Catalogue of fossil Scarabaeoidea (Coleoptera: Polyphaga) of the Mesozoic and Tertiary

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Catalogue of named fossil Scarabaeoidea (Lamellicornia)

The present catalogue is based on the printed version published in 2000 in Invertebrate Taxonomy (Krell, 2000a) but it is updated up to 2003 and includes also some older references that were overlooked. However, it does not include some taxonomic and nomenclatural remarks included in the printed version. All named fossil taxa of Scarabaeoidea are listed according to their current classification. The classification of Scarabaeoidea follows the proposed system of Browne & Scholtz (1998, 1999) and Lawrence & 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 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.

The following species were not included in the printed catalogue:
Cretocoma tologoica Nikolaev, 2002
Paralucanus mesozoicus Nikolajev, 2000
Prototrox transbaikalicus Nikolaev, 2000

Onthophagus rugulosus (Heer, 1870), listed by Ponomarenko & Kirejtshuk (http://www.zin.ru/Animalia/Coleoptera/eng/paleosy1.htm, accessed 30.March 2004) has been described as *Elytridium rugulosum* and originally classified as a possible carabid (Heer 1870: 78). It is the middle part of one elytron which lacking any character which might reveal its family.
The genus names ‘Mimaphodius Nikolajev, 1993’, ‘Protogeotrupes Nikolajev’ and ‘Cretoglaphyrus Nikolajev’ listed by Ponomarenko & Kirejtshuk (l.c.) are not yet described and, therefore, nomina nuda.

The author would like to update this catalogue regularly. To have your work included, please provide the author with reprints or pdf files of your papers containing new fossil taxa of Scarabaeoidea or mentioning known taxa or only the presence of Scarabaeoidea in a lagerstätte. Thank you for your cooperation.

(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 1998b: 30; Browne & Scholtz 1999: 54 ("Glaresidae-like"); Krell 2000a: 874.

(***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; Scudder 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; Krell 2000a: 874.

Aphodiites prologaeus. – Balthasar 1963: 78; Iablokoff-Khnzorian 1977: 137 (family identity doubtful); Morón Ríos 1984: 117; Morón 2003: 12.

Doubful (no appendages present).

Familia **Trogidae**

Trox antiquus Wickham

Trox antiquus Wickham, 1909: 129 (Oligocene, Florissant, U.S.A.). – Wickham 1920: 358; Krell 2000a: 874.

(***Trox oustaleti*** Scudder)

Trox oustaleti Scudder, 1879a: 178B (Eocene, Nine-mile Creek, British Columbia, Canada). – Scudder 1890: 487, pl. 2; Scudder 1895a: 35; Scudder 1900: 105; Handlirsch 1907: 839; Handlirsch 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; Krell 2000a: 875.

Doubful (only one elytron).

Subfamilia **Prototroginae** Nikolaev, 2000: 63 (transl. p. 426)

Genus ***Prototrox*** Nikolaev

Prototrox Nikolaev, 2000a: 65 (transl. p. 427) (type species by original designation: *Prototrox transbaikalicus* Nikolaev). - Nikolajev, 1999: 178 (nomen nudum); Krell 2000a: 890 (nomen nudum); Nikolaev 2002: 54 (transl. p. 281).

Prototrox transbaikalicus Nikolaev

Prototrox transbaikalicus Nikolaev 2000a: 65 (transl. p. 428) (Lower Cretaceous, Argun' formation, Semen Creek, Chita District, Transbaikalia, Russia).

Familia **Passalidae**

Passalus (Passalus) indormitus Cockerell

Passalus (?) *indormitus* Cockerell, 1927a: 65 (Oligocene, John Day Series, Oregon, U.S.A.).

Passalus indormitus. – Reyes-Castillo 1970: 73; Morón 2003: 13.

Passalus (Passalus) indormitus. – Reyes-Castillo 1977: 652; Krell 2000a: 875.

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); Krell 2000a: 875.

Familia **Lucanidae**

Subfamilia **Lucaninae**

(***Lucanus fossilis*** Wickham)

Lucanus fossilis Wickham, 1913b: 293 (Oligocene, Florissant, U.S.A.). – Wickham 1920: 358; Maes 1992: 17; Krell 2000a: 875.

Doubtful (only one elytron).

(***Platycerus***) ***sepultus*** Germar

Lucanus. – Goldfuss 1831: 118; Keferstein 1834: 329; Scudder 1886: 74.

Platycerus sepultus Germar, 1837a: 7, pl. 7 (Oligocene, "in carbone fossili territorii Rheni prope Bonnam", Germany). – Germar 1837b: 423: ("1 *Lucanus*", *Platycerus sepultus*); Malepeyre 1838: 267; Bronn 1848b: 992; Bronn 1849: 623; Giebel 1852b: 653; Giebel 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; Krell 2000a: 875.

Systenocerus sepultus. – Statz 1952: 1 (generic affiliation doubtful).

Platycerus zherichini Nikolajev

Platycerus zherichini Nikolajev, 1990: 122 (1991: 121) (Oligocene, Pozhar region, Russia). – Krell 2000a: 875.

Genus ***Succiniplatycerus*** Nikolajev

Succiniplatycerus Nikolajev, 1990: 122 (1991: 120) (type species by original designation: *Platycerus berendti* Zang, 1905). – Jarzembowski 2000: (3); Krell 2000a: 875.

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); Krell 2000a: 875.

Dorcus (Eurytrachelus) primigenius Deichmüller

Dorcus (Eurytrachelus) primigenius Deichmüller, 1881: 303, pl. 21 (Eocene, Ku_lín [Kutschlin] near Bílina [Bilin], Czechia). – Leuthner 1885: 482; Scudder 1891: 514; Po_ta 1900: 265; Handlirsch 1907: 842; Houlbert 1915: 6; _íha 1979: 26; Maes 1992: 92; Krell 2000a: 875.

Genus ***Miocenidorcus*** Riou

Miocenidorcus Riou 1999: 126 (type species by original designation: *Miocenidorcus andancensis* Riou). – Riou, 1988: 98 (unpublished); Krell 2000a: 875.

Miocenidorcus andancensis Riou

Miocenidorcus andancensis Riou, 1999: 126, 133 (Miocene, Andance, France). – Riou, 1988: 99 (unpublished); Krell 2000a: 875.

Subfamilia **Paralucaninae** Nikolajev, 2000b

Genus ***Paralucanus*** Nikolajev

Paralucanus Nikolajev, 2000b: S329 (type species by original designation: *Paralucanus mesozoicus* Nikolajev).

Paralucanus mesozoicus Nikolajev

Paralucanus mesozoicus Nikolajev, 2000b: S330 (Upper Jurassic, Shara-Tag, Mongolia).

Subfamilia **Syndesinae**

Ceruchus fuchsii Wickham

Ceruchus fuchsii Wickham, 1911: 58 (Oligocene, Florissant, U.S.A.). – Wickham 1920: 358; Rodeck 1938: 293; Maes 1992: 11; Krell 2000a: 875.

Subfamilia **Chiasognathinae**

Genus ***Protognathinus*** Chalumeau & Brochier

Protognathinus Chalumeau & Brochier, 2001: 595 (type species by monotypy: *Protognathinus spielbergi* Chalumeai & Brochier

Protognathinus spielbergi Chalumeau & Brochier

Protognathinus spielbergi Chalumeau & Brochier, 2001: 595 (Eocene, Grube Messel, Germany).

Subfamilia **Aesalinae**

Genus ***Cretaesalus*** Nikolajev

Cretaesalus Nikolajev, 1993: 90 (type species by original designation: *Gretaesalus ponomarenkoi* Nikolajev [lapsus calami for *Cretaesalus*]). – Nikolaev 1999: 178; Krell 2000a: 875; Nikolaev 2002: 54 (transl. p. 281).

Cretaesalus ponomarenkoi Nikolajev

Cretaesalus ponomarenkoi Nikolajev, 1993: 90 (U Cretaceous, Kzyl-Zhar, Kazakhstan). – Krell 2000a: 875.

S u b f a m i l i a i n c e r t a

Genus ***Dorcasoides*** Motschulsky

Dorcasoides Motschulsky, 1856: 27, 30 (type species by monotypy: *Dorcasoides bilobus* Motschulsky). – Scudder 1881-1885: 795; Scudder 1886: 74; Handlirsch 1925: 245; Maes 1992: 95; Carpenter 1992: 300; Poinar 1992: 147; Krell 2000a: 875; Schweigert, 2003..

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); Scudder 1891: 513; Zittel 1895: 505; Zang 1905: 199; Handlirsch 1907: 842; Broili 1921: 675; Broili 1924: 696; Carpenter 1992: 300; Maes 1992: 95; Krell 2000a: 876.

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; Krell 2000a: 876.

Ceruchites hahnei Statz

Ceruchites hahnei Statz, 1952: 5 (Oligocene, Rott, Germany). – Sphon 1973: 51; Carpenter 1992: 300; Krell 2000a: 876.

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; Krell 2000a: 876.

Palaeognathus. – Bibliography: Spahr 1981: 65, additional: Deville 1991: 16; Maes 1992: 68; Scholtz & Chown 1995: 364; Schweigert 2003: 179.

Paleognathus succini Waga

Paleognathus succini Waga, 1883: 191 (Eocene, Baltic Amber). – Bibliography: Spahr 1981: 65, additional: Paulian 1988: 394; Carpenter 1992: 300; Krell 2000a: 876; Chalumeai & Brochier 2001: 593 ("probablement […] Lampriminae").

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). – Krell 2000a: 876.

Genus ***Cretobolbus*** Nikolajev

Cretobolbus Nikolajev, 1996: 95 (transl. p. 221) (type species by original designation: *Cretobolbus rohdendorfi* Nikolajev, 1996). – Nikolaev 1999: 178; Krell 2000a: 876; Nikolaev 2002: 54 (transl. p. 281).

Cretobolbus rohdendorfi Nikolajev

Cretobolbus rohdendorfi Nikolajev, 1996: 96 (transl. p. 222) (L Cretaceous, Baysa, Russia). – Krell 2000a: 876.

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 1996: 91 (transl. p. 217), 1999: 178; Krell 2000a: 876 (subfamily affiliation according to Nikolaev 1996); Nikolaev 2002: 54 (transl. p. 281).

Protoscarabaeus: Scholtz 1990: 1029; Scholtz & Chown 1995: 358.

(***Proteroscarabaeus magnus*** Nikolajev)

Proteroscarabaeus magnus Nikolajev, 1996: 91 (transl. p. 217) (L Cretaceous, Baysa, Russia). – Krell 2000a: 876.

Doubtful (only one elytron).

(***Proteroscarabaeus nikritini*** Nikolajev)

Proteroscarabaeus nikritini Nikolajev, 1996: 93 (transl. p. 217) (L Cretaceous, Baysa, Russia). – Krell 2000a: 876.

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). – Krell 2000a: 876.

