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**Catalogue of fossil Scarabaeoidea
(Coleoptera: Polyphaga) of the
Mesozoic and Tertiary
- Version 2007 -**

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Catalogue of fossil Scarabaeoidea (Coleoptera: Polyphaga) of the Mesozoic and Tertiary – Version 2007 –

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Abstract. – A catalogue and bibliography of fossil Scarabaeoidea (Lamellicornia) updated to November 2007 is presented. Of 264 described fossil species, 9 currently are considered as belonging to other taxa and 31 are doubtful due to a limited set of preserved characters. 224 fossil species and 13 ichnospecies probably or reliably belong to the Scarabaeoidea.

The present catalogue of fossil Scarabaeoidea (scarab beetles, chafers, stag beetles and relatives) and their trace fossils is based on a former version published in 2000 in *Invertebrate Taxonomy* (Krell 2000a) and a supplement in Krell (2006). It is updated up to November 2007 and also includes older references that were overlooked in the former versions. All named fossil taxa of Scarabaeoidea are listed according to their current classification (Beutel & Leschen 2005). Of 264 fossil scarabaeoid species described, 224 probably or reliably belong to Scarabaeoidea, 31 are lacking key characters and are considered doubtful, and 9 belong to other taxa. After recent revisions (Genise 2004; Laza 2006), 13 ichnospecies (trace fossils) of Scarabaeoidea are accepted.

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

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Catalogue of named fossil Scarabaeoidea (Lamellicornia)¹

Familia **PARALUCANIDAE** Nikolajev

Paralucaninae Nikolajev 2000b, upgraded to family by Nikolajev 2007b: 13

Genus ***Paralucanus*** Nikolajev

Paralucanus Nikolajev 2000b: S329 (type species by original designation: *Paralucanus mesozoicus* Nikolajev). – Krell 2006: 141; Nikolajev 2007b: 13, 213.

Paralucanus mesozoicus Nikolajev

Paralucanus mesozoicus Nikolajev 2000b: S330 (Upper Jurassic, Shara-Teg, Gov'-Altai' Aymag, Mongolia). – Krell 2006: 133, 141; Nikolajev 2007b: 14f, 213.

Paralucanus mesozoicus. – Nikolajev 2007b: 205.

Familia **LUCANIDAE**

Subfamilia **Protolucaninae** Nikolajev 2007b: 18

Genus ***Protolucanus*** Nikolajev

Protolucanus Nikolajev 2007b: 18, 213 (type species by original designation: *Protolucanus jurassicus* Nikolajev).

Protolucanus jurassicus Nikolajev

Protolucanus jurassicus Nikolajev 2007b: 18f, 213 (U Jura, Anda-Zhuduk, Mongolia).

Subfamilia **Ceruchitinae** Nikolajev 2006b: 133

Genus ***Ceruchites*** Statz

Ceruchites Statz 1952: 5 (type species by monotypy: *Ceruchites hahnei* Statz). – Carpenter 1992: 300; Krell 2000a: 876; Nikolajev 2006b: 133.

Ceruchites hahnei Statz

Ceruchites hahnei Statz 1952: 5 (Oligocene, Rott, Germany). – Sphon 1973: 51; Carpenter 1992: 300; Franciscolo 1997: 50; Krell 2000a: 876; Nikolajev 2006b: 133.

Subfamilia **Lucaninae**

Genus ***Protognathinus*** Chalumeau & Brochier

Protognathinus Chalumeau & Brochier, 2001: 595 (type species by monotypy: *Protognathinus spielbergi* Chalumeau & Brochier). – Krell 2006: 142.

¹ Species lacking diagnostic characters of Scarabaeoidea such as single elytra are in brackets. A genus name in brackets indicates that the generic placement of the species is doubtful. Abbreviations: L: Lower, M: Middle, U: Upper.

Protognathinus spielbergi Chalumeau & Brochier

Protognathinus spielbergi Chalumeau & Brochier, 2001: 595 (Eocene, Grube Messel, Germany). – Brauckmann & Gröning 2003; Krell 2006: 122f, 142.

Genus ***Cretolucanus*** Nikolajev

Cretolucanus Nikolajev 2007b: 21, 213 (type species by original designation: *Cretolucanus longus* Nikolajev).

Cretolucanus longus Nikolajev

Cretolucanus longus Nikolajev 2007b: 22f, 205, 213 (L Cretaceous, Pad Semen, Russia).

Cretolucanus ordinarius Nikolajev

Cretolucanus ordinarius Nikolajev 2007b: 22, 24, 213 (L Cretaceous, Pad Semen, Russia).

Cretolucanus sibericus Nikolajev

Cretolucanus sibericus Nikolajev 2007b: 22, 25, 213 (L Cretaceous, Pad Semen, Russia).

Lucanus fossilis Wickham

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

Only one elytron, but of typical lucanid shape.

(*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 1914: 716; Houlbert 1915: 6; Nikolajev 1990: 121 (transl. p. 119) (generic and even family affiliation doubtful; may belong near *Ceruchus*); Maes 1992: 14; Franciscolo 1997: 50; Krell 2000a: 875.

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

Platycerus zherichini Nikolajev

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

Platycerus zherichini. – Franciscolo 1997: 50.

Genus ***Succiniplatycerus*** Nikolajev

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

According to Larsson (1978: 152) Zang "describes a total of 5 species of *Systemocerus*" 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) Nikolajev

Platycerus berendti Zang 1905: 199 (Eocene, Baltic Amber). – Bibliography: Spahr 1981: 65; additional: Hieke & Pietrzeniuk 1984: 313.

Platycerus berendtii. – Maes 1992: 12.

Succiniplatycerus berendti. – Nikolajev 1990: 122 (1991: 120); Franciscolo 1997: 49f; Krell 2000a: 875.

Dorcus (Eurytrachelus) primigenius Deichmüller

Dorcus (Eurytrachelus) primigenius Deichmüller 1881: 303, pl. 21 (Eocene, Kučlín [Kutschlin] near Bílina [Bilin], Czech Republic). – Leuthner 1885: 482; Scudder 1891: 514; Počta 1900: 265; Handlirsch 1907: 842; Houlbert 1914: 716; Houlbert 1915: 6; Říha 1979: 26; Maes 1992: 92; Franciscolo 1997: 50; 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 **Aesalinae**

Genus ***Cretaesalus*** Nikolajev

Cretaesalus Nikolajev 1993: 90 (type species by original designation: *Gretaesalus ponomarenkoi* Nikolajev [lapsus calami for *Cretaesalus*]). – Nikolajev 1999: 178; Krell 2000a: 875; Nikolajev 2002: 54 (transl. p. 281); Nikolajev 2005b: 113; Nikolajev 2007b: 26, 213.

Cretaesalus ponomarenkoi Nikolajev

Cretaesalus ponomarenkoi Nikolajev 1993: 90 (U Cretaceous, Kzyl-Zhar, Kazakhstan). – Franciscolo 1997: 50; Krell 2000a: 875; Nikolajev 2007b: 26f, 206, 213.

Subfamilia **Syndesinae**

Ceruchus fuchsii Wickham

Ceruchus fuchsii Wickham 1911: 58 (Oligocene, Florissant, U.S.A.). – Wickham 1920: 358; Rodeck 1938: 293; Maes 1992: 11; Franciscolo 1997: 50; Krell 2000a: 875.

Subfamilia **incerta**

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: 179.

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 subsequent 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; Franciscolo 1997: 49; Krell 2000a: 876.

Dorcasoides nigrescens. – Motschulsky 1856: pl. (lapsus calami? – see Scudder 1891: 513); Franciscolo 1997: 49.

Dorcasoides bibolus. – Houlbert 1914: 716; Houlbert 1915: 6.

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; Franciscolo 1997: 50; 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; Franciscolo 1997: 49f.

Palaeognathus succinifer. – Leuthner 1885: 482.

Paläognathus succini. – Handlirsch 1908: 1356.

Paleognathus succini. – Laurentiaux 1953: 477.

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; Krell 2006: 133.

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 **LITHOSCARABAEIDAE** Nikolajev

Lithoscarabaeinae Nikolajev 1992: 76 (transl. p. 96), upgraded to family by Nikolajev 2007b: 41.

Genus *Baisarabaeus* Nikolajev

Baisarabaeus Nikolajev 2005a: 117 (type species by original designation: *Baisarabaeus rugosus* Nikolajev). – Krell 2006: 143; Nikolajev 2007b: 44, 47, 213.

Baisarabaeus rugosus Nikolajev

Baisarabaeus rugosus Nikolajev 2005a: 119 (L Cretaceous, Baysa, Russia). – Krell 2006: 143; Nikolajev 2007b: 45f, 213, 220.

Genus ***Lithoscarabaeus*** Nikolajev

Lithoscarabaeus Nikolajev 1992: 78 (transl. p. 97) (type species by original designation: *Proteroscarabaeus baissensis* Nikritin). – Nikolajev 1999: 178; Krell 2000a: 888; Nikolajev 2002: 54 (transl. p. 281); Nikolajev 2005a: 118; Nikolajev 2005b: 113; Nikolajev 2007b: 43, 213.

Lithoscarabaeus baissensis (Nikritin) Nikolajev

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

Proteroscarabaeus daissensis. – Morón 2003: 12.

Lithoscarabaeus baissensis. – Nikolajev 1992: 78 (transl. p. 97); Krell 2000a: 888; Nikolajev 2007b: 41, 43f, 47, 131, 207, 213, 220.

Familia **TROGIDAE*****Trox antiquus*** Wickham

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

Trox cretaceus Nikolajev

Trox cretaceus Nikolajev 2007b: 102f, 105, 206, 215 (L Cretaceous, Bon-Tsagan, Mongolia).

(*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).

Trox sibericus Nikolajev

Trox sibericus Nikolajev 2007b: 104f, 215, 220 (L Cretaceous, Baysa, Russia).

Genus ***Cretomorgus*** Nikolajev²

Cretomorgus Nikolajev 2007b: 106, 215 (type species by original designation: *Cretomorgus ikhbogdensis* Nikolajev).

Cretomorgus ikhbogdensis Nikolajev

Cretomorgus ikhbogdensis Nikolajev 2007b: 107f, 215 (L Cretaceous, Shar-Tologoy, Mongolia).

² Belongs to Omorginae Nikolajev 2005 according to Nikolajev (2007: 106).

Subfamilia **Prototroginae** Nikolajev 2000: 63 (transl. p. 426)³

Genus **Prototrox** Nikolajev

Prototrox Nikolajev 2000a: 65 (transl. p. 427) (type species by original designation: *Prototrox transbaikalicus* Nikolajev). – Nikolajev 1999: 178 (nomen nudum); Krell 2000a: 890 (nomen nudum); Nikolajev 2002: 54 (transl. p. 281); Nikolajev 2005a: 118; Krell 2006: 141; Nikolajev 2007b: 67, 214.

Prototrox transbaikalicus Nikolajev

Prototrox transbaikalicus Nikolajev 2000a: 65 (transl. p. 428) (Lower Cretaceous, Argun' formation, Semen Creek, Olengui River basin, Chita District, Transbaikalia, Russia. Paratype: Barremian–Aptian, Bon-Tsagan series, Bayan-Hongor Aymag, Mongolia). – Krell 2006: 141; Nikolajev 2007b: 67f, 209, 214.

Subfamilia **Avitortorinae** Nikolajev 2007b: 110

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; Nikolajev 1992: 80 (transl. p. 101) (Scarabaeidae); Nikolajev 1999: 178; Krell 2000a: 888; Nikolajev 2002: 54 (transl. p. 281); Nikolajev 2005a: 117; Nikolajev 2007b: 105, 110f, 215.

Avitortor dolchiodactylus Nikolajev

Avitortor dolchiodactylus Nikolajev 2007b: 118, 208, 215 (L Cretaceous, Bon-Tsagan, Mongolia).

Avitortor leptoscelis (Nikritin) Nikolajev

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. – Nikolajev 1992: 80 (transl. p. 101); Krell 2000a: 888; Nikolajev 2007b: 116f [117: one specimen was misidentified as *Geotrupoides sulcatus* Nikritin], 209, 215, 220.

