Phylogeny and Evolution of Subterranean and Endogean Cholevidae (= Leiodidae Cholevinae) Proceedings of XX I.C.E. Firenze, 1996 | Mus. reg. Sci. nat. Torino, 1998: 41-178

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Phylogenetic problems, current classification and generic catalog of world Leiodidae (including Cholevidae)

ABSTRACT

Subterranean and endogean cholevines are placed in the context of a world-wide review of the past and present classification of related Staphylinoidea. Arguments are presented for recognizing a single large monophyletic family, Leiodidae, rather than a series of less well-defined families including Cholevidae, Leptinidae, etc. The sister group of this Leiodidae *sensu lato* is probably Agyrtidae. Six leiodid subfamilies are recognized, all but the first probably being monophyletic: Camiarinae, Catopocerinae, Leiodinae (=Anisotominae), Coloninae, Cholevinae (=Catopinae, Leptodirinae) and Platypsyllinae (=Leptininae). Outstanding phylogenetic problems at the subfamily and tribal levels are discussed.

Keys for identification, diagnoses, and brief summaries of the biology and knowledge of larvae of each subfamily and tribe are given. A new subtribe, Eunemadina, is separated from Nemadina. A complete generic catalog includes indication of the distribution and number of named species for each genus, and genera examined. Also provided in appendices are summaries of new taxonomic changes (10 new generic, 1 subgeneric and 9 species synonymies, 3 species resurrected from synonymy, 22 new generic combinations, and 2 new family placements) and nomenclatural problems.

Cholevinae display the greatest diversity in subterranean habits, with more than 160 genera and 750 species in the Leptodirini (=Bathysciini) in the Palearctic region.

Key words: Leiodidae, Cholevidae, phylogeny, classification, generic catalog

INTRODUCTION

It is now more than a century since the famous (or infamous) American entomologist Thomas Casey (1893: 510) accurately referred to the old family Silphidae as "that ollapodrida of discordances". Since then, a great deal of work by many authors has led to a better understanding of real relationships among the beetles once placed in this dumping ground. Important advances came from broadly comparative morphological studies of all

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Coleoptera, for example, male genitalia by Sharp & Muir (1912), wing venation and folding patterns by Forbes (1926), larvae by Böving & Craighead (1931), and a synthesis of these and other characters by Crowson (1955). More intensive taxonomic work on "silphids" by Portevin and others helped. However, it was the monumental work of Réné Jeannel, spanning more than half of this century (1906-1964), that established the main lineages of the former silphids that we recognize today, including all of the groups combined here in a family Leiodidae. Jeannel's work has had an enormous impact, and has stood the test of time and subsequent study rather well: nearly 90% of all the species, genera and higher taxa named by Jeannel are still recognized as valid today. This can be contrasted with certain other prolific systematists that have worked even more recently in these groups: more than half of the species and 3/4 of the genera named by Hlisnikovský have been synonymized within 35 years! However, even Jeannel made some errors of fact and interpretation, and I will return to some of these shortly.

The family Leiodidae as recognized here is a large worldwide group of more than 3,000 named species. Although most of these are "little brown beetles" scarcely noticed by most collectors of larger showy insects including silphids proper, the species show extraordinary ecological and morphological adaptations to special habitats such as deep soil and caves and fungi of many kinds, and some are highly modified mammalian parasites or inquilines of social insects. The apparent great age of the group (known from early Cretaceous fossils but probably older) has resulted in a large number of geographic "relicts" including many "Gondwanan" oddities such as Camiarinae. These factors combine to make leiodids of great interest to evolutionary biologists and biogeographers.

However, in spite of the considerable resulting attention this group has received from many capable and prolific systematists, many problems concerning the family limits, classification, biology and evolution of these beetles await resolution. Taxonomic confusion, resulting from a checkered history of family concepts and shifting alliances of individual genera, continues to the present. Anywhere from one to five families are recognized by different authors, and some genera still appear regularly under two or three different families in the *Zoological Record* including very inappropriate ones such as Silphidae. This symposium on cave beetles seeks to review and resolve some of these problems for the largest and perhaps most interesting of all leiodid groups, the remarkable leptodirines that represent one of the world's greatest radiations of cave-adapted insects.

The present contribution, however, focuses less on leptodirines proper than on the other leiodids. My main objective in this is to place leptodirines in the context of the classification and phylogeny of the family as a whole, and thus provide the kind of background necessary for understanding phylogeny and evolution in leptodirines. But I also hope to resolve some taxonomic problems in these other leiodids and provide resources that will facilita-

te study of the entire family. The specific goals of this work are to (1) review evidence for the monophyly and relationships of Leiodidae as a group, and its major subdivisions (subfamilies and tribes); (2) make some changes to higher-level (above genus) classification required by this review; (3) present diagnoses and keys to these major groups, as a means of identification as well as for future placement of problematic taxa; (4) present a complete catalog of genus-group names of Leiodidae, resolving or calling attention to problems of nomenclature, and providing basic data on each currently recognized genus such as overall distribution and number of described species to help document the diversity of each higher group; (5) make some lower-level taxonomic changes discovered incidentally to the overall review, such as new generic or species synonymies; and (6) provide extensive references to the systematics, biology and larval descriptions for each higher group, to serve as a general resource for further work on the family. Although a formal phylogenetic analysis of the higher taxa of leiodids has long been an objective of my studies, the sheer size and complexity of this group in combination with time constraints have precluded including such an analysis here.

Much of my research and study of types directed toward these objectives was completed years ago, as part of a general review of the classification of staphylinoid beetles that sought to delimit monophyletic families and correctly place many problematic taxa. A draft manuscript on leiodids with many of the results was circulated to numerous specialists on this family in 1983. Although many of these results have been published and used in various ways by myself and others (e.g., Lawrence & Newton, 1982, 1995; Newton, 1983a, 1983b, 1984, 1985, 1991; Newton & Thayer, 1992, 1995; Peck, 1990; Wheeler, 1984a; various leiodine revisions of Daffner and others), the justification for many changes and the full set of keys, diagnoses and generic lists have not yet appeared. The growing interest in this family as illustrated by this symposium, and the support of its organizers, have encouraged me to revise and complete this work.

Family limits

The groups here combined to form Leiodidae were included in Silphidae by most 19th century authors, although Thomson (1859) had separated most of them as the families Catopidae and Anisotomidae. Recognition of Leiodidae in the present sense as a natural unit distinct from Silphidae has been generally accepted since the work of Jeannel (1936), but was already suggested by earlier studies including comparative morphological work on male genitalia (Sharp & Muir, 1912), wing folding and venation (Forbes, 1926) and larvae (Böving & Craighead, 1931). Jeannel and many other European authors have recognized 5 families: Leiodidae (=Anisotomidae), Colonidae, Camiaridae, Catopidae (=Cholevidae, =Leptodiridae), and

Leptinidae (including Platypsyllidae). Crowson (1955), Hatch (1957), Peck (1973) and others have recognized only 2 families: Leptinidae and Leiodidae (the latter including Jeannel's other families). More recently, Crowson (1981), Lawrence & Newton (1982, 1995), Newton & Thayer (1992) and Peck (1990) have included Leptinidae in Leiodidae.

There seems to be little justification for the recognition of more than one family for Leiodidae as used here. This family is clearly monophyletic (Lawrence & Newton, 1982), demonstrated especially by a series of unusual antennal characters including a usually "interrupted" antennal club with segment 8 reduced compared to segments 7 and 9, a periarticular gutter on segments 7, 9 and 10, and vesicles extending internally from this gutter in many taxa (Corbière-Tichané, 1973a, 1974, 1977; Peck, 1977a; Angelini & De Marzo, 1983; further discussion below). Leptinidae have been maintained as a separate family by most authors of the past half century, but this appears to be based primarily on the erroneous belief that leptinids, with open procoxal cavities, differ from leiodids which reputedly have closed cavities (Jeannel, 1936). Closure of the procoxal cavities was given great weight by Jeannel (1936:8) who thought that closure was correlated with disappearance of the mesothoracic spiracles. In fact, all Leiodidae I have examined possess fairly large, functional mesothoracic spiracles. Further, open procoxal cavities are found in numerous genera of Leiodidae belonging to 3 of the 5 non-leptinid subfamilies recognized here (see later). Open cavities are either ancestral for the family or have been multiply derived from closed cavities. In either case there is no basis for separation of Leptinidae from Leiodidae on this character. Leptinids possess the unique antennal structure of Leiodidae, and in all other respects are derivable from a leiodid-like ancestor.

Jeannel's multi-family division of Leiodidae has been widely accepted but is also, in my view, difficult to support. Jeannel (1936) did not question the monophyly of Leiodidae in the broad sense when he first proposed this series of families, as is clear from his phyletic diagram (Jeannel, 1936:18), although he later coined a group name Catopiaria (Jeannel & Paulian, 1944: 97-98; Jeannel & Jarrige, 1949: 265) for a larger group that included Hydraenidae and Ptiliidae among other groups now placed in other suborders or superfamilies. Rather, Jeannel's recognition of several families here seemed to be based on degree of difference, of the same sort that led him to propose some 45 families for what most biologists called the family Carabidae (see Jeannel, 1949). This fragmentation of Carabidae never gained wide acceptance and has been abandoned by most systematists today, but the analogous division of Leiodidae has been widely adopted at least in Europe (a region with well-known inclination toward fragmentation!). However, neither Jeannel nor later proponents of a multi-family system for Leiodidae have demonstrated any phylogenetic necessity for such a division, for example by demonstrating that any of these units is more closely related to another family of beetles than to other leiodids.

The morphological basis for separating Leiodidae into a series of families is also based on dubious and often erroneous distinctions, as already noted above in the case of open or closed procoxal cavities. Jeannel (1936) separated Catopidae from the other families by their possession of a broad, rather than triangular, postcoxal process of the pronotum. Actually, a broad notal process is also found within his Camiaridae (e.g. *Camiarus*) and his Liodidae (*Cyrtusa* Group of Leiodini), while a triangular closure is found in some Catopidae (Eucatopini). Jeannel's Colonidae and Ptomaphagini (Catopidae) actually have the notal process indistinguishably fused to the sternal process; his attribution of a particular shape to the notal process in these taxa is based on the shape of a secondary carina. Jeannel (1936) also separated Catopidae from the other families by the nature of the contact of the mesepisternum with the mesocoxal cavities: no contact (Catopidae) versus broad contact (other families). In many members of these latter families the mesosternal-mesepisternal suture is obsolete, but when present as in *Colon* and various genera of Camiaridae and many Leiodidae the mesepisternal-mesocoxal cavity contact is very small and differs little if at all from the condition in Catopidae; only within certain tribes of Leiodidae is the broad contact noted by Jeannel found. The larval mandibular character cited by Jeannel (1936: 8) to separate Catopidae from the other families also does not do so. The characterization of the other families is actually based on the genus *Anisotoma*, whose larvae have an unusual molar surface adapted for feeding on slime mold spores (Lawrence & Newton, 1980). Recently discovered larvae of other tribes of Leiodinae and of Catopocerinae and some Camiarinae (present sense) have mandibles that do not differ in any consistent way from those of Catopidae (Newton, 1991).

In summary, neither the characters used by Jeannel (1936), nor those used by others or discovered by me, appear to justify the separation of Leiodidae in the present sense into 2 or more families. In general, Jeannel's families are here considered subfamilies. In fact, distinguishing these subfamilies from one another is far from a simple task, and difficulties here have resulted in recent movement of groups or genera between subfamilies, as will be discussed later. Subfamily distinctions, especially between the three larger subfamilies Camiarinae, Leiodinae and Cholevinae, are likely to blur even further as many new taxa of the former primitive group are described and others are adequately studied.

In addition to the above considerations of the status of major groups, various individual genera have been moved into or out of Leiodidae in the recent past, and two more are added in the present work: *Lomechon* Wasmann (from Leiodidae to Ptilodactylidae) and *Termitoglobus* Reichensperger (from Endomychidae to Leiodinae: Scotocryptini); see Taxonomic Changes (Appendix A). Earlier removals of taxa sometimes included or implied to be in or near Leiodidae were discussed, e.g., by Newton (1985) and Newton & Thayer (1992, 1995); these include the gene-

ra *Dasycerus*, *Empelus*, *Glypholoma*, *Micragyrtes* and *Microsilpha*, all now placed in Staphylinidae. Several families once placed near Leiodidae (or parts thereof), such as Corylophidae, Clambidae, Sphaeriidae and Hydroscaphidae, have been removed to other superfamilies (e.g., Crowson, 1955; Lawrence & Newton, 1982, 1995).

Reorganization of Leiodidae

In the course of a generic revision of the family "Silphidae" (now the families Silphidae and Agyrtidae), and differentiation of these groups from Staphylinidae, I have examined Leiodidae more intensively than any other non-"silphid" family. This was in part because of the nearness of Agyrtidae to Leiodidae, which makes differentiation of the two families difficult, and in part because so many of the genera removed from "Silphidae" have had to be placed in Leiodidae. Although the work of Jeannel, Szymczakowski, Laneyrie, Guéorguiev, Peck, Zwick, Perreau, Giachino and others has established a generally satisfactory worldwide classification of Cholevinae (present sense), it was quickly apparent that Leiodinae (present sense) were in a relatively chaotic state at the tribal level with many poorly characterized and unplaced or misplaced genera. Many isolated and primitive leiodid genera, especially from Austral or south temperate areas, have been left "floating" in the family after removal from subfamilies or tribes in which they clearly did not belong. For these reasons, I have attempted to critically examine at least 1 species (where possible the type species) of each genus of non- Cholevine leiodid as well as a representative sample of cholevine genera, and to develop a revised classification of the family based on these studies. Although I have also been intensively studying larvae of Leiodidae and have seen representatives of all subfamilies and tribes recognized here except Coloninae, Glacicavicolini (Catopocerinae) and Estadiini (Leiodinae), these studies need more time and more space than can be accomodated here and will be mentioned only briefly. It is possible to say now that larval characters support the recognition of Leiodidae in the present sense as a single family, and that they appear to generally support the following classification which is based on adult structure.

Although I have not been able to examine every genus of doubtful placement in the family, I feel that enough taxa have been examined, and enough new characters found, to justify some changes in the subfamily and tribal organization of the family. Leiodinae are divided into a larger than usual number of tribes, most of which are defined in a novel manner. This reflects better the diversity within Leiodinae, which is comparable to that found in Cholevinae but which has been largely overlooked because of inadequate study. Camiarinae is expanded by addition of Neopelatopini (from Leiodinae), Agyrtodini (from Cholevinae), and a few previously unplaced

genera. This converts Camiarinae into a "group of convenience" which is doubtfully monophyletic and badly in need of further study (see discussion under that subfamily), but it removes discordant groups from Leiodinae and Cholevinae (see, e.g., Zwick, 1979; Perreau, 1989) and increases the likelihood that those two subfamilies are monophyletic. Finally, Jeannel's subfamily Nemadinae is modified not only by removal of Agyrtodini to Camiarinae but also by removal of Oritocatopini to the equivalent of a separate subfamily in Jeannel's system (tribe here).

The classification of Leiodidae proposed here is summarized in Table 1. A more detailed discussion of the basis for this classification, and illustration of many of the characters considered in constructing it, are presented below under "Phylogenetic considerations" and reviewed in the main catalog section.

Tab. 1 - Current classification of Leiodidae at the level of tribe and above, with numbers of described genera and species through 1995, and genera of adults and larvae examined for this study.

	Described through 1995		Genera examined*	
	Species	Genera	Adults	Larvae
CAMIARINAE, sensu novo				
NEOPELATOPINI (ex Leiodinae)	12	6	6+	4+
CAMIARINI	16	6	6+	2+
AGYRTODINI (ex Cholevinae)	50	14	14+	6+
CATOPOCERINAE				
CATOPOCERINI	15	1	1+	1+
GLACICAVICOLINI	1	1	1	---
LEIODINAE (= Liodinae, Anisotominae)				
SOGDINI (= Hydnobiini, Triarthrini)	54	8	6+	4+
ESTADIINI	12	1	1	---
LEIODINI, sensu novo	285	17	11+	2
PSEUDOLIODINI, sensu novo	117	10	9+	5
SCOTOCRYPTINI, sensu novo	42	9	4+	5+
AGATHIDIINI (= Anisotomini)	654	9	8+	2
COLONINAE	138	2	1	---
CHOLEVINAE (= Catopinae, Leptodirinae)				
ANEMADINI (= Nemadini, Paracatopini)	229	25	23	7+
CHOLEVINI (= Catopini)	337	24	12	4+
LEPTODIRINI (= Bathysciini)	757	162	23	1
ORITOCATOPINI	19	3	3	2
EUCATOPINI	12	1	1	1
PTOMAPHAGINI	251	9	5	4
PLATYPSYLLINAE (= Leptininae)	13	4	3	3
TOTALS	3013	312	138+	53+

*Examined as cleared microscope slide preparations; "+" indicates that undescribed genera of adults, or unidentified larval types, were also studied in these groups

Family group names

A full listing and nomenclatural data on family-group names is included here, mainly following Newton & Thayer (1992) with slight changes and one additional synonym (Hadesiini).

Generic catalog and placements

The catalog of included genera, subgenera and synonyms, and nomenclatural data on these names, are intended to be complete and up to date. The distribution and number of species given for each genus are based on an actual checklist of world species, compiled from the most recent revision or list (in many cases the Coleopterorum Catalogus) plus entries in the Zoological Record through Vol. 131 (1994/1995). This checklist has been checked by, or compared against unpublished catalogs or lists prepared by, several specialists on Leiodidae including M. Perreau (Cholevinae, Platypsyllinae), S. Peck (North American and West Indies leiodids), F. Angelini (Agathidiini), P. Gnaspini (Ptomaphagini), and A. Casale, P. M. Giachino, J. M. Salgado-Costas and S. Zoia (Leptodirini). In some cases (mainly southern hemisphere genera) where I have actually studied relevant types and much recently collected material at the generic and species level, the actual generic distribution known to me is indicated, and the number of species actually seen is indicated after "Note:", but the number of species given in parentheses after distribution is always based on described species only. Undescribed genera that I am aware of are mentioned in the comments for each group.

Unexamined genera are assigned on the basis of published information; those of doubtful placement are noted and discussed. It should be assumed that representative species of all examined genera agree with the key characters and diagnoses of the subfamilies and tribes in which they are placed. There are many instances, mainly in Leiodinae, where tribal placement here conflicts with published descriptions (e.g., tarsal formulae) and placements. In these cases some of the published data is wrong, but I have not attempted to point out every such instance.

Abbreviations: "**e**", "**w**", "**n**", "**s**" and "**c**" with reference to geographic distribution refer to "east", "west", "north", "south" and "central", respectively; "**des.**" = designated by, "**orig.**" = original, and "**syn.**" = synonymized by.

Examined taxa

A code in square brackets [] after the name and author in the generic catalog indicates whether I have critically examined adults of any species of

that genus, and how. A "T" indicates the type species of the generic name, "S" one or more other species. A "c" after one of these letters indicates that a cleared (and usually dissected) specimen of at least one sex was studied as a microscope slide preparation using a compound microscope at up to 400X magnification (see Methods); otherwise, uncleared specimens were studied with a dissecting microscope at magnifications below 100X. Thus, an indication "[T, Sc]" after a generic name indicates that I have studied a whole specimen(s) of the type species, and a cleared slide preparation of at least one other species, placed in this genus. Many other species were examined in less detail. Many of the species studied were represented by types, but this is not indicated except for those taxa discussed in Appendix A, "Taxonomic Changes". Examined larvae are indicated under "Comments" for each tribe or subfamily. The total number of taxa of adults and larvae examined for each tribe or subfamily is indicated in Table 1.

METHODS

When possible, specimens of each sex intended for critical study were cleared in hot 1N KOH until clear of soft tissues, stained with chlorazol black, and prepared with dissection as either permanent microscope slides in a xylene-based synthetic medium (Permount®) or as temporary depression slides in glycerin. Certain rare specimens, including some types, were temporarily cleared in hot lactic acid and studied (without dissection) in depression slides, then washed and remounted as dry preparations. All of these slides were studied at magnifications up to 400X with a differential-interferen-

Tab. 2 - Scheme of Jeannel (1936: p. 6) dividing Staphylinoidea into family groups (translated and with change of taxon and structure names to current usage).

I. Procoxal cavity open, postcoxal process of pronotum [="epimere"] free
Mesothoracic spiracle functional, easily visible
A. HYDRAENIDAE, PTILIIDAE, [Hydroscaphidae, Sphaeriidae]
Primitive families, larva with mandibular mola
B. STAPHYLINIDAE, PSELAPHIDAE, SCYDMAENIDAE, SILPHIDAE, SCAPHIDIIDAE
Derived families, larva without mandibular mola

II. Procoxal cavity closed, postcoxal process of pronotum fused to prosternal process
Mesothoracic spiracle atrophied, not visible
A. LEIODIDAE, PLATYPSYLLIDAE, COLONIDAE, CAMIARIDAE, [Clambidae]
Pronotal process triangular
Mesocoxal cavity transverse, mesepisternum bordering a part of the cavity
Larva with a tuberculate mola
B. CHOLEVIDAE
Pronotal process quadrangular
Mesocoxal cavity not transverse, mesepisternum not reaching the cavity
Larva with a plicate mola

ce compound microscope. Some characters such as presence of antennal vesicles and number of functional abdominal spiracles could be determined only with such preparations. Most of these slide preparations will be deposited in the Field Museum.

PHYLOGENETIC CONSIDERATIONS

Although a formal phylogenetic analysis cannot be completed at this time, it is possible and probably useful to present some summary of characters and character states that have been used by others or found useful by me to justify the recognition of major groups within Leiodidae. Jeannel's (1936: 8) table of major groups of staphylinoids and supporting characters, reproduced here as Table 2, may be taken as the starting point for the modern classification of leiodids. The group II of this table corresponds to Leiodidae in the present broad sense, after removal of Clambidae (now placed in another superfamily of beetles). Jeannel gave profound weight to the supposed closure of the procoxal cavities, which he thought was always correlated with great reduction of the "prothoracic" (actually mesothoracic) spiracle immediately behind the procoxae. Jeannel further divided this group into a family Cholevidae (formerly a subfamily of Silphidae), and a series of other families, using as characters the shape of the pronotal postcoxal process, shape of

Tab. 3 - Mesothoracic spiracles and procoxal closure in Staphylinoidea. Symbols: (▲) closed by triangular notal process; (■) closed by quadrangular notal process; (●) closed by complete fusion of notal and sternal processes, suture absent.

1. Mesothoracic spiracles are never atrophied or invisible, and their size is dependent on the size of the beetle, not whether or not the procoxal cavities are closed.

2. Closure of the procoxal cavities has occurred many times independently, in:
   HYDRAENIDAE (some, e.g., *Hydraena*)
   PTILIIDAE (many, e.g., *Ptenidium*)
   SCYDMAENIDAE (many, e.g., *Euconnus*)
   SCAPHIDIIDAE (many, e.g., Scaphisomatini)
   STAPHYLINIDAE (some, e.g., Leptochirini)
   LEIODIDAE:
      [CATOPOCERINAE, PLATYPSYLLINAE: none]
      CAMIARINAE:
         NEOPELATOPINI (some; ▲)
         CAMIARINI (most; ▲, ■)
         AGYRTODINI (■)
      LEIODINAE:
         SOGDINI (some, including only some *Hydnobius* spp.; ▲)
         ESTADIINI (some *Dietta* spp.; ▲)
         LEIODINI (■)
         PSEUDOLIODINI, SCOTOCRYPTINI, AGATHIDIINI (▲)
         COLONINAE (●)
         CHOLEVINAE (■, except ▲ in Eucatopini, ● in Ptomaphagini and many Leptodirini)

the mesocoxae, contact of the mesepisternum with the mesocoxal cavities, and surface of the larval mola. These non-cholevid families were not clearly differentiated in a similar table or key, and no explanation was given for why these groups were treated as families rather than subfamilies.

According to my study, not a single one of the characters used by Jeannel in his Group II is correct as shown! Problems with the procoxal closure and atrophy of the adjacent spiracle are shown in Tab. 3. The mesothoracic spiracle is present in every leiodid and other staphylinoid beetle I have studied. In smaller beetles, the spiracle is relatively smaller in relation to the size of the beetle than in larger beetles, so that it is more difficult to see in a leiodid than in a large silphid or agyrtid, for example. More importantly, closure of

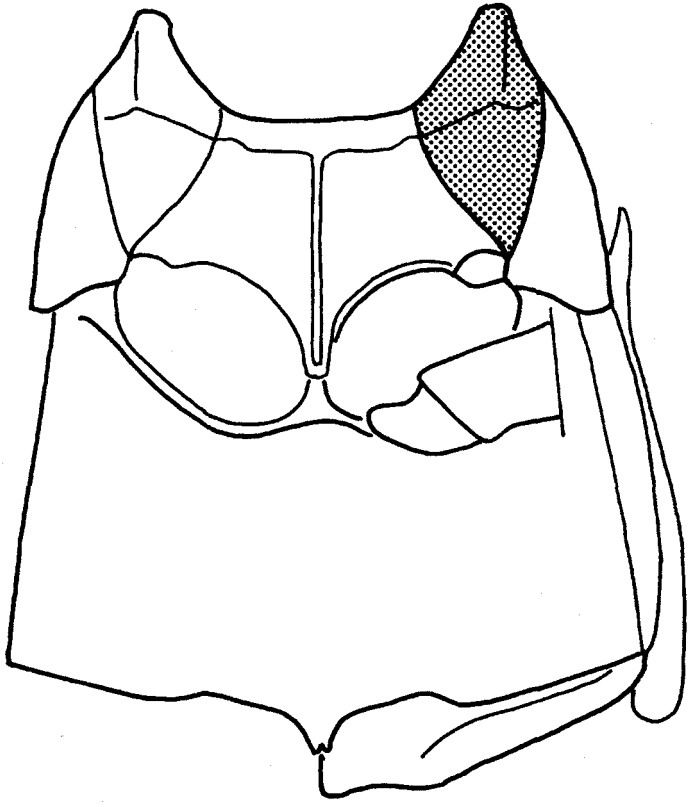

Fig. 1 - *Neopelatops edwardsi* Jeannel (Camiarinae: Neopelatopini), meso- and metasternum, diagram showing mesepisternum (stippled).

the procoxal cavities is not at all a universal feature of Leiodidae, nor absent in the other families, but has a complex distribution as shown in Tab. 3. There is little doubt that open procoxal cavities are symplesiomorphous in Staphylinoidea compared to closed cavities, but closure has clearly occurred many times, within at least five other families of staphylinoids besides Leiodidae. Further, closure has probably occurred at least 9 times within Leiodidae, at least once in each of the groups shown here. Finally, the shape of the pronotal process varies in complex fashion within this family, so that quadrangular and triangular processes occur within each of the three larger subfamilies. Thus, this character is not even useful for the family or subfamily divisions recognized by Jeannel.

Jeannel's use of the structure of the mesepisternum to separate leiodid groups has similar problems. Fig. 1 illustrates the condition that I consider primitive in Staphylinoidea, in which the mesepisternum contacts the mesocoxal cavity at one point. This condition is very widespread in Staphylinoidea and occurs in the most primitive leiodids, as in this camiarine. This plesiomorphic condition, Condition 1, is modified in several ways within leiodids as shown in Tab. 4. Condition 2, used by Jeannel for Cholevinae, does characterize most but not all cholevines. However, Condition 4, used by Jeannel for all other leiodids, is in fact restricted to certain tribes of Leiodinae. Other leiodines have a less derived condition, 3, as illustrated in

Tab. 4 - Mesepisternum shape and contact with mesocoxal cavity in Staphylinoidea.

Condition 1: (plesiomorphic): Mesepisternum contacts mesocoxal cavity at a single point; mesosternal-mesepisternal suture nearly straight
- STAPHYLINOIDEA: Most families, including Agyrtidae
- LEIODIDAE:
  - CAMIARINAE (most)
  - COLONINAE
  - CHOLEVINAE: ORITOCATOPINI (but mesepisternal-epimeral suture greatly reduced)

Condition 2: (=1) but mesepisternum does not quite contact mesocoxal cavity
- CHOLEVINAE: ANEMADINI, CHOLEVINI, LEPTODIRINI, PTOMAPHAGINI

Condition 3: (=1) but mesosternal-mesepisternal suture strongly curved
- LEIODINAE: SOGDINI, ESTADIINI, LEIODINI

Condition 4: (=3) but mesepisternum contacts mesocoxal cavity broadly
- LEIODINAE: PSEUDOLIODINI, SCOTOCRYPTINI, AGATHIDIINI

Condition 5: Mesosternal-mesepisternal suture and/or mesepisternal-epimeral suture indistinct or absent, so that mesepisternal shape and contact with mesocoxal cavities not determinable
- CATOPOCERINAE
- PLATYPSYLLINAE
- CHOLEVINAE: EUCATOPINI
- CAMIARINAE (some)
- LEIODINAE (some)

various recent works by Daffner and Baranowski. The remaining leiodids have the sutures on one or both sides of the mesepisternum obliterated to the extent that it is impossible to determine its limits or the extent of contact with the mesocoxal cavities. Thus here, as in the case of procoxal closure, the character is more complex than indicated by Jeannel, and is useful but at a lower systematic level than he used it.

The same can be said for the remaining character used by Jeannel in his "family" division of leiodids, the plicate versus tuberculate mola of the larva. These conditions represent extremes of a continuum of molar surfaces,

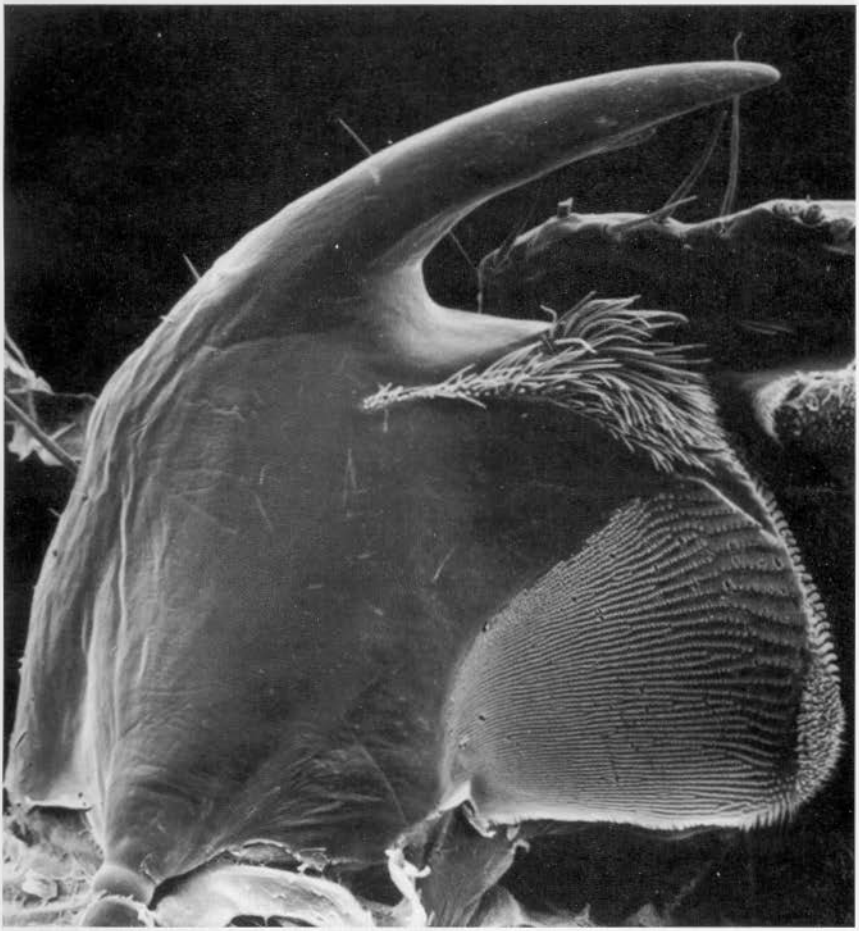

Fig. 2 - Mature larva, right mandible, ventral, of *Necrophilus hydrophiloides* Guérin-Méneville (Agyrtidae), 150X.

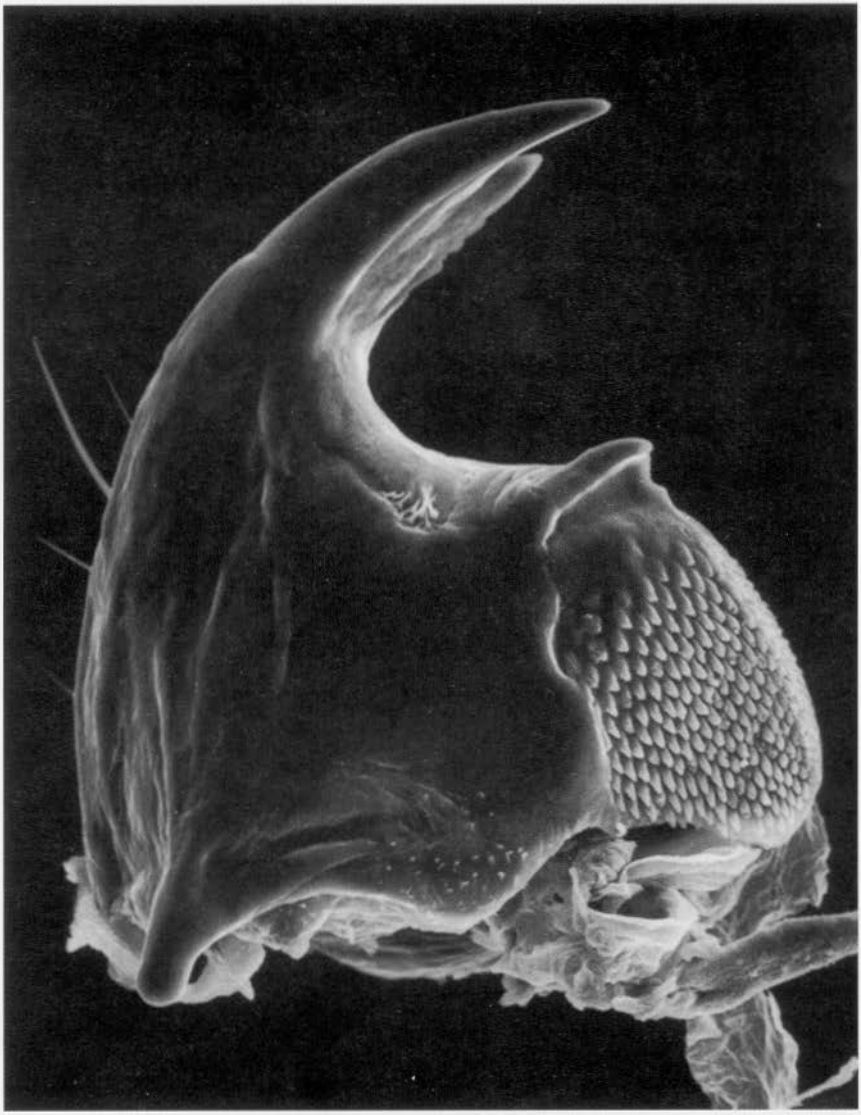

Fig. 3 - Mature larva, right mandible, ventral, of *Anistoma errans* Brown (Leiodinae: Agathidiini), 320X.

which are highly correlated with the type of food. Fig. 2, of the larval mandible of an agyrtid (*Necrophilus*), shows a "plicate" mola, actually consisting of rows of fine teeth. This condition is probably plesiomorphic for leiodids, found not only in cholevines but in at least some larvae of all known subfamilies including most Leiodinae. In contrast, a mola with large scattered teeth or tubercles is found only in Agathidiini such as *Anisotoma* (Fig. 3), and in certain camiarines, which feed on Myxomycetes with large tough spores that must be crushed.

If these characters used by Jeannel (1936) are not useful for separating the groups he recognized, then we must seek other evidence that will test the validity of these groups and provide evidence for their relationships and the classification to be adopted. A number of potentially useful characters have become evident through the work of other specialists on leiodids, and through

Tab. 5 - Probable synapomorphies of family groups of Staphylinoidea, modified and augmented from Lawrence & Newton (1982). Numbers in () refer to internodes in Fig. 12.

HYDRAENIDAE + PTILIIDAE
- Genital segment permanently everted, well sclerotized
- Ovipositor with gonocoxites connate or fused to each other
- Larva: apex of maxillary palp with complex 3-part appendage
- Larva: anal membranes with 2 hooks
- Pupa: only 1 pair functional abdominal spiracles
- etc.

STAPHYLINIDAE (s.l.) + SILPHIDAE + SCYDMAENIDAE
- Elytra truncate, exposing some abdominal segments dorsally (reversed in certain groups)
- Wing with unique hinge and folding pattern
- Aedeagus specialized, with large muscle-filled basal bulb and small basal foramen
- Larva: mandible without molar lobe
- Larva: labrum of 3-5 sclerites, without tormae
- Larva: tentorium specialized, bridge directed posteriorly
- etc.

(1) AGYRTIDAE + LEIODIDAE (s.l.)
- Antenna with open sensilla-filled periarticular gutter on several preapical segments
- Larva: anterior arms of epicranial suture bifurcate
- Larva: unique hypopharyngeal muscle disks present

(2) AGYRTIDAE
- Aedeagus very asymmetrical, parameres greatly reduced and fused to one another or absent

(3) LEIODIDAE (s.l.)
- Antenna with "interrupted" 5-segmented club, segment 8 smaller than segments 7 or 9 (reversed in Coloninae?)
- Antenna with periarticular gutter of segments 7, 9 and 10 nearly enclosed (sometimes reversed)
- Wing without discrete anal lobe, venation reduced
- Aedeagus with "lame ventral" (modified basal piece?) attached to parameres
- Larva: maximum of 5 stemmata ("ocelli") on each side of head
- Larva: setal field of mandible reduced, not reaching mesal edge

general morphological work on beetles. Still more are apparent from my own character survey in this group. From here on, I will present evidence from all of these sources, covering more than 50 character systems of adults and larvae, that does seem to provide support for most of the groups recognized by Jeannel and others. These will be in the form of a list of apparent synapomorphies that unite various taxa. Of course, these lists and the chosen character polarities must be considered preliminary until more taxa and characters are surveyed and a full phylogenetic analysis is completed, but I hope they will provide an indication of which groups are likely to be monophyletic and which are not, and provide a basis for the classification shown in Table 1 and presented in detail in the main catalog section.

