

THE PROTHORAX OF COLEOPTERA: (EXCEPT BOSTRICHIFORMIA-CUCUJIFORMIA)

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ABSTRACT. Variation in prothoracic structure is documented for a portion of the Polyphaga and for the three other suborders of Coleoptera. The structural diversity detected through examination, and usually dissection, of over 350 genera is presented in 166 figures representing 121 genera.

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INTRODUCTION

The prothorax is the most variable element of the extremely diverse locomotory system of Coleoptera. Parallelism and convergence are dominant themes in prothorax evolution. For this reason, characters of high weight are not common. However, comparison of transformation series between higher taxa can yield improved hypotheses on both phyletic and biological diversification of the higher categories of beetles (Hlavac, in press). Such inferences need to be based on prior analysis of within-group variation. This type of basic data on comparative structure is presented below; the Cucujiformia are to be treated in a similar fashion.

An introduction to morphology and the major elements of variation of the coleopterous prothorax is given elsewhere (Hlavac, 1972).

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MATERIALS AND METHODS

The number of forms dissected within a higher taxon depended roughly on a group's size and systematic complexity as well as on the amount of variation detected. Variation was estimated by routine dissection of common genera and in external examination of specimens from a nearly complete synoptic collection of beetle tribes.

Usually three dry, determined specimens per species were relaxed in hot water and removed from pins or points. The prothoraces of two examples were isolated while the whole relaxed third specimen was placed in alcohol along with the heads and remaining parts of the other two. Detached structures were treated in warm 10% potassium hydroxide for about five minutes and then flushed with a stream of water from a hypodermic syringe. If large amounts of solid muscle tissue remained, treatment continued until the tissue was soft enough to be flushed out. After the pericoxal membrane was ruptured and the coxa was moved laterally, one prothorax was sliced parasagittally with a razor blade leaving the sternal projection untouched. If the notopleural joint was membranous, the pleuron and coxa were

then detached from the smaller section. The larger section was then examined in lateral view. If the internal boundaries of the endopleuron, sternal and notal rim-folds, as well as the enclosed portions of the coxa and trochantin, were not readily visible in very strong transmitted light, the section was bleached and cleared along with the unsectioned prothorax in hydrogen peroxide with a few drops of KOH. The detached pleuron and coxa were cleared separately, or if necessary, stained with Chlorazol Black.

The standard study series then consisted of: one whole relaxed specimen, one whole cleared prothorax, and one sectioned cleared prothorax with pleuron and coxa detached on one side. Routine outline drawings of lateral views were done using the sections and were checked with the non-KOH'd specimen to correct any distortion caused by processing.

Depending on size, dissected prothoraces as well as other parts were placed in glycerine and studied in plant-quarantine type watch glasses or in low-form Stender dishes. For detailed study and drawing, dissected parts were positioned in a layer of fine sand at the bottom of a glycerine-filled container.

Drawings were made with a grid mounted in the 12.5× eyepiece of a Leitz dissecting scope. The most informative single view of a beetle thorax is a lateral one parallel to the coxal long axis; figures of entire prothoraces included here are drawn in this position.

Suborder **ARCHOSTEMATA**

CUPEDIDAE

Figures 1-4, 141

Pleuron large, rigid; forms lateral wall of prothorax. Anterior pleural flange small, external, or enclosed, or absent with an internal fold. Trochantin motile, external.

Head prognathous, posterior aspect enclosed by prothorax. Cervical sclerites

absent. Sternal flange with paired internal regions, as in Adephaga.

Anterior pleural fold, including the flange, visible externally only in *Priacma* (Figs. 1, AFL), it is enclosed by the notum in *Prolixocupes* and *Cupes* (Fig. 2). In *Tetraphalerus* and *Omma* (Figs. 3, 4) the anterior pleural fold is reduced and internalized by a lobe on the sternal flange. The anterior configuration of *Tetraphalerus* and *Omma* is similar to that of the Adephaga (Hlavac, 1972, figs. 10–14).

The anterior rim-fold in the cupedines is divided into two regions by the origin of the cervical membrane, the anterior region is the pleural flange. In *Prolixocupes* and *Priacma* (Hlavac, 1972, figs. 2, 11–13) the pleural flange is long and slender, it rests on but is not attached to the sternum. In *Cupes*, however, the flange is short, squat and is attached to the sternum by an anterior extension of the pleurosternal joint.

Sternal attachment region of the ventral pleural rim-fold present only in the cupedines, where the joint is long, straight and tightly membranous, and is either horizontal or slightly inclined. In *Tetraphalerus* the very long, curved pleurosternal joint is solid anteriorly with a distinct suture but without rim-folds, while posteriorly it appears semimembranous with pleural and sternal folds. The sternum and pleuron of *Omma* are solidly fused together, no suture is present.

Pleurotrochantinal joint membranous, external in the cupedines but in the ommadines it is concealed by the broad ventral surface of the pleural fold which forms a small trochantinal cowling.

Below the endopleural invagination, which is the actual site of membranous notopleural attachment, a notal rim-fold surface overlaps, conceals and may articulate with a section of the pleuron as in Myxophaga. The band of enclosed pleuron is broadest in *Cupes*, less so in *Priacma* and quite narrow in ommadines, and is less heavily pigmented than surrounding external regions and lacks setae. Overlap

continues behind the endopleuron, but consists here of the margins of posterior folds or flanges, and the enclosed pleuron is setose and has normal pigmentation. Boundary of overlap sometimes marked by a slight carina on the pleuron. Evans (1974) has incorrectly identified this carina as a "pleural ridge" that is an apophysis or invagination homologous to that found in other holometabolous orders, but absent in Coleoptera. Posterior flange extends behind coxa to overlap and interlock with the mesepisternum, flange largest in ommadines.

Endopleuron small, flat in cross section, does not come near the dorsal wall of the notum.

Trochantin triangular and external (cupedines) or quadrate and partially enclosed (ommadines). Sternotrochantinal joint loosely membranous. The trochantin is capable of mediolateral movement about the pleural attachment.

In the cupedines the sternal projection extends below and slightly behind the coxae, e.g., *Priacma*, while in the ommadines it is small and extends between the coxae.

Coxa squat, articular region very large (about .6 total length), only a small amount of which is enclosed by the pleuron (Fig. 14).

In the cupedines, the sternal projection extends below the coxal apex, the coxae are partially housed by the cryptosternum and by large cavities in the mesepisternum. The coxal rotation axis is parallel to the long axis; coxal motion is restricted to simple rotation. The coxal mechanism of *Omma* may be similar to that of the cupedines. In *Tetraphalerus* the coxal apex extends far below the very small projection and posteriorly the coxae are not enclosed by mesepisternal cavities. In addition, the sternellum bears a pair of large condyles just below the trochantinal apex that are inserted into cavities in the coxae. The rotation axis extends from the pleurocoxal to the sternocoxal articulation and is not parallel to the long axis. Since the coxal

apex is free and the rotation axis is not aligned with the long axis, the coxal apex moves anteroposteriorly as the coxa rotates.

There are two different types of propleuron-mesepisternal interlocking devices in the Cupedidae. In the cupedines, the posterior fold of the pleuron is expanded into a condyle above the coxal articulation that is placed into a cavity on the mesepisternum. In the ommadines, the cavity is on the pleuron and the condyle on the mesepisternum. The prosternal projection fits into a small (*Priacma*) or large (*Cupes*) fossa on the mesosternum. It is possible the notum may be motile around the pleuron, such movements could help clamp the prothorax onto the mesothorax.

The anterior configurations of *Cupes* and *Prolixocupes* on one hand and the ommadines on the other can be derived along two pathways from a *Priacma*-like configuration. Each pathway involves reduction and either enclosure or internalization of the anterior pleural fold. The similarity of the anterior configurations of Adephaga and the ommadines raises questions on the possible relationships between these groups or on the likelihood of parallel development.

The lack of a large sternal projection in the ommadines, especially *Tetraphalerus*, may not be primitive but may be part of a specialized mechanism to permit anteroposterior movement of the coxal apex. The trochantin of the ommadines is more enclosed by the pleuron and sternum and may be more motile than that of cupedines.

MICROMALTHIDAE

Figure 5

A uniquely simplified configuration, endopleuron absent, notum, pleuron, trochantin and sternum fused together without even the slightest vestige of sutures.

Head prognathous, completely enclosed posteriorly by the prothorax, cervical sclerites absent. Notum, pleuron, trochantin and sternum solidly fused together, sutures

absent. Posterior flange expanded into a small condyle that articulates with the concave dorsal face of the coxa. Coxa rests against but does not articulate with the dorsally curved posterior rim of the prosternum. Posteriorly, the coxae are housed in large, divided, mesosternal cavities. A small projection on the coxa near the apex fits into a groove on the ventral rim of the mesosternal concavity to form a procoxa-mesosternal articulation. Sternellum small, vertical, quadrate.

Suborder ADEPHAGA

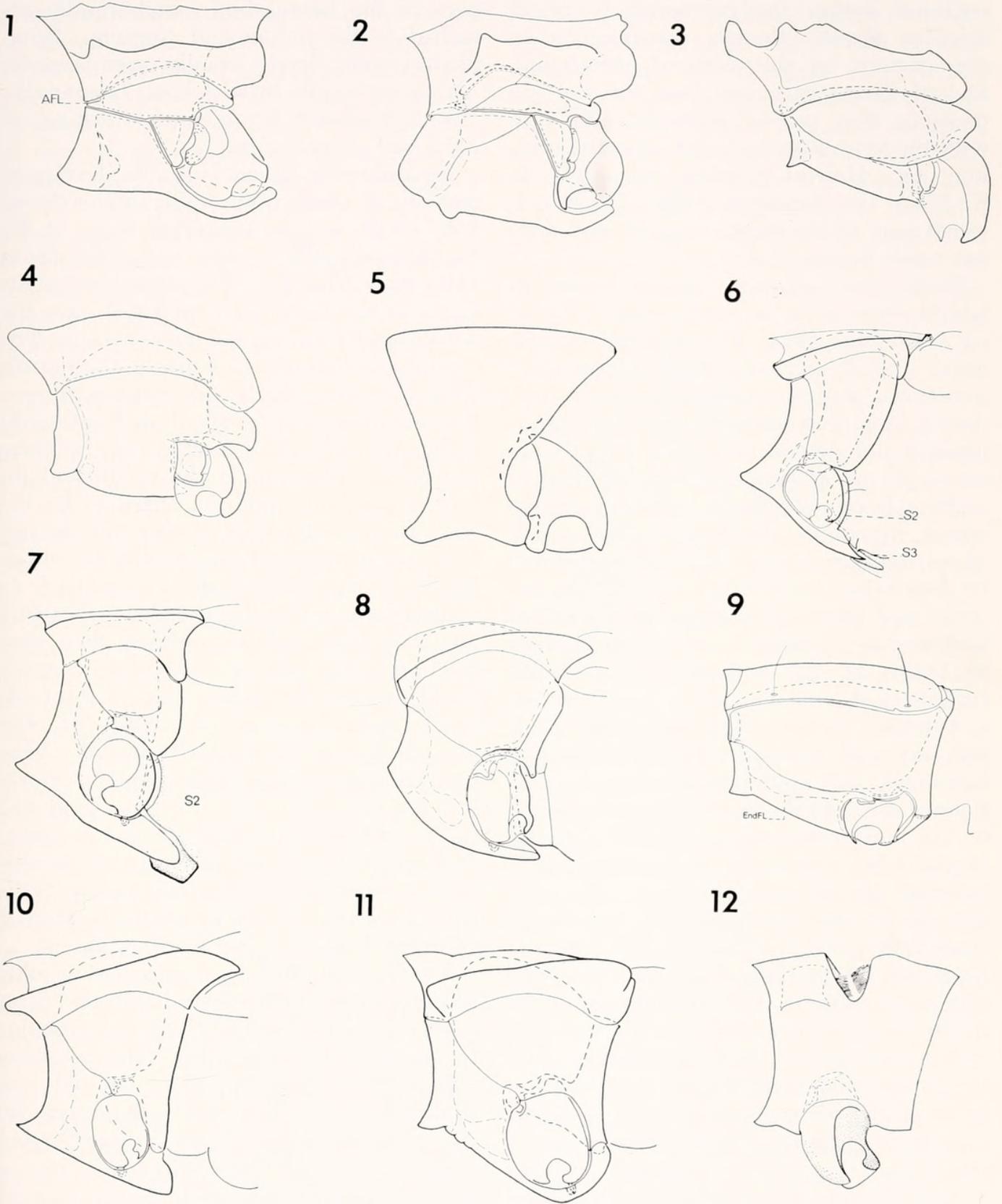
Figures 6-12, 142-143, 149-158

Pleuron a prominent part of body wall, rigid. Anterior pleural fold internal. Trochantin small, motile, enclosed.

Head usually prognathous and deeply

ABBREVIATIONS USED IN FIGURES

-
- AF, anterior fold, of pleuron.
 - AFL, anterior flange, of pleuron.
 - Artic, articular region of coxa.
 - CRN, crenulations.
 - CrS, cryptosternum.
 - Cw, cowling.
 - CxBr, post coxal bridge.
 - EndFL, endoflange.
 - EndPL, endopleuron.
 - ICxSP, intercoxal septum.
 - Invg, endopleural invagination.
 - LCnd, lateral condyle of notum.
 - MCnd, median condyle of notum.
 - NCnd, notal condyle, coxal articular.
 - NCw, notal cowling.
 - NPj, notal projection.
 - PL, pleuron.
 - PLCnd, pleural condyle, coxal articular.
 - PLPj, pleural projection.
 - PL-RFM, pleural rim-fold margin.
 - Pr, proprioceptor(s).
 - R, elytral ridge.
 - RFM, rim-fold margin.
 - S, prosternum.
 - S2, mesosternum.
 - S3, metasternum.
 - SL, sternellum.
 - SPj, sternal projection.
 - Tn, trochantin.
 - Tn-RFM, trochantinal rim-fold margin.
 - ZF, zone of fusion between pleuron and trochantin.



Figures 1-12. Archostemata, Adephaga. 1. *Priacma serrata*. 2. *Cupes concolor*. 3. *Tetraphalerus wagneri*. 4. *Omma stanleyi*. 5. *Micromalthus debilis*. 6. *Agabus striatus*. 7. *Amphizoa insolens*. 8. *Carabus nemoralis*. 9. *Clivina impressifrons*. 10. *Metrius contractus*. 11. *Ozaena elevata*. 12. *Paussus* sp.

enclosed within the prothorax. Cervical sclerites absent, though proprioceptors are present in the cervical membrane. Sternal flange with two long internal expansions that project ventrally and fuse with the ventral sternal wall near the midline, e.g., *Metrius*, *Clivina* (Figs. 157, 9, EndFL). In *Amphizoa* (Fig. 7) the internal part of the flange is small and does not reach the sternum.

Notum low, relatively inconspicuous in lateral view even in high volume forms, e.g., *Clivina* (Fig. 9). Lateral margin usually small and only slightly expanded, sometimes absent (*Apotomus*, *Tricondyla*, *Agra*), large and flattened only in *Sphalломорpha* and *Adelotopus* where it probably covers all movements of the proleg. Dorsal midline frequently bears a slender groove which represents the invagination crease of an internal carina. Transverse grooves or depressions near either or both the anterior and posterior margins of the dorsal surface may be present and represent zones of fusion of the anterior and posterior flanges to the notal wall.

Anterior pleural fold present though reduced and internal. In all *Adephaga* examined, the anterior sternal and notal flanges are joined via membrane (*Omus*) or via membrane and a dorsally directed sternal lobe, *Amphizoa*, or by fusion. The anterior pleural rim-fold is in all cases covered by the sternal flange. Membrane from the pleural invagination first joins the notal and sternal flanges and then runs into cervical membrane. The pleuron contributes neither cervical membrane nor a sclerotized surface to support the head. Externally, the notum and sternum are developed in front of the apex of the pleural fold and may be slightly separated (*Nebria*), meet edge on (*Carabus*, *Amphizoa*), overlap (*Ozaena*), or be tightly to solidly connected (*Clivina*, *Galeritula*, *Lebia*, *Helluomorphoides*). The anterior configuration of the *Adephaga* is similar to that of *Omma* and *Tetraphalerus* (Hlavac, 1972, figs. 11–14).

Pleuron large, rigid, forms a conspicuous

part of the lateral body wall, rigidly attached to the notum and sternum. Notopleural joint long, usually membranous, sometimes solidly fused (*Agra*, *Tricondyla*) always enclosed by edge-on meeting of notal and pleural rims.

Endopleuron broad, usually developed dorsally to come quite close to the dorsal notal wall but is separated from it by the *notopleuralis* muscle, e.g., *Amphizoa* (Hlavac, 1972, fig. 9); sometimes it is fused to the notal wall in which case the *notopleuralis* is absent (e.g., *Agra*, *Tricondyla*, *Galeritula*). Commonly, this muscle consists of very short, widely-spaced fibers, that are most densely distributed anteriorly and posteriorly. The function of the *notopleuralis* is obscure. If the origin and insertion are both rigid, as seems to be the case, then contraction of this muscle can have no mechanical effect. On the other hand, if the endopleuron is subject to ventral bending as the muscles originating on its ventral surface contract, then contraction or the mere presence of this muscle could counter this force. Pleural rim-folds specialized relative to those of the *Myxophaga* and most *Archostemata*. Ventral rim-fold not distinct, modified anteriorly into a rigid carinate pleurosternal joint and posteriorly into a complex coxal housing. The pleurosternal suture marks an invagination crease and varies from nearly vertical (*Agabus*, Fig. 6) to nearly horizontal (*Clivina*, Fig. 9), it is sometimes absent.

Trochantinal and coxal articulation folds of sternum and pleuron are broad and form cowlings which enclose the coxal articular region and the trochantin. The cowlings either meet edge-on or the sternal rim slightly overlaps the notal rim. Posteriorly, the pleural fold is fused to the lateral pleural wall. It bears along its rim a ventrally projecting condyle that is inserted into a groove on the coxa to form the pleurocoxal articulation (Fig. 142).

Posterior pleural fold may be evaginated ventrally to form a projection which may be joined, in one of 3 ways, to the sternal

projection to form a complete collar or set of closed coxal cavities: it may overlap (*Ozaena*, *Metrius*, Fig. 157); enclose the pleural tip into sternal groove or cavity (*Clivina*, *Helluomorphoides*, Figs. 153–154) or enclose the sternal tip into cavity on pleural apex, e.g., *Omophron* (Bell, 1967, fig. 17). The projection may be short with a free apex (*Carabus*, Figs. 8, 149 PLPj) or the projection may be absent (*Agabus*, *Amphizoa*, Figs. 6–7). Dorsally, the posterior pleural fold forms a long flange that is always fused, near its inner margin, to the pleural wall.

The region of fusion of the ventral fold above the coxa, and of the posterior fold to the pleural wall is sometimes marked by a suturelike groove similar in cross section to the notal invagination crease-flange assemblies. This groove has been erroneously called the pleural suture (apophysis) by many authors who use it as a landmark to divide the pleuron into an anterior episternum and a posterior epimeron, but who do not attempt to explain its origin off the pleurosternal suture. A pleural suture and a proepimeron do not occur in the prothorax of the Coleoptera and are present in only a few Holometabola (Hlavac, 1972: 134–139).

Posterior to the endopleural invagination the notopleural joint varies from tightly membranous to solidly fused. In *Metrius*, *Rhysodes* and *Amphizoa* (Fig. 7) the rims of the notum and pleuron meet edge-on and are readily separated in a KOH'd specimen. The membrane from the pleural invagination curves medially and joins the intersegmental membrane. In many forms a small (*Trachypachus*) or large (*Carabus*, *Zacotus*) ventral lobelike expansion of the notal flange increases the length of the membranous notopleural connection. Solid fusion of the notal and pleural flanges and their rims is found in some carabids (*Galeritula*, *Lebia*, *Helluomorphoides*).

Coxal articular region enclosed, always small, and less than .25 total length of coxa. The articular region is distinctly

produced above the coxal foramen in some, e.g., *Amphizoa* (Fig. 142) while in most carabids with closed coxal cavities this region is greatly reduced and is developed little above the level of the coxal foramen, e.g., *Helluomorphoides* (Figs. 143, 153), see section on promesothoracic joint below. A groove on the dorsal surface of the articular region receives the pleural condyle to form the pleurocoxal articulation (Fig. 142 PLCnd). In most Adephaga, a peg on the coxa is inserted into a cavity on the cryptosternum to form a sternocoxal articulation (Figs. 142–143) which restricts coxal motion to rotation. The sternocoxal articulation is absent but coxal flexation does not seem possible in the Gyrinidae, Dytiscini and Laccophilini and in the paussines (Evans, 1965). Proprioceptors are present near the pleurocoxal articulation and near the trochantincoxal joint (Fig. 143, PR).

Trochantin small (Figs. 142, 143, Tn), enclosed except in some forms, e.g., *Carabus* where a small section may be visible externally when the coxa is rotated far posteriorly. The trochantin is loosely attached to the sternum and pleuron but tightly joined to and moves freely with the coxa. The *nototrochantinalis* muscle serves as an accessory anterior coxal rotator.

Promesothoracic joint. The great structural and mechanical diversity in intersegmental attachment can be divided into two groups: (1) terrestrial forms (Caraboidea) with variable prothoracic mechanisms and (2) rigid body aquatic families plus *Omophron*.

