobes as well as a slightly more developed furcasternum. The eutrochantin of this form has a convexly-rounded apodeme extending slightly cephalad. The Silphid (Fig. 42), which follows the Staphylinid, is probably of equal primitiveness and is placed here since the cervical sclerites have reduced to one pair, although the furcasternum and eutrochantin are less developed than those of the Staphylinid. The Orthoperid (Fig. 43) probably originated from Staphylinid-like ancestors and has developed longer postcoxal lobes and a long prosternal lobe as well as having lost one pair of cervical sclerites. The eutrochantin forms a cephalad-extending apodeme which indicates a development over that of the Staphylinid.

The remaining members of this group have evidently developed from the same ancestors as the Orthoperid type as is indicated by the eutrochantin. The postcoxal lobes, prosternal lobe, and furcasternum of the Histerid (Fig. 44) and Scarabaeid (Fig. 45) show further developments in this line, and the eutrochantin of these forms continues extending the apodeme cephalad, where it is joined to the anterior edge of the trochantin. The cervical sclerites remain primitive in these two representatives but are reduced to but one pair in the Lucanid (Fig. 46) and Passalid (Fig. 47). The eutrochantin in these latter two forms has developed further and forms a large, convex, cephalad-extending apodeme. The furcasternum in these forms extends more dorsad than laterad and the postcoxal lobes extend to the well developed prosternal lobe.

Group V

Colydiidae, Elmidae, Pythidae.

The three representatives of this line of development do not readily fit into a phylogenetic pattern. It is possible that this group arose from Lymexylonid-like (Fig. 15) ancestors, since mesally the basisternum is produced caudally to form a prosternal lobe. Only in the Colydiid (Fig. 48) and Pythid (Fig. 50) is there evidence of postcoxal lobes. The Colydiid is the only form in this group possessing cervical sclerites, and but one pair is present. It is possible that the Colydiid arose from an ancestor common to the Anobiid (Fig. 31), although the cervical sclerites would place the Colydiid earlier than the Anobiid. The Elmid (Fig. 49) and Pythid are placed near the Colydiid since the prosternal lobe and furcasternum are but moderately developed, and only the slight postcoxal lobes of the Pythid have led the author to place it after the Elmid, although if the furcasternum and prosternal lobe are considered, the Elmid would be the more recent form. Since this group does not fit into any definite arrangement, and, since the slight development of postcoxal lobes indicate primitiveness, these forms have been grouped in this position.

Group VI

Cephaloidae, Dermestidae, Oedmeridae, Cleridae, Cryptophagidae, Chrysomelidae, Mycetophagidae, Phalacridae, Mordellidae, Leiodidae.

The furcasternum in this group is well developed, narrow arms extending to the postcoxal lobes in the more primitive forms, while greatly broadened arms extend to the postcoxal lobes in the more recent forms. Likewise, the prosternal lobe and postcoxal lobes are short in the primitive forms of the group and develop in the more recent forms. The cervical sclerites in the more primitive forms include two pairs, which reduce to one pair and finally none in the more recent forms, although several specimens which have developed the other structures, do retain the cervical sclerites.

The most primitive member of this group, the Cephaloid (Fig. 51), possibly arose from ancestors related to the Pyrochroid (Fig. 17). The cervical sclerites of the Pyrochroid and Cephaloid are similar, as are all structures except the furcasternum. The furcasternum of the Cephaloid has broadened extensively and extends to the postcoxal lobes. In the Dermestid (Fig. 52) the postcoxal lobes have developed further and the prosternal lobe is slightly longer, while the cervical sclerites consist of two pairs. In the Oedmerid (Fig. 53) the postcoxal lobes are less developed, while the prosternal lobe is longer and the cervical sclerites consist of two pairs. This form has possibly developed along slightly different lines than has the Dermestid. The Clerid (Fig. 54) has short postcoxal lobes, a long prosternal lobe, and cervical sclerites reduced to one pair. The Cryptophagid (Fig. 55), Chrysomelid (Fig. 56), Mycetophagid (Fig. 57), and Phalacrid (Fig. 58) have evidently developed from Clerid-like ancestors and have developed the prosternal lobe as well as the postcoxal lobes. In the Mycetophagid and Phalacrid the furcasternum forms broader junctions with the postcoxal lobes than are apparent in the early members of this group. In addition, the members of this group shown in Figs. 55-58 have lost the cervical sclerites.

The Mordellid (Fig. 59) and Leiodid (Fig. 60) have been placed in this group since the furcasternum and postcoxal lobes follow the trends of the earlier members of this group. The precoxal bridges and basisternum are slender and the prosternal lobe, although slender, is well developed. These forms, however, possess cervical sclerites and must have arisen from earlier members of this group through intermediate stages or lines not shown in this brief study. The postcoxal lobes and furcasternum, however, place these members as of more recent origin than the presence of cervical sclerites indicates.

Group VII

Serropalpidae, Hydrophilidae, Endomychidae, Coccinellidae.

It is possible that this group originated from Pyrochroid-like ancestors which may have been similar to those of the Cephaloid of the preceding group. The furcasternum and postcoxal lobes of this group show a greater development than those of the preceding group.

The Serropalpid (Fig. 61) has moderately long postcoxal lobes, a well developed furcasternum, and a very short prosternal lobe. The Hydrophilid (Fig. 62) has been placed after the Serropalpid because of the greater postcoxal development, although the cervical sclerites would indicate an interchange of positions. The Endomychidae (Fig. 63) shows continued development of the furcasternum and prosternal lobe, while the cervical sclerites consist of but one pair and the postcoxal lobes remain about the same as those of earlier members of the group. The Coccinellid (Fig. 64), which follows, shows a greater development of the postcoxal lobes and prosternal lobe, although the furcasternum appears somewhat less developed and the cervical sclerites still consist of one pair. The trochantin of these members is fairly long and aids in indicating a not too recent origin for this group.

Group VIII

Scaphidiidae, Ptinidae, Scydmaenidae, Bostrychidae, Colonidae, Platypodidae.

The development of this group appears mainly in the furcasternum, the postcoxal lobes and prosternal lobe developing very slowly. It appears very likely that this group originated from ancestors derived from Lycid (Fig. 14) and Phengodid (Fig. 19) like precursors.

The Scaphidiid (Fig. 65) has short postcoxal lobes and a broad furcasternum which joins the postcoxal lobes, and is the only member of the group possessing cervical sclerites. The prosternal lobe consists of a short pointed posterior extension of the basisternum. The Ptinid (Fig. 66) differs from its immediate predecessor only in the lack of cervical sclerites. In the Scydmaenid (Fig. 67) the postcoxal lobes are slightly more developed and greatly developed furcasternum forms broad junctions with the postcoxal lobes. In the Bostrychid (Fig. 68) the furcasternum is equally well developed and forms broader junctions with the lengthened postcoxal lobes, while the prosternal lobe is still short and pointed. In the Colonid (Fig. 69) the prosternal lobe is slightly more developed and the junctions of furcasternum and postcoxal lobes are very broad. The furcasternum of the Platypodid (Fig. 70) is well developed and forms broad junctions with the postcoxal lobes, while the prosternal lobe is pointed and longer than that of its predecessors in the group. In this family the pronotum and precoxal bridges have fused. Despite the fact that the family Platypodidae is usually placed with the Scolytids, Curculionids, etc., morphological evidence based on the prothoracic structures seems to place this family late in this line of development.

Group IX

Byturidae, Bruchidae, Lathridiidae, Nilionidae.

