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The fossil record of Mesozoic and Tertiary Scarabaeoidea (Coleoptera : Polyphaga)

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Abstract. Lack of characters, similarity of stem species of adelphotaxa and the necessity to know the extant world fauna of the studied group of fossils are the main difficulties in palaeontology of beetles. The paucity of characters of most of the fossils of supposed Scarabaeoidea prevents their inclusion in a reliable phylogenetic analysis. Only rarely can an autapomorphy of Scarabaeoidea be seen in a fossil classified as a member of this group. Therefore, the classification of Mesozoic and Tertiary fossils is often tentative. Based on a critical literature review of all recorded fossil Scarabaeoidea from the Mesozoic and Tertiary, the minimum age for families and/or subfamilies of this group is determined. An annotated catalogue of named fossils and ichnofossils of Scarabaeoidea and of their lagerstätten is given. 238 fossil species and subspecies of this group have been described, of which 27 are doubtful, eight already identified as belonging to other taxa, and two subspecies synonymised with extant taxa. 189 species and 12 ichnospecies probably or reliably belong to the Scarabaeoidea. Nomenclatural acts: *Hongscarabaeus*, nom. nov. for *Proscarabaeus* Hong, 1982 (nec Schrank, 1781); *Onthophagus urusheeri*, nom. nov. for *Onthophagus urus* Heer, 1847 (nec Ménétries, 1832); *Aphodius anteactus*, nom. nov. for *Aphodius antiquus* Heer, 1847 (nec Faldermann, 1835); *Aphodius theobaldi*, nom. nov. for *Aphodius incertus* Théobald, 1937 (nec Ballion, 1878); *Anomala palaeobrunnea*, nom. nov. for *Anomala brunnea* (Hong, 1985) (nec Klug, 1855); *Eophyllocerus scrobiculatus* Haupt, 1950 is designated as the type species of *Eophyllocerus* Haupt, 1950; *Cangabola* Lengerken, 1955 is a junior synonym of *Coprinisphaera* Sauer, 1955.

'*Mais en présence des Coléoptères, sauf très rares exeptions, tout spécialiste sérieux ne peut que se récuser*'.
R. Jeannel (1942: 191) on fossil faunas.

Introduction

The scarab and stag beetles (Scarabaeoidea or Lamellicornia) are a cosmopolitan monophyletic group of Coleoptera : Polyphaga comprising around 28 000 described extant species. 238 fossil species, subspecies and ichnospecies have been named and an immense number of fossil individuals recorded. Most of the latter are from Quaternary deposits (Buckland and Coope 1991) and often unnecessarily called subfossils. (I follow Spilman's (1976) definition of a fossil, slightly modified: remnants of an organism, a replacement of an organism, or the work or evidence of an organism that lived in the past and was naturally preserved rather than buried by man.) The oldest fossils that were claimed to belong to Scarabaeoidea are from the Lower Jurassic. The present review reanalyses the literature on fossil Scarabaeoidea from the Mesozoic and Tertiary, evaluates the classification of some described taxa, and determines the minimum age of major taxa.

Identification of Scarabaeoidea

For reliable identification of a specimen as belonging to the Scarabaeoidea, it has to show at least one autapomorphy of this taxon that ideally should not be reduced in any terminal subordinated taxon at any period. That means it should be a synapomorphy recognisable in all taxa of Scarabaeoidea. Since all fossils claimed to be Scarabaeoidea so far are imagos, only imaginal synapomorphies are of interest here. According to Lawrence and Britton (1991) and Hansen (1997*a*), these are:

1. Antennae with lamellate club. This character is exclusive to Scarabaeoidea and present in all their taxa. Therefore, it is sufficient to diagnose a specimen as belonging to the superfamily. However, it is a very fragile structure generally not preserved in fossils.
2. Pronotum and fore legs adapted to burrowing (procoxae enlarged, pronotum enlarged to include enlarged coxal musculature, protibiae dilated apically, usually with teeth

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on its outer margin). Similar adaptations of the fore legs are convergently expressed in other taxa of Coleoptera, such as Tenebrionidae (Koch 1961; Medvedev 1965), Histeridae, Carabidae (Baehr 1979) and Curculionidae. In some species of these families, the shape of the fore tibiae is very similar to that of Scarabaeoidea, and burrowing adaptions of leg structures alone are therefore not sufficient to diagnose a specimen as belonging to Scarabaeoidea. Similarly, burrowing adaptions of the hind legs occur in taxa other than Scarabaeoidea.

3. Reduced wing venation and intrinsic spring mechanism for folding of alae. This feature is specific to Scarabaeoidea but rarely visible in fossil specimens.
4. Prosternal intercoxal process widened apically behind procoxae.

If none of these apomorphies are recognisable, it is possible to identify Scarabaeidae approximately by means of coxal and leg structures alone (Lawrence *et al.* 2000), if the ventral side is clearly visible, and assuming that no other extinct taxon possessed the same features. By these auxiliary characters many of the Mesozoic fossils from Baysa and Chinese lagerstätten were recognised or defined as being Scarabaeoidea (enlarged coxae, transverse meso- and metacoxae, the latter not widely separated, enlarged femora and apically widened tibiae).

Problems in classification and phylogenetical systematics of fossil Scarabaeoidea

Three fundamental problems complicate the interpretation of scarab fossils.

1. Most of the fossils are incompletely preserved. In particular, the antennae, which are essential for reliable identification of Scarabaeoidea, are mostly lacking, and the alae are nearly always hidden. Scarabaeoidea generally yield only a few useful characters when fossilised, since their body is mostly compact and evenly and strongly sclerotised. When compressed and fossilised, usually only the body outline and a few legs are recognisable. Incompleteness of specimens combined with an urge to classify them has led to curious odysseys of some named fossils through different orders, classes or even kingdoms (Théodoridès 1952). Examples from the Scarabaeoidea are *Progeotrupes jurassicus* Oppenheim which, according to Ponomarenko (1971), is a cockroach, *Scarabaeides deperditus* Germar that belonged temporarily to Hydrophilidae (Weyenbergh 1873) but was later considered to be a water bug (Heteroptera Belostomatidae) (Deichmüller 1886), and *Troxites germari* Goldenberg, described as a species of Trogidae, later considered a weevil (Scudder 1879*b*), then 'probably a fruit' (Scudder 1886) and in the end interpreted as a part of a crustacean (Schlechtendal 1912).
2. The stem species of adelphotaxa are likely to be rather similar even if the extant adelphotaxa differ clearly because speciations need not to be accompanied by morphological saltations and because further divergence usually occurs over time. It is unpredictable when morphological divergence began to be recognisable.
3. In the Tertiary and Mesozoic and to a lesser extent even in the Quaternary, faunas are composed of different biogeographical elements (as defined according to present distribution patterns) than today (e.g. Théodoridès 1952; Zherichin 1971; Storch 1990). Hence, for classification of Tertiary and older fossils the whole extant world fauna has to be considered (Obenberger 1957). This causes problems especially at the generic level since revisions of suprageneric taxa are generally regionally limited and comparative taxonomic and synonymical treatment of all genera of a suprageneric taxon are mostly lacking, even in worldwide revisions. Moreover, most genera still are typologically defined rather than phylogenetically diagnosed. Thus, most Tertiary fossil Scarabaeoidea, were classified in an extant genus only because the latter resembles the shape of the fossil and was known to the classifying author. In most of these cases, the fossil does not show any diagnostic character of the extant genus, much less any generic autapomorphy. This applies also to other insect groups (e.g. Brachycera; Hennig 1966). Likewise, in Mesozoic scarab fossils, the lack of crucial characters (apomorphies of higher taxa) has usually resulted in a simple comparison of their overall shape with that of extant species. Secondary characters, like the number of tibial denticles or keels (which may vary even within extant genera), have been inflated to diagnostic characters of taxa at subfamily level (Nikolaev 1992). This 'stopgap' classification may be the only feasible way of handling Mesozoic fossils but has sometimes led to optimistic reconstructions with hardly any basis in the fossil itself (Nikolaev 1996). Even such well-preserved specimens as the type of *Pro-teroscarabaeus yeni* Grabau remain of doubtful systematic position ('the description contains no characters that formally justify its inclusion in the family Scarabaeidae'; Ponomarenko 1991*a*).

Recent attempts to reconstruct scarabaeoid phylogeny at suprageneric level using character-rich fossils suffer from neglecting out-group comparison and lead, therefore, to irreproducible results (Nikolaev 1998*a*). Only Scarabaeoidea from Lebanese Amber (Crowson 1981: 673; Poinar 1992: 151) or single well-preserved specimens from lagerstätten like Santana may lead to well-founded phylogenetic hypotheses, although these are not yet studied (in preparation). Therefore, the systematics of Mesozoic Scarabaeoidea is still at a preliminary stage.

According to established opinion, living species of beetles are not older than Pleistocene (Hatch 1926; Crowson 1981). If extant insect species are recorded from the Tertiary, their identifications are either tentative (Gersdorf 1971; Riou 1988), later revised (Matthews 1976), or based on forgeries

(Hennig 1966; Grimaldi *et al.* 1994). Morphological constancy over hundreds of thousands or even millions of years of a 'species' documented in the fossil record, as indicated, e.g. by ELIAS (1991) and Coope (1994) in Coleoptera of the northern hemisphere, says nothing about the frequency and the duration of speciation processes. It indicates only a long-term morphological constancy (a low rate of anagenesis) in a successful clade. Branching, i.e. speciation, is not recognised if one clade remained morphologically constant (Hennig 1966). Hence, even if we cannot distinguish Tertiary fossils from extant species, we cannot be sure that they really belong to the extant species.

How old are the Scarabaeoidea?

We can never determine the absolute age of a taxon from its fossil record since it is extremely unlikely that one of the first individuals of the stem species of this taxon ever fossilised. Even if we could find such a fossil we cannot prove, nor even detect that it really belongs to a population existing just after the speciation of this stem species. We can only estimate a minimum age of taxa according to their occurrence in the fossil record (Scholtz and Chown 1995; Hansen 1997*b*).

According to current opinion (Crowson 1981; Ross and Jarzembowski 1993; Donovan 1994; Scholtz and Chown 1995; Hansen 1997*b*) Scarabaeoidea are known from the Lower Jurassic (Lower Lias) and may have developed in the Triassic (Morón Ríos 1984). This claim is based on two specimens. *Aphodiites protogaeus* Heer, 1865 has been described from the Lower Lias of Switzerland. It was originally thought to belong to Aphodiinae, but later Scholtz *et al.* (1994) noted that, 'The diagnostic characters attributed to *Aphodiites* could equally apply to a *Glaresis*-like beetle', without, however, re-examining the original specimen. Heer's original figure shows the remains of a beetle without appendages and any clear evidence of it belonging to Scarabaeoidea. It could well belong to Glaresidae, but equally plausibly to Chrysomelidae or any other family of oval beetles, as already concluded by Handlirsch (1906). *Opiselleipon grave* Bode, 1953 was described from the Upper Lias of Lower Saxony without indication to which family it may belong. Crowson (1981) presumed it to be a scarabaeid, but since the remains lack all appendages and the posterior part of elytra and abdomen, there is no real evidence enabling it to be classified in the Scarabaeoidea. A '*Melolontha* ?' described from the Lower Lias of England (Brodie 1845) based on a fossil resembling the outline of the pygidium of some extant species of *Melolontha*, is so incomplete that we cannot even be sure it is an insect. Hence, no reliable scarabaeoid fossils are known from the Lower Jurassic or earlier.

Although Ponomarenko (1995) gave the minimum age for Scarabaeoidea as Middle Jurassic, the fossil record of this era is even less promising. Phillips (1871) listed '*Melolonthidium*' from the Stonesfield Slate, England without any description or figure. It might refer to the *Melolontha* of Murchison (1845: 67) represented by a single elytron from Stonesfield. Therefore, the identity of this fossil remains doubtful.

From the Upper Jurassic, we know a single fossil likely to belong to Scarabaeoidea: *Holcorobeus nigrimontanus* from Karatau, Kazakhstan (Nikolaev 1992), which shows legs and coxae of a typical scarab appearance. The Chinese localities Laiyang and Jiuquan from where some Scarabaeoidea have been described, were supposed to be of Upper Jurassic age, but most authors now agree that they are Lower Cretaceous in age (Lin 1994; Ponomarenko 1995; Hong 1998). Therefore, it is likely that Scarabaeoidea already existed in the Upper Jurassic. Only from the Lower Cretaceous Baysa site are beetle fossils known with alae showing the typical scarabaeoid spring mechanism (Nikolaev 1992, 1994, 1995*a*, 1995*b*, 1998*a*). A specimen from the Lower Cretaceous Santana formation in Brazil shows the typical lamellicorn antennae (unpublished data). The proven first occurrence of Scarabaeoidea in the fossil record of Coleoptera is, therefore, Lower Cretaceous in age.

The age of major taxa of Scarabaeoidea

Based on the catalogue below, Fig. 1 shows the minimum age of extant families and subfamilies of Scarabaeoidea. I have adopted the system proposed by Browne and Scholtz (1998, 1999) with some modifications and additions within the Scarabaeidae. In Scarabaeidae, only extant subfamilies represented in the fossil record are shown. The age of adelphotaxa is determined by the oldest fossil of either of the two lineages. The diagram summarises our current knowledge, but it has to be borne in mind that the classification of the Mesozoic fossils is tentative.

The fossil record of Scarabaeoidea

All described species and literature records of fossil Scarabaeoidea are compiled in the catalogue below. 238 fossil species and ichnospecies have been described. I consider 27 species dubious, eight species were previously identified as belonging to other taxa and two subspecies are synonymised with extant species. The remaining 189 species and 12 ichnospecies probably or reliably belong to Scarabaeoidea.

Catalogue of named fossil Scarabaeoidea (Lamellicornia)

All named fossil taxa of Scarabaeoidea are listed according to their current classification. The classification of Scarabaeoidea follows the proposed system of Browne and Scholtz (1998, 1999) and Lawrence and Newton (1995). Species of doubtful identity are in brackets; such instances are only indicated if the fossils definitively lack any diagnostic character of Scarabaeoidea. These specimens are

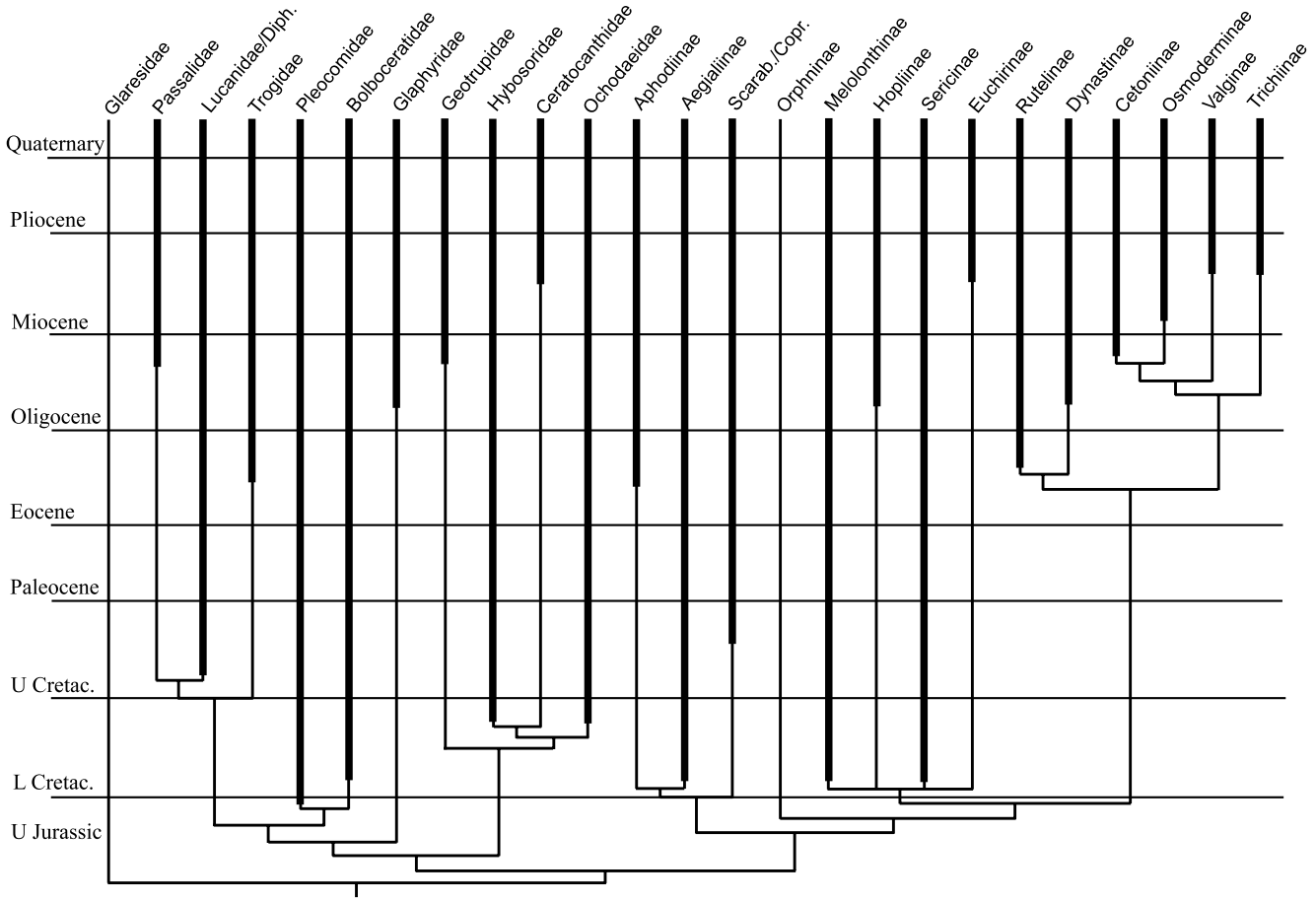

Fig. 1. Fossil record of Scarabaeoidea based on the phylogenetic system. Thick lines begin with the first fossil record of a clade. Continuous lines do not indicate continuous fossil record. The Pleocomidae may start only in lowest Cretaceous, if the Chinese localities formerly attributed to uppermost Jurassic are indeed Cretaceous. Abbreviations: Cretac., Cretaceous; Copr., Coprinae; Diph., Diphyllostomatidae; L, Lower; Scarab., Scarabaeidae; U, Upper.

mostly single elytra. A genus name in brackets indicates that the placement of the species in the genus is doubtful. Abbreviations: L: Lower, M: Middle, U: Upper.

