Phenetic and cladistic relationships among tenebrionid beetles (*Coleoptera*)

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ABSTRACT. The higher classification of Tenebrionidae is analysed using numerical phenetic, numerical cladistic and traditional Hennigian methods. In all, eighty characters are examined for about 335 taxa; definitive analyses are made on combinations of eighteen to seventy characters for thirty-three OTUs. At lower levels of relationship (genera and closely related tribes) phenetic and cladistic classifications are shown to be congruent, but at higher levels (tribes and subfamilies) there is marked discordance with phenetic results being more stable. A consensus classification is more similar to the Hennigian cladogram than is any single computer generated cladogram. Two main tribal groups — the Lagrioid and Tenebrionoid groups — are suggested which differ in defensive glands, female anatomy, wing and mouthpart morphology, larval characters and other features. The Tenebrionoid group consists of three main subdivisions — the tenebrionine, coelometopine and diaperine lineages. Changes in classificatory position are recommended for eighty-seven genera and tribes (listed in Appendix E) and implied for numerous others.

Introduction

After practically a century of inattention from taxonomists, the higher classification of Tenebrionidae and related families has recently been subjected to close scrutiny, and major changes in composition and position of tenebrionid taxa have been suggested. Early attempts to classify these beetles are discussed in some depth by Watt (1967, 1974a) and Doyen & Lawrence (1979), and will be considered here only in regard to specific taxa or taxonomic changes.

Recent analyses of tenebrionid higher classification have incorporated previously unstudied characters. Thus, Doyen (1972) pointed out the importance of the abdominal defensive glands and several highly correlated features. Watt (1974a) revealed the significance of a number of unstudied characters

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of both adults and larvae. His classification is based in large part upon characters of the larvae. For example, similarities between adults of *Diaperis* and other members of Diaperini (*sensu* Gebien, 1938–44) are rejected as convergent, and larval similarities between *Diaperis* and Boletophagini are used as a basis for Watt's Diaperinae. Previously unstudied characters were also surveyed by Fiori (1977), who compared the details of the subelytral cavity and elytral interlocking mechanism in eight tribes of Tenebrionidae. Fiori's results, based on a single structure which serves multiple functions of defence, moisture retention (Cloudsley-Thompson, 1964) and possibly heat balance (Ahearn & Hadley, 1969; Hadley, 1970), are difficult to interpret. The structures involved are simple and, in our view, subject to extensive convergence. In any case, classifications based on a single complex of characters are almost never entirely correct, especially in a taxon as

large and diversified as Tenebrionidae. Medvedev (1977) surveyed the microstructure of the antennal sensoriae over most families of Heteromera, including Alleculidae, Lagriidae and eighty species of Tenebrionidae in forty-eight tribes. As suggested by his choice of family level names, Medvedev believed that his data supported the traditional classification of Tenebrionoidea into three families. This conclusion disagrees with those of several recent studies (Skopin, 1964; Doyen, 1972; Watt, 1974a; Doyen & Lawrence, 1979; Tschinkel & Doyen, 1980), and Medvedev's data are reanalysed and used to supplement our own observations below.

In the present study we analyse the cladistic and phenetic relationships among Tenebrionidae, including Lagriinae and Alleculinae (*sensu* Watt, 1974a). Characters of both adults and larvae are considered, but the former greatly outnumber the latter, and the overall results derive mainly from patterns of variation in adults. This bias is unavoidable, since relatively few tenebrionid larvae have been associated with the mature forms and characterized in terms of the important taxonomic structures. Additionally, larvae are relatively simple in structure, compared to the adult beetles, and present relatively few features that can be used by the taxonomist. Watt (1974a: 382) viewed simplicity and uniformity in structure as an advantage for analysis of relationship, believing that larval classifications of these insects are, on the whole, more satisfactory than those based on adults. However, simplicity of structure makes convergence or parallel evolution more difficult to detect. For example, enlarged anterior legs occur in cladistically diverse larvae which inhabit soil (e.g. the 'Pedobionta' of Skopin, 1964). Similarly, larvae which tunnel through rotting wood usually possess strong, recurved urogomphi, regardless of cladistic derivation. In general we feel that adult characters are more robust indicators of relationship than those of the larvae. Important exceptions include taxa in which the highly modified adults show only unique apomorphies (e.g. Cossyphodinae) or have retained mostly plesiomorphous features (e.g. Toxicini). Specific disagreements between our results and those based primarily on larvae are detailed and discussed where appropriate below.

Many of the characters used in the following analyses are based on similarities and differences in internal structures. Internal organ systems are scarcely utilized in studies of tenebrionid higher classification (as well as that of most families of Coleoptera), although our results indicate that internal structures offer many important characters. Two of these internal organ systems have been the subject of extensive comparative studies: (1) abdominal defensive glands (Kendall, 1968, 1974; Tschinkel, 1975a, b; Tschinkel & Doyen, 1980) and (2) internal female reproductive tract (Tschinkel & Doyen, 1980). The last study also detailed variation in ovipositor structure. We believe that similarities and differences in these organ systems, especially in the structure of the female reproductive tract, have great taxonomic value. Accordingly, the results of the studies cited above are outlined below. Other neglected features which appear to have substantial taxonomic value include internal skeletal anatomy (particularly the metendosternite and the tentorium), structure of the labrum-epipharynx, and wing configuration and venation. Variation in these traits is discussed in some detail. Finally, many characters traditionally held to be taxonomically important, including most of those introduced by Watt and Medvedev, were included in our analyses, with the aim of verifying their classificatory importance.

Our concept of Tenebrionidae coincides with that of Watt (1974a), including Alleculidae, Lagriidae and Nilionidae, as well as highly modified forms such as *Cossyphus* and *Cossyphodes,* and excluding Zopheridae, which are probably more closely related to Colydiidae (Doyen & Lawrence, 1979). The limits of Tenebrionidae are discussed in more detail by Doyen & Lawrence (1979) and Watt (1974a), who provides the best morphological definition of the family.

Philosophical basis of classification

The recent history of systematics has been characterized by two divergent methods of specifying relationships and of defining taxonomic groups. On the one hand, the phenetic approach to classification, developed primarily in North America, recognizes overall similarity as the primary or only measure of

defining taxa, holding that patterns of evolutionary diversification are unknowable, except under extraordinary circumstances (e.g. continuous fossil record, etc.). For nearly all real situations, according to pheneticists, the most stable classifications would result from estimates of overall similarity. Operationally defined methods of measuring similarity and for translating similarity relationships into classifications form the bulk of 'phenetic' literature, most of which was contributed by mathematicians or mathematical biologists. In retrospect it appears that few practising taxonomists have wholeheartedly embraced phenetics, in part because the original claims of operationalism and stability proved to be greatly overstated. As shown by numerous studies, changes in combinations of similarity coefficients, clustering algorithms and character sets, produce different (sometimes drastically so) phenetic results. In addition, the cladistic approach to classification has risen in popularity, partly at the expense of the phenetic school.

The cladistic school of classification arose in Europe and has become widely appreciated by North American taxonomists only during the last 15 years. Rather than using overall similarity to estimate relationship and derive classifications, cladistics attempts to define taxonomic groups by estimating evolutionary branching sequences. As in the case of phenetics, operationally defined methods have been propounded for deriving branching sequences from phenetic data, and several numerical cladistic methods have been proposed. In all of these methods character states must be designated primitive (plesiomorphous) or derived (apomorphous). As character states evolve from primitive to derived, distinctive combinations of characteristics are produced in different lineages. These character state combinations are analysed by cladistic methods to reconstruct the branching patterns. Obviously the initial selection of characters and their polarity has overwhelming influence on the resulting analysis. Aside from its profoundly different way of treating phenetic data, the cladistic school has also addressed the problem of translating results of cladistic analysis into classifications. Most proponents of cladism hold that the most stable classifications, and those with the highest information content, recognize only monophyletic (= holophyletic, *sensu* Ashlock, 1971, 1974) taxa. Several workers (Michener, 1977; Brothers, 1975) have combined phenetic and cladistic approaches, with resulting classifications that are not purely monophyletic. The resulting debate (Nelson, 1978, 1979; Michener, 1978; Brothers, 1978; McGinley & Michener, 1980), sometimes acrimonious, indicates the profoundly different views among the taxonomic community regarding translation of relationships into classifications.

As pointed out by Ashlock (1979), Hull (1979) and Duncan (1980a), insistence on strictly monophyletic classifications introduces problems into general purpose classifications. For example, the naming of numerous sister groups renders many classifications incomprehensible to non-specialists. The insect classification proposed by Boudreaux (1979) is an example in point (see also review by Kristensen, 1979). Stability is perhaps the most important aspect of classification for general biologists, and little evidence exists that cladistic classifications are more stable than phenetic or intuitively derived ones. In fact, we present evidence later that cladistic results, at least when based on numerical analyses, suffer from the same or greater degree of instability as numerical phenetic results.

Probably most taxonomists find it more satisfying to base their classifications primarily on evolutionary branching sequences, regardless of considerations such as stability. However, when phenetic differentiation is pronounced, many workers will probably choose to recognize paraphyletic taxa, as urged by Ashlock (1974, 1979) and Duncan (1980a). Certainly this practice would seem to favour increased stability, since phenetically divergent groups will usually retain their phenetic distinctiveness, regardless of cladistic changes caused by reinterpretation of homology, revised judgements of character polarity, or analysis of new suites of characters. This eclectic approach is the one we have adopted in the analysis and discussion which follow. While we have attempted to discover the cladistic relationships among tenebrionid beetles, in many instances no unique or even strongly preferable result has been obtained,

and several alternative cladograms are presented. We have estimated degree of divergence (or convergence) using numerical phenetic methods, and our suggestions in regard to changes in classification result partly from phenetic considerations.

Materials and Methods

Selection of OTUs

Initially this study was intended to investigate the higher classification of the tribe Tenebrionini (*sensu* Gebien, 1938–44). Consequently members of this group are strongly represented in subsequent analyses. As morphological comparisons were made, it became evident that many of the traditionally recognized subfamilies and tribes were not monophyletic, and the scope was increased to encompass the entire part of the family with defensive glands. When it became apparent from both their presence and absence in Lagriinae that defensive glands had probably evolved more than once, we decided to include the glandless Tentyriinae as well, but only as a few exemplars, since Tentyriinae number about 8000 species, or about half of the entire family.

Of necessity, taxonomic representation, even among those taxa with defensive glands, is variable (Appendix A). We attempted to include members of every tribe or subfamily recognized in recent catalogues or analyses of higher classification, but have been unable to dissect some uncommon taxa, such as Cossyphodinae. Whenever possible a member of the type genus of each tribe was examined. The number of genera studied depends on the size and diversity of the respective tribes. For tribes or subfamilies which are highly canalized, with variation mostly in structural detail, relatively few genera were examined. Examples include Alleculinae, Amarygmini, Helopini and Strongyliini. In contrast, higher taxa which showed significant structural variation (e.g. Lagriinae, Diaperini and Tenebrionini), or which revealed important deviations from patterns of variation common to most Tenebrionidae (e.g. Phrenapatini, Goniaderini and Adeliini), are represented by more genera. Several species each were examined in the genera *Tenebrio*, *Damatris* and *Platydema*

to ensure that variation at this level was only in structural detail, not in major patterns of variation.

The total number of species we examined is approximately 335 but lack of one sex, missing structures in damaged specimens or limited availability of rare taxa reduced the number included in numerical analyses (Appendix A). Most of the additional taxa are listed in Tschinkel & Doyen (1980), where categorization according to defensive gland, ovipositor and female reproductive tract structure is given. Since the total number of species greatly exceeded computer limitations, preliminary grouping into clusters of closely related OTUs was necessary. These clusters, mostly corresponding to tribal units or groups of tribes in the Gebien classification, are shown in Appendix B. The constitution of these composite OTUs is listed in Appendix D and discussed under computational procedures.

Selection and coding of characters

Characters selected for final analysis and the states of each character are described in Appendix C. Character states were coded in graded linear series when possible, so that the most divergent states were at opposite extremes. Features for which the pattern of divergence was too complex to arrange in a graded series were coded as several characters in an additive binary manner (Sokal & Sneath, 1963; Farris *et al.*, 1970). Additive binary coding throughout would have made interpretation of the results simpler, but would have required deletion of many characters, since the original data set contained 249 states (available cladistic programs accepted only seventy binary characters). Primitiveness or derivedness were judged primarily by character state distribution among Tenebrionidae and, when possible, by 'out group' comparison with closely related families of beetles. Thus, character states occurring commonly in Tenebrionoidea were normally judged primitive. However, distribution of states of some characters is variable within several families or poorly known outside Tenebrionidae. This is particularly true of the characters of the female reproductive tract and mouthparts. Since it was impossible for us to survey such features widely throughout the Heteromera, our judgements are based

in these cases almost entirely on character state distributions within Tenebrionidae. The resulting character state trees can be inferred from Appendix C.

All numerical analyses were based on un-weighted characters, but in effect weighting was achieved by successively eliminating low value characters, as described below. In the intuitive analyses the character weights indicated in Appendix C were used in assessing the importance of character state reversals in each cladogram. The weighting scale is similar to that suggested by Hecht & Edwards (1976), with weights ranging from 0 to 4. A weight of 0 would be assigned to characters which have been lost or reduced independently several times. The clearest example involves wings, which apparently have been lost hundreds of times in Tenebrionidae.

Computational procedures

Relationships among taxa were explored through numerical phenetic and cladistic approaches. Preliminary consolidation was done by lumping species which shared nearly all character states (e.g. species within one genus or closely related genera). Initial clustering into units approximately equivalent to the tribe was done by analysing the maximum number of taxa acceptable to phenetic (135) or cladistic (70) programs. Most genera clearly fell into clusters of closely related taxa. These clusters were enlarged by adding closely similar taxa, and exemplar character state values were assigned to each cluster. Many characters were invariant within clusters. Where important character variation occurred taxa representing each state were included for characters given high weight. For example, four OTUs were chosen to represent the variation in ovipositor, female reproductive tract and defensive gland characters in the coelometopine lineage. For characters in which losses or reversal appeared to be common, the state judged to be primitive to each cluster was assigned. For example, wingedness and its associated characters are primitive to all lineages, although winglessness predominates in some. Some genera did not clearly belong to any cluster in the initial analyses (e.g. *Meneristes, Menephilus, Rhy-*

pasma, etc.), and were entered as separate OTUs. In this manner thirty-three OTUs were selected for analysis and assigned character state values (Appendix B). Most of the OTUs correspond to presently recognized tribes or groups of tribes, whose names appear in Appendices B and D and Figs. 49–62. One additional OTU, designated PLES and represented by the hypothetical primitive state for every character, was included to establish polarity and to root the cladograms. The larger clusters were analysed separately, as discussed below.

Phenetic similarity was assessed by using the taxonomic distance coefficient (Sneath & Sokal, 1973). Clustering was by the unweighted pair group method using arithmetic averages (UPGMA). Prim networks were constructed from the same similarity matrices, and the networks converted into evolutionary trees by rooting them at PLES. For convenience of comparison with cladograms, OTUs at nodes were placed on stems whose length is considered zero. An analogous operation is done in numerical cladistic analysis so that extant taxa are not ancestral to one another.

Cladistic relationships were assessed intuitively and with the Wagner tree method of Farris (1970, 1973). In Farris' program, WAGNER, the length of each segment or stem is determined by the number of character state changes along it. The branching pattern is determined by minimizing the total number of character state changes over the entire tree. The trees shown here were all rooted by including the hypothetical OTU, PLES, with all primitive character states. PLES and the remainder of the tree are always jointly connected to the basalmost node in the tree.

The thirty-three OTUs selected for final analysis were analysed on the basis of five different character sets: (1) The entire set of seventy adult characters (70A). (2) A set of sixty-three characters of adults and seven of larvae (70AL). The seven adult characters showing the greatest amount of homoplasy were omitted, based on statistics ('C-ratios') produced by WAGNER. (3) and (4) Sets of thirty-eight and eighteen characters with the lowest homoplasy values. Both adult and larval characters were included. (5) A set of forty-four characters (adult and larval) selected
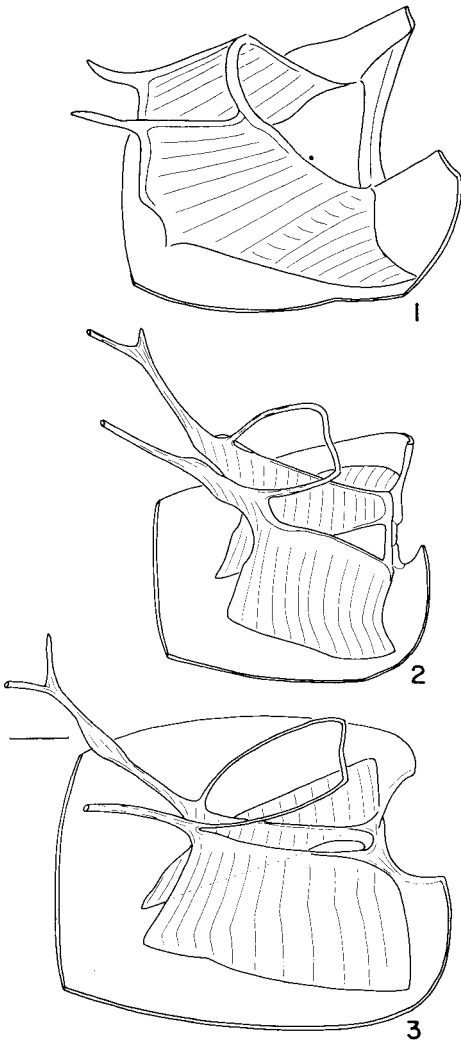
FIGS. 1–3. Corporotentoria; lateral oblique aspect, cranial walls removed: 1, *Tenebrio molitor* Linnaeus; 2, *Corticeus rufipes* Fabricius; 3, *Diaperis boleti* Linnaeus. Scale = 0.18 mm (Figs. 1, 2), 0.125 mm (Fig. 3).

tend to be triangular in lateral aspect, rather than trapezoidal. Weakly arched tentorial bridges occur in a few Cnodalonini and Tenebrionini; in these cases the posterior arms are rectilinear and the bridge occupies the normal, posterior position, suggesting convergence. The functional significance of the unusual arched tentorial bridge is unknown. It does not appear to bear muscle insertions, and the gut and nerve cord in *Diaperis* and *Bolitophagus* occupy the usual position above the bridge. In the genus *Araeoschizus* (subfamily Tentyriinae) the tentorial bridge is strongly arched and bent ventrally at the dorsal apex (Doyen & Lawrence, 1979; Fig. 33). This certainly represents an independent development of this feature.

Labral configuration (characters 6–10)

Watt (1974a) noted that an elongate labrum (Figs. 4–6) was common to the taxa he included in Lagriinae, as well as Cossyphinae (Fig. 7). The labrum is elongate in several other taxa (*Belopus*, *Adelonia*, *Rhypasma*; Fig. 8) which have never been included in Lagriinae. It is subquadrate or slightly longer than broad in Toxicini (Fig. 9) and in *Nycteropus* and related genera. We follow Watt in assuming that an elongate labrum is derived in the lagriine tribes, but the subquadrate labrum of Toxicini suggests a primitive, retained feature.

The labrum also varies in disposition of the tormal arms and in symmetry of the epipharynx. In most Tenebrionidae the medial tormal arms extend nearly perpendicularly toward the midline, just behind the posterior margin of the labrum (Figs. 9–11). This condition applies to Tenebrioninae (*sensu* Watt, 1974a), as well as Alleculinae and many Tentyriinae. In these beetles the medial arms are relatively slender and bent posteriorly at right angles near their mesal extremities. Three additional configurations are evident: (1) In Lagriinae the medial arms are inclined diagonally into the epipharyngeal membrane. This configuration is exaggerated in Goniaderini, Pycnocerini and Cossyphini (Figs. 4–6). The arms are inclined slightly anterad in Toxicini (Fig. 9) and *Nycteropus*. In Adeliini, *Rhypasma*, *Belopus* and *Adelonia* (Figs. 7 and 8) the medial arms are transverse, but bend anterad near their extremities. This configuration is probably derived from the lagrioid pattern. (2) In Diaperini (*sensu* Gebien), Bolitophagini and Hypophloeini, the medial arms are relatively stout, short and adnate to the labrum distally. In these taxa the arms curve posteromedially and lack the abrupt bend found in Tenebrioninae. (3) In many Tentyriinae the medial arms are long and slender, curving obliquely posterad and clearly separated from the base of the labrum (Fig.
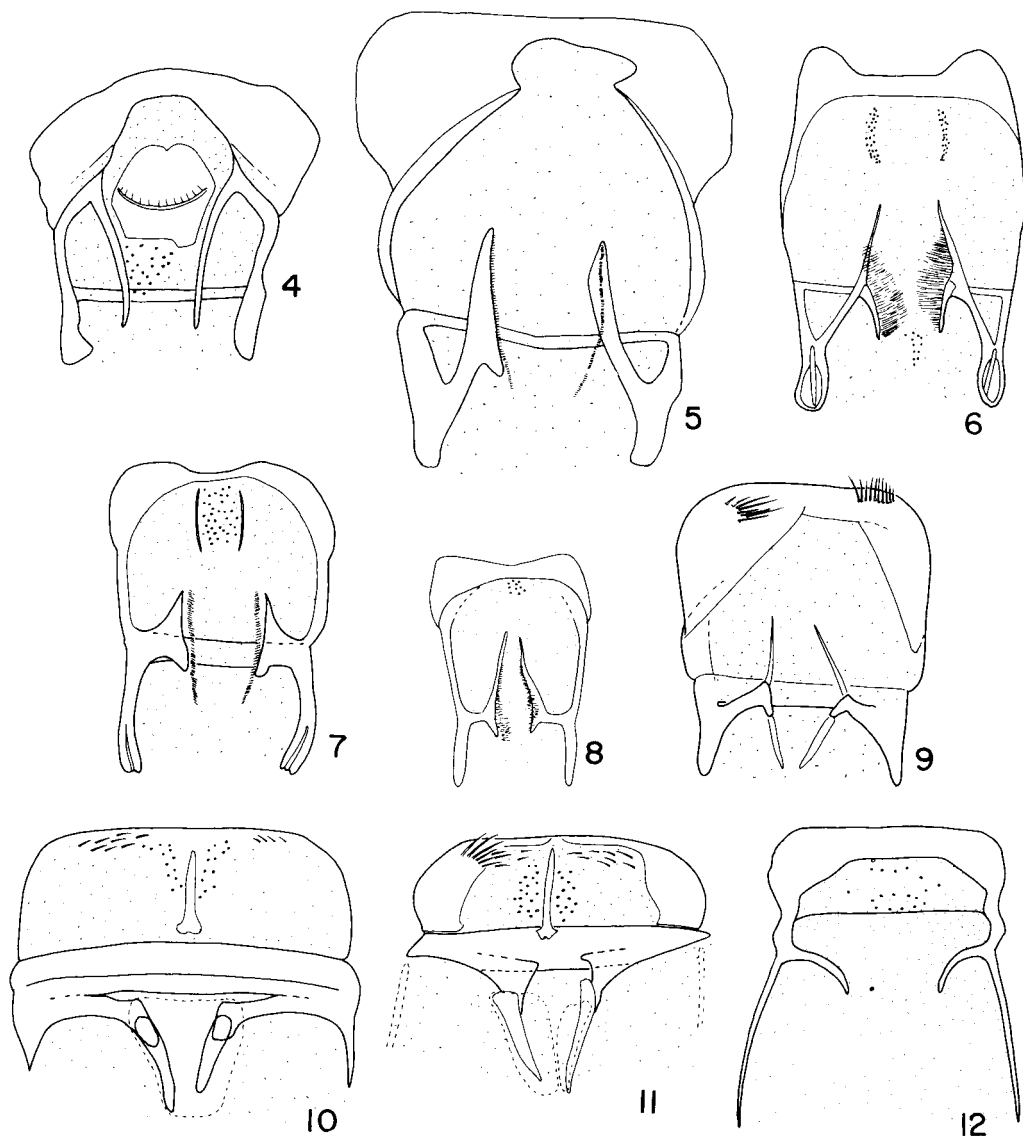
FIGS. 4–12. Epipharyngeal surfaces of labra: 4, *Goniadera nicaraguensis* Champion; 5, *Metallonotus metallicus* Fabricius; 6, *Cossyphus laevis* Laporte; 7, *Adelium* sp.; 8, *Rhypasma costaricensis* Marcuzzi; 9, *Crypaeus elongatus* Schaufuss; 10, *Phaleromela globosa* LeConte; 11, *Diaperis boleti*; 12, *Alaephus pallidus* Horn. Scale = 0.125 mm (Figs. 6, 8, 9, 10, 11), 0.18 mm (Fig. 12), 0.25 mm (Figs. 4, 5, 7).

12). The medial arms are abruptly bent or not.

Elongation of the labrum is associated with pronounced asymmetry of the epipharynx (Figs. 4–9). Asymmetry is most pronounced in Goniaderini and Pycnocerini, where it involves configuration of the tormae as well as shape of the epipharynx. In other Lagriinae and in *Belopus, Adelonia, Rhypasma* and Toxicini it involves only the enlargement of the sclerotized right margin of the labrum. This sclerotized right lobe may bear a tuft of medially directed setae. Mild asymmetry, especially in setation, occurs sporadically in Tenebrionini (e.g. *Tenebrio*, Fig. 10), and may be a primitive characteristic.
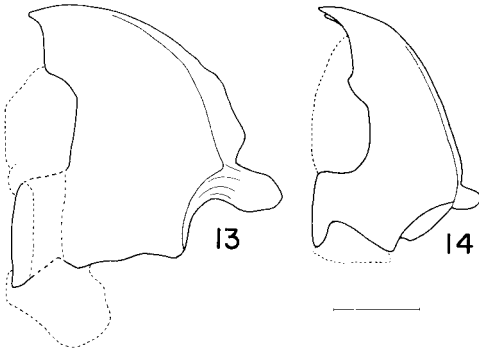
FIGS. 13–14. Mandibles, dorsal aspect; prostheca and submola indicated by dashed lines: 13, *Cibdelis blaschkei* Mannerheim, showing relatively stout configuration typical of Tenebrionoid Tenebrionidae; 14, *Statira subnitida* LeConte, showing elongate shape characterstic of some Lagrioids, Helopini, and some Tentyrioids. Scale = 0.3 mm (Fig. 13), 0.18 mm (Fig. 14).

Mandibular configuration (characters 11–14)

Typically the mandibles of Tenebrionidae are relatively stout, massive structures with a strong mola presumably adapted for crushing. Apically a pair of incisor teeth are evident. Medially a dentiform retinaculum usually projects a short distance before the mola, which is subquadrate and planar or nearly so (Figs. 15 and 16). As indicated in Appendices B and C, this description applies to the great majority of Tenebrionidae, including Tenebrioninae, Alleculinae, Diaperinae, etc. Variations from this pattern are as follows: (1) The mandibles of Helopini and many Statirini are relatively slender and elongate, with the incisor and molar lobes remote and the retinaculum reduced (Fig. 14). The mandibles of many Tentyriinae, especially Tentyriini and related tribes, are also relatively slender and elongate, but differ in other features from those of Helopini, as described below. A few taxa, such as Phrenapatini and Hypophloeini, have highly specialized mandibles which have become elongate. (2) The shape of the mola varies considerably from its subquadrate, planar configuration in Tenebrionini and related tribes (Figs. 15 and 16). In most Lagriinae (except Belopini) the mola is longitudinally elongate (Figs. 17 and 18) and bears one to three strong, transverse ridges. The anterior part of the mola in this group is

frequently sharply angulate when viewed normally. In Tentyriinae and related tribes the mola is relatively small and usually transversely elongate (Figs. 19 and 20), becoming lunate in taxa such as *Grammicus, Stenosis* and *Araeoschizus*. (3) Molar sculpturing varies from planar to coarsely ridged or toothed to finely, transversely striate, but for the most part these textures are complexly distributed across subfamilies and tribes. The mola is always planar or with subdued ridges or teeth in Tentyriinae and Opatrinae. Coarsely ridged or toothed molas occur in many Lagriinae (including Belopini), in *Zolodinus* and in Ulomini (*sensu stricto*). Fine, transverse striations (Fig. 16) occur on the molas of Alleculinae, Helopini, Strongyliini, Amarygmini and in nearly all Diaperini (exceptions: *Ceropria induta* Wiedemann; *Platydema detersum* Walker). Fine striations are distributed without apparent taxonomic pattern in Tenebrionini, Coelometopini, Amarygmini, Phaleriini and the other tribes of Watt's Tenebrioninae. Watt (1974a) listed the striate condition as primitive for Tenebrionidae. However, both striate and non-striate molar sculpturing is widespread among other Heteromera, and the non-striate condition occurs in many primitive Tenebrionidae, including Lagriinae, Tentyriinae and Zolodininae. Taxa with striate molar surfaces include some which feed on finely particulate material such as pollen (Alleculidae: Medvedev, 1977) and others which are often associated with decaying wood or fungus. In other families striate molas are frequently associated with shearing of fungal hyphae, wood fibres and similar materials (J. F. Lawrence, in litt.), and this is probably the function in many Tenebrionidae. Since the striate condition probably evolved independently several times, we have designated the planar condition as primitive (Appendix C).