The postcoxal lobes in this line of development are well developed and extend to or nearly to the prosternal lobe, while the furcasternum is also well developed. The Byturid (Fig. 71), which possesses one pair of cervical sclerites, is the only member of this group having such structures, and this family is considered the most primitive of the group. It is quite probable that this group arose from ancestors related to the Mordellid (Fig. 59) and Leoidid (Fig. 60), since both of these representatives possess cervical sclerites, a well developed furcasternum, and shorter postcoxal lobes than those of this group. The postcoxal lobes of the Byturid extend to the well developed prosternal lobe and are also joined by the well developed furcasternum. The postcoxal lobes and prosternal lobe of the Bruchid (Fig. 72) are slightly less developed than those of the Byturid, while the furcasternum is more highly developed and the cervical sclerites are lacking. The Lathridiid (Fig. 73)has the postcoxal lobes meeting the long, well developed prosternal lobe, and the furcasternum appears to be secondarily cut up into fragments. The Nilionid (Fig. 74) has well developed furcasternum and postcoxal lobes, and, since the eutrochantin is more developed, is arranged following the Lathridiid. The eutrochantin of the Bruchid is long and could possibly indicate a more primitive position in the group for this form. It appears, however, that the members of this group for this form, are very similar and should probably be placed merely as a group with no attempt at phylogenetic arrangement.

Group X

Monommidae, Tenebrionidae, Nitidulidae, Alleculidae, Languriidae.

With the exception of the Monommid (Fig. 11), this group has a well developed prosternal lobe and well developed postcoxal lobes that are joined by the furcasternum. This group possibly had its origin from ancestors similar to the Cryptophagid (Fig. 55). The Monommid has short postcoxal lobes and a moderately developed furcasternum, which, however, does not extend to the postcoxal lobes. The prosternal lobe is well developed. The Tenebrionid (Fig. 75) closely follows the Monommid, although in this form the postcoxal lobes nearly meet the prosternal lobe and the furcasternum is more developed. The suture (x) in both forms is nearly identical as is also the eutrochantin. The Nitidulid (Fig. 76) is placed here since it has well developed postcoxal lobes, furcasternum, and prosternal lobe, while still retaining one pair of cervical sclerites. The condition of the cervical sclerites seems to indicate a more primitive position than does the eutrochantin, and this form may actually be much later in this group or possibly in some other group. The Alleculid (Fig. 77) shows a similar development to that of the

Tenebrionid and is possibly more recent, since the long trochantin of the Tenebrionid has become shorter in this form. The Languriid (Fig. 78) shows similar development of the postcoxal lobes, furcasternum, and prosternal lobe, and, although the sternum is much longer, the morphological structures closely relate this form to the preceding forms.

Group XI

Cerambycidae, Cupesidae, Gyrinidae, Dytiscidae, Carabidae, Cicindelidae, Rhysodidae, Haliplidae, Paussidae.

The moderate lengthened postcoxal lobes, well developed furcasternum, and narrow prosternal lobe of the most primitive Cerambycid (Fig. 7) indicates a possible origin of the Cerambycids from ancestors related to the Serropalpid (Fig. 61) and Endomychid (Fig. 63). The Cerambycids have lost the cervical sclerites, and in the Cerambycids (Figs. 7 & 8) the postcoxal lobes are well developed. The eutrochantin, as was pointed out above, sets up a line of development leading to that of the Adephagous type, wherein the apodeme is totally reduced and the articulating condyles closely apposed. It has also been shown that the suture (d) of the Adephaga is secondarily formed, and it is probable that the Adephagous beetles (Figs. 80-85) arose from Cerambycid-like ancestors which developed secondary sutures in much the same manner as would be possible through Monommid-like (Fig. 11) precursors which have a similarly situated groove (g). The Cupesidae (Fig. 79) has been placed here since it has the secondary suture (d). The furcasternum and postcoxal lobes of the Cupesid are poorly developed, however, and the eutrochantin is similar and possibly more primitive than that of the Adephaga. The Adephaga are arranged mainly on the basis of postcoxal lobe development; from the short lobes of the Gyrinid (Fig. 80) and Dytiscid (Fig. 81), through the longer lobes of the Carabid (Fig. 12) and Cicindelid (Fig. 82), to the prosternal lobe-touching lobes of the Rhysodid (Fig. 83), to the mesally fused lobes of the Paussid (Fig. 85). The prosternal lobe develops at about the same rate as the postcoxal lobes, and for this reason the Haliplid (Fig. 84) is placed after the Rhysodid, although the postcoxal lobes of the Haliplid are less developed. The prosternal lobe of the Paussid, however, is narrow and less developed, and has possibly been secondarily reduced by "crowding" of the furcasternum. Whatever the exact position of this group, morphological evidence based on the prothorax precludes the primitive condition given the Adephagous beetles by most writers. This morphological study of the prothorax actually shows the Adephaga to be well advanced along the Coleopterous path of evolution.

Group XII

Rhipiphoridae, Anthicidae, Lagriidae, Lyctidae, Monotommidae, Brenthidae, Curculionidae, Anthribidae, Scolytidae, Proterhinidae.

This line of development, which starts with the Rhipiphorid (Fig. 86), possibly arose from ancestors related to the Serropalpid (Fig. 61) and Endomychid (Fig. 63), as did those of group XI, and has followed a line of development leading to the highest development of trends exhibited by beetles. The postcoxal lobes of the Rhipiphorid are of only moderate length, while the furcasternum is well developed and the prosternal lobe is short and pointed. In the Anthribid (Fig. 87) the postcoxal lobes and prosternal lobe are more developed, while the furcasternum remains about the same. In the Lagriid (Fig. 88) the postcoxal lobes and prosternal lobe are further developed, the furcasternum remaining static. In the Lyctid

(Fig. 89) the postcoxal lobes and prosternal lobe are well developed and the furcasternum is greatly developed. The Monotommid (Fig. 90) is placed here since the coxal cavities are closed and the prosternal lobe is greatly developed. The furcasternum appears to be less developed, however, and it is possible that this form may be of somewhat less recent origin than this position indicates. The Brenthid (Fig. 91) has postcoxal lobes which join mesally and the furcasternum is well developed, a mesal, pentagonal sclerite lying between the postcoxal lobes and prosternal lobe and possibly being a portion of the furcasternum. In the Curculionid (Fig. 92) a similar appearance is given, although the prosternal lobe has shortened. The Curculionid (Fig. 93) has the postcoxal lobes fused, and only a suture lying between the prosternal lobe and the postcoxal lobes (or furcasternum to which the lobes are fused) is visible. The Anthribid (Fig. 94) shows a similar fusion of sclerites, and the Scolytid (Fig. 95) and Proterhinid (Fig. 96), which follow the Anthribid, are placed here since they have apparently followed a development similar to that of Figs. 92, 93, & 94. The author, however, has simply placed these latter specimens here and does not attempt to call any one form more recent than similar types. Fusion or partial fusion of the precoxal bridges and pronotum occurs in all of the members of this group, and this is evidently a late stage of development. In Figs. 93-96 the sclerites have so fused as to preclude any definite demarking of particular sclerites.

As has been stated above, this phylogenetic arrangement of twelve groups should be considered as very tentative. While the most primitive and most recent beetles are somewhat accurately placed from a phylogenetic standpoint in Groups I and XII, the arrangement of the intermediate groups must be considered as very tentative until more work is done. It should be apparent, however, that the Adephagous beetles placed in Group XI are rather highly evolved and not of a primitive origin as is generally assumed.

SUMMARY

Morphological evidence shows that the prothoracic sclerites of the Polyphaga and Adephaga are homologous. The reduced eutrochantin of the Adephaga has been shown to be homologous to the eutrochantin of the Polyphaga. The upper pleural region joins the precoxal bridge, while the lower pleural region is joined to the trochantin. The overlapping pronotum in both groups is made up of pronotum alone, the longitudinal suture on the inflexed portion of the Adephagous pronotum being secondarily formed.

The Polyphaga are characterized by the presence of a eutrochantin consisting of the trochantin and lower pleural region. The pleural suture of the lower pleural region forms an internal ridge or apodeme. The upper pleural region is joined to the precoxal bridge, although it has become rudimentary or completely fused with the precoxal bridge. The overlapping pronotum is made up of pronotum alone.

