Phylogeny and classification of the staphyliniform beetle families (Coleoptera)

By MICHAEL HANSEN

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Abstract

The socalled Staphyliniform series of beetles is a very large assemblage of approximately 60.000 described species, placed in several families, subfamilies and lower taxonomic categories. Few attempts have been made to reveal the basal phylogeny and evolution of the group on a modern cladistic basis. The purpose of the present study is to review this subject and provide a phylogenetically justified basis for the classification of higher taxa within the Staphyliniformia. Numerous species, representing all families and subfamilies (as well as most tribes) have been studied to define the taxa appropriate for cladistic analysis. Computerized analyses have been based on the distribution of approximately 120 morphological characters (adults and larvae) in 30 staphyliniform subgroups, mostly representing families or subfamilies, and 7 representatives of more-or-less related groups of beetles. The results of the analyses indicate that the current concept of Staphyliniformia does not represent a natural (monophyletic) group and that the Scarabaeoidea should be included in the assemblage. Staphyliniformia + Scarabaeoidea seem to form a monophyletic group, which have recently been referred to as the »hydrophiloid lineage« (more-or-less equivalent of the traditional concept of Haplogastra). Within this lineage, four superfamilies are recognized here: Scarabaeoidea (not treated in further detail here), Hydrophiloidea, Histeroidea, and Staphylinoidea, the last being probably the sistergroup of the first three. In Hydrophiloidea 6 families are recognized (Helophoridae, Epimetopidae, Georissidae, Hydrochidae, Spercheidae, Hydrophilidae), in Histeroidea 3 families (Sphaeritidae, Synteliidae, Histeridae), and in Staphylinoidea 10 families (Hydraenidae, Ptiliidae, Agyrtidae, Leiodidae, Scydmaenidae, Scaphidiidae, Empelidae, Staphylinidae, Apateticidae, Silphidae). Apart from the inclusion of the Scarabaeoidea in the »staphyliniform« assemblage, the results of the present analyses agree in several regards with the ideas of Lawrence and Newton (1982), and the classification proposed here is more concordant with their system than with others proposed so far. The major differences are 1) recognition of Hydrophiloidea and Histeroidea as separate superfamilies, 2) recognition of six families, rather than just one, within Hydrophiloidea, 3) recognition of Agyrtidae, Leiodidae, Hydraenidae and Ptiliidae as a monophyletic group, 4) family status of Scaphidiidae, Empelidae and Apateticidae, and 5) various modifications within Staphylinidae, e.g., the recognition of Pselaphinae (earlier Pselaphidae) as a formal subfamily of Staphylinidae. In addition to a phylogenetic discussion of the taxa, diagnoses and keys to adults and larvae of families and subfamilies are provided, along with notes on their ecology and distributions.

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Introduction

The Staphyliniformia constitute one of the major groups of beetles of the suborder Polyphaga. It includes an immense number of species from all regions of the world. Almost 60.000 species have been named and many new are described every year. The structural and biological diversity is enormous. Most staphyliniforms are small or average sized beetles, often less than 5 mm long and rarely more than 10 mm, but larger forms occur in some families, notably Hydrophilidae, Silphidae and the staphylinid subfamily Staphylininae. The family Ptiliidae includes the smallest known beetles, only about 0.35 mm long. The vast majority of staphyliniforms are ground dwellers and typically inhabit more-or-less moist habitats, but there are adaptations to almost all kinds of habitats including aquatic ones. Many species occur in various kinds of rotting plant debris, rotten wood, fungi, dung, carrion etc., some in open land, others in forests, certain forms are cavernicolous or subterranean. Some are associated with nests of birds, mammals or social insects and have in some cases become extremely specialized to such habits. Even parasitic forms occur. A wide variety of feeding habits are exhibited by the Staphyliniformia. Many of them, including the presumedly most primitive forms, are saprophagous, some are mycophagous, and others are predatory. Other types of feeding habits such as coprophagy, necrophagy, algophagy and phytophagy, are also known from the staphyliniforms, but are less common. In some cases larvae and adults exhibit different feeding habits.

The existing classifications of the group disagree in several cases and in regard to all taxonomic levels. Not even the sheer number of families are generally agreed upon, and particularly the systematic status and limits of, e.g., Hydrophilidae, Leiodidae, Silphidae, Scydmaenidae, Pselaphidae and Staphylinidae have been subject to debate. Currently about 12-20 families are recognized as valid. In some cases the different numbers of recognized families are equally justified from our knowledge about phylogeny, and the formal status of the taxa is simply a matter of subjectivity (e.g., Hydrophilidae vs. Hydrophiloidea). But more often the divergences reflect to various extent the lack of a philosophical basis for the classification. Only few attempts have been made to analyse the phylogeny of the entire Staphyliniformia on a strict cladistic basis, and none have made use of the recently developed computer programs, which allow us to deal with very large amounts of data. The same is also true on a much lower taxonomic level, and actually only few subgroups of staphyliniformia (and other beetles as well) have been subject to a thorough cladistic analysis (with or without the aid of computer programs). Although the cladistic philosophy, i.e., that classification must reflect evolutionary history on a strict genealogical basis (without inclusion of paraphyletic groups), has been broadly accepted, several novel classifications are supported by little or no explanation. However, the understanding of the necessity for a strict cladistic approach in phylogenetic reconstruction is undoubtedly growing, and progress is being made continuously.

The present study deals with the phylogeny and classification of the beetles of the polyphagan series Staphyliniformia, to which the superfamilies Hydrophiloidea, Histeroidea and Staphylinoidea have currently been referred. All three superfamilies are here recognized as valid, although it should be noted that some authors prefer to include the Histeroidea in Hydrophiloidea (which is equally justified phylogenetically).

Due to the large number of species, it is of course impossible to analyse the entire Staphyliniformia at the species level. Not only would it be impossible to examine so many species within a reasonable time, but the amount of data would also be far beyond the capacity of any persons mind or any computer. Rather, we have to base such phylogenetic reconstruction on a series of smaller analyses at different taxonomic levels, in which taxa are grouped into demonstably monophyletic units for further analysis.

The major scope of the present study has been to analyse and reconstruct the basal phylogeny of the staphyliniform series and to examine its possible monophyly and relationship to other beetles, as well as the interrelationship and systematic status of the included superfamilies and families. Therefore the basic taxonomic units for analysis have mostly been families and (to some extent) subfamilies, and since only a fraction of the existing species could be examined, a certain degree of generalization has been necessary. To avoid too extensive generalizations representatives of almost all formal taxa to level of tribe (or sometimes subtribe) have been examined, but in the absence of existing analyses of most staphyliniform subgroups, misinterpretations are almost inevitable. I hope that possible misinterpretations and errors will be excused and that, in spite of many unanswered questions, the present study will provide a basis for further investigations of the phylogeny of the staphyliniform beetles, at higher as well as more detailed taxonomic levels.

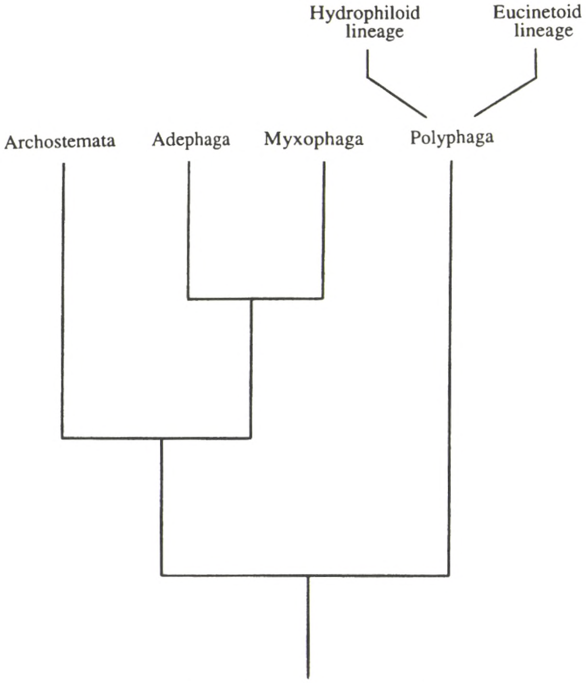

Fig. 1. Phylogenetic relationship of the major groups of Coleoptera as proposed by Kukalová-Peck and Lawrence (1993).

Basal phylogeny and major groups of Coleoptera

It seems to be generally accepted that the Coleoptera can be divided into four major lineages (suborders), Archostemata, Adephaga, Myxophaga and Polyphaga, all of which are probably monophyletic, at least when extant forms are considered. But different hypothesis about the relationship between the coleopteran suborders exist. The Archostemata are normally believed to include the most primitive (generalized) beetles, and could be the sistergroup of other beetles (Hennig, 1953), while Myxophaga might be the sistergroup of Polyphaga (e.g., Crowson, 1981). On the other hand, a sistergroup relationship between Polyphaga and Archostemata, Adephaga and Myxophaga has also been suggested and may be more likely as indicated by recent studies of the hindwing structure, which are also in favor of a sistergroup relationship between Myxophaga and Adephaga rather than Polyphaga (Kukalová-Peck and Lawrence, 1993) (fig. 1).

Whether or not the basal phylogeny of the Coleoptera as a whole has been fully understood, it seems that the major phylogenetic problems lie within the large suborder Polyphaga, which includes more than 90% of the known Coleoptera and exhibits a much greater diversity, biologically as well as structurally, than the other three suborders. The difficulties of reconstructing the phylogeny within Polyphaga is reflected by the several conflicting hypotheses concerning the subdivision of the group.

It should be mentioned that early classifications were predominantly based on the knowledge of the fauna of the northern hemisphere (particularly Europe) and should generally be considered "practical" rather than reflecting true phylogenetic relationships (although they may often do so). This "practical" approach (as opposed to an evolutionary one) could easily give rise to irrelevant discussions about whether one set of characters or another would provide the "best" classification (e.g., larval versus adult characters). Although the knowledge of the phylogeny of Coleoptera has gradually improved over the years, it is obvious that the most important step forwards has been the recognition of the necessity of using cladistic methodology in reconstructing phylogeny.

One of the first major works dealing with coleopteran phylogeny on a more modern cladistic basis), and the most widely accepted one, is that of Crowson, first issued in its entirety in 1955. In his work six major lineages ("series") of Polyphaga were recognized. Two of them (Staphyliniformia, Scarabaeiformia) were placed in one group, Haplogastra, the remainder (Dascilliformia, Bostrichiformia, Cucujiformia, Stylopiformia) in another, Symphiogastra (= Heterogastra). These two major groups of Polyphaga had earlier been treated as separate suborders (Paulian, 1949).

Crowson's Stylopiformia included only a single superfamily, Stylopoidea, with the much discussed families Mengeidae and Stylopidae (now more families are recognized), which have at times been considered closely related to the cucujiform (tenebrionoid) family Rhipiphoridae, or placed in a separate insect order (Strepsiptera). Later Crowson (1960) downgraded his Stylopiformia and suggested a close relationship to the cucujiform (lymexylonoid) family Lymexylonidae, but more recent evidence indicates a probable sistergroup relationship with the entire Coleoptera (Lawrence and Newton, 1982; Kukalová-Peck and Lawrence, 1993). Whether or not the Stylopoidea are beetles, there is no indication that they have evolved from a staphyliniform group, or that they are in any way closely related to that "series", so the question of their relationship seems to be of minor importance in regard to the present study.

The division of Polyphaga into Haplogastra and Symphiogastra (= Heterogastra), based upon the presence or absence, respectively, of a distinct (separate) pleural sclerite of abdominal segment 2 seems hard to justify, because it is inconstant within many groups (Crowson, 1960). However, this division may be supported by other evidence. Having studied the morphology of hindwings in a large number of different Coleoptera Kukalová-Peck and Lawrence (1993) suggested a basal split of the Polyphaga into two major groups: a "hydrophiloid lineage" (more-or-less equivalent of Haplogastra) and a "eucinetoid lineage" (more-or-less equivalent of Symphiogastra).

Crowson (1960) removed the Dascillidae from his ("symphiogastran") Dascilliformia - a name which for obvious reasons was replaced with Elateriformia – and suggested that the dascillids were likely to be regarded as an archaic group of the ("haplogastran") Scarabaeiformia. But this position of the Dascillidae as well as the "Dascilloid" ancestry of the Scarabaeiformia was questioned by Lawrence and Newton (1982), who pointed out the relatively "isolated" position of the latter. They included both the Dascilloidea and the Scarabaeoidea in an "elateriform lineage", but subsequently Lawrence (1988) excluded the latter again and placed it in a separate series, Scarabaeiformia. Although the Scarabaeiforms exhibit a suite of highly derived features, they also possess a number of primitive characters, which may be indicative of a relatively basal position within the Polyphaga.

The Elateriformia (earlier Dascilliformia) was redefined by Lawrence (1988), who recognized only four superfamilies (Dascilloidea, Byrrhoidea, Psephenoidea, Elateroidea), and excluded the Eucinetoidea and Scarabaeoidea.

The Eucinetoidea (now Scirtoidea), including Decliniidae, Eucinetidae, Clambidae and Scirtidae (= Helodidae), should probably be considered a primitive elateriform superfamily (e.g., Crowson, 1955; Lawrence and Newton, 1982, 1995) but has at times been placed in a separate series, Eucinetiformia (Crowson, 1981; Lawrence and Britton, 1991). Lawrence, Nikitsky and Kirejtshuk (1995) considered the Scirtoidea as a basal group within Elateriformia, possibly the sistergroup of other elateriforms. It seems to be an archaic polyphagan group.

Bostrichiformia (including two superfamilies: Dermestoidea and Bostrichoidea) was still retained as a separate series by Crowson (1960), but can probably not be justified. More recently, it has been considered a primitive (paraphyletic) group related to the Cucujiformia (Lawrence and Newton, 1982). The superfamily Dermestoidea is now included in the Bostrichoidea, except for the very primitive family Derodontidae, which is placed in a separate superfamily.

There appears to be general agreement of the concept of the Cucujiformia, and that it represents a monophyletic group (Crowson, 1955, 1960; Lawrence and Newton, 1982; Lawrence and Britton, 1991); the major problem may be whether or not the Stylopoidea (Strepsiptera) is to be included (cf. above).

The composition of the last of Crowson's (1955) series, i.e., Staphyliniformia, which is the subject of the present study, has been almost universally accepted. But, as outlined below, there is still considerable disagreement among authors in regard to the internal hierachy of the group, and neither the basal splits within Staphyliniformia nor the exact relationship to other beetles have been adequately explained so far. Not even the most essential question, i.e., whether the group is monophyletic has been firmly documented, and apart from the possibly autapomorphic nature of the segmented urogomphi in the larvae, no character has yet been suggested in support of its monophyly.

Review of the systematics of Staphyliniformia

A close relationship of several staphyliniform subgroups has long been admitted, but the concept of the entire assemblage as a possible monophyletic group is of more recent date. The Staphyliniformia was first proposed by Lameere (1900) for a group including the families Silphidae (in a very broad sense), Histeridae, Staphylinidae, Pselaphidae, Platypsyllidae and Pulicidae (= Siphonaptera). Ganglbauer (1895, 1899, 1904) treated a roughly equivalent group under the name Staphylinoidea, but used more families, viz., Staphylinidae, Pselaphidae, Scydmaenidae, Silphidae (s.lat.), Clambidae, Leptinidae, Platypsyllidae, Corylophidae, Sphaeriidae (= Microsporidae), Trichopterygidae (= Ptiliidae), Hydroscaphidae, Scaphidiidae and Histeridae. Other families, which are now considered part of the Staphyliniformia, were referred to more distantly related family groups, some of which have now been abandonned. Thus, Sphaeritidae and Synteliidae were referred to Clavicornia, which formed part of the large "dumping group" Diversicornia. Hydrophilidae and Georissidae were also first included in the Diversicornia by Ganglbauer, but a close relationship between the two families was not admitted. While the Hydrophilidae was subsequently placed in a separate group, Palpicornia (roughly corresponding to Hydrophiloidea), of equivalent rank with Staphylinoidea and Diversicornia, the Georissidae was retained in the Diversicornia (near Dryopidae).

A close relationship between Histeridae and Hydrophilidae (excl. Hydraenidae) was suggested by Bøving and Craighead (1931) on the basis of larval similarities. The two authors actually transferred the Histeridae from Staphylinoidea to Hydrophiloidea and, in contrast, included the Hydraenidae in Staphylinoidea rather than Hydrophiloidea.

Later, other of Ganglbauer's "staphylinoid" families were excluded from the superfamily: Microsporidae (= Sphaeriidae), Hydroscaphidae (both now in Myxophaga), Clambidae (now in Eucinetoidea), and Corylophidae (now in Cucujoidea) (e.g., Crowson, 1955, Lawrence and Britton, 1991). Also "Thorictidae" and "Gnostidae" have earlier (by some authors) been considered closely related to staphyliniform groups – Histeridae and Scydmaenidae, respectively – but are now believed to belong to the Bostrichoidea, and are included in Dermestidae (Lawrence and Britton, l.c.) and Ptinidae (Crowson, l.c.), respectively.

Crowson (l.c.) included the Dasyceridae (earlier referred to Latridiidae) in the Staphylinoidea, but did not consider Hydraenidae part of the superfamily. He suggested a close relationship between the Hydrophiloidea (to which he referred Georissidae), the Histeroidea (including Sphaeritidae and Synteliidae, both earlier in "Clavicornia") and the Staphylinoidea (in the slightly modified sense), and placed them in the series Staphyliniformia.

The composition of this series, as defined by Crowson, has been generally agreed upon by subsequent authors, but the concepts of the families (and lower taxa), as well as their relationships within Staphyliniformia, has been widely divergent, particularly in regard to the position of Hydraenidae, composition and taxonomic status of the Hydrophilidae (and allies), Leiodidae (and allies), the current concept of Staphylinidae, and the family rank of Scydmaenidae, Scaphidiidae, Silphidae (s.str.), Micropeplidae, Dasyceridae and Pselaphidae.

An extensive splitting of the Staphylinidae into several smaller families was suggested by Coiffait (1972), but was not accompanied by any phylogenetic justification and was not followed by subsequent authors.

Tikhomirova (1973) reviewed the morphology, ecology and evolution of the Staphylinidae, and though this paper is not a phylogenetic analysis in any modern sense, it is a valuable source of comparative morphology of staphylinoids.

In an important paper on classification and phylogeny of beetles, Lawrence and Newton (1982) outlined the relationship between the major subgroups of Staphyliniformia. They recognized only two superfamilies, Hydrophiloidea (incl. Histeroidea) and Staphylinoidea, and listed several possible apomorphies in support of the monophyly of both groups. Within Staphylinoidea, three groups were recognized, viz. a Ptiliid-Hydraenid group, an Agyrtid-Leiodid group and a Staphylinid group, all of which appeared to be well justified as monophyletic. In the Staphylinid group (roughly equivalent of the old "Brachelytra") they included, in addition to the Staphylinidae, the "traditional" families Scydmaenidae, Scaphidiidae, Silphidae (s.str.), Micropeplidae, Dasyceridae and Pselaphidae, and considered them likely to be subordinate groups of Staphylinidae. A division of the Staphylinidae (including these smaller "families") into four major groups was proposed, but otherwise Lawrence and Newton did not go into detail concerning the phylogeny of the staphylinid subfamilies.

More recently, an attempt at a more detailed classification of Staphylinidae and allied groups was presented by Naomi (1985). He divided the assemblage into three families: 1) Oxytelidae including Oxytelinae, Pseudopsinae, Osoriinae, Piestinae, Micropeplinae, Proteininae (s.lat.) and Omaliinae; 2) Staphylinidae (s.str.) including Paederinae, Staphylininae (s. lat.), Phloeocharinae, Tachyporinae, Habrocerinae, Trichophyinae and Aleocharinae (s.lat.); and 3) Oxyporidae including Oxyporinae, Megalopsidiinae, Steninae, Euaesthetinae, Leptotyphlinae and a group consisting of the 6 subfamilies traditionally constituting the Pselaphidae. He also considered Scydmaenidae, Scaphidiidae and Silphidae as valid families.

However, although Naomi's approach was claimed to be cladistic, there are serious objections to his analytical procedure, e.g., inadequate data sampling and the reliance on phylogenetic reconstruction based on "underlying autapomorphies" (i.e., apomorphies that are not present in the most plesiomorphic taxa of a group, but are assumed to have evolved repeatedly within the group as a result of "common inherited factors" (Sæther, 1979)). Moreover, his use of family group names are somewhat casual and, in some cases, not following the principles of zoological nomenclature. Naomi's classification was strongly criticised by Newton and Thayer (1988).

The Hydrophiloidea (excl. Histeroidea) were revised and reclassified on the basis of a cladistic analysis on the suprageneric level by Hansen (1991b), who recognized 6 hydrophiloid families (rather than only one). Although excluding the Histeroidea from Hydrophiloidea, Hansen agreed with e.g., Lawrence and Newton (1982) in regard to the probable sister-group relationship between hydrophiloids and histeroids. Beutel (1994) made a phylogenetic analysis of the Hydrophiloidea (excl. Histeroidea) based on characters of the head of adults and larvae and suggested a somewhat different phylogeny of the group. He retained the six families recognized by Hansen but included the Hydraenidae (here referred to Staphylinoidea) (see phylogenetic discussion under Hydrophiloidea).

Phylogenetic studies based on cladistic methodology have been made of a number of other staphyliniform subgroups, but generally only groups below the family level. The state of knowledge about staphyliniform phylogeny was discussed by Newton and Thayer (1992), who gave an outline of the current classification and a catalogue of all family-group names used in the series. More recently the phylogeny of two large sections of the Staphylinidae – Tachyporinae and allies, and Omaliinae and allies – has been analyzed by Ashe and Newton (1993) and Newton and Thayer (1995), respectively.

Basis for classification

The naming and classification of living organisms has a long history. Early classifications (like the Linnaean one) appeared long before ideas about evolution had developed and were in the absence of this philosophical basis merely practical in essence. But they proved to be a very useful tool in the study of organisms and communication between scientists. As the ideas about evolution appeared and became accepted, a quite new basis for classifying living organisms was provided. But although the classifications gradually improved in regard to reflecting true phylogenetic relationships between species, the groupings were still based almost entirely on general similarity. A more competent methodology for phylogenetic reconstruction was developped by the German

Willi Hennig and outlined in his classical works from 1950 and 1966. Hennig emphasized the importance of distinguishing between "primitive" and "derived" characters – plesiomorphies and apomorphies, respectively – and that only groups based on apomorphies can be justified as natural (i.e., monophyletic) entities. Although some authors still use certain cladistic terms (e.g., plesiomorphic vs. apomorphic) in a rather casual manner and more-or-less intentionally recognize paraphyletic groups as valid, there is growing agreement that classification should reflect phylogeny and hence, cladistic methodology is steadily becoming more widely accepted and used.

There has been some controversy about appropriate cladistic methodology, but phylogenetic analysis based on parsimony is now widely (though not generally) accepted and has also been applied in available computer programs designed for phylogenetic reconstruction (e.g., Hennig86, PAUP). A further discussion of this subject is considered to be beyond the scope of the present work. The basic hypothesis in regard to this mode of phylogenetic reconstruction is that the best estimate of a phylogeny (based on the available character data) is the one involving the lowest degree of homoplasy (convergences/parallelisms and character reversals), so that derived characters shared by two or more taxa are taken to be indicative of relationship unless they are in conflict with other characters of higher number and/or reliability (weight), in which case they must be interpreted as convergences. In the present work only groups that are found likely to be monophyletic have been recognized, whereas paraphyletic groups are not accepted.

The relation between phylogeny and classification has been a much debated subject (see, e.g., Nelson 1972), but it is now widely accepted that we should strive for a type of classification that reflects the phylogenetic relationship of organisms. There are several ways in which this can be achieved, e.g., by naming every monophyletic group of a given tree. Another recommended convention which is, in my opinion, much more useful is the phyletic sequencing convention suggesting that "monophyletic groups [of an asymmetrical tree] could be placed at the same categorial rank and listed in order of their branching sequence" (e.g., Wiley, 1981). The great benefits of this convention are that 1) it can exactly reflect phylogenetic relationship without every branch point having to be named, 2) it will keep the number of formal rank categories at a minimum, and 3) it permits a higher degree of stability with regard to the formal rank of taxa even when the phylogeny is not adequately resolved, because a change in the position of a taxon does not necessarily give rise to a change of its rank.

Material and methods

Definition and selection of taxa

Definition of terminal of taxa

As already mentioned, the Staphyliniformia is an extremely species-rich group of beetles, and an analysis of its basal phylogeny can not possibly be based on all included species. Therefore one has to rely on already established compositions of the different subgroups to a certain taxonomic level. Families that have been excluded from the Staphyliniformia by previous authors (cf. above) are here ignored. The terminal taxa ("ingroups") that form the basis for the present analyses are delimited, so that they can be regarded as reasonably well justified monophyletic groups. In most cases, more-or-less well established, "traditional" families could be selected. The major exception in the present context is the "Staphylinidae" which, as indicated by previous authors (e.g., Lawrence and Newton, 1982), might be expected to be paraphyletic with respect to the "families" Pselaphidae, Dasyceridae, Scaphidiidae, Micropeplidae, Silphidae (s.str.) and Scydmaenidae, or at least some of them. Thus, it was obviously necessary to split the Staphylinidae into several minor units. Basically the existing subfamilies or, in some cases, groups of closely related subfamilies were identified as terminal taxa. A total of 37 terminal taxa have been identified (including the outgroups discussed below). Definitions and compositions of the terminal taxa are given below in connection with the phylogenetic discussion.

The character distribution of each terminal taxon was obtained from examination of one or (in most cases) several species, representing as many of its subgroups as possible. When a character showed variation within a terminal taxon, the character state assumed to represent the ground plan of the taxon was chosen. Hence, the terminal taxa defined throughout the study represent their hypothetical ancestors (or groundplan, if one prefers that term), rather than actual species. The main objection to this method might be that it involves a certain amount of initial assumptions and generalizations in regard to character distribution and -polarization. However when the assumptions can be based on hypotheses about the relationships *within* a terminal taxon, the risk of misinterpretations are minimized. And it must be realized that assumptions and generalizations will always be necessary at some level. Furthermore, the characters used here have been defined so that they show no or relatively little variation within each terminal taxon, and therefore initial assumptions about character polarity within terminal taxa are few compared to characters that are constant within a given taxon.

Alternatively, one could select one or more species from each terminal taxon and use them as terminal taxa instead. But this method has other and, at least for this study, probably more serious disadvantages and requires that large fractions of missing data must be included, e.g., because larvae are unknown for many species, which are in other regards the most informative representatives for their respective groups. Moreover, a selected species could have too many derived characters compared to the ancestor of the group, which could also distort the outcome of a phylogenetic analysis.

Selection of outgroups

It seems obvious that, like some of the other polyphagan "series", the Staphyliniformia (notably the Hydrophiloidea) includes some forms, which must be regarded as very primitive Polyphaga and that they probably originate from a very early polyphagan stock. Hence, the questions about basal Staphyliniform phylogeny is (at least with the present knowledge) intimately connected to the question about basal polyphagan phylogeny. Because of the uncertainty about the monophyly and sistergroup relationship of the Staphyliniformia it was found necessary to include a series of different outgroups in the phylogenetic analyses rather than just a single one. Outgroups were selected from the presumedly more archaic groups of some of the major polyphagan lineages ("series") mentioned above, i.e., such representatives that would appear most generalized compared to the assumed polyphagan groundplan, as well as from the other three suborders of Coleoptera.

Because of the dubious but probably quite basal position of the Scarabaeiformia within Polyphaga and the possibly close relationship to the Staphyliniformia as suggested by some previous authors, it is obvious to include a primitive Scarabaeiform family among the outgroups. Within this group, the Trogidae seem to have a relatively basal position. The family posseses a suite of primitive (but also certain highly derived) characters (e.g., Crowson, 1955), and is considered to be an appropriate group for study in the present context. It includes only a few genera, of which *Trox* was selected here for examination.

The Elateriformia (incl. the former Eucinetiformia) include some forms which are in many regards primitive Polyphaga, particularly the Scirtoidea. Since the Scirtidae are in some regards to be considered relatively derived members of that superfamily (Lawrence and Newton, 1982), and the clambids might show too many structural reductions that are directly related to their minute size, it is believed that the best representative is to be selected from the Euctinetidae, and that *Eucinetus* is an adequate choice.

Due to the probable relationship between the Bostrichiformia and the (apparently well founded) Cucujiformia, with the former possibly representing a primitive paraphyletic "-stem group" of the latter, it appears justified to select a primitive bostrichiform as representative for this large group of beetles. The most obvious group seems to be the Derodontidae, from which *Laricobius* was used as an outgroup.

In addition to the outgroups selected among primitive Polyphaga, it was found necessary to include also some non-polyphagan outgroups in the analyses, particularly in order to secure a reasonably reliable determination of character polarity at the most basal polyphagan level, in case the Staphyliniformia (or part of the group) should turn out to be the sistergroup of other Polyphaga (which could not initially be rejected). Due to divergent hypotheses about the relationship between the coleopteran suborders it was found appropriate to include representatives from each of the remaining suborders.

Archostemata includes the apparently most generalized beetles, and although the few modern forms possibly constitute a monophyletic assemblage, the group as a whole – i.e., when the wide variety of fossil forms are considered – is most likely paraphyletic. The genera studied here are *Tetraphalerus* (Ommatidae) and *Priacma* (Cupedidae).

Adephaga appears to be a well defined monophyletic group. It was recently shown that the Gyrinidae are very likely to be the sistergroup of the other adephagan families (Beutel and Roughley, 1988), and that it has not evolved from a dytiscoid ancestor, as often assumed. Thus, due to this basal position within the suborder, it seemed obvious to include a gyrinid genus among the outgroups. Since the primitive genus *Spanglerogyrus* was not available, a species of *Gyrinus* was selected. But as the gyrinids are – in spite of their basal position – in many regards highly specialized, it was found appropriate to include an additional outgroup selected among the Adephaga. It is generally believed that the Trachypachidae represent an ancient family. Undoubtedly, it is an early offshoot of primitive "caraboids", and because it is moreover near to the hypothetical ancestor of the "Hydradephaga" (excl. Gyrinidae and ?Haliplidae), it would seem to be an adequate choice. The family includes only two small genera, *Trachypachus* and *Systolosoma*, the latter of which was selected for the present study.

Myxophaga. There has been some dispute about the status and relationship of this group. Originally, Crowson (1955) included Microsporidae (= Sphaeriidae), Lepiceridae (= Cyathoceridae), Hydroscaphidae and Calypteromeridae (including only *Calyptomerus*) in the group. However, the latter family was subsequently excluded from the Myxophaga (and again included in Clambidae), while a new family, Torridincolidae, has been added. The phylogeny within the group is not clear as illustrated by the different hypotheses about its origin/sistergroup relationship. Crowson (e.g., 1960) suggested that it was closest related to Polyphaga, but others have mentioned that the Myxophaga may have evolved from forms currently placed in the (fossil) "archostematan" family Schizophoridae (cf. Lawrence and Newton, 1982). Most recently it has been suggested that Myxophaga and Adephaga are sistergroups (Kukalová-Peck and Lawrence, 1993). For the present study, *Microsporus* (Microsporidae) was selected as a representative of the Myxophaga.

Certainly, many more outgroups could be selected, but for the purpose of this study the choice of outgroups is believed to be adequate. It should not be expected, however, that the analyses based on the groups considered here will resolve the basal phylogeny of the Polyphaga as a whole (though they may to some extent), much less the entire order of Coleoptera.

It may be worth to emphasize here that the distinction between outgroups and ingroups is merely an operational one based on the assumption that the ingroups do in fact form a monophyletic group. We may find, if more than one outgroup is included in the analysis, that in some cases a so-called outgroup actually turns out to be a subordinate member of the ingroup assemblage and – contrary to initial assumptions – must be categorized as an ingroup. Hence, the inclusion of several presumed outgroups may provide some kind of test as to whether the ingroups do consititute a monophylum. This can never be revealed from the inclusion of only a single outgroup.

Preparation of specimens

Specimens of adult beetles used for this study were obtained from various institutions and private collections (see Acknowledgement). In order to identify and define characters that are relevant for the phylogenetic analysis of the Staphyliniformia a number of species (mostly dry specimens) representing a wide variety of different staphyliniform subgroups, as well as the above mentioned outgroups, were prepared as follows.

Initially, the elytra were removed from the specimen and mounted on a card, so one could be examined from above and the other from below. Then the hindwings (if present) were removed, and the one mounted (in its folded condition) with the elytra, the other softened, unfolded and mounted in euparal on a slide. The specimen, thus deprived of its wings, was macerated in KOH at room temperature for a period of some hours to a day, depending on the size of the specimen. Smaller species were in most cases sufficiently cleared after treatment in KOH, but larger or heavily pigmented specimens had to be treated for a few minutes in hydrogen peroxide, which is very efficient in bleaching the specimens and thus faciliating the examination of wide variety of skeletal characters. Subsequently, the specimen was transferred to absolute alcohol, and when airbubbles (mainly resulting from treatment with peroxide) had disappeared, it was placed in glycerin for study. After study the specimens were transferred to small glass or plastic tubes (kept in a mixture of glycerin and alcohol), except for some dissected parts that were mounted in euparal on slides. Not all the species examined here could be given this treatment, so some generalizations had to be made in regard to characters that could only be observed in cleared specimens. I have not found it necessary to mention for each examined species which characters could not be examined, but have rather indicated cleared species in the list of studied taxa given below.

Taxa studied

Adults of the following species were examined during the course of this study. The classification indicated here agrees largely with that of Newton and Thayer (1992), except for the recognition of six (rather than one) families of Hydrophiloidea, familiy status of Scaphidiidae, and the downgrading of the Pselaphidae to a subfamily of Staphylinidae (in consequence, current "pselaphid" subgroups are also tentatively downgraded). Moreover, Aphaenostemminae is included in the Omaliinae, whereas Microsilphinae is given separate subfamily status (cf. phylogenetic discussion).

The examination of most of species was based upon dry specimens, but some representatives of nearly all major groups have been dissected and cleared as described above. These species have been indicated by a *.

HYDROPHILOIDEA. – Helophoridae (*Helophorus brevipalpis**). – Epimetopidae (*Eumetopus flavidulus**). – Georissidae (*Georissus crenulatus**). – Hydrochidae (*Hydrochus brevis**). – Spercheidae (*Spercheus emarginatus**). – Hydrophilidae: Horelophinae (*Horelophus walkeri*), Hydrophilinae (*Berosus luridus**, *Anacaena globulus**, *Enochrus coarctatus**), Sphaeridiinae (*Pseudohydrobius flavus**, *Coelostoma orbiculare**, *Cercyon melanocephalum**, *Sphaeridium scarabaeoides**). – Reconstruction of the hydrophiloid groundplan was further based on data that were obtained in connection with a previous study of virtually all hydrophiloid genera (Hansen, 1991b).

SPHAERITIDAE: (*Sphaerites glabratus**).

SYNTELIIDAE: (*Syntelia histeroides*).

HISTERIDAE. – Niponiinae (*Niponius obtusiceps*). – Abraeinae: Abraeini (*Abraeus globosus**), Acritini (*Acritus nigricornis*), Plegaderini (*Plegaderus vulneratus*), Teretriini (*Teretrius picipes*). – Trypeticinae (*Trypeticus indicus*). – Trypanaeinae (*Trypanaeus thoracicus*). – Saprininae (*Saprinus semistriatus**). – Dendrophilinae: Bacaniini (*Bacanius punctiformis*), Dendrophilini (*Dendrophilus punctatus**), Paromalini (*Paromalus flavicornis*). – Onthophilinae (*Onthophilus striatus*). – Tribalinae (*Epierus pulicarius, Tribalus scaphidiformis*). – Histerinae: Exosternini (*Pachycraerus cyanescens*), Histerini (*Atholus bimaculatus**, *Hister unicolor*), Hololeptini (*Hololepta plana*), Omalodini (*Omalodes angulatus*), Platysomatini (*Platysoma compressum*). – Hetaeriinae (*Hetaerius ferrugineus*). – Chlamydopsinae (*Chlamydopsis* sp.).

AGYRTIDAE. – Lyrosomatini (*Lyrosoma ovipenne*). – Pterolomatini (*Pteroloma forstroemi**). – Agyrtini (*Agyrtes castaneus**, *Pelatines latus, Ecanus glaber, Necrophilus hydrophiloides**).

LEIODIDAE. – Catopocerinae: Glacicavicolini (*Glacicavicola bathyscioides*), Catopocerini (*Catopocerus cryptophagoides*). – Platypsyllinae (*Leptinus testaceus**, *Platypsyllus castoris**). – Coloninae (*Colon serripes** (+ sp.)). – Camiarinae: Neopelatopini (*Ragytodes ocellifer, Neopelatops* sp.), Agyrtodini (*Agyrtodes* sp.). – Leiodinae: Estadiini (*Dietta sperata*), Scotocryptini (*Scotocryptus inquilinus*), Sogdini (*Hydnobius punctatus*), Leiodini (*Leiodes polita**, *L. cinnamomea*), Pseudoliodini (*Dermatohomoeus kaszabi*), Agathidiini (*Anisotoma humeralis**, *A. glabra, Agathidium atrum*). – Cholevinae: Ptomaphagini (*Ptomaphagus medius*), Anemadini (*Anemadus acicularis, Nemadus colonoides*), Cholevini (*Nargus wilkini**, *N. velox, Choleva agilis, Catops picipes**, *Catopsimorphus orientalis*), Leptodirini (*Platycholeus leptinoides, Adelopsella bosnica, Bathyscia montana, Bathysciotes khevenmuelleri, Troglodromus bucheti, Aphaobius milleri, Drimeotus kovacsi, Pholeuon ha-*

zayi, Leptodirus hohenwarti, Apholeuon nudus, Anthroherpon ganglbaueri).

HYDRAENIDAE. – Hydraeninae: Hydraenidini (*Hydraenida ocellata*), Hydraenini (*Hydraena riparia*, Limnebius truncatellus**). – Prosthetopinae (*Prosthetops megacephalus*). – Ochthebiinae (*Ochthebius marinus**). – Reconstruction of the hydraenid groundplan was further based on data that were obtained in connection with a previous study of most hydraenid genera (Hansen, 1991a).

PTILIIDAE. – Ptiliinae: Nossidiine section (*Nossidium pilosellum**), Ptiliine section (*Ptenidium pusillum*, Dipentium parvum, Ptiliolum kunzei, Bambara sublutea, Skidmorella magnifica*), Pterycine section (*Pteryx suturalis*, Ptinella aptera*). – Acrotrichinae (*Acrotrichis intermedia**). – Cephaloplectinae (*Limulodes paradoxa*).

SCYDMAENIDAE. – Scydmaeninae: Eutheiini (*Eutheia schaumi**), Cephenniini (*Cephennium thoracicum**), Cyrtoscydmini (*Stenichnus collaris, Euconnus hirticollis**), Scydmaenini (*Scydmaenus tarsatus**). – Mastiginae: Clidicini (*Clidicus* sp., *Papusus macer*), Leptomastacini (*Leptomastax coquereli*), Mastigini (*Mastigus palpalis**).

SCAPHIDIIDAE. – Scaphidiini (*Ascaphium tibiale, Scaphium immaculatum*, Scaphidium quadrimaculatum**). – Cypariini (*Cyparium mikado*). – Heteroscaphini (*Bironium nigrolineatum*). – Scaphisomatini (*Scaphisoma agaricinum**). – Toxidiini (*Toxidium aberrans*).

EMPELIDAE: (*Empelus brunnipennis**).

STAPHYLINIDAE. – Microsilphinae (*Microsilpha* sp.*). – Omaliinae: Aphaenostemmini (*Aphaenostemmus testaceus*), Anthophagini (*Olophrum piceum*, Brathinus oculatus, Anthophagus caraboides*), Coryphiini (*Coryphium angusticolle*), Eusphalerini (*Eusphalerum minutum*), Omaliini (*Omalium rivulare*, Xylodromus depressus*). – Proteininae: Anepiini (*Anepius koebelei*), Nesoneini (*Nesoneus acuticeps*), Proteinini (*Metopsia clypeata, Megarthrus depressus*, M. denticollis, Proteinus brachypterus**). – Micropeplinae (*Micropeplus porcatus**). – Neophoninae (*Neophonus bruchi**). – Dasycerinae (*Dasycerus sulcatus**). – Pselaphinae (= Pselaphidae auct.): Faronini (*Faronus lafertei*), Euplectini (Euplectina: *Euplectus piceus*, Trimium brevicorne*; Trogastrina: *Phtegnomus naso*), Batrisini (Batrisina: *Batrisodes venustus*, Batrisus formicarius*), Goniacerini (Trichonycina: *Trichonyx sulcicollis*; Brachyglutina: *Brachygluta fossulata**; Bythinina: *Bryaxis bulbifer*; Tychina: *Tychus niger*), Pselaphini (Pselaphina: *Pselaphus heisei**; Ctenistina: *Chennium bituberculatum*; Tyrina: *Tyrus mucronatus*), Clavigerini (Clavigerina: *Articerodes syriacus, Claviger testaceus**).

Phloeocharinae (*Phloeocharis subtillissima**). – Olisthaerinae (*Olisthaerus substriatus**). – Tachyporinae: Deropini (*Derops longicornis*), Mycetoporini (*Mycetoporus brunneus**), Tachyporini (*Tachyporus obtusus*, Tachinus proximus*, T. rufipes*). – Trichophyinae (*Trichophya pilicornis*). – Habrocerinae (*Habrocerus capillaricornis**). – Aleocharinae: Pygostenini (*Pygostenus eppelsheimi* (+ spp.)), Hypocyphtini (*Cypha longicornis, Oligota inflata*), Gymnusini (*Gymnusa brevicollis**), Myllaenini (*Myllaena dubia*), Diglottini (*Diglotta mersa*), Pronomaeini (*Pronomaea rostrata*), Hygronomini (*Hygronoma dimidiata**), Homalotini (*Gyrophaena affinis, Homalota plana, Leptusa fumida*), Termitusini (*Termitusa sjoestedti*), Phytosini (*Phytosus balticus*), Autaliini (*Autalia impressa*), Falagriini (*Falagria caesa*), Dorylophilini (*Derema bickmanni*), Athetini (*Atheta graminicola*, Amischa analis*), Lomechusini (*Drusilla canaliculata, Zyras cognata, Lomechusa emarginata*), Hoplandriini (*Tinotus morion*), Oxypodini (*Dinarda maerkelii, Meotica exilis, Phloeopora testacea, Ilyobates subopacus, Oxypoda lividipennis*, Ischnopoda atra*), Aleocharini (*Aleochara curtula*, A. lanuginosa*).

Trigonurinae (*Trigonurus crotchii*). – Piestinae (*Piestus spinosus, Siagonium quadricorne*). – Osoriinae: Eleusinini (*Eleusis kraatzi* (+ spp.)), Thoracophorini (*Thoracophorus corticinus*), Osoriini (*Osorius brasiliensis* (+ spp.)), Leptochirini (*Leptochirus mexicanus, Thoracochirus variolosa, Priochirus sanguinosus*). – Oxytelinae (*Syntomium aeneum*, Coprophilus striatulus*, Carpelimus bilineatus, Oxytelus rugosus, Apocellus sphaericollis*).

Oxyporinae (*Oxyporus rufus**). – Megalopsidiinae (*Megalopinus punctatus*). – Steninae (*Stenus juno*, S. binotatus, Dianous coerulescens*). – Euaesthetinae: Stenaesthetini (*Stictocranius puncticeps*), Euaesthetini (*Euaesthetus bipunctatus*, Edaphus nitidus*). – Solieriinae (*Solierius obscurus*). – Leptotyphlinae (*Leptotyphlus brevicornis*). – Pseudopsinae (*Pseudopsis sulcata, Zalobius spinicollis*). – Paederinae: Paederini (*Echiaster* sp., *Paederus riparius, Astenus immaculatus, Rugilus rufipes, Lithocharis ochracea, Scopaeus sulcicollis, Domene scabricollis, Lathrobium brunnipes*, L. elongatum*, Pseudocryptobium spinola, Ochthephilum fracticorne, Dolicaon illyricus*), Pinophilini (*Procirrus lefebvrei, Pinophilus laticeps, Palaminus* sp.). – Staphylininae: Xantholinini (*Xantholinus tricolor*, X. linearis, Eulissus chalybaeus, Plagionocerus fulgens*), Othiini (*Othius punctulatus*), Diochini (*Diochus schaumi*), Platyprosopini (*Platyprosopus consularis*), Staphylinini (*Erichsonius cinerascens, Philonthus fuscipennis, Staphylinus dimidiaticornis*, Platydracus stercorarius, Phanolinus pretiosus, Xanthopygus cyanelytrius, Creophilus maxillosus, Quedius xanthopus, Atanygnathus terminalis*).

APATETICIDAE: (*Nodynus leucofasciatus*).

SILPHIDAE. – Silphinae (*Thanatophilus rugosus, Necrophila americana, Silpha obscura*, Ptomaphilus lacrymosa, Protone-*

crodes surinamensis, Necrodes litoralis, Diamesus osculans). – Nicrophorinae (*Nicrophorus humator, Ptomascopus plagiatus**).

ARCHOSTEMATA. – OMMATIDAE: (*Tetraphalerus* sp.*). – CUPEDIDAE: (*Priacma serrata*).

ADEPHAGA. – GYRINIDAE: (*Gyrinus marinus**). – TRACHYPACHIDAE: (*Systolosoma* sp.*).

MYXOPHAGA. – MICROSPORIDAE: (*Microsporus acaroides**).

POLYPHAGA. – EUCINETIDAE: (*Eucinetus haemorrhoidalis**). – DERODONTIDAE: (*Laricobius erichsoni**). – TROGIDAE: (*Trox scaber**).

Definition and selection of characters

The basic unit used for describing taxa, i.e., the "character", is often referred to as an objectively defined unit, and taxa are often more-or-less categorically described as being defined by a certain number of characters, as if the number of characters is an absolute measure for its validity. But, although it is indeed impossible to discuss phylogeny without referring to characters in this way, it must be realized that a character is always subjectively defined and that characters may be of very different nature. For example, the presence/absence of a certain structure may be considered as a single character, but if the structure shows some complexity, it is often preferable to look at it as a suite of different characters. There is no objective method for determining which alternative is the most adequate in the given context. And as the phylogenetic models are calculated on the basis of numbers of characters, characters should be very carefully defined. Inclusion of very simple and very complex characters in an analysis should be avoided, and probably the best way of achieving reasonably comparable characters would be to strive for a relatively high degree of resolution of the characters. But it would still be illusive to assume that all characters can be defined so they are quite equivalent. And there may be problems in regard to the definition of characters of certain segmentally homologous structures (e.g., legs or antennal segments of insects), i.e., when similar features of different segments are to be considered one "repeated" character or more independent characters. Probably, these problems may also be reduced to some degree when the number of characters are maximized.

The development of computer programs for reconstruction of phylogeny allows us to deal with much larger amounts of data than it was possible just few years ago. And such programs are still being improved, so technically a higher degree of objectivity can now be applied to the phylogenetic analyses. When phylogenetic models are calculated, most programs basically assign equal importance (weight) to the characters, but there are a variety of options by which characters can be individually weighted. Phylogenetic reconstruction based on equally weighted characters may work well if one has succeded in defining characters so they are reasonably equivalent, but this will always be a matter of reliance and can probably never be objectively established. More likely, there are in any assemblage of characters some, which deserve higher weight than others. In some cases the phylogenetic hypothesis may not be affected by the weight assigned to a particular character, but in others the weight can be crucial for the result.

Perhaps the major problem of character weighting lies in the fact that we can not even be sure that a character is equally liable to change from one state to another in a given group of organisms. Take, for example, the long or short elytra of different groups of Staphyliniformia. It is generally believed that the short elytra of most Staphylinidae is a derived feature at a certain taxonomical level and that some forms have secondarily developed longer elytra. However, there is no indication that the character – long versus short elytra – is equally likely to change in both directions, and we can hardly justify the assumption that the "same" character in other families (e.g., Ptiliidae) is equally likely to change. However, operationally such assumptions have to be made at some level, and it should also be admitted that in many cases this discussion is more academic than concrete, particularly when the degree of character compatibility is high. Some groups of taxa may be so well defined with regard to the number of characters that the weight of each character becomes of minor importance. But taxonomic groups that are supported only by a single or a few characters may often be sensitive to even slight manipulations of the data matrix and are often not very reliable. The fact that modern technology allows us to achieve objectively calculated phylogenetic models must not make us forget that the most fundamental problem in phylogenetic reconstruction is how we define the characters, on which the phylogenetic analyses are based.

The characters used in the present study were obtained from examination of the taxa listed above and from the literature. A major difficulty in identifying and defining suitable characters for higher classification of a group like Staphyliniformia lies in the great variation of character states that often occur when larger groups are considered.

When a character state for a group of taxa shall be determined, it must be the one that is ancestral for this group. In the simplest case a character is constant within the group and can therefore also be assumed to be ancestral. But in many cases, when we deal with higher classification/ phylogeny, many characters occur in different states within a group, and it must therefore be examined which state can be regarded as the ancestral (plesiomorphic). Because the polarization of character states can only be based on outgroup comparison, and the sistergroup relationships of several Staphyliniform subgroups was usually not clear, it was impossible to determine the ancestral state of many characters. This means that several characters, which may be useful for phylogenetic analysis at a lower taxonomic level, have to be excluded from the present analysis.

But there are still many characters which are, in spite of some variation (also within terminal taxa), potentially informative about phylogeny on a higher taxonomic level. In the present study, 119 such characters form the basis of the phylogenetic analysis. As it will be seen from the list of characters given below, there is hardly any character that has not already been used at some taxonomic level in the Staphyliniformia. Thus, almost any modification in regard to the phylogeny presented here (compared with previous hypotheses) is based on reinterpretation of characters, so although some characters might be considered "new", it is rather the present interpretation that is new.

In regard to the selection of characters I have focused on integumental structures. Visceral structures were not included, because of the scarcity of suitable material. As to the character distribution within terminal taxa, adult characters were primarily obtained from examination of the above mentioned species, while larval characters were mainly obtained from various literature sources (Dybas, 1976; Frank, 1991; Lawrence, 1991; Newton, 1991; Paulian, 1941; etc.).

List of characters

The following list includes all characters that have been used in this study for the phylogenetic analysis. Most characters have been defined as two-state characters, but some include several states. All multistate characters have been considered unordered (non-additive) to avoid "a priori" assumptions about transformation series. Likewise, no "a priori" assumptions about character polarity between terminal taxa were made.

Characters that were tentatively included in an initial phylogenetic analysis, but which turned out to be difficult to define adequately (and uninformative in the present context) are not included in the list. Since numerous characters were included at various stages in the course of the study, I have made no attempt to list all characters that have been discarded. Autapomorphies for single terminal taxa are also omitted from the list of characters, but they have been mentioned under the relevant taxa. A few characters were excluded from the analyses because of difficulties in obtaining sufficient comparative data. Such characters are not listed here but may be mentioned under the relevant taxa in the phylogenetic discussion.

The relative importance of different characters, as revealed by the phylogenetic analyses, is outlined in the phylogenetic discussion, and a survey of character statistics is given in the appendix.

Characters of adults (both sexes):

1. Clypeus moderate sized or rather small, at lateral margin < $1^1/_2$ x as long as frons (measured from anterior margin of eye to frontoclypeal suture) (fig. 18) (0) – Clypeus large (fig. 14) (1)

   The size of clypeus is usually small (as defined here). A larger clypeus occur in Hydrophiloidea, Hydraenidae, Scaphidiidae and Silphidae, occasionally also in subordinate members of other groups.

2. Frontoclypeal suture grooved (0) – Frontoclypeal suture visible but not grooved (1) – Frontoclypeal suture not distinct (2)

   A frontoclypeal suture is detectable in many groups of Staphyliniformia. It is grooved in Hydrophiloidea (except more derived forms), Sphaeritidae, Hydraenidae (most forms) and some Staphylinidae (e.g., Neophoninae), as well as in some of the outgroups (Gyrinidae, Eucinetidae). The suture has disappeared in several groups, e.g., Synteliidae. Histeridae (most), Ptiliidae, Apateticidae, some Staphylinidae (Steninae, Staphylininae, Solieriinae, Micropeplinae, Pselaphinae), and some of the outgroups.

3. Head not constricted behind eyes (fig. 16, 19) (0) – Head abruptly constricted immediately behind eyes (fig. 12) (1) – Head with constricted neck well behind eyes (fig. 17, 20) (2)

   This character is rather variable. Most of the outgroups as well as Histeroidea and some of the presumedly more archaic staphylinoid families, Agyrtidae and Leiodidae (most forms, including the more primitive ones), and a few others do not have a constricted neck. Most other groups, however, do have a more-or-less constricted neck. Hydrophiloidea (except the more derived forms), Hydraenidae (most spp.) and to some extent Ptiliidae have the head more-or-less strongly constricted immediately behind the eyes. In others, e.g., Scydmaenidae, Silphidae (most) and the majority of the Staphylinidae the constriction lies more-or-less behind the eyes.

4. A pair of ocelli present on vertex (fig. 20) (seldom a single median ocellus) (0) – Ocelli absent (1)

   The presence of ocelli is usually considered an archaic feature within Coleoptera. Paired ocelli are present in Agyrtidae (some), Leiodidae (the presumedly primitive genus *Ragytodes*), Hydraenidae (most), some Staphylinidae (Omaliinae and some allied subfamilies), and Derodontidae. In the genus *Metopsia* (Staphylinidae: Proteininae) only a single median ocellus is present.

5. Interocular grooves (= dorsal tentorial pits) present (fig. 20, 24) (0) – Interocular grooves absent (1)

   Interocular grooves are present in various groups of Staphyliniformia: Hydraenidae, some Staphylinidae (Omaliinae, Proteininae, Micropeplinae, Dasycerinae, Pselaphinae, etc.) and in one of the outgroups (Derodontidae). Such grooves are also found in certain subordinate members of a few other groups.

6. Gular sutures separate throughout (so submentum is not separated from gula by constriction by the sutures) (fig. 26) (0) – Gular sutures confluent (fig. 27), completely or at least for long distance (so submentum forms a well defined sclerite) (1) – Gular sutures not distinct (2)

   The appearance of the gular sutures varies considerably, but most groups have them well separated (at least primitively). Only in Synteliidae, Histeridae, Hydraenidae, Scaphidiidae and Staphylinidae: Neophoninae are they probably primitively confluent. In Ptiliidae the gular sutures could not be detected.

7. Pair of cervical sclerites present (fig. 26, 114) (0) – Cervical sclerites absent (1)

   The presence of cervical sclerites is usually referred to as characteristic of the suborder Polyphaga as opposed to the other three coleopteran suborders in which such sclerites are constantly absent. There are, however, also some staphyliniforms in which cervical sclerites are apparently absent: Ptiliidae, Scydmaenidae and certain Staphylinidae (Solieriiinae, Micropeplinae, Dasycerinae, Pselaphinae).

8. Mandibles with moderately developed apices, at least one of which is visible externally, when mandibles are abducted (0) – Mandibles with small weak apices, which are concealed, when mandibles are abducted (1)

   The extent to which the mandibles are projecting varies considerably between (as well as within) groups, but in most taxa they are visible. Howver, in Hydrophiloidea (most), Hydraenidae, Ptiliidae and a few staphylinid subfamilies (Proteininae, Micropeplinae, Dasycerinae) they are hardly visible when abducted. In Hydraenidae and Ptiliidae their apices are usually weaker than in the other groups.

9. Mandibles with mola (fig. 34, 37) (0) – Mandibles without mola (fig. 35, 36) (1)

   The presence of a mola is typical of most groups, but the mola may be more-or-less well developed. A mola is absent in Scydmaenidae, Silphidae and some Staphylinidae (Microsilphinae, Staphylininae, Paederinae, Pselaphinae). The absence of a mola is usually correlated with predatory feeding habits.

10. Inner face of mandibles (or at least one of them) with a projecting, movable lobe ("prostheca") (fig. 34) (0) – Inner face of mandibles without movable lobe (1)

    The morphology of the inner edge of the mandibles varies but most differences may be significant only at lower taxonomic levels. The presence of a movable lobe is unusual, presumedly a basal feature of Hydraenidae and Microsporidae. A similar lobe is also found in some derived Hydrophiloidea (Berosini).

11. Lacinia short, not reaching apex of galea (fig. 38, 45) (0) – Lacinia elongated, at least reaching apex of galea (fig. 40, 44) (1)

    The relative length of the lacinia varies considerably. It is mostly of the "short" type, but is longer in various, not closely related groups. Several of the terminal taxa include both forms with short and long laciniae and the character is probably not very significant at higher taxonomic levels.

12. 4th segment of maxillary palpi at least about as large as 3rd (i.e., both c. as wide and as long) (fig. 46, 47, 49) (0) – 4th segment of maxillary palpi markedly smaller than 3rd (i.e., both narrower and shorter) (fig. 48, 51, 52) (1)

    The relative size of the 4th segment of the maxillary palpi is somewhat variable. There is hardly no doubt that a relatively large 4th segment is a plesiomorphic coleopteran feature and it is apparently also a basal characteristic of most staphyliniform groups. A small 4th segment is assumed to be basal only for Ptiliidae, Scydmaenidae and a few staphylinid subfamilies (Microsilphinae, Leptotyphlinae, Solieriinae) but occur also in subordinate members of several other groups.

13. 1st segment of labial palpi not longer than 2nd (0) – 1st segment of labial palpi longer than 2nd (1)

    A short basal segment of the labial palpi is the normal condition in Staphyliniformia, but in Scaphidiidae, Empelidae and some Staphylinidae, as well as subordinate members of several other groups, it is longer. The character is probably more significant at lower taxonomic levels and may not be very informative in the present context.

14. 3rd segment of labial palpi not narrower than 2nd (0) – 3rd segment of labial palpi narrower than 2nd (1)

    A rather variable character which is apparently, as the preceding, more informative at lower taxonomic levels.

15. Antennae not used in respiration (0) – Antennae used to break surface film and form air funnel in aquatic respiration (1)

    The habit of using the antennae as auxiliary organs in respiration is a well known feature of aquatic Hydrophiloidea and Hydraenidae. In both groups the antennae are used to break the surface film of the water and – via a "tube" formed by the antennae and the postocular portion of the head – create contact between atmospheric air and an air reservoir "carried" on the ventral face of the beetle's body. This habit is, by nature, only found in aquatic forms, but as both groups are almost certainly basally aquatic in the adult stage, the unique function of the antennae is undoubtedly also basal.

16. Antennae 11-segmented (0) – Antennae 10-segmented (1) – Antennae 9-segmented (2)

    There is no doubt that the plesiomorphic coleopteran number of antennal segments is 11. Only very few beetles have a higher number of segments, but in several groups reductions in the number occur. Only two groups of Staphyliniformia seem to have a reduced number as part of their groundplan: Hydrophiloidea and Micropeplinae, both with an ancestral number of 9.

17. Antennae inserted on dorsal face of head, not below side margin (0) – Antennae inserted on lateral side of head, or somewhat dorsally, but below side margin (occasionally below anterior margin) (1)

    The antennae are usually inserted below a lateral edge of the head, but in some groups the insertion is more dorsal. Within Staphyliniformia only the Silphidae seem to have dorsally inserted antennae as a basal feature, but similar conditions occur in subordinate members of various other groups, e.g., Scydmaenidae, Scaphidiidae, and a few staphylinid subfamilies, notably Steninae and Aleocharinae.

18. 8th (morphological) antennal segment simple (0) – 8th (morphological) antennal segment cupuliform (fig. 59, 61, 66) (1)

In most staphyliniforms with the "complete" number (11) of antennal segments the 8th segment is simple, i.e., not differing from the preceding segments. In some groups, however, notably the histeroid families and Silphidae segment 8 is more-or-less enlarged and cupuliform, forming a transition between the proximal (simple) segments and the three apical (enlarged) club-segments. In Hydrophiloidea the apical portion of the antennae is similar, i.e., a cupuliform segment precedes a 3-segmented club, but the total number of antennal segments is reduced to 9 (or fewer). In this group the reduction of segments probably involved the small segments proximal to the cupule (Hansen, 1991b, 1995), so the cupule is actually the 8th morphological segment.

19. Antennae filiform, or with gradually developed club of about 5 segments, with gradual increase in pubescence apically (fig. 68, 82) (0) – Antennae with club of 1 apical segment (fig. 91) (1) – Antennae with 2-3 apical segments forming rather well defined club, which is not sharply delimited from preceding segments in regard to pubescence (fig. 83, 89) (2) – Antennae with well differentiated club of 3 densely pubescent segments, pre-club segments nearly glabrous (fig. 59, 63, 64) (3) – Antennae with well differentiated club of 5 densely pubescent segments, pre-club segments nearly glabrous (fig. 76, 77) (4) – Antennae with 7 distal segments forming an elongate club (5)

Apparently the filiform or apically gradually thickened type of antenna is the plesiomorphic coleopteran type, but in various groups of Staphyliniformia the antennae are more-or-less evidently clubbed apically. In some forms the club is particularly well defined by being densely pubescent in contrast to preceding glabrous or almost glabrous segments. This type is found in at least the more primitive forms of Hydraenidae and Scaphidiidae, both with 5-segmented club, and in Hydrophiloidea, Histeroidea, Silphidae (and Scarabaeoidea), all of which have – at least primitively – 3-segmented clubs.

20. Antennal segments without periarticulate grooves (0) – Penultimate 3-4 antennal segments each with apical periarticular open groove, which bears dense concentration of sensilles (fig. 72) (1) – Periarticular grooves nearly enclosed, opening to distal surface of segments only through a narrow slit (fig. 73) (2)

The presence of sensilla-filled, periarticular grooves on penultimate antennal segments is characteristic of Agyrtidae and Leiodidae. It has been suggested that the more open grooves of Agyrtidae is a precursor of the more enclosed vesicles found in Leiodidae (Lawrence and Newton, 1982). Vesicles similar to those of Leiodidae are also found in the scydmaenid genus *Eutheia*, but may not be a basal characteristic of that family. Otherwise such grooves or vesicles has not been found among the staphyliniforms examined here.

21. Pronotum with sharp lateral ridge separating dorsal portion from ventral portion (hypomeron) (0) – Pronotum without dis-

tinct lateral ridge, or with very fine ridge located far down on pronotal sides, so pronotum is rather evenly convex to procoxae (cross-section) (1)

Normally the pronotum has more-or-less sharp lateral edges but in certain Staphylinidae (Neophoninae, Stenine group, Pselaphinae) a lateral canthus is absent or very blunt so that pronotum is more-or-less evenly rounded in cross-section. A lateral canthus is also absent in most Scydmaenidae (but not the presumedly primitive forms) and in subordinate members of a few other groups.

22. Pronotum without accessory posterior ridge (fig. 101-113) (0) – Pronotum with accessory posterior ridge below posterior margin (=locking device) (fig. 93-98) (1)

The presence of an accessory transverse ridge below the posterior pronotal margin, serving as a locking device against the elytral base, seems to be confined to the Polyphaga and is likely to be a basal characteristic of that suborder. Among the taxa examined here such a locking device is found in Hydrophiloidea, Histeroidea, Scarabaeoidea, Eucinetidae and Derodontidae, but it is absent in all taxa currently referred to Staphylinoidea (incl. Hydraenidae).

23. Propleuron invaginated, not visible externally (often fused to trochantin, so the exposed "trochantin" sometimes may include a small portion of the pleuron) (0) – Propleuron visible externally (at least in part), separating sternum from notum (except at anterior margin) (1)

An invaginated propleuron is generally considered autapomorphic for the Polyphaga. None of the Polyphaga examined here make any exception and the character is included only to contribute to the resolution of the basal phylogeny of the Coleoptera.

24. Procoxal fissure present/open, trochantin exposed (fig. 110, 114) (0) – Procoxal fissure absent/closed (fig. 103), trochantin concealed (1)

The appearance of the procoxal fissure is somewhat variable, even within some groups treated here as terminal taxa. In most groups it is open so that the trochantin is exposed, but several groups have the fissure closed, e.g., Synteliidae, Histeridae, Ptiliidae, Scydmaenidae, Scaphidiidae and some Staphylinidae (Stenine group, Dasycerinae, Pselaphinae and a few others). A closed or strongly narrowed procoxal fissure is also found in subordinate members of a few other groups (e.g, Leiodidae: Cholevinae).

25. Hypomeron without processes (fig. 110, 112, 113) (0) – Hypomeron on each side with a mesally directed process behind procoxae; hypomeral processes not closing coxal cavities (fig. 97, 107) (1) – Hypomeral processes closing procoxal cavities posteriorly (fig. 93, 104) (2)

In most groups of Staphyliniformia the postcoxal hypomeral processes are more-or-less well developed. They are absent (or extremely blunt) in Scydmaenidae, Scaphidiidae, Empelidae, Silphidae (most) and several Staphylinidae (e.g., Tachyporine group, Paederinae, Staphylininae, Leptotyphlinae, Solieriinae, Micropeplinae, Pselaphinae). More rarely they completely close the procoxal cavities posteriorly as in Synteliidae and a few subordinate members of, e.g., Hydrophiloidea, Hydraenidae and Staphylinidae: Osoriinae.

26. Prosternum without intercoxal process (at most bluntly angulate in middle before coxae) (as fig. 95) (0) – Prosternal intercoxal process present, but not widened behind procoxae (fig. 102, 109, 112) (1) – Prosternal intercoxal process widened behind procoxae (fig. 93) (2)

Normally a more-or-less well developed intercoxal process is present, at least as a short anterior, acute angular projection. In a few groups, e.g., Dasycerinae and Pselaphinae, the projection is so obtuse that it is not interpreted as an intercoxal process, and in others, e.g., Synteliidae and subordinate members of a few other groups, the intercoxal process reaches posteriorly beyond the procoxae and is more-or-less expanded behind these.

27. Procoxal cavities not closed internally (except for a rather small portion anteromedially adjacent to intercoxal process) (fig. 105, 112, 113) (0) – Procoxal cavities (or at least their major part) closed internally (fig. 96, 103, 108) (1)

In most groups the procoxal cavities are not closed internally, i.e., a sclerotized "inner wall" forms no more than small anteromedian extensions from the intercoxal process. In other groups this sclerotized "wall" is more markedly extended so it occupies at least the major portion of the coxal cavities, which are then referred to as "closed internally". Closed cavities are found in Hydrophiloidea, Histeridae, Leiodidae, Hydraenidae, Ptiliidae, Scaphidiidae and a few Paederinae.

28. Mesothoracic spiracles concealed under hypomeron (0) – Mesothoracic spiracles (at least partly) exposed (fig. 109, 113, 114) (1)

Exposed mesothoracic spiracles are characteristic of most Staphylinidae (except Pselaphinae, Dasycerinae, Stenine group and a few others), Silphidae, Scaphidiidae, Empelidae and Histeridae. In other groups, Hydrophiloidea, Sphaeritidae, Agyrtidae, Leiodidae, Hydraenidae, Ptiliidae and Scydmaenidae the mesothoracic spiracles are concealed under the hypomeron.

29. Connecting membrane between pro- and mesosternum without sclerites (0) – With one pair of transverse sclerites (peritremes) in which spiracles are located laterally (fig. 114) (sclerites sometimes connected medially by an extra sclerite) (1) – With a median sclerite or pair of sclerites not associated with mesothoracic spiracular sclerites (and located more-or-less behind them) (2)

The presence of sclerites in the pro-mesothoracic connecting membrane is characteristic of several groups. In Empelidae and the staphylinid subfamilies Omaliinae, Microsilphinae, Proteininae and the Oxyteline group the sclerites enclose the mesothoracic spiracles, whereas in Apateticidae, Silphidae and Staphylinidae: Pseudopsinae they do not.

30. Mesosternum broad anteriorly (at least about 1/3 of anterior mesothoracic width) (fig. 114) (0) – Mesosternum narrow anteriorly (1)

Within Staphyliniformia an anteriorly narrow mesosternum seems to be unique to Hydrophiloidea. Only very few few hydrophiloids (e.g., Georissidae, Hydrochidae, Chaetarthriini) have an anteriorly more-or-less broad mesosternum, but in these forms the condition is undoubtedly secondary (Hansen, 1991b).

31. Mesosternum delimited from mesepisterna by a suture (fig. 114) (0) – Mesosternum intimately fused to mesepisterna (1)

Primitively, mesosternum and mesepimera are delimited by distinct sutures but in various groups they have become intimately fused (e.g., Hydraenidae, Ptiliidae, Neophoninae, Stenine group, Oxyporinae, Micropeplinae, and subordinate members of a few other groups). Similarly the mesepimera are normally well demarcated, but they also may be fused to the episterna, e.g., in Ptiliidae. Probably the fusion of at least mesosternum and mesepisterna is not always an irreversible process.

32. Mesepisterna and mesepimera delimited by a suture (fig. 114) (0) – Mesepisterna and mesepimera intimately fused (1)

    See the previous character.

33. Mesocoxal fissure open, mesotrochantin exposed (fig. 114) (0) – Mesocoxal fissure closed, mesotrochantin concealed (1)

    Most groups of Staphyliniformia have an exposed mesotrochantin. It is concealed in, e.g., Hydrophiloidea, Histeroidea, Hydraenidae, Ptiliidae and some Staphylinidae (Stenine group, Leptotyphlinae, Solieriinae, Micropeplinae, Dasycerinae, Pselaphinae).

34. Mesocoxal cavities sharply demarcated posteriorly, by a ridge (fig. 114) (0) – Mesocoxal cavities not demarcated by ridge posteriorly (1)

    Normally the mesocoxal cavities are delimited posteriorly by a more-or-less pronounced ridge. However, in Scydmaenidae and a few subordinate members of certain staphylinid subfamilies (Aleocharinae, Staphylininae) such ridges are absent and the coxal cavities are not sharply delimited posteriorly.

35. Metepisterna exposed (0) – Metepisterna concealed (1)

    The metepisterna are normally more-or-less exposed with most exceptions found only in subordinate members of various groups (e.g., Histeridae. Leiodidae). However, in Scydmaenidae (except some presumedly derived forms) and in Empelidae, Dasycerinae, Pselaphinae they are typically concealed. Probably the concealed metepisterna is a basal characteristic of these groups.

36. Ventral surface of body without plastron (0) – Most of ventral surface with plastron (coating of fine hydrofuge pubescence) (1)

    Within Staphyliniformia there is a great variation in regard to the development of the pubescence on the ventral face of the body and the differences are in most cases only of phylogenetic significance at lower taxonomic levels. Hydrophiloidea and Hydraenidae, however, have a plastron-like type of pubescence that differ from that of the other groups studied here. It is undoubtedly an adaptation to the aquatic mode of life exhibited by these beetles. Some terrestrial forms of the Hydrophiloidea and Hydraenidae (in both cases subordinate groups) may have rudimentary, more sparse or even no ventral pubescence.

37. Laterosternites of 2nd abdominal segment not distinct (0) – Laterosternites of 2nd abdominal segment distinct (1)

    The presence or absence of distinct, separate laterosternites ("pleural sclerites") of 2nd abdominal segment has often been used as the main criterion for a division of polyphagan beetles into two major groups, Haplogastra and Symphiogastra, with or without separate sclerites, respectively (e.g., Crowson, 1955). However, as pointed out by several authors (e.g., Crowson, 1960) the character is rather variable and do not allow for a clear distinction between such two major groups. Most Staphyliniformia (referred to "Haplogastra") do have a distinct, separate 2nd laterosternite, but several groups do not, e.g., Histeridae, Scaphidiidae and some Staphylinidae.

38. Abdominal segments 3 – 6/7 with one paratergite on each side (fig. 115, 127) (sometimes hardly defined) (0) – With two paratergites on each side (fig. 116) (1)

    This character relates particularly to the Staphylinidae, most of which have on abdominal segments 3-6(-7) distinct, separate sclerites on either side of the tergite proper. These sclerites are usually referred to as "paratergites", a term which have been adopted here, but they seem to be homologous with the deflexed lateral portions of the sternites (laterosternites) of non-staphylinids. In most Staphylinidae (as in non-staphylinids) the paratergites are present as a single sclerite on either side of the tergite, but in some staphylinids (Tachyporine group, Oxyporinae, Staphylininae, Paederinae, Leptotyphlinae, Solieriinae and presumedly subordinate members of the Stenine and Oxyteline groups) the paratergites are double, i.e., each of them divided longitudinally into an inner and an outer sclerite.

39. Abdominal segment 8 exposed at least dorsally (when elytra opened) (fig. 117) (0) – Abdominal segment 8 completely invaginated within segment 7 (1)

Normally the 8th abdominal tergum is exposed at least when the elytra are opened. However, in Sphaeritidae, Synteliidae and Histeridae the entire segment 8 is completely invaginated within segment 7. Apparently this feature is unique to three families.

40. Abdominal sternum 8 (and segment 9) – in repose – retracted in abdomen (tergum 8 may be exposed dorsally when elytra are opened) (0) – Abdominal segment 8 (but not 9) everted, so both tergum and sternum are exposed (1) – Also segment 9 (+10) everted (2)

In Hydrophiloidea, Histeroidea, Agyrtidae and Leiodidae the abdominal sternum 8 is, in repose, retracted into the abdomen. In Histeroidea the entire segment 8 is invaginated (cf. previous character) but in the other groups only the sternal portion is concealed. In some Leiodidae a small portion of this retractable 8th sternite is narrowly visible, but only in some more derived forms of the family (e.g., Cholevinae) is it exposed to a greater extent and, hence, the basal condition for Leiodidae is here interpreted as "retracted". In Hydraenidae, Ptiliidae and all families of the Staphylinid group (sensu Lawrence and Newton, 1982) the 8th abdominal segment is evidently exposed, sometimes also segments 9 and 10. A distinction between "only segment 8 exposed" and "segments 8-9 (-10) exposed" is tentatively used here but may not be of any significance, at least not within the Staphylinid group, because segments 9 and 10 are in many staphylinids probably only retracted in dried specimens (the major source of material available for examination). Hence, the observation that, e.g., Silphidae should have segments 9 and 10 exposed whereas other members of the Staphylinid group (notably Staphylinidae) should not, may be an artefact. However, the distinction does not in this case distort the results of the phylogenetic analysis.

41. Abdominal tergo-sternal membrane long on segments 1-6(-7) (fig. 117) (0) – Abdominal tergo-sternal membrane long on segments 1-3 (and partly 4), very short on following segments (1) – Abdominal tergo-sternal membrane long only on segments 1-2, very short on following segments (2)

Long tergo-sternal membranes of abdominal segments 1-6 are typical of forms that have normally developed elytra which more-or-less completely cover the abdomen. In Staphyliniformia these groups are Hydrophiloidea, Sphaeritidae, Synteliidae, Agyrtidae, Leiodidae, Ptiliidae, Scydmaenidae and Staphylinidae: Dasycerinae. In other groups (Histeridae, Scaphidiidae, Empelidae) long tergo-sternal membranes are restricted to the first 3-4 abdominal segments and in these the elytra are still relatively long but truncate apically, leaving 2-3 abdominal segments uncovered. The remainder of the staphyliniforms, i.e., Apateticidae, Silphidae (only presumedly primitive forms) and Staphylinidae (except Dasycerinae) generally have very short tergo-sternal membranes except on segments 1-2 (the only constantly concealed segments).

42. Intersegmental membranes between abdominal segments 3 to 7 short, about 1/8 length of adjacent segments (at least on ventral face) (fig. 117) (0) – Intersegmental membranes between abdominal segments 3 to 7 longer, at least about 1/4 length of adjacent segments (fig. 115, 116) (1)

    Short abdominal intersegmental membranes are typical of forms without or with little abdominal flexibility, i.e., Hydrophiloidea, Histeroidea, Agyrtidae, Leiodidae, Hydraenidae, Ptiliidae, Scydmaenidae and a few Staphylinidae (Proteininae, Micropeplinae, Dasycerinae, Pselaphinae), as well as the outgroups studied here. Longer membranes are typical of Scaphidiidae, Empelidae, Apateticidae, Silphidae and Staphylinidae apart from the aboven mentioned exceptions.

43. Intersegmental membranes between abdominal segments 3 to 7 clear (0) – Intersegmental membranes between abdominal segments 3 to 7 with "brick wall" pattern of minute sclerites (fig. 115, 128) (1)

    The development of a specialized type of intersegmental membrane with minute sclerites arranged in a close "brick-wall" pattern is relatively well correlated with the elongation of the membranes (cf. previous character) and probably serve to reinforce the membranes without loosing their flexibility. Such membrane structure is typical of Scaphidiidae, Empelidae, Apateticidae, Silphidae and Staphylinidae (except Proteininae, a few Oxytelinae and most members of the Tachyporine group). Otherwise, within Staphyliniformia similar membrane structure is only found in intersternal membranes of the leiodid genus *Colon*.

44. Abdominal spiracles 1-8 functional (occasionally, the 8th are indistinct) (0) – Abdominal spiracle 7 (and possibly 8) atrophied, non-functional, other spiracles functional (1) – Abdominal spiracles 4-6 atrophied, non-functional (2)

    In most groups the abdominal spiracles on segments 1-7 (and usually 8) are well developed and apparently all functional but different reductions occur in various groups. As pointed out by Lawrence and Newton (1982) the spiracles of segment 7 (-8) are atrophied in Hydrophiloidea and Histeroidea while in certain Staphylinidae (Proteininae, Neophoninae, Micropeplinae, Dasycerinae, Pselaphinae) they are atrophied on segments 3 or 4 to 6.

45. Abdominal spiracles located in membrane between terga and sterna, except for segments 7 and/or 8 where they may be located in the terga (fig. 117, 123) (0) – Abdominal spiracles placed in terga from segment 2 or 3 through segment 8 (but sometimes atrophied on segments 4-6) (fig. 115, 116) (1) – Abdominal spiracles placed in terga from segment 4 or 5 through segment 8 (2)

    The abdominal spiracles are normally located in the tergosternal membrane in forms with weakly sclerotized abdominal terga, i.e., forms with the abdomen concealed (and protected) by well developed elytra, viz. Hydrophiloidea, Histeroidea, Agyrtidae, Leiodidae, Hydraenidae, Ptiliidae and Staphylinidae: Dasycerinae. In Scydmaenidae (at least its presumedly more primitive forms) and Scaphidiidae, both of which have the posterior targa more-or-less sclerotized, the spiracles are located in the terga from segment 4 (or 5) to 8. In the remaining groups, i.e., Empelidae, Apateticidae, Silphidae and Staphylinidae (except Dasycerinae), almost all with well sclerotized terga (except on segments 1 and 2), the spiracles are located in the terga on all segments except 1 and 2.

46. Patches of "wing folding" setae covering much of abdominal tergum 7 (often also present on one or more of preceding terga) (as fig. 123) (0) – Patches of "wing folding" setae present on abdominal terga 3-6 (possibly also tergum 2), absent from following terga (1) – Patches of "wing folding" setae present on abdominal terga 3-5 (possibly also tergum 2), absent from following terga (2) – Patches of "wing folding" setae present on abdominal terga 3-4, or 4 alone (fig. 115) (possibly also tergum 2), absent from following terga (3) – Patches of "wing folding" setae present on abdominal tergum 3 (possibly also tergum 2), absent from following terga (4) – Patches of "wing folding" setae absent on from abdominal tergum 3 and following terga (possibly present on tergum 2) (5)

Most beetles with normally developed elytra and hind wings have a large patch (or a pair of patches) of minute and dense, mesally directed spines or microtrichiae on one or more of the abdominal terga. These patches which take part in the folding of the hind wings are here referred to as "wing folding patches" and their microtrichiae as "wing folding setae". In Hydrophiloidea, Agyrtidae, Leiodidae and Ptiliidae they are present on tergum 7 and some of the preceding terga; in Ptiliidae the wing folding patches are of a specialized unique type (see discussion of that family below). In Sphaeritidae and Synteliidae (with exposed tergum 7) wing folding patches are absent from tergum 7 but present on preceding terga. In Histeridae the wing folding patches are present only only on anterior three or four (concealed) terga. Similar reductions of the probably primitive ("hydrophiloid") type is seen in Scydmaenidae, Scaphidiidae, Empelidae, Apateticidae, Silphidae and particularly Staphylinidae. In most staphylinids wing folding setae are absent from all terga except the (constantly concealed) terga 1-2. However, in Omaliinae and some Tachyporinae pairs of small rudimentary patches can be seen on one or more of the exposed terga.

47. Only abdominal tergum 7 and/or 8 (and sometimes the following) well sclerotized (0) – 6th, and the following abdominal terga well sclerotized (1) – 5th, and the following abdominal terga well sclerotized (2) – 4th, and the following abdominal terga well sclerotized (3) – 3rd (sometimes also 2nd), and the following abdominal terga well sclerotized (4)

The degree of sclerotization of the abdominal terga may be difficult to determine but has tentatively been included as a character here. It is correlated more-or-less with the degree of abdominal exposure so that forms with strongly abbreviated elytra and markedly exposed abdomen (e.g., most Staphylinidae) have strongly sclerotized terga except on (concealed) segments 1-2; groups with fully developed elytra which more-or-less completely cover the abdomen have generally weakly sclerotized terga, but there are also groups with a concealed abdomen having fairly well sclerotized terga (e.g., some Histeridae).

48. Abdominal sternum 8 without gland openings near anterior margin (0) – Abdominal sternum 8 with short median "ap-

odeme" flanked by a pair or more-or-less separated gland openings near anterior margin (fig. 119-121) (1)

The presence of a "sternum 8 gland complex" is often considered unique to a group of staphylinid subfamilies referred to as the "Omaliine group" (e.g., Lawrence and Newton, 1982; Thayer, 1987). The taxa currently referred to this group are Omaliinae, Microsilphinae, Proteininae, Neophoninae, Micropeplinae, Dasycerinae, Pselaphinae and Empelinae (here Empelidae). In Pselaphinae the "sternum 8 glands" are somewhat rudimentary or absent and in Micropeplinae they are apparently constantly absent. Other types of abdominal glands are found in various groups of Staphylinidae but are only present in subordinate members of groups which are here treated as terminal taxa for the phylogenetic analysis.

49. Abdominal sternum 2 not visible externally (at least not as separate sclerite) (0) – Abdominal sternum 2 visible at least laterally, on each side of hind coxae (1)

Within Staphyliniformia the first (basal) ventrite is normally composed of sterna 2 and 3 which are more-or-less intimately fused. In most groups the sternum 2 portion of the ventrite seems to be concealed under the posterior coxae so that the visible portion of firts ventrite corresponds to sternum 3. However, in some groups such as Silphidae a well demarcated sternum 2 is exposed laterally (as typically found in Adephaga). Certain Staphylinidae (most Oxytelinae) have a separate and exposed sternum 2, no doubt a derived feature within the Oxyteline group.

50. Abdominal sternum "2+3" completely carinate medially (0) – Abdominal sternum "2+3" carinate medially (at least between hind coxae, but not completely) (1) – Abdominal sternum "2+3" not carinate (2)

In most staphyliniform groups the basal ventrite (composed of sternum 2 and 3) are more-or-less carinate anteriorly between the metacoxae. This carina is often continuous with an (exposed) acute intercoxal process (see next character), but a carina may also be present in forms with more broadly rounded intercoxal process. A carina is absent in Histeridae, Scydmaenidae, Scaphidiidae, Silphidae and various Staphylinidae. A completely carinate basal ventrite is found in subordinate members of various staphyliniform groups, e.g., Hydrophiloidea.

51. Abdominal sternum "2+3" with an acute intercoxal process (fig. 125) (0) – Abdominal sternum "2+3" without, or with low rounded, intercoxal process (fig. 126) (1)

An acute intercoxal process is found in Hydrophiloidea, Agyrtidae, Hydraenidae, Ptiliidae (at least the more primitive forms) and a few Staphylinidae (Trigonurinae, Oxyteline group, Solieriinae, Dasycerinae, Pselaphinae). In other staphyliniforms the intercoxal process is more-or-less broadly rounded or very low and insignificant (or absent).

52. Abdominal sternum "2+3" with well defined concavities for reception of hind coxae, cavities delimited posteriorly by a carina (fig. 125) (0) – Abdominal sternum "2+3" without such concavities, without transverse carina (fig. 126) (1)

The presence of well defined metacoxal cavities in the basal ventrite is undoubtedly a plesiomorphic feature within Staphyliniformia, shared by Hydrophiloidea, Histeroidea, Agyrtidae, Leiodidae, Hydraenidae, Ptiliidae, Scydmaenidae, Scaphidiidae and Empelidae. In the other families, Apateticidae, Silphidae and (most) Staphylinidae such cavities are not sharply defined and the metacoxae are not so tightly "fixed" to the abdominal base, allowing for greater abdominal flexibility. It might be mentioned that the abdominal flexibility of most of the forms lacking well defined metacoxal cavities is further increased by prolongation of the abdominal intersegmental membranes (cf. character 42).

53. Inflexed dorsal portion of abdominal sterna not demarcated from ventral portion (seldom very bluntly so on the anterior sternites) (0) – Inflexed dorsal portion of abdominal sterna demarcated, but not separated from ventral portion by an articulation (1) – Inflexed dorsal portion of abdominal sterna articulated to ventral portion (2)

Normally the lateral portions of the exposed abdominal sternites are more-or-less sharply inflexed with the result that the inflexed portion (laterosternite) becomes more-or-less dorsal. Apparently the plesiomorphic condition within Staphyliniformia is sharply deflexed laterosternites; this is typical of Hydrophiloidea, Sphaeritidae, Agyrtidae, Leiodidae, Hydraenidae and Ptiliidae. In Synteliidae and Histeridae the laterosternites are not more than bluntly deflexed, whereas in most Staphylinoidea (except the ones already mentioned) the laterosternites become separated from the remainder of the sternite by a narrow membrane and are often more dorsal (particularly in Staphylinidae, where they are often referred to as "paratergites"). Some Staphylinidae have the tergal and sternal components of each exposed segment fused into a solid ring (e.g., Osoriinae, some Steninae, some Tachyporinae).

54. Inflexed dorsal portion of abdominal sterna (laterosternite) with microtrichiae (sometimes partly modified for stridulation) (0) – Inflexed dorsal portion of abdominal sterna (laterosternite) without microtrichiae (1)

The presence of microtrichiae on the laterosternites seems to be more-or-less correlated with the development of the elytra, i.e., they are present only on segments concealed by the elytra, but they may be absent even in forms with long elytra. Probably these microtrichiae are often forming the abdominal component of an elytral-abdominal locking device, i.e., when similar microtrichiae are present on the contacting portion of the ventral elytral face (cf. Hammond, 1979). Microtrichiae are present in Hydrophiloidea, Sphaeritidae, Synteliidae, Agyrtidae, Leiodidae and Hydraenidae, but otherwise absent except possibly on segments 1-2. In some forms, notably within Hydrophiloidea, the microtrichiae of part of laterosternite 3 have been modified to form a stridulatory file (e.g. Berosini).

55. Tibial spurs present (0) – Tibial spurs absent, or not well defined among other apical spines or setae (1)

Tibial spurs, i.e. a pair of more-or-less strongly developed spines at mesal apex of the tibiae, is present in most groups. The size of the spurs varies considerably but even when they are relatively small, they are still markedly more developed than other tibial spines. In some Staphylinidae, however, tibial spurs are not detectable (Proteininae, Neophoninae, Stenine group, Micropeplinae, Dasycerinae, Pselaphinae).

56. Tarsi with basal segments distinct, though sometimes short; tarsi not appearing as composed of a single long thin segment (fig. 143, 144) (0) – Tarsi very thin, almost appearing as composed of a single long segment, because basal segments are very small (fig. 142) (1)

The apparently 1-segmented tarsi are unique for Ptiliidae and Microsporidae.

57. Anterior coxae not projecting (0) – Anterior coxae projecting (1)

    The degree of projection of the anterior coxae varies but may still be a usefull character even at higher taxonomic levels. More-or-less strongly projecting anterior coxae are found in most groups of Staphyliniformia, and little (or not) projecting anterior coxae are probably only a basal feature of Synteliidae, Histeridae, Ptiliidae, Phloeocharinae and Micropeplinae.

58. Middle coxae globular or almost so (or slightly elongate) (fig. 114, 135) (0) – Middle coxae transverse, i.e., at least 1/3 wider than long (fig. 134) (1)

    More-or-less globular (or even slightly elongate) mesocoxae is apparently a basal characteristic of most staphyliniform groups. Only in Agyrtidae, Leiodidae and Empelidae more transverse coxae seems to be the normal (and basal) condition. Transverse coxae are also found in almost all Hydrophilidae, but not in the preseumedly more primitive families of Hydrophiloidea.

59. Posterior coxae "transverse", i.e., expanded caudally and laterally (fig. 141) (0) – Posterior coxae "triangular"/"conical", i.e., neither expanded laterally nor caudally (except sometimes when a coxal plate is developed to conceal the femur) (fig. 136-138, 140) (1)

    The shape of the posterior coxae is somewhat variable in Staphyliniformia, even within some of the groups treated here as terminal taxa. However, it seems that two major types can be distinguished: a "transverse" type in which the coxae are expanded caudally and laterally, and a "triangular" type without such expansions; the latter type may still be transverse in the sense that the coxae may be wider than long. The mentioned expansions should not be confused with the "coxal plates" covering the posterior femora in repose (cf. next character). The "transverse" type of coxa is the most widely distributed type within Staphyliniformia, but "triangular" coxae occur in Ptiliidae, Scydmaenidae and several Staphylinidae (Trigonurinae, Omaliinae, Proteininae, Micropeplinae, Stenine and Oxyteline groups, Pseudopsinae, Staphylininae, etc.).

60. Posterior coxae with oblique posterior face (fig. 138, 140) (0) – Posterior coxae with excavate posterior face, which conceals a smaller or greater portion of femur in repose (fig. 136, 137) (1)

    Normally the posterior face of the metacoxae is more-or-less simply oblique (in some forms vertical), but in certain groups it is more-or-less evidently excavate for the reception of the posterior femora, sometimes even with a pronounced extension ("coxal plate") covering the entire posterior leg (when retracted) from below. Such excavate posterior coxae are probably a basal characteristic of Ptiliidae, Empelidae, Apateticidae (only mesally) and a few staphylinid subfamilies (notably Habrocerinae of the Tachyporine group).

61. Posterior coxae almost contiguous (0) – Posterior coxae more-or-less broadly separated (1)

    Most Staphyliniformia have almost contiguous posterior coxae but in Histeridae, Scydmaenidae, Scaphidiidae and Micropeplinae they are normally (and no doubt primitively) well separated.

62. Posterior coxae reaching to lateral edges of body (or nearly so) (0) – Posterior coxae ending laterally distinctly before lateral edges of body (1)

    Usually the posterior coxae reaches almost to the lateral edges of the body but in some forms they are more-or-less "abbreviated" laterally, e.g., in Synteliidae, Histeridae, Scaphidiidae, Apateticidae and some Staphylinidae (Trigonurinae, Stenine group, Pseudopsinae, Micropeplinae).

63. Tarsi 5-segmented (0) – Tarsi with less than 5 segments (1)

Primitively most staphyliniform groups have 5-segmented tarsi but reductions in the number occurs within several groups. There are only few groups in which a lower number can be assumed to be basal, viz. Ptiliidae with 3 segments and some staphylinid subfamilies: Neophoninae, Leptotyphlinae, Dasycerinae and Pselaphinae, all with 3-segmented tarsi (2-segmented in some Leptotyphlinae and some Pselaphinae), and Micropeplinae with 4-segmented tarsi.

64. Elytra without ridge or lamina on ventral face (0) – Elytra with sublateral ridge or lamina on ventral face, at least in or anterior to middle (fig. 155) (1) – Elytra with sublateral ridge or lamina posteriorly on ventral face (2)

Within Staphyliniformia a few groups have a pronounced ridge or lamina on the ventral face of the elytra (a locking device keeping the elytra tightly fixed to the body). In Histeridae such a ridge may be constantly present and is undoubtedly a basal feature, but otherwise such a structure is found only in subordinate members of groups treated here as terminal taxa (e.g., Hydrochidae and Georissidae within Hydrophiloidea).

65. Epipleura demarcated from dorsal elytral portion by a ridge/line (0) – Epipleura not demarcated from dorsal elytral portion (1)

In most groups of Staphyliniformia the epipleura are sharply demarcated from the dorsal portion of the elytra. But in some groups, e.g., Scydmaenidae and several staphylinid subfamilies (Phloeocharinae, Aleocharinae, Paederinae, Staphylininae, Solieriinae, etc.) the epipleura are not defined, i.e. the elytral edges are only bluntly inflexed laterally.

66. Ventral face of elytra with "medio-lateral" microspinose binding patch (in addition to a more anterior "baso-lateral" patch) (as fig. 154) (0) – "Medio-lateral" binding patch absent (but "baso-lateral" patch often present) (1) – "Medio-lateral" binding patch present and strongly iridescent (2)

In many staphyliniforms (as well as other beetles) the elytra have on the ventral face more-or-less extensive areas densely covered with microscopic spines or microtrichiae. Their main function is probably to serve as some kind of locking device, binding the elytra to the body (see also character 54). Hammond (1979) referred to these areas of the elytron as "binding-patches", and distinguished between "baso-lateral", "medio-lateral", "apico-lateral" and "apico-sutural" binding patches. Within Staphyliniformia it is mainly the presence or absence of a medio-lateral binding patch that seems to be of potential phylogenetic significance. Such a patch is apparently only present in Hydrophiloidea, Sphaeritidae, Hydraenidae, Empelidae and two staphylinid subfamilies: Dasycerinae and Neophoninae (strongly iridescent in these two).

67. Elytra not truncate posteriorly, concealing abdomen completely (or at least first 7 segments, i.e., except for extreme apex) (0) – Elytra truncate posteriorly, covering about first 5 or 6 abdominal segments (1) – Elytra truncate posteriorly, covering only about first 2 or 3 abdominal segments (2)

This character is to some degree correlated with the degree of sclerotization of abdominal terga (char. 47), i.e., forms with abbreviated and truncate elytra always have at least the exposed tergites well sclerotized. However, although most groups with well developed (long) elytra have generally weakly sclerotized abdominal terga, some such groups may have well sclerotized terga (e.g., Histeridae, Scaphidiidae).

68. Hindwings without medial hinge (0) – Medial hinge present (1)

A medial hinge is generally present in the hindwings of Archostemata, Adephaga and Myxophaga but is absent in Polyphaga (Kukalová-Peck and Lawrence, 1993). The character is only included here to contribute to the resolution of the basal phylogeny of the Coleoptera. It should be noted that a suggestion of a medial hinge is found in the polyphagan family Eucinetidae; it probably represents a rudiment of the presumedly more archaic condition (well developed hinge) as seen in the other three suborders.

69. Folded hindwings cover at least about abdominal terga 1-4 (often 1-5 or more) (0) – Folded hindwings cover about abdominal terga 1-2 (seldom 1-3) (1)

In Staphyliniformia the folded hindwings primitively cover at least the first four abdominal segments, but in some derived Staphylinoidea (Apateticidae, Silphidae, Staphylinidae) they cover only the first two or three segments. It may be worth to mention that even in staphylinids with long elytra (e.g., Microsilphinae) the folded hindwings still cover only first 2-3 abdominal segments.

70. Folded hindwings overlap by less than 1/2 the width of one folded wing at their apices (0) – Folded hindwings overlap completely at their apices (1)

Within Staphyliniformia a relatively low degree of overlapping of the folded hindwings are typical of Hydrophiloidea, Agyrtidae, Leiodidae, Hydraenidae, Ptiliidae and Scaphidiidae, whereas other groups, viz. Histeroidea and the remainder of the Staphylinoidea, exhibit a high degree of overlapping.

71. Transverse wing folding pattern consisting of hinge ("apical hinge") distal to radial cell/crossvein ("r4") (with or without subsequent transverse folds) (fig. 145-147) (0) – Transverse wing folding pattern not involving hinge (fig. 148-150) (1) – Transverse wing folding pattern including a hinge ("radial hinge") proximal to radial cell/crossvein ("r4") (fig. 153) (2)

The presence of an "apical hinge" distal to the radial crossvein "r4" (sensu Kukalová-Peck and Lawrence, 1993) is probably a basal coleopteran feature which has been retained in Hydrophiloidea and Histeroidea (as well as all outgroups examined here). The apical hinge is completely absent in all Staphylinoidea (incl. Hydraenidae), but within this superfamily a similar hinge, "radial hinge", has evolved proximal to "r4" in Scydmaenidae, Scaphidiidae, Empelidae, Apateticidae, Silphidae and Staphylinidae. As pointed out by Lawrence and Newton (1982) the "radial hinge is undoubtedly a novel structure, non-homologous with the "apical hinge" of other groups.

72. Hindwing anal lobe present (fig. 145-148, 153) (0) – Anal lobe absent (fig. 149-150) (1)

The presence of an anal lobe is typical of most Staphyliniformia and is undoubtedly also a basal coleopteran feature. Usually, but not always, the lobe is demarcated from the remainder of the wing by a more-or-less pronounced excision in the posterior margin of the wing. The anal lobe varies in size from comparatively large (e.g. most Hydrophiloidea) to very small (e.g., Omaliinae, Aleocharinae). It seems to be completely absent in Leiodidae, Hydraenidae, Ptiliidae, Scydmaenidae and some Staphylinidae (e.g., Neophoninae, Micropeplinae, Pselaphinae).

73. Hindwing with distinct medial loop (fig. 145-147) (0) – Medial loop absent (or not evident) (fig. 148-150, 153) (1)

The presence of a medial loop in undoubtedly a basal characteristic of the Coleoptera, retained in Hydrophiloidea, Histeroidea and the outgroups examined here. In all groups currently referred to Staphylinoidea (incl. Hydraenidae) a medial loop is absent or at most very indistinct.

74. Medial field, posterior to medial bar, with (at least) 4 veins running freely towards posterior wing margin (fig. 145, 146) (0) – With 3 such veins (fig. 147, 153) (1) – With 2 such veins (fig. 148) (2) – With 1 such vein (fig. 149, 150) (3) – Hindwing without distinct veins posterior to the medial bar (4)

The medial field, as defined by Kukalová-Peck and Lawrence (1993), is the portion of the wing between the medial bar (or the fold next to it) and the posterior wing margin, delimited proximally from the anal field (anal lobe) by an anal fold. The number of veins in the medial field varies considerably between groups, sometimes also within groups, and may in some cases be more depending on absolute wing size rather that systematic relationship.

75. Hindwing with oblong cell (fig. 145) (0) – Oblong cell absent (fig. 146-150, 153) (1)

The presence of an oblongum cell is restricted to the suborders Archostemata, Adephaga and Myxophaga and is merely included here to contribute to the resolution of the basal phylogeny of Coleoptera.

76. Hindwing with wedge cell (fig. 145, 146) (0) – Wedge cell absent (or not evident) (fig. 147-150, 153) (1)

The presence of a wedge cell is undoubtedly a basal coleopteran feature, found in Archostemata, Adephaga and several archaic groups of Polyphaga. In Staphyliniformia it seems to be restricted to Hydrophiloidea (most forms, except some clearly derived ones).

Characters of adults (males):

77. Lateral sclerites of abdominal tergum 9 not joined dorsally at base (except sometimes in a single point) (as fig. 179) (0) – Lateral sclerites of abdominal tergum 9 joined in a narrow basal bridge dorsally (1) – Abdominal tergum 9 entire, moderately to rather long, though often with apical excavation for tergum 10 (as fig. 174, 183) (2)

The male abdominal terga 9 and 10 are often somewhat modified. Tergum 9 usually forms a pair of anterolateral sclerites flanking an undivided posteromedian tergum 10. In most of the outgroups examined here, as well as in some staphylinoids, the 9th tergum is evidently divided medially (by narrow membranous zone or by the 10 tergum). Within Staphyliniformia the two halves of tergum 9 are, however, more commonly joined basally, either by a narrow bridge (e.g., Hydrophiloidea, some Staphylinoidea), or so broadly connected that tergum 9 must be considered entire (e.g., Agyrtidae, Leiodidae, Hydraenidae, Ptiliidae and some Staphylinidae).

78. Aedeagus symmetrical (0) – Aedeagus asymmetrical (1)

The aedeagus of most staphyliniforms is symmetrical but different kinds of asymmetry can be seen in various groups. In Sphaeritidae the asymmetry involves only the basal piece but in others such as

Agyrtidae, Hydraenidae and some staphylinid subfamilies, notably Leptotyphlinae and Pselaphinae, both the parameres and the median lobe may be very asymmetrical.

79. Aedeagus everted symmetrically from abdominal apex (0) – Aedeagus everted asymmetrically from abdominal apex (1)

An asymmetrical eversion of the aedeagus from the abdominal apex was mentioned by Lawrence and Newton (1982) as a characteristic of what they referred to the Staphylinid group of Staphylinoidea, i.e. the families Scydmaenidae, Scaphidiidae, Empelidae, Apateticidae, Silphidae and Staphylinidae. Apparently, all other groups of Staphyliniformia evert the aedeagus symmetrically.

80. Median foramen of aedeagus large, basal (fig. 161) (0) – Median foramen of aedeagus small, ventral (fig. 170) (aedeagus often rotated to various extent, lying more-or-less on its side in abdomen) (1)

The basal position of the median foramen is undoubtedly a basal characteristic of the Coleoptera. It is retained in Hydrophiloidea, Histeroidea, Agyrtidae, Leiodidae, Hydraenidae and Ptiliidae (as well as the outgroups examined here). The remainder of the Staphylinoidea , i.e., the Staphylinid group (cf. previous character), share a derived type of aedeagus in which the median foramen is quite small and has moved to a more ventral position. It should be mentioned that – by using the term "ventral" – I follow the interpretation of Brundin (e.g., 1953); others (e.g., Lawrence and Newton, 1982) interpret the position as dorsal. The interpretation is complicated by the fact that the aedeagus often lies in a more-or-less rotated position within the abdomen.

81. Basal piece of aedeagus present, large (shield-like) (fig. 158, 160-163) (0) – Basal piece of aedeagus small (strap-like) (almost as fig. 159) (1) – Basal piece of aedeagus absent (fig. 164-171) (2)

The presence of a basal piece in the male genitalia is undoubtedly a plesiomorphic feature within Coleoptera, and in Polyphaga as well. In Staphyliniformia a well developed basal piece is present in Hydrophiloidea and Histeroidea, but absent or rudimentary in Staphylinoidea. When a basal piece is present in the latter superfamily (e.g., some Agyrtidae and a few Staphylinidae: Microsilphinae, Proteininae, Neophoninae, Pseudopsinae, etc.) it is almost always nothing more than a narrow transverse strap-like sclerite. The only staphylinoid examined here, in which a relatively well developed basal piece seems to be present, is the leiodid genus *Colon*, but due to the presumed subordinate position of this genus, the basal piece is in this case considered to represent a secondary structure.

82. Median lobe of aedeagus long, tubular, apparently without intrinsic mechanism for evagination of internal sac (fig. 159, 164-168) (0) – Median lobe short, basally forming large bulb with musculature for evagination of internal sac by fluid pressure (fig. 169-171) (1)

The bulbous type of aedeagus was described as a characteristic of the Staphylinid group of Staphylinoidea (Lawrence and Newton, 1982). It is apparently a constant and unique feature of this group. Other taxa studies here all seem to have genitalia of the first, more primitive type in which there is apparently no intrinsic mechanism for evagination of the internal sac. This type is here referred to as "long", but it may actually be quite short in some forms (e.g., Ptiliidae). Some species of the hydraenid genus *Limnebius* have fairly voluminous genitalia reminiscent of the "bulbous" staphylinid type, but they are apparently similar only in external shape.

83. Parameres paired, separate (sometimes more-or-less fused in basal portion) (fig. 160, 164-166, 169) (0) – Parameres fused to single ventral plate (1) – Parameres fused to a tube enclosing median lobe (fig. 161-163) (2)

Parameres are primitively paired, separate and symmetrical. This is the structure found in most groups of Staphyliniformia, but modifications are found within many groups and can in some cases by assumed to be basal for a terminal taxon (as defined here). Hence, in Histeridae the parameres are fused to a tube enclosing the median lobe (except apically or subapically). Other histeroids (Sphaeritidae, Synteliidae) have partly fused parameres which are, however, separate for a fairly long distance in apical portion; a similar modification is found in the derived hydrophilid genus *Helochares* (obviously convergent). In Agyrtidae the parameres are fused to a single ventral plate similar to that of most Staphylininae (another obvious convergency). Several forms have lost the parameres, but apparently the absence of parameres are not basal to any of the groups defined here as terminal taxa.

Characters of adults (females):

84. Abdominal tergum 9 divided, forming pair of lateral sclerites ("paraprocts" of ovipositor) articulated posteriorly to tergum 10 (fig. 173, 178, 179) (0) – Abdominal tergum 9 forming a continuous bridge anterior to tergum 10 (fig. 183) (1) – Abdominal tergum 9 forming a single sclerite anterior to tergum 10 (fig. 174) (2)

Usually the 9th tergum of the female is divided, but in some Staphylinidae (Stenine group, Pseudopsinae, Paederinae, some Staphylininae, etc.) the two halves are joined by a rather well developed bridge anteriorly. In Hydraenidae and Ptiliidae the 9th tergum forms a simple, entire sclerite without apical excision for tergum 10.

85. Gonocoxites separate, short, cylindrical or somewhat flattened (0) – Gonocoxites separate, moderately long, narrow and rather cylindrical (fig. 178, 181) (1) – Gonocoxites separate, broad and flattened, often short (fig. 172, 176, 184) (2) – Gonocoxites connate or fused (fig. 175, 177) (3)

The shape of the gonocoxites varies considerably between groups, sometimes also within groups. Relatively short, cylindrical or somewhat flattened gonocoxites are found in various staphyliniform groups (Leiodidae, Scydmaenidae, Scaphidiidae, Silphidae, some Staphylinidae, etc.). Similar, but relatively longer and more slender gonocoxites are found in Hydrophiloidea, Agyrtidae, Empelidae, Apateticidae and some Staphylinidae (e.g., Tachyporinae), but the distinction between "short" and "long" gonocoxites is sometimes problematic and may not be phylogenetically significant at higher taxonomic levels. The broad and flattened, paired gonocoxites as found in Sphaeritidae, Histeridae , Oxyporinae and the Stenine group, seems to represent more distinctive types. The most remarkable modification seems to be found in Hydraenidae and Ptiliidae, which – as noted by Lawrence and Newton (1982) – have flattened and connate or fused goncoxites reminiscent of an apical abdominal sternite (a similar modification may to be basal of Leptotyphlinae). Sometimes the gonocoxites are absent (e.g., most Aleocharinae).

86. Stylus situated apically or almost apically on gonocoxite (fig. 180, 182) (0) – Stylus

situated ventrally-mesally on gonocoxite (fig. 172, 176) (1) – Styli absent (fig. 175, 177, 184) (2)

In most staphyliniforms the gonocoxites bear apical styli, but a remarkable exception is found in Sphaeritidae and Histeridae (probably also the related family Synteliidae, which could not be examined here). In these groups the styli are situated ventrally-mesally on the gonocoxites (the latter furthermore unusually broad and flat in these groups, cf. previous character). Styli are apparently completely absent in Hydraenidae, Ptiliidae, Scydmaenidae and some Staphylinidae (Stenine group, Leptotyphlinae, Solieriinae, Micropeplinae, Pselaphinae).

87. Valvifers (= paired lateral sclerites composing 9th sternite, bearing the coxites in female) present (fig. 172, 175, 180) (0) – Valvifers absent (or not evident) (fig. 182) (1)

Apparently valvifers are present in most staphyliniforms. They seem to be absent only in some Staphylinidae (Omaliinae, Microsilphinae, Proteininae, Neophoninae).

88. Spermatheca without "sperm pump" (fig. 178, 188-190) (0) – Spermatheca with "sperm pump" (i.e., with lightly sclerotized, flexible central portion separating more heavily sclerotized proximal and distal portions, which are connected by muscles) (fig. 185-187) (1)

The spematheca varies greatly between and within the various groups of Staphyliniformia, both in regard to the degree of sclerotization and to shape and relative size. Most of this variation is at best significant at low taxonomic levels, but there is one type of spermatheca which seems to be significant at a higher level. It is the type described here as "with sperm pump". This type seems to be present only in Hydraenidae and Ptiliidae and has been suggested as a synapomorphy by Hansen (1995).

Characters of eggs:

89. Eggs laid singly (sometimes in mass), without silken covering (0) – Eggs laid singly, upturned free side covered by silk web (but not enclosed in cocoon) (1) – Eggs laid singly or in mass, in protecting cocoon of silk (fig. 191-192) (2)

Apparently most staphyliniforms place their eggs in holes or crevices without protecting them with a web. The construction of a protective silk web (Hydraenidae) or a proper silk cocoon completely enclosing groups of eggs (Hydrophiloidea) are undoubtedly adaptations to life in or near aquatic habitats. The production of such webs or eggcases have often been considered evidence for a close relationship between the two groups, but not only the degree of cover, also the mode of web construction differ in the two groups and the character does not necessarily indicate a close relationship (Hansen, 1995).

Characters of larvae:

90. Head prognathous (0) – Head rather declined or hypognathous (1)

According to descriptions most groups have a more more-or-less prognathous head. A hypognathous head has been described for Micropeplinae (Newton, 1991 as Micropeplidae) and apparently this is the only staphyliniform with a truely hypognathous head. A more-or-less declined head seems to be typical of a few other groups (Hydraenidae, Ptiliidae, Dasycerinae), which are tentatively also coded as "hypognathous" for the analysis. However, the significance of the character may not be great at higher taxonomic levels within Staphyliniformia.

91. Cephalic egg bursters absent (0) – Cephalic egg bursters present in first instar larvae (1)

Egg-bursters, i.e., cuticular spines on the head or body of first instar larvae, and used for rupturing the chorion of the egg, have been recorded from various groups of beetles (e.g., Emden, 1946). In at least two staphyliniform groups (Hydraenidae, Hydrophiloidea) egg-bursters have been recorded as present on the head ("cephalic egg-bursters") (Emden, 1946; Crowson, 1981); these groups have not egg-bursters on other parts of the body. Cephalic egg-bursters are unknown from other staphyliniform groups, but it must be mentioned that data have only been available for few groups.

92. Head without fimbriate, lightly sclerotized lobes on each side over mandibles (fig. 194, 197-201) (0) – Head with fimbriate, lightly sclerotized lobes ("epistomal lobes") on each side over mandibles (fig. 193, 195, 196) (1)

The presence of epistomal lobes are characteristic of Hydrophiloidea and Histeroidea (e.g., Bøving and Henriksen, 1938; Newton, 1991). Such lobes are apparently absent in all other Staphyliniformia. They are also absent in the hydrophiloid family Spercheidae, but this is assumed to be a secondary feature because Spercheidae is probably a subordinate group within the Hydrophiloidea (Hansen, 1991b). It should be mentioned, however, that Spercheidae is sometimes considered the sistergroup of other hydrophiloids (e.g., Beutel, 1994), but such a relationship relies on the hypothesis that Hydraenidae are the sistergroup of Hydrophiloidea rather than a subordinate group of Staphylinoidea. This position of the Hydraenidae has been refuted by previous authors (Bøving and Craighead, 1931; Lawrence and Newton, 1982; Hansen, 1991b, 1995).

93. Epistomal (fronto-clypeal) suture present (fig. 197) (0) – Epistomal suture absent (1)

Within Staphyliniformia an epistomal suture has apparently only been recorded from Hydraenidae (cf. Bøving and Henriksen, 1938).

94. Dorsal ecdysial lines of head with basal stem (fig. 197-201) (0) – Dorsal ecdysial lines of head without basal stem (fig. 193, 194, 196) (1)

Most staphyliniforms have a basal stem of the dorsal ecdysial lines on the head. A stem is absent in Hydrophiloidea (except for a very short stem in some presumedly derived forms), Sphaeritidae and Micropeplinae.

95. Anterior arms of dorsal ecdysial lines of head not bifurcate, each ending in or near antennal foramen (fig. 199-201) (0) – Anterior arms of dorsal ecdysial lines of head each bifurcate, with outer branch ending in or near antennal foramen, and inner branch directed anteriorly (fig. 198) (1)

Bifurcate anterior arms of the dorsal ecdysial lines of the head were described as typical of Agyrtidae and Leiodidae (Lawrence and Newton, 1982). Although not all members of these families exhibit this feature, it is tentatively assumed to be a basal character of them both. Apparently, all other Staphyliniformia have simple, not bifurcate anterior arms of the dorsal ecdysial lines of the head.

96. Head with 6 stemmata on each side (fig. 193) (0) – 5 stemmata on each side (1) – 4 stemmata on each side (2) – 3 stemmata on each side (3) – 2 stemmata on each side (4) – 1 stemma on each side (5) – Stemmata absent (6)

The number of stemmata varies considerably between (and within) groups. The maximum number found within Staphyliniformia, and probably the overall primitive number, is 6 on each side of the head. This number is assumed to basal for several groups though many of them include forms with a lower number as well. In some groups the number is reduced to 5 (or secondarily fewer) on each side (Leiodidae, Hydraenidae, Scaphidiidae, Phloeocharinae), in others 3 (secondarily fewer) on each side (Scydmaenidae), 2 (or fewer) on each side (Pselaphinae) or 1 (or 0) on each side (Histeridae, Ptiliidae). In a few groups stemmata are basally completely absent (Sphaeritidae, Synteliidae, Leptotyphlinae, Micropeplinae).

97. Labrum free, distinct (sometimes subdivided) (fig. 197-199) (0) – Labrum fused to head capsule to form nasale (fig. 193-196, 201) (1)

Many staphyliniforms have a free, i.e. articulated, labrum and there is hardly no doubt that this is a basal coleopteran characteristic. However, several groups have the labrum intimately fused to the head capsule. In Staphyliniformia groups with a fused labrum include Hydrophiloidea, Histeroidea, Scydmaenidae and several Staphylinidae (Stenine group, Oxyporinae, Pseudopsinae, Paederinae, Staphylininae, Leptotyphlinae, Pselaphinae). In the vast majority of these forms the fusion of the labrum is apparently intimately correlated with predatory habits, perhaps even extraoral digestion).

98. Apodemes (tormae) extending from posterolateral corners of labrum to adoral surface of mouth (epipharynx) (0) – Tormae absent (1)

Within Staphyliniformia tormae are present in Agyrtidae and Leiodidae (Newton, 1991), but apparently absent in other staphyliniform groups (cf. Lawrence and Newton, 1982).

99. Mandibles short, with dentate, tuberculate or spinose molar lobe (interacting with molar lobe of opposing mandible) (fig. 205, 206) (0) – Mandibles without molar area (though sometimes with glabrous pseudomola) (fig. 202-204, 207-209) (1)

The presence of a mola is usually considered a plesiomorphic polyphagan feature (Lawrence and Newton, 1982). In Staphyliniformia a mola has been retained in the presumedly more primitive families of Staphylinoidea (Agyrtidae, Leiodidae, Hydraenidae, Ptiliidae) but seems to be absent in all other groups.

100. Mandibles with prostheca (fig. 205, 206) (0) – Mandibles without prostheca (fig. 202-204, 207-209) (1)

The presence of a prostheca is closely correlated with the presence of a mola (cf. previous character). However, a mesal appendage is present in the mandibles of Proteininae. This appendage was tentatively interpreted as a prostheca but is probably a non-homologous (novel) structure because it is not shared with any closely related groups. However, since Proteininae is quite isolated from forms with a true prostheca the interpretation has no effect on the results of the phylogenetic analysis.

101. Mandibles with densely setose area on ventral surface which extends to mesal edge between mola and retinaculum (0) – Mandibles with penicillus at mesal base (fig. 202-204) (1) – Mandibles with reduced setose area only on mesal edge between mola and retinaculum (2) – Mandibles without setose area on mesal or ventral surface (3)

In most Staphylinoidea the mandibles are without setose area on mesal or ventral face, but sometimes a densely setose area is present on ventral face (Agyrtidae) or on mesal edge between mola and retinaculum (Hydraenidae). Histeroidea and Hydrophiloidea (except presumedly more derived forms) are unique in having a penicillus as the mesal base of the mandibles.

102. Cardo present at base of maxilla (fig. 212, 218) (0) – Cardo apparently absent (fig. 227) (1)

The absence of cardines has been mentioned as a unique feature of Synteliidae and Histeridae by Lawrence and Newton (1982). They are apparently present in all other Staphyliniformia.

103. Lacinia (inner lobe of mala) well developed (sometimes fused with galea) (fig. 216-223) (0) – Lacinia present only as a few apical setae on stipes (or not evident) (fig. 212, 214, 215) (1)

A lacinia is apparently generally present in the groups currently referred to Staphylinoidea (incl. Hydraenidae) but it may be more-or-less intimately fused with the galea in some groups (cf. next character). In Hydrophiloidea and Histeroidea it is absent or represented only by a few setae on the mesal face of stipes. The lacinia-like appendage of Spercheidae is interpreted as a novel (non-homologous) structure, possibly connected with specialized mode of filter-feeding in this family, because Spercheidae is probably a subordinate member of the Hydrophiloidea (cf. Hansen, 1991, 1995) (see also comments on Spercheidae under character 92).