(Family **GLARESIDAE**)

(Genus ***Aphodiites*** Heer)

Aphodiites Heer, 1865: 90, pl. 8 (type species by monotypy: *Aphodiites protogaeus* Heer). – Scudder 1886: 73; Crowson 1981: 664 (‘Possible Scarabaeoids’), 679 (‘probably attributable to this superfamily’); Dellacasa 1988: 361; Paulian 1988: 390; Cambefort 1991: 51 (‘undifferenciated Laparosticti’); Carpenter 1992: 318 (‘Little-known genus’, suborder and family uncertain); Scholtz *et al.* 1994: 275 (‘The diagnostic characters [...] could equally apply to a *Glaresis*-like beetle’); Scholtz & Chown 1995: 358 (‘glaresid-like’); Nikolaev 1998*b*: 30; Browne & Scholtz 1999: 54 (‘Glaresidae-like’).

The name *Aphodiites* Heer is valid according to Article 20 (ICZN 1999) because the author states implicitly that the fossil does not belong to the extant genus *Aphodius* Illiger, 1798, but is only similar to it (‘Es sieht den im Dünger lebenden Aphodien so ähnlich [...]’).

(***Aphodiites protogaeus*** Heer)

(*Aphodiites protogaeus* Heer, 1865: 90, pl. 8); (Jurassic, L Lias, Schambelen, Aargau, Switzerland). – Heer 1883: 100, pl. 8; Scudder 1881–1885: 794; id. 1891: 190; Handlirsch 1906: 441, pl. 41 (‘Es ist auch hier keinerlei Anhaltspunkt vorhanden, um die Familie mit einiger Sicherheit erkennen zu können. So gut wie um eine Scarabaeide kann es sich auch um eine Chysomelide, Tenebrionide usw. handeln.’); Théodoridès 1952: 32 (‘très sceptiques sur la position systématique exacte de ce Coléoptère’); Dellacasa 1983: 28f (‘la sua attribuzione agli Scarabaeoidea è estremamente dubitativa’); Dellacasa 1988: 361; Scholtz 1990: 1029; Carpenter 1992: 318.

Aphodiites prologaeus. – Balthasar 1963: 78; Iablokoff-Khnzorian 1977: 137 (family identity doubtful); Morón Ríos 1984: 117.

Doubful (no appendages present).

Familia **TROGIDAE**

Trox antiquus Wickham

Trox antiquus Wickham, 1909: 129 (Oligocene, Florissant, USA.). – Wickham 1920: 358.

(***Trox oustaleti*** Scudder)

Trox oustaleti Scudder, 1879*a*: 178B (Eocene, Nine-mile Creek, British Columbia, Canada). – Scudder 1890: 487, pl. 2; id. 1895*a*: 35; id. 1900: 105; Handlirsch 1907: 839; id. 1910: 99 (‘Of this order of insects, which, as far as the trustworthiness of the identification is concerned, is distinctly a discredit to paleoentomology, a series of forms from British Columbia has been brought to light, the interpretation of which lacks adequate support.’); Wickham 1920: 358.

Doubful (only one elytron).

Familia **PASSALIDAE**

Passalus (Passalus) indormitus Cockerell

Passalus (?) *indormitus* Cockerell, 1927*a*: 65 (Oligocene, John Day Series, Oregon, USA.).
Passalus indormitus. – Reyes-Castillo 1970: 73.
Passalus (Passalus) indormitus. – Reyes-Castillo 1977: 652.

Genus ***Serrulus*** Hong

Serrulus Hong, 1983: 6 (type species by original designation: *Serrulus sinicus* Hong).

Serrulus sinicus Hong

Serrulus sinicus Hong, 1983: 6, 13 (Miocene, Shanwang, China). – Zhang 1989: 149, pl. 40 (Passalidae).

Familia **LUCANIDAE**

Subfamilia **LUCANINAE**

(***Lucanus fossilis*** Wickham)

Lucanus fossilis Wickham, 1913*b*: 293 (Oligocene, Florissant, USA.). – Wickham 1920: 358; Maes 1992: 17.

Doubtful (only one elytron).

(Platycerus) sepultus Germar

Lucanus. – Goldfuss 1831: 118; Keferstein 1834: 329; Scudder 1886: 74.
Platycerus sepultus Germar, 1837*a*: 7, pl. 7 (Oligocene, ‘in carbone fossili territorii Rheni prope Bonnam’, Germany). – Germar 1837*b*: 423: (‘1 *Lucanus*’, *Platycerus sepultus*); Malepeyre 1838: 267; Bronn 1848*b*: 992; id. 1849: 623; Giebel 1852*b*: 653; id. 1856: 29; Goss 1878: 331; Scudder 1891: 567; Handlirsch 1907: 842; Houlbert 1915: 6; Nikolaev 1990: 121 (transl. p. 119) (generic and even family affiliation doubtful; may belong near *Ceruchus*); Maes 1992: 14.
Systenocerus sepultus. – Statz 1952: 1 (generic affiliation doubtful).

Platycerus zherichini Nikolajev

Platycerus zherichini Nikolajev, 1990: 122 (1991: 121) (Oligocene, Pozhar region, Russia).

Genus ***Succiniplatycerus*** Nikolajev

Succiniplatycerus Nikolajev, 1990: 122 (1991: 120) (type species by original designation: *Platycerus berendti* Zang, 1905). – Jarzembowski 2000: (3).

According to Larsson (1978: 152) Zang ‘describes a total of 5 species of *Systenocerus*’ from Baltic Amber. This is wrong, since Zang described only the following species and mentioned one other stag beetle species (*Dorcasoides bilobus* Motsch.).

Succiniplatycerus berendti (Zang) Nikolaev

Platycerus berendti Zang, 1905: 199 (Eocene, Baltic Amber). – Bibliography: Spahr 1981: 65, additional: Hieke & Pietrzeniuk 1984: 313.
Platycerus berendtii. – Maes 1992: 12.
Succiniplatycerus berendti. – Nikolaev 1990: 122 (1991: 120).

Dorcus (Eurytrachelus) primigenius Deichmüller

Dorcus (Eurytrachelus) primigenius Deichmüller, 1881: 303, pl. 21 (Eocene, Kučlín [Kutschlin] near Bílina [Bilin], Czechia). – Leuthner 1885: 482; Scudder 1891: 514; Počta 1900: 265; Handlirsch 1907: 842; Houlbert 1915: 6; Říha 1979: 26; Maes 1992: 92.

Genus ***Miocenidorcus*** Riou

Miocenidorcus Riou 1999: 126 (type species by original designation: *Miocenidorcus andancensis* Riou). – Riou, 1988: 98 (unpublished).

Miocenidorcus andancensis Riou

Miocenidorcus andancensis Riou, 1999: 126, 133 (Miocene, Andance, France). – Riou, 1988: 99 (unpublished).

Subfamilia **SYNDESINAE**

Ceruchus fuchsii Wickham

Ceruchus fuchsii Wickham, 1911: 58 (Oligocene, Florissant, USA.). – Wickham 1920: 358; Rodeck 1938: 293; Maes 1992: 11.

Subfamilia **AESALINAE**

Genus ***Cretaesalus*** Nikolajev

Cretaesalus Nikolajev, 1993: 90 (type species by original designation: *Gretaesalus ponomarenkoi* Nikolajev [lapsus calami for *Cretaesalus*]). – Nikolaev 1999: 178.

Cretaesalus ponomarenkoi Nikolajev

Cretaesalus ponomarenkoi Nikolajev, 1993: 90 (U Cretaceous, Kzyl-Zhar, Kazakhstan).

Subfamilia incerta

Genus ***Dorcasoides*** Motschulsky

Dorcasoides Motschulsky, 1856: 27, 30 (type species by monotypy: *Dorcasoides bilobus* Motschulsky). – Scudder 1881–1885: 795; id. 1886: 74; Handlirsch 1925: 245; Maes 1992: 95; Carpenter 1992: 300; Poinar 1992: 147.

Dorcasoides bilobus Motschulsky

Dorcasoides bilobus Motschulsky, 1856: 27 (fossil, without further data; Motschoulsky 1868 listed the species among 'Insectes contenus dans le succin' which was interpreted as from Baltic Amber [Eocene] by following authors). – Motschoulsky 1868: 103; Scudder 1881–1885: 794 (fig. 1028); id. 1891: 513; Zittel 1895: 505; Zang 1905: 199; Handlirsch 1907: 842; Broili 1921: 675; id. 1924: 696; Carpenter 1992: 300; Maes 1992: 95.
Dorcasoides nigrescens. – Motschulsky 1856: pl. (lapsus calami? – see Scudder 1891: 513).
Dorcasoides bibolus. – Houlbert 1915: 6.

Genus ***Ceruchites*** Statz

Ceruchites Statz, 1952: 5 (type species by monotypy: *Ceruchites hahnei* Statz). – Carpenter 1992: 300.
The name *Ceruchites* Statz is valid according to Article 20 (ICZN 1999) because the author introduced it explicitly for a new genus.

Ceruchites hahnei Statz

Ceruchites hahnei Statz, 1952: 5 (Oligocene, Rott, Germany). – Sphon 1973: 51; Carpenter 1992: 300.

Genus ***Paleognathus*** Waga

Paleognathus Waga, 1883: 191 (type species by monotypy: *Paleognathus succini* Waga). – Bibliography: Spahr 1981: 65, additional: Carpenter 1992: 300f; Poinar 1992: 147.
Palaeognathus. – Bibliography: Spahr 1981: 65, additional: Deville 1991: 16; Maes 1992: 68; Scholtz & Chown 1995: 364.

Paleognathus succini Waga

Paleognathus succini Waga, 1883: 191 (Eocene, Baltic Amber). – Bibliography: Spahr 1981: 65, additional: Paulian 1988: 394; Carpenter 1992: 300.
Palaeognathus succini. – Bibliography: Spahr 1981: 65, additional: Kozur 1984: 594f; Müller 1989: 245f; Maes 1992: 68.
Palaeognathus succinifer. – Leuthner 1885: 482.
Paläognathus succini. – Handlirsch 1908: 1356.
Paleognatius succini. – Laurentiaux 1953: 477.

Familia **BOLBOCERATIDAE**

Bolboceras inermis Piton

Bolboceras inermis Piton, 1940: 175 (Eocene, Menat, France).

Genus ***Cretobolbus*** Nikolajev

Cretobolbus Nikolajev, 1996: 95 (transl. p. 221) (type species by original designation: *Cretobolbus rohdendorfi* Nikolajev, 1996). – Nikolaev 1999: 178.

Cretobolbus rohdendorfi Nikolajev

Cretobolbus rohdendorfi Nikolajev, 1996: 96 (transl. p. 222) (L Cretaceous, Baysa, Russia).

Familia **PLEOCOMIDAE**

Genus ***Proteroscarabaeus*** Grabau

Proteroscarabaeus Grabau, 1923: 173 (type species by original designation: *Proteroscarabaeus yeni* Grabau). – Ping 1928: 18; Crowson 1974: 68 ('suggestive of Hybosoridae. If it is truly Scarabaeid, then it has possible affinities to [...] Aclopinae'); Nikritin 1977: 124 (1991: 168); Lin 1980: 230; Crowson 1981: 667 ('modern-looking Scarabeoids'); Ponomarenko 1990: 66; Carpenter 1992: 301; Nikolaev 1999: 178 (subfamily affiliation according to Nikolaev 1996).
Protoscarabaeus: Scholtz 1990: 1029; Scholtz & Chown 1995: 358.

(***Proteroscarabaeus magnus*** Nikolajev)

Proteroscarabaeus magnus Nikolajev, 1996: 91 (transl. p. 217) (L Cretaceous, Baysa, Russia).
Doubtful (only one elytron).

(***Proteroscarabaeus nikritini*** Nikolajev)

Proteroscarabaeus nikritini Nikolajev, 1996: 93 (transl. p. 217) (L Cretaceous, Baysa, Russia).
Doubtful (only one elytron).

Proteroscarabaeus robustus Zhang

Proteroscarabaeus dalaziensis (nomen nudum). – Lin 1994: 309 (according to Lin, in litt. 2000).
Proteroscarabaeus robustus Zhang, 1997: 90f, 103 (L Cretaceous, Zhixin Basin, China).

Proteroscarabaeus yeni Grabau

Proteroscarabaeus yeni Grabau, 1923: 175 (L Cretaceous, Laiyang, China). – Ping 1928: 19; Handlirsch 1939: 167; Balthasar 1963: 78; Ponomarenko 1977*a*: 6 (1991*a*: 2); Nikritin 1977: 126 (1991: 171) (L Cretaceous, Baysa, and Chita region, Pad Semen site); Iablokoff-Khnzorian 1977: 137 (oldest reliable Lamellicornia fossil; belonging to an extinct family-group taxon); Morón Ríos 1984: 117; Hong & Wang 1990: 114f; Carpenter 1992: 301; Zhang 1992*b*: 134; Nikolaev 1992: 79 (transl. p. 99); Lin 1994: 305; Nikolaev 1996: 94 (transl. p. 219).

Familia **GLAPHYRIDAE**

Glaphyrus antiquus Heer

Glaphyrus antiquus Heer, 1862: 79, pl. 6 (Miocene, Öhningen 'Insektenschicht des untern Bruches', Germany). – Heer 1865: 380; id. 1883: 406; Handlirsch 1907: 839.

Amphicoma defuncta Wickham

Amphicoma defuncta Wickham, 1910: 49 (Oligocene, Florissant, USA.). – Wickham 1920: 358; White 1995: 3.

Familia **GEOTRUPIDAE**

Subfamilia **GEOTRUPINAE**

Geotrupes atavus Oustalet

Geotrupes atavus Oustalet, 1874: 199, pl. 3 (Oligocene, Aix en Provence, France). – Goss 1878: 339; Scudder 1891: 524; Handlirsch 1907: 839; Meunier 1921: 4; Théobald 1937: tabl. 11; Théodoridès 1952: 46.

Gymnopleurus atavus. – Meunier 1921: 12 ('gehört wahrscheinlich auch zur Gattung *Gymnopleurus*').

Geotrupes germari Heer

Geotrupes germari Heer, 1862: 71, pl. 6 (Miocene, Öhningen, Kesselstein, Germany). – Heer 1865: 379; Oustalet 1874: 200; Heer 1883: 405; Scudder 1891: 524; Handlirsch 1907: 839; Meunier 1921: 4.

Geotrupes jiaoyanshanensis (Hong) Zhang

Obitiscarabaeus jiaoyanshanense Hong, 1983: 6, 13 (Miocene, Shanwang, China). – Hong 1985: 40, pl. 21; Zhang 1989: 172.

Geotrupes jiaoyanshanensis. – Zhang 1989: 152, 172.

(***Geotrupes messelensis*** Meunier)

Geotrupes messelensis Meunier, 1921: 11, pl. 2 (Eocene, Messel, Germany). – Théodoridès 1952: 46; Koenigswald 1987: 140.

Doubtful (poor preservation).

Geotrupes rottensis Statz

Geotrupes rottensis Statz, 1952: 7 (Oligocene, Rott, Germany). – Sphon 1973: 52.

Geotrupes vetustus Germar

Geotrupes vetustus Germar, 1837*a*: 6, pl. 6 (Oligocene, 'e carbone fossili territorii Rheni prope Bonnam', Germany). – Malepeyre 1838: 267; Brullé 1839: 20; Germar 1849: 57; Heer 1847: 62; Bronn 1849: 624 (Dynastidae); Giebel 1852*b*: 653; id. 1856: 35; Heer 1862: 72; Goss 1878: 331; Scudder 1891: 525; Handlirsch 1907: 839; Meunier 1921: 4; Statz 1952: 2.

(Genus ***Geotrupoides*** Handlirsch)

Geotrupoides Handlirsch, 1906: 545 (type species by monotypy: *Geotrupoides lithographicus* Deichmüller). – Nikritin 1977: 119 (1991: 162); Crowson 1981: 667 ('modern-looking Scarabeoids'), 679 ('could well be an early representative of the Geotrupidae [...] line'); Schlüter 1987: 133; Hong & Wang 1990: 115; Scholtz 1990: 1029; Carpenter 1992: 300; Scholtz & Chown 1995: 358; Nikolaev 1998*b*: 30.

(Geotrupoides) fortus Ren, Zhu & Lu

Geotrupoides fortus Ren *et al*., 1995: 436 (L Cretaceous, Chifeng City, Inner Mongolia, China).

Ren *et al.* classified this species as being close to *G. sulcatus* Nikritin which is currently in *Holcorobeus*. Hence, the generic affiliation of the *G. fortus* is doubtful.

Geotrupoides jiaoheensis Hong

Geotrupoides jiaoheense Hong, 1992: 415, pl. 161 (L Cretaceous, Jilin Province, China).

Generic affiliation needs revision since genus is dubious.

(***Geotrupoides lithographicus*** (Deichmüller) Handlirsch)

Geotrupes lithographicus Deichmüller, 1886: 69 (U Jurassic, Eichstädt [Lithographischer Schiefer], Germany). – Scudder 1891: 206; Iablokoff-Khnzorian 1977: 137 (family identity doubtful); Ponomarenko 1980: 113, pl. 16 (photo of holotype).

Geotrupoides lithographicus. – Handlirsch, 1906: 545, pl. 45 ('kann man doch nicht sicher sagen, dass die Form zu den Scarabaeiden gehört, solange weder Fühler noch Beine bekannt sind'); Théodoridès 1952: 32; Nikritin 1977: 119 (1991: 162); Ponomarenko 1980: 119; Morón Ríos 1984: 117; Hong & Wang 1990: 115f (*G. lingraphicus*, lapsus calami); Hong 1992: 415f.

Geotrupides lithographicus. – Balthasar 1963: 78 ('die Einreihung zu den Scarabaeoidea [ist] nur eine gewagte Annahme').

After having studied the holotype Ponomarenko (1980) claimed that this fossil belongs to 'Scarabaeidae' (= Scarabaeoidea), but further classification is not possible. However, this interpretation remains questionable since only traces of the coxae and neither tibiae nor antennae are present.

Geotrupoides nodosus Hong & Wang

Geotrupoides nodosus Hong & Wang, 1990: 116, 180, pl. 21 (L Cretaceous, Laiyang, China).

Generic affiliation needs revision since genus is doubtful.

Geotrupoides saxosus Zhang

Geotrupoides saxosus Zhang, 1997: 90, 103 (U Cretaceous, Zhixin Basin, China). – Lin 1994: 309 (nomen nudum).

Generic affiliation needs revision since genus is doubtful.

Geotrupoides songyingziensis Hong

Geotrupoides songyingziense Hong, 1984: 170, pl. 71 (L Cretaceous, Yixian, China).

Generic affiliation needs revision since genus is doubtful.

Genus ***Orrhodomala*** Zhang

Orrhodomala Zhang, 1989: 154, 425 (type species by original designation: *Orrhodomala protista* Zhang).

Orrhodomala protista Zhang

Orrhodomala protista Zhang, 1989: 154, 425 (Miocene, Shanwang, China).