The Adephaga are characterized by a secondary longitudinal suture that cuts off the inflexed pronotum. The eutrochantin is small and reduced, and the major functional coxal condyle may be on the inflexed pronotum. The upper pleural region apparently has joined the precoxal bridge in the same manner as shown by the Polyphaga. The overlapping pronotum is made up of pronotum alone.

A comparative study of the prothoracic sclerites shows the families of Coleoptera to be poorly grouped in many of the superfamilies. Superfamilies frequently include families that are entirely unrelated when the prothoracic sclerites are compared.

The author has grouped the studied families of Coleoptera into a very tentative phylogenetic arrangement of twelve groups based on the prothoracic sclerites. This grouping shows the families of Group I to be the most primitive and the families of Group XII to be the most recent. The Adephagous beetles are included in a group that is well along the road of evolution and far from the primitive state usually assigned them.

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Abbreviations

a	transverse suture on inflexed pronotum
ao	secondary or auxiliary condyle
ap	apodeme or internal ridge
b	transverse infolding or groove on inflexed pronotum
bs	basisternum
c	lateral or median carina
cc	coxal cavity
cvs	cervical sclerite
cx	coxa
d	subnotal suture or fold
e	postpseudopleural suture, (secondary suture on inflexed pronotum or lateral plate)
em	epimeron
eps	episternum
etn	eutrochantin
fa	furcal arm
fp	furcal pit
fs	furcasternum
g	longitudinal infolding or groove on inflexed pronotum
h	secondary invagination or suture
p	lateral plate, pleuron, pseudopleurum, (Adephaga)
pc	precoxal bridge, precoxale
pn	pronotum
ps	pleural suture
psl	prosternal lobe
px	postcoxal lobe or bridge
s	sulcus
sp	spiracle (mesothoracic)
tn	trochantin
x	precoxal suture or fold
y	precoxal suture or fold (Fig. 12)

Explanation of Figures

Plate 1.

Fig. 1	Cryptocercus punctulatus	(Orthoptera)
Fig. 2	Stagmomantis carolina	(Orthoptera)
Fig. 3	Taeniopteryx nivalis Fitch	(Plecoptera)
Fig. 4	Cantharis rotundicollis Say	(Cantharidae)
Fig. 5	Trixagus chevrolati Bonv.	(Trixagidae)
Fig. 6	Lycopolemius rouyeri Pic.	(Cantharidae)
Fig. 7	Criocephalus agrestis Kby.	(Cerambycidae)
Fig. 8	Saperda tridentata Oliv.	(Cerambycidae)
Fig. 9	Oberea bimaculata Oliv.	(Cerambycidae)
Fig. 10	Schistocerca americana	(Orthoptera)
Fig. 11	Hyporrhagus opuntiae Horn	(Monommidae)
Fig. 12	Harpalus caliginosus Fab.	(Carabidae)

Plate 2.

Fig. 13	Lucidota corrusca L.	(Lampyridae)
Fig. 14	Eros aurora Hbst.	(Lycidae)
Fig. 15	Melittomma sp.	(Lymexylonidae)
Fig. 16	Epicauta cinerea Forst.	(Meloidae)
Fig. 17	Neopyrochroa flabellata	(Pyrochroidae)
Fig. 18	Malachius aeneus L.	(Malachiidae)
Fig. 19	Phengodes plumosa Oliv.	(Phengodidae)
Fig. 20	Dasytes niger L.	(Dasytidae)
Fig. 21	Tenebroides marginicolle Melsh.	(Temnochilidae)
Fig. 22	Dryops auriculatus Geoff.	(Dryopidae)
Fig. 23	Cucujus clavipes Fab.	(Cucujidae)
Fig. 24	Nosodendron unicolor Say	(Nosodendridae)

Plate 3.

Fig. 25	Byrrhus cyclophorus Kbs.	(Byrrhidae)
Fig. 26	Cyphon concinnus Lec.	(Cyphonidae)
Fig. 27	Dascillus cervina L.	(Dascillidae)

Fig. 28	Ptilodactyla serricollis Say	(Ptilodactylidae)
Fig. 29	Decarthron stigmosum Brend.	(Pselaphidae)
Fig. 30	Eurysphindus hirtus Lec.	(Sphindidae)
Fig. 31	Hadrobregmus carinatus Say	(Anobiidae)
Fig. 32	Chalcophora virginiensis Drury	(Buprestidae)
Fig. 33	Euthysanius lautus Lec.	(Plastoceridae)
Fig. 34	Aeolus dorsalis Say	(Elateridae)
Fig. 35	Cebrio bicolor Fab.	(Cebrionidae)
Fig. 36	Psephenus lecontei Lec.	(Psephenidae)

Plate 4.

Fig. 37	Isorhips ruficornis Say	(Melasidae)
Fig. 38	Megalodacne fasciata Fab.	(Erotylidae)
Fig. 39	Heterocerus near undatus	(Heteroceridae)
Fig. 40	Sandalus niger Knoch	(Rhipiceridae)
Fig. 41	Staphylinus maculosus Grav.	(Staphylinidae)
Fig. 42	Silpha inaequalis Fab.	(Silphidae)
Fig. 43	Anthobium convexum Faur.	(Orthopteridae)
Fig. 44	Hister obtusatus Harris	(Histeridae)
Fig. 45	Phyllophaga fusca Froehlich	(Scarabaeidae)
Fig. 46	Pseudolucanus capreolus L.	(Lucanidae)
Fig. 47	Passalus cornutus Fab.	(Passalidae)
Fig. 48	Bothrideres geminatus Say	(Colydiidae)

Plate 5.

Fig. 49	Stenelmis crenata Say	(Elmidae)
Fig. 50	Pytho niger Kby.	(Pythidae)
Fig. 51	Cephaloon lepturides Newm.	(Cephaloidae)
Fig. 52	Dermestes lardarius L.	(Dermestidae)
Fig. 53	Nacerda melanura L.	(Oedmeridae)
Fig. 54	Enoclerus quadriguttatus Oliv.	(Cleridae)
Fig. 55	Antherophagus ochraceus Melsh.	(Cryptophagidae)
Fig. 56	Calligrapha sp.	(Chrysomelidae)
Fig. 57	Typhaea fumata L.	(Mycetophagidae)
Fig. 58	Stilbus nitidus Melsh.	(Phalacridae)
Fig. 59	Mordella scutellaris Fab.	(Mordellidae)
Fig. 60	Leiodes discolor Melsh.	(Leiodidae)

Plate 6.

Fig. 61	Melandrya striata Say	(Serropalpidae)
Fig. 62	Hydrophilus triangularis Say	(Hydrophilidae)
Fig. 63	Lychoperdina ferruginea Lec.	(Endomychidae)
Fig. 64	Anatis quindecimpunctata Oliv.	(Coccinellidae)
Fig. 65	Scaphisoma convexum Say	(Scaphidiidae)
Fig. 66	Ptinus fur L.	(Ptinidae)
Fig. 67	Connophron fossiger Lec.	(Scydmaenidae)
Fig. 68	Xylobiops basillare Say	(Bostrychidae)
Fig. 69	Colon magnicolle Mann	(Colonidae)
Fig. 70	Platypus compositus Say	(Platypodidae)
Fig. 71	Byturus bakeri Bar.	(Byturidae)
Fig. 72	Bruchus obtectus Say	(Bruchidae)

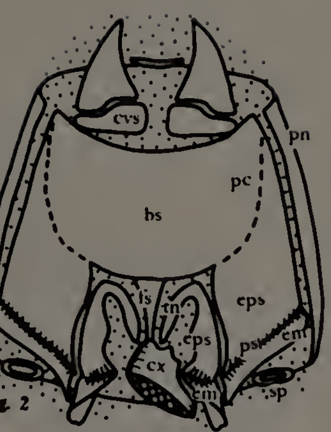
Plate 7.

