COMPARATIVE ANATOMY OF THE DEFENSIVE GLANDS, OVIPOSITORS AND FEMALE GENITAL TUBES OF TENEBRIONID BEETLES (COLEOPTERA)

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Abstract—With the ultimate objective of determining higher phylogenetic relationships, the cuticular portions of the defensive glands, ovipositors and female genital tubes of 247 species from 178 genera were studied after clearing in sodium hydroxide. On the basis of these studies, the following evolutionary hypotheses are put forward. The most primitive tenebrionids are the lagriine groups and their allies. Ancestral tenebrionids were without defensive glands and some modern groups still are. Defensive glands evolved 4 times independently, once between sterna 8 and 9, and 3 times between sterna 7 and 8. Only one of the 7/8 glands shows much diversification beyond the primitive state. Primitively, these glands are simple, eversible, conical pouches with the gland tissue scattered on the reservoir dorsum. Advanced glands show increased reservoir size, localization of gland tissue, contriction of exit ducts, and specializations of reservoir walls.

Ancestral tenebrionids have a female tube consisting of a blind, primary bursa copulatrix with ventral entry of the common oviduct and dorsal entry of the single, slender spermathecal gland tube. This condition persists in the lagriines and their allies. A strong tendency to evolve a separate, non-glandular spermatheca has led to its evolution at least 4 times independently. These are (1) a multiple, short-tubular spermatheca derived from the bursa copulatrix; (2) a single, short- to long-tubular spermatheca from the same source; (3) a cannister-shaped spermatheca derived from the basal portion of the spermathecal gland; and (4) a saccate spermatheca derived from the apical portion of the spermathecal gland. These 4 configurations are strong characters defining major lines of tenebrionid evolution.

The ancestral ovipositor was probably elongate and appendage-like, and this condition is still present in some lagriines and their allies. The primitive ovipositor contains 2 sets of sclerites. The proximal paraprocts are rather simple and cyclindrical. The distal coxites are divided ventrally into 4 lobes with the fourth lobe bearing the gonostyles terminally. The paraprocts are stiffened ventrally by a pair of longitudinal baculi, while the first lobe of the coxites (the valvifer) are stiffened by a pair of transverse baculi. Much of the evolutionary change has involved reductions of various structures, but reorientation of the baculi and elongation and shortening of paraprocts and coxites have been important in certain groups. There is a strong tendency for the gonostyles to move to a lateral or dorsolateral position, and this is often accompanied by a reduction of the fourth lobe of the coxites.

On the basis of these and other characters, several major lines of tenebrionid evolution become apparent: (1) the lagriines and their allies, probably including the adeliines, pycnocerines and goniaderines; (2) the diaperines and their allies; (3) the coelometopines, cnodalonines, strongyliines, talanines and their allies; (4) the tenebrionines, opatrines, helopines, toxicines, amarygmines and their allies. Some groups, such as the bolitophagines, share features with more than a single lineage and are difficult to place. Phylogeny within the major lines is discussed in general terms, as is the importance of internal characters for higher classification of Tenebrionidae.

INTRODUCTION

INSECTS contain a great number of cuticular structures that are internal insofar as they cannot be readily seen without dissection or preparation. Topologically of course, no cuticular structures are truly internal, but the linings of exocrine glands, the hindgut, foregut, crop, parts of the male and female genital tubes, tracheae, and skeletal apodemes are all structures inside the apparent exterior surface of the insect. In addition, many insects have telescoped genital segments which are externally visible only upon extrusion. Interest in the use of such "internal" cuticular characters in insect systematics has flickered sporadically over almost a century, but there have been very few concerted, comprehensive efforts to apply such and other characters to the problems of higher systematics. For example, in Coleoptera, comparisons have been made of the central nervous system (Peyerimhoff, 1903), the malpighian tubules (Marcus, 1930); Stammner, 1934), the musculature of the male genitalia (Pu, 1938) and the musculature of the pharyngeal region (Dorsey, 1943). However, specific phylogenetic interpretations resulting from these studies have been sparse, often because too few taxa were examined. A notable exception is the work of Crowson (1938, 1942, 1955) on the metendosternite, where morphological comparisons were broadly used to analyze the higher classification.

Among the Coleoptera external genital structures (aedeagus and ovipositor) have been the most popular "internal" characters since the pioneering studies of Verhoeff (1893a, b, 1918), Wandolleck (1905) and Sharp and Muir (1912), who sketched out phylogenetic affinities as well as functions of the male genitalia. Bordas (1900) and Newell (1918) studied the comparative morphology of both sexes in many insects, and identified the segmental source of many of the structures. The external morphology of the ovipositors of 125 genera in 65 families of beetles was compared by Tanner (1927) who provided good drawings as well as descriptions. On the basis of 6 species, he concluded that the ovipositor was rather uniform throughout the family Tenebrionidae. The significance of male genitalia for higher classification of Coleoptera was reconsidered by Jeannel and Paulian (1944), who also considered the skeletal morphology of the abdomen. The female genitalic characters of Tenebrionidae have never been compared, other than among the few species included in the studies listed above.

Comparisons of internal genitalic structures have mostly included relatively few species, often representing distantly related taxa. For example, Williams (1945) provided brief descriptions and illustrations of the female internal reproductive structures of 12 families of beetles. Surtees (1961) compared the spermathecae in a number of stored products Coleoptera, including 6 species of Tenebrionidae, in which he noted 3 different spermathecal types. Many other studies limited to a single family have included too few species to allow phylogenetic interpretations. For example, Karg (1962) examined the sclerites in the bursa copulatrix of 12 species of Elateridae, describing a variety of toothed plates and spines of rather counterselective appearance. Watt (1970; 1974a, b) described the internal female tracts of a few tenebrionids and closely related families, and indicated that the structures might have classificatory value.

In more comprehensive studies, Varma (1955) assessed the taxonomic value of the spermatheca for Chrysomelidae, and Schuler (1960, 1962) did the same for the tribe Bembidiini and the genus *Chlaenius* (Carabidae). All of these studies revealed a basically similar structure of the spermathecal capsule throughout the taxon, with variation only in detail.

Among recent assessments of the systematic value of internal characters of Coleoptera, many have considered both male and female structures, and occasionally other internal systems within individual families. Thus, the work of Nüsslin (1911–12) on the male and female reproductive organs and proventriculus of bark beetles is followed by those of Aslam (1961) on a number of the internal organ systems of Curculionidae, of Gupta (1965) on the alimentary canal and male and female reproductive systems of Meloidae, and Ekis and Gupta (1971) comparing the alimentary canals of Cleridae.

Most authors concluded that internal characters had systematic value, but typically, other than offering a few suggested relationships, they did not apply the characters to the solution of specific systematic problems. For example, Crowson (1972) discussed in detail the phylogenetic significance of earlier work on the alimentary canal in Cleridae. An exception to this is Blaisdell (1909) who relied heavily upon both male and female external genitalic characters in his revision of the tribe Eleodini and based his subgeneric classification of *Eleodes* on ovipositor structure. Similarly, Wilson (1930) suggested various changes in higher classification of Cucujoidea based on the male genitalia. He dismissed females characters as being too uniform to be of systematic value. In general, male external genitalia have been used extensively in recent revisionary work at the generic level throughout the Coleoptera. Terminology and homology have thus come to be important, and both Wood (1952) and Gilbert (1952) dealt with these subjects. Female structures have been relatively little used in revisionary systematics; they are included with male structures by Michener (1944) and in Lindroth's glossary (1957).

Abdominal defensive glands occur in several families of Coleoptera, but have been investigated on a comparative basis only in the Carabidae (Moore and Wallbank, 1967) and the Tenebrionidae (Kendall, 1968, 1974; Tschinkel, 1975a, b). Both authors offered tentative suggestions regarding systematic importance, but no comprehensive applications have been made to the systematics of either family.

The higher classification of Tenebrionidae is considered difficult, because of the large number of species (estimated at ca. 15,000 by Watt, 1974b) and because of the extreme degree of variation in external morphological features. The limits of the family have recently been clarified by excluding Zopheridae and several small families (Watt, 1974b; Doyen and Lawrence, 1979) and by the inclusion of Alleculidae, Lagriidae, and Nilionidae as subfamilies of Tenebrionidae (Doyen, 1972; Watt, 1974b). The latter changes are also suggested by Kendall (1974) on the basis of similarities in defensive gland structure. The results reported here support these changes, and in the following discussions we shall refer to Tenebrionidae in the sense used by Watt (1974b) and Doyen and Lawrence (1979).

Despite recent attention and critical re-examination of taxa and characters, the tribal classification of Tenebrionidae is still essentially that of Lacordaire (1859). Doyen (1972) suggested a simplified subfamily classification, and Watt (1974b) proposed a classification into 12 sub-families, based on extensive comparison of external characters of adults and larvae. Both of the modified classifications seem inadequate in the light of information presented here. Doyen and Lawrence (1979) reviewed recent changes in the higher classification of Tenebrionidae, recognizing 2 major groupings, based on presence or absence of abdominal defensive glands and associated characters. Nearly all genera fit clearly into one or the other of these groups, which were designated the tenebrionoid (glands present) and the tentyrioid lineages. These designations will be used in subsequent discussions.

The ultimate goal of our work is a revision of the higher classification of the

Tenebrionidae. We have relied heavily upon internal cuticular structures for this purpose, because from preliminary investigations it appeared that these features were frequently conservative and would be useful in delineating phylogenetic patterns. Our findings dramatically illustrate the value of internal characters for documenting the higher classification of the Tenebrionidae. When patterns of similarity and differences shown by internal characters are considered, it becomes clear that, even within the fraction of the family we dealt with, many of the tribes and subfamilies are composed of several phylogenetic lines, and single phylogenetic lines are often placed into several tribes.

In this paper we shall deal with the description, variation and phylogeny of the female genital tube, the ovipositor, and the defensive glands of the members of the tenebrionoid lineage, as defined above (see also Doyen and Lawrence, 1979). The tentyrioid lineage, as well as a complete analysis of other characters and revision of the higher classification, will be the subject of future papers.

MATERIALS AND METHODS

Taxonomic unit and selection of material

It is necessary to establish the taxonomic level below which one can reasonably expect uniformity of characters at the prevailing level of discrimination. In our study, we found that variation below the generic level was usually variation of detail, not of basic structure. We found this for almost all characters in all genera of which we had more than one species. For this reason, although most of our specimens were identified to species, we dealt with the genus as the primary taxonomic unit of our study.

Whenever possible, type genera of the various tribes were included for examination. Additional genera were selected to represent obvious diversity in external features, but often availability determined tribal representation. Overall, we examined 247 species as indicated in Appendix IV. All the tenebrionoid tribes recognized by Gebien (1938–44) are represented by at least one genus. The Tenebrionini, Coelometopini, Cnodalonini and related tribes are disproportionately represented by about 100 species, because we encountered many misclassified genera in this group. Only 10 genera representing the enormous tentyrioid lineage (about 10,000 species) were examined for critical characters for comparison with the tenebrionoid groups.

Preparation of specimens

Most of the specimens were dried museum specimens, except a few fresh or alcohol-preserved. In all but the very smallest species, the abdomen was broken out of the dried specimen and cleared by boiling in 5–10% NaOH for 5–10 min. The remainder of the beetle was used for the study of the mouthparts, wings and internal skeletal anatomy. After clearing, cuticular remains of the abdomens were rinsed in water several times before dissection. The terga were completely removed with forceps, exposing the internal structures (Fig. 1). The reproductive and digestive structures were separated as a unit from the sterna and defensive glands. This was accomplished by tearing along the membrane between sterna 8 and 9, i.e. just posterior to the defensive glands. The hindgut was then removed just distal to the anus and discarded. (It has already been removed in Fig. 1.) The defensive glands were next separated from the sterna by cutting or tearing along the posterior margin of sternum 7 (Fig. 2). Because many of the cuticular structures were very delicate and difficult to see, all parts were next stained with Chlorazol Black E in alcohol. The resulting increased visibility of all structures allowed the final clean-up by removal of tracheae and other extraneous structures. Female structures and defensive glands were dehydrated in 100% alcohol and brought through alcohol:xylene (1:1) to xylene from which they were mounted on slides in Canada balsam for study. When drawings were made, a Wild M-5 Dissecting Stereomicroscope with drawing tube was used.

The characters and their subdivisions

Defensive glands. The defensive glands of Tenebrionidae form at least 3, and possibly 4, independently derived lineages. One of these lineages has been extensively treated previously (Tschinkel, 1975b; Kendall, 1974). All glands consist of a cuticular reservoir with associated secretory tissue. The position of the secretory tissue could be determined by the location of the fine tubules or ducts through which the secretion drains into the reservoirs from the gland cells (Tschinkel, 1975b).

Female structures. The cuticular structures of the female reproductive system are conveniently divided into the ovipositor and the cuticular portions of the female genital tube with its associated structures.

(a) *The ovipositor.* The ovipositor bears the vulva at its posterior tip (Figs. 1, 3). The ovipositor tube contains 2 pairs of sclerites. The proximal paraprocts usually carry a pair of rod-like baculi, which probably lend rigidity. The
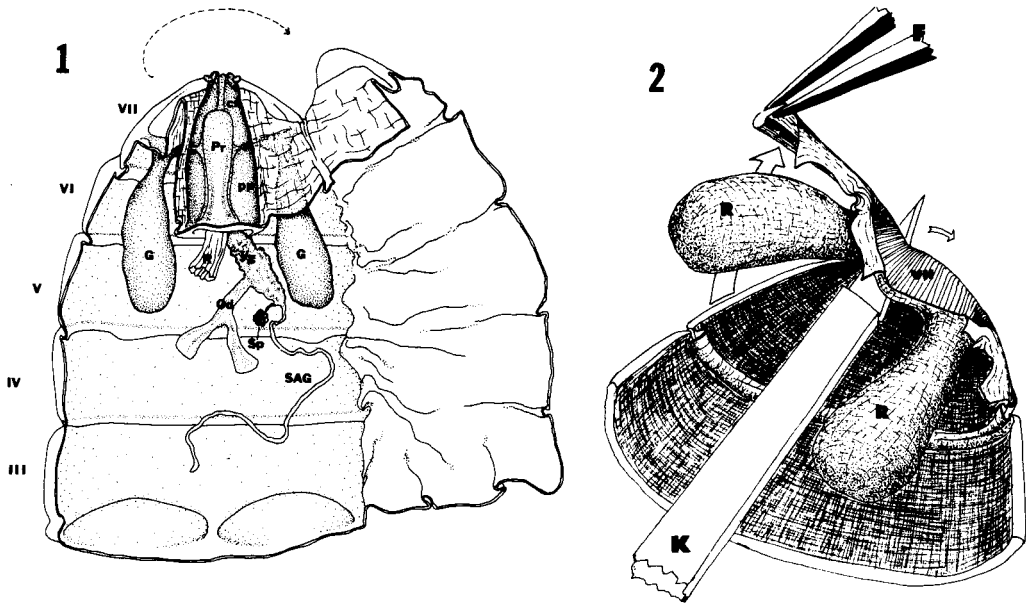
FIG. 1. Dissection of a cleared female abdomen, showing ovipositor, defensive glands (G), and some internal reproductive organs. Glands are attached on intersegmental membrane between segments 7 and 8, and ovipositor begins with segment 9. Ovipositor is made up of paraprocts and coxites (pp. cx), and dorsal proctiger (Pr), under which lies anus. Vagina (Vg) is continuous with ovipositor at vulva and receives common oviduct (Od), spermatheca (Sp) and spermathecal accessory gland (SAG). Abdominal segments are numbered in roman numerals. Rectum (R) is left of vagina.

FIG. 2. Dissection of gland reservoirs from sterna. Dorsal portion of sternite VII with attached reservoirs (R) is cut from the remainder of the sternites with a knife (K) while being pulled upward with the forceps (F).

apical coxites are ventrally subdivided into 4 lateral lobes by slight folds, grooves or areas of sclerotization (Fig. 3). Lobe 1 (the valvifer) is usually stiffened by a pair of baculi, while the apical lobe 4 forms the ovipositor tip and bears the gonostyles. The membranous dorsal and ventromedial regions of the coxites usually show some pleating that allows expansion during the passage of the egg. The vulva commonly lies at the level of the third or fourth lobes.

The dorsomedial portion of the female terminalia is composed of the proctiger, bearing the anus at its posterior margin. The proctiger, a single, medial sclerite, is often poorly defined and usually has a pair of proctigeral baculi at its lateral margins. In a few species with very elongate coxites, there is an additional pair of baculi linking the "normal" baculi of the paraprocts with the proctigeral baculi.

(b) *The female genital tube.* Proceeding from the ovipositor toward the insect's head (Fig. 4), the structures encountered are the tube-like or bag-like vagina (Vg) into whose ventral side opens the common or median oviduct (Od) which forks into the lateral oviducts. The apical ends of the lateral oviducts are the limits of ectodermal tissue and therefore of cuticular lining.

Tenebrionids fall into 2 classes with respect to spermathecal structures—those that have only a single structure, glandular throughout (Fig. 4A), and those with 2 separate structures, a glandular tube and a non-glandular spermatheca (Fig. 4B, C). In order to make this distinction clear in the following descriptions and discussion, we have called the solo, all-glandular structure the spermathecal gland (SG). The non-glandular (presumably sperm storage) structure we have called the spermatheca (Sp), and the glandular tube which always accompanies it the spermathecal accessory gland (SAG). These names are in line with the useage of Happ and Happ (1970), but it should be noted that Watt (1974b) consistently misidentified the spermatheca as the spermathecal gland, and the spermathecal accessory gland as the spermatheca. The glandular portions of all these structures can be recognized by the presence on their surfaces of the fine tubules and end structures of the gland cells (Happ and Happ, 1970).

The vagina may end in a blind sac, which we shall call the primary bursa copulatrix. Alternatively, the vagina may bear a spermathecal accessory gland and a non-glandular spermatheca at its anterior apex. In the latter case, there is no bursa copulatrix (Fig. 4B), although some species have evolved a dorsal secondary bursa copulatrix (Fig. 4C). In other beetles, the vagina may receive a spermathecal gland, or a spermathecal accessory gland dorsally. In the latter case, the non-glandular spermatheca is borne on the accessory gland, rather than on the vagina directly (Fig. 16). After ovulation but before oviposition, eggs may be stored in the calyx of the oviducts, in the vagina, or possibly in the bursa copulatrix.
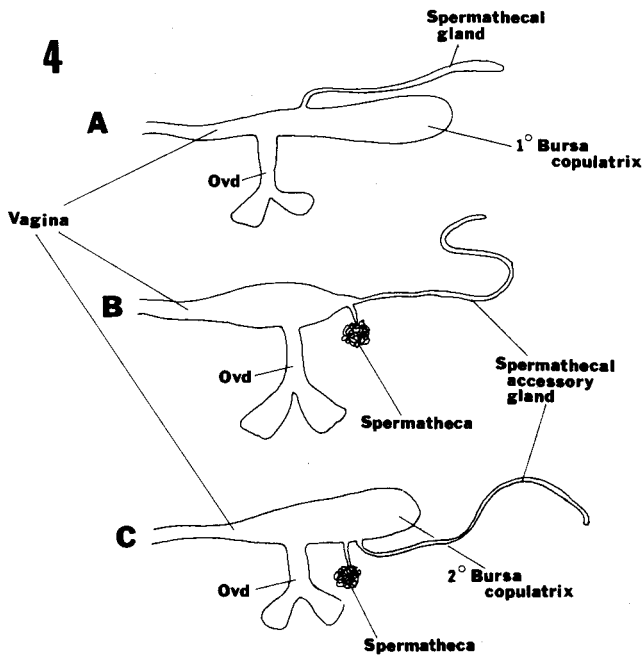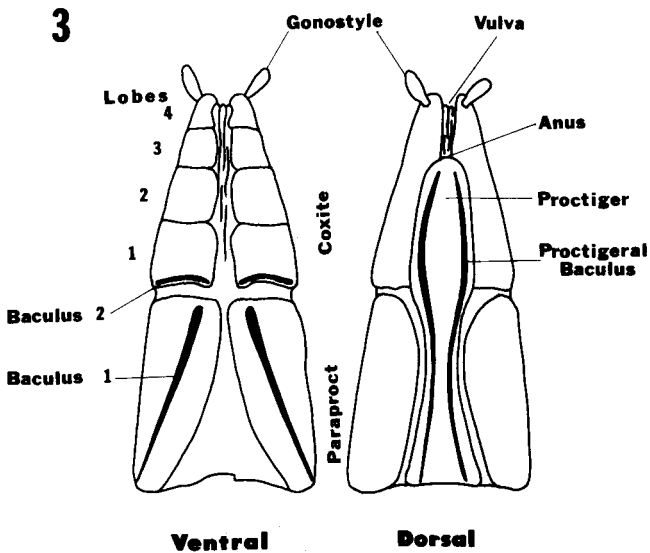
FIG. 3. A typical tenebrionid ovipositor, showing major parts. In ventral view can be seen baculi of the paraprocts, the 4 lobes of the coxites (1–4), baculi of the coxites which lie in first lobe, and pleated membrane which makes up midventral surface. Vulva lies near posterior tip, and gonostyles are borne on fourth lobe of the coxites. In dorsal view can be seen proctiger with its baculi and pleated membrane making up middorsal surface.