Among caraboids, major differences are found in the completeness of the posterior collar and in the geometry of pro- and mesosternal articulation surfaces. Two major grades of development are recognized. The low grade mechanism of a few tribes is structurally uniform. The sternal projection extends behind and below the coxal apex, its articular surface is only slightly raised and is at a distinct angle to the narrow posterior margin of the intercoxal

septa, e.g., *Carabus* (Figs. 8, 149–152). The internal septa extends between the long coxae for only a short distance. The mesosternum is divided into a nearly vertical anterior region bearing a pair of concavities, sometimes separated by a median carina, that can receive the procoxae; and a ventral, horizontal, slightly concave posterior region that receives the dorsal surface of the prosternal projection. As the prothorax moves ventrally, the prosternal projection moves along the ventral surface of the mesosternum and the procoxae come to rest against the mesosternal concavities, blocking additional ventral motion. Dorsal movement of the prothorax increases the space between the coxae and mesosternum and results in the exposure of intersegmental membrane (Figs. 150–152).

A low grade ventral motility mechanism has been found in *Trachypachus*, *Systolosoma*, *Nebria*, *Leistus*, *Hiletus*, *Opisthius*, *Carabus*, *Calosoma*, *Ceroglossus* and in *Sphaeroderus*. All of these forms have open coxal cavities. Poorly developed though probably fully functional postcoxal bridges occur in the trachypachidines, *Leistus* and *Carabus*; in *Hiletus* the bridge is broad and heavily sclerotized.

The high grade ventral motility mechanism can be derived from a configuration similar to that of *Carabus* by performing four operations:

- (1) Developing the sternal projection dorsally above the level of the coxal apex, broadening its articular surface.
- (2) Developing the intercoxal septa dorsally and expanding it laterally over the median curvature of the coxa so that a broad surface is formed that curves posteroventrally from the apophysis and is continuous with the projection flange (Figs. 149, 153, 157).
- (3) Reducing the length of the coxae, especially the articular region.
- (4) Remolding the anterior part of the mesosternum to form an enclosable,

slightly curving, nearly horizontal surface distinctly above the plane of the mesosternum proper.

This mechanism is an improvement over the low grade type in two respects. Since the pro- and mesosternal articular surfaces are above the most ventral sections of the pro- and mesosternum, there is a large ventral clearance permitting extensive ventral motion of the prothorax. Secondly, there is a broad overlap of pro- and mesosternal surfaces; dorsal movement of the prothorax will not expose ventral intersegmental membrane (Figs. 152, 156).

The high grade mechanism occurs, with significant variation, in many tribes of Carabidae and is associated with closed coxal cavities, except in *Gehringia*.

Of the forms examined, *Mystropomus* and *Metrius* (Figs. 10, 157) are the least modified over the low grade type. The coxae of *Metrius* are long (L/W 1.7), the intercoxal septa is not expanded and is much narrower than the relatively low articular surface of the projection.

As the flange is developed dorsally, and the internal septum expanded laterally while the coxae are reduced in length, the length of the actual articular surface is increased from simply that of the projection proper to the combined lengths of the projection and the septum. As these changes are occurring, an increasingly smaller amount of the coxa is visible in posterior view (Figs. 153, 157). The amount of coxa visible in posterior view between the pleural and sternal flanges is a measure of the development of the ventral motility mechanism. This varies from a large amount of coxal exposure, though less than in *Metrius* in some forms examined belonging to Sloane's "Carabidae clausae" and "Carabidae uniperforatae" (*Ozaena*, *Psydrus*, *Nomius*, *Promecognathus*, *Loricera*, *Rhysodes*), to little coxal exposure, similar to *Clivina*, in others (*Pterostichus*, *Zacotus*, *Ega*).

The least amount of coxa is visible in certain forms with a broad flangelike post-

coxal bridge. In *Helluomorphoides* (Figs. 153–156), for example, the pleural projection is broadened ventrally and the flange is developed anteriorly over the coxa. The ventral surface of the pleural flange is approximately coplanar with that of the sternal flange. The postcoxal bridge itself is slender and separates pericoxal from intersegmental membrane (Fig. 153, CxBr). The cavity between the pleural and sternal projections and the postcoxal bridge is the second foramen of the “biperforate” cavity of Sloane (1923). This foramen is large in some (*Agra*, *Lebia*, *Pentagonica* and *Omus*), but much smaller in others (*Anthia*, *Apotomus*, *Pangaeur*, and *Helluomorphoides*), and secondarily lost in *Sphallomorpha*.

In *Omophron*, the prosternal projection is long, broad and flattened. It rests on and completely covers the mesosternum; the intercoxal septum is not expanded over the coxae and is at a distinct angle to the projection. Large mesosternal concavities house part of the procoxae. A median groove on the projection receives a ridge on the mesosternum forming a ventral interlocking mechanism. A dorsal mechanism is formed from a pair of ridges on the elytra inserted into paired grooves on the notal flange. The pleural projection is developed laterad of the coxae and joined with the sternal projection. The prothorax is not moved as these beetles dig, rather the entire oval dorsal surface of the body is used to push and compress substrate. The prothorax is not moved during walking or running.

Omophron, then, is a rigid-body form with a ventral mechanism similar to that of the low grade forms described above. The combination of closed coxal cavities and mesosternal housing of the procoxae suggests that closed coxal cavities originated or have shifted function to increase the integrity of the already rigid joint by increasing the surface area of intersegmental overlap. A similar configuration is found in the curious African cicindeline *Platychila*.

The aquatic Adephaga, like most other aquatic Coleoptera, are rigid-body forms; their ventral motility mechanism can be derived from the low grade type of carabids. The ventral intersegmental connection of *Amphizoa* (Figs. 7, 158), differs little from that of *Carabus* (Figs. 8, 151). In *Agabus* (Fig. 6) the prosternal projection is divided into a thick, anterior portion that fits into a deep cavity on the mesosternum and a thin, tapering, posterior section that is placed in a metasternal groove. The promesothoracic interlocking mechanism of *Peltodytes* and *Haliphus* is extremely complex. The long, broad, prosternal projection bears a pair of anterior cavities that receive expansions of the mesosternum, and a posterior condyle that is placed in a metasternal cavity. In *Dineutes* and *Gyrinus* the prosternal projection consists only of an internal septum, the mesosternum is developed anteriorly between the coxae, the perpendicular edges of the mesosternum and projection meet edge-on. A thick, heavily sclerotized, postcoxal bridge is present in all aquatic Adephaga.

Bell (1966) concluded that the Haliplidae, Gyrinidae and the dytiscoid families represent three independent invasions of the aquatic zone. This conclusion was based in part on the assumption that open coxa cavities and postcoxal bridges occur together only in the aquatic Adephaga and trachypachidines. However, postcoxal bridges occur with open coxal cavities in *Hiletus*, *Leistus* and *Carabus*.

A postcoxal bridge is present in many Adephaga; it is formed from sclerotization of intersegmental membrane between slight expansions of the pleural flange and the sternellum (Figs. 153, 157, 158, CxBr, SL). In some carabids the postcoxal bridge is thicker but may not be more heavily sclerotized than the surrounding intersegmental membrane, e.g., *Metrius*, the ozaenines examined, possibly *Gehringia* as well as *Carabus*, *Notiophilus*, *Leistus*, *Scarites*, *Morion*, *Terehus*, some *Bembidion*, *Trachypachus* and *Systolosoma*. In these forms it

may be difficult to see the bridge after treatment with KOH. In the cicindelids examined, in the aquatic families and in *Hiletus* the bridge is thick and heavily sclerotized while in the tribes included in Sloane's "Carabidae Biperforatae" it is variable though always quite distinct.

Even an only slightly developed post-coxal bridge is probably effective in isolating pericoxal membrane from the effects of forces generated by prothoracic movement.

Paussines: Paussid beetles are myrmecophiles; most have prothoracic trichomes (Darlington, 1950:57-58). In many advanced paussids a pair of trichomes is located on the lateral margin of the notum and is joined by a deep transverse cleft or groove (Fig. 12). The development of these organs has caused many modifications of prothoracic structure, including: (1) Extensive development of the prothorax posterior to the coxa to house the trichome glands (compare *Ozaena*, Fig. 11, with *Paussus*, Fig. 12). (2) Reduction of the prothorax, including the endopleuron, anterior to the coxa. (3) Posterior development and fusion of the pleural projections to one another.

In the primitive paussids the prothorax is not developed posteriorly, the notopleural suture extends the full length of the prothorax and the pleural projections overlap the sternal projection as in *Ozaena*, e.g., *Protopaussus*, *Megalopaussus*, *Caribodomemmus*, *Arthropterus*, and some species of *Homopterus*. In *Homopterus bolivianus* Kolbe the pleural projections are slightly developed and fused posterior to the sternal projection.

Suborder **MYXOPHAGA**

Figures 13-16, 120-122

Pleuron variable in size, rigid, forms part of body wall; fused to trochantin. Anterior pleural flange external or enclosed.

Head prognathous, cervical sclerites absent.

Notum encloses a very low volume in *Hydroscapha* and *Sphaerius*, somewhat larger in *Lepicerus* where it bears a pair of anterolateral cavities that house the antennal club, and in *Hintonia* (= *Ptyopteryx*) where it bears a complex of interlocking devices on the posterior face.

In *Lepicerus*, *Hydroscapha* and *Sphaerius* the small anterior pleural flange is visible externally (Figs. 13-16). In *Hintonia* (Fig. 16) the notum and sternum and their flanges are developed anterior to the apex of the pleuron. The rim of the notum is housed in a cavity on the broad dorsal sternal face, and this region of overlap encloses the pleural flange. Internally, cervical membrane originates from the pleural flange as in other Myxophaga.

Pleuron apparently incapable of motion, joined broadly to notum via membrane slightly above the notal rim so that a small amount of the pleuron as well as the actual notopleural joint are both concealed. Endopleuron with ventral surface broadly concave in *Lepicerus* and *Hintonia*; however in *Hydroscapha* it is concave basally but compressed, flattened apically into a long horizontal region that is seen highly foreshortened in Fig. 121. The endopleuron of *Sphaerius* is strongly compressed from the base to the apex and is nearly horizontal and triangular in outline (Figs. 120-122).

Pleuron largest in *Hydroscapha*, comparatively reduced in *Hintonia* (Figs. 120-122). The anterior pleural fold includes the pleural flange in front of the cervical membrane and a small (*Lepicerus*) or large (*Sphaerius*) internal region behind it (Fig. 122, AFL, RFM). The ventral portion of the rim-fold includes the small inclined sternal attachment region above the trochantin and the coxal articulation behind it. Coxal fold broad or narrow and peninsulalike in *Hintonia*, encloses a small part of the articular region, except in *Hydroscapha*, where it is developed anteriorly to enclose most of the articular region. A tall and broad posterior pleural

flange is present in *Lepicerus*, in *Hydroscapha* it is tall and narrow.

The trochantin is solidly fused to the pleuron; there is no trace of either a suture, paired rim-folds or an internal zone of fusion.

Pleurosternal and trochantinosternal joints both membranous.

The sternum of *Hydroscapha* and *Sphaerius* is not folded extensively while that of *Lepicerus* and *Hintonia* is more structurally complex. Exosternum narrow, except *Hintonia*, reaches coxal apex or extends slightly below it. Sternal projection very small and acts as coxal separator in *Hydroscapha* where it arises from the cryptosternum, and in *Sphaerius* where it originates from the sternum and extends in front of the anterior sternal margin. Projection large in *Lepicerus* and *Hintonia* where it extends below and behind the coxae.

Sternacostal suture distinct in *Sphaerius* but in *Hydroscapha* it runs alongside of and may be confused with a slight fold that separates a concave, anterior region (housing the coxa) from a convex, posterior region (including most of the horizontal sternellum). In *Lepicerus* and *Hintonia* the sternellum is smaller and vertical.

In *Lepicerus* and *Hydroscapha* the cryptosternum and the inner face of the pleuron come quite close together, overlap slightly, or may actually touch. Pericoxal membrane is then either completely separated from intersegmental membrane, forming dorsal closure of the coxal cavities, or there may be only a slight region of continuity between the two membranous regions.

Coxal articular region varies from .3 (*Sphaerius*), to about .2 (total coxal length in the other genera). Coxa elongate to squat, in *Lepicerus* a ridge on the coxa near the apex articulates with a groove in the endosternum. The very broad posterior notal and pleural flanges suggest that Myxophaga are rigid-body forms.

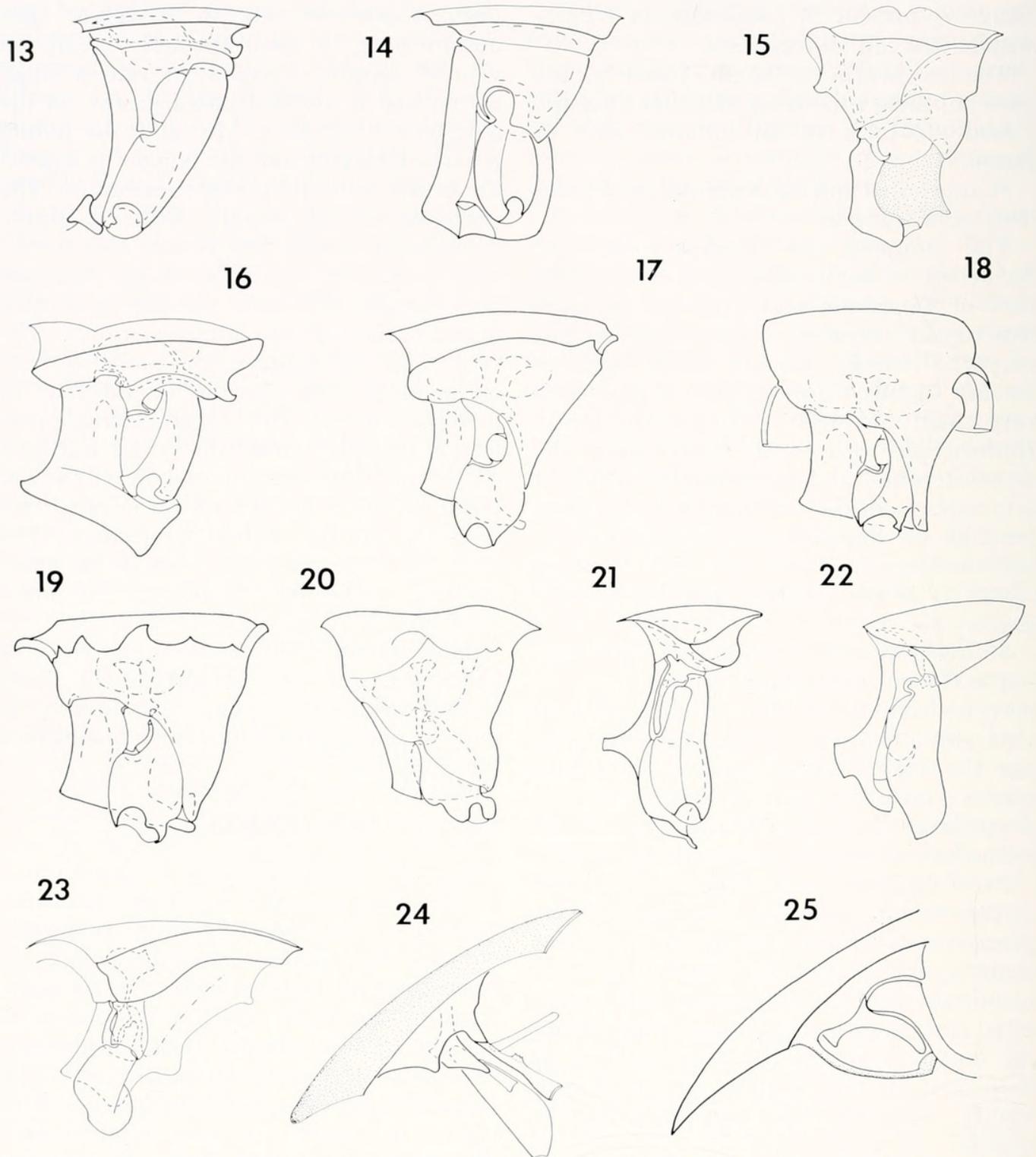
A promesothoracic interlocking mecha-

nism is present only in *Hintonia*. The notum bears a small posterior wall, its ventral margin is expanded into a small carina that is inserted into a groove on the anterior elytral face. Medially, the notum is arched dorsally and the flange fits against the broad, similarly folded mesonotum. The posterior dorsal margin bears a single crenulation which fits against the scutellum. Laterally, the notal flange becomes very broad and rests on the tomentose dorsal surface of the mesepisternum. The very small notal projection probably rests on a slight shelf on the lateral face of mesepisternum. The broad sternal projection extends behind the coxae and rests on the mesosternum; a condyle on the anterior margin of the sternum is inserted into a cavity on the sternal projection. The procoxae are partially housed in small cavities on the anterior face of the mesosternum.

The broad flattened profemora of *Sphaerius* can be brought to lie flush against the mesosternum. In addition, its inner surface has a long cavity that houses the protibia.

Suborder POLYPHAGA

Pleuron greatly reduced in length and width relative to that of other suborders, varies from largely external to completely enclosed by notal or sternal cowlings or both; may be motile but is never an element of the body wall. Reduction most evident in the external region which extends from the notal rim to the trochantin (e.g., Fig. 128 PL, stippled portion). This section is largest in certain primitive taxa (Eucinetoidae, Staphylindidae, Derodontoidae) and may be much wider than the trochantin (Figs. 17–22, 123–128). A result of pleural reduction is the enclosure of the dorsal aspect of the pleurocoxal articulation by notal rim-folds. An anterior pleural fold, formed from an evaginated ventral pleural rim-fold is present in some members of the same primitive groups and inserts between the notum and sternum; this



Figures 13–25. Myxophaga, Derodontoidea, Eucinetidae. 13. *Sphaerius politus*. 14. *Hydroscapha natans*. 15. *Lepicerus horni*. 16. *Hintonia britskii*. 17. *Laricobius rubidus*. 18. *Peltastica tuberculata*. 19. *Derodontus maculatus*. 20. *Nothoderodontus gourlayi*. 21. *Prionocyphon lembatus*. 22. *Eucinetus infumatus*. 23. Undescribed Clambid. 24. *Clambus gibbosus*. 25. *Loricaster* sp.

structure is homologous with the anterior flange of Archostemata and Myxophaga (Figs. 1, 122, 123, 125, AFL; Hlavac, 1972,

figs. 10–18). The enclosed region of the pleuron, between the notal rim and the endopleural invagination, highly variable in size and sensitive to pleurocoxal mechanics (Figs. 123–134, area between dotted

line and notopleural membrane). Endopleuron quite variable in height relative to that of the notum and in degree of basal compression and apical expansion (Figs. 123–136 EndPL).

Pleuron and trochantin fused. Boundary between these sclerites present internally in only a few groups and indicates joining of rim-fold surfaces (Figs. 123, 124, 128 ZF). Pleural and trochantral rim-folds and a zone of fusion are absent in most Polyphaga and all Myxophaga which prevents accurate determination of the site of attachment.

For purposes of terminology the trochantinopleural boundary is taken to be at the level of the most ventral point of a distinct dorsal coxal articulation. Trochantin and coxal articular region vary greatly in relative size (Figs. 135, 136, 144–148 Artic) and may be almost completely exposed (Figs. 19, 21, 22, 42–44, 53–55, 89–97, 99–104, 111–119) or wholly enclosed (Figs. 20, 56–66, 80–84, 106–109).

The pleuron, endopleuron and trochantin may be motile and function to aid coxal rotation or cause coxal flexation via a lever mechanism with the region of the pleuron just below the invagination serving as a fulcrum (e.g., Figs. 53–54, 132–133). In many cases the pleuron is rigidly fused to the notum and the endopleuron may be fused to the notal wall.

Notum and sternum, while joined primitively by membranous rim-fold joints, are often solidly fused together and in some cases the notosternal suture is absent.

EUCINETOIDEA

Figures 21–25, 123, 125, 126, 166

Very small, low volume prothoraces, part of a variable compaction mechanism. Pleuron rigid, large externally, may bear a small anterior fold and a zone of fusion to the trochantin. Coxae elongate, external; sternum thin.

Head in rest position hypognathous to opisthognathous; its posterior face is flattened and lies flush against either the procoxae, mesosternum or metasternum,

partially to wholly concealing the proleg. One or two cervical sclerites present.

Notum small with very large flattened lateral margins in clambids. Notal projection absent, except in *Loricaster* (Fig. 25), where it is fused with and does not extend below the cryptosternum.

Thin lateral arms of sternum attached via membrane to notum, above coxal articulation. Without sternal projection but with large sternellum and distinct basicoxal suture as well as an intersegmental sclerite bearing a spinasternum in *Clambus*, or with a broad cryptosternum in *Loricaster*. In eucinetids and helodids, there is no intersegmental sclerite and the sternum is evaginated medially to form a projection. Sternellar projection small, fused with sternal projection.

Pleuron immovable, joined to notum near rim with large external component above coxal articulation and with anterior fold. In *Sarabandus* (Fig. 123) pleural and trochantinal rim-folds are present as well as a distinct zone of fusion between these sclerites. Fusion zone almost entirely obliterated in *Prionocyphon* (Figs. 21, 25). In the eucinetids and clambids only the pleural rim-fold is present (Figs. 22, 126).

Trochantincoxal articulation normal, except in *Eucinetus* where it is quite compressed. Pleurocoxal articulation large. Coxae long and narrow, usually entirely external, with a slight articulation against unfolded notal rim.

Promesothoracic interlocking mechanism similar in eucinetids and helodids. Lateral rim of notum rests on the infolded mesepisternum. Anterior faces of mesosternum and episternum concave, partially house procoxae. Medial mesosternal fossa receives apex of the prosternal projection.

In *Clambus* a dorsal interlocking mechanism consists of three mesothoracic elements: the rim of the scutum, an episternal condyle, and an elytral carina, that fits into an elongate groove on the posterior notal flange.

Eucinetoids are moderately to very highly

compacted beetles. A measure of compaction is the number of appendages enclosed in rest position. In helodids, the anterodorsal face of the procoxa is hidden by the head while the posterior coxal face is only slightly enclosed by mesosternal cavities. In eucinetids only a slender lateral section of the procoxae is visible, between the head and the mesothorax. In both groups, the lateral margin of the pronotum is not expanded.