Avitortor ovalis Nikolajev

Avitortor ovalis Nikolajev 2007b: 113f, 215, 220 (L Cretaceous, Baysa, Russia).

Avitortor parallelus Nikolajev

Avitortor parallelus Nikolajev 2007b: 114f, 209, 215 (L Cretaceous, Bon-Tsagan, Mongolia).

Avitortor primitivus Ponomarenko

Avitortor primitivus Ponomarenko 1977b: 42 (1991b: 55) (L Cretaceous, Baysa, Russia). – Nikolajev 1992: 80 (transl. p. 101) (Scarabaeidae); Krell 2000a: 888; Nikolajev 2007b: 112, 208, 215, 220.

³ According to Nikolajev (2007:66) subfamily of Eremazidae Iablokoff-Khnzorian 1977 which he upgraded to family.

(Family **GLARESIDAE**)(Genus ***Aphodiites*** Heer)

Aphodiites Heer 1865: 90, pl. 8 (type species by monotypy: *Aphodiites protogaesus* Heer). – Scudder 1886: 73; Crowson 1981: 664 (“Possible Scarabaeoids”), 679 (“probably attributable to this superfamily”); Dellacasa 1988: 361; Paulian 1988: 390; Cambefort 1991: 51 (“undifferentiated 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”); Nikolajev 1998b: 30; Browne & Scholtz 1999: 54 (“Glaresidae-like”); Krell 2000a: 874; Nikolajev 2007b: 70, 217.

(*Aphodiites protogaesus* Heer)

Aphodiites protogaesus 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; Krell 2000c: (4); Krell 2006: 124f; Nikolajev 2007b: 70, 217.

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

Doubful (no appendages present).

***Glaresis cretacea* Nikolajev**

Glaresis cretacea Nikolajev 2007b: 71, 76, 214, 220 (L Cretaceous, Baysa, Russia).

Genus ***Cretoglaresis*** Nikolajev

Cretoglaresis Nikolajev 2007b: 72, 214 (type species by original designation: *Cretoglaresis nana* Nikolajev).

***Cretoglaresis nana* Nikolajev**

Cretoglaresis nana Nikolajev 2007b: 73, 210, 214, 220 (L Cretaceous, Baysa, Russia).

Genus ***Lithoglaresis*** Nikolajev

Lithoglaresis Nikolajev 2007b: 74, 214 (type species by original designation: *Lithoglaresis ponomarenkoi* Nikolajev).

***Lithoglaresis ponomarenkoi* Nikolajev**

Lithoglaresis ponomarenkoi Nikolajev 2007b: 74–76, 211, 214, 220 (L Cretaceous, Baysa, Russia).

Familia **PLEOCOMIDAE**Genus ***Proteroscarabaeus*** Grabau

Proteroscarabaeus Grabau 1923: 173 (type species by original designation: *Proteroscarabaeus yeni* Grabau). – Ping 1928: 18; Crowson 1974: 68 (“suggestive of Hybosoridae. If it is truly Scarabaeid, then it has possible affinities to [...] Aclopininae”); Nikritin 1977: 124 (1991: 168); Lin 1980: 230; Crowson 1981: 667 (“modern-looking Scarabeoids”); Ponomarenko 1990: 66; Carpenter 1992: 301; Nikolajev 1996: 91 (transl. p. 217) 1999: 178; Krell 2000a: 876; Nikolajev 2002: 54 (transl. p. 281); Tan *et al.* 2004: 683, 685; Nikolajev 2005a: 118; Nikolajev 2005b: 113; Nikolajev 2007b: 31f, 195, 213.

Proteroscarabaeus: 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; Nikolajev 2007b: 33f, 213, 220.

Doubtful (only one elytron).

(*Proteroscarabaeus nikritini* Nikolajev)

Proteroscarabaeus nikritini Nikolajev 1996: 93 (transl. p. 217) (L Cretaceous, Baysa, Russia). – Krell 2000a: 876; Nikolajev 2007b: 33, 213, 220.

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; Krell 2006: 129; Nikolajev 2007b: 213.

***Proteroscarabaeus yeni* Grabau**

Proteroscarabaeus yeni Grabau 1923: 175 (L Cretaceous, Laiyang, China). – Anonymous 1924: 311; 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-Khuzorian 1977: 137; Morón Ríos 1984: 117; Hong & Wang 1990: 114f; Carpenter 1992: 301; Zhang 1992b: 134; Nikolajev 1992: 79 (transl. p. 99); Lin 1994: 305; Nikolajev 1996: 94 (transl. p. 219); Krell 2000a: 876; Morón 2003: 12; Tan *et al.* 2004: 683; Krell 2006: 129, 133; Nikolajev 2007b: 32, 34, 213.

Subfamilia ***Cretocominae*** Nikolajev

Cretocomini Nikolajev 2002: 53 (transl. p. 281), upgraded to subfamily by Krell 2006: 142.

Genus ***Cretocoma*** Nikolajev

Cretocoma Nikolajev 2002: 54 (transl. p. 281) (type species by original designation: *Cretocoma tologoica*). – Krell 2006: 142; Nikolajev 2007b: 36, 38, 206, 213.

***Cretocoma tologoica* Nikolajev**

Cretocoma tologoica Nikolajev 2002: 54 (transl. p. 281) (L Cretaceous, Shar-Tologoy, Bayan-Hongor Aymag, Mongolia). – Krell 2006: 142; Nikolajev 2007b: 35–37, 213.

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; Nikolajev 1998b: 30; Krell 2000a: 877; Tan *et al.* 2004: 685; Nikolajev 2007b: 142, 217.

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

Geotrupoides fortus Ren *et al.* 1995: 436 (L Cretaceous, Chifeng City, Inner Mongolia, China). – Krell 2000a: 877; Nikolajev 2007b: 217.

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.

Geotrupoides jiaohensis. – Nikolajev 2007b: 217.

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; Nikolajev 2007b: 217.

Geotrupoides 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; Nikolajev 2007b: 217.

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; Nikolajev 2007b: 217.

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; Nikolajev 2007b: 217.

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 species by original designation: *Cretogeotrupes convexus* Nikolajev). – Nikolajev 1999: 178; Krell 2000a: 878; Nikolajev 2002: 54 (transl. p. 281); Nikolajev 2005a: 117; Nikolajev 2007b: 98, 215.

Cretogeotrupes convexus Nikolajev

Cretogeotrupes convexus Nikolajev 1992: 81 (transl. p. 102) (L Cretaceous, Baysa, Russia). – Krell 2000a: 878; Krell 2006: 133; Nikolajev 2007b: 99, 215, 220.

Familia **BOLBOCERATIDAE*****Bolboceras inermis*** Piton

Bolboceras inermis Piton 1940: 175 (Palaeocene, Menat, France). – Krell 2000a: 876.

Genus ***Cretobolbus*** Nikolajev

Cretobolbus Nikolajev 1996: 95 (transl. p. 221) (type species by original designation: *Cretobolbus rohdendorfi* Nikolajev). – Nikolajev 1999: 178; Krell 2000a: 876; Nikolajev 2002: 54 (transl. p. 281); Nikolajev 2005a: 118; Nikolajev 2005b: 113; Nikolajev 2007b: 94, 214.

Cretobolbus rohdendorfi Nikolajev

Cretobolbus rohdendorfi Nikolajev 1996: 96 (transl. p. 222) (L Cretaceous, Baysa, Russia). – Krell 2000a: 876; Krell 2006: 133; Nikolajev 2007b: 95, 210, 214, 220.

Familia **OCHODAEIDAE**

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

Genus ***Cretochodaeus*** Nikolajev

Cretochodaeus Nikolajev 1995a: 79 (type species by original designation: *Cretochodaeus mongolicus* Nikolajev). – Nikolajev 1999: 178; Krell 2000a: 878; Nikolajev 2002: 54 (transl. p. 281); Nikolajev 2005a: 117; Nikolajev 2007b: 62, 214.

Cretochodaeus mongolicus Nikolajev

Cretochodaeus mongolicus Nikolajev 1995a: 79 (L Cretaceous, Bon-Tsagan, Mongolia). – Krell 2000a: 878; Nikolajev 2007b: 62f, 207, 214.

(*Cretochodaeus striatus* Nikolajev)

Cretochodaeus striatus Nikolajev 1995a: 80 (L Cretaceous, Bon-Tsagan, Mongolia). – Krell 2000a: 878; Nikolajev 2007b: 60, 64.

Cretochodaeus striatulus. – Nikolajev 2007b: 214.

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

Genus ***Miochodaeus*** Nikolajev

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

Miochodaeus proaevus (Germar) Nikolajev

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.

Miochodaeus proaevus. – Nikolajev 1995a: 81; Krell 2000a: 878.

Subfamilia **Ochodaeinae**Genus ***Lithochodaeus*** Nikolajev

Lithochodaeus Nikolajev 2007b: 58, 214 (type species by original designation: *Lithochodaeus cretaceus* Nikolajev).

Lithochodaeus cretaceus Nikolajev

Lithochodaeus cretaceus Nikolajev 2007b: 59, 214 (L Cretaceous, Bon-Tsagan, Mongolia).

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.

Coprologus. – 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; Nikolajev 1996: 96 (transl. p. 222) (doubts the former classification as belonging to the Bolboceratidae, "presumably belongs to the Hybosoridae"); Krell 2000a: 878.

Coprologus gracilis. – Giebel 1852b: 653.

Genus ***Procoilodes*** Ocampo

Procoilodes Ocampo, 2002: 123 (type species by original designation: *Procoilodes adrastus* Ocampo). – Krell 2006: 142.

Procoilodes adrastus Ocampo

Procoilodes adrastus Ocampo, 2002: 125 (Miocene, Dominican Amber). – Krell 2006: 142.

Genus ***Tyrannasorus*** Ratcliffe & Ocampo

Tyrannasorus Ratcliffe & Ocampo, 2001: 351 (type species by original designation: *Tyrannasorus rex* Ratcliffe & Ocampo). – Krell 2006: 142.

Tyrannasorus rex Ratcliffe & Ocampo

Tyrannasorus rex Ratcliffe & Ocampo, 2001: 353 (Miocene, Dominican Amber). – Ocampo 2002: 123; Krell 2006: 142.

Subfamilia **Anaidinae** Nikolajev(Genus ***Cretanoides*** Nikolajev)

Cretanoides Nikolajev 1996: 94 (transl. p. 219) (type species by original designation: *Cretanoides trogopterus* Nikolajev). – Nikolajev 1999: 178; Krell 2000a: 878; Nikolajev 2002: 54 (transl. p. 281); Nikolajev 2005a: 118; Nikolajev 2007b: 87, 214.

(***Cretanoides trogopteris*** Nikolajev)

Cretanoides trogopteris Nikolajev 1996: 95 (transl. p. 220) (L Cretaceous, Baysa, Russia). – Krell 2000a: 878; Nikolajev 2007b: 88, 214, 220.
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; Nikolajev 2002: 54 (transl. p. 281); Nikolajev 2005a: 117; Nikolajev 2005d: 27; Nikolajev 2007b: 81, 214.

Cretohybosorus buryaticus Nikolajev

Cretohybosorus buryaticus Nikolajev 1999: 179 (L Cretaceous, Baysa, Russia). – Krell 2000a: 878; Nikolajev 2007b: 80, 82f, 208, 214, 220.

Cretohybosorus striatulus Nikolajev

Cretohybosorus striatulus Nikolajev 1999: 179 (L Cretaceous, Baysa, Russia). – Krell 2000a: 878; Nikolajev 2005d: 27; Nikolajev 2007b: 80, 84, 214, 220.

Hybosorus lividus Heer

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

Genus ***Jurahybosorus*** Nikolajev

Jurahybosorus Nikolajev 2005d: 27 (type species by original designation: *Jurahybosorus mongolicus* Nikolajev). – Krell 2006: 142; Nikolajev 2007b: 79, 214.

Jurahybosorus mongolicus Nikolajev

Jurahybosorus mongolicus Nikolajev 2005d: 27 (U Jurassic, Bayan-Teg, Mongolia). – Krell 2006: 133, 142; Nikolajev 2007b: 80f, 214.