FIG. 4. Schematic diagrams of cuticular parts of representative female genital tubes of Tenebrionidae. Structures are judged as glandular if their surface bears secretory tubules of gland cells. The name spermathecal gland is used when there is no separate, non-glandular sperm-storage structure. Ovd = oviduct.

OBSERVATIONS—THE PRIMITIVE STRUCTURES AND THEIR EVOLUTION

The defensive glands

Although the primitive state for tenebrionids is probably the absence of glands, the ancestral tenebrionid must have had a strong tendency for the intersegmental membranes 7/8 and 8/9 to become increasingly glandular. This, combined with the elaboration of the intersegmental membrane into reservoirs, ultimately produced the 3 or 4 major, apparently non-homologous gland lineages described below.

(1) *The adeliine glands.* In the Adeliini, a pair of reservoirs has evolved between sterna 8 and 9, rather than the much more common 7/8 position. That this region has a tendency to become glandular is indicated by the presence in the same position of very large colleterial glands in *Lagria* (Fig. 15) and *Derolagria*. It is even possible that this defensive gland is homologous with these colleterial glands. In any case, the defensive gland cells are scattered over the dorsal surface and empty individually into the reservoir. This gland type is restricted to the Adeliini where it is always found as long-tapering sacs (Fig. 5) which are everted in use (Eisner *et al.*, 1974). Other than the increase in reservoir length, they seem to have undergone little evolutionary specialization, and are quite uniform in appearance among different genera.

(2) *The pycnocerine glands.* In this minor line, the incipient gland field between sterna 7 and 8 became elaborated into a single, small, medial reservoir, rather than paired reservoirs. The gland cells are scattered on the dorsal surface and empty into the reservoir individually (see also Kendall, 1974). This gland type seems to have undergone little specialization and was found only in its primitive state (Pycnocerini, possibly Phrenapatini) (Fig. 6).

(3) *The lagriine glands.* It is uncertain whether these glands are homologous with the fourth and most common type. In the lagriine glands (Fig. 7) cuticular structures and their location between sterna 7 and 8 are similar to the common tenebrionid glands. However, the glands of *Lagria* are musculated (Kendall, 1968), while those of non-lagriine tenebrionids are apparently not. However, this has not been specifically checked for many species. Because we examined cleared specimens, musculation was undetected.

(4) *The common tenebrionid glands.* By far the major line of glands is that of paired reservoirs between sterna 7 and 8. This design has become highly diversified throughout the large majority of tenebrionid species. In the apparent primitive state, these glands consist of a pair of small, conical pouches that are partially in communication with one another (have common volume). The relatively small amount of secretion is produced by gland cells that are scattered over the entire dorsal surface of the reservoirs and empty into them by individual tubules. In use, the reservoirs are everted by hemolymph pressure and the film of secretion is thus aired (Lengerken, 1925; Kendall, 1968, 1974). The glands of *Tenebrio* and *Idiobates* conform well to most of these primitive features (Fig. 8). Additionally, cells of most advanced tenebrionid defense glands are differentiated into two distinct populations but those of *Tenebrio* are undifferentiated (Kendall, 1974).

Evolutionary trends of the common tenebrionid gland

Since only the fourth major gland type has become specialized beyond its primitive state, a discussion of evolutionary trends of gland structure need not concern itself with the other
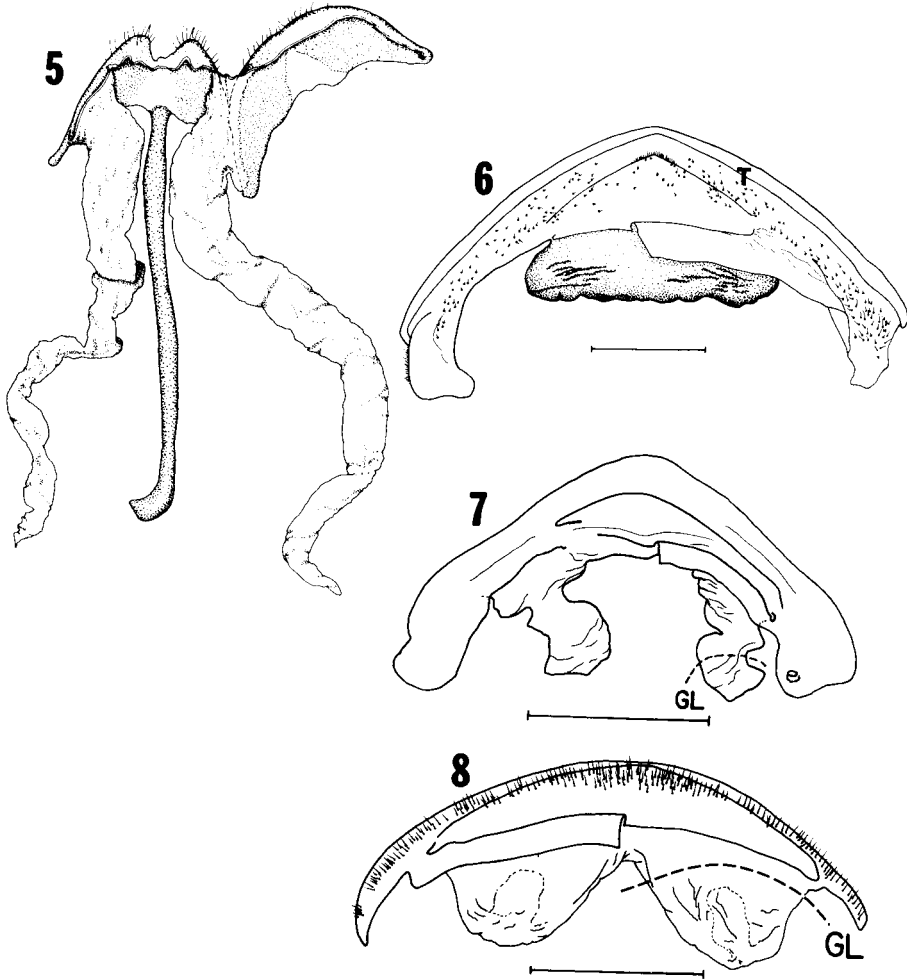
FIG. 5. Defensive glands of *Adelium auratrum* Pascoe are long pouches attached at intersegmental membrane 8/9. This preparation is of a female. Ovipositor has been removed along cut edges, and spiculum ventrale of segment 8 is seen in midventral position. Glands of adeliines are not homologous with those of other tenebrionids.

FIG. 6. Defensive gland of *Chiroscelis digitata* is a single, medial pouch between sterna 7 and 8, and is probably not homologous with paired reservoir glands of most tenebrionids. Note apparently primitive feature of trough-like sculpturing (T) of margins of dorsal plate of sternite 7.

FIG. 7. Defensive glands of *Derolagria* sp. In uncleared state, reservoirs are musculated. GL = limits of gland tubule terminations.

FIG. 8. Defensive glands of *Tenebrio molitor* showing primitive state of the 7/8 paired glands which are homologous with major lines of tenebrionid glands. Partly everted reservoir tips (dotted lines) are an advanced feature. GL = limits of field of gland tubule terminations.

3 types. Tschinkel (1975b) has discussed evolutionary trends within the major lineage in detail. Figure 9 summarizes the gland characters along with their primitive and advanced states. Our reasoning for the primitiveness of characters is based on the assumption that the glands arose from the unspecialized intersegmental membranes. The primitive reservoirs were thus necessarily wider at their basal ends, shared a common volume, had more or less smooth cuticule, and had glandular cells uniformly scattered over the dorsal reservoir

surface. All of these characters became modified, often independently, in the course of gland evolution, so that any given gland may consist of a mosaic of primitive and advanced features. The major characters that undergo specialization are reservoir size, shape and wall structure, presence of common volume, mode of basal reservoir attachment, and termination of gland cell tubules (Fig. 9). Many of the advanced states may have evolved convergently several times. This is apparent in the occurrence of concentrated secretory tubule terminations along a basal line or in a duct. Reservoir shapes probably evolved by a variety of independent pathways.
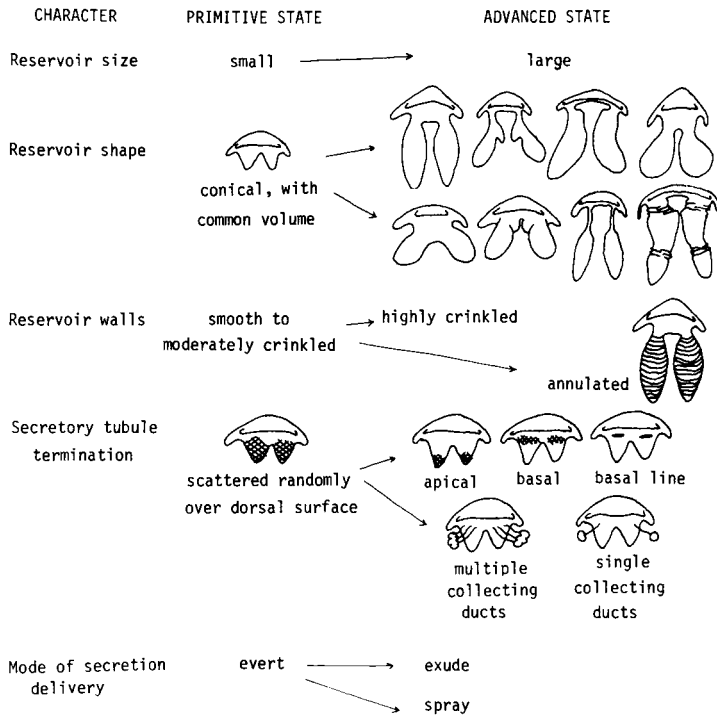

FIG. 9. Major trends in the evolution of the 7/8 paired defensive glands of Tenebrionidae. Secretory tubules are very fine cuticular tubules which drain gland cells and survive KOH clearing. They show where gland was in life and are indicated by cross-hatching in this figure. Reservoir shapes are intended as a sampling of shapes represented among tenebrionids.

Phylogeny of the defensive glands

The greatest variety of non-homologous glands, as well as the glandless condition, is found in those groups deemed primitive on the basis of other unrelated characters. For example, 3 gland types and glandlessness are found in the related tribes Phrenepatini, Lagriini, Pycnocerini, Goniaderini and Adeliini (Fig. 10), and members of most of these tribes exhibit notably primitive ovipositor and reproductive tract characteristics as well (Figs. 17, 37).

The character state tree proposed in Fig. 10 is based upon the localization of the secretory tubule termination as a primary character, with loss of common volume, sclerite shape, reservoir shape and constriction into exit ducts playing secondary roles. The pattern that results is in general agreement with the probable relationships of the genera as surmised from
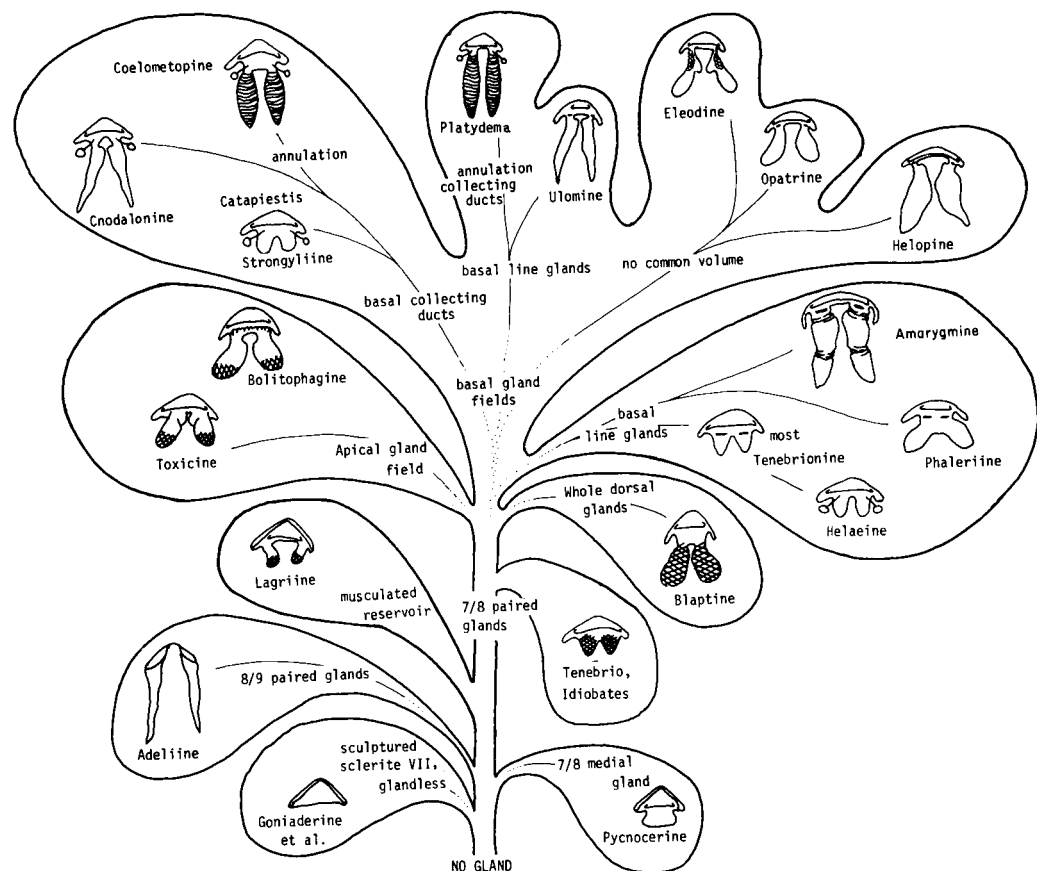
Fig. 10. Phylogeny of tenebrionid defensive glands. Primitive tenebrionids were glandless, and apparently evolved 4 independent lineages of glands. Of these, only *Tenebrio* line shows much further diversification. Genera included in each type are listed in Appendix I.

a large number of other characters (Doyen and Tschinkel, unpublished). It is certainly not the only possible phylogenetic arrangement, for many of the characters could conceivably have been derived independently one or more times. For example, it seems likely that there is a very strong trend leading to the "basal line" arrangement of secretory tubules, and it is almost certain that this characteristic evolved independently a number of times, as discussed below. In fact, it is impossible to construct a cladistic scheme in which all gland characters are uniquely derived.

Since Tenebrioidae were originally glandless, the *Tenebrio* type of gland (Fig. 8) is placed, not at the root of the entire gland family tree, but near the stem of the major lineage of tenebrionid glands (Fig. 10). The minor lineages and glandlessness (adeliine, pyconcerine, goniaderine) thus represent basal branches. These minor lineages all share the peculiar trough-like sculpturing of the posterior margin of the dorsal part of sternum 7 (Fig. 6). This trough is absent from all other glands, though its great reduction may have lead to the "squared-off" coelometopine margin. Evolutionary relationships of these primitive tenebrionids will be discussed in more detail elsewhere.

The *Tenebrio* type of gland apparently evolved into a number of more or less distinct branches. The primitive feature of whole-dursal tubule terminations is retained in the blaptine glands, which are modified only in the enlargement of the reservoirs and changes in the shape of sternum 7. Kendall (1974) also notes that tubules appear more dense basally, that they are aggregated into bundles and that the secretory cells are differentiated into two distinct populations.

Concentration of the tubules into the apical reservoir region lead to the toxicine–bolitophagine glands, with the former being distinguished by ventromedial pouches and the latter by basal–dorsal pouch-folds. Both types are partly everted in use.

Most tenebrionid gland fields drain basally in some way, and probably evolved from an intermediate stage in which the tubules became basally localized. From this situation, they readily became concentrated into basal lines of tubules or enlarged collecting ducts. The primitive, eversible glands found in a very large number of Tenebrionini and related groups are of this type (see Appendix I), as are the somewhat modified phaleriine glands in which the common volume is enlarged. Somewhat more modified into 2 distinct regions and of uncertain affinity are the amarygmine glands with their distinctive lateral reinforcing prongs on sternum 7 (Fig. 11) (Tschinkel, 1975a). It is uncertain whether the amarygmines are properly placed in this branch or not.

The details of the diversification of the remaining glands are unclear. Basal gland fields, a primitive feature, are retained in all eleodine and some opatrine glands, as well as those of *Diaperis, Nilio* and *Tribolium* (Tschinkel, 1975b). The Eleodini and Opatrini share a trend toward bilobed reservoirs in many opatrines and all eleodines, and by the consistent absence of common volume. This last trait also links them in a somewhat tenuous manner with the helopines which often have basal lines of tubule terminations.

The basal gland fields presumably become specialized as basal lines and to basal collecting ducts in the remaining lineages. Basal gland fields are retained in a few ulomines (see Appendices I, IV), while most have basal lines or collecting ducts, and the same diversity is found in the diaperines. The diaperines are clearly specialized in the helical annulation of the reservoir walls, so that they fill and empty accordion-fashion, rather than collapsing dorsoventrally, as in the primitive condition. The helical bands appear to be composed of folded cuticle in the reservoir walls (Kendall, 1974). The glands of ulomines and diaperines are not strongly similar but certain members of these tribes are associated on the basis of other characters, as discussed below.

In the lineage leading to the Coelometopine glands, collecting ducts apparently arose before reservoir enlargement took place or annulation was developed. Such taxa as *Catapiestis* lack the characteristic features of coelometopine glands, but are strongly linked to the Cnodalonini and Coelometopini by other major characters. Moreover, *Strongylium atrum* has glands with some coelometopine features such as incipient annulation (Fig. 12). The gland structure of the Heleaeini, Cyphaleini and probably the Nyctozoilini is similar to that of the Strongyliini. However, these Australian tribes differ profoundly from the coelometopine lineage in many other features. Similarities in internal female genital characters indicate that they arose from the tenebrionine lineage independently of the coelometopines (Fig. 10).