104. Galea (outer lobe of mala) not fused with lacinia, jointlike, movable (fig. 222) (0) – Galea present as a small (fixed) appendage on lacinia (fig. 216-218) (1) – Galea completely fused to lacinia, fixed (fig. 219, 220) (2) – Galea completely fused to lacinia, articulated basally to maxilla (fig. 221) (3) – Galea absent (fig. 212-215) (4)

A galea seems to be generally present in Staphylinoidea (incl. Hydraenidae). In some of them it is present as a small fixed appendage on lacinia (Agyrtidae, Leiodidae, Hydraenidae, Ptiliidae, Slphidae). In others the galea and lacinia are completely fused and may form a fixed appendage on the stipes (Scydmaenidae, Scaphidiidae and most Staphylinidae except Pseudopsinae, Paederinae and Staphylininae). In the three last mentioned staphylinid subfamilies the fused lacinia and galea – often collectively referred to as "mala" – is articulated to the stipes. Micropeplinae is unique within Staphyliniformia in having a joint-like, articulated galea. Hydrophiloidea and Histeroidea are unique in having no distinct galea. But both of these superfamilies have an apical articulated appendage on mesal face of the first palpal segment. Bøving and Henriksen (1938) interpreted this appendage (in Hydrophiloidea) as a "galea" and the first palpal segment as "palpifer", but Moulins (1959) pointed out that there is no justification for assuming these homologies. He argued that the position of the appendage, as well as the absence of muscles leading to it, strongly suggests that it is not a true galea.

105. Galea without apical fringes (0) – Galea with characteristic fringes apically (fig. 217) (1)

A fringed galea has been described as a characteristic of Agyrtidae, Leiodidae, Hydraenidae and Ptiliidae (Dybas, 1976; Newton, 1991). Apparently this feature is unique within Staphyliniformia. The character has not been coded here for Hydraenidae because some members of this family (Ochthebiinae) do not have a fringed galea, and it was not clear which of the two alternatives would represent the plesiomorphic condition of the family.

106. Maxillary palpi 3-segmented (fig. 212-215, 223) (0) – Maxillary palpi 4-segmented (fig. 216-222) (1)

The number of segments in the maxillary palpi is obviously a very constant character, significant even at a high taxonomic level. In Hydrophiloidea and Histeroidea the palpi are 4-segmented whereas in Staphylinoidea (incl. Hydraenidae) they are almost always 3-segmented.

107. Segment 1 of maxillary palp without articulated appendage (fig. 216-223) (0) – Segment 1 of maxillary palp bearing articulated appendage at mesal apex, the appendage having 2 or more sensilla at its apex (fig. 212-215) (1)

The presence of an articulated appendage on mesal apex of basal palpal segment was described as a unique feature of Hydrophiloidea and Histeroidea by Lawrence and Newton (1982). Bøving and Henriksen (1938) erroneously referred to this segment (in Hydrophiloidea) as a "galea" (see also character 104 above).

108. Apical segment of maxillary palpi with several simple sensilla at apex (0) – Apical segment of maxillary palpi with large, oblique sensory appendage of complex structure (fig. 216, 217) (1)

The presence of characteristic, complex sensory appendage was mentioned as a hydraenid-ptiliid synapomorphy by Lawrence and Newton (1982). Apparently the character is unique within Staphyliniformia.

109. Ligula present (fig. 225, 226, 229-233) (0) – Ligula absent (fig. 224, 227, 228) (1)

A ligula is present in most staphyliniform groups, at least basally. It seems to be completely absent, however, in all Histeroid families, in Scydmaenidae, and in Pselaphinae.

110. Antennal foramen well separated from mandibular foramen (e.g., fig. 197) (0) – Antennal foramen only separated from mandibular foramen by a narrow strip of membrane (e.g., fig. 195) (1)

The narrow separation of antennal and mandibular foramina ("antennal foramen contiguous with buccal cavity") has been mentioned as characteristic of Synteliidae and Histeridae by Lawrence and Newton (1982). They do not mentioned anything about the condition in presumed sister-group of these two families, Sphaeritidae, and nor do existing descriptions of the sphaeritid larva (but the illustrations of Nikitsky, 1976 indicates it may be similar). Hence, since larvae of the latter has not been available for study, the condition in Sphaeritidae remain dubious. With this possible exception apparently all other staphyliniforms have the antennal and mandibular foramina well separated.

111. Sensory appendage of preapical antennal segment on anterior (inner) side of the latter (fig. 236, 237) (0) – Sensory appendage of preapical antennal segment on posterior (outer) side of the latter (fig. 234) (1)

Within Staphyliniformia a fairly sharp distinction can be made between Staphylinoidea and Hydrophiloidea+Histeroidea. In almost all Staphylinoidea (incl. Hydraenidae) except Steninae and some Pselaphinae the preapical antennal segment has the sensory appendage on its inner face, whereas in Hydrophiloidea and Histeroidea the sensory appendage is constantly on the outer face on the preapical antennal segment.

112. Legs composed of 6 segments (including claw) (fig. 240) (0) – Legs composed of 5 segments, or less (including claw) (fig. 241-243) (1)

The presence of 6 segments in the legs is normally considered the basal condition in Coleoptera. This number has been retained in Archostemata and Adephaga, but all Polyphaga and Myxophaga have at most 5 segments. The character is included here primarily to contribute to the resolution of the basal coleopteran phylogeny.

113. Thoracic or abdominal egg bursters absent (0) – Egg bursters present as pair of spines on dorsum of abdominal tergum 1 in first instar larvae (1) – Egg bursters present as pair of spines on metanotum in first instar larvae (sometimes also a pair on mesonotum) (2)

As described under character 91, different types of egg-bursters have been recorded from first instar larvae of various beetles, including several staphyliniform groups. Emden (1946) and Crowson (1981) distinguish between "cephalic" (character 91) and "thoraco-abdominal" egg-bursters. However, the last type should rather be considered as at least two different types, "thoracic" and "abdominal", because there is no indication that presence or absence of thoracic egg-bursters is correlated with presence or absence of abdominal egg-bursters. In most of the taxa considered here (for which data has been available) thoracic and abdominal egg-bursters are absent, but abdominal egg-bursters are found in Histeridae and thoracic egg-bursters in at least some Oxytelinae and in Scarabaeoidea. It must be emphasized that data on this character is very scarce.

114. Each abdominal segment 1-9 with single large tergum, seldom divided medially by ecdysial line (and often undivided sternum) (0) – Abdomen largely membraneous, each segment without single large tergum and sternum (1)

Within Staphyliniformia well developed abdominal terga are typical for the vast majority of Staphylinoidea (incl. Hydraenidae). In some forms the terga are narrowly divided medially by an ecdysial line (e.g., Staphylininae) or they may have apparently reduced sclerotization (Ptiliidae). In Hydrophiloidea and Histeroidea the abdomen is largely membranous, sometimes (notably in the presumedly more primitive forms) with several smaller sclerites, but without single large tergites. The hydrophiloid families Hydrochidae and Epimetopidae may make an exception (adequate material was not available for study), but as the two are probably both subordinate members of the superfamily (Hansen, 1991b), their characteristics – if different – are probably secondary.

115. Spiracles annular (fig. 254) (0) – Spiracles biforous (fig. 256) (sometimes except on segment 8) (1) – Spiracles annular-biforous (fig. 255) (2) – Spiracles cribriform (fig. 257) (3)

The general type of abdominal spiracles in Staphylinoidea (incl. Hydraenidae) is the annular one. Some families, Agyrtidae and Leiodidae, also include forms with annular-biforous spiracles (Newton, 1991) and it is not clear which type is actually ancestral for these two families. Biforous spiracles have been described for Hydrophiloidea (e.g., Bøving and Henriksen, 1938) and Histeroidea (e.g., Newton, 1991). In the more derived Hydrophiloidea most abdominal spiracles have become more-or-less reduced and non-functional, except those of segment 8. These are, in return, enlarged and annular (no doubt secondarily!) and have become embedded into a specialized cavity ("stigmatic atrium").

116. Urogomphi absent (fig. 470) (0) – Urogomphi 1-segmented (i.e., not divided, though often articulated at base) (fig.

248, 251) (1) – Urogomphi 2-segmented (fig. 249, 250) (2) – Urogomphi 3-segmented (fig. 244) (3) – Urogomphi 4-segmented (fig. 245) (4)

The presence of articulated urogomphi has been mentioned as a synapomorphy (the only one, actually) for the entire Staphyliniformia (e.g., Lawrence and Newton, 1982). There is, howver, a considerable variation in regard to the apparance of the urogomphi throughout this large assemblage. Most groups of Staphylinoidea have 2-segmented urogomphi (articulated at base), but in certain groups they are "1-segmented", i.e. without any division (though they may be articulated at base). Groups with "1-segmented urogomphi include Ptiliidae, Scydmaenidae (only the presumedly primitive forms), Omaliinae, Leptotyphlinae, Micropeplinae, Dasycerinae, Pselaphinae (sometimes absent). In some presumedly derived members of certain staphylinoid groups (e.g., Ptiliidae, Scydmaenidae, Scaphidiidae, Pselaphinae) the urogomphi are completely absent. In Hydrophiloidea 3-segmented urogomphi (as found in Helophoridae and Epimetopidae) are assumed to represent the basal condition, but most other, more derived hydrophiloids have more-or-less rudimentary urogomphi, which are usually 2-segmented. In these forms the reduction of the urogomphi seems to be correlated with the development of a stigmatic atrium, which involves modifications of abdominal segment 9 (and, hence, the urogomphi). In Histeroidea the urogomphi are generally well developed, 4-segmented in Sphaeritidae and 2-segmented in Histeridae.

117. Urogomphi (at their bases) articulated to dorsal apex of 9th abdominal segment (fig. 249) (0) – Urogomphi solidly "fixed" to 9th abdominal segment (fig. 251) (1)

As mentioned under the previous character, the presence of articulated urogomphi is a typical feature of most Staphyliniformia. However, in some groups of Staphylinoidea, all of which have "1-segmented" (i.e., undivided) urogomphi, these have been solidly fixed to the 9th abdominal tergum. These groups are Scydmaenidae and some staphylinid subfamilies (Micropeplinae, Dasycerinae, Pselaphinae).

118. Abdominal segment 10 unarmed (0) – Abdominal segment 10 with one pair of large hooks on eversible anal lobes (fig. 249) (1) – Abdominal segment 10 with 2 pairs of large hooks on eversible anal lobes (2) – Abdominal segment 10 with numerous fine teeth or hooks on eversible anal lobes (3) – Abdominal segment 10 with 3 pairs of large hooks on eversible anal lobes (4)

In Staphyliniformia there is some variation in regard to the arming of the 10th abdominal segments. Hydrophiloidea and Histeroidea, as well as some Staphylinoidea (most Staphylinidae) have an unarmed segment 10. Hydraenidae and Ptiliidae have eversible anal lobes of segment 10 armed with a pair of large hooks (suggested as synapomorphy by Lawrence and Newton, 1982). Similar, but undoubtedly non-homologous hooks are found in some of the outgroups considered here, i.e., Gyrinidae (with 2 pairs of hooks) and Microsporidae (with 3 pairs of hooks). In Agyrtidae, Leiodidae, Scydmaenidae, Scaphidiidae, Silphidae and a some Staphylinidae (Micropeplinae, Pselaphinae) the arming consists of numerous fine teeth or hooks.

Habitat:

119. Adult terrestrial (0) – Adult aquatic (1)

Adult Staphyliniformia are generally

terrestrial, but there are two groups which are predominantly and undoubtedly basally aquatic, at least in the adult stage: Hydraenidae and Hydrophiloidea. The larvae of both groups are probably primitively terrestrial. In Hydraenidae this mode of life seems to have been retained throughout the family, but in Hydrophiloidea larvae of most derived families have become aquatic; an exception is made by the hydrophilid subfamily Sphaeridiinae, in which both larvae and adults have become secondarily terrestrial. The aquatic habits (and related structural features) of Hydraenidae and Hydrophiloidea have often been considered indicative of a close relationship between the two groups, but several other morphological details tend to refute this hypothesis.

Data matrix

The character distribution of terminal taxa, which form the basis for the present phylogenetic analysis is summarized in the data matrix given here (Table 1a-e). Characters of undetermined state are denoted by a "–". The formal ranks of terminal taxa correspond to the ranks proposed in other sections of this work, and the taxonomic compositions of the taxa are outlined under the phylogenetic discussion.

Analytical procedure

The data that form the basis for the phylogenetic analysis include 37 terminal taxa and 119 characters. In the initial analytical phase more characters were included (>150) but a series of preliminary analyses revealed the necessity of modifying the character set. In these preliminary analyses the computer programs Hennig86 (Farris, 1988), PAUP (Swofford, 1993), and MacClade (Maddison and Maddison, 1992), were used. Numerous such analyses were performed, based on various modifications of the data matrix, such as exclusion of some taxa, deactivation of different characters, different weighting of characters, etc. The main purpose of such manipulations were to examine stability of tree topology and check the initial codings and definitions of characters. Some poorly defined characters were redefined or discarded, and autapomorphies of single terminal taxa were also omitted. Characters that were ambiguous (i.e., inconstant within a terminal taxon) were checked, and when justified, reinterpreted on the basis of these preliminary analyses.

In the final phase (i.e., on the basis of the optimized character matrix) analyses were performed by the use of Hennig86, PAUP and Nona and Pee-Wee (Goloboff, 1993b, 1993c). All characters were treated as unordered (nonadditive) for reasons already mentioned under the list of characters.

TABLE 1 (a):

Character no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Trogidae	0	2	0	1	1	0	0	0	0	1	0	0	0	0	0	1	1	0	3	0	0	1	0	1	2
Hydrophiloidea	1	0	1	1	1	0	0	1	0	1	0	0	0	0	1	2	1	1	3	0	0	1	0	0	1
Sphaeritidae	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	1	1	3	0	0	1	0	0	1
Synteliidae	0	2	0	1	1	1	-	0	0	1	-	0	0	0	0	0	1	1	3	0	0	1	0	1	2
Histeridae	0	2	0	1	1	1	0	0	0	1	0	0	0	0	0	0	1	1	3	0	0	1	0	1	1
Agyrtidae	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1
Leiodidae	0	1	0	0	1	0	0	0	0	1	1	0	0	1	0	0	1	0	0	2	0	0	0	0	1
Hydraenidae	1	0	1	0	0	1	0	1	0	0	0	0	0	1	1	0	1	0	4	0	0	0	0	0	1
Ptiliidae	0	2	1	1	1	2	1	1	0	1	0	1	0	1	0	0	1	0	2	0	0	0	0	1	1
Scydmaenidae	0	1	2	1	1	0	1	0	1	1	0	1	0	1	0	0	1	0	0	0	0	0	0	1	0
Scaphidiidae	1	1	0	1	1	1	0	0	0	1	0	0	1	0	0	0	1	0	4	0	0	0	0	1	0
Empelidae	0	2	0	1	1	0	0	0	0	1	0	0	1	1	0	0	1	0	2	0	0	0	0	0	0
Microsilphinae	0	1	0	0	1	0	0	0	1	1	1	1	1	0	0	0	1	0	2	0	0	0	0	0	1
Omaliinae	0	1	2	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Proteininae	0	2	2	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Micropeplinae	0	2	1	1	0	0	1	1	0	1	0	0	0	0	0	2	1	0	1	0	0	0	0	0	0
Neophoninae	0	0	2	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1
Dasycerinae	-	2	2	1	0	0	1	1	0	1	1	0	1	1	0	0	1	0	2	0	0	0	0	1	1
Pselaphinae	0	2	2	1	0	0	1	0	1	1	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0
Phloeocharinae	0	1	2	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	0	0	0	0	0	0	1
Tachyporine group	0	1	0	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0
Trigonurinae	0	1	2	1	1	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1
Oxyteline group	0	1	2	1	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Oxyporinae	0	1	2	1	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1
Stenine group	0	2	2	1	1	0	0	0	0	1	0	0	0	0	0	0	1	0	2	0	1	0	0	1	1
Solieriinae	0	2	2	1	1	0	1	0	0	1	0	1	0	1	0	0	1	0	0	0	0	0	0	1	0
Leptotyphlinae	0	1	2	1	0	0	0	0	0	1	-	1	1	0	0	0	1	0	0	0	1	0	0	1	0
Pseudopsinae	0	1	2	1	1	0	-	0	0	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1
Staphylinine group	0	2	2	1	1	0	0	0	1	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Apateticidae	-	2	2	1	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Silphidae	1	1	2	1	1	0	0	0	1	1	0	0	0	1	0	0	0	1	3	0	0	0	0	0	0
Ommatidae/Cupedid.	0	2	2	1	1	2	1	0	1	1	-	0	0	0	0	0	1	0	0	0	0	0	1	0	0
Microsporidae	0	1	0	1	1	0	1	1	0	0	-	1	0	-	0	0	0	1	2	0	0	0	1	0	0
Gyrinidae	0	0	0	1	1	0	1	1	1	1	1	0	0	0	0	2	1	0	5	0	0	0	1	1	0
Trachypachidae	0	1	0	1	1	0	1	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	1	1	0
Eucinetidae	0	0	0	1	1	0	0	1	0	1	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0
Derodontidae	0	1	2	0	0	0	0	1	0	1	1	0	0	0	0	0	1	0	2	0	0	1	0	0	1

Analyses were made to find 1) shortest trees (i.e., most parsimonious trees based on equally weighted characters); 2) trees resulting from weighting of specific characters that have been considered of major significance by previous authors; and 3) trees resulting from the use of standard weighting procedures such as "successive weighting" (Farris, 1969) and "implied

TABLE 1 (b):

Character no.	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
Trogidae	2	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Hydrophiloidea	1	1	0	0	1	0	0	1	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1
Sphaeritidae	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	0	1
Synteliidae	2	0	-	-	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	4	0	0	1
Histeridae	1	1	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	0	3	3	0	0	2
Agyrtidae	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Leiodidae	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Hydraenidae	1	1	0	0	0	1	0	1	0	0	1	1	0	0	2	0	0	0	0	0	0	0	0	0	1
Ptiliidae	1	1	0	0	-	1	1	1	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	1
Scydmaenidae	1	1	0	0	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	2	2	1	0	0	2
Scaphidiidae	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	2	2	3	0	0	2
Empelidae	1	0	1	1	0	0	0	0	0	1	0	-	0	0	1	1	1	1	0	1	3	4	1	0	1
Microsilphinae	1	0	1	1	0	0	0	0	0	0	0	1	0	0	1	2	1	1	0	1	3	4	1	0	2
Omaliinae	1	0	1	1	0	0	0	0	0	0	0	1	0	0	1	2	1	1	0	1	3	4	1	0	1
Proteininae	1	0	1	1	0	0	0	0	0	0	0	1	0	0	1	2	0	0	2	1	4	4	1	0	2
Micropeplinae	1	0	1	1	-	1	0	1	0	0	0	1	0	0	1	2	0	1	2	1	5	4	0	0	2
Neophoninae	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	2	1	1	2	1	4	4	1	0	1
Dasycerinae	0	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0	0	1	2	0	5	2	1	0	1
Pselaphinae	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	2	0	1	2	1	5	4	1	0	1
Phloeocharinae	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	2	1	1	0	1	5	4	0	0	1
Tachyporine group	1	0	1	0	0	0	0	0	0	0	0	1	1	0	1	2	1	1	0	1	5	4	0	0	1
Trigonurinae	1	0	1	-	0	0	0	0	0	0	0	1	0	0	1	2	1	1	0	1	4	4	0	0	1
Oxyteline group	1	0	1	1	0	0	0	0	0	0	0	1	0	0	1	2	1	1	0	1	5	4	0	0	1
Oxyporinae	1	0	0	0	0	1	0	0	0	0	0	1	1	0	1	2	1	1	0	1	5	4	0	0	2
Stenine group	1	0	0	0	-	1	0	1	0	0	0	1	0	0	1	2	1	1	0	1	5	4	0	0	1
Solieriinae	1	0	0	0	0	0	1	1	0	0	0	-	1	0	1	2	1	1	0	1	5	4	0	0	1
Leptotyphlinae	1	-	1	-	0	0	0	1	-	0	0	1	1	0	1	2	1	-	0	1	5	4	0	0	1
Pseudopsinae	1	0	1	2	0	0	0	0	0	0	0	1	0	0	1	2	1	1	0	1	5	4	0	0	1
Staphylinine group	1	0	1	0	0	0	0	0	0	0	0	1	1	0	1	2	1	1	0	1	5	4	0	0	1
Apateticidae	1	0	1	2	0	0	0	0	0	0	0	1	0	0	1	2	1	1	0	1	2	4	0	0	1
Silphidae	1	0	1	2	0	0	0	0	0	0	0	1	0	0	2	2	1	1	0	1	2	3	0	1	2
Ommatidae/Cupedid.	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Microsporidae	1	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Gyrinidae	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	2
Trachypachidae	2	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1
Eucinetidae	1	0	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Derodontidae	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

weighting" (Goloboff, 1993a). The specific options used for the calculation of the trees are stated below in connection with the results.

In the tree searching phase of the analyses no particular attention was given to where the trees should be rooted. It should be mentioned that whereas the analyses performed by PAUP produced unrooted trees, Hennig86 and Nona (by

TABLE 1 (c):

Character no.	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
Trogidae	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Hydrophiloidea	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Sphaeritidae	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1
Synteliidae	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	1	1
Histeridae	1	0	0	1	0	0	0	0	0	0	1	1	0	1	0	1	1	0	0	1	0	0	0	1	1
Agyrtidae	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	2	1
Leiodidae	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	3	1
Hydraenidae	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	3	1
Ptiliidae	0	0	1	1	0	1	0	0	1	1	0	0	1	0	0	1	0	0	0	0	1	1	1	4	1
Scydmaenidae	1	0	2	1	0	0	1	0	1	0	1	0	0	0	1	1	1	0	0	1	2	1	1	3	1
Scaphidiidae	1	0	2	1	0	0	1	0	0	0	1	1	0	0	0	1	1	0	0	0	2	0	1	2	1
Empelidae	1	0	-	1	0	0	1	1	0	1	0	0	0	0	0	0	1	0	0	1	2	0	1	3	1
Microsilphinae	1	1	2	1	0	0	1	0	1	0	0	0	0	0	0	1	1	0	1	1	2	0	1	3	1
Omaliinae	1	1	2	1	0	0	1	0	1	0	0	0	0	0	0	1	1	0	1	1	2	0	1	2	1
Proteininae	1	1	2	1	1	0	1	0	1	0	0	0	0	0	0	1	2	0	1	1	2	0	1	2	1
Micropeplinae	1	0	2	1	1	0	0	0	1	0	1	1	1	0	0	1	2	0	1	1	2	1	1	3	1
Neophoninae	1	1	2	1	1	0	1	0	0	0	0	0	1	0	0	2	2	0	1	1	2	1	1	3	1
Dasycerinae	0	0	1	1	1	0	1	0	0	0	0	0	1	0	0	2	0	-	-	-	-	-	-	3	1
Pselaphinae	0	0	2	1	1	0	1	0	0	0	0	0	1	0	0	1	2	0	1	1	2	1	1	3	1
Phloeocharinae	1	1	2	1	0	0	0	0	0	1	0	0	0	0	1	1	2	0	1	1	2	1	1	3	1
Tachyporine group	1	1	2	1	0	0	1	0	0	0	0	0	0	0	0	1	2	0	1	1	2	0	1	3	1
Trigonurinae	0	1	2	1	0	0	1	0	1	0	0	1	0	0	0	1	2	-	1	1	-	0	1	3	1
Oxyteline group	0	1	2	1	0	0	-	0	1	0	0	0	0	0	0	1	2	0	1	1	2	0	1	2	1
Oxyporinae	1	1	2	1	0	0	1	0	0	0	0	0	0	0	0	1	2	0	1	1	2	0	1	0	1
Stenine group	1	1	2	1	1	0	1	0	1	0	0	1	0	0	0	1	2	0	1	1	2	0	1	2	1
Solieriinae	0	0	2	1	0	0	1	0	0	0	0	0	0	0	1	1	2	0	1	1	2	-	1	3	1
Leptotyphlinae	1	1	2	1	0	0	1	0	1	0	0	-	1	-	1	-	2	-	-	-	-	-	-	-	-
Pseudopsinae	1	1	2	1	0	0	1	0	1	0	0	1	0	-	0	1	2	-	-	-	-	-	-	-	-
Staphylinine group	1	1	2	1	0	0	1	0	1	0	0	0	0	0	1	1	2	0	1	1	2	0	1	0	1
Apateticidae	1	1	2	1	0	0	1	0	0	1	0	1	0	0	0	1	1	0	1	1	2	0	1	1	1
Silphidae	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	2	0	1	1	2	0	1	1	1
Ommatidae/Cupedid.	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
Microsporidae	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	1	0	1	0	0	0	1	0	2	0
Gyrinidae	1	1	1	0	0	0	1	1	0	1	0	0	0	2	0	1	0	1	0	0	0	0	0	0	0
Trachypachidae	0	1	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Eucinetidae	0	0	1	1	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Derodontidae	0	0	1	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1

default) root the trees between the first taxon of the matrix and the remaining taxa (e.g., below node 71 in fig. 2). However, if no presumption about global or local polarity is made, then an entire tree can be rerooted on any of its branches, with each of these trees being of equal length (Maddison and Maddison, 1992). That is, with regard to the discussion of tree

TABLE 1 (d):

Character no.	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
Trogidae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	5	0	0	0	1
Hydrophiloidea	0	1	0	0	0	0	0	0	0	1	0	0	0	2	0	1	1	1	1	0	0	1	1	1	1
Sphaeritidae	1	2	1	0	0	0	0	0	0	2	1	0	0	0	0	-	1	1	1	0	6	1	1	1	1
Synteliidae	1	-	-	-	-	0	0	0	-	-	-	-	-	-	0	-	1	1	0	0	6	1	1	1	1
Histeridae	1	1	0	0	0	0	0	2	0	2	1	0	0	0	0	0	1	1	0	0	5	1	1	1	1
Agyrtidae	1	2	1	0	0	1	0	1	0	1	0	0	0	0	0	-	0	1	0	1	0	0	0	0	0
Leiodidae	1	2	0	0	0	-	0	0	0	0	0	0	0	0	0	-	0	1	0	1	1	0	0	0	0
Hydraenidae	1	2	1	0	0	2	0	0	2	3	2	0	1	1	1	1	0	0	0	0	1	0	-	0	0
Ptiliidae	1	2	0	0	0	2	0	0	2	3	2	0	1	0	1	-	0	1	0	-	5	0	-	0	0
Scydmaenidae	1	0	0	1	1	2	1	0	0	0	2	0	0	0	0	-	0	1	0	0	3	1	1	1	1
Scaphidiidae	1	0	0	1	1	2	1	0	0	0	0	0	0	0	0	-	0	1	0	0	1	0	1	1	1
Empelidae	1	-	0	-	1	2	1	0	-	1	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Microsilphinae	1	-	1	1	1	1	1	0	0	0	0	1	0	-	-	-	-	-	-	-	-	-	-	-	-
Omaliinae	1	2	0	1	1	2	1	0	0	1	0	1	0	-	0	-	0	1	0	0	0	0	1	1	1
Proteininae	1	0	0	1	1	1	1	0	0	0	0	1	-	-	0	-	0	1	0	0	0	0	1	1	0
Micropeplinae	1	0	0	1	1	1	1	0	0	0	2	0	0	-	1	-	0	1	1	0	6	0	1	1	1
Neophoninae	1	2	0	1	1	1	1	0	0	0	0	1	0	-	-	-	-	-	-	-	-	-	-	-	-
Dasycerinae	1	-	0	1	1	2	1	0	-	-	-	-	-	-	1	-	0	1	0	0	0	0	1	1	1
Pselaphinae	1	-	1	1	1	2	1	0	-	3	2	0	0	-	0	-	0	1	0	0	4	1	1	1	1
Phloeocharinae	1	1	0	1	1	2	1	0	0	1	0	0	0	-	0	-	0	1	-	-	1	0	-	1	1
Tachyporine group	1	0	0	1	1	2	1	0	0	1	0	0	0	0	0	-	0	1	0	0	0	0	1	1	1
Trigonurinae	1	-	-	-	1	2	1	0	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-	-	-
Oxyteline group	1	1	0	1	1	2	1	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0	1	1	1
Oxyporinae	1	0	0	1	1	2	1	0	0	2	0	0	0	0	0	-	0	1	0	0	0	1	1	1	1
Stenine group	1	2	0	1	1	2	1	0	1	2	2	0	0	0	0	-	0	1	0	0	0	1	1	1	1
Solieriinae	1	0	0	-	1	2	1	0	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Leptotyphlinae	-	-	1	1	1	2	1	0	0	3	2	0	-	-	-	-	-	-	-	-	6	1	-	-	-
Pseudopsinae	-	2	0	-	-	1	-	0	1	-	-	-	-	-	-	-	-	-	-	-	0	1	-	-	-
Staphylinine group	1	-	0	1	1	2	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	1
Apateticidae	1	0	0	1	1	2	1	0	0	1	0	0	0	-	-	-	-	-	-	-	0	-	-	-	-
Silphidae	1	0	0	1	1	2	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1
Ommatidae/Cupedid.	0	0	0	0	0	0	0	0	-	-	-	-	0	-	0	0	0	0	1	-	-	0	-	0	1
Microsporidae	1	-	-	-	-	-	-	-	-	0	0	0	0	0	1	-	0	0	1	-	2	1	1	0	1
Gyrinidae	0	0	0	0	0	2	0	0	0	2	2	1	0	0	0	-	0	1	0	0	0	1	1	1	1
Trachypachidae	0	0	0	1	0	2	0	0	0	1	2	0	0	0	0	1	0	1	0	0	0	1	1	1	1
Eucinetidae	0	1	0	0	0	0	0	0	1	1	0	0	0	-	-	-	0	1	0	0	1	0	-	0	0
Derodontidae	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	1	0	0	1	0	0	0	-	0	0

length the attachment of the root is of no importance. The only presumption made at this stage (to give meaning to comments about "staphyliniform subgroups") was that the root (as here) would lie "outside" the Staphyliniformia. A discussion of the exact attachment of the root in the preferred cladogram is given below.

Character changes between nodes and

TABLE 1 (e):

Character no.	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119
Trogidae	3	0	0	1	0	1	0	0	1	0	0	1	2	1	3	0	-	3	0
Hydrophiloidea	1	0	1	4	-	1	1	0	0	0	1	1	0	1	1	3	0	0	1
Sphaeritidae	1	0	1	4	-	1	1	0	1	-	1	1	-	1	1	4	0	-	0
Synteliidae	1	1	1	4	-	1	1	0	1	1	1	1	-	1	1	4	0	0	0
Histeridae	1	1	1	4	-	1	1	0	1	1	1	1	1	1	1	2	0	0	0
Agyrtidae	0	0	0	1	1	0	0	0	0	0	0	1	-	0	-	2	-	3	0
Leiodidae	3	0	0	1	1	0	0	0	0	0	0	1	-	0	-	2	0	3	0
Hydraenidae	2	0	0	1	-	0	0	1	0	0	0	1	0	0	0	2	0	1	1
Ptiliidae	3	0	0	1	1	0	0	1	0	0	0	1	-	1	0	1	0	1	0
Scydmaenidae	3	0	0	2	0	0	0	0	1	0	0	1	-	0	0	1	1	3	0
Scaphidiidae	3	0	0	2	0	0	0	0	0	0	0	1	-	0	0	2	0	3	0
Empelidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Microsilphinae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Omaliinae	3	0	0	2	0	0	0	0	0	0	0	1	-	0	0	1	0	0	0
Proteininae	3	0	0	2	0	0	0	0	0	0	0	1	-	0	0	2	0	0	0
Micropeplinae	3	0	0	0	0	0	0	0	0	0	0	1	-	0	0	1	1	3	0
Neophoninae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Dasycerinae	3	0	0	2	0	0	0	0	0	0	0	1	-	0	0	1	1	0	0
Pselaphinae	3	0	0	2	0	0	0	-	1	0	0	1	-	0	0	1	1	3	0
Phloeocharinae	3	0	0	2	0	0	0	0	0	-	0	1	-	0	0	2	0	-	0
Tachyporine group	3	0	0	2	0	0	0	0	0	0	0	1	-	0	0	2	0	0	0
Trigonurinae	-	-	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-	0
Oxyteline group	3	0	0	2	0	0	0	0	0	0	0	1	2	0	0	2	0	0	0
Oxyporinae	3	0	0	2	0	0	0	0	0	0	0	1	-	0	0	2	0	0	0
Stenine group	3	0	0	2	0	0	0	0	0	0	1	1	-	0	0	2	0	0	0
Solieriinae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Leptotyphlinae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	0
Pseudopsinae	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	2	-	-	0
Staphylinine group	3	0	0	3	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0
Apateticidae	-	-	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-	0
Silphidae	3	0	0	1	0	0	0	0	0	0	0	1	0	0	0	2	0	3	0
Ommatidae/Cupedid.	3	0	0	0	0	0	0	0	0	0	-	0	0	1	0	0	-	0	0
Microsporidae	-	0	0	1	0	0	-	-	0	0	1	1	-	0	-	0	-	4	1
Gyrinidae	3	0	0	0	0	1	0	0	1	0	-	0	-	1	-	0	-	2	1
Trachypachidae	3	0	1	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0
Eucinetidae	3	0	0	1	0	0	0	0	0	0	0	1	-	-	0	0	-	-	0
Derodontidae	1	0	0	1	0	0	0	0	0	0	0	1	0	0	2	1	1	-	0

between nodes and terminal taxa (i.e., apomorphies) were identified and listed by the use of the APO command of Nona. Lists of "node changes" under each character were obtained by using the command CHANGE of the same program. It should be noted that Nona (by default) produces these list on the premise that the tree is rooted between the first taxon (here

Archostemata) and the remaining taxa. If the tree is rerooted character state polarization becomes reversed along the branches between this and the new root. In some cases the character states at a particular node were listed as ambiguous, and whenever possible, the actual state was determined from the premise that repeated losses are more likely than repeated gains.

Phylogenetic analysis

Results

SHORTEST TREES. – As a first step in the analysis Hennig86 was used to calculate the shortest, i.e., most parsimonious trees on the basis of equally weighted characters. Since the number of taxa was too large to allow for the use of exact algorithms of this program, the options MHENNIG* and BB* (calculates multiple trees using branch breaking) were used to calculate shortest tree(s). The result was 9 equally parsimonious trees (length = 537, consistensy index = 32, retention index = 58).

To confirm the results of the Hennig86 analysis, a search for shortest trees were also performed by the use of Nona. This program has some more facilities than Hennig86, which may be useful when the data set is too large to allow for exact calculations of the trees. The problem with the approximated algorithms is that they do not guarantee to produce the shortest tree(s) and/or all of them. That is, for some data sets, there exist groups or "islands" of trees that (within the same island) are much more similar to each other than to trees from different islands; once such an island is reached in search of shortest trees by the use of approximated algorithms, trees from different islands cannot be obtained (e.g., Maddison and Maddison, 1992). Depending on the starting point (input order of taxa) the procedure of finding shortest trees may therefore stop at a "local" rather than the "global" optimum. By trying several different starting trees, however, the chances improve that at least some of them will produce globally rather than locally optimal trees.

Hence, to minimize the risk of using inadequate input order, a series of analyses were performed on the basis of randomized input order of taxa, using the option MULT of Nona. This command creates a single tree which is submitted to branch-swapping and retain (by default) up to 20 trees. When * is added to the command, branch swapping is more exhaustive. Shortest trees were found by the use of the commands HOLD100 (keeps 100 trees in memory), HOLD/20 (sets 20 as maximum number of trees to be kept in each replication of MULT) and MULT*50 (do 50 tree searches with exhaustive branch swapping based on randomized input order). This resulted, in 33 out of 50 replications, in 9 trees of length 537, i.e., exactly the same result as found by the Hennig86 analysis.

Finally the same analysis was made by using PAUP with the following heuristic search settings: Addition sequence simple; 1 tree held at each step during stepwise addition; tree-bisection-reconnection (TBR) branch-swapping performed; MULPARS option in effect; (steepest descent option not in effect); initial MAXTREES setting = 100; branches having maximum length zero collapsed to yield polytomies; (topological constraints not enforced); (trees unrooted). The result is identical with that of the Hennig86 and Nona analyses.

A strict consensus tree of the 9 equally parsimonious trees was computed (length 546), using the option NELSEN of Nona (fig. 2). It will be seen that this consensus tree has one unresolved polytomy (at node 70) and one unresolved trichotomy (at node 49), and that it is otherwise fully resolved. Furthermore, it must be mentioned that with the exception of the taxa included in the "staphylinid group" (clade 67) this tree is identical to trees calculated on the basis of the initial larger number of charac-

Fig. 2. Strict consensus of 9 equally parsimonious 537-step trees (shortest trees) based on equally weighted characters (W = 1) (see text). Numbers denote clades referred to in the section on analytical procedure, but are not identical with the numbers referred to under the phylogenetic discussion ("evaluation of preferred cladogram").

ters (i.e., including those which have been discarded, cf. above).

WEIGHTING OF SELECTED CHARACTERS. – Two characters (no. 44 and 48) have been considered of major significance as defining an "omaliine group" of staphylinid subfamilies (sensu Lawrence and Newton, 1982) including a "proteinine subgroup" (= Proteininae, Neophoninae, Micropeplinae, Dasycerinae and

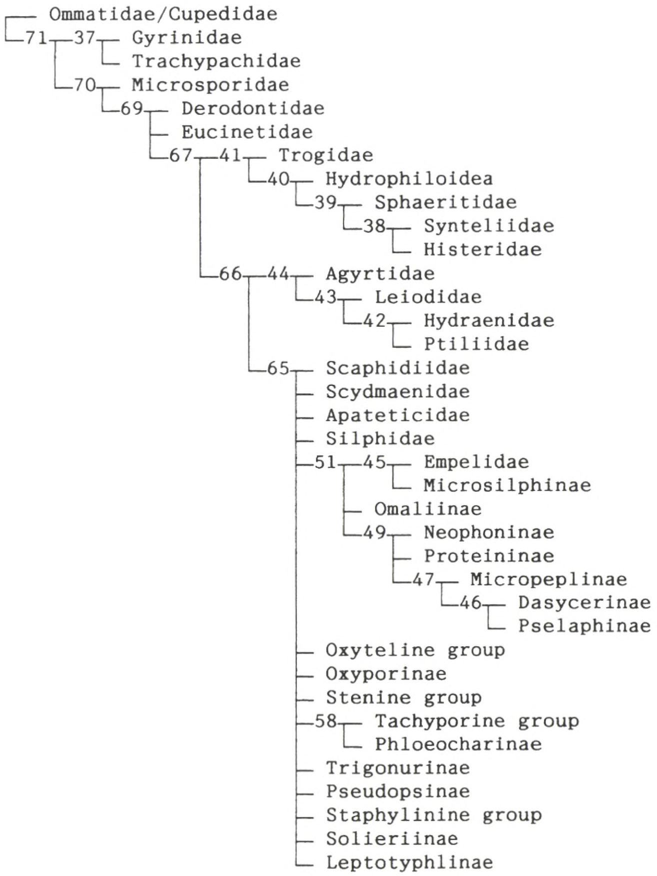

Fig. 3. Strict consensus of 150 equally parsimonious trees based on higher weighting of characters no. 44 and 48 (see text). Numbers denote clades referred to in the section on analytical procedure, but are not identical with the numbers referred to under the phylogenetic discussion ("evaluation of preferred cladogram").

Pselaphinae). Such a relationship was, however, not revealed in the "shortest trees". Therefore several analyses, each based on different weightings of the two characters, were made to find the minimum weight required of each of them in order to constrain the taxa currently included in the "omaliine group". These analyses were made in Hennig86 by use of the same tree searching commands as mentioned in the previous section (MHENNIG*, BB*).

It turns out that when the weight 10 (or more) is given to the sternum 8 gland (char. 48), Empelidae, Micropeplinae, Dasycerinae and Pselaphinae become included in the "omaliine group", but a close relationship between the latter three and Proteininae and Neophoninae is not revealed. On the other hand, when the weight 7 (or more) is given to the atrophy of spiracles 4-6 (char. 44), the entire "proteinine subgroup" (with Micropeplinae, Dasycerinae and Pselaphinae) appears as a monophyletic subgroup within the omaliine group, but this does not result in the inclusion of Empelidae. Only when the characters 44 and 48 are given higher weights simultaneously (weight at least 7 and 4, respectively), both Empelidae and a monophyletic "proteinine subgroup" will appear as members of the "omaliine group".

The result of the analysis, in which both characters were given higher weights, is 150

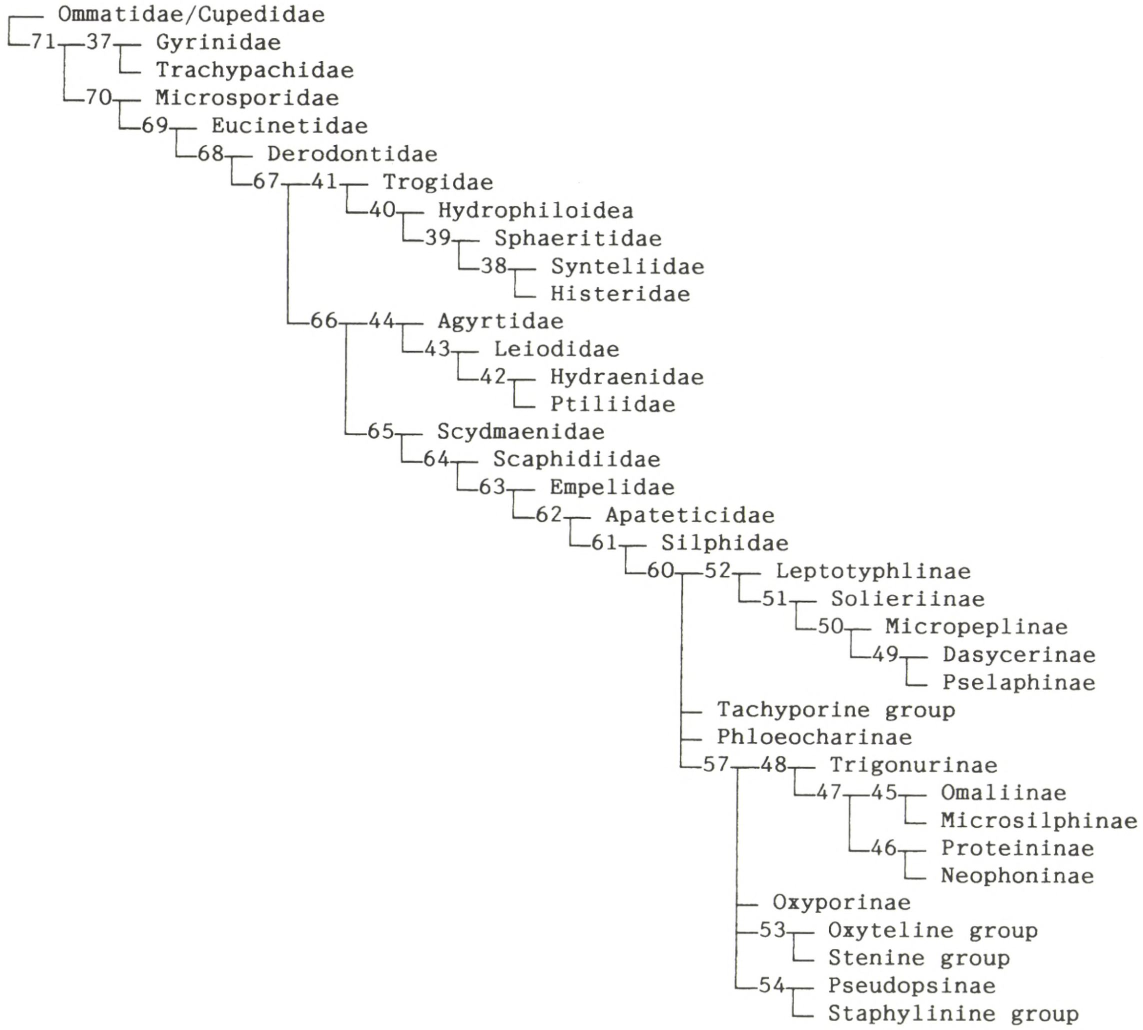

Fig. 4. Strict consensus of 8 equally parsimonious trees based on successive weighting of characters analysed with Hennig86 (see text). Numbers denote clades referred to in the section on analytical procedure, but are not identical with the numbers referred to under the phylogenetic discussion ("evaluation of preferred cladogram").

equally parsimonious trees, which (with characters reweighted to 1) have a length of 543 (i.e., 6 steps longer than the shortest trees). A strict consensus tree of the 150 trees (computed using the option NELSEN in Nona) is given in fig. 3. When this cladogram is compared to the previous one (strict consensus of shortest trees, fig. 2), it will be noted that there is an unresolved trichotomy at node 69 (Polyphaga) and that the entire staphylinid group (clade 65 in this tree) forms an almost unresolved polytomy (except for the taxa constrained by the weighting of characters 44 and 48). Otherwise the tree is resolved and identical with the previous alternative (fig. 2).

Fig. 5. Preferred cladogram, based on successive weighting of characters analysed with PAUP (see text). The cladogram forms the basis for the following phylogenetic discussion. Numbers denote clades referred to in this section.

SUCCESSIVE WEIGHTING. – A widely used method of weighting characters according to their "fits" is the successive weighting (implemented in Hennig86 and PAUP). Initially the analysis were performed in Hennig86. The reweighting of the characters (based on their distribution in one or more initial trees) is achieved by using the command XSTEPS W (weights characters according to fits, as the product of character consistency and character retention indices scaled to lie in the range 0-10) followed by the command BB* (calculating multiple trees by branch breaking), and repeating the procedure until the tree length stabilizes. Because the result may depend on the tree file input, the procedure was effected

Fig. 6. Strict consensus of 4 equally parsimonious trees based on weighting procedure implemented in Pee-Wee (see text). Numbers denote clades referred to in the section on analytical procedure, but are not identical with the numbers referred to under the phylogenetic discussion ("evaluation of preferred cladogram").

on the basis of 1) all equally parsimonious trees, 2) the consensus tree, and 3) an unresolved tree (option TR;BB* of Hennig86). The result was identical in all three cases, viz. 8 trees. To compare their length with the most parsimonious tree(s) and calculate the number of extra steps applied, all characters were reweighted (given weight =1, using the command CC/1 0.) and the length calculated (using the command XSTEPS L). The length of the 8 trees, thus calculated, varied from 548 to 551, i.e., 11-14 steps longer than the most parsimonious ones. A strict consensus tree, computed by the (Nona) NELSEN command, is shown in fig. 4.

It will be seen that the consensus tree has two unresolved polytomies (at node 57 and 60), and that it is otherwise fully resolved. Furthermore, it must be noted that apart from taxa within the "staphylinid group" (now clade

65!), the tree is identical with the consensus tree calculated on the basis of equally weighted characters ("shortest tree"), except that the tetratomy of the latter is now resolved. Comparison of the two consensus trees (figs. 2, 4) implies that the phylogeny of the non-staphylinid-group taxa is rather well founded. Within the "staphylinid group" the most drastic change is the shift in position of the Scydmaenidae from a subordinate position within Staphylinidae (clade 64 in shortest tree, fig. 2) to a basal position within the entire staphylinid group (clade 65 in successive weighting tree, fig. 4).

There is one thing in regard to the successive weighting procedure of Hennig86 that may in some cases result in inadequate trees. This concerns the values of the weights assigned to the characters. As mentioned this weight expresses the "fits" of the characters on a scale from 0-10. Since no decimals are used the weights are generally more-or-less inaccurate, i.e. a character with the actual "weight" of 1.1 and another with the actual "weight" 1.9 would both appear as having a weight of 1. In this regard a more exact calculation can be done by using PAUP in which weights can be set to lie between 0 and 1000 (but still calculated in the same way as in Hennig86). For this reason a successive weighting analysis was also performed in PAUP.

On the basis of the shortest trees (see above) characters were reweighted by maximum value of rescaled consistency indices (in the scale from 0-1000). The heuristic search settings (tree-bisection-reconnection (TBR) branch-swapping performed, etc.) are the same as mentioned under procedure for finding shortest trees). The procedure was repeated until the result stabilized. The result differ somewhat from that of Hennig86. Only one tree was found (length 94103) (Fig. 5). With all characters reweighted to 1, the length of this tree is 542, i.e. 5 steps longer than the shortest trees. This is less than the extra steps required in the trees found by the Hennig86 analysis.

The result of the PAUP analysis differs mainly from that of the Hennig86 analysis in being unambiguous and fully resolved. Differences between the trees computed by the two analyses are restricted to the slightly different positions of Apateticidae (sistergroup of Silphidae, rather than Silphidae + Staphylinidae) and certain staphylinid subfamilies, notably Oxyporinae and the Oxyteline group. Since the PAUP tree is based on a more detailed calculation of character "fits" it is preferred in favour of the Hennig86 trees.

IMPLIED WEIGHTING. – Another method for weighting characters according to their homoplasy has been proposed by Goloboff (1993a) and implemented in his computer program Pee-Wee. This method is based on searching of trees with maximum total fit (with character fits defined as a concave function of homoplasy), rather than trees of minimum length as in Hennig86, PAUP and Nona. Hence, to see the effect of using this method compared to that of successive weighting, an analysis was made in Pee-Wee (with default value of the concavity constant K = 3). The tree searching commands used in this analysis are the same as given above under search for shortest trees with by use of Nona (HOLD100, HOLD/20, MULT*50). This procedure resulted in 4 trees of maximum fit = 677.3 (in 10 out of 50 replications). With all characters reweighted to 1, this corresponds to tree lengths of 547, i.e., 10 steps longer than the shortest trees.

A strict consensus of these trees is shown in fig. 6. Apart from the position of Agyrtidae (sistergroup of Leiodidae rather than Leiodidae + Hydraenidae + Ptiliidae) and changes in the position of certain taxa within the Staphylinid group (here clade 65) this tree is identical with the preceding trees.

Discussion

Although the analyses outlined above resulted in a quite low number (9) of equally most parsimonious trees, and the strict consensus of these is very well resolved, there are several properties about these trees that need commenting. That is, the relationship of taxa within the "staphylinid group" (fig. 2, clade 67) as suggested by this analysis may be problematic, primarily because it involves many homoplasies and most subclades are supported by few indicated apomorphies, most of which must be considered more-or-less weak characters. This was also illustrated in the initial analyses (with now discarded characters included), where slight changes in the character matrix resulted in drastic changes in tree topology within the "staphylinid group".

One of the more curious features of this tree is the position of the Micropeplinae, Dasycerinae and Pselaphinae ("Pselaphidae" auct.), here referred to collectively as the "pselaphine group" (fig. 2, clade 52). These subfamilies have generally been regarded as closely related to Proteininae and Neophoninae (fig. 2, clade 48, possibly particularly Neophoninae) of the "omaliine group" (cf. fig. 2, clade 49), on the basis of atrophied spiracles on abdominal segments 4-6 (char. 44). Moreover, except for Micropeplinae, members of the pselaphine group have (like the entire "omaliine group") paired gland openings at the anterior margin of sternum 8 (char. 48). The latter feature is known otherwise only in Empelidae, which has been considered part of this assemblage by some authors, rather than having the isolated (more basal) position as indicated in the cladogram (fig. 2). Hence, this cladogram may not be the most satisfactory alternative and should not be immediately accepted.

In order to constrain the "omaliine group" as currently defined (i.e., including the pselaphine group and Empelidae), one would have to assign relatively high weights (7 and 4, respectively) to both of these characters (44 and 48) simultaneously. Although they may deserve special attention, the same might be true for several other characters used in this analysis, and I find no justification for assigning a higher weight only to these two particular characters. Therefore, trees based on such assumptions are rejected and not discussed in further detail.

A more fundamental question is whether the shortest tree(s) is actually the most reliable estimate of a phylogeny. Although such trees are often treated in this way, I find their reliability debatable. Admittedly, these trees require the lowest number of extra "ad hoc" hypotheses about character changes, but only on the premise that all characters are considered of equal reliability (weight). As discussed above in the section on "Definition and selection of characters" I find no justification for regarding all characters of equal importance (weight). And it must be realized that assuming equal weight of all characters is just as much a hypothesis of weighting as assuming different weights of different characters.

Hence, the most fundamental question actually seems to be whether all characters can be regarded as equally reliable or if some are more reliable than others, i.e., whether they deserve equal or different weights. Not least because of the very nature of characters, i.e., as highly subjectively defined features, I find it hard to believe that they could successfully be treated as equally reliable. Rather, I believe that characters should be given weight on the basis of their distribution and degree of homoplasy as revealed in the most parsimonious cladograms they produce. For this reason I regard the shortest trees to be inferior compared to trees resulting from "successive" or "implied" weighting. Under this assumption I find it to be of minor importance, if a tree based on differently weighted characters is some steps longer than the shortest possible tree, because the two alternatives relies on different starting hypotheses about weighting of characters.

Regarding the two trees produced by "successive" and "implied" weighting, respectively (figs. 5, 6), they differ only in the position of some taxa within Staphylinoidea. One noteworthy property of the tree resulting from "implied weighting" is that the "omaliine group" of staphylinids (discussed above) appear as a monophyletic taxon, except that Empelidae is still excluded from the group and indicated to have a relatively basal position within the staphylinid group of Staphylinoidea. There are, however, some peculiar features of this tree that seem to make it less preferable than that resulting from the PAUP-analysis using successive weighting, e.g., the relatively basal position of Phloeocharinae (outside Staphylinidae in the current sense) and the distant position of Oxyporinae and the Stenine group, as well as of Pseudopsinae and the Staphylinine group.

Phloeocharinae is usually regarded as closely related to (or part of) the tachyporine group Staphylinidae, and its strongly abbreviated elytra (char. 67) and well sclerotized abdominal terga 3-8 (char. 47) having no wing folding patches (char. 46) are all typical staphylinid features indicating that a position "below" Apateticidae and Silphidae may be doubtful. It is, however, probably still a fairly "primitive" group of staphylinids (as indicated in the "successive weighting"-tree, fig. 5).

The distant position of Oxyporinae and the Stenine group of staphylinids as indicated in the "implied weighting"-tree is also somewhat surprising and in conflict with current hypotheses. These groups share several unusual derived features which I find more likely to be synapomorphies that convergences, e.g., absence of a sharp lateral canthus on pronotum (char. 21), fused mesosternum and mesepisterna (char. 31), and broad, flattened female gonocoxites (char. 85).

Furthermore, the distant position of Pseudopsinae and the Staphylinine group of staphylinids (in the "implied weighting"-tree) is debatable. Although there has been some uncertainty concerning the exact relationship of the Pseudopsinae, they have recently been found to share at least one unique larval feature which suggest them as being the sister group of the Staphylinine group associated with the within Staphylinidae, i.e., the (completely fused) galea and lacinia articulated to the maxilla (Newton, 1990; Lawrence and Newton, 1995).

The main objection to discard the "implied weighting"-tree in favor of the "successive weighting"-tree seems to be that it will imply the rejection of a close relationship between the staphylinid subfamilies currently referred to the "omaliine group". The principal derived feature supporting monophyly of this group, i.e., presence of a "sternum 8 gland" (char. 48), would indeed seem to be a reliable autapomorphy. However, since neither the implied weighting nor the successive weighting indicate that Empelidae (with the same or at least very similar "stenum 8 glands") is closely related to the other taxa currently included in the "omaliine group", this feature may not be as unique as currently assumed. It is still possible (though less parsimonious), however, that such glands have evolved only once, but then one would have to assume that they have been lost again several times.

In conclusion, although the successively weighted PAUP tree may be less preferable in a few regards, it is found to be the one that presents the overall best estimate of phylogenetic relationships (the statistics of this tree are given above, those of the characters are given in the appendix). It might also be argued that the higher number of extra steps required to explain the "implied weighting"-trees may make these trees slightly inferior to the PAUP tree (though this may not necessary be relevant). Hence, the following phylogenetic discussion is based on an evaluation of this tree.

The preferred cladogram, as discussed so far, is in principle an unrooted tree (in the above discussion of this and other trees it was assumed that the root lies outside the Staphyliniformia). As mentioned in the introduction, recent evidence is in favour of the hypothesis that Polyphaga is the sistergroup of the other three suborders of beetles. Several characters of the hindwings were listed by Kukalová-Peck and Lawrence (1993) in support of this (I refer to their paper for a complete list of characters and a discussion of these matters), but have not been included in the present study. For this reason, the phylogenetic relationship of Archostemata, Myxophaga, Adephaga and primitive Polyphaga (Derodontidae, Eucinetidae) revealed by the present analyses differ slightly from the relationship of the same groups suggested by Kukalová-Peck and Lawrence (l. c.). However, because of the inclusion of other characters specifically relating to basal coleopteran phylogeny, the positions of taxa representing other basal coleopteran lineages are assumed to be fairly reliable (given the taxa available, at least). This may be of some importance because changes in the position among outgroup taxa may affect the position of the ingroup as well as topology of relationships among ingroup taxa. This may emphasize the importance of using more than one outgroup and treat them in the same way as taxa initially categorized as ingroups (Nixon and Carpenter, 1993).

Based on the hypothesis that Polyphaga is the sistergroup of Archostemata, Adephaga and Myxophaga (which is not contradicted by the present analysis), the root of the preferred cladogram is attached between the nodes 69 and 70. The rooting of the tree at this point is found to be the most pertinent choice; it also seems to provide the most adequate explanation for characters in addition to those of the hindwings (see below).

Evaluation of preferred cladogram

The following discussion of the phylogeny and character changes is based on the cladogram shown in fig. 5 (rooted as described above). It will primarily focus on the phylogenetic relationships of the taxa included in the "hydrophiloid lineage" (= Staphyliniformia incl. Scarabaeoidea, clade 67). Unambiguous character changes are indicated with an asterisk (*). The evaluation of the cladogram is divided into four subsections: 1) a brief outline of the outgroup taxa; 2) an evaluation of the clades within the hydrophiloid lineage; 3) an evaluation of terminal taxa within the hydrophiloid lineage; and 4) an evaluation of the characters.

Outgroups

The selection of outgroups has already been discussed and partly evaluated in a previous section. In the present section, I have merely listed characters that were indicated by the present analysis as possible autapomorphies, but a further evaluation of the outgroups is considered to be beyond the scope of this study. It must therefore be emphasized that these lists are probably more-or-less incomplete, because they mainly include characters that have been selected as potentially relevant for phylogenetic reconstruction within the Staphyliniformia. Moreover, since the number of examined outgroups is limited, and their inter-relationships may not be satisfactorily resolved (see introduction), it is possible that some of the indicated apomorphies given below are not valid for the particular outgroups examined here.

CLADE 70 (Archostemata, Myxophaga and Adephaga). – The monophyly of Archostemata, Myxophaga and Adephaga and the sistergroup relationship between these and the Polyphaga has recently been suggested on the basis of characters in the hindwing (Kukalová-Peck and Lawrence, 1993). This hypothesis is followed here and the present cladogram was rooted accordingly (as described in the previous section). Among the characters examined in the present study, the absence of cervical sclerites in the adults (7:1) is indicated as a possible autapomorphy for the present clade. Moreover, the hindwing has a distinct abrupt medial hinge (68:0) at the point where the medial bar has a weak zone in some primitive Polyphaga (e.g., *Eucinetus*, here also coded as 68:0). Crowson (1981) considered cervical sclerites to have been lost in the coleopteran ancestor and secondarily developed in Polyphaga, but it seems more likely that the cervical sclerites of Polyphaga are homologous with those of other insects. The abrupt medial hinge of the hindwing was regarded as apomorphic by Kukalová-Peck and Lawrence (1993). A few characters (no. 66, 100, 111) might be added to the list of apomorphies, but must remain dubious at present (cf. clade 69).

CLADE 71 (Archostemata + Adephaga). – A sistergroup relationship between Archostemata and Adephaga was suggested by the present analysis on the basis of the following possible synapomorphies: Mandibles without mola (9:1), mesothoracic spiracles concealed (28:0), laterosternites of 2nd abdominal segment distinct (37:1, misleading), first abdominal ventrite without transverse ridge delimiting metacoxal cavities (52:1), larval galea articulated to lacinia (104:0). It is uncertain if the mandibles were exposed or concealed (8:01), and whether an acute intercoxal process (51:0) was present at the base of this clade. The indication that 6 rather than 5 segments in the legs of larvae (112:0) should be a synapomorphy for Archostemata and Adephaga is undoubtedly erroneous, and the lower number in Myxophaga and Polyphaga is a derived feature, which has evolved independently in the latter two. All characters suggested here as possible synapomorphies of Archostemata and Adephaga seem to be quite weak and are in conflict with more substantial evidence of the hindwings, indicating that it is more likely that Adephaga and Myxophaga are sistergroups, and that the Archostemata is the sistergroup of both these suborders (cf. Kukalová-Peck and Lawrence, 1993).

CLADE 37 (Adephaga). – Among the characters examined in the present study, the following were indicated as possible autapomorphies for the Adephaga, but it must be emphasized that the list of characters is incomplete. At least some of the characteristics are well established adephagan autapomorphies, but a closer examination of the general significance of the characters is beyond the scope of this study. Possible apomorphies are: procoxal fissure closed, trochantin concealed (24:1), mesocoxal fissure closed, trochantin concealed (33:1), posterior coxae transverse (59:0; not clearly apomorphic), basal piece of aedeagus absent (81:2), styli absent (86:2; probably, but not clearly apomorphic), fronto-clypeal suture absent in larvae (93:1; probably, but not clearly apomorphic), dorsal ecdysial lines of larval head with basal stem (94:0; not clearly apomorphic), labrum fused to head capsule in larvae

(97:1; not clearly autapomorphic), larval mandibles without molar area (99:1), larval ligula absent (109:1).

CLADE 69 (Polyphaga). – Among the characters examined in the present study, the following were indicated as possible autapomorphies for the Polyphaga. Most of them have been established as such by previous authors. In regard to the interpretation about character polarity, I have relied on current hypotheses, because no outgroup for the entire Coleoptera has been included in this study and the Polyphaga seems to be the sistergroup of other Coleoptera. It is emphasized that the list of characters is incomplete: Pronotum with accessory posterior ridge (below posterior margin), serving as a locking device against the elytral bases (22:1), propleuron invaginated in prothorax (cryptopleuron) and often fused with the trochantin (23:0), oblongum cell absent (75:1), larval leg with no more than 5 segments (112:1, convergent in Myxophaga, cf. clade 71). The interpretation of the following characters is dubious. They may be listed as apomorphies for the Polyphaga, but it is equally likely that their alternative character states are a synapomorphic for Archostemata, Myxophaga and Adephaga (clade 70): Ventral face of elytra with medio-lateral binding patch (66:0<1), larval mandible with prostheca (100:0<1), sensory appendage of penultimate antennal segment in larvae on anterior (inner) side of the segment (111:0<1); the same is probably true for the transverse shape of the posterior coxae (59:0<1).

CLADE 68 (Derodontidae + hydrophiloid lineage (clade 67)). – The sistergroup relationship between Derodontidae and the hydrophiloid lineage indicated by the present analysis is only supported by two possible synapomorphies: Hypomeron with a mesally directed postcoxal process on each side (25:1), and hindwing without medial hinge (or weak zone) (68:0). These characters are in conflict with more substantial evidence for a closer relationship between Derodontidae, Eucinetidae and remaining Polyphaga (i.e., excl. the hydrophiloid lineage), collectively referred to as the "eucinetoid lineage" (cf. Kukalová-Peck and Lawrence, 1993).

OMMATIDAE/CUPEDIDAE (ARCHOSTEMATA). – Adult characters: head without distinct frontoclypeal suture (2:2; not clearly apomorphic; suture sometimes grooved), neck constricted well behind eyes (3:2), gular sutures indistinct (6:2), mandibles exposed (8:0; not clearly apomorphic, cf. clade 71), mesocoxal cavities not sharply demarcated posteriorly (34:1), first ventrite without intercoxal process (51:1; not clearly apomorphic; cf. clade 71), anterior coxae not projecting (57:0). – Larval characters: first instar larva without cephalic egg bursters (91:0; although this is not clearly apomorphic, the distribution of such egg bursters among other groups of beetles, may well justify the assumption that they were present in the coleopteran groundplan), abdomen largely membranous, without well defined terga and sterna (114:1).

ANNOTATIONS TO CHARACTERS: *Tetraphalerus* (Ommatidae) examined; some characters also examined in *Priacma* (Cupedidae); larval characters are cupedid (after Lawrence, 1991). – 2. Frontoclypeal suture indistinct in *Tetraphalerus* (grooved in *Priacma*). – 11. Character state not determined (maxilla only with single lobe). – 23. Prosternum and hypomeron contacting each other anteriorly in *Tetraphalerus* (completely separated by propleuron in *Priacma*). – 26. Prosternum with very short intercoxal process in *Tetraphalerus* (large process in *Priacma*). – 37. Laterosternite 2 distinct, but fused to 3rd. – 46. Abdomen with wing folding patches on tergum 7 only. – 57. Anterior coxae weakly projecting in *Tetraphalerus* (not projecting in *Priacma*). – 58. Mesocoxae slightly elongate. – 60. Hind coxae with excavate posterior margin into which femur fits, but without "coxal plate". – 68. Hindwing medial hinge weak, very near proximal crossvein delimiting oblong cell. – 91. Larva: 1. instar cephalic eggbursters apparently absent (Cupedidae: Crowson, 1981). – 113. Larva: 1. instar thoracic/abdominal eggbursters apparently absent (Cupedidae: Crowson, 1981).

MICROSPORIDAE (MYXOPHAGA). – Adult characters: left mandible with movable appendage on inner face (10:0), apical (4th) segment of maxillary palpi much smaller than penultimate (12:1), antennae inserted dorsally on head (17:0), with cupuliform segment 8 (18:1) and 3-segmented club (19:2), mesosternum fused to episterna (31:1), metepisterna concealed (35:1), inflexed dorsal portion of abdominal sterna without microtrichia (54:1; probably, but not clearly apomorphic), tibiae without distinct apical spurs (55:1), tarsi very thin, with basal segments very small and somewhat retracted into tibial apices (56:1), middle coxae transverse (58:1), hindwing without anal lobe (72:1), only 2 veins posterior to medial bar (74:2) and no wedge cell (76:1); adults are at least "sub"-aquatic (119:1). – Larval characters: head hypognathous (90:1), with only 4 stemmata on each side (96:2) and labrum apparently fused to head capsule (97:1; probably, but not clearly apomorphic), legs with only 5 segments (112:1) (see clade 71), 10th abdominal segment with 3 pairs of large hooks on eversible anal lobes (118:4).

ANNOTATIONS TO CHARACTERS: 11. Character state not determined (maxilla only with single lobe). – 14. Character state not determined (labial palpi only 2-segmented). – 23. Propleuron visible externally, separating pronotum (hypomeron) from prosternum, but also with invaginated part. – 26. Prosternal intercoxal process present, somewhat T-shaped (but, like entire prosternum, very short). – 46. Abdomen with wing folding patches on terga 4-7. – 57. Anterior coxae only moderately projecting. – 60. Hind coxae with excavate posterior margin and large "coxal plate". – 63. Tarsi apparently 5-segmented, but basal 4 segments very short, indistinctly demarcated and partly retracted into tibial apex; apical segment long and thin. – 84. Female tergum 9 not distinct (apparently divided dorsally). – 86. Female gonocoxites extremely small and short, situated mesally to tridentate lateral "lobes" of tergum 9. – 94. Larva: epicranial stem indistinct. – 115. Larva: spiracles present on abdominal segments 1-8, forming vesicular gills. – 119. Adult at least "sub"-aquatic (larvae aquatic, judging from presence of gills).

GYRINIDAE (ADEPHAGA). – Adult characters: frontoclypeal suture grooved (2:0), mandibles concealed when abducted (8:1; not clearly apomorphic, cf. clade 71), antennae 9-segmented (16:2) (not a basal feature for the family), with 7 distal segments forming an elongate club (19:5), procoxal cavities closed internally (27:1), abdominal segment 8 everted so both tergum and sternum are exposed (40:1), first ventrite not carinate (not even between posterior coxae) (50:2) and with low rounded intercoxal process (51:1; not clearly apomorphic, cf. clade 71), middle coxae transverse (58:1), ventral face of elytra with sublateral ridge or lamina posteriorly (64:2), female gonocoxites broad and flattened (85:2), valvifers apparently absent (membranous?) (87:1); adult (and larva) aquatic (119:1). – Larval characters: maxillary palpus 4-segmented (106:1), abdomen largely membranous, without distinct terga and sterna (114:1, probably, but not clearly apomorphic), 10th segment with two pairs of large hooks on eversible anal lobes (118:2).

ANNOTATIONS TO CHARACTERS: Primarily based on *Gyrinus* sp., unless otherwise mentioned; larval characters are general gyrinid characters (after Spangler, 1991). – 16. Antennae 9-segmented (not representing primitive condition for Gyrinidae, which primitively have 11 segments (Holmen, 1987). – 22. Pronotum without accessory ridge (though laterally with vertical portion "beneath"/inside posterior corners). – 23. Prosternum separated from hypomeron by the large exposed propleuron (except at a single point at anterior margin). – 46. Abdomen with wing folding patches on posterior portions of terga 3-7 (microtrichiae somewhat posteriorly directed). – 67. Elytra hardly truncate, but not covering segment 8. – 72. Hindwing apparently with jugal lobe, but lobe not demarcated from rest of wing. – 76. Hindwing wedge cell confluent with basal cell. – 77. Male tergum 9 very reduced (membranous), only a small sclerite posteriorly on each side. – 104. Larva: galea palp-like, 2-segmented. – 111. Larva: sensory appendage on penultimate antennal segment apparently absent. – 115. Larva: spiracles absent (filamentous gills), except on abdominal segment 1-3 in last instar larvae.

TRACHYPACHIDAE (ADEPHAGA). – Adult characters: mandibles exposed (8:0; not clearly apomorphic, cf. clade 71), prosternum with well developed intercoxal process widened apically (26:2), abdominal sternum 2 visible on each side of posterior coxae (49:1), basal ventrite with acute intercoxal process (51:0; not clearly apomorphic, cf. clade 71), ventral face of elytra with extensive lateral binding patch for its entire length (66:0), aedeagus everted asymmetrically from the abdomen (79:1), female gonocoxites long, narrow and cylindrical (85:1; not clearly apomorphic). – Larval characters: lacinia absent (103:1), abdominal segment 9 with 1-segmented urogomphi (116:1). – The presence of cephalic egg bursters in first instar larvae (91:1) (not known for Trachypachidae, but recorded from Carabidae) may be a plesiomorphic feature, see also under Archostemata).

ANNOTATIONS TO CHARACTERS: Primarily based on *Systolosoma* sp. (adult characters), unless otherwise mentioned; larval characters are those of *Trachypachus* (after Lindroth, 1960) or, when mentioned, general carabid characters. – 22. Pronotum without accessory ridge (though laterally with vertical portion "beneath"/inside posterior corners). – 23. Prosternum separated from hypomeron by the large exposed propleuron (except at a single point at anterior margin). – 46. Abdomen with wing folding patches on terga 6-8 (only on rather narrow posterior portion on tergum 6). – 60. Hind coxae with excavate posterior face and small "coxal plate" mesally. – 72. Hindwing apparently with anal lobe, but lobe not demarcated from rest of wing. – 76. Wedge cell confluent with basal cell. – 89. (General carabid character, not described specifically for *Trachypachus*). – 91. Larva: 1. instar with frontal eggbursters (general carabid character: Emden, 1946; Crowson, 1981). – 102. (General carabid character, not described specifically for *Trachypachus*). – 104. Larva: galea palp-like, 2-segmented. – 112. (General carabid character, not described specifically for *Trachypachus*). – 113. Larva: 1. instar without thoracic or abdominal eggbursters (general carabid character; Emden, 1946; Crowson, 1981).

EUCINETIDAE (POLYPHAGA). – Adult characters: frontoclypeal suture grooved (2:0), mesosternum narrow anteriorly (30:1), mesocoxal fissure closed (33:1), abdominal segment 8 everted so both sternum and tergum are exposed (the latter concealed by the elytra, though) (40:1), inflexed dorsal portion of abdominal sterna without microtrichiae (54:1; apomorphic status dubious), ventral face of elytra with sublateral ridge or lamina before middle (64:1), tergum 9 of male and female with lateral sclerites joined dorsally by a narrow anterior bridge (77:1, 84:1), gonocoxites moderately long, narrow and rather cylindrical (85:1; not clearly apomorphic). – Larval characters: epistomal suture absent (93:1; apomorphic status dubious), dorsal ecdysial lines with basal stem (94:0; apomorphic status dubious), head with only 5 pairs of stemmata (96:1).

ANNOTATIONS TO CHARACTERS: Adult characters based on examination of *Eucinetus haemorrhoidalis*; larval characters are after Lawrence (1991), unless otherwise mentioned. – 3. Eyes sitting dorsally but reaching sides of head where they are delimited by a sharp canthus from the ventral face of head; viewed from certain angles in ventral view head could appear as abruptly narrowed immediately behind eyes, but the general appearance (dorsal view) is "head not constricted". – 23. Prosternum contacts hypomeron (just below, inside body cavity is a well developed cryptopleuron). – 39. Abdomen with all 10 terga exposed, when elytra are removed (tergum 9 very short, tergum 10 large). – 46. Abdomen with wing folding patches on terga 7-8 (but microtrichiae directed posteriorly rather than mesally). – 60. Hind coxae with deeply excavate posterior face and large "coxal plates" concealing femora in repose. – 68. Medial bar of hindwing with weak zone distally (?primitive coleopteran (polyphagan) feature). – 71. Hindwing with very weak costal hinge, distal to radial cell. – 76. Hindwing wedge cell present, but partly open on anterior face. – 87. Valvifers apparently present, but only well sclerotized on narrow lateral portion. – 90. Larva: head prognathous (or somewhat hypognathous). – 97. Larva: labrum free (or sometimes partly fused to head capsule). – 100. Larva: prostheca present, a blunt fixed hyaline lobe (seldom apparently absent). – 111. Larva: sensorium of penultimate antennal segment apparently in anterior face (cf. Bøving and Craighead, 1931: plate 26A).

DERODONTIDAE (POLYPHAGA). – Adult characters: head with constricted neck well behind eyes (3:2) and a pair of ocelli (4:0) and interocular grooves (5:0) on frons, antennae with more-or-less well defined 3-segmented club (19:2), tibiae without distinct apical spurs (55:1), hindwing with only 3 veins posterior to medial bar (74:1). – Larval characters: mandibles with penicillus at mesal edge (101:1), spiracles annular-biforous (115:2), pair of undivided (fixed) urogomphi present (116:1). – The presence of cephalic egg bursters in first instar larvae (91:1) may be a plesiomorphic feature, see also under Archostemata).

ANNOTATIONS TO CHARACTERS: Adult characters primarily based on examination of *Laricobius erichsoni*; larval characters are general derodontid characters (after Lawrence, 1991). – 2. Frontoclypeal suture fine in *Nothoderodontus* and *Peltastica*, absent in *Laricobius* (probably secondary). – 9. Mandibles with narrow mola. – 19. Antennae almost gradually thickened apically, but with suggestion of 3-segmented club (in *Peltastica* with distinct 3-segmented club). – 28. Mesothoracic spiracles apparently exposed (difficult to identify). – 58. Mesocoxae almost globular (slightly more transverse in *Peltastica*). – 59. Hind coxae rather transverse, but with latero-caudal portion narrow and vertical. – 60. Hind coxae with excavate posterior face (but not forming large "coxal plate"). – 91. Larva: 1. instar with frontal eggbursters (*Laricobius*: Crowson, 1981). – 93. Larva: frontoclypeal suture vaguely indicated or absent. – 100. Larva: prostheca present, tooth-like and fixed (reduced in *Laricobius*). – 104. Larva: galea and lacinia primitively well developed; sometimes reduced (*Laricobius*). – 113. Larva: 1. instar without thoracic or abdominal eggbursters (*Laricobius*: Crowson, 1981). – 116. Larva: usually (and primitively?) with pair of fixed (1-segmented) urogomphi (absent in *Laricobius*).

Ingroup clades

In this section each clade within the hydrophiloid lineage (Staphyliniformia incl. Scarabaeoidea) is discussed in turn in a "root-to-terminal branch" sequence. The clades are identified by the numbers attached to the nodes of the cladogram (fig. 5). Supporting apomorphies, as indicated by the present analysis, are listed and commented on.

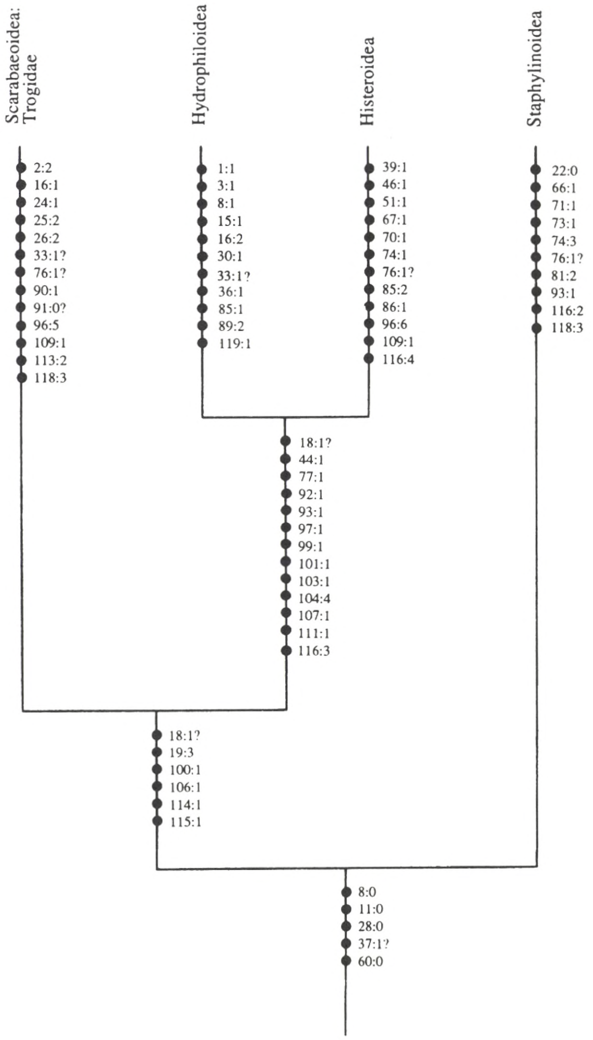

Fig. 7. Phylogenetic relationship and apomorphies of the superfamilies of the "Hydrophiloid lineage" (sensu Kukalová-Peck and Lawrence, 1993), equivalent of "Staphyliniformia" incl. Scarabaeoidea. Unique autapomorphies that were omitted from the analysis are not indicated here (see also text).

CLADE 67 (Hydrophiloid lineage)
[= Staphyliniformia incl. Scarabaeoidea]

This clade (fig. 7) was consistently indicated as a monophyletic group by the present analyses, regardless of how characters were weighted (cf. previous section). It constitue the (paraphyletic) Staphyliniformia and the Scarabaeoidea and is thus equivalent of the Haplogastra (sensu Crowson, 1955). Recently, Kukalová-Peck and Lawrence (1993) referred to the group as the "hydrophiloid lineage" of Polyphaga, a term which I have adopted here. Although it would seem from the sheer number of supporting characters that the group is well defined, it will be seen that all characters are fairly weak (one of them possibly even misleading). However, the probable monophyly of the group was also concluded by Kukalová-Peck and Lawrence (l.c.), who examined a great number of morphological details in the hindwings of Coleoptera, including features not studied in the present analysis. The possible characters that may justify the monophyly of the hydrophiloid lineage are as follows:

8:0*. Mandibles more-or-less exposed, not concealed under labrum when abducted. Although this was indicated by a possible apomorphy for this clade by the present analysis, the character is considered of little significance, because it is subject to some degree of homoplasy, and only few primitive Polyphaga were included in the analysis.

11:0*. Lacinia short, not reaching apex of galea. Like the previous character, and for the same reasons as mentioned there, this character is considered of little significance.

28:0*. Mesothoracic spiracles concealed under the hypomeron (reversals occur within several Staphylinoidea and Histeroidea).

37:1*. Laterosternites of 2nd abdominal segment distinct (indistinct in some subgroups). Although this was indicated as a derived feature within the Polyphaga, it may actually be primitive. The limited number of primitive polyphagan beetles included in the analyses do not provide sufficient basis for a reliable interpretation of character polarity.

60:0*. Posterior coxae with oblique, non-excavate posterior face. This may be the most reliable of the possible apomorphies suggested by the present analysis, since it seems that more-or-less excavate posterior coxae was part of the polyphagan ground plan (cf. Lawrence and Newton, 1982). The excavate posterior coxae of certain staphylinoids (e.g., Ptiliidae) is no doubt a derived feature.

The loss of a wedge cell in the hindwing (76:1) was indicated as an apomorphy for this clade, but since a well developed wedge cell is present in the Hydrophiloidea (see that), it seems more likely that it has been lost independently in Histeroidea, Scarabaeoidea and Staphylinoidea.

It was indicated that articulated urogomphi (117:0) is a basal character for the present clade, in which case it should also be regarded as autapomorphic. However, this would imply that the absence of urogomphi in the Scarabaeoidea should be explained as a secondary loss. It seems equally likely that articulated urogomphi have evolved independently in the Staphylinoidea and the Hydrophiloidea-Histeroidea.

The presence of a prostheca in the larval mandibles (100:0) is – in spite of indicated ambiguity – assumed to be an ancestral feature (i.e. no character change) in the hydrophiloid lineage, independently lost in clade 41 (Scarabaeoidea-Hydrophiloidea-Histeroidea) and clade 65 (staphylinid group).

The hindwing characters examined and regarded as apomorphies by Kukalová-Peck and Lawrence (l.c.) are the following:

a) Radial cell primitively eyelet-like but weakened proximally by the obliteration of the base of RA_{3+4}.
b) Radial bar with a single apical hinge, reinforced by the pinching together of RA_{3+4} with the anterior wing margin.
c) RA_{4} and RP_{1} approaching one another and remaining parallel or fused together to form a Y-shaped support for the anterior apical wing margin and large apical field.

The recognition of the reinforcement of the apical hinge as an autapomorphy for the entire hydrophiloid lineage is in my view somewhat questionable, because it is actually shown only by Scarabaeoidea, Hydrophiloidea and Histeroidea, whereas in Staphylinoids it is rudimentary or absent. If scarabaeoids, hydrophiloids and histeroids form a monophyletic group, as it has been indicated by the present analysis, the reinforcement of the apical hinge is more likely another autapomorphy for that group.

CLADE 41 (Scarabaeoidea + clade 40 (Hydrophiloidea-Histeroidea))
A fairly distinctive and probably well justified monophyletic group, supported by a number of fairly strong apomorphies. Some of the derived features of the clade has been given as synapomorphic for Hydrophiloidea and Histeroidea by authors who did not consider these two closely related to the Scarabaeoidea. The following apomorphies may define the clade:

19:3*. Antennae short, with well differentiated, densely pubescent, 3-segmented club, preclub segments nearly glabrous. Some derived scarabaeoids have the club composed of more than 3 segments, and in others its pubescence may be rudimentary (probably secondary). The character was mentioned as a hydrophiloid-histeroid synapomorphy by Lawrence and Newton (1982), who did not consider these two closely related to the Scarabaeoidea.

100:1. Larval mandibles without prostheca (also in the staphylinid group; probably convergent (see clade 65)).

106:1*. Maxillary palpi of larvae 4-segmented (3-segmented in Passalidae (Scarabaeoidea) and 5-segmented in some Histeridae; probably secondary. Four-segmented maxillary palpi are also found in Gyrinidae, but in none of the other taxa studied here. Though this character occur in a number of other beetles, 3-segmented maxillary palpi seems to be the usual condition among the more primitive polyphagan beetles. Hence, it seems likely that the 4-segmented maxillary palpi is a derived feature for the present clade, as indicated by the present analysis.

114:1*. Abdomen largely membranous in larvae, each segment without single large tergum and sternum (the character was mentioned as a hydrophiloid-histeroid synapomorphy by Lawrence and Newton (1982), who did not consider these two closely related to the Scarabaeoidea).

115:1. Spiracles of larvae biforous. It was initially assumed that the cribriform spiracle-type is an ancestral scarabaeoid characteristic, but the suggested sistergroup relationship between Scarabaeoidea and the the hydrophiloid-histeroid group, indicates that this may not be true, because the cribriform type could have evolved from the biforous type. As some presumedly primitive scarabaeoids (some Geotrupidae, some Trogidae) actually have biforous spiracles, it could be assumed that this type is basal to the Scarabaeoidea, and consequently an autapomorphy of the present clade.

It seems likely that the cupuliform shape of the 8th (morphological) antennal segment (18:1) is another apomorphy of the present clade, though it has earlier been proposed as a synapomorphy of Hydrophiloidea and Histeroidea (e.g., Hansen, 1991b). However, because the selected representative of the Scarabaeoidea (*Trox*) has a simple segment 8, this was not immediately indicated by the present analysis. But several other scarabaeoids (including the presumedly primitive Geotrupidae) have a more-or-less cupuliform segment 8, and it seems likely that this condition is ancestral to the Scarabaeoidea. If this is true, the character must be regarded as a synapomorphy for Scarabaeoidea, Hydrophiloidea and Histeroidea.

Another derived feature – the reinforcement of the apical hinge in the hindwing – was considered an autapomorphy of the entire hydrophiloid lineage (clade 67) by Kukalová-Peck and Lawrence (1993). However, this is not found in Staphylinoidea and it seems more likely to be autapomorphic for the present clade (see under clade 67).

The absence of a larval ligula (109:1) could be interpreted as a basal apomorphy of clade 41 (Scarabaeoidea-Hydrophiloidea-Histeroidea), but this would imply that a ligula in is a secondary structure in Hydrophiloidea, which is found less likely. Probably, the ligula has been independently lost in Scarabaeoidea and Histeroidea (as well as some presumedly derived Hydrophiloidea). Similarly, concealed mesotrochantins (33:1) could be considered as a basal apomorphy of the present clade (with character reversed in Sphaeritidae and Synteliidae), but perhaps more likely the trochantins have become concealed independently in Scarabaeoidea, Hydrophiloidea and Histeridae. Moreover, the appearance of the frontoclypeal suture (char. 2) was indicated as basally ambiguous for this clade (see, e.g., Scarabaeoidea).

CLADE 40 (Hydrophiloidea + Histeroidea)

The two superfamilies comprising this clade have by some authors been referred to as a single superfamily, Hydrophiloidea [s.lat.] (e.g., Lawrence and Newton, 1982), but I have preferred to treat them as separate, because of the profound structural and biological differences between them. However, there is hardly any doubt that they constitute a well defined, and strongly supported monophyletic group, although there has been some disagreement about their sistergroup relationships. Some authors (e.g., Crowson, 1955, 1981) consider the Hydraenidae as the most closely related group of the Hydrophiloidea, but this hypothesis can hardly be maintained, and was rejected by the present analysis. The monophyly of the hydrophiloid-histeroid group is supported by the following apomorphies:

44:1*. Spiracles of abdominal segment 7 atrophied (almost unique) (also mentioned by Lawrence and Newton, 1982). Apparently atropied spiracles 6-8 are found in certain Scydmaenidae (*Cephennium*) (no doubt convergent).

77:1*. Male tergum 9 with lateral sclerites joined dorsally in a narrow bridge anteriorly (also in several staphylinoids; probably convergent).

92:1*. Head with a fimbriate (epistomal) lobe on anteriorly on each side (unique) (secondarily reduced in *Spercheus*).

93:1. Larva without epistomal (frontoclypeal) suture (also found in Staphylinoidea, see that; probably convergent).

97:1*. Labrum fused to head capsule in larvae (also in some members of the staphylinid group; no doubt convergent) (also mentioned by Lawrence and Newton, 1982).

99:1*. Larval mandibles with reduced molar area (also in the staphylinid group; no doubt convergent) (also pointed out by Lawrence and Newton, 1982).

101:1*. Larval mandibles with penicillus at mesal base (unique) (a more distally inserted penicillus is found in Derodontidae; no doubt a convergence) (absent in Spercheidae and Hydrophilidae; probably secondarily lost).

103:1*. Lacinia absent in larvae (possibly indicated by a few apical setae on stipes in some forms) (unique within Staphyliniformia) (also pointed out by Lawrence and Newton, 1982). The lacinia-like appendage of *Spercheus* is regarded as a secondary structure, probably correlated with the specialized filter-feeding habits of this genus.

104:4*. Galea absent in larvae (apparently unique) (also pointed out by Lawrence and Newton, 1982).

107:1*. First segment of larval maxillary palpus with mesal, subapical articulated appendage (unique) (also pointed out by Lawrence and Newton, 1982).

111:1*. Sensory appendage of penultimate antennal segment situated on the posterior (outer) face of the segment (also in the stenine group of Staphylinidae; no doubt convergent).

116:3. Urogomphi present, articulated (possibly 3-segmented). The exact number of segments is impossible to interpret, but it seems likely that at least the hydrophiloid ancestor had 3 segments in the urogomphi (like the primitive hydrophiloid genera *Helophorus* and *Epimetopus*); other hydrophiloids have no more than 2 segments. However, the most primitive histeroids (*Sphaerites* and *Syntelia*) have 4 segments, whereas there are not more than 2 segments in the urogomphi of Histeridae. The presence of articulated urogomphi has been considered a synapomorphy for Hydrophiloidea, Histeroidea and the Staphylinoidea (e.g., Lawrence and Newton, 1982). But, if the Scarabaeoidea is the sistergroup of Hydrophiloidea and Histeroidea (as suggested here), it is equally likely that articulated urogomphi have evolved independently in Staphylinoidea and the hydrophiloid-histeroid group, though the absence of urogomphi in Scarabaeoidea could be due to secondary loss.

Other characters were mentioned as apomorphies for this clade by Lawrence and Newton (1982), but were not included in this analysis, because sufficient comparative data could not be obtained: a) tentorium in larvae with posterior arms attached directly to head, with a short bridge attached well above venter of head; b) final larval instar without ecdysial lines on head; c) pupae without functional spiracles on first abdominal segment.

Certain characters, some of which have been suggested as hydrophiloid-histeroid synapomorphies by previous authors, are of a more dubious nature or may have to be reinterpreted:

An undoubtedly basal characteristic of this clade, is the cupuliform shape of the 8th (morphological) antennal segment (18:1). In the Hydrophiloidea, the cupule has become the actual 6th, 5th or 4th segment due to reductions in the number of antennal segments (presumedly involving the segments proximal to the cupule). Although the cupuliform shape of this segment was indicated as a hydrophiloid-histeroid autapomorphy in the present analysis, it is likely that the apomorphy should also include the Scarabaeoidea (see under clade 41).

It is possible that the absence of a basal stem in the dorsal ecdysial lines of the larval head (94:1) is autapomorphic for this clade, but the presence of a basal stem in Synteliidae and Histeridae complicates the interpretation of the character, and the basal stem may have been independently lost in Sphaeritidae and Hydrophiloidea.

The biforous nature of the spiracles of Hydrophiloidea and Histeroidea (115:1) has been regarded as a synapomorphy for the two superfamilies (e.g., Lawrence and Newton, 1982), and could also be interpreted as such on the basis of the present analysis. However, as the assumed hydrophiloid-histeroid sistergroup, suggested by the present analysis (Scarabaeoidea), may also have biforous spiracles as an ancestral character, it seems likely that the synapomorphy should include all three subfamilies (cf. clade 41).

The short antennae with well-defined, densely pubescent, 3-segmented club of the adults (19:3) and the largely membranous abdomen of the larvae (114:1) were suggested as hydrophiloid-histeroid synapomorphies by Lawrence and Newton (l.c.), but are probably more basal features, shared with Scarabaeoidea (see clade 41).

In contrast to the statement of Lawrence and Newton (1982), adult hydrophiloids and histeroids do not have the 7th abdominal segment invaginated.

CLADE 39 (Histeroidea)

The families of this clade, Sphaeritidae, Synteliidae and Histeridae (fig. 9), constitute a well established and undoubtedly monophyletic group, defined by several strong autapomorphies.

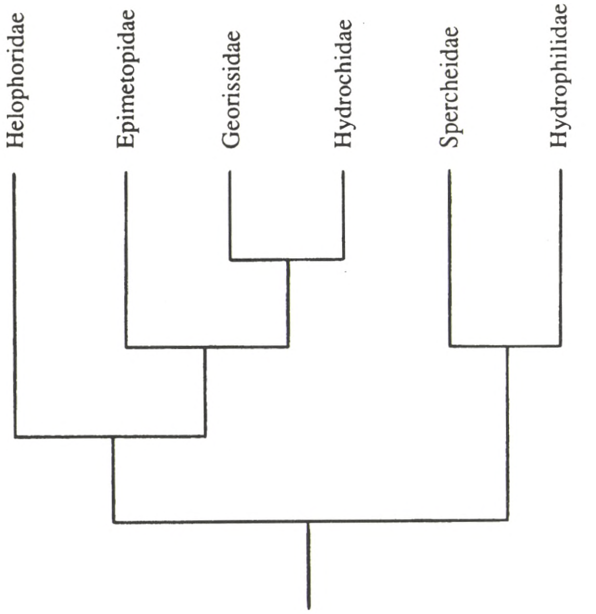

Fig. 8. Phylogenetic relationship of the families of Hydrophiloidea (after Hansen, 1991b); for a discussion of the families, see Hansen (l.c.).

39:1*. 8th abdominal segment completely invaginated within segment 7 (unique).

46:1*. Patches of wing folding setae absent from abdominal segment 7 (but still present on at least some of terga 3-6).

51:1*. First abdominal ventrite with rounded (not acute) intercoxal process.

67:1*. Elytra truncate posteriorly, covering only first 5 or 6 abdominal segments (also pointed out by Lawrence and Newton, 1982).

70:1*. Folded hindwings overlap completely at their apices.

74:1*. Hindwing with no more than 3, often weak, veins posterior to the medial bar.

85:2. Female gonocoxites broad and flattened, scoop-like (also pointed out by Lawrence and Newton, 1982). Broad and flat gonocoxites are also found in Gyrinidae and a few staphylinids (no doubt convergent). The basal condition of this character was indicated as ambiguous for Hydrophiloidea and Histeroidea (clade 40), but it is assumed that the long and slender gonocoxites of Hydrophiloidea and the broad and flat gonocoxites of Histeroidea both evolved from a relatively short, non-flattened type (state 0).

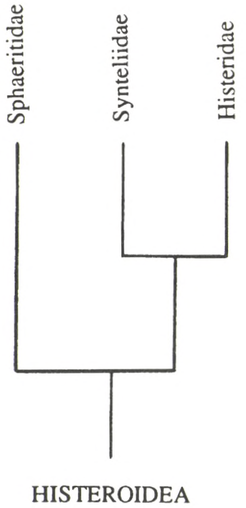

Fig. 9. Phylogenetic relationship of the families of Histeroidea. Apomorphies of the families are given in the text.

86:1*. Styli situated ventrally-mesally on the gonocoxites (unique) (also pointed out by Lawrence and Newton, 1982).

96:6*. Larva without stemmata. Since stemmata are absent in the more primitive members of the Histeroidea (Sphaeritidae, Synteliidae), it is possible that this is ancestral for the Histeroidea. However, some Histeridae have a single stemma on each side of the head (secondary?) (see also under Histeridae). Since, the assumed histeroid sistergroup, Hydrophiloidea, have the presumed primitive number of stemmata (6 on each side), there is hardly any doubt that the reduced number (1 or 0) in Histeroidea is an autapomorphy.

109:1. Larval ligula absent (also in scarabaeoids and some Hydrophiloidea; probably convergent) (see also Scarabaeoidea).

116:4. Urogomphi 4-segmented. Since this is found in both of the presumedly most primitive histeroid families (Sphaeritidae, Synteliidae), it could be regarded as an ancestral histeroid feature. However, Histeridae have no more that 2 segments in the urogomphi (probably the basal condition of the family), and in some members of that family the urogomphi are 1-segmented (or even absent). But the character is difficult to interpret, because the assumed histeroid sistergroup, Hydrophiloidea, seems to have 3-segmented urogomphi as the basal condition (and no histeroids share this number of segments).

The presence of egg bursters on first abdominal tergum in first instar larvae (113:1) and the close association between antennal foramen and buccal cavity in larvae (110:1) could be other histeroid autapomorphies (see under clade 38 (Synteliidae-Histeridae)).

Possibly the absence of a wedge cell in the hindwing (76:1) is another apomorphy, though this was not indicated by the analysis (see under Hydrophiloidea); if so, histeroids are convergent with scarabaeoids and staphylinoids in this regard.

Moreover, exposed mesotrochantins (33:0) could represent a basal apomorphy of the Histeroidea (reversed in Histeridae), but it seems more likely that this is a more basal, plesiomorphic feature (see also Histeridae).

A few more possible autapomorphies were mentioned by Lawrence and Newton (1982), viz. the very compact antennal club, very prominent and acute mandibles, and the carnivorous feeding habits of the adults.

CLADE 38 (Synteliidae + Histeridae)
A distinctive and undoubtedly monophyletic group, as already recognized by previous authors. It is characterized by a number of fairly strong (some unique) apomorphies:

2:2. Frontoclypeal suture not distinct (exceptions occur within a few Histeridae (e.g., *Epierus*), but are probably secondary; the arcuate, transverse groove on the head of some histerids is almost certainly derived). A frontoclypeal suture is assumed to be basally present in clade 41 (Scarabaeoidea-Hydrophiloidea-Histeroidea).

6:1*. Gular sutures confluent.

24:1*. Procoxal fissure closed, trochantin concealed.

47:3. 4th and the following abdominal terga sclerotized, no more than first three terga membranous (this has been further developed in some Histeridae (e.g., *Hister*) and, particularly, Synteliidae, in which also the first three terga have become sclerotized) (see also under Synteliidae).

53:0*. Inflexed portion of abdominal sterna hardly, or very bluntly, demarcated from the ventral portion.

57:0*. Anterior coxae not projecting.

62:1*. Posterior coxae not reaching lateral edges of body.

66:1*. Ventral face of elytra without (or with indistinct) medio-basal binding patch, but normally with more anterior patch (in Histeridae, on mesal face of the sublateral lamina).

102:1*. Cardo apparently absent in the larval maxilla (unique).

110:1. Antennal foramen almost contiguous with buccal cavity, only separated by a narrow membranous strip (unique). This was also pointed out as a synteliid-histerid synapomorphy by Lawrence and Newton (1982). It is possible that the character also should include Sphaeritidae (which could not be examined) and the apomorphy is valid for the entire Histeroidea.

Lawrence and Newton (l.c.) also mentioned the presence of egg bursters on first abdominal tergum in first instar larvae (113:1) and presence of two (rather than three) larval instars as synapmorphies of Synteliidae and Histeridae. However, to my knowledge, neither the presence or absence of such egg bursters nor the number of larval instars has been described for Sphaeritidae, and it is possible that these features are autapomorphic for the entire Histeroidea.

The presence of a basal stem in the dorsal ecdysial lines of the larval head in Synteliidae and Histeridae (94:0) may be another synapomorphy (convergent with Scarabaeoidea), but could also be a more basal feature (see also under Hydrophiloidea).

CLADE 66 (Staphylinoidea)

A well established and well justified monophyletic group (fig. 10). Apart from the inclusion of the Hydraenidae – rejected by some authors, but strongly confirmed by the present analysis – there seems to be general agreement about the systematic limits of the Staphylinoidea as well as its formal rank of superfamily. Its monophyly is supported by a number of apomorphies, some of which (notably char. 73 and 81) have long been recognized as such:

22:0*. Pronotum without accessory ridge (locking device) below posterior margin). A remarkably constant feature (no exceptions were seen), unique among the taxa examined (except for non-polyphagan beetles); the presence of an accesory posterior pronotal ridge seem to be an ancestral character for the Polyphaga.

66:1*. Ventral face of elytra without mediolateral binding patch (apparent reversals occur in some subgroups of this clade, e.g., Hydraenidae).

71:1. Hindwings without "apical hinge" (distal to the radial cell). Hence, there are no hinges involved in the folding of the hindwings in the presumedly more primitive members of the Staphylinoidea. But in more derived staphylinoids a "radial hinge" (proximal to the radial cell) has evolved. The character was pointed out, e.g., by Lawrence and Newton (1982) (see also clade 65).

73:1*. Hindwing without medial loop (unique within the Staphyliniformia incl. Scarabaeoidea).

74:3*. Hindwings with only one vein posterior to the medial bar. The loss of such veins seems not to be irreversible (see under Agyrtidae), and character reversals have taken place in several staphylinoid subgroups.

81:2*. Basal piece of aedeagus absent (membranous). A narrow, transverse, strap-like basal piece occur in certain staphylinoids, e.g., Agyrtidae (*Pteroloma*) and a some members of a few staphylinid subfamilies (e.g., Pseudopsinae, Microsilphinae, Proteininae, Neophoninae), but seems to have evolved independently in these groups.

93:1. Larva without epistomal (frontoclypeal) suture (probably convergent with Hydrophiloidea and Histeroidea). The character was indicated as basally ambiguous for the Hydrophiloid lineage (clade 67), but it is assumed to be more likely that a suture has become independently lost in Staphylinoidea and clade 40 (Hydrophiloidea-Histeroidea), rather than having evolved independently in Scarabaeoidea. However, within Staphylinoidea it is indicated that an epistomal suture has evolved secondarily in Hydraenidae.

116:2*. Urogomphi present, articulated (2-segmented). The presence of articulated urogomphi has been considered a synapomorphy for Hydrophiloidea, Histeroidea and the Staphylinoidea (e.g., Lawrence and Newton, 1982). But, if the Scarabaeoidea is the sistergroup of Hydrophiloidea and Histeroidea (as suggested here), it may be more likely that articulated urogomphi have evolved independently in Staphylinoidea and the hydrophiloid-histeroid group, unless the absence of urogomphi in Scarabaeoidea is explained as due to secondary loss. The absence of urogomphi, as well as 1-segmented (sometimes even fixed) urogomphi, found in some staphylinoids, are undoubtedly derived features within the group.

118:3. Larva with abdominal segment 10

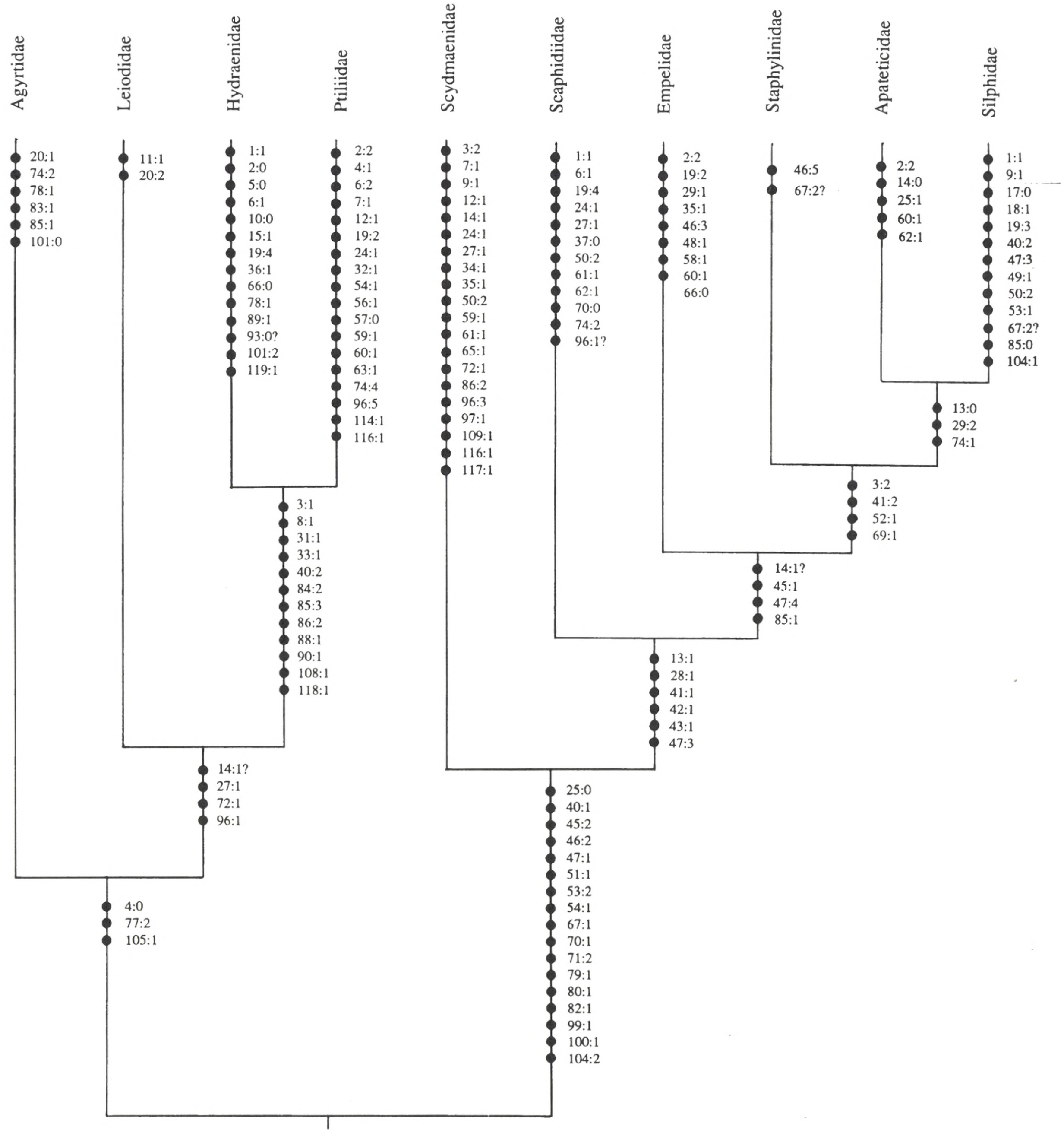

Fig. 10. Phylogenetic relationship and apomorphies of the families of Staphylinoidea (for composition of the families, see text). Unique autapomorphies that were omitted from the analysis are not indicated here (see text).

bearing numerous fine teeth on eversible anal lobes (lost in several Staphylinidae). In Hydraenidae and Ptiliidae the anal lobes are provided with a pair of larger hooks rather than numerous fine teeth (probably a secondary modification). The character was indicated as basally ambiguous in the Hydrophiloid lineage (clade 67) because numerous fine teeth are also present on 10th segment in Scarabaeoidea. However, in that group they are of a different appearance and probably not homologous.

A narrow 3rd segment of the labial palpi (14:1) could be interpreted as a possible autapomorphy but the character is actually basally ambiguous in Staphylinoidea. It might be more plausible to regard a narrower segment 3 as having evloved independently in some groups within Staphylinoidea (e.g., clade 43, Scydmaenidae and clade 63, subsequently reversed in the latter. A very weak character at higher taxonomic levels.

It is possible that internally closed procoxal cavities (27:1) could be apomorphic, but the character is basally ambiguous in the Staphylinoidea and it is equally likely that they have become independently closed in various subordinate groups (e.g., clade 43 (Leiodidae-Hydraenidae-Ptiliidae), Scydmaenidae, Scaphidiidae).

Also the presence of a basal stem in the dorsal ecdysial lines in the larva (94:0) is possibly an autapomorphy, but its significance is difficult to interpret because a similar condition is found in Scarabaeoidea and some Histeroidea (see also under Hydrophiloidea).

It is possible that the absence of a wedge cell in the hindwing (76:1) is apomorphic, though this was not indicated by the analysis (see below under Hydrophiloidea); if so, staphylinoids are convergent with scarabaeoids and histeroids in this regard.

Another derived feature of the staphylinoids, mentioned by several previous authors, is the presence of only four (rather than six) malpighian tubules. Due to the scarcity of well preserved material of several groups, the character was not included in the present study.

CLADE 44 (Agyrtidae + clade 43 (Leiodidae-Hydraenidae-Ptiliidae))

A reasonably well defined group, which was already recognized by Dybas (1976) (as the "Leptinid association"). Its monophyly was refuted by Lawrence and Newton (1982), who considered the supporting characters as plesiomorphies and regarded Agyrtidae and Leiodidae as sistergroups (see also under these families), but the present study seems to confirm the monophyly. It is defined by the following possible autapomorphies.

4:0*. Head with a pair of ocelli. This is likely to be a basal characteristic of the group, although only presumedly primitive members of the families do have ocelli (the complete absence of ocelli in Ptiliidae is probably also secondary). The traditional assumption that presence of ocelli is an overall primitive character, is not necessarily true, and it seems likely that ocelli have evolved independently in this group and some Staphylinidae (Omaliinae and related subfamilies) (unless several independent losses of ocelli are accepted).

77:2*. Male tergum 9 more-or-less entire (but often excavated posteriorly). This is also found in certain Staphylinidae (e.g., Pseudopsinae, the stenine group, Omaliinae), probably convergent.

105:1*. Larval galea with characteristic fringes apically (absent in some Hydraenidae and some Leiodidae, probably due to secondary loss). This feature has been regarded as plesiomorphic by some authors (ancestral to the entire Staphylinoidea), but the present analysis do not provide any support for this hypothesis. Rather, it is indicated that the fringed galea is a uniquely derived feature for the present clade.

The presence of apodemes (tormae) extending from posterolateral corners of labrum (98:0) was indicated as apomorphic by the analysis, but this is usually regarded a primitive feature, and it seems not likely that tormae should have evolved independently in this group. Probably, they have been lost in the staphylinid group (clade 65). Also the presence of a prostheca in the mandibles of larvae (100:0) could be interpreted as an autapomorphy of the present clade because the character was indicated as basally ambiguous for Staphylinoidea (clade 66), but it seems more likely to be a plesiomorphic feature (see also clade 65).

Transverse middle coxae of the adults (58:1) and bifurcate arms of dorsal ecdysial arms in larvae (95:1) could be interpreted as apomorphic for this clade (with reversal in Hydraenidae and Ptiliidae), but it seems to be equally likely that Agyrtidae and Leiodidae are convergent in these respects. Another derived larval feature found in Agyrtidae and Leiodidae was mentioned by Lawrence and Newton (l.c.), viz. the presence of "a unique pair of hypopharyngeal muscle discs". This was considered suggestive of a sistergroup relationship between Agyrtidae and Leiodidae, but may be basal to the present clade (not recorded from Hydraenidae and Ptiliidae). Because of the absence of adequate comparative data, I did not include this character in the present analysis.

It should be mentioned that Lawrence and Newton (l.c.) considered Agyrtidae and Leiodidae more closely related with the staphylinid group on the basis of certain larval characters "shared by at least the more primitive members" of these groups: "numerous frayed setae (fig. 258); long, multiannulate apical segment of urogomphus (fig. 252); multidentate anal lobes". The first two characters were not included in the present analysis because of difficulties in obtaining sufficient comparative data, but at least the frayed setae occur scattered throughout the staphylinid group (cf. Frank, 1991). On the basis of the present analysis it seems that the presence of frayed setae and multidentate anal lobes are likely to be ancestral Staphylinoid features (or that they have developed independently a number of times within the group).

CLADE 43 (Leiodidae + clade 42 (Hydraenidae-Ptiliidae)

A relatively well defined and apparently monophyletic group, which is characterized by at least three possible apomorphies.

27:1. Procoxal cavities closed internally (also in a few other staphylinoids, e.g., Scydmaenidae, Scaphidiidae; probably convergent). The basal condition of this character in Staphylinoidea (clade 66) is ambiguous, but it is tentatively assumed that the internally closed coxal cavities of this clade represents a derived feature.

72:1*. Hindwings without anal lobe. The anal lobe has also been lost in a few other staphylinoids, e.g., Scydmaenidae and some Staphylinidae, probably convergent.

96:1*. Larva with 5 (or fewer) stemmata on each side of the head; similar reductions from the presumedly ancestral number (i.e., 6 pairs) occur in numerous other groups.

It is possible that the narrow third segment of the labial palpi (14:1) is also apomorphic (secondarily wider, e.g., in the hydraenid genus *Limnebius*); a narrow segment 3 is also found in several members of the staphylinid group (clade 65), possibly convergent. However, the character is basally ambiguous in Staphylinoidea (clade 66, see that) and even in the Leiodid group (clade 44) so it is also possible that a narrow segment represents a plesiomorphic feature and that the wider segment of, e.g., Agyrtidae is a secondary feature.

CLADE 42 (Hydraenidae + Ptiliidae)

A very well defined and undoubtedly monophyletic group, as suggested by previous authors (cf. Lawrence and Newton, 1982) and confirmed by the present analysis (see also under Hydrophiloidea). It is characterized by several significant apomorphies, some of which are unique:

3:1*. Head more-or-less constricted immediately behind eyes (some derived Hydraenidae have the constriction well behind the eyes, and in many Ptiliidae the constriction is not very strong).

8:1*. Mandibles with weak apices, concealed when mandibles are abducted (also pointed out by Lawrence and Newton, 1982). Other staphylinoid groups may also have concealed mandibles, but normally not so weak mandibular apices.

31:1*. Mesosternum fused to mesepisterna (in the hydraenid genus *Limnebius* mesosternum is well demarcated from the episterna, but this is undoubtedly a secondary feature).

33:1*. Mesocoxal fissure closed, trochantin concealed.

40:2*. Abdominal segments 8-9 everted (also pointed out by Lawrence and Newton, 1982). These segments are also everted (but still more-or-less retractable) in members of, e.g., the staphylinid group (probably convergent).

84:2*. Female tergum 9 entire (also in a few staphylinid subfamilies; no doubt convergent).

85:3*. Female gonocoxites connate or fused (also pointed out by Lawrence and Newton, 1982).

86:2*. Styli absent or vestigial (also in some members of the staphylinid group; no doubt convergent).

88:1*. Spermatheca with sperm pump (unique).

90:1*. Head of larva somewhat declined (apparently a weak character, only tentatively included here).

108:1*. Apical segment of larval maxillary palpus with apical sensory appendage (unique) (also pointed out by Lawrence and Newton, 1982).

118:1*. 10th abdominal segment of larva with a pair of large hooks on eversible anal lobes (unique) (also pointed out by Lawrence and Newton, 1982). Such hooks are absent in the ptiliid subfamily Cephaloplectinae (probably secondary).

According to Lawrence and Newton (1982), pupae of this group are characterized by having functional spiracles on segment one only.

The globular middle coxae (58:0) could be interpreted as an autapomorphy (reversal within clade 44), but it is also possible that transverse middle coxae have evolved independently in Agyrtidae and Leiodidae. The simple (rather than bifurcate) anterior arms of dorsal ecdysial lines in larvae (95:0) might be a synapomorphy of this clade, but could not be examined in Ptiliidae (ecdysial lines indistinct). It seems, however, more likely that bifurcate arms have evolved independently in Agyrtidae and Leiodidae (see these).

CLADE 65 (Staphylinid group)

[= Scydmaenidae, Scaphidiidae, Empelidae, Apateticidae, Silphidae and Staphylinidae]

A very well defined and undoubtedly monophyletic group, characterized by several very weighty apomorphies, some of which are unique:

25:0*. Hypomeron without distinct processes behind anterior coxae (reversed in some staphylinid subgroups).

40:1*. 8th abdominal segment everted, so both its tergum and sternum are visible. Within Staphylinoidea, this is shared with certain Leiodidae (e.g., Cholevinae), Hydraenidae and Ptiliidae (probably convergent).

45:2*. Abdominal spiracles placed in terga from segments 4 or 5 through segment 8 (this has been further modified in the more derived families of this group (clade 63), which also has the spiracles of segment 3 (or 2-3) are located in the terga, rather than in the tergo-sternal membrane).

46:2*. Abdomen with patches of wing folding setae present on no more than terga 2-5, i.e., reduced from terga 6 and 7 (further reduced in several subgroups of this clade).

47:1. Abdomen with no more than first five segments membranous, 6th and the following terga well sclerotized (this has been further developed in clades 64 and 63). The character was indicated as basally ambiguous for the present clade because it was (like other characters) treated as unordered in the analysis. Actually it seems to present a transformation series of progressively more sclerotized abdominal terga, i.e., first 6 terga basally membranous in clade 66, first 5 terga basally membranous in clade 65 (the present one), first 3 terga membranous in clade 64 and only first 2 terga membranous in clade 63.

51:1*. First ventrite with rounded intercoxal process (or without distinct process); an acute intercoxal process has secondarily evolved in certain Staphylinidae.

53:2*. Inflexed dorsal portion of abdominal sterna articulated to ventral portion. In some derived Staphylinidae, the abdominal sterna are solidly fused with the corresponding terga to form complete rings (e.g., some Paederinae, some Steninae, Osoriinae and some Tachyporinae).

54:1*. Inflexed dorsal portion of abdominal sterna without microtrichia (also in Ptiliidae, no doubt convergent).

67:1*. Elytra truncate posteriorly, covering only about first 5 or 6 segments. More strongly abbreviated elytra have developed in Silphidae and Staphylinidae, whereas several (presumedly derived) Scydmaenidae have longer and non-truncate elytra, which completely cover the abdomen.

70:1. Folded hindwings overlap completely at their apices (the only partially overlapping folded wings of Scaphidiidae is considered to be derived, although it is also possible that the complete overlap of the folded hindwings has evolved independently in Scydmaenidae and the empelid-apateticid-silphid-staphylinid group (clade 63).