Genus ***Leptosorus*** Nikolajev

Leptosorus Nikolajev 2006a: 12 (type species by original designation: *Leptosorus zherikhini* Nikolajev). – Nikolajev 2007b: 85, 214.

Leptosorus zherikhini Nikolajev

Leptosorus zherikhini Nikolajev 2006a: 13 (L Cretaceous, Baysa, Russia). – Nikolajev 2007b: 80, 85f, 208, 214, 220.

Phaeochrous tertiarium (Deichmüller) Nikolajev

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

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

Subfamilia **Mimaphodiinae** Nikolajev 2007aGenus **Mimaphodius** Nikolajev

Mimaphodius Nikolajev 2007a (type species: *Mimaphodius pusillus* Nikolajev). – Nikolajev 2007b: 90, 214.

Mimaphodius pusillus Nikolajev

Mimaphodius pusillus Nikolajev 2007a (L Cretaceous, Baysa, Russia). – Nikolajev 2007b: 90, 214, 220.

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.

Subfamilia **Cretoglaphyrinae** Nikolajev

Cretoglaphyrini Nikolajev 2005c: 70; upgraded to subfamily by Krell 2006: 142.

Genus **Cretoglaphyrus** Nikolajev

Cretoglaphyrus Nikolajev 2005c:70 (type species by original designation: *Cretoglaphyrus rohdendorfi* Nikolajev). – Krell 2006: 133, 142; Nikolajev 2007b: 44, 49, 213.

(*Cretoglaphyrus calvescens* Nikolajev)

Cretoglaphyrus calvescens Nikolajev 2005c: 73 (L Cretaceous, Pad Semen, Russia). – Krell 2006: 142; Nikolajev 2007b: 50–52, 213.
Doubtful (only one elytron).

(*Cretoglaphyrus leptopterus* Nikolajev)

Cretoglaphyrus leptopterus Nikolajev 2005c: 73 (L Cretaceous, Pad Semen, Russia). – Krell 2006: 142; Nikolajev 2007b: 50f, 213.
Doubtful (only one elytron).

Cretoglaphyrus olenguicus Nikolajev

Cretoglaphyrus olenguicus Nikolajev 2005c: 75 (L Cretaceous, Pad Semen, Russia). – Krell 2006: 142; Nikolajev 2007b: 53f, 213.

Cretoglaphyrus rohdendorfi Nikolajev

Cretoglaphyrus rohdendorfi Nikolajev 2005c: 72 (L Cretaceous, Baysa, Russia). – Krell 2006: 142; Nikolajev 2007b: 50f, 213.

(*Cretoaglaphyrus transbaikalicus* Nikolajev)

Cretoaglaphyrus transbaikalicus Nikolajev 2005c: 73 (L Cretaceous, Pad Semen, Russia). – Krell 2006: 142; Nikolajev 2007b: 51f, 213.

Doubtful (only one elytron).

***Cretoaglaphyrus zherikhini* Nikolajev**

Cretoaglaphyrus zherikhini Nikolajev 2005c: 74 (L Cretaceous, Pad Semen, Russia). – Krell 2006: 142; Nikolajev 2007b: 51, 53, 55, 207, 213, 220.

Familia **SCARABAEIDAE**Subfamilia **Aphodiinae**Tribus **Aegialiini*****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* Nikolajev**

Cretaegialia Nikolajev 1994: 5 (type species by original designation: *Cretaegialia rhypariformis* Nikolajev). – Nikolajev 1999: 178; Krell 2000a: 880; Nikolajev 2002: 54 (transl. p. 281); Nikolajev 2005a: 118; Nikolajev 2005b: 113; Krell 2006: 133; Nikolajev 2007b: 123, 215.

***Cretaegialia aphodiiformis* Nikolajev**

Cretaegialia aphodiiformis Nikolajev 1994: 7 (L Cretaceous, Baysa, Russia). – Krell 2000a: 880; Nikolajev 2007b: 126f, 210, 221.

Cretaegialia aphodiiformes. – Nikolajev 2007b: 214.

***Cretaegialia rhypariformis* Nikolajev**

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

Cretaegialia rhypariformis Nikolajev 1994: 6 (L Cretaceous, Baysa, Russia). – Krell 2000a: 880; Nikolajev 2007b: 124, 210, 221.

Cretaegialia rhypariformes. – Nikolajev 2007b: 214.

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 Łomnicki

Aphodius boryslavicus Łomnicki 1894: 83, pl. 7 (Pleistocene, Borysław, Poland). – Krell 2000a: 881; Krell 2006: 132.

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 description sensu Art. 12 ICZN]. – Schmidt 1910: 140 (“*Aphod.? Bosniaskii*”).

Aphodius bosniaskii. – Dellacasa 1983: 29; Dellacasa 1988: 400; Krell 2000a: 881; Dellacasa & Dellacasa 2006: 14.

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 (Palaeocene, Menat, France). – Krell 2000a: 881; Krell 2006: 133.

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; Daeschler *et al.* 1993: 31; Krell 2000a: 881; Krell 2006: 132.

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

Aphodius rhinocerontis Łomnicki

Aphodius rhinocerontis Łomnicki 1894: 81, pl. 7 (Pleistocene, Borysław, Poland). – Krell 2000a: 881; Krell 2006: 132.

Aphodius ruthenus Łomnicki

Aphodius ruthenus Łomnicki 1894: 82, pl. 7 (Pleistocene, Borysław, Poland). – Krell 2000a: 882; Krell 2006: 132.

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 Łomnicki

Aphodius subater Łomnicki 1894: 80, pl. 7 (Pleistocene, Borysław, Poland). – Krell 2000a: 882; Krell 2006: 132.

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; Krell 2006: 121.

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.

Tribus **Aulonocnemini**Genus ***Protopalnia*** Nikolajev

Protopalnia Nikolajev 2007b: 128, 215 (type species by original designation: *Protopalnia magadanica* Nikolajev).

Protopalnia magadanica Nikolajev

Protopalnia magadanica Nikolajev 2007b: 129, 215 (U Cretaceous, Obeshchayushchiy, Magadanskaya Oblast, Russia).

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; Krell 2006: 132.

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

Choeridium? [= *Ateuchus*] *ebenium* Horn. – Daeschler *et al.* 1993: 31.

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; Krell 2006: 132.

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.

Heliocoprís antiquus Fujiyama

Heliocoprís 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.

Genus ***Cretonitis*** Nikolajev

Cretonitis Nikolajev 2007b: 131 (type species by original designation: *Cretonitis copripes* Nikolajev).

Cretonitis copripes Nikolajev

Cretonitis copripes Nikolajev 2007b: 132, 221 (L Cretaceous, Baysa, Russia).

Cretonitis ikhbogdensis Nikolajev. – Nomen nudum, lapsus calami, Nikolajev 2007: 214.

(***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). Heyden may have confused 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; Krell 2006: 132.

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; Krell 2006: 132.

Phanaeus antiquum Horn. – Daeschler *et al.* 1993: 31.

Phanaeus labrae (Pierce) Miller

Palaeocopris labrae 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 labrae. – Halffter 1959: 176.

Phanaeus labrae. – Miller *et al.* 1981: 627; Krell 2000a: 880; Krell 2006: 132.

Genus ***Prionocephale*** Lin

Prionocephale Lin 1980: 230 (type species by original designation: *Prionocephale deplanate* Lin). – Krell 2000a: 880; Paetel 2001: 234; Nikolajev 2007b: 130, 215.

Prionocephale deplanate Lin

Prionocephale deplanate Lin 1980: 230 (U Cretaceous, Zheijiang, China). – Lin 1994: 314; Krell 2000a: 880; Krell 2006: 131, 133; Nikolajev 2007b: 214.

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 **Aclopinae**Tribus **Aclopini**Genus ***Cretaclopus*** Nikolajev

Cretaclopus Nikolajev 2004: 35 (type species by original designation: *Geotrupoides longipes* Ponomarenko). – Krell 2006: 128f, 142; Nikolajev 2007b: 175, 216.

Cretaclopus longipes (Ponomarenko) Nikolajev

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

Holcorobeus (Holcorobeus) longipes. – Nikolajev 1992: 83 (transl. p. 104); Krell 2000a: 889.

Cretaclopus longipes. – Nikolajev 2004: 35; Nikolajev 2007b: 176, 216.

Genus ***Juraclopus*** Nikolajev

Juraclopus Nikolajev 2005b: 112 (type species: *Juraclopus rohdendorfi* Nikolajev). – Nikolajev 2004: 34 [as "in litt." and figured]; Krell 2006: 128, 142; Nikolajev 2007b: 173, 180, 216.

Juraclopus rohdendorfi Nikolajev

Juraclopus rohdendorfi Nikolajev 2005b:113 (Fig. 2) (U Jurassic, Karatau, Kazakhstan). – Nikolajev 2004: 34 [as "in litt." and figured]; Krell 2006: 124f, 133, 142; Nikolajev 2007b: 173f, 177, 212, 216.

Tribus **Holcorobeini** Nikolajev 1992: 81 (transl. p. 102)
(classified as tribe of Aclopinae by Nikolajev 2004)

Genus ***Antemnacrassa*** Gomez Pallerola

Antemnacrassa Gomez Pallerola 1979: 340 (type species by monotypy: *Antemnacrassa monreali* Gomez Pallerola). – Nikolajev 2004: 38 (removed from synonymy); Nikolajev 2005a: 117; Krell 2006: 142; Nikolajev 2007b: 142, 144, 151, 171, 173, 178, 216.

Antemnocrassa – Nikolajev 1992: 82 (synonymi of *Holcorobeus* Nikritin).

(*Antemnacrassa albomaculata* Nikolajev)

Antemnacrassa albomaculata Nikolajev 2004: 42 (L Cretaceous, Shar-Tologoy, Bayan-Leg, Mongolia). – Krell 2006: 143; Nikolajev 2007b: 144, 168, 216.

Doubful (only one elytron).

Antemnacrassa albosulcata Nikolajev

Antemnacrassa albosulcata Nikolajev 2004: 39 (U Jurassic, Karatau, Kazakhstan). – Krell 2006: 124, 143; Nikolajev 2007b: 144, 154f, 177, 216.

(*Antemnacrassa geminata* Nikolajev)

Antemnacrassa geminata Nikolajev 2004: 41 (L Cretaceous, Pad Semen, Russia). – Krell 2006: 143; Nikolajev 2007b: 144, 166, 216.

Doubful (only one elytron).

Antemnacrasa incerta (Ponomarenko) Nikolajev

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

Holcorobeus (Holcorobeus) incertus. – Nikolajev 1992: 83 (transl. p. 104); Krell 2000a: 889.

Antemnacrasa incerta. – Nikolajev 2004: 41; Krell 2006: 142; Nikolajev 2007b: 152, 169, 216.

Antemnacrasa kazakhstanica Nikolajev

Antemnacrasa kazakhstanica Nikolajev 2007b: 156f, 216 (U Jura, Karatau, Kazakhstan).

Antemnacrasa latitibialis (Nikolajev) Nikolajev

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

Antemnacrasa latitibialis. – Nikolajev 2007b: 163f, 216, 221.

Antemnacrasa maculata (Nikolajev) Nikolajev

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

Antemnacrasa maculata. – Nikolajev 2004: 40; Krell 2006: 142; Nikolajev 2007b: 162f, 211, 216, 221.

(*Antemnacrasa magna* Nikolajev)

Antemnacrasa magna Nikolajev 2004: 41 (L Cretaceous, Baysa, Russia). – Krell 2006: 143; Nikolajev 2007b: 144, 165, 216, 221.

Doubful (only one elytron).

Antemnacrasa monreali Gomez Pallerola

Antemnacrasa monreali Gomez Pallerola 1979: 340 (L Cretaceous, Montsec, Spain). – Gomez Pallerola 1986: 720f; Nikolajev 2004: 38; Nikolajev 2007b: 151, 216.

Holcorobeus (Holcorobeus) monreali. – Nikolajev 1992: 83 (transl. p. 104); Krell 2000a: 889.

(*Antemnacrasa nebulosa* Nikolajev)

Antemnacrasa nebulosa Nikolajev 2004: 41 (L Cretaceous, Baysa, Russia). – Krell 2006: 143; Nikolajev 2007b: 144, 165, 216, 221.