Reservoir enlargements coupled with medial movement of the reservoir attachments and a distinctive reservoir shape characterize the cnodalonine glands. A few of these show incipient annulation. Reservoir enlargement and medial attachment also characterize the definitive coelometopine glands, but the most distinctive feature of these is the uniform annulation by
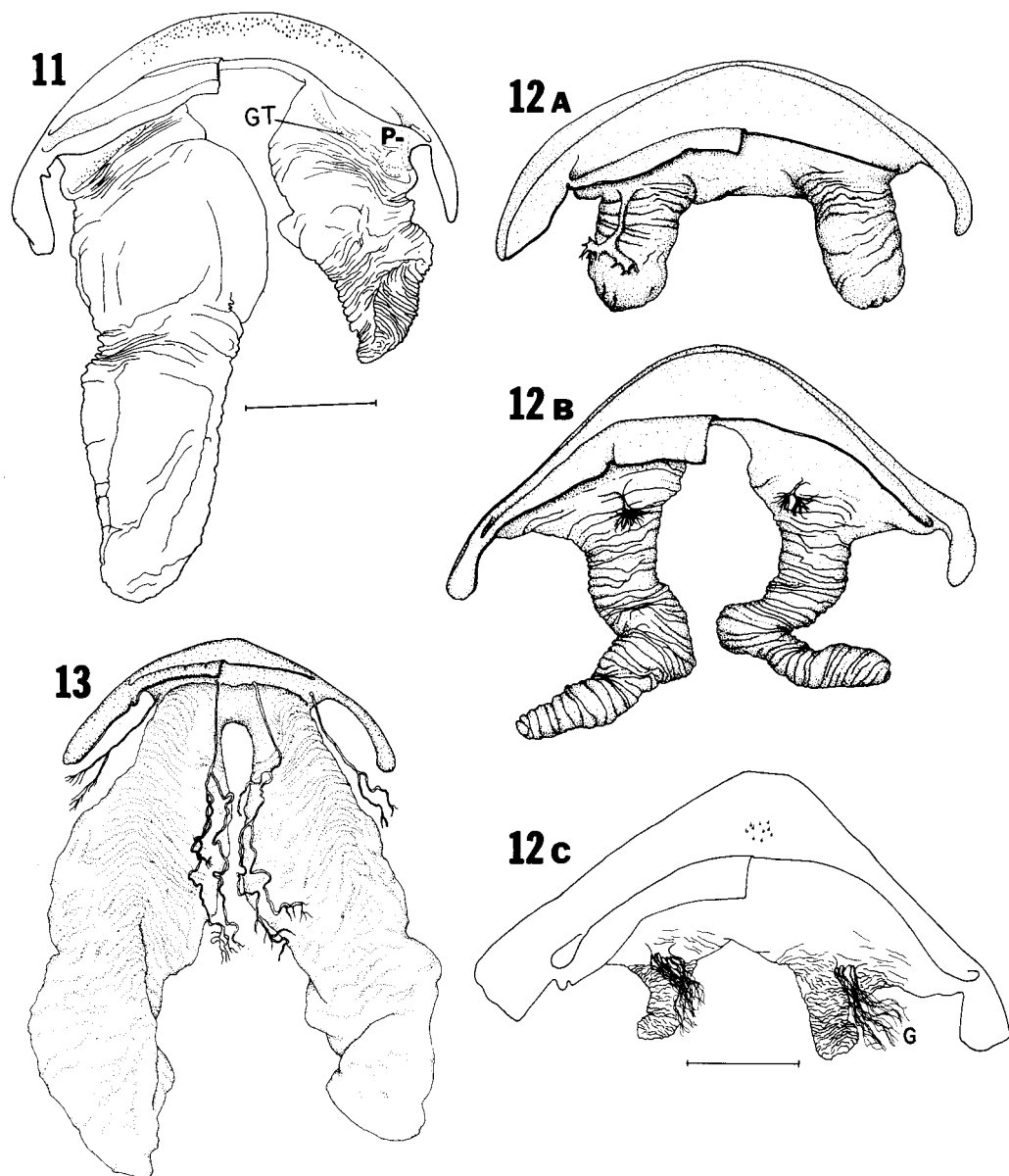
FIG. 11. Defensive gland of *Psorodes gratilla*, showing sclerotized prong (P) characteristic of most amarygmine glands. Also characteristic is division into 2 distinctive regions by reservoir folding. GT = gland tubule termination loci.

FIG. 12. Three glands primitive to coelometopine line. (A) *Catapiestis tonkineus* shows very little advancement over *Tenebrio* gland except that gland tissue drains through collecting ducts (lost on beetle's left side). (B) *Strongylium atrum* differs from (C) more typical strongyliine gland (*Strongylium purpureipenne*) in showing elongation and incipient annulation of reservoirs, both coelometopine characters. Gland drainage is again by collecting ducts as is typical of coelometopines.

FIG. 13. Defensive gland of *Eucyrtus laosensis*. This and other cnodalonine glands show a number of coelometopine features, indicating relatedness. Some species show incipient annulation of reservoir walls.

sclerotization of the reservoir walls. As outlined above, glands of the *Platydema* type also show annulation of the reservoir walls, and those of *Diaperis* and *Nilio* sometimes show weak annulation.

The multiple, independent derivation of a feature as distinctive as gland annulation requires explanation. There are 3 sources of evidence supporting multiple derivation of annulation.

(1) There are consistent minor differences between diaperine and coelometopine glands (Fig. 14): Common volume is always prominent in the coelometopines but reduced or absent in glands of the *Platydema* type. All coelometopine glands drain by collecting ducts, while those of the *Platydema* type often drain by basal line. Almost all coelometopine reservoirs are attached medially, while those of the *Platydema* type, with a few exceptions, are balanced. In the ceolometopines, the posterior margin of sternum 7 is usually "squared off" in cross-section, sometimes with a shallow groove, while it is simple in the *Platydema* type (Fig. 14a,b). The annular bands of the *Platydema* type result from a folding of the gland wall while in the coelometopine type, they are modified (sclerotized) cuticle (Kendall, 1974).

(2) Partial annulation of reservoirs has arisen independently in at least 2 other unrelated taxa. For example, the glands of *Argoporis* (Fig. 14c) and *Cerenopus*, otherwise similar to those of *Tenebrio*, show lateral cuticular ribbing and folding which is similar in general aspect to the annulation of the coelometopines and *Platydema*. The overall form of the glands of *Tauroceras angulatus* is quite different from that of coelometopines or the *Platydema* type, yet the reservoirs of *T. angulatum* are stiffened by cuticular bands (Fig. 14e) that have probably evolved independently. In general, many gland reservoirs tend to crinkle or fold in an annular fashion, though not stiffened by cuticular bands (e.g. Fig. 14d), suggesting a preadaptation for evolution of typical annulation.

(3) Numerous differences in other organ systems suggest a long, independent evolutionary history for the diaperine and coelometopine lineages. Differences are particularly striking in the internal female reproductive tract and ovipositor (see below), and in the configuration of the internal skeletal elements and the flying wings (Doyen and Lawrence, 1979).

The female genital tube

Primitive state. The primitive arrangement of the female genital tube is essentially that of *Lagria* (Fig. 15)—a simple vagina ending in a blind, large primary bursa copulatrix, with the common oviduct entering ventrally and the spermathecal gland dorsally. There is no separate, differentiated spermatheca and the spermathecal gland tube is glandular throughout its length. This configuration is considered primitve for the following reasons: (1) it tends to be associated with species judged primitive on a number of other characters; (2) it is simple in structure and detail; (3) it can be found in species that clearly belong to different lineages on the basis of other characters. It is unlikely to have arisen several times independently by reduction of other types. It is more reasonable to consider the specialized structures to have arisen from the simple lagriine type; (4) it leads to a more parsimonious phylogenetic tree for the Tenebrionidae when the lagriine type of female tract is considered primitive; (5) according to the probable evolution of the insect "internal" female genital tract (Snodgrass, 1935), the primary gonopore comes to lie in a genital atrium at the level of segment 8–9. The secondary genital opening (vulva) is thus the posterior termination of the genital atrium (vagina–bursa copulatrix). Part of the wall of the atrium becomes specialized to serve as a sperm storage organ, and may be glandular in nature (spermatheca and accessory gland). According to this scheme, the specialized structures are added in a stepwise
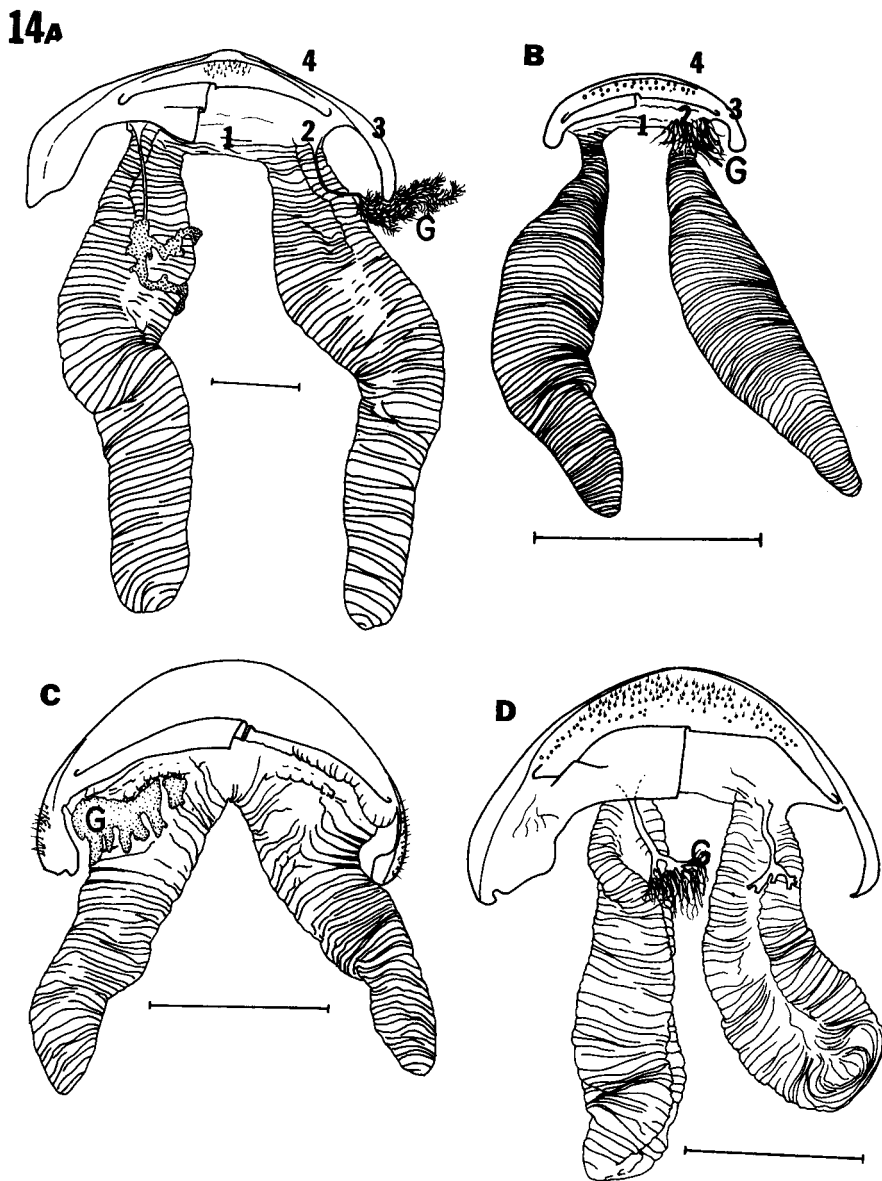
Fig. 14. A comparison of a typical coelometopine gland (A) with a *Platydema* type gland (B), illustrating major consistent differences discussed in the text: (1) common volume; (2) gland tubule termination; (3) sternal marginal sculpturing; (4) position of insertion of reservoirs. A *Alobates pennsylvanica*. B. *Neomida bicornis*. At bottom are 2 glands which show independent evolution of something resembling annulation. C. *Argoporis rugipes*, with cuticular ribs laterally, annular folding throughout. Except for ribs, annular bands are absent. D. *Zophius* sp. showing type of annular folding occasionally encountered throughout tenebrionidae. Helical bands are absent. G = gland location.

fashion. The lagriine type would thus be the most primitive tenebrionid female tube. However, other families of Heteromera have not been sufficiently surveyed to determine whether the lagriine type of arrangement is widespread, and further outgroup analysis could modify some of the above conclusions.

FIG. 14. E. Defensive gland of *Taurocerus angulatum*. A species of uncertain affinities whose glands show annulation which has probably evolved independently of that found in coelometopine and diaperine glands.

The putative evolutionary scheme of Snodgrass (1935) is supported by Srivastava's (1956) study of the postembryonic development of the female rep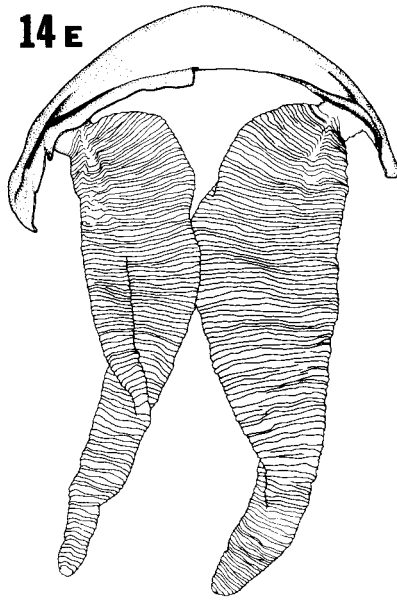roductive system in *Tribolium castaneum*, a tenebrionid. Development proceeds via 2 separate invaginations of the body wall, the posterior one giving rise to the primordial bursa copulatrix and spermatheca, and the anterior one to the common and lateral oviducts. Later in development, the 2 tubes fuse in such a way that the original opening of the oviducts is lost and the external genital opening is via the bursal–spermathecal invagination on segment 9. It may be noted that development of the internal tract in female ditrysian Lepidoptera proceeds in a similar fashion, but the original invagination to the bursa copulatrix remains as a copulatory opening in the adult and the gonopore is formed by a secondary, posterad extension of the common oviduct (Dodson, 1937).

Evolutionary trends of the female tube. The morphological changes in the specialization of the female reproductive organs are best visualized by examining trends in each character separately. Figure 16 outlines the multiple evolutionary fates of the bursa copulatrix and the spermathecal gland. There is little change in the vagina other than more or less extensive crinkling or extension of its walls, and the occasional appearance of distinctive sclerites in its walls (e.g. Amarygmini, Fig. 32).

It is clear from Fig. 16 that there is a strong tendency to form a separate, specialized spermatheca, which has evolved independently and non-homologously at least 4, perhaps 5, different times. The source structure is either the primary bursa copulatrix, which has given rise to 2 independent spermathecae (single and multiple openings), or the spermathecal gland, whose apical end evolved into the coelometopine spermatheca, and whose basal end produced the diaperine spermatheca.

That the primary bursa did, indeed, give rise to spermathecae is supported by the observation that spermathecae presumed to be bursa-derived never occur together with a primary bursa copulatrix. Furthermore, the bursa of *Metallonotus* (Fig. 21) is divided into a cluster of rather large, membranous tubes whose walls are similar to the vaginal walls. This
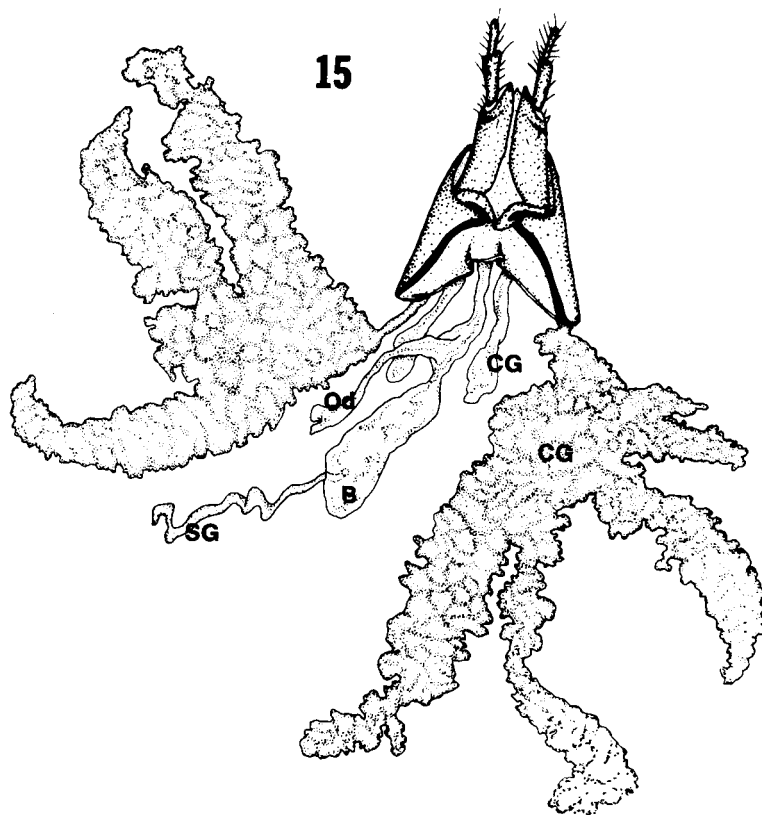
FIG. 15. Ventral view of female culicular structures of *Lagria* sp. showing primitive female genital tube with its primary bursa copulatrix (B), spermathecal gland (SG) entering vagina dorsally and common oviduct (Od) entering ventrally. This species also has 2 pairs of colleterial glands (CG), one of them very large. Ovipositor is essentially primitive, except for enlargement of lobe 2 and its partial fusion with lobe 3 of the coxites.

could represent an intermediate condition between the lagriine and the adeliine types. It at least indicates how a primary bursa might have given rise to a spermatheca.

In those species that retain the primitive, primary bursa copulatrix, there is relatively little specialization. The junction between the bursa and the vagina may become constricted (Fig. 18), or the walls of the bursa may develop various types of sclerites. Many diaperines and their allies show a sclerotization of the blind bursal end into what somewhat resembles a window (Figs. 29a, 30), or in the extreme, an elongate, olive-shaped structure resulting from a half-rolled circle of cuticle (Fig. 29b). Other sclerites occasionally appear in various taxa, apparently derived independently (Fig. 19).

The most widespread configuration we found was the bursa-derived spermatheca with a single opening (though the spermathecal tube could be either branched or not). In this type, there is no bursa copulatrix unless a secondary, dorsal bursa has evolved. This has occurred independently a number of times, as discussed below.

Phylogeny of the female tube (Fig. 17)

The configuration of the primitive lagriine tube is shared by a number of related taxa, such as *Lagria, Derolagria* and *Goniadera*. Constriction of the bursa copulatrix to produce a distal sac with the spermathecal tube opening at the constriction is the major change differentiating
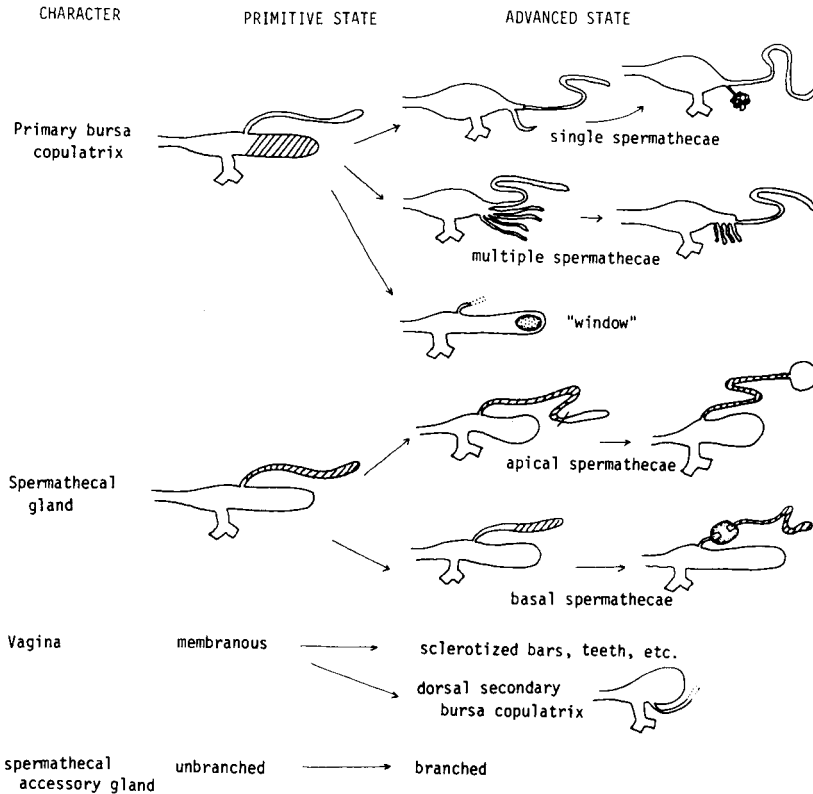
FIG. 16. Major trends in the evolution of features of female genital tube. Portion under consideration is shaded.

the female tubes of such genera as *Anaedus* (Fig. 18), *Catamerus, Phymatestes, Luprops* and possibly *Laena*. All of these female tubes are basically lagriine in their configuration and modes of specialization.

Figure 17 illustrates the evolutionary relationships indicated by the characteristics of the female reproductive tract. Besides the basal branch representing *Anaedus*, there are 4 major lineages, based primarily on the origin of the spermatheca and its subsequent modification. The order of derivation of types of spermathecae is not clear from present evidence, and the arrangement of the major lineages in Fig. 17 is arbitrary. On the basis of other characters, the adeliine lineage is most primitive. In this branch the primary bursa copulatrix has given rise to a non-glandular spermatheca with multiple openings into the vagina just ventral to the spermathecal accessory gland (Fig. 20). This condition is found in all Adeliini and Pycnocerini, and in *Damatris* (Cnodalonini). A possible intermediate stage is represented by *Metallonotus*, where the spermathecal tubes are membranous and large (Fig. 21).

In the second major lineage, a non-glandular spermatheca evolved from the apical portion of the spermathecal gland. This configuration characterizes the coelometopine–strongyliine–cnodalonine group of taxa. The cnodalonines (*Hemicera, Eucyrtus*) show the fewest derived features, differing from the primitive lagriines only in that the distal tip of the spermathecal tube is non-glandular and sclerotized, and that the spermathecal tube is very long (Fig. 22). The primary bursa is present and the spermathecal tube originates dorsal to

Glyptotus et al.

most Coelometopines

Diaperine

Nilio

Graptopezus etc.