71:2. Hindwing with a "radial hinge" (proximal to the radial cell). The development of such a hinge seems to be a unique feature, as already pointed out by Lawrence and Newton (1982). It should be noted that the character was indicated as basally ambiguous for Staphylinoidea (clade 66), but that alternative interpretations of the "radial hinge" are most unlikely, i.e., there is no trace of a hinge in other Staphylinoidea which could suggest that a "radial hinge" was basally present in the superfamily, and the proximal location of the "radial hinge" makes it almost impossible to be considered a derivate of a "apical hinge".

79:1*. Aedeagus everted asymmetrically from the abdomen (also pointed out by Lawrence and Newton, 1982).

80:1*. Median foramen of aedeagus small, ventral rather than basal (there is some disagreement about which side is morphologically ventral. I have followed the interpretation of Brundin (e.g., 1953), but other authors would claim that the median foramen is dorsal; the interpretation is complicated by the fact that the aedeagus of often more-or-less rotated in the abdomen).

82:1*. Median lobe of aedeagus forming large basal bulb with musculature for evagination of internal sac (also pointed out by Lawrence and Newton, 1982).

99:1*. Larval mandibles without mola (the relatively broad mandibular bases in some members of certain staphylinid subfamilies (Piestinae, Oxytelinae, Omaliinae, Aleocharinae) are probably independently derived ("pseudomola")) (also pointed out by Lawrence and Newton, 1982).

100:1. Larval mandibles without prostheca (a "prostheca"-like appendage is present in a few Staphylinidae (Proteininae, some Omaliinae); no doubt secondary). The character was indicated as basally ambiguous for Staphylinoidea (clade 66), but it is considered most likely that a prostheca was basally present in that clade and has been lost independently in the staphylinid group and non-staphylinoid taxa.

104:2*. Galea completely fused to lacinia (not distinct as a separate fixed appendage) (a distinct galea-like appendage is secondarily present in e.g., Silphidae, and some staphylinid subfamilies (e.g., Micropeplinae).

A few more derived characteristics were mentioned by Lawrence and Newton (1982), viz. a compact, usually characteristically asymmetrical, hindwing folding pattern, and certain larval characteristics, such as labrum (if free) divided into three or five sclerites and lacking tormae, and tentorium with posterior arms attached directly to ventral surface of head and bridge directed posteriorly.

In addition to the mentioned autapomorphies of the Staphylinid group closed procoxal fissures (24:1), internally closed procoxal cavities (27:1), basally non-carinate sternum 2+3 (50:2) and well separated posterior coxae (61:1) could be interpreted as derived, but all of these features must then have reversed again in clade 63 (Staphylinid group excl. Scydmaenidae and Scaphidiidae). Hence, it is probably more likely to consider them independently derived in Scydmaenidae and Scaphidiidae (see also under these).

CLADE 64 (Scaphidiidae + clade 63 (Empelidae-Apateticidae-Silphidae-Staphylinidae)

A characteristic and apparently well justified monophyletic group, characterized by a number of relatively strong apomorphies:

13:1*. First segment of labial palpi longer than second (a very weak character, which shows reversals in many taxa of this clade, e.g., Apateticidae, Silphidae, and most members of clades 48 and 59 within Staphylinidae).

28:1*. Mesothoracic spiracles at least partly exposed (spiracles have been secondarily concealed in some Staphylinidae (e.g., the stenine group).

41:1*. Abdominal tergo-sternal membranes very short on 4rd (or 5th) and the following segments (long only on segments 1-3). A further reduction of tergo-sternal membranes occur in clade 62 (Apateticidae-Silphidae-Staphylinidae), in which also segment 3 has very short tergo-sternal membranes.

42:1*. Intersegmental membranes between abdominal segments 3 to 7 long (a few reversals occur in the Staphylinidae, notably the pselaphine group (clade 47)).

43:1*. Intersegmental membranes between abdominal segments 3 to 7 with characteristic "brick-wall" pattern of minute sclerites. This is a very characteristic and almost unique feature (a similar pattern was otherwise oberserved only in the leiodid genus *Colon*). This membrane-structure has been secondarily reduced only in a few staphylinid groups, notably Proteininae and the more derived members of the tachyporine group (Tachyporinae partim, Habrocerinae, Trichophyinae, Aleocharinae). Lawrence and Newton (1982) considered this feature to be a groundplan character of the entire staphylinid group (clade 65), and considered the "clear" abdominal intersegmental membranes of the Scydmaenidae to be a derived feature of that family. But the position of the Scydmaenidae, indicated by the present analysis, suggests that the absence of "brick-wall" membranes in this family is a plesiomorphic feature.

47:3. Abdomen with no more than first three segments membranous, 4th and the following terga well sclerotized (see also clade 65). This has been further developed in clade 63 (Empelidae-Apateticidae-Silphidae-Staphylinidae), in which also the 3rd tergum has become sclerotized (reversals occur in Silphidae and the staphylinid subfamily Dasycerinae).

CLADE 63 (Empelidae + clade 62 (Apateticidae-Silphidae-Staphylinidae)

The monophyly of this clade is supported by three possible apomorphies, of which at least the first two seem to be fairly reliable.

45:1*. Abdominal spiracles placed in terga from segments 2 or 3 through segment 8 (sometimes atrophied on segments 4-6) (see also under the staphylinid group, clade 65). A remarkably constant feature, which seems to have reversed only in the staphylinid subfamily Dasycerinae, in which the terga have become secondarily membranous.

47:4. Abdomen with not more than two first terga membranous, tergum 3 and the following well sclerotized (see also under clade 64); reversals seem to occur only in the staphylinid subfamily Dasycerinae and in Silphidae. It should be noted that a distinction between "sclerotized" and "membranous" terga may sometimes be difficult because the degree of sclerotization varies.

85:1*. Female: Gonocoxites moderately long and cylindrical (rather than short and cylindrical); the relative length of the gonocoxites is somewhat variable and may not be very significant at such high taxonomic level (several reversals occur).

The open procoxal fissures (24:0), internally open procoxal cavities (27:0), basally carinate sternum 2+3 (50:1) and contiguous posterior coxae (61:0), all of which are basal features of this clade, are probably plesiomorphic (see Scydmaenidae).

It is possible that the narrow third segment of the labial palpi (14:1) is also apomorphic (secondarily wider in several groups); a narrow segment 3 is also found in Scydmaenidae and clade 43 (Leiodidae-Hydraenidae-Ptiliidae), possibly convergent. However, the character is basally ambiguous in Staphylinoidea (clade 66, see that) so it is also possible that a narrow segment represents a plesiomorphic feature.

CLADE 62 (clade 45 (Apateticidae-Silphidae) + clade 61 (Staphylinidae))

A relatively well defined and probably monophyletic group, supported by at least four, fairly strong apomorphies.

3:2*. Head with constricted neck (well behind eyes); reversed in some Staphylinidae (notably the tachyporine group). Some silphids have the head constricted immediately behind the eyes, probably a secondary condition.

41:2*. Abdominal tergo-sternal membranes very short on third and the following segments (long only on segments 1-2) (see also clade 64). The character has reversed only in the derived staphylinid subfamily Dasycerinae.

52:1*. First ventrite without well defined cavities for the reception of posterior coxae (apparent reversals occur in certain Staphylinidae, e.g., Solierinae + pselaphine group (clade 48) and some members of the oxyteline group).

69:1*. Folded hindwings only covering first 2-3 abdominal segments (apparently a unique feature, only reversed in a few presumedly derived silphids).

The relatively short elytra, covering only about first 3 segments (rather than 5 or 6 segments) (67:2) may be an autapomorphy of this clade (with reversal in Apateticidae), but was indicated as ambiguous. Hence, it is also possible that the higher degree of abdominal exposure has evolved independently in Silphidae and Staphylinidae.

The absence of cephalic egg bursters in first instar larvae (91:0) is probably a basal feature of this clade, but as the state of the character is unknown in Scydmaenidae, Scaphidiidae, Empelidae and Apateticidae, it is very likely that their absence is basal for the entire staphylinid group (clade 65). However, their presence in some primitive staphylinoids (Hydraenidae) may suggest that cephalic egg bursters is a groundplan character of the Staphylinoidea (i.e., assuming that this can be regarded as a primitive coleopteran feature, see above under Archostemata). The scarcity of available data makes difficult to discuss the character in greater detail.

CLADE 45 (Apateticidae + Silphidae)

A moderately well defined clade, supported at least three possible apomorphies, of which at least one (29) seems to be fairly reliable. It could be mentioned that the two genera that here constitute the Apateticidae, *Apateticus* and *Nodynus*, have been included in the Silphidae by some authors. However, considering the number of taxa that have earlier been referred to the silphids (see that), a previous inclusion of apateticids in that family is not very surprising. I have here preferred to maintain apateticids and silphids as separate families, although they may be sistergroups as indicated here.

13:0*. First segment of labial palpi not longer than second (apparently a reversal within clade 64 (the staphylinine group excl. Scydmaenidae; convergent in clade 48 and clade 59) (a rather weak character).

29:2*. Pro-mesothoracic connecting membrane with a pair of sclerites not associated with mesothoracic spiracles (often also with median sclerite) (convergent in Pseudopsinae).

74:1*. Medial field of hind wing with 3 veins (rather than a single) (apparently a reversal within Staphylinoidea). Since the number of such veins seems to be correlated to some extent with size, the phylogenetic significance may not be great (see also under Agyrtidae).

CLADE 61 (Staphylinidae)

This taxon is more-or-less equivalent of the traditional concept of Staphylinidae, with the main exception that the pselaphines are included as a subfamily of comparatively subordinate position. It could be argued that it is equally justified to include the silphids and apateticids (clade 45) as a subfamilies, since they seem to be the sistergroup of staphylinids as here defined (cf. clade 62), and if they are, the empelids may also be included (cf. clade 63), and also the scaphidiids (cf. clade 64) and the scydmaenids (cf. clade 65). However, though all of these have at various times been suggested to be staphylinids, I have preferred to keep them as separate families, particularly to avoid unnecessary changes in family rank of the Silphidae and Scydmaenidae, which are both habitually quite distinctive. The same can also be said about the Scaphidiidae, Empelidae and Apateticidae for that matter. The phylogeny of the Staphylinidae is still not well understood, and though the monophyly of several subgroups may be reasonably well established, there is still uncertainty about the basal splits within the family. Only a single possible, unambiguous apomorphy seems to support the monophyly of the Staphylinidae (as here delimited), and the family can not be considered adequately defined at present.

46:5*. Abdominal tergum 3 (and the following terga) without patches of wing folding setae. Apparent reversals occur in some groups (some Tachyporinae, Trigonurinae and several Omaliinae and related subfamilies).

The relatively short elytra, covering only about first 3 segments (rather than 5 or 6 segments) (67:2) may be an autapomorphy (convergent with Silphidae), but the basal condition for clade 62 (Apateticidae-Silphidae-Staphylinidae) is ambiguous. It is also possible that the higher degree of abdominal exposure may be basal of clade 62 with subsequent reversal in Apateticidae.

CLADE 50 (Phloeocharinae + clade 49 (Leptotyphlinae-Solieriinae-Micropeplinae-Dasycerinae-Pselaphinae))

A rather weakly defined group, whose monophyly only relies upon two, not very strong apomorphies:

65:1*. Epipleura not demarcated from dorsal elytral portion (reversed in the Micropeplinae-Dasycerinae-Pselaphinae clade); non-demarcated elytra also in the staphylinine group, and Scydmaenidae probably convergent.

72:1*. Hindwings without anal lobe (also in Leiodidae, Hydraenidae, Ptiliidae, Scydmaenidae and Neophoninae; undoubtedly convergent).

CLADE 49 (Leptotyphlinae + clade 48 (Solieriinae-Micropeplinae-Dasycerinae-Pselaphinae))

A rather poorly defined clade. Its possible monophyly may be supported by the following autapomorphies which, however, all show some degree of homoplasy:

5:0. Head with interocular grooves; the absence of grooves in Solieriinae is probably secondary, but it is also possible that the grooves have evolved independently in Leptotyphlinae and the pselaphine group (clade 47).

24:1*. Procoxal fissure closed, trochantin concealed (also in the stenine group and some members of the oxyteline group; probably convergent); trochantin secondarily exposed in Micropeplinae.

33:1*. Mesocoxal fissure closed, trochantin concealed (also in the stenine group and some Osoriinae; probably convergent).

85:3*. Female gonocoxites apparently fused (secondarily separate in Micropeplinae and (?)Solieriinae). There is some uncertainty with regard to the interpretation of what is the gonocoxites in some if the taxa of this clade (others could not been examined), and the character is here only tentatively included among the apomorphies.

86:2*. Styli absent (shared with the stenine and oxyteline groups and some members of the staphylinine group; probably convergent).

116:1*. Urogomphi 1-segmented (articulated in Leptotyphlinae, solidly fixed in the more derived groups of this clade (cf. clade 47)).

A very small apical segment of the maxillary palpi (12:1) and the double paratergites (38:1) could also be apomorphic for the present clade, in which case the two characters have reversed in the pselaphine group (clade 47). It may be more plausible to regard the small segment as well as the double paratergites, found in Leptotyphlinae and Solieriinae, as parallelisms (see also these taxa).

CLADE 48 (Solieriinae + clade 47 (Micropeplinae-Dasycerinae-Pselaphinae))

The subfamilies Micropeplinae, Dasycerinae and Pselaphinae, which form part of this clade, resemble Proteininae and Neophoninae (clade 55) in a number of respects, but as mentioned under the latter, the similarities were indicated as having evolved convergently. A closer relationship between the three first mentioned subfamilies and Solieriinae was suggested by the present analysis and supported by the following possible apomorphies.

2:2*. Frontoclypeal suture not distinct (this is also found in several other staphylinids, and although it is probably autapomorphic for the present clade, the character is relatively weak).

7:1*. Cervical sclerites (apparently) absent. Loss of cervical sclerites is rather unusual among polyphagan beetles, and within Staphylinoidea it seems to be shared only with the Ptiliidae and the Scydmaenidae (probably convergent).

13:0*. First segment of labial palpi not shorter than second (apparently a reversal within clade 64 (Staphylinine group excl. Scydmaenidae); a rather weak character.

52:0*. Basal ventrite with well developed and sharply delimited concavities for the reception of posterior coxae. Such well demarcated concavities are also found in a few other staphylinids (e.g., Piestinae and some Osoriinae, probably convergent), but can hardly be regarded a groundplan character of the family.

The presence of an acute intercoxal process of basal ventrite (51:0) could also be considered an autapomorphy of the present clade, in which case it has been secondarily lost in Micropeplinae. It is perhaps more likely that such a process has evolved independently in Solieriinae and in clade 46 (Dasycerinae-Pselaphinae) (see also these). Similarly, the interpretation of the concealed mesothoracic spiracles (28:0) as a possible apomorphy of the present clade is dubious (see clade 46).

CLADE 47 (Micropeplinae + clade 46 (Dasycerinae-Pselaphinae))
This clade, here referred to as the "pselaphine group", seems to form a relatively well defined assemblage. In addition to the three subfamilies included in the present analysis the clade probably also contain the recently described subfamily Protopselaphinae (see under Pselaphinae and clade 46). Although the group may not possess any uniquely derived features, its monophyly seems to be justified by several reasonably strong apomorphies:

5:0. Frons with a pair of interocular pits; similar small pits are found in Leptotyphlinae (possibly convergent). The character was indicated as basally ambiguous for clade 49 and it is therefore possible that the presence of interocular pits is a basal feature of that clade and has been secondarily lost in Solieriinae.

42:0*. Abdominal intersegmental membranes short (in Dasycerinae the abdominal terga are largely membranous, but the membranes between the sterna are short). Probably the short intersegmental membranes of Proteininae is a convergence).

44:2*. Abdominal spiracles atrophied on segments 4-6. A similar condition is found in Proteininae and Neophoninae (clade 55) and has been considered indicative for a close relationship between the present clade and these subfamilies. However, as explained earlier it is possible that the spiracles have become reduced independently in the two groups (see also under analytical procedure).

55:1*. Tibial spurs absent (or not evident); this is also found in Proteininae, Neophoninae, the stenine group, and a few Oxytelinae (probably convergent).

63:1. Tarsi 4-segmented (the number of segment further reduced in Dasycerinae and Pselaphinae, cf. clade 46). The number of tarsal segments was indicated as basally ambiguous for clade 48 and clade 49, but assuming that reductions in the number of tarsal segments are more likely than an increase in number, the reduced number of segments in the present clade is convergent with reduced number in Leptotyphlinae. It is also most likely that the basal number of segments is different in the two taxa, i.e., 4 in the present clade and 3 in Leptotyphlinae.

65:0*. Epipleura well demarcated from dorsal portion of elytra (reversal within clade 50).

117:1. Urogomphi fixed (not articulated). This is clearly a derived feature, and probably an autapomorphy for this clade (perhaps inclusive Solieriinae whose larvae are not yet known).

It is possible that the absence of an anal lobe in the hindwings (72:1) is also an apomorphy of this clade, but the interpretation is somewhat uncertain, because the wings could not be examined in the indicated sistergroup of this clade, Solieriinae, and because only apterous species of Dasycerinae were available).

CLADE 46 (Dasycerinae + Pselaphinae)
A comparatively well defined and probably monophyletic taxon, supported by several possible apomorphies. Most of the characters are moderately strong, and there are no unique ones among them. Collectively, these characters seem to provide reliable justification for the monophyly of this clade:

26:0*. Prosternum without distinct intercoxal process.

28:0. Mesothoracic spiracles concealed by the hypomeron (apparently also in Solieriinae, probably convergent). Because the character was indicated as basally ambiguous for clade 48 is it also possible that the spiracles were basally concealed in this clade (Solieriinae-Micropeplinae-Dasycerinae-Pselaphinae) and have secondarily become exposed in Micropeplinae.

35:1*. Metepisterna concealed (occasionally, in a few Pselaphinae, very narrowly visible).

48:1*. Abdominal sternum 8 with paired, more-or-less separated (or apparently confluent) gland openings at anterior margin (fig. 121, 122); the absence of such openings in a number of Pselaphinae are believed to be due to secondary losses. Similar gland openings are also found in Omaliinae and allies (clade 56) and in the Empelidae, and have been considered as evidence for a close relationship between these groups (the "omaliine group" sensu Lawrence and Newton, 1982). But as mentioned previously this could not be supported by the present analysis, and it is possible that such gland complex has evolved independently in these groups (see also under analytical procedure).

51:0. First ventrite with an acute intercoxal process (in several derived Pselaphinae the intercoxal process has become broader and more bluntly rounded). An acute intercoxal process is also found in several other staphylinids, e.g., Solieriinae (probably convergent). The character was indicated as basally ambiguous for clade 48, so it is also possible that the presence of an acute intercoxal process is a basal apomorphy of that clade (Solieriinae-Micropeplinae-Dasycerinae-Pselaphinae) and has secondarily become lost in Micropeplinae (as well as in derived Pselaphinae).

The 3-segmented tarsi is probably a further reduction of the 4-segmented tarsi (63:1), which is considered a basal apomorphy of the pselaphine group (clade 47) and, hence, a synapomorphy for Dasycerinae and Pselaphinae. Some derived Pselaphinae have only two segments in the tarsi, but this is undoubtedly a still further reduction.

This clade probably also includes the subfamily Protopselaphinae described by Newton and Thayer (1995) (after the present analysis was done) and considered the sistergroup of Pselaphinae (see that). All the above mentioned possible apomorphies are also valid for that subfamily (except perhaps the acute intercoxal process of the first ventrite, which was not mentioned in the description of the taxon).

CLADE 60 (Tachyporine group + clade 59 (Oxyporinae-Stenine group-Pseudopsinae-Staphylinine group-Trigonurinae-Omaliinae-Microsilphinae-Proteininae-Neophoninae))

A rather weakly defined clade, whose monophyly is only supported by a single, not very strong apomorphy:

118:0*. Larva: Abdominal segment 10 unarmed (rather than with numerous fine teeth or hooks on eversible anal lobes). Also in Dasycerinae, probably convergent.

CLADE 59 (clade 53 (Oxyporinae-Stenine group-Pseudopsinae-Staphylinine group) + clade 58 (Trigonurinae-Omaliinae-Microsilphinae-Proteininae-Neophoninae)

A relatively well supported and apparently monophyletic clade, defined by the following apomorphies:

13:0*. First segment of labial palpi not longer than second (apparently a reversal within clade 64 (the staphylinine group excl. Scydmaenidae; convergent in clade 45 and clade 48) (a rather weak character).

25:1*. Postcoxal processes of hypomera distinct (reversal within Staphylinid group (clade 65), probably convergent with Phloeocharinae, Dasycerinae and Apateticidae (further reversed in the staphylinine group). A rather weak character.

59:1*. Posterior coxae "triangular", i.e., not expanded caudally and laterally; also in Leptotyphlinae, Micropeplinae, Ptiliidae, Scydmaenidae, probably convergent); reversed in Oxyporinae and Neophoninae.

77:2*. Male: Abdominal tergum 9 entire (also Leiodid group (clade 44), no doubt convergent). The character has apparently reversed in Oxyporinae and Proteininae, and is modified in the Oxyteline group. It was not coded for some taxa in which it was ambiguous, e.g. the staphylinine group (entire in Paederinae, divided in Staphylininae) and the variation is greater than immediately indicated.

85:0*. Female: Gonocoxites relatively short (rather than long and narrow) (apparently reversed in Omaliinae, modified in Oxyporinae and the stenine group); relatively short gonocoxites are found in several other groups, e.g., Silphidae, probably convergent.

CLADE 58 (Oxyteline group + clade 57 (Trigonurinae-Omaliinae-Microsilphinae-Proteininae-Neophoninae)

A rather weakly supported clade, defined only by a single unambiguous apomorphy (which could, however, not be examined in Trigonurinae):

29:1*. Pro-mesothoracic connecting membrane with a pair of transverse sclerites in which mesothoracic spiracles are located laterally (also in Empelidae and Micropeplinae, apparently convergent).

It is possible that the presence of an acute intercoxal process on the basal ventrite (51:0) is also autapomorphic (with reversal in clade 56), but the character is ambiguous and impossible to interpret adequately on the present basis (see also the oxyteline group).

CLADE 57 (Trigonurinae + clade 56 (Omaliinae-Microsilphinae-Proteininae-Neophoninae)

A rather poorly supported group whose monophyly relies only upon a single, not very strong character.

46:4*. Abdominal tergum 3 with patches of "wing folding" setae. Although such patches are often considered rudiments of more extensive patches (as found in beetles with fully developed, non-abbreviated elytra and functional hindwings) and have been considered a plesiomorphic condition within the Staphylinidae, the present analysis rather indicates that such patches were absent in the staphylinid ancestor and hence, that the presence of "wing folding" setae in this clade is a derived feature (further developed in Omaliinae and Microsilphinae, in which wing folding patches are normally also present tergum 4).

It is possible that the absence of distinct valvifers (87:1) is also apomorphic, but the character could not be examined in Trigonurinae and may be found only in clade 56).

CLADE 56 (clade 54 + clade 55)
[= Omaliinae, Microsilphinae, Proteininae, Neophoninae]

The subfamilies of this clade seems to constitute a fairly well justified monophyletic group. Some authors (e.g., Lawrence and Newton, 1982; Thayer, 1987; Newton and Thayer, 1995) include the pselaphine group (clade 47) and Empelidae in this assemblage on the basis of atrophied spiracles on abdominal segments 4-6 in the former and paired gland openings anteriorly on sternum 8 in them both. However, as explained earlier (cf. analytical procedure) this hypothesis could not be supported by the present analysis unless these two characters were "a priori" assumed to deserve higher weight than other characters examined in connection with this study. The subfamily Glypholomatini, recently proposed for the formerly omaliine genus *Glypholoma* (not studied here) also belongs to this clade (see under clade 54). The monophyly of the present clade is supported by the following possible autapomorphies.

4:0*. Head with a pair of ocelli. This is almost certainly a basal characteristic of this group, and the absence in a few Omaliinae and Proteininae is due to secondary losses (some proteinines have a single median ocellus). However, the traditional assumption that presence of ocelli is an overall primitive character, can not be confirmed by the present analysis, unless several independent losses are considered more likely (no other member of the staphylinid group have ocelli). Given the present position of the omaliine group, I find it more likely that the presence of ocelli is a derived feature in this particular case.

5:0. Head with interocular grooves (= dorsal tentorial pits); this is also found in other staphylinids, probably convergent. The absence of such grooves in Microsilphinae and a few Omaliinae is probably a secondary feature within this clade. Alternatively (but perhaps less likely) the interocular grooves of Omaliinae and Proteininae-Neophoninae have evolved independently.

48:1*. Abdominal sternum 8 with paired, more-or-less separated gland openings at anterior margin. Similar gland openings are also found in Dasycerinae and some Pselaphinae (clade 46) as well as in Empelidae, but may have evolved independently in these (see also under these groups).

81:1. Aedeagus with strap-like basal piece (not found in Omaliinae, possibly secondary, see also that subfamily). As discussed below under Agyrtidae it is possible that a basal piece is absent (or membranous) in the staphylinoid groundplan and that the presence of a strap-like, sclerotized basal piece in certain staphylinoids should be interpreted as secondary. A similar (strap-like) basal piece is also found in Micropeplinae and some Pseudopsinae (probably convergent).

87:1. Valvifers absent (membranous?). The character could not be examined in the indicated sistergroup of this clade (Trigonurinae), so it is possible that the absence of distinct valvifers is a more basal feature (apomorphy of clade 57?).

It is possible that a "wide" third segment of the labial palpi (14:0) is also apomorphic for this clade, but as the character is basally ambiguous for clades 57-59, the interpretation is is uncertain and it could also be a more basal (plesiomorphic) feature. Also the absence of acute intercoxal process on basal ventrite (51:1) is difficult to interpret, and may be plesiomorphic (see oxyteline group).

CLADE 54 (Omaliinae + Microsilphinae)

The monophyly of this clade is only supported by two relatively weak, possible apomorphies.

46:3*. Abdominal terga 3 and 4 (or 4 alone) with paired patches of "wing folding" setae (except in certain apterous forms, e.g., *Olophrum*, in which the absence is probably secondary). Such patches are often considered rudiments of more extensive patches (as found in beetles with fully developed, non-abbreviated elytra and functional hindwings), and have been considered a plesiomorphic condition within the Staphylinidae. However, the presently indicated position of Omaliinae and Microsilphinae rather suggest that the wing folding patches of these subfamilies represent a derived feature (which has evolved convergently, e.g., in certain Tachyporinae).

67:1*. Elytra covering about first 5 or 6 abdominal segments. It was provisionally assumed that long elytra are a basal feature of the Omaliinae and that abbreviated elytra is secondary within this subfamily. If this is true, the long elytra can be considered a synapomorphy of Microsilphinae and Omaliinae (long elytra are also found in some Proteininae, but may not be basal for that subfamily). However, several Omaliinae do have abbreviated elytra and are habitually "typical" staphylinids, so it is also possible that long elytra have evolved independently in Microsilphinae and part of Omaliinae. It must also be noted that the monophyly of Omaliinae is not well established and that it may turn out to be paraphyletic. The recently proposed subfamily Glypholomatinae (formerly included in Omaliinae and not included in the present analysis) may also belong here (see also under Omaliinae).

CLADE 55 (Proteininae + Neophoninae)

The two subfamilies constituting seem to form a well defined, monophyletic group, defined by at least two possible apomorphies:

44:2*. Abdominal spiracles atrophied and non-functional on segments 4-6 (this is also found in the pselaphinae group (clade 47), probably convergent).

55:1*. Tibiae without distinct apical spurs (in Staphylinidae otherwise only found in the stenine group, the pselaphine group (clade 47), and a few Oxytelinae, probably convergent).

The presence of interocular grooves on the frons (5:0) could be interpreted as a derived feature, but since it is shared with most Omaliinae, it may be a more basal feature (apomorphy for clade 56), indicating that the absence of grooves in Microsilphinae (and a few Omaliinae) is secondary.

The presence of a straplike basal piece in the male genitalia (81:1) could also be interpreted as an apomorphy of this clade (convergent with Microsilphinae), but is perhaps more likely to be an apomorphy of clade 56 with secondary reduction in Omaliinae.

It will be noted that Proteininae and Neophoninae are strikingly similar to Micropeplinae, Dasycerinae and Pselaphinae with regard to the characters mentioned here, and that these subfamilies are often considered closely related ("proteinine subgroup" sensu Thayer, 1987). Although this might actually prove to be true, a close relationship could not be supported by the present analysis, from which it is suggested that the similarities should rather be explained as convergences (see under analytical procedure).

CLADE 53 (Oxyporinae-Stenine group-Pseudopsinae-Staphylinine group)

This clade is equivalent of Lawrence and Newton's (1982) "staphylinine group", except that they also included Leptotyphlinae (and "possibly Scydmaenidae and Silphidae"). A close relationship between clade 53 and the latter three taxa was not supported by the present analysis. The following characters (particularly 97) may support the monophyly of this clade:

74:0*. Medial field of hind wing with 4 veins (rather than a single) (apparently a reversal within Staphylinoidea; the number of veins secondarily reduced in the Stenine group; not examined in Pseudopsinae).

84:1. Female abdominal tergum 9 forming continuous bridge anterior to tergum 10 (probably autapomorphic, but reversed in Oxyporinae as well as in some Staphylininae). An alternative interpretation is that an undivided tergum 9 is plesiomorphic for this clade (i.e., no change of the character) and that the derived condition has evolved independently in the stenine group and in clade 52 (Pseudopsinae + the staphylinine group).

97:1*. Larva: Labrum fused to head capsule (also in a Leptotyphlinae, Pselaphinae, Scydmaenidae and Hydrophiloidea + Histeroidea, probably convergent).

CLADE 51 (Oxyporinae + Stenine group)

A fairly well defined group, whose monophyly is supported by the following, fairly reliable apomorphies:

21:1*. Pronotum without sharp lateral ridge separating dorsal portion from hypomera (also in Leptotyphlinae, Pselaphinae and Neophoninae, no doubt convergent).

28:0*. Mesothoracic spiracles concealed under hypomera (no doubt a secondary feature, i.e., reversal within clade 64 (Staphylinid group excl. Scydmaenidae); also in Solieriinae, Dasycerinae and Pselaphinae, convergent).

31:1*. Mesosternum intimately fused to mesepisterna (also in Neophoninae, Micropeplinae, Ptiliidae and Hydraenidae, no doubt convergent).

85:2*. Female: Gonocoxites relatively broad and flattened (also in Histeroidea, but here of somewhat different appearance, no doubt convergent).

CLADE 52 (Pseudopsinae + staphylinine group)

A comparatively well defined and probably monophyletic taxon, supported by at least one fairly reliable (unique) character.

104:3. Larval galea and lacinia completely fused (mala) and basally articulated to the maxilla (unique).

It is possible that a narrow segment 3 of labial palpi (14:1) is another apomorphy of this clade, but because the character is basally ambiguous for clade 59 and clade 53, this characteristic could also be interpreted as more basal (plesiomorphic).

Ingroup terminal taxa

Principally, the terminal taxa were defined and selected in a way that would justify each of them as being monophyletic. However, some of them lack obvious (unique) autapomorphies and their monophyly may not be strongly supported, so possible autapomorphies depends on the exact relationship to other taxa.

In addition to the possible autapomorphies revealed by the present analysis (listed by their character numbers), certain autapomorphies (mostly unique ones), which were excluded from the analyses, are listed (as "a, b, c, ...", etc.). Furthermore, annotations to certain characters have been summarized under the terminal taxa. Remarks are primarily based on variation (etc.) of the examined species, but also to some extent on data obtained from various literature sources. Each taxon is discussed in turn in the same order as classified in the (following) systematic part.

SCARABAEOIDEA

The scarabaeoids, primarily represented by Trogidae, were originally regarded as an outgroup, but the present analyses indicates that they are more closely related to the Hydrophiloidea and the Histeroidea than these two are to the Staphylinoidea. For this reason, the list of autapomorphies may be somewhat less complete than it is in the other staphyliniform subgroups, though the monophyly of Scarabaeoidea can hardly be questioned. Scholtz (1990) discussed several adult and larval character systems and gave an outline of the evolutionary trends within Scarabaeoidea. The phylogeny was discussed in more detail by Scholtz et al. (1994) and Browne and Scholtz (1995) who presented evidence that the Glaresidae (earlier placed in or near Trogidae) are the most primitive of living scarabaeoids, representing the sister group of all other scarabaeoids. The latter may fall into two major groups, i.e., a "passalid" and a "scarabaeid" lineage (sensu Browne and Scholtz, l.c.). The passalid lineage includes the families usually referred to as more-or-less "primitive" scarabaeoids (Passalidae, Lucanidae, Trogidae, Geotrupidae, etc.), and the scarabaeid lineage includes the taxa traditionally referred to Scarabaeidae.

In addition to certain coxal and tibial adaptations for burrowing, specializations in the venation and folding of the hindwing, lamellate antennal club, and distinctive grub-like, usually C-shaped larvae (e.g., Lawrence and Newton, 1982; Scholtz, 1990; Kukalová-Peck and Lawrence, 1993), the following autapomorphies can be mentioned:

2:2. Frontoclypeal suture not distinct (possibly a trogid apomorphy; many scarabaeoids lack a frontoclypeal suture, but others (e.g., geotrupids, some melolonthines) have a distinct suture). A frontoclypeal suture is assumed to be basally present in clade 41 (Scarabaeoidea-Hydrophiloidea-Histeroidea).

16:1*. Antennae 10-segmented (although it is traditionally assumed that the ancestral scarabaeoid had 11-segmented antennae (as found in some of the more primitive families, e.g., Geotrupidae), the antennae of most of the primitive scarabaeoid families, including Glaresidae, are actually 10-segmented (Scholtz et al., 1994). It is therefore possible that 10 is the ancestral number of antennal segments in Scarabaeoidea).

24:1*. Procoxal fissure closed, trochantin concealed (probably general scarabaeoid apomorphy; only Diphyllostomatidae and Pleocomidae form an exception (Scholtz et al., 1994) but since these families seem to have a somewhat subordinate position within Scarabaeoidea (Scholtz, 1990; Browne and Scholtz, 1995), the exposure of the trochantins in these families may be considered secondary (unlike what Scholtz et al. (l.c.) assumed)).

25:2*. Hypomeron with mesally directed processes, which close the procoxal cavities posteriorly (probably general scarabaeoid apomorphy; the only exception within the superfamily is Pleocomidae, in which the cavities are open posteriorly (Scholtz, 1990), but since this family seems to have a somewhat subordinate position within Scarabaeoidea (Browne and Scholtz, l.c.), its open coxal cavities is probably of secondary nature rather than primitive as claimed by Scholtz et al. (1994)).

26:2*. Prosternal intercoxal process widened apically behind procoxae (probably general scarabaeoid apomorphy).

33:1. Mesotrochantin concealed (possibly convergent with Hydrophiloidea and Histeridae). The character could also be interpreted as basal to clade 67 (Hydrophiloid lineage) with reversal in Sphaeritidae and Synteliidae.

90:1*. Larval head hypognathous (general scarabaeoid autapomorphy).

91:0. The general absence of cephalic egg bursters in first instar larvae of Scarabaeoidea may be considered apomorphic, i.e., if such egg bursters are part of coleopteran ground plan (see also under Archostemata).

96:5*. Larva with not more than a single stemma on each side of head.

109:1. Larval ligula absent (general scarabaeoid autapomorphy). The absence of a ligula could also be interpreted as a basal apomorphy of clade 41 (Scarabaeoidea-Hydrophiloidea-Histeroidea), but this would imply that a ligula in is a secondary structure in Hydrophiloidea.

113:2*. First instar larvae with a pair of egg bursters on metanotum (apparently a general scarabaeoid feature).

118:3. The presence of numerous fine teeth on abdominal segment 10 of larvae is probably also a scarabaeoid autapomorphy. It is also indicated as a basal feature of Staphylinoidea (but here of different appearance) and could therefore be interpreted as basal to the entire Hydrophiloid lineage with reversals in Hydrophiloidea, Histeroidea and some subordinate taxa of Staphylinoidea.

Possibly the absence of a wedge cell (76:1) in the hindwing is another apomorphy, though this was not indicated by the analysis (see below under Hydrophiloidea); if so, scarabaeoids are convergent with histeroids and staphylinoids in this regard.

Some characters, indicated as possible autapomorphies, are of a more dubious nature, and their phylogenetic significance is not quite clear:

The presence of a basal stem in the dorsal ecdysial lines of larvae (94:0) may be an autapomorphy (ambiguous), but is difficult to interpret because it is shared with Histeridae and Synteliidae (see also under Hydrophiloidea).

The presence of apodemes (tormae) extending from posterolateral corners of labrum in larvae (98:0) was indicated as apomorphic by the analysis, but this is usually regarded a primitive feature, and it seems not likely that tormae should have evolved independently in the Scarabaeoidea.

The presence of cribriform spiracles in the larvae (115:3) was initially considered a general and basal feature of the scarabaeoids. However, there are some of the presumedly primitive scarabaeoids, i.e., some *Trox* and some geotrupids, that have biforous spiracles. Since the sistergroup of the scarabaeoids suggested by the present analysis (Hydrophiloidea + Histeroidea) are characterized by having biforous spiracles, it is likely that the Scarabaeoidea also have biforous spiracles as part of their groundplan, so the specialized cribriform spiracles is not autapomorphic for the entire Scarabaeoidea (see also under clade 41).

ANNOTATIONS TO CHARACTERS:
Primarily based on *Trox scaber* (adult characters); larval characters partly based on general description of scarabaeoids (after Carlson, 1991).

1. Clypeus not demarcated, but small judging from antennal insertions.
20. Antennae without periarticular grooves in penultimate segments (but with some enclosed "vesicles" in terminal segment).
44. Abdominal spiracles 1-7 distinct (not distinct on segment 8 in *Trox scaber*, but variable in the family).
72. Hindwings with well developed, but weakly demarcated anal lobe.
76. Hindwing wedge cell not evident (possibly confluent with basal cell, but entire cell open distally).
91. Larva: 1. instar without cephalic eggbursters (Emden, 1946).
96. Larva: some *Trox* with 1 stemma on each side (others without stemmata).
100. Larva: prostheca apparently absent.
113. Larva: 1. instar with pair of eggbursters on metanotum (at least in Lucanidae, Passalidae, "Scarabaeidae": Emden, 1946).
118. (General scarabaeoid character, not mentioned for *Trox*).

HYDROPHILOIDEA

The present concept of this superfamily is restricted to include the families Helophoridae, Epimetopidae, Geosissidae, Hydrochidae, Spercheidae and Hydrophilidae (s. str.). It should be noted that some authors regard all these families as constituting a single family, Hydrophilidae (s. lat.), and include the families of Histeroidea (Sphaeritidae, Synteliidae, Histeridae) in the Hydrophiloidea. Although this may be justified from a phylogenetic basis, I still prefer to regard Histeroidea and Hydrophiloidea as separate subfamilies. However, it can hardly be justified to include Hydraenidae in the Hydrophiloidea. The placement of the Hydraenidae within Staphylinoidea, suggested by Bøving and Craighead (1931) and others, is confirmed by the present analyses. The phylogeny of the families included here in the Hydrophiloidea was discussed by Hansen (1991b, 1995) and Beutel (1994). It seems to be well established that the most primitive hydrophiloids are included in the small families (Helophoridae, Epimetopidae, Georissidae, Hydrochidae, Spercheidae). Their relationship, as proposed by Hansen (l.c.), is shown in fig. 8.

Beutel's (l.c.) ideas about basal hydrophiloid phylogeny differ somewhat from the one presented here. Basically, he argues for a sister group relationship between Hydraenidae and Hydrophiloidea on the basis of shared features in the head of larvae and adults. There are, however, in my opinion two fundamental problems with his approach. Firstly, his conclusions are based on a limited set of characters (only cephalic characters are used). Secondly, he seems to focus particularly on common features of Hydraenidae and Hydrophiloidea and polarize the characters one by one by outgroup comparison without giving any indication of what might be the possible sister group of Hydraenidae + Hydrophiloidea. That is, groups like Histeroidea and Ptiliidae are "a priori" treated as outgroups, though some previous authors have actually suggested sister group relationships between 1) Histeroidea and Hydrophiloidea and 2) Ptililidae and Hydraenidae. Beutel lists the following 11 features (10 adult, 1 larval) in support of the hypothesis about a hydraenid-hydrophiloid sister group relationship.

(1) Head strongly retracted, with transverse posterodorsal ridge. – The degree of retraction of the head is however a very variable feature which is difficult to define, and several related groups (e.g., Histeridae, Scarabaeoidea) have the head retracted to at least the same extent. The presence of a transverse posterodorsal ridge is postulated to be basal to Hydraenidae and Hydrophiloidea and secondarily reduced in Hydrophilidae. Although this is probably true, a similar ridge occur in various other groups as well (e.g., some Histeridae and Trogidae), and the character is subject to a higher degree of homoplasy that indicated by Beutel.

(2) Lateral margins of clypeus distinctly longer than those of frons anterior to eyes (= char. no. 1 in the present analysis). – Although unusual, this feature is not unique to Hydraenidae and Hydrophiloidea. It is also found in some staphylinoids (e.g., Scaphidiidae and Silphidae), and the present analysis indicates that in all of these groups the feature has evolved convergently.

(3) Antennae with breathing function (= char. no. 15 in the present analysis). – This is certainly one of the more unusual features, known only from Hydraenidae and Hydrophiloidea. However, as mentioned below, it may have evolved convergently in the two groups, possibly as a result of some degree of "preadaptation".

(4) Antennal base not visible from above, furrows and anterolateral pouch present. – There is a considerable variation as to how large a portion of the antennal base is concealed. The vast majority of the taxa examined in the present study have the antennae inserted on the sides of the head below a lateral ridge or canthus, and it is primarily the degree of expansion of this canthus that determines if and to what degree the antennal base is hidden. Although the canthus is generally fairly strongly expanded in Hydraenidae and Hydrophiloidea, the same is true also for Scarabaeoidea. The antennal base is also concealed in some Leiodidae (Leiodinae) and – in contrast to the statement of Beutel – in Ptiliidae. Subocular furrows are far from unique to Hydraenidae and Hydrophiloidea. Besides showing some variation within these groups, such furrows are also present, e.g., in most Scarabaeoidea and Histeroidea. Due to variation I find it difficult to distinguish clearly between a subocular "concavity" (which is a fairly general feature) and a subocular "furrow", and the character seems to be of little value at higher taxonomic levels. The prothoracic pouch (antennal groove) was regarded as a basal hydrophiloid feature by Beutel, who claimed that it "is secondarily [!] absent in *Spercheus* and Hydrophilidae". This statement may, however, only be justified if Hydraenidae is actually the sister group of Hydrophiloidea. If, as suggested by Hansen (1991b) *Spercheus* and Hydrophilidae are the sister group of Helophoridae, Epimetopidae, Georissidae and Hydrochidae, it is equally likely that the absence of such pouches is an ancestral hydrophiloid feature. The interpretation is crucially depending on the sister group relationship of Hydrophiloidea. It must also be pointed out that "prothoracic pouches" are present in in a number of more-or-less closely related taxa (e.g., Histeridae). Hence, regardless of which phylogenetic hypothesis is preferred, convergences must be accepted.

(5) Postocular emargination present. – This, undoubtedly derived feature, could be interpreted as a hydraenid-hydrophiloid synapomorphy. But the degree of emargination varies considerably in both groups, and several exceptions occur, e.g., in Georissidae (already mentioned by Beutel) and in Hydrophilidae (Horelophinae, most Sphaeridiinae). Apparently, at least within Hydrophiloidea the presence of this emargination seems to be inti-

mately correlated with aquatic life. This may not be so surprising, because the posterior emargination of the eye is actually an expansion of the temporal area, which plays an important role in aquatic "respiration" (these beetles renew their airsupply through a "tube" formed by the antenna and the postocular region of the head). Hence, if the hydraenid-hydrophiloid mode of aquatic "respiration" has evolved convergently (cf. above), then it is most likely that the same is true for the postocular emargination. Furthermore, it is emphasized that similar a emargination occurs in other groups, e.g., Ptiliidae (though less pronounced than in most hydraenids and aquatic hydrophiloids) and some Silphidae not examined by Beutel (e.g., *Oiceoptoma* and, notably, *Ptomaphila*).

(6) Mentum enlarged and strongly sclerotized. – This is a rather problematic character, mainly because it is difficult to define adequately (it was excluded from the present analysis for this reason). Admittedly, the mentum of Hydraenidae and Hydrophiloidea is generally quite large compared to most related groups and may indicate relationship, but because of the great variation in size and shape, the caracter may be of limited significance, especially at higher taxonomic levels. At least, a more precise distinction between "small" and "large" is desirable.

(7) Distal galeomere composed by several fimbriate lamellae. – As mentioned by Beutel, this is most likely a ground plan character of Hydraenidae and Hydrophiloidea, and it is possibly also a derived feature. Exceptions within these groups (e.g., Ochthebiinae and Megasternini, respectively) can well be explained as secondary. However, because the morphology and "armature" of the galea varies greatly in presumedly related groups (e.g., Scarabaeoidea, cf. Scholtz, 1990) it is not very surprising if "fimbriate lamellae" have evolved convergently in Hydraenidae and Hydrophiloidea, which must be concluded from the present analysis.

(8) Maxillary palp elongated. – This is indeed a variable character, and although the maxillary palps are generally relatively long (and sometimes very long) in Hydraenidae and Hydrophiloidea, this is less pronounced among the presumedly primitive forms of both groups. Several other beetles have similarly long maxillary palpi, e.g., many Scydmaenidae, some Leiodidae and various Staphylinidae (e.g., Pselaphinae, Steninae). The character is probably of minor significance at higher taxonomic levels as it was also admitted by Beutel ("this derived character state should not be overvalued").

(9) Large hypopharyngeal suspensorium present. – Beutel finds this character to be present in *Hydraena*, *Ochthebius*, *Hydrochus*, *Helophorus*, and Hydrophilidae. It is absent in Cupedidae, Adephaga, Silphidae, Ptiliidae, Staphylinidae and Histeridae. Hence, the assumption that it may represent a synapomorphy of Hydraenidae and Hydrophiloidea seems to be justified. However, the interpretation is somewhat weakened by the fact that its presence is indicated as dubious in *Spercheus*, *Epimetopus* and *Georissus*, and because Beutel gives no information about the character in the examined species of Leiodidae (incl. "Leptinidae") and Scydmaenidae. It is therefore impossible to evaluate any possible homoplasies. I have not examined the character.

(10) Cerebrum shifted posteriorly. – Beutel considers this feature as a synapomorphy of Hydraenidae and Hydrophiloidea (the character state is not known in *Spercheus*, *Georissus* and *Epimetopus*). The more central position of cerebrum in the head capsule, found in Silphidae, Staphylinidae and Histeridae, was assumed to be plesiomorphic (Beutel mentions nothing about the character state in examined species of Leiodidae (incl. "Leptinidae"), Scydmaenidae and Cupedidae). A problem with this hy-

pothesis may be that the brain of Ptiliidae has a posterior position similar to that of Hydraenidae and Hydrophiloidea, but Beutel merely states that it is "considered as a result of parallelism". However, admitting that an assumption about parallelism is necessary, it might be considered equally likely that the parallelism is between Hydrophiloidea and a hydraenid-ptiliid group. This would be the interpretation resulting from the present analysis.

(11) Cephalic eggbursters present [in first instar larvae] (= char no. 91 in the present analysis). – The character has been considered as a synapomorphy of Hydraenidae and Hydrophiloidea by Beutel (1994) and others. But because of the scarcity of available data the interpretation is somewhat uncertain. On the basis of the present analysis, it is found to be equally likely that cephalic eggbursters are actually an ancestral feature of the Coleoptera, retained in some Adephaga and primitive Polyphaga, but lost in most Polyphaga and Archostemata (character state unknown in Myxophaga). Possibly, such eggbursters have evolved secondarily in some groups.

Although most of these characters can be regarded as derived and therefore indicative of a sister group relationship between Hydraenidae and Hydrophiloidea, I find no justification for regarding them as more significant than other characters systems (e.g., wings, genitalia) that would have led to different conclusions. Several of them (especially 1, 2, 4, 6, 8) are quite variable or (11) inadequately known and seems to be of limited significance for reconstruction of phylogeny at higher taxonomic levels. This is to some extent ignored by Beutel who considers "the head ... the most complex structure of the insect body". Although such a statement may be justified, the complexity is not really reflected in most of the characters used for his phylogenetic reconstruction. Most characters are just as variable as many other characters from other parts of the body. It does not mean that they are uninformative, only that they must be evaluated with same degree of caution as any other character. Apparently, Beutel relies too much on the above 11 features, i.e., to the extent that other characters can be evaluated from the presumption that all of these are true synapomorphies. Hence, it is striking that, except for one weakly defined character – clypeus "strongly enlarged" rather than "moderately long" – all his characters given as autapomorphies of Hydrophiloidea (excl. Hydraenidae) are shared with Histeroidea. Although the phylogeny presented by Beutel (based on a total of 39 characters) is the most parsimonious one given the characters he uses, the addition of only two or three conflicting characters (and there are several such characters!) may completely alter the result.

Admittedly, Beutel discusses other characters that have been proposed by previous authors to support alternative hypotheses about the relationship of Hydraenidae and Hydrophiloidea. But throughout the discussion he tends to reject characters supporting sister group relationships between 1) Hydraenidae and Ptiliidae and 2) Hydrophiloidea and Hydraenidae, either by given examples of convergences from quite distantly related groups (e.g., comparing the derived type of mandibles found in Ptiliidae and Hydraenidae with that of Elmidae), or by simply stating that "polarity ... is not sufficiently clarified" (e.g., anal hooks of larvae of Ptiliidae and Hydraenidae) or "convergency ... cannot be excluded" (e.g., wing folding with simple convex and concave folds and without a hinge; medial loop poorly developed or absent; phallobase small and strap-like or absent; only four Malpighian tubules). Other characters supporting a ptiliid-hydraenid relationship (everted genital segments, connate/fused female gonocoxites) are mentioned but not commented on. Moreover, Beutel claims that "none of the proposed autapomorphies of adult and larval Hydrophiloidea [incl. Hydraenidae] is found in the adults of Histeroidea". But this is only true because he initially assumes that Hydraenidae are a basal group of Hydrophiloidea. Otherwise, there are a number of derived features that are shared by Hydrophiloidea (excl. Hydraenidae) and Histeroidea, including several of Beutel's "own" cephalic characters. And the statement that a mandibular penicillus, as found in Histeridae [actually Histeroidea], is absent in Hydrophiloidea, is not true. Most of the presumedly primitive hydrophiloids (at least Helophoridae, Epimetopidae and Hydrochidae) do have a penicillus more-or-less similar to that of histeroids.

Beutel concludes his discussion by refering to the phylogenetic analysis of Hydrophiloidea by Hansen (1991b), mentioning that it would be beyond the scope of his paper to discuss the results and procedures applied there in detail. He does, however, comment on a few characters used in that study, but does not really discuss characters that might be in conflict with his own hypothesis. At least 6 cephalic (!) characters, not considered by Beutel, were used by Hansen in support of a different hypothesis about basal phylogeny within Hydrophiloidea. It would have been desirable if Beutel had discussed these characters as well. Beutel's comments about Hansen's character polarity determination seems to rely on some kind of misconception. Apparently, he assumes that the character states "0" and "1" are by definition plesiomorphic and apomorphic, respectively, and that polarity must be determined prior to analysis. But none of these assumptions are true. The character states (0, 1, 2, etc.) are only operational symbols and character polarity is determined by rooting the trees after these have been calculated.

It should be obvious that any hypothesis about the phylogenetic relationship of these groups need to consider a certain degree of convergency. The number of possible synapomorphies given by Beutel (11 cephalic and 3 others) is by far exceeded by the number found in the present analysis (based on many different characters). That is, the inclusion of Hydraenidae in Staphylinoidea is here supported by 9-10 derived characters, to which must be added 3 synapomorphies with Agyrtidae-Leiodidae-Ptiliidae, 3-4 synapomorphies with Leiodidae-Ptiliidae, and 12-13 synapomorphies with Ptiliidae. Hydrophiloidea, on the other hand, is found to share 5-6 derived features with Scarabaeoidea and Histeroidea and further 12-13 synapomorphies with Histeroidea. The characters are discussed under the relevant clades (note that several of the characters are rather strong, and that Beutel's hypothesis is not rejected on the basis of the sheer number of characters).

On the basis of the present phylogenetic hypothesis, the following adult autapomorphies may support the monophyly of Hydrophiloidea:

a) Head with coronal suture or, in primitive forms, groove (a rudimentary suture or groove is also found in some not very closely related groups (a few Hydraenidae, a few Agyrtidae, a few Leiodidae and a few Osoriinae and Piestinae, probably convergent).

1:1*. Clypeus large (convergent in several other groups).

3:1*. Head abruptly constricted immediately behind eyes; in the more derived forms (most Hydrophilidae) the head is hardly constricted.

8:1*. Mandibles almost concealed under clypeus.

15:1*. Antennae used to break surface film in aquatic respiration. This behavior is also found in the Hydraenidae and has been considered one of the more important synapomorphies for Hydraenidae and Hydrophiloidea, but the outcome of the present analyses strongly indicates that this is a matter of convergence. Moreover, a similar behaviour is shown by some coprophilous scarabaeoids, when they are placed in water (cf. Hrbácek, 1950). This may suggest that the potential of using the antennae as auxiliary organs in aquatic respiration was present before the hydrophiloids and the hydraenids became aquatic, i.e., even before the lineages leading to them separated (Hansen, 1995).

16:2*. Antennae with 9 (or fewer) segments.

27:1*. Procoxal cavities closed internally (also in Histeridae and in certain Staphylinoidea, e.g., Leiodidae, Hydraenidae, Ptiliidae, Scydmaenidae, Scaphidiidae; convergent).

30:1*. Mesosternum very narrow anteriorly. It has secondarily become wider in a few forms (Georissidae, Hydrochidae, a few derived Hydrophilidae).

33:1. Mesotrochantin concealed (possibly convergent with Scarabaeoidea and Histeridae). The character could also be interpreted as basal to clade 67 (Hydrophiloid lineage) with reversal in Sphaeritidae and Synteliidae.

36:1*. Ventral surface with fine and dense, hydrofuge pubescence. This is also found in the Hydraenidae and has been considered synapomorphic for Hydraenidae and Hydrophiloidea, but the outcome of the present analyses strongly indicates that this is a matter of convergence.

85:1. Female gonocoxites moderately long, narrow and cylindrical. The basal condition of this character was indicated as ambiguous for Hydrophiloidea and Histeroidea (clade 40), but it is assumed that the long and slender gonocoxites of Hydrophiloidea and the broad and flat gonocoxites of Histeroidea both evolved from a relatively short, non-flattened type (state 0).

89:2*. Eggs laid in groups (rarely singly) enclosed in a silk cocoon. A similar feature is found in the Hydraenidae and has been considered one of the more important synapomorphies for Hydraenidae and Hydrophiloidea but, as pointed out by Hansen (1995) the similarity is probably rather superficial, because hydraenids lay their eggs singly and merely cover them with a web, which is constructed in a different manner. Moreover, because eggs are only known from a few genera and exceptions are known, it is not even clear if this habit was present in the hydraenid ancestor. Anyway, the outcome of the present analyses indicates that this is a matter of convergence.

119:1*. Adult aquatic; some more derived forms (notably Sphaeridiinae) have secondarily become terrestrial. The aquatic habits of Hydraenidae, often considered evidence for close relationship to the Hydrophiloidea, is almost certainly a parallelism, as indicated by the outcome of the present analyses.

Other characters were indicated as possible apomorphies by the present analyses, but their significance is somewhat dubious:

It was indicated by the analyses that the absence of a distinct wedge cell is an apomorphy for the entire hydrophiloid lineage (clade 67) and that a wedge cell has evolved independently in Hydrophiloidea (76:0). However, this is believed to be very unlikely. Rather, it has been lost independently in Scarabaeoidea, Histeroidea and Staphylinoidea.

The presence of cephalic egg bursters in first instar larvae (91:1) may be a plesiomorphic feature, i.e., they might be part of coleopteran ground plan (see also under Archostemata).

The absence of a basal stem of the dorsal ecdysial lines of head (94:1) is difficult to interpret. It may be convergent in regard to Sphaeritidae, but it is also possible that basal stem was lost in the hydrophiloid-histeroid ancestor and has reversed in Synteliidae and Histeridae. The character is also ambiguous in the entire Hydrophiloid lineage and all of the more basal clades (i.e., no. 66-71).

ANNOTATIONS TO CHARACTERS:

2. Frontoclypeal suture primitively grooved; in derived forms still visible, but not grooved.
3. Head primitively constricted immediately behind eyes (as in Helophorid group, Spercheidae); but in most Hydrophilidae hardly constricted.
5. Interocular grooves primitively and generally absent, but present in Hydrochidae (secondary).
6. Gular sutures probably primitively separate; but in Helophoridae, Epimetopidae, Georissidae, and Hydrochidae confluent.
10. Mandibles sometimes with projecting lobe on inner face (Hydrophilidae: Berosini).
16. Antennae primitively 9-segmented; in some derived forms with only 7 or 8 segments.
18. 8th morphological segment are considered to be represented by the cupule in Hydrophiloids, though as result of assumed reduction in the number of preceding segments, it appears as the actual segment 4, 5 or 6.
24. Procoxal fissure in most primitive forms narrowly open, exposing trochantin (but in Helophoridae closed: secondary?); in more derived forms often more open.
25. Hypomeron with processes behind procoxae, but only in a few derived forms (e.g., Hydrochidae, Hydrophilidae:*Helobata*) meeting with an intercoxal process to form complete closure of procoxal cavities.
26. Prosternal intercoxal process primitively present, but short, and for most of its length concealed beneath procoxae; only in few derived forms with well developed intercoxal process (e.g., Hydrochidae, Hydrophilidae:*Helobata*, some Megasternini); intercoxal process completely absent in Georissidae.
51. Intercoxal process of abdominal sternum 2+3 primitively and generally acute; more blunt and broader only in Georissidae (secondary).
61. Posterior coxae primitively and generally contiguous (or nearly so), but broadly separated in Georissidae (secondary).
63. Tarsi primitively 5-segmented; only 4-segmented in Georissidae, in middle and hind tarsi of *Cymbiodyta* and *Helocombus*, and in male anterior tarsi of *Berosus* (Hydrophilidae).
64. Ventral face of elytra normally without sublateral ridge/lamina, except in Hydrochidae and Georissidae (secondary).
70. Folded hindwings overlap only c. $^1/_2$ the width of one folded wing apically (but overlap more, often almost completely, for some distance in middle).
72. Hindwing anal lobe mostly (and primitively) present, though sometimes not well demarcated from rest of wing; sometimes absent (e.g., Megasternini).
74. Hindwings primitively with 4 veins posterior to medial bar; sometimes with 5 (Coelostomatini) or 3 such veins, seldom fewer.
76. Hindwing wedge cell generally present; seldom absent (e.g., Megasternini).
91. Larva: 1. instar with frontal eggbursters, according to Emden (1946) and Crowson (1981); exceptions occur in at least some Hydrophilidae.
92. Larva: epistomal lobes normally well developed; only missing in Spercheidae (secondary).
94. Larva: dorsal ecdysial lines primitively without basal stem (sometimes with short stem).
103. Larva: lacinia rudimentary or absent; except in Spercheidae (a secondary? lacinia-like appendage present).
109. Larva: ligula mostly present (primitive condition?); absent in Helophorid lineage (except for short ligula in *Epimetopus*) and some clearly derived hydrophilids (*Berosus, Laccobius*).
113. Larva: 1. instar without thoracic or abdominal eggbursters (Emden, 1946; Crowson, 1981).
115. Larva: abdominal spiracles primitively biforous (Helophoridae, Georissidae); sometimes reduced, except on segment 8, which has enlarged, apparently annular spiracles (Hydrochidae, Spercheidae, and Hydrophilidae; spiracles absent in *Berosus*).
116. Larva: urogomphi probably primitively 3-segmented (as in Helophoridae and Epimetopidae); but in most forms reduced and small, 2- or 1-segmented (in Spercheidae only present as small setiferous tubercles on tergum 9).
117. Larva: urogomphi probably primitively articulated basally to abdominal segment 9 (as apparently in, e.g., Epimetopidae); basal segment of urogomphi fixed to abdominal segment in Helophoridae (secondary?).

SPHAERITIDAE

This family includes only the holarctic genus *Sphaerites* with 3 species. They are in many ways very primitive histeroids and it is difficult to identify autapomorphies for the family. In the present study only a single species has been examined, so the possible autapomorphies listed below (and suggested by the outcome of the analyses) must be regarded tentative:

77:2*. Male tergum 9 relatively long, apparently entire (though with apical excavation for tergum 10).

78:1*. Aedeagus with asymmetrically twisted basal piece (otherwise symmetrical).

The absence of a basal stem of the dorsal ecdysial lines of head (94:1) is of dubious significance. It may be convergent in regard to Hydrophiloidea, but it is also possible that basal stem was lost in the hydrophiloid-histeroid ancestor and has evolved independently in Synteliidae and Histeridae.

SYNTELIIDAE

A small family, comprising only the genus *Syntelia* with 2 species in temperate areas of central Mexico and 3 in central Asia. The following characters of the adults are possible autapomorphies of the family:

25:2*. Hypomeron with narrow, mesally directed processes that contact the apex of the prosternal intercoxal process and thereby close the procoxal cavities posteriorly.

26:2*. Prosternal intercoxal process widened behind procoxae; the process is partly concealed in posterior half by the procoxae, but its apical portion is abruptly raised to the level of coxae.

47:4. All abdominal terga sclerotized. Although the character was indicated as ambiguous for a hypothetical synteliid-histerid ancestor, there is little doubt that the sclerotization of all terga in Synteliidae is a further modification of the condition of found in Histeridae and assumed to represent the basal synteliid-histerid condition (terga sclerotized from segment 4 onwards).

The rudimentary elytral striation is probably also an autapomorphy, although the sister-group of Synteliidae (Histeridae) also have partly rudimentary striae. In Synteliidae 10 striae (the ancestral coleopteran number) can be detected: 1, 5, 6 and 10 are rather complete, 2 and 4 are rather long but interrupted, and 3, 7, 8 and 9 only present at the extreme apex.

HISTERIDAE

A large and diverse family whose systematic limits are generally agreed upon (only one subfamily, Niponiinae, has sometimes been given rank of separate family). However, the internal hierarchy of the family is not well founded on a phylogenetic basis. Primarily, the division of the family into two major groups, Abraeomorphae (= Saprinomorphae) and Histeromorphae, based respectively on the absence or presence of an anterior prosternal lobe, seems to be artificial. As long as a more thorough cladistic analysis of the histerids has not been made, the phylogenetic status of the different subfamilies is also to some extent obscure and at least some of them are probably paraphyletic. Crowson (1955) considered the genus *Teretrius* (Abraeinae: Teretriini) as one of the most primitive histerids, but still the basal splits within the family are not obvious. In spite of these problems, the family as a whole seems to be a well defined monophyletic group. It can be defined by the following possible autapomorphies:

27:1*. Procoxal cavities closed internally (also in Hydrophiloidea and in certain Staphylinoidea, e.g., Leiodidae, Hydraenidae, Ptiliidae, Scydmaenidae, Scaphidiidae; convergent).

33:1. Mesotrochantin concealed (possibly convergent with Scarabaeoidea and Hydrophiloidea). The character could also be interpreted as basal to clade 67 (Hydrophiloid lineage) with reversal in Sphaeritidae and Synteliidae.

37:0*. Laterosternite of 2nd abdominal segment not distinct.

41:1*. Abdominal tergo-sternal membrane very short on 5th and following segments (long only on segment 1-3).

46:3*. Patches of wing folding setae absent from abdominal tergum 5 (and the following ones).

50:2*. First ventrite ("sternum 2+3") not carinate, not even between posterior coxae.

54:1*. Laterosternites without or with very rudimentary clothing of microtrichia.

61:1*. Posterior coxae broadly separated.

64:1*. Ventral face of elytra with a sublateral ridge or lamina, at least anterior to middle.

83:2*. Parameres fused to a tube enclosing the median lobe (unique); a partial fusion of the parameres is found in Sphaeritidae and Synteliidae, but both families have parameres separate for some distance in the apical portion.

116:2*. Urogomphi of larvae 2-segmented (rather than 4-segmented, which is possibly the primitive histeroid condition); in some, presumedly derived forms, the urogomphi are 1-segmented or even absent.

Other characters, indicated as possible apomorphies by the outcome of the analyses, are of somewhat dubious significance:

The (at least partly) exposed mesothoracic spiracles (28:1) is possibly another histerid autapomorphy, but it could not be examined in Synteliidae, so possibly the apomorphy includes this family as well.

The absence of cephalic egg bursters in first instar larvae (91:0) (Emden, 1946; Crowson, 1981) may be a derived feature, i.e., if they are part of coleopteran ground plan (see also under Archostemata). However, even if the derived nature of absence of cephalic egg bursters is accepted, its status as a possible histerid autapomorphy is questionable, because it may also turn out to include Sphaeritidae and Synteliidae, which could not be examined for the character.

The presence of a single stemma on each side of the head (96:5) in some Histeridae may be an apomorphy for the family, because stemmata are absent in the two more primitive histeroid families (Sphaeritidae, Synteliidae). However, since stemmata are also absent in some Histeridae, it is not certain that the presence of stemmata is an apomorphy for the entire family.

Initially, I had only recorded the presence of egg bursters on first abdominal tergum from first instar larvae of Histeridae (113:1). However, the character was given as a synteliid-histerid synapomorphy by Lawrence and Newton (1982), and it is even possible that it includes the Sphaeritidae and is an autapomorphy for the entire Histeroidea (see above under clade 38 (Synteliidae-Histeridae)).

The rudimentary striation is probably also an autapomorphy, although the sistergroup of Histeridae (Synteliidae) also have partly rudimentary striae. In Histeridae 10 striae (the ancestral coleopteran number) is probably the primitive number (detectable in, e.g., *Hister*), but at least the 4 lateral ones are greatly reduced; some groups have no distinct striae.

ANNOTATIONS TO CHARACTERS:

1. Clypeus probably primitively small (general condition), but variable in size; rather large, e.g., in Tribalinae:*Epierus* and Tryponaeinae (in the latter produced into a rostrum).
2. Frontoclypeal suture mostly not detectable (probably primitive), but seldom present and not grooved (as, e.g., Tribalinae:*Epierus*); in some Histerinae a groove is present, but it is probably secondary (a result of two lateral interocular grooves, which bends towards midline anteriorly and eventually may be united medially).
8. Mandibular apices primitively and generally protruding and very distinct; except Trypanaeinae in which the clypeus is produced into a rostrum that conceals mandibles completely in dorsal view.
9. Mandibles probably primitively with a mola (well developed in, e.g., Dendrophilinae and Abraeinae); mola sometimes indistinct, e.g., *Saprinus* (secondary).
16. Antennae primitively 11-segmented with 3-segmented compact club (as seen in, e.g., Histerinae:*Hister*, Tribalinae etc.); sometimes club-segments partly fused (Dendrophilinae: *Dendrophilus*), or completely fused to a single large segment (*Saprinus, Abraeus, Trypanaeus* etc.); exceptionally with only 7 segments preceding club.
17. Antennae primitively and generally inserted laterally under lateral canthus of frons; only in Abraeinae inserted at a more dorsal/mesal position (near inner margin of eyes), but still the frontal canthus can be detected (secondary).
35. Metepisterna generally exposed, except, e.g., *Abraeus* (secondary).
37. Laterosternite of segment 2 not distinct as separate sclerite (though probably represented by the anterior portion of the apparent 3rd).
46. Abdominal tergum 4 extensively covered with microtrichiae (other terga without microtrichiae).

47. Abdomen generally well sclerotized from tergum 4, but the first three terga often more-or-less corneous (soft in *Abraeus*, rather soft in *Dendrophilus*; but rather sclerotized in *Hister*).
59. Posterior coxae transverse, but not very much so (due to their broad separation).
65. Epipleura narrow, but well demarcated by a fine groove (not deflexed).
72. Hindwing generally with well developed and demarcated anal lobe; sometimes not demarcated from rest of wing (e.g., *Abraeus*).
113. Larva: 1. instar with pair of eggbursters on abdominal tergum 1 (Emden, 1946; Crowson, 1981).
116. Larva: urogomphi probably primitively 2-segmented; but sometimes 1-segmented or (Trypeticinae, Trypanaeinae, some *Teretrius*) absent.

AGYRTIDAE

The genera constituting in this family were earlier treated as a subfamily of the Silphidae (roughly corresponding to the traditional tribes Lyrosomatini and Agyrtini). However, they differ from typical silphids (Silphinae, Nicrophorinae) in many regards, including both larval and adult features. Whereas typical silphids share a number of derived characters with the staphylinid group, there is no evidence for including agyrtids in this assemblage. Lawrence and Newton (1982) refer to agyrtids as the "least specialized of all staphylinoids", and suggested that the group be given status as separate family. The phylogeny of the family is not yet sufficiently understood and the possible autapomorphies supporting its possible monophyly are few. Currently, three tribes are recognized, viz. Pterolomatini, Lyrosomatini and Agyrtini, but it is not clear which of them include the most primitive forms. The presence of a pair of ocelli and a relatively well developed basal piece of the aedeagus in *Pteroloma* may suggest that this genus is relatively primitive (see also below), but the genus also exhibit some characters (e.g., 6 rather than 5 ventrites) which are probably more derived. The following possible autapomorphies may support the monophyly of the Agyrtidae:

20:1*. Penultimate 3-4 antennal segments each with apical, periarticular open groove which bears dense concentration of sensilla. As suggested by Lawrence and Newton (1982) it is possible that these grooves can be considered as precursors to the more closed vesicles found in the Leiodidae, in which case they should be considered plesiomorphic within clade 44 and having been further developed in the Leiodidae and lost in Hydraenidae and Ptiliidae. However, such grooves are absent in some Agyrtidae (e.g., *Pteroloma*) so it is even possible that they were not even part of the agyrtid groundplan.

74:2*. Hindwing with two (rather than just one) vein posterior to medial bar (the acquisition of an extra vein may not be so significant or surprising; it seems that the number of such veins is to some extent correlated with the size of the species and that veins that have apparently disappeared, e.g., as a result of size reduction, are not always irreversibly lost and may reappear if the size increases again). Larger forms (e.g., *Necrophilus*) may even have 3 such veins (Kukalová-Peck and Lawrence, 1993) and others (e.g., *Pteroloma*) have only one such vein.

78:1*. Aedeagus asymmetrical. This was given as an autapomorphy by Lawrence and Newton (1982), and though it is possible that an asymmetrical aedeagus is a groundplan character of the Agyrtidae, there is some variation in the family. The asymmetry is evident in *Pteroloma*, but restricted to the aedeagal base in *Ecanus*; in *Agyrtes* the aedeagus seems to be symmetrical.

83:1*. Parameres fused to a single ventral plate (parameres sometimes absent, e.g., in *Agyrtes*.)

85:1*. Female gonocoxites moderately long, narrow and cylindrical.

101:0*. Mandibles with densely setose area on ventral face.

The presence of a rudimentary, strap-like basal piece of the aedeagus (81:1) has normally been considered a plesiomorphic staphylinoid feature. But since a basal piece is not found in other of the presumedly most primitive staphylinoid families (Hydraenidae, Ptiliidae, Leiodidae (except *Colon*, cf. below)), it is possible that the basal piece was absent or, perhaps more likely, rudimentary and entirely membranous in the staphylinoid groundplan, and the presence of a more-or-less well sclerotized basal piece in (at least some) Agyrtidae may actually be apomorphic. It is possible that a sclerotized strap-like basal piece is an agyrtid groundplan character, but there is some variation and its presence is not always evident. Thus, the very distinct basal piece found in, e.g., *Pteroloma* may be autapomorphic to that particular genus.

The transverse middle coxae (58:1) could be interpreted as an autapomorphy (convergent with Leiodidae), but it is also possible that this is a basal characteristic for clade 44, and that the more globular coxae of Hydraenidae and Ptiliidae represents a secondary feature.

The bifurcate anterior arms of dorsal ecdysial lines in larvae (95:1) is a characteristic shared with Leiodidae and has been suggested as a possible synapomorphy for these two families (Lawrence and Newton, 1982). But the indications of the present analysis are rather that the bifurcation of the frontal arms has evolved convergently in Agyrtidae and Leiodidae, or that it is a plesiomorphic feature within clade 44, which has reversed in Hydraenidae and Ptiliidae.

ANNOTATIONS TO CHARACTERS:

1. Clypeus small in *Agyrtes* and *Pteroloma* (probably primitive condition), sometimes larger (e.g., *Necrophilus*, *Pelatines*).
4. Probably paired ocelli are primitively present, as in *Pteroloma*; but most other taxa (i.e., all the ones examined) have no ocelli.
9. Possibly a mola is primitively present (narrow mola present in *Pteroloma*; mola absent in *Agyrtes*).
28. Mesothoracic spiracles hardly exposed in *Agyrtes* (probably primitive condition); partly exposed in *Pteroloma*.
37. A suggestion of a separate 2nd laterosternite present.
40. Abdominal segment 8 normally not exposed (except for the tergum below the elytra), but exposed in *Pteroloma* (secondary).
100. Larva: prostheca present, rounded or toothlike.
115. Larva: spiracles annular (primitive condition?), or "modified annular", or annular-biforous.

LEIODIDAE

The family is here defined in a broad sense, including the subfamilies Camiarinae, Leiodinae, Catopocerinae, Coloninae, Cholevinae and Platypsyllinae. This concept of the family agrees with that of Lawrence and Newton (1982) and, apart from the inclusion of Platypsyllinae, with Crowson's (1955) Anisotomidae. The leiodids have earlier been referred to the Silphildae (auct.), and some of them (notably Cholevinae) are still treated as silphids by some authors. However, typical silphids share a number of derived features with the members of the staphylinid group (see this). The lack of a such features in the leiodids excludes these beetles from the staphylinid group and indicates that they are only distantly related to typical silphids. Rather, the leiodids seem to belong among the more primitive staphylinoids (near Agyrtidae). So far, the internal phylogeny of Leiodidae has not been well explained. Lawrence and Newton (1982) defined the family in the broad sense (as in the present work), noting that "the interrelationships of the subfamilies are not yet clear".

It seems that the Camiarinae are generally the least derived of the leiodid subfamilies (although not necessarily primitive in all respects). They include the genus *Ragytodes*, the only leiodid in which ocelli are present (probably a groundplan character of the clade 44), and which may therefore be considered one of the most primitive genera. The taxonomic limits of the Camiarinae have been subject to varying opinions. Jeannel (1936) defined it rather narrowly (corresponding to the tribus Camiarini). Subsequently, other groups (Neopelatopini, Agyrtodini) have been referred to the subfamily (Newton, 1985), apparently merely on the basis of plesiomorphic characters. Although the subgroups of Camiarinae may be well defined, there seems to be no evidence supporting the possible monophyly of the entire subfamily.

The Leiodinae seems to be a monophyletic subfamily, defined by at least one autapomorphy, viz. the metepisterna concealed by the elytra (exceptionally very narrowly visible, as in *Anisotoma*). Other leiodids have the metepisterna visible from below (in Platypsyllinae the metepisterna are fused with metasternum).

The Catopocerinae are a small group of uncertain relationship and status, including only two genera (*Catopocerus*, *Glacicavicola*).

The Coloninae differ from other leiodid subfamilies, e.g., by the morphology of the antennae, which have a more-or-less well defined, not interrupted club (i.e., segment 8 not smaller than both 7 and 9). This very atypic condition is undoubtedly secondary within the family, because the Coloninae share some presumedly derived leiodid features with the Cholevinae (and to some degree Platypsyllinae), e.g., presence of a posterior transverse line or fine ridge dorsally on head (probably homologous to the strong ridge of Cholevinae and Platypsyllinae), and similar, dense pubescence of the body. Most forms of the more primitive leiodid subfamilies are glabrous or very finely pubescent, or (some Camiarinae) have a less dense and more erect pubescence of different appearance. The increase in the number of distinct ventrites shown by Cholevinae and Platypsyllinae (see below) is not found in Coloninae, in which there are only 4 ventrites in the / (usually 5 in ?). Other derived features of Coloninae are found in the structure of the male genitalia (complex with apparently secondarily developed basal piece) and the abdominal intersegmental membranes which, between the ventrites, have a "brick-wall" pattern of small hexagonal sclerites similar to that of most Staphylinidae and related families.

In the Cholevinae (Catopinae) the hypomeral projections (behind procoxae) are quadrangular (fig. 107) rather than of the normal (plesiomorphic) leiodid, triangular type (Jeannel, 1936). This seems to be unique within the family and may be considered an autapomorphy supporting the monophyly of the subfamily (somewhat modified in the more derived Leptodirini). As now defined, the Cholevinae includes the tribe Leptodirini (Bathysciini), a large group of cavernicolous, mostly blind species, which exhibit a great morphological diversity. Although the Leptodirini share a few apomorphic features (4-segmented / -protarsi and more-or-less separate posterior coxae), which support their monophyly, many of the more derived Leptodirini are so modified that their relationships would be very obscure, were it not for the forms that link them morphologically to more typical cholevines (see, e.g., Jeannel, 1911). In the most primitive forms vestigial eyes are present and the general habitus is rather typical "cholevine", e.g., they have a distinct transverse dorsal ridge at the rear of the head, typical leiodid antennae with small 8th segment, and transverse pronotum with sharp lateral canthus. However, in some of the more derived Leptodirini (e.g., *Leptodirus*) there is no posterior transverse ridge on the head, antennal segment 8 equals 7 and 9 in size, and pronotum is elongate and without lateral canthus. Moreover, the antennae are inserted more dorsally on the head, though delimited mesally by a longitudinal ridge (corresponding to the lateral canthus of more typical leiodids). In addition to the characteristic shape of the hypomeral processes (cf. above), the following characters, apparently all derived within Leiodidae, support the inclusion of the Leptodirini in Cholevinae: 1) Small (rudimentary) conical apical segment of maxillary palpus (as in most presumedly more derived cholevines); 2) posterior transverse dorsal ridge of head (except in derived forms); 3) narrowing of procoxal fissure; and 4) presence of 6 visible abdominal sternites (probably, the ancestral leiodid condition was 5 distinct sternites, as found in Camiarinae and Leiodinae, though sometimes a small retractable 6th ventrite can be seen in these subfamilies). These characters, except the quadrangular hypomeral processes, are also shared with the Platypsyllinae.

The Platypsyllinae (Leptininae) are a small group of partly very derived forms, which are more-or-less ectoparasitic on smaller mammals. The monophyly is supported several derived features of the adults, e.g., concealed mandibles, small and globular (rather than projecting) anterior coxae, presence of prosternal intercoxal process (extremely large in *Platypsyllus*), loss of eyes (no doubt convergent with the loss of eyes in most Leptodirini, cf. above), and fusion of metepisterna and metasternum, as well as the parasitic habits. The close phylogenetic relationship of the extremely aberrant *Platypsyllus* (having strongly abbreviated elytra and small, apparently 3-segmented antennae) – earlier placed in a monotypic family of uncertain affinities – to the much less derived *Leptinus* was pointed out by Jeannel (e.g., 1936). Although family rank is often retained for this group, there is evidence for a more subordinate taxonomic position within the Leiodidae. The presence of a transverse posterior ridge (canthus) dorsally on the head, a constricted neck, and 6 rather than 5 distinct ventrites indicate a close relationship with the Cholevinae. However, the Platypsyllinae do not have the derived (quadrangular) shape of the hypomeral processes typical of the Cholevinae, and can hardly be included in that subfamily. Probably the two subfamilies are sistergroups.

The Leiodidae, as here delimited, seems to be a well defined monophyletic group, which may be supported by the following autapomorphies:

a) Antennal segment 8 reduced in size, smaller than both segment 7 and 9. This is a very unusual feature (though not unique) and is undoubtedly part of the leiodid groundplan. A small segment 8 is found throughout the apparently primitive genera of all leiodid subfamilies, except Coloninae (which seems to include relatively derived leiodids, cf. above) and the highly specialized Platypsyllinae. Other exceptions are found only in more subordinate groups (e.g., a few genera of the cholevine tribus Leptodirini, and *Triarthron* of the leiodine tribus Sogdini).

11:1*. Lacinia elongated, at least reaching apex of galea (the shorter lacinia of Cholevinae:Leptodirini is probably secondary).

20:2*. Penultimate antennal segments with apical periarticular, sensilla-filled, nearly enclosed grooves ("internal vesicles" of Lawrence and Newton, 1982), which open to distal surface only by a narrow slit. Such grooves are unique and seem to be generally present throughout the family; the more open grooves of *Leptinus* as well as the apparently rudimentary grooves of *Platypsyllus* (with strongly modified antennae) are undoubtedly secondary features. Lawrence and Newton (l.c.) suggested that these enclosed grooves of Leiodidae may be homologous with the similar, but open (apparently more primitive) grooves found in most Agyrtidae (see under that family).

The transverse middle coxae of adults (58:1) and bifurcate frontal arms of dorsal ecdysial lines in larvae (95:1) may also be interpreted as apomorphic features, but their significance is doubtful because they are shared with Agyrtidae and are equally likely to represent plesiomorphies within clade 44 (see under Agyrtidae).

ANNOTATIONS TO CHARACTERS:

2. Frontoclypeal suture primitively and generally present as a fine line (not distinct in *Colon*).

3. Head probably primitively not constricted immediately behind eyes, but in most Cholevinae strongly constricted immediately behind eyes (also in Platypsyllinae strongly constricted, apparently at same place, though absence of eyes makes interpretation difficult).
4. Probably primitively, as in some Camiarinae (*Ragytodes*) paired ocelli are present, but in the other subfamilies ocelli are absent.
7. Cervical sclerites primitively present, but apparently absent in Coloninae and Platypsyllinae.
8. Mandibular apices normally projecting and exposed; concealed in Platypsyllinae and a few Camiarinae (*Myrmecholeva*) (secondary).
9. Probably, a mandibular mola is primitively (and often) present (as, e.g., *Anisotoma, Catops,* (?some) Leptochirini); however, mola indisctinct in, e.g., *Leiodes.*
12. 4th segment of maxillary palpi as large (or larger) than 3rd (probably primitive); small in Coloninae and several Cholevinae.
17. Antennae generally inserted laterally under lateral canthus of frons; in Coloninae and some Cholevinae:Leptodirini inserted at a more mesal position (though still inserted outside/"below" a sublateral ridge).
19. Antennae primitively with gradually developed club of about 5 segments, and with gradual increase in pubescence (e.g., Camiarinae); but often with well developed, typically 5-segmented (interrupted) club (Leiodinae, many Cholevinae); club seldom 4-segmented (Coloninae) or 3-segmented (some Leiodinae); antennae aberrant in *Platypsyllus*, apparently 3-segmented (the apparent 3rd segment is composed of 7 or 8 very short and very closely aggregated segments).
21. Pronotum primitively and generally with sharp lateral canthus separating dorsal portion from hypomeron; canthus absent only in a few Cholevinae:Leptodirini (secondary).
24. Procoxal fissure usually open, but very narrow in some derived forms (e.g., Cholevinae).
25. Hypomeron with processes, that apparently not closes procoxal cavities posteriorly; however, often they are intimately "fused" with the posterior margin of the internal wall of the coxal cavities, so an extremely narrow posterior closure of procoxal cavities is apparent (as, e.g., Camiarinae, Leiodinae).
26. Prosternal intercoxal process primitively present, but short; only in Platypsyllinae with well developed intercoxal process (narrow in *Leptinus*, large and broad in *Platypsyllus*).
27. Procoxal cavities normally completely closed internally (except, e.g., *Leptinus*, in which the closure is not quite complete).
31. Mesosternum mostly well defined from episterna; but sometimes fused to them (e.g., *Leptinus*).
32. Mesepisterna and mesepimera generally not fused (except *Leptinus*).
35. Metepisterna primitively exposed; in Leiodinae concealed or (*Anisotoma*) only very narrowly exposed (secondary); in *Leptinus* fused with metasternum (secondary).
37. Laterosternite 2 present, but (at least) partly fused with 3rd.
40. Abdominal segment 8 primitively not or hardly exposed (except for the tergum); sometimes more-or-less exposed (e.g., Cholevinae, *Leptinus*) (secondary).
43. Abdominal intersegmental membranes generally clear; only in Coloninae with "brick-wall" membrane (reminiscent of staphylinid type) between sternites (secondary).
61. Posterior coxae primitively and generally almost contiguous; somewhat separated in some Cholevinae:Leptodirini (secondary).
62. Hind coxae reaching lateral edges of body (except, e.g., *Leptinus*).
63. Tarsi primitively all 5-segmented, but reductions in the number occur; e.g., some Leiodinae (tarsal formula 5:5:4, 5:4:4, 4:4:4, 4:3:3, or 3:3:3, sometimes with sexual dimorphism), and some Cholevinae:Leptodirini (anterior tarsi 4-segmented in females, and sometimes also males).
66. Ventral face of elytra normally without medio-lateral patch of microspines (except, e.g., *Anisotoma*), but baso-lateral patch present.
67. Elytra generally not truncate, fully concealing abdomen; in some derived forms truncate at apex (e.g., Cholevinae: *Ptomaphagus*), or even abbreviated (e.g., Platypsyllinae: *Platypsyllus*).
68. Hindwings absent in Cholevinae:Leptodirini and Platypsyllinae.
74. Hindwing normally with 1 vein posterior to medial bar, occasionally with 2 such veins (e.g., *Catops*: secondary?).
78. Aedeagus primitively and generally symmetrical; secondarily asymmetrical in a few Cholevinae.
81. Basal piece of aedeagus apparently generally absent (membranous?), except in *Colon* (secondary).
85. Female: Gonocoxites probably primitively short; but sometimes (e.g., Coloninae) moderately long.
94. Larva: dorsal ecdysial lines of head variable, rarely absent.
95. Larva: frontal arms probably primitively bifurcate anteriorly (but not always).

96. Larva: primitively with 5 stemmata on each side, but often fewer.
99. Larva: mola normally (and primitively) present, but sometimes absent.
100. Larva: prostheca primitively present as membranous or partly sclerotized lobe; sometimes absent.
103. Larva: galea and lacinia only exceptionally completely fused (*Platypsyllus*).
104. Larva: galea and lacinia only exceptionally completely fused (*Platypsyllus*).
105. Larva: galea probably primitively with fimbriate apex (as, e.g., *Anisotoma*); sometimes with setose or glabrous apex.
114. Larva: sclerotization of body variable.
115. Larva: spiracles probably primitively annular (also in *Platypsyllus*); sometimes "modified annular" or annular-biforous.
116. Larva: urogomphi probably primitively 2-segmented, but in some Leiodinae and some Platypsyllinae 1-segmented.
117. Larva: urogomphi primitively articulated at base; seldom fixed.
118. Larva: abdominal segment 10 probably primitively with numerous fine teeth, but sometimes unarmed (*Platypsyllus* and others).

HYDRAENIDAE

A quite distinctive and no doubt monophyletic family whose taxonomic limits are well established and generally agreed upon. It was earlier included in the Hydrophiloidea, but the shared features (mainly resulting from adaptations to aquatic life) are now usually considered to be parallelisms, because they are outnumbered by several conflicting characters, which seem to be of more fundamental importance (see discussion under Hydrophiloidea). And, as explained under Hydrophiloidea, some of the similarities appear to be rather superficial. The internal hierarchy and classification of Hydraenidae has been discussed by Perkins (1980), Hansen (1991a) and Perkins and Balfour-Browne (1994). Three subfamilies are currently recognized, Hydraeninae (including two tribes, Hydraenidini and Hydraenini), Prosthetopinae (with five tribes) and Ochthebiinae. The aberrant genus *Limnebius*, which were earlier placed in its own subfamily, is now considered a derived member of the tribe Hydraenini (subtribe Limnebiina). There is hardly any doubt that the most primitive Hydraenidae are to be found among those currently included in the tribe Hydraenidini and that the current subfamily division of the Hydraenidae is not quite adequate, i.e., Hydraeninae is probably paraphyletic. The monophyly of Hydraenidae is supported by several possible apomorphies:

a) 6th antennal segment cupuliform (fig. 76, 78); in forms with a reduced number of proximal antennal segments the morphological 6th segment may be the actual segment 4 or 5 (fig. 77). In some clearly derived forms it is only weakly cupuliform. Apparently this is a unique character; the antennal cupule of the Hydrophiloidea is interpreted as the 8th morphological segment, though (as result of reduction in the number of segments), it often appears as the actual 6th.
b) Male genitalia with the apparent internal sac of aedeagus permanently everted (unique) (fig. 166-168).

1:1*. Clypeus large (convergent in several other groups).

2:0. Frontoclypeal suture grooved. The character was indicated as ambiguous for a hypothetical hydraenid-ptiliid ancestor (clade 42), but it is assumed that this ancestor had a distinct, non-grooved suture as in related taxa. The suture would then have become grooved in Hydraenidae and lost in Ptiliidae.

5:0*. Head with a pair of interocular grooves on frons. Such grooves are absent only in some clearly derived forms (e.g., *Limnebius*).

6:1. Gular sutures confluent, so the gula is reduced to a small posterior sclerite. This is probably a hydraenid autapomorphy, but it should be mentioned that, in the sistergroup of Hydraenidae (Ptiliidae), gular sutures are not distinct, so it is impossible to tell if the gular sutures were already confluent in the common hydraenid-ptiliid ancestor.

10:0*. Mesal face of mandibles with a projecting, movable lobe ("prostheca").

15:1*. Antennae used to break surface film in aquatic respiration (convergent in Hydrophiloidea, see under that).

19:4. Antennae with well differentiated 5-segmented, hydrofuge pubescent club (pre-club segments nearly glabrous). In some derived forms (e.g., *Podaena*) the club is more weakly demarcated and almost glabrous or (e.g., *Prosthetops*) the number of club segments is reduced. The character was indicated as ambiguous for a hypothetical hydraenid-ptiliid ancestor, but it is assumed that the sharply demarcated 5-segmented club of Hydraenidae (and the 3-segmented club of Ptiliidae) is a modification of the weakly or more gradually developed (ca. 5-segmented) club found in related taxa (at least more primitive groups of Agyrtidae and Leiodidae).

36:1*. Ventral surface of body with dense, hydrofuge pubescence (convergent in Hydrophiloidea, see under that).

66:0*. Ventral face of elytra with medio-lateral binding patch of microscopic spines (also in several other groups; possibly convergent).

78:1*. Aedeagus asymmetrical, often very complex.

89:1*. Eggs covered by a silk web. I have tentatively followed previous authors in considering this a basal hydraenid feature, though this is not necessarily true (see also above under Hydrophiloidea, which are superficially similar in this regard).

93:0*. The presence of epistomal (fronto-clypeal) suture was indicated as a hydraenid autapomorphy by the outcome of the analyses. Such a suture is absent in other Staphylinoidea as well as in Hydrophiloidea and Histeroidea, but is present in other relatively basal groups of polyphagan beetles (e.g., Scarabaeoidea, and to some extent Derodontidae), and it may be more likely that this suture has been lost independently in, e.g., the hydrophiloid-histeroid group and other Staphylinoidea.

101:2*. Larval mandibles with rudimentary setose area on mesal edge.

119:1*. Adults aquatic (convergent with Hydrophiloidea, see under that).

The presence of cephalic egg-bursters (91:1) (Emden, 1946; Crowson, 1981) has been considered a derived feature, and a possible synapomorphy with Hydrophiloidea, but it is equally likely, on the basis of our present knowledge, that it is a plesiomorphic feature (see also under Hydrophiloidea and Derodontidae).

ANNOTATIONS TO CHARACTERS:

2. Frontoclypeal suture primitively grooved, except *Limnebius*, in which only a fine line is visible (secondary).
3. Primitively, head is abruptly constricted immediately behind eyes; in some derived forms (*Podaena* etc.) constricted further behind eyes.
4. Paired ocelli present in Prosthetopinae, most Ochthebiinae and Hydraeninae: Hydraenidini (+ *Mesoceration*); absent in most Hydraeninae: Hydraenini.
12. 4th segment of maxillary palpi probably primitively (at least) as large as 3rd; in Ochthebiinae markedly smaller (secondary).
14. 3rd segment of labial palpi generally narrower than 2nd, except in *Limnebius* (secondary), but not shorter.
16. Antennae primitively 11-segmented (e.g., most Hydraeninae: Hydraenidini and *Podaena*); many reductions occur: 10, 9 or 8 segments in some taxa.
25. Hypomeron with processes behind procoxae, but only in a few derived forms (Hydraeninae: *Hydraena, Adelphydraena, Coelometopon*) meeting with an intercoxal process to form complete closure of procoxal cavities.
26. Prosternal intercoxal process primitively present, but short, and for most of its length concealed beneath procoxae; only in few derived forms with well developed intercoxal process (Hydraeninae: *Hydraena, Adelphydraena, Coelometopon*).
31. Mesosternum normally indistinctly demarcated from mesepisterna (or completely fused to them); but in, e.g., *Limnebius* well demarcated (secondary).
44. Spiracles small, but probably all functional (only *Ochthebius* examined).
47. 6th abdominal tergum coriaceous (like 7th), but hardly to be considered well sclerotized.
51. Intercoxal process of abdominal sternum 2+3 primi-

tively and generally acute; sometimes blunt and broader (e.g., some Ochthebiinae).

61. Posterior coxae primitively and generally contiguous (or nearly so), but more broadly separated, e.g., in some Ochthebiinae (secondary).
67. Elytra primitively complete and rounded posteriorly; in *Limnebius* truncate (secondary), but still covering abdomen, except for extreme apex.
83. Parameres primitively present, paired; sometimes one of them rudimentary or absent (e.g., *Parhydraenida*), or without parameres (some genera of both Hydraeninae and Ochthebiinae).
90. Larva: head semi-hypognathous to prognathous.
105. Larva: galea with fringes in *Hydraena*, not in *Ochthebius* – primitive condition doubtful.
108. Larva: apical segment of maxillary palpi "frequently with minute appendage (perhaps a sensillum)" (-Bøving and Henriksen, 1938).
113. Larva: 1. instar without thoracic or abdominal egg-bursters (Emden, 1946; Crowson, 1981).

PTILIIDAE

A well defined, no doubt monophyletic family, which is supported by several autapomorphies. There is general agreement of the taxonomic composition of the family except that one subfamily, Cephaloplectinae (= Limulodinae), has sometimes been given rank of separate family. Currently, four subfamilies are recognized, viz. Ptiliinae, Nanosellinae, Acrotrichinae and Cephaloplectinae. Whereas the latter three subfamilies seem to be relatively characteristic and probably monophyletic, the Ptiliinae are obviously a paraphyletic group, which includes the more primitive members of the family. Among the described genera, *Nossidium* seems to be the most generalized ptiliid, and it is likely that it forms the sistergroup of all other ptiliids and should be placed in a separate subfamily. It is the only described ptiliid genus in which parameres are present in the male genitalia and its hindwings are not so modified as those of other ptiliids (except *Motschulskyum*). A phylogenetic analysis and of the Ptiliidae is in preparation by M. Sörensson (pers. comm.). The following apomorphies may define the family:

a) Antennal segment 3 inserted in deeply concave apex of segment 2 (unique) (fig. 79, 80).
b) Abdominal terga with curved transverse strigae (unique); such strigae are least evolved in *Nossidium* (fig. 123), in which they present a transitional state between mesally directed microtrichia (of other beetles) and typical "strigae" of more derived ptiliids (fig. 124). The strigae are possibly lost in the apterous Cephaloplectinae (not examined).
c) Abdominal terga each with a transverse carina bearing macrosetae (unique) (fig. 124); in the primitive genus *Nossidium* only the rows of macrosetae are present (fig. 123). Such carinae and setae are absent (lost) in Cephaloplectinae, probably correlated with loss of hindwings.
d) Hindwings fringed with very long barbed setae (unique) (fig. 151, 152); setae a little shorter and apparently more coarsely and sparsely barbed in the primitive genus *Nossidium.*

2:2. Frontoclypeal suture absent. The character was indicated as ambiguous for a hypothetical hydraenid-ptiliid ancestor (clade 42), but it is assumed that this ancestor had a distinct, non-grooved suture as in related taxa. The suture would then have become lost in Ptiliidae and grooved in Hydraenidae.

4:1*. Head without ocelli; probably a reversal within clade 44 (convergent with some members of the other families of this clade, i.e., Agyrtidae, Leiodidae and Hydraenidae).

6:2. Gular sutures absent. The character was indicated as ambiguous for a hypothetical hydraenid-ptiliid ancestor, but this is only a result of the gular sutures being confluent in Hydraenidae instead of separate as in other related groups. The absence of sutures in Ptiliidae is unique among related taxa.

7:1*. Cervical sclerites absent.

12:1*. Apical (4th) segment of maxillary palpus markedly smaller than penultimate.

19:2. Antennae with relatively well defined 3-segmented club (not sharply delimited in regard to pubescence); normally the middle (3rd-8th) antennal segments are very thin and, like the club, with erect setae; the thicker antennae of Cephaloplectinae and some Nanosellinae are probably secondary. The character was indicated as ambiguous for a hypothetical hydraenid-ptiliid ancestor, but it is assumed that the 3-segmented club of Ptiliidae (and the sharply demarcated 5-segmented club of Hydraenidae) is a modification of the weakly or more gradually developed (ca. 5-segmented) club found in related taxa (at least more primitive groups of Agyrtidae and Leiodidae).

24:1*. Procoxal fissure absent, trochantin concealed.

32:1*. Mesosternum and mesepisterna fused.

54:1*. Inflexed dorsal portion of abdominal sterna without microtrichia.

56:1*. Tarsi very thin, almost appearing as composed of a single long segment (basal segments very small and to some degree retracted into tibial apices).

57:0*. Anterior coxae not projecting.

59:1*. Posterior coxae "triangular", neither expanded laterally nor caudally (except in some genera with large "coxal plate" concealing the femur in repose).

60:1*. Posterior coxae with excavate posterior face, which conceals a smaller or greater portion of femur in repose, sometimes with large coxal plate.

63:1*. Tarsi 3-segmented (apparently 1-segmented, cf. above under char. 56).

74:4*. Hindwings without distinct veins posterior to medial bar (could only be examined in *Nossidium*; almost all other ptiliids have extremely modified/rudimentary wing venation).

96:5*. Larvae with no more than a single stemma on each side of head (stemmata have only been recorded from a single, *Nossidium*-like species (Dybas, 1976); in other ptiliids stemmata are completely absent).

114:1*. Abdomen largely membranous, normally without distinct terga or sterna.

116:1*. Urogomphi 1-segmented (absent in some forms, e.g., *Nanosella*).

ANNOTATIONS TO CHARACTERS:

1. Clypeus not demarcated, but small, judging from antennal placement.
3. Head constricted immediately behind eyes, but to a much lesser extent than Hydraenidae (only in Cephaloplectinae strongly constricted, apparently at same place, though absence of eyes makes interpretation difficult).
16. Antennae primitively 11-segmented, but in Cephaloplectinae with 10 or fewer segments (secondary).
23. Pronotum (i.e., the hypomeron) joins with prosternum, but is not demarcated by a suture.
26. Prosternal intercoxal process primitively short and with its major portion concealed under procoxae, but in Cephaloplectinae the process is extremely large and well developed (not widened behind procoxae).
30. Character state not determined (mesosternum completely fused to mesepisterna).
35. Metepisterna primitively very narrowly exposed (its major portion vertical), often concealed under elytra.
38. Abdominal segments generally with one paratergite on each side; only in *Nossidium* there is a suggestion of 2 (secondary?).
47. Primitively, abdominal terga 1-6 are not well sclerotized (e.g., *Nossidium*); some derived taxa with shortened elytra have fewer non-sclerotized terga, e.g., only tergum 1-3 in *Pteryx*, and only tergum 1-2 in *Acrotrichis* and Cephaloplectinae.
50. Primitively, abdominal sternum 2+3 carinate anteromedially between hind coxae (as, e.g., *Nossidium*); in most other, more derived, taxa non-carinate (*Ptenidium, Pteryx, Acrotrichis*, Cephaloplectinae, etc.).
51. Primitively, abdominal sternum 2+3 with acute intercoxal process (as, e.g., *Nossidium*); most other, more derived, taxa with broader process (*Ptenidium, Pteryx, Acrotrichis*, Cephaloplectinae etc.).
61. Posterior coxae primitively contiguous (as in *Nossidium*); in all other forms seen more-or-less separate (secondary).
62. Hind coxae reaching lateral edges of body in *Nossidium* (primitive condition); in several other ptiliids not reaching so far laterally.
65. Primitively, epipleura are well developed and well demarcated (deflexed), as in *Nossidium*; narrower and demarcated by a fine line in *Ptenidium*; not or hardly demarcated in other taxa.

67. Elytra primitively covering abdomen and not truncate (e.g., *Nossidium, Ptenidium, Ptilium*), but in several derived forms truncate and leaving part of the abdomen exposed (e.g., *Pteryx*, most *Ptinella, Acrotrichis*, and especially Cephaloplectinae).
69. Primitively (and generally), hindwings cover about abdominal terga 1-5 (hindwings absent in, e.g., Cephaloplectinae).
73. Hindwings without medial loop (only *Nossidium* has veins that are more-or-less comparable to those of other beetles; venation extremely reduced in other ptiliids).
82. Aedeagus primitively long and tubular (e.g., *Nossidium*, Cephaloplectinae), but often abbreviated (e.g., *Acrotrichis*).
83. Parameres primitively present ("leiodid-like"), as in *Nossidium*; in all others absent (secondary).
88. Spermatheca with "sperm pump" generally very well developed; short in *Nossidium*; apparently rudimentary (dentiform-conical) in Cephaloplectinae.
94. Larva: dorsal ecdysial lines of head mostly indistinct (indicated, e.g., in some *Acrotrichis*).
108. Larva: apical segment of maxillary palpi with apparent sensory appendage ("terminal tuft" sensu Dybas, 1976).
118. Larva: usually with one pair of anal hooks (absent in Cephaloplectinae).

SCYDMAENIDAE

A quite distinctive family, whose systematic limits are now generally agreed upon. The relationship to other staphylinoids is, however, somewhat obscure. Scydmaenids has often been regarded as closely related to pselaphids, but their resemblance to these are undoubtedly superficial. Crowson (1955) indicated that they might be allied to the Leiodidae (Anisotomidae of Crowson). More recently, Lawrence and Newton (1982) suggested that they should be included in a group of staphylinid subfamilies (together with Oxyporinae, Megalopsidiinae, Steninae, Euaesthetinae, Leptotyphlinae, Paederinae, Staphylinae and perhaps Silphidae). Naomi (1985) considered the Scydmaenidae as the sistergroup of Scaphidiidae and placed them next to his "Oxyporidae" (i.e., Oxyporinae, Megalopsidiinae, Steninae, Euaesthetinae, Leptotyphlinae, and Pselaphinae (s.lat.)). Neither of these relationships could be confirmed by the present analysis. Rather the scydmaenids seem to have a more basal position within the staphylinid group (justifying their formal rank of separate family). Two subfamilies of scydmaenids are currently recognized, viz. Scydmaeninae and Mastiginae, but the phylogeny of the family seems to be inadequately known and it is seems likely that at least the Scydmaeninae constitute a paraphyletic group. Probably, *Eutheia* (of the scydmaenine tribe Eutheiini) can be regarded as one of the least derived scydmaenids. It exhibits such presumedly plesiomorphic features as, e.g., presence of a lateral canthus on pronotum, relatively broad neck and weakly developed antennal club; also the relatively well developed urogomphi of the larva (cf. below) is suggestive of a basal position within the family. The following possible autapomorphies, some of which are depending on the exclusion of the family from the above mentioned assemblage of staphylinid subfamilies, may support the monophyly of the Scydmaenidae:

a) Femora more-or-less clavate, i.e., with narrow basis and swollen distal portion (fig. 135, 139) (apparently almost unique).
b) Larva with stemmata, when present, aggregated (apparently unique within Staphylinoidea).

3:2*. Head with abruptly constricted neck (well behind eyes); probably convergent with the more derived members of the staphylinid group.

7:1*. Cervical sclerites absent.

9:1*. Mandibles without mola (probably convergent with, e.g., some staphylinid subfamilies).

12:1*. Apical (4th) segment of maxillary palpi markedly smaller than penultimate; the large apical segment of some Mastiginae (*Mastigus*) is undoubtedly a secondary feature.

14:1. Third segment of labial palpi narrower than second. The basal staphylinoid condition of this character is ambiguous, but it is assumed that the condition found in Scydmaenidae is derived (convergent in several other staphylinoids) (see also clade 66).

24:1. Procoxal fissure closed, trochantin concealed. The basal condition of this character in the staphylinid group (clade 65) is not certain, but it is assumed that the closed fissure of Scydmaenidae is derived (hence, convergent with Scaphidiidae).

27:1. Procoxal cavities closed internally. The basal condition of this character in the staphylinid group (actually the entire Staphylinoidea, clade 66) is ambiguous, but it is tentatively assumed that the internally closed coxal cavities of Scydmaenidae represents a derived feature (hence, convergent with Scaphidiidae).

34:1*. Mesocoxal cavities not demarcated by a ridge posteriorly; except for a few Staphylininae (e.g., *Xantholinus*) and a few Aleocharinae (*Hygronoma*), all other staphylinoids (as well as scarabaeoids, hydrophiloids and histeroids) have the mesocoxal cavities delimited posteriorly.

35:1*. Metepisterna concealed (as in the presumedly primitive genus *Eutheia* and most other Scydmaeninae; in *Scydmaenus* and Mastiginae the episterna are exposed, but this is tentatively regarded as secondary).

50:2. Basal ventrite not at all carinate. The basal condition of this character in the staphylinid group (clade 65) is ambiguous, but it is assumed that the completely non-carinate basal ventrite of Scydmaenidae is derived and, hence, convergent with Scaphidiidae (several other taxa are similar, but more clearly convergent).

59:1*. Posterior coxae triangular or more-or-less conical, neither expanded laterally nor caudally (probably convergent with some staphylinid subfamilies).

61:1. Posterior coxae more-or-less broadly separated. The basal condition of this character in the staphylinid group (clade 65) is ambiguous, but it is assumed that the broadly separated posterior coxae of Scydmaenidae represents a derived feature (convergent with Scaphidiidae).

65:1*. Epipleura not demarcated from dorsal portion of elytra; only in the genus *Mastigus* (but not other Mastiginae) is there a weak suggestion of a very blunt ridge laterally on the elytra, but this is almost a secondary feature (probably convergent with, e.g., some staphylinid subfamilies).

72:1*. Hindwing without anal lobe (probably convergent with Ptiliidae, Hydraenidae, Leiodidae, and a few Staphylinidae).

86:2*. Female gonocoxites without styli (probably convergent with, e.g., some staphylinid subfamilies).

96:3*. Larval head with no more than 3 stemmata on each side (sometimes with 1 or 0) (several parallelisms).

97:1*. Larva with labrum fused to head capsule (probably convergent with, e.g., some staphylinid subfamilies).

109:1*. Larval ligula absent.

116:1*. Larva with 1-segmented (not 2-segmented) urogomphi; this is probably the ancestral scydmaenid condition; the urogomphi are best developed in the presumedly primitive Eutheiini, smaller in some groups, and have been completely lost in most scydmaenids (probably convergent with, e.g., Dasycerinae, Micropeplinae and Pselaphinae).

117:1*. Larva with fixed (not articulated) urogomphi (urogomphi lost in most forms, see under the previous character); probably convergent with, e.g., Dasycerinae, Micropeplinae and Pselaphinae (Pselaphidae auct.).

Naomi (1985) mentioned a few more possible scydmaenid autapomorphies, notably the presence of two pairs of large foveae at the pronotal base. Although such foveae are not always present, they are found in most forms including the presumedly more primitive ones (e.g., *Eutheia*). Likewise, the presence of foveae at the elytral base may be an autapomorphy.

The complete absence of elytral striae is probably also an autapomorphy of the Scydmaenidae (convergent in several other groups); only *Clidicus* (Mastiginae) has striae, but this is probably secondary (only 6 striae are present, but they are evenly spaced, so there is no obvious homologies to the primitive polyphagan 10 striae).

ANNOTATIONS TO CHARACTERS:

2. Frontoclypeal suture probably primitively present as fine line (as most Scydmaeninae); grooved in Mastiginae; sometimes indistinct (e.g., *Eutheia*).
4. Apparently ocelli are generally absent; but in *Eutheia*, the frons may have a pair of interocular paler spots, which could represent rudiments of ocelli.
5. Interocular grooves generally (and primitively) absent; secondary grooves present in some *Nevraphes* spp. (Scydmaeninae).
6. Gular sutures generally present, separate; sometimes indistinct *(Scydmaenus)*.
11. Lacinia normally (and primitively) not reaching apex of galea, except in *Mastigus* (secondary).
17. Antennae primitively inserted somewhat laterally; in Scydmaeninae inserted below a distinct lateral frontal canthus; in Mastiginae inserted more mesally on dorsum of head, but still demarcated posteromedially by a ridge.
19. Antennae primitively gradually, and not strongly thickened distally; often with c. 3 apical segments more-or-less enlarged and forming a more-or-less well demarcated club (secondary).
20. Antennal segments probably primitively without periarticular grooves; however, in *Eutheia*, penultimate segments have grooves similar to those of Leiodidae (though more "open"). Provisionally, the grooves of *Eutheia* are considered secondary, but it should be mentioned that the *Eutheia* has a suggestion of "leiodid" antennal club (i.e., interrupted by small segment 8).
21. Pronotum probably primitively with lateral ridge separating dorsal portion from hypomeron (as, e.g., *Eutheia, Cephennium, Nevraphes* etc.), but without such ridge in most others (secondary).
25. Hypomeron generally (and primitively) without processes, except for a very blunt and short process in *Mastigus* (secondary).
26. Prosternal intercoxal process variable, generally present, but short.
30. Mesosternum sometimes fused to mesepisterna, e.g., in *Mastigus* (secondary).
33. Mesocoxal fissure open, primitively exposing trochantin (as in *Eutheia*); trochantin sometimes not distinctly exposed.
37. Laterosternite 2 primitively distinct (as, e.g., *Eutheia*); indistinct ("absent") in others, e.g., *Mastigus*, which has very reduced dorsal tergites.
38. Normally (and primitively), one paratergite is present on each side (*Scydmaenus* etc.); in *Eutheia* abdominal sternites have sublateral ridges, giving the appearance of two paratergites being present (secondary).
40. Generally with segment 8 exposed; in *Mastigus* (not all Mastiginae) also the 9th is exposed (secondary).
44. Abdominal spiracles primitively present on segment 1-8 (e.g., *Scydmaenus*); apparently reductions occur in *Cephennium* (spiracles only distinct on 1-5), *Mastigus* (spiracles indistinct).
45. Abdominal spiracles located in terga, near lateral edge, in segment 4-8 (sometimes terga are more membranous).
46. Abdomen with patches of microtrichiae on terga 1-5 in *Eutheia* (probably primitive state); however, in most other (winged) forms, with more developed patches covering also tergum 7 (e.g., *Scydmaenus*); in wingless forms patches are absent (*Cephennium, Mastigus*).
47. Abdomen with tergites 6-8 sclerotized in *Eutheia* (primitive condition?); in most taxa only 7-8 are sclerotized (secondary?); in *Scydmaenus*, terga becomes gradually less sclerotized anteriorly, but are generally slightly sclerotized.
52. Coxal cavities of abdominal sternum 2+3 generally present; but in *Mastigus* their posterior ridge has become obsolete (probably secondary).
58. Mesocoxae generally globular; but in *Mastigus* somewhat conically projecting (not transverse).
60. Posterior coxae normally with oblique posterior face (but in *Eutheia* excavate and with small "coxal plate" mesally).
62. Posterior coxae primitively reaching lateral edges of body (e.g., as in *Eutheia*), but variable and in some forms not reaching so far laterally.
64. Ventral face of elytra normally without sublateral ridge or lamina (only in *Scydmaenus* with small anterior lamina, and in *Cephennium* with weak ridge anteriorly).
65. Generally, epipleura are not at all demarcated; only in *Mastigus* is there a suggestion of a very blunt ridge laterally on elytra (this is probably secondary, since it is not distinct in other Mastiginae).
66. Ventral face of elytra without medio-lateral patch of microspines, but baso-lateral patch present in some forms (e.g., *Scydmaenus, Mastigus*).

67. Elytra probably primitively truncate and covering about abdominal terga 1-6 (as in *Eutheia*; in *Cephennium* covering 1-7); in most other taxa, the elytra are rounded at apex and conceals abdomen completely (secondary?).
74. Hindwing with 1 vein posterior to (and rather close to) medial bar (sometimes not distinct).
106. Larva: maxillary palpi usually (and probably primitively) 3-segmented (but 2-segmented in *Eutheia*, 4-segmented in *Mastigus*).
114. Larva: thoracic and abdominal terga consisting of one or (secondarily?) more sclerites.
118. Larva: abdominal segment 10 probably primitively with several hooks, but sometimes unarmed.

SCAPHIDIIDAE

A very distinctive group, which is no doubt monophyletic. Although there is general agreement in regard to the systematic limits of the group, its formal rank has been subject to some dispute. Traditionally, it has been considered a distinct family but more recently some authors have included it (as a subfamily) in the Staphylinidae, near the subfamilies Piestinae, Osoriinae and Oxytelinae (e.g., Lawrence and Newton, 1982). A close relationship to these subfamilies could not be confirmed by the present analyses, and neither could a sistergroup relationship with the Scydmaenidae (suggested by Naomi, 1985). Rather, the scaphidiids appear to have a relatively basal position within the staphylinid group, which may justify them as having rank of separate family. The phylogeny of the group is not well understood and the present division into tribes (see, e.g., Newton and Thayer, 1992) may have to be modified to some extent. However, it will probably be safe to regard such genera as, e.g., *Scaphium* and *Ascaphium* as some of the most primitive forms (cf. Crowson, 1955). In addition to the distinctive, wedge-like body form (fig. 344-346), the following autapomorphies may support the monophyly of the Scaphidiidae:

a) First ventrite very long, at least as long as the three following ventrites combined (unique).
b) Pronotum more-or-less produced posteromedially to form a subtriangular or rounded projection in front of scutellum (fig. 344-346).

1:1*. Clypeus relatively long (also in some other groups, e.g., Hydrophiloidea, Hydraenidae and Silphidae, no doubt convergent).

6:1*. Gular sutures confluent, gula reduced to a short transverse triangle at the rear of the head.

19:4*. Antennae with well differentiated, densely pubescent, 5-segmented club (pre-club segments nearly glabrous); this is very obvious in the more primitive forms (*Ascaphium*, *Scaphium*, *Scaphidium*), but in more derived forms (e.g., *Scaphisoma*) the club becomes less strongly demarcated though it is still distinct. In some derived forms segment 8 becomes smaller than adjacent segments, so the antennae are similar to those of the Leiodidae.

24:1. Procoxal fissure closed, trochantin concealed (probably convergent with Scydmaenidae). This seems to be almost general for the family and is found in such primitive forms as, e.g., *Ascaphium*; however, in *Scaphium* there is a very small opening, but this is tentatively considered as secondary. The basal condition of this character in the staphylinid group (clade 65) is not certain, but it is assumed that the closed fissure of Scaphidiidae is derived (hence, convergent with Scydmaenidae).

27:1. Procoxal cavities closed internally. The basal condition of this character in the staphylinid group (actually the entire Staphylinoidea, clade 66) is ambiguous, but it is tentatively assumed that the internally closed coxal cavities of Scaphidiidae represents a derived feature (hence, convergent with Scydmaenidae).

37:0*. Laterosternites of 2nd abdominal segment not distinct.

50:2. Basal ventrite not at all carinate. The basal condition of this character in the staphylinid group (clade 65) is ambiguous, but it is assumed that the completely non-carinate basal ventrite of Scaphidiidae is derived and, hence, convergent with Scydmaenidae (several other taxa are similar, but more clearly convergent).

61:1. Posterior coxae broadly separated (secondarily almost contiguous in Toxidiini). The basal condition of this character in the staphylinid group (clade 65) is ambiguous, but it is assumed that the broadly separated posterior coxae of Scaphidiidae represents a derived feature (convergent with Scydmaenidae).

62:1*. Posterior coxae ending laterally distinctly before lateral edges of body.

70:0. Folded hindwings overlap by less than half the width of one folded wing at their apices (possibly a reversal within the Staphylinid group, which may be basally characterized by completely overlapping wings, see also under clade 65).

74:2*. Hindwing with two (rather than just one) vein posterior to the medial bar; this is probably the primitive condition within the family, but more derived forms (e.g., *Scaphisoma*) have only one such vein. As discussed above (cf. Agyrtidae), the number of such veins is probably correlated with the size of the species, so its phylogenetic significance may not be great.

96:1*. Larval head with 5 pairs of stemmata. Although this is apparently the usual condition within the family there are deviations with regard to the number of stemmata (sometimes 6 pairs, sometimes 3 pairs). Therefore the initial assumption that 5 pairs is the basal number for the family may not necessarily be true. If 6 pairs of stemmata is the ancestral scaphidiid feature, no character change has taken place.