Fig. 73	Melanophthalma distinguenda Com.	(Lathridiidae)
Fig. 74	Nilio lanatum Germ.	(Nilionidae)
Fig. 75	Tenebrio picipes Hbst.	(Tenebrionidae)
Fig. 76	Omosita colon L.	(Nitidulidae)
Fig. 77	Isomira quadristriata Couper	(Alleculidae)
Fig. 78	Acropteroxys gracilis Newn.	(Languriidae)
Fig. 79	Cupes capitatus Fab.	(Cupesidae)
Fig. 80	Dineutes nigrior Rbts.	(Gyrinidae)
Fig. 81	Acilius semisulcatus Aube	(Dytiscidae)
Fig. 82	Omus dejeani Rehe.	(Cicindelidae)
Fig. 83	Clinidium sculptile Newn.	(Rhysodidae)
Fig. 84	Peltodytes shermani (Rbts.)	(Haliplidae)

Plate 8.

Fig. 85	undertermined Paussid sp.	(Paussidae)
Fig. 86	Macrosiagon limbatum Fab.	(Rhipiphoridae)
Fig. 87	Notoxus monodon Lec.	(Anthicidae)
Fig. 88	Anthromacra aenea Say	(Lagriidae)
Fig. 89	Lyctus linearis Goeze	(Lyctidae)
Fig. 90	Monotoma americana Aube	(Monotomidae)
Fig. 91	Eupsalis minuta Drury	(Brenthidae)
Fig. 92	Lixus concavus Say	(Curculionidae)
Fig. 93	Cryptorhynchus lapathi L.	(Curculionidae)
Fig. 94	Euparius marmoreus Oliv.	(Anthribidae)
Fig. 95	Dendroctonus piceaperda Hopk.	(Scolytidae)
Fig. 96	Proterhinus maurus Perkins	(Proterhinidae)

Fig. 1



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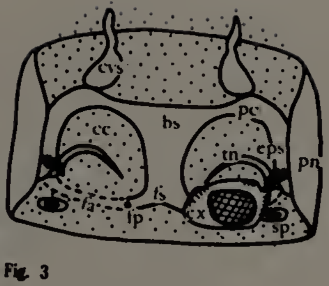

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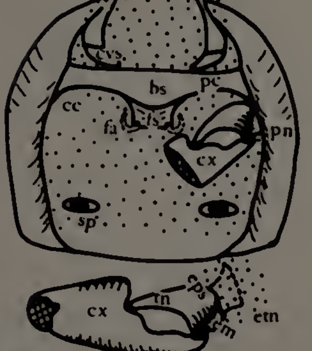

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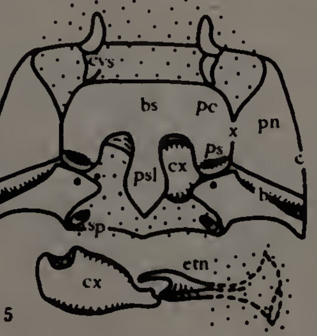

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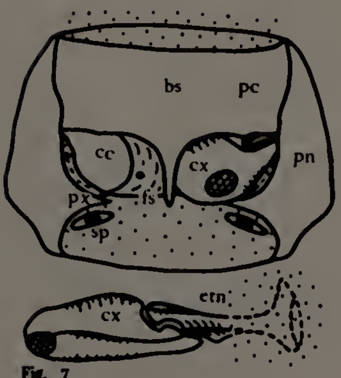

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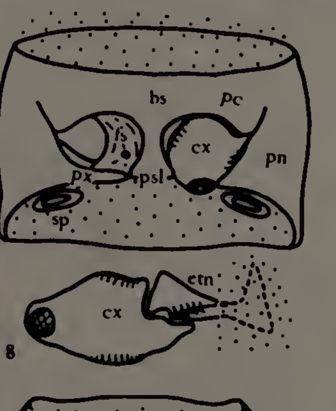

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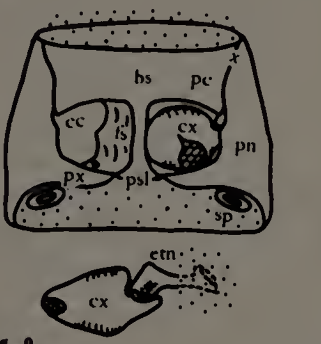

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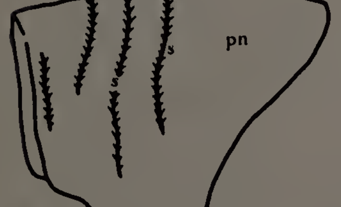

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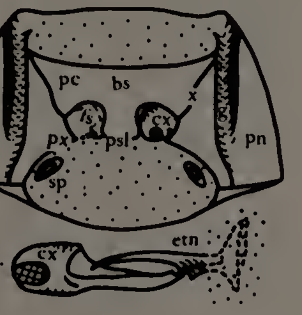

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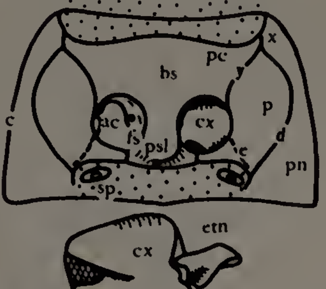
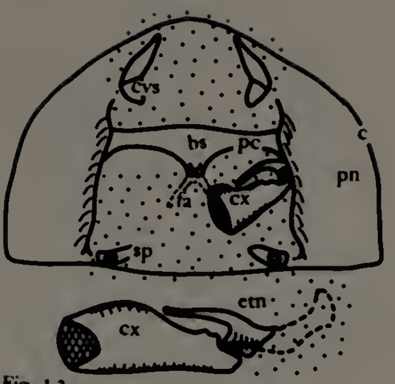


Fig. 12

Plate 1



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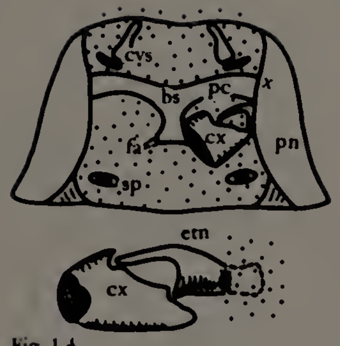

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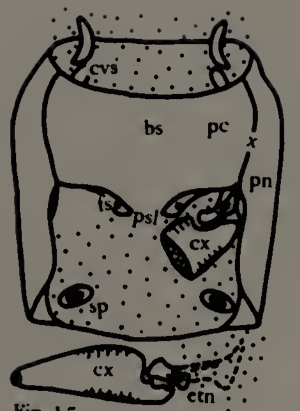

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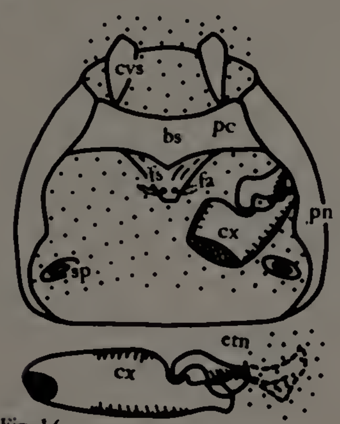

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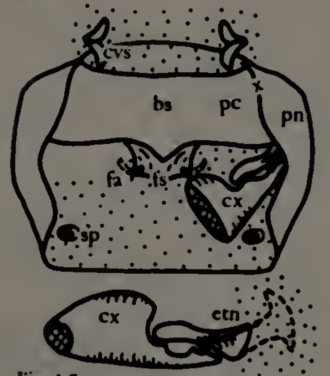

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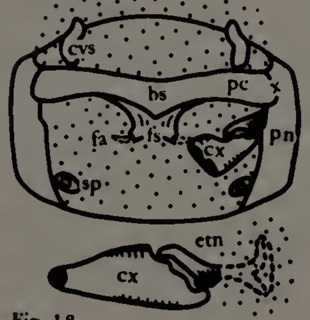