Hypophloeine

Alobates et al

Coelometopine types

BASAL SPERMATHECA

Phaleriine

Ipthimus et al.

Cnodalonine

APICAL SPERMATHECA

Adeliine

Amarygmine

Toxicine

Tenebrionine

MULTIPLE, BURSA-DERIVED SPERMATHECA

Metallonotus

and many others

SINGLE, BURSA-DERIVED SPERMATHECA

Eleodine

Aneadus et al.
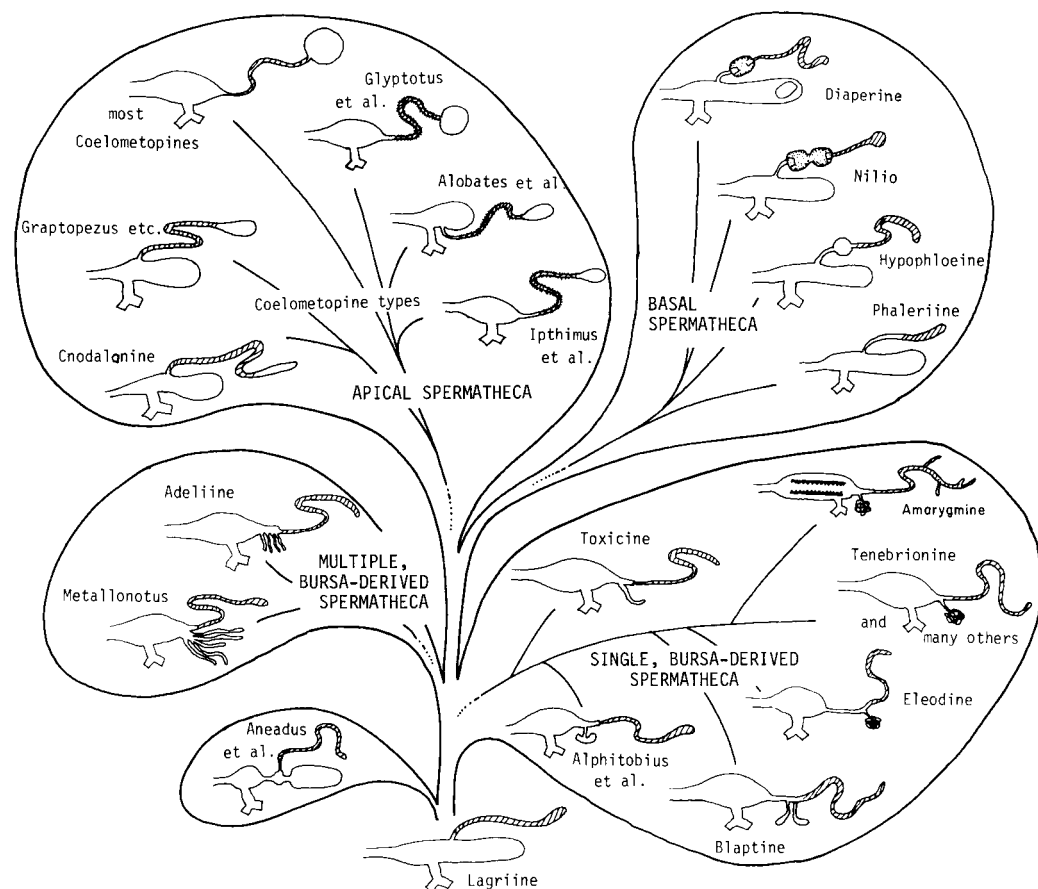
Alphitobius et al.

Blaptine

Lagriine

FIG. 17. Phylogeny of the female genital tube. Four major branches of advanced tubes are based primarily on source and type of spermatheca. Glandular regions are hatched. Species belonging in each of types are listed in Appendix II.

the median oviduct. *Damatris* (Cnodalonini) resembles the coelometopines on the basis of all its other characters, but its female tube is very similar to that of the Adeliini. While retention of such a primitive feature is not necessarily indicative of close relationship, it indicates that the coelometopine lineage arose independently of other lineages, probably from a lagrioid progenitor.

Expansion of the non-glandular apex of the spermathecal tube into a tapered spermatheca and annulation of the walls of the tube must have occurred early in the differentiation of the characteristic coelometopine structures. The character states are represented in such genera as *Polypleurus, Graptopezus* (Fig. 24), *Xylopinus* and *Tonkinius*, which still retain the primary bursa copulatrix, and the next major evolutionary change was probably loss of the bursa to produce a bursa-less female tube with a tapered spermatheca at the apex of the annulate duct opening at the anterior end of the vagina. Only some *Iphthiminus* species have this configuration, and most members of this group have evolved a secondary bursa by a dorsal expansion of the vagina (*Alobates, Iphthiminus* (part), *Promethis, Setenis, Taraxides*). Why these taxa do not simply retain the primary bursa is puzzling. Perhaps the spermathecal tube merely changes its point of origin, which would be indistinguishable from the evolution of a
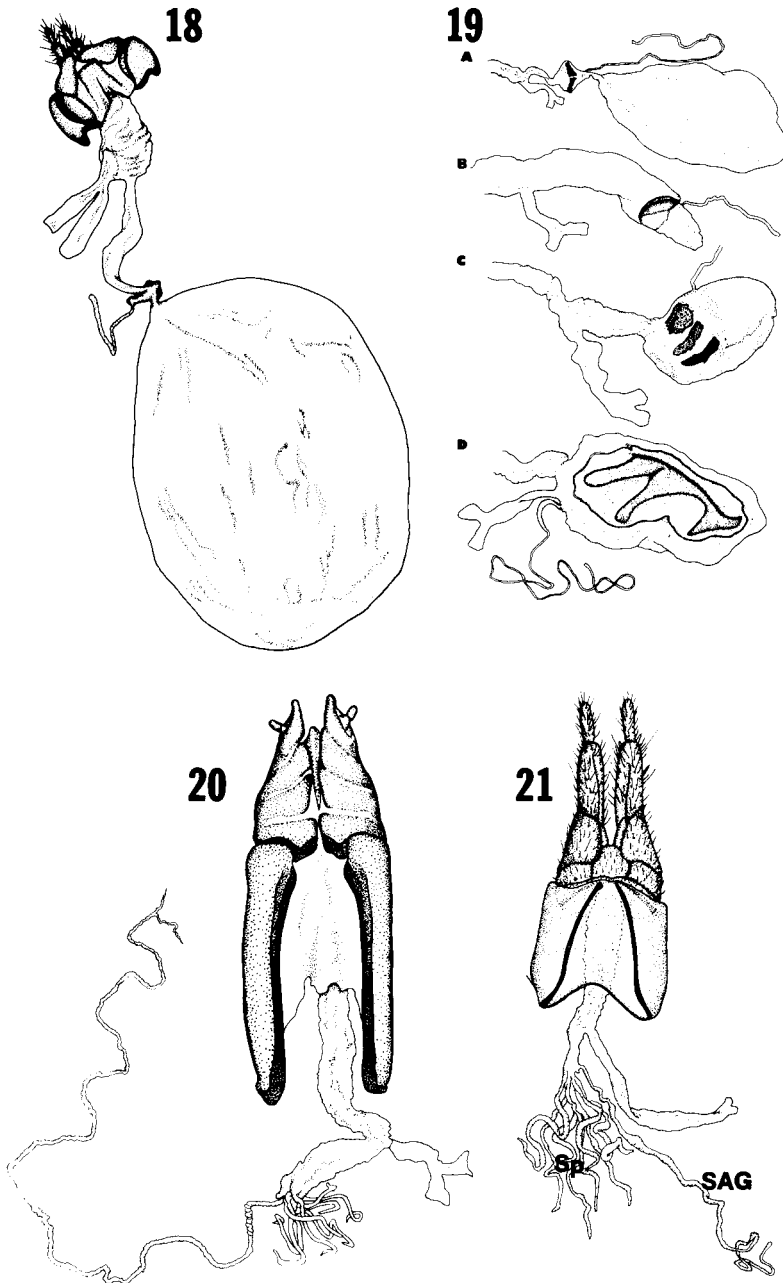
FIG. 18. Female cuticular structures of *Anaedus punctatissimus* (ventral view). Ovipositor is primitive but greatly reduced and desclerotized. Female genital tube is primitive except for constriction separating enlarged primary bursa copulatrix from vagina.

FIG. 19. Sclerites in primary bursa copulatrix of tenebrionids. (A) *Phymatestes exsculptus*. (B) *Goniadera nicaraguensis*. (C) *Lobopoda* sp. (D) *Nesogena viridicupria*.

FIG. 20. Female cuticular structures of *Cardiothorax caparatus*. Ovipositor is highly sclerotized and rather specialized. Female genital tube shows multiple spermatheca derived from primary bursa copulatrix of primitive female tract.

FIG. 21. Female cuticular structures of *Metallonotus metallicus*. Primary bursa copulatrix is divided into tubes which probably comprise a spermatheca (Sp). SAG = spermathecal accessory gland.
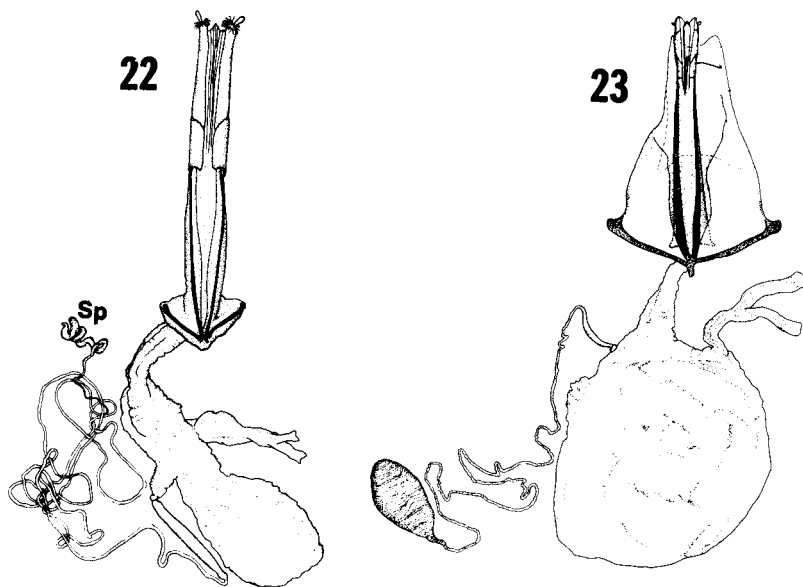
FIG. 22. Ovipositor and female tube of *Hemicera curta*, showing typical cnodalonine configuration. Primary bursa copulatrix is present, spermatheca (Sp) is apical, non-glandular portion of spermathecal tube, and ovipositor is typically coelometopine except that coxite lobes 3 and 4 are fused. Gonostyles are nearly terminal, and lobes 2, 3, and 4 are more sclerotized than in most coelometopines.

FIG. 23. Cuticular female structures of *Polopinus nitidus* (ventral view), showing typical and highly derived coelometopine ovipositor, most of whose length is made up by lobe 1 of the coxites. Note also re-orientation of baculi of the paraprocts and coxites. Female genital tube shows relatively primitive state for coelometopines. Apical spermatheca is gradually expanded and lightly sclerotized, and primary bursa copulatrix is still present.

secondary bursa. However, the attachment of the accessory gland remains quite constant in other tenebrionids in which the primary bursa is retained, and secondary development is more likely.

The evolution of the tapered spermatheca into an abrupt, saccate, usually membranous organ, followed by the loss of annulation of the spermathecal accessory gland marks the final stages of the distinctive coelometopine female tube (Fig. 25). Its most derived condition is thus as follows: a bursa-less vagina with an apical, smooth spermathecal accessory gland ending distally in a membranous, abruptly saccate spermatheca. A large fraction of coelometopine and all strongyliine (Fig. 26) taxa have this type of female tube. Only a few genera are at variance in showing an annulate of fine-annulate accessory gland (*Coelocnemms, Glyptotus, Paroeatus*). These may be transitional to the non-annulate condition. Only rarely does a secondary bursa evolve in this group (*Amenophis, Menephilus*, Fig. 39), so that the definitive coelometopine female tube lacks any bursa whatsoever, though many have a distensible vagina.

The third major lineage, represented by the Diaperini and relatives, is characterized by the evolution of a basal spermatheca from the spermathecal gland. In analogy with the cnodalonines, the first step is the evolution of a basal, non-glandular portion of the spermathecal tube. This state is found in the Phaleriini (Fig. 27), where only the apical half is glandular. Although the Phaleriini are probably not directly ancestral to the diaperine groups, they illustrate what may have been the first step in the evolution of the diaperine
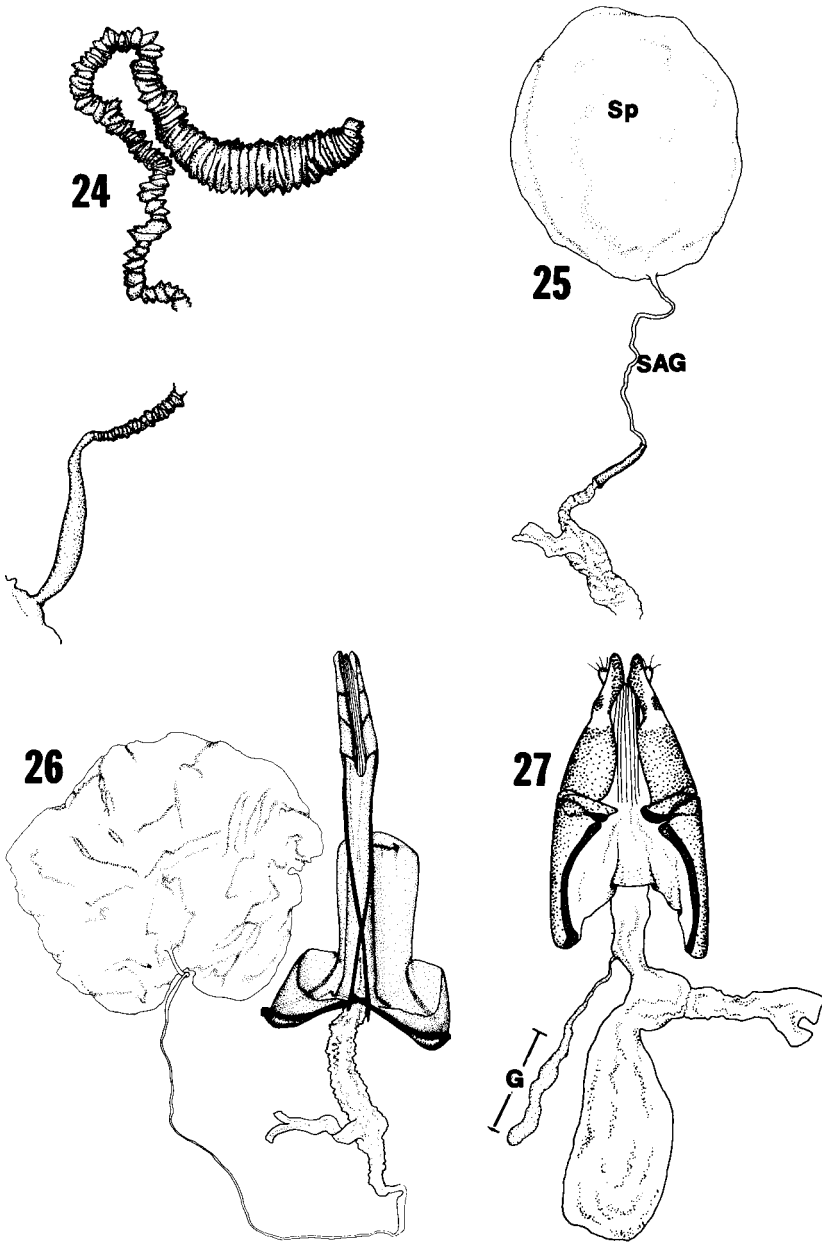
FIG. 24. *Graptopezus crenaticollis*, a relatively primitive coelometopine spermatheca and accessory gland, showing strong annular structure throughout and gradually expanded spermatheca at apex of spermathecal accessory gland.

FIG. 25. Female cuticular genital tube of a typical, definitive, coelometopine, *Upis ceramboides*, showing abruptly expanded apical spermatheca (Sp), connected to a bursa-less vagina by spermathecal accessory gland (SAG).

FIG. 26. Female cuticular structures of a typical strongyliine, *Strongylium haemorrhoidale*, showing that Strongyliini have typical coelometopine female structures. Spermatheca is enormous and very delicately membranous.

FIG. 27. Female cuticular structures of *Phaleria punctipes* (ventral view) showing highly modified ovipositor and essentially primitive female tube. Spermathecal tube is basally non-glandular. This represents an advanced character and a possible precursor to basal spermatheca of diaperines. G = glandular portion.

spermatheca. In the next stage, the proximal, non-glandular portion becomes enlarged or saccate, as in *Hypophloeus* (= *Corticeus*) and *Platydema ellipticum* (Fig. 28). This sac then becomes sclerotized into the characteristic and unmistakable capsular ("check valve") spermatheca of the diaperine taxa (Figs. 29, 30), with *Nilio* (Fig. 31) showing a slight variation with a double capsule. All of the taxa in the diaperine line retain the primitive, primary bursa copulatrix with a dorsal insertion of the spermathecal tube. In the most definitive diaperine type, the anterior wall of the primary bursa is sclerotized into specialized transparent structures ("window" or "olive") of unknown function. These are found in *Diaperis* (Fig. 30), *Ceropria* (Fig. 29a), *Clamoris, Palembus, Alphitophagus,* and most *Platydema* (Fig. 29b).

The fourth major type of female reproductive tract is characterized by a second, independent evolution of the primary bursa into a spermatheca. In this case, the bursa seems at first to have been reduced to a rather short, unbranched tube (some Toxicini) (Fig. 32) or T-shaped sac (*Alphitobius, Neatus, Tenebrio guineensis*). Later evolution of the spermatheca probably occurred through tube elongation, coiling and branching (Figs. 34, 35, 42, 43, 44). These definitive spermathecae are often mildly branched, sclerotized (Fig. 33) and tightly coiled, and may be extremely long and thin (Figs. 43, 45). Since the primary bursa forms the spermatheca in this group, the female tube is characteristically bursa-less for most of these taxa. Secondary, dorsal bursae are occasionally found, but the primary bursa is always absent.

A diverse array of taxa, including Opatrinae, Alleculinae, Helopini, and Tenebrionini share this configuration of female tube (see Appendices II, IV). In addition, most of the few members that we have examined from the tentyrioid lineage show this configuration. Apparently, further evolution of these taxa did not include serious modification of the female tube, and other characters are more useful in revealing interrelationships within this group.

It is difficult to decide how diversification within this branch took place, except that short, unbranched or saccate spermathecae are probably primitive. The Amarygmini (including Meracanthini) are distinguished by 2 unique features—a highly branched spermathecal accessory gland (Fig.35), and the presence of 4 long, toothed sclerites in the vaginal walls— but they cannot be directly derived from other taxa within the lineage. The Eleodini are moderately well distinguished by a long, tubular extension of the anterior vagina (Fig. 46), but this structure is not useful in indicating relationship.