It is likely that some degree of reduction of the elytral striae also represents a scaphidiid autapomorphy. In the presumedly primitive genera *Ascaphium* and *Scaphium* the elytra have only 6 distinct striae, apparently representing striae 1-6 of the ancestral polyphagan 10 striae (i.e., there is a broad non-striate interstice lateral to 6th stria). Hence, it seems likely that the presence of not more than 6 (?or 7, as in *Cyparium*) is a basal, autapomorphic characteristic of the family; all other scaphidiids seen have only a sutural stria.

ANNOTATIONS TO CHARACTERS:

3. Head generally without constricted neck (a weak suggestion is found in *Scaphium* and especially *Ascaphium*, but they are still considered "without neck", although they may represent the primitive condition for the group); sometimes slightly constricted immediately behind eyes (*Scaphidium*: probably secondary).
8. Mandibular apices projecting, but because of the enlarged labrum they are only narrowly visible.
17. Primitively (as in *Ascaphium* and *Scaphium*), antennae are inserted laterally under lateral canthus of frons, though very near level of anterior margin of eyes; in more derived forms the antennae are inserted more dorsally and closer together, but still a fine "lateral" canthus can be seen (except in Heteroscaphini, which have the antennae inserted near the posteromesal corners of the eyes).
25. Hypomeron generally (and primitively) without projections, as in *Ascaphium* and most other forms examined; only *Scaphium* has very blunt and short projections (secondary).
41. Abdominal tergo-sternal membranes short, but first from segment 5 (and to some extent 4; segments 1-3 largely non-sclerotized dorsally).
47. Abdominal terga sclerotized from the 4th (tergum 4 not as strongly sclerotized as 5).
72. Primitively with demarcated anal lobe (as in *Scaphium* and *Scaphidium*, smaller and less demarcated in the latter); sometimes without anal lobe (e.g., *Scaphisoma*).
93. Larva: frontoclypeal suture probably primitively absent (but in some forms with transverse line joining the frontal arms anteriorly).
114. Larva: thoracic and abdominal terga consisting of one or (secondarily?) more sclerites.
116. Larva: urogomphi primitively 2-segmented (as in *Scaphium*); but sometimes 1-segmented (*Cyparium*) or absent (some *Baeocera*).

EMPELIDAE

This group includes only a single odd species, *Empelus brunnipennis*, from western North America. The systematic position of this species has been subject to some dispute. It was originally placed in near the genus *Clambus*

(Clambidae), at that time included in the Silphidae (auct.), and was later transferred to the Leiodidae (Crowson, 1955, as "Anisotomidae"). Subsequently, Crowson (1960) considered it as one of the most primitive staphylinoids and later (Crowson, 1981), he listed "Empelidae" as a distinct staphylinoid family. Hammond (1971) suggested a close relationship with the Proteininae. The first formal description of the group was given by Newton and Thayer (1992) who considered it a primitive member (of uncertain affinities) of the omaliine group. Newton and Thayer (1995) maintained it in this systematic position but the present analysis indicates that *Empelus* may have a more basal position within the staphylinid group, and for this reason it is tentatively treated as a distinct family. In addition to the distinctive body form (compact, dorsally convex, with power of rolling up and hypognathous head), the following characters are possible autapomorphies of the Empelidae:

2:2*. Frontoclypeal suture absent.

19:2*. Antennae with 3-segmented club.

29:1*. Promesothoracic connecting membrane with pair of sclerites associated with mesothoracic spiracles and connected by a narrow sclerotized bar (also found in some staphylinids, e.g., Oxytelinae, Omaliinae and Proteininae, probably convergent).

35:1*. Metepisterna concealed.

46:3*. Abdominal tergum 5 without patches of wing folding setae (reduction) (also reduced in, e.g., most Staphylinidae, probably convergent).

48:1*. Abdominal sternum 8 with a pair of gland openings at anterior margin. This structure is often regarded as uniquely derived for a group of staphylinids ("omaliine group", cf., e.g., Lawrence and Newton, 1982), but it was indicated by the present analysis that this may not be the situation. Hence, it is possible that the "omaliine" type of gland complex has evolved independently in Empelidae, in Dasycerinae-Pselaphinae (Staphylinidae), and in Omaliinae-Microsilphinae-Proteininae-Neophoninae (Staphylinidae).

58:1*. Middle coxae transverse.

60:1*. Posterior coxae with excavate posterior face, which conceals basal portion of femur in repose.

66:0*. Ventral face of elytra with medio-lateral binding patch.

Several of these autapomorphies were also found by Newton and Thayer (1995) who further mentioned, e.g., antennal groove present immediately below eye; tarsal empodium with only one seta; femora with tibial grooves. Other characters given by Newton and Thayer (l.c.), e.g., the long elytra and the absence of ocelli, rely on a subordinate position of *Empelus* within the omaliine group of Staphylinidae and was therefore not indicated as apomorphies in the present analysis.

ANNOTATIONS TO CHARACTERS:

67. Elytra slightly obliquely truncate posteriorly; no more than 3 abdominal segments exposed.
72. Anal lobe of hindwing very small, fringed with 6-7 long setae.

MICROSILPHINAE

This group includes only the genus *Microsilpha* (Newton, 1985; Newton and Thayer, 1995). The systematic position of the genus has been subject to some dispute. It was originally referred to Silphidae (auct.), then to different parts of the Leiodidae, and is now considered closely related to the omaliine (and allied) Staphylinidae. Its affinities with this group of subfamilies seems undeniable but the exact relationship is not evident. Lawrence and Newton (1982) regarded the group as a distinct subfamily, and though Newton and Thayer (1992) included it as a tribe (Microsilphini) in Omaliinae, they (Newton and Thayer, 1995) subsequently considered it of subfamily rank. The following characters may support the monophyly of the Microsilphinae:

3:0*. Head without constricted neck.

5:1. Head without interocular grooves, probably a reversal within clade 56 (the character could also be interpreted as a basal feature of clade 56, in which case interocular grooves have evolved independently in Omaliinae and Proteininae-Neophoninae (clade 55)).

9:1*. Mandibles without mola.

11:1*. Lacinia elongated, reaching apex of galea.

12:1*. 4th segment of maxillary palpi markedly smaller than 3rd.

13:1*. First segment of labial palpi longer than second.

19:2*. Antennae with 3-segmented club.

50:2*. First ventrite not carinate (not even between posterior coxae) (convergent with, e.g., Proteininae and Micropeplinae).

78:1*. Aedeagus with asymmetrical parameres.

Also the 5-segmented maxillary palpi and 4-segmented labial palpi (i.e., each with an "extra" minute apical segment) are autapomorphic. A number of additional autapomorphies are given by Newton and Thayer (1995), e.g., apices of antennal segments 9-10 and apical excavation of segment 11 with dense fields of large setiform sensilla; spiracles of abdominal segment 8 reduced and non-functional; male genital segment with Y-shaped anteroventral sclerite. The long elytra was also considered autapomorphic by Newton and Thayer but – as is the case with certain other features – this interpretation is more crucially depending on a correctly reconstructed phylogeny because it is shared with several fairly closely related taxa.

The presence of a straplike basal piece in the male genitalia (81:1) could also be interpreted as an apomorphy of Microsilphinae (convergent with Proteininae and Neophoninae (clade 55)), but is perhaps more likely to be an apomorphy of clade 56 with secondary reduction in Omaliinae.

ANNOTATIONS TO CHARACTERS:

14. Labial palpi with small 4th (novel?) segment.

54. Laterosternites without microtrichiae (except for rudiments on segment 2 and 3).

66. Ventral face of elytra apparently without medio-lateral patch of microspines, i.e., a weak patch is present more anteriorly (baso-lateral?).

72. Hindwing with well demarcated, small anal lobe (lobe fringed with long setae).

77. Character state not determined (male tergum 9 and 10 apparently nearly membranous).

87. Female sternum 9 apparently membranous.

OMALIINAE

The present concept of this group is roughly that of Newton and Thayer (1992), except for the exclusion of the Microsilphinae (cf. above) and the inclusion of the genus *Aphaenostemmus* (considered a primitive member of uncertain relationship of the omaliine group and placed in a separate subfamily, Aphaenostemminae, by Newton and Thayer). Recently (after the present analysis was done), Newton and Thayer (1995) reviewed the phylogenetic status of the Omaliinae and in this work the definition of the subfamily agrees with the present one. They also excluded the presumedly primitive genus *Glypholoma* and placed it in a new subfamily, Glypholomatinae (not studied or included in the present analysis). However, the monophyly of the Omaliinae is still not very well supported and should be considered tentative. Only a few possible (weak) omaliine apomorphies were suggested by the present analysis:

74:2*. Medial field of hindwing with 2 veins (rather than only one); apparently a reversal within Staphylinoidea (clade 66), convergent in several other groups (e.g., Proteininae). The character is probably very weak because it often seems to be more depending on size than on phylogenetic relationship (see also under Agyrtidae).

81:2. Aedeagus without basal piece (probably a reversal within clade 56, for which the presence of a straplike (secondary) basal piece may be ancestral); it is also possible, but perhaps less plausible, that a straplike basal piece (81:1) has evolved independently in Microsilphinae and Proteininae-Neophoninae.

85:1*. Female gonocoxites moderately long, narrow and cylindrical (also found in other staphylinids, probably convergent).

116:1. Urogomphi 1-segmented (apparently a general and probably basal omaliine feature). It is likely that 1-segmented urogomphi is an omaliine autapomorphy but insufficient knowledge about larvae in the indicated sistergroup (Microsilphinae) makes the character impossible to interpret adequately at present.

ANNOTATIONS TO CHARACTERS:

2. Primitively probably with clypeus finely demarcated, but in most forms not demarcated.
5. Primitively with interocular grooves; these seldom absent (e.g., *Xylodromus* and *Olophrum*).
11. Lacinia probably primitively shorter than galea (as in *Omalium*); but lacinia and galea prolonged and almost equally long in *Olophrum* (secondary).
12. 4th segment of maxillary palpi generally as large as 3rd; only in Coryphiini small (secondary).
13. Generally, labial palpi with 1st segment not longer than 2nd (seldom, e.g., *Olophrum* slightly longer).
14. Labial palpi with segment 3 narrow in, e.g., *Omalium* and *Anthophagus*, as wide as 2nd, e.g., in *Olophrum*. – Primitive condition doubtful (as *Olophrum*?).
25. Hypomeron with very blunt processes (hardly situated behind procoxae, rather a result of enlarged procoxal fissure).
26. Prosternal intercoxal process very short.
29. Mesothoracic spiracles connected by narrow sclerotized bar (apparently consisting of two lateral and a median sclerite).
46. Abdominal terga 3-4 normally with "wing folding" patches of microtrichia (except, e.g., the apterous *Olophrum*).
50. Abdominal sternum 2+3 probably primitively carinate anteriorly (as *Omalium*), but carina may be blunt (*Olophrum*).
59. Hind coxae rather triangular, but with narrow expansion latero-caudally.
63. Tarsi primitively 5-segmented (except Corneolabini: 4-segmented, cf. Thayer, 1987).
67. Elytra generally truncate posteriorly (except, e.g., some *Eusphalerum*); often long, covering about abdominal terga 1-6 (primitive condition?), but in several Omaliinae (incl. Aphaenostemmini) covering only about 1-2 or 3 (secondary?).
72. Hindwing with anal lobe well demarcated, very small, fringed with long setae (only *Omalium* examined).
96. Larva: probably primitively with 6 stemmata on each side (as, e.g., *Olophrum*), but mostly with 5 (*Omalium, Anthobium, Lesteva* etc.); occasionally without stemmata.
97. Larva: labrum free (apparently subdivided).
99. Larva: mandibles without mola, but sometimes rather broad at base (with pseudomola).
100. Larva: prostheca primitively absent, but in some forms with (secondary) prostheca-like appendage on mesal face.
109. Larva: ligula primitively present (as in, e.g., *Omalium*); but sometimes absent.

PROTEININAE

A small, relatively well defined group of Staphylinidae. There seems to be general agreement about the systematic limits of the subfamily, though sometimes the genus *Metopsia* has been placed in a separate subfamily regarded as the sistergroup of the remaining Proteininae (e.g., Naomi, 1985). Newton and Thayer (1995) recognized five tribes (listed in a sequence from presumedly primitive to more derived forms): Silphotelini, Nesoneini, Austrorhysini, Anepiini and Proteinini (incl. *Metopsia*). The monophyly of the entire subfamily seems to be reasonably well established and may be supported by the following autapomorphies:

2:2. Frontoclypeal suture not distinct. The character was indicated as ambiguous for a hypothetical proteinine-neophonine ancestor (clade 55), but it is assumed that the basal condition of clade 55 was the presence of a non-grooved frontoclypeal suture (as in related taxa), which has become absent in Proteininae and grooved in Neophoninae.

8:1*. Mandibles concealed (when abducted) (also in Micropeplinae and Dasycerinae; probably convergent).

42:0*. Abdominal intersegmental membranes relatively short, hardly one-sixth the length of the adjacent segments (also in the pselaphine group (clade 47); probably convergent).

43:0*. Abdominal intersegmental membranes clear, without the normal staphylinid "brick wall" pattern of minute sclerites (convergent only in a few other staphylinid groups: derived members of the tachyporine group (e.g., Aleocharinae, Habrocerinae, some Tachyporinae), and a few Oxytelinae (*Euphanias*).

74:2*. Medial field of hindwing with 2 veins (rather than only one); apparently a reversal within Staphylinoidea (clade 66), convergent in several other groups (e.g., Omaliinae); the presence of only one such vein in *Megarthrus* is assumed to be secondary. The character is probably very weak because it often seems to be more depending on size than on phylogenetic relationship (see also under Agyrtidae).

77:0*. Lateral sclerites of male abdominal tergum 9 not joined dorsally at base (apparently a reversal within clade 59.

The very long and slender shape of the maxillary mala (fig. 219) found in known proteinine larvae seems to be a unique autapomorphic feature of the subfamily.

It is possible that the presence of a mesal process ("prostheca") (100:0) is also a proteinine autapomorphy, but as the character is not known from the presumed sistergroup (Neophoninae), it can not be adequately interpreted at present. A similar process is found in a few Omaliinae but this may be convergent.

Another possible proteinine autapomorphy may be the presence of a single median ocellus (rather than paired ocelli) (char. 4), but this is only found in a single genus (*Metopsia*), which may not be considered the most primitive proteinine. The absence of ocelli in all other members of the subfamily, including the forms that are normally considered to be the most primitive, suggests that the single ocellus in *Metopsia* is an autapomorphy for that particular genus, and that it is more likely the absence of ocelli that should be considered autapomorphic at the subfamily level. Anyway, it is most likely that the Proteininae have evolved from forms with paired ocelli.

A completely non-carinate first ventrite (50:2) was indicated as a proteinine autapomorphy, but after the analysis was completed I became aware that the character is not constant within the subfamily, so the significance of the character is uncertain; possibly the basal condition is an anteriorly carinate basal ventrite (a non-carinate ventrite is also found in, e.g., Microsilphinae, no doubt convergent).

ANNOTATIONS TO CHARACTERS:

25. Hypomeral process short, but probably primitively distinct; absent in *Proteinus* and *Megarthrus* (secondary?).
29. Pro-mesothoracic connecting membrane with large triangular sclerites (in which spiracles are located) in most Proteininae.
46. Primitively with patches of microtrichiae on abdominal terga 2 (posterior corners) and 3 (almost entire tergite), as in *Metopsia* and *Megarthrus*; in *Proteinus* absent on tergum 3 (secondary).
63. Tarsi primitively 5-segmented, sometimes 3- or 4-segmented.
67. Elytra primitively truncate, covering first 2 (or 3) abdominal terga; seldom non-truncate and completely covering abdomen (*Silphotelus*).
72. Anal lobe of hindwing well demarcated, very small, fringed with long setae (examined in *Megarthrus* and *Proteinus*).
81. Aedeagus in primitive forms with strap-like basal piece.
83. Parameres primitively present and paired (in some Proteinini fused or absent).
85. Female gonocoxites mostly present; but sometimes absent (e.g., *Alloproteinus*).
87. Female: valvifers absent (i.e., sternum 9 membranous) in primitive forms; secondarily more sclerotized.
96. Larva: primitively with 6 stemmata on each side, sometimes fewer (i.e., 3 in *Proteinus*).
97. Larva: labrum free (subdivided?).
99. Larva: mandibles without mola, but generally rather broad at base (suggestion of pseudomola).
116. Larva: urogomphi probably primitively 2-segmented (as *Proteinus*); possibly sometimes 1-segmented (as recorded for *Megarthrus* by Paulian, 1941).

MICROPEPLINAE

A relatively small, characteristic and no doubt monophyletic group. Due to its very distinctive general facies, the group has often been given family rank, and some authots (e.g., Paulian, 1941; Crowson, 1955) even doubted its inclusion in the Staphylinoidea. Paulian suggested a close relationship with the cucujoid families Nitidulidae or Latridiidae. However, the inclusion of Micropeplinae in the Staphylinoidea is well justified and there is strong evidence that the micropeplines are a subordinate group of the Staphylinidae (e.g., Thayer, 1987, and present analysis). A close relationship with the Dasycerinae and Pselaphinae (also often considered distinct families) was suggested by previous authors (e.g., Lawrence and Newton, 1982; Thayer, 1987) and has been confirmed by the present analysis, but a close relationship with Proteininae and Omaliinae as suggested by these authors was not indicated here (see also under Neophoninae). The monophyly of the Micropeplinae can be supported by at least the following autapomorphies:

a) Prothorax with well-developed grooves for reception of the antennae (fig. 112) (unique).
b) Larval legs 4-segmented (i.e., trochanter and femur fused (Newton, 1991)); apparently unique.

3:1*. Head abruptly constricted immediately behind eyes (temporae not distinct) (very unusual within Staphylinidae).

8:1. Mandibles concealed (when abducted) (also in Dasycerinae, probably convergent). Alternatively, concealed mandibles could be interpreted as a basal autapomorphy of clade 47 (Micropeplinae-Dasycerinae-Pselaphinae) with subsequent reversal in Pselaphinae.

14:0*. Third segment of labial palpi not narrower than second.

16:2*. Antennae 9-segmented (almost unique within Staphylinidae).

19:1*. Antennae with apical club of one large segment (almost unique within Staphylinidae).

24:0*. Trochantin of anterior legs exposed.

29:1*. Promesothoracic connecting membrane with a pair of sclerites associated with the mesothoracic spiracles and connected by a narrow sclerotized bar (also found in other staphylinids, e.g., Oxytelinae, Omaliinae and Proteininae, probably convergent).

31:1*. Mesosternum fused with mesepisterna.

50:2*. First ventrite not carinate (not even between posterior coxae).

57:0*. Anterior coxae not projecting (i.e., hardly raised above the level of the elevated mesal portion of prosternum).

59:1*. Posterior coxae triangular, not expanded caudally and laterally.

61:1*. Posterior coxae broadly separated (very unusual within Staphylinidae).

62:1*. Posterior coxae not reaching lateral edges of body.

81:1*. Aedeagus with straplike basal piece (probably a secondary feature; see also under Agyrtidae).

85:0*. Gonocoxites separate, relatively short (possibly fused to valvifers). The presence of separate gonocoxites is apparently a reversal within clade 49, in which gonocoxites were indicated as primitively fused. However, there is some uncertainty with regard to the interpretation of this character (see clade 49).

90:1. Head of larva hypognathous (possibly convergent with Dasyscerinae, in which the head is moderately declined). Alternatively, but perhaps less likely, a declined head is a basal apomorphy of the pselaphine group (clade 47) and has become secondarily prognathous in Pselaphinae. In any case, the head is apparently more declined than both Dasycerinae and Pselaphinae, and hence, the character can still be regarded as an autapomorphy of Micropeplinae.

94:1*. Dorsal ecdysial lines of larval head without basal stem.

96:6. Stemmata absent. The character was indicated as ambiguous at clade 47, i.e. either 6 or 0 stemmata might be present. But assuming that repeated losses (rather than gains) of stemmata are more likely, the lower number of stemmata in the different taxa of clade 47 (i.e. also Pselaphinae) is resulting from independent reductions.

104:0*. Galea of larva articulated (not fused) with lacinia, joint-like.

The presence of 3 longitudinal costae on each elytron is probably another autapomorphy, paralleled in certain other staphylinid subfamilies (Dasycerinae, Pseudopsinae, some Osoriinae, etc.). In addition to some of the characters given above Newton and Thayer (1995) listed several possible adult autapomorphies, e.g., antennal groove present immediately below eye; elytral apex with lateral locking notch (also found in Pselaphinae); abdominal segment 3 (as well as 4—6) with reduced spiracles; abdominal tergum 3 (usually also 4-6 or 4-7) with internal projections touching the internal surface of foveae of the corresponding sternum.

Some of the other possible autapomorphies given by Newton and Thayer (l.c.), as well as certain characters given by Naomi (1985), are of more dubious significance because they are also found in fairly closely related taxa and may prove to be synapomorphies for Micropeplinae and other taxa (e.g., the reduced number of tarsal segments).

Exposed mesotoracic spiracles (28:1) and absence of acute intercoxal process on basal ventrite (51:0) could also be interpreted as apomorphic for Micropeplinae, but both characters are ambiguous and are probably rather just plesiomorphic features (see also under Solieriinae).

ANNOTATIONS TO CHARACTERS:

5. Interocular grooves present, but small and situated in transverse neck constriction line.
30. Character state not determined (mesosternum fused with mesepisterna).
35. Metepisterna very narrowly exposed, except posteriorly, where they are broader.
52. The posterior ridge of coxal cavities of abdominal sternum 2+3 becoming somewhat obsolete laterally.
63. Tarsi 4-segmented. – Many authors records them as 3-segmented, but this is not the case with the examined species (*M. porcatus*), and Thayer (1987) states 4-segmented tarsi to be the general condition.
65. Epipleura apparently well demarcated (by the outermost ridge in *Micropeplus*); the socalled "pseudepipleuron" is the lateral deflexed elytral portion.
84. Female: 9th tergum apparently membranous, without sclerites.
87. Valvifers interpreted as present (but difficult to identify).
114. Larva: thoracic and abdominal terga consisting of one or (secondarily?) more sclerites.

NEOPHONINAE

This group includes only a single, very remarkable species, *Neophonus brucki*, whose systematic relationship has been somewhat unclear. It was originally placed in its own tribe, but later included in the "oxyteline" tribe Proteinini (more-or-less equivalent of Proteininae) (e.g., Blackwelder, 1952). More recently, Thayer (1987) reexamined the genus, discussed its systematic position and placed it in a separate subfamily belonging to the socalled "proteinine subgroup" of the omaliine group. The monophyly of the "proteinine subgroup" could not be supported by the present analysis, i.e., some of the subfamilies included by Thayer (Micropeplinae, Dasycerinae, Pselaphinae) was indicated to form a group which is not closely related to other members of the "proteinine subgroup" (Proteininae, Neophoninae). Based on the relationship suggested by the present analysis, Neophoninae may be characterized by the following autapomorphies:

2:0. Head with well-demarcated fronto-clypeal groove. The character was indicated as ambiguous for a hypothetical proteinine-neophonine ancestor (clade 55), but it is assumed that the basal condition of clade 55 was the presence of a non-grooved frontoclypeal suture (as in related taxa), which has become slightly grooved in Neophoninae and absent in Proteininae.

6:1*. Gular sutures confluent, gula reduced to a small posterior triangle on the constricted neck.

11:1*. Lacinia elongated, reaching apex of galea (also, e.g., Dasycerinae, probably convergent).

21:1*. Pronotum with rather weak lateral canthus (coded as absent).

29:0*. Pro-mesothoracic connecting membrane without sclerites (probably secondary loss, i.e., a reversal within clade 58).

31:1*. Mesosternum fused with mesepisterna.

37:0*. Laterosternites of 2nd abdominal segment not distinct.

59:0*. Posterior coxae transverse, expanded caudally and laterally (reversal within clade 59).

63:1*. Tarsi 3-segmented.

66:2*. Ventral face of elytra with strongly iridescent medio-lateral binding patch; the presence of a medio-lateral binding patch is found in some other staphylinid groups (as well as several non-staphylinids), but the very iridescent appearance was otherwise only observed in Dasycerinae (probably convergent).

72:1*. Hindwing without anal lobe.

In addition to some of these characters (e.g., the fused gular sutures) Newton and Thayer (1995) also mentioned, e.g., the presence of adhesive setae on basal segment in all tarsi of both sexes as autapomorphic.

ANNOTATIONS TO CHARACTERS:

35. Metepisterna only partly exposed.
46. Patches of microtrichiae present on abdominal terga 2 (posterior corners) and 3 (almost entire tergite).

DASYCERINAE

A small, undoubtedly monophyletic group, including only the very remarkable genus *Dasycerus* that may have a superficial resemblance to members of the cucujoid family Latridiidae. Actually, the dasycerines were formerly regarded as a subfamily of latridiids, and although they are still placed there in some recent works, the staphylinoid nature of the dasycerines has been recognized for long (e.g., Crowson, 1955). The group is often given rank of family (no doubt due to the distinctive general facies), but there is strong evidence for regarding them as highly modified staphylinids (e.g., Lawrence and Newton, 1982; Thayer, 1987). A close relationship to the pselaphines, proposed by previous authors, has been confirmed by the present analysis. The monophyly of Dasycerinae may be supported by the following autapomorphies:

a) Antennae very thin and hairlike, middle segments spindle-shaped (reminiscent of those of most ptiliids: fig. 79).
b) Larva: anterior portion of mandible with dense array of slender teeth (fig. 210) (unique).

8:1. Mandibles concealed (when abducted) (also in Micropeplinae, probably convergent). Alternatively, concealed mandibles could be interpreted as a basal autapomorphy of clade 47 (Micropeplinae-Dasycerinae-Pselaphinae) with subsequent reversal in Pselaphinae.

11:1*. Lacinia elongated, reaching apex of galea (also, e.g., Neophoninae, probably convergent).

13:1*. First segment of labial palpi longer than 2nd.

19:2*. Antennae with 3 apical segments forming a loose club (not sharply defined in regard to pubescence) (antennae with 3-segmented club are also found in some (derived) Pselaphinae, but this is most likely convergent).

25:1*. Hypomeron with well developed mesally directed postcoxal processes.

41:0*. Abdominal tergo-sternal membrane

long on segments 1-7 (in the examined species, *D. sulcatus*, the entire terga 1-7 are membranous; certain presumedly primitive species have more sclerotized terga and may therefore have shorter tergo-sternal membranes, but this could not be examined here).

45:0*. Abdominal spiracles located in membrane between terga and sterna rather than in the terga (in the examined species terga 1-7 are entirely membranous).

47:2*. Abdominal terga only sclerotized from the 5th (rather than the 3rd), anterior terga more membranous. This is assumed to be the primitive condition for the family (cf. Löbl, 1986); in more derived forms (like *D. sulcatus* examined here) the sclerotization of abdominal terga is further reduced, and terga 1-7 are entirely membranous.

53:1*. Inflexed dorsal portion of abdominal sterna demarcated, but not separated from ventral portion by an articulation.

66:2*. Ventral face of elytra with strongly iridescent medio-lateral binding patch; the presence of a medio-lateral binding patch is found in some other staphylinid groups (as well as several non-staphylinids), but the very iridescent appearance was otherwise only observed in Neophoninae (probably convergent).

67:0*. Elytra not or only slightly truncate posteriorly, completely concealing abdomen (sometimes except for extreme apex).

90:1. Head of larva somewhat declined (probably convergent with Micropeplinae, in which the head is hypognathous). Alternatively, but perhaps less likely, a declined head is a basal apomorphy of the pselaphine group (clade 47) and has become secondarily prognathous in Pselaphinae.

118:0. Abdominal segment 10 unarmed (rather than with numerous fine teeth) (reversal within Staphylinoidea, apparently convergent in some other Staphylinidae (clade 60)).

The presence of well defined longitudinal striae or series of punctures is probably also a dasycerine autapomorphy; the primitive number of striae within the subfamily seems to be 9 (exclusive an epipleural row of punctures), but in some species, e.g., *Dasycerus sulcatus*, only 8 striae (exclusive the epipleural row) are present.

Other probable adult autapomorphies were mentioned by Newton and Thayer (1995), e.g., dorsum incrusted (probably detritus adhering to sticky secretions of cuticular glands); each elytron with 3 discal costae having tubercles or spines; antennae inserted on frontal stalks; tarsal empodium without setae. The last characteristic is also found in the Pselaphinae but is probably a matter of convergence, because the presumed sistergroup of the latter, Protopselaphinae (see below under Pselaphinae), has a normally bisetose empodium (Newton and Thayer, l.c.).

ANNOTATIONS TO CHARACTERS:

68-73. Character state not determined (only apterous forms could be examined).

74. Only 1 vein present present posterior to medial bar ("one anal vein": Lawrence, 1982); hindwings absent in most species, including the one examined here (*D. sulcatus*).

114. Larva: thoracic and abdominal terga consisting of one or (secondarily?) more sclerites.

PSELAPHINAE

The concept of this group is equivalent of the Pselaphidae (incl. Clavigerinae, sensu auct.). The systematic limits and the monophyly of the group seem to be well established and generally accepted. It has been considered a separate family since the early part of the 19th century and is still given family rank by most authors, although its probably subordinate position within the Staphylinidae has been recognized for some time. Crowson (1955) regarded the Pselaphidae (as a family) as particularly closely related to the Steninae rather than to the Scydmaenidae as suggested by several previous authors (e.g., Bøving and Craighead, 1931). A more-or-less concordant view was presented by Naomi (1985) who split the traditional Staphylinidae into three families and included the "pselaphids" (as 6 separate subfamilies) in one of them, "Oxyporidae", with the subfamilies Oxyporinae, Megalopsidiinae, Steninae, Euaesthetinae and Leptotyphlinae. Naomi's classification was strongly criticised by Newton and Thayer (1988), and has not been followed by subsequent authors, who have generally retained the family rank of the "pselaphids". Although "pselaphids" are probably a subordinate staphylinid group, the relationship to the mentioned subfamilies is indeed questionable, and others (e.g., Lawrence and Newton, 1982; Thayer, 1987) have suggested a closer relationship with Dasycerinae and Micropeplinae. This latter alternative is strongly supported by the results of the present analysis. Thus, when Dasycerinae and Micropeplinae and, for that matter, several other staphylinid groups are regarded as subfamilies, the "Pselaphidae" can not retain its family rank.

Recently Newton and Thayer (1995) formally downgraded the entire Pselaphidae to a subfamily of Staphylinidae. In consequence, they changed the rank of all current subfamilies to "supertribes" and also proposed a new supertribe, "Bythinoplectitae", for the former Faroninae (minus Faronini, which became "Faronitae"). I would rather prefer to regard all of these "supertribes" as tribes, current tribes as subtribes and tentatively abandon current subtribes (as well as the "extra" ranks between current family and subfamily and between current subfamily and tribe, which are not formally valid). Hence, seven tribes are recognized here, viz. Faronini, Euplectini, Bythinoplectini, Batrisini, Goniacerini, Pselaphini and Clavigerini. The most primitive members of the group are generally believed to be those included in the Faronini (cf. Newton, 1985; Newton and Thayer, 1995), while the most derived are probably those of Pselaphini and particularly Clavigerini. However, the phylogeny of the group as a whole seems to be in need of a thorough phylogenetic analysis. Most likely, such analyses will give rise to further modifications of the internal hierachy of the Pselaphinae and reveal that some of the tribes (e.g., Pselaphini) are not monophyletic. Newton and Thayer (l.c.) also proposed a new subfamily, Protopselaphinae, for a new genus, *Protopselaphus*, which is likely to be the sistergroup of the Pselaphinae. This genus could be not studied or included in the present analysis.

The Pselaphinae can be defined by numerous adult autapomorphies. The presence of a "unique system of distinctive cuticular foveae" was mentioned by previous authors (e.g., Newton and Chandler, 1989). Newton and Thayer (1995) indicated that basally within the subfamily such foveae were present of dorsal and ventral side of head, on pronotum, on mesosternum and on the elytra. But there is an immense variation in regard to the number and position of such foveae throughout the subfamily, and foveae may be completely absent from one or more of the mentioned body portions. Several other unique autapomorphies were mentioned by Newton and Thayer, notably the following: apex of sternite 3 and basal impression of sternite 4 with dense "fringe" of setae over and in impression; at least abdominal sternite 4 with long internal projections touching the foveae of the corresponding tergite; elytra with sutural stria (absent in a few derived forms); maxillary palpi with unsclerotized digitiform 5th segment; labial palpi with sensillum at or on base of 3rd segment (see also Newton and Thayer, l.c.). The following characters of the present analysis may further support the monophyly of the Pselaphinae:

37:0*. Laterosternites of 2nd abdominal segment not evident (largely membranous) (also in a few other staphylinid groups; probably convergent).

78:1*. Aedeagus asymmetrical. This is almost general for the group and is found even in the presumedly most primitive forms (Faronini); the symmetrical aedeagus of a few forms (e.g., *Plectophloeus* is almost certainly a secondary feature). The asymmetrical aedeagus of Leptotyphlinae is almost certainly a parallelism.

96:4. Head of larva normally with 2 stemmata on each side (basal condition?); forms with 1 or 0 stemmata may have evolved from forms with 2, but as some forms have 3 pairs of stemmata, it is possible that this was the basal condition for the subfamily. It is still apomorphic, however, since the pselaphines probably evolved from forms with 6 pairs of stemmata (as in the closely related Dasycerinae). The character was, however, indicated as ambiguous for a hypothetical pselaphine-dasycerine ancestor (clade 46), i.e. either 6, 2 or 0 stemmata might be present. But assuming that losses (rather than gains) of stemmata are more likely, the lower number of stemmata in Pselaphinae is interpreted as the derived condition.

97:1*. Labrum fused to head capsule in the larva (also in some other staphylinid subgroups; probably convergent).

109:1*. Larval ligula absent (also in some Omaliinae, some Tachyporinae; no doubt convergent).

The absence of a mandibular mola (9:1) and absence of lateral pronotal canthus (21:1) were indicated as pselaphine autapomorphies in the present analysis, but can not be regarded as such because they are shared with the presumed sistergroup, Protopselaphinae, (not be studied or included in this analysis, see above).

ANNOTATIONS TO CHARACTERS:

1. Clypeus not demarcated, but quite small judging from antennal position.
6. Gula broad, but strongly narrowed anteriorly, and though it may be very narrow at posterior tentorial pits, it is seldom (and probably only secondarily) constricted from submentum; gular sutures normally distinct, but disappeared in some derived forms (e.g., *Pselaphus, Claviger*).
12. Maxillary palpi normally 4-segmented with large apical segment; occasionally (secondarily) 3-segmented (e.g., *Chennium*).
16. Antennae primitively 11-segmented; in many taxa with fewer segments (e.g., Clavigerini, which may have as few as 2 segments); very rarely with 12 segments.
19. Antennae primitively gradually, and only slightly thickened distally (as Faronini:*Faronus*); often (and in most other taxa) with 1-3 apical segments enlarged and forming a club; aberrant in Clavigerini.
21. Pronotum with no more than a fine, rather ventrolaterally situated line separating dorsal portion from hypomeron; in many taxa not even with trace of any line (i.e., pronotum regularly convex transversely to prosternum).
23. Pronotum (i.e., the hypomeron) joins with prosternum, but is not demarcated by a suture.
25. Primitively (and normally) hypomeron is not projecting behind procoxae; a few forms with very blunt angular suggestion of projection (secondary).
31. Mesosternum primitively probably not fused with mesepisterna (as in *Euplectus*), though often fused with them.
32. Mesepisterna primitively appearing as separate sclerites; but in many derived forms (e.g., *Pselaphus*) fused with epimera.
35. Metepisterna normally (and probably primitively) concealed; seldom very narrowly exposed.
42. Abdominal intersegmental membranes relatively long, but due to long segments they are not 1/4 as long.
48. Sternum 8 with very small defensive glands opening anteriorly on sternite ("omaliine type"), distinct in, e.g., some Batrisina (cf. Nomura, 1991); probably primitively present, but reduced several times in Pselaphinae (cf. Nomura, l.c.). A very small anteromedian opening (closely situated paired openings?) is present in *Euplectus* (fig. 122) (present observation).
50. Abdominal sternite 2+3 primitively carinate anteromedially between coxae (as, e.g., *Faronus* and *Euplectus*); in many others non-carinate (secondary).
51. Intercoxal process of abdominal sternite 2+3 narrow and acute in primitive forms (*Faronus, Euplectus* etc.); but mostly (in derived forms) broader, and rounded.
55. Tibiae normally not with distinct apical spurs (all apical "spines" at tibial apex fine and alike); seldom a suggestion of spurs can be detected (secondary).
61. Posterior coxae primitively contiguous (as, e.g., *Faronus, Euplectus*); otherwise normally (secondarily) more-or-less separated.
64. Ventral face of elytra normally without sublateral ridge/lamina (except for anterior lamina in *Claviger*).

65. Epipleura probably primitively demarcated by fine line, as in *Euplectus*, *Batrisodes*, and some Goniacerini (Trichonychina, but not other subtribes). Not demarcated in *Faronus* (secondary?), in some Goniacerini and most Pselaphini and Clavigerini (secondary).
66. Ventral face of elytra without medio-lateral patch of microspines; normally also without baso-lateral patch (except, e.g., *Pselaphus*; secondary).
77. Character state not determined (male tergum 9 and 10 apparently nearly membranous, at least dorsally).
83. Apparently, primitive pselaphines (like some Faronini) have relatively normal, paired parameres, but in most taxa (all tribes) the parameres are strongly modified (one asymmetrical paramere, or parameres absent). – The interpretation is complicated by the often very complex morphology of genitalia (having several socalled "apophyses" of uncertain nature).
84. Female: 9th tergite apparently membranous.
85. Female gonocoxites apparently absent (the "large" paired sclerites are interpreted as valvifers ("9th sternite hind lobe" of Nomura, 1991, who also records paired "9th sternite fore lobes").
87. Valvifers interpreted as present (see also char. 85).
106. Larva: maxillary palpi primitively 3-segmented; sometimes 2-segmented.
111. Larva: sensorium of penultimate antennal segment anteroventral in Faronini (primitive condition); but in the majority of other forms ventral to posterior, rarely apical (in forms with lost apical antennal segment).
114. Larva: thoracic and abdominal terga consisting of one or (secondarily?) more sclerites.
116. Larva: urogomphi 1-segmented, fixed, generally small, sometimes absent.
118. Larva: abdominal segment 10 probably primitively with numerous fine teeth, but sometimes unarmed.

PHLOEOCHARINAE

A small group of staphylinids, consisting of less than 10, mostly poorly known genera, the phylogenetic relationship of which is not well understood. The inclusion of Olisthaeriinae, considered by some authors, has not been followed here. Still, the concept of the subfamily has been subject to some dispute, and it is likely that the group is highly artificial. Its systematic position is not obvious, but it has usually been regarded as most closely related to the tachyporine group of subfamilies (cf. Lawrence and Newton, 1982). As the nominal type genus of the subfamily, *Phloeocharis* (the only one known to me), seems to differ from other members of the tachyporine group and exhibits some presumedly primitive features (e.g., constricted neck, single paratergites on abdominal segments), it has tentatively been excluded from the group although Ashe and Newton (1993) regarded it as a more subordinate. Because the characters examined here are almost exclusively those of *Phloeocharis*, the possible autapomorphies given below for the subfamily should be considered tentative, though they probably are valid for at least some of the other genera currently referred to it.

11:1*. Lacinia at least reaching apex of galea (also found in, e.g., the tachyporine group, possibly convergent).

25:1*. Postcoxal processes of hypomera well developed (apparently a reversal within clade 65, convergent in several other staphylinids, notably clade 59).

37:0*. Laterosternite of 2nd abdominal segment not distinct.

57:0*. Anterior coxae not projecting (within Staphylinidae only convergent in Micropeplinae and a few derived members of, e.g., the oxyteline group).

60:1*. Posterior coxae with small excavation mesally on posterior face.

77:1*. Male tergum 9 with lateral sclerites joined dorsally by a narrow anterior bridge.

96:1. Larva with 5 stemmata on each side of head (in *Phloeocharis* (cf. Newton, 1990), sometimes fewer (3 pairs). Other forms have been reported to have 6 stemmata (cf. Frank, 1991), but since no particular genus was referred to (and the composition of the subfamily is uncertain), I tentatively regard 5 stemmata as the basal number for the subfamily. The apomorphy can be expressed as "loss on one pair of ocelli". The character was indicated as ambiguous at clade 50, i.e. either 6, 5 or 0 stemmata might be present. But assuming that repeated losses (rather than gains) of stemmata are more likely, the lower number of stemmata in the different taxa of clade 50 is resulting from independent reductions.

ANNOTATIONS TO CHARACTERS:

9. Mola small, but present.
28. Mesothoracic spiracles only partly exposed.
42. Abdominal intersegmental membrane rather short (though still coded as "long").
59. Hind coxae expanded caudally and laterally, but only rather narrowly so.
97. Larva: Labrum apparently subdivided.
99. Larva: Mandibles rather broad at base, with suggestion of a pseudomola.
116. Larva: urogomphi interpreted as 2-segmented by Frank (1991), though the ability of segment 2 to articulate is doubtful.

TACHYPORINE GROUP

A large and diverse group, which includes the subfamilies Olisthaerinae, Tachyporinae, Habrocerinae, Trichophyinae and Aleocharinae (s. lat.). Moreover, the Phloeocharinae are usually considered part of this assemblage, which have collectively been referred to as the tachyporine group (e.g., Lawrence and Newton, 1982). Although no clear autapomorphies for the group as a whole has yet been recognized, Lawrence and Newton (l.c.) characterized it as "widely accepted as a natural unit of predominantly predatory species lacking the specializations of other groups". A phylogenetic analysis of the group was presented by Ashe and Newton (1993), but still without giving conclusive evidence for its possible monophyly. I have tentatively followed this view, except that I have here excluded the subfamilies Phloeocharinae (as explained under that) and Pseudopsinae (included by Lawrence and Newton, l.c., but considered of uncertain position within the Staphylinidae by Newton, 1982a). The relationship between the subfamilies placed in the tachyporine group is not well understood, and it seems likely that some of the subfamilies (notably Tachyporinae) may not be monophyletic. Possibly, the more primitive members of the group are to be found among the Olisthaeriinae and the tachyporine tribe Mycetoporini, both of which lack the derived features of typical Tachyporinae (e.g., more-or-less strongly lobed abdominal tergum 8, fig. 384, 386), Habrocerinae (highly modified genital segments and genitalia in male and strongly excavate posterior coxae), Trichophyinae (absence of well-demarcated epipleura, shared with Aleocharinae) and Aleocharinae (e.g., dorsally inserted antennae, uniquely derived complex aedeagal structure including large segmented parameres (fig. 171); as pointed out by Hammond (pers. comm.) the parameres of Aleocharinae may not be entirely homologous with the parameres of other staphylinids). Moreover, Mycetoporini and (possibly) Olisthaeriinae seem, unlike the other members of the group, to have retained certain plesiomorphic staphylinid features, e.g., the "brick-wall" pattern of minute sclerites in the abdominal intersegmental membranes (this was difficult to detect in Olisthaeriinae, but it seems that a very fine, rudimentary "brick-wall" pattern is present). Also the (currently) tachyporine genus *Derops* seems to be a primitive member of uncertain relationship within the group. On the basis of the present analysis, only a few weak possible autapomorphies can be suggested in support of the monophyly of the tachyporine group.

3:0*. Head without constricted neck. This is an almost general and apparently basal characteristic of the group. Exceptions seem to occur only in some of the more derived forms, e.g., Trichophyinae and a few Aleocharinae (e.g., *Autalia, Falagria, Drusilla*). The absence of a neck is a very unusual feature within the Staphylinidae, which almost certainly has a more-or-less constricted or demarcated neck as groundplan character). The absence of a distinct neck in, e.g., Microsilphinae and some members of the oxyteline group (e.g., *Osorius*), is most likely convergent.

11:1*. Lacinia at least reaching apex of galea (also found in, e.g., Phloeocharinae, possibly convergent). A shorter lacinia occur in some forms (Tachyporinae), but this is tentatively assumed to be secondary.

38:1*. Abdominal segments 3 – 6 (7) with 2 pairs of paratergites. This is no doubt a derived staphylinid feature (paratergites are only exceptionally and no doubt secondarily not distinct, e.g., *Sepedophilus*). The two pairs of paratergites on the abdominal terga of the staphylinine group, Oxyporinae, Megalopsidiinae, Solieriinae, Leptotyphlinae, and derived Oxytelinae have probably evolved independently.

ANNOTATIONS TO CHARACTERS:

8. Mandibular apices primitively exposed (as in most forms); secondarily concealed in Habrocerinae, Trichophyinae, and many Aleocharinae (e.g., Hypocyphtini, Gymnusini, Myllaenini, Pronomaeini, some Homalotini, Autaliini).
9. Mandibles primitively with mola; large in Tachyporinae and Habrocerinae, variable in Aleocharinae (e.g: moderate sized in *Gymnusa*, absent in *Oxypoda*).
12. 4th segment of maxillary palpi primitively c. as large as 3rd (as in Olisthaerinae, several Tachyporinae (some Bolitocharini + some Tachyporini), Habrocerinae, Trichophyinae); in Aleocharinae 4th segment is minute (secondary).
13. Labial palpi generally with segment 1 longer than 2 (only in *Olisthaerus* hardly longer).
14. Labial palpi with segment 3 generally narrower than 2 (but often longer); some Aleocharinae (e.g., *Thamiaraea*) have 2-segmented labial palpi.
16. Antennae generally 11-segmented, except in Hypocyphtini (with 10 segments).
17. Antennae generally and primitively inserted laterally "below" lateral edge of frons; in Aleocharinae the canthus has become indistinct and is (with antennal insertions) situated more dorsally, so antennae appear inserted "freely" on frons (anteriorly between eyes); exceptions within Aleocharinae are Hypocyphtini (*Cypha*, in particular), in which a fine canthus demarcates antennal insertion posteromedially, and Pygostenini, which have a strong (secondary?) transverse canthus running across frons immediately behind antennal insertions.
21. Lateral ridge of pronotum demarcating dorsal porion from hypomeron generally very sharp; except in few Aleocharinae (e.g., *Falagria*).
25. Hypomeron generally without processes, except *Olisthaerus* (secondary?).
26. Prosternal intercoxal process probably primitively present, as in *Olisthaerus* and some Tachyporinae (short); in all others absent.
29. Pro-mesosternal connecting membrane probably primitively without sclerites; but in Tachyporinae:*Tachinus*, Habrocerinae and Aleocharinae with rather large, transverse, often triangular sclerites, in which spiracles are located; sometimes also with median sclerite (e.g., *Gymnusa*).
31. Mesosternum primitively well demarcated, but in several Aleocharinae fused to mesepisterna.
34. Mesocoxal cavities normally demarcated posteriorly by ridge; the ridge is fine in several Aleocharinae, though only exceptionally absent (*Hygronoma*).
42. Abdominal intersegmental membranes variable, but generally long.
43. Abdominal intersegmental membranes primitively with brick-wall pattern (as Tachyporinae: *Mycetoporus*); pattern lost in other Tachyporinae (*Tachinus, Tachyporus*), Habrocerinae, Aleocharinae.
46. Abdominal terga usually without "wing folding patches", but in a few Tachyporinae (*Tachinus, Derops*) with small paired, patches on terga 3-5 (secondary?).
50. Abdominal sternum 2+3 generally not carinate (probably derived condition); carinate anteriorly only in *Olisthaerus* and *Mycetoporus.*
53. Paratergites only exceptionally not demarcated (Tachyporinae: *Sepedophilus*).
58. Meoscoxae globular, or often even slightly elongate.
59. Hind coxae generally typically transverse; only in Habrocerinae of the "triangular" type, but this is concealed by development of a very large "coxal plate".
60. Primitively, hind coxae not excavate on posterior face, but in *Tachinus* and *Gymnusa* with small excavation mesally; in *Habrocerus* deeply excavate and with very large "coxal plate" covering femur in repose.
65. Epipleura demarcated by a sharp ridge in Olisthaerinae, Tachyporinae, and Habrocerinae (probably primitive condition); not demarcated in Trichophyinae and Aleocharinae (except Dinardini and Pygostenini, in which epipleura are secondarily demarcated).
72. Generally with well demarcated anal lobe, moderate sized in Tachyporinae, small and fringed with long setae in Habrocerinae and Aleocharinae, number of setae variable in the latter subfamily (many in *Aleochara*, not quite as many in *Oxypoda*, few setae in e.g *Atheta*); no jugal lobe in Aleocharinae:*Hygronoma.*
74. Hindwing normally with 1 vein posterior to medial bar, as in Olisthaerinae (with weak suggestion of a 2nd vein), some Tachyporinae (*Tachyporus*), Habrocerinae, and Aleocharinae (the single vein only distinct in basal half, or indistinct; only *Aleochara* and *Oxypoda* with 3 longitudinal pigmented areas, probably not veins). – Only *Mycetoporus* and *Tachinus* have

2 distinct anal veins, the latter also with suggestion of a third.

85. Female gonocoxites primitively present, as in Tachyporinae and Aleocharinae: *Gymnusa*; absent in other Aleocharinae.
87. Female: valvifers present (primitive condition), or appearing absent (most Aleocharinae).
96. Larva: probably primitively with 6 stemmata on each side (as in Tachyporinae (*Tachyporus, Tachinus*), and Habrocerinae). – Reductions occur in some Tachyporinae (5 or 3), and all Aleocharinae (normally 1, seldom 0).
97. Larva: labrum free (apparently subdivided in *Tachyporus*, not in Aleocharinae); a few Aleocharinae apparently have an almost fused labrum.
99. Larva: mandibles without mola, but sometimes more-or-less broad at base and (e.g., few Aleocharinae) with suggestion of pseudomola.
109. Larva: ligula primitively present (*Tachyporus*, Aleocharinae); but in some Tachyporinae absent.
116. Larva: urogomphi normally 2-segmented (all subfamilies, though unknown in Olisthaerinae); aberrant in a few Aleocharinae (e.g., 1-segmented in 1st instar *Aleochara*, absent in 3rd instar *Aleochara*) (cf. Paulian, 1941).

TRIGONURINAE

This group includes the single genus *Trigonurus* whose systematic position has been subject to dispute. It has been placed in the Silphidae by some authors (e.g., Madge, 1980), in the Staphylinidae (often included in Piestinae) by others (e.g., Newton, 1982b), but the affinities with these groups are not evident, and more recently *Trigonurus* has been placed in a separate subfamily within the Staphylinidae (e.g., Newton and Thayer, 1992). The phylogenetic relationship indicated by the present analyses (near Omaliinae and allied subfamilies) is weakly supported and by no means conclusive. Lawrence and Newton (1995) refers to it as a primitive relative of the oxyteline group (in the present sense). They actually include it in their concept of the "oxyteline group" together with "Apateticinae" and "Scaphidiinae" (the latter two were indicated as more basal, not closely related groups in the present analysis). In spite of the relatively distinctive facies of the Trigonurinae, it is difficult to identify obvious autapomorphies in support of its monophyly, mainly because such would depend largely on the exact relationship of the group. Only one character was indicated as unambiguously autapomorphic by the present analysis:

62:1*. Posterior coxae not reaching the lateral edges of the body (this is also found in a few other staphylinids, e.g., Pseudopsinae, Micropeplinae and the stenine group, and in Apateticidae, probably convergent).

The presence of 9 elytral series of punctures may be another autapomorphy (convergent in several other staphylinoids).

It is possible that the narrow segment 3 of the labial palpi (14:1) and the presence of an acute intercoxal process on the basal ventrite (51:0) are also autapomorphic, but the characters are basally ambiguous for clade 59 and clade 58, respectively. It seems therefore equally likely that the characters are not derived only for Trigonurinae.

ANNOTATIONS TO CHARACTERS:

28. Mesothoracic spiracles exposed (Blackwelder, 1936).
35. Metepisterna exposed, but only posteriorly.
42. Abdominal intersegmental membranes apparently long (only dried specimen examined).
57. Anterior coxae projecting, but rather weakly so.
72. Hindwing apparently with anal lobe that is not demarcated from rest of wing (cf. Bernet Kempers, 1923: fig.119 – not described).

73-76. (After Bernet Kempers, l.c.).

80-83. (After Blackwelder, 1936).

OXYTELINE GROUP

The group include the subfamilies Piestinae, Osoriinae and Oxytelinae, as delimited by Newton and Thayer (1992). It can be noted that this concept of Piestinae does not include *Apateticus*, *Nodynus* (here Apateticidae), *Trigonurus* (now Trigonurinae) and a few genera now referred to Pseudopsinae (Newton, 1982a), and that some forms earlier referred to Piestinae (or "Piestini") (Eleusinini, Leptochirini, Thoracophorini) are now placed in Osoriinae because of their un-margined abdomen. The phylogeny of the Oxytelinae was reviewed by Newton (1982b) who listed a number of apomorphies for the subfamily, e.g., the presence of a well defined abdominal sternum 2 (secondarily fused to sternum 3 in some genera, according to Newton), abdominal tergum 9 with openings of a pair of large glandular reservoirs. But apart from this, the phylogeny within the oxyteline group is poorly understood, and the exact relationship between the Piestinae, Osoriinae and Oxytelinae is not obvious. Probably, some or all of the Piestinae and Osoriinae form the sistergroup of Oxytelinae (they lack the mentioned oxyteline autapomorphies) (cf. Newton, 1982a), and it is possible that the most generalized forms of the entire oxyteline group are included in the Piestinae, though these can hardly be regarded as generally primitive. The following possible autapomorphies may support the monophyly of the oxyteline group:

a) Labrum, mandibular prostheca and galea with numerous multifid or plumose setae (cf. Newton, 1982a).
b) Saprophagous adult (and larval) feeding habits (cf. Newton, 1982a, 1982b).
c) Larval ligula transverse, broadly truncate (cf. Newton, 1982a, 1982b).
d) Larval cervicosternum triangular, consisting of a single sclerite (not three-segmented as usually among staphylinid larvae) (cf. Newton, 1982a, 1982b).

74:2*. Medial field of hind wing with only 2 veins (rather than 1) (reversal within Staphylinoidea; see also comments under Agyrtidae). The presence of 2 veins is assumed to represent the basal condition of the oxyteline group (as found, e.g., in *Coprophilus* and *Deleaster*), but some Oxytelinae (e.g., *Syntomium*) have only 1 vein.

77:1*. Male abdominal tergum 9 not entire, lateral sclerites only connected by a very narrow anterior bridge (apparently absent in most forms); reversal within clade 59.

86:2*. Female: Styli absent (also in some other staphylinids, e.g, stenine group and clade 49; probably convergent).

It is possible that the presence of a pair of egg bursters on metanotum in first instar larvae (113:2) represents another autapomorphy of the oxyteline group, but the significance is not clear, because it has only been studied in the oxyteline genus *Platysthetus* (Emden, 1946; Crowson, 1981) (and presence or absence of egg bursters is unrecorded in several related taxa).

Another autapomorphy may involve the elytra, which are probably primitively striate within the oxyteline group, as in Piestinae and Oxytelinae:*Coprophilus*, which both have 7 striae (apparently 1-7 present, 8-10 absent); in Osoriinae:*Thoracophorus* suggestions of serial punctures are present between elytral carinae; in other taxa the striae are lost except for the sutural stria. If elytral striae are a groundplan character of this group (which has not yet been adequately revealed), it seems that not only their presence, but also their number (7 rather than 10) are probable autapomorphies.

Finally, it is possible that the presence of an acute intercoxal process on the basal ventrite (51:0) is also autapomorphic (convergent in Trigonurinae), but the character is basally ambiguous for clade 58 and it is therefore also possible that the character is not derived for the oxyteline group alone. I have followed Newton (1982b) in regarding the absence of such a process in the Oxytelinae as secondary (autapomorphy), probably resulting from modifications of the abdominal basis, involving the development of a separate sternum 2.

ANNOTATIONS TO CHARACTERS:

2. Frontoclypeal suture variable, but probably primitively present and not grooved.
3. Head probably primitively with constricted neck somewhat behind eyes, but many exceptions occur in

all three subfamilies; in some Osoriinae:Leptochirini narrowed immediately behind eyes (secondary).

5. Interocular grooves generally absent (except *Deleaster*, probably secondary).
6. Gular sutures probably primitively separate (as Piestinae), though often close); in Oxytelinae primitively separate (cf. Newton, 1982b); in Osoriinae confluent (perhaps except posteriorly).
11. Lacinia shorter than galea in Oxytelinae (primitive condition); as long as galea in Osoriinae:*Osorius* (secondary).
12. 4th segment of maxillary palpi generally as large as 3rd; only in Osoriinae:Thoracophorini and few Oxytelinae smaller (secondary).
14. 3rd segment of labial palpi as wide as 2nd (only in *Osorius*, which have dilated segment 2, narrower, but still long (secondary)).
19. Antennae generally gradually thickened apically, but in *Syntomium* with 3-segmented club (secondary).
21. Pronotum primitively with lateral ridge separating dorsal portion from hypomeron; in Osoriinae:Leptochirini (and some others) with fine ridge situated more ventrally on pronotal side; lateral ridge absent in Osoriinae:Thoracophorini (secondary).
24. Procoxal fissure generally open and trochantin exposed, except some Oxytelinae and *Leptochirus* (secondary).
25. Hypomeron generally and primitively with processes that do not form complete closure of procoxal cavities; but in Osoriinae:*Leptochirus* forming complete closure, and in some Oxytelinae (e.g., *Oxytelus*) almost absent.
26. Prosternal intercoxal process present, but not widened behind (except Osoriinae:*Leptochirus*; secondary).
31. Mesosternum generally not fused to mesepisterna (except *Osorius*).
33. Mesocoxal fissure probably primitively open and with exposed trochantin (e.g., *Coprophilus* and some other Oxytelinae); closed in *Osorius* (secondary).
35. Metepisterna generally exposed, except in Osoriinae:Thoracophorini.
38. Primitively one paratergite on each side; derived Oxytelinae:Oxytelini have two; in Osoriinae paratergites are not demarcated.
43. "Brick wall" structure of abdominal intersegmental membranes generally present (only absent in Oxytelinae:*Euphanias*, cf. Newton, 1982b).
49. Abdominal sternum 2 primitively not visible as separate sclerite; except most Oxytelinae (secondary).
50. Abdominal sternum 2+3 carinate basally in Piestinae and Osoriinae (notably Leptochirini) (primitive condition); non-carinate in most (not all) Oxytelinae.
51. Intercoxal process of abdominal sternum 2+3 present (acute) in Piestinae and Osoriinae (notably Leptodirini); absent in all Oxytelinae.
52. Abdominal sternum 2+3 with well defined coxal cavities in Piestinae and some Osoriinae (Leptochirini, *Thoracophorus*), indistinct or absent in *Osorius* and Oxytelinae (latter condition probably primitive).
53. Paratergite generally articulated to tergum, except in Osoriinae (secondarily fused).
55. Apical spurs generally present on tibiae (not detectable in *Syntomium*; secondary).
57. Anterior coxae projecting in Oxytelinae and Osoriinae:Osoriini, not projecting in other Osoriinae and in Piestinae. – Primitive condition doubtful!
63. Tarsi primitively 5-segmented, but in Osoriinae:*Lispinus* 4-segmented, and in several Oxytelinae:Oxytelini 3- (or even 2-) segmented.
65. Epipleura primitively demarcated by a ridge; in several Oxytelinae:Oxytelini the ridge is situated more ventrally on pronotal side; in some Osoriinae:Leptochirini without ridge.
72. Hindwing with well demarcated anal lobe, not fringed with long setae (in *Syntomium* small: secondary).
90. Larva: Head normally prognathous, but in some Osoriinae rather hypognathous.
91. Larva: 1. instar without cephalic eggbursters (Emden, 1946; Crowson, 1981).
96. Larva: possibly primitively with 6 stemmata on each side, as *Lispinus* (cf. Paulian, 1941). However, this number of stemmata in *Lispinus* was questioned by Newton (1982b), who recorded only 4 stemmata on each side of the head in this genus; thus, according to Newton (l.c.) the number of stemmata varies as follows in the oxyteline group: Piestinae (1, 4), Osoriinae (0-4), Oxytelinae (0, 1, 3, 4).
97. Larva: labrum free (apparently generally subdivided, at least in Piestinae and Oxytelinae).
99. Larva: mandibles without mola, but in some Piestinae and some Oxytelinae with broad base (pseudomola).
100. Larva: prostheca normally and primitively absent (but in some, not all, Piestinae with prostheca like appendage).
116. Larva: urogomphi 2-segmented in Piestinae (probably primitive condition); 1-segmented in Oxytelinae (small in *Syntomium*, otherwise well developed) and most Osoriinae (incl. *Leptochirus*).

OXYPORINAE

A small and distinctive, rather uniform group of staphylinids, including only a single genus, *Oxyporus*. The monophyly of the group is indisputable and can be supported by the following autapomorphies:

a) Apical segment of labial palpi very large and broadly triangular (fig. 58) (unique) (cf. 14:0).
b) Antennae short with very transverse segments 6-10 (fig. 88).
c) Metasternal process between mesocoxae very large and very broadly separating mesocoxae (unique within Staphylinidae).
d) Mentum with two long projections anteriorly (fig. 54).
e) Larva with apical portion of mandibles finely denticulate (fig. 209); this is apparently unique within Staphylinidae, but is convergent in a few Scaphidiidae.
f) Larval ligula membranous (cf. 109:0).
g) Larval maxilla with 3-lobed mala.

38:1*. Abdominal segments 3-6 with 2 paratergites on each side (only basally on segment 3 and 4 distinctly separated by a membrane, otherwise apparently only delimited by a fine ridge). Paired abdominal paratergites are also found in the staphylinine-group, Solieriinae, Leptotyphlinae, some Oxytelinae, Megalopsidiinae, and the Tachyporine group (excl. Phloeocharinae), but this is probably convergent.

50:2*. First ventrite not carinate (not even basally between coxae).

59:0*. Posterior coxae transverse, but only moderately expanded caudally and laterally (reversal within clade 59).

77:0*. Lateral sclerites of male abdominal tergum 9 not joined dorsally at base (reversal within clade 59).

84:0. Lateral sclerites of female abdominal tergum 9 divided dorsally at base (probably a reversal within clade 53, see also that).

ANNOTATIONS TO CHARACTERS:

3. Head constricted well behind eyes, but with very broad neck.
9. Mandibles with small, rather narrow mola.
31. Mesosternum fused to mesepisterna (but suture suggested in cleared specimens).
58. Mesocoxae elongate.
65. Epipleura well demarcated, but lateral elytral ridge moved somewhat down on the side, so epipleura become very narrow.
99. Larva: mandibles without mola, but rather broad at base (weak pseudomola).

STENINE GROUP

This group includes the staphylinid subfamilies Megalopsidiinae, Steninae and Euaesthetinae, which seem to form a reasonably well defined monophyletic group. The Megalopsidiinae (with the genus *Megalopinus*) may be the least derived of these subfamilies, e.g., in having well developed apical segments of maxillary palpi and labial palpi, well developed and -demarcated epipleura, and perhaps a free labrum in the larva (the latter may be a secondary feature). But the megalopsidiines posses also certain apparently derived features, e.g., paired paratergites of the abdomen and strong, protruding mandibles (fig. 22), which give them a resemblance to the Oxyporinae (tentatively regarded as convergences). Other derived characters of Megalopsidiinae include, e.g., a pattern of sparse foveae on the head and a bifurcate labrum (fig. 22). The Steninae is a quite distinctive subfamily, comprising only the genera *Stenus* and *Dianous*, and are derived, e.g., in having the antennae inserted dorsally on the head (anteriorly between eyes) (fig. 24). The Euaesthetinae have like Steninae slender, falciform mandibles in the adults (regarded synapomorphic). The subfamily includes several genera whose relationships seem to be poorly understood; the current division of the subfamily into five tribes based on the number of tarsal segments and margined/non-margined abdomen is probably artificial and needs to be critically reviewed. I know of no autapomorphy of the Euaesthetinae (except possibly the dentate labrum, fig. 33). Naomi (1985) mentioned a reduced number (4) of segments in the posterior tarsi as the only derived feature, but some presumedly primitive euaesthetines have 5-segmented tarsi (Newton, 1985). The following apomorphies may define the entire stenine-group:

2:2*. Frontoclypeal suture absent.

19:2*. Antennae with 2-3 apical segments forming well defined club (not sharply delimited in regard to pubescence); the club is very pronounced in Megalopsidiinae and Euaesthetinae, while in Steninae (with generally slender antennae) it is less strongly developed. A few other groups of staphylinids also have clubbed antennae (e.g., some members of the omaliine group, a few Oxytelinae and some Leptotyphlinae), but this is probably convergent.

24:1*. Procoxal fissure closed, trochantin concealed (also in other staphylinid groups, probably convergent).

33:1*. Mesocoxal fissure closed, trochantin concealed (also in other staphylinid groups, probably convergent).

55:1*. Apical tibial spurs absent (i.e., not detectable) (in Staphylinidae otherwise found only in Proteininae, Neophoninae, Micropeplinae, Dasycerinae, Pselaphinae and a few Oxytelinae).

62:1*. Posterior coxae ending laterally distinctly before lateral edges of body (also in a few other staphylinid groups, e.g., Trigonurinae, Pseudopsinae, Micropeplinae, probably convergent).

74:2*. Medial field of hind wing with only 2 veins (rather than 4) (reduction within clade 53)

86:2*. Female: Styli absent (also in some other staphylinids, e.g, oxyteline group and clade 49; probably convergent).

111:1*. Larva: sensory appendage of preapical antennal segment on posterior (outer) face of the latter (unique within Staphylinidae); in Steninae it is still morphologically posterior, but has become anterior as result of antennal rotation (Frank, 1991).

ANNOTATIONS TO CHARACTERS:

8. Mandibular apices primitively exposed; concealed in Steninae (labrum large).
12. 4th segment of maxillary palpi extremely small in Steninae and Euaesthetinae (probably the derived condition), large in Megalopsidiinae (probably primitive).
13. Labial palpi with segment 1 short in *Euaesthetus* (primitive condition?), much longer than 2nd in *Stenus* and *Megalopus*.
14. Labial palpi with segment 3 large in Megalopsidiinae (primitive condition?), very small in *Euaesthetus*, disappeared in *Stenus*.
17. Antennae primitively inserted laterally under lateral canthus of frons, as in Megalopsidiinae and Euaesthetinae, a little more dorsally/medially in Euaesthetinae; in Steninae inserted dorsally just inside anterior margin of eyes, and not under distinct canthus.
25. Hypomeron with processes (not closing procoxal cavities) in Steninae and Euaesthetinae (primitive condition?); processes hardly present in Megalopsidiinae.
30. Character state not determined (mesosternum fused with mesepisterna).
38. Abdominal segments normally with one paratergite on each side, but in Megalopsidiinae with two on each side (probably secondary). In some *Stenus* and some Euaesthetinae the paratergites are not demarcated (fused to terga).
50. Abdominal sternite 2+3 carinate anteriorly; in *Euaesthetus* almost completely carinate (secondary).
53. Primitively, paratergites are articulated to sternites, but in some *Stenus* and some Euaesthetinae not demarcated (fused to terga).
65. Epipleura well developed and demarcated in Megalopsidinae; generally narrower in Euaesthetinae and Steninae, and in *Stenus* only finely demarcated.
72. Hindwing anal lobe well developed and well demarcated in *Stenus* (entire wing extremely reduced in *Euaesthetus*).
85. Female: apparent gonocoxites present in *Stenus* (probably not in *Euaesthetus*, which only appears to have the valvifers).
97. Larva: labrum fused to head capsule in Steninae and Euaesthetinae (the articulated labrum of Megalopsidiinae (cf. Newton, 1991) is possibly a secondary feature).
104. Larva: lacinia+galea (i.e., mala) fixed, small or very small.

SOLIERIINAE

The phylogenetic relationship of this monotypic subfamily has been subject to some dispute.

It has usually been placed near (or in) the Omaliinae, but its similarity to primitive pselaphines has also been noted. However, Newton and Thayer (1992) stated that it can hardly be included in Omaliinae or anywhere in the "omaliine group" of staphylinid subfamilies (in which they included Pselaphinae), because it lacks the "typical omaliine sternum 8 glands" and have two pairs of paratergites on abdominal segments. Recently, Newton and Thayer (1995) has suggested a close relationship with Pseudopsinae, Paederinae, Staphylininae and Leptotyphlinae. In the present analysis, a close relationship between Solieriinae and Micropeplinae, Dasycerinae and Pselaphinae was indicated. Occupying this systematic position, the subfamily can be defined by the following possible autapomorphies:

a) Pronotum with characteristic pattern of five basal foveae (fig. 433) (unique).

12:1. Apical segment of maxillary palpi much smaller than penultimate (also found in several other staphylinids, e.g., Leptotyphlinae, probably convergent). Alternatively, but perhaps less likely, a reduced apical segment of the maxillary palpi could be a basal feature of clade 49 and have become secondarily well developed again in clade 47.

28:0. Mesothoracic spiracles apparently concealed under the hypomeron (difficult to identify in available specimens); concealed spiracles are also found in clade 46 (probably convergent). The character was indicated as basally ambiguous for clade 48, so it is also possible that the spiracles were basally concealed in this clade (Solieriinae-Micropeplinae-Dasycerinae-Pselaphinae) and has secondarily become exposed in Micropeplinae.

32:1*. Mesepisterna fused with the mesepimera.

38:1. Abdominal segments with 2 paratergites on each side (also found in other groups of Staphylinidae, e.g., Leptotyphlinae, probably convergent). Alternatively, but perhaps less likely, doubled paratergites could be a basal apomorphy of clade 49 and have become secondarily simple again in clade 47.

51:0. First ventrite (sternum "2+3") with acute intercoxal process (also found in certain other staphylinids, e.g., Dasycerinae and primitive Pselaphinae, probably convergent). The character was indicated as basally ambiguous for clade 48, so it is also possible that the presence of an acute intercoxal process is a basal apomorphy of this clade (Solieriinae-Micropeplinae-Dasycerinae-Pselaphinae) and has secondarily become lost in Micropeplinae (as well as derived Pselaphinae).

It is possible that the absence of interocular grooves (5:1) is a derived feature within clade 49, but it could also be a plesiomorphic feature, i.e., if interocular grooves have evolved independently in Leptotyphlinae and the pselaphine group (clade 47) (see also the latter).

ANNOTATIONS TO CHARACTERS:

1. Clypeus not demarcated, but small judging from position of antennal insertions.
3. Head constricted somewhat behind eyes, but temporae much shorter than eyes.
26. Prosternal intercoxal process very short, but acute (coded as present).
35. Metepisterna exposed, but only very narrowly so.
82. Basal bulb of median lobe present but small (and entire median lobe narrow and elongate).
85. Character state not determined (female gonocoxites present (Newton and Thayer, 1992), but shape not described).
86. Styli absent (Newton and Thayer, l.c.).

LEPTOTYPHLINAE

A distinctive group of very small and slender, exclusively subterranean and blind staphylinids. The systematic position of the Leptotyphlinae has not been agreed upon. Lawrence and Newton (1982) placed them in a group of staphylinids with the subfamilies Oxyporinae, Megalopsidiinae, Steninae, Euaesthetinae, Paederinae and Staphylininae, but did not discuss the relationship in further detail. Naomi

(1985) referred these subfamilies to different groups, the first four to what he called "Oxyporidae", the last two to "Staphylinidae (s.nov.)" (including also the subfamilies of the tachyporine group). Naomi considered Leptotyphlinae and Pselaphinae as sistergroups (based on the 3-segmented tarsi of both groups) and included them as a sistergroup to Euaesthetinae in his "Oxyporidae". None of these two relationships of the Leptotyphlinae were supported by the present analysis. Although Leptotyphlinae may not be so distantly related to the Pselaphinae there is no evidence for a sistergroup relationship, and none of them seem to be closely related to Euaesthetinae. Currently, five tribes are recognized (Newton and Thayer, 1992), but this division may only to some extent reflect natural groups. So far no attempt has been made to reconstruct the phylogeny of the entire subfamily on a cladistic basis, and it is not obvious which group(s) can be considered the most primitive. However, the monophyly of the entire subfamily seems to be well established, and is supported by several adult autapomorphies:

a) Eyes completely absent (parallelisms are found in a few clearly derived members of other staphylinid subfamilies (Omaliinae, Pselaphinae, Aleocharinae) and in other families, notably Leiodidae (Scotocryptini, Catopocerinae, Platypsyllinae, most Leptodirini) and Ptiliidae (e.g., Cephaloplectinae)).
b) Elytra completely fused basally to mesothorax, so there is no articulation and the elytron is immovable (unique, according to Coiffait, 1959).
c) Hindwings absent (this is a general characteristic of the superfamily, and though wings have been lost in several other groups, the Leptotyphlinae is the the only staphylinid subfamily in which wings are basally absent).

5:0. Frons with a pair of small "interocular" pits (sometimes referred to as ocelles); similar grooves are found in clade 47 (possibly convergent). The character was indicated as basally ambiguous for clade 49 and it is therefore possible that the presence of interocular pits is a basal feature of that clade and has been secondarily lost in Solieriinae.

12:1. Apical segment of maxillary palpi much smaller than penultimate (also found in several other staphylinids, e.g., Solieriinae, probably convergent). Alternatively, but perhaps less likely, a reduced apical segment of the maxillary palpi could be a basal feature of clade 49 and have become secondarily well developed again in clade 47. Some forms have the 3rd segment enlarged, but most species have rather the 2nd segment enlarged and occasionally the 3rd segment is so small that it is only as large or even smaller than 4th (probably secondary).

14:0*. Apical (3rd) segment of labial palpi as wide as penultimate (only rarely, and probably secondarily, slightly narrower); sometimes an extremely small accessory 4th segment is present (no doubt derived).

21:1*. Pronotum without distinct lateral canthus.

38:1. Abdominal segments with 2 paratergites on each side (also found in other groups of Staphylinidae, e.g., Solieriinae, probably convergent). Alternatively, but perhaps less likely, doubled paratergites could be a basal apomorphy of clade 49 and have become secondarily simple again in clade 47.

59:1*. Posterior coxae "triangular", i.e., not expanded laterally and caudally (also found in other groups of Staphylinidae, probably convergent).

63:1. Tarsi with no more than 3 segments (sometimes only 2-segmented). The number of tarsal segments was indicated as basally ambiguous for clade 49, but assuming that reductions in the number of tarsal segments are more likely than an increase in number, the reduced number of segments in Leptotyphlinae is convergent with the reduced number in the pselaphine group (clade 47 (see also that clade).

78:1*. Aedeagus asymmetrical; some forms (e.g., *Cyrtotyphlus*, *Megatyphlus*) have a relatively simple aedeagus, but in most forms it is quite complex.

96:6. Larva without stemmata. The character was indicated as ambiguous at clade 49, i.e. either 6 or 0 stemmata might be present. But assuming that repeated losses (rather than gains) of stemmata are more likely, the lower number of stemmata in the different taxa of clade 49 is resulting from independent reductions.

97:1*. Labrum fused to head capsule in larva (also found in other staphylinids, probably convergent).

ANNOTATIONS TO CHARACTERS:
Since only dry (un-cleared) specimens were available for this study, the determination of character states have been based partly on descriptions by Coiffait (1959).

3. Neck slightly constricted, but broad, apparently "well behind eyes" (though eyes are absent).
6. Gular sutures separate, except at a point at "posterior tentorial pits" (gula thus not continuous with submentum) in all forms, except *Leptotyphlus* (secondary?).
10. Mandibles sometimes with projecting lobe on inner face (secondary?).
11. Lacinia generally as long as galea; seldom shorter (e.g., *Megatyphlus* – secondary?).
17. Antennae inserted under "side margin", but inserted somewhat closer together (like Staphylininae) and appearing rather dorsal, were it not for the canthus above the insertions.
19. Antennae generally and probably primitively gradually widened apically; sometimes with rather well defined club consisting of 3 segments (*Eotyphlus*) or 2 segments (*Cyrtotyphlus*).
23. Pronoto-sternal suture absent except for weak vestige in *Megatyphlus*.
24. Anterior coxae with concealed trochantin (only in *Megatyphlus* with slightly exposed trochantin; secondary?).
37. Paratergites of abdominal segment 2 apparently distinct.
48. Sternum 8 without openings for glands at anterior margin (Coiffait, 1959: e.g., figs 78-79 – not described).
51. Abdominal sternum 2+3 apparently without intercoxal process.
53. Inflexed dorsal portion of abdominal sterna apparently articulated to ventral portion.
58. Mesocoxae slightly elongate.
83. Parameres present, paired (generally asymmetrical).
84. Female tergum 9 apparently divided medially (Coiffait (l.c.) describes the 9th segment as composed of two "hemisternites" and two ventral "sternelles" in *Megatyphlus* etc.; possibly Coiffait's "hemisternites" are homologous with the divided tergum 9). – In some forms (*Leptotyphlus* etc.), the sclerites of segment 9 are described as forming a fused ring (secondary?).
85. Gonocoxites apparently fused (but interpretation tentative).
86. Styli generally absent (in *Gynotyphlus*, socalled "styli" are described by Coiffait (l.c.); but they are not typical styli according to his figures, and may be non-homologous structures.
87. Valvifers probably present (=? "sternelles" of Coiffait); paired in *Megatyphlus* etc., fused in *Epalxotyphlus*, *Leptotyphlus* etc. (secondary).

PSEUDOPSINAE

A small, rather well-defined group of staphylinids. Formerly, it included only a single genus, but the concept of the group was expanded by Newton (1982a), who included further three genera (earlier placed in the Piestinae). He listed a number of possible autapomorphies (a-h, and others discussed below) in support of the monophyly of the group.

a) Pronotum and elytra longitudinally carinate or costate.
b) Punctation of head and pronotum reticulate.
c) Epipharynx with globosetae present, forming median patch (secondarily forming transverse row on anterior edge).
d) Mandibles with one or more large subapical teeth on mesal edge.
e) Mandibles with thin (reduced) molar lobes bearing mesial microtrichia (secondarily without mola).
f) Hypopharynx with two pairs of lobes (secondarily with six lobes or with median pair of lobes largely fused to lateral pair).
g) Abdominal tergum 9 with fine "stridulatory"

file on each side (unique within Staphylinidae).

h) Stylus reduced, knoblike (secondarily absent).

In addition to these characters, the following possible autapomorphies can be mentioned:

11:1*. Lacinia elongated, reaching apex of galea (at least in *Pseudopsis* (Blackwelder, 1936)); this is also found in other staphylinid groups, e.g., several members of the Tachyporine group, but is almost certainly convergent. However, since it could not be examined in the other genera of the subfamily the possible autapomorphic status should be regarded tentative.

29:2*. Pro-mesothoracic connecting membrane with a pair of sclerites (or a median sclerite) not associated with the mesothoracic spiracles (similar sclerites are also present in Silphidae and Apateticidae, no doubt convergent). The presence of such sclerites was also regarded as a pseudopsine autapomorphy by Newton (1982a).

62:1*. Posterior coxae not reaching lateral edges of body (this is also found in a few other staphylinids, e.g., Trigonurinae, Micropeplinae and the stenine group, and in Apateticidae, no doubt convergent).

81:1*. Aedeagus with straplike basal piece. Newton (1982a) considered the presence of a basal piece as a plesiomorphic groundplan character of the Pseudopsinae and explained its absence in some forms as secondary loss. It may be most likely that a basal piece is part of the pseudopsine groundplan but, as discussed above (cf. Agyrtidae), it is possible that a basal piece was absent (or membranous) in the staphylinoid groundplan, so the presence of a straplike, sclerotized basal piece in certain staphylinoids should be regarded as secondary (derived). A similar basal piece is also found in, e.g., Microsilphinae, Proteininae, and Micropeplinae (probably convergent).

The entire tergum 9 of the female (with large apical excavation for tergum 10 (cf. Newton, 1982a)) (84:1) was regarded as an autapomorphy by Newton (1982a), but is probably a more basal feature (see clade 53). Newton also considered the more-or-less constricted neck (3:2) and the absence of tergal wing folding patches (46:5) as pseudopsine autapomorphies, but both features are almost certainly more basal and probably part of the staphylinid groundplan (here indicated as basal for clade 62 and clade 61, respectively).

ANNOTATIONS TO CHARACTERS:

3. Head with neck pronouncedly constricted well behind eyes in *Zalobius*; neck broader and weaker demarcated in *Pseudopsis* (secondary?).
6. Gular sutures separate, though almost confluent for some distance in middle (at least in *Zalobius*).
10. Mandibles without inner lobe (prostheca) (Blackwelder, 1936: fig.15i).
12. 4th segment of maxillary palpi as large as 3rd, but narrow (long) in *Pseudopsis*.
24. Procoxal fissure open and trochantin exposed in *Zalobius* and *Pseudopsis* (but according to Newton (1982a) sometimes closed).
28. Mesothoracic spiracles exposed (Newton, 1982a: fig.3).
30. Mesosternum considered broad, though not quite 1/3 of anterior mesothoracic width in *Zalobius*; apparently not fused to mesepisterna (i.e., at least demarcated by a ridge).
38. Abdominal segments with one paratergite on each side in *Pseudopsis* (Newton, 1982a mentions, that *Zalobius* has 2, but this could no be observed in the specimens examined here; possibly the the thick lateral sternal edge was taken for a second paratergite).
50. Abdominal sternum 2+3 carinate anteriorly in *Zalobius* (sometimes not carinate, according to Newton, 1982a).
59. Hind coxae triangular, but with very slight (not demarcated) expansion laterocaudally.
63. Tarsi normally 5-segmented (but in some *Pseudopsis* 3-segmented, cf. Newton, 1982a).
65. Epipleura well demarcated, but lateral canthus situated rather ventrally, so epipleura become very narrow; a "false lateral elytral canthus" is formed by the third longitudinal ridge (apparently representing the true 7th elytral interstice, though this can not be confirmed due to absence of distinct elytral striation).
78. Aedeagus symmetrical (primitive?) or asymmetrical (Newton, 1982a).

83. Parameres present (primitive condition) or absent (Newton, l.c.).

STAPHYLININE-GROUP

This group, as delimited here, includes the staphylinid subfamilies Paederinae and Staphylininae (incl. Xantholinini) and is thus not equivalent of the more broadly defined "staphylinine group" of, e.g., Lawrence and Newton (1982). These two subfamilies seem to form a reasonably well defined monophyletic assemblage, which may be defined by the following possible autapomorphies:

a) Larval head constricted posteriorly (apparently unique, except that it is also weakly constricted in Euaesthetinae and Megalopsidiinae).

2:2*. Frontoclypeal suture not distinct (this is also found in other groups of Staphylinidae, but is indicated as convergent by the present analysis); the presence of a suture in a few genera (e.g., *Eulissus* and *Pseudocryptobium*) is most likely secondary.

9:1*. Mandibles without mola (also in certain other staphylinid subfamilies, apparently convergent).

25:0*. Hypomeron without postcoxal processes. The significance of this character is not great, and though absence of such processes is probably basal to the staphylinine group, blunt processes occur in some forms, particularly within Paederinae. Moreover, several other staphylinids lack hypomeral processes (apparently convergent).

38:1*. Abdominal segments 3 to 6 (or 7) with 2 paratergites on each side (also found in other staphylinid groups, probably convergent). In some derived Paederinae (e.g., *Procirrus* and *Palaminus*) segments 3 to 6 have terga and sterna fused to solid rings without any indication of paratergites.

65:1*. Epipleura not demarcated from dorsal portion of the elytra (also found in some other Staphylinidae, e.g., Phloeocharinae, Leptotyphlinae and derived members of a few other groups; probably convergent). The extremely narrow suggestions of epipleura found in some Paederini, as well as the well demarcated epipleura of *Pseudocryptobium*, are undoubtedly secondary features.

Naomi (1985) mentioned a few more characters as autapomorphic for the staphylinine group (e.g., very strongly constricted occiput and large, broad, shallow and contiguous mesocoxal cavities), but their significance is not clear. Particularly the contiguous mesocoxal cavities are shared with numerous other Staphylinidae.

ANNOTATIONS TO CHARACTERS:

3. Head generally with pronouncedly constricted neck well behind eyes; however, in Platyprosopini only weakly demarcated (secondary).
6. Gular sutures separate but often close, except in Xantholinini, where they are fused for most of their length (secondary).
14. Labial palpi generally with 3rd segment a little narrower than 2nd (e.g., Paederinae, Xantholinini); sometimes as wide (*Staphylinus*).
17. Antennal insertions relatively anterior in Staphylininae (particularly Xantholinini), but still inserted under a canthus.
21. Pronotum primitively with lateral ridge separating dorsal portion from hypomeron, as in Staphylininae and Paederinae:Pinophilini (*Pinophilus*); in some Paederinae:Pinophilini only distinct posteriorly (*Procirrus*), or not distinct (*Palaminus*); in Paederini the ridge is situated more ventrally on the side and has generally become very fine or indistinct (secondary).
26. Primitively, a short acute prosternal intercoxal process is present (as Paederinae); absent in Staphylininae (secondary).
27. Procoxal cavities normally open internally (except in a few Paederinae).
28. Mesothoracic spiracles mostly (and primitively) exposed (Staphylininae and some Paederinae), but variably located in Paederinae and sometimes even concealed.
34. Mesocoxal cavities demarcated posteriorly by a very fine ridge (ridge disappeared in *Xantholinus*).
50. Abdominal sternum 2+3 carinate anteriorly in Paederinae (primitive condition), not carinate in Staphylinini.

53. In some Paederinae (e.g., *Procirrus* and *Palaminus*) paratergites are not demarcated (fused to terga).
57. Anterior coxae are strongly projecting, but directed somewhat caudally (rather than ventrally).
58. Mesocoxae often more-or-less elongate (particularly in Xantholinini).
74. Hindwings normally with 4 veins posterior to medial bar (brachypterous *Xantholinus* only with 2 such veins).
77. Male tergum 9 undivided in Paederinae; divided medially by tergum 10 in Staphylininae (incl. Xantholinini). – Primitive condition doubtful.
78. Aedeagus primitively symmetrical; sometimes asymmetrical (e.g., Staphylininae:some *Philonthus*).
83. Parameres primitively present and paired (e.g., Xantholinini, Platyprosopini, Othiini); in other Staphylininae fused to single median plate, or occasionally (e.g., *Heterothops*) absent; parameres and apical portion of median lobe very reduced in size in Xantholinini; parameres absent in some (most?) Paederinae or (e.g., *Lathrobium*) apparently fused to a single median plate ("sternal lobe" sensu Bordini, 1982).
84. Female tergum 9 entire in *Lathrobium* and *Xantholinus* (primitive condition?); almost divided in Othius (secondary?).
85. Female gonocoxites primitively present (as in most Staphylininae, except Xantholinini); apparently fused to valvifers (or absent?) in some Paederinae).
86. Styli often absent.
87. Female: valvifers normally separate (primitive condition); fused medially in Xantholinini (secondary).
91. Larva: 1. instar cephalic eggbursters absent (Staphylinini: Crowson, 1981).
96. Larva: primitively with 6 stemmata on each side (as in some Paederinae); other Paederinae have 5 pairs of stemmata or no stemmata. – Staphylininae with fewer stemmata (Xantholinini 1 or 2; Staphylinini 4).
106. Larva: maxillary palpi probably primitively 3-segmented (as, e.g., *Paederus*, some Staphylinini); 4-segmented in some Paederini, some Staphylinini and in Xantholinini.
113. Larva: 1. instar thoracic/abdominal eggbursters absent (Staphylinini: Crowson, 1981).
116. Larva: urogomphi normally 2-segmented (only in some Staphylinini aberrant: 3-segmented in *Creophilus*, and according to Frank (1991) sometimes forming single bulbous segment).

APATETICIDAE

A small group, including only the genera *Apateticus* and *Nodynus* whose systematic position have been subject to some debate. They have been included in the Silphidae by some authors (e.g., Madge, 1980), in the Staphylinidae (often included in Piestinae) by others (e.g., Newton, 1982b), but the affinities of these beetles are not evident, and more recently they have been placed in a separate subfamily within the Staphylinidae (e.g., Newton and Thayer, 1992). The present analysis supports the hypothesis of a close (sistergroup) relationship with the Silphidae (s.str.), but because the latter is a very distinctive taxon as presently defined, I hesitate to include *Apateticus* and *Nodynus* in that family. Rather, I tentatively suggest that Apateticinae of previous authors are raised to family rank, which is equally justified on the basis of the results of the present analysis. Assuming the phylogenetic position of the Apateticidae as a sistergroup of Silphidae (s.str.), its monophyly can be supported by the following autapomorphies.

2:2*. Frontoclypeal suture absent.

14:0*. Third segment of labial palpi as wide as 2nd, not narrower (reversal within clade 63; similar reversals found in several other subgroups of that clade, probably convergent).

25:1*. Hypomeron with mesally directed postcoxal processes.

60:1*. Posterior coxae with excavate posterior face in about mesal half.

62:1*. Posterior coxae not reaching lateral edges of body.

The presence of 9 elytral striae (rather than the ancestral polyphagan 10 striae) may be another autapomorphy for the Apateticidae; apparently the reduced number of striae results from the loss of the 8th stria (similar reductions in the number of elytral striae are found in several other staphylinoids).

The relatively long elytra, covering about first 5 or 6 segments (rather than just two or three) (67:1) may be an autapomorphy, but the basal condition for clade 62 (Apateticidae-Silphidae-Staphylinidae) is ambiguous. It is also possible that the higher degree of abdominal exposure, assumed to be basal of Silphidae and Staphylinidae, has evolved independently in these two families, and that Apateticidae are merely plesiomorphic with regard to this character.

ANNOTATIONS TO CHARACTERS:

3. Neck constricted well behind eyes, but very broad.
28. Mesothoracic spiracles large, partly (slightly) exposed.
49. Abdominal sternum 2 fused to 3, but apparently demarcated laterally by a transverse ("intersegmental"?) ridge.
57. Anterior coxae only moderately projecting.

SILPHIDAE

The present concept of the Silphidae is restricted to include the forms currently placed in Nicrophorinae and Silphinae (incl. Necrodini) (e.g., Lawrence and Newton, 1982; Newton and Thayer, 1992). Other forms, earlier included in the family, are not closely related to the typical silphids and have been referred to other families (Agyrtidae, Leiodidae). In this restricted sense, the silphids constitute a quite distinctive and no doubt monophyletic group, which is normally given family rank but which, according to Lawrence and Newton (l.c.), possibly should be included in a group of staphylinid subfamilies (together with Oxyporinae, Megalopsidiinae, Steninae, Euaesthetinae, Leptotyphlinae, Paederinae, Staphylinae and perhaps Scydmaenidae). Although the position of the Silphidae as a member of the staphylinid group is confirmed by the present analysis, a subordinate position within Staphylinidae is not indicated. Apparently, the silphids occupy a more basal position within the staphylinid group, for which reason their rank of distinct family can be justified. However, Naomi's (1985) hypothesis about silphids representing the most primitive Staphylinoidea and his statement that their inclusion in the staphylinid group is "practically based on symplesiomorphies" is based on complete ignorance of the evidence presented previously by Lawrence and Newton (l.c.). The phylogeny within the Silphidae seems not to be well understood, and the division of the family into Silphinae and Nicrophorinae is most likely artificial, leaving the first of the subfamilies as a paraphyletic assemblage. Thus, it seems most likely that the most primitive forms should be found among those with more-or-less abbreviated elytra rather than those with entire elytra. Possibly, the necrodine genus *Diamesus* (with strongly abbreviated elytra) can be considered one of the more primitive silphids, i.e., it seems plausible that a *Diamesus*-like form have given rise, along one lineage, to the necrophorine genera (*Ptomascopus, Nicrophorus*) and, along another – via forms such as *Necrodes* – to the more typical Silphini. A more thorough phylogenetic analysis need to be made before the phylogeny of the silphids can be adequately explained. The monophyly of the family can be supported by the following possible autapomorphies:

a) Each elytron with a subapical bulge situated between the outer 2 (of 3) longitudinal ridges (fig. 156) (unique); such bulge seems to be generally present throughout the family, but may be more-or-less pronounced (only exceptionally indistinct).

1:1. Clypeus relatively large. The character was ambiguous for a hypothetical silphid-apateticid ancestor (clade 45), because the character could not be examined in Apateticidae, but other related taxa have a smaller clypeus, so probably the larger clypeus of Silphidae is a derived feature; a large clypeus is also found in Hydrophiloidea, Hydraenidae and Scaphidiidae (no doubt convergent).

9:1*. Mandibles without mola (probably convergent with, e.g., some staphylinid subfamilies).

17:0*. Antennae inserted on dorsal face of head; in Nicrophorinae, the insertions are demarcated posteromedially by a fine ridge (convergent with, e.g., some staphylinid subfamilies (Aleocharinae, Steninae)).

18:1*. Antennal segment 8 cupuliform (segments 7 and 6 often forms a transition to the proximal, simple segments); the cupuliform shape of segment 8 less pronounced in a few Silphini (e.g., *Silpha*), no doubt secondary (convergent with Histeroidea, Hydrophiloidea, and several Scarabaeoidea).

19:3*. Antennae with well defined, densely pubescent, 3-segmented club (pre-club segments nearly glabrous).

40:2*. Abdominal segment 9 and 10 everted. The character may be an artefact (see note under this character in List of characters in previous section).

47:3*. Only abdominal tergum 4 and the following well sclerotized, i.e. tergum 3 (secondarily) less sclerotized (reversal within clade 63).

49:1*. Abdominal sternum 2 well demarcated and visible at least laterally, on each side of posterior coxae.

50:2*. Basal ventrite not at all carinate (also found in, e.g., Scydmaenidae and Scaphidiidae, probably convergent).

53:1*. Inflexed portion of abdominal sterna demarcated (but not articulated) to ventral portion (secondary fusion?).

85:0*. Gonocoxites rather short, a little flattened (apparently a reversal within clade 63, at least in regard to the relative length).

104:1. Larval galea present as a small (fixed) appendage on lacinia (not completely fused to it); possibly a silphid autapomorphy, but not examined in the presumed sistergroup (Apateticidae).

The relatively short elytra, covering only about first 3 segments (rather than 5 or 6 segments) (67:2) may be an autapomorphy (convergent with Staphylinidae (clade 61), but the basal condition for clade 62 (Apateticidae-Silphidae-Staphylinidae) is ambiguous. It is also possible that the higher degree of abdominal exposure may be basal of clade 62 with subsequent reversal in Apateticidae.

ANNOTATIONS TO CHARACTERS:

1. Clypeus large (only demarcated in *Nicrophorus*).
2. Frontoclypeal suture possibly primitively present as a fine line (as *Nicrophorus*), but indistinct in other Nicrophorini and in Silphini.
3. Head apparently primitively with constricted neck somewhat behind eyes, as in *Nicrophorus, Ptomascopus* and *Silpha*; in other forms the constriction is nearer to the hind margin of eyes (*Diamesus, Necrodes* and to some extent *Ptomaphila*), but this is probably secondary.
6. Gular sutures generally separate, except *Ptomascopus* (secondary).
12. 4th segment of maxillary palpi generally as long as 3rd, but sometimes slightly narrower.
13. 1st segment of labial palpi probably primitively c. as long as 2nd (as in Nicrophorini); elongated in many Silphini (secondary).
25. Hypomeron probably primitively without projections (as in Nicrophorini and particularly Silphini:*Diamesus*); in some Silphini a short, very blunt projection appears to be present (secondary), but probably only as a result of the pronounced enlargement of the procoxal fissure.
46. Wing folding patches present on abdominal terga 3-5 (large, paired); seldom only present on terga 3-4 (*Diamesus*: secondary?).
47. Abdominal terga sclerotized from the 4th in *Diamesus* and Nicrophorini (though 4th may be slightly softer than 5th) (primitive condition); in other Silphini first sclerotized from tergum 5 or 6 (secondary).
60. Hind coxae generally (and primitively?) with oblique posterior face; but in Nicrophorini:*Nicrophorus* excavate mesally.
66. Ventral face of elytra probably primitively without medio-lateral patch of microspines (except posteriorly in *Silpha*); sometimes, notably in Nicrophorini with extensively microspinose, almost pubescent ventral face (secondary).
67. Elytra truncate and covering abdominal terga 1-3 in *Diamesus* (primitive condition?), truncate and covering terga 1-5 in Nicrophorini and some Silphini; only in *Silpha* and a few other Silphini rounded posteriorly and almost completely covering abdomen (secondary).
69. Folded hindwings cover abdominal terga 1-3 in *Diamesus* and *Ptomaphila* (probably others); sometimes also covering tergum 4 (e.g., *Silpha*) (secondary).

70. Folded hindwings primitively overlap completely (as *Ptomascopus, Diamesus* etc.); in *Silpha* less overlapping (secondary).
72. Hindwing with anal lobe, but lobe not demarcated from rest of wing (examined in *Ptomascopus, Thanatophilus* and *Silpha*).
74. Hindwing with 3 veins posterior to medial bar; (in brachypterous *Silpha* only with 2 such veins).
80. Median foramen of aedeagus small and apparently ventral in *Nicrophorus* (probably primitive condition); but larger and more basal in *Silpha* (secondary).
82. Median lobe of aedeagus rather bulbous in *Nicrophorus* (probably primitive condition); less bulbous and appearing more tubular in *Silpha* (secondary).
91. Larva: 1. instar cephalic eggbursters absent (at least in *Blitophaga*, cf. Emden, 1946).
96. Larva: probably primitively with 6 stemmata on each side (Silphini); but sometimes only 1 (Nicrophorini).
113. Larva: 1. instar thoracic/abdominal eggbursters absent (at least in *Blitophaga*, cf. Emden, 1946).
116. Larva: urogomphi probably primitively 2-segmented (as in Nicrophorini and some Silphini); other Silphini have 1-segmented urogomphi.
118. Larva: abdominal segment 10 probably primitively with numerous fine teeth (as in Silphini); segment unarmed in Nicrophorini).

Evaluation of characters

The phylogenetic significance of the characters included in the present study are briefly discussed on the basis of the results of the phylogenetic analysis. A complete list of character variation is given in the appendix.

Strong and unique apomorphies are few, and almost all the included characters are subject to homoplasy. Even some of the apparently unique apomorphies within the Staphyliniformia may not be unique when other groups of Coleoptera are considered. Thus, although autapomorphies are by definition unique of nature, their images as unique morphological (or other) features are probably quite rare (this is often less obvious, when only taxa of lower ranks are considered). But it does not mean that the characters are uninformative. When all characters are regarded collectively, parallelisms or reversals are often relatively obvious.

Our present knowledge about the morphology (and variation) of adult staphyliniform beetles is quite comprehensive and seems to provide a great potential for phylogenetic reconstruction. Although character polarities are in many cases insufficiently understood, the reason for this is often that the characters have not yet been adequately analysed (i.e., on the basis of modern cladistic methods). Our knowledge about larval morphology is increasing, but still far more fragmentary, and although larvae seems to be generally more conservative than adults in regard to character changes, we rarely have a detailed knowledge about the variation of a particular character in a particular taxon. Hence, when larval and adult characters seem conflicting, it is possible that the latter should be considered more reliable.

In recent years the use of molecular data in phylogenetic reconstruction has been growing, but because such data are hardly available for staphyliniform beetles, only morphological characters have been used in the present analysis.

There is, however, one item about morphological characters (as used here) that may be worth mentioning: they are all phenotypic, but determined genetically. This may sound elementary, but can greatly affect our understanding and imagination as to how characters may vary between taxa. Actually we only know little about the genetic basis for morphological characters at a detailed level. It is generally believed that once a character has been lost, it can not evolve again. This is of course essentially true, because a "re-evolved" character is not homologous with the original character. But when this statement refers to morphological (phenotypic) characters, we can not assume that a change results from an irreversible change in the gene(s) that code for the character, i.e., the change/loss of a morphological structure may not always be the result of a complete change/-

loss of its genetic basis. In some cases – judging from the morphological character distribution between taxa – it seems more likely that the gene(s) have been deactivated by a (reversible and possibly fairly simple) mechanism, which does not alter the genetic code itself, and that the gene(s) are potentially able to be expressed phenotypically again, if the deactivating mechanism is lost or destroyed. Whether such a phenotypic "regain" is successful will probably depend primarily on its selective advantage or disadvantage and on how long (i.e., for how many generations) the character has been deactivated; it seems likely that inactive genes gradually disintegrate as the result of random mutations, because it is not (like phenotypic characters) subject to selective pressure.

Examples of such characters within Staphyliniformia may be the presence or absence of dorsal ocelli in the adults and the number of veins in the hindwings. But without a detailed knowledge about the genetic mechanisms responsible for morphological variation, we cannot tell how common such "reversible" changes are compared to "irreversible" changes in the genome.

Head and mouthparts (adults)

The head capsule shows some characteristics, which seem to be relatively significant though none of them can be considered very strong at a higher taxonomic level. In most forms, the clypeus (1) is generally small but a few groups, notably Hydrophiloidea, Hydraenidae, and Silphidae, have independently developed a larger clypeus. The appearance of the fronto-clypeal suture (2) is very variable and of little significance. The posterior constriction of the head (3) may be more informative; only few groups have the head constricted immediately behind eyes (e.g., primitive Hydrophiloidea, Hydraenidae, Ptiliidae, Micropeplinae and some derived members of certain other groups), others (e.g., most members of the staphylinid group) have a more-or-less constricted neck well behind the eyes (i.e., there are well developed temples behind the eyes), and a non-constricted head is found in e.g., Histeroidea, Scarabaeoidea and some primitive Staphylinoidea (Agyrtidae, many Leiodidae). Interocular grooves (5) seem to have evolved independently in Hydraenidae, Omaliinae (and allies), and Leptotyphlinae and the pselaphine group, as well as a few derived members of other groups. The gular sutures (6) are separate in most groups, but have become confluent in the more derived Histeroidea, Hydraenidae, Scaphidiidae, Neophoninae, and in derived members of some other groups; they are rarely indistinct (e.g., Ptiliidae, derived Pselaphinae).

The presence of ocelli (4) of some primitive Polyphaga (e.g., Derodontidae, many Hydraenidae and a few Agyrtidae and Leiodidae) is usually referred to as an archaic feature of these beetles. This could be true, but it should be noted that it will imply several independent losses of ocelli (e.g., in the Scarabaeoidea-Hydrophiloidea-Histeroidea lineage, as well as some or all members of staphylinoid families, most other Polyphaga, and the other three coleopteran suborders. The ocelli of certain staphylinid subfamilies (notably Omaliinae) is indicated by the present analysis to have evolved independently.

Cervical sclerites (7), which are generally present in most Polyphaga, seem to have been lost a few times in the Staphylinoidea (Ptiliidae, Scydmaenidae, and the pselaphine group and allies).

The degree of exposure of the mandibles (8) is quite variable and possibly only significant at a relatively low taxonomic level, whereas the presence or absence of a mandibular mola (9) and a prostheca (10) may be more informative on a higher level. Primitively, a mola is present, but it has been lost independently in e.g., Scydmaenidae, Silphidae, the staphylinine group, Pselaphinae, and some derived members of other groups; a well developed prostheca is found only in a few groups (e.g., Hydraenidae).

The relative length of lacinia (11), apical segment of maxillary palpi (12), and 1st and 3rd segment of the labial palpi (13, 14) are only moderately informative on a higher taxonomic level and show some degree of homoplasy, between and within the terminal taxa. These characters would probably be more significant at lower taxonomic levels.

Antennae (adults)
The antennae provide several important characters. They are primitively 11-segmented (16) and filiform or only slightly and gradually thickened apically (19). Reductions in the number of segments have taken place a number of times, e.g., in Hydrophiloidea (9 or fewer segments), Micropeplinae (9 segments), and subordinate members of a few other groups (Histeridae, Hydraenidae, Ptiliidae, and a few staphylinids, e.g., some Pselaphinae), but increase in the number of segments are extremely rare (a few Pselaphinae).

In some forms the distal segments form a more-or-less well defined club, which is often 3-segmented (e.g., Ptiliidae, some Scydmaenidae, Empelidae, Steninae, Microsilphinae, Dasycerinae, some Pselaphinae). In Hydrophiloidea, Histeroidea and (most) Scarabaeoidea the 3-segmented club is densely pubescent and sharply contrasting the glabrous pre-club segments; some Histeridae have the club segments intimately fused. Two-segmented clubs are found, e.g., in certain derived Pselaphinae, 4-segmented clubs, e.g., in some derived Scydmaenidae. In other groups the club is 5-segmented, pubescent and sharply contrasting the pre-club segments (e.g., Hydraenidae, Scaphidiidae). A special antennal morphology is found in the Leiodidae. Most members of this family have 11-segmented antennae with a 5-segmented, interrupted club; although the club is not always well demarcated (e.g., in the more primitive forms) the 8th antennal segment is almost invariably smaller than adjacent segments. Greatly modified antennae are found in some highly specialized, myrmecophilous or parasitic forms (e.g., the pselaphine tribe Clavigerini and the leiodid genus *Platypsyllus*).

In some groups, notably Hydrophiloidea, Histeroidea, Scarabaeoidea the segment preceding the club has become more-or-less cupuliform (18). In these groups the cupule represents the 8th segment (although, in Hydrophiloidea, it appears as the 6th, 5th or 4th, due to reduction of pre-club segments). A similar cupule has evolved independently in Silphidae. In Hydraenidae, the club is also preceded by a cupule, but in this family the cupule is formed by the 6th antennal segment. In the aquatic Hydrophiloidea and Hydraenidae the antennae are used as auxiliary organs in aquatic respiration (15) (a function, which seems to have evolved in a primitive form in certain scarabaeoids, as well).

In some groups, the penultimate antennal segments have sensilla-filled, periarticular grooves apically (20). Such grooves are present, notably in Agyrtidae and the closely related Leiodidae. In the first mentioned these grooves are open, while in the second they form almost enclosed vesicles, which open to distal surface only through a narrow slit. Similar vesicles are found in a few other groups (e.g., the scydmaenid genus *Eutheia*), probably convergent.

Normally, the antennae are inserted laterally on the head, below a more-or-less sharp, sometimes thickened canthus (17). But in some groups, the insertions have become more dorsal, e.g., some Histeridae, some Leiodidae, some Scaphidiidae, Silphidae, and certain Staphylinidae (Steninae, Aleocharinae).

Thorax (adults)
In most forms the pronotum has a well de-

fined, sharp lateral edge, which separates the dorsal portion from the deflexed ventral portions (hypomera) (21), but this ridge has become obsolete or absent in some forms, e.g., the stenine group, Leptotyphlinae, Neophoninae and Pselaphinae, as well as derived members of certain other staphylinid groups, some Leiodidae and many Scydmaenidae. Primitively, in Polyphaga, the pronotum has an accessory posterior ridge below the posterior margin, serving as a locking device, which prevents the prothorax from rotating (22); such a ridge has been lost in the Staphylinoidea, and in the more derived members of the superfamily there is a higher degree of flexibility between pro- and mesothorax.

The invagination of the propleuron (23) is a distinctive characteristic of polyphagan beetles, with no exceptions found in the Staphyliniformia. In most of these beetles, the trochantin is still exposed (in an open procoxal fissure) (24), but a number of groups have the trochantin concealed and the procoxal fissure closed, e.g., derived Histeroidea, Scydmaenidae, Scaphidiidae, the stenine group, Dasycerinae and Pselaphinae. In primitive staphyliniforms (and Scarabaeoidea), the hypomera are expanded into a mesally directed process on each side behind the procoxae (25). Such processes are rudimentary or absent in most members of the staphylinid group, and when present in Staphylinidae, they may have evolved secondarily. In certain groups (Hydrochidae, a few Hydrophilidae, Synteliidae, some Hydraenidae, some Osoriinae, etc.) the hypomeral processes are very well developed and may, in combination with an expanded intercoxal process, form a complete posterior closure of the procoxal cavities. The appearance of the prosternal intercoxal process (26) is quite variable. In most forms it is present, but relatively short, sometimes stronger developed (e.g., Hydrochidae, some Hydrophilidae, some Hydraenidae, some Ptiliidae, a few Leiodidae, only rarely in Staphylinidae), or virtually absent (Staphylininae, Dasycerinae, Pselaphinae, most members of the tachyporine group). There is some variation in regard to the internal closure of the procoxal cavities (27). It seems that open cavities represent the primitive staphyliniform (and scarabaeoid) condition and that the closed cavities of the Hydrophiloidea, derived Histeroidea and certain staphylinoids (the Leiodid-hydraenid-ptiliid group, Scydmaenidae and Scaphidiidae) are parallelisms; other groups, such as Sphaeritidae, Agyrtidae, Silphidae and Staphylinidae (except a few Paederinae) have at least the major part of the procoxal cavities open internally. In the more primitive staphyliniforms, the mesothoracic spiracles are concealed under the hypomeron, but in the staphylinid group (excl. Scydmaenidae), the spiracles have become exposed (secondarily concealed in a few members of Staphylinidae, e.g., the stenine group); a few other groups have also somewhat exposed mesothoracic spiracles, e.g., Histeridae and certain Agyrtidae. In Apateticidae, Silphidae and certain Staphylinidae (Pseudopsinae), the promesothoracic connecting membrane has one or a pair of sclerites (not associated with spiracles), and in certain other staphylinids (the oxyteline group, Micropeplinae, Omaliinae (and allies), and some (derived?) members of the tachyporine group) sclerites associated with the spiracles are present.

The anterior width of mesosternum (30) seems to be a relatively constant character. Normally, it takes up at least one-third of the anterior mesothoracic width, but in Hydrophiloidea (with only few secondary exceptions) it is strongly narrowed anteriorly. Primitively, it is well demarcated from the mesepisterna by a suture (32), but in several groups it is completely fused with these (some Hydrophilidae, most Hydraenidae, Ptiliidae, some Leiodidae, and a number of staphylinid subfamilies). The mesocoxal fissure is normally open, exposing the trochantin (33), but in Hydrophiloidea, Histeridae, Hydraenidae, Ptiliidae and certain staphylinid subfamilies, it is closed. The mesocoxal cavities are normally sharply demarcated posteriorly by a ridge (34), but their demarcation has become obsolete and the ridge absent in a few, not closely related groups (Scydmaenidae, Xantholinini, a few Aleocharinae).

The degree of exposure of the metepisterna (35) is somewhat variable and the character may be of more significance at a lower taxonomic level. They are usually more-or-less broadly visible from below, but in certain forms completely concealed by the elytra (some Hydrophilidae, many Ptiliidae, some Leiodidae, most Scydmaenidae, a few Osoriinae, Dasycerinae, Pselaphinae, etc.).

Abdomen (adults)

The vestiture of the ventral face of abdomen is quite variable throughout the Staphyliniformia and hardly contribute significant phylogenetic information at a higher taxonomic level. However, two groups (Hydrophiloidea and Hydraenidae) are remarkable in having (independently) developed a very dense clothing of hydrofuge pubescence (plastron) (36) on the entire ventral surface of the body as an adaptation to aquatic life.

The presence/absence of distinct laterosternites of 2nd abdominal segment (37), earlier used for a basal division of the Polyphaga, is a somewhat variable character and of no great importance.

In most forms the abdominal sterna have a sharply demarcated, deflexed lateral/dorsal portion (53). In the more derived Histeroidea this demarcation has become more blunt (or obsolete), while in the staphylinid group the dorsal portion is separated from the ventral portion by a narrow membrane, and has become a separate sclerite (paratergite). Within the staphylinid group, the primitive condition is to have a single paratergite on each side of segments 3 – 6/7 (38), but some forms have evolved paired paratergites (e.g., Paederinae, Staphylininae, Solieriinae, Leptotyphlinae, Oxyporinae and most members of the tachyporine group). Some staphylinids have secondarily fused terga and sterna.

Primitively, in the Staphyliniformia, the deflexed portions of the sterna are covered with microtrichia (54), which contacts patches of similar spines on the ventral face of the elytra and probably serves as locking device between the elytra and the abdomen. In some forms, which have a ventral, sublateral, laminar locking-device on the elytra (e.g., Histeridae), the spines on the laterosternites have become rudimentary. In the staphylinid group these spines have also been reduced, and there is no such locking device between elytra and the abdomen (in most staphylinids the elytra are strongly abbreviated and do not contact the abdominal segments, except for the two first).

The abdominal terga, which are primitively concealed under the elytra bear extensive patches of more-or-less mesally directed microspines, which take part in the folding of the hindwings (46). Primitively, such wing folding patches are present on the 7th and preceding terga, but in some forms (Histeroidea and the staphylinid group), the 7th tergum has become exposed and has lost the wing folding patches. In the more derived members of the staphylinid group (notably Staphylinidae) the wing folding patches have become reduced on the preceding terga as well, probably in connection with the higher degree of exposure of the abdominal segments. Some groups have small paired wing folding patches on first exposed terga (e.g., Omaliinae, some Tachyporinae) and a few forms (with long elytra) have even more extensive patches, but this may be secondary. The Ptiliidae have these patches present on most terga, but modified to transverse, curved "strigae".

It is possibly primitive for the Staphyliniformia (and Scarabaeoidea) to have 5 distinct ventrites (segments 3-7) and the 8th tergum not concealed by the 7th. In the Histeroidea, however, segment 8 is completely invaginated within segment 7 (39). On the other hand, in the hydraenid-ptiliid group and the staphylinid group (as well as certain derived members of, e.g., Hydrophilidae, Agyrtidae and Leiodidae, at least the 8th abdominal segment has become everted (probably convergently).

Within the staphylinid group there seems to be a series of modifications of the abdominal morphology correlated with the abbreviation of the elytra. Primitively, as in Scydmaenidae, the tergo-sternal membranes are still long on segments 1-6 (41) and only tergum 6 to 8 have become sclerotized (47) (both features probably correlated with the full or only slightly abbreviated elytra). In Scaphidiidae and Empelidae, the tergo-sternal membranes are long only on segments 1-3 (and partly 4), terga 4 to 8 (or Empelidae: 3 to 8) sclerotized, and the elytra at least slightly truncate apically. In the more derived members of the staphylinine group, Apateticidae, Silphidae and Staphylinidae, only the basal two segments have a long tergo-sternal membrane and the 3rd tergum has become well sclerotized (apparently secondarily less sclerotized in Silphidae). In Apateticidae the elytra are still relatively long, covering most of the abdomen, but broadly truncate posteriorly. But Silphidae and Staphylinidae have more-or-less strongly abbreviated elytra, which probably primitively cover no more than first 2-3 abdominal segments (several Silphidae and some Staphylinidae, notably Dasycerinae, Glypholomatinae, Microsilphinae, some Omaliinae and some Proteininae have secondarily developed longer elytra). Similar modifications of the abdomen are found in certain other groups, in which the elytra have become abbreviated (e.g., some Ptiliidae).

Other specializations of the staphylinid group (excl. Scydmaenidae) are the high abdominal flexibility (notably in Silphidae and Staphylinidae) resulting from the elongation of the intersegmental membranes (42), as well as the reinforcement of the membranes by the development of a dense system of minute sclerites arranged in a characteristic "brick-wall" pattern (43). Both these features have been lost in certain groups of Staphylinidae, but rarely in combination (Proteininae). Another character correlated with the high abdominal flexibility is the loss (in Apateticidae, Silphidae and Staphylinidae) of sharply defined metacoxal cavities on the first ventrite (52). In certain staphylinids with reduced abdominal flexibility, such cavities seem to have evolved secondarily (e.g., Micropeplinae, Dasycerinae, Pselaphinae).

The number (44) and position (45) of abdominal spiracles seem to provide significant evidence about phylogeny at a higher taxonomic level. Primitively (and normally) abdominal segments 1-8 have functional spiracles located in the tergo-sternal membranes. In Hydrophiloidea and Histeroidea the spiracles are atrophied on segment 7, and in Proteininae and Neophoninae, as well as the pselaphine group, they are atrophied on segments 4-6. The atrophy of spiracles 4-6 is often regarded as indicative of a close relationship of the pselaphine group to Proteininae and Neophoninae (e.g., Lawrence and Newton, 1982; Thayer, 1987), but is indicated as a parallelism by the present analysis. Sometimes, the 8th spiracles are indistinct, and in certain Scydmaenidae, other reductions of the spiracles can be found. In the staphylinid group, the spiracles are placed in the terga rather than in the tergo-sternal membranes, either from segments 4 or 5 onwards (primitively, as in Scydmaenidae and Scaphidiidae) or from segments 2 or 3 onwards (as in the remainder of the group). In the very derived Dasycerinae, with secondarily long elytra, the abdominal terga have become greatly reduced and largely membranous.