First, Table 5 summarizes the characters that were already used by Lawrence & Newton (1982) to justify the recognition of three monophyletic

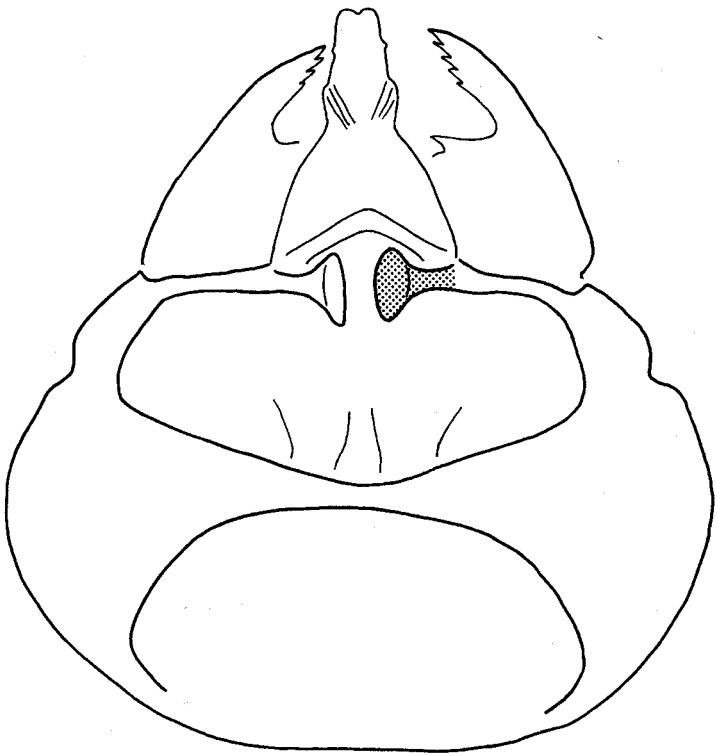

Fig. 4 - *Agyrtodes atropos* (Blackburn) (Camiarine: Agyrtodini), larva, head, ventral, schematic diagram showing internal hypopharyngeal disks (one stippled).

groups of families in Staphylinoidea. The family groups here are quite similar to those of Jeannel discussed earlier, except for the removal of Agyrtidae from Silphidae and its association with Leiodidae. The first two family groups are each strongly supported by a number of uniquely derived characteristics, while Agyrtidae and Leiodidae are united by fewer and less well known derived characters. These two families thus seem to be less removed from the common ancestor of staphylinoids than the other groups. The most important of the synapomorphies they share is the presence of a unique pair of muscle disks in the hypopharynx of the larva (Fig. 4). A mass of muscle tissue extends directly between these in uncleared specimens, as illustrated by Deleurance-Glaçon (1963) in *Bathysciola* (Leptodirini), but the function of this structure is unknown. The disks are reduced in size in those leiodid larvae that have reduced molar lobes, as in *Agathidium* larvae that feed on Myxomycete plasmodia, so they are probably related in some way to the grinding action of the mandibles. Within certain Cholevinae, as mentioned later, a unique hypopharyngeal bar replaces these disks. Such disks are unknown in the otherwise similar larvae of Hydraenidae and Ptiliidae, and in other beetles. The bifurcate anterior arms of the larval epicranial suture appear to be unique also.

The sensilla-filled periarticular gutters of several preapical antennal segments of adults are unusual, but somewhat similar conditions occur elsewhe-

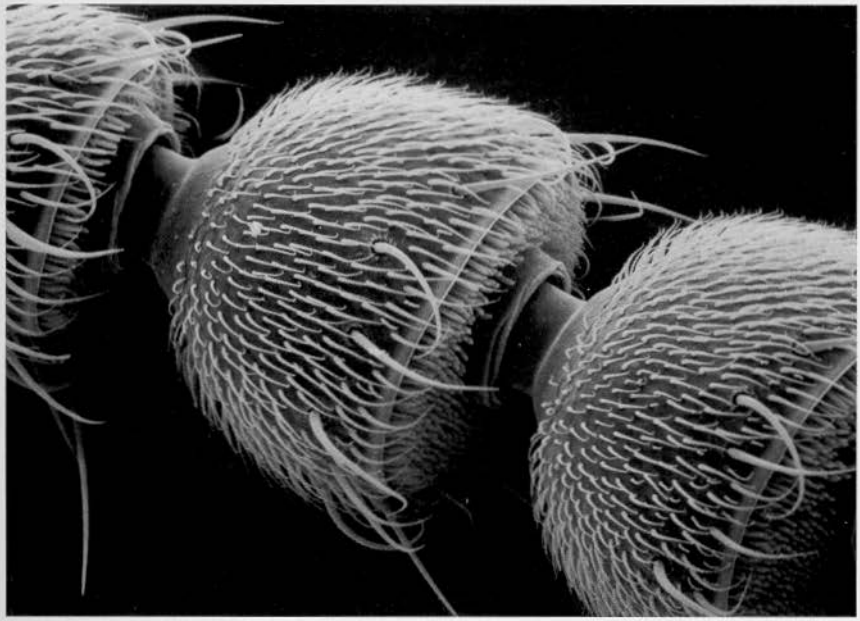

Fig. 5 - Antenna of *Necrophilus pettitii* Horn (Agyrtidae), segment 8 (200X).

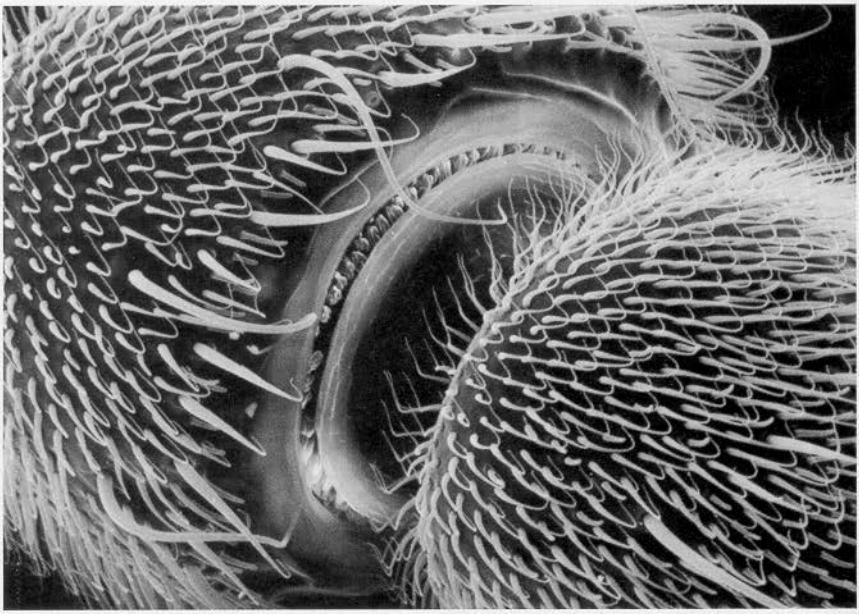

Fig. 6 - Antenna of *Hydnobius crestonensis* Hatch (Leiodinae: Sogdini), apex of segment 10 (460X).

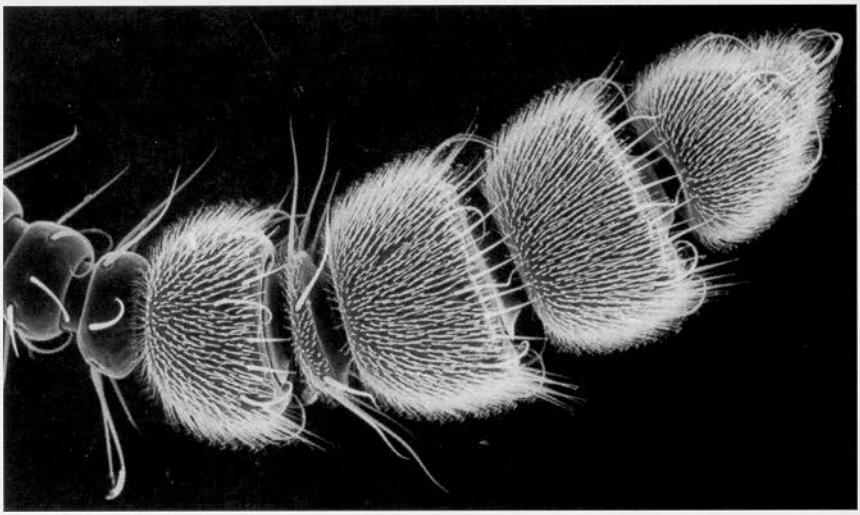

Fig. 7 - Antenna of *Hydnobius crestonensis,* apical 7 segments (120X).

re and a few more derived members of both Agyrtidae and Leiodidae have modified or lost these. Fig. 5 of a preapical antennal segment of an adult *Necrophilus* shows the open, sensilla-filled periarticular gutter found in most agyrtids. This is the likely precursor to the more enclosed gutter found in most leiodids, as in *Hydnobius* (Fig. 6) with several sensilla visible through the narrow slit opening of the gutter. The gutter is usually absent on the reduced eighth antennal segment of the "interrupted" antennal club in leiodids (Fig. 7). However, there is much variation within the family in the development of this gutter, including secondary opening of the slit as in *Glacicavicola* and many *Catopocerus*. Most remarkable is the development of "vesicles", or further sensilla-filled chambers, extending internally from the gutter. These are best developed in Leiodinae, Coloninae and Cholevinae, as illustrated for example by Corbière-Tichané (1973a, 1974, 1977) and Peck (1977a).

Agyrtidae are the most primitive group of Staphylinoidea overall, and their only synapomorphies evident to me are in the structure of the aedeagus, which is always highly asymmetrical with parameres modified or lost. Leiodidae in the broad sense appears to be a well-defined and monophyletic group with at least 6 synapomorphies. These include the characteristic "interrupted" antennal club with a reduced eighth segment, and the near-enclosure of the antennal periarticular gutter compared to the open gutter found in most Agyrtidae. Other synapomorphies include the loss of a discrete anal lobe of the wing, and somewhat reduced venation; a characteristic "lame ventral" of the tegmen of the aedeagus, which may be a modified basal piece of other Coleoptera; and in larvae the loss of one stemma and reduction of the large setal field of the mandible found in Agyrtidae.

Within Leiodidae, support for monophyly of individual subfamilies varies greatly, and the extremes are shown in Table 6. At one extreme, the two small subfamilies Coloninae and Platypsyllinae are each very well defined by a large suite of synapomorphies, including many unique characteristics as well as a few shared with each other or with other leiodids. These shared synapomorphies are not strong ones, however, and I would be hesitant to link either of these with another subfamily at this time.

At the other extreme, the south temperate group Camiarinae in the broad sense used by me has no synapomorphies at all, and it is unlikely that this group is monophyletic. It is possible to recognize a series of probably monophyletic generic groups within this subfamily, as I attempted to do in a biogeographical review (Newton, 1985), but these groups intergrade. This fascinating group requires much more attention than it has received. At least 10 undescribed genera and more than a hundred undescribed species are known in collections, so there is relatively more descriptive taxonomic work to be done here than in other subfamilies. These are the least derived of all leiodids and retain some notable primitive features that are lost or modified in other leiodids, including true adult ocelli in two genera, 5 larval stemmata rather than 3 or fewer as in all other subfamilies, and the frequent presence of a Y-shaped epistomal suture (this last also occurs in Catopocerinae). The genus *Ragytodes* (Fig. 8), from southern South America, illustrates some of

Tab. 6 - Probable synapomorphies of leiodid subfamilies Coloninae, Platypsyllinae and Camiarinae. Numbers in () refer to internodes in Fig. 12.

(4) COLONINAE
Antenna with "uninterrupted" club, segment 8 not reduced compared to 7 and 9
Arms of tentorium medially fused
Mandibles with reduced, smooth molar lobes
Cervical sclerites absent
Procoxal cavities closed by complete fusion of notal process and prosternum
Elytra not striate
Protarsi of both sexes dilated and with adhesive setae
Mesotarsi of neither sex dilated or with adhesive setae
Abdominal intersegmental membranes with "brick-wall" pattern
Abdominal spiracles 7-8 absent
Male tergum 8 connate with dorsum of genital segment
Aedeagus highly specialized, homologies uncertain
Female with only 4 visible abdominal sterna
Ovipositor with proximal gonocoxites fused to one another
Biology: hypogean fungi? (suspected, not demonstrated)

(5) PLATYPSYLLINAE
Head with elevated occipital crest which overlaps pronotum in repose
Cervical sclerites absent
Elytra not striate
Flightless, eyes reduced or absent
Pro- and mesotarsi of both sexes dilated and with adhesive setae
Larva: stemmata absent
Larva: lacinia with large scooplike apex
Biology: obligate associates or ectoparasites of mammals

CAMIARINAE
NO synapomorphies

these characters (e.g., ocelli) and problems. Jeannel (1936, 1962) placed this genus in his tribe Neopelatopini of Leiodinae, while Hlisnikovský (1964b) independently named it in Silphidae. This genus has the characteristic antennae and wings noted above for Leiodidae, but lacks the appearance, antennal insertions or other characters of Leiodinae; lacks the characteristic head and procoxal cavity closure of cholevines; and lacks the enlarged maxillary palps and other characters of Camiarini in the strict sense. Another example of a problem genus is *Catopsolius*, from New Zealand (Fig. 9). In addition to a generalized morphology comparable to *Ragytodes*, this photograph illustrates another problem in the study of some of these genera: this species is known only from this type and a few other specimens, none of them collected recently. In fact, some of the largest New Zealand camiarines are known from single specimens, and may be extinct even before they are described.

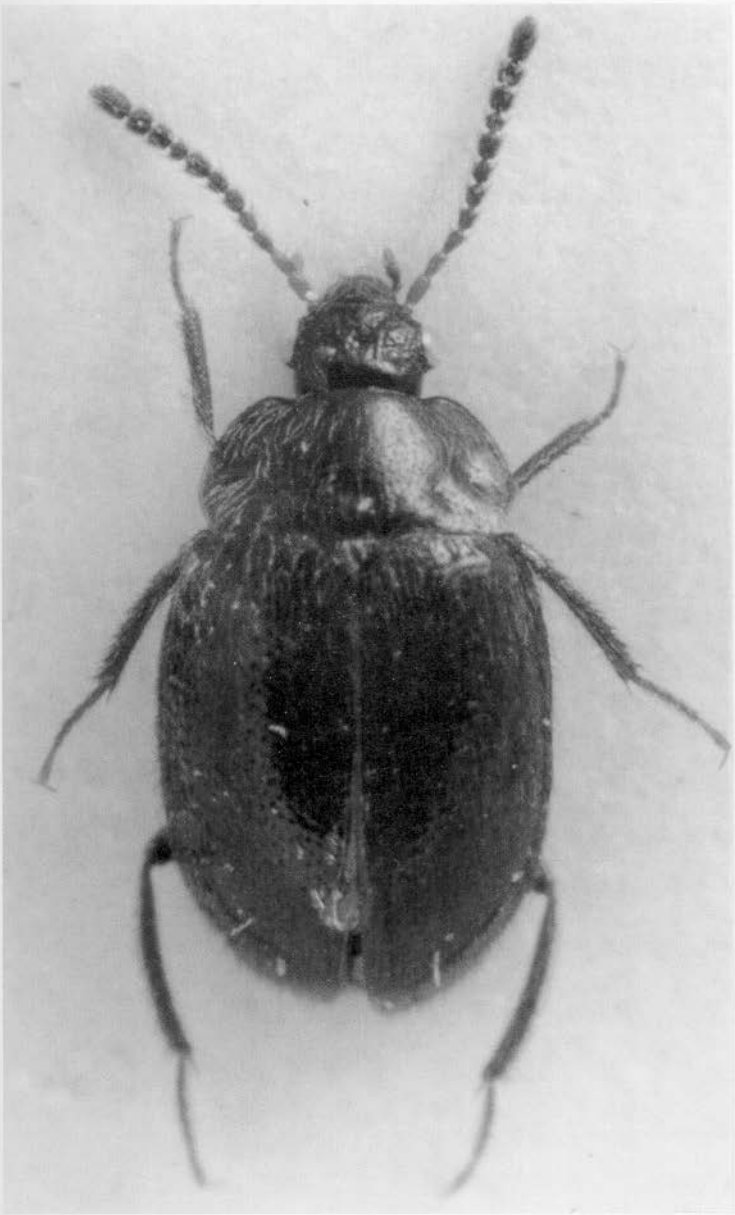

Fig. 8 - Light photograph of *Ragytodes ocellifer* Jeannel (Camiarinae: Neopelatopini) (paratype of synonym *Tricholoma kaszabi* Hlisnikovský).

Fig. 9 - Light photograph of *Catopsolius laevicollis* Sharp (Camiarinae: Neopelatopini) (syntype).

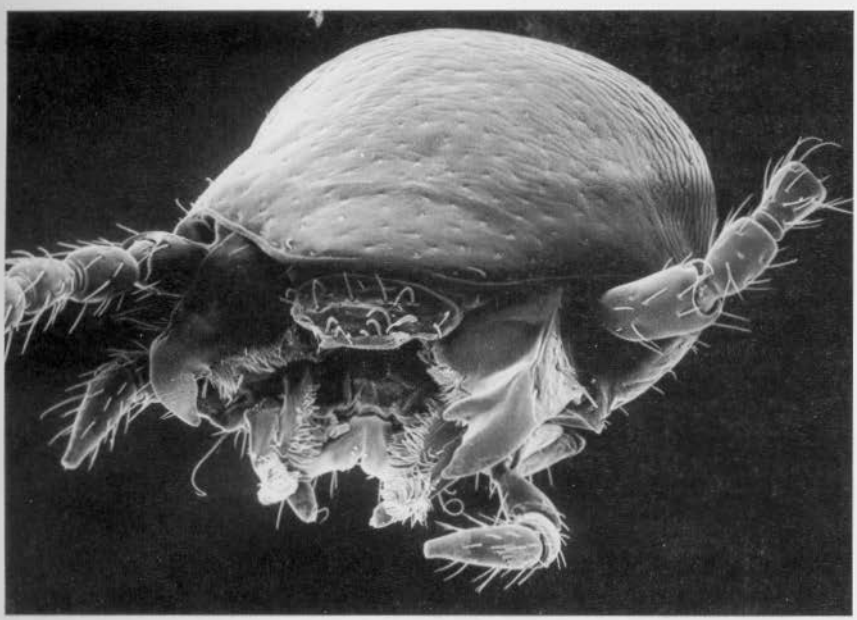

Fig. 10 - *Catopocerus appalachianus* Peck (Catopocerinae: Catopocerini), head (120X).

One synapomorphy that may link two leiodid subfamilies, in combination with other characters such as nearly "glabrous" body and large flat head, is an antennal insertion that is concealed from above, as in *Catopocerus* (Fig. 10). This feature, which I thank Richard Leschen for pointing out, seems to be a general characteristic of Leiodinae also, but is not found in the highly modified cave beetle *Glacicavicola* placed in Catopocerinae. These two subfamilies (Tab. 7) also share some larval characters, notably loss of subbasal abdominal carinae. Catopocerinae are rather weakly supported as monophyletic by their elongate prosternum and well-separated metacoxae.

Leiodinae have been a difficult group to delimit, but in addition to the synapomorphies shared with Catopocerinae leiodines have the characteristic strongly curved mesosternal-mesepisternal suture mentioned earlier, and some other adult and larval traits that suggest that this group is monophyletic (after removal of the tribe Neopelatopini placed here by Jeannel). Within this subfamily, two distinctive sets of tribes can be recognized, each with clear synapomorphies. Members of one of these groups, Sogdini through Leiodini, have specialized mouthparts and hypogean larvae that are probably correlated with a general association with hypogean fungi,

Tab. 7 - Probable synapomorphies of leiodid subfamilies Catopocerinae and Leiodinae, and of groups of tribes of Leiodinae. Numbers in () refer to internodes in Fig. 12.

(6) CATOPOCERINAE + LEIODINAE
Antennal insertion concealed in dorsal view (except *Glacicavicola*, reversed?)
Head relatively flattened and broad, half or more as wide as pronotum
Body apparently "glabrous"
Larva: transverse subbasal abdominal carinae absent
Larva: galeal fringe greatly reduced (except some Agathidiini)

(7) CATOPOCERINAE
Prosternum elongate, longer than coxal cavities
Metacoxae separated by 1/3 or more of their width
Flightless, eyeless
Larva: stemmata absent
Biology: humicoles, subterranean

(8) LEIODINAE
Antennal segments 7, 9 and 10 usually with vesicles
Arms of tentorium medially fused
Mesosternal-mesepisternal suture strongly curved
Cervical sclerites with broadly rounded outer projection
Larva: maximum of 3 stemmata on each side of head

(9) SOGDINI + ESTADIINI + LEIODINI
Lacinia with dense setal brush along entire mesal edge
Mandibles with reduced, non-contiguous molar lobes
Labrum deeply emarginate
Larva: hypogean, reverse C-shaped (Estadiini unknown)
Larva: body with simple setae only (" ")
Biology: hypogean fungi? (not known in Estadiini)

(10) PSEUDOLIODINI + SCOTOCRYPTINI + AGATHIDIINI
Tarsal formula always reduced, maximum 5-5-4 (♂), 5-4-4 (♀)
Clypeus subquadrangular
Procoxal cavities closed by triangular notal process
Aedeagus with "lame dorsal" extended dorsally from base of parameres
Biology: epigean fungi

although the biology of Estadiini and many genera of the other two tribes is unknown. Most members of the other group, Pseudoliodini through Agathidiini, have more typical leiodid mouthparts and larvae, and most are associated with epigean fungi, including Myxomycetes for most Agathidiini. However, many scotocryptines are obligate associates of social insects, found in nests of fungus-growing termites and stingless bees.

Finally, we come to the largest and in many ways best-studied subfamily, Cholevinae, the focus of this symposium (Tab. 8). After removal of Jeannel's tribe Agyrtodini, which several authors including Zwick (1979), Perreau (1989) and I (Newton, 1985) have suggested, cholevines can be recognized

Tab. 8 - Probable synapomorphies of leiodid subfamily Cholevinae and of some included lower taxa. Numbers in () refer to internodes in Fig. 12.

(11) CHOLEVINAE
Head shape molded to that of pronotum, line of contact delimited by carina or crest
Procoxal cavities closed by quandrangular notal process (triangular in Eucatopini)
Elytra not striate (rarely very indistinctly striate)
Abdominal spiracle 8 greatly reduced or absent
Antennal segments 7, 9 and 10 usually with 1-2 vesicles each
Larva: maximum 1 stemma on each side of head (except *Prionochaeta* with 3)
Biology: saprophages/scavengers at dung, carrion, vertebrate and insect nests

(12) ANEMADINI + CHOLEVINI
Mesocoxal cavities widely contiguous
Head with strongly elevated occipital crest (except Anemadini: Paracatopina)
Maxillary palp segment 4 reduced, shorter than 3
Larva: hypopharyngeal bar present, muscle disks reduced or absent
Larva: lacinia with a single apical tooth

(13) LEPTODIRINI
Female protarsus 4-segmented
Tarsal empodium with single non-articulated "seta"
Maxillary palp segment 4 reduced, shorter than 3
Metacoxae slightly separated
Male genital segment short, ringlike

PLATYCHOLEINA (=*Platycholeus* only)
Unique elytral-abdominal tergum 8 interlock system present
Tergum of male genital segment with deep impression
Aedeagus with "lame ventral" reduced and straplike
Biology: inhabit rotting logs (+/- with ants or termites)

LEPTODIRINI (remaining)
Flightless, eyes reduced or absent
Spermatheca "Type 1" (Perreau 1989)
Post-mesocoxal carina curved, not angulate
Biology: humicoles, subterranean

(14) ORITOCATOPINI + EUCATOPINI + PTOMAPHAGINI
Epistomal suture absent
Mesosternal process strongly developed, separating mesocoxal cavities
Male mesotarsus not dilated, without adhesive setae
Female spiculum ventrale absent (Perreau 1989)
Spermatheca "Type 2" (Perreau 1989)

by their characteristic head shape. The head is molded to fit closely against the front of the pronotum, forming a smooth contour, but this shape is lost in many of the more modified cave-dwelling Leptodirini. A somewhat similar but less developed head shape occurs in Coloninae, and a more developed overlapping of head and pronotum in Platypsyllinae, but these may be independently acquired conditions. The other synapomorphies listed here for

cholevines are consistent with monophyly of this group but not unique to it.

Within cholevines, the definitions and relationships among the subgroups are not at all well established or agreed upon. For example, the tribe Anemadini as used here, and by Perreau (1989), has been treated historically as two groups, Nemadini and Anemadini, while Giachino & Vailati (1993) recognized three groups which are widely separated in their phylogenetic diagram. Although possible phylogenetic relationships among all cholevine groups have been diagrammed and discussed by these authors as well as Szymczakowski (1964a), synapomorphies linking the various groups have generally not been established, and a full phylogenetic analysis not completed.

One group of three tribes, Oritocatopini, Eucatopini and Ptomaphagini, was recently recognized by Perreau (1989), based on a characteristic spermatheca and loss of the female spiculum ventrale. Other synapomorphies noted here also support this group, including a strongly developed mesosternal process which is found elsewhere in Cholevinae only in leptodirines, where it is lost in the most highly modified taxa. (In other leiodid subfamilies, the mesocoxae are separated but usually by a combination of less developed mesosternal plus metasternal processes.) However, relationships among these three tribes are not clear. Historically, Eucatopini and Ptomaphagini have been associated or combined because each has a tibial comb and a modified aedeagus lacking a distinct tegmen (except for parameres), but these conditions are possibly symplesiomorphous or not homologous, respectively. Eucatopini and Oritocatopini are unique among winged leiodids in having the mesepisternal-epimeral suture greatly reduced or absent, and also are the only cholevines to retain normal maxillary palps with a large apical segment and a reduced, but possibly functional, spiracle on the 8th abdominal segment. Ptomaphagines have a reduced apical maxillary palp segment as found in other cholevines.

The two tribes Anemadini and Cholevini have usually been associated with one another, and with the remaining tribe Leptodirini. Anemadini, including Jeannel's group Nemadinae, is still not demonstrably monophyletic, even after removal of Agyrtodini and Oritocatopini as noted earlier and elimination of the rather artificial division between anemadines and nemadines. However, Anemadini and Cholevini together do share several synapomorphies, including two unusual ones: widely confluent mesocoxal cavities, and a unique hypopharyngeal bar in larvae that is correlated with great reduction or loss of the hypopharyngeal muscle disks found in all other leiodids.

Last, and in some ways the most problematic of all, is the enormous group Leptodirini. This group does seem to be monophyletic, as indicated by the unique 4-segmented female protarsi and some other synapomorphies. One of these not noticed before is the presence of a non-articulated "seta" on the tarsal empodium (Fig. 11); all other examined leiodids appear to have 2 articulated empodial setae, although one of these may be greatly reduced. However, evidence linking leptodirines to other cholevines is rather contra-

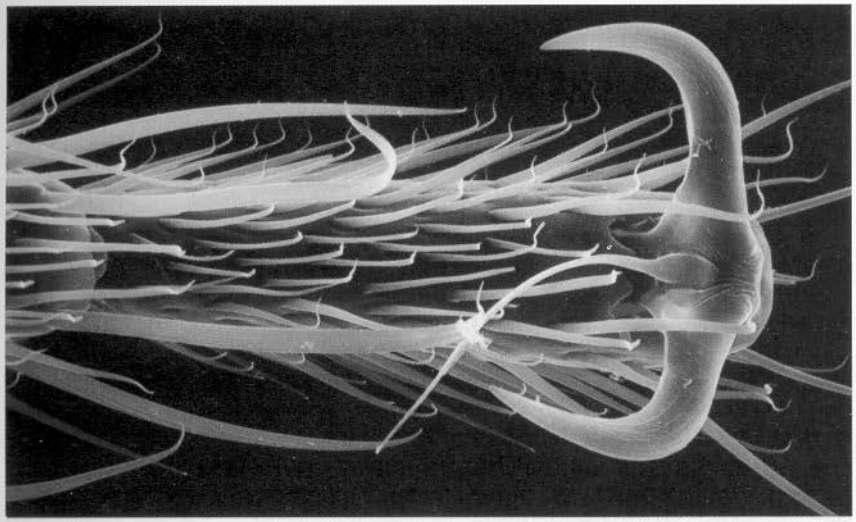

Fig. 11 - *Platycholeus* n. sp. (Cholevinae: Leptodirini), ♂ protarsus, apex, ventral (700X).

dictory. For example, with the exception of the most highly modified genera, leptodirines lack the widely confluent mesocoxal cavities of the previous group (Anemadini + Cholevini), and the few leptodirine larvae I have examined (including *Platycholeus*) lack the unique hypopharyngeal bar of that group. Hence, the short ringlike genital segment that was used by Jeannel to link Leptodirini and Cholevini may not be a synapomorphy for these groups. Except for having a well-developed mesosternal process separating the mesocoxae, leptodirines also lack the synapomorphies of the Oritocatopini-Ptomaphagini group of tribes.

Within leptodirines, there has been much discussion and controversy over the course of evolution in this group, which are reviewed in more detail by Giachino et al. (1998). Recently, Giachino & Etonti (1995) proposed a revolutionary interpretation, suggesting that the otherwise highly modified genera *Antroherpon* and *Remyella* may form a sister group to all other leptodirines. This interpretation, based on characters of the aedeagus and genital segment, is difficult to reconcile with other evidence and comparison with outgroups. It seems more likely that the rather long genital segment of these two genera, and very short straight aedeagus, are specializations within leptodirines. I would suggest instead that the most primitive leptodirines are probably those implicit in Jeannel's (1924) monograph, namely the primitive members of Jeannel's Division 1 (or Pholeuina) such as *Platycholeus*, *Sciaphyes* and *Adelopsella*. In these genera, the genital segment, although short, has a distinct tergum, pleurites and sternum, while these sclerites are fused into a single ring in most other leptodirines, apparently including *Antroherpon* and *Remyella*.

The North American genus *Platycholeus*, the only confirmed New World leptodirine and the only one with flight wings and well-developed eyes, combines certain additional primitive features, such as a simple membranous spermatheca, with likely autapomorphies such as an enlarged fringed galea, a reduced parameral basal lobe of the aedeagus, and special abdominal tergal structures. The mesosternal process is well developed, and metacoxae only narrowly separated. The prolegs lack a tibial comb or apical basket, and males have 5-segmented protarsi and mesotarsi with one segment dilated and bearing adhesive setae. And last, the seta-like process of the tarsal empodium (Fig. 11) is not split as it is in most other leptodirines.

If we combine all the groupings that I have indicated above are supported by some synapomorphies into a single phylogenetic diagram, it would look something like Fig. 12. Lineages that seem to be supported as monophyletic are indicated by single lines, those that are probably paraphyletic by double lines. Clearly, there are many unresolved questions here. Completion of formal phylogenetic analyses might add further resolution. Of course, such analyses may also indicate that some of these groups are not justified. At least, even at this stage, this is a concrete proposal that can be tested by study of additional characters and taxa.

Several conclusions can reasonably be drawn from this and other studies so far. (1) Leiodidae in the present sense is a clearly defined, monophyletic group. Its sister group, and only close relative, is the small family Agyrtidae. (2) The six leiodid subfamilies, often treated as families, are less clearly defined and of uncertain relationship to one another. Some taxa, for example Neopelatopini and Agyrtodini, are of uncertain relationships and have been moved between subfamilies. (3) The subfamily Camiarinae includes the least derived leiodids, and the other subfamilies are derivable from it. It is not demonstrably monophyletic, but moving several controversial taxa into it increases the likelihood that the remaining five subfamilies are monophyletic. (4) The recognition of a single family Leiodidae with a series of subfamilies can better represent situations (1) - (3) above, and is more consistent with the classification of the rest of Staphylinoidea and Coleoptera, than the recognition of 5-6 families. Most of the characters originally proposed by Jeannel (1936) to justify these family divisions are erroneous. (5) Resolution of phylogenetic relationships among the leiodid subfamilies will be difficult until the taxonomic and morphological diversity of Camiarinae is better understood. Taxa currently included in this group (plus a large number of undescribed genera and species) appear to bridge the gap between otherwise distinctive subfamilies such as Leiodinae and Cholevinae. (6) Finally, even within the best-known leiodid group, Cholevinae, many questions remain concerning the definition of and relationships among the subgroups. Lepto-

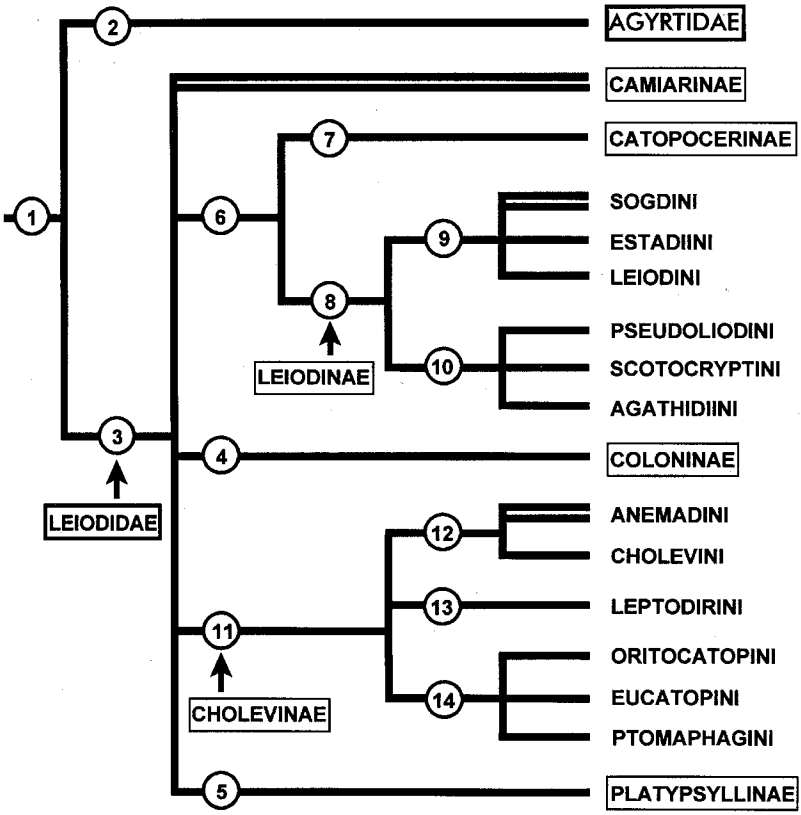

Fig. 12 - Diagram of inferred relationships among subfamilies and some tribes of Leiodidae, based on phylogenetic discussion in text. Numbers along internodes refer to lists of probable synapomorphies in Tabs. 5, 6, 7 and 8. Double lines indicate probable paraphyletic groups.

dirini may be a more basal group of cholevines than previously thought. Better knowledge of the extra-European Leptodirines may be critical to understanding the enormous and complex European radiation of this group.

General references

This section is a brief and no doubt incomplete review of the main literature on leiodids from various perspectives, similar to the one on Coleoptera as a whole at the beginning of Lawrence & Newton (1995). It is intended as an introduction to not only taxonomic literature (including main catalogs) but selected references to morphology, biology, ecology and larvae. Works on these subjects that pertain to only a single leiodid tribe or subtribe are generally not mentioned here but included in the discussion for the appropriate group in the main text.

Regional reviews (main recent ones only; see also Jeannel 1936): Europe: Giachino & Vailati (1993), Peez (1971), Szymczakowski (1971b). Asia: Angelini & Švec (1994), Hisamatsu & Hayashi (1985), Lafer (1989), Nakane (1955), Szymczakowski (1964a). South Africa: Angelini & Peck (1984), Jeannel (1964). Australia, New Zealand: Jeannel (1958), Matthews (1982), Szymczakowski (1966, 1973), Zwick (1979). North America: Arnett (1963), Downie & Arnett (1996), Hatch (1933, 1957), Peck (1973, 1990). Central and South America: Jeannel (1957b, 1962), Matthews (1887-88), Peck (1977c), Salgado Costas (1992b), Szymczakowski (1965, 1976).

Catalogs: *Coleopterorum Catalogus* (last complete world species catalog, Csiki, 1910; Hatch, 1928, 1929b; Jeannel, 1914b); *Genera Insectorum* (*Platypsyllus* only, Desneux, 1906); Cholevinae excluding Leptodirini (world species, Jeannel, 1936); Leptodirini only (world species, Laneyrie, 1967, 1970; world genera, Guéorguiev, 1976); suprageneric taxa only (Newton & Thayer, 1992). Regional catalogs on Coleoptera including leiodids are listed in Lawrence & Newton (1995); additions since then include checklists for Denmark (Hansen, 1996) and Italy (Angelini et al., 1995). Works intended for publication that have been completed at least in draft form include a world catalog of species of Cholevinae and Platypsyllinae (M. Perreau); a catalog of North American and West Indies species of Leiodidae (S. Peck); a catalog and keys to genera of Neotropical Leiodidae (S. Peck, P. Gnaspini & A. Newton); and a world checklist of all leiodid species (A. Newton).

Morphology: Feeding, digestive tract: Leschen (1993), Strambi (1970). Male/female genitalia: Iablokoff-Khnzorian (1980), Jeannel (1955a), Perreau (1989), Sharp & Muir (1912). Thorax: Brown (1933), Hlavac (1975). Wing folding and venation: Blum (1979), Forbes (1926), Kukalová-Peck & Lawrence (1993).

Larvae: Böving & Craighead (1931), Costa et al. (1988), Casale (1975a), Dybas (1976), Newton (1991), Paulian (1941), Zwick (1979), Zwick in Klausnitzer (1978).