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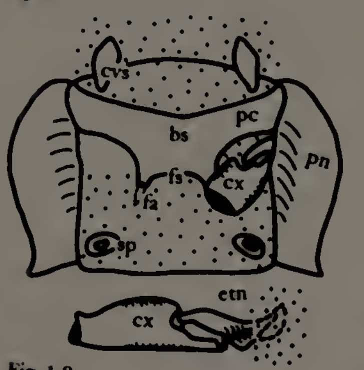

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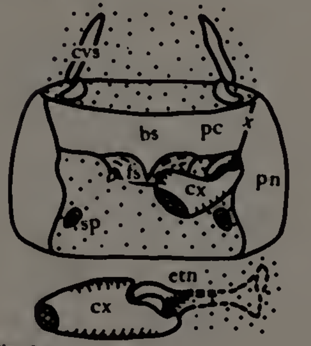

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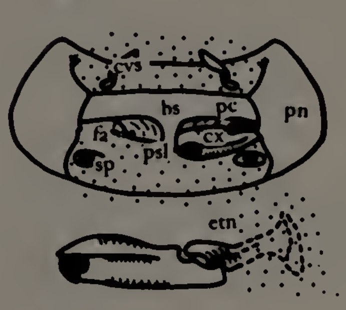

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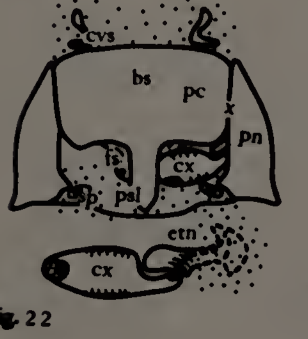

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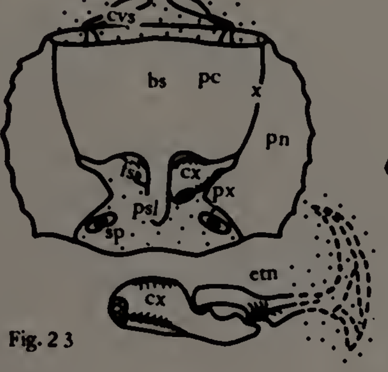

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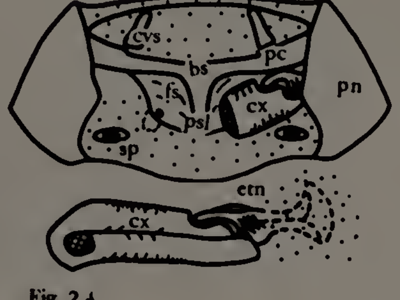
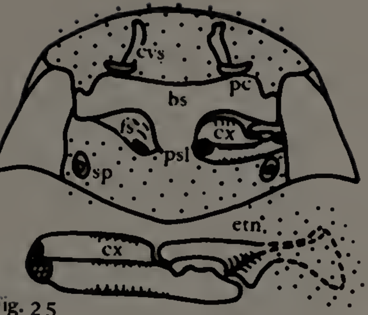


Fig. 24

Plate 2



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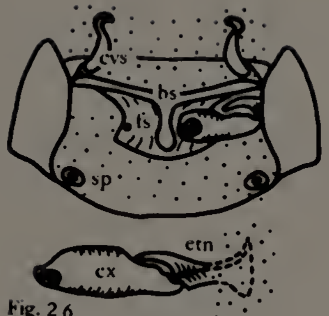

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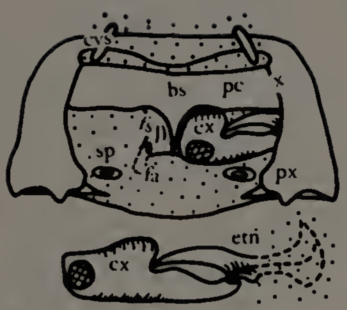

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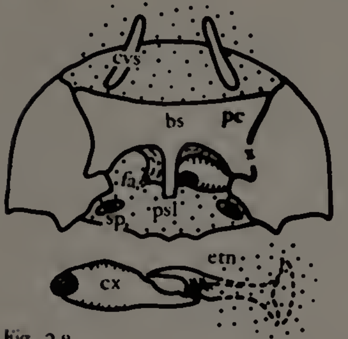
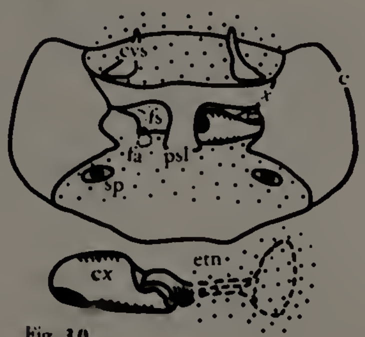


Fig. 28

Fig. 29



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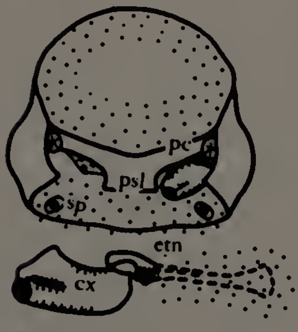

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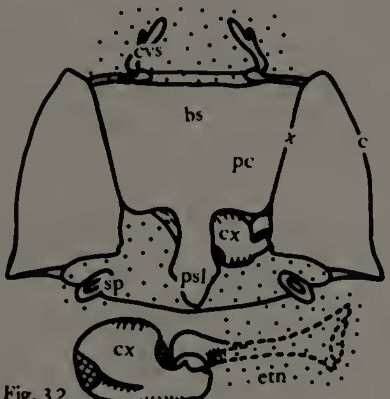

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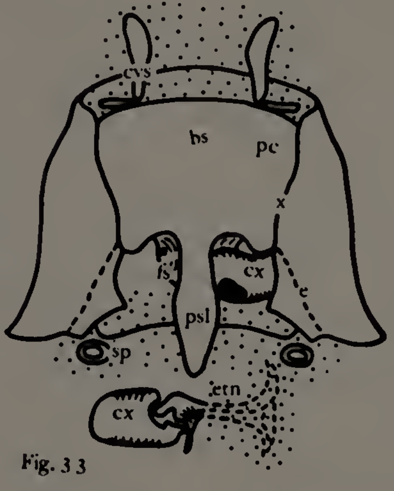

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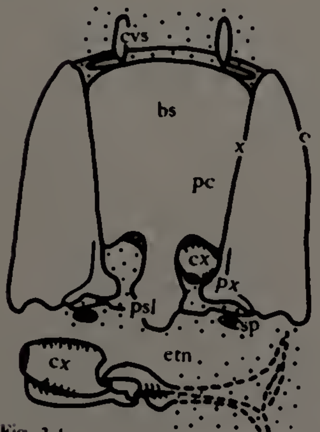

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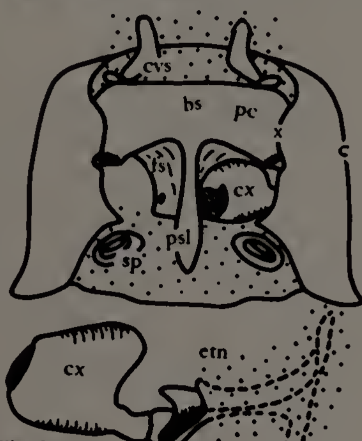

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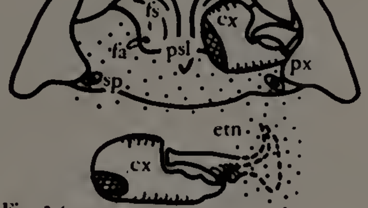

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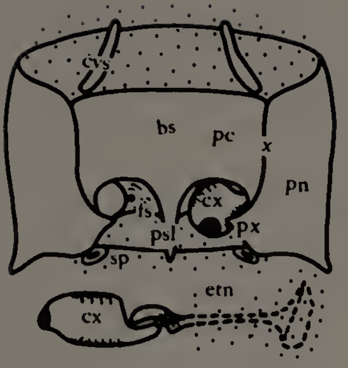