Doubful (only one elytron).

Antemnacrasa nigrimontana (Nikolajev) Nikolajev

Holcorobeus nigrimontanus Nikolajev 1992: 83 (transl. p. 105) (U Jurassic, Karatau, Kazakhstan). – Krell 2000a: 889; Krell 2000c: (4); Grimaldi & Engel 2004 380; Krell 2006: 142.

Antemnacrasa nigrimontana. – Nikolajev 2004: 38; Krell 2006: 124; Nikolajev 2007b: 152f, 177, 216.

Antemnacrasa picturata (Nikritin) Nikolajev

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

Holcorobeus (Holcorobeus) picturatus. – Nikolajev 1992: 83 (transl. p. 104); Krell 2000a: 889.

Antemnacrasa picturata. – Nikolajev 2004: 40; Krell 2006: 142; Nikolajev 2007b: 158, 216, 221.

Antemnacrasa punctata (Ponomarenko) Nikolajev

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

Holcorobeus (Holcorobeus) punctatus. – Nikolajev 1992: 83 (transl. p. 104); Krell 2000a: 889.

Antemnacrasa punctata. – Nikolajev 2004: 42; Krell 2006: 142; Nikolajev 2007b: 167, 216.

Antemnacrasa sulcata (Nikritin) Nikolajev

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. – Nikolajev 1992: 83 (transl. p. 104); Krell 2000a: 889.

Antemnacrasa sulcata. – Nikolajev 2004: 40; Nikolajev 2007b: 151f, 159f, 209, 216, 221.

Antemnacrasa vitimensis (Nikritin) Nikolajev

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

Holcorobeus vitimensis. – Nikolajev 1992: 83 (transl. p. 104); Krell 2000a: 889.

Antemnacrasa vitimensis. – Nikolajev 2004: 40; Krell 2006: 142; Nikolajev 2007b: 161f, 216, 221.

Genus ***Holcorobeus*** Nikritin

Holcorobeus Nikritin 1977: 127 (1991: 172) [*"Holcoribeus"*, lapsus calami, since all species are named *Holcorobeus*] (type species: *Holcorobeus vittatus* Nikritin). – Crowson 1981: 667 ("modern-looking Scarabeoids"); Schlüter 1987: 133; Nikolajev 1992: 82 (transl. p. 103); Nikolajev 1998b (classified as Aclopininae, but without giving an explanation); Nikolajev 1999: 178; Jarzembowski 2000: (8); Krell 2000a: 889; Nikolajev 2002: 54 (transl. p. 281); Nikolajev 2004: 36; Nikolajev 2005a: 118; Nikolajev 2005b: 112, 114; Nikolajev 2007b: 142, 145, 149–151, 173, 177f, 216.

Holcoribeus Nikritin (see above). – Ponomarenko 1990: 68; Carpenter 1992: 300 ("Family assignment doubtful"); Tan *et al.* 2004: 685.

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

Holcorobeus atosulcatus Nikolajev

Holcorobeus (Holcorobeus) atosulcatus Nikolajev 1992: 84 (transl. p. 106) (L Cretaceous, Baysa, Russia). – Krell 2000a: 889; Nikolajev 2007b: 144, 147f, 216, 221.

Holcorobeus atosulcatus. – Nikolajev 2004: 37.

Holcorobeus evittatus Zhang

Holcoribeus evittatus Zhang 1992a: 334 (L Cretaceous, Laiyang Formation, China). – Krell 2000a: 889; Nikolajev 2007b: 216.

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

(*Holcorobeus nigrovittatus* Nikolajev)

Holcorobeus nigrovittatus Nikolajev 1992: 86 (transl. p. 108) (L Cretaceous, Baysa, Russia). – Krell 2000a: 889; Nikolajev 2004: 37; Nikolajev 2007b: 144, 148, 216, 221.

Doubtful (only one elytron).

Holcorobeus vittatus Nikritin

Holcorobeus vittatus Nikritin 1977: 128 (1991: 173) (L Cretaceous, Baysa, Russia). – Nikolajev 1992: 83 (transl. p. 104); Krell 2000a: 890; Ponomarenko 2002: 182; Grimaldi & Engel 2004: 380; Nikolajev 2004: 36; Nikolajev 2007b: 145–147, 216, 221.

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

Holcorobaeus vittatus. – Nikolajev 2007b: 212.

Genus **Mesaclopus** Nikolajev

Mesaclopus Nikolajev 1992: 86 (transl. p. 108) (as subgenus of *Holcorobeus*; type species by original designation: *Holcorobeus mongolicus* Nikolajev). – Krell 2000a: 890; Nikolajev 2004: 42 (upgraded to genus); Nikolajev 2007b: 142f, 170, 216.

Mesaclopus mongolicus (Nikolajev) Nikolajev

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

Mesaclopus mongolicus. – Nikolajev 2004: 42; Nikolajev 2007b: 171, 216.

Genus **Mongolrobeus** Nikolajev

Mongolrobeus Nikolajev 2004: 37 (type species by original designation: *Mongolrobeus zherikhini* Nikolajev). – Krell 2006: 142; Nikolajev 2007b: 142, 149, 216.

Mongolrobeus zherikhini Nikolajev

Mongolrobeus zherikhini Nikolajev 2004: 37 (L Cretaceous; Dund-Uul, Bon-Tsagan, Bayan-Hongor Aymag, Mongolia). – Krell 2006: 142; Nikolajev 2007b: 150, 178, 216.

Subfamilia **Euchirinae****Cheirotonus otai** Ueda

Cheirotonus otai Ueda 1989: 107 (Miocene, Tottori, Japan). – Krell 2000a: 887; Krell 2006: 133.

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 subsequent designation by Krell (2000: 882): *Eophyllocerus scrobiculatus* Haupt). – Crowson 1981: 680; Scholtz & Chown 1995: 364; Krell 2000a: 882; Krell 2006: 122.

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; Krell 2006: 122.

Macroductylus pluto Wickham

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

Macroductylus propheticus Wickham

Macroductylus 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, Mokřina [Krottensee] near Kynšperk n. O., Czech Republic). – Scudder 1891: 552; Počta 1900: 264; Handlirsch 1907: 840; Říha 1977: 22; Říha 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 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 1936a: 18 ("*latero-sinuatus*"), Piton 1936b: 22; 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 indistinct).

(*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.

Tribe **Hopliini*****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.

Tribe **Sericini**Genus ***Cretoserica*** Nikolajev

Cretoserica Nikolajev 1998a: 83 (transl. p. 519) (type species by original designation: *Cretoserica latitibialis* Nikolajev). – Nikolajev 1999: 178; Krell 2000a: 888; Nikolajev 2002: 54 (transl. p. 281); Nikolajev 2005a: 117; Nikolajev 2007b: 189, 191, 216.

Cretoserica latitibialis Nikolajev

Cretoserica latitibialis Nikolajev 1998a: 83 (transl. p. 520) (L Cretaceous, Baysa, Russia). – Krell 2000a: 888; Nikolajev 2007b: 190, 216, 221.

Genus ***Lithanomala*** Nikolajev

Lithanomala Nikolajev 1992: 79 (transl. p. 100) (type species by original designation: *Proteroscarabaeus oblongus* Ponomarenko). – Nikolajev 1998a: 82 (transl. p. 519); Nikolajev 1999: 178; Krell 2000a: 886; Nikolajev 2005a: 118; Nikolajev 2005b: 113; Krell 2006: 133; Nikolajev 2007b: 185, 191, 216.

Lithanomala crassa (Ponomarenko) Nikolajev

Proteroscarabaeus crassus Ponomarenko 1990: 66, pl. 6 (L Cretaceous, Leskovo, Russia).
Lithanomala crassa. – Nikolajev 1992: 80 (transl. p. 100); Krell 2000a: 886; Nikolajev 2007b: 187f, 216.

Lithanomala oblonga (Ponomarenko) Nikolajev

Proteroscarabaeus oblongus Ponomarenko 1990: 66, pl. 6 (L Cretaceous, Leskovo, Russia).
Lithanomala oblonga. – Nikolajev 1992: 79 (transl. p. 100); Krell 2000a: 886; Nikolajev 2007b: 186, 212, 216.

Lithanomala sibirica (Ponomarenko) Nikolajev

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

Lithanomala sibirica. – Nikolajev 1992: 80 (transl. p. 100); Krell 2000a: 886; Nikolajev 2004: 188f, 216.

***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.

***Serica cockerelli* Wickham**

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

***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; Krell 2006: 132.

***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 ***Cretomelolonthinae*** Nikolajev

Cretomelolonthini Nikolajev 1998: 80 (transl. p. 515), upgraded to subfamily by Nikolajev 2007b: 181.

Genus ***Cretomelolontha*** Nikolajev

Cretomelolontha Nikolajev 1998a: 81 (transl. p. 516) (type species by original designation: *Cretomelolontha transbaikalica* Nikolajev). – Nikolajev 1999: 178; Krell 2000a: 884; Nikolajev 2002: 54 (transl. p. 281); Nikolajev 2005a: 117; Nikolajev 2007b: 181, 216.

Cretomelolontha transbaikalica Nikolajev

Cretomelolontha transbaikalica Nikolajev 1998a: 82 (transl. p. 517) (L Cretaceous, Baysa, Russia). – Krell 2000a: 884; Krell 2006: 133; Nikolajev 2007b: 182f, 212, 216, 221.

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*** Frič

Anomalites Frič 1885: 163 (type species by monotypy: *Anomalites fugitivus* Frič). – Scudder 1881–1885: 794; Scudder 1886: 74; Handlirsch 1925: 246; Carpenter 1992: 300, 330; Krell 2000a: 885; Krell 2006: 121.

Anomalites fugitivus Frič

Anomalites fugitivus Frič 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: Rhabdophoridae).

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; Krell 2006: 133.

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 **Dynastinae*****Ligyris compositus*** Wickham

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

(*Ligyris*) *effetus* Wickham

Ligyris 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.

Genus ***Oryctoantiquus*** Ratcliffe & Smith

Oryctoantiquus Ratcliffe & Smith in Ratcliffe, Smith & Erwin 2005: 128 (type species by original designation: *Oryctoantiquus borealis* Ratcliffe & Smith). – Krell 2006: 143.

Oryctoantiquus borealis Ratcliffe & Smith

Oryctoantiquus borealis Ratcliffe & Smith in Ratcliffe, Smith & Erwin 2005: 130 (M Eocene, Clarno Formation, West Branch Creek, Oregon, U.S.A.). – Krell 2006: 133, 143.

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 1914: 721; 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 1914: 721; 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 **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.

Tribus **Trichiini*****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; 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; Krell 2006: 133.

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

Genus ***Cretoscarabaeus*** Nikolajev

Cretoscarabaeus Nikolajev 1995b: 147 (transl. p. 186) (type species by original designation: *Cretoscarabaeus gibbosus* Nikolajev). – Nikolajev 1999: 178; Krell 2000a: 887; Nikolajev 2002: 54 (transl. p. 281); Nikolajev 2005a: 117; Nikolajev 2005b: 113; Krell 2006: 127; Nikolajev 2007b: 136, 215.

Cretoscarabaeus gibbosus Nikolajev

Cretoscarabaeus gibbosus Nikolajev 1995b: 147 (transl. p. 186) (L Cretaceous, Baysa, Russia). – Krell 2000a: 887; Nikolajev 2007b: 135–137, 207, 215, 221.

Cretoscarabaeus lentiginosus Nikolajev

Cretoscarabaeus lentiginosus Nikolajev 1995b: 148 (transl. p. 188) (L Cretaceous, Baysa, Russia). – Krell 2000a: 887; Nikolajev 2007b: 138f, 215, 221.

FAMILIAE INCERTAE SEDIS

Genus ***Aliscarabaeus*** Hong

Aliscarabaeus Hong 1983: 5 (type species by original designation: *Aliscarabaeus granulatus* Hong). – Hong 1985: 37 (*Aliscarabaeus*, 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 ***Cretoabaeus*** Nikolajev

Cretoabaeus Nikolajev 1995b: 149 (transl. p. 189) (type species by original designation: *Cretoabaeus elongatus* Nikolajev). – Nikolajev 1999: 178; Krell 2000a: 887; Nikolajev 2005a: 118; Krell 2006: 127; Nikolajev 2007b: 135; Nikolajev 2007b: 192, 217.