Biology and ecology: Chandler & Peck (1992), Giachino & Tosti-Croce (1986), Hammond (1990), Kistner (1982), Leschen (1993), Newton (1984), Peck (1998a), Peck & Anderson (1985), Peschke et al. (1987), Růžička (1994), Shubeck et al., (1981), Wheeler (1984a).

Leiodidae Fleming, 1821

Leiodesidae Fleming, 1821: 51 (incorrect original spelling). Type genus: *Leiodes* Latreille, 1796.
Liodini Reitter, 1884: 91 (based on unjustified emendation). Type genus: *Leiodes* Latreille, 1796 (as Liodes, unjustified emendation by Erichson, 1845).

DIAGNOSIS:

Size 1-8mm. Form variable, usually ovoid, moderately flattened to strongly convex. Antenna 11-, rarely 10-segmented, usually with variably developed club of 5 segments with reduced 8th segment, club rarely of 4, 3, or other number of segments or antenna filiform; segments 7 and 9-10, 9-10, 8-10, or (10- segmented antenna) 7-9 or 8-9 each with apical periarticular gutter which is usually nearly enclosed, opening through a narrow slit to apical surface of segment; same segments often with internal vesicles opening into periarticular gutter. Elytra usually entire, covering abdomen; sometimes apically truncate, exposing abdominal tergum 8; rarely (*Platypsyllus*) shortened and exposing several abdominal terga. Hind wings with characteristic folding pattern consisting of convex and concave transverse folds, hinge absent; discrete anal lobe absent. Abdominal intersegmental membranes short, without pattern (except *Colon* with long membranes bearing brick wall pattern). Aedeagus without basal bulb, usually symmetrical, usually with pair of long parameres which often have basal lobes or a free basal piece.

KEY TO SUBFAMILIES OF LEIODIDAE

1. Head with distinct occipital carina or elevated crest, or if absent (some Cholevinae: Leptodirini) then tarsi 4-5-5 segmented in female (and often in male) 2
   Head without occipital carina or crest; tarsi never 4-5-5 segmented 3

2(1). Occipital crest overlaps pronotum when head in repose; cervical sclerites absent; procoxal cavities internally open behind ..... Platypsyllinae
   Occipital carina or crest (when present) rests against front of pronotum when head in repose; cervical sclerites present; procoxal cavities internally closed behind ..... Cholevinae

3(1). Antenna 11-segmented, segment 8 usually as large as segments 9-10 and bearing similar periarticular gutter and internal vesicles (except *Colon* (*Tricolon*)); cervical sclerites absent; intersegmental membranes between abdominal sterna long, with brick-wall pattern of minute sclerites; female with 4 visible abdominal sterna ..... Coloninae
   Antenna 11-segmented, segment 8 smaller than segments 9-10 and without periarticular gutter or internal vesicles, or antenna 10-segmented; cervical sclerites present; abdominal intersegmental membranes short and without minute sclerites; female with 5 or 6 visible abdominal sterna 4

4(3). Antennal insertions concealed in dorsal view (except *Glacicavicola*); head relatively flattened and broad, usually about half or more as wide as pronotum; dorsum apparently glabrous (but often with numerous very short hairs visible at high magnification); mesosternal-mesepisternal suture (if present) strongly curved 5

Antennal insertions visible in dorsal view; head relatively convex and narrow, usually less than half as wide as pronotum; dorsum usually clothed with long setae, rarely apparently glabrous; mesosternal-mesepisternal suture (if present) more or less straight . . . . . .Camiarinae

5(4). Prosternum in front of coxae longer than coxal width; hind coxae separated by about a third or more of their width; tarsi 5-5-5 segmented . . . . . .Catopocerinae
Prosternum in front of coxae much shorter than coxal width (except *Perkovskius*); hind coxae not separated, or if separated then tarsi reduced, at least hind tarsi 3 segmented . . . Leiodinae

Camiarinae Jeannel, 1911, *sensu novo*

Camiarinae Jeannel, 1911a: 192. Type genus: *Camiarus* Sharp, 1878.

DIAGNOSIS:

In addition to the absence of an occipital carina or crest, 11-segmented antenna with reduced 8th segment, relatively narrow and convex head and a usually setose dorsum, Camiarinae have: epistomal suture present or absent, with or without "stem"; cervical sclerites with more or less acute outer projection; procoxal cavities open or closed behind; postcoxal process of pronotum triangular or blunt; mesocoxal cavities separated by narrow mesosternal process; tarsi 5-5-5 segmented (reduced in 2 undescribed genera); and all abdominal spiracles functional or spiracles of 8th segment atrophied.

COMMENTS:

Originally proposed for *Camiarus* because of the enlarged 4th palpal segment of that genus, this subfamily was later used by Hatch (1928) as a depository for Leiodidae of uncertain position. Jeannel (1936) removed most of the extraneous genera and recharacterized the group as the family Camiaridae. Later (Jeannel, 1957b) he added a new genus and further modified his characterization. Jeannel's (1958) final concept of the group is here accepted as the tribe Camiarini, discussed further below.

To Camiarini, I am adding Jeannel's tribes Neopelatopini (from Leiodinae) and Agyrtodini (from Cholevinae) to form a subfamily Camiarinae. Several authors have commented on the difficulties of including Agyrtodini in Cholevinae, and the tribe was tentatively excluded by Zwick (1979) and Perreau (1989). Neopelatopini likewise make a characterization of Leiodinae more difficult if included in that subfamily. Neopelatopini, Agyrtodini and Camiarinae share many characters, and there are indications (see below) of a close relationship between genera of the 3 tribes; in fact it is difficult to delimit the tribes so that closely related genera are placed in the same tribe. Virtually all of the characters common to the 3 tribes, however, are likely to be primitive for Leiodidae as a whole or at least for a majority

of the subfamilies recognized here. The monophyly of Camiarinae in the present sense is therefore very much in doubt, and the group is proposed here as one of convenience rather than as a probable natural unit. The 3 included tribes are also of dubious monophyly (see below), but formal changes would best await a more detailed study of the entire group. I am aware of at least 10 distinctive undescribed genera of the subfamily, whose study and description will almost certainly require alteration of the tribal and subfamily classification presented here. Until this can be completed, I prefer to avoid any more drastic changes at the family-group level in Camiarinae.

Key to Tribes of Camiarinae

1. Fourth segment of maxillary palp enlarged, at least 1.5X as wide as 3rd segment; metepisternum with small tongue-like process which overlaps elytron in repose ..... Camiarini
   Fourth segment of maxillary palp less than 1.5X as wide as 3rd; metepisternum without tongue-like process (except *Chelagyrtodes* and *Dictydiella*) 2

2(1). Procoxal cavities internally open behind or closed by more or less triangular notal process; abdominal segment 8 with functional spiracles ..... Neopelatopini
   Procoxal cavities internally closed behind by broad, blunt notal process; spiracles of abdominal segment 8 atrophied ..... Agyrtodini

Neopelatopini Jeannel, 1962, *sensu novo*

Neopelatopini Jeannel, 1962: 487. Type genus: *Neopelatops* Jeannel, 1936.

Diagnosis:

In addition to the characters indicated in the key, Neopelatopini have: epistomal suture present, with or without "stem"; mandible with or without well developed molar lobe bearing grinding surfaces; and aedeagus with basoventral parameral lobe reduced or absent, with or without long free parameres.

Distribution: Australia, New Zealand, s Neotropical.

Comments:

The tribe, originally proposed for the 3 described genera from Chile and Argentina, was expanded by Newton (1985) with the addition of *Eublackburniella* and *Myrmicholeva* (Australia), problematic genera which had been transferred from Cholevinae to Leiodinae by Szymczakowski (1966) and Jeannel (1936), respectively. These genera fit the original characterization of Neopelatopini well and it is surprising that Jeannel did not include them.

Newton (1985) briefly characterized three groups within this tribe: *Neopelatops; Ragytodes* Group (*Ragytodes, Eublackburniella, Myrmicholeva,* and two undescribed genera from eastern Australia, one of which has since been found also in western New Guinea); and *Sphaeropelatops* Group (*Sphaeropelatops* and one undescribed genus from New Zealand). Two additional genera, noted by Newton (1985) as Camiarinae *incertae sedis*, are assignable to this tribe as defined here: *Catopsolius* (=*Asphaerites*) from New Zealand, and an additional undescribed genus from southeastern Australia. The addition of these genera, and the position of neopelatopines as perhaps the least derived of all leiodids, clearly indicate the need for further detailed study of this group.

Neopelatops, Catopsolius and some of the undescribed genera resemble Leiodinae in lacking the dorsal vestiture of long setae found in other Camiarinae, but there is little else to support a close relationship of these genera to Leiodinae. The reduction of the basal lobes of the parameres, cited by Jeannel (1936) as characteristic of all Leiodinae including Neopelatopini, is in fact restricted to certain tribes and genera of Leiodinae in the present sense. The reduction of basal parameral lobes in Neopelatopini is probably an independent development, which has also occured elsewhere in Leiodidae (e.g. in some Camiarini and in Ptomaphagini and Paracatopina). *Neopelatops* larvae have 5 stemmata on each side of the head as in other known camiarine larvae, while all known leiodine larvae have 3 or fewer stemmata.

Myrmicholeva is unique among all Staphylinoidea in possessing acute, piercing-sucking mouthparts in both adults and larvae (personal observations). Together with *Eublackburniella*, the genus possesses a pair of deep, setose cavities in the concealed portion of the scutellum; similar cavities are found in *Inocatops* (Camiarini) and in reduced form in some of the undescribed genera of Neopelatopini and in the Australian species of *Neopelatops*.

Four *Neopelatops* species have been found commonly as adults and larvae on fruiting bodies of slime molds (Newton, 1984). *Myrmicholeva* was originally reported as being myrmecophilous (Lea, 1910), but this has not been substantiated by recent collections which are primarily from forest litter. Little is known of the habits of the other genera, although *Eublackburniella* species are also usually found in forest litter, and species of the undescribed New Zealand genus allied to *Sphaeropelatops* are commonly associated with rotting logs and in some cases found near slime molds (personal observations).

Larvae: Newton (1991). Examined: *Eublackburniella* sp. (Australia: W. A.); *Myrmicholeva acutifrons* Lea; *M.* sp. (Australia: W. A.); *Neopelatops edwardsi* Jeannel; *N.* sp. (Australia: Vic.); undet. genera and species (Chile, New Zealand).

GENERIC CATALOG:

Catopsolius Sharp [Tc] New Zealand (2 spp.)
Catopsolius Sharp, 1886: 383. Type sp.: *Catopsolius laevicollis* Sharp, 1886 (monotypy).
Asphaerites Broun, 1893: 1067 (NEW SYNONYMY; see Appendix A). Type sp.: *Asphaerites nitidus* Broun, 1893 (monotypy).

Eublackburniella Jeannel [T, Sc] Australia (2 spp.)
Eublackburniella Jeannel, 1938: 257 (new name for *Blackburniella* Jeannel). Note: 8+ new spp. seen, throughout Australia.
Blackburniella Jeannel, 1936: 114 (preoccupied, not Chapin ,1924). Type sp.: *Cholevomorpha extranea* Blackburn, 1903 (orig. des.).

Myrmicholeva Lea [T, Sc] Australia (4 spp.)
Myrmicholeva Lea, 1910: 190. Type sp.: *Myrmicholeva lata* Lea, 1910 (des. Hatch, 1928:208). Note: 8+ new spp. seen.

Neopelatops Jeannel [Tc, Sc] s Chile, sw Argentina, e Australia (2 spp.)
Neopelatops Jeannel, 1936: 12. Type sp.: *Neopelatops edwardsi* Jeannel, 1936 (monotypy). Note: 6+ new spp. seen from Australia (Newton, 1984; 1985).

Ragytodes Jeannel [Tc] s Chile, sw Argentina (1 sp.)
Ragytodes Jeannel, 1936: 14. Type sp.: *Ragytodes ocellifer* Jeannel, 1936 (monotypy).
Tricholoma Hlisnikovský, 1964b: 309 (NEW SYNONYMY; see Appendix A).
Type sp.: *Tricholoma kaszabi* Hlisnikovský, 1964 (=*R. ocellifer* Jeannel, 1936) (orig. des.).

Sphaeropelatops Jeannel [T, Sc] s Chile, s Brazil (1 sp.)
Sphaeropelatops Jeannel, 1962: 489. Type sp.: *Sphaeropelatops globosus* Jeannel, 1962 (orig. des.). Note: 2 new spp. seen (Chile, s Brazil).

Camiarini Jeannel, 1911

DIAGNOSIS:

In addition to the characters used in the key, Camiarini lack an epistomal suture; the molar lobe of the mandible is weak or membranous; the spiracles of abdominal segment 8 are functional or atrophied; and the aedeagus has long free parameres with or without basoventral lobes.

DISTRIBUTION: New Zealand, s Chile and Argentina, se Australia.

COMMENTS:

The sternal structures that Jeannel (1936, 1958) emphasized as family characters (i.e., very transverse mesepimeron, small and moderately separated hind coxae, oblique metasternal-pleural suture and broad metapleural-abdominal contact) are found only in *Inocatops* and *Neocamiarus*; the other

genera have a normal disposition of sternal sclerites. Nevertheless, the traditional character of enlarged 4th palpal segment plus the previously overlooked metepisternal-elytral clamp do support the association of these genera in a single tribe.

The named genera form two distinctive generic groups, called the *Inocatops* and *Camiarus* Groups by Newton (1985). *Inocatops* and *Neocamiarus*, in addition to sharing the derived sternal characters cited above, have functional spiracles on the 8th abdominal segment and a normal bisetose tarsal empodium, while the other genera (*Camiarus* Group) have the 8th abdominal spiracles atrophied and have a unisetose empodium. But *Neocamiarus*, from Chile, differs from the other genera (all from New Zealand or Australia) in having the procoxal cavities open behind. *Inocatops* differs from all other genera in having a pair of deep, setose cavities in the concealed portion of the scutellum, exactly as in the Australian genera *Eublackburniella* and *Myrmecholeva* of Neopelatopini. Finally, the 4 genera with atrophied 8th abdominal spiracles also have the procoxal cavities closed by a more or less broadened notal process as in Agyrtodini, which also have the atrophied spiracles. Three undescribed genera have also been seen that will require reassessment of this group, two from New Zealand placed in the *Camiarus* group by Newton (1985) and a recently discovered genus from southeastern Australia (personal observations). Clearly, more detailed study of the relationships of the genera of Camiarini to each other and to genera of the other camiarine tribes is needed.

Very little is known about the habits of Camiarini. The genera of "normal", ovoid habitus (*Neocamiarus*, *Inocatops*, *Baeosilpha*, *Zenocolon*) are not uncommon in forest litter. Species of *Camiarus* and *Camiarites* (and the undescribed genera), of long-legged "scydmaenid" habitus, are quite rare. All species except *Baeosilpha rufescens* are flightless.

Larvae: Jeannel (1957b, 1958). Examined: *Neocamiarus kuscheli* Jeannel; undet. genera and species (New Zealand).

Generic Catalog:

Baeosilpha Broun [Tc] — New Zealand (1 sp.)
Baeosilpha Broun, 1895: 84. Type sp.: *Baeosilpha rufescens Broun*, 1895 (monotypy).

Camiarites Jeannel [Tc, S] — New Zealand (2 spp.)
Camiarites Jeannel, 1957b: 58. Type sp.: *Camirus convexus* Sharp, 1876 (orig. des.). Note: 1 new sp. seen.
Camiarinus; Jeannel, 1962: 497 (misspelling of *Camiarites*).

Camiarus Sharp [Tc, S] — New Zealand (2 spp.)
Camiarus Sharp, 1878: 36 (new name for *Camirus* Sharp). Note: 1 new sp. seen.
Camirus Sharp, 1876a: 23 (preoccupied, not Stål 1860). Type sp.: *Camirus thoracicus* Sharp, 1876 (des. Hatch, 1928:210).

Inocatops Broun [T, Sc] New Zealand (9 spp.)
Inocatops Broun, 1893: 1066. Type sp.: *Camiarus concinnus* Broun, 1880 (des. Hatch, 1928:211).

Neocamiarus Jeannel [Tc] s Chile, sw Argentina (1 sp.)
Neocamiarus Jeannel, 1957b: 59. Type sp.: *Neocamiarus kuscheli* Jeannel, 1957 (orig. des.).

Zenocolon Broun [Tc] New Zealand (1 sp.)
Zenocolon Broun, 1917: 387. Type sp.: *Zenocolon laevicollis* Broun, 1917 (monotypy).

Agyrtodini Jeannel, 1936

Agyrtodini Jeannel, 1936: 99. Type genus: *Agyrtodes* Portevin, 1907.

DIAGNOSIS:

In addition to characters indicated in the key, Agyrtodini have: epistomal suture present or not, with or without "stem"; mandible with well developed molar lobe bearing grinding surfaces; spiracles of abdominal segment 8 atrophied; and aedeagus with long free parameres bearing basoventral lobes which usually meet ventrally.

DISTRIBUTION: Australia, New Zealand, South Africa, s Neotropical.

COMMENTS:

This tribe is used in the established sense (Jeannel, 1936; 1962; 1964; Szymczakowski, 1966; 1973; Zwick, 1979). It has been previously included in Cholevinae because of the blunt notal process closing the procoxal cavities, and the genera share a reduced or atrophied 8th abdominal spiracle with Cholevinae, but these characters occur elsewhere in Leiodidae (e.g. in some Camiarini and some Leiodini) and by themselves do not justify inclusion of the tribe in Cholevinae. Agyrtodini have no trace of the occipital carina or crest that characterizes nearly all Cholevinae in the present sense (the few exceptions involve highly modified cavernicolous Leptodirini that have probably lost this cholevine character secondarily). *Chelagyrtodes* and *Dictydiella* have an elytral-metepimeral clamp similar to that of Camiarini, but these and the other genera of Agyrtodini lack an enlarged 4th palpal segment.

Newton (1985) recognized two distinctive generic groups in this tribe, a clearly derived *Agyrtodes* Group with specialized mouthparts and the *Eupelates* Group with more generalized mouthparts. The six genera of the *Agyrtodes* Group *(Agyrtodes, Agyrtolasia, Cholevomorpha, Zeagyrtes, Zeagyrtoma* and *Zearagytodes*) have a large complex brush on the lacinia, which is likely correlated with feeding on fungi (confirmed only for the last-named genus). In addition to the remaining named genera, the *Eupelates*

Group includes an undescribed genus from Tasmania and at least one from southern Chile.

Adults and larvae of *Zearagytodes* species are found commonly on bracket fungi (Polyporaceae), and some of the other genera including *Agyrtodes* and *Paragyrtodes* are commonly associated with decaying logs. *Eupelates* and *Dasypelates* (=*Pelatonoma*) species are frequently found at carrion and other decaying organic matter. The habits of most genera and species are very poorly known. (Zwick, 1979; Newton, 1984)

Larvae: Newton (1991), Zwick (1979). Examined: *Agyrtodes atropos* (Blackburn); *Cholevomorpha picta* Blackburn; *Dictydiella turneri* Jeannel; *Eupelates transversestrigosus* (Fairmaire & Germain); *Paragyrtodes modestus* Szymczakowski; *Zearagytodes maculifer* (Broun); undet. genera and species (Australia, Chile).

Generic Catalog:

Afropelates Jeannel [Sc] — South Africa (3 spp.)
Afropelates Jeannel, 1964: 223. Type sp.: *Afropelates leleupi* Jeannel, 1964 (orig. des.).

Agyrtodes Portevin [Tc, Sc] — e Australia, s Chile, New Zealand (15 spp.)
Agyrtodes Portevin, 1907: 75. Type sp.: *Agyrtodes ovatus* Portevin, 1907 (monotypy). Note: see Appendix A; 2 new spp. seen (N.Z.), more in Australia?.
Ragytes Portevin, 1914a: 196. Type sp.: *Ragytes luteipes* Portevin, 1914 (=*A. monticola* (Broun, 1893)) (monotypy).

Agyrtolasia Szymczakowski [T, Sc] — e Australia (1 sp.)
Agyrtolasia Szymczakowski, 1973: 99. Type sp.: *Agyrtolasia calliptera* Szymczakowski, 1973 (orig. des.). Note: 1 new sp. seen.

Chelagyrtodes Szymczakowski [T, Sc] — New Zealand (1 sp.)
Chelagyrtodes Szymczakowski, 1973: 102. Type sp.: *Chelagyrtodes crowsoni* Szymczakowski, 1973 (orig. des.). Note: 13+ new spp. seen.

Chiliopelates Jeannel, *sensu novo* (see Appendix A) [T, Sc] — s Chile, Argentina (12 spp.)
Chiliopelates Jeannel, 1964: 222 (as subgenus of *Dasypelates*). Type sp.: *Dasypelates pictus* Jeannel, 1957 (orig. des.). Note: published May 1964; additional n. spp. seen.
Topaliola Hlisnikovský, 1964b: 311 (NEW SYNONYMY; see Appendix A).
Type sp.: *Topaliola crenulata* Hlisnikovský, 1964 (as *Topalia crenulata*) (orig. des.). Note: published "1964".
Topalia Hlisnikovský, 1964b: 312 (misspelling of *Topaliola*; not Balogh & Csiszár, 1963).

Cholevomorpha Blackburn [Tc] — se Australia (1 sp.)
Cholevomorpha Blackburn, 1891: 89. Type sp.: *Cholevomorpha picta* Blackburn, 1891 (monotypy). Note: 1 new sp. seen.

Dasypelates Portevin, *sensu novo* (see Appendix A) [Tc, Sc] — s Chile, sw Argentina (2 spp.)
Dasypelates Portevin, 1907: 74. Type sp.: *Dasypelates gracilis* Portevin, 1907 (monotypy). Note: 1 new sp. seen.
Pelatonoma Jeannel, 1957b: 50 (NEW SYNONYMY; see Appendix A). Type sp.: *Pelatonoma pubescens* Jeannel, 1957 (=*D. gracilis* Portevin, 1907) (orig. des.).

Dictydiella Jeannel [Tc] South Africa (2 spp.)
Dictydiella Jeannel, 1936: 121. Type sp.: *Dictydiella turneri* Jeannel, 1936 (orig. des.).

Eupelates Portevin [Tc] s Chile, sw Argentina (1 sp.)
Eupelates Portevin, 1907: 73. Type sp.: *Choleva transversestrigosa* Fairmaire & Germain, 1859 (monotypy). Note: revised by Salgado (1992b).

Paragyrtodes Szymczakowski [T, Sc] e Australia (3 spp.)
Paragyrtodes Szymczakowski, 1966: 598. Type sp.: *Paragyrtodes modestus* Szymczakowski, 1966 (orig. des.). Note: 1 new sp. seen.

Ragytodina Jeannel [Tc, Sc] s Chile, sw Argentina (2 spp.)
Ragytodina Jeannel, 1957b: 49. Type sp.: *Ragytodina tuberculosa* Jeannel, 1957 (orig. des.).
Topalella Hlisnikovský, 1964b: 314 (NEW SYNONYMY; see Appendix A). Type sp.: *Topalella rugosa* Hlisnikovský, 1964 (=*R. tuberculosa* Jeannel, 1957) (orig. des.).

Zeagyrtes Broun [Tc, S] New Zealand, ?Australia (2 spp.)
Zeagyrtes Broun, 1917: 386. Type sp.: *Zeagyrtes vitticollis* Broun, 1917 (monotypy). Note: dubious Australian record in Szymczakowski (1973:99).

Zeagyrtoma Szymczakowski [T, Sc] New Zealand (2 spp.)
Zeagyrtoma Szymczakowski, 1966: 588. Type sp.: *Mesocolon undulata* Broun, 1880 (orig. des.). Note: 5 new spp. seen.

Zearagytodes Jeannel [Tc, S] New Zealand (3 spp.)
Zearagytodes Jeannel, 1936: 108. Type sp.: *Mesocolon maculifer* Broun, 1880 (orig. des.). Note: *Z. concinnus* (Broun) transferred from genus *Scaphisoma* (Scaphidiidae or Staphylinidae: Scaphidiinae) by Newton in Klimaszewski et al. (1996); 4+ new spp. seen.

Catopocerinae Hatch, 1927 (1880)

Catopocerini Hatch, 1927: 4 (new name for Pinodytini [genus = junior synonym]; maintained, Art. 40b). Type genus: *Catopocerus* Motschulsky, 1869.
Pinodytini Horn, 1880: 248 (replaced, Art. 40b). Type genus: *Pinodytes* Horn, 1880 (=*Catopocerus* Motschulsky, 1869).

DIAGNOSIS:

In addition to the characters mentioned in the key, Catopocerinae have: eyes and wings absent; mandibles with contiguous grinding molar lobes; epistomal suture with or (*Glacicavicola*) without "stem"; cervical sclerites with rounded outer projection, or reduced; postcoxal process of pronotum triangular; procoxal cavities open behind; mesocoxal cavities separated by mesoplus metasternal processes; tarsi 5-5-5; and all abdominal spiracles functional.

DISTRIBUTION: Nearctic, e Palearctic, ?Chile.

COMMENTS:

Catopocerus and *Glacicavicola* were placed in a single subfamily by Newton (1985) and Peck (1990), in the latter case in separate tribes. This subfamily is not clearly defined on synapomorphies, but these two genera are fundamentally very similar in structure and seem to be more closely related to one another than to any other leiodids; the remarkable differences in body form are no greater than occur within some subtribes of Leptodirini. There is significant variation in adult and larval structure within the genus *Catopocerus*, even within the USA. For example, examined species from eastern USA have several teeth each on antennal segments 7, 9 and 10; male with meso- as well as protarsi dilated; aedeagal parameres glabrous; and larvae with an entire ligula and undivided maxillary lobe. Examined species from western USA have no antennal teeth; male with protarsi only dilated; aedeagal parameres bisetose; and larvae with a bilobed ligula and maxillary lobe divided in apical third into galea and lacinia. The undescribed genus from southern Chile tentatively attributed to Catopocerinae by Newton (1985) resembles the western *Catopocerus* in many ways, and an associatiated larva is nearly identical to the western USA *Catopocerus* larvae, but adults have 3-segmented tarsi, closed procoxal cavities and other significant differences from both North American catopocerine genera.

Catopocerus species are most commonly found in forest litter; a few species have been collected on subterranean fungi or in cave entrance zones (Peck, 1975; Newton, 1984). *Glacicavicola bathyscioides* is a highly modified troglobite from both lava tube and limestone caves in Idaho and Wyoming (Westcott, 1968; Peck, 1974; 1982a). Perkovsky (1989a), Lafer (1989).

Larvae: Newton (1991). Examined: *Catopocerus appalachianus* Peck; *C. ulkei* Brown; *C. ?rothi* Hatch; *C. ?pusio* (Horn); undet. genus, sp. (Chile).

KEY TO TRIBES OF CATOPOCERINAE

1. Epistomal suture with median stem; labrum entire; gular sutures widely separated; pronotum transverse, laterally margined, subequal in width to both elytra together; metasternum longitudinally carinate; abdominal sternites free; "pleurites" of male genital segment connected in front of tergite; body form normal, ovoid, flattened, appendages short . . . . . .Catopocerini

   Epistomal suture without stem; labrum apically emarginate; gular sutures more or less fused medially; pronotum elongate, not laterally margined, narrower than one elytral width; metasternum not carinate; abdominal sternites 3-4 connate; "pleurites" of male genital segment not connected in front of tergite; body form *Leptodirus*-like, convex, appendages very long and slender . . . . . .Glacicavicolini

GENERIC CATALOG:

Catopocerini Hatch, 1927 (1880)

Catopocerus Motschulsky [Tc, Sc] Nearctic, Russia (e Siberia) (15 spp.)

Catopocerus Motschulsky, 1870c: 351. Type sp.: *Catopocerus politus* Motschulsky, 1870 (=*C. cryptophagoides* (Mannerheim, 1852)) (monotypy). Note: type species from "North America", species synonymy needs confirmation; partial revision, Peck (1975), Perkovsky (1989a).

Homoeosoma Austin, 1880: 16 (attributed to Horn; preoccupied, not Curtis 1833). Type sp.: *Catops cryptophagoides* Mannerheim, 1852 (monotypy). Note: as *Homaeosoma* in Neave (1939-40).

Pinodytes Horn, 1880: 248. Type sp.: *Catops cryptophagoides* Mannerheim, 1852 (monotypy).

Typhloleiodes Hatch, 1935: 116. Type sp.: *Typhloleiodes subterraneus* Hatch, 1935 (orig. des.).

Glacicavicolini Westcott, 1968

Glacicavicolinae Westcott, 1968: 1. Type genus: *Glacicavicola* Westcott, 1968.

Glacicavicola Westcott [Tc] nw USA (Idaho, Wyoming) (1 sp.)

Glacicavicola Westcott, 1968: 3. Type sp.: *Glacicavicola bathyscioides* Westcott, 1968 (orig. des.). Note: reviewed by Peck (1974, 1982a).

Leiodinae Fleming, 1821 (=Anisotominae)

DIAGNOSIS:

In addition to the apparently glabrous dorsum and broad flattened head, Leiodinae share the following: epistomal suture (if present) never with "stem"; cervical sclerites with broadly rounded outer projection; postcoxal process of pronotum triangular (except blunt in *Cyrtusa* Group of Leiodini); procoxal cavities open or closed behind; mesocoxal cavities separated, often widely, by meso- and/or metasternal process; tarsi 5-5-5 or with reduced segmentation; and abdominal spiracles 1-8 all functional (except those on segment 8 in the *Cyrtusa* Group).

COMMENTS:

Leiodinae have generally been divided into only two tribes, Leiodini and Agathidiini (as Anisotomini), on the basis of presence of antennal grooves on the ventral surface of the head, carinae on the tibiae and/or sexual dimorphism in tarsal segmentation in the latter tribe. These characters are not congruent and have led to confusion in the placement of several genera. Brown

(1937) has argued persuasively that antennal grooves have probably appeared independently in 2 or more groups of Leiodinae, and suggested restricting the tribe Agathidiini to those genera with a sexually dimorphic tarsal formula. This appears to result in a natural grouping for that tribe but leaves in Leiodini a diverse assemblage of generic groups that are no more closely related to one another than to Agathidiini. Various family-group names have been erected for scattered genera of Leiodini through the years, in most cases without adequate characterizations and on a restricted geographic basis. By using some new characters as well as older ones, it is possible to divide Leiodini into six tribes that make use of these existing names, resulting in what I believe to be a more natural arrangement of Leiodinae than any proposed earlier. This arrangement has already come into some use in phylogenetic discussions and classification (e.g., Newton, 1984; Wheeler, 1984a, 1984b).

Key to tribes of Leiodinae

1. Labrum deeply emarginate apically; mandibles with molar lobes usually reduced, smooth, not contiguous; lacinia with dense brush of setae along entire mesal edge, galeal brush relatively much smaller; tarsal formula 5-5-5, 5-5-4, or (rarely) 4-4-4, not sexually dimorphic 2
Labrum shallowly or not at all emarginate apically; mandibles with well-developed, contiguous molar lobes bearing grinding surfaces; lacinia with setal brush concentrated along apical half of mesal edge, galeal brush subequal or larger in size; tarsal formula 5-4-4 or more reduced, or sexually dimorphic (5-5-4 or 5-5-3 in male, more reduced in female) 4

2(1). Tarsal formula 5-5-4 or (*Cyrtusoma*) 4-4-4; transverse, lightly sclerotized structure bearing minute teeth present immediately behind tergum 7 . . . . . .Leiodini
Tarsal formula 5-5-5; above structure absent (except *Stereus*?) 3

3(2). Mesocoxae very narrowly separated; first tarsal segment as long as or longer than second segment . . . . . .Sogdini
Mesocoxae separated by about their length; first tarsal segment much shorter than second segment . . . . . .Estadiini

4(1). All tarsi 3-segmented; abdominal sternum 3 (first visible) with transverse carina . . . .Scotocryptini
At least protarsi of 4 or 5 segments; abdominal sternum 3 without transverse carina 5

5(4). Head without antennal grooves below; tarsal formula usually 5-4-4, rarely 4-4-4 or 4-3-3, not sexually dimorphic (except *Cainosternum*: 5-5-4 male, 5-4-4 female, and *Perkovskius*: 5-5-3 male, 4-4-3 female); elytron usually transversely striolate; aedeagus with free parameres . . . . . .Pseudoliodini
Head with antennal grooves below; tarsi usually sexually dimorphic, 5-5-4 in male, 5-4-4 or 4-4-4 in female, rarely 4-4-4 in both sexes; elytron not transversely striolate; aedeagus with parameres more or less fused at base to median lobe . . . . . .Agathidiini

Sogdini Lopatin, 1961 (=Hydnobiini, Triarthrini)

Sogdiidae Lopatin, 1961:121 (incorrect original spelling). Type genus: *Sogda* Lopatin, 1961 (= senior synonym of *Trichohydnobius* Vogt, 1961).

Hydnobiini Jeannel, 1962:492. Type genus: *Hydnobius* Schmidt, 1841.

Triarthrini Jeannel, 1962:486 (junior homonym of Triarthridae Ulrich, 1930 [Trilobita: Olenidae: *Triarthrus* Green]; needs application to ICZN). Type genus: *Triarthron* Märkel, 1840 (not cited).

Triarthriina; Perkovsky, 1991:20 (incorrect subsequent spelling). Type genus: *Triarthron* Märkel, 1840.

DIAGNOSIS:

In addition to characters given in the key, Sogdini have procoxal cavities either open or closed behind; mesocoxae separated primarily by either meso- or metasternal process; and aedeagus with free parameres bearing basoventral lobes which may meet ventrally.

DISTRIBUTION: Holarctic and southern temperate (s Afrotropical, Australia, New Zealand, s Neotropical).

COMMENTS:

This tribe, as Hydnobiini, was first separated from Leiodini by the presence of an unreduced tarsal formula and supposed genitalic differences (Jeannel, 1962). The unique sclerotization posterior to tergum 7 of Leiodini (see under that tribe) is apparently absent here. Jeannel (1962) also created a separate tribe for *Triarthron* because of its 3-segmented antennal club, but Daffner (1983) rejected this separation; Perkovsky (1991) agreed but still recognized a subtribe "Triarthriina" for *Triarthron* and *Stereus*. The segregation of these genera from *Hydnobius* and other genera based only on this antennal character seems unwarranted in the absence of other differential characters and in view of the frequency of occurence of this and other changes in club formation within other tribes and smaller generic groups of Leiodinae. Although Daffner (1983) stated that the genus *Deltocnemis* had only 4-segmented tarsi, Perkovsky (1991) corrected this to 5-segmented and synonymized this genus with *Stereus*. The tribe must be known by the older name Sogdini Lopatin (1961), based on the name for a new family and genus that was subsequently recognized as belonging to this tribe (Perkovsky, 1988).

Sogdines are a classic "amphitropical" group, well represented in both north and south temperate zones but virtually absent from the tropics proper. Newton (1985) briefly characterized a distinctive suite of four undescribed genera ('BCDE' Group) from south temperate areas, and noted a fifth undescribed genus from southeastern Australia and Tasmania (since then also found in New Zealand).

The little available information on habits of Sogdini indicates that some species, perhaps all, breed in subterranean fungi (Newton, 1984). Similar habits are known or suspected for members of the closely related tribes Estadiini and Leiodini, which with Sogdini form a probably monophyletic unit of Leiodinae. In addition to sharing several derived features of the mouthparts, members of the 3 tribes have several well- developed vesicles in antennal segments 9-10 (sometimes in 7 also) and the few known larvae have in common a dorsally-curved hypogean body form; at least some of these characters may be associated with feeding on subterranean fungi. Sogdini lack the more specialized features of the other 2 tribes and have no known uniquely derived ones. Thus, Sogdini may well be paraphyletic with respect to Leiodini and/or Estadiini.

Larvae: Newton (1991). Examined: *Hydnobius crestonensis* Hatch; *?Isocolon* sp. (New Zealand); undet. genera and spp. (Australia, Chile, New Zealand).

Generic Catalog:

Euliodes Portevin [T] South Africa (Basutoland) (1 sp.)
Euliodes Portevin, 1937: 31. Type sp.: *Euliodes subglobosa* Portevin, 1937 (monotypy).

Hydnobius Schmidt [Sc] Holarctic, n India, n China (29 spp.)
Hydnobius Schmidt, 1841: 193. Type sp.: *Anisotoma punctatum* Sturm, 1807 (des. Thomson 1859:58). Note: The Palearctic spp. were revised by Daffner (1983). The species *Hydnobius tropicus* Motschulsky, 1866, from Sri Lanka, is not a leiodid and belongs in Hydrophilidae: Sphaeridiinae based on study of the type by Perkovsky (1992).

Hydnodiaetus Jeannel [Tc, Sc] s Chile, sw Argentina (2 spp.)
Hydnodiaetus Jeannel, 1962: 495. Type sp.: *Hydnodiaetus brunneus* Jeannel, 1962 (orig. des.). Note: see Appendix A; 1 new sp. seen.
Kaszabella Hlisnikovský, 1964c: 321 (NEW SYNONYMY; see Appendix A). Type sp.: *Kaszabella striata* Hlisnikovský, 1964 (=*H. brunneus* Jeannel, 1962) (orig. des.).

Isocolon Broun [T, Sc] New Zealand (5 spp.)
Isocolon Broun, 1893: 1070. Type sp.: *Isocolon hilaris* Broun, 1893 (monotypy).
Allocatops Broun, 1893: 1435 (NEW SYNONYMY; see Appendix A). Type sp.: *Allocatops ovalis* Broun, 1893 (monotypy).

Metahydnobius Portevin [Tc, Sc] s Chile, sw Argentina (5 spp.)
Metahydnobius Portevin, 1942: 78. Type sp.: *Hydnobius forticornis* Champion, 1918 (monotypy). Note: genus and type species overlooked by Jeannel (1962); 2 new spp. seen from Bolivia and Peru; see Appendix A.
Hydnobiotus Jeannel, 1962: 492 (NEW SYNONYMY; see Appendix A). Type sp.: *Hydnobiotus bimaculatus* Jeannel, 1962 (orig. des.).