Abdominal defensive glands have evolved a number of times, and at different positions, within the Staphylinidae. Some of them are present only in subordinate groups of the terminal taxa of the present analysis (Tachyporine group: Aleocharinae; Oxyteline group: Oxytelinae; Staphylinine group: Staphylininae), but one type of gland, ending in paired openings near the anterior margin of the 8th sternum (48), seems to be basal for a number of terminal taxa, viz. Empelidae, Omaliinae, Microsilphinae, Proteininae, Neophoninae, Dasycerinae and probably Pselaphinae. Some authors (Lawrence and Newton, l.c.; Thayer, l.c.; Newton and Thayer, 1995) consider these taxa as closely related on the basis of the shared gland structure and refer to them as the "omaliine group" (also including Micropeplinae, in which the absence of such gland complex is explained as secondary, and the recently proposed subfamilies Glypholomatinae and Protopselaphinae (not studied here)). It is, however, indicated by the present analysis that a "sternum 8 gland complex" may have evolved independently three times within Staphylinoidea: 1) in Empelidae, 2) in Omaliinae, Glypholomatinae, Microsilphinae, Proteininae and Neophoninae, and 3) in Dasycerinae, Protopselaphinae and Pselaphinae (see also above under Results and Discussion). It is also possible – perhaps more likely (but less parsimonious) – that such a gland complex evolved once and subsequently became reduced in a number of lineages.

Legs (adults)

The legs posses a number of phylogenetically important features, though most of them may be more significant at lower taxonomic levels.

The morphology of the coxae includes some important characteristics of major groups, particularly the degree of projection of the anterior coxae (57) and the globular vs. transverse shape of the middle coxae (58). The shape of the posterior coxae, e.g., whether or not they are expanded caudally and laterally (59) and whether or not they have excavate posterior face (60) are subject to a higher degree of homoplasy. Mostly, the posterior coxae are almost contiguous (61), but in Georissidae, Histeridae, some Hydraenidae, most Ptiliidae, some Leiodidae, Scydmaenidae, Scaphidiidae and a few subgroups of Staphylinidae, they have (independently) become more-or-less broadly separated. The posterior coxae usually reach the lateral edges of the body (or nearly so), but sometimes they end well before the lateral edge (e.g., Synteliidae, Histeridae, a few staphylinid subfamilies, and certain derived members of Ptiliidae, Leiodidae and Scydmaenidae).

The presence of one or (unually two) stronger spines (tibial spurs) at the tibial apices is a general feature of most Staphyliniforms, but in some groups tibial spurs have become undetectable (lost?), e.g., in the stenine, proteinine and pselaphine groups of Staphylinidae.

The tarsi are primitively 5-segmented, but various reductions in the number of segments occur throughout the Staphyliniformia (63); only few groups have basally less than 5 segments (Ptiliidae, Leptotyphlinae, Neophoninae, Micropeplinae, Dasycerinae, Protopselaphinae, Pselaphinae). In Ptiliidae the basal tarsal segments are very small and partly retracted into the tibial apices, while the apical segment is very long and thin (56).

Elytra

There are not many elytral characteristics that seem to be important at higher taxonomic levels. One of the more obvious features is the relative length of the elytra (67). Primitively, the elytra are well developed and conceal the abdomen completely, but in several forms the elytra are more-or-less abbreviated, so a smaller or greater portion of the abdomen has become exposed. In Histeroidea and the more primitive members of the staphylinid group, the elytra cover about the first 5 or 6 abdominal segment, but in the more derived members of the staphylinid group (Staphylinidae and primitive Silphidae) no more than the first 2 or 3 abdominal segments are covered. Several silphids and some staphylinids have secondarily become longer elytra. Some Ptiliidae and a few Leiodidae also have more-or-less abbreviated elytra.

Certain groups, e.g., Georissidae, Hydrochidae and Histeridae, have developed a sublateral ridge or lamina on the ventral face of the elytra (64), which serves to lock the elytra tightly to the abdomen. In other groups the elytra may be "locked" to the abdomen by means of a "medio-lateral binding patch" (66), i.e., a patch of dense microscopical spines on the ventral face of the elytra. Such a patch seems to have been lost in derived Histeroidea and in most Staphylinoidea, though it is present in some staphylinoids (Hydraenidae, certain Staphylinidae). Most staphylinoids have a more anterior ("baso-lateral") binding patch, which may be confluent with the apparent mediobasal patch, so the major part of the ventral face of the elytra is covered by such small spines (e.g., some Silphidae). The phylogenetic significance of such binding patches may not be great at a higher taxonomic level.

Normally the epipleura are sharply defined from the dorsal portion of the elytra (65), but in a number of groups the epipleura have become indistinctly defined (lost?), e.g., some Ptiliidae, Scydmaenidae, the staphylinine group, Solieriinae, Leptotyphlinae, some Steninae, Trichophyinae and Aleocharinae.

The elytral striation may also contribute important information about phylogeny, but hardly at a higher taxonomic level. Due to a high degree of variation, I did not find it possible to include striation characters in the present analysis, but a few comments might be worth here. First, it should be noted that the primitive coleopteran (and staphyliniform) number of elytral striae is undoubtedly 10 (probably plus an extra basal stria, the scutellary stria or striole, between the inner two striae). This number has been retained in most Hydrophiloidea, primitive Histeroidea, primitive Scarabaeoidea (Trogidae etc.) and some primitive Staphylinoidea (Hydraenidae etc.) (the scutellary stria is lost in most forms). The term "stria", as used here, also includes primary series of punctures as well as indications of such (even if they can only be observed when the elytron is examined from below).

Deviations from this number of striae are in most cases due to reductions of striae. In Histeridae at least the four lateral striae are greatly reduced, and a similar condition is found in the closely related Synteliidae which, however, still have a relatively complete 10th stria. In Agyrtidae and Leiodidae, there are normally only 9 complete striae, the 10th being reduced to a basal rudiment, which is more-or-less confluent with the 9th. Most members of the staphylinid group lack striae, and it is possible that elytral striae were basally absent in that group. However striae occur scattered throughout the group, and may have evolved independently a number of times. The number of striae varies: 6 evenly spaced striae in a few derived Scydmaenidae (*Clidicus*), 6-7 striae (and broad smooth lateral "interstice") in certain Scaphidiidae, Piestinae and Oxytelinae (*Coprophilus*), 9 striae (apparantly loss of stria 8) in Apateticidae and Trigonurinae, 8 or 9 in some Dasycerinae. Other groups (e.g., some Hydraenidae) have a higher number of elytral striae. The sheer presence or absence of distinct striae is of no importance at a higher taxonomic level.

Hindwings

The hindwings provide several very important characteristics. Some characters, like the presence of an oblongum cell (75) and a wedge cell (76), as well as the presence of an apical hinge (71) on the anterior margin of the wing (distal to the radial cell), are probably basal characteristics of the Coleoptera. Some of these characters (the wedge cell and the apical hinge), as well as a median loop (73) (but not the oblongum cell), have been retained in the more primitive Polyphaga (e.g., Hydrophiloidea). In Scarabaeoidea, Histeroidea and Staphylinoidea there is no distinct wedge cell (probably independent losses), and in the latter the median loop and the apical hinge have been lost. More derived members of the Staphylinoidea (i.e., the staphylinid group) have developed a secondary "radial hinge" at the anterior margin of the wing (proximal to the radial cell), probably in response to the high degree of wing folding.

Most Staphylinoidea have the veins of the medial field (posterior to the medial bar) more-or-less reduced in number (74), probably to some degree correlated with reduction of size. Reductions of these veins are also found in other groups and may not be irreversible.

Primitively, a well developed anal lobe is present (72), but it has been lost a number of times, e.g., in the leiodid-hydraenid-ptiliid group, in Scydmaenidae, a few staphylinid subgroups and in some derived members of Hydrophilidae. In several Staphylinidae, it is very small, fringed with a number of long setae.

The folded hindwings cover at least the first 4-5 abdominal terga in most groups (69) and overlap by less than half the width of one folded wing at their apices (70). However, in the staphylinid group the folding is more complex and the folded wings overlap completely at their apices (except Scaphidiidae). In Apateticidae, Silphidae and Staphylinidae the folded wings cover no more than first 2 (or 3) terga. Completely overlaping wings are also found in the Histeroidea.

In the Ptiliidae a highly specialized type of hindwing is found, in which the wing membrane is reduced to a narrow strip bordered by a fringe of very long, dense, barbed setae (only the most archaic ptiliids, e.g., *Nossidium*, have a more well developed wing membrane).

Male genitalia

The 9th tergum (77, 84) is normally more-or-less completely divided into two lateral sclerites, but often the sclerites are connected by a narrow anterior bridge (Hydrophiloidea (?), Histeridae (?), some Staphylinidae). In Sphaeritidae (?) and the more primitive staphylinoid families (Hydraenidae, Ptiliidae, Agyrtidae (?), Leiodidae (?)) as well as in certain staphylinids (e.g., the stenine group and Pseudopsinae) the 9th tergum is more-or-less entire, but with large apical emargination for tergum 10.

The male genitalia exhibit several phylogenetically important characteristics. In the primitive polyphagan type (e.g., Hydrophiloidea), they are symmetrical and have a well developed basal piece, paired parameres, a relatively simple median lobe, and the median foramen is situated basally. This type is found in a more-or-less typical form in the Hydrophiloidea, Scarabaeoidea and Histeroidea (somewhat modified in more derived members of the latter two).

In Staphylinoidea the basal piece is strongly reduced, normally membranous and indistinguishable (81), but sometimes (secondarily?) present as a narrow, transverse sclerotized strap; the more well-developed basal piece of the leiodid genus *Colon* is probably an autapomorphy for that genus. In the more derived Staphylinoidea (i.e., the staphylinid group) the median lobe of aedeagus form a large basal bulb with musculature for evagination of the internal sac (82), the median foramen has become small and situated at the morphologically ventral side rather than basally (80), and the aedeagus is everted asymmetrically from the abdomen (79).

Different kinds of asymmetry (78) have evolved in a number of groups, e.g., Sphaeritidae, some Hydrophilidae, Agyrtidae, Hydraenidae, Leptotyphlinae, Pselaphinae and some Staphylininae. In some forms, the asymmetry involves mainly the basal piece (e.g., Hydrophilidae: Megasternini), in others mainly the parameres (e.g., some species of *Philonthus* (Staphylininae)), but often all the aedeagal components are involved (e.g., most Hydraenidae, Pselaphinae). In many Hydraenidae the (permanently everted) internal sac is also very asymmetrical.

The parameres (83) are sometimes fused to a single ventral plate (Agyrtidae, most Staphylininae), or to a tube enclosing the median lobe (Histeridae and the hydrophilid genus *Helochares*). Loss of parameres have taken place a number of times, e.g., within Hydraenidae, Ptiliidae (most genera), some Agyrtidae, Paederinae and some Staphylininae. A unique type of paramere – large, three-segmented – is characteristic of the large staphylinid subfamily Aleocharinae.

Female genitalia

There is some variation in regard to the shape of the gonocoxites (85), and it seems that the shape is generally not very informative in regard to phylogeny at a higher taxonomic level. They are mostly relatively short, cylindrical or somewhat flattened. The most significant exceptions may be found in Histeroidea (broad, flattened, scoop-like) and the hydraenid-ptiliid group (connate or fused, appearing as an apical sternite). In certain staphylinids they are absent (e.g., Xantholinini, most Aleocharinae and some Proteininae). The styli are (when present) primitively situated apically on the gonocoxites, but in Histeroidea they are more ventral/mesal. Styli have been lost in a number of different staphylinoids.

In most staphyliniforms, the 9th sternum is present as a pair of lateral sclerites (valvifers) (87), but in some staphylinid subfamilies, e.g., Omaliinae, Microsilphinae, Proteininae, Neophoninae, they are not evident (sternum 9 membranous).

The spermatheca (88) is generally extremely variable, both in shape and in degree of sclerotization, and only significant at a very low taxonomic level. However, a specialized type is shared by the Hydraenidae and Ptiliidae, in which it has a lightly sclerotized, flexible central portion separating more heavily sclerotized proximal and distal portions, which are connected by muscles ("sperm pump").

Eggs

The most important character related to the eggs (89) seems to be the the construction of silk webs for protection of the eggs, shown by Hydrophiloidea and Hydraenidae. In the Hydrophiloidea eggs are normally laid in groups, completely enclosed in a cocoon, whereas the Hydraenidae lay the eggs singly and merely cover them by a web (or leave them uncovered).

Head and mouthparts (larvae)

The head of most staphyliniforms is prognathous (90), but certain forms (e.g., Hydraenidae, Ptiliidae, Dasycerinae and Micropeplinae) have a more-or-less declined or hypognathous head.

The phylogenetic significance of the presence or absence of cephalic egg bursters in first instar larvae (91) is somewhat unclear due to lack of adequate data, but their presence among certain presumedly primitive polyphagan groups (Derodontidae, Hydrophiloidea, Hydraenidae) as well as some Adephaga may suggest that they represent an archaic coleopteran feature. Such egg bursters have not been recorded from Scarabaeoidea, Histeroidea and Staphylinoidea except Hydraenidae.

Primitively, the labrum forms a separate sclerite (97), but in several groups it has become fused to the head capsule to form a nasale (e.g., Hydrophiloidea, Histeroidea, Scydmaenidae and some staphylinid subfamilies, such as, Pseudopsinae, Paederinae, Staphylininae, Steninae, Euaesthetinae, Oxyporinae and Pselaphinae). In some primitive staphylinoid families (Agyrtidae, Leiodidae) a pair of postero-lateral apodemes (tormae) rise from the labrum (98) (probably a plesiomorphic feature). Tormae are absent (lost) in Hydrophiloidea, Histeroidea and more derived Staphylinoidea (i.e., the staphylinid group). In Hydrophiloidea and Histeroidea a fimbriate lobe ("epistomal lobe") is present on each side at the anterior margin (92).

A distinct fronto-clypeal suture (93) is rarely present in the Staphyliniformia (e.g., Hydraenidae), but dorsal ecdysial lines (94) are generally found. These are often Y-shaped, i.e., with basal median stem, but sometimes (e.g., most Hydrophiloidea, Sphaeritidae, Micropeplinae) more-or-less V-shaped, without basal stem. In Agyrtidae and some Leiodidae the anterior arms of the dorsal ecdysial lines are bifurcate (95).

The number of stemmata (96) is extremely variable, and primarily phylogenetically significant at lower taxonomic (e.g., generic) levels. Apparently, the primitive number is 6 on each side, but reductions have taken place in numerous groups, and it is even possible that loss of stemmata is not always irreversible (cf. Histeroidea).

Important characters are found in the mandibles. Primitively, they have a basal, dentate, tuberculate or spinose molar area (99) and (probably) a well-developed prostheca (100), but in Hydrophiloidea, Histeroidea and the staphylinid group of Staphylinoidea the mola and the prostheca is rudimentary or absent. Relatively broad-based mandibles (with glabrous pseudomola) are present, e.g., in some Piestinae, Oxytelinae, Omaliinae and Aleocharinae (probably secondary), and Proteininae and some Omaliinae have a prostheca-like appendage on the mesal face of the mandibles (probably also a secondary feature). In most forms, the mandibles are more-or-less glabrous (101), but in, e.g., Agyrtidae they have a densely setose area on ventral surface which extends to mesal edge, and in Hydraenidae there is a setose area on the mesal face. Histeroidea and (primitive) Hydrophiloidea share the presence of a brush of setae (penicillus) at the mesal base of the mandibles.

The maxillae normally have a well-developed cardo (102), but in the derived Histeroidea (i.e., Synteliidae and Histeridae) cardo is apparently absent. The inner lobe of the maxilla (lacinia) is normally well-developed (103), but has become strongly rudimentary or absent in Hydrophiloidea and Histeroidea (the well-developed lacinia-like lobe in *Spercheus* is considered to be of secondary nature). The outer lobe, galea (104), is probably primitively (within Staphyliniformia) present as a small, fixed appendage on the lacinia, but in most members of the staphylinid group it has become completely fused to the lacinia (forming a solid mala). The articulated galea of Micropeplinae and the articulated mala of the staphylinine group are undoubtedly derived features within Staphylinidae. In Hydraenidae, Ptiliidae, Agyrtidae and Leiodidae, the galea is characteristically fringed apically (105). It has been suggested that this is a basal staphylinoid feature lost secondarily in other staphylinoids (Lawrence and Newton, 1982), but as mentioned by others (e.g., Dybas, 1976) and indicated by the present analysis, it is more likely a synapomorphy for the four families. In Hydrophiloidea and Histeroidea the galea is completely lost.

The maxillary palpus (106) may be 3-segmented (Staphylinoidea) or 4-segmented (Scarabaeoidea, Hydrophiloidea, Histeroidea) (a few Histeridae have 5-segmented palpi). It was indicated by the present analysis that 4-segmented palpi represent the derived condition within Staphyliniformia (incl. Scarabaeoidea). Hydrophiloidea and Histeroidea are unique in having an articulated, subapical appendage at the mesal face of the basal segment of the palpi (which has sometimes been referred to as a "galea"). A complex sensory appendage at the apical segment of the palpi is found in Hydraenidae and Ptiliidae (108).

A distinct ligula (109) is present in most forms, but has been lost a number of times (e.g., Scarabaeoidea, some Hydrophiloidea, Histeroidea, Scydmaenidae, some Omaliinae, Pselaphinae, some Tachyporinae).

Antennae (larvae)

Generally, the antennal foramen is well separated from mandibular foramen (110), but in Synteliidae and Histeridae it is only separated by a narrow strip of membrane. The penultimate antennal segment usually bears a sensory appendage (111), which is (probably primitively) situated on the anterior (inner) side of the segment (as in Staphylinoidea and (when distinct) Scarabaeoidea). However, in Hydrophiloidea and Histeroidea, as well as the stenine group of Staphylinidae, the appendage is situated on the posterior (outer face) of the penultimate segment.

Thorax (larvae)

The presence of a pair of egg bursters on metanotum in first instar larvae (113) has been recorded from Scarabaeoidea and certain Staphylinidae (Oxytelinae), but since comparative data are insufficient, the phylogenetic significance of such egg bursters is not clear. There is, however, hardly any doubt that metanotal egg bursters are derived and that they have evolved independently in Scarabaeoidea and (some) Staphylinidae.

Abdomen (larvae)

Among the Staphyliniformia, the Histeridae seem to be unique in having a pair of egg bursters on abdominal tergum 1 in first instar larvae (113). Such "abdominal" egg bursters have often been classed with "thoracic" egg bursters and collectively referred to as "thoraco-abdominal" (Emden, 1946; Crowson, 1981), as opposed to "cephalic" egg bursters (as in, e.g., Hydraenidae). However, the different distribution of thoracic and abdominal egg bursters among taxa requires a distinction between the two types. Due to lack of sufficient comparative data, the phylogenetic implications of abdominal egg bursters is not obvious.

Probably the presence of single, well defined, more-or-less sclerotized abdominal terga and sterna (114) is a primitive staphyliniform feature. But in Scarabaeoidea, Hydrophiloidea and Histeroidea the abdomen has become largely membranous, without single, large terga and sterna (in Hydrophiloidea and Histeroidea a number of small, rudimentary sclerites are often present). The abdominal spiracles (115) were possibly primitively annular (some members of the presumedly primitive staphylinoid families, Agyrtidae and Leiodidae, have annular-biforous spiracles, however). In the Scarabaeoidea, Hydrophiloidea and Histeroidea the spiracles have become biforous (secondarily cribriform in the majority of the scarabaeoids). The enlarged, annular spiracles of segment 8 in derived Hydrophiloidea are undoubtedly a derived feature.

The presence of articulated urogomphi (116, 117) has been mentioned as one of the principal characteristics of the Staphyliniformia, and there is hardly any doubt that it is a derived feature within Polyphaga. However, it is possible that articulated urogomphi have evolved independently in the hydrophiloid-histeroid group and in Staphylinoidea; alternatively they could be a basal autapomorphy for the entire "hydrophiloid lineage" (= Staphyliniformia incl. Scarabaeoidea) and have become secondarily lost in the Scarabaeoidea. In Hydrophiloidea and Histeroidea the urogomphi are probably primitively 3- or 4-segmented, and in Staphylinoidea they are no doubt primitively 2-segmented. Reductions (more rarely complete losses) of the urogomphi occur in all three superfamilies, and in certain staphylinoids (e.g., Scydmaenidae, the pselaphine group) they have become fixed and undivided.

In several groups the 10th abdominal segment is armed with more-or-less numerous, fine or strong spines or hooks (118). The appearance of these hooks or spines seems to be of some phylogenetic importance, even at a higher taxonomic level. Most characteristic within Staphyliniformia is perhaps the pair of large hooks shared by Hydraenidae and (most) Ptiliidae.

Legs (larvae)

The legs are typically 5-segmented (normal polyphagan condition), but reductions in the number of segments occur in derived members of certain groups (e.g., some terrestrial Hydrophilidae).

Habitat

The habitat of the Staphyliniformia is primarily terrestrial, but two groups, Hydrophiloidea and Hydraenidae, have become aquatic (at least as adults) (119).

Conclusions

1. The monophyly of the Staphyliniformia, consisting of Hydrophiloidea, Histeroidea and Staphylinoidea, can not be confirmed, because the first two superfamilies seem to be more closely related to the Scarabaeoidea than to the Staphylinoidea. However, if the Scarabaeoidea are included in this assemblage, its monophyly appears to be justified. Such a group, more-or-less equivalent of the Haplogastra, has recently been referred to as the hydrophiloid lineage of Polyphaga (Kukalová-Peck and Lawrence, 1993). A similar conclusion concerning the relationship of the Scarabaeoidea was reached by Scholtz et al. (1994) and Browne and Scholtz (1995), who suggested the group might be the sister group of Histeroidea or "Hydrophiloidea" (incl. Histeroidea), respectively. In the latter paper "Hydrophiloidea" (incl. Histeroidea) was used as an outgroup in a phylogenetic analysis of the Scarabaeoidea.

2. The four superfamilies constituting the hydrophiloid lineage are all well defined monophyletic groups. Their systematic compositions have been established by previous authors. Histeroidea and Hydrophiloidea are here treated as separate superfamilies because of their pronounced structural and biological differences (though the inclusion of Histeroidea in Hydrophiloidea is equally justified from a sheer phylogenetic point of view). Scarabaeoidea is the sistergroup of Hydrophiloidea and Histeroidea, and the three combined form the sistergroup of the Staphylinoidea.

3. The position of Hydraenidae within the Staphylinoidea (as sistergroup of the Ptiliidae), suggested by some previous authors, is confirmed. The similarities with the Hydrophiloidea – aquatic habits as well as correlated structural modifications – are interpreted as parallelisms rather than synapomorphies.

4. The Staphylinoidea includes two major groups, which are probably both monophyletic: 1) a Leiodid group (= "Catopiaria", "Leptinid association") containing the families Agyrtidae, Leiodidae, Hydraenidae and Ptiliidae, and 2) a Staphylinid group (= "Brachelytra") containing the families Scydmaenidae, Scaphidiidae, Empelidae, Apateticidae, Silphidae and Staphylinidae. The monophyly of the first group was questioned by Lawrence and Newton (1982), who considered Agyrtidae and Leiodidae as more closely related to the staphylinid group than to Hydraenidae and Ptiliidae, but such a relationship was not indicated by the present analysis.

5. Within the staphylinid group, the Scydmaenidae seem to represent the first offshoot, Scaphidiidae the next, then Empelidae and then Staphylinidae (s.lat.), while Silphidae (s.str.) and Apateticidae are probably sistergroups. The subordinate position of the Scydmaenidae, Scaphidiidae, Empelidae, Apateticidae and Silphidae within Staphylinidae, suggested by some authors (e.g., Lawrence and Newton, 1982) could not be confirmed (unless the concept of Staphylinidae is broadened to include all members of the staphylinid group).

6. The phylogeny within Staphylinidae is not well explained. Although several well defined and undoubtedly monophyletic groups, more-or-less equivalent of current subfamilies, can be recognized, their relationships are in most cases relatively weakly supported. The omaliine group (sensu Thayer, 1987), which is often considered a monophyletic taxon including some of the most primitive staphylinids (cf.

Lawrence and Newton, 1982) was not indicated as such by the present analysis. Rather, it was suggested that it consists of three, not closely related lineages: 1) Empelidae, 2) Micropeplinae, Dasycerinae, Protopselaphinae and Pselaphinae, and 3) Omaliinae, Glypholomatinae, Microsilphinae, Proteininae and Neophoninae. The first of these may be a relatively primitive member of the staphylinid group and is here excluded from the Staphylinidae, whereas the other two are more-or-less subordinate members of the Staphylinidae. These suggestions are far from conclusive and not in accordance with a more thorough analysis of these subfamilies, recently presented by Newton and Thayer (1995).

7. The Pselaphidae are a subordinate group of the Staphylinidae, closely related to Dasycerinae and Micropeplinae. This was suggested by previous authors (e.g., Lawrence and Newton, 1982; Thayer, 1987; Newton and Thayer, 1995) and is confirmed by the present analysis. Consequently, the taxon must be downgraded to a subfamily (Pselaphinae) of Staphylinidae, as recently proposed formally by Newton and Thayer (1995).

Systematic part

This section includes keys and diagnoses of the current families and subfamilies of Staphyliniformia (= Hydrophiloidea, Histeroidea and Staphylinoidea). The Scarabaeoidea are included in the key to superfamilies below but are not treated in further detail.

The structural and biological diversity of the Staphyliniformia (not less the entire hydrophiloid lineage) is enormous, and it is virtually impossible to give a general morphological characteristic of the entire group, which will clearly distinguish it from other beetles (cf. phylogenetic discussion above). I refer to existing general keys to the coleopteran families, e.g., Lawrence and Britton (1991) (adults of most families) and Lawrence (1991) (larvae).

The superfamilies are more easily recognized, and each of them shows a series of unique features that allows for a more adequate characterization. Also lower taxonomic categories (families, subfamilies) can usually be satisfactorily defined morphologically, though their phylogenetic status may be uncertain. The families, as recognized in here, have been discussed in the previous section on phylogeny, and are believed to represent monophyletic groups (possibly except Staphylinidae which is poorly supported, cf. phylogenetic discussion). The same is probably true for most subfamilies, though exceptions are found within some families, and current subfamilies are included in the keys given below. An evaluation of some of these subfamilies will require thorough phylogenetic analyses at more detailed taxonomic levels. Taxa of tribal or lower ranks have not been included in the present work, because many of them badly need reviewing and may be poorly (or not) justified phylogenetically, sometimes also morphologically.

The keys given below are based primarily on more easily observable morphological features. These may not always be the most important diagnostic characters, so the latter have been given under the respective families or subfamilies. The phylogenetically most important characters are not always useful when higher taxonomic categories are considered, because many of them are too often subject to reversals; such characters are discussed in the previous section about evaluation of taxa. For all families and subfamilies are also given notes about the number of described genera and species, geographical distribution, bionomy, and (when relevant) systematic status.

Apart from the inclusion of the Scarabaeoidea in the "staphyliniform" assemblage, the results of the present analysis agree in several regards with the ideas of Lawrence and Newton (1982) and Newton and Thayer (1992), and the classification proposed here is more concordant with their system than with others proposed so far. The major differences are 1) recognition of Hydrophiloidea and Histeroidea as separate superfamilies, 2) recognition of six families, rather than just one, within Hydrophiloidea, 3) recognition of Agyrtidae, Leiodidae, Hydraenidae and Ptiliidae as a monophyletic group, 4) family status of Scaphidiidae, Empelidae and Apateticidae, and 5) various modifications within Staphylinidae, e.g., the inclusion of Pselaphinae (earlier Pselaphidae) as a formal subfamily. With regard to the classification of staphylinid subfamilies I have hesitated from introducing new changes based merely on the results of the present analysis. Because possible alternatives to the current classification of staphylinid subfamilies – recently summarized by Lawrence and Newton (1995) – are not well supported, I have here adopted their classification, except that I consider Empelidae, Apateticidae and Scaphidiidae as distinct families.

The classification of subfamilies, families and higher taxa adopted here can be summarized as follows (a complete survey of family-group names within Staphyliniformia, including authorships and publication dates of names, as well as all synonyms, is given by Newton and Thayer (1992)).

HYDROPHILOID LINEAGE (= Staphyliniformia incl. Scarabaeoidea)

A. HYDROPHILOID SUB-LINEAGE
  I. SCARABAEOIDEA (not treated here)
  II. HYDROPHILOIDEA
    1. Helophoridae
    2. Epimetopidae
    3. Georissidae
    4. Hydrochidae
    5. Spercheidae
    6. Hydrophilidae
      Horelophinae
      Hydrophilinae
      Sphaeridiinae
  III. HISTEROIDEA
    1. Sphaeritidae
    2. Synteliidae
    3. Histeridae
      Niponiinae
      Abraeinae
      Trypeticinae
      Trypanaeinae
      Saprininae
      Dendrophilinae
      Onthophilinae
      Tribalinae
      Histerinae
      Hetaeriinae
      Chlamydopsinae

B. STAPHYLINOID SUB-LINEAGE
  IV. STAPHYLINOIDEA
    a. Leiodid group (= Catopiaria, Leptinid association)
      1. Agyrtidae
      2. Leiodidae
        Camiarinae
        Leiodinae (= Anisotominae)
        Coloninae
        Cholevinae (= Catopinae)
        Platypsyllinae (= Leptininae)
        Catopocerinae
      3. Hydraenidae
        Hydraeninae
        Prosthetopinae
        Ochthebiinae
      4. Ptiliidae
        Ptiliinae
        Nanosellinae
        Acrotrichinae
        Cephaloplectinae
          (= Limulodinae)
    b. Staphylinid group (= Brachelytra)
      5. Scydmaenidae
        Scydmaeninae
        Mastiginae
      6. Scaphidiidae
      7. Empelidae
      8. Staphylinidae
        Glypholomatinae
        Microsilphinae
        Omaliinae
        Proteininae
        Micropeplinae
        Neophoninae
        Dasycerinae
        Protopselaphinae
        Pselaphinae
        Phloeocharinae
        Olisthaerinae
        Tachyporinae
        Trichophyinae
        Habrocerinae
        Aleocharinae

Trigonurinae
Piestinae
Osoriinae
Oxytelinae
Oxyporinae
Megalopsidiinae
Steninae
Euaesthetinae
Solieriinae
Leptotyphlinae
Pseudopsinae
Paederinae
Staphylininae
9. Apateticidae (stat.n.)
10. Silphidae
Silphinae
Nicrophorinae

Key to superfamilies of the Hydrophiloid lineage

1. Adult: Pronotum without accessory posterior ridge below posterior margin, not forming a locking device with the elytral bases (fig. 101-113). Hindwings (when present) without distinct medial loop and without apical hinge distal to radial cell (fig. 148-150, 153) (but often with a hinge proximal to radial cell). Antennae (fig. 68-92) mostly filiform or gradually thickened apically, sometimes clubbed; if a sharply defined 3-segmented club is present, then abdominal segments 7-9 are usually everted (antennae strongly modified in some myrmecophilous forms). – Larva: Maxillary palpi (fig. 216-222) almost always 3-segmented, abdomen usually with well developed terga and sterna (seldom membranous), spiracles annular or annular-biforous . .Staphylinoidea

– Adult: Pronotum with accessory posterior ridge below posterior margin, forming a locking device with the elytral bases (fig. 93-98). Hindwings (when present) with distinct, but sometimes (Histeroidea) reduced medial loop and strong, reinforced apical hinge distal to radial cell (fig. 146, 147). Antennae (fig. 59-67) with densely pubescent club of 3 (sometimes fused) segments, if club is partly glabrous or formed by more than 3 segments, it is more-or-less lamellate. – Larva: Maxillary palpi (fig. 212-215, 223) normally 4-segmented, abdomen largely membranous, without single large sterna and terga, spiracles biforous or cribriform (sometimes annular on segment 8) 2

2. Adult: Antennal club asymmetrical, lamellate, formed by apical 3-7 segments (fig. 39). At least anterior tibiae almost always dentate on outer face, usually more-or-less flattened. Pygidium, when exposed, formed by the 8th tergum. – Larva: Grub-like and normally C-shaped, head hypognathous, maxilla with well defined galea and lacinia (fig. 223) (often fused to a single lobe), urogomphi always absent . . . . Scarabaeoidea

– Adult: Antennal club almost symmetrical, never lamellate, always formed by apical 3 segments (which are sometimes solidly fused, however) (fig. 60-67). Tibiae not dentate on outer face, or if dentate (some Histeroidea) the pygidium is formed by the 7th tergum. – Larva: More-or-less campodeiform, never C-shaped, head prognathous or even directed somewhat upwards, maxilla without galea and lacinia (fig. 212, 214, 215) (except in Spercheidae (fig. 213), where a lacinia-like appendage is present), urogomphi normally present, 1-4 segmented, but often small (fig. 244-248) 3

3. Adult: Antennae with no more than 6 segments preceding the club (fig. 60-63), the latter always distinctly 3-segmented (except a few Georyssidae). Mandibles not protruding, their major portion concealed (fig. 11-14). Clypeus never rostriform. Elytra rounded posteriorly, completely covering the abdomen, except sometimes for the extreme apex (= tergum 8) (fig. 259-280). Ventral face of body almost always with more-or-less extensive, normally hydrofuge pubescence. – Larva: Head with 6 (rarely 5), normally well separated stemmata on each side. Antennal foramen well separated from buccal cavity. Abdomen often with stigmatic atrium formed primarily by the 8th and 9th abdominal segments (fig. 246-247) . . . . Hydrophiloidea

– Adult: Antennae with 8 segments preceding the club (exceptionally only 7) (fig. 64-67), the club-segments often fused and appearing as a single large segment. Mandibles stronlgy protruding, their major portion exposed (fig. 15, 16) (except in few forms with rostriform clypeus). Elytra truncate posteriorly, at least pygidium (= tergum 7) exposed (fig. 281-298). Ventral face of body glabrous. – Larva: Head with no more than a single stemma on each side, often without stemmata. Antennal foramen almost contiguous with buccal cavity (also Sphaeritidae?). Abdomen never with stigmatic atrium . . . . .Histeroidea

Hydrophiloidea

The diagnostic features of adults of this superfamily include the presence of an accessory posterior ridge (locking device) below posterior margin (fig. 93-96), presence of medial loop, wedge cell (rarely open at distal end) and apical hinge (distal to radial cell) in the hindwing (fig. 146), and the presence of a well developed basal piece in the male genitalia (fig. 158-160). Head with distinct, well developed, sometimes grooved, coronal suture (fig. 11-14). Elytra completely covering abdomen, except (rarely) for extreme apex, not truncate apically. Abdominal segment 8 not completely invaginated within segment 7 (fig. 117). Females with styli situated apically on the gonocoxites (fig. 178). Larvae are characterized by 4-segmented maxillary palpi, absence of galea and lacinia (Spercheidae with lacinia-like, probably non-homologous appendage) (fig. 212-214), usually absent or rudimentary and subdivided tergites and sternites, biforous spiracles (apparently annular on segment 8 in more derived forms), and presence of a pair of projecting epistomal lobes at anterior margin of head (fig. 193) (except Spercheidae: fig. 194). Larvae of the families Hydrochidae, Spercheidae, Hydrophilidae are unique in having a respiratory chamber (stigmatic atrium) formed by dorsal portions of abdominal segments 8 and 9 (fig. 246, 247). Larvae without stigmatic atrium are very similar to histeroid larvae, but are separated from these by characters mentioned in the key above. A unique feature of the Hydrophiloidea is the construction of an egg case (fig. 191, 192), which is usually placed among debris, in soil, or attached to vegetation (certain Hydraenidae also protect their eggs by a layer of silk, but they never enclose the eggs in a case).

The formal rank of the hydrophiloid subgroups is not generally agreed upon. Traditionally, two families have been recognized (Hydrophilidae s.lat., Georissidae), but there is no phylogenetic justification for such a classification. Hence, some authors (e.g., Lawrence and Newton, 1982; Newton and Thayer, 1992) recognize only a single family (Hydrophilidae) equivalent of the Hydrophiloidea in the present sense. However, family rank seems to be more and more commonly used for some of the more archaic hydrophiloid groups, notably Georissidae, Spercheidae and Hydrochidae (e.g., Crowson, 1955, 1981). If these three groups are considered as valid families, the same rank must – for phylogenetic reasons – be given to Helophoridae and Epimetopidae (Hansen, 1991b). The reasons for excluding the Hydraenidae from the hydrophiloids are discussed in the previous phylogenetic section). Six families are recognized in the present work.

Key to families of Hydrophiloidea (adults and larvae)

1. ADULT: Head and pronotum at least partly covered with more-or-less dense, small granules, each usually with fine central setiferous puncture, granulation only exceptionally obscured (by fusion of granules). Middle coxae almost globular, not more than 1/3 x wider than long (as fig. 114, 135). Gula strongly narrowed anteriorly, gular sutures confluent or closely aggregated in their anterior half or more (almost as fig. 27). Frontoclypeal suture grooved. – LARVA: Mandibles with brush of hairs (penicillus) at mesal base (fig. 202). Ligula absent (fig. 224). Abdominal segment 8 without sclerotized tergal shield (fig. 448-450) 2

– ADULT: Head and pronotum not granulate (except hydrophilid genus Acidocerus), usually simply punctate, rarely with irregular rugulose-punctate sculpture. Middle coxae more transverse (fig. 134) (except Spercheidae and hydrophilid genus Amphiops). Gula usually only moderately narrowed anteriorly, gular sutures well separated throughout (as fig. 26) (except a few Hydrophilidae). Frontoclypeal suture fine or indistinct, very rarely grooved. – LARVA: Mandibles without penicillus. Ligula usually present, variable (fig. 225, 226). Abdominal segment 8 with differentiated sclerotized tergal shield (fig. 246, 247, 451-456) 5

2. ADULT: Eyes partly or almost completely divided by lateral canthus into dorsal and ventral portions (fig. 28). Basal ventrite very short and inconspicuous, number of apparent ventrites therefore only four. Pronotum projecting anteromedially, concealing head from above (fig. 28, 260). – LARVA: Stemmata closely aggregated. First antennal segment shorter than 2nd. Urogomphi long, 3-segmented. Posterior margin of abdominal tergum 8 with four projecting lobes . . . . . . Epimetopidae

– ADULT: Eyes complete, not at all divided by lateral canthus. Basal ventrite well developed, often longer than following, number of ventrites evidently five. Pronotum rarely with pronounced anteromedian projection (except Georissidae). – LARVA: Stemmata less closely aggregated. First antennal segment longer than 2nd. Urogomphi short, 1- or 2-segmented, or if long and 3-segmented, then posterior margin of abdominal tergum 8 without projections 3

3. ADULT: Pronotum with 7 longitudinal grooves (fig. 259) which are only exceptionally partly indistinct (in species with very extensive granulation). Ventral face of body with rather uniform, dull appearance due to very fine microsculpture and dense (but not velvety) pubescence, without large pitlike punctures, tubercles or granules. Abdominal ventrites not separated by grooves. – LARVAE: Urogomphi long, 3-segmented (fig. 244). Abdominal spiracles 1-8 well developed and functional. Legs well developed, with all normal 5 segments (fig. 241) . . . . Helophoridae

– ADULT: Pronotum without such grooves, but with variable pattern of impressions, sometimes with raised tubercles. Ventral face of body either dull with fine microsculpture and extremely dense, velvety pubescence and numerous large pitlike punctures (Hydrochidae), or somewhat shining and glabrous and covered with more-or-less sparse granules (Georissidae). Abdominal ventrites separated by transverse grooves. – LARVAE: Urogomphi short or rudimentary, 1- or 2-segmented (fig. 248, or as 246). Abdominal spiracles 1-7 rudimentary and non-functional, if not, then legs very short and stumpy, with reduced segmentation (fig. 243) 4

4. ADULT: Pronotum with pronounced anterior shelflike projection concealing head from above (fig. 261). Anterior coxae and trochanters fused to large plates, completely concealing the very reduced prosternum (fig. 131). Procoxal cavities not closed posteriorly (fig. 95). Posterior coxae very broadly separated. – LARVAE: Legs very short and stumpy, with reduced segmentation. Abdomen without stigmatic atrium, segment 8 and 9 not modified, the latter with very small, 1-segmented urogomphi (fig. 248) . . . . Georissidae

– ADULT: Pronotum without anterior projection, not concealing head from above (fig. 262). Anterior coxae and trochanters normal, not fused to large plates and not concealing the well developed prosternum. Procoxal cavities closed posteriorly (fig. 93). Posterior coxae very narrowly separated. – LARVAE: Legs very well developed, with usual 5 segments (as fig. 241). Abdomen with stigmatic atrium, i.e., pocket formed between tergal portions of segment 8 and 9, the latter with larger, 2-segmented urogomphi (almost as fig. 246) . . . . Hydrochidae

5. Antennae (fig. 60) 7-segmented, segments 2 and 4 (in addition to apical three) with dense hydrofuge pubescence and separated only by very small and inconspicuous (3rd) segment, entire antenna thus appearing 6-segmented with 5-segmented pubescent club. Lateral glabrous portions of hypomeron broad, defined from the remainder, pubescent portion by sharp ridge (fig. 94). Head strongly and very abruptly constricted immediately behind eyes (fig. 12), the latter defined from temporae by ridge. – LARVA: Maxilla with large lacinia-like lobe projecting from mesal face of stipes (fig. 213). Head with 5 stemmata on each side. Epistomal lobes absent (fig. 194) . . . . Spercheidae

– Antennae (fig. 61-63) 7-, 8- or 9-segmented, always with pubescence restricted to apical three segments and never appearing 6-segmented. Lateral glabrous portions of hypomeron of variable width, often well defined from the remainder, (normally) pubescent portion, but never by sharp ridge. Head almost always much weaker (and never very abruptly) narrowed behind eyes (fig. 13, 14), these normally not defined from temporae by ridge. – LARVA: Stipes without projecting lobe (fig. 214). Head with 6, sometimes very closely aggregated stemmata on each side. Epistomal lobes present (fig. 193), left and right lobe sometimes dissimilar . . . . Hydrophilidae

HELOPHORIDAE

(Adult: fig. 259; larva: fig. 448)

Length about 2-9 mm. Body elongate with outline more-or-less interrupted between pronotum and elytra. The granulate sculpture and unique pattern of 7 longitudinal grooves on pronotum easily distinguish the family from other hydrophiloids (and other staphyliniforms as well). Larvae are easily recognized from other hydrophiloid larvae by the long 3-segmented urogomphi in combination with a simple, not lobate tergum 8; they strongly resemble some histeroid larvae but can be recognized by, e.g., the presence of 6 pairs of stemmata (rather than 1 or 0).

This family contains only the genus *Helophorus*, with about 175 described species. Adults are usually aquatic, and feed mainly on decaying vegetable matter (a few species have terrestrial adults). The larvae are terrestrial, and normally predacious; only larvae of the entirely terrestrial species have been reported as vegetarian (pests of various crops). The distribution is predominantly holarctic, but a few species extend into central America and the afrotropical region.

EPIMETOPIDAE

(Adult: fig. 260)

Length about 1-4 mm. Body oval or ovoid with outline more-or-less interrupted between pronotum and elytra. The granulate sculpture of head and pronotum, in combination with the partly or almost completely divided eyes and short basal ventrite distinguish the family from other hydrophiloids (as well as other staphyliniforms). Larvae are easily recognized by the long 3-segmented urogomphi in combination with the quadrilobed tergum 8.

This family contains 2 genera and about 25 described species. They are reported as aquatic, but little is known about their biology; aquatic habits of the larvae have not been documented, and it is possible than they (like in Helophoridae) are terrestrial. Neither larval nor adult feeding seems to have been observed. Females carry the eggs in a bag below the abdomen (only Spercheidae and a few genera of Hydrophilidae have a similar behavior). The family is distributed in tropical America (*Epimetopus*) and Africa and southeast Asia (*Eumetopus*).

GEORISSIDAE

(Adult: fig. 261; larva:. fig. 449)

Length about 1-2 mm. Body broadly oval with outline more-or-less interrupted between pronotum and elytra. The granulate sculpture of head and pronotum, in combination with rudimentary prosternum without any trace of intercoxal process, fused anterior coxae and trochanters, and very large basal ventrite distinguish the family from other hydrophiloids (as well as other staphyliniforms). Larvae are easily recognized from other hydrophiloid larvae by the minute 1-segmented urogomphi in combination with complete absence of a stigmatic atrium.

This family contains only the genus *Georissus* with about 75 described species. They inhabit wet soil, often near the edges of water. Little has been published on the life history of georissids, and apparently nothing has been reported on their feeding habits. Probably, the larvae are (like other hydrophiloids) predacious, while the adults may feed primarily on algae. The adults cover themselves with layers of fine soil particles. The family is distributed worldwide.

HYDROCHIDAE

(Adult: fig. 262; larva: fig. 450)

Length about 1.5-6 mm. Body more-or-less elongate with outline distinctly interrupted between pronotum and elytra. The extremely dense, velvety pubescence on the ventral surface of body, in combination with the presence of numerous large pitlike punctures or foveae on ventral face of body, and a semitransparent lobe apically on 5th ventrite (fig. 118) distinguish the family from other hydrophiloids (as well as other staphyliniforms). Larvae have a distinct respiratory chamber (stigmatic atrium) formed by dorsal portions of abdominal segments 8 and 9, and are similar to spercheids and hydrophilids in this regard; they differ from the latter two, e.g., by the absence of differentiated tergal shield on abdominal segment 8.

This family contains only the genus *Hydrochus*, with more than 150 described species. Hydrochids are aquatic both as larva and as adult.

Larvae are probably predacious, but apparently feeding has not been observed. The adults feed mainly on decomposing vegetable matter. The family is distributed worldwide.

SPERCHEIDAE

(Adult: fig. 263; larva: fig. 451)

Length about 1.5-7 mm. Body oval or ovoid, strongly convex, with outline more-or-less interrupted between pronotum and elytra. The family is easily recognized by the unique antennal morphology, i.e., apparently 6-segmented with 5-segmented pubescent club (see key). Larvae with small respiratory chamber (stigmatic atrium) formed by dorsal portions of abdominal segments 8 and 9 and with sclerotized tergal shield on abdominal segment 8; a well developed lacinia-like appendage on the maxilla and the absence of epistomal lobes distinguish spercheid larvae from other hydrophiloid larvae.

This family contains only the genus *Spercheus* with about 15 described species. Spercheids are aquatic both as larva and as adult. Larvae are predators on various smaller invertebrates, and have also been recorded as filter feeders (feeding on particles from the surface of the water). Adults are probably mainly feeding on decomposing vegetable matter. Females carry the eggs in a bag below the abdomen (only Epimetopidae and a few genera of Hydrophilidae have a similar behavior). The family is widely distributed and occur in all major biogeographic regions, except the nearctic.

HYDROPHILIDAE

(Adults: fig. 264-280; larvae: fig. 452-456)

Length about 0.7-50 mm (usually 1.5-30 mm). Body usually more-or-less broadly oval with outline not interrupted between pronotum and elytra, rarely (Horelophinae) elongate. The vast majority of hydrophilids are characterized by more-or-less oblique (sometimes almost vertical) epipleura and rather evenly convex, relatively smooth dorsal surface, without grooves or impressions on pronotum (except Horelophinae and a few Sphaeridiinae:Megasternini). Moreover, they are recognized by the absence of granulate sculpture on head and pronotum (except *Acidocerus*), in combination with 7- to 9-segmented antennae having not more than three apical segments pubescent. Larvae with well developed respiratory chamber (stigmatic atrium) formed by dorsal portions of abdominal segments 8 and 9 (except *Berosus*) and with sclerotized tergal shield on abdominal segment 8 (similar to spercheid larvae, but differing as noted in key above).

This family contains more than 2200 described species, placed in almost 150 genera and 3 subfamilies. Most hydrophilids are aquatic or semiaquatic and occur in a variety of different habitats, e.g., among submerged vegetation along edges of streams or pools, partly flooded sand or gravel, spray zone or water film on rock faces; some species are halobionts, and a few may inhabit hot springs. Most species of the subfamily Sphaeridiinae are terrestrial, inhabiting various kinds of decomposing organic matter, particularly in damp places (adults of certain sphaeridiines are pollinators of flowers). The larvae are predators on insect larve, worms, snails and other invertebrates, while adults usually feed on decomposing vegetable matter (or are to some degree omnivorous). The distribution is worldwide.

It is not possible at present to give a key to larvae of hydrophilid subfamilies. Not only are larvae of Horelophinae unknown, but no diagnostic characters have yet been found that may separate the other two subfamilies. Although larvae of certain derived Sphaeridiinae (Megasternini, Sphaeridiini) may be easily recognized from those of Hydrophilinae, larvae of the more primitive Sphaeridiinae are extremely hydrophiline-like. Furthermore, the knowledge of sphaeridiine larvae is very fragmentary and larvae of several subgroups are still unknown.

Key to subfamilies of Hydrophilidae (adults)

1. Body elongate, outline interrupted between pronotum and elytra. Pronotum (fig. 264) widest anterior to middle with sides somewhat S-shaped, rounded anteriorly, sinuate posteriorly. Antennae long, distinctly longer than width of head. Epipleura not obliquely hanging down, body not lowered into elytral cavity ....Horelophinae
– Body less elongate, outline normally not distinctly interrupted between pronotum and elytra. Pronotum (e.g., fig. 266) almost always widest at, or very near, base and with rather evenly rounded sides, very rarely slightly sinuate posteriorly. Antennae almost always much shorter than width of head. Epipleura more-or-less strongly oblique, hanging down so body becomes lowered into elytral cavity, rarely (e.g., some Megasternini) almost horizontal 2
2. Labrum well sclerotized, not paler than clypeus, usually not concealed by clypeus (fig. 14). Labial palpi (fig. 57) of moderate size, segment 2 without subapical wreathlike tuft of setae, rarely with more than a few setae apically on inner and outer face, segment 3 usually asymmetrical with more straight inner face, not smaller than segment 2, almost always with long subapical seta on outer face, otherwise without or with much smaller setae (rarely, labial palpi bear numerous long setae and have apical segment 3 smaller than 2: some Chaetarthriini with basal ventrites covered by hyaline mass and fringe of long stiff setae). Antennal club more-or-less loosely segmented (fig. 63). Clypeus not strongly deflexed anterolaterally, never excised in front of eyes .... Hydrophilinae
– Labrum usually rather soft and pale, paler than clypeus, more-or-less retracted under clypeus (fig. 13), if not, then antennal club compact (as fig. 61) (except rygmodine genus Cylorygmus). Labial palpi (fig. 53, 56) often small, segment 2 with subapical wreathlike tuft of setae (except some Omicrini (fig. 29) with clypeus strongly deflexed anterolaterally and deeply excised in front of eyes), segment 3 often smaller than 2, often symmetrical, usually bearing numerous long setae, but never with single long subapical seta on outer face. Basal ventrites never covered by hyaline mass or fringe of long setae .... Sphaeridiinae

HORELOPHINAE (Adult: fig. 264). The subfamily includes only the monotypic New Zealand genus *Horelophus*. The species has been collected from rocks in the spray zone of water falls and may be hygropetric. Immature stages are unknown.

HYDROPHILINAE (Adults: fig. 265-271; larvae: fig. 252-254). The subfamily is currently divided into 6 tribes (sometimes partly treated as separate subfamilies) and contains about 50 genera and almost 1400 described species. Most forms are aquatic. The distribution is worldwide.

SPHAERIDIINAE (Adults: fig. 272-280; larvae: fig. 455, 456). The subfamily is currently divided into 9 tribes and contains more than 90 genera and almost 750 described species. The vast majority of the species are terrestrial, occuring in moist conditions in various kinds of decomposing organic matter. The distribution is worldwide.

Histeroidea

The diagnostic features of adults of this superfamily include the presence of an accessory posterior ridge (locking device) below posterior margin (fig. 97, 98), presence of medial loop and apical hinge (distal to radial cell) in the hindwing, absence of a wedge cell (fig. 147), and the presence of a well developed basal piece in the male genitalia (fig. 161-165). Head without coronal suture (fig. 15, 16). Elytra truncate posteriorly, one or two abdominal segments exposed. Abdominal segment 8 completely invaginated within segment 7. Females with styli situated ventrally-mesally on the gonocoxites (fig. 172, 176). Larvae are characterized by 4-segmented (sometimes 5-segmented) maxillary palpi, absence of galea and lacinia (fig. 215, 227), absent or rudimentary and subdivided tergites and sternites, biforous spiracles, and presence of a pair of projecting epistomal lobes at anterior margin of head (fig.

195, 196); they are very similar to certain primitive hydrophiloids but differ as noted in the key above.

Three families are currently recognized, and their systematic status is now broadly accepted.

Key to families of Histeroidea (adults and larvae)

1. ADULT: Elytra with 9 complete striae each. Antennae (fig. 64) not geniculate, with club clearly 3-segmented. Anterior tibiae spinose, but not dentate at external edge. Only one abdominal tergite exposed behind elytra. Body broadly oval (fig. 281), pronotum not narrowed posteriorly. – LARVA: Mandibles broadly and abruptly expanded at base (fig. 203). Head without epicranial stem and with frontal arms separated at base. Urogomphi 4-segmented, long (fig. 245) (only instar 1 larvae known) .... Sphaeritidae
– ADULT: Elytral with less than 9 complete striae, striae often incomplete, sometimes completely absent. Antennae (fig. 65-67) geniculate, club often without or with indistinct segmentation. Anterior tibiae mostly dentate (often also spinose) at external edge. At least two abdominal tergites exposed behind elytra, if not (Synteliidae), then body rather elongate with pronotum narrowed posteriorly (fig. 282). – LARVA: Mandibles not broadly and abruptly expanded at base (fig. 204). Head with epicranial stem and lyriform or V-shaped frontal arms (1. instar) or such lines absent (2. instar). Urogomphi usually 1- or 2-segmented or absent, rarely (Synteliidae) 4-segmented 2
2. ADULT: All coxae narrowly separated in midline, anterior coxae somewhat projecting. Only one abdominal segment exposed behind elytra. Tarsi with distinct bisetose empodium (fig. 143). Antennal club evidently 3-segmented. – LARVA: Urogomphi 4-segmented. Labium consisting of distinct prementum and mentum (as fig. 228), the latter separated from head capsule by suture .... Synteliidae
– ADULT: All coxae broadly separated in midline, anterior coxae not at all projecting. Usually two abdominal segments exposed behind elytra. Tarsi without distinct empodium (fig. 144). Antennal club usually without evident segmentation. – LARVA: Urogomphi 1- or 2-segmented, sometimes absent. Labium consisting of prementum only, mentum indistinguishable, fused to head capsule (fig. 227) .... Histeridae

SPHAERITIDAE

(Adult: fig. 281)

Length about 4-6 mm. Body broadly oval with outline not interrupted between pronotum and elytra, pronotum not narrowed behind. The presence of 9 complete striae on each elytron, non-geniculate antennae, as well as the broad shape in combination with almost contiguous coxae distinguish the family from other histeroids. Larvae are easily recognized from all other staphyliniforms (except Synteliidae) by the long 4-segmented urogomphi; they can be separated from synteliid larvae as noted in the key above.

This family contains only the genus *Sphaerites* with 3 known species. Sphaeritids occur in decomposing, probably usually fermenting organic matter, e.g., rotting vegetables, fruits, or fungi, fermenting tree sap, dung and carrion. Adults have been observed feeding on sap exuded from tree stumps, but are probably also predators on, e.g., maggots. Larvae are probably predacious, but feeding has never been recorded. The distribution is holarctic (Europe, China, western North America).

SYNTELIIDAE

(Adult: fig. 282; larva: fig. 457)

Length about 12-25 mm. Body elongate, rather parallelsided, but with outline somewhat interrupted between pronotum and elytra, pronotum narrowed behind. The rudimentary elytral striation (most striae incomplete) and the geniculate antennae, in combination with narrowly separated coxae distinguish the family from other histeroids. Larvae are easily recognized from all other staphyliniforms (except Sphaeritidae) by the long 4-segmented urogomphi posteriorly; they can be separated from sphaeritid larvae as noted in the key above.

This family contains only the genus *Syntelia* with 5 known species. Synteliids occur mainly under the bark of decaying logs, but one species inhabit rotting cacti. They are predacious both as larvae and adults, feeding on insect larvae, e.g., maggots. The family is known from central Mexico (2 species) and eastern Asia (3 species).

HISTERIDAE

(Adults: fig. 283-298; larvae: fig. 458, 459)

Length about 0.5-20 (usually 1.5-12 mm). Body broadly oval, normally very compact, more rarely elongate and cylindrical, outline not interrupted between pronotum and elytra, pronotum not narrowed behind. The broadly separated coxae and (usually) two, rather than one, exposed abdominal segments distinguish the family from other histeroids. Larvae are characterized by the complete fusion of mentum to the head capsule and by having 1- or 2-segmented urogomphi (or urogomphi absent).

This family contains about 3800 described species, placed in about 300 genera and 11 subfamilies. Histerids occur in a variety of habitats, e.g., in dung, carrion, under bark, in rotting fungi and in other kinds of decomposing or fermenting organic matter; some inhabit nests of ants, mammals or birds, others are characteristic of sand dunes. Both larvae and adults are predacious and feed particularly on immature stages of Diptera and other insects; adults of some forms (*Bacanius*) have been reported to feed on fungi. The distribution is worldwide.

The immature stages of histerids are poorly known and larvae of several subfamilies have not been described. The larval key given below is adopted from Newton (1991).

Key to subfamilies of Histeridae (adults)

1. Pronotum and elytra with longitudinal carinae (fig. 292) . . . . Onthophilinae
– Pronotum and elytra without longitudinal carinae . . 2
2. Head about as wide, and usually almost as long, as pronotum, with pronounced triangular anteromedian emargination and projecting anterior corners (fig. 283). Body narrowly elongate, cylindrical. Mandibles not concealed . . . . Niponiinae
– Head much narrower and shorter than pronotum, without anteromedian emargination and projecting anterior corners. Body less elongate, or (Trypanaeinae, Trypeticinae) clypeus more-or-less rostriform, concealing mandibles completely (or almost so) from above . . . 3
3. Mandibles concealed or almost concealed under long rostriform clypeus. Body narrowly elongate, cylindrical (fig. 287, 288) 4
– Mandibles not at all concealed, clypeus not rostriform. Body almost always much less elongate, normally broadly rounded 5
4. Prosternum with narrow and deep, sharply defined antennal groove on each side of very abruptly raised mesal portion (fig. 99). Clypeus not projecting beyond mandibular apices (fig. 287) . . . . Trypeticinae
– Prosternum without such antennal grooves, simple and rather flat on each side of less abruptly raised mesal portion (fig. 100). Clypeus projecting beyond mandibular apices (fig. 288) . . . . Trypanaeinae
5. Prosternum with large projecting anteromedian lobe defined by more-or-less distinct transverse line (fig. 97) 6
– Prosternum without such lobe or line (fig. 98) 9
6. Antennal club not tomentose, rather cylindrical, truncate at apex (fig. 297). Antennal grooves present on anterior margin of prothorax, partly enclosed in anterior corners, so antennae (when retracted) are concealed by prosternum in ventral view. Dorsal face of body with sparse erect setae or pruinose . . . . Hetaeriinae
– Antennal club tomentose, rounded or oval. Antennal grooves situated more ventrally on prothorax, or hardly defined; if partly enclosed in anterior corners (Tribalinae), then dorsal face of body glabrous 7
7. Labrum without setiferous punctures. Prothorax with antennal grooves situated ventrally near anterior corners, not in front of coxae (grooves indistinct in Hololeptini) . . . . Histerinae
– Labrum with setiferous punctures. Prothorax with antennal grooves situated more mesally, in front of coxae 8
8. Antennal grooves at least partly closed ventrally by prosternum, antennae (when retracted) not visible from

below. Anterior tibiae with rather fine spines on outer edge (fig. 132) . . . . Tribalinae
- Antennal grooves not closed ventrally by prosternum, antennae (when retracted) visible from below. Anterior tibiae with rather strong spines on outer edge (fig. 133) . . . . Dendrophilinae

9. Antennal club elongate (fig. 67). Prothorax with antennal grooves partly closed ventrally by prosternum, antennae (when retracted) partly concealed from below. Elytra often with conspicuous foveae and/or brushes of long setae near base . . . . Chlamydopsinae
- Antennal club short, broadly oval (fig. 66). Prothorax with antennal grooves not closed ventrally by prosternum, antennae (when retracted) not concealed from below. Elytra without foveae or brushes of long setae 10

10. Antennae inserted on frons, in groove near inner margins of eyes (fig. 15) . . . . Abraeinae
- Antennae inserted below lateral margin of frons, in front of eyes (fig. 16) . . . . Saprininae

Key to subfamilies of Histeridae (larvae)

1. Maxillary palpi 4-segmented, labial palpi 2-segmented 2
- Maxillary palpi 5-segmented, labial palpi 3-segmented 4

2. Dorsum of prementum with membranous setose area at base. Mesonotum of five sclerites above level of spiracles . . . . Saprininae
- Dorsum of prementum without membranous setose area (except *Dendrophilus*). Mesonotum of three sclerites above level of spiracles 3

3. Prementum without lateral lobes or dorsal teeth . . . . Histerinae
- Prementum on each side with small, acute, obtuse, spiniform or setose lobe . . . . . Dendrophilinae, Tribalinae

4. Antennal segments 1 and 2 of about equal size. Maxilla articulated to head by normal monocondylic joint . . . . Abraeinae
- Antennal segment 2 about half as long as, and much narrower than segment 1. Maxilla eversible, attached to head by long connecting membrane . . . . Trypanaeinae, Trypeticinae

NIPONIINAE (Adult: fig. 283). Includes only the genus *Niponius* with about 20 described species from east Asia and Australia. The group was earlier considered a distinct family.

ABRAEINAE (Adults: fig. 284-286). The subfamily is currently divided into 5 tribes and contains about 25 genera and almost 400 described species. It is widely distributed (all major biogeographic regions).

TRYPETICINAE (Adult: fig. 287). The subfamily contains 3 genera and about 50 described species. It is widely distributed in tropical Africa and east Asia, including Japan and New Guinea.

TRYPANAEINAE (Adult: fig. 288). The subfamily contains 3 genera and about 75 described species, confined to central and south America.

SAPRININAE (Adult: fig. 289; larva: fig. 458). The subfamily contains about 35 genera and almost 600 described species. The distribution is worldwide.

DENDROPHILINAE (Adults: fig. 290, 291). The subfamily is currently divided into 4 tribes and contains about 25 genera and more than 350 described species. It is widely distributed (all major biogeographic regions).

ONTHOPHILINAE (Adult: fig. 292). The subfamily contains 7 genera and almost 75 described species. It is widely distributed (all major biogeographic regions).

TRIBALINAE (Adult: fig. 293). The subfamily contains about 10 genera and almost 200 described species. It is widely distributed (all major biogeographic regions).

HISTERINAE (Adults: fig. 294-296; larva: 459). This is the largest of the histerid subfamilies. It is currently divided into 5 tribes and contains about 100 genera and almost 1600 described species. The distribution is worldwide.

HETAERIINAE (Adult: fig. 297). The subfamily contains about 100 genera and almost 400 described species. Most species are obligate myrmecophiles. It is widely distributed and are represented in all major biogeographical regions, except the Australian.

CHLAMYDOPSINAE (Adult: fig. 298). The subfamily contains about 10 genera and 50 described species. Most species are obligate myrmecophiles. The vast majority of the species are Australian, but a few occur in the neotropics and east Asia.

Staphylinoidea

The diagnostic features of adults of this superfamily include the absence of an accessory posterior ridge (locking device) below posterior margin (fig. 101-113), absence of medial loop, wedge cell and apical hinge (distal to radial cell) in the hindwing (fig. 148-151, 153), and the absence of a basal piece in the male genitalia (fig. 164-171) (rarely with rudimentary strap-like basal piece, or Leiodidae:Coloninae with apparently well developed basal piece). Head without or (rarely) with short, rudimentary coronal suture (fig. 17-25). Elytra completely covering abdomen, or more-or-less abbreviated and truncate posteriorly, so a smaller or larger portion of the abdomen is exposed. Abdominal segment 8 not completely invaginated within segment 7. Females with styli (if present) situated more-or-less apically on the gonocoxites (fig. 180, 182). Larvae are characterized by 3-segmented (very rarely 4-segmented) maxillary palpi with distinct (often fused) galea and lacinia (fig. 216-222), usually well developed terga and sterna, annular or annular-biforous spiracles, and absence of epistomal lobes (fig. 197-201).

There is not general agreement about the family division within Staphylinoidea. Some of the families recognized here are by other authors divided into smaller families (cf. Ptiliidae, Leiodidae), or have been considered subordinate members of other families (cf. Scaphidiidae, Empelidae and Apateticidae). Other groups have often been considered as distinct families but are here included in the Staphylinidae (Dasycerinae, Micropeplinae, Pselaphinae). In the present work ten families are recognized.

Key to families of Staphylinoidea (adults and larvae)

1. ADULT: Ventral face of body with very dense, more-or-less extensive, hydrofuge pubescence (plastron). Antennae about 2/3 x width of head, usually with 5-segmented pubescent club preceded by a more-or-less cupuliform segment (fig. 76, 77), but sometimes with fewer and more weakly pubescent club-segments and/or indistinct cupule (fig. 78). Elytra fully developed, entirely covering abdomen, except sometimes for extreme apex. – LARVA: Abdominal segment 10 with a pair of hooks (anal hooks) on eversible anal lobes (fig. 249, 250). Head with 5 stemmata on each side . . . . Hydraenidae

– ADULT: Ventral face of body glabrous or pubescent, but never with plastron of dense, hydrofuge pubescence. Antennae almost always much longer than width of head, never with 5-segmented pubescent club preceded by a cupule; if antennae shorter, then elytra abbreviated, exposing a large portion of abdomen. – LARVA: Abdominal segment 10 without anal hooks, or (Ptiliidae) head without stemmata or (rarely) with a single stemma on each side 2

2. ADULT: Posterior coxae excavate posteriorly, forming more-or-less developed coxal plates for at least half of coxal length (fig. 136). Tarsi (fig. 142) very thin, 3-segmented, but with two basal segments very small and very long and slender apical segment forming almost entire tarsus. Hindwings (when present) narrow or very narrow, fringed with long or very long setae, feather-like (fig. 151). Spermatheca sclerotized, with well developed sperm pump (fig. 186, 187). Very small species, length not exceeding 2 mm. – LARVA: Mandibles normally with distinct mola and prostheca (as fig. 206). Abdominal segment 9 with a pair of 1-segmented articulated urogomphi (except Nanosellinae), segment 10 with anal hooks (as fig. 249) (except Cephaloplectinae). Stemmata usually absent, rarely a single pair present . . . . Ptiliidae

– ADULT: Posterior coxae not excavate, not forming coxal plates, or such are only indicated at extreme mesal edges of coxae (except Empelidae and the staphylinid subfamilies Habrocerinae and Glypholomatinae). Tarsi 5-segmented or with fewer segments, but never as in Ptiliidae. Hindwings (when present) not very narrow, fringed with short or very short setae, never feather-like. Spermatheca sclerotized or not, without distinct sperm pump. Often larger forms, more than 2 mm long. – LARVA: Mandibles without distinct mola, or if mola present then prostheca absent or urogomphi 2-segmented or head with at least 2 pairs of stemmata . . . 3

3. ADULT: Abdominal segment 8 usually retracted, so only 5 ventrites (sternum 3-7) are distinct (sometimes with

small retractable 6th ventrite); if a 6th ventrite is evident, antennae with segment 8 smaller than 7 and 9 and (usually) more-or-less developed 5-segmented club (fig. 71), or antennae apparently 3-segmented (fig. 75), or elytra fully developed, not at all truncate posteriorly, with 9 punctate striate, or head with sharp transverse occipital carina. Mesocoxal cavities delimited posteriorly by a ridge. Basal ventrite not enlarged, much shorter than 2-4 combined. Elytra almost always completely covering abdomen except sometimes for extreme apex (abbreviated elytra occur only in the eyeless, strongly depressed leiodid subfamily Platypsyllinae). Hindwings (when present) without hinge at anterior margin (fig. 148, 149). Aedeagus without large basal bulb, median foramen basal (fig. 164, 165). – LARVA: Labrum free, consisting of single sclerite. Mandibles with mola (fig. 205) or a membranous setose lobe at mesal base (very rarely simple) 4

– ADULT: Abdominal segment 8 everted, so at least 6 ventrites (sternum 3-7) are distinct. Antennal segment 8 not distinctly smaller than 7 and 9; exceptions occur in Scydmaenidae-Scydmaeninae (with mesocoxal cavities not delimited posteriorly), Scaphidiidae (with greatly enlarged basal ventrite), and Pselaphinae (with strongly abbreviated elytra). Antennae not apparently 3-segmented. Forms with fully developed, not truncate elytra never with 9 punctate elytral striate (except a few Omaliinae). Head without sharp occipital carina. Hindwings (when present) with hinge (radial hinge) at anterior margin proximal to radial cell (fig. 153). Aedeagus with more-or-less developed basal bulb (fig. 169, 171), median foramen ventral, small (aedeagus often more-or-less rotated within abdomen). – LARVA: Labrum fused to head capsule, or if free, usually subdivided into more sclerites. Mandibles without mola (fig. 207-209), mesal surface simple or slightly expanded, rarely with fixed, rigid or partly sclerotized process 5

4. ADULT: Antennae 11-segmented, gradually thickened distally, without sharply defined club, segment 8 not smaller than 7 and 9 (fig. 68); penultimate 3-4 segments with open, sensilla-filled periarticular grooves at their distal surfaces (fig. 72) (rarely without such grooves). Procoxal cavities not closed internally (fig. 105). Hindwings with anal lobe (fig. 148). – LARVA: Head with 6 stemmata on each side . . . . Agyrtidae

– ADULT: Antennae normally 11-segmented with more-or-less defined club of 3, 4 or 5 segments, segment 8 almost always smaller than 7 and 9 (fig. 69-71) (except Coloninae with 4-segmented club: fig. 74, and *Platypsyllus* with highly modified, apparently 3-segmented antennae: fig. 75); penultimate antennal segments with enclosed, sensilla-filled vesicles opening to distal surfaces through narrow slits (fig. 73). Procoxal cavities closed internally (fig. 106-108). Hindwings without anal lobe (fig. 149). – LARVA: Head with 5 or fewer stemmata on each side . . . . Leiodidae

5. ADULT: Elytra fully developed, rarely truncate apically, never with longitudinal carinae, abdomen completely covered or (rarely) only its extreme apex exposed. Body without power of rolling up. Femora more-or-less clavate, with long narrow basal portion and swollen distal portion (fig. 135, 139). Mesocoxal cavities not demarcated posteriorly. Basal ventrite not enlarged, much shorter than 2-4 combined. Sternum 8 without gland openings. – LARVA: Labrum fused to head capsule. Urogomphi absent or (rarely) a pair of fixed, undivided urogomphi present. Antennal sensorium short and broad, domelike or conical (fig. 237) . . Scydmaenidae

– ADULT: Elytra truncate and often strongly abbreviated, so a smaller or greater portion of abdomen is exposed, if not, then basal ventrite at least as long as 2-4 combined (Scaphidiidae), elytra with 3 longitudinal carinae each (Silphidae: fig. 156), body with power of rolling up (Empelidae), or abdominal sternum 8 with paired gland openings at anterior margin (a few Staphylinidae: fig. 120, 121). Femora not clavate (fig. 137, 138). Mesocoxal cavities demarcated posteriorly by distinct ridge (fig. 114) (except a few Staphylinidae with strongly abbreviated elytra). – LARVA: If labrum fused to head capsule, then urogomphi present and articulated basally or (Pselaphinae) antennal sensorium elongate and palpiform, setiform or bifid 6

6. ADULT: Basal ventrite very large, at least as long as 2-4 combined. Body of characteristic wedge-like form (fig. 244-246), elytra truncate apically but long and covering major portion of abdomen. – LARVA: Labrum free, anterior margin with crenulate emargination (fig. 211) . . . . Scaphidiidae

– ADULT: Basal ventrite not enlarged, much shorter than 2-4 combined. Body form variable, but very rarely wedge-like, elytra often strongly abbreviated and covering only a small portion of abdomen. – LARVA: Labrum variable, often fused to head capsule, anterior margin without crenulate emargination 7

7. ADULT: Elytra fully developed, without striae, ridges or tubercles, only narrowly truncate at apex, concealing most of abdomen, so that not more than three abdominal segments are exposed. Head without ocelli. Posterior coxae excavate throughout their lengths for reception of posterior femora (fig. 137). Antennae with 3-segmented club (fig. 83). Body (fig. 347) with power of rolling up, habitus reminiscent of the eucinetoid family Clambidae. – (LARVA: unknown) . . . . Empelidae

– ADULT: Elytra more-or-less abbreviated and broadly truncate at apex, concealing smaller portion of abdomen, so that five or six abdominal segments are exposed; if elytra cover greater portion of abdomen, then they have distinct striae, ridges or tubercles, or head with a pair of ocelli. Posterior coxae not excavate throughout their lengths (except Staphylinidae-Habrocerinae with very thin, filiform antennae and Staphylinidae-Glypholomatinae with striate elytra). Body almost always without power of rolling up, habitus never clambid-like 8

8\. ADULT: Elytra with 9 striae or regular series of punctures, at least about 2 x as long as pronotum, truncate apically, not more than three abdominal segments exposed. Head without ocelli. Tarsi 5-segmented. Body relatively broad, pronotum almost twice as wide as long. – (LARVA: Insufficiently described, see diagnosis below) . . . . Apateticidae

– ADULT: Elytra without striae or serial punctures, or if such are present, then elytra strongly abbreviated (5-6 abdominal segments exposed) or head with a pair of ocelli and/or tarsi 3-segmented. Body often very elongate, pronotum rarely twice as wide as long 9

9\. ADULT: Elytra at least 2 x as long as pronotum, concealing at least first three (usually more) abdominal segments; each elytron normally with three longitudinal, rarely interrupted ridges and a more-or-less developed bulge posteriorly between outer two ridges (fig. 156). Large forms, length about 7 to 45 mm. – LARVAE: Maxillae with large and broad mala divided in apical fourth, its outer lobe (galea) with dense brush of setae (fig. 218). Thoracic and abdominal terga with lateral lobes extending beyond sternal edges (fig. 474, 475), or abdominal terga each with four spinose projections along posterior margin (fig. 476). Urogomphi articulated, 1- or 2-segmented . . . . Silphidae

– ADULT: Elytra usually strongly abbreviated, much less than 2 x as long as pronotum, and concealing only first two abdominal segments; if longer, then without ridges and posterior bulge and body size much less than 7 mm. – LARVAE: Mala variable, but not large and broad with outer lobe bearing dense brush. Thoracic and abdominal terga without such lobes or projections (except Micropeplinae with fixed, undivided urogomphi) . . . . Staphylinidae

AGYRTIDAE

(Adults: fig. 299-301; larva: fig. 460)

Length about 4-14 mm. Body oval to broadly oval with outline not or hardly interrupted between pronotum and elytra, or somewhat carabid-like, with strongly interrupted body outline. Elytra covering abdomen completely. Agyrtids are distinguished from other staphylinoids by the combination of five distinct ventrites and internally open procoxal cavities (the aberrant *Pteroloma*, with six distinct ventrites, can be recognized from members of other staphylinoid families by its carabid-like habitus with long filiform antennae and somewhat cordiform pronotum, in combination with presence of 9 elytral striae). Other characteristics of Agyrtidae include the presence of open, periarticular, sensilla-filled grooves on distal end of penultimate 3-4 antennal segments (except *Pteroloma*), and absence of radial hinge but presence of anal lobe in the hindwing; a pair of ocelli sometimes present. The male genitalia are without large basal bulb, usually more-or-less asymmetrical, internal sac not everted; parameres fused to single ventral plate, or absent. Larvae have a free labrum, mandibular mola, and 6 stemmata on each side of the head. Urogomphi 2-segmented, long.

This family contains about a dozen genera and approximately 60 described species (three tribes, but no formal subfamilies are currently recognized, cf. Newton and Thayer, 1992). Agyrtids occur in different kinds of decaying animal or vegetable matter, e.g., small carcasses, feces, leaf litter, etc.; some forms (*Lyrosoma*) are confined to marine beaches. They are probably saprophages and scavengers, but little has been published about their biology; some species may be predators as adults (Newton, 1991). The distribution is predominantly holarctic but includes also New Zealand.

LEIODIDAE

(Adults: fig. 302-320; larvae: fig. 461-466)

Length about 1-7 mm. Body oval to broadly oval with outline not or more-or-less interrupted between pronotum and elytra, sometimes with pronotum markedly narrower than elytra. Elytra covering abdomen completely, sometimes except for extreme apex, very rarely (some Platypsyllinae) abbreviated, so as many as 5 abdominal segments are exposed. Leiodids are recognized from other staphylinoids by the combination of 5 (rarely 4) distinct ventrites and internally closed procoxal cavities, or (if with 6 ventrites) the configuration of the antennae. The antennal characteristics include the presence of enclosed, sensilla-filled vesicles opening through narrow slits on distal end of penultimate 3-4 antennal segments (apparently vestigial in *Platypsyllus* with highly modified, apparently 3-segmented antennae), and size reduction of antennal segment 8, which is normally smaller than 7 (not in Coloninae). Hindwings without radial hinge and anal lobe. Ocelli absent (except in the camiarine genus *Ragytodes*). The male genitalia are without large basal bulb, usually symmetrical, internal sac not everted; parameres present, not fused. Larvae have a free labrum, mandibles with mola or a membranous setose lobe at mesal base (very rarely simple), and 5 or fewer stemmata on each side of the head. Urogomphi 2- or 1-segmented, sometimes fixed.

This family is here treated in a relatively broad sense, including groups that are sometimes given rank of distinct families (see below under subfamilies). As presently defined, the family contains about 2500 species, which are placed in more than 300 genera and 6 subfamilies. Leiodids occur in leaf litter, carrion, fungi, rotting wood, and other kinds of decomposing organic matter; some live in nests of ants, termites, mammals, and birds, and several are obligate cave dwellers. Most species are saprophages and scavengers, but mycophagy occur in a number of Leiodinae, Coloninae and Catopocerinae; some are associated with hypogeous fungi, others with slime molds. The distribution is worldwide.

The present knowledge of the immature stages of Leiodidae is poor and larvae of the subfamilies Coloninae and Catopocerinae unknown. It has not been possible to provide a reasonably reliable key to subfamilies based on larval characters at present.

Key to subfamilies of Leiodidae (adults)

1. Anterior coxae small, rounded. Eyes absent. Vertex with sharp transverse occipital carina above anterior pronotal margin (fig. 30). Antennae 11-segmented, filiform with segment 8 hardly smaller than 7 and 9, or strongly modified, apparently 3-segmented, i.e., segments distal to 2nd forming a very compact elongate club (fig. 75). Body strongly depressed. Species more-or-less ectoparasitic on mammals .... Platypsyllinae

– Anterior coxae large, transverse or conically projecting. Eyes usually present (except Catopocerinae, the leiodine Scotocryptini and the cholevine Leptodirini). Vertex without sharp occipital carina (except most Cholevinae). Antennae usually 11-segmented (rarely 10-segmented) with 5-segmented club, segment 8 usually markedly smaller than 7 and 9 (except Coloninae with 4-segmented club). Body normally more convex. Species not ectoparasitic on mammals 2

2. Eyes absent. Maxillary palpi with apical segment markedly longer than penultimate (fig. 50). Dorsal face of body glabrous. Metepisterna exposed. Tarsi 5-segmented .... Catopocerinae

Eyes present, if not, then maxillary palpi with apical segment smaller than penultimate (fig. 51), and either (most Leptodirini) dorsal face of body usually pubescent and anterior tarsi 4-segmented (at least in /), or (Scotocryptini) metepisterna concealed and tarsi 3-segmented 3

3. Dorsal face of body almost always shining and usually glabrous. Metepisterna normally completely concealed under elytra or (e.g., *Anisotoma*) very narrowly visible. Postcoxal process of hypomeron long and pointed, nearly or evidently reaching apex of prosternal intercoxal process (fig. 106). Metasternum at a distinctly "lower" (more ventral) horizontal level than abdomen, posterior coxae with vertical posterior face. Tarsi with 3-5 segments, often heteromerous and if so, then anterior tarsus with one more segment than posterior tarsus ... . Leiodinae

– Dorsal face of body densely pubescent, normally rather dull (except in the camiarine *Neopelatops* and a few Leptodirini). Metepisterna almost always exposed. Postcoxal process of hypomeron usually short and obtuse, not nearly reaching apex of prosternal intercoxal process (fig. 107). Metasternum usually in same horizontal level as abdomen, posterior coxae not with vertical posterior face. Tarsi 5-segmented, anterior tarsi sometimes 4-segmented 4

4. Head with sharp transverse occipital carina (as fig. 30), if not (some Leptodirini), then eyes absent (or metepisterna concealed) and anterior tarsi 4-segmented at least in ♀. Apical segment of maxillary palpi almost always smaller than pentultimate, more-or-less conical (fig. 51). Antennae weakly clubbed or with loose club, segment 8 almost always smaller than 7 and 9. Trochantin of anterior legs almost always concealed . . Cholevinae

– Head without occipital carina. Eyes present, well developed. Metepisterna exposed. Anterior tarsi 5-segmented in both sexes. Apical segment of maxillary palpi not smaller than penultimate (fig. 49), or antennal club compact and segment 8 large, not smaller than 7 and 9 (fig. 74). Trochantin of anterior legs exposed 5

5. Antennae with well developed, 4-segmented, compact club, segment 8 and 9 of same size, larger than 7 (fig. 74). Apical segment of maxillary palpi smaller than penultimate, more-or-less conical (as fig. 51). Abdomen with 4 or 5 ventrites . . . . Coloninae

– Antennae hardly or weakly clubbed, segment 8 at least slightly smaller than 9 and 7 (as fig. 71). Apical segment of maxillary palpi larger than penultimate (fig. 49), sometimes more-or-less securiform. Abdomen with 5 or 6 ventrites . . . . Camiarinae

CAMIARINAE (Adults: fig. 302, 303; larva: fig. 461). The subfamily is currently divided into 3 tribes, containing more than 30 genera. The group has sometimes been treated as a distinct family. It is confined to the southern hemisphere (Australia, New Zealand, South America, South Africa).

LEIODINAE (= Anisotominae) (Adults: fig. 304-310; larvae: fig. 462, 463). A large subfamily, which is currently divided into 6 tribes and contains about 60 genera. The distribution is worldwide.

COLONINAE (Adult: fig. 311). The subfamily includes only the isolated genus *Colon* with more than 100 known species. The genus has sometimes been placed in a separate family. The distribution includes primarily temperate regions of the northern and southern hemispheres, and only few species are known from the tropics.

CHOLEVINAE (= Catopinae) (Adults: fig. 312-316; larva: fig. 464). A large subfamily, which has often been treated as a separate family, or (without phylogenetic justification) referred to Silphidae rather than to Leiodidae: The group is currently divided into 6 tribes (and several subtribes) containing more than 200 genera. The majority (about two thirds) of the genera are placed in the tribe Leptodirini (= Bathyscini), an almost exclusively west palearctic group of predominantly eyeless and wingless, often highly modified cavernicoles, which were earlier excluded from the Cholevinae and considered a separate subfamily (or family). Cholevines are distributed worldwide.

PLATYPSYLLINAE (= Leptininae) (Adults: fig. 317, 318; larva: fig. 465). The subfamily contains only 4 genera and 7 known species, all confined to nests of smaller mammals or (*Leptinus*) occasionally social Hymenoptera. They have often been placed in a separate family, sometimes even in two families (one including the highly modified *Platypsyllus*, the other including the remaining 3 genera), but their relationship with other leiodids are probably rather subordinate. The group is entirely holarctic.

CATOPOCERINAE (Adults: fig. 319, 320; larva: fig. 466). A small subfamily of uncertain phylogenetic status, currently divided into 2 tribes, each containing one very isolated genus. The group is only known from North America.

HYDRAENIDAE

(Adults: fig. 321-327; larvae: fig. 467, 468)

Length about 0.5-3 mm. Body elongate to oval, usually with outline interrupted between pronotum and elytra, the latter covering abdomen completely or leaving only extreme apex exposed, not or only slightly and narrowly truncate at apex. Hydraenids are distinguished from other staphylinoids by the short antennae, about 2/3 as long as width of head, and the dense hydrofuge pubescence covering much of the ventral surface of body. Other characteristics include the absence of radial hinge in the hindwing, 7 (rarely 6) distinct ventrites, and often presence of a pair of ocelli. The male genitalia are without large basal bulb (some *Limnebius* with entire aedeagus somewhat bulbous), more-or-less asymmetrical, with internal sac permanently everted (fig. 166-168); parameres mostly present and often asymmetrical, sometimes absent. Larvae have a free labrum, 5 stemmata on each side of head, and a pair of anal hooks on eversible lobes of abdominal segment 10. Urogomphi present, 2-segmented.

This family contains over 1100 described species, placed in about 30 genera and 3 subfamilies. Adult hydraenids occur in a variety of aquatic and semiaquatic habitats, e.g., among submerged vegetation along edges of streams or pools, partly flooded sand or gravel, spray zone or water film on rock faces; some species are halobionts and a few are terrestrial. The larvae are terrestrial, but are usually found at damp margins of aquatic habitats. Hydraenids are usually said to be phytophagous and to feed on algae (predatory habits have been mentioned by some authors, but this may be an error). The distribution is worldwide.

The family was earlier considered closely related to the families of Hydrophiloidea (and is still by some authors) because of the aquatic habits and related structural modifications. However, as explained in the previous section on phylogeny (and as indicated by the diagnostic features mentioned here), hydraenids differ drastically from hydrophiloids in several regards. The similarities of the two groups are almost certainly convergences or, to some degree, retained archaic features.

Key to subfamilies of Hydraenidae (adults and larvae)

1. ADULT: Maxillary palpi (fig. 48) short, about 1/2 to 2/3 x as long as width of head, apical segment minute, much shorter and narrower than penultimate. Anterior, posterior and (usually) lateral margins of pronotum at least narrowly bordered by semitransparent hyaline membrane (fig. 101). – LARVA: Urogomphi almost contiguous basally (fig. 249). Galea (fig. 218) without fringed margins .... Ochthebiinae

– ADULT: Maxillary palpi (fig. 46, 47) usually rather long, apical segment not minute, at least as long as penultimate, if not, then palpi at least as long as width of head. Pronotum without hyaline margins. – LARVA: Urogomphi well separated basally (fig. 250). Galea (fig. 217) with fringed margins (larvae of Prosthetopinae unknown) 2

2. Prothorax with well developed, usually deep antennal grooves ventrally on each side of prosternum (sometimes covered ventrally by the expanded hypomera); if such grooves are indistinct, then ocelli are absent or frons concave between strongly protruding and elevated eyes. – LARVA: as described in previous couplet .... Hydraeninae

– Prothorax without well developed antennal grooves, at most with shallow concavities at anterior margin. Head always with ocelli, frons not concave, eyes not strongly elevated and protruding. – LARVA: unknown .... Prosthetopinae

HYDRAENINAE (Adults: fig. 321-324; larva: fig. 467). The subfamily is currently divided into 2 tribes and contains 15 genera and more than 650 described species. The group includes several primitive hydraenid genera, which probably have a more basal phylogenetic position within the family than is indicated by the current classification. Probably, this subfamily is paraphyletic. Hydraeninae is distributed worldwide.

PROSTHETOPINAE (Adult: fig. 325). The subfamily was recently proposed for a group of genera some of which were earlier included in Hydraeninae (Perkins and Balfour-Browne, 1994). It is divided into 5 tribes and contains 7 genera and 40 described species. The subfamily is restricted to the afrotropical region, particularly South Africa.

OCHTHEBIINAE (Adults: fig. 326, 327; larva: fig. 468). The subfamily contains 7 genera and more than 400 described species, and is distributed worldwide.

PTILIIDAE

(Adults: fig. 328-336; larvae: fig. 469, 470)

Length about 0.35-2 mm. Body elongate to oval, sometimes relatively short and wide, outline interrupted between pronotum and elytra, or not. Elytra covering abdomen completely or somewhat abbreviated and truncate posteriorly, so last about 3-4 abdominal segments are exposed. Ptiliids are distinguished from other staphylinoids by the 3-segmented (apparently 1-segmented), very thin tarsi, the narrow or very narrow, extensively fringed, usually feather-like hindwings, and more-or-less well developed coxal plates of the hind coxae (coxal plates are also found in Empelidae and the staphylinid subfamily Habrocerinae). Other characteristics include the absence of radial hinge in the hindwing, 6 or 7 distinct ventrites, and complete absence of ocelli. The male genitalia are without large basal bulb, symmetrical, internal sac not everted, parameres absent or (very rarely) present. Larvae have a free labrum and resemble hydraenid larvae in having a pair of anal hooks on eversible lobes of abdominal segment 10 (except in Cephaloplectinae), but differ in having no or (rarely) only a single pair of stemmata, and 1-segmented urogomphi (absent in Nanosellinae).

This family contains about 65 genera and 600 described species. The current division into 4 subfamilies is followed here, but must be regarded as highly tentative (see also below under the subfamilies). Ptiliids occur in a variety of habitats, e.g., leaf litter, rotten wood, fungi, dung, carrion, mosses, etc.; some forms live in nests of ants. Apparently, most species feed primarily on spores or hyphae of fungi. The distribution is worldwide.

Key to subfamilies of Ptiliidae (adults and larvae)

1. ADULT: Prosternal intercoxal process broad and long, projecting backwards over mesosternum (fig. 104). Eyes absent. Antennae short, retractable into grooves on ventral side of head. – LARVAE: Abdomen without anal hooks . . . . Cephaloplectinae
– ADULT: Prosternal intercoxal process narrow, not projecting backwards over mesosternum (fig. 103). Eyes usually present. Antennae usually not retractable into grooves on ventral side of head. – LARVAE: Abdomen with pair of anal hooks on eversible anal lobes 2
2. ADULT: Elytra usually more-or-less truncate apically (fig. 334), abdomen relatively long, at least about three segments exposed behind elytra. Pygidium composed of last two tergites completely fused. Basal ventrite without femoral lines. Body usually rather flat. – LARVA: Urogomphi present, 1-segmented (larvae identical with those of Ptiliinae with regard to urogomphi) . . . . . Acrotrichinae
– ADULT: Elytra usually rather long and attenuate to rounded apically (fig. 329, 330), abdomen relatively short, at most its extreme apex exposed behind elytra (except most *Ptinella*-spp.: fig. 332). Last two tergites not or (*Ptiliodes*) only partly fused. Basal ventrites often with femoral lines. Body usually convex. – LARVA: Urogomphi similar or absent 3
3. ADULT: Metasternum with pair of longitudinal ridges (metasternal lines), rising from outer edges of mesocoxal cavities, directed backwards and curved slightly towards midline; lines rarely (e.g., *Kuschelidium*) reduced to anterior vestiges. – LARVA: Urogomphi absent . . . . Nanosellinae
– ADULT: Metasternum without such lines; rarely (*Oligella*) with similar, weak lines. – LARVA: Urogomphi present, 1-segmented . . . . Ptiliinae

PTILIINAE (Adults: fig. 328-333). This subfamily consists of approximately 40 genera and almost 300 described species. The group is undoubtedly paraphyletic and contains several groups of genera that are apparently not closely related. It includes the most archaic ptiliids (*Nossidium* and a few undescribed allies), which are probably the sistergroup of all other ptiliids and might warrant a separate subfamily. The distribution is worldwide.

NANOSELLINAE (Adult: fig. 336). The group contains about a dozen genera and about 25 described species. Nanosellines are not well separated from the Ptiliinae, and they should probably be included as a subordinate group within the latter subfamily (possibly near *Oligella*). The group is widely distributed (nearctic, neotropical, palearctic, and australian regions).

ACROTRICHINAE (Adult: fig. 334; larva: fig. 469). The subfamily contains about 7 genera and about 150 described species. It is widely distributed and occur in all major biogeographic regions.

CEPHALOPLECTINAE (= Limulodinae) (Adult: fig. 335; larva: fig. 470). The subfamily contains about 5 genera and 30 described species, all of which are obligate myrmecophiles. They may have a superficial resemblance to small staphylinids (truncate elytra and long, exposed abdomen), and some of them have earlier been placed in that family. Cephaloplectines are confined to the neotropical, nearctic and australian regions. The group has often been given status as separate family (as "Limulodidae").

SCYDMAENIDAE

(Adults: fig. 337-343; larvae: fig. 471, 472)

Length about 0.5-7 mm (usually 1-3 mm). Body usually of characteristic antlike shape, with outline more-or-less abruptly interrupted between pronotum and elytra, occasionally oblong or ovate. Elytra covering abdomen completely, sometimes except for extreme apex, not or (rarely) narrowly truncate at apex. Scydmaenids are distinguished from other staphylinoids by the combination non-demarcated mesocoxal cavities and more-or-less clavate femora with long narrow basal portion and swollen distal portion (non-demarcated mesocoxal cavities are, within Staphylinoidea, shared only with a few staphylinids with strongly abbreviated elytra, and clavate femora with the leiodid genus *Glacicavicola* and some Leptodirini, which have sharply defined mesocoxal cavities). Other scydmaenid features include the presence of a radial hinge (proximal to radial cell) in the hindwing, absence of ocelli, and 6 distinct ventrites. The male genitalia with large basal bulb, usually symmetrical, internal sac not everted; parameres present (paired), or absent. Larvae have the labrum fused to the head capsule, mandibles without mola, 3 (closely aggregated), 1 or 0 stemmata on each side of the head; urogomphi absent, or (rarely) a pair of fixed, undivided urogomphi present. Scydmaenid larvae may resemble those of certain staphylinids, notably Pselaphinae, but can be recognized by shorter and broader, domelike or conical antennal sensorium.

This family contains more than described 4000 species, placed in almost 100 genera and 2 subfamilies. Scydmaenids occur in leaf litter, rotting wood, mosses, etc., particularly in moist places; some species live in nests of ants or mammals. At least some species are known to be predators of mites, and predatory habit is believed to be general for the family, but published observations are few. The distribution is worldwide.

Key to subfamilies of Scydmaenidae (adults and larvae)

1. ADULT: Antennae (fig. 81) not geniculate, or (Scydmaenini) with three apical segments enlarged, forming distinct club; basal segment usually much shorter than 2+3, rarely as long, if grooved apically (Scydmaenini), then groove is dorsal. Metepisterna usually concealed, or if exposed, then not or only slightly narrowed anteriorly, separating anterior metasternal corners from elytral margins. – LARVA: Antennae inserted laterally on head (fig. 470), 3-segmented, rarely 2-segmented, with sensorium on segment 2, anterad or anterodorsad of segment 3 or its unarticulated remnant (fig. 237) .... Scydmaeninae

– ADULT: Antennae (fig. 82) geniculate, three apical segments not enlarged; basal segment at least as long as 2-4 combined, grooved apically on lateral or ventral face. Metepisterna at least partly exposed, narrowed anteriorly so anterior metasternal corners reach (or almost reach) elytral margins. – LARVA: Antennae inserted more dorsomedially on head, either markedly so (Leptomastax: fig. 472) or, if this is less pronounced, antennae 4-segmented with sensorium placed apically on segment 4 .... Mastiginae

SCYDMAENINAE (Adults: fig. 337-340; larva: fig. 471). This is by far the largest scydmaenid subfamily, including the vast majority of the known species. It is currently divided into 10 tribes and contains more than 80 genera. The Scydmaeninae include several primitive genera, which probably have a more basal phylogenetic position within the family than is indicated by the current classification. Probably, this subfamily is paraphyletic. The distribution is worldwide.

MASTIGINAE (Adults: fig. 341-343; larva: fig. 472). The subfamily is currently divided into 3 tribes and contains about 7 genera and more than 50 species. It is distributed in the western palearctic, Africa, southeast Asia and north and central America.

SCAPHIDIIDAE

(Adults: fig. 344-346; larva: fig. 473)

Length about 1-7 mm. Body of characteristic, more-or-less wedge-like shape, outline not interrupted between pronotum and elytra, the latter covering most of abdomen, but truncate posteriorly and leaving abdominal apex exposed. Scaphidiids are easily recognized from other staphylinoids by the very large basal ventrite, which is at least as long as the following three ventrites combined. A characteristic (shared with Empelidae, Apateticidae, Silphidae and most Staphylinidae) is the presence of minute sclerites in the abdominal intersegmental membranes arranged in a distinctive brick-wall pattern (among other staphylinoid families, such membrane structure was only seen in the leiodid genus *Colon*). Other scaphidiid features include the presence of a radial hinge (proximal to radial cell) in the hindwing, absence of ocelli, and 6 distinct ventrites. The male genitalia with large basal bulb, usually symmetrical, internal sac not everted; parameres present (paired). Larvae are recognized by having a free labrum with a crenulate emargination at anterior margin. Head usually with 5 (sometimes 6 or 3) stemmata on each side of head. Urogomphi 1- or 2-segmented, or absent.

This family contains about 50 genera and 1200 described species (five tribes and several subtribes are currently recognized (cf. Newton and Thayer, 1992)). Scaphidiids occur in leaf litter, rotting wood, etc., where they feed on various kinds of fungi; some are associated with tree fungi, others with mushrooms, and certain forms are associated with slime molds. The distribution is worldwide.

The Scaphidiidae have traditionally been treated as a distinct family but Kasule (1966) and others include them in the Staphylinidae (near Oxytelinae and allies). Leschen (1993) regarded scaphidiids and apateticids as probable sistergroups and included them both in the Staphylinidae. Although there seems to be evidence for such a relationship it was not revealed by the present analysis. Here, a more basal position of scaphidiids (and apateticids) within the Staphylinoidea is indicated. Consequently, the family rank of Scaphidiidae has been maintained.

EMPELIDAE

(Adult: fig. 347)

Lenght about 1.5 mm. Body ovoid, very convex, with outline not interrupted between pronotum and elytra, the latter completely without striae, ridges or tubercles, slightly truncate at apex, covering most of the abdomen, so that not more than 3 abdominal segments are exposed. Empelids are distinguished from other staphylinoids by the distinctive clambid-like facies, i.e., body with power of rolling up, head hypognathous, elytra non-striate and posterior coxae excavate throughout their lengths, in combination with the presence of 6 distinct ventrites. A characteristic (shared with Scaphidiidae, Apateticidae, Silphidae and most Staphylinidae) is the presence of minute sclerites in the abdominal intersegmental membranes arranged in a distinctive brick-wall pattern (among other staphylinoid families, such membrane structure was only seen in the leiodid genus *Colon*). Other empelid features include the presence of a radial hinge (proximal to radial cell) in the hindwing, and absence of ocelli. The male genitalia with large basal bulb, symmetrical, internal sac not everted; parameres present (paired). Like some subfamilies of Staphylinidae, Empelidae has a pair of gland openings anteriorly on sternum 8 (fig. 119). Immature stages are unknown.

The family contains only a single species, *Empelus brunnipennis*, distributed in western North America. It has been found in forest leaf litter and wet debris along small forest streams (Newton and Thayer, 1995).

The systematic status of the group has been (and probably still is) subject to debate. It was originally placed near the genus *Clambus* (Clambidae, at that time included in the silphids), subsequently transferred to Leiodidae, and later again considered a very primitive staphylinoid group, for which Crowson (1981) used the name Empelidae. However, the group was not formally described until recently, when Newton and Thayer (1992) proposed it as a distinct staphylinid subfamily and (based on the shared sternum 8 gland complex) considered it closely related to Omaliinae and allies. This subordinate position was also concluded by Newton and Thayer (1995) from an analysis of the omaliine group of staphylinid subfamilies. However, the present analysis tends to support the hypothesis about a more basal position within Staphyliniformia and, hence, Empelidae is tentatively regarded here as a distinct family.

STAPHYLINIDAE

(Adults: fig. 354-447; larvae: fig. 477-492)

Length about 0.5-50 mm (usually 1-20 mm). Body usually very elongate, occasionally ovate. Most staphylinids have strongly abbreviated elytra with truncate posterior margin, and abdominal terga (from about segment 3) exposed and strongly sclerotized; similarly abbreviated elytra are only found in a few Ptiliidae, the leiodid genus *Platypsyllus*, and a few Silphidae (notably *Diamesus*) (for separation, see these families). Certain staphylinids have, however, longer elytra which may cover most of the abdomen (occasionally the entire abdomen). Long elytra are found in the subfamilies Glypholomatinae, Omaliinae, Microsilphinae, Proteininae, Neophoninae and Dasycerinae, some of which are habitually very atypic staphylinids, but which can be recognized from non-staphylinids (except Empelidae) by the presence of paired gland openings anteriorly on sternum 8 (fig. 120, 121); Empelidae differ from these subfamilies by its ability to "roll up" and (except Glypholomatinae) excavate posterior coxae.

Most staphylinids (except, e.g., Aleocharinae, many Tachyporinae, Proteininae and, to some extent, Staphylininae) share with scaphidiids, empelids, apateticids and silphids a characteristic brick-wall pattern of minute sclerites in the abdominal intersegmental membranes (among other staphylinoid families, such membrane structure was seen only in the leiodid genus *Colon*). Other characteristics of Staphylinidae include the presence of a radial hinge (proximal to radial cell) in the hindwing, and 6-7 distinct ventrites. The male genitalia with more-or-less developed, usually large basal bulb, symmetrical or sometimes asymmetrical, internal sac not everted; parameres present (paired or rarely fused), occasionally absent. Larvae variable; mandibles without mola (rarely with pseudomola), labrum free (often subdivided) or completely fused to head capsule, urogomphi usually present, articulated, and 1- or 2-segmented (for separation from larvae of other families, see under these and key to families above).

This family is here used in a relatively broad sense, including groups that are often treated as distinct families (notably Micropeplinae, Dasycerinae and Pselaphinae); other groups that have sometimes been treated as staphylinid subfamilies are excluded here (see also the phylogenetic discussion in the previous section). As mentioned in the introduction to the systematic part I have largely followed Lawrence and Newton (1982, 1995) with regard to the classification of staphylinid subfamilies. According to these authors (but not shown by the present analysis) these subfamilies fall into four major groups: 1) an omaliine group (Glypholomatinae-Pselaphinae); 2) a tachyporine group (Phloeocharinae-Aleocharinae); 3) an oxyteline group (Trigonurinae-Oxytelinae); and 4) a staphylinine group (Oxyporinae-Staphylininae). Lawrence and Newton also included Empelidae in the omaliine group, and Scaphidiidae and Apataticidae in the oxyteline group, but as outlined in the phylogenetic discussion these three taxa seem to have more basal positions within Staphylinoidea and are therefore considered distinct families in the present context.

As defined here, the Staphylinidae contain more than 40.000 species, placed in about 3000 genera and (here) 28 subfamilies. Staphylinids occur in a variety of different habitats, e.g., in leaf litter, rotten wood, fungi, dung, carrion, banks of rivers and lakes, seashores, etc.; some live in nests of ants, termites, mammals or birds. Most forms are predaceous, but some feed on fungal spores or hyphae, or algae. The distribution is worldwide.

Larvae have been described for most subfamilies (except Glypholomatinae, Microsilphinae, Neophoninae, Protopselaphinae, Olisthaerinae and Solieriinae), but those of Trigonurinae, Megalopsidiinae, Leptotyphlinae and Pseudopsinae have only been very briefly characterized (Newton, 1982b, 1990). With regard to the larvae, the following key to staphylinid subfamilies is partly based on the keys of Frank (1991), Lawrence (1991) and Newton (l.c.).

Key to subfamilies of Staphylinidae (adults)

1. Antennae inserted on dorsal surface of head behind level of anterior margin of eyes (fig. 19, 24) (or in corresponding position in eyeless forms); if inserted in front of eyes (*Cypha*), then 10-segmented and pronotum very transverse, semicircular, widest basally (fig. 415) 2
– Antennae inserted at anterior or lateral margins of head in front of eyes (fig. 18, 20-23, 25), rarely 10-segmented and if so, then pronotum not very transverse and semicircular 3
2. Posterior coxae small (almost as fig. 140), oval and distinctly separated. Anterior coxae enclosed at base, with trochantins concealed. Eyes very large and protruding (fig. 24) . . . . Steninae
– Posterior coxae large (fig. 141), very transverse and contiguous. Anterior coxae not enclosed, with trochantins exposed. Eyes not very large and protruding, sometimes absent . . . . Aleocharinae
3. Elytra completely covering abdomen, rounded or only slightly truncate apically, with regular longitudinal series of punctures, interstices often partly ridged. Head without ocelli. Habitus somewhat reminiscent of the cucujoid family Latridiidae (fig. 369) . . . Dasycerinae
– Elytra abbreviated and truncate apically, leaving at least 2-3 abdominal segments uncovered, or if longer, then without serial punctures or head with pair of ocelli dorsally between eyes (fig. 20). Habitus never Latridiid-like 4
4. Prothorax with sharply defined antennal grooves ventrally (fig. 112). Antennae 9-segmented with 1-segmented club (fig. 91). Elytra with longitudinal, usually sharp ridges (fig. 367), exposed abdominal terga usu-

ally also with pronounced longitudinal ridge-like projections . . . . Micropeplinae

– Prothorax without such antennal grooves. Antennae normally 11-segmented, never 9-segmented with 1-segmented club. Elytra mostly without ridges, abdominal terga without ridges 5

5\. Antennae with well developed 2-segmented club (fig. 89). Eyes very large and protruding (fig. 22). Labrum deeply emarginate and partly concealed, so that only a pair of narrow setose processes are visible (fig. 22) . . . . Megalopsidiinae

– Antennae without distinct club, or if clubbed, then eyes much smaller (sometimes absent), or labrum different, with visible portion not restricted to a pair of narrow setose processes 6

6\. Labial palpi very large, with large transverse, crescent-shaped apical segment (fig. 58). Middle coxae very broadly separated. Mandibles strongly protruding (fig. 21) . . . . Oxyporinae

– Labial palpi small, often inconspicuous, apical segment not enlarged or transverse crescent-shaped, normally minute. Middle coxae not broadly separated, normally almost contiguous. Mandibles variable, often much less protruding 7

7\. Eyes completely absent. Neck broad, weakly differentiated (as fig. 21). Elytra immovably fused basally to mesothorax. Very small, thread-like forms, usually about 1 mm long (always less than 2 mm) . . . . Leptotyphlinae

– Eyes present, or if (very rarely) absent, then neck narrower and more abruptly differentiated or body form much broader. Elytra always articulated basally to mesothorax, not solidly fused. Mostly larger and less elongate, not thread-like forms 8

8\. Posterior coxae with well developed coxal plates, i.e., strongly excavate throughout their lenghts for reception of posterior femora (almost as fig. 136). Antennae filiform, very thin and hairlike, with sparse erect setae (fig. 86). Elytra not striate, covering only first two abdominal segments. Epipleura defined by a sharp ridge . . . . Habrocerinae

– Posterior coxae without coxal plates, i.e., not excavate except sometimes at mesal end; if distinctly excavate (Glypholomatinae) then elytra striate, covering most of abdomen. Antennae variable, if somewhat thin and hairlike, then epipleura not demarcated by ridge . . 9

9\. Pronotum and elytra with longitudinal ridges (fig. 435). Abdominal segments with paratergites separating sternal and ventral halves (as fig. 115), tergum 9 entire, with large apical emargination for reception of tergum 10 (almost as fig. 183) . . . . Pseudopsinae

– Pronotum and elytra without longitudinal ridges, or if ridges present, then abdominal segments without distinct paratergites, i.e., sternal and ventral halves of each segment fused to solid ring, or tergum 9 divided medially by tergum 10 (except sometimes at extreme anterior margin) 10

10\. Tarsi 3-segmented or (rarely) 2-segmented. Ocelli absent. Elytra with small pitlike foveae basally and sharp sutural stria (fig. 157) (absent in a few eyeless forms). Abdomen without dorso-ventral flexibility . . . . Pselaphinae

– Tarsi usually 5-segmented, rarely 4-segmented, or if 2- or 3-segmented, then a pair of ocelli present (fig. 20), or elytra without basal foveae and sutural stria (and eyes present). Abdomen usually more-or-less flexible dorso-ventrally 11

11\. Antennae with distinct 2-segmented club (as fig. 49). Antennae inserted at anterior margin of head mesal to outer edges of mandibles (almost as fig. 25). Labrum broad, entire, its anterior margin dentate (fig. 33) . . . . Euaesthetinae

– Antennae without distinct club, or if clubbed, then rather inserted on sides of head, lateral to outer edges of mandibles (as fig. 18). Labrum different 12

12\. Abdomen with conspicuous, rigid, black macrosetae, at least present on segment 8 (fig. 129). Head normally without differentiated neck (fig. 18), rarely with suggestion of constriction. Epipleura demarcated by distinct line or (usually) sharp ridge. Antennae inserted laterally in front of eyes (fig. 18), but not below raised margin (rarely below fine line) 13

– Abdomen without macrosetae, or if macrosetae present, then head with well defined, abruptly constricted neck (fig. 23, 25), or epipleura not demarcated from remainder of elytra. Antennae inserted below more-or-less strongly raised sidemargin (or anterior margin) 14

13\. Body depressed. Head with fine sharp frontoclypeal groove (fig. 18). Pronotum widest slightly behind middle, narrowed behind, sides sinuate posteriorly (fig. 380). Abdominal tergum 8 simply rounded posteriorly (fig. 380) . . . . Olisthaerinae

– Body not depressed. Head without frontoclypeal groove (sometimes indicated as fine suture). Pronotum normally widest at base, narrowed only in front (fig. 382-386); if narrowed behind and with sides sinuate posteriorly, then abdominal tergum 8 deeply bifurcate (fig. 129) . . . . Tachyporinae

14\. Elytra with 9 regular longitudinal series of punctures. Head without ocelli. Pronotum widest at base (fig. 418) . . . . Trigonurinae

– Elytra without serial punctures, or if series present, then usually differing in number, and head with ocelli or pronotum distinctly narrowed behind 15

15\. Tarsi 3-segmented. Pronotum without lateral carina delimiting dorsal and ventral portions. Elytra without striae. Antennae with more-or-less defined 3-segmented club . . . . Protopselaphinae

– Tarsi usually 5- (or 4-) segmented; if 3-segmented then pronotum with more-or-less sharp lateral carina delimiting dorsal and ventral portions, or elytra striate. Antennae rarely with 3-segmented club 16

16. Anterior coxae only slightly projecting. Epipleura hardly demarcated from remainder of elytra. Abdominal segments with well developed paratergites separating sternal and tergal halves (as fig. 115) . . . . Phloeocharinae

– Anterior coxae strongly projecting (fig. 110, 130), if not, then epipleura more-or-less sharply demarcated, or abdominal segments without distinct paratergites, i.e., sternal and tergal halves of each segment fused to solid ring 17

17. Antennae filiform, extremely slender and hairlike, segments with wreaths of long setae (as fig. 86). Epipleura not demarcated from remainder of elytra . . . . Trichophyinae

– Antennae not very slender, segments usually without wreaths of long setae. Epipleura demarcated or not 18

18. Anterior coxae very long and projecting (fig. 110, 130). Epipleura not demarcated from remainder of elytra (except in few Paederinae). Tarsi 5-segmented, middle and posterior tarsi very rarely 4-segmented 19

– Anterior coxae shorter, but still often projecting. Epipleura demarcated by distinct line or ridge, if not, then anterior coxae small and globular or tarsi 3-segmented 21

19. Posterior coxae transverse, not projecting, expanded caudally and laterally (almost as fig. 141). Pronotum widest anterior to middle, narrowed behind, with transverse series of five deep foveae posteriorly (fig. 433). Body pubescent, but without distinct macrosetae . . . . Solieriinae

– Posterior coxae triangular, conically projecting, hardly expanded caudally and laterally (fig. 140). Pronotum of variable shape, without deep foveae posteriorly. Body almost always with more-or-less numerous, black rigid macrosetae (e.g., as fig. 444) 20

20. Antennae inserted anteriorly at sides of head, lateral to outer edges of mandibles (fig. 23). Abdominal intersegmental membranes with distinct brick-wall pattern of minute sclerites (as fig. 115, 128). Basal ventrite carinate anteromedially . . . . Paederinae

– Antennae inserted at anterior margin of head, mesal to outer edges of mandibles (fig. 25). Abdominal intersegmental membranes at most with indistinct brick-wall pattern of minute sclerites. Basal ventrite usually not carinate anteromedially . . . . Staphylininae

21. Trochanters relatively large, those of posterior legs at least 1/4 x as long as femoral length (fig. 138). Abdominal sternum 8 with characteristic paired gland openings at anterior margin (fig. 120) (only visible by dissection). Ocelli often present (fig. 20) 22

– Trochanters smaller, those of posterior legs not more than 1/5 x as long as femoral length. Abdominal sternum 8 without such gland openings. Ocelli always absent 26

22. Head without ocelli or with single median ocellus. Abdominal tergum 3 (if exposed) without pair of small patches of microtrichiae. Abdominal intersegmental membranes relatively short, without pattern of minute sclerites . . . . Proteininae

– Head with pair of ocelli between eyes (fig. 20), if not, then abdominal tergum 3 exposed and with pair of small patches of microtrichiae (as fig. 115). Abdominal intersegmental membranes longer, with distinct brick-wall pattern of minute sclerites (fig. 115, 128) 23

23. Posterior coxae excavate posteriorly for reception of posterior femora, which are largely concealed from below when retracted. Elytra long, covering all but apical 1-3 abdominal segments in dorsal view, each elytron with 11 punctate striae . . . . Glypholomatinae

– Posterior coxae not excavate, posterior femora not concealed from below. Elytra often shorter and concealing smaller portion of abdomen; if striate, then with no more than 9-10 striae 24

24. Elytra with regular series of punctures. Tarsi 3-segmented . . . . Neophoninae

– Elytra without serial punctures, or tarsi 5-segmented 25

25. Elytra long (fig. 355), covering major portion of abdomen, not more than 2-3 abdominal segments exposed, no trace of elytral striae or series of punctures. Antennae with more-or-less differentiated 3-segmented club (fig. 87). 4th segment of maxillary palpi much smaller than 3rd, bearing a minute 5th segment (fig. 52) . . . . Microsilphinae

– Elytra usually shorter, leaving about 5-6 abdominal segments exposed; if longer, then antennae filiform, without club, or elytra with serial punctation (or both), and 4th segment of maxillary palpi not smaller than 3rd . . . . Omaliinae

26. Abdominal segments without paratergites, sternal and ventral halves of each segment fused to solid ring, abdomen usually cylindrical or slightly flattened, rarely depressed . . . . Osoriinae

– Abdominal segments with well developed paratergites separating sternal and ventral halves of segments (as fig. 115, 116), abdomen usually moderately flattened 27

27. Anterior coxae small, globular, coxal cavities narrowly closed posteriorly (fig. 111). Abdomen with 6 distinct ventrites (sternum 3-8), basal ventrite with well defined cavities for reception of posterior coxae and with well developed, acute intercoxal process (as fig. 125) . . . . Piestinae
– Anterior coxae larger, conically projecting, coxal cavities not closed posteriorly (as fig. 109, 110). Abdomen usually with 7 distinct ventrites (sternum 2-8), basal ventrite without or (rarely) with weakly defined cavities for reception of posterior coxae, without or with low, rudimentary intercoxal process (almost as fig. 126) . . . . Oxytelinae

Key to subfamilies of Staphylinidae (larvae)

1. Mandibles truncate apically, apical portion with dense array of slender teeth (fig. 210). Body oval, not or slightly flattened (fig. 480). Head with 6 stemmata on each side . . . . Dasycerinae
– Mandibles more-or-less pointed, without array of slender teeth (rarely with minute spines on apical portion). Body usually very elongate, if broader (Micropeplinae), then flattened and head without stemmata 2
2. Body relatively broad and flattened, terga with lateral projecting lobes (fig. 479). Head without median epicranial suture . . . . Micropeplinae
– Body usually very elongate, terga without lateral projections. Head with median epicranial suture (fig. 200, 201) 3
3. Maxillae with articulated mala (fig. 221) 4
– Maxillae with fixed mala (fig. 219, 220) 6
4. Antennae 3-segmented . . . . Pseudopsinae
– Antennae 4-segmented 5
5. Head with 5 or 6 (rarely 1) stemmata on each side. Ventral face of prothorax with transverse, somewhat crescent-shaped sclerite anteriorly . . . . . . Paederinae
– Head usually with 4 or (Xantholinini) 1 or 2 stemmata on each side. Ventral face of prothorax with less transverse, triangular sclerite anteriorly . . . . Staphylininae
6. Labrum completely fused to head capsule (rarely finely demarcated) 7
– Labrum articulated to head capsule 10
7. Head with 3 or fewer stemmata on each side. Urogomphi 1-segmented, fixed or indistinctly articulated at base, sometimes absent 8
– Head with 6 stemmata on each side. Urogomphi 2-segmented (rarely 1-segmented), distinctly articulated at base 9
8. Stemmata usually present, 1-3 on each side . . . . Pselaphinae
– Stemmata absent . . . . Leptotyphlinae
9. Maxilla with trilobed mala (fig. 220). Mandibles stout and deeply bifid, apical portion finely serrate (fig. 209) . . . . Oxyporinae
– Maxilla not trilobed. Mandibles falciform, simply pointed, serrate only at mesal edge 10
10. Head without differentiated neck. Ligula broad, bilobed (fig. 229) . . . . Steninae
– Head with differentiated neck. Ligula small, acute (fig. 230) . . . . Euaesthetinae
11. Maxilla with very long and slender mala (fig. 219). Urogomphi 2-segmented . . . . Proteininae
– Maxilla with shorter mala, or if mala relatively long, then urogomphi 1-segmented 12
12. Mandibles with 2 or more subapical teeth, more-or-less widened and scoop-like apically (fig. 207), inner edge not serrate. Ligula transverse, truncate (fig. 231-233). Head with 4 or fewer stemmata on each side 13
– Mandibles mostly with single tooth and 1 or 2 preapical teeth, rather narrow at apex, inner edge often serrate. Ligula variable. If mandibles and ligula as above, then head with 5 or 6 stemmata on each side 15
13. Left and right mandibles almost symmetrical, with same number of preapical teeth. Maxillary palpi with segment 2 not longer than segment 1, if longer, then urogomphi falciform . . . . Oxytelinae
– Left and right mandibles with different dentition, or with scoop-like or mola-like lobes near apex. Maxillary palpi with segment 2 longer than segment 1. Urogomphi straight 14
14. Head with two large sclerites (mentum, submentum) between prementum and posterior tentorial pits (fig. 231). Stemmata 4 or 1 on each side . . . . Piestinae
– Head with single large sclerite (fused mentum and submentum) between prementum and posterior tentorial pits (fig. 232). Stemmata 1-4 on each side, or absent . . . . Osoriinae
15. Head with single stemma on each side, or (rarely) stemmata absent. Abdominal segment 8 with median dorsal glandular structure (fig. 253), or urogomphi minute . . . . Aleocharinae
– Head with at least 2 stemmata on each side, or if stemmata absent, then abdominal segment 8 without such glandular structure and urogomphi well developed 16
16. Head with 2 stemmata on each side . . Trichophyinae
– Head with at least 3 stemmata on each side, or (rarely) stemmata absent 17
17. Head with broad, but distinctly differentiated neck . . . . Megalopsidiinae
– Head without differentiated neck 18
18. Head with 6 stemmata on each side. Ligula bilobed . . . . Trigonurinae

– Head with 5 or fewer stemmata on each side, if 6 stemmata present on each side, ligula different, conical or short and obtuse, or absent 19
19. Urogomphi 1-segmented .... Omaliinae
– Urogomphi 2-segmented 20
20. Head with 6 stemmata on each side, or if fewer, antennae 4-segmented .... Tachyporinae
– Head with 5 or fewer stemmata on each side. Antennae 3-segmented 21
21. Head with 5 stemmata on each side arranged in single, irregularly curved line .... Habrocerinae
– Head with 5 stemmata on each side arranged in two groups (three anterior, two posterior), or with only 3 stemmata on each side .... Phloeocharinae

GLYPHOLOMATINAE (Adult: fig. 354). A small subfamily recently proposed by Newton and Thayer (1995) for the genus *Glypholoma* with 4 species from southern South America and 1 species from southeastern Australia. The genus was originally placed in Silphidae but was transferred to Staphylinidae-Omaliinae by Newton (1975).