There is considerable variation in the compaction mechanisms of clambids. All, however, have large, flat lateral prothoracic margins. In *Loricaster* the mesosternum is inflected dorsally. The entire proleg is enclosable within a cavity formed by the margins of the head and pronotum resting against the elytra and mesothorax. The flat mesofemur is external. The tibia and tarsi are housed under it. In *Clambus*, *Sphaerotherax*, the anterior part of the metasternum is also inflected dorsally, the anterior margin of the head then rests against the metasternum enclosing both the pro- and mesolegs. In *Calyptomerus* the anterior margin of the head rests on the metathorax and the pro- and mesoleg are enclosed (Fig. 166). In each of these genera, the anterior margin of the head rests on a pterothoracic sternite, forming, along with the pronotal margins, a cavity that can completely enclose the proleg and sometimes the mesoleg as well.

The flat surfaces of the mesosternum and most of the metasternum are inflected far dorsally above the ventral plane in *Clambus*, *Sphaerotherax*, and *Calyptomerus* (Fig. 166). The flat ventral surface of the head and the prothorax rest against these inflected surfaces and can completely enclose the thin, poorly sclerotized pro- and mesolegs.

In *Loricaster* the posterior notal flange bears a small posterior wall. Bearing a groove that houses an elytral carina. Mesosternum inflected dorsally nearly 90° from ventral plane of the metasternum. Proleg and mesocoxa poorly sclerotized and can

be enclosed. Mesofemur sclerotized and flat, exposed and can conceal tibia and tarsus under it when animal is compacted.

An undescribed genus (Fig. 23), known from Micronesia and the West Indies, differs from other eucinetoids in many characters: (1) The notum is produced below the level of the notosternal joint enclosing most of the trochantin and coxal articular region. (2) The pleuron lacks an anterior fold and is without a large external component. (3) Endopleuron with slender stalklike base and expanded apex. (4) Cryptosternum is fused to the notal projection. (5) The coxa is differentiated into a narrow apical region enclosed within the notum and a squat external portion. (6) The compacting mechanism does not involve the head's resting against the meso- or metasternum enclosing at least the proleg as in other clambids. The mesosternum is, however, inflected approximately 45° and bears a pair of concave regions, separated by a carina, for reception of the posterior faces of the procoxae. The head covers only the anterior coxal face; cavities under the notal margin house, but do not enclose, the antennal apex and part of the leg.

The prothorax of this form can be derived from that of other eucinetoids by employing common transformations, e.g., enclosure of coxae and differentiation of the endopleuron. The inflected mesosternum could indicate derivation from a form with a *Clambus*- or *Loricaster*-like compaction mechanism.

DERODONTOIDEA

Figures 17-20, 127

Low volume configurations with closed coxal cavities except *Laricobius*, and with deep coxal enclosure in *Nothoderodontus*. Pleuron rigid, usually bears a large anterior fold. Pleural and trochantinal rim-folds and zone of fusion between them are all absent.

Head prognathous, deeply inserted within prothorax. The single cervical sclerite is enclosed.

Lateral rim of notum expanded and flattened (*Peltastica*, Fig. 18) or less developed but with toothed margin (*Derodontus*, *Nothoderodontus*, Figs. 19, 20) or not expanded and without serrate margin (*Laricobius*, Fig. 17). Projection broad, reaches sternal projection except in *Laricobius*.

Notosternal joint membranous. Cryptosternum with concavity for reception of anterior face of trochantin and for housing the anterior pleural fold.

Pleuron immovable, joined to notum near rim, except *Nothoderodontus* where extensive dorsal development of the notal rim-fold results in enclosure of the entire coxal articular region. Endopleuron with longitudinal crease forming a ventral carina. Anterior pleural fold large, distinct externally in *Peltastica* and *Laricobius* (Fig. 127), smaller and enclosed in *Derodontus*, absent in *Nothoderodontus*. Pleural and trochantinal rim-folds and zone of fusion are absent or very obscure. Anterior face of trochantin large, housed within concavity in cryptosternum. Small portion of articular region and part of posterior face of the squat coxa housed within notum except in *Nothoderodontus* where anterior expansion of the ventral portion of the notal projection encloses the lateral coxal face (Fig. 20). Coxae extend below level of sternal projection. Pleurocoxal articulation compressed, with strong groove-ridge device.

Apices of notal and sternal projections overlap, though are not tightly fused in *Peltastica* and *Derodontus*, forming a complete articulation collar and closed coxal cavities. In *Laricobius* the notal projection is separated from the sternal projection (Fig. 17); a groove in the mesosternum and two concave regions house the prosternal projection and part of the procoxae respectively.

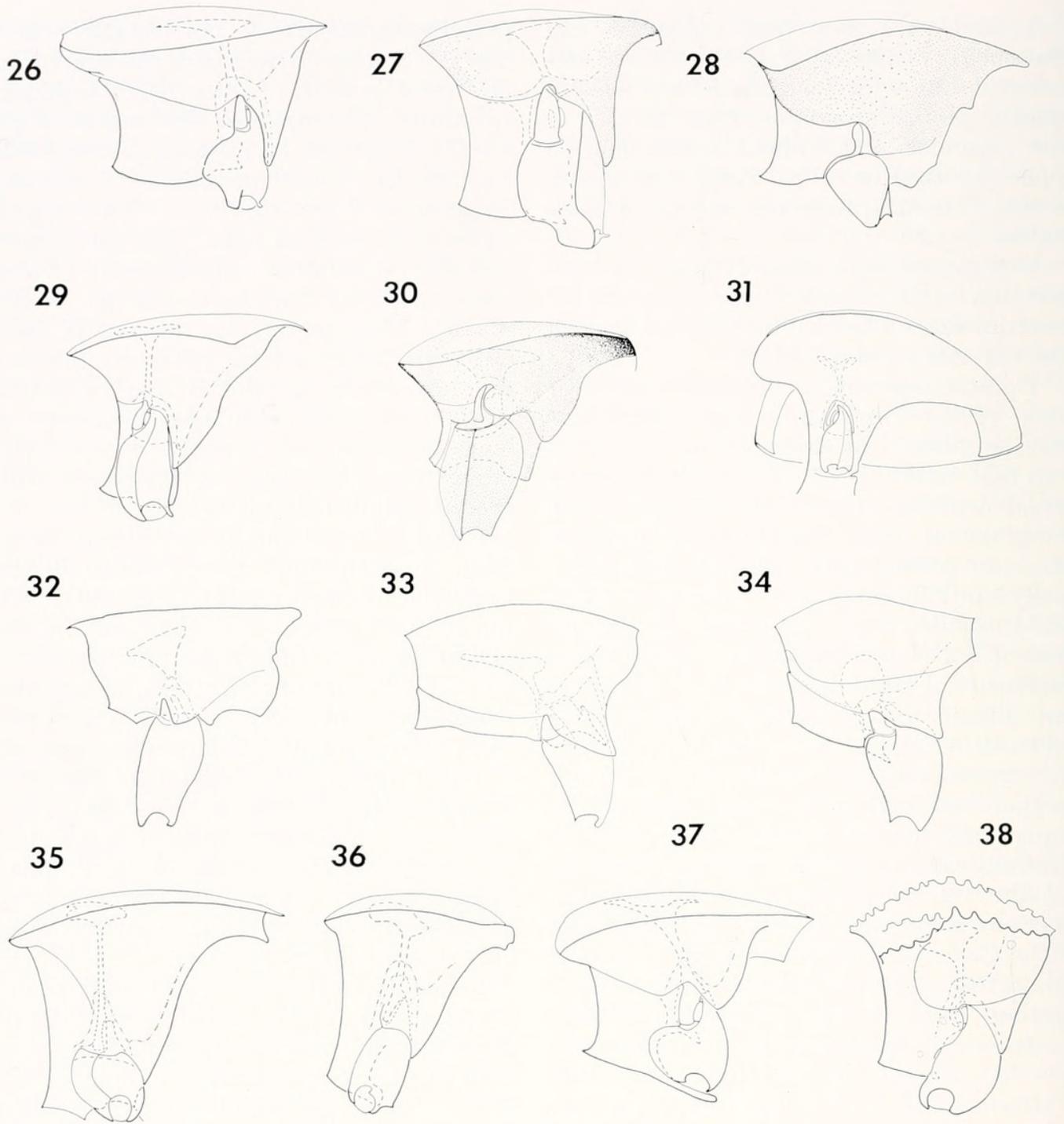
STAPHYLINOIDEA

The immense prothoracic diversity of staphylinoids has resulted from multiple, variably parallel transformations of a

primitive/generalized polyphagous prothorax. Similar generalized configurations are found in each of three major lineages: Leiodidae (*Catopocerus*, *Hydnodbius*, Figs. 26–27); Silphidae (*Lyrosoma*, *Necrophilus*, Figs. 39–40); and Staphylinidae (*Omalium*, *Trigonurus*, Figs. 45, 46). Unspecialized forms with reduced coxal articular regions include: *Leptinillus*, *Micropeplus*, *Dasycerus*, and the hydraenids (Figs. 37–38, 67–70). Divergence from this sort of stem array has taken several pathways, leading to forms capable of extensive coxal flexation as well as those with deep enclosure of long and squat coxal articular regions. The latter cases may also be associated with specialized pleurocoxal mechanisms.

Different mechanisms permitting large scale coxal flexation have evolved in the Leiodidae (*Prionochoeta*, Fig. 30), Silphidae (*Necrodes*, Fig. 42); and in the Staphylinidae (*Philonthus*, Fig. 54). Extensive enclosure of elongate coxal articular regions is found in several taxa: Staphylinidae (*Stenus*, *Bledius*, *Leptochirus*, Figs. 56, 57, 51); Pselaphidae (*Sonoma*, Fig. 61); Scydmaenidae (*Clidicus*, Fig. 62). Enclosure of a relatively squat coxa and loss of pleural motility is found in Ptiliidae (Figs. 35–36) and some Scaphidiidae (*Scaphisoma*, Fig. 60), and a few scydmaenids (*Connophron*, Fig. 66).

Reduction of the length and width of the sternum as part of a compaction system or as an element of a flexation mechanism or both can be found in the Leiodidae (Figs. 28–30, 32); Silphidae (Figs. 39–42); Staphylinidae (Figs. 54–55); Scaphidiidae (Figs. 59–60); Scydmaenidae (Figs. 61–63); Pselaphidae (Figs. 64–66). Ventral closure of the coxal cavities is uncommon but found in *Leptochirus* and *Hydraena* (Figs. 51, 70), an elongate notal projection extending far below the trochantin is more widely distributed (Figs. 26–27, 39–40, 45–48). Dorsal closure common (Figs. 29–31, 35, 61, 69). The extensive variation within most families is considered at length below.



Figures 26–38. Staphylinoidea. 26. *Catopocerus* sp. 27. *Hydnobius matthewsi*. 28. *Camiarus* sp. 29. *Anisotoma polita*. 30. *Prionochaeta opaca*. 31. *Agathidium* sp. 32. *Astagobius angustatus*. 33. *Glacicavicola bathyscioides*. 34. *Brathinus nitidus*. 35. *Acratrichis* sp. 36. *Nossidium* sp. 37. *Leptinillus valious*. 38. *Dasycerus carolinensis*.

LEIODIDAE

Figures 26–33, 131, 163, 165

The diversity of prothoracic configurations and pleurocoxal mechanisms within the leiodids examined can be divided into four groups.

- (1) Generalized high volume forms with open coxal cavities, where the notal projection is a bar to coxal flexation, e.g., *Catopocerus*, *Hydnobius* (Figs. 26, 27).
- (2) Anteriorly compacted forms with reduced sterna and dorsally closed

- coxal cavities which prevent coxal flexation, sometimes with a leg enclosure mechanism, e.g., *Anisotoma*, *Agathidium* (Figs. 29, 31).
- (3) Compacted forms as in (2) but with partially to almost completely enclosed trochantins and with a complex of structural modifications to permit coxal flexation, e.g., *Prionochaeta* (Fig. 30).
- (4) Uncompacted troglitic forms with long legs, elongate prothoraces and with coxae capable of flexation, e.g., *Glacivicola*, *Astagobius* (Figs. 32-33).

Description: Head-prothoracic joint variable; the forms studied can be divided into three groups. In *Hydnobius*, *Catopocerus*, *Camiarus* and *Neocamiarus*, the prognathous head is simply enclosed within the prothorax, the anterolateral region of the notum is not curved medially and the sternum is broad in front of the coxae. In *Colon* and *Platycholeus* the hypognathous head is also simply enclosed, but the sternum in front of the coxa is thin. The anterolateral region of the notum of *Anisotoma* and *Agathidium* curves medially, the hypognathous head rests against it and the thin sternum. In *Ptomaphagus*, *Catops*, *Nemadus* and *Prionochaeta* (Fig. 30) the notum is also curved medially and the sternum is narrow in front of the coxae. In addition, the posterior region of the head is divided into a distinct narrow neck, enclosed within the prothorax, and a large flat area which rests against the notum, sternum and coxae. Cervical sclerites always present.

Lateral margin of notum greatly expanded in *Agathidium* (Figs. 31, 165) as part of a clambid-like enclosure mechanism, less so in other leiodines, notum expanded only posteriorly in catopoids. In *Catopocerus* and in most species of *Hydnobius*, the notal projection is triangular in cross section, blocks coxal flexation posteriorly and is not connected to the sternum (Figs. 26, 27). The notal projection of *Anisotoma* and

Agathidium is triangular in cross section and blocks coxal flexation, but the posterolateral edge of the sternum fits into slight groove on the inner face of the notum closing the coxal cavities dorsally. In the catopids, the notal projection is flat (not a barrier to coxal flexation) and is broadly joined to the sternum. There is variation in the posterior notosternal connection. In *Catops* and *Platycholeus*, the notum simply overlaps the sternum; while in *Prionochaeta* they must edge-on anteriorly and overlap posteriorly. In *Ptomaphagus* the entire joint is edge-on with a distinct suture; the suture is lost in *Colon*.

In *Catopocerus*, *Hydnobius*, and *Anisotoma* the notum, posterior to the coxae, curves, medially forming a cavity under the lateral margin for reception of the proleg. In catopoids, the notum above the coxae is curved outwards, but posteriorly it curves inwards and is entirely mesad of the coxae (Figs. 30, 163), and not a barrier to posterior coxal flexation. These curvatures are slightly developed in *Camiarus*. Notal rim-fold produced ventrally to form long condyle in *Catopocerus*, *Hydnobius*, *Agathidium*, and *Anisotoma*, which articulates with the coxa and pleuron.

Notosternal joint rigid, horizontal or nearly so, slightly inclined in *Catopocerus*, articulation folds distinct only in *Hydnobius*, suture absent in *Colon*.

The sternum extends well in front of coxae and the cryptosternum is slender in *Catopocerus*, *Hydnobius*, *Camiarus*, *Neocamiarus* (Figs. 26, 27). In *Agathidium* and *Anisotoma* (Figs. 31, 29) and in the other catopoid genera, the sternum does not extend far in front of the coxae (see head-prothorax joint above) and the cryptosternum is broad. Projection produced ventrally to form a small intercoxal septa.

Pleuron motile, attached to notum near rim except in *Platycholeus* and *Ptomaphagus*. Endopleuron with a long compressed base and an expanded apex in *Catopocerus* (Fig. 131); and with a squat base in *Ptomaphagus*; endopleuron intermediate in

other forms examined. Slender flat coxal articular face of trochantin folded approximately 90° from sternal face in *Catopocerus*, *Hydnobius*, and *Agathidium*. In the catopoids, the coxal face is distinctly concave and is capable of enclosing the entire coxal articular region. Only the trochantinal rim-fold is distinct in the genera examined.

Articular region of coxa small, less than .35 total coxal length, short and compressed in catopoids to form slender neck which fits into a trochantinal concavity (Fig. 147). Coxa extends below sternum, ranges from squat and small (*Catopocerus*, *Camiarus*) to elongate and very large (*Prionochaeta*). Coxal and trochantinal enclosure quite variable. In *Catopocerus*, *Hydnobius*, *Agathidium* and *Anisotoma* the notal and sternal cowlings are small, the pleuron articulates near the notal rim; only a small part of the trochantin and coxa are enclosed. In the catopoids, these cowlings are enlarged, do not overlap, there is always at least a small space between them; enclosure least developed in *Colon*, most so in *Ptomaphagus*.

The pronotum rests broadly on the mesonotum and elytra, while laterally the rim of the mesepisternum is slightly enclosed within the prothorax. In forms with dorsally closed coxal cavities the posterior sternal flange encloses the rim of the mesosternum. When the pronotum rests on the elytra and the mesothoracic rim is enclosed within the prothorax, little prothoracic motion seems possible (Fig. 163).

The procoxae of the catopoid genera are capable of flexing through a large angle. This is made possible through modifications of the sternum, notal curvature, and of the pleurocoxal articulation and its enclosure. The slender sternum is not only part of the compaction device but also permits the coxae to move further anteriorly than a broad sternum extending to the coxal apex. Posteriorly, the sternum curves inwardly, permitting posterior flexation.

In *Anisotoma* (Fig. 29) the notal projection is laterad of the inner coxal face;

posterior coxal flexation is geometrically impossible. In the catopoids, closed coxal cavities are retained, coxal flexation is made possible by curving the notum and coxal articulation outwards anteriorly, and curving the notum sharply inwards posteriorly. These modifications bring the entire coxa laterad of the notal projection and permits a large angle of posterior flexation (Fig. 30).

Enclosure of the trochantin and coxal articular region is a general adaptive improvement that serves to project membrane connecting moving parts. Coxal and trochantinal enclosure in forms capable of flexation requires more internal space or smaller, more compact moving parts than would be required in forms capable only of coxal rotation. The trochantin and coxal articular region are sharply reduced in anisotomids capable of flexation. The amount of coxal enclosure is variable; sternal and notal cowlings almost completely enclose the coxae and trochantin in *Ptomaphagus*, less so in *Prionochaeta* and *Camiarus* (Figs. 28, 31). The coxal articular region is compressed into a small, slender neck (Fig. 147) and is enclosed within the concave articulation face of the trochantin.

Bathysciinae and *Glacicavicola*

The prothorax of many of the troglobitic bathysciines is elongate and nearly circular in cross section. However, their pleurocoxal mechanism is easily derivable from that of catopoids. In *Astagobius*, most of the slender coxal neck and trochantin are enclosed (Fig. 32). Posterior to the coxal articulation the notum and sternum are solidly joined and curve inwardly.

The prothorax of *Glacicavicola* (Fig. 33) is also elongate. However, it is developed in front of the coxae, with a long notosternal joint. The coxa and the trochantin are partially enclosed. The notal projection is large, extends laterad of the coxae, and covers a portion of it below the pleural articulation. Coxal flexation is possible

since the inner surface of the notal projection is flat. The coxae simply move under it as in some silphids. A pleurocoxal mechanism of this type is readily derived from that of a generalized staphylinoid (*Lyrosoma*, *Hydnobius*, *Catopocerus*).

SILPHIDAE

Figures 39–42, 129–130, 162

Generalized configurations with relatively high volume and coxae capable only of rotation, e.g., *Lyrosoma*, *Necrophilus* (Figs. 39–40) or variably reduced forms, with low enclosed volume and coxae capable of a high degree of flexation, e.g., *Nicrophorus*, *Necrodes* (Figs. 41–42).

Notum with large flat expanded margins in *Necrophilus* (Fig. 40), *Pelatines*, *Silpha* and *Necrodes* (Fig. 42). Notal projection acutely triangular in outline, reaches below trochantin and is triangular in cross section, blocking flexation in *Pteroloma*, *Lyrosoma*, *Pelatines*; long though not a bar to flexation in *Necrophilus*. Inner surface of the notal projection is flat, broad in outline, and reaches slightly above the trochantin in *Silpha*; projection is at level of trochantin in *Nicrophorus*, but in *Necrodes* it extends just below the dorsal pleurocoxal articulation.

Notosternal joint horizontal or nearly so, tightly membranous. Notal and sternal rim-folds present.

Sternum highly variable in horizontal and vertical development; the extremes are *Lyrosoma* and *Necrodes*. Sternal projection thin, acts as coxal separator, reduced in the silphines and nicrophorines.

Pleuron motile. Endopleuron with squat base and expanded apex in *Lyrosoma* (Fig. 129), *Pteroloma*, *Necrophilus* and *Pelatines*. However, in *Nicrophorus* (Fig. 130), *Silpha* and *Necrodes* it is expanded immediately above the apophysis. Exopleuron with anterior pleural fold that articulates with the sternum as well as with an external dorsal pleurocoxal articulation in *Necrophilus* and *Pelatines*. In other genera the posterodorsal edge of the sternum is inserted into a small

cavity on the ventral surface of the pleural fold. Trochantin long folded lengthwise. Internally, a pleural rim-fold is present but does not extend far below the pleurocoxal articulation. Zone of fusion between pleural and trochantinal rim-folds usually present.

Coxa articular region large (.35–.56 coxal length). Coxae capable of flexation in forms with reduced or flat notal projections, e.g., *Nicrophorus*, *Necrodes*.

Promesothoracic joint variable. Mesosternal cavities for reception of procoxae present in *Pelatines*, *Necrophilus* and *Lyrosoma*.

Spiracular sclerites present, median sclerites present in *Silpha*, *Necrodes*, and *Nicrophorus*.