Coxal closure (characters 18–19, 46)

The procoxae are closed externally by extensions of the notum in all Tenebrionidae except *Zolodinus*. Internal closure, which results from a secondary fusion of the furcal arms of the proendosternite with the external postcoxal bridge (Fig. 21), is complete in the great majority of species. This character is
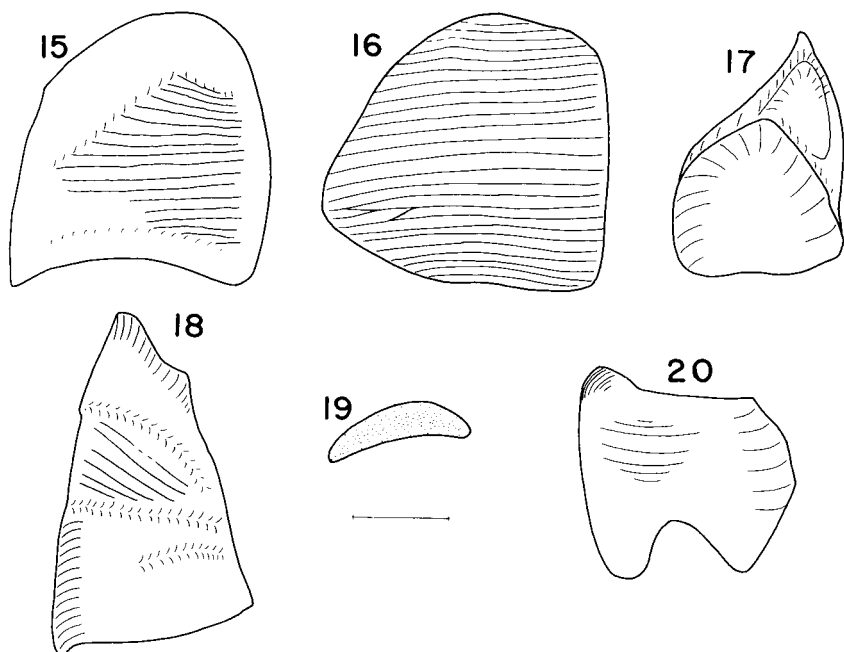
FIGS. 15–20. Molar surfaces of mandibles, normal view: 15, *Rhinandrus elongatus* Horn; the anterior and posterior rims are slightly elevated; the transverse striations are somewhat irregular and partly obscured, possibly by wear; 16, *Telacis opaca* LeConte; the molar surface is almost flat; 17, *Lagria grandis* Gyllenhall, showing the large posterior concave surface, separated by a sharp ridge from the smaller anterior concavity which is bordered by a distinct ridge; 18, *Goniadera nicaraguensis* Champion; there are three transverse ridges, and the anterior and posterolateral borders are raised; 19, *Bothrotes canaliculatus* (Say); the anterior left angle is declivous; the right lateral margin is upturned; 20, the strongly transverse mola of *Araeoschizus sulcicollis* LeConte. Scale: 0.21 mm (Fig. 15), 0.09 mm (Fig. 16), 0.18 mm (Figs. 17–20).
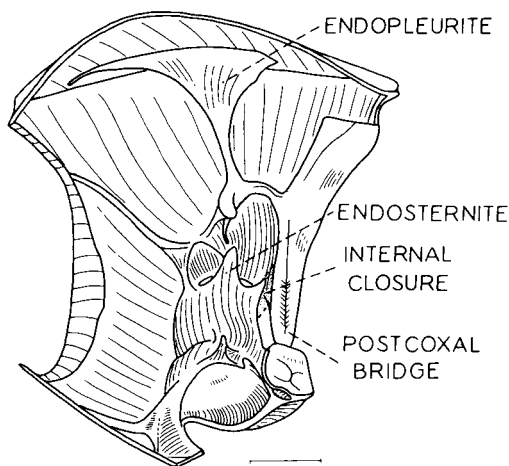

FIG. 21. Internal view of skeletal anatomy of *Tenebrio molitor,* showing externally closed, internally open procoxal cavities. The stippled area limited by dashed lines indicates the position of the internal closure resulting from fusion of the posterior lobe of the prosternal apophysis with the postcoxal bridge (after Doyen, 1966). Scale: 0.5 mm.

variable in the Tenebrionini, where every condition from internally closed to internally open occurs, sometimes in the same genus. For example, in *Tenebrio molitor* Linnaeus the procoxal cavities are open internally; in *T.guineensis* Imhoff they are partially closed, and in *T.tenebrioides* Beauvoir (= *Neatus tenebrioides*), completely closed. In the Cyphaleini and related tribes procoxal cavities are always open internally. Procoxal closure has obviously developed gradually in Tenebrionidae and, judging from the degree of variation in the tribe Tenebrionini, may have occurred independently several times. The open procoxal cavities of *Zolodinus* are certainly a primitive feature, and may indicate derivation from forerunners of some group such as Cyphaleini in which internally open cavities are retained.

The mesocoxal cavities are closed laterally by the mesepimeron in most Tenebrionidae. This condition is widespread in Coleoptera,

and is undoubtedly primitive for Tenebrionidae. In some Diaperini, some Ulomini, and in Archeoglenini and Hypophloeini the closure is effected by the meso- and metasterna, which meet lateral to the coxal cavities. Other members of Diaperini and Ulomini and many Bolitophagini show variable degrees of apposition of the meso- and metasterna. Closure by the sterna is widespread in Tentyriinae, and in some genera, such as *Batulius,* apposition of the sterna is variable (Doyen & Lawrence, 1979). In addition, closure of the sterna occurs rarely in Tenebrioninae (*Alphitobius, Apocrypha, Cryptacus*) and Lagriinae (*Paratenetus, Cossyphus, Lorelus,* etc.). In Phrenapatinae a unique closure mechanism involving the apparently adnate trochantin is present (Doyen & Lawrence, 1979). The apparent multiple evolution of sternal closure of the mesocoxal cavities reduces the value of this character for cladistic analysis, although its common occurrence in tribes such as Diaperini and Ulomini provides supporting evidence of relationship.

Number of elytral striae (character 20)

Tentyriinae, Lagriinae, and Zolodininae retain the primitive number of ten striae. A partial tenth stria occurs laterally in *Cryphaeus* and *Toxicum,* and the elytra are clearly tenstriate in *Adelonia, Belopus* and *Rhypasma,* which should be transferred to Lagriinae, and in *Dysantes.* It needs to be pointed out here only that retention of primitive characteristics is of little cladistic significance, and that reduction to nine-striate elytra occurs so widely in Tenebrionidae that it has little classificatory value.

Mesendosternite and metendosternite structure (characters 21–23, 47, 67–68)

The primitive configuration of the mesendosternite is probably similar to that of *Tenebrio molitor* (Fig. 22), in which the apophyses arise from the coxal inflexions, running first subhorizontally in an anterior or oblique direction, then curving dorsally and laterally to terminate as a slender process in the vicinity of the elytral articulation. Two structural specializations, both evolved independently many times, are common in Tenebrionidae. First, the length of the dorsal part of the apophyses decreases, so that in the extreme condition the dorsal arm is lost. Secondly, the thickened flanges at the bases of the apophyses become enlarged as attachment surfaces for ventral longitudinal muscles inserting on the prosternal apophyses (Fig. 23). In the most extreme condition the flanges are modified as concave, round muscle disks, oriented in the vertical plane (Fig. 24). Such muscle disks commonly occur in wingless species, and are particularly widespread in Tentyriinae, and also common in Coelometopini, where they show a confusing generic distribution. The mesendosternite in Diaperini and related tribes usually runs obliquely in a dorsolateral direction, without a horizontal portion, but is not always distinctive. The changes in dorsal arm length and basal flange
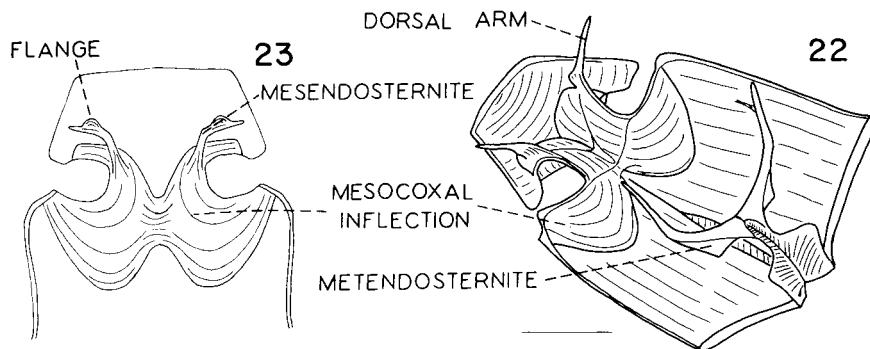
FIGS. 22–23. Internal skeletal features of pterothorax: 22, *Tenebrio molitor,* posterior oblique view, showing relatively primitive metendosternite and mesendosternite (after Doyen, 1966); 23, *Sphaerotus diversus* Pic, dorsal view, showing shortened dorsal arms of mesendosternite. Scale: 1 mm (Fig. 22), 1.4 mm (Fig. 23).
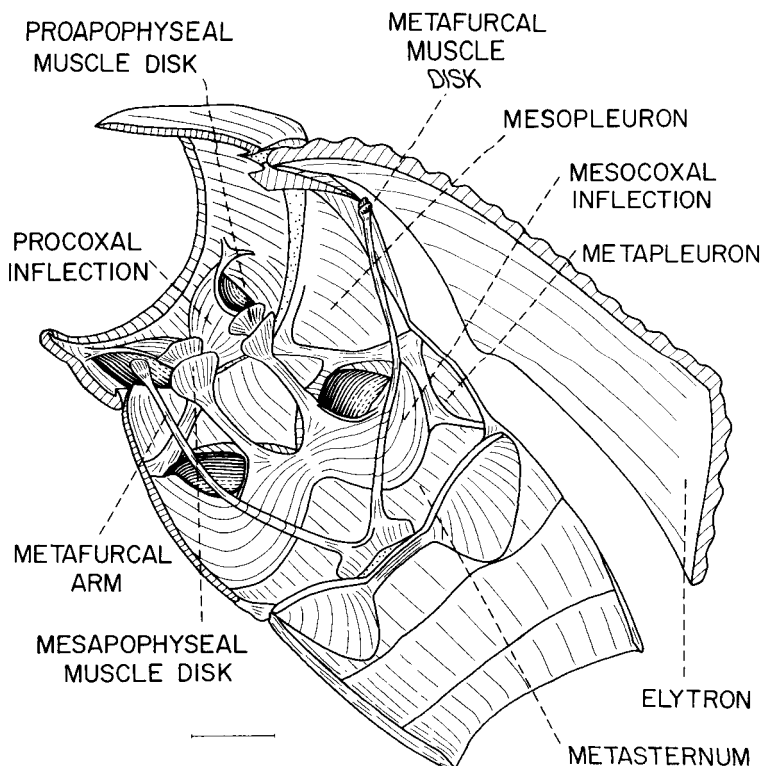
FIG. 24. Internal skeletal anatomy of *Adesmia nassata* Erichson, posterior oblique view, showing specialized, terminally expanded arms of mesendosternite and the very long arms of the metendosternite, with apical tendonous connections to the mesonotum (after Doyen, 1968). Scale: 1 mm.

structure are clearly subject to convergence, and these characters have been given low weight in the analyses.

Metendosternite structure is of the cucujoid type designated by Crowson (1938, 1944, 1967), but the configurations found in Tenebrionidae encompass virtually the entire range of variation in the Cucujoidea. Primitively in Tenebrionidae the metendosternite was probably similar to that of *Phaleria punctipes* LeConte (Fig. 25), with the stalk slightly shorter than the arms, the anterior tendons medial and the laminae relatively large. Subapically the arms form a ventral flange. Structures similar to this occur in scattered species from diverse tribes, but modifications, especially reduction of the laminae, are commonplace. The most profound modifications occur in flightless taxa, especially Tentyriinae, where only a relatively few primitive species retain wings. In flightless species the alae are always lost and the proportions and orientation

of the metendosternite become drastically altered, often in one of two ways. In genera such as *Argoporis, Cerenopus* and *Misolampus* the arms are shortened and broadened (Fig. 26) and are often held against the mesocoxal inflections by a sheet-like tendon. In genera such as *Blaps, Pimelia* and many Tentyriinae the arms become very elongate and are often enlarged apically as a disk which rests near the apex of the metapleural wing process (Fig. 24). Both types of modifications occur across phylogenetically diverse assemblages of taxa. Other common modifications are clearly related to gross changes in body form. In strongly flattened beetles such as *Catapiestus* and *Doliema* the stalk is much reduced in length (Fig. 28), while in beetles with a dorsoventrally deep body, such as Amarygmini and some Strongyliini, the stalk is elongate (Fig. 29). Another feature of potential taxonomic use is the development of the apices of the arms, either as a large, terminal flange as
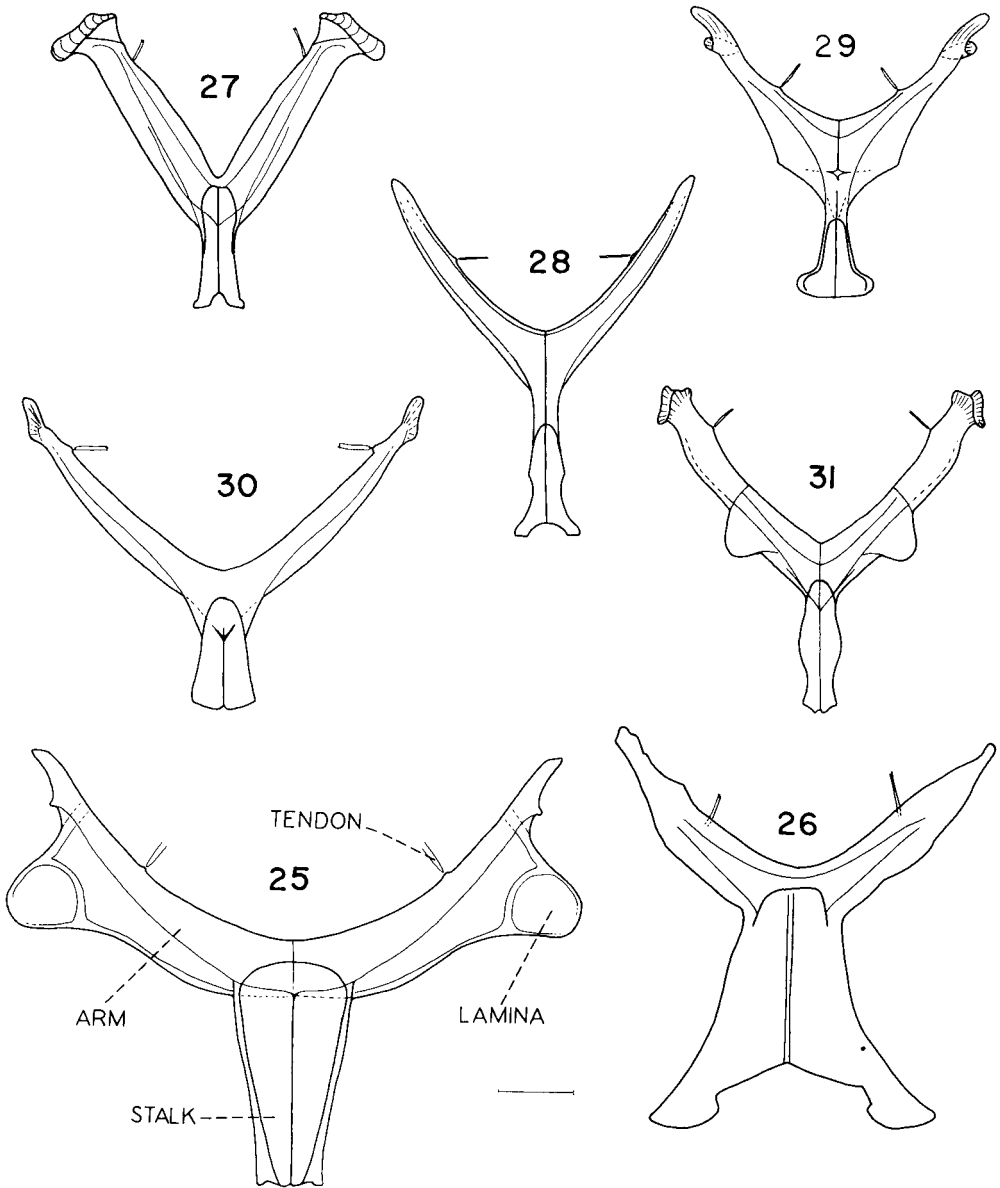
FIGS. 25–31. Metendosternites, normal view of posterior surface: 25, *Phaleria punctipes* LeConte, showing large posteroventral laminae; 26, *Sphaerotus diversus*; 27, *Doliema plana* Olivier, with greatly enlarged apical muscle disks; 28, *Strongylium tenuicolle* Say; 29, *Necrobioides bicolor* Fairmaire, showing subapical muscle attachment flange; 30, *Bolitophagus corticola* Say; 31, *Platydema detersum* Walker; note the distinct laminae, which are usually lost in *Platydema.* Scale: 0.25 mm (Fig. 25), 0.7 mm (Fig. 26), 0.2 mm (Fig. 27), 0.5 mm (Figs. 28–31).

in Diaperini and related tribes (Figs. 30 and 31), or as a small, subterminal flange, as in Tenebrionini, Coelometopini, Cyphaleini and others (Figs. 25 and 29). In general, however, variation in metendosternite structure depends on many independent parameters and is so complex that its use in analyses of relationship risks confusing convergence with patristic similarity. Consequently the metendosternite characters are given low to moderate weights.

*Wing configuration and venation
(characters 24–28)*

In general, wing shape and venation show little variation in Tenebrionidae. The most important differences involve the relative size of the apical membrane, the form of the recurrent vein and cell, and the form of the apical wing fleck. The subcubital fleck, which Watt believed to be present only in his Toxicinae and Zolodininae, occurs sporadically in many tribes from most subfamilies (see Appendix B). Its presence is clearly a retained plesiomorphic feature, with little taxonomic significance.
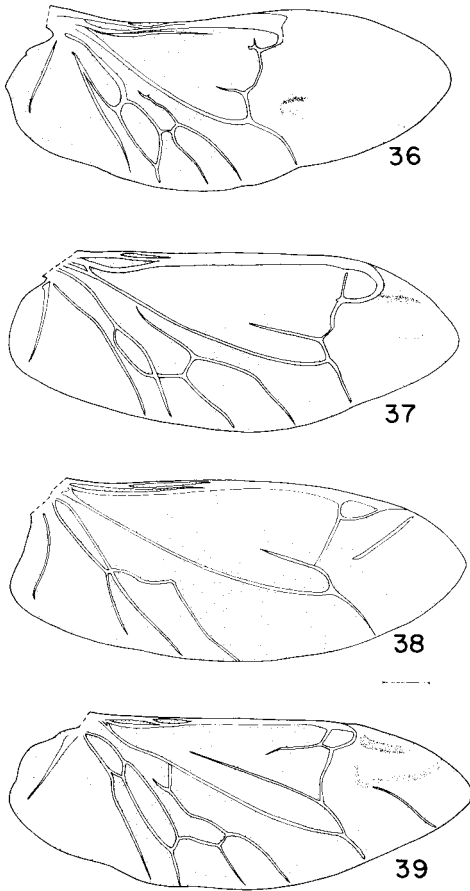
(1) Apical membrane. The veinless apical membrane typically constitutes about a quarter of the total wing length (Fig. 32). In Diaperini and related tribes the membrane is much longer, constituting at least a third of the total wing length, and sometimes as much as half, as in *Diaperis* (Fig. 33). The membrane length is intermediate in many Ulomini, a few Opatrini, Coelometopini and Cnodalonini and in a few other taxa, such as *Cryphaeus, Calymmus* and *Dysantes*. It is long in *Leichenum* (Opatrini), *Tetraphyllus* (Cnodalonini), *Trachyscelis* (Trachyscelini) and *Paratenetus* (Goniaderini). Relative membrane length is inversely correlated with body size and elytral length. As noted by Hammond (1979), increased wing area occurs in minute insects of various orders, notably Hymenoptera and Diptera, as well as Coleoptera. The negative correlation between membrane length and elytral length is related to the requirements of wing folding in Coleoptera. To shorten the wing so that it can be retracted beneath the elytra, the veinless apical portion is folded upon itself and/or beneath the veined wing base. When the body becomes extremely foreshortened, as in *Diaperis*, the basal part of the wing, bearing the veins, is also shortened. The apical membranous portion of the wing must become relatively larger in order to maintain constant wing area, and apparently requires complex modes of wing folding, involving structures external to the wings (Hammond, 1979). An elongate membrane has apparently evolved several times in Tenebrionidae with short globular bodies. In Diaperini and related tribes, however, the membrane is uniformly long, regardless of
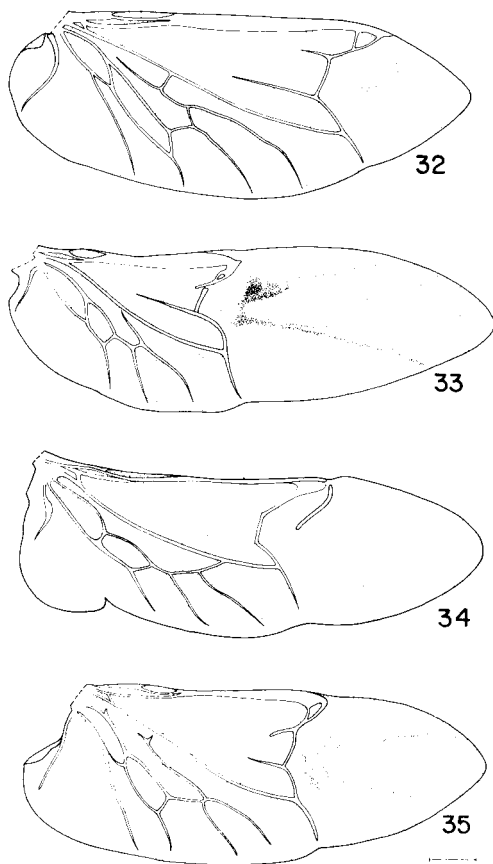
FIGS. 32–35. Right wings: 32, *Neatus tenebrioides* Beauvoir; 33, *Diaperis boleti*; 34, *Corticeus rufipes*; 35, *Platydema detersum*. Scale: 0.48 mm (Fig. 32), 0.55 mm (Figs. 33, 35), 0.38 mm (Fig. 34).

relative elytral length (e.g. *Corticeus*, Fig. 34). Wings of this group are distinctive in several other features, and the long membrane probably represents a synapomorphy for this lineage.

(2) Size and configuration of recurrent cell. In typical Tenebrionidae the recurrent cell is relatively large (Fig. 32). It is closed medially by the radial cross-vein, and the interior of the cell is membranous, not thickened and pigmented by encroachment of the surrounding veins. In Diaperini and related tribes the size of the recurrent cell is (1) reduced by approximation of the radial cross-vein to the recurrent radius (*Phaleria, Platydema*; Fig. 35), or (2) the recurrent cell is open due to loss of the radial cross-vein (*Neomida, Nilio, Corticeus*; Fig. 34). In *Phaleromella picta* Mannerheim

FIGS. 36–39. Right wings: 36, *Bolitotherus cornutus* Panzer; 37, *Goniadera nicaraguensis*; 38, *Cossyphus* sp.; 39, *Amarygmus metallicus* Perty. The vein-like thickenings in the apical membranes of *Cossyphus* and *Amarygmus* are strongly condensed flecks, rather than veins. Scale: 0.59 mm (Figs. 36, 37, 39), 0.38 mm (Fig. 38).

the radial cross-vein is extremely faint and apparently absent in some specimens. In *Diaperis* the radial cross-vein is strong and practically contiguous to the recurrent radius. These different configurations suggest that the open recurrent cell probably arose in two separate ways. In Bolitophagini, which share the elongate wing membrane with Diaperini, the recurrent cell is also relatively small, but is polygonal rather than wedge shaped (Fig. 36). In addition the anterior vein (combined costal, subcostal and radial) is apically thickened and the radiomedian cross-vein is characteristically bowed toward the wing apex. It is unclear whether this configuration

is homologous with that in the Diaperini. In *Calymmus* and *Ozolais,* in which the apical membrane is relatively short, the radial crossvein is absent. Other characters suggest that these genera are related to *Toxicum.*

(3) Apical flecks. The prevailing configuration (Figs. 32, 35, 36) consists of an irregular, diffuse pigmented area, difficult to compare and of little taxonomic use. A few taxa, such as *Corticeus* (Fig. 34), have highly distinctive flecking, but these are mostly autapomorphies. The only major taxonomic group sharing a distinct state for this character is the Lagriinae, in which the fleck is a strong horizontal bar extending from the apex of the recurrent cell, sometimes subtended by a second fleck. This character state is strongly developed in Goniaderini and Pycnocerini (Fig. 37), less clearly so in Laenini, and modified in Cossyphini (Fig. 38). In Lagriini the apical fleck is diffuse and irregular. A strikingly similar bar shaped fleck occurs in Amarygmini (Fig. 39). Amarygmini, by all other characters, are clearly members of the Tenebrioninae, so that the specialized apical flecks must have developed convergently. Presumably the flecking is involved with wing folding, which may be similar in Lagriinae and Amarygmini.

Abdominal glands and related structures (characters 29–30, 40–42, 53–56, 69–70)

(1) Abdominal membrane and hinge position (characters 29 and 30). In nearly all Tenebrionidae which possess abdominal defensive glands, the membranes between visible sternites 3–5 (morphologically sternites 5–7) are external. In this group the sternites are hinged laterally (Fig. 40). When the sternites are deflexed, as when defensive secretions are released, the large, external membrane allows the medial part of the sclerite to rotate dorsad, increasing its scope of movement. In the Tentyriinae, which lack glands, the hinging membrane is always internal, and the articulation between sternites is medial (Fig. 41). This arrangement affords less deflexion. In Belopini and Zolodinini, which lack glands, the hinging membrane is internal and medial. In Goniaderini, although glands are absent, the membranes are external and lateral, suggesting secondary gland loss. Similarly, *Cossyphini*
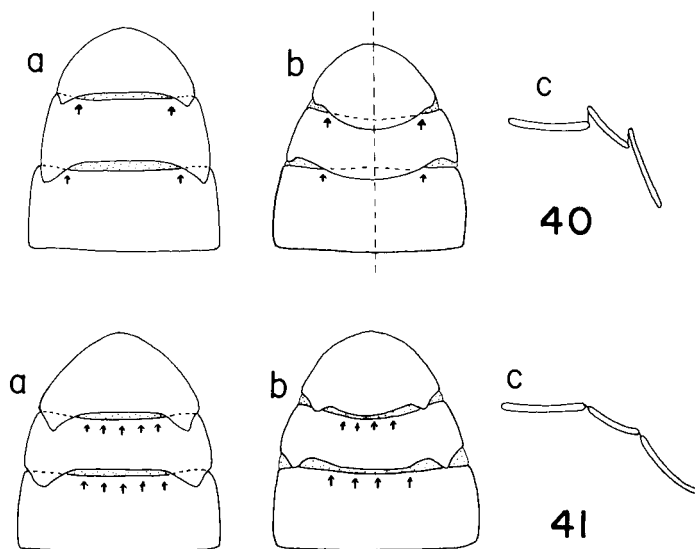
FIGS. 40–41. Abdominal hinging mechanisms, diagrammatic; arrows indicate hinge position: a, Sternites elevated, and b, sternites depressed, dorsal view; c, median longitudinal section of depressed sternites: 40, tenebrionoid type of hinge, 41, tentyrioid type of hinge.

lack glands and have the membranes internal, but lateral, as in Lagriini, from which they are probably derived. In Toxicini and Dysantini, which have small but well-developed glands, the membranes are internal and lateral. In the latter tribe the margins of the sternites are greatly thickened, so that the membranes are hidden in deep slits; this may have been the mode by which internal membranes originated in Toxicini as well. The high correlation of internal membranes with absence of defensive glands suggests that these are biologically important structures. Probably external membranes can be exploited by predators, particularly piercing feeders such as spiders, and become internalized quickly if glands are lost.

(2) Reservoir position (characters 53–55). Evolutionary trends and variation of this important organ system are discussed in detail by Tschinkel & Doyen (1980). Presumably the primitive condition for Tenebrionidae is absence of glands, as in all Tentyriinae, and in closely related families. Glands and reservoirs apparently evolved at least three, probably four times independently, producing distinctive structural arrangements. First, in Adeliini, reservoirs open between sternites 8 and 9, rather than the much more common position between 7 and 8. Adeliine glands are

distinctively shaped as very long, tapered sacs. Second, in Pycnocerini, a very shallow medial reservoir opens between sternites 7 and 8. This arrangement apparently occurs in *Phrenapates*, as well. Third, in the Lagriini, the paired reservoirs open between sternites 7 and 8, but bear a complex musculature apparently involved with expulsion of secretions (Kendall, 1968). We have not examined musculature, and do not know the distribution of this character state. Fourth, in the major tenebrionid lineage, paired reservoirs emptied by haemolymph pressure open between sternites 7 and 8. Small, eversible reservoirs, incompletely separated from one another and with secretory tissue covering the entire dorsal surface, were probably primitive for this type of gland. This configuration occurs in *Tenebrio molitor*. In other taxa with glands of this type, additional specializations are apparent. These involve the structure of the reservoir wall (character 56), size (character 40), shape (characters 41 and 69), and the distribution of the tubules which convey the secretion from the glandular cells to the reservoir (character 42).