MICROSILPHINAE (Adult: fig. 355). The subfamily includes only the genus *Microsilpha* with approximately 30 species (only 4 described) (Newton and Thayer, 1995). It is distributed in Southern Australia, New Zealand and southern South America. *Microsilpha* was earlier considered to belong to Silphidae or Leiodidae. It has also been included in the Omaliinae but was most recently considered of subfamily rank (Newton and Thayer, l.c.).

OMALIINAE (Adults: fig. 356-362; larva: fig. 477). A relatively large subfamily, including certain long-winged forms (e.g., *Brathinus, Deinopteroloma*) which were earlier placed in other families; the genus *Aphaenostemmus*, sometimes placed in a distinct subfamily, is here included in the Omaliinae. Thus defined, the subfamily contains more than 100 genera placed in 7 tribes by Newton and Thayer (1995). It is widely distributed (all major biogeographical regions).

PROTEININAE (Adults: fig. 363-366; larva: fig. 478). A relatively small subfamily, now divided into 5 tribes (Newton and Thayer, 1995) and containing about a dozen genera and approximately 130 described species. It is widely distributed (all major biogeographical regions), primarily in temperate regions of northern and southern hemispheres.

MICROPEPLINAE (Adult: fig. 367; larva: fig. 479). A small subfamily, containing 5 genera and about 60 described species. The group has often been considered a distinct family. Micropeplines are primarily holarctic but extend into the oriental, neotropical and afrotropical regions.

NEOPHONINAE (Adult: fig. 368). The subfamily includes only the genus *Neophonus* with a single species from southern South America.

DASYCERINAE (Adult: fig. 369; larva: fig. 480). The subfamily contains only the genus *Dasycerus* with about 15 described species. The genus has often been placed in a distinct family, or included in the Latridiidae (Cucujoidea) because of superficial resemblance in general habitus. Dasycerines are primarily holarctic but extend into the oriental region.

PROTOPSELAPHINAE. A small subfamily, recently proposed by Newton and Thayer (1995) for the genus *Protopselaphus* with 8 known species, all from the oriental region (Malaysia).

PSELAPHINAE (Adults: fig. 370-378; larva: fig. 481). The subfamily as here defined is equivalent of the Pselaphidae of previous authors. Although family rank has usually been assigned to the group, there is no phylogenetic justification for this (unless several traditional staphylinid subfamilies are considered distinct families). As a result of the change in formal rank of the entire group, lower taxonomic categories should also be downgraded (at least to some degree). Newton and Thayer (1995) who also changed Pselaphidae to Pselaphinae proposed that current subfamilies be substituted by "supertribes" (see under Pselaphinae in Phylogenetic discussion above), but I have here preferred to treat these taxa simply as tribes, primarily to avoid the informal concept of supertribes (otherwise not used within Staphyliniformia). Hence, the tribes used here are Faronini, Euplectini, Bythinoplectini, Batrisini, Goniacerini, Pselaphini and Clavigerini. The Pselaphinae are a very large group, which contain approximately 1100 genera and more than 8000 described species. They are distributed worldwide, and particularly abundant in warmer regions.

PHLOEOCHARINAE (Adult: fig. 379). The concept of this subfamily has been subject to some dispute and, at least earlier, it was more-or-less a "dumping ground" for species that could not be assigned to other subfamilies. As presently delimited, Phloeocharinae is a relatively small group, containing about 7 genera and less than 50 described species. The subfamily is distributed in the holarctic regions (extending into central America) and in the australian region.

OLISTHAERINAE (Adult: fig. 380). A small subfamily, containing only a single genus, *Olisthaerus*, with only a few species distributed in the holarctic region. The genus has sometimes been included in the Phloeocharinae.

TACHYPORINAE (Adults: fig. 381-386; larva: fig. 482). The subfamily is currently divided into 7 tribes, containing about 30 genera and several hundred species. The distribution is world wide.

TRICHOPHYINAE (Adult: fig. 387). The subfamily includes only the genus *Trichophya* with a dozen described species. It is primarily holarctic, but extends into central America and southeast Asia.

HABROCERINAE (Adult: fig. 388). A small subfamily, containing only 2 small genera, *Habrocerus* with a few species in the holarctic region, and *Nomimocerus* with a single species in southern Chile.

ALEOCHARINAE (Adults: fig. 389-417; larvae: fig. 483, 484). A very large subfamily, currently divided into about 50 tribes (and numerous subtribes). It contains about 1000 genera and several thousand species, distributed in all parts of the world.

TRIGONURINAE (Adult: fig. 418). This subfamily includes only the genus *Trigonurus* with about a dozen described species. The distribution is holarctic.

PIESTINAE (Adult: fig. 419; larva: fig. 485). The subfamily as now restricted contains 7 genera (Lawrence and Newton, 1995). It is widely distributed and represented in all major biogeographical regions (except the afrotropical).

OSORIINAE (Adults: fig. 420-423; larvae: fig. 486, 487). A relatively large subfamily, currently divided into 4 tribes (and several subtribes), containing almost 100 genera. It is widely distributed (all major biogeographic regions), particularly in warmer climates.

OXYTELINAE (Adults: 424-427; larva: fig. 488). A relatively large subfamily containing well over 1500 described species and about 50 genera. It is currently divided into two tribes. The distribution is worldwide.

OXYPORINAE (Adult: fig. 428; larva: fig. 489). A relatively small subfamily, containing only a single holarctic genus, *Oxyporus*, with approximately 50 described species.

MEGALOPSIDIINAE (Adult: fig. 429). The subfamily includes only the genus *Megalopinus*, with several species distributed in the neotropical, australian, oriental and afrotropical regions.

STENINAE (Adult: fig. 430; larva: fig. 490). The subfamily contains 2 genera, *Stenus* and *Dianous*, with a couple of thousand species, distributed worldwide.

EUAESTHETINAE (Adults: fig. 431, 432). The subfamily is currently divided into 6 tribes, and contains about 25 genera. It is widely distributed (all major biogeographical regions).

SOLIERIINAE (Adult: fig. 433). The subfamily contains only the genus *Solierius*, with a single rare species from southern Chile and Argentina.

LEPTOTYPHLINAE (Adult: fig. 434). The subfamily is currently divided into 5 tribes and contains more than 30 genera and several hundred described species. The vast majority of the described species are from the western palearctic (mediterranean), but leptotyphlines are also known from the afrotropical, nearctic and neotropical regions, and Australia. All species are minute, blind and wingless soil dwellers with very restricted distributions, and have probably been overlooked in many parts of the world.

PSEUDOPSINAE (Adult: fig. 435). A small subfamily which, as now defined, contains 4 genera (three of them earlier in Piestinae). The group is primarily holarctic, but extends into the neotropical region.

PAEDERINAE (Adults: fig. 436-440; larva: fig. 491). A large subfamily currently divided into 2 tribes (and several subtribes), containing almost 150 genera. The distribution is worldwide.

STAPHYLININAE (Adults: fig. 441-447; larva: fig. 492). A large subfamily, used here in a broad sense, including Xantholinini and related tribes (which have sometimes been placed in a distinct subfamily). Thus defined, Staphylininae is currently divided into 5 tribes (and several subtribes), containing more than 250 genera. The distribution is worldwide.

APATETICIDAE **stat.n.**
(Adult: fig. 348)

Lenght about 5-10 mm. Body rather broadly oval, its outline not or slightly interrupted between pronotum and elytra, the latter relatively long, at least about 2 x as long as pronotum, each with 9 striae or regular series of punctures, truncate apically, and covering most of the abdomen, so that not more than 3 abdominal segments are exposed. Apateticids are recognized from other staphylinoids by the long, striate elytra (exposing 3 abdominal segments), in combination with the absence of ocelli and the 5-segmented tarsi. A characteristic (shared with Scaphidiidae, Empelidae, Silphidae and most Staphylinidae) is the presence of minute sclerites in the abdominal intersegmental membranes arranged in a distinctive brick-wall pattern (among other staphylinoid families, such membrane structure was only seen in the leiodid genus *Colon*). Other empelid features include the presence of a radial hinge (proximal to radial cell) in the hindwing, and 6 distinct ventrites. The male genitalia with large basal bulb, symmetrical, internal sac not everted; parameres present (paired). Larvae have 6 pairs of stemmata and transverse, quadrilobed ligula (cf. Newton, 1982b) (no further information about larval morphology has been available to me).

The family contains only two genera, *Apatetica* and *Nodynus*, and about 25 described species, restricted to east Asia. Newton (1984) refers to these beetles as saprophages associated with decaying trees, but otherwise little seems to be known about their biology.

The systematic position of the two genera included here has been, and may still be, subject to debate. They have been referred to Silphidae by some authors, while others regard them as staphylinids and include them in Piestinae or, more recently, in a separate subfamily (e.g., Newton and Thayer, 1992). Lawrence and Newton (1995) refer to the group as a primitive member of the oxyteline group of staphylinid subfamilies (to which they also refer the scaphidiids and Trigonurinae; see also above under Scaphidiidae). Although further examinations may render this to be more likely, such a hypothesis could not be confirmed by the present analysis. Here it was indicated that apateticids may constitute the sistergroup of Silphidae (both of which collectively may form the sistergroup of Staphylinidae in the present sense). Therefore Apateticidae is tentatively proposed as a distinct family.

SILPHIDAE

(Adults: fig. 349-353; larvae: fig. 474-476)

Lenght about 7-45 mm. Body ovate to moderately elongate, with outline not or only slightly interrupted between pronotum and elytra, the latter relatively long and usually covering most of the abdomen, rounded or more-or-less truncate posteriorly and sometimes leaving part of the abdomen (occasionally as many as ca. 5 last segments) exposed. Elytra never striate, usually with 3 longitudinal ridges each, and a more-or-less developed bulge posteriorly between outer two ridges (fig. 156). Silphids share with scaphidiids, empelids, apateticids and most staphylinids a characteristic brick-wall pattern of minute sclerites in the abdominal intersegmental membranes (among other staphylinoid families, such membrane structure was only seen in the leiodid genus *Colon*). Other features of Silphidae include the presence of a radial hinge (proximal to radial cell) in the hindwing, absence of ocelli, and 6-7 distinct ventrites. The male genitalia with large basal bulb, symmetrical, internal sac not everted; parameres present (paired). Larvae are recognized by their large and broad mala divided in apical fourth and bearing dense brush of setae on the outer lobe (galea), in combination with the thoracic and abdominal terga having lateral lobes extending beyond sternal edges, or abdominal terga having spinose projections along posterior margin. Urogomphi articulated, 1- or 2-segmented.

This family contains about 200 species, placed in about 25 genera and 2 subfamilies. Most silphids are carrion feeders or scavengers, but some are phytophagous and others predators (of snails or caterpillars). The distribution is primarily holarctic, but a few genera extend into tropical Africa, South America and Southeast Asia, and two occur in Australia.

Key to subfamilies of Silphidae (adults and larvae)

1. ADULT: Antennae 11-segmented, segment 2 well developed, not retracted into apex of basal segment (fig. 85). Abdominal tergum 5 without stridulatory files. – LARVA: Body flattened, thoracic and abdominal terga with a lateral lobe extending beyond sternal edges (fig. 474). Head with 6 stemmata on each side. Anal lobes with numerous fine teeth .... Silphinae

– ADULT: Antennae apparently 10-segmented, segment 2 very short and strongly retracted into apex of basal segment (fig. 84). Abdominal tergum 5 with pair of longitudinal stridulatory files (fig. 127). – LARVA: Body less flattened, thoracic and abdominal terga either with two lateral processes on each side (fig. 475) or not extended laterally (fig. 476). Head with 1 stemma on each side. Anal lobes without teeth .... Nicrophorinae

SILPHINAE (Adults: fig. 349-352; larva: fig. 474). The subfamily is often divided into 2 tribes, and contains about 20 genera and approximately 125 described species. The Silphinae include several, presumedly primitive genera, which seem to have a more basal phylogenetic position within the family than is indicated by the current classification. Probably, the subfamily is paraphyletic. It is primarily distributed in the northern hemisphere, but extends into tropical Africa (incl. Madagascar), South America, Southeast Asia and Australia.

NICROPHORINAE (Adult: fig. 353; larvae: 475, 476). The subfamily includes 2 genera and about 75 described species. Most species belong to the genus *Nicrophorus*, which is known to be subsocial, burying small mammal or bird carcasses and guarding their offspring. Nicrophorines are primarily holarctic but extends into southeast Asia and south America.

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Appendix

The appendix includes a list of apomorphies, list of node changes, and list of statistics of characters in the preferred cladogram (PAUP analysis, successive weighting: fig. 5). The list of apomorphies includes only unambiguous characters (for ambiguous character changes, see under node changes and the phylogenetic discussion).

List of apomorphies:

MICROSPO:
char 10: 1 —> 0
char 12: 0 —> 1
char 17: 1 —> 0
char 18: 0 —> 1
char 19: 0 —> 2
char 31: 0 —> 1
char 35: 0 —> 1
char 55: 0 —> 1
char 56: 0 —> 1
char 58: 0 —> 1
char 72: 0 —> 1
char 74: 0 —> 2
char 76: 0 —> 1
char 90: 0 —> 1
char 96: 0 —> 2
char 119: 0 —> 1
GYRINIDA:
char 2: 1 —> 0
char 16: 0 —> 2
char 19: 0 —> 5
char 27: 0 —> 1
char 40: 0 —> 1
char 50: 1 —> 2
char 58: 0 —> 1
char 64: 0 —> 2
char 87: 0 —> 1
char 106: 0 —> 1
char 118: 0 —> 2
char 119: 0 —> 1
TRACHYPA:
char 26: 1 —> 2
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char 66: 1 —> 0
char 79: 0 —> 1
char 103: 0 —> 1
char 116: 0 —> 1
EUCINETI:
char 2: 1 —> 0
char 30: 0 —> 1
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char 40: 0 —> 1
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char 77: 0 —> 1
char 84: 0 —> 1
char 96: 0 —> 1
DERODONT:
char 3: 0 —> 2
char 4: 1 —> 0
char 5: 1 —> 0
char 19: 0 —> 2
char 55: 0 —> 1
char 74: 0 —> 1
char 101: 3 —> 1
char 115: 0 —> 2
char 116: 0 —> 1
TROGIDAE:
char 16: 0 —> 1
char 24: 0 —> 1
char 25: 1 —> 2
char 26: 1 —> 2
char 90: 0 —> 1
char 96: 0 —> 5
char 98: 1 —> 0
char 113: 0 —> 2
HYDROPHI:
char 1: 0 —> 1
char 3: 0 —> 1
char 8: 0 —> 1
char 15: 0 —> 1
char 16: 0 —> 2
char 30: 0 —> 1
char 36: 0 —> 1
char 76: 1 —> 0
char 89: 0 —> 2
char 119: 0 —> 1
SPHAERIT:
char 77: 1 —> 2
char 78: 0 —> 1
SYNTELII:
char 25: 1 —> 2
char 26: 1 —> 2
HISTERID:
char 37: 1 —> 0
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char 50: 1 —> 2
char 54: 0 —> 1
char 61: 0 —> 1
char 64: 0 —> 1
char 83: 0 —> 2
char 96: 6 —> 5
char 116: 4 —> 2
HYDRAENI:
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char 5: 1 —> 0
char 10: 1 —> 0
char 15: 0 —> 1
char 36: 0 —> 1
char 66: 1 —> 0
char 78: 0 —> 1
char 89: 0 —> 1
char 93: 1 —> 0
char 101: 3 —> 2
char 119: 0 —> 1
PTILIIDA:
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char 7: 0 —> 1
char 12: 0 —> 1
char 24: 0 —> 1
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char 54: 0 —> 1
char 56: 0 —> 1
char 57: 1 —> 0
char 59: 0 —> 1
char 60: 0 —> 1
char 63: 0 —> 1
char 74: 3 —> 4
char 96: 1 —> 5
char 114: 0 —> 1
char 116: 2 —> 1
AGYRTIDA:
char 20: 0 —> 1
char 74: 3 —> 2
char 78: 0 —> 1
char 81: 2 —> 1
char 83: 0 —> 1

```
    char 85: 0 —> 1
    char 101: 3 —> 0
  LEIODIDA:
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    char 20: 0 —> 2
  EMPELIDA:
    char 2: 1 —> 2
    char 19: 0 —> 2
    char 29: 0 —> 1
    char 35: 0 —> 1
    char 46: 2 —> 3
    char 48: 0 —> 1
    char 58: 0 —> 1
    char 60: 0 —> 1
    char 66: 1 —> 0
  OMALIINA:
    char 74: 3 —> 2
    char 85: 0 —> 1
  MICROSIL:
    char 3: 2 —> 0
    char 9: 0 —> 1
    char 11: 0 —> 1
    char 12: 0 —> 1
    char 13: 0 —> 1
    char 19: 0 —> 2
    char 50: 1 —> 2
    char 78: 0 —> 1
  PROTEINI:
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    char 43: 1 —> 0
    char 50: 1 —> 2
    char 74: 3 —> 2
    char 77: 2 —> 0
  MICROPEP:
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    char 14: 1 —> 0
    char 16: 0 —> 2
    char 19: 0 —> 1
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    char 29: 0 —> 1
    char 31: 0 —> 1
    char 50: 1 —> 2
    char 57: 1 —> 0
    char 59: 0 —> 1
    char 61: 0 —> 1
    char 62: 0 —> 1
    char 81: 2 —> 1
    char 85: 3 —> 0
    char 94: 0 —> 1
    char 104: 2 —> 0
  NEOPHONU:
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    char 11: 0 —> 1
    char 21: 0 —> 1
    char 29: 1 —> 0
    char 31: 0 —> 1
    char 37: 1 —> 0
    char 59: 1 —> 0
    char 63: 0 —> 1
    char 66: 1 —> 2
    char 72: 0 —> 1
  DASYCERU:
    char 11: 0 —> 1
    char 13: 0 —> 1
    char 19: 0 —> 2
    char 25: 0 —> 1
    char 41: 2 —> 0
    char 45: 1 —> 0
    char 47: 4 —> 2
    char 53: 2 —> 1
    char 66: 1 —> 2
    char 67: 2 —> 0
    char 118: 3 —> 0
  PSELAPHI:
    char 9: 0 —> 1
    char 21: 0 —> 1
    char 37: 1 —> 0
    char 78: 0 —> 1
    char 97: 0 —> 1
    char 109: 0 —> 1
  SOLIERIU:
    char 32: 0 —> 1
  OXYTELIN:
    char 74: 3 —> 2
    char 77: 2 —> 1
    char 86: 0 —> 2
  APATETIC:
    char 2: 1 —> 2
    char 14: 1 —> 0
    char 25: 0 —> 1
    char 60: 0 —> 1
    char 62: 0 —> 1
  SILPHIDA:
    char 9: 0 —> 1
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    char 18: 0 —> 1
    char 19: 0 —> 3
    char 40: 1 —> 2
    char 47: 4 —> 3
    char 49: 0 —> 1
    char 50: 1 —> 2
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    char 85: 1 —> 0
  SCAPHIDI:
    char 1: 0 —> 1
    char 6: 0 —> 1
    char 19: 0 —> 4
    char 37: 1 —> 0
    char 62: 0 —> 1
    char 74: 3 —> 2
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  SCYDMAEN:
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    char 9: 0 —> 1
    char 12: 0 —> 1
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    char 59: 0 —> 1
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  TACHYPOR:
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  PHLOEOCH:
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  OXYPORIN:
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  STENINAE:
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  LEPTOTYP:
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    char 21: 0 —> 1
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PSEUDOPS:
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STAPHYLI:
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char 54: 0 —> 1
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char 79: 0 —> 1
char 80: 0 —> 1

char 82: 0 —> 1
char 99: 0 —> 1
char 104: 1 —> 2
Node 66:
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char 66: 0 —> 1
char 73: 0 —> 1
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char 11: 1 —> 0
char 28: 1 —> 0
char 37: 0 —> 1
char 60: 1 —> 0
char 76: 0 —> 1
char 117: 1 —> 0
Node 68:
char 25: 0 —> 1
char 68: 1 —> 0
Node 69:
(—> ambiguous character polarity:
= Node 69 or 70 in rerooted tree)
char 7: 1 —> 0
char 22: 0 —> 1
char 23: 1 —> 0
char 66: 1 —> 0
char 75: 0 —> 1
char 111: 1 —> 0
Node 70:
(—> reversed character polarity:
= Node 71 in rerooted tree)
char 9: 1 —> 0
char 28: 0 —> 1
char 37: 1 —> 0
char 52: 1 —> 0
char 104: 0 —> 1
char 112: 0 —> 1
Node 71:
(—> reversed character polarity:
= Archstemata in rerooted tree)
char 2: 2 —> 1
char 3: 2 —> 0
char 6: 2 —> 0
char 34: 1 —> 0
char 57: 0 —> 1

List of characters:

Character (1)
node 0: 0
node 45: 0 —> 01
SCAPHIDI: 0 —> 1
SILPHIDA: 01 —> 1
HYDRAENI: 0 —> 1
HYDROPHI: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Histeridae, Agyrtidae
Character (2)
node 0: 2
node 71: 1
node 55: 1 —> 012
node 48: 1 —> 2
node 42: 1 —> 012
node 41: 1 —> 012
node 40: 012 —> 02
node 38: 02 —> 2
STAPHYLI: 1 —> 2
STENINAE: 1 —> 2
APATETIC: 1 —> 2
NEOPHONU: 012 —> 0
PROTEINI: 012 —> 2
EMPELIDA: 1 —> 2
PTILIIDA: 012 —> 2
HYDRAENI: 012 —> 0
SPHAERIT: 02 —> 0
HYDROPHI: 02 —> 0
TROGIDAE: 012 —> 2
EUCINETI: 1 —> 0
GYRINIDA: 1 —> 0
VARIATION WITHIN TERMINAL TAXA: Hydrophiloidea, Histeridae, Hydraenidae, Leiodidae, Scydmaenidae, Silphidae, Staphylinine group, Oxyteline group, Omaliinae, (Archostemata), (Derodontidae)

Character (3)
node 0: 2
node 71: 0
node 62: 0 —> 2
node 42: 0 —> 1
TACHYPOR: 2 —> 0
SCYDMAEN: 0 —> 2
MICROPEP: 2 —> 1
MICROSIL: 2 —> 0
HYDROPHI: 0 —> 1
DERODONT: 0 —> 2
VARIATION WITHIN TERMINAL TAXA: Hydrophiloidea, Hydraenidae, Ptiliidae, Leiodidae, Silphidae, Staphylinine group, Oxyteline group, Pseudopsinae, Tachyporine group

Character (4)
node 0: 1
node 56: 1 —> 0
node 44: 1 —> 0
PTILIIDA: 0 —> 1
DERODONT: 1 —> 0
VARIATION WITHIN TERMINAL TAXA: Hydraenidae, Agyrtidae, Leiodidae, Scydmaenidae, Proteininae

Character (5)
node 0: 1
node 56: 1 —> 01
node 55: 01 —> 0
node 49: 1 —> 01
node 47: 01 —> 0
LEPTOTYP: 01 —> 0

SOLIERIU: 01 —> 1
MICROSIL: 01 —> 1
OMALIINA: 01 —> 0
HYDRAENI: 1 —> 0
DERODONT: 1 —> 0
VARIATION WITHIN TERMINAL TAXA: Hydrophiloidea, Hydraenidae, Scydmaenidae, Oxyteline group, Omaliinae

Character (6)
node 0: 2
node 71: 0
node 42: 0 —> 012
node 38: 0 —> 1
SCAPHIDI: 0 —> 1
NEOPHONU: 0 —> 1
PTILIIDA: 012 —> 2
HYDRAENI: 012 —> 1
VARIATION WITHIN TERMINAL TAXA: Hydrophiloidea, Scydmaenidae, Silphidae, Staphylinine group, Leptotyphlinae, Oxyteline group, Pselaphinae

Character (7)
node 0: 1
node 69: 1 —> 0
node 48: 0 —> 1
SCYDMAEN: 0 —> 1
PTILIIDA: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Leiodidae

Character (8)
node 0: 0
node 71: 01
node 70: 01 —> 1
node 67: 1 —> 0
node 47: 0 —> 01
node 42: 0 —> 1
PSELAPHI: 01 —> 0
DASYCERU: 01 —> 1
MICROPEP: 01 —> 1
PROTEINI: 0 —> 1
HYDROPHI: 0 —> 1
TRACHYPA: 01 —> 0
GYRINIDA: 01 —> 1
VARIATION WITHIN TERMINAL TAXA: Histeridae, Leiodidae, Stenine group, Tachyporine group

Character (9)
node 0: 1
node 70: 1 —> 0
STAPHYLI: 0 —> 1
SCYDMAEN: 0 —> 1
SILPHIDA: 0 —> 1
PSELAPHI: 0 —> 1
MICROSIL: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Histeridae, Agyrtidae, Leiodidae, Pseudopsinae, Tachyporine group

Character (10)
node 0: 1
HYDRAENI: 1 —> 0
MICROSPO: 1 —> 0
VARIATION WITHIN TERMINAL TAXA: Hydrophiloidea, Leptotyphlinae

Character (11)
node 0: ?
node 71: 1
node 67: 1 —> 0
PSEUDOPS: 0 —> 1
PHLOEOCH: 0 —> 1
TACHYPOR: 0 —> 1
DASYCERU: 0 —> 1
NEOPHONU: 0 —> 1
MICROSIL: 0 —> 1
LEIODIDA: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Leiodidae, Scydmaenidae, Leptotyphlinae, Oxyteline group, Omaliinae, Tachyporine group

Character (12)
node 0: 0
node 49: 0 —> 01
node 47: 01 —> 0
LEPTOTYP: 01 —> 1
SCYDMAEN: 0 —> 1
SOLIERIU: 01 —> 1
MICROSIL: 0 —> 1
PTILIIDA: 0 —> 1
MICROSPO: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Hydraenidae, Leiodidae, Scydmaenidae, Silphidae, Leptotyphlinae, Stenine group, Oxyteline group, Omaliinae, Pselaphinae, Tachyporine group

Character (13)
node 0: 0
node 64: 0 —> 1
node 59: 1 —> 0
node 48: 1 —> 0
node 45: 1 —> 0
DASYCERU: 0 —> 1
MICROSIL: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Silphidae, Stenine group, Omaliinae, Tachyporine group

Character (14)
node 0: 0
node 66: 0 —> 01
node 63: 01 —> 1
node 59: 1 —> 01
node 56: 01 —> 0
node 52: 01 —> 1
node 51: 01 —> 0
node 43: 01 —> 1
LEPTOTYP: 1 —> 0
TRIGONUR: 01 —> 1
SCYDMAEN: 01 —> 1
SCAPHIDI: 01 —> 0
APATETIC: 1 —> 0
OXYTELIN: 01 —> 0
MICROPEP: 1 —> 0
AGYRTIDA: 01 —> 0
VARIATION WITHIN TERMINAL TAXA: Hydraenidae, Staphylinine group, Leptotyphlinae, Stenine group, Oxyteline group, Omaliinae

Character (15)
node 0: 0
HYDRAENI: 0 —> 1
HYDROPHI: 0 —> 1

Character (16)
node 0: 0
MICROPEP: 0 —> 2
HYDROPHI: 0 —> 2
TROGIDAE: 0 —> 1
GYRINIDA: 0 —> 2
VARIATION WITHIN TERMINAL TAXA: Hydrophiloidea, Histeridae, Hydraenidae, Ptiliidae, Pselaphinae, Tachyporine group, (Gyrinidae), (Trogidae/Scarabaeoidea)

Character (17)
node 0: 1
SILPHIDA: 1 —> 0
MICROSPO: 1 —> 0
VARIATION WITHIN TERMINAL TAXA: Histeridae, Leiodidae, Scydmaenidae, Scaphidiidae, Silphidae, Stenine group, Tachyporine group

Character (18)
node 0: 0
node 40: 0 —> 1
SILPHIDA: 0 —> 1
MICROSPO: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Silphidae

Character (19)
node 0: 0
node 42: 0 —> 024
node 41: 0 —> 3
STENINAE: 0 —> 2
SCAPHIDI: 0 —> 4
SILPHIDA: 0 —> 3
DASYCERU: 0 —> 2
MICROPEP: 0 —> 1
MICROSIL: 0 —> 2
EMPELIDA: 0 —> 2
PTILIIDA: 024 —> 2
HYDRAENI: 024 —> 4
DERODONT: 0 —> 2
GYRINIDA: 0 —> 5
MICROSPO: 0 —> 2
VARIATION WITHIN TERMINAL TAXA: Hydraenidae, Leiodidae, Scydmaenidae, Scaphidiidae, Leptotyphlinae, Stenine group, Oxyteline group, Pselaphinae, (Derodontidae)

Character (20)
node 0: 0
LEIODIDA: 0 —> 2
AGYRTIDA: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Agyrtidae, Leiodidae, Scydmaenidae

Character (21)
node 0: 0
node 51: 0 —> 1
LEPTOTYP: 0 —> 1
PSELAPHI: 0 —> 1
NEOPHONU: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Leiodidae, Scydmaenidae, Staphylinine group, Oxyteline group, Tachyporine group

Character (22)
node 0: 0
node 69: 0 —> 1
node 66: 1 —> 0

Character (23)
node 0: 1
node 69: 1 —> 0
VARIATION WITHIN TERMINAL TAXA: Leptotyphlinae

Character (24)
node 0: 0
node 65: 0 —> 01
node 63: 01 —> 0

node 49: 0 —> 1
node 38: 0 —> 1
node 37: 0 —> 1
STENINAE: 0 —> 1
SCYDMAEN: 01 —> 1
SCAPHIDI: 01 —> 1
MICROPEP: 1 —> 0
PTILIIDA: 0 —> 1
TROGIDAE: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Hydrophiloidea, Leiodidae, Scaphidiidae, Leptotyphlinae, Oxyteline group, Pseudopsinae

Character (25)
node 0: 0
node 68: 0 —> 1
node 65: 1 —> 0
node 59: 0 —> 1
STAPHYLI: 1 —> 0
PHLOEOCH: 0 —> 1
APATETIC: 0 —> 1
DASYCERU: 0 —> 1
SYNTELII: 1 —> 2
TROGIDAE: 1 —> 2
VARIATION WITHIN TERMINAL TAXA: Hydrophiloidea, Hydraenidae, Leiodidae, Scydmaenidae, Scaphidiidae, Silphidae, Staphylinine group, Stenine group, Oxyteline group, Omaliinae, Proteininae, Pselaphinae, Tachyporine group

Character (26)
node 0: 1
node 46: 1 —> 0
SYNTELII: 1 —> 2
TROGIDAE: 1 —> 2
TRACHYPA: 1 —> 2
VARIATION WITHIN TERMINAL TAXA: Hydrophiloidea, Hydraenidae, Ptilliidae, Leiodidae, Scydmaenidae, Staphylinine group, Oxyteline group, Tachyporine group, (Archostemata)

Character (27)
node 0: 0
node 66: 0 —> 01
node 63: 01 —> 0
node 43: 01 —> 1
SCYDMAEN: 01 —> 1
SCAPHIDI: 01 —> 1
AGYRTIDA: 01 —> 0
HISTERID: 0 —> 1
HYDROPHI: 0 —> 1
GYRINIDA: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Leiodidae, Staphylinine group

Character (28)
node 0: 0
node 70: 0 —> 1
node 67: 1 —> 0
node 64: 0 —> 1
node 51: 1 —> 0
node 48: 1 —> 01
node 46: 01 —> 0
node 38: 0 —> 01
SOLIERIU: 01 —> 0
MICROPEP: 01 —> 1
HISTERID: 01 —> 1
VARIATION WITHIN TERMINAL TAXA: Agyrtidae, Staphylinine group

Character (29)
node 0: 0
node 58: 0 —> 1
node 45: 0 —> 2
PSEUDOPS: 0 —> 2
NEOPHONU: 1 —> 0
MICROPEP: 0 —> 1
EMPELIDA: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Proteininae, Tachyporine group

Character (30)
node 0: 0
HYDROPHI: 0 —> 1
EUCINETI: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Hydrophiloidea, Scydmaenidae

Character (31)
node 0: 0
node 51: 0 —> 1
node 42: 0 —> 1
NEOPHONU: 0 —> 1
MICROPEP: 0 —> 1
MICROSPO: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Hydraenidae, Leiodidae, Oxyteline group, Pselaphinae, Tachyporine group

Character (32)
node 0: 0
SOLIERIU: 0 —> 1
PTILIIDA: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Leiodidae, Pselaphinae

Character (33)
node 0: 0
node 49: 0 —> 1
node 42: 0 —> 1
node 41: 0 —> 01
node 37: 0 —> 1
STENINAE: 0 —> 1
HISTERID: 01 —> 1
SYNTELII: 01 —> 0
SPHAERIT: 01 —> 0
HYDROPHI: 01 —> 1
TROGIDAE: 01 —> 1
EUCINETI: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Scydmaenidae, Oxyteline group

Character (34)
node 0: 1
node 71: 0
SCYDMAEN: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Staphylinine group, Tachyporine group

Character (35)
node 0: 0
node 46: 0 —> 1
SCYDMAEN: 0 —> 1
EMPELIDA: 0 —> 1
MICROSPO: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Histeridae, Leiodidae, Scydmaenidae, Oxyteline group, Pselaphinae

Character (36)
node 0: 0
HYDRAENI: 0 —> 1
HYDROPHI: 0 —> 1

Character (37)
node 0: 1
node 70: 1 —> 0
node 67: 0 —> 1
PHLOEOCH: 1 —> 0
SCAPHIDI: 1 —> 0
PSELAPHI: 1 —> 0
NEOPHONU: 1 —> 0
HISTERID: 1 —> 0
VARIATION WITHIN TERMINAL TAXA: Scydmaenidae

Character (38)
node 0: 0
node 49: 0 —> 01
node 47: 01 —> 0
STAPHYLI: 0 —> 1
LEPTOTYP: 01 —> 1
OXYPORIN: 0 —> 1
TACHYPOR: 0 —> 1
SOLIERIU: 01 —> 1
VARIATION WITHIN TERMINAL TAXA: Staphylinine group, Stenine group, Oxyteline group, Tachyporine group

Character (39)
node 0: 0
node 39: 0 —> 1

Character (40)
node 0: 0
node 65: 0 —> 1
node 42: 0 —> 2
SILPHIDA: 1 —> 2
EUCINETI: 0 —> 1
GYRINIDA: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Agyrtidae, Leiodidae, Scydmaenidae

Character (41)
node 0: 0
node 64: 0 —> 1
node 62: 1 —> 2
DASYCERU: 2 —> 0
HISTERID: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Dasycerinae

Character (42)
node 0: 0
node 64: 0 —> 1
node 47: 1 —> 0
PROTEINI: 1 —> 0
VARIATION WITHIN TERMINAL TAXA: Tachyporine group

Character (43)
node 0: 0
node 64: 0 —> 1
PROTEINI: 1 —> 0
VARIATION WITHIN TERMINAL TAXA: Leiodidae, Oxyteline group, Tachyporine group

Character (44)
node 0: 0
node 55: 0 —> 2
node 47: 0 —> 2

node 40: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Scydmaenidae, (Trogidae/Scarabaeoidea)

Character (45)
node 0: 0
node 65: 0 —> 2
node 63: 2 —> 1
DASYCERU: 1 —> 0
VARIATION WITHIN TERMINAL TAXA: Scydmaenidae

Character (46)
node 0: 0
node 65: 0 —> 2
node 61: 2 —> 5
node 57: 5 —> 4
node 54: 4 —> 3
node 39: 0 —> 1
EMPELIDA: 2 —> 3
HISTERID: 1 —> 3
VARIATION WITHIN TERMINAL TAXA: Scydmaenidae, Silphidae, Omaliinae, Proteininae, Tachyporine group

Character (47)
node 0: 0
node 65: 0 —> 0134
node 63: 0134 —> 4
node 38: 0 —> 034
SCYDMAEN: 0134 —> 1
SCAPHIDI: 0134 —> 3
SILPHIDA: 4 —> 3
DASYCERU: 4 —> 2
HISTERID: 034 —> 3
SYNTELII: 034 —> 4
VARIATION WITHIN TERMINAL TAXA: Ptiliidae, Scydmaenidae, Silphidae, Dasycerinae

Character (48)
node 0: 0
node 56: 0 —> 1
node 46: 0 —> 1
EMPELIDA: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Pselaphinae

Character (49)
node 0: 0
SILPHIDA: 0 —> 1
TRACHYPA: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Oxyteline group

Character (50)
node 0: 1
node 65: 1 —> 12
node 63: 12 —> 1
OXYPORIN: 1 —> 2
SCYDMAEN: 12 —> 2
SCAPHIDI: 12 —> 2
SILPHIDA: 1 —> 2
MICROPEP: 1 —> 2
PROTEINI: 1 —> 2
MICROSIL: 1 —> 2
HISTERID: 1 —> 2
GYRINIDA: 1 —> 2
VARIATION WITHIN TERMINAL TAXA: Ptiliidae, Staphylinine group, Stenine group, Oxyteline group, Pselaphinae, Pseudopsinae, Tachyporine group

Character (51)
node 0: 1
node 71: 01
node 70: 01 —> 0
node 65: 0 —> 1
node 58: 1 —> 01
node 56: 01 —> 1
node 48: 1 —> 01
node 46: 01 —> 0
node 39: 0 —> 1
TRIGONUR: 01 —> 0
OXYTELIN: 01 —> 0
SOLIERIU: 01 —> 0
MICROPEP: 01 —> 1
TRACHYPA: 01 —> 0
GYRINIDA: 01 —> 1
VARIATION WITHIN TERMINAL TAXA: Hydrophiloidea, Hydraenidae, Ptiliidae, Oxyteline group, Pselaphinae

Character (52)
node 0: 1
node 70: 1 —> 0
node 62: 0 —> 1
node 48: 1 —> 0
VARIATION WITHIN TERMINAL TAXA: Scydmaenidae, Oxyteline group

Character (53)
node 0: 1
node 65: 1 —> 2
node 38: 1 —> 0
SILPHIDA: 2 —> 1
DASYCERU: 2 —> 1

VARIATION WITHIN TERMINAL TAXA: Staphylinine group, Stenine group, Oxyteline group, Pseudopsinae, Tachyporine group

Character (54)
node 0: 0
node 70: 0 —> 01
node 68: 01 —> 0
node 65: 0 —> 1
PTILIIDA: 0 —> 1
HISTERID: 0 —> 1
EUCINETI: 01 —> 1
MICROSPO: 01 —> 1

Character (55)
node 0: 0
node 55: 0 —> 1
node 47: 0 —> 1
STENINAE: 0 —> 1
DERODONT: 0 —> 1
MICROSPO: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Oxyteline group, Pselaphinae

Character (56)
node 0: 0
PTILIIDA: 0 —> 1
MICROSPO: 0 —> 1

Character (57)
node 0: 0
node 71: 1
node 38: 1 —> 0
PHLOEOCH: 1 —> 0
MICROPEP: 1 —> 0
PTILIIDA: 1 —> 0
VARIATION WITHIN TERMINAL TAXA: Oxyteline group, (Archostemata)

Character (58)
node 0: 0
node 44: 0 —> 01
node 42: 01 —> 0
EMPELIDA: 0 —> 1
LEIODIDA: 01 —> 1
AGYRTIDA: 01 —> 1
GYRINIDA: 0 —> 1
MICROSPO: 0 —> 1

Character (59)
node 0: 1
node 71: 01
node 69: 01 —> 0
node 59: 0 —> 1
node 37: 01 —> 0
LEPTOTYP: 0 —> 1
OXYPORIN: 1 —> 0
SCYDMAEN: 0 —> 1
NEOPHONU: 1 —> 0
MICROPEP: 0 —> 1
PTILIIDA: 0 —> 1
MICROSPO: 01 —> 1
VARIATION WITHIN TERMINAL TAXA: Tachyporine group

Character (60)
node 0: 1
node 67: 1 —> 0
PHLOEOCH: 0 —> 1
APATETIC: 0 —> 1
EMPELIDA: 0 —> 1
PTILIIDA: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Ptiliidae, Scydmaenidae, Silphidae, Tachyporinae group

Character (61)
node 0: 0
node 65: 0 —> 01
node 63: 01 —> 0
SCYDMAEN: 01 —> 1
SCAPHIDI: 01 —> 1
MICROPEP: 0 —> 1
HISTERID: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Hydrophiloidea, Hydraenidae, Ptiliidae, Leiodidae, Pselaphinae

Character (62)
node 0: 0
node 38: 0 —> 1
PSEUDOPS: 0 —> 1
STENINAE: 0 —> 1
TRIGONUR: 0 —> 1
SCAPHIDI: 0 —> 1
APATETIC: 0 —> 1
MICROPEP: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Ptiliidae, Leiodidae, Scydmaenidae

Character (63)
node 0: 0
node 49: 0 —> 01
node 47: 01 —> 1
LEPTOTYP: 01 —> 1
SOLIERIU: 01 —> 0
NEOPHONU: 0 —> 1

PTILIIDA: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Hydrophiloidea, Leiodidae, Oxyteline group, Omaliinae, Proteininae

Character (64)
node 0: 0
HISTERID: 0 —> 1
EUCINETI: 0 —> 1
GYRINIDA: 0 —> 2
VARIATION WITHIN TERMINAL TAXA: Hydrophiloidea, Scydmaenidae, Pselaphinae

Character (65)
node 0: 0
node 50: 0 —> 1
node 47: 1 —> 0
STAPHYLI: 0 —> 1
SCYDMAEN: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Ptiliidae, Scydmaenidae, Staphylinine group, Stenine group, Oxyteline group, Pselaphinae, Tachyporine group

Character (66)
node 0: 1
node 69: 1 —> 0
node 66: 0 —> 1
node 38: 0 —> 1
DASYCERU: 1 —> 2
NEOPHONU: 1 —> 2
EMPELIDA: 1 —> 0
HYDRAENI: 1 —> 0
TRACHYPA: 1 —> 0
VARIATION WITHIN TERMINAL TAXA: Leiodidae, Scydmaenidae, Silphidae, Pselaphinae

Character (67)
node 0: 0
node 65: 0 —> 1
node 62: 1 —> 12
node 61: 12 —> 2
node 54: 2 —> 1
node 39: 0 —> 1
SILPHIDA: 12 —> 2
APATETIC: 12 —> 1
DASYCERU: 2 —> 0
VARIATION WITHIN TERMINAL TAXA: Hydraenidae, Ptiliidae, Leiodidae, Scydmaenidae, Silphidae, Omaliinae, Proteininae

Character (68)
node 0: 1
node 68: 1 —> 0
VARIATION WITHIN TERMINAL TAXA: Histeridae

Character (69)
node 0: 0
node 62: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Ptiliidae

Character (70)
node 0: 0
node 65: 0 —> 01
node 63: 01 —> 1
node 39: 0 —> 1
SCYDMAEN: 01 —> 1
SCAPHIDI: 01 —> 0
VARIATION WITHIN TERMINAL TAXA: Silphidae

Character (71)
node 0: 0
node 66: 0 —> 012
node 65: 012 —> 2
node 44: 012 —> 1

Character (72)
node 0: 0
node 50: 0 —> 1
node 43: 0 —> 1
SCYDMAEN: 0 —> 1
NEOPHONU: 0 —> 1
MICROSPO: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Hydrophiloidea, Scaphidiidae

Character (73)
node 0: 0
node 66: 0 —> 1

Character (74)
node 0: 0
node 66: 0 —> 3
node 53: 3 —> 0
node 45: 3 —> 1
node 39: 0 —> 1
STENINAE: 0 —> 2
SCAPHIDI: 3 —> 2
OXYTELIN: 3 —> 2
PROTEINI: 3 —> 2
OMALIINA: 3 —> 2
AGYRTIDA: 3 —> 2
PTILIIDA: 3 —> 4
DERODONT: 0 —> 1
MICROSPO: 0 —> 2
VARIATION WITHIN TERMINAL TAXA: Hydrophiloidea, Agyrtidae, Scydmaenidae, Scaphidiidae, Silphi-

dae, Staphylinine group, Oxyteline group, Proteininae, Tachyporine group

Character (75)
node 0: 0
node 69: 0 —> 1

Character (76)
node 0: 0
node 67: 0 —> 1
HYDROPHI: 1 —> 0
MICROSPO: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Hydrophiloidea

Character (77)
node 0: 0
node 59: 0 —> 2
node 44: 0 —> 2
node 40: 0 —> 1
OXYPORIN: 2 —> 0
PHLOEOCH: 0 —> 1
OXYTELIN: 2 —> 1
PROTEINI: 2 —> 0
SPHAERIT: 1 —> 2
EUCINETI: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Staphylinine group

Character (78)
node 0: 0
LEPTOTYP: 0 —> 1
PSELAPHI: 0 —> 1
MICROSIL: 0 —> 1
AGYRTIDA: 0 —> 1
HYDRAENI: 0 —> 1
SPHAERIT: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Agyrtidae, Staphylinine group, Leptotyphlinae, Pselaphinae, Pseudopsinae

Character (79)
node 0: 0
node 65: 0 —> 1
TRACHYPA: 0 —> 1

Character (80)
node 0: 0
node 65: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Silphidae

Character (81)
node 0: 0
node 66: 0 —> 2
node 56: 2 —> 12
node 55: 12 —> 1
node 37: 0 —> 2
PSEUDOPS: 2 —> 1
MICROPEP: 2 —> 1
MICROSIL: 12 —> 1
OMALIINA: 12 —> 2
AGYRTIDA: 2 —> 1
VARIATION WITHIN TERMINAL TAXA: Agyrtidae, Proteininae, Pseudopsinae

Character (82)
node 0: 0
node 65: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Ptiliidae, Silphidae

Character (83)
node 0: 0
AGYRTIDA: 0 —> 1
HISTERID: 0 —> 2
VARIATION WITHIN TERMINAL TAXA: Hydraenidae, Ptiliidae, Agyrtidae, Staphylinine group, Proteininae, Pselaphinae, Pseudopsinae

Character (84)
node 0: ?
node 71: 0
node 53: 0 —> 01
node 52: 01 —> 1
node 42: 0 —> 2
STENINAE: 01 —> 1
OXYPORIN: 01 —> 0
EUCINETI: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Staphylinine group

Character (85)
node 0: ?
node 71: 012
node 70: 012 —> 01
node 68: 01 —> 0
node 63: 0 —> 1
node 59: 1 —> 0
node 51: 0 —> 2
node 49: 1 —> 3
node 42: 0 —> 3
node 40: 0 —> 012
node 39: 012 —> 2
SILPHIDA: 1 —> 0
MICROPEP: 3 —> 0
OMALIINA: 0 —> 1

AGYRTIDA: 0 —> 1
HYDROPHI: 012 —> 1
EUCINETI: 01 —> 1
TRACHYPA: 012 —> 1
GYRINIDA: 012 —> 2
MICROSPO: 01 —> 0
VARIATION WITHIN TERMINAL TAXA: Leiodidae, Staphylinine group, Stenine group, Proteininae, Tachyporine group

Character (86)
node 0: ?
node 71: 02
node 70: 02 —> 0
node 49: 0 —> 2
node 42: 0 —> 2
node 39: 0 —> 1
node 37: 02 —> 2
STENINAE: 0 —> 2
SCYDMAEN: 0 —> 2
OXYTELIN: 0 —> 2
VARIATION WITHIN TERMINAL TAXA: Staphylinine group

Character (87)
node 0: ?
node 71: 0
node 57: 0 —> 01
node 56: 01 —> 1
GYRINIDA: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Staphylinine group, Proteininae, Tachyporine group

Character (88)
node 0: 0
node 42: 0 —> 1

Character (89)
node 0: ?
node 71: 0
HYDRAENI: 0 —> 1
HYDROPHI: 0 —> 2

Character (90)
node 0: 0
node 49: 0 —> 01
node 42: 0 —> 1
PSELAPHI: 01 —> 0
DASYCERU: 01 —> 1
MICROPEP: 01 —> 1
TROGIDAE: 0 —> 1
MICROSPO: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Oxyteline group

Character (91)
node 0: 0
node 71: 01
node 62: 01 —> 0
HYDRAENI: 01 —> 1
HISTERID: 01 —> 0
HYDROPHI: 01 —> 1
TROGIDAE: 01 —> 0
DERODONT: 01 —> 1
TRACHYPA: 01 —> 1

Character (92)
node 0: 0
node 40: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Hydrophiloidea

Character (93)
node 0: 0
node 71: 01
node 66: 01 —> 1
node 40: 01 —> 1
node 37: 01 —> 1
HYDRAENI: 1 —> 0
TROGIDAE: 01 —> 0
DERODONT: 01 —> 0
EUCINETI: 01 —> 1
MICROSPO: 01 —> 0
VARIATION WITHIN TERMINAL TAXA: Scaphidiidae

Character (94)
node 0: 1
node 71: 01
node 66: 01 —> 0
node 38: 01 —> 0
node 37: 01 —> 0
MICROPEP: 0 —> 1
SPHAERIT: 01 —> 1
HYDROPHI: 01 —> 1
TROGIDAE: 01 —> 0
DERODONT: 01 —> 1
EUCINETI: 01 —> 0
MICROSPO: 01 —> 1
VARIATION WITHIN TERMINAL TAXA: Hydrophiloidea, Leiodidae

Character (95)
node 0: ?
node 71: 0
node 44: 0 —> 01

LEIODIDA: 01 —> 1
AGYRTIDA: 01 —> 1
HYDRAENI: 01 —> 0
VARIATION WITHIN TERMINAL TAXA: Leiodidae

Character (96)
node 0: ?
node 71: 0
node 50: 0 —> 016
node 49: 016 —> 06
node 46: 06 —> 046
node 43: 0 —> 1
node 39: 0 —> 6
LEPTOTYP: 06 —> 6
PHLOEOCH: 016 —> 1
SCYDMAEN: 0 —> 3
SCAPHIDI: 0 —> 1
PSELAPHI: 046 —> 4
DASYCERU: 046 —> 0
MICROPEP: 06 —> 6
PTILIIDA: 1 —> 5
HISTERID: 6 —> 5
TROGIDAE: 0 —> 5
EUCINETI: 0 —> 1
MICROSPO: 0 —> 2
VARIATION WITHIN TERMINAL TAXA: Histeridae, Ptiliidae, Leiodidae, Scydmaenidae, Scaphidiidae, Silphidae, Staphylinine group, Oxyteline group, Omaliinae, Proteininae, Pselaphinae, Phloeocharinae, Tachyporine group, (Trogidae)

Character (97)
node 0: 0
node 71: 01
node 69: 01 —> 0
node 53: 0 —> 1
node 40: 0 —> 1
node 37: 01 —> 1
LEPTOTYP: 0 —> 1
SCYDMAEN: 0 —> 1
PSELAPHI: 0 —> 1
MICROSPO: 01 —> 1
VARIATION WITHIN TERMINAL TAXA: Stenine group, Oxyteline group, Tachyporine group

Character (98)
node 0: ?
node 71: 1
node 44: 1 —> 0
TROGIDAE: 1 —> 0

Character (99)
node 0: 0
node 65: 0 —> 1
node 40: 0 —> 1
node 37: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Leiodidae, Oxyteline group, Omaliinae, Tachyporine group

Character (100)
node 0: 1
node 69: 1 —> 01
node 65: 01 —> 1
node 55: 1 —> 01
node 44: 01 —> 0
node 41: 01 —> 1
PROTEINI: 01 —> 0
DERODONT: 01 —> 0
EUCINETI: 01 —> 0
VARIATION WITHIN TERMINAL TAXA: Leiodidae, Oxyteline group, Omaliinae, (Derodontidae)

Character (101)
node 0: 3
node 40: 3 —> 1
AGYRTIDA: 3 —> 0
HYDRAENI: 3 —> 2
DERODONT: 3 —> 1

Character (102)
node 0: 0
node 38: 0 —> 1

Character (103)
node 0: 0
node 40: 0 —> 1
TRACHYPA: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Hydrophiloidea, Leiodidae

Character (104)
node 0: 0
node 70: 0 —> 1
node 65: 1 —> 2
node 52: 2 —> 3
node 45: 2 —> 12
node 40: 1 —> 4
SILPHIDA: 12 —> 1
MICROPEP: 2 —> 0
VARIATION WITHIN TERMINAL TAXA: Leiodidae, (Derodontidae)

Character (105)
node 0: 0
node 44: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Hydraenidae, Leiodidae

Character (106)
node 0: 0
node 41: 0 —> 1
GYRINIDA: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Scydmaenidae, Staphylinine group, Pselaphinae

Character (107)
node 0: 0
node 40: 0 —> 1

Character (108)
node 0: 0
node 42: 0 —> 1

Character (109)
node 0: 0
node 41: 0 —> 01
node 39: 01 —> 1
node 37: 0 —> 1
SCYDMAEN: 0 —> 1
PSELAPHI: 0 —> 1
HYDROPHI: 01 —> 0
TROGIDAE: 01 —> 1
VARIATION WITHIN TERMINAL TAXA: Hydrophiloidea, Omaliinae, Tachyporine group

Character (110)
node 0: 0
node 39: 0 —> 01
node 38: 01 —> 1

Character (111)
node 0: ?
node 71: 1
node 69: 1 —> 0
node 40: 0 —> 1
STENINAE: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Stenine group, Pselaphinae

Character (112)
node 0: 0
node 70: 0 —> 1

Character (113)
node 0: 0
node 58: 0 —> 02
node 39: 0 —> 01
OXYTELIN: 02 —> 2
HISTERID: 01 —> 1
TROGIDAE: 0 —> 2

Character (114)
node 0: 1
node 71: 01
node 70: 01 —> 0
node 41: 0 —> 1
PTILIIDA: 0 —> 1
TRACHYPA: 01 —> 0
GYRINIDA: 01 —> 1
VARIATION WITHIN TERMINAL TAXA: Leiodidae, Scydmaenidae, Scaphidiidae, Dasycerinae, Pselaphinae

Character (115)
node 0: 0
node 41: 0 —> 013
node 40: 013 —> 1
TROGIDAE: 013 —> 3
DERODONT: 0 —> 2
VARIATION WITHIN TERMINAL TAXA: Hydrophiloidea, Agyrtidae, Leiodidae, (Trogidae)

Character (116)
node 0: 0
node 66: 0 —> 2
node 54: 2 —> 12
node 49: 2 —> 1
node 40: 0 —> 034
node 39: 034 —> 4
SCYDMAEN: 2 —> 1
OMALIINA: 12 —> 1
PTILIIDA: 2 —> 1
HISTERID: 4 —> 2
HYDROPHI: 034 —> 3
DERODONT: 0 —> 1
TRACHYPA: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Hydrophiloidea, Histeridae, Ptiliidae, Leiodidae, Scydmaenidae, Scaphidiidae, Silphidae, Staphylinine group, Oxyteline group, Omaliinae, Proteininae, Pselaphinae, Tachyporine group, (Derodontidae)

Character (117)
node 0: ?
node 71: 1
node 67: 1 —> 0
node 49: 0 —> 01
node 47: 01 —> 1
SCYDMAEN: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Hydrophiloidea, Leiodidae

Character (118)
node 0: 0

node 70: 0 —> 034
node 67: 034 —> 03
node 66: 03 —> 3
node 60: 3 —> 0
node 42: 3 —> 1
node 40: 03 —> 0
DASYCERU: 3 —> 0
TROGIDAE: 03 —> 3
GYRINIDA: 0 —> 2
MICROSPO: 034 —> 4
VARIATION WITHIN TERMINAL TAXA: Ptiliidae, Leiodidae, Scydmaenidae, Silphidae, Pselaphinae

Character (119)
node 0: 0
HYDRAENI: 0 —> 1
HYDROPHI: 0 —> 1
GYRINIDA: 0 —> 1
MICROSPO: 0 —> 1
VARIATION WITHIN TERMINAL TAXA: Hydrophiloidea, Hydraenidae

Character statistics:
(NS = number of states, NC = number of changes (steps), CI = consistency index, RI = retention index, RC = rescaled consistency index (= "weight"))

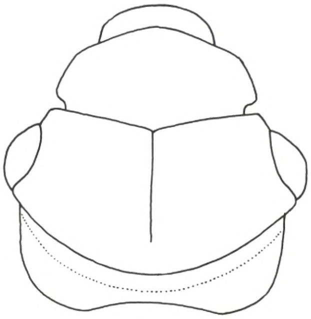
Char.	NS	NC	CI	RI	RC
1	2	4	0.250	0.000	0.000
2	3	15	0.133	0.278	0.037
3	3	9	0.222	0.562	0.125
4	2	4	0.250	0.571	0.143
5	2	6	0.167	0.375	0.062
6	3	6	0.333	0.200	0.067
7	2	4	0.250	0.667	0.167
8	2	8	0.125	0.222	0.028
9	2	6	0.167	0.286	0.048
10	2	2	0.500	0.000	0.000
11	2	8	0.125	0.300	0.038
12	2	6	0.167	0.000	0.000
13	2	6	0.167	0.167	0.028
14	2	9	0.111	0.385	0.043
15	2	2	0.500	0.000	0.000
16	3	4	0.500	0.000	0.000
17	2	2	0.500	0.000	0.000
18	2	3	0.333	0.600	0.200
19	6	13	0.385	0.333	0.128
20	3	2	1.000	0/0	0/0
21	2	4	0.250	0.250	0.062
22	2	2	0.500	0.833	0.417
23	2	1	1.000	1.000	1.000
24	2	9	0.111	0.333	0.037
25	3	9	0.222	0.533	0.119
26	3	4	0.500	0.333	0.167
27	2	6	0.167	0.286	0.048
28	2	7	0.143	0.600	0.086
29	3	6	0.333	0.429	0.143
30	2	2	0.500	0.000	0.000
31	2	5	0.200	0.333	0.067
32	2	2	0.500	0.000	0.000
33	2	8	0.125	0.462	0.058
34	2	2	0.500	0.000	0.000
35	2	4	0.250	0.250	0.062
36	2	2	0.500	0.000	0.000
37	2	7	0.143	0.143	0.020
38	2	5	0.200	0.000	0.000
39	2	1	1.000	1.000	1.000
40	3	5	0.400	0.750	0.300
41	3	4	0.500	0.882	0.441
42	2	3	0.333	0.875	0.292
43	2	2	0.500	0.938	0.469
44	3	3	0.667	0.857	0.571
45	3	3	0.667	0.938	0.625
46	6	7	0.714	0.900	0.643
47	5	7	0.571	0.786	0.449
48	2	3	0.333	0.667	0.222
49	2	2	0.500	0.000	0.000
50	2	9	0.111	0.000	0.000
51	2	8	0.125	0.500	0.062
52	2	3	0.333	0.882	0.294
53	3	4	0.500	0.867	0.433
54	2	5	0.200	0.600	0.120
55	2	5	0.200	0.429	0.086
56	2	2	0.500	0.000	0.000
57	2	5	0.200	0.200	0.040
58	2	5	0.200	0.000	0.000
59	2	9	0.111	0.385	0.043
60	2	5	0.200	0.556	0.111
61	2	4	0.250	0.000	0.000
62	2	7	0.143	0.143	0.020
63	2	4	0.250	0.400	0.100
64	3	3	0.667	0.000	0.000

65	2	4	0.250	0.250	0.062
66	3	8	0.250	0.250	0.062
67	3	6	0.333	0.800	0.267
68	2	1	1.000	1.000	1.000
69	2	1	1.000	1.000	1.000
70	2	3	0.333	0.833	0.278
71	3	2	1.000	1.000	1.000
72	2	5	0.200	0.500	0.100
73	2	1	1.000	1.000	1.000
74	5	13	0.308	0.500	0.154
75	2	1	1.000	1.000	1.000
76	2	3	0.333	0.600	0.200
77	3	9	0.222	0.417	0.093
78	2	6	0.167	0.000	0.000
79	2	2	0.500	0.909	0.455
80	2	1	1.000	1.000	1.000
81	3	7	0.286	0.583	0.167
82	2	1	1.000	1.000	1.000
83	3	2	1.000	0/0	0/0
84	3	4	0.500	0.500	0.250
85	4	14	0.214	0.267	0.057
86	3	7	0.286	0.545	0.156
87	2	2	0.500	0.750	0.375
88	2	1	1.000	1.000	1.000
89	3	2	1.000	0/0	0/0
90	2	5	0.200	0.200	0.040
91	2	4	0.250	0.000	0.000
92	2	1	1.000	1.000	1.000
93	2	5	0.200	0.000	0.000
94	2	6	0.167	0.000	0.000
95	2	2	0.500	0.000	0.000
96	7	13	0.462	0.222	0.103
97	2	7	0.143	0.538	0.077
98	2	2	0.500	0.500	0.250
99	2	3	0.333	0.750	0.250
100	2	4	0.250	0.500	0.125
101	4	4	0.750	0.750	0.562
102	2	1	1.000	1.000	1.000
103	2	2	0.500	0.750	0.375
104	5	6	0.667	0.867	0.578
105	2	1	1.000	1.000	1.000
106	2	2	0.500	0.800	0.400
107	2	1	1.000	1.000	1.000
108	2	1	1.000	1.000	1.000
109	2	5	0.200	0.429	0.086
110	2	1	1.000	1.000	1.000
111	2	3	0.333	0.667	0.222
112	2	1	1.000	1.000	1.000
113	3	3	0.667	0.000	0.000
114	2	4	0.250	0.571	0.143
115	4	3	1.000	1.000	1.000
116	5	10	0.400	0.538	0.215
117	2	3	0.333	0.600	0.200
118	5	7	0.571	0.625	0.357
119	2	4	0.250	0.000	0.000

Plates

PLATE 1 (Details of adults)

Fig. 11. *Georissus crenulatus* (Georissidae), head, dorsal
Fig. 12. *Spercheus emarginatus* (Spercheidae), head, dorsal
Fig. 13. *Coelostoma orbiculare* (Hydrophilidae-Sphaeridiinae), head, dorsal
Fig. 14. *Laccobius minutus* (Hydrophilidae-Hydrophilinae), head, dorsal (cl = clypeus)
Fig. 15. *Abraeus globosus* (Histeridae-Abraeinae), head, dorsal
Fig. 16. *Saprinus semistriatus* (Histeridae-Saprininae), head, dorsal
Fig. 17. *Scydmaenus tarsatus* (Scydmaenidae-Scydmaeninae), head, dorsal
Fig. 18. *Olisthaerus substriatus* (Staphylinidae-Olisthaerinae), head, dorsal (cl = clypeus)
Fig. 19. *Aleochara curtula* (Staphylinidae-Aleocharinae), head, dorsal



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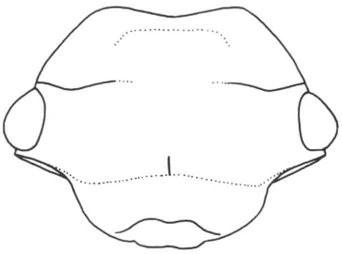

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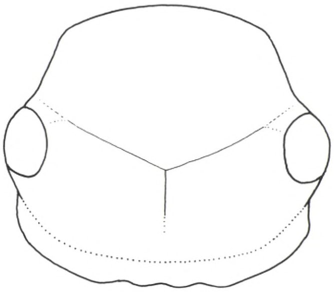

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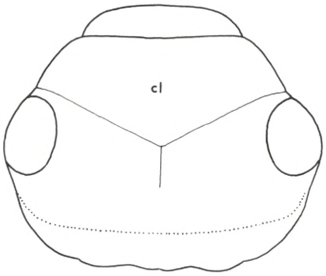

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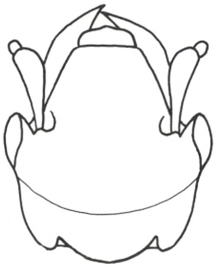

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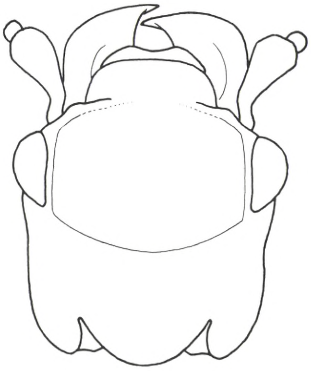

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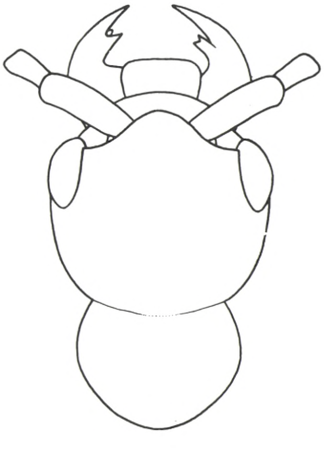

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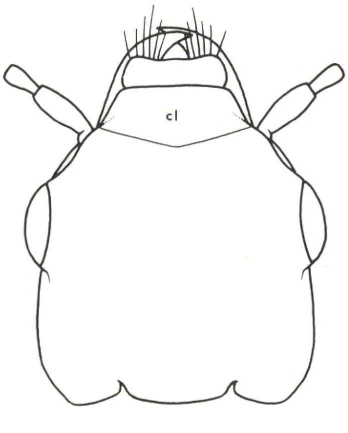

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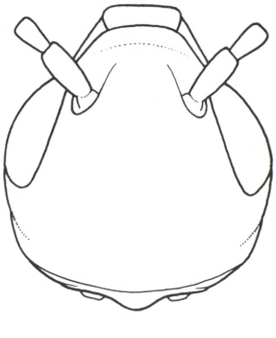

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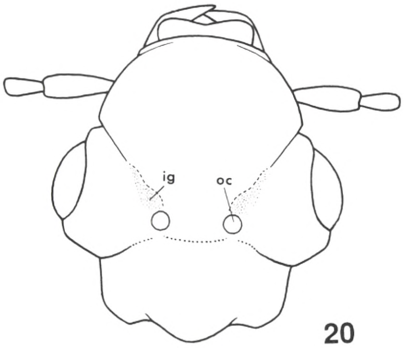
PLATE 2 (Details of adults)

Fig. 20. *Omalium rivulare* (Staphylinidae-Omaliinae), head, dorsal (ig = interocular groove, oc = ocellus)
Fig. 21. *Oxyporus rufus* (Staphylinidae-Oxyporinae), head, dorsal
Fig. 22. *Megalopinus punctatus* (Staphylinidae-Megalopsidiinae), head, dorsal (la = labrum)
Fig. 23. *Lathrobium brunnipes* (Staphylinidae-Paederinae), head, dorsal
Fig. 24. *Stenus juno* (Staphylinidae-Steninae), head, dorsal
Fig. 25. *Staphylinus dimidiaticornis* (Staphylinidae-Staphylininae), head, dorsal
Fig. 26. *Anisotoma humeralis* (Leiodidae-Leiodinae), head, ventral (mouthparts omitted) (cs = cervical sclerites, gs = gular suture, gu = gula)
Fig. 27. *Scaphidium quadrimaculatum* (Scaphidiidae), head, ventral (mouthparts omitted) (gs = fused gular sutures)
Fig. 28. *Eumetopus flavidulus* (Epimetopidae), head, dorso-lateral



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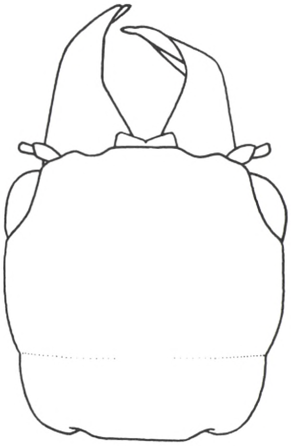

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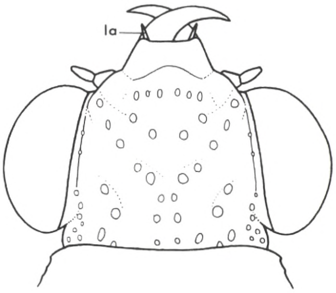

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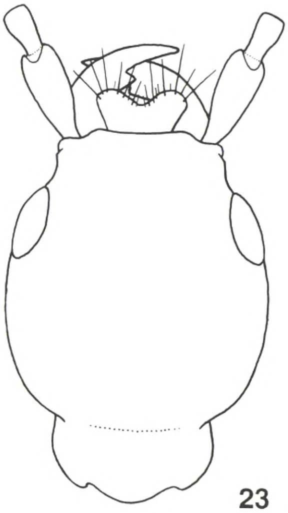

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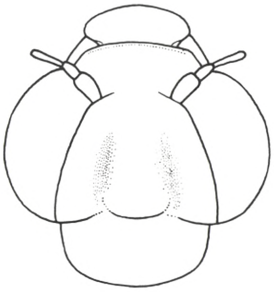

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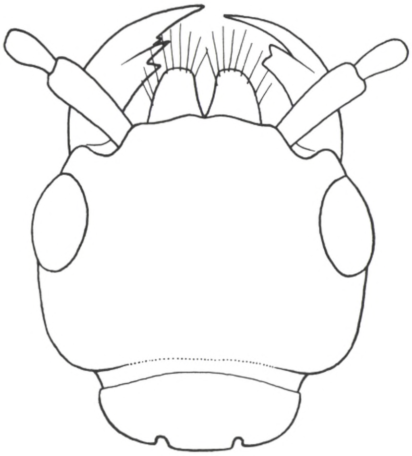

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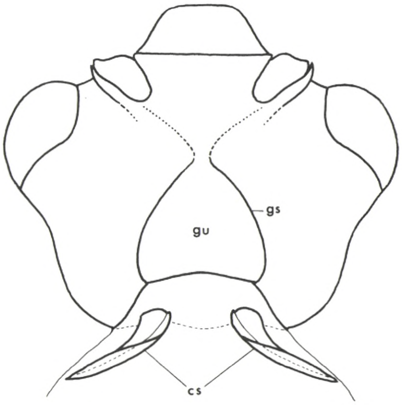

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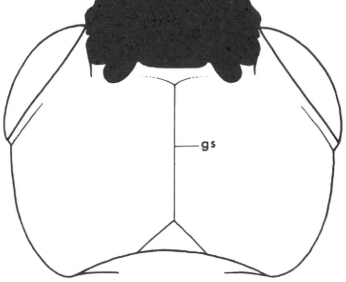

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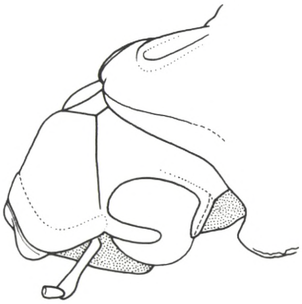

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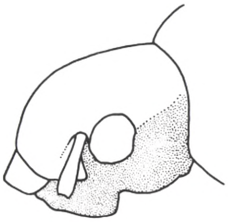
PLATE 3 (Details of adults)

Fig. 29. *Omicrus brevipes* (Hydrophilidae-Sphaeridiinae), head, lateral
Fig. 30. *Leptinus testaceus* (Leiodidae-Platypsyllinae), head, lateral (ca = posterior transverse carina)
Fig. 31. *Petasopsis brevitarsis* (Hydrophilidae-Sphaeridiinae), mandible
Fig. 32. *Saprinus semistriatus* (Histeridae-Saprininae), mandible
Fig. 33. *Euaesthetus bipunctatus* (Staphylinidae-Euaesthetinae), labrum
Fig. 34. *Hydraena riparia* (Hydraenidae-Hydraeninae), mandible (mo = mola, pr = prostheca)
Fig. 35. *Staphylinus dimidiaticornis* (Staphylinidae-Staphylininae), mandible
Fig. 36. *Xantholinus tricolor* (Staphylinidae-Staphylininae), mandible
Fig. 37. *Omalium rivulare* (Staphylinidae-Omaliinae), mandible (mo = mola)
Fig. 38. *Cercyon melanocephalus* (Hydrophilidae-Sphaeridiinae), ♂ maxilla (ga = galea, la = lacinia)
Fig. 39. *Saprinus semistriatus* (Histeridae-Saprininae), maxilla
Fig. 40. *Anisotoma humeralis* (Leiodidae-Leiodinae), maxilla (ga = galea, la = lacinia)
Fig. 41. *Triarthron maerkelii* (Leiodidae-Leiodinae), maxilla



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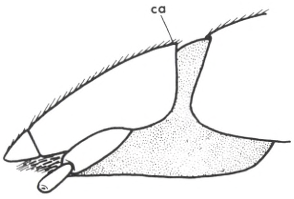

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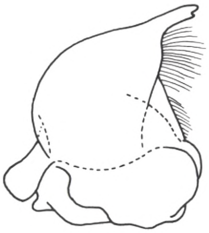

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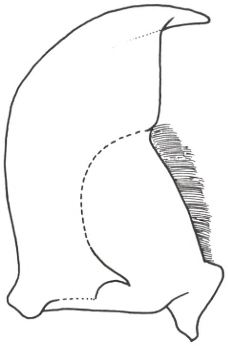

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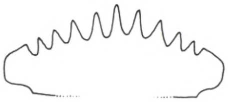

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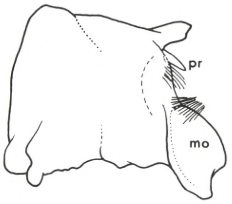

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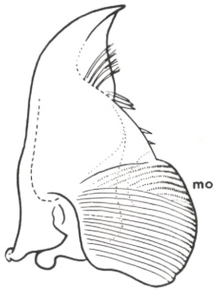

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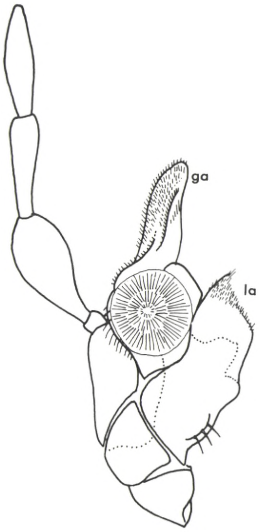

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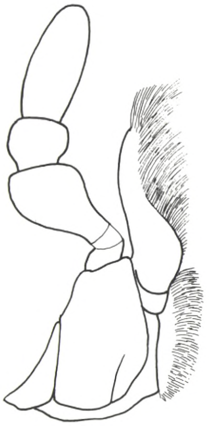

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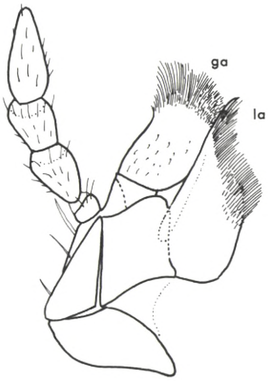

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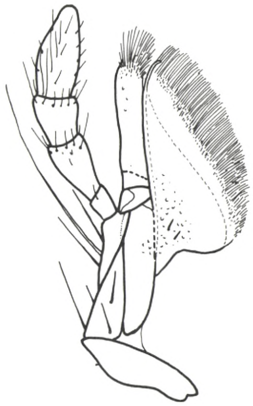

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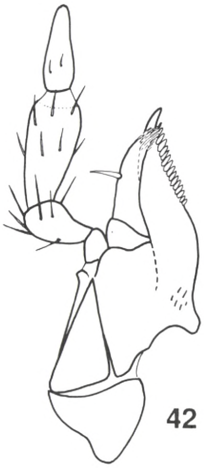
PLATE 4 (Details of adults)

Fig. 42. *Colon serripes* (Leiodidae-Coloninae), maxilla
Fig. 43. *Empelus brunnipennis* (Empelidae), maxilla
Fig. 44. *Aleochara curtula* (Staphylinidae-Aleocharinae), maxilla (ga = galea, la = lacinia)
Fig. 45. *Omalium rivulare* (Staphylinidae-Omaliinae), maxilla (ga = galea, la = lacinia)
Fig. 46. *Limnebius crinifer* (Hydraenidae-Hydraeninae), maxillary palpus
Fig. 47. *Hydraena reyi* (Hydraenidae-Hydraeninae), ♂ maxillary palpus
Fig. 48. *Ochthebius dilatatus* (Hydraenidae-Ochthebiinae), maxillary palpus
Fig. 49. *Neopelatops* sp. (Leiodidae-Camiarinae), maxillary palpus
Fig. 50. *Glacicavicola bathyscioides* (Leiodidae-Catopocerinae), maxillary palpus
Fig. 51. *Catops picipes* (Leiodidae-Cholevinae), maxillary palpus
Fig. 52. *Microsilpha* sp. (Staphylinidae-Microsilphinae), maxillary palpus
Fig. 53. *Elocomosta nigra* (Hydrophilidae-Sphaeridiinae), labium
Fig. 54. *Oxyporus rufus* (Staphylinidae-Oxyporinae), mentum
Fig. 55. *Empelus brunnipennis* (Empelidae), labial palpus
Fig. 56. *Coelostoma orbiculare* (Hydrophilidae-Sphaeridiinae), labial palpus
Fig. 57. *Limnoxenus niger* (Hydrophilidae-Hydrophilinae), labial palpus
Fig. 58. *Oxyporus rufus* (Staphylinidae-Oxyporinae), labial palpus



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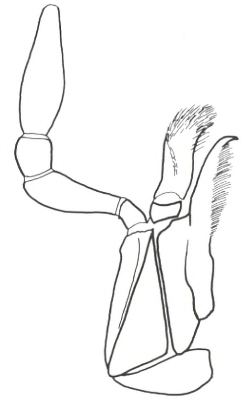

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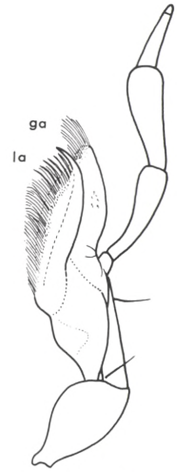

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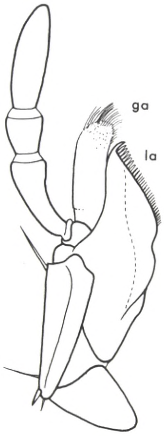

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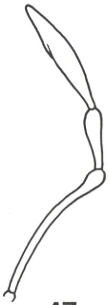

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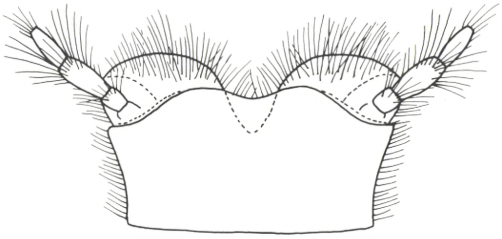

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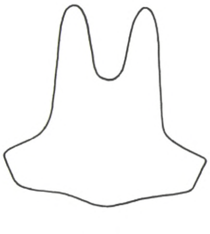

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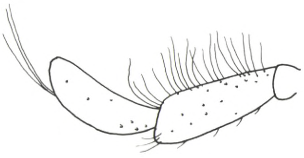

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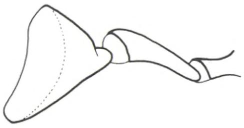

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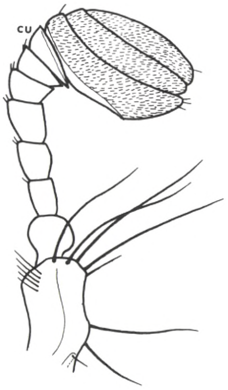
PLATE 5 (Details of adults)

Fig. 59. *Geotrupes stercorosus* (Geotrupidae), antenna (cu = cupule (8th segment))
Fig. 60. *Spercheus emarginatus* (Spercheidae), antenna
Fig. 61. *Sphaeridium scarabaeoides* (Hydrophilidae-Sphaeridiinae), antenna (cu = cupule (8th morphological segment)
Fig. 62. *Hydrochus brevis* (Hydrochidae), antenna
Fig. 63. *Helochares punctatus* (Hydrophilidae-Hydrophilinae), antenna
Fig. 64. *Sphaerites glabratus* (Sphaeritidae), antenna
Fig. 65. *Atholus bimaculatus* (Histeridae-Histerinae), antenna
Fig. 66. *Saprinus semistriatus* (Histeridae-Saprininae), antenna (cu = cupule (8th segment))
Fig. 67. *Chlamydopsis* sp. (Histeridae-Chlamydopsinae), antenna
Fig. 68. *Agyrtes castaneus* (Agyrtidae), antenna
Fig. 69. *Anisotoma humeralis* (Leiodidae-Leiodinae), antenna
Fig. 70. *Leiodes cinnamomea* (Leiodidae-Leiodinae), antenna
Fig. 71. *Catops picipes* (Leiodidae-Cholevinae), antenna
Fig. 72. *Agyrtes castaneus* (Agyrtidae), 10th antennal segment
Fig. 73. *Bathysciola silvestris* (Leiodidae-Cholevinae), 7th antennal segment (redrawn from Jeannel, 1911)



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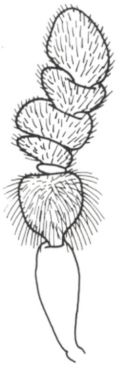

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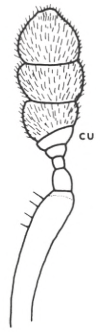

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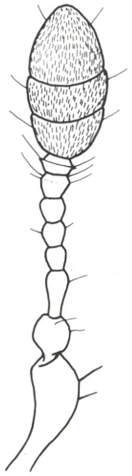

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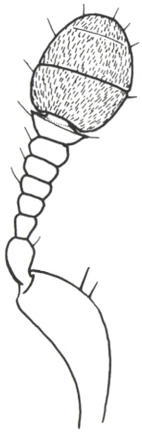

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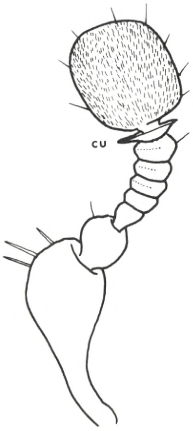

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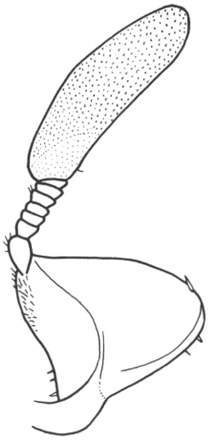

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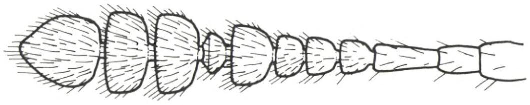

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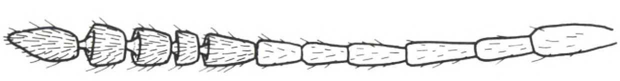

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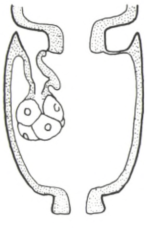

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PLATE 6 (Details of adults)

Fig. 74. *Colon serripes* (Leiodidae-Coloninae), antenna
Fig. 75. *Platypsyllus castoris* (Leiodidae-Platypsyllinae), antenna
Fig. 76. *Hydraenida ocellata* (Hydraenidae-Hydraeninae), antenna
Fig. 77. *Ochthebius minimus* (Hydraenidae-Ochthebiinae), antenna
Fig. 78. *Prosthetops megacephalus* (Hydraenidae-Prosthetopinae), antenna
Fig. 79. *Nossidium pilosellum* (Ptiliidae-Ptiliinae), antenna
Fig. 80. *Limulodes* sp. (Ptiliidae-Cephaloplectinae), antenna
Fig. 81. *Scydmaenus tarsatus* (Scydmaenidae-Scydmaeninae), antenna
Fig. 82. *Mastigus* sp. (Scydmaenidae-Mastiginae), antenna
Fig. 83. *Empelus brunnipennis* (Empelidae), antenna
Fig. 84. *Nicrophorus germanicus* (Silphidae-Nicrophorinae), antenna
Fig. 85. *Oiceoptoma thoracica* (Silphidae-Silphinae), antenna
Fig. 86. *Habrocerus capillaricornis* (Staphylinidae-Habrocerinae), antenna
Fig. 87. *Microsilpha* sp. (Staphylinidae-Microsilphinae), antenna
Fig. 88. *Oxyporus rufus* (Staphylinidae-Oxyporinae), antenna
Fig. 89. *Megalopinus punctatus* (Staphylinidae-Megalopsidiinae), antenna


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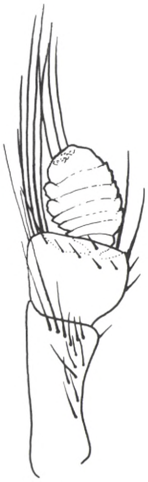
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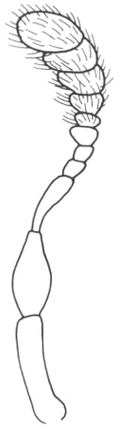
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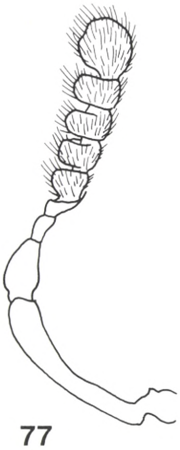
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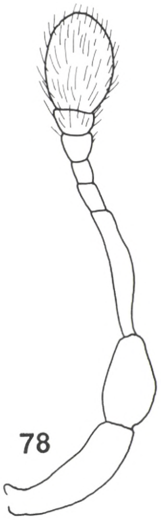
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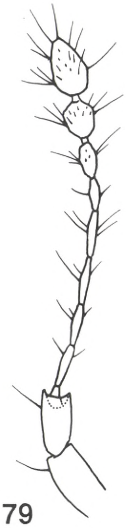
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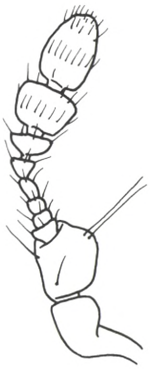
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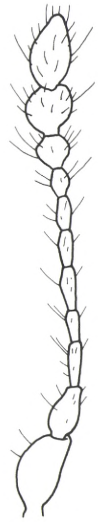
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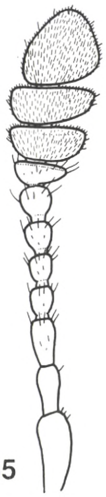
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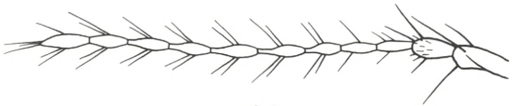
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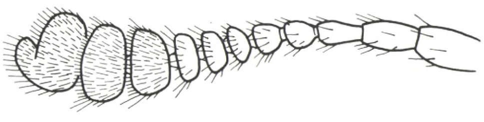
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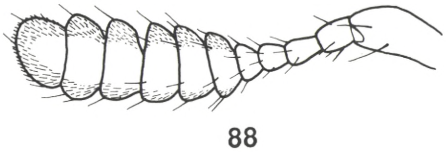
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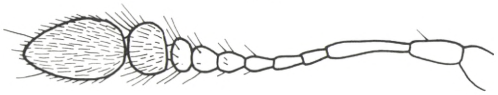
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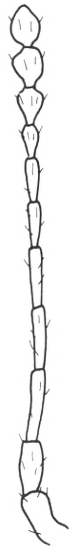
PLATE 7 (Details of adults)

Fig. 90. *Stenus* sp. (Staphylinidae-Steninae), antenna
Fig. 91. *Micropeplus* sp. (Staphylinidae-Micropeplinae), antenna
Fig. 92. *Claviger longicornis* (Staphylinidae-Pselaphinae), antenna
Fig. 93. *Hydrochus brevis* (Hydrochidae), prothorax, ventral (hp = hypomeral process)
Fig. 94. *Spercheus emarginatus* (Spercheidae), prothorax, ventral (r = ridge)
Fig. 95. *Georissus crenulatus* (Georissidae), prothorax, ventral
Fig. 96. *Cercyon melanocephalus* (Hydrophilidae-Sphaeridiinae), prothorax, ventral (apr = accessory posterior ridge)
Fig. 97. *Atholus bimaculatus* (Histeridae-Histerinae), prothorax, ventral (hp = hypomeral process)
Fig. 98. *Saprinus semistriatus* (Histeridae-Saprininae), prothorax, ventral (apr = accessory posterior ridge)



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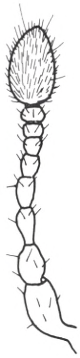

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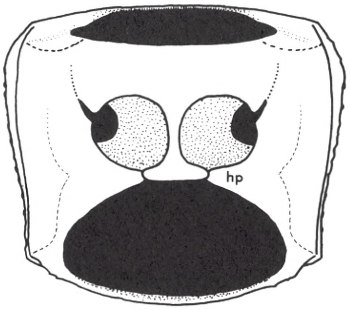

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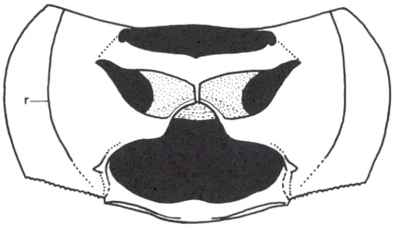

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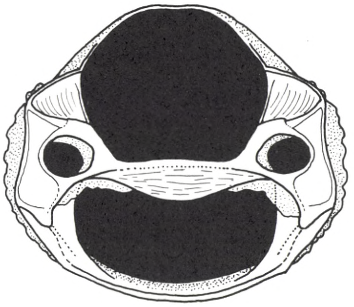

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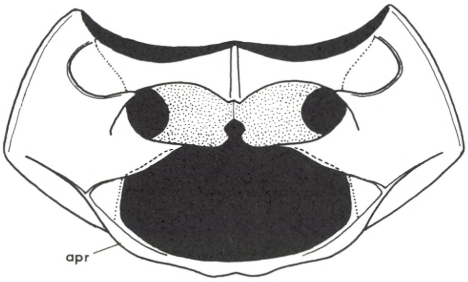

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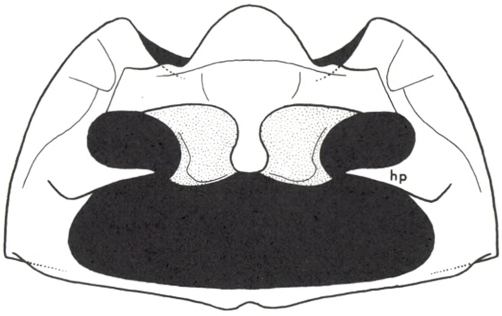

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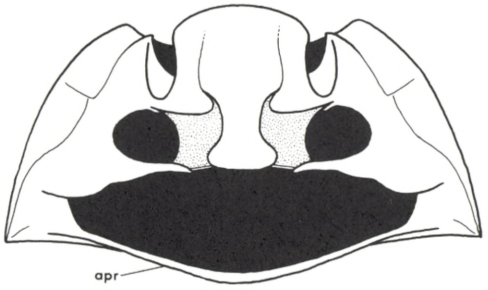

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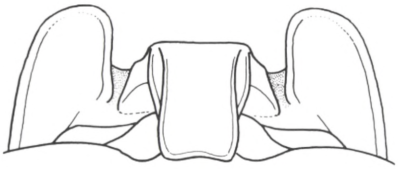
PLATE 8 (Details of adults)

Fig. 99. *Trypeticus indicus* (Histeridae-Trypeticinae), anterior portion of prothorax, ventral
Fig. 100. *Trypanaeus thoracicus* (Histeridae-Trypanaeinae), anterior portion of prothorax, ventral
Fig. 101. *Ochthebius dilatatus* (Hydraenidae-Ochthebiinae), prothorax, ventral (sm = semitransparent membrane)
Fig. 102. *Limnebius crinifer* (Hydraenidae-Hydraeninae), prothorax, ventral
Fig. 103. *Nossidium pilosellum* (Ptiliidae-Ptiliinae), prothorax, ventral
Fig. 104. *Limulodes* sp. (Ptiliidae-Cephaloplectinae), prothorax, ventral (hp = hypomeral process)
Fig. 105. *Agyrtes castaneus* (Agyrtidae), prothorax, ventral
Fig. 106. *Anisotoma humeralis* (Leiodidae-Leiodinae), prothorax, ventral
Fig. 107. *Catops picipes* (Leiodidae-Cholevinae), prothorax, ventral (hp = hypomeral process)
Fig. 108. *Leptinus testaceus* (Leiodidae-Platypsyllinae), prothorax, ventral



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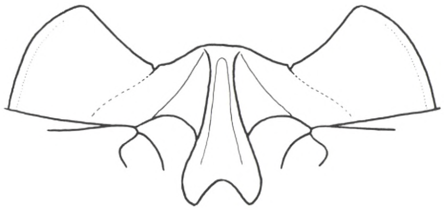

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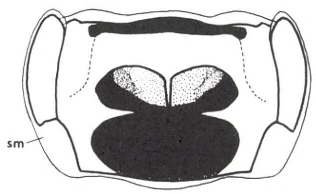

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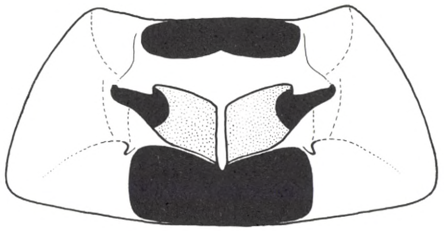

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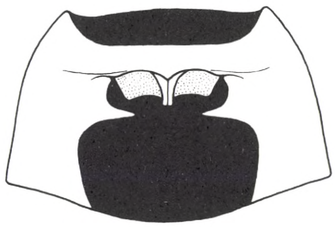

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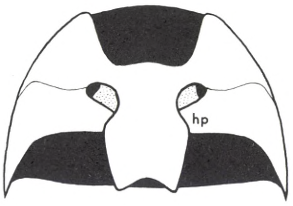

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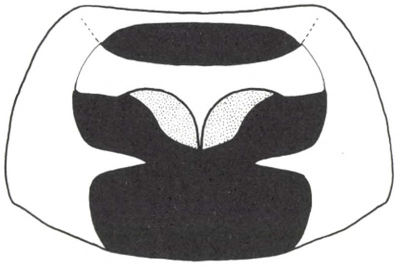

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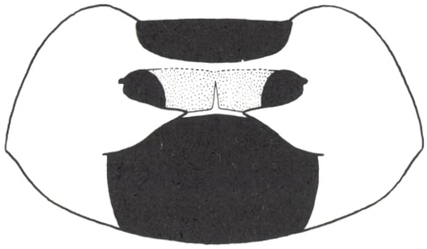

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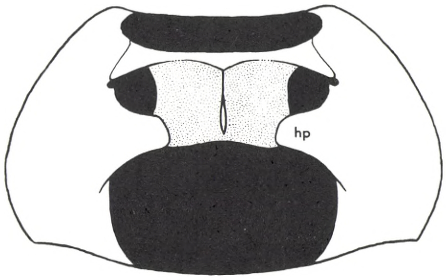

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PLATE 9 (Details of adults)

Fig. 109. *Thanatophilus sinuatus* (Silphidae-Silphinae), prothorax, ventral (sp = spiracle)

Fig. 110. *Nehemitropia lividipennis* (Staphylinidae-Aleocharinae), prothorax with one leg, ventral (tr = trochantin)

Fig. 111. *Piestus spinosus* (Staphylinidae-Piestinae), prothorax, ventral

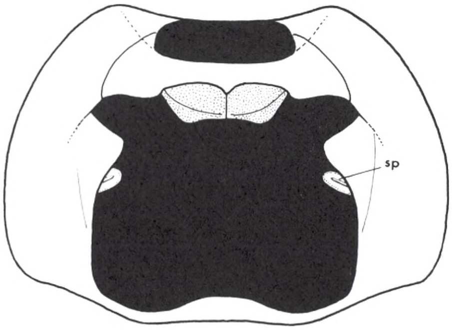
Fig. 112. *Micropeplus fulvus* (Staphylinidae-Micropeplinae), prothorax, ventral (ag = antennal groove)

Fig. 113. *Phacophallus parumpunctatus* (Staphylinidae-Staphylininae), prothorax, ventral (sp = spiracle)

Fig. 114. *Tachinus proximus* (Staphylinidae-Tachyporinae), prothorax, mesothorax and anterior portion of metathorax, ventral (cs = cervical sclerite, mep = mesepimeron, mes = mesepisternum, ms = mesosternum, pe = peritreme, ri = ridge delimiting mesocoxal cavity, sp = spiracle, tr = trochantins)

Fig. 115. *Omalium rivulare* (Staphylinidae-Omaliinae), 4th tergum and anterior portion of 5th tergum (im = intersegmental membrane, ps = patches of wing folding setae, pt = paratergite, sp = spiracle)

Fig. 116. *Aleochara curtula* (Staphylinidae-Aleocharinae), 3rd and anterior portion of 4th tergum (im = intersegmental membrane, pt = paratergites, sp = spiracle)



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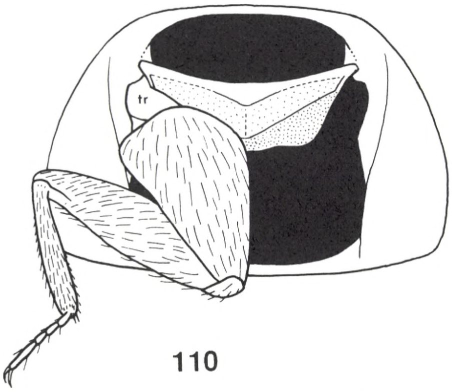

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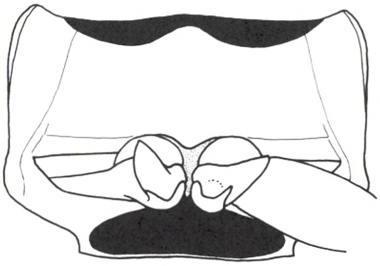

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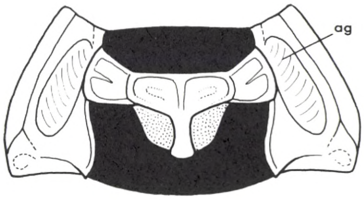

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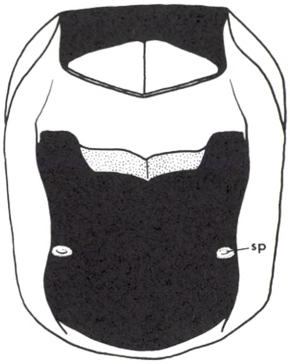

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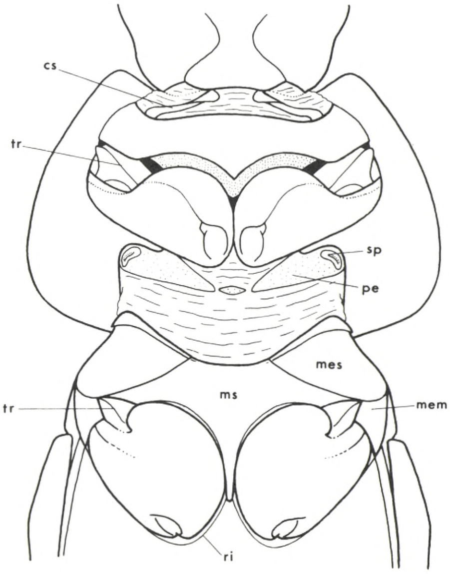

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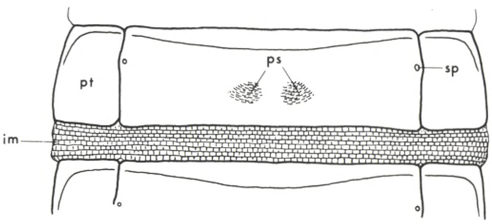

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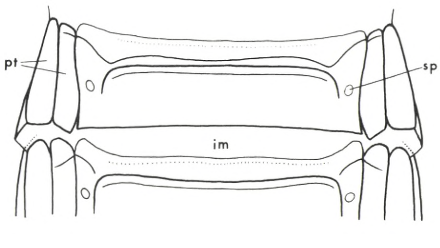

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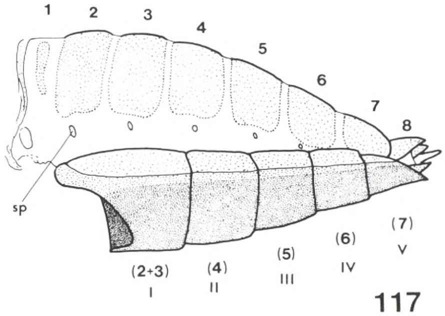
PLATE 10 (Details of adults)

Fig. 117. *Helophorus* sp. (Helophoridae), abdomen, lateral (1-8 = abdominal segments, I-V = visible ventrites, sp = spiracle)
Fig. 118. *Hydrochus ignicollis* (Hydrochidae), 7th sternite with apical, semitransparent lobe
Fig. 119. *Empelus brunnipennis* (Empelidae), 8th sternite
Fig. 120. *Omalium rivulare* (Staphylinidae-Omaliinae), 8th sternite (ap = apodeme, go = gland openings)
Fig. 121. *Dasycerus sulcicollis* (Staphylinidae-Dasycerinae), 8th sternite
Fig. 122. *Euplectus piceus* (Staphylinidae-Pselaphinae), 8th sternite
Fig. 123. *Nossidium pilosellum* (Ptiliidae-Ptiliinae), 4th and 5th terga (ps = patch of wing folding setae, sp = spiracle)
Fig. 124. *Ptenidium pusillum* (Ptiliidae-Ptiliinae), 4th and 5th terga
Fig. 125. *Helophorus grandis* (Helophoridae), basal ventrite (= sternum 2+3) (cc = coxal cavity, ip = intercoxal process)
Fig. 126. *Thanatophilus sinuatus* (Silphidae-Silphinae), basal ventrite (= sternum 2+3)
Fig. 127. *Ptomascopus plagiatus* (Silphidae-Nicrophorinae), 5th tergite (sf = stridulatory file)
Fig. 128. *Omalium rivulare* (Staphylinidae-Omaliinae), detail of abdominal intersegmental membrane, showing brickwall pattern of minute sclerites
Fig. 129. *Derops longicornis* (Staphylinidae-Tachyporinae), abdominal apex (segment 7ff), dorsal



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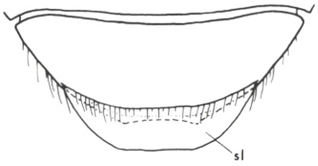

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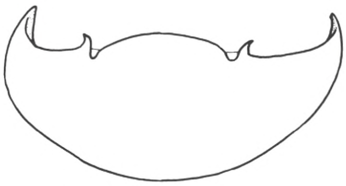

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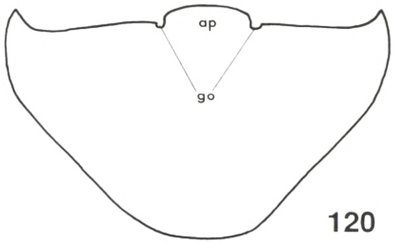

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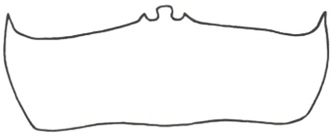

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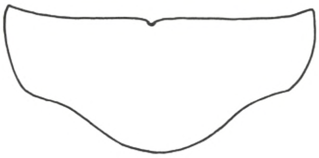

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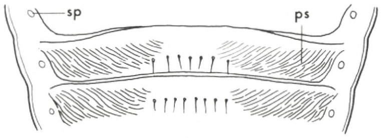

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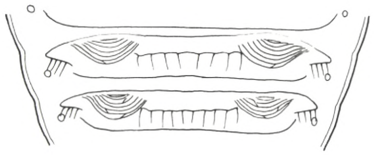

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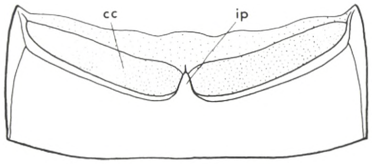

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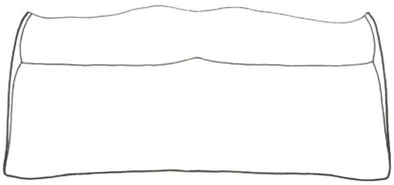

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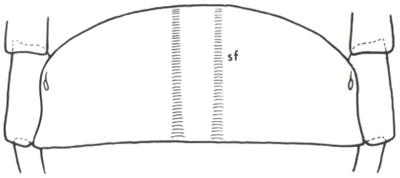

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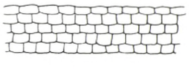

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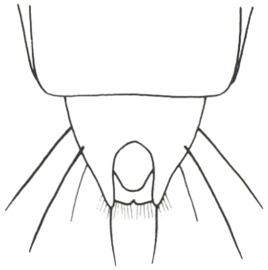

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PLATE 11 (Details of adults)

Fig. 130. *Nehemitropia lividipennis* (Staphylinidae-Aleocharinae), prothorax with anterior leg, lateral

Fig. 131. *Georissus crenulatus* (Georissidae), anterior leg, ventral (tr+cx = fused trochanter and coxa)

Fig. 132. *Tribalus scaphidiformis* (Histeridae-Tribalinae), anterior tibia and tarsus, dorsal

Fig. 133. *Dendrophilus punctatus* (Histeridae-Dendrophilinae), anterior tibia and tarsus, dorsal

Fig. 134. *Sternolophus* sp. (Hydrophilidae-Hydrophilinae), middle coxa, trochanter and femur, ventral

Fig. 135. *Mastigus palpalis* (Scydmaenidae-Mastiginae), middle coxa, trochanter and femur, ventral

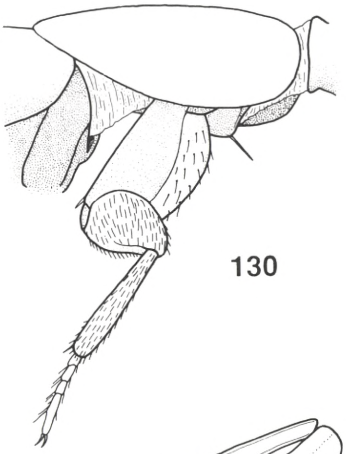
Fig. 136. *Acrotrichis* sp. (Ptiliidae-Acrotrichinae), posterior leg, ventral (cp = coxal plate)

Fig. 137. *Empelus brunnipennis* (Empelidae), posterior leg, ventral (cp = coxal plate)

Fig. 138. *Omalium rivulare* (Staphylinidae-Omaliinae), posterior coxa, trochanter and femur, ventral

Fig. 139. *Scydmaenus tarsatus* (Scydmaenidae), middle femur

Fig. 140. *Staphylinus dimidiaticornis* (Staphylinidae-Staphylininae), posterior coxa, trochanter and femur, ventral



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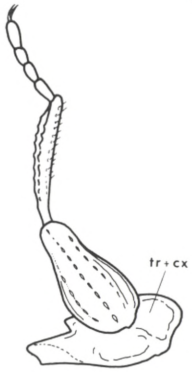

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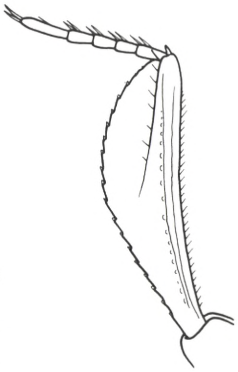

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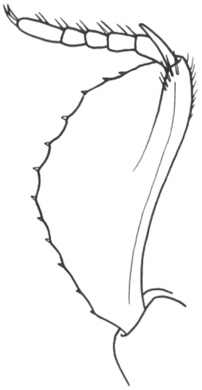

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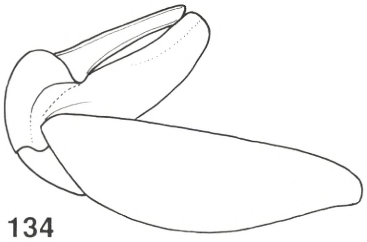

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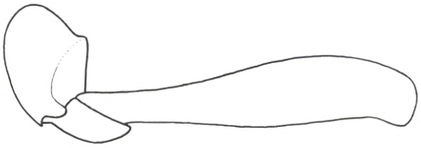

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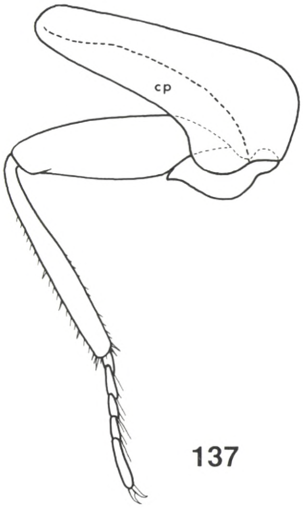

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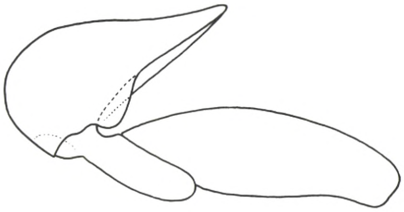

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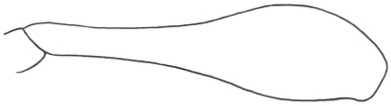

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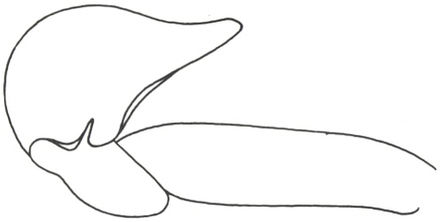

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PLATE 12 (Details of adults)

Fig. 141. *Aleochara curtula* (Staphylinidae-Aleocharinae), posterior coxa, trochanter and femur, ventral

Fig. 142. *Nossidium pilosellum* (Ptilidae-Ptiliinae), posterior tarsus

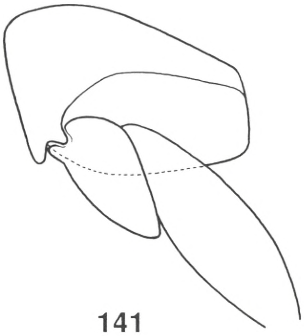
Fig. 143. *Syntelia histeroides* (Synteliidae), posterior tarsus

Fig. 144. *Atholus bimaculatus* (Histeridae-Histerinae), posterior tarsus

Fig. 145. *Systolosoma* sp. (Trachypachidae), hind wing (Veins: AA = Anal Anterior, AP = Anal Posterior, CuA = Cubitus Anterior, RA = Radius, Anterior, RP = Radius Posterior, MP = Media Posterior, cr = crossvein, ml = median loop, r4 = distal radial crossvein. – Cells: bc = basal cell, oc = oblongum cell, wc = wedge cell, Hinges: ah = anterior hinge, mh = medial hinge, rh = radial hinge. – Lobes and fields: al = anal lobe, mf = medial field) (nomenclature after Kukalová-Peck and Lawrence, 1993)

Fig. 146. *Enochrus fuscipennis* (Hydrophilidae-Hydrophilinae), hind wing (abbreviations as in fig. 145)

Fig. 147. *Sphaerites glabratus* (Sphaeritidae), hind wing (abbreviations as in fig. 145)



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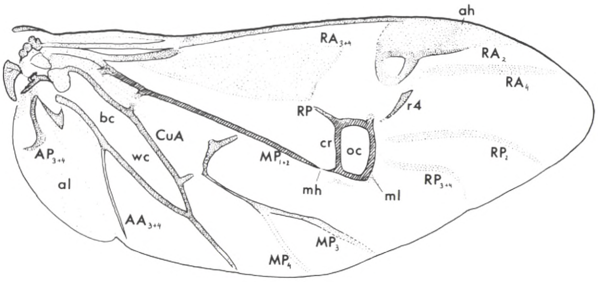

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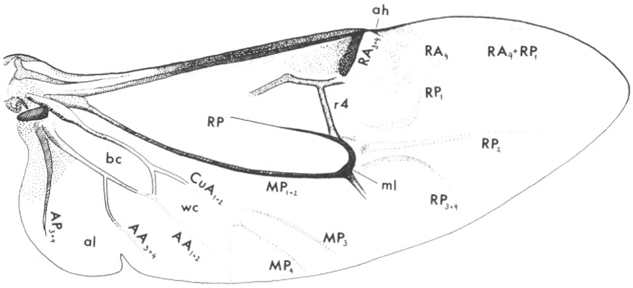

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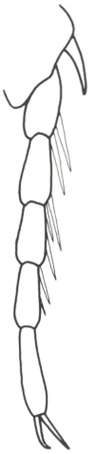

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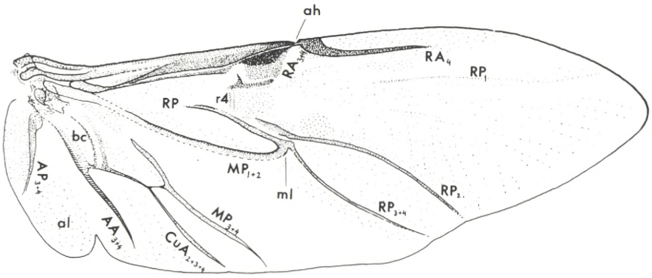

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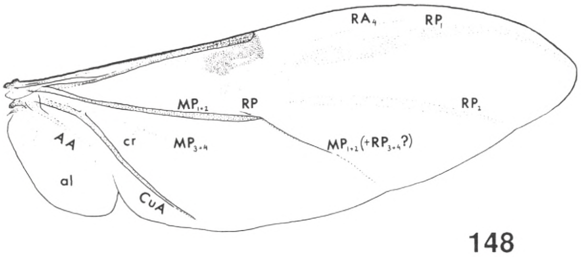
PLATE 13 (Details of adults)

Fig. 148. *Agyrtes castaneus* (Agyrtidae), hind wing (abbreviations as in fig. 145)
Fig. 149. *Nargus wilkinii* (Leiodidae-Cholevinae), hind wing (abbreviations as in fig. 145)
Fig. 150. *Hydraena riparia* (Hydraenidae-Hydraeninae), hind wing (abbreviations as in fig. 145)
Fig. 151. *Nephanes titan* (Ptiliidae-Acrotrichinae), hind wing
Fig. 152. *Ptenidium* sp. (Ptiliidae-Ptiliinae), detail of wing fringe setae
Fig. 153. *Thanatophilus sinuatus* (Silphidae-Silphinae), hind wing (abbreviations as in fig. 145)
Fig. 154. *Rhizophagus dispar* (Monotomidae-Rhizophaginae), left elytron, ventral (al = apico-lateral binding patch, as = apico-sutural binding patch, bl = baso-lateral binding patch, ml = medio-lateral binding patch)



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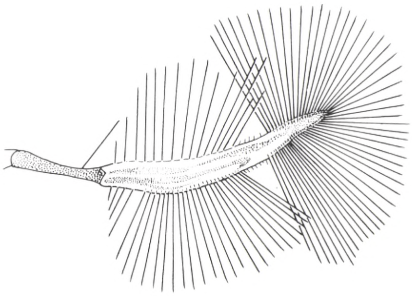

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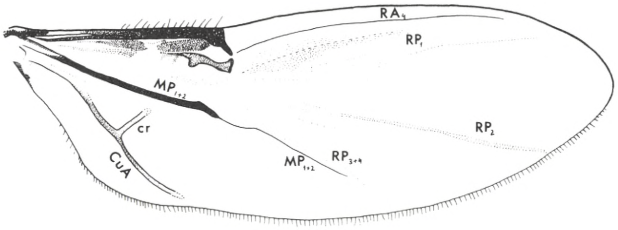

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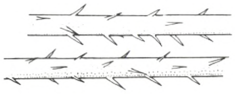

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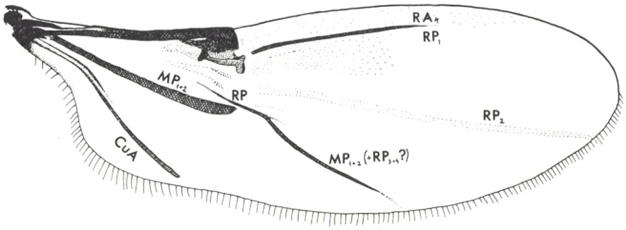

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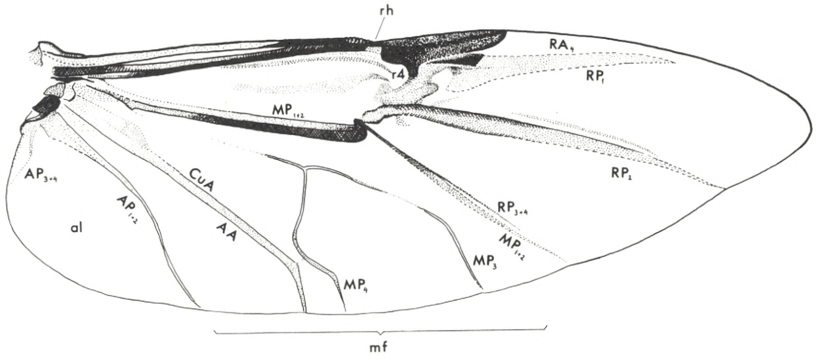

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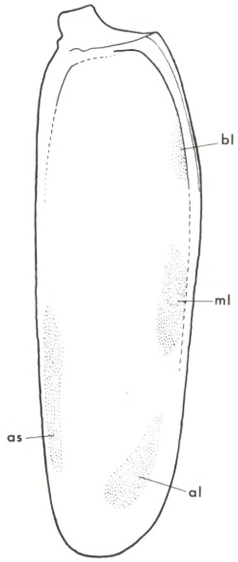

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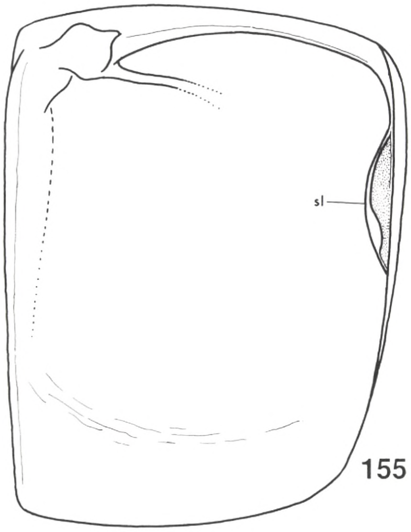
PLATE 14 (Details of adults)

Fig. 155. *Atholus bimaculatus* (Histeridae-Histerinae), left elytron, ventral (sl = sublateral lamina)
Fig. 156. *Oiceoptoma thoracica* (Silphidae-Silphinae), left elytron, dorsal
Fig. 157. *Trichonyx sulcicollis* (Staphylinidae-Pselaphinae), left elytron, dorsal
Fig. 158. *Hydrochus brevis* (Hydrochidae), ♂-genitalia, dorsal (bp = basal piece, ml = median lobe, pa = paramere)
Fig. 159. *Helochares punctatus* (Hydrophilidae-Hydrophilinae), ♂-genitalia, dorsal (bp = basal piece, ml = median lobe, pa = paramere)
Fig. 160. *Helophorus aquaticus* (Helophoridae), ♂-genitalia, dorsal (bp = basal piece, ml = median lobe, pa = paramere)
Fig. 161. *Hister unicolor* (Histeridae-Histerinae), ♂-genitalia, dorsal (bp = basal piece, mf = median foramen, ml = median lobe, pa = parameres)
Fig. 162. *Saprinus* sp. (Histeridae-Saprininae), ♂-genitalia, dorsal (bp = basal piece, ml = median lobe, pa = parameres)
Fig. 163. Same, lateral (bp = basal piece, pa = paramere)
Fig. 164. *Leiodes oblonga* (Leiodidae-Leiodinae), ♂-genitalia, dorsal (ml = median lobe, pa = paramere)
Fig. 165. *Hydnobius punctatus* (Leiodidae-Leiodinae), ♂-genitalia, dorsal (ml = median lobe, pa = paramere)
Fig. 166. *Hydraena riparia* (Hydraenidae-Hydraeninae), ♂-genitalia, lateral (is = everted internal sac, ml = median lobe, pa = paramere)
Fig. 167. *Ochthebius dilatatus* (Hydraenidae-Ochthebiinae), ♂-genitalia, lateral (is = everted internal sac, ml = median lobe, pa = parameres)
Fig. 168. *Hydraena gracilis* (Hydraenidae-Hydraeninae), ♂-genitalia, lateral (is = everted internal sac, ml = median lobe)



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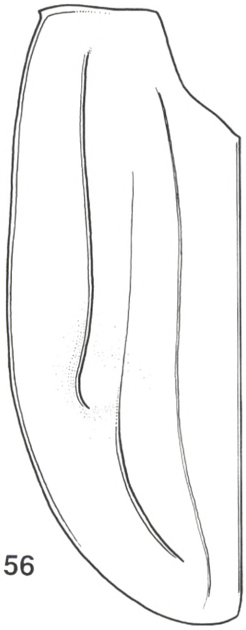

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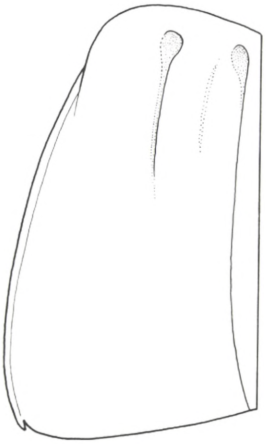

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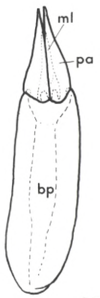

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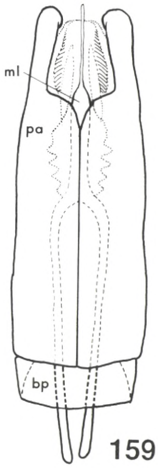

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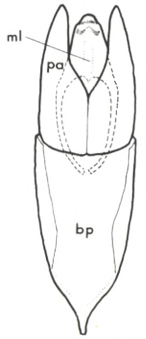

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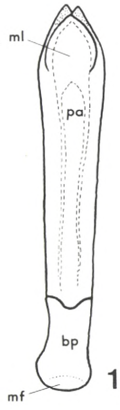

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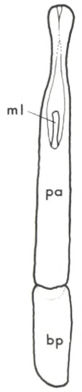

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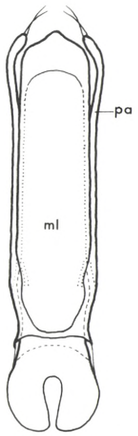

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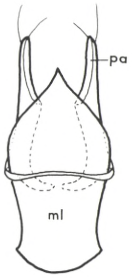

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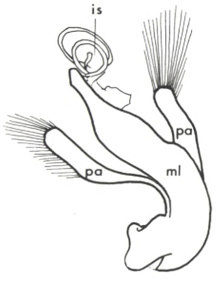

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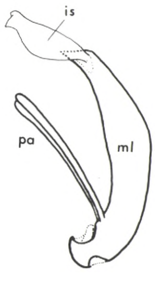

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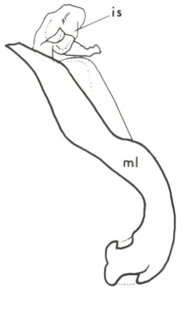

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PLATE 15 (Details of adults)

Fig. 169. *Stenus sculptilis* (Staphylinidae-Steninae), ♂-genitalia, dorsal (ml = median lobe, pa = paramere)

Fig. 170. *Philonthus aeneus* (Staphylinidae-Staphylininae), ♂-genitalia, lateral (ml = median lobe, pa = paramere)

Fig. 171. *Cypha longicornis* (Staphylinidae-Aleocharinae), ♂-genitalia, dorsal (ml = median lobe, pa = parameres)

Fig. 172. *Sphaerites glabratus* (Sphaeritidae), ♀, ovipositor, ventral (gc = gonocoxite, st = stylus, va = valvifer, s8 = sternum 8)

Fig. 173. Same, dorsal (gc = gonocoxite, t8 = tergum 8, t9 = tergum 9, t10 = tergum 10)

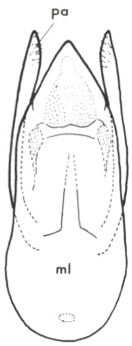
Fig. 174. *Ochthebius marinus* (Hydraenidae-Ochthebiinae), ♀ abdominal apex, dorsal (t9 = tergum 9, t10 = tergum 10)

Fig. 175. Same, ventral (gc = fused gonocoxites, va = valvifers)

Fig. 176. *Saprinus* sp. (Histeridae-Saprininae), ♀, gonocoxites, ventral (st = stylus)