Subfamilia **CRETOGEOTRUPINAE** Nikolajev, stat. nov.

Cretogeotrupinae Nikolajev, 1996: 97 (transl. p. 222).

Since Nikolaev treats Geotrupidae, Ochodaeidae and Hybosoridae as subfamilies, he introduced the subordinated taxa as tribes. Following Lawrence and Newton (1995) and Browne and Scholtz (1999), I consider the former taxa as families. Hence the subordinated taxa must be at subfamily level. This formal classificatory act does not imply any interpretation on the value of these taxa.

Genus ***Cretogeotrupes*** Nikolajev

Cretogeotrupes Nikolajev, 1992: 80 (transl. p. 101), type genus (type species by original designation: *Cretogeotrupes convexus* Nikolajev). – Nikolaev 1999: 178.

Cretogeotrupes convexus Nikolajev

Cretogeotrupes convexus Nikolajev, 1992: 81 (transl. p. 102) (L Cretaceous, Baysa, Russia).

Familia **HYBOSORIDAE**

Genus ***Coprologus*** Heer

Coprologus Heer, 1847: 60 (type species by monotypy: *Coprologus gracilis* Heer). – Stitzenberger 1851: 100; Rogg 1852: 22; Giebel 1856: 35; Scudder 1881–1885: 795; id. 1886: 74; Handlirsch 1907: 839; id. 1925: 246; Balthasar 1963: 79; Carpenter 1992: 330.

Caprologus. – Giebel 1852b: 653.

Coprologus gracilis Heer

Coprologus gracilis Heer, 1847: 60, pl. 2 (Miocene, Öhningen, Germany). – Bronn 1849: 624; Giebel 1856: 35; Heer 1865: 379; id. 1883: 405; Nikolaev 1996: 96 (transl. p. 222) (doubts the former classification as belonging to the Bolboceratidae, 'presumable belongs to the Hybosoridae').

Caprologus gracilis. – Giebel 1852b: 653.

Subfamilia **ANAIDINAE** Nikolajev, stat. nov.

(Genus ***Cretanaides*** Nikolajev)

Cretanaides Nikolajev, 1996: 94 (transl. p. 219) (type species by original designation: *Cretanaides trogopterus* Nikolajev). – Nikolaev 1999: 178.

(***Cretanaides trogopterus*** Nikolajev)

Cretanaides trogopterus Nikolajev, 1996: 95 (transl. p. 220) (L Cretaceous, Baysa, Russia).

Doubtful (only one elytron).

Subfamilia **HYBOSORINAE**

Genus ***Cretohybosorus*** Nikolajev

Cretohybosorus Nikolajev, 1999: 178 (type species by original designation: *Cretohybosorus buryaticus* Nikolajev).

Cretohybosorus buryaticus Nikolajev

Cretohybosorus buryaticus Nikolajev, 1999: 179 (L Cretaceous, Baysa, Russia).

Cretohybosorus striatulus Nikolajev

Cretohybosorus striatulus Nikolajev, 1999: 179 (L Cretaceous, Baysa, Russia).

Hybosorus lividus Heer

Hybosorus lividus Heer, 1862: 77, pl. 6 (Miocene, Öhningen, Germany). – Scudder 1891: 534; Handlirsch 1907: 838.

Phaeochrous tertiarium (Deichmüller) Nikolaev

Bolboceras tertiarium Deichmüller, 1881: 304 (Eocene, Kučlín [Kutschlin] near Bílina [Bilin], Czechia). – Scudder 1891: 474; Počta 1900: 265; Handlirsch 1907: 838; Ríha 1979: 26.

Phaeochrous tertiarium (Deichmüller). – Nikolaev, 1996: 96 (transl. p. 222).

Familia **OCHODAEIDAE**

Subfamilia **CRETOCHODAEINAE** Nikoloaev, stat. nov.

Cretochodaeinae Nikolaev, 1995*a*: 78 (transl. p. 120), stat. nov.

Genus ***Cretochodaeus*** Nikolajev

Cretochodaeus Nikolajev, 1995*a*: 79 (type species by original designation: *Cretochodaeus mongolicus* Nikolajev). – Nikolaev 1999: 178.

Cretochodaeus mongolicus Nikolajev

Cretochodaeus mongolicus Nikolajev, 1995a: 79 (L Cretaceous, Bon-Tsagan, Mongolia).

(***Cretochodaeus striatus*** Nikolajev)

Cretochodaeus striatus Nikolajev, 1995a: 80 (L Cretaceous, Bon-Tsagan, Mongolia).

Doubtful (very incomplete, lacking legs and head appendages).

Genus ***Mioochodaeus*** Nikolajev

Mioochodaeus Nikolajev, 1995*a*: 81 (type species by original designation: *Geotrupes proaevus* Germar).

Mioochodaeus proaevus (Germar) Nikolaev

Geotrupes proaevus Germar, 1849: 57, pl. 2 (Oligocene, Orsberg near Rott, Germany). – Giebel 1852*b*: 653; id. 1856: 36; Scudder 1891: 525; Handlirsch 1907: 838.

Geotrupes proavus. – Goss 1878: 331; Meunier 1921: 4.

Mioochodaeus proaevus. – Nikolaev, 1995*a*: 81.

Familia **SCARABAEIDAE**

Subfamilia **SCARABAEINAE** (incl. Coprinae)

Anachalcos mfwangani Paulian

Anachalcos mfwangani Paulian, 1976: 1 (Miocene, Lake Victoria, Kenya).

Genus ***Ateuchites*** Meunier

Ateuchites Meunier, 1898*a*: 114 (type species by monotypy: *Ateuchites grandis* Meunier). – Handlirsch 1925: 246; Théodoridès 1952: 34; Balthasar 1963: 79; Iablokoff-Khnzorian 1977: 137; Carpenter 1992: 300.

The name *Ateuchites* Meunier is valid according to Article 20 (ICZN 1999) because the author states implicitly that the fossil does not belong to the extant genus *Ateuchus* Weber, 1801, but is only related to it ('cet articulé est voisin des Lamellicornes du genre *Ateuchus*').

Ateuchites grandis Meunier

Ateuchites grandis Meunier, 1898*a*: 114 (Oligocene, Armissan, Aude, France). – Handlirsch 1907: 836; Carpenter 1992: 300.

Choeridium ebenium Horn

Choeridium ebenium Horn, 1876: 245 (Pleistocene, Irvingtonian, Port Kennedy caves, Pennsylvania, USA.). – Scudder 1890: 490, pl. 1; Wickham 1920: 358; Théodoridès 1952: 36.

Choeridium ? *ebenium* Horn. – Lesley 1889: xiii; Scudder 1891: 490; id. 1900: 104; Handlirsch 1908: 1126.

Copris druidum Heer

Copris druidum Heer, 1862: 73, pl. 6 (Miocene, Öhningen, Kesselstein, Germany). – Heer 1865: 378f; id. 1883: 404f; Scudder 1891: 500; Handlirsch 1907: 837.

Copris (Copris) kartlinus Kabakov

Copris (Copris) kartlinus Kabakov, 1988: 110 (Pliocene, Kisatibi formation, Georgia).

Copris leakeyorum Paulian

Copris leakeyorum Paulian, 1976: 1 (Miocene, Lake Victoria, Kenya).

Copris pristinus Pierce

Copris pristinus Pierce, 1946a: 124; (Pleistocene, Rancho La Brea tar pits, Los Angeles, USA.). – Halffter 1959: 176; Matthews 1961: 35, 67, 69; Matthews & Halffter 1968: 160 (*rembuchei*-Gruppe); Sphon 1973: 52; Miller *et al*. 1981: 626; Stock & Harris 1992: 70, 84; Miller 1997: 188.

Copris subterraneus Heer

Copris subterranea Heer, 1862: 74, pl. 3 (Miocene, Öhningen, Kesselstein, Germany). – Heer 1865: 379; id. 1883: 405; Scudder 1891: 501; Handlirsch 1907: 837.

Gymnopleurus deperditus Heer

Gymnopleurus deperditus Heer, 1862: 73, pl. 6 (Miocene, Öhningen, Kesselstein, Germany). – Handlirsch 1907: 836; Meunier 1921: 11.

(***Gymnopleurus eocaenicus*** Meunier)

Gymnopleurus eocaenicus Meunier, 1921: 12, pl. 3 (Eocene, Messel, Germany). – Koenigswald 1987: 140.

Gymnopleurus eocenicus.– Théodoridès 1952: 46.

Doubtful (poor preservation).

Gymnopleurus rotundatus Heer

Gymnopleurus rotundatus Heer, 1862: 73, pl. 6 (Miocene, Öhningen, Kesselstein, Germany). – Heer 1865: 378f; id. 1883: 404f; Scudder 1891: 527; Handlirsch 1907: 837; Meunier 1921: 11.

Gymnopleurus sisyphus Heer

Gymnopleurus sisyphus Heer, 1847: 64, pl. 7 (Miocene, Öhningen, Germany). – Bronn 1849: 625; Stitzenberger 1851: 100; Giebel 1852b: 653; id. 1856: 38; Heer 1862: 72; Scudder 1891: 527; Handlirsch 1907: 839; Meunier 1921: 11f.

Heliocopris antiquus Fujiyama

Heliocopris antiquus Fujiyama, 1968: 203 (Miocene, Noto, Japan). – Harusawa 1994: 23.

Metacatharsius rusingae Paulian

Metacatharsius rusingae Paulian, 1976: 2 (Miocene, Lake Victoria, Kenya).

Oniticellus amplicollis Heer

Oniticellus amplicollis Heer, 1862: 76, pl. 6 (Miocene, Öhningen, Kesselstein, Germany). – Heer 1865: 378f; id. 1883: 404f; Scudder 1891: 558; Handlirsch 1907: 837.

(***Onitis magus*** Heyden)

Onitis magus Heyden, 1862: 65, pl. 10 (Oligocene, Rott, Germany). – Krantz 1867: 315; Scudder 1891: 558; Handlirsch 1907: 837.

Onitis magnus. – Statz 1952: 2.

Zonitis. – After Janssens (in Balthasar 1963: 79); [it is rather a species of *Zonitis* (Meloidae) and Heyden may have mixed up the names. Slender tibiae without denticles indicate that it is not an *Onitis*].

Doubtful (tibiae structure untypical for Scarabaeoidea; poorly preserved).

Onthophagus bisontinus Heer

Onthophagus bisontinus Heer, 1862: 76, pl. 76 (Miocene, Öhningen, 'Insektenschicht des unteren Bruches', Germany). – Heer 1865: 379; id. 1883: 405; Scudder 1891: 559; Handlirsch 1907: 837.

Onthophagus crassus Heer

Onthophagus crassus Heer, 1862: 75, pl. 6 (Miocene, Öhningen, Kesselstein, Germany). – Heer 1865: 379; id. 1883: 405; Oustalet 1874: 196; Scudder 1891: 559; Handlirsch 1907: 837.

Onthophagus everestae Pierce

Onthophagus everestae Pierce, 1946a: 131 (Pleistocene, Los Angeles, USA). – Sphon 1973: 52; Miller et al. 1981: 627f; Wilson 1986: 101; Stock & Harris 1992: 70, 84; Miller 1997: 187f.

Onthophagus luteus Oustalet

Onthophagus luteus Oustalet, 1874: 194, pl. 2 (Oligocene, Aix en Provence, France). – Goss 1878: 339; Scudder 1891: 559; Handlirsch 1907: 837; Théobald 1937: tabl. 11; Théodoridès 1952: 46.

Onthophagus ovatulus Heer

Onthophagus ovatulus Heer, 1847: 64, pl. 7 (Miocene, Öhningen, Germany). – Bronn 1849: 624; Giebel 1852*b*: 653; id. 1856: 39; Heer 1865: 379; id. 1883: 405; Scudder 1891: 559; Handlirsch 1907: 837.

Onthophagus prodromus Heer

Onthophagus prodromus Heer, 1862: 75, pl. 6 (Miocene, Öhningen, Kesselstein, Germany). – Heer 1865: 378f; id. 1883: 404f; Scudder 1881–1885: 795; Oustalet 1874: 196; Scudder 1891: 559; Handlirsch 1907: 837.

Onthophagus statzi Krell

Onthophagus muelleri Statz, 1952: 8 (nec Novak, 1921) (Oligocene, Rott, Germany).
Onthophagus mulleri. – Sphon 1973: 52.
Onthophagus statzi Krell, 1990: 187.

Onthophagus urusheeri**,** nom. nov.

Onthophagus urus Heer, 1847: 62, pl. 2 (Miocene, Öhningen, Germany). – Stitzenberger 1851: 100; Giebel 1852*b*: 653; id. 1856: 39; Bronn 1849: 624; Heer 1862: 76; id. 1865: 379; id. 1883: 405; Scudder 1891: 559; Handlirsch 1907: 837.
Onthophagus urus Heer, 1847, is preoccupied by *Onthophagus urus* Ménétries, 1832: 175, and is to be replaced by the new name *Onthophagus urusheeri* [derivatio nominis: the urus (= aurochs) of Heer].

Phanaeus antiquus Horn

Phanaeus antiquus Horn, 1876: 245 (Pleistocene, Irvingtonian, Port Kennedy caves, Pennsylvania, USA.). – Goss 1878: 340; Scudder 1890: 489, pl. 1; id. 1891: 565; id. 1900: 104; Handlirsch 1908: 1126; Wickham 1920: 358; Théodoridès 1952: 36.

Phanaeus labreae (Pierce) Miller

Palaeocopris labreae Pierce, 1946a: 130 (Pleistocene, Rancho La Brea tar pits, Los Angeles, USA.). – Matthews 1961: 35 ('appears to be a composite of two genera'); Sphon 1973: 52; Stock & Harris 1992: 84; Wilson 1986: 101.
Paleocopris labreae. – Halffter 1959: 176.
Phanaeus labreae. – Miller *et al*. 1981: 627.

Genus ***Prionocephale*** Lin

Prionocephale Lin, 1980: 230 (type species by original designation: *Prionocephale deplanate* Lin).
The taxon resembles to extant telecoprid dung beetles. Therefore, I classify it as belonging to the Scarabaeinae.

Prionocephale deplanate Lin

Prionocephale deplanate Lin, 1980: 230 (U Cretaceous, Zheijang, China). – Lin 1994: 314.
Prionocephale deplanae. – Lin 1983: 394.

Genus ***Scelocopris*** Zhang

Scelocopris Zhang 1989: 150, 425 (type species by original designation: *Scelocopris enertheus* Zhang).

Scelocopris enertheus Zhang

Scelocopris enertheus Zhang, 1989: 151, 425 (Miocene, Shanwang, China).

Subfamilia **AEGIALIINAE**

Aegialia rupta Scudder

Aegialia rupta Scudder, 1890: 489, pl. 8 (Eocene, Green River, Wyoming, USA.). – Scudder 1891: 461; id. 1900: 104; Handlirsch 1907: 838; Wickham 1920: 358; Dellacasa 1988: 359.

Genus ***Cretaegialia*** Nikolayev

Cretaegialia Nikolayev, 1994: 5 (type species by original designation: *Cretaegialia rhypariformis* Nikolayev). – Nikolaev 1999: 178.

Cretaegialia aphodiiformis Nikolayev

Cretaegialia aphodiiformis Nikolayev, 1994: 7 (L Cretaceous, Baysa, Russia).

Cretaegialia rhypariformis Nikolayev

Geotrupoides sulcatus Nikritin, 1977: 120 [part.]. – Nikolayev 1994: 6.
Cretaegialia rhypariformis Nikolayev, 1994: 6 (L Cretaceous, Baysa, Russia).

Subfamilia **APHODIINAE**

Tribus **APHODIINI**

Aphodius aboriginalis Wickham

Aphodius aboriginalis Wickham, 1912: 22 (Oligocene, Florissant, USA.). – Wickham 1913*a*: 17; id. 1913*c*: 360; id. 1914*b*: 455; id. 1920: 358; Dellacasa 1988: 400.

Aphodius anteactus, nom. nov.

Aphodius antiquus Heer, 1847: 66, pl. 7 (Miocene, Öhningen, Germany). – Bronn 1849: 624; Stitzenberger 1851: 100; Giebel 1852*b*: 653; id. 1856: 40; Scudder 1891: 468; Handlirsch 1907: 838; Schmidt 1910: 140; Dellacasa 1988: 400.

Aphodius antiquus Heer is preoccupied by *Aphodius antiquus* Faldermann, 1835: 367, and is to be replaced by the new name *Aphodius anteactus* [derivatio nominis: anteactus, Mediaeval Latin: bygone].

Aphodius boryslavicus Łomnicki

Aphodius boryslavicus Łomnicki 1894: 83, pl. 7 (Pleistocene, Borysław, Poland).

Aphodius bosniaskii Handlirsch

? Aphodius bosniaskii Handlirsch, 1907: 838 (Miocene, Gabbro, Livorno, Italy) [only length and location given, no real description, which, however, may be considered as a formal one sensu Article 12 (ICZN 1999)]. – Schmidt 1910: 140 (‘*Aphod*.? *Bosniaskii*’).

Aphodius bosniaskii. – Dellacasa 1983: 29; Dellacasa 1988: 400.

Aphodius brevipennis Heer

Aphodius brevipennis Heer, 1862: 77, pl. 6 (Miocene, Öhningen, Kesselstein, Germany). – Scudder 1891: 468; Handlirsch 1907: 838; Schmidt 1910: 140; Dellacasa 1988: 400.

Aphodius charauxi Piton

Aphodius charauxi Piton, 1940: 176 (Eocene, Menat, France).

Aphodius florissantensis Wickham

Aphodius florissantensis Wickham, 1911: 59 (Oligocene, Florissant, USA.). – Wickham 1912: 23; id. 1913*a*: 17; id. 1914*b*: 456; id. 1920: 358; Dellacasa 1988: 400.

Aphodius granarioides Wickham

Aphodius granarioides Wickham, 1913*a*: 17 (Oligocene, Florissant, USA.). – Wickham 1912: 23 (nomen nudum); id. 1913*b*: 295; id. 1920: 358; Théodoridès 1952: 35; Dellacasa 1988: 400.

Although Wickham described this species as new in the Proceedings of the United States National Museum 45, no. 1982, published on June 13, 1913 (as indicated on the title page), the formal original description is in the key on page 17 of the Bulletin from the Laboratories of Natural History 6(4) (= New Series No. 57), since the latter is published on April 26, 1913 (as indicated on the title page).

Aphodius helvolus Statz

Aphodius helvolus Statz, 1952: 6 (Oligocene, Rott, Germany). – Sphon 1973: 52; Dellacasa 1991: 36.