(3) Sternite VII configuration (character 70). The posterior dorsal margin of sternite VII is rounded in cross section in most tene-
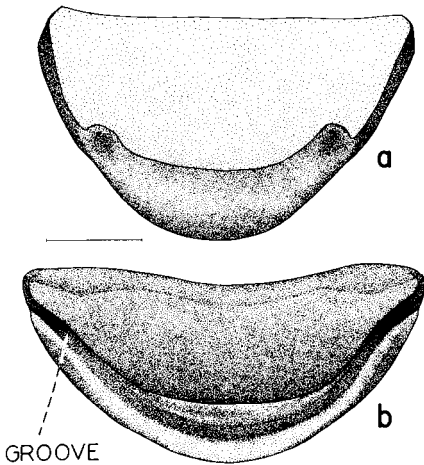
FIG. 42. Dorsal aspect of seventh (fifth visible) sternites: a, *Eleodes armata* LeConte; the arcuate projections mark the attachment point of the defence reservoirs; b, *Phrenapates bennetti* Kirby, showing submarginal groove which receives elytra. Scale: 1 mm.

brionids, fitting flat against the elytra at rest. In Lagriinae, including Cossyphini, and in Phrenapatinae sternite VII bears a trough just inside the margin (Fig. 42). The sharp edges of the epipleura fit into this trough. A less distinctive configuration occurs in many Coelometopini and Cnodalonini, where the hind border of sternite VII is more or less squared off in cross section. The inflected portion of sternite VII varies greatly in shape. Some of these shapes are distinctive and taxonomically delimited, but most are connected by intermediates and it is not clear which states are primitive, which derived. The triangular shape always occurs in conjunction with a marginal trough.

Structures of defensive glands and reservoirs are useful at all levels of classification, but as mentioned by Tschinkel & Doyen (1980), most of the characters (such as annulate reservoirs) are relatively simple, and have often arisen independently more than once. Some major dichotomies in tenebrionid evolution might be clarified by further study of gland systems.

Ovipositor structure (characters 34–39, 49–52)

Characteristics of the ovipositor are described in detail by Tschinkel & Doyen (1980). The primitive ovipositor probably resembled

that of certain Lagriini, with long, terminal gonostyles; coxites consisting of four distinct lobes, the apical lobe elongate; and elongate or subquadrate paraprocts. Reduction of gonostyles and of the apical coxite lobe have apparently occurred independently numerous times in Tenebrionidae, producing an ovipositor similar to that of *Tenebrio*. In addition, the following changes have occurred in various taxa: extreme reduction or extreme elongation of the first lobe of the coxite; shift in orientation of the baculi of the first coxite lobe from longitudinal to transverse; changes in shape and location of the coxites. Most of these changes involve relatively simple structural modifications which occurred independently more than once, judging by distributions of other characters. However, distinctive ovipositor types occur in several tribes, such as Coelometopini (characters 35–37 and 39), Eleodini (characters 34–36 and 38) or Meracanthini (characters 34 and 52). In general, the ovipositor has been ignored by taxonomists, although its taxonomic value is at least as great as that of male genitalia.

Aedeagal structure (characters 31–33)

Despite its extensive use in descriptive taxonomy, no structural comparisons across the entire family exist. Compared to the ovipositor, aedeagal structure is rather simple and uniform except for details, and its value in higher classification limited. In all Tentyriinae the aedeagus is rotated $180°$ from the normal position, so that the tegmen is ventral. This orientation also occurs in Zolodininae and in some Amarygmini, Cyphaleini (and related tribes), and Coelometopini (and related tribes), probably independently. In dried specimens of many taxa the aedeagus appears to be partially rotated. This is a preservation artifact.

Primitively, the median lobe probably was connected to a long, glabrous membrane, allowing relatively free movement in and out of the enveloping fused parameres, and this condition occurs in diverse taxa. In *Tenebrio* and a few closely related genera the connecting membrane is setose. The length of the connecting membrane is reduced in many taxa, often until the median lobe is adnate to the parameres (Fig. 43). This modification

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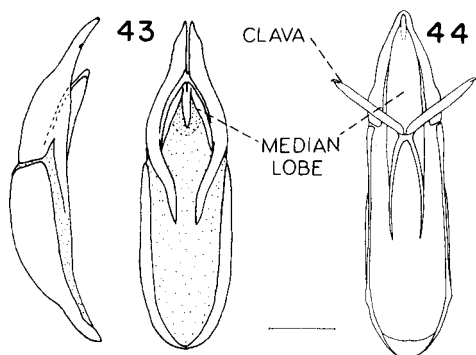
FIGS. 43–44. Aedeagal configurations: 43, *Coeloc-nemis califomica* Mannerheim, lateral and ventral; the median lobe is adnate to the basal piece of the aedeagus; 44, *Eleodes armata* ventral, showing partially extended clavae. Scale: 0.6 mm.

Additional variation involves details of structure of spermathecae or spermathecal glands. For example, spermathecae derived from the bursa (character 57) may consist of multiple tubes, or of a single tube of variable thickness and length. Spermathecae derived from the basal part of the accessory gland (character 58) may be simply saccate (*Platy-dema elliptacum* Fabricius) or modified as an ovoid capsule (*Diaperis*, etc.). Spermathecae derived from the distal part of the accessory gland (character 59) are either gradually tapered, or abruptly bulbous. Frequently associated with the basal gland spermatheca is a stiff, transparent region in the bursa copulatrix (character 65, state 2).

occurs in some genera of practically every tribe, and in nearly all members of some tribes such as Coelometopini. In a number of distantly related taxa the median lobe is absent. Clearly these reductional changes are of limited cladistic use. More valuable is the specialization of the parameres to produce distinctive 'clavae' which rotate at their proximal ends and diverge as the median lobe is extended (Fig. 44). Clavae are restricted to the Opatrini and Pedinini, but do not occur in all genera.

Internal female reproductive tract (characters 57–66)

This organ system was dealt with in detail by Tschinkel & Doyen (1980). The primitive arrangement is apparently as in *Lagria,* where a spermathecal gland is present, but not a separate spermatheca. Most significant variation involves origin and structure of a definitive spermatheca. In Tenebrionidae the spermatheca may arise *de novo* from the bursa copulatrix or it may be derived from either the basal or apical portion of the spermathecal glands. The first arrangement is extremely widespread, occurring in most of Watt's Tenebrioninae, as well as several other subfamilies. Spermathecae derived from the basal part of the spermathecal gland occur only in Diaperini and related tribes. Spermathecae derived from the distal part of the gland are restricted to Coelometopini and related tribes.

Antennal sensoriae (characters 71–73)

Characters and character states describing these structures were based on Medvedev (1977) and verified under high power dissecting microscopes for certain taxa. The commonest type of sensillae are simple setiform structures. These occur in all species observed, and are the only sensillae present in Tentyriinae, Lagriinae, Phrenapatinae, Toxicinae, and many Tenebrioninae, including *Tenebrio,* Boletophagini, Helopini, Opatrini, and Cyphaleini and related tribes. Compound structures, termed tenebrionoid sensoriae by Medvedev, were apparently evolved by consolidation of individual sensillae. These organs, which may be almost 0.1 mm in diameter, consist of a large disk-shaped base from which protrude up to twenty sensory cones. Tenebrionoid sensoriae are distributed most densely on segments 8–11, often in characteristic patterns on the rims or sides of the segments. This type of sensorial structure occurs uniformly throughout most tribes of Tenebrioninae, in Nilioninae, Alleculinae and in Diaperini and related tribes. This distribution suggests either (1) that tenebrionoid sensoriae evolved early in the main tenebrionine lineage and have been lost in some taxa, or (2) tenebrionoid type sensoriae evolved independently more than once. Medvedev describes structural variation which may indicate multiple evolution. For example, the sensorial base (character 73) is elevated in Diaperini and Phaleriini, but not in other taxa with tenebrionoid sensoriae.

Placoid sensoriae, present only in Ulomini (s.s.) and in *Scotobius* and *Ammophorus*, are of uncertain taxonomic significance.

Larval structures (characters 74–80)

The seven larval characters included in this analysis are a subset of those listed by Watt (1974a). His eight additional characters were deleted because they represent autapomorphies, are highly variable in one or more taxa, or, more frequently, because character states could not validly be assigned to a high proportion of the taxa considered here. For example, we have been able to examine only three genera of diaperine larvae and three of bolitophagine larvae, and feel uncertain of the taxonomic distribution of the mandibular tubercle which Watt regards as a synapomorphy shared by Bolitophagini and *Diaperis.*

The larval characters included in our analysis differentiate mainly the Tentyriinae and Lagriinae from the typical Tenebrionidae. In Tentyriinae the mandibles bear a tuft of stout setae dorsally at the base (character 74) and have the forelegs greatly enlarged for digging (character 76). The postcoxale forms a prominent, hemispherical bulge behind the procoxae. Similar, less extreme modifications appear in larvae of *Blaps* and some species of *Eleodes.* Like those of Tentyriinae, larvae of these genera are soil dwellers, and their mandibular and leg specializations could be independently derived.

The mandibular mola (character 77) in tenebrionid larvae is either planar or striate. Watt regards the planar mola of larvae as a primitive feature (derived in adults), apparently on the basis of its widespread distribution among Tenebrionidae. As in adults, it seems possible that striate molas could be an adaptation for feeding on fibrous materials.

Spiracles with a peripheral ring of 'air-tubes' (character 75) are widespread in Heteromera, and are probably primitive in Tenebrionidae, as indicated by Watt. Since the loss of tubes produces the simple, annular spiracle, this character is of relatively low cladistic value.

In typical Tenebrionidae the ninth sternite is greatly reduced and segment 10 and the anus are preterminal and ventral (character 78; Fig. 47). In a few larvae, such as that of *Corticeus,* the anus is terminal and the sternite and
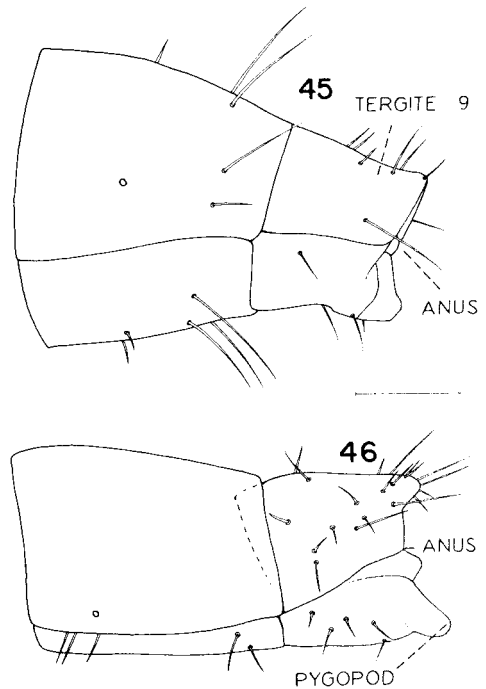
FIGS. 45–46. Apical abdominal segments of larvae, lateral aspect: 45, *Neomida* sp. (Mexico), showing terminal anus; 46, *Phaleromela globosa,* showing slight enlargement of tergite 9 and distinct pygopods. Scale: 0.25 mm.

tergite of segment 9 are subequal (Fig. 45). In Diaperini, Bolitophagini and Phaleriini, an intermediate condition exists, with sternite 9 slightly reduced and the anus subterminal (Fig. 46). In Lagriinae the structure of the abdomen is somewhat different than in other Tenebrionidae, with explanate lateral margins. Segment 9 is reduced and mostly retracted into segment 8. Tergite 9 is somewhat larger than sternite 9, and the anus subterminal (Fig. 48).

Urogomphi (character 79) represent an extremely labile feature in beetle larvae, occurring on segments 8 and/or 9. They are widespread among larvae which bore through rotten wood (but absent in Alleculinae), and perhaps represent an adaptation for providing traction for backward movement. Loss of urogomphi must have occurred independently numerous times, and this must be considered a weak character.

The great majority of tenebrionid larvae have three antennal segments (character 80).
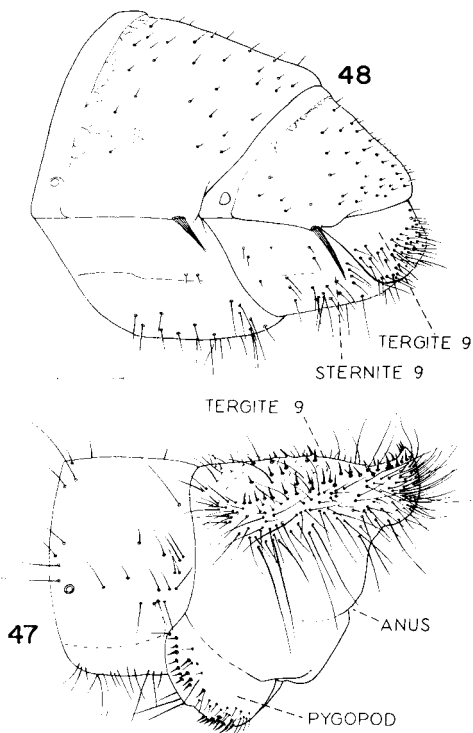
FIGS. 47–48. Apical abdominal segments of larvae, lateral aspect: 47, *Eusattus reticulatus* (Say), showing greatly enlarged tergite 9; 48, *Goniadera* (?) sp. (Mexico), showing the operculate ninth tergite closed tightly against the sternite. Scale: 0.6 mm (Fig. 47), 0.5 mm (Fig. 48).

In Lagriinae, Gnathidiinae and some Nilioninae two segments are present, the apical one much enlarged and bearing specialized sensoriae. Reduction to two antennal segments is certainly a derived feature in Heteromera, and it seems likely that segment loss has recurred independently in Tenebrionidae. It may be pointed out that the terminal segment is greatly reduced in Hypophloeini and Phrenapatini, with enlargement of segment 2.

Results

Cladograms

Major features of relationship and aspects of analysis or interpretation of general application are discussed below. Details of taxonomic relationship, characterization of cladistic lineages and sequences of character changes are treated separately later.

Topography. The cladograms based on seventy and thirty-eight characters are similar in that the first dichotomy produces two major branches which bear exactly the same terminal taxa (Figs. 49 and 50). These major divisions are termed the Lagrioid and Tenebrionoid branches throughout the following account. In addition, for several minor branches there is an identity in included OTUs over all four cladograms. For example, *Menephilus, Catapiestus, Strongyliini, Coelometopini* and *Damatris* form a monophyletic group in all analyses. Similarly, Opatrini–Ulomini is always monophyletic, and in both 70 character analyses, Helopini–Opatrini–Ulomini is monophyletic. In all analyses Diaperini–Hypophloeini is monophyletic; Bolitophagini and Phalerini are added as sister groups in all but the 38 character cladogram. The cluster *Meneristes–Bius–Metaclisa* occurs within a monophyletic unit in all but the 70 character (adult) cladogram; *Nycteropus* and *Nycterinus* sometimes join this unit. Other groups which are always (or usually) monophyletic are: *Tentyriini–Pimeliini–Zolodinini*–(Phrenapatini), *Rhypasma–Adelonia–Belopus*–(*Paratenetus*), and Adeliini–Pycnocerini. A general similarity is also apparent in the topographic position of many of the clusters mentioned above. For example, *Menephilus–Catapiestus*–Strongyliini–Coelometopini–*Damatris* always occurs as a highly derived branch on the Tenebrionoid side of the primary dichotomy. Diaperini–Hypophloeini–Bolitophagini–(Phaleriini) always appears as a relatively primitive branch on the same side of the tree. Likewise, Toxicini always occupies a primitive position on the Tenebrionoid branch.

The Lagrioid side of the primary dichotomy may be divided into two groups of OTUs. The first group includes taxa which always cluster separately from the Tenebrionoid branch (Lagriini–Goniaderini–Adeliini–Pycnocerini–Cossyphini–Phrenapatini; see Fig. 52). The second group includes taxa which cluster with the Tenebrionoid branch in the 44 character analysis (*Paratenetus–Belopus–Adelonia–Rhypasma* and Zolodinini–Tentyriini–Pimeliini). The differences in position of these clusters are the largest displacements among the cladograms and represent a previously recognized problem in
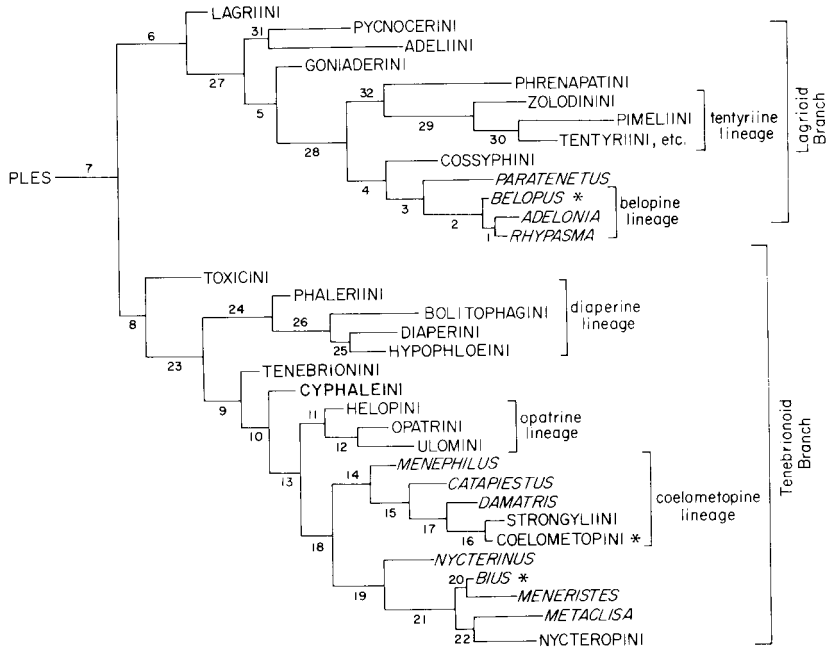
Synapomorphies

STEM 1: 51(1); 57(1)
STEM 2: 1(2); 5(1); 8(2); 9(2); 12(2); 13(1); 46(1); 73(1); 74(0); 75(0)
STEM 3: 7(2); 14(2); 32(2); 66(2); 78(0)
STEM 4: 46(2); 51(2); 76(0); 77(0); 79(0)
STEM 5: 1(2); 40(0); 41(0); 56(0)
STEM 6: 8(3); 13(2); 14(3); 18(3); 24(3); 27(3); 28(3); 32(3); 41(2); 44(2); 80(2)
STEM 7: 3(2); 11(2); 18(2); 24(2); 30(2); 55(2); 57(2); 73(2); 78(2); 79(2)
STEM 8: 1(2); 25(2); 40(2); 66(2)
STEM 9: 15(2); 25(1); 40(1); 49(3); 73(1); 78(3)
STEM 10: 26(1); 32(3); 41(2); 42(5)
STEM 11: 24(3); 26(2); 51(2)
STEM 12: 11(2); 34(3); 37(2); 38(1); 49(2)
STEM 13: 18(3); 40(2); 67(2); 69(1); 76(1)
STEM 14: 15(3); 31(2); 56(2); 57(1); 59(2); 70(1)
STEM 15: 24(3); 37(2); 38(3); 39(2); 62(2); 65(2)
STEM 16: 24(2); 49(2); 75(1); 77(1); 79(2)
STEM 17: 15(2); 36(3); 37(3); 59(3); 40(3); 52(2)
STEM 18: 41(1); 71(2)
STEM 19: 11(2); 24(1); 40(1); 42(4); 69(2); 74(0); 76(0); 80(0)
STEM 20: 15(3); 42(5)
STEM 21: 18(1); 20(1); 26(2); 32(2); 41(2); 67(1); 78(0)
STEM 22: 24(2); 42(2)
STEM 23: 6(1); 11(1); 20(3); 34(2); 42(4); 49(2); 76(2); 79(1)
STEM 24: 3(1); 5(4); 18(3); 24(3); 25(3); 26(3); 57(1); 64(2); 66(1); 73(3); 78(3)
STEM 25: 58(2); 61(2); 69(1)
STEM 26: 8(1); 9(2); 10(1); 34(1); 42(3); 49(1); 76(1); 77(2); 79(2)
STEM 27: 6(1); 6(3); 26(1); 42(0); 55(1); 69(0); 70(3); 73(1)
STEM 28: 1(5); 10(1); 26(2); 28(2); 29(2); 30(1); 6(2); 44(1); 73(2); 80(1)
STEM 29: 1(1); 6(1); 14(2); 15(2); 24(1); 26(1); 31(3); 34(2); 66(2); 73(1); 78(3)
STEM 30: 8(1); 9(1); 10(2); 12(1); 70(2); 74(2); 76(2)
STEM 31: 32(2); 34(2); 49(2); 66(2)
STEM 32: 8(2); 9(2); 12(2); 13(1); 35(1); 36(1)

Apomorphies

ADELONIA: 36(1); 64(2); 66(1); 71(2)
ADELIINI: 8(2); 9(2); 24(0); 25(0); 26(0); 27(0); 28(0); 35(1); 40(3); 44(3); 50(2); 54(2); 69(4)
BELOPINI: 32(3)
BIUS: 9(2)
BOLITOPHAGINI: 20(4); 26(1); 27(1); 32(3); 38(3); 42(1); 57(2); 64(1); 66(2); 67(2); 71(1); 75(2)
CATAPIESTUS: 10(1); 31(3); 40(1); 56(1); 62(3); 69(2)
COELOMETOPINI: 15(3)
COSSYPHINI: 6(3); 19(1); 20(1); 28(1); 39(2); 47(1); 64(2); 70(2)
DAMATRIS: 47(3); 57(2); 59(1); 62(1); 63(1)
DIAPERINI: 36(1); 40(3); 41(2); 42(5); 56(2); 61(3); 65(2)
GONIADERINI: 4(2); 7(2); 52(2); 57(1)
HELAEINI: 15(1); 18(1); 24(1); 31(2); 75(2)
HELOPINI: 15(1); 32(2); 79(2)
HYPOPHLOEINI: 19(1); 46(2); 73(1); 78(1); 79(1)
LAGRIINI: 2(2); 4(2); 57(1)
MENERISTES: 11(1); 27(0); 31(3); 37(2); 38(3); 39(2)
MENEPHILUS: 27(3); 49(2); 66(1)
METACLISA: 11(1); 18(2); 25(2); 26(1); 31(2); 32(3); 40(3); 49(2); 69(1); 70(1)
NYCTEROPUS: 1(4); 7(2); 10(1); 27(3); 34(1); 38(1); 41(2); 71(1)
NYCTERINUS: 24(0); 26(0); 27(3); 38(0); 69(3); 71(1)
OPATRINI: 42(4); 50(2); 51(1); 74(2); 76(2)
PARATENETUS: 1(4); 3(3); 4(2); 10(3); 25(3); 26(3); 29(1); 30(2); 44(2)
PHALERIINI: 11(2); 34(3); 58(1)
PHRENAPATINI: 1(4); 20(3); 25(2); 26(3); 27(2); 29(1); 30(2); 32(2); 36(1); 37(0); 38(0); 39(0); 40(1); 49(0); 53(2); 57(1); 77(2)
PIMELIINI: 9(0); 20(1); 24(0); 25(0); 26(0); 27(0); 28(0); 30(2); 34(3); 47(1); 57(1); 70(1)
PYCNOCERINI: 5(3); 7(2); 15(3); 34(3); 35(3); 38(3); 44(1); 50(0); 53(2); 67(2); 75(0); 79(1)
RHYPASMA: 1(1); 6(3)
STRONGYLIINI: 41(2); 56(1); 62(3)
TENEBRIONINI: 7(2); 32(1); 69(3)
TENTYRIINI: 14(1); 19(1); 24(3); 26(2); 46(2)
TOXICINI: 1(4); 7(2); 9(2); 10(1); 18(1); 30(1); 42(1); 75(2)
ULOMINI: 6(2); 7(2); 10(1); 13(1); 14(3); 25(2); 40(3); 41(1); 41(1); 72(2)
ZOLODININI: 15(3); 18(1); 35(2); 49(2); 50(2); 75(2); 79(2)

FIG. 49. WAGNER cladogram based on seventy characters (adult and larval). Stem numbers on clado-gram correspond to numbers in the synapomorphy lists. Lengths of stems are proportional to the number of character state changes between nodes. Taxa denoted by asterisks have no apomorphies, but are placed on stems of unit length for clarity. Total length of the tree (= total number of character state changes) is 448; deviation ratio = 0.89. For further explanation, see text).

higher classification (Doyen & Lawrence, 1979; Tschinkel & Doyen, 1980) which will be discussed below. Other major differences in cladistic structure involve: (1) Phrenapatini, which sometimes appears as the sister group of Zolodinini−Tentyriini−Pimeliini, or sometimes is embedded in the Lagrioid branch; (2) the position of Zolodinini−Tentyriini−Pimeliini within the Lagrioid branch; (3) the position of *Belopus−Adelonia−Rhypasma* within the Lagrioid branch. In general, the position of terminal taxa in the Lagrioid branch is inconstant, with most varying in position from relatively primitive to relatively derived. For example, Lagriini is the sister-group of the rest of the Lagrioid lineage in two analyses, relatively derived in one and intermediate in the last. Similarly, the position of Adeliini is relatively primitive in two cladograms (44 character; 70 character, adult) and relatively derived in two (38 character, 70 character adult + larval). The positions of terminal taxa are more stable on the Tenebrionoid branch, but Tenebrionini, Cyphaleini and Helopini, as well as the clusters Opatrini−Ulomini and *Meneristes−Bius, Metaclisa−Nycteropus* and Helopini, vary significantly in cladistic position and in sister group relations.

Finally, one aspect of general topographic pattern should be mentioned. Certain groups of OTUs form discrete clusters which bear sister-group relationships which can be conveniently recognized in classifications. For example, a subfamily Diaperinae could be distinguished on the 44 character cladogram, coordinate with the entire remaining Tenebrionoid branch except for Toxicini. Most OTUs, however, are isolated on branches which diverge one at a time from the remainder of the tree. This topographic pattern, which is analogous to chaining in single-linkage phenograms, is particularly clear in the Tenebrionoid branch of the 70 character adult analysis, and is generally prevalent in the Lagrioid branch in all analyses. Whether or not cladograms accurately represent the evolutionary branching patterns among these taxa will be discussed in detail below. Regardless of evolutionary considerations, chained cladogram topography presents severe problems in constructing taxonomic and nomenclatural hierarchies, since the numerous branching levels require equally numerous taxonomic categories, if strictly cladistic classifications are desired.

Farris (1969) suggests that 'correct' cladograms may be derived by heavily weighting those characters which show the least homoplasy in successive analysis. Homoplasy is measured in relation to the tree derived from each analysis, beginning with all characters and ending with a character set which minimizes deviation from the hypothetically correct result. The deviation index is measured as

$$d = (Q, P) = 2 \frac{[q(i, j) − p(i, j)]^2}{t(t − 1)}$$

where Q and P are the matrices of differences between OTUs in each cladogram and its corresponding Prim network (Farris, 1969); t is the number of OTUs. This procedure was followed in the present study by eliminating the most homoplastic characters after each analysis, ultimately producing an 18 character cladogram (not shown).

The relatively drastic reduction to eighteen characters reduced homoplasy to a low level (0.14) but also eliminated most of the detail evident in analyses with the additional characters. The 18 character cladogram underscored the integrity of the coelometopine, diaperine and tentyriine groups which remain discrete lineages. Most of the other OTUs, particularly those of the tenebrionine and lagriine lineages, were independently derived as two major multifurcations. This pattern reflects the reduced number of characters, and does not necessarily indicate that these OTUs should be recognized as separate lineages. Because of the higher degree of homoplasy in the characters defining these lineages, however, their composition and relationships are less certain than for the clusters discussed above.

Homoplasy. In the ensuing discussion parallelism and reversal are not differentiated, since they have similar effects in confounding cladistic analysis. Details of character state transformations important in defining taxa are discussed separately later, and only the magnitude and distribution of homoplasy are considered here.