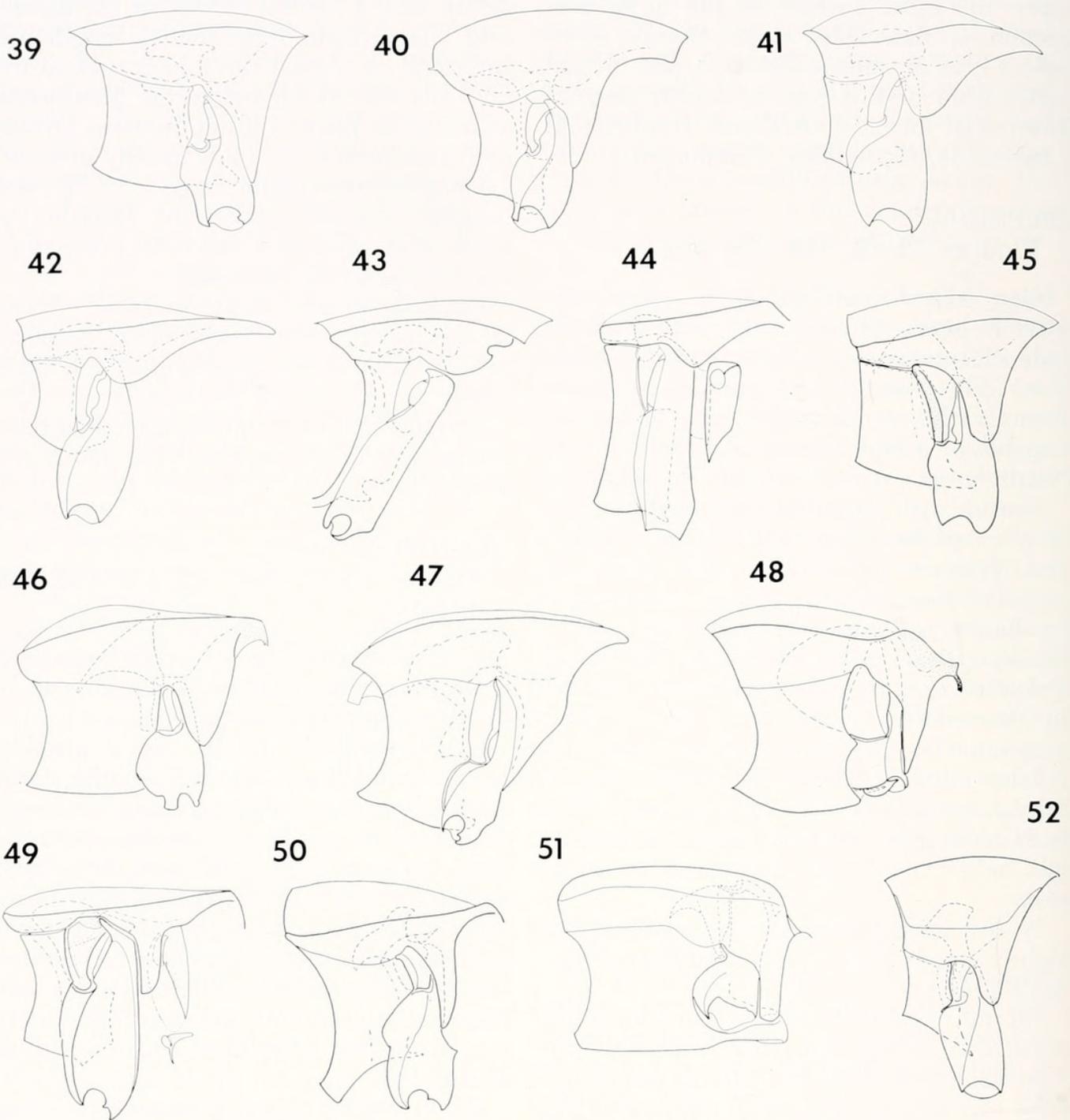
STAPHYLINIDAE

Figures 43–58, 124, 128, 132–133, 136, 144–146

The great diversity of prothoracic configurations within the staphylinids can be divided into three groups:

(A) *Generalized forms*. Coxal articular region long (about .30 total length) dorsal articulation normally enclosed. A main sequence array of configurations ranging from high volume forms with large nota and sterna, the latter extending close to the apex and far in front of the relatively small coxae, e.g., *Nodynus*, *Trigonurus*, *Omalium*, *Osorius* (Figs. 45–47, 50), to low volume forms with low nota and variable sterna, e.g., *Empelus*, *Proteinus*, *Tachinus* (Figs. 43–44, 49).

(B) *Forms capable of high coxal flexation*. Derivable from the generalized type by: 1. reducing the sternum so that it extends slightly in front of and just below the trochantin; 2. reducing both the height of the notum and the length of its projection; 3. increasing the length and width of the coxae while decreasing as well as enclosing the articular region. A continuous series probably exists between the forms capable of flexation and the highly modified forms included here, e.g., *Lathrobium*, *Philonthus*, *Aleochara* (Figs. 53–55).



Figures 39–52. Staphylinoidea. 39. *Lyrosoma opaca*. 40. *Necrophilus hydrophiloides*. 41. *Nicrophorus* sp. 42. *Necrodes surinamensis*. 43. *Empelus brunnipennis*. 44. *Protenus sulcatus*. 45. *Omalium marginatus*. 46. *Trigonurus crotchii*. 47. *Nodynus leucofasciatus*. 48. *Piestus* sp. 49. *Tachinus fimbriatus*. 50. *Osorius stipes*. 51. *Leptochirus* sp. 52. *Oxyporus lateralis*.

(C) *Forms with internalized coxae.* Derivable from the generalized type by enclosing the articular region of the coxa through: 1. dorsal growth of the notal cowlings, e.g., *Piestus*, *Leptochirus* (Figs. 48, 51); 2. overlap and fusion of notal

and sternal cowlings, e.g., *Stenus*, *Oxytelus*, *Bledius* (Figs. 56–58).

Description: Head prognathous in most forms, hypognathous in *Conosomus*, *Aleochara*, *Habrocerus* and in *Gymnusa*. Cervical sclerites present.

Height of notum and development of its lateral margins highly variable. Lateral margins expanded in *Megarthus*, *Habrocerus*, *Tachinus*, and *Conosomus*, but much reduced in *Bledius*, *Stenus*, and *Oxyporus*, where the notum is ovoid in cross section.

Notal projection variable. Among the Proteininae the notal projection is small and broadly curved in *Proteinus* (Fig. 44), *Megarthus* and in the genera figured by Steel (1969), except *Spiphotelus* and *Alloproteinus*, where it is long and triangular in outline. These two genera lack large spiracular sclerites. In the omaliines examined as well as in *Trigonurus*, *Siagonium*, *Oxyporus*, *Osorius*, *Pinophilus*, *Lathrobium* and *Tachinus* the notal projection is long, reaches the level of the trochantal apex and is triangular in outline (Figs. 46, 52, 50, 53, 49). The projection extends below the trochantin in *Piestus* and *Leptochirus* (Figs. 48, 51); in the latter it is attached to the sternal projection. A short projection is present in *Bledius* (Fig. 58). In *Oxytelus* and *Stenus* the notum is developed far ventrally, its margin is horizontal (Figs. 57, 56). A thin, small notal projection distinctly less sclerotized than the surrounding regions occurs in *Creophilus*; the projection is absent in *Thinophilus* and *Philonthus* (Fig. 54). A small projection is present in *Xenodosa* but absent in *Aleochara* (Fig. 55). In *Conosomus* the short projection originates posterior to the coxa and articulates with the spiracular sclerites.

Membranous notosternal joint present in the omaliines and proteinines examined as well as in *Tachinus*, *Conosomus*, *Aleochara* and *Habrocerus*. Solid joint with distinct suture found in the piestines, osoriines and in *Oxyporus*, *Lathrobium* and *Pinophilus*; suture very faint in *Stenus* and *Philonthus*. Notosternal suture absent in *Bledius*, *Oxytelus*.

Ventral and anterior development of sternum varies from greatly reduced in *Philonthus* and *Aleochara* (Figs. 54, 55), where the notosternal joint is dorsad of the posterior notal margin and extends slightly

below and not far in front of the trochantin; to well developed in high volume forms where it extends close to and far in front of the coxal apex, e.g., *Trigonurus*, *Leptochirus* (Figs. 46, 51). Sternal projection short, vertical, acts as a coxal separator in the proteinines, omaliines examined as well as in *Piestus*, *Trigonurus*, *Osorius*, *Oxyporus*, *Bledius*, *Stenus*, *Lathrobium* and *Pinophilus*. Sternal projection absent in *Tachinus*, *Habrocerus*, *Aleochara*, *Xenodosa* and the staphylinines examined. In *Leptochirus* (Fig. 51) a broad sternal projection extends behind the coxae and is united with the notal projections at the level of the coxal apex forming closed coxal cavities, its dorsal surface is enlarged posteriorly into a flange that articulates with the mesosternum. Dorsal surface of projection forms a flange in *Osorius*. Coxal cavities may also be closed by sclerotization of intersegmental membrane that either includes the spiracles (*Pinophilus*) or does not (*Conosomus*).

Pleuron motile. Endopleuron with sharply constricted base and large expanded apex in *Trigonurus* (Fig. 46) though it is somewhat constricted and then expanded in *Oxyporus* and *Lispinus* (Fig. 52). In the other forms examined the endopleuron is not differentiated into a base and apex, its dorsal surface may be horizontal and ranges from slightly concave in *Empelus*, *Proteinus* and *Anthobium* (Figs. 43–44, 124) to highly concave, almost globose, in *Philonthus* and *Lathrobium* (Figs. 133, 132), or its surface may be flat and vertical as in *Piestus* (Fig. 48).

Trochantin and exopleuron highly variable, latter usually broad, pleurocoxal articulation is enclosed, except *Tachinus*. A small low anterior pleural fold may be present, but only in *Proteinus* (Fig. 128) and *Megarthus* does it have a distinct articulation with the sternum. In forms where the trochantin is not enclosed, it may be folded lengthwise, usually nearly 90°, forming sternal and coxal attachment surfaces. However, in *Habrocerus*, *Xantholinus* and *Lathrobium* (Figs. 53, 133) the

trochantin is flat, almost folded back on itself, and is laterad of the sternum. The trochantin is flat and not folded lengthwise in forms where it is enclosed, e.g., *Oxytelus*, *Bledius*, *Stenus*. Internally, a pleural rim-fold is usually present, may be external and may extend far below the pleurocoxal articulation in forms with broad endopleura, e.g., *Omalium*, *Proteinus*, *Anthobium* and *Tachinus* (Figs. 45, 44, 128, 49, 128 PL stippled region). In forms with narrow endopleura the rim-fold is present but does not extend far below the dorsal coxal articulation, e.g., *Trigonurus*, *Oxyporus*. The pleural rim-fold appears to be absent in *Oxytelus*, *Bledius*, and *Stenus*. An external line of fusion in the solid zone between the pleural and trochantinal rim-folds is present only in *Tachinus* (Fig. 49). A zone of fusion between pleural and trochantinal rim-folds is usually visible internally (Figs. 124 A, B, ZF).

Pleuronotal joint, and quality of pleural motion, highly variable. Pleuron may be capable of rotation and a slight amount of flexation in the proteinines, omaliines examined as well as in *Siagonium*, *Trigonurus*, *Oxyporus*, and *Tachinus*. In *Osorius*, a large ventrally directed condyle on the notal fold articulates with a small concave region on the dorsal face of the coxa. Among the forms with deep coxal internalization, there are no condyles in *Piestus* and *Stenus*, but in *Oxytelus* and *Bledius* a small evagination on the pleuron, below the apophysis and anterior to the coxae, is inserted into a cavity in the notal cowling, while in *Leptochirus* a large notal condyle articulates with both the coxa and pleuron. In the high flexing forms, the margin of the curved invagination encloses a large flat pleural surface which is in contact with and moves against the flat surface of the notal cowling during flexation, e.g., *Philonthus*, *Lathrobium* (Figs. 132–133).

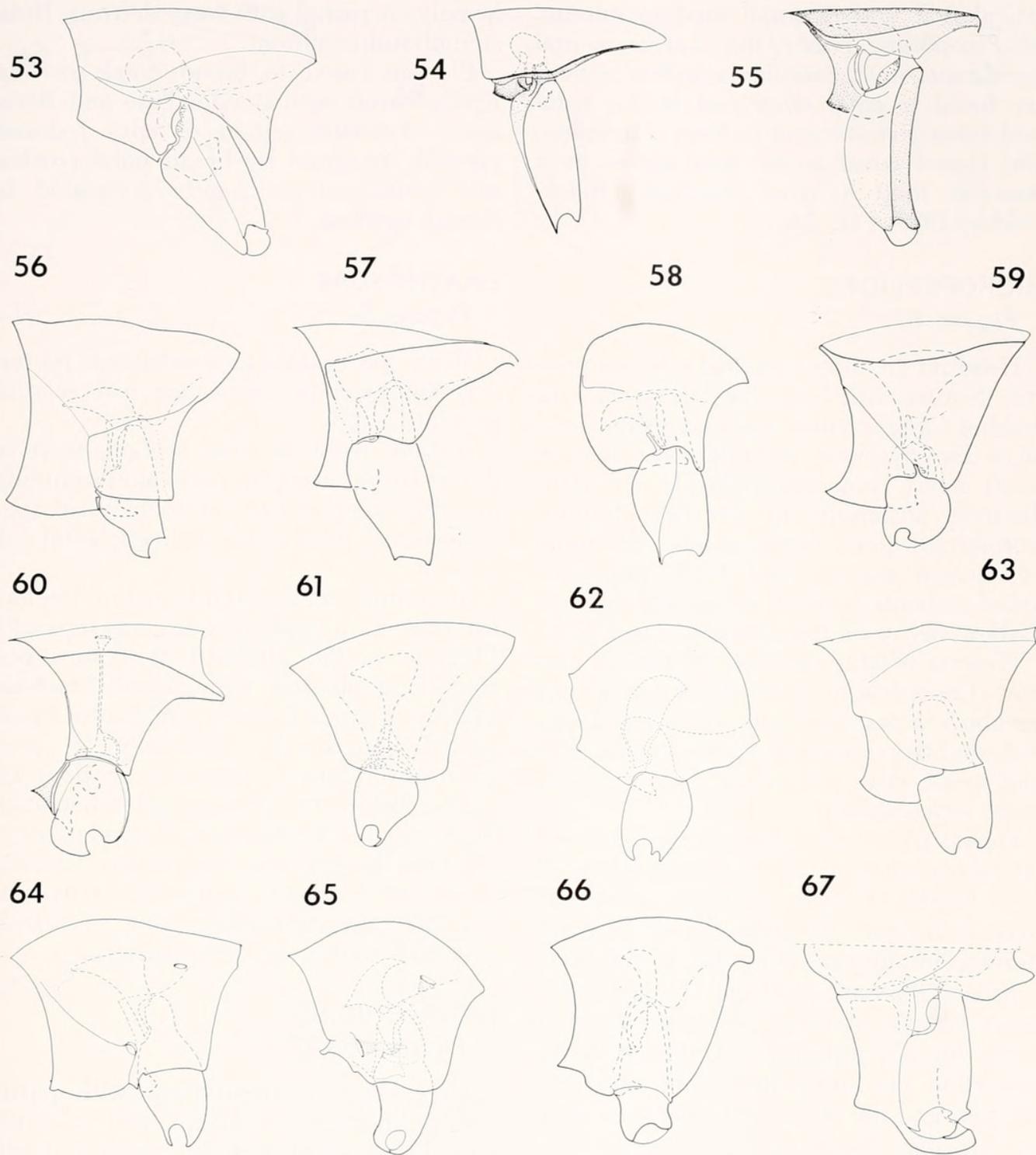
Coxal structure, enclosure and motility highly variable. In many generalized forms, only the strong dorsal pleurocoxal articulation is enclosed within the notum, and a

portion of the coxae may be enclosed by the notal projection, e.g., *Proteinus*, *Omalium*, *Trigonurus*, *Tachinus* and *Oxyporus* (Figs. 44–46, 49, 52). In these forms the pleural articular region of the coxa is broad and generally more than .30 coxal length as in *Trigonurus* (Fig. 144). Dorsal development of the pleurocoxal cowling results in enclosure of the entire articular region in *Oxytelus* and *Bledius* (Figs. 57–58) or of enclosure below the articular region as in *Stenus* (Fig. 56). The articular region is about .60 total coxal length in both *Piestus*, where it is partially enclosed, and in *Leptochirus* (Figs. 48, 51, 145), where it is entirely enclosed. The very narrow articular region is reduced to less than .25 coxal length in high flexing forms such as *Philonthus* (Figs. 54, 146), where it is partially enclosed and in *Aleochara* and *Lathrobium*, where the articular region is almost entirely external. Coxal flexation is prevented by the shape and position of the notal projection in *Leptochirus*, *Piestus*, *Bledius*, by the contours of coxal cowling in *Stenus* and by a long coxal carina which is inserted into a groove in the cryptosternum in *Lispinus* and *Osorius*.

Pleurocoxal articulation usually well-developed, involving a conical projection on the coxa that is inserted into a depression on the pleuron.

Promesothoracic joint highly variable and not studied in detail. In generalized forms the notal projection rests on the mesepisternum and the pronotum rests on the mesonotum and elytra resulting in somewhat rigid (*Trigonurus*) to relatively loose connections (*Omalinae*). In some of these forms there are small cavities in the mesosternum for reception of the procoxae. The very loose joint in some of the high flexing forms, e.g., Staphylininae, is similar to that of higher silphids, e.g., *Nicrophorus* (Fig. 41). A motile joint with structural integrity is found only in *Leptochirus*.

Mesothoracic spiracle surrounded by sclerotized margin that is usually produced ventrally and is triangular in outline. In the



Figures 53–67. Staphylinoidea. 53. *Lathrobium prahae*. 54. *Philonthus cyannipennis*. 55. *Aleocharara lata*. 56. *Stenus juno*. 57. *Oxytelus fuscipennis*. 58. *Bledius* sp. 59. *Scaphium castanipes*. 60. *Schaphisoma castanum*. 61. *Connophron flavicarse*. 62. *Clidicus* sp. 63. *Chevrolatia amoena*. 64. *Sonoma tulnae*. 65. *Tmesiphorus costailis*. 66. *Fustiger fuschi*. 67. *Micropeplus laticollis*.

piestines and in most omaliines examined, the slender spiracular sclerites reach but are not fused with a median intersegmental sclerite. However, in the omaliine genera *Phaleopterus* and *Trigonoderus*, the median

sclerite is absent. The spiracular sclerite in *Proteinus* (Fig. 44), *Megarthus* and *Tachinus* (Fig. 49) is large and articulates with and is partially enclosed by the notum; in the latter two genera there is also an

articulation with a small median sclerite. In *Pinophilus*, either the intersegmental membrane, the spiracular sclerites or both are fused to each other and to the notal projection and sternum to form a functionally closed coxal cavity that serves as a posterior limit to coxal flexation (Blackwelder, 1936, Fig. 238).

MICROPEPLIDAE

Figure 67

Head prognathous, cervical sclerites present. Notum with large flat lateral margins bearing large cavities on their ventral surfaces for reception of antennae. A very small notal projection extends for short distance anteriorly to overlap sternum. Notosternal joint membranous. Sternum: exosternum narrow and high, projection broad, extends beneath coxae and fits into shallow cavity on the mesosternum.

Pleuron motile attached to notum near rim. Endopleuron small, does not extend far above notosternal joint, with broad base and slightly expanded apex. Pleural rim-fold small, does not extend below pleurocoxal articulation.

Dorsal pleurocoxal articulation enclosed, articular region of coxa not constricted, .31 total length. Groove on inner surface of coxa, near apex, fits into groove on endosternum limiting coxal motion to rotation.

Promesothoracic joint may be rigid, posterior margin of notal projection fits into cavity on mesepisternum, while the sternal projection fits into a depression on mesosternum and the elytra and pronotum overlap broadly. Small mesothoracic spiracles attached to a slender creased sclerite.

DASYCERIDAE

Figure 38

Head prognathous, cervical sclerites present. Notum with slightly produced lateral margin that is lined with a row of elongate seta-bearing projections. Such projections along with those on the notal disc are most

heavily encrusted with waxy detritus. Notosternal suture absent.

Pleuron fused to broad notal cowling. Endopleuron with slender base and flared apex. Articular region of coxa reduced, partially enclosed by broad notal cowling and projection; trochantin concealed by sternal cowling.

BRATHINIDAE

Figure 34

Head prognathous, constricted posteriorly into slender neck, cervical sclerites present.

Notum ovoid in cross section, with reduced lateral margins, projection triangular in outline reaches level of trochantinal apex. Notosternal joint rigid, inclined, notal fold present.

Sternum extends slightly below trochantin, projection small, acts as coxal separator. Pleuron motile, attached to notum near rim. Endopleuron with broad base and slightly expanded, apex. Trochantin broad, folded lengthwise. Internally a small pleural rim-fold is present but does not extend below the pleurocoxal articulation. Coxa capable of flexation. Articular region .26 total length, not compressed laterally, dorsal articulation of projection cavity type.