Aphodius inundatus Wickham

Aphodius inundatus Wickham, 1914*a*: 262 (Oligocene, Florissant, USA.). – Wickham 1920: 358; Théodoridès 1952: 35; Dellacasa 1988: 400.

Aphodius krantzi Heyden & Heyden

Aphodius krantzi Heyden & Heyden, 1866: 138, pl. 22 (Oligocene, Rott, Germany). – Krantz 1867: 315; Goss 1878: 333; Scudder 1891: 468; Handlirsch 1907: 838; Schmidt 1910: 140; Statz 1952: 2; Dellacasa 1988: 400.

Aphodius laminicola Wickham

Aphodius laminicola Wickham, 1910: 49 (Oligocene, Florissant, USA.). – Wickham 1911: 59; id. 1912: 22f; id. 1913*a*: 17; id. 1914*b*: 456; id. 1920: 358; Dellacasa 1988: 400; White 1995: 4.

Aphodius mediaevus Wickham

Aphodius mediaevus Wickham, 1914*b*: 455 (Oligocene, Florissant, USA.). – Wickham 1920: 358; Dellacasa 1988: 400.

Aphodius meyeri Heer

Aphodius meyeri Heer, 1847: 67, pl. 7 (Miocene, Öhningen, Germany). – Bronn 1849: 624; Stitzenberger 1851: 100; Giebel 1852*b*: 653; id. 1856: 40; Scudder 1891: 468; Handlirsch 1907: 838; Schmidt 1910: 140; Dellacasa 1988: 400.

Aphodius praeemptor Wickham

Aphodius praeemptor Wickham, 1913*a*: 17, pl. 6 (Oligocene, Florissant, USA.). – Wickham 1914*b*: 456; id. 1920: 358; Dellacasa 1988: 400.

Aphodius precursor Horn

Aphodius precursor Horn, 1876: 245 (Tertiary/Pleistocene, Bone Caves of Port Kennedy, Pennsylvania, USA.). – Goss 1878: 340; Scudder 1890: 488, pl. 1; id. 1900: 105; Wickham 1920: 358.

Aphodius praecursor. – Lesley 1889: v; Scudder 1891: 469; Handlirsch 1908: 1126; Schmidt 1910: 140; Dellacasa 1988: 400.

Aphodius rhinocerontis Łomnicki

Aphodius rhinocerontis Łomnicki 1894: 81, pl. 7 (Pleistocene, Borysław, Poland).

Aphodius ruthenus Łomnicki

Aphodius ruthenus Łomnicki 1894: 82, pl. 7 (Pleistocene, Borysław, Poland).

Aphodius schlickumi Statz

Aphodius schlickumi Statz, 1952: 6 (Oligocene, Rott, Germany). – Dellacasa 1991: 36; Lutz 1996: 45.

Aphodius senex Wickham

Aphodius senex Wickham, 1914*b*: 456 (Oligocene, Florissant, USA.). – Wickham 1920: 358; Dellacasa 1988: 400.

Aphodius shoshonis Wickham

Aphodius shoshonis Wickham, 1912: 23 (Oligocene, Florissant, USA.). – Wickham 1913*a*: 17; Wickham 1914*b*: 455; Wickham 1920: 358; Dellacasa 1988: 400.

Aphodius subater Łomnicki

Aphodius subater Łomnicki 1894: 80, pl. 7 (Pleistocene, Borysław, Poland).

Aphodius theobaldi, nom. nov.

Aphodius incertus Théobald, 1937: 126, pl. 10 (Oligocene, Sannoisien du Gard, France). – Théodoridès 1952: 46.

Aphodius incertus Théobald, 1937, is preoccupied by *Aphodius incertus* Ballion, 1878: 282, and is to be replaced by the new name *Aphodius theobaldi* [derivatio nominis: after Nicolas Théobald, author of the original name of this species].

Tribus **EUPARIINI**

Ataenius europaeus Quiel

Ataenius europaeus Quiel, 1910: 187 (Eocene, Baltic Amber). – Kolbe 1925: 150; Dellacasa 1988: 412.

Ataenius patescens Scudder

Ataenius patescens Scudder, 1893: pl. 1 (not described, only figured; Oligocene, Florissant, USA.). – Scudder 1900: 104, pl. 11 (description); Handlirsch 1907: 838; Schmidt 1910: 140; Wickham 1910: 48; id. 1912: 22; id. 1913*b*: 295; id. 1913*c*: 360; id. 1914*b*: 453; id. 1920: 358; Dellacasa 1988: 412.

Ataenius restructus (Wickham) Wickham

Aphodius restructus Wickham, 1912: 22 (Oligocene, Florissant, USA.). – Wickham 1913*a*: 17; Dellacasa 1988: 400.

Ataenius restructus. – Wickham 1914*b*: 454; id. 1920: 358.

Oxyomus nearcticus Wickham

Oxyomus nearcticus Wickham, 1914*b*: 453 (Oligocene, Florissant, USA.). – Wickham 1920: 358; Dellacasa 1988: 403.

Saprosites cascus Britton

Saprosites cascus Britton, 1960: 36 (Eocene, Bognor Regis, Sussex, England). – Jarzembowski 1992: 94.

Saprosites succini (Zang) Kolbe

Aphodius succini Zang, 1905: 204 (Eocene, Baltic Amber). – Handlirsch 1908: 1356; Schmidt 1910: 140.

Ataenius succini. – Quiel 1910: 187; Dellacasa 1988: 412.

Saprosites succini. – Kolbe 1925: 150; Hieke & Pietrzeniuk 1984: 316.

Subfamilia **MELOLONTHINAE**

(*Diplotaxis aurora* Wickham)

Diplotaxis aurora Wickham, 1913*b*: 294 (Oligocene, Florissant, USA.). – Wickham, 1912: 26; id. 1920: 358; Vaurie 1960: 414 (doubts generic affiliation because of the described characters).

Doubtful (only one elytron).

(Diplotaxis) simplicipes Wickham

Diplotaxis ? *simplicipes* Wickham, 1912: 25 (Oligocene, Florissant, USA.). – Wickham 1920: 358; Vaurie 1960: 414 (doubts generic affiliation because of the described structures of the legs).

Genus *Eophyllocerus* Haupt

Eophyllocerus Haupt, 1950: 56 (type species by present designation: *Eophyllocerus scrobiculatus* Haupt [it is the first mentioned species with most specimens found]). – Crowson 1981: 680; Scholtz & Chown 1995: 364.

Eophyllocerus scrobiculatus Haupt

Eophyllocerus scrobiculatus Haupt, 1950: 57 (Eocene, Geiseltal, Germany). – Krumbiegel 1982: 15; Müller 1989: 244.

Eophyllocerus glaucinus Haupt

Eophyllocerus glaucinus Haupt, 1950: 58 (Eocene, Geiseltal, Germany). – Krumbiegel 1982: 15.

Macrodactylus pluto Wickham

Macrodactylus pluto Wickham, 1912: 24 (Oligocene, Florissant, USA.). – Wickham 1913*b*: 294; id. 1920: 358; Rodeck 1938: 294.

Macrodactylus propheticus Wickham

Macrodactylus propheticus Wickham, 1912: 25 (Oligocene, Florissant, USA.). – Wickham 1920: 358; Rodeck 1938: 294.

Melolontha greithiana Heer

Melolontha greithiana Heer, 1847: 67 (Oligocene, Greith, Switzerland). – Bronn 1848*a*: 720; id. 1849: 624; Heer 1865: 378, 380; id. 1883: 406; Scudder 1891: 551; Handlirsch 1907: 840.

Melolontha greithana. – Giebel 1852*b*: 652; id. 1856: 32; Goss 1879: 145.

(***Melolontha solitaria*** Novák)

Melolontha solitaria Novák, 1878: 92, pl. 3 (Miocene, Mokřina [Krottensee] near Kynšperk n. O., Czechia). – Scudder 1891: 552; Počta 1900: 264; Handlirsch 1907: 840; Říha 1977: 22; id. 1979: 26.

Doubtful (only one elytron).

Genus ***Melolonthites*** Heer (collective group)

Melolonthites Heer, 1847: 71 (as a collective group, this taxon has no type species [Article 13.3.2 (ICZN 1999)], though a the type species was designated by Carpenter 1992: *Melolonthites aciculatus* Heer.). – Bronn 1848*a*: 720; id. 1849: 624; Rogg 1852: 22; Giebel 1856: 33; Scudder 1886: 74; id. 1895: 120; Handlirsch 1925: 246; Théodoridès 1952: 36; Carpenter 1992: 323 (suborder and family uncertain).

The name *Melolonthites* Heer is valid according Art. 20 ICZN because the author states implicitly that the fossil does not belong to the extant genus *Melolontha* Fabricius, 1775, but is introduced explicitly for a collective group (sensu Art. 42.2.1 ICZN ('Unter diesem Namen fasse ich mehrere Fragmente von Käfern zusammen, welche mir zur Familie der Melolonthiden oder Melittophilen zu gehören scheinen, die aber so beschaffen sind, dass ich sie keiner bekannten Gattung mit etwelcher Sicherheit zuzutheilen vermöchte. Der Name ist daher nur als ein provisorischer zu betrachten, welcher wegfallen wird, wie einmal vollständigere Exemplare eine genauere Bestimmung möglich machen werden.').

(***Melolonthites aciculatus*** Heer)

Melolonthites aciculata Heer, 1847: 71, pl. 2 (Miocene, Öhningen, Germany). – Stitzenberger 1851: 100; Giebel 1852*b*: 652; id. 1856: 33.

Melolonthites aciculatus. – Bronn 1848*a*: 720; id. 1849: 624; Scudder 1891: 552; Handlirsch 1907: 840; Carpenter 1992: 323.

Doubtful (only one abdomen [5 sternites]).

(***Melolonthites collinsi*** Wickham)

Melolonthites collinsi Wickham, 1929: 149 (Eocene, Holcomb, Tennessee, USA.). – Wickham 1933: 104.

Doubtful (only one elytron).

Melolonthites deperditus Heer

Melolonthites deperdita Heer, 1847: 71, pl. 2 (Miocene, Öhningen, Germany). – Stitzenberger 1851: 100; Giebel 1852*b*: 652; id. 1856: 33.

Melolonthites deperditus. - Bronn 1848*a*: 720; id. 1849: 624; Scudder 1891: 552; Handlirsch 1907: 840.

Melolonthites interemtus Cockerell

Melolonthites interemtus Cockerell, 1926: 319 (Oligocene, Kudia River, Siberia, Russia) (only part of an ala; 'placed in Heer's blanket-genus *Melolonthites* merely to avoid proposing a new generic name').

(***Melolonthites kollari*** Heer)

Melolonthites kollari Heer, 1847: 72, pl. 7 (Miocene, 'in den Kohlen zu Parschlug in Steiermark', Austria). – Bronn 1848*a*: 720; id. 1849: 624; Giebel 1856: 33; Scudder 1891: 552; Handlirsch 1907: 840; Beier 1952: 131.

Melolonthites kolleri. – Giebel 1852*b*: 652.

Doubtful (described after only a drawing of one elytron).

(***Melolonthites laterosinuatus*** Piton in Piton & Théobald)

Melolonthites laterosinuatus Piton in Piton & Théobald, 1935: 78, pl. 3 (Mio/Pliocene, Cinérites de Varennes, France). – Piton 1936: 18 ('*latero-sinuatus*').

Doubtful (only one elytron).

(***Melolonthites lavateri*** Heer)

Melolonthites lavateri Heer, 1847: 73, pl. 7 (Miocene, Öhningen, Germany). – Bronn 1848*a*: 720; id. 1849: 624; Stitzenberger 1851: 100; Giebel 1852*b*: 652; id. 1856: 34; Scudder 1891: 552; Handlirsch 1907: 840.

Doubtful (only one elytron).

(***Melolonthites obsoletus*** Heer)

Melolonthites obsoleta Heer, 1847: 73, pl. 2 (Miocene, Öhningen, Germany). – Stitzenberger 1851: 100; Giebel 1852*b*: 652; id. 1856: 34.

Melolonthites obsoletus. – Bronn 1848a: 720; id. 1849: 624; Scudder 1891: 552; Handlirsch 1907: 840.

Doubtful (only one elytron, abdomen and a part of the thorax indistinctly visible).

(***Melolonthites parschlugianus*** Heer)

Melolonthites parschlugiana Heer, 1847: 72 (Miocene, 'in den Kohlen zu Parschlug in Steiermark', Austria). – Unger 1870: 3, pl. 1.

Melolonthites parschlugianus. – Bronn 1848*a*: 720; Scudder 1891: 552; Handlirsch 1907: 840; Beier 1952: 131.

Melolonthites parschluganus. – Bronn 1849: 624.

Melolonthites parschlugana. – Giebel 1852*b*: 652; id. 1856: 33.

Doubtful (described after only a drawing of one elytron).

Phyllophaga avus (Cockerell) Cockerell

Melolonthites avus Cockerell, 1921: 36, pl. 8 (Eocene, White River, Green River Formation, Colorado, USA.).

Phyllophaga avus. – Cockerell 1925: 10 (Eocene, Roan Mountains, Green River Formation, Colorado, USA.); Wickham 1927: 55.

Phyllophaga disrupta Cockerell

Phyllophaga disrupta Cockerell, 1927*b*: 587 (Oligocene, Florissant, USA.). – Wickham 1933: 104.

(***Phyllophaga extincta*** (Wickham) Wickham)

Lachnosterna ? extincta Wickham, 1916: 9 (Oligocene, Florissant, USA.). – Rodeck 1938: 294.

Phyllophaga extincta. – Wickham 1920: 358.

Doubtful (only one elytron).

Rhizotrogus longimanus Heer

Rhizotrogus longimanus Heer, 1847: 69, pl. 7 (Miocene, Öhningen, Germany). – Bronn 1849: 624; Stitzenberger 1851: 100; Giebel 1852*b*: 652; id. 1856: 32; Heer 1865: 380; id. 1883: 406; Scudder 1891: 576; Handlirsch 1907: 839.

Listrochelus puerilis Wickham

Listrochelus puerilis Wickham, 1914*b*: 459, pl. 6 (Oligocene, Florissant, USA.). – Wickham 1920: 358.

Tribus **CRETOMELOLONTHINI** Nikolajev

Cretomelolonthini Nikolajev, 1998: 80 (transl. p. 515).

Genus ***Cretomelolontha*** Nikolajev

Cretomelolontha Nikolajev, 1998*a*: 81 (transl. p. 516) type genus (type species by original designation: *Cretomelolontha transbaikalica* Nikolajev). – Nikolaev 1999: 178.

Cretomelolontha transbaikalica Nikolajev

Cretomelolontha transbaikalica Nikolajev, 1998*a*: 82 (transl. p. 517) (L Cretaceous, Baysa, Russia).

Subfamilia **DYNASTINAE**

Ligyrus compositus Wickham

Ligyrus compositus Wickham, 1911: 59 (Oligocene, Florissant, USA.). – Wickham 1914*b*: 461; id. 1920: 358; Rodeck 1938: 294.

(Ligyrus) effetus Wickham

Ligyrus effetus Wickham, 1914*b*: 461 (Oligocene, Florissant, USA.). – Wickham 1920: 358. The generic classification was founded 'by the facies', that means *not* by characters. Therefore, the generic affiliation is doubtful.

(***Oryctes pluto*** Weyenbergh)

Oryctes pluto Weyenbergh 1869*a*: 282, pl. 27 (Jurassic, U Malm, Solnhofen, Germany). – Weijenbergh 1869*b**: [232]; id. 1874: 102 or 109 (There are two printings with slightly different arrangement of the text.); Goss 1879: 148; Winkler 1878: 95; Scudder 1891: 216; Winkler 1896: 313 ('Coléoptère sp. Meunier'); Meunier 1897, pl. 10 ('Aucun organe de ce fossile n'étant suffisamment conservé, on doit se borner à dire que cette empreinte est celle d'un grand coléoptère.'); Houlbert 1915: 64 ('n'est pas déterminable').

Oryctes grandis Weijenb. – Weijenbergh 1869*b* [nomen nudum].

Pentodon bellerophon Heyden & Heyden

Pentodon bellerophon Heyden & Heyden, 1866: 139, pl. 23 (Oligocene, Rott, Germany). – Krantz 1867: 315; Scudder 1891: 564; Handlirsch 1907: 841; Houlbert 1915: 64; Statz 1952: 3.

(***Pentodon proserpinae*** (Heer) Heer)

Scarabaeus proserpinae Heer, 1862: 78, pl. 6 (Miocene, Öhningen, Kesselstein, Germany). – Scudder 1891: 578.

Pentodon proserpinae. – Heer 1865: 379; id. 1883: 405; Scudder 1891: 564; Handlirsch 1907: 841; Houlbert 1915: 64.

Doubtful (only one elytron).

Strategus cessatus Wickham

Strategus cessatus Wickham, 1914*b*: 461 (Oligocene, Florissant, USA.). – Wickham 1920: 358; Ratcliffe 1976: 123, 169 [only elytron, but revised by Ratcliffe].

Subfamilia **RUTELINAE**

Adoretus recticlypeus Zhang

Adoretus recticlypeus Zhang, 1989: 167, pl. 47 (Miocene, Shanwang, China). – Zhang *et al.* 1994: 110.

Adoretus rhinus Zhang, Sun & Zhang

Adoretus rhinus Zhang, Sun & Zhang, 1994: 109, pl. 16 (Miocene, Shanwang, China).

Anomala amblobelia Zhang

Magniscarabaeus furvus part. – Hong 1985: 83.

Anomala amblobelia Zhang, 1989: 158, 160, 164, 174, pl. 42 (Miocene, Shandong, China).

Anomala brachytarsia Zhang, Sun & Zhang

Anomala brachytarsia Zhang, Sun & Zhang, 1994: 104, 107f, pl. 16 (Miocene, Shanwang, China).

Anomala endoxa Zhang, Sun & Zhang

Anomala endoxa Zhang, Sun & Zhang, 1994: 103, 106f, pl. 16 (Miocene, Shanwang, China).

Anomala eversa Zhang

Anomala eversa Zhang, 1989: 158, 165, 167, pl. 44 (Miocene, Shanwang, China).

Anomala exterranea Wickham

Anomala exterranea Wickham, 1914*b*: 459 (Oligocene, Florissant, USA.). – Wickham 1920: 358.

Anomala fugax Heer

Anomala fugax Heer, 1862: 80, pl. 6 (Miocene, Öhningen, Kesselstein, Germany). – Heer 1865: 380; id. 1883; 406; Scudder 1891: 465; Handlirsch 1907: 841.

Anomala furva (Hong & Wang) Zhang

Magniscarabaeus furvus Hong & Wang in Hong, 1983: 5, 13 (Miocene, Shanwang, China). – Hong 1985: 38, pl. 17; Hong & Wang 1986: 7; id. 1987: 120.

