A genus level revision of the subfamily Cardiophorinae Candèze

(Insecta: Coleoptera: Elateridae)

By

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Abstract

Phylogenies are presented for Clicking Elateroidea and Elateridae: Cardiophorinae. Subfamilies Hypnoidinae Schwarz (or tribe Hypnoidini of Dendrometrinae) and Negastrinae Nakane and Kishii are placed in synonymy with Cardiophorinae. Tribe Nyctorini Semenov-Tian-Shanskij and Pjatakova of Cardiophorinae is synonymised under Cardiophorini. All 35 genera of higher Cardiophorinae are keyed and their genus level classification is revised. The genus *Exoeolus* Broun is transferred from Cardiophorinae to Hemiopinae; fossil genus *Crioraphes* Iablokoff-Khnzorian is transferred to Elaterinae; fossil genera, *Pseudocardiophorites* Dolin, and *Protocardiophorus* Dolin are transferred to clicking Elateroidea *insertae sedis*. The genera *Lesnelater* Fleutiaux (Physodactylinae, syn.nov of *Pachyelater* Lesne, Dendrometrinae), *Margogastrius* Schwarz (Physodactylinae), *Pachyelater*, *Teslasena* Fleutiaux (syn.nov of *Globothorax* Fleutiaux) and species *Negastrius americanus* (Horn) (as type of *Floridelater* gen.nov) are transferred to Cardiophorinae. Other new genera include *Austrocardiophorus* (type species = *Cardiophorus humeralis* Fairmaire and Germain), *Chileaphricus* gen.nov. (type species = *Aphricus chilensis* Fleutiaux). *Paradicronychus* Dolin and Gurjeva is found to be nomen nudum and not separate from *Cardiophorus* Eschscholtz . The genus *Patriciella* Van Zwaluwenburg is synonymised under *Aphricus* LeConte. The subgenera *Diocarphus* Fleutiaux (of *Phorocardius*), *Metacardiophorus* Gurjeva (of *Cardiophorus*) and *Zygocardiophorus* Iablokoff-Khnzorian and Mardjanian (of *Cardiophorus*) are raised to

genus rank. Generic definitions of the genera *Aptopus* Eschscholtz, *Cardiophorus* Eschscholtz and *Paracardiophorus* Schwarz are restricted, and those of *Blaiseus* Fleutiaux, *Cardiodontulus* Van Zwaluwenburg and *Horistonotus* Candèze are expanded. *Coptostethus* Wollaston was found to belong at subgenus rank and *Dicronychus* Brullé and *Platynychus* Motschulsky at genus rank. Species *Lesnelater madagascariensis* Fleutiaux is synonymised under *Pachyelater madagascariensis* (Lesne). The hypothesis of a Jurassic origin of higher Cardiophorinae is supported by phylogenetic and biogeographic evidence, despite finding that previously published fossil evidence was invalid.

Nomenclatural Disclaimer

Although this dissertation contains phrases such as “new species,” “new synonymy,” and “new genus” (to name a few), it is not issued for the public and permanent scientific record or for the purposes of zoological nomenclature. A similar form of this work will soon be published in a scientific journal. That upcoming version will validate all of the nomenclatural acts seen within.

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CHAPTER 1

Introduction to the Subfamily Cardiophorinae

1.1 Introduction to the family Elateridae

1.1.1 Distribution, biology

The Elateridae, or click beetles, are among the most abundant beetle families in many terrestrial habitats. This large family, with 10 000 described species is the 9th most speciose beetle family (Johnson 2002b). Although there are 23 valid subfamily names in recent use, only about five of these are widely used. This is partly due to nomenclatural inconsistency, but also because some subfamilies are rare or geographically isolated. Of these, Elaterinae is the most diverse, followed by Agrypninae, Cardiophorinae, Dendrometrinae and Negastrinae. All five major subfamilies have worldwide distributions although Dendrometrinae is Holarctic centred and Agrypninae is most abundant and diverse in warm temperate and tropical areas.

Elaterid larvae, or wireworms, are elongate and cylindrical and ingest only extra-orally digested liquid food (Eidt 1959). Larvae of most species live in decaying wood, litter or soil. Other larval habitats include riparian sand and gravel (e.g. Leseigneur 1972), termite colonies (Costa et al. 1992), bromeliads (Costa et al. 1988) and tunnels made by Cerambycidae in living trees (Dushem 1922). Some Elateridae, such as the crop pest *Conoderus exsul* (Sharp), exhibit better larval survival on plant diets but are also facultative predators (Williams and Galbreath 1987). Some species act as predators beneficial to horticulture, for example *Pyrophorus luminosus* (Illiger) preys on scarabaeid

sugar cane pests (Wolcott 1923). Larvae can be collected by sifting soil and litter, peeling tree-bark and excavating decaying trees and using underground bait stations.

Adult Elateridae are 2-60 mm long and can be collected at lights, in traps baited with wine or pheromones, on and in the soil, on and under tree bark and on foliage (especially newly emerged leaves) and flowers. Some adult Elateridae feed on flowers, leaves, sap flows and soft-bodied insects. Although many elaterids are cryptically coloured, some are bright, bioluminescent, or marked with contrasting eyespots. At least one species is chemically defended against predators (Dettner and Beran 2000). Most, or all, elaterid species can propel their bodies into the air using a complex set of thoracic structures (Leseigneur 1972), although the primary function of this ability remains unclear. Many species have adult life spans of only a few weeks, and fly during this time to find mates and oviposition sites.

1.1.2 Previous phylogenetic research

Elateridae remains one of the largest beetle families for which there are no well-supported general phylogenetic hypotheses. Previous phylogenetic analysis of Elateridae have included small taxon samples and, with one exception (Calder et al. 1993), few characters. Early phylogenetic analyses by Hyslop (1917), Jagemann (1955), Ôhira (1962) and Dolin (1978a) were performed manually based on the author's best explanation of morphological evidence observed in adults, larvae and fossils. All of these, except Jagemann (1955), considered Cardiophorinae to be either the sister group to the remaining subfamilies, or one of several offshoots from a single basal lineage based

on the distinctiveness of Cardiophorine larvae. Although these early phylogenies have provided important characters for quantitative analyses, their own findings are no longer considered persuasive because of their informal methods. Similarly, phylogenies of the Elateridae of a single country or region are not considered here, because of their small taxon samples.

Computational, parsimony based phylogenetic analysis, has produced more objective, repeatable findings about elaterid relationships. The first study, by Lawrence (1987) included all Elateridae as one operational taxonomic unit (OTU, i.e. one row of data in a phylogenetic matrix), and therefore did not test elaterid monophyly. This tree was used to support an earlier, largely ignored, placement of Cebrionidae as a subfamily of Elateridae. However, this finding was partially contradicted by the findings of the same study, since these 2 OTUs were placed as sister taxa in only some of the 20 most parsimonious trees. The finding most relevant to the present work is that the Clicking Elateroidea formed a monophyletic group, including Elateridae, Cebrionidae, Eucnemidae, Cerophytidae and Throscidae. Subsequent studies have focused on the phylogeny of this clade.

A second study, by Calder et al. (1993) included 25 OTUs and 94 adult and larval morphological characters for 18 elaterid genera and eight outgroup taxa. This study used entire genera as OTUs and thereby risked error wherever the genera included were non-monophyletic. This study, like that of Lawrence (1987) found that the clicking Elateroidea are a monophyletic group, including representatives of Elateridae (including Cebrioninae and Lissominae), Cerophytidae, Throscidae and Eucnemidae. A strict

consensus of their results was mostly uninformative about whether these families render Elateridae non-monophyletic. One exception to this was that one of two elaterid clades in the basal polytomy of clicking Elateroidea included *Lissomus* and *Drapetes*, which were previously considered to be part of Throscidae sensu Crowson (1955), or their own family (e.g. Costa 1988). The strict consensus of these results did suggest that the nearest relatives of the one included cardiophorine genus belonged to Elaterinae. However, these findings do not rule out the possibility that one of the five elaterid subfamilies unrepresented in the study is more closely related to Cardiophorinae. Additionally, if the current subfamilies are not monophyletic, which remains unknown, other true subfamilies could be concealed within them. Although these are the best elaterid cladograms available, they do not indicate which subfamilies are the nearest neighbours to Cardiophorinae. Because of this, a larger taxon sample is needed to test cardiophorine monophyly.

Results of the third and most recent study, by Muona (1995), indicated that Elateridae are not rendered paraphyletic by Cerophytidae. This finding agrees with some, but not all of the most parsimonious trees of Calder et al. (1993). Muona's study also indicated that Anischiidae, a family not included in previous studies, may render Elateridae paraphyletic. While both Muona's study and that of Calder et. al (1993) found that members of Throscidae rendered Elateridae paraphyletic, Muona found that Throscidae (*Sensu* Crowson 1955) was monophyletic. This is unlike the optimal topologies of Calder et. al (1993), which found that only Lissominae, from a polyphyletic Throscidae belonged within Elateridae. Muona's study provides little information about

the placement of Cardiophorinae, because it included only eight elaterid genera. Muona found that Calder's larval data provided a phylogenetic signal that was incongruent with the adult morphological data of both authors and also conclusions of all earlier non-computational taxonomists. This study's findings about the monophyly of Elateridae and the placement of Cardiophorinae are only weakly supported, and provide little useful information for designing a test of cardiophorine monophyly.

1.1.3 Rationale, taxonomic background and current status

Although the central questions that my thesis seeks to answer are about the membership and internal relationships of Cardiophorinae, additional knowledge about Elateridae is required to answer them. Phylogenetic analyses used for robust testing of cardiophorine monophyly must include representatives of all other groups with which cardiophorines might be confounded. Identification of these groups requires a phylogenetic analysis including Cardiophorinae, all other elaterid subfamilies and all other beetle families that might render Elateridae non-monophyletic.

The monophyly of Elateridae has been questioned recently because of disagreement about the addition of species formerly considered non-elaterids. Major examples include the recent disagreement about the addition of family Cebrionidae (Lawrence 1987) and the subfamily Lissominae (formerly of Throscidae) to Elateridae (Calder et al. 1993). Recent phylogenetic analyses (Calder et al. 1993, Lawrence 1987, Muona 1995) are individually inconclusive or contradict each other weakly on these subjects and the possible inclusion of the remainder of Throscidae in Elateridae. None of

these studies are full tests of elaterid monophyly because they include only partially overlapping subsets of elaterid subfamilial diversity.

Although there are many stable, broadly recognised elaterid subfamilies, tribes and genera, the subfamily level classification of Elateridae has long troubled researchers. Many researchers have commented on the difficulty of defining subfamilies and the relationships between them (e.g. Candèze, Calder). Historically, 56 subfamily names have been published, 23 of which have been used since 1995. This number of subfamilies is excessive considering that the more diverse, but better studied families Cerambycidae, Chrysomelidae and Curculionidae have only 13, 10 and six subfamilies respectively (Lawrence and Newton 1995). Other evidence of discordant subfamilial classification is that different authors use conflicting classifications, continuing to use several names placed in synonymy by others.

1.1.4 Phylogeny: outgroup of Elateridae

Previous studies indicate that Artematopodidae are a possible sister group to clicking elateroids, but beyond the range of possible elaterid paraphyly (Calder et al. 1993, Lawrence 1987, Muona 1995). In order to represent these groups, and to facilitate comparability to earlier studies the following taxa should be used as outgroups:

Artematopodidae (*Macropogon*); Eucnemidae (*Fornax*, *Phyllocerus* (Closely related (Muona 1993) genera *Onichodon* and *Anelastes* were encoded instead of these)); Eulichadidae (*Eulichas*); Cerophytidae (*Cerophytum*); and Throscidae (*Aulonothroscus*).

1.2 Introduction to the subfamily Cardiophorinae

1.2.1 Taxonomic background of Cardiophorinae and current status

Although it is one of the largest and most universally recognised elaterid subfamilies, hypotheses about the membership and internal taxonomic structure of Cardiophorinae have never been tested phylogenetically. Additionally, no single work including keys and descriptions for all Cardiophorine genera has been published since Schwarz (1906). Since the publication of the most recent taxonomic catalogue of Cardiophorinae (Schenkling 1925), 13 new genera, six subgenera and hundreds of species have been described. For these reasons, it is difficult to identify many cardiophorines and impossible to determine whether the current nomenclature reflects evolutionary history. Additionally, inconsistencies in the use of genus level names also make genus level identifications difficult using literature alone.

Cardiophorinae has 29 described extant genera worldwide (Appendix 1) and also four fossil genera, which together include about 1100 species. Previous researchers have described genera based mainly on various combinations of the following character systems: number of mandibular teeth; length and vertical position of lateral pronotal carina; number of tarsal claw points; presence/absence of tarsal lobes as well as the distinctive characteristics of one or a few species. These generic concepts represent historical efforts to group species by overall similarity and to set distinctive species apart. However, it remains unknown whether any of these genera are monophyletic, and similar studies of other groups indicate that many probably are not.

Historically, Eschscholtz (1829) named three Cardiophorine genera, in his initial division of the genus *Elater*. During the 19th century 15 additional Cardiophorine genera were described, of which four to seven are now in synonymy according to various authors. Candèze (1860) wrote the first genus-level revision of Cardiophorinae, as part of a four-volume subfamily, genus and species level revision of Elateridae (Candèze 1857-63). The most recent genus level revision was published by Schwarz (1906). Thirteen of the new genera (14), fossil genera (four) and subgenera (seven) described in the 20th century are from Asia, four are from Africa, two from the Neotropics and two from Australia. Fifteen of these genus-level names are based on species first described in the 20th century. Fleutiaux, Ôhira and six Russian authors made most of these genus level changes. Despite this recent proliferation of genus names, more than 90% of all species remain in a few genera described in the 19th century: *Cardiophorus* (663), *Horistonotus* (109), *Paracardiophorus* (86), *Dicronychus* (74); *Cardiotarsus* (59) and *Esthesopus* (54). The monophyly and membership of all genus level groups remain untested hypotheses because phylogenetic analysis has never been applied to any of these genera.

Cardiophorinae was effectively divided into two tribes when Gurjeva (1974b) transferred the monotypic tribe Nyctorini from Elaterinae into Cardiophorinae. This transfer was made without comment, thus suggesting that Gurjeva did not realize that Nyctorini was not originally part of Cardiophorinae. For this reason, it seems possible that the division of Cardiophorinae into two tribes (Cardiophorini and Nyctorini) was accidental. Dolin (1975a) placed Nyctorini in synonymy under Cardiophorini, effectively eliminating the tribal level classification. Stibick (1979a) removed Nyctorini from

synonymy because, although he dismissed two of its diagnostic characters as suspect, he was unable to identify other Cardiophorinae with absent [short] prosternal lobes. One hypothesis tested by this work is that *Nyctor* is the sister group to the remainder of Cardiophorinae, and thereby also testing the validity of subfamily Nyctorini.

1.2.2 Distribution, biology

Cardiophorinae are known from all continents except Antarctica and from most large islands from the temperate and tropical zones. While larvae of *Horistonotus uhleri* Horn are known to attack roots of corn, cotton, oats, peanuts and tobacco (Gibson 1916), the dominant larval feeding mode of most species is nevertheless expected to be carnivory, because of their large exodont mandibles. Most larval cardiophorines inhabit soil (especially sandy soil) and rotting wood or hollow trees (Palm 1972) and are sometimes among the most abundant insects attracted to lights in desert habitats. Cardiophorines are likely to be trophically important where they are abundant. They are also important as pollinators: for example one South African orchid is pollinated primarily by a single species of *Cardiophorus* (Peter and Johnson 2005). Many Cardiophorinae are rare or localized to sand deposits or ancient forests (e.g. Douglas 2003, Girard 2003, Platia and Gudenzi 2000b) and probably at risk of extinction. Presently only one species, *Cardiophorus gramineus*, has formal conservation protection (as one of two insects considered extirpated from Sweden (Forslund 2000)).

1.2.3 Phylogeny: outgroup of Cardiophorinae

While any non-cardiophorine elaterid could reasonably be the outgroup for phylogenetic analysis of Cardiophorinae (Nixon and Carpenter 1993) the problem of outgroup selection is complicated by uncertainty about ingroup monophyly. Non-computational analyses of Elaterid phylogeny have concluded that the sister group of Cardiophorinae is the rest of Elateridae based on larval characters (Hyslop 1917, Ôhira 1962), or both ((Physorhininae + Pomachiliinae + Elaterinae) + (Diminae + Hypnoidinae)) based on adult characters (Jagemann 1955), or Negastrinae alone based on adult morphological characters (Stibick 1979a), or Elaterinae alone based partly on stratigraphic and adult morphological evidence (Dolin 1978a). The analysis by Calder et al. (1993) suggests that Elaterinae is the sister group to Cardiophorinae, although no Negastrinae were included in that analysis. None of these hypotheses however, have been rigorously tested. Therefore the only way to identify the ingroup and sister group of Cardiophorinae and thereby test its phylogenetic limits is to first conduct a phylogenetic analysis of Elateridae in general.

1.2.4 Phylogeny: monophyly of Cardiophorinae

Although not tested phylogenetically, the monophyly of Cardiophorinae as a group has never, to my knowledge, been questioned. This group has been universally recognised since its description in 1859 (Candèze, as a subtribe). Possible non-monophyly is evident, however, from inconsistencies in which characters are used to

separate Cardiophorinae from Negastrinae and from questions about the placement of three genera. Several apparent synapomorphies unite Negastrinae and Cardiophorinae, the most distinctive of which include the meeting of the mesosterna and metasterna laterad of the mesocoxal cavities, the absence of the anal cell of the wing and basally fused parameres. The characters used to distinguish these two subfamilies since their description (Candèze 1860, Negastrinae as part of Cryptohypnites) are the short cardiophorine prosternal process, the broad prosternum of most Negastrinae and the heart-shaped scutellum of most Cardiophorinae. However Stibick (1979a) noticed that these were not universal and has omitted the prosternal width character and qualified the other two characters with the terms “usually” and “normally.” These diagnostic problems are also evident in difficulties placing the three genera *Agrypnella*, *Cardiohypnus* and *Rivulicola*. Although these were described in Cardiophorinae because of their heart shaped scutella, they were later moved to Negastrinae because of evidence from other characters. For these reasons, the monophyly of Cardiophorinae is not evident from previous analysis of adult morphology.

Other putative evidence for cardiophorine monophyly comes from the distinctiveness of known cardiophorine larvae. The peculiar characteristics of these are widely considered possible synapomorphies (Hyslop 1921, Ôhira 1962, Stibick 1979a, Calder 1996). These characteristics include: deeply cleft mandibles, thread-like abdomen with extra pseudosegmentation and digitate anal lobes (Stibick 1979a). Although this type of larvae is known from Europe (Palm 1972), Central Asia (Atamuradov 1993), northeast Asia (Dolin and Gurjeva 1975), Japan (Ôhira 1962), Australia (Calder 1996),

New Zealand (collections only), North America (Tenhet 1941) and South America (Costa et al. 1988), the larvae of most genera and species remain unknown. Because of this, it remains unknown whether these probable synapomorphies are ancestral to Cardiophorinae alone, to Cardiophorinae and other taxa, or to only a subgroup of Cardiophorinae. Although these strong larval morphological characters exist and are possible evidence for the cardiophorine monophyly, too few larvae are known for them to be used for an actual test of monophyly.

The monophyly of Cardiophorinae remains in need of testing, because it has not been demonstrated through analyses of larval or adult morphology to date. Phylogenetic analysis of adult morphology appears to be the best method available for such a test. Phylogenetic analysis is better for testing such hypotheses than traditional taxonomic methods, because it can incorporate more data, and do so in a way that is relatively unbiased by the opinions of the investigator. Adult morphological data is the best data available in this, because unlike data from DNA sequences, behaviour and larval morphology, it is available for nearly all known species of Cardiophorinae.

1.2.5 Phylogeny: phylogeny within Cardiophorinae

The only published phylogenetic hypotheses published concerning Cardiophorinae are those implied by its classification into tribes, genera and subgenera. The phylogenetic analyses presented here are the first efforts aimed at testing these hypotheses using computational tools.

1.3 Hypotheses Tested

1.3.1 Subdivisions within Elateridae: the position and membership of Cardiophorinae

Because phylogenetic analysis examines millions of possible topologies, it is not possible to discuss each hypothesis evaluated in finding an optimal tree. However, several central hypotheses must be evaluated formally here. The first hypothesis is that Cardiophorinae are a monophyletic group. This hypothesis is tested here by analysis of 2 datasets. The first includes several cardiophorine genera, non-cardiophorines suspected to belong in Cardiophorinae and representatives of as many other subfamilies and tribes of other clicking elateroid groups as possible. Analysis of this dataset is intended to identify the closest relatives of Cardiophorinae and any groups with which they might be confounded. Although incidental to this study, this analysis is also the most thorough test of elaterid monophyly, subfamily monophyly and assessment of within family relationships to date.

Using the closest relatives of Cardiophorinae identified here (Chapter 2), a second dataset is designed to test whether these taxa render Cardiophorinae non-monophyletic. Designed to be an effective test, this dataset includes a broad sample of these associated taxa as well as an outgroup that is beyond the expected range of possible Cardiophorinae non-monophyly. It also includes the type species of the type genus of both Cardiophorine tribes and the type species of all but three genera (one of which is represented by another species). These types are required to include the full recognised diversity of

Cardiophorinae and also the taxa most likely to render Cardiophorinae non-monophyletic.

1.3.2 Age of Cardiophorinae

Dolin (1976) has suggested that Cardiophorinae were present in the Upper Jurassic, based on putative cardiophorine genera that he described from fossils. Iablokoff-Khnzorian (1961) described another putative cardiophorine genus from (more recent) Baltic amber. By including these species in phylogenetic analyses of clicking Elateroidea it is possible to test whether the available evidence supports the placement of these fossil genera within Cardiophorinae. This thereby tests whether these fossils can legitimately be used to infer the age of Cardiophorinae.

1.3.3 Subdivisions Within Cardiophorinae and Biogeographic Hypotheses

The only previously stated phylogenetic hypotheses about relationships within Cardiophorinae are those implied by the tribal, generic and subgeneric classification. The second dataset provides an effective test of the monophyly of both tribes because it includes all their constituent genera (except for two of Cardiophorini). Thoroughly testing the monophyly of all cardiophorine genera is beyond the scope of this study because it would require inclusion of an additional 1000 species. However, it is nevertheless useful to include multiple exemplars of each genus, wherever possible, to improve the power of phylogenetic inference and for a preliminary test of genus-level monophyly. To these ends, it helps to include the type species of all subgenera and any morphological oddities.

Further testing is accomplished by adding at least one species from any world biogeographic region where the genus occurs, other than that of the type locality. These species are the best to include a priori, because they are the most likely to cause rejection of hypotheses of generic monophyly.

This phylogeny will also be used to test four biogeographic hypotheses of regional monophyly for Cardiophorinae: New World Cardiophorinae; New World *Cardiophorus*; Neotropical Cardiophorinae; Australian Cardiophorinae. The finding that any of these groups are monophyletic would suggest a single origin of the fauna of that landmass. Non-monophyly of these faunas could indicate either one or more trans-oceanic dispersal events, or that regional faunas predate ancient continental vicariance events.

1.4 Research Objectives

1. To test whether Cardiophorinae is a monophyletic group, and if necessary to redefine the limits of Cardiophorinae, to ensure that it is monophyletic.
2. To provide a description of Cardiophorinae and its tribes and keys and diagnoses for all 31 genera.
3. To provide a rigorous phylogenetic analysis of Cardiophorinae and Elateridae which will allow better understanding of the evolution and general biology of these groups.

CHAPTER 2

Subdivisions within Elateridae: the Position, Membership and Age of Cardiophorinae

2.1 Introduction

Phylogenetic analysis of clicking Elateroidea is necessary, as discussed in section 1.1, for choosing outgroups for use in testing the monophyly of Cardiophorinae in Chapter 3. Such a phylogeny is also needed to test published fossil-based hypotheses about the age of Cardiophorinae for the reasons presented in section 1.3.2. Furthermore, such a phylogenetic analysis is expected to provide additional insights into the phylogeny of clicking elateroids, which are beyond the goals of this thesis.

I present here the most detailed analysis of clicking Elateroidea to date, using 55 exemplars that include much of the morphological variation within the group. These include representatives of 16 of 17 subfamilies listed in Lawrence and Newton (1995). The type species of the type genera of most of these subfamilies were included to ensure that these exemplars truly reflected the named subfamilies. Taxon sampling emphasized Elateridae because my primary goals were to test the monophyly of Cardiophorinae and identify its possible sister groups for later use as outgroups. This sampling bias was chosen because the Elateridae, as traditionally defined, are considered by all previous workers to include the closest relatives of Cardiophorinae.

Because the monophyly of no elaterid subfamilies have been previously tested, this study includes multiple exemplars of the 7 most speciose subfamilies. These

exemplars also include the type genera for 12 additional subfamily names considered synonymized in Lawrence and Newton (1995). This study is intended as a framework to help guide future taxonomic studies and not as a basis for reclassification of the clicking Elateroidea.

2.2 Materials and Methods

2.2.1 Specimens examined

Specimens examined for morphological coding belonged to 16 insect collections (Table 2.1). Codens listed here follow those listed in Arnett et al. (1993), except where other letters are preferred by individual collections. Most of these 158 specimens of 58 species were borrowed and encoded at Carleton University, although a few were coded while visiting museums in Brussels (ISNB) and Paris (MNHN). Among these specimens were 29 primary type, allotype or paratype specimens representing 16 species.

Table 2.1. Codens for insect collections from which specimens were examined.

CMNC	Canadian Museum of Nature, Ottawa, Ontario, Canada
CNCI	Canadian National Collection of Insects, Arachnids, and Nematodes, Agriculture and Agri-Food Canada, Eastern Cereal and Oilseed Research Centre, Ottawa Ontario, Canada
HBDC	Hume Douglas Insect Collection (personal collection), Ottawa, Ontario, Canada
ISNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
JNIC	John Nunn Insect Collection, Dunedin, New Zealand
LSUK	Linnean Society, London, United Kingdom
MCZC	Museum of Comparative Zoology, Harvard University, Cambridge Massachusetts, USA
MNHN	Muséum National d'Histoire Naturelle, Entomologie, Paris, France
NHM	The Natural History Museum [formerly British Museum (Natural History), BMNH], London, England
NZAC	New Zealand Arthropod Collection, Landcare Research, Auckland, New Zealand
PIN	Paleontological Institute, Russian Academy of Sciences, Moscow, Russia
SANC	South African National Collection of Insects, Pretoria, South Africa
UCMP	University of California Museum of Palaeontology, Berkeley, California, USA. UCMP is the depository of one type specimen that was unavailable for examination.
USNM	United States National Museum (Natural History), Washington, District of Columbia, USA
ZMHB	Museum für Naturkunde der Humboldt-Universität, Berlin, Germany
ZMUC	University of Copenhagen, Zoological Museum, Copenhagen, Denmark

Wherever possible, species identifications were verified by comparison to type specimens (Appendix 7). Information from type specimens was often used in coding species. Lectotypes were not designated in this work, because it was considered preferable to leave that choice to authors of future species level revisions. For *Agriotes sputator* Linnaeus, type series included specimens of multiple species and no lectotype had been designated. For this species, the type specimen that was used in this study was the only one that matched the definition of the genus and species used by recent authors. For other type series without designated lectotypes, specimen labels were followed to determine which specimen would be considered the type here. Unofficial lectotype designations or beginning of series specimen determination labels of the original authors were considered indicative of type status.

For this study, 56 ingroup and two outgroup species were coded for phylogenetic analysis (Appendices 5-7). Of these, 19 were missing genitalic data for one sex. For two extant species, material was unavailable for both the aedeagal and female genitalic characters. Non-genitalic characters were coded from male specimens only, except for one species, for which only females were available. It was impossible to code most characters, including all genitalic characters for the three included fossil taxa. Literature was used to supplement coding of four species for which some characters could not be examined (Calder 1996, Calder et al. 1993, Costa et al. 1994, Platia 1994). All terminal taxa were single species except for two distinctive genera, which were coded using males and females of different species. For the genus *Anischia* Fleutiaux, males were coded from an unidentified male from Panama, and female genitalia were coded using

information from a drawing of an unidentified species provided by Dr. John Lawrence of CSIRO, Australia. The genus *Thylacosternus* was encoded using a male specimen of *T. vittatus* Champion and a female of *T. rubricollis* Bonvouloir.

2.2.2 Specimen preparation and examination

Specimens were relaxed for examination by placement in nearly boiling distilled water for 10-30 minutes. Wings were photographed in water on a glass microscope slide under a cover slip. Male and female genitalia were prepared and examined as outlined in Calder (1996). Specimens were examined using a Leica Wild M-10 dissecting microscope and all structures examined were photographed using an attached Nikon Coolpix 995 digital camera. Image files were catalogued in a database using Portfolio v6.0. Measurements were made using either an ocular micrometer or from digital photographs using Corel® Photo-Paint 12 software. Drawings were made using these digital photographs. Vestiture has been omitted from drawings except where taxonomically informative.

Structural terms follow those of Douglas (2003), which are based on those used by Calder (1996) and Casari (1998). Wing venation follows Kukalova-Peck and Lawrence (2004). The incomplete carina on the sides of the pronotum of some Cardiophorinae (e.g. *Cardiophorus gramineus* Scopoli), traditionally referred to as the submarginal line, is considered here as homologous with the lateral carinae of other Elateridae (e.g. *Elater ferrugineus*) and is referred to as such. This decision was based on examination of many Cardiophorinae, including species with complete and incomplete carinae of similar

appearance. In some species (e.g. *Paraplatynychus mixtus* Fleutiaux) this carina follows the edge of the pronotum, while in others the dorsal part of the pronotum appears expanded laterally beyond this line. In species with only one carina extending anteriorly from the hind angles it was not possible to determine whether this was the pronotal lateral carina or the hind angle carina. This is because both extend to the anterior edge of the pronotum in some species and both are near the side of the pronotum.

Additional tarsal claw points of some species, including rectangular basal points (including flange *sensu* Stibick 1971), are counted as claw apices. Unlike Douglas (2003), the sclerotised base of the spermathecal gland duct inside the bursa copulatrix and appendages thereof are not considered here as homologous with the distal sclerites of the bursa copulatrix. This change was adopted because *Phorocardius florentini* Fleutiaux was found to have both kinds of structures. Additionally the term “glandular reservoir”, used in Calder 1996 and Douglas 2003 to refer to an extension or appendage of the bursa copulatrix, is replaced here by the more descriptive term “pedunculate anterior sac”.

2.2.3 Choice of optimality criteria

Since the abandonment of phenetic methods, and until 2001 (Lewis), morphological phylogenetics had used parsimony exclusively as an optimality criterion because that was the only one available. However, it is now also possible to analyse data using model-based Bayesian methods. In this section I briefly introduce both Bayesian and parsimony methods and describe my rationale for using both, but I favour the results of Bayesian analyses for interpretation.

Parsimony, the oldest widely accepted method of phylogenetic analysis, uses the principle of Occam's razor to choose between the possible phylogenetic trees for a set of taxa. Occam's razor posits that when choosing between explanations for a phenomenon, one should favour ones with fewer unnecessary assumptions, and is used in phylogenetics to argue that the simplest phylogenetic explanation for the data is probably the most accurate. Parsimony is operationalised by choosing the shortest phylogenetic tree, or the one that posits the fewest evolutionary changes. While it is widely recognised that the shortest tree often differs somewhat from the true phylogeny, the same is true for all methods, and parsimony remains the favourite of many. Parsimony does not require additional information about evolutionary processes (i.e. evolutionary models and parameter settings are not estimated prior to analysis). For this reason, parsimony is viewed by many as making fewer assumptions than model-based methods, although agreement on the nature of these assumptions is elusive (Sober 2004).

Aside from questions about its underlying assumptions, the most serious shortfall of parsimony is that it does not make use of branch length information when counting the computational cost of evolutionary changes (Holder and Lewis 2003). This can be expected to result in phylogenetic error, especially in parts of trees with relatively long or short branches. This difficulty is apparently corroborated empirically by parsimony's relative susceptibility to long-branch attraction (Felsenstein 1978, Huelsenbeck 1995, Bergsten 2005), whereby branches with many evolutionary changes tend to be grouped together based on coincidentally shared changes (or homoplasy).

A primary goal of Bayesian phylogenetic analysis of morphological data is to solve the problem of long-branch attraction. Before discussing this, however, a brief introduction to Bayesian methods is needed. Bayesian analysis of a morphological data matrix began with a set of randomly chosen initial topologies and prior probability distributions for all active parameters (here: character state frequencies prior = Symmetric dirichlet with fixed (-1.00) variance parameter; shape prior = Uniform (0.00,200.00); topology prior = all topologies equally probable a priori; branch lengths prior = branch lengths are unconstrained: exponential (10.0)). A model of evolution is also selected from among the three available for morphological analysis. Once the data, model and parameters are chosen, Markov-chain based phylogenetic analysis is performed using MrBayes (Huelsenbeck and Ronquist 2001, Ronquist and Huelsenbeck 2003 (the only available software for Bayesian analysis of morphological data)).

The Markov chain Monte Carlo algorithm makes a randomly selected change to each chain (or set of initial parameters) in the analysis and then recalculates the relative posterior-probability density of the new state, given the model and data. If the new state has a higher posterior-probability density than the old one, the change is accepted and another change is made to the new state. If the proposed change has a lower posterior-probability density, the change will usually be rejected and the chain returns to its former state. However, changes to less probable states will be accepted a set proportion of the time, especially when the probable density is only slightly lower. These steps are repeated several million times, and the simultaneously running chains periodically exchange information to fully explore parameter space. Overall, the chains tend to spend

most time exploring areas of high posterior-probability density. This is particularly true of the cold chain, the chain least likely to accept a change to a lower posterior-probability density. Together they explore parameter space such that the number of cycles that the cold chain spends visiting a particular parameter state (e.g. a topology or branch length) is proportional to the probability that the parameter state is correct. For this reason, a majority rule consensus of trees sampled after an initial burn-in period is a well-tested estimate of phylogeny. The proportion of trees showing a particular clade, or the posterior probability of that clade, is expected to be proportional to the probability of that clade being correct.

Again, the major expected advantage of using Bayesian analyses for morphological data is that they handle branch length information more effectively than parsimony. Bayesian analyses are based on evolutionary models, and thus unlike parsimony, consider a set of branch lengths for all characters simultaneously. Empirically, the only study comparing the two methods for morphological data (Wiens 2005), found that accuracy of Bayesian analyses equalled or exceeded that of parsimony under a variety of conditions. In that simulation study, Bayesian analyses performed better at avoiding long branch attraction, and for using incomplete or fossil taxa, although reconstruction of very long branches was poor using both methods. For this reason Bayesian analysis appears to be most accurate method available for phylogenetic analysis of morphological data.

Although Bayesian analysis is now in widespread use for molecular data, recent criticisms have questioned the reliability of its results. The first criticism is that Bayesian

probabilities may be too liberal (Suzuki et al. 2002) compared to more conservative maximum-likelihood non-parametric bootstrap scores. However, this argument is not currently relevant to choosing Bayesian analysis for morphology data since there is no publicly available maximum likelihood-based phylogenetic method for which bootstrap support is a useful measure. A second concern, that Bayesian analysis is vulnerable to supporting a wrong bifurcating topology when polytomy is the correct answer (Holder and Lewis 2003), is possibly valid. Because it is not yet known whether true polytomies are common in nature, and because no more reliable method is known, Bayesian analysis is nevertheless considered the preferred method here.

Bayesian analysis was used for all analyses, because the available evidence indicates that it is the most accurate method available for phylogenetic reconstruction. However, parsimony analyses were also performed because that technique remains widely accepted. Additionally, parsimony is still the only phylogenetic optimality criterion available for evaluating trees with gap-weighted data. The preferred measures of support for parsimony analysis, decay indices (Bremer 1988) and non-parametric bootstrap (Felsenstein 1985) resampling were calculated, and corrected for branch length (Zander 2004) for all tests to compare results of parsimony and Bayesian analyses.

2.2.4 Data Selection and Taxon Sampling

Adult morphological characters were selected for phylogenetic analysis because larval morphological data and DNA sequence are much less available. Larval data is scarce and unreliable, because larvae of most species are unknown, and because it is

often impossible to verify the accuracy of published larval associations. Although DNA sequence data is desirable, it is difficult to obtain suitable specimens for such projects including taxa from all biogeographic regions. Unlike specimens available for morphological analysis, for which even rare species from many regions can be borrowed from museums, specimens for DNA-based research generally must be collected fresh. This is because most museums do not yet have extensive, well-curated collections of appropriately preserved specimens for DNA analysis.

Despite these expected difficulties, material for DNA analysis was collected throughout the project, but the difficulty of obtaining exemplars of focal genera and higher taxa prevented use of DNA data. Additionally, difficulties were encountered identifying primers for PCR amplification and sequencing of suitable genes for this analysis. Many commonly used gene regions were unusable because they evolve either too rapidly or too slowly for testing these genus and subfamily level hypotheses. Efforts to amplify two ribosomal genes, 16S (mitochondrial ribosomal) and 28S (nuclear ribosomal), using primers from both the literature and ones designed for Elateroidea (with the assistance of Prof. Myron Smith, Carleton University) were unsuccessful. Efforts to include DNA sequence data in this project were discontinued because of these difficulties in obtaining material and functional primers for appropriate genes.

There are several reasons why adult morphological data is a good choice for phylogenetic studies that use a single data type. Firstly, a thorough review of type species and their morphological characters is necessary to relate phylogenetic findings to the existing taxonomic literature. Secondly the goal of inclusion of all subgroups of the focal

taxon is most likely to be met with morphological analyses. Such sampling is important for revisionary studies, which must treat all of these subgroups. Strong taxon sampling is also important for breaking long phylogenetic branches, and thereby reducing the problem of long-branch attraction. Here, morphological data allowed the best-possible taxon sampling, because nearly all species selected a priori were available for morphology coding. Additionally, inferences from morphological data are more reliable than those made from a single gene region because morphological datasets can be expected to sample genetic information from many parts of the genome. This helps avoid error commonly introduced by only considering the phylogeny of a single gene. The morphology data used here is expected to reflect many parts of the genome because they include information from nearly all externally visible sclerites and also male and female internal and external genitalia. Finally, such morphological matrices can later be analysed in combination with molecular datasets. Separate and (where appropriate) combined analyses of multiple character systems are widely considered to provide the most reliable and informative trees possible (de Queiroz et al. 1995, Nylander et al. 2004).

Ideally, phylogenetic analysis of a higher taxon should include all member species and any species that might render them non-monophyletic. However, for large groups like Clicking Elateroidea it is only feasible to include a well chosen sample of these taxa. To be taxonomically meaningful, a tree for a group of families should include the type genera for all available subfamily-group names within them. Preferably, several morphologically divergent exemplars of each of these should be included as a preliminary test of subfamily level monophyly.

Ingroup taxon sampling for this analysis included 55 representatives of all four clicking elateroid families (*sensu* Muona 1995). Sampling was heaviest in Elateridae because the primary goal was to identify outgroups for analysis of Cardiophorinae (Appendix 7). *Macropogon* (Artematopodidae) and *Eulichas* (Eulichadidae) were selected as outgroups because they were identified as elateroids outside the clicking elateroid clade (Lawrence 1987), and to reflect the taxon sampling of previous studies.

Within Elateridae, this study included type genera of 23 of the 26 subfamily names used since 1994. Two of the missing subfamilies (Denticollinae and Melanactinae) are widely considered junior synonyms of Dendrometrinae (Ruiz 1996, Johnson 2002c), which was represented by five other genera. One valid subfamily, Subprotelaterinae, was unrepresented because no specimens could be obtained. Tribal level sampling was heaviest in subfamilies Elaterinae (7/9 tribes) and Dendrometrinae (2/3 tribes) which have been considered possible sister groups of Cardiophorinae. Seven genera of subfamily Negastrinae were included, because that subfamily is also considered a possible sister-group to Cardiophorinae. Non-type specimens were identified by comparison to types (23/58 species, Appendix 6), and labelled with unique identifier numbers (Appendix 5). Where types could not be examined, specimens identified by experienced workers (9/57 species) (Appendix 7) were examined. One species was new to science. The remaining 25 species were identified using published taxonomic literature alone. All identifications of non-type specimens, and verifications of type status were performed using published taxonomic literature (Appendix 7).

The type species of *Exoeolus* (formerly *Brounaeolus*), New Zealand's only known cardiophorine genus was initially known from only two female type specimens. Revision of this genus indicated that two other species from the same locality, but known from male holotypes only, were actually conspecific (Douglas 2005). Subsequent to this revisionary work, it was possible to encode *Exoeolus* using both males and females. While seeking additional specimens of *Exoeolus* for this revision, several males of an undescribed species from New Zealand that apparently belonged to Cardiophorinae were provided by Dr. R. Leschen of NZAC. This species was also added to the phylogenetic matrix.

2.2.5 Morphological character coding

Morphological character selection should use a uniform methodology to consider all observed morphological variation as a potential source of characters. To do otherwise may introduce bias, especially if apparently homoplasious characters are rejected (Poe and Wiens 2000). Similarly, even characters showing within-species polymorphism should not be excluded, because doing so reduces phylogenetic signal (Wiens 2000). Frequency coding, the method identified by Wiens (2000) as the most effective for coding within-species polymorphism, has not been widely tested. This method is also not widely accepted because it effectively considers allele frequencies to be species characteristics (instead of as population characteristics only). Simulation and congruence studies by Wiens (2000) found that majority coding, coding polymorphisms as their most common form, also performs better than excluding polymorphic characters. Although this

coding method is seldom discussed, it is often practiced unknowingly when rare morphological variants are excluded from character analysis as an artifact of small sample sizes.

This study used majority coding of polymorphisms, coding polymorphic characters as their most commonly observed form for each species. This was done partly because the number of available specimens of most species was too low to practice frequency coding. Sample sizes were small because many included species are rare, and specimens in collections are too valuable to allow semi-destructive examination of numerous specimens. Exemplars used in this study often originate from a single collection series, which often was the type series. This is because the species-level taxonomy of many genera is too poorly developed to allow certainty that any other putative conspecifics really are the same species. For qualitatively defined characters, majority coding was practiced by coding the character state most commonly observed in each species. For 24 quantitatively coded morphometric characters (Appendix 8), the value entered for each species was the mean of a series of ratios of pairs of length measurements. One morphometric character was defined angularly in degrees. For the one quantitatively coded meristic character, values entered were means of counts of rows of spines on a sclerite.

Morphological character selection and coding were performed together. All observed variation was evaluated as a potential source of characters following a uniform procedure to avoid bias. This procedure was to examine all observed variation and describe all suitable variation as characters. To be considered suitable, variation between

homologous structures must allow diagnosis between at least one pair of species in the majority of cases. Characters must be primary statements of homology such that a character state shared between two species can reasonably be considered to be possible evidence of homology, without reference to other phylogenetic evidence. For a character to be considered suitably repeatable and objective for use, it must also be possible to describe all of its states simply and accurately (either qualitatively or quantitatively). An initial list of candidate characters was assembled from the adult morphological character lists of Calder et al. (1993, 62 characters) and Muona (1995, 63 characters, many similar to those from Calder et al. 1993), with additional characters added from published keys and taxon descriptions. This preliminary list was edited to remove or modify those that did not meet the outlined criteria.

Additional phylogenetic characters were identified from examination of clicking Elateroid specimens. Characters relevant to Cardiophorinae and Negastrinae were identified by complete disarticulation of two specimens of each sex of the following species: *Aptopus pullatus* Horn; *Esthesopus parvus* Horn; *Cardiophorus fenestratus* LeConte; *Horistonotus simplex* LeConte; *Negastrius arnetti* Stibick; and *Paradonus pectoralis* (Say). The other characters were added following examination of additional species for coding using the same criteria. Because each character state was photographed for each species, it was often possible to revisit species to code additional characters without re-examination of specimens.

Morphological characters, once identified, may be coded either qualitatively or quantitatively. Coding based on qualitative descriptions can be clear and objective where

variation is discrete and simple to describe (e.g. presence or absence of a structure). However quantitative descriptions are more objective and repeatable where there is overlapping variation between some species or where limits of qualitative character states require substantial choices by the investigator (Wiens 2001). Thus because of the heterogeneous nature of phylogenetic character sets, the goals of simplicity and objectivity are together served best using a combination of qualitative and quantitative character descriptions.

All 154 characters that could not be described as ratios of lengths, or as counts were treated qualitatively as binary or multistate characters. Qualitative characters included the presence or absence of structures, or the carefully defined curvatures of particular sclerites (e.g. notched vs. uniformly convex). A type species was assigned for each qualitatively defined character state. Efforts were made to keep the list of species used as character-types as small as possible by using the same species as the type of multiple character states. Following the above criteria, all qualitative characters identified as showing non-overlapping variation between at least two species were considered for possible use. Subsequent characters showing apparent developmental or genetic non-independence from previous ones were then excluded from this set. Many excluded characters were parts of outlines of sclerites that uniformly reflected the outlines of adjacent sclerites that were already used as characters (to avoid encoding the shape of the same suture, or interface twice). Repetitive serially homologous characters and other apparently correlated characters (e.g. shapes of adjacent antennomeres 4-10) were excluded for the same reason. All remaining qualitative characters were included in the

set. Autapomorphic characters were also encoded because they provide branch length information for Bayesian analysis and characters for taxon diagnoses.

In addition to circumventing some sources of coding bias, quantitative coding allows inclusion of information about distances between character states (Thiele 1993). This means that small and large differences between character states are considered with weights proportionate to their differences. The first method for quantitative coding is gap-weighting (Thiele 1993) which allows sorting of quantitative characters into 10-30 states. Step-matrix gap-weighting (Wiens 2001) allows division of continuous characters into 1000 discrete partitions. Gap-weighting with 10 categories was used here to correspond to the maximum number of character states possible in MrBayes v.3.1.2 (Huelsenbeck and Ronquist 2001, Ronquist and Huelsenbeck 2003), although the current versions of MrBayes do not yet process continuous data. To implement Thiele's (1993) method for a given character, the mean trait value (x) for that character is converted to a score (x_s) between 0 and 9 by range-standardizing the data according to the following formula

$$x_s = \frac{x - \min}{\max - \min} \times 9$$

where "min" is the minimum (lowest) mean species value of the trait across all species and "max" the maximum. Scores are then rounded to the nearest integer.

Because the two phylogenetic software packages used allow different types of data, gap-weighted and qualitatively coded data were adjusted to suit the software used.

Where gap-weighted and qualitative data are used together in a matrix, it is necessary to increase the weight of qualitative data to avoid effectively reducing the weight of these characters by a factor equal to the range of codings used in gap-coding quantitative traits. For this reason, where gap-weighted data was used in Paup* v. 4.0b8 (Swofford 2001) all qualitatively coded characters were reweighted from weight one to weight 10. Gap-weighted characters were converted to binary characters for analysis in MrBayes by recoding character states (0-4 to 0 and states 5-9 to 1) because MrBayes does not allow gap-weighted data. While this method loses some of the detailed phylogenetic signal that gap coding attempts to capture, it retains the advantage of removing subjective decisions from coding quantitative data.

The final morphological data set included 178 characters, of which 24 were coded quantitatively and 154 qualitatively (Appendix 8). These characters include 440 character states (after binary coding of quantitative characters), of which 75 are autapomorphic.

2.2.6 Model selection

Three morphological models are available for Bayesian analysis of morphological data. Of these, the Tuffley and Steel (1997) model, which emulates parsimony, was not used because it would be redundant in addition to regular parsimony analysis. The remaining two models are both based on the generalized Jukes-Cantor model for k states (Mkv), corrected for acquisition bias (Lewis 2001). For Bayesian analysis of morphological data, the important choice was whether or not to include gamma distributed rate variation between morphological characters (Mkv + G). The best model

for phylogenetic analysis of Bayesian data is the simplest one that reflects evolutionary processes well enough to provide accurate results. This is because, while additional parameters may provide a more realistic model of evolution, their estimation also introduces additional risk of error. While computer programs exist for testing many models for molecular sequence data none test models for morphological data.

Bayes factors were used here because they allow comparison of alternate models based on both these criteria and because they can be used to compare models for all types of phylogenetic data. Additionally, Bayes factors are based on integration over the probability of all parameter values, making them arguably more useful than maximum likelihood point estimates (Nylander et al. 2004). Bayes factors allow comparison of how well alternate models, M_0 and M_1 , describe the processes generating a data set X . Bayes factors are widely viewed as a comparison of the predictive likelihoods of the models (Kass and Raftery 1995, Nylander et al. 2004).

The Bayes factor in favor of model 1 over model 0, B_{10} , is calculated as the ratio of the model likelihoods, given the data. Using MrBayes, Bayes factors are calculated as twice the difference between harmonic means of the estimated natural log likelihoods for two runs of phylogenetic analysis, under the two different evolutionary models selected for comparison. Bayes factors can be interpreted using the following table.

Table 2.2. Interpretation of Bayes factors (from Kass and Raftery 1995).

$2 \log_e$	Evidence against M_0
0 to 2	not worth more than a bare mention
2 to 6	positive
6 to 10	strong
>10	very strong

2.2.7 Measures of confidence

Although both decay analysis and bootstrap resampling were performed under the parsimony optimality criterion, the preferred measure of support for interior nodes of phylogenetic trees was Bayesian posterior probability (PP). It is difficult to compare the reliability of PPs with those resulting from analyses with different mechanisms like parsimony. Comparison of PPs with bootstrap analysis of more similar, model-based, non-Bayesian maximum-likelihood results would probably be more useful. However previous studies have indicated that PP are higher than (Yoshiyuki et al 2002), lower than (Wilcox et al. 2002), or not directly comparable to (Douady et al. 2003) bootstrap values from maximum likelihood analysis based on the same models. A recent study addressing these inconsistencies (Zander 2004), indicates that PP values are predictably liberal at branch lengths typical for morphological studies (under 35). Because of this bias PP values were corrected using Zander's table when assessing clade credibilities for hypothesis testing.

2.2.8 Tests of monophyly

Testing of hypotheses of monophyly was performed by determination of the posterior probability of the focal clade. For focal clades absent from all trees sampled during Bayesian analysis, the posterior probability was considered to be equal to one divided by the number of trees sampled (Miller et al. 2002). These values were compared to alpha values selected by Bonferroni correction of $\alpha = 0.05$ for the number of non-mutually exclusive hypotheses to be tested for each analysis (Tables 2.7, 2.8).

2.2.9 Phylogenetic analyses

As explained in the choice of optimality criteria, phylogenetic analysis was performed using both parsimony and Bayesian methods. Bayesian analysis was performed using the program MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001, Ronquist and Huelsenbeck 2003), which utilizes the Metropolis-Hastings-Green Markov Chain Monte Carlo algorithm. Prior probability distributions were left at uniform default values. The gamma distribution was approximated using the default setting of four rate classes. The setting for the likelihood parameters used were Mkv (nst=1, coding=variable) and Mkv (nst=1, coding=variable, rates=gamma). Searches began with randomly selected starting trees and were run for 8-20 million cycles (until the standard deviation of split frequencies between parallel runs was below 0.01). Samples of trees from the MCMC chain were taken every 100 cycles, which resulted in 80-200 thousand trees depending on the total number of cycles. At the completion of the run, the “average standard deviation of split frequencies” (a metric in MrBayes to determine convergence of the simulation) was below the recommended value of 0.01 (MrBayes documentation). The last 60-180 thousand trees of each run were used to compute a majority rule consensus tree assigning posterior probabilities of tree topology. Each matrix was analysed three times to test repeatability. Among these, the analysis with the highest average harmonic mean log likelihood was used for phylogenetic inference.

Parsimony analysis of the gap-weighted coded and non gap-weighted matrices was performed using Paup* (Swofford 2001). The heuristic search procedure was used with

1000 random replications of stepwise-addition, with the branch-swapping algorithm (maxtrees set to auto-increase, multrees option in effect, Appendix 9). Bootstrap values were generated through 1000 replicates of bootstrapping using the same settings but with maxtrees set to 1000 and the number of replicates of stepwise addition reduced to 10 to reduce processing time. Decay index scores were calculated using PRAP (Müller 2004) for decay analysis of a strict consensus of all trees found in initial parsimony analysis. MacClade 3 (Maddison & Maddison 1992) was used to view character evolution on trees generated by all methods.

2.3 Results

2.3.1 Model selection

In this study, Bayes factors showed strong support for models including gamma-distributed rate variation between characters over models that did not include this type variation (Table 2.3). Results of analyses including gamma-distributed rate variation were used for all phylogenetic inferences in Chapters 2 and 3. Tables RA1-RA3 and RB1 show parameter estimates for three independent pairs of MCMC runs.

2.3.2 Comparison of analysis types

Bayesian analysis of the dataset with all extant taxa, with some taxa deleted, and then with three fossil taxa added, and analysis of a larger sample of Cardiophorinae, Negastrinae and Hypnoidinae (Chapter 3) indicated varying levels of branch support (Figs. 38, 41, 44, 47), but few contradictory clades. The same was not true for parsimony analysis of the same taxa (Figs. 39, 40, 42, 43, 45, 46, 48, 49). These parsimony analyses often disagreed with one another on the monophyly of clades (e.g. Negastrinae and Hypnoidinae) and all showed only moderate bootstrap and decay index support for even the strongest clades. Analyses in which binary coding was used for quantitative characters were more consistent with one another and with Bayesian analyses than were results of gap-weighting.

2.3.3 Phylogenetic inferences for extant taxa

Bayesian analysis of all extant taxa in the original matrix indicated over 95% probability of monophyly of Clicking Elateroidea minus *Cerophytum*, (Fig. 38) as tested with the two outgroups used (branch length = 18, raw posterior probability (PP) = 1.00, corrected for branch length according to Zander (2004)). Support for Clicking Elateroidea plus *Cerophytum* included was approximately equivocal. Within Clicking Elateroidea, *Pityobius* appears, with weak support, as the sister group to the two most diverse lineages. One of these two lineages (weak elaterine clade) included the families Eucnemidae and Throscidae within a paraphyletic Elateridae, as were the following subfamilies of uncertain association with Elateridae: Anischniinae; Cebrioninae; Lissominae; Thylacosterninae. This clade is called “weak” because support for it and its basal nodes was weak enough to fall near or within the support values expected if the true phylogeny was a polytomy (<0.05). The other clade (cardiophorine-hypnoidine clade) contains the three of four cardiophorines (including the type genus), and also *Agriotes*, all encoded Hypnoidinae Schwarz (1906, placed by many as Dendrometrinae: Hypnoidini) and Negastrinae (Nakane and Kishii 1956).

There was strong support for the monophyly of three of four included cardiophorines. However *Exoeolus*, the only cardiophorine genus known from New Zealand prior to this study, was resolved as a possible sister group to *Hemiops* in the weak elaterine clade. There was also moderately strong support (PP = .88, Fig. 38) for the monophyly of the three-cardiophorine genera, plus an undescribed species from New Zealand, *Negastris americanus* (Horn) from Negastrinae, plus two genera of

Physodactylinae (*Margogastrius*, *Teslasena*) and one from Dendrometrinae (*Pachyelater*). The remaining Negastrinae were found to form a moderately supported clade. Hypnoidinae were found to be a basal grade to Cardiophorinae plus Negastrinae (plus the three physodactylina genera and Cardiophorinae sp.nov. from New Zealand, minus *Exoeolus*) with approximately equivocal support at each of the three nodes where it was paraphyletic.

Parsimony analysis of the same data yielded conflicting results. The single most parsimonious tree for gap-weighted analysis indicated that both Cardiophorinae and Negastrinae were rendered paraphyletic by taxa that were not found to be closely related in other analyses, or in other publications (Fig. 40). Hypnoidinae was found to be polyphyletic, a result also never suggested by previous work. None of these findings had bootstrap support (BS) over 50%. A strict consensus of most parsimonious trees for the binary-coded matrix included a broad basal polytomy but did not contradict the Bayesian tree in the placement of any Cardiophorinae, Negastrinae or Hypnoidinae (Fig. 39). This tree included identical, but less resolved negastrine (decay index (D) = 1, BS <50%) and cardiophorine clades (D = 2, BS <50%) that were consistent with Bayesian results. The three members of Cardiophorinae as traditionally defined were recovered with a decay index of 4 (10 including more basal changes in cardiophorine clade) and bootstrap support of 64%.

In an attempt to improve resolution of the cardiophorine-hypnoidine clade, analysis was redone without the taxa in this clade for which one sex was missing (*Teslasena*, *Margogastrius*, *Pachyelater*, sp.nov). This was done because missing data

are known to confound phylogenetic analysis, perhaps especially where the missing data differs between species. This appeared to be the case in this clade of eight taxa because no females were known for three taxa and no males for one. However, other non-cardiophorines for which data for females were missing were not excluded, because preliminary analyses indicated that their inclusion or exclusion had little effect on the distribution of sampled topologies.

Bayesian analysis of the data set with these four taxa deleted resulted in a mostly unchanged topology, in which all nodes with more than 50% support in the previous analysis were uncontradicted by the second (Fig. 41). Support for the monophyly of the cardiophorine-hypnoidine clade (branch length = 15.7, raw posterior probability = 99%) and Cardiophorinae (branch length = 36.5, raw posterior probability = 99%), increased to over 95% after correction for branch length. Similarly, support for the paraphyly of Hypnoidinae increased to 86-99% at three consecutive nodes. Support for the monophyly of Negastrinae minus *Negastrius americanus* declined. Results of hypothesis testing by examination of posterior probabilities reject the hypothesis of Cardiophorinae monophyly (Table 2.7) below the Bonferroni corrected α value of 0.005. Support for the monophyly of Hypnoidinae (sensu Stibick 1976) was low, and that for Negastrinae was approximately equivocal. Hypotheses of monophyly of several other named subgroups of clicking Elateroidea were also clearly rejected (Table 2.7), however these results are beyond the scope of this thesis.

Parsimony analysis of this data yielded similar results to those from the complete data set. Gap-weighted parsimony analysis (Fig. 43) resulted in the same paraphyletic and

polyphyletic arrangements of Cardiophorinae, Negastrinae and Hypnoidinae (BS <50%) that were found in gap-weighted analysis of all taxa. Analysis of binary-coded data again supported the monophyly of Cardiophorinae without *Exoeolus* (Fig. 42, D = 5, BS = 62%, Fig. 42). Corrected for branch length (14), this clade has less than 95% credibility based on either measure of support. However, in this analysis, Cardiophorinae plus Negastrinae were found to be monophyletic with low support (D = 2, BS <50%), but Negastrinae was not recovered as monophyletic (with or without *Negastrius americanus*).