Proteroscarabaeus yeni Grabau

Proteroscarabaeus yeni Grabau, 1923: 175 (L Cretaceous, Laiyang, China). – Ping 1928: 19; Handlirsch 1939: 167; Balthasar 1963: 78; Ponomarenko 1977a: 6 (1991a: 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 1992b: 134; Nikolaev 1992: 79 (transl. p. 99); Lin 1994: 305; Nikolaev 1996: 94 (transl. p. 219); Krell 2000a: 876; Morón 2003: 12.

Tribus **Cretocomini** Nikolaev, 2002: 53 (transl. p. 281)

Genus ***Cretocoma*** Nikolaev

Cretocoma Nikolaev, 2002: 54 (transl. p. 281) (type species by original designation: *Cretocoma tologoica*).

Cretocoma tologoica Nikolaev

Cretocoma tologoica Nikolaev, 2002: 54 (transl. p. 281) (L Cretaceous, Shar Tolgoy, Bayan-Hongor Aymag, Mongolia)

Familia **Glaphyridae**

Glaphyrus antiquus Heer

Glaphyrus antiquus Heer, 1862: 79, pl. 6 (Miocene, Öhningen "Insektenschicht des untern Bruches", Germany). – Heer 1865: 380; Heer 1883: 406; Handlirsch 1907: 839; Krell 2000a: 876.

Glaphyrus. – Kolbe 1932: 150.

Amphicoma defuncta Wickham

Amphicoma defuncta Wickham, 1910: 49 (Oligocene, Florissant, U.S.A.). – Wickham 1920: 358; White 1995: 3; Krell 2000a: 876.

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; Krell 2000a: 877.

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; Krell 2000a: 877.

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; Krell 2000a: 877.

(***Geotrupes messelensis*** Meunier)

Geotrupes messelensis Meunier, 1921: 11, pl. 2 (Eocene, Messel, Germany). – Théodoridès 1952: 46; Koenigswald 1987: 140; Krell 2000a: 877.

Doubtful (poor preservation).

Geotrupes rottensis Statz

Geotrupes rottensis Statz, 1952: 7 (Oligocene, Rott, Germany). – Sphon 1973: 52; Krell 2000a: 877.

Geotrupes vetustus Germar

Geotrupes vetustus Germar, 1837a: 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 1852b: 653; Giebel 1856: 35; Heer 1862: 72; Goss 1878: 331; Scudder 1891: 525; Handlirsch 1907: 839; Meunier 1921: 4; Statz 1952: 2; Krell 2000a: 877.

(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 1998b: 30; Krell 2000a: 877.

(***Geotrupoides***) ***fortus*** Ren, Zhu & Lu

Geotrupoides fortus Ren *et al.*, 1995: 436 (L Cretaceous, Chifeng City, Inner Mongolia, China). – Krell 2000a: 877.

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). – Krell 2000a: 877.

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; Krell 2000a: 877; Morón 2003: 12.

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). – Krell 2000a: 877.

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); Krell 2000a: 877.

Generic affiliation needs revision since genus is doubtful.

Geotrupoides songyingziensis Hong

Geotrupoides songyingziense Hong, 1984: 170, pl. 71 (L Cretaceous, Yixian, China). – Krell 2000a: 877.

Generic affiliation needs revision since genus is doubtful.

Genus ***Orrhodomala*** Zhang

Orrhodomala Zhang, 1989: 154, 425 (type species by original designation: *Orrhodomala protista* Zhang). – Krell 2000a: 877.

Orrhodomala protista Zhang

Orrhodomala protista Zhang, 1989: 154, 425 (Miocene, Shanwang, China). – Krell 2000a: 877.

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

Genus ***Cretogeotrupes*** Nikolajev

Cretogeotrupes Nikolajev, 1992: 80 (transl. p. 101), type genus (type species by original designation: *Cretogeotrupes convexus* Nikolajev). – Nikolaev 1999: 178; Krell 2000a: 878; Nikolaev 2002: 54 (transl. p. 281).

Cretogeotrupes convexus Nikolajev

Cretogeotrupes convexus Nikolajev, 1992: 81 (transl. p. 102) (L Cretaceous, Baysa, Russia). – Krell 2000a: 878.

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; Scudder 1886: 74; Handlirsch 1907: 839; Handlirsch 1925: 246; Balthasar 1963: 79; Carpenter 1992: 330; Krell 2000a: 878.

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; Heer 1883: 405; Nikolaev 1996: 96 (transl. p. 222) (doubts the former classification as belonging to the Bolboceratidae, "presumable belongs to the Hybosoridae"); Krell 2000a: 878.

Caprologus gracilis. – Giebel 1852b: 653.

Genus ***Procoilodes*** Ocampo

Procoilodes Ocampo, 2002: 123 (type species by original designation: *Procoilodes adrastus* Ocampo).

Procoilodes adrastus Ocampo

Procoilodes adrastus Ocampo, 2002: 125 (Miocene, Dominican Amber).

Genus ***Tyrannasorus*** Ratcliffe & Ocampo

Tyrannasorus Ratcliffe & Ocampo, 2001: 351 (type species by original designation: *Tyrannasorus rex* Ratcliffe & Ocampo).

Tyrannasorus rex Ratcliffe & Ocampo

.Tyrannasorus rex Ratcliffe & Ocampo, 2001: 353 (Miocene, Dominican Amber). – Ocampo 2002: 123.

Subfamilia **Anaidinae** Nikolajev

(Genus ***Cretanaides*** Nikolajev)

Cretanaides Nikolajev, 1996: 94 (transl. p. 219) (type species by original designation: *Cretanaides trogopterus* Nikolajev). – Nikolaev 1999: 178; Krell 2000a: 878; Nikolaev 2002: 54 (transl. p. 281).

(***Cretanaides trogopterus*** Nikolajev)

Cretanaides trogopterus Nikolajev, 1996: 95 (transl. p. 220) (L Cretaceous, Baysa, Russia). – Krell 2000a: 878. Doubtful (only one elytron).

Subfamilia **Hybosorinae**

Genus ***Cretohybosorus*** Nikolajev, 1999

Cretohybosorus Nikolajev, 1999: 178 (type species by original designation: *Cretohybosorus buryaticus* Nikolajev). – Krell 2000a: 878; Nikolaev 2002: 54 (transl. p. 281).

Cretohybosorus buryaticus Nikolajev

Cretohybosorus buryaticus Nikolajev, 1999: 179 (L Cretaceous, Baysa, Russia). – Krell 2000a: 878.

Cretohybosorus striatulus Nikolajev

Cretohybosorus striatulus Nikolajev, 1999: 179 (L Cretaceous, Baysa, Russia). – Krell 2000a: 878.

Hybosorus lividus Heer

Hybosorus lividus Heer, 1862: 77, pl. 6 (Miocene, Öhningen, Germany). – Scudder 1891: 534; Handlirsch 1907: 838; Krell 2000a: 878.

Phaeochrous tertiarium (Deichmüller) Nikolaev

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

Phaeochrous tertiarium (Deichmüller). – Nikolaev, 1996: 96 (transl. p. 222); Krell 2000a: 878.

Familia **Ochodaeidae**

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

Genus ***Cretochodaeus*** Nikolajev

Cretochodaeus Nikolajev, 1995a: 79 (type species by original designation: *Cretochodaeus mongolicus* Nikolajev). – Nikolaev 1999: 178; Krell 2000a: 878; Nikolaev 2002: 54 (transl. p. 281).

Cretochodaeus mongolicus Nikolajev

Cretochodaeus mongolicus Nikolajev, 1995a: 79 (L Cretaceous, Bon-Tsagan, Mongolia). – Krell 2000a: 878.

(***Cretochodaeus striatus*** Nikolajev)

Cretochodaeus striatus Nikolajev, 1995a: 80 (L Cretaceous, Bon-Tsagan, Mongolia). – Krell 2000a: 878.

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

Genus ***Mioochodaeus*** Nikolajev

Mioochodaeus Nikolajev, 1995a: 81 (type species by original designation: *Geotrupes proaevus* Germar). – Krell 2000a: 878.

Mioochodaeus proaevus (Germar) Nikolaev

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

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

Mioochodaeus proaevus. – Nikolaev, 1995a: 81; Krell 2000a: 878.

Familia **Scarabaeidae**

Subfamilia **Scarabaeinae** (incl. **Coprinae**)

Anachalcos mfwangani Paulian

Anachalcos mfwangani Paulian, 1976: 1 (Miocene, Lake Victoria, Kenya). – Krell 2000a: 879.

Genus ***Ateuchites*** Meunier

Ateuchites Meunier, 1898a: 114 (type species by monotypy: *Ateuchites grandis* Meunier). – Handlirsch 1925: 246; Théodoridès 1952: 34; Balthasar 1963: 79; Iablokoff-Khnzorian 1977: 137; Carpenter 1992: 300; Krell 2000a: 879; Paetel 2001: 234.

Ateuchites grandis Meunier

Ateuchites grandis Meunier, 1898a: 114 (Oligocene, Armissan, Aude, France). – Handlirsch 1907: 836; Carpenter 1992: 300; Krell 2000a: 879.

Choeridium ebenium Horn

Choeridium ebenium Horn, 1876: 245 (Pleistocene, Irvingtonian, Port Kennedy caves, Pennsylvania, U.S.A.). – Scudder 1890: 490, pl. 1; Wickham 1920: 358; Théodoridès 1952: 36; Krell 2000a: 879.

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

Copris druidum Heer

Copris druidum Heer, 1862: 73, pl. 6 (Miocene, Öhningen, Kesselstein, Germany). – Heer 1865: 378f; Heer 1883: 404f; Scudder 1891: 500; Handlirsch 1907: 837; Krell 2000a: 879.

Copris (Copris) kartlinus Kabakov

Copris (Copris) kartlinus Kabakov, 1988: 110 (Pliocene, Kisatibi formation, Georgia). – Krell 2000a: 879.

Copris leakeyorum Paulian

Copris leakeyorum Paulian, 1976: 1 (Miocene, Lake Victoria, Kenya). – Krell 2000a: 879.

Copris pristinus Pierce

Copris pristinus Pierce, 1946a: 124; (Pleistocene, Rancho La Brea tar pits, Los Angeles, U.S.A.). – 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; Krell 2000a: 879; Morón 2003: 12.

Copris subterraneus Heer

Copris subterranea Heer, 1862: 74, pl. 3 (Miocene, Öhningen, Kesselstein, Germany). – Heer 1865: 379; Heer 1883: 405; Scudder 1891: 501; Handlirsch 1907: 837; Krell 2000a: 879.

Gymnopleurus deperditus Heer

Gymnopleurus deperditus Heer, 1862: 73, pl. 6 (Miocene, Öhningen, Kesselstein, Germany). – Handlirsch 1907: 836; Meunier 1921: 11; Krell 2000a: 879.

(***Gymnopleurus eocaenicus*** Meunier)

Gymnopleurus eocaenicus Meunier, 1921: 12, pl. 3 (Eocene, Messel, Germany). – Koenigswald 1987: 140; Krell 2000a: 879; Paetel 2001: 234.

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; Heer 1883: 404f; Scudder 1891: 527; Handlirsch 1907: 837; Meunier 1921: 11; Krell 2000a: 879.