Anomala furva. – Zhang 1989: 158, 162, 164, 166f, 173, pl. 43; Zhang *et al.* 1994: 104, pl. 15.

Anomala turua. – Sun 1995: 38.

Anomala lochmocola Zhang

Anomala lochmocola Zhang, 1989: 158, 164, pl. 45 (Miocene, Shanwang, China).

Anomala orcina Zhang, Sun & Zhang

Anomala orcina Zhang, Sun & Zhang, 1994: 103, 105, pl. 15 (Miocene, Shanwang, China).

Anomala palaeobrunnea, nom. nov.

Magniscarabaeus brunneus Hong, 1985: 39, pl. 42 (Miocene, Shanwang, China). – Hong & Wang 1987: 119ff.

Anomala brunnea. – Zhang 1989: 158, 160f.

Since *Anomala brunnea* (Hong) is a junior secondary homonym of *Anomala brunnea* Klug, 1855 (extant species from Moçambique), the former is to be replaced by a nomen novum, *Anomala palaeobrunnea* [derivatio nominis: παλαιός = ancient, brunneus = brown, the original specific name].

(***Anomala***) ***primigenia*** Heyden & Heyden

Anomala primigenia Heyden & Heyden, 1866: 138, pl. 22 (Oligocene, Rott, Germany). – Krantz 1867: 315; Goss 1878: 333; Scudder 1891: 465; Handlirsch 1907: 840; Ohaus 1940: 74; Statz 1952: 2 (generic affiliation doubtful).

Anomala punctulata Zhang

Anomala punctulata Zhang, 1989: 158, 165, pl. 44 (Miocene, Shanwang, China).

Anomala scia Zhang

Anomala scia Zhang, 1989: 158, 166, pl. 45 (Miocene, Shanwang, China).

Anomala scudderi Wickham

Anomala scudderi Wickham, 1914*b*: 460 (Oligocene, Florissant, USA.). – Wickham 1920: 358.

Anomala synemosyna Zhang

Anomala synemosyna Zhang, 1989: 158, 161, pl. 42 (Miocene, Shanwang, China).

(***Anomala***) ***thetis*** Heyden & Heyden

Anomala thetis Heyden & Heyden, 1866: 139, pl. 24 (Oligocene, Rott, Germany). – Krantz 1867: 315; Goss 1878: 333; Scudder 1891: 465; Handlirsch 1907: 840; Ohaus 1940: 74; Statz 1952: 2 (generic affiliation doubtful).

(***Anomala***) ***tumulata*** Heyden & Heyden

Anomala tumulata Heyden & Heyden, 1866: 138, pl. 23 (Oligocene, Rott, Germany). – Krantz 1867: 315; Goss 1878: 333; Scudder 1891: 465; Handlirsch 1907: 841; Meunier 1920: 48 (no Lamellicornia); Ohaus 1940: 74; Statz 1952: 2 (Menier's specimen: no Lamellicornia; Heydens' specimen may be one; generic affiliation doubtful).

Anomala ursa Zhang, Sun & Zhang.

Anomala ursa Zhang, Sun & Zhang, 1994: 104, 108f, pl. 16 (Miocene, Shanwang, China).

Genus ***Anomalites*** Frič

Anomalites Frič, 1885: 163 (type species by monotypy: *Anomalites fugitivus* Frič). – Scudder 1881–1885: 794; id. 1886: 74; Handlirsch 1925: 246; Carpenter 1992: 300, 330.

The name *Anomalites* Frič is valid according Article 20 (ICZN 1999) because the author states implicitly that the fossil does not belong to the extant genus *Anomala* Samouelle, 1819, but is only related to it ('ich schlage daher vor, die Verwandtschaft mit *Anomala* durch den Namen *Anomalites* anzudeuten').

Anomalites fugitivus Frič

Anomalites fugitivus Frič, 1885: 163 (Tertiary, Süßwasserquarz Nogent le Rotrou, France). – Handlirsch 1907: 841; Carpenter 1992: 300.

Genus ***Zhangsunia***, nom. nov.

Dolichopoda Zhang, Sun & Zhang, 1994: 101, 279 (type species by original designation: *Dolichopoda extumida* Zhang, Sun & Zhang). – Jarzembowski 2000: (6).

Dolichopoda Zhang, Sun & Zhang, 1994, is preoccupied by *Dolichopoda* Bolivar, 1880: 72 (Ensifera: Rhaphidophoridae), and is, therefore, to be replaced by the new name *Zhangsunia* [derivatio nominis: after the authors of the original name, Zhang Junfeng, Sun Bo, and Zhang Xiyu; gender: feminine].

Zhangsunia extumida (Zhang, Sun & Zhang), comb. nov.

Dolichopoda extumida Zhang, Sun & Zhang, 1994: 101f (Miocene, Shanwang, China).

Holotrichia cressona Zhang, Sun & Zhang

Holotrichia cressona Zhang, Sun & Zhang, 1994: 102f (Miocene, Shanwang, China).

Holotrichia spatha Zhang

Holotrichia spatha Zhang, 1989: 156 (Miocene, Shanwang, China).

Mimela rhenana (Heyden) Ohaus in Statz

Anoplognathus rhenanus Heyden, 1862: 65, pl. 10 (Oligocene, Rott, Germany). – Krantz 1867: 315; Scudder 1891: 465; Handlirsch 1907: 841; Ohaus 1940: 74.

Mimela rhenana (Heyden). – Ohaus in Statz, 1952: 2.

Genus ***Miolachnosterna*** Wickham

Miolachnosterna Wickham, 1914*b*: 458 (type species by original designation: *Miolachnosterna tristoides* Wickham). – Théodoridès 1952: 36; Carpenter 1992: 301.

Miolachnosterna tristoides Wickham

Miolachnosterna tristoides Wickham, 1914*b*: 458, pl. 8 (Oligocene, Florissant, USA.). – Wickham 1920: 358; Carpenter 1992: 301.

Genus ***Pelidnotites*** Cockerell

Pelidnotites Cockerell, 1920: 463 (type species by monotypy: *Pelidnotites atavus* Cockerell). – Carpenter 1992: 301.

The name *Pelidnotites* Cockerell is valid according Article 20 (ICZN 1999) because the author introduced it explicitly for a new genus.

Pelidnotites atavus Cockerell

Pelidnotites atavus Cockerell, 1920: 462 (Eocene, U Ypresian – Lutetian, Bournemouth, England). – Carpenter 1992: 301; Jarzembowski 1996: 210.

Genus ***Petraeianus*** Zhang

Petraeianus Zhang, 1989: 168, 426 (type species by original designation: *Petraeianus ruderatus* Zhang).

Petraeianus ruderatus Zhang

Petraeianus ruderatus Zhang, 1989: 168, 426 (Miocene, Shanwang, China).

Genus ***Petulantis*** Zhang, Sun & Zhang

Petulantis Zhang, Sun & Zhang, 1994: 110, 279 (type species by original designation: *Petulantis yimengensis* Zhang, Sun & Zhang).

Petulantis yimengensis Zhang, Sun & Zhang

Petulantis yimengensis Zhang, Sun & Zhang, 1994: 110, pl. 17 (Miocene, Shanwang, China).

Subfamilia **HOPLIINAE**

Hoplia striatipennis Wickham

Hoplia striatipennis Wickham, 1914*b*: 457 (Oligocene, Florissant, USA.). – Wickham 1920: 358.

Lepitrix germanica Heer

Lepitrix germanica Heer, 1862: 80, pl. 6 (Miocene, Öhningen, Germany). – Heer 1865: 378, 380; id. 1883: 406; Scudder 1891: 546; Handlirsch 1907: 839.

Subfamilia **SERICINAE**

Genus ***Lithanomala*** Nikolajev

Lithanomala Nikolaev, 1992: 79 (transl. p. 100) (type species by original designation: *Proteroscarabaeus oblongus* Ponomarenko). – Nikolaev 1998*a*: 82 (transl. p. 519); id. 1999: 178.

Lithanomala crassa (Ponomarenko) Nikolaev

Proteroscarabaeus crassus Ponomarenko, 1990: 66, pl. 6 (L Cretaceous, Leskovo, Russia).
Lithanomala crassa. – Nikolaev, 1992: 80 (transl. p. 100).

Lithanomala oblonga (Ponomarenko) Nikolaev

Proteroscarabaeus oblongus Ponomarenko, 1990: 66, pl. 6 (L Cretaceous, Leskovo, Russia).
Lithanomala oblonga. – Nikolaev, 1992: 79 (transl. p. 100).

Lithanomala sibirica (Ponomarenko) Nikolaev

Proteroscarabaeus sibiricus Ponomarenko, 1990: 68, pl. 6 (L Cretaceous, Leskovo, Russia).
Lithanomala sibirica. – Nikolaev, 1992: 80 (transl. p. 100).

Maladera spinitibialis Statz

Maladera spinitibialis Statz, 1952: 9 (Oligocene, Rott, Germany).
Maladera ? spinitibialis. – Sphon 1973: 52.

Genus ***Mioserica*** Zhang

Mioserica Zhang, 1989: 157, 426 (type species by original designation: *Mioserica margelis* Zhang).

Mioserica margelis Zhang

Mioserica margelis Zhang, 1989: 157, 426 (Miocene, Shanwang, China).

(Serica) antediluviana Wickham

Serica antediluviana Wickham, 1912: 23 (Oligocene, Florissant, USA.). – Wickham 1914*a*: 263; id. 1920: 358; Rodeck 1938: 294.

According to the description, the specimen shows no character allowing to classify it as belonging to the Sericinae.

(Serica) cockerelli Wickham

Serica cockerelli Wickham, 1914*a*: 262 (Oligocene, Florissant, USA.). – Wickham 1920: 358; Théodoridès 1952: 35.

According to the description, the specimen shows no character allowing to classify it as belonging to the Sericinae.

Serica kanakoffi Pierce

Serica kanakoffi Pierce, 1946*b*: 132 (Pleistocene, Rancho La Brea tar pits, Los Angeles, USA.). – Sphon 1973: 53; Miller *et al.* 1981: 627; Stock & Harris 1992: 84.

Serica minutula Heer

Serica minutula Heer, 1862: 79, pl. 6 (Miocene, Öhningen, Kesselstein, Germany). – Heer 1865: 380; id. 1883: 406; Scudder 1891: 579; Handlirsch 1907: 839.

Subfamilia **CETONIINAE**

(***Cetonia defossa*** Weyenbergh)

Cetonia (?) *defossa* Weyenbergh, 1869*a*: 282, pl. 37 (*Amphicoma* ?) (U Jurassic, Solnhofen, Germany). – Weijenbergh 1869*b**: [232]; id. 1874: 103 [‘*defosfa*’, lapsus calami] or 109 [‘*defossa*’]; Goss 1879: 148; Winkler 1878: 96; Altena 1958.

Cetonia defossa. – Weijenbergh 1869*b*: [232]; Scudder 1891: 197; Meunier 1897: 235, pl. 10 (‘indéterminable empreinte de coléoptère’).

? Ditomoptera defossa (Coleoptera incert. sed.). – Handlirsch 1906: 546 (classification doubted by Altena 1958)

Genus ***Genonota*** Zhang

Genonota Zhang, 1989: 170, 426 (type species by original designation: *Genonota mochthera* Zhang).

Genonota mochthera Zhang

Genonota mochthera Zhang, 1989: 170f, 426, pl. 46 (Miocene, Shanwang, China).

Genonota scola Zhang

Genonota scola Zhang, 1989: 170f, pl. 47 (Miocene, Shawang, China).

Macronota shandongiana Zhang

Macronota shandongiana Zhang, 1989: 169, pl. 45 (Miocene, Shandong, China).

Subfamilia **TRICHIINAE**

Gnorimus aedilis (Heer) Frentzen

Trichius (Gnorimus) aedilis Heer, 1862: 81, pl. 6 (Miocene, Öhningen, Kesselstein, Salamanderschicht, Germany). – Heer 1865: 378, 380; Scudder 1891: 591.

Trichius aedilis. – Heer 1883: 404f; Scudder 1891: 591; Handlirsch 1907: 841.

Gnorimus aedilis. – Frentzen 1927: 141.

Trichius amoenus Heer

Trichius amoenus Heer, 1847: 74, pl. 7 (unknown locality). – Bronn 1849: 624; Stitzenberger 1851: 100; Giebel 1852*b*: 652; id. 1856: 30; Heer 1865: 380 (deducing: Switzerland); id. 1883: 405; Scudder 1891: 591; Handlirsch 1907: 841; Frentzen 1927: 141.

Trichius lugubris Heer

Trichius (Gnorimus) lugubris Heer, 1862: 81, pl. 6 (Miocene, Öhningen, Germany). – Heer 1865: 380; Scudder 1891: 591.

Trichius lugubris. – Heer 1883: 405; Scudder 1891: 591; Handlirsch 1907: 841; Frentzen, 1927: 141.

Trichius rotundatus Heer

Trichius rotundatus Heer, 1862: 82, pl. 6 (Miocene, Öhningen, Kesselstein, Germany). – Scudder 1891: 591; Handlirsch 1907: 841.

Trichius unifasciatus Heer

Trichius (Trichius) unifasciatus Heer, 1862: 82, pl. 6 (Miocene, Öhningen, Kesselstein, Germany). – Scudder 1891: 592; Handlirsch 1907: 842.

Subfamilia **VALGINAE**

Valgus oeningensis Heer

Valgus oeningensis Heer, 1862: 82, pl. 6 (Miocene, Öhningen, Kesselstein, Germany). – Heer 1865: 378, 380; id. 1883: 404–406; Scudder 1891: 594; Handlirsch 1907: 842; Frentzen 1927: 141.

Subfamilia **EUCHIRINAE**

Cheirotonus otai Ueda

Cheirotonus otai Ueda, 1989: 107 (Miocene, Tottori, Japan).

Subfamilia **CRETOSCARABAEINAE** Nikolajev

Cretoscarabaeinae Nikolajev, 1995*b*: 147 (transl. p. 185).

Genus ***Cretoscarabaeus*** Nikolajev

Cretoscarabaeus Nikolajev, 1995*b*: 147 (transl. p. 186), type genus (type species by original designation: *Cretoscarabaeus gibbosus* Nikolajev). – Nikolaev 1999: 178.

Cretoscarabaeus gibbosus Nikolajev

Cretoscarabaeus gibbosus Nikolajev, 1995*b*: 147 (transl. p. 186) (L Cretaceous, Baysa, Russia).

Cretoscarabaeus lentiginosus Nikolajev

Cretoscarabaeus lentiginosus Nikolajev, 1995*b*: 148 (transl. p. 188) (L Cretaceous, Baysa, Russia).

Genus ***Cretorabaeus*** Nikolajev

Cretorabaeus Nikolajev, 1995*b*: 149 (transl. p. 189) (type species by original designation: *Cretorabaeus elongatus* Nikolajev). – Nikolaev 1999: 178.

Cretorabaeus elongatus Nikolajev

Cretorabaeus elongatus Nikolajev, 1995*b*: 149 (transl. p. 189) (L Cretaceous, Baysa, Russia).

Subfamilia **LITHOSCARABAEINAE** Nikolajev

Lithoscarabaeinae Nikolaev, 1992: 76 (transl. p. 96).

Genus ***Lithoscarabaeus*** Nikolajev

Lithoscarabaeus Nikolaev, 1992: 78 (transl. p. 97), type genus (type species by original designation: *Proteroscarabaeus baissensis* Nikritin). – Nikolaev 1999: 178.

Lithoscarabaeus baissensis (Nikritin) Nikolaev

Proteroscarabaeus baissensis Nikritin, 1977: 124 (1991: 168) (L Cretaceous, Baysa, Russia). – Hong & Wang 1990: 115.
Lithoscarabaeus baissensis. – Nikolaev 1992: 78 (transl. p. 97).

Familiae incertae sedis

Genus ***Aliscarabaeus*** Hong

Aliscarabaeus Hong, 1983: 5 (type species by original designation: *Aliscarabaeus granulatus* Hong). – Hong 1985: 37 (*Alscarabaeus*, lapsus calami).

Aliscarabaeus granulatus Hong

Aliscarabaeus granulatus Hong, 1983: 5, 13 (Miocene, Shanwang, China). – Hong 1985: 37f, pl. 16.

Genus ***Avitortor*** Ponomarenko

Avitortor Ponomarenko, 1977*b*: 42 (1991*b*: 54) (originally classified as belonging to Gyrinidae) (type species by original designation: *Avitortor primitivus* Ponomarenko). – Schlüter 1987: 132; Nikolaev 1992: 80 (Scarabaeidae); id. 1999: 178.

Avitortor primitivus Ponomarenko

Avitortor primitivus Ponomarenko, 1977*b*: 42 (1991*b*: 55) (L Cretaceous, Baysa, Russia). – Nikolaev 1992: 80 (transl. p. 101) (Scarabaeidae).

Avitortor leptoscelis (Nikritin) Nikolaev

Geotrupoides leptoscelis Nikritin, 1977: 122 (1991: 165) (L Cretaceous, Baysa, Russia). – Hong 1984: 171; Hong & Wang 1990: 116 (*G. ceptoscelis*, lapsus calami); Hong 1992: 416.
Avitortor leptoscelis. – Nikolaev 1992: 80 (transl. p. 101).

Genus ***Cretoserica*** Nikolajev

Cretoserica Nikolajev, 1998*a*: 83 (transl. p. 519) (type species by original designation: *Cretoserica latitibialis* Nikolajev), incertae subfamiliae. – Nikolaev 1999: 178.

Cretoserica latitibialis Nikolajev

Cretoserica latitibialis Nikolajev, 1998*a*: 83 (transl. p. 520) (L Cretaceous, Baysa, Russia).

Genus ***Hongscarabaeus***, nom. nov.

Proscarabaeus Hong, 1982: 126 (type species by original designation: *Proscarabaeus brunneus* Hong). – Xiao *et al.* 1994: 81; Nikolaev 1998*b*: 30.
Proscarabaeus Hong, 1982, is preoccupied by *Proscarabaeus* Schrank, 1781 (Coleoptera Meloidae) and is, therefore, to be replaced by the new name *Hongscarabaeus* [derivatio nominis: the scarab of Hong, author of the original name; gender: masculine].

Hongscarabaeus brunneus (Hong), comb. nov.

Proscarabaeus brunneus Hong, 1982: 126 (L Cretaceous, Jiuquan, China).

(Genus ***Hybosorites*** Nikolajev)

Hybosorites Nikolajev, 1996: 98 (type species by original designation: *Hybosorites fissuratus* Nikolajev). – Nikolaev 1999: 178.
The name *Hybosorites* Nikolajev is valid according Article 20 (ICZN 1999), because the author introduced it explicitly for a new genus.