Cretoabaeus elongatus Nikolajev

Cretoabaeus elongatus Nikolajev 1995b: 149 (transl. p. 189) (L Cretaceous, Baysa, Russia). – Krell 2000a: 887; Nikolajev 2007b: 192f, 217, 221.

Genus ***Hongscarabaeus*** Krell

Hongscarabaeus Krell, 2000a: 888

Proscarabaeus Hong 1982: 126 (type species by original designation: *Proscarabaeus brunneus* Hong). – Xiao *et al.* 1994: 81; Nikolajev 1998b: 30; Tan *et al.* 2004: 685; 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). – Nikolajev 1999: 178; Krell 2000a: 888; Nikolajev 2005a: 118; Nikolajev 2007b: 194.

Hyboosorites. – Nikolajev 2007b: 217.

(***Hybosorites fissuratus*** Nikolajev)

Hybosorites fissuratus Nikolajev 1996: 98 (L Cretaceous, Baysa, Russia). – Krell 2000a: 888; Nikolajev 2007b: 194, 217, 221.

Doubtful (only one elytron).

Genus ***Mesoscarabaeus*** Hong

Mesoscarabaeus Hong 1982: 123 (type species by original designation: *Mesoscarabaeus corneus* Hong). – Nikolajev 1998b: 30; Krell 2000a: 888; Tan *et al.* 2004: 685; Nikolajev 2007b: 217.

Mesoscarabaeus corneus Hong

Mesoscarabaeus corneus Hong 1982: 124 (L Cretaceous, Jiuquan, China). – Krell 2000a: 888; Nikolajev 2007b: 217.

Mesoscarabaeus morulosus Hong

Mesoscarabaeus morulosus Hong 1982: 125 (L Cretaceous, Jiuquan, China). – Krell 2000a: 888; Nikolajev 2007b: 217.

PRESUMED SCARABAEOIDEA

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; Nikolajev 2007b: 217.

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; Krell 2000c: (4); Nikolajev 2007b: 217.

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; Nikolajev 2007b: 217.

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; Nikolajev 2007b: 217.

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 ***Palaeocopriss*** Pierce

Palaeocopriss Pierce 1946a: 130 (type species by monotypy: *Palaeocopriss labreae* Pierce 1946). – Edmonds 1972: 855 (“morphological resemblance to this genus with *Phanaeus*”).
Paleocopriss. – 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.). – Spohn 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; Krell 2000c: (4).

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.

“*Protogeotrupes* Nikolajev” listed in the “Taxonomic list of fossil beetles of suborder Scarabaeina (Part 2)” by A.G. Ponomarenko & A.G. Kirejtshuk (<http://www.zin.ru/Animalia/Coleoptera/eng/paleosy1.htm>, accessed 18 November 2007) is still undescribed.

**ICHNOTAXA (FOSSIL PUPAL CHAMBERS, NESTS, AND BROODBALLS) OF
SCARABAEOIDEA**

Ichnofamilia **COPRINISPHAERIDAE** Genise, 2004: 426

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; Hasiotis *et al.* 1994: fig. 149; Genise & Cladera 1995: 78; Buatois *et al.* 1998: 226; Genise & Laza 1998: 220; González *et al.* 1998; Genise 1999: 110; Buatois *et al.* 2000; Genise 2000a: 50, 53, 55; Genise 2000c: 115; Genise *et al.* 2000: 49ff; Krell 2000a: 890; Verde 2000: 112f; Bellosi *et al.* 2001; Genise *et al.* 2001; Retallack 2001: 291; De 2002: 65; Hasiotis 2002: 79f, 132; Genise 2003: 19; Mikulás & Genise 2003: 341, 344; Aramayo *et al.* 2004; Bellosi 2004; Bellosi & Genise 2004: 15, 20, 22, 24f; Bellosi *et al.* 2004: 33, 35; Buatois & Mángano 2004: 312, 327; Dieni & Genise, 2004a: 29; Dieni & Genise 2004b: 31; Genise 2004: 421, 424f, 427, 444f; Genise & Cladera 2004: 632, 636; Genise *et al.* 2004a: 366, 370–372, 376; Genise *et al.* 2004b; Genise & Bellosi 2004: 41; Hasiotis 2004: 184f, 188, 190, 200, 236, 238f, 250; Hembree & Hasiotis 2004; Pieńkowski 2004: 8, 12; Bellosi *et al.* 2005; De 2005: 233, 235, 239, 243, 245–248; Sánchez *et al.* 2005; Chure *et al.* 2006: 243; Genise *et al.* 2006: 243f; Hasiotis 2006: 401; Hasiotis & Bourke 2006: 217f; Laza 2006: 220; Sánchez *et al.* 2006; Sánchez *et al.* 2007; Bromley *et al.* 2007: 144, 146; Buatois & Mángano 2007: 286–289, 315; Düringer *et al.* 2007: 333, 350; Ekdale *et al.* 2007: 570; Genise 2007; Hasiotis 2007: 265; Hasiotis *et al.* 2007: 174, 182, 192; Hunt & Lucas 2007: 59f, 63; Krause *et al.* 2007; MacEachern *et al.* 2007a: 54–58, 61; MacEachern *et al.* 2007b: 114; Melchor *et al.* 2007: 16; Verde & Genise 2007; Verde *et al.* 2007: 342f.
- Cangabola* Lengerken 1955: 937 (type species by monotypy: *Cangabola ecuadoriensis* Sauer).
- Coprinsphaera*. – Sauer 1956: 550; Halffter & Matthews 1966: 154; Retallack 1991: 182, 296; Düringer *et al.* 2000b: 264; Laza 2006: 220 (lapsus calami).
- “bolas de Cangagua”. – Estrada 1941: 433, figs 1, 2–7; Sauer 1950: 344, 348–350.
- “Nido fósil de escarabajo”. – Camacho 1966: 488–490.
- “Paleonidos de escarabéidos”. – Spalletti & Mazzoni 1977: 265, 267.
- “nidos de escarabajos peloteros”. – Fontaine *et al.* 1995.
- “nódulos [...] como producto de la actividad de escarabajos estercoleros”. – Iriondo & Kröhling 1996: 43.
- Devincenzia* Roselli 1939: 81 (type species by monotypy: *Devincenzia murguiai* Roselli; preoccupied by *Devincenzia* Kraglievich 1932 – see Genise & Bown 1994: 109) (syn.).
- Devicenzichnus* Roselli 1976: 167 (type species by monotypy: *Devicenzichnus murguiai* Roselli). – Martinez 1982: 48; Buatois *et al.* 1998: 226; González *et al.* 1998: 39 (syn.); Genise 2000a: 53 (syn.).
- Devinzenichnus*. – Genise 1993: 50 (synonym of *Coprinisphaera*); Hasiotis *et al.* 1994: fig. 148; Genise & Laza 1998: 213 (syn.).
- Fontanai* Roselli 1939: 79 (type species by monotypy: *Fontanai kraglievichi* Roselli). – Genise & Laza 1998: 213 (“is a dung beetle brood mass”); González *et al.* 1998: 39 (as synonym of *Coprinisphaera*); Genise 2000c: 115; Genise *et al.* 2000: 49, 51, 53f, 58f; Krell 2000a: 891; Verde 2000: 112; Genise 2004: 421, 425, 426, 444; Genise *et al.* 2006: 243f (to be suppressed);

Laza 2006: 220 ("new synonym"); Buatois & Mángano 2007: 288 (as valid); MacEachern *et al.* 2007a: 58 (as valid).

Fontanaichnus Roselli 1976: 167 (type species by monotypy: *Fontanaichnus kraglievichi* Roselli). – Retallack 1990: 219; Donovan 1994: 209; Buatois *et al.* 1998: 226 (syn. of *Fontana*); Genise *et al.* 2006: 243f (to be suppressed).

Madinaichnus Roselli 1987: 23 (type species by monotypy: *Madinaichnus larranagai* Roselli). – Hasiotis *et al.* 1994 (probably synonym of *Devincenzichnus*); Genise & Laza 1998: 213; Buatois *et al.* 1998: 226; González *et al.* 1998: 39 (as synonym of *Coprinisphaera*); Genise 1999: 110 (supposed synonymy with *Coprinisphaera*); Genise 2000a: 53 (syn.); Genise *et al.* 2000: 54; Krell 2000a: 891; Verde 2000: 112.

Martinezichnus Roselli 1987: 22 (type species by monotypy: *Martinezichnus francisi* Roselli). – Hasiotis *et al.* 1994 (probably synonym of *Devincenzichnus*); Genise & Cladera 1995: 78; Genise & Laza 1998: 213; Buatois *et al.* 1998: 226; González *et al.* 1998: 39 (as synonym of *Coprinisphaera*); Genise 1999: 110 (supposed synonymy with *Coprinisphaera*); Genise 2000a: 53 (syn.); Genise *et al.* 2000: 54; Krell 2000a: 891; Verde 2000: 112.

Microicoichnus Roselli 1987: 49 (type species by monotypy: *Microicoichnus lafurcadai* Roselli). – Hasiotis *et al.* 1994 (probably synonym of *Devincenzichnus*); Buatois *et al.* 1998: 226; Genise & Laza 1998: 213; González *et al.* 1998: 39 (as synonym of *Coprinisphaera*); Genise 1999: 110 (supposed synonymy with *Coprinisphaera*); Genise 2000a: 53 (syn.); Genise *et al.* 2000: 54; Krell 2000a: 891; Verde 2000: 112.

***Coprinisphaera ecuadoriensis* Sauer**

"bolas". – Bruet 1950.

Coprinisphaera ecuadoriensis Sauer 1955: 123 (U Pleistocene, Cangagua Formation, northern Ecuador). – Sauer 1956: 555; Sauer 1959: 119ff; Häntzschel 1962: W189; Sauer 1965: 271f; Häntzschel 1975: W52; Martínez 1982: 48; Genise & Bown 1994: 109; Genise 1999: 110; Genise 2000b: 28; Krell 2000a: 890; Genise *et al.* 2006: 243f; Sánchez *et al.* 2007.

Cangabola ecuadoriensis. – Lengerken 1955: 937.

Coprinisphaera ecuadoriensis. – Sauer 1956: 550.

Coprinisphaera ecuadorensis. – Halffter & Matthews 1966: 154.

Coprinisphaera ecuadorensis. – Genise 1993: 50.

Coprinisphaera frenguelli Genise & Bown 1994: 110 (Miocene, Pinturas Formation, Estancia Ana Maria, Prov. Santa Cruz, Argentina). – Hasiotis *et al.* 1994: fig. 149 (*frenguelli*); Buatois *et al.* 1998: 226; Genise 2000a: 51 (*frenguelli*); Krell 2000a: 891; Laza 2006: 221 (syn.).

Madinaichnus larranagai Roselli 1987: 23 (U Cretaceous – L Tertiary, Uruguay) (holotype shown in Hasiotis *et al.* 1994: fig. 148). – Krell 2000a: 891; Laza 2006: 220 (syn.).

***Coprinisphaera kheprij* Laza**

Coprinisphaera kheprij Laza, 2006: 229 (L Miocene, Sarmiento Formation, Gran Barranca, Chubut Prov., Argentina). – Sánchez *et al.* 2007.

***Coprinisphaera kraglievichi* (Roselli) Laza**

Fontana *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"); Genise 2000a: 51, 53; Krell 2000a: 891; Genise 2004: 427; Genise *et al.* 2006: 243.

Fontanaichnus kraglievichi. – Roselli 1976: 167; Retallack 1990: 219 ("Likely fossil nests of dung beetles"); Donovan 1994: 209 ("Possible fossil nests of dung beetles").

Coprinisphaera kraglievichi. – Laza 2006: 228; Sánchez *et al.* 2007.

Coprinisphaera murguiai (Roselli) Genise & Bown

Devincenzia murguiai Roselli 1939: 81 (U Cretaceous, Colonia, Uruguay) (holotype shown in Hasiotis *et al.* 1994: fig. 148). – Genise 1983: 50.