Sogda Lopatin [S] Palearctic (4 spp.)
Sogda Lopatin, 1961: 121. Type sp.: *Sogda pavlovskii* Lopatin, 1961 (orig. des.).
Trichohydnobius Vogt, 1961: 154 (as subgenus of *Hydnobius*). Type sp.: *Hydnobius perrisii* Fairmaire, 1855 (=*S. suturalis* (Zetterstedt, 1828)) (orig. des.). Note: as genus, Daffner (1983); syn. Perkovsky (1988).

Stereus Wollaston [Tc] Palearctic, China (4 spp.)
Stereus Wollaston, 1857: 148 (preoccupied?, not Mannerheim 1846 [unjustified emendation of *Sthereus* Motschulsky]). Type sp.: *Stereus cercyonides* Wollaston, 1857 (monotypy). Note: revised by Daffner (1983), Perkovsky (1991).
Deltocnemis Sahlberg [S] Russia (Siberia), Mongolia, Turkestan, China (1 sp.)
Deltocnemis Sahlberg, 1886: 87. Type sp.: *Deltocnemis hamatus* Sahlberg, 1886 (monotypy). Note: as genus, Daffner (1983); as subgenus of *Stereus*, Perkovsky (1991).
Stereus s. str. [Tc] Madeira, Canary Islands, Tunisia (3 spp.)
Pseudotriarthron Normand, 1938: 346. Type sp.: *Pseudotriarthron numidicum* Normand, 1938 (monotypy). Note: syn. Daffner (1983).

Triarthron Märkel [Sc] Europe, Japan, Nearctic (3 spp.)
Triarthron Märkel, 1840: 141. Type sp.: *Triarthron maerkelii* Märkel, 1840 (monotypy).
Triarthrum Agassiz, 1847: 375 (unjustified emendation of *Triarthron*).

Estadiini Portevin, 1914

Estadiini Portevin, 1914b: 199. Type genus: *Estadia* Fairmaire, 1903 (=*Dietta* Sharp, 1876).
Eustadiini; Hatch, 1928: 77 (based on misspelled type genus). Type genus: *Estadia* Fairmaire, 1903 (as *Eustadia*).

DIAGNOSIS:

As in Sogdini, except for the very widely separated mesocoxae and unusually short 1st tarsal segment noted in the key. Periarticular gutters of antennal segments 7 and 9-10 are widely open, and procoxal cavities are open or narrowly closed behind by a triangular notal process.

DISTRIBUTION: Afrotropical including Madagascar, Australia, Neotropical (Mexico to Peru).

COMMENTS:

Decelle (1988) reviewed the controversial placement of the genera *Estadia* and *Dietta* as Leiodidae or Silphidae, and synonymized them. *Dietta* may represent a highly specialized offshoot of Sogdini, and perhaps should be placed in that tribe. The wide but very disjunct distribution of this distinctive genus is remarkable.

The biology is unknown, but some specimens of the Australian *D. sperata* have been collected in burrows of Geotrupidae (H. F. Howden, personal communication).

Larvae unknown.

GENERIC CATALOG:

Dietta Sharp [Tc, Sc] e+s Africa, Madagascar, Australia, Mexico to Peru (12 spp.)
Dietta Sharp, 1876b: 78. Type sp.: *Dietta sperata* Sharp, 1876 (monotypy). Note: undet. specimens seen from Mexico, Honduras, Costa Rica, Ecuador and Peru (FMNH, SEMC, SBPC).
Estadia Fairmaire, 1903: 183 (not Sellards 1909). Type sp.: *Estadia capito* Fairmaire, 1903 (monotypy). Note: syn. Decelle (1988).
Eustadia; Hatch, 1928: 77 (misspelling of *Estadia*).

Leiodini Fleming, 1821

Anisotomidae Erichson, 1845: 41 (based on misidentified type genus). Type genus: *Anisotoma* of Schmidt, 1841 (not Panzer, 1797; =*Leiodes* Latreille, 1796).

DIAGNOSIS:

In addition to the unique sclerotized area behind tergum 7 and other characters mentioned in the key, Leiodini have procoxal cavities closed by either a triangular or blunt notal process; mesocoxae separated primarily by either meso- or metasternal process; and aedeagus with free parameres with or without basoventral lobes which, if present, may meet ventrally.

DISTRIBUTION: Worldwide.

COMMENTS:

As here defined, the tribe excludes *Colenis* and allies and *Hydnobius* and allies, both usually with other tarsal formulae and lacking the post-7th-tergal structure. *Colenis* and allies as well as all other members of the following tribes lack the specialized mouthparts (see tribal key above) shared by Leiodini, Estadiini and Sogdini. The tribe is most closely related to, and possibly derivable from, Sogdini.

The genera may be divided into two groups. *Leiodes, Ecarinosphaerula, Hypoliodes* and perhaps the unexamined *Chobautiella* form the "*Leiodes* Group", characterized by having an oblique mesosternum narrowly dividing the mesocoxae and functional spiracles on abdominal segments 1-8. The remaining genera of the tribe form the more derivative "*Cyrtusa* Group", first recognized as a unit and characterized by Brown (1937). In this group the mesosternum is almost vertical before the mesocoxae which are rather widely separated by a metasternal process, the epistomal suture is absent, the spiracles of abdominal segment 8 are atrophied, and the postcoxal process of the pronotum is blunt rather than acute. Some of these genera (as well as

Hypoliodes) have antennal grooves and thus have been referred to Agathidiini by some authors. Several of them have the 8th antennal segment greatly reduced or completely absent, producing 10-segmented antennae otherwise unknown in Leiodidae. An undescribed genus of the *Leiodes* Group occurs in southern Chile.

Some species of the genus *Leiodes* are well-known inhabitants of truffles and other hypogean fungi (Arzone, 1970; 1971; Baranowski, 1993; Lyszkowski, 1995; Newton, 1984). Very little is known about the other genera, but they are assumed to have similar habits (see under Sogdini).

Larvae: Arzone (1970, 1971), Klausnitzer (1978). Diagnosis: Body reverse C-shaped; stemmata 3 minute in close vertical group, 1 minute, or absent; stridulatory ridges on abd. T8 (at least), asperate area on head. Examined: *Leiodes* spp. (Alaska, Mexico, South Africa, Sweden); *Zeadolopus* spp. (New Caledonia, New Zealand).

GENERIC CATALOG:

Afrocyrtusa Daffner — Rwanda, Burundi, e Zaire (1 sp.)
Afrocyrtusa Daffner, 1990b: 62. Type sp.: *Afrocyrtusa hansmuehlei* Daffner, 1990 (orig. des.).

Anogdus LeConte [Sc] — Nearctic, ?South Africa (11 spp.)
Anogdus LeConte, 1866: 369. Type sp.: *Anogdus capitatus* LeConte, 1866 (monotypy). Note: generic placement of South African sp. *A. trimeni* Champion, 1925 is doubtful.
Neocyrtusa Brown, 1937: 161. Type sp.: *Pallodes obsoletus* Melsheimer, 1844 (orig. des.). Note: syn. Daffner (1989b).

Chobautiella Reitter — Algeria, Morocco, Canary Islands (1 sp.)
Chobautiella Reitter, 1900: 229. Type sp.: *Trachyscelis anisotomoides* Fairmaire, 1876 (monotypy). Note: revised by Daffner (1983).

Cyrtusa Erichson [Sc] — Holarctic, s India, ?Afrotropical, ?Neotropical (14 spp.)
Cyrtusa Erichson, 1842: 221. Type sp.: *Anisotoma subtestaceum* Gyllenhal, 1813 (des. Thomson 1859:58). Note: partially revised, restricted by Daffner (1982, 1983, 1989b); generic placement of 6 African and Neotropical species doubtful.
Caenocyrta Brown, 1937: 172. Type sp.: *Amphicyllis picipennis* LeConte, 1863 (=*C. subtestacea* (Gyllenhal, 1813)) (orig. des.). Note: syn. Daffner (1989b).

Cyrtusamorpha Daffner — Russia, Mongolia, ?Turkestan (5 spp.)
Cyrtusamorpha Daffner, 1983: 129 (see Appendix B). Type sp.: *Chobautiella sumakovi* Sahlberg, 1913 (orig. des.). Note: Perkovsky (1990b) syn. type species with *Leiodes ciliaris*, but continued using *Cyrtusamorpha* in sense of Daffner (1983).

Cyrtusoma Daffner — s India, Sri Lanka (3 spp.)
Cyrtusoma Daffner, 1982: 203. Type sp.: *Cyrtusoma foveola* Daffner, 1982 (orig. des.).
Cyrtusoma s. str. — s India, Sri Lanka (2 spp.)
Paracyrtusoma Daffner — s India (1 sp.)
Paracyrtusoma Daffner, 1982: 206. Type sp.: *Cyrtusoma bullata* Daffner, 1982 (as *Paracyrtusoma bullata*) (orig. des.).

Ecarinosphaerula Hatch [T] sw USA (Nevada) (1 sp.)
Ecarinosphaerula Hatch, 1929a: 2 (as subgenus of *Leiodes*). Type sp.: *Anisotoma ecarinata* Horn, 1880 (orig. des.).

Hypoliodes Portevin [Tc] Afrotropical (Ethiopia to Zimbabwe) (7 spp.)
Hypoliodes Portevin, 1908: 27. Type sp.: *Hypoliodes rothschildi* Portevin, 1908 (monotypy). Note: revised by Daffner (1987a).

Incacyrtusa Daffner [Tc] Peru (1 sp.)
Incacyrtusa Daffner, 1990a: 32. Type sp.: *Incacyrtusa eucera* Daffner, 1990 (orig. des.).

Isoplastinus Portevin Tanzania (Zanzibar) (1 sp.)
Isoplastinus Portevin, 1907: 75. Type sp.: *Isoplastinus alluaudi* Portevin, 1907 (monotypy).

Isoplastus Horn [Tc] e Nearctic, Mexico (1 sp.)
Isoplastus Horn, 1880: 295 (not Skuse 1889). Type sp.: *Isoplastus fossor* Horn, 1880 (monotypy). Note: revised by Daffner (1989b), 2 spp. synonymized (needs checking).

Leiodes Latreille [Sc] Holarctic, n Oriental, n Neotropical (to Panama), s Africa (177 spp.)
Leiodes Latreille, 1796: 22 (no species listed). Type sp.: *Sphaeridium ferrugineum* Fabricius, 1787 (subsequent monotypy by Latreille 1802:163). Note: revised by Daffner (1983), Baranowski (1993); latter did not use subgenera.
Anisotoma of Schmidt, 1841: 143 (misidentification of *Anisotoma* Panzer).
Liodes Erichson, 1845: 87 (unjustified emendation of *Leiodes* Latreille; used in misidentified sense of Schmidt 1841 (=*Anisotoma*)). Note: used in correctly identified sense by Reitter (1884:96).
Oosphaerula Ganglbauer, 1896: 181. Type sp.: *Anisotoma badium* Sturm, 1807 (des. Hatch 1929b:39; *Liodes carpathica* Gang. des. Daffner 1983:108). Note: syn. Baranowski (1993).
Oreosphaerula Ganglbauer, 1899: 228. Type sp.: *Anisotoma nitidula* Erichson, 1845 (des. Hatch 1929b:37).
Pseudohydnobius Ganglbauer, 1899: 208. Type sp.: *Anisotoma punctulatum* Gyllenhal, 1810 (monotypy).
Trichosphaerula Fleischer, 1904: 261. Type sp.: *Anisotoma scita* Erichson, 1845 (=*L. ferruginea* (Fabricius, 1787)) (monotypy). Note: Daffner (1983:105), corrected misidentification of Reitter etc.
Pteromerula Fleischer, 1905: 314. Type sp.: *Anisotoma pallens* Sturm, 1807 (des. Hatch 1929b:15).
Parahydnobius; Fleischer, 1908: 29 (lapsus for *Pseudohydnobius*).
Strigoliodes Fleischer, 1908: 32 (unavailable, not formally proposed). Type sp.: *Leiodes rugosa* Stephens, 1829 (monotypy). Note: suggested for *L. rugosa* and possibly other spp., but withheld.
Eremosphaerula Hlisnikovský, 1967: 260. Type sp.: *Liodes terricola* Hlisnikovský, 1967 (=*L. sparreschneideri* (Strand, 1943)) (orig. des.).

Liocyrtusa Daffner [Tc, Sc] Holarctic, India, Thailand, China (11 spp.)
Liocyrtusa Daffner, 1982: 209. Type sp.: *Anisotoma minutum* Ahrens, 1812 (orig. des.). Note: revised by Daffner (1983, 1989b).

Lionothus Brown [T, Sc] Nearctic, n Neotropical (Mexico, Colombia) (3 spp.)
Lionothus Brown, 1937: 170. Type sp.: *Lionothus ulkei* Brown, 1937 (orig. des.). Note: revised by Daffner (1989b).
Pseudocyrtusa Portevin, 1942: 78. Type sp.: *Pseudocyrtusa australis* Portevin, 1942 (monotypy). Note: syn. Newton (1983b).

Ovocyrtusa Daffner [Tc, Sc] s Chile (5 spp.)
Ovocyrtusa Daffner, 1985: 10. Type sp.: *Ovocyrtusa atricornis* Daffner, 1985 (orig. des.).

Xanthosphaera Fairmaire [Tc] Austria, Hungary, w Russia (1 sp.)
Xanthosphaera Fairmaire, 1859: 29. Type sp.: *Xanthosphaera barnevillii* Fairmaire, 1859 (monotypy). Note: revised by Daffner (1983); recorded from Russia (Ulyanovsk) by Perkovsky & Isayev in 1992.

Zeadolopus Broun [T, Sc] worldwide (except Afrotropical) (42 spp.)
Zeadolopus Broun, 1903: 614. Type sp.: *Zeadolopus spinipes* Broun, 1903 (monotypy).
Apheloplastus Brown, 1937: 173. Type sp.: *Cyrtusa egena* LeConte, 1853 (orig. des.). Note: syn. Newton (1983b).

Pseudoliodini Portevin, 1926, *sensu novo*

Pseudoliodini Portevin, 1926: 75. Type genus: *Pseudoliodes* Portevin, 1926.
Dermatohomoeini Hlisnikovský, 1963: 311. Type genus: *Dermatohomoeus* Hlisnikovský, 1963.

DIAGNOSIS:

In addition to characters given in the key, Pseudoliodini have the procoxal cavities closed by a triangular notal process, mesocoxae usually rather widely separated by a metasternal process, male tenent setae usually on protarsus only, and free parameres of the aedeagus with basodorsal lobes which may meet dorsally. Tarsi are 5-4-4 segmented in both sexes of most genera, but 4-3-3 in *Agaricophagus*, 4-4-4 in an undescribed New Zealand genus, and sexually dimorphic in *Cainosternum* (5-5-4 male, 5-4-4 female) and *Perkovskius* (5-5-3 male, 4-4-3 female).

DISTRIBUTION: Worldwide.

COMMENTS:

This tribe does not correspond to any previously defined group. *Colenis* has usually been placed in Leiodini. Pseudoliodini, including the genera *Pseudoliodes*, *Pseudocolenis*, *Liodinella* and *Delios*, was separated from Leiodini by the absence of external protibial teeth and by a more slender antennal club (Portevin, 1926). A virtual continuum exists in these characters between *Colenis*, retained in Leiodini by Portevin, and his Pseudoliodini. When Hlisnikovský, (1963) erected Dermatohomoeini for the two new genera *Dermatohomoeus* and *Bironellia*, he failed to provide any differential characters for the tribe, nor can I find any characters to justify tribal separation from *Colenis* and allies. The generic classification has been extensively revised by H. Daffner in a series of publications (noted under individual genera in the generic catalog below). Although Pseudoliodini have not been repor-

ted from New Zealand, *Colenisia* and an apparently undescribed genus with all tarsi 4-segmented have been found there.

The two most anomalous genera included here, both with sexually dimorphic tarsal formulae, are *Cainosternum* and *Perkovskius*. *Cainosternum* was placed in Agathidiini by Wheeler (1986) because it has the same sexually dimorphic tarsal formula as most members of that tribe. However, in all of the many other respects in which Pseudoliodini and Agathidiini differ (with the latter group more derived), *Cainosternum* agrees with Pseudoliodini, and I place it here. Either the sexually dimorphic tarsi have arisen independently in *Cainosternum* and Agathidiini (as has happened in other leiodids), or *Cainosternum* is a very basal member of Agathidiini lacking most of the derived features of that tribe. *Perkovskius*, placed with doubt in Cholevinae: Leptodirini by Lafer (1989) who also suggested it might belong in Catopocerinae, is even more problematic. I can find no basis for relating this genus to any Cholevinae, and the antennal insertion and other characters clearly relate it to Catopocerinae or Leiodinae. It most closely resembles a large *Catopocerus* in appearance, and two characters (prosternum as long as the procoxal width, and slightly separated metacoxae) support a possible relationship to catopocerines. However, the reduced and sexually dimorphic tarsi (5-5-3, not 5-5-4 in the male paratype examined by me); procoxal cavities narrowly closed by a triangular notal process; quadrangular shape of the epistomal suture; aedeagus with basodorsal lobes; and other structures indicate placement in Leiodinae and particularly the primitive tribe Pseudoliodini. Further study of both these rare genera is needed, and eventually one or both may be placed elsewhere, but for the present I place both tentatively in Pseudoliodini.

Some pseudoliodine species are found frequently on epigean fungi, especially Polyporaceae and Agaricales, while a few inhabit decaying or fermenting organic matter. Many are of unknown feeding habits but are collected commonly in forest leaf litter. Newton (1984), Wheeler (1984a, 1984b, 1986), Peck (1998b).

Larvae: Newton (1991). Examined: *Colenis impunctata* LeConte; *C.* spp. (Mexico, Panama, USA); *Colenisia* spp. (Australia: N.S.W., Tas.); *Dermatohomoeus* sp. (Australia: N.S.W.); *Neohydnobius* sp. (Chile); *?Pseudcolenis* sp. (Japan); undet. genera and spp. (Gabon, Japan, New Caledonia).

GENERIC CATALOG:

Agaricophagus Schmidt [Tc] — Europe to Caucasus (5 spp.)

Agaricophagus Schmidt, 1841: 191. Type sp.: *Agaricophagus cephalotes* Schmidt, 1841 (monotypy). Note: revised by Daffner (1983); tarsi unique (m,f 433).

Allocolenisia Daffner — India, Thailand (2 spp.)

Allocolenisia Daffner, 1990c: 1004. Type sp.: *Allocolenisia multistriata* Daffner, 1990 (orig. des.).

Ansibaris Reitter [Tc] Caucasus, Turkey (5 spp.)
Ansibaris Reitter, 1883: 111. Type sp.: *Ansibaris alexiiformis* Reitter, 1883 (monotypy). Note: revised by Daffner (1989a).

Cainosternum Notman [Tc] e USA (1 sp.)
Cainosternum Notman, 1921: 148. Type sp.: *Cainosternum imbricatum* Notman, 1921 (monotypy). Note: revised by Wheeler (1986), placed in Agathidiini; tarsi dimorphic (m 554, f 544).

Colenis Erichson [Tc, Sc] Holarctic, n Neotropical (to Panama), ?n India (9 spp.)
Colenis Erichson, 1842: 221. Type sp.: *Anisotoma dentipes* Gyllenhal, 1810 (=*C. immunda* (Sturm, 1807)) (des. Thomson, 1859:58). Note: current spp., distribution uncertain; partial revision, Peck (1998b).
Mathewsionia Hlisnikovský, 1965: 397 (NEW SYNONYMY; see Appendix A). Type sp.: *Colenis punctulata* Matthews, 1887 (orig. des.). Note: genus apparently based on misinterpretation of generic characterization of Matthews (1887-88) for the two included species.
Carcharodes Hlisnikovský, 1965: 400 (see Appendices A, B; preoccupied, not Strand 1912; also spelled *Carcharodus*). Type sp.: *Colenis macrocephaloides* Hlisnikovský, 1965 (=*C. bonnairii* Jacquelin du Val, 1859) (monotypy). Note: both spellings preoccupied.
Carcharodus; Hlisnikovský, 1965: 399,409 (misspelling of *Carcharodes*; not Huebner 1819).

Colenisia Fauvel [Tc, Sc]Afrotrop., Japan, Oriental, New Guinea, New Caled., Australia, N. Z. (44 spp.)
Colenisia Fauvel, 1903: 287. Type sp.: *Colenisia caledonica* Fauvel, 1903 (monotypy). Note: revised by Daffner (1991 and included references).
Liocolenis Portevin, 1905b: 422. Type sp.: *Liocolenis pygmaea* Portevin, 1905 (monotypy). Note: syn. Daffner (1988c).
Colensia; Hatch, 1929a: 3 (misspelling of *Colenisia*). Note: also used by Hatch (1929b).
Bironellia Hlisnikovský, 1963: 306. Type sp.: *Bironellia guineensiana* Hlisnikovský, 1963 (orig. des.). Note: syn. Daffner (1986).
Freyonymus Hlisnikovský, 1968: 144. Type sp.: *Freyonymus reticulatus* Hlisnikovský, 1968 (orig. des.). Note: syn. Daffner (1987b).
Besuchetus Hlisnikovský, 1972: 140. Type sp.: *Besuchetus ceylanicus* Hlisnikovský, 1972 (orig. des.). Note: syn. Daffner (1991).

Dermatohomoeus Hlisnikovský [Sc] c Africa, Oriental, New Guinea to Solomon I., Australia (27 spp.)
Dermatohomoeus Hlisnikovský, 1963: 301. Type sp.: *Dermatohomoeus guineensis* Hlisnikovský, 1963 (orig. des.). Note: partially revised by Daffner (1988b); n. spp. seen from Madagascar.
Acanthodiaprepus Hlisnikovský, 1972: 135. Type sp.: *Acanthodiaprepus silvaticus* Hlisnikovský, 1972 (orig. des.). Note: syn. Daffner (1988b).

Neohydnobius Jeannel [Tc, Sc] s Chile, sw Argentina (2 spp.)
Neohydnobius Jeannel, 1962: 496 (see Appendix A). Type sp.: *Neohydnobius brevis* Jeannel, 1962 (orig. des.). Note: originally placed in Hydnobiini; 2+ new spp. seen.
Microhydnobius; Jeannel, 1962: 492 (lapsus for *Neohydnobius*).
Loxorhabdus Hlisnikovský, 1964c: 323 (NEW SYNONYMY; see Appendix A; also spelled *Loxorhadbus*). Type sp.: *Loxorhabdus argentinicus* Hlisnikovský, 1964 (orig. des.).

Perkovskius Lafer [Tc] Russia (e Siberia) (1 sp.)
Perkovskius Lafer, 1989: 318. Type sp.: *Perkovskius ussuriensis* Lafer, 1989 (orig. des.). Note: placement tentative; Lafer (1989) as Leptodirini or possibly Catopocerinae; tarsi dimorphic (m 553, f 443); spelled *Petrovskius* in Zoological Record.

Pseudcolenis Reitter [Tc, Sc] Oriental, Japan, New Guinea (21 spp.)

Pseudcolenis Reitter, 1884: 92 (see Appendix B). Type sp.: *Pseudcolenis hilleri* Reitter, 1884 (monotypy). Note: revised by Daffner (1988a).

Pseudocolenis Fauvel, 1885: 315 (unjustified emendation of *Pseudcolenis* (cited as correction). Note: Reitter (1885:334) also used *Pseudocolenis*, without comment.

Pseudcolenis s. str. [Tc, Sc] Oriental, Japan (20 spp.)

Delios Portevin, 1903b: 335. Type sp.: *Delios bouvieri* Portevin, 1903 (monotypy). Note: syn. Daffner (1988a).

Liodinella Portevin, 1905b: 422. Type sp.: *Liodinella strigosa* Portevin, 1905 (monotypy). Note: syn. Daffner (1988a).

Pseudoliodes Portevin, 1926: 78. Type sp.: *Pseudocolenis grandis* Portevin, 1905 (orig. des.). Note: syn. Daffner (1988a).

Pseudcolenisia Daffner New Guinea (1 sp.)

Pseudcolenisia Daffner, 1988a: 155. Type sp.: *Pseudcolenis sedlaceki* Daffner, 1988 (orig. des.). Note: for 1 sp. only, rest in s.str.?.

Scotocryptini Reitter, 1884, *sensu novo*

Scotocryptini Reitter, 1884: 91. Type genus: *Scotocryptus* Girard, 1874.

DIAGNOSIS:

In addition to characters in the key, Scotocryptini have antennal grooves on the ventral surface of the head; procoxal cavities closed by a triangular notal process; mesocoxae separated by a metasternal process; mesosternum with a nearly vertical keel before the coxae; femora with grooves for reception of the tibiae; and parameres of the aedeagus short, fused to the median lobe and without basal lobes.

DISTRIBUTION: Worldwide except New Zealand, southern South America.

COMMENTS:

Until recently, this tribe included only four Neotropical genera (*Parabystus, Scotocryptodes, Scotocryptus* and *Synaristus*) with wings and eyes greatly reduced or absent. Matthews (1887) pointed out that the unique transversely carinate abdominal sternum 3 is also found in *Aglyptinus* and *Creagrophorus*, genera which have been placed in Agathidiini by most authors. Wheeler (1979b) further characterized these genera and their close relationship to Scotocryptini, calling the combined group the "*Aglyptinus* Association". The African genera *Cyrtusiola* and *Popeus* also share numerous derived characters with the above New World genera, as indicated in the tribal key and diagnosis. In the context of the present tribal reorganization of Leiodinae, the *Aglyptinus* Association is best treated as a separate tribe, to which the name Scotocryptini is applicable. In addition to described species

known from the New World, Africa, England, southeast Asia and New Guinea, I have seen many undescribed species from Madagascar, southeast Asia (including a distinctive new genus), Sulawesi, and Australia, suggesting that the tribe is virtually worldwide in distribution. According to the detailed original description, the genus *Termitoglobus* Reichensperger (1915), originally placed in Endomychidae, does not belong there (J. Pakaluk, personal communication), and is clearly a scotocryptine.

Scotocryptus and the 3 other flightless genera originally included in Scotocryptini are known to be inquilines in the nests of stingless bees (Hymenoptera: Apidae: Meliponinae), where they probably feed on the fecal masses of the bees (Roubik & Wheeler, 1982). *Aglyptinus* species are commonly found on epigean fungi, especially Polyporaceae (Newton, 1984), and *Creagrophorus* species have been bred from puffballs (Wheeler, 1979b). Species of *Popeus*, as well as those of the new genus from southeast Asia, have been collected from the fungus gardens of large termite nests (D. H. Kistner, personal communication), and *Termitoglobus* was also collected with termites (Reichensperger, 1915). Species of *Cyrtusiola* as well as undescribed and generically unplaced Australian and Madagascan species have been found in forest litter.

Larvae: Costa et al. (1988), Paulian (1941), Wheeler (1979b, 1985). Examined: *Aglyptinus puertoricensis* Peck; *A.* spp. (Australia, Mexico, Panama); *Creagrophorus* sp. (Panama); *Cyrtusiola* sp. (South Africa); *Parabystus inquilinus* (Matthews); *Scotocryptus* sp.; undet. genus, sp. (Madagascar).

GENERIC CATALOG:

Aglyptinus Cockerell [Tc, Sc] Neotropical, e Nearctic, England, New Guinea (21 spp.)
Aglyptinus Cockerell, 1906: 240 (new name for *Aglyptus* LeConte). Note: more widely distributed (Australia etc.).
Aglyptus LeConte, 1866: 369 (preoccupied, not Foerster 1856). Type sp.: *Colenis laevis* LeConte, 1853 (monotypy).
Aglyptonotus Champion, 1913: 65 (new name for *Aglyptus* LeConte).

Creagrophorus Matthews [Sc] West Indies, Mexico to Panama, Japan, n India (6 spp.)
Creagrophorus Matthews, 1887: 82. Type sp.: *Creagrophorus hamatus* Matthews, 1887 (des. Hatch 1929b:57). Note: revised by Wheeler (1979b).

Cyrtusiola Hlisnikovský [T, Sc] South Africa, Zimbabwe, Rwanda (2 spp.)
Cyrtusiola Hlisnikovský , 1974: 773. Type sp.: *Cyrtusiola punctatipennis* Hlisnikovský, 1974 (orig. des.).

Parabystus Portevin [Tc] Guatemala, Panama (1 sp.)
Parabystus Portevin, 1907: 80. Type sp.: *Scotocryptus inquilinus* Matthews, 1887 (monotypy).

Popeus Hlisnikovský [S] Afrotropical (4 spp.)
Popeus Hlisnikovský, 1974: 778. Type sp.: *Popeus mirabilis* Hlisnikovský, 1974 (orig. des.). Note: revised by Daffner (1984).

Scotocryptodes Portevin [S] Bolivia (1 sp.)
Scotocryptodes Portevin, 1907: 78. Type sp.: *Scotocryptodes germaini* Portevin, 1907 (monotypy).

Scotocryptus Girard [S] Neotropical (Mexico to Brazil) (5 spp.)
Scotocryptus Girard, 1874a: 574; 1874b: cv. Type sp.: *Scotocryptus meliponae* Girard, 1874 (monotypy).
Scotocryptopsis Portevin Brazil (1 sp.)
Scotocryptopsis Portevin, 1937: 36. Type sp.: *Scotocryptus parasitus* Reitter, 1884 (monotypy).
Scotocryptus s. str. Neotropical (Mexico to Brazil) (4 spp.)
Apharia Reitter, 1881: 87. Type sp.: *Apharia melitophila* Reitter, 1881 (monotypy).

Synaristus Portevin Peru (1 sp.)
Synaristus Portevin, 1907: 79. Type sp.: *Synaristus pilosus* Portevin, 1907 (monotypy).

Termitoglobus Reichensperger, NEW PLACEMENT (ex Endomychidae) South Africa (Natal) (1 sp.)
Termitoglobus Reichensperger, 1915: 10 (as genus of Endomychidae). Type sp.: *Termitoglobus ovulum* Reichensperger, 1915 (monotypy). Note: ex Endomychidae (J. Pakaluk, in litteris 1992); found with "*Termes*".

Agathidiini Westwood, 1838 (=Anisotomini)

Agathidiidae Westwood, 1838: 10 (new name for Anisotomidae [genus as junior synonym]). Type genus: *Agathidium* Illiger, 1798.
Anisotomidae Stephens, 1828: 99 (unavail., Art. 11f(i)1 [type genus implied junior synonym of *Leiodes*]). Type genus: *Anisotoma* Panzer, 1797 (not cited).
Anisotomidae Reitter, 1884: 91. Type genus: *Anisotoma* Panzer, 1797 (as Illiger).

DIAGNOSIS:

In addition to the usually sexually dimorphic tarsal segmentation, connate parameres bearing indistinct basal lobes, and antennal grooves on the ventral surface of the head, Agathidiini have procoxal cavities closed by a triangular notal process, mesocoxae separated by a metasternal process, tibiae each with a pair of dorsal carinae, and male tenent setae usually present on pro- and mesotarsi.

DISTRIBUTION: Holarctic, Afrotropical, Oriental, Neotropical (Mexico to Bolivia).

COMMENTS:

Scotocryptini and some genera allied to *Cyrtusa* (Leiodini) which also have antennal grooves are excluded from Agathidiini, here used in the restricted sense suggested by Brown (1937). Portevin (1926) divided the tribe into Anisotomini and Agathidiini, but based on characters that do not seem to justify such a split; this division has not been followed by recent workers. Wheeler (1979a) reviewed the tribe but did not mention many of the

Palearctic genera; Angelini (1995) included a key to all genera and, in numerous other publications noted there, has extensively revised the Old World fauna of the largest genus, *Agathidium*. Wheeler (1986) placed the genus *Cainosternum* in Agathidiini because of its similar sexually dimorphic tarsal formula, but other characters of the one known species are more consistent with its placement in Pseudoliodini (see above). This tribe has not been reported from South America, but undescribed species referable to the African genus *Pseudoagathidium* or a related new genus have been seen from several countries from Bolivia north to Mexico (personal observations). Two distinctive new genera have also been discovered in southeastern Asia (Angelini, *in litteris*) and Panama (personal observations).

All Agathidiini whose habits are known feed primarily or exclusively on slime molds (Myxomycetes) as adults and larvae. Most *Anisotoma* species and some subgenera of *Agathidium* (especially *Cyphoceble* and *Neoceble*) are found on fruiting bodies and feed primarily on spores, while species of the nominal subgenus of *Agathidium* and at least one species of *Anisotoma* have been associated with slime mold plasmodia. Angelini (1995), Angelini & De Marzo (1980), Lawrence & Newton (1980), Newton (1984), Newton & Stephenson (1990), Stephenson et al. (1994), Wheeler (1979a, 1980, 1984a, 1984b, 1986).

Larvae: Angelini & De Marzo (1984), Morimoto & Hayashi (1986), Newton (1991), Ratajczak (1995), Wheeler (1979a, 1984a, 1990). Diagnosis: Stemmata 2, large, well separated, dorsal usually larger than ventral or apparently separated into 2 stemmata; mola with coarse teeth not arranged in rows. Larvae of *Agathidium* (s. str.), known to feed on slime mold plasmodia rather than fruiting bodies with spores, lack mandibular molae. Examined: *Agathidium* (*Agathidium*) *oniscoides* Beauvois; *A.* (*Cyphoceble*) *angulare* Mannerheim; *A.* (*C.*) *mollinum* Fall; *A.* (*Neoceble*) *kumaonicum* Angelini & De Marzo; *A.* (*N.*) *pulchrum* LeConte; *A.* spp. (Mexico, USA); *Anisotoma basalis* (LeConte); *A. blanchardi* (Horn); *A. confusa* (Horn); *A. discolor* (Melsheimer); *A. geminata* (Horn); *A. horni* Wheeler; *A. inops* Brown.

GENERIC CATALOG:

Afroagathidium Angelini & Peck [Tc]Ghana, Zaire, South Africa, Taiwan, Malaysia (Sarawak) (5 spp.)
Afroagathidium Angelini & Peck, 1984: 422. Type sp.: *Afroagathidium capense* Angelini & Peck, 1984 (orig. des.).

Agathidium Panzer [Sc] Holarctic, Oriental, New Guinea, Mexico, Guatemala (553 spp.)
Agathidium Panzer, 1797: 13 (see Appendix B). Type sp.: *Tetratoma globosa* Herbst, 1792 (=*A. seminulum* (Linnaeus, 1758)) (monotypy). Note: as Illiger in Kugelann, 1798 (Neave 1939-40), but that refers to this page of Panzer!; 49 spp. not assigned to subgenus (48 Nearctic to Guatemala, 1 Java).
Volvoxis Kugelann, 1794: 535 (NOT preoccupied by *Volvox* Linnaeus). Type sp.: *Tetratoma globosa* Herbst, 1792 (= *A. seminulum* (Linnaeus, 1758)) (new des.).

Agathidium Illiger, 1798: 81 (new name for *Volvoxis* Kugelann, 1794 (in part), supposedly preocc. by *Volvox* Linnaeus, 1758).

Agathidium s. str. [Sc] Palearctic, Oriental (271 spp.)

Chaetoceble Sainte-Claire-Deville se France (1 sp.)

Chaetoceble Sainte-Claire-Deville, 1899: 292. Type sp.: *Agathidium pilosum* Sainte-Claire-Deville, 1899 (orig. des.).

Cyphoceble Thomson [Sc] Palearctic, Oriental (19 spp.)

Cyphoceble Thomson, 1859: 59. Type sp.: *Anisotoma staphylaeum* Gyllenhal, 1810 (=*A. nigrinum* Sturm, 1807) (orig. des.).

Saccoceble Gozis, 1886: 17. Type sp.: *Agathidium discoideum* Erichson, 1845 (orig. des.).

Euryceble Hlisnikovský Malaysia (Sarawak), Indonesia (Sumatra), New Guinea (5 spp.)

Euryceble Hlisnikovský, 1964a: 123. Type sp.: *Agathidium antennatum* Hlisnikovský, 1964 (orig. des.).

Macroceble Angelini Oriental (Nepal, n India, Malaysia, Taiwan) (24 spp.)

Macroceble Angelini, 1993: 30. Type sp.: *Agathidium shermathangense* Angelini & De Marzo, 1981 (orig. des.).

Microceble Angelini & De Marzo Oriental, Pakistan, Japan (97 spp.)

Microceble Angelini & De Marzo, 1986: 439. Type sp.: *Agathidium grouvellei* Portevin, 1907 (orig. des.).

Neoceble Gozis [Sc] Palearctic, Oriental (86 spp.)

Neoceble Gozis, 1886: 16. Type sp.: *Agathidium marginatum* Sturm, 1807 (orig. des.).

Stigmoceble Hlisnikovský, 1964a: 119. Type sp.: *Agathidium longicorne* Portevin, 1908 (orig. des.). Note: syn. with subgenus *Neoceble*, Angelini (1986).

Rhabdoelytrum Hlisnikovský [Tc, Sc] sw USA (1 sp.)

Rhabdoelytrum Hlisnikovský, 1964a: 31. Type sp.: *Agathidium sexstriatum* Horn, 1880 (orig. des.).

Amphicyllis Erichson [Tc] Europe to Caucasus, n Iran, Siberia (2 spp.)

Amphicyllis Erichson, 1845: 93. Type sp.: *Sphaeridium globus* Fabricius, 1792 (des. Thomson 1859:58, Hatch, 1929b:58).

Anisotoma Panzer [Sc] Holarctic, Nepal, China, Taiwan, n Neotropical (to Panama) (59 spp.)

Anisotoma Panzer, 1797: 8 (see Appendix B). Type sp.: *Tritoma glabra* Fabricius, 1787 (des. Hatch, 1929b:50; "*A. picea* (Illig.)" des. Thomson 1859:58). Note: as Knoch in Kugelann, 1798 (Neave); 2 orig. spp. (*picea* Kug., *glabra* Kug.).