The ovipositor:

Primitive state (Fig. 36). From general considerations of the origin and evolution of the insect ovipositor, the primitive tenebrionid ovipositor is probably more or less like that of certain Lagriini. Since the insect ovipositor is thought to have arisen from parts of abdominal appendages (coxites and coxal styles; Snodgrass, 1935), we judged that long, terminal gonostyles and free and elongate fourth lobes on the coxites are the primitive states. Otherwise stated, the more appendage-like ovipositors are primitive, and the less appendage-like ones are derived from them largely by reduction. This hypothesis is also supported by the widespread distribution of appendage-like gonostyles in Chalcodryidae, Zopheridae and other Heteromera believed to be closely related to Tenebrionidae (Watt, 1974a,b; Doyen and Lawrence, 1979). Other primitive features of the ovipositor are: (1) an elongate to subquadrate pair of paraprocts that form a cylindrical unit abutting but not enclosing the coxites. The paraproct baculi are oriented longitudinally on the ventral side; (2)
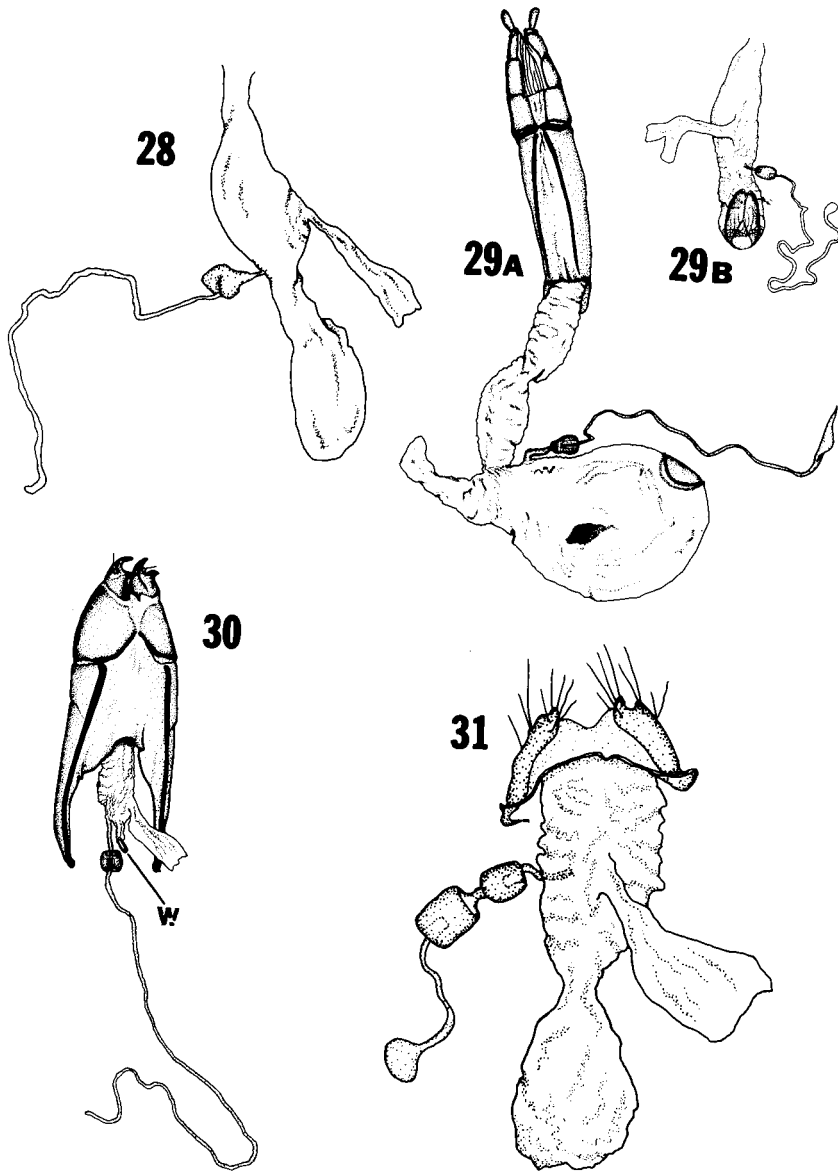
FIG. 28. Female genital tube of *Platydema ellipticum*. Basal portion of spermathecal tube has been expanded into a non-glandular, membranous sac. Primitive primary bursa copulatrix is present.

FIG. 29. (A) Cuticular female structures of a typical *Platydema* type, *Ceropria induta*. Ovipositor exhibits reduced 1st and 4th coxite lobes but has terminal gonostyles. Basal spermatheca is sclerotized into typical "check-valve" structure, and primary bursa copulatrix bears slightly sclerotized "window" common in many diaperines. Bursal teeth are unique to *Ceropria*. (B) *Platydema americanum* showing extreme development of bursal sclerite.

FIG. 30. Cuticular female structures of *Diaperis boleti* (ventral view). Ovipositor is highly specialized, heavily sclerotized and unique for genus. Female tract, on the other hand, is typically diaperine, showing definitive basal spermatheca, and (although reduced) primary bursa copulatrix with "window" (W).

FIG. 31. Cuticular female structures of *Nilio villosus* in ventral view. Ovipositor is greatly reduced and desclerotized, and its relationships cannot be determined. Female tract, on the other hand, is typically diaperine except that basal spermatheca is a double structure, and tip of spermathecal accessory gland is expanded. As in other diaperines, a primary bursa copulatrix is present.
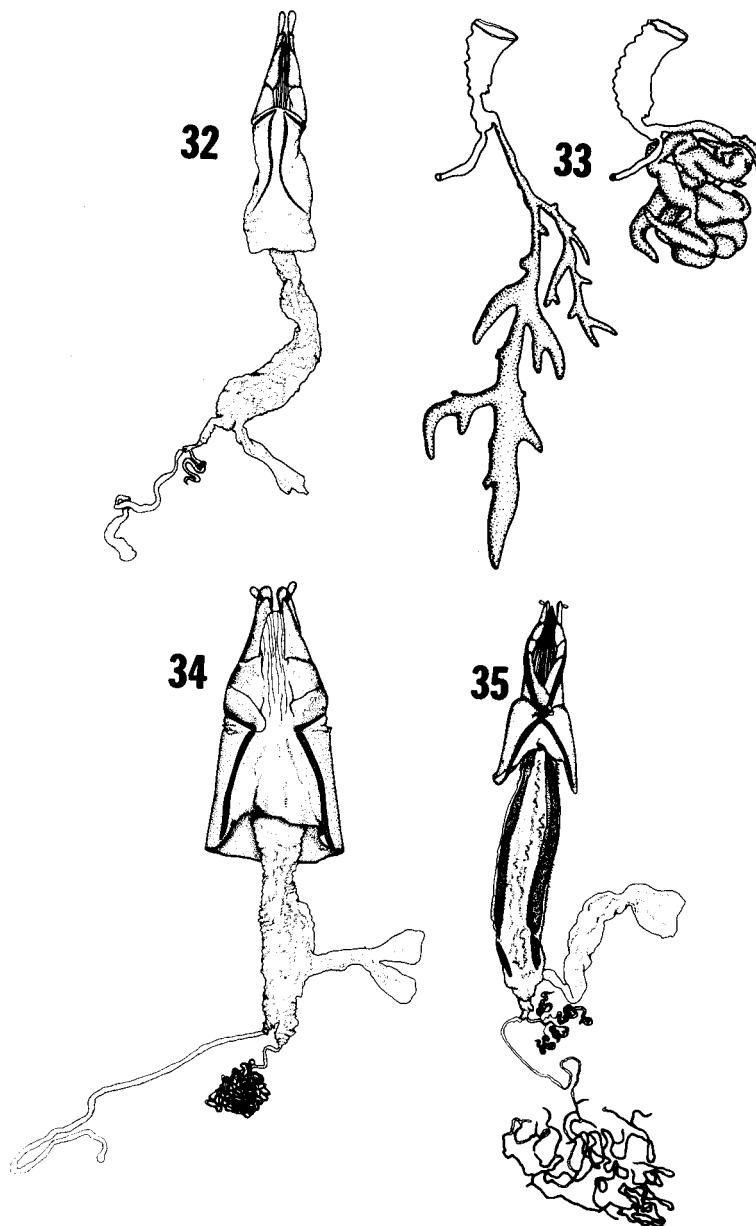
FIG. 32. Female cuticular structures of *Toxicum quadricorne* (ventral view) showing typical toxicine aspects. Single, short, tubular spermatheca has been derived from primary bursa copulatrix which is therefore absent. Ovipositor shows reduced fourth and first coxite lobes, but has terminal gonostyles. Dark, cuticular torus at base of spermatheca is characteristic of many toxicines, but is not found in other groups.

FIG. 33. Spermatheca of *Zophobas rugipes* Kirsch in normal and unrolled state. Spermatheca is sclerotized and rather brittle.

FIG. 34. Female cuticular structures of *Tenebrio molitor* Linn. (ventral view). Ovipositor shows reduced, lateral fourth coxite lobes with lateral gonostyles. Female tube is typical of those with a single, bursa-derived spermatheca in lacking a primary bursa copulatrix.

FIG. 35. Cuticular female structures of a typical amarygmine, *Plesiophthalmus* sp., in ventral view. In ovipositor, typical amarygmine features are long first coxite lobe and its oblique baculi. Four heavy, toothed, sclerotized bars in vagina and branched spermathecal accessory glands are characteristic of and unique to amarygmines.

CHARACTER	PRIMITIVE STATE	ADVANCED STATES
1 Position of gonostyles	terminal	lateral dorso-lateral
2 Shape of lobe 4	long, cylindrical, finger-like	disc-like or short
3 Length of lobe 1	subequal to each other lobe	Longer than lobes 1-3 Shorter than any lobe
4 Orientation of lobe 1 baculus	transverse	Oblique Longitudinal, very long
5 Length of paraproct	subequal CX	Much shorter than CX Much longer than CX
6 Orientation of PP baculus	longitudinal	Oblique Transverse
7 Relation of paraprocts to coxites	abutting	PP partly enclosing CX

1,2,6,7   3   1,2,3,4,   1,2,4   1,2,5
                            5,6,7   6,7

Advanced   none
characters

FIG. 36. Major trends in evolution of ovipositors. A range of ovipositor types is depicted at bottom to allow visualization of characters and changes. Numbers of characters which are advanced are listed under each type. Types are not exhaustive for family.

the coxites are each composed of 4 subequal, ventral lobes or segments. The fourth (apical) lobes are distal to the vulva, cylindrical and thus free along their medial margins. They bear the gonostyles terminally at their apical ends; (3) the position of the vulva is at the level of the second or third lobe of the coxites.

Evolutionary trends. The major evolutionary changes which transform these primitive character states are listed in Fig. 36. Some of the more conspicuous trends, some of which may have occurred independently several times, are: (1) movement of the gonostyles from a terminal to a lateral or even dorsolateral position; (2) this is often accompanied by a reduction of lobe 4 which may become disc-like and attached laterally to lobe 3. This process causes the vulva to appear to lie more distal to the ovipositor, but its relation to the lobes often remains the same in actuality; (3) extreme reduction of the first lobe of the coxites so that it is much shorter than the other lobes; (4) extreme elongation of the first lobe of the coxites so that it is much longer than all other lobes combined. This is usually accompanied by an equal elongation of the lobe 1 baculi and a shift in their orientation from transverse to logitudinal; (5) the paraprocts may become triangular in ventral view. In this condition, the paraprocts usually partly enclose the coxites at their distal end. Orientation of the paraproct baculi changes from longitudinal to oblique in some groups or transverse in others; (6) orientation of the lobe 1 baculi of the coxites may change from transverse to oblique. This

often correlates with a reduction in the coxites; (7) loss of lobation in the coxites, so that the entire structure appears more or less unitized.

Ovipositors vary greatly in the degree of their sclerotization, but this is a rather labile feature of relatively little systematic value.

Phylogeny of the ovipositor (Fig. 37)

The closest approximation to the hypothetically primitive condition is found in the Goniaderini and Lagriini (e.g. *Phymatestes,* Fig. 38). A substantial amount of the change that occurs during ovipositor evolution is reduction of the component parts. Especially the posterior ovipositor tip is subject to reduction, with lobe 4 and the gonostyles becoming smaller and lateral in position.

Unfortunately, much of the change in the ovipositor character states could probably have occurred independently a number of times, especially the reduction of primitive structures. This makes it difficult to place some of the ovipositor types in unequivocal phylogenetic relationships. Nevertheless, there clearly exist a number of distinctive ovipositor types which define certain taxa. The specialized ovipositors of the Coelometopini, the Amarygmini and the Eleodini provide the strongest examples.
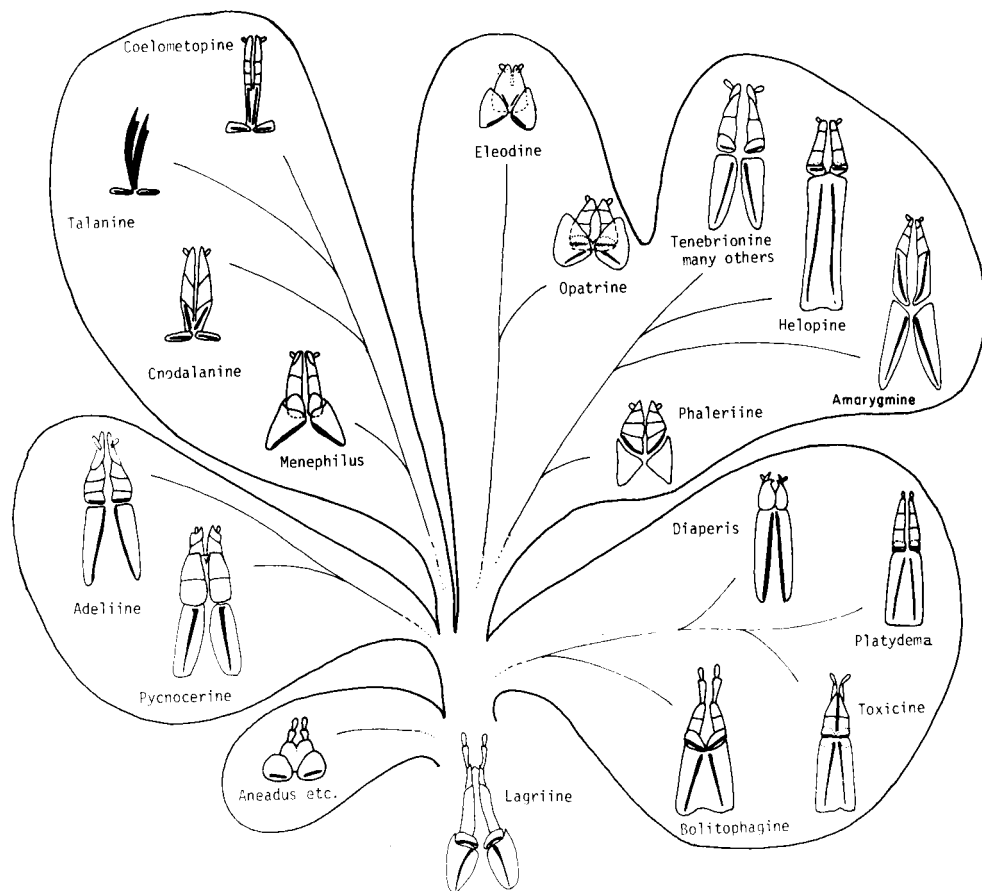

FIG. 37. Phylogeny of the ovipositor. Genera composing each type are listed in Appendix III. Major changes defining branches are position of gonostyles, orientation of baculi, and changes in relative development of paraprocts and coxites.

The ovipositors of genera such as *Catamerus* and *Anaedus* (Fig. 18) are clearly related to the primitive lagriine ovipositor in having terminal gonostyles on free fourth lobes. They seem to be derived from the lagriine ovipositors by overall reduction and desclerotization, resulting in rather poorly formed paraprocts and coxites without (or with indistinct) baculi.

The changes that led to the coelometopine ovipositor must have occurred quite early in tenebrionid phylogeny, because some species with coelometopine ovipositors have primitive glands and/or female tubes. It is difficult to be certain about the order in which the changes took place, and Fig. 39 gives only one possible sequence. The gonostyles move from their terminal to a lateral position and the paraprocts become shortened and enclose the base of the coxites. The baculi of the paraprocts become diagonal in orientation, as in *Menephilus* (Fig. 40), *Zophophilus* and *Catapiestus*, and ultimately become entirely transverse, as in the definitive coelometopine and cnodalonine ovipositors (Figs. 23, 16). The shape of the paraprocts also changes from the primitive elongate (Fig. 39a) to subtriangular (Fig. 39b) (*Menephilus, Zophophilus, Catapiestus*), to triangular or even elongate-transverse (Fig. 39c). In the coxites, most of the change is confined to the first lobe and its baculus. The first lobe elongates, often extremely, and its baculus changes from a transverse orientation to a longitudinal one (Figs. 23, 26). Lobe 4 becomes shortened and sessile, while lobes 2 and 3 show little change. Within the coelometopine–cnodalonine line, lobes 2, 3, and 4 show very little change from this characteristic pattern (Appendix III), except that lobes 3 and 4 are fused in most cnodalonines.

The talanine ovipositor (Fig. 41) represents an extreme specialization of the coelometopine type. The coxites are heavily sclerotized into a pair of blade-like structures that are fused basally with the enlarged baculi of the paraprocts so that the entire ovipositor operates as a rigid unit. The lobation of the coxites is no longer apparent, though faint suture lines suggest its presence.

Most of the adeliine and pycnocerine ovipositors are well sclerotized (Fig. 42), with lateral gonostyles, but the fact that certain adeliines (*Scirotrana parallela*) have terminal gonostyles with free, cylindrical fourth lobes indicates a strong relationship to the lagriines. Many adeliines have free fourth lobes but they are not cylindrical. In the pycnocerines, the fourth lobe is often elaborately sculptured and heavily sclerotized (Fig. 42).

The toxicine and bolitophagine ovipositors (Figs. 43, 44) retain a number of primitive features—the gonostyles are terminal and the fourth lobes are free. In the bolitophagines, the fourth lobes are usually quite long, while in the Toxicini they are reduced and medially flattened. The first lobe in Toxicini is often reduced and narrow.

The *Tenebrio* (Fig. 34) and helopine (Fig. 45) ovipositors differ from the preceding primarily in that the gonostyles are lateral and the fourth lobes are not free, but are often reduced to a somewhat lateral position on the third lobe. Many helopines have elongate paraprocts (Fig. 45), an apparently derived character.

The ovipositors of *Platydema* and related genera (Fig. 29) are not clearly differentiated from those of toxicines (Figs. 32, 43). The gonostyles are terminal in both, and the reduced first lobe is folded under the second. The major difference seems to be that the fourth lobe is shorter and usually sessile in the diaperines.

The amarygmine ovipositor (Fig. 35) is an easily recognizable, distinct type, but it is difficult to determine its origin. The gonostyles are lateral, the first lobes are usually long with oblique baculi, and the entire ovipositor has a distinctive shape.

The opatrine ovipositor shows a gradation from rather *Tenebrio*-like to quite specialized (Fig. 46). Within this line, the *Tenebrio*-like ovipositor is probably primitive—the gonostyles
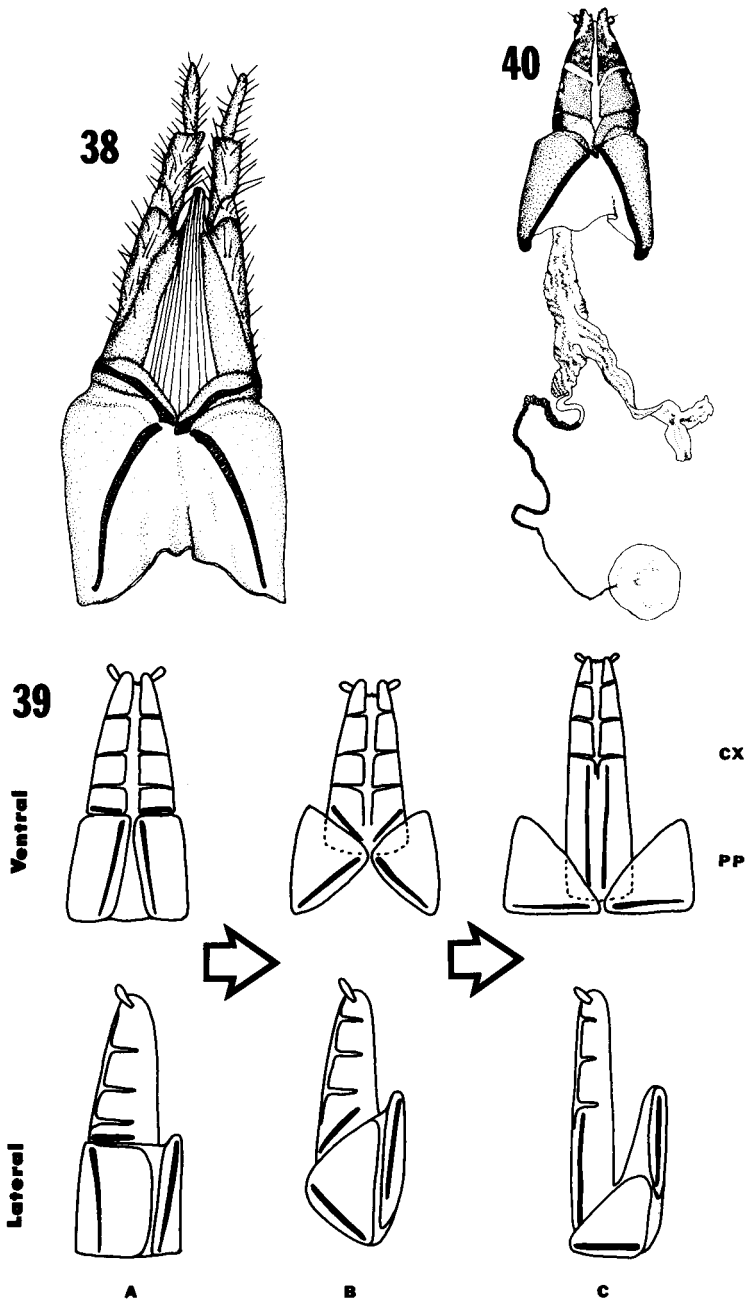
FIG. 38. Ovipositor of *Phymatestes exsculptus* (ventral view). With exception of modification of shape of coxite lobes 2 and 3, ovipositor is typically primitive and lagriine.