(***Hybosorites fissuratus*** Nikolajev)

Hybosorites fissuratus Nikolajev, 1996: 98 (L Cretaceous, Baysa, Russia).
Doubtful (only one elytron).

Genus ***Mesoscarabaeus*** Hong

Mesoscarabaeus Hong, 1982: 123 (type species by original designation: *Mesoscarabaeus corneus* Hong). – Nikolaev 1998*b*: 30.

Mesoscarabaeus corneus Hong

Mesoscarabaeus corneus Hong, 1982: 124 (L Cretaceous, Jiuquan, China).

Mesoscarabaeus morulosus Hong

Mesoscarabaeus morulosus Hong, 1982: 125 (L Cretaceous, Jiuquan, China).

(Genus **Opiselleipon** Bode)

(*Opiselleipon* Bode, 1953: 230; pl. 11 (type species by monotypy: *Opiselleipon gravis* Bode); not assigned to a family by the author. – Crowson 1981: 664 ('Possible Scarabaeoids'), 679 ('Scarabaeoid-like appearance'); Carpenter 1992: 324 ('Little-known genus', suborder and family uncertain); Scholtz & Chown 1995*a*: 358.

(***Opiselleipon grave*** Bode)

Opiselleipon gravis Bode, 1953: 230, pl. 11 (L Jurassic, Hondelage near Braunschweig, Germany). – Scholtz 1990: 1029; Carpenter 1992: 324.

Tribus **HOLCOROBEINI** Nikolajev

Holcorobeini Nikolajev, 1992: 81 (transl. p. 102).

Genus ***Holcorobeus*** Nikritin

Holcorobeus Nikritin, 1977: 127 (1991: 172) [‘*Holcoribeus*’, lapsus calami, since all species are named *Holcorobeus*], type genus (type species: *Holcorobeus vittatus* Nikritin). – Crowson 1981: 667 (‘modern-looking Scarabeoids’); Schlüter 1987: 133; Nikolaev 1998*b* (classified as Aclopinae, but without giving an explanation); id. 1999: 178; Jarzembowski 2000: (8).

Holcoribeus Nikritin (see above). – Ponomarenko 1990: 68; Carpenter 1992: 300 (‘Family assignment doubtful’).

Antemnacrassa Gomez Pallerola 1979: 340 (syn. Nikolaev 1992: 82 who called it *Antemnocrassa*).

Since the differences between *Holcorobeus* and *Geotrupoides* (sensu Nikolaev) are fluid, the undiscussed transference of some species from the latter to the first genus by Nikolaev (1992) is questionable.

Subgenus ***Holcorobeus*** Nikritin

Holcorobeus Nikritin, 1977: 127 (1991: 172) (‘*Holcoribeus*’; see above); subgenus introduced by Nikolaev 1992: 82 (transl. p. 103).

Holcorobeus (Holcorobeus) atrosulcatus Nikolajev

Holcorobeus (Holcorobeus) atrosulcatus Nikolajev, 1992: 84 (transl. p. 106) (L Cretaceous, Baysa, Russia).

Holcorobeus (Holcorobeus) evittatus Zhang

Holcoribeus evittatus Zhang, 1992*a*: 334 (L Cretaceous, Laiyang Formation, China).

Legs lacking exept for hind coxae and femora. On this basis, the classification is not reliable.

Holcorobeus (Holcorobeus) incertus Ponomarenko

? Holcoribeus incertus Ponomarenko 1990: 68, pl. 6 (L Cretaceous, Turga Formation, Russia; Gidari Formation: Karabon, Pavlovka, Russia).

Holcorobeus (Holcorobeus) incertus. – Nikolaev, 1992: 83 (transl. p. 104).

Holcorobeus (Holcorobeus) latitibialis Nikolajev

Holcorobeus (Holcorobeus) latitibialis Nikolajev, 1992: 84 (transl. p. 106) (L Cretaceous, Baysa, Russia).

Holcorobeus (Holcorobeus) longipes (Ponomarenko) Nikolaev

Geotrupoides longipes Ponomarenko, 1986: 98, pl. 8 (L Cretaceous, Myangad, Mongolia).

Holcorobeus (Holcorobeus) longipes. – Nikolaev, 1992: 83 (transl. p. 104).

Holcorobeus (Holcorobeus) maculatus Nikolajev

Holcorobeus (Holcorobeus) maculatus Nikolajev, 1992: 85 (transl. p. 107) (L Cretaceous, Baysa, Russia).

Holcorobeus (Holcorobeus) monreali (Gomez Pallerola) Nikolaev

Antemnacrassa monreali Gomez Pallerola 1979: 340 (L Cretaceous, Montsec, Spain). – Gomez Pallerola 1986: 720f.

Holcorobeus (Holcorobeus) monreali. – Nikolaev, 1992: 83 (transl. p. 104).

Nikolaev synonymised *Antemnacrassa* with *Holcorobeus* without explanation, although the former was described as having long, strong antennae. He saw only the published photographs but claimed that these ‘antennae’ does not belong to a beetle (pers. comm.).

Holcorobeus (Holcorobeus) nigrimontanus Nikolajev

Holcorobeus nigrimontanus Nikolajev, 1992: 83 (transl. p. 105) (U Jurassic, Karatau, Kazakhstan).

(Holcorobeus (Holcorobeus) nigrovittatus Nikolajev)

Holcorobeus nigrovittatus Nikolajev, 1992: 86 (transl. p. 108) (L Cretaceous, Baysa, Russia).

Doubtful (only one elytron).

Holcorobeus (Holcorobeus) picturatus Nikritin

Holcorobeus picturatus Nikritin, 1977: 129 (1991: 175) (L Cretaceous, Baysa, Russia).

Holcorobeus (Holcorobeus) picturatus. – Nikolaev 1992: 83 (transl. p. 104).

Holcorobeus (Holcorobeus) punctatus (Ponomarenko) Nikolaev

Proteroscarabaeus punctatus Ponomarenko, 1986: 97f, pl. 8 (L Cretaceous, Gurvan-Erenii-Nuru, Mongolia).

Holcorobeus (Holcorobeus) punctatus. – Nikolaev, 1992: 83 (transl. p. 104).

Holcorobeus (Holcorobeus) sulcatus (Nikritin) Nikolaev

Geotrupoides sulcatus Nikritin, 1977:120 (1991: 163) (L Cretaceous, Baysa, Russia). – Hong 1984: 170; Hong & Wang 1990: 116 (*G. sdulcatus*, lapsus calami); Hong 1992: 416; Ren *et al.* 1995: 436; Zhang 1997: 90.

Holcorobeus (Holcorobeus) sulcatus. – Nikolaev 1992: 83 (transl. p. 104).

Holcorobeus (Holcorobeus) vitimensis (Nikritin) Nikolaev

Geotrupoides vitimensis Nikritin, 1977: 123 (1991: 167) (L Cretaceous, Baysa, Russia). – Hong & Wang 1990: 116; Hong 1992: 416.

Holcorobeus vitimensis. – Nikolaev, 1992: 83 (transl. p. 104).

Holcorobeus (Holcorobeus) vittatus Nikritin

Holcorobeus vittatus Nikritin, 1977: 128 (1991: 173) (L Cretaceous, Baysa, Russia). – Nikolaev 1992: 83 (transl. p. 104).
Holcoribeus vittatus. – Carpenter 1992: 301; Zhang 1992*a*: 334f.

Subgenus ***Mesaclopus*** Nikolajev

Mesaclopus Nikolajev, 1992: 86 (transl. p. 108) (type species by original designation: *Holcorobeus mongolicus* Nikolajev).

Holcorobeus (Mesaclopus) mongolicus Nikolajev

Holcorobeus (Mesaclopus) mongolicus Nikolajev, 1992: 86 (transl. p. 108) (U Jurassic–L Cretaceous, Khutel–Khara, Mongolia).

Presumed Scarabaeoidea

Genus ***Tetragonides*** Bode

Tetragonides Bode, 1953: 225, pl. 11 (type species by monotypy: *Tetragonides magnus* Bode) – Carpenter 1992: 326 ('Little-known genus.', suborder and family uncertain).

Tetragonides magnus Bode

Tetragonides magnus Bode, 1953: 225 (L Jurassic, Hondelage, Germany) ('Die Gestalt erinnert an die der (?) Lucaniden.'). – Carpenter 1992: 326.

Fossil taxa later synonymised with recent taxa

Genus ***Magniscarabaeus*** Hong & Wang

Magniscarabaeus Hong & Wang in Hong, 1983: 5 (type species by original designation: *Magniscarabaeus furvus* Hong & Wang). – Hong & Wang 1986: 6.
= *Anomala* Samouelle, 1819. – Zhang 1989: 162.

Genus ***Obitiscarabaeus*** Hong

Obitiscarabaeus Hong, 1983: 6 (type species by original designation: *Obitiscarabaeus jiaoyanshanensis* Hong). – Hong 1985: 40.
= *Geotrupes* Latreille, 1796. – Zhang 1989: 152.

Genus ***Palaeocopris*** Pierce

Palaeocopris Pierce, 1946*a*: 130 (type species by monotypy: *Palaeocopris labreae* Pierce, 1946). – Edmonds 1972: 855 ('morphological resemblance to this genus with *Phanaeus*').
Paleocopris. – Halffter 1959: 176.
= *Phanaeus* MacLeay, 1819. – Miller *et al.* 1981: 627.

Canthon simplex antiquus Pierce

Canthon simplex antiquus Pierce, 1946*a*: 120 (Pleistocene, Rancho La Brea tar pits, Los Angeles, USA). – Spohn 1973: 52.
Boreocanthon simplex antiquus. – Halffter 1959: 176.
= *Canthon (Boreocanthon) simplex* LeConte. – Miller *et al.* 1981: 626; Stock & Harris 1992: 84.

Canthon praticolus retustus Pierce

Canthon praticolus vetustus Pierce, 1946*a*: 122 (Pleistocene, Rancho La Brea tar pits, Los Angeles, USA). – Sphon 1973: 52.
Boreocanthon praticola vetustus. – Halffter 1959: 176.
= *Canthon (Boreocanthon) praticola* LeConte. – Miller *et al.* 1981: 626; Stock & Harris 1992: 84.

Nomina nuda and unpublished names

Genus *Melolonthidium* Phillips, 1871: 174; M Jurassic, Stonesfield Slate, England; without indication. – Brodie 1873: 23; Goss 1879: 143; Handlirsch 1907: 572.
Genus *Prototrox* Nikolajev, 1999: 178 (Mesozoic, without indication; description in press).
Genus *Pseudopentodon* Filhol, 1892: 2 (without indication).
Pseudopentodon blanchardi Filhol, 1892: 2 (Eocene-Oligocene, Quercy, France; without indication). – Handschin 1944: 2, 19, 21; id. 1950: 138 (*Pseudopantodon*); Théodoridès 1952: 47.

Ichnotaxa, fossil nests and broodballs of Scarabaeoidea

Ichnogenus ***Coprinisphaera*** Sauer

Coprinisphaera Sauer, 1955: 123 (type species by monotypy: *Coprinisphaera ecuadoriensis* Sauer). – Häntzschel 1962: W189; id. 1975: W52; Martinez 1982: 48; Genise 1993: 50; Donovan 1994: 209; Genise & Cladera 1995: 78; Buatois *et al.* 1998: 226; Genise & Laza 1998: 220; Genise 1999: 110; Genise *et al.* 2000: 49ff.
Cangabola Lengerken, 1955: 937 (type species by monotypy: *Cangabola ecuadoriensis* Sauer), **syn. nov.** (Lengerken (10.viii.1955) introduced the generic name *Cangabola* unintentionally by citing from and referring to letters of Walther Sauer. *Cangabola* seems to be the name that Sauer used in his correspondence for the ichnofossils he finally described as *Coprinisphaera* (iv.1955). Since Lengerken introduced "*Cangabola ecuadoriensis* W. Sauer" with description and photographs, *Cangabola* is available according to Code Art. 13.1. and 13.3. However, it has the same type species as *Coprinisphaera* and is, therefore, a synonym of the latter.)
Coprinsphaera. – Sauer 1956: 550; Halffter & Matthews 1966: 154; Retallack 1991: 182, 296; Duringer *et al*. 2000: 264.
Devincenzia Roselli, 1939: 81 (type species by monotypy: *Devincenzia murguiai* Roselli; preoccupied by *Devincencia* Kraglievich, 1932 – see Genise & Bown 1994: 109). (syn.)
Devicenzichnus Roselli, 1976: 167 (type species by monotypy: *Devicenzichnus murguiai*). – Martinez 1982: 48; Buatois *et al.* 1998: 226. (syn.)
Devinzenzichnus. – Genise 1993: 50 (synonym of *Coprinisphaera*); Genise & Laza 1998: 213. (syn.)

Coprinisphaera ecuadoriensis Sauer

'bolas'. – Bruet 1950.
Coprinisphaera ecuadoriensis Sauer, 1955: 123 (U Pleistocene, northern Ecuador). – Sauer 1956: 555; id. 1959: 119ff; Häntzschel 1962: W189; id. 1975: W52; Martinez 1982: 48; Genise & Bown 1994: 109; Genise 1999: 110.
Cangabola ecuadoriensis. – Lengerken 1955: 937.
Coprinsphaera ecuadoriensis. – Sauer 1956: 550.
Coprinsphaera ecuadorensis. – Halffter & Matthews 1966: 154.
Coprinisphaera ecuadorensis. – Genise 1993: 50.

Coprinisphaera frenguellii Genise & Bown

Coprinisphaera frenguellii Genise & Bown, 1994: 110 (Miocene, Estancia Ana Maria, Prov. Santa Cruz, Argentina). – Buatois *et al.* 1998: 226.

Coprinisphaera murguiai (Roselli) Genise & Bown

Devincenzia murguiai Roselli, 1939: 81 (U Cretaceous, Colonia, Uruguay). – Genise 1983: 50.
Devincenzichnus murguiai. – Roselli 1976: 166f; Genise 1993: 50; Genise & Bown 1994: 109.
Devicenzichnus murguiai. – Roselli 1976: 167; Martinez 1982: 48.
Devincenzichnus murguiae. – Retallack 1990: 219.
Devinzenzichnus murgiiae. – Donovan 1994: 209.
Coprinisphaera murguiai. – Genise & Bown 1994: 109.

Ichnogenus ***Eatonichnus*** Bown, Hasiotis, Genise, Maldonaldo & Browers

Eatonichnus Bown, Hasiotis, Genise, Maldonaldo & Browers, 1997: 52 (type species by original designation: *Xenohelix utahensis* Gilliland & LaRocque; 'might be constructions of dung beetles'). – Genise & Bown 1998: 222; Genise & Laza 1998: 214, 218; Genise 1999: 110; Genise *et al*. 2000: 53f, 57 ('possible dung beetle nest').

Eatonichnus claronensis Bown, Hasiotis, Genise, Maldonaldo & Browers

Eatonichnus claronensis Bown, Hasiotis, Genise, Maldonaldo & Browers, 1997: 54 (Eocene, J.G. Eaton locality, Utah, USA.). – Genise & Bown 1998: 222.

Eatonichnus utahensis (Gilliland & La Rocque) Bown, Hasiotis, Genise, Maldonaldo & Browers

Xenohelix? utahensis Gilliland & La Rocque, 1952: 502, pl. 59 (Eocene, Bald Knoll Canyon, Utah, USA.). – Kilpper 1962: 56.
Eatonichnus utahensis. – Bown *et al.* 1997: 52; Genise & Laza 1998: 222.

Ichnogenus ***Fontanai*** Roselli

Fontanai Roselli 1939: 79 (type species by monotypy: *Fontanai kraglievichi* Roselli). – Genise & Laza 1998: 213 ('is a dung beetle brood mass'); Genise *et al.* 2000: 49, 51, 53f, 58f.
Fontanaichnus Roselli 1976: 167 (type species by monotypy: *Fontanaichnus kraglievichi*). – Retallack 1990: 219; Donovan 1994: 209; Buatois *et al.* 1998: 226, (syn.).

Fontanai kraglievichi Roselli

Fontanai kraglievichi Roselli, 1939: 79 (U Cretaceous-L Tertiary, Asencio Formation, Uruguay). – Genise 1993: 53 (classification impossible); Genise & Bown 1994: 112 ('insufficiently known to meaningfully interpret them').
Fontanaichnus kraglievichi. – Roselli 1976: 167; Retallack 1990: 219 ('Likely fossil nests of dung beetles'); Donovan 1994: 209 ('Possible fossil nests of dung beetles').

Ichnogenus ***Madinaichnus*** Roselli

Madinaichnus Roselli, 1987: 23 (type species by monotypy: *Madinaichnus larranagai*). – Genise & Laza 1998: 213; Buatois *et al.* 1998: 226; Genise 1999: 110; Genise *et al.* 2000: 54.
Genise (1999) supposed *Madinaichnus*, *Martinezichnus*, and *Microicoichnus* to be synonymous to *Coprinisphaera*.

Madinaichnus larranagai Roselli

Madinaichnus larranagai Roselli, 1987: 23 (U Cretaceous – L Tertiary, Uruguay).

Ichnogenus ***Martinezichnus*** Roselli

Martinezichnus Roselli, 1987: 22 (type species by monotypy: *Martinezichnus francisi* Roselli). – Genise & Cladera 1995: 78; Genise & Laza 1998: 213; Buatois *et al.* 1998: 226; Genise 1999: 110; Genise *et al.* 2000: 54.

Martinezichnus francisi Roselli

Martinezichnus francisi Roselli, 1987: 22 (Cretaceous, Asencio Formation, Uruguay?). – Genise & Cladera 1995: 78f.

Ichnogenus ***Microicoichnus*** Roselli

Microicoichnus Roselli, 1987: 49 (type species by monotypy: *Microicoichnus lafurcadai* Roselli). – Buatois *et al.* 1998: 226; Genise & Laza 1998: 213; Genise 1999: 110; Genise *et al.* 2000: 54.

Microicoichnus lafurcadai Roselli

Microicoichnus lafurcadai Roselli, 1987: 49 (U Cretaceous – L Tertiary, Uruguay).

Ichnogenus ***Monesichnus*** Roselli

Monesichnus Roselli, 1987: 39 (type species by monotypy: *Monesichnus ameghinoi* Roselli). – Laza *et al.* 1994; Bown *et al.* 1997: 55f ('might be constructions of dung beetles'); Buatois *et al.* 1998: 226; Genise & Laza 1998: 218; Genise *et al.* 2000: 49, 51, 53f, 58f.

Monesichnus ameghinoi Roselli

Monesichnus ameghinoi Roselli, 1987: 39 (U Cretaceous – L Tertiary, Asencio Formation, Uruguay). – Laza *et al.* 1994; Bown *et al.* 1997: 56; Genise & Laza 1998; Genise 1999: 110.