Pentatoma Schneider, 1792: 339 (preoccupied, not Olivier 1789). Type sp.: *Sphaeridium humerale* Fabricius, 1792; not in Sherborn 1902, ?=*Sphaeridium humerale* Olivier, 1790 (des. Hatch, 1929b:50).

Anisotoma Illiger, 1798: 69 (attributed to Knoch). Type sp.: none des.? (13 orig.spp., including "*piceum* Panzer" and "*glabrum* Panzer").

Leiodes of Schmidt, 1841: 132 (misidentification of *Leiodes* Latreille).

Eucyrta Portevin, 1927: 82 (preoccupied, not Felder 1874). Type sp.: *Eucyrta didymata* Portevin, 1927 (des. Hatch, 1929b:57). Note: syn. Wheeler (1979a).

Cyrtoplastus Reitter [Tc] Palearctic, China, Taiwan (8 spp.)

Cyrtoplastus Reitter, 1884: 110. Type sp.: *Cyrtoplastus seriatopunctatus* Reitter, 1884 (=*C. seriepunctatus* (Brisout, 1867)) (des. Hatch, 1929b:64).

Liodopria Reitter [Sc] Palearctic, Oriental (7 spp.)

Liodopria Reitter, 1909: 256. Type sp.: *Anisotoma serricorne* Gyllenhal, 1813 (monotypy).

Pseudoagathidium Angelini [Sc] Afrotropical, South Africa (8 spp.)
Pseudoagathidium Angelini, 1993: 29. Type sp.: *Agathidium burgeoni* Portevin, 1937 (orig. des.).

Sphaeroliodes Portevin [T] Japan, Russia (e Siberia) (2 spp.)
Sphaeroliodes Portevin, 1905b: 419. Type sp.: *Sphaeroliodes rufescens* Portevin, 1905 (monotypy).

Stetholiodes Fall [Tc, Sc] n India, Nepal, Vietnam, China, Japan, e USA (10 spp.)
Stetholiodes Fall, 1910: 4. Type sp.: *Stetholiodes laticollis* Fall, 1910 (monotypy).
Agathodes Portevin, 1926: 80 (preoccupied, not Guénée 1854). Type sp.: *Agathodes striatipenne* Portevin, 1926 (monotypy).
Agathidiodes Portevin, 1944: 169 (new name for *Agathodes* Portevin). Note: syn. Newton (1983a).

Coloninae Horn, 1880 (1859)

Colones Horn, 1880: 266 (maintained, Art. 40b). Type genus: *Colon* Herbst, 1797.
Myloechina Thomson, 1859: 60 (replaced, Art. 40b). Type genus: *Myloechus* Latreille, 1807 (=*Colon* Herbst, 1797).

DIAGNOSIS:

Coloninae are readily recognized by the characters given in the key. They also have: open to largely closed periarticular gutters on antennal segments 8-10 (rarely 7-10 or 9-10); epistomal suture absent; mandibles with reduced, smooth molar lobes; procoxal cavities closed behind by fusion of notal process to sternum; mesocoxal cavities separated by mesosternal process; tarsi all 5-segmented, anterior tarsi of *both* sexes usually dilated and with tenent setae; spiracles of abdominal segments 7-8 atrophied; tergum 8 of male connate with dorsum of genital segment; aedeagus highly specialized; and proximal gonocoxites of ovipositor fused to one another.

DISTRIBUTION: Worldwide.

COMMENTS:

Coloninae are isolated from the other subfamilies by possession of a large number of unique and probably derivative features that may indicate a highly specialized but yet unknown natural history. Little is known about the biology of the group, although the species are often assumed to be associated with hypogean fungi (Newton, 1984). The group was extensively revised by Szymczakowski (e.g., 1964b, 1965, 1969b).

Larvae unknown.

GENERIC CATALOG:

Colon Herbst [Tc, Sc] worldwide (few in tropics) (135 spp.)
Kolon Herbst, 1797: 224 (designated an incorrect original spelling and corrected to *Colon* by ICZN (1995b)). Type sp.: *Kolon viennensis* Herbst, 1797 (des. Thomson, 1859: 60; *Myloechus brunneus* Latreille, 1807, des. Shuckard, 1839:158 (not orig. incl.)). Note: 2 spp. not assigned to subgenus.
Colon Illiger, 1801: 133 (designated as correct original spelling of *Kolon* by ICZN (1995b)).
Chelicolon Szymczakowski [Tc] Australia, s Chile, Argentina (10 spp.)
Chelicolon Szymczakowski, 1964b: 501. Type sp.: *Colon melbournense* Blackburn, 1892 (orig. des.).
Colon s. str. [Tc] c+n Europe, Burma, Nearctic (14 spp.)
Desmidocolon Szymczakowski [Sc] Australia, New Guinea (3 spp.)
Desmidocolon Szymczakowski, 1964b: 493. Type sp.: *Colon pugioniferum* Szymczakowski, 1964 (orig. des.).
Eurycolon Ganglbauer [Tc] Holarctic (8 spp.)
Eurycolon Ganglbauer, 1899: 146. Type sp.: *Colon latus* Kraatz, 1850 (monotypy).
Curvimanon Fleischer, 1909: 46. Type sp.: *Colon rufescens* Kraatz, 1850 (des. Szymczakowski, 1969b:306; *Catops bidentatus* Sahlberg des. Hatch, 1928:214 (not orig. incl.)). Note: syn. with subgenus *Eurycolon*, Szymczakowski (1969b).
Mesagyrtes Broun [Tc] New Zealand (1 sp.)
Mesagyrtes Broun, 1895: 85 (not Ponomarenko 1977). Type sp.: *Mesagyrtes scabripes* Broun, 1895 (=*C. hirtale* (Broun, 1880)) (monotypy). Note: reduced to subgenus of *Colon*, Szymczakowski (1964b).
Myloechus Latreille [Tc, Sc] Holarctic, Mexico, n Oriental, c Africa (76 spp.)
Myloechus Latreille, 1807: 30. Type sp.: *Myloechus brunneus* Latreille, 1807 (monotypy).
Myloecus Agassiz, 1847: 242 (unjustified emendation of *Myloechus*).
Platycolon Portevin [Sc] Afrotropical, South Africa (18 spp.)
Platycolon Portevin, 1907: 73. Type sp.: *Colon sulcicolle* Portevin, 1907 (monotypy).
Striatocolon Peck & Stephan Nearctic (1 sp.)
Striatocolon Peck & Stephan, 1996: 687. Type sp.: *Colon thoracicum* Horn, 1880 (orig. des.).
Tricolon Peck & Stephan Nearctic (2 spp.)
Tricolon Peck & Stephan, 1996: 684. Type sp.: *Colon pacificum* Peck & Stephan, 1996 (orig. des.).

Colonellus Szymczakowski Indonesia (Sumatra), Sri Lanka (3 spp.)
Colonellus Szymczakowski, 1964b: 480. Type sp.: *Colonellus fleischeri* Szymczakowski, 1964 (orig. des.).

Cholevinae Kirby, 1837 (=Catopinae, Leptodirinae)

Cholevidae Kirby, 1837: 108. Type genus: *Choleva* Latreille, 1796.

DIAGNOSIS:

In addition to the internally closed coxal cavities and the usual (and probably ancestral) presence of an occipital carina or crest, Cholevinae have: epistomal suture (if present) never with "stem"; cervical sclerites with acute to rounded outer projection; mesocoxal cavities contiguous or separated by mesosternal process; tarsi 5-5-5 or 4-5-5 segmented; and abdominal spiracle 8 highly reduced or atrophied.

COMMENTS:

Zwick (1979) pointed out that the name Cholevinae must replace the more familiar name Catopinae for this subfamily, which is often treated as a family. The classification adopted here is basically that established by Jeannel (1936) as modified by Jeannel (1964), Szymczakowski (1964a, 1966, 1973), Zwick (1979), and Perreau (1989), with reduction of subfamilies to tribes as suggested by Peck (1973). The main recent changes in this subfamily concern what is here called Anemadini. Jeannel (1936) recognized two subfamilies, Nemadinae and Anemadinae, for this group, including 3 tribes in the former subfamily on the basis of a shared aedeagal type that is almost certainly primitive for Cholevinae if not for Leiodidae as a whole. Of Jeannel's tribes of Nemadinae, Agyrtodini are here excluded from Cholevinae and placed in Camiarinae (see above); Oritocatopini are made a separate tribe of Cholevinae, allied more closely to Eucatopini than to Nemadini; and following Perreau (1989) Nemadini is combined with Jeannel's Anemadinae to form a single group Anemadini (using the oldest name). Perreau (1989), Giachino & Vailati (1993), Newton (1985), etc.

KEY TO TRIBES OF CHOLEVINAE

1. Mesocoxal cavities narrowly separated by prolonged mesosternal process 2
   Mesocoxal cavities contiguous (narrowly separated in some Japanese *Cholevodes* only) 5
2(1). Epistomal suture present; female (and sometimes male) protarsi 4-segmented; head without strongly elevated occipital crest, with or without occipital carina; metacoxae more or less separated . . . . . .Leptodirini
   Epistomal suture absent; all tarsi 5-segmented; head with strongly elevated occipital crest, or occipital carina; metacoxae contiguous 3
3(2). Head with strongly elevated occipital crest; maxillary palp with segment 4 shorter than 3, conical; abdominal tergum 7 with basolateral carina . . . . . .Ptomaphagini
   Head with occipital carina which is weak or absent mesally; maxillary palp with segment 4 much longer than 3, fusiform; abdominal tergum 7 not carinate 4
4(3). Prosternum normal, horizontal before coxae; postcoxal process of pronotum broadly rounded; protibia without external comb of short spines . . . . . .Oritocatopini
   Prosternum flared ventrad to form precoxal cowling; postcoxal process of pronotum acutely triangular; protibia with external comb of short spines . . . . . .Eucatopini
5(1). Male genital segment reduced, short and ringlike; elytra not transversely striolate . .Cholevini
   Male genital segment well developed, tubular; elytra usually transversely striolate (but many exceptions) . . . . . .Anemadini

Anemadini Hatch, 1928

Anemadina Hatch, 1928: 159. Type genus: *Anemadus* Reitter, 1884.
Anemadinae Jeannel, 1936: 179 (as new). Type genus: *Anemadus* Reitter, 1884.

DIAGNOSIS:

In addition to characters mentioned in the tribal key, Anemadini have: head with elevated occipital crest; epistomal suture present (Anemadina, Paracatopina) or absent; 4th segment of maxillary palp shorter than 3rd and conical (except *Catoposchema* with long parallel-sided segment 4); postcoxal process of pronotum broad, blunt; abdominal spiracle 8 atrophied; and parameres of aedeagus with basoventral lobes which usually meet ventrally, and may be articulated to parameres, or (Paracatopina) without basoventral lobes.

DISTRIBUTION: Holarctic, Oriental, Australia, New Zealand, Neotropical.

COMMENTS:

As Zwick (1979), Newton (1985) and Perreau (1989) pointed out, Jeannel's (1936) subfamilies Anemadinae and Nemadinae were unnatural groups, and difficult to distinguish from one another. Nemadinae, in particular, was defined by Jeannel (1936) mainly on the basis of structures of the aedeagus and male genital segment that are probably plesiomorphies not only for Cholevinae but all Leiodidae. Anemadini is used here in the sense of Jeannel's (1936) subfamilies Anemadinae plus Nemadinae combined, but excluding his nemadine tribes Oritocatopini and Agyrtodini (here made a separate tribe of Cholevinae and removed to Camiarinae, respectively; see above). Four of the subtribes provisionally retained here were recognized by Jeannel (1936) as subtribes of his Nemadini or tribes of his Anemadinae, but these groups need reevaluation. Giachino & Vailati (1993, Fig. 114) separated these groups very widely, associating "Anemadinae" with "Cholevinae" and "Leptodirinae", and "Nemadinae" and "Paracatopinae" with "Ptomaphaginae". However, these authors provided no morphological evidence to justify these associations or the separation of "Anemadinae" from "Nemadinae", and their scheme is clearly contradicted, for example, by evidence presented by Perreau (1989) for association of his Ptomaphaginae with Eucatopinae and Oritocatopinae rather than with Nemadinae and Paracatopinae. Problems with the placement of the genus *Anemadiola* Szymczakowski, transferred from "Anemadinae" to "Nemadinae" by Giachino & Vailati (1993) but questioned by Perreau (1996), illustrate the difficulties in separating these groups. Nevertheless, strong evidence for monophyly of Anemadini as used here and by Perreau (1989) is still lacking, and the group may be paraphyletic with respect to Cholevini and/or Leptodirini.

One change made here is the formal removal from Nemadina of the large austral generic group referred to by Newton (1985) as the "*Eunemadus*

Group", here named as the **new subtribe** Eunemadina (type genus, *Eunemadus* Portevin). This group, plus the two New Zealand genera of Paracatopina, differ significantly from the remaining examined genera of Nemadina, and from Anemadina and Eocatopina, as indicated in the subtribal key below.

Most species of Anemadini are attracted to carrion, dung and other decomposing organic matter, including vertebrate nests. Some species of

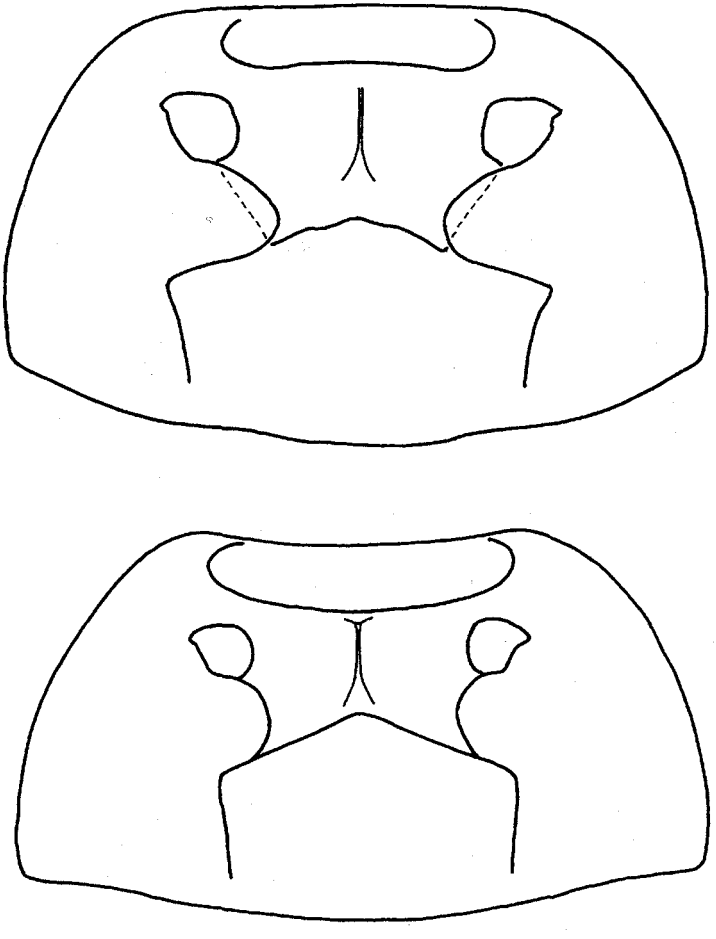

Fig. 13-14 - Prothorax, cleared and legs removed, ventral, of: 13, *Eunemadus chilensis* Portevin (Cholevinae: Anemadini: Eunemadina); 14, *Nemadus integer* Fall (Cholevinae: Anemadini: Nemadina)

Nemadus and *Eocatops* are myrmecophilous, while some *Nargomorphus* species are fungivorous, and some *Speonemadus* species are cavernicolous (Jeannel, 1936). Giachino & Vailati (1993) thoroughly revised Anemadina. (Jeannel, 1936; Newton, 1984, 1985)

Larvae: Gnaspini (1993b), Jeannel (1922b), Newton (1991), Peyerimhoff (1907), Samuelson (1964), Tanaka (1972), Zwick (1979), Zwick in Klausnitzer (1978). Examined: *Dissochaetus vanini* Gnaspini; *Nargiotes blackburni* (Portevin); *Nargomorphus filitarsis* Szymczakowski; *Nemadus hornii* Hatch; *N.* spp. (USA); *Paracatops* spp. (New Zealand); *Pseudonemadus adelaidae* (Blackburn); undet. genera and spp. (Australia, Chile, Japan).

Key to subtribes of Anemadini

1. Metepisternum with small tongue-like process which overlaps elytron in repose; post-mesocoxal carina bordering mesocoxal cavity throughout, not angulate; procoxal cavity closure as in Fig. 13, with broad overlap between notal and sternal processes; antenna not compact, segments 7, 9 and 10 without periapical carina 2
   Metepisternum without tongue-like process; post-mesocoxal carina angularly separated from mesocoxal cavity except at base and apex of coxa; procoxal closure as in Fig. 14, with little overlap between notal and sternal processes; antenna compact and with periapical carina on segments 7, 9 and 10 (except Anemadina) 3
2(1). Epistomal suture present; parameres of aedeagus lacking basal lobes ..... .Paracatopina
   Epistomal suture absent; parameres of aedeagus with basal lobes that meet ventrally ..... .Eunemadina **new subtribe**
3(2). Male mesotarsus with basal 2 segments dilated; epistomal suture present ..... .Anemadina
   Male mesotarsus with at most 1 basal segment dilated; epistomal suture usually absent 4
4(3). Protibia with several apical spines of varying length but without distinct periarticular comb of small spines; paramere of aedeagus with at most 3 setae; female sternite 8 with anterior projection ..... .Nemadina **sensu novo**
   Protibia with well-developed periarticular comb of small spines; paramere of aedeagus with 6 setae; female sternite 8 without anterior projection ..... .Eocatopina

Generic catalog:

Anemadina Hatch, 1928

Anemadiola Szymczakowski — Japan, Taiwan (3 spp.)

Anemadiola Szymczakowski, 1963b: 112. Type sp.: *Anemadiola inordinata* Szymczakowski, 1963 (orig. des.). Note: moved to Nemadina by Giachino & Vailati (1993), reviewed and placement questioned by Perreau (1996), returned to Anemadina (Perreau *in litteris*, 1998); 2 of 3 spp. have 2 male mesotarsal segments dilated.

Anemadus Reitter [Tc, Sc] — s Europe to n India, Taiwan, Japan (30 spp.)

Anemadus Reitter, 1884: 58. Type sp.: *Catops strigosus* Kraatz, 1852 (des. Jeannel, 1922b:41, Hatch, 1928:159). Note: revised by Giachino & Vailati (1993), updated by Perreau (1996).

Namadeus Jeannel, 1936: 203. Type sp.: *Catops acicularis* Kraatz, 1852 (orig. des.). Note: syn. Giachino & Vailati (1993).

Cholevodes Portevin [Sc] Japan (Honshu, Kyushu) (1 sp.)
Cholevodes Portevin, 1928: 1. Type sp.: *Cholevodes tenuitarsis* Portevin, 1928 (monotypy). Note: revised by Giachino & Vailati (1993), Nishikawa (1994).

Speonemadus Jeannel [Sc] w Mediterranean (10 spp.)
Speonemadus Jeannel, 1922b: 53 (as subgenus of *Anemadus*). Type sp.: *Anemadus escalerae* Uhagón, 1898 (orig. des.). Note: revised by Giachino & Vailati (1993).
Hormosacus Jeannel, 1936: 209. Type sp.: *Choleva subcostata* Reiche, 1864 (orig. des.). Note: syn. Giachino & Vailati (1993).

Nemadina Jeannel, 1936, *sensu novo*

Nemadinae Jeannel, 1936: 96. Type genus: *Nemadus* Thomson, 1867.

Micronemadus Jeannel [Tc] Russia (e Siberia), Japan, Taiwan, China, Sumatra, n India (1 sp.)
Micronemadus Jeannel, 1936: 173. Type sp.: *Catops pusillimus* Kraatz, 1877 (orig. des.).

Nemadus Thomson [Tc, Sc] Holarctic, Nepal, n India (23 spp.)
Nemadus Thomson, 1867: 351. Type sp.: *Catops colonoides* Kraatz, 1851 (monotypy). Note: most spp. not assigned to subgenus.
Eonargus Iablokoff-Khnzorian Armenia (1 sp.)
Eonargus Iablokoff-Khnzorian, 1959: 65. Type sp.: *Eonargus nidicola* Iablokoff-Khnzorian, 1959 (orig. des.). Note: to subgenus of *Nemadus*, Iablokoff-Khnzorian (1975).
Laferius Perkovsky Russia (e Siberia) (1 sp.)
Laferius Perkovsky, 1994: 13. Type sp.: *Nemadus kurbatovi* Perkovsky, 1994 (orig. des.). Note: also including *N. brachyderus*?, other spp.? (Perkovsky, 1994).
Nemadus s. str. [Tc, Sc] Holarctic, Nepal, n India (21 spp.)

Eocatopina Jeannel, 1936

Eocatopina Jeannel, 1936: 124. Type genus: *Eocatops* Peyerimhoff, 1924.

Eocatops Peyerimhoff [Tc] w+c Palearctic (16 spp.)
Eocatops Peyerimhoff, 1924: 36. Type sp.: *Eocatops ambiguus* Peyerimhoff, 1924 (orig. des.).
Eocatops s. str. [Tc] w+c Palearctic (15 spp.)
Eonemadus Perreau Pakistan (1 sp.)
Eonemadus Perreau, 1991: 564. Type sp.: *Eocatops loebli* Perreau, 1991 (orig. des.).

Eunemadina Newton, *new subtribe*

Type genus: *Eunemadus* Portevin, 1914

Austrocholeva Zwick [Tc] se Australia (2 spp.)
Austrocholeva Zwick, 1979: 27. Type sp.: *Austrocholeva platypus* Zwick, 1979 (orig. des.).

Austronargus Zwick [Sc] s Australia (2 spp.)
Austronargus Zwick, 1979: 31. Type sp.: *Austronargus tidbinbillae* Zwick, 1979 (orig. des.).

Austronemadus Zwick [Tc] se Australia (2 spp.)
Austronemadus Zwick, 1979: 33. Type sp.: *Choleva macleayi* Blackburn, 1903 (orig. des.). Note: 1 new sp. seen.

Catoposchema Jeannel [Tc] se Australia (1 sp.)
Catoposchema Jeannel, 1936: 134. Type sp.: *Catoposchema tasmaniae* Jeannel, 1936 (orig. des.). Note: 1 sp. to *Austronargus*, Zwick (1979).

Dissochaetus Reitter [Sc] Nearctic, Neotropical (30 spp.)
Dissochaetus Reitter, 1884: 39. Type sp.: *Dissochaetus hetschkoi* Reitter, 1884 (des. Jeannel 1922b:41, Hatch 1928:163). Note: checklist, Gnaspini (1991).
Dissochaetus Portevin, 1902: 513 (as new, for "*Dissochaetus* Reitter in litt."). Type sp.: *Catops spinipes* Murray, 1856 (monotypy). Note: 3 other spp. "very likely" belong to genus (Portevin).

Eunemadus Portevin [Tc] s Chile, sw Argentina (1 sp.)
Eunemadus Portevin, 1914a: 192. Type sp.: *Eunemadus chilensis* Portevin, 1914 (des. Hatch, 1928:208).

Falkocholeva Hatch [Tc] s Chile, sw Argentina, Falkland Islands (1 sp.)
Falkocholeva Hatch, 1928: 208. Type sp.: *Choleva falklandica* Waterhouse, 1879 (=*F. cribellata* (Fairmaire & Germain, 1859)) (orig. des.).
Falkocholeva Jeannel, 1936: 156 (as new [*Falkocholeva* Hatch, 1928 considered nomen nudum]). Type sp.: *Choleva falklandica* Waterhouse, 1879 (=*F. cribellata* (Fairmaire & Germain, 1859)) (orig. des.).

Falkonemadus Szymczakowski [Tc, Sc] Falkland Islands (1 sp.)
Falkonemadus Szymczakowski, 1961a: 160. Type sp.: *Falkonemadus sphenisci* Szymczakowski, 1961 (orig. des.).

Nargiotes Jeannel [T, Sc] Australia (3 spp.)
Nargiotes Jeannel, 1936: 141. Type sp.: *Choleva antipodum* Blackburn, 1891 (=*N. blackburni* (Portevin, 1905)) (orig. des.). Note: see Appendix B; 2+ new spp. seen; Jeannel (1936:142) considered *antipodum* not homonym of *antipoda* Kirsch..

Nargomorphus Jeannel [Tc, Sc] Australia (20 spp.)
Nargomorphus Jeannel, 1936: 136. Type sp.: *Choleva victoriensis* Blackburn, 1891 (orig. des.). Note: revised by Szymczakowski (1963a, 1973), Zwick (1979).

Nemadiolus Jeannel [Sc] s Chile (4 spp.)
Nemadiolus Jeannel, 1936: 161. Type sp.: *Nemadiolus germaini* Jeannel, 1936 (orig. des.).

Nemadiopsis Jeannel [Sc] s Chile, sw Argentina, Ecuador (8 spp.)
Nemadiopsis Jeannel, 1936: 159. Type sp.: *Choleva fastidiosa* Fairmaire & Germain, 1859 (orig. des.). Note: new spp. seen, Peru and Bolivia.

Nemadotropis Szymczakowski [Tc] s Chile (1 sp.)
Nemadotropis Szymczakowski, 1971a: 408. Type sp.: *Nemadotropis stenosoma* Szymczakowski, 1971 (orig. des.).

Paranemadus Zwick [Sc] se Australia (1 sp.)
Paranemadus Zwick, 1979: 36. Type sp.: *Paranemadus striatopunctatus* Zwick, 1979 (orig. des.).

Pseudonemadus Portevin [T, Sc] Indonesia, New Guinea, Australia, New Zealand (42 spp.)
Pseudonemadus Portevin, 1914a: 193. Type sp.: *Catops integer* Portevin, 1903 (des. Jeannel 1922b:40, Hatch, 1928:209). Note: revised by Peck (1985).

Leptonemadus Zwick [Tc] se Australia (2 spp.)
Leptonemadus Zwick, 1979: 24. Type sp.: *Pseudonemadus transvestitus* Zwick, 1979 (orig. des.).
Pseudonemadus s. str. [T, Sc] Indonesia, New Guinea, Australia, New Zealand (38 spp.)
Archaeonemadus Jeannel, 1936: 127. Type sp.: *Archaeonemadus modiglianii* Jeannel, 1936 (orig. des.). Note: syn. Szymczakowski (1964a).
Triardronia Szymczakowski e Australia (2 spp.)
Triardronia Szymczakowski, 1966: 615. Type sp.: *Catops australis* Erichson, 1842 (orig. des.).

Rangiola Jeannel [T] se Australia (2 spp.)
Rangiola Jeannel, 1936: 139. Type sp.: *Rangiola punctipennis* Jeannel, 1936 (orig. des.).

Paracatopina Jeannel, 1936

Paracatopini Jeannel, 1936: 181. Type genus: *Paracatops* Portevin, 1907.

Mesocolon Broun [Sc] New Zealand (9 spp.)
Mesocolon Broun, 1880: 153 (see Appendix B). Type sp.: *Mesocolon undulata* Broun, 1880 (des. Hatch, 1928:212; *M. clathratum* Broun, 1880, des. Jeannel, 1936:190). Note: Hatch type sp. designation = *Zeargyrtoma*!; see Appendix A.

Paracatops Portevin [Sc] New Zealand and nearby islands (15 spp.)
Paracatops Portevin, 1907: 69. Type sp.: *Choleva antipoda* Kirsch, 1877 (as *antipoda*, without derivation but probably adjective [genus considered feminine]) (monotypy).
Cnemopsilus Portevin, 1914a: 190. Type sp.: *Cnemopsilus femoratus* Portevin, 1914 (=*P. lugubris* (Sharp, 1882)) (monotypy).
Dolichocatops Portevin, 1914a: 191. Type sp.: *Dolichocatops schenklingi* Portevin, 1914 (=*P. relatus* (Broun, 1893)) (monotypy).
Austrocatops Brookes, 1951: 26. Type sp.: *Austrocatops campbellicus* Brookes, 1951 (monotypy).

Cholevini Kirby, 1837 (=Catopini)

Catopides Chaudoir, 1845: 195 (Latinized?). Type genus: *Catops* Paykull, 1798 (as Fabricius).
Catopidae Thomson, 1859: 59. Type genus: *Catops* Paykull, 1798. Note: first Latinized use?

DIAGNOSIS:

As for Anemadini, except for the characters noted in the tribal key.

DISTRIBUTION: Holarctic, Oriental.

COMMENTS:

The genera of Cholevini have been about evenly divided into 2 groups (Jeannel, 1936). Szymczakowski (1956) noted problems with this division, and moved *Rybinskiella* from what is here called Cholevina to Catopina;

Iablokoff-Khnzorian (1975) further questioned and rejected this division completely. Perreau (1989) acknowledged problems with most of the characters used to separate these groups but continued to recognize them as probably natural groupings. They are retained here as subtribes, but further study is clearly needed.

Species of the tribe have habits similar to those of Anemadini, but are more frequently associated with vertebrate nests. *Catopsimorphus, Attumbra, Attaephilus* and *Philomessor* species are myrmecophilous. Jeannel (1936).

Larvae: Blas & Vives (1978), Böving & Craighead (1931), Casale (1975a), Huen (1955), Jeannel (1922b), Morimoto & Hayashi (1986), Paulian (1941), Peyerimhoff (1906), Silvestri (1912), Strambi (1963), Tanaka (1972), Zwick in Klausnitzer (1978). Examined: *Catops egenus* (Horn); *C. nigricans* (Spence); *C.* spp. (Germany, USA); *Choleva oblonga oblonga* Latreille; *C. sturmi* Brisout; *Prionochaeta opaca* (Say); *Sciodrepoides watsoni watsoni* (Spence).

Key to subtribes of Cholevini

1. Epistomal suture present (except *Prionochaeta*); main tibial spur spinose; paramere of aedeagus normal, apex more or less dilated and blunt; male mesotarsus usually with all segments slender ..... Cholevina
   Epistomal suture absent; main tibial spur more or less smooth; paramere of aedeagus usually very slender, tapered to fine point; male mesotarsus usually with expanded basal segment ... . Catopina

Generic Catalog:

Cholevina Kirby, 1837

Attaephilus Motschulsky — c Europe to Caucasus, Iran (16 spp.)

Attaephilus Motschulsky, 1870c: 350 (new name for *Myrmecophilus* Motschulsky; also spelled *Attaephillus*). Note: to subgenus of *Catopsimorphus*, Iablokoff-Khnzorian (1975); missp. *Attaphilus*, Reitter 1906:244.

Myrmecophilus Motschulsky, 1844: 817 (preoccupied, not Berthold, 1827). Type sp.: *Myrmecophilus paradoxus* Motschulsky, 1844 (monotypy).

Attophilus Jacobson, 1910: 608 (unjustified emendation of *Attaephilus*; as subgenus of *Catopomorphus*).

Jeannelella Roubal, 1925: 68. Type sp.: *Jeannelella paradoxa* Roubal, 1925 (=*A. arenarius* (Hampe, 1852)) (monotypy).

Attumbra Gozis [Sc] — w+c Palearctic (13 spp.)

Attumbra Gozis, 1886: 17. Type sp.: *Catopsimorphus josephinae* Saulcy, 1862 (orig. des.).

Anthobiomorpha Obenberger, 1917: 12. Type sp.: *Anthobiomorpha malyi* Obenberger, 1917 (monotypy).

Catopsimorphus Aubé [Tc] — Mediterranean to Caucasus, nw Iran (17 spp.)

Catopsimorphus Aubé, 1850: 324. Type sp.: *Catopsimorphus orientalis* Aubé, 1850 (monotypy).

Catopomorphus Schaum, 1851: 176 (unjustified emendation of *Catopsimorphus*).

Attiscurra Gozis — Mediterranean (5 spp.)
Attiscurra Gozis, 1886: 17. Type sp.: *Catopsimorphus marqueti* Fairmaire, 1857 (orig. des.).
Catopsimorphus s. str. [Tc] — Mediterranean to Caucasus, nw Iran (8 spp.)
Weiratherella Jeannel — Mediterranean (4 spp.)
Weiratherella Jeannel, 1929: 82. Type sp.: *Weiratherella clavalis* Jeannel, 1929 (orig. des.).

Choleva Latreille [Tc] — w+c Palearctic, Mongolia, Oriental (n India, Vietnam) (58 spp.)
Choleva Latreille, 1796: 14 (no species listed; see Appendix B). Type sp.: *Catops sericeus* Fabricius; not in Sherborn, 1902, ?=*Catops sericeus* Paykull, 1798/*Tritoma sericea* Fabricius, 1787 (=*C. fuscus* (Panzer, 1794)) (subsequent monotypy by Latreille, 1802:122); *agilis* Ill. by Westwood 1838:11, Thomson ... Note: 1 sp. nomen nudum?, not assigned to subgenus.
Choleva s. str. [Tc] — w+c Palearctic, Mongolia (46 spp.)
Cholevopsis Jeannel — Europe to Turkey, Israel (9 spp.)
Cholevopsis Jeannel, 1922b: 43. Type sp.: *Catops spadiceus* Sturm, 1839 (orig. des.).
Protocatops Perreau — Nepal, n India, Vietnam (2 spp.)
Protocatops Perreau, 1995: 973 (as subgenus of *Choleva*). Type sp.: *Choleva henroti* Szymczakowski, 1961 (orig. des.).

Nargus Thomson [Sc] — w+c Palearctic, n India, Taiwan (46 spp.)
Nargus Thomson, 1867: 349. Type sp.: *Choleva velox* Spence, 1815 (monotypy). Note: *N. taiwanensis* Perreau not assigned to subgenus, to new subgenus in Perreau (manuscript).
Demochrus Thomson [Tc] — w+c Palearctic (27 spp.)
Demochrus Thomson, 1867: 350. Type sp.: *Choleva anisotomoides* Spence, 1815 (monotypy).
Nargus s. str. — w+c Palearctic, n India (18 spp.)

Philomessor Jeannel — w Mediterranean, Armenia (5 spp.)
Philomessor Jeannel, 1936: 304. Type sp.: *Catops brevicollis* Kraatz, 1852 (orig. des.). Note: to subgenus of *Catopsimorphus*, Iablokoff-Khnzorian (1975).
Attumbrinus Jeannel — Algeria, Morocco (2 spp.)
Attumbrinus Jeannel, 1936: 307. Type sp.: *Catopomorphus cloueti* Portevin, 1907 (orig. des.). Note: to subgenus of *Catopsimorphus*, Iablokoff-Khnzorian (1975).
Philomessor s. str. — w Mediterranean, Armenia (3 spp.)

Prionochaeta Horn [Tc] — Nearctic, e Palearctic, China (4 spp.)
Prionochaeta Horn, 1880: 260. Type sp.: *Catops opacus* Say, 1825 (monotypy). Note: reviewed by Peck (1977b).

Takobiella Růžička — Tajikistan (1 sp.)
Takobiella Růžička, 1992: 243. Type sp.: *Takobiella strejceki* Růžička, 1992 (orig. des.).

Catopina Chaudoir, 1845

Catopides Chaudoir, 1845: 195 (Latinized?). Type genus: *Catops* Paykull, 1798 (as Fabricius).
Catopidae Thomson, 1859: 59. Type genus: *Catops* Paykull, 1798. Note: first Latinized use?

Apocatops Zwick [Tc] — Europe (2 spp.)
Apocatops Zwick, 1968: 13. Type sp.: *Catops nigrita* Erichson, 1837 (orig. des.).

Apterocatops Miyama — Japan (Shikoku) (2 spp.)
Apterocatops Miyama, 1985: 15. Type sp.: *Apterocatops tsurugisanus* Miyama, 1985 (orig. des.).

Catopidius Jeannel [Tc] sw Europe, Madeira (2 spp.)
Catopidius Jeannel, 1922b: 45. Type sp.: *Catops depressus* Murray, 1856 (orig. des.).

Catopodes Portevin Japan, China, Nepal (3 spp.)
Catopodes Portevin, 1914c: 214. Type sp.: *Catops fuscifrons* Kraatz, 1877 (monotypy).

Catops Paykull [Sc] Holarctic, n India, China, Taiwan, n Borneo, Mexico (122 spp.)
Catops Paykull, 1798: 342. Type sp.: *Catops sericeus* Paykull, 1798; referred to *Tritoma sericea* Fabricius, 1787 [Sherborn, 1902] (=*C. fuscus* (Panzer, 1794)) (des. Jeannel, 1922b:44; *Helops fuscus* Panzer des. Thomson, 1859:59, Hatch, 1928:188 (not orig. incl.)).
Sciodrepa Thomson, 1859: 60. Type sp.: *Catops alpinus* Gyllenhal, 1827 (orig. des.; *Catops fumatus* Spence des. Hatch, 1928:202).
Lasiocatops Reitter, 1901a: 47 (as subgenus of *Catops*). Type sp.: *Catops alpinus* Gyllenhal, 1827 (des. Jeannel 1922b:44).

Catoptrichus Murray [Tc] w Nearctic (1 sp.)
Catoptrichus Murray, 1856: 461. Type sp.: *Catops frankenhaeuseri* Mannerheim, 1852 (monotypy).

Chionocatops Ganglbauer Switzerland, Austria (Alps) (1 sp.)
Chionocatops Ganglbauer, 1899: 137 (as subgenus of *Catops*). Type sp.: *Catops bugnioni* Tournier, 1873 (monotypy).

Cholevinus Reitter [Tc] Palearctic (6 spp.)
Cholevinus Reitter, 1901a: 39 (as subgenus of *Catops*). Type sp.: *Catops pallidus* Ménétries, 1832 (des. Jeannel, 1922b:45).

Cryocatops Jeannel Russia (Siberia) (3 spp.)
Cryocatops Jeannel, 1936: 421. Type sp.: *Cryocatops starokadomskyi* Jeannel, 1936 (orig. des.).

