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Catalogue of species-group names assigned to *Copris* Geoffroy, *Coptodactyla* Burmeister, *Litocopris* Waterhouse, *Microcopris* Balthasar, *Paracopris* Balthasar, *Pseudocopris* Ferreira, *Pseudopedaria* Felsche, *Sinocopris* Ochi, Kon and Bai, and *Thyregis* Blackburn
(Coleoptera: Scarabaeidae: Scarabaeinae: Coprini)

Jiri Zidek

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Catalogue of species-group names assigned to *Copris* Geoffroy, *Coptodactyla* Burmeister, *Litocopris* Waterhouse, *Microcopris* Balthasar, *Paracopris* Balthasar, *Pseudocopris* Ferreira, *Pseudopedaria* Felsche, *Sinocopris* Ochi, Kon and Bai, and *Thyregis* Blackburn (Coleoptera: Scarabaeidae: Scarabaeinae: Coprini)

Jiri Zidek
jrzidek@gmail.com

Abstract. Presented are species-group names published in the nine coprine genera (Coleoptera: Scarabaeidae: Scarabaeinae: Coprini) having only one lateral carina on each elytron. The data include authorships, dates and pages of original descriptions, geographic distributions, and references to works pertinent to the topic.

Key words. Genera, species, synonyms, geographic distributions, literature.

Introduction

The subject taxa are united by having only one lateral carina on each elytron. The species have been described either as *Copris* s. str., or placed in subgenera of *Copris* Geoffroy, or regarded as belonging to separate genera. Ferreira (1961b) included in this group also the genus *Copridaspidus* Boucomont, which however has two lateral carinae on each elytron, as do e.g. *Catharsius* Hope and *Metacatharsius* Paulian regarded as belonging in the tribe Dichotomiini (Montreuil 1998; Philips et al. 2004; Davis et al. 2008).

Balthasar's (1939a, 1958) subgenera *Microcopris* (10 species in China and southeastern Asia) and *Paracopris* (22 species in India, Nepal, China and southeastern Asia) were maintained as such by Nguyen-Phung (1988c), Cambefort and Nguyen-Phung (1996) and Marchisio and Zunino (2012), whereas Löbl et al. (2006) and Král and Bezděk (2016) treated them as separate genera. Ferreira (1960, 1961b, 1972) accepted *Paracopris* and *Litocopris* (four Afrotropical species) as subgenera of *Copris*, but elevated *Microcopris* to genus (1961b: 91) and assigned (1960: 4) *Copris lunaticeps* Gillet to a new genus, *Pseudocopris*. Cambefort and Nguyen-Phung (1996) and Davis et al. (2008) treated *Litocopris* as a genus, and Löbl et al. (2006) and Král and Bezděk (2016) synonymized it with *Copris*. As far as I am aware, *Coptodactyla* Burmeister (17 Australian species), *Pseudopedaria* Ferreira (four Afrotropical species) and *Thyregis* Blackburn (four Australian species) have always been treated as genera. In absence of a consensus, all of these taxa, as well as *Sinocopris* Ochi, Kon and Bai (19 species in India, China, Japan, Korean peninsula, e. Siberia and southeastern Asia), are here regarded as genera.

The name *Copris* was long attributed to O. F. Müller (1764), but in 1994 the International Commission on Zoological Nomenclature ruled *Copris* and some other genera of Geoffroy (1762) conserved, and the name thus became available from the latter work (ICZN 1994; Branco 2007: 10). Of the nine genera included in this catalogue it is by far the largest (over 200 species) and most widely distributed, with roughly equal numbers of species inhabiting the Afrotropical (109) and Holarctic–Oriental (99) regions, 32 of them in the Nearctic subregion and Neotropical region. Only one Afrotropical species (*C. diversus* Waterhouse) extends to Madagascar and one Palearctic species (*C. pueli* Mollandin de Boissy) is confined to northern Africa. One Nearctic–Neotropical species (*C. incertus* Say) has been introduced into Hawaii, New Zealand and Vanuatu (Thomas 1961, Gutierrez et al. 1988), one Oriental species (*C. fricator* (Fabricius)) has been introduced into North America (Matthews 1961), and two Palearctic (*C. hispanus* (Linnaeus), *C. lunaris* (Linnaeus)) and three Afrotropical species (*C. diversus* Waterhouse, *C. elphenor* Klug, *C. fallaciosus* Gillet) have been introduced into Australia (Doube et al. 1991, Cassis and Weir 1992).

Afrotropical members of *Copris* were revised by Ferreira (1961b, 1972), Nguyen-Phung (1987, 1988a–c, 1989), Nguyen-Phung and Cambefort (1986a, b, 1987), Cambefort (1992a, b) and Cambefort and Nguyen-Phung (1996). The latter two authors revised 33 species, described 24 new species, and

divided them and a majority of the remaining species into 48 groups. Relatively few Afrotropical species have not been treated or at least mentioned in their works; they are *C. ares* Zelenka, *C. basilewskyi* Ferreira, *C. brittoni* Ferreira, *C. freyi* Ferreira, *C. hartli* Frey, *C. hybridus* Gillet, *C. mourgliai* Zelenka, *C. perturbator* Péringuey and *C. scorpion* Zelenka.