2.3.4 Phylogenetic inferences for fossil taxa

Addition of the three fossil taxa to the matrix, from which the 4 single-sex cardiophorine clade species had been deleted, resulted in an overall reduction in Bayesian posterior probability values and a change in the position in the position of Eucnemidae plus Throscidae plus *Lissomus* plus *Anischia* (Fig. 44). All of the three fossil taxa were placed in weakly supported positions near the base of the tree, and none within the hypnoidine-cardiophorine clade. *Crioraphes* was found to be the sister taxon to *Melanotus* in Bayesian and parsimony analyses (Figs. 44 and 45).

Hypotheses that any of the three fossil genera formed a monophyletic group together with Cardiophorinae were found to have low probability (raw PP = <0.000005-0.03). Among these, only the data for *Crioraphes* was lower than the Bonferroni corrected alpha value for clade rejection (Table 2.8).

Parsimony analysis of this data yielded similar results to those from the complete data set. Gap-weighted parsimony analysis provided little phylogenetic resolution (Fig. 46). As in the previous section, analysis of binary-coded data again found moderate support for the monophyly of extant Cardiophorinae ($D = 5$, $BS = 62\%$) and Cardiophorinae plus Negastrinae were found to be monophyletic ($D = 0$, $BS < 50\%$), but not Hypnoidinae (Fig. 46). The three fossil taxa were placed in the wide basal polytomy and not in association with Cardiophorinae, except for *Crioraphes*, which was again placed as the sister taxon of *Melanotus*.

Table 2.3. Calculation of factors for comparison of phylogenetic models with or without gamma-distributed rate variation (Mkv $\pm$ gamma) for analyses in chapters 2 and 3. Values for ln L without gamma is for a single run of the analysis, value with gamma is average of three runs (from tables RA1-RA4). Bayes factor values >10 are considered very strong evidence in favor of the model with the greater Ln L (Table 2).

Analysis	2X ln L -Gamma	2X ln L +Gamma	Bayes factor
All Clicking Elateroidea (CE)	-10676	-9638	1039
CE -3 taxa	-10042	-9095	947
CE -3 taxa +fossils	-10018	-9118	900
Cardiophorinae	-12837	-11719	1118

Table 2.4. Model parameters and standard deviation of split frequencies for simultaneous parallel runs estimated by MrBayes v.3.1.2 (Mkv+G) for 3 independent pairs of MCMC runs of 8-20 million cycles each based on 60-180 X10³ samples for all included extant Clicking Elateroidea. MrBayes “sump” (summarize parameters) command does not provide variance and 95% CI values for ln L. Potential scale reduction factors for all parameters for all runs were 1.000-1.001.

Run	Parameter	Mean	Variance	95% CI
1	TL	10.350029	0.544793	8.969000 - 11.864000
2	TL	10.356472	0.569039	8.920000 - 11.858000
3	TL	10.370918	0.552480	8.976000 - 11.897000
1	alpha	0.699013	0.008596	0.530652 - 0.891460
2	alpha	0.699218	0.008543	0.531145 - 0.890987
3	alpha	0.698502	0.008585	0.530303 - 0.891229
1	ln L	-4839.73		
2	ln L	-4801.23		
3	ln L	-4817.43		
1	σ Split	0.008364		
2	σ Split	0.007483		
3	σ Split	0.007067		

Table 2.5. Model parameters and standard deviation of split frequencies for simultaneous parallel runs estimated by MrBayes v.3.1.2 (Mkv+G) for 3 independent MCMC runs of 8-12 million cycles each based on 60-100 X10³ samples for all included extant Clicking Elateroidea except cardiophorine clade species coded from only one sex. MrBayes “sump” (summarize parameters) command does not provide variance and 95% CI values for ln L. Potential scale reduction factors for all parameters for all runs were 1.000-1.001.

Run	Parameter	Mean	Variance	95% CI
1	TL	9.816262	0.516963	8.449000 - 11.267000
2	TL	9.843525	0.516379	8.472000 - 11.276000
3	TL	9.816878	0.527945	8.434000 - 11.287000
1	alpha	0.697563	0.009554	0.521108 - 0.901303
2	alpha	0.696559	0.009552	0.520609 - 0.900647
3	alpha	0.696896	0.009523	0.520354 - 0.900116
1	ln L	-4584.75		
2	ln L	-4518.05		
3	ln L	-4540.81		
1	σ Split	0.007809		
2	σ Split	0.006483		
3	σ Split	0.006404		

Table 2.6. Model parameters and standard deviation of split frequencies for simultaneous parallel runs estimated by MrBayes v.3.1.2 (Mkv+G) for 3 independent MCMC runs of 8-12 million cycles each based on 60-100 X10³ samples for all included extant and fossil Clicking Elateroidea except cardiophorine clade species coded from only one sex. MrBayes “sump” (summarize parameters) command does not provide variance and 95% CI values for ln L. Potential scale reduction factors for all parameters for all runs were 1.000-1.000.

Run	Parameter	Mean	Variance	95% CI
1	TL	10.239145	0.538547	8.833000 - 11.723000
2	TL	10.228091	0.544875	8.819000 - 11.707000
3	TL	10.232714	0.560630	8.801000 - 11.747000
1	alpha	0.703498	0.009540	0.525490 - 0.906706
2	alpha	0.703239	0.009528	0.525422 - 0.906035
3	alpha	0.702872	0.009594	0.524387 - 0.906835
1	ln L	-4542.92		
2	ln L	-4560.62		
3	ln L	-4574.00		
1	σ Split	0.006266		
2	σ Split	0.008934		
3	σ Split	0.008101		

Table 2.7. Tests of prior hypotheses of monophyly based on Bayesian analysis (Fig. 41) of Clicking Elateroidea in which 4 cardiophorine clade species coded from only one sex are omitted. Genera apparently not overtly placed by original authors were considered wild to increase the generality of tests. Monophyly was considered tested if two or more taxon members were included in the analysis.

Hypothesis probability	citation (not original author)	posterior
Agrypninae	Gurjeva 1974a	0.816036
Agrypninae	(Stibick 1979a)	0.228638
Athoinae	(Dolin 1975a)	<0.000008*
Cardiophorinae ¹	genera in Appendix 1	<0.000008*
Denticollinae	(Stibick 1979a)	0.000025*
Elaterinae	Gurjeva 1974a	0.000008*
Elaterinae	(Stibick 1979a)	<0.000008*
Hypnoidinae	(Stibick 1979a)	0.020499
Negastriinae ¹	(Stibick 1971)	0.579175
Throscidae	(Crowson 1955) ($\pm$ <i>Oestodes</i> , <i>Anischia</i>)	0.919792
Elateridae: Lissominae	(Calder <i>et al.</i> 1993) ($\pm$ <i>Anischia</i>)	0.000017*
Elateridae ²	(Stibick 1979a)	0.048765
Clicking Elateroidea	(Muona 1995)	0.529233

¹With or without *Negastrius americanus*.

²With or without *Physodactylus*, Cebrioninae, *Anischia*, *Thylacosternus*, *Lissomus*.

* Significant at $\alpha = 0.004$, based on Bonferroni correction for nine non-mutually exclusive hypotheses.

Table 2.8. Tests of hypotheses of monophyly of Cardiophorinae plus three fossil cardiophorine genera based on Bayesian analysis of Clicking Elateroidea (Fig. 44).

Negastrius americanus was treated as wild to increase the generality of the tests.

Hypothesis	citation	posterior probability
<i>Crioraphes</i>	Iablokoff-Khnzorian 1961	<0.000005*
<i>Protocardiophorus</i>	Dolin 1976	0.01997
<i>Pseudocardiophorites</i>	Dolin 1976	0.034505

* significant at $\alpha = 0.017$, based on Bonferroni correction for three non-mutually

exclusive hypotheses.

2.4 Discussion

2.4.1 Phylogenetic data coding

Gap-weighting is a relatively new technique and its results here lack internal consistency and disagree with non-gap-weighted parsimony and Bayesian analyses as well as existing classifications. Because of this evidence that these results are inaccurate and unstable, there is no reason to place confidence in analyses of gap-weighted data. Because of this apparent weakness, results of gap-weighted parsimony are not discussed in detail here. However quantitatively measured characters coded as binary data (as used in the other parsimony analyses and all Bayesian analyses) is much more consistent between analyses and is more concordant with most pre-phylogenetic work. Because analysis including some binary-coded quantitative characters does appear to meet these basic requirements of informativeness, it is used here to make taxonomic conclusions, where there is sufficient branch support. For the reasons outlined in the Materials and Methods section, Bayesian results are generally preferred here for interpretation over parsimony results where there is conflict.

2.4.2 Monophyly of Cardiophorinae

Cardiophorinae, as previously defined, was found to be polyphyletic because it included *Exoeolus* Broun, although the other three cardiophorine genera included were recovered as a strongly supported clade by both Bayesian (Fig. 41) and parsimony (Fig. 42) analyses. Although the posterior probability indicating that it belongs there is only 0.30 (Fig. 41, in other Elateridae), it seems best to transfer *Exoeolus* to Hemiporinae,

because that is the best supported hypothesis. Its placement in that little studied subfamily from the Oriental region should be regarded as tentative, as should be the validity of Hemiopinae.

Re-analysis of the matrix with fossil taxa included found little evidence that the three fossil putative Cardiophorines actually belong to Cardiophorinae (both Bayesian Fig. 44 and parsimony Fig. 45). It was possible to encode enough data from *Crioraphes* Iablokoff-Khnzorian, which was preserved in amber, to clearly reject the hypothesis that it belongs in Cardiophorinae. This genus appears similar to *Ampedus* and was placed, with weak support, by Bayesian and binary-coded parsimony analyses as the sister taxon to *Melanotus*. Because both these taxa are currently placed in Elaterinae, it seems best that *Crioraphes* should also be transferred to that subfamily. The finding that support for monophyly for each of the two remaining fossil genera plus Cardiophorinae was low (PP = 0.02, 0.04), but insufficient for Bonferroni corrected hypothesis rejection, is probably mainly due to missing data. This is because only 8-9 of 172 characters could be coded for either of these limestone-preserved fossils. With so few characters visible, it would be surprising to gain enough information to place them anywhere with confidence. It should be remembered here that Bonferroni correction for multiple hypothesis tests from a single phylogeny is not standard practise, and may be unnecessary. In any case, taxonomic decisions must be based on the best supported (or least refuted) hypothesis and should not be restricted by arbitrary alpha values. For these reasons, it seems best that *Protocardiophorus* Dolin 1976 and *Pseudocardiophorites* Dolin 1976 should be removed from Cardiophorinae and considered Clicking Elateroidea *insertae sedis*. Even this

placement is uncertain because the inclusion of these fossils in the analysis reduced the posterior support for the monophyly of Clicking Elateroidea (minus *Cerophytum*) to only 0.74.

The finding that Clicking Elateroidea is monophyletic, but that Elateridae is probably not monophyletic (Raw PP = 0.05, not significant after correction for multiple hypothesis testing (Table 2.7)) indicates that changes to the family level classification of this group are most likely required. However, such changes are beyond the scope of this work.

2.4.3 Sister group of Cardiophorinae

A major goal of these analyses was to identify outgroups for analysis of a larger subset of Cardiophorinae. Analysis of all extant taxa using both Bayesian and parsimony analysis suggests that the closest relatives to Cardiophorinae belong to Physodactylinae or Dendrometrinae. These genera were included in this analysis because they were suspected a priori of being fossorial cardiophorines. These genera, *Margogastrius*, *Pachyelater*, *Teslasena* and sp.nov. from New Zealand should all be included in a phylogenetic analysis of Cardiophorinae either as outgroups, or as probable cardiophorines.

Since well-supported topologies (Fig. 41) indicate Negastrinae Nakane and Kishii (1956) and Hypnoidinae Schwarz (1906, considered a tribe Hypnoidini of Dendrometrinae by most recent authors) contain successively more distant relatives of the included cardiophorines they appear to be the best outgroups for analysis of

Cardiophorinae. However, these results also indicate that Negastrinae may be paraphyletic (Table 2.7, PP = 0.57) and that Hypnoidinae is rendered paraphyletic by Negastrinae by Cardiophorinae plus Negastrinae (raw PP = 0.02, but >0.05 after Bonferroni correction). Thus, in order to avoid unnecessary recognition of paraphyletic subfamilies, Negastrinae (Nakane and Kishii 1956) and Hypnoidinae (Schwarz 1906) should be synonymised under the senior name Cardiophorinae (Candèze 1859). All three subfamilies should be referred to collectively as Cardiophorinae *sensu lato*. Interestingly, these three former subfamilies were similarly included in Cardiophorinae *sensu* Heyden *et al.* 1906. Cardiophorinae and the former negastriine genera should be referred to as Cardiophorinae *sensu stricto*. The former Cardiophorinae, also the most derived group, will be referred to here as higher Cardiophorinae.

Using the former Negastrinae and Hypnoidinae both (or basal Cardiophorinae) as outgroups remains useful for the original aim of the study, which is to infer the phylogeny of Cardiophorinae (now higher Cardiophorinae). Monophyly of Cardiophorinae *sensu lato* was already tested in this section by analysis with members of most other subfamilies. Because of this, only the closest relatives of this group will be needed to root the trees and further test the monophyly Cardiophorinae *sensu lato*. *Agriotes*, the most likely sister group of Cardiophorinae according to all Bayesian analyses, was included as an outgroup based on this reasoning. *Adrastus*, *Elater*, *Agrypnus* and *Prosternon* were also chosen as outgroups for analysis of Cardiophorinae, to represent less frequently sampled possible sister groups of Cardiophorinae *sensu lato*.

2.4.4 Taxonomic conclusions

The extant genus *Exoeolus* and the fossil genera *Crioraphes*, *Pseudocardiophorites* and *Protocardiophorus* should be transferred from Cardiophorinae to other subfamilies or to Clicking Elateroidea *insertae sedis*. Subfamilies Hypnoidinae and Negastrinae should be synonymised under Cardiophorinae. The three former subfamilies should be referred to collectively as Cardiophorinae *sensu lato*. Cardiophorinae plus Negastrinae should be referred to as Cardiophorinae *sensu stricto*. The former Cardiophorinae will be referred to here as higher Cardiophorinae.

2.4.5 Further family and subfamily level research.

Additional resolution of the higher classification is needed to determine whether Cardiophorinae *sensu lato* render any other named taxa within Clicking Elateroidea paraphyletic. If so, Cardiophorinae would require further expansion or synonymisation under a senior family-group name.

CHAPTER 3

Subdivisions within Cardiophorinae: the monophyly and phylogenetic structure of Cardiophorinae

3.1 Introduction

For the reasons presented in section 1.2, phylogenetic analysis of Cardiophorinae and its nearest relatives is necessary for testing the monophyly of it and its tribes and larger genera. This analysis is also exploratory, because it tests millions of unarticulated hypotheses about possible intergeneric relationships. To ensure that the included exemplars reflect established genera, I have encoded the type species of as many cardiophorine genera as possible. Because the results of phylogenetic analysis of clicking elateroids (Chapter 2) indicate that the closest relatives of Cardiophorinae are negastriines, exemplars of seven of eight negastriine genus groups recognised by Stibick (1971) are included as outgroups.

This phylogenetic analysis is used here to revise the genus-level classification of Cardiophorinae. This revision includes transfers of genera into and out of Cardiophorinae, descriptions of new genera and synonymisation of extra genus names. A key to genera is provided (Appendix 4), along with diagnoses (Appendix 3) and a bibliographic synonymy of genus level names (Appendix 2). Because it was possible to examine fewer than half of the over 1100 described cardiophorine species, no checklists are provided here. Because many species of each genus were not examined, it is not possible to accurately redescribe the genera of previous authors.

3.2 Materials and Methods

Sections on specimen preparation and examination, choice of optimality criteria, morphological character coding, model selection, measures of confidence, test of monophyly, phylogenetic analysis and taxonomic changes are not provided here. This was done to avoid repetition of methods and rationales described in chapter two that also apply here.

3.2.1 Specimens examined

Specimens examined for morphological coding belonged to 29 insect collections (Table 3.1). Codens listed here follow those listed in Arnett et al. (1993), except where other codens are preferred by individual collections. Most of these 224 specimens of 77 species were borrowed and encoded at Carleton University, although a few were coded at museums in Brussels (ISNB) and Paris (MNHN). Among these specimens were 61 type, type series or paratype specimens representing 41 species. Types of an additional 307 species, which were not coded for phylogenetic analysis, were photographed at NHM (London), ISNB and MNHN. Notes from examination of types of 85 more North American cardiophorine species for a previous project (Douglas 2003) were also consulted to ensure that taxon sampling reflected much of the range of morphological diversity of the group.

Table 3.1. Codens for insect collections from which specimens were examined*.

AMNH	American Museum of Natural History, New York, New York, USA
NHM	The Natural History Museum [formerly British Museum (Natural History), BMNH], London, England
BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii, USA
CASC	California Academy of Science, Department of Entomology, San Francisco, California, USA
CMNC	Canadian Museum of Nature, Ottawa, Ontario, Canada
CNCI	Canadian National Collection of Insects, Arachnids, and Nematodes, Agriculture and Agri-Food Canada, Ottawa Ontario, Canada
CUIC	Cornell University Insect Collection, Department of Entomology, Cornell University, Ithaca, New York, USA
DEBU	University of Guelph Insect Collection, Guelph, Ontario, Canada
DEIC	Institut für Pflanzenschutzforschung, Eberswalde, Germany
FSCA	Florida State Collection of Arthropods, Department of Plant Industry, Gainesville, Florida, USA
HBDC	Hume Douglas Insect Collection (personal collection), Ottawa, Ontario, Canada
ISNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
LSUK	Linnean Society, London, United Kingdom
MCZC	Museum of Comparative Zoology, Harvard University, Cambridge Massachusetts, USA
MNHN	Muséum National d'Histoire Naturelle, Entomologie, Paris, France
MSUC	Michigan State University, Department of Entomology Museum, East Lansing Michigan, USA
MZHF	University of Helsinki, Zoological Museum, Helsinki, Finland
MZSP	Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil
NZAC	New Zealand Arthropod Collection, Landcare Research, Auckland, New Zealand
SANC	South African National Collection of Insects, Pretoria, South Africa
SEMC	Snow Entomological Museum, Kansas State Biological Survey, University of Kansas, Lawrence, Kansas, USA
TAMU	Insect Collection, Department of Entomology, Texas A&M University, College Station, Texas, USA
TARI	Taiwan Agricultural Research Institute, Taichung, Taiwan [Republic of China]
UCMP	University of California Museum of Palaeontology, Berkeley, California, USA
USNM	United States National Museum (Natural History), Washington, District of Columbia, USA
ZMAS	Russian Academy of Sciences, Zoological Institute, St. Petersburg, Russia
ZMHB	Museum für Naturkunde der Humboldt-Universität, Berlin, Germany
ZMUC	University of Copenhagen, Zoological Museum, Copenhagen, Denmark

Table 3.1 Continued.

ZMUM Zoological Museum of Moscow Lomonosov State University, Moscow,
Russia

* MZHF, TARI, UCMP are depositories (or expected depositories) of type specimens that were unavailable for examination.

Wherever possible, species identifications were verified by comparison to type specimens. Information from type specimens was often used in coding species. Lectotypes were not designated in this work, because it was considered preferable to leave that choice to authors of future species level revisions. For *Agriotes sputator* Linnaeus, type series included multiple species and no lectotype had been designated. For this species, the type specimen that was used in this study was the only one that matched the definition of the genus and species used by recent authors. For other type series without published lectotypes, specimen labels were followed to determine which specimen would be considered the type in this study. Unofficial lectotype designations or beginning of series specimen determination labels of the original authors were considered indicative of type status.

For this study, 69 ingroup and eight outgroup species were coded for phylogenetic analysis (Appendices 6-8). Of these, 21 were missing genitalic data for one sex. For two species, material was unavailable for both the aedeagal and female genitalic characters. Non-genitalic characters were coded from male specimens only, except for six species, for which only females were available. Wherever possible, coding of species for which

some characters could not be examined was done partially from literature Calder (1996), Gurjeva (1966), Ôhira (1963).

3.2.2 Data selection and taxon sampling

The principles of data selection and taxon sampling used here are introduced in section 2.2.4. Initial character selection for this analysis was done in combination with that for analysis of Clicking Elateroidea. Of all characters examined, a partially overlapping subset was found to be suitable for this analysis (Appendix 8)

Ideally, phylogenetic analysis of a higher taxon should include all member species and all species that might render them non-monophyletic. However, for large groups like Cardiophorinae it is only feasible to include a well-chosen sample of these taxa. To be taxonomically meaningful, phylogenetic analysis of a subfamily should include the type species for all available genus-group names within that subfamily. Preferably, several morphologically divergent exemplars of each of these should be included as a preliminary test of the monophyly of the genera and to increase analytical power. Species from all biogeographic regions should also be considered as exemplars of genera in an effort to include both branches of ancient biogeographical divergences.

This phylogenetic analysis included 56 cardiophorine species, including the type species of four genera and one new species identified as possible higher Cardiophorinae in this thesis (Chapter two). Of greatest interest were the type species of 25 of 32 valid and subjectively synonymised genus-level names for Cardiophorinae (Appendix 7). Four of the remaining genera (*Aptopus*, *Coptostethus*, *Dicronychus*, *Triplonychoidus*) were represented by non-type species only, and four were entirely unavailable for inclusion.

Taxon sampling was heaviest in the genera *Cardiophorus*, *Horistonotus*, *Paracardiophorus*, *Dicronychus*, *Cardiotarsus* and *Esthesopus* because they are most diverse and occur on multiple continents. Non-type specimens were identified by comparison with types (types were examined for 40 species) or specimens identified by experienced workers (three species, Appendix 7). All non-type specimens examined were also labelled with unique identifier numbers. Four distinctive species that were new to science were included to represent the diversity of Cardiophorinae more fully. Neither *Exoeolus*, nor any of the four fossil taxa were included because they were all found to belong to other subfamilies (Chapter 2), except for *Mionelater* Becker, which was unavailable for examination. All identifications of non-types were evaluated using published keys and descriptions (Appendix 7), and five species were identified using literature alone.

This analysis also included 24 other taxa that did not belong to Cardiophorinae. Previous analysis of Clicking Elateroidea (Chapter two) indicated that Negastrinae were the sister group to, or a basal grade of Cardiophorinae. Because of this, 16 exemplars of - 30 negastriine genera were included to further test the monophyly of Cardiophorinae. These genera include representatives of seven of Stibick's (1971) eight unnamed groups of negastriine genera. Three genera of Dendrometrinae: Hypnoidini (or subfamily Hypnoidinae), including the type genus *Hypnoidus*, were included as well as *Adrastus*, because analysis of clicking elateroids indicated that these were the most likely sister groups to Cardiophorinae + Negastrinae. The type species of the genera *Elater*, *Agriotes*,

Athous and *Agrypnus* were included as outgroups, although only *Elater* was formally defined as an outgroup in the analysis.

Phylogenetic analysis was conducted using 137 characters (Appendix 8), of which 25 were coded quantitatively and 112 qualitatively. These characters include 376 character states (after binary coding of quantitative characters), of which 40 are autapomorphic.

3.2.3 Taxonomic changes and synonymies

A pre-revision bibliographic synonymy of Cardiophorinae was assembled (Appendix 1) to ensure that the revised taxonomy (Appendix 2) correctly reflects the existing classification and to clarify inconsistencies in the use of genus level names.

This search for any use of genus group names in Cardiophorinae began with a manuscript catalogue provided by Prof. Paul Johnson (South Dakota State University, USA) and Schenkling's most recent (1925) world catalogue for all historically and currently recognized cardiophorine names. The *Genera Insectorum* (Schwarz 1906) and the *Biologia Centrali-Americana* (Champion 1894-1897) were also consulted. Since earlier names and applications were sometimes not cited in these works, a general search was made through them to track names and their origins. Following this procedure, the following monographs, reviews, faunal lists and faunal works were also examined: Candèze (1860, 1891); Gistel (1834, 1848, 1856); Gemminger and Harold (1869); Heyden et al. (1898, 1906); Jakobson (1913); Jacquelin du Val (1859); Kiesenwetter (1858); Lacordaire (1857); Stein and Wiese (1877). In addition, the following lists of

genus-group names and the works that they cited were also examined: Agassiz (1846); Scudder (1882 a-b), Waterhouse (1902, 1912), Lucas (1920).

The following faunal studies and lists were examined to find taxonomic changes within Cardiophorinae since Schenkling's 1925 Catalogue: *Zoological Record* (Thomson 1864 onwards); Blackwelder (1944); Cobos (1970b); Dajoz (1963); Fleutiaux (1929a, b, 1930, 1931, 1932a, b, c, 1935b, 1947a, b); Golbach (1994); Gurjeva (1966); Leseigneur (1972); Miwa (1934); Neboiss (1956, 1961). In addition Neave (1939) was checked for homonyms of all genus level names.

3.3 Results

3.3.1 Phylogenetic inferences

Bayesian analysis of the entire Cardiophorinae, Negastrinae and Hypnoidinae matrix resulted in trees that largely agree with results of analysis of clicking Elateroidea in general (Chapter 2). They agree in the finding of a well supported monophyletic Cardiophorinae (raw PP = 0.96) and Cardiophorinae plus Negastrinae (raw PP = 1.00), which together render Hypnoidinae paraphyletic (Fig. 47). Among these strongly supported clades, only Cardiophorinae plus Negastrinae had support above 95% after correction for branch length (branch length = 28.2, correction according to Table 4 of Zander 2004). As in previous analyses, the most likely sister group of this hypnoidine-cardiophorine clade was indicated to be *Agriotes*. However, unlike previous analyses, Cardiophorinae here renders Negastrinae broadly paraphyletic. Rejection of monophyly was strong (Table 3.3) although support for each of the 5 paraphyletic nodes was weak to moderate (PP = 31-72%). This change was at least partly due to the nearly threefold increase in the number of included negastriine species from previous analyses.

Within Cardiophorinae there are several clades with moderately high support, but because the tree was generally pectinate-shaped, these do not divide the tree into large subdivisions. Branches were short and clade support was low in the mid-region of this tree, especially among the paraphyletic genus *Cardiophorus*. Clades with more than 90% support within Cardiophorinae include *Blaiseus* plus an undescribed new species of Cardiophorinae from South Africa (PP = 0.90), *Paracardiophorus* plus *Cardiophorus cardisce* plus *C. luridipes* (PP = 1.00, $\geq 95\%$ after correction for branch length) and the

Brazilian genera *Globothorax* plus *Teslasena* (PP = 1.00, $\geq 95\%$ after correction for branch length).

Support for all a priori hypotheses of monophyly was weak to absent (Table 3.3). Hypotheses of monophyly of Cardiophorinae and Negastrinae were both significantly rejected and the raw probability of monophyly of Hypnoidinae was found to be 0.004 (although >0.05 after Bonferroni correction Table 3.3). Uncorrected probabilities that the 10 genera tested were truly monophyletic ranged from <0.000008 to 0.328603, and hypotheses of monophyly were significantly rejected for all except *Horistonotus* (Table 3.3). Similarly, all tested published hypotheses of generic synonymy were found to have low support and three of four were clearly rejected. All a priori biogeographical hypotheses of monophyly were also clearly rejected.

Results of parsimony analysis corroborated those of Bayesian analysis, or were idiosyncratic. Analysis of gap-weighted data also found that Cardiophorinae was monophyletic (bootstrap support (BS) $<50\%$) and rendered Negastrinae paraphyletic (Fig. 49, BS $< 50\%$). Hypnoidinae remained paraphyletic, but due to part of Negastrinae alone. However this analysis placed the elaterine genus *Adrastus* between Cardiophorinae and Negastrinae, which is a topology not suggested previously. Similarly, the topologies within Cardiophorinae and Negastrinae differ greatly from any other result.

Results of parsimony analysis of this binary-coded quantitative data were intermediate between those of the Bayesian analysis and gap-weighted parsimony analysis, with low branch support (Fig. 48). *Adrastus* was again included in the hypnoidine-cardiophorine clade, this time between Negastrinae (paraphyletic) and

Hypnoidinae (monophyletic $D=1$, $BS < 50\%$). Cardiophorinae was found to be monophyletic ($D=2$, $BS < 50\%$), and unlike for gap-coded data, its internal topology largely agreed with that indicated by Bayesian analysis.

Table 3.2. Model parameters and standard deviation of split frequencies for simultaneous parallel runs estimated by MrBayes v.3.1.2 (Mkv+G) for 3 independent MCMC runs of 8-12 million cycles each based on 60-100 $\times 10^3$ samples. MrBayes “sump” (summarize parameters) command does not provide variance and 95% CI values for $\ln L$. Potential scale reduction factors for all runs were 1.000-1.001.

Run	Parameter	Mean	Variance	95% CI
1	TL	14.011084	0.941761	12.211000 - 16.005000
2	TL	13.922824	0.967234	12.135000 - 15.971000
3	TL	13.933538	0.963059	12.138000 - 15.969000
1	alpha	0.880679	0.012285	0.682745 - 1.117785
2	alpha	0.887496	0.012646	0.687924 - 1.127197
3	alpha	0.886625	0.012580	0.687730 - 1.127290
1	$\ln L$	-5828.16		
2	$\ln L$	-5903.75		
3	$\ln L$	-5847.03		
1	σ Split	0.009913		
2	σ Split	0.008995		
3	σ Split	0.008686		

Table 3.3. Tests of hypotheses of monophyly of and within Cardiophorinae *sensu lato* based on Bayesian analysis (Fig 47). *Negastrius americanus* was treated as wild to increase the generality of the tests. Monophyly was considered tested if two or more taxon members were included in the analysis (“-” = not tested). The monophyly of monotypic genera could not be tested (mt = monotypic).

Hypothesis and citation	posterior probability
Subfamilies	
Cardiophorinae <i>auctorum</i>	<0.000008*
Cardiophorinae (w <i>Negastrius americanus</i> and Physodactylinae spp.)	<0.000008*
Negastriinae (<i>sensu</i> Stibick 1979a)	0.000108*
Hypnoidinae (<i>sensu</i> Stibick 1976)	0.004833
Tribes	
Cardiophorini Candèze 1859 (as redefined in chapter 2)	0.000267*
Nyctorini Semenov-Tian-Shanskij & Pjatakova 1936	mt
Genera of higher Cardiophorinae	
<i>Allocardiophorus</i> Ôhira 1989	-
<i>Aphricus</i> LeConte 1853 (+/- <i>Aphricus</i> sp.nov from N. Zealand)	0.001650*
<i>Aptopus</i> Eschscholtz 1829	0.000033*
<i>Blaiseus</i> Fleutiaux 1931	mt
<i>Buckelater</i> Costa 1973	mt
<i>Cardiodontulus</i> Van Zwaluwenburg 1963	mt
<i>Cardiophorellus</i> Cobos 1970a	-
<i>Cardiophorellus</i> : subg. <i>Parapleonomus</i> Cobos 1970a	mt
<i>Cardiophorus</i> Eschscholtz 1829	<0.000008*
C.: subg. <i>Cardiophorus</i>	<0.000008*
C.: subg. <i>Coptostethus</i> Wollaston.	-
C.: subg. <i>Lasiocerus</i> Buysson 1912	mt
C.: subg. <i>Metacardiophorus</i> Gurjeva 1966	mt
C.: subg. <i>Perrinellus</i> Buysson 1899	0.064749
C.: subg. <i>Zygocardiophorus</i> Iablokoff-Khnzorian and Mardjanian 1981	mt
<i>Cardiotarsus</i> Eschscholtz 1836 (+/- <i>Cardiotarsus mjobergi</i>)	0.003642*
<i>Craspedostethus</i> Schwarz 1898b	-
<i>Dicronychus</i> Brullé 1832	-
<i>Displatynychus</i> Ôhira 1987	-
<i>Esthesopus</i> Eschscholtz 1829	0.016291
<i>Exoeolus</i> Broun 1893	-
<i>Globothorax</i> Fleutiaux 1891a	-

Table 3.3 Continued

Hypothesis and citation	posterior probability
<i>Horistonotus</i> Candèze 1860	0.328603*
<i>Margogastrius</i> Schwarz 1903c	mt
<i>Mionelater</i> Becker 1963	mt
<i>Neocardiophorus</i> Gurjeva 1966	-
<i>Nyctor</i> Semenov-Tian-Shanskii and Pjatakova 1936	mt
<i>Odontocardus</i> Fleutiaux 1931	-
<i>Pachyelater</i> Lesne 1897b	mt
<i>Paracardiophorus</i> Schwarz 1895b	<0.000008*
<i>Paradicronychus</i> Dolin and Gurjeva 1975 (<i>nomen nudem</i>)	-
<i>Paraplatynychus</i> Fleutiaux 1931	-
<i>Patriciella</i> Van Zwaluwenburg 1953	mt
<i>Phorocardius</i> Fleutiaux 1931	0.000583*
<i>Phorocardius</i> : subg. <i>Phorocardius</i>	-
<i>Phorocardius</i> : subg. <i>Diocarphus</i> Fleutiaux 1947a	mt
<i>Platynychus</i> Motschulsky 1858	-
<i>Ryukyucardiophorus</i> Ôhira 1973a	-
<i>Teslasena</i> Fleutiaux 1892	-
<i>Triplonychoidus</i> Schwarz 1906	-
<i>Triplonychus</i> Candèze 1860	-
<i>Tropidiplus</i> Fleutiaux 1903a	-
Synonymies (putative synonyms of <i>Cardiophorus</i> were not tested because monophyly of <i>Cardiophorus</i> alone was rejected)	
<i>Dicronychus</i> (= <i>Paradicronychus</i> (<i>nomen nudem</i>)): Platia 1994	0.069549
<i>Dicronychus</i> (= <i>Platynychus</i>): Méquignon 1931 ¹	<0.000008*
<i>Craspedostethus</i> (= <i>Tropidiplus</i>): Schwarz 1906	0.000008*
<i>Paracardiophorus</i> (= <i>Craspedostethus</i>): Cobos 1970a.	<0.000008*
New a priori biogeographic hypotheses	
New World Cardiophorinae	<0.000008*
New World <i>Cardiophorus</i> ($\pm$ <i>cardisce</i> , <i>luridipes</i> , <i>brevis</i>)	0.000108*
Neotropical Cardiophorinae ($\pm$ <i>P. humeralis</i> , <i>A. chilensis</i> , <i>C. brevis</i>)	<0.000008*
Australian Cardiophorinae ($\pm$ <i>Cardiodontulus</i> , <i>Aphricus</i> sp.nov)	<0.000008*

¹with or without *Cardiotarsus*, *Coptostethus*, *Phorocardius* spp. and *Paraplatynychus*.

* significant at $\alpha = 0.002$, based on Bonferroni correction for 22 non-mutually exclusive hypotheses.

3.4 Discussion

3.4.1 Monophyly of Cardiophorinae

Results discussed here are based on Bayesian analysis, unless stated otherwise. The term “parsimony analysis” refers to non-gap-coded parsimony only.

Although Bayesian tests of monophyly (Fig. 47, Table 3.3) and parsimony (Fig. 48) show that Cardiophorinae is not monophyletic (as defined by recent authors, with or without the three fossil genera and *Exoeolus*), there is however a well supported clade that includes only a few additional species. Cardiophorinae can be corrected to reflect a large monophyletic group by adding a few species and genera from other subfamilies (*Margogastrius*, *Negastrius americanus*, *Teslasena*, sp.nov. (from New Zealand) and *Pachyelater*) and removing *Exoeolus* and the three fossil genera discussed in the previous chapter. Three of these four taxa also require further taxonomic alterations, as discussed below. These additions to higher Cardiophorinae should be considered necessary for its recognition as a natural group, however the formal changes to Cardiophorinae should extend far beyond this.

Results of this analysis (Fig. 47) also show strong support for the paraphyly of Negastrinae and Hypnoidinae and monophyly of Cardiophorinae plus Negastrinae plus Hypnoidinae as identified in Chapter 2 (although both of these results are weakly contradicted by parsimony). In this analysis, support for the monophyly of Negastrinae was below 0.05 after Bonferroni correction (Table 3.3). The strength of this rejection is surprising, considering that support for each of the five paraphyletic nodes in the consensus topology was only 0.31-0.72. Bonferroni corrected evidence for rejection of

hypnoidine monophyly was slightly above 0.05, although the raw probability was 0.005. However, support for the monophyly of Cardiophorinae *sensu stricto* and *sensu lato* is respectively 9000 and 16 times higher than that for Negastrinae or Hypnoidinae alone. Further phylogenetic analysis, including at least all genera of the former Hypnoidinae and Negastrinae, would be important future work to further test the membership of Cardiophorinae *sensu lato*.

3.4.2 Tribal classification of Cardiophorinae *sensu lato*

The existing tribal classification of (higher) Cardiophorinae is incorrect according to both Bayesian and Parsimony analyses. This is because Nyctorini renders the only other tribe, Cardiophorini, paraphyletic (Figs. 47-49, Table 3.3). Because Nyctorini (Semenov-Tian-Shanskij and Pjatkova 1936) is monotypic, that name contains no information other than that it appeared distinctive compared to other Cardiophorinae known to its authors. The diagnostic characters, its short anterior prosternal lobe and sexual size dimorphism are homoplastic characters found in many fossorial elaterids. For these reasons Nyctorini should become a junior synonym of Cardiophorini, effectively eliminating tribal level classification of Cardiophorinae. Because of the generally pectinate shape of the inferred phylogeny of Cardiophorinae *sensu lato* (Figs. 47, 48), there are no apparent major natural divisions within it that lend themselves to a convenient tribal level classification. For this reason all Cardiophorinae *sensu lato* should be placed in tribe Cardiophorini.

3.4.3 Genera of Cardiophorinae

Because the genera of former subfamilies Negastrinae and Hypnoidinae were generally represented in the matrix by a single species, no changes will be made to the classification of most of genera. The only exception to this is *Negastrius* Thomson, from which *Negastrius americanus* (Horn) is transferred to higher Cardiophorinae (as gen.nov.). However since Johnson (2001) did not alter genus diagnoses when transferring *Cardiophorus* (*Coptostethus*) *americanus* (Horn) into *Negastrius*, no re-adjustments to diagnoses are required here.

Of other interest, three genera which were previously transferred from Cardiophorinae form a well supported clade (PP > 0.95 after correction for branch length, length = 27, raw probability = 1.00) within the Negastrine grade in both Bayesian and parsimony (D = 5, BS = 75) analyses (Figs. 47, 48). These three distinctive genera, *Agrypnella*, *Cardiohypnus* and *Rivulicola* are restricted to riparian habitats in the Neotropics, South Asia and Australia respectively and may all be relicts of a single Gondwanian lineage. The Australian genus is especially interesting because it is the only known negastrine grade taxon known from that continent. They are all distinctive among the negastrine grade for their scale-like or apically broadened setae and complex elytral markings. All three were once placed in Cardiophorinae because of their heart shaped scutella (with emarginate anterior edges) and general body shape. They were all later separately transferred to Negastrinae based, at least in part, on their convex prosternal sides. Surprisingly, despite their apparent affinities with both former subfamilies, this group does not appear to be the sister group to higher Cardiophorinae.

Fleutiauxellus, a negastrine of more typical appearance is the most likely sister group to Cardiophorinae based on other characters, including the presence of a pedunculate anterior sac of its bursa copulatrix.

Among the higher Cardiophorinae, many changes are required, which are discussed here in phylogenetic order. The most basal higher cardiophorine (Fig. 47) currently belongs to the significantly non-monophyletic (Table 3.3) genus *Aphricus* LeConte (also paraphyletic by parsimony analysis, Fig. 48). This genus is probably rendered paraphyletic by the fossorial Australian genus *Patriciella* Van Zwaluwenburg plus an undescribed species that appears similar to *Aphricus* from New Zealand. In order to avoid recognising a clearly paraphyletic genus, *Aphricus chilensis* is designated here as the type of the new genus *Chileaphricus*. Despite the only moderate support (PP = 0.80, D = 1) for the monophyly of the type species of *Aphricus* (from California, USA) plus *Patriciella* and the new species from New Zealand, the best taxonomic practice appears to be to consider them all a single genus (by synonymising *Patriciella* under *Aphricus*). If truly monophyletic, this clade also displays an interesting relictual biogeographic history. Most or all known species are rare or uncommon in their native habitats and are known from males only. This suggests that the females are flightless soil dwellers and that their current disjunct distribution is probably not due to recent dispersal. It seems more likely that this group spread to occupy its current range during the Jurassic, prior to the break-up of Gondwana. Possible further evidence for such ancient vicariance events is that the most likely sister group to these three taxa is the small African genus *Pachyelater* (PP =

0.61). Further collecting effort focused on this group is needed to discover new species and female semaphoronts in order to make stronger phylogenetic inferences.

Blaiseus Fleutiaux is another basal member of higher Cardiophorinae, with a surprising relictual distribution. This genus was known, until the present, from a single male type specimen from Vietnam. Another single male of an undescribed congener from South Africa was examined during this project. Although support for the monophyly of these two was only 0.90 (also supported by parsimony, $D = 3$, $BS = 81$), the characters uniting them are distinctive. One such synapomorphy is their unique split parameres (Fig. 27). Another uncoded apparent synapomorphy is the pair of basal points on the aedeagal median lobe. During this project, other undescribed males were examined from China, Malaysia, Honduras and Mexico. The rareness of all these species, the absence of female specimens and their odd disjunct distribution suggests that *Blaiseus* represent another ancient relictual lineage.

Pachyelater Lesne (1897b) is a muscular fossorial cardiophorine genus, the type species of which (*P. madagascariensis*) is known only from Ambohibeloma, and Ankeramadinika Madagascar. Fleutiaux (1935b) described the genus *Lesnelater* based on males from Ambohibeloma that Lesne (1906) associated with *P. madagascariensis*. Fleutiaux's splitting of Lesne's species and genus was evidently incorrect because these males and females share the following diagnostic characteristics, which distinguish them from all other cardiophorine genera: anterior edge of the scutellum broadly concave; tarsi and tarsal claws simple; mandibles bidentate; protibiae apically expanded and flattened. That these males and females share a common locality is further evidence of

conspecificity. Because of these arguments, and because Fleutiaux argued for dividing *Pachyelater* into two genera based only on their general body shape, the best decision seems to be to synonymise the name *Lesnelater* under *Pachyelater*. Because this genus falls within higher Cardiophorinae in this analysis, it should be transferred from Dendrometrinae to Cardiophorinae. Knowing both sexes of *Pachyelater* may help infer the probable morphology of the unknown *Aphricus* females (as redefined to include spp. from Australia and New Zealand) if they are sister taxa, as suggested by the inferred phylogeny (Fig. 47). If so, females of *Aphricus* spp. may be larger and more adapted for digging than the males and have reduced eyes and ovipositor and lack bursa copulatrix sclerites. However, because many basal cardiophorines appear to be fossorial, discovering that all *Aphricus* females were fossorial would not alone confirm this relationship.

Margogastrius Schwarz, a genus known from only two damaged female type specimens from coastal Tanzania was placed with weak branch support as the sister taxon of *Blaiseus* (although they are not closely related according to parsimony, Fig. 48). No taxonomic change is recommended for this genus because of uncertainty about its correct phylogenetic position. It is hoped that examining internal genitalia of the remaining undissected type specimen will yield further phylogenetic information. No associated males have been identified with external morphology or distribution similar to that of these females.

Although the historically enigmatic species *Negastrius americanus* (Horn) clearly belongs to higher Cardiophorinae, the characters examined in both male and female

specimens did not yield strong evidence for its placement in any other genus using parsimony or Bayesian analysis. For this reason, and because the available evidence suggests that it is the sister taxon to all remaining higher Cardiophorinae, I propose to place it in the new monotypic genus *Floridelater* (type species = *Coptostethus americanus* Horn). This genus has been collected by sifting sand on beach dunes by the Gulf of Mexico in USA. Perhaps sifting at beaches elsewhere will yield congeners that will provide more evidence about this species' phylogenetic position.

Two genera, *Neocardiophorus* Gurjeva and *Nyctor* Semenov-Tian-Shanskij and Pjatakova, and also *Cardiophorus* subg. *Metacardiophorus* Gurjeva form a weakly supported grade between the genera already discussed and the remaining higher Cardiophorinae (PP = 0.86, also part of a similar grade in parsimony analysis Fig. 48). These three monotypic groups are all known from central Asia and are thus perhaps more likely to actually represent a distinct lineage. Among these, only *Nyctor* is known from both sexes, so the future discovery of the females of the other two genera could provide further phylogenetic evidence to better understand their phylogenetic history. Meanwhile, no changes should be made to the classification of the first two genera. Since subg. *Metacardiophorus* is evidently not closely related to the nominate subgenus, it should be raised to genus rank.

The nominate subgenus of *Cardiophorus* Eschscholtz, which contains half of all described higher cardiophorine species, was found to be significantly non-monophyletic. Instead it was found to be a weakly supported grade, which was represented as a polytomy by parsimony analysis. Subgenus *Cardiophorus* is mixed in this weak grade

with numerous genera including *Platynychus*, *Paracardiophorus*, *Dicronychus*, *Aptopus*, *Phorocardius*, *Tropidiphus*, *Displatynychus*, *Cardiotarsus* and a clade of 11 genera mainly from the southern hemisphere. Unfortunately because of this paraphyly and non-resolution, there is as yet no basis for an improved definition of *Cardiophorus*. One of the remaining subgenera of Cardiophorinae, the monotypic *Zygocardiophorus*, appears to be the sister group to *Cardiophorus* plus the remainder of higher Cardiophorinae (PP = 0.89, D = 1) and thus should be raised to genus rank. It is not possible to comment on the position of subg. *Lasiocerus* here because its type was not located for examination.

The genus *Paradicronychus* was described by Dolin and Gurjeva (1975) without a formal type designation, and is therefore not an available name, because of IZCN regulations for genera described after 1930. This genus was described based on larval characteristics only. Although larvae of many higher cardiophorines from the former USSR are known, larval morphology of the world fauna remains too weak to define genera based on larvae alone. Both kinds of analysis placed *C. inflatus* within the weak grade of *Cardiophorus* and other genera. Because of this result, and because no adult characters could be identified to distinguish it from *Cardiophorus*, *Paradicronychus* should be placed in synonymy under the nominate subgenus of *Cardiophorus*.

The remaining two subgenera of *Cardiophorus*, subg. *Coptostethus* (Wollaston) and subg. *Perrinellus* Buysson are based on single, evolutionarily labile, characters and should be disregarded or used with caution, although they are not formally synonymised here. The first, *Coptostethus*, is a name historically applied to various short-winged Cardiophorinae, with little regard for other characters. For example, species currently

assigned to *Coptostethus* from the Azores Archipelago include ones with tarsal claws with one or two apices, a distinction that was historically considered diagnostic at the genus level (although the accuracy of this criterion is questioned below, in discussion of *Dicronychus*). The rank of *Coptostethus* should subgenus (of *Cardiophorus*) and not genus, because Golbach's 1994 placement of *Coptostethus* at genus rank was made without reference to Cobos' (1970b) transfer to subgeneric rank. This suggests that Golbach's placement was not intended to overturn Cobos' findings. Some *Cardiophorus* from Africa and Eurasia that are possibly adapted for fossorial life have been grouped into subg. *Perrinellus*. Although Bayesian analysis failed to conclusively reject the hypothesis that the two encoded *Perrinellus* species are monophyletic, support for their monophyly was low (PP = 0.06). Evidence that numerous other higher cardiophorines have similar modifications for digging may be further evidence that these characters are highly homoplastic and that this assemblage is artificial.

Among the remaining genera historically confounded with *Cardiophorus*, the most basal is *Paracardiophorus* Schwarz. There was significant evidence that this genus is non-monophyletic (Table 3.3), evidently because it was polyphyletic (Figs. 47, 48), including superficially similar species from Australia and Chile. It is argued below that these should be part of a new genus. The type species of *Paracardiophorus* forms a fully supported clade with two North American *Cardiophorus* species (PP > 0.95 after correction for branch length, length = 12, raw probability = 1.00), which is also indicated by parsimony analysis (D = 2, BS = 57). These and all other North American species displaying the synapomorphies of this group should be transferred to *Paracardiophorus*.

This redefined genus is beyond the known range of *Cardiophorus* paraphyly (after status change of subg. *Metacardiophorus*). *Paracardiophorus* is the most likely (PP = 0.67) sister group of the remainder of Cardiophorinae.

Globothorax Fleutiaux and *Teslasena* Fleutiaux (Physodactylinae) are a fully supported (Raw PP = 1.00, D = 2) clade within the weak grade of *Cardiophorus* and other genera. Like the other genera within this poorly resolved grade, these two should not be synonymised with the paraphyletic *Cardiophorus*. *Teslasena* should be considered a junior synonym of *Globothorax*, because of the well-supported monophyly of these two species, which is based on external morphological characters alone. It seems likely that *Teslasena* and *Globothorax* are dimorphic males and females of a single fossorial genus, because both are known from only one sex and their known ranges are sympatric in Brazil (although *Globothorax* has been recorded from Bolivia, but not *Teslasena*). Interestingly, these genera were both described by Fleutiaux, who also divided the similarly dimorphic males and females of *Pachyelater madagascariensis* Lesne into two genera. In both cases, the females are approximately twice the size of males and have reduced compound eyes, so that they appear quite different. Parsimony analysis also found that these two genera were sister taxa (Fig. 48), supporting this new synonymy. However, that analysis placed them as the sister taxon to the Neotropical genus *Triplonychus*, a placement that seems more likely based on the similarity of their posterior bursa copulatrix sclerites and sympatry in a region lacking *Cardiophorus* species.

Dicronychus was coded here based on *D. cinereus*, which was considered a senior synonym of the type species at the time of the beginning of this study. Since then Platia and Gudenzi (2003) have returned the type species to valid status. However, this change probably makes little difference to the taxonomic accuracy of these findings because *D. cinereus* and the type species are very similar and because no clear evidence has been presented indicating that they are not conspecific. Furthermore this change was made without reference to any type specimen(s) for the type species (*D. obesus* (Brullé), now *D. brullei* Platia and Gudenzi), thus making this distinction unverifiable.

There is little evidence for the monophyly of genera *Dicronychus* Brullé and *Platynychus* Motschulsky (PP = 0.07, Fig. 47, Table 3.3, also not recovered by parsimony analysis, Fig. 48), therefore *Platynychus* should be removed from synonymy under *Dicronychus*, where it has been placed by some authors. Furthermore neither should be considered a synonym of *Cardiophorus*, as done by some authors, at least until the problems surrounding that genus are resolved. However, since both *Platynychus* and *Dicronychus* are distinguished from *Cardiophorus* by the presence or absence of a second tarsal claw tooth (Fig. 23), there may be no reliable basis on which to distinguish them from that genus even at the species level because of apparent intraspecific variation in this character. Such variation may underly the partly sympatric pair of species *Cardiophorus aptopoides* Candèze and *C. brevis* champion from Mexico, which are distinguishable by this tarsal claw character but are otherwise morphologically identical (including aedeagal shape and regional colour variants). A similar otherwise possibly identical *Cardiophorus-Dicronychus* pair of species (*Cardiophorus varius*, Cate et al.

(2002) and *D. hoberlandti* Cate et al. (2002)) from Iran also may be an example of a single species that exhibits dimorphic claw shape.

The genus *Cardiophorellus* Cobos also falls within the paraphyletic nominate subgenus of *Cardiophorus*. The type species of *Cardiophorellus* is much like *Cardiophorus* except that the anterior edge of its scutellum is broadly concave and not emarginate, and its mandibles are simple. Due to phylogenetic uncertainty surrounding the placement of this genus, there is no obvious best taxonomic placement for *Cardiophorellus*. Because of this uncertainty, and because *Cardiophorellus* is readily diagnosed, it seems best to continue to consider *Cardiophorellus* a valid genus. The type specimen of the monotypic subgenus *Cardiophorellus* (*Parapleonomus*) Cobos could not be found at MNHN (Paris), thus it is impossible to comment on its validity or rank. Diagnosis of *Cardiophorellus* here differs from that of Cobos 1970a because he considered the anterior prosternal lobe reduced, whereas it is not reduced by the definition used here (whether or not it conceals the labium when the head is withdrawn).

Similarly to some previous genera, *Aptopus* Eschscholtz seems to be *Cardiophorus* with added synapomorphies, the most apparent of which is its pectinate tarsal claws. Although the hypothesis of *Aptopus* monophyly was clearly rejected (Table 3.3, Fig. 47, also rejected by parsimony, Fig. 48), this result does not reflect the genus *Aptopus*, as it is known by most. This is because the dissimilar species *A. agrestis* (Erichson) was one of two included in the matrix. Apart from its pectinate claws, this species most closely resembles those *Horistonotus* species with costate elytral intervals. Because phylogenetic analysis weakly suggested that *A. agrestis* was the most likely

sister taxon to *Horistonotus simplex*, and because this species is overall much more compatible with the current (paraphyletic) concept of *Horistonotus*, such *Aptopus* species with carinae following the lateral edge of the pronotum should be transferred to *Horistonotus*. However, because the type specimen of *A. agrestis* was not examined, this species is not transferred to *Horistonotus* here. The concept of *Aptopus* used here is that of modern authors (e.g. Aranda 1998, also Section 1 of Candèze 1860) because the type specimen of the type species, *A. tibialis* Eschscholtz, are lost or were unavailable for examination and because the only published species description lacks detail (eight words only).

The oriental genus *Phorocardius* Fleutiaux was described to include *Cardiophorus*-like species with apically bidentate tarsal claws (Fig. 24, Not Fig. 23), however the nominate subgenus plus subg. *Diocarpus* Fleutiaux are not a monophyletic pair (Table 3.3). Because of this, the most accurate classification is to recognize *Diocarpus* as a distinct genus despite the uncertainty due to their positions in the weak grade including *Cardiophorus* and other genera.

Tropidiplus Fleutiaux is a distinctive east African genus that is also part of the *Cardiophorus* weak grade. The hypothesis (Schwarz 1906) that *Tropidiplus* is a synonym of *Craspedostethus* was clearly rejected (Table 3.3). Similarly *Displatynychus* Ôhira was a subgenus of *Platynychus* until Ôhira (1987) raised it to genus rank. Phylogenetic analysis (Fig. 47) here suggests that Ôhira (1987) was correct, and that these genera are not sister taxa or even close relatives.

The genus *Cardiotarsus* Eschscholtz includes species from Africa, Mauritius, S. and E. Asia and Australia. This analysis included the type species (*C. capensis*, known here from females only), another (undescribed) African species and *C. mjobergi*, Australia's only known species. Bayesian hypothesis testing (Table 3.3) significantly rejected the hypothesis that even the two African species were monophyletic (also not recovered by parsimony, Fig. 48). It seems best to not make major changes to this biologically inaccurate (but easily diagnosable) genus until the phylogeny of this, *Cardiophorus* and other nearby genera is better understood. However, *Cardiotarsus mjobergi* was placed at the base of the (weakly supported) apical clade composed of six Australian and South American species. It seems most appropriate to transfer *C. mjobergi* to the genus *Cardiodontulus*, from Papua New Guinea, because it matches the current definition of that genus. This placement appears likely to be accurate, because both are from the Australian biogeographic region, and because support for the clade including *Cardiodontulus*, but not *C. mjobergi*, is weak (PP = 0.65). Although the type specimen of *C. mjobergi* was not examined, I am confident in the identification of the specimens examined because they were from near the type locality, which is in an apparently well-collected area near a major city, and because of Calder's (1996) illustrated publication on the genus in Australia. The remaining apical clade of 15 taxa (PP = 0.81, Fig. 47) is composed mainly of Australian and Neotropical genera, plus two South Asian genera and one from Africa. This clade was also inferred by parsimony (Fig. 48), but with *Globothorax* and *Teslasena* added. Among these, the monophyly of each of *Odontocardus* Fleutiaux, *Triplonychoidus* Schwarz, *Paraplatynychus* Fleutiaux,

Triplonychus Candèze, *Cardiodontulus* Van Zwaluwenburg, *Craspedostethus* Schwarz and *Buckelater* Costa were not tested. These genera remain unaltered, except as noted previously for *Cardiodontulus*. Two large Neotropical genera (that extend into temperate N. America) *Esthesopus* and *Horistonotus* are both clearly not monophyletic (Table 3.3). However the definitions and status of these genera should be maintained until more detailed phylogenetic analysis of this clade is available. However, the definition of *Horistonotus* is broadened here to include species similar to *Aptopus agrestis*.

Of the apical three species in the weakly supported apical clade of this phylogram (Fig. 47), two belong to the polyphyletic genus *Paracardiophorus*. These species from Australia and Chile are rendered paraphyletic (also at low probability) by *Buckelater*, from Brazil. Because the included Australian and South American *Paracardiophorus* are identical in most characters including their kinds of male and female genitalia, it appears best to place them into a new genus along with other species from both continents that share their diagnostic characters. The type species of this new genus, *Austrocardiophorus*, is *Cardiophorus humeralis* Fairmaire and Germain (1860) from Chile (more recently placed in *Paracardiophorus*). This solution is considered preferable to formal association with the monotypic *Buckelater* because its female genitalic characters remain unknown, which contributes greatly to uncertainty about its placement.

3.4.4 Taxonomic conclusions

Tribe Nyctorini is placed in synonymy under the tribe Cardiophorinae. No tribal arrangement of Cardiophorinae is proposed here because no useful, phylogenetically

accurate groupings were identified. This is because the former Hypnoidinae and Negastrinae are a basal grade to the remainder of Cardiophorinae *sensu lato*, such that a sister tribe to the remainder of Cardiophorinae would be too small for these groupings to be taxonomically useful. The taxonomic changes to the genera of higher Cardiophorinae recommended based on the results of these analyses are listed in Table 3.4.

Table 3.4. Genera and subgenera for which status, rank or membership has been changed or clarified.