Dreposcia Jeannel [Tc] Palearctic (3 spp.)
Dreposcia Jeannel, 1922b: 45. Type sp.: *Catops umbrinus* Erichson, 1837 (orig. des.).
Munsteria Krogerus, 1931: 10. Type sp.: *Catops colletti* Münster, 1912 (=*D. brevipalpis* (Reitter, 1901), ssp.) (orig. des.).
Münsteria; Jeannel, 1936: 331 (misspelling of *Munsteria*; not *Muensteria* Deslongchamps 1835, Knebel 1909).

Dzungarites Jeannel Turkestan (1 sp.)
Dzungarites Jeannel, 1936: 419. Type sp.: *Catops roubali* Lebedev, 1930 (orig. des.).

Fissocatops Zwick Europe to Caucasus (3 spp.)
Fissocatops Zwick, 1968: 14. Type sp.: *Catops westi* Krogerus, 1931 (orig. des.).

Himalops Perreau Nepal (1 sp.)
Himalops Perreau, 1986: 29. Type sp.: *Himalops ovipalpis* Perreau, 1986 (orig. des.).

Mesocatops Szymczakowski e Russia, Japan, Nepal, Burma, China, Taiwan (6 spp.)
Mesocatops Szymczakowski, 1961b: 130. Type sp.: *Mesocatops latitarsis* Szymczakowski, 1961 (orig. des.).

Rybinskiella Reitter [S] Palearctic, n India (11 spp.)
Rybinskiella Reitter, 1906: 243. Type sp.: *Choleva magnifica* Rybiński, 1902 (=*R. daurica* (Motschulsky, 1845)) (monotypy). Note: in catalog; described by Reitter (1907:333); placement, Szymczakowski (1956).

Eurybinskiella Iablokoff-Khnzorian — Russia (e Siberia) (1 sp.)
Eurybinskiella Iablokoff-Khnzorian, 1970: 54. Type sp.: *Rybinskiella levushkini* Iablokoff-Khnzorian, 1970 (monotypy).
Rybinskiella s. str. — Czechoslovakia to Ukraine (1 sp.)
Sintania Pic — c+e Palearctic, n India (9 spp.)
Sintania Pic, 1908: 59 (attributed to Rost). Type sp.: *Sintania himalayica* Pic, 1908 (des. Jeannel 1922b:47). Note: genus and both original spp. attributed to "Rost".

Sciodrepoides Hatch [Tc] — Holarctic, China (10 spp.)
Sciodrepoides Hatch, 1933: 224 (as subgenus of *Catops*). Type sp.: *Choleva watsoni* Spence, 1815 (orig. des.).

Leptodirini Lacordaire, 1854 (1849) (=Bathysciini)

Leptodérides Lacordaire, 1854: 195 (kept for Stagobiini, Art. 40b; not Latinized; avail., Art. 11f(iii); based on unjustified emendation). Type genus: *Leptodirus* Schmidt, 1832 (as *Leptoderus,* unjustified emendation by Schmidt 1852).
Leptoderini Gutfleisch & Bose, 1859: 202 (based on unjustified emendation). Type genus: *Leptodirus* Schmidt, 1832 (as *Leptoderus*, unjustified emendation by Schmidt 1852). Note: first Latinized use?
Leptoderidae Kraatz, 1859: 35 (based on unjustified emendation). Type genus: *Leptodirus* Schmidt, 1832 (as *Leptoderus*, unjustified emendation by Schmidt 1852). Note: first Latinized use?
Leptodirites; Abeille de Perrin, 1878: 145 (not formal Latin name?). Type genus: *Leptodirus* Schmidt, 1832.
Gynomorphi Jeannel, 1910a: 14 (unavail., not based on genus).
Brachyscapiti Jeannel, 1910a: 19 (unavail., not based on genus).
Euryscapiti Jeannel, 1910a: 7 (unavail., not based on genus).
Téléomorphes Jeannel, 1914a: 71 (unavail., not based on genus).
Leptodiridae; Hatch, 1933: 188. Type genus: *Leptodirus* Schmidt, 1832.
Leptodirina Guéorguiev, 1974a: 841 (as new subtribe). Type genus: *Leptodirus* Schmidt, 1832 (not cited).

DIAGNOSIS:

In addition to the characters noted in the tribal key, Leptodirini have: head with or without occipital carina; 4th segment of maxillary palp shorter than 3rd, conical; postcoxal process of pronotum broad, blunt; tarsal empodium with 1 or 2 non-articulated setiform lobes; abdominal spiracle 8 atrophied; and parameres of aedeagus with basoventral lobes meeting ventrally.

DISTRIBUTION: Palearctic, w Nearctic, ?Venezuela.

COMMENTS:

As Silfverberg (1990) and Newton & Thayer (1992) noted, the correct name for this group is Leptodirini, not Bathysciini. This is by far the largest unit of Leiodidae, with about half of the named genera, and is easily the most intensively studied group of the family. Jeannel (especially 1911a, 1924,

1955a) established the foundation of the present classification, using male genitalia and other characters in an effort to determine phylogenetic relationships often obscured by the high degree of adaptive modifications to cave existence shown by many species. Guéorguiev (1974a, 1974b, 1976) formalized Jeannel's elaborate system of mostly informal groups into a system of subtribes. However, Laneyrie (1967, 1970, 1974) extended some of Jeannel's later (e.g., 1955a) ideas into a novel and somewhat discordant classification that has led to continuing controversy over the classification and phylogeny of this group. For further comment, see especially Casale et al. (1991a), Dupré (1992), Giachino & Etonti (1995), Laneyrie (1978, 1979), Perreau (1989), Pretner (1970), Racovitza (1974), and especially the contribution of Giachino et al. (1998) in this volume. As Perreau (1989) noted, the lack of concordance in many seemingly good characters that have been used demonstrates the need for more and better characters before any resolution of the course of evolution in this enormous group is likely.

In spite of the undoubtedly artificial features of the classification of Guéorguiev (1976), I have decided to use a modification of his classification here, because (1) it is a formal classification, using family-group names instead of informal terms for generic groups; (2) all genera known to that time were placed in it; (3) his identification key is simple, and allows genera not known to him to be placed in the classification rather easily. In contrast, a classification proposed by Casale et al. (1991a) and Giachino et al. (1998) is possibly more natural, but formal groups are not used, and not all genera have been assigned to groups; an identification key supplied by these authors is given as an alternative below. To aid correlation of the classification of Guéorguiev as modified here with that of Jeannel (1924), Casale et al. (1991a) and Giachino et al. (1998), alternative informal terms are given in square brackets under formal subtribal names at the head of each subtribe below.

The classification used here is modified from that of Guéorguiev (1976) by addition of the subtribe Platycholeina (which has generally been ignored in that and other recent European classifications); merging of Ghidiniina with Pholeuina (see Vailati, 1988); and considering all subtribes as belonging to one tribe, Leptodirini. The various subtribes have usually been divided between two tribes of one subfamily: Antroherponini with a few highly specialized genera in two subtribes (Antroherponina and Spelaeobatina), and Leptodirini (formerly Bathysciini) with the remaining subtribes. Recently (e.g., Casale et al., 1991a) the antroherponine subtribes have been associated with different subtribes of Leptodirini, which includes most of the diversity of the group, including the five genera found outside the western Palearctic region (*Sciaphyes*, *Coreobathyscia*, and *Fusi* of eastern Asia; *Platycholeus* of western North America; and *Neotropospeonella* supposedly from Venezuela). Certainly, the classification into seven subtribes here is in need of serious revision. Pholeuina, in particular, is based on plesiomorphic cha-

racter states and is very likely to be paraphyletic with respect to the remaining subtribes with the exception of Platycholeina, which is perhaps the most doubtfully included group. *Platycholeus* species have fully developed hind wings (contrary to Jeannel, 1922b) and have better-developed eyes than any of the other genera, most of which are blind and all of which have the hind wings greatly reduced or absent according to Jeannel and later authors. However, *Platycholeus* does have virtually all derived characters that have been identified for Leptodirini, and is likely to be a relict basal member of this group as Jeannel (1922b, 1924) supposed, rather than unrelated to it.

The genus *Neotropospeonella* Pace (1985, 1987) from Venezuela, far outside the range of this group, resembles "typical" European cave leptodirines in structure, and in my opinion is likely to be based on mislabeled European specimens; geographic confirmation and collection of males are needed before much can be made of this discovery. This genus is listed below as "Leptodirini *incertae sedis*". In contrast, the Siberian genus *Perkovskius* Lafer (1989), originally placed with doubt in Leptodirini, does not belong here and is moved to Leiodinae: Pseudoliodini (see above).

A majority of leptodirine species are restricted to caves, and form one of the largest and most dramatic radiations of cave-adapted beetles. Some genera, such as *Leptodirus* and *Antroherpon*, are among the most highly specialized of all cavernicolous insects. Many species of the least modified genera of the tribe are found in forest litter or soil, which is presumably the ancestral habitat and preadaptive to cave entry. The winged, enigmatic genus *Platycholeus* is also unusual in distribution (the only confirmed New World genus of an otherwise Palearctic group) and habitat (all species associated with decaying conifer logs, including *P. leptinoides* (Crotch) with log-nesting termites of the genus *Zootermopsis*, *P. opacellus* Fall with log-nesting ants of the genus *Lasius*, and an undescribed species that is freeliving under bark; personal observations). Reviews of the extensive literature on the evolution and biology of Palearctic Leptodirini are given by Deleurance-Glaçon (1963), Laneyrie (1967), Racovitza (1974, 1980) and Guéorguiev (1976); see also Casale et al. (1991a), Giachino et al. (1998), Crouau-Roy (1987), and Sbordoni et al. (1982).

Larvae: Capra (1924), Casale (1975b), Casale et al. (1990), Cerruti (1955), Corbière-Tichané (1967, 1973b), Decu & Juberthie (1969), Deleurance-Glaçon (1963), Franciscolo (1956), Rossi (1976), Sendra et al. (1987). Examined: *Platycholeus* n. sp. (USA: Washington).

Key to subtribes of Leptodirini

(Modified from Guéorguiev, 1976 and Giachino et al., 1998; excludes *Neotropospeonella*, listed below as incertae sedis)

1. Wings and eyes present; tarsungulus with a single large setiform projection, thus apparently "unisetose"; spermatheca not sclerotized; tergite of male genital segment short but free, well sclerotized and with large median impression; basal lobe of aedeagal parameres reduced to a thin strap; western Nearctic ..... Platycholeina

Wings extremely reduced or absent, eyes usually absent (present but small, e.g., in *Adelopsella*); spermatheca sclerotized at least at each end; tarsungulus usually with a split setiform projection, thus apparently "bisetose"; tergite of male genital segment short and usually fused to pleurites to form a ring (tergite free in *Adelopsella, Sciaphyes*), lightly sclerotized and without median impression; basal lobe of aedeagal parameres usually a well-developed lamina; Palearctic 2

2(1). Antennae inserted on the middle third of the head length (including labrum and neck); tarsal claws normal, long and slender 3
Antennae inserted on the posterior third of the head length (including labrum and neck); tarsal claws rather wide, ventral surface concave 6

3(2). Male protarsi 5-segmented 4
Male protarsi 4-segmented 5

4(3). Protibia without an externo-apical comb of short spines, but with at least one well-developed external spine near apex; meso- and metatibiae armed with well-developed external spines, usually without periapical combs ..... .Pholeuina
Protibia without large external spines, but usually with an externo-apical comb of short spines; meso- and metatibiae without external spines, usually with periapical combs .... .Leptodirina

5(3). Protibia without an externo-apical comb of short spines, but with 2-3 well-developed external spines near apex; meso- and metatibiae without periapical combs, but armed with well-developed external spines ..... .Bathysciina
Protibia without large external spines, but with an externo-apical comb of short spines; meso- and metatibiae with periapical combs ..... .Bathysciotina

6(2). Male protarsi 5-segmented; mesosternum not carinate ..... .Antroherponina
Male protarsi 4-segmented; mesosternum more or less carinate ..... .Spelaeobatina

ALTERNATIVE KEY TO SUBTRIBES OR GENERIC GROUPS OF LEPTODIRINI

(Provided by Giachino et al. (1998); referenced to generic groups of Casale et al. (1991a)

1. Inner sac of aedeagus with a basal, dorsal flagellum. Male protarsi 5-segmented .....
..... .Supraflagellates (= Pholeuina, pars auctorum)
Inner sac of aedeagus with a basal, Y-shaped ventral piece.(Infraflagellates) 2

2(1). Male protarsi 5-segmented .....
..... .Infraflagellates, pars (=Pholeuina, pars + Leptodirina + Antroherponina, auctorum)
Male protarsi 4-segmented (Teleomorphes) 3

3(2). Aedeagus of large size ..... .Teleomorphes, pars (= Bathysciina, pars, auctorum)
Aedeagus of very reduced size .....
..... .Teleomorphes, pars (=Bathysciina, pars + Spealaeobatina auctorum)

GENERIC CATALOG:

Platycholeina Horn, 1880

[=Division I (in part) of Jeannel, 1924]

Platycholei Horn, 1880: 254. Type genus: *Platycholeus* Horn, 1880.

Platycholeus Horn [Tc, Sc] w Nearctic (2 spp.)

Platycholeus Horn, 1880: 254. Type sp.: *Ptomaphagus leptinoides* Crotch, 1874 (monotypy). Note: as genus *incertae sedis*, Guéorguiev (1976); 1 new sp. seen, BC-OR, genus under review by Newton.

Pholeuina Reitter, 1886 (=Pholeuonina)

[=Division I (Euryscapes) + Division IV (Brachyscapes in part) of Jeannel, 1924]

Pholeuones Reitter, 1886b: 314 (incorrect original spelling). Type genus: *Pholeuon* Hampe, 1856. Note: type genus is senior homonym of *Pholeuon* L. Koch, 1873 (Araneae).
Ghidiniina Guéorguiev, 1974a: 841. Type genus: *Ghidinia* Pavan, 1938 (not cited). Note: synonymized by Vailati (1988)
Pholeuonina Guéorguiev, 1974a: 841 (as new subtribe; incorrect original spelling). Type genus: *Pholeuon* Hampe, 1856 (not cited).

Adelopsella Jeannel [Tc] — Croatia, Bosnia, Montenegro (1 sp.)
Adelopsella Jeannel, 1908b: 182. Type sp.: *Bathyscia bosnica* Reitter, 1884 (monotypy).

Albaniola Jeannel — Albania, n Greece, Macedonia (Yugoslavia) (12 spp.)
Albaniola Jeannel, 1924: 43. Type sp.: *Bathyscia merditana* Apfelbeck, 1907 (orig. des.).

Anillochlamys Jeannel — Spain (9 spp.)
Anillochlamys Jeannel, 1909b: 471. Type sp.: *Bathyscia tropica* Abeille, 1881 (orig. des.).
Anillochlamys s. str. — Spain (Alicante, Castellón, Valencia) (6 spp.)
Paranillochlamys Zariquiey — Spain (Tarragona) (3 spp.)
Paranillochlamys Zariquiey, 1940: 529. Type sp.: *Paranillochlamys velox* Zariquiey, 1940 (monotypy). Note: as probable syn., Guéorguiev (1976); as subgenus, Bellés (1987).

Antrocharidius Jeannel — Spain (Tarragona) (1 sp.)
Antrocharidius Jeannel, 1910c: 283. Type sp.: *Antrocharidius orcinus* Jeannel, 1910 (monotypy).

Antrocharis Abeille [Tc] — France (Ariège) (1 sp.)
Antrocharis Abeille, 1878: 149 (new name for *Antrodietus* Abeille [as *Antrodictus*] (unnecessary, see Appendix B)).
Antrodietus Abeille, 1876: 29 (NOT preoccupied by *Antrodiaetus* Ausserer 1871). Type sp.: *Leptoderus querilhaci* Lespès, 1857 (des. Jeannel 1910a:11). Note: spelled *Antrodioetus*, Laneyrie (1967); NOT preoccupied (nor is *Antrodictus*, cited 1878).
Antrodictus; Abeille, 1878: 151 (misspelling of *Antrodietus*).

Aranzadiella Español — Spain (Guipúzcoa) (1 sp.)
Aranzadiella Español, 1972: 60. Type sp.: *Aranzadiella leizaolai* Español, 1972 (orig. des.).

Archeoboldoria Ghidini — Italy (Piemonte) (1 sp.)
Archeoboldoria Ghidini, 1938: 69. Type sp.: *Bathysciola doderona* Jeannel, 1924 (orig. des.). Note: spelled *Archaeoboldoria*, Laneyrie (1967:619); revised by Vailati (1988), elevated from subgenus of *Boldoria*.

Atticiella Coiffait — Greece (Attica) (1 sp.)
Atticiella Coiffait, 1955b: 208. Type sp.: *Atticiella lindbergi* Coiffait, 1955 (orig. des.).

Banatiola Decu — Romania (Banat) (1 sp.)
Banatiola Decu, 1967: 434. Type sp.: *Banatiola vandeli* Decu, 1967 (orig. des.). Note: as *Banatolia* in Neave (1939-40) supplement.

Bathysciella Jeannel — France (Pyrénées-Atlantiques) (1 sp.)
Bathysciella Jeannel, 1906: 23. Type sp.: *Bathyscia jeanneli* Abeille, 1904 (monotypy).

Bathysciola Jeannel [Sc] — sw Palearctic (s Europe to Caucasus, Israel) (79 spp.)
Bathysciola Jeannel, 1910a: 9 (see Appendix B). Type sp.: *Bathyscia aubei* Kiesenwetter, 1850 (orig. des.). Note: *Catopsinus* has priority.

Catopsinus Motschulsky, 1870a: 58. Type sp.: *Catops pusillus* Motschulsky, 1840 (monotypy). Note: as "nom. nud." in Jeannel (1911a), etc., but published in list with valid species.
Salfia Tamanini, 1955: 4. Type sp.: *Bathysciola ruffoi* Tamanini, 1955 (orig. des.). Note: as syn., not subgenus, Angelini et al. (1995), Zoia (1998).

Bellesia Fresneda & Hernando — Spain (Huesca) (1 sp.)
Bellesia Fresneda & Hernando, 1994: 57. Type sp.: *Speonomus espanyoli* Auroux & Bellés, 1974 (orig. des.).

Beronia Guéorguiev — Bulgaria (1 sp.)
Beronia Guéorguiev, 1960a: 607. Type sp.: *Beronia micevi* Guéorguiev, 1960 (orig. des.). Note: placement?, females only.

Besuchetiola Rampini & Zoia — ne Turkey (1 sp.)
Besuchetiola Rampini & Zoia, 1991: 795. Type sp.: *Besuchetiola priapus* Rampini & Zoia, 1991 (orig. des.).

Bithyniella Jeannel — nw Turkey (2 spp.)
Bithyniella Jeannel, 1955c: 117 (as subgenus of *Bathysciola*). Type sp.: *Bathysciola strinatii* Jeannel, 1955 (monotypy). Note: elevated from subgenus of *Bathysciola*, Rampini & Zoia (1991).
Bithynella; Guéorguiev, 1976: 106 (misspelling of *Bithyniella*).
Parabithyniella Rampini & Zoia, 1991: 792. Type sp.: *Parabithyniella viti* Rampini & Zoia, 1991 (orig. des.). Note: syn. Rampini & Zoia (1993).

Boldoria Jeannel — n Italy (16 spp.)
Boldoria Jeannel, 1924: 117 (as subgenus of *Bathysciola*). Type sp.: *Bathysciola aculeata* Jeannel, 1924 (orig. des.). Note: revised by Vailati (1988).
Hartigia Müller, 1928: 188 (as subgenus of *Bathysciola*; preoccupied, not Schiödte 1838, Robineau-Desvoidy 1863, Rondani 1871). Type sp.: *Bathysciola baldensis* Müller, 1928 (orig. des.).
Hartigiella Müller, 1935: 62 (new name for *Hartigia* Müller). Note: type species moved to *Boldoria* by Vailati (1988).
Ghidinia Pavan, 1939: 106. Type sp.: *Ghidinia morettii* Pavan, 1939 (monotypy). Note: revised, syn. with *Boldoria* by Vailati (1988).

Breuilia Jeannel — Spain (Asturias, Cantabria) (1 sp.)
Breuilia Jeannel, 1909b: 467. Type sp.: *Adelops triangulum* Sharp, 1872 (orig. des.).

Breuilites Salgado — Spain (Asturias) (1 sp.)
Breuilites Salgado, 1980: 158. Type sp.: *Breuilites eloyi* Salgado, 1980 (orig. des.).

Bureschiana Guéorguiev — Bulgaria (Rhodopes), Greece (Thrace) (3 spp.)
Bureschiana Guéorguiev, 1963: 391. Type sp.: *Bureschiana drenskii* Guéorguiev, 1963 (orig. des.).

Canavesiella Giachino — Italy (Piemonte) (2 spp.)
Canavesiella Giachino, 1993: 349. Type sp.: *Canavesiella lanai* Giachino, 1993 (orig. des.).

Capraiola Zoia & Rampini — n Iran (1 sp.)
Capraiola Zoia & Rampini, 1994: 790. Type sp.: *Capraiola orientalis* Zoia & Rampini, 1994 (orig. des.).

Cavazzutiella Casale & Giachino — sw Turkey (1 sp.)
Cavazzutiella Casale & Giachino, 1985: 221. Type sp.: *Cavazzutiella taurica* Casale & Giachino, 1985 (orig. des.).

Ceuthophyes Jeannel [Tc] Albania, Macedonia (Yugoslavia) (4 spp.)
Ceuthophyes Jeannel, 1924: 43. Type sp.: *Ceuthophyes karamani* Jeannel, 1924 (orig. des.).
Ceutophyes; Laneyrie, 1967: 592,608 (misspelling of *Ceuthophyes*). Note: misspelling used also by Pretner (1968).

Closania Jeannel Romania (2 spp.)
Closania Jeannel, 1928a: 272. Type sp.: *Closania winkleri* Jeannel, 1928 (monotypy).

Coiffaitiola Jeannel Turkey (1 sp.)
Coiffaitiola Jeannel, 1955b: 3. Type sp.: *Coiffaitiola rudis* Jeannel, 1955 (orig. des.).

Coreobathyscia Szymczakowski Korea (1 sp.)
Coreobathyscia Szymczakowski, 1975: 464. Type sp.: *Coreobathyscia solivaga* Szymczakowski, 1975 (orig. des.). Note: placement in Pholeuina here based on original description, requires confirmation.

Cryptobathyscia Vailati Italy (Lombardia) (1 sp.)
Cryptobathyscia Vailati, 1980: 58. Type sp.: *Cryptobathyscia gavardensis* Vailati, 1980 (orig. des.). Note: revised by Vailati (1988).

Cytodromus Abeille France (Drôme, Isère) (3 spp.)
Cytodromus Abeille, 1876: 30. Type sp.: *Pholeuon dapsoides* Abeille, 1875 (monotypy).

Dalmatiola Jeannel Croatia (Korcula Island) (1 sp.)
Dalmatiola Jeannel, 1924: 42. Type sp.: *Bathyscia curzolensis* Ganglbauer, 1902 (orig. des.).

Dellabeffaella Capra n Italy (2 spp.)
Dellabeffaella Capra, 1924: 154 (as *Della Beffaella*). Type sp.: *Royerella roccae* Capra, 1924 (monotypy). Note: elevated from subgenus of *Royerella* and revised by Vailati (1988).

Diaprysius Abeille France (Ardèche, Gard, Hérault) (10 spp.)
Diaprysius Abeille, 1878: 149 (as subgenus of *Antrocharis*). Type sp.: *Pholeuon caudatum* Abeille, 1875 (des. Jeannel 1910a:9).
Ardecheus Reitter, 1908: 115. Type sp.: *Diaprysius serullazi* Peyerimhoff, 1904 (monotypy).

Drimeotus Miller [Tc] Romania (w Carpathians) (14 spp.)
Drimeotus Miller, 1856b: 635. Type sp.: *Drimeotus kovacsii* Miller, 1856 (monotypy).
Bihorites Jeannel Romania (Bihar mts.) (3 spp.)
Bihorites Jeannel, 1923: 442. Type sp.: *Drimeotus laevimarginatus* Moczarski, 1912 (orig. des.).
Drimeotinus Jeannel Romania (Transylvania, Turda-Aries) (2 spp.)
Drimeotinus Jeannel, 1923: 439. Type sp.: *Drimeotus ormayi* Reitter, 1889 (orig. des.).
Drimeotus s. str. [Tc] Romania (Bihar mts., Bihor) (7 spp.)
Fericeus Reitter Romania (Bihar mts.) (1 sp.)
Fericeus Reitter, 1884: 13. Type sp.: *Drimeotus kraatzi* Frivaldszky & Frivaldszky, 1857 (monotypy).
Trichopharis Knirsch Romania (Bihar mts.) (1 sp.)
Trichopharis Knirsch, 1925a: 43. Type sp.: *Drimeotus blidarius* Knirsch, 1925 (monotypy). Note: spelled *Trichophanis*, Laneyrie (1967:616).

Eskualdunella Coiffait France (Pyrénées-Atlantiques) (1 sp.)
Eskualdunella Coiffait, 1950: 65. Type sp.: *Eskualdunella delespierrei* Coiffait, 1950 (orig. des.).

Espanoliella Guéorguiev Spain (Cantabria, Vizcaya) (4 spp.)
Espanoliella Guéorguiev, 1976: 126. Type sp.: *Breuilia tibialis* Jeannel, 1909 (orig. des.). Note: revised by Salgado (1994).

Euryspeonomus Jeannel — Spain (Guipúzcoa, Navarra) (5 spp.)
Euryspeonomus Jeannel, 1919: 134 (as subgenus of *Speonomus*). Type sp.: *Speonomus breuili* Jeannel, 1919 (orig. des.). Note: elevated from subgenus of *Speonomus,* Bellés et al. (1978).
Euryspeonomus s. str. — Spain (Guipúzcoa, Navarra) (3 spp.)
Urbasolus Español — Spain (Guipúzcoa, Navarra) (2 spp.)
Urbasolus Español, 1948: 238 (as subgenus of *Speonomus*). Type sp.: *Speonomus eloseguii* Español, 1948 (orig. des.). Note: to subgenus of *Euryspeonomus,* Bellés et al. (1978).

Fusi Perkovsky — Russia (e Siberia) (1 sp.)
Fusi Perkovsky, 1989b: 139. Type sp.: *Fusi nyujwa* Perkovsky, 1989 (orig. des.). Note: priority over *Fuxi*, published 23 November 1989, teste Perkovsky (*in litteris* 1996); placement in Pholeuina here based on original description, requires confirmation.
Fuxi Lafer, 1989: 318 (attributed to Perkovsky). Type sp.: *Fuxi njuywa* Lafer, 1989 (attributed to Perkovsky) (monotypy). Note: published 19 December 1989, teste Perkovsky (*in litteris* 1996).

Gesciella Giachino & Guéorguiev — France (Ariège) (1 sp.)
Gesciella Giachino & Guéorguiev, 1989: 403. Type sp.: *Gesciella delioti* Giachino & Guéorguiev, 1989 (orig. des.).

Hoffmannella Müller — Croatia (Dalmatia) (1 sp.)
Hoffmannella Müller, 1912: 300 (as subgenus of *Bathyscia*). Type sp.: *Bathyscia makarensis* Müller, 1912 (orig. des.).

Hussonella Jeannel — Greece (Macedonia), Macedonia (Yugoslavia) (2 spp.)
Hussonella Jeannel, 1934c: 95. Type sp.: *Hussonella remyi* Jeannel, 1934 (orig. des.).
Babuniella Karaman — Macedonia (Yugoslavia) (1 sp.)
Babuniella Karaman, 1954: 70. Type sp.: *Hussonella ovata* Karaman, 1954 (monotypy).
Hussonella s. str. — Greece (Macedonia) (1 sp.)

Insubriella Vailati — Italy (Lombardia) (1 sp.)
Insubriella Vailati, 1990: 214. Type sp.: *Insubriella paradoxa* Vailati, 1990 (orig. des.).

Iranobathyscia Zoia & Rampin — n Iran (1 sp.)
Iranobathyscia Zoia & Rampini, 1994: 786. Type sp.: *Iranobathyscia jeanneli* Zoia & Rampini, 1994 (orig. des.).

Isereus Reitter — France (Alpes-Maritimes, Isère) (4 spp.)
Isereus Reitter, 1886a: 100. Type sp.: *Trocharanis xambeui* Argod, 1885 (monotypy).

Josettekia Bellés & Deliot — Spain (Navarra) (1 sp.)
Josettekia Bellés & Deliot, 1983: 237. Type sp.: *Josettekia angelinae* Bellés & Deliot, 1983 (orig. des.).

Karadeniziella Casale & Giachino — Turkey (1 sp.)
Karadeniziella Casale & Giachino, 1989: 170. Type sp.: *Karadeniziella omodeoi* Casale & Giachino, 1989 (orig. des.).

Kobiella Español & Bellés — Spain (Guipúzcoa) (1 sp.)
Kobiella Español & Bellés, 1980: 33. Type sp.: *Speocharidius galani* Español, 1970 (orig. des.).

Magdelainella Jeannel — Bosnia, Serbia, Albania (5 spp.)
Magdelainella Jeannel, 1924: 73. Type sp.: *Bathyscia serbica* Müller, 1904 (orig. des.).

Knirschiella Guéorguiev — Albania (1 sp.)
Knirschiella Guéorguiev, 1976: 127. Type sp.: *Bathysciola ravasinii* Müller, 1922 (orig. des.).
Magdelainella s. str. — Bosnia, Serbia (4 spp.)

Maroniella Casale & Giachino — ne Greece (1 sp.)
Maroniella Casale & Giachino, 1985: 226. Type sp.: *Maroniella beroni* Casale & Giachino, 1985 (orig. des.).

Mehadiella Csiki — Romania (Banat) (1 sp.)
Mehadiella Csiki, 1899: 247 (new name for *Frivaldszkya* Ganglbauer (unnecessary, see Appendix B).
Frivaldszkya Ganglbauer, 1899: 100 (NOT preoccupied by *Frivaldskia* Schiner, 1861). Type sp.: *Adelops paveli* Frivaldszky, 1880 (monotypy).

Monguzziella Vailati — ne Italy (1 sp.)
Monguzziella Vailati, 1993: 262. Type sp.: *Monguzziella grottoloi* Vailati, 1993 (orig. des.).

Muelleriella Jeannel — Greece, Crete (5 spp.)
Muelleriella Jeannel, 1924: 39 (as *Mülleriella*). Type sp.: *Bathyscia kerkyrana* Reitter, 1884 (orig. des.).

Notidocharis Jeannel — Spain (Asturias, Burgos, Cantabria, León) (7 spp.)
Notidocharis Jeannel, 1956a: 5. Type sp.: *Adelops uhagoni* Sharp, 1872 (orig. des.). Note: revised by Giachino & Salgado (1989).

Ochridiola Sbordoni — Macedonia (Yugoslavia) (1 sp.)
Ochridiola Sbordoni, 1971: 29. Type sp.: *Ochridiola marinae* Sbordoni, 1971 (orig. des.).

Oresigenus Jeannel — Spain (Asturias) (1 sp.)
Oresigenus Jeannel, 1948a: 73. Type sp.: *Oresigenus jaspei* Jeannel, 1948 (monotypy). Note: to subgenus of *Speocharis*, Bellés et al. (1978), but as genus, Salgado (*in litteris* 1996), etc.

Ovobathysciola Jeannel — Sardinia (3 spp.)
Ovobathysciola Jeannel, 1924: 118 (as subgenus of *Bathysciola*). Type sp.: *Bathyscia majori* Reitter, 1884 (orig. des.).

Pangaeoniola Etonti & Etonti — Greece (Macedonia) (1 sp.)
Pangaeoniola Etonti & Etonti, 1985: 31. Type sp.: *Pangaeoniola casalei* Etonti & Etonti, 1985 (orig. des.).

Parabathyscia Jeannel — Italy, France, Corsica, s England (33 spp.)
Parabathyscia Jeannel, 1908a: 308 (as subgenus of Bathyscia). Type sp.: *Bathyscia spagnoloi* Fairmaire, 1882 (des. Jeannel 1910a:9).
Ligurobathyscia Zoia — Italy (Liguria) (1 sp.)
Ligurobathyscia Zoia, 1986: 333. Type sp.: *Parabathyscia brigantii* Zoia, 1980 (orig. des.).
Parabathyscia s. str. — Italy, France, Corsica, s England (32 spp.)
Platybathyscia Capra, 1920: 11 (as subgenus of *Bathysciola*). Type sp.: *Bathyscia grouvellei* Abeille, 1882 (orig. des.). Note: syn. with subgenus *Parabathyscia,* Zoia (1986).

Paraspeonomus Coiffait — France (Ariège) (1 sp.)
Paraspeonomus Coiffait, 1952: 41. Type sp.: *Paraspeonomus vandeli* Coiffait, 1952 (orig. des.).

Paratroglophyes Fourès — France (Ariège) (2 spp.)
Paratroglophyes Fourès, 1954: 5. Type sp.: *Paratroglophyes carrerei* Fourès, 1954 (orig. des.). Note: author as "Coiffait, 1954" in Laneyrie, (1967), Guéorguiev (1976); used by Coiffait (1955a:108) but attributed to Fourès.

Patriziella Jeannel — Sardinia (2 spp.)
Patriziella Jeannel, 1956b: 106. Type sp.: *Patriziella sardoa* Jeannel, 1956 (orig. des.).

Perriniella Jeannel — Spain (Gerona) (2 spp.)
Perriniella Jeannel, 1910b: clxi. Type sp.: *Perriniella faurai* Jeannel, 1910 (orig. des.).

Phacomorphus Jeannel — France (Pyrénées-Atlantiques), Spain (Navarra) (10 spp.)
Phacomorphus Jeannel, 1908c: 60 (as subgenus of *Speonomus*). Type sp.: *Bathyscia mascarauxi* Sainte-Claire-Deville, 1905 (monotypy). Note: as genus (Laneyrie, 1967; Guéorguiev, 1976; etc.) or as subgenus of *Speonomus* (Laneyrie, 1988; Dupré, 1989; etc.).
Phacomorphoides Dupré — France (Pyrénées-Atlantiques) (3 spp.)
Phacomorphoïdes Dupré, 1996: 13 (as subgenus of *Speonomus*; validation of *Phacomorphoides* Dupré 1989 by designation of type species). Type sp.: *Bathyscia alexinae* Jeannel (orig. des.).
Phacomorphoides Dupré, 1989: 85 (as subgenus of *Speonomus*; nomen nudum, no type species designated).
Phacomorphus s. str. — France (Pyrénées-Atlantiques), Spain (Navarra) (7 spp.)

Pholeuon Hampe [Sc] — Romania (w Carpathians) (7 spp.)
Pholeuon Hampe, 1856: 463 (as *Poleuon*, emended on basis of evidence in original publication [derivation, abbreviation]; not *Pholeuon* Koch, 1873). Type sp.: *Pholeuon angusticolle* Hampe, 1856 (monotypy).
Parapholeuon Ganglbauer — Romania (Bihar mts., Bihor) (2 spp.)
Parapholeuon Ganglbauer, 1887: 95. Type sp.: *Pholeuon gracile* Frivaldszky, 1861 (monotypy).
Pholeuon s. str. [Sc] — Romania (Bihar & Apuseni mts.) (5 spp.)
Apropeus Reitter, 1884: 13. Type sp.: *Pholeuon leptodirum* Frivaldszky & Frivaldszky, 1857 (monotypy). Note: spelled *Apropus*, Laneyrie (1967:616).
Irenellum Csiki, 1911: 106. Type sp.: *Pholeuon mihoki* Csiki, 1911 (=*P. angusticolle* Hampe, 1856, ssp.) (monotypy).

Protopholeuon Jeannel — Romania (Bihar mts.) (1 sp.)
Protopholeuon Jeannel, 1923: 452. Type sp.: *Pholeuon hungaricum* Csiki, 1904 (monotypy).

Pseudoboldoria Ghidini — Italy (Lombardia) (14 spp.)
Pseudoboldoria Ghidini, 1938: 63. Type sp.: *Bathyscia kruegeri* Müller, 1914 (orig. des.). Note: elevated from subgenus of *Boldoria* and revised by Vailati (1988).

Pseudochlamys Comas — Spain (Gerona) (1 sp.)
Pseudochlamys Comas, 1977: 136. Type sp.: *Anillochlamys raholai* Zariquiey, 1922 (orig. des.). Note: also as subgenus of *Anillochlamys* (Salgado *in litteris*, 1996).

Purkynella Knirsch — Macedonia (Yugoslavia) (1 sp.)
Purkynella Knirsch, 1926: 59 (as *Purkyně̈lla;* also spelled *Purkyně̈la*). Type sp.: *Purkynella rambouseki* Knirsch, 1926 (orig. des.). Note: spelling *-ella* 2x, *-ela* 1x; Neave (1939-40) as *-ela*.

Quaestus Schaufuss — n Spain (38 spp.)
Quaestus Schaufuss, 1861: 424 (unjustified rejection by Jeannel (1909b:464); see Appendix B). Type sp.: *Quaestus arcanus* Schaufuss, 1861 (des. Jeannel 1924:53). Note: as "gen.

fals.", Jeannel (1924:53), in error; resurrected as valid name, Perreau (1993); *Q. bergidi* to new genus, Salgado (*in litteris* 1996).

Quaestus s. str. Note: resurrected as valid name, Perreau (1993). n Spain (34 spp.)

Quaesticulus Schaufuss, 1861: 426 (unjustified rejection by Jeannel (1909b:464)). Type sp.: *Quaesticulus adnexus* Schaufuss, 1861 (monotypy). Note: as "gen. fals.", Jeannel (1924:53), in error.

Speocharis Jeannel, 1909b: 463. Type sp.: *Quaestus arcanus* Schaufuss, 1861 (orig. des.).

Sajadytes Salgado Spain (Cantabria) (1 sp.)

Sajadytes Salgado, 1992a: 101. Type sp.: *Speocharis canis* Salgado, 1992 (orig. des.).

Speogeus Salgado Spain (Asturias) (3 spp.)