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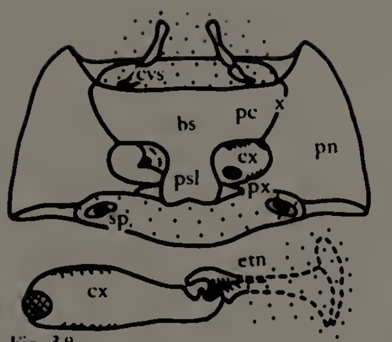

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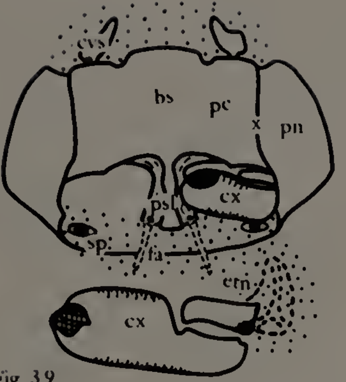

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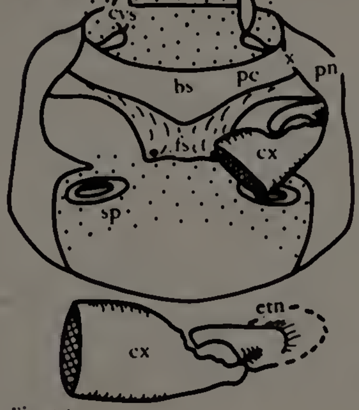
Fig. 40



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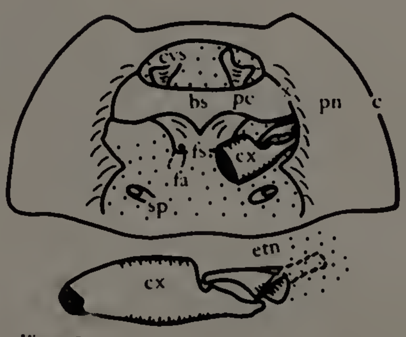

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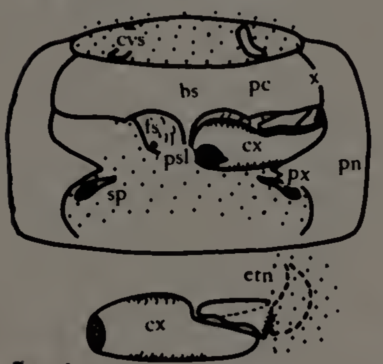

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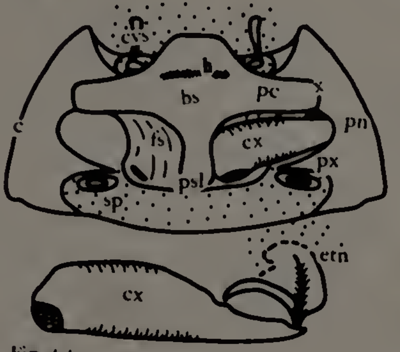

Fig. 44

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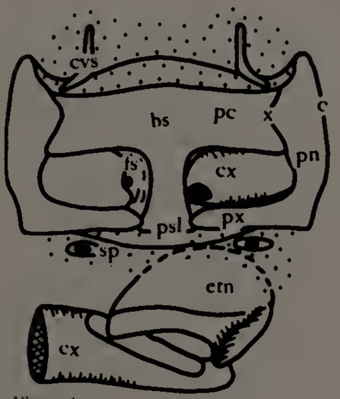

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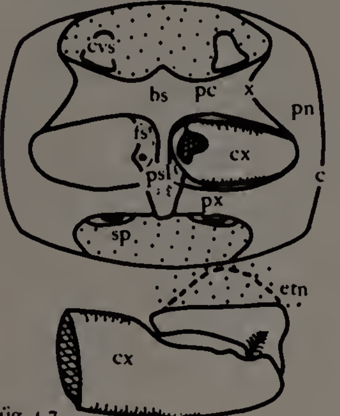

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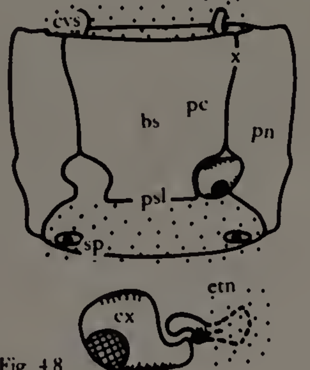

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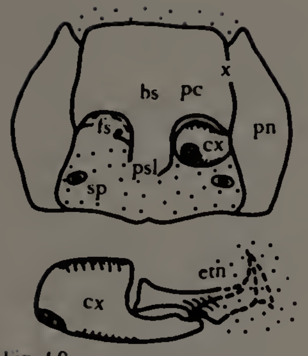
Plate 4



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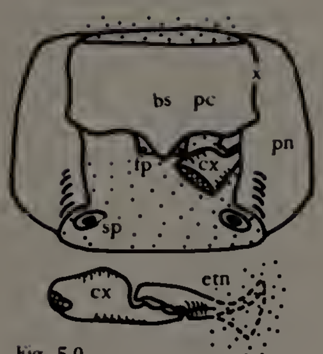

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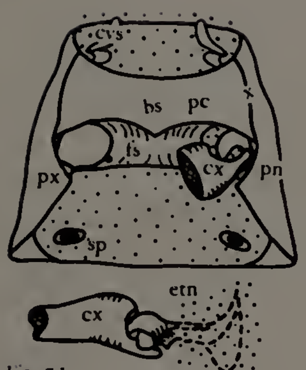

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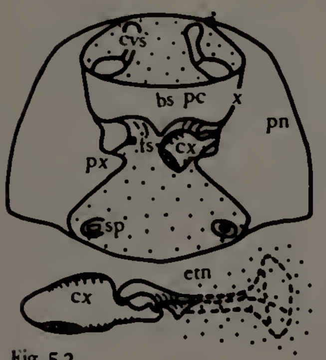

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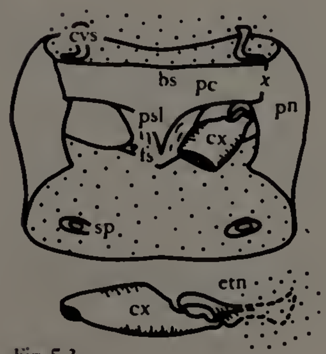

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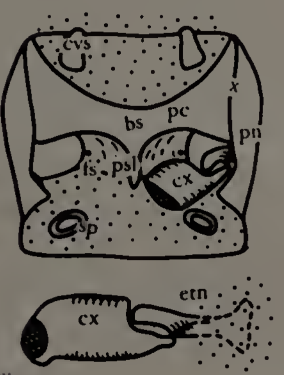

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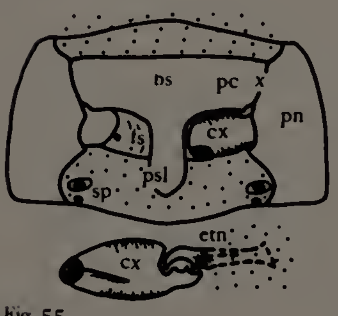

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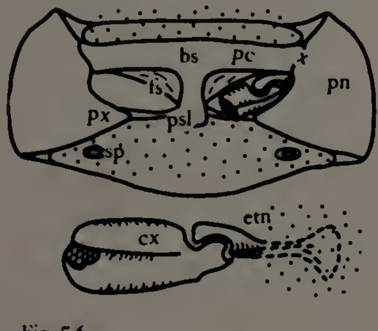

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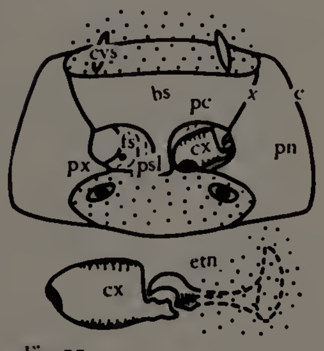