Gymnopleurus sisyphus Heer

Gymnopleurus sisyphus Heer, 1847: 64, pl. 7 (Miocene, Öhningen, Germany). – Bronn 1849: 625; Stitzenberger 1851: 100; Giebel 1852b: 653; Giebel 1856: 38; Heer 1862: 72; Scudder 1891: 527; Handlirsch 1907: 839; Meunier 1921: 11f; Krell 2000a: 879.

Heliocopris antiquus Fujiyama

Heliocopris antiquus Fujiyama, 1968: 203 (Miocene, Noto, Japan). – Harusawa 1994: 23; Krell 2000a: 879.

Metacatharsius rusingae Paulian

Metacatharsius rusingae Paulian, 1976: 2 (Miocene, Lake Victoria, Kenya). – Krell 2000a: 879.

Oniticellus amplicollis Heer

Oniticellus amplicollis Heer, 1862: 76, pl. 6 (Miocene, Öhningen, Kesselstein, Germany). – Heer 1865: 378f; Heer 1883: 404f; Scudder 1891: 558; Handlirsch 1907: 837; Krell 2000a: 879, 2000b: 177.

(***Onitis magus*** Heyden)

Onitis magus Heyden, 1862: 65, pl. 10 (Oligocene, Rott, Germany). – Krantz 1867: 315; Scudder 1891: 558; Handlirsch 1907: 837; Krell 2000a: 879.

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; Heer 1883: 405; Scudder 1891: 559; Handlirsch 1907: 837; Krell 2000a: 880.

Onthophagus crassus Heer

Onthophagus crassus Heer, 1862: 75, pl. 6 (Miocene, Öhningen, Kesselstein, Germany). – Heer 1865: 379; Heer 1883: 405; Oustalet 1874: 196; Scudder 1891: 559; Handlirsch 1907: 837; Krell 2000a: 880.

Onthophagus everestae Pierce

Onthophagus everestae Pierce, 1946a: 131 (Pleistocene, Los Angeles. U.S.A.). – Sphon 1973: 52; Miller *et al.* 1981: 627f; Wilson 1986: 101; Stock & Harris 1992: 70, 84; Miller 1997: 187f; Krell 2000a: 880.

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; Krell 2000a: 880.

Onthophagus ovatulus Heer

Onthophagus ovatulus Heer, 1847: 64, pl. 7 (Miocene, Öhningen, Germany). – Bronn 1849: 624; Giebel 1852b: 653; Giebel 1856: 39; Heer 1865: 379; Heer 1883: 405; Scudder 1891: 559; Handlirsch 1907: 837; Krell 2000a: 880.

Onthophagus prodromus Heer

Onthophagus prodromus Heer, 1862: 75, pl. 6 (Miocene, Öhningen, Kesselstein, Germany). – Heer 1865: 378f; Heer 1883: 404f; Scudder 1881-1885: 795; Oustalet 1874: 196; Scudder 1891: 559; Handlirsch 1907: 837; Krell 2000a: 880.

Onthophagus statzi Krell

Onthophagus muelleri Statz, 1952: 8 (nec Novak, 1921) (Oligocene, Rott, Germany).

Onthophagus mulleri. – Sphon 1973: 52.

Onthophagus statzi Krell, 1990: 187. – Krell 2000a: 880.

Onthophagus urusheeri Krell

Onthophagus urusheeri Krell, 2000a: 880.

Onthophagus urus Heer, 1847: 62, pl. 2 (Miocene, Öhningen, Germany). – Stitzenberger 1851: 100; Giebel 1852b: 653; Giebel 1856: 39; Bronn 1849: 624; Heer 1862: 76; Heer 1865: 379; Heer 1883: 405; Scudder 1891: 559; Handlirsch 1907: 837; preoccupied by *Onthophagus urus* Ménétries, 1832: 175.

Phanaeus antiquus Horn

Phanaeus antiquus Horn, 1876: 245 (Pleistocene, Irvingtonian, Port Kennedy caves, Pennsylvania, U.S.A.). – Goss 1878: 340; Scudder 1890: 489, pl. 1; Scudder 1891: 565; Scudder 1900: 104; Handlirsch 1908: 1126; Wickham 1920: 358; Théodoridès 1952: 36; Krell 2000a: 880.

Phanaeus labreae (Pierce) Miller

Palaeocopris labreae Pierce, 1946a: 130 (Pleistocene, Rancho La Brea tar pits, Los Angeles, U.S.A.). – 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; Krell 2000a: 880.

Genus ***Prionocephale*** Lin

Prionocephale Lin, 1980: 230 (type species by original designation: *Prionocephale deplanate* Lin). – Krell 2000a: 880; Paetel 2001: 234.

Prionocephale deplanate Lin

Prionocephale deplanate Lin, 1980: 230 (U Cretaceous, Zheijang, China). – Lin 1994: 314; Krell 2000a: 880.

Prionocephale deplanae. – Lin 1983: 394.

Genus ***Scelocopris*** Zhang

Scelocopris Zhang 1989: 150, 425 (type species by original designation: *Scelocopris enertheus* Zhang). – Krell 2000a: 880; Paetel 2001: 234.

Scelocopris enertheus Zhang

Scelocopris enertheus Zhang, 1989: 151, 425 (Miocene, Shanwang, China). – Krell 2000a: 880.

Subfamilia **Aegialiinae**

Aegialia rupta Scudder

Aegialia rupta Scudder, 1890: 489, pl. 8 (Eocene, Green River, Wyoming, U.S.A.). – Scudder 1891: 461; Scudder 1900: 104; Handlirsch 1907: 838; Wickham 1920: 358; Dellacasa 1988: 359; Krell 2000a: 880.

Genus ***Cretaegialia*** Nikolayev

Cretaegialia Nikolayev, 1994: 5 (type species by original designation: *Cretaegialia rhypariformis* Nikolayev). – Nikolaev 1999: 178; Krell 2000a: 880; Nikolaev 2002: 54 (transl. p. 281).

Cretaegialia aphodiiformis Nikolayev

Cretaegialia aphodiiformis Nikolayev, 1994: 7 (L Cretaceous, Baysa, Russia). – Krell 2000a: 880.

Cretaegialia rhypariformis Nikolayev

Geotrupoides sulcatus Nikritin, 1977: 120 [part.]. – Nikolayev 1994: 6.

Cretaegialia rhypariformis Nikolayev, 1994: 6 (L Cretaceous, Baysa, Russia). – Krell 2000a: 880.

Subfamilia **Aphodiinae**

Tribus **Aphodiini**

Aphodius aboriginalis Wickham

Aphodius aboriginalis Wickham, 1912: 22 (Oligocene, Florissant, U.S.A.). – Wickham 1913a: 17; Wickham 1913c: 360; Wickham 1914b: 455; Wickham 1920: 358; Dellacasa 1988: 400; Krell 2000a: 881.

Aphodius anteactus Krell

Aphodius anteactus Krell, 2000a: 881.

Aphodius antiquus Heer, 1847: 66, pl. 7 (Miocene, Öhningen, Germany). – Bronn 1849: 624; Stitzenberger 1851: 100; Giebel 1852b: 653; Giebel 1856: 40; Scudder 1891: 468; Handlirsch 1907: 838; Schmidt 1910: 140; Dellacasa 1988: 400; preoccupied by *Aphodius antiquus* Faldermann, 1835: 367.

Aphodius boryslavicus _omnicki

Aphodius boryslavicus _omnicki 1894: 83, pl. 7 (Pleistocene, Borys_aw, Poland). – Krell 2000a: 881.

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 Art. 12 ICZN]. – Schmidt 1910: 140 ("*Aphod*.? *Bosniaskii*").

Aphodius bosniaskii. – Dellacasa 1983: 29; Dellacasa 1988: 400; Krell 2000a: 881.

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; Krell 2000a: 881.

Aphodius charauxi Piton

Aphodius charauxi Piton, 1940: 176 (Eocene, Menat, France). – Krell 2000a: 881.

Aphodius florissantensis Wickham

Aphodius florissantensis Wickham, 1911: 59 (Oligocene, Florissant, U.S.A.). – Wickham 1912: 23; Wickham 1913a: 17; Wickham 1914b: 456; Wickham 1920: 358; Dellacasa 1988: 400; Krell 2000a: 881.

Aphodius granarioides Wickham

Aphodius granarioides Wickham, 1913a: 17 (Oligocene, Florissant, U.S.A.). – Wickham 1912: 23 (nomen nudum); Wickham 1913b: 295; Wickham 1920: 358; Théodoridès 1952: 35; Dellacasa 1988: 400; Krell 2000a: 881.

Aphodius helvolus Statz

Aphodius helvolus Statz, 1952: 6 (Oligocene, Rott, Germany). – Sphon 1973: 52; Dellacasa 1991: 36; Krell 2000a: 881.

Aphodius inundatus Wickham

Aphodius inundatus Wickham, 1914a: 262 (Oligocene, Florissant, U.S.A.). – Wickham 1920: 358; Théodoridès 1952: 35; Dellacasa 1988: 400; Krell 2000a: 881.

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; Krell 2000a: 881.

Aphodius laminicola Wickham

Aphodius laminicola Wickham, 1910: 49 (Oligocene, Florissant, U.S.A.). – Wickham 1911: 59; Wickham 1912: 22f; Wickham 1913a: 17; Wickham 1914b: 456; Wickham 1920: 358; Dellacasa 1988: 400; White 1995: 4; Krell 2000a: 881.

Aphodius mediaevus Wickham

Aphodius mediaevus Wickham, 1914b: 455 (Oligocene, Florissant, U.S.A.). – Wickham 1920: 358; Dellacasa 1988: 400; Krell 2000a: 881.

Aphodius meyeri Heer

Aphodius meyeri Heer, 1847: 67, pl. 7 (Miocene, Öhningen, Germany). – Bronn 1849: 624; Stitzenberger 1851: 100; Giebel 1852b: 653; Giebel 1856: 40; Scudder 1891: 468; Handlirsch 1907: 838; Schmidt 1910: 140; Dellacasa 1988: 400; Krell 2000a: 881.

Aphodius praeemptor Wickham

Aphodius praeemptor Wickham, 1913a: 17, pl. 6 (Oligocene, Florissant, U.S.A.). – Wickham 1914b: 456; Wickham 1920: 358; Dellacasa 1988: 400; Krell 2000a: 881.

Aphodius precursor Horn

Aphodius precursor Horn, 1876: 245 (Tertiary/Pleistocene, Bone Caves of Port Kennedy, Pennsylvania, U.S.A.). – Goss 1878: 340; Scudder 1890: 488, pl. 1; Scudder 1900: 105; Wickham 1920: 358; Krell 2000a: 881.

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

Aphodius rhinocerontis _omnicki

Aphodius rhinocerontis _omnicki 1894: 81, pl. 7 (Pleistocene, Borys_aw, Poland). – Krell 2000a: 881.

Aphodius ruthenus _omnicki

Aphodius ruthenus _omnicki 1894: 82, pl. 7 (Pleistocene, Borys_aw, Poland). – Krell 2000a: 882.