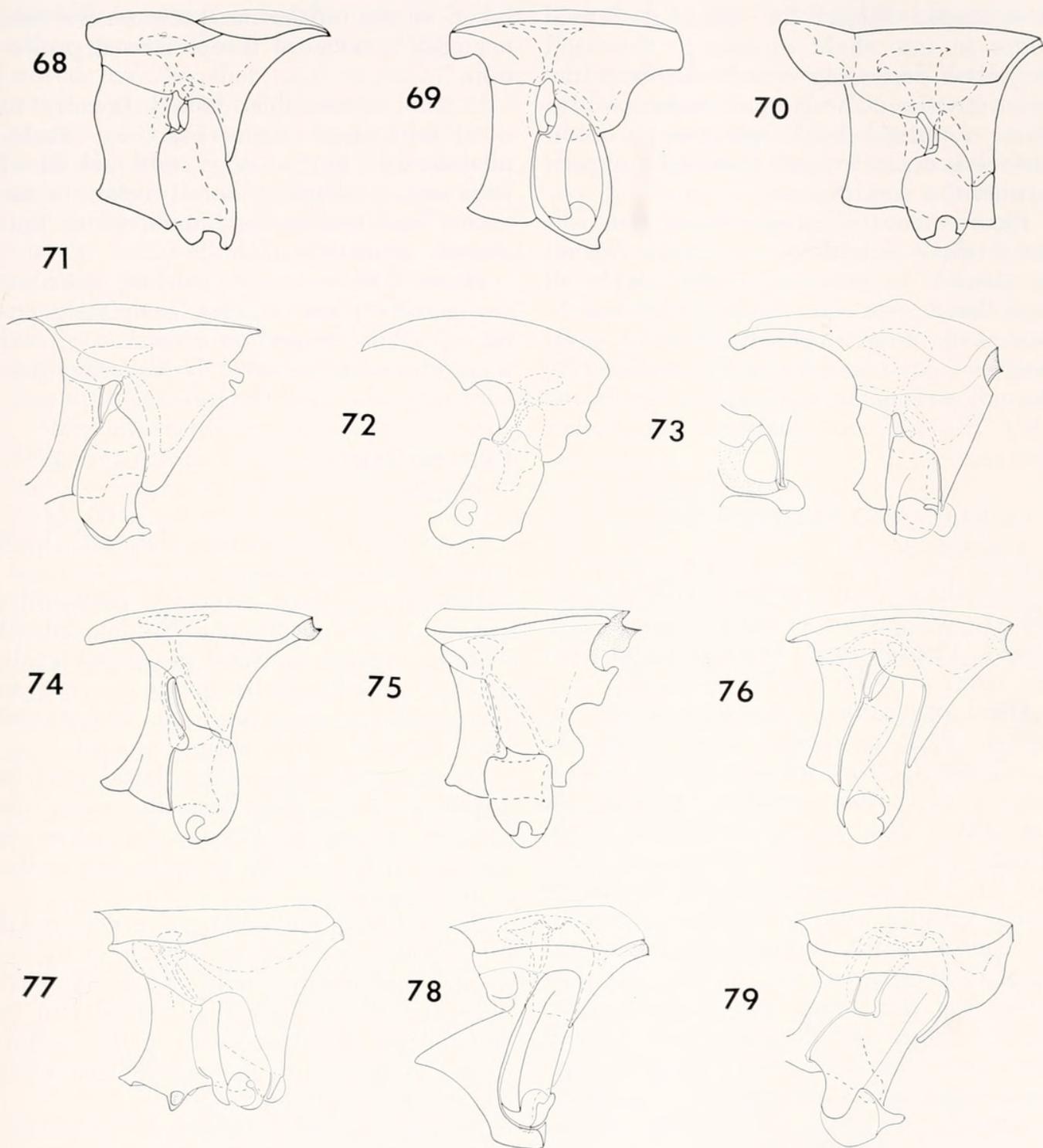
Loose promesothoracic joint, with small procoxal cavities on the mesosternum.

HYDRAENIDAE

Figures 68-70

Generalized configurations with partial trochantincoxal enclosure and ventrally closed coxal cavities in *Hydraena*, but with dorsally closed coxal cavities in *Limnebius*.

Head prognathous, posterior aspect enclosed by prothorax, cervical sclerites present. Anterior face of notum bears a pair of cavities which enclose some of the eyes, the antennae are housed in a slight (*Limnebius*) or elongate (*Hydraena*, *Ochthebius*) posterior elements of these cavities. In *Hydraena*, the long maxillary palpi can be placed in narrow grooves extending from



Figures 68–79. Staphylinoida, Hydrophiloidea, Histeroidea, Scarabaeoidea. 68. *Ochthebius* sp. 69. *Limnebius piceus*. 70. *Hydraena pennsylvanica*. 71. *Spercheus* sp. 72. *Georhyssus californicus*. 73. *Epimetopus costatus*. 74. *Enochrus pygmaeus*. 75. *Helophorous* sp. 76. *Sphaerites politus*. 77. *Syntelia mexicana*. 78. *Hister sulcatus*. 79. *Pleocoma* sp.

below the antennal cavities to the posterior margin of the notum.

Notal projection present, not connected with sternum only in *Ochthebius* (Fig. 68). Rigid notosternal joint, horizontal to

slightly inclined, suture difficult to see in *Limnebius*. Cryptosternum variable, solidly fused to notum producing dorsal closure of coxal cavities in *Limnebius* (Fig. 69). In *Hydraena* (Fig. 70) the sternal projection

is expanded behind the coxae; its lateral edges fit into slight cavities in the notal projection producing ventral closure of the coxal cavities. The sternal projection also forms a vertical coxal separator; its dorsal surface is expanded and flattened and rests against the mesosternum.

Pleuron movable, attached to notum near rim. Stalk of endopleuron squat (*Hydraena*) or slender (*Limnebius*, *Ochthebius*), all with flared apex. Trochantin folded lengthwise with large rim-fold. Most of coxal articular region and trochantin enclosed by sternal and notal cowlings in *Hydraena* (Fig. 70), less coxal enclosure in the other genera.

PTILIIDAE AND LIMULODIDAE

Figures 34, 35

Specialized configurations with dorsally closed coxal cavities or with cavities nearly closed. Pleuron rigid, trochantin and slender coxal articular region enclosed.

Head prognathous, posterior aspect inserted into prothorax, deeply so in *Limulodes*. Cervical sclerites absent. Lateral margin of notum greatly expanded in *Limulodes*, less so in *Acratrichis*, only slightly expanded in *Nossidium* and *Nannosella*. The notal projection of *Acratrichis* fused broadly with sternum at level of trochantinal apex, forming dorsally closed coxal cavities, suture absent (Fig. 35). In *Nossidium* the notum and sternum come close together but do not touch, a notal short projection that arches over the posterior coxal face is also present (Fig. 34).

Notosternal joint solid, suture absent except in *Acratrichis*. Complete enclosure of coxal articular region and trochantin has resulted from the fusion, after overlap, of the notal and sternal cowlings. Only a small area of overlap is present in *Nossidium*.

Exosternum slender, cryptosternum broad, small median projection forms coxal separator. However, in *Limulodes* a long, broad projection extends beneath the pro- and mesocoxae and reaches the metasternum. A

broad carina on the mesosternum fits into a medial groove on the prosternal projection.

Pleuron immovable, joined broadly to notal fold above coxa (Fig. 35). Endopleuron with long slender stalk and flared apex which extends to dorsal surface of the notum in *Limulodes* and *Acratrichis*. Trochantin slender, enclosed.

Coxae globose or cylindrical, articular region short, narrow and completely enclosed. Notal projection (*Nossidium*) and a coxosternal articulation (*Limulodes*) prevent posterior coxal flexation.

LEPTINIDAE

Figure 37

Generalized, somewhat flattened high volume configurations.

Head prognathous, narrowed posteriorly, cervical sclerites absent. Notum, lateral margins expanded. Notal projection small, reaches middle of trochantin, except in *Platypyllus* where it is absent. Notosternal joint inclined, solid, suture present.

Sternal projection reaches coxal apex in *Leptinus*, expanded beneath coxae in *Leptinillus* and in *Platypyllus* where it extends far beyond the coxae to rest on the mesosternum.

Pleuron with long connection with notal fold above coxa may be capable of movement. Endopleuron with slender stalked base and flared apex that extends up to and touches the dorsal wall of the notum. Coxae globose, articular region somewhat compressed, .38 total length.

Promesothoracic connection unspecialized except in *Platypyllus* where the notum broadly overlaps the elytra. The long sternal projection rests on the mesosternum and the intersegmental membrane is unusually short, thick and tough.

SCAPHIDIIDAE

Figures 59, 60

High notal volume variably specialized configurations. Pleuron rigid, and fused

dorsally to notum in *Scaphisoma*, but not in other genera. Coxal articular region narrowed may be short and enclosed along with region slightly below it. External portion of coxa about as long as wide.

Head hypognathous in *Scaphisoma*, nearly prognathous in *Scaphium*, intermediate in *Scaphidium*, posterior aspect completely enclosed by prothorax, cervical sclerites present. Notum with neither expanded lateral margin nor posterior concavity for reception of part of the proleg; projection absent. Notosternal suture rigid, sharply inclined.

Sternum relatively broad in *Scaphium* (Fig. 59) less so in *Scaphidium*. The sternum is compressed dorsally in *Scaphisoma* (Fig. 60) into a narrow peninsula but is expanded at the level of the trochantin. In front of coxa it is molded into a small flat triangular vertical region on which the head rests. Sternal projection forms vertical coxal separator, and in *Scaphisoma* it is fused with the notal flange at the level of the coxal constriction, forming dorsally closed coxal cavities.

Pleuron rigid, with long notal joint above coxa. Endopleuron large with a broad base in *Scaphium* and *Scaphidium*, apex in contact with wall of notum. However, the slender stalk of *Scaphisoma* is only slightly expanded before fusing with the notum. Trochantin and pleuron solidly fused to notum and reduced to a medially projecting shelf in *Scaphisoma*; not reduced in other genera.

Coxae capable only of rotation, constricted and enclosed below the narrow articular region, latter reduced to .16 total coxal length in *Scaphisoma*. A coxal carina in *Scaphium* and *Scaphidium* is inserted into a groove on the rim of the cryptosternum.

Trochantin, articular region of coxae and the constricted portion below it are completely enclosed in *Scaphisoma* and *Scaphidium*, while in *Scaphium* the rims of the cowlings do not overlap, but are quite close

together at the level of the trochantinal apex.

Promesothoracic joint is rigid. In *Scaphidium* a condyle on the mesepisternum fits into a concavity on the posterior notal flange, while in *Scaphium* an elongate ridge on the flange is inserted into a furrow on the mesepisternum. The notal flange is *Scaphisoma* bears both a condyle, which is placed into a concavity on the mesepisternum, and also a long furrow which receives the sharp edge of the episternum. The anterior face of the mesosternum bears two large concavities for housing the procoxae.

SCYDMAENIDAE

Figures 61–63

High notal volume specialized configurations leading to forms with very reduced horizontal sterna, e.g., *Connophron* (Fig. 61). Coxa enclosed below trochantin. Pleuron rigid.

Head prognathous, not constricted posteriorly in *Cephennium*. In the other genera examined the head is hypognathous and constricted posteriorly to form a large globose articular region that is only partially enclosed within the prothorax. Cervical sclerites present, small.

Notum highly developed in some but without expanded lateral margins or posterior medial curvature, projection absent. Notosternal suture rigid when present, inclined in *Chevrolatia*, horizontal in *Cephennium*.

Sternum variable. In *Chevrolatia* (Fig. 63), *Lophioderus*, *Ascydmus*, *Veraphis* and *Mastigus*, the exosternum is distinct with a lateral connection to the notum, while in *Leptoscydmus* and *Clidicus* (Fig. 62) an exosternum is present, but the notosternal suture is absent. The exosternum of *Cephennium* is reduced to a small triangular region below the notosternal suture. In *Scydmaenus*, *Eumicrus* and *Connophron* (Fig. 61) the notum is expanded ventrally so that its lateral margin is actually ventrad

of the approximately horizontal sternum. In *Connophron*, at least, there is no differentiation of the sternum into exo- and cryptosternum. Sternal projection absent, except in *Cephennium* where it is vertical and reaches the coxal apex. Posterior sternal and notal flanges fused at level of trochantin in *Connophron* forming dorsally closed coxal cavities, projections widely separate in *Clidicus*, less so in *Cephennium*.

Pleuron apparently immovable, attached broadly onto notum. Endopleuron with slender stalk and expanded apex in *Connophron* (Fig. 61) and *Cephennium*; not so differentiated in *Clidicus* (Fig. 62). Trochantin completely enclosed, long and broad in *Clidicus*, short and narrow in *Connophron* and *Cephennium*.

Coxae capable only of rotation, constricted and enclosed for short distance below trochantinal apex. Articular region of *Connophron* not parallel with long axis; coxal rotation causes anteroposterior movement of the coxal apex. Articular region long, broad in *Chevrolatia*, *Clidicus*, shorter and compressed in *Connophron* and *Cephennium*.

Trochantin completely enclosed by dorsal development of notal cowling in *Clidicus* and by overlap of notal and sternal cowlings in *Connophron*; probably by a combination of the two methods in *Chevrolatia*.

In most scydmaenids the pronotum rests broadly on the elytra and mesothorax, the prosternum overlaps the anterior rim of the mesosternum; the latter bears a pair of large concavities, usually separated by a carina, for the reception of the procoxae. In rest position, the prothorax may not be capable of much movement. The promesothoracic joint of the Clidicini seems less rigid, and lacks large mesosternal concavities.

PSELAPHIDAE

Figures 64–66

High notal volume specialized configurations with reduced sterna and with the coxae enclosed far below the trochantin.

Head prognathous in *Sonoma*, *Euplectus*, *Fustiger* inclined somewhat ventrally in *Tmesiphorus*, constructed posteriorly into a large globose condyle that is partially inserted into the prothorax. Cervical sclerites absent.

Notum developed far ventrally, with a long cowling; projection absent, without expanded lateral margins and posterior medial curvatures.

Notosternal suture faint and inclined in *Sonoma* where it extends along a shallow groove, absent in *Euplectus*, *Tmesiphorus*, and *Fustiger*. Sternum variable, exosternum relatively long in *Euplectus* and *Sonoma* (Fig. 64) smaller in *Tmesiphorus* and *Fustiger* (Figs. 65, 66).

Pleuron rigid or capable of slight movement, attached to notum far above notal rim but only slightly above the coxa. Endopleuron with broad base and moderately expanded apex. Trochantin long, enclosed. Coxae probably capable only of rotation, long, enclosed by notum far below trochantin. Articular region long, not constricted.

The pronotum rests broadly and snugly on the mesothorax; the procoxae are housed by an undivided cavity on the mesosternum.

HYDROPHILOIDEA

Figures 71–75

(Except *Georyssus*). Specialized configurations with dorsally closed coxal cavities and in *Epimetopus* ventral closure as well. Coxal articular region and trochantin always partially enclosed, completely so in *Helophorus*, *Hydrochus* and *Georyssus*. Pronotum-elytra interlocking device always present, while a strong ventral interlocking mechanism is present in some Hydrophilinae.

Broad, prognathous head deeply inserted into prothorax. Cervical sclerites present.

Lateral margin of notum varies from reduced in *Epimetopus* to large and flattened in *Enochrus*. Posterior wall and

notal carina present, former bears striate crenulations in *Spercheus*.

The notal projection of *Epimetopus* (Fig. 73) is long and gradually narrowed below the dorsal closure, its apex rests on the sternal projection; a large foramen is enclosed between the notal projection and the cryptosternum. In *Helobata* and *Hydrochus*, however, the dorsal closure is very broad and the short blunt projection reaches the sternal projection but no foramen is enclosed. In the other genera examined a short, blunt projection extends slightly below the dorsal closure, e.g., *Enochrus* (Fig. 74).

Notosternal joint short, horizontal or nearly so, rigid to tightly membranous with internal carina.

Exosternum reduced, extends little in front of coxae in *Chaetarthria* and *Berosus*, slender in other genera, does not reach coxal apex; with low carina along ventral midline in *Enochrus*, *Berosus* and *Sphaeridium* while in *Tropisternus* and *Hydrophilus* the exosternum is broadly produced ventrally and bears on its posterior surface a large fossa. Dorsal surface of projection expanded and flattened forming a posterior sternal flange, in *Sphaeridium* it is highly concave.

Pleuron motile, except *Sphaeridium*, attached to notum near rim. Endopleuron with slender stalk and expanded apex, comes close to dorsal wall of notum, except in *Spercheus* (Fig. 71) where the base is squat. Trochantin usually slender, with narrow rim fold. What may be a pleuro-trochantinal suture is present in *Spercheus*. In *Sphaeridium*, the pleuron is broadly fused to the notal rim and the endopleuron comes close to the dorsal wall of the notum. The trochantin is thin, poorly sclerotized and moves, along with the pericoxal membrane, as the coxa rotates.

Coxa capable of rotation only. Articular region long and narrow, usually more than .3 total length except in *Epimetopus* where it is short (.2 total length) and broad.

Coxal enclosure variable, occurs only

through development of notal and sternal cowlings below notosternal joint. Little enclosure in *Chaetarthria*, coxal articular region and most of trochantin enclosed in majority of genera examined, e.g., *Epimetopus*, *Spercheus*, *Enochrus*. In *Sphaeridium* the cowlings come close together while in *Helophorus* (Fig. 75) they overlap to the level of the trochantinal apex and in *Hydrochus* cowling overlap extends below the trochantinal apex.

Promesothoracic joint relatively complex, not studied in detail. Notal carinae inserted into cavities in the elytra. Dorsal margin of notum usually overlaps dorsal margin of elytra; they meet edge-on in *Epimetopus*, *Hydrochus* and in *Spercheus*, where finely striate notal crenulations interdigitate against the finely striate dorsal rims of the scutellum and elytra. Dorsal surface of sternal projection generally in contact with mesosternum. In some hydrophilines a large mesosternal keel is inserted into a fossa on the posterior face of a sternal projection forming an interlocking device which could prevent lateral movements of the prothorax. In *Sphaeridium* a blunt condyle on the mesosternum is received by a cavity in the sternal projection.

Georyssus

The prothorax of *Georyssus* (Fig. 72) is modified to form part of a highly developed head-prothorax-mesothorax compacting mechanism. The head in rest position is opisthognathous and housed in a large, complex cavity formed posteriorly by the nearly continuous vertical faces of the pro- and mesosternum and laterally by the large, flattened medial coxal surfaces. The coxae are produced, below the trochanteral insertions, into large medially curving plates that partially cover the mouthparts and labrum. The antenna is housed in a large cavity formed from the notum and the small lateral regions of the sternum. The notosternal suture and probably a zone of cowling overlap occur in

this cavity. The flattened medial surface of the femora can close the entrance to the antennal cavity.

Coxal articular region and trochantin enclosed. Endopleuron with broad base and horizontal apex. Coxal cavities closed dorsally. Posterior wall and small notal carina present.

HISTEROIDEA

Figures 76–78, 137–139

Specialized rigid body, high notal volume configurations with extreme dorsal enclosure of the trochantin and coxa and with a complex compacting mechanism, e.g., *Hister* (Fig. 78) OR with partial coxal enclosure but without compacting and interlocking mechanisms, e.g., *Sphaerites*, *Syntelia* (Figs. 76, 77). There is great variation in the pleurocoxal mechanism leading up to a scarabaeoid type in *Hister*, compare Figures 139, 140.

Head is hypognathous in *Sphaerites*, *Hister* and in *Saprinus* where it is, in rest position, deeply enclosed within the pronotum partially to wholly concealing the eyes; head prognathous in *Syntelia* and *Hololepta*. A small (*Saprinus*) or large (*Hister*) anterior expansion of the sternum conceals the mouth parts up to near the mandibular apices, while laterally a slit cavity device houses the antennae. Cervical sclerites present.

Posterior notal wall present, its ventral rim only slightly expanded. Notal projection long in *Sphaerites* (Fig. 76) and *Saprinus*, short in *Hister* (Fig. 78) and *Hololepta*. Notal projection is attached to the sternal projection forming ventrally closed cavities only in *Syntelia* (Fig. 77).

Notosternal joint solid, suture inclined ventrad from coxa in *Hololepta* and *Saprinus*, only slightly so in *Hister* and *Sphaerites*. Sternal and notal folds distinct in *Sphaerites*, reduced in other genera.

In *Saprinus* and *Hister*, the exosternum is produced medially into a large horizontal flange, laterally it is narrowed and bears a

groove and a cavity that house the basal antennal segments and the antennal club respectively. *Sphaerites* and *Syntelia* lack both an expanded sternum and an antennal housing mechanism, a slightly expanded sternum is present in *Hololepta*. Cryptosternum narrow in *Sphaerites*, broad, reaching level of notal projection, in *Saprinus*, *Hister* and *Hololepta*. Sternal projection slender, acts as coxal separator and does not reach coxal apex in *Syntelia* and *Sphaerites*, while in the other genera examined it is broad and extends beneath the coxa.

Pleuron motile, attached to notum at or near level of dorsal wall. Endopleuron distinctly shifted anteroventrally in *Hister* (Fig. 139), less so in *Saprinus* (Fig. 138), relatively unmodified in *Sphaerites* (Fig. 137) with a triangular ventral carinae in *Hister* and *Saprinus*. Trochantin broad, partially exposed in *Sphaerites* where it is folded lengthwise nearly 90° and has a large rim-fold; boundary between pleuron and trochantin obscure, it may form the ventral margin of pleurocoxal articulation cavity. In *Saprinus* there is a distinct zone of fusion between the trochantin and exopleuron below the pleurocoxal articulation, fusion zone compressed in *Hister*.

Coxae very long, capable only of rotation. Articular region broad, about .3 total length, enclosed except in *Sphaerites*. Coxa articulates with sternal projection via a groove-ridge device in *Hister* and *Hololepta*.

Sphaerites, *Saprinus* and *Hister* represent successive steps in the development of a scarabaeoid type pleurocoxal mechanism. In *Sphaerites* the pleurocoxal cowling is developed far dorsally but is not fused to the lateral or dorsal notal walls and does not bear a condyle; the pleurocoxal articulation is of the projection-cavity type and is similar to that of other staphyliniforms, as is the structure of the trochantin and endopleuron (Fig. 137). In *Saprinus* the cowling bears a strut that is fused to the lateral notal wall and comes close to, but is not fused with, the dorsal notal wall. A pleural projection articulates with the con-

cave dorsal face of the coxa, while the endopleuron extends ventrally as a slender peninsula (Fig. 138). In *Hister* the cowl-ing is fused not only to the lateral notal wall, via a strut, but also to the dorsal wall. It bears a large condyle that is inserted into a cavity formed from the pleural projection and from the coxa above the pleural articulation. The endopleuron is developed and expanded far ventrally (Fig. 139).