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- Aptopus* Eschscholtz 1829. Definition narrowed to exclude *Horistonotus*-like species.
- Austrocardiophorus* **gen. nov.** Type sp. *Cardiophorus humeralis* Fairmaire and Germain 1860. *Blaiseus* Fleutiaux 1931. New diagnosis, but spp.nov. not described here.
- Cardiodontulus* Van Zwaluwenburg 1963. *Cardiotarsus mjobergi* Carter transferred into genus.
- Cardiophorus*: subg. *Coptostethus* Wollaston 1854 was found to belong at subgenus rank.
- Chileaphricus* **gen.nov.** Type species, *Aphricus chilensis* Fleutiaux.
- Dicronychus* Brullé was found to belong at genus rank.
- Diocarpus* Fleutiaux 1947. **stat.nov.**, raised to genus rank.
- Floridelater* **gen.nov.** Type species *Coptostethus americanus* Horn. Type species transferred to Cardiophorinae from Negastrinae.
- Horistonotus* Candèze 1860. Definition expanded to include species near *Aptopus agrestis*.
- Margogastrus* Schwarz 1903. Transferred to Cardiophorinae from Physodactylinae.
- Metacardiophorus* Gurjeva 1966. **stat.nov.**, raised to genus rank.
- Lesnelater* Fleutiaux 1935 (Physodactylinae) **syn.nov.** of *Pachyelater* Lesne 1897.
- Pachyelater* Lesne 1897. Transferred from Dendrometrinae to Cardiophorinae.
- Paradicronychus* **gen.nov.** (Type species *Cardiophorus inflatus* Candèze), **syn.nov.** of *Cardiophorus* Eschscholtz 1829.
- Paracardiophorus* Schwarz 1895. Redefined based on North American and Eurasian spp.
- Patriciella* Van Zwaluwenburg 1953 **syn.nov.** of *Aphricus* LeConte 1853.
- Platynychus* Motschulsky was found to belong at genus rank.
- Teslasena* Fleutiaux 1892 (Physodactylinae), **syn.nov.** of *Globothorax* Fleutiaux 1891.
- Zygocardiophorus* Iablokoff-Khnzorian and Mardjanian 1981. **stat.nov.**, raised to genus rank.

3.4.5 Biogeographic hypotheses

All four a priori hypotheses of regional monophyly were clearly rejected (Table 3.3). These are: New World higher Cardiophorinae; New World *Cardiophorus* ($\pm$ *cardisce*, *luridipes*, *brevis*); Neotropical higher Cardiophorinae ($\pm$ *Austrocardiophorus humeralis*, *Chileaphricus chilensis*, *Cardiophorus brevis*); Australian higher Cardiophorinae ($\pm$ *Cardiodontulus*, *Aphricus* sp.nov). The rejection of all these hypotheses and the wide distribution of Cardiophorinae species indicates that either multiple lineages pre-date continental vicariance events or that intercontinental dispersal has occurred.

The disjunct, apparently relictual, distributions of genera *Aphricus* and *Blaiseus* are possible evidence that the major lineages do pre-date continental vicariance events. The finding that these and other basal members of higher Cardiophorinae are also known from small or monotypic genera throughout the world, including biogeographically disjunct areas like New Zealand and Chile, suggests that such an ancient origin is probably correct. The current apparent flightlessness of females of most basal genera may be further evidence against widespread intercontinental dispersal.

Further possible evidence for such ancient vicariance events is the southern biased distribution of the apical 17 taxa of Fig. 47 (PP = 0.77). Of these taxa, two are from the Oriental Region, three are Ethiopian, two are Australian and nine are Neotropical (two genera with some spp. also found in USA and S. Canada). This clade, which apparently includes most of the large Australian and Neotropical faunas is absent from the Palearctic region (and rarer than *Cardiophorus* in most of N. America). This mainly southern

distribution pattern suggests that this clade may have dispersed through Gondwana during the Jurassic or Cretaceous periods. Thus although putative fossil cardiophorines from the upper Jurassic were found not to be Cardiophorinae (Chapter 2), it nevertheless seems likely that higher Cardiophorinae were present during that period. The distribution of basal Cardiophorinae (formerly Negastrinae and Hypnoidinae, including clades with relictual distributions) throughout all world biogeographic regions suggests that these basal divergences are also ancient and global, which also corroborates the hypothesis of a pre-Cretaceous origin of higher Cardiophorinae.

3.4.6 Future research

Additional phylogenetic research with more taxon sampling is needed throughout Cardiophorinae to test generic monophyly and improve understanding of intergeneric relationships. Additional collecting and taxon sampling would be particularly useful among the basal higher cardiophorines, for which only two of nine genera are known from both sexes.

Some areas of the tree have low clade support and short branch lengths. These may approximate a hard polytomy, and thus it might be impossible to infer branching patterns using morphology alone. It is hoped that combined analysis of multiple gene regions plus morphology might resolve these regions, once specimens suitable for DNA sequencing have been collected.

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Figures 1-4. Frontoclypeal area of Clicking Elateroidea (scale bar = 0.5 mm). 1, *Eucnemidae Onichodon orchesoides*, (anterodorsal view); 2, *Selenodon speratus*, (anterodorsal view); 3, *Cardiophorus convexus*, (anteroventral view); 4, *Cardiophorus gramineus*, (dorsal view). CE = compound eye; SC = supra-antennal carina; SG = supra-orbital groove. Figs. 5-6. Latero-ventral view of hypomeron of Cardiophorinae (scale bar = 1 mm). 5, *Cardiophorus gagates* Erichson; 6, *Paracardiophorus propinquus* Lanchester. Ant = anterior.

Fig. 7. Lateral view of prosternal process of *Cardiophorus erythropus* Erichson (scale bar = 0.5 mm). A = longitudinal distance from procoxa to dorsal apex; Ant = Anterior; B = longitudinal distance from procoxa to end at halfway between dorsal and ventral apices; C = longitudinal distance from procoxa to ventral apex; D = vertical distance between dorsal and ventral apices. Dorsal and ventral apices are considered points where profile of respective surface is 45° from horizontal. Figures 8-11. Dorsal view of scutellum of Cardiophorinae (scale bar = 0.5 mm). 8, *Esthesopus castaneus*; 9 *Blaiseus bedeli*; 10, *Cardiophorus gramineus*; 11, *Floridelater americanus*. Figure 12. Latero-ventral view of mesepimeron and mesepisternum of *Paracardiophorus fenestratus* (LeConte) showing measurement of angle (a) of anterolateral corner of mesepisternum (scale bar = 0.5 mm). MST = mesepisternum; MRN = mesepimeron.

Figure 13-15. Ventral view of left side of mesocoxal cavity of Elateridae (After Johnson 2002b, scale bar = 1 mm). 13, Elaterinae sp.; 14, *Hypnoidus* sp.; 15, Cardiophorinae sp. Lat = lateral; MCX = mesocoxae MRN = mesepimeron; MST = mesepisternum; MS = Mesosternum. Figure 16. Lateral view of metasternum of *Zygocardiophorus nigratissimus* (scale bar = 0.5 mm). LC = lateral carina; MTP = metepisternum; MTS = metasternum. Figure 17-18. Dorsal view of anterior end of left elytron of Cardiophorinae (scale bar = 0.5 mm). 17, *Cardiophorus gramineus*; 18, *Paracardiophorus cardisce*. Scut = scutellum.

Figures 19-20. Hind wing of Clicking Elateroidea (scale bar = 1 mm). 19, *Anelastes druryi*; 20, *Blaiseus bedeli*. Vein names follow Kukalova-Peck and Lawrence (2004). Figures 21-22. Left metacoxal plate and metepisternum of Clicking Elateroidea (scale bar = 0.5 mm). 21, *Aulonothroscus punctatus*; 22, *Cardiophorus gramineus*. MCX = metacoxal plate; MTS = metepisternum.

Figures 23-24. Metatarsal claws of Cardiophorinae (scale bar = 0.5 mm). 23, *Dicronychus cinereus*; 24, *Diocarpus solitarius*. Figures 25-27. Dorsal view of aedeagus of Cardiophorinae (scale bar = 0.5 mm). 25, *Hypnoidus riparius*; 26, *Paracardiophorus cardisce*; 27, *Blaiseus bedeli*. PM = Paramere, ML = Median Lobe, BS = Basal Strut, PB = Phallobase.

Figures 28. Ventral view of ovipositor apex of *Agriotes sputator* (scale bar = 0.5 mm). C = coxites, B = baculae, S = styli. Figure 29. Bursa copulatrix of *Cardiophorus togatus* (scale bar = 0.5 mm). AnS = anterior sac; DS = distal sclerites, PS = proximal sclerites, SD = spermathecal gland duct, V = vagina.

Figures 30-33. Proximal sclerites of the bursa copulatrix of Cardiophorinae (top end of sclerite extends furthest into bursa) (scale bar = 0.5 mm). 30, *Paracardiophorus cardisce* (Say); 31, *Platynychus mixtus* Fleutiaux; 32, *Globothorax chevrolati* Fleutiaux; 33, *Esthesopus parvus* Horn. Figures 34-35. Distal sclerites of the bursa copulatrix of Cardiophorinae (scale bar = 0.5 mm). 34, *Cardiophorus inflatus* Candèze; 35, *Cardiophorus gramineus* (Scopoli). Figures 36-37. Sclerotised base of spermathecal gland duct of Cardiophorinae (scale bar = 0.5 mm). 36, *Paracardiophorus cardisce* (Say); 37, *Paracardiophorus musculus* (Erichson). SD = spermathecal gland duct.

Figure 38. Inferred phylogeny of extant Clicking Elateroidea based on 175 non-gap-weighted adult morphological characters. Tree is an all-compatible phylogram with branch lengths estimated by MrBayes, of 180000 post-burnin trees. Model = Mk_v+G. Values are posterior probabilities. Scale bar indicates 0.1 changes per character. Sex is indicated for members of cardiophorine clade coded from one sex only.

Figure 39. Inferred phylogeny of extant Clicking Elateroidea based on 134 parsimony informative non-gap-weighted adult morphological characters. Tree is a strict consensus of 116 most parsimonious trees of 1008 steps, CI = 0.25. Values above branches are decay indices, values below branches are bootstrap indices (above 50%).

Figure 40. Inferred phylogeny of extant Clicking Elateroidea based on 137 parsimony informative adult morphological characters (some gap-weighted). Tree is a single parsimonious tree of 1184 steps (reweighting removed), CI = 0.21. Values below branches are bootstrap indices (above 50%).

Figure 41. Inferred phylogeny of extant Clicking Elateroidea based on 175 non-gap-weighted adult morphological characters, with all four cardiophorine clade species coded from only one sex omitted. Tree is an all-compatible phylogram with branch lengths estimated by MrBayes, of 120000 post-burnin trees. Model = MkV+G. Values are posterior probabilities. Scale bar indicates 0.1 changes per character.

Figure 42. Inferred phylogeny of extant Clicking Elateroidea based on 134 parsimony informative non-gap-weighted adult morphological characters, with all 4 cardiophorine clade species coded from only one sex omitted. Tree is a strict consensus of 416 most parsimonious trees of 956 steps, CI = 0.26. Values above branches are decay indices, values below branches are bootstrap indices (above 50%).

Figure 43. Inferred phylogeny of extant Clicking Elateroidea based on 137 parsimony informative adult morphological characters (some gap-weighted), with all 4 cardiophorine clade species coded from only one sex omitted. Tree is a single most parsimonious tree of 1121 steps (reweighting removed), CI = 0.22. Values below branches are bootstrap indices (above 50%).

Figure 44. Inferred phylogeny of extant and fossil (indicated by arrows) Clicking Elateroidea based on 175 non-gap-weighted adult morphological characters with cardiophorine clade species coded from only one sex omitted. Tree is an all-compatible phylogram with branch lengths estimated by MrBayes, of 200000 post-burnin trees. Model = Mkv+G. Values are posterior probabilities. Scale bar indicates 0.1 changes per site.

Figure 45. Inferred phylogeny of extant and fossil (indicated by arrows) Clicking Elateroidea based on 134 parsimony informative non-gap-weighted adult morphological characters, with cardiophorine clade species coded from only one sex omitted. Tree is a strict consensus of 148 most parsimonious trees of 956 steps, CI = 0.265. Values above branches are decay indices, values below branches are bootstrap indices (above 50%).

Figure 46. Inferred phylogeny of extant and fossil (indicated by arrows) Clicking Elateroidea based on 137 parsimony informative adult morphological characters (some gap-weighted), with cardiophorine clade species coded from only one sex omitted. Tree is a strict consensus of 2651 most parsimonious trees of 1124 steps (reweighting removed), CI = 0.22. Values below branches are bootstrap indices

Figure 47. Inferred phylogeny of Cardiophorinae *sensu lato* based on 159 non-gap-weighted adult morphological characters. Tree is an all-compatible phylogram with branch lengths estimated by MrBayes, of 120000 post-burnin trees. Model = Mk_v+G. Values are posterior probabilities. Scale bar indicates 0.1 changes per site. D, P, and N are members of Dendrometrinae, Physodactylinae and Negastrinae within the Cardiophorine clade. Genus name "C." indicates *Cardiophorus*.

Figure 48. Inferred phylogeny of Cardiophorinae *sensu lato* based on 139 parsimony informative non-gap-weighted adult morphological characters. Tree is a strict consensus of 412 most parsimonious trees of 1083 steps, CI = 0.17. Values above branches are decay indices, values below branches are bootstrap indices (above 50%). D, P, and N are members of Dendrometrinae, Physodactylinae and Negastrinae within the Cardiophorine clade. Genus name "C." indicates *Cardiophorus*.

Figure 49. Inferred phylogeny of Cardiophorinae *sensu lato* based on 140 parsimony informative adult morphological characters (some gap-weighted). Tree is a strict consensus of 4 most parsimonious trees of 1473 steps (reweighting removed), CI = 0.17. Values below branches are bootstrap indices (above 50%). D, P, and N are members of Dendrometrinae, Physodactylinae and Negastriinae within the Cardiophorine clade. Genus name "C." indicates *Cardiophorus*.

Appendix 1. Synonymy of Cardiophorinae prior to revision.

A complete bibliographic synonymy is presented here to accurately document the nomenclatural history of the group. Several references were unavailable for examination, as is noted in the text. Methods used to develop synonymy are listed in Materials and Methods section. The following abbreviations refer to kinds of reference and taxonomic rank: catal., catalogue; check., checklist; comb.nov., species transferred to a different genus; distn., distribution; gen., genus/genera; rev., revision; sp.nov, one new species; spp.nov., more than one new species; subg., subgenus.

Cardiophorinae Candèze 1859 (in chronological order)

Cardiophorites Candèze 1859: 4. Key only.

-Type gen.: *Cardiophorus* Eschscholtz, 1829.

-Name recognised by: Candèze 1860: 100; Candèze 1865: 39 (spp.nov.); Candèze 1878: XXXVI (spp.nov.); Candèze 1882: 77 (spp.nov.); Candèze 1891a: 120 (catal.); Candèze 1891b: 778 (spp.nov.); Candèze 1893: 45 (spp.nov.); Candèze 1893: 45 (spp.nov.); Candèze 1897: 55 (spp.nov.); Candèze 1889: 105 (spp.nov.); Candèze 1900: 93 (sp.nov.).

Cardiophori LeConte 1861: 166;

Cardiophorina Thomson 1864: 109 (spp. of Scandinavia, includes *Negastrius*).

Cardiophorini Champion 1895: 415.

-Name recognised by: Schwarz 1906: 160 (gen. level rev., catal.).

-Synonymised under Cardiophorinae by Leseigneur 1972: 129 (spp. of France).

-Synonymy followed by Gurjeva 1974b: 77 (thoracic characters); Dolin 1988: 7 (spp. of Ukraine).

Aptopina Jakobson 1913: 760.

-Type gen.: *Aptopus* Eschscholtz, 1829.

-Synonymy verified by inclusion of Cardiophorina in synonymy under **Aptopina**.

-Synonymised under Cardiophorinae by Gurjeva 1974b: 77 (thoracic characters)

-Synonymy followed by Dolin 1988: 7 (spp. of Ukraine).

Cardiophorinae Hyslop 1917: 259 (phylogeny of Elateridae).

-Name recognised by: Leng (1920: 175); 1927: 105 and 1930: 4; Schenkling: 1925: 218 (catal., distn.); Miwa 1927: 105 (key to gen. of Japanese Empire); Miwa 1930: 1 (key to gen. and spp. of Formosa); Carter 1939: 309 (spp. of Australia); Blackwelder 1944: 301 (checkl.); Fleutiaux 1941: 27 (key to subfamilies); Neboiss 1956: 39 (checkl., Australia); Fleutiaux 1947a: 341 (spp. of French Indochina); Fleutiaux 1947b: 111 (spp. of Antilles); Nakane and Kishii 1956: 204 (subfamilies of Elateridae of Japan); Tsherepanov 1957: 234 (spp. of W. Siberia); Van Zwaluwenburg 1957: 62 (spp. of Micronesia); Arnett 1960: 508 (gen. of USA); Neboiss 1961: 18 (checkl., Australia); Iablokoff-Khnzorian 1961: 93 (fossils, Oligocene); Dajoz: 1963: 165 (spp. of

Europe and Mediterranean region); Gurjeva 1969: 157 (larval evolution); Cobos 1970a: 221 (spp. of Congo); Ôhira 1970: 216 (types from S.E. Asia), Lanchester 1971: 35 (spp. of N.W. USA); Ôhira 1971: 212 (types from S.S. Asia); Leseigneur 1972: 129 (spp. of France); Ôhira 1973a: 28 (spp. of Ryukyu Arch.); Ôhira 1973b: 38 (spp. of Ceylon); Costa 1973: 33 (gen.nov); Gurjeva 1974b: 77 (thoracic characters); Dolin 1975a: 1632 (wing venation, translated dolin 1975b); Dolin 1976 (2 new fossil gen.); Dolin 1978a: 8 (phylogeny of Elateridae); Dolin 1978b: 72 (larvae of USSR); Stibick 1979a: 181 (classification of Elateridae); Lohse 1979: 181 (spp. of central Europe); Golbach 1979a: 399 (key to gen. of S.S. America); Iablokoff-Khnzorian and Mardjanian 1981: 247 (subg.nov); Golbach 1994: 24 (key to S.S. American genera); Aranda 1998: 124 (note); Ôhira 1989: 79 (gen.nov); Atamuradov 1993: 118 (larvae, central Asia); Lawrence and Newton 1995: 784 (synonymy list); Lawrence et al. 1995 (subfamily larval diagnosis); Aranda 2003: 139 (spp.nov.); Lawrence et al. 2000 (subfamily diagnosis).

Cardiopherinae Hyslop 1917: 263 misspelling of Cardiophorinae.

Esthesopinae Fleutiaux 1919: 76 (incorrectly includes senior synonym,

Cardiophorites Candèze, in synonymy).

-Type gen.: *Esthesopus* Eschscholtz, 1829.

-Name recognised by: Fleutiaux 1931c: 306 (Catal. French Indochina); Miwa 1934: 25 (spp. of Japanese Empire); Van Zwaluwenburg 1963: 339 (spp. of Papua New Guinea).

-Synonymised under Cardiophorinae by Schenkling: 1925: 218 (catal., distn.); Fleutiaux 1941: 27 (key to subfamilies); Leseigneur 1972: 129 (spp. of France); Laurent 1974: 21 (spp. of S.S. Africa); Dolin 1988: 7 (spp. of Ukraine).

Esthesopini, Fleutiaux 1932c: 36 (tribe of Elaterinae).

-Type gen.: *Esthesopus* Eschscholtz, 1829.

Dicronychidae *sensu* Chûjô and Ôhira 1965: 28 (not Fleutiaux).

-Elevation, in error of Dicronychinae Fleutiaux 1919: 101 to family rank. Name, based on misapplication of homonym *Dicronychus sensu* Laporte (replaced by *Eudicronychus* Méquignon 1931) to Cardiophorinae (not *Dicronychus* Brullé).

Cardiophorini Candèze, 1859

-Cardiophorites Candèze 1859: 4. Key only.

-Type gen.: *Cardiophorus* Eschscholtz, 1829.

-Name recognised by: Candèze 1860: 100; Candèze 1865: 39 (spp.nov.); Candèze 1878: XXXVI (spp.nov.); Candèze 1882: 77 (spp.nov.); Candèze 1891a: 120 (catal.); Candèze 1893: 45 (spp.nov.); Candèze 1893: 45 (spp.nov.); Candèze 1897: 55 (spp.nov.); Candèze 1889: 105 (spp.nov.); Candèze 1900: 93 (sp.nov).

-Cardiophorini, Champion 1895: 415.

-Name recognised by: Schwarz 1906: 160 (gen. level rev., catal.); Heyden et al. 1906: 392 (catal., tribe includes *Cryptohypnus* and *Hypnoidus*); Hyslop 1917: 259 (phylogeny of Elateridae); Schenkling 1925: 218 (checkl.); Stibick 1979a: 181 (classification of Elateridae); Gurjeva 1974b: 77 (thoracic characters); Dolin 1975a: 1632 (wing venation); Dolin 1978b: 16 (larvae of USSR); Dolin 1988: 7 (spp. of Ukraine).

-Synonymised under *Esthesopinae* by Miwa 1934: 26 (spp. of Japanese Empire).

Genera in Alphabetical order:

Allocardiophorus Ôhira 1989: 79 *Paracardiophorus nigroapicalis* Miwa 1927: 109.

-Type species fixed by original designation.

Aphricus LeConte 1853: 501. Type species: *A. californicus* LeConte 1853: 502.

-Type species fixed by original monotypy.

-Described in *Cebrionites*.

-Name recognised by: Lacordaire 1857: 233 (gen. of Elateridae, in *Campylides*); Candèze 1863: 471 (spp. level rev. of Elateridae, in *Campylides*); Harold 1869: 1602 (catal.); Henshaw 1885: 66 (catal., in *Plastoceridae*); Candèze 1891a: 217 (catal., *Plastocerites*); Schwarz 1907b: 8 (gen. level rev., catal.), Woodworth 1913: 197 (checkl., California USA); Leng 1920: 166 (catal.); Fleutiaux 1940: 103; Knull 1957: 201 (key to spp.); Arnett 1960: 509 (gen. of USA, transferred to *Cardiophorinae*); Golbach

1979a: 400 (key to Argentinean gen.); Golbach 1994: 24 (key to gen. of S.S. America); Johnson 2002b: 168 (gen. of USA).

Aptopus Eschscholtz 1829: 32. Type species: *A. tibialis* Eschscholtz 1829: 32.

-Type species fixed by Hyslop 1921: 629.

-Name recognised by: Dejean 1836: 99 (catal.); Candèze 1860: 230 (spp. level rev. of Elateridae); Harold 1869: 1553 (catal.); Horn 1885: 33 (sp.nov. U.S.A); Henshaw 1885: 66 (catal.); Candèze 1889: 111 (spp.nov.); Candèze 1891a: 134 (catal.); Candèze 1891b: 781 (sp.nov., Burma); Champion 1895: 418 (spp. of central America); Schwarz 1906: 175 (gen. level rev., catal.); Schaeffer 1916 (spp.nov.); Leng 1920: 175 (catal.); Schenkling: 1925: 254 (catal., distn.); Blackwelder 1944: 302 (checkl.); Arnett 1960: 508 (gen. of USA); Dolin 1975a: 1632 (wing venation); Golbach 1979a: 400 (key to Argentinean gen.); Golbach 1994: 24 (key to gen. of S. America); Aranda 1996: 444 (key to Argentinean spp.); Aranda 1998: 130 (gen. descr. from S. American spp.); Johnson 2002b: 168 (gen. of USA); Aranda 2003: 139 (spp.nov.).

-Synonymised under *Cardiophorus* by Lacordaire 1857: 193.

-Incorrectly synonymised under the junior name *Priopus* Laporte by Laporte 1840: 251.

Apsopus Schwarz 1906: 180, incorrect subsequent spelling of *Aptopus*.

-Misspelling verified by inclusion of the correct reference page for *Aptopus* Eschscholtz.

Eniconyx Horn 1885: 51. Type species: *Eniconyx pullatus* Horn 1885: 52

- Type species fixed by Hyslop 1921: 644.
- Described in Elateridae.
- Name recognised by: Henshaw 1885: 66 (catal.); Candèze 1891a: 217 (catal., in Plastoceridae); Waterhouse 1902: 123; Leng 1920: 166 (catal., in Plastoceridae).
- Synonymised under *Aptopus* by Arnett 1960: 508.

Enisonyx Candèze 1891a: 217, incorrect subsequent spelling of *Eniconyx*.

- Misspelling verified by reference to Horn publication and spp. epithets belonging to *Eniconyx*.
- Misspelling followed by: Schwarz 1907b: 7 (gen. level rev., catal.).

Blaiseus Fleutiaux 1931c: 307. Type species: *B. bedeli* Fleutiaux 1931c: 308.

- Type species fixed by original monotypy.
 - Name recognised by: Fleutiaux 1947a: 343 (spp. of French Indochina).
- Blaseus* Gurjeva 1974a: 112, incorrect subsequent spelling of *Blaiseus*.
- Verified by placement in context of other cardiophorine genera.
 - Misspelling followed by: Gurjeva 1974b: 78 (thoracic characters).

Buckelater Costa 1973: 33. Type species: *B. argutus* Costa 1973: 35.

- Type species fixed by original designation.
- Name recognised by: Golbach 1979a: 399 (key to Argentinean gen.); Golbach 1994: 24 (key to gen. of S. America).

Cardiodontulus Van Zwaluwenburg 1963: 341. Type species: *C. brandti* Van

Zwaluwenburg 1963: 341.

-Type species fixed by original designation.

Cardiophorellus Cobos 1970a: 222. Type species: *C. gracilicornis* Cobos 1970a: 223.

-Type species fixed by original monotypy of nominate subg.

Cardiophorellus: subg. *Parapleonomus* Cobos 1970a: 222. Type species: *C. inermis*

Cobos 1970a: 222.

-Type species fixed by original designation.

Cardiophorus Eschscholtz 1829: 34. Type species: *Elater thoracicus* Fabricius 1801:

236, now regarded as a synonym of *Cardiophorus gramineus* (Scopoli, 1763).

-Type species fixed by Westwood 1838: 26.

-Name recognised by: Dejean 1833: 91 (catal.); Dejean 1836: 103 (catal.);

Eschscholtz 1836: Table; Germar 1839: 196 (key to gen. of Elateridae);

Erichson 1840: (spp. level rev.); Redtenbacher 1849: 300 (spp. of Austria);

LeConte 1853: 496 (spp. of USA, also includes *Horistonotus* spp.);

Lacordaire 1857: 193 (gen. of Elateridae); Redtenbacher 1858: 495 (spp. of

Austria); Jacquelin du Val 1859: 141 (gen. of Europe); Thomson 1859: 104

(gen. of Scandinavia); Candèze 1860: 106 (spp. level rev. of Elateridae);

Thomson 1864: 116 (spp. of Scandinavia); Harold 1869: 1546 (catal.);

Candèze 1875: 16 (spp.nov.); Horn 1871: 301 (spp.nov. U.S.A); Redtenbacher

1874: 537 (spp. of Austria); Henshaw 1885: 66 (catal.); Candèze 1889: 105

(spp.nov.); Candèze 1891a: 121 (catal.); Candèze 1891b: 778 (spp.nov.);

Heyden et al. 1891: 205 (catal.); Candèze 1892: 805 (sp.nov); Champion 1895: 416 (spp. of central America); Candèze 1897: 55 (sp.nov.); Jäger 1897: 356; Buysson 1891: 134 (note); Candèze 1893: 45 (sp.nov.); Fleutiaux 1893: 687 (sp.nov); Schwarz 1895a: 37 (sp.nov); Schwarz 1895b: 40 (key to gen.); Schwarz 1896: 148 (sp.nov); Buysson 1899: 279 (note); Blanchard 1889: 1 (spp. of N. America); Candèze 1900: 93 (sp.nov); Buysson 1902: 286 (spp. of France and Rhine Valley); Schwarz 1902: 259 (sp.nov); Schwarz 1903c: 370 (sp.nov.); Schwarz 1905: 289 (sp.nov.); Schwarz 1906: 162 (gen. level rev., catal.); Heyden et al. 1906: 393 (catal., Europe); Buysson 1910: 138 (note); Buysson 1911: 22 (spp. of Egypt); Buysson 1912: 128 (sp.nov. Russia); Jakobson 1913: 761 (key, catal., Europe); Woodworth 1913: 197 (checkl., California USA); Buysson 1914: 41 (sp.nov); Fleutiaux 1918b: 225 (sp.nov. Indochina); Fleutiaux 1919: 76 (sp.nov. east Africa); Leng 1920: 175 (catal.); Fleutiaux 1921: 14 (spp. record, English Africa); Buysson 1924: 207 (spp. of Morocco); Cockerell 1925: 9 (sp.nov. Eocene fossil); Schenkling 1925: 219 (catal., distn.); Méquignon 1931: 207 (note); Miwa 1927: 106 (key to gen. of Japanese Empire); Miwa 1930: 1 (key to gen. and spp. of Formosa); Miwa 1934: 26 (spp. of Japanese Empire); Fleutiaux 1931c: 313 (catal., French Indochina); Fleutiaux 1932b: 20 (spp. of Mozambique); Carter 1939: 310 (spp. of Australia transferred to *Paracardiophorus*); Jagemann 1940: 55 (spp. Europe); Normand 1941: 331 (sp.nov, N. Africa); Blackwelder 1944: 301 (checkl.); Van Zwaluwenburg

1947: 111 (spp. of Australia); Fleutiaux 1947a: 344 (spp. of French Indochina); Cobos 1954: 86 (checkl., Sierra Nevada, Spain); Binaghi 1955: 4 (note); Jagemann 1955: 136 (spp. of Czechoslovakia); Neboiss 1956: 39 (transferred all Australian spp. to *Paracardiophorus*, checkl., Australia); Tsherepanov 1957: 234 (spp. of W. Siberia); Cobos 1959: 468 (sp.nov. Brazil); Arnett 1960: 508 (gen. of USA); Cobos 1961: 63 (spp. of Morocco); Ôhira 1962: 177 (higher classification, larvae); Chûjô and Ôhira 1965: 28 (spp. of Japan); Dajoz 1963: 165 (spp. of Europe and Mediterranean region); Gurjeva 1966: 64 (spp. of central Asia); Leiler 1967: 89-109 (larvae and pupae, Europe); Gurjeva 1969: 156 (larval evolution); Cobos 1970a: 232 (spp.nov. Congo); Cobos 1970b: 29 (spp. of Canary Islands); Ôhira 1970: 216 (types from S.E. Asia); Ôhira 1971: 212 (types from S. Asia); Lanchester 1971: 35 (spp. of N.W. USA); Leseigneur 1972: 130 (spp. of France); Laurent 1974: 22 (spp. of S. Africa); Gurjeva 1974b: 78 (thoracic characters); Gurjeva 1974c: 170 (spp.nov, Afghanistan); Dolin 1975a: 1632 (wing venation); Dolin 1978a: 8 (phylogeny of Elateridae); Dolin 1978b: 73 (larvae of USSR); Chassain 1979: 194 (spp. of Saudi Arabia); Golbach 1979a: 400 (key to Argentinean gen.); Lohse 1979: 181 (spp. of central Europe); Iablokoff-Khnzorian and Mardjanian 1981: 247 (subg.nov); Dolin 1988: 7 (spp. of Ukraine); Bousquet 1991: 185 (catal.); Kompantseva 1991: 18 (key: larvae of Tajikistan); Vats and Chauhan 1991: 11 (spp. N. India); Atamuradov 1993: 118 (larvae, central Asia); Downie and Arnett 1996: 821 (spp. N.E. N.

America); Platia and Gudenzi 2000a: 601, 2002: 28 (spp. of Turkey); Platia and Gudenzi 2000b: 136 (spp. of Greece); Johnson 2002b: 168 (gen. of USA); Cate et al. 2002: 46 (spp. nov, Iran); Platia et al. 2002: 76 (sp. nov, Iran); Douglas 2003: 493 (spp. of E. N. America) ; Lucht 2005: 198, 199 (distn., bionomics).

Cardiophorus Motschulsky 1858: 59, incorrect subsequent spelling of *Cardiophorus*.

-Verified as *Cardiophorus* ref. by mention of *C. curiatus* in same passage.

Cardiophorua Cobos 1954: 86, incorrect subsequent spelling of *Cardiophorus*.

-Verified by cardiophorine context.

Cardiosphorus Gurjeva 1974b: 70, incorrect subsequent spelling of *Cardiophorus*.

-Verified by ref. to fig. of cordate scutellum.

Caloderus Stephens 1830: 269. Type species: *Elater thoracicus* Fabricius 1801: 236.

-Type fixed by Hyslop 1921: 632.

-Name recognised by Laporte 1840: 249 (with *Cardiophorus* in synonymy).

-Synonymised under *Cardiophorus* by Westwood 1838: 26 (gen. of British Insects).

-Synonymy followed by: Lacordaire 1857: 138 (gen. of Elateridae); Candèze 1860: 106 (spp. level rev. of Elateridae); Harold 1869: 1546 (catal.); Candèze 1891a: 121 (catal.); Champion 1895: 416 (spp. of central America); Schwarz

1906: 162 (gen. level rev., catal.); Schenkling: 1925: 220 (catal., distn.);
Leseigneur 1972: 130 (spp. of France); Dolin 1988: 10 (spp. of Ukraine).

Cardiophorus: subg. *Coptostethus* Wollaston.

-Current rank ambiguous.

-Rank lowered to subgenus by Cobos 1970b: 34.

-Subg. rank recognised by: Cobos 1978: 145 (spp. Atlantic Islands); Johnson
2001: 58 (*C. (Coptostethus) americanus* transferred to *Negastrius*).

Coptostethus Wollaston 1854: 238. Type species: *C. femoratus* Wollaston 1854:
240.

-Type species fixed by original monotypy.

-Gen. status recognised by Lacordaire 1857: 196 (gen. of Elateridae); Candèze
1860: 104; Harold 1869: 1546 (catal.); Horn 1871: 303 (sp.nov. U.S.A);
Henshaw 1885: 66 (catal.); Fleutiaux 1891a; Candèze 1891a: 121 (catal.);
Candèze 1889: 105 (spp.nov.); Schwarz 1906: 161 (gen. level rev., catal.);
Jakobson 1913: 761 (key, catal., Europe); Leng 1920: 175 (sp. of N.
America); Schenkling: 1925: 218 (catal., distn.); Blackwelder 1944: 301
(checkl.); Arnett 1960: 508 (gen. of USA); Dajoz 1963: 173 (spp. of Europe
and Mediterranean region); Laurent 1974: 22 (spp. of S. Africa); Gurjeva
1974b: 78 (thoracic characters); Golbach 1979a: 400 (without comment, key
to Argentinean gen.); Golbach 1994: 24 (key to gen. of S. America); Aranda
1998: 130 (key to gen.).

Coptostethus Candèze 1860: 504, incorrect subsequent spelling of *Coptostethus*.

-Verified by listing of correct spp.

-Misspelling followed by: Aranda 1998: 124 (list of gen., but not key).

Cardiophorus: subg. *Metacardiophorus* Gurjeva 1966: 91. Type species: *C. sogdianus*
Gurjeva 1966: 91.

-Type species fixed by original designation.

Cardiophorus: subg. *Perrinellus* Buysson 1899: 282. Type species: *Athous argentatus*
Abeille de Perrin 1894: 92.

-Type species fixed by original designation.

-Genus rank recognised by: Waterhouse 1902: 279; Buysson 1910: 145 (note);
Buysson 1911: 22 (spp. of Egypt).

-Treated as subgenus of *Cardiophorus* by Schwarz 1906: 172 (genus level
revision, catal.).

-Subgenus rank followed by: Heyden et al. 1906: 394 (catal. Europe);

Schenkling: 1925: 220 (catal., distn.); Jagemann 1940: 55 (spp. Europe);

Cobos 1950: 155 (note); Cobos 1954: 86 (Faunal list, Sierra Nevada, Spain);

Gurjeva 1966: 88 (spp. of central Asia); Platia 1994: 354 (spp. of Italy).

-Not recognized as a natural group by Dajoz 1963: 165 (spp. of Europe and
Mediterranean region).

Cardiophorus: subg. *Lasiocerus* Buysson 1912: 129. Type species: *C. schusteri* Buysson
1912: 128.

-Type species fixed by original monotypy.

-Current rank and status ambiguous.

-Described at genus rank.

-Synonymised under *Cardiophorus*: subg. *Perrinellus* by Schenkling: 1925: 237 (catal., distn.).

-Synonymy (under *Cardiophorus*, without recognition as subgenus) followed by Dolin 1988: 10 (spp. of Ukraine).

-As subgenus of *Cardiophorus* Platia 1994: 354 (spp. of Italy, without comment).

-Mentioned, but neither recognized, nor synonymised by Dajoz 1963: 165 (spp. of Europe and Mediterranean region).

Perinellus Schwarz 1906: 172, incorrect subsequent spelling of *Perrinellus*.

-Verified by corroboration: correct species listed.

Cardiophorus: subg. *Zygocardiophorus* Iablokoff-Khnzorian and Mardjanian 1981: 247.

Type species: *C. nigratissimus* Buysson 1891: 134.

-Type species fixed by original designation.

Zygocardiophorus Platia 1994: 354, incorrect subsequent spelling of *Zygocardiophorus*.

-Verified by correct page and date of original publication.

Cardiotarsus Eschscholtz 1836: published in identification table opposite p.5, without associated spp. Type species: *C. capensis* Candèze 1860: 226.

-Type species fixed by Hyslop 1921: 633.

-Name recognised by: Dejean 1833: 91 (*nomen nudem*, (indication not valid because associated species name was unavailable) catal.); Dejean 1836: 103 (catal.); Germar 1839: 198 (key to gen. of Elateridae); Lacordaire 1857: 192 (gen. of Elateridae); Candèze 1860: 225 (spp. level rev. of Elateridae); Harold 1869: 1552 (catal.); Candèze 1889: 111 (sp.nov.); Candèze 1891a: 133 (catal.); Candèze 1891b: 780 (sp.nov.); Candèze 1897: 55 (spp.nov.); Schwarz 1902: 261 (sp.nov.); Schwarz 1905: 289 (sp.nov.); Schwarz 1906: 174 (gen. level rev., catal.); Fleutiaux 1918b: 231 (sp.nov., Indochina, now *Odontocardus*); Schenkling: 1925: 253 (catal., distn.); Fleutiaux 1919: 97 (sp. record, east Africa); Miwa 1927: 105 (key to gen. of Japanese Empire); Miwa 1930: 4 (key to gen. and spp. of Formosa); Fleutiaux 1931c: 328 (catal. French Indochina); Fleutiaux 1932c: 36 (spp. of Mascarene Is.); Miwa 1934: 27 (spp. of Japanese Empire); Carter 1939: 309 (spp. of Australia); Fleutiaux 1947a: 369 (spp. of French Indochina); Neboiss 1956: 46 (checkl., Australia); Cobos 1970a: 223 (key to gen., Congo); Ôhira 1970: 216 (types from S.E. Asia); Laurent 1974: 34 (spp. of S. Africa); Gurjeva 1974b: 78 (thoracic characters); Dolin 1975a: 1632 (wing venation); Kishii 1992: 8 (sp.nov., Taiwan); Calder 1996: 360 (checkl., Australia).

Craspedostethus Schwarz 1898b: 414. Replacement name for *Craspedonotus* Schwarz.

-Name recognised by: Waterhouse 1902: 88; Schenkling: 1925: 252 (catal., distn.); Dajoz 1963: 172 (spp. of Europe and Mediterranean region); Chassain 1979: 206 (rejecting placement in *Paracardiophorus* by Cobos 1970a based

on sclerites of bursa copulatrix, spp. of Saudi Arabia); Cate et al. 2002: 52 (sp.nov, Iran).

-Considered a subg. of *Paracardiophorus* by: Cobos 1970a: 227 (spp.nov. Congo).

Craspedonotus Schwarz 1898a: 148. Type species: *C. rufiventris* Schwarz 1898a: 148.

-Type species fixed by Hyslop 1921: 636.

-Junior homonym of *Craspedonotus* Schaum 1863 (Carabidae).

Crioraphes Iablokoff-Khnzorian (fossil, Oligocene) 1961: 93. Type species: *C. rohndendorfi* Iablokoff-Khnzorian 1961: 94.

-Type species fixed by original monotypy.

Dicronychus Brullé 1832: 138. Type species: *Elater obesus* Brullé 1832: 138, now referred to by replacement name *Dicronychus brullei* Platia and Gudenzi (2003).

-Current rank and status ambiguous.

-Type fixed by Méquignon 1931: 208.

-Originally described *Dicronychus* as a subgroup of *Elater* (and considered Eschscholtz the author).

-Raised to genus rank by Eschscholtz 1836: Table.

-Genus rank followed by: Schwarz 1897: 9 (note); Schwarz 1903c: 365 (sp.nov.); Schwarz 1905: 282 (sp.nov.); Fleutiaux 1932a: 170 “Gen *Dicronychus* Brullé, 1832”; Fleutiaux 1947a: 348 (spp. of French

Indochina); Arnett 1955: 608 (note on types); Ôhira 1962: 177 (higher classification, larvae); Ôhira 1970: 230 (types from S.E. Asia); Ôhira 1971: 212 (types from S. Asia); Leseigneur 1972: 151 (spp. of France); Ôhira 1973b: 38 (spp. of Ceylon); Laurent 1974: 23 (spp. of S. Africa); Gurjeva 1974b: 78 (thoracic characters); Lohse 1979: 184 (spp. of central Europe); Iablokoff-Khnzorian and Mardjanian 1981: 247 (subg.nov); Platia 1994: 381 (spp. of Italy); Cate et al. 2002: 55 (sp.nov, Iran); Platia and Gudenzi 2003: 27 (spp. of Greece); Platia and Gudenzi 2004: 9 (spp. of Turkey); Lucht 2005: 198, 199 (distn., bionomics).

-Synonymised under *Cardiophorus* by Lacordaire 1857: 138 (gen. of Elateridae).

-Synonymy followed by: Candèze 1860: 106 (spp. level rev. of Elateridae); Harold 1869: 1546 (catal.); Candèze 1891a: 121 (catal.); Heyden et al. 1891: 205 (catal.); Champion 1895: 416 (spp. of central America); Schwarz 1906: 162 (gen. level rev., catal.); Schenkling: 1925: 220 (catal., distn.); Dolin 1975a: 1621 (wing venation); Dolin and Gurjeva 1975: 118 (note on larvae); Dolin 1988: 10 (spp. of Ukraine); Vats and Chauhan 1991: 11 (spp. N. India, no formal synonymy, but includes *Cardiophorus* spp. with diagnostic characters of *Dicronychus*).

-As subg. of *Cardiophorus*: Méquignon 1931: 207 (as senior synonym of subg. *Platynychus*).

-Subg. rank followed by: Binaghi 1955: 4 (note); Lawrence and Newton (1995: 855).

Eudicronychus Méquignon; sensu Chûjô and Ôhira 1965: 28.

-Error verified by inclusion of spp. assigned to *Dicronychus* Brullé.

Gauroderus Thomson 1859: 104. Type species: *Elater cinereus* Herbst 1784: 114.

-Type species fixed by original designation.

-Considered an objective junior generic synonym of *Dicronychus* by Méquignon 1931: 207 because type sp. is a subjective synonym of the type of *Dicronychus* (treated as subg. of *Cardiophorus*).

-Synonymy followed by Miwa 1934: 26 (spp. of Japanese Empire);

Fleutiaux 1947a: 348 (spp. of French Indochina); Leseigneur (1972: 151);

Platia (1994: 380).

-Synonymised under *Cardiophorus* by Harold 1869: 1546 (catal. with *Dicronychus*).

-Synonymy under *Cardiophorus* followed by: Candèze 1891a: 121

(catal.); Champion 1895: 416 (spp. of central America); Schwarz 1906:

162 (gen. level rev., catal.); Schenkling: 1925: 220 (catal., distn.).

-Considered a junior synonym of *Platynychus* (as subg. of *Cardiophorus*) by Heyden et al. 1906: 394 (catal. Europe).

Displatynychus Ôhira 1987: 92.

-Raised to gen. rank by Ôhira 1999.

Platynychus: subg. *Displatynychus* Ôhira 1987: 92. Type species: *Cardiophorus adjutor* Candèze 1875: 17.

-Type species fixed by original designation.

Esthesopus Eschscholtz 1829: 32. Type species: *E. castaneus* Eschscholtz 1829: 32.

-Type species fixed by original monotypy.

-Name recognised by: Eschscholtz 1836: table; Germar 1839: 197 (key to gen. of Elateridae); Candèze 1860: 274 (spp. level rev. of Elateridae); Harold 1869: 1555 (catal.); Horn 1885: 41 (spp. of U.S.A); Steinheil 1875: 131 (spp. of “Neu-Granada”); Henshaw 1885: 66 (catal.); Candèze 1891a: 137 (catal.); Champion 1895: 439 (spp. of central America); Schwarz 1902: 269 (sp.nov); Schwarz 1903a: 75 (spp.nov.); Schwarz 1906: 179 (gen. level rev., catal.); Woodworth 1913: 198 (checkl., California USA); Leng 1920: 175 (catal.); Schenkling: 1925: 260; Blackwelder 1944: 303 (checkl.); Fleutiaux 1947: 111 (spp. of Antilles); Arnett 1960: 509 (gen. of USA); Becker 1973b: 1531 (diagnostic note); Dolin 1975a: 1632 (wing venation); Dolin 1978: 8 (phylogeny of Elateridae); Golbach 1979a: 400 (key to Argentinean gen.); Golbach 1994: 24 (key to gen. of S. America); Downie and Arnett 1996: 822 (spp. N.E. N. America); Johnson 2002b: 168 (gen. of USA).

Esthesops Woodworth 1913: 197, incorrect subsequent spelling of *Esthesopus*.

-Verified by correct spelling elsewhere in document.

Esthosopus Eschscholtz 1836: table, incorrect subsequent spelling of *Esthesopus*.

- Verified by possession of following key characters: 4th tarsomere laminate, claws serrate.

Ethesopus Germar 1839: 197, incorrect subsequent spelling of *Esthesopus*.

- Verified by mention of correct type sp.

Exoeolus Broun 1893: 1133. Type species: *E. rufescens* Broun 1893: 1134.

- Type species fixed by Hyslop 1921: 646 (spelled *Exaeolus*).
- Name recognised by Waterhouse 1902: 140; Neave 1939: 391 (list of gen. names); Douglas 2005: 29 (revision).

Exaeolus; Schwarz 1906: 161, incorrect subsequent spelling of *Exoeolus*.

- Verified by reference to valid *Exoeolus* species.
- Misspelling followed by: Hyslop 1921: 646 (note on types); Schenkling: 1925: 219 (catal., distn.).

Brounaeolus Hyslop 1921: 631. Replacement name for *Exaeolus sensu* Schwarz.

- Misspelled name was junior homonym of *Exaeolus* Gozis 1886: 22 (Coleoptera: Elateridae).
- Replacement name followed by: Schenkling: 1925: 219 (catal., distn.).

Globothorax Fleutiaux 1891a: ccxxxii. Type species: *G. chevrolati* Fleutiaux 1891a: ccxxxiii.

- Type species fixed by original monotypy.
- Name recognised by: Waterhouse 1902: 149; Schwarz 1906: 181 (gen. level rev., catal.); Schenkling: 1925: 263 (catal., distn.); Blackwelder 1944: 303

(checkl.); Golbach 1979a: 401 (new sp., key to species); Golbach 1994: 24 (key to gen. of S. America).

Globotorax Aranda 1998: 126, 128, 130 (key to gen.), incorrect subsequent spelling of *Globothorax*.

-Verified by reference to correct author and year and appearance in context with other Cardiophorine genera.

Horistonotus Candèze 1860: 243. Type species: *H. flavidus* Candèze 1860: 250.

-Type species fixed by Hyslop 1921: 650.

-Name recognised by: Harold 1869: 1554 (catal.); Steinheil 1875: 131 (spp. of “Neu-Granada”); Horn 1871: 302 (sp.nov. U.S.A); Horn 1885: 33 (spp. of U.S.A); Henshaw 1885: 66 (catal.); Candèze 1889: 111 (sp.nov.); Candèze 1891a: 135 (catal.); Fleutiaux 1895: 172 (sp.nov.); Schwarz 1895b: 40 (key to gen.); Champion 1895: 428 (spp. of central America); Schwarz 1897: 9 (note); Schwarz 1902: 261 (spp.nov.); Schwarz 1903a: 74 (sp.nov.); Schwarz 1906: 176 (gen. level rev., catal.); Woodworth 1913: 198 (checkl., California USA); Leng 1920: 175 (catal.); Schenkling: 1925: 255 (catal., distn.); Van Dyke 1932: 329 (spp.nov. USA); Carter 1939: 310 (sp. of Australia transferred to *Paracardiophorus*); Blackwelder 1944: 302 (checkl.); Fleutiaux 1947: 111 (spp. of Antilles); Neboiss 1956: 46 (transferred all Australian spp. to *Paracardiophorus*, checkl., Australia); Arnett 1960: 509 (gen. of USA); Lanchester 1971: 48 (spp. of N.W. USA); Becker 1973b: 1531 (diagnostic note); Dolin 1975a: 1632 (wing venation); Golbach 1979b: 411 (sp.nov, key

to Argentinean spp.); Bousquet 1991: 178 (catal.); Golbach 1994: 24 (key to gen. of S. America); Downie and Arnett 1996: 821 (spp. N.E. N. America); Wells 2000: 416 (key to the spp. of USA and Canada); Johnson 2002b: 168 (gen. of USA).

Horisonotus Woodworth 1913: 197, incorrect subsequent spelling of *Horistonotus*.

-Verified by two references to valid *Horistonotus* spp.

Horizonotus Carpenter 1992: 331, incorrect subsequent spelling of *Horistonotus*.

-Verified by reference to name spelled correctly by Wickham (1916).

Mionelater Becker 1963: 125. Type species: *M. planatus* Becker 1963: 126.

-Type species fixed by original designation.

-Chiapas, Mexico Miocene fossil in amber.

Neocardiophorus Gurjeva 1966: 95. Type species: *N. mamajevi* Gurjeva 1966: 95.

-Type species fixed by original designation.

-Name recognised by: Gurjeva 1974b: 78 (thoracic characters); Dolin 1978b: 81 (larvae of USSR); Iablokoff-Khnzorian and Mardjanian 1981: 246 (note).

Odontocardus Fleutiaux 1931c: 332. Type species: *Cardiotarsus vitalisi* Fleutiaux 1918b: 231.

-Type species fixed by original designation.

-Name recognised by: Fleutiaux 1947a: 376 (spp. of French Indochina).

Odontocarduus Gurjeva 1974a: 112, incorrect subsequent spelling of

Odontocardus.

-Verified by reference to cardiophorine genera.

-Misspelling followed by: Gurjeva 1974b: 78 (thoracic characters).

Paracardiophorus Schwarz 1895b: 40. Type species: *Cardiophorus musculus* Erichson 1840: 299.

-Type species fixed by Hyslop 1921: 660.

-Name and genus rank recognised by: Schwarz 1902: 259 (sp.nov);

Waterhouse 1902: 265; Schwarz 1903d: 390 (sp.nov.); Schwarz 1906: 172

(gen. level rev., catal.); Jakobson 1913: 761 (key, catal., Europe); Schenkling:

1925: 249 (catal., distn.); Miwa 1927: 106 (key to gen. of Japanese Empire);

Miwa 1930: 6 (key to gen. and spp. of Formosa); Fleutiaux 1932b: 21 (spp. of

Mozambique); Miwa 1934: 26 (spp. of Japanese Empire); Carter 1939: 309

(spp. of Australia); Jagemann 1940: 55 (spp. Europe); Blackwelder 1944: 302

(checkl.); Jagemann 1955: 152 (spp. of Czechoslovakia); Neboiss 1956: 40

(checkl., Australia); Tsherepanov 1957: 244 (spp. of W. Siberia); Neboiss

1961: 18 (checkl., Australia); Leseigneur 1972: 156 (spp. of France); Dajoz

1963: 172 (spp. of Europe and Mediterranean region); Cobos 1970a: 225

(sp.nov. Congo); Ôhira 1973b: 38 (spp. of Ceylon); Gurjeva 1974b: 78

(thoracic characters); Dolin 1975a: 1632 (wing venation); Dolin 1978b: 73

(larvae of USSR); Chassain 1979: 210 (sp.nov. Saudi Arabia); Golbach

1979a: 400 (key to Argentinean gen.); Lohse 1979: 186 (spp. of central

Europe); Iablokoff-Khnzorian and Mardjanian 1981: 246 (note); Dolin 1988: 9 (spp. of Ukraine); Golbach 1994: 24 (key to gen. of S. America); Calder 1996: 360 (checkl., Australia); Ôhira 1997: 1 (note).

-As subg. of *Cardiophorus* Buysson 1902: 290 (originally called a group of *Cardiophorus*).

-Subg. rank followed by Heyden et al. 1906: 394 (catal. Europe); Fleutiaux 1931c: 314.

Paracardiophorus Lucht 2005: 198-199, incorrect subsequent spelling of *Paracardiophorus*.

-Verified by association of type species name, author and range.

Paracarpiphonus Fleutiaux 1928: 284, incorrect subsequent spelling of *Paracardiophorus*.

-Verified by published correction, Fleutiaux 1929a: 23.

Paracapiophonus Arnett 1955: 614 (note on types), incorrect subsequent spelling of *Paracardiophorus*.

-Verified by reference to Fleutiaux's (different) misspelling of *Paracardiophorus*.

Paradicronychus Dolin and Gurjeva 1975: 116 (*nomen nudum*)

-No type species designated for this name, published after 1930, therefore name is not available.

-Name recognised by: Dolin 1978b: 81 (larvae of USSR).

-As synonym of *Dicronychus*: Platia 1994: 380 (spp. of Italy, synonymised without comment).

Paraplatynychus Fleutiaux 1931c: 315.

-Raised to gen. rank by Ôhira 1970: 230 (without comment, types from S.E. Asia). Made new combination *Paraplatynychus costatus* (Fleutiaux, 1931) from *Platynychus* (*Paraplatynychus*) *costatus*.

Platynychus: subg. *Paraplatynychus* Fleutiaux 1931c: 315. Type species:

Platynychus mixtus Fleutiaux 1931c: 326.

-Type species fixed by original designation.

-Treated as a subg. of *Dicronychus* by Fleutiaux 1947a: 348 (spp. of French Indochina).

Patriciella Van Zwaluwenburg 1953: 20. Replacement name for *Patricia* Van Zwaluwenburg.

-Name recognised by: Neboiss 1961: 28 (checkl., Australia); Calder 1996: 360 (checkl., Australia).

-Moved to Cardiophorinae by Calder 1996: 377.

Patricia Van Zwaluwenburg 1947: 113. Type species: *P. australica* Van Zwaluwenburg 1947: 114.

-Type assigned by original designation.

-Name recognised by: Neboiss 1956: 64 (checkl., Australia).

-Described in Physodactylinae.

-Junior homonym of *Patricia* Fox 1940 (Lepidoptera).

Phorocardius Fleutiaux 1931c: 308. Type species: *Cardiophorus florentini* Fleutiaux 1893: 687.

-Type species fixed by original designation.

-Name recognised by: Miwa 1934: 26 (spp. of Japanese Empire); Fleutiaux 1947a: 363 (spp. of French Indochina); Ôhira 1971: 207 (types from S. Asia); Gurjeva 1974b: 78 (thoracic characters).

Phorocardius: subg. *Diocarpus* Fleutiaux 1947a: 364. Type species: *P. solitarius* Fleutiaux 1931c: 309.

-Type species fixed by monotypy.

Platynychus Motschulsky 1858: 58. Type species: *P. indicus* Motschulsky 1858: 59.

-Type species fixed by Hyslop 1921: 665. This fixation is valid and non-reversible, although disputed by Méquignon 1930: 96.

-Current rank and status ambiguous.

-Gen. rank recognised by: Fleutiaux 1931c: 315 (catal. French Indochina); Fleutiaux 1932b: 25 (spp. of Mozambique); Miwa 1934: 26 (spp. of Japanese Empire); Fleutiaux 1947a: 348 (spp. of French Indochina, with putative diagnostic chars for this and *Dicronychus*); Jagemann 1955: 147 (spp. of Czechoslovakia); Van Zwaluwenburg 1957: 62 (spp. of Micronesia); Van Zwaluwenburg 1963: 339 (spp. of Papua New Guinea); Dajoz 1963: 171 (but with *P. cinereus* (valid name of *Dicronychus* type sp.) incorrectly named as type species, spp. of Europe and Mediterranean region); Chassain 1979: 195

(spp. of Saudi Arabia); Ôhira 1987: 92 (description of new subg. of *Platynychus*).

-Treated as synonym of *Cardiophorus* by Harold 1869: 1546 (catal., *pars.*).

-Synonymy under *Cardiophorus* followed by: Candèze 1891a: 121 (*Pars.*, catal.); Dolin 1988: 10 (spp. of Ukraine).

-Treated as subg. of *Cardiophorus* by Buysson 1902: 329 (including *E. cinereus*, senior synonym of type species of *Dicronychus*).

-subg. rank followed by Heyden et al. 1906: 394 (catal. Europe); Schenkling: 1925: 219 (catal., distn.); Jagemann 1940: 55 (spp. Europe); Gurjeva 1966: 92 (spp. of central Asia); Cobos 1970a: 223 (key to gen., Congo); Dolin and Gurjeva 1975: 118 (note on larvae, misspelled).

-Treated as a synonym of *Dicronychus* by Méquignon 1931: 207 (note, *Dicronychus* here considered a subg. of *Cardiophorus*).

-Synonymy followed by: Leseigneur 1972: 151 (spp. of France); Ôhira 1973b: 38C (made *Dicronychus comptus* (Candèze) comb.nov. from *Cardiophorus (Platynychus) comptus*; Schenkling 1925: 238 (catal., distn.); Lohse 1979: 184 (spp. of central Europe); Iablokoff-Khnzorian and Mardjanian 1981: 246 (note).

-Ôhira 1970: 230 moved one *Platynychus* sp. to *Dicronychus* and elevated *Paraplatynychus* to gen. rank w/o comment. These transfers are considered possible evidence of acceptance of synonymisation of *Platynychus* under *Dicronychus*.