Devincenzichnus murguiai. – Roselli 1976: 166f; Genise 1993: 50; Genise & Bown 1994: 109.

Devincenzichnus murguiai. – Roselli 1976: 167; Martinez 1982: 48.

Devincenzichnus murguiae. – Retallack 1990: 219.

Devincenzichnus murguiae. – Donovan 1994: 209.

Coprinisphaera murguiai. – Genise & Bown 1994: 109; Krell 2000a: 891; Laza 2006: 227; Sánchez *et al.* 2007.

Martinezichnus francisi Roselli 1987: 22 (Cretaceous, Asencio Formation, Uruguay?) (holotype shown in Hasiotis *et al.* 1994: fig. 148). – Genise & Cladera 1995: 78f; Krell 2000a: 891; Laza 2006: 227 (syn.).

Microicoichnus lafurcadai Roselli 1987: 49 (U Cretaceous–L Tertiary, Uruguay) (holotype shown in Hasiotis *et al.* 1994: fig. 148). – Krell 2000a: 891; Laza 2006: 227 (syn.).

Coprinisphaera tonnii Laza

Coprinisphaera kheprii Laza 2006: 230 (L Miocene, Sarmiento Formation, Gran Barranca, Chubut Prov., Argentina). – Sánchez *et al.* 2007.

Coprinisphaera ichnosp.

Coprinisphaera ichnosp. nov. [not named]. – Dieni & Genise, 2004a: 29; Dieni & Genise 2004b: 31 (M Eocene, Bartoniano, Monte di Malo, Vicenza, Italy).

Ichnogenus ***Eatonichnus*** Bown, Hasiotis, Genise, Maldonado & Browsers

Eatonichnus Bown, Hasiotis, Genise, Maldonado & Browsers 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 *et al.* 1998: 12; Genise 1999: 110; Genise 2000a: 53; Genise 2000c: 115; Genise *et al.* 2000: 53f, 57 (“possible dung beetle nest”); Krell 2000a: 891; Genise *et al.* 2001; Genise 2004: 421, 424f, 430, 444; Bohacs *et al.* 2007: 79, 82–83, 85, 97, 103–104; Buatois & Mángano 2007: 289, 315; MacEachern *et al.* 2007a: 57f.

Eatonichnus claronensis Bown, Hasiotis, Genise, Maldonado & Browsers

Eatonichnus claronensis Bown, Hasiotis, Genise, Maldonado & Browsers 1997: 54 (Eocene, J.G. Eaton locality, Utah, U.S.A.). – Genise & Bown 1998: 222; Genise 2000a: 51; Krell 2000a: 891; Genise *et al.* 2001; Krause *et al.* 2007.

Eatonichnus utahensis (Gilliland & La Rocque) Bown, Hasiotis, Genise, Maldonado & Browsers

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; Genise *et al.* 2001.

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 2000: 115; Genise *et al.* 2000: 49, 51, 53f, 58f;

Krell 2000a: 891; Verde 2000: 112; Mikulás & Genise 2003: 340; Genise 2004: 421, 424, 430, 444f; Genise *et al.* 2004a: 366, 372, 376; Buatois & Mángano 2007: 288; MacEachern *et al.* 2007a: 58; Verde & Genise 2007.

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 *et al.* 1998; González *et al.* 1998; Genise 1999: 110; Genise 2000a: 53; Krell 2000a: 891; Mikulás & Genise 2003: 346; Bellosi *et al.* 2004: 33; Genise & Cladera 2004: 632.

Ichnogenus ***Quirogaichnus*** Laza⁴

Quirogaichnus Laza, 2006: 231 (type species by original designation: *Quirogaichnus coniunctus* Laza). – Sánchez *et al.* 2005 (nomen nudum); Sánchez *et al.* 2006 (Miocene and Pleistocene).

Quirogaichnus coniunctus Laza

Quirogaichnus coniunctus Laza, 2006: 231 (U Miocene, Cerro Azul Formation, Guaminí, Buenos Aires Prov., Argentina).

(Ichnogenus ***Rebuffoichnus*** Roselli⁵)

Rebuffoichnus Roselli 1987: 24 (type species by monotypy: *Rebuffoichnus casamiquelai* Roselli). – Buatois *et al.* 1998: 226; Genise & Laza 1998: 213; Genise *et al.* 2000: 54; Krell 2000a: 892; Verde 2000: 112; 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); Genise 2000a: 53 (“familias no identificadas”); Krell 2000a: 892; Genise *et al.* 2002a: 230f; Genise *et al.* 2002b; Mikulás & Genise 2003: 341, 343, 344; Genise & Bellosi 2004: 34; Genise *et al.* 2007: 546, 554, 556f.

Ichnofamilia **PALLICHNIDAE** Genise, 2004: 432

(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); Genise 2004: 435 (“pupation chambers of Coleoptera, probably Curculionidae”).

⁴ *Quirogaichnus* Laza has not been formally attributed to Coprinisphaeridae, but fits the definition of this ichnofamily as given by Genise (2004: 426).

⁵ *Rebuffoichnus sciuttoii* Genise *et al.* 2007, despite being in the same ichnogenus as the beetle traces *R. casamiquelai*, has been assigned to Hymenoptera, hence being neglected here.

idae, Tenebrionidae or Scarabaeidae"; similar statement in Genise & Cladera 2004: 629), 444, 446. – Since the assignment of this ichnogenus to scarabaeid tracemakers is doubtful, the ichnospecies *F. gobiensis* Johnston *et al.* 1996, and *F. parvus* Johnston *et al.* 1996 (syn. ad *F. gobiensis* according to Genise 2004: 433) are not listed separately.

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 2000a: 50; Genise *et al.* 2000: 53; Krell 2000a: 891; Dieni & Genise 2004a: 29; Dieni & Genise 2004b: 31; Genise 2004: 421, 425, 444, 446; Genise *et al.* 2004; Bellosi *et al.* 2005; MacEachern *et al.* 2007a: 56, 58; Sánchez *et al.* 2007.

Pallichnus dakotensis Retallack

Pallichnus dakotensis Retallack 1984: 581 (U Oligocene, Brule Formation, Badlands National Park, South Dakota, U.S.A.). – Genise 1993: 50; Krell 2000a: 891; Genise *et al.* 2007: 546f, 550; Hembree & Hasiotis 2007: 125, 127, 129, 132–134.

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; Genise 2000: 115; Krell 2000a: 892; Hasiotis 2002: 79f, 132; Genise 2004: 433, 444, 446; De 2005: 240; Hasiotis *et al.* 2007: 182; MacEachern *et al.* 2007a: 56.

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); Hasiotis *et al.* 1994: fig. 149; Bown *et al.* 1997: 56; Genise & Laza 1998: 222; Genise 1999: 110; Krell 2000a: 892; Genise *et al.* 2004a: 375; Smith *et al.* 2004.

NOT ASSIGNED TO ICHNOFAMILY

Ichnogenus ***Lazaichnus*** Mikuláš & Genise

Lazaichnus Mikuláš & Genise, 2003: 345 (type species by original designation: *Lazaichnus fistulosus* Mikuláš & Genise). – Sánchez *et al.* 2007.

Lazaichnus fistulosus Mikuláš & Genise

Lazaichnus fistulosus Mikuláš & Genise 2003: 345 (U Cretaceous–LTertiary Asencio Formation, Uruguay). – External holes with internal gallery in *Monesichnus ameghinoi*, possibly created by cleptoparasitic dung beetles.

(Ichnogenus ***Macanopsis*** Macsotay)

Macanopsis Macsotay 1967: 32. – Hembree & Hasiotis 2007: 125, 127, 129, 132–134 (authors call burrows with dung balls at the end "*Macanopsis* isp.–*Pallichnus dakotensis*"; however, *Macanopsis* was introduced for marine burrows and later used also for burrows in fluvial sediments (Fernandes & Carvalho 2006); it seems inappropriate to use this ichnogenetic name for any sort of burrow disregarding the creating animal.)

UNNAMED SCARAB TRACE FOSSILS

Africa

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

Europe

L Jurassic (Lias α 1-2), Sołtyków, Poland: *Coprinisphaera* sp. (Pieńkowski 2004), neither described nor figured.

North America

Pliocene, Jalisco, México: "bola-nido" (Morón Ríos 1984: 27).

L Miocene, Harrison Formation, Eagle Crags, Nebraska, U.S.A.: "*Daemonelix* ball" (Barbour 1897a: 11, 26, 1897b: 308), "remains superficially similar to dung pellets and cakes and the brood chambers of burrow-stuffing, dung beetles" (Retallack 1990: 223).

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 with dung beetle traces (Chin 1995; Chin & Gill 1996).

OTHER FOSSILS ORIGINALLY DESCRIBED AS SCARABAEOIDEA OR SCARAB ICHNOTAXA

Genus *Oryctes* Oppenheim (not valid)

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

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

Oryctes fossilis (Oppenheim) Houlbert

Oryctes 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: Adepaga incertae sedis.

Oryctes fossilis. – Houlbert 1914: 721; 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). – Weyenbergh 1869b*: [232]; Weyenbergh 1874: 102 or 109⁶; 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 1914: 721; Houlbert 1915: 64 ("n'est pas déterminable"); Krell 2000a: 884.

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

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

⁶ There are two printings with slightly different arrangement of the text.

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).

Prosynactus scissus Bode

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

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 (Jurassic, 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 deperditus*" [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. – Weyenbergh 1869b: [233] (Heteroptera, Geocoris).

Scarabaeoides deperditus, *Scarabaeides 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 (Jurassic, 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 Frič (ichnospecies)

Xyloryctes planus Frič 1877: 16, pl. 3 (Carboniferous, Nyřan near Plzen, Czech Republic; 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 Frič (ichnospecies)

Xyloryctes septarius Frič 1877: 15, pl. 3 (U Carboniferous, Swinná near Radnitz, Bohemia, Czech Republic). – 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.

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

Onthophagus rugulosus (Heer 1870), listed in the "Taxonomic list of fossil beetles of suborder Scarabaeina (Part 2)" by A.G. Ponomarenko & A.G. Kirejtshuk (<http://www.zin.ru/Animalia/Coleoptera/eng/paleosy1.htm>, accessed 18 November 2007) was described as *Elytridium rugulosum* and originally classified as a possible carabid (Heer 1870: 78). It is the middle part of one elytron which is lacking any character revealing its family.

Tertiary and Mesozoic lagerstätten with fossils of Scarabaeoidea

Pliocene (5.3–1,8 Myr)⁷

Europe

Kisatibi, Kisatibi Formation, Akhaltsikh District, Georgia (L): *Copris (Copris) kartlinus* (Kabakov 1988).

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

Willershausen, Harz, northern Germany (U): *Aphodius (Acrossus) rufipes* (L.), Aphodiinae sp., *Mimela* sp., *Oryctes nasicornis* L. (Gersdorf 1971), Coprinae sp., Cetoniinae sp. (reliable) (Gersdorf 1976); *Lucanus cervicalis* (= *cervus* (L.)) (Schweigert 2003).

Africa

Laetoli, Tanzania (3.46–3.76 Myr): structure resembling a dung ball of *Helicopris* (Sands 1987: 423) (= *Coprinisphaera* isp. according to Genise *et al.* 2000).

Makapansgat, South Africa: ichnofossils of coprophagans (Kitching 1980).

Palaeo-lake Chad system, Kouba Olanga, Kossom Bougoudi and Kollé, Chad (5 Myr): fossil brood-balls of dung beetles (Düringer *et al.* 1999, 2000a,b; Schuster *et al.* 2000).

North America

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

South America

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

Las Grutas, Vorohué Formation, Necochea, Buenos Aires Prov., Argentina: *Coprinisphaera tonnii* (Laza 2006).

Maimará Formation, Jujuy Prov., Argentina (L): ichnofossils: *Coprinisphaera ecuadoriensis*, *C. murguiai* (Laza 2006).

Quequén Salado river, Irene Formation, Buenos Aires Prov., Argentina (L-M; Montehermosan): ichnofossils: *Coprinisphaera* isp. (Aramayo *et al.* 2004).