FIG. 39. Hypothetical pathway in evolution of typical coelometopine ovipositor, shown in both ventral and lateral view (pp = paraprocts; cx = coxites).

FIG. 40. Cuticular female structures of *Menephilus lucens* (ventral view) showing its partially coelometopine nature. Female tube is typically coelometopine with its apical spermatheca and absence of primary bursa copulatrix (actually, a small secondary bursa is present). Ovipositor, however, shows little coelometopine character as such, but has oblique buculi in the paraprocts and lateral gonostyles which could indicate that it evolved before coelometopine ovipositor was complete.
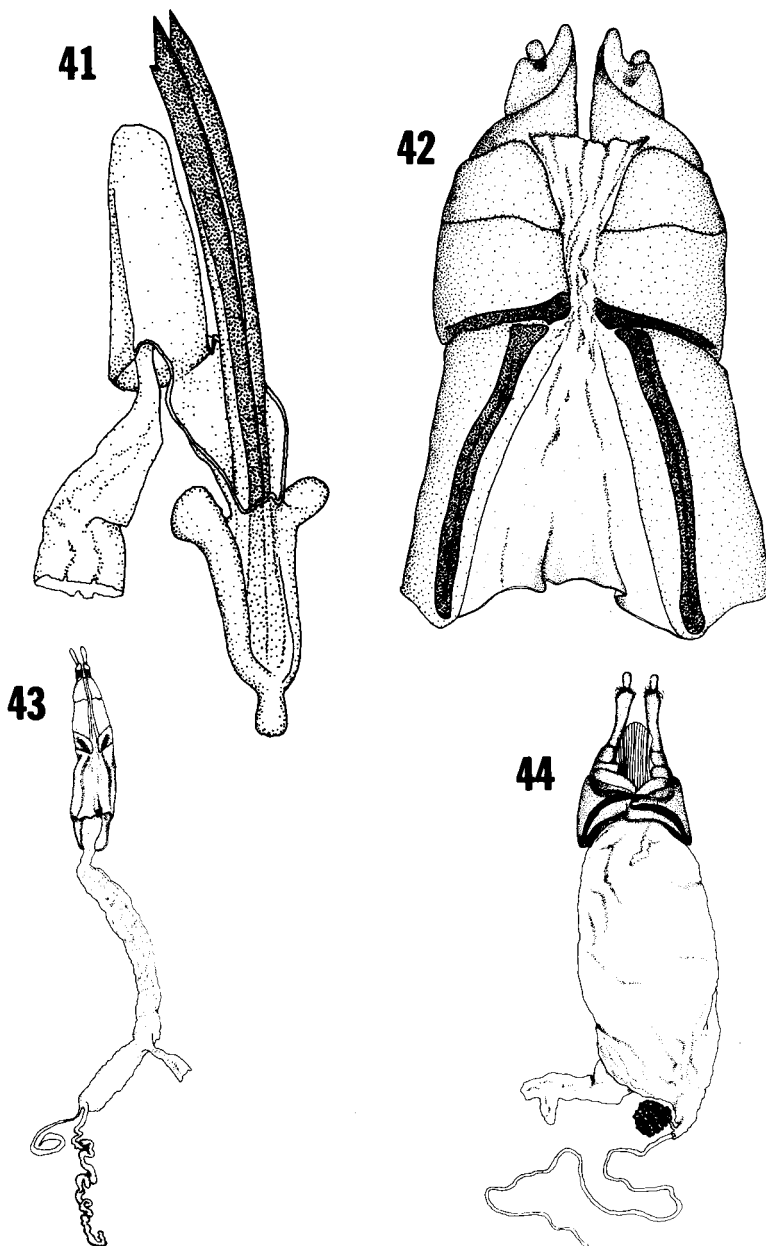
FIG. 41. Cuticular structures of ovipositor of *Talanus stenochinus* in ventral view. The coxites have become sclerotized into a pair of blade-like structures and fused basally with enlarged baculi of the paraprocts. Entire ovipositor is thus a rigid unit. Lobation of the coxites and all but the baculi of the paraprocts are no longer apparent. Proctiger has been pulled slightly to left during preparation but remains connected to ovipositor by membranous sheath.

FIG. 42. Ovipositor of *Prioscelis serratus* (ventral view) showing its heavily sclerotized and sculptured state. Coxite lobes 3 and 4 are fused, and ovipositor is quite specialized.

FIG. 43. Cuticular female structures of *Arthromacra aenea* in ventral view. Both ovipositor and female tube are largely toxicine. Gonostyles are terminal on short, but free, fourth coxite lobes, vagina bears a single, bursa-derived spermatheca and primary bursa copulatrix is therefore absent.

FIG. 44. Female cuticular structures of *Bolitophagus corticola* (ventral view). Long, free fourth coxite lobes and terminal gonostyles are primitive characters, but oblique baculi in the paraprocts are not. Primary bursa copulatrix has given way to a single, long tubular spermatheca.

are lateral, lobation is apparent and subequal, and the paraprocts and coxites simply abut, their baculi being longitudinal and oblique in orientation, respectively. In more specialized ovipositors the gonostyles evolve to lie dorsolaterally, lobation is reduced or absent, the baculi of both paraprocts and coxites become obliquely oriented and the paraprocts enclose the coxites. In its extreme, this description fits most eleodine ovipositors (Fig. 46), which are clearly derived from the opatrine, since many intermediates can be found.

Other ovipositors and female tubes of interest

Both the ovipositor and the female tube of *Zolodinus zealandicus* (Fig. 47) are derived, although the ovipositor is difficult to place in the present scheme. In general, it seems more similar to the ovipositors of the tentyrioid lineage than to the tenebrionoid tribes, in that the paraprocts are accentuated and well sclerotized and the lobation of the coxites is not very apparent. Overall, it forms a rod-like unit of much greater rigidity than most tenebrionoid ovipositors. The configuration of the female tube fits into the bursa-derived, single spermatheca line, as do many tentyrioids as well as Tenebrionini, Opatrini and others. Although *Zolodinus* is primitive in a number of characters (see Watt, 1974b; Doyen and Lawrence, 1979), the sum of the evidence presented here suggests that it is related to the tenebrionine-opatrine lineage as defined by the female reproductive tract.

Figure 48 shows an extreme development of the baculi in one of the amarygmine species, *Chalcopterus laevicollis* Bless. The baculi of the paraprocts are much longer than the body of the paraproct, so that they are carried in invaginated pouches projecting toward the animal's head. The function of this extreme development is unknown.

The spermathecae in several American Scaurini are extremely thin tubules. *Apsena rufipes* is the example shown in Fig. 49. *Argoporis* is similar.

DISCUSSION

One of the compelling lessons we learned in the course of this study was the necessity for using a large number of taxa as a basis for phylogenetic analysis. Selecting a few representatives from the taxa under study is error-prone. Thus, for example, Turner (1927) concluded, on the basis of 6 or 7 species, that tenebrionid ovipositors were rather uniform in structure. As it happened, most of the species he examined were closely related, but he also overlooked the profound differences between the ovipositors of *Eleodes* and *Coelocnemis*, perhaps because he studied them in the extended position. For all the organ systems we studied, variation was so great that, had we randomly selected a few taxa here and a few there, we would not have been able to determine relationships on the one hand, or on the other hand, would have concluded that certain taxa (e.g. tribes) were homogeneously of a certain character, when, in reality, the taxon consisted of members of several phyletic lines lumped together. A case in point would be the Tenebrionini. A small random sample of genera would possibly net only those belonging to the type having *Tenebrio*-like glands, ovipositors and female tracts. If the sample were drawn somewhat differently (e.g. from a collection with a different geographic bias), it is equally possible that all the genera would show coelometopine types for these same organ systems. The point is simply that the true systematics and phylogeny of larger taxa can almost never be worked out by examining one or a few genera from intermediate taxonomic categories such as tribes or subfamilies. Only by investigating a substantial fraction of the taxa in each higher unit can valid conclusions be generated. In our study, we analyzed some 3% of all tenebrionid species, but about 6% of the species in the tribes under consideration, and up to 60% of the genera of some tribes such as
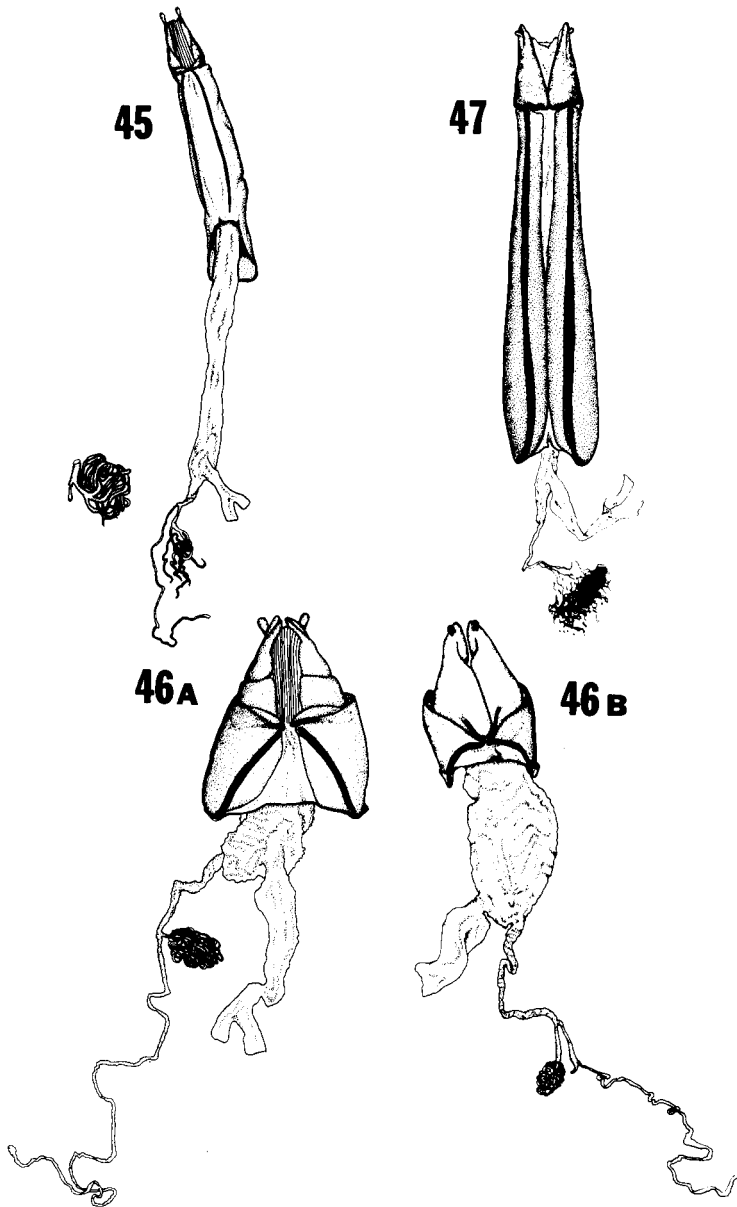
FIG. 45. Cuticular female structures of *Helops discretus* in ventral view. This ovipositor shows extreme elongation of the paraprocts common among many Helopini. Rather coarse, branched spermathecae are also common in this tube. Spermatheca is also shown in rolled state at twice magnification. Neither character is highly distinctive or universal, and Helopini are not sharply differentiated from similar groups.

FIG. 46. Female cuticular structures of *Opatrinus minimus* (left), and *Eleodes clavicornis* (right). Certain shared features of both ovipositors and female tube indicate that Eleodini are derived from same stock as Opatrini. Both have shortened ovipositors with paraprocts partly enclosing coxites, oblique orientation of baculi-1, and long "stem" connecting accessory gland and coiled spermatheca to vagina. Eleodini differ in that baculi-2 are obliquely oriented and lobation of coxites is often absent. Other differences are of degree only.

FIG. 47. Female cuticular structures of *Zolodinus zealandicus* Blanch. (ventral view). Ovipositor is sclerotized into a thick, rod-like structure, and a bursa-derived, single spermatheca is present. In both of these characters, *Zolodinus* resembles many tentyrioids, as also in reduction in size of the coxites.

Spermathecal accessory gland was lost in this preparation, but is a single, long tube (Watt, 1974b).
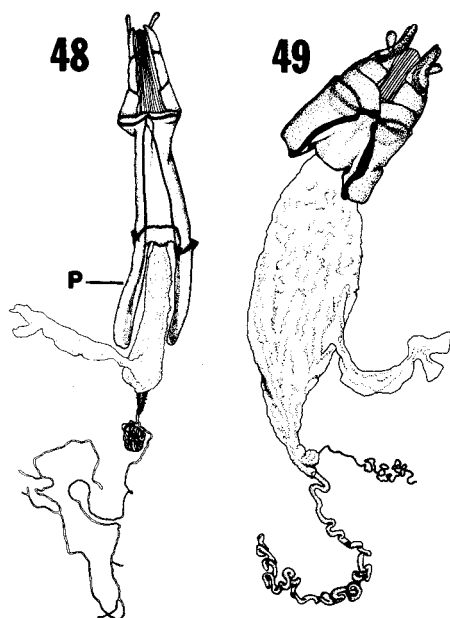
FIG. 48. The cuticular female structures of *Chalcopteroides laevicollis* (ventral view). Development of baculi-1 is so extreme that they lie in invaginated pockets (P) of intersegmental membrane projecting into abdomen.

FIG. 49. Female cuticular structures of *Apsena rufipes* (ventral view) showing very thin spermatheca and distinctively sclerotized ovipositor.

Coelometopini. Because of the high degree of convergence in external features among tribes such as Tenebrionini and Coelometopini, it is expected that additional misclassifications will be revealed by further comparisons. Indeed, it may prove necessary to examine internal features of most genera in some tribes.

Value of internal characters in classification of Tenebrionidae

Most comparisons of internal organ systems of Coeloptera have yielded information of systematic interest. As documented on the previous pages, the present study is certainly no exception. Not all the features we studied are of equal importance, however, and the taxonomic level at which relationships are revealed varies. Analysis of character variation and its systematic implications will be discussed more thoroughly in future papers, but it is appropriate here to appraise briefly and to compare the usefulness of the various organs and organ systems.

The single most diagnostic feature, we believe, is the structural variation in the female genital tract. Three distinct arrangements of bursa copulatrix, spermatheca, and spermathecal accessory glands occur through a very large proportion of the species examined, without intermediates. Intermediacy occurs only with the generalized type of female tract, found in the lagriine lineage, which is believed to be primitive in many other adult and larval features (see Watt, 1974b). In other words, the permutations of structure of the female genital tube define the 3 large lineages that include the great majority of all beetles

in the tenebrionoid Tenebrionidae. Further analysis may be required to ascertain whether these lineages arose independently from lagriine ancestors, or diverged later, possibly from a *Tenebrio*-like beetle. In any case, variation in the female tube should probably be represented at the subfamily level in classifications.

Several individual structures of the female tube are of considerable taxonomic value. The configuration of the spermatheca, spermathecal accessory gland, and occasionally of the bursa copulatrix or vagina may be uniform and distinct through one or several closely related tribes. Examples include the toothed vaginal walls of the Amarygmini (Fig. 35) and the thickened, capsular spermathecae of the Diaperini and related tribes (Fig. 29).

Several features of the abdominal defensive glands and ovipositors are clearly of taxonomic importance, but less so than the structures of the female genital tube. For example, distinctive annulate gland reservoirs characterize the Coelometopini, but similar reservoirs occur in Diaperini. The position and form of the gland secretory tubule attachments to the reservoirs, and the shape of the reservoirs is often distinctive, but similarities frequently occur among taxa which are obviously unrelated on the basis of numerous other features. For example, condensation of the secretory tubules into a few or a single collecting duct has apparently arisen independently in at least part of the Helaeini, Coelometopini, Ulomini and Diaperini (Fig. 10). The most distinctive feature of the ovipositor is the peculiar transverse position of the paraprocts, which is one of the chief defining characters of the coelometopine lineage. Several other tribes or groups of tribes have ovipositors with idiosyncratic features (e.g. *Diaperis*; Fig. 30), but these are frequently approached by structures in distantly related taxa. More than the other organs considered here, the ovipositor shows a pattern of convergent reduction in several features over many different lineages. In general, the gonostyles tend to become shorter and smaller and lateral in position in all the major lineages, and the lobation of the coxites becomes consolidated and obscured.

Combinations of the various characters are very frequently unique to tribes or groups of closely related genera. For example, enlarged medially lobed gland reservoirs in conjunction with very short ovipositor and tightly coiled spermatheca differentiate the Eleodini, although any single character is inadequate. As yet unrecognized clusters of correlated characters of this sort probably have very great potential for future clarification of the phylogenetic relationships within the Tenebrionidae.

Functional correlates

As for the details of internal structure of most insects, very little is known of the function of the structures described here. The significance of the various reservoir designs was pondered by Tschinkel (1975b), who noted that all eversible glands must be tapered toward the apex to allow their use. The spiral annulation of the reservoirs of Coelometopini and certain other tribes probably facilitates distension as the reservoirs fill, and may aid in their complete emptying. The significance of other features of the glands, especially of the condensation of tubule terminations into one or a few collecting ducts, is problematic.

Knowledge of the functional significance of the extensive variation in the internal female tract is almost entirely lacking. From the location of spermatozoa from *in vivo* preparations, it is certain that the structures designated as spermathecae actually function in sperm storage in all the major types of genital tube, except the lagriine, which we have been unable to examine. Similar observations were reported by Surtees (1961) for several species of stored products tenebrionids. The reason for the diversity in shape, size, spatial configuration, and, for the accessory glands, in branching is entirely unknown.

Construction of the ovipositor is broadly correlated with the type of substrate where eggs are laid. For example, the Eleodini, Opatrini, and related tribes, and the Phaleriini oviposit in soil. The ovipositor is short, the lobation of the coxites is obscured by increasing sclerotization, so that the cuticle becomes leathery. In nature, some *Eleodes* construct oviposition burrows. In laboratory situations, many species of this category deposit their eggs indiscriminately in surface objects, including sand or soil. It is interesting that the other major group of soil-dwelling tenebrionids, including nearly the entire tentyrioid lineage, shows a distinctly different ovipositor design. As described below, the paraprocts are elongate, often greatly so. The apices of the coxites are often flattened and cornified or strongly sclerotized as spatulate digging devices. The lobation to the coxites is obscured and the gonostyles, usually greatly reduced, are inserted anteriorly and dorsally.

In many species which are known to oviposit on harder substrates, such as rotting wood or fungus, the ovipositor is relatively elongate. The eggs are inserted into cracks and crevices in the substrate. The ovipositor apparently has an important tactile function, and usually remains relatively weakly sclerotized and flexible. The coelometopine group and most diaperines exemplify this type of adaptation. The functions of the long, finger-like gonostyli of lagriines, or the highly modified ovipositors of genera such as *Diaperis* (Figs. 30, 37) and *Talanus* (Figs. 37, 41) are unknown.

Major lineages in the evolution of the Tenebrionidae

Without resorting to the formal analysis of phenetic or cladistic methods, which will be presented later, it is possible to make a number of generalizations about evolutionary differentiation of the major lineages of Tenebrionidae. From the evidence presented above, it is clear that these major lineages are characterized by radical differences in certain internal structures and accompanied by many consistent minor differences as well. Where knowledge is available, these lineages often include species of similar general life habits (e.g. fungus beetles or those associated with dead wood). Each lineage is also associated with a spectrum of threshold groups that possess some but not all of the definitive features. Such threshold taxa are probably early branches from the major lines, and are always outnumbered by the taxa of the definitive lineage.