-Treated as subg. of *Dicronychus*: Fleutiaux 1947a: 348 (spp. of French Indochina); Chûjô and Ôhira 1965: 28.

-Subg. rank recognised by: Ôhira 1973a: 32 (spp. of Ryukyu Arch.).

Platynychus Motschulsky 1858: 59, incorrect subsequent spelling of

Platynychus.

-Verified by reference to correct spelling in earlier paragraph.

Platynichus Dolin and Gurjeva 1975: 118, incorrect subsequent spelling of

Platynychus.

-Verified by use as subg. of *Cardiophorus*, which contains sp. “*C.*

(*Platynichus*) *cinereus* (Herbst)”.

Platynychnus Méquignon 1931: 208 (note), incorrect subsequent spelling of

Platynychus.

-Verified by use of correct spelling elsewhere in note and reference to correct publication date.

Protocardiophorus Dolin 1976: 71. Type species: *P. ancestralis* Dolin 1976: 71.

-Fossil, Upper Jurassic.

-Type species fixed by original designation.

Pseudocardiophorites Dolin 1976: 72. Type species: *P. fragilis* Dolin 1976: 73.

-Fossil, Upper Jurassic.

-Type species fixed by original designation.

Ryukyucardiophorus Ôhira 1973a: 32. Type species: *Paracardiophorus loochooensis*

Miwa 1934: 255.

-Type species fixed by original designation.

Triplonychoidus Schwarz 1906: 181. Type species: *Triplonychus trivittatus* Champion 1895: 427.

-Type species fixed by Hyslop 1921: 672.

-Name recognised by: Waterhouse 1912: 308; Neave 1939: 565 (list of genus names); Golbach 1979a: 400 (key to gen. of S. America).

Triplonychoides Hyslop 1921: 672, incorrect subsequent spelling of *Triplonychoidus* Schwarz.

-Misspelling followed by Schenkling: 1925: 263 (catal., distn.); Blackwelder 1944: 303 (checkl.); Golbach 1994: 24 (key to gen. of S. America).

Triplonychus Candèze 1860: 236. Type species: *T. acuminatus* Candèze 1860: 238.

-Type species fixed by Hyslop 1921: 672.

-Name recognised by: Harold 1869: 1553 (catal.); Candèze 1891a: 135 (catal.); Champion 1895: 426 (spp. of central America); Schwarz 1906: 180 (gen. level rev., catal.); Schenkling: 1925: 262 (catal., distn.); Blackwelder 1944: 303 (checkl.); Golbach 1979a: 400 (key to gen. of S. America); Golbach 1994: 24 (key to gen. of S. America).

Tropidiplus Fleutiaux 1903a: 251. Type species: *T. tellinii* Fleutiaux 1903a: 251.

-Type species fixed by original monotypy.

-Synonymised under *Craspedostethus* by Schwarz 1906: 174 (gen. level rev., catal.).

-Synonymised under *Paracardiophorus* as part of s.g. *Craspedostethus* (stat.nov) by Cobos 1970a.

-Name recognised by: Waterhouse 1912: 310; Fleutiaux 1932b: 22 (spp. of Mozambique, apparently ignoring synonymy by Schwarz); Chassain 1979: 206 (rejecting placement in *Paracardiophorus* based on sclerites of bursa copulatrix, spp. of Saudi Arabia).

Nyctorini Semenov-Tian-Shanskij and Pjatkova 1936: 101.

-Type Gen.: *Nyctor* Semenov-Tian-Shanskij and Pjatkova 1936.

-Described in Elaterinae.

-Tribe recognised by Gurjeva 1974b: 78 (Apparently transferred to Cardiophorinae without comment.

-Synonymised under Cardiophorini by Dolin 1975a: 1632.

-Synonymy rejected by Stibick 1979: 181 (without explanation).

Nyctor Semenov-Tian-Shanskij and Pjatkova 1936: 101 *N. expallidus* Semenov-Tian-Shanskij and Pjatkova 1936: 102.

-Type species fixed by original designation.

-Name recognised by: Dolin 1975a: 1632 (wing venation).

Appendix 2. Revised Synonymy of higher Cardiophorinae

A complete bibliographic synonymy is presented here to accurately document the nomenclatural history of the group. All family-group names in synonymy under Cardiophorinae *sensu lato* are also listed here. Several references were unavailable for examination, as is noted in the text. Methods used to develop synonymy are listed in Materials and Methods section. The following abbreviations refer to kinds of reference and taxonomic rank: catal., catalogue; check., checklist; comb.nov., species transferred to a different genus; distn., distribution; gen., genus/genera; rev., revision; sp.nov, one new species; spp.nov., more than one new species; subg., subgenus.

Cardiophorinae Candèze 1859 (in chronological order)

Cardiophorites Candèze 1859: 4. Key only.

-Type gen.: *Cardiophorus* Eschscholtz, 1829.

-Name recognised by: Candèze 1860: 100; Candèze 1865: 39 (spp.nov.); Candèze 1878: XXXVI (spp.nov.); Candèze 1882: 77 (spp.nov.); Candèze 1891a: 120 (catal.); Candèze 1891b: 778 (spp.nov.); Candèze 1893: 45 (spp.nov.); Candèze 1893: 45 (spp.nov.); Candèze 1897: 55 (spp.nov.); Candèze 1889: 105 (spp.nov.); Candèze 1900: 93 (sp.nov).

Cryptohypnites Candèze 1859: 4. Key only.

-Type genus: *Cryptohypnus* Eschscholtz, 1836.

-Synonymised under Hypnoidinae by: Fleutiaux 1919: 74.

Cardiophori LeConte 1861: 166;

Cardiophorina Thomson 1864: 109 (spp. of Scandinavia, includes *Negastrius*).

Cryptohypnini Champion 1895: 407 (spp. of Central America).

-Synonymised under Hypnoidinae by Schenkling 1925: 199 (catal., distn.);

Stibick 1976: 190 (revision of world Hypnoidinae).

-Synonymised under Negastrinae by: Gurjeva 1969: 156 (larval evolution).

Cardiophorini Champion 1895: 415.

-Name recognised by: Schwarz 1906: 160 (gen. level rev., catal.).

-Synonymised under Cardiophorinae by Leseigneur 1972: 129 (spp. of France).

-Synonymy followed by Gurjeva 1974b: 77 (thoracic characters); Dolin 1988: 7 (spp. of Ukraine).

Hypnoidini Schwarz 1906: 150.

-Type genus: *Hypnoidus* Stephens, 1830.

Hypnoidina Jakobson 1913: 734 .

-Name recognised by: Blackwelder 1944: 293 (catal.).

-Synonymised under Hypnoidinae by: Schenkling 1925: 199 (catal., distn.);

-Synonymy followed by: Stibick 1976: 190 (revision of world Hypnoidinae).

Aptopina Jakobson 1913: 760.

-Type gen.: *Aptopus* Eschscholtz, 1829.

-Synonymy verified by inclusion of *Cardiophorina* in synonymy under *Aptopina*.

-Synonymised under *Cardiophorinae* by Gurjeva 1974b: 77 (thoracic characters)

-Synonymy followed by Dolin 1988: 7 (spp. of Ukraine).

Cardiophorinae Hyslop 1917: 259 (phylogeny of *Elateridae*).

-Name recognised by: Leng (1920: 175); 1927: 105 and 1930: 4; Schenkling: 1925: 218 (catal., distn.); Miwa 1927: 105 (key to gen. of Japanese Empire); Miwa 1930: 1 (key to gen. and spp. of Formosa); Carter 1939: 309 (spp. of Australia); Blackwelder 1944: 301 (checkl.); Fleutiaux 1941: 27 (key to subfamilies); Neboiss 1956: 39 (checkl., Australia); Fleutiaux 1947a: 341 (spp. of French Indochina); Fleutiaux 1947b: 111 (spp. of Antilles); Nakane and Kishii 1956: 204 (subfamilies of *Elateridae* of Japan); Tsherepanov 1957: 234 (spp. of W. Siberia); Van Zwaluwenburg 1957: 62 (spp. of Micronesia); Arnett 1960: 508 (gen. of USA); Neboiss 1961: 18 (checkl., Australia); Iablokoff-Khnzorian 1961: 93 (fossils, Oligocene); Dajoz: 1963: 165 (spp. of Europe and Mediterranean region); Gurjeva 1969: 157 (larval evolution); Cobos 1970a: 221 (spp. of Congo); Ôhira 1970: 216 (types from S.E. Asia), Lanchester 1971: 35 (spp. of N.W. USA); Ôhira 1971: 212 (types from S.S. Asia); Leseigneur 1972: 129 (spp. of France); Ôhira 1973a: 28 (spp. of Ryukyu Arch.); Ôhira 1973b: 38 (spp. of Ceylon); Costa 1973: 33 (gen.nov); Gurjeva 1974b: 77 (thoracic characters); Dolin 1975a: 1632 (wing venation,

translated Dolin 1975b); Dolin 1976 (2 new fossil gen.); Dolin 1978a: 8 (phylogeny of Elateridae); Dolin 1978b: 72 (larvae of USSR); Stibick 1979a: 181 (classification of Elateridae); Lohse 1979: 181 (spp. of central Europe); Golbach 1979a: 399 (key to gen. of S.S. America); Iablokoff-Khnzorian and Mardjanian 1981: 247 (subg.nov); Golbach 1994: 24 (key to S.S. American genera); Aranda 1998: 124 (note); Ôhira 1989: 79 (gen.nov); Atamuradov 1993: 118 (larvae, central Asia); Lawrence and Newton 1995: 784 (synonymy list); Lawrence et al. 1995 (subfamily larval diagnosis); Aranda 2003: 139 (spp.nov.); Lawrence et al. 2000 (subfamily diagnosis).

Cardiopherinae Hyslop 1917: 263 misspelling of Cardiophorinae.

Hypnoidinae Fleutiaux 1919: 74.

-Gurjeva 1974b: 75 (thoracic characters); places *Hypnoidus*, *Ascoliocerus* and *Hypolithus* in Athoinae: Athoini.

Esthesopinae Fleutiaux 1919: 76 (incorrectly includes senior synonym,

Cardiophorites Candèze, in synonymy).

-Type gen.: *Esthesopus* Eschscholtz, 1829.

-Name recognised by: Fleutiaux 1931c: 306 (Catal. French Indochina); Miwa 1934: 25 (spp. of Japanese Empire); Van Zwaluwenburg 1963: 339 (spp. of Papua New Guinea).

-Synonymised under Cardiophorinae by Schenkling: 1925: 218 (catal., distn.); Fleutiaux 1941: 27 (key to subfamilies); Leseigneur 1972: 129 (spp. of

France); Laurent 1974: 21 (spp. of S.S. Africa); Dolin 1988: 7 (spp. of Ukraine).

Hypolithinae Fleutiaux 1928c: 252 .

-Type genus: *Hypolithus* Eschscholtz, 1829.

-Synonymised under Hypnoidinae by: Shenkling 1925: 199 (catal., distn.);

-Reduced to synonymy under Ctenicerinae by Nakane and Kishii 1956: 203 (subfamilies of Elateridae of Japan).

Esthesopini, Fleutiaux 1932c: 36 (tribe of Elaterinae).

-Type gen.: *Esthesopus* Eschscholtz, 1829.

Negastriinae Nakane and Kishii 1956: 203 (subfamilies of Elateridae of Japan).

-Type genus: *Negastrius* Thomson 1859.

-Effectively in synonymy under Denticollinae (because *Negastrius* is placed there without note of synonymy): Lane and Lanchester 1971: 19 (spp. of N.W. USA).

Dicronychidae *sensu* Chûjô and Ôhira 1965: 28 (not Fleutiaux).

-Elevation, in error of Dicronychinae Fleutiaux 1919: 101 to family rank.

Name, based on misapplication of homonym *Dicronychus sensu* Laporte (replaced by *Eudicronychus* Méquignon 1931) to Cardiophorinae (not *Dicronychus* Brullé).

Hypnomorphini Dolin 1978a: 11.

-Type genus: *Hypnoidus* Stephens, 1830.

Cardiophorini Candèze, 1859

-Cardiophorites Candèze 1859: 4. Key only.

-Type gen.: *Cardiophorus* Eschscholtz, 1829.

-Name recognised by: Candèze 1860: 100; Candèze 1865: 39 (spp.nov.);
Candèze 1878: XXXVI (spp.nov.); Candèze 1882: 77 (spp.nov.); Candèze
1891a: 120 (catal.); Candèze 1893: 45 (spp.nov.); Candèze 1893: 45
(spp.nov.); Candèze 1897: 55 (spp.nov.); Candèze 1889: 105 (spp.nov.);
Candèze 1900: 93 (sp.nov).

-Cardiophorini, Champion 1895: 415.

-Name recognised by: Schwarz 1906: 160 (gen. level rev., catal.); Heyden et
al. 1906: 392 (catal., tribe includes *Cryptohypnus* and *Hypnoidus*); Hyslop
1917: 259 (phylogeny of Elateridae); Schenkling 1925: 218 (checkl.); Stibick
1979a: 181 (classification of Elateridae); Gurjeva 1974b: 77 (thoracic
characters); Dolin 1975a: 1632 (wing venation); Dolin 1978b: 16 (larvae of
USSR); Dolin 1988: 7 (spp. of Ukraine).

-Synonymised under Esthesopinae by Miwa 1934: 26 (spp. of Japanese
Empire).

Nyctorini Semenov-Tian-Shanskij and Pjatakova 1936: 101. Syn. nov.

-Type Gen.: *Nyctor* Semenov-Tian-Shanskij and Pjatakova 1936.

-Described in Elaterinae.

-Tribe recognised by Gurjeva 1974b: 78 (Apparently transferred to
Cardiophorinae without comment.

-Synonymised under *Cardiophorini* by Dolin 1975a: 1632.

-Synonymy rejected by Stibick 1979: 181 (without explanation).

Genera in Alphabetical order:

Allocardiophorus Ôhira 1989: 79 *Paracardiophorus nigroapicalis* Miwa 1927: 109.

-Type species fixed by original designation.

Aphricus LeConte 1853: 501. Type species: *A. californicus* LeConte 1853: 502.

-Type species fixed by original monotypy.

-Described in Cembrionites.

-Name recognised by: Lacordaire 1857: 233 (gen. of Elateridae, in Campylides); Candèze 1863: 471 (spp. level rev. of Elateridae, in Campylides); Harold 1869: 1602 (catal.); Henshaw 1885: 66 (catal., in Plastoceridae); Candèze 1891a: 217 (catal., Plastocerites); Schwarz 1907b: 8 (gen. level rev., catal.), Woodworth 1913: 197 (checkl., California USA); Leng 1920: 166 (catal.); Fleutiaux 1940: 103; Knull 1957: 201 (key to spp.); Arnett 1960: 509 (gen. of USA, transferred to Cardiophorinae); Golbach 1979a: 400 (key to Argentinean gen.); Golbach 1994: 24 (key to gen. of S.S. America); Johnson 2002b: 168 (gen. of USA).

Patriciella Van Zwaluwenburg 1953: 20. **Syn.nov.**

Replacement name for *Patricia* Van Zwaluwenburg.

-Name recognised by: Neboiss 1961: 28 (checkl., Australia); Calder 1996: 360 (checkl., Australia).

-Moved to Cardiophorinae by Calder 1996: 377.

Patricia Van Zwaluwenburg 1947: 113. Type species: *P. australica* Van Zwaluwenburg 1947: 114.

-Type assigned by original designation.

-Name recognised by: Neboiss 1956: 64 (checkl., Australia).

-Described in Physodactylinae.

-Junior homonym of *Patricia* Fox 1940 (Lepidoptera).

Aptopus Eschscholtz 1829: 32. Type species: *A. tibialis* Eschscholtz 1829: 32.

-Type species fixed by Hyslop 1921: 629.

-Name recognised by: Dejean 1836: 99 (catal.); Candèze 1860: 230 (spp. level rev. of Elateridae); Harold 1869: 1553 (catal.); Horn 1885: 33 (sp.nov.

U.S.A); Henshaw 1885: 66 (catal.); Candèze 1889: 111 (spp.nov.); Candèze 1891a: 134 (catal.); Candèze 1891b: 781 (sp.nov., Burma); Champion 1895:

418 (spp. of central America); Schwarz 1906: 175 (gen. level rev., catal.);

Schaeffer 1916 (spp.nov.); Leng 1920: 175 (catal.); Schenkling: 1925: 254

(catal., distn.); Blackwelder 1944: 302 (checkl.); Arnett 1960: 508 (gen. of

USA); Dolin 1975a: 1632 (wing venation); Golbach 1979a: 400 (key to

Argentinean gen.); Golbach 1994: 24 (key to gen. of S. America); Aranda

1996: 444 (key to Argentinean spp.); Aranda 1998: 130 (gen. descr. from S.

American spp.); Johnson 2002b: 168 (gen. of USA); Aranda 2003: 139

(spp.nov.).

-Synonymised under *Cardiophorus* by Lacordaire 1857: 193.

-Incorrectly synonymised under the junior name *Priopus* Laporte by Laporte 1840: 251.

-Definition restricted here to exclude species near *Aptopus agrestis* (Erichson).

Apsopus Schwarz 1906: 180, incorrect subsequent spelling of *Aptopus*.

-Misspelling verified by inclusion of the correct reference page for *Aptopus* Eschscholtz.

Eniconyx Horn 1885: 51. Type species: *Eniconyx pullatus* Horn 1885: 52

-Type species fixed by Hyslop 1921: 644.

-Described in Elateridae.

-Name recognised by: Henshaw 1885: 66 (catal.); Candèze 1891a: 217 (catal., in Plastoceridae); Waterhouse 1902: 123; Leng 1920: 166 (catal., in Plastoceridae).

-Synonymised under *Aptopus* by Arnett 1960: 508.

Enisonyx Candèze 1891a: 217, incorrect subsequent spelling of *Eniconyx*.

-Misspelling verified by reference to Horn publication and spp. epithets belonging to *Eniconyx*.

-Misspelling followed by: Schwarz 1907b: 7 (gen. level rev., catal.).

Austrocardiophorus **gen. nov.** Type sp. *Cardiophorus humeralis* Fairmaire and Germain 1860.

Blaiseus Fleutiaux 1931c: 307. Type species: *B. bedeli* Fleutiaux 1931c: 308.

-Type species fixed by original monotypy.

-Name recognised by: Fleutiaux 1947a: 343 (spp. of French Indochina).

Blaseus Gurjeva 1974a: 112, incorrect subsequent spelling of *Blaiseus*.

-Verified by placement in context of other cardiophorine genera.

-Misspelling followed by: Gurjeva 1974b: 78 (thoracic characters).

Buckelater Costa 1973: 33. Type species: *B. argutus* Costa 1973: 35.

-Type species fixed by original designation.

-Name recognised by: Golbach 1979a: 399 (key to Argentinean gen.);

Golbach 1994: 24 (key to gen. of S. America).

Cardiodontulus Van Zwaluwenburg 1963: 341. Type species: *C. brandti* Van Zwaluwenburg 1963: 341.

-Type species fixed by original designation.

- *Cardiotarsus mjobergi* Carter is here transferred to this genus.

Cardiophorellus Cobos 1970a: 222. Type species: *C. gracilicornis* Cobos 1970a: 223.

-Type species fixed by original monotypy of nominate subg.

Cardiophorellus: subg. *Parapleonomus* Cobos 1970a: 222. Type species: *C. inermis* Cobos 1970a: 222.

-Type species fixed by original designation.

Cardiophorus Eschscholtz 1829: 34. Type species: *Elater thoracicus* Fabricius 1801: 236, now regarded as a synonym of *Cardiophorus gramineus* (Scopoli, 1763).

-Type species fixed by Westwood 1838: 26.

-Name recognised by: Dejean 1833: 91 (catal.); Dejean 1836: 103 (catal.);

Eschscholtz 1836: Table; Germar 1839: 196 (key to gen. of Elateridae);

Erichson 1840: (spp. level rev.); Redtenbacher 1849: 300 (spp. of Austria);
 LeConte 1853: 496 (spp. of USA, also includes *Horistonotus* spp.);
 Lacordaire 1857: 193 (gen. of Elateridae); Redtenbacher 1858: 495 (spp. of Austria); Jacquelin du Val 1859: 141 (gen. of Europe); Thomson 1859: 104 (gen. of Scandinavia); Candèze 1860: 106 (spp. level rev. of Elateridae);
 Thomson 1864: 116 (spp. of Scandinavia); Harold 1869: 1546 (catal.);
 Candèze 1875: 16 (spp.nov.); Horn 1871: 301 (spp.nov. U.S.A); Redtenbacher 1874: 537 (spp. of Austria); Henshaw 1885: 66 (catal.); Candèze 1889: 105 (spp.nov.); Candèze 1891a: 121 (catal.); Candèze 1891b: 778 (spp.nov.);
 Heyden et al. 1891: 205 (catal.); Candèze 1892: 805 (sp.nov); Champion 1895: 416 (spp. of central America); Candèze 1897: 55 (spp.nov.); Jäger 1897: 356; Buysson 1891: 134 (note); Candèze 1893: 45 (spp.nov.); Fleutiaux 1893: 687 (sp.nov); Schwarz 1895a: 37 (sp.nov); Schwarz 1895b: 40 (key to gen.); Schwarz 1896: 148 (sp.nov); Buysson 1899: 279 (note); Blanchard 1889: 1 (spp. of N. America); Candèze 1900: 93 (sp.nov); Buysson 1902: 286 (spp. of France and Rhine Valley); Schwarz 1902: 259 (sp.nov); Schwarz 1903c: 370 (spp.nov.); Schwarz 1905: 289 (spp.nov.); Schwarz 1906: 162 (gen. level rev., catal.); Heyden et al. 1906: 393 (catal., Europe); Buysson 1910: 138 (note); Buysson 1911: 22 (spp. of Egypt); Buysson 1912: 128 (spp.nov. Russia); Jakobson 1913: 761 (key, catal., Europe); Woodworth 1913: 197 (checkl., California USA); Buysson 1914: 41 (sp.nov); Fleutiaux 1918b: 225 (spp.nov. Indochina); Fleutiaux 1919: 76 (spp.nov. east Africa);

Leng 1920: 175 (catal.); Fleutiaux 1921: 14 (spp. record, English Africa);
 Buysson 1924: 207 (spp. of Morocco); Cockerell 1925: 9 (sp.nov. Eocene
 fossil); Schenkling 1925: 219 (catal., distn.); Méquignon 1931: 207 (note);
 Miwa 1927: 106 (key to gen. of Japanese Empire); Miwa 1930: 1 (key to gen.
 and spp. of Formosa); Miwa 1934: 26 (spp. of Japanese Empire); Fleutiaux
 1931c: 313 (catal., French Indochina); Fleutiaux 1932b: 20 (spp. of
 Mozambique); Carter 1939: 310 (spp. of Australia transferred to
Paracardiophorus); Jagemann 1940: 55 (spp. Europe); Normand 1941: 331
 (sp.nov, N. Africa); Blackwelder 1944: 301 (checkl.); Van Zwaluwenburg
 1947: 111 (spp. of Australia); Fleutiaux 1947a: 344 (spp. of French
 Indochina); Cobos 1954: 86 (checkl., Sierra Nevada, Spain); Binaghi 1955: 4
 (note); Jagemann 1955: 136 (spp. of Czechoslovakia); Neboiss 1956: 39
 (transferred all Australian spp. to *Paracardiophorus*, checkl., Australia);
 Tsherepanov 1957: 234 (spp. of W. Siberia); Cobos 1959: 468 (sp.nov.
 Brazil); Arnett 1960: 508 (gen. of USA); Cobos 1961: 63 (spp. of Morocco);
 Ôhira 1962: 177 (higher classification, larvae); Chûjô and Ôhira 1965: 28
 (spp. of Japan); Dajoz 1963: 165 (spp. of Europe and Mediterranean region);
 Gurjeva 1966: 64 (spp. of central Asia); Leiler 1967: 89-109 (larvae and
 pupae, Europe); Gurjeva 1969: 156 (larval evolution); Cobos 1970a:
 232 (spp.nov. Congo); Cobos 1970b: 29 (spp. of Canary Islands); Ôhira 1970:
 216 (types from S.E. Asia); Ôhira 1971: 212 (types from S. Asia); Lanchester
 1971: 35 (spp. of N.W. USA); Leseigneur 1972: 130 (spp. of France); Laurent

1974: 22 (spp. of S. Africa); Gurjeva 1974b: 78 (thoracic characters); Gurjeva 1974c: 170 (spp.nov, Afghanistan); Dolin 1975a: 1632 (wing venation); Dolin 1978a: 8 (phylogeny of Elateridae); Dolin 1978b: 73 (larvae of USSR); Chassain 1979: 194 (spp. of Saudi Arabia); Golbach 1979a: 400 (key to Argentinean gen.); Lohse 1979: 181 (spp. of central Europe); Iablokoff-Khnzorian and Mardjanian 1981: 247 (subg.nov); Dolin 1988: 7 (spp. of Ukraine); Bousquet 1991: 185 (catal.); Kompantseva 1991: 18 (key: larvae of Tajikistan); Vats and Chauhan 1991: 11 (spp. N. India); Atamuradov 1993: 118 (larvae, central Asia); Downie and Arnett 1996: 821 (spp. N.E. N. America); Platia and Gudenzi 2000a: 601, 2002: 28 (spp. of Turkey); Platia and Gudenzi 2000b: 136 (spp. of Greece); Johnson 2002b: 168 (gen. of USA); Cate et al. 2002: 46 (spp.nov, Iran); Platia et al. 2002: 76 (sp.nov, Iran); Douglas 2003: 493 (spp. of E. N. America); Lucht 2005: 198, 199 (distn., bionomics).

Cardiophorus Motschulsky 1858: 59, incorrect subsequent spelling of *Cardiophorus*.

-Verified as *Cardiophorus* ref. by mention of *C. curiatus* in same passage.

Cardiophorua Cobos 1954: 86, incorrect subsequent spelling of *Cardiophorus*.

-Verified by cardiophorine context.

Cardiosphorus Gurjeva 1974b: 70, incorrect subsequent spelling of *Cardiophorus*.

-Verified by ref. to fig. of cordate scutellum.

Caloderus Stephens 1830: 269. Type species: *Elater thoracicus* Fabricius 1801: 236.

-Type fixed by Hyslop 1921: 632.

-Name recognised by Laporte 1840: 249 (with *Cardiophorus* in synonymy).

-Synonymised under *Cardiophorus* by Westwood 1838: 26 (gen. of British Insects).

-Synonymy followed by: Lacordaire 1857: 138 (gen. of Elateridae); Candèze 1860: 106 (spp. level rev. of Elateridae); Harold 1869: 1546 (catal.); Candèze 1891a: 121 (catal.); Champion 1895: 416 (spp. of central America); Schwarz 1906: 162 (gen. level rev., catal.); Schenkling: 1925: 220 (catal., distn.); Leseigneur 1972: 130 (spp. of France); Dolin 1988: 10 (spp. of Ukraine).

Paradicronychus Dolin and Gurjeva 1975: 116 (*nomen nudum*)

-No type species designated for this name, published after 1930, therefore name is not available.

-Name recognised by: Dolin 1978b: 81 (larvae of USSR).

-As synonym of *Dicronychus*: Platia 1994: 380 (spp. of Italy, synonymised without comment).

-**Syn.nov** of *Cardiophorus*.

Cardiophorus: subg. *Coptostethus* Wollaston.

-Rank lowered to subgenus by Cobos 1970b: 34.

-Subg. rank recognised by: Cobos 1978: 145 (spp. Atlantic Islands); Johnson 2001: 58 (*C. (Coptostethus) americanus* transferred to *Negastrius*).

Coptostethus Wollaston 1854: 238. Type species: *C. femoratus* Wollaston 1854: 240.

-Type species fixed by original monotypy.

-Gen. status recognised by Lacordaire 1857: 196 (gen. of Elateridae); Candèze 1860: 104; Harold 1869: 1546 (catal.); Horn 1871: 303 (sp.nov. U.S.A); Henshaw 1885: 66 (catal.); Fleutiaux 1891a; Candèze 1891a: 121 (catal.); Candèze 1889: 105 (spp.nov.); Schwarz 1906: 161 (gen. level rev., catal.); Jakobson 1913: 761 (key, catal., Europe); Leng 1920: 175 (sp. of N. America); Schenkling: 1925: 218 (catal., distn.); Blackwelder 1944: 301 (checkl.); Arnett 1960: 508 (gen. of USA); Dajoz 1963: 173 (spp. of Europe and Mediterranean region); Laurent 1974: 22 (spp. of S. Africa); Gurjeva 1974b: 78 (thoracic characters); Golbach 1979a: 400 (without comment, key to Argentinean gen.); Golbach 1994: 24 (key to gen. of S. America); Aranda 1998: 130 (key to gen.).

Coptosthetus Candèze 1860: 504, incorrect subsequent spelling of *Coptostethus*.

-Verified by listing of correct spp.

-Misspelling followed by: Aranda 1998: 124 (list of gen., but not key).

Cardiophorus: subg. *Perrinellus* Buysson 1899: 282. Type species: *Athous argentatus* Abeille de Perrin 1894: 92.

-Type species fixed by original designation.

-Genus rank recognised by: Waterhouse 1902: 279; Buysson 1910: 145 (note); Buysson 1911: 22 (spp. of Egypt).

-Treated as subgenus of *Cardiophorus* by Schwarz 1906: 172 (genus level revision, catal.).

-Subgenus rank followed by: Heyden et al. 1906: 394 (catal. Europe);

Schenkling: 1925: 220 (catal., distn.); Jagemann 1940: 55 (spp. Europe);

Cobos 1950: 155 (note); Cobos 1954: 86 (Faunal list, Sierra Nevada, Spain);

Gurjeva 1966: 88 (spp. of central Asia); Platia 1994: 354 (spp. of Italy).

-Not recognized as a natural group by Dajoz 1963: 165 (spp. of Europe and Mediterranean region).

Cardiophorus: subg. *Lasiocerus* Buysson 1912: 129. Type species: *C. schusteri* Buysson 1912: 128.

-Type species fixed by original monotypy.

-Described at genus rank.

-Synonymised under *Cardiophorus*: subg. *Perrinellus* by Schenkling: 1925: 237 (catal., distn.).

-Synonymy (under *Cardiophorus*, without recognition as subgenus) followed by Dolin 1988: 10 (spp. of Ukraine).

-As subgenus of *Cardiophorus* Platia 1994: 354 (spp. of Italy, without comment).

-Mentioned, but neither recognized, nor synonymised by Dajoz 1963: 165 (spp. of Europe and Mediterranean region).

Perinellus Schwarz 1906: 172, incorrect subsequent spelling of *Perrinellus*.

-Verified by corroboration: correct species listed.

Cardiotarsus Eschscholtz 1836: published in identification table opposite p.5, without associated spp. Type species: *C. capensis* Candèze 1860: 226.

-Type species fixed by Hyslop 1921: 633.

-Name recognised by: Dejean 1833: 91 (*nomen nudem*, (indication not valid because associated species name was unavailable) catal.); Dejean 1836: 103 (catal.); Germar 1839: 198 (key to gen. of Elateridae); Lacordaire 1857: 192 (gen. of Elateridae); Candèze 1860: 225 (spp. level rev. of Elateridae); Harold 1869: 1552 (catal.); Candèze 1889: 111 (sp.nov.); Candèze 1891a: 133 (catal.); Candèze 1891b: 780 (sp.nov.); Candèze 1897: 55 (spp.nov.); Schwarz 1902: 261 (sp.nov.); Schwarz 1905: 289 (sp.nov.); Schwarz 1906: 174 (gen. level rev., catal.); Fleutiaux 1918b: 231 (sp.nov., Indochina, now *Odontocardus*); Schenkling: 1925: 253 (catal., distn.); Fleutiaux 1919: 97 (sp. record, east Africa); Miwa 1927: 105 (key to gen. of Japanese Empire); Miwa 1930: 4 (key to gen. and spp. of Formosa); Fleutiaux 1931c: 328 (catal. French Indochina); Fleutiaux 1932c: 36 (spp. of Mascarene Is.); Miwa 1934: 27 (spp. of Japanese Empire); Carter 1939: 309 (spp. of Australia); Fleutiaux 1947a: 369 (spp. of French Indochina); Neboiss 1956: 46 (checkl., Australia); Cobos 1970a: 223 (key to gen., Congo); Ôhira 1970: 216 (types from S.E. Asia); Laurent 1974: 34 (spp. of S. Africa); Gurjeva 1974b: 78 (thoracic characters); Dolin 1975a: 1632 (wing venation); Kishii 1992: 8 (sp.nov., Taiwan); Calder 1996: 360 (checkl., Australia). *Cardiotarsus mjobergi* Carter is here recommended for transfer to *Cardiodontulus* Van Zwaluwenburg.

Chileaphricus gen.nov. Type species, *Aphricus chilensis* Fleutiaux.

Craspedostethus Schwarz 1898b: 414. Replacement name for *Craspedonotus* Schwarz.

-Name recognised by: Waterhouse 1902: 88; Schenkling: 1925: 252 (catal., distn.); Dajoz 1963: 172 (spp. of Europe and Mediterranean region); Chassain 1979: 206 (rejecting placement in *Paracardiophorus* by Cobos 1970a based on sclerites of bursa copulatrix, spp. of Saudi Arabia); Cate et al. 2002: 52 (sp.nov, Iran).

-Considered a subg. of *Paracardiophorus* by: Cobos 1970a: 227 (spp.nov. Congo).

Craspedonotus Schwarz 1898a: 148. Type species: *C. rufiventris* Schwarz 1898a: 148.

-Type species fixed by Hyslop 1921: 636.

-Junior homonym of *Craspedonotus* Schaum 1863 (Carabidae).

Dicronychus Brullé 1832: 138. Type species: *Elater obesus* Brullé 1832: 138, now referred to by replacement name *Dicronychus brullei* Platia and Gudenzi (2003).

-Type fixed by Méquignon 1931: 208.

-Originally described *Dicronychus* as a subgroup of *Elater* (and considered Eschscholtz the author).

-Raised to genus rank by Eschscholtz 1836: Table.

-Genus rank followed by: Schwarz 1897: 9 (note); Schwarz 1903c: 365 (sp.nov.); Schwarz 1905: 282 (sp.nov.); Fleutiaux 1932a: 170 "Gen

Dicronychus Brullé, 1832”; Fleutiaux 1947a: 348 (spp. of French Indochina); Arnett 1955: 608 (note on types); Ôhira 1962: 177 (higher classification, larvae); Ôhira 1970: 230 (types from S.E. Asia); Ôhira 1971: 212 (types from S. Asia); Leseigneur 1972: 151 (spp. of France); Ôhira 1973b: 38 (spp. of Ceylon); Laurent 1974: 23 (spp. of S. Africa); Gurjeva 1974b: 78 (thoracic characters); Lohse 1979: 184 (spp. of central Europe); Iablokoff-Khnzorian and Mardjanian 1981: 247 (subg.nov); Platia 1994: 381 (spp. of Italy); Cate et al. 2002: 55 (sp.nov, Iran); Platia and Gudenzi 2003: 27 (spp. of Greece); Platia and Gudenzi 2004: 9 (spp. of Turkey); Lucht 2005: 198, 199 (distn., bionomics).

-Synonymised under *Cardiophorus* by Lacordaire 1857: 138 (gen. of Elateridae).

-Synonymy followed by: Candèze 1860: 106 (spp. level rev. of Elateridae); Harold 1869: 1546 (catal.); Candèze 1891a: 121 (catal.); Heyden et al. 1891: 205 (catal.); Champion 1895: 416 (spp. of central America); Schwarz 1906: 162 (gen. level rev., catal.); Schenkling: 1925: 220 (catal., distn.); Dolin 1975a: 1621 (wing venation); Dolin and Gurjeva 1975: 118 (note on larvae); Dolin 1988: 10 (spp. of Ukraine); Vats and Chauhan 1991: 11 (spp. N. India, no formal synonymy, but includes *Cardiophorus* spp. with diagnostic characters of *Dicronychus*).

-As subg. of *Cardiophorus*: Méquignon 1931: 207 (as senior synonym of subg. *Platynychus*).

-Subg. rank followed by: Binaghi 1955: 4 (note); Lawrence and Newton (1995: 855).

Eudicronychus Méquignon; sensu Chûjô and Ôhira 1965: 28.

-Error verified by inclusion of spp. assigned to *Dicronychus* Brullé.

Gauroderus Thomson 1859: 104. Type species: *Elater cinereus* Herbst 1784: 114.

-Type species fixed by original designation.

-Considered an objective junior generic synonym of *Dicronychus* by

Méquignon 1931: 207 because type sp. is a subjective synonym of the type of *Dicronychus* (treated as subg. of *Cardiophorus*).

-Synonymy followed by Miwa 1934: 26 (spp. of Japanese Empire);

Fleutiaux 1947a: 348 (spp. of French Indochina); Leseigneur (1972: 151);

Platia (1994: 380).

-Synonymised under *Cardiophorus* by Harold 1869: 1546 (catal. with *Dicronychus*).

-Synonymy under *Cardiophorus* followed by: Candèze 1891a: 121

(catal.); Champion 1895: 416 (spp. of central America); Schwarz 1906:

162 (gen. level rev., catal.); Schenkling: 1925: 220 (catal., distn.).

-Considered a junior synonym of *Platynychus* (as subg. of *Cardiophorus*) by

Heyden et al. 1906: 394 (catal. Europe).

Diocarphus Fleutiaux 1947a: 364. **stat.nov.**, raised to genus rank.

Phorocardius: subg. *Diocarphus* Fleutiaux 1947a: 364. Type species: *P. solitarius*

Fleutiaux 1931c: 309.

-Type species fixed by monotypy.

Displatynychus Ôhira 1987: 92.

-Raised to gen. rank by Ôhira 1999.

Platynychus: subg. *Displatynychus* Ôhira 1987: 92. Type species: *Cardiophorus adjutor* Candèze 1875: 17.

-Type species fixed by original designation.

Esthesopus Eschscholtz 1829: 32. Type species: *E. castaneus* Eschscholtz 1829: 32.

-Type species fixed by original monotypy.

-Name recognised by: Eschscholtz 1836: table; Germar 1839: 197 (key to gen. of Elateridae); Candèze 1860: 274 (spp. level rev. of Elateridae); Harold 1869: 1555 (catal.); Horn 1885: 41 (spp. of U.S.A); Steinheil 1875: 131 (spp. of "Neu-Granada"); Henshaw 1885: 66 (catal.); Candèze 1891a: 137 (catal.); Champion 1895: 439 (spp. of central America); Schwarz 1902: 269 (sp.nov); Schwarz 1903a: 75 (spp.nov.); Schwarz 1906: 179 (gen. level rev., catal.); Woodworth 1913: 198 (checkl., California USA); Leng 1920: 175 (catal.); Schenkling: 1925: 260; Blackwelder 1944: 303 (checkl.); Fleutiaux 1947: 111 (spp. of Antilles); Arnett 1960: 509 (gen. of USA); Becker 1973b: 1531 (diagnostic note); Dolin 1975a: 1632 (wing venation); Dolin 1978: 8 (phylogeny of Elateridae); Golbach 1979a: 400 (key to Argentinean gen.); Golbach 1994: 24 (key to gen. of S. America); Downie and Arnett 1996: 822 (spp. N.E. N. America); Johnson 2002b: 168 (gen. of USA).

Esthesops Woodworth 1913: 197, incorrect subsequent spelling of *Esthesopus*.

-Verified by correct spelling elsewhere in document.

Esthosopus Eschscholtz 1836: table, incorrect subsequent spelling of

Esthesopus.

-Verified by possession of following key characters: 4th tarsomere laminate, claws serrate.

Ethesopus Germar 1839: 197, incorrect subsequent spelling of *Esthesopus*.

-Verified by mention of correct type sp.

Floridelater **gen.nov.** Type species *Coptostethus americanus* Horn. Type species transferred to Cardiophorinae from Negastrinae (*Negastrius americanus* (Horn)).

Globothorax Fleutiaux 1891a: ccxxxii. Type species: *G. chevrolati* Fleutiaux 1891a: ccxxxiii.

-Type species fixed by original monotypy.

-Name recognised by: Waterhouse 1902: 149; Schwarz 1906: 181 (gen. level rev., catal.); Schenkling: 1925: 263 (catal., distn.); Blackwelder 1944: 303 (checkl.); Golbach 1979a: 401 (new sp., key to species); Golbach 1994: 24 (key to gen. of S. America).

Teslasena Fleutiaux 1892: 410. **Syn.nov.**

-Type species, *Anelastes femoralis* Lucas 1857: 71, fixed by original monotypy.

-Name recognised by: Schwarz 1897: 9 (note); Fleutiaux 1899: 206 (sp.nov.); Schwarz 1906: 313 (gen. level rev., catal.); Schenkling: 1927: 509 (catal., distn.).

-Described in Elaterinae: Physodactylini.

Globotorax Aranda 1998: 126, 128, 130 (key to gen.), incorrect subsequent spelling of *Globothorax*.

-Verified by reference to correct author and year and appearance in context with other Cardiophorine genera.

Horistonotus Candèze 1860: 243. Type species: *H. flavidus* Candèze 1860: 250.

-Type species fixed by Hyslop 1921: 650.

-Name recognised by: Harold 1869: 1554 (catal.); Steinheil 1875: 131 (spp. of "Neu-Granada"); Horn 1871: 302 (sp.nov. U.S.A); Horn 1885: 33 (spp. of U.S.A); Henshaw 1885: 66 (catal.); Candèze 1889: 111 (sp.nov.); Candèze 1891a: 135 (catal.); Fleutiaux 1895: 172 (sp.nov.); Schwarz 1895b: 40 (key to gen.); Champion 1895: 428 (spp. of central America); Schwarz 1897: 9 (note); Schwarz 1902: 261 (sp.nov.); Schwarz 1903a: 74 (sp.nov.); Schwarz 1906: 176 (gen. level rev., catal.); Woodworth 1913: 198 (checkl., California USA); Leng 1920: 175 (catal.); Schenkling: 1925: 255 (catal., distn.); Van Dyke 1932: 329 (sp.nov. USA); Carter 1939: 310 (sp. of Australia transferred to *Paracardiophorus*); Blackwelder 1944: 302 (checkl.); Fleutiaux 1947: 111 (spp. of Antilles); Neboiss 1956: 46 (transferred all Australian spp. to *Paracardiophorus*, checkl., Australia); Arnett 1960: 509 (gen. of USA); Lanchester 1971: 48 (spp. of N.W. USA); Becker 1973b: 1531 (diagnostic note); Dolin 1975a: 1632 (wing venation); Golbach 1979b: 411 (sp.nov, key to Argentinean spp.); Bousquet 1991: 178 (catal.); Golbach 1994: 24 (key to

gen. of S. America); Downie and Arnett 1996: 821 (spp. N.E. N. America); Wells 2000: 416 (key to the spp. of USA and Canada); Johnson 2002b: 168 (gen. of USA).

-Definition expanded here to include species near *Aptopus agrestis* (Erichson).

Horisonotus Woodworth 1913: 197, incorrect subsequent spelling of *Horistonotus*.

-Verified by two references to valid *Horistonotus* spp.

Horizonotus Carpenter 1992: 331, incorrect subsequent spelling of *Horistonotus*.

-Verified by reference to name spelled correctly by Wickham (1916).

Margogastrius Schwarz 1903b: 80. Replacement name for *Gastrimargus* Schwarz.

-Name recognised by: Schwarz 1906: 312 (gen. level rev., catal.); Schenkling: 1927: 509 (catal., distn.).

-Transferred here to Cardiophorinae.

Gastrimargus Schwarz 1902: 309 *G. schneideri* Schwarz 1902: 310.

-Type species fixed by original monotypy.

-Junior homonym of *Gastrimargus* Spix, 1823.

Metacardiophorus Gurjeva 1966: 91. **stat.nov.**, raised to genus rank.

Cardiophorus: subg. *Metacardiophorus* Gurjeva 1966: 91. Type species: *C. sogdianus* Gurjeva 1966: 91.

-Type species fixed by original designation.

Mionelater Becker 1963: 125. Type species: *M. planatus* Becker 1963: 126.

-Type species fixed by original designation.

-Chiapas, Mexico Miocene fossil in amber.

Neocardiophorus Gurjeva 1966: 95. Type species: *N. mamajevi* Gurjeva 1966: 95.

-Type species fixed by original designation.

-Name recognised by: Gurjeva 1974b: 78 (thoracic characters); Dolin 1978b: 81 (larvae of USSR); Iablokoff-Khnzorian and Mardjanian 1981: 246 (note).

Nyctor Semenov-Tian-Shanskij and Pjatkova 1936: 101 *N. expallidus* Semenov-Tian-Shanskij and Pjatkova 1936: 102.

-Type species fixed by original designation.

-Name recognised by: Dolin 1975a: 1632 (wing venation).

Odontocardus Fleutiaux 1931c: 332. Type species: *Cardiotarsus vitalisi* Fleutiaux 1918b: 231.

-Type species fixed by original designation.

-Name recognised by: Fleutiaux 1947a: 376 (spp. of French Indochina).

Odontocardus Gurjeva 1974a: 112, incorrect subsequent spelling of *Odontocardus*.

-Verified by reference to cardiophorine genera.

-Misspelling followed by: Gurjeva 1974b: 78 (thoracic characters).

Pachyelater Lesne 1897b: 117 Replacement name for *Parelater* Lesne.

-Name recognised by: Lesne 1906: 172 (male association, sp.nov., key to spp.); Fleutiaux 1918a: 170 (sp.nov. E. Africa); Fleutiaux 1921: 17 (distn., Kenya, not placed in any subfamily); Schenkling

1927: 503 (catal., distn., in Denticollinae); Fleutiaux 1929b: 241

(catal., list of types, not placed in any subfamily).

-Transferred here to Cardiophorinae.

Lesnelater Fleutiaux 1935a: 116. **Syn.nov.**

-Described as (called replacement name) for males assigned to *Pachyelater* by Lesne 1906: 172.

-Type species *Lesnelater madagascariensis* Fleutiaux (= *Pachyelater madagascariensis* Lesne 1897 **syn.nov.**), fixed by original designation (although this combination was not used in original publication),).

-Original placement in Physodactylinae.

-Name recognised by: Fleutiaux 1935b: 242 (sp.nov. Angola); Arnett 1955: 612 (note on type sp.).

Parelater Lesne 1897a: 102. *P. madagascariensis* Lesne 1897: 102.

-Type species fixed by original monotypy.

-Not originally placed in any subfamily by Lesne, but possible proximity to Cebriionidae, Cardiophorinae and Physodactylinae mentioned.

-Junior homonym of *Parelater* Candèze 1882: 70 (Coleoptera: Elateridae), not *Parelater* Candèze 1865: 29 as according to Neave 1939: 607.

Paracardiophorus Schwarz 1895b: 40. Type species: *Cardiophorus musculus* Erichson 1840: 299.

-Type species fixed by Hyslop 1921: 660.

- Name and genus rank recognised by: Schwarz 1902: 259 (sp.nov);
 Waterhouse 1902: 265; Schwarz 1903d: 390 (sp.nov.); Schwarz 1906: 172
 (gen. level rev., catal.); Jakobson 1913: 761 (key, catal., Europe); Schenkling:
 1925: 249 (catal., distn.); Miwa 1927: 106 (key to gen. of Japanese Empire);
 Miwa 1930: 6 (key to gen. and spp. of Formosa); Fleutiaux 1932b: 21 (spp. of
 Mozambique); Miwa 1934: 26 (spp. of Japanese Empire); Carter 1939: 309
 (spp. of Australia); Jagemann 1940: 55 (spp. Europe); Blackwelder 1944: 302
 (checkl.); Jagemann 1955: 152 (spp. of Czechoslovakia); Neboiss 1956: 40
 (checkl., Australia); Tsherepanov 1957: 244 (spp. of W. Siberia); Neboiss
 1961: 18 (checkl., Australia); Leseigneur 1972: 156 (spp. of France); Dajoz
 1963: 172 (spp. of Europe and Mediterranean region); Cobos 1970a: 225
 (sp.nov. Congo); Ôhira 1973b: 38 (spp. of Ceylon); Gurjeva 1974b: 78
 (thoracic characters); Dolin 1975a: 1632 (wing venation); Dolin 1978b: 73
 (larvae of USSR); Chassain 1979: 210 (sp.nov. Saudi Arabia); Golbach
 1979a: 400 (key to Argentinean gen.); Lohse 1979: 186 (spp. of central
 Europe); Iablokoff-Khinzorian and Mardjanian 1981: 246 (note); Dolin 1988:
 9 (spp. of Ukraine); Golbach 1994: 24 (key to gen. of S. America); Calder
 1996: 360 (checkl., Australia); Ôhira 1997: 1 (note).
- Genus membership revised here to include North American spp. and exclude
 Australian and S. American spp.
- As subg. of *Cardiophorus* Buysson 1902: 290 (originally called a group of
Cardiophorus).

-Subg. rank followed by Heyden et al. 1906: 394 (catal. Europe);

Fleutiaux 1931c: 314.

Paracardiophorus Lucht 2005: 198-199, incorrect subsequent spelling of

Paracardiophorus.

-Verified by association of type species name, author and range.

Paracarpiphonus Fleutiaux 1928: 284, incorrect subsequent spelling of

Paracardiophorus.

-Verified by published correction, Fleutiaux 1929a: 23.

Paracapiophonus Arnett 1955: 614 (note on types), incorrect subsequent spelling of *Paracardiophorus*.

-Verified by reference to Fleutiaux's (different) misspelling of

Paracardiophorus.

Paraplatynychus Fleutiaux 1931c: 315.

-Raised to gen. rank by Ôhira 1970: 230 (without comment, types from S.E.

Asia). Made new combination *Paraplatynychus costatus* (Fleutiaux, 1931) from *Platynychus* (*Paraplatynychus*) *costatus*.

Platynychus: subg. *Paraplatynychus* Fleutiaux 1931c: 315. Type species:

Platynychus mixtus Fleutiaux 1931c: 326.

-Type species fixed by original designation.

-Treated as a subg. of *Dicronychus* by Fleutiaux 1947a: 348 (spp. of French Indochina).

Phorocardius Fleutiaux 1931c: 308. Type species: *Cardiophorus florentini* Fleutiaux 1893: 687.

-Type species fixed by original designation.

-Name recognised by: Miwa 1934: 26 (spp. of Japanese Empire); Fleutiaux 1947a: 363 (spp. of French Indochina); Ôhira 1971: 207 (types from S. Asia); Gurjeva 1974b: 78 (thoracic characters).

Platynychus Motschulsky 1858: 58. Type species: *P. indicus* Motschulsky 1858: 59.

-Type species fixed by Hyslop 1921: 665. This fixation is valid and non-reversible, although disputed by Méquignon 1930: 96.

-Gen. rank recognised by: Fleutiaux 1931c: 315 (catal. French Indochina); Fleutiaux 1932b: 25 (spp. of Mozambique); Miwa 1934: 26 (spp. of Japanese Empire); Fleutiaux 1947a: 348 (spp. of French Indochina, with putative diagnostic chars for this and *Dicronychus*); Jagemann 1955: 147 (spp. of Czechoslovakia); Van Zwaluwenburg 1957: 62 (spp. of Micronesia); Van Zwaluwenburg 1963: 339 (spp. of Papua New Guinea); Dajoz 1963: 171 (but with *P. cinereus* (valid name of *Dicronychus* type sp.) incorrectly named as type species, spp. of Europe and Mediterranean region); Chassain 1979: 195 (spp. of Saudi Arabia); Ôhira 1987: 92 (description of new subg. of *Platynychus*).

-Treated as synonym of *Cardiophorus* by Harold 1869: 1546 (catal., *pars.*).

-Synonymy under *Cardiophorus* followed by: Candèze 1891a: 121 (*Pars.*, catal.); Dolin 1988: 10 (spp. of Ukraine).

-Treated as subg. of *Cardiophorus* by Buysson 1902: 329 (including *E. cinereus*, senior synonym of type species of *Dicronychus*).

-subg. rank followed by Heyden et al. 1906: 394 (catal. Europe);

Schenkling: 1925: 219 (catal., distn.); Jagemann 1940: 55 (spp. Europe);

Gurjeva 1966: 92 (spp. of central Asia); Cobos 1970a: 223 (key to gen.,

Congo); Dolin and Gurjeva 1975a: 118 (note on larvae, misspelled).

-Treated as a synonym of *Dicronychus* by Méquignon 1931: 207 (note, *Dicronychus* here considered a subg. of *Cardiophorus*).

-Synonymy followed by: Leseigneur 1972: 151 (spp. of France); Ôhira

1973b: 38C (made *Dicronychus comptus* (Candèze) comb.nov. from

Cardiophorus (Platynychus) comptus; Schenkling 1925: 238 (catal.,

distn.); Lohse 1979: 184 (spp. of central Europe); Iablokoff-Khnzorian

and Mardjanian 1981: 246 (note).

-Ôhira 1970: 230 moved one *Platynychus* sp. to *Dicronychus* and elevated

Paraplatynychus to gen. rank w/o comment. These transfers are

considered possible evidence of acceptance of synonymisation of

Platynychus under *Dicronychus*.

-Treated as subg. of *Dicronychus*: Fleutiaux 1947a: 348 (spp. of French Indochina); Chûjô and Ôhira 1965: 28.

-Subg. rank recognised by: Ôhira 1973a: 32 (spp. of Ryukyu Arch.).

Platynychus Motschulsky 1858: 59, incorrect subsequent spelling of

Platynychus.

-Verified by reference to correct spelling in earlier paragraph.

Platynichus Dolin and Gurjeva 1975a: 118, incorrect subsequent spelling of *Platynychus*.

-Verified by use as subg. of *Cardiophorus*, which contains sp. “*C. (Platynichus) cinereus* (Herbst)”.

Platynychnus Méquignon 1931: 208 (note), incorrect subsequent spelling of *Platynychus*.

-Verified by use of correct spelling elsewhere in note and reference to correct publication date.

Ryukyucardiophorus Ôhira 1973a: 32. Type species: *Paracardiophorus loochooensis* Miwa 1934: 255.

-Type species fixed by original designation.

Triplonychoidus Schwarz 1906: 181. Type species: *Triplonychus trivittatus* Champion 1895: 427.

-Type species fixed by Hyslop 1921: 672.

Triplonychoides Hyslop 1921: 672, incorrect subsequent spelling of *Triplonychoidus* Schwarz.

-Misspelling followed by Schenkling: 1925: 263 (catal., distn.); Blackwelder 1944: 303 (checkl.); Golbach 1994: 24 (key to gen. of S. America).

Triplonychus Candèze 1860: 236. Type species: *T. acuminatus* Candèze 1860: 238.

-Type species fixed by Hyslop 1921: 672.

-Name recognised by: Harold 1869: 1553 (catal.); Candèze 1891a: 135 (catal.); Champion 1895: 426 (spp. of central America); Schwarz 1906: 180 (gen. level rev., catal.); Schenkling: 1925: 262 (catal., distn.); Blackwelder 1944: 303 (checkl.); Golbach 1979a: 400 (key to gen. of S. America); Golbach 1994: 24 (key to gen. of S. America).

Tropidiplus Fleutiaux 1903a: 251. Type species: *T. tellinii* Fleutiaux 1903a: 251.

- Type species fixed by original monotypy.
- Synonymised under *Craspedostethus* by Schwarz 1906: 174 (gen. level rev., catal.).
- Synonymised under *Paracardiophorus* as part of s.g. *Craspedostethus* (stat.nov) by Cobos 1970a.
- Name recognised by: Waterhouse 1912: 310; Fleutiaux 1932b: 22 (spp. of Mozambique, apparently ignoring synonymy by Schwarz); Chassain 1979: 206 (rejecting placement in *Paracardiophorus* based on sclerites of bursa copulatrix, spp. of Saudi Arabia).

Zygocardiophorus Iablokoff-Khnzorian and Mardjanian 1981: 247. **Stat.nov.** raised to genus rank.

- Type species, *C. nigratissimus* Buysson 1891: 134, fixed by original designation.

Zigocardiophorus Platia 1994: 354, incorrect subsequent spelling of *Zygocardiophorus*.

- Verified by correct page and date of original publication.

Cardiophorus: subg. *Zygocardiophorus* Iablokoff-Khnzorian and Mardjanian

1981: 247. Type species: *C. nigratissimus* Buysson 1891: 134.

-Type species fixed by original designation.

Appendix 3. Diagnoses

Diagnosis of Cardiophorinae (*sensu lato*)

Head with supra-antennal carina extending mesally or anteromesally from antennal fossa (Figs. 1, 2); mesocoxal cavity closed to mesepimeron and mesepisternum by extension of mesosternum in most (Fig. 15), if open to mesepimeron (Fig. 14) or both (Fig. 13), then stylus of ovipositor absent or wider than long; if claws with basal setae, then anterior edge of scutellum emarginate mesally (Fig. 10).

Description of Cardiophorinae (*sensu lato*)

Length 2-15 mm. Integument black, brown, yellow and/or red, some with spots or lines on pronotum or elytra; setae simple or wider at midlength than at base. Body without concavities for reception of tarsi. **Head:** Antennae weakly serrate; antennomere 1 with dorso-lateral carina in some, antennal sensory elements beginning on 3 or 4; mandibles with apices unidentate or bidentate. Labrum flat or evenly convex; area between antennal fossa and compound eye unsculptured, or with carina, groove or pit(s). Frons convex; with supra-antennal carinae complete across frontoclypeal region (Fig. 3), although not concave between carinae and anterior edge in some, supra-antennal carina forked near juncture with compound eye in many (Fig. 4); frons with supra-orbital groove present (Fig. 3) or absent. **Prothorax:** Pronotum with punctures round or elongate, situated on or between tubercles in some; hind angles with or without carinae dorsally; sublateral carinae and incisions present or absent; posterior edge of pronotum with 1 to 3

apices mesally; lateral carinae complete or effaced anteriorly (Figs. 5, 6) possibly entirely effaced in some), ventrad of lateral edge of pronotum in some; hind angles complete dorsally (5) or truncate so that apex is composed of hypomerion only (Fig. 6); dorsal carina of hind angle single, absent to complete; hypomerion hind edge with sinuation (Fig. 6) or rectangular emargination (Fig. 5) immediately meso-ventrad of hind angles; procoxal cavities open or closed. Prosternum with lateral edges concave to convex in ventral view, effaced in a few; pronotosternal suture not depressed anteriorly sufficiently to guide antennae; anterior prosternal lobe long or short, covering labium in most; prosternal process straight or curved dorsad, ventral surface carinate laterally, or not.