Speogeus Salgado, 1985: 262. Type sp.: *Speocharis avicularis* Salgado, 1985 (orig. des.).

Radevia Knirsch Bulgaria (1 sp.)

Radevia Knirsch, 1925b: 60. Type sp.: *Radevia hanusi* Knirsch, 1925 (monotypy). Note: revised by Giachino & Guéorguiev (1996).

Rhodopiola Guéorguiev Bulgaria (Rhodopes) (1 sp.)

Rhodopiola Guéorguiev, 1960b: 721. Type sp.: *Rhodopiola cavicola* Guéorguiev, 1960 (monotypy).

Royerella Jeannel e France, Switzerland (4 spp.)

Royerella Jeannel, 1910a: 9. Type sp.: *Adelops tarissani* Bedel, 1878 (orig. des.). Note: subgenus *Dellabeffaella* elevated to genus, Vailati (1988).

Sbordoniola Zoia & Rampini n Iran (6 spp.)

Sbordoniola Zoia & Rampini, 1994: 794. Type sp.: *Bathyscia persica* Abeille, 1881 (orig. des.).

Sciaphyes Jeannel [Tc] Russia (e Siberia) (1 sp.)

Sciaphyes Jeannel, 1910a: 7. Type sp.: *Bathyscia sibirica* Reitter, 1887 (orig. des.).

Sengletiola Zoia & Rampini n Iran (1 sp.)

Sengletiola Zoia & Rampini, 1994: 782. Type sp.: *Sengletiola motschulskyi* Zoia & Rampini, 1994 (orig. des.).

Sophrochaeta Reitter [Tc] Romania (s Carpathians) (17 spp.)

Sophrochaeta Reitter, 1884: 17 (as subgenus of *Bathyscia*). Type sp.: *Adelops insignis* Frivaldszky, 1880 (des. Jeannel 1910a:20).

Cernella Jeannel Romania (s Carpathians) (1 sp.)

Cernella Jeannel, 1930a: 38. Type sp.: *Bathyscia reitteri* Frivaldszky, 1884 (monotypy).

Sophrochaeta s. str. [Tc] Romania (s Carpathians) (16 spp.)

Spelaeochlamys Dieck Spain (Alicante) (2 spp.)

Spelaeochlamys Dieck, 1870: 93. Type sp.: *Spelaeochlamys ehlersi* Dieck, 1870 (monotypy).

Speocharidius Jeannel Spain (Guipúzcoa) (3 spp.)

Speocharidius Jeannel, 1919: 130. Type sp.: *Speocharidius breuili* Jeannel, 1919 (orig. des.).

Speocharinus Español & Escolà Spain (Cantabria) (1 sp.)

Speocharinus Español & Escolà, 1977: 25 (as subgenus of *Speocharis*). Type sp.: *Speocharis llosesi* Español & Escolà, 1977 (monotypy). Note: to genus, Bellés et al. (1978).

Speodiaetus Jeannel France (Alpes-Maritimes, Bouches-du-Rhône, Var) (2 spp.)

Speodiaetus Jeannel, 1908a: 296. Type sp.: *Adelops galloprovincialis* Fairmaire, 1860 (monotypy).

Ochsiella Jeannel — France (Alpes-Maritimes) (1 sp.)
Ochsiella Jeannel, 1947: 2. Type sp.: *Bathyscia bucheti* Abeille, 1905 (monotypy). Note: spelled *Ochiella*, Guéorguiev (1976:107).
Speodiaetus s. str. — France (Bouches-du-Rhône, Var) (1 sp.)

Speonomus Jeannel [Sc] — s France, n Spain, Sardinia (75 spp.)
Speonomus Jeannel, 1908a: 299. Type sp.: *Adelops pyreneus* Lespès, 1857 (des. Jeannel, 1909a:510).
Batinoscelis Jeannel — Sardinia (3 spp.)
Batinoscelis Jeannel, 1924: 147. Type sp.: *Bathyscia lostiae* Dodero, 1904 (orig. des.).
Machaeroscelis Jeannel [Tc] — France (Ariège, Haute-Garonne) (2 spp.)
Machaeroscelis Jeannel, 1924: 148. Type sp.: *Adelops infernus* Dieck, 1869 (orig. des.).
Metaspeonomus Coiffait — France (Ariège) (1 sp.)
Metaspeonomus Coiffait, 1959: 175. Type sp.: *Speonomus alticola* Coiffait, 1959 (=*S. monticola* Coiffait, 1963) (orig. des.).
Naspunius Fresneda et al. — Spain (Huesca) (1 sp.)
Naspunius Fresneda *et al.*, 1994: 111. Type sp.: *Speonomus eseranus* Lagar, 1974 (orig. des.). Note: incl. type species only, based on details of internal sac.
Parvospeonomus Bellés & Escolà — s France, ne Spain (5 spp.)
Parvospeonomus Bellés & Escolà, 1977: 34. Type sp.: *Speonomus urgellesi* Español, 1964 (orig. des.).
Speonomidius Jeannel — Spain (Guipúzcoa, Navarra) (1 sp.)
Speonomidius Jeannel, 1924: 164. Type sp.: *Bathyscia mazarredoi* Uhagón, 1881 (=*S. crotchi* (Sharp, 1872), ssp.) (orig. des.).
Speonomites Jeannel — Spain (Lérida) (2 spp.)
Speonomites Jeannel, 1910b: cl. Type sp.: *Speonomites velox* Jeannel, 1910 (orig. des.).
Speonomus s. str. — s France, n Spain (60 spp.)

Tismanella Jeannel — Romania (Gorj) (2 spp.)
Tismanella Jeannel, 1928a: 271. Type sp.: *Tismanella chappuisi* Jeannel, 1928 (monotypy).

Trocharanis Reitter — France (Aude, Ariège) (1 sp.)
Trocharanis Reitter, 1884: 12. Type sp.: *Antrocharis mestrei* Abeille, 1878 (monotypy).

Troglocharinus Reitter — ne Spain (17 spp.)
Troglocharinus Reitter, 1908: 116 (as subgenus of *Troglophyes*). Type sp.: *Troglophyes ferreri* Reitter, 1908 (monotypy).
Speophilus Jeannel — ne Spain (10 spp.)
Speophilus Jeannel, 1911b: xciii (new name for *Perrinia* Reitter). Note: syn. Guéorguiev (1976); as subgenus, Bellés et al. (1978).
Perrinia Reitter, 1884: 16 (preoccupied, not Adams 1854). Type sp.: *Adelops kiesenwetteri* Dieck, 1869 (monotypy).
Trapezodirus Jeannel, 1924: 172 (as subgenus of *Speophilus*). Type sp.: *Speophilus carrodillae* Jeannel, 1911 (orig. des.). Note: syn. with subgenus *Speophilus*, Bellés et al. (1978).
Troglocharinus s. str. — ne Spain (7 spp.)

Troglodromus Sainte-Claire-Deville — France (Alpes-Maritimes, Var) (3 spp.)
Troglodromus Sainte-Claire-Deville, 1901: 59. Type sp.: *Cytodromus bucheti* Sainte-Claire-Deville, 1898 (des. Jeannel, 1910a:10).

Troglophyes Abeille — s France, ne Spain (7 spp.)
Troglophyes Abeille, 1894: xxvii. Type sp.: *Troglophyes gavoyi* Abeille, 1894 (orig. des.).

Ceretophyes [Anonymous] ne Spain (2 spp.)
Ceratophyes [Anonymous], 1990: 262 (as *Ceratophyes*; validation of *Ceretophyes* Comas & Escolà by designation of type species; see Appendix B). Type sp.: *Speophilus cenarroi* Español, 1955 (as *Troglophyes cenarroi*) (orig. des.). Note: Designation valid (ICZN 1985, Art. 69(a)vi).
Ceretophyes Comas & Escolà, 1989: 142 (nomen nudum, no type species designated).
Troglophyes s. str. s France (5 spp.)

Typhlochlamys Español Spain (Alicante) (2 spp.)
Typhlochlamys Español, 1975: 121. Type sp.: *Typhlochlamys bardisai* Español, 1975 (orig. des.).

Viallia Pavan Italy (Lombardia) (4 spp.)
Viallia Pavan, 1950: 55. Type sp.: *Viallia alfanoi* Pavan, 1950 (orig. des.). Note: revised and moved to Pholeuina, Vailati (1988).

Zariquieyella Jeannel Croatia (Dalmatia) (1 sp.)
Zariquieyella Jeannel, 1928b: 297 (new name for *Hoffmannia* Knirsch).
Hoffmannia Knirsch, 1928: 101 (preoccupied, not Gemmellaro, 1888). Type sp.: *Hoffmannia biokovensis* Knirsch, 1928 (orig. des.).

Leptodirina Lacordaire, 1854 (1849)

[=Division V (Brachyscapes in part) of Jeannel, 1924]

Stagobiinae Schiödte, 1849: 16 (replaced, Art. 40b). Type genus: *Stagobius* Schiödte, 1847 (=*Leptodirus* Schmidt, 1832).

Adelopidius Apfelbeck Bosnia (7 spp.)
Adelopidius Apfelbeck, 1907a: 305; 1907b: 320. Type sp.: *Pholeuonopsis sequensi* Reitter, 1902 (monotypy).

Antrosedes Reitter Bosnia, Herzegovina (2 spp.)
Antrosedes Reitter, 1912a: 326. Type sp.: *Antrosedes speluncarius* Reitter, 1912 (monotypy).

Apholeuonus Reitter [Sc] Bosnia, Herzegovina (5 spp.)
Apholeuonus Reitter, 1889: 297. Type sp.: *Hexaurus nudus* Apfelbeck, 1889 (monotypy). Note: revised by Giachino & Guéorguiev (1995).

Astagobius Reitter [Tc] Slovenia, Croatia (2 spp.)
Astagobius Reitter, 1886b: 315 (no species listed). Type sp.: *Leptoderus angustatus* Schmidt, 1852 (subsequent monotypy by Ganglbauer, 1899:83).

Balcanobius Guéorguiev Bulgaria (1 sp.)
Balcanobius Guéorguiev, 1965: 393. Type sp.: *Balcanobius etropolensis* Guéorguiev, 1965 (orig. des.).

Bathyscimorphus Jeannel Slovenia, Croatia (4 spp.)
Bathyscimorphus Jeannel, 1910a: 21. Type sp.: *Bathyscia byssina* Schiödte, 1847 (orig. des.). Note: 5 spp. teste Zoia (1998), but no reference for *B. sagarum* Pretner or Jeannel?.

Bathysciopsis Müller Bosnia (1 sp.)
Bathysciopsis Müller, 1941: 213. Type sp.: *Bathysciopsis sternalis* Müller, 1941 (monotypy).

Beroniella Giachino & Guéorguiev — Bulgaria (1 sp.)
Beroniella Giachino & Guéorguiev, 1991: 193. Type sp.: *Beroniella tetevensis* Giachino & Guéorguiev, 1991 (orig. des.). Note: implied placement in Leptodirina.

Beskovia Guéorguiev — Bulgaria (1 sp.)
Beskovia Guéorguiev, 1960b: 723 (as *Beškovia*). Type sp.: *Beskovia bulgarica* Guéorguiev, 1960 (monotypy). Note: reviewed by Giachino & Guéorguiev (1996).

Bulgariella Karaman — Bulgaria (1 sp.)
Bulgariella Karaman, 1958: 225. Type sp.: *Bulgariella tranteevi* Karaman, 1958 (monotypy). Note: published 10 March 1958; given priority by Laneyrie (1967).
Tranteeviella Pretner, 1958: 59. Type sp.: *Tranteeviella bulgarica* Pretner, 1958 (=*B. tranteevi* Karaman, 1958) (monotypy). Note: published 23 May 1958; given priority by Guéorguiev (1976).

Ceuthmonocharis Jeannel [Tc] — Italy (Como), Slovenia (7 spp.)
Ceuthmonocharis Jeannel, 1914a: 68 (new name for *Hohenwartia* Jeannel (unnecessary, see Appendix B)).
Ceuthmonocharis s. str. [Tc] — Italy (Como), Slovenia (6 spp.)
Hohenwartia Jeannel, 1910a: 21 (NOT preoccupied by *Hohenwarthia* Letourneux & Bourguignat 1887). Type sp.: *Adelops freyeri* Miller, 1855 (orig. des.).
Rectipenis Pretner — Slovenia (1 sp.)
Rectipenis Pretner, 1959: 270. Type sp.: *Ceuthmonocharis matjasici* Pretner, 1959 (monotypy).
Rectipennis; Pretner, 1968: 27 (misspelling of *Rectipenis*). Note: also spelled *Rectipennis* by Pretner (1970), Laneyrie (1970), etc.?.

Charonites Apfelbeck — Bosnia (4 spp.)
Charonites Apfelbeck, 1907a: 304; 1907b: 314. Type sp.: *Charonites matzenaueri* Apfelbeck, 1907 (monotypy).

Elladoherpon Casale — Greece (Macedonia) (1 sp.)
Elladoherpon Casale, 1983: 261. Type sp.: *Elladoherpon inopinatum* Casale, 1983 (orig. des.).

Genestiellina Giachino — Bulgaria (1 sp.)
Genestiellina Giachino, 1996:167 (new name for *Genestiella* Giachino).
Genestiella Giachino, 1992: 316 (preoccupied, not Fennah 1969; see Appendix B). Type sp.: *Genestiella gueorguievi* Giachino, 1992 (orig. des.).

Haplotropidius Müller — Croatia (Dalmatia), Bosnia, Herzegovina (5 spp.)
Haplotropidius Müller, 1903: 89 (as subgenus of *Apholeuonus*). Type sp.: *Apholeuonus pubescens* Müller, 1903 (des. Jeannel, 1910a:22).

Icharonia Reitter — Bosnia, Herzegovina (1 sp.)
Icharonia Reitter, 1912b: 334. Type sp.: *Icharonia leonhardiana* Reitter, 1912 (monotypy).

Katobatizon Knirsch — Bosnia (1 sp.)
Katobatizon Knirsch, 1928: 109. Type sp.: *Katobatizon antennarium* Knirsch, 1928 (orig. des.).
Anomalocerina Knirsch, 1928: 112 (attributed to Weirather; pub. in syn. *Katobatizon).* Type sp.: *Anomalocerina zariquieyi* Knirsch, 1928 (=*K. antennarium* Knirsch, 1928 (pub. in syn.)) (monotypy).

Laneyriella Guéorguiev — Croatia (Dalmatia), Montenegro, Albania (7 spp.)
Laneyriella Guéorguiev, 1976: 127. Type sp.: *Bathyscia ganglbaueri* Apfelbeck, 1907 (orig. des.).

Leonhardia Reitter — Bosnia, Herzegovina (2 spp.)
Leonhardia Reitter, 1901b: 128. Type sp.: *Leonhardia hilfi* Reitter, 1901 (monotypy).

Leptodirus Schmidt [Tc] — Slovenia, Croatia, ?ne Italy (1 sp.)
Leptodirus Schmidt, 1832a: 83; 1832b: 9. Type sp.: *Leptodirus hochenwartii* Schmidt, 1832 (monotypy). Note: Neave (1939-40) gave priority to Schmidt, 1832b over Schmidt, 1832a (cited as 1834).
Stagobius Schiödte, 1847: 78. Type sp.: *Stagobius troglodytes* Schiödte, 1847 (=*L. hochenwartii* Schmidt, 1832) (monotypy).
Leptoderus Schmidt, 1852: 381 (misspelling of *Leptodirus*). Note: used 4x, not noted as new spelling, no reference to earlier papers.

Leptostagus Karaman — Macedonia (Yugoslavia) (1 sp.)
Leptostagus Karaman, 1954: 72. Type sp.: *Leptostagus babunae* Karaman, 1954 (orig. des.).

Parapropus Ganglbauer [Sc] — Slovenia, Bosnia, Croatia (7 spp.)
Parapropus Ganglbauer, 1899: 85 (as subgenus of *Propus*; attributed to Apfelbeck 1898 [not found]). Type sp.: *Propus ganglbaueri* Ganglbauer, 1899 (attributed to "Apfelbeck, Verh. Zool. Bot. Ges. Wien 1898" [no such publication found]) (monotypy).
Leptonotus Motschulsky, 1870b: 253 (preoccupied, not Kaup 1853). Type sp.: *Leptoderus sericeus* Schmidt, 1852 (monotypy).
Propus Abeille, 1878: 149 (as subgenus of *Leptodirus*; preoccupied, not Oken 1816, Cope 1874). Type sp.: *Leptoderus sericeus* Schmidt, 1852 (monotypy).

Petkovskiella Guéorguiev — Macedonia (Yugoslavia) (1 sp.)
Petkovskiella Guéorguiev, 1976: 128. Type sp.: *Leptostagus stygius* Karaman, 1954 (orig. des.).

Pholeuonella Jeannel — Croatia (Dalmatia), Herzegovina, Montenegro (2 spp.)
Pholeuonella Jeannel, 1910a: 8. Type sp.: *Adelops erberii* Schaufuss, 1863 (orig. des.).
Protopholeuonella Laneyrie, 1967: 596. Type sp.: *Adelops erberii* Schaufuss, 1863 (monotypy). Note: isogenotypic with *Pholeuonella* Jeannel, latter not in catalog, unknown to Laneyrie?

Pholeuonidius Jeannel — n Italy (4 spp.)
Pholeuonidius Jeannel, 1911a: 267. Type sp.: *Bathyscia halbherri* Reitter, 1887 (orig. des.).

Protobracharthron Reitter — Bosnia (1 sp.)
Protobracharthron Reitter, 1889: 297. Type sp.: *Hexaurus reitteri* Apfelbeck, 1889 (monotypy).

Radziella Casale & Jalžić — Croatia (Dalmatia) (1 sp.)
Radziella Casale & Jalžić, 1988: 349. Type sp.: *Radziella styx* Casale & Jalžić, 1988 (orig. des.).

Roubaliella Jeannel — Croatia (Dalmatia) (1 sp.)
Roubaliella Jeannel, 1925: 74. Type sp.: *Roubaliella biokovensis* Jeannel, 1925 (orig. des.). Note: placement, Casale et al. (1994).

Setnikia Breit — Bosnia (1 sp.)
Setnikia Breit, 1913a: 13. Type sp.: *Setnikia leonhardi* Breit, 1913 (monotypy).

Spelaeodromus Reitter — Croatia (1 sp.)
Spelaeodromus Reitter, 1884: 13. Type sp.: *Pholeuon pluto* Reitter, 1881 (monotypy).

Spelaites Apfelbeck — Croatia (Dalmatia) (1 sp.)
Spelaites Apfelbeck, 1907a: 303 (as *Spelaïtes* and *Spaelaïtes*; see Appendix B). Type sp.: *Spelaites grabowskii* Apfelbeck, 1907 (monotypy). Note: Greek derivation given, correctly transliterated as *Spelaites* or *Spelaetes*, not *Spaelaites* (error).
Spelaetes Apfelbeck, 1907b: 315. Type sp.: *Spelaites grabowskii* Apfelbeck, 1907 (monotypy).

Speoplanes Müller — Croatia (Dalmatia) (1 sp.)
Speoplanes Müller, 1911a: 2 (as subgenus of *Apholeuonus*). Type sp.: *Apholeuonus giganteus* Müller, 1911 (orig. des.).

Bathysciina Horn, 1880

[=Division II (Théléomorphes in part) of Jeannel, 1924]

Bathysciae Horn, 1880: 251. Type genus: *Bathyscia* Schiödte, 1847.
Oriotini Reitter, 1889: 296 (based on misspelled type genus). Type genus: *Oryotus* Miller, 1856 (as *Oriotus*).
Bathysciina Guéorguiev, 1974a: 841 (as new subtribe). Type genus: *Bathyscia* Schiödte, 1847 (not cited).

Anillocharis Reitter — Herzegovina, Montenegro (4 spp.)
Anillocharis Reitter, 1903b: 231. Type sp.: *Anillocharis ottonis* Reitter, 1903 (orig. des.).

Anisoscapha Müller — Bosnia, Croatia (Dalmatia) (2 spp.)
Anisoscapha Müller, 1917: 616 (as subgenus of *Proleonhardella*). Type sp.: *Proleonhardella winkleri* Müller, 1917 (orig. des.).

Antrodulus Knirsch — Herzegovina (2 spp.)
Antrodulus Knirsch, 1927: 11. Type sp.: *Antrodulus occultus* Knirsch, 1927 (orig. des.).

Aphaobiella Guéorguiev — Slovenia (2 spp.)
Aphaobiella Guéorguiev, 1976: 100 (validation of *Aphaobiella* Pretner by designation of type species; see Appendix B). Type sp.: *Aphaobius budnarlipoglavseki* Pretner, 1949 (des. Guéorguiev, 1976:100). Note: syn. of *Lotheria*?, Szymczakowski (1971b).
Aphaobiella Pretner, 1949: 143 (as subgenus of *Aphaobius*; nomen nudum, no type species designated).

Aphaobius Abeille [Tc] — Slovenia, Austria, ne Italy (3 spp.)
Aphaobius Abeille, 1878: 148. Type sp.: *Adelops milleri* Schmidt, 1855 (monotypy).

Aphaotus Breit — ne Italy (3 spp.)
Aphaotus Breit, 1914: 58. Type sp.: *Aphaotus jureceki* Breit, 1914 (des. Lucas, 1920:108, Jeannel, 1924:239).

Augustia Zariquiey — Herzegovina (1 sp.)
Augustia Zariquiey, 1927: 152. Type sp.: *Augustia weiratheri* Zariquiey, 1927 (monotypy).

Bathyscia Schiödte [Tc] — ne Italy, Yugoslavia, Greece, Bulgaria, w Ukraine (11 spp.)
Bathyscia Schiödte, 1847: 79. Type sp.: *Bathyscia montana* Schiödte, 1847 (des. Jeannel 1910a:16). Note: revised by Casale et al. (1990).
Bathyscina Reitter, 1908: 117 (as subgenus of *Bathyscia*; no species listed). Type sp.: none des.? (9 species added by Jeannel, 1908a:299). Note: Jeannel (1910a:36, 1911a:410, 1914a:72) reinterpreted as synonym of *Bathyscia* s.str., proposed *Speonesiotes* (1910a:38) to replace *Bathyscina* of Jeannel, 1908a, not Reitter, 1908; Reitter (1913:155) argued *Speonesiotes* = *Bathyscina*.

Blattochaeta Reitter — Montenegro, Herzegovina (5 spp.)
Blattochaeta Reitter, 1910: 164 (as subgenus of *Bathyscia*). Type sp.: *Bathyscia marianii* Reitter, 1910 (orig. des.).

Blattodromus Reitter — Herzegovina (1 sp.)
Blattodromus Reitter, 1904: 153 (as subgenus of *Pholeuonopsis*). Type sp.: *Pholeuonopsis herculeana* Reitter, 1904 (monotypy).

Cansiliella Paoletti — n Italy (2 spp.)
Cansiliella Paoletti, 1972: 119. Type sp.: *Cansiliella tonielloi* Paoletti, 1972 (orig. des.).

Halbherria Conci & Tamanini — n Italy (5 spp.)
Halbherria Conci & Tamanini, 1951: 125. Type sp.: *Aphaotus tamaninii* Müller, 1931 (orig. des.).
Halbheria Guéorguiev, 1976: 99 (misspelling of *Halbherria*).

Hexaurus Reitter — Bulgaria (4 spp.)
Hexaurus Reitter, 1884: 15. Type sp.: *Pholeuon merklii* Frivaldszky, 1879 (monotypy). Note: revised by Zerche (1990).

Huetheriella Jeannel — Turkey (2 spp.)
Huetheriella Jeannel, 1934a: 21; 1934b: 164 (as *Hütheriella*). Type sp.: *Huetheriella maximiliani* Jeannel, 1934 (monotypy, orig. des.). Note: placement, Casale & Giachino (1990).

Leonhardella Reitter [Tc] — Bosnia, Herzegovina, Montenegro (7 spp.)
Leonhardella Reitter, 1903a: 209. Type sp.: *Leonhardella angulicollis* Reitter, 1903 (monotypy).
Leonhardella s. str. [Tc] — Bosnia, Herzegovina, Montenegro (4 spp.)
Leonhardellina Guéorguiev — Herzegovina, Montenegro (3 spp.)
Leonhardellina Guéorguiev, 1976: 102 (validation of *Leonhardellina* Jeannel by designation of type species; see Appendix B). Type sp.: *Leonhardella antennaria* Apfelbeck, 1907 (des. Guéorguiev 1976:102).
Victorella Reitter, 1908: 111 (preoccupied, not Kent 1870; no species listed). Type sp.: *Leonhardella antennaria* Apfelbeck, 1907 (des. Jeannel, 1924:248 (first spp. added?)).
Leonhardellina Jeannel, 1948b: 94 (nomen nudum, no type species designated). Note: not proposed as new name for *Victorella* Reitter.

Lessiniella Pavan — n Italy (2 spp.)
Lessiniella Pavan, 1941: 201. Type sp.: *Lessiniella trevisioli* Pavan, 1941 (orig. des.). Note: revised by Piva (1993), related to *Aphaotus*.

Lotharia Mandl — Austria (Carinthia) (1 sp.)
Lotharia Mandl, 1944: 106. Type sp.: *Lotharia angulicollis* Mandl, 1944 (monotypy). Note: possibly same as *Aphaobiella* (Szymczakowski, 1971b); as genus *incertae sedis* because male unknown (Guéorguiev, 1976).

Netolitzkya Müller — Bulgaria (2 spp.)
Netolitzkya Müller, 1913: 2. Type sp.: *Aphaobius maneki* Müller, 1909 (monotypy).

Orostygia Müller — n Italy, ?Austria (9 spp.)
Orostygia Müller, 1912: 301. Type sp.: *Orostygia moczarskii* Müller, 1912 (monotypy).

Oryotus Miller [Tc] — Slovenia, n Italy (7 spp.)
Oryotus Miller, 1856a: 627. Type sp.: *Oryotus schmidtii* Miller, 1856 (monotypy).

Phaneropella Jeannel — Italy to Turkey, Georgia (6 spp.)
Phaneropella Jeannel, 1910a: 15. Type sp.: *Adelops lesinae* Reitter, 1881 (orig. des.). Note: revised by Casale et al. (1991b).

Epiroella Casale *et al.* — Greece (Epirus) (2 spp.)
Epiroella Casale *et al.*, 1991b: 202. Type sp.: *Phaneropella muelleriana* Paoletti, 1975 (orig. des.).

Hittitia Casale et al. — Turkey (1 sp.)
Hittitia Casale *et al.*, 1991b: 207. Type sp.: *Bathyscia turcica* Reitter, 1884 (orig. des.).

Phaneropella s. str. — Italy, Yugoslavia, Georgia (2 spp.)

Uludagites Casale *et al.* — Turkey (1 sp.)
Uludagites Casale *et al.*, 1991b: 213. Type sp.: *Phaneropella minuta* Casale *et al.*, 1991 (orig. des.).

Pholeuonopsis Apfelbeck — Bosnia, Herzegovina, Serbia, Montenegro (12 spp.)
Pholeuonopsis Apfelbeck, 1901: 14. Type sp.: *Pholeuonopsis ganglbaueri* Apfelbeck, 1901 (monotypy).

Pholeuodromus Breit — Bosnia, Herzegovina (2 spp.)
Pholeuodromus Breit, 1913b: 354. Type sp.: *Pholeuodromus leonhardi* Breit, 1913 (=*P. breiti* (Jeannel, 1924)) (monotypy).

Pholeuonopsis s. str. — Bosnia, Herzegovina, Serbia (8 spp.)

Scotosites Knirsch — Montenegro (1 sp.)
Scotosites Knirsch, 1929: 88. Type sp.: *Pholeuonopsis spaethi* Knirsch, 1929 (orig. des.).

Silphanillus Reitter — Herzegovina (1 sp.)
Silphanillus Reitter, 1903a: 210. Type sp.: *Silphanillus leonhardi* Reitter, 1903 (monotypy).

Pisidiella Jeannel — Turkey (4 spp.)
Pisidiella Jeannel, 1930b: 226. Type sp.: *Pisidiella spatulifera* Jeannel, 1930 (orig. des.).

Pretneria Müller — Slovenia (2 spp.)
Pretneria Müller, 1931: 198 (as subgenus of *Aphaobius*). Type sp.: *Aphaobius latitarsis* Müller, 1931 (monotypy).

Proleonhardella Jeannel — Bosnia, Serbia (8 spp.)
Proleonhardella Jeannel, 1910a: 16. Type sp.: *Bathyscia matzenaueri* Apfelbeck, 1907 (orig. des.).

Pholeuonillus Breit — Bosnia (1 sp.)
Pholeuonillus Breit, 1913b: 355. Type sp.: *Bathyscia adolfi* Reitter, 1911 (monotypy).

Proleonhardella s. str. — Bosnia, Serbia (7 spp.)
Proleonhardia Jeannel, 1910a: 21. Type sp.: *Bathyscia neumanni* Apfelbeck, 1901 (orig. des.). Note: syn. Müller (1917) (see Jeannel, 1924:242).

Prospelaeobates Giachino & Etonti — Slovenia, Croatia (2 spp.)
Prospelaeobates Giachino & Etonti, 1996:64. Type sp.: *Prospelaeobates vrezeci* Giachino & Etonti, 1996 (orig. des.)

Speophyes Jeannel — France (Hérault) (1 sp.)
Speophyes Jeannel, 1910a: 15. Type sp.: *Adelops lucidulus* Delarouzée, 1860 (orig. des.).

Weiratheria Zariquiey — Montenegro (1 sp.)
Weiratheria Zariquiey, 1927: 155. Type sp.: *Weiratheria bocki* Zariquiey, 1927 (monotypy).

Bathysciotina Guéorguiev, 1974

[=Division III (Théléomorphes in part) of Jeannel, 1924]

Bathysciotina Guéorguiev, 1974a: 841. Type genus: *Bathysciotes* Jeannel, 1910 (not cited).

Bathyscidius Jeannel — Croatia (Dalmatia), Montenegro, Macedonia (Yugoslavia), Albania (4 spp.)
Bathyscidius Jeannel, 1910a: 15. Type sp.: *Bathyscia tristicula* Apfelbeck, 1907 (orig. des.).

Bathysciotes Jeannel [Tc] — Croatia, Slovenia, ne Italy (1 sp.)
Bathysciotes Jeannel, 1910a: 15. Type sp.: *Adelops khevenhuelleri* Miller, 1852 (orig. des.).

Neobathyscia Müller — n Italy (10 spp.)
Neobathyscia Müller, 1917: 639. Type sp.: *Bathyscia antrorum* Dodero, 1900 (des. Jeannel 1924:277).

Pseudobathyscidius Karaman — Serbia (1 sp.)
Pseudobathyscidius Karaman, 1964: 30 (as subgenus of *Bathyscidius*). Type sp.: *Bathyscidius serbicus* Karaman, 1964 (monotypy).

Ravasinia Müller — Albania (1 sp.)
Ravasinia Müller, 1922: 89 (as subgenus of *Leonhardella*). Type sp.: *Leonhardella lonae* Müller, 1922 (monotypy).

Redensekia Karaman — Croatia (1 sp.)
Redensekia Karaman, 1953: 109 (as *Redenšekia*). Type sp.: *Redensekia likana* Karaman, 1953 (monotypy).

Speonesiotes Jeannel — Yugoslavia, Albania (21 spp.)
Speonesiotes Jeannel, 1910a: 15. Type sp.: *Adelops narentinus* Miller, 1861 (orig. des.).
Albanella Müller — Montenegro, Albania (3 spp.)
Albanella Müller, 1914: 1006 (not Harris & Lalicker 1934). Type sp.: *Speonesiotes lonae* Müller, 1914 (orig. des.).
Crivosiella Jeannel — Montenegro (2 spp.)
Crivosiella Jeannel, 1924: 287. Type sp.: *Speonesiotes huemmleri* Jeannel, 1924 (orig. des.).
Kulzeria Zariquiey — Croatia (Dalmatia), Herzegovina, Montenegro (5 spp.)
Kulzeria Zariquiey, 1927: 157. Type sp.: *Adelops dorotkana* Reitter, 1881 (des. Guéorguiev 1976:103).
Speonesiotes s. str. — Croatia (Dalmatia), Bosnia, Herzegovina, Montenegro (11 spp.)

Sphaerobathyscia Müller — Slovenia, ne Italy (1 sp.)
Sphaerobathyscia Müller, 1917: 637. Type sp.: *Bathyscia hoffmanni* Motschulsky, 1856 (monotypy).

Antroherponina Jeannel, 1910

[=*Antroherpon* phyletic series of Jeannel, 1924]

Antroherpona Jeannel, 1910a: 25. Type genus: *Antroherpon* Reitter, 1889.
Hadesiini Absolon, 1913: 108. Type genus: *Hadesia* Müller, 1911.
Antroherponina Guéorguiev, 1974a: 841 (as new subtribe). Type genus: *Antroherpon* Reitter, 1889.

Antroherpon Reitter [Sc] — Croatia (Dalmatia), Bosnia, Herzegovina, Montenegro, Albania (26 spp.)
Anthroherpon Reitter, 1889: 294 (see Appendix B). Type sp.: *Leptoderus cylindricollis* Apfelbeck, 1889 (des. Jeannel, 1910a:26). Note: spelled *Anthroherpon* five times in original publication; revised by Giachino & Guéorguiev (1993).

Antroherpon Apfelbeck, 1894: 511 (misspelling of *Anthroherpon*). Note: possibly other earlier publication?
Eumecosoma Müller, 1901: 29 (preoccupied, not Schiner 1866). Type sp.: *Antroherpon stenocephalum* Apfelbeck, 1901 (monotypy).
Antrophilon Absolon, 1913: 100. Type sp.: *Antrophilon primitivum* Absolon, 1913 (orig. des.). Note: omitted from Laneyrie (1967), Guéorguiev (1976) catalogs.
Protantroherpon Absolon, 1913: 108. Type sp.: *Leptoderus cylindricollis* Apfelbeck, 1889 (des. Jeannel 1924:400). Note: probably intended as subgenus.
Euantroherpon Absolon, 1913: 108. Type sp.: *Leptoderus hoermanni* Apfelbeck, 1889 (des. Jeannel 1924:400). Note: probably intended as subgenus.

Hadesia Müller — Herzegovina, ?Montenegro (1 sp.)
Hadesia Müller, 1911b: 175. Type sp.: *Hadesia vasiceki* Müller, 1911 (monotypy).

Leptomeson Jeannel — Croatia (Dalmatia), Bosnia, Herzegovina (4 spp.)
Leptomeson Jeannel, 1924: 420 (as subgenus of *Antroherpon*). Type sp.: *Antroherpon leonhardi* Reitter, 1902 (orig. des.).

Parantrophilon Noesske — Herzegovina (1 sp.)
Parantrophilon Noesske, 1914: 17. Type sp.: *Parantrophilon spelaebatoides* Noesske, 1914 (monotypy).

Remyella Jeannel [Tc] — Serbia, Montenegro (1 sp.)
Remyella Jeannel, 1931: 260. Type sp.: *Remyella scaphoides* Jeannel, 1931 (orig. des.). Note: revised by Giachino & Etonti (1995).

Spelaeobatina Guéorguiev, 1974

[=*Spelaeobates* phyletic series of Jeannel, 1924]

Spelaeobatina Guéorguiev, 1974a: 841. Type genus: *Spelaeobates* Müller, 1901.

Spelaeobates Müller [Sc] — Croatia (Dalmatia) (6 spp.)
Spelaeobates Müller, 1901: 16. Type sp.: *Spelaeobates novaki* Müller, 1901 (des. Jeannel 1910a:25). Note: belongs near *Prospelaeobates* in Bathysciina (Giachino & Etonti, 1996).
Pretneriella Guéorguiev [Sc] — Croatia (Dalmatia) (5 spp.)
Pretneriella Guéorguiev, 1976: 129. Type sp.: *Spelaeobates pharensis* Müller, 1901 (orig. des.).
Spelaeobates s. str. — Croatia (Dalmatia) (1 sp.)

Leptodirini *incertae sedis*

Neotropospeonella Pace — Venezuela (1 sp.)
Neotropospeonella Pace, 1985: 542; 1987: 195. Type sp.: *Neotropospeonella decui* Pace, 1985 (orig. des.). Note: known from females only, placement doubtful; locality needs confirmation.

Oritocatopini Jeannel, 1936

Oritocatopini Jeannel, 1936: 116. Type genus: *Oritocatops* Jeannel, 1921.

DIAGNOSIS:

In addition to the characters in the tribal key, Oritocatopini have: mesepisternal-epimeral suture absent or (*Afrocatops*) indistinct; abdominal spiracle 8 minute but probably non-functional; and parameres of aedeagus with basoventral lobes which meet ventrally and are articulated to parameres.

DISTRIBUTION: Afrotropical (Kenya to South Africa).

COMMENTS:

This tribe is recognized in the sense of Jeannel (1964). Jeannel (1936, 1964) placed Oritocatopini together with Agyrtodini and Nemadini in his subfamily Nemadinae, but Perreau (1989) demonstrated that Oritocatopini are more closely allied to Eucatopini and Ptomaphagini and combined these three as tribes of one subfamily, Eucatopinae. Among Cholevinae, only Oritocatopini and Eucatopini have an elongated apical segment of the maxillary palp and minute but probably non-functional spiracles of abdominal segment 8, both probable plesiomorphies compared to the short apical maxillary palp segment and complete absence of spiracles on abdominal segment 8 in other cholevines, but only these two tribes have lost the mesepisternal-epimeral suture (weakly indicated in *Afrocatops*).

Chappuisiotes lobeliae occurs commonly, as adults and larvae, in dead inflorescences of *Lobelia telekii* on Mt. Elgon. Species of *Oritocatops* and *Afrocatops* are found in litter of moist montane forests, but at least some *Afrocatops* species are commonly found at carrion and dung. Jeannel (1964); S. B. Peck (personal communication).

Larvae: Paulian (1941). Examined: *Afrocatops natalensis* (Jeannel); *Chappuisiotes lobeliae* (Jeannel).