Even superficial perusal of the apomorphy lists in Figs. 49−52 will show that homoplasy

LAGRIINI
GONIADERINI
ADELIINI
PYCNOCERINI
COSSYPHINI
PARATENETUS
BELOPUS ∗
RHYPASMA
ADELONIA ∗
PHRENAPATINI
ZOLODININAE
PIMELIINI   } tentyriine lineage
TENTYRIINI
} Lagrioid Branch

PLES

TOXICINI
BOLITOPHAGINI
DIAPERINI
HYPOPHLOEINI   } diaperine lineage
PHALERIINI
NYCTERINUS
TENEBRIONINI ∗
CYPHALEINI ∗
MENERISTES
BIUS ∗
METACLISA
NYCTEROPINI
HELOPINI
OPATRINI
ULOMINI   } opatrine lineage
MENEPHILUS
CATAPIESTUS
STRONGYLIINI
COELOMETOPINI
DAMATRIS
} Tenebrionoid Branch

Synapomorphies

STEM 1: 51(1)
STEM 2: 8(2); 74(0)
STEM 3: 6(2); 14(2); 28(2); 78(0)
STEM 4: 29(2); 44(1); 51(2); 80(0)
STEM 5: 6(3); 42(0); 55(1); 56(0); 69(0); 70(3)
STEM 6: 8(3); 14(3); 28(1); 44(2); 80(2)
STEM 7: 3(2); 42(1); 55(2); 78(2)
STEM 8: 25(2)
STEM 9: 3(1); 6(1); 8(1); 20(3); 25(3)
STEM 10: 8(2); 34(2); 49(2)
STEM 11: 3(2); 25(1); 49(3); 78(3)
STEM 12: 42(5)
STEM 13: 69(3)
STEM 14: 69(1)
STEM 15: 37(2); 49(2)
STEM 16: 34(3)
STEM 17: 42(4)
STEM 18: 58(2); 61(2); 69(1)
STEM 19: 59(2); 70(1)
STEM 20: 39(2); 62(3); 63(2)
STEM 21: 36(3); 37(3); 39(3); 52(2)
STEM 22: 62(2); 56(2)
STEM 24: 20(1); 74(0); 78(0); 80(0)
STEM 26: 42(2)
STEM 28: 36(1)
STEM 29: 6(1); 34(2); 78(3)
STEM 30: 8(1); 74(2); 70(2)
STEM 31: 34(2); 49(2); 56(1)
STEM 32: 35(1); 74(1); 78(2); 80(1)

Apomorphies

ADELIINI: 8(2); 25(0); 28(0); 35(1); 44(3); 50(2); 54(2); 69(4)
BOLITOPHAGINI: 20(4)
CATAPIESTUS: 49(3); 69(2)
COSSYPHINI: 19(1); 20(1); 39(2); 47(1); 70(2)
DAMATRIS: 47(3); 49(3); 59(1); 62(1); 63(1)
DIAPERINI: 40(2); 61(3); 36(2); 42(5); 56(2)
GONIADERINI: 52(2)
HELOPINI: 51(2)
HYPOPHLOEINI: 19(1); 42(3); 78(1)
LAGRIINI: 42(2)
MENERISTES: 37(2); 39(2)
MENEPHILUS: 37(1); 56(2)
METACLISA: 25(2); 49(2); 69(1); 70(1)
NYCTEROPINI: 34(1); 42(1)
NYCTERINUS: 74(0); 80(0)
OPATRINI: 42(4); 50(2); 74(2)
PARATENETUS: 3(3); 25(3); 29(1); 44(2)
PHALERIINI: 34(3)
PHRENAPATIINI: 14(3); 20(3); 25(2); 29(1); 34(0); 35(0); 36(0); 37(0); 39(0); 49(0); 53(2)
PIMELIINI: 20(1); 25(0); 28(0); 34(3); 47(1); 70(1)
PYCNOCERINI: 34(3); 35(3); 44(1); 53(2); 50(0)
RHYPASMA: 6(3)
TENTYRIINI: 14(1); 19(1)
ULOMINI: 6(2); 14(3); 25(2); 51(2); 72(2)
ZOLODININI: 35(2); 49(2); 50(2)

FIG. 50. WAGNER cladogram based on thirty-eight characters with highest consistency ratios in the 70 character analysis. Conventions are explained in Fig. 49. Total tree length is 186; deviation ratio = 0.80.

is extremely common in all four data sets. In fact, only nine characters (2, 28, 35, 54, 55, 58, 61, 65, 72) show no homoplasy at all, and the maximum number of non-homoplastic characters for any single analysis is nine. The number of uniquely derived character states is considerably higher (e.g. fifty for the 38 character analysis), but homoplasy is still extensive. For the 38 character analysis 60% of the character states are not uniquely derived; for the 44 character analysis 77% of the character states are not unique. Even in the 18 character analysis eleven characters show at least one reversal or parallelism. Such extensive homoplasy may be interpreted in two ways. If parallelism, convergence and
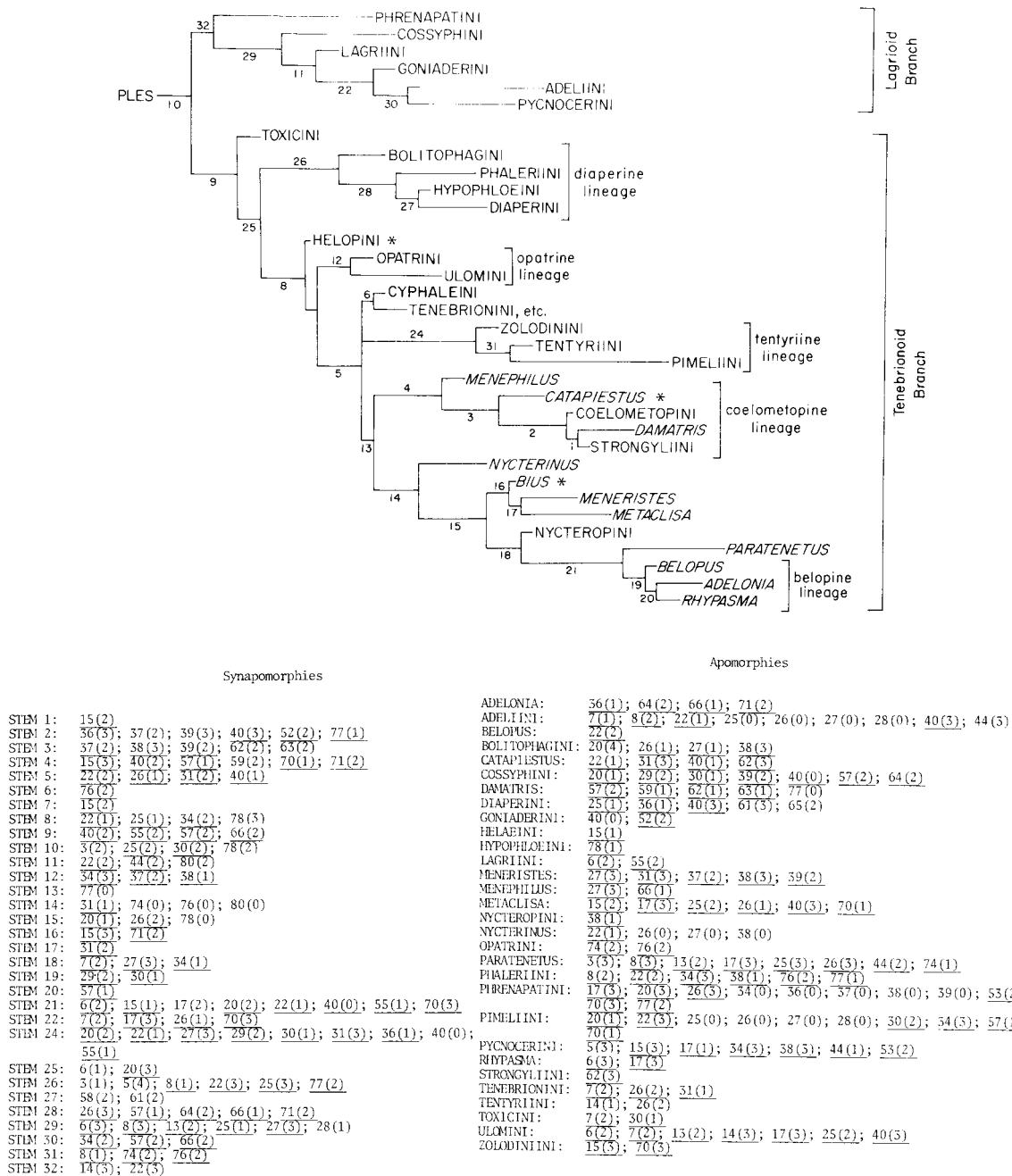
FIG. 51. WAGNER cladogram based on forty-four characters used in intuitive analysis (Fig. 58). Conventions are explained in Fig. 49. Total tree length is 263; deviation ratio = 0.52.

Synapomorphies

STEM 1:   15(2)
STEM 2:   36(3); 37(2); 39(3); 40(3); 52(2); 77(1)
STEM 3:   37(2); 38(3); 39(2); 62(2); 63(2)
STEM 4:   15(3); 40(2); 57(1); 59(2); 70(1); 71(2)
STEM 5:   22(2); 26(1); 31(2); 40(1)
STEM 6:   76(2)
STEM 7:   15(2)
STEM 8:   22(1); 25(1); 34(2); 78(3)
STEM 9:   40(2); 55(2); 66(2)
STEM 10: 3(2); 25(2); 30(2); 78(2)
STEM 11: 22(2); 44(2); 80(2)
STEM 12: 34(3); 37(2); 38(1)
STEM 13: 77(0)
STEM 14: 31(1); 74(0); 76(0); 80(0)
STEM 15: 20(1); 26(2); 78(0)
STEM 16: 15(3); 71(2)
STEM 17: 31(2)
STEM 18: 7(2); 27(3); 34(1)
STEM 19: 29(2); 30(1)
STEM 20: 57(1)
STEM 21: 6(2); 15(1); 17(2); 20(2); 22(1); 40(0); 55(1); 70(3)
STEM 22: 7(2); 17(3); 26(1); 70(2)
STEM 24: 20(2); 22(1); 27(3); 29(2); 30(1); 31(3); 36(1); 40(0);
          55(1)
STEM 25: 6(1); 20(3)
STEM 26: 3(1); 5(4); 8(1); 22(3); 25(3); 77(2)
STEM 27: 58(2); 61(2)
STEM 28: 26(3); 57(1); 64(2); 66(1); 71(2)
STEM 29: 6(3); 8(3); 13(2); 25(1); 27(3); 28(1)
STEM 30: 34(2); 57(2); 66(2)
STEM 31: 8(1); 74(2); 76(2)
STEM 32: 14(3); 22(3)

Apomorphies

ADELONIA: 36(1); 64(2); 66(1); 71(2)
ADELIINI: 7(1); 8(2); 22(1); 25(0); 26(0); 27(0); 28(0); 40(3); 44(3)
BELOPUS: 22(2)
BOLITOPHAGINI: 20(4); 26(1); 27(1); 38(3)
CATAPIESTUS: 22(1); 31(3); 40(1); 62(3)
COSSYPHINI: 20(1); 29(2); 30(1); 39(2); 40(0); 57(2); 64(2)
DAMATRIS: 57(2); 59(1); 62(1); 63(1); 77(0)
DIAPERINI: 25(1); 36(1); 40(3); 61(3); 65(2)
GONIADERINI: 40(0); 52(2)
HELAEINI: 15(1)
HYPOPHLOEINI: 78(1)
LAGRIINI: 6(2); 55(2)
MENERISTES: 27(3); 31(3); 37(2); 38(3); 39(2)
MENEPHILUS: 27(3); 66(1)
METACLISA: 15(2); 17(3); 25(2); 26(1); 40(3); 70(1)
NYCTEROPINI: 38(1)
NYCTERINUS: 22(1); 26(0); 27(0); 38(0)
OPATRINI: 74(2); 76(2)
PARATENETUS: 3(3); 8(3); 13(2); 17(3); 25(3); 26(3); 44(2); 74(1)
PHALERINI: 8(2); 22(2); 34(3); 38(1); 76(2); 77(1)
PHRENAPATINI: 17(3); 20(3); 26(3); 34(0); 36(0); 37(0); 38(0); 39(0); 53(2)
               70(3); 77(2)
PIMELIINI: 20(1); 22(3); 25(0); 26(0); 27(0); 28(0); 30(2); 54(3); 57(1)
               70(1)
PYCNOCERINI: 5(3); 15(3); 17(1); 34(3); 38(3); 44(1); 53(2)
RHYPASMA: 6(3); 17(3)
STRONGYLIINI: 62(3)
TENEBRIONINI: 7(2); 26(2); 31(1)
TENTYRIINI: 14(1); 26(2)
TOXICINI: 7(2); 30(1)
ULOMINI: 6(2); 7(2); 13(2); 14(3); 17(3); 25(2); 40(3)
ZOLODINIINI: 15(3); 70(3)

reversal are common evolutionary phenomena, then most characters might be expected to show homoplasy. The other interpretation is that better, less homoplastic characters exist, but remain to be detected. While it is certain that additional valuable characters will be discovered, they will not eliminate the homoplasy which is evident, even in complex

characters such as configuration of the internal female reproductive tract, distinctive patterns of wing venation or specialized defensive gland structures. For example, the coelometopine lineage is characterized by a unique arrangement of the female reproductive system, a unique and highly specialized ovipositor, and derived defensive gland characters. Yet the distribution of character states is such in these taxa, which always cluster together, that at least one of these characters must be reversed. In Figs. 50 and 51 characters 57 and 59, describing the configuration of the reproductive system, are always reversed in *Damatris*, and character 56, describing defensive reservoir structure, is always reversed in *Strongyliini*. Similar considerations attend characters 40, 53, 54 and 55, describing defensive gland origin. On all the cladograms glands are evolved independently more than once and lost in at least one lineage. In most characters homoplasy is much more abundant, especially as multiple evolution of indistinguishable character states, often in remotely related taxa. We conclude that character state reversal and parallelism are extremely common evolutionary phenomena, at least in speciose groups such as the Insecta. Homoplasy, if indeed so widespread, implies a high degree of uncertainty for most cladistic results, since, as shown by Felsenstein (1978), phylogenies estimated by parsimony or compatibility methods will not converge on the true phylogeny when parallel changes exceed nonparallel ones. Particularly suspect are conclusions based on assumptions of polarity or irreversibility of changes in simple characters such as setal numbers, cuticular sculpturing, or colour.

In general the degree of homoplasy is reduced by eliminating weaker characters, using Farris' method as described above. Thus, the deviation ratio decreases from 1.08 (70 characters, adults only) to 0.14 (18 characters). It should be pointed out, however, that the difference between the 70 character (adult + larval) and 38 character analyses is small (0.89 v. 0.80). In contrast, the ratio for the 44 character analysis is considerably lower (0.52). The 44 character set was selected from an intuitively based cladogram, constructed before computer analysis. The branching pattern in this intuitive cladogram was quite different than that in Fig. 51, and comparison
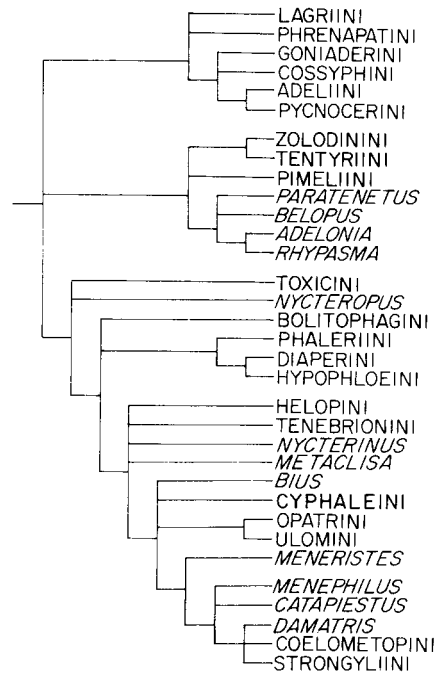

FIG. 52. Consensus diagram for four cladograms (70 characters, adults; 70 characters, adults and larvae; 44 characters; 38 characters). Lengths of stems are arbitrary.

indicated that the computer derived version was preferable in certain aspects, and certainly more parsimonious. Nevertheless, the homoplasy figures suggest that character selection can be efficiently accomplished using traditional methods of cladistic analysis.

Consensus cladogram (Fig. 52). The consensus cladogram represents the relationships shared by the four larger data sets (70A, 70A + L, 44, 38). The 18 character cladogram was omitted because of its extremely simplified structure, which would have dominated the consensus tree.

In Fig. 52 the OTUs divide into three major branches. In the computer analyses these correspond to: (1) the Lagrioid branch, exclusive of the tentyriine and belopine clusters; (2) the combined tentyriine and belopine groups; (3) the Tenebrionoid branch. The diaperine and coelometopine lineages are distinct, as before, and Opatrini–Ulomini remains as a monophyletic unit, as do Adeliini– Pycnocerini and *Rhypasma–Adelonia*. Toxicini and *Nycteropus* appear at the base

of the Tenebrionoid branch, as in Figs. 49–51. Comparison of Figs. 52 and 48 shows that the consensus cladogram is obviously more similar to the intuitively derived diagram, than to any of the computer produced versions. The implications of this are discussed below.

Phenograms

Phenograms were computed for the three character sets indicated in Table 1 and compared with the corresponding cladograms. The 44 character and 70 character (A + L) phenograms are shown here (Figs. 53 and 54). The hypothetical OTU PLES was included, although phenograms do not accommodate judgements of ancestry or character state precedence.

Comparison of Figs. 53 and 54 with the corresponding cladograms reveals a high level of similarity in OTU composition of terminal clusters (Table 1). In fact, for the diaperine, tentyriine and lagriine groups, cluster com-

position is more constant than in the cladograms. The tenebrionine group, which varies considerably among cladistic analyses, has a more predictable composition in the phenograms, and includes the members of the opatrine group, except in the 70 character analysis, where they appear as a distinct subgroup. It might be expected that the coelometopine, diaperine and tenyriine clusters would coincide in cladistic and phenetic analyses, since these are highly derived groups which share many apomorphines. The tenebrionine group, in contrast, shares almost entirely primitive features, and never appears as a discrete cluster in cladistic analyses. The belopine lineage, with many primitive features shared with the lagriine lineage, others with Toxicini, clusters erratically in cladistic analyses, depending on character selection. The belopine cluster is always discrete in phenetic diagrams. PLES, with all primitive character states, clusters with Toxicini, in a highly derived position.
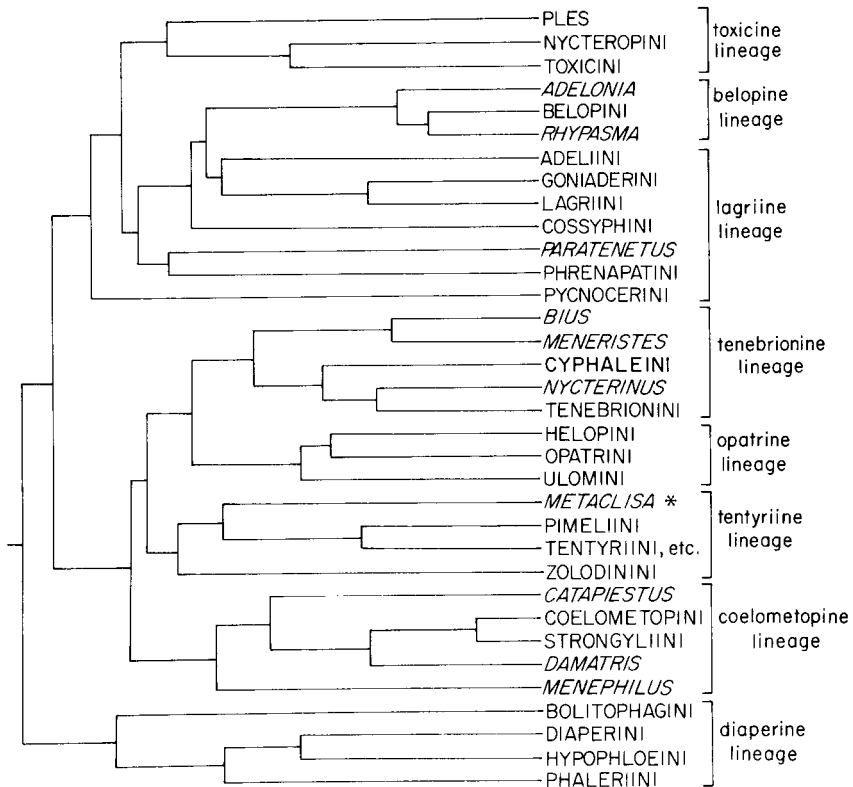

FIG. 53. Phenogram (UPGMA, taxonomic distance) based on seventy characters (adult and larval). Cophenetic correlation coefficient = 0.75.
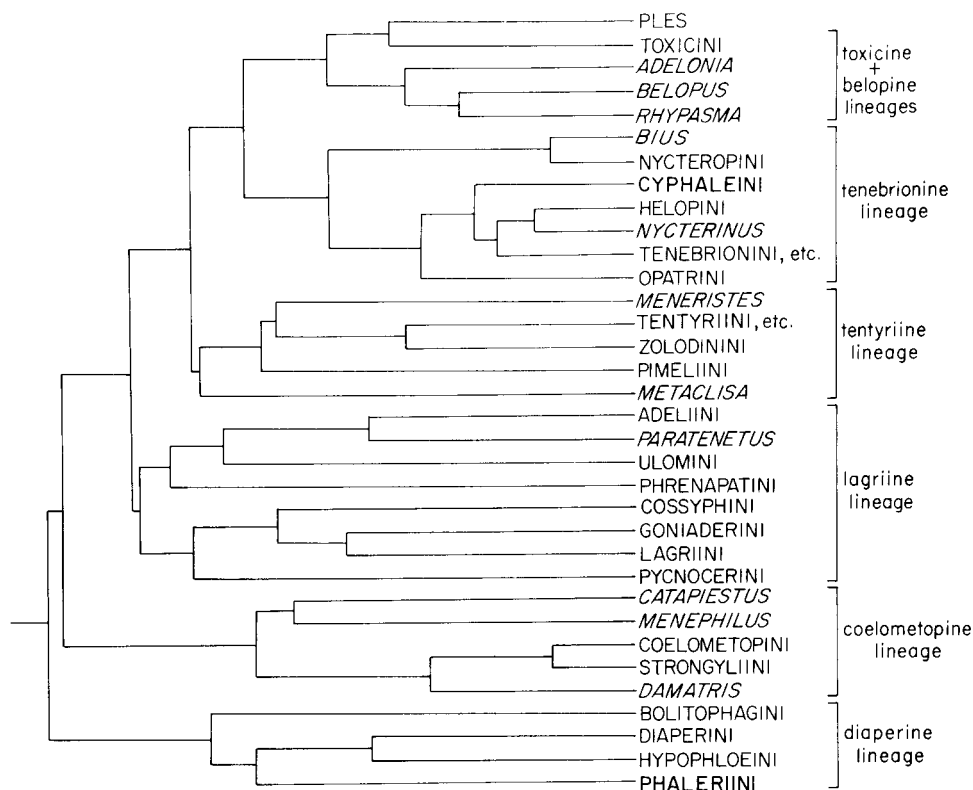
FIG. 54. Phenogram (UPGMA, taxonomic distance) based on the forty-four characters used in intuitive analysis (Fig. 58). Cophenetic correlation coefficient = 0.76.

Within the major lineages, correspondence between the phenograms and cladograms is very clear. In the coelometopine group, for example, Coelometopini, Strongyliini and *Damatris* are always most closely related, with *Menephilus* and *Catapiestus* peripheral members. Similarly, Hypophloeini and Diaperini are the closest members of the diaperine cluster, with Bolitophagini and Phaleriini peripheral. Thus, it appears that phenetic and cladistic estimates converge at high levels of relationship.

At lower levels of relationship huge differences separate the phenograms and cladograms. In the phenograms, the most derived clusters always branch from near the base of the diagram. For example, the diaperine cluster forms the initial branch in the 44 and 70 character phenograms; the coelometopine cluster is the second branch in the 44 character phenogram and is the first branch in the 38 character phenogram (not shown). OTUs

which are basal (and therefore primitive) on the cladograms always appear as members of terminal branches on the phenograms. The best example is PLES; Toxicini, *Nycteropus,* Helopini, *Belopus* and Zolodinini are others.

Relationships among the major groups indicated by cladistic analyses are also confounded. In the computer derived cladistic results the Lagrioid branch forms the sister group to all other Tenebrionidae (Figs. 49–51). In the phenograms the lagriine group is embedded in the large cluster which contains the tenebrionine group as well as many primitive OTUs whose relationships cannot be specified from the cladograms. Similarly, the topographic relationships of other major clusters (diaperine, coelometopine, etc.) to one another, are grossly altered in the phenograms.

Finally, a few OTUs occupy inexplicable positions. In the 44 character phenogram, *Meneristes* joins the tentyriine group, and in
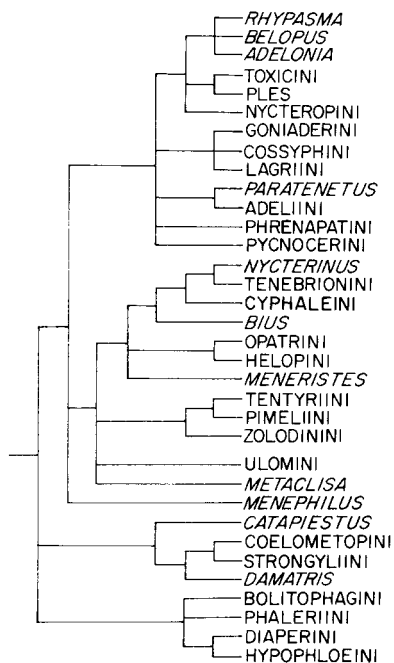
FIG. 55. Consensus diagram for three phenograms
(70 characters, adults and larvae; 44 characters; 38
characters).

the 44 and 70 (A + L) phenograms, *Metaclisa*
joins the tentyriine group. Both *Meneristes*
and *Metaclisa* share primitive features with
members of the tentyriine group, but share
no derived features with tentyriines, which
lack glands, have a different abdominal sternite
structure, etc. In the 38 character phenogram
Phaleriini clusters with the tenebrionine
group, rather than the diaperine. This may
indicate an alternative relationship not speci-
fied in the cladograms, since Phaleriini share
some derived characters with the tenebrionine
group, as detailed later.

The consensus phenogram (Fig. 55) shows
most of the features evident in the pheno-
grams based on the different character sets.
As before the coelometopine and diaperine
lineages are distinct, and appear at the base
of the diagram. The Lagrioid cluster, including
PLES, appears in a relatively derived position,
coordinate with the large tenebrionine cluster
and *Menephilus*, which is separated from the
coelometopine cluster. A few other OTUs,
such as Ulomini, are isolated in relatively basal
positions. This is expected, since their position
varied among the phenograms used to con-
struct the consensus.

Prim networks

Prim networks represent the shortest
phenetic pathway through a matrix of OTU x
OTU similarities. The deviation index of
Farris (1969; WAGNER program) is based on
comparisons between cladograms and Prim
networks derived from the same data sets.
Farris' networks and cladograms are based
on Manhattan distances; the Prim networks
presented here are derived from Euclidean
distance matrices. Primnets corresponding to
all the cladograms were constructed; those
based on thirty-eight and forty-four charac-
ters are illustrated here. OTUs which occur at
nodes are placed on short (zero length) stems
and the networks are rooted at PLES, con-
verting them to tree diagrams for ease of
comparison with cladograms and phenograms.
Extending stems for nodal OTUs also avoids
the impression that extant taxa have evolved
from one another.

As indicated by inspection of Figs. 56 and
57 and Table 1, the topography of the Prim
networks is generally similar to that of the
corresponding cladograms, with greater differ-
ences from the phenograms. This is especially
evident in the placement of the OTUs which
comprise the tenebrionine lineage in the
phenograms. In both Prim networks and
cladograms this group is fragmented, reflecting
the primitive nature of the characters they
share. There are additional minor differences
in character identity between the Prim net-
works and cladograms — in the placement of
Phrenapatini and *Paratenetus,* for example.
The largest divergence is between the place-
ment of the tentyriine cluster in the 38
character network, where it occurs as a
relatively specialized member of the Tene-
brionoid branch of the tree. In the corres-
ponding cladogram, these OTUs attach to the
Lagrioid side of the tree as its most specialized
branch. As mentioned earlier and discussed
below, the true relationships of the tentyriine
lineage are problematic, with similarities to
both sides of the tree. It may be recalled that
in the 44 character cladogram the tentyriine
lineage appeared on the Tenebrionoid side of
the tree.

There are additional differences between
the cladograms and Prim networks. Some of
these, such as the differing placements of
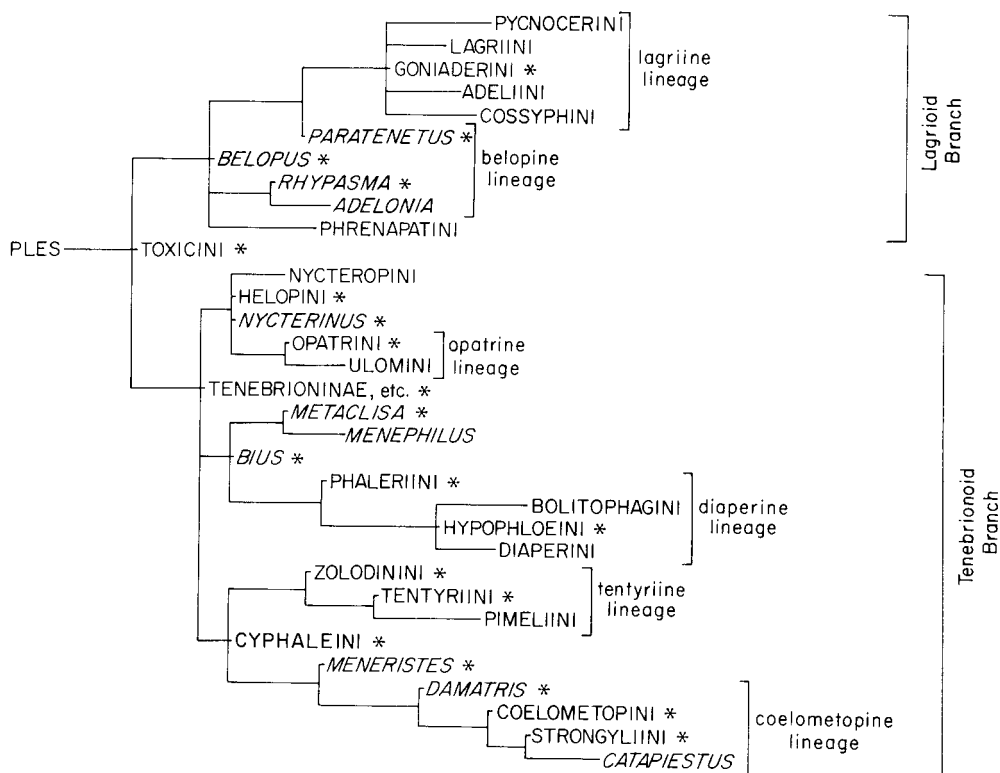*Paratenetus* and Phrenapatini, are difficult to

FIG. 56. Minimum spanning tree constructed from Prim network (taxonomic distance) based on thirty-eight characters. The lengths of horizontal lines between nodes correspond to Prim network distances; vertical lines are arbitrary. The tree is rooted at PLES. Lengths of stems for taxa denoted by asterisks are zero; short stems are shown for clarity.

assess, because the position of these OTUs is generally variable. In other regards the Prim networks seem poorer than the cladograms in OTU placement. For example, *Meneristes* replaced *Menephilus* in the coelometopine lineage in the 38 character network. The diaperine lineage appears on a terminal branch with *Bius, Metaclisa* and *Menephilus* in the same diagram. These arrangements are not suggested in any other analysis, nor by intuition.