Aphodius schlickumi Statz

Aphodius schlickumi Statz, 1952: 6 (Oligocene, Rott, Germany). – Dellacasa 1991: 36; Lutz 1996: 45; Krell 2000a: 882.

Aphodius senex Wickham

Aphodius senex Wickham, 1914b: 456 (Oligocene, Florissant, U.S.A.). – Wickham 1920: 358; Dellacasa 1988: 400; Krell 2000a: 882.

Aphodius shoshonis Wickham

Aphodius shoshonis Wickham, 1912: 23 (Oligocene, Florissant, U.S.A.). – Wickham 1913a: 17; Wickham 1914b: 455; Wickham 1920: 358; Dellacasa 1988: 400; Krell 2000a: 882.

Aphodius subater _omnicki

Aphodius subater _omnicki 1894: 80, pl. 7 (Pleistocene, Borys_aw, Poland). – Krell 2000a: 882.

Aphodius theobaldi Krell

Aphodius theobaldi Krell, 2000a: 882.

Aphodius incertus Théobald, 1937: 126, pl. 10 (Oligocene, Sannoisien du Gard, France). – Théodoridès 1952: 46; preoccupied by *Aphodius incertus* Ballion, 1878: 282.

Tribus **Eupariini**

Ataenius europaeus Quiel

Ataenius europaeus Quiel, 1910: 187 (Eocene, Baltic Amber). – Kolbe 1925: 150; Dellacasa 1988: 412; Krell 2000a: 882.

Ataenius patescens Scudder

Ataenius patescens Scudder, 1893: pl. 1 (not described, only figured; Oligocene, Florissant, U.S.A.). – Scudder 1900: 104, pl. 11 (description); Handlirsch 1907: 838; Schmidt 1910: 140; Wickham 1910: 48; Wickham 1912: 22; Wickham 1913b: 295; Wickham 1913c: 360; Wickham 1914b: 453; Wickham 1920: 358; Dellacasa 1988: 412; Krell 2000a: 882.

Ataenius restructus (Wickham) Wickham

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

Ataenius restructus. – Wickham 1914b: 454; Wickham 1920: 358; Krell 2000a: 882.

Oxyomus nearcticus Wickham

Oxyomus nearcticus Wickham, 1914b: 453 (Oligocene, Florissant, U.S.A.). – Wickham 1920: 358; Dellacasa 1988: 403; Krell 2000a: 882.

Saprosites cascus Britton

Saprosites cascus Britton, 1960: 36 (Eocene, Bognor Regis, Sussex, England). – Jarzembowski 1992: 94; Krell 2000a: 882.

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; Krell 2000a: 882.

Subfamilia **Melolonthinae**

(***Diplotaxis aurora*** Wickham)

Diplotaxis aurora Wickham, 1913b: 294 (Oligocene, Florissant, U.S.A.). – Wickham, 1912: 26; Wickham 1920: 358; Vaurie 1960: 414 (doubts generic affiliation because of the described characters); Krell 2000a: 882.

Doubtful (only one elytron).

(***Diplotaxis***) ***simplicipes*** Wickham

Diplotaxis ? *simplicipes* Wickham, 1912: 25 (Oligocene, Florissant, U.S.A.). – Wickham 1920: 358; Vaurie 1960: 414 (doubts generic affiliation because of the described structures of the legs); Krell 2000a: 882.

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; Krell 2000a: 882.

Eophyllocerus scrobiculatus Haupt

Eophyllocerus scrobiculatus Haupt, 1950: 57 (Eocene, Geiseltal, Germany). – Krumbiegel 1982: 15; Müller 1989: 244; Krell 2000a: 882.

Eophyllocerus glaucinus Haupt

Eophyllocerus glaucinus Haupt, 1950: 58 (Eocene, Geiseltal, Germany). – Krumbiegel 1982: 15; Krell 2000a: 882.

Macrodactylus pluto Wickham

Macrodactylus pluto Wickham, 1912: 24 (Oligocene, Florissant, U.S.A.). – Wickham 1913b: 294; Wickham 1920: 358; Rodeck 1938: 294; Krell 2000a: 882.

Macrodactylus propheticus Wickham

Macrodactylus propheticus Wickham, 1912: 25 (Oligocene, Florissant, U.S.A.). – Wickham 1920: 358; Rodeck 1938: 294; Krell 2000a: 882.

Melolontha greithiana Heer

Melolontha greithiana Heer, 1847: 67 (Oligocene, Greith, Switzerland). – Bronn 1848a: 720; Bronn 1849: 624; Heer 1865: 378, 380; Heer 1883: 406; Scudder 1891: 551; Handlirsch 1907: 840; Krell 2000a: 882.

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

(***Melolontha solitaria*** Novák)

Melolontha solitaria Novák, 1878: 92, pl. 3 (Miocene, Mok_ina [Krottensee] near Kyn_perk n. O., Czechia). – Scudder 1891: 552; Po_ta 1900: 264; Handlirsch 1907: 840; _íha 1977: 22; _íha 1979: 26; Krell 2000a: 883.

Doubtful (only one elytron).

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

Melolonthites Heer, 1847: 71 (as a collective group, this taxon has no type species [Art. 13.3.2 ICZN], though a the type species was designated by Carpenter 1992: *Melolonthites aciculatus* Heer.). – Bronn 1848a: 720; Bronn 1849: 624; Rogg 1852: 22; Giebel 1856: 33; Scudder 1886: 74; Scudder 1895: 120; Handlirsch 1925: 246; Théodoridès 1952: 36; Carpenter 1992: 323 (suborder and family uncertain); Krell 2000a: 883.

(***Melolonthites aciculatus*** Heer)

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

Melolonthites aciculatus. – Bronn 1848a: 720; Heer 1849: 624; Scudder 1891: 552; Handlirsch 1907: 840; Carpenter 1992: 323; Krell 2000a: 883.

Doubtful (only one abdomen [5 sternites]).

(***Melolonthites collinsi*** Wickham)

Melolonthites collinsi Wickham, 1929: 149 (Eocene, Holcomb, Tennessee, U.S.A.). – Wickham 1933: 104; Krell 2000a: 883.

Doubtful (only one elytron).

Melolonthites deperditus Heer

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

Melolonthites deperditus. - Bronn 1848a: 720; Bronn 1849: 624; Scudder 1891: 552; Handlirsch 1907: 840; Krell 2000a: 883.

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"). – Krell 2000a: 883.

(***Melolonthites kollari*** Heer)

Melolonthites kollari Heer, 1847: 72, pl. 7 (Miocene, "in den Kohlen zu Parschlug in Steiermark", Austria). – Bronn 1848a: 720; Bronn 1849: 624; Giebel 1856: 33; Scudder 1891: 552; Handlirsch 1907: 840; Beier 1952: 131; Krell 2000a: 883.

Melolonthites kolleri. – Giebel 1852b: 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*"); Krell 2000a: 883.

Doubtful (only one elytron).

(***Melolonthites lavateri*** Heer)

Melolonthites lavateri Heer, 1847: 73, pl. 7 (Miocene, Öhningen, Germany). – Bronn 1848a: 720; Bronn 1849: 624; Stitzenberger 1851: 100; Giebel 1852b: 652; Giebel 1856: 34; Scudder 1891: 552; Handlirsch 1907: 840; Krell 2000a: 883.

Doubtful (only one elytron).

(***Melolonthites obsoletus*** Heer)

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

Melolonthites obsoletus. – Bronn 1848a: 720; Bronn 1849: 624; Scudder 1891: 552; Handlirsch 1907: 840; Krell 2000a: 883.

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 1848a: 720; Scudder 1891: 552; Handlirsch 1907: 840; Beier 1952: 131; Krell 2000a: 883.

Melolonthites parschluganus. – Bronn 1849: 624.

Melolonthites parschlugana. – Giebel 1852b: 652; Giebel 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, U.S.A.). – Morón 2003: 13.

Phyllophaga avus. – Cockerell 1925: 10 (Eocene, Roan Mountains, Green River Formation, Colorado, U.S.A.); Wickham 1927: 55; Krell 2000a: 883.

Phyllophaga disrupta Cockerell

Phyllophaga disrupta Cockerell, 1927b: 587 (Oligocene, Florissant, U.S.A.). – Wickham 1933: 104; Krell 2000a: 883; Morón 2003: 13.

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

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

Phyllophaga extincta. – Wickham 1920: 358; Krell 2000a: 883.

Doubtful (only one elytron).

Rhizotrogus longimanus Heer

Rhizotrogus longimanus Heer, 1847: 69, pl. 7 (Miocene, Öhningen, Germany). – Bronn 1849: 624; Stitzenberger 1851: 100; Giebel 1852b: 652; Giebel 1856: 32; Heer 1865: 380; Heer 1883: 406; Scudder 1891: 576; Handlirsch 1907: 839; Krell 2000a: 883.

Listrochelus puerilis Wickham

Listrochelus puerilis Wickham, 1914b: 459, pl. 6 (Oligocene, Florissant, U.S.A.). – Wickham 1920: 358; Krell 2000a: 884; Morón 2003: 12.

Tribus **Cretomelolonthini** Nikolajev 1998

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

Genus ***Cretomelolontha*** Nikolajev

Cretomelolontha Nikolajev, 1998a: 81 (transl. p. 516) type genus (type species by original designation: *Cretomelolontha transbaikalica* Nikolajev). – Nikolaev 1999: 178; Krell 2000a: 884; Nikolaev 2002: 54 (transl. p. 281).

Cretomelolontha transbaikalica Nikolajev

Cretomelolontha transbaikalica Nikolajev, 1998a: 82 (transl. p. 517) (L Cretaceous, Baysa, Russia). – Krell 2000a: 884.

Subfamilia **Dynastinae**

Ligyrus compositus Wickham

Ligyrus compositus Wickham, 1911: 59 (Oligocene, Florissant, U.S.A.). – Wickham 1914b: 461; Wickham 1920: 358; Rodeck 1938: 294; Krell 2000a: 884.

(***Ligyrus***) ***effetus*** Wickham

Ligyrus effetus Wickham, 1914b: 461 (Oligocene, Florissant, U.S.A.). – Wickham 1920: 358; Krell 2000a: 884. The generic classification was founded "by the facies", that means *not* by characters. Therefore, the generic affiliation is doubtful.

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; Kolbe 1932: 150; Statz 1952: 3; Krell 2000a: 884.

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

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

Pentodon proserpinae. – Heer 1865: 379; Heer 1883: 405; Scudder 1891: 564; Handlirsch 1907: 841; Houlbert 1915: 64; Kolbe 1932: 150; Krell 2000a: 884.

Doubtful (only one elytron).

Strategus cessatus Wickham

Strategus cessatus Wickham, 1914b: 461 (Oligocene, Florissant, U.S.A.). – Wickham 1920: 358; Ratcliffe 1976: 123, 169 [only elytron, but revised by Ratcliffe]; Krell 2000a: 884; Morón 2003: 13.