GENERIC CATALOG:

Afrocatops Jeannel [Tc] — South Africa, Tanzania (7 spp.)
Afrocatops Jeannel, 1964: 235. Type sp.: *Oritocatops natalensis* Jeannel, 1936 (orig. des.).

Chappuisiotes Jeannel [Tc] — Kenya (Mt. Elgon) (1 sp.)
Chappuisiotes Jeannel, 1957a: 327. Type sp.: *Oritocatops lobeliae* Jeannel, 1936 (orig. des.).

Oritocatops Jeannel [Sc] — Kenya, Rwanda, Burundi, e Zaire (11 spp.)
Oritocatops Jeannel, 1921: 236. Type sp.: *Oritocatops kenyensis* Jeannel, 1921 (orig. des.).

Eucatopini Jeannel, 1921

Eucatopini Jeannel, 1921: 233. Type genus: *Eucatops* Portevin, 1903.

DIAGNOSIS:

In addition to the characters in the tribal key, Eucatopini have: mesepisternal-epimeral suture absent; elytron with microstriated area ventrally near apex; small sclerite present behind each posterior corner of abdominal tergum 7; reflexed portion of abdominal sternum 7 produced into erect flap; abdominal spiracle 8 minute but probably non-functional; and aedeagus highly specialized (see Jeannel, 1936).

DISTRIBUTION: Neotropical (Mexico to n Argentina, Dominican Republic).

COMMENTS:

Eucatops is isolated from all other Cholevinae by possession of numerous unique specializations noted in the tribal key and diagnosis above. The genus has more in common with Oritocatopini than with other Cholevinae (see under that tribe). Jeannel (1936) associated this group with ptomaphagines based on the shared presence of a protibial comb and some aedeagal characters. This supposed relationship was justifiably questioned by Perreau (1989) and Gnaspini (1994), although Perreau placed these groups plus Oritocatopini together in one subfamily. The unusual structures on the dorsum of abdominal segment 7 and opposing striations on the underside of the elytra possibly form a stridulatory system, which is present in both sexes.

The species occur on dung, carrion, fungi and other decomposing organic matter but are not common (Gnaspini, 1994; personal observations).

Larvae undescribed. Examined: *Eucatops* sp. (Panama).

GENERIC CATALOG:

Eucatops Portevin [Sc] Neotropical (Mexico to n Argentina, Dominican Republic) (12 spp.)
Eucatops Portevin, 1903a: 162. Type sp.: *Eucatops curvipes* Portevin, 1903 (des. Jeannel 1922b:39). Note: reviewed, checklist by Gnaspini (1994); species seen to Mexico, Dominican Rep. (Peck, 1977c).

Eucatops s. str. Neotropical (Mexico to n Argentina, Dominican Republic) (9 spp.)
Acanthocatops Bruch, 1918: 193. Type sp.: *Acanthocatops formicetorum* Bruch, 1918 (monotypy).

Sphaerocatops Portevin Bolivia, Brazil, n Argentina (3 spp.)
Sphaerocatops Portevin, 1907: 67 (new name for *Spathosternum* Portevin).
Spathosternum Portevin, 1903a: 165 (preoccupied, not Krauss 1877). Type sp.: *Spathosternum haemorrhoidale* Portevin, 1903 (monotypy).

Ptomaphagini Jeannel, 1911

Ptomaphagini Jeannel, 1911a: 193. Type genus: *Ptomaphagus* Illiger, 1798.
Ptomaphagina Hatch, 1928: 164. Type genus: *Ptomaphagus* Illiger, 1798.

DIAGNOSIS:

In addition to characters used in the tribal key Ptomaphagini have: postcoxal process of pronotum fused to sternum; abdominal spiracle 8 atrophied; terga 7 and 8 more or less connate; and aedeagus without basal lobes on parameres.

DISTRIBUTION: Holarctic, Oriental, Neotropical.

COMMENTS:

This tribe was reviewed by Peck (1973), and a new review with description of several new genera and phylogenetic analysis of nearly all genera has been completed by Gnaspini (1996; received too late to incorporate results here). This tribe was divided into 2 groups (recognized as subtribes here) by Szymczakowski (1964a, 1969a): Ptomaphaginina with *Pandania, Proptomaphaginus* and *Ptomaphaginus*, and the nominal subtribe with the remaining genera. However, the above-cited work of Gnaspini does not support the monophyly of Ptomaphaginina and he does not use subtribes. The genus *Acrotrychiopsis* Normand (1946) was originally placed in " Liodidae" (Leiodinae of present classification) but clearly does not belong there, and I tentatively place it here. Based on the original description (the unique type has not been available), *Acrotrychiopsis* has mesocoxae separated by a strong mesocoxal process, transverse elytral striolations and an aedeagus of the ptomaphagine type, but apparently lacks the tibial periapical comb characteristic of ptomaphagines.

The species are found around carrion, dung and other decomposing matter, in forest litter, and in caves. Some species, including all those of *Acrotrychiopsis, Echinocoleus* and *Synaulus*, are myrmecophilous. Peck (1973, 1976, 1979,1984, 1986, etc.).

Larvae: Böving & Craighead (1931), Decu (1973), Gnaspini (1993c), Jeannel (1922b), Peyerimhoff (1907), Zwick in Klausnitzer (1978). Examined: ?*Adelopsis* sp. (Panama); *Echinocoleus setiger* Horn; *Proptomaphaginus puertoricensis* Peck; *Ptomaphagus hirtus* (Tellkampf); *P. valentinei* Jeannel; undet. genera, spp. (Japan, Mexico, Nicaragua, USA).

KEY TO SUBTRIBES OF PTOMAPHAGINI

(Modified from Peck, 1973)

1. Protibia with periapical comb of short spines only; mesepimeron trapezoidal, wider on outer edge than inner edge ..... Ptomaphagina
   Protibia with comb of short spines along external edge as well as around apex; mesepimeron transverse, as wide at inner edge as at outer edge ..... Ptomaphaginina

GENERIC CATALOG:

Ptomaphagina Jeannel, 1911

Acrotrychiopsis Normand — Tunisia (1 sp.)
Acrotrychiopsis Normand, 1946: 38. Type sp.: *Acrotrychiopsis dorylophilus* Normand, 1946 (monotypy). Note: placement tentative, questioned by Gnaspini (*in litteris* 1996).

Adelopsis Portevin [Sc] — Neotropical, se USA (55 spp.)
Adelopsis Portevin, 1907: 71. Type sp.: *Adelopsis heterocera* Portevin, 1907 (monotypy). Note: partially revised by Peck (1979), Gnaspini & Peck (1996).
Adelopsis s. str. [Sc] — Neotropical, se USA (52 spp.)
Iutururuca Gnaspini — Brazil (3 spp.)
Iutururuca Gnaspini, 1993a: 79. Type sp.: *Adelopsis leo* Gnaspini, 1993 (orig. des.).

Echinocoleus Horn [T, Sc] — s USA (3 spp.)
Echinocoleus Horn, 1885: 136. Type sp.: *Echinocoleus setiger* Horn, 1885 (monotypy). Note: revised by Peck (1976), Peck & Gnaspini (1997, as subgenus of *Ptomaphagus*).

Paulipalpina Gnaspini & Peck — Brazil, Costa Rica, Panama (4 spp.)
Paulipalpina Gnaspini & Peck, 1996: 434. Type sp.: *Adelopsis claudicans* Szymczakowski, 1980 (orig. des.).

Ptomaphagus Hellwig [Sc] — Holarctic, n Oriental, Neotropical (97 spp.)
Ptomaphagus Hellwig, 1795: 358 (attributed to Knoch; published in synonymy with *Tritoma*). Type sp.: *Tritoma sericea* Fabricius, 1787 (=*P. subvillosus* (Goeze, 1777)) (monotypy). Note: partial revision, Peck (1973, 1977c, 1984); evolution, Peck (1984, 1986); 1 sp. from Argentina not assigned to subgenus.
Ptomaphagus Illiger, 1798: 84 (attributed to Knoch). Type sp.: *Helops sericeus* Panzer, 1801 (=*P. subvillosus* (Goeze, 1777)?) (des. Thomson, 1859:60, Jeannel, 1922b:42 (not orig. incl.); *Pt. truncatus* Ill. des. Westwood, 1838:11, Shuckard, 1839:158 (not orig. incl.)).
Ptomatophagus Agassiz, 1847: 316 (unjustified emendation of *Ptomaphagus*).
Adelops Tellkampf [Sc] — North & Central America (61 spp.)
Adelops Tellkampf, 1844: 318 (not Dejean 1833 [nomen nudum? in Scarabaeoidea]). Type sp.: *Adelops hirtus* Tellkampf, 1844 (monotypy).
Merodiscus Jeannel — se Europe (Slovakia to Ukraine) (2 spp.)
Merodiscus Jeannel, 1934d: 162. Type sp.: *Catops validus* Kraatz, 1852 (orig. des.).
Ptomaphagus s. str. — Palearctic, n Oriental (Nepal, ne Burma, Taiwan) (27 spp.)
Tupania Szymczakowski — Mexico, Brazil (6 spp.)
Tupania Szymczakowski, 1961a: 146. Type sp.: *Ptomaphagus forticornis* Matthews, 1888 (orig. des.).

Synaulus Portevin — Algeria, Tunisia (2 spp.)
Synaulus Portevin, 1903a: 157 (new name for *Myrmecobius* Lucas).
Myrmecobius Lucas, 1846: 233 (preoccupied, not Waterhouse 1836). Type sp.: *Myrmecobius agilis* Lucas, 1846 (monotypy).

Ptomaphaginina Szymczakowski, 1964

Ptomaphaginini Szymczakowski, 1964a: 66. Type genus: *Ptomaphaginus* Portevin, 1914.

Pandania Szymczakowski — Indonesia (Sumatra) (1 sp.)
Pandania Szymczakowski, 1964a: 148. Type sp.: *Pandania oxytropis* Szymczakowski, 1964 (orig. des.).

Proptomaphaginus Szymczakowski [Sc] — Mexico, West Indies (6 spp.)
Proptomaphaginus Szymczakowski, 1969a: 88. Type sp.: *Proptomaphaginus apodemus* Szymczakowski, 1969 (orig. des.).

Ptomaphaginus Portevin [Sc] — Oriental, Japan (82 spp.)
Ptomaphaginus Portevin, 1914a: 194. Type sp.: *Ptomaphaginus longitarsis* Portevin, 1914 (monotypy). Note: 11 spp. belong in new genus (Perreau, *in litteris* 1998).
Euptomaphagus Hatch, 1928: 158. Type sp.: *Ptomaphagus cilipes* Portevin, 1907 (orig. des.).

Platypsyllinae Ritsema, 1869 (=Leptininae)

Platypsyllidae Ritsema, 1869b: 38. Type genus: *Platypsyllus* Ritsema, 1869 (senior homonymic synonym of Platypsyllus Westwood 1869).
Leptinidae [implied] LeConte, 1866: 368 (unavail., name not given). Type genus: *Leptinus* Müller, 1817.
Achreioptera Westwood, 1869: 118 (as order; unavail., not based on genus; for *Platypsyllus* Westwood, 1869, not Ritsema, 1869).
Platypsyllidae LeConte, 1872: 799. Type genus: *Platypsyllus* Ritsema, 1869 (senior homonymic synonym of *Platypsyllus* Westwood, 1869).
Leptinidae LeConte, 1872: 802. Type genus: *Leptinus* Müller, 1817.

DIAGNOSIS:

In addition to characters given in the subfamily key, Platypsyllinae have: eyes and wings reduced or absent; epistomal suture present or absent, if present then without "stem" ; prosternum with or without ventral intercoxal lobe separating procoxae; mesocoxal cavities separated by mesosternal process; tarsi all 5-segmented, with tenent setae on 4 or all 5 segments of pro- and mesotarsi of both sexes; elytra entire or abbreviated; abdominal spiracles 1-8 functional; and aedeagus with long free parameres bearing basoventral processes.

DISTRIBUTION: Holarctic.

COMMENTS:

A close relationship of the louse-like ectoparasite *Platypsyllus* (Platypsyllidae) to *Leptinus* and *Leptinillus* (Leptininae of Silphidae) was well established by Jeannel (1922a) and Bugnion & du Buysson (1924). Together with *Silphopsyllus*, the genera have usually remained united in a subfamily or family since then.

All platypsyllines are associated with mammal hosts. In *Leptinus* species the association is a loose one; the life cycle is completed in the nests of ground-dwelling mammals, and adults enter the fur of the hosts to feed, but adults are frequently found in other habitats and the species are apparently not host-specific. The other three genera are host-specific ectoparasites on aquatic or semiaquatic mammals, as follows: *Silphopsyllus desmanae* on *Desmana moschata*; *Leptinillus aplodontiae* on *Aplodontia rufa*; and *L. validus* and *Platypsyllus castoris* on *Castor* spp. *Platypsyllus castoris* is the most highly modified species and spends its entire life cycle in the fur of the host, leaving briefly only to pupate. All species are thought to feed on dead skin and secretions of the hosts. Besuchet (1980), Dessart (1993), Ising (1969), Parks & Barnes (1955), Pavlovsky (1956), Peck (1982b), Semenov & Dobzhansky (1927), Winter (1979), Wood (1965).

Larvae: Böving & Craighead (1931), Ising (1969), Newton (1991), Peterson (1960), Semenov & Dobzhansky (1927), Wood (1965). Examined: *Leptinillus validus* (Horn); *Leptinus orientamericanus* Peck; *Platypsyllus castoris* Ritsema.

Generic Catalog:

Leptinillus Horn [Tc] — Canada, n+w USA (2 spp.)
Leptinillus Horn, 1882: 113. Type sp.: *Leptinus validus* Horn, 1872 (monotypy).

Leptinus Müller [Tc, Sc] — w Palearctic, Nearctic (9 spp.)
Leptinus Müller, 1817: 266. Type sp.: *Leptinus testaceus* Müller, 1817 (monotypy). Note: revised by Besuchet (1980), Peck (1982b).

Platypsyllus Ritsema [Tc] — w Palearctic, Nearctic (1 sp.)
Platypsyllus Ritsema, 1869a: [23]. Type sp.: *Platypsyllus castoris* Ritsema, 1869 (monotypy).
Platypsyllus Westwood, 1869: 118 (synonymic homonym of *Platypsyllus* Ritsema). Type sp.: *Platypsyllus castorinus* Westwood, 1869 (=*P. castoris* Ritsema, 1869) (monotypy).
Platypsylla; LeConte, 1872: 801 (misspelling of *Platypsyllus*).

Silphopsyllus Olsufiev [T] — Russia (European) (1 sp.)
Silphopsyllus Olsufiev, 1923: 84. Type sp.: *Silphopsyllus desmanae* Olsufiev, 1923 (orig. des.).

Extinct taxa

Nyujwa Perkovsky — Russia (Buryat ASSR) (1 sp.)
Nyujwa Perkovsky, 1990a: 118 (extinct genus and species, Cretaceous). Type sp.: *Nyujwa zherichini* Perkovsky, 1990 (orig. des.). Note: placed by author in Cholevinae: Agyrtodini, but probably belongs in Leiodinae (note antennal insertion, strong antennal club, shape of epistomal suture).

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RIASSUNTO

Problemi filogenetici, classificazione e catalogo generico dei Leiodidae mondiali (Cholevidae inclusi)

Nel presente contributo i Colevini endogei e sotterranei sono correlati ad un'analisi delle classificazioni passate e presenti degli Staphylinoidea. L'Autore porta argomenti a favore del riconoscimento di una singola grande famiglia monofiletica, quella dei Leiodidae, piuttosto che una serie, meno ben definita, di famiglie, includente Cholevidae, Leptinidae, etc. Il sister group dei Leiodidae *sensu lato* è rappresentato probabilmente dagli Agyrtidae. La famiglia Leiodidae comprende, nell'accezione dell'Autore, sei sottofamiglie probabilmente monofiletiche: Camiarinae, Catopocerinae, Leiodinae (= Anisotominae), Coloninae, Cholevinae (= Catopinae, Leptodirinae) e Platypsyllinae (= Leptininae). L'Autore discute inoltre alcuni rilevanti problemi filogenetici a livello di sottofamiglie e di tribù.

Vengono fornite chiavi di identificazione, diagnosi e un breve riassunto delle conoscenze sulla biologia e sulle larve delle singole sottofamiglie e tribù. Una nuova sottotribù, quella degli Eunemadina, è separata dai Nemadina.

Viene fornito un catalogo generico completo, comprendente indicazioni circa la distribuzione e il numero di specie conosciute di ciascun genere. Inoltre, in appendice sono riassunti i nuovi cambiamenti tassonomici (10 nuove sinonimie generiche, 1 subgenerica e 9 specifiche; 3 specie rivalutate; 22 nuove combinazioni generiche e 2 spostamenti di famiglia) e alcuni problemi di nomenclatura. Dal presente contributo risulta evidente che i Cholevinae presentano la più grande diversità nell'ambiente sotterraneo, con più di 160 generi e 750 specie di Leptodirini (= Bathysciini) nella regione paleartica.

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APPENDIX A. TAXONOMIC CHANGES

The definitions of many higher taxa, especially tribes of Leiodinae and Camiarinae and subtribes of Anemadini, are modified in the above work, with resulting changes in the placement of many genera. In this section, I will not attempt to list such changes, but only summarize those formal taxonomic changes that result in new names, new synonymies or generic combinations, or changes in family placement. Most of these changes are an incidental result of my study of types of poorly known taxa to determine generic placement, and are presented here although many do not appear elsewhere in this work (e.g., new species-group synonymies). Full references for all genus-group and higher-level names are given in the generic catalog.

Agyrtodes Portevin

A. labralis (Broun), **RESURRECTED** as valid species, not synonym of *A. monticola* (Broun)
A. nemoralis (Broun), **RESURRECTED** as valid species, not synonym of *A. monticola* (Broun)
A. nebulosus (Broun)
=*A. varius* (Broun), **NEW SYNONYMY**
=*A. varius* Jeannel, **NEW SYNONYMY**

In his revision of *Agyrtodes,* Jeannel (1936) listed the names *labralis* Broun and *varius* Broun, found on specimens in the Broun collection (in BMNH), as "*in lit.*" because he could find no record of their publication. Jeannel listed *A. labralis* as a synonym of *A. monticola* (Broun), and proposed a new species *A. varius* Jeannel for *A varius* Broun based on the two Broun specimens bearing this name. In fact, both species had been described by Broun, as *Mesocolon labralis* Broun (1921:611) and *Mesocolon varius* Broun (1886:946). Based on my examination of syntypes (in BMNH) of these and other Broun species placed in *Agyrtodes* by Jeannel (1936), and on other material of this genus from New Zealand, the above changes in status are proposed.

Catopsolius Sharp
=*Asphaerites* Broun, **NEW SYNONYMY**
C. nitidus (Broun), **NEW COMBINATION** (ex *Asphaerites*)

Broun (1893), in describing *Asphaerites nitidus*, noted that *Catopsolius laevicollis* Sharp (1886)

was a "cognate form" but failed to point out any significant differences between these genera. They have generally been kept together while bouncing from Silphidae to Camiarinae (Jeannel, 1922b) and Leiodidae sensu stricto (Jeannel, 1936), and indicated as "possibly congeneric" by Newton (1985) who placed them as "Camiarinae *incertae sedis*". Based on my study of syntypes of both species (in BMNH), the species are certainly distinct but I can find no characters that would seem to justify their continued generic separation, thus I propose the above generic synonymy.

Chiliopelates Jeannel, **SENSU NOVO**
=*Dasypelates* of Jeannel (1936, 1962) and other authors (type species misidentified)
=*Topaliola* Hlisnikovský, **NEW SYNONYMY**
C. cekalovici (Salgado Costas), **NEW COMBINATION** (ex *Dasypelates*)
C. crenulatus (Hlisnikovský), **NEW COMBINATION** (ex *Topaliola*)
C. edeniensis (Jeannel), **NEW COMBINATION** (ex *Dasypelates*)
C. fasciatus (Jeannel), **NEW COMBINATION** (ex *Dasypelates*)
C. kuscheli (Jeannel), **NEW COMBINATION** (ex *Dasypelates*)
C. latipennis (Jeannel), **NEW COMBINATION** (ex *Dasypelates*)
C. monticola (Jeannel), **NEW COMBINATION** (ex *Dasypelates*)
C. naumanni (Szymczakowski), **NEW COMBINATION** (ex *Dasypelates*)
C. obscurus (Pic), **NEW COMBINATION** (ex *Dasypelates*)
C. ornatus (Jeannel), **NEW COMBINATION** (ex *Dasypelates*)
=*Topaliola ornata* Hlisnikovský, **NEW SYNONYMY**
C. pictus (Jeannel), **NEW COMBINATION** (ex *Dasypelates*)
C. ventricosus (Jeannel), **NEW COMBINATION** (ex *Dasypelates*)

Removal of *Dasypelates gracilis* Portevin, the type species of *Dasypelates* Portevin, to the genus *Pelatonoma* Jeannel (see under *Dasypelates* below) leaves the remaining species of *Dasypelates* as used by Jeannel (1936, 1957b, 1962) and later authors in need of a new name. The subgeneric name *Chiliopelates* Jeannel (1964) is available for this, and is adopted here in place of *Dasypelates* of authors.

Examination of holotypes (in HNHM) of the two named species of *Topaliola* Hlisnikovský (1964b), a genus placed in Silphidae: Pterolomini without comment, indicates that these species belong in *Chiliopelates*. One of these species, *T. ornata* Hlisnikovský, is a synonym of *C. ornatus* (Jeannel) (types seen in MNHN), while the other, *T. crenulata* Hlisnikovský, is apparently a valid species. This placement and probable synonymy of *Topaliola* were noted by Newton (1985).

Colenis Erichson
=*Mathewsionia* Hlisnikovsky, **NEW SYNONYMY**
=*Carcharodes* or *Carcharodus* Hlisnikovský, (preoccupied subgeneric name)

Hlisnikovský (1965) named a new genus *Mathewsionia* for the two Central American species *Colenis punctulata* Matthews and *C. crassicornis* Matthews, noting as characteristic only that "die Vorderhüften vorn und hinten offen sind" [the procoxal cavities are open before and behind]. There is no indication that Hlisnikovský saw specimens of these species; his characterization of the genus seems to be based on Matthews' (1887:86) generic description of *Colenis* as having procoxal cavities "open in front and behind". Matthews no doubt meant that these coxal cavities were externally "open" in the sense of not being visibly bordered before and behind by the prosternum, and examination of types of these species (in BMNH) confirmed that the procoxal cavities are internally closed as in other *Colenis*. Thus, *Mathewsionia* is best treated as a synonym and its two species retained in *Colenis* unless and until valid characters can be found to separate it from *Colenis*. In the same work, Hlisnikovský (1965) established a new subgenus *Carcharodes* (also spelled *Carcharodus*) for a new species *Colenis macrocephaloides*. Both spellings of this name are preoccupied (by *Carcharodes* Strand and *Carcharodus* Huebner), leaving this subgenus without a valid name. A new name has been proposed by S. Peck (1998b).

Dasypelates Portevin, **SENSU NOVO** (type species misidentified by Jeannel)
=*Pelatonoma* Jeannel, **NEW SYNONYMY** (isogenotypic)

D. gracilis Portevin

=*Pelatonoma pubescens* Jeannel, **NEW SYNONYMY**

D. nebulosus (Jeannel), **NEW COMBINATION** (ex *Pelatonoma*)

Labeled syntypes of *Dasypelates gracilis* Portevin (examined in MNHN) are females, and no males of this species were known to Jeannel (1962:512). However, Portevin (1914a:74) reported seeing males as well as females, and I have seen males in MNHN labeled as *D. gracilis* and apparently from the same series of specimens as the types (from the Strobl collection). These males match syntype females of *D. gracilis* closely, but have the distinctive male genitalia and secondary sexual characters of the genus *Pelatonoma* Jeannel (1957b) which was separated from *Dasypelates* on the basis of these male characters. Further, males and females of *D. gracilis* match male and female type specimens (in MNHN) of *Pelatonoma pubescens* Jeannel, the type species of *Pelatonoma*. Since *D. gracilis* is the type species of *Dasypelates*, this generic name must move with *D. gracilis* and becomes a senior synonym of *Pelatonoma*. I have retained Jeannel's distinction between his concept of *Dasypelates* and *Pelatonoma*, based on the distinctive male characters of species of the latter genus which include comb-like projections of sternite VII that were overlooked by Jeannel (see Salgado Costas, 1992: Fig. 8), but note that Jeannel himself could not distinguish females of these genera even at the species level.

EUNEMADINA **NEW SUBTRIBE** (see under Anemadini in text)

Hydnodiaetus Jeannel

=*Kaszabella* Hlisnikovský, **NEW SYNONYMY** (isogenotypic)

H. brunneus Jeannel

=*Kaszabella striata* Hlisnikovský, **NEW SYNONYMY**

H. consobrinus (Fairmaire and Germain), **NEW COMBINATION** (ex *Hydnobius)*

Based on my study of the holotype (in MNHN) of *Hydnodiaetus brunneus* Jeannel (1962) and the holotype (in HNHM) of *Kaszabella striata* Hlisnikovský (1964c), these type species of monobasic genera are conspecific, hence I propose the new synonymies above. This genus belongs in Sogdini where Jeannel placed it; Hlisnikovský erroneously cited a 5-5-4 tarsal formula for his species, but Szymczakowski (1976) corrected this error. Study of a syntype (in MNHN) of *Hydnobius consobrinus* Fairmaire & Germain (1859), a species overlooked in Jeannel's (1962) review of the Chilean leiodid fauna, shows that this species also belongs in *Hydnodiaetus* but is not conspecific with *H. brunneus*.

Isocolon Broun

=*Allocatops* Broun, **NEW SYNONYMY**

I. ovale (Broun), **NEW COMBINATION** (ex *Allocatops*)

Broun (1893) described these two New Zealand genera from a single species each without providing any differential characters. Study of the single specimen in the Broun collection (in BMNH) of *Allocatops ovalis* Broun shows that this species does not differ in any way that would justify generic separation from the several species now included in *Isocolon*, including the type species *I. hilare* Broun (holotype in BMNH examined). Thus I propose the above generic synonymy.

Lomechon Wasmann: **NEW FAMILY PLACEMENT**, removed from family Leiodidae to Ptilodactylidae

Jeannel (1922b:40, 1936:26) noted that the odd myrmecophilous genus and species *Lomechon alfaroi* Wasmann (1897) from Costa Rica, originally placed in Silphidae: Cholevini, had antennae and other structures that were inconsistent with placement in Cholevinae and suggested instead that the species might belong in Endomychidae. From the description and figures of Wasmann it does seem that there is no basis for placing this species in Leiodidae *sensu lato*, and it is excluded from the family here. John Lawrence (personal communication) suggested from the figures that it might belong in Ptilodactylidae, and Robert Anderson (*in litteris*, 1997) confirmed this based on a newly collected specimen.

Metahydnobius Portevin

=*Hydnobiotus* Jeannel, **NEW SYNONYMY**

M. basipunctatus (Hlisnikovský), **NEW COMBINATION** (ex *Leiodes*)

M. bicolor (Jeannel), **NEW COMBINATION** (ex *Hydnobiotus*)

M. bimaculatus (Jeannel), **NEW COMBINATION** (ex *Hydnobiotus*)

M. forticornis (Champion)

=*Leiodes gilvicornis* Hlisnikovský, **NEW SYNONYMY**

M. hybridiformis (Hlisnikovský), **NEW COMBINATION** (ex *Leiodes*)

In his review of the Chilean leiodid fauna, Jeannel (1962) apparently overlooked the proposal by Portevin (1942) of a new genus *Metahydnobius* for *Hydnobius forticornis* Champion (1918), a Chilean species also overlooked by Jeannel. Based on my study of the holotype (in BMNH) of this species, *Metahydnobius* is very close to Jeannel's (1962) genus *Hydnobiotus*, with the same unusual "interrupted" mesosternal keel (Jeannel, 1962: Fig. 30) and similar type of aedeagus. *M. forticornis* has transverse striolations on the elytra which are lacking in the two *Hydnobiotus* species, and is unicolored rather than bicolored, but such differences do not seem to warrant generic separation. The addition of three more species (below) further obscures any differences between these genera, and they are here synonymized.

Szymczakowski (1976) noted that all three "*Liodes* (s. str.)" species described by Hlisnikovský (1964c) had a 5-5-5 tarsal formula and belonged in "Hydnobiini", but did not try to place these species into a valid genus. Based on my study of holotypes of all three species (in HNHM), all belong in *Metahydnobius* as recognized here. One, *L. gilvicornis*, is identical to *M. forticornis* and is here synonymized with that species, while the other two species are apparently valid.

Neohydnobius Jeannel

=*Loxorhabdus* Hlisnikovský, **NEW SYNONYMY**

N. argentinicus (Hlisnikovský), **NEW COMBINATION** (ex *Loxorhabdus*)

Study of the holotype (in MNHN) of *Neohydnobius brevis* Jeannel (1962) shows that contrary to its description this genus and species has a 5-4-4 tarsal formula and is winged, not apterous; it belongs in the tribe Pseudoliodini, not "Hydnobiini" were Jeannel (1962) and Szymczakowski (1976) placed it. Study of the holotype (in HNHM) of *Loxorhabdus argentinicus* Hlisnikovský (1964c) shows that this genus and species likewise belongs in Pseudoliodini and is very similar in all respects to *Neohydnobius brevis*, but evidently not conspecific with it; thus the above generic synonymy is proposed.

Mesocolon Broun and *Pseudonemadus* Portevin

Mesocolon puncticeps Broun, **RESURRECTED COMBINATION, REMOVAL FROM SYNONYMY**

Pseudonemadus lituratus (Broun)

=*Mesocolon strigicollis* Broun, **NEW COMBINATION, NEW SYNONYMY**

Jeannel (1936) placed *Mesocolon puncticeps* as a junior synonym of *Pseudonemadus lituratus*, and treated *Mesocolon strigicollis* as a valid species of *Mesocolon*. Examination of types of these three Broun names (in BMNH) demonstrates that Jeannel (1936) apparently somehow reversed the correct placement of *M. puncticeps* and *M. strigicollis*: the former species belongs in *Mesocolon*, and can be treated as a valid species of that genus pending revision, while the latter belongs in *Pseudonemadus* and is a synonym of *P. lituratus*.

Ragytodes Jeannel

=*Tricholoma* Hlisnikovský, **NEW SYNONYMY** (isogenotypic)

R. ocellifer Jeannel

=*Tricholoma kaszabi* Hlisnikovský, **NEW SYNONYMY**

Examination of the holotype and allotype (in HNHM) of *Tricholoma kaszabi* Hlisnikovský, 1964b, a genus and species placed in Silphidae and considered closely related to the genus *Camioleum* Lewis (now placed in Staphylinidae: Omaliinae, see Newton & Thayer, 1995), shows that this species belongs in Leiodidae: Neopelatopini and is a synonym of *Ragytodes ocellifer* Jeannel (1936, 1962) (paratypes in MNHN examined). This placement and probable synonymy were noted by Szymczakowski (1976).

Ragytodina Jeannel
=*Topalella* Hlisnikovský, **NEW SYNONYMY** (isogenotypic)
R. tuberculosa Jeannel
=*Topalella rugosa* Hlisnikovský, **NEW SYNONYMY**
Study of the holotype (in HNHM) of *Topalella rugosa* Hlisnikovský (1964b), a genus and species placed in Silphidae: Pterolomini near *Topaliola* Hlisnikovský, shows that this species also belongs in Leiodidae: Agyrtodini and is a synonym of *Ragytodina tuberculosa* Jeannel (1957b) (types in MNHN examined). This placement and probable synonymy were noted by Newton (1985).

Termitoglobus Reichensperger: **NEW FAMILY PLACEMENT**, removed from family Endomychidae to Leiodidae: Leiodinae: Scotocryptini (see under Scotocryptini)

Appendix B. Nomenclatural problems and changes

A number of nomenclatural problems were uncovered during this study that require resolution. In some cases, newly discovered type species designations, original spellings, and other problems would require name changes for names in wide use in order to conform to current rules of zoological nomenclature (ICZN 1985). However, at this writing these rules are under review, and some proposed changes to the rules (ICZN 1995a) might eliminate the need to make many of these changes by making it easier to conserve names in current use over prior names or original spellings that have not been in use. Some problems of type fixation require further study for resolution. This list calls attention to all nomenclatural problems known to me, but I have implemented currently required changes only when these have already been made by others or are unavoidable. Full references for all names are given in the generic catalog.

Agathidium Panzer: This may have been an unnecessary new name for *Volvoxis* Kugelann (NOT preoccupied by *Volvox* Linnaeus; ICZN 1985, Art. 56b). No change is made here.

Anisotoma Panzer: It is not clear which of the two originally included species (*Volvoxis picea* Kugelann and *glabra* Fabricius) was first designated as type species. The former species is now in *Leiodes*, the latter in *Anisotoma*. Solution: determine the first valid type species designation and, if *picea*, apply for conservation of *Anisotoma* by approving later designations of *glabra* as type species? No change is made here.

Antrocharis Abeille: This was an unnecessary new name for *Antrodietus* Abeille (NOT preoccupied by *Antrodiaetus* Ausserer; ICZN 1985, Art. 56b). No change is made here.

Antroherpon Reitter: The correct original spelling is *Anthroherpon*, used five times in the original publication. If this spelling is adopted, then the subtribal name based on this genus must also be corrected to Anthroherponina. No change is made here.

Aphaobiella Pretner: This name was a nomen nudum as proposed (no type species designation), but was validated by designation by Guéorguiev (1976) who is here credited with the name.

Bathysciola Jeannel: *Catopsinus* Motschulsky was incorrectly treated by Jeannel (1911a) as a nomen nudum, but is an available name (ICZN 1985, Art. 12b(5)) and has priority for this genus if its type species, *Catops pusillus* Motschulsky, truly belongs in *Bathysciola*. No change is made here.

Carcharodes or *Carcharodus* Hlisnikovský: Both of these original spellings are preoccupied, leaving this subgenus of *Colenis* without a name. Solution: a new name has been proposed by S. Peck (1998b).

Ceretophyes Comas & Escolà: This name was a nomen nudum as proposed (no type species designation), but was validated by designation in the Zoological Record (Anonymous, 1990) where the name was misspelled *Ceratophyes*; the name is here attributed to [Anonymous] (1990).

Ceuthmonocharis Jeannel: This was an unnecessary new name for *Hohenwartia* (NOT preoccupied by *Hohenwarthia* Letourneux & Bourguignat; ICZN 1985, Art. 56b). No change is made here.

Choleva Latreille: Fixation of "*Catops sericeus* Fabricius" as the type species by subsequent monotypy by Latreille (1802) makes *Choleva* a senior isogenotypic synonym of *Catops*, leaving *Cholevopsis* as the valid name for *Choleva* of later authors. Solution: apply for conservation of *Catops* and *Choleva* by approving Jeannel's (1922b) later designation of *Luperus cisteloides* Frölich as type species of *Choleva*? No change is made here.

Cyrtusamorpha Daffner: Daffner (1983) was unable to locate types of the species he designated as type species for this genus, *Chobautiella sumakovi* Sahlberg, which he considered to be a senior synonym of *Curtusa seriepunctata* Hlisnikovský. According to Perkovsky (1990b) who studied an authentic specimen, *Chobautiella sumakovi* Sahlberg actually belongs in *Leiodes* and is a junior synonym of *Leiodes ciliaris* (Schmidt). Although Perkovsky (1990b) continued to use *Cyrtusamorpha* in the sense of Daffner (1983), this was nomenclaturally incorrect since this name then became a synonym of *Leiodes* and the former genus *Cyrtusamorpha* was left without a name. This case of a misidentified type species could be best solved by application to ICZN for designation of *Cyrtusa seriepunctata* Hlisnikovský, the species actually studied by Daffner (1983), as type species of *Cyrtusamorpha*.

Leonhardellina Jeannel: This name was a nomen nudum as proposed (no type species designation), but was validated by designation by Guéorguiev (1976) who is here credited with the name.

Mehadiella Csiki: This was an unnecessary new name for *Frivaldszkya* Ganglbauer (NOT preoccupied by *Frivaldskia* Schiner; ICZN 1985, Art. 56b). No change is made here.

Mesocolon Broun: Fixation of *Mesocolon undulata* Broun as the type species by Hatch (1928) makes *Mesocolon* a senior isogenotypic synonym of *Zeagyrtoma*, leaving *Mesocolon* of later authors without a valid name. Solution: apply for conservation of *Mesocolon* and *Zeagyrtoma* by approving Jeannel's (1936) later designation of *Mesocolon clathratum* Broun as type species of *Mesocolon*? No change is made here.

Nargiotes blackburni (Portevin) and *N. antipodum* (Blackburn): Jeannel (1936:142, footnote) argued that *Choleva antipodum* Blackburn was not preoccupied by *Choleva antipoda* Kirsch because the species epithets were of different derivation, and therefore Portevin (1905a) was incorrect to propose the replacement name *Choleva blackburni* for *C. antipodum* Blackburn. However, since neither Blackburn (1891) nor Kirsch (in Kiesenwetter & Kirsch 1877) indicated any basis for name derivation, it seems prudent to accept Portevin's (1905a) interpretation of these names as primary homonyms and use *N. blackburni* (Portevin) as the current valid name for *N. antipodum* (Blackburn).

Pseudocolenis Reitter: The correct original spelling is *Pseudcolenis*, already used by Daffner (1988a, etc.), and used here.

Spelaetes Apfelbeck: The correct original spelling is *Spelaites*, which is adopted here.

Speocharis Jeannel: *Quaestus* Schaufuss and *Quaesticulus* Schaufuss are available names that were unjustly rejected by Jeannel (1909b, 1924) who did not like the characters cited by Schaufuss. Both Schaufuss names have priority for this genus and nominal subgenus. Perreau (1993) pointed out this problem and followed priority, choosing *Quaestus* as the valid name for the genus, and this is followed here.

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