Ichnogenus ***Pallichnus*** Retallack

Pallichnus Retallack, 1984: 580 (type species by original designation: *Pallichnus dakotensis* Retallack). – Genise 1993: 50; Genise & Bown 1994: 109; Buatois *et al.* 1998: 226; Genise 1999: 110; Genise *et al.* 2000: 53.

Pallichnus dakotensis Retallack

Pallichnus dakotensis Retallack, 1984: 581 (Oligocene, South Dakota, USA.). – Genise 1993: 50.

(Ichnogenus ***Rebuffoichnus*** Roselli)

Rebuffoichnus Roselli, 1987: 24 (type species by monotypy: *Rebuffoichnus casamiquelai*). – Buatois *et al.* 1998: 226; Genise & Laza 1998: 213; Genise *et al.* 2000: 54.

(***Rebuffoichnus casamiquelai*** Roselli)

Rebuffoichnus casamiquelai Roselli 1987: 24 (U Cretaceous – L Tertiary, Asencio Formation, Uruguay). – Genise *et al.* 1999: 29 (pupal chamber of Coleoptera – Curculionidae, Scarabaeidae or Tenebrionidae).

Ichnogenus ***Scaphichnium*** Bown & Kraus

Scaphichnium Bown & Kraus, 1983: 106 (type species by original designation: *Scaphichnium hamatum* Bown & Kraus). – Buatois *et al.* 1998: 226; Genise & Laza 1998: 214, 218.

Scaphichnium hamatum Bown & Kraus

Scaphichnium hamatum Bown & Kraus, 1983: 106 (L Eocene, Willwood formation, Wyoming, USA.). – Hasiotis *et al.* 1993 (classified as traces of Scarabaeoidea); Bown *et al.* 1997: 56; Genise & Laza 1998: 222; Genise 1999: 110.

Unnamed trace fossils

[More possible traces of dung beetles have been compiled by Retallack (1990: 223).]

Africa. Pleistocene, Rutana, Burundi: 'loges fossiles des coprophages' (Basilewsky 1951).

Pliocene (2–3 Myr), Makapansgat Limeworks, South Africa (Kitching 1980).

Pliocene (3,46–3,76 Myr), Laetoli, Tanzania: structure resembling a dung ball of *Heliocopris* (Sands 1987: 423) (= *Coprinisphaera* sp. according to Genise *et al.* 2000).

Asia. U Miocene, Dhok Patan Formation, Pakistan: *Coprinisphaera* sp. (Retallack 1991: 182, 296).

North America. Pliocene, Jalisco, México: 'bola-nido' (Morón Ríos 1984: 27).

L Eocene, Golden Valley Formation, North Dakota, USA.: striae in coprolites 'appear to have been made by scatophagous beetles' (Jepsen 1963: 680).

U Cretaceous, Two Medicine Formation, Montana, USA.: coprolites (Chin & Gill 1996).

South America. U Pleistocene, Buenos Aires and Lujan; Santa Fé, Tezanos Pinto; Tucumán, Tafí del Valle: *Coprinisphaera* sp. (Genise *et al.* 2000).

U Pleistocene, Sopas, Uruguay: *Coprinisphaera* sp. (Genise *et al.* 2000).

L Pleistocene, Los Galpones, Argentina: 'bolas' of cf. *Canthon* (Frenguelli 1938*a*, *b*; *Coprinisphaera* sp. according to Genise *et al.* 2000).

U Pliocene (– L Pleistocene), Chapadmalal and San Andrés Formation, Buenos Aires, Argentina: *Coprinisphaera* sp. (Genise *et al.* 2000).

U Pliocene, Piquete Formation, Sierra de Vaqueros, Salta, Argentina: cf. *Phanaeus, Megathopa; Coprinisphaera* sp. (Alonso *et al.* 1982; Genise *et al.* 2000).

U Miocene, Las Flores, San Juan, Argentina: 'nidos de escarabeidos' (Contreras 1996; *Coprinisphaera* sp. according to Genise *et al.* 2000).

U Miocene, Collón-Curá Formation, Río Negro and Neuquén, Argentina: 'peras' of cf. *Megathopa,* cf. *Onthophagus*, etc. (Frenguelli 1938*a*, 1939; Laza 1986*a*; *Coprinisphaera* sp. according to Genise *et al.* 2000).

U Miocene, Paso de las Carretas, San Luis, Argentina: "nidos' de escarabideos' (Pascual & Bondesio 1981:125; *Coprinisphaera* sp. according to Genise *et al.* 2000).

U Miocene, Andalhualá, Catamarca, Argentina: *Coprinisphaera* sp. (Genise *et al.* 2000).

U Miocene, Cerro Azul, La Pampa/Buenos Aires, Argentina: *Coprinisphaera* sp. (Genise *et al.* 2000).

U Miocene–L Pliocene, Monte Hermoso, Buenos Aires, Argentina: *Coprinisphaera* sp. (ichnofossil) (Genise *et al.* 2000).

U Oligocene, Colhue-Huapi Formation, Argentina (U): *Coprinisphaera* sp. (Laza 1986*b*, Genise *et al.* 2000).

Oligocene, Ludados lustrosos, Mendoza, Argentina: *Coprinisphaera* sp. (Genise *et al.* 2000).

U Eocene, Musters Formation, Chubut Province, Argentina: *Coprinisphaera* sp. (Genise *et al.* 2000).

M Eocene, Laguna del Mate, Chubut Province, Argentina: 'similar fossils of *Coprinisphaera*' (Retallack 1990: 218).

L Eocene, Santa Cruz, Punta Casamayor, Los Leones, and Chubut, Comodoro Rivadavia, Argentina: 'peras' of cf. *Megathopa* and cf. *Phanaeus* (Frenguelli 1938*a*, *b*; Laza 1986*b*; *Coprinisphaera* sp. according to Genise *et al.* 2000).

Palaeocene, Rio Chico, Chubut, Argentina: *Coprinisphaera* sp. (Genise *et al.* 2000).

Palaeocene (?), Comallo, Rio Negro, Uruguay: fossil nests (Retallack 1990: 217).

Tertiary (Oligocene?), Chubut, Cañadón del Loco, Argentina: 'nidos de escarabeidos' (Frenguelli 1941).

Antarctica. Eocene, Isla Marambio (Seymour), La Meseta formation, Peninsula Antartica: 'un molde interno de nido de escarabeido integrante de la subtribu Phanaeina (Scarabaeinae)' (Laza & Reguero 1990; *Coprinisphaera* sp. according to Genise *et al.* 2000).

Other fossils originally described as Lamellicornia

Genus ***Oryctites*** Oppenheim (not valid)

Oryctites Oppenheim, 1888: 238. – Ponomarenko 1971: 72 (transl. p. 67): Adephaga incertae sedis.

Since Oppenheim only indicates a fossil species of *Oryctes* Illiger, 1798 ('Für *Oryctes* spricht noch der Umstand...'), the name *Oryctites* Oppenheim is not valid according to Article 20 (ICZN 1999).

(***Oryctes***) ***fossilis*** (Oppenheim) Houlbert

Oryctites fossilis Oppenheim, 1888: 238, pl. 31, fig. 2 (Jurassic, U Malm, Solnhofen, Germany). – Scudder 1891: 216; Meunier 1898*b*: 112, 133, pl. 23; Ponomarenko 1971: 67: Adephaga incertae sedis.

Oryctes fossilis. – Houlbert 1915: 64 ('Handlirsch assure que cette identification est inexacte').

? Cerambycinus fossilis (Cerambycidae). – Handlirsch 1906: 547 ('gewiss kein '*Oryctes*").

Genus ***Progeotrupes*** Oppenheim

Progeotrupes Oppenheim, 1888: 239 (type species by monotypy: *Progeotrupes jurassicus* Oppenheim). – Broili 1921: 675; id. 1924: 697; Laurentiaux 1953: 476. – belongs to Blattodea (see below).

Progeotrupes jurassicus Oppenheim

Progeotrupes jurassicus Oppenheim, 1888: 239, pl. 31 (Jurassic, U Malm, Solnhofen, Germany). – Scudder 1891: 217; Meunier 1898*b*: 109 ('C'est avec le plus grand doute, que je place ce coléoptère près des Lamellicornes du genre *Geotrupes*'); Handlirsch 1906: 549, pl. 45 [1907] ('Hat sicher nichts mit *Geotrupes* zu tun.'); Ponomarenko 1971: 80 (transl. p. 75) (Blattodea).

Geotrupes jurassicus. – Meunier 1898*b*: 133.

Genus ***Prosynactus*** Bode

Prosynactus Bode, 1953: 224 (type species by monotypy: *Prosynactus scissus* Bode) ('Ein Typ, der an manche (?) Lucaniden erinnert.'). – belongs to Tachypachidae (see below).

Prosynactus scissus Bode

Prosynactus scissus Bode, 1953: 224, pl. 11 (Lias, Beienrode, Germany). – Ponomarenko 1992: 180 (belongs to Coleoptera Tachypachidae).

Genus ***Scarabaeides*** Germar

Scarabaeides Germar, 1839: 218 (type species by monotypy: *Scarabaeides deperditus* Germar). – Giebel 1846: 148; Bronn 1848*b*: 1119; id. 1849: 625; Weyenbergh 1873: 240.

Mesobelostomum Haase, 1890: 21 (Heteroptera: Belostomatidae); synonym of *Scarabaeides* because of identical type species.

Scarabaeides deperditus Germar

'*Scarabaeus* (der Gattung *Phileurus* nahe stehend)'. – Germar 1837*b*: 422.

Scarabaeides deperditus Germar, 1839: 218 (Malm, Solnhofen, Germany). – Brodie 1845: 109; Bronn 1848*b*: 1119; id. 1849: 625; Giebel 1852*a*: 207; Quenstedt 1852*a*: 313 ('Wäre es ein Käfer, so sollte man doch Reste von Flügeldecken erwarten.'), 786 (index: '*Scarabaeoides depertitus*' [lapsus calami]; id. 1852*b*: pl. 5; Giebel 1856: 36 ('Die Stellung des Thieres bleibt völlig zweifelhaft.'); Hagen 1862: 110 ('grosse Aehnlichkeit mit *Belostoma*; ein Käfer ist es bestimmt nicht.'), 113 (ad Hemiptera); Weyenbergh 1869*a*: 249 (ad Hemiptera); Goss 1879: 147; Scudder 1886: 73 ('Belostomidae'); id. 1891: 176 ('Belostomatidae'); Zittel 1895: 504.

Scarabaeoides deperditus. – Weijenbergh 1869*b*: [233] (Heteroptera, Geocorises).

Scaraboeides deperditus, Scarabeides deperditus. – Brodie 1873: 21.

Scarabaeus deperditus. – Weyenbergh 1874: 88f, 103 or 109; Winkler 1878: 96; Scudder 1891: 176.

Hydrophilus deperditus. – Weyenbergh 1873: 239; id. 1874: 84 or 89, 103 or 109; Winkler 1878: 96; id. 1896: 309.

Belostomum deperditus. – Assmann 1877: 192.

Belostoma deperditum. – Deichmüller 1886: 61; Meunier 1896: 93; Winkler 1896: 309.

Belostoma deperdita. – Scudder 1891: 176.

Mesobelostomum deperditum. – Haase 1890: 21; Handlirsch 1906: 637, pl. 51 (1907); id. 1925: 210; Müller 1989: 247.

Genus ***Tetragonotrachelus*** Bode

Tetragonotrachelus Bode, 1953: 224 (type species by monotypy: *Tetragonotrachelus gracilis* Bode) ('Äußerlich etwas an den Lucanidentyp erinnernd.').

Synonym of *Prosynactus* Bode, 1953: 224 (Coleoptera Tachypachidae) (Ponomarenko 1992: 181).

Tetragonotrachelus gracilis Bode

Tetragonotrachelus gracilis Bode, 1953: 224, pl. 11 (Lias, Beidenrode, Germany).

Prosynactus gracilis. – Ponomarenko 1992: 181 (belongs to Coleoptera: Tachypachidae).

Genus ***Troxites*** Goldenberg

Troxites Goldenberg, 1854: 36 (type species by monotypy: *Troxites germari* Goldenberg). – Giebel 1856: 36; Goldenberg 1867: 7; Gerstaecker 1868: 289 ('Zugehörigkeit zu der Ordnung der Coleopteren zumindest sehr zweifelhaft'); Scudder 1879*b*: 19 ('curculionid'); id. 1881–1885: 794 ('dürfte eine fossile Frucht sein'); id. 1886: 73 ('probably a fruit').

The name *Troxites* Goldenberg is nomenclaturally valid according to Article 20 (ICZN 1999), because the author introduced it explicitly for a new genus that is rather of the type of a collective group.

Troxites germari Goldenberg

Troxites germari Goldenberg, 1854: 36 (Carboniferous; Steinkohlen, Altenwald near Saarbrücken). – Giebel 1856: 36; Goldenberg 1867: 7; Brodie 1873: 27; Goldenberg 1873: 7, pl. 2; id. 1877: 50; Scudder 1879*b*: 17; Goss 1880: 297; Scudder 1891: 97f ('Probably not an insect.'); Handlirsch 1906: 342 (refers to the next author's interpretation); Schlechtendal 1912: 159ff, pl. 1 ('unzweifelhaft das Bruchstück einer Crustacee etwa ? *Arthropleura armata*, vielleicht haben wir in ihm ein Stückchen Fühler oder Bein'); Handlirsch 1919: 81 ('*Arthropleura*-Fühlerglied'); id. 1922: 221 ('Arthropleurarest'); Waterlot 1934: 262 ('fossile à affinité douteuse').

Xyloryctes planus Frič (ichnospecies)

Xyloryctes planus Frič, 1877: 16, pl. 3 (Carboniferous, Nyřan near Plzen, Czechia; Oberhohndorf, Germany). – Scudder 1879*b*: 17; id. 1891: 98 ('coleopteroid'); Handlirsch 1905: 328 ('Die Deutung dieser Gebilde als Bohrlöcher von Coleopteren erscheint mir gewagt.'); id. 1919: 590 (arthropod origin questionable); id. 1922: 219 (no insect).

Xyloryctes septarius Frič (ichnospecies)

Xyloryctes septarius Frič, 1877: 15, pl. 3 (U Carboniferous, Swinná near Radnitz, Bohemia, Czechia). – Scudder 1879*b*: 17; id. 1891: 98 ('coleopteroid'); Handlirsch 1905: 337 (not from an insect); id. 1919: 590 (arthropod origin questionable); id. 1922: 219 (no insect).

Frič never claimed that these ichnofossils were lebensspuren of Scarabaeoidea. However, he gave them the ichnogeneric name *Xyloryctes*. I suppose that he did not realise that this name was already proposed for extant Dynastinae from America (*Xyloryctes* Hope, 1837).

Tertiary and Mesozoic lagerstätten with fossils of Scarabaeoidea

Pliocene (>1.8 Myr)

Europe. Willershausen, Harz, northern Germany (U): *Aphodius (Acrossus) rufipes* (L.), Aphodiinae spec., *Mimela* spec., *Oryctes nasicornis* L. (Gersdorf 1971), Coprinae sp., Cetoniinae sp. (reliable) (Gersdorf 1976).
Boulder-Formation, Mundesley, England: cfr. *Copris lunaris* (Lyell 1840: 175).
Kisatibi formation, Georgia (L?): *Copris (Copris) kartlinus* (Kabakov 1988).

Africa. Makapansgat, South Africa: ichnofossils of coprophagans (Kitching 1980).
Kouba Olanga, palaeo-lake Chad system, Chad (5 Myr): fossil brood-balls of dung beetles (Duringer *et al*. 2000).
Pliocene (3,46–3,76 Myr), Laetoli, Tanzania: *Coprinisphaera* sp, (Sands 1987: 423; Genise *et al.* 2000: 55).

North America. Jalisco, México: ichnofossils of coprophagans (Morón Ríos 1984).

South America. Piquete Formation, Sierra de Vaqueros, Salta, Argentina (U): ichnofossils of coprophagans ('bolas') (Alonso *et al.* 1982; *Coprinisphaera* sp. according to Genise *et al.* 2000: 55).
Chapadmalal and San Andrés Formation (transition to Pleistocene), Buenos Aires, Argentina: *Coprinisphaera* sp. (Genise *et al.* 2000).

Transition Mio/Pliocene

Europe. Simetite (Sicilian resin): (*Scarabaeus bilobus* L.) (= *Caelosis biloba*) (Ferrara 1805: 136 [wrong determination as already indicated by Krell 1996: 18]; Kohring & Schlüter 1989: 45).
Cinérites de Varennes, France: (*Melolonthites laterosinuatus*) (Piton & Théobald 1935).

North America. Beaufort Formation, Prince Patrick Island, Canada (3–5,7 Myr): *Aegialia* sp. (Matthews 1976, Matthews *et al.* 1990).

South America. Monte Hermoso, Buenos Aires, Argentina (U Miocene-L Pliocene): *Coprinisphaera* sp. (ichnofossil) (Genise *et al.* 2000: 55).

Miocene (>5Myr)

Europe. Montagne d'Andance, Ardeche, France (U, Turolian): *Miocenidorcus andancensis*, cf. *Geotrupes stercorarius*, *Thyphoeus* sp. [= *Typhaeus* sp.], cf. *Amphimallon ater* (Riou 1988: 103ff, 1999).
Habichtswald near Kassel, Germany (L): cfr. *Aphodius* (Landgrebe 1843); doubtful (legs and antennae absent).
Öhningen, Badenia, Germany (M, Sarmat, Serravallian, 14,5 Myr): *Coprologus gracilis, Geotrupes germari, Gymnopleurus deperditus, G. rotundatus, G. sisyphus, Copris druidum, C. subterraneus, Onthophagus bisontinus, O. crassus, O. ovatulus, O. prodromus, O. urusheeri, Oniticellus amplicollis, Aphodius anteactus, A. brevipennis, A. meyeri, Hybosorus lividus, Rhizotrogus longimanus, (Melolonthites aciculatus), M. deperditus, (M. lavateri), (M. obsoletus)* [The *Melolontha* listed by Keferstein (1834: 331) likely refers to one of these *Melolonthites* species.] *Lepitrix germanica, Anomala fugax, Serica minutula, Gnorimus aedilis, Trichius amoenus, T. lugubris, T. rotundatus, T. unifasciatus, Valgus oeningensis, Glaphyrus antiquus, Pentodon proserpinae* (Heer 1847, 1862, 1865, Frentzen 1927), *Lucanus* sp. (Serres 1829: 235), *Geotrupes* sp., cf. *Trichius* sp. (obviously not considered by Heer) (Scudder 1895*b*: 120).
Parschlug, Styria, Austria (U): *(Melolonthites kollari), (M. parschlugianus)* (Heer 1847).
Mokřina (Krottensee) near Kynšperk n. O., Cypris Shale, Cheb Basin, Bohemia, Czechia (L, Burdigalian): (*Melolontha solitaria*) (Novák, 1878).
Gabbro, Livorno, Italy (L, Messinian): *Aphodius bosniaskii* (Handlirsch 1908).
Euboea (Evia), Greece (L): *Geotrupes* spec. (Bachmayer *et al.* 1971).