Subfamilia **Rutelinae**

Adoretus recticlypeus Zhang

Adoretus recticlypeus Zhang, 1989: 167, pl. 47 (Miocene, Shanwang, China). – Zhang *et al.* 1994: 110; Krell 2000a: 884.

Adoretus rhinus Zhang, Sun & Zhang

Adoretus rhinus Zhang, Sun & Zhang, 1994: 109, pl. 16 (Miocene, Shanwang, China). – Krell 2000a: 884.

Anomala amblobelia Zhang

Magniscarabaeus furvus part. – Hong 1985: 83.

Anomala amblobelia Zhang, 1989: 158, 160, 164, 174, pl. 42 (Miocene, Shandong, China). – Krell 2000a: 884.

Anomala brachytarsia Zhang, Sun & Zhang

Anomala brachytarsia Zhang, Sun & Zhang, 1994: 104, 107f, pl. 16 (Miocene, Shanwang, China). – Krell 2000a: 884.

Anomala endoxa Zhang, Sun & Zhang

Anomala endoxa Zhang, Sun & Zhang, 1994: 103, 106f, pl. 16 (Miocene, Shanwang, China). – Krell 2000a: 884.

Anomala eversa Zhang

Anomala eversa Zhang, 1989: 158, 165, 167, pl. 44 (Miocene, Shanwang, China). – Krell 2000a: 884.

Anomala exterranea Wickham

Anomala exterranea Wickham, 1914b: 459 (Oligocene, Florissant, U.S.A.). – Wickham 1920: 358; Krell 2000a: 884.

Anomala fugax Heer

Anomala fugax Heer, 1862: 80, pl. 6 (Miocene, Öhningen, Kesselstein, Germany). – Heer 1865: 380; Heer 1883; 406; Scudder 1891: 465; Handlirsch 1907: 841; Krell 2000a: 884.

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; Hong & Wang 1987: 120.

Anomala furva. – Zhang 1989: 158, 162, 164, 166f, 173, pl. 43; Zhang *et al.* 1994: 104, pl. 15; Krell 2000a: 884.

Anomala turua. – Sun 1995: 38.

Anomala lochmocola Zhang

Anomala lochmocola Zhang, 1989: 158, 164, pl. 45 (Miocene, Shanwang, China). – Krell 2000a: 885.

Anomala orcina Zhang, Sun & Zhang

Anomala orcina Zhang, Sun & Zhang, 1994: 103, 105, pl. 15 (Miocene, Shanwang, China). – Krell 2000a: 885.

Anomala palaeobrunnea Krell

Anomala palaeobrunnea Krell, 2000a: 885.

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

Anomala brunnea. – Zhang 1989: 158, 160f; junior secondary homonym of *Anomala brunnea* Klug, 1855 (extant species from Moçambique).

(***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); Krell 2000a: 885.

Anomala punctulata Zhang

Anomala punctulata Zhang, 1989: 158, 165, pl. 44 (Miocene, Shanwang, China). – Krell 2000a: 885.

Anomala scia Zhang

Anomala scia Zhang, 1989: 158, 166, pl. 45 (Miocene, Shanwang, China). – Krell 2000a: 885.

Anomala scudderi Wickham

Anomala scudderi Wickham, 1914b: 460 (Oligocene, Florissant, U.S.A.). – Wickham 1920: 358; Krell 2000a: 885.

Anomala synemosyna Zhang

Anomala synemosyna Zhang, 1989: 158, 161, pl. 42 (Miocene, Shanwang, China). – Krell 2000a: 885.

(***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); Krell 2000a: 885.

(***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); Krell 2000a: 885.

Anomala ursa Zhang, Sun & Zhang.

Anomala ursa Zhang, Sun & Zhang, 1994: 104, 108f, pl. 16 (Miocene, Shanwang, China). – Krell 2000a: 885.

Genus ***Anomalites*** Fri_

Anomalites Fri_, 1885: 163 (type species by monotypy: *Anomalites fugitivus* Fri_). – Scudder 1881-1885: 794; Scudder 1886: 74; Handlirsch 1925: 246; Carpenter 1992: 300, 330; Krell 2000a: 885.

Anomalites fugitivus Fri_

Anomalites fugitivus Fri_, 1885: 163 (Tertiary, Süßwasserquarz Nogent le Rotrou, France). – Handlirsch 1907: 841; Carpenter 1992: 300; Krell 2000a: 885.

Genus ***Zhangsunia*** Krell

Zhangsunia Krell, 2000a: 885.

Dolichopoda Zhang, Sun & Zhang, 1994: 101, 279 (type species by original designation: *Dolichopoda extumida* Zhang, Sun & Zhang). – Jarzembowski 2000: (6); preoccupied by *Dolichopoda* Bolivar, 1880: 72 (Ensifera: Rhaphidophoridae).

Zhangsunia extumida (Zhang, Sun & Zhang) Krell

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

Zhangsunia extumida. – Krell 2000a: 885.

Holotrichia cressona Zhang, Sun & Zhang

Holotrichia cressona Zhang, Sun & Zhang, 1994: 102f (Miocene, Shanwang, China). – Krell 2000a: 885.

Holotrichia spatha Zhang

Holotrichia spatha Zhang, 1989: 156 (Miocene, Shanwang, China). – Krell 2000a: 885.

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; Krell 2000a: 885.

Genus ***Miolachnosterna*** Wickham

Miolachnosterna Wickham, 1914b: 458 (type species by original designation: *Miolachnosterna tristoides* Wickham). – Théodoridès 1952: 36; Carpenter 1992: 301; Krell 2000a: 885.

Miolachnosterna tristoides Wickham

Miolachnosterna tristoides Wickham, 1914b: 458, pl. 8 (Oligocene, Florissant, U.S.A.). – Wickham 1920: 358; Carpenter 1992: 301; Krell 2000a: 886; Morón 2003: 13.

Genus ***Pelidnotites*** Cockerell

Pelidnotites Cockerell, 1920: 463 (type species by monotypy: *Pelidnotites atavus* Cockerell). – Carpenter 1992: 301; Krell 2000a: 886.

Pelidnotites atavus Cockerell

Pelidnotites atavus Cockerell, 1920: 462 (Eocene, U Ypresian - Lutetian, Bournemouth, England). – Carpenter 1992: 301; Jarzembowski 1996: 210; Krell 2000a: 886.

Genus ***Petraeianus*** Zhang

Petraeianus Zhang, 1989: 168, 426 (type species by original designation: *Petraeianus ruderatus* Zhang). – Krell 2000a: 886.

Petraeianus ruderatus Zhang

Petraeianus ruderatus Zhang, 1989: 168, 426 (Miocene, Shanwang, China). – Krell 2000a: 886.

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

Petulantis Zhang, Sun & Zhang, 1994: 110, 279 (type species by original designation: *Petulantis yimengensis* Zhang, Sun & Zhang). – Krell 2000a: 886.

Petulantis yimengensis Zhang, Sun & Zhang

Petulantis yimengensis Zhang, Sun & Zhang, 1994: 110, pl. 17 (Miocene, Shanwang, China). – Krell 2000a: 886.

Subfamilia **Hopliinae**

Hoplia striatipennis Wickham

Hoplia striatipennis Wickham, 1914b: 457 (Oligocene, Florissant, U.S.A.). – Wickham 1920: 358; Krell 2000a: 886.

Lepitrix germanica Heer

Lepitrix germanica Heer, 1862: 80, pl. 6 (Miocene, Öhningen, Germany). – Heer 1865: 378, 380; Heer 1883: 406; Scudder 1891: 546; Handlirsch 1907: 839; Krell 2000a: 886.

Subfamilia **Sericinae**

Genus ***Lithanomala*** Nikolajev

Lithanomala Nikolaev, 1992: 79 (transl. p. 100) (type species by original designation: *Proteroscarabaeus oblongus* Ponomarenko). – Nikolaev 1998a: 82 (transl. p. 519); Nikolaev 1999: 178; Krell 2000a: 886.

Lithanomala crassa (Ponomarenko) Nikolaev

Proteroscarabaeus crassus Ponomarenko, 1990: 66, pl. 6 (L Cretaceous, Leskovo, Russia).

Lithanomala crassa. – Nikolaev, 1992: 80 (transl. p. 100); Krell 2000a: 886.

Lithanomala oblonga (Ponomarenko) Nikolaev

Proteroscarabaeus oblongus Ponomarenko, 1990: 66, pl. 6 (L Cretaceous, Leskovo, Russia).

Lithanomala oblonga. – Nikolaev, 1992: 79 (transl. p. 100); Krell 2000a: 886.

Lithanomala sibirica (Ponomarenko) Nikolaev

Proteroscarabaeus sibiricus Ponomarenko, 1990: 68, pl. 6 (L Cretaceous, Leskovo, Russia).

Lithanomala sibirica. – Nikolaev, 1992: 80 (transl. p. 100); Krell 2000a: 886.

Maladera spinitibialis Statz

Maladera spinitibialis Statz, 1952: 9 (Oligocene, Rott, Germany). – Krell 2000a: 886.

Maladera ? spinitibialis. – Sphon 1973: 52.

Genus ***Mioserica*** Zhang

Mioserica Zhang, 1989: 157, 426 (type species by original designation: *Mioserica margelis* Zhang). – Krell 2000a: 886.

Mioserica margelis Zhang

Mioserica margelis Zhang, 1989: 157, 426 (Miocene, Shanwang, China). – Krell 2000a: 886.

(***Serica***) ***antediluviana*** Wickham

Serica antediluviana Wickham, 1912: 23 (Oligocene, Florissant, U.S.A.). – Wickham 1914a: 263; Wickham 1920: 358; Rodeck 1938: 294; Krell 2000a: 886.

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

(***Serica***) ***cockerelli*** Wickham

Serica cockerelli Wickham, 1914a: 262 (Oligocene, Florissant, U.S.A.). – Wickham 1920: 358; Théodoridès 1952: 35; Krell 2000a: 886.

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

Serica kanakoffi Pierce

Serica kanakoffi Pierce, 1946b: 132 (Pleistocene, Rancho La Brea tar pits, Los Angeles, U.S.A.). – Sphon 1973: 53; Miller *et al.* 1981: 627; Stock & Harris 1992: 84; Krell 2000a: 886.

Serica minutula Heer

Serica minutula Heer, 1862: 79, pl. 6 (Miocene, Öhningen, Kesselstein, Germany). – Heer 1865: 380; Heer 1883: 406; Scudder 1891: 579; Handlirsch 1907: 839; Krell 2000a: 886.

Subfamilia **Cetoniinae**

(***Cetonia defossa*** Weyenbergh)

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

Cetonia defossa. – Weijenbergh 1869b: [232]; Scudder 1891: 197; Meunier 1897: 235, pl. 10 ("indéterminable empreinte de coléoptère"); Krell 2000a: 887.

? 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). – Krell 2000a: 887.

Genonota mochthera Zhang

Genonota mochthera Zhang, 1989: 170f, 426, pl. 46 (Miocene, Shanwang, China). – Krell 2000a: 887.

Genonota scola Zhang

Genonota scola Zhang, 1989: 170f, pl. 47 (Miocene, Shawang, China). – Krell 2000a: 887.