Mesothorax: Scutellum with anterior edge convex (Fig. 8) to emarginate (Fig. 10), posterior apex rounded to pointed (Figs. 8, 10). Mesosternum with anterior edges convex or concave laterad of mesosternal cavity; mesosternal cavity with lateral edges straight or sinuate anterad of mesocoxae. Mesepisternum and mesepimeron not reaching mesocoxal cavity in most (Fig. 15); mesotrochantin not exposed in most. Elytra with 9 striae (obscured in some), intervals flattened to costate; apices without spines. Hind wings, notched in anal area or not, wedge cell absent in most (Fig. 20). **Legs:** Tibiae with 2 apical spurs; tarsi simple or with tarsomere 4 lobed; tarsal claws each with 1-8 apices; metacoxal plate covers 1/8-2/3 of metatrochanter with legs withdrawn. **Abdomen:** Ventrites 1-4 fused, ventrite 5 articulating with 4. **Male genitalia:** Urosternite 8 straight to anteriorly pointed, with 2 lateral posterior lobes, without medial posterior lobe; abdominal segment 9 with tergite and sternites articulated at sides or base; phallobase of aedeagus not fused with parameres; parameres articulated at base (Fig. 25) or fused

basally (Figs. 26, 27), articulated in posterior half in some, with or without apicolateral or apicomedial expansions, apex forked in some (Fig. 27), sides with 0-30 setae; median lobe with basal struts approximately 0.2-2.1 times length of median lobe, median lobe simple or split, tapered or with triangular apical expansion. **Female genitalia:** Ovipositor with baculae present or absent; coxites flexible to heavily sclerotised; styli present (Fig. 28) or absent. Bursa copulatrix with colleterial glands pedunculate to indiscernible; with 0-1 capsule-like sclerotised spermathecae; clusters of free spines, or spine bearing sclerites present (Figs. 30-35), or absent; common spermathecal gland and spermathecal duct unmodified if present; spermathecal gland duct with row of diverticulae in some, base sclerotised inside bursa in some (Figs. 36, 37); anterior end of bursa with 0-2 anterior pedunculate sacs (Fig. 29) if 2, then sharing common attachment to bursa).

Diagnosis of Cardiophorinae (*sensu stricto*)

If procoxal cavities not closed to mesepisternum and mesepimeron, then scutellum emarginate anteriorly; hind wing without wedge cell; male aedeagus with paramere bases fused together into tube both dorsally and ventrally, articulated apically of bases, or rigid (Figs. 26, 27); female ovipositor without styli.

Description of Cardiophorinae (*sensu stricto*)

Length 2-15 mm. Integument black, brown, yellow and/or red, some with spots or lines on pronotum or elytra; setae simple or wider at midlength than at base. Body without concavities for reception of tarsi. **Head:** Antennae weakly serrate; antennomere 1

with dorso-lateral carina in some, antennal sensory elements beginning on 3 or 4; mandibles with apices unidentate or bidentate. Labrum flat or evenly convex; area between antennal fossa and compound eye unsculptured, or with carina, groove or pit(s). Frons convex; with supra-antennal carinae complete across frontoclypeal region (Fig. 3), although not concave between carinae and anterior edge in some, supra-antennal carina forked near juncture with compound eye in many (Fig. 4); frons with supra-orbital groove present (Fig. 3) or absent. **Prothorax:** Pronotum with punctures round or elongate, situated on or between tubercles in some; hind angles with or without carinae dorsally; sublateral carinae and incisions present or absent; posterior edge of pronotum with 1 to 3 apices mesally; lateral carinae complete or effaced anteriorly (Figs. 5, 6) possibly entirely effaced in some), ventrad of lateral edge of pronotum in some; hind angles complete dorsally (5) or truncate so that apex is composed of hypomeron only (Fig. 6); dorsal carina of hind angle single, absent to complete; hypomeral hind edge with sinuation (Fig. 6) or rectangular emargination (Fig. 5) immediately meso-ventrad of hind angles; procoxal cavities open or closed. Prosternum with lateral edges concave to convex in ventral view, effaced in a few; pronotosternal suture not depressed anteriorly sufficiently to guide antennae; anterior prosternal lobe long or short, covering labium in most; prosternal process straight or curved dorsad, ventral surface carinate laterally, or not. **Mesothorax:** Scutellum with anterior edge convex (Fig. 8) to emarginate (Fig. 10), posterior apex rounded to pointed (Figs. 8, 10). Mesosternum with anterior edges convex or concave laterad of mesosternal cavity; mesosternal cavity with lateral edges straight or sinuate anterad of mesocoxae. Mesepisternum and mesepimeron not reaching mesocoxal

cavity in most (Fig. 15); mesotrochantin not exposed in most. Elytra with 9 striae (obscured in some), intervals flattened to costate; apices without spines. Hind wings, notched in anal area or not, wedge cell absent (Fig. 20). **Legs:** Tibiae with 2 apical spurs; tarsi simple or with tarsomere 4 lobed; tarsal claws each with 1-8 apices; metacoxal plate covers 1/8-2/3 of metatrochanter with legs withdrawn. **Abdomen:** Ventrites 1-4 fused, ventrite 5 articulating with 4. **Male genitalia:** Urosternite 8 straight to anteriorly pointed, with 2 lateral posterior lobes, without medial posterior lobe; abdominal segment 9 with tergite and sternites articulated at sides or base; phallobase of aedeagus not fused with parameres; parameres fused basally (Figs. 26, 27), articulated in posterior half in some, with or without apicolateral or apicomedial expansions, apex forked in some (Fig. 27), sides with 0-30 setae; median lobe with basal struts approximately 0.2-1.7 times length of median lobe, median lobe simple or split, tapered or with triangular apical expansion. **Female genitalia:** Ovipositor with baculae present or absent; coxites flexible to heavily sclerotised; styli absent. Bursa copulatrix with colleterial glands pedunculate to indiscernible; with 0-1 capsule-like sclerotised spermathecae; spine bearing sclerites present (Figs. 30-35), or absent; common spermathecal gland and spermathecal duct unmodified if present; spermathecal gland duct with row of diverticulae in some, base sclerotised inside bursa in some (Figs. 36, 37); anterior end of bursa with 0-2 anterior pedunculate sacs (Fig. 29) if 2, then sharing common attachment to bursa).

Diagnosis of higher Cardiophorinae (the genera of Cardiophorinae *sensu stricto* that are treated in this work)

If procoxal cavities not closed to mesepisternum and mesepimeron, then scutellum emarginate anteriorly. Prosternum with lateral edges near midlength straight or concave, not effaced. Also, hind wing without wedge cell; all setae evenly tapered; males with aedeagus with paramere bases fused together into tube both dorsally and ventrally, articulated apicad of bases or rigid (Figs. 26, 27); females with ovipositor lacking styli, bursa copulatrix without sclerotised spermathecal capsules.

Diagnoses of genera of altered status or membership

Diagnoses presented here distinguish each genus from all other Cardiophorinae (*sensu lato*)

***Aphricus* LeConte 1853**

Aphricus LeConte 1853: 501. Type species: *A. californicus* LeConte 1853: 502.

Patriciella Van Zwaluwenburg 1953: 20. **Syn.nov.**

Replacement name for *Patricia* Van Zwaluwenburg.

Patricia Van Zwaluwenburg 1947: 113. Type species: *P. australica* Van Zwaluwenburg 1947: 114.

-Junior homonym of *Patricia* Fox 1940 (Lepidoptera).

Diagnosis: Prosternum with sides concave or parallel; mesosternum and metasternum connate laterad of mesocoxal cavity (Fig. 15); aedeagus with parameres fused basally, articulated beyond midlength (Fig. 26), apices with more than 3 setae, not divided. Also labrum concave in lateral view. Females unknown.

(Range: USA, Australia, New Zealand)

***Aptopus* Eschscholtz 1829**

Aptopus Eschscholtz 1829: 32. Type species: *A. tibialis* Eschscholtz 1829: 32.

-Definition restricted here to exclude species near *Aptopus agrestis* (Erichson).

Apsopus Schwarz 1906: 180, incorrect subsequent spelling of *Aptopus*.

-Misspelling verified by inclusion of the correct reference page for *Aptopus* Eschscholtz.

Diagnosis: Pronotum with lateral carina effaced anteriorly, not visible in dorsal view; tarsi simple, tarsal claws with at least 5 points on each. Also, bursa copulatrix with both proximal (Fig. 30) and distal sclerites (Figs. 34, 35).

(Range: Argentina to SW North America)

***Austrocardiophorus* (gen.nov.)**

Austrocardiophorus gen. nov. Type sp. *Cardiophorus humeralis* Fairmaire and Germain 1860.

Diagnosis: Pronotum with carina along lateral edge visible in dorsal view, effaced anteriorly; procoxal cavities closed; scutellum with anterior edge broadly concave (Fig. 9); tarsi and tarsal claws simple. Also, female bursa copulatrix with one pair of bilobed sclerites (Fig. 31).

(Range: Chile and Australia)

***Blaiseus* Fleutiaux 1931**

Blaiseus Fleutiaux 1931c: 307. Type species: *B. bedeli* Fleutiaux 1931c: 308.

Blaseus Gurjeva 1974a: 112, incorrect subsequent spelling of *Blaiseus*.

Diagnosis: Mandibles simple; aedeagus with parameres split vertically into dorsal and ventral lobes; median lobe of aedeagus broadest near apex (Fig. 27). Male abdominal segment 9 with tergite and sternite articulated at base. Most species with protibiae broadened, apparently for digging. Females unknown.

(Range: Vietnam, China, Malaysia, South Africa, Mexico, Honduras)

***Cardiodontulus* Van Zwaluwenburg 1963**

Cardiodontulus Van Zwaluwenburg 1963: 341. Type species: *C. brandti* Van Zwaluwenburg 1963: 341.

- *Cardiotarsus mjobergi* Carter is here transferred to this genus.

Diagnosis: Pronotum with carina along lateral edge effaced anteriorly, not hidden in dorsal view; procoxal cavities closed; tarsomere 4 lobed, tarsal claws with 2 points; bursa copulatrix with one pair of bilobed sclerites.

(Range: Papua New Guinea, Australia)

***Cardiophorus* (*Cardiophorus*) Eschscholtz 1829**

Cardiophorus Eschscholtz 1829: 34. Type species: *Elater thoracicus* Fabricius 1801:

236, now regarded as a synonym of *Cardiophorus gramineus* (Scopoli, 1763).

Cardiaphorus Motschulsky 1858: 59, incorrect subsequent spelling of

Cardiophorus.

Cardiophorua Cobos 1954: 86, incorrect subsequent spelling of *Cardiophorus*.

Cardiosphorus Gurjeva 1974b: 70, incorrect subsequent spelling of

Cardiophorus.

Caloderus Stephens 1830: 269. Type species: *Elater thoracicus* Fabricius 1801:

236.

Melanotus, *sensu* Gistel 1834: 11, not Eschscholtz 1829: 32 *Elater thoracicus*

Fabricius 1801: 236.

Paradicronychus Dolin and Gurjeva 1975: 116 (*nomen nudum*)

-Here placed as **syn.nov** of *Cardiophorus*.

Diagnosis: Mandibles bidentate or tridentate; labrum convex in lateral view; scutellum with anterior edge emarginate (Fig. 10); tarsi and tarsal claws simple; pronotum with

lateral carina effaced anteriorly, hidden by lateral expansion of pronotum in dorsal view; bursa copulatrix with proximal (largest, or only) sclerites ovoid (Fig. 30).

(Paraphyletic, Range: North America, Eurasia, Africa)

***Cardiophorus (Coptostethus) femoratus* Wollaston.**

Cardiophorus: subg. *Coptostethus* Wollaston.

Coptostethus Wollaston 1854: 238. Type species: *C. femoratus* Wollaston 1854: 240.

Coptosthetus Candèze 1860: 504, incorrect subsequent spelling of *Coptostethus*.

Diagnosis: Mandibles bidentate; pronotum with lateral carina effaced anteriorly, not hidden by lateral expansion of pronotum in dorsal view; prosternum with anterior edge produced as lobe, concealing labium when head not extended; scutellum with anterior edge emarginate, anterolateral edges evenly rounded, posterior end pointed (Fig. 10); tarsi and tarsal claws simple.

Type locality: Porto Santo Island, Madeira Archipelago, from a cave, females unknown. The relatedness of this species to brachypterous Cardiophorinae from the Canary Archipelago. and S. Africa also placed in subg. *Coptostethus* has not been demonstrated. Some *Coptostethus* spp. from the Canary Archipelago have tarsal claws with 2 apices (Fig. 23).

***Cardiophorus (Perrinellus) argentatus* Buysson 1899**

Cardiophorus: subg. *Perrinellus* Buysson 1899: 282. Type species: *Athous argentatus*

Abeille de Perrin 1894: 92.

Cardiophorus: subg. *Lasiocerus* Buysson 1912: 129. Type species: *C. schusteri*

Buysson 1912: 128.

Perinellus Schwarz 1906: 172, incorrect subsequent spelling of *Perrinellus*.

Diagnosis: Mandibles bidentate; supra-antennal carina without longitudinal split next to compound eyes (Fig. 3); pronotum with hind angles not truncate dorsally (Fig. 5); pronotum with lateral carina effaced anteriorly, not hidden by lateral expansion of pronotum in dorsal view, reaching less than half way to anterior edge; prosternum with anterior edge produced as lobe, concealing labium when head not extended; procoxal cavities open; scutellum with anterior edge emarginate (Fig 10), anterolateral edges straight or concave posterior to anterolateral corners (Fig. 8), posterior end pointed; tarsi and tarsal claws simple.

Type locality: Israel, other spp from N. Africa, Ceylon, Central Asia, probably not monophyletic. *Lasiocerus* du Buysson, described from Algeria for long antennae with dense setae, and later synonymised under subg. *Perrinellus* was not located for examination, and may not match these key characteristics.

***Chileaphricus* gen.nov.**

***Chileaphricus* gen.nov.** Type species, *Aphricus chilensis* Fleutiaux.

Diagnosis: Labrum convex in lateral view; area between antenna fossa and edge of compound eye with carina connecting fossa and eye or with 2 pits with non-depressed

area between them; frons with supra-orbital groove present (Fig. 4); pronotum with carina on lateral edge effaced anterad of posterior third; prosternum with anterior edge short, arcuate, exposing labium, lateral edges near midlength straight or concave, not effaced; scutellum with anterior edge emarginate (Fig. 10); tarsi and tarsal claws simple; aedeagus with 3 or more setae on each paramere. Also mesocoxal cavity open to both mesepimeron and mesepisternum (Fig. 13), mesotrochantin not hidden (in type specimen); hind wing membrane not notched in anal area.

(Range: Chile)

***Floridelater* gen.nov.**

***Floridelater* gen.nov.** Type species *Coptostethus americanus* Horn. Type species transferred to Cardiophorinae from Negastrinae (*Negastrius americanus* (Horn)).

Diagnosis: Scutellum with anterior edge broadly concave; posterior apex bilobed (Fig. 11). Also short winged; tarsi and tarsal claws simple; pronotum more than half as long as elytra.

(Range: USA, Coastal dunes by Gulf of Mexico)

***Globothorax* Fleutiaux 1891**

***Globothorax* Fleutiaux 1891a: ccxxxii.** Type species: *G. chevrolati* Fleutiaux 1891a: ccxxxiii.

Teslasena* Fleutiaux 1892: 410. *Syn.nov.

-Type species, *Anelastes femoralis* Lucas 1857: 71.

Globotorax Aranda 1998: 126, 128, 130 (key to gen.), incorrect subsequent spelling of *Globothorax*.

Diagnosis: Protibiae flattened and broadened apically, apparently for digging, tarsi simple, tarsal claws with 2-3 teeth; bursa copulatrix with proximal (only) sclerites parallel sided (Fig. 32). Also, anterior edge of scutellum straight, females with compound eyes nearly flat and antennae reaching only 2/3 of distance to pronotal hind angles.

(Range: Brazil, Bolivia)

***Pachyelater* Lesne 1897**

Pachyelater Lesne 1897b: 117 Replacement name for *Parelater* Lesne.

-Transferred here to Cardiophorinae.

Lesnelater Fleutiaux 1935a: 116. **Syn.nov.**

-Type species *Lesnelater madagascariensis* Fleutiaux (= *Pachyelater madagascariensis* Lesne 1897 **Syn.nov.**)

Parelater Lesne 1897a: 102. *P. madagascariensis* Lesne 1897: 102.

-Junior homonym of *Parelater* Candèze 1882: 70 (Coleoptera: Elateridae).

Diagnosis: Mandibles bidentate; labrum convex in lateral view; pronotum with lateral carina effaced anteriorly, not hidden in dorsal view; procoxal cavities open; protibiae flattened and broadened apparently for digging; prosternum with anterior edge short, exposing labium; pronotum with setae on disc not on tubercles; scutellum with anterior edge broadly concave, posterior end not bilobed (Fig. 9); mesepisternum with

anteromesal corners rounded; anterior edge of elytra rounded or straight in dorsal view (Fig. 18); tarsi and tarsal claws simple. Also, aedeagus of males with parameres undivided (Fig. 26). Females with compound eyes reduced, antennae reaching only halfway to pronotal hind angles reduced ovipositor with baculae of ovipositor shorter than coxites; bursa copulatrix without sclerites.

(Range: Madagascar, W. Africa)

***Paracardiophorus* Schwarz 1895**

Paracardiophorus Schwarz 1895b: 40. Type species: *Cardiophorus musculus* Erichson 1840: 299.

-Genus membership revised here to include North American spp. and exclude Australian and S. American spp.

Paracarpiphonus Fleutiaux 1928: 284, incorrect subsequent spelling of *Paracardiophorus*.

Paracapiophonus Arnett 1955: 614 (note on types), incorrect subsequent spelling of *Paracardiophorus*.

Diagnosis: Supra-antennal carina with longitudinal split next to compound eyes (Fig. 4); scutellum with anterior edge emarginate (Fig. 10); tarsi and tarsal claws simple; bursa copulatrix with internal elbowed sclerotisation of base of spermathecal gland duct (Figs. 36, 37). Also most species with pronotal hind angles truncate dorsally so that apex is composed of only the narrow hypomeral portion (Fig. 6); posterior edges of hypomeron mesad of hind angles straight or sinuate (Fig. 6).

(Range: Holarctic)

Appendix 4. Key to genera of extant Cardiophorinae, based on adult morphology

- 1 Aedeagus with parameres pivoting at base (Fig. 25), not fused. If mesocoxal cavities closed to mesepimeron and mesepisternum then dorsal vestiture with scale-like setae and anterior edge of scutellum convex anteriorly; hind wing with or without wedge cell; ovipositor with or without styli *Cardiophorinae sensu lato* (hypnoidine grade of genera revised by Stibick (1976, 1978, 1979b, 1980a, 1980b).
- Aedeagus with paramere bases fused together into tube both dorsally and ventrally, articulated apicad of bases or rigid (Figs. 26, 27). If procoxal cavities not closed to mesepisternum and mesepimeron, then scutellum emarginate anteriorly; hind wing without wedge cell; ovipositor without styli, [*Cardiophorinae sensu stricto*] 2
- 2 (1) Prosternum with lateral edges near midlength convex, or partially effaced due to fusion with pronotum; if scutellum emarginate anteromesally, then with dorsal vestiture of scale-like or apically broadened setae; some with tubercles between setal punctures on pronotum; bursa copulatrix with symmetrical pair of spine bearing sclerites absent, or connected to each other by semi-sclerotised tissue; some with sclerotised spermathecae negastriine grade of genera (revised by Stibick (1971), with subsequent changes by Calder 1996, Dolin 1976, Dolin 1992, Dolin and Girard 1998, Golbach 1994, Kishii 1976)
- Prosternum with lateral edges near midlength straight or concave, not effaced. Most with scutellum emarginate anteromesally; setae evenly tapered in all; none with tubercles between pronotal setae; most with minute serrations along upper edge of

- elytral epipleurae and/or at sides of urosternites 3-7; bursa copulatrix of most with symmetrical pair of separate, spine bearing sclerites (proximal sclerites); without sclerotised spermathecal capsules [higher Cardiophorinae] 3
- 3 (2) Pronotum with complete carina at lateral edge or on hypomeron, reaching from hind angle to anterior edge of prothorax (from Oriental and Ethiopian realms)4
- Pronotum with lateral carina effaced anteriorly (ventrad of edge of pronotum in some, called submarginal line of earlier publications), [to rest of Cardiophorinae] 5
- 4 (3) Scutellum with anterior edge abruptly emarginate; tarsal claws without basal point; tarsal claws with basal setae (possibly absent in some); bursa copulatrix with proximal sclerites ovoid (Fig. 30). In type species (*T. tellinii*) urosternite 7 has multiple longitudinal grooves and second longitudinal carina near lateral edge (Eritrea, Ethiopia, Mozambique, Kenya) *Tropidiplus* Fleutiaux 1903.
- Scutellum with mesal portion of anterior edge broadly concave; tarsal claws with both basal and apical points, without basal setae; bursa copulatrix with proximal sclerites bilobed (Fig. 31), (southeast Asia) *Paraplatynychnus* Fleutiaux 1931.
- 5 (3) Pronotum with lateral carina present (short and thin in some) but hidden in dorsal view by swollen pronotum (= submarginal line); proximal (largest) sclerites of bursa copulatrix ovoid or absent (Fig. 30) 6
- Pronotum with carina extending anteriad from hind angles following lateral edge or completely effaced; proximal (largest) sclerites of bursa copulatrix ovoid, bilobed, parallel sided, partially membranous, or absent 21
- 6 (5) Tarsomere 4 with ventral lobe or pad extending beyond base of tarsomere 5 7

- Tarsomere 4 without ventral lobe or pad extending beyond base of tarsomere 5 8
- 7 (6) Tarsal claws without basal point (Africa, Mauritius, S. and E. Asia, Japan,
Taiwan)... *Cardiotarsus* Eschscholtz 1836, part (type species keys here, genus not
monophyletic).
- Tarsal claws with both basal and apical points (Cambodia, Vietnam, Laos, Philippines)
..... *Odontocardus* Fleutiaux 1931.
- 8 (6) Tarsal claws with 3 or more points (SW North America to Argentina)
..... *Aptopus* Eschscholtz 1829.
- Tarsal claws with single apical point or both basal and apical points 9
- 9 (8) Tarsal claws with 2 points (figs. 23, 24) 10
- Tarsal claws only 1 point 15
- 10 (9) Procoxal cavities open 11
- Procoxal cavities closed 12
- 11 (10) Tarsal claws with second point near apex; hind wing membrane not notched in
anal area (S. and S.E. Asia) *Phorocardius* Fleutiaux 1931.
- Tarsal claws with second point at base; hind wing membrane notched in anal area
(Eurasia, Africa) *Dicronychus* Brullé 1832.
Monophyly unknown, widely confused with *Platynychus*. Some apterous spp.
currently assigned to *Cardiophorus* s.g. *Coptostethus* key to here.
- 12 (10) Anterior edge of scutellum with arcuate concavity (Ryukyu Islands, Japan)
..... *Ryukyucardiophorus* Ôhira 1973 (not examined).
- Anterior edge of scutellum emarginate 13

- 13 (12) Head with area between antenna fossa and edge of compound eye unsculptured;
 bursa copulatrix with paired distal sclerites (pair farthest from vagina, at base of
 spermathecal gland duct) present and fused into a “U” shape; base of spermathecal
 gland duct inside bursa without tube-like sclerotisation (Eurasia) *Platynychus*
 Motschulsky 1858 (monophyly unknown, widely confused with *Dicronychus*).
- Head with area between antennal fossa and edge of compound eye with carina
 connecting fossa and eye, or with 2 pits with non-depressed area between them or
 with a single pit; bursa copulatrix without paired distal sclerites (i.e. a second pair,
 farther from vagina, at base of spermathecal gland duct); base of spermathecal gland
 duct with tube-like sclerotisation (without paired plate-like appendages) 14
- 14 (13) Head with area between antennal fossa and edge of compound eye with carina
 connecting fossa and eye, or with 2 pits with non-depressed area between them; tarsal
 claws with ventral surface convex mesad of basal apex (Fig. 23) (Japan)
 Displatynychus Ôhira 1987.
- Head with area between antennal fossa and eye with a single pit (Vietnam); tarsal
 claws with ventral surface concave mesad of basal apex (Fig. 24)
 Diocarpus Fleutiaux 1947 (stat.nov., monotypic, *D. solitarius* Fleutiaux).
- 15 (9) Mandibular apex unidentate (simple) 16
- Mandibular apex bidentate or tridentate 18
- 16 (15) Head with supra-orbital groove absent; posterior edges of hypomeron mesad of
 hind angles without rectangular or semicircular indentations (Uzbekistan, known
 from males only)..... *Metacardiophorus* Gurjeva 1966 (stat.nov.).

- Head with supra-orbital groove present (Figs. 3, 4); posterior edges of hypomeron mesad of hind angles with rectangular or semicircular indentations 17
- 17 (16) Scutellum with mesal portion of anterior edge broadly concave; prosternum with anterior edge short, exposing labium; protibiae with posterior surface convex, weakly modified for digging (S. Africa, known from males only) ... *Cardiophorellus* Cobos 1970 (3 spp., Congo,). Subgenus *Parapleonomus* was not located for examination, and may not match key characteristics.
- Scutellum with mesal portion of anterior edge abruptly emarginate; prosternum with anterior edge not short, produced as lobe, concealing labium; protibiae with posterior surface flattened and broadened apically, apparently strongly modified for digging (Tanzania, known from females only)
..... *Margogastrius* Schwarz 1903 (monotypic, *M. schneideri* Schwarz).
- 18 (15) Edge of elytra in dorsal view between anterior-most point and humeral angle arcuate or straight, without sinuation (Fig. 18); bursa copulatrix containing a tube-like sclerotisation of base of spermathecal gland duct (Figs. 36, 37) 19
- Edge of elytra in dorsal view between anterior-most point and humeral angle sinuate or tuberculate (Fig 17); base of spermathecal gland duct not sclerotised 20
- 19 (18) Elytron with apical shelf-like extension; elytra black without markings; sclerotisation of base of spermathecal gland duct without paired plate-like appendages (S.W. Asia)..... *Zygocardiophorus* Iablokoff-Khnzorian and Mardjanian 1981, stat.nov. (monotypic, *Z. nigratissimus* (Buysson) 1891).

- Elytron without apical shelf-like extension; elytra with or without pale spots; bursa copulatrix with tube-like sclerotisation of base of spermathecal gland duct, some also with L shaped or with paired plate-like appendages (Holarctic)
 Paracardiophorus Schwarz 1895, part.
- 20 (18) Pronotum with carina extending from dorsal surface of hind angles to anterior quarter; dorsal surface of labrum flat in side view; bursa copulatrix with a pair of semi-membranous concave sclerites, or none (Cameroon to Iran)
 Craspedostethus Schwarz 1898.
- Pronotum with dorsal hind angle carina not reaching anterior half; labrum convex in side view; bursa copulatrix with spiny ovoid proximal sclerites, most also with separate or fused distal sclerites (a second pair next to spermathecal gland duct), , (North America, Eurasia, Africa) *Cardiophorus* Eschscholtz 1829 (Paraphyletic).
- 21 (5) Tarsomere 4 lobed or lamellate 22
- No tarsomeres lobed or lamellate 27
- 22 (21) Tarsal claws with 2 points (Fig. 23) 23
- Tarsal claws with 1 point 25
- 23 (22) Scutellum with mesal portion of anterior edge straight (Fig. 8), (South and North America) *Esthesopus* Eschscholtz 1829.
- Scutellum with mesal portion of anterior edge broadly concave (Figs. 9, 11) or abruptly emarginate (Fig. 10) 24
- 24 (23) Procoxal cavities closed; elytra with apical half of interval 9 flattened or rounded (Australia, Papua New Guinea) *Cardiodontulus* Van Zwaluwenburg 1963.

- Procoxal cavities open, apical half of elytral interval 9 costate
 Triplonychoidus Schwarz 1906 (Mexico to South America).
- 25 (22) Mandibles with apices simple and aedeagus with free portion of parameres split vertically into dorsal and ventral lobes (Fig. 27); median lobe. Male abdominal segment 9 with tergite and sternite articulated at base. Most species with protibiae broadened, apparently for digging (known from males only China, Vietnam, Malaysia, South Africa, Mexico, Honduras) *Blaiseus* Fleutiaux 1931, part.
- Mandibles with 2-3 points; hind wing with CuA1 not forked; tergite and sternite of male abdominal segment 9 articulated at sides; aedeagus with parameres not split; protibiae not modified for digging 26
- 26 (25) Distance between antennae equal to $\frac{1}{4}$ width of head (measured across outsides of compound eyes), nasale oriented ventrally; procoxal cavities closed; notched in anal area (known from males only, Brazil)
 Buckelater Costa 1973 (monotypic, *B. argutus* Costa 1973).
- Distance between antennae more than $\frac{1}{4}$ width of head; nasale oriented anteroventrally; procoxal cavities open; hind wing membrane not notched in anal area (S. Africa)
 Cardiotarsus Eschscholtz 1836, part (undescribed species near *C. philautus* Candèze 1860).
- 27 (21) Tarsal claws with number of points (including basal tooth) more than 1; bursa copulatrix with 1 pair of sclerites 28
- Tarsal claws with apical point only; bursa copulatrix with 0-4 sclerites 31

- 28 (27) Protibiae flattened and broadened apically, apparently modified for digging;
 elytral intervals 1-8 rounded; sclerites of bursa copulatrix parallel sided (Fig. 32).
 Females with compound eyes and antennae reduced (Bolivia, Brazil).....
 Globothorax Fleutiaux 1891.
- Protibiae not apparently modified for digging; some with apical half of elytral intervals
 1-9 costate; bursa copulatrix with proximal sclerites ovoid or parallel sided (Figs. 30,
 32)..... 29
- 29 (28) Tarsal claws with 2 points only; bursa copulatrix with proximal sclerites ovoid
 (Fig. 30), (USA to Argentina, not monophyletic); ... *Horistonotus* Candèze 1860, part
 (type species keys here).
- Tarsal claws with more than two points 30
- 30 (29) Tarsal claws each with 3 points; elytra with apical half of intervals 1-8 costate;
 head with area between antenna fossa and edge of compound eye with either carina
 connecting fossa and eye, or with 2 pits with non-depressed area between; urosternite
 7 with second carina mesad of lateral carina (S. and Central America)
 Triplonychus Candèze 1860.
- Tarsal claws each with 7 or more points; head with area between antenna fossa and
 edge of compound eye with a single pit; elytra with apical half of intervals 1-8 all
 flattened or rounded; urosternite 7 without second carina mesad of lateral carina
 (Brazil) *Horistonotus agrestis* Candèze 1860, comb.nov.
- 31 (27) Scutellum with mesal portion of anterior edge convex to broadly concave (Figs.
 8, 9, 11) 32

- Scutellum with mesal portion of anterior edge abruptly emarginate 36
- 32 (31) Procoxal cavities closed; mesepisternum with mesally concave projection of anteromesal corners; anterior edge of elytra in dorsal view between anterior-most point and humeral angle sinuate or tuberculate (Fig. 17); bursa copulatrix with bilobed sclerites (Fig. 31), (Chile and Australia) *Austrocardiophorus* gen.nov.
- Procoxal cavities open; mesepisternum with anteromesal corners rounded; anterior edge of elytra evenly rounded (Fig. 18), straight, or sinuate in dorsal view; bursa copulatrix (for genera with known females) with a pair of ovoid sclerites, or without sclerites 33
- 33 (32) Scutellum with posterior apex bilobed; prosternum with anterior edge produced as lobe, concealing labium when head not extended; pronotum with setae on disc on tubercles; hind wing with veins weakly sclerotised, wing area less than half of elytral area (USA, coastal dunes by Gulf of Mexico) *Floridelater* gen.nov.
- Scutellum with posterior apex not bilobed; prosternum with anterior edge short, exposing labium; pronotum with setae on disc not on tubercles; hind wing with venation well developed, some or all with wing area greater than elytral area 34
- 34 (33) Aedeagus with paramere apices forked (Fig. 27) (females unknown, undescribed spp., S. Africa, Honduras) *Blaiseus* Fleutiaux 1931 (part).
- Aedeagus with paramere apices not forked 35
- 35 (34) Labrum flat in lateral view; protibiae modified for digging, or not *Aphricus* LeConte 1853, (part).

- Labrum convex dorsally in lateral view; protibiae apparently modified for digging,
posterior surface flattened and broadened apically; *Pachyelater* Lesne 1897.
- 36 (31) Prosternum with anterior edge short, exposing labium 37
- Prosternum with anterior edge not short, produced as lobe, concealing labium when
head not extended 39
- 37 (36) Head with area between antenna fossa and edge of compound eye unsculptured;
hind wing membrane notched in anal area (between AA3+4 and AP); parameres with
2 setae each (central Asia)
..... *Nyctor expallidus* Semenov-Tian-Shanskii & Pjatakova 1936.
- Head with area between antenna fossa and edge of compound eye with carina
connecting fossa and eye or with 2 pits with non-depressed area between them; hind
wing membrane notched or unnotched in anal area; parameres of aedeagus with 3 or
more setae on each 38
- 38 (37) Labrum flat in lateral view; frons without supra-orbital groove; prosternum with
anterior edge notched at midline; mesocoxal cavity closed to mesepimeron and
mesepisternum by extension of mesosternum; mesotrochantin hidden
..... *Aphricus* LeConte 1853 (part).
- Labrum convex in side view; frons with supra-orbital groove; prosternum with anterior
edge at midline arcuate; mesocoxal cavity open to both mesepimeron and
mesepisternum (Fig. 13), mesotrochantin not hidden (Chile) ... *Chileaphricus* gen.nov.

- 39 (36) Mandibles with apices simple, scutellum pointed at posterior apex; urosternites 3-7 with or without serrations along sides (Uzbekistan, monotypic, known from males only) *Metacardiophorus* Gurjeva 1966, stat.nov. (monotypic, *M. sogdianus* Gurjeva).
- Mandibles with 2 points, scutellum pointed or rounded at posterior apex; urosternites 3-7 without serrations along sides 40
- 40 (39) Pronotum with carina along lateral edge reaching more than halfway to anterior edge; bursa copulatrix with pair proximal sclerites partially membranous between spines (Ryukyu Islands, Japan) *Allocardiophorus* Ôhira 1989.
- Pronotum with carina along lateral edge restricted to hind angles, or not reaching more than halfway to anterior edge; female bursa copulatrix with 1 pair of solid sclerites or unknown, but almost certainly not semi-membranous between spines 41
- 41 (40) Scutellum with anterolateral edges evenly rounded (Fig. 10)..... 42
- Scutellum with anterolateral edges straight or concave posterior to anterolateral corners (Fig. 8) 43
- 42 (40) Scutellum with posterior apex evenly rounded (central Asia, known from males only) *Neocardiophorus* Gurjeva 1966.
- Scutellum with posterior apex pointed; wings incapable of flight (cave inhabiting species from Porto Santo Island, Madeira Archipelago) *Cardiophorus* (*Coptostethus*) *femoratus*. The relatedness of this species to brachypterous *Cardiophorinae* from the Canary Archipelago and S. Africa also placed in s.g.

Coptostethus has not been demonstrated. Some *Coptostethus* spp. from the Canary Is. have tarsal claws with 2 apices.

- 43 (41) Supra-antennal carina without longitudinal split next to eyes (Fig. 3); pronotum with hind angles not truncate dorsally; posterior edges of hypomeron mesad of hind angles with rectangular or semicircular indentations; procoxal cavities open; parameres approximately cylindrical near apex (Isreal)... *Cardiophorus* (*Perrinellus*) *argentatus* Buysson 1899 (other spp from N. Africa, Ceylon, Central Asia, probably not monophyletic with this). *Lasiocerus* du Buysson, described from Algeria for long antennae with dense setae, and later synonymised under s.g. *Perrinellus* was not located for examination, and may not match these key characteristics.
- Supra-antennal carina with longitudinal split next to eyes (Fig. 4); most species with pronotal hind angles truncate dorsally so that apex is composed of only the narrow hypomeral portion; most species with posterior edges of hypomeron mesad of hind angles straight or sinuate; procoxal cavities open or closed; free portion of parameres cylindrical to paddle-like; bursa copulatrix with proximal sclerites ovoid, distal sclerites absent; base of spermathecal gland duct sclerotised inside bursa copulatrix (Holarctic) *Paracardiophorus* Schwarz 1895 (part).

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Appendix 5. Label data from non-type specimens of species coded for phylogenetic analyses.

Details on use and identification in are presented Appendix 3. Unicode = code used on labels; Photo = code used for photographs; Dep. = specimen depository.

Unicode	Photo	Genus Species Author	Labels (checked)	Sex	Dep.
HDCU001	P001	<i>Platynychus adjutor</i> Candèze	[handwritten] "KU.79"; "Japan./G.Lewis./1910-320"	M	NHM
HDCU002	P002	<i>Platynychus adjutor</i> Candèze	[difficult to read] "Nowaba/ 6.80"; "DATA/ under card"	F	NHM
HDCU003	P003	<i>Platynychus adjutor</i> Candèze	Japan./ G. Lewis/ 1910-320."	M	NHM
HDCU004	P004	<i>Exoeolus rufescens</i> (Broun)	"Yoyogi/ (Tokyo)/ 9-vi-1953/ A.Kato"; "9"; "Adjutor Cand/ ex Ôhira"	M	NHM
HDCU005	P005	<i>Aphricus sp.nov.</i>	"Tisbury/ 10/12/14"; "A.E.Brookes/ Collection"; "Brounaeolus Hyslop"; "N Z Arthropod/ Collection, NZAC/ Private Bag 92170/ AUCKLAND/ New Zealand"	M	NZAC
HDCU006	P006	<i>Exoeolus rufescens</i> (Broun)	"Rika Valley/ Clarence River/KA 12 Mar 69/ R.J.B. Power"; "Swept grass Coprosoma"; "Brounaeolus Hyslop"; "N Z Arthropod/ Collection, NZAC/ Private Bag 92170/ AUCKLAND/ New Zealand"; "nr Brounaeolus/ det. R.A. Leschen"	M	NZAC
HDCU007	P007	<i>Exoeolus rufescens</i> (Broun)	"New Zealand DN/ Dunedin Town/ Belt/ 21-Jun97"; "In blocky/ decayed wood/ in Griselinia bole"; "Voucher specimen/ "Beetles of/ Dunedin" project./ JT Nunn coll."	M	JNIC
HDCU008	P008	<i>Exoeolus rufescens</i> (Broun)	"New Zealand DN/ Swampy Summit/ Dunedin Belt/ 20-Oct-00"	M	JNIC
HDCU009	P009	<i>Exoeolus rufescens</i> (Broun)	"New Zealand SL/ Matai Falls/ Catlins/ 6-Oct-02"; "Mixed broadleaf/ forest floor/ litter"	M	JNIC

Unicode	Photo	Genus Species Author	Labels (checked)	Sex	Dep.
HDCU010	P010	<i>Oedostethus femoralis</i> LeConte	"CANADA Québec/ Brome Co. Glen-/ Sutton 24.VII.1985/ Larochelle, Larivière"; [handwritten] "Oedostethus/ femoralis LeC./ Dét.: P. Bélanger, 1987"	F	CNCI
HDCU011	P011	<i>Oedostethus femoralis</i> LeConte	"CANADA Québec/ Brome Co.; Glen-/ Sutton 24.VII.1985/ Larochelle, Larivière"; [handwritten] "Oedostethus/ femoralis LeC./ Dét.: P. Bélanger, 1987"	F	CNCI
HDCU012	P012	<i>Oedostethus femoralis</i> LeConte	"CANADA Québec/ Brome Co.; Glen-/ Sutton 24.VII.1985/ Larochelle, Larivière"	M	CNCI
HDCU013	P013	<i>Negastrius pulchellus</i> (Lin.)	"Jarov/ Boh.v.54./A.Olexa"; [handwritten] "Hypnoidus/ pulchellus/ L./ Det.Olexa 73"	F	CNCI
HDCU014	P014	<i>Negastrius pulchellus</i> (Lin.)	"589"; "Fennia/ Ik Ollila/ 12/6 1932/ K Lahtivirta"; [handwritten] "Hypnoidus/ pulchellus L."	F	CNCI
HDCU015	P015	<i>Arrhaphes diptychus</i> Candèze	"Coll. R.I.Sc.N.B/ Inde/ Tenasserim/ Thagata/ Fea. Apr. 1887"; "Collection/ E. Candèze"; [handwritten] "Arrhaphes/ diptychus Cd. Dét. E. Candèze"	F	ISNB
HDCU016	P016	<i>Arrhaphes diptychus</i> Candèze	"Coll. R.I.Sc.N.B/ Inde/ Tenasserim/ Thagata/ Fea. Apr. 1887"; "Collection/ E. Candèze"; [handwritten] "Arrhaphes/ diptychus Cd. Dét. E. Candèze"	M	ISNB
HDCU017	P017	<i>Quasimus minutissimus</i> (Germar)	"Zbraslav/ Boh. C. VI53./ A. Olaxa"; [handwritten] "Quasimus/ minutissimus/ Germ./ Det. Olexa '73"	M	CNCI
HDCU018	P018	<i>Quasimus minutissimus</i> (Germar)	"Zbraslav/ Boh. C. VI53./ A. Olaxa"; [handwritten] "Quasimus/ minutissimus/ Germ./ Det. Olexa '73"	F	CNCI
HDCU020	P020	<i>Cardiophorus gramineus</i> Scopoli	"Schleissheim/ 28.5.04"; "München/ k.Ku zer"; [handwritten] "Cardiophorus/ gramineus Scop."	F	CNCI
HDCU021	P021a	<i>Rivulicola variegatus</i> Macleay	Specimen on left: [partly handwritten] "N.S. Wales/ Minto (W.W.F.)/ on/ apple trunk/ 16-VI-1903"	M	NHM
HDCU022	P021b	<i>Rivulicola variegatus</i> Macleay	Specimen on right: [partly handwritten] "N.S. Wales/ Minto (W.W.F.)/ on/ apple trunk/ 16-vi-1903"	M	NHM

Unicode	Photo	Genus Species Author	Labels (checked)	Sex	Dep.
HDCU023	P022	<i>Rivulicola variegatus</i> Macleay	[handwritten] "Kuranda/ 26-6-38/ C.G.C."; [handwritten] "kuranda"; "A.E. Clarke/ Collection./ B.M.1957-24"; "♀ genitalia in/ water soluble resin/ Dimethyl Hydrantoin/ Formaldehyde); [handwritten] "abdomen missing 19 III 85."	F	NHM
HDCU024	P023	<i>Cardiophorus gramineus</i> Scopoli	[handwritten] "ROMA: E.U.R./ 16.V.'58.PARENTI"	F	CNCI
HDCU025	P024	<i>Rivulicola variegatus</i> (Macleay)	[handwritten] "kuranda"; "A.E. Clarke/ Collection./ B.M.1957-24"; [handwritten] "Cryptohypnus/ variegatus MacI"	F	NHM
HDCU026	P025	<i>Agrypnella eburnea</i> Champion	"Santarem,Para/Brazil IV-27-/1963 F.Werner"; [partly handwritten] "Agrypnella/ nr. eburnea/ MCZ has 3/ Det. E.C. Becker 1985"; [partly handwritten] "Agrypnella/ eburnea/ BMNH -Homotype/ Det.HDouglass 2004"	M	CNCI
HDCU029	P028	<i>Cardiohypnus mirabilis</i> (Candèze)	6 specimens on pin with six labels reading: "Haldwani Div./ Kumaon,/ India. H.G.C."; 1X "H.G.Champion Coll./ B.M. 1953-156." 4 specimens and 4 labels remaining on original pin, 2 removed to separate pins.		NHM
HDCU030	P028a	<i>Cardiohypnus mirabilis</i> (Candèze)	"Haldwani Div./ Kumaon,/ India. H.G.C."	M	NHM
HDCU031	P028b	<i>Cardiohypnus mirabilis</i> (Candèze)	"Haldwani Div./ Kumaon,/ India. H.G.C."	F	NHM
HDCU032	P028c	<i>Cardiohypnus mirabilis</i> (Candèze)	Topmost of 4 specimens on HDCU029	M	NHM
HDCU033	P029	<i>Agrypnella squamifer(a)</i> (Candèze)	[blue disc, handwritten] "Santar/ em"; [handwritten] "squamifer/ Cdz./ (named from type)."; [partly handwritten] "mentioned/ B.C.A.III.(1)415"	F	NHM

Unicode	Photo	Genus Species	Author	Labels (checked)	Sex	Dep.
HDCU035	P031	<i>Physorhinus erythrocephalus</i>	(Fabricius)	"Santa Margarita/ Hill, TRINIDAD/ May 1959"; [handwritten] "Taken at/ light"; [partly handwritten] "Physorhinus/ erythrocephalus/ (Fab.)/ E.C. Becker 1968"; "Physorhinus/ erythrocephalus (Fab.)/ det. D. Schaaf 1970". Female genitalia in attached microvial.	F	CNCI
HDCU036	P032	<i>Physorhinus erythrocephalus</i>	(Fabricius)	"Santa Margarita/ Hill, TRINIDAD/ May 1959"; [partly handwritten] "Physorhinus/ erythrocephalus/ (Fab.)/ E.C. Becker 1968"; [handwritten] "Taken at/ light"; "Physorhinus/ erythrocephalus (Fab.)/ det. D. Schaaf 1970"	F	CNCI
HDCU037	P033	<i>Physorhinus erythrocephalus</i>	(Fabricius)	"BRAZIL,SP,Faz./ Campininas,Mogi Guacu,/ XII-29-31- 1969,/ JM & BA Campbell"	M	CNCI
HDCU038	P034	<i>Aphricus californicus</i>	LeConte	"Congress Jct./ Ar. 7-28-33/ R.H.Beamer"; [partly handwritten] "Aphricus/ californicus/ LeC./ Det.HDouglass 2004"	M	CNCI
HDCU039	P035	<i>Aptopus pullatus</i>	(Horn)	"AZ, Pima Co., Sta. Rita/ Mts., Madera Can./ 1450m, 7 Aug 2002/ Spraying tree trunks w./ Raid@, H.Douglas"	M	HBDC
HDCU040	P036	<i>Aptopus pullatus</i>	(Horn)	"Baboquivari, Mts./ Ariz. VII-24-41/ E. L. Todd"; [partly handwritten] "Aptopus ♀?/ pullatus (Horn)/ Det.Hdouglas 2003"	F	SEMC
HDCU041	P037	<i>Anchastus digitatus</i>	LeConte	"Gainesville,Fla./ 20IV-1952/ J.R. Vockeroth"; [partly handwritten] "Anchastus/ digitatus LeC./ E.C. Becker 1959"	M	CNCI
HDCU042	P038	<i>Porthmidius austriacus</i>	Schrank	[handwritten] "Austria"; "Keisenwetter"; [handwritten] "Porthmidius/ austriacus/ Schrank"; "Sammlung/ CI Müller"; [partly handwritten] "Porthmidius/ Austriacus/ Schrank./ det. E.C.Becker 1970"	M	CNCI
HDCU043	P039	<i>Porthmidius austriacus</i>	Schrank	"Zvolen/ Slov. V.56./ A. Olexa; [Handwritten] "Porthmidius/ austriacus/ Det Olexa'72"	F	CNCI
HDCU044	P040	<i>Porthmidius austriacus</i>	Schrank	[handwritten] "Austria"; "Sammlung/ CI Müller"	M	CNCI

Unicode	Photo	Genus Species Author	Labels (checked)	Sex	Dep.
HDCU045	P041	<i>Melanotus castanipes</i> (Paykull)	[handwritten] "Forst. Rosengarien/ bie Hamburg/ 28.XII.1977/ Leg. M.Zeising"	F	CNCI
HDCU046	P042	<i>Melanotus castanipes</i> (Paykull)	[handwritten] "Forst. Göhrde/ bei Hamburg/8.II.1966/ Leg. M. Zeising"	M	CNCI
HDCU047	P043	<i>Megapenthes lugens</i> (Redtenbacher)	[handwritten, nearly illegible] "Gaibien"	F	CNCI
HDCU048	P044	<i>Megapenthes lugens</i> (Redtenbacher)	[handwritten] "Megapenthes/ lugens"	F	CNCI
HDCU049	P045	<i>Negastrius pulchellus</i> (Lin.)	[handwritten] "Europe"	M	CNCI
HDCU050	P046	<i>Elater ferrugineus</i> (Lin.)	unlabeled	M	CNCI
HDCU051	P047	<i>Elater ferrugineus</i> (Lin.)	[handwritten] "L. ferrugi/ neus. 20.6/ Tero. Ital"; "343"	F	CNCI
HDCU052	P048	<i>Megapenthes lugens</i> (Redtenbacher)	"Forêt de/ Fontainebleau/ J. Chassain"; [handwritten] "Gorges aux/ Loups/ Fagus/ 4.IV.1969"	M	HBDC
HDCU053	P049	<i>Esthesopus castaneus</i> Eschscholtz	[handwritten] "Brazil"; "Sammlung/ CI Müller"; [partly handwritten] "Esthesopus/ castaneus Esch./ E.C. Becker 1959"	M	CNCI
HDCU054	P050	<i>Esthesopus castaneus</i> Eschscholtz	[handwritten] "Fry/ Rio. Jan/"; "Fry Coll./ 1905. 100."; "Esthesopus/ castaneus Er/ C.M.F. von Hayek det. 1985"; [handwritten] "Mandibles open"	F	NHM
HDCU055	P051	<i>Esthesopus castaneus</i> Eschscholtz	[handwritten] "Bahia"; "Coll. Janson./ Ex Mniszech."; [handwritten] "Esthesopus/ castaneus Esch./ Cand. Cdz./ ex. Coll. De Mniszech."	F	NHM
HDCU056	P052	<i>Anchastus digitatus</i> LeConte	[partly handwritten, dates ambiguous] "Emery Un. Field/ Sta. Newton, Ga./ Baker Co. Light/ V-7-14 1952"; [partly handwritten] "Anchastus/ digitatus (LeC.)/ Det.Becker 1975"	F	CNCI
HDCU057	P053	<i>Craspedostethus rufiventris</i> (Schwarz)	"Kamerun/ Conradt"; "Coll. Kraatz"	M	DEIC
HDCU058	P054	<i>Craspedostethus rufiventris</i> (Schwarz)	"Kamerun/ Conradt"; "Coll. Kraatz"	M	DEIC

Unicode	Photo	Genus Species Author	Labels (checked)	Sex	Dep.
HDCU060	P056	<i>Phorocardius florentini</i> Fleutiaux	"Tonkin/ Florentin"; "MUSÉUM PARIS/ Coll. E. FLEUTIAUX"	M	MNHN
HDCU061	P057	<i>Phorocardius florentini</i> Fleutiaux	"Tonkin/ Florentin"; "MUSÉUM PARIS/ Coll. E. FLEUTIAUX". Abdomen on sepearte glass slide HD-04.	F	MNHN
HDCU062	P058	<i>Globothorax Chevrolati</i> Fleutiaux	"261"; [handwritten] "Brésil"; "Collection Chevrolat". Abdomen on separate glass slide labeled HD-05.	F	MNHN
HDCU063	P059	<i>Cardiophorus (Perinellus)</i> <i>angustatus</i> Fleutiaux	"MAHATSINJO/ près Tananarive"	M	MNHN
HDCU064	P060	<i>Cardiophorus (Perinellus)</i> <i>angustatus</i> Fleutiaux	"MAHATSINJO/ près Tananarive"	M	MNHN
HDCU065	P061	<i>Teslasena femoralis</i> Fleutiaux	"MUSEUM PARIS/ GOYAZ à CUYUBA/ DE CASTELNAU 6-47"; [white disc, handwritten] "6/47"; [partly handwritten] "Teslasena/ FLEUTIAUX det."	M	MNHN
HDCU066	P062	<i>Physodactylus henningi</i> Fischer	[handwritten] "de Contendas"; [handwritten] "clavipes barty"; [handwritten] "clavipes pesty/ Brésil"; [handwritten] "Drepanius/ Pesty"; [partly handwritten] "Physodactylus/ Henningi/ Fischer/ 1940 FLEUTIAUX det."	M	MNHN
HDCU067	P063	<i>Tropidiplus tellinii</i> Fleutiaux	[handwritten] "Bir Donan/ 20.X.49"; [partly handwritten] "Tropidiplus/ tellini Fleut/ C.M.F.von Hayek det/ 1965". Abdomen on separate glass slide labeled HD-06.	F	MNHN
HDCU068	P064	<i>Platynychus mixtus</i> Fleutiaux	"MUSEUM PARIS/ HAUT - TONKIN/ CAO BANG/ CHRISSEMENT VILLAIN/ 1925"/ [partly handwritten] "mixtus fleut./ FLEUTIAUX det."; paraplathynychus/ C.M.F. von Hayek/ det. 1965". Abdomen on separate glass slide labeled HD-07.	F	MNHN
HDCU069	P065	<i>Platynychus mixtus</i> Fleutiaux	"Hué"; [handwritten] "Fl 200 mx"	M	MNHN
HDCU070	P066	<i>Platynychus mixtus</i> Fleutiaux	"Hué"; [handwritten]	M	MNHN
HDCU071	P067	<i>Odontocardus vitalisi</i> Fleutiaux	[partly handwritten] "MUSEUM PARIS/ Laos/ ou Cambodge/ Bonette 1911"	M	MNHN

Unicode	Photo	Genus Species Author	Labels (checked)	Sex	Dep.
HDCU072	P068	<i>Odontocardus vitalisi</i> Fleutiaux	[partly handwritten] "MUSEUM PARIS/ Laos/ ou Cambodge/ Bonette 1911"/ [partly handwritten] "Cardiotarsus/ Vitalisi/ Fleut./ FLEUTIAUX det."; [handwritten] " Laos ou Cambodge/ Bonnotte/ 1911. Abdomen on separate glass slide labeled HD-08.	F	MNHN
HDCU073	P069	<i>Athous argentatus</i> Perrin	[♂]; [handwritten] "Jerusalem/ D David"; "MUSEUM PARIS/ Collection Léon Fairmaire/ 1906"	M	MNHN
HDCU074	P070	<i>Hemiops flava</i> Laporte	"Nilgiri Hills/ S.India V. 1961/ P.S. Nathan"	M	CNCI
HDCU075	P071	<i>Hemiops flava</i> Laporte	"NEPAL nr Simra/ Adhabhar 600 ft./ 27 Aug. 1967, Can, Nepal Exped."; [partly handwritten] "Hemiops/ flava/ Det H Ohira 1971/ E.C. Becker"	M	CNCI
HDCU076	P072	<i>Agrypnus murinus</i> Lin.	[Partly handwritten] "Suisse-Lausanne/ Vidy/ 6 VI 42/ J. Aubert"	M	CNCI
HDCU077	P073	<i>Agrypnus murinus</i> Lin.	"France, Landes/ Parentis/ VI. 1977/ Vuillaume"	F	CNCI
HDCU078	P074	<i>Cebrio gigas</i> Fabricius	"Aix-Provence"; "Collectio/ M. Fassati"; [partly handwritten] "Cebrio gigas/ Det. M. Fassati 1956"	M	CNCI
HDCU079	P075	<i>Semiotus furcatus</i> (Fabricius)	"BRAZIL, Amazonas/ Estirao do Ecuador/ (Rio Jaurai)X.1979/ M.Alvarenga"	F	CNCI
HDCU080	P076	<i>Semiotus furcatus</i> (Fabricius)	"BRAZIL, Amazonas/ Estirao do Ecuador/ (Rio Jaurai)X.1979/ M.Alvarenga"	F	CNCI
HDCU081	P077	<i>Pityobius anguinus</i> LeConte	"CANADA: QUEBEC/ (Deux-Montagnes) Parc/ Paul-Sauvé 26.VI.1990/ Serge Laplante"; Pityobius/ anguinus/ LeConte/ Det. S. Laplante'90"	M	CNCI
HDCU082	P078	<i>Pityobius anguinus</i> LeConte	"Fredrickton, N.B./ VII.13.1928/ W.J. Brown"	F	CNCI
HDCU083	P079	<i>Semiotus furcatus</i> (Fabricius)	"PERU-MADRE de DIOS/ Manu Res. Zone/ Pakitza B.S. 320 m/ 11°56.7'S, 71°17.0'W/ D. Brzoska 16-X-2000"	M	HBDC
HDCU084	P080	<i>Prosternon tessellatum</i> (Lin.)	"ENGLAND, London,/ Richmond Park, 7VI04/ HDouglas"	M	HBDC
HDCU085	P081	<i>Prosternon tessellatum</i> (Lin.)	"ENGLAND, London,/ Richmond Park, 7VI04/ HDouglas"	F	HBDC