Asia. Dhok Patan Formation, Pakistan (U): *Coprinisphaera* sp. (Retallack 1991: 182, 296).
Shanwang, Shandong, China (M, Serravallian-Langhian; 15.5–17 Myr): *Geotrupes jiaoyanshanensis*, *Orrhodomala protista*, *Onthophagus* sp., *Phalops* sp., *Scelocopris enertheus, Adoretus recticlypeus, A. rhinus, Aliscarabaeus granulatus*, *Anomala amblobelia*, *A. brachytarsia, A. endoxa, A. eversa, A. furva*, *A. lochmocola, A. orcina, A. palaeobrunnea, A. punctulata, A. scia, A. ursa, Zhangsunia extumida, Genonota mochthera, G. scola, Holotrichia cressona, H. spatha*, *Macronota shandongiana*, *Mioserica margelis*, *Petraeianus ruderatus*, *Petulantis yimengensis*, *Serrulus sinicus* (Hong 1983, 1985, Zhang *et al.* 1994, Zhang 1989).
Noto, Takaya, Yanagida Formation, Japan (M): *Heliocopris antiquus*, *Phyllopertha*? sp. (Fujiyama 1968).
Seki, Masaragawa Formation, Sado Island, Japan (L): *Aphodius* ? sp. (doubtful, only one elytron) (Fujiyama 1985).
Tottori Group, Kokufu Town, Japan (M): *Cheirotonus otai* (Ueda 1989).

Africa. Lake Victoria, Kenya: *Anachalcos mfwangani* (Mfwangano Island), *Copris leakeyorum* (Rusinga Island), *Metacatharsius rusingae* (Rusinga I.), Rutelinae, Cetoniinae (Paulian 1976).

North America. Ruby River, Montana, USA. (U): Rutelinae (tentatively) (Zuidema 1950: 121).
Clarkia, Idaho, USA. (L, 17–20 Myr): *Lucanus* sp., *Osmoderma* sp., *Geotrupes* sp. (Lewis 1985: 251ff).
Meighen Island, Canada (U): *Aegialia* sp. (Matthews 1977).
Dominican Amber: Ceratocanthidae, Lucanidae, *Canthidium* sp., *Rhyparus*, *Termitodius* (Poinar 1992: 151, 285; Poinar & Poinar 1999: 165, 205; Wu without date: 187).

South America. Río Negro, Collón-Curá Formation, and Neuquén, Argentina (U): ichnofossils of coprophagans (*Megathopa* and *Onthophagus*), *Coprinisphaera* sp. (Frenguelli 1938*a*; Genise *et al.* 2000: 55).
San Luis, Paso de las Carretas, Argentina (U): ichnofossils of scarabs, *Coprinisphaera* sp. (Pascual & Bondesio 1981: 125; Genise *et al.* 2000: 55).
Las Flores, San Juan, Argentina (U): 'nidos de escarabeidos' (Contreras 1996; *Coprinisphaera* sp. according to Genise *et al.* 2000: 55).
Andalhualá, Catamarca and Cerro Azul, La Pampa/Buenos Aires, Argentina (U): *Coprinisphaera* sp. (ichnofossil) (Genise *et al.* 2000: 55).
Santacrucian, Pinturas, Patagonia, Argentinia (L): *Coprinisphaera frenguellii* (ichnofossil) (Genise & Bown 1994).

Oligocene (>24 Myr)

Europe. Rott, Siebengebirge, Germany (U, Chattian, 25 Myr): *Geotrupes rottensis*, *(Onitis) magus*, *Miochodaeus proaevus, Onthophagus statzi, Aphodius helvolus, A. krantzi, A.. schlickumi, Melolontha spec., Mimela rhenana, Anomala primigenia, A. thetis, A. tumulata, Maladera spinitibialis, Pentodon bellerophon, Ceruchites hahnei* (Germar 1849, Heyden 1862, Heyden & Heyden 1866, Statz 1952, Krell 1990); presumably: *Geotrupes vetustus, (Platycerus) sepultus* (Germar 1837*a*).
Enspel, Westerwald, Germany (U): Scarabaeoidea (Wedmann 1998).
Greith (Kohlengrube), Hohenrhone, Switzerland: *Melolontha greithiana* (Heer 1847).
Brunstatt, Alsatia, France (M): *Ammoecius* ? sp. [= *Aphodius (Ammoecius)* sp.] (Förster 1890: 102).
Aix en Provence, France (U, Stampian): *Onthophagus luteus, Geotrupes atavus* (Oustalet 1874), *Sisyphus* sp., *Melolontha* sp.,

Pachypus sp. (Serres 1829: 221f), *Cetonia* sp. ('resembling *C. hirtellus'* and 'like *C. stictica*, Fab.') (Curtis 1829: 295); ? *Geotrupes, Melolontha* (*Rhizotrogus*) [single elytron] (Hope 1847).
Célas, Gard, France (L, Sannoisian): *Aphodius theobaldi* (Théobald 1937).
Puy Saint-Jean, Auvergne, France (U; ca. 22 Myr [-L Miocene?]): '*Helicopris* sp. (?)' [= *Heliocopris*] (Rudel 1940: 15).
Armissan, Aude, France: *Ateuchites grandis* (Meunier 1898*a*).
Barachek Creek, Pozhar Region, Russia: *Platycerus zherichini* (Nikolaev 1991).

Asia. Kudia River, Primorye Province, Russia (L): *Melolonthites interemtus* (Cockerell 1926).

North America. John Day Series (lower division), Oregon, USA. (U): *Passalus indormitus* (Cockerell 1927*a*).
Ruby Paper Shales, Montana, USA. (U): 'scarab' (Becker 1961: 38, pl. 31).
Florissant, Colorado, USA. (L): *Trox antiquus, Ataenius patescens, A. restructus, Oxyomus nearcticus*, *Aphodius aboriginalis, A. florissantensis, A. granarioides, A. inundatus, A. laminicola, A. mediaevus, A. praeemptor, A. senex, A. shoshonis, Phyllophaga disrupta, (P. extincta), Macrodactylus pluto, M. propheticus, (Diplotaxis aurora), (Diplotaxis) simplicipes, Listrochelus puerilis, Anomala exterranea, A. scudderi, Miolachnosterna tristoides, Hoplia striatipennis, (Serica) antediluviana, (S.) cockerelli, Ligyrus compositus, (L.) effetus, Strategus cessatus, Amphicoma defuncta, Ceruchites fuchsii, (Lucanus fossilis)* (Cockerell 1927*b*, Wickham 1909, 1910, 1911, 1912, 1913*a*, *b,* 1914*a*, *b*).
South Dakota: *Pallichnus dakotensis* (ichnofossil) (Retallack 1984).

South America. Colhue-Huapi Formation, Argentina (U): *Coprinisphaera* sp. (ichnofossil) (Laza 1986*b*, Genise *et al*. 2000: 54).
Santa Cruz and Chubut, Argentina: ichnofossils of coprophagans, *Coprinisphaera* sp. (ichnofossil) (Frenguelli 1938*a*, *b*; Genise *et al*. 2000: 54).
Ludados lustrosos, Mendoza, Argentina: *Coprinisphaera* sp. (ichnofossils) (Genise *et al*. 2000: 54).

Eocene–Oligocene

Europe. Quercy near Toulouse, France (U Eocene to U Oligocene): *Aphodius* sp., *Pseudopentodon blanchardi* nom. nud. (Filhol 1892; Handschin 1944, 1950).
Glarus shales, Switzerland (U Eocene – L Oligocene): 'HANNETON. Scarabaeus' [= *Melolontha* s.l. spec.] (Bertrand 1763: 259).

Eocene (>37Myr)

Europe. Gurnet Bay, Bembridge Limestone, Isle of Wight (U): *Dorcus* sp. (Brodie 1845: 47; Goss 1878: 325; Woodward 1878, 1879).
Kučlín (Kutschlin) near Bílina (Bilin), Bohemia, Czechia (U, U Priabonian): *Dorcus (Eurytrachelus) primigenius, Phaeochrous tertiarium* (Deichmüller 1881).
Bournemouth, Bagshot Beds, England (M, U Ypresian – Lutetian): *Pelidnotites atavus* (Cockerell 1920).
Geiseltal near Halle, Germany (M, M – U Geiseltalian): *Eophyllocerus scrobiculatus, E. glaucinus* (Haupt 1950).
Messel near Darmstadt, Germany (M, L Geiseltalian): (*Geotrupes messelensis*), (*Gymnopleurus eocaenicus*) (Meunier 1921), Lucanidae (Lutz 1988*b*), many more species (Krell, in prep.).
Eckfelder Maar, Eifel, Germany (M, U Geiseltalian): Scarabaeidae, Melolonthinae (Lutz 1988*a*).
Baltic Amber: *Paleognathus succini* (Waga 1883); *Succiniplatycerus berendti* (Zang 1905), *Dorcasoides bilobus* (Motschulsky 1856); *Ataenius europaeus* (Quiel 1910); *Saprosites succini* (Zang 1905); *Aphodius*, *Trox* (Helm 1886: 277), some more species (Krell, in prep.).
Bognor Regis, London Clay, England (L): *Saprosites cascus*, *Onthophagus* spec. (Britton 1960: 36f).

North America. British Columbia, Canada (M): Ninemile creek: (*Trox oustaleti*) (Scudder 1879*a*, Handlirsch 1910); Princeton: Scarabaeidae (Wilson 1977).
Green River, Colorado/Wyoming, USA. (L – M): *Aegialia rupta* (Scudder 1890), *Phyllophaga avus* (Cockerell 1921, 1925); unidentified specimen of Scarabaeidae (Grande 1984: 249).
Willwood Formation, Slick Creek and Fifteenmile Creek, Bighorn Basin, Wyoming, USA. (L): *Scaphichnium hamatum* (Bown & Kraus 1983: 106; Hasiotis *et al.* 1993).
Holcomb Property, Henry County, Tennessee, USA. (L): (*Melolonthites collinsi*) (Wickham 1929).
J.G. Eaton Locality, Claron Formation, Kane County, Utah, USA. (L): *Eatonichnus claronensis*, *E.* sp. (ichnofossils) (Bown *et al.* 1997).
Golden Valley Formation, North Dakota, USA. (L): striae in coprolites 'appear to have been made by scatophagous beetles' (Jepsen 1963: 680).
Bald Knoll Canyon, Colter and Claron Formation, Sevier and Garfield County, Utah, USA: *Eatonichnus utahensis* (Bown *et al.* 1997).

South America. Musters Formation, Chubut Province, Argentina (U): *Coprinisphaera* sp. (Genise *et al.* 2000: 54).
Laguna del Mate, Chubut Province, Argentina (M): 'similar fossils of *Coprinisphaera*' (Retallack 1990: 218).
Santa Cruz, Punta Casamayor, Los Leones, and Chubut, Comodoro Rivadavia, Argentina (L): 'peras' of cf. *Megathopa* and cf. *Phanaeus* (Frenguelli 1938*a*, *b*; Laza 1986*b*; *Coprinisphaera* sp. according to Genise *et al.* 2000: 54).

Antarctica. Isla Marambio: ichnofossils of coprophagans (Laza & Roguero 1990).

Palaeocene (>54 Myr)

Europe. Menat, Puy-de-Dôme, France (U, Thanetian, 56 Myr): *Bolboceras inermis*, *Aphodius charauxi* (Piton 1940).

South America. Rio Chico, Chubut, Argentina: *Coprinisphaera* (Genise *et al*. 2000: 54).

Tertiary (without specification)

Europe. Nogent le Rotrou ('Süßwasserquarz'), France: *Anomalites fugitivus* (Frič 1885).

Upper Cretaceous (>65 Myr)

Asia. Kzyl-Zhar, Southern Kazakhstan (Turonian): *Cretaesalus ponomarenkoi* (Nikolajev 1993).
Zheijang Province, Ho Jia, Zhu Xi, China (Turonian? – Santonian): *Prionocephale deplanate* (Lin 1980).

Africa. Orapa, Botswana (Cenomanian – Coniacian): Scarabaeidae (Photo) (McKay & Rayner 1986: 11f).

North America. Two Medicine Formation, Montana, USA. (Campanian): Coprolithes and fossil soil with nesting traces (Chin & Gill 1996).

South America. (U Cretaceous – L Tertiary) Asencio Formation, Cantera Maldonado, Nueva Palmira, Departamento Colonia, Uruguay: *Coprinisphaera murguiai, Fontanai kraglievichi, Madinaichnus* sp., *Martinezichnus francisi, Microicoichnus* sp. *Monesichnus ameghinoi, Rebuffoichnus* sp. (ichnotaxa) (Roselli 1939, Genise & Cladera 1995, Genise & Laza 1998).

Lower Cretaceous (>98 Myr)

Europe. Las Hoyas, Cuenca, Spain (Barremian): Scarabaeidae (Martínez-Delclós 1989: 76).
Montsec, Spain (U Berriasian – L Valanginian): Scarabaeidae (Martínez-Delclós & Ruiz de Loizaga 1993); *Holcorobeus monreali* (Gomez Pallerola 1986, Nikolaev 1992).

Asia. Lebanon (Amber, Aptian): termitophilous species of Scarabaeoidea (Crowson 1981: 669, 673); 'Corythodérine' (= Corythoderini) (Paulian 1988: 394).
Baysa, Zazin series, Transbaykalia, Russia (Valanginian-Hauterivian): *Avitortor leptoscelis, A. primitivus*, *Cretogeotrupes convexus*, *Cretohybosorus buryaticus, C. striatulus, Holcorobeus atrosulcatus*, *H. latitibialis*, *H. maculatus, H. nigrovittatus, H. picturatus*, *H. sulcatus*, *H. vitimensis, H. vittatus, Proteroscarabaeus yeni,* (*P. magnus*), (*P. nikritini*), *Lithoscarabaeus baissensis*, *Cretaegialia aphodiiformis,* C. *rhypariformis,* (*Cretanaides trogopterus*), *Cretobolbus rohdendorfi*, (*Hybosorites fissuratus*), *Cretomelolontha transbaikalica, Cretoserica latitibialis*, *Cretoscarabaeus gibbosus*, *C. lentiginosus*, *Cretorabaeus elongatus* (Ponomarenko 1977*b*, Nikritin 1977, Nikolaev 1992, 1994, 1995*b*, 1996, 1998*a*, 1999).
Pad Semen, Argun series, Transbaykalia, Russia: *Proteroscarbaeus yeni, Lithoscarabaeus baissensis* (Nikritin 1977).
Leskovo, Transbaykalia, Russia: *Lithanomala crassa*, *L. oblonga*, *L. sibirica* (Ponomarenko 1990, Nikolaev 1992).
Turga, Transbaykalia, Russia: *Holcorobeus incertus* (Ponomarenko 1990).
Gurvan-Erenii-Nuru, Mongolia: *Holcorobeus punctatus* (Ponomarenko 1986).
Myangad, Mongolia: *Holcorobeus longipes* (Ponomarenko 1986).
Bon-Tsagan, Mongolia (U Neocomian – L Aptian): *Cretochodaeus mongolicus*, (*C. striatus*) (Nikolaev 1995*a*).
Chifeng, Inner Mongolia, China: (*Geotrupoides*) *fortus* (Ren *et al.* 1995).
Laiyang Formation, Shandong Province, China (Barremian – Hauterivian): *Geotrupoides nodosus* (Hong & Wang 1990), *Holcorobeus evittatus* (Zhang 1992*a*), *Proteroscarabaeus yeni, P. baissensis* (Grabau 1923; Hong & Wang 1990). There has been some discussion about whether this formation belongs to Lower Cretaceous, to Upper Jurassic (Zhang 1992*b*), or to both (see Lin 1994). Here I adopt the view of Lin (1994) and Hong (1998).
Jiuquan Basin, Chijinpu Formation, Gansu Province, China (Valanginian; according to Hong 1998): *Mesoscarabaeus corneus, M. morulosus, Hongscarabaeus brunneus* (Hong 1982).
Yixian, Hebei Province, China (Tithonian? – Berriasian) [^{40}Ar-^{39}Ar dating gave inconsistent results. According to Smith *et al.* (1995), the entire Yixian Formation is Cretaceous (122 Myr), whereas Lo *et al.* (1999) found it to be Upper Jurassic to Lower Cretaceous (136–155 Myr)]: *Geotrupoides songyingziensis* (Hong 1984).
Jilin Province, China: *Geotrupoides jiaoheensis* (Hong 1992).

South America. Santana, Brazil: Scarabaeidae (Grimaldi & Maisey 1990: 7; Grimaldi 1991: 400 [colour photo]), some more specimens (Krell, in prep.).

Transition Upper Jurassic/Lower Cretaceous

Asia. Khutel-Khara; Mongolia: *Holcorobeus (Mesaclopus) mongolicus* (Nikolaev 1992).

Upper Jurassic (Malm, 144 Myr)

Europe. Lithographischer Schiefer, Bavaria, Germany (L Tithonian): (*Geotrupoides lithographicus*) (Eichstätt) (Deichmüller 1886), (*Cetonia defossa*), (*Oryctes pluto*) (Solnhofen) (Weyenbergh 1869*a*).

Asia. Karatau, Kazakhstan (Oxfordian – Kimmeridgian): *Holcorobeus nigrimontanus* (Nikolaev 1992).

Middle Jurassic (Dogger, >163 Myr)

No reliable records: '*Melolonthidium*' of Philips (1871) from the Stonesfield Slate, England, was not described and has to be confirmed. It might refer to the doubtful *Melolontha* (or '*Melolontha* ?') from the same lagerstätte classified and figured by Murchison (1845: 68, 107, pl. 4).

Lower Jurassic (Lias, >188 Myr)

No reliable records: the family identity of *Opiselleipon grave* Bode and *Tetragonides magnus* Bode (Lias from Hondelage, Germany), *Aphodiites protogaeus* Heer (Lower Lias, Schambelen, Switzerland) and *Melolontha* ? sp. (Lower Lias, Cracombe, England; Brodie 1845: 101, pl. 9) is untraceable.

Carboniferous (>286 Myr)

No records: *Troxites germari* Goldenberg from the hard coals of Saarbrücken, Germany, and the ichnotaxa *Xyloryctes planus* Fričand *X. septarius* Frič from the Upper Carboniferous of Germany and Bohemia, are not fossils or traces of Scarabaeoidea.

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