Macronota shandongiana Zhang

Macronota shandongiana Zhang, 1989: 169, pl. 45 (Miocene, Shandong, China). – Krell 2000a: 887.

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; Kolbe 1931: 117; Kolbe 1932: 150; Krell 2000a: 887.

Gnorimus lugubris (Heer) Kolbe

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; Krell 2000a: 887.

Gnorimus lugubris. – Kolbe 1931: 117; Kolbe 1932: 150

Trichius amoenus Heer

Trichius amoenus Heer, 1847: 74, pl. 7 (unknown locality). – Bronn 1849: 624; Stitzenberger 1851: 100; Giebel 1852b: 652; Giebel 1856: 30; Heer 1865: 380 (deducing: Switzerland); Heer 1883: 405; Scudder 1891: 591; Handlirsch 1907: 841; Frentzen 1927: 141; Krell 2000a: 887.

Trichius rotundatus Heer

Trichius rotundatus Heer, 1862: 82, pl. 6 (Miocene, Öhningen, Kesselstein, Germany). – Scudder 1891: 591; Handlirsch 1907: 841; Krell 2000a: 887.

Trichius unifasciatus Heer

Trichius (Trichius) unifasciatus Heer, 1862: 82, pl. 6 (Miocene, Öhningen, Kesselstein, Germany). – Scudder 1891: 592; Handlirsch 1907: 842; Kolbe 1931: 117; Krell 2000a: 887.

Subfamilia **Valginae**

Valgus oeningensis Heer

Valgus oeningensis Heer, 1862: 82, pl. 6 (Miocene, Öhningen, Kesselstein, Germany). – Heer 1865: 378, 380; Heer 1883: 404-406; Scudder 1891: 594; Handlirsch 1907: 842; Frentzen 1927: 141; Kolbe 1931: 117; Krell 2000a: 887.

Subfamilia **Euchirinae**

Cheirotonus otai Ueda

Cheirotonus otai Ueda, 1989: 107 (Miocene, Tottori, Japan). – Krell 2000a: 887.

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

Genus ***Cretoscarabaeus*** Nikolajev

Cretoscarabaeus Nikolajev, 1995b: 147 (transl. p. 186), type genus (type species by original designation: *Cretoscarabaeus gibbosus* Nikolajev). – Nikolaev 1999: 178; Krell 2000a: 887; Nikolaev 2002: 54 (transl. p. 281).

Cretoscarabaeus gibbosus Nikolajev

Cretoscarabaeus gibbosus Nikolajev, 1995b: 147 (transl. p. 186) (L Cretaceous, Baysa, Russia). – Krell 2000a: 887.

Cretoscarabaeus lentiginosus Nikolajev

Cretoscarabaeus lentiginosus Nikolajev, 1995b: 148 (transl. p. 188) (L Cretaceous, Baysa, Russia). – Krell 2000a: 887.

Genus ***Cretorabaeus*** Nikolajev

Cretorabaeus Nikolajev, 1995b: 149 (transl. p. 189) (type species by original designation: *Cretorabaeus elongatus* Nikolajev). – Nikolaev 1999: 178; Krell 2000a: 887.

Cretorabaeus elongatus Nikolajev

Cretorabaeus elongatus Nikolajev, 1995b: 149 (transl. p. 189) (L Cretaceous, Baysa, Russia). – Krell 2000a: 887.

Subfamilia **Lithoscarabaeinae** Nikolajev, 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; Krell 2000a: 888; Nikolaev 2002: 54 (transl. p. 281).

Lithoscarabaeus baissensis (Nikritin) Nikolaev

Proteroscarabaeus baissensis Nikritin, 1977: 124 (1991: 168) (L Cretaceous, Baysa, Russia). – Hong & Wang 1990: 115.

Proteroscarabaeus daissensis. – Morón 2003: 12

Lithoscarabaeus baissensis. – Nikolaev 1992: 78 (transl. p. 97); Krell 2000a: 888.

Familiae Incertae Sedis

Genus ***Aliscarabaeus*** Hong

Aliscarabaeus Hong, 1983: 5 (type species by original designation: *Aliscarabaeus granulatus* Hong). – Hong 1985: 37 (*Alscarabaeus*, lapsus calami); Krell 2000a: 888.

Aliscarabaeus granulatus Hong

Aliscarabaeus granulatus Hong, 1983: 5, 13 (Miocene, Shanwang, China). – Hong 1985: 37f, pl. 16; Krell 2000a: 888.

Genus ***Avitortor*** Ponomarenko

Avitortor Ponomarenko, 1977b: 42 (1991b: 54) (originally classified as belonging to Gyrinidae) (type species by original designation: *Avitortor primitivus* Ponomarenko). – Schlüter 1987: 132; Nikolaev 1992: 80 (transl. p. 101) (Scarabaeidae); Nikolaev 1999: 178; Krell 2000a: 888; Nikolaev 2002: 54 (transl. p. 281).

Avitortor primitivus Ponomarenko

Avitortor primitivus Ponomarenko, 1977b: 42 (1991b: 55) (L Cretaceous, Baysa, Russia). – Nikolaev 1992: 80 (transl. p. 101) (Scarabaeidae); Krell 2000a: 888.

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); Krell 2000a: 888.

Genus ***Cretoserica*** Nikolajev

Cretoserica Nikolajev, 1998a: 83 (transl. p. 519) (type species by original designation: *Cretoserica latitibialis* Nikolajev), incertae subfamiliae. – Nikolaev 1999: 178; Krell 2000a: 888; Nikolaev 2002: 54 (transl. p. 281).

Cretoserica latitibialis Nikolajev

Cretoserica latitibialis Nikolajev, 1998a: 83 (transl. p. 520) (L Cretaceous, Baysa, Russia). – Krell 2000a: 888.

Genus ***Hongscarabaeus*** Krell

Hongscarabaeus Krell, 2000a: 888

Proscarabaeus Hong, 1982: 126 (type species by original designation: *Proscarabaeus brunneus* Hong). – Xiao *et al.* 1994: 81; Nikolaev 1998b: 30; preoccupied by *Proscarabaeus* Schrank, 1781 (Coleoptera Meloidae).

Hongscarabaeus brunneus (Hong) Krell

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

Hongscarabaeus brunneus. – Krell 2000a: 888.

(Genus ***Hybosorites*** Nikolajev)

Hybosorites Nikolajev, 1996: 98 (type species by original designation: *Hybosorites fissuratus* Nikolajev). – Nikolaev 1999: 178; Krell 2000a: 888.

(***Hybosorites fissuratus*** Nikolajev)

Hybosorites fissuratus Nikolajev, 1996: 98 (L Cretaceous, Baysa, Russia). – Krell 2000a: 888.

Doubtful (only one elytron).

Genus ***Mesoscarabaeus*** Hong

Mesoscarabaeus Hong, 1982: 123 (type species by original designation: *Mesoscarabaeus corneus* Hong). – Nikolaev 1998b: 30; Krell 2000a: 888.

Mesoscarabaeus corneus Hong

Mesoscarabaeus corneus Hong, 1982: 124 (L Cretaceous, Jiuquan, China). – Krell 2000a: 888.

Mesoscarabaeus morulosus Hong

Mesoscarabaeus morulosus Hong, 1982: 125 (L Cretaceous, Jiuquan, China). – Krell 2000a: 888.

(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 1995a: 358; Krell 2000a: 888.

(***Opiselleipon grave*** Bode)

Opiselleipon gravis Bode, 1953: 230, pl. 11 (L Jurassic, Hondelage near Braunschweig, Germany). – Scholtz 1990: 1029; Carpenter 1992: 324; Krell 2000a: 888.

Tribus **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 1998b (classified as Aclopinae, but without giving an explanation); Nikolaev 1999: 178; Jarzembowski 2000: (8); Krell 2000a: 889; Nikolaev 2002: 54 (transl. p. 281).

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); Krell 2000a: 889.

Holcorobeus (Holcorobeus) atrosulcatus Nikolajev

Holcorobeus (Holcorobeus) atrosulcatus Nikolajev, 1992: 84 (transl. p. 106) (L Cretaceous, Baysa, Russia). – Krell 2000a: 889.

Holcorobeus (Holcorobeus) evittatus Zhang

Holcoribeus evittatus Zhang, 1992a: 334 (L Cretaceous, Laiyang Formation, China). – Krell 2000a: 889.

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); Krell 2000a: 889.

Holcorobeus (Holcorobeus) latitibialis Nikolajev

Holcorobeus (Holcorobeus) latitibialis Nikolajev, 1992: 84 (transl. p. 106) (L Cretaceous, Baysa, Russia). – Krell 2000a: 889.

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); Krell 2000a: 889.

Holcorobeus (Holcorobeus) maculatus Nikolajev

Holcorobeus (Holcorobeus) maculatus Nikolajev, 1992: 85 (transl. p. 107) (L Cretaceous, Baysa, Russia). – Krell 2000a: 889.

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); Krell 2000a: 889.

Holcorobeus (Holcorobeus) nigrimontanus Nikolajev

Holcorobeus nigrimontanus Nikolajev, 1992: 83 (transl. p. 105) (U Jurassic, Karatau, Kazakhstan). – Krell 2000a: 889.

(***Holcorobeus (Holcorobeus) nigrovittatus*** Nikolajev)

Holcorobeus nigrovittatus Nikolajev, 1992: 86 (transl. p. 108) (L Cretaceous, Baysa, Russia). – Krell 2000a: 889.

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); Krell 2000a: 889.

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); Krell 2000a: 889.

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); Krell 2000a: 889.

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); Krell 2000a: 889.

Holcorobeus (Holcorobeus) vittatus Nikritin

Holcorobeus vittatus Nikritin, 1977: 128 (1991: 173) (L Cretaceous, Baysa, Russia). – Nikolaev 1992: 83 (transl. p. 104); Krell 2000a: 890.

Holcoribeus vittatus. – Carpenter 1992: 301; Zhang 1992a: 334f.

Subgenus ***Mesaclopus*** Nikolajev

Mesaclopus Nikolajev, 1992: 86 (transl. p. 108) (type species by original designation: *Holcorobeus mongolicus* Nikolajev). – Krell 2000a: 890.

Holcorobeus (Mesaclopus) mongolicus Nikolajev

Holcorobeus (Mesaclopus) mongolicus Nikolajev, 1992: 86 (transl. p. 108) (U Jurassic-L Cretaceous, Khutel-Khara, Mongolia). – Krell 2000a: 890.

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); Krell 2000a: 890.

Tetragonides magnus Bode

Tetragonides magnus Bode, 1953: 225 (L Jurassic, Hondelage, Germany) ("Die Gestalt erinnert an die der (?) Lucaniden."). – Carpenter 1992: 326; Krell 2000a: 890.

Fossil taxa later synonymised with extant 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; Krell 2000a: 890.

Genus ***Obitiscarabaeus*** Hong

Obitiscarabaeus Hong, 1983: 6 (type species by original designation: *Obitiscarabaeus jiaoyanshanensis* Hong). – Hong 1985: 40.