Sierra de Vaqueros, Piquete Formation, Salta, Argentina (U): ichnofossils ("bolas") of coprophagans (cf. *Phanaeus*, *Megathopa*) (Alonso *et al.* 1982), *Coprinisphaera* isp. according to Genise *et al.* (2000: 55).

Transition Mio/Pliocene:

Europe

Simetite (Sicilian resin): (*Scarabaeus bilobus* L.) (= *Caelosis biloba*) (Ferrara 1805: 136 [wrong identification; Krell 1996: 18]; Kohring & Schlüter 1989: 45).

Varenes (cinerites), France: (*Melolonthites laterosinuatus*) (Piton & Théobald 1935).

North America

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

⁷ Dating according to the standard time scale of the International Commission on Stratigraphy (Gradstein *et al.* 2005).

South America

Buenos Aires, Monte Hermoso Formation, Argentina (U Miocene–L Pliocene): ichnofossils: *Coprinisphaera* isp. (Genise *et al.* 2000: 55).

Miocene (23.3–5.3 Myr)

Europe

Montagne d'Andance, Ardeche, France (U, Turolian): *Miocenidorcus andancensis*, cf. *Geotrupes stercorarius*, *Thyphoeus* sp. [= *Typhaeus* sp.], cf. *Amphimallon ater* (Riou 1988: 103ff, 1999).

Habichtswald near Kassel, Germany (L): cf. *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*)⁸, *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).

Mokřina (Krottensee) near Kynšperk n. O., Cypris Shale, Cheb Basin, Bohemia, Czech Republic (L, Burdigalian): (*Melolontha solitaria*) (Novák 1878).

Gabbro, Livorno, Italy (L, Messinian): *Aphodius bosniaskii* (Handlirsch 1908).

Euboea (Evia), Greece (L): *Geotrupes* sp. (Bachmayer *et al.* 1971).

Asia

Dhok Patan Formation, Pakistan (U): ichnofossils: *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 rectidypeus*, *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).

Yanagida Formation, Noto, Takaya, Japan (M): *Heliocopris antiquus*, *Phyllopertha?* sp. (Fujiyama 1968).

Masaragawa Formation, Seki, Sado Island, Japan (L): *Aphodius?* sp. (doubtful, only one elytron) (Fujiyama 1985).

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

Africa

Lake Victoria, Kenya (L, 16–23 Myr): *Anachalcos mfwangani* (Mfwangano Island), *Copris leakeyorum* (Rusinga Island), *Metacatharsius rusingae* (Rusinga I.), Rutelinae, Cetoniinae (Paulian 1976).

⁸ The *Melolontha* listed by Keferstein (1834: 331) likely refers to one of these *Melolonthites* species.

North America

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).

Las Breas de San Felipe, Cuba (Miocene–Pleistocene): Scarabaeidae sp. (Valdés 1999).

South America

Arroyo Feo, Pinturas Formation, Santacrucian, Santa Cruz Prov., Argentina (L): ichnofossils: *Coprinisphaera ecuadoriensis* (ichnofossil) (Genise & Bown 1994 [as *C. frenguelli*]; Laza 2006).

Andalhualá, Catamarca, Argentina (U): ichnofossils: *Coprinisphaera* isp. (Genise *et al.* 2000: 55).

Bajada del Diablo, Sarmiento Formation, Puesta Almendra Member, Chubut Prov., Argentina (M Eocene–L Miocene): ichnofossils: *Coprinisphaera* isp. (Bellosi *et al.* 2005); *Lazaichnus* sp., *Coprinisphaera ecuadoriensis*, *C. kheprii*, *C. kraglievichi*, *C. murguiai*, *C. tonnii* (Laza 2006; Sánchez *et al.* 2007).

Cañadón, Sarmiento Formation, Los Leones, Chubut Prov., Argentina (M Eocene–L Miocene): ichnofossils: Pallettole di Scarabeide (Frenguelli 1938b; Fossa-Mancini 1941; Laza 1986b); *C. ecuadoriensis*, *C. kheprii*, *C. murguiai* (Laza 2006).

Cerro Azul Formation, La Pampa/Buenos Aires, Argentina (U): ichnofossils: *Coprinisphaera* isp. (Genise *et al.* 2000); *Quirogaichnus coniunctus* (Laza 2006).

Cerro del Humo, Sarmiento Formation, Puesta Almendra Member, Chubut Prov., Argentina (M Eocene–L Miocene): ichnofossils: *Coprinisphaera* isp. (Bellosi *et al.* 2005); *Lazaichnus* sp., *Coprinisphaera ecuadoriensis*, *C. kheprii*, *C. kraglievichi*, *C. murguiai*, *C. tonnii* (Laza 2006; Sánchez *et al.* 2007).

Gran Barranca, Sarmiento Formation, Colhue-Huapi, Chubut Prov., Argentina (M Eocene–L Miocene): ichnofossils: *Coprinisphaera ecuadoriensis* (Laza 2006; McCartney 1933: "characteristic layers of spherical concretions"; Spalletti & Mazzoni 1977: 265 "paleonidos de escarabéidos"); *C. kheprii*, *C. murguiai*, *C. tonnii* (Laza 2006); *C. kraglievichi* (Sánchez *et al.* 2007).

Laguna del Mate, Sarmiento Formation ("Musters Formation"), Chubut Province, Argentina (M Eocene–L Miocene): ichnofossils: "nidos de escarabajos" (Andreis 1972), "similar fossils of *Coprinisphaera*" (Retallack 1990: 218); *Coprinisphaera* isp. (Genise *et al.* 2000: 54); *Coprinisphaera ecuadoriensis* (Laza 2004).

Las Flores, Asencio Formation, San Juan, Argentina (U): ichnofossils: "nidos de escarabidos" (Contreras 1996), *Coprinisphaera* isp. (Genise *et al.* 2000: 55); *C. kraglievichi* (Laza 2006).

North of Musters Lake, Sarmiento Formation, Chubut Prov., Argentina (M Eocene–L Miocene): ichnofossils: *Coprinisphaera ecuadoriensis*, *C. kraglievichi* (Laza 2006).

Paso de las Carretas, San Luis, Argentina (U): ichnofossils: "'nidos' de escarabideos" (Pascual & Bondesio 1981: 125), *Coprinisphaera* isp. according to Genise *et al.* (2000: 55).

Punta Casamayor, Sarmiento Formation, Santa Cruz Prov., Argentina (M Eocene–L Miocene): ichnofossils: "bolas", probably of *Megathopa* (Frenguelli 1938a,b); "bolas alimenticias de escarabidos" (Fossa-Mancini 1941), *Coprinisphaera ecuadoriensis*, *C. murguiai*, *C. tonnii* (Laza 2006).

Río Negro, and Neuquén, Collón-Curá Formation, Argentina (U): ichnofossils: "peras" of cf. *Megathopa*, cf. *Onthophagus*, etc. (Frenguelli 1938a, 1939a,b; Fossa-Mancini 1941; Camacho

1966: 490; Laza 1986; Genise 2000a: 50), *Coprinisphaera* sp. according to Genise *et al.* (2000: 55), *C. ecuadoriensis* according to Laza (2006: 220).

Rosado Member, Sarmiento Formation, Chubut Prov., Argentina (M Eocene–L Miocene): ichnofossils: *Pallichnus* sp. (Bellosi *et al.* 2005; Sánchez *et al.* 2007).

Sierra de Talquino, Sarmiento Formation, Puesta Almendra Member, Chubut Prov., Argentina (M Eocene–L Miocene): ichnofossils: *Coprinisphaera* isp. (Bellosi *et al.* 2005); *Lazaichnus* sp., *Coprinisphaera ecuadoriensis*, *C. kheprij*, *C. kraglievichi*, *C. murguiai*, *C. tonnii* (Laza 2006; Sánchez *et al.* 2007).

Valle Hermoso, Sarmiento Formation, Chubut Prov., Argentina (M Eocene–L Miocene): ichnofossils: *Coprinisphaera ecuadoriensis*, *C. murguiai* (Laza 2006).

Vera Member, Sarmiento Formation, Chubut Prov., Argentina (M Eocene–L Miocene): ichnofossils: *Coprinisphaera* isp. (Sánchez *et al.* 2007).

Oligocene (33.9–23.3 Myr)

Europe

Rott, Siebengebirge, Germany (U, Chattian, 25 Myr): *Geotrupes rottensis*, (*Onitis*) *magus*, *Onthophagus statzi*, *Miochodaeus proaevus*, *Aphodius helvolus*, *A. krantzi*, *A. schlickumi*, *Melolontha* sp., *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, Alsacia, France (M): *Ammoecius* ? sp. [= *Aphodius* (*Ammoecius*) sp.] (Förster 1890: 102).

Aix en Provence, France (U, Stampian): *Geotrupes atavus*, *Onthophagus luteus* (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?]): "*Helicopriss* sp. (?)" [= *Heliocopriss*] (Rudel 1940: 15).

Armissan, Aude, France: *Ateuchites grandis* (Meunier 1898a).

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

Asia

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

North America

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): *Ceruchites fuchsii*, (*Lucanus fossilis*), *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*), *Macroductylus pluto*, *M. propheticus*, (*Diplotaxis aurora*), (*Diplotaxis simplicipes*), *Listrochelus puerilis*, *Anomala exterranea*, *A. scudderi*, *Miolachnosterna tristoides*, *Hoplia striatipennis*, *Serica antediluviana*, *S. cockerelli*, *Ligyris compositus*, (*L. effetus*), *Strategus*

cessatus, *Amphicoma defuncta* (Cockerell 1927b; Wickham 1909, 1910, 1911, 1912, 1913a,b, 1914a,b).

Brule Formation, Badlands National Park, South Dakota, U.S.A.: ichnofossils: "casts of pupa cases or larval burrows" (Clark & Kietzke 1967: 124); *Pallichnus dakotensis* (Retallack 1984).

South America

Comodoro Rivadavia, Deseado Formation (currently Sarmiento Formation), Chubut Prov., Argentina: ichnofossils: peras (Frenguelli 1938a; Fossa-Mancini 1941); Pallettole di Scarabeide (Frenguelli 1938b; Camacho 1966: 490; Laza 1986b), *Coprinisphaera* sp. according to Genise *et al.* (2000: 54).

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

Cañadón del Loco, Chubut, Argentina (Tertiary, Oligocene?): "nidos de escarabeidos" (Frenguelli 1941); *Coprinisphaera* isp. (Genise 2004).

Asencio Formation/Fray Bentos Formation, Sartori, Nueva Palmira, Uruguay: ichnofossils: (*Monesichnus ameghinoi*) (Genise *et al.* 1998; ?*Monesichnus*, Verde 2000: 112; probably hymenopteran ichnofossil, Genise & Cladera 2004: 632).

Eocene–Oligocene:

Europe

Quercy near Toulouse, France (U Eocene to U Oligocene): *Aphodius* sp., *Pseudopentodon blanchardi* nom. nud. (Filhol 1892; Handschin 1944, 1950).

Glarus shales, Switzerland (U Eocene–L Oligocene): "HANNETON. *Scarabaeus*" [= *Melolontha* s.l. sp.] (Bertrand 1763: 259).

Eocene (55.8–33.9 Myr)

Europe

Gurnet Bay, Bembridge Marls, Isle of Wight (U): *Dorcus* sp. (Brodie 1878: 4; Goss 1878: 325; Woodward 1878, 1879) = *Pentodon* (Krell, submitted).

Kučín (Kutschlin) near Bílina (Bilin), Bohemia, Czech Republic (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).

Bartoniano (palaeosol), Monte di Malo, Vicenza, Italy (M): ichnofossils: *Coprinisphaera* isp. (Dieni & Genise 2004a,b).

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* sp. (Britton 1960: 36f).

Africa

Mahenge, Tanzania (M): Scarabaeoidea (Kaiser *et al.* 2006: 422, 425).