Promesothoracic joint relatively loose in *Sphaerites*; the perpendicular posterior face of notum rests against the elytra blocking dorsal rotation. The mesosternum is without cavities for reception of the prosternal projection and procoxae. *Syntelia* is a somewhat pedunculate form; the prothorax is capable of rotation above the plane of the elytra.

Saprinus and *Hister* are rigid-body compacted forms. Dorsally, the perpendicular faces of the notum and elytra lie against one another, and a small notal carina is inserted into a groove on the elytra or mesepisternum. The mesepisternum is developed far in front of the elytra forming a broad shelf on which the pronotum rests. The mesepisternum also curves medially and meets the notal projection to form a cavity that can house the profemur in rest position. The mesosternum bears a pair of divided cavities that receive the procoxae and in *Hister* it also bears a cavity that receives the prosternal projection. In *Saprinus* the prosternal projection overlaps the mesosternum for a short distance; ventral motion of the prothorax is blocked by a vertical ridge on the projection.

SCARABAEOIDEA

Figures 79–84, 140, 148

Moderate to high notal volume forms with a uniform, specialized, pleurocoxal mechanism with extensive ventral shift of the endopleuron. Coxal cavities closed ventrally, except *Pleocomma*.

Notal height and enclosed volume varies

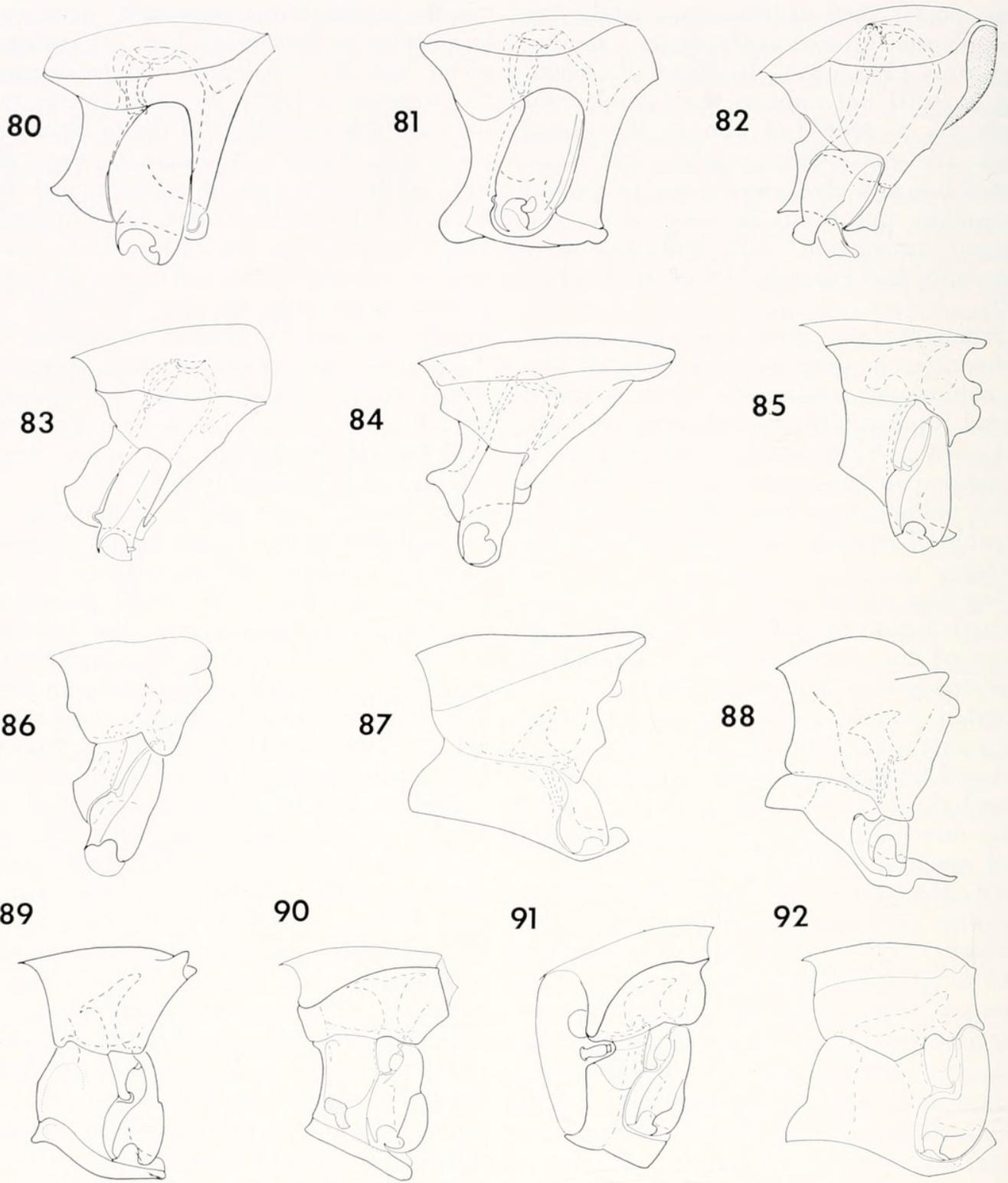
greatly in the forms examined. The very low notum of *Pleocomma* (Fig. 79) encloses about half the exopleuron and trochantin; the sternum is high. In many forms the notum reaches the level of the trochantinal apex, e.g., *Popilius*, *Cerucheus* (Figs. 80, 81), while in a few it is developed far below the trochantinal apex, e.g., *Phyllophaga*, *Copris* (Figs. 83, 82) and the sternum is reduced. Size and shape of notal projection variable, its apex is loosely or tightly enclosed by grooves or cavities on the sternal projection forming ventrally closed coxal cavities, except in *Pleocomma* (see Ritcher, 1969, Figs. 2–10). Posterior wall sometimes present but never bears interlocking mechanisms.

Notosternal joint solid, inclination of suture varies from straight and horizontal to slightly inclined and curved.

Exosternum narrow, normally extends to just above coxal apex, comes close to being horizontal in some high notal volume forms, e.g., *Copris*. Sternal projection compound, very large evagination of sternellum forms a large flange, and laterally bears grooves or a pit that receives the notal projections.

Pleuron motile, attached to notum at level of dorsal wall, rotates, along with the coxa, about notal condyle (Fig. 140). Endopleuron vertical, shifted anteriorly so that most of it is anterior to rather than above the exopleuron. A distinct pleural invagination is present dorsally but is obscure anteriorly. The exo- and endopleura are developed ventrally resulting in reduction of the trochantin. In *Lichnanthe* (Fig. 134) the trochantin and its internal rim fold are somewhat reduced, comparable to the condition in *Hister* (Fig. 139), but in most other Scarabaeoidea, e.g., *Phyllophaga* (Figs. 83, 140), the endopleuron reaches quite close to the trochantinal apex so that the rim fold is either greatly reduced and difficult to see or is absent. Ventral surface of endopleuron usually carinate.

Pleurocoxal articulation and manner in which both articulate with and rotate about the notal condyle without appreciable vari-



Figures 80–92. Scarabaeoidea, Elateriformia. 80. *Ceruchus piceus*. 81. *Popilius disjunctus*. 82. *Corpis fri-cator*. 83. *Phyllophaga* sp. 84. *Euphoria lambalis*. 85. *Dascillus davidsoni*. 86. *Sandalus niger*. 87. *Brachy-psectra fulva*. 88. *Cerophytum elateroides*. 89. *Eurypogon niger*. 90. *Artematopus puncticollis*. 91. *Byrrhus americanus*. 92. *Heterocerus pallidus*.

ation in the scarabaeoids examined. A bar-like pleural evagination with a concave surface articulates with the coxa, and receives a portion of the notal condyle. The

coxa extends above the pleural articulation and bears a concave surface that articulates with the notal condyle (Fig. 148).

Coxa always with strong notal articu-

lation as described above, capable of rotation only, articular region broad (varies from .25-.4 total length), wholly enclosed, except in *Pleocoma*. A very broad attachment surface for posterior rotator muscles always present, coxal foramen large, ovoid, usually extends far below articular region (Fig. 148). In many forms examined, a coxal carina is inserted into a groove in the cryptosternum, e.g., *Phyllophaga*, *Popilius*, while in *Copriss* the groove is on the coxa and the ridge on the cryptosternum. Otherwise, a coxo-sternal articulation may be absent, e.g., *Ceruchus*.

Series ELATERIFORMIA

A large assemblage of limited diversity. Putative stem form with membranous notosternal joint, generalized pleurocoxal mechanism, low notal volume, and a suite of promesothoracic interlocking devices including striate crenulations which serve as a defense mechanism or as a semipermanent rigid joint (e.g., Ptilodactylidae, and some dascilloids, psephenids, dryopids). Major elements of variation: (1) Malacodermization, involving variable reduction of interlocking devices as well as exposure of head and trochantin and possible extensive exposure of intersegmental membrane, plus variable modification of the pleurocoxal mechanism to permit extensive flexation; Psephenidae (*Eubrianax*, *Pheneps*); Dryopidae (*Lara*, *Potamophilus*); Dascillidae (*Anorus*, karumines); Cantharoidea, Cebriionidae (*Scaptolenus*), Artematopidae, Rhipiceridae (*Sandalus*), Ptilodactylidae (Some exotic anchytarsines). (Figs. 86, 93, 97, 110, 113-116.) (2) Development of a quasi-permanent rigid-body configuration involving reduction of the assumed primitive interlocking structures, e.g., Artematopidae, Byrrhidae, Elmidae, Buprestoidea. (Figs. 90, 91, 98, 106, 107, 118, 119.) (3) Transformation of interlocking devices into the articulations of a startle defense mechanism has occurred in the elaterids

and possibly in some members of related families. (4) Compaction of pro- and meso-legs in thoracic cavities so that they lie flush against surrounding surfaces e.g., Chelonariidae, Psephenidae (*Dicranopselaphus*), Byrrhidae, Throscidae, Eucnemidae, Buprestidae (*Tachys*). (Figs. 91, 105, 166.) Enclosure of antennae and mouthparts also common.

Pleurocoxal mechanism generalized in most taxa, with the motile trochantin exposed or only slightly enclosed e.g., *Dascillus*, *Eurypogon*, *Dicranopselaphus*, *Stenocolus* (Figs. 85, 89, 94, 100). Deep enclosure of an elongate coxal articular region found only in *Ptilodactyla* and related genera and in *Cerophytum*. Enclosure less extensive in *Brachypsectra* (Figs. 87, 88, 104). Enclosure of a reduced coxa and trochantin is associated with loss of pleural motility in most elateroids; pleural fusion and coxal reduction without enclosure characterizes the buprestoids (Figs. 106-109, 118-119). Coxal cavities never closed.

The promesothoracic joint of many elateriforms consists of a complex set of interlocking mechanisms. Three major zones of contact bear specialized attachment structures: (1) Posterior dorsal face of the notum and the anterior region of the mesonotum plus the elytra; (2) Posterolateral region of the notum and the mesepisternum, and sometimes the mesepimeron as well; (3) The prosternal projection against a cavity or groove on the mesosternum. In addition, the coxae are often housed in paired cavities formed from the inflected anterior faces of the mesosternum and sometimes the mesepisternum (Figs. 159-161).

The entire posterior dorsal rim of the notum bears hemicylindrical transversely striate crenulations in many groups (Ptilodactylidae, all; Chelonariidae; Psephenidae, e.g., *Sclerocyphon*; Dryopidae only *Pelonomus*; some species of *Dascillus* and *Rhipicera marginata* (Fig. 159, Crn)). These

crenulations may fit against a complementary set on the elytra and scutellum. In other elateriforms, notal striations may be present but without crenulations (*Callihipidae*), or with at most a single pair (*Elateriodes*). In most groups, even those without crenulations or striations, the notal rim is slightly expanded to form triangular paramedial projections which fit against the elytra-scutellum (Fig. 160). In *Brachypsectra* only these projections bear faint striations.

In many forms the ventral margin of the posterior notal face bears a pair of globose condyles which fit into concavities on the mesonotum (Figs. 159–160 MCnd). The posterior face bears a pair of ridges which are placed in cavities on the anterior face of the elytra (Figs. 159–160 R). The lateral region of these notal carinae is sometimes expanded into a lateral condyle. Laterally the notal projection may be modified to increase the degree of intersegmental overlap and can also bear interlocking devices. A flattened lobelike expansion which extends far behind the posterior wall may rest against concavities on the mesopleuron or elytra (Figs. 94, 100–105, 161). A condyle, groove or both at the base of this notal lobe interlocks with complementary structures on the mesepisternum (Fig. 159 NPj, LCnd). The sternal projection is often broad and housed in mesosternal cavities. Variation in attachment devices of rigid-body forms, which may not be mechanical, will be treated elsewhere, as will evidence supporting the tentative hypotheses for their having evolved from ancestors with interlocking mechanisms.

ARTEMATOPOIDEA

ARTEMATOPIDAE

Figures 89–90

Rigid-body forms without an interlocking system involving crenulations or striations on the posterior notal face; and with a generalized pleurocoxal mechanism.

BRACHYPSECTRIDAE

Figure 87

Posterior notal face with striations only on paramedial projections. Coxa and trochantin partially enclosed by cowlings. Sternal projection narrow, apparently capable of movement in a long, deep, mesosternal fossa similar to that of elateroids.

CEROPHYTIDAE

Figure 89

Quasi-rigid body forms of questionable systematic position, included here as a preliminary hypothesis. Posterior notal wall reduced, and with a unique and non-elateroid pleurocoxal mechanism. Coxal articular region long and completely enclosed along with the trochantin by cowlings. Endopleuron relatively small. The mode of coxal enclosure and geometry of pleurocoxal mechanism resemble that of *Ptilodactyla* and *Brachypsectra*.

DASCILLIODEA

Figures 85–86

Generalized, pleurocoxal mechanism-forms show much variation in degree of reduction of elateriformlike interlocking devices and in structural integrity. Striate crenulations present only in some species of *Dascillus* (Dominican Republic, India) and in *Rhipicerca marginata*. Sternal projection lies far above coal apex in *Anorus* and *Karumia*, in the latter the posterior notal face is greatly reduced and lacks attachment devices. This malacodermization sequence is associated with specialized life cycles, including larviform females, parasitism and possibly termitophily.

BYRRHOIDEA

BYRRHIDAE

Figure 91

Generalized pleurocoxal mechanism forms with a rigid promesothoracic attachment but without interlocking devices on pos-

terior notal face. Head enclosed to mouthparts. Antenna concealed between the legs and prothorax, pro- and mesothoracic appendages may lie flush in deep cavities as in Figure 164.

DRYOPOIDEA

PTILODACTYLIDAE

Figures 100, 102-105, 159-161

(Except Ptilodactylinae) Generalized configurations with the elateriform promesothoracic joint well developed. Complex variation present in the head-prothoracic joint and in relative heights of notum, sternum and trochantin.

Ptilodactylinae. As above, but with the elongate coxal articular region completely enclosed by overlap of cowlings and by dorsal migration of the notopleural articulation (Figs. 104, 159-161).

CHELONARIIDAE

Figures 105, 164

Generalized pleurocoxal mechanism and elateriform type promesothoracic joint but with a very highly developed compaction system.

Anterior contours of head lie flush with notum and sternum, mouthparts concealed. Compacted pro- and mesolegs lie together in continuous pro- and mesothoracic depressions and are flush with surrounding surfaces (Fig. 165).

CALLIPHIPIDAE

Figure 101

Generalized configurations with a well-developed elateriform interlocking system quite similar to that of Ptilodactylidae, but with lateral crenulations weakly developed or absent. Sternum does not extend to coxal apex and does not enclose mouthparts.

PSEPHENIDAE

Figures 93-95

Generalized configurations with a somewhat (*Eubrianax*, *Sclerocyphon*) to very

reduced elateriform interlocking system (*Psephenus*, *Pheneps*) where crenulations are absent and the posterior notal face is simple. Head usually hypognathous and deeply enclosed except in *Psephenus*; *Mataeopsephus* and *Pheneps* when it is nearly prognathous and the mouthparts are exposed.

HETEROCERIDAE

Figure 92

Pleurocoxal mechanism generalized. Prognathous head deeply enclosed, sternal flange broad. Promesothoracic joint loose, motile. Elements of interlocking system lacking, notum does not extend far beyond coxa.

LIMNICHIDAE

Figure 96

Rigid body forms without an interlocking system and with a generalized pleurocoxal mechanism. Head hypognathous, enclosed to eyes, mouthparts concealed (except *Thaumastodinae*). Antenna concealed between body wall and variably compacted pro- and mesolegs.

DRYOPIDAE

Figure 99

Rigid body forms with a generalized pleurocoxal mechanism. Hypognathous head enclosed to eyes; mouthparts, antennae concealed by sternum. Crenulations and associated elateriform interlocking structures present only in *Pelonomus*.

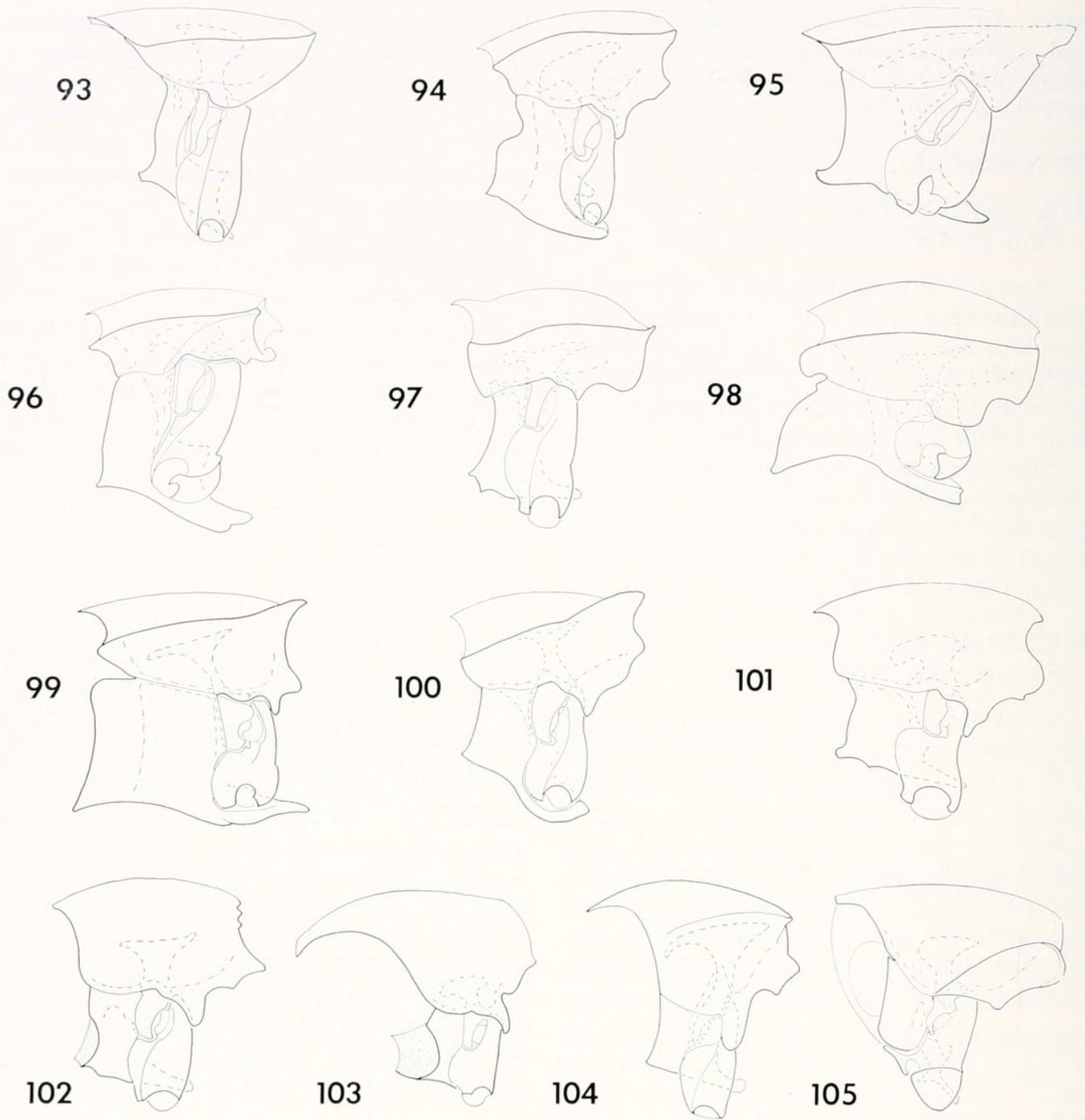
ELMIDAE

Figures 97, 98

Moderately variable configurations with the Larinae, Potomophilinae differing sharply from the Elminae.

In *Lara* (Fig. 97) the head is not deeply enclosed, the mouthparts and coxae extend below the narrow sternum, the trochantin is exposed and the promesothoracic joint is loose.

In *Stenelmis* (Fig. 98) the head, mouth-



Figures 93–105. Elateriformia. 93. *Eubrianx edwardsi*. 94. *Dicranopselaphus* sp. 95. *Psephenus* sp. 96. *Lutrochus geniculatus*. 97. *Lara amphipennis*. 98. *Stenelmis crenata*. 99. *Pelonomus obscurus*. 100. *Stenocolus scutellaris*. 101. *Zenoa picea*. 102. *Anchycteis velutina*. 103. *Araeopidius monachus*. 104. *Ptilodactyla serricollis*. 105. *Chelonarium lecontei*.

parts and coxal apices are enclosed by the broad sternum, the coxal articular region is reduced and enclosed by variable development to overlap of sternal and notal cowlings. Promesothoracic joint rigid, inter-

locking structures reduced. In some elmines e.g., *Cleptelmis* and *Heterlimnis* the mesepisternum is developed into a cowling which encloses much of the procoxa; the prosternal cowling encloses the trochantin.