= *Geotrupes* Latreille, 1796. – Zhang 1989: 152; Krell 2000a: 890.

Genus ***Palaeocopris*** Pierce

Palaeocopris Pierce, 1946a: 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; Krell 2000a: 890.

Canthon simplex antiquus Pierce, 1946a: 120 (Pleistocene, Rancho La Brea tar pits, Los Angeles, U.S.A.). – Spohn 1973: 52.

Boreocanthon simplex antiquus. – Halffter 1959: 176.

= *Canthon (Boreocanthon) simplex* LeConte. – Miller *et al.* 1981: 626; Stock & Harris 1992: 84; Krell 2000a: 890.

Canthon praticolus vetustus Pierce, 1946a: 122 (Pleistocene, Rancho La Brea tar pits, Los Angeles, U.S.A.). – Sphon 1973: 52.

Boreocanthon praticola vetustus. – Halffter 1959: 176.

= *Canthon (Boreocanthon) praticola* LeConte. – Miller *et al.* 1981: 626; Stock & Harris 1992: 84; Krell 2000a: 890.

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; Krell 2000a: 890.

Genus *Pseudopentodon* Filhol, 1892: 2 (without indication). – Krell 2000a: 890.

Pseudopentodon blanchardi Filhol, 1892: 2 (Eocene-Oligocene, Quercy, France; without indication). – Handschin 1944: 2, 19, 21; Handschin 1950: 138 (*Pseudopantodon*); Théodoridès 1952: 47; Krell 2000a: 890.

Ichnotaxa, fossil nests and broodballs of Scarabaeoidea

Ichnogenus ***Coprinisphaera*** Sauer

Coprinisphaera Sauer, 1955: 123 (type species by monotypy: *Coprinisphaera ecuadoriensis* Sauer). – Häntzschel 1962: W189; Häntzschel 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; Krell 2000a: 890.

Cangabola Lengerken, 1955: 937 (type species by monotypy: *Cangabola ecuadoriensis* Sauer)

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; Sauer 1959: 119ff; Häntzschel 1962: W189; Häntzschel 1975: W52; Martinez 1982: 48; Genise & Bown 1994: 109; Genise 1999: 110; Krell 2000a: 890.

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; Krell 2000a: 891.

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; Krell 2000a: 891.

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"); Krell 2000a: 891.

Eatonichnus claronensis Bown, Hasiotis, Genise, Maldonaldo & Browers

Eatonichnus claronensis Bown, Hasiotis, Genise, Maldonaldo & Browers, 1997: 54 (Eocene, J.G. Eaton locality, Utah, U.S.A.). – Genise & Bown 1998: 222; Krell 2000a: 891.

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

Xenohelix? utahensis Gilliland & La Rocque, 1952: 502, pl. 59 (Eocene, Bald Knoll Canyon, Utah, U.S.A.). – Kilpper 1962: 56.

Eatonichnus utahensis. – Bown *et al.* 1997: 52; Genise & Laza 1998: 222; Krell 2000a: 891.

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; Krell 2000a: 891.

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"); Krell 2000a: 891.

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; Krell 2000a: 891.

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). – Krell 2000a: 891.

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; Krell 2000a: 891.

Martinezichnus francisi Roselli

Martinezichnus francisi Roselli, 1987: 22 (Cretaceous, Asencio Formation, Uruguay?). – Genise & Cladera 1995: 78f; Krell 2000a: 891.

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; Krell 2000a: 891.

Microicoichnus lafurcadai Roselli

Microicoichnus lafurcadai Roselli, 1987: 49 (U Cretaceous – L Tertiary, Uruguay). – Krell 2000a: 891.

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; Krell 2000a: 891.

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; Krell 2000a: 891.

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; Krell 2000a: 891.

Pallichnus dakotensis Retallack

Pallichnus dakotensis Retallack, 1984: 581 (Oligocene, South Dakota, U.S.A.). – Genise 1993: 50; Krell 2000a: 891.

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; Krell 2000a: 892.

Scaphichnium hamatum Bown & Kraus

Scaphichnium hamatum Bown & Kraus, 1983: 106 (L Eocene, Willwood formation, Wyoming, U.S.A.). – Hasiotis *et al.* 1993 (classified as traces of Scarabaeoidea); Bown *et al.* 1997: 56; Genise & Laza 1998: 222; Genise 1999: 110; Krell 2000a: 892.

u n n a m e d t r a c e f o s s i l s : [1]

A f r i c a : Pleistocene, Rutana, Burundi: "loges fossiles des coprophages" (Basilewsky 1951).

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

[1] more possible traces of dung beetles are compiled by Retallack (1990: 223)

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).

A s i a : U Miocene, Dhok Patan Formation, Pakistan: *Coprinisphaera* sp. (Retallack 1991: 182, 296).

N o r t h A m e r i c a : Pliocene, Jalisco, México: "bola-nido" (Morón Ríos 1984: 27).

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

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

S o u t h A m e r i c a : 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 1938a, 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 1938a, 1939; Laza 1986a; *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 1986b, 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 1938a, b; Laza 1986b; *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).

A n t a r c t i c a : 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

Ichnogenus ***Fictovichnus*** Johnston, Eberth & Anderson

Fictovichnus Johnston, Eberth & Anderson, 1996: 521 (type species by original designation: *Fictovichnus gobiensis* Johnston, Eberth & Anderson) (pupal chambers of Scarabaeidae, Tenebrionidae, or Curculionidae), containing the ichnospecies *F. gobiensis* and *F. parvus* Johnston, Eberth & Anderson, 1996. - Genise *et al.* 2002a: (probably [junior] synonym of *Rebuffoichnus* Roselli, 1987 [Curculionidae]); Genise *et al.* 2002b (pupal chamber of Curculionidae).

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

Oryctites Oppenheim, 1888: 238. – Ponomarenko 1971: 72 (transl. p. 67): Adephaga incertae sedis; Krell 2000a: 892.

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 Art. 20 ICZN.

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

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

Oryctes fossilis. – Houlbert 1915: 64 ("Handlirsch assure que cette identification est inexacte"); Krell 2000a: 892.

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

(***Oryctes pluto*** Weyenbergh)

Oryctes pluto Weyenbergh 1869a: 282, pl. 27 (Jurassic, U Malm, Solnhofen, Germany). – Weijenbergh 1869b*: [232]; Weijenbergh 1874: 102 or 109[2]; 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"); Krell 2000a: 884.

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

Pseudohydrophilus avitus (Heyden, 1847) Handlirsch, 1906 (Blabera avita Heyden, 1847: 100). – Handlirsch 1906: 544; belongs to Hydrophilidae.

Genus ***Progeotrupes*** Oppenheim

Progeotrupes Oppenheim, 1888: 239 (type species by monotypy: *Progeotrupes jurassicus* Oppenheim). – Broili 1921: 675; Broili 1924: 697; Laurentiaux 1953: 476; Krell 2000a: 892. – belongs to Blattodea (see below).

Progeotrupes jurassicus Oppenheim

Progeotrupes jurassicus Oppenheim, 1888: 239, pl. 31 (Jurassic, U Malm, Solnhofen, Germany). – Scudder 1891: 217; Meunier 1898b: 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); Krell 2000a: 893.

Geotrupes jurassicus. – Meunier 1898b: 133.

Genus ***Prosynactus*** Bode

Prosynactus Bode, 1953: 224 (type species by monotypy: *Prosynactus scissus* Bode) ("Ein Typ, der an manche (?) Lucaniden erinnert."); Krell 2000a: 893. – belongs to Tachypachidae (see below).

[2] There are two printings with slightly different arrangement of the text.

Prosynactus scissus Bode

Prosynactus scissus Bode, 1953: 224, pl. 11 (Lias, Beienrode, Germany). – Ponomarenko 1992: 180 (belongs to Coleoptera Tachypachidae); Krell 2000a: 893.

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; Krell 2000a: 892; Genise *et al.* 2002a: (probably [senior] synonym of *Fictovichnus* Johnston, Eberth & Anderson, 1996 [Curculionidae]); Genise *et al.* 2002b (probably pupal chamber of Curculionidae, but separate from *Fictovichnus*).

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); Krell 2000a: 892; Genise *et al.* 2002a: 230f; Genise *et al.* 2002b.

Genus ***Scarabaeides*** Germar

Scarabaeides Germar, 1839: 218 (type species by monotypy: *Scarabaeides deperditus* Germar). – Giebel 1846: 148; Bronn 1848b: 1119; Bronn 1849: 625; Weyenbergh 1873: 240; Krell 2000a: 893.

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

Scarabaeides deperditus Germar

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

Scarabaeides deperditus Germar, 1839: 218 (Malm, Solnhofen, Germany). – Brodie 1845: 109; Bronn 1848b: 1119; Bronn 1849: 625; Giebel 1852a: 207; Quenstedt 1852a: 313 ("Wäre es ein Käfer, so sollte man doch Reste von Flügeldecken erwarten."), 786 (index: "*Scarabaeoides depertitus*" [lapsus calami]; Quenstedt 1852b: 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 1869a: 249 (ad Hemiptera); Goss 1879: 147; Scudder 1886: 73 ("Belostomidae"); Scudder 1891: 176 ("Belostomatidae"); Zittel 1895: 504; Krell 2000a: 893.

Scarabaeoides deperditus. – Weijenbergh 1869b: [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; Weyenbergh 1874: 84 or 89, 103 or 109; Winkler 1878: 96; Winkler 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); Handlirsch 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."); Krell 2000a: 893.

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

Tetragonotrachelus gracilis Bode

Tetragonotrachelus gracilis Bode, 1953: 224, pl. 11 (Lias, Beidenrode, Germany); Krell 2000a: 893.

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 1879b: 19 ("curculionid"); Scudder 1881-1885: 794 ("dürfte eine fossile Frucht sein"); Scudder 1886: 73 ("probably a fruit"); Krell 2000a: 893.

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; Goldenberg 1877: 50; Scudder 1879b: 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"); Handlirsch 1922: 221 ("Arthropleurarest"); Waterlot 1934: 262 ("fossile à affinité douteuse"); Krell 2000a: 893.

Xyloryctes planus Fri_ (ichnospecies)

Xyloryctes planus Fri_, 1877: 16, pl. 3 (Carboniferous, Ny_an near Plzen, Czechia; Oberhohndorf, Germany). – Scudder 1879b: 17; Scudder 1891: 98 ("coleopteroid"); Handlirsch 1905: 328 ("Die Deutung dieser Gebilde als Bohrlöcher von Coleopteren erscheint mir gewagt."); Handlirsch 1919: 590 (arthropod origin questionable); Handlirsch 1922: 219 (no insect); Krell 2000a: 893.

Xyloryctes septarius Fri_ (ichnospecies)

Xyloryctes septarius Fri_, 1877: 15, pl. 3 (U Carboniferous, Swinná near Radnitz, Bohemia, Czechia). – Scudder 1879b: 17; Scudder 1891: 98 ("coleopteroid"); Handlirsch 1905: 337 (not from an insect); Handlirsch 1919: 590 (arthropod origin questionable); Handlirsch 1922: 219 (no insect); Krell 2000a: 893.