One feature of the Prim networks may be of some significance in deriving classifications. This is their reduced number of branching levels, which is brought about by the tendency for multifurcations to occur at nodes represented by primitive OTUs. For example, four major branches and *Nycterinus* are connected to the same node in the 44 character network. In the corresponding cladogram the same OTUs entail four levels of branching which

would require nine rather than four names. For many data sets multifurcations are probably more realistic than the bifurcations sought by strict cladistic procedure.

Hennigian argumentation scheme

Before the definitive computer analyses were completed, the relationships among the thirty-three taxa chosen for analysis were expressed in an intuitive phylogenetic diagram (Fig. 58). The taxonomic groups distinguished in Fig. 58 are mostly the same as those in the computer-generated cladograms, and the branching relationships are similar as well. The important features which should be noted in Fig. 58 are: (1) the Lagrioid branch is reduced by the removal of the belopine and tentyriine lineages; (2) the belopine and tentyriine lineages are derived independently; (3) we included the Toxicini and Nycteropini
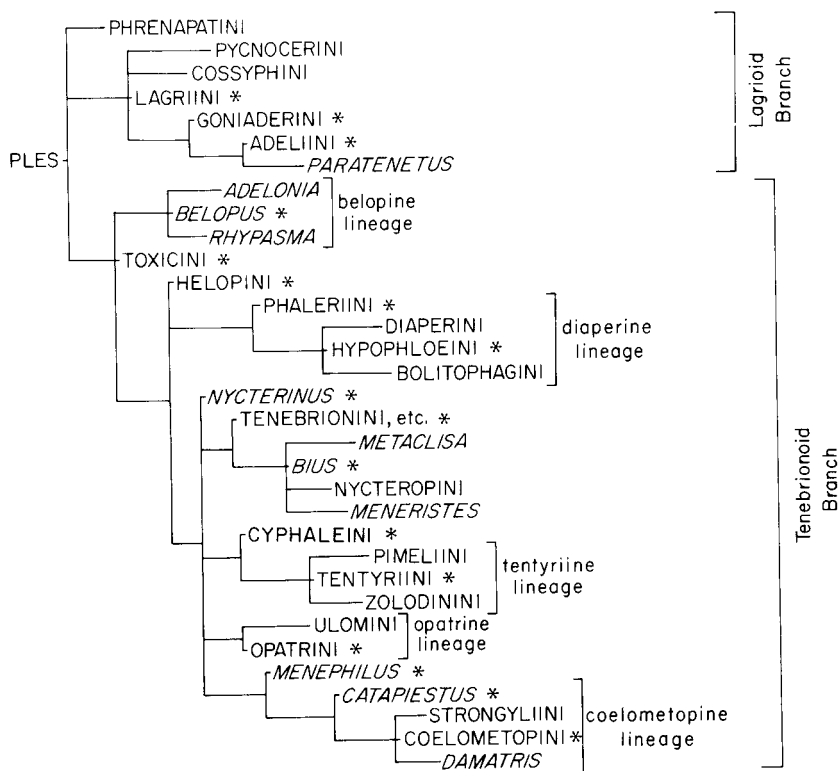
PHRENAPATINI
PYCNOCERINI
COSSYPHINI
LAGRIINI *
GONIADERINI *
ADELIINI *
PARATENETUS

PLES

ADELONIA
BELOPUS *   belopine
RHYPASMA   lineage

TOXICINI *
HELOPINI *
PHALERIINI *
DIAPERINI
HYPOPHLOEINI *   diaperine
BOLITOPHAGINI   lineage

NYCTERINUS *
TENEBRIONINI, etc. *
METACLISA
BIUS *
NYCTEROPINI
MENERISTES

CYPHALEINI *
PIMELIINI
TENTYRIINI *   tentyriine
ZOLODININI   lineage

ULOMINI   opatrine
OPATRINI * lineage

MENEPHILUS *
CATAPIESTUS *
STRONGYLIINI   coelometopine
COELOMETOPINI *   lineage
DAMATRIS

Lagrioid Branch

Tenebrionoid Branch

FIG. 57. Minimum spanning tree constructed from Prim network based on forty-four characters. Conventions as in Fig. 56.

in an enlarged tenebrionine–ulomine branch. As before, the diaperine and coelometopine lineages are very clearly defined, but the latter has a more basal position on the tree. Inspection of Figs. 49–52 and 58 will reveal that the pattern of major branches in the consensus cladogram is more similar to the intuitive diagram than to any of the computer versions. This point is considered at length below.

Taxonomic interpretations

In the following sections references to character changes and suites of characters diagnostic of particular OTUs or clusters of OTUs are keyed to the apomorphy lists below the cladistic diagrams and to the list of characters and character states in Appendix D. Character names are used throughout for ease of comprehension, followed by characters and character state numbers in parentheses. For example, (14:3) refers to character 14, state 3, an

elongate mola; (14) refers merely to character 14, molar shape. Stem numbers subtending groups of OTUs are reference points for the character changes, and are used here unless the latinized names of lineages apply to the same group of OTUs. For example, stem 32 in Fig. 54 is also referred to as the lagrioid lineage, whereas stem 29 in the same diagram has no latinized name. Discussion is limited to the more important characters, diagnostic of major lineages, with reference to reversals or parallelisms where appropriate. Complete reconstructions of character changes and suites of characters diagnostic of each stem can be extracted from the apomorphy lists and cladograms.

Lagrioid branch

The primary dichotomy on all the computer derived cladograms (Figs. 49–51) splits the OTUs into two major branches, though these differ in the placement of the tentyriine
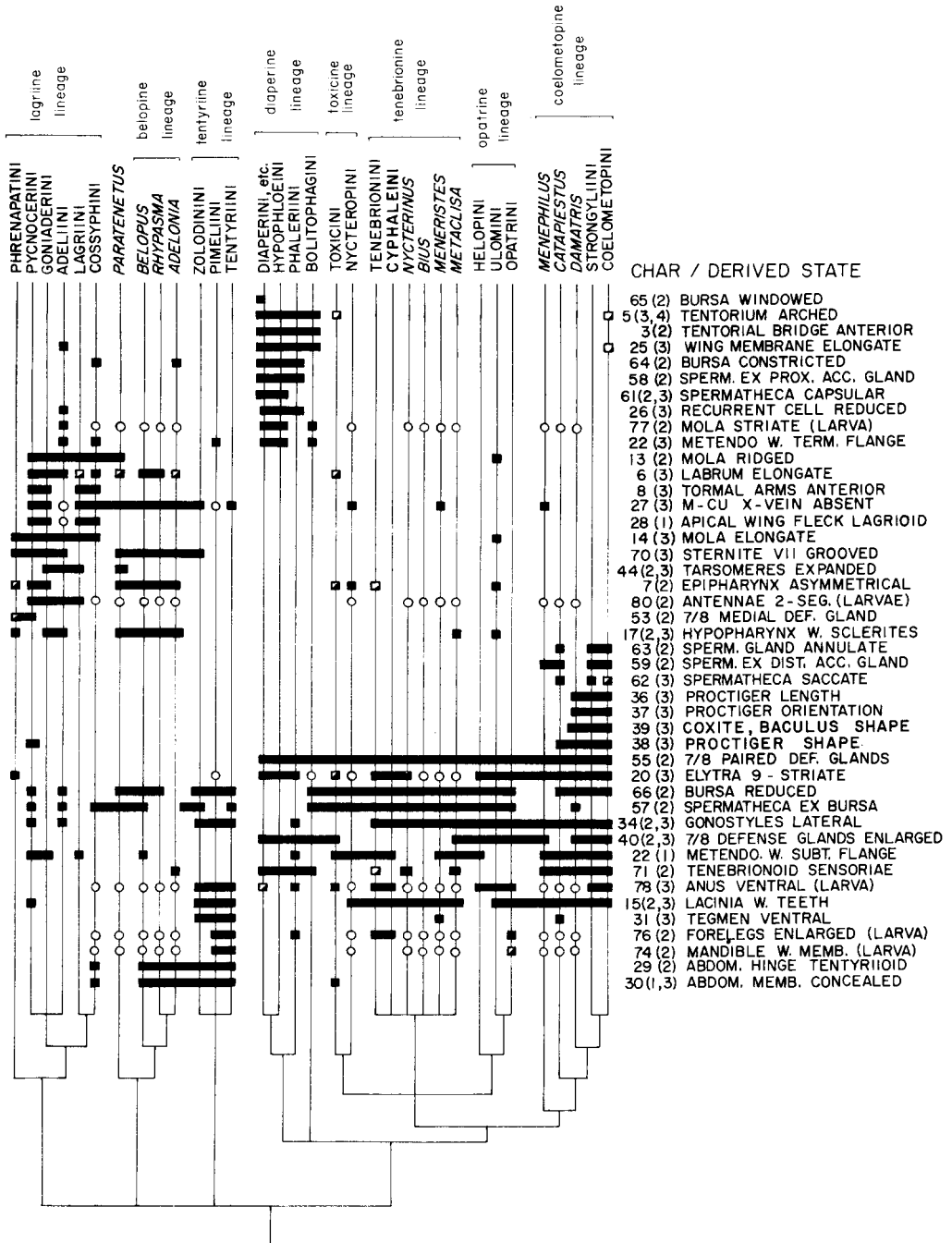
FIG. 58. Hennigian argumentation scheme based on forty-four intuitively selected characters. Derived character states are indicated by solid squares or bars. Presence of both primitive and derived states is indicated by partly solid squares. Missing or inapplicable data are indicated by circles.

and belopine clusters in the 44 character analysis. These major branches, earlier designated the Lagrioid and Tenebrionoid branches, also appear in the 38 character Prim network, and in a modified form on the other Prim networks. In the phenograms the Lagrioid taxa do not form a primary branch, but always retain their integrity as a major cluster.

The characters which define the Lagrioid branch correspond to exactly which taxa are included. In Fig. 51, where the tentyriine and belopine groups join the Tenebrionoid branch, only two characters change at stem 32. In Fig. 50, where the tentyriine and belopine lineages are included on the Lagrioid branch, five apomorphies are listed for stem 6, but all are reversed in more derived taxa. For example, specialized, two-segmented larval antennae (80:2) is reversed in stem 32 to the normal, three-segmented condition (80:1). Similarly, molar shape (14:3), the specialized apical wing fleck (28:3) and the expanded preapical tarsomere are reversed in stems 3 and 4, and the anteriorly oblique tormal arms in stem 2. Even if the tentyriine and belopine lineages are excluded from the Lagrioid branch, as in Figs. 51 and 52, it remains undefined by uniquely derived, unreversed characters (14:3 also occurs in ULOM; 22:3 is reversed in stem 11). In the 70 character analyses (Fig. 49) many more apomorphies are listed for the Lagrioid branch, but without exception are subject to reversal in more derived taxa or parallelism elsewhere in the tree.

Examination of Fig. 58 shows that while the Lagrioid group of taxa share many derived features, none is shared by every member. This mosaic distribution of characters explains why nonhomoplastic arrangements are not possible. Fig. 58 also clearly depicts the three lagrioid subgroups mentioned earlier. The cluster of taxa traditionally included in Lagriidae is always coordinate to the remainder of Tenebrionidae. As shown in Fig. 58, even this reduced group of OTUs shares only one uniquely derived feature (two-segmented larval antennae), but is strongly differentiated by a suite of derived character states shared by most members: elongate labrum (6:3); anteriorly oblique terminal arms (8:3); specialized apical wing fleck (28:1); asymmetrical epipharynx (7:2); elongate mola

(14:3); expanded tarsomeres (44:2,3). On the basis of these characters Phrenapatini and Cossyphini should probably be included in the central Lagrioid group, although both show similarities to other taxa. Inspection of Fig. 58 and the computer derived cladograms (Figs. 49–51) shows that all these taxa tend to be strongly autapomorphous. For example, on the 44 character cladogram Adeliini is distinguished by nine apomorphies, five of them unique to the entire tree; Phrenapatini is distinguished by eleven apomorphies (five unique; all losses of structures); Pycnocerini by seven apomorphies (one unique), and Cossyphini by seven (none unique). Additional apomorphies are indicated on the 70 character diagrams, but all of these are derived more than once. This strong tendency toward autapomorphy suggests that, after developing a clear set of synapomorphies, the lagrioid taxa have subsequently diverged over a long period. Such an evolutionary history is also suggested by their geographic distributions. While Lagriini are widespread, Adeliini are largely restricted to Australia and surrounding areas (a few species occur in Chile and probably southern Africa), Goniaderini to South America or nearly so, and Pycnocerini to the Old World tropics (very largely Africa). On all the cladograms Adeliini and Pycnocerini are sister taxa, and Goniaderini is their sister on the 44 character analysis. This branching sequence does not match the sequence of continental separations, probably because of undetected homoplasy. It seems likely that more comprehensive analyses will show that the major lagrioid taxa were isolated at the times that the modern continents became established. The relationships of Cossyphini and Phrenapatini vary considerably among analyses, but each shares a peculiar derived feature with a member of the core lagrioid group, which may explain their origin. Phrenapatini have more autapomorphous features than any other OTU in the cladograms. Among these are included complete loss of the ovipositor, which bears important distinguishing characters in several of the lagrioid taxa. In *Phrenapates* the membrane between sternites 7 and 8 is invaginated to produce a pouch. It was not clear from our preparations whether this pouch is glandular, but it is morphologically similar to the medial, unpaired (defen-

sive?) glands of Pycnocerini. In addition, Pycnocerini and Phrenapatini are similar in their highly specialized body configuration, with stout, cylindrical trunks, enlarged prothorax, stout, short legs and short, clavate or capitate antennae. Larvae of these two groups are quite distinctive and very different, so that the relationships of Phrenapatini remain problematic.

Cossyphini are exceedingly flattened beetles which resemble the dead leaves among which they are frequently encountered (Cloudsley-Thompson, 1977). Aside from sharing several features with the Lagrioid taxa, they show one striking similarity to *Lagria* and related genera. In both groups the posteroventral extensions of the pronotum meet in the midline and overlap behind the prosternal process. (This character is not included in the analyses described here.) It is likely that the Cossyphini represent a highly derived branch of the tribe Lagriini.

Watt (1974a) placed Lupropini, Laenini, Goniaderini and Phobeliini as subtribes of Adeliini. As reported earlier (Tschinkel & Doyen, 1980), these taxa differ in profound characters. Adeliini are unique among Tenebrionidae in having defensive glands opening between abdominal sternites 8 and 9, rather than the more usual position between sternites 7 and 8, although the glands produce substances similar to those of other tenebrionids (Eisner *et al.*, 1974). In Goniaderini glands are entirely lacking; in Lupropini and Laenini glands are similar to those of Lagriini and open between sternites 7 and 8. We have not examined *Phobelius* (the sole member of

Phobeliini), but predict that it is a derived member of Goniaderini. Our preliminary cladistic analysis of the relationships of these tribes (Fig. 59) is inconclusive. As indicated by Watt, Lupropini, etc., share many characters with Adeliini. However, our results indicate that Pycnocerini should also be included if an enlarged, monophyletic Adeliini is to be recognized. Lupropini and Laenini, on the basis of defensive gland position, appear to be the most primitive members of Lagriini. Because of these contradictory character distributions, it would seem wisest at present to recognize all these taxa at the tribal level. *Stilpnonotus* was previously classified in a separate tribe or subfamily of Lagriidae (Borchman, 1936; Blackwelder, 1945). It lacks defensive glands and in skeletal morphology is very similar to *Conomorphus* (Salpingidae), where it should be transferred.

In contrast to the relatively closely related core groups of Lagrioid taxa, the members of the belopine and tentyriine lineages are definitely more remote, and in our intuitive analysis are not placed on the lagrioid branch at all. Of the two, the belopines are clearly more similar to the core lagriines, sharing derived similarities in labral configuration (6:3; 7:2), molar sculpturing (12:2) and sculpturing of the seventh abdominal sternite (70:3) (Figs. 50, 51, 58 and 59). In lacking glands they are similar to Goniaderini, and in structure of the hinge mechanism of sternites 6 and 7, to Cossyphini as well as the Tentyriine lineage. This suite of characters suggests that the belopines are a derived branch of the Lagrioid lineage, and on most cladograms Cossyphini appear as their sister taxon. *Paratenetus*, which is usually placed in Goniaderini (erroneously in Heterotarsini in catalogues), clusters with the belopines in Figs. 49–52, and at the base of the branch including belopines and tentyriines in Fig. 59. Its relationships need further study, but *Paratenetus* differs from other Goniaderini in mouthpart structure and wing venation (Fig. 58), and should tentatively be moved to the belopine lineage.

In the 44 character analysis (Fig. 51) the belopine cluster moves from the Lagrioid to the Tenebrionoid branch of the cladogram. This is apparently because three of the characters (40, 57, 66) whose derived states define
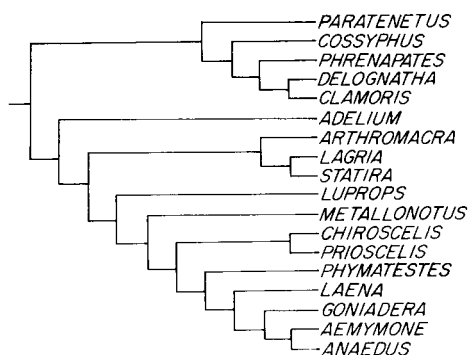

FIG. 59. WAGNER cladogram for selected genera of Lagrioid Tenebrionidae. Apomorphies and synapomorphies are deleted.

PARATENETUS
COSSYPHUS
PHRENAPATES
DELOGNATHA
CLAMORIS
ADELIUM
ARTHROMACRA
LAGRIA
STATIRA
LUPROPS
METALLONOTUS
CHIROSCELIS
PRIOSCELIS
PHYMATESTES
LAENA
GONIADERA
AEMYMONE
ANAEDUS

the Tenebrionoid branch in the 44 character analysis, were omitted from the 38 character analysis, since their consistency ratios were relatively low. In addition other characters defining stems 8 (character 22), 7 (character 15), 5 (22, 26, 31, 40) and 14 (31) were not used in the 38 character analysis. Although the belopine group appears on the Lagrioid branch in the 70 character analyses, many of the apomorphies listed in Fig. 49 are reversed in the path leading to the belopine group. Moreover, in the Prim network for the 70 character (A + L) analyses (not shown) the belopines appear on the Tenebrionoid side of the diagram. The larvae of this group have been described (Byzova, 1958), and apparently do not share the peculiar body shape and antennal morphology of lagrioid larvae. However, the descriptions are inadequate and association with adults uncertain. Detailed knowledge of larvae may allow correct placement of the belopine lineage, as well as the tentyriine lineage, discussed next.

The tentyriine lineage represents the largest group of tenebrionids in number of species. As might be expected for such a large group, the tentyriines are extremely diversified, especially in external characters such as leg and coxal structure. They also exhibit a range of variation in structure of the female reproductive tract from multiple accessory glands without a spermatheca to a bursal derived spermatheca. In several characters we compared, including ovipositor structure, wing morphology, abdominal sternite configuration and larval morphology, they are relatively uniform. One important organ system, the defensive glands and reservoirs, is absent in all known species. Finally, we examined only about a dozen species from the approximately fifty tribes and 8000 species that are recognized. Therefore our conclusions regarding primitive characteristics of this group, the origin of its derived features and its relationship to other taxa, must be considered preliminary.

The proper position of the tentyriine lineage is unclear, since it shares derived characters with both the Lagrioid and Tenebrionoid branches of the tree. The tentyriine abdominal structure (characters 29 and 30) and lack of defensive glands (53, 54, 55) are shared with the belopine group, and it is tempting to imagine that both groups evolved

from some glandless group of Lagrioids such as the Goniaderini. However, the position of the belopines is uncertain (see above) and the tentyriines themselves show only a single derived lagriine feature (27:3, m-cu vein absent). Moreover, the presence of sclerotized maxillary teeth (15:2), enlarged larval forelegs (76:2) and a membrane on the larval mandible (74:2) are shared with some members of the Tenebrionoid branch. The gross morphology of tentyriine larvae, though specialized, is suggestive of the Tenebrionoid, rather than the Lagrioid branch, and the larva of *Zolodinus* (Zolodinini) differs from primitive tenebrionoid larvae (Helaeini, Tenebrionini) in only a few features (cf. below, and Watt, 1974a).

The tentyriine lineage clusters on the Lagrioid branch of the tree on all except the 44 character computer analysis, but its position varies. In the cladogram based on adult features (not shown) the tentyriines are sister group to the remaining Lagrioids. If they are included in the analysis of Lagrioid OTUs alone (Fig. 59), the belopine and tentyriine clusters, along with *Paratenetus* also form the sister group to all other Lagrioid taxa. This position requires an initial change of many primitive character states and their subsequent reversal. In the 70 character (A + L) and 38 character cladograms (Figs. 49 and 50), the tentyriines are the most derived member of the Lagrioid branch and sister group to the belopines or one of the belopine OTUs.

On the 44 character cladogram (Fig. 51) and in the Prim networks (Figs. 56 and 57), the tentyriines shift to the Tenebrionoid side of the tree, clustering closest to the Cyphaleini or Opatrini. The belopine lineage never clusters close to the tentyriines in these diagrams, suggesting that their similarities, mainly involving loss of defensive glands, may be convergent. As in the case of the belopines, the exact position of the tentyriines depends on choice of characters, but the resulting changes in the cladograms are complex and difficult to understand. As discussed later, such sensitivity to character change is an important property of these parsimony determined cladograms, especially in deriving classifications from numerical results. It seems best to reserve judgment

when the evidence is so conflicting, and derive the tentyriines independently of the Lagrioid and Tenebrionoid lineages, as in Fig. 58.

Pimeliini differs from Tentyriini in having a membrane visible between the apical abdominal sternites (character 30), but shares nearly all other derived features with Tentyriini. On the 70 character (A) cladogram it is the sister taxon of Adeliini, a result of similarities in primitive character states (8:2) and similarity due to secondary losses of flight apparatus, with only a single valid synapomorphy (35:1). Zolodinini likewise share numerous derived features with Tentyriini (Fig. 58). The unusual features of Zolodinini (open front coxal cavities, subcubital fleck on wing, ten-striate elytra) are primitive conditions. Forecoxal cavities are open internally in Cyphaleini and many Tenebrionini; in the genus *Tenebrio* they may be internally open, barely closed, or broadly closed by a stout bridge. Subcubital flecks occur widely in taxa of the Tenebrionoid branch (Appendix B), and at least partial tenth striae are present in *Toxicum, Cryphaeus* and Dysantini. No important autapomorphies are known for Zolodinini, for either larvae or adults. Thus, it seems that the subfamilial status accorded them by Watt (1974a) is undeserved. Zolodinini may be the sister group of Tentyriini—Pimeliini, but Pimeliini may be the sister to Tentyriini, and more detailed investigation will undoubtedly reveal a complex genealogy for the Tentyriini. Recognition of every level of bifurcation would result in an impractical classification. It would seem more appropriate to recognize Zolodinini at the tribal level, coordinate with the diversified tribes of the tentyrioid group. It should be re-emphasized that larvae of Zolodinini do not differ significantly from primitive members of the Tenebrionoid side of the trees. This is the best evidence supporting a tenebrionoid origin for the tentyriine lineage. Alternatively, Zolodinini could represent a specialized derivative of some Tenebrionoid group, perhaps related to Cyphaleini, with only convergent similarities to Tentyriinae.

Tenebrionoid branch

This branch includes all those tenebrionids which possess non-musculate paired defensive glands with reservoirs opening between sternites 7 and 8. This is the only unique apomorphy shared by the entire assemblage, but nine-striate elytra (20:3), ventral larval anus (78:3) and tenebrionoid antennal sensoriae are nearly ubiquitous. Other features listed as apomorphies in Fig. 49 are either later reversed or occur also in the Lagrioid branch. On the 38 character cladogram (Fig. 50) the single apomorphy of the Tenebrionoid branch (wing membrane of intermediate length; 25:2) is reversed in stem 11; on the 44 character cladogram (Fig. 51) all the indicated apomorphies are in fact diagnostic of only part (sometimes a small part) of the tenebrionoid taxa. Inspection of Fig. 58 shows that evolution of the subgroups of the Tenebrionoid branch has been strongly mosaic, with many individual OTUs lacking character states that are otherwise diagnostic of larger groups. For example, the spermatheca is derived from the bursa copulatrix in the great majority of OTUs, and is listed as an apomorphy of the entire branch in Fig. 51. However, the bursal derived spermatheca is absent in two specialized clusters (coelometopine and diaperine), where the accessory gland has been transformed into the spermatheca (Fig. 58). Similarly, such specialized features as helical thickening of the defensive reservoir walls and reduction of secretory tubules to a few or even a single collecting duct have apparently evolved independently several times (Tschinkel & Doyen, 1980). Additionally, many OTUs in this group show few or no apomorphic features other than those characteristic of the entire Tenebrionoid branch. Numerically the Tenebrionoid branch constitutes one of the dominant groups of tenebrionids, with approximately 8000 species listed in Gebien's (1938—44) catalogue.

The distribution of character states in Fig. 58 indicates that the Tenebrionoid branch consists of three major lineages, although these are not always clearly demarked in the computer derived cladograms. Two of these lineages, the diaperine and the coelometopine, are strongly differentiated by derived characteristics. The third, the tenebrionine lineage, includes many taxa with predominantly plesiomorphous characteristics, and is difficult to differentiate, especially from the coelometopines, which are superficially similar.

On all the computer derived cladograms the toxicines are the sister group of the rest of the Tenebrionoid branch. Indeed, Toxicini are the most primitive members of the Tenebrionoid branch in several characters. The forecoxal cavities are open internally; the wings have a distinct subcubital fleck; in some species a partial tenth elytral stria is present; the ovipositor is primitive, with large, terminal gonostyles; the defensive glands are small and eversible; etc. In addition, the toxicines have a few features that are found predominantly in the Lagrioid branch (epipharynx asymmetrical, labrum subquadrate or even rather elongate). These are apparently the characters which led Watt (1974a) to recognize Toxicinae as a separate subfamily. However, despite the retention of these primitive features, the toxicines are differentiated by only a single uniquely derived character, the concealed abdominal membranes (30:1) (Fig. 51). In Fig. 51 no apomorphies are present, so that Toxicini is the sister group of the remaining Tenebrionoid branch, but has a stem length of 0. As shown in Fig. 58, most of the similarities of the toxicine group are with the tenebrionine lineage, where they are treated below. One tribe, the Bolitophagini, shares features of both the diaperine and tenebrionine lineages, and will be discussed separately below.

Diaperine lineage

In terms of synapomorphies, the diaperine lineage is among the most distinctive in the entire family. As shown in Fig. 58, the important characters include internal skeletal features (characters 3, 5, 22), wing shape and venation (25, 26), mouthparts (77) and reproductive tract configuration (58, 61, 64, 65). Some of these, such as an elongate wing membrane (25:3) and an arched tentorial bridge (3:1) occur rarely in distantly related taxa, where they are certainly convergent. The development of the spermathecal accessory gland and its subsequent elaboration as a complex, capsular structure are unique among Tenebrionidae.

The distinctiveness of the diaperine lineage is reflected in the constancy with which it appears as a separate, distinct cluster in all computer analyses. In the cladograms the diaperine cluster is discrete in all but the 38

character analysis, where the Phaleriini and Bolitophagini cluster separately. However, in the 38 character Prim network (Fig. 56), Phaleriini and Bolitophagini return to the diaperine cluster. In the phenograms the diaperines constitute the most distinct cluster in the tree and do not vary in composition.

Despite this apparent cohesiveness, the exact limits of the diaperine lineage are unclear. While Diaperini, etc., and Hypophloeini are unquestionably sister taxa, the relationships of Phaleriini and Bolitophagini are problematic, and they alternate as the most primitive member of the diaperine lineage. Bolitophagini share with the diaperines an arched tentorial bridge (5:3, 4), elongate wing membrane (25:3), striate mola in the larva (77:2) and an enlarged, terminal flange on the metendosternite arms (22:3). These are mostly rather simple characters, and could have arisen convergently through adaptation to the fungivorous habit common to Bolitophagini and most diaperines. For example, an elongate wing membrane has apparently arisen several times in taxa with a foreshortened body, as explained above under character selection. Furthermore venation is somewhat different in Bolitophagini and the diaperines, again suggesting convergence in membrane length. More importantly the most unique apomorphy of the diaperine lineage, the accessory gland-derived spermatheca (59:2) is not shared with any Bolitophagini. Rather, the bolitophagine spermatheca is derived from the bursa copulatrix, as in the toxicine, tenebrionine and opatrine lineages.