Unicode	Photo	Genus Species Author	Labels (checked)	Sex	Dep.
HDCU086	P082	<i>Tetralobus flabellicornis</i> (Lin.)	"Nanga Eboko/ Cameroun Afr./ Dr.Lenczy 1959"	F	CNCI
HDCU087	P083	<i>Tetralobus flabellicornis</i> (Lin.)	"Ibdan, NIGERIA/ 1.XII.1961/ D.C. Eidt"	M	CNCI
HDCU088	P084	<i>Hemiops flava</i> Laporte	"NEPAL nr Simra/ Adhabhar 600 ft./ 27 Aug. 1967, Can, Nepal Exped."; [partly handwritten] "Hemiops/ flava/ Det H Ohira 1971/ E.C. Becker"	M	CNCI
HDCU089	P085	<i>Lissomus bicolor</i> Chevrolat	"NICARAGUA: GrenadaDept./ Volcan Mombacho Res. Nat./ N11°50' W85°58.8', 1150m-/ MV and UV lights, research stn. 3.VI.02, H.Douglas"	F	HBDC
HDCU091	P087	<i>Lissomus bicolor</i> Chevrolat	"NICARAGUA: GrenadaDept./ Volcan Mombacho Res. Nat./ N11°50' W85°58.8', 1150m-/ 850m forest beating/ 3.VI.02, H.Douglas"	F	HBDC
HDCU092	P088	<i>Lissomus bicolor</i> Chevrolat	"HONDURAS: Yoro/ PN Pico Pijol, 1300/ N15°09.4' W 87°37.6'/ 11.V.02, forest beating/ H.Douglas"	F	HBDC
HDCU096	P092	<i>Eudicronychus</i> sp.	"Chimala,1400m./ 58mi.E. of Mbeya/ TANGANYIKA"	M	CNCI
HDCU097	P093	<i>Eudicronychus</i> sp.	"Chimala,1400m./ 58mi.E. of Mbeya/ TANGANYIKA"	M	CNCI
HDCU098	P094	<i>Eudicronychus</i> sp.	"Chimala,1400m./ 58mi.E. of Mbeya/ TANGANYIKA"	M	CNCI
HDCU107	P103	<i>Lissomus bicolor</i> Chevrolat	"MEX., Dos Amates/ V.C.,VI-16-17-1969?,D.Bright/ &J.M.Campbell"; [handwritten] "L. bicolor/ Det. Cobos '72"	M	CNCI
HDCU108	P104	<i>Athous vittatus</i> (Fabricius)	[partly handwritten] "CZECHOSLOVAKIA/ Mor. Bor. 24.v.1963/ Moravicany/ leg.V.Korbel"	M	CNCI
HDCU109	P105	<i>Athous vittatus</i> (Fabricius)	[partly handwritten] "CZECHOSLOVAKIA/ Mor. Bor. 24.v.1963/ Moravicany/ leg.V.Korbel"	M	CNCI
HDCU110	P106	<i>Athous vittatus</i> (Fabricius)	[partly handwritten] "CZECHOSLOVAKIA/ Mor. Bor. 24.v.1963/ Moravicany/ leg.V.Korbel"	F	CNCI
HDCU111	P107	<i>Athous vittatus</i> (Fabricius)	[partly handwritten] "CZECHOSLOVAKIA/ Mor. Bor. 24.v.1963/ Moravicany/ leg.V.Korbel"	F	CNCI

Unicode	Photo	Genus Species	Author	Labels (checked)	Sex	Dep.
HDCU112	P108	<i>Dima elateroides</i>	Charpentier	[handwritten] "Hung."; "Kiesenwetter"; "Sammlung/ CI. Müller"	M	CNCI
HDCU113	P109	<i>Dima elateroides</i>	Charpentier	"Hung."; [handwritten] "Moïrkel."; "Sammlung/ CI Müller"; [handwritten] "Dima/ elateroides Charp."	M	CNCI
HDCU114	P110	<i>Pyrophorus notilucus</i> (Linneus)		"PERU, Huallaga/ Aquaytin,400m./ IX-1961"; [partly handwritten] "Pyrophorus/ notilucus/ L, 1758/ C. Costa det. 1969"	M	CNCI
HDCU115	P111	<i>Pyrophorus notilucus</i> (Linneus)		"PERU, Huallaga/ Aquaytin,400m./ IX-1961"; [partly handwritten] "Pyrophorus/ notilucus/ L, 1758/ C. Costa det. 1969"	M	CNCI
HDCU116	P112	<i>Pyrophorus notilucus</i> (Linneus)		"PERU, Huallaga/ Aquaytin,400m./ IX-1961"; [partly handwritten] "Pyrophorus/ notilucus/ L, 1758/ C. Costa det. 1969"	M	CNCI
HDCU117	P113	<i>Pyrophorus notilucus</i> (Linneus)		"PERU, Huallaga/ Aquaytin,400m./ IX-1961"; [partly handwritten] "Pyrophorus/ notilucus/ L, 1758/ C. Costa det. 1969"	M	CNCI
HDCU118	P114	<i>Pyrophorus notilucus</i> (Linneus)		"PERU, Huallaga/ Aquaytin,400m./ IX-1961"; [partly handwritten] "Pyrophorus/ notilucus/ L, 1758/ C. Costa det. 1969"	M	CNCI
HDCU119	P115	<i>Pyrophorus notilucus</i> (Linneus)		"HONDURAS: Dept. Cortez/ PN CerroAzul-Meambar/ LosPinos, N14°52.4' 87°54.7'/ 800m, 10.V.02 on log, H. Douglas"	F	HBDC
HDCU120	P116	<i>Esthesopus parvus</i>	Horn	"AZ, Santa Cruz Co./ Peña Blanca Campgr./ 6 Aug 2002/ H. Douglas BL"	F	HBDC
HDCU121	P117	<i>Esthesopus parvus</i>	Horn	"AZ, Pima Co.,Green Valley, on tree bark, 860m, 5 AUG/ 2002 H.Douglas"	?	HBDC
HDCU122	P118	<i>Oestodes tenuicollis</i> "Randall"		[partly handwritten] "Whiteface Mt./ trail, N.Y./ VII-10-1914"; [handwritten] "E.Shoemaker/ collector"; "Shoemaker/ ion 1956"	M	USNM

Unicode	Photo	Genus Species Author	Labels (checked)	Sex	Dep.
HDCU123	P119	<i>Selenodon speratus</i> (Fall)	"OKLAHOMA: Latimer Co./ -VIII-83/ Karl Stephan"; "Selonodon speratus (Fall)/ det. K. Galley 1990"	M	CNCI
HDCU124	P120	<i>Selenodon speratus</i> (Fall)	"OKLAHOMA: Latimer Co./ July 1982/ K. Stephan"; "Selonodon speratus (Fall)/ det. K. Galley 1990"	M	CNCI
HDCU125	P121	<i>Selenodon speratus</i> (Fall)	"OKLAHOMA: Latimer Co./ 5MI. W. Red Oak/ VII-80/ Karl H. Stephan"; [partly handwritten] "Selonodon/ speratus ? (Fall)/ det. K. Stephan 1986"	F	CNCI
HDCU127	P123	<i>Oestodes tenuicollis</i> Randall	"Shoemaker/ tion 1956"; [orange disk without writing]; [white disk] "c."; [partly handwritten] "Whiteface Mt./ trail, N. Y./ VII-9-1914"; [handwritten] "8850"; [partly handwritten] "Genitalia prep./ E-1955 ♀/ A.Calder 1991"	F	USNM
HDCU128	P124	<i>Oestodes tenuicollis</i> Randall	[partly handwritten] "Wilmington N.Y./ VII-4-1914/ E.Shoemaker"; "Shoemaker/ tion 1956"; [partly handwritten] "Genitalia prep./ E-1696 ♀/ A.A.Calder 1987"	F	USNM
HDCU129	P125	<i>Oxyntopterus strachani</i> Hope	"Le-2"; [partly handwritten] "Ile-Ife, Nigeria/ 13 Mar 1970/ Col. J.T.Medler"; "Oxyntopterus/ strachani Hope/ dét. L. Laurent"	M	CNCI
HDCU130	P126	<i>Oxyntopterus strachani</i> Hope	[handwritten] "Legon, Ghana/ III.2.1971/ R.Taylor"	F	CNCI
HDCU131	P127	<i>Anelastes druryi</i> Kirby	[partly handwritten] "La Laja/ Chih. Mex./ July 16, 1960"/ Anelastes/ druryi Kby./ E.C. Becker 1962"; with abdomen on card; genitalia in microvial	M	CNCI
HDCU132	P128	<i>Anelastes druryi</i> Kirby	[partly handwritten] "10 mi.W.El Salto,/ Dgo.MEX.VII.5/ 1964 H.F, Howden"	F	CNCI
HDCU133	P129	<i>Anelastes druryi</i> Kirby	"10 mi.W.El Salto,/ Dgo.MEXICO, 9000'/ June 20 -July 6, 1964/ J.E.H. Martin"	M	CNCI
HDCU134	P130	<i>Anelastes druryi</i> Kirby	[partly handwritten] "10 mi.W.El Salto,/ Dgo.MEX.VII.6/ 1964 H.F, Howden"	F	CNCI
HDCU135	P131	<i>Hypnoidus riparius</i> (Fabricius)	[partly handwritten] "Jilmeica/ Boh. 16.V.48/ A. Olexa"; [handwritten] "Hypnoidus/ riparius/ F./ Det. Olexa '73"	F	CNCI

Unicode	Photo	Genus Species Author	Labels (checked)	Sex	Dep.
HDCU136	P132	<i>Hypnoidus riparius</i> (Fabricius)	[partly handwritten] "Le Sancy/ P. Ole D./ 1.VII.72/ G. Minet"	F	CNCI
HDCU137	P133	<i>Hypnoidus riparius</i> (Fabricius)	[partly handwritten] "Le Sancy/ P. Ole D./ 1.VII.72/ G. Minet"	?	CNCI
HDCU138	P134	<i>Adrastus pallens</i> (Fabricius)	"Germany/ Holstein, Plön/ 26 . Vii. 1964/ G. G. E. Scudder"; [partly handwritten] "Adrastus/ pallens F. 1967/ Wellschmeid det."	M	CNCI
HDCU139	P135	<i>Adrastus pallens</i> (Fabricius)	[partly handwritten] "22.VII.1924 Finl./ Kuolemajärvi/ M.Ivaschinzeff"; [partly handwritten] "Adrastus ♀/ pallens Fabr./ Dr. Wellschmeid det. 1962"	F	CNCI
HDCU140	P136	<i>Promopelus elegans</i> Laurent	"Pt.St.johns,Cape/ Prov., S. Africa, XII.7-16, 1970/ H. & M. Townes"	M	CNCI
HDCU141	P137	<i>Anischia</i> sp.	"PANAMA: Darién, Cana/ Biological Station/ Serranía de Pirre, 1000 m/ 7°45'18"N,77°41'6"W/ 07 Jun 1996; J.Ashe./ R.Brooks PAN1AB96 095/ ex: fungusy log"; [label with barcode] "SM0042049/ KUNHM-ENT"; [partly handwritten] "Anishia/ sp./ Det.HDouglas 2005"	M	SEMC
HDCU142	P138	<i>Anisomerus sylvestris</i> Girard	"Ghana, Tafo/ IV-1968/ E.O. Boafo"	M	CNCI
HDCU143	P139	<i>Anisomerus sylvestris</i> Girard	"Ghana, Tafo/ May-Aug. 1966/ E.O. Boafo"	F	CNCI
HDCU144	P140	<i>Thylacosternus rubricollis</i> Bonvouloir	"COSTA RICA Guan. Pr./ 3-6 Km. NW Canas/ June 2, 7 1980/ La Pacifica J. Wappes"; [partly handwritten] "Thylacosternus/ ? Rufficollis/ Bonv./ Det./ E.C.Becker 1982"	F	CNCI
HDCU145	P141	<i>Cardiophorus gramineus</i> (Scopoli)	[handwritten partly illegible] "Cerva U _____"; [green square]; "BROOKLYN/ MUSEUM/ COLL. 1929"; USNM 2036286"	F	USNM
HDCU146	P142	<i>Aptopus agrestis</i> Erichson	"Faz.Aceiro/ Jatai, Goiás - Brasil/ X. 1962/ Exp.Dep.Zool."	M	MZSP
HDCU147	P143	<i>Aptopus agrestis</i> Erichson	"Faz.Aceiro/ Jatai, Goiás - Brasil/ X. 1962/ Exp.Dep.Zool."	M	MZSP

Unicode	Photo	Genus Species Author	Labels (checked)	Sex	Dep.
HDCU148	P144	<i>Cardiotarsus capensis</i> Candèze	"Winburg, OFS./ Aug.,1918./ C.W. Mally./ SN. 2543."; [partly handwritten] "ac.c.2450/ Ag Dp S Afr"; "NATIONAL COLL./ OF INSECTS/ Pretoria,S.Afr"	M	SANC
HDCU149	P145	<i>Cardiotarsus capensis</i> Candèze	"Winburg, OFS./ Aug.,1918./ C.W. Mally./ SN. 2543."; [partly handwritten] "ac.c.2450/ Ag Dp S Afr"; "NATIONAL COLL./ OF INSECTS/ Pretoria,S.Afr"	M	SANC
HDCU150	P146	<i>Cardiotarsus capensis</i> Candèze	"Winburg, OFS./ Aug.,1918./ C.W. Mally./ SN. 2543."; [partly handwritten] "ac.c.2450/ Ag Dp S Afr"; "NATIONAL COLL./ OF INSECTS/ Pretoria,S.Afr"	F	SANC
HDCU151	P147	<i>Triplonychus plagiatus</i> Erichson	[handwritten] "35935"; [handwritten] "Brasil/ Puru"; "Fry Coll./ 1905.100."; [handwritten] "35935=/ Brazil Para/ Higgins" [partly handwritten] "Triplonychus/ plagiatus/ Er. Det.Hdouglass 2005"	F	NHM
HDCU152	P148	<i>Triplonychus plagiatus</i> Erichson	"Coll./ Janson."; "Ega./ Amazons./ Bates." [partly handwritten] "Triplonychus/ plagiatus/ Er. Det.Hdouglass 2005"	M	NHM
HDCU153	P149	<i>Cardiophorus nigratissimus</i> Buysson	"Turkey-Gaziantep/ 18 km NW Kilis/ Kara Deresi river"; "m 420, 30.V.2002/ C.Giusto-S.Zoia"; "CARDIOPHORUS/ nigratissimus Buys./ det Platia 002"	M	HBDC
HDCU154	P150	<i>Cardiophorus nigratissimus</i> Buysson	"Turkey-Gaziantep/ 18 km NW Kilis/ Kara Deresi river"; "m 420, 30.V.2002/ C.Giusto-S.Zoia"; "CARDIOPHORUS/ nigratissimus Buys./ det Platia 002"	F	HBDC
HDCU155	P151	<i>Cardiophorus nigratissimus</i> Buysson	"Turkey-Gaziantep/ 18 km NW Kilis/ Kara Deresi river"; "m 420, 30.V.2002/ C.Giusto-S.Zoia"; "CARDIOPHORUS/ nigratissimus Buys./ det Platia 002"	M	HBDC
HDCU156	P152	<i>Cardiophorus nigratissimus</i> Buysson	"Turkey-Gaziantep/ 18 km NW Kilis/ Kara Deresi river"; "m 420, 30.V.2002/ C.Giusto-S.Zoia"; "CARDIOPHORUS/ nigratissimus Buys./ det Platia 002"	F	HBDC

Unicode	Photo	Genus Species Author	Labels (checked)	Sex	Dep.
HDCU157	P153	<i>Dicronychus cinereus</i> (Herbst)	[Italy, partly handwritten] "RAVENNA/ P. S. VITALE/ 16vi84/ LEG. CALLEGARI"; "DICRONYCHUS/ cinereus (Hbst.)/ det. Platia 002"	f	HBDC
HDCU158	P154	<i>Coptostethus brunneipennis</i> Wollaston	[Spain, handwritten] "IS. TENERIFE/ MASS. TENO/ Mt. DE L'AGUA/ 5.2.1991 m.800/ I. Gudenzi"; "COPTOSTETHUS/ brunneipennis Wol/ det. Platia 2002"	F	HBDC
HDCU159	P155	<i>Coptostethus brunneipennis</i> Wollaston	[Spain, handwritten] "IS. TENERIFE/ MASS. TENO/ Mt. DE L'AGUA/ 5.2.1991 m.200/ I. Gudenzi"; "COPTOSTETHUS/ brunneipennis Wol/ det. Platia 2002"	M	HBDC
HDCU160	P156	<i>Negastrius americanus</i> (Horn)	"USA, FL, St. Theresa,/ 7.V.2000, sifting sand &/ grass, sheltered beach,/ H.Douglas"	F	HBDC
HDCU161	P157	<i>Negastrius americanus</i> (Horn)	"USA, FL, St. Theresa,/ 7.V.2000, sifting sand &/ grass, sheltered beach,/ H.Douglas"	M	HBDC
HDCU162	P158	<i>Cardiophorus cardisce</i> (Say)	"Canada, ON, Lanark Co./ Almonte, on sand 16.V.04/ HDouglas, MLarivee"	M?	HBDC
HDCU163	P159	<i>Cardiophorus cardisce</i> (Say)	"Canada, QC, Co. Pontiac, Bristol Mines, 45°30' 00" N 76°21'00"W , 20.IV.03 SandDune/ Pit, on sand, 11 AM HDouglas, Mlarivee"	M	HBDC
HDCU164	P160	<i>Horistonotus simplex</i> LeConte	"AZ Santa Cruz Co./ Pena Blanca Campgr./ 6 Aug 2002/ H.Douglas BL"	F	HBDC
HDCU165	P161	<i>Esthesopus parvus</i> Horn	"AZ Santa Cruz Co./ Pena Blanca Campgr./ 6 Aug 2002/ H.Douglas BL"	F	HBDC
HDCU166	P162	<i>Esthesopus parvus</i> Horn	"AZ Santa Cruz Co./ Pena Blanca Campgr./ 6 Aug 2002/ H.Douglas BL"	M	HBDC
HDCU167	P163	<i>Cardiophorus togatus</i> Horn	"MEXICO:Nuevo Leon/ 37 km Linares, 1545 m/ 20 March 1991, Brooks/ Leschen. #29. Ex:beating"; [partly handwritten] "Cardiophorus/ togatus/ Horn/ Det.Hdouglas 2005". [Based on elevation this must be 37 km W of Linares]	M	SEMC

Unicode	Photo	Genus Species Author	Labels (checked)	Sex	Dep.
HDCU168	P164	<i>Cardiophorus luridipes</i> Candèze	"CALIFORNIA:/ Riverside Co./ 16 May 1924/ W. Benedict"	F	HBDC
HDCU169	P165	<i>Cardiophorus luridipes</i> Candèze	"CALIFORNIA:/ Riverside Co./ 16 May 1924/ W. Benedict"; [partly handwritten] "Cardiophorus/ luridipes/ Cand./ Det.Hdouglas 2003"	M	HBDC
HDCU170	P166	<i>Cardiophorus undescribed</i>	"Rep. Of Congo/ Voka/ V.1978 G. Onore"	F	HBDC
HDCU171	P167	<i>Cardiophorus convexulus</i> LeConte	[handwritten] "ON, Sandbanks/ PP. VI.16.2000/ Beating, H.Douglas"; "Cardiophorus/ convexulus LeC./ Det.Hdouglas 2002"	M	HBDC
HDCU172	P168	<i>Cardiophorus brevis</i> Champion	"Mex: Oaxaca/ 20 mi. W. Pinotepa/ Nacional/ VI.23.1983"	M	HBDC
HDCU173	P169	<i>Cardiophorus brevis</i> Champion	"Mex: Oaxaca/ 20 mi. W. Pinotepa/ Nacional/ VI.23.1983"	F	HBDC
HDCU174	P170	<i>Blaiseus transvaalensis</i> <i>sp.nov</i>	"Lydenburg dist./ Transvaal"; "Janson coll./ 1903-130."	M	HBDC
HDCU175	P171	<i>Blaiseus transvaalensis</i> <i>sp.nov</i>	[handwritten] "Ayres"; [handwritten] "P.B. Spei/ Transvaal"; "Fry Coll./ 1905-100"	M	HBDC
HDCU176	P172	<i>Cardiotarsus mjoberbi</i> Carter	"Australia, Qld. Mt./ Glorious 27°19' S/ 152°45' E, 1-5.XII.1997/ T. Hiller Malaise"	M	HBDC
HDCU177	P173	<i>Cardiotarsus mjoberbi</i> Carter	"Australia, Qld. Mt./ Glorious 27°19' S/ 152°45' E, 1-5.XII.1997/ T. Hiller Malaise"	F	HBDC
HDCU178	P174	<i>Paradonus pectoralis</i> (Say)	"USA, NY, Essex Co./ Crown Pt, splashing gravel beach under L. Champlain/ bridge,19.VII.03 Hdouglas"	F	HBDC
HDCU179	P175	<i>Paradonus pectoralis</i> (Say)	"USA, NY, Essex Co./ Crown Pt, splashing gravel beach under L. Champlain/ bridge,19.VII.03 Hdouglas"	M	HBDC
HDCU180	P176	<i>Paradonus pectoralis</i> (Say)	"Canada, ON, Carleton/ Crown Pt. 45°31'00"N-/ 76°08'00"W, 8.VI.03./ sand/ rock beach hand/ coll. J.Holland Leg."	F	HBDC

Unicode	Photo	Genus Species Author	Labels (checked)	Sex	Dep.
HDCU181	P177	<i>Neohypdonus gentilis</i> (LeConte)	"Saskatoon/ Saskatchewan/ VI-22-1974/ E.J.Kitely"	M	CNCI
HDCU182	P178	<i>Neohypdonus gentilis</i> (LeConte)	"Saskatoon/ Saskatchewan/ VI-22-1974/ E.J.Kitely"	F	CNCI
HDCU183	P179	<i>Migiwa curatus</i> (Candèze)	[partly handwritten] "Mt. Fuji. JAPAN/ 3.VIII.1964/ M. Suda leg."; [handwritten] "Negastris/ curatus/ [+7 japanese characters]"	M	CNCI
HDCU184	P180	<i>Migiwa curatus</i> (Candèze)	"Mt.Koya,Nara-ken/ Japan 17-VII-55/ S. Mizobe"	F	CNCI
HDCU185	P181	<i>Monadicus sp.</i>	"Argentina,Prov.Bs.As/ Bs.As., San Isidro/ 10-15.I.1982/ H & A Howden"	M	CNCI
HDCU186	P182	<i>Monadicus sp.</i>	"Argentina,Prov.Bs.As/ Bs.As., San Isidro/ 10-15.I.1982/ H & A Howden"	F	CNCI
HDCU187	P183	<i>Pronegastris humeralis</i> (Candèze)	"Mimune(Mie)/ 1955-VI.18-21/ H.Ôhira.Coll"	F	CNCI
HDCU188	P184	<i>Pronegastris humeralis</i> (Candèze)	"Mimune(Mie)/ 1955-VI.18-21/ H.Ôhira.Coll"; [handwritten] "Negastris/ (Pronegastris)/ humeralis/ Cand."	F	CNCI
HDCU189	P185	<i>Fleutiauxellus maritimus</i> (Candèze)	[partly handwritten] "Grünwald/ 23.5.49."; "München/ Bühlmann"; [handwritten] "Hypnoidus/ maritimus Cand."	M	CNCI
HDCU190	P186	<i>Fleutiauxellus maritimus</i> (Candèze)	"ЗАКАРПАТБЕ/ СКОДЬ/ ПЕС НА ГОРАХ/ vii. 1966r."; [partly handwritten] "Negastris/ maritimus (Cand.)/ W. Dolin det. 1969"	F	CNCI
HDCU191	P187	<i>Neoarhaphes americanus</i> (Champion)	"Paraiso CZ/ PanApr 22 11/ EASchwarz"	M	CNCI
HDCU192	P188	<i>Neoarhaphes americanus</i> (Champion)	"COSTA RICA. Punt./ 3 km N. Guacimal/ 800m 26.V.1979/ H & A Howden"	F	CNCI
HDCU193	P189	<i>Paracardiophorus subcruciatus</i> Carter	"Australia, Qld. Mt./ Glorious 27°19' S./ 152° 45' E, 1-5.XII.1997/ T. Hiller Malaise"	F	HBDC
HDCU194	P190	<i>Paracardiophorus humeralis</i> (Fairmaire and Germain)	[handwritten] "CACHAGUA/ W. Aconcagua/ 18-IX-1974/ Col.P.VIDAL"	F	HBDC

Unicode	Photo	Genus Species Author	Labels (checked)	Sex	Dep.
HDCU195	P191	<i>Yukoana carinicornis</i> (Lewis)	[handwritten] "Mt. Mikuni/ 14-V-1966/ K.Baba"; [partly handwritten] "Yukoana/ carinicornis/ (Lewis, 1894)/ H.Ôhira Det. 1969"	M	CNCI
HDCU196	P192	<i>Yukoana carinicornis</i> (Lewis)	[handwritten] "Kurokawa/ N. Echigo/ 21.-V, 1967/ K. Baba"; [handwritten] "Y. carinicornis/ Det. Ôhira 1967"	F	CNCI
HDCU197	P193	<i>Aulonothroscus punctatus</i> <i>Bonvouloir</i>	[partly handwritten] "LIMBOUR/ TOURAINE, QUÉ./ 17.vi 1974/ R Sexton, Touraine, Que"; "Ex/ Acer saccharum"	M	CNCI
HDCU198	P194	<i>Aulonothroscus punctatus</i> <i>Bonvouloir</i>	[partly handwritten] "LIMBOUR/ TOURAINE, QUÉ./ 27.vi 1974/ R Sexton, Touraine, Que"; "Ex/ Acer N./ sp."	F	CNCI
HDCU199	P195	<i>Macropogon piceus</i> LeConte	"Sault au Mouton/ Qué.21.VII.1981"	F	CNCI
HDCU200	P196	<i>Macropogon piceus</i> LeConte	"Que., Forestville/ 23 July 1971/ E.C. Becker"	F	CNCI
HDCU201	P197	<i>Macropogon piceus</i> LeConte	"Ste Rose Nord/ Qué.16.VII.1981"	M	CNCI
HDCU202	P198	<i>Macropogon piceus</i> LeConte	[handwritten] "Rigaud/ Quebec/ VII.23.1973/ E.J.Kitely"; [handwritten] "Eurypogon/ harrisii Melsh/ Det: 1974/ J.M. Campbell"; [handwritten] "Macropogon/ piceus Lec/ Det 82 C.Chantal"	M	CNCI
HDCU203	P199	<i>Cerophytum elateroides</i> (Latreille)	"Wien"; "♂"; [partly handwritten] "Cerophytum/ elateroides Latr./ det. W. Lucht"	M	CNCI
HDCU204	P200	<i>Cerophytum elateroides</i> (Latreille)	[handwritten] "bei Wien/ Austria"; [handwritten] "Kahlenberg/ A. I."; "♀"; [partly handwritten] "Cerophytum/ elateroides Latr./ det. W. Lucht"	F	CNCI
HDCU205	P201	<i>Eulichas sp.</i>	[partly handwritten] "Malaysia/ Ulu Gombak/ Kuala Lumpur/ Aug 21.1971/ R. E. Parrot"	M	CNCI
HDCU206	P202	<i>Eulichas sp.</i>	[partly handwritten] "Malaysia/ Cameron Highlands/ Tanah Rata/ March. 1977"	F	CNCI
HDCU207	P203	<i>Berninelsonius hyperboreus</i> (Gyllenhal)	"Y.T., British Mts./ "June Cr.", 320m/ 3km NW Firth R./ 69°13',140°05'/ J.M.Campbell"; "25.VI.1984/ 84-32, misc./ beetles ex/ around camp"	M	CNCI

Unicode	Photo	Genus Species Author	Labels (checked)	Sex	Dep.
HDCU208	P204	<i>Berninelsonius hyperboreus</i> (Gyllenhal)	"Y.T., British Mts./ "June Cr.", 320m/ 3km NW Firth R./ 69°13',140°05' J.M.Campbell"; "29.VI.1984/ 84-37, sifting/ Salix & Alnus/ litter"	F	CNCI
HDCU209	P205	<i>Onichodon orchesides</i> Newman	"St.Lawrence Isl./ Nat.Park,ONT./ McDonald Is."; [partly handwritten] "24.VII. 1976/ Reid/ Code 4201-0"; "Onichodon/ orchesides Newm/ J.Muona det. 5/ 96"	M	CNCI
HDCU210	P206	<i>Onichodon orchesides</i> Newman	[partly handwritten] "6 mi.W.Richmond,Ont/ 8.VI.1972/ J. E. H. Martin"; "on/ sugar maple"	F	CNCI
HDCU211	P207	<i>Heteroderes sordidus</i> LeConte	"AZ Cochise Co. Sierra/ Vista, Ramsay Canyon/ UV light 30Jul2002 H./ Douglas"	M	HBDC
HDCU212	P208	<i>Heteroderes sordidus</i> LeConte	"AZ Cochise Co. Sierra/ Vista, Ramsay Canyon/ UV light 30Jul2002 H./ Douglas"	F	HBDC
HDCU213	P209	<i>Heteroderes sordidus</i> LeConte	"AZ Cochise Co. 3 km w of/ Wilcox on SR 186 1280m/ Dunes UV light 28Jul2002/ H. Douglas"	F	HBDC
HDCU214	P210	<i>Thylacosternus vittatus</i> Champion	"Honduras, Sta.Bar./ 13km.SE.ElMochito/ July 31, 1977 CW&L/ O'Brien &Marshall"		CNCI
HDCU215	TQ	<i>Paracardiophorus humeralis</i> (Fairmaire and Germain)	[purple, partly handwritten] "Coll. R. I. Sc. N. B/ santiago/ ex. Coll. Mnizech"; "Collection/ E. Candèze"; "(Bitactus cdz.)/ Humeralis/ Frm./ Chili. C. mn"; [partly handwritten] "Cardiophorus humeralis Fairm./ dét. E. Candèze"; [partly handwritten] "Paraplatynychus/ C.M.F. von Hayek/ det. 1960"; [handwritten] "cardiophorus/ humeralis/ no6i5"	F	ISNB
HDCU222	P2B1	<i>Cardiotarsus</i> sp. (nr. <i>Philautus</i> Candèze 1860)	"Pietermaritzburg,/ Natal, S. Afr./ 23.XI.-5.XII.70/ H. & M. Townes"	F	CNCI
HDCU223	P2B2	<i>Cardiotarsus</i> sp. (nr. <i>Philautus</i> Candèze 1860)	"Pietermaritzburg,/ Natal, S. Afr./ 23.XI.-5.XII.70/ H. & M. Townes"	M	CNCI
HDCU224	P2B3	<i>Dicrepidius ramicornis</i> (Beavois)	"Bahamas.AndrosI.RedBays./ LewisCoppit.Shadrack/ Russel'sPlace.Jbrowne./ 17.VIII.1987.high/ interior coppice/ blk.lt. 87-207J"	M	CNCI

Unicode	Photo	Genus Species Author	Labels (checked)	Sex	Dep.
HDCU225	P2B4	<i>Dicrepidius ramicornis</i> (Beavois)	"Bahamas.AndrosI.RedBays./ LewisCoppit.Shadrack/ Russel'sPlace.Jbrowne./ 17.VIII.1987.high/ interior coppice/ blk.lt. 87-207J"	F	CNCI
HDCU226	P2B5	<i>Dicrepidius ramicornis</i> (Beavois)	"Bahamas.AndrosI.RedBays./ LewisCoppit.Shadrack/ Russel'sPlace.Jbrowne./ 17.VIII.1987.high/ interior coppice/ blk.lt. 87-207J"	F	CNCI
HDCU227	P2B6	<i>Agriotes sputator</i> (Linnaeus)	"Sydney, N.S./ VI-7-1965/ W.J.Brown"	F	CNCI
HDCU228	P2C1	<i>Agriotes sputator</i> (Linnaeus)	"North Sydney/ N.S. VI-19-1965/ W.J. Brown"	F	CNCI
HDCU229	P2C2	<i>Agriotes sputator</i> (Linnaeus)	"Sydney, N.S./ VI-7-1965/ W.J.Brown"	M	CNCI
HDCU230	P2C3	<i>Zorochros demustoides</i> (Herbst)	"ITALIA,Marche/ diut.Novafeltria/ 25.IV.1983,G.Platia/ cive F.Marecchia"	M	CNCI
HDCU231	P2C4	<i>Zorochros demustoides</i> (Herbst)	"ITALIA,Marche/ diut.Novafeltria/ 25.IV.1983,G.Platia/ cive F.Marecchia"	F	CNCI
HDCU232	P2C5	<i>Ampedus sanguineus</i> (Fabricius)	"Fennia"; [nearly illegible] "Lempaula/ M. Pohiola"	F	CNCI
HDCU233	P2C6	<i>Ampedus sanguineus</i> (Fabricius)	"LAZIO:CADICOTTA/ 1-II-'59/ leg. A. Parenti" on own pin.	M	CNCI
HDCU234	P2D1	<i>Tropihypnus bimargo</i> (Reitter)	"Ферг. хр. у перева-/ ла Калдама 2000 м/ Заславскій"; [handwritten Russian label]; "Middle Asia/ Fezganski Mount."; "Tropihypnus bi-/ margo Rtt./ Gurjeva det."	F	CNCI
HDCU235	P2D2	<i>Tropihypnus bimargo</i> (Reitter)	"Ферг. хр. у перева-/ ла Калдама 2000 м/ Заславскій"; "Tropihypnus bimar-/ go Rtt./ Gurjeva det."	M	CNCI
HDCU236	P7A1	<i>Aptopus pullatus</i> (Horn)	"AZ, Pima Co. Bog/ Springs Campground/ 1500m, 3 Aug 2002/ H.Douglas BL"	M	HBDC

Unicode	Photo	Genus Species Author	Labels (checked)	Sex	Dep.
HDCU237	P7A2	<i>Aptopus pullatus</i> (Horn)	"AZ, Pima Co. Bog/ Springs Campground/ 1500m, 3 Aug 2002/ H.Douglas BL"	M	HBDC
HDCU238	P7A3	<i>Aptopus pullatus</i> (Horn)	"AZ, Pima Co. Bog/ Springs Campground/ 1500m, 3 Aug 2002/ H.Douglas BL"	M	HBDC
HDCU239	P7A4	<i>Horistonotus simplex</i> LeConte	"AZ Santa Cruz Co./ Pena Blanca Campgr./ 6 Aug 2002/ H.Douglas BL"	F	HBDC
HDCU240	P7A5	<i>Horistonotus simplex</i> LeConte	"AZ Santa Cruz Co./ Pena Blanca Campgr./ 6 Aug 2002/ H.Douglas BL"	M	HBDC
HDCU241	P7A6	<i>Horistonotus simplex</i> LeConte	"AZ Santa Cruz Co./ Pena Blanca Campgr./ 6 Aug 2002/ H.Douglas BL"	M	HBDC
HDCU242	P7B1	<i>Horistonotus simplex</i> LeConte	"AZ Santa Cruz Co./ Pena Blanca Campgr./ 6 Aug 2002/ H.Douglas BL"	F	HBDC
HDCU243	P7B2	<i>Esthesopus parvus</i> Horn	"AZ Santa Cruz Co./ Pena Blanca Campgr./ 6 Aug 2002/ H.Douglas BL"	M	HBDC
HDCU244	P7B3	<i>Esthesopus parvus</i> Horn	"AZ Santa Cruz Co./ Pena Blanca Campgr./ 6 Aug 2002/ H.Douglas BL"	F	HBDC
HDCU245	P7B4	<i>Esthesopus parvus</i> Horn	"AZ Santa Cruz Co./ Pena Blanca Campgr./ 6 Aug 2002/ H.Douglas BL"	M	HBDC
HDCU246	P7B5	<i>Esthesopus parvus</i> Horn	"AZ Santa Cruz Co./ Pena Blanca Campgr./ 6 Aug 2002/ H.Douglas BL"	F	HBDC
HDCU259	PBA1	<i>Cardiophorus convexus</i> (Say)	"USA, FL, Clay Co. SR #21, 10kmNW Keystone Hts., scrub beating 21.V.00 H.Douglas"	M	HBDC
HDCU260	PBA2	<i>Cardiophorus convexus</i> (Say)	"USA, FL, Clay Co. SR #21, 10kmNW Keystone Hts., scrub beating 21.V.00 H.Douglas"	M	HBDC
HDCU261	PBA3	<i>Cardiophorus convexus</i> (Say)	"USA, FL, Clay Co. SR #21, 10kmNW Keystone Hts., scrub beating 21.V.00 H.Douglas"	F	HBDC
HDCU262	PBA4	<i>Cardiophorus convexus</i> (Say)	"USA, FL, Clay Co. SR #21, 10kmNW Keystone Hts., scrub beating 21.V.00 H.Douglas"	F	HBDC

Unicode	Photo	Genus Species Author	Labels (checked)	Sex	Dep.
HDCU263	PBA5	<i>Paracardiophorus subcruciatus</i> Carter	"Australia, Qld. Mt./ Glorious 27°19' S,/ 152° 45' E, 1-5.XII.1997/ T. Hiller Malaise"	M	HBDC
HDCU264	PBA6	<i>Paracardiophorus subcruciatus</i> Carter	"Australia, Qld. Mt./ Glorious 27°19' S,/ 152° 45' E, 1-5.XII.1997/ T. Hiller Malaise"	F	HBDC
HDCU265	PBB1	<i>Cardiophorus gramineus</i> (Scopoli)	"CZECHOSLOVAKIA, Bohemia/ MOCHOV 14.9.1988/ J.Mertlik leg."; "CARDIOPHORUS/ gramineus/ (Scopoli , 1763)/ J. MERTLIK det. 2003"	M	HBDC
HDCU266	PBB2	<i>Dicronychus cinereus</i> (Herbst)	[Italy] "PIAMONTE (CN)/ Vinadio, m 1000/ 27.V.01 DeGiovanni"; "DICRONYCHUS/ cinereus (Hbst.)/ det. Platia 002"	M	HBDC
HDCU267	PBB3	<i>Paracardiophorus musculus</i> (Erichson)	"CZ-Bohemia bor.(5454)/ Dosky env./ 17.5.1997/ JOSEF MERTLIK LGT."; "Paracardiophorus musculus Er. 1840 (J. Mertlik det.)"	F	HBDC
HDCU268	PBB4	<i>Paracardiophorus musculus</i> (Erichson)	"CZ-Bohemia bor.(5454)/ Dosky env./ 17.5.1997/ JOSEF MERTLIK LGT."; "Paracardiophorus musculus Er. 1840 (J. Mertlik det.)"	M	HBDC
HDCU274	PBC4	<i>Cardiophorus holosericeus?</i> Candèze	"Rep. Of Congo/ Voka/ V.1978 G. Onore"	M	HBDC
HDCU275	PBC5	<i>Cardiophorus holosericeus?</i> Candèze	"Rep. Of Congo/ Voka/ V.1978 G. Onore"	F	HBDC
HDCU278	PBD2	<i>Paracardiophorus humeralis</i> (Fairmaire and Germain)	[Chile] "EL MANZANO/ CORD.SANTIAGO/ 11-SEPT.-1988"	M	HBDC
HDCU279	PBD3	<i>Paracardiophorus humeralis</i> (Fairmaire and Germain)	[Chile] "EL MANZANO/ CORD.SANTIAGO/ 11-SEPT.-1988"	F	HBDC
HDCU280	PBD4	<i>Paracardiophorus subcruciatus</i> Carter	"Australia, Qld. Mt. Glorious 27°19' S, 152° 45' E, 1-5.XII.1997, malaise, T. Hiller"	F	HBDC
HDCU281	PBD5	<i>Paracardiophorus subcruciatus</i> Carter	"Australia, Qld. Mt. Glorious 27°19' S, 152° 45' E, 1-5.XII.1997, malaise, T. Hiller"	F	HBDC

Unicode	Photo	Genus Species Author	Labels (checked)	Sex	Dep.
		<i>Cardiophorus gramineus</i>			
HDCU282	PBD6	(Scopoli)	"München/ H Kulzer"; "Schleissheim/ 9.6.04."	F	HBDC
HDCU283	P5 A2	<i>Cardiophorus cardisce</i> (Say)	Canada, ON, Prince Edward Co., 1-Jun-19, Brimley Leg.	F	CUIC
HDCU284	P5 A3	<i>Cardiophorus cardisce</i> (Say)	USA, FL, Daytona, iii.15', ED Ball Leg.	F	FMNH
HDCU285	P6 A5	<i>Cardiophorus cardisce</i> (Say)	USA, FL, Marineland, 5-Apr-41, LW Clausen Leg.	M	AMNH
HDCU286	P2 A12	<i>Cardiophorus cardisce</i> (Say)	USA, NY, Long Island, Riverhead, 2-Aug-35, R Latham Leg.	M	CUIC
HDCU287	P2 B1	<i>Cardiophorus cardisce</i> (Say)	USA, KS, Clay Co., 20-Apr-14, Blaisdell Leg.	M	CASC
HDCU288	P2 C6	<i>Cardiophorus cardisce</i> (Say)	USA, GA, Tybee Is, iv.20, RW Wenzel Leg.	M	CASC
		<i>Cardiophorus convexulus</i>			
HDCU289	P4 C6	LeConte	USA, NH, Mt. Plst., July', A Fenyes Leg.	F	CASC
		<i>Cardiophorus convexulus</i>			
HDCU290	P1 H1	LeConte	USA, MI, Oakland Co., 14-Jun-07, AW Andrews Leg.	F	MSUC
		<i>Cardiophorus convexulus</i>			
HDCU291	P1 H2	LeConte	USA, OH, Hocking Co., 19-May-53, D & J Knull Leg.	M	FMNH
HDCU292	P1 A5	<i>Cardiophorus convexus</i> (Say)	Canada, ON, Pt. Pelee, 27-Jun-79, KL Bailey Leg.	M	DEBU
			USA, FL, Putnam Co., Ravine Gardens S.P., 18-Mar-89, C & S Staines Leg.	M	FSCA
HDCU293	P1 C10	<i>Cardiophorus convexus</i> (Say)	"USA, NC, Dare Co. Kill/ Devil Hills 24.V.00/ beating on/by dunes/ H.Douglas"	M	HBDC
HDCU294	P3 B6	<i>Cardiophorus convexus</i> (Say)	Canada, ON, Sandbanks Provincial Park, 16-Jun-00, H Douglas Leg.	F	HBDC
HDCU295	P4 A3	<i>Cardiophorus convexus</i> (Say)	USA, FL, Tarpon Sprs, 16-May-43, B Malkin Leg.	F	AMNH
HDCU296	P5 D1	<i>Cardiophorus convexus</i> (Say)	USA, TX, Caldwell Co., Ca. 5 Mi. E. McMahan, 3-Jun-84, E Riley Leg.	F	TAMU
HDCU297	P1 F4	<i>Cardiophorus convexus</i> (Say)	USA, NE, Sioux Co., Monroe Canyon, 27-Jun-11, FH Shoemaker Leg.	F	CASC
HDCU298	P1 F6	<i>Cardiophorus convexus</i> (Say)			
HDCU299	P5 B2	<i>Cardiophorus togatus</i> Horn	USA, TX, Llano Co., 13-Apr-63, D & J Knull Leg.	F	CNCI

Appendix 6. Label data from type specimens of species coded for phylogenetic analyses.

Details on use and identification in Appendix 3. Kind = kind of type specimen (A = allotype; H = holotype; L = lectotype; N = neotype; P = paratype; PL = paralectotype; S = syntype; T = type of unknown kind); Dep. = specimen depository. Type numbers are part of a larger list, and not all consecutive.

Kind	Type #	Species	Label	Sex	Dep.
H	T001	<i>Cardiodontulus brandti</i> Van Zwaluwenburg	"NEW GUINEA: PAPUA/ Kiunga, Fly River/ IX-10-17-1957"; "Wm. W. Brandt/ Collector"; "♂"; [red] "Holotype"; "Cardiodontulus/ brandti/ ♂/ Van Zwal./ Holotype/ No."; [pink] "HT - 6047/ BISHOP MUSEUM"	M	BPBM
P	T002	<i>Cardiodontulus brandti</i> Van Zwaluwenburg	[genitalia in microvial, and left wing and urosternites 3-7 mounted on a card] "NEW GUINEA: PAPUA/ Kiunga, Fly River/ IX-10-17-1957"; "Wm. W. Brandt/ Collector"; "♂"; [yellow] "Paratype"; "Cardiodontulus/ brandti/ ♂/ Van Zwal."	M	BPBM
L	T003	<i>Exoeolus rufescens</i> Broun	[circular with blue margin] "SYN/ TYPE"; [handwritten] "2013"; [handwritten] "♀"; "Dunedin"; "New Zealand/ Broun Coll./ Brit. Mus./ 1922-482."; [handwritten] "exaeolus rufescens"; "LECTOTYPE/ Exoeolus/ rufescens/ Broun desig./ Douglas 2004"; [with genitalia in microvial attached to pin]	F	NHM
PL	T004	<i>Exoeolus rufescens</i> Broun	[circular with blue margin] "SYN/ TYPE"; [handwritten] "2013"; [handwritten] "♀"; "Dunedin"; "New Zealand/ Broun Coll./ Brit. Mus./ 1922-482."	F	NHM

Kind	Type #	Species	Label	Sex	Dep.
T	T005	<i>Cardiophorus inflatus</i> Candèze	[handwritten] "Mantchouria"; "Collection/ E. Candèze"; [handwritten] "n.sp./ inflatus/ Cdz/ Mandchuria"; [partly handwritten] "Cardiophorus/ inflatus cd./ dét. E. Candèze"; "♀"; [partly handwritten] "Holotype. C. inflatus/ C.M.F.von Hayek.Cand/ det.,1957"; [red] "Holotype"; [with ♀ genitalia on slide on pin]	F	ISNB
H	T008	<i>Agrypnella eburnea</i> Champion	[circular with red margin] "TYPE"; [handwritten] "Santarem"; "Coll./ Janson"; "Janson coll./ 1903-130."; [handwritten] "agrypnella/ eburnea, Ch./ type"	M	NHM
S	T009	<i>Cardiophorus mirabilis</i> Candèze	[circular with blue margin] "SYN/ TYPE"; [handwritten] "Cardiophorus/ mirabilis/ Inde or. Cdz"	?	NHM
L	T010	<i>Triplonychus trivittatus</i> Champion	Left hand specimen on card labeled: [disk with blue border] "SYN_/ TYPE"; "Tolé,/ Panama./ Champion."; "♂"; [partly handwritten] "B.C.A.Coll.III[1]./ Triplonychus/ trivittatus/ Ch."; [red label, partly handwritten] "LECTOTYPE Spcm on/ left/ Triplonychus/ trivittatus/ Champion/ desig. P.J. Johnson 2001"	M	NHM
PL	T011	<i>Triplonychus trivittatus</i> Champion	Right hand specimen [formerly left] on card labeled: [disk with blue border] "SYN_/ TYPE"; [disk with red border] "TYPE"; "Bugaba/ 800-1500 ft./ Champion"; "♂"; [partly handwritten] "B.C.A.Coll.III[1]./ Triplonychus/ trivittatus/ Ch."	M	NHM
S	T012	<i>Elater thoracicus</i> Fabricius	Pin unlabeled, in box with card: "Elater thoracicus F./ 2 syntypes/ UNIVERSITES/ ZOOLOGISKE MUSEUM/ UNIVERSITETSPARKEN 15/ DK-2100 KØBENHAVN Ø"	?	ZMUC
S	T013	<i>Elater thoracicus</i> Fabricius	Pin unlabeled, in box with card: "Elater thoracicus F./ 2 syntypes/ UNIVERSITES/ ZOOLOGISKE MUSEUM/ UNIVERSITETSPARKEN 15/ DK-2100 KØBENHAVN Ø"	?	ZMUC
S	T014	<i>Elater testaceus</i> Fabricius	Pin unlabeled, in box with card: "Elater testaceus F./ Holotype/ UNIVERSITES/ ZOOLOGISKE MUSEUM/ UNIVERSITETSPARKEN 15/ DK-2100 KØBENHAVN Ø"	?	ZMUC

Kind	Type #	Species	Label	Sex	Dep.
T	T015	<i>Elater erythrocephalus</i> Fabricius	[green square without writing]; [red] "TYPE"; [handwritten] "Essequibo./ Smidt/ Mus.J.Lund/ Elater/ erythrocephalus. Fabr."; [red, handwritten] "Lectotype ♂"	M	ZMUC
T	T016	<i>Oedostethus femoralis</i> LeConte	[green disc without writing]; [red label, partly handwritten] "Type/ 2461"; [handwritten] "Oedostethus/ femoralis/ Kansas. Lec."	M	MCZC
S	T017	<i>Eniconyx pullatus</i> Horn	"Ari"; [partly handwritten red] "LectoTYPE/ 3405"; [HW] "Eniconyx/ pullatus/ Horn"; [partly handwritten, red] "MCZ/ SynType/33774"	M	MCZC
S	T018	<i>Eniconyx pullatus</i> Horn	"Ari"; [partly handwritten blue] "PARA-TYPE/ 3405"	M	MCZC
T	T019	<i>Anchastus longulus</i> LeConte	"Enterprise/ May 8 Fla"; "1082"; [handwritten] "a. longulus/ Lec."; [red label, partly handwritten] "Type 2414"	F?	MCZC
H	T020	<i>Aphricus californicus</i> LeConte	[gold disc without writing]; [red] "Type./ 2623"; [handwritten] "Aphricus/ californicus/ S.D. Lec."	M	MCZC
S	T021	<i>Pityobius anguinus</i> LeConte	[red-black disc without writing]; [partly handwritten] "Type./ 2543"; [handwritten] "Pityobius/ anguinus/ Ga. Lec."; [aedeagus in microvial attached to pin and head]; [pronotum and pro and mesolegs in a separate glass vial]	M	MCZC
S	T022	<i>Pityobius anguinus</i> LeConte	[red-black disc without writing]; [handwritten] "anguinus 2"	F	MCZC
S	T023	<i>Pityobius anguinus</i> LeConte	[red-black disc without writing]; [handwritten] "anguinus 3"	M	MCZC
S	T024	<i>Lesnelater madagascariensis</i> Fleutiaux	"Madagascar; Ambohibeloma."; [handwritten] "Pachyelater/ madagascarensis/ ♂ presummé, type/ syn./ P. Lesne vid. 1906"; MUSÉUM PARIS/ 1952/ COLL A. OBERTHUR"	M	MNHN
S	T025	<i>Lesnelater madagascariensis</i> Fleutiaux	"Madagascar; Ambohibeloma."; [handwritten] "Pachyelater/ madagascarensis/ ♂ presummé, type/ syn./ P. Lesne vid. 06"; MUSÉUM PARIS/ 1952/ COLL A. OBERTHUR"	M	MNHN

Kind	Type #	Species	Label	Sex	Dep.
S	T026	<i>Pachyeleter madagascariensis</i> Lesne	"Madagascar; Ambohibeloma."; [handwritten] " Pachyelater/ madagascareinsis/ P. Lesne vid. 06"; MUSÉUM PARIS/ 1952/ COLL A. OBERTHUR"; [with 6 antennomeres attached mounted on card attached to pin]. Abdomen on card, genitalia on separate glass slide HD-01	F	MNHN
S	T027	<i>Pachyeleter madagascariensis</i> Lesne	"Madagascar; Ambohibeloma."; [handwritten] " Pachyelater/ madagascareinsis/ Lesne/ P. Lesne vid. 06"; MUSÉUM PARIS/ 1952/ COLL A. OBERTHUR". Abdomen on card, genitalia on separate glass slide HD-02	F	MNHN
P	T028	<i>Cardiophorellus gracilicornis</i> Cobos	"Odzala/ Congo/ Octobre"; "MUSÉUM PARIS/ MISSION/ A. DESCARPENTRIES/ ET. A. VILLIERS/ 1963-1964"; [red] "PARATYPUS/ A. COBOS"	M	MNHN
P	T029	<i>Cardiophorellus gracilicornis</i> Cobos	"Odzala/ Congo/ Octobre"; "MUSÉUM PARIS/ MISSION/ A. DESCARPENTRIES/ ET. A. VILLIERS/ 1963-1964"; [red] "PARATYPUS/ A. COBOS"	M	MNHN
H	T030	<i>Crioraphes rhodendorfi</i> Iablokoff-Khnzorian	[Partly handwritten] "Палеонтологический инст. АН СССР/ No 364/460/ Crioraphes/ rohdendorfi sp.n., gen.n./ Jablokov-Khnzorian S.M./ Местн./ Янтарное (Palmicken)/ Калинингр. Обл./ Колл. П. 3. Виноградов-Никитин"	?	PIN
H	T031	<i>Pseudocardiophorites fragilis</i> Dolin	[Partly handwritten] "Палеонтологический инст. АН СССР/ Pseudocardiophorites/ fragilis Dolin, 1976 No 2554/688/ голотип/ Мест. Каратау (Иухайловка)/ Возр. Уз (карабастауская свтма)/ Сборы 196 г./ Издание Вестник Зоологии АН УССР/ Год 1976 стр. 73, табл. 2 фиг., 4/ Автор В.Г. Долин рис. 1/5а-б"	?	PIN
H	T032	<i>Protocardiophorus ancestralis</i> Dolin	[Partly handwritten] "Палеонтологический инст. АН СССР/ Protocardiophorus/ ancestralis Dolin, 1976 No 2066/2571/ голотип/ Мест. Каратау (Иухайловка)/ Возр. Уз (карабастауская свтма)/ Сборы 196 г./ Издание Вестник Зоологии АН УССР/ Год 1976 стр. 73, табл. 2 фиг., 3/ Автор В.Г. Долин рис. 1/4а-б"	?	PIN

Kind	Type #	Species	Label	Sex	Dep.
T	T033	<i>Phorocardius solitarius</i> Fleutiaux	[handwritten] "Tonkin/ Zhan Moi/ Vitalis Juin ##"; [red] "TYPE"; "MUSÉUM PARIS/ Coll. E. FLEUTIAUX"; [partly handwritten] "Phorocardius/ solitarius/ Fleut. Type/ COLLECTION FLEUTIAUX"; [handwritten] "griffes très/ __lement bifides/4' art, targes/ tronqué/ carrément_". Body on card with abdomen, genitalia on seperate glass slide, HD-03.	F	MNHN
T	T034	<i>Blaiseus bedeli</i> Fleutiaux	"RÉG. DE LUC-NAM/ (TONKIN) L.BLAISE"; "MUSEUM PARIS/ (COLL. PH.FRANÇOIS)/ COLL. L. BEDEL 1922"; "TYPE"; [partly handwritten] "Blaiseus/ Bedeli Fleut./ type/ FLEUTIAUX det."	M	MNHN
T	T035	<i>Cardiophorus florentini</i> Fleutiaux	"Tonkin/ Florentin"; [red] "Type"; "MUSÉUM PARIS/ Coll. E. FLEUTIAUX"; [handwritten] "Cardiophorus/ Florentini/ Fleut. Type"; [partly handwritten] "Fleut., Ann./ Soc. Ent. Fr./ 1894. P. 687/ Collection FLEUTIAUX"; [partly handwritten] "C. Florentini/ Fleut. type/ Collection FLEUTIAUX"	?	MNHN
T	T036	<i>Aphricus chilensis</i> Fleutiaux	"TYPE"; [handwritten] "chili/ coll. Vienna"; [partly handwritten] "aphricus/ chilensis/ type/ COLLECTION FLEUTIAUX". Head and thorax in capsule on separate pin labeled: [handwritten] "found loose/ in box/ CHM. 3.81"	M	MNHN
T	T037	<i>Globothorax chevrolati</i> Fleutiaux	"Type"; "Collection Chevrolat"; [handwritten] "Globothorax/ chevrolati/ Fleut. type/ Bresil"; [partly handwritten] "Globothorax/ chevrolati/ Fleut. type/ Bresil/ Collection FLEUTIAUX"; [partly handwritten] "Fleut. E.R./ Soc. Ent. Belge/ 1891 p233/ Collection FLEUTIAUX"	F	MNHN
T	T038	<i>Cardiophorus (Perrinellus) angustatus</i> Fleutiaux	"MAHATSINJO/ près Tananarive"; [handwritten] "Mahatsinjo/ Près Beforona"; "Type"; [partly handwritten] "Cardiophorus/ s.g. Perrinellus/ angustatus/ type/ Collection FLEUTIAUX"	M	MNHN
T	T039	<i>Anelastes femoralis</i> Lucas	"MUSEUM PARIS/ GOYAZ À CUYUBA/ DE CASTELNAU 6-47"; [handwritten] "anelastes/ femoralis Lucas"; [handwritten] "type"; [partly handwritten] "type de/ Lucas/ FLEUTIAUX det."	M	MNHN

Kind	Type #	Species	Label	Sex	Dep.
S	T040	<i>Tropidiplus tellinii</i> Fleutiaux	[handwritten] "Cheren/ Eritrea XI"; [partly handwritten] "Syntype/ Tropidiplus/ telinii Fleut. 1903./ C.M.F.von Hayek det/ 1964"; [partly handwritten] "Tropidiplus/ telinii Fleut/ C.M.F.von Hayek det/ 1963"	M	MNHN
T	T041	<i>Platynychus indicus</i> Motschulsky	[handwritten] "Platynychus/ indicus/ Motsch./ Ind.or"; [handwritten] "Ind. Or."; [red rectangle]	F	ZMUM
T	T042	<i>Cardiotarsus vitalisi</i> Fleutiaux	[handwritten] "Pnom Penh/ Vitalis"; "Type"; [partly handwritten] "Cardiotarsus/ Vitalisi Fleut./ type/ Ann. Soc. Ent. Fr. 1918/ Collection FLEUTIAUX"; [with part of antennae on card]	?	MNHN
T	T043	<i>Athous argentatus</i> Abeille de Perrin	[handwritten] "Jaffa/ bic"; [handwritten] "athous/ argentatus/ ab."	M	MNHN
P	T044	<i>Patricia australica</i> Van Zwaluwenburg	"SirGraham/ MooreID/ Waustralia"; "20Feb1945/ Bmalkin"; "♂"; [partly handwritten] "Patricia australica/ ♂ Van. Z"; [yellow, partly handwritten] "PARATYPE/ CNC No. 13633"	M	CNCI
P	T045	<i>Buckelater argutus</i> Costa	[handwritten] "Barueri/ SP, Brasil/ 21.XI.1955/ K.Lenko col./ 7270". Wing on microslide labeled: [handwritten]: "Costa, 73"; [red, partly handwritten] "Buckelater/ argutus/ paratipo/ C Costa det 1973"	M	MZSP
P	T046	<i>Buckelater argutus</i> Costa	[handwritten] "Barueri/ SP, Brasil/ 21.XI.1955/ K.Lenko col./ 7270". Legs and antennae on microslide labeled: [handwritten]: "Costa, 73"; [red, partly handwritten] "Buckelater/ argutus/ paratipo/ C Costa det 1973"	M	MZSP
P	T047	<i>Buckelater argutus</i> Costa	Body in microvial, labelled: [partly handwritten] "K. Lenko-Leg."; [handwritten] "21.XI.1955/ Barueri/ S. Paolo/ 7270". Mouthparts and genitalia on 2 microslides labeled: [handwritten]: "Costa, 73"; [red partly handwritten] "Buckelater/ argutus/ paratipo/ C Costa det 1973"	M	MZSP
P	T048	<i>Buckelater argutus</i> Costa	[head thorax and abdomen on point]; [handwritten] "Ponta Grolla/ XII-1938/ Camargo col". Mouthparts and genitalia on microslides labeled: [handwritten]: "Costa, 73"; [red, partly handwritten] "Buckelater/ argutus/ paratipo/ C Costa det 1973"	M	MZSP