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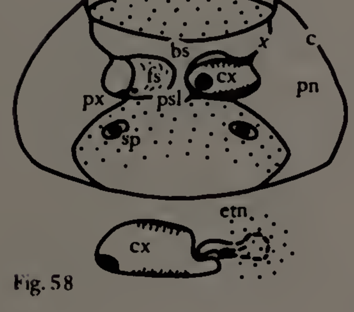
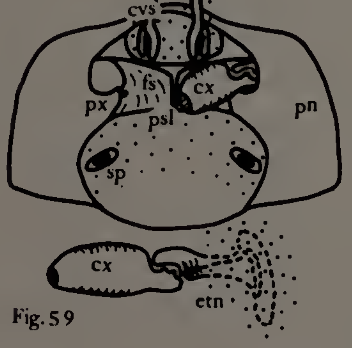


Fig. 58



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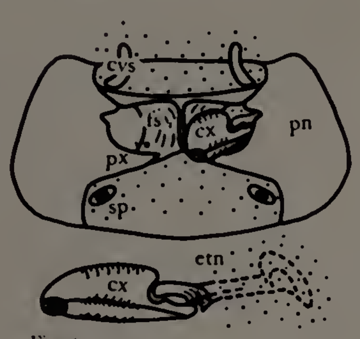
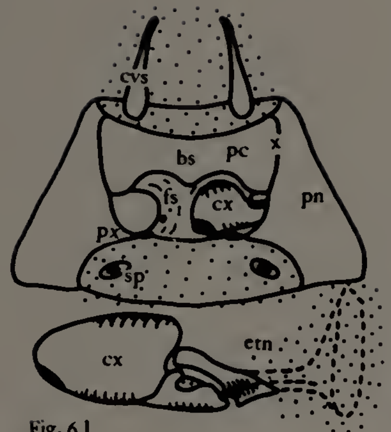


Fig. 60

Plate 5



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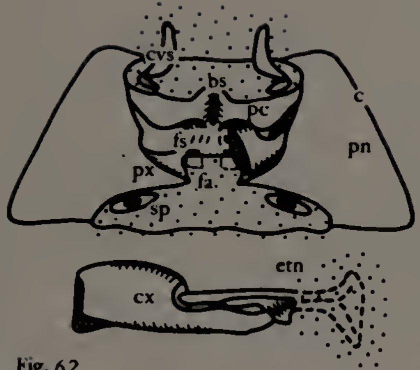

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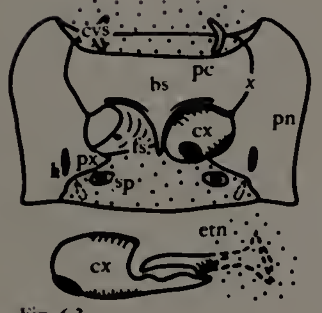

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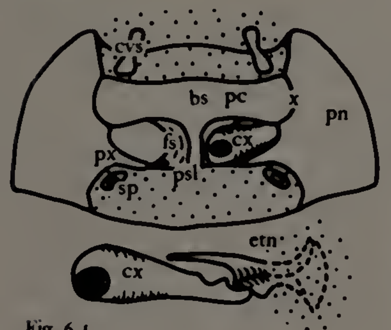

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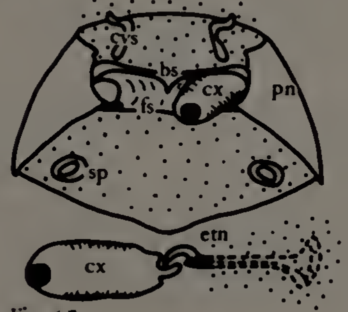

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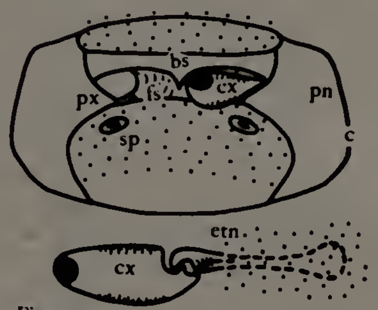

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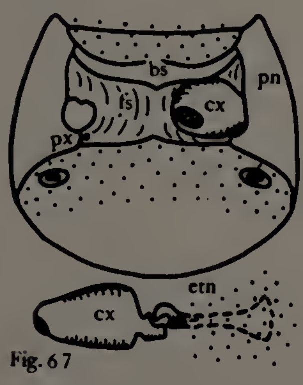

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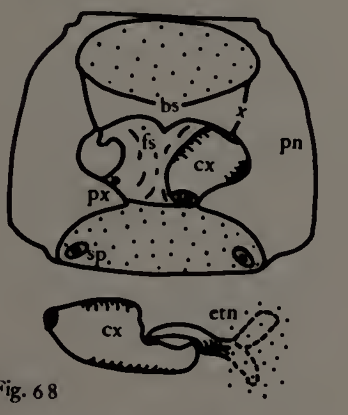

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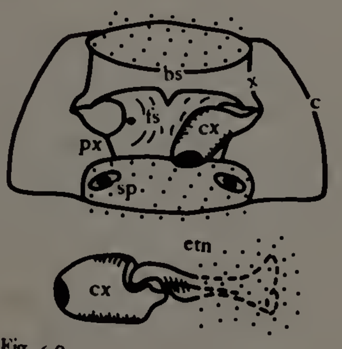

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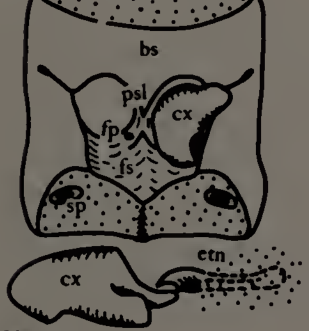

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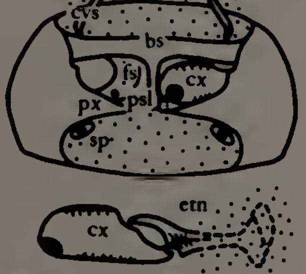

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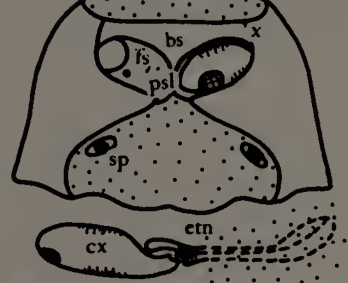
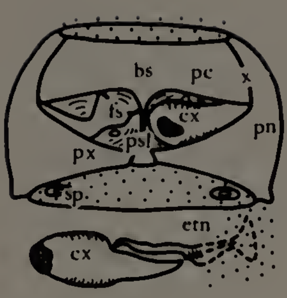


Fig. 72

Plate 6



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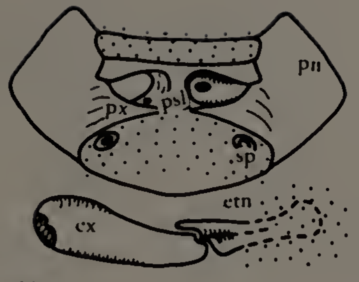

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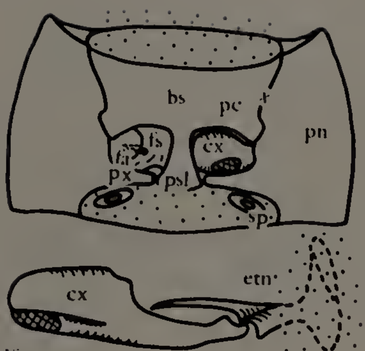

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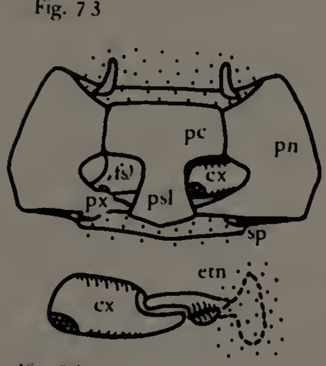