The most primitive genera should probably not be called a lineage, because they have not diverged much from the ancestral state. These are the "lagriine" genera whose female tracts contain a primitive bursa copulatrix, and a single spermathecal gland without a spermatheca. The ovipositor is finger-like with terminal gonostyles, and 3 of the 4 gland types as well as the glandless condition are represented. When glandlessness occurs, it is probably primitive. The tribe Lagriini (*sensu* Watt, 1974b) matches most closely these criteria, and in a typological sense defines this grouping. However, the Goniaderini, Pycnocerini and Adeliini, though differing in some strikingly apomorphous features, share many features with the Lagriini. The Cossyphini and Phrenopatini, accorded subfamily status by Watt (1974b), share features of the female tube as well as other characters with the lagrioid tribes, and should probably be placed here as well. The genera *Rhypasma* and *Adelonia*, of problematic systematic position, have both the ovipositor and the female tube of the lagriine configuration and are tentatively placed here. The Apocryphini, included in Watt's (1947b) Lagriinae, belong to the tenebrionine lineage (Doyen and Kitayama, 1980) discussed below.

The fate of the bursa copulatrix and the source of a non-glandular spermatheca define all of the other major lineages. In the diaperine line, the primitive bursa is retained throughout,

and a spermatheca is formed from the base of the spermathecal gland. The defensive glands are usually annulate, except in some threshold species. In most members of this group the spermatheca becomes further modified as a thick-walled capsular structure. Included here would be the Diaperini, Nilionini, Hypophloeini, Phaleriini and some genera now placed in the Ulomini. *Crypticus* (Crypticini) shares some features with Phaleriini, but has a lagriine type female tube, and may be a threshold member of the diaperine lineage. It may be noted that this lineage is highly composite on the basis of previous classifications.

In the coelometopine line, the primitive bursa is at first retained but later lost in most species, and the spermatheca is formed from the apex of the spermathecal gland. The ovipositor is of the unmistakable coelometopine type with re-oriented baculi on both paraprocts and coxites. The defensive glands are annulate throughout, except for some of the threshold genera. The coelometopine genera form an exceedingly uniform, characteristic and unambiguous group, many of whose genera were previously placed into several different tribes. Included here would be the Coelometopini, Cnodalonini, Misolampini, Misolampidiini, Strongyliini, Talanini, and many genera previously placed in the Tenebrionini.

All the remaining tenebrionids with defensive glands belong to the tenebrionine lineage. In this lineage, the spermatheca is derived from the primitive bursa, but has a single opening. The definitive ovipositor has lateral gonostyles and is somewhat to greatly reduced, and the defensive glands lie between the seventh and eighth sterna in a variety of shapes and styles. This very large lineage can be further subdivided into sublines. Probably the earliest subline is the toxicine in which the spermatheca is yet short and small, and the ovipositor still has terminal gonostyles, although the fourth lobes are reduced from their primitive length. The defensive glands are eversible and rather primitive, though of a quite distinctive type.

It is possible that the Australian tribes Helaeini, Cyphaleini, and Nyctozoilini should be grouped into another subline, but we cannot as yet sharply define them. The opatrine sublineage on the other hand, is characterized by a strong trend toward reduction and loss of lobation of the ovipositor, and the dorsal movement of the gonostyles. The female tract is fairly typical for the tenebrionine lineage, but the defensive glands are often 2-lobed, without common volume. In specialized tribes such as the Eleodini, these trends are quite distinctive, but the sublineage is not sharply separated from the tenebrionine lineage. However, most of the genera share the clavae of the aedeagus as a uniting character as well.

As might be expected, there are a number of groups which do not fit easily into these lineages, or which straddle 2 of them. The genus *Damatris*, for example, is a perfectly ordinary coelometopine in every way, except that it has an adeliine spermatheca, rather than the expected apical one.

A number of groups are difficult to place in relation to others because key structures are unique and without intermediate links to other taxa. Some examples would be *Centronopus, Hegemona, Rhipidandrus* and *Micranterius*. It is possible that further study will turn up species that will shed light on the relationships of such groups.

On the other hand, our data do not agree with some of the present classification. For example, *Nilio* is usually placed into a separate subfamily (or family), yet is clearly closely related to *Platydema* and other diaperines. *Nilio*, like *Diaperis*, seems to be an early offshoot of the diaperine line, and both genera have a specialized ovipositor and distinctive defense glands with some primitive features.

Primitive relationships of the tentyrioid lineage
We have examined in detail only 10 species of tentyrioids, and thus cannot relate this

group to the stem tenebrionids with much confidence. There is, nevertheless, little doubt that they are derived from tenebrionoid stock, and some tentative speculations on their phylogeny can be made. All tentyrioids we examined had easily recognizable ovipositor which were not primitive. Typically, the paraprocts exceed the coxites in length and are well sclerotized with strong baculi. The coxites are short, have small or no gonostyles, and are joined to the paraprocts in such a way as to form a rather stiff, rod-like structure of the whole ovipositor–proctiger assembly (Fig. 47). A primitive bursa copulatrix was absent, although 2 species had a dorsal, secondary bursa. Three types of spermatheca were found: (1) multiple, bursa-derived, reminiscent of the adeliine type; (2) single, short, bursa-derived spermatheca, reminiscent of some toxicines; (3) spermathecal glands without a separate, differentiated spermatheca, as in lagriines.

The genera *Zolodinus* and *Tanylypa* were placed by Watt (1974b) in a subfamily Zolodininae, as the sister group to his Pimeliinae. We have examined both genera, which certainly share many features such as glandlessness with the tentyrioid lineage, and also have an ovipositor similar to those of some tentyrioids. However, many primitive members of the tenebrionoid line (e.g. Goniaderini) also lack glands. The female tube of *Zolodinus* is of the tenebrionine type described above (which also occurs in certain tentyrioids). In general, Zolodinini share several features of the larvae with Cyphaleini, Halaeini, and Nyctozoilini (see Doyen and Lawrence, 1979). Thus, the proper position of Zolodininae cannot be clarified at present, but an early derivation from the tenebrionine–opatrine lineage is probably most likely.

It seems likely that tentyrioid phylogeny will be as complex as that of the tenebrionoid line. Two generalizations seem reasonable at this point: (1) the tentyrioids did not diverge from the most primitive tenebrionoids (Lagriini), but rather branched off from some more advanced form. This we conclude from the derived and fairly uniform ovipositor, and the consistent absence of the primitive bursa copulatrix; (2) the divergence from the tenebrionoid line was early enough that a diversity of spermathecal types is found among the tentyrioids. Thus, the tentyrioid lineage should probably be considered as a moderately early ejectum from the stew pot that gave rise to the major tenebrionoid lineages.

We have also tentatively concluded that the tentyrioid tenebrionids are secondarily glandless, since their affinities are greater for tenebrionoid groups with glands than for those that are primitively glandless. Perhaps gland loss is an adaptation for the generally xeric conditions under which these beetles live. It should be pointed out that this interpretation of gland presence and absence differs strongly from the earlier interpretations of Doyen (1972) and Watt (1974b), who assumed that the tentyrioid line was primitively glandless.

We emphasize that all these conclusions are tentative. If the great variation among tenebrionids also holds for tentyrioids, future work may show our generalizations for the latter to be dismally incorrect.

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APPENDIX I

Classification of tenebrionid defensive glands. The classes are those in Fig. 10 and Appendix IV. An asterisk indicates that the gland deviates somewhat from its class. Abbreviations following each class name are those used in Appendix IV, where a full listing of species appears.

No Gland

Adelonia
Aemymone
Anaedus
Belopus
Cossyphus
Goniadera

Paratenetus
Clamoris (= Phthora)
Phymatestes
Rhypasma
Zolodinus
Tanylypa

Pycnocerine (PYCN)

Catamerus
Chiroscelis
Metallonotus

Prioscelis

Adeliine (ADEL)

Adelium   *Otrintus*
Cardiothorax   *Seirotrana*

Lagriine (LAGR)

Derolagria   *Luprops**
Lagria   *Sora**

Blaptine (BLAP)

Blaps

Toxicine (TOXI)

Calymmus   *Nycteropus*
Cryphaeus   *Ozolais*
Diceroderes   *Toxicum*
Dysantes

Bolitophagine (BOLI)

Bolitophagus   *Eleates*
Bolitotherus   *Megeleates*

Tenebrionine (TENE)

Alphitobius   *Lepispilus**   *Tenebrio*
Apsena   *Meneristes*   *Xystrophus*
*Argoporus**   *Neatus*   *Zophobas*
*Cerenopus**   *Nycterinus*
Crypticus   *Pedinus*
Epantius   *Rhinandrus*
Idiobates   *Scotobius*
                           *Sympetes**

Phaleriine (PHAL)

Phaleria   *Phaleromela*

Amarygmine (AMAR)

Amarygmus   *Platolenes*
Chalcopteroides   *Plesiophthalmus*
Eupezus   *Psorodes*
Meracantha

Catapiestus Type (CATA)

*Antimachus**   *Cuphotes*
Asphalus   *Mimopeus (= Cilibe)*
Catapiestus   *Pterohelaeus*
                                                           Strongylium

Cnodalonine (CNOD)

Arthrodactyla   *Hemicera*
Camaria   *Platycrepis*
Eucyrtus   *Talanus**
Hapsida

Coelometopine (COEL)

Alobates
Amenophis   *Necrobioides*
Bradymerus   *Nuptis*
Choastes   *Oeatus*
Cibdelis   *Oedemutes*
Coelocnemis   *Oenopion*
Coelometopus   *Paroeatus*
Cyrtosoma   *Polopinus*
Damatris   *Polypleurus*
Derosphaerus   *Promethis*
Dicraeosis   *Pseudobax*
Eccoptosoma   *Setenis*

Encyalesthus
Euthysternum
Glyptotus
Graptopezus
Haplandrus
Heliofugus
Hypaulax
Ilus
Iphthiminus
Menephilus
Merinus
Misolampidius
Misolampus
Mylaris*

Sphaerotus
Taphrosoma*
Taraxides
Temnophthalmus
Tetraphyllus
Tonkinius
Upis
Xylopinus
Zophophilus

Platydema Type (PLAT)

Alphitophagus
Ceropria
Doliema
Gnatocerus
Liodema

Neomida
Palembus
Platydema

Diaperis Type (DIAP)

Diaperis

Nilio

Ulomine (ULOM)

Eutochia
Hypophloeus
Tribolium

Uleda*
Uloma

Opatrine (OPAT)

Blapstinus
Eurynotus
Heterotarsus
Nesogena

Opatrinus
Opatrum
Pseudoblaps
Ulus

Eleodine (ELEO)

Eleodes (incl. *Amphidora, Cratidus*)
Lariversius
Neobaphion

Trichoderulus*
Trogloderus

Helopine (HELO)

Helops
Lygestira
Nautes
Nyctozoilus

Probaticus
Tarpela

Centronopus (CENT) (not illustrated)

Centronopus

Scotobaenus

Unclassified or of uncertain affinity (UNCL)

Achrostus
Apocrypha
Arthromacra
Bius
Ectyche
Hegemona
Lobopoda
Macellocerus

Menimus
Metaclisa
Micrantereus
Pentaphyllus
Praogena

Rhipidandrus
Scaurus
Statira
Tauroceras
Titaena
Ulosonia

APPENDIX II

Classification of tenebrionid female genital tubes. The classes are those in Fig. 17 and Appendix IV. An asterisk indicates that the tube deviates somewhat from its class. Other conventions as in Appendix I.

I. PRIMITIVE SPERMATHECAL GLAND
Lagriine (LAGR)

Adelonia   *Lobopoda**
Clamoris (= Phthora)   *Luprops*
Delognatha   *Menimus*
Derolagria   *Phrenapates*
Goniadera   *Rhypasma*
Lagria   *Ulosonia*

Anaedus Type (ANAE)

Anaedus
Phymatestes

II. MULTIPLE BURSA-DERIVED SPERMATHECA
Adeliine (ADEL)

Adelium   *Praogena**
Cardiothorax   *Prioscelis*
Cossyphus   *Seirotrana*
Damatris   *Sora*
Otrintus

Metallonotus Type (META)

Metallonotus

III. SINGLE, BURSA-DERIVED SPERMATHECA
Toxicine (TOXI)

*Arthrodactyla**   *Diceroderes*
Arthromacra   *Dysantes*
Belopus   *Ozolais*
Calymmus   *Toxicum*
Cryphaeus

Alphitobius Type (ALPH)

Alphitobius   *Neatus*   *Tenebrio (part)*

Blaptine (BLAP)

Blaps

Eleodine (ELEO)

Eleodes (incl. *Amphidora, Cratidus*)   *Trichoderulus*
Lariversius   *Trogloderus*
Neobaphion

Tenebrionine (TENE)

Achrostus	*Helops*	*Pterohelaeus*
Antimachus	*Heterotarsus**	*Rhinandrus*
*Apsena**	*Idiobates*	*Rhipidandrus*
Argoporus	*Lepispilus*	*Scaurus*
Asphalus	*Lygestira*	*Scotobius*
Bius	*Megeleates*	*Tarpela*
*Blapstinus**	*Meneristes*	*Tauroceras*
Bolitophagus	*Metaclisa*	*Tenebrio* (part)
Bolitotherus	*Mimopeus*	*Titaena*
Cerenopus	*Nycteropus*	*Tribolium*
Eleates	*Nyctozoilus**	*Uleda*
Epantius	*Opatrinus*	*Uloma*
*Eurynotus**	*Opatrum*	*Ulus*
Eutochia	*Pedinus*	*Xystropus*
	Probaticus	*Zolodinus**
	*Pseudoblaps**	*Zophobas*

Amarygmine (AMAR)

*Chalcopteroides**   *Platolenes*
Eupezus   *Plesiophthalmus*
Meracantha   *Psorodes*

IV. Spermatheca derived apically from accessory gland
Cnodalonine (CNOD)

Eucyrtus   *Mylaris**
Hemicera   *Taphrosoma**

Coelometopine (COEL)

Graptopezus   *Coelometopine*
subtype   subtype
  Graptopezus   *Amenophis*   *Misolampus*
  Polopinus   *Bradymerus*   *Necrobioides*
  Polypleurus   *Camaria*   *Nuptis*
  Promethis   *Catapiestus*   *Oeatus*
  Tonkinius   *Choastes*   *Oedemutes*
  Xylopinus   *Cibdelis*   *Oenopion*
Iphthiminus   *Coelometopus*   *Pseudebax*
subtype   *Cuphotes*   *Sphaerotus*
  Coelocnemis   *Cyrtosoma*   *Strongylium*
  Iphthiminus   *Derosphaerus*   *Talanus*
Alobates   *Eccoptostoma*   *Temnophthalmus*
subtype   *Encyalesthus*   *Tetraphyllus*
  Alobates   *Euthysternum*   *Upis*
  Setenis   *Haplandrus*   *Zophophilus*
  Taraxides   *Hapsida*
Glyptotous   *Heliofugus*
subtype   *Ilus*
  Glyptotus   *Menephilus*
  Paroeatus   *Merinus*
                        Misolampidius

V. Spermatheca derived basally from accessory gland
Phalerine (PHAL)

Crypticus   *Phaleria*   *Phaleromela*

Hypophloeine (HYPO)
Hypophloeus

Diaperine (DIAP)

Alphitophagus   *Gnatocerus*
Ceropria   *Neomida*
Diaperis   *Nilio*
Doliema   *Palembus*
                                                      Platydema

Centronopus Type (CENT)

Centronopus   *Scotobaenus*

Unclassified (UNCL)

Ectyche   *Nycterinus*
Hegemona   *Paratenetus*
Leichenum   *Pentaphyllus*
Nesogena   *Statira*

APPENDIX III

Classification of tenebrionid ovipositors. The classes are those in Fig. 37 and Table IV. An asterisk denotes that the ovipositor deviates somewhat from its class. Other conventions as in Appendix I.

Lagriine (LAGR)

*Adelonia**   *Menimus**
Cossyphus   *Metallonotus**

Goniadera
Laena*
Lagria
Lobopoda*
Luprops*

Paratenetus
Phymatestes
Rhypasma*
Seirotrana

Bolitophagine (BOLI)

Bolitophagus
Bolitotherus
Eleates

Hypophloeus
Megeleates

Toxicine (TOXI)

Arthrodactyla*
Arthromacra*
Belopus
Calymmus
Cryphaeus
Diceroderes

Dysantes
Nycteropus*
Ozolais
Sora
Statira*
Toxicum
Uleda*

Platydema Type (PLAT)

Alphitophagus
Ceropria
Doliema
Gnatocerus

Neomida
Palembus
Platydema

Diaperis Type (DIAP)
Diaperis

Phaleriine (PHAL)
Crypticus   Phaleria   Phaleromela

Amarygmine (AMAR)

Chalcopteroides*
Eupezus
Meracantha

Platolenes
Plesiophthalmus
Psorodes

Helopine (HELO)

Helops
Lygestira
Nyctozoilus*

Probaticus
Tarpela

Coelometopine (COEL)

Alobates
Amenophis
Bradymerus
Camaria
Choastes
Cibdelis
Coelocnemis
Coelometopus
Cuphotes
Cyrtosoma
Damatris
Derosphaerus
Eccoptostoma
Encyalesthus
Euthysternum

Glyptotus
Graptopezus
Haplandrus
Heliofugus
Ilus
Iphthiminus
Merinus
Misolampidius
Misolampus
Mylaris
Necrobioides
Nuptis
Oeatus
Oedemutes
Oenopion

Paraoeatus
Polopinus
Polypleurus
Promethis
Pseudobax
Setenis
Sphaerotus
Strongylium
Taraxides
Temnophthalmus
Tonkinius
Upis
Xylopinus

Talanine (TALA)
Talanus

Cnodalonine (CNOD)

Eucyrtus
Hapsida

Hemicera
Taphrosoma

Menephilus Type (MENE)

Catapiestus   *Zophophilus*
Menephilus

Adeliine (ADEL)

Adelium   *Otrintus*
Cardiothorax

Pycnocerine (PYCN)

Chiroscelis   *Prioscelis*

Anaedus Type (ANAE)

Aemymone   *Catamerus*
Anaedus   *Derolagria*

Tenebrionine (TENE)

Tenebrio subtype   *Cerenopus* subtype   *Meneristes* subtype
  Alphitobius   *Apsena*   *Meneristes*
  *Bius**   *Argoporis*
  Ectyche   *Cerenopus*
  *Eurynotus**   *Epantius*
  Idiobates
  Metaclisa   *Uloma* subtype
  Neatus   *Eutochia*
  *Nycterinus**   *Uloma*
  Rhinandrus
  Tenebrio   *Asphalus* subtype
  Titaena   *Antimachus*
  Tribolium   *Asphalus*
  *Ulosonia**   *Mimopeus*
  *Xystropus**   *Pterohelaeus*
  Zophobas   *Scotobius*

Opatrine (OPAT)

Blapstinus   *Pedinus*
Heterotarsus   *Pseudoblaps**
*Opatrinus**   *Scaurus**
Opatrum   *Ulus*

Eleodine (ELEO)

Eleodes (incl. *Amphidora, Cratidus*)   *Trichoderulus*
Lariversius   *Trogloderus*
Neobaphion

Centronopus Type (CENT)

Centronopus   *Scotobaenus*

Lepispilus Type (LEPI)

Lepispilus   *Achrostus*

Unclassified or of uncertain affinity (UNCL)

Anemia   *Nesogena*
Apocrypha   *Nilio*
Blaps   *Pentaphyllus*
Clamoris (= *Phthora*)   *Phrenapates*
Delognatha   *Praogena*
Hegemona   *Rhipidandrus*
Leichenum   *Tauroceras*
Micrantereus   *Zolodinus*

APPENDIX IV

Alphabetical listing of species investigated and the classification of their defensive gland, female tube and ovipositor. Abbreviations are the same as in Appendices I–III. Asterisks indicate that the structure deviates from its class. The present taxonomic position is that listed by Gebien (1938–1944).