ELATEROIDEA

Specialized, high notal-volume configurations with reduced and enclosed coxal articular regions. Pleuron rigid, may be fused to dorsal wall of notum; trochantin (sometimes extremely reduced) forms merely a part of the coxal articulation along with the notal rim-fold. Interlocking devices almost always present in rigid-body forms but these structures are modified into a "jumping" mechanism, in the Elateridae and probably some eucnemids. Notal crenulations usually absent or only a few occur; striations common.

CEBRIONIDAE

Figure 110

A reduction sequence complicated by sexual dimorphism. The prothorax of some, e.g., *Aplastus*, *Euthysanius*, differs little in structure from that of other elaterioids. In others, *Cebrio*, *Scaptolenus*, the length of the sternum and the height of the notum are reduced while notal and sternal cowlings are also reduced to varying degrees exposing the coxal-articular region.

THROSCIDAE

Figure 106

Rigid-body compacted forms. Head deeply enclosed; mouthparts concealed; antennae enclosed in grooves. Pro- and mesolegs concealed in thoracic cavities and lie flush with surrounding surfaces. In the Balginae, the rims of elytra and pronotum are curved ventrally as in elaterids, these structures are coplanar in other subfamilies.

EUCNEMIDAE

Figure 107

Elateroidea with variation in antennal enclosure, compaction. Also variation in the promesothoracic joint.

In the Melasinae the legs are not compacted, the antennae not concealed in grooves, and in some the promesothoracic joint appears motile and is quite elaterid-

like, e.g., *Anelastes*. While in the gastraulacines and eucnemines, the pro- and mesolegs are compacted in cavities, the antennae concealed in pronotal grooves.

PEROTHOPIDAE

Figure 108

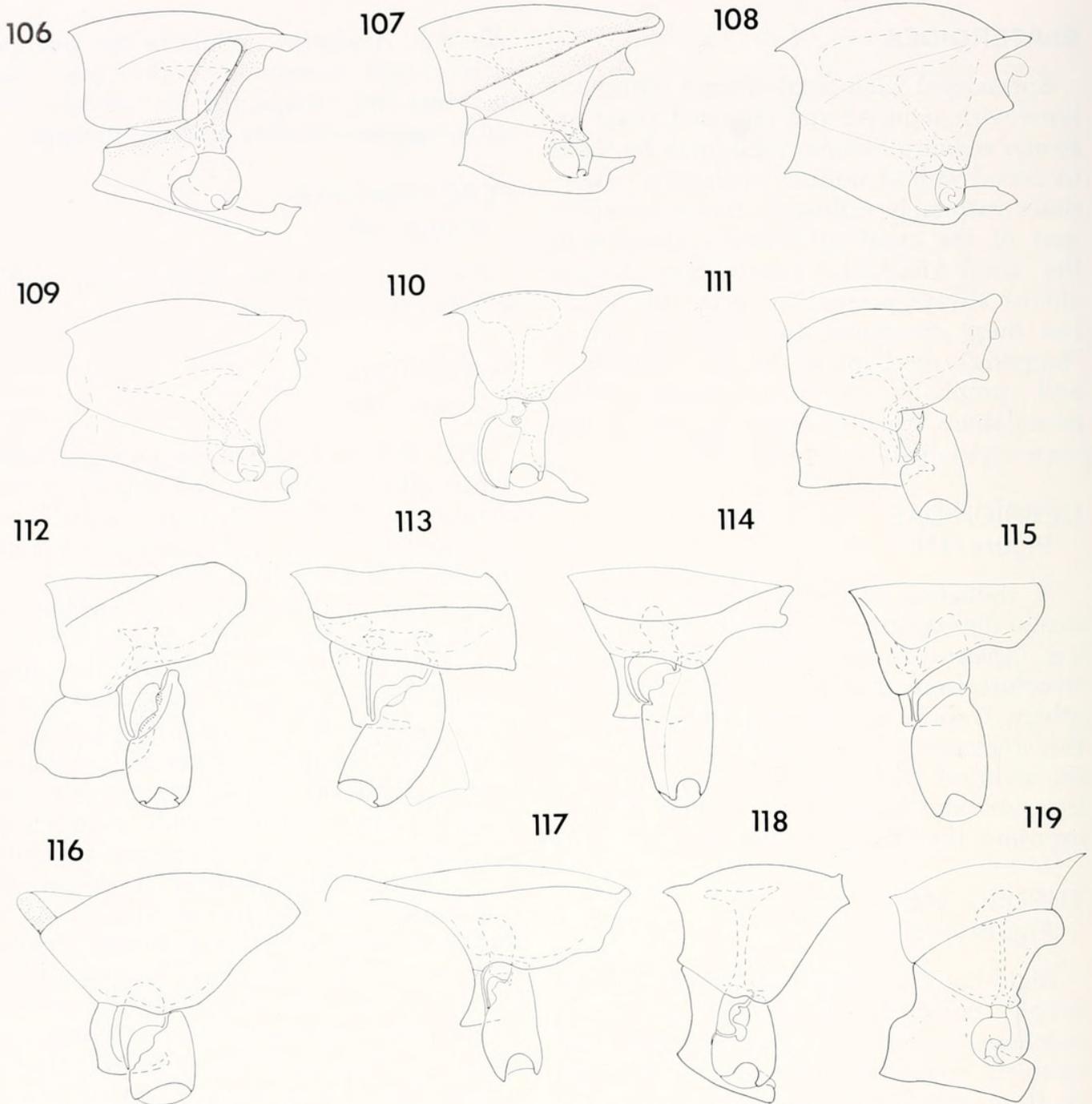
Elateroidea with the endopleuron solidly fused to the notal wall.

ELATERIDAE

Figure 109

High to very high volume configurations with slight variation in the degree of trochantinal reduction. Pleuron always fused at notopleural joint and sometimes against the dorsal notal wall as well.

Elements of the interlocking mechanism of other elateriforms are modified into the intersegmental articulations of the click mechanism of elaterids, see above and Figures 159–161. In preclick position, a notch near the tip of the sternal projection is placed on the rim of the mesosternal fossa, thereby creating a wide ventral gap and exposing membrane between segments. Strong articulations between the dorsal rim of the pronotum and the mesothorax-elytra form a fulcrum resulting in dorsal arching of the prothorax above the elytral plane, as the sternal projection slides forward. These dorsal articulations are formed primarily by the insertion of paired dorsal notal condyles into cavities and by placement of ridges into elytral concavities, e.g., (Fig. 159 MCnd, R.). Dorsal arching is made possible through clearances formed by sharp ventral sloping of contiguous pro- and mesothoracic surfaces and through dorsoventral compression of the posterior notal face. The click or jumping mechanism of elaterids has then evolved from the defensive promesothorax interlocking system of related forms. The click mechanism is doubtless a defense adaptation as well, but a dynamic one, working by violently rapid body movements and serving to either startle or to



Figures 106–119. Elateroidea, Cantharoidea, Buprestoidea. 106. *Drapetes* sp. 107. *Fornax bicolor*. 108. *Perothops muscida*. 109. *Cardiophorus gagates*. 110. *Scaptolenus* sp. 111. *Homaligus fontisbellaquei*. 112. *Drilus flavescens*. 113. *Podabrus* sp. 114. *Zarhipis integripennis*. 115. *Telegeusis* sp. 116. *Eros aurora*. 117. *Photinus pyralis*. 118. *Schizopus laetus*. 119. *Acmaeodera gibbula*.

mechanically break free from predators. The latter effect is aided by a rather streamlined, hard-to-grab body contours, and by smooth or silky cuticular surfaces.

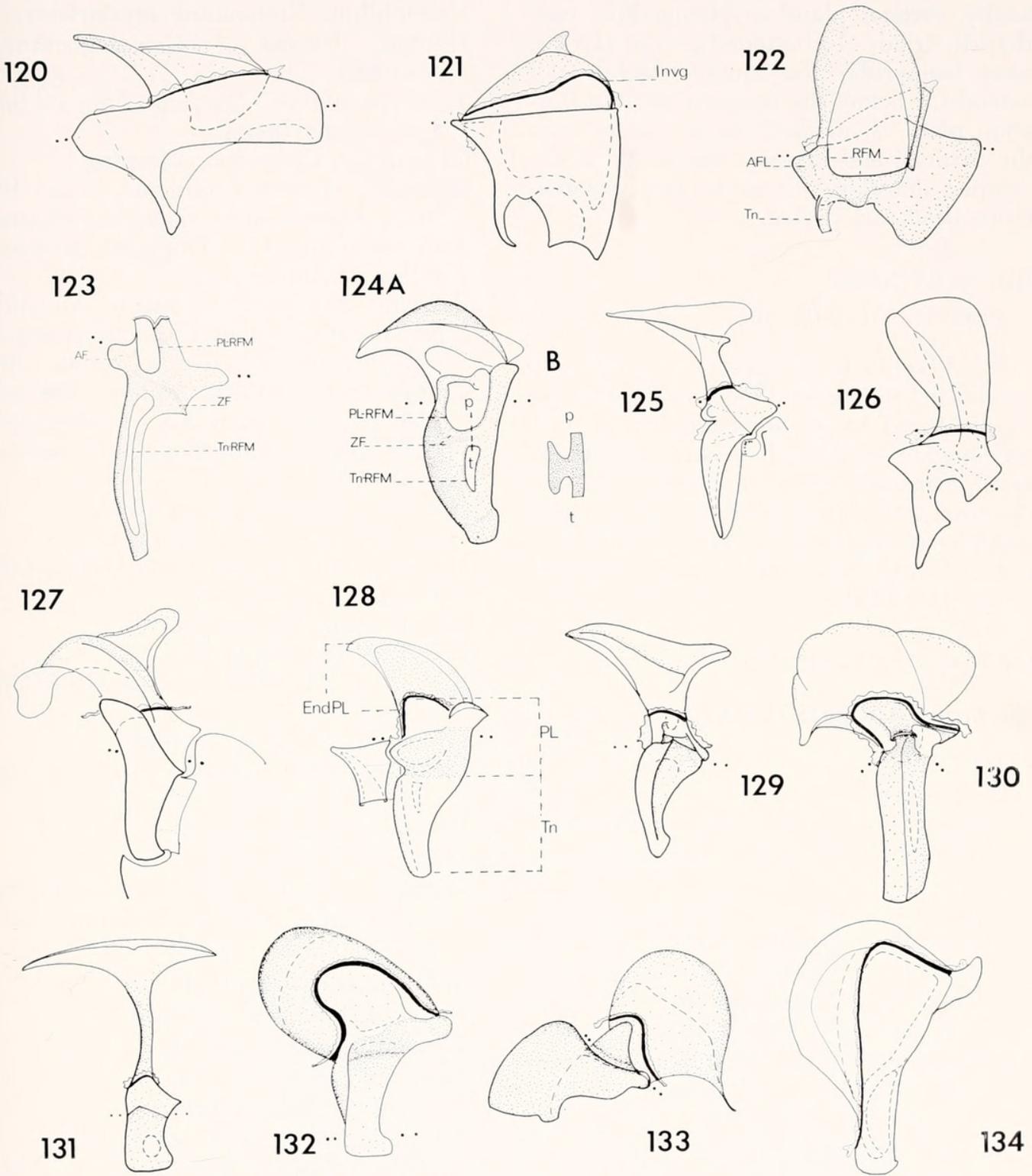
CANTHAROIDEA

Figures 111–117

Terminal elements of a malacodermization sequence, or series of sequences,

resulting in reduced structural integrity, exposure of membrane, and a high degree of coxal flexation. Prothoracic structure and mechanics effected by flattening of the body in a few groups.

Sternum, promesothoracic joint, and trochantal enclosure least modified in *Homaligus* (Fig. 111). Elongate coxae extend far below the sternum and flex in a



Figures 120–134. Pleura, Myxophaga, Polyphaga, mostly external views. 120. *Sphaerius politus*. 121. *Hydroscapha natans*. 122. *Lepicerus horni*, internal view. 123. *Sarabandus robustus*, basal aspect, internal view. 124A. *Anthobium pothos*, internal view; B. section through p-t. 125. *Prionocyphon limbatus*. 126. *Eucinetus infumatus*. 127. *Peltastica tuberculata*. 128. *Proteinus sulcatus*. 129. *Lyrosoma opaca*. 130. *Nicrophorus* sp. 131. *Catopocerus* sp. 132. *Philonthus cyannipennis*. 133. *Lathrobium prahae*. 134. *Lichnanthe vulpina*. Endopleural invagination (Invg) indicated by heavy line below sinuous membrane. Level of notal rim indicated by a pair of dots on either side of the pleuron.

nearly vertical plane in phengodids, cantharids, drilids. In flattened groups (lycids, most lampyrids) the squat coxae do not extend far below the sternum and the flexion plane is inclined sharply away from the vertical, and in some the notum is developed anteriorly to cover the hypognathous head and proleg.

BUPRESTOIDEA

Figures 118–119, 135

Rigid-body forms with a uniformly specialized pleurocoxal mechanism. Pleuron rigidly fused to notum; endopleuron with an elongate, stalklike base and a relatively small, expanded apex which comes close to the notal wall. Coxal articular region, quite small in schizopines (Fig. 118), even further reduced in buprestids, never enclosed (Figs. 119, 135).

MATERIAL EXAMINED

Suborder **ARCHOSTEMATA**

CUPEDIDAE

Ommadinae

Ommadini, *Omma stanleyi* (Fig. 4).

Tetraphalerini, *Tetraphalerus wagneri* (Fig. 3).

Cupedinae

Priacmini, *Priacma serrata* (Fig. 1, 141).

Cupedini, *Cupes concolor* (Fig. 2), *Prolixocupes lobiceps*.

MICROMALTHIDAE *Micromalthus debilis* (Fig. 5).

Suborder **ADEPHAGA**

CARABIDAE

Carabini, *Carabus nemoralis* (Figs. 8, 149–152), *Calosoma calidum*, *Ceroglossus* sp., *Pamborus guerini*.

Cychrini, *Sphaeroderus canadensis*.

Nebriini, *Nebria* sp., *Leistus ferruginosus*, *Pelophila borealis*.

Opisthiini, *Opisthius richardsoni*.

Notiophilini, *Notiophilus semistriatus*.

Hiletini, *Hiletus* (= *Camaragnathus*) *versutus*.

Trachypachidini, *Trachypachus gibbsi*, *Systolosoma brevis*.

Gehringiini, *Gehringia olympica*.

Ozaenini, *Metrius contractus* (Figs. 10, 157), *Mystropomus regularis*, *Ozaena elevata* (Fig. 11), *Tropopsis marginicollis*, *Pachyteles* sp.

Paussini, *Protopaussus bakeri*, *Megalopaussus amplipennis*, *Carabidomemmus pallidus*, *Homopterus bolivianus*, *Arthropterus brevis*, *Cerapterus lafertei*, *Pleuropterus alternans*, *Pentaplatartarus gestroi*, *Platyrhopalopsis melloi*, *Paussus* sp. (Fig. 12).

Omophonini, *Omophon ovale*.

Cicindelini, *Cicindela rapanda*.

Megacephalini, *Omus dejeani*, *Platychila pallida*.

Ctenostomini, *Ctenostoma* sp.

Collyrini, *Tricondyla* sp.

Rhysodini, *Rhysodes hamatus*, *Clinidium* sp.

Loriccerini, *Loricera pilicornis*.

Promecognathini, *Promecognathus laevissimus*.

Enceladini, *Enceladus* sp.

Saigonini, *Saigonum* sp.

Scaritini, *Scarites substriatus*, *Clivinia impressifrons* (Fig. 9), *Ardistomis viridis*.

Apotomini, *Apotomus* sp.

Nomiini, *Nomius pygmaeus*.

Broscini, *Zacotus matthewsi*.

Psydrini, *Psydrus piceus*.

Trechini, *Trechus loculentus*.

Bembidini, *Bembidion putrule*.

Pogonini, *Pogonus texanus*.

Patrobini, *Patrobus longicornis*.

Morionini, *Morion monilicornis*.

Pterostichini, *Pterostichus adnoxus*.

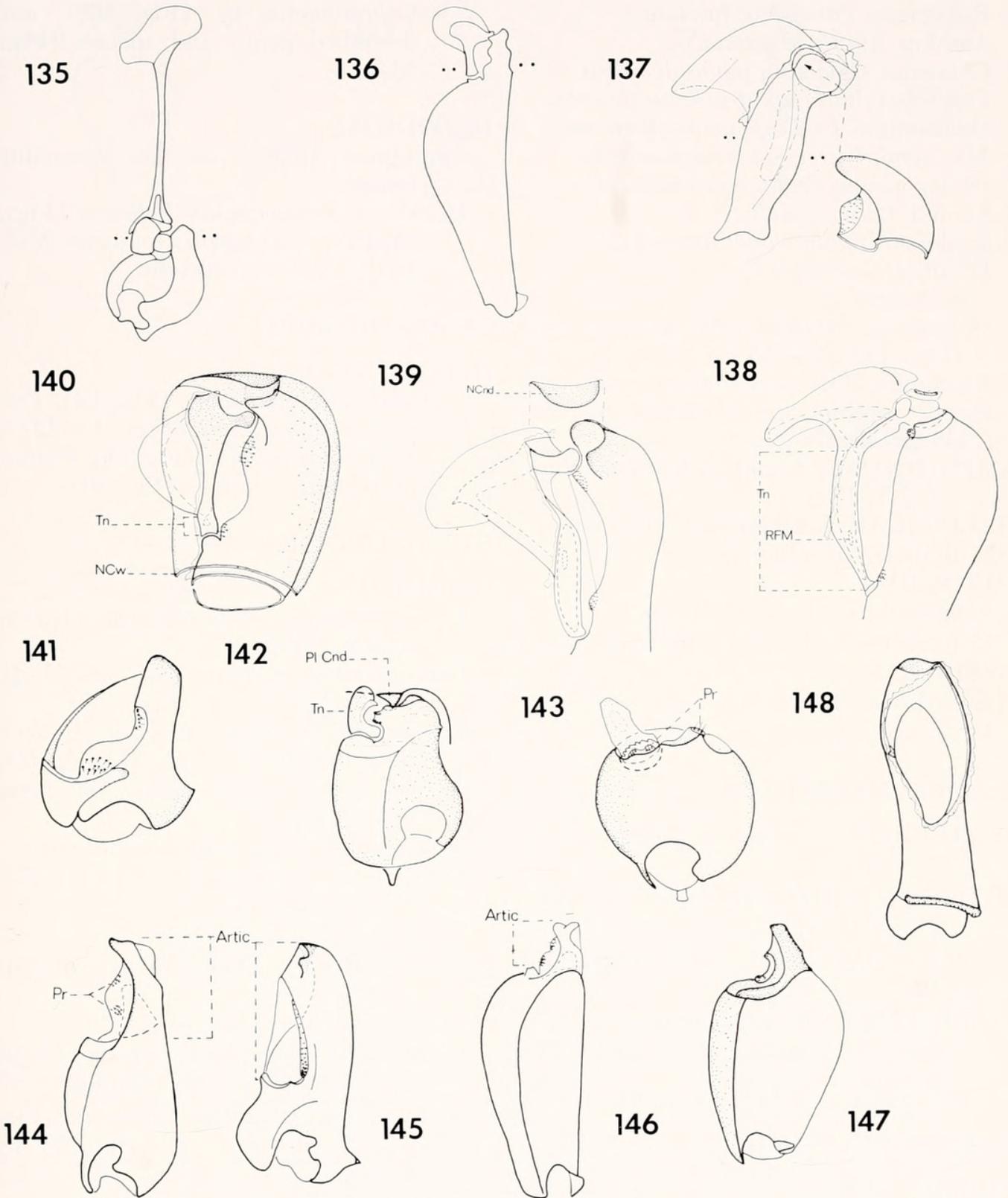
Lachnophorini, *Ega sallei*.

Harpalini, *Harpalus pleuritidus*.

Licinini, *Rembus assimilis*.

Peleciini, *Pelecium* sp.

Cyclosomini, *Cyclosoma flexosus*.



Figures 135–148. Pleuro-coxal Mechanisms. 135–136. Pleuron and coxa, Lateral views; 135. *Acmeodera gibbula*, 136. *Philonthus cyannipennis*, 137–140. Pleuro-coxal articulation, Histeroidea, Scarabaeoidea, Lateral Views; 137. *Sphaerites politus*, pleuron and coxal apex, 138. *Saprinus pennsylvanicus*, 139. *Hister sulcatus*, 140. *Phyllophaga* sp., notal cowling considered transparent. 141–148. Coxae, mostly lateral views; 141. *Priacma serrata*, 142. *Amphizoa insolens*, 143. *Helluomorphoides texana*, 144. *Trigonurus crotchii*, 145. *Leptochirus* sp., 146. *Philonthus cyannipennis*, 147. *Prionochaeta opaca*, 148. *Phyllophaga* sp. internal view.

Panagaeini, *Panagaeus fasciatus*.
 Anthiini, *Anthia biguttata*.
 Chlaenini, *Chlaenius pennsylvanicus*.
 Ctenodactylini, *Leptotrachelus dorsalis*.
 Odacanthini, *Colliuris pennsylvanicus*.
 Masoreini, *Tetragonoderus fasciatus*.
 Pentagonicini, *Pentagonica nigricollis*.
 Lebiini, *Lebia grandis*.
 Zuphiini, *Zuphium americanus*.
 Dryptini, *Geleritula* sp.

Agrini, *Agra* sp.

Helluonini, *Helluomorphoides texana*
 (Figs. 143, 153–156).

Brachinini, *Brachinus janthinipennis*.