Kind	Type #	Species	Label	Sex	Dep.
P	T049	<i>Buckelater argutus</i> Costa	[point-mounted]; [handwritten] "Serra Caraça - 1380m/ MG - Brasil XI - 961/ Kloss,Lenko,/ Martins & Silva col."; [red, partly handwritten] "Buckelater/ argutus/ paratipo/ C Costa det 1973"	M	MZSP
T	T050	<i>Horistonotus flavidus</i> Candèze	[purple, partly handwritten] "Coll. R. I. Sc. N. B./ Bresil NOVO FRIBURGO"; "Collection/ E. Candèze"; [handwritten] "Flavidus/ N.Frib. cde"; [partly handwritten] "Horistonotus/ flavidus Cd./ dét. E. Candèze"	F	ISNB
T	T051	<i>Horistonotus flavidus</i> Candèze	[purple, partly handwritten] "Coll. R. I. Sc. N. B./ Bresil NOVO FRIBURGO"; "Collection/ E. Candèze"; [partly handwritten] "Horistonotus/ flavidus Cd./ dét. E. Candèze"	F	ISNB
H	T052	<i>Nyctor expallidus</i> Semenov-Tian-Shanskij	[partly handwritten] "Nyctor expallidus/ Typ. ♂. M./ A. Semenov-Tian-Shansky det.V.22"; [red disk]; [hand written, approx.] "Фарад/ 1. VI. 05/ Сумаков"/ [red] "Holotypus"	M	ZMAS
P	T053	<i>Nyctor expallidus</i> Semenov-Tian-Shanskij	[handwritten, approx.] "Фарад/ Сумаков 1907"/ [red] "Paratypus"	M	ZMAS
A	T054	<i>Nyctor expallidus</i> Semenov-Tian-Shanskij	"Nyctor expallidus/ m. Typ.♀/ A. Semenov-Tian-Shansky det. V.22"; "Ремедекъ/ 12.VI.1905/ Ю. [illegible, probably Beckmann]"; [red] "Allotypus"	M	ZMAS
P	T055	<i>Neocardiophorus mamajevi</i> Gurjeva	[handwritten, approx.] "Кызыпкыт/ 2. Кулдмжук-Тай/Мамаев 20.III.961"; [handwritten] "Песуак. Фада"; [red, partly handwritten] "Paratypus/ Neocardiophorus/ mamajevi Gurjeva"	M	ZMAS
P	T056	<i>Cardiophorus</i> (<i>Metacardiophorus</i>) <i>sogdianus</i> Gurjeva	[handwritten, approx.] "Гузар, Пеиджи-/ кеетк. об./ Бромписим S.V. 956"; [red, partly handwritten] "Paratypus/ Cardiopho-/ rus (metacardiophorus)/ sogdianus Gurjeva"	M	ZMAS

Kind	Type #	Species	Label	Sex	Dep.
T	T058	<i>Gastrimargus schneideri</i> Schwarz	[body and ovipositor on card] "Africa or./ Micindani/ EX COLL. F. SCHNEIDER"; "Coll.Schwarz"; "Dtsch.Entomol./ Institut Berlin"; [red] "LECTOTYPE ♀"; [handwritten, glued onto next label] "Margogastrius/ Schneideri/ Schw."; [handwritten on blue label, partly covered] "Schneideri/ Schw."; [partly handwritten] "Margogastrius/ schneideri/ Schwarz/ C. Girard vid. 1974"; [partly handwritten] "S/F. !?/ Cardiophorinae/ C. Girard det. 1974"	F	DEIC
T	T059	<i>Gastrimargus schneideri</i> Schwarz	"Africa or./ Micindani/ EX COLL. F. SCHNEIDER"; "Coll.Schwarz"; "Dtsch.Entomol./ Institut Berlin"; [handwritten] "Margogastrius/ Schneideri/ Schw."; [red] "PARALECTOTYPE ♀"; "Margogastrius/ schneideri/ Schwarz/ C. Girard vid. 1974"; [partly handwritten] "S/F. !?/ Cardiophorinae/ C. Girard det. 1974"	F	DEIC
T	T060	<i>Craspedostethus rufiventris</i> Schwarz	[green, handwritten] "Kameroun"; "Coll. Schwarz"; [red] "Lectotypus"; [handwritten] "rufiventris/ Schw."; "Dtsch.Entomol./ Institut Berlin"; [partly handwritten] "Lectotype/ Craspedostethus/ rufiventris Schw./ C. M. F. von Hayek/ det. 1963"; "DEI/ Eberswalde"; [handwritten] "Craspedostethus/ rufiventris/ Schw."	F	DEIC
T	T061	<i>Craspedostethus rufiventris</i> Schwarz	[green, handwritten] "Kameroun/ Kraals"; "Coll. Schwarz"; [red] "Paralectotypus"; [handwritten] "Dtsch.Entomol./ Institut Berlin"; [partly handwritten] "Paralectotype/ Craspedostethus/ rufiventris Schw./ C. M. F. von Hayek/ det. 1963"; "DEI/ Eberswalde"	F	DEIC
L	T062	<i>Cardiophorus convexulus</i> LeConte	"#1157 Maine", "convexus", "true type of convexulus J.C. Brimley"; "LECTOTYPE/ Cardiophorus/ convexulus/ LeConte, desig./ Douglas 2002"	F	MCZC
N	T063	<i>Elater convexa</i> Say	"ILL" "convexus/ (Say) fide Walsh"; "NEOTYPE/ Elater convexa/ Say Desig./ Douglas 2002"	M	MCZC
L	T064	<i>Cardiophorus togatus</i> Horn	"Tex"; "female" (symbol); "LectoType 3331"; "C. togatus Horn" "MCZ type 33727"; "LECTOTYPE/ Cardiophorus/ togatus/ Horn, desig./ Douglas 2002"	F	MCZC

Kind	Type #	Species	Label	Sex	Dep.
T	T065	<i>Cardiophorus luridipes</i> Candèze	[blank square]; [green, handwritten] "Calif/ Mufeim"; "405."; [handwritten] "C. luridipes"; "Collection/ Chevrolat"; [partly handwritten] "typique Cand./ Mon./ Collection Fleutiaux"; [red] "Type"	F	MNHN
T	T066	<i>Elater ferrugineus</i> Linnaeus	[Handwritten] "11 ferrugineus"; "20"	?	LSUK
T	T067	<i>Elater ferrugineus</i> Linnaeus	unlabeled	F	LSUK
T	T068	<i>Elater flabellicornis</i> Linnaeus	[torn, handwritten] "flabellicoformis"; [handwritten] "flabellicornis"; "1"	M	LSUK
T	T069	<i>Elater sputator</i> Linnaeus	[Handwritten] "I5 Sputator"; "24"	?	LSUK
T	T070	<i>Elater sputator</i> Linnaeus	unlabeled	?	LSUK
T	T071	<i>Elater sputator</i> Linnaeus	unlabeled	?	LSUK
T	T072	<i>Elater sputator</i> Linnaeus	unlabeled	?	LSUK
T	T073	<i>Elater sputator</i> Linnaeus	unlabeled	?	LSUK
T	T074	<i>Elater cardisce</i> Say	[pink disc = Middle States: Maryland; Delaware; New York; New Jersey; Pennsylvania; Connecticut?; Rhode Island?]; "C. cardisce/ Coney Is./ Say"; "NEOTYPE/ Elater/ cardisce/ Say, desig./ Douglas 2002"	M	MCZC
T	T075	<i>Cardiotarsus capensis</i> Lacordaire	[green, handwritten] "Cardiotarsus/ capensis mini./ L. ad Cap. Bon. Sp. D. - at"; [handwritten, partly illegible] "T__ge"; [handwritten] "Cardiotarsus/ capensis Cdze/ see Candèze"; "Janson coll./ ex Dejean./ 1903-130."; [handwritten] "dr 314"; [partly handwritten] "♀ genitalia/ see slide Coll./ TYPE."	F	NHM
T	T076	<i>Esthesopus castaneus</i> Eschscholtz	[handwritten] "Castaneus./ E./ Brasilia./ Rio Jan."; [handwritten] "Esthesopus"	F	ZMUM
T	T077	<i>Cardiophorus musculus</i> Erichson	[handwritten] "165."; [handwritten] "16599"; [microslide with handwritten label] "♀ genitalia/ musculus Er."; [red] "Lektotypus/ Nr."; [partly handwritten] "Lectotype/ Cardiophorus/ musculus Er./ C.M.F. von Hayek./ det. 1960"; [handwritten] "musculus/ Er./ Blankherb. Kn./ Austr. Dahl"	F	ZMHB

Kind	Type #	Species	Label	Sex	Dep.
T	T078	<i>Cardiophorus musculus</i> Erichson	"♀"; [handwritten] "16599"; [red] "Paratypus/ Nr."; [partly handwritten] "Cardiophorus/ musculus Er./ C.M.F. von Hayek./ det. 1960"; "Hist.-Coll. (Coleoptera)/ Nr. 16599/ Cardiophorus musculus Er./ Austria, Dahl/ Zool. Mus. Berlin"	F	ZMHB
T	T079	<i>Cardiophorus musculus</i> Erichson	"♂"; [handwritten] "gibbicollis/ Mg.s.Dhl"; [handwritten] "16599"; [red] "Paratypus/ Nr."; [partly handwritten] "Cardiophorus/ musculus Er./ C.M.F. von Hayek./ det. 1960"; "Hist.-Coll. (Coleoptera)/ Nr. 16599/ Cardiophorus musculus Er./ Austria, Dahl; Zool. Mus. Berlin"	M	ZMHB
T	T080	<i>Elater cinereus</i> Herbst	[female genitalia on card]; "♀"; [handwritten] "16647"; [handwritten] "Berlin"; [handwritten] "cinereus/ Hbt Larch. Er./ pilosus Payk./ Equiseti Gyll"; "Hist.-Coll. (Coleoptera)/ Nr. 16641/ Cardiophorus cinereus Hrbst./ Berolin; Zool. Mus. Berlin"; [partly handwritten] "Dicronychus/ cinereus (Herbst)/ J.Chassain det. 82"	F	ZMHB
T	T081	<i>Elater minutissimus</i> Germar	"17525"; [handwritten, partly illegible] "minutissimus/ Germ. Faun./ des ?? Sp?????"; [handwritten] "minutis/ firmus/ Tirol/ Italia"; "Hist.-Coll. (Coleoptera); Nr. 17525; Cryptohypnus minutissimus/ Germ./ Italia - Tyrol/ Zool. Mus. Berlin";	?	ZMHB
T	T082	<i>Elater dermestoides</i> Herbst	"17509"; [handwritten] "Europa"; [handwritten] "dermestoides/ Herbst"; [red] "LECTOTYPE ♂/ L.Leseigneur 1968"; [partly handwritten] "Zorochrus/ dermestoides Hbst/ Leseigneur det. 1968". With previously dissected ♂ genitalia on glass slide labeled: [handwritten] "Zorochrus/ dermestoides/ Herbst/ genitalia ♂"; [red] "LECTOTYPE ♂/ no 17509/ L.Leseigneur 1968"	M	ZMHB
T	T083	<i>Triplonychus acuminatus</i> Candèze	[male genitalia on card attached to pin]; [circular with blue margin] "SYN-/ TYPE"; [circular with red margin] "Type"; "Type"; "Cayenne."; [handwritten, green] "LacorDaire"; [green card]; "Coll.Janson/ Ex Laferte"; [handwritten, green] "Cayennensis var/ Cayenne. Bugt."; [handwritten] "H. acuminatus/ CDZ"; [handwritten] "Triplonychus/ acuminatus/ Type Cdze"	M	NHM

Kind	Type #	Species	Label	Sex	Dep.
T	T088	<i>Horistonotus simplex</i> LeConte	[green disc]; [red, partly handwritten] "Type 2399"; [handwritten] "Horistonotus/ simplex Lec."	M?	MCZC
T	T089	<i>Monocrepidius sordidus</i> LeConte	[gold disc]; [red, partly handwritten] "Type 2422"; [handwritten] "M. sordidus/ Gila Lec."	?	MCZC
T	T090	<i>Esthesopus parvus</i> Horn	[handwritten] "E./ parvus/ Horn"; "LectoTYPE/ 3345"; [red] M.C.Z./ Type/ 33734"; "Ariz"	F	MCZC
T	T091	<i>Macropogon piceus</i> LeConte	[blue disc]; [red, partly handwritten] "Type 2327"; [handwritten] "Macropogon/ piceus Lec."	?	MCZC
T	T092	<i>Cebrio speratus</i> Fall	[partly handwritten] "Hope Ark/ 6/18/26"; [partly handwritten] "Type/ speratus"; [red] "M.C.Z./ Type/ 24339"; "H. C. Fall/ COLLECTION"	M	MCZC
S	T093	<i>Cardiophorus adjutor</i> Candèze	[circular with blue margin] "SYN-/ TYPE"; "Japan./ G. Lewis./ 1910-320"; [partly handwritten] "SYNTYPE/ Cardiophorus/ adjutor Cand 73/ C.M.F. von Hayek/ 1985 O.T.O"	F	NHM
T	T094	<i>Platynychus mixtus</i> Fleutiaux	"Hué"; [partly handwritten] "mixtus Fleut/ Type/ Fairmaire Cand./ pars - Fleut. 1889/ Collection FLEUTIAUX"; [red] "TYPE"; [handwritten] "Fl 201 mx"; [partly handwritten] "♀ genitalia/ See slide Coll./ No. TYPE"; [partly handwritten] "Paraplatynychus/ C. M. F. von Hayek/ det. 1965"; ♀ genitalia removed to glass microslide labeled: [partly handwritten] "mixtus Fleut./ type/ fairmairei Cand/ pars Fleut 1889/ Hué"	F	MNHN
H	T095	<i>Coptostethus americanus</i> Horn	[handwritten] "Coptostethus/ americanus/ Horn"; [red] "HoloTYPE/ 3335"; [red] M.C.Z./ Holotype/ 33729; "La."	?	MCZC

Appendix 7. Specimens coded and identification information sources used for species used in phylogenetic analysis.

Ch = chapter (2 = Clicking Elateroidea analysis; 3 = Cardiophorinae analysis); F = female; M = male; other lit. = literature other than original species description used for identification; det. label = author of identification labels attached to non-type specimens; t.sp. = is type species for its genus (yes/no).

Species	Ch	Specimens Coded	Type #	Other lit.	Det. label	t.sp.
<i>Adrastus pallens</i> (Fabricius) 1792	2	M: P134, F: P135		Leseigneur 1972	Wellschmeid det. 1962	n
<i>Agriotes sputator</i> (Linnaeus) 1758	2	M: P2C2; F: P2B6, P2C1	T069- T073	Leseigneur 1972	none	y
<i>Agrypnella eburnea</i> Champion 1895	2,3	M: t, P025; F P029	T008	Champion 1895	Det. E.C. Becker 1985	y
<i>Agrypnus murinus</i> (Linnaeus) 1758	2,3	M: P072; F: P073		Leseigneur 1972	none	y
<i>Ampedus sanguineus</i> (Fabricius) 1801	2	M: P2C6; F: P2C5		Leseigneur 1972	none	y
<i>Anchastus digitatus</i> LeConte 1853	2	M: P036	T019	Van Dyke 1932	Becker 1957- 1959	y
<i>Anelastes druryi</i> Kirby 1818	2	M: P127, P129; F: P128		Muona 2000	E.C. Becker 1962	?
<i>Anischia</i> sp.	2	M: P137		Champion 1895	Douglas 2005	n
<i>Anisomerus sylvestris</i> Girard 1971	2	M: P138		-		n

Species	Ch	Specimens Coded	Type #	Other lit.	Det. label	t.sp.
<i>Aphricus californicus</i> LeConte 1853	3	M: t, P034	T020	Knull 1957	Douglas 2004	y
<i>Aphricus chilensis</i> Fleutiaux 1940	3	M: t	T036	-	Type	n
<i>Aptopus agrestis</i> Candèze 1860	3	M: P142, P143		-	none	n
<i>Aptopus pullatus</i> (Horn) 1884	3	M: P7A1-3; F: P036	T017, T018	Horn 1884, Schaeffer 1916	none	y
<i>Arhaphes diptychus</i> Candèze 1860	2,3	M: P015; F: P016		Candèze 1860)	Dét. E. Candèze"	y
<i>Athous vittatus</i> Fabricius 1792	2,3	M: P104, P105; F: P106, P107		Leseigneur 1972	none	y
<i>Aulonthroscus punctatus</i> (Bonvouloir) 1859	2	M: P193; F: P194		Blanchard 1917	none	?
<i>Berninelsonius hyperboreus</i> (Gyllenhal) 1827	2,3	M: P203; F: P204		Stibick 1979b	none	y
<i>Blaiseus bedeli</i> Fleutiaux 1931	3	M: t	T034	-	Type	y
sp.undescr. nr. <i>Aphricus</i> , S. Africa	3	M: P169, P170		Fleutiaux 1931	NA	n
<i>Buckelater argutus</i> Costa 1973	3	M: t, M: P098-102	T045- T049	-	paratypes	y
<i>Cardiodontulus brandti</i> Van Zwaluwenburg 1963	3	M: para-t; F: none	T001, T002	-	paratypes	y
<i>Cardiohypnus mirabilis</i> (Candèze) 1860	3	M: P028a, c; F: P028b	T009	Candèze 1860, Fleutiaux 1947a	none	y

Species	Ch	Specimens Coded	Type #	Other lit.	Det. label	t.sp.
<i>Cardiophorellus gracillicornis</i> Cobos 1970	3	M: para-t	T028, T029	Cobos 1970a	paratypes	y
<i>Cardiophorus (Coptostethus) brunneipennis</i> Wollaston 1864	3	M: P155; F: P154		Cobos 1970b	Platia 2002	n
<i>Cardiophorus (Metacardiophorus) sogdianus</i> Gurjeva 1966	3	M: para-t	T056	-	Type	y
<i>Cardiophorus (Perrinellus) angustatus</i> Fleutiaux 1933	3	M: P059, P060; F: none	T038	-	type series	n
<i>Cardiophorus brevis</i> Candèze 1887	3	M: P168; F: P169		Champion 1895	none	n
<i>Cardiophorus cardisce</i> (Say) 1834	3	M: P6A5, P2A12, P2C6, P2B1, P158, P159; F: P5A2, P5A3, FAB8	T074	Douglas 2003	Douglas 2003	n
<i>Cardiophorus convexulus</i> LeConte 1853	3	M: P167, P1H3; F: P1H1, P3H3	T062	Douglas 2003	Douglas 2003	n
<i>Cardiophorus convexus</i> (Say) 1823	3	M: P1A5, P1C10, P3B6, PBA1, PBA2, F: P1F4, P1F6, P4A3, P5D1, PBA3, PBA4	T063	Douglas 2003	Douglas 2003	n

Species	Ch	Specimens Coded	Type #	Other lit.	Det. label	t.sp.
<i>Cardiophorus gramineus</i> (Scopoli) 1763	2,3	M: PBB1; F: P020, P023, P141	T012, T013	Leseigneur 1972	Anonymous	y
<i>Cardiophorus inflatus</i> Candèze 1882	3	F: t	T005	-	type	y
<i>Cardiophorus luridipes</i> Candèze 1860	3	M: P165; F: t, P164	T065	Blanchard 1889	Blanchard 1889	n
<i>Cardiophorus</i> (<i>Zygocardiophorus</i>) <i>nigratissimus</i> Buysson 1891	3	M: P149, P151; F: P150, P152		Platia and Gudenzi 2002	det Platia 002	y
<i>Cardiophorus</i> sp. undescr., Congo	3	M: PBC4; F: C5		Candèze 1860	none	n
<i>Cardiophorus togatus</i> Horn 1871	3	M: P163, P1G9, P1G10; F: P5B2	T064	Douglas 2003	Douglas 2003	n
<i>Cardiotarsus capensis</i> Lacordaire 1857	3	P144-146 & 2M & 3F	T075	Candèze 1860	none	y
<i>Cardiotarsus mjobergi</i> Carter 1939	3	M: P172; F: P173		Carter 1939	none	n
<i>Cardiotarsus</i> sp. nr. <i>C.</i> <i>philautus</i> Candèze 1860	3	M P2B2, F P2B1		Candèze 1860	none	n
<i>Cebrio gigas</i> Fabricius 1787	2	M: P074		Schwarz 1912, Chevrolat 1874	Det. M. Fassati 1956	?
<i>Cerophytum elateroides</i> Latreille 1804	2	M: P199; F: P200		Johnson 2002a	det. W. Lucht	?
<i>Craspedostethus rufiventris</i> Schwarz 1898	3	M: P053; F: t	T060, T061	Schwarz 1898a	none	y

Species	Ch	Specimens Coded	Type #	Other lit.	Det. label	t.sp.
<i>Crioraphes rohdendorfi</i> Iablokoff-Khnzorian 1961	2	t in Amber	T030	-	type	y
<i>Dicrepidius ramicornis</i> Beauvois 1805	2	M: P2B3; F: P2B4-5		Candèze 1859	none	y
<i>Dicronychus cinereus</i> Herbst 1784	3	M: t series ts, PBB2; F: ts, P153	T080	Leseigneur 1972	Platia 2002	y
<i>Dima elateroides</i> Charpentier 1825	2	M: P108, P109		Platia 1994	Anonymous	y
<i>Elater ferrugineus</i> Linnaeus 1758	2,3	M: P046; F: P047	T066, T067	Leseigneur 1972	Anonymous	y
<i>Esthesopus castaneus</i> Eschscholtz 1829	3	M: P049; F: t, P050, P051	T076	Candèze 1860	Becker '59, Hayek '85	y
<i>Esthesopus parvus</i> Horn 1884	3	M: P7B2, P7B4; F: P7B3, P116, P117	T090	Horn 1884	none	n
<i>Eudicronychus</i> sp.	2	M: P092, P093, P094		Girard 1991	none	?
<i>Eulichas</i> sp.	2	M: P201; F: P202		Jäch, M.A. 1995	none	?
<i>Exoeolus rufescens</i> Broun 1893	2	M: P004	T003	Douglas 2005	none	y
<i>Fleutiauxellus maritimus</i> Curtis 1840	3	M: P185; F: P186		Leseigneur 1972	W. Dolin det. 1969	y
<i>Globothorax chevrolati</i> Fleutiaux 1891	3	F: t	T037	-	type	y
<i>Hemiops flava</i> Laporte 1833	2	M: P071, P084		Schimmel 1996, Candèze 1863	none	y

Species	Ch	Specimens Coded	Type #	Other lit.	Det. label	t.sp.
<i>Heteroderes sordidus</i> LeConte 1853	2	M: P207; F: P208	T089	Van Dyke 1932	none	n
<i>Horistonotus flavidus</i> Candèze 1860	2,3	M: P097; F: P095, t, P096 t-series	T050, T051	Candèze 1860	types	y
<i>Horistonotus simplex</i> LeConte 1863	3	M: P7A5, P7A6; F: P7A4, P7B1, P160	T088	Wells 2000	none	n
<i>Hypnoidus riparius</i> Fabricius 1792	2,3	M: P133; F: P131, P132		Stibick 1979b	Det. Olexa '73	y
<i>Lesnelater madagascariensis</i> Lesne 1897	2,3	M: t;	T024, T025	-	types	y
<i>Lissomus bicolor</i> Chevrolat 1835	2	M: P103; F: , P085, P087, P088		Champion 1895	Det. Cobos '72	?
<i>Macropogon piceus</i> LeConte 1861	2	M: P197, P198; F: P195, P196	T091	Young 2002	C. Chantal 1974	?
<i>Margogastrius schneideri</i> Schwarz 1902	2,3	F: t series	T058, T059	types	-	y
<i>Megapenthes lugens</i> Redtenbacher 1842	2	M: P043, P044		Leseigneur 1972	provided by C. Girard	y
<i>Melanotus castanipes</i> Paykull 1800	2	M: P042, F: P041		Leseigneur 1972	none	n
<i>Migiwa curatus</i> Candèze 1875	3	M: P179; F: P180		Kishii 1956	det. [Japanese characters]	n
<i>Monadicus</i> sp.	3	M: P181; F: P182		Candèze 1860	none	n
<i>Negastrius americanus</i> Horn 1871	2,3	M: P157, F: P156	T095	-	none	n

Species	Ch	Specimens Coded	Type #	Other lit.	Det. label	t.sp.
<i>Negastrius pulchellus</i> Fabricius 1801	2,3	F: P013, P014	Lost	Leseigneur 1972	Det.Olexa 73	y
<i>Neorhaphes americanus</i> Champion 1895	3	M: P187; F: P188		Costa 1966	none	n
<i>Neocardiophorus mamajevi</i> Gurjeva 1966	3	M: para-t	T055	-	type	y
<i>Neohypdonus gentilis</i> LeConte 1866	2,3	M: P177; F: P178		Stibick 1990	none	y
<i>Nyctor expallidus</i> Semenov- Tian-Shanskii & Pjatakova 1936	3	M: t; F: allo-t	T052- T054	-	type	y
<i>Odontocardus vitalisi</i> Fleutiaux 1918	3	M: P067; F: P068	T042	Fleutiaux 1947a	Fleutiaux	y
<i>Oedostethus femoralis</i> LeConte 1853	2,3	M: t, P012; F: P010	T016	Stibick 1990	P. Bélanger	y
<i>Oestodes tenuicollis</i> Randall 1838	2	M: P018		Johnson 2002b	none	y
<i>Onichodon orchesides</i> Newman 1838	2	M: P204; F: P205		Muona 2000	J.Muona det. 5/96	?
<i>Oxynopterus strachani</i> Hope 1842	2	M: P125; F: P126		Laurent & Taminaux 1960	dét. L. Laurent	n
<i>Pachyelater</i> Lesne 1897	2,3		T026, T027	Lesne 1897b, 1906	types	y
<i>Paracardiophorus humeralis</i> Fairmaire and Germain 1860	3	M: PBD2; F: PBD3, P190, HDCU215		Fairmaire and Germain 1860	Candèze, von Hayek	n

Species	Ch	Specimens Coded	Type #	Other lit.	Det. label	t.sp.
<i>Paracardiophorus musculus</i> Erichson 1840	2,3	F: PBB3; M: PBB4	T077- T079	Leseigneur 1972	J. Mertlik	y
<i>Paracardiophorus subcruciatus</i> Carter 1939	3	M: PBA5; F: PBA6, P189	not found	-	none	n
<i>Paradonus pectoralis</i> Say 1836	3	M: P175; F: P176		Stibick 1990 van Zwaluwenburg 1947	none	y
<i>Patriciella australica</i> Van Zwaluwenburg 1947	3	M: paratype	T044		paratype	y
<i>Cardiophorus Perrinellus argentatus</i> Abeille de Perrin 1894	3	M: t, P069	T043	Buysson 1899	none	y
<i>Phorocardius florentini</i> Fleutiaux 1894	3	M: P056; F: P057, t sex?	T035	Fleutiaux 1947a	none	y
<i>Phorocardius solitarius</i> Fleutiaux 1931a	3	F: t	T033	Fleutiaux 1947a	none	y
<i>Physodactylus henningi</i> Fisher 1823	2	M: P062		-	Fleutiaux	y
<i>Physorhinus erythrocephalus</i> Fabricius 1801	2	M: t, P033; F: P032	T015	Schaaf 1970	Schaaf, 1970	y
<i>Pityobius anguinus</i> LeConte 1853	2	M: P077; F: P078	T021- T023	Johnson 2002b	S. Laplante 1970	y
<i>Platynychus adjutor</i> Candèze 1875	3	M: P003, F: P002	T093	Ôhira 1987	none	y
<i>Platynychus indicus</i> Motschulsky 1858	3	F: t	T041	-	type	y

Species	Ch	Specimens Coded	Type #	Other lit.	Det. label	t.sp.
<i>Platynychus mixtus</i> Fleutiaux 1931a	3	M: P065, P066; F: P064	T094	Fleutiaux 1947a	Fleutiaux	y
<i>Porthmidius austriacus</i> Schränk 1781	2	M: P038, P040; F: P039		Leseigneur 1972	E.C.Becker 1970; Olexa'72	y
<i>Promopelus elegans</i> Laurent 1966	2	M: P136		-	none	y
<i>Pronegastrius humeralis</i> Candèze 1863	3	F: P183, P184		Ôhira 1963	From Ohira Coll.	y
<i>Prosternon tessellatum</i> Linnaeus 1758	2	M: P080; F: P081		Leseigneur 1972	none	y
<i>Protocardiophorus</i> <i>ancestralis</i> Dolin 1976b	2	Fossil t	T032	-	type	y
<i>Pseudocardiophorites fragilis</i> Dolin 1976b	2	Fossil t	T031	-	type	y
<i>Pyrophorus notilucus</i> Linnaeus 1758	2	M: P010-014; F: P015		Costa 1975, Champion 1895	C. Costa det. 1969	y
<i>Quasimus minutissimus</i> Germar 1817	2,3	M: P017; F: P018	T081	Leseigneur 1972	Olexa '73	y
<i>Rivulicola variegatus</i> Macleay 1872	3	M: P021a, b; F: P022		-	Anonymous det. K. Galley	y
<i>Selonodon speratus</i> Fall 1928	2	M: P119, P120; F: P121	T092	Galley 1999	1990	n
<i>Semiotus furcatus</i> Fabricius 1775	2	M: P079; F: P075, P076		Chassain 2001 Broun1893, Douglas 2003	none	y
sp.undescr., New Zealand	2,3	M: P005			none	n

Species	Ch	Specimens Coded	Type #	Other lit.	Det. label	t.sp.
<i>Teslasena femoralis</i> Lucas 1857	2,3	M: P061	T039	Fleutiaux 1892	Fleutiaux	y
<i>Tetralobus flabellicornis</i> Linnaeus 1758	2	M: P083; F: P082	T068	Laurent 1964a, b, c, 1965, 1967	none	y
<i>Thylacosternus rubricollis</i> Bonvouloir 1875	2	F: P140;			Becker 1962	?
<i>Thylacosternus vittatus</i> champion 1897	2	M: P210			none	?
<i>Triplonychoides trivittatus</i> Champion 1895	3	M: t	T010, T011	Champion 1895	none	y
<i>Triplonychus plagiatus</i> Erichson 1840	3	M: P148 & 6 others; F: P147	T083	Candèze 1860	Douglas 2005	n
<i>Tropidiplus tellinii</i> Fleutiaux 1903a	3	M: t; F: P063	T040	Fleutiaux 1903	von Hayek 1965	y
<i>Tropihypnus bimargo</i> Reitter 1896	2,3	M: P2D2; F: P2D1		Stibick 1968	Gurjeva det	y
<i>Yukoana carinicollis</i> Lewis 1894	3	M: P191; F: P192		Kishii 1970	Det. Ôhira 1967	n
<i>Zorochros demustoides</i> Herbst 1806	3	M: P2C4; F P2C3	T082	Leseigneur 1972	none	y

**Appendix 8. Morphological characters used for phylogenetic analysis of Clicking
Elateroidea and Cardiophorinae**

Quantitative characters are indicated by the term "Quant."; described here are the measurements and ratios used to obtain data for quantitative coding. Longitudinal distance refers to the portion of the distance between two points that is parallel to the longitudinal axis of the specimen's body (e.g. measurements a-c, Fig. 1). Species named in brackets are designated as types for character states. Type designations of character states for which the type species has not been identified to species level should be viewed as temporary. Three columns at left are: #, character number; #E, character number for analysis of Clicking Elateroidea (Chapter 2); #C, character number for analysis of Cardiophorinae (Chapter 3). An "x" indicates that the character was not used for that analysis because it was invariant.

#	#E	#C	Character Description (O = ordered multistate character)
1	1	1	Antennae: 0) with 11 antennomeres [<i>Cardiophorus gramineus</i>]; 1) with 12 antennomeres [<i>Pityobius anguinus</i>].
2	2	x	Antennomere 1 with row of bristles on posterior surface (apparent eye cleaning organ): 0) absent [<i>Elater ferrugineus</i>]; 1) present [<i>Anelastes femoralis</i>].
3	3	2	Quant. Lengths of antennomeres: (2)/(3).
4	4	3	Quant. Lengths of antennomeres: (4)/(3).

#	#E	#C	Character Description (O = ordered multistate character)
5	5	4	Quant. Antennomere 11: (length)/(maximum height).
6	x	5	Antennomere 1 with dorsolateral carina: 0) absent [<i>Elater ferrugineus</i>]; 1) present [<i>Zorochros demustoides</i>].
7	6	6	Antennae with sensory elements beginning on antennomere: 0) 3 [<i>Cardiophorus gramineus</i>]; 1) 4 [<i>Elater ferrugineus</i>]; 2) 5 [<i>Macropogon piceus</i>]; 3) 9 [<i>Anischia</i> sp.]. Observations of rough microsculpture, apicoventral lobes or presence of vestiture types absent from antennomeres 1 and 2 were considered evidence of sensory elements. (O)
8	7	7	Quant. Antennal fossa: (width of fossa)/(minimum distance from fossa to eye).
9	8	8	Head with area between antenna fossa and edge of compound eye: 0) unsculptured [<i>Cardiophorus gramineus</i>]; 1) with carina connecting fossa and eye [<i>Esthesopus castaneus</i>] or with 2 pits with non depressed area between them [<i>Cardiotarsus mjobergi</i>]; 2) with a single pit [<i>Horistonotus flavidus</i>]; 3) with groove connecting fossa and eye [<i>Anelastes druryi</i>]; 4) with multiple punctures similar to those on frons [<i>Macropogon piceus</i>].
10	9	9	Mandibular apex: 0) unidentate (simple) [<i>Cebrio gigas</i>]; 1) bidentate [<i>Paracardiophorus musculus</i>]; 2) tridentate [<i>Buckelater argutus</i>]. (O)
11	10	x	Labrum: 0) exposed [<i>Cardiophorus gramineus</i>]; 1) concealed by frontoclypeal region [<i>Anelastes druryi</i>].

#	#E	#C	Character Description (O = ordered multistate character)
12	11	10	Labrum: 0) entire, evenly convex dorsally [<i>Cardiophorus gramineus</i>]; 1) entire, with mesal longitudinal groove [<i>Hemiops flava</i>]; 2) entire, flat [<i>Cebrio gigas</i>] or broadly concave [<i>Craspedostethus rufiventris</i>]; 3) emarginate mesally [<i>Tetralobus flabellicornis</i>].
13	12	x	Supra-antennal carina: 0) following contour of antennal fossa (Fig. 1), ending near base of mandible [<i>Lissomus bicolor</i>]; 1) extending mesally (Fig. 3) or anteromesally away from antennal fossa [<i>Cardiophorus gramineus</i>]; 2) absent (Fig. 2) [<i>Cebrio gigas</i>].
14	13	11	Supra-antennal carina with longitudinal split next to eyes: 0) absent (Fig. 3) [<i>Elater ferrugineus</i>]; 1) present (Fig. 4) [<i>Cardiophorus gramineus</i>].
15	14	12	Quant. Frontoclypeal region: (distance between supra-antennal carina and labrum at midline)/(minimum distance between antennal fossae).
16	15	13	Frontoclypeal region with carinae from bases of mandibles extending meso-dorsad to supra-antennal carina: 0) absent [<i>Cardiophorus gramineus</i>]; 1) present [<i>Dicrepidius ramicornis</i>].
17	16	14	Fronto-clypeus at midline in side view, with concavity between antero-ventral edge (adjacent to labrum) and supra-antennal carina: 0) absent [<i>Agriotes sputator</i>]; 1) present [<i>Cardiophorus gramineus</i>]; ?) not measurable because supra-antennal carinae do not extend mesally from antennal fossae [<i>Cebrio gigas</i>].

#	#E	#C	Character Description (O = ordered multistate character)
18	x	15	Fronto-clypeus with crenulations on anterior margin: 0) absent [<i>Elater ferrugineus</i>]; 1) present [<i>Neoarhaphes americanus</i>].
19	17	x	Head with mesal vertical carina of frontoclypeal region: 0) absent [<i>Elater ferrugineus</i>]; 1) present [<i>Cerophytum elateroides</i>].
20	18	x	Frons with spines above antennae: 0) absent [<i>Elater ferrugineus</i>]; 1) present [<i>Semiotus furcatus</i>].
21	19	16	Frons with mesal groove: 0) absent [<i>Elater ferrugineus</i>]; 1) present [<i>Floridelater americanus</i>].
22	20	17	Frons with supra-orbital groove: 0) absent (Figs. 1, 2) [<i>Elater ferrugineus</i>]; 1) present (Figs. 3, 4) [<i>Cardiophorus gramineus</i>].
23	21	18	Quant. (ocular index) compound eyes: (maximum distance between outer edges of compound eyes)/(minimum distance between inner edges of eyes).
24	22	x	Galea and lacinia: 0) not reduced, reaching closed mandibles [<i>Cardiophorus gramineus</i>]; 1) reduced, not reaching closed mandibles [<i>Anelastes druryi</i>].
25	23	19	Apical segment of maxillary palp: 0) securiform or subtriangular (apex truncate, sides expanded apically) [<i>Cardiophorus gramineus</i>]; 1) oblong-ovate (apex rounded, sides equally curved) [<i>Patriciella australica</i>]; 2) lanceolate [<i>Adrastus pallens</i>]; 3) forked [<i>Anischia</i> sp.]; 4) bottle shaped (lageniform) [<i>Arhaphes diptychus</i>].

#	#E	#C	Character Description (O = ordered multistate character)
26	24	20	Apical segment of labial palp: 0) securiform or subtriangular [<i>Cardiophorus gramineus</i>]; 1) oblong-ovate [<i>Patriciella australica</i>]; 2) lanceolate [<i>Adrastus pallens</i>]; 3) bottle shaped [<i>Arhaphes diptychus</i>].
27	25	21	Mentum: 0) without macrosetae [<i>Cardiophorus gramineus</i>]; 1) with macrosetae [<i>Elater ferrugineus</i>].
28	26	x	Profemur with carina surrounding posterior surface: 0) absent [<i>Elater ferrugineus</i>]; 1) present [<i>Cerophytum elateroides</i>].
29	27	22	Pronotum with space between punctures on disc: 0) flat [<i>Cardiophorus gramineus</i>]; 1) with tubercles [<i>Zorochros demustoides</i>] or raised ridges [<i>Negastrius pulchellus</i>]. (O)
30	28	23	Pronotum with setae that are dorsoventrally compressed, and/or wider at midlength than at base: 0) absent [<i>Cardiophorus gramineus</i>]; 1) present [<i>Agrypnella squamifer</i>].
31	29	24	Head and pronotum with integument: 0) unicoloured [<i>Negastrius pulchellus</i>]; 1) with strongly contrasting light and dark areas [<i>Cardiophorus gramineus</i>].
32	30	25	Pronotum with hind angles: 0) not truncate dorsally (Fig. 5) [<i>Cardiophorus gramineus</i>]; 1) truncate dorsally (Fig. 6) so that only narrow hypomeral portion of hind angle remains in dorsal view [<i>Cardiophorus cardisce</i>]; 2) notched dorsally with dorsal surface of pronotum reaching apex of hind angle [<i>Agrypnella eburnea</i>].

#	#E	#C	Character Description (O = ordered multistate character)
33	x	26	Pronotum with lateral edge of hind angle with tubercle: 0) absent [<i>Cardiophorus gramineus</i>]; 1) present [<i>Platynychus indicus</i>].
34	31	27	Hind angles of pronotum with carina adjacent to lateral pronotal carina: 0) absent [<i>Athous vittatus</i>]; 1) present, but not reaching anterior edge of pronotum [<i>Elater ferrugineus</i>]; 2) present, reaching anterior edge of pronotum [<i>Quasimus minutissimus</i>]. (O)
35	32	x	Hind angles of pronotum with third carina, next to mesal edge (additional to lateral carina): 0) absent [<i>Cardiophorus gramineus</i>]; 1) present [<i>Anchastus digitatus</i>].
36	33	x	Pronotum with bioluminescent spots: 0) absent [<i>Elater ferrugineus</i>]; 1) present [<i>Pyrophorus notilucus</i>].
37	34	x	Pronotum with concavity on posterior edge immediately mesad of hind angles in dorsal view: 0) present [<i>Elater ferrugineus</i>]; 1) absent [<i>Macropogon piceus</i>].
38	35	28	Pronotum at middle of posterior edge with: 0) arcuate indentation between 2 apices [<i>Elater ferrugineus</i>]; 1) point or lobe between 2 apices (= 3 apices) [<i>Cardiophorus gramineus</i>]; 2) single arcuate lobe (= 1 apex) [<i>Athous vittatus</i>]; 3) single rectangular lobe (= 1 apex) [<i>Tetralobus flabellicornis</i>]; 4) 3 points recessed between 2 longer lobes [<i>Hemiops flava</i>].

#	#E	#C	Character Description (O = ordered multistate character)
39	36	x	Posterior edge of pronotum with crenulations: 0) absent [<i>Elater ferrugineus</i>]; 1) present [<i>Oxyntopterus strachani</i>].
40	37	29	Pronotum with sublateral incisions: 0) absent, and longitudinal carinae absent [<i>Elater ferrugineus</i>]; 1) present, without longitudinal carinae [<i>Dicrepidius ramicornis</i>]; 2) present, and with longitudinal carinae [<i>Cardiophorus gramineus</i>]. (O)
41	38	30	Pronotum with lateral carina: 0) reaching from anterior edge to posterior or lateral edge of hind angle [<i>Elater ferrugineus</i>]; 1) effaced anteriorly (ventrad of edge of pronotum in some) [<i>Cardiophorus gramineus</i>]; 2) effaced posteriorly [<i>Anelastes druryi</i>]; 3) absent [<i>Exoeolus rufescens</i>].
42	39	x	Pronotum with lateral carinae: 0) not serrate [<i>Elater ferrugineus</i>]; 1) serrate [<i>Thylacosternus sp.</i>].
43	40	31	Pronotum extending laterally beyond lateral carina: 0) for entire length (Figs. 5, 6) [<i>Cardiophorus gramineus</i>]; 1) not at all [<i>Elater ferrugineus</i>]; 2) only in anterior half [<i>Agriotes sputator</i>]; 3) only in posterior half [<i>Melanotus castanipes</i>].
44	41	32	Posterior edges of hypomeron mesad of hind angles: 0) with rectangular or semicircular indentations (Fig. 5) [<i>Cardiophorus gramineus</i>]; 1) straight or shallowly sinuate (Fig. 6) [<i>Elater ferrugineus</i>]; 2) convex [<i>Prosternon tessellatum</i>].

#	#E	#C	Character Description (O = ordered multistate character)
45	42	x	Hypomeron with pockets for reception of antennae: 0) absent [<i>Elater ferrugineus</i>]; 1) present, vertical [<i>Aulonthroscus punctatus</i>]; 2) present, immediately below, and parallel to lateral pronotal carina [<i>Onichodon orchesoides</i>]. (See also char. 50.
46	43	33	Hypomeron with loop shaped carinae near procoxae: 0) absent [<i>Elater ferrugineus</i>]; 1) present [<i>Arhaphes diptychus</i>].
47	44	34	Prosternum with anterior edge: 0) short, exposing labium [<i>Physodactylus henningi</i>]; 1) not short, produced as lobe, concealing labium when head not extended [<i>Cardiophorus gramineus</i>].
48	45	35	Prosternum with anterior edge at midline: 0) arcuate [<i>Elater ferrugineus</i>]; 1) notched [<i>Aphricus</i> sp.nov. N. Zealand]; 2) with tubercle [<i>Esthesopus castaneus</i>].
49	46	36	Prosternum with lateral edges near midlength: 0) straight [<i>Cardiophorus gramineus</i>] to weakly concave [<i>Elater ferrugineus</i>]; 1) convex [<i>Negastrius pulchellus</i>].
50	47	37	Pronotosternal sutures with anterior end: 0) closed [<i>Cardiophorus gramineus</i>]; 1) open, produced into a groove large enough to guide, but not conceal, antennae [<i>Agriotes sputator</i>]; 2) excavated deeply enough to conceal part of length of antennae [<i>Agrypnus murinus</i>]. (O)

#	#E	#C	Character Description (O = ordered multistate character)
51	48	38	Pronotosternal sutures: 0) not effaced, pronotum and prosternum not fused [<i>Elater ferrugineus</i>]; 1) partly [<i>Arhaphes diptychus</i>] or completely [<i>Neoarhaphes americanus</i>] effaced, pronotum and prosternum fused.
52	49	39	Prosternal process with "V" shaped carina on sides of ventral surface: 0) absent or interrupted [<i>Elater ferrugineus</i>]; 1) complete, connected basally to carinae surrounding procoxal cavities [<i>Paracardiophorus musculus</i>].
53	50	40	Quant. Prosternal process: (length of portion of prosternal process extending posteriad of procoxae)/(maximum width of exposed part of procoxae in ventral view).
54	51	41	Quant. Prosternal process (Fig. 7, c/a): (longitudinal distance from posterior edge of procoxae to ventral apex of prosternal process)/(longitudinal distance from posterior edge of procoxae to dorsal apex of prosternal process).
55	52	42	Quant. Prosternal process (Fig. 7, b/a): (longitudinal distance from posterior edge of procoxae to posterior end of prosternal process, halfway between dorsal and ventral apices)/(longitudinal distance from posterior edge of procoxae to dorsal apex of prosternal process).
56	53	43	Quant. Prosternal process (Fig. 7, d/a): (vertical distance between dorsal and ventral apices of prosternal process)/(longitudinal distance from posterior edge of procoxae to dorsal apex of prosternal process).

#	#E	#C	Character Description (O = ordered multistate character)
57	54	44	Prosternal process (anteriad of ventral apex) with angle between ventral surface and ventral surface of middle of prosternum anterior to procoxae: 0) less than 30° (horizontal) [<i>Elater ferrugineus</i>]; 1) more than 30° (inclined dorsally) [<i>Dima elateroides</i>].
58	55	45	Procoxal cavities: 0) open [<i>Elater ferrugineus</i>]; 1) closed [<i>Paracardiophorus musculus</i>].
59	56	x	Prothorax with lateral extension of procoxa and articular region of pleurotrochantin: 0) well-developed and at least as long as shortest coxal diameter [<i>Macropogon piceus</i>]; 1) highly reduced (less than 1/5 as long as shortest coxal diameter) or absent [<i>Elater ferrugineus</i>].
60	57	x	Prothorax with pleurotrochantin or endopleuron (if trochantin absent): 0) freely movable [<i>Macropogon piceus</i>]; 1) fused to the notum at a point near the junction of the notosternal suture and the wall of the coxal cavity [<i>Elater ferrugineus</i>].
61	58	x	Promesothoracic clicking mechanism: 0) absent [<i>Macropogon piceus</i>]; 1) present [<i>Elater ferrugineus</i>].
62	59	46	Protibiae near apex with posterior surface: 0) convex, not modified for digging [<i>Cardiophorus gramineus</i>]; 1) flattened, concave or broadened apically, apparently modified for digging [<i>Cebrio gigas</i>].

#	#E	#C	Character Description (O = ordered multistate character)
63	60	47	Pronotum with punctures on disc: 0) elongate [<i>Athous vittatus</i>]; 1) not elongate [<i>Cardiophorus gramineus</i>]; 2) absent, setae on tubercles [<i>Anelastes druryi</i>].
64	61	48	Scutellum with mesal portion of anterior edge: 0) straight [<i>Pyrophorus notilucus</i>] or convex [<i>Elater ferrugineus</i>]; 1) broadly concave [<i>Athous vittatus</i>]; 2) abruptly emarginate [<i>Cardiophorus gramineus</i>]; 3) indistinct because not raised above anterior part of mesoscutum [<i>Cebrio gigas</i>].
65	62	49	Scutellum with anterolateral edges: 0) convex throughout [<i>Cardiophorus gramineus</i>]; 1) straight [<i>Athous vittatus</i>] or concave posterior to anterolateral corners [<i>Agriotes sputator</i>].
66	63	50	Scutellum with posterolateral edges: 0) with straight [<i>Cardiophorus gramineus</i>] or concave portion [<i>Rivulicola variegatus</i>], meeting at acute to obtuse angle; 1) convex throughout [<i>Elater ferrugineus</i>] evenly rounded or with convex sides meeting at an obtuse angle; 2) with straight portion, apex truncate [<i>Blaiseus bedeli</i>]; 3) concave, apex bilobed [<i>Floridelater americanus</i>].

#	#E	#C	Character Description (O = ordered multistate character)
67	64	51	Sides of mesosternal cavity with antero-ventral angles in side view: 0) prominent and rounded [<i>Cardiophorus gramineus</i>]; 1) prominent and angulate, acute to 140° (concave ventrad of antero-ventral angle in some, appearing able to fit procoxae) [<i>Esthesopus castaneus</i>]; 2) 160°-180° and hidden by mesocoxae in side view [<i>Elater ferrugineus</i>]; 3) excavated in amphitheatre shape [<i>Arhaphes diptychus</i>].
68	65	x	Sides of mesosternal cavity reaching anterior edge of mesosternum: 0) as separate carinae [<i>Elater ferrugineus</i>]; 1) as single merged carina [<i>Aulonothroscus punctatus</i>]; 2) as "V" shape, merging at edge [<i>Macropogon piceus</i>]; 4) not at all, carinae truncated before reaching edge [<i>Cerophytum elateroides</i>].
69	66	52	Sides of mesosternal cavity posterior to anterior edge of mesocoxae in ventral view: 0) U shaped [<i>Cardiophorus gramineus</i>]; 1) straight, forming a V [<i>Elater ferrugineus</i>]; 2) with anteromesal projection [<i>Arhaphes diptychus</i>]; 3) narrowed to parallel sided posterior extension, entire cavity bottle shaped (lageniform) in ventral view [<i>Anchastus digitatus</i>]; 4) with 3 obtuse angles and 4 sides [<i>Cardiophorus convexulus</i>].
70	67	53	Sides of mesosternal cavity anterior to mesocoxae: 0) sinuate [<i>Cardiophorus gramineus</i>]; 1) straight (parallel or anteriorly convergent) [<i>Semiotus furcatus</i>]; 2) concave [<i>Lissomus bicolor</i>]; 3) convex [<i>Anelastes druryi</i>].

#	#E	#C	Character Description (O = ordered multistate character)
71	68	54	Anterior edge of mesosternum: 0) concave laterad of anterior protrusions of mesosternal fossa [<i>Elater ferrugineus</i>]; 1) convex laterad of anterior protrusions of mesosternal fossa [<i>Negastrius pulchellus</i>] or evenly convex, uninterrupted by mesosternal fossa [<i>Zoroachros demustoides</i>].
72	69	55	Mesepisternum with anterior projection of anteromesal corners relative to junction with mesosternum: 0) present, concave mesally forming an acute point (Fig. 16) [<i>Cardiophorus gramineus</i>]; 1) present, rounded (Fig. 13) [<i>Elater ferrugineus</i>] to obtusely angulate, but not concave mesally [<i>Ampedus sanguineus</i>]; 2) absent, abruptly angulate (Fig. 14) [<i>Cebrio gigas</i>].
73	70	56	Mesepisternum with circular pit at anteromesal corner: 0) absent [<i>Elater ferrugineus</i>] (some with groove [<i>Athous vittatus</i>]); 1) present [<i>Agrypnus murinus</i>].
74	71	57	Angle of anterolateral corner of mesepisternum (angle between tangents of edge of sclerite at lowest part of concavity immediately mesad of angle, and an equidistant point on lateral edge): 0) approximately right angled (80°-100°, Fig. 12) without notch immediately mesad of angle [<i>Cardiophorus gramineus</i>]; 1) approximately right angled with notch immediately mesad of corner [<i>Tropihypnus bimargo</i>]; 2) obtuse or evenly curved (Fig. 13) [<i>Ampedus sanguineus</i>]; 3) with rectangular projection [<i>Cebrio gigas</i>]; 4) acute, less than 70° [<i>Macropogon piceus</i>].

#	#E	#C	Character Description (O = ordered multistate character)
75	72	x	Mesepisternum and mesepimeron with suture between them: 0) visible as a ridge or groove throughout length (Fig. 12) [<i>Elater ferrugineus</i>]; 1) effaced for most of length [<i>Onichodon orchesoides</i>].
76	73	58	Quant. Mesepimeron: (maximum width, measured parallel to anterior edge)/(maximum length, measured perpendicular to width).
77	74	x	Posterior lobe of mesepimeron: 0) present [<i>Elater ferrugineus</i>]; 1) absent [<i>Tetralobus flabellicornis</i>].
78	75	59	Mesotrochantin: 0) visible [<i>Elater ferrugineus</i>] or partly concealed by mesosternum; 1) not visible [<i>Cardiophorus gramineus</i>].
79	76	60	Mesocoxal cavity: 0) open to both mesepimeron and mesepisternum (Fig. 13) [<i>Elater ferrugineus</i>]; 1) open to mesepimeron only (Fig. 14) [<i>Agriotes sputator</i>]; 2) closed to mesepimeron and mesepisternum by extension of mesosternum (Fig. 15) [<i>Cardiophorus gramineus</i>]. (O)
80	77	x	Suture between meso- and metasternum at midline: 0) visible, groove-like [<i>Elater ferrugineus</i>]; 1) effaced [<i>Semiotus furcatus</i>] or visible only as indistinct line.
81	78	61	Quant. Midleg: (trochanter length)/(femur length).
82	79	62	Quant. Exposed portion of metepisternum: (length)/(width). Width measured at midlength, not including portion covered by closed elytra.
83	80	x	Carina between mesocoxal cavity and metasternum: 0) visible throughout length [<i>Elater ferrugineus</i>]; 1) hidden by mesocoxae [<i>Cebrio gigas</i>].

#	#E	#C	Character Description (O = ordered multistate character)
84	81	63	Carina between mesocoxal cavity and metasternum: 0) without adjoining carinae extending onto metasternum [<i>Elater ferrugineus</i>]; 1) with carinae extending onto metasternum as an arc [<i>Lissomus bicolor</i>] or closed loop posterior to coxae [<i>Quasimus minutissimus</i>].
85	82	64	Metasternum with ratio of width of lateral carina (Fig. 16, c) to distance between it and carina surrounding mesocoxal cavities at level of posterior third of mesocoxae (Fig. 16, d): 0) less than 0.5 [<i>Cardiophorus gramineus</i>]; 1) greater than 0.5 [<i>Quasimus minutissimus</i>].
86	83	x	Metasternum with pockets for reception of midlegs (edges not joined to any other carinae): 0) absent [<i>Elater ferrugineus</i>]; 1) present [<i>Aulonothroscus punctatus</i>].
87	84	65	Edge of elytra in dorsal view between anterior most point and humeral angle: 0) sinuate or tuberculate [<i>Cardiophorus gramineus</i>]; 1) arcuate or straight [<i>Elater ferrugineus</i>]; 2) cleft by anterior extension of stria, with small tubercles laterad of cleft [<i>Rivulicola variegatus</i>].
88	85	66	Number of puncture rows or striae on elytra: 0) ambiguous (striae poorly defined or absent on basal half) [<i>Cebrio gigas</i>]; 1) 9 [<i>Elater ferrugineus</i>]; 2) more than 9 [<i>Eulichas sp.</i>].
89	86	67	Elytra with intervals 1-8 on basal third: 0) all flattened or rounded [<i>Elater ferrugineus</i>]; 1) partly or completely costate [<i>Negastrius pulchellus</i>].

#	#E	#C	Character Description (O = ordered multistate character)
90	x	68	Elytra with apical half of intervals 1-8: 0) all flattened or rounded [<i>Elater ferrugineus</i>]; 1) with at least some partly or completely costate [<i>Aphricus californicus</i>].
91	87	69	Elytra with apical half of interval 9: 0) flattened or rounded [<i>Elater ferrugineus</i>]; 1) costate [<i>Triplonychoidus trivittatus</i>].
92	88	70	Elytra: 0) without spots or markings [<i>Elater ferrugineus</i>] (some with basal markings or longitudinal stripe); 1) with distinct transverse markings or spots that are not confluent with anterior edge [<i>Negastrius pulchellus</i>].
93	89	71	Upper edge of elytral epipleura: 0) with minute regular serrations [<i>Cardiophorus gramineus</i>]; 1) without serrations [<i>Elater ferrugineus</i>].
94	90	72	Elytral apex with punctures at least 1.5X diameter of largest on anterior half: 0) absent [<i>Elater ferrugineus</i>]; 1) present, single [<i>Paracardiophorus subcruciatus</i>] or multiple [<i>Agrypnella eburnea</i>].
95	x	73	Elytron with apical shelf like extension: 0) absent [<i>Elater ferrugineus</i>]; 1) present [<i>Cardiophorus nigratissimus</i>].
96	91	x	Elytra with ventral (hidden) apical fin parallel to striae: 0) absent [<i>Elater ferrugineus</i>]; 1) present [<i>Macropogon piceus</i>].
97	92	x	Elytra with apical spine(s): 0) absent [<i>Elater ferrugineus</i>]; 1) present [<i>Oxynopterus strachani</i>].

#	#E	#C	Character Description (O = ordered multistate character)
98	93	74	Hind wing: 0) with venation well developed, wing area greater than elytral area [<i>Elater ferrugineus</i>]; 1) with veins weakly sclerotised, wing area less than half of elytral area [<i>Dima elateroides</i>].
99	94	75	Hind wing membrane: 0) not notched in anal area [<i>Elater ferrugineus</i>]; 1) notched in anal area (between AA3+4 and AP) [<i>Negastrius pulchellus</i>].
100	95	76	Hind wing with apical concavity: 0) absent [<i>Elater ferrugineus</i>]; 1) present [<i>Berninelsonius hyperboreus</i>].
101	96	77	Quant. Hind wing, radial cell: (length)/(width).
102	97	78	Quant. Hind wing: proximal, posterior angle of radial cell (measured as angle (in degrees) between tangents of: anterior edge of cell, at 1/3 distance from posterior angle to anterior edge of cell; and posterior edge of cell at an equal distance from angle).
103	98	x	Hind wing with r3 proximad of radial cell: 0) free (Fig. 19) [<i>Elater abruptus</i>]; 1) joined to costa by a crossvein [<i>Tetralobus flabellicornis</i>]; ?) absent (Fig. 20) [<i>Blaiseus bedeli</i>].
104	99	79	Hind wing with vein AA3: 0) joining CUA posterior to divergence from AA4 [<i>Elater ferrugineus</i>]; 1) joining CUA at divergence from AA4 [<i>Esthesopus castaneus</i>]; 2) joining CUA, AA4 not continuing posteriorly [<i>Negastrius pulchellus</i>].
105	100	80	Hind wing with wedge cell: 0) present (Fig. 19) [<i>Elater ferrugineus</i>]; 1) absent (Fig. 20) [<i>Cardiophorus gramineus</i>].