Watt (1974a) combined Bolitophagini and *Diaperis* as his subfamily Diaperinae, based on (1) the carinate outer tibial margins of adults; (2) a dorsal tubercle on the mandibles of larvae. Carinate tibial margins also occur in *Amenophis* (coelometopine lineage; forelegs only), *Pterohelaeus* and *Titaena* (Tenebrionine lineage), *Belopus* (lagriine lineage), *Calymmus* and *Ozolais* (Toxicine lineage) and in *Hypophloeus*. The mandibular tubercle is known only from *Diaperis* and Bolitophagini, and varies considerably in the latter (J. F. Lawrence, in litt.). Moreover the tubercle is a simple structure which could easily be homoplastic. Watt also points out that larvae of *Diaperis* and Bolitophagini share spiracles with a peripheral ring of air-tubes and a terminal anus

(primitive features). Peripheral air-tubes have been retained in many distantly related taxa, as shown by Watt. The position of the larval anus is not constant in the diaperine group. In *Hypophloeus* and *Menimus* the anus is distinctly terminal (Fig. 45), but in *Diaperis* and Bolitophagini the ninth segment is slightly enlarged and the anus becomes sub-terminal. In *Platydema* the seventh segment is further enlarged and the anus distinctly sub-terminal (Fig. 46). In the tenebrionine, opatrine and coelometopine lineages the reduced tenth segment and ninth sternite sub-tend the much enlarged ninth tergite (Fig. 47). Other differences cited by Watt between *Diaperis* and other diaperines are variable (e.g. presence of laminae on metendosternite; position of anterior tendons of metendoster-nite; antennal shape).

Important larval differences between the diaperine and bolitophagine groups include the following (J. F. Lawrence, in litt.): (1) In *Diaperis* and *Neomida,* but not Bolitophagini the frons is produced forward forming a distinct, horn-like process. (2) In *Diaperis* and *Neomida* the first antennal segment is much smaller than the second. (3) The gula, submentum and mentum are clearly demarcated by sutures in *Diaperis* and *Neomida,* indistinct in Bolitophagini (see also Hayashi, 1966). (4) The ninth tergum of *Diaperis* has a small, median tubercle, which could be derived from the larger median process in genera such as *Platydema.* Bolitophagini usually have two small urogomphi, and never have the median process. (5) Ventral pygopods are present in Diaperini (including *Diaperis*), absent in Bolitophagini.

Diaperis is strongly autapomorphous, especially in ovipositor and defensive gland structure, but its similarities in important diagnostic features of the female reproductive tract are unmistakably with other diaperines, not bolitophagines. The proper position of Bolitophagini remains unclear. The results presented here indicate that it may be the most primitive member of the diaperine lineage. Alternatively Bolitophagini could represent an independent specialization for the fungivorous mode of life, perhaps from a toxicine ancestor.

Phaleriini were included by Watt in his subfamily Tenebrioninae, based on the
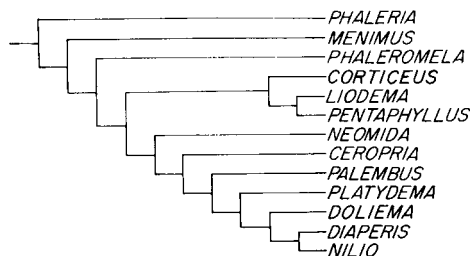

FIG. 60. WAGNER cladogram for selected genera of the diaperine lineage.

position of the larval anus and the mandibular structure. The ovipositor structure, with shortened proctiger and coxite and small, lateral gonostyles also suggests tenebrionine or opatrine affinities. The wings and tentorium are modified as in the diaperines, and the base of the accessory gland is enlarged, apparently as a spermatheca, suggesting that Phaleriini are an early derivative of the diaperine lineage. This is the position usually accorded Phaleriini in catalogues, apparently based on general similarity in external features of adults. The shortened ovipositor with reduced gonostyles occurs in most tenebrionoids which oviposit in soil (e.g. Helaeini, Opatrini, Tenebrionini) and has probably arisen independently several times.

Hypophloeini and Gnathidiini were combined as the subfamily Hypophloeinae by Doyen & Lawrence (1979), based primarily on characteristics of the larvae. Most of these features could not be included in the present analyses, since larvae of so many taxa are unknown. Therefore, the fact that Gnathidiini (*Menimus*) does not cluster next to Hypophloeini in Fig. 60 is misleading. The present results do suggest that subfamily status for Hypophloeinae is inappropriate, unless other diaperine tribes are similarly elevated.

Under Diaperini are included several taxa usually recognized at the tribal or even sub-family level (Fig. 60). *Nilio*, originally placed in a separate family, has been included as a subfamily of Tenebrionidae in recent treatments (Doyen, 1972; Watt, 1974a). The present analysis suggests that it represents a highly derived member of the diaperine lineage which should be given no more than tribal status. This conclusion is based primarily on the presence of a typical diaperine female reproductive tract. In wing structure, the

strongly reduced ovipositor, and in several larval characteristics *Nilio* is strongly autapomorphous.

In Fig. 60 *Doliema*, which is placed in Ulomini in all existing classifications, clusters between *Platydema* and *Diaperis*. The same position was held by *Doliema* in preliminary analyses. Fig. 60 includes relatively few genera of the entire diaperine lineage, and must be considered very preliminary. Nevertheless, on the basis of all important diagnostic features *Doliema* belongs in the core diaperine group. As discussed in detail below (see Tenebrionine–Toxicine–Opatine   lineages), the Ulomini are clearly polyphyletic. Besides *Doliema, Gnatocerus, Echoceras* and probably many more 'ulomine' genera belong in the diaperine lineage, close to *Platydema*. It may also be mentioned here that closure of the mesocoxal cavities by the sterna (19:1), usually considered diagnostic for Ulomini, is approached in many Diaperini, where the mesepimeron becomes very narrow. In *Pentaphyllus, Hypophloeus, Menimus* and *Phaleria* the cavities are entirely closed by the sterna.

Coelometopine lineage

In terms of the characters analysed here, the coelometopine lineage is the most clearcut major group of Tenebrionidae. The characters which differentiate the coelometopines are unequivocal, and with the exception of a few genera are fully expressed in all members. Moreover, the exceptions mostly involve only one or a few of the differentiating features, and are useful in explaining how the specialized coelometopine characters may have evolved. On the basis of external structures, the coelometopine group is weakly differentiated, and has always been confused with the tenebrionine lineage. The similarity between these two is especially striking among genera which inhabit the same types of niche, for example the Cyphaleini and Coelometopini, which both occur predominantly on decaying wood and are frequently flightless.

Three important features define the coelometopine group: (1) a highly specialized ovipositor, with modifications involving the proctiger (36:3; 37:3; 38:3), and coxites (39:3), which function in a different manner from other Tenebrionidae (Tschinkel &

Doyen, 1980). (2) The derivation of the spermatheca from the distal part of the accessory gland (59:2; 62:3; 63:2). (3) Very large defensive reservoirs strengthened by helical thickenings of the cuticular wall (56:2) and glands opening via a few large collecting ducts (42:5). The last character has arisen convergently in certain Diaperini, but then differs from the coelometopine condition in details (Tschinkel & Doyen, 1980).

All the definitive coelometopine characters are present in nearly all genera of the tribes Coelometopini, Misolampini, Eutelini, and in many genera now placed in Tenebrioninae (see Appendix E). The old division between Coelometopini and Tenebrionini was based primarily on presence or absence of wings, a variable feature in both. In terms of the characters analysed here, the genera of the coelometopine lineage vary only in details of structure, and should be placed in a single tribe for which we propose the name Coelometopini Lacordaire, 1859: 358.

Cnodalonini   as   presently   constituted include many species which share defensive gland, female reproductive tract and ovipositor characteristics with Coelometopini. Among the taxa we examined, this group includes *Cyrtosoma, Euthysternum, Oedemutes, Pseudebax* and *Tetraphyllus*. Another group of genera have glands which lack annular thickenings, have the spermatheca only slightly enlarged, and have coxite lobes 3 and 4 of the ovipositor fused. This group includes *Eucyrtus, Hapsida, Hemicera* and *Platycrepis*. Still other genera, including *Camaria, Graptopezus, Mylaris, Taphrosoma, Tauroceras* and *Talanus,* combine features from the first two groups (see Tschinkel & Doyen, 1980, for details). *Cnodalon,* the generitype, was unavailable for dissection, but superficially it resembles *Cyrtosoma,* which is typically Coelometopine. We have not examined enough genera to know whether the abrupt termination of the epipleuron at about the level of the fourth visible sternite is diagnostic of Cnodalonini. At present the boundary between Cnodalonini and Coelometopini remains unclear.

Besides the major taxonomic rearrangements described above, *Bradymerus* and *Dicraeosis,* both previously included in Bolitophagini, must be moved into the coelometopine group, based on the structure of their defensive

glands, ovipositor and female reproductive tract. The spermatheca is not inflated, indicating membership in Cnodalonini. With Bolitophagini these genera share only superficial similarities in surface sculpturing and body shape. *Hapsida,* previously placed in Diaperini, has a typical coelometopine ovipositor. The female reproductive tract and defensive reservoirs are as in Cnodalonini. *Hapsida* shares only superficial similarity in body shape and antennal form with Diaperini, and should be placed in Cnodalonini.

Damatris, presently included in Cnodalonini, possesses all the important coelometopine features except the female reproductive tract. In *Damatris* multiple glands leave the bursa copulatrix, an apparently primitive condition which occurs elsewhere in belopines and some lagriines. Retention of this primitive feature in a taxon which is so clearly coelometopine indicates that the coelometopine lineage could not have evolved from some group with a single bursa derived spermatheca, as indicated on all the computer generated cladograms. On all the cladograms the bursa derived spermatheca is gained, then secondarily lost when the coelometopine spermatheca is evolved; the coelometopine spermatheca is then lost and the multiple tube arrangement regained in *Damatris.* While this pattern may minimize homoplasy over all characters, it seems more likely that *Damatris* has retained the ancestral reproductive tract.

The other major groups composing the coelometopine lineage lack additional diagnostic features. In Strongyliini and Talanini the defensive reservoirs, which have no helical thickenings, are small conical pouches, similar to those of Cyphaleini and Tenebrionini. Strongyliini are unusual in being frequently brightly coloured, diurnal and relatively weakly sclerotized. Thus, it is not clear whether the small defence reservoirs are primitive or a secondary reduction. Talanini (not included in analyses reported here) are similar to Strongyliini in all characters except the construction of the ovipositor. In *Talanus* the ovipositor is specialized as a strongly sclerotized, blade-like structure, adapted for piercing or slicing. The proctigers retain the characteristic orientation and movement of coelometopines, and Talanini appears to be a specialized derivative of Strongyliini. *Ainu,*

with one species from Japan, has been included in Strongyliini. The reproductive tract and defence system support this placement, but the ovipositor is developed as a short, vertically oriented pair of sclerotized blades. Whether this structure is homologous with the blade-like ovipositor of *Talanus* is unclear, since the proportions and shapes of the coxites and proctiger are quite different. *Praogena, Nesogena,* and closely related genera from southern Africa, presently placed in Strongyliini, belong in the tenebrionine lineage according to all important characters, possibly near Helaeini.

Two genera we examined do not fit the present tribal classification. *Catapiestus* has the female reproductive tract typically coelometopine, but has small defence reservoirs without thickenings and has the ovipositor unmodified except for proctiger shape. *Menephilus* has helical thickenings around the large defence reservoirs, and has a simple (non-saccate) spermatheca derived from the distal accessory gland. In other characters it is similar to members of the tenebrionine and opatrine lineages. *Catapiestus* and *Menephilus* are clearly peripheral members of the coelometopine cluster, and on cladistic grounds alone would have to receive higher taxonomic rank, perhaps at the tribal level.

The coelometopine lineage almost certainly arose from some primitive member of the Tenebrionoid group, or a precursor to it. Coelometopines and the Tenebrionoids share numerous features of skeletal morphology, including general similarity in mouthparts, wings, and male genitalia. Larvae of the two groups seem to differ only in detail, and often occupy similar feeding niches. In the 44 character and 70 character (A + L) cladograms (Figs. 49 and 51) the sister group to the coelometopines is the cluster *Bius−Meneristes−Metaclisa−Nycteropus.* In the 70 character cladogram common volume of defensive reservoirs (41:1) and presence of tenebrionoid antennal sensoriae (71 : 2) are listed as apomorphies. Both features appear to have been evolved independently several times, even in groups as diverse as the coelometopines and diaperines. The single apomorphy in the 44 character analysis, reservoir shape (69:3) is an extremely labile feature. These apomorphies are unconvincing, and can be regarded as

computational noise. In the 38 character and 70 character (A) analyses the sister to the coelometopines is the opatrine group. The only apomorphy which could indicate a real relationship is the oblique proctiger orientation (37:2), which occurs in *Catapiestus* and a few other coelometopines. For all coelometopines their highest phenetic similarities outside the coelometopine group are with Cyphaleini and Helopini. For *Menephilus,* which has more primitive characters than any other coelometopine, the similarities to Helopini and Cyphaleini are greater than to the other coelometopine taxa. Both Helopini and Cyphaleini include many genera which use rotting wood as a larval feeding substrate, as in many coelometopines, and larvae of helopines and coelometopines usually have complex urogomphi. However, Helopini and Cyphaleini as well as all tenebrionines have a bursa-derived spermatheca. If their similarities to Coelometopini indicate cladistic relationship, the divergence must have occurred before the spermatheca differentiated. It is also possible that bursa derived spermathecas have evolved more than once. Some evidence for this exists in the great diversity of structure among bursal derived spermathecas, as discussed below.

Tenebrionine, toxicine and opatrine lineages

This assemblage is united by having the spermatheca derived from the bursa copulatrix (57:2), which is reduced (66:2), as in the coelometopines. As shown in Fig. 58, a bursa derived spermatheca is also present in Bolitophagini, as well as in many tentyriines, belopines and some lagriines. The distribution of this character, which disagrees with the numerous features delimiting these major groups, suggests that derivation of a spermatheca from the bursa copulatrix has occurred several times independently. Reduction in the size of the bursa has occurred in all lineages except the diaperine. Multiple evolution of the bursa derived spermatheca is also suggested by variation in spermathecal structure. In Adeliini, Pycnocerini and *Damatris,* similar multiple spermathecal tubes are present (one may be enlarged). In the toxicines a single, simple short spermathecal tube is present. In some *Tenebrio, Alphitobius* and their close relatives the spermatheca is T-shaped.

In Eleodini, Meracanthini and most Opatrini it is very elongate and coiled into a tight ball. In addition, the branching and relative diameter of the spermathecal tube varies considerably, as do details of accessory gland and bursa structure (see Tschinkel & Doyen, 1980, for details).

In most other characters members of this complex show a mosaic of primitive and derived states. For example, tenebrionoid sensoriae (71:2) are absent in Toxicini (including Nycteropini), some Tenebrionini (including *Tenebrio*), Cyphaleini, Helopini, Opatrini and Ulomini. Small, eversible defence glands (40:1) are retained in Tenebrionini and Cyphaleini; a primitive ovipositor with large, terminal gonostyli (34:1) occurs in Toxicini and Nycteropini; laminae or flanges on the metendosternite (21:1), subcubital wing flecks (24:1), and internally open procoxal cavities (18:1) are other primitive features which commonly occur in this group, especially in the tribes Toxicini, Tenebrionini and the cluster of Australian tribes related to Cyphaleini. At the same time, many of the tribes included here are distinguished by autapomorphous features. For example, alleculines universally have the tarsal claws pectinate, yet in other features clearly belong to the tenebrionine group, and probably warrant no more than tribal status, although recognized as a family in most classifications. The specific constellations of characters which distinguish various subgroups among these beetles with bursa derived spermathecas are described in somewhat more detail below, but in general their interrelationships are unresolved by the characters we studied. The recognition that the coelometopine taxa are distinct from the tenebrionines leaves the latter less heterogeneous. Nevertheless, the tenebrionine–toxicine–opatrine complex remains a dumpcan assemblage, with numerous small tribes of uncertain relationship.

Among the OTUs with bursal derived spermathecas, three subgroups are distinguished on the cladograms. For purposes of discussion we have called these the toxicine, opatrine and tenebrionine lineages, although the characters distinguishing them are less fundamental than for the diaperine, coelometopine and other lineages. The characteristics of toxicines were discussed at some length

above. They are most notable because of their large number of primitive character states. As noted previously, the toxicines are the sister group to the rest of the Tenebrionoid branch of the tree in all computer generated cladograms, but are never distinguished by unique (nonhomoplastic) apomorphies. The most important apomorphies are probably: (1) clubbed antennae (1:4), which are uncommon in Tenebrionidae, and, as noted by Watt, suggest a relationship between Toxicini and Nycteropini; (2) labral and epipharyngeal structure (7:2; 9:2); (3) concealed position of abdominal sternite membrane (30:3). The other apomorphies listed in Figs. 49—51 represent unlikely reversals to primitive states or simple characters which occur in one to many unrelated taxa. Note that in the 38 character cladogram Toxicini is the sister group to all other members of the Tenebrionoid branch of the tree, but has no apomorphies. Toxicini certainly differ from Tenebrionini, but most peculiar toxicine features are plesiomorphous, and scarcely warrant recognition at the subfamily level, as proposed by Watt (1974a).

Watt (1974a) placed *Nycteropus* and its relatives in his Toxicinae. The most important character shared by Nycteropini and Toxicini is the clubbed antennae. The epipharynx is asymmetrical (7 : 2) in members of both groups, but this also occurs in Ulomini and some Tenebrionini. The most distinctive apomorphy of Toxicini, the concealed abdominal membranes, does not occur in Nycteropini. Thus, the sister group relationship between Toxicini and Nycteropini (Fig. 58) must be considered tentative. Watt (1974a) remarked that Dysantini were in some respects intermediate between his Diaperinae (= *Diaperis* + Bolitophagini) and Toxicinae, but included them in Diaperini. Dysantini which we examined have a spermatheca which is clearly bursal derived, an asymmetrical epipharynx (7:2), tormal

arms as in Toxicini (8, 9), a sclerotized ligula (17:3), a distinct subcubital wing fleck (24:1), invaginated abdominal membranes (30:3), primitive ovipositor with large, terminal gonostyles (34:1), and short, conical defence reservoirs, with the gland tubule terminations on the apical half of the reservoirs (69:3; 42:1). With Diaperini the dysantines share no important characters (the wing membrane is intermediate in length in *Calymmus* and *Dysantes*). The dysantines clustered with Toxicini in all preliminary analyses, and were not run as separate OTUs in Figs. 49—51. A cladogram of the taxa we examined is shown in Fig. 61, which places *Toxicum* and *Cryphaeus* as relatively derived members. In some features (wing membrane length; apical distribution of secretory tubule terminations on defensive reservoirs; antennal structure; gonostyle position and size; bursal structure) Dysantini are similar to Bolitophagini, suggesting that Bolitophagini may ultimately be derived from the toxicine lineage via Dysantini. The similarities of Bolitophagini to the diaperines could be in response to similar feeding substrates (conchs of wood-rotting polypore fungi). Discovery of the larvae of Dysantini may clarify this problem.

The opatrine cluster includes the subfamily Opatrinae (*sensu* Medvedev, 1968) and Gebien's (1938—44) Helopini and Ulomini (s.s.). This combination of taxa has not been recognized previously, but recurs in nearly all the analyses presented here. However, the apomorphies uniting these taxa mostly involve losses of characters (24:3) or simple states which could easily evolve convergently (26:2; 41:2; 68:2). Dorsal or dorsolateral gonostyles (34:3) and an obliquely oriented subquadrate proctiger (37:2; 38:1) are probably the strongest apomorphies, but relate only Opatrini and Ulomini, although Helopini is cladisotically very near. It should be pointed out that Ulomini in the sense used here includes only *Uloma* and closely related genera (we examined *Uloma, Eutochia, Uleda, Antimachus* and *Alegoria*). *Gnatocerus, Echoceras* and *Doliema* belong to the diaperine lineage, and many other 'Ulomine' genera are probably diaperines. *Tribolium, Alphitobius, Ulosonia* and *Metaclisa* (included in Ulomini or Cnodalonini in catalogues) belong in the Tenebrionine lineage. Ulomini
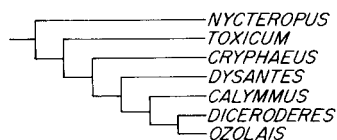

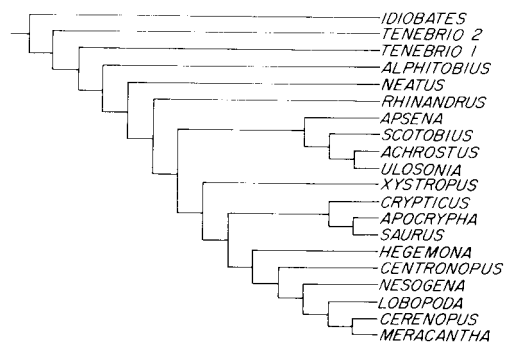FIG. 61. WAGNER cladogram for selected genera of the toxicine lineage.

FIG. 62. WAGNER cladogram for selected genera of the tenebrionine lineage.

in this restricted sense is a phenetically compact group sharing many adult and larval features and common feeding substrate (punky, rotten wood). It is important to stress that there are major differences between Ulomini and Opatrini, especially in the larvae. The apparent relationships between them need to be critically examined over more taxa and characters.

Even without Helopini and Ulomini, the opatrine lineage is one of the dominant groups of Tenebrionidae. Among species with defensive glands, only members of the opatrine lineage have been very successful at entering the arid environments dominated by the glandless Tentyriinae. In the steppe and desert regions, especially in the Old World, these beetles are extremely diversified and abundant. If a subfamily Opatrinae is to be recognized, it would have to be on the basis of number of species and diversity in superficial characters such as body shape and leg morphology. Our examination of about twenty-five species from several subtribes (Appendix A) indicates little differentiation from the tenebrionine lineage in mouthpart structure, skeletal morphology, wing venation, ovipositor structure and female reproductive tract organization. Many subgroups of Opatrinae possess a curious apomorphic character in males. The lateral lobes are modified as a pair of 'clavae', hinged basally, with apices rotating outward as the median lobe is protruded. It is not clear from our limited sample whether this character state is primitive to the entire Opatrinae, being subsequently lost in many taxa. Alternately, clavae could have evolved in a restricted group of Opatrinae.

Among more distinctive opatrines we examined are: (1) *Pedinus*, which lacks clavae on the aedeagus and is distinctive in body shape. In other features *Pedinus* clearly belongs to the opatrine group. American members of Pedinini (*Blapstinus, Opatrinus*, etc.) are typical opatrines, and probably not closely related to *Pedinus*, although some *Blapstinus* lack clavae. *Opatrinus* has mistakenly been included in Tenebrionini in some faunal works (Arnett, 1960). (2) *Blaps* and *Eleodes*. Some members of these genera share great superficial similarity in body shape, probably because of their similar ambulatory habits. They differ in configuration of the spermatheca, *Eleodes* possesses clavae, *Blaps* does not, and the defensive glands and reservoirs are different (Tschinkel & Doyen, 1980). They appear to represent highly modified, but probably not very closely related, opatrine derivatives.

The tenebrionine lineage proper includes an ill-defined assemblage sharing mostly primitive features. In the computer generated cladograms the tenebrionine OTUs tend to form chains of single taxa which are sisters of very large heterogeneous clusters (examine especially Fig. 49). As shown in the phenograms (Figs. 53 and 54), mutual similarity among these OTUs is high, although they also have high similarity to other taxa. For example, *Bius, Metaclisa* and *Nycterinus* cluster unpredictably with different OTUs or clusters in the cladograms and Prim networks, but are phenetically close to Tenebrionini. Taxa with predominantly primitive features typically show similarities to diverse taxonomic groups. In the present analyses many characters change polarity several times in the computer generated cladograms, so that primarily plesiomorphous character states may be secondarily derived. In this situation taxonomic position may change radically, depending on the combination of characters analysed. *Bius*, etc., should be classified in Tenebrionini until discovery of their larvae or of more diagnostic characters indicates a different taxonomic position.

Within the tenebrionine lineage several quasi-distinct clusters can be distinguished. Tenebrionini (s.s.) are characterized by a densely setose connecting membrane between the median and lateral lobes of the aedeagus

(32:1). This group includes *Tenebrio*, *Neatus*, *Idiobates* and *Bius*. On the basis of external features *Neatus* and *Idiobates* have been included in *Tenebrio* in some classifications. A setose connecting membrane also occurs in *Toxicum quadricorne* Fabricius, and may indicate a close relationship between Toxicini and Tenebrionini. *Tribolium, Alphitobius, Zophobus, Achrostus, Lordoderus* and *Rhinandrus* share many features with this group, and properly belong in Tenebrionini. In these taxa plesiomorphous character states are frequent and autapomorphies are common. In the sense proposed here, Tenebrionini is a relatively small tribe, with most species apparently native to the Old World tropics.

The Australian tribes Helaeini, Cyphaleini and Nyctozoilini always clustered together in preliminary computer analyses. Very few characters are shared by all members of this group, which shows plesiomorphous states for many characters. However, many apomorphous states occur predominantly among the cyphaleine taxa, but not in every OTU, apparently causing them to cluster together. For example, reservoir shape (69:3), mesendosternite configuration (67:2; 68:2), visible labro-clypeal membrane, pubescent tarsi (43:2), defence glands lacking common volume (41:2), and several derived features of the ovipositor occur in most of the cyphaleine group. *Titaena*, previously placed in Cnodalonini, should be included in the cyphaleine group. According to the characters we analysed, the tribes Helaeini, Cyphaleini and Nyctozoilini cannot be differentiated by significant characters and should probably be combined. It may be noted that among the taxa we studied, no Tenebrionini (s.s.) occur naturally in Australia. *Meneristes* is difficult to classify, but its relationships seem to be with Cyphaleini.

The remaining tribes of the tenebrionine lineage do not cluster into taxonomically meaningful units. Their positions vary, sometimes drastically, among different analyses, and the apomorphies defining clusters are weak. The tribes included in this problem group are: Alleculini, Amarygmini (including Meracanthini), Apocryphini, Cerenopini, Crypticini, Nycterini, Scaurini and Scotobiini. Despite the lack of convincing similarities among these taxa, many are strikingly autapomorphous in external features, and have long been recognized nomenclaturally. The best example is Alleculini, which was universally given family status until quite recently (Doyen, 1972; Watt, 1974a), but Amarygmini, Apocryphini and Saurini are probably equally distinct. The relationships indicated by the WAGNER analyses of some genera of the Tenebrionine group that we examined are shown in Fig. 62 (Cyphaleini, etc., were analysed separately). Note that *Idiobates, Tenebrio* and *Neatus* cluster together at the base of the cladogram, but with a chained linkage pattern. The alleculine OTUs (*Xystropus, Lobopoda*) are isolated from one another, apparently because *Xystropus* retains primitive features such as laminae on the metendosternite, small defensive reservoirs with common volume, and less consolidated gland tubule terminations. This displacement emphasizes the minor nature of the characters defining Alleculini, and also reflects the characters we chose to analyse, of course. It must be stressed that only a fraction of the pertinent genera are represented in Fig. 62, and the suggested relationships are extremely tentative.

General Discussion

Value of cladistic and phenetic approaches

It has been claimed that cladistic classifications are superior to phenetic ones, not only philosophically, but also because cladistic classifications should be more stable and predictive. A philosophical preference for cladistic or phylogenetic classifications appears to stem from the desire among taxonomists for natural arrangements — i.e. those which reflect evolutionary branching relationships, rather than arrangements designed for convenience or other unnatural reasons. It seems clear from comparisons of phenetic and cladistic analyses of the same data sets (Duncan, 1980; Schuh & Polhemus, 1980; Baverstock *et al.*, 1979) as well as for computational reasons (Farris, 1973, 1979) that phenetic classifications are less natural than cladistic ones. This conclusion is strongly supported by the analyses presented above: inspection of Figs. 49–52 and 57 will readily show that the computer generated cladograms are much more similar than the phenograms to the best

intuitive cladogram that we were able to construct. However, the results presented here indicate that phenograms are efficient indicators of cladistic relationship among relatively closely related OTUs. At more distant levels phenograms become progressively poorer as descriptors of cladistic relationship. It should be noted that relative in this context refers to levels of relationship within a given study. A phenogram would probably portray species groups accurately, for example, but not the relationships among groups. The ability of phenograms to detect groups of closely related OTUs suggests a use in preliminary screening to reduce numbers of OTUs before cladistic analysis. Some of the groups would be based on primitive shared characters (as the tenebrionine group here), but phenetic similarities could be estimated from derived character states only. Moreover, for purposes of classification, clustering phenetically similar OTUs together could sometimes be advantageous, since simpler classifications would result.