North America

- Ninemile Creek, British Columbia, Canada (M): (*Trox oustaleti*) (Scudder 1879a; Handlirsch 1910).
 Princeton British Columbia, Canada (M): Scarabaeidae (Wilson 1977).
 Bald Knoll Canyon, Colter and Claron Formation, Sevier and Garfield County, Utah, U.S.A.: ichnofossils: *Eatonichnus utahensis* (Bown *et al.* 1997).
 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): ichnofossils: *Eatonichnus claronensis*, *E.* isp. (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).
 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); ichnofossils: *Eatonichnus* isp. (Bohacs *et al.* 2007).
 Wasatch Formation (Wyoming, U.S.A.): ichnofossils: *Eatonichnus* (Bohacs *et al.* 2007).
 West Branch Creek, Clarno Formation, Oregon, U.S.A. (M): *Oryctoantiquus borealis* (Ratcliffe *et al.* 2005).
 White River Formation, Logan County, Colorado, U.S.A. (U Eocene–M Oligocene): ichnofossils: *Coprinisphaera* isp. (ichnotaxon) (Hambree & Hasiotis 2004).
 Willwood Formation, Slick Creek and Fifteenmile Creek, Bighorn Basin, Wyoming, U.S.A. (L): ichnofossils: *Scaphichnum hamatum* (Bown & Kraus 1983: 106; Hasiotis *et al.* 1993; Smith *et al.* 2004); *Coprinisphaera* isp. (Smith *et al.* 2004).

South America

- Cantera Las Flores/Canteras Maldonado, Espiga and Prati, Asencio Formation, Nueva Palmira, Departamento Colonia, Uruguay (U Cretaceous–L Tertiary; L Eocene according to Bellosi *et al.* 2004): ichnofossils: *Coprinisphaera ecuadoriensis*, *C. kraglievichi*, *C. murguiai* (also from Cantera Chileno, Sire, Faldasel Cerro, Carmelo; Laza 2006); (*Lazaichnus fistulosus*, *Microicoichnus* isp., *Monesichnus ameghinoi*) (Roselli 1939; Genise & Cladera 1995; Genise & Laza 1998; González *et al.* 1998; Laza 2006).

Antarctica

- Isla Marambio (Seymour), La Meseta Formation, Peninsula Antartica: ichnofossils: "un molde interno de nido de escarabeido integrante de la subtribu Phanaeina (Scarabaeinae)" (Laza & Reguero 1990), *Coprinisphaera* sp. according to Genise *et al.* (2000), identified by Laza (2006) as *C. ecuadoriensis* and *C. murguiai*.

Palaeocene (65.5–55.8 Myr)

Europe

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

South America

- Rio Chico, Peñas Coloradas Formation, Río Chico Group, Chubut, Argentina (U Palaeocene–M Eocene): ichnofossils: *Coprinisphaera* isp. (Genise *et al.* 2000: 54), *Eatonichnus* isp. (Genise *et al.* 2001); *Eatonichnus claronensis*, no *Coprinisphaera* (ichnofossils) (Krause *et al.* 2007).
 Koluel-Kaike Formation, Chubut Prov., Argentina (?Palaeocene–Eocene): *Coprinisphaera ecuadoriensis*, *C. murguiai* (Laza 2006).

Comallo, Rio Negro, Argentina (?Palaeocene): fossil nests, probably of *Megathopa* (Frenguelli 1938a,b, 1939b, 1940; Fossa-Mancini 1941; Retallack 1990: 217), *Coprinisphaera* isp. (Genise 2004).

Tertiary (without specification): Europe
Nogent le Rotrou ("Süßwasserquarz"), France: *Anomalites fugitivus* (Frič 1885).

MESOZOICUM

Upper Cretaceous (89.3–65.5 Myr)

Asia

Pisdura ("Pijdura"), Lameta Formation, India (Maastrichtian): feeding traces on coprolites possibly created by coprophagous beetles (Matley 1941: 539).

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

North America

Two Medicine Formation, Montana, U.S.A. (Campanian): coprolithes and fossil soil with nesting traces (Chin 1995, Chin & Gill 1996).

South America

Asencio Formation, Departamento Colonia, Uruguay (U Cretaceous–L Tertiary), see Eocene (Bellosi *et al.* 2004).

Cañadón Puerta del Diablo, Laguna Palacios Formation, Patagonia, Argentina (U): ichnofossils: *Rebuffoichnus casamiquelai* (Genise & Bellosi 2004).

Middle Cretaceous (112.0–89.3 Myr)

Asia

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

Obeshchayushchiy, Magadanskaya Oblast, Russia (Cenomanian): *Protopalnia magadanica* (Nikolajev 2007b).

Pad Semen, Argun Formation, Transbaykalia, Russia (?Albian): (*Antemnacrassa geminata*) (Nikolajev 2004); *Cretoglaphyrus olenguicus*, *C. zherikhini*, (*C. leptopterus*), (*C. transbaikalicus*), (*C. calvescens*), *Lithoscarabaeus baissensis*, *Proteroscarabaeus yeni* (Nikritin 1977); *Prototrox transbaikalicus* (Nikolajev 2000a); *Cretolucanus longus*, *C. ordinarius*, *C. sibericus* (Nikolajev 2007b).

Africa

Orapa, Botswana (Turonian): Scarabaeidae (photo) (McKay & Rayner 1986: 11f).

Lower Cretaceous (> 98 Myr)

Europe

Las Hoyas, Cuenca, Spain (Barremian): Scarabaeidae (Martínez-Delclós 1989: 76).

Montsec, Spain (L Valanginian–U Berriasian): Scarabaeidae (Martínez-Delclós & Ruiz de Loizaga 1993); *Holcorobeus monreali* (Gomez Pallerola 1986; Nikolajev 1992).

Asia

Lebanon (Amber, Aptian): termitophilous species of Scarabaeoidea (Crowson 1981: 669, 673); "Corythodérine" (= Corythoderini) (Paulian 1988: 394).

Baysa, Zazinskaya Formation, Transbaykalia, Russia (Valanginian–Hauterivian): *Glaresis cretacea*, *Cretoglaresis nana*, *Lithoglaresis ponomarenkoi*, *Trox sibericus*, *Avitortor leptoscelis*, *A. ovalis*, *A. primitivus*, *Antemnacrasa latitibialis*, *A. maculata*, (*A. magna*), (*A. nebulosa*), *A. picturata*, *A. sulcata*, *A. vitimensis*, *Baisarabaeus rugosus*, *Cretobolbus rohdendorfi*, *Cretogeotrupes convexus*, *Cretoglaphyrus rohdendorfi*, *Cretohybosorus buryaticus*, *C. striatulus*, *Mimaphodius pusillus*, *Holcorobeus atrosulcatus*, *H. nigrovittatus*, *H. vittatus*, *Proteroscarabaeus yeni* [not in faunal list of Nikolajev 2007b: 220], (*P. magnus*), (*P. nikritini*), *Lithoscarabaeus baissensis*, *Cretaegialia aphodii-formis*, *C. rhypariformis*, (*Cretanoides trogopterus*), (*Hybosorites fissuratus*), *Leptosorus zherikhini*, *Cretonitis copripes*, *Cretomelolontha transbaikalica*, *Cretoserica latitibialis*, *Cretoscarabaeus gibbosus*, *C. lentiginosus*, *Cretorabaeus elongatus* (Ponomarenko 1977b; Nikritin 1977; Nikolajev 1992, 1994, 1995b, 1996, 1998a, 1999, 2004, 2005a,c, 2007).

Leskovo, Leskovskaya Formation, Transbaykalia, Russia (L Neocomian): *Lithanomala crassa*, *L. oblonga*, *L. sibirica* (Ponomarenko 1990; Nikolajev 1992).

Turga, Turginskaya Formation, Transbaykalia, Russia (L Neocomian): *Antemnacrasa incerta* (Ponomarenko 1990).

Gurvan-Erenii-Nuru, Gobi-Altay, Mongolia (L Neocomian): *Antemnacrasa punctatus* (Ponomarenko 1986).

Shar-Tologoy, Bayan-Hongor Aymag, Mongolia: *Cretomorgus ikhbogdensis*, (*Antemnacrasa albo-maculata*), *Cretocoma tologoica* (Nicolajev 2002, 2004, 2007)

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

Bon-Tsagan, Mongolia (U Neocomian–L Aptian): *Cretochodaeus mongolicus*, (*C. striatus*) (Nicolajev 1995a); *Mongolrobus zherikhini* (Nicolajev 2004); *Prototrox transbaikalicus* (Nicolajev 2000a); *Lithochodaeus cretaceus*, *Trox cretaceus*, *Avitortor parallelus*, *A. dolchiodactylus* (Nicolajev 2007b).

Chifeng, Inner Mongolia, China: (*Geotrupoidea*) *fortus* (Ren *et al.* 1995).

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

Jiuquan Basin, Chijinpu Formation, Gansu Province, China (Valanginian, according to Hong 1998): *Mesoscarabaeus corneus*, *M. morulosus*, *Hongscarabaeus brunneus* (Hong 1982).

Laiyang Formation, Shandong Province, China (Barremian–Hauterivian): *Geotrupoidea 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).

Yixian, Hebei Province, China (Tithonian?–Berriasian)⁹: *Geotrupoidea songyingziensis* (Hong 1984).

South America

Santana, Brazil: Scarabaeidae (Grimaldi & Maisey 1990: 7; Grimaldi 1991: 400 [colour photo]; Grimaldi & Engel 2004: 380 [colour photo]); some more specimens (vid. Krell).

Transition Upper Jurassic/Lower Cretaceous

Khutel-Khara, Mongolia: *Mesaclopus mongolicus* (Nicolajev 1992).

⁹ ⁴⁰Ar-³⁹Ar 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).

Upper Jurassic (Malm, 161.2–145.5 Myr)

Europe

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

Asia

Karatau, Kazakhstan (Oxfordian–Kimmeridgian): *Antemnacrasa albosulcata*, *A. nigrimontana* (Nikolajev 1992, 2004); *A. kazakhstanica* (Nikolajev 2007b); *Juraclopus rohdendorfi* (Nikolajev 2005b).

Anda-Zhuduk, Mongolia (Thitonian): *Protolucanus jurassicus* (Nikolajev 2007b).

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

Bayan-Teg, Mongolia: *Jurahybosorus mongolicus* (Nikolajev 2005d).

North America

Morrison Formation, Rocky Mountain Region, USA: ichnofossils: dung beetle nests (Hasiotis 1999), *Coprinisphaera* sp. (Hasiotis 2004); questioned by Bromley *et al.* (2007).

Middle Jurassic (Dogger, 175.6–161.2 Myr)

No reliable records: "*Melolonthidium*" of Philips (1871) from the Stonesfield Slate, England, was not described and needs confirmation. 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, 199.6-175.6 Myr)

No reliable records: The family identity of *Opiselleipon grave* Bode and *Tetragonides magnus* Bode (Lias ϵ from Hondelage, Germany), *Aphodiites protogaeus* Heer (Lower Lias, Schambelen, Switzerland) and *Melolontha* ? sp. (Lower Lias, Cracombe, England; Brodie 1845: 101, pl. 9) cannot be determined. "*Coprinisphaera* sp." from the lower Jurassic of Sołtyków, Poland (Pieńkowski 2004) is neither figured nor described.

Upper Triassic (228.0-199.6 Myr)

No reliable records: Traces of coprophagy on coprolites from the Chinle Formation (Arizona, U.S.A.; Carnian–Norian) were tentatively assigned to Diptera larvae or fungal hyphae. "Dung beetles are clearly too large as possible tracemakers for burrows of the Chinle coprolithes" (Wahl *et al.* 1998: 146), but Krell (2006: 131) disagreed with this statement.

Lower Triassic (251.0-245.0 Myr)

No reliable records: Burrows backfilled with sediment and surface marks in coprolites of the Arcadia formation, southeastern Queensland, Australia (Northwood 2005: 60) were supposedly created by coprophagous invertebrates; dung beetles as tracemakers possible, but speculative (Krell 2006).

Carboniferous (359.2-299.0 Myr)

No records: *Troxites germari* Goldenberg from the hard coals of Saarbrücken, Germany, and the ichnotaxa *Xyloryctes planus* Frič and *X. septarius* Frič from the Upper Carboniferous of Germany and Bohemia, are neither fossils nor traces of Scarabaeoidea.

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