#	#E	#C	Character Description (O = ordered multistate character)
106	101	81	Hind wing vein MP3 and MP4 separating: 0) distal to intersection with CUA1 [<i>Cardiophorus gramineus</i>]; 1) proximal [<i>Elater ferrugineus</i>] to or at same level as [<i>Macropogon piceus</i>] intersection with CUA1. (CUA1 interrupted in some).
107	102	82	Hind wing with CuA1: 0) uninterrupted (Fig. 20) [<i>Elater ferrugineus</i>]; 1) interrupted or not reaching MP3+4 or MP4 [<i>Cardiophorus gramineus</i>].
108	x	83	Hind wing with CuA1 0) not forked [<i>Elater ferrugineus</i>]; 1) forked at junction with MP3+4 forming additional closed cell [<i>Blaiseus bedeli</i>].
109	103	84	Hind wing with MP3+4 with proximal extension of crossvein mp1+2-mp3+4: 0) present [<i>Elater ferrugineus</i>]; 1) absent (Figs. 19, 20) [<i>Cardiophorus gramineus</i>].
110	104	85	Apex of hind wing with anterior field sclerotisation (Muona1993): 0) absent [<i>Negastrius pulchellus</i>]; 1) single (Fig. 20) [<i>Elater ferrugineus</i>]; 2) double (Figs 19) [<i>Adrastus pallens</i>]. (O)
111	105	86	Apex of hind wing with median field (Muona1993): 0) unsclerotised [<i>Hypnoidus riparius</i>]; 1) sclerotised (Figs. 19, 20) [<i>Elater ferrugineus</i>].
112	106	87	Apex of hind wing with posterior field (Muona1993): 0) unsclerotised [<i>Hypnoidus riparius</i>]; 1) sclerotised (Figs. 19, 20) [<i>Elater ferrugineus</i>].
113	107	88	Quant. Metacoxal plate: (width)/(length at widest point mesad of trochanter attachment).

#	#E	#C	Character Description (O = ordered multistate character)
114	108	89	Metacoxae with posterior excavation: 0) sufficient to cover at least 2/3 area of trochanter with hind legs withdrawn (Fig. 22) [<i>Cardiophorus gramineus</i>]; 1) insufficient to cover 2/3 of trochanter with hind legs withdrawn [<i>Athous vittatus</i>].
115	109	90	Metacoxal plate: 0) not reaching metepisternum or shorter than 1/3 posterior width of metepisternum laterad of intersection with metepisternum (Fig. 22) [<i>Cardiophorus gramineus</i>]; 1) reaching more than halfway across metepisternum and longer than 1/3 posterior width of metepisternum laterad of intersection with metepisternum (Fig. 21) [<i>Aulonthroscus punctatus</i>].
116	110	x	Metacoxae: 0) connate [<i>Elater ferrugineus</i>]; 1) separated [<i>Anischia</i> sp.].
117	111	x	Metacoxae with posterior surface oriented: 0) posteriorly [<i>Elater ferrugineus</i>]; 1) posteroventrally [<i>Dima elateroides</i>].
118	x	91	Metacoxal plate with mesally directed hook: 0) absent [<i>Elater ferrugineus</i>]; 1) present [<i>Cardiohypnus mirabilis</i>].
119	112	92	Metatibia with number of apical spurs: 0) 2 [<i>Elater ferrugineus</i>]; 1) 0 [<i>Lissomus bicolor</i>].
120	113	93	Quant. Dorsal lengths of tarsomeres of hind leg: (1)/(2).

#	#E	#C	Character Description (O = ordered multistate character)
121	114	94	Metatarsi with only the following tarsomeres lobed or lamellate: 0) none [<i>Elater ferrugineus</i>]; 1) 3 [<i>Anchastus digitatus</i>]; 2) 4 [<i>Cardiotarsus capensis</i>]; 3) 3, 4 [<i>Monadicus sp.</i>]; 4) 1, 2, 3 [<i>Athous vittatus</i>]; 5) 2, 3, 4 [<i>Aulonthroscus punctatus</i>]; 6) 1, 2, 3, 4 [<i>Tetralobus flabellicornis</i>].
122	115	95	Metatarsal claws with basal setae: 0) absent [<i>Elater ferrugineus</i>]; 1) present, multiple in some [<i>Agrypnus murinus</i>].
123	116	96	Metatarsal claws with number of points (including flange <i>sensu</i> Stibick 1971)): 0) 1 [<i>Elater ferrugineus</i>]; 1) 2 [<i>Dicronychus cinereus</i>]; 2) 3 or more [<i>Melanotus castanipes</i>].
124	117	x	Urosternite 3 with rimmed oval depressions for reception of hind femur: 0) absent [<i>Elater ferrugineus</i>]; 1) present [<i>Lissomus bicolor</i>].
125	118	97	Urosternites 3-6 with size of adjacent punctures: 0) approximately uniform [<i>Elater ferrugineus</i>]; 1) of 2 size classes [<i>Paracardiophorus musculus</i>].
126	119	98	Urosternites 3-7 with elongate punctures: 0) absent [<i>Athous vittatus</i>] or limited to urosternites 6 and 7; 1) throughout [<i>Ampedus sanguineus</i>].
127	120	99	Lateral edges of urosternites 3-7 with serrations: 0) present on at least some [<i>Cardiophorus gramineus</i>]; 1) absent [<i>Elater ferrugineus</i>].
128	121	x	Urosternite 7: 0) without spines [<i>Elater ferrugineus</i>]; 1) with mesal row of spines [<i>Thylacosternus vittatus</i>].

#	#E	#C	Character Description (O = ordered multistate character)
129	x	100	Urosternites 6 and 7 with multiple longitudinal ridges: 0) absent [<i>Elater ferrugineus</i>]; 1) present [<i>Tropidiplus tellinii</i>].
130	122	x	Abdomen with number of fused urosternites: 0) 4 (1 free sclerite) [<i>Elater ferrugineus</i>]; 1) 5 (0 free sclerites) [<i>Anelastes druryi</i>], 2) 3 (2 free sclerites) [<i>Anischia</i> sp.].
131	x	101	Urosternite 7 (and in some 6) with second carina mesad of lateral carina: 0) absent [<i>Cardiophorus gramineus</i>]; 1) present [<i>Tropidiplus tellinii</i>].
132	123	x	Abdominal tergites 2-7: 0) weakly sclerotised, flexible [<i>Elater ferrugineus</i>]; 1) rigidly sclerotised [<i>Thylacosternus</i> sp.].
133	124	102	Male urosternite 8 with mesal third of anterior sclerotised band (anterior margin between bases of anterior lobes): 0) straight, bisinuate [<i>Arhaphes diptychus</i>] or arcuate [<i>Paracardiophorus musculus</i>], width uniform or interrupted mesally [<i>Cardiophorus gramineus</i>]; 1) anteriorly angulate, width uniform [<i>Zorochros demustoides</i>]; 2) broadened mesally, anteriorly arcuate [<i>Ampedus sanguineus</i>], interrupted laterally in some [<i>Physorhinus erythrocephalus</i>]; 3) indistinguishable from posterior lobes, because sclerite of uniform length across width or longest mesally [<i>Patriciella australica</i>]; 4) indistinguishable from posterior lobes, because posterior lobes connate basally [<i>Lesnelater madagascariensis</i>]; 5) absent (entirely unsclerotised) although posterior lobes present [<i>Dicrepidius ramicornis</i>].

#	#E	#C	Character Description (O = ordered multistate character)
134	125	103	Sclerotised basal band of male urosternite 8: 0) not extending laterally beyond posterior lobes (i.e. posterior edge of sclerite convex from apex of lobes to sides of sclerite) [<i>Elater ferrugineus</i>]; 1) extending laterally beyond slope of lobes (posterior edge of sclerite sinuate from apex of lobes to sides of sclerite) [<i>Paracardiophorus musculus</i>].
135	126	104	Tergite and sternite of male abdominal segment 9 articulated at: 0) sides [<i>Elater ferrugineus</i>]; 1) base [<i>Blaiseus bedeli</i>].
136	x	105	Male urosternite 9 with anterior end: 0) not pointed [<i>Elater ferrugineus</i>]; 1) pointed [<i>Paradonus pectoralis</i>].
137	127	106	Quant. Length of male urotergites: (9 [measured at point of greatest length])/ (10 [measured at midline]).
138	128	107	Male urotergites 9 and 10: 0) not fused mesally [<i>Elater ferrugineus</i>]; 1) fused mesally [<i>Fleutiauxellus maratimus</i>].
139	129	108	Male urotergite 9 in male with shape of apical emargination: 0) "U" [<i>Elater ferrugineus</i>]; 1) intermediate between "U" and "V" [<i>Ampedus sanguineus</i>]; 2) "V" [<i>Agrypnus murinus</i>]; 3) rectangular [<i>Oxynopterus strachani</i>].
140	130	x	Aedeagus with phallobase: 0) bilaterally symmetrical [<i>Elater ferrugineus</i>]; 1) asymmetrical [<i>Eudicronychus</i> sp.].

#	#E	#C	Character Description (O = ordered multistate character)
141	131	109	Aedeagus with antero-dorsal concavity or sinuosity of phallobase in dorsal view: 0) simple [<i>Elater ferrugineus</i>]; 1) with mesal convexity [<i>Cardiophorus gramineus</i>].
142	132	110	Aedeagus with posterior emargination of phallobase: 0) deep and evenly concave [<i>Elater ferrugineus</i>]; 1) reduced, concavity nearly absent [<i>Pityobius anguinus</i>]; 2) produced mesally [<i>Athous vittatus</i>].
143	133	111	Quant. Aedeagus: (width of posterodorsal concavity cavity of phallobase [0 if absent])/(maximum width of phallobase).
144	134	112	Quant. Aedeagus: (length of phallobase [longitudinal distance between anterior and posterior most points])/(maximum width of phallobase).
145	135	113	Quant. Median lobe of aedeagus: (length of apical portion [portion posterad of concavity between basal struts])/(length of concavity between basal struts).
146	136	114	Quant. Aedeagus: (length of entire median lobe [including basal struts])/(maximum width of phallobase).
147	137	115	Quant. Aedeagus: (length of parameres)/(maximum width of phallobase).
148	138	116	Quant. Aedeagus: (length of overlap between phallobase and parameres)/(maximum width of phallobase).
149	139	x	Aedeagus with phallobase: 0) not fused to base of parameres [<i>Elater ferrugineus</i>]; 1) fused to parameres ventrally [<i>Lissomus bicolor</i>].

#	#E	#C	Character Description (O = ordered multistate character)
150	140	117	Aedeagus with parameres: 0) articulated basally, pivoting at base [<i>Elater ferrugineus</i>]; 1) articulated apicad of bases (bases free), not forming a tube [<i>Physorhinus erythrocephalus</i>]; 2) articulated apicad of base, bases fused together into a tube both dorsally and ventrally (parameres rigid in some) [<i>Cardiophorus gramineus</i>]; 3) not articulated, fused together dorsally only [<i>Eudicronychus sp.</i>]; 4) fused with median lobe [<i>Selonodon speratus</i>]; 5) articulated basally, with extra sclerite between them [<i>Aulonothroscus punctatus</i>].
151	x	118	Parameres in species with parameres articulated beyond bases with abrupt narrowing immediately apicad of point of articulation: 0) absent [<i>Cardiophorus gramineus</i>]; 1) present [<i>Cardiophorus cardisce</i>]; ?) parameres articulated basally.
152	141	119	Aedeagus with parameres with pre-apical or apical expansions: 0) absent [<i>Elater ferrugineus</i>]; 1) present, lateral or ventral [<i>Agriotes sputator</i>]; 2) absent, but serrate pre-apically [<i>Anelastes druryi</i>]; 3) present, mesal side [<i>Cardiophorus luridipes</i>].
153	142	x	Parameres with preapical depressions (i.e. scooped): 0) absent [<i>Elater ferrugineus</i>]; 1) present [<i>Hemiops flava</i>].
154	x	120	Parameres with ratio of lateral width to dorsoventral depth of free portion: 0) less than 2 [<i>Cardiophorus gramineus</i>]; 1) greater than 2 [<i>Cardiophorus luridipes</i>].

#	#E	#C	Character Description (O = ordered multistate character)
155	x	121	Parameres with number of apices: 0) 1 [<i>Elater ferrugineus</i>]; 1) 2 [<i>Blaiseus bedeli</i>].
156	143	122	Parameres in dorsal view with profile of mesal edge of apices: 0) not concave [<i>Elater ferrugineus</i>]; 1) concave [<i>Dicrepidius ramicornis</i>].
157	144	123	Parameres with number of setae on each: 0) 0 [<i>Agriotes sputator</i>]; 1) 1 [<i>Hypnoidus riparius</i>]; 2) 2 [<i>Cardiophorus gramineus</i>]; 3) 3 or more [<i>Elater ferrugineus</i>]. (O)
158	145	124	Parameres with setae: 0) restricted to sides, basad of apicolateral expansions [<i>Dicronychus cinereus</i>] or of apical arc in species without expansions [<i>Esthesopus parvus</i>]; 1) restricted to apex, apicad of apicolateral expansions if present [<i>Athous vittatus</i>] or to apical arc if expansions absent [<i>Selonodon speratus</i>]; 2) both apicad and basad of apicolateral expansions [<i>Pyrophorus notilucus</i>] or apical arc; ?) with position uncertain because apical arc not distinguishable and apicolateral expansions absent.
159	146	125	Parameres with apices: 0) opaque or otherwise not abruptly translucent [<i>Cardiophorus gramineus</i>]; 1) abruptly translucent [<i>Dicrepidius ramicornis</i>].
160	147	x	Aedeagus with parameres asymmetrically twisted: 0) no [<i>Elater ferrugineus</i>]; 1) yes [<i>Anisomerus sylvestris</i>].

#	#E	#C	Character Description (O = ordered multistate character)
161	148	x	Aedeagus with spine-like setae on parameres: 0) absent [<i>Elater ferrugineus</i>]; 1) present [<i>Heteroderes sordidus</i>].
162	149	x	Aedeagus with parameres with patch of setae on inner edge: 0) absent [<i>Elater ferrugineus</i>]; 1) present [<i>Semiotus furcatus</i>].
163	150	126	Aedeagus with median lobe with apex in side view: 0) without globular expansion [<i>Elater ferrugineus</i>], straight or down turned; 1) with globular expansion [<i>Esthesopus castaneus</i>], straight or down turned; 2) without expansion, but abruptly upturned [<i>Agrypnella eburnea</i>]; 3) split into dorsal and ventral lobes with partially sclerotised sac protruding [<i>Onichodon orchesoides</i>].
164	151	x	Aedeagus with apex of median lobe in dorsal view: 0) unsplit [<i>Elater ferrugineus</i>]; 1) bilobed apically [<i>Heteroderes sordidus</i>].
165	152	x	Aedeagus with lateral preapical expansions of median lobe: 0) absent [<i>Elater ferrugineus</i>]; 1) present [<i>Heteroderes sordidus</i>].
166	153	x	Female urosternite 8 and Urotergite 8: 0) not joined basally, separated by membranous tissue [<i>Elater ferrugineus</i>]; 1) fused basally by a thin sclerotised strip [<i>Lissomus bicolor</i>].
167	154	127	Female urosternite 8 with lateral sclerotisations: 0) joined at or near apex [<i>Elater ferrugineus</i>]; 1) not joined apically [<i>Zoroachros demustoides</i>].

#	#E	#C	Character Description (O = ordered multistate character)
168	155	128	Female urosternite 8 with lateral sclerotisation: 0) joined to sclerotised spiculum [<i>Elater ferrugineus</i>]; 1) separated from sclerotised spiculum by membranous tissue or intermittent sclerotisation [<i>Cardiophorus gramineus</i>].
169	x	129	Female urosternite 8 with spiculum: 0) present [<i>Elater ferrugineus</i>]; 1) absent [<i>Lesnelater madagascariensis</i>].
170	156	130	Ovipositor with sclerites of coxites: 0) narrow, occupying less than 1/2 width of coxites at midlength [<i>Cardiophorus gramineus</i>]; 1) heavy, occupying more than half of width of coxites at midlength [<i>Elater ferrugineus</i>].
171	157	131	Quant. Ovipositor: (paraproct length)/(coxite length).
172	158	132	Ovipositor with apical stylus: 0) absent [<i>Cardiophorus gramineus</i>]; 1) present [<i>Agriotes sputator</i>].
173	159	x	Ovipositor with baculae and coxites: 0) not fused [<i>Elater ferrugineus</i>]; 1) fused [<i>Thylacosternus sp.</i>].
174	160	133	Vagina with colleterial glands: 0) absent [<i>Cardiophorus gramineus</i>] or feebly developed, less than hemispherical [<i>Rivulicola variegatus</i>]; 1) hemispherical, not pedunculate at base [<i>Elater ferrugineus</i>]; 2) globose, and pedunculate at base [<i>Athous vittatus</i>]. (O)

#	#E	#C	Character Description (O = ordered multistate character)
175	161	134	Vagina with colleterial glands attached: 0) on either side of common oviduct [<i>Elater ferrugineus</i>]; 1) anterior to common oviduct [<i>Anisomerus sylvestris</i>]; 2) posterior to common oviduct [<i>Athous vittatus</i>].
176	162	x	Vagina with diverticulae of colleterial glands: 0) absent [<i>Elater ferrugineus</i>]; 1) present [<i>Tetralobus flabellicornis</i>].
177	x	135	Bursa copulatrix with spermathecal gland duct opening (or shared spermatheca-spermathecal gland duct): 0) away from base of blind sac [<i>Cardiophorus gramineus</i>]; 1) adjacent to base of blind sac [<i>Paracardiophorus musculus</i>].
178	163	136	Spermathecal gland (or shared) duct opening: 0) at distal (anterior) end of bursa copulatrix [<i>Elater ferrugineus</i>]; 1) between vagina [<i>Esthesopus parvus</i>] and midlength of bursa [<i>Cardiophorus gramineus</i>].
179	164	137	Bursa copulatrix with spermathecal gland duct attached to: 0) main bursa [<i>Cardiophorus gramineus</i>] or extension of bursa: non-tubular [<i>Cebrio gigas</i>] or tubular [<i>Elater ferrugineus</i>]; 1) spermatheca [<i>Anelastes druryi</i>] or shared duct [<i>Oedostethus femoralis</i>].
180	165	138	Female spermathecal gland duct with single row of diverticulae: 0) present [<i>Cardiophorus gramineus</i>]; 1) absent (but duct present) [<i>Elater ferrugineus</i>].
181	166	139	Number of coil type spermathecae: 0) 0 [<i>Cardiophorus gramineus</i>]; 1) 1 [<i>Agriotes sputator</i>]; 2) 1 [<i>Pyrophorus notilucus</i>].

#	#E	#C	Character Description (O = ordered multistate character)
182	167	140	Female with number of sclerotised capsule type spermathecae: 0) 0 [<i>Cardiophorus gramineus</i>]; 1) 1 [<i>Elater ferrugineus</i>]; 2) 2 [<i>Aulonthroscus punctatus</i>].
183	x	141	Bursa copulatrix with blind pedunculate sac attached to: 0) apical part of main bursa [<i>Cardiophorus gramineus</i>]; 1) basal part of main bursa (near median oviduct) [<i>Onichodon orchesoides</i>].
184	168	142	Bursa copulatrix with number of blind pedunculate sacs: 0) 0; 1) 1 [<i>Cardiophorus gramineus</i>]; 2) 2 [<i>Horistonotus simplex</i>]; 3) 5 [<i>Eulichas</i> <i>sp.</i>].
185	169	143	Bursa copulatrix with number of non-pedunculate blind tubular extensions: 0) 0 [<i>Cardiophorus gramineus</i>]; 1) 1 [<i>Elater ferrugineus</i>]; 2) 2 or more [<i>Melanotus castanipes</i>].
186	170	144	Bursa copulatrix with free spines (i.e. not part of sclerite with multiple spines): 0) absent [<i>Cardiophorus gramineus</i>]; 1) present [<i>Melanotus</i> <i>castanipes</i>].
187	171	145	Bursa copulatrix with free spines: 0) not combined into paired, discrete, ovoid patches [<i>Melanotus castanipes</i>]; 1) present and combined into paired discrete ovoid patches, with individual spines separated by membranous tissue [<i>Exoeolus rufescens</i>]; 2) present and combined into flexible paired discrete ovoid patches, but with some spines partially fused [<i>Physorhinus erythrocephalus</i>]. (O)

#	#E	#C	Character Description (O = ordered multistate character)
188	172	x	Bursa copulatrix with free spines arranged into a column of overlapping spines: 0) no (none) [<i>Melanotus castanipes</i>]; 1) yes (at least some) [<i>Physorhinus erythrocephalus</i>].
189	173	146	Bursa copulatrix with rugose, spineless, partially sclerotised patches: 0) absent [<i>Cardiophorus gramineus</i>]; 1) present [<i>Horistonotus simplex</i>].
190	x	147	Bursa copulatrix with single dorsal and ventral sclerites both: 0) absent [<i>Negastrius pulchellus</i>]; 1) present [<i>Oedostethus femoralis</i>].
191	x	148	Bursa copulatrix with single dorsal and ventral sclerites: 0) both bilaterally symmetrical [<i>Oedostethus femoralis</i>]; 1) not both symmetrical [<i>Quasimus minutissimus</i>].
192	x	149	Bursa copulatrix, of species with single symmetrical dorsal and ventral sclerite of bursa copulatrix, with ventral sclerite: 0) fully sclerotized at midline [<i>Oedostethus femoralis</i>]; 1) divided or weakly sclerotised along midline [<i>Neoarhaphes americanus</i>].
193	x	150	Bursa copulatrix with single dorsal and ventral sclerites: 0) both not ring-like, opaque at center [<i>Oedostethus femoralis</i>]; 1) with at least dorsal sclerite ring-like, and transparent at center [<i>Arhaphes diptychus</i>].
194	x	151	Quant. (meristic) Bursa copulatrix with paired proximal sclerites: (count # of rows of spines, including outer row, which surrounds most of sclerite in most species).

#	#E	#C	Character Description (O = ordered multistate character)
195	x	152	Bursa copulatrix with proximal sclerites (defined as pair of spine bearing sclerites closest to vagina (for species with only 1 pair of sclerites: defined as proximal if not surrounding base of spermathecal gland duct): 0) absent [<i>Craspedostethus rufiventris</i>]; 1) present [<i>Cardiophorus gramineus</i>]; 2) absent but with 3 asymmetrical spine bearing sclerites [<i>Agriotes sputator</i>].
196	x	153	Bursa copulatrix with points of proximal sclerites: 0) simple [<i>Cardiophorus gramineus</i>]; 1) pinnate [<i>Cardiotarsus capensis</i>].
197	x	154	Bursa copulatrix with proximal sclerites: 0) ovoid [<i>Cardiophorus gramineus</i>]; 1) bilobed [<i>Platynychus mixtus</i>]; 2) parallel sided [<i>Globothorax chevrolati</i>]; 3) with multiple acute lobes [<i>Esthesopus parvus</i>].
198	x	155	Bursa copulatrix with placement of proximal sclerites: 0) symmetrical [<i>Cardiophorus gramineus</i>]; 1) asymmetrical [<i>Cardiophorus brunnipennis</i>].
199	x	156	Quant. Bursa copulatrix: (length of largest spines of proximal sclerites [measured as smallest possible distance between a line connecting 2 adjacent spines and the deepest part of the concavity between them])/(length of posterior sclerites).

#	#E	#C	Character Description (O = ordered multistate character)
200	174	157	Bursa copulatrix with paired distal sclerites (pair farthest from vagina, at base of spermathecal gland duct or shared duct): 0) absent [<i>Elater ferrugineus</i>]; 1) present [<i>Cardiophorus inflatus</i>], fused together in some at wall of bursa [<i>Cardiophorus gramineus</i>].
201	x	158	Bursa copulatrix with distal sclerites: 0) separate from each other [<i>Cardophorus inflatus</i>]; 1) fused at one end (at wall of bursa) into a "U" [<i>Cardiophorus gramineus</i>]; 2) fused at both ends to form a loop [<i>Aptopus pullatus</i>].
202	x	159	Bursa copulatrix with distal sclerites: 0) smooth [<i>Cardiophorus gramineus</i>]; 1) rugose [<i>Dicronychus cinereus</i>].
203	x	160	Bursa copulatrix with distal sclerites: 0) flexible and at least in part weakly sclerotised and membranous [<i>Cardiophorus convexus</i>]; 1) entirely sclerotised [<i>Cardiophorus gramineus</i>].
204	175	161	Bursa copulatrix with tube-like sclerotisation of base of spermathecal gland duct: 0) absent [<i>Cardiophorus gramineus</i>]; 1) present, without paired plate like appendages [<i>Paracardiophorus musculus</i>]; 2) present, with paired plate like appendages [<i>Cardiophorus cardisce</i>]. (O)
205	176	162	Habitat: 0) restricted to riparian areas [<i>Negastrius pulchellus</i>]; 1) not restricted to riparian areas [<i>Elater ferrugineus</i>]. (Not used to infer phylogeny)

#	#E	#C	Character Description (O = ordered multistate character)
206	177	163	Bursa copulatrix with multiple parallel linear sclerites: 0) absent [<i>Elater ferrugineus</i>]; 1) present [<i>Athous vittatus</i>].
207	178	x	Bursa copulatrix with sclerites with three spines: 0) absent [<i>Elater ferrugineus</i>]; 1) present (set of four) [<i>Lissomus bicolor</i>].
208	179	x	Bursa copulatrix with ring-shaped sclerite circling bursa: 0) absent [<i>Elater ferrugineus</i>]; 1) present [<i>Tetralobus flabellicornis</i>].

Appendix 9. Nexus files used for phylogenetic analysis

There are six matrices below. The first three are for chapter 2. (Clicking Elateroidea), and the rest are for Chapter 3. (Cardiophorinae). Within each set of three, the first is for Bayesian analysis, the second parsimony with binary coded quantitative characters, the third for parsimony with gap-weighted parsimony analysis. For analyses of Clicking Elateroidea, to add fossil taxa (Protocar Pseudoca Crioraph) or to remove Cardiophorinae coded from only one sex (Lesnelat, Margogas, NZAphric, Teslasen), change the taxa listed for exclusion in this line: “delete Protocar Pseudoca Crioraph;”.

4.1 Clicking Elateroidea, Mr. Bayes.

#NEXUS

[ElatMB64

Fossorial chars and habitat deleted (also including mandibular apex shape) (# 10 47 62 removed, (here counter #s 9 44 59).

That was Matrix done using Characters 25MA.XLS]

BEGIN Data;

DIMENSIONS NTAX=58 NCHAR=179;

format datatype=Standard missing=?;

MATRIX

```
Adrastus 00000100100100?1000000220000001000002002100100001000000111001110010
010201000000000011000110000000001101201111000000200010000000020101000000
0001310000000000000100?010100000?00001000
Agriotes 00100000100100?0000000011000001000002002100100101001000111010112000
010200001000000011000100000000000100101100000000000110002000020001000000
01000?000000000100100?001?10?10??0001000
Agrypnus 00100100100100110010000000100011220001020000010100101101011100210100
11102000120100010211011100010000?1???0000000000000111000100000000101001
0210020000020000010?00?0???0000???0?00000
Agrypnus 00100100100100?000000000100100100010000110010020010000011101011201
00112000120000000010001000000000100010111001001000010000000020?0000000
00100310000000000010001000??10011000011000
Ampedus_ 000001001001000100000001100000100000000110010010?000000011101011201
00102000000000000110001000000000010010100100000000011000200001000100000
001003100000000000101010000?00211000001000
```


Hypnoidu 000001001001100000010000100100100000200110010100101100011100111200
 001020000101000001100010000000?00010010000000000000111000000000?0000000
 000001000000000000000020000?00000?00000000
 Lesnelat 00000000100100?1000000011000000000100?0?100000000?0001011?1111020100
 1000101200000001100000000000002111?1010100000000000?0004100000?000000002
 10020000000000?100010000100100?000?000
 Lissornus 0010010210000?000001000100000000000001100100200000000111010101002
 110201111011010010000100001000000000101111001060010010105?00020?00000001
 0101320000000100100022010100010?0?0?01010
 Macropog 00001204202200?0001000010000?000120000110000000?0?0?0000010112310
 120400000000000011000101000000000100000101000050000010101000020?0000000
 00010?000000001000100?0001?020?0?1001000
 Margogas ?000?002000100010001?022100000000010110100010000?0?0?01011112100?0?
 ?0?0?1011?00?000110001000?
 ?0?
 Megapent 001001001001000100000001100000100000000110010000011100011101011200
 00102000000000000011000100000000000010011100100000000011000200000010100001
 00101311000000001001012000101021000001000
 Melanotu 0000010010010001000000010000010001020031001001010110101110111201
 0010200000000000001100010000000000001101101000000020011000200000000100000
 00100310000000001011010000100021000001000
 NegastAm 000000001001100100100001100000?000002?0?10010000001101011112103200
 101020101201000001100010001?0?
 2000200000000001000000?000100210?0?0001000
 Negastru 00100100100110010000001100100010001000011001010011100001110?1112000
 110200012010000001101100001000021??00000000000000001100010000001?0011010
 2001300000000001000010000100000?00000000
 Neohypdo 000000011001100100010001100000100010000110010100001000011101111200
 11102000120100000010011000010000211??100011000000000001000000000010100001
 02001311000000001000010011101000?0000?000
 Oedostet 0000000010011001000100001000001000100001100101001000000111011112001
 110201?120000000010001000010000211?11000010000001000100000000100010000010
 200131100000000100000?011101000?00000000
 Oestodes 00000000100100?0000000111000001000102001100000000000000111010012010
 0102000000000000011000100001001001000100111000000000010002000000001000000
 0100310000000000101010011101010?00000000
 Onichodo 0000010121?00?000100001000010000000000001020001001000000111010122210
 11021?01?000000011000100000001?01?0121100000002010001010300?1?0001011100
 31010?000030000100100?0?0?00210?0001000
 Oxynopte 0010101000110?000001000100100000001000110010000000000011101111000
 002020000010000001000010010000000010010101000000000001000200003000000000
 00101300000000000000101?000100021000001000
 Paracard 000000001001100100010000100001?000102?0?100100001000001111012100000
 000001012010000001000100001000001011101000000000001000000100000101000000
 23002?000000000100000?000000100?0010000
 Physodac 000001000021000100000011100010000000010210000000000101011111011001
 0010200000000000001100010000000000010021101000000?00001000500002000000001
 00100210000000?
 Physorhi 0000010010010001000000000000101100000001000100101111000111010112000
 010200011000000011001100000000000100111000000020000010002000100100000010
 1000300000000001001102?0?0?00111010001000
 Pityobiu 100011001001000100001000100000000000001100100000011000111010112010
 010200000000000011000100000000000100101111000060000010000000000011000000
 01010?000000000100000?010100020?0001000
 Porthmid 0000010010010001000100001000001100000002000100100001000111010112010
 010201000000000011000100000000000100201000000010000010002000000001000000
 010031000000000001000000100121200001000
 Promople 001111001002??000000111000001000000101100000000000000111011112010
 010200000000000011000100000000000000100010000000000010002000000001000000
 0100320000000?
 Prostern 000001001001000000000001000001000000001200100000011000111000112002
 0000000000000000011000100000000000010010011100000000000000000020101000000
 0101210000000000001010010100010?0001000
 Protocar ?0?
 ?0?
 ?0?


```

Pseudoca ?????????????????0????????????0???0????????????0????????????1?????????????
????????????????????0????????????????1????????0????0????????????????????????
????????????????????????????????
Pyrophor 0000010010010001000010001000101010200001100101100100000111010110001
00120000001000001100010000000010010001011010000010000100050010107000000000
0101320000000000100022000120001000001000
Quasimus 001001001001100100000011000000200010000110010110100100011101110200
0110100?12010011010000100001000?1???000000000020000110001000000?0000000
020012000000000010000? ??????????0?00001000
Selonodo 000001000002????00000011100010100020030?1000000000000000111113112?10
120200010000100011000100000000100110101010000000000010000001020101000000
40003100000000001000?0001??100??0001000
Semiotus 0000000010010001010000001000101000200001200100000110000111011011011
1102000001110000110001001000010001001001110000600000000000000020000000000
0101320001000000011020000100020?0001000
Teslasen ?000?000000100010001100000000?000000?0?00000000000111111110100000
01000101201000000101010000000101101010101000000010001000400002????????????
????????????????????????????????????
Tetralob 0010010010310101000000001000001000300001100100000100000111010011000
1002001000000000001000100000011101101101101000061000010000001020020000000
00010?0000000000011020100?10000?0001001
Thylacos 0000110010000???000000110000100000200011100001201000000111011112011
110200100000000011000100000001000000101011001160000011010000010? ????????1?
1013100000001001101070???00100?00001000
Tropihyp 0000010010011001000100011001101000002001100101001110000111000110001
010100012000000001100100000000021100100100000000001110001000020000000000
000111100000000000000100???00000?0000000
;
end;

```

```

begin mrbayes;
outgroup Macropog;
delete Protocar Pseudoca Crioraph;
exclude 9 44 59 176; [fossorial reduced and habitat]
log start filename=ElatMB64.log.txt replace;
lset nst=1 coding=variable rates=gamma;
ctype ordered: 6 9 27 31 37 47 54 76 104 144 160 171 175;
showmodel;
mcmc ngen=8000000 samplefreq=100 printfreq=1000 nchains=4 savebrlens=yes;
sump filename=ElatMB64.nex printtofile=yes;
sumt filename=ElatMB64.nex burnin=20000 showtreeprobs=no contype=all
displayeq=0;
log stop;
END;

```

4.2 Clicking Elateroidea, binary quantitative parsimony.

The matrix has been deleted from the nexus file, because it is identical to the previous matrix.

```

#NEXUS
[ElatMB64

```

Fossorial chars and habitat deleted (also including mandibular apex shape) (# 10 47 62 removed, (here counter #s 9 44 59).

Matrix done using Characters 25MA.XLS]

begin taxa;

dimensions ntax=58;

taxlabels

Adrastus	Agriotes	Agrypnel	Agrypnus	Ampedus_	Anchastu
Anelaste	Anischia	Anisomer	NZAphric	Arhaphes	
Athous__	Aulonoth	Berninel	Cardioph	Cebrio__	
Cerophyt	Crioraph	Dicrepid	Dima_____	Elater__	
Eudicron	Eulichas	Exoeolus	Hemiops_	Heterode	
Horiston	Hypnoиду	Lesnelat	Lissomus	Macropog	
Margogas	Megapent	Melanotu	NegastAm	Negastri	
Neohypdo	Oedostet	Oestodes	Onichodo	Oxynopte	
Paracard	Physodac	Physorhi	Pityobiu	Porthmid	
Promople	Prostern	Protocar	Pseudoca	Pyrophor	
Quasimus	Selonodo	Semiotus	Teslasen	Tetralob	
Thylacos	Tropihyp				

;

end;

begin characters;

dimensions nchar=179;

format symbols = "0 1 2 3 4 5 6";

MATRIX

[Deleted to save space. Identical to previous matrix]

;

end;

begin assumptions;

CHARSET ORDERED = 6 9 27 31 37 47 54 76 104 144 160 171 175;

TYPESET * normal = unord: all, ord: ordered;

end;

begin paup;

log file=ElatMB64.log;

delete Protocar Pseudoca Crioraph;

outgroup Macropog;

exclude 9 44 59 176; [fossorial reduced and habitat]

set maxtrees=100 increase=auto;

hsearch addseq=random nreps=1000;

savetrees file=ElatMB64.trees;

contree/ treefile = consensus.tre;

end;

4.3 Clicking Elateroidea, gap-weighted parsimony.

#NEXUS

[Reweighted to account for quant coding scale

ElatMB64

Fossorial chars and habitat deleted (also including mandibular apex shape) (# 10 47 62 removed, (here counter #s 9 44 59).

Matrix done using Characters 25MA.XLS]

begin taxa;

dimensions ntax=58;

taxlabels

Adrastus	Agriotes	Agrypnel	Agrypnus	Ampedus_	Anchastu
Anelaste	Anischia	Anisomer	NZAphric	Arhaphes	
Athous_	Aulonoth	Berninel	Cardioph	Cebrio_	
Cerophyt	Crioraph	Dicrepid	Dima_	Elater_	
Eudicron	Eulichas	Exoeolus	Hemiops_	Heterode	
Horiston	Hypnoideu	Lesnelat	Lissomus	Macropog	
Margogas	Megapent	Melanotu	NegastAm	Negastri	
Neohypdo	Oedostet	Oestodes	Onichodo	Oxynopte	
Paracard	Physodac	Physorhi	Pityobiu	Porthmid	
Promople	Prostern	Protocar	Pseudoca	Pyrophor	
Quasimus	Selonodo	Semiotus	Teslasen	Tetralob	
Thylacos	Tropihyp				

;

end;

begin characters;

dimensions nchar=179;

format symbols = "0 1 2 3 4 5 6 7 8 9";

MATRIX

```

Adrastus 00311100100101?10000202200000010000002002100100001232200111001110010
010206000033000011000110000024001101201611000200200010000004020109214330
0001310000000000002100?010100000?70001000
Agriotes 00611010100100?0000020011000001000002002100100101445100111010112000
010203001042000011000100000042000100101500000100000110002001020008113230
01000?000000000104100?001?10?10?70001000
Agrypnel 00611101001130100001001000112200010200000010100145631011100210100
11102030120530010211011100010140?1???00020000010000111000100100000519338
0210020000020000011?00?0?7?0000???0?00000
Agrypnus 00821110100101?000002000100100100010000110010020062310011101011201
0011203012034000001000100000032001000101611001201000010000002020?0002222
00100310000000000013001000??10011000011000
Ampedus_ 002411001001010100002001100000100000000110010010?33210011101011201
001020300002400001100010000004200010010130100030000011000200101000711323
001003100000000000141010000?00211000001000

```



```

Pseudoca ?????????????????0????????????0????????????0????????????1????????????
????????????????????0????????????????1????????0????????????????????
????????????????????
Pyrophor 0041112010010101000060001000101010200001100101100733100111010110001
001202000053000011000100000045001000101601000201000010005007010700112120
0101320000000000110022000120001000001000
Quasimus 005111001001120100002011000000200010000110010110133720011101110200
0110104?12053011010000100001012??1???000300000020000110001001000?0013441
020012000000000010100?????????0?00001000
Selonodo 003221200002????00004011100010100020030?100000000344000111113112?10
120204010032100011000100000021100110101310000100000010000005020107202110
40003100000000001300?0001??100?00001000
Semiotus 0001001010010101010030001000101000200001200100000954200111011011011
1102020001550000110001001000450001001007110003600000000000002020003213330
0101320001000000081020000100020?00001000
Teslasen ?011?0100001020100015000000000?000000?0?00000000024591111110100000
01000601206200000101010000001601101010121000020010001000400202??????????
????????????????????????????????????
Tetralob 0051412010310701000040001000001000300001100100000632200111010011000
100202100030000001000100000099101101101701000161000010000009020023211030
00010?00000000000051020100?10000?00001001
Thylacos 0020511010000???000020110000100000200011100001201303100111011112011
110204100031000011000100000035000000101311001960000011010002010?????????1?
10131000000010017010?0???00100?00001000
Tropihyp 0031111010011201000120011001101000002001100101001554100111000110001
010103012044000001100100000013021100100600000100001110001000020003121230
00011110000000000300100???00000?00000000

```

```

;
end;

```

```

begin assumptions;
    CHARSET ORDERED = 3-7 9 14 21 27 31 37 47 50-54 73 76 78 79 96 97 104
107 113 127 133-138 144 157 160 171 175; [ordered + quant]
    TYPESET * normal = unord: all, ord: ordered;
end;

```

```

begin paup;
log file=ElatMB64.log;
delete Protocar Pseudoca Crioraph;
outgroup Macropog;
exclude 9 44 59 176; [fossorial reduced and habitat]
weights 10:all, 1:1 2 6 8-13 15-20 22-49 54-72 74-77 80-95 98-106 108-112 114-126
128-132 139-156 158-179;
set maxtrees=100 increase=auto;
hsearch addseq=random nreps=1000;
savetrees file=ElatMB64.trees;
describe;
contree/ treefile = consensus.tre;
describe;
end;

```

4.4 Cardiophorinae, Mr. Bayes.

#NEXUS

[CardMB53, with double #gens and 2 million burnin.

Like fossorial chars, habitat excluded: 10 47 62 (counters: 9 34 46)

Matrix done using Characters 25MB.XLS, none excluded]

BEGIN Data;

DIMENSIONS NTAX= 78 NCHAR=163;

format datatype=Standard missing=?;

MATRIX

```

Adrastus 000001001000?100002200000010202101000010000000011101001021000100110
00011000001011001201011001002001000000102101110100?000131000000010??1010
0?000?00?????0??0?0???010
Agriotes 010000001000?000000110000010202101001011010000101120001020011000110
00010000010001000101000001000011002000002001110000?10000?000100110??01?1
0??10?00????20?0?0???010
Agrypnel 010001001010010000010011202120000101001111010002101011102012110121
100111001000?1????000000000000011100100000000100011201000200200010?0?????0
0?00?00?0?????0???0???000
Agrypnus 010001001000?00000001010001100110100200100000010112100112012010001
000010000010010000101011011010001000000102?00000100?1000310000011010?0??
10?011000????0?0?0?0???110
Aphricus 00010000121011001000100000?10??100000000010100111021101000120000110
10010000001110000101111000000101000000100?00100102010002000?????????????
?????????????????????1?
AphriChi 00010101101001001011100000?10??100000000110100121?20001021000100110
1001000000111010110101000000001000000001?00100102000013000?????????????
?????????????????????
AphricNZ 01110101120001000001000000?11??10010001000010012102100100112100011
000010000001110000100010000000?01000000100101101112010013000?????????????
?????????????????????
AptopusA 000000021210010011000000000111100100001111001012101000000012100001
001000001000010100101010000003100000000100??100102000002000?????????????
?????????????????????
AptopusP 000100001010010011000000000121000100000000010012101000000012110001
0000000010000101001010100000021000000000021010001020100020001000000?0101
000100?00??1100011210110
Arhaphes 000001001010010000431000001200101101011100000010113210100012010011
000010001000110??1000001001000001000000000101000102000012000?0000010??11
11?000?01101?0?0?0???000
Athous_ 010001001000010010001000000200120100000100000001112000102000110011
000010000010001000100011001400000000000100121110000?1000310000001122?001
000211010????0?0?0?0???011
Berninel 0000010210100000100010000010201101000011110000101120001020010100110
0001000010000100000001000000101000000102001001100?00010?1000000120?0010
0?001200????0?0?0?0???000
BlaiseuB 00000000020101001022100000?10??101000010001101111200001020120000010
10000000011010011111010000200001000010000001101102000113?01?????????????
?????????????????????
BlaiseuT 00000010000101001022100000?10??0000000000000101111020001021120100110
1001000000101001?000010000000000100??10??021100002000103?01?????????????
?????????????????????
Buckelat 000100002000?1000000000000?12??001000010100010111010000001121000210
010010010011101?1101000001200000000100002?00101112000002000?????????????
?????????????????????
Cardiodo 00010101101001001100000000?12??001000010100010111010000000121000010
00001001010010000101000000201100000000001101101112000002010?????????????
?????????????????????

```



```

Paracard 00000000101001001000100010712??101000010000010121000000001121000010
00010001010010101101000000000100000100000101000102031002?000100100?10000
00100?00??00100010??100
Paracsub 00000101201001001000000000?12??001000010000010111000000000121000010
0010100100011010110100000100011000000000?1011011120000120000100000?00010
01200?10??0101000???010
Paradonu 010001001010010010111000001100110101000111000011110001102012010010
000010001000?1100?10000000000001001001101000101112000001?00110000??0?1
00??0?00??0??0?0?0??000
Paraplat 00000101101001001100100000?11??001000010000010111010000000121000010
110000010011110011010100010011000100000021010001020000020000100000?00??0
00100?10??1101000???1?0
Patricie 00000001020001001011100000?10??1000000000111011211011010011210000100
001100101101???1101010000000101003?00101?01100102010013001????????????????
????????????????????
Phorocard 0000000010100100107000010011110001000010001000121010001001120000010
00000000011010100101010000001100000000000?000001020100020000100100?10000
00100?00??11000010011?0
PhorDiac 00000002101001001000?00000112100010000110000101210100000?0121100010
0000000100101????10100000000111000?0????????????????????????????1100100?1000000
100?00??11000100??1?0
PlatIndi 00000000101001000100010000111110101000010001010121010000000120000010
0001000101101010110100000?00100100?0????????????????????????????1100100?0100000
100?00??11000111010?0
Pronegas 0???10010100100101111000011001101010011000000111122111020120000010
001001?0????????????00000020000100?0?????10?????20000132?00000000?001100?
000?00?0??0??0?0??0?0
Quasimus 010001001010010000110000002100110101101001000011102001101012101110
000010001000?1???0000000002000110010000000?00001102000012000010000?0?????
???0?01101?0??0?0??010
Rivulico 00000100100001000001011000?12??001010010001100121010101020121001210
00110001000?1?101100000000000010100100010010100110200001300011000000?0111
0?000?00???????0????000
Teslasen ?00?0000000001001000000000?00?0000000001111101000001000121000010
1100000100101001010001001001004000102????????????????????????????????
????????????????????
Tripehus 00010001220101001100100100?11??001000000101110101?011000000121000010
110000010010101001010001002100010000002000000102000002?000001100????0
0???0?10??0102000??0?0
Tripoide 000100000101001001100000100?11??001000010000000121010000000121000010
01000001000110101101000000201000000000102101100102100002000?0????????????
????????????????????
Tropidip 000000001000010010000000011200101000010000010121011001000121000010
01100?00??0100000??1?0
Tropihyp 0000010010100100100110110010201101010011110000001100101010120100011
00010000000211000100000000000111001000002000100100?0001111000001010????0
0?00?00??0??0?0?0??000
YukoanaC 000001021010010010001000002100110101101101000011000001102012110110
000010001000210?0?000001000200011001000100?00001102000002?000100?0?0?111
01?000?00??1?0??0?0??0?0
Zorochro 000011001010010010111000011001101011011100000111120111020120100010
0011000100021???1000000001000101001000000?001011020000030001101000?00110
1?000?00????0??0?0??000
;
end;
```

```
begin mrbayes;  
outgroup ElaterFe;  
delete GloboTes;  
log start filename=CardMB53.log.txt replace;  
lset nst=1 coding=variable rates=gamma;
```

```

exclude 9 34 46 162; [fossorial, habitat]
ctype ordered: 6 9 22 27 29 37 44 60 85 123 133 145 161;
showmodel;
mcmc ngen=8000000 samplefreq=100 printfreq=1000 nchains=4 savebrlens=yes;
sump filename=CardMB53.nex printtofile=yes;
sumt filename=CardMB53.nex burnin=20000 showtreeprobs=no contype=all
displaygeq=0;
log stop;
END;

```

4.5 Cardiophorinae, binary quantitative parsimony.

The matrix has been deleted from the nexus file, because it is identical to the previous matrix.

#NEXUS

[Paup format

Like CardMB52.nex but with fewer fossorial chars excluded: 10 47 62 (counters: 9 34 46)

That was Like CardMB51.nex but made with chars the following fossorial complex chars excluded: 47 54 57 62 67 72 87 113 (counters: 34 41 44 46 51 55 65 88)

That was Matrix redone using Characters 25MB.XLS, none excluded]

begin taxa;

dimensions ntax=78;

taxlabels

Adrastus	Agriotes	Agrypnel	Agrypnus	Aphricus	AphriChi
AphricNZ	AptopusA	AptopusP	Arhaphes	Athous__	
Berninel	BlaiseuB	BlaiseuT	Buckelat	Cardiodo	
Cardiohy	Cardphrl	CardAngu	CardPerr	CardBrev	
Coptoste	CardCard	CardCvxl	CardCvxs	CardGram	
CardInfl	CardLuri	Zygocard	Metacard	CardspC_	
CardToga	CartCape	CartMjob	CartPhil	Craspedo	
Dicronyc	Displaty	ElaterFe	Esthesop	EsthParc	
Fleutiau	Globotho	GloboTes	Horiston	HoriSimp	
Hypnoidu	Lesnelat	Margogas	MigiwaCu	Monadicu	
NegaAmer	Negastri	Neoarhap	Neocardi	Neohypdo	
Nyctor__	Odontoca	Oedostet	ParacHum	Paracard	
Paracsub	Paradonu	Paraplat	Patricie	Phorocar	
PhorDioc	PlatIndi	Pronegas	Quasimus	Rivulico	
Teslasen	Tripchus	Tripoide	Tropidip	Tropihyp	
YukoanaC	Zorocho				

;

```

end;

begin characters;
    dimensions nchar=163;
    format symbols = "0 1 2 3 4 5";

MATRIX
[Deleted to save space. Identical to previous matrix]
;
end;

begin assumptions;
    CHARSET ORDERED = 6 9 22 27 29 37 44 60 85 123 133 145 161;
    TYPESET * normal = unord: all, ord: ordered;
end;

begin paup;
log file=CardMB53.log;
delete GloboTes;
outgroup ElaterFe;
exclude 9 34 46 162 uninf;
set maxtrees=100 increase=auto;
hsearch addseq=random nreps=1000;
savetrees file=CardMB53.trees;
contree/ treefile = consensus.tre;
end;

```

4.6 Cardiophorinae, gap-weighted parsimony.

#NEXUS

[Paup format, Reweighted to account for quant coding scale
Fossorial chars and habitat deleted (also including mandibular apex shape): 10 47 62
(counters: 9 34 46)
Matrix done using Characters 25MB.XLS, none excluded]

```

begin taxa;
dimensions ntax=78;
taxlabels

```

Adrastus	Agriotes	Agrypnel	Agrypnus	Aphricus	AphriChi
AphricNZ	AptopusA	AptopusP	Arhaphes	Athous__	
Berninel	BlaiseuB	BlaiseuT	Buckelat	Cardiodo	
Cardiohy	Cardphrl	CardAngu	CardPerr	CardBrev	
Coptoste	CardCard	CardCvxl	CardCvxs	CardGram	

CardInfl	CardLuri	Zygocard	Metacard	CardspC_
CardToga	CartCape	CartMjob	CartPhil	Craspedo
Dicronyc	Displaty	ElaterFe	Esthesop	EsthParc
Fleutiau	Globotho	GloboTes	Horiston	HoriSimp
Hypnoidu	Lesnelat	Margogas	MigiwaCu	Monadicu
NegaAmer	Negastri	Neoarhap	Neocardi	Neohypdo
Nyctor__	Odontoca	Oedostet	ParacHum	Paracard
Paracsub	Paradonu	Paraplat	Patricie	Phorocar
PhorDioc	PlatIndi	Pronegas	Quasimus	Rivulico
Teslasen	Tripchus	Tripoide	Tropidip	Tropihyp
YukoanaC	Zorochro			

;

end;

begin characters;

dimensions nchar=163;

format symbols = "0 1 2 3 4 5 6 7 8 9";

MATRIX

```

Adrastus 0312011010017100012200000010202101000013232000011101001025003500110
00011000045011001201111005002001000000902109854630?000131000000410??1010
0?000?00????0??0?0???010
Agriotes 0711002010007000010110000010202101001015451000101120001022015300110
00010000093001000101100005000011002000402008674430?10000?000100610??01?1
0??10?00????20?0?0???010
Agrypnel 071101201012010000010011202120000101001556310002101011102112550121
100111001024?1???0000000040001110010004000053036820100020020001270?????0
0?00?000??????0?0???000
Agrypnus 093101201000?00001001010001100110100200813100010112100112112460001
000010000063010000101111016010001000000602?00242520?1000310000015010?0??
10?011000???0?0?0?0???110
Aphricus 0336001012111100120010000?10??100000003463100111021101003123300110
10010000036110000101911001000101000000900?00534642010002000?????????????
?????????????????????1?
AphriChi 02350121101201001111100000?10??100000003793100121?20001025004500110
10010000045110101101010002000001000000401?00534532000013000?????????????
?????????????????????
AphricNZ 06990121120301000301000000?11??10010001203210012102100100512540011
000010000035110000100010002000?01000000500107725552010013000?????????????
?????????????????????
AptopusA 011400421213010015000000000111100100001675401012101000000412630001
001000001034010100101110001003100000000500???513622000002000?????????????
?????????????????????
AptopusP 022700201011010016000000000121000100000244410012101000000412550001
0000000010440101001011100000021000000003021064246320100020001000200?0101
000100?00???7100061210110
Arhaphes 032301201011010004431000001200101101011944000010113210100312490011
000010001031110??1000201007000001000000200108413522000012000?003010??11
11?000?01101?0?0?0?0???000
Athous_ 052301301001010012001000000200120100000634000001112000102100570011
000010000051001000100111009400000000000800127790330?1000310000006122?001
0002110107???0?0?0?0???011
Berninel 0201012210100000100010000010201101000016650000101120001021014500110
00010000143001000000110003000101000000502005026710?00010?1000004120?0010
0?001200????0?0?0?0???000
BlaiseuB 02140020020501001422100000?10??101000013427101111200001024124300010
1000000005901001111010004200001000010200006705632000113?01?????????????
?????????????????????

```



```

Odontoca ???0?1110140100160000000011110001000003333010121010000003125300010
0000000104401010010111000?2011000000002010063235020000120011000900?000?0
00100?00???31000810010?0
Oedostet 0202001010100100110010000011001101010014230000111120111023123500010
00010001023211???11001010040010010000004010065146520000131100100400???1110
1?000?01000?0??0?0???000
ParacHum 03120120101201001101000000?11??00100000254301011110000000312420001
000000001026010100101110004000101000000200?006135420000020000000400?0001
001200?10???0101000???0?0
Paracard 02140020101201001200100010?12??101000012224010121000000006125200010
00010001054010101101000003000100000100400105233532031002?000100500?10000
00100?00???3100050???100
Paracsub 02140101201401001400000000?12??001000013343010111000000004127300010
0010100103311010110110000600011000000030?1078267520000120000100400?00010
01200?10???0101000???010
Paradonu 061001201011010011111000001100110101000567100011110001102212470010
000010001021?1100?100000003000001001001601002928792000001?00110020???0?1
00???0?00???0?0?0?0?0???000
Paraplat 02120111101301001500100000?11??001000014344010111010000002129300010
11000001025110011011100050011000100004021073146320000020000100400?00???0
00100?10???7101000???1?0
Patricie 00130011020201001111100000?10??1000000032751011211011010051252000100
001100105501???1101110001000101003?00501?06524532010013001???????????????
????????????????????
Phorocar 0204001010120100137000010011110001000013335000121010001008124200010
00000000055010100101110002001100000000200?00225220100020000100600?10000
00100?00???71000110011?0
PhorDioe 02120012101301001300?00000112100010000154430101210100000?3126500010
0000000104501???10110000300111000? ?????????????????????????????1100700?1000000
100?00???7100060???1?0
PlatIndi 0302001010100100120010000111110101000013435010121010000001124200010
0001000106501010110110000?00100100? ?????????????????????????????1100500?0100000
100?00???61000511010?0
Pronegas 0???110010100100111111000011001101010015441000111122111024124300010
0001001?0 ?????????????10000320000100? ??????10? ??????20000132?00000300?01100?
000?00???0?0?0?0?0???0?0
Quasimus 050101001012010001110000002100110101101437200011102001101312541110
000010001012?1???000100003200011001000400?00225712000012000010020? ??????
?????0?01101?0?0?0?0???010
Rivulico 03010120100201000101011000?12??001010014346100121010101024125201210
00110001022?1?10110010000400010100100070010601683200001300011003000?0111
0?000?00 ??????0?0???000
Teslasen ?00?0020000201001400000000?00?000000002369111101000001004126300010
01010000037110100101010006001001004000502 ?????? ?????? ?????? ??????
????????????????????
Tripchus 01160021220701001600100100?11??001000003545110101011000003126100010
11000001045010100101110005002100010000402000313532000002?000001600? ??????
0???0?10? ???3102000???0?0
Tripoide 00170010101401001500000100?11??001000013343000121010000004125200010
01000001024110101101000004201000000000602107513532100002000? ?????? ??????
????????????????????
Tropidip 0312002010020100130000000011200101000012232010121011001003125400010
11000001026010100101010003010?1011010010?0133214020100020000100500?10000
01100?00???3100040???1?0
Tropihyp 0301013010110100120110110010201101010017551000001100101011124600011
00010000034211000100100003000111001000102003531520?0001111000005010? ??????
0?000?00 ??????0?0?0?0???000
YukoanaC 042201021012010012001000002100110101101635200011000001102212550110
000010001022210?0?000101003200011001000600?00317912000002?000100?0?0?111
01?000?00???1?0?0?0?0???0?0
Zorocho 0411112010100100111111000011001101011015540000111120111023120500010
0011000100221???1000000005000101001000300?006187420000030001101300?0110
1?000?00 ??????0?0?0?0???000
;
end;

```



```

begin assumptions;
  CHARSET ORDERED = 2-4 6 7 9 12 18 22 27 29 37 40-44 58 60-62 77-78 85
88 93 106 111-116 123 131 133 145 151 156 161;
  TYPESET * normal = unord: all, ord: ordered;
end;

begin paup;
log file=CardMB53.log;
delete GloboTes;
outgroup ElaterFe;
exclude 9 34 46 162 uninf;
weights 10:all, 1:1 5 6 8-11 13-17 19-39 44-57 59-60 63-76 79-87 89-92 94-105 107-110
117-130 132-150 152-155 157-163;
set maxtrees=100 increase=auto;
hsearch addseq=random nreps=1000;
savetrees file=CardMB53.trees;
contree/ treefile = consensus.tre;
end;

```