In certain respects, the computer produced cladograms shown here are no better than phenograms, and have additional problems of their own. Schuh & Polhemus (1980), citing Platnick (1978), suggested that many desirable properties of classifications — including naturalness, predictivity and stability — are equivalent. Our results strongly indicate that naturalness and stability need not be strongly correlated. The three computer generated cladograms illustrated (Figs. 49—51) show numerous minor dislocations of OTUs, many small discordances in cluster membership, and even some major structural differences. Table 1 compares stability of the terminal clusters for the cladograms, phenograms and primnets, respectively. Since no phenogram was derived for adult characters only, two figures are listed for the cladistic analyses. The first is based on all four cladograms. The second omits the cladogram based on seventy adult characters. The lowest average stability figure (0.63) is for all cladistic analyses combined. If the 70 character adult cladogram is omitted the average increases to 0.73, still markedly lower than that for the phenograms (0.88), which show the least change in memberships in the terminal clusters.

Stability at lower branching levels is much more difficult to compare since the major clusters circumscribed by the phenograms and cladograms are so drastically different. Quantitative indices of similarity have been used to compare branching diagrams of different types, such as phenograms and cladograms (Phipps, 1971; Slobodchikoff & Johnson, 1973; Duncan *et al.*, 1980). The results of some of these comparisons are interesting. Duncan, for instance, was able to show that various cladistic approaches yielded relatively similar results, while Prim networks and phenograms were respectively more divergent. However, the same conclusion is generally apparent from inspection of cladistic and phenetic interpretations of the same data. Such indices suffer the disadvantage of averaging differences and similarities, since they are based on correlative comparisons of the number of nodes separating pairs of OTUs. These indices are equivalent to cophenetic correlation coefficients between phenograms, and, like cophenetic coefficients, may have similar numerical values for very different comparisons. Vague indices of this sort are of little systematic value, and were omitted from this study.

Schuh & Polhemus (1980) used consensus trees (Adams, 1972) to compare stability of numerical cladistic and phenetic classifications of leptopodomorph Hemiptera. They concluded that cladograms were definitely more stable, because more of their original structure was retained in the consensus tree. Consensus trees for the cladograms (70A, 70A + L, 44, 38 characters) and phenograms (70A + L, 44, 38) are shown in Figs. 61 and 62. The consensus tree for phenograms has twelve dichotomies, seven trichotomies and two quadrotomies. The consensus tree for the cladograms has seven dichotomies, nine trichotomies, one quadrotomy and one pentotomy. Since four cladograms were condensed and only three phenograms, the consensus trees are not entirely equivalent. Nevertheless, it seems evident that the amount of structure shared by the phenograms is approximately equivalent to that shared by the cladograms. We hasten to reiterate that the cladogram consensus is vastly closer to our intuitive interpretation of tenebrionid relationships.

The variable positions of the belopine and tentyriine clusters on the different cladograms

TABLE 1. Comparison of results of different methods of analysis, showing cluster membership of each OTU (left column) in cladograms, phenograms and primnets. Numbers at tops of columns refer to the number of characters analysed. Cluster membership is indicated by the four-letter upper-case abbreviations, which are defined in the text under Computational Procedures. Parentheses around cluster membership designations indicate a single OTU or the most similar OTU, without cluster membership. Numerical values for each taxon represent the reciprocal of the number of different cluster memberships for the cladograms (CLAD), phenograms (PHEN), Prim networks (PRIM), respectively. Two values are shown for the cladograms. A, values for all four analyses; B, values for all except the analysis based on seventy adult characters. Abbreviations not explained in the text are as follows: Adel, *Adelonia*; Adlm, Adeliini; Belo, *Belopus*; Bius, *Bius*; Coss, Cossyphini; Goni, Goniaderini; Hela, Cyphaleini; Helo, Helopini; Mene, *Meneristes*; Meta, Metaclisa; Nycp, Nycteropus; Para, *Parateneus*; Phrn, Phrenapatini; Pycn, Pycnocerini; Toxi, Toxicini; Ulom, Ulomini; Zolo, Zolodinini.

| | CLUSTER MEMBERSHIP | | | | | | | | | | MEMBERSHIP STABILITY | | | | |
| | CLADOGRAMS | | | | PHENOGRAMS | | | PRIMNETS | | | CLAD | | | | |
OTU	38	44	70(A)	70(A+L)	38	44	70(A+L)	38	44	70(A+L)	A	B	PHEN	PRIM	X̄
CATAPIESTUS	COEL	COEL	COEL	COEL	COEL	COEL	COEL	COEL	COEL	COEL	1.	1.	1.	1.	1.
COELOMETOPINI	COEL	COEL	COEL	COEL	COEL	COEL	COEL	COEL	COEL	COEL	1.	1.	1.	1.	1.
DAMATRIS	COEL	COEL	COEL	COEL	COEL	COEL	COEL	COEL	COEL	COEL	1.	1.	1.	1.	1.
STRONGYLIINI	COEL	COEL	COEL	COEL	COEL	COEL	COEL	COEL	COEL	COEL	1.	1.	1.	1.	1.
MENEPHILUS	COEL	COEL	COEL	COEL	COEL	COEL	COEL	COEL	COEL	COEL	1.	1.	1.	1.	.88
MENERISTES	NYCP	NYCP	(Hela)	NYCP	TENE	TENT	TENE	(Meta)	NYCP	(Bius)	.5	1	.5	.5	.58
METACLISA	NYCP	NYCP	(Meta)	NYCP	TENE	TENT	TENE	(Meta)	NYCP	(Mene)	.5	1	1	.33	.71
BIUS	NYCP	NYCP	(Bius)	NYCP	TENE	TENE	TENE	(Bius)	NYCP	(Mene)	.5	1	1	.33	.71
NYCTEROPUS	NYCP	BELO	(Toxi)	BELO	TENE	TENE	(Toxi)	(Nycp)	NYCP	(Toxi)	.33	.5	.5	.5	.46
NYCTERINUS	(Tene)	(Nyct)	(Nyct)	NYCP	TENE	TENE	TENE	(Nyct)	(Nyct)	(Nyct)	.5	.5	1	1	.75
CYPHALEINI	(Hela)	(Tene)	(Hela)	(Hela)	TENE	TENE	TENE	(Hela)	TENT	(Hela)	.5	.5	1	.5	.65
TENEBRIONINI	(Nyct)	(Tene)	(Tene)	(Tene)	TENE	TENE	TENE	(Tene)	NYCP	(Tene)	.33	.33	1	.5	.54
HELOPINI	(Helo)	(Helo)	(Helo)	OPAT	TENE	TENE	OPAT	(Helo)	OPAT	(Helo)	.5	.5	.5	1	.63
OPATRINI	OPAT	OPAT	OPAT	OPAT	TENE	TENE	OPAT	OPAT	OPAT	(Opat)	1.	1.	.5	1.	.88
ULOMINI	OPAT	OPAT	OPAT	OPAT	TENF	LAGR	OPAT	OPAT	OPAT	(Ulom)	1.	1.	.33	1.	.71
TOXICINI	(Toxi)	(Toxi)	(Nycp)	(Toxi)	BELO	BELO	(Nycp)	(Toxi)	(Toxi)	(Nycp)	.5	1	.5	.5	.63
PHALERIINI	(Phal)	DIAP	DIAP	DIAP	TENE	DIAP	DIAP	DIAP	DIAP	DIAP	.5	.5	.5	1	.63
BOLITOPHAGINI	(Bole)	DIAP	DIAP	DIAP	DIAP	DIAP	DIAP	DIAP	BELO	DIAP	.5	.33	1	1	.75
HYPOPHLOEINI	DIAP	DIAP	DIAP	DIAP	DIAP	DIAP	DIAP	DIAP	DIAP	DIAP	1.	1.	1.	1.	1.
DIAPERINI	DIAP	DIAP	DIAP	DIAP	DIAP	DIAP	DIAP	DIAP	DIAP	DIAP	1.	1.	1.	1.	1.
ADELONIA	TENT	BELO	BELO	BELO	BELO	BELO	BELO	(Belo)	BELO	(Adel)	.33	.5	1	.5	.58
BELOPUS	TENT	BELO	BELO	BELO	BELO	BELO	BELO	BELO	BELO	BELO	.33	.5	1	1	.71
RHYPASMA	TENT	BELO	BELO	BELO	BELO	BELO	BELO	BELO	BELO	BELO	.33	.5	1	1	.71
TENTYRIINI	TENT	TENT	TENT	TENT	TENT	TENT	TENT	TENT	TENT	TENT	1.	1.	1.	1.	1.
ZOLODININI	TENT	TENT	TENT	TENT	TENT	TENT	TENT	TENT	TENT	(Zolo)	.5	1	1	.5	.88
PIMELIINI	TENT	TENT	TENT	TENT	TENT	TENT	TENT	TENT	TENT	TENT	1.	1.	1.	1.	.88
PHRENAPATINI	TENT	LAGR	TENT	TENT	(Pycn)	LAGR	(Para)	(Phrn)	(Phrn)	(Para)	.5	.5	.33	.5	.46
PARATENETUS	TENT	BELO	LAGR	BELO	LAGR	LAGR	(Phrn)	LAGR	LAGR	(Phrn)	.33	.5	.5	.5	.46
COSSYPHINI	TENT	LAGR	LAGR	BELO	(Coss)	LAGR	(Coss)	LAGR	LAGR	(Coss)	.33	.33	.5	.5	.42
LAGRIINI	(Lagr)	LAGR	LAGR	(Lagr)	LAGR	LAGR	LAGR	LAGR	LAGR	LAGR	.5	.5	1.	1	.75
PYCNOCERINI	(Adlm)	LAGR	LAGR	(Adlm)	(Phrn)	LAGR	LAGR	LAGR	LAGR	LAGR	.5	.5	.5	1	.63
GONIADERINI	(Goni)	LAGR	LAGR	(Goni)	LAGR	LAGR	LAGR	LAGR	LAGR	LAGR	.5	.5	1.	1	.75
ADELIINI	(Pycn)	LAGR	LAGR	(Pycn)	LAGR	LAGR	LAGR	LAGR	LAGR	LAGR	.5	.5	1.	1.	.74
X̄											.63	.73	.88	.77	

(Figs. 49—51) points out a general problem with the WAGNER program. Since branching sequence is determined by a parsimony criterion, each OTU is assigned a specific position, even if it shares derived characters with more than one relative. Altering the balance of synapomorphies can cause such OTUs to shift position radically, as in the case of the tentyriine and belopine clusters here. UPGMA phenograms, based on average linkage clustering, are not so susceptible to such major dislocations. Problem taxa with mosaic affinities are easily recognized in intuitive cladistic analysis. Most taxonomists would probably assign them an uncommitted, basal position in diagrams of relationships, as we have done with the belopine and tentyriine clusters in Fig. 56.

Other, less serious problems with the cladograms produced by WAGNER involve (1) the creation of dichotomies where none exist, and (2) the tendency toward chained branching patterns which are difficult to convert to classifications. Examples of artificial dichotomies on the 44 character cladogram (Fig. 51) are the OTUs, *Bius,* Coelometopini and Helopini and stem 23, all of which have stem lengths of zero. Since the stem lengths and character changes are included with the WAGNER output, these artificial dichotomies may be rejected at the discretion of the investigator.

Less tractable is the problem of chained branching structure. In all the cladograms shown here the group of OTUs traditionally included in the Tenebrionini were subject to chaining. These OTUs share many primitive features but have few shared, derived features. It is not clear whether their chained branching pattern is a function of our particular data set or of the WAGNER program, but the difficulty in placing them in a dichotomized classification is readily apparent at the intuitive level. Hence, in Fig. 58 these taxa were placed as branches of a multifurcated stem. The consensus diagram representing the four computer generated cladograms shows a similar arrangement (Fig. 52).

In many respects, traditional Hennigian argumentation schemes are the most convenient method of analysis of cladistic data. They quickly convey patterns of synapomorphy, and clearly show clusters of closely

related taxa. OTUs which have mixed affinities to distantly related groups are readily apparent. Perhaps most importantly, Hennigian diagrams may be constructed relatively quickly and cheaply: rough weighting of characters is easily accomplished, problem taxa become readily apparent, missing data can be ignored, and competing arrangements can be compared. Moreover, at least in our experience, intuitively derived arrangements have a reasonably high probability of approximating computer produced cladograms. Comparison of Figs. 49—51 and Fig. 58 with the consensus cladogram (Fig. 52) clearly shows that our intuitively derived arrangement is more similar to the consensus than is any single computer produced diagram. Consensus trees would appear to be an efficient way to remove the less reliable details from computer generated classifications, and should probably be used routinely.

Taxonomic implications

We refrain from presenting a formal reclassification of Tenebrionidae, until the scope of our studies can be expanded to include the entire family and more larval features. Aside from lack of data for some groups of the beetles, unresolved contradictions in character state distributions prevent unequivocal classification of other groups. Discordance of this type is particularly prevalent between character sets drawn from adults versus those drawn from larvae. More detailed analysis, and, especially, characterization of larvae of critical taxa, will probably be required to explain these disagreements. At the same time, continuing study will undoubtedly reveal unexpected relationships. For example, Watt (1974a: 408) proposed Gnathidiinae for *Menimus* Sharp and a small group of closely related genera. Doyen & Lawrence (1979: 362) demonstrated that *Corticeus* Pillar and Mitterpacher should be included in the same taxon as *Menimus,* and changed the subfamily name to Hypophloeinae because of priority. In this paper we present strong evidence that the Hypophloeinae are derived from the same lineage as Diaperini, and probably do not warrant recognition at the subfamily level. Until greater stability in higher classification can be achieved, it seems

most appropriate to delineate relationships and define taxonomic groupings without involving nomenclatural changes. In any case, the Gebien (1938–44) classification will probably be used by non-specialists until a new world catalogue appears.

The taxonomic implications of our results are discussed at length above, so only a few salient points need be mentioned here.

The value of several morphological characters not previously used in tenebrionid classifications is documented. We believe that the configuration of the internal female reproductive tract is pivotal in illuminating the major lines of evolution within the family, and will enable facile placement of many heretofore misclassified species. The systematic value of this organ system was suspected by Watt (1974b), but no comparisons of its configuration existed before that of Tschinkel & Doyen (1980). The present study, in which the characters of the female tract are used in conjunction with other external and internal characters, re-emphasizes the importance of the reproductive tract characters. Preliminary investigations we have made on Colydiidae and other families indicate that the female reproductive system will be an important taxonomic feature for the entire Tenebrionoidea, and preliminary surveys of Carabidae show extensive variation (D. H. Kavanaugh, J. Liebherr, personal communication). It seems likely that this organ system will provide useful characters throughout the Coleoptera.

Organs or organ systems of substantial but subsidiary value include: (1) ovipositor structure; (2) defence glands, reservoirs and associated structures; (3) mouthparts, especially the structure of the epipharynx; (4) internal skeletal anatomy, especially the tentorium and the metendosternite; (5) wing venation and configuration. Internal skeletal anatomy has been surveyed in other families (e.g. Dytiscidae: Riha, 1955) where it shows variation comparable to that in Tenebrionidae. Despite difficulties in interpreting the functional significance and polarity of some internal skeletal features, they seem to have broad taxonomic application below the family level. Wing venation has been surveyed in Coleoptera (Forbes, 1922; Graham, 1922; Wilson, 1930), but not intensively within

families. Ovipositor structure seems to have been neglected at all levels. Both these organs show complex variation in Tenebrionidae, and need further investigation in other families.

Our results suggest major revision of the higher classification of Tenebrionidae. Lagriinae (= Lagriidae of authors) which was previously transferred to Tenebrionidae (Doyen, 1972; Watt, 1974a), appears to represent the most primitive branch of the family. Phrenapatini and Cossyphini, considered subfamilies by Watt, should be transferred to Lagriinae. *Belopus, Rhypasma* and *Adelonia* share several features with the Lagriinae, and are probably specialized members of that lineage. Thus, it appears that Lagriinae may be the sister group of the remaining Tenebrionidae. If this conclusion is validated by future studies of larvae, and by more extensive comparison of Tentyriinae, then it might be most convenient to return Lagriidae to family status.

The remaining Tenebrionidae fall into two major groups. The Tenebrionoid branch of the cladograms includes all those species with paired, non-musculate defensive glands opening between sternites 7 and 8. The Tentyrioid branch includes species without defensive glands and lacking the distinctive apomorphies of the Lagrioid group. It is not clear from present evidence whether the Tentyrioid lineage is derived from the Lagrioid or the Tenebrionoid branch. It is also possible that future comparisons will show that Tentyrioids differentiated before the Lagrioid and Tenebrionoid branches diverged, as postulated by Watt (1974a) and Doyen (1972). Determining the proper position of the Tentyrioids remains the major task in working out the main lines of evolution in Tenebrionidae.

The Tenebrionoid branch consists of three main lineages, the diaperine, coelometopine and tenebrionine, along with several smaller groups of less certain affinity. The most primitive Tenebrionoid tribes appear to be Toxicini and Nycteropini (Figs. 49–52, 58), and these should probably be accorded subfamily status, as proposed by Watt (1974a). Bolitophagini shares characters with Diaperini, Toxicini and Tenebrionini. Its position is uncertain, but subfamily status may be warranted. Two large lineages, the diaperine

and coelometopine, are well distinguished by features that are often strikingly specialized. The diaperine lineage includes Diaperini, Hypophloeini, Gnathidiini, Nilionini, and some genera of Ulomini. Phaleriini probably represents the most primitive member of the diaperine line. This grouping partly corresponds to the tribal arrangement in the Gebien (1938–44) catalogue. The coelometopine lineage includes the tribes Coelometopini, Cnodalonini, Misolampini, Eutelini, Strongyliini and Talanini, as well as many genera formerly placed in Tenebrionini or other tribes (Appendix E). This large, diverse group does not correspond to any previously recognized higher category. Both the diaperine and coelometopine lineages could conveniently be recognized at the subfamily level, but need to be more completely defined by examining pertinent characters in a wider array of taxa.

In contrast to the well-defined diaperines and coelometopines, the tenebrionine lineage is very poorly resolved by the characters we studied. The more generalized members of this group (*Tenebrio,* Cyphaleini, etc.) share many features with Toxicini. Tribes such as Amarygmini show abundant autapomorphies, but are difficult to relate to other taxa. In general, our analyses defined only two groups within the tenebrionine lineage (Opatrini–Ulomini and Cyphaleini–Helaeini–Nyctozoilini). This situation may be remedied in part by examination of more species from large tribes, but it seems likely that additional characters will be needed to clarify cladistic relationships.

Acknowledgments

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Appendix A. Conspectus of taxa investigated

Arrangement of tribes follows the catalogue of Gebien (1938–44). Tribes recognized by Watt (1974a) and Doyen & Lawrence (1979) are included in their appropriate position. Numbers in parentheses following genera indicate number of species examined if greater than 1. Asterisks indicate taxa included in numerical analyses.

Subfamily: Tribe	Genera examined

Tentyriinae[1,3]
    Eurymetopini: *Metaponium, Armalia*
    Epitragini: *Bothrotes*
    Vacronini[1]: *Eupsophulus*
    Tentyriini: *Tentyria*
    Praocini: *Praocis*
    Physogasterini: *Entomochilus*
    Coniontini: *Eusattus*
    Erodiini: *Erodius*
    Platyopini: *Platyope*
    Pimeliini: *Pimelia**

Tenebrioninae[1]
    Scaurini: *Apsena** (2), *Argoporis, Cerenopus**, *Eulabis, Scaurus**
    Scotobiini: *Scotobius**
    Platyopini: *Platyope*
    Blaptini: *Blaps**
    Eleodiini: *Amphidora** (2), *Cratidus, Eleodes** (4), *Lariversius, Neobaphion, Nycterinus, Trichoderulus, Trogloderus*
    Platyscelini: *Platyscelis*
    Pedinini: *Heterotarsus*[*2], *Opatrinus** (3), *Pedinus**, *Pseudoblaps**, *Ulus**
    Opatrini[3]: *Anemia, Leichenum, Lobodera, Melanesthus, Opatrum*
    Trachyscelini: *Trachyscelis*
    Phaleriini: *Phaleria** (2), *Phaleromela** (2)
    Crypticini: *Crypticus** (2)
    Bolitophagini: *Bolitophagus** (2), *Bolitotherus**, *Bradymerus** (2), *Dicraeosis**, *Eleates, Megeleates**

Appendix A (continued)

Subfamily: Tribe	Genera examined

Dysantini: *Calymmus*, Dysantes*, Ozolais**

Rhipidandrini: *Eledona, Rhipidandrus** (2)

Diaperini: *Alphitophagus, Apsida** (2), *Ceropria*, Diaperis** (3), *Liodema, Neomida*, Pentaphyllus*, Palembus*, Platydema** (4)

Hypophloeini[1]: *Hypophloeus** (2)

Gnathidiini: *Menimus**

Nilionini[2]: *Nilio** (2)

Phrenapatini: *Delognatha*, Clamoris** (= *Phthora*), *Phrenapates**

Ulomini: *Alegoria, Alphitobius*, Antimachus*, Cynaeus, Doliema** (3), *Eutochia*, Gnatocerus, Tribolium, Uleda*, Uloma** (3), *Ulosonia**

Helaeini: *Pterohelaeus*, Sympetes**

Nyctozoilini: *Mimopeus* (= *Cilibe*), *Nyctozoilus**

Cossyphini: *Cossyphus** (2)

Eutelini: *Diceroderes*, Nodotelus* (= *Eutelus*), *Polposipus*

Coelometopini: *Asphalus*, Centronopus*, Cibdelis*, Coelocnemis*, Coelometopus*; Hypaulax, Oenopion*, Polopinus*, Polypleurus*, Pseudhadrus, Rhinandrus** (2), *Scotobaenus, Scotobates**

Tenebrionini: *Achrostus*, Alobates** (3), *Amenophis** (2), *Bius*, Catapiestus*, Choastes*, Derosphaerius** (2), *Eccoptostoma, Encyalesthus** (2), *Glyptotus, Graptopezus, Haplandrus*, Idiobates*, Ilus, Iphthiminus** (3), *Lordodera, Meneristes*, Menephilus** (2), *Merinus, Mylaris** (= *Nyctobates*), *Neatus*, Necrobioides, Nuptis*, Oeatus, Paroeatus*, Promethis*, Setenis** (3), *Taphrosoma*, Taraxides* (2), *Temnophthalmus, Tenebrio** (3), *Tonkineus, Upis, Xylopinus, Zophobas*, Zophophilus*

Zolodinini[2]: *Tanylypa, Zolodinus**

Belopini[2]: *Adelonia** (2), *Belopus*, Rhypasma*

Toxicini[2]: *Arthrodactyla*, Cryphaeus** (2), *Macelloceras, Nycteropus*, Toxicum**

Subfamily: Tribe	Genera examined

Goniaderini: *Goniadera*, Phymatestes**

Heterotarsini: *Aemymone*, Anaedus** (2), *Coxelinus, Heterotarsus*, Luprops, Paratenetus*, Prateus*

Pycnocerini: *Catamerus, Chiroscelis*, Metallonotus*, Prioscelis**

Cyphaleini: *Lepispilus*, Lygestira**

Cnodalonini: *Camaria*, Cyrtosoma*, Damatris** (3), *Eucyrtus, Euthysternum, Hemicera, Metaclisa*, Oedemutes, Pseudebax, Tetraphyllus, Titaena**

Apocryphini: *Apocrypha**

Adeliini: *Adelium** (3), *Cardiothorax, Laena*, Micrectyche, Otrintus, Seirotrana*

Misolampini: *Heliofugus*, Misolampidius, Misolampus*, Osdara, Sphaerotus*

Helopini: *Hegemona*, Helops** (3), *Nautes, Probaticus*, Stenotrichus, Tarpela**

Talanini: *Talanus** (2)

Helopinini: *Micranterius**

Amarygmini[2]: *Amarygmus* (2), *Chalcopterus, Eupezus, Meracantha*, Platolenes, Psorodes, Pyanisia*

Strongyliini: *Ainu, Cuphotes*, Nesogena*, Praogena, Strongylium** (4)

Alleculinae[1,2]: *Lobopoda*, Stenochidus, Telacis* (2), *Xystrophus**

Lagriinae (see also, Adeliini, Pycrocerini, Goniaderini, Heterotarsini

Lagriini: *Arthromacra*, Lagria** (2), *Statira*

Stilpnonotini: *Stilpnonotus*

Incertae sedis: *Myrmechyxenus*

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[1] *Sensu* Doyen & Lawrence (1979). [2] *Sensu* Watt (1974a). [3] Composite set of characters primitive to subfamily or tribe used in numerical analysis.

Appendix B. Character state matrix

Character state matrix for major taxonomic categories and individual taxa represented in definitive analyses (Figs. 49–58). Zeros indicate missing or inapplicable data. Characters and character states are described in Appendix C. Composition of categories is listed in Appendix D.

```
                    1 2 3 4 5 6 7 8 9 10 ...                                        40
PLES            1 1 1 2 2 1 2 1 2 1 1 1 2 1 1 1 1 2 2 1 2 2 1 1 2 2 2 1 1 1 2 1 1 2 2 1 2 1 1
ADELONIA        2 1 2 1 2 2 2 2 2 1 2 2 1 2 1 1 2 3 2 2 1 1 2 3 1 2 3 2 2 1 1 2 1 1 2 1 1 2 1 0
ADELIINI        1 1 2 1 2 3 1 2 2 2 1 2 3 1 1 3 5 2 2 3 1 2 0 0 0 0 0 1 2 1 2 1 2 1 2 1 2 1 3
BELOPUS         2 1 2 1 2 2 2 2 1 2 2 1 2 1 1 2 3 2 2 1 2 5 3 1 2 3 2 2 1 1 3 1 1 2 2 1 2 1 0
BIUS            2 1 2 1 2 1 1 2 2 2 2 1 1 2 3 1 1 1 2 1 1 2 2 1 1 2 2 2 1 2 1 2 1 2 2 2 1 2 1 1
BOLITOPHAGINI   2 1 1 4 1 1 1 2 1 1 1 2 1 1 1 3 2 4 3 3 3 3 3 3 1 1 2 1 2 1 3 1 1 2 2 1 3 1 2
CATAPIESTUS     2 1 2 1 2 1 1 2 1 1 1 1 2 3 1 1 3 2 3 5 1 5 5 1 1 2 2 1 2 3 3 1 2 2 2 3 5 2 1
COELOMETOPINI   2 1 2 1 2 1 1 2 1 2 1 1 1 2 3 1 1 3 2 3 1 2 2 2 1 1 2 2 1 2 2 5 1 2 2 3 3 3 5 3
COSSYPHINI      3 1 2 1 3 1 3 1 1 2 1 2 3 1 1 3 1 1 3 1 1 2 3 1 3 1 2 3 1 2 1 1 1 3 1 1 2 2 1 2 2 0
DAMATRIS        2 1 2 1 2 1 1 2 1 2 1 1 2 2 1 1 3 2 3 3 2 1 3 1 3 1 1 2 2 1 2 3 1 2 2 3 5 5 5 3
DIAPERINI       2 1 1 1 4 1 1 1 2 1 1 1 2 1 1 1 3 2 3 1 3 3 3 3 3 2 2 1 2 1 2 1 1 1 2 1 1 2 1 3
GONIADERINI     2 1 2 2 2 3 2 3 1 2 2 1 2 3 1 1 3 3 2 2 3 2 2 3 1 1 3 1 1 2 1 3 1 1 2 2 1 2 1 0
HELAEINI        2 1 2 1 2 1 1 2 1 2 1 1 1 2 1 1 1 1 2 1 1 1 3 2 2 1 1 2 2 3 1 2 2 3 1 2 1 2 1 1
HELOPINI        2 1 2 1 2 1 1 2 1 2 1 1 1 2 1 1 3 2 3 2 1 2 3 1 2 2 2 2 1 2 1 2 1 2 2 2 1 2 1 2
HYPOPHLOEINI    2 1 1 1 4 1 1 1 2 1 1 1 2 1 1 1 3 1 3 3 3 3 3 3 3 3 5 2 2 1 2 1 2 1 1 1 2 2 1 2 1 2
LAGRIINI        1 2 2 2 2 2 1 3 1 2 2 1 2 3 1 1 1 3 2 2 3 2 1 2 3 1 2 3 1 1 2 1 3 1 1 1 2 1 1 1
MENERISTES      2 1 2 1 2 1 1 2 1 2 1 1 1 2 3 1 1 1 2 1 3 2 3 1 1 2 0 2 1 2 3 2 1 2 2 2 1 3 2 1
MENEPHILUS      2 1 2 1 2 1 1 2 1 2 1 1 1 2 3 1 1 3 2 3 2 2 2 2 1 1 3 2 1 2 2 3 1 2 2 2 1 2 1 2
METACLISA       2 1 2 1 2 1 1 2 1 2 1 1 1 2 1 1 2 2 1 3 2 2 1 2 2 2 2 1 2 2 3 1 2 2 1 2 2 1 1 3
NYCTEROPUS      4 1 2 1 2 1 2 2 1 2 2 1 1 2 2 1 1 2 1 2 3 2 1 2 3 2 1 2 1 2 1 2 1 1 1 1 1 1 1
NYCTERINUS      2 1 2 1 2 1 1 2 1 2 2 1 1 3 2 3 3 1 2 0 1 0 0 2 1 2 1 3 1 2 2 2 1 0 1 1
OPATRINI        2 1 2 1 2 1 1 2 1 2 1 1 1 2 1 1 3 2 5 2 1 2 3 1 2 3 1 2 2 1 2 1 3 2 3 2 2 2 1 1 2
PARATENETUS     4 1 5 2 2 2 3 1 3 2 1 2 2 1 1 3 3 2 2 1 1 2 3 3 3 3 2 1 2 1 2 1 2 1 2 1 2 1 0
PHALERIINI      2 1 1 1 4 1 1 2 1 2 2 1 1 2 1 1 1 3 2 3 1 2 2 3 3 3 2 2 1 2 1 2 1 3 2 2 2 1 1 2
PHRENAPATINI    4 1 2 1 2 2 1 2 2 1 2 1 3 1 1 3 3 2 3 3 3 5 3 2 3 2 2 1 2 1 2 1 0 0 0 0 0 0 1
PIMELIINI       1 1 2 1 2 1 1 1 0 2 1 1 2 2 1 1 3 2 1 3 3 1 0 0 0 0 0 0 2 2 3 3 1 3 1 1 1 2 1 0
PYCNOCERINI     1 1 2 1 3 3 5 2 3 1 2 2 1 2 3 3 1 1 3 2 2 3 2 1 3 1 1 3 1 1 2 1 2 1 3 3 2 1 3 1 1
RHYPASMA        1 1 2 1 2 3 2 2 2 1 2 2 1 2 1 1 3 3 2 2 1 1 2 3 1 2 3 2 2 1 1 2 1 1 2 2 1 2 1 0
STRONGYLIINI    2 1 2 1 2 1 1 2 1 2 1 1 1 2 1 1 3 2 3 3 3 2 1 1 2 2 1 1 2 2 1 2 2 3 3 5 5 5 3
TENEBRIONINI    2 1 2 1 2 1 1 2 1 1 1 2 2 1 1 2 2 3 1 2 2 2 2 1 2 2 2 1 2 1 1 1 2 2 1 2 1 0
TENTYRIINI      1 1 2 1 2 1 1 1 2 2 1 1 1 2 1 1 3 1 2 1 1 2 3 1 2 3 2 2 1 3 3 1 2 1 1 1 2 1 0
TOXICINI        4 1 2 1 2 2 2 2 2 1 2 1 2 1 1 2 1 1 1 1 2 3 2 3 2 2 2 2 2 1 1 2 1 1 1 2 2 1 2
ULOMINI         2 1 2 1 2 2 2 2 1 1 2 1 2 3 2 1 3 3 2 3 2 1 3 5 3 2 2 2 2 1 2 1 3 1 3 2 2 2 1 1 3
ZOLODININI      1 1 2 1 2 1 1 2 2 1 2 2 1 2 3 1 1 1 2 2 2 1 3 1 1 1 3 2 2 1 3 5 1 2 2 1 1 2 1 0
```