	Gland	♀tube	Ovipos.	Present tribe
Achrostus amariformis Fairm.	UNCL	TENE	LEPI	Tenebrionini
Adelonia sulcatulus Champ.	none	LAGR	LAGR*	Tenebrionini
Adelium auratrum Pasc.	ADEL	ADEL	ADEL	Adeliini
Adelium plicigerum Pasc.	ADEL	ADEL	ADEL	Adeliini
Adelium sp.	ADEL	ADEL	ADEL	Adeliini
Aemymone cariosa Fairm.	none	——	ANAE	Heterotarsini
Alobates morio Fab.	COEL	COEL	COEL	Tenebrionini
Alobates pennsylvanica DeG.	COEL	COEL	COEL	Tenebrionini
Alphitophagus bifasciatus Say	PLAT	DIAP	PLAT	Diaperini
Alphitobius diaperinus Panz.	TENE	ALPH	TENE	Ulomini
Amarygmus metallicus Perty	AMAR	——	——	Amarygmini
Amenophis elongata Thom.	COEL	COEL	COEL	Tenebrionini
Amenophis iphthimoides Qued.	COEL	COEL	COEL	Tenebrionini
Anaedus punctatissimus Blanch.	none	ANAE	ANAE	Heterotarsini
Anemia sardoa Géné	——	——	UNCL	Opatrini
Antimachus sp.	CATA*	TENE	TENE*	Ulomini
Apocrypha anthicoides Esch.	UNCL	——	UNCL	Apocryphini
Apsena pubescens LeC.	TENE	TENE*	TENE*	Scaurini
Apsena rufipes Esch.	TENE	TENE	TENE*	Scaurini
Argoporis alutacea Csy.	TENE*	TENE	TENE*	Scaurini
Arthrodactyla elongatea Klug	CNOD	TOXI*	TOXI*	Tenebrionini
Arthrodactyla intermedia Fairm.	CNOD	TOXI*	TOXI*	Tenebrionini
Arthromacra aenea Say	UNCL	TOXI*	TOXI*	Lagriini
Asphalus ebeninus Pasc.	CATA	TENE	TENE*	Coelometopini
Belopus elongatus Herbst	none	TOXI*	TOXI	Tenebrionini
Bius estriatus LeC.	UNCL	TENE	TENE	Tenebrionini
Blaps rugosa Gebl.	BLAP	BLAP	UNCL	Blaptini
Blapstinus longicollis Champ.	OPAT	TENE	OPAT	Pedinini
Blapstinus sulcatus LeC.	OPAT	TENE	OPAT	Pedinini
Bolitophagus corticola Say	BOLI	TENE	BOLI	Bolitophagini
Bolitophagus reticulatus Linn.	BOLI	——	——	Bolitophagini
Bolitotherus cornutus Panz.	BOLI	TENE	BOLI	Bolitophagini
Bradymerus amicorum Fairm.	COEL	COEL	COEL	Bolitophagini
Calymmus cucullatus Pasc.	TOXI	TOXI	TOXI	Dysantini
Camaria nr. *plicifrons* Geb.	CNOD*	COEL	COEL	Cnodalonini
Cardiothorax caperatus Pasc.	ADEL	ADEL	ADEL	Adeliini
Catamerus revoili Fairm.	PYCN	——	ANAE	Pycnocerini
Catapiestus tonkineus Pic	CATA	COEL	MENE	Tenebrionini
Centronopus calcaratus Fab.	CENT	CENT	CENT	Coelometopini
Centronopus supressus Say	CENT	CENT	CENT	Coelometopini
Cerenopus concolor Lec.	TENE*	TENE	TENE*	Scaurini
Ceropria induta Wied.	PLAT	DIAP	PLAT	Diaperini
Ceropria laticollis Fairm.	PLAT	DIAP	PLAT	Diaperini
Chalcopteroides laevicollis Bless.	AMAR	AMAR*	AMAR*	Amarygmini
Chiroscelis digitata Fab.	PYCN	——	PYCN	Pycnocerini
Choastes purpurea Champ.	COEL	COEL	COEL	Tenebrionini
Cibdelis blaschkei Mann.	COEL	COEL	COEL	Coelometopini
Clamoris (= *Phthora*) *americana* Horn	none	LAGR	†	Phrenapatini
Coelocnemis magna LeC.	COEL	COEL	COEL	Coelometopini
Coelometopus clypeatus Germ.	COEL	COEL	COEL	Coelometopini
Cossyphus laevis Lap.	none	ADEL	LAGR	Cossyphini
Cryphaeus cornutus Fisch.	TOXI	TOXI	TOXI	Tenebrionini
Cryphaeus elongatus Schaufuss	TOXI	TOXI	TOXI	Tenebrionini
Crypticus dactylispinus Mars.	TENE	PHAL	PHAL	Crypticini
Crypticus obsoletus Say	TENE	PHAL	PHAL	Crypticini

Cuphotes unicolor Champ.	CATA	COEL	COEL	Strongyliini
Cyrtosoma denticolle Chev.	COEL	COEL	COEL	Cnodalonini
Damatris acidiferus Coq.	COEL	ADEL	COEL	Cnodalonini
Damatris formosus Lap. & Brll.	COEL	ADEL	COEL	Cnodalonini
Damatris vadoni Ardoin	COEL	ADEL	COEL	Cnodalonini
Delognatha puncticollis Bates	———	———	†	Phrenapatini
Derolagria sp.	LAGR	LAGR	ANAE	(Lagriidae)
Derosphaerus globicollis Thom.	COEL	COEL	COEL	Tenebrionini
Derosphaerus morosus Motsch.	COEL	COEL	COEL	Tenebrionini
Diaperis boleti Linn.	DIAP	DIAP	DIAP	Diaperini
Diaperis maculata Oliv.	DIAP	DIAP	DIAP	Diaperini
Diaperis rufipes Horn.	DIAP	———	———	Diaperini
Diceroderes mexicanus Sol.	TOXI	TOXI	TOXI	Eutelini
Dicraeosis carinatus Geb.	COEL	———	———	Bolitophagini
Doliema bifurcata Champ.	PLAT	DIAP	PLAT	Ulomini
Doliema pallida Say	PLAT	DIAP	PLAT	Ulomini
Doliema plana Oliv.	PLAT	DIAP	PLAT	Ulomini
Dysantes biluna Walk.	TOXI	TOXI	TOXI	Dysantini
Eccoptostoma robusta Geb.	COEL	COEL	COEL	Tenebrionini
Ectyche sp.	UNCL	UNCL	TENE*	Amphidorini
Eleates occidentalis Csy.	BOLI	TENE	BOLI	Bolitophagini
Eleodes arcuata Csy.	ELEO	ELEO	ELEO	Eleodini
Eleodes beameri Blais.	ELEO	ELEO	ELEO	Eleodini
Eleodes clavicornis Esch.	ELEO	ELEO	ELEO	Eleodini
Eleodes extricata Say	ELEO	ELEO	ELEO	Eleodini
Eleodes goryi Sol.	ELEO	ELEO	ELEO	Eleodini
Eleodes (= *Amphidora*) *littoralis* Esch.	ELEO	ELEO	ELEO	Eleodini
Eleodes longicollis LeC.	ELEO	ELEO	ELEO	Eleodini
Eleodes (= *Amphidora*) *nigropilosa* LeC.	ELEO	ELEO	ELEO	Eleodini
Eleodes (= *Cratidus*) *osculans* LeC.	ELEO	ELEO	ELEO	Eleodini
Eleodes subnitens LeC.	ELEO	ELEO	ELEO	Eleodini
Eleodes tricostata Say	ELEO	ELEO	ELEO	Eleodini
Encyalesthus miseticolor Pic	COEL	COEL	COEL	Tenebrionini
Encyalesthus nitidipennis Fairm.	COEL	COEL	COEL	Tenebrionini
Epantius obscurus LeC.	TENE	TENE	TENE*	Scaurini
Eucyrtus laosensis Pic	CNOD	CNOD	CNOD	Cnodalonini
Eucyrtus sp.	CNOD	CNOD	CNOD	Cnodalonini
Eupezus longipennis Gerst.	AMAR	AMAR	AMAR	Amarygmini
Eurynotus capensis Fab.	OPAT	TENE*	TENE*	Opatrini
Euthysternum attenuatum Fairm.	COEL	COEL	COEL	Cnodalonini
Eutochia pulla Erich.	ULOM	TENE	TENE*	Ulomini
Glyptotus cribratus LeC.	COEL	COEL	COEL	Tenebrionini
Gnatocerus cornutus Fab.	PLAT	DIAP	PLAT	Ulomini
Goniadera nicaraguensis Champ.	none	LAGR	LAGR	Goniaderini
Graptopezus crenaticollis Macl.	COEL	COEL	COEL	Tenebrionini
Haplandrus fulvipes Hbst.	COEL	COEL	COEL	Tenebrionini
Hapsida chrysomelina Lacord.	CNOD	———	CNOD	Diaperini
Hapsida purpureomicans Bates .	CNOD	COEL	CNOD	Diaperini
Hegemona filibuster Thom.	UNCL	UNCL	UNCL	Helopini
Heliofugus impressus Guer.	COEL	COEL	COEL	Misolampini
Helops arizonensis Horn	HELO	———	———	Helopini
Helops discretus LeC.	HELO	TENE	HELO	Helopini
Helops simulator Blais.	HELO	TENE	HELO	Helopini
Hemicera curta Pic	CNOD	CNOD	CNOD	Cnodalonini
Heterotarsus inflatus Lacord.	OPAT	TENE*	OPAT	Heterotarsini
Hypaulax ovalis Bates	COEL	———	———	Coelometopini
Hypophloeus rufipes Fab.	ULOM	HYPO	BOLI	Hypophloeini
Hypophloeus unicolor Pill. & Mitt.	ULOM	HYPO	BOLI	Hypophloeini
Idiobates castaneus Knoch	TENE	TENE	TENE	Tenebrionini
Ilus apicicornis Champ.	COEL	COEL	COEL	Tenebrionini
Iphthiminus bellardi Truqui	COEL	COEL	COEL	Tenebrionini
Iphthiminus croaticus Truqui	COEL	COEL	COEL	Tenebrionini
Iphthiminus italicus Truqui	COEL	COEL	COEL	Tenebrionini
Iphthiminus serratus Mann.	COEL	COEL	COEL	Tenebrionini

Laena reitteri Weise	none	————	LAGR*	Adeliini
Lagria grandis Gyll.	LAGR	LAGR	LAGR	(Lagriidae)
Lagria chinensis Fairm.	LAGR	LAGR	LAGR	(Lagriidae)
Lariversius tibialis Blais.	ELEO	ELEO	ELEO	Eleodini
Leichenum variegatum Küster	TENE	UNCL	UNCL	Opatrini
Lepispilus sulcicollis Boisd.	TENE*	TENE	LEPI	Cyphaleini
Liodema kirschi Bates	PLAT	————	— ——	Diaperini
Lobopoda hirta Champ.	UNCL	LAGR*	LAGR*	(Alleculidae)
Luprops shanghaicus Mars.	LAGR*	LAGR	LAGR*	Heterotarsini
Lygestira simplex Westw.	HELO	TENE	HELO	Cyphaleini
Macellocerus acuminatus Klug	UNCL	——— ..	———	Tenebrionini
Megeleates sequoiorum Csy.	BOLI	TENE	BOLI	Bolitophagini
Menephilus lucens Marseul	COEL	COEL	MENE	Tenebrionini
Meneristes laticollis Pasc.	TENE	TENE	TENE*	Tenebrionini
Menimus rugicollis Geb.	UNCL	LAGR	LAGR*	Gnathidiini
Meracantha contracta Beauv.	AMAR	AMAR	AMAR	Amarygmini
Merinus laevis Oliv.	COEL	COEL	COEL	Tenebrionini
Metaclisa marginalis Horn	UNCL	TENE	TENE*	Cnodalonini
Metallonotus metallicus Fab.	PYCN	META	LAGR*	Pycnocerini
Micrantereus seriegranosus Fairm.	UNCL	—— —	UNCL	Helopini
Mimopeus sp. (=Cilibe)	CATA	TENE	TENE*	Nyctozoilini
Misolampidius clavicrus Mars.	COEL	COEL	COEL	Misolampini
Misolampus lusitannicus Breme	COEL	COEL	COEL	Mislolampini
Mylaris gigas Linn.	COEL*	CNOD*	CNOD*	Tenebrionini
Nautes viridimicans Horn	HELO	———	— ——	Helopini
Neatus tenebrioides Beauv.	TENE	ALPH	TENE	Tenebrionini
Necrobioides bicolor Fairm.	COEL	COEL	COEL	Tenebrionini
Neobaphion planipennis LeC.	ELEO	ELEO	ELEO	Eleodini
Neomida bicornis Fab.	PLAT	DIAP	PLAT	Diaperini
Nesogena viridicuprea Fairm.	OPAT	UNCL	UNCL	Strongyliini
Nilio villosus Fab.	DIAP*	DIAP*	UNCL	(Nilionidae)
Nuptis caliginosus Champ.	COEL	COEL	COEL	Tenebrionini
Nycterinus genei Sol.	TENE	UNCL	TENE*	Eleodini
Nycterinus rugiceps Curt.	TENE	UNCL	TENE*	Eleodini
Nycteropus anthracinus Klug	TOXI	———	———	Tenebrionini
Nycteropus ebeninus Klug	TOXI	TENE	TOXI*	Tenebrionini
Nyctozoilus reticulatus Bates	HELO*	TENE*	HELO*	Nyctozoilini
Oeatus chevrolati Champ.	COEL	COEL	COEL	Tenebrionini
Oedemutes varicolor Geb.	COEL	COEL	COEL	Cnodalonini
Oenopion zopheroides Horn	COEL	COEL	COEL	Coelometopini
Opatrinus aciculatus LeC.	OPAT	TENE	OPAT*	Pedinini
Opatrinus minimus Beauv.	OPAT	TENE	OPAT*	Pedinini
Opatrum sabulosum Linn.	OPAT	TENE	OPAT	Opatrini
Otrintus behri Germ.	ADEL	ADEL	ADEL	Adeliini
Ozolais gibbipennis Geb.	TOXI	TOXI	TOXI	Dysantini
Palembus ocularis Csy.	PLAT	DIAP	PLAT	Diaperini
Paratenetus punctatus Spinola	none	UNCL	LAGR	Heterotarsini
Paroeatus opacus Geb.	COEL	COEL	COEL	Tenebrionini
Pedinus strabonis Seidlitz	TENE	TENE	OPAT*	Pedinini
Pedinus sp.	TENE	TENE	OPAT*	Pedinini
Pentaphyllus californicus Horn	UNCL	UNCL	UNCL	Diaperini
Phaleria longula LeC.	PHAL	PHAL	PHAL	Phaleriini
Phaleria punctipes LeC.	PHAL	PHAL	PHAL	Phaleriini
Phaleromela globosa LeC.	PHAL	PHAL	PHAL	Phaleriini
Phaleromela picta Mannh.	PHAL	PHAL	PHAL	Phaleriini
Phrenapates bennetti Kby.	none	LAGR	†	Phrenapatini
Phymatestes exsculptus Perty	none	ANAE	LAGR	Goniaderini
Platolenes nr. *angustus* Geb.	AMAR	AMAR	AMAR	Amarygmini
Platycrepis violaceus Kraatz	CNOD	———	———	Cnodalonini
Platydema americanum Lap & Brll.	PLAT	DIAP	PLAT	Diaperini
Platydema ellipticum Fab.	PLAT	DIAP*	PLAT	Diaperini
Platydema oregonense LeC.	PLAT	DIAP	PLAT	Diaperini
Platydema subcostatum Lap. & Brll.	PLAT	DIAP	PLAT	Diaperini
Plesiophthalmus nigrocyaneus Motsch.	AMAR	AMAR	AMAR	Amarygmini

Species				
Plesiophthalmus sp.	AMAR	AMAR	AMAR	Amarygmini
Polopinus nitidus LeC.	COEL	COEL	COEL	Coelometopini
Polypleurus geminatus Sol.	COEL	COEL	COEL	Coelometopini
Praogena nigritarsus Mäkl.	UNCL	ADEL*	UNCL	Strongyliini
Prioscelis serrata Fab.	PYCN	ADEL	PYCN	Pycnocerini
Probaticus anthracinus turdus Germ.	HELO	TENE	HELO	Helopini
Promethis nigra Bless.	COEL	COEL	COEL	Tenebrionini
Pseudabax chalceus Geb.	COEL	COEL	COEL	Cnodalonini
Pseudoblaps javana Wied.	OPAT	TENE*	OPAT*	Opatrini
Psorodes calcaratus Fab.	AMAR	AMAR	AMAR	Meracanthini
Pterohelaeus parallelus Breme	CATA	TENE	TENE*	Helaeini
Rhinandrus elongatus Horn	TENE	TENE	TENE	Coelometopini
Rhipidandrus peninsularis Horn	UNCL	TENE	†	Rhipidandrini
Rhypasma costaricensis Marcuzzi	none	LAGR*	LAGR*	Stenosini
Scaurus sp.	UNCL	TENE	OPAT*	Scaurini
Scotobaenus parallelus LeC.	CENT	CENT	CENT	Coelometopini
Scotobius gayi Sol.	TENE	TENE	TENE*	Scotobiini
Seirotrana parallela Germ.	ADEL	ADEL	LAGR	Adeliini
Setenis foveicollis Fairm.	COEL	COEL	COEL	Tenebrionini
Setenis semisulcata Fairm.	COEL	COEL	COEL	Tenebrionini
Setenis sulcigera Boisd.	COEL	COEL	COEL	Tenebrionini
Sora rostrifera Fairm.	LAGR*	ADEL	TOXI	(Lagriidae)
Sphaerotus diversus Pic	COEL	COEL	COEL	Misolampini
Statira subnitida LeC.	UNCL	UNCL	TOXI*	(Lagriidae)
Strongylium atrum Champ.	CATA	COEL	COEL	Strongyliini
Strongylium haemorrhoidale Fab.	CATA	COEL	COEL	Strongyliini
Strongylium maculicolle Champ.	CATA	COEL	COEL	Strongyliini
Strongylium tenuicolle Say	CATA	COEL	COEL	Strongyliini
Strongylium sp.	CATA	COEL	COEL	Strongyliini
Sympetes sp.	TENE*	———	———	Helaeini
Talanus longicornis Champ.	———	———	TALA	Talanini
Talanus subexeratus Mäkl.	———	———	TALA	Talanini
Talanus stenochinus LeC.	CNOD*	COEL	TALA	Talanini
Tanylypa sp.	none	TENE	UNCL	Tenebrionini
Taphrosoma doorknob Kirsch.	COEL*	CNOD*	CNOD	Tenebrionini
Taraxides punctatus Fab.	COEL	COEL	COEL	Tenebrionini
Taraxides laevigatus Fab.	COEL	COEL	COEL	Tenebrionini
Tarpela micans Fab.	HELO	TENE	HELO	Helopini
Tauroceras angulatum Pic.	UNCL	TENE	UNCL	Tenebrionini
Tetraphyllus latreillei Lap. & Brll.	COEL	COEL	———	Cnodalonini
Temnophthalmus scalaris Geb.	COEL	COEL	COEL	Tenebrionini
Tenebrio guineensis Imhoff	TENE	ALPH	TENE	Tenebrionini
Tenebrio molitor Linn.	TENE	TENE	TENE	Tenebrionini
Tenebrio obscurus Fab.	TENE	TENE	TENE	Tenebrionini
Titaena sp.	UNCL	TENE*	TENE*	Cnodalonini
Tonkinius sculptilus Fairm.	COEL	COEL	COEL	Tenebrionini
Toxicum quadricorne Fab.	TOXI	TOXI	TOXI	Tenebrionini
Tribolium confusum Duv.	ULOM	TENE	TENE	Ulomini
Trichoderulus longipilosus Blais	ELEO*	ELEO	ELEO	Eleodini
Trogloderus costatus LeC.	ELEO	ELEO	ELEO	Eleodini
Uleda diaperoides Lap.	ULOM*	TENE	TOXI*	Ulomini
Uloma imberbis LeC.	ULOM	TENE	TENE*	Ulomini
Uloma punctulata LeC.	ULOM	TENE	TENE*	Ulomini
Ulosonia biimpressa Latr.	UNCL	LAGR	TENE*	Ulomini
Ulus crassus LeC.	OPAT	TENE	OPAT	Pedinini
Upis ceramboides Linn.	COEL	COEL	COEL	Tenebrionini
Xylopinus saperdioides Oliv.	COEL	COEL	COEL	Tenebrionini
Xystropus californicus Horn	TENE	TENE	TENE*	(Alleculidae)
Zolodinus zelandicus Blanch.	none	TENE*	UNCL	Tenebrionini
Zophobas morio Fab.	TENE	TENE	TENE	Tenebrionini
Zophobas rugipes Kirsch	TENE	TENE	TENE	Tenebrionini
Zophobas subnitens Horn	TENE	TENE	TENE	Tenebrionini
Zophophilus podager Geb.	COEL	COEL	MENE	Tenebrionini

†Unsclerotized ovipositor.