Pseudomorphini, *Sphallomorpha* sp., *Ade-
 lotopus dytiscoides*.

AMPHIZOIDAE, *Amphizoa insolens* (Figs.
 7, 142, 158).

HALIPLIDAE, *Haliplus* sp., *Peltodytes* sp.

HYGROBIIDAE, *Hygrobia* sp.

DYTISCIDAE

Laccophilinae, *Laccophilus* sp.

Colymbetinae, *Agabus striatus* (Fig. 6).

GYRINIDAE

Enhydrinae, *Dineutes* sp.

Gyriniinae, *Gyrinus* sp.

Suborder MYXOPHAGA

SPHAERIIDAE, *Sphaerius politus* (Figs.
 13, 120).

HYDROSCAPHIDAE, *Hydroscapha natans*
 (Figs. 14, 121).

LEPICERIDAE, *Lepicerus horni* (Figs. 15,
 122).

TORRIDINICOLIDAE, *Hintonia* (= *Ptyo-
 pteryx*) *britskii* (Fig. 16), *Ytu
 artemis*.

Suborder POLYPHAGA

EUCINETOIDEA

EUCINETIDAE

Eucinetus infumatus (Figs. 22, 126),
Euscaphurus saltator.

CLAMBIDAE

Clambus gibbosus (Fig. 24), *Sphaero-
 thorax* sp., *Loricaster* sp. (Fig. 25),

Calyptomeres sp. (Fig. 166), un-
 described genus and species (Fig.
 23).

HELODIDAE

Atopidinae, *Atopida castanea*, *Veronatus
 tarsalis*.

Helodinae, *Prionocyphon limbatus* (Figs.
 21, 125), *Sarabandus robustus* (Fig.
 123), *Cyphon coracinus*.

DERODONTOIDEA

DERODONTIDAE

Derodontus maculatus (Fig. 19), *Pel-
 tastica tuberculata* (Figs. 18, 127),
Laricobius rubidus (Fig. 17), *Notho-
 derodontus gourlayi* (Fig. 20).

STAPHYLINOIDEA

LEIODIDAE

Glacicavicolinae, *Glacicavicola bathy-
 scioides* (Fig. 33).

Catopocerinae, *Catopocerus* sp. (Figs.
 26, 131).

Leiodinae, *Anisotoma globosa*, *Hydno-
 bius matthewsi* (Fig. 27), *Agathi-
 dium* sp. (Figs. 31, 165), *Anisotoma
 polita* (Fig. 29).

Scotocryptinae, *Parabystus inquilinus*.

Camiarinae, *Camiarus* sp. (Fig. 28),
Neocamiarus sp.

Coloninae, *Colon* sp.

Ptomaphaginae, *Ptomaphagus caverni-
 cola*.

Nemadinae, *Nemadus* sp.

Catopinae, *Prionochoeta opaca* (Figs.
 30, 147, 163); *Catops alsiosus*.

Bathysciinae, *Astagobius angustatus* (Fig.
 32), *Leptodirus* sp., *Platycholeus
 leptinoides*.

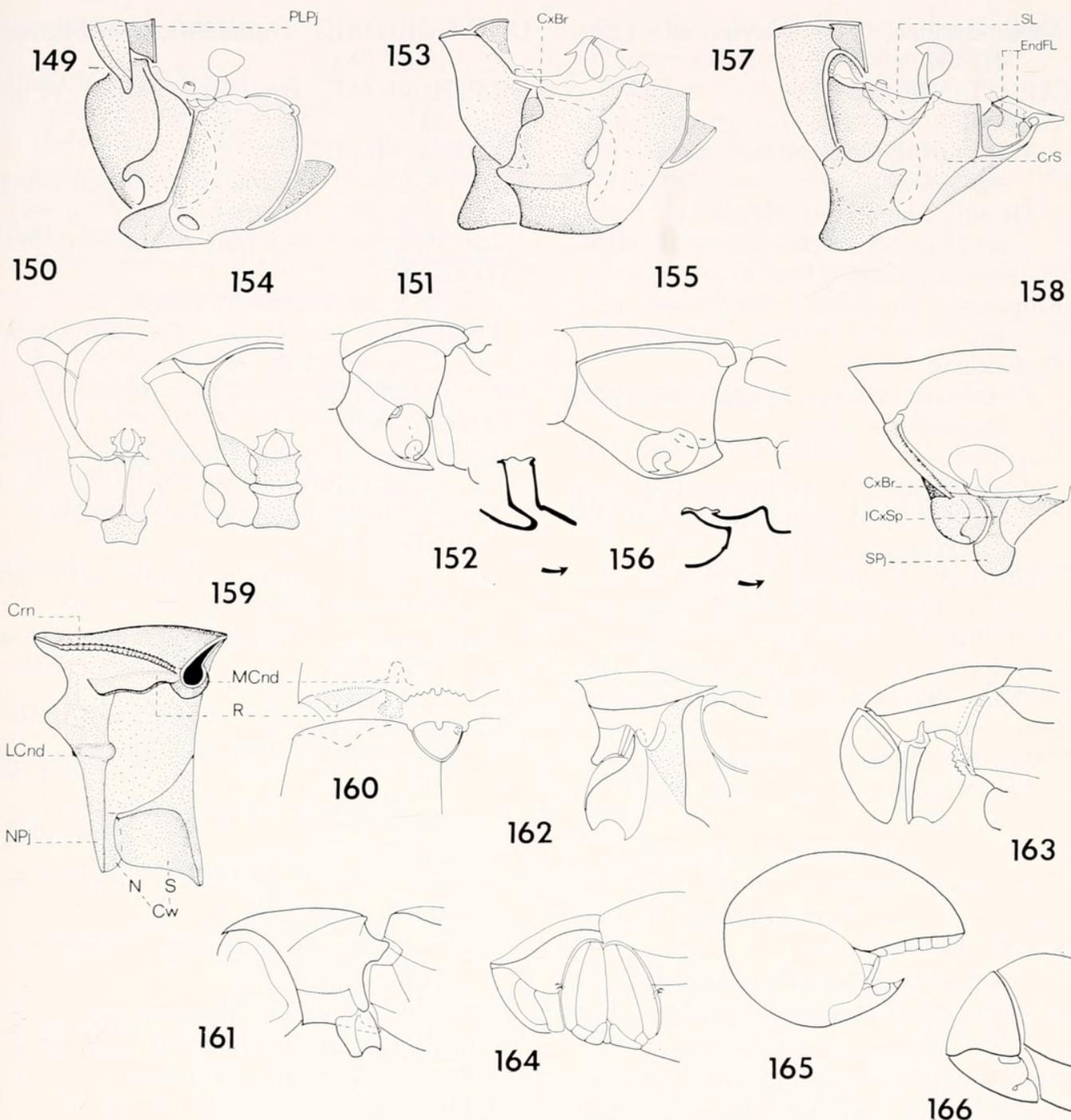
SILPHIDAE

Agyrtinae

Necrophilini, *Necrophilus hydrophiloi-
 des* (Fig. 40).

Agyrtini, *Agyrtes longulus*, *Pelatines
 latus*.

Pterolominae



Figures 149–166. Intersegmental Attachments. Figs. 149–157. Pro-mesothoracic Joint of Adephaga. Figs. 149–152. *Carabus nemoralis*. 149. Postero-ventral aspect of prothorax, right coxa removed; postero-medial view of parasagittal section. 150. Lateral view of prothorax and adjacent tagmata. 151. Posterior view of prothorax parasagittal section. 152. Section through midline of prosternal projection and rim of mesosternum; arrow indicates mode of overlap as the entire prothorax moves downwards. Figs. 153–156. *Helluomorphoides texana*; sequence as in Figs. 149–152. 157. *Metrius contractus*, view as in Fig. 149. 158. *Amphizoa insolens*, view as in Fig. 151. Figs. 159–161. *Ptilodactyla serricollis*, promesothoracic interlocking system. 159. Postero-medial view of parasagittal section of prothorax, coxa and pleuron removed. 160. Dorsal view of intersegmental attachment. 161. Lateral view. Figs. 162–166. Lateral views, various Polyphaga. 162. *Nicrophorus* sp. 163. *Prionochaeta opaca*. 164. *Chelonarium lecontei*. 165. *Agathidium* sp. 166. *Calyptomerus* sp.

Pterolomini, *Pteroloma caraboides*.
 Lyrosomini, *Lyrosoma opaca* (Figs. 39, 129).
 Silphinae

Silphini, *Silpha inaequalis*, *Silpha americana*.
 Necrodini, *Necrodes surinamensis* (Figs. 42, 162).

- Nicrophorinae, *Nicrophorus* sp. (Figs. 41, 130).
- STAPHYLINIDAE
- Piestinae
- Trigonurini, *Trigonurus crotchii* (Figs. 46, 144).
- Piestini, *Siagonium punctatum*, *Piestus* sp. (Fig. 48), *Apatetica* sp., *Nodynus leucofasciatus* (Fig. 47).
- Empelinae *Empelus brunnipennis* (Fig. 43).
- Proteininae
- Proteinus sulcatus* (Figs. 44, 128); *Megarthus pictus*.
- Omaliinae
- Anthophagini, *Anthobium pothos* (Fig. 124), *Amphichroum testaceum*, *Trigonodemus striatus*.
- Omaliini, *Omaliium marginatus* (Fig. 45), *Phlaeopterus longipalpus*.
- Oxytelinae
- Oxytelini, *Oxytelus fuscipennis* (Fig. 57), *Bledius* sp. (Fig. 58).
- Osoriinae
- Lispinini, *Lispinus californicus*.
- Leptochirini, *Leptochirus* sp. (Figs. 51, 145).
- Osoriini, *Osorius stipes* (Fig. 50).
- Oxyporinae, *Oxyporus lateralis* (Fig. 52).
- Steninae, *Stenus junco* (Fig. 56).
- Paederinae
- Pinophilini, *Pinophilus picipes*.
- Paederini, *Lathrobium prahae* (Figs. 53, 133).
- Staphylininae
- Staphylinini, *Philonthus cyannipennis* (Figs. 54, 132, 136, 146), *Thinopinus pictus*, *Creophilus maxillosus*.
- Quediini, *Quedius fulvicollis*.
- Habrocerinae, *Habrocerus capillaricornis*.
- Tachyporinae
- Tachyporini, *Tachinus fimbriatus* (Fig. 49).
- Aleocharinae
- Myrmedoniini, *Xenodusa* sp.
- Aleocharini, *Aleochara lata* (Fig. 55).
- MICROPEPLIDAE, *Micropeplus laticollis* (Fig. 67).
- DASYCERIDAE, *Dasycerus carolinensis* (Fig. 38).
- BRATHINIDAE, *Brathinus nitidus* (Fig. 34).
- HYDRAENIDAE
- Hydraeninae, *Hydraena pennsylvanica* (Fig. 70), *Ochthebius* sp. (Fig. 68).
- Limnebiinae, *Limnebius piceus* (Fig. 69).
- PTILIIDAE
- Nanosellinae, *Nanosella fungi*.
- Ptiliinae, *Acratrachis* sp. (Fig. 35), *Nossidium* sp. (Fig. 34).
- LIMULODIDAE, *Limulodes paradoxus*.
- LEPTINIDAE
- Leptininae, *Leptinus testaceus*, *Leptinillus validus* (Fig. 37).
- Platypsyllinae, *Platypsyllus castoris*.
- SCAPHIDIIDAE
- Scaphidiini, *Scaphium castanipes* (Fig. 59), *Scaphidium* sp.
- Scaphisomini, *Scaphisoma castaneum* (Fig. 60).
- SCYDMAENIDAE
- Scydmaeninae
- Chevrolatiini, *Chevrolatia amoena* (Fig. 63).
- Leptoscydmini, *Leptoscydmus cavi-frons*.
- Cephenniini, *Cephennium carporosum*.
- Eutheini, *Veraphis* sp.
- Euconnini, *Connophron flavicarse* (Fig. 61).
- Lophioderini, *Lophioderus* sp.
- Scydmaenini, *Scydmaenus perforatus*.
- Eumicrini, *Eumicrus grossus*.
- Clidicinae
- Clidicini, *Clidicus* sp. (Fig. 62), *Lep-tomastix emeryi*.
- Mastigini, *Mastigus dalmatinus*.
- PSELAPHIDAE
- Faroninae
- Faronini, *Sonoma tulnae* (Fig. 64).
- Pselaphinae
- Euplectini, *Euplectus confluens*.
- Tmesiphorini, *Tmesiphorus costalis* (Fig. 65).
- Clavigerinae
- Fustigerini, *Fustiger fuchsi* (Fig. 66).

HYDROPHILOIDEA

HYDROPHILIDAE

Sphercheinae, *Spercheus* sp. (Fig. 71).

Helophorinae, *Helophorus* sp. (Fig. 75).

Epimetopinae, *Epimetopus costatus* (Fig. 73).

Hydrochinae, *Hydrochus callosus*.

Hydrophilinae, *Hydrophilus triangularis*,
Tropisternus lateralis, *Hydrochara*
sp.

Berosinae, *Berosus striatus*.

Hydrobiinae, *Sperchopsis tessellatus*, *Enochrus pygmaeus nebulosus* (Fig. 74),
Helobata striata.

Chaetarthriinae, *Chaetarthria* sp.

Sphaeridiinae, *Sphaeridium scarabaeoides*.

GEORYSSIDAE

Georyssus californicus (Fig. 72).

HISTEROIDEA

SPHAERITIDAE

Sphaerites politus (Figs. 76, 137).

SYNTELIIDAE

Syntelia mexicana (Fig. 77).

HISTERIDAE

Saprininae, *Saprinus pennsylvanicus* (Fig. 138).

Histerinae, *Hister sulcatus* (Figs. 78, 139), *Hololepta fossularis*.

SCARABAEOIDEA

LUCANIDAE

Syndesinae, *Ceruchus piceus* (Fig. 80).

Lucaninae, *Pseudolucanus capriolus*.

PASSALIDAE

Pseudacanthinae, *Popilius disjunctus*
(Fig. 81).

SCARABAEIDAE

Scarabaeinae, *Copris fricator* (Fig. 82),
Dichotomius (= *Pinotus*) sp.

Aphodiinae, *Aphodius* sp.

Chironinae, *Chiron* sp.

Pleocominae, *Pleocoma* sp. (Fig. 79),
Acoma brunnea.

Glaphyrinae, *Lichnanthe vulpina* (Fig. 134).

Ochodaerinae, *Ochodaeus biarmatus*.

Ceratocanthinae, *Cloeotus globosus*.

Troginae, *Trox gemmulatus*.

Geotrupinae, *Geotrupes semiopacus*.

Rutelinae, *Anomala binotata*.

Melolonthinae, *Phyllophaga* sp. (Figs. 83, 140, 148).

Dynastinae, *Bothynus* sp.

Trichiinae, *Osmoderma* sp., *Gnorimella maculosa*

Cetoniinae, *Euphoria lambalis* (Fig. 84).

ELATERIFORMIA

ARTEMATOPOIDEA

ARTEMATOPIDAE, *Artematopus puncti-collis* (Fig. 90).

Eurypogon niger (Fig. 89), *Macropogon testaceipennis*.

Macropogon villosus, *Allopogonia villosus*.

BRACHYPSECTRIDAE, *Brachypsectra fulva* (Fig. 87).

CEROPHYTIDAE, *Cerophytum elateroides* (Fig. 88).

DASCILLOIDEA

DASCILLIDAE

Dascillinae, *Dascillus davidsoni* (Fig. 85),
D. cervinus, *D. plumbeus*.

Karumiinae, *Anorus piceus*, *A. arizonicus*,
Karumia estafilinoides.

RHIPICERIDAE, *Sandalus niger* (Fig. 86),
Rhipicera marginata, *Arrhaphipterus sckelkownikoffi*.

BYRRHOIDEA

BYRRHIDAE

Byrrhinae.

Amphicyrtini, *Amphicyrta chrysomelina*,
Lioon speculara.

Simplocarini, *Simplocaria tessellata*.

Morychini, *Morychus subsetosus*.

Byrrhini, *Byrrhus americanus* (Fig. 91),
Cytilus sp.

- Pedilophorini, *Listemus acuminatus*, *Pedilophorus* sp.
- SYNCALYPTINAE
Syncalypta spinosa. *Curimopsis* sp.,
Microchaetes sp.
- DRYOPOIDEA
- PTILODACTYLIDAE
Anchytarsinae, *Anchytarsus bicolor*, *Anchycteis velutina* (Fig. 102), *Odon-tonyx trivittis*, *Araeopidius monachus* (Fig. 103), *Octoglossa* sp., *Paralichas guerni*, *Epilichas atricolor*, *Therius suturalis*.
Eulichadinae(idae), *Eulichas mus*, *Stenocolus scutellaris* (Fig. 100).
Ptilodactylinae, *Ptilodactyla serricollis* (Figs. 104, 159–161), *Lachnodactyla arizonica*, *Chaetodactyla lyciformis*.
- CHELONARIIDAE, *Chelonarium lecontei* (Figs. 105, 166), *Chelonarium* spp.
- CALLIRHIPIDAE, *Zenoa picea* (Fig. 101), *Horatocera nipponica*, *Callirhipis* sp.
- PSEPHENIDAE
Psepheninae, *Psephenus* spp. (Fig. 95), *Mataeopsephus* sp., *Pheneps gracilis*.
Eubrianacinae, *Eubrianax edwardsi* (Fig. 93).
Eubriinae, *Ectopria nervosa*, *Acneus 4-maculatus*, *Eubria palustris*, *Sclerocyphon* sp., *Dicranopselaphus* sp. (Fig. 94), *Tychepsephus felix*, *Schinostethus* sp.
- HETERO CERIDAE
Auglyini, *Auglyles auromicans*.
Tropicus, *Tropicus pusillus*.
Heterocerini, *Heterocerus pallidus* (Fig. 92).
- LIMNICHIDAE
Limnichinae, *Eulimnichus analis*, *Limnichites nebulosus*, *Byrrhinus* sp., *Limnichus analis*.
Bothriophorinae, *Physemus minutus*.
Cephalobyrrhinae, *Throscinus* sp.
Thaumastodinae, *Martinius ripisaltater*, *Pseudoeucinetus* sp.
- Lutrochinae, *Lutrochus geniculatus* (Fig. 96).
- DRYOPIDAE, *Helichus fastigiatus*, *Pelonomus obscurus* (Fig. 99); *Dryops arizonensis*.
- ELMIDAE
Larinae
Larini, *Lara amphipennis* (Fig. 97).
Potamophilini, *Potamophilus* spp.
Elminae
Elmini, *Stenelmis crenata* (Fig. 98).
Ancyronychini, *Ancyronyx variegatus*.
- ELATEROIDEA
- CEBRIONIDAE, *Selonodon bicolor*, *Scaptolenus* sp. (Fig. 110), *Cebrio gigas*, *Euthysanius laurus*, *Aplastus piceicollis*, *Octinodes megalops*.
- THROSCIDAE
Throscinae, *Aulonothroscus* sp., *Trixagus* spp., *Pactopus horni*.
Lissominae, *Lissomus bicolor*, *Drapetes* sp. (Fig. 106).
Balginae, *Cussolenis mutabilis*, *Thylacosternus* sp.
- EUCNEMIDAE
Melasinae, *Melasis rufipennis*, *Cryptosoma* sp., *Isorhipis ruficornis*, *Anelastes druryi*, *Palaeoxenus dohrni*.
Dirhaginae, *Dirhagus triangularis*.
Gastraulacinae, *Gastraulacus* sp.
Eucneminae, *Fornax bicolor* (Fig. 107), *Pterotarsus* sp.
- PEROTHOPIDAE, *Perothops mucida* (Fig. 108).
- ELATERIDAE
Pyrophorinae, *Alaus* spp., *Chalcolepidius* sp.
Elaterinae, *Pityobius anguinus*, *Ctenicera* sp., *Agriotes* sp.
Melanactinae, *Melanactes piceus*.
Oestodinae, *Oestodes tenuicollis*.
Negastrinae, *Negastrinus belumbis*.
Hypolithinae, *Athous* sp.
Adrastinae, *Glyphonyx testaceus*.
Melanotinae, *Melanotus* spp.
Cardiophorinae, *Cardiophorus gagates* (Fig. 109).

CANTHAROIDEA

HOMALISIDAE, *Homalilus fontisbella-quei* (Fig. 111).

DRILIDAE, *Drilus flavescens* (Fig. 112),
Selasia sp.

TELEGEUSIDAE, *Telegeusis* sp. (Fig. 115).

PHENGODIDAE, *Phengodes* spp., *Zarhipis integripennis* (Fig. 114).
Mastinocerus sp.

LAMPYRIDAE

Lampyrinae, *Lamprocera* sp., *Pleotomus pallens*.

Photinus pyralis (Fig. 117), *Lucidota punctata*.

Photurinae, *Photurus* sp.

Luciolinae, *Luciola* sp.

Pterotinae, *Pterotus obscuripennis*.

Rhagophthalminae, *Ochotyra semiusla*.

CANTHARIDAE

Chauliognathinae, *Chauliognathus pennsylvanicus*.

Cantharinae, *Podabrus* sp. (Fig. 113).
Cantharis sp., *Malthodes* sp.

LYCIDAE

Lycini, *Lycus* sp.

Calopterini, *Calopteron* sp.

Dictyopterini, *Eros aurora* (Fig. 116).

Platerodini, *Plateros modestus*.

BUPRESTOIDEA

SCHIZOPODIDAE, *Schizopus laetus* (Fig. 118), *Dystaxia elegans*.

Glyptoscelimorpha marmorata

BUPRESTIDAE

Julodinae, *Sternocera pulchra*.

Acmaeoderinae, *Acmaeodera gibbula*
(Figs. 119, 135).

Buprestinae, *Dicerca divaricata*.

Agrilinae, *Brachys tessellata*.

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