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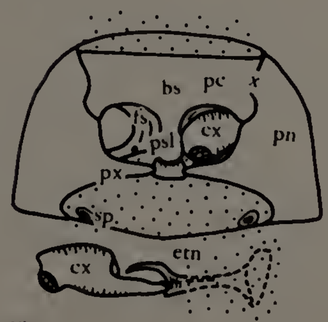

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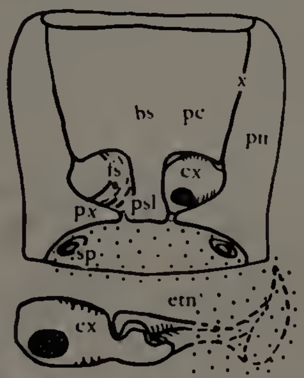

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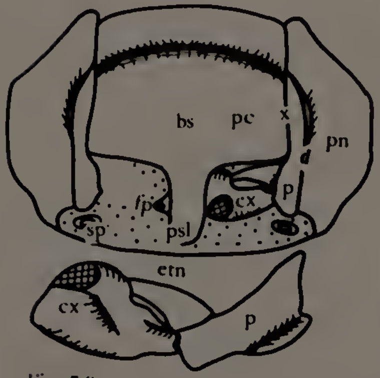

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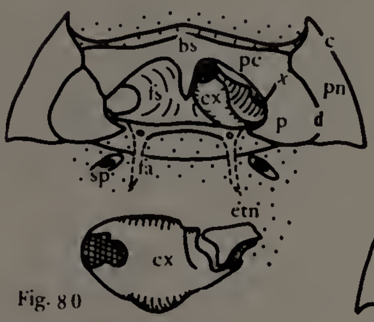

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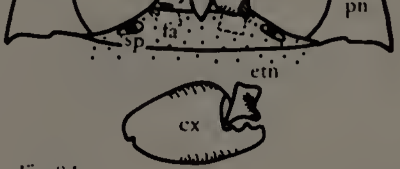

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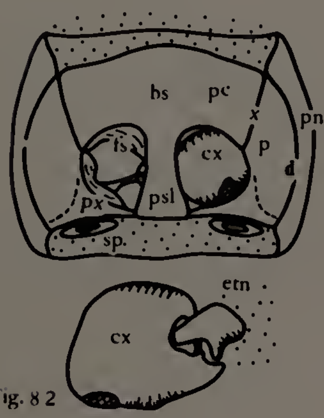

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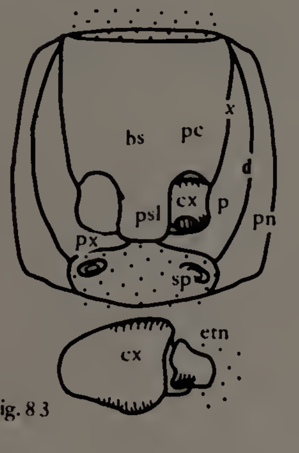

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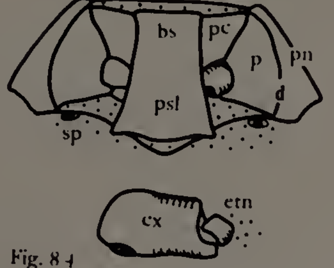
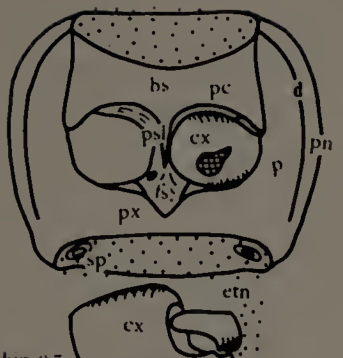


Fig. 84

Plate 7



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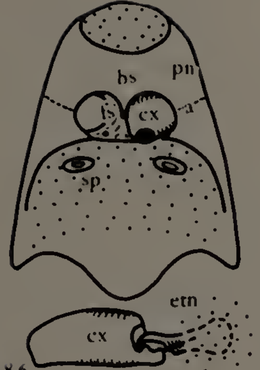

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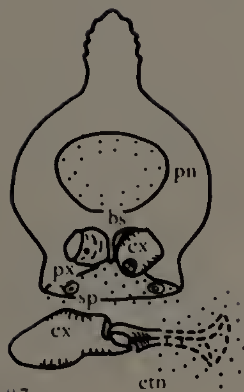

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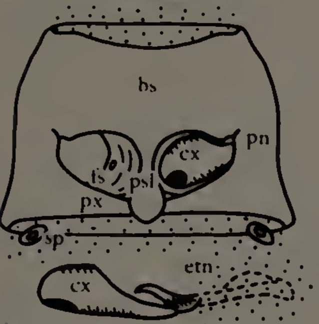

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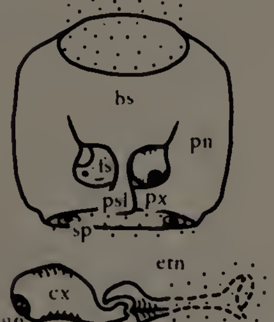

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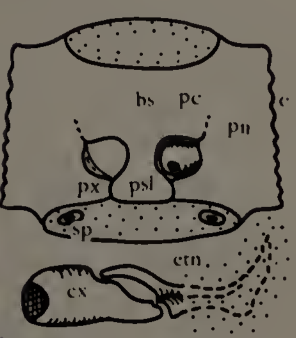

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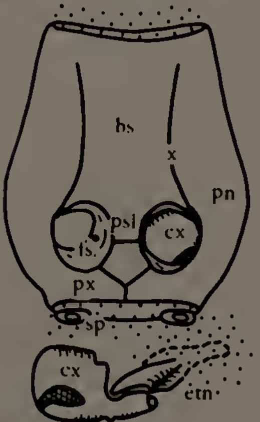

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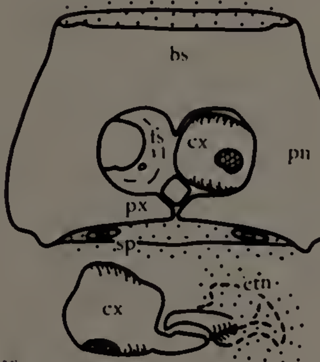

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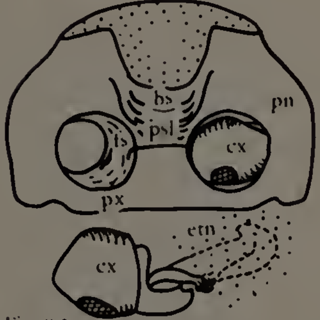

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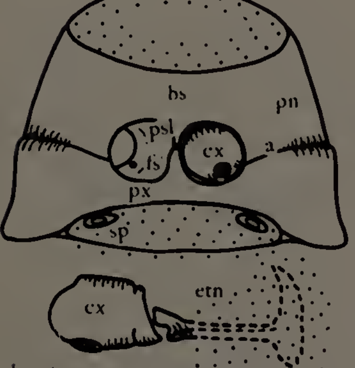

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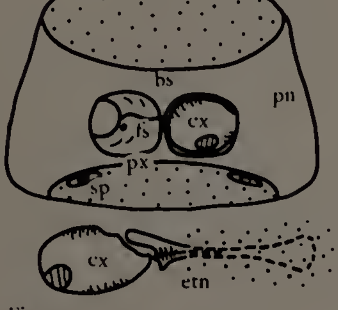

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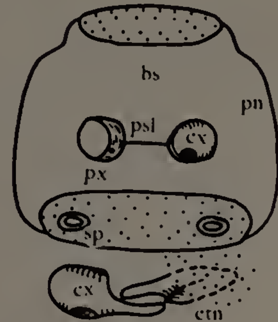

Fig. 96

Plate 8

Approved by

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Graduate Committee

Date May 18 1948