Fri_ never claimed that these ichnofossils were lebensspuren of Scarabaeoidea. However, he gave them the ichnogeneric name *Xyloryctes*. I suppose that he did not realize 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)

E u r o p e : 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); *Lucanus cervicalis* (= *cervus* (L.)) (Schweigert 2003).

Boulder-Formation, Mundesley, England: cfr. *Copris lunaris* (Lyell 1840: 175).

Kisatibi formation, Georgia (L?): *Copris (Copris) kartlinus* (Kabakov 1988).

A f r i c a : 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).

N o r t h A m e r i c a : Jalisco, México: ichnofossils of coprophagans (Morón Ríos 1984).

S o u t h A m e r i c a : 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).

T r a n s i t i o n M i o / P l i o c e n e : E u r o p e : Simetite (Sicilian resin): (*Scarabaeus bilobus* L.) (= *Caelosis biloba*) (Ferrara 1805: 136 [wrong determination; Krell 1996: 18]; Kohring & Schlüter 1989: 45).

Cinérites de Varennes, France: (*Melolonthites laterosinuatus*) (Piton & Théobald 1935).

N o r t h A m e r i c a : Beaufort Formation, Prince Patrick Island, Canada (3-5,7 Myr): *Aegialia* sp. (Matthews 1976, Matthews *et al.* 1990).

S o u t h A m e r i c a : Monte Hermoso, Buenos Aires, Argentina (U Miocene-L Pliocene): *Coprinisphaera* sp. (ichnofossil) (Genise *et al.* 2000: 55).

Miocene (> 5 Myr)

E u r o p e : 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)*[3], *Lepitrix germanica, Anomala fugax, Serica minutula, Gnorimus aedilis, G. lugubris, Trichius amoenus, 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 1895b: 120).

Parschlug, Styria, Austria (U): *(Melolonthites kollari), (M. parschlugianus)* (Heer 1847).

Mok_ina (Krottensee) near Kyn_perk 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).

A s i a : 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).

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[3] The *Melolontha* listed by Keferstein (1834: 331) likely refers to one of these *Melolonthites* species.

Tottori Group, Kokufu Town, Japan (M): *Cheirotonus otai* (Ueda 1989).

A f r i c a : Lake Victoria, Kenya: *Anachalcos mfwangani* (Mfwangano Island), *Copris leakeyorum* (Rusinga Island), *Metacatharsius rusingae* (Rusinga I.), Rutelinae, Cetoniinae (Paulian 1976).

N o r t h - A m e r i c a : Ruby River, Montana, U.S.A. (U): Rutelinae (tentatively) (Zuidema 1950: 121).

Clarkia, Idaho, U.S.A. (L, 17-20 Myr): *Lucanus* sp., *Osmoderma* sp., *Geotrupes* sp. (Lewis 1985: 251ff).

Meighen Island, Canada (U): *Aegialia* sp. (Matthews 1977).

Dominican Amber: *Tyrannasorus rex* (Ratcliffe & Ocampo 2001), *Procoilodes adrastus* (Ocampo 2002); Ceratocanthidae, Lucanidae, *Canthidium* sp., *Rhyparus*, *Termitodius* (Poinar 1992: 151, 285; Poinar & Poinar 1999: 165, 205; Wu without date: 187).

S o u t h - A m e r i c a : Río Negro, Collón-Curá Formation, and Neuquén, Argentina (U): ichnofossils of coprophagans (*Megathopa* and *Onthophagus*), *Coprinisphaera* sp. (Frenguelli 1938a; 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)

E u r o p e : Rott, Siebengebirge, Germany (U, Chattian, 25 Myr): *Geotrupes rottensis*, (*Onitis*) *magus*, *Mioochodaeus 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 1837a).

Enspel, Westerwald, Germany (U): Scarabaeoidea (Wedmann 1998, 2000: 47).

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 1898a).

Barachek Creek, Pozhar Region, Russia: *Platycerus zherichini* (Nikolaev 1991).

A s i a : Kudia River, Primorye Province, Russia (L): *Melolonthites interemtus* (Cockerell 1926).

N o r t h A m e r i c a : John Day Series (lower division), Oregon, U.S.A. (U): *Passalus indormitus* (Cockerell 1927a).

Ruby Paper Shales, Montana, U.S.A. (U): "scarab" (Becker 1961: 38, pl. 31).

Florissant, Colorado, U.S.A. (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 1927b, Wickham 1909, 1910, 1911, 1912, 1913a, b, 1914a, b).

South Dakota: *Pallichnus dakotensis* (ichnofossil) (Retallack 1984).

S o u t h A m e r i c a : Colhue-Huapi Formation, Argentina (U): *Coprinisphaera* sp. (ichnofossil) (Laza 1986b, Genise *et al.* 2000: 54).

Santa Cruz and Chubut, Argentina: ichnofossils of coprophagans, *Coprinisphaera* sp. (ichnofossil) (Frenguelli 1938a, b; Genise *et al.* 2000: 54).

Ludados lustrosos, Mendoza, Argentina: *Coprinisphaera* sp. (ichnofossils) (Genise *et al.* 2000: 54).

E o c e n e – O l i g o c e n e : E u r o p e : 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 (> 37 Myr)

E u r o p e : Gurnet Bay, Bembridge Limestone, Isle of Wight (U): *Dorcus* sp. (Brodie 1845: 47; Goss 1878: 325; Woodward 1878, 1879).

Ku_lín (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 1988b), *Protognathus spielbergi* (Chalumeau & Brochier 2001), many more species (Krell, in prep.).

Eckfelder Maar, Eifel, Germany (M., U Geiseltalian): Scarabaeidae, Melolonthinae (Lutz 1988a).

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).

N o r t h A m e r i c a : British Columbia, Canada (M): Ninemile creek: (*Trox oustaleti*) (Scudder 1879a, Handlirsch 1910); Princeton: Scarabaeidae (Wilson 1977).

Green River, Colorado/Wyoming, U.S.A. (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, U.S.A. (L): *Scaphichnium hamatum* (Bown & Kraus 1983: 106; Hasiotis *et al.* 1993).

Holcomb Property, Henry County, Tennessee, U.S.A. (L): (*Melolonthites collinsi*) (Wickham 1929).

J.G. Eaton Locality, Claron Formation, Kane County, Utah, U.S.A. (L): *Eatonichnus claronensis*, *E.* sp. (ichnofossils) (Bown *et al.* 1997).

Golden Valley Formation, North Dakota, U.S.A. (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, U.S.A.: *Eatonichnus utahensis* (Bown *et al.* 1997).

S o u t h A m e r i c a : 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 1938a, b; Laza 1986b; *Coprinisphaera* sp. according to Genise *et al.* 2000: 54).

A n t a r c t i c a : Isla Marambio: ichnofossils of coprophagans (Laza & Roguero 1990).

Palaeocene (> 54 Myr)

E u r o p e : Menat, Puy-de-Dôme, France (U, Thanetian, 56 Myr): *Bolboceras inermis*, *Aphodius charauxi* (Piton 1940).

S o u t h A m e r i c a : Rio Chico, Chubut, Argentina: *Coprinisphaera* (Genise et al. 2000: 54).

T e r t i a r y (w i t h o u t s p e c i f i c a t i o n) : E u r o p e : Nogent le Rotrou ("Süßwasserquarz"), France: *Anomalites fugitivus* (Fri_ 1885).

MESOZOICUM

Upper Cretaceous (> 65 Myr)

A s i a : Kzyl-Zhar, Southern Kazakhstan (Turonian): *Cretaesalus ponomarenkoi* (Nikolajev 1993).

Zheijang Province, Ho Jia, Zhu Xi, China (Turonian?-Santonian): *Prionocephale deplanate* (Lin 1980).

A f r i c a : Orapa, Botswana (Cenomanian-Coniacian): Scarabaeidae (Photo) (McKay & Rayner 1986: 11f).

N o r t h A m e r i c a : Two Medicine Formation, Montana, U.S.A. (Campanian): Coprolithes and fossil soil with nesting traces (Chin & Gill 1996).

S o u t h A m e r i c a : (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* (ichnotaxa) (Roselli 1939, Genise & Cladera 1995, Genise & Laza 1998).

Lower Cretaceous (> 98 Myr)

E u r o p e : 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).

A s i a : 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 1977b, Nikritin 1977, Nikolaev 1992, 1994, 1995b, 1996, 1998a, 1999).

Pad Semen, Argun series, Transbaykalia, Russia: *Proteroscarbaeus yeni, Lithoscarabaeus baissensis* (Nikritin 1977), *Prototrox transbaikalicus* (Nikolaev 2000a).

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).

Shar Tolgoy, Bayan-Hongor Aymag, Mongolia: *Cretocoma tologoica* (Nikolaev 2002)

Myangad, Mongolia: *Holcorobeus longipes* (Ponomarenko 1986).

Bon-Tsagan, Mongolia (U Neocomian – L Aptian): *Cretochodaeus mongolicus*, (*C. striatus*) (Nikolaev 1995a).

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 1992a), *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 1992b), 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)[4]: *Geotrupoides songyingziensis* (Hong 1984).

Jilin Province, China: *Geotrupoides jiaoheensis* (Hong 1992).

S o u t h A m e r i c a : Santana, Brazil: Scarabaeidae (Grimaldi & Maisey 1990: 7; Grimaldi 1991: 400 [colour photo]), some more specimens (Krell, in prep.).

T r a n s i t i o n U p p e r J u r a s s i c / L o w e r C r e t a c e o u s : Khutel-Khara; Mongolia: *Holcorobeus (Mesaclopus) mongolicus* (Nikolaev 1992).

Upper Jurassic (Malm, > 144 Myr)

E u r o p e : Lithographischer Schiefer, Bavaria, Germany (L Tithonian): (*Geotrupoides lithographicus*) (Eichstätt) (Deichmüller 1886), (*Cetonia defossa*), (*Oryctes pluto*) (Solnhofen) (Weyenbergh 1869a).

A s i a : Karatau, Kazakhstan (Oxfordian – Kimmeridgian): *Holcorobeus nigrimontanus* (Nikolaev 1992).

Shara-Teg Mountain, Gov'-Altai' Aymag, Mongolia: *Paralucanus mesozoicus* (Nikolajev 2000b).

Middle Jurassic (Dogger, > 163 Myr)

N o r e l i a b l e r e c o r d s : "*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)

N o r e l i a b l e r e c o r d s : 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)

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[4] ^{40}Ar-^{39}Ar dating gave inconsistent results. According to Smith *et al.* (1995), the entire Yixian Formation is Cretaceous (122 Ma), whereas Lo *et al.* (1999) found it to be Upper Jurassic to Lower Cretaceous (136-155 Ma).

N o r e c o r d s : *Troxites germari* Goldenberg from the hard coals of Saarbrücken, Germany, and the ichnotaxa *Xyloryctes planus* Fri_ and *X. septarius* Fri_ from the Upper Carboniferous of Germany and Bohemia, are no fossils or traces of Scarabaeoidea.

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