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                    41 42 ...                                                        78
PLES            1 2 1 1 1 1 2 2 1 1 1 1 1 1 1 1 1 1 1 2 1 1 1 1 1 1 1 2 2 1 1 1 1 1 1 1 1 1
ADELONIA        0 0 1 1 2 1 2 2 1 1 1 1 1 1 0 1 1 1 1 1 1 1 1 2 1 1 1 1 0 3 2 1 1 0 0 0 0 0 0
ADELIINI        2 0 2 3 2 1 2 3 2 2 1 1 2 1 2 1 1 2 1 1 1 1 1 2 1 2 4 3 1 1 1 1 1 1 1 2 2 2
BELOPUS         0 0 1 1 2 1 2 2 1 1 2 1 1 1 0 2 1 1 3 1 1 1 1 2 1 1 0 3 1 1 1 0 0 0 0 0 0 0
BIUS            2 5 1 1 2 1 2 2 3 1 1 1 1 2 1 2 1 1 4 1 1 1 1 2 1 1 2 2 1 1 1 0 0 0 0 0 0 0
BOLITOPHAGINI   1 1 1 1 2 1 2 1 1 1 1 1 2 1 2 1 1 4 1 1 1 1 2 2 2 2 2 1 2 1 2 1 2 2 1
CATAPIESTUS     1 5 2 1 2 1 2 3 3 1 1 1 1 2 1 1 2 1 1 3 2 1 2 1 1 1 0 1 0 3 0 1
COELOMETOPINI   1 5 2 1 2 1 2 2 2 1 1 2 1 1 2 2 1 1 2 2 1 1 1 2 1 1 1 1 1 1 1 3 2 1
COSSYPHINI      0 0 1 1 1 3 1 3 1 2 1 1 1 1 0 2 1 1 2 1 1 2 1 1 1 3 0 2 1 1 2 1 1 0 0 2 0 0
DAMATRIS        1 5 2 1 2 1 3 3 3 1 1 2 1 1 2 2 2 1 1 2 1 1 1 1 1 1 0 1 0 3 0 1
DIAPERINI       2 5 1 1 2 1 2 1 1 1 1 1 1 1 2 2 1 2 1 1 3 1 1 2 2 1 1 1 1 2 2 1 2 1 1 1 2 2 1
GONIADERINI     0 0 2 2 2 1 2 3 1 1 2 1 1 1 0 1 1 1 1 1 1 1 1 1 3 0 3 1 1 1 1 1 1 1 1 2 2 2
HELAEINI        2 5 2 1 2 1 2 2 3 1 1 1 1 1 4 1 1 1 1 2 1 1 1 2 2 1 1 1 1 2 1 5 1 1
HELOPINI        2 5 2 1 2 1 2 5 3 1 2 1 1 1 2 1 2 1 1 4 1 1 1 1 2 2 2 1 2 1 2 1 1 1 1 1 1 3 2 1
HYPOPHLOEINI    1 3 1 1 2 2 2 1 1 1 1 1 1 2 1 1 2 1 1 2 1 1 2 1 1 1 1 1 2 2 1 1 1 1 2 1 1 1
LAGRIINI        2 2 2 2 2 1 2 2 1 1 1 1 2 1 1 1 1 2 1 1 1 1 2 1 1 1 2 1 1 1 1 2 2 2
MENERISTES      2 5 1 1 2 1 2 2 3 1 1 1 1 2 1 1 4 5 1 1 1 1 2 1 2 2 2 1 1 1 0 0 0 0 0 0 0
MENEPHILUS      1 5 2 1 2 1 2 1 2 1 1 1 1 2 2 1 1 2 1 1 1 1 1 1 2 3 1 1 2 1 1 1 0 1 0 3 0 1
METACLISA       2 2 1 1 2 1 2 2 2 1 1 1 1 2 1 1 4 1 1 1 1 1 2 1 1 1 1 2 1 1 0 0 0 0 0 0 0 0
NYCTEROPUS      1 1 2 1 2 1 2 2 3 1 1 1 1 2 1 2 1 1 4 1 1 1 1 1 2 1 1 2 2 1 1 0 0 0 0 0 0 0
NYCTERINUS      1 4 1 1 2 1 2 2 3 1 1 1 1 2 1 2 1 1 4 1 1 1 1 2 2 3 2 2 1 1 0 0 0 0 3 0 0
OPATRINI        2 4 1 1 2 1 2 2 2 1 1 1 1 2 1 1 4 1 1 1 1 2 1 2 3 1 2 1 1 2 1 2 3 1 1 1
PARATENETUS     0 0 2 2 1 2 2 2 1 1 2 1 1 1 0 2 1 1 2 1 1 1 1 1 2 1 1 0 3 1 1 2 1 1 0 0 0 0 0
PHALERIINI      1 4 1 1 2 1 2 1 2 1 1 1 1 2 1 1 1 1 1 1 1 2 1 1 1 2 2 2 1 2 1 1 2 1 1 2 1 1
PHRENAPATINI    0 0 1 1 1 1 2 1 0 1 1 2 1 1 0 1 1 1 1 1 1 1 1 1 1 2 0 3 1 1 2 1 1 2 2 1 1
PIMELIINI       0 0 1 1 2 1 1 2 1 1 1 1 1 0 1 1 1 1 1 1 1 2 1 3 0 1 1 1 1 2 1 1 2 1 1
PYCNOCERINI     2 0 1 1 2 1 2 3 2 0 1 2 1 1 1 2 1 1 2 1 1 1 1 2 2 2 0 3 1 1 1 1 0 1 1 2 1 2
RHYPASMA        0 0 1 1 2 1 2 3 1 1 1 1 1 0 1 1 1 1 1 1 1 2 1 1 0 3 1 1 0 0 0 0 0 0 0 0
STRONGYLIINI    2 5 2 1 2 1 2 3 2 1 2 1 1 2 1 1 3 2 1 2 1 1 1 1 1 1 1 1 1 1 3 2 1
TENEBRIONINI    1 4 1 1 2 1 2 2 3 1 1 1 1 2 1 2 1 1 4 1 1 1 1 2 1 1 3 2 1 1 1 1 1 1 1 3 2 1
TENTYRIINI      0 0 1 1 2 2 2 2 1 1 1 1 1 1 1 0 2 1 1 3 1 1 1 1 2 1 1 0 2 1 1 1 2 1 2 3 1 1
TOXICINI        1 1 2 1 2 2 2 1 1 1 1 1 2 1 1 1 1 2 1 1 1 1 2 1 2 3 1 1 2 1 2 1 2 1 2 2 1
ULOMINI         1 5 1 1 2 1 2 2 2 1 2 1 1 2 1 2 1 1 4 1 1 1 1 2 2 2 1 2 1 2 1 1 1 1 1 3 1 1
ZOLODININI      0 0 2 1 2 1 2 2 2 2 1 1 1 1 0 2 1 1 4 1 1 1 1 2 1 2 0 3 1 1 1 1 2 1 1 3 2 1
```

Appendix C. Characters and character states

States labelled (P) are considered primitive; those labelled (D), derived. Subscripts ($D_{1.1}$, $D_{1.2}$, etc.) indicate morphoclines. Character suites used in the analyses discussed in the text are indicated in the columns on the left. Relative weights of each character are indicated in parentheses following the character state descriptions.

38	44	70A	70 A + L	Characters and states
				Adult characters
		X	X	1. Antennal form: 1. Filiform or serrate (P); 2. Moniliform or gradually calvate ($D_{1.1}$); 3. Strongly clavate ($D_{1.2}$); 4. Capitate ($D_{1.3}$). (2)
X	X	X	X	2. Antenna, terminal segment: 1. Unmodified (P); 2. Elongate (D). (2)
X	X	X	X	3. Tentorial bridge position: 1. Posterior (P); 2. Anterior (D_1); 3. Absent (D_2). (2)
		X	X	4. Tentorial bridge: 1. Present (P); 2. Absent (D). (0)
	X	X	X	5. Tentorial bridge configuration: 1. Doubly arched (D_1); 2. Straight (P); 3. Slightly arched ($D_{1.1}$); 4. Strongly arched ($D_{1.2}$). (3)
X	X	X	X	6. Labrum, shape: 1. Transverse (D_1); 2. Subquadrate (P); 3. Elongate (D_2). (2)
	X	X	X	7. Labrum, symmetry: 1. Symmetrical (P); 2. Asymmetrical (D). (2)
X	X	X	X	8. Medial tormal arms: 1. Posteriorly oblique (D_1); 2. Transverse (P); 3. Anteriorly oblique (D_2). (3)
		X	X	9. Medial tormal arms: 1. Long, slender (P); 2. Short, thick (D). (1)
		X	X	10. Posterior tormal arms: 1. Robust, short (D_1); 2. Slender (P); 3. Bifurcate (D_2). (2)
		X	X	11. Mandible, mola: 1. Not planar (P); 2. Planar (D). (2)
		X	X	12. Mola: 1. Not coarsely striate (P); 2. Coarsely striate (D). (2)
	X	X	X	13. Mola: 1. Not irregularly ridged (P); 2. Irregularly ridged (D). (2)
X	X	X	X	14. Mola, shape: 1. Transversely elongate or lunate (D_1); 2. Subquadrate (P); 3. Longitudinally elongate (D_2). (2)
	X	X	X	15. No. lacinial teeth: 1. 0 (P); 2. 1 ($D_{1.1}$); 3. 2 ($D_{1.2}$). (2)
X		X	X	16. Labium size: 1. Small (P); 2. Large (D). (1)
	X	X		17. Hypopharynx: 1. Ligula membranous (P); 2. Ligula with small sclerites ($D_{1.1}$); 3. Ligula sclerotized ($D_{1.2}$). (1)
		X	X	18. Procoxal cavities, internal closure: 1. Open (P); 2. Barely closed ($D_{1.1}$); 3. Broadly closed ($D_{1.2}$). (1)
X		X	X	19. Mesocoxal cavities: 1. Closed by sterna (D_1); 2. By mesepimeron (P); 3. By trochantin (D_2). (1)
X	X	X	X	20. No. elytral striae: 1. Estriate (D_1); 2. 10-striate (P); 3. 9-striate ($D_{2.1}$); 4. Estriate ($D_{2.2}$). (1)
		X		21. Metendosternite, alae: 1. Large (P); 2. Moderate ($D_{1.1}$); 3. Absent ($D_{1.2}$). (1)
	X			22. Metendosternite, terminal flange: 1. Small, subterminal (D_1); 2. Absent (P); 3. Large, terminal (D_2). (2)
	X	X		23. Metendosternite, tendon position: 1. Medial (D_1); 2. Intermediate (P); 3. Apical (D_2). (0)
		X	X	24. Subcubital wing fleck: 1. Strong (P); 2. Weak ($D_{1.1}$); 3. Absent ($D_{1.2}$). (1)
X	X	X	X	25. Apical wing membrane: 1. < 0.25 wing length (P); 2. 0.26– 0.35 wing length ($D_{1.1}$); 3. > 0.36 wing length ($D_{1.2}$). (2)
	X	X	X	26. Recurrent cell: 1. Large (D_1); 2. Moderate (P); 3. Small, absent (D_2). (2)
	X	X	X	27. M-CU cross-vein(s): 1. Proximal and distal to 1A–2A (P); 2. Proximal only (D_1); 3. Absent (D_2). (2)
X	X	X	X	28. Apical wing fleck: 1. Longitudinal bar(s) (D_1); 2. Diffuse, irregular or absent (P); 3. Transverse bar (D_2). (2)
X	X	X	X	29. Abdominal hinge position: 1. Lateral (P); 2. Medial (D). (2)
	X	X	X	30. Abdominal membrane exposure: 1. Concealed (P); 2. External ($D_{1.1}$); 3. Secondarily invaginated ($D_{1.2}$) (2)
	X	X	X	31. Aedeagus orientation: 1. Tegmen dorsal (P); 2. Lateral ($D_{1.1}$); 3. Ventral ($D_{1.2}$). (2)

Appendix C (continued)

38	44	70A	70 A + L	Characters and states
		X	X	32. Aedeagus, connecting membrane: 1. Glabrous (P); 2. Setose (D_1); 3. Absent (D_2). (2)
		X		33. Aedeagus, median lobe: 1. Free, with clavae (D_1); 2. Free, without clavae (P); 3. Sessile ($D_{2.1}$); 4. Reduced, absent ($D_{2.2}$). (2)
X	X	X	X	34. Ovipositor, gonostyle position: 1. Terminal (P); 2. Lateral ($D_{1.1}$); 3. Dorsal or dorsolateral ($D_{1.2}$). (2)
X		X	X	35. Ovipositor coxite: 1. Weakly sclerotized, rounded (P); 2. Sclerotized, spatulate (D_1); 3. Otherwise modified (D_2). (3)
X	X	X	X	36. Proctiger length: 1. Much longer than coxite (D_1); 2. Subequal to coxite (P); 3. Much shorter than coxite (D_2). (2)
X	X	X	X	37. Proctiger orientation: 1. Longitudinal (P); 2. Oblique ($D_{1.1}$); 3. Transverse ($D_{1.2}$). (3)
	X	X	X	38. Proctiger shape: 1. Subquadrate (D_1); 2. Linear (P); 3. Triangular (D_2). (2)
X	X	X	X	39. Coxite (baculus) shape: 1. Transverse (P); 2. Oblique ($D_{1.1}$); 3. Longitudinal ($D_{1.2}$). (2)
	X	X	X	40. Defence gland size: 1. Small (P); 2. Intermediate ($D_{1.1}$); 3. Large ($D_{1.2}$). (1)
		X	X	41. Defence gland common volume: 1. Present (P); 2. Absent (D). (1)
X		X	X	42. Gland tubule terminations: 1. Apical half of reservoir (D_1); 2. Evenly distributed (P); 3. Basal half ($D_{2.1}$); 4. Basal line ($D_{2.2}$); 5. Few large ducts ($D_{2.3}$). (2)
		X		43. Tarsal vestiture: 1. Bristles, spines (P); 2. Silky (D). (2)
X	X	X	X	44. Fourth tarsomere shape: 1. Filiform (P); 2. Expanded, spatulate ($D_{1.1}$); 3. Apically emarginate ($D_{1.2}$). (2)
		X		45. Eye emargination: 1. Entire or barely emarginate (P); 2. Emarginate ($D_{1.1}$); 3 Divided ($D_{1.2}$). (1)
		X	X	46. Mesotrochantin position: 1. Exposed (P); 2. Concealed ($D_{1.1}$); 3. Greatly reduced or absent ($D_{1.2}$). (2)
X		X	X	47. Metendosternite, arms: 1. Long (D_1); 2. Intermediate (P); 3. Short (D_2). (1)
		X		48. Maxillary palp shape: 1. Cylindrical (D_1); 2. Slightly securiform (P); 3. Strongly securiform (D_2). (1)
X		X	X	49. Coxite, lobe 4 structure: 1. Free, cylindrical (P); 2. Free, triangular ($D_{1.1}$); 3. Sessile ($D_{1.2}$). (2)
X		X	X	50. Coxite lobe 1 shape: 1. $\simeq$ lobes 2, 3, 4 combined (P); 2. $\geqslant$ lobes 2, 3, 4 combined (D). (3)
X		X	X	51. Coxite lobe 1 shape: 1. Not shortened (P); 2. Much shorter than lobes, 2, 3, 4 combined (D). (2)
X	X	X	X	52. Coxite lobe 1 development: 1. Distinct (P); 2. Undifferentiated (D). (1)
X		X	X	53. Median defence reservoir: 1. Absent (P); 2. Present (D). (4)
X		X	X	54. Paired defence reservoir, sternites 8/9: 1. Absent (P); 2. Present (D). (4)
X	X	X	X	55. Paired defence reservoir, sternites 7/8: 1. Absent (P); 2. Present (D). (2)
X		X	X	56. Defence reservoir wall: 1. Not pleated (P); 2. Accordion pleated (D). (3)
	X	X	X	57. Spermatheca derived from bursa copulatrix (type 1): 1. No (P); 2. Yes (D). (2)
X	X	X	X	58. Spermatheca derived proximally from accessory gland (type 2): 1. No (P); 2. Yes (D). (4)
X	X	X	X	59. Spermatheca derived distally from accessory gland (type 3): 1. No (P); 2. Yes (D). (4)
		X		60. Spermathecal (type 1) structure: 1. Undifferentiated (P); 2. Multiple, independent tubes ($D_{1.1}$); 3. Single short, thick tube ($D_{1.2}$); 4. Single long, thin tube ($D_{1.3}$); 5. Single, saccate ($D_{1.4}$). (2)
X	X	X	X	61. Spermathecal structure (type 2): 1. Undifferentiated (P); 2. Saccate ($D_{1.1}$); 3. Capsular ($D_{1.2}$). (3)
X	X	X	X	62. Spermathecal structure (type 3): 1. Undifferentiated or cylindrical (P); 2. Gradually enlarged ($D_{1.1}$); 3. Abruptly saccate ($D_{1.2}$). (2)

Appendix C (continued)

38	44	70A	70 A + L	Characters and states
X	X	X	X	63. Spermathecal accessory gland: Not annulate (P); 2. Annulate (D). (2)
	X	X	X	64. Bursa copulatrix shape: 1. Not constricted (P); 2. Constricted (D). (2)
X	X	X	X	65. Bursa copulatrix structure: 1. Without fenestration (P); 2. With apical fenestration (D). (4)
	X	X	X	66. Bursa copulatrix size: 1. Large, saccate (P); 2. Reduced, absent (D). (1)
		X	X	67. Mesendosternite, dorsal arm: 1. Extending almost to pleural wing process (P); 2. Markedly shortened (D). (1)
		X		68. Mesendosternite, horizontal arm: 1. Slender (P); 2. Flanged basally ($D_{1.1}$); 3. Disc shaped ($D_{1.2}$). (2)
X		X	X	69. Defence reservoir shape: 1. Long straight, saccate ($D_{2.2}$); 2. Short straight, saccate ($D_{2.1}$); 3. Short, conical (P); 4. Elongate conical (D_1). (2)
X	X	X	X	70. Sternite 7 marginal cross-section: 1. Squared-off (D_1); 2. Rounded (P); 3. Dorsally grooved (D_2). (3)
	X		X	71. Tenebrionoid antennal sensoriae: 1 . Absent (P); 2. Present (D). (2)
X			X	72. Placoid antennal sensoriae: 1. Absent (P); 2. Present (D). (3)
			X	73. Antennal sensorial base: 1. Flat (P); 2. Elevated (D). (2)

Larval characters

38	44	70A	70 A + L	Characters and states
X	X		X	74. Mandible, base with setose membrane: 1. No (P); 2. Yes (D). (3)
			X	75. Spiracle with peripheral air tubes: 1. Yes (P); 2. No (D). (3)
	X		X	76. Forelegs enlarged: 1. No (P); 2. Yes (D). (1)
	X		X	77. Mandibular mola: 1. Planar or tuberculate (P); 2. Striate (D). (2)
X	X		X	78. Anus position: 1. Terminal (P); 2. Subterminal ($D_{1.1}$); 3. Ventral ($D_{1.2}$). (2)
			X	79. Urogomphi: 1. Absent (P); 2. Present (D). (1)
X	X		X	80. No. antennal segments: 1. 3 (P); 2. 2 (D). (3)

Appendix D. Tribal composition of composite OTUs referred to in Figs. 49—58 and 61—62

Genera examined from each tribe are listed in Appendix A. Changes in tribal membership are listed in Appendix E. For tribal names appearing in Figs. 49—58 but not here, generic representation is given in Appendix A.

OTU	Included tribes (*sensu* Gebien, 1938—44)
Bolitophagini	Bolitophagini, Rhipidandrini
Coelometopini, etc.	Coelometopini, Misolampini, Nodotelini, Tenebrionini (in part), Cnodalonini
Diaperini, etc.	Diaperini, Nilionini[1], Ulomini (in part)
Goniaderini	Goniaderini, Heterotarsini (except *Heterotarsus*)
Cyphaleini, etc.	Helaeini, Cyphaleini, Nyctozoilini
Lagriini, etc.[1]	Lagriini, Statirini, Laenini, Lupropini
Tenebrionini, etc.	Alleculini, Amarygmini, Apocryphini, Coelometopini (in part), Scotobiini, Tenebrionini (in part), Ulomini (in part)
Tentyriini, etc.	Asidinae, Tentyriinae (except Pimeliini)
Opatrini, etc.	Eleodiini, Helopinini, Opatrini, Pedinini

[1] Not included in Gebien (1938—44).

Appendix E. Alphabetical listing of generic and tribal rearrangements alluded to in text

Present taxonomic position from Gebien (1938–44) catalogue unless indicated otherwise.

Taxon	Present tribe or subfamily	Proper lineage/tribe
Adelonia	Tenebrionini	belopine; Belopini
Aemymone	Heterotarsini	lagriine; Goniaderini
Ainu	Strongyliini	coelometopine; Cnodalonini
Alobates	Tenebrionini	coelometopine; Coelometopini
Alphitobius	Ulomini	tenebrionine; Tenebrionini
Amenophis	Tenebrionini	coelometopine; Coelometopini
Anaedus	Heterotarsini	lagriine; Goniaderini
Arthrodactyla	Tenebrionini	toxicine (?); Nycteropini
Asphalus	Coelometopini	tenebrionine; Cyphaleini
Belopus	Tenebrionini	belopine
Bolitophagini	Diaperinae[1]	bolitophagine
Bradymerus	Bolitophagini	coelometopine; Cnodalonini
Calymmus	Dysantini	toxicine; Dysantini
Catapiestus	Tenebrionini	coelometopine
Centronopus	Coelometopini	tenebrionine
Choastes	Tenebrionini	coelometopine; Coelometopini
Cnodalonini	near Cyphaleini	coelometopine; Coelometopini
Cossyphus	Cossyphinae	lagriine; Cossyphini
Coxelinus	Heterotarsini	lagriine; Lupropini
Cryphaeus	Tenebrionini; Toxicinae	toxicine; Toxicini
Cyphaleini	near Cnodalonini	tenebrionine; Cyphaleini
Derosphaerius	Tenebrionini	coelometopine; Coelometopini
Diceroderes	Nodotelini (Eutelini)[4]	toxicine; Dysantini
Dicraeosis	Bolitophagini	coelometopine; Cnodalonini
Doliema	Ulomini	diaperine
Dysantes	Dysantini	toxicine; Dysantini
Eccoptostoma	Tenebrionini	coelometopine; Coelometopini
Encyalesthus	Tenebrionini	coelometopine; Coelometopini
Glyptotus	Tenebrionini	coelometopine; Coelometopini
Gnathidiini	Hypophloeinae[2]	diaperine; Gnathidiini
Gnatocerus	Ulomini	diaperine
Graptopezus	Tenebrionini	coelometopine; Coelometopini
Haplandrus	Tenebrionini	coelometopine; Coelometopini
Hapsida	Diaperini	coelometopine; Cnodalonini
Helaeini	near Cnodalonini	tenebrionine; Cyphaleini
Heliofugus	Misolampini	coelometopine; Coelometopini
Hypophloeini	Hyphloeinae[2]	diaperine; Hypophloeini
Ilus	Tenebrionini	coelometopine; Coelometopini
Iphthiminus	Tenebrionini	coelometopine; Coelometopini
Macellocerus	Tenebrionini	toxicine (?); Nycteropini
Menephilus	Tenebrionini	coelometopine[5]
Meneristes	Tenebrionini	tenebrionine, Cyphaleini?
Merinus	Tenebrionini	coelometopine; Coelometopini
Metaclisa	Cnodalonini	tenebrionine; Tenebrionini
Micrectyche	Adeliini	tenebrionine; Cyphaleini (?)
Misolampidius	Misolampini	coelometopine; Coelometopini
Misolampus	Misolampini	coelometopine; Coelometopini
Mylaris (= Nyctobates)	Tenebrionini	coelometopine; Coelometopini
Necrobioides	Tenebrionini	coelometopine; Coelometopini
Nesogena	Strongyliini	tenebrionine
Nilio	Nilioninae[1]	diaperine; Nilionini
Nodotelus (= Eutelus)	Nodotelini (Misolampini)[4]	coelometopine; Coelometopini
Nuptis	Tenebrionini	coelometopine; Coelometopini
Nycterinus	Eleodiini	tenebrionine
Nycteropus	Tenebrionini	toxicine (?); Cyphaleini
Nyctozoilini	near Cnodalonini	tenebrionine; Cyphaleini
Oeatus	Tenebrionini	coelometopine; Coelometopini
Opatrinus	Tenebrionini[3]	Opatrine

Appendix E (continued)

Taxon	Present tribe or subfamily	Proper lineage/tribe
Osdara	Nodotelini (Misolampini)[4]	coelometopine; Coleometopini
Ozolais	Dysantini	toxicine
Paratenetus	Heterotarsini	belopine (?)
Paroeatus	Tenebrionini	coelometopine; Coelometopini
Phaleriini	Tenebrioninae	diaperine; Phaleriini
Phrenapatini	Phrenapatinae[1,2]	Lagriinae; Phrenapatini
Polposipus	Nodotelini (Misolampini)[4]	coelometopine; Coelometopini
Praogena	Strongyliini	tenebrionine
Promethis	Tenebrionini	coelometopine; Coelometopini
Rhinandrus	Coelometopini	tenebrionine; Tenebrionini
Rhypasma	Tentyriinae	belopine
Scotobaenus	Coelometopini	tenebrionine
Setenis	Tenebrionini	coelometopine; Coelometopini
Sphaerotus	Mislampini	coelometopine; Coelometopini
Stilpnonotus	Lagriinae; Stilpnonotini	Salpingidae; near Conomorphus
Strongyliini	near Amarygmini	coelometopine; Strongyliini
Talanus	Talanini	coelometopine; Talanini
Talanini	near Amarygmini	coelometopine; Talanini
Taphrosoma	Tenebrionini	coelometopine; Coelometopini
Taraxides	Tenebrionini	coelometopine; Coelometopini
Temnophthalmus	Tenebrionini	coelometopine; Coelometopini
Titaena	Cnodalonini	tenebrionine; Cyphaleini
Tonkineus	Tenebrionini	coelometopine; Coelometopini
Tribolium	Ulomini	tenebrionine; Tenebrionini (?)
Ulosonia	Ulomini	tenebrionine
Upis	Tenebrionini	coelometopine; Coelometopini
Xylopinus	Tenebrionini	coelometopine; Coelometopini
Zolodinus	Zolodininae[1]	tentyriine; Zolodinini
Zophophilus	Tenebrionini	coelometopine; Coelometopini

[1] Watt (1974a). [2] Doyen & Lawrence (1979). [3] Arnett (1960). [4] Kulzer (1950); Koch (1950). [5] We examined *Menephilus cylindricus* Herbst (generitype) and *M.lucens* Marseul, which are both clearly in the coelometopine lineage. Some Australian species such as *M.colydioides* Erichson are in the tenebrionine lineage (E. G. Matthews, in litt.).