Fig. 177. *Hydraena* sp. (Hydraenidae-Hydraeninae), ♀, fused gonocoxites, ventral

Fig. 178. *Hydrobius fuscipes* (Hydrophilidae-Hydrophilinae), ♀ genitalia (bu = bursa, gc = gonocoxite, sp = spermatheca, st = stylus, t9 = tergum 9, t10 = tergum 10)



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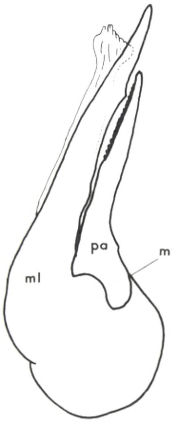

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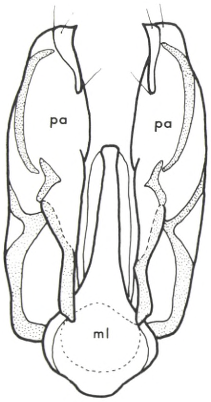

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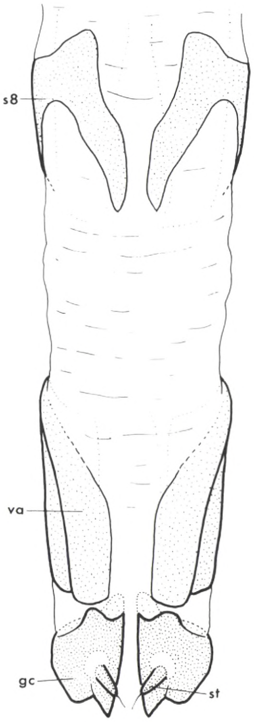

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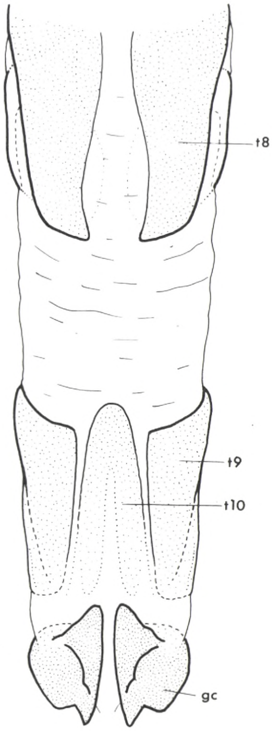

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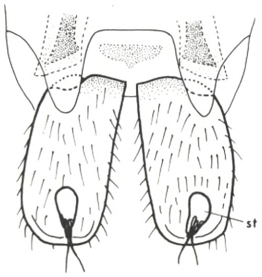

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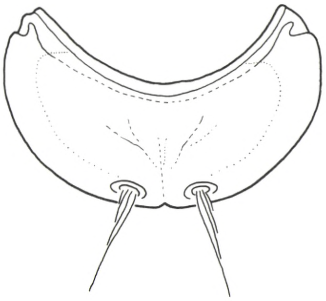

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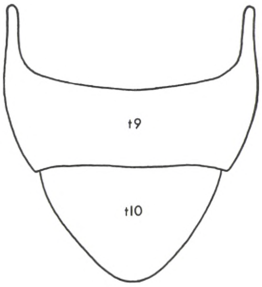

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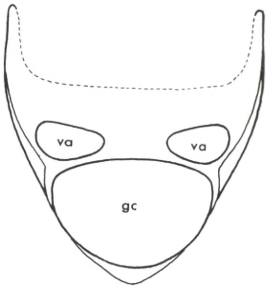

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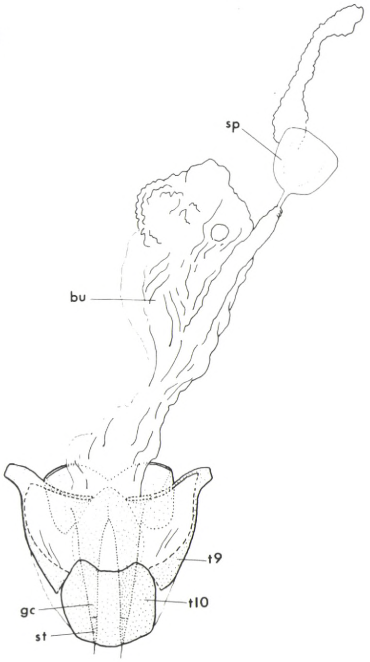

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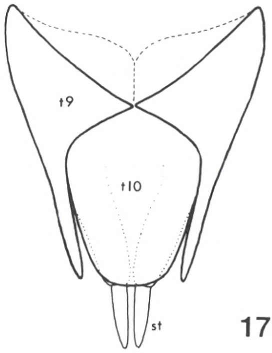
PLATE 16 (Details of adults; egg cases)

Fig. 179. *Gymnusa brevicollis* (Staphylinidae-Aleocharinae), ♀ abdominal apex, dorsal (st = stylus, t9 = tergum 9, t10 = tergum 10)
Fig. 180. Same, ventral (gc = gonocoxite, st = stylus, va = valvifer, t9 = ventral reflexed portion of tergum 9)
Fig. 181. *Omalium rivulare* (Staphylinidae-Omaliinae), ♀ abdominal apex, dorsal (gc = gonocoxite, t9 = tergum 9, t10 = tergum 10)
Fig. 182. Same, ventral (gc = gonocoxite, st = stylus, t9 = ventral reflexed portion of tergum 9)
Fig. 183. *Stenus juno* (Staphylinidae-Steninae), ♀ abdominal apex, dorsal (gc = gonocoxite, t9 = tergum 9, t10 = tergum 10)
Fig. 184. Same, ventral (gc = gonocoxite, va = valvifer, t9 = ventral reflexed portion of tergum 9)
Fig. 185. *Hydraena* sp. (Hydraenidae-Hydraeninae), spermatheca (cp = central portion, dp = distal portion, pp = proximal portion)
Fig. 186. *Ptenidium pusillum* (Ptiliidae-Ptiliinae), spermatheca
Fig. 187. *Acrotrichis intermedia* (Ptiliidae-Acrotrichinae), spermatheca
Fig. 188. *Aleochara curtula* (Staphylinidae-Aleocharinae), spermatheca
Fig. 189. *Atheta longicornis* (Staphylinidae-Aleocharinae), spermatheca
Fig. 190. *Atheta graminicola* (Staphylinidae-Aleocharinae), spermatheca
Fig. 191. *Helophorus* sp. (Helophoridae), egg case
Fig. 192. *Enochrus* sp. (Hydrophilidae-Hydrophilinae), egg case



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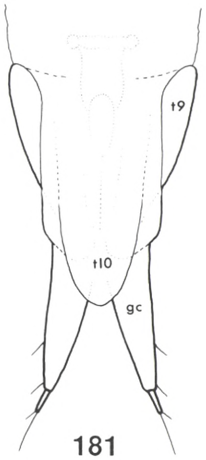

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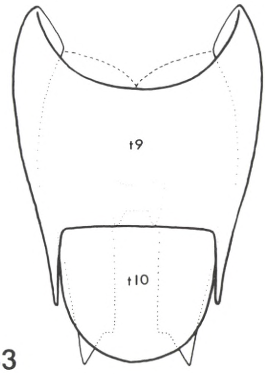

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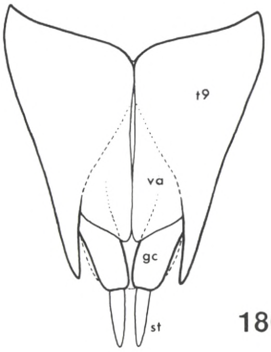

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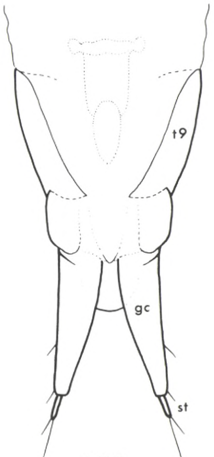

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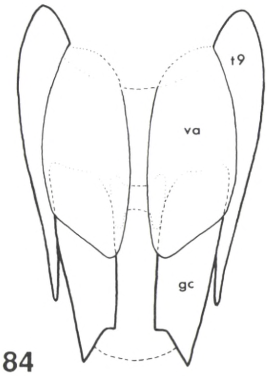

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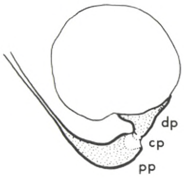

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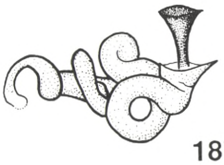

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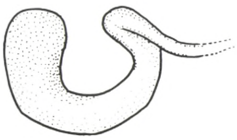

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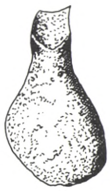

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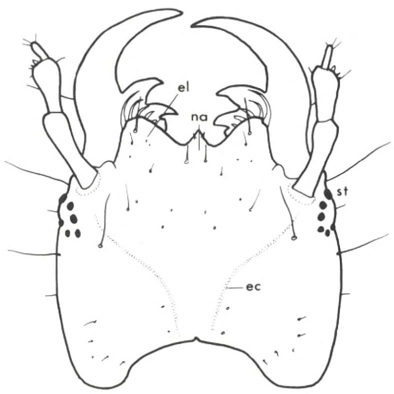
PLATE 17 (Details of larvae)

Fig. 193. *Helophorus* (Helophoridae), head, dorsal (maxillae and labium omitted) (ec = ecdysial line, el = epistomal lobe, na = nasale, st = stemmata)
Fig. 194. *Spercheus* (Spercheidae), head, dorsal (maxillae and labium omitted)
Fig. 195. *Dendrophilus* (Histeridae-Dendrophilinae), head, dorsal (redrawn from Vienna, 1980)
Fig. 196. *Sphaerites* (Sphaeritidae), head, dorsal (maxillae and labium omitted) (el = epistomal lobe) (redrawn from Nikitsky, 1976)
Fig. 197. *Ochthebius* (Hydraenidae-Ochthebiinae), head, dorsal (maxillae and labium omitted) (ec = ecdysial line, ep = epistomal suture, la = labrum)
Fig. 198. *Prionochaeta* (Leiodidae-Cholevinae), head, dorsal (based on Bøving and Craighead, 1931)
Fig. 199. *Silpha* (Silphidae-Silphinae), head, dorsal (maxillae omitted)
Fig. 200. *Oxyporus* (Staphylinidae-Oxyporinae), head, dorsal (left antenna omitted) (redrawn from Kasule, 1966)
Fig. 201. *Philonthus* (Staphylinidae-Staphylininae), head, dorsal (maxillae and labium omitted) (na = nasale) (based on Kasule, 1966)



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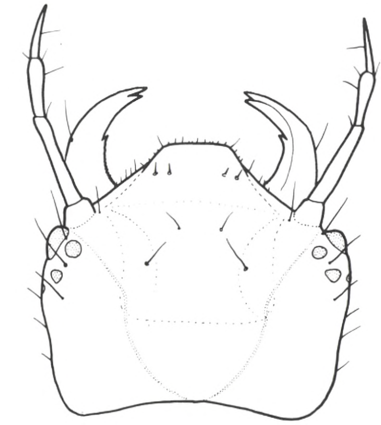

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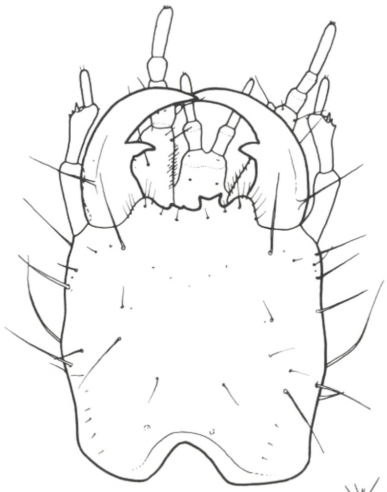

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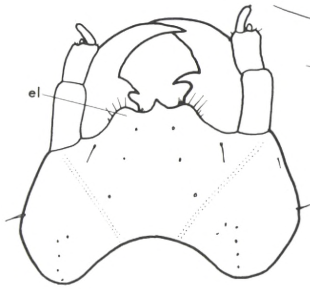

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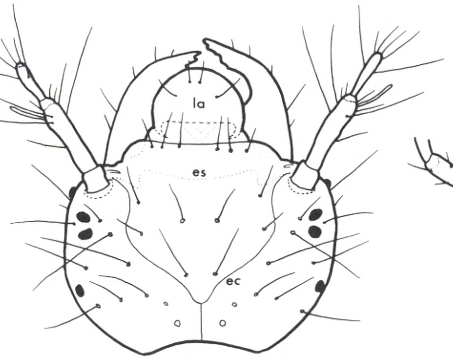

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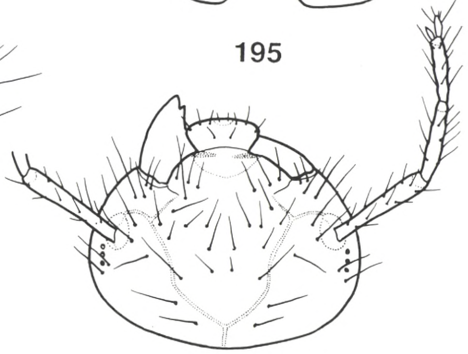

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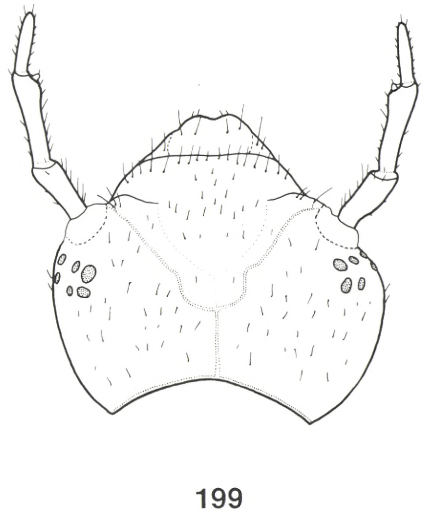

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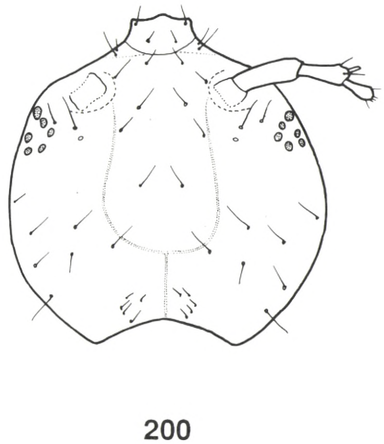

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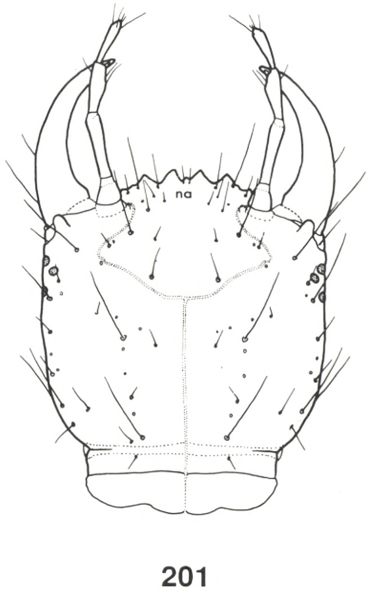

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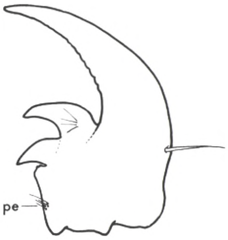
PLATE 18 (Details of larvae)

Fig. 202. *Helophorus* (Helophoridae), mandible (pe = penicillus)
Fig. 203. *Sphaerites* (Sphaeritidae), mandible (pe = penicillus) (redrawn from Nikitsky, 1976)
Fig. 204. *Saprinus* (Histeridae-Saprininae), mandible (pe = penicillus) (based on Bøving and Craighead, 1931)
Fig. 205. *Catops* (Leiodidae-Cholevinae), mandible (mo = mola, pr = prostheca) (redrawn from Kasule, 1966)
Fig. 206. *Ochthebius* (Hydraenidae-Ochthebiinae), mandible (mo = mola, pr = prostheca) (redrawn from Bøving and Henriksen, 1938)
Fig. 207. *Anotylus* (Staphylinidae-Oxytelinae), mandible (redrawn from Kasule, 1966: "*Oxytelus*")
Fig. 208. *Limnoxenus* (Hydrophilidae-Hydrophilinae), mandible (redrawn from Berge Henegouwen, 1975)
Fig. 209. *Oxyporus* (Staphylinidae-Oxyporinae), mandible (redrawn from Kasule, 1966)
Fig. 210. *Dasycerus* (Staphylinidae-Dasycerinae), apical portion of mandible, anterior aspect (-based on Newton, 1991)
Fig. 211. *Scaphidium* (Scaphidiidae), labrum (redrawn from Kasule, 1966)
Fig. 212. *Helophorus* (Helophoridae), maxilla (ap = appendage of first palpal segment, ca = cardo, st = stipes)
Fig. 213. *Spercheus* (Spercheidae), maxilla (st = stipes)
Fig. 214. *Helochares* (Hydrophilidae-Hydrophilinae), maxilla (st = stipes)
Fig. 215. *Sphaerites* (Sphaeritidae), maxilla (pa = palpus, st = stipes) (redrawn from Nikitsky, 1976)
Fig. 216. *Ochthebius* (Hydraenidae-Ochthebiinae), maxilla (ga = galea, la = lacinia, pa = palpus, sa = sensory appendage) (redrawn from Richmond, 1920)
Fig. 217. *Hydraena* (Hydraenidae-Hydraeninae), maxilla (ga = galea, la = lacinia) (redrawn from Richmond, 1920)



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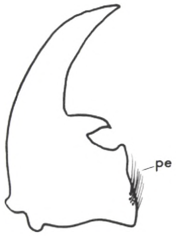

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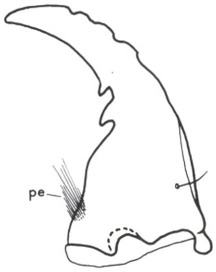

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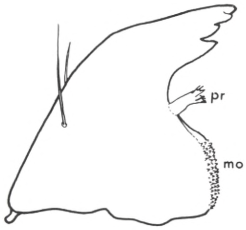

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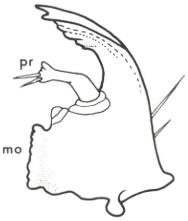

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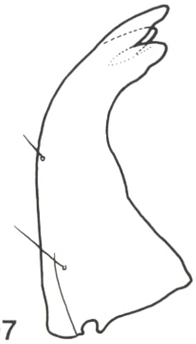

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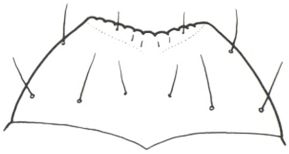

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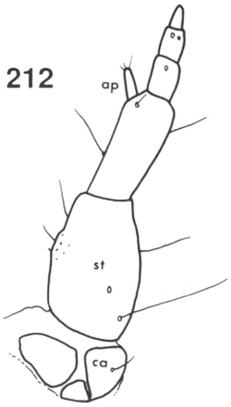

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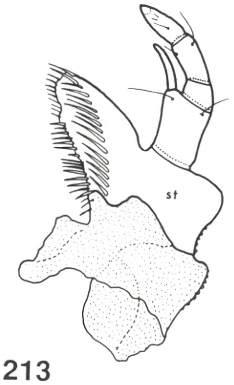

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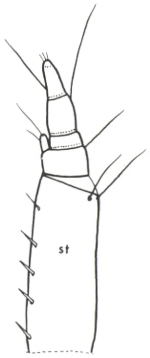

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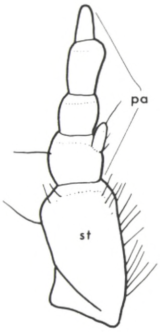

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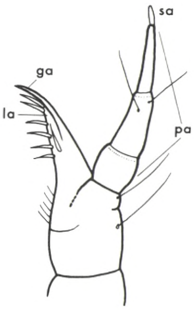

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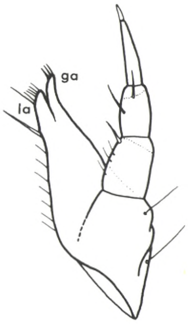

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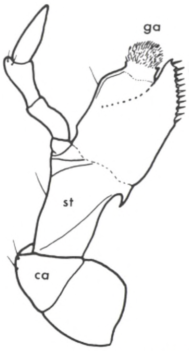
PLATE 19 (Details of larvae)

Fig. 218. *Ptomaphila* (Silphidae-Silphinae), maxilla (ca = cardo, ga = galea, la = lacinia, st = stipes) (redrawn from Paulian, 1941)
Fig. 219. *Megarthrus* (Staphylinidae-Proteininae), maxilla (ga+la = fused galea and lacinia (= mala)) (redrawn from Kasule, 1966)
Fig. 220. *Oxyporus* (Staphylinidae-Oxyporinae), maxilla (ga+la = fused galea and lacinia (= mala)) (redrawn from Paulian, 1941)
Fig. 221. *Paederus* (Staphylinidae-Paederinae), maxilla (ga+la = fused galea and lacinia (= mala))
Fig. 222. *Micropeplus* (Staphylinidae-Micropeplinae), maxilla (ga = galea, la = lacinia) (redrawn from Kasule, 1966)
Fig. 223. *Dorcus* (Lucanidae), maxilla (ga = galea, la = lacinia) (redrawn from Schiødte, 1874)
Fig. 224. *Helophorus* (Helophoridae), labium
Fig. 225. *Paracymus* (Hydrophilidae-Hydrophilinae), labium (redrawn from Richmond, 1920)
Fig. 226. *Cymbiodyta* (Hydrophilidae-Hydrophilinae), labium (redrawn from Richmond, 1920)
Fig. 227. *Teretrius* (Histeridae-Abraeinae), labrum and maxillae (pm = prementum, st = stipes) (based on Bøving and Craighead, 1931)
Fig. 228. *Sphaerites* (Sphaeritidae), labium (m = mentum, pm = prementum, sm = submentum) (redrawn from Nikitsky, 1976)
Fig. 229. *Stenus* (Staphylinidae-Steninae), labium (li = ligula) (redrawn from Kasule, 1966)
Fig. 230. *Euaesthetus* (Staphylinidae-Euaesthetinae), labium (li = ligula) (redrawn from Kasule, 1966)
Fig. 231. *Piestus* (Staphylinidae-Piestinae), labium (m = mentum, sm = submentum) (redrawn from Frank, 1991)
Fig. 232. *Osorius* (Staphylinidae-Osoriinae), labium (m+sm = fused mentum and submentum) (redrawn from Frank, 1991)



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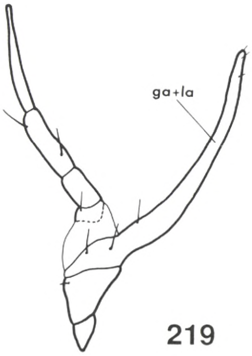

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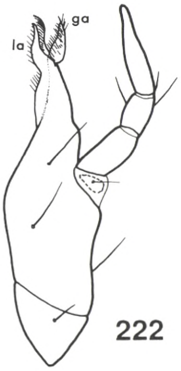

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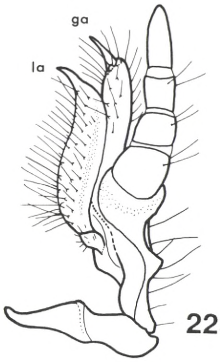

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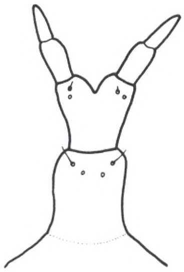

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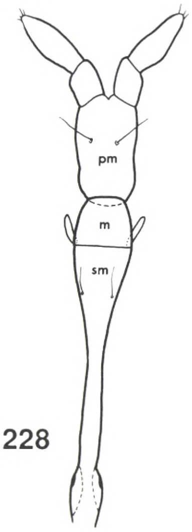

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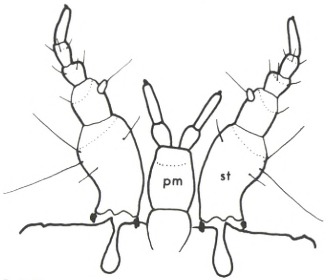

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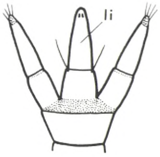

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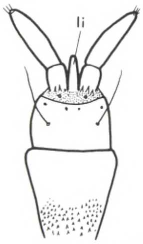

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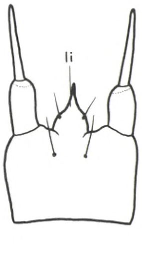

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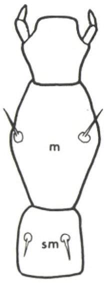

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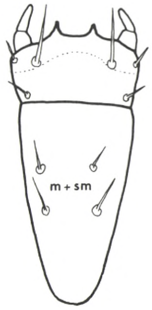

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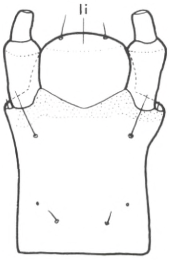
PLATE 20 (Details of larvae)

Fig. 233. *Anotylus* (Staphylinidae-Oxytelinae), labium (li = ligula) (redrawn from Kasule, 1966: "*Oxytelus*")
Fig. 234. *Helochares* (Hydrophilidae-Hydrophilinae), right antenna, dorsal (sa = sensory appendage) (redrawn from Richmond, 1920)
Fig. 235. *Sphaerites* (Sphaeritidae), right antenna, dorsal (sa = sensory appendage) (redrawn from Nikitsky, 1976)
Fig. 236. *Catops* (Leiodidae-Cholevinae), right antenna, dorsal (sa = sensory appendage)
Fig. 237. *Cephennium* (Scydmaenidae-Scydmaeninae), right antenna, dorsal (sa = sensory appendage) (redrawn from Paulian, 1941)
Fig. 238. *Mastigus* (Scydmaenidae-Mastiginae), left antenna, dorsal (sa = sensory appendage) (based on Newton, 1991)
Fig. 239. *Gyrophaena* (Staphylinidae-Aleocharinae), right antenna, dorsal (sa = sensory appendage) (redrawn from Paulian, 1941)
Fig. 240. *Haliplus* (Haliplidae), posterior leg (redrawn from Bøving and Craighead, 1931)
Fig. 241. *Helophorus* (Helophoridae), middle leg (redrawn from Richmond, 1920)
Fig. 242. *Ochthebius* (Hydraenidae-Ochthebiinae), leg (redrawn from Bøving and Henriksen, 1938)
Fig. 243. *Georissus* (Georissidae), middle leg (redrawn from Emden, 1956)
Fig. 244. *Helophorus* (Helophoridae), 9th abdominal tergum with urogomphi
Fig. 245. *Sphaerites* (Sphaeritidae), urogomphi (redrawn from Nikitsky, 1976)



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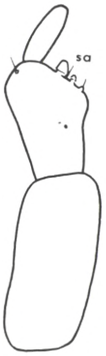

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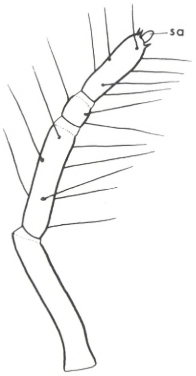

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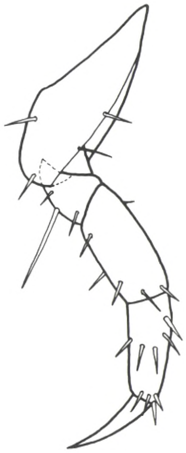

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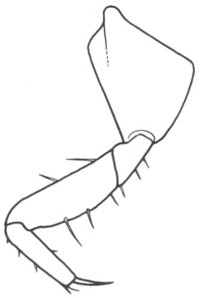

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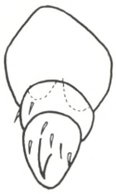

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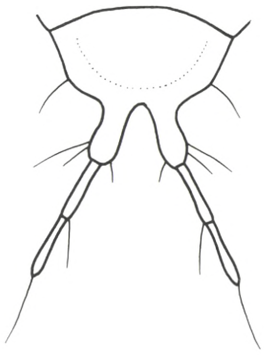

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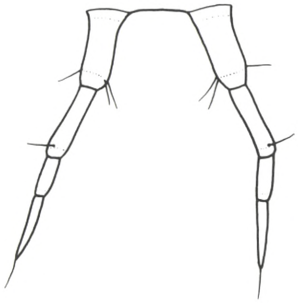

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PLATE 21 (Details of larvae)

Fig. 246. *Enochrus* (Hydrophilidae-Hydrophilinae), abdominal apex, dorsal (tr = tracheae from spiracles of segment 8, t8 = tergal shield of segment 8, ur = urogomphus) (redrawn from Richmond, 1920)

Fig. 247. *Spercheus* (Spercheidae), abdominal apex with stigmatic atrium, dorso-posterior aspect (an = anus, sp = spiracle of segment 8, s9 = sternum 9, t8 = tergal shield of segment 8, t9 = tergum 9, t10 = tergum 10, ur = rudiment of urogomphus)

Fig. 248. *Georissus* (Georissidae), abdominal segments 8-10, dorsal (ur = urogomphus) (redrawn from Emden, 1956)

Fig. 249. *Ochthebius* (Hydraenidae-Ochthebiinae), abdominal segments 9 and 10, dorsal (ah = anal hooks, t9 = tergum 9, t10 = tergum 10, ur = urogomphus)

Fig. 250. *Hydraena* (Hydraenidae-Hydraeninae), abdominal segments 9 and 10, dorsal

Fig. 251. *Leptomastax* (Scydmaenidae-Mastiginae), 9th abdominal tergum with urogomphi (based on Vit and De Marzo, 1989)

Fig. 252. *Catops* (Leiodidae-Cholevinae), urogomphus

Fig. 253. *Gyrophaena* (Staphylinidae-Aleocharinae), abdominal apex, dorsal (ag = abdominal gland, t8 = tergum 8, t9 = tergum 9, ur = urogomphus) (redrawn from Paulian, 1941)

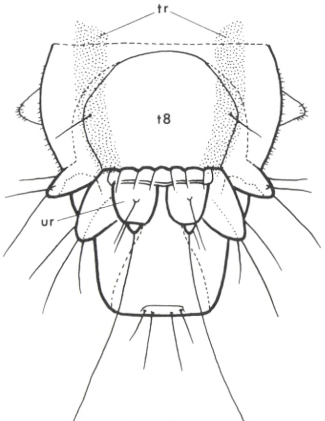
Fig. 254. *Thinopinus* (Staphylinidae-Staphylininae), spiracle (annular) (redrawn from Bøving and Craighead, 1931)

Fig. 255. *Cryptophagus* (Cryptophagidae-Cryptophaginae), spiracle (annular-biforous) (redrawn from Bøving and Craighead, 1931)

Fig. 256. *Hister* (Histeridae-Histerinae), spiracle (biforous) (redrawn from Bøving and Craighead, 1931)

Fig. 257. *Trox* (Trogidae), spiracle (cribriform) (redrawn from Bøving and Craighead, 1931)

Fig. 258. *Catops* (Leiodidae-Cholevinae), plumose seta



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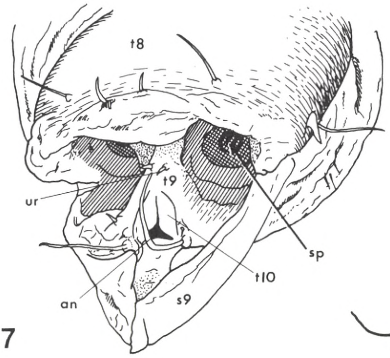

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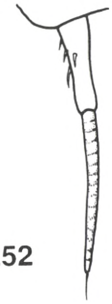

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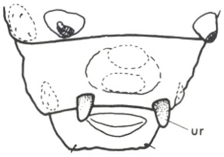

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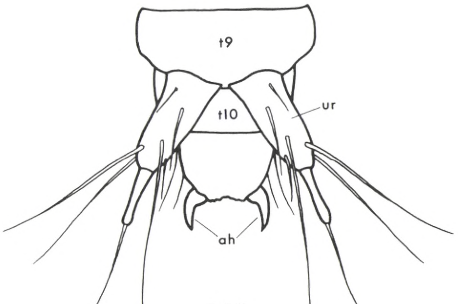

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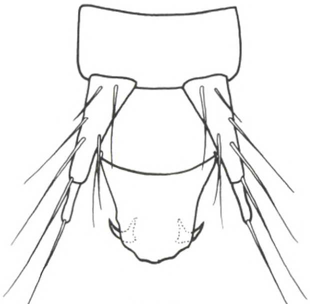

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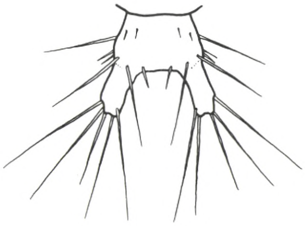

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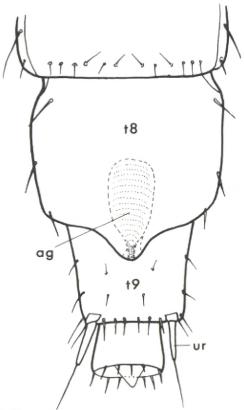

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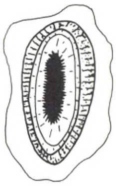

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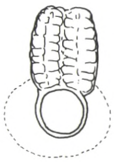

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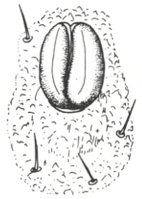

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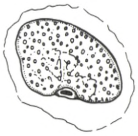

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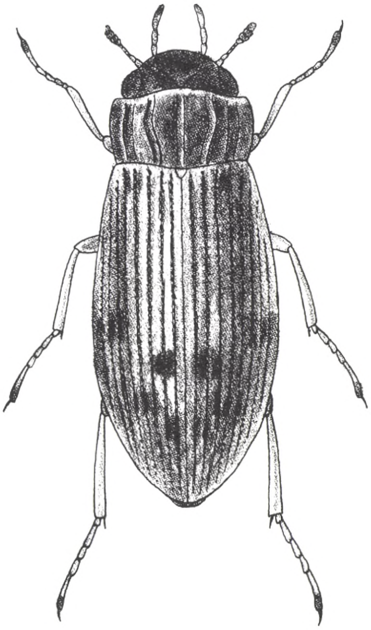
PLATE 22 (Habitus of adults)

Fig. 259. *Helophorus minutus*, Helophoridae, 2.9 mm (after V. Hansen)
Fig. 260. *Epimetopus thermarum*, Epimetopidae, 2.2 mm
Fig. 261. *Georissus crenulatus*, Georissidae, 1.8 mm (after V. Hansen)
Fig. 262. *Hydrochus elongatus*, Hydrochidae, 3.8 mm (after V. Hansen)



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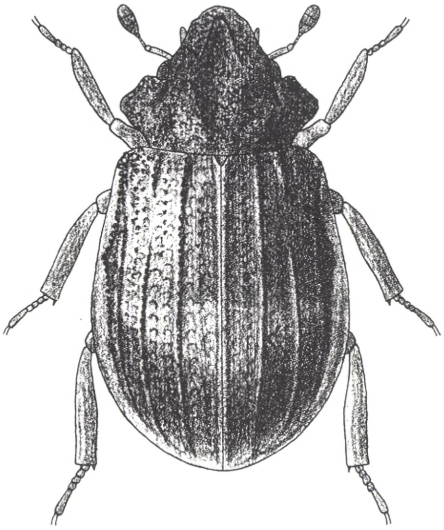

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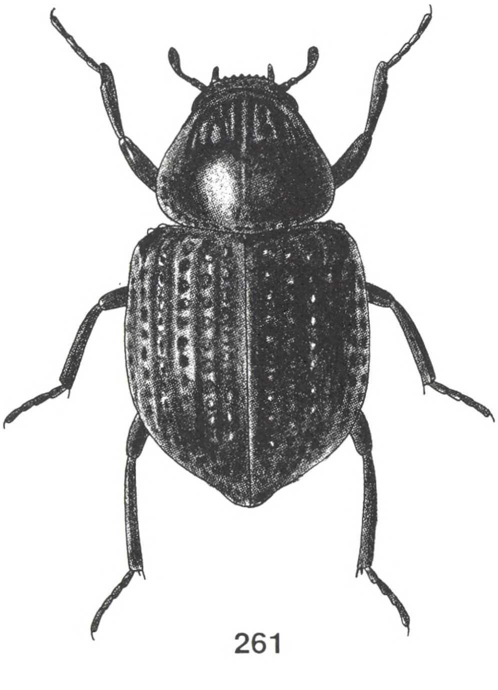

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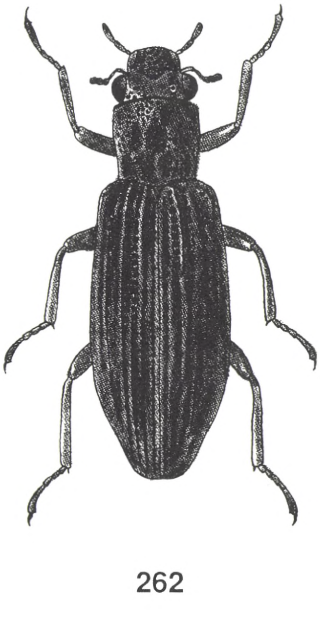

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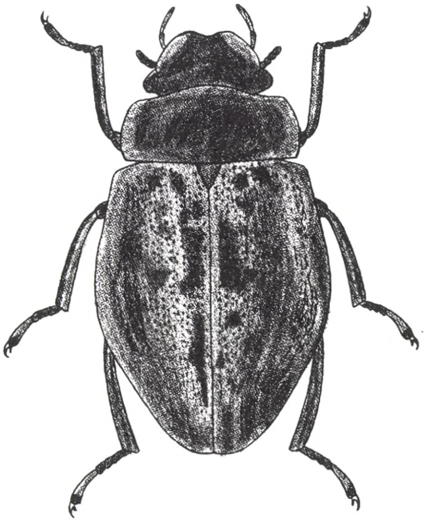
PLATE 23 (Habitus of adults)

Fig. 263. *Spercheus emarginatus*, Spercheidae, 6.0 mm (after V. Hansen)
Fig. 264. *Horelophus walkeri*, Hydrophilidae-Horelophinae, 2.6 mm
Fig. 265. *Sperchopsis tessellata*, Hydrophilidae-Hydrophilinae (Sperchopsini), 7.0 mm
Fig. 266. *Berosus luridus*, Hydrophilidae-Hydrophilinae (Berosini), 4.0 mm (after V. Hansen)



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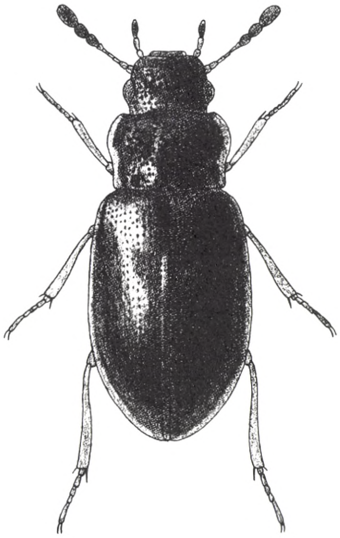

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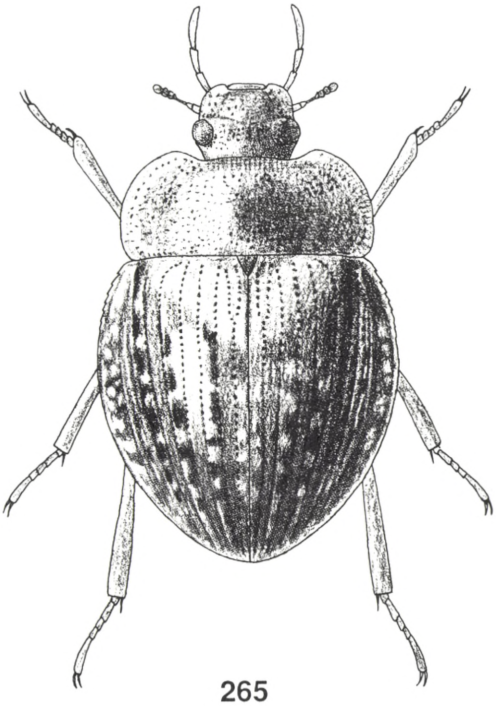

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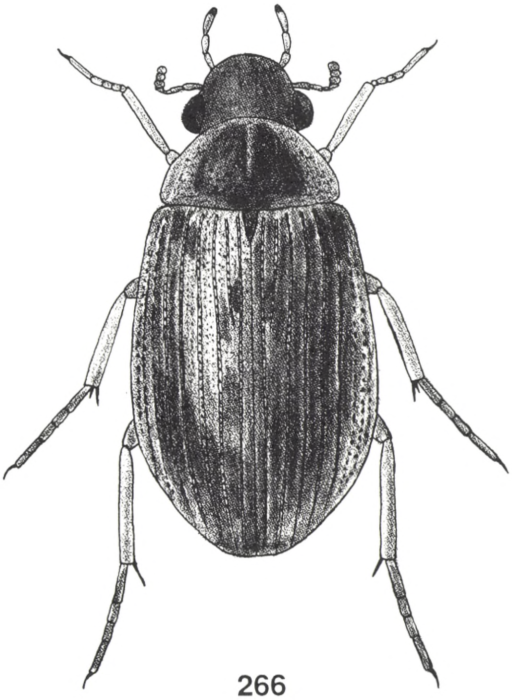

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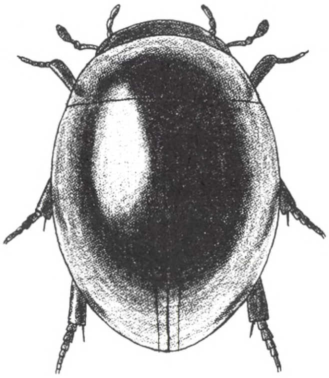
PLATE 24 (Habitus of adults)

Fig. 267. *Chaetarthria seminulum*, Hydrophilidae-Hydrophilinae (Chaetarthriini), 1.5 mm (after V. Hansen)

Fig. 268. *Anacaena limbata*, Hydrophilidae-Hydrophilinae (Anacaenini), 2.6 mm (after V. Hansen)

Fig. 269. *Laccobius sinuatus*, Hydrophilidae-Hydrophilinae (Laccobiini), 3.6 mm (after V. Hansen)

Fig. 270. *Agraphydrus punctatellus*, Hydrophilidae-Hydrophilinae (Hydrophilini), 2.6 mm



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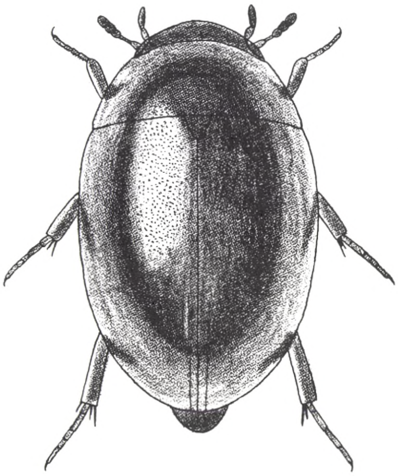

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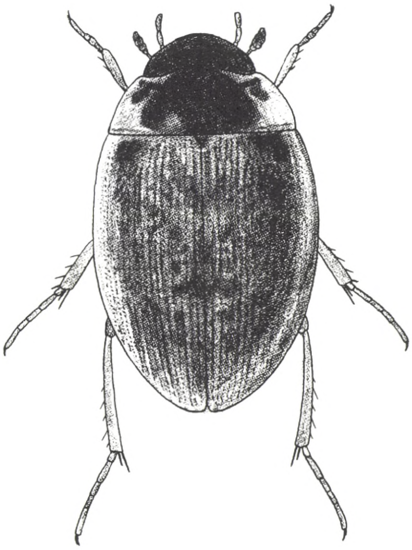

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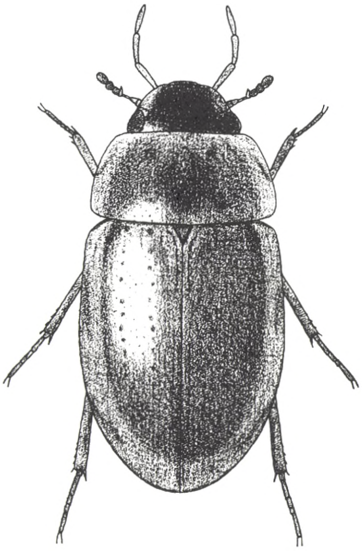

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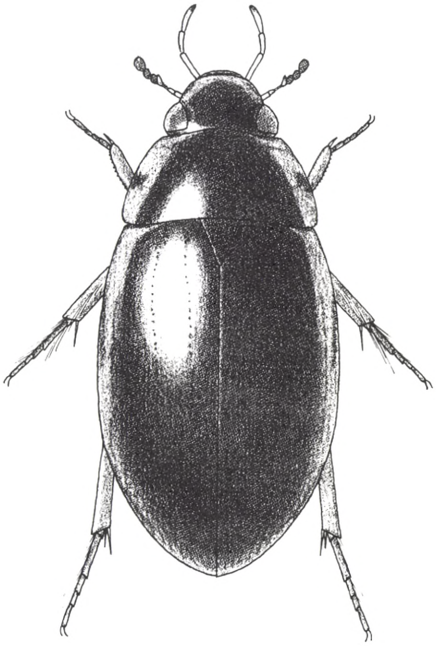
PLATE 25 (Habitus of adults)

Fig. 271. *Sternolophus rufipes*, Hydrophilidae-Hydrophilinae (Hydrophilini), 11.0 mm
Fig. 272. *Rygmodus modestus*, Hydrophilidae-Sphaeridiinae (Rygmodini), 5.8 mm
Fig. 273. *Tormissus magnulus*, Hydrophilidae-Sphaeridiinae (Tormissini), 7.7 mm
Fig. 274. *Andotypus ashworthi*, Hydrophilidae-Sphaeridiinae (Andotypini), 4.4 mm



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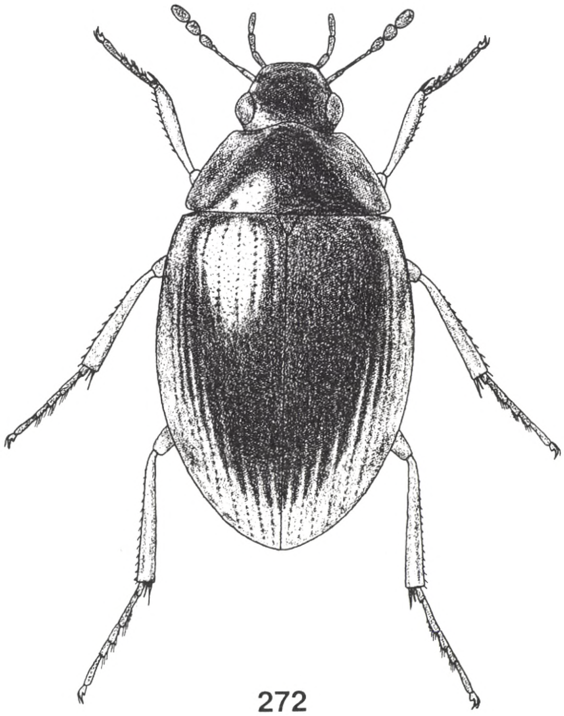

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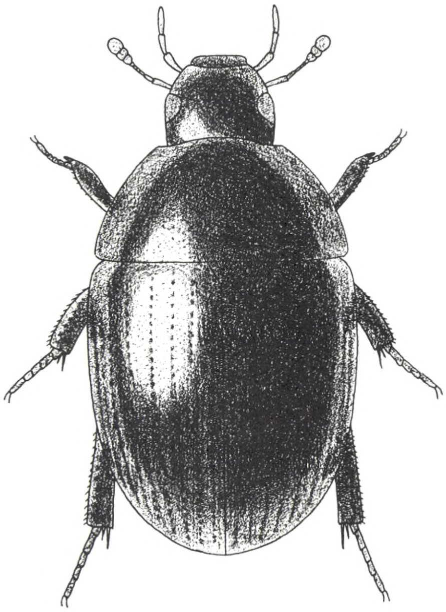

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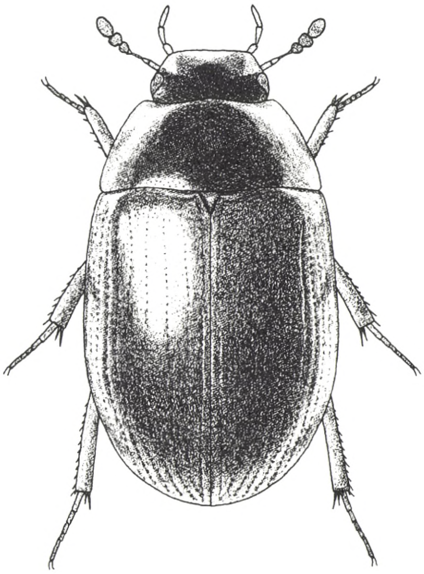

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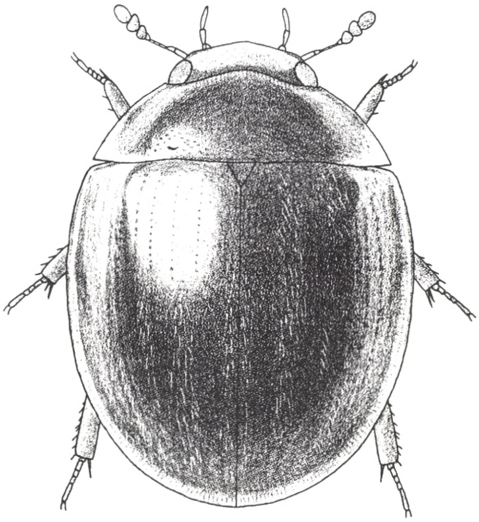
PLATE 26 (Habitus of adults)

Fig. 275. *Borborophorus pubescens*, Hydrophilidae-Sphaeridiinae (Borborophorini), 3.5 mm
Fig. 276. *Coelostoma orbiculare*, Hydrophilidae-Sphaeridiinae (Coelostomatini), 4.4 mm (after V. Hansen)
Fig. 277. *Protosternum atomarium*, Hydrophilidae-Sphaeridiinae (Protosternini), 1.7 mm
Fig. 278. *Noteropagus politus*, Hydrophilidae-Sphaeridiinae (Omicrini), 1.5 mm



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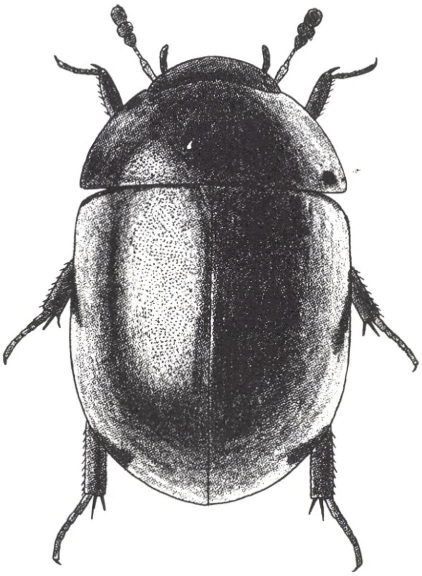

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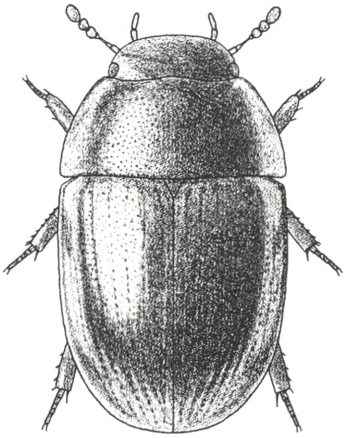

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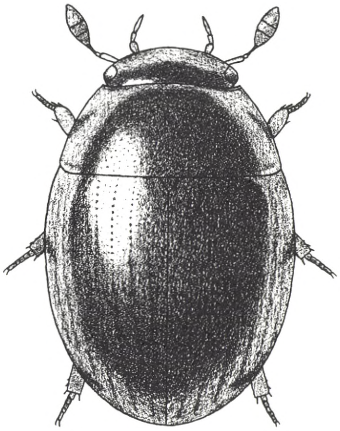

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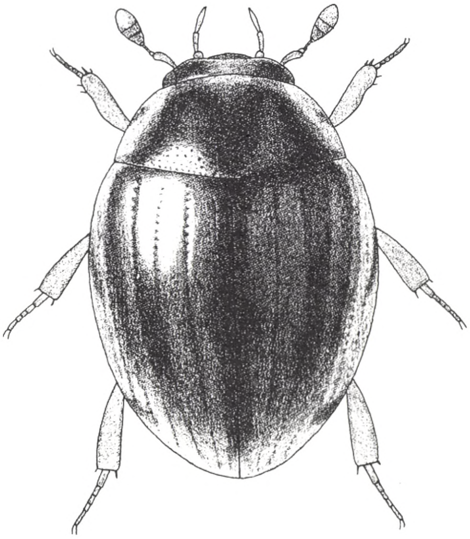
PLATE 27 (Habitus of adults)

Fig. 279. *Pachysternum nigrovittatum*, Hydrophilidae-Sphaeridiinae (Megasternini), 2.6 mm
Fig. 280. *Sphaeridium scarabaeoides*, Hydrophilidae-Sphaeridiinae (Sphaeridiini), 6.0 mm (after V. Hansen)
Fig. 281. *Sphaerites glabratus*, Sphaeritidae, 5.7 mm (after V. Hansen)
Fig. 282. *Syntelia histeroides*, Synteliidae, 12.5 mm



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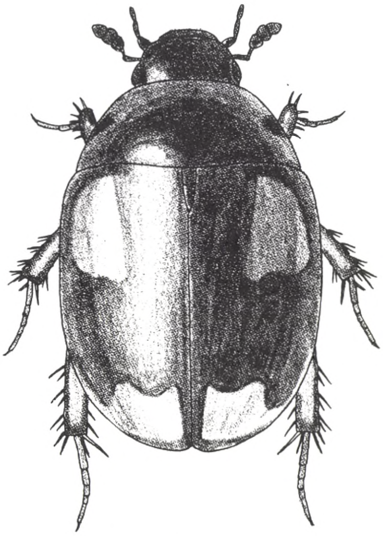

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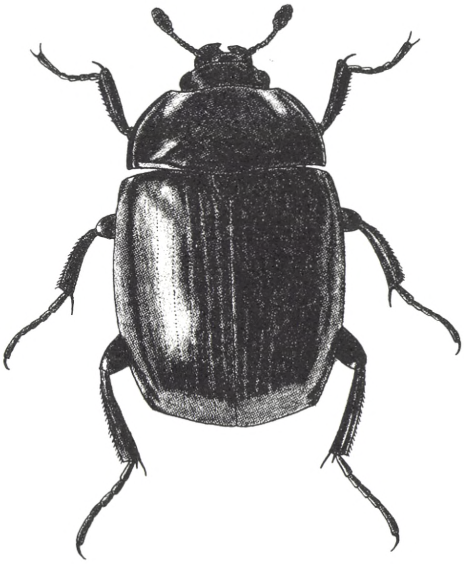

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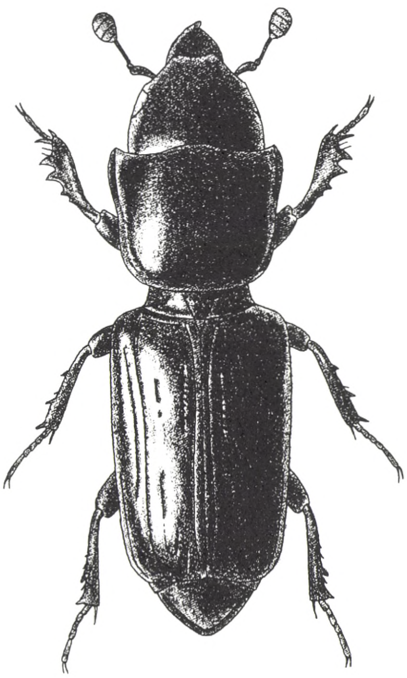

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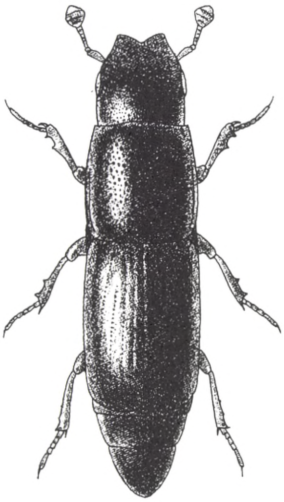
PLATE 28 (Habitus of adults)

Fig. 283. *Niponius obtusiceps*, Histeridae-Niponiinae, 4.4 mm
Fig. 284. *Abraeus globosus*, Histeridae-Abraeinae (Abraeini), 1.5 mm (after V. Hansen)
Fig. 285. *Plegaderus dissectus*, Histeridae-Abraeinae (Plegaderini), 1.3 mm (after V. Hansen)
Fig. 286. *Teretrius picipes*, Histeridae-Abraeinae (Teretriini), 2.3 mm



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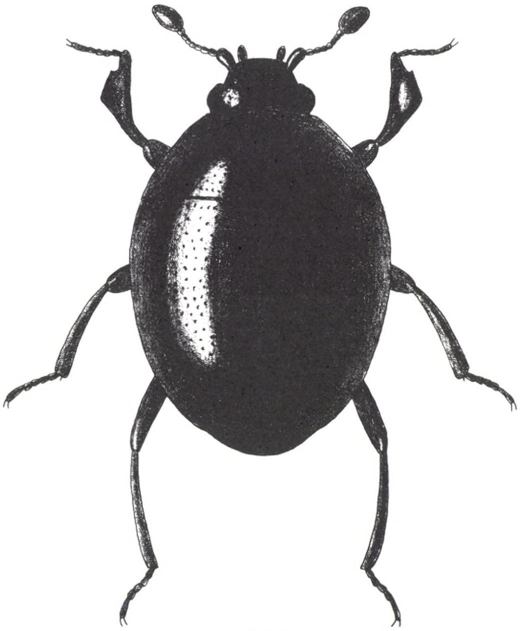

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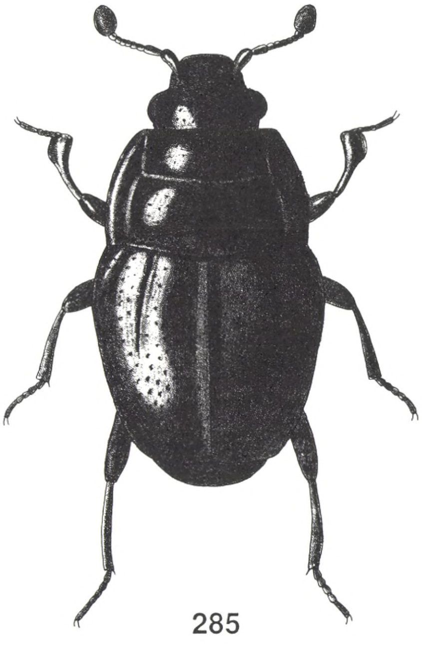

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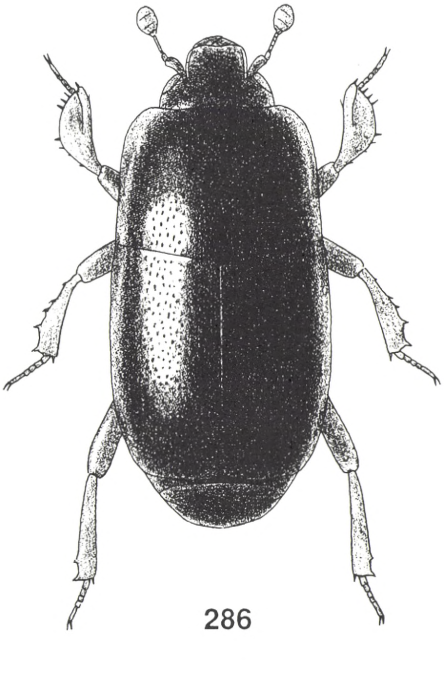

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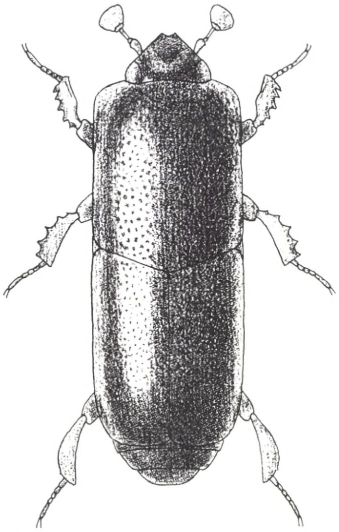
PLATE 29 (Habitus of adults)

Fig. 287. *Trypeticus indicus*, Histeridae-Trypeticinae, 3.3 mm
Fig. 288. *Trypanaeus thoracicus*, Histeridae-Trypanaeinae, 8.5 mm
Fig. 289. *Saprinus semistriatus*, Histeridae-Saprininae, 5.0 mm (after V. Hansen)
Fig. 290. *Dendrophilus punctatus*, Histeridae-Dendrophilinae (Dendrophilini), 3.3 mm



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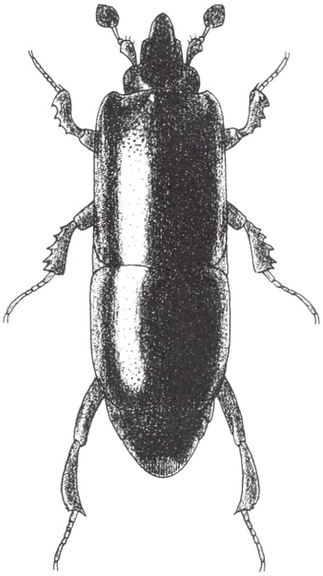

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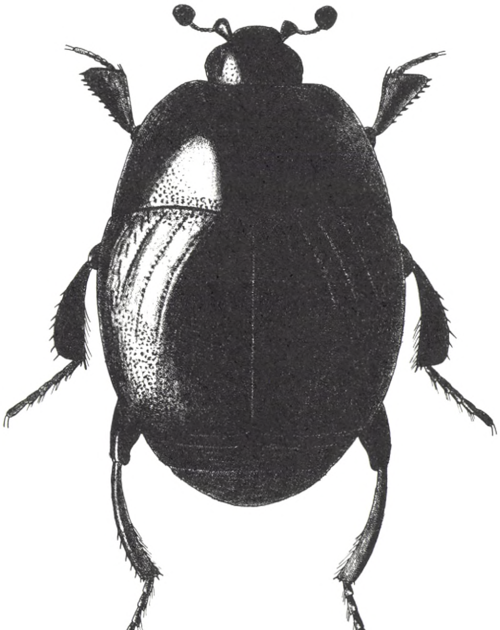

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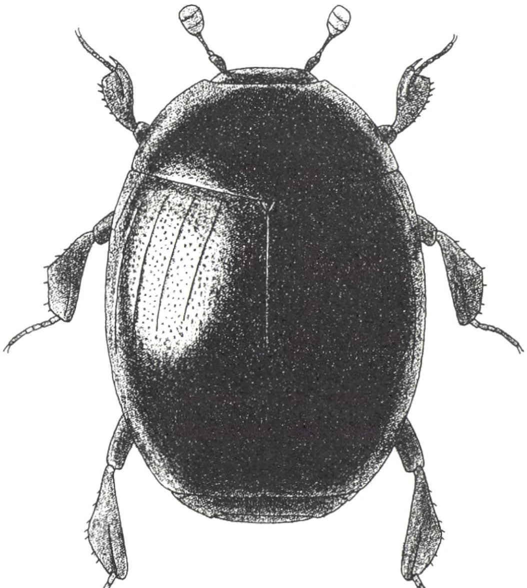

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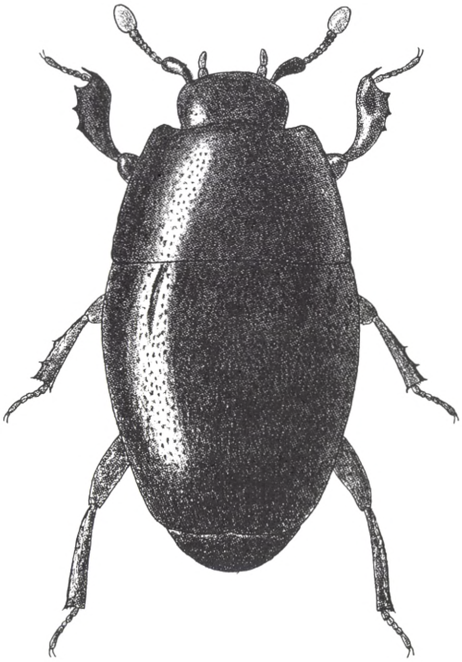
PLATE 30 (Habitus of adults)

Fig. 291. *Paromalus flavicornis*, Histeridae-Dendrophilinae (Paromalini), 2.2 mm (after V. Hansen)
Fig. 292. *Onthophilus sulcatus*, Histeridae-Onthophilinae, 3.0 mm (after V. Hansen)
Fig. 293. *Tribalus scaphidiformis*, Histeridae-Tribalinae, 2.4 mm
Fig. 294. *Margarinotus brunneus*, Histeridae-Histerinae (Histerini), 7.0 mm (after V. Hansen)



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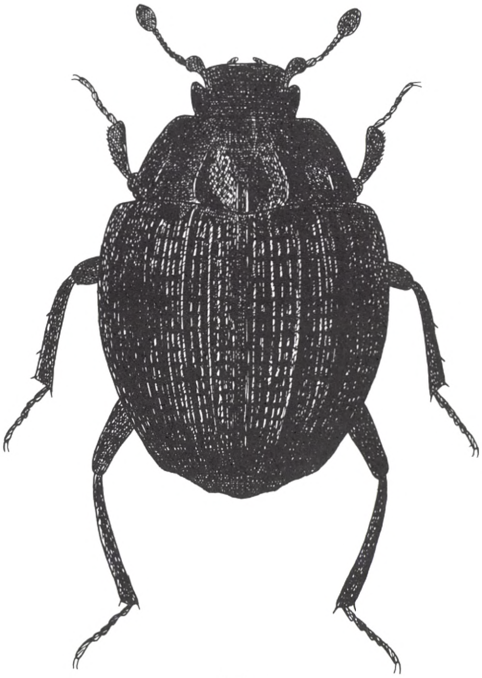

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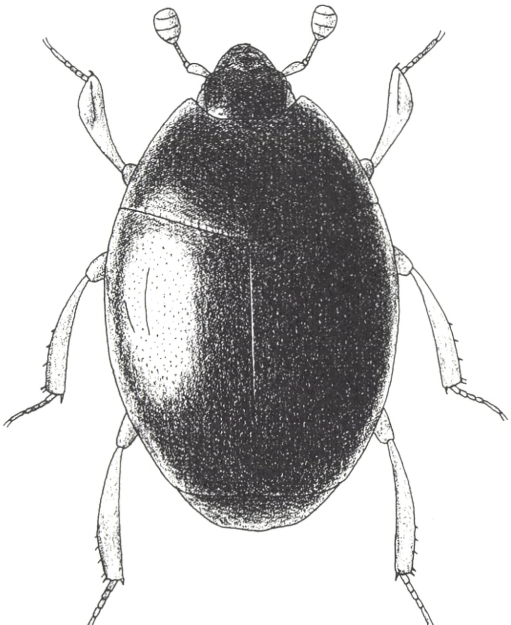

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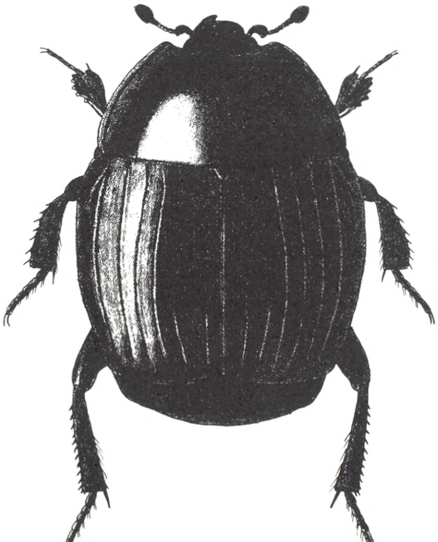

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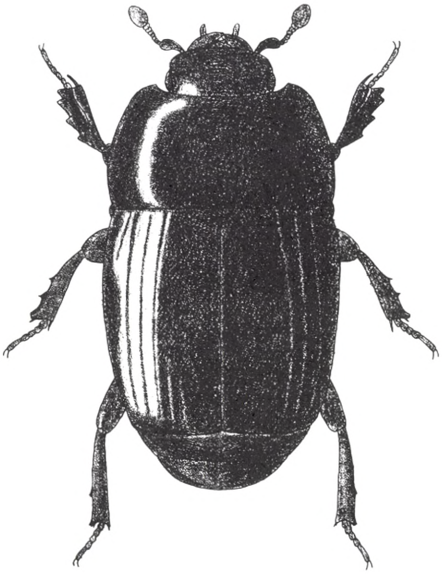
PLATE 31 (Habitus of adults)

Fig. 295. *Platysoma compressum*, Histeridae-Histerinae (Platysomatini), 3.5 mm (after V. Hansen)
Fig. 296. *Hololepta plana*, Histeridae-Histerinae (Hololeptini), 8.8 mm
Fig. 297. *Hetaerius ferrugineus*, Histeridae-Hetaeriinae, 1.6 mm (after V. Hansen)
Fig. 298. *Chlamydopsis* sp., Histeridae-Chlamydopsinae, 4.3 mm



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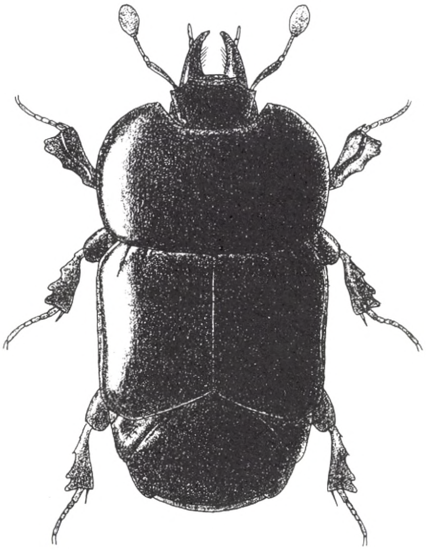

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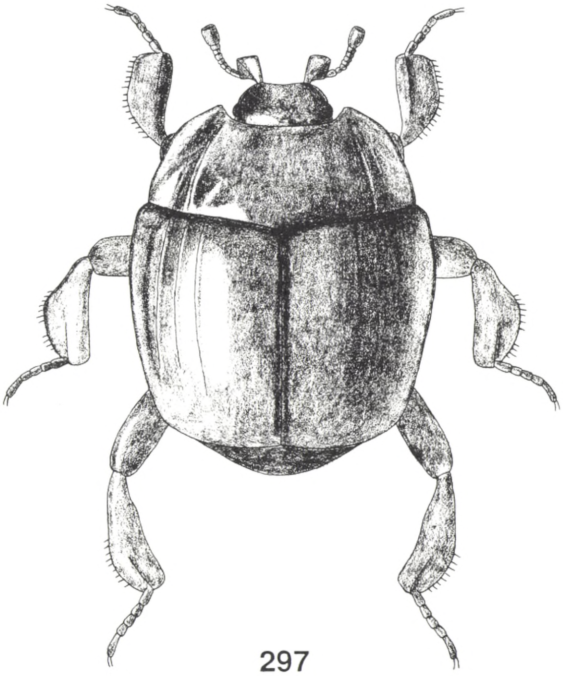

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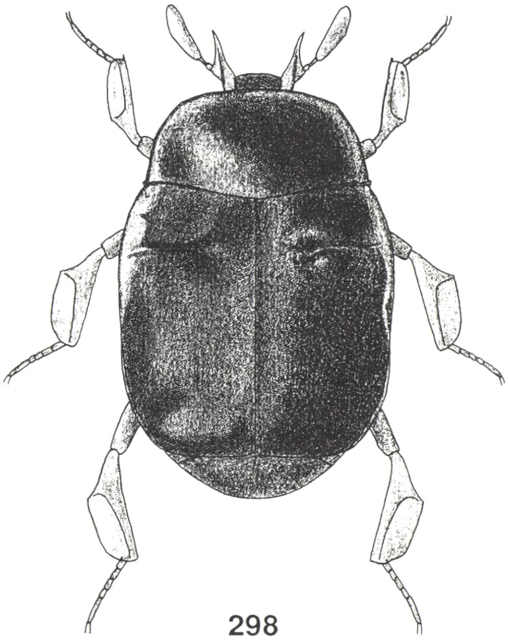

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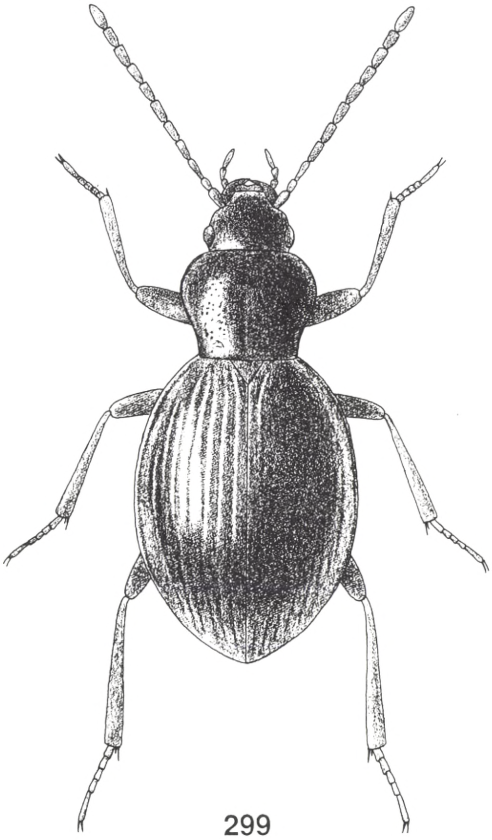
PLATE 32 (Habitus of adults)

Fig. 299. *Lyrosoma ovipenne*, Agyrtidae (Lyrosomatini), 4.0 mm
Fig. 300. *Pteroloma forstroemi*, Agyrtidae (Pterolomatini), 6.7 mm
Fig. 301. *Agyrtes bicolor*, Agyrtidae (Agyrtini), 4.5 mm (after V. Hansen)



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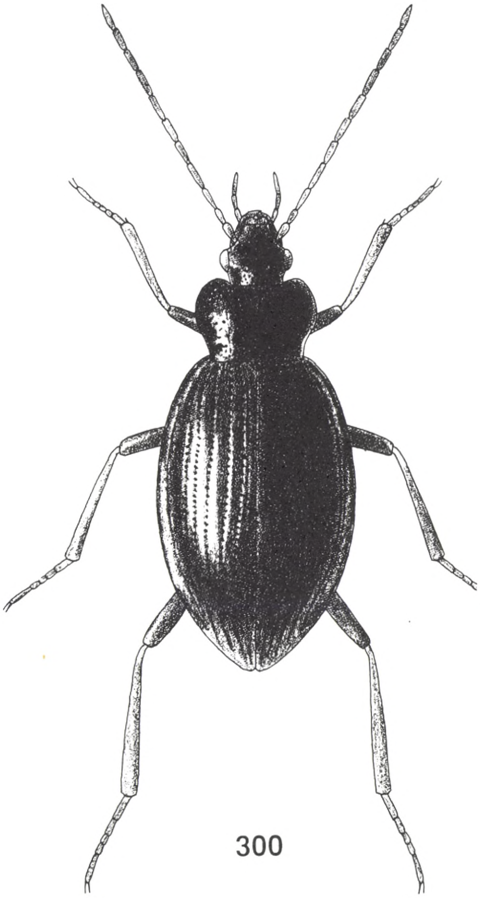

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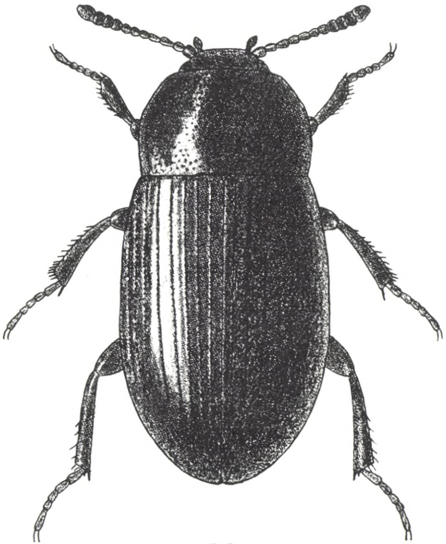

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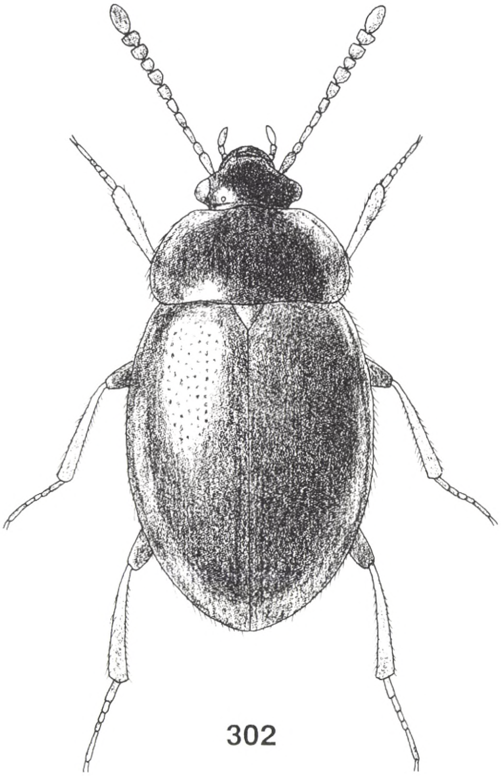
PLATE 33 (Habitus of adults)

Fig. 302. *Ragytodes ocellifer*, Leiodidae-Camiarinae (Neopelatopini), 3.9 mm
Fig. 303. *Agyrtodes* sp., Leiodidae-Camiarinae (Agyrtodini), 2.4 mm
Fig. 304. *Scotocryptus inquilinus*, Leiodidae-Leiodinae (Scotocryptini), 2.2 mm
Fig. 305. *Dietta sperata*, Leiodidae-Leiodinae (Estadiini), 4.0 mm



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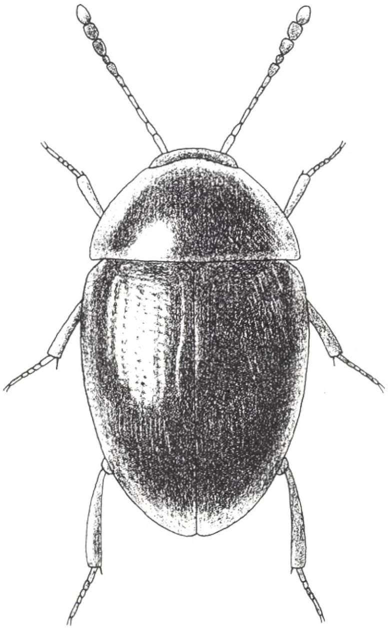

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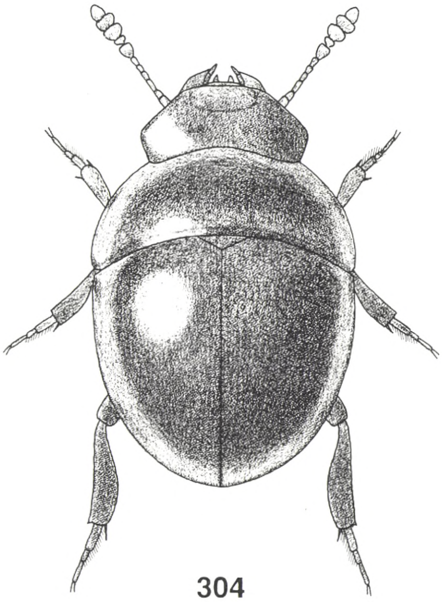

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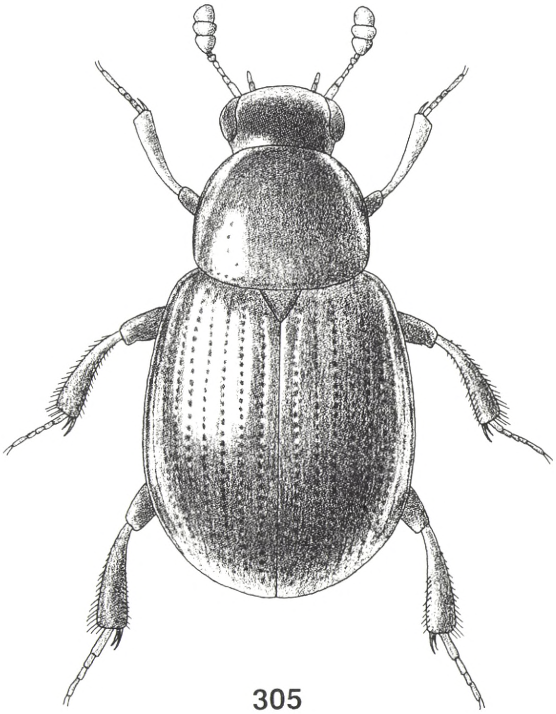

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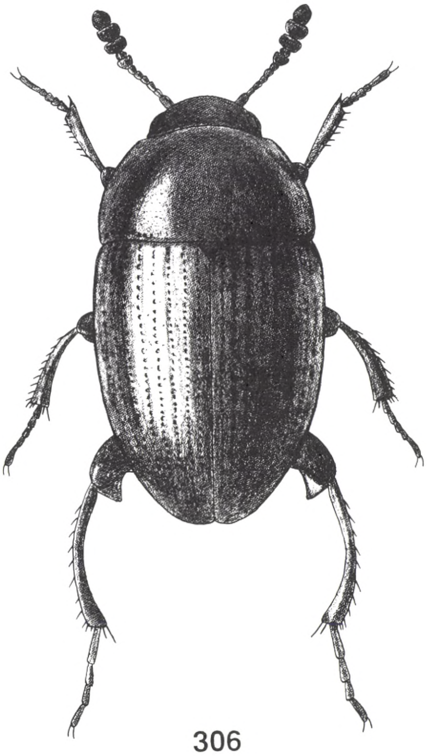
PLATE 34 (Habitus of adults)

Fig. 306. *Leiodes polita*, Leiodidae-Leiodinae (Leiodini), 3.0 mm (after V. Hansen)
Fig. 307. *Hydnobius multistriatus*, Leiodidae-Leiodinae (Sogdini), 2.4 mm (after V. Hansen)
Fig. 308. *Dermatohomoeus kaszabi*, Leiodidae-Leiodinae (Pseudoliodini), 1.4 mm
Fig. 309. *Anisotoma humeralis*, Leiodidae-Leiodinae (Agathidiini), 3.5 mm (after V. Hansen)



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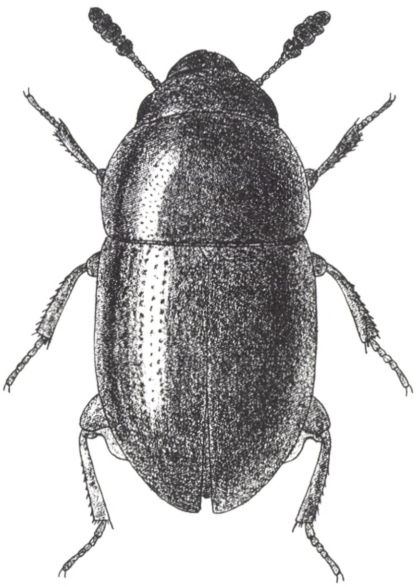

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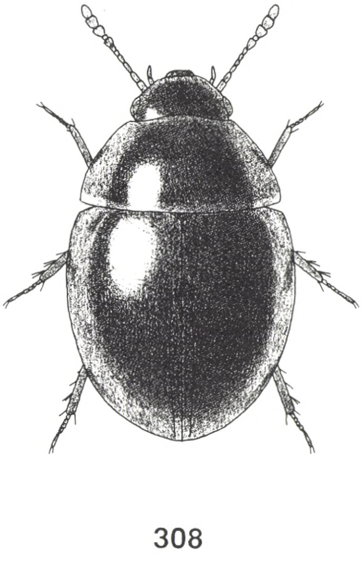

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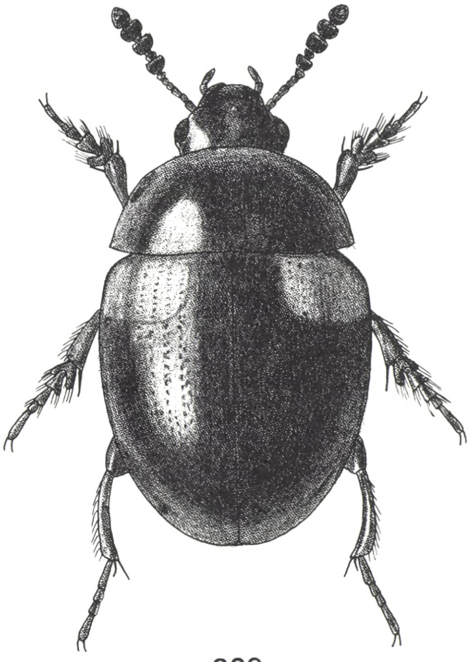

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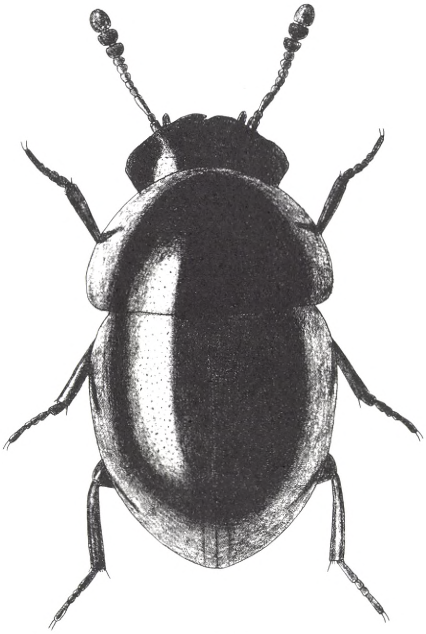
PLATE 35 (Habitus of adults)

Fig. 310. *Agathidium atrum*, Leiodidae-Leiodinae (Agathidiini), 3.0 mm (after V. Hansen)
Fig. 311. *Colon dentipes*, Leiodidae-Coloninae, 2.5 mm (after V. Hansen)
Fig. 312. *Ptomaphagus subvillosus*, Leiodidae-Cholevinae (Ptomaphagini), 3.0 mm (after V. Hansen)
Fig. 313. *Choleva oblonga*, Leiodidae-Cholevinae (Cholevini), 5.2 mm (after V. Hansen)



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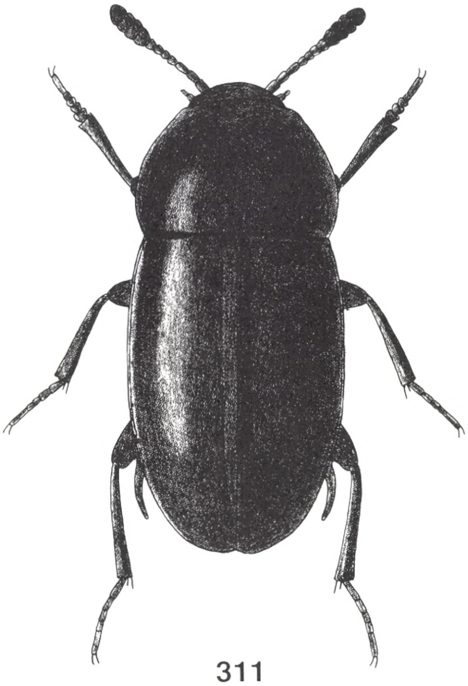

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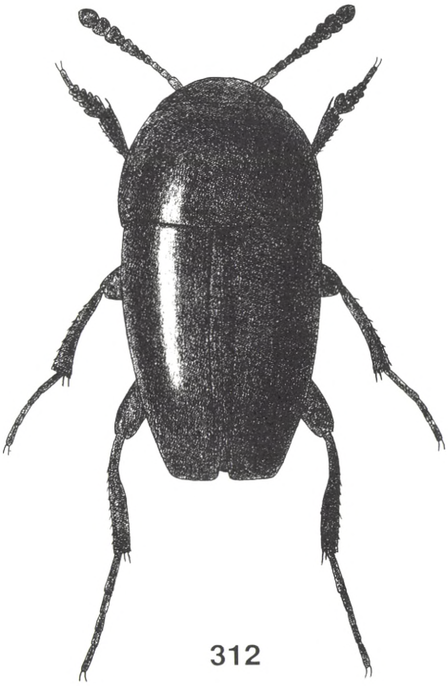

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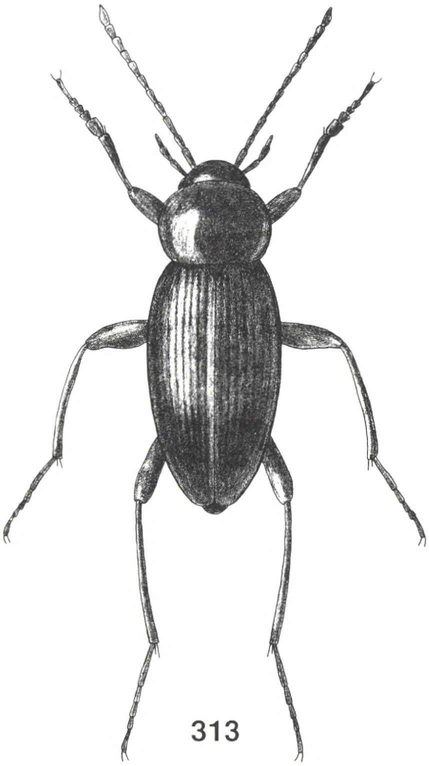

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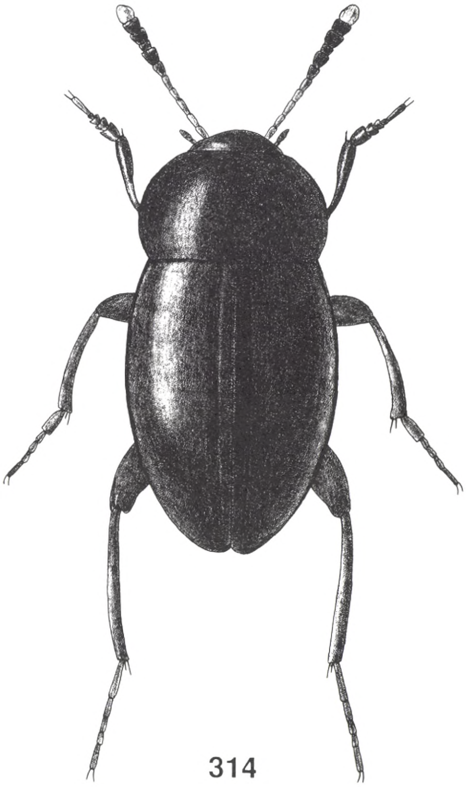
PLATE 36 (Habitus of adults)

Fig. 314. *Catops westi*, Leiodidae-Cholevinae (Cholevini), 3.5 mm (after V. Hansen)
Fig. 315. *Leptodirus hohenwarti*, Leiodidae-Cholevinae (Leptodirini), 7.0 mm
Fig. 316. *Pholeuon kazayi*, Leiodidae-Cholevinae (Leptodirini), 4.9 mm
Fig. 317. *Leptinus testaceus*, Leiodidae-Platypsyllinae, 2.0 mm (after V. Hansen)



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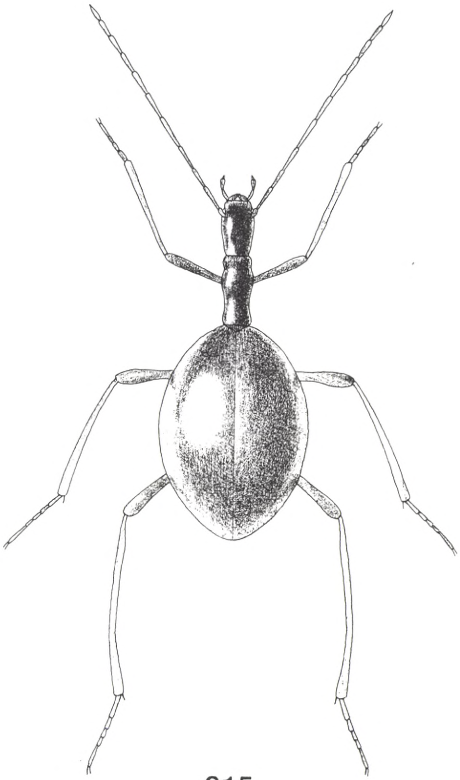

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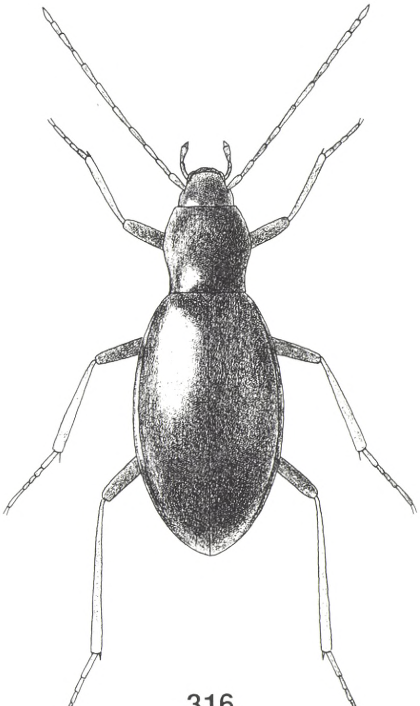

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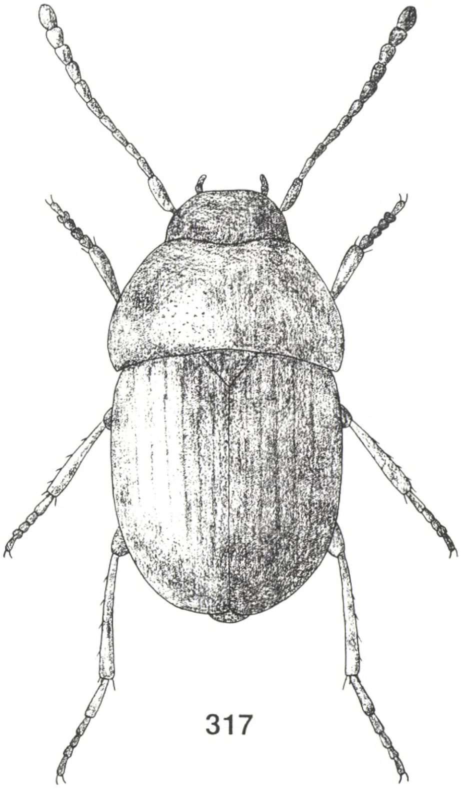

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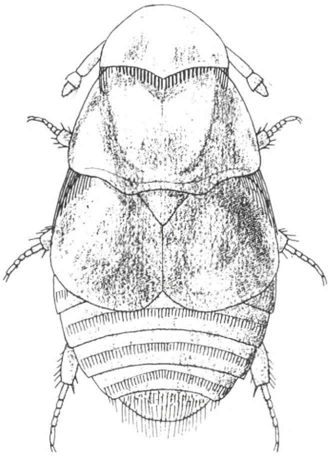
PLATE 37 (Habitus of adults)

Fig. 318. *Platypsyllus castoris*, Leiodidae-Platypsyllinae, 2.1 mm
Fig. 319. *Catopocerus cryptophagoides*, Leiodidae-Catopocerinae (Catopocerini), 1.5 mm
Fig. 320. *Glacicavicola bathyscioides*, Leiodidae-Catopocerinae (Glacicavicolini), 4.8 mm
Fig. 321. *Hydraenida ocellata*, Hydraenidae-Hydraeninae (Hydraenidini), 2.0 mm



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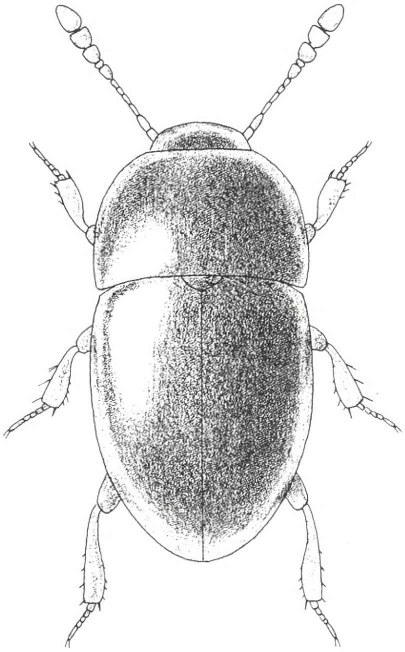

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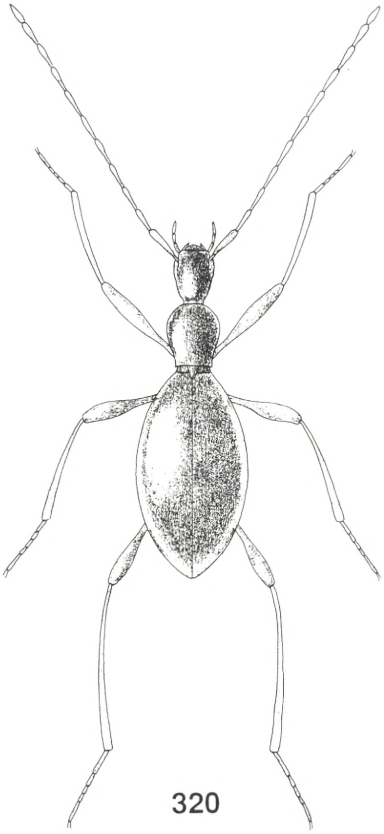

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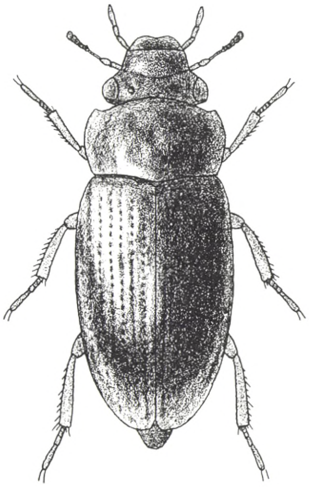

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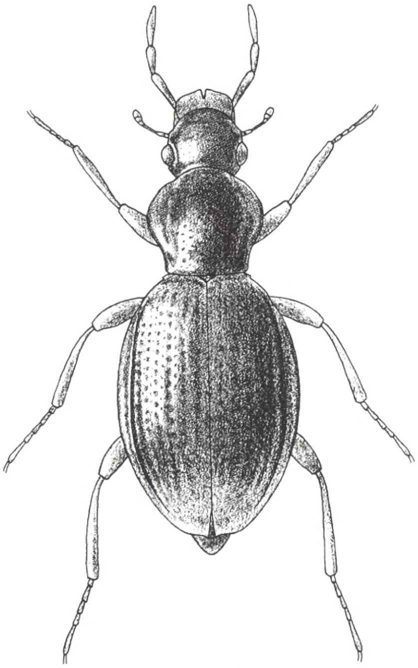
PLATE 38 (Habitus of adults)

Fig. 322. *Podaena maclellani,* Hydraenidae-Hydraeninae (Hydraenini), 2.2 mm
Fig. 323. *Limnebius parvulus,* Hydraenidae-Hydraeninae (Hydraenini), 2.2 mm (after V. Hansen)
Fig. 324. *Hydraena gracilis,* Hydraenidae-Hydraeninae (Hydraenini), 2.2 mm (after V. Hansen)
Fig. 325. *Prosthetops megacephalus,* Hydraenidae-Prosthetopinae (Prosthetopini), 2.6 mm



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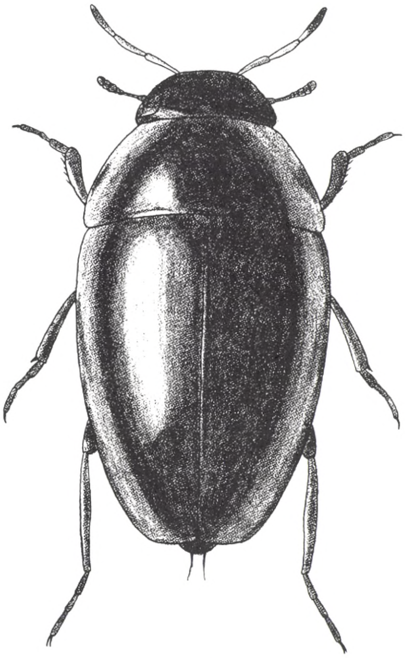

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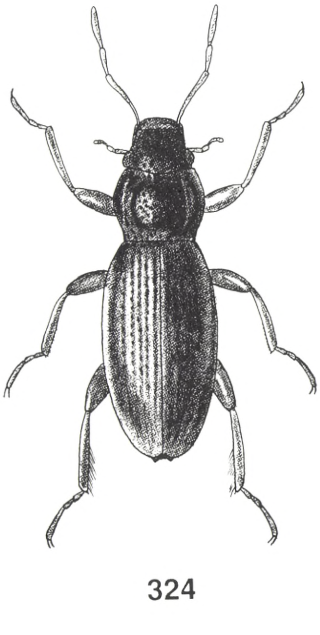

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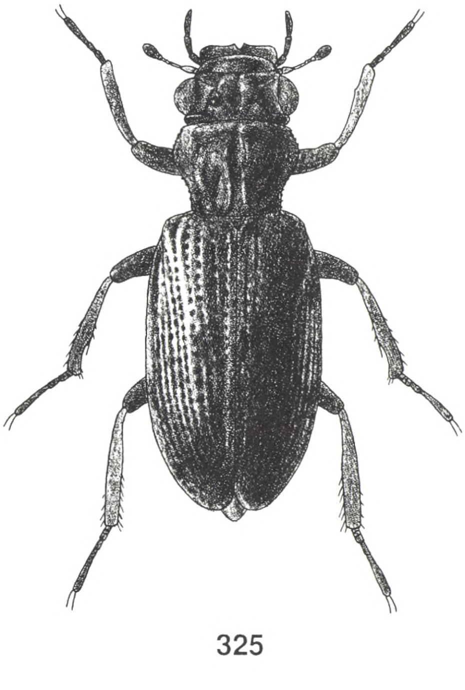

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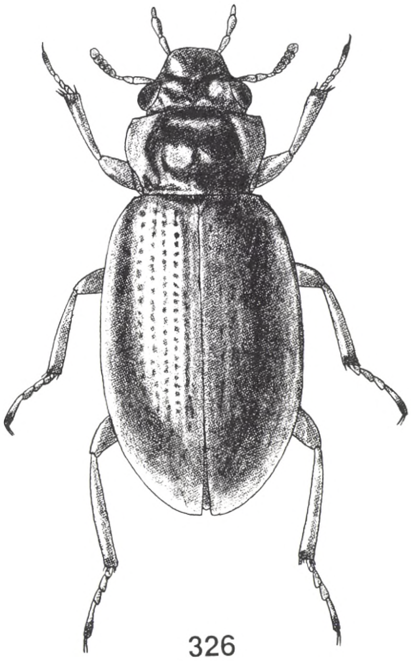
PLATE 39 (Habitus of adults)

Fig. 326. *Ochthebius marinus*, Hydraenidae-Ochthebiinae, 2.0 mm (after V. Hansen)
Fig. 327. *Meropathus zelandicus*, Hydraenidae-Ochthebiinae, 2.5 mm
Fig. 328. *Nossidium pilosellum*, Ptiliidae-Ptiliinae (Nossidine section), 1.2 mm
Fig. 329. *Ptenidium pusillum*, Ptiliidae-Ptiliinae (Ptiliine section), 1.0 mm (after V. Hansen)



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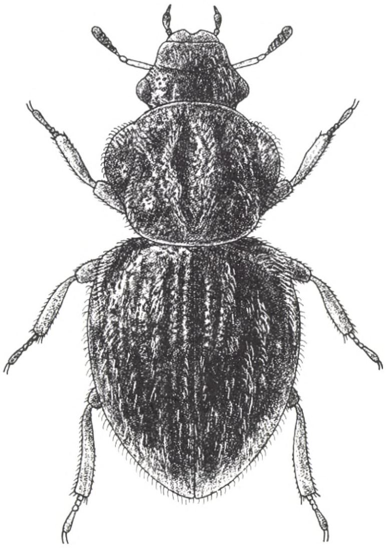

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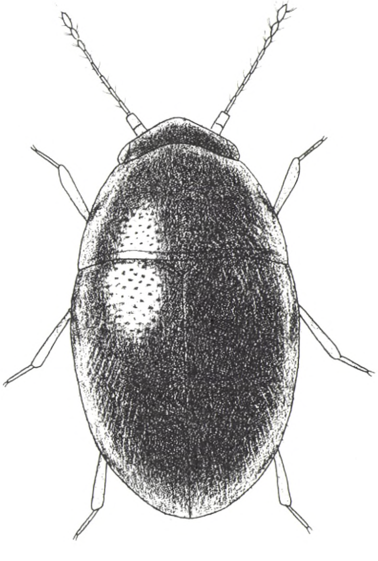

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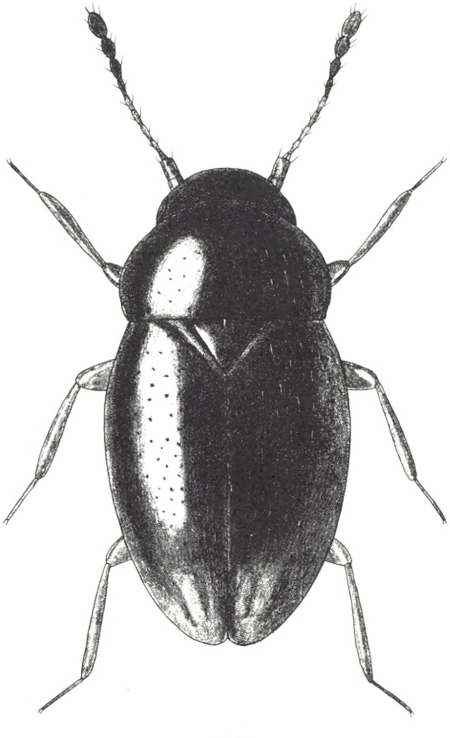

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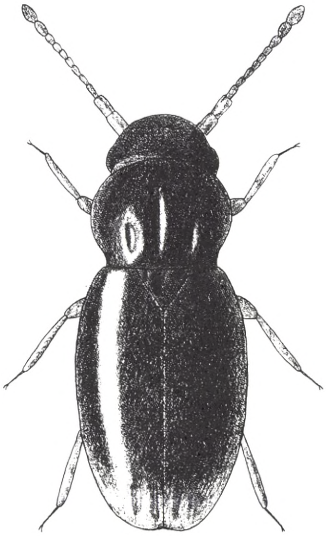
PLATE 40 (Habitus of adults)

Fig. 330. *Ptilium minutissimum*, Ptiliidae-Ptiliinae (Ptiliine section), 0.6 mm (after V. Hansen)
Fig. 331. *Pteryx suturalis*, Ptiliidae-Ptiliinae (Pterycine section), 0.8 mm (after V. Hansen)
Fig. 332. *Ptinella aptera*, Ptiliidae-Ptiliinae (Pterycine section), 0.6 mm (after V. Hansen)
Fig. 333. *Actidium boudieri*, Ptiliidae-Ptiliinae (Actidiine section), 0.6 mm (after V. Hansen)



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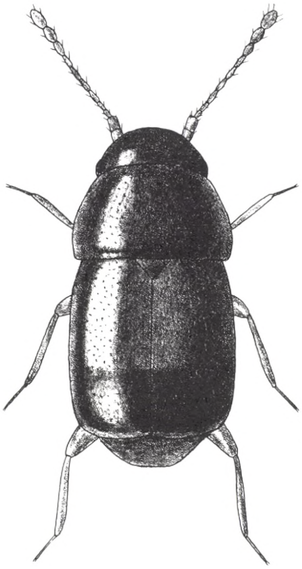

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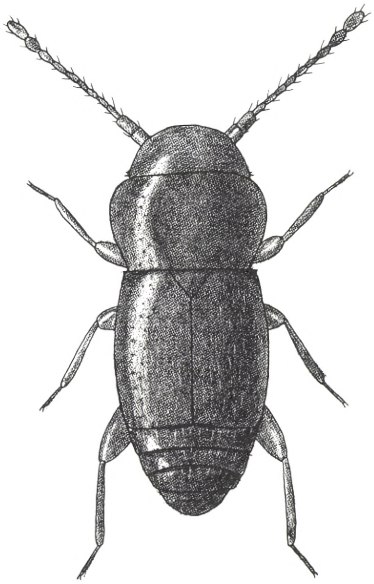

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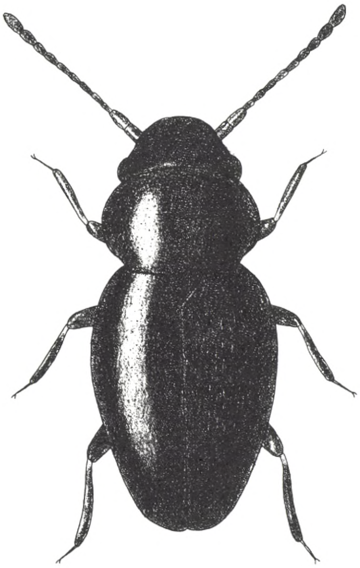

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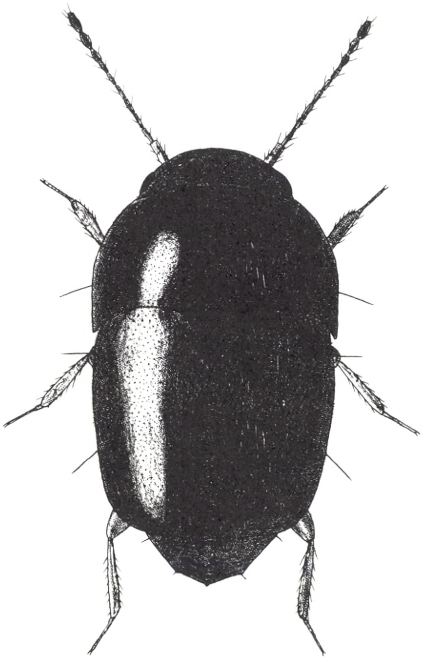
PLATE 41 (Habitus of adults)

Fig. 334. *Acrotrichis grandicollis*, Ptiliidae-Acrotrichinae, 0.9 mm (after V. Hansen)
Fig. 335. *Limulodes paradoxus*, Ptiliidae-Cephaloplectinae, 1.0 mm
Fig. 336. *Nanosella* sp., Ptiliidae-Nanosellinae, 0.4 mm
Fig. 337. *Eutheia schaumi*, Scydmaenidae-Scydmaeninae (Eutheiini), 1.3 mm (after V. Hansen)



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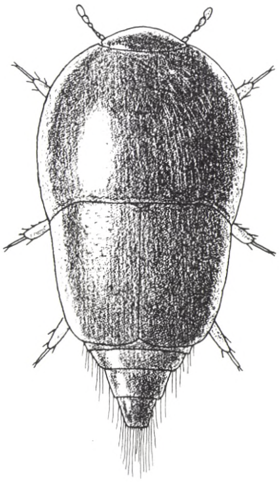

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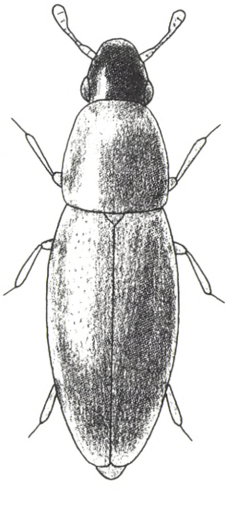

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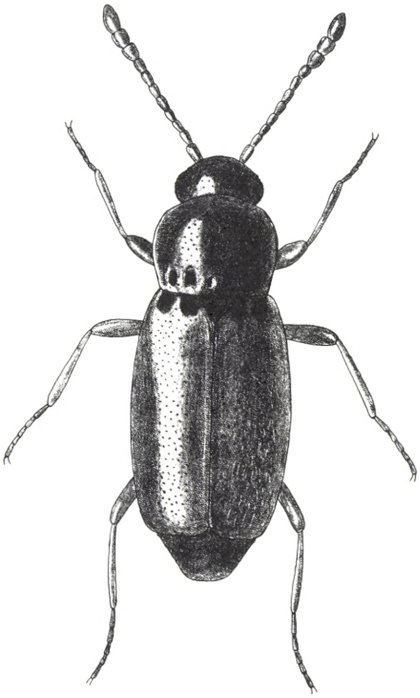

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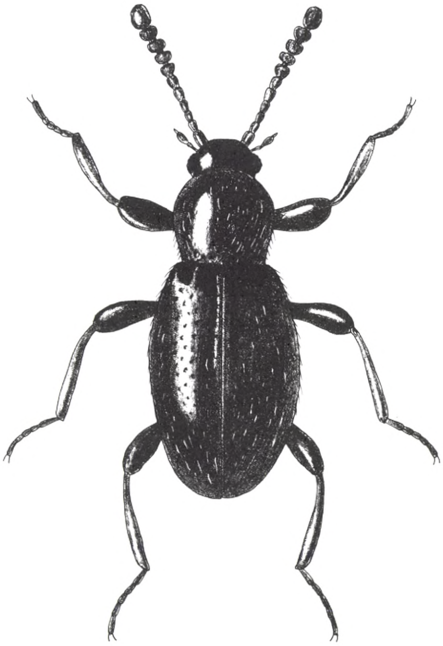
PLATE 42 (Habitus of adults)

Fig. 338. *Stenichnus collaris*, Scydmaenidae-Scydmaeninae (Cyrtoscydmini), 1.4 mm (after V. Hansen)
Fig. 339. *Euconnus rutilipennis*, Scydmaenidae-Scydmaeninae (Cyrtoscydmini), 1.6 mm (after V. Hansen)
Fig. 340. *Scydmaenus tarsatus*, Scydmaenidae-Scydmaeninae (Scydmaenini), 2.0 mm (after V. Hansen)
Fig. 341. *Leptomastax cocquereli*, Scydmaenidae-Scydmaeninae (Leptomastacini), 1.9 mm



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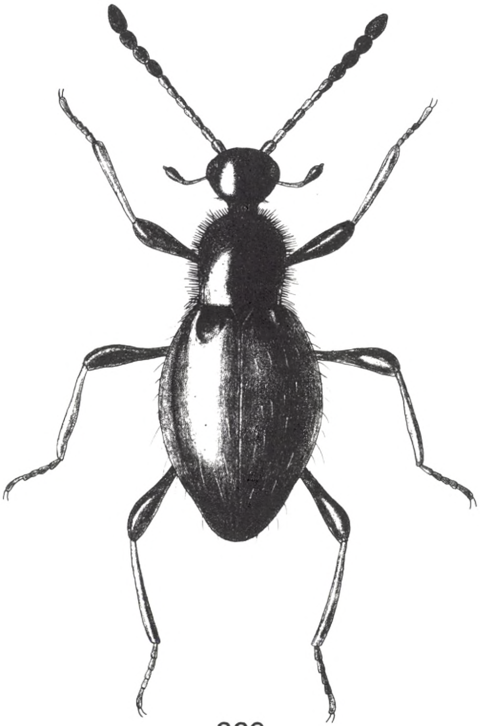

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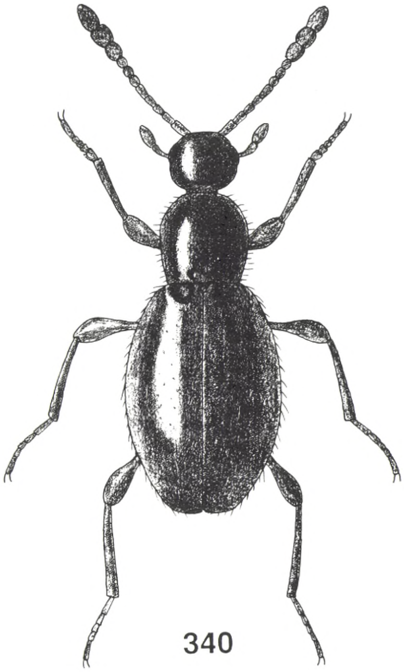

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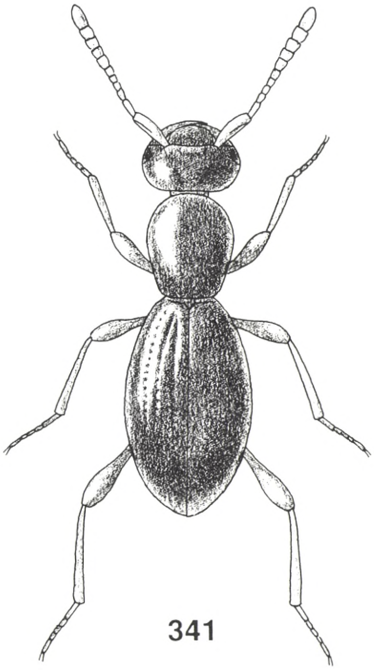

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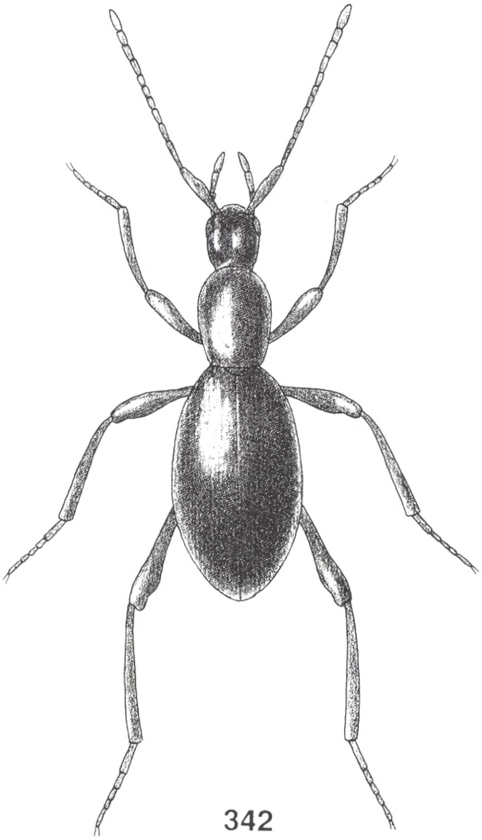
PLATE 43 (Habitus of adults)

Fig. 342. *Mastigus palpalis,* Scydmaenidae-Mastiginae (Mastigini), 3.5 mm
Fig. 343. *Clidicus* sp., Scydmaenidae-Mastiginae (Clidicini), 6.7 mm
Fig. 344. *Scaphidium quadrimaculatum,* Scaphidiidae (Scaphidiini), 5.5 mm (after V. Hansen)
Fig. 345. *Scaphisoma agaricinum,* Scaphidium (Scaphisomatini), 1.8 mm (after V. Hansen)



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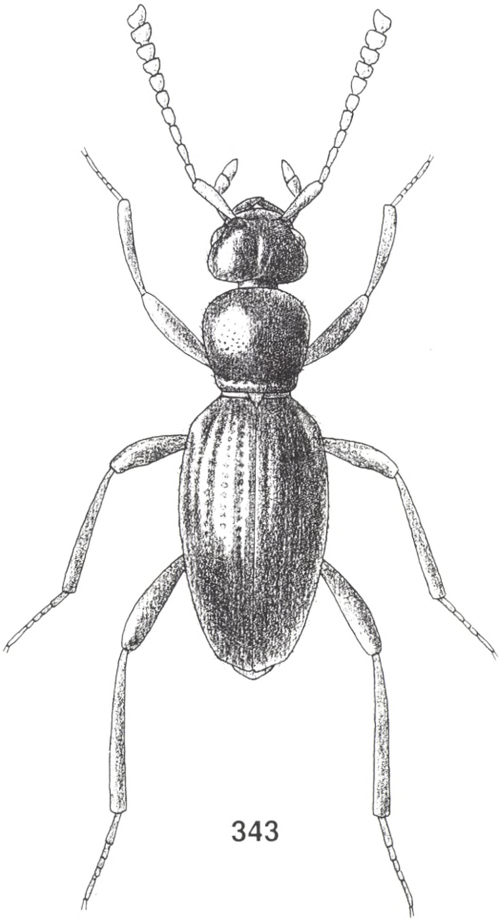

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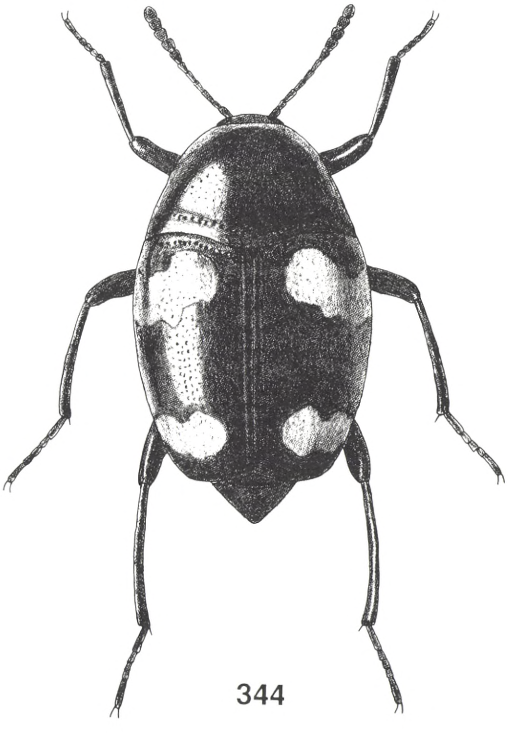

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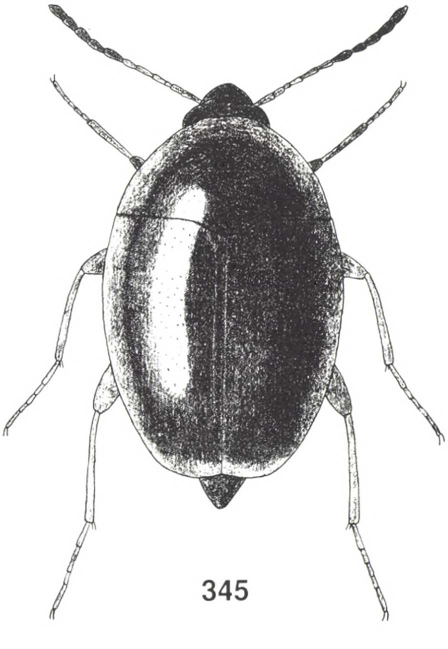

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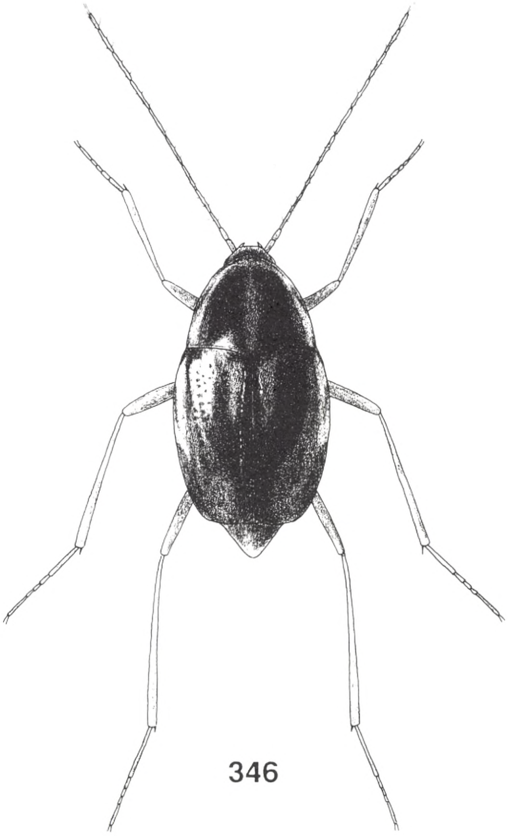
PLATE 44 (Habitus of adults)

Fig. 346. *Bironium nigrolineatum*, Scaphidiidae (Heteroscaphini), 2.9 mm
Fig. 347. *Empelus brunnipennis*, Empelidae, 1.5 mm
Fig. 348. *Nodynus leucofasciatus*, Apateticidae, 10.0 mm
Fig. 349. *Diamesus osculans*, Silphidae-Silphinae, 30 mm



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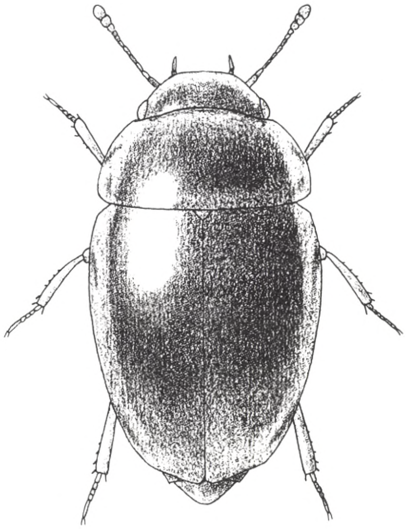

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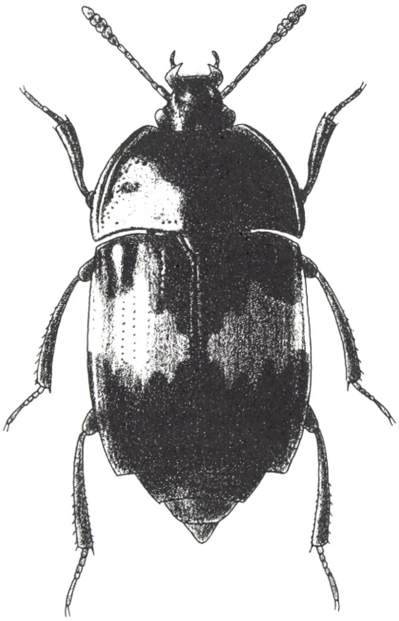

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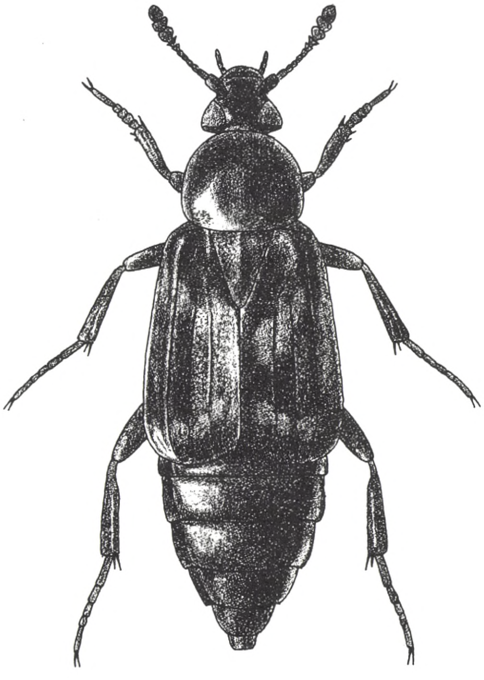

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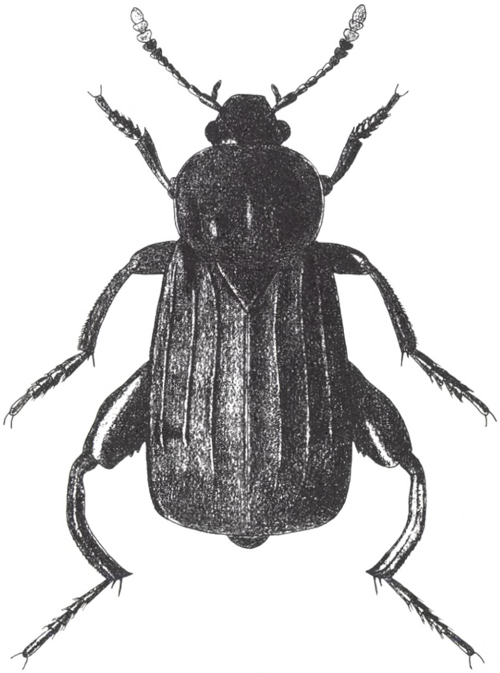
PLATE 45 (Habitus of adults)

Fig. 350. *Necrodes litoralis*, Silphidae-Silphinae, 20 mm (after V. Hansen)
Fig. 351. *Oiceoptoma thoracica*, Silphidae-Silphinae, 14 mm (after V. Hansen)
Fig. 352. *Silpha carinata*, Silphidae-Silphinae, 17 mm (after V. Hansen)
Fig. 353. *Nicrophorus investigator*, Silphidae-Nicrophorinae, 20 mm (after V. Hansen)



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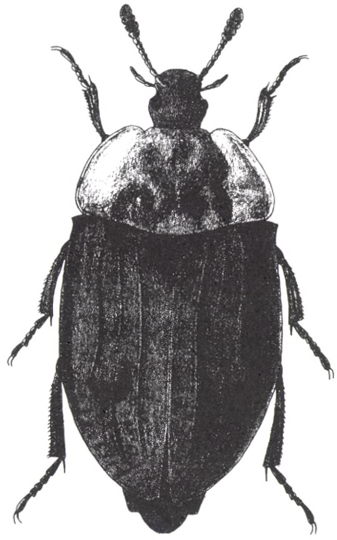

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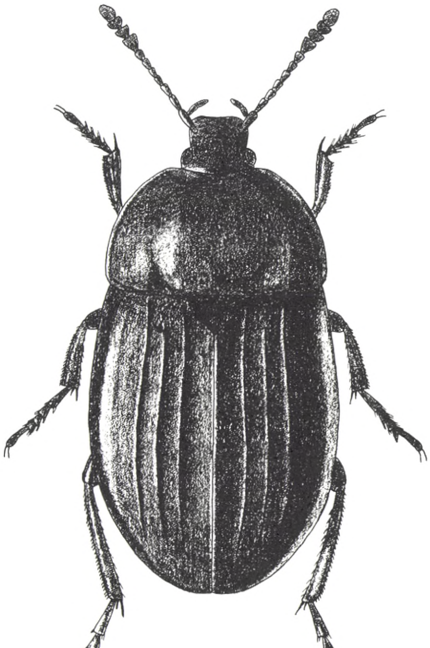

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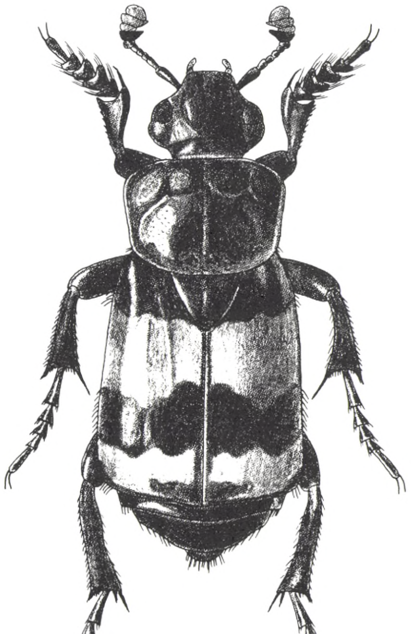

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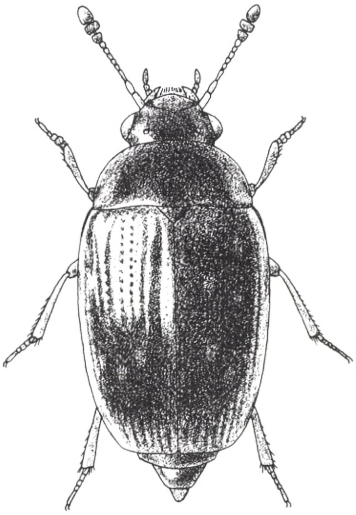
PLATE 46 (Habitus of adults)

Fig. 354. *Glypholoma rotundulum*, Staphylinidae-Glypholomatinae, 2.2 mm
Fig. 355. *Microsilpha* sp., Staphylinidae-Microsilphinae, 2.6 mm
Fig. 356. *Omalium rivulare*, Staphylinidae-Omaliinae (Omaliini), 3.8 mm (after V. Hansen)
Fig. 357. *Micralymma marinum*, Staphylinidae-Omaliinae (Omaliini), 2.9 mm
Fig. 358. *Eusphalerum minutum*, Staphylinidae-Omaliinae (Eusphalerini), 2.5 mm (after V. Hansen)
Fig. 359. *Anthophagus caraboides*, Staphylinidae-Omaliinae (Anthophagini), 4.7 mm (after V. Hansen)



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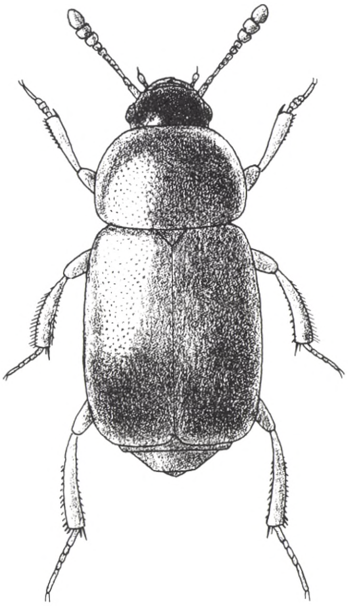

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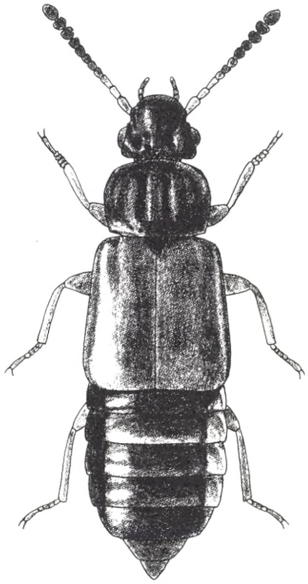

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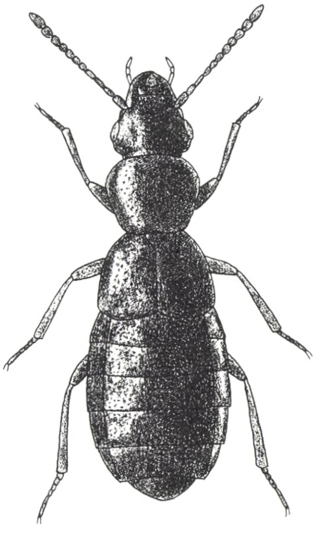

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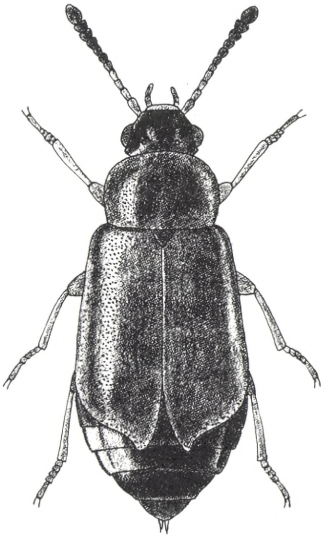

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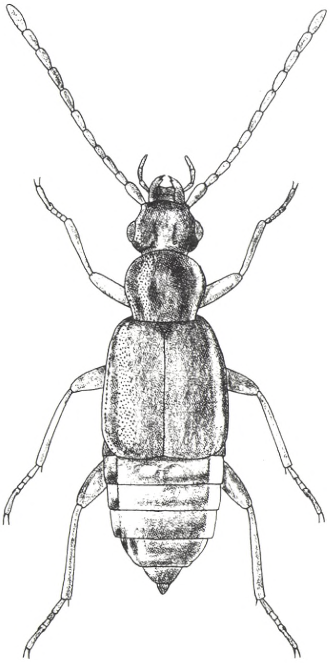

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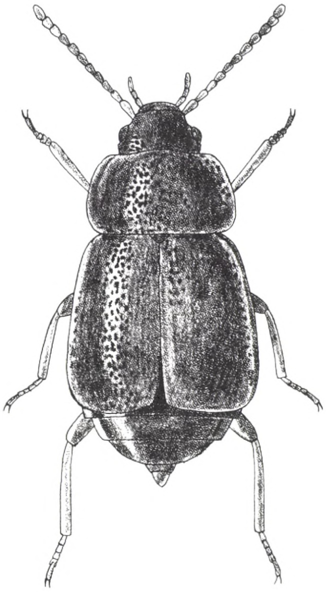
PLATE 47 (Habitus of adults)

Fig. 360. *Olophrum piceum*, Staphylinidae-Omaliinae (Anthophagini), 5.0 mm (after V. Hansen)
Fig. 361. *Aphaenostemmus testaceus*, Staphylinidae-Omaliinae (Aphaenostemmini), 3.5 mm
Fig. 362. *Coryphium angusticolle*, Staphylinidae-Omaliinae (Coryphiini), 2.8 mm
Fig. 363. *Nesoneus acuticeps*, Staphylinidae-Proteininae (Nesoneini), 2.0 mm
Fig. 364. *Anepius koebelei*, Staphylinidae-Proteininae (Anepiini), 2.3 mm
Fig. 365. *Metopsia clypeata*, Staphylinidae-Proteininae (Proteinini), 2.7 mm (after V. Hansen)



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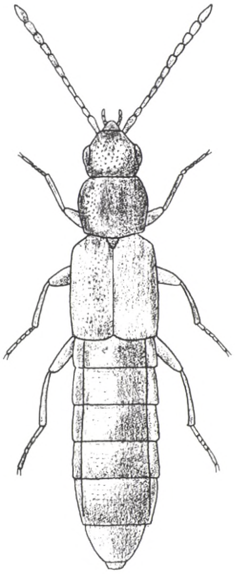

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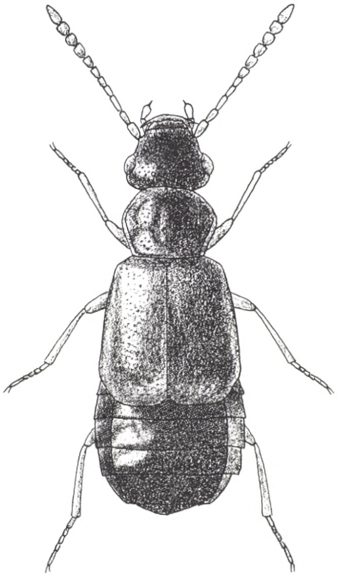

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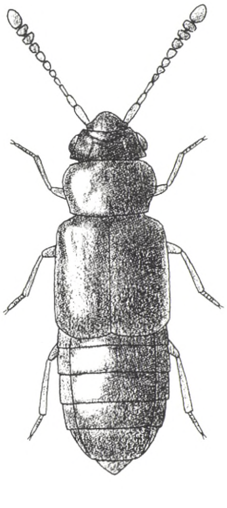

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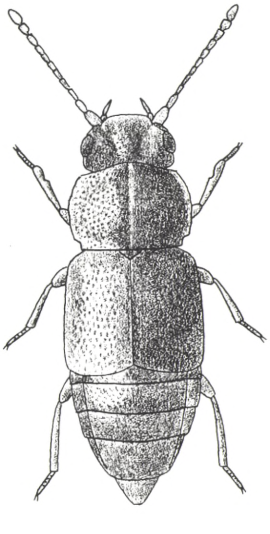

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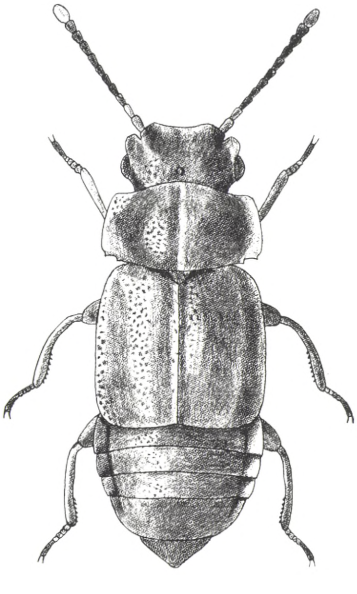

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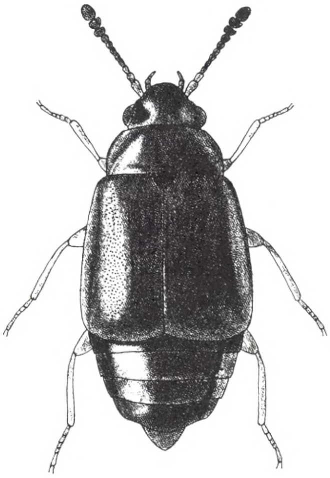
PLATE 48 (Habitus of adults)

Fig. 366. *Proteinus brachypterus*, Staphylinidae-Proteininae (Proteinini), 1.8 mm (after V. Hansen)
Fig. 367. *Micropeplus porcatus*, Staphylinidae-Micropeplinae, 2.4 mm (after V. Hansen)
Fig. 368. *Neophonus brucki*, Staphylinidae-Neophoninae, 3.3 mm
Fig. 369. *Dasycerus sulcatus*, Staphylinidae-Dasycerinae, 1.8 mm
Fig. 370. *Faronus lafertei*, Staphylinidae-Pselaphinae (Faronini), 1.5 mm



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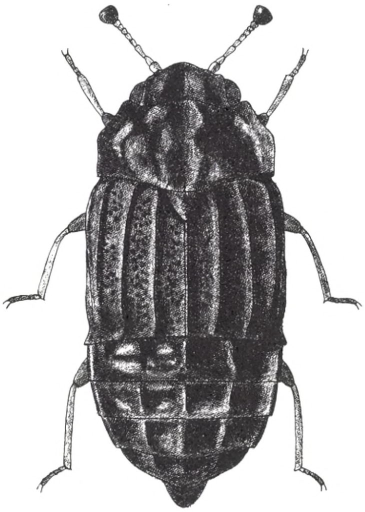

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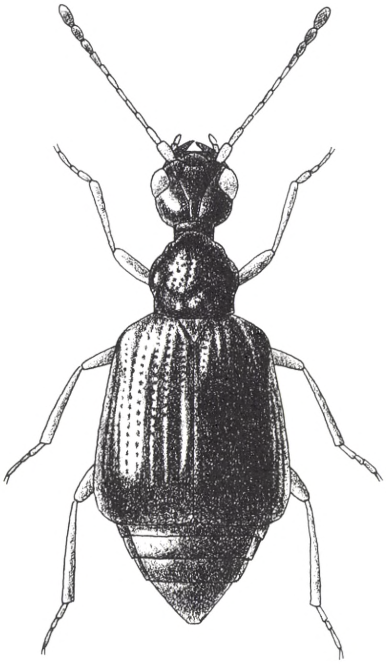

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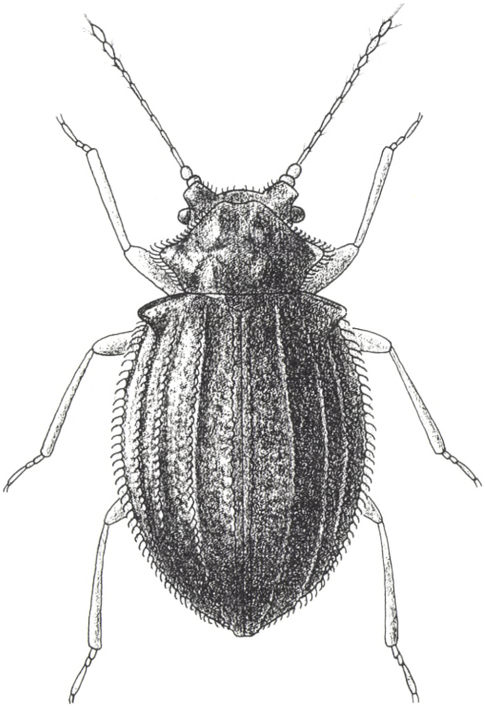

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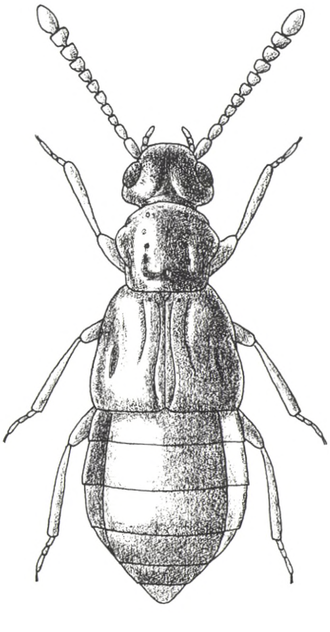

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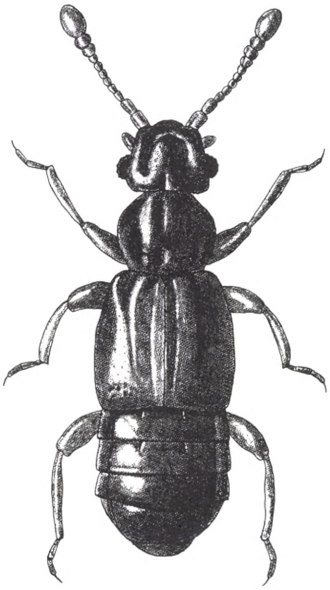
PLATE 49 (Habitus of adults)

Fig. 371. *Euplectus nanus*, Staphylinidae-Pselaphinae (Euplectini), 1.5 mm (after V. Hansen)
Fig. 372. *Batrisodes venustus*, Staphylinidae-Pselaphinae (Batrisini), 2.0 mm (after V. Hansen)
Fig. 373. *Trichonyx sulcicollis*, Staphylinidae-Pselaphinae (Goniacerini), 3.0 mm (after V. Hansen)
Fig. 374. *Rybaxis longicornis*, Staphylinidae-Pselaphinae (Goniacerini), 1.9 mm (after V. Hansen)



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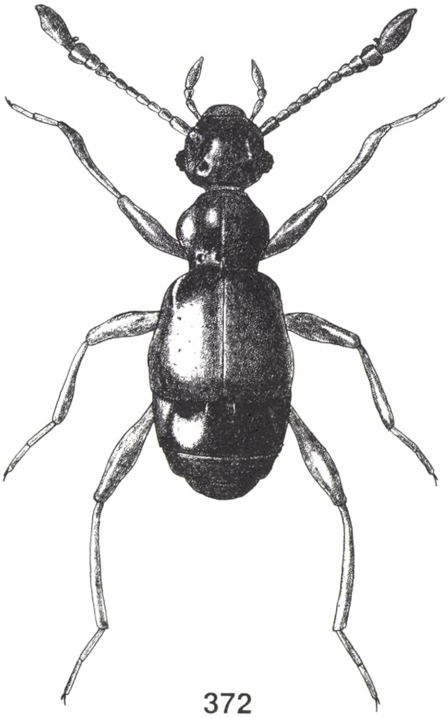

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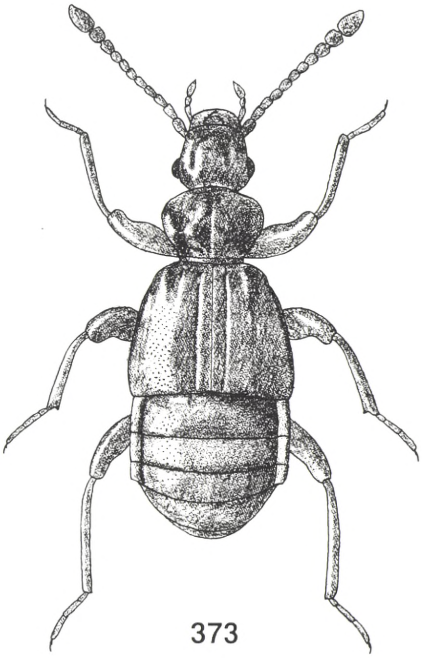

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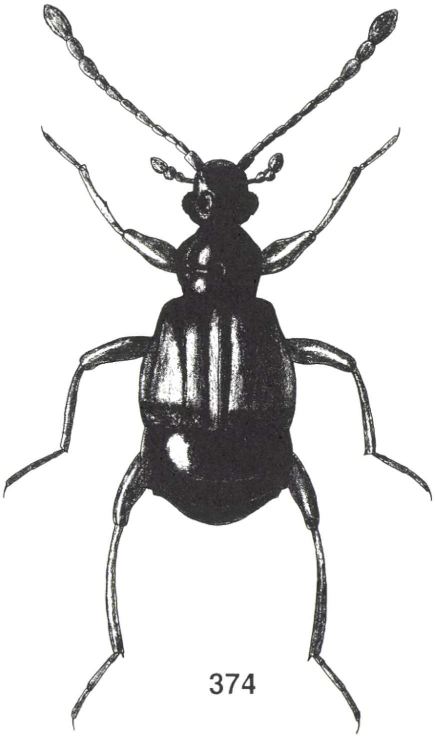

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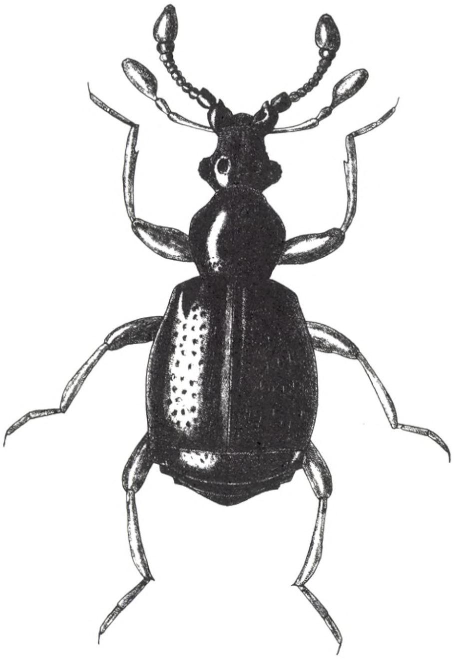
PLATE 50 (Habitus of adults)

Fig. 375. *Bryaxis bulbifer*, Staphylinidae-Pselaphinae (Goniacerini), 1.3 mm (after V. Hansen)
Fig. 376. *Tychus niger*, Staphylinidae-Pselaphinae (Goniacerini), 1.4 mm (after V. Hansen)
Fig. 377. *Pselaphus heisei*, Staphylinidae-Pselaphinae (Pselaphini), 1.7 mm (after V. Hansen)
Fig. 378. *Claviger testaceus*, Staphylinidae-Pselaphinae (Clavigerini), 2.2 mm (after V. Hansen)



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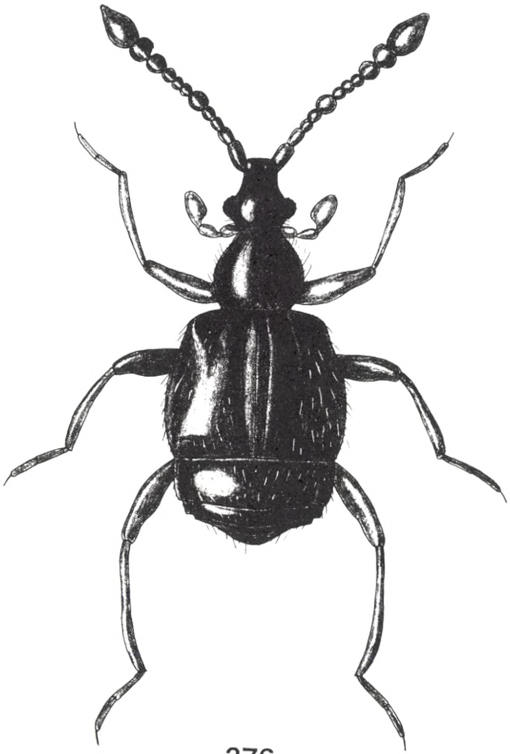

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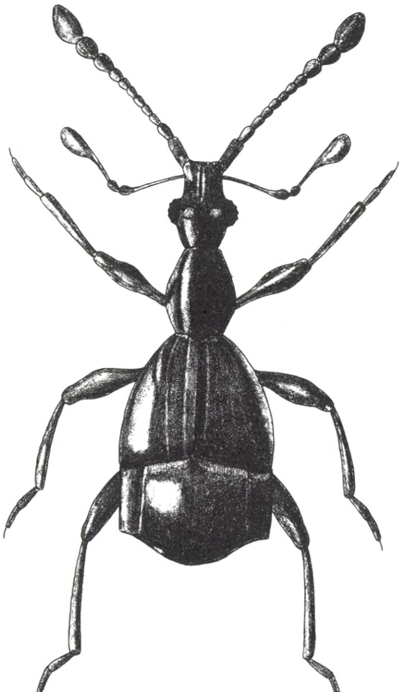

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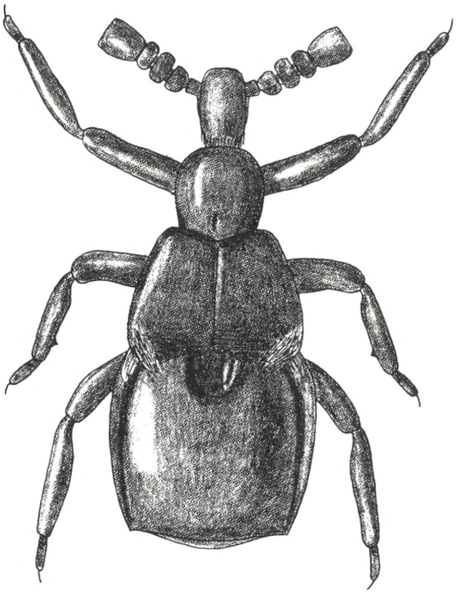

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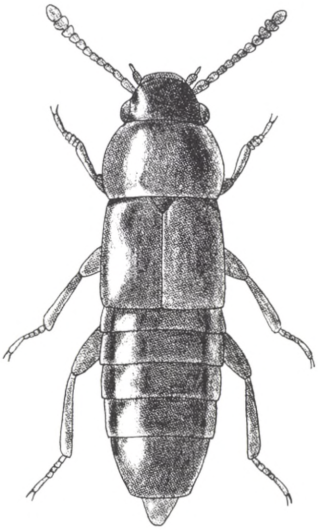
PLATE 51 (Habitus of adults)

Fig. 379. *Phloeocharis subtillissima*, Staphylinidae-Phloeocharinae, 1.7 mm (after V. Hansen)
Fig. 380. *Olisthaerus substriatus*, Staphylinidae-Olisthaerinae, 6.0 mm
Fig. 381. *Derops longicornis*, Staphylinidae-Tachyporinae (Deropini), 4.7 mm
Fig. 382. *Mycetoporus lepidus*, Staphylinidae-Tachyporinae (Mycetoporini), 4.5 mm (after V. Hansen)
Fig. 383. *Lordithon lunulatus*, Staphylinidae-Tachyporinae (Mycetoporini), 5.5 mm (after V. Hansen)
Fig. 384. *Sepedophilus litoreus*, Staphylinidae-Tachyporinae (Tachyporini), 4.5 mm (after V. Hansen)



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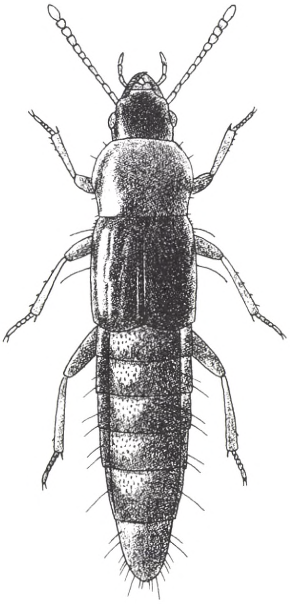

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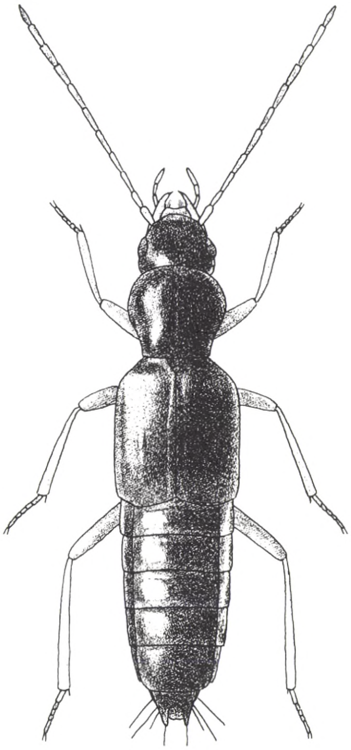

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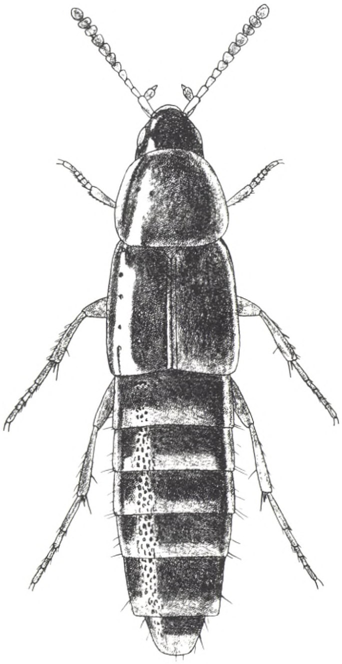

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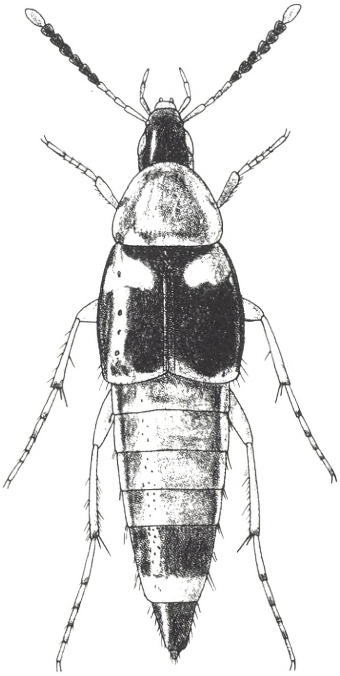

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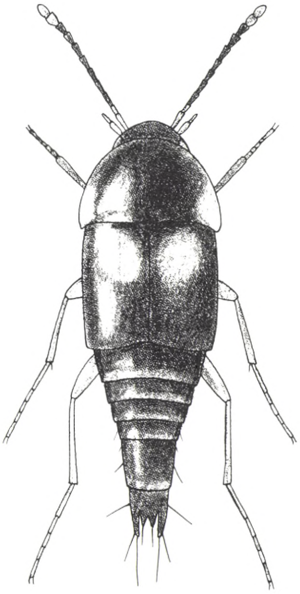

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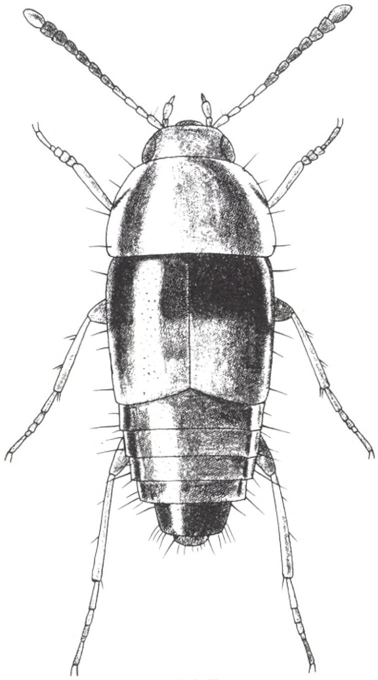
PLATE 52 (Habitus of adults)

Fig. 385. *Tachyporus obtusus*, Staphylinidae-Tachyporinae (Tachyporini), 3.7 mm (after V. Hansen)
Fig. 386. *Tachinus elongatus*, Staphylinidae-Tachyporinae (Tachyporini), 8.0 mm (after V. Hansen)
Fig. 387. *Trichophya pilicornis*, Staphylinidae-Trichophyinae, 2.7 mm (after V. Hansen)
Fig. 388. *Habrocerus capillaricornis*, Staphylinidae-Habrocerinae, 3.3 mm (after V. Hansen)
Fig. 389. *Gymnusa brevicollis*, Staphylinidae-Aleocharinae (Gymnusini), 5.2 mm (after V. Hansen)
Fig. 390. *Deinopsis erosa*, Staphylinidae-Aleocharinae (Deinopsini), 3.3 mm (after V. Hansen)



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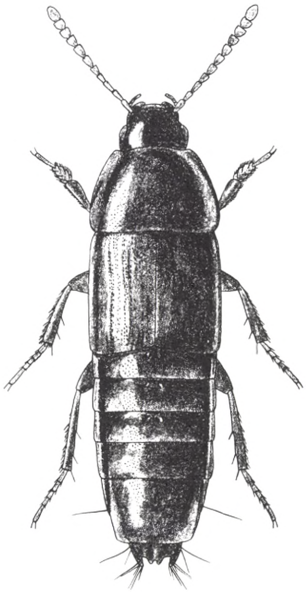

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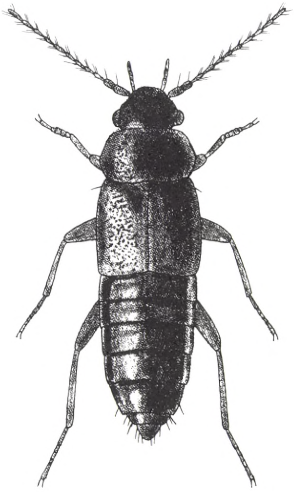

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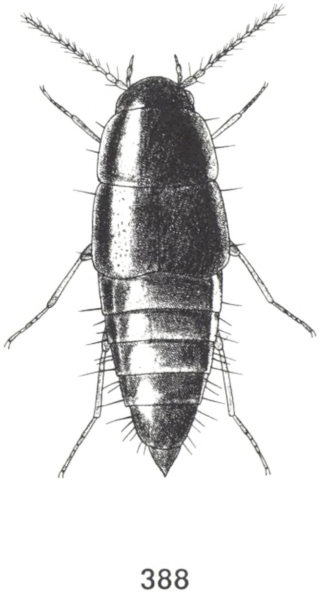

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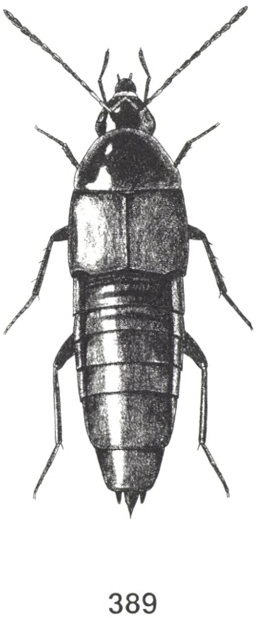

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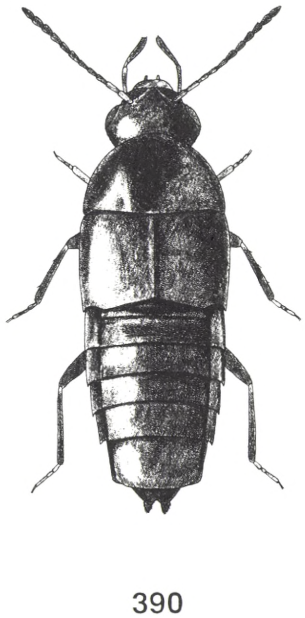

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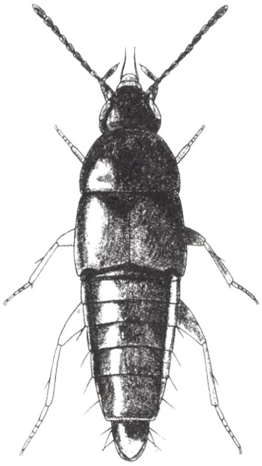
PLATE 53 (Habitus of adults)

Fig. 391. *Myllaena intermedia*, Staphylinidae-Aleocharinae (Myllaenini), 2.3 mm (after V. Hansen)
Fig. 392. *Aleochara bipustulata*, Staphylinidae-Aleocharinae (Aleocharini), 3.0 mm (after V. Hansen)
Fig. 393. *Tinotus morion*, Staphylinidae-Aleocharinae (Hoplandrini), 2.0 mm (after V. Hansen)
Fig. 394. *Oxypoda annullaris*, Staphylinidae-Aleocharinae (Oxypodini), 2.3 mm (after V. Hansen)
Fig. 395. *Ocyusa maura*, Staphylinidae-Aleocharinae (Oxypodini), 2.2 mm (after V. Hansen)
Fig. 396. *Calodera riparia*, Staphylinidae-Aleocharinae (Oxypodini), 3.0 mm (after V. Hansen)



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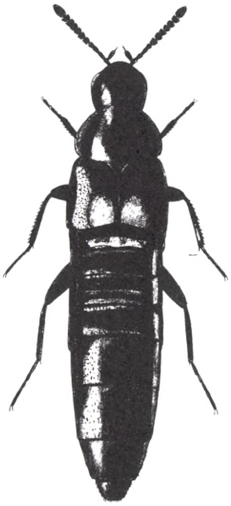

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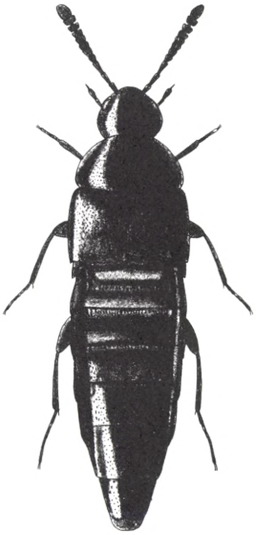

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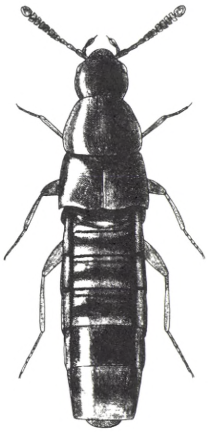

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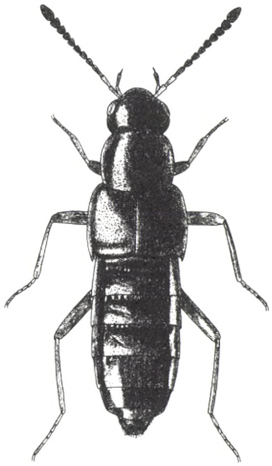

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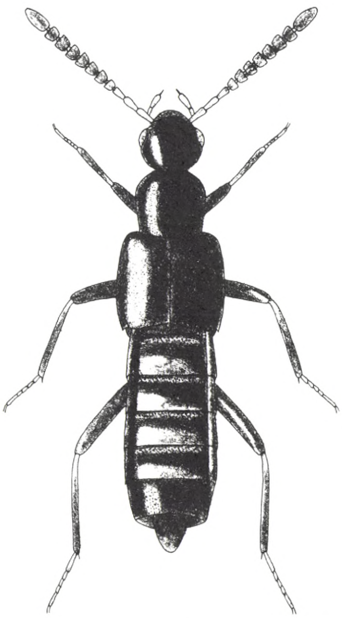

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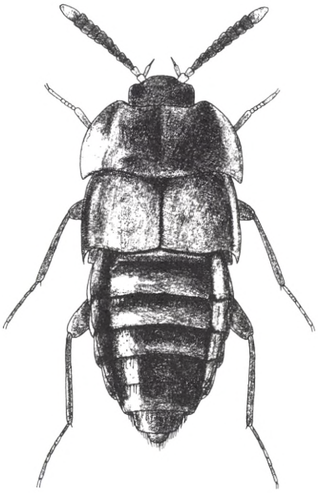
PLATE 54 (Habitus of adults)

Fig. 397. *Dinarda maerkelii*, Staphylinidae-Aleocharinae (Oxypodini), 4.7 mm (after V. Hansen)
Fig. 398. *Meotica apicalis*, Staphylinidae-Aleocharinae (Oxypodini), 1.6 mm (after V. Hansen)
Fig. 399. *Ischnopoda constricta*, Staphylinidae-Aleocharinae (Oxypodini), 3.0 mm (after V. Hansen)
Fig. 400. *Geostiba circellaris*, Staphylinidae-Aleocharinae (Athetini), 3.2 mm (after V. Hansen)
Fig. 401. *Atheta graminicola*, Staphylinidae-Aleocharinae (Athetini), 4.2 mm (after V. Hansen)
Fig. 402. *Amischa analis*, Staphylinidae-Aleocharinae (Athetini), 2.1 mm (after V. Hansen)



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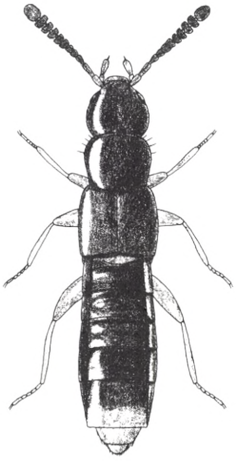

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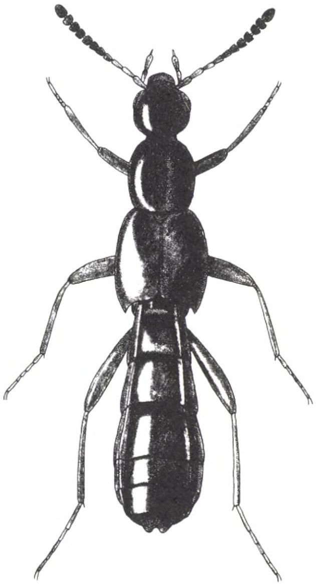

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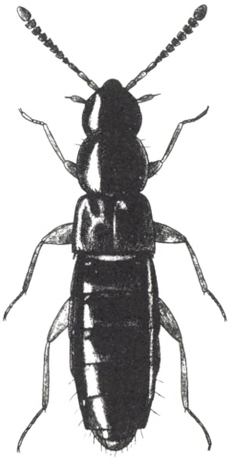

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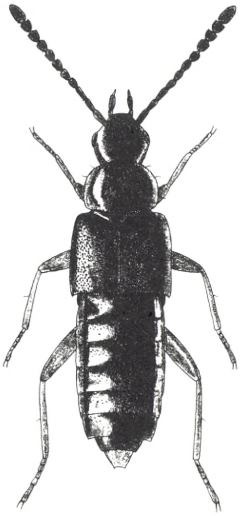

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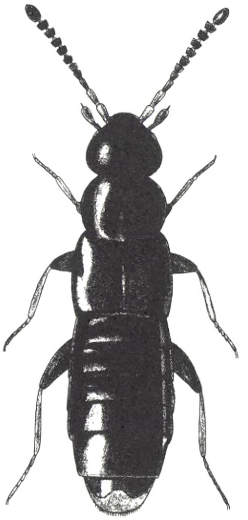
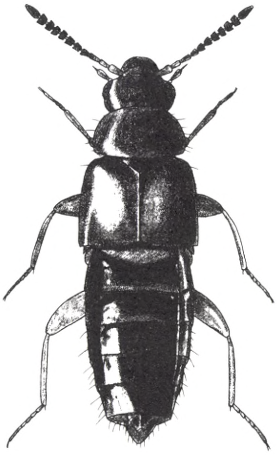


402

PLATE 55 (Habitus of adults)

Fig. 403. *Thamiaraea cinnamomea*, Staphylinidae-Aleocharinae (Athetini), 4.5 mm (after V. Hansen)
Fig. 404. *Falagria caesa*, Staphylinidae-Aleocharinae (Falagriini), 2.4 mm (after V. Hansen)
Fig. 405. *Drusilla canaliculata*, Staphylinidae-Aleocharinae (Lomechusini), 4.5 mm (after V. Hansen)
Fig. 406. *Zyras humeralis*, Staphylinidae-Aleocharinae (Lomechusini), 6.0 mm (after V. Hansen)
Fig. 407. *Lomechusa emarginata*, Staphylinidae-Aleocharinae (Lomechusini), 4.3 mm (after V. Hansen)
Fig. 408. *Gyrophaena affinis*, Staphylinidae-Aleocharinae (Homalotini), 1.7 mm (after V. Hansen)



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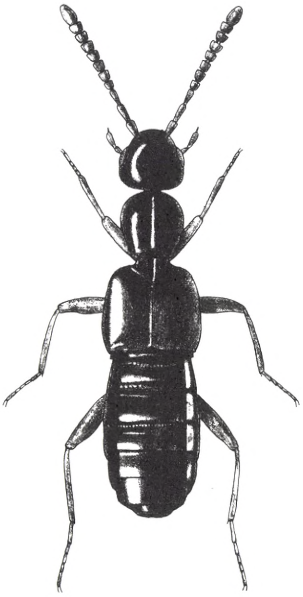

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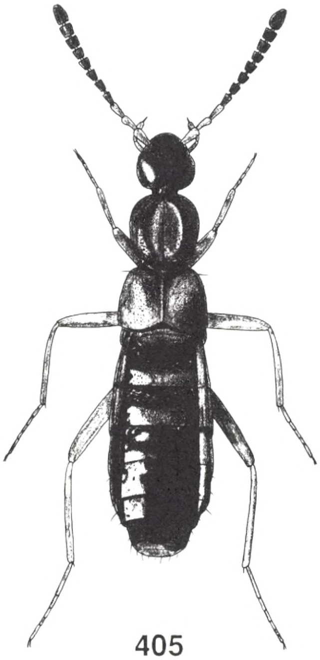

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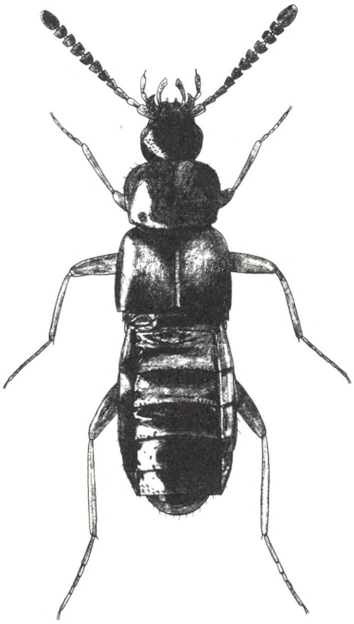

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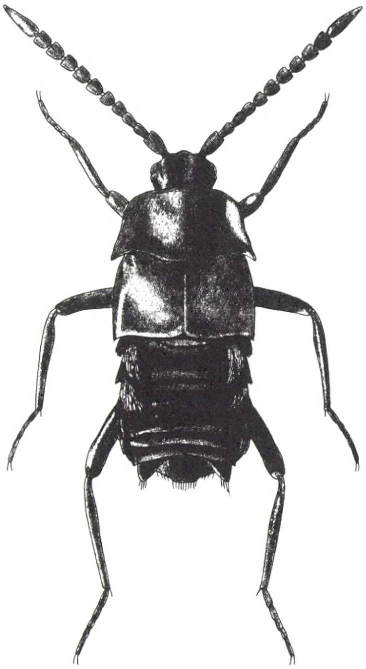

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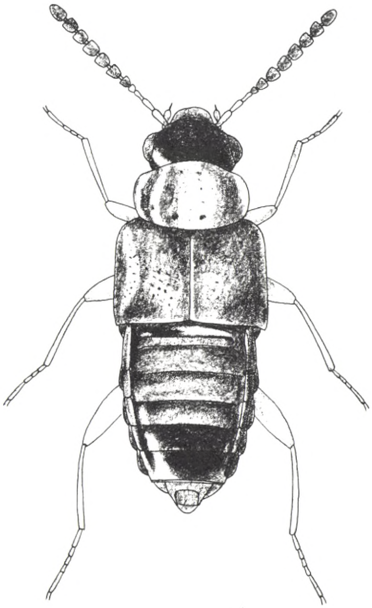

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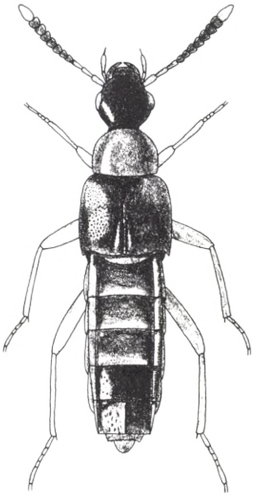
PLATE 56 (Habitus of adults)

Fig. 409. *Bolitochara lunulata*, Staphylinidae-Aleocharinae (Homalotini), 4.2 mm (after V. Hansen)
Fig. 410. *Homalota plana*, Staphylinidae-Aleocharinae (Homalotini), 2.7 mm (after V. Hansen)
Fig. 411. *Phytosus balticus*, Staphylinidae-Aleocharinae (Phytosini), 2.2 mm (after V. Hansen)
Fig. 412. *Diglotta submarina*, Staphylinidae-Aleocharinae (Diglottini), 2.0 mm (after V. Hansen)
Fig. 413. *Hygronoma dimidiata*, Staphylinidae-Aleocharinae (Hygronomini), 2.7 mm (after V. Hansen)
Fig. 414. *Oligota inflata*, Staphylinidae-Aleocharinae (Hypocyphtini), 1.0 mm (after V. Hansen)



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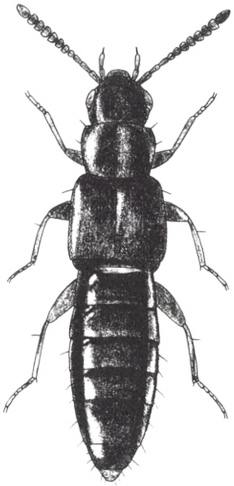

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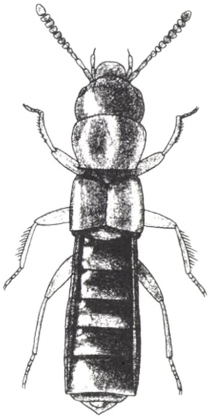

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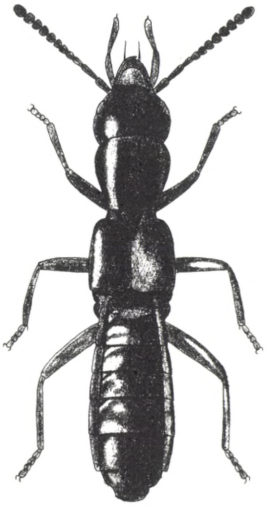

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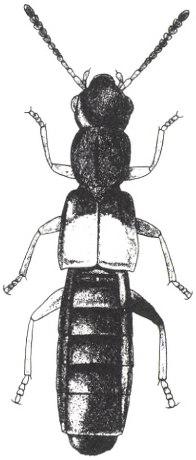

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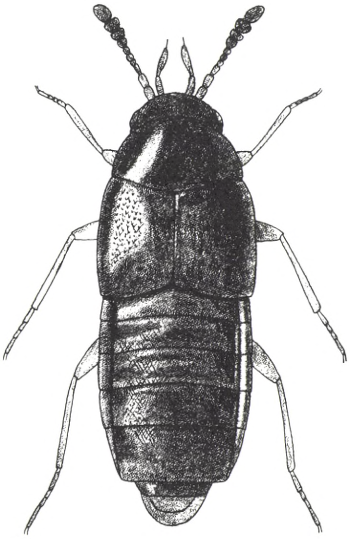

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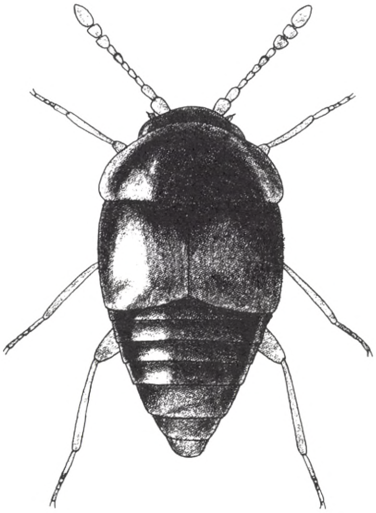
PLATE 57 (Habitus of adults)

Fig. 415. *Cypha discoidea*, Staphylinidae-Aleocharinae (Hypocyphtini), 1.2 mm (after V. Hansen)
Fig. 416. *Termitusa sjoestedti*, Staphylinidae-Aleocharinae (Termitusini), 1.3 mm
Fig. 417. *Pygostenus eppelsheimi*, Staphylinidae-Aleocharinae (Pygostenini), 2.3 mm
Fig. 418. *Trigonurus crotchii*, Staphylinidae-Trigonurinae, 4.1 mm
Fig. 419. *Piestus spinosus*, Staphylinidae-Piestinae, 8.0 mm
Fig. 420. *Thoracophorus corticinus*, Staphylinidae-Osoriinae (Thoracophorini), 2.2 mm



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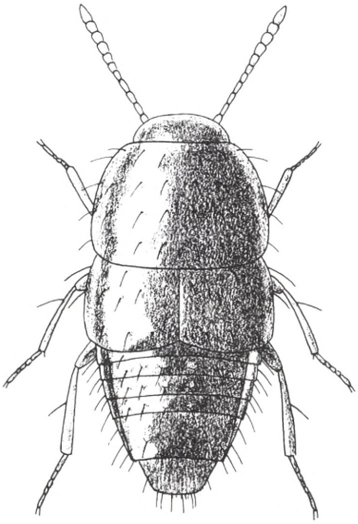

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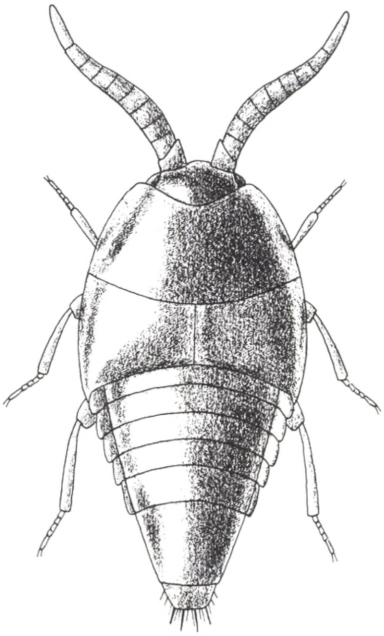

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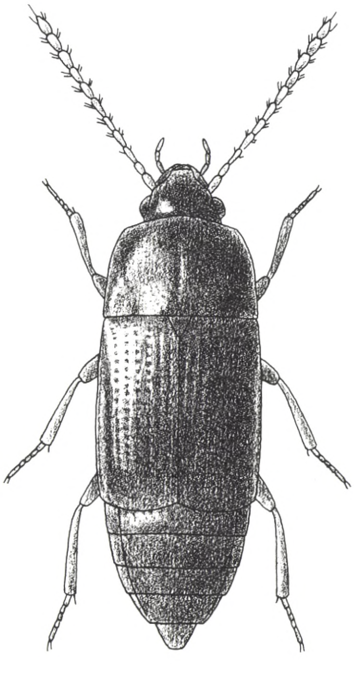

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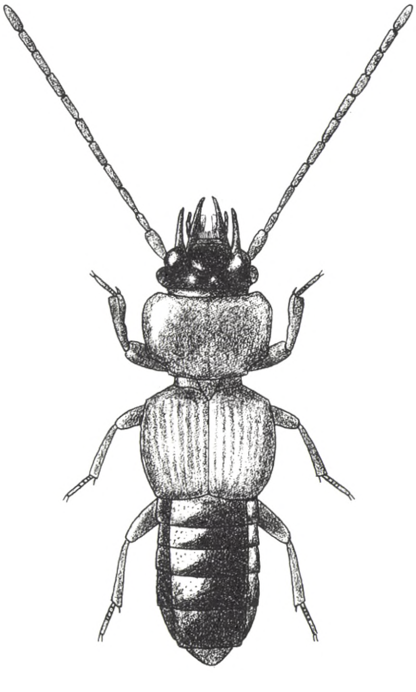

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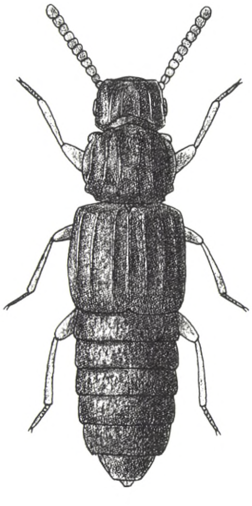

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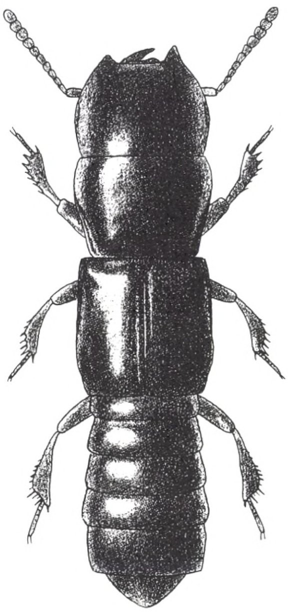
PLATE 58 (Habitus of adults)

Fig. 421. *Osorius brasiliensis*, Staphylinidae-Osoriinae (Osoriini), 12.0 mm
Fig. 422. *Leptochirus mexicanus*, Staphylinidae-Osoriinae (Leptochirini), 16.0 mm
Fig. 423. *Eleusis kraatzi*, Staphylinidae-Osoriinae (Eleusinini), 3.0 mm
Fig. 424. *Syntomium aeneum*, Staphylinidae-Oxytelinae, 2.3 mm (after V. Hansen)
Fig. 425. *Coprophilus striatulus*, Staphylinidae-Oxytelinae, 6.5 mm (after V. Hansen)
Fig. 426. *Anotylus rugosus*, Staphylinidae-Oxytelinae, 4.7 mm (after V. Hansen)



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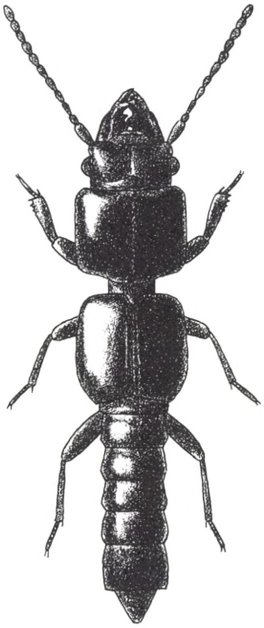

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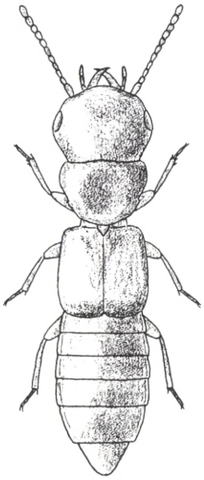

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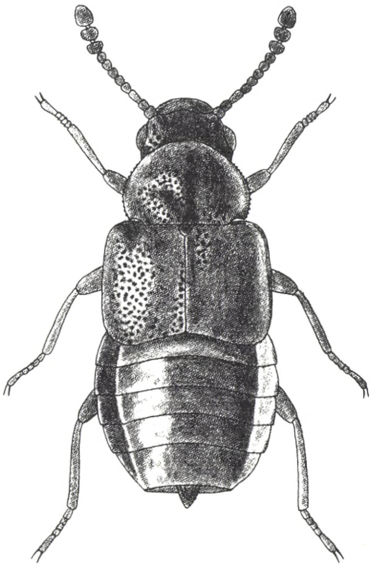

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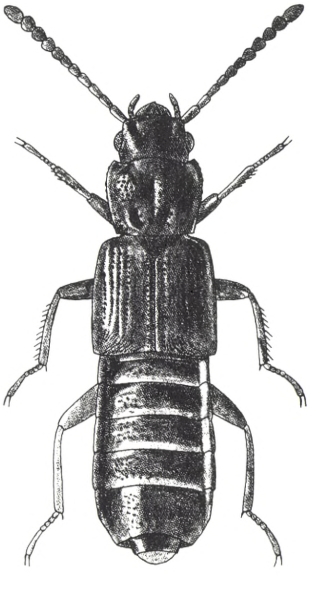

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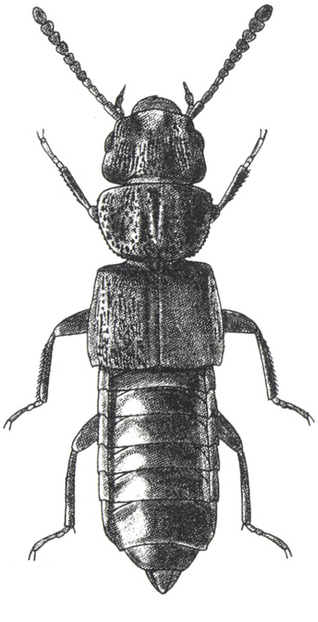

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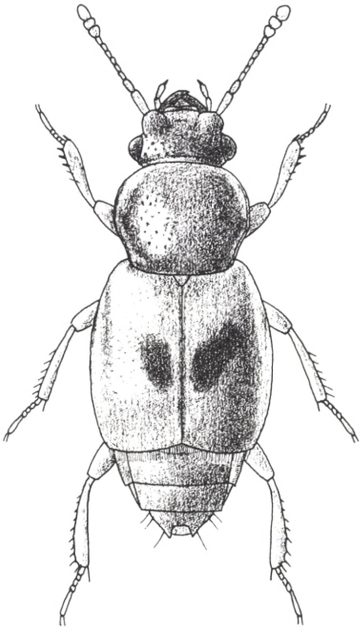
PLATE 59 (Habitus of adults)

Fig. 427. *Sartallus signatus*, Staphylinidae-Oxytelinae, 4.5 mm
Fig. 428. *Oxyporus rufus*, Staphylinidae-Oxyporinae, 9.0 mm (after V. Hansen)
Fig. 429. *Megalopinus punctatus*, Staphylinidae-Megalopsidiinae, 3.8 mm
Fig. 430. *Stenus clavicornis*, Staphylinidae-Steninae, 5.2 mm (after V. Hansen)
Fig. 431. *Euaesthetus bipunctatus*, Staphylinidae-Euaesthetinae (Euaesthetini), 1.7 mm (after V. Hansen)



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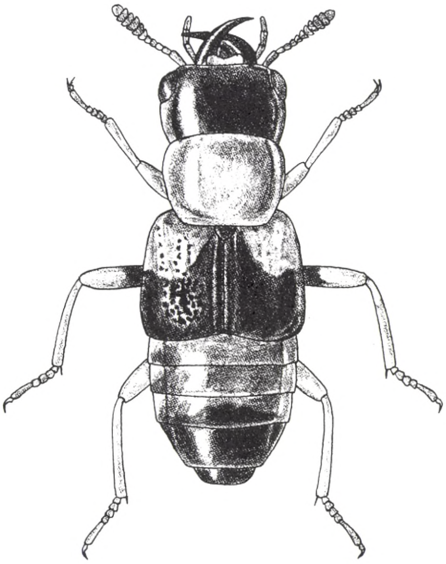

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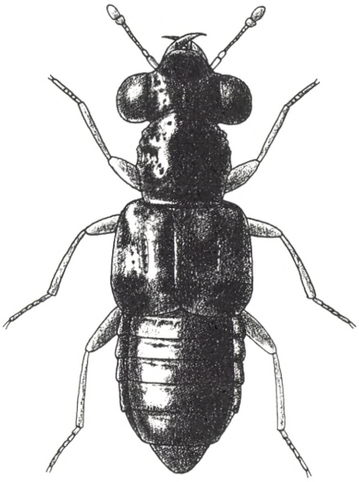

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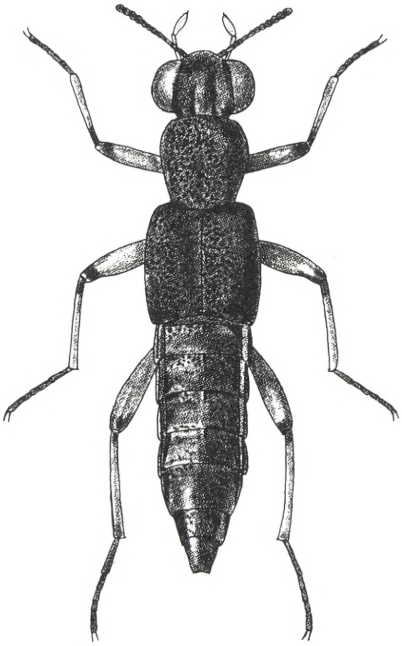

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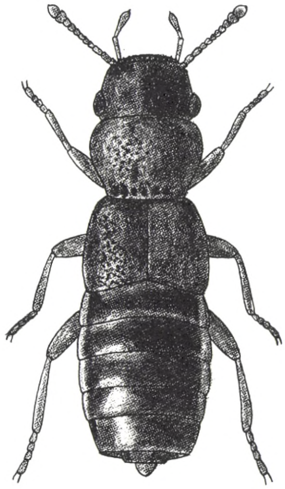

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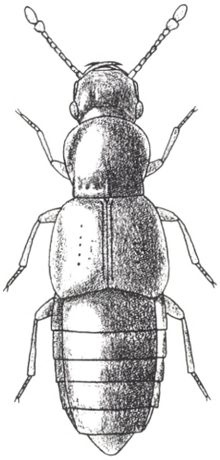
PLATE 60 (Habitus of adults)

Fig. 432. *Edaphus nitidus,* Staphylinidae-Euaesthetinae (Euaesthetini), 1.2 mm
Fig. 433. *Solierius obscurus,* Staphylinidae-Solieriinae, 2.2 mm
Fig. 434. *Leptotyphlus brevicornis,* Staphylinidae-Leptotyphlinae (Leptotyphlini), 0.9 mm
Fig. 435. *Pseudopsis sulcata,* Staphylinidae-Pseudopsinae, 3.3 mm
Fig. 436. *Paederus riparius,* Staphylinidae-Paederinae (Paederini), 7.5 mm (after V. Hansen)
Fig. 437. *Rugilus orbiculatus,* Staphylinidae-Paederinae (Paederini), 4.3 mm (after V. Hansen)



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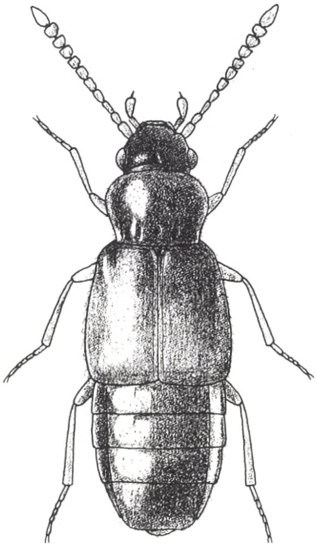

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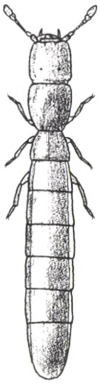

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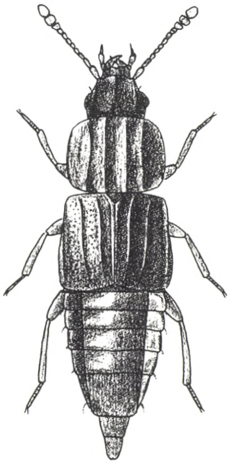

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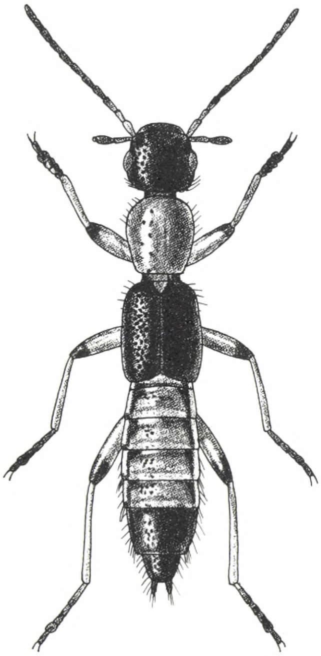

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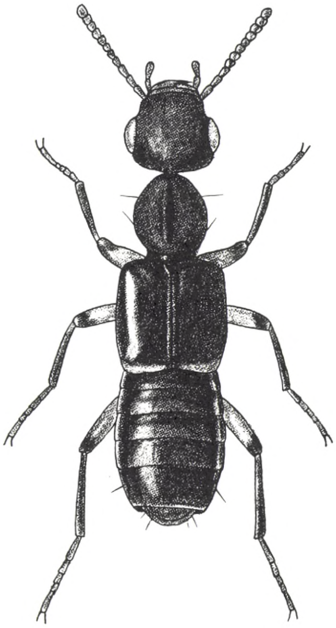

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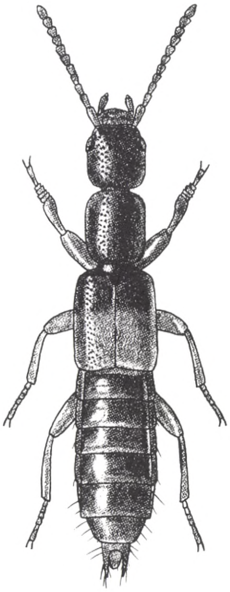
PLATE 61 (Habitus of adults)

Fig. 438. *Lathrobium elongatum*, Staphylinidae-Paederinae (Paederini), 8.5 mm (after V. Hansen)
Fig. 439. *Ochthephilum fracticorne*, Staphylinidae-Paederinae (Paederini), 5.5 mm (after V. Hansen)
Fig. 440. *Palaminus* sp., Staphylinidae-Paederinae (Pinophilini), 4.0 mm
Fig. 441. *Gyrohypnus liebei*, Staphylinidae-Staphylininae (Xantholinini), 7.5 mm (after V. Hansen)
Fig. 442. *Othius punctulatus*, Staphylinidae-Staphylininae (Othiini), 12.0 mm (after V. Hansen)
Fig. 443. *Platyprosopus consularis*, Staphylinidae-Staphylininae (Platyprosopini), 15.5 mm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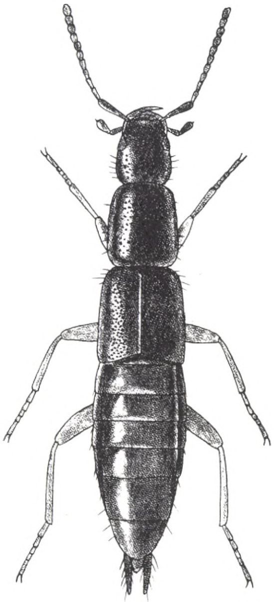
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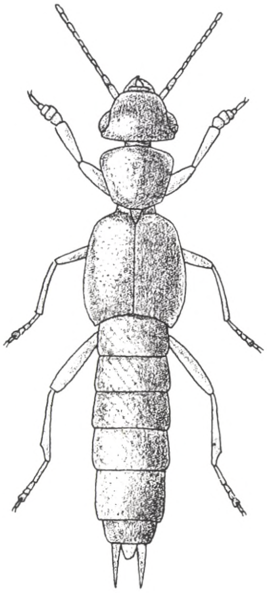
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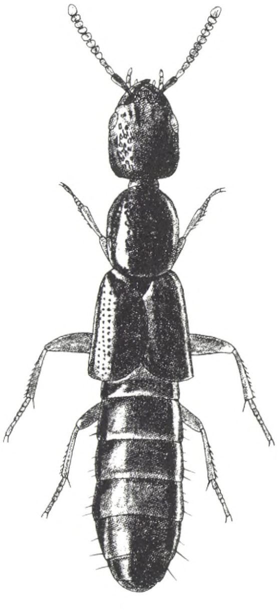
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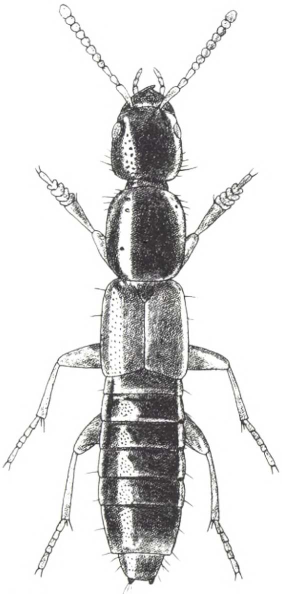
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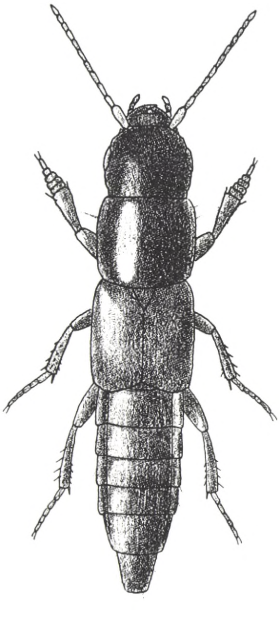
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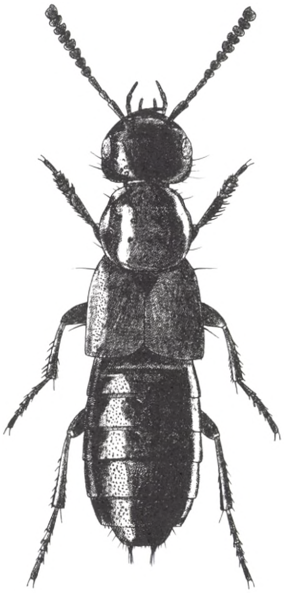
PLATE 62 (Habitus of adults)

Fig. 444. *Philonthus politus*, Staphylinidae-Staphylininae (Staphylinini), 12.0 mm (after V. Hansen)
Fig. 445. *Platydracus stercorarius*, Staphylinidae-Staphylininae (Staphylinini), 14.0 mm (after V. Hansen)
Fig. 446. *Emus hirtus*, Staphylinidae-Staphylininae (Staphylinini), 25 mm (after V. Hansen)
Fig. 447. *Quedius fumatus*, Staphylinidae-Staphylininae (Staphylinini), 8.0 mm (after V. Hansen)



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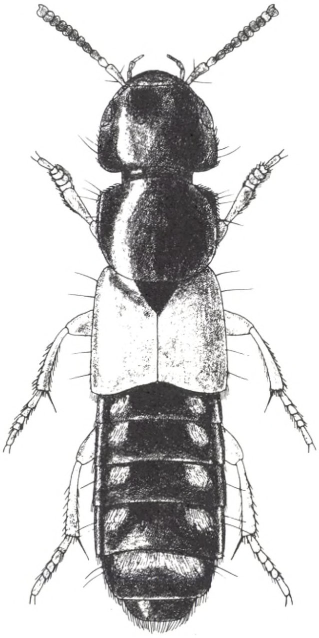

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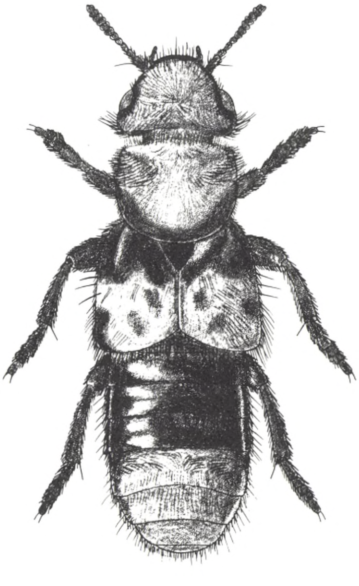

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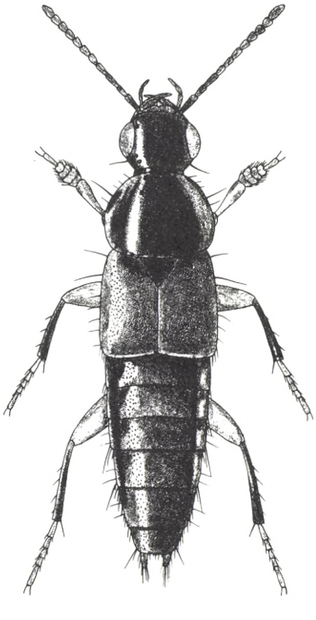
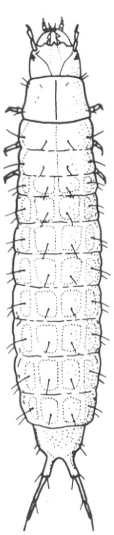


447

PLATE 63 (Habitus of larvae)

Fig. 448. *Helophorus* sp., Helophoridae
Fig. 449. *Georissus crenulatus*, Georissidae (redrawn from Emden, 1956)
Fig. 450. *Hydrochus squamifer*, Hydrochidae (redrawn from Richmond, 1920)
Fig. 451. *Spercheus emarginatus*, Spercheidae (redrawn from Bøving and Henriksen, 1938)
Fig. 452. *Berosus spinosus*, Hydrophilidae-Hydrophilinae (Berosini) (redrawn from Bøving and Henriksen, 1938)
Fig. 453. *Laccobius agilis*, Hydrophilidae-Hydrophilinae (Laccobiini) (redrawn from Richmond, 1920)
Fig. 454. *Hydrobius fuscipes*, Hydrophilidae-Hydrophilinae (Hydrophilini) (redrawn from Bøving and Henriksen, 1938)



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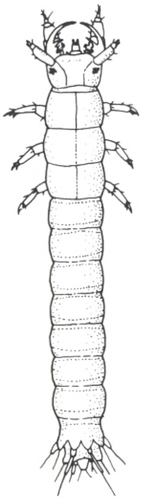

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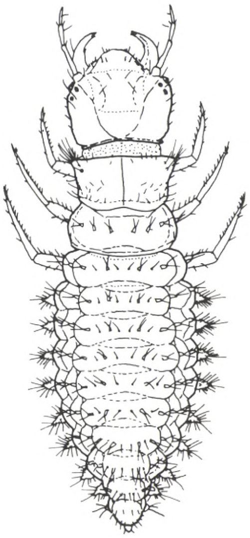

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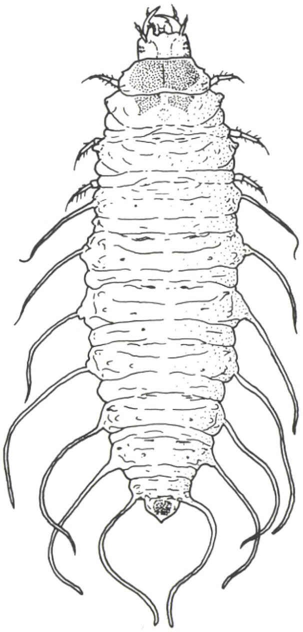

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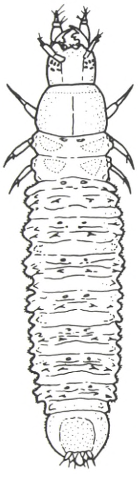

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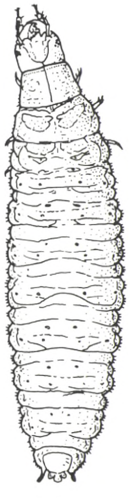

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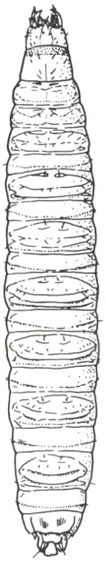
PLATE 64 (Habitus of larvae)

Fig. 455. *Coelostoma orbiculare*, Hydrophilidae-Sphaeridiinae (Coelostomatini) (redrawn from Bøving and Henriksen, 1938)
Fig. 456. *Sphaeridium* sp., Hydrophilidae-Sphaeridiinae (Sphaeridiini)
Fig. 457. *Syntelia histeroides*, Synteliidae (redrawn from Newton, 1991)
Fig. 458. *Chalcionellus hauseri*, Histeridae-Saprininae (redrawn from Vienna, 1980)
Fig. 459. *Hololepta plana*, Histeridae-Histerinae (Hololeptini) (redrawn from Vienna, 1980)
Fig. 460. *Necrophilus hydrophiloides*, Agyrtidae (Agyrtini) (redrawn from Newton, 1991)
Fig. 461. *Neocamiarus kuscheli*, Leiodidae-Camiarinae (Camiarini) (redrawn from Jeannel, 1958)
Fig. 462. *Leiodes cinnamomea*, Leiodidae-Leiodinae (Leiodini) (redrawn from Daffner, 1983)



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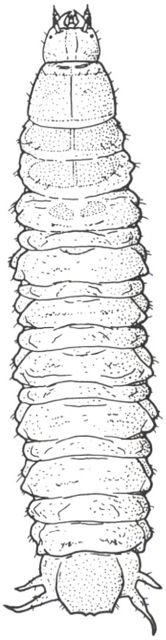

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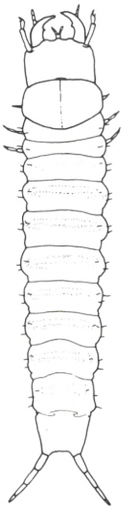

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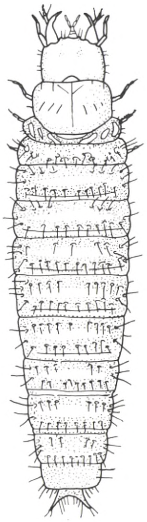

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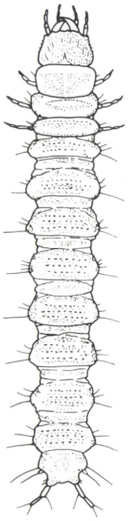

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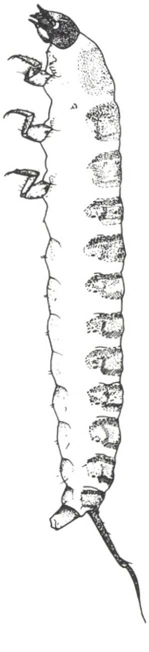

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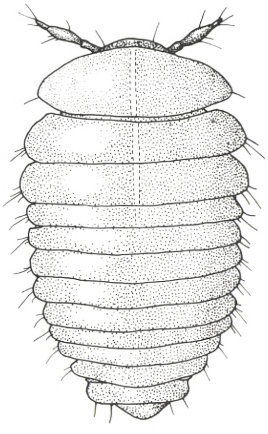

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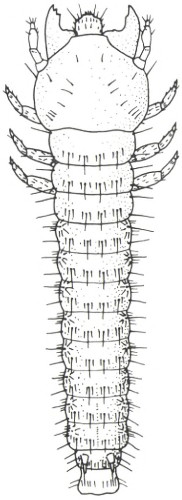

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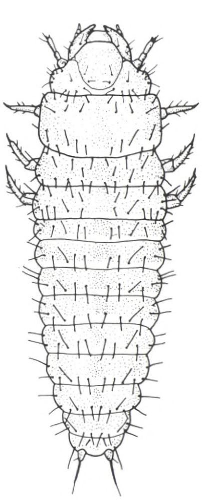
PLATE 65 (Habitus of larvae)

Fig. 463. *Scotocryptodes germaini*, Leiodidae-Leiodinae (Scotocryptini) (redrawn from Costa and al., 1988)
Fig. 464. *Catops fusca*, Leiodidae-Cholevinae (Cholevini) (redrawn from Schiødte, 1862)
Fig. 465. *Leptinus* sp., Leiodidae-Platypsyllinae (redrawn from Newton, 1991)
Fig. 466. *Catopocerus appalachianus*, Leiodidae-Catopocerinae (redrawn from Newton, 1991)
Fig. 467. *Hydraena pennsylvanica*, Hydraenidae-Hydraeninae (Hydraenini) (redrawn from Richmond, 1920)
Fig. 468. *Ochthebius minimus*, Hydraenidae-Ochthebiinae (redrawn from Bøving and Henriksen, 1938)
Fig. 469. *Acrotrichis discolor*, Ptiliidae-Acrotrichinae (redrawn from Costa and al., 1988)
Fig. 470. *Limulodes parki*, Ptiliidae-Cephaloplectinae (redrawn from Dybas, 1991)



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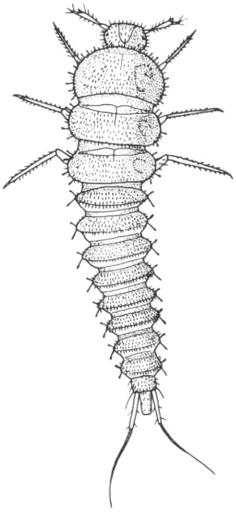

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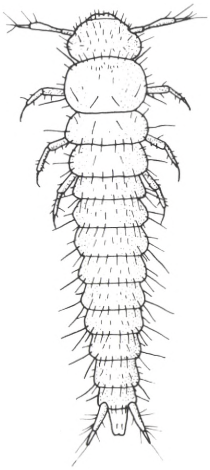

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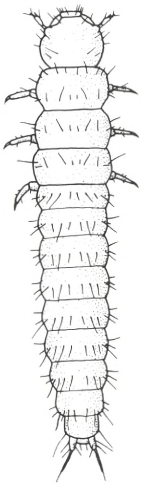

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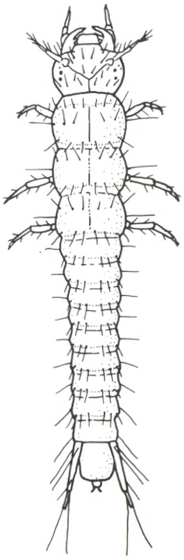

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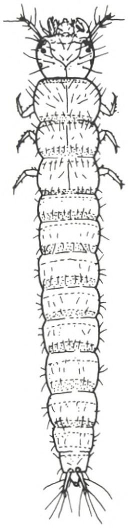

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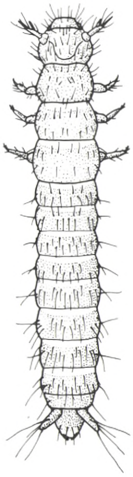

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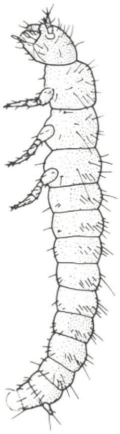

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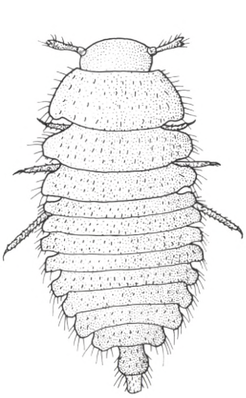
PLATE 66 (Habitus of larvae)

Fig. 471. *Scydmaenus* sp., Scydmaenidae-Scydmaeninae (Scydmaenini) (redrawn from Bøving and Craighead, 1931: "*Eumicrus*")
Fig. 472. *Leptomastax hypogaeus*, Scydmaenidae-Mastiginae (Leptomastacini) (redrawn from Vit and De Marzo, 1991)
Fig. 473. *Scaphisoma agaricinum*, Scaphidiidae (Scaphisomatini) (redrawn from Perris, 1877)
Fig. 474. *Silpha carinata*, Silphidae-Silphinae (redrawn from Paulian, 1941)
Fig. 475. *Ptomascopus morio*, Silphidae-Nicrophorinae (redrawn from Anderson, 1982)
Fig. 476. *Nicrophorus investigator*, Silphidae-Nicrophorinae (redrawn from Anderson, 1982)
Fig. 477. *Omalium* sp., Staphylinidae-Omaliinae (Omaliini) (redrawn from Lawrence and Britton, 1991)
Fig. 478. *Proteinus* sp., Staphylinidae-Proteininae (Proteinini) (redrawn from Bøving and Craighead, 1931)



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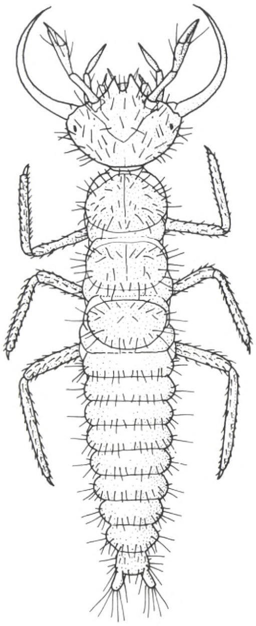

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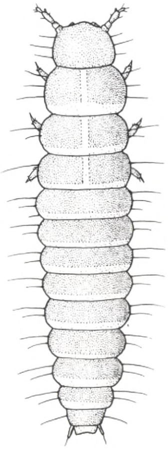

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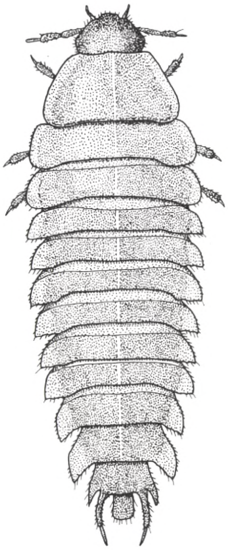

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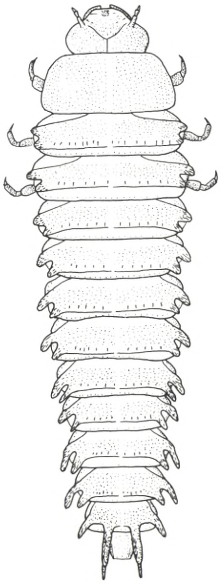

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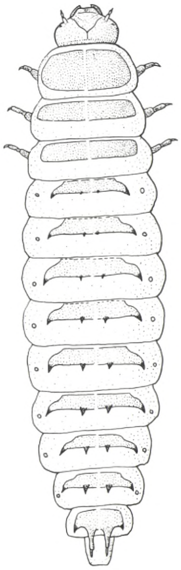

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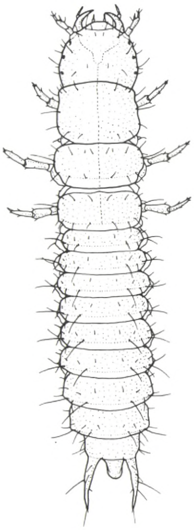

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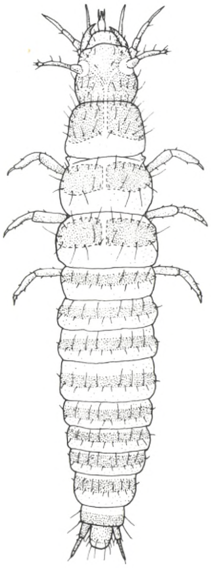

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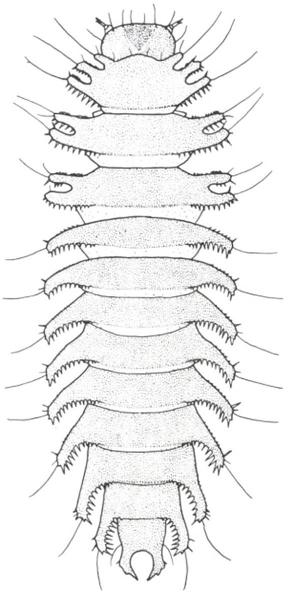
PLATE 67 (Habitus of larvae)

Fig. 479. *Micropeplus neotomae*, Staphylinidae-Micropeplinae (redrawn from Newton, 1991)
Fig. 480. *Dasycerus* sp., Staphylinidae-Dasycerinae (redrawn from Newton, 1991)
Fig. 481. *Euplectus* sp., Staphylinidae-Pselaphinae (Euplectini) (redrawn from Bøving and Craighead, 1931)
Fig. 482. *Tachinus rufipes*, Staphylinidae-Tachyporinae (Tachyporini) (redrawn from Schiødte, 1873)
Fig. 483. *Aleochara algarum*, Staphylinidae-Aleocharinae (Aleocharini) (redrawn from Paulian, 1941)
Fig. 484. *Atheta* sp., Staphylinidae-Aleocharinae (Athetini) (redrawn from Frank, 1991)
Fig. 485. *Piestus* sp., Staphylinidae-Piestinae (redrawn from Frank, 1991)



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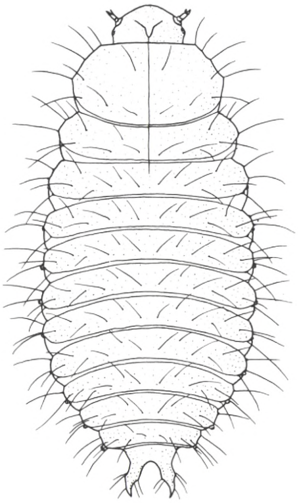

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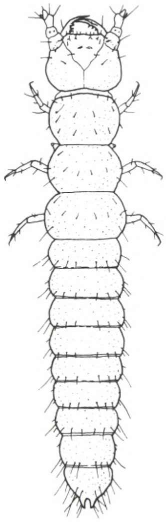

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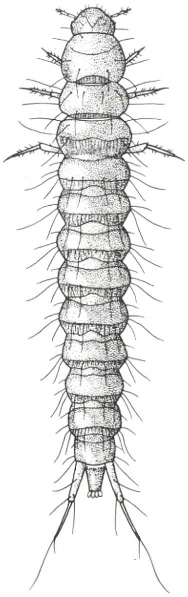

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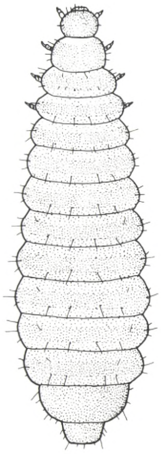

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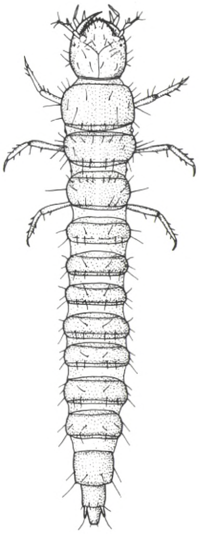

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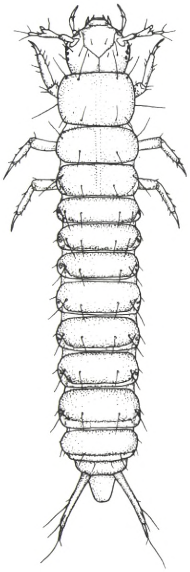

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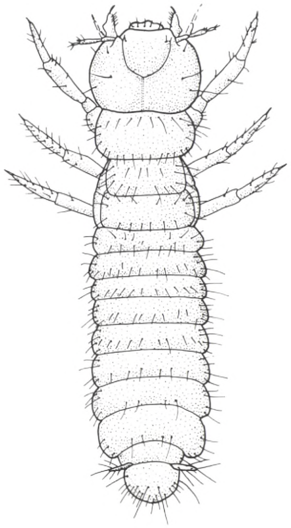
PLATE 68 (Habitus of larvae)

Fig. 486. *Osorius* sp., Staphylinidae-Osoriinae (Osoriini) (redrawn from Costa and al., 1988)
Fig. 487. *Leptochirus* sp., Staphylinidae-Osoriinae (Leptochirini) (redrawn from Costa and al., 1988)
Fig. 488. *Oxytelus* sp., Staphylinidae-Oxytelinae (Oxytelini) (redrawn from Frank, 1991)
Fig. 489. *Oxyporus maxillosus*, Staphylinidae-Oxyporinae (redrawn from Schiødte, 1864)
Fig. 490. *Stenus comma*, Staphylinidae-Steninae (redrawn from Schiødte, 1873)
Fig. 491. *Paederus* sp., Staphylinidae-Paederinae (Paederini) (redrawn from Bøving and Craighead, 1931)
Fig. 492. *Philonthus nitidus*, Staphylinidae-Staphylininae (Staphylinini) (redrawn from Schiødte, 1864)



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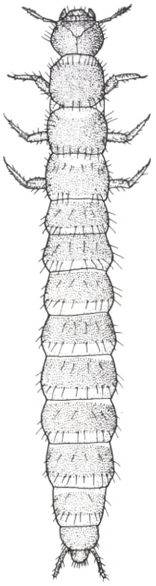

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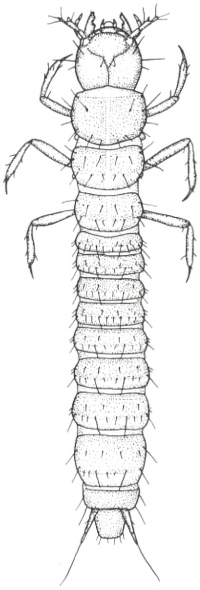

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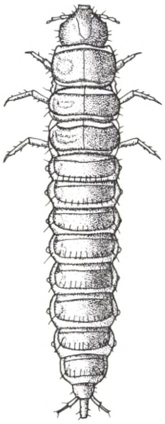

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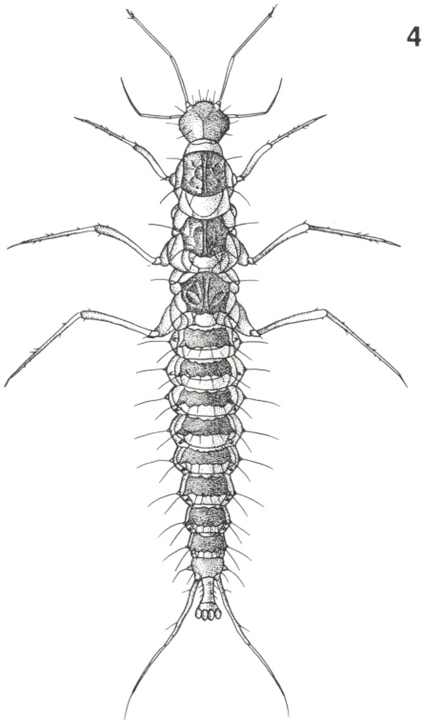

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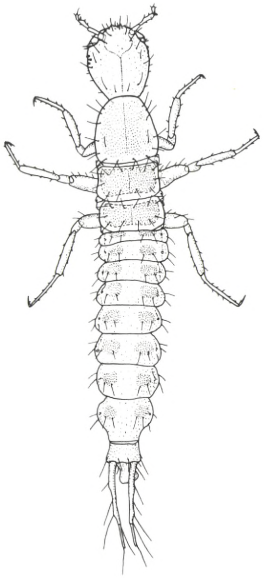

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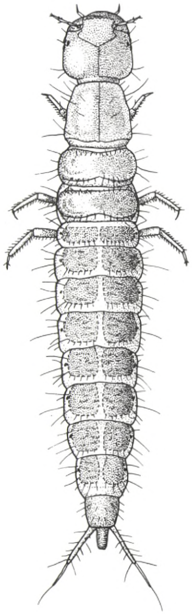

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Submitted to the Academy January 1997.
Published September 1997.

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Abstract, Summary. – An abstract in English is compulsory. It should count 10-15 lines, outline main features, stress novel information and conclusions, and end with the author's name, title, and institutional and/or private postal address. – Papers in Danish may be provided with a summary in another language by agreement between author and Editor.

Typescript. – Page 1 should contain title, author's name and the name of the Academy. Page 2: Abstract, author's name and address. Page 3: Table of contents if necessary. Captions should be supplied on separate sheets. Footnotes should be avoided if at all possible; if indispensable, they, too, should be typed on separate sheets. Consult a *recent* issue of the series for general layout.

Typewrite with double space throughout and leave a 4 cm margin *right*. Indicate desired position of illustrations and tables with pencil in margin *and repeat it in the galley proof.*

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