Of the approximately 70 Palearctic and Oriental *Copris* species presumed valid in this catalogue most were re-described by Balthasar (1963), leaving only those described subsequently and two, *C. consobrinus* (Lansberge) and *C. marcus* (Gillet), that he regarded as synonyms of *C. doriae* (Harold) (*Microcopris*) and *C. nevinsoni* Waterhouse, respectively. Balthasar's work contains a key to both sexes and provides a good platform for further studies. Most recently Kabakov (2006) revised the six species inhabiting Russia and the neighboring countries (*C. armeniacus* Faldermann, *C. hispanus* (Linnaeus), *C. lunaris* (Linnaeus), *C. ochus* (Motschulsky) (*Sinocopris*), *C. pecuarius* (Lewis) (*Sinocopris*) and *C. tripartitus* (Waterhouse)), included three more species in his key (*C. acuticollis* (Motschulsky) = *C. acutidens* Motschulsky, *C. pueli* Mollandin de Boissy and *C. umbilicatus* (Abeille de Perrin)), and mentioned a fossil species, *Copris kartlinus* Kabakov, 1988 from the early Pliocene of Georgia [Gruzia] (not included in this catalogue). Finally Ochi and Kon (2004a, b, 2005, 2010, 2014), Ochi, Kon and Bai (2007, 2009), Ochi, Kon and Kawahara (2005, 2008, 2019), Ochi, Kon and Pham (2019) and Ochi, Kusui and Pham (2019) described nearly 30 species, most of them *Paracopris* and *Microcopris*, from Nepal, China (Guanxi, Guizhou, Quinhai, Shanxi, Sichuan, Yunnan, Xizang) and southeastern Asia (Cambodia, Laos, Malay peninsula, Malaysia-Sabah, Myanmar, Vietnam).

All western hemisphere species belong to *Copris* s. str., which was revised by Matthews (1961) who treated 22 previously known species and described one species (*C. lecontei*) and one subspecies (*C. fricator cartwrighti* Robinson) as new. Nine New World species have been described since 1961, bringing the number up to 32. Mexico has the most species (22), followed by Central America (13), followed by the USA (10). Only two species (*C. incertus* Say and *C. laeviceps* Harold) extend from Mexico into western South America. Eight species extend from Mexico into Central America and four others extend from Mexico into the USA, but no species occurs in all three regions. Woodruff (1973) presented accounts of the species occurring in Florida (*C. gopheri* Hubbard, *C. howdeni* Matthews and Halffter, *C. inemarginatus* Blatchley and *C. minutus* (Drury)), and Kohlmann (2003) reviewed the Mexican species except *C. warneri*, which was described subsequently (McCleve and Kohlmann 2005).

The following catalogue is a compilation intended to serve for orientation in the vast number of species names, their original generic / subgeneric assignments and pertinent references. A word of caution is in order concerning the dates of Ferreira's papers in the Instituto de Investigação Científica de Moçambique periodicals, especially the Revista de Entomologia de Moçambique, which were often released a year or more after the date indicated on the title page and at the bottom of each following page of the monograph. This is also evidenced by the authoress referring to species described by her as new in another Revista paper released only a year later. Unfortunately, the real date of publication is apparent only from a hardly noticeable small-print statement in the center of otherwise empty outside back cover, which is not included in pdf versions of papers available in on-line bibliographies, and I have not been able to find these discrepancies corrected anywhere in on-line library records.

The genera and species are listed alphabetically and, for convenience, names of species belonging to all other included genera are left in the first and longest *Copris* list, where they are annotated by the generic name in boldface (e.g. "see ***Litocopris***"). As in any work of this nature, omissions can be expected and reporting them would be appreciated. The cut-off date of the literature search is December 2019.

Catalogue

Synonyms and homonyms are preceded by en dashes (–), subspecies are preceded by asterisks (*). Countries / states with longer names are abbreviated: DRC = Democratic Republic of the Congo, PNG = Papua New Guinea, PRC = Peoples' Republic of the Congo, RSA = Republic of South Africa, USA = United States of America; NSW = New South Wales (Australia), NT = Northern Territory (Australia), WA = Western Australia, WNG = Western New Guinea (Indonesia).

Copris Geoffroy

Geoffroy 1762: 87; type sp. *Scarabaeus lunaris* Linnaeus, 1758.

–*Insulicopris* Tsukamoto 1974: 1; type sp. *Copris brachypterus* Nomura, 1964.

–*Pilularius* Schrank 1798: 394; type sp. *Pilularius lunus* Schrank, 1798 (= *Scarabaeus lunaris* Linnaeus, 1758).

–*Palaeocopris* Pierce 1946: 130; type sp. *Palaeocopris labreae* Pierce, 1946 = *Phanaeus labreae* (Pierce) [late Pleistocene of California, see Miller et al. 1981: 627, Edmonds 1994: 91].

Species-group taxa

–*achates* Péringuey 1901: 346, 365; = *cornifrons*

–*acuticeps* Felsche; see **Coptodactyla**

–*acuticollis* (Motsch.) of Kabakov 2006: 87 [key]; = *acutidens*
acutidens Motschulsky 1860: 13; China (Fujian, Hubei, Sichuan), Japan.

afgoi Cambefort 1992b: 181; Somalia.

agnus Sharp 1875: 47; Borneo, Java, Malaysia, Singapore.

algol Nguyen-Phung 1989: 202; Kenya, Tanzania.

–*amabile* Ferreira 1958a: 3; = *amabilis* Kolbe

amabilis Kolbe 1914: 311; DRC, Uganda.

–*ammon* (Fabricius 1781: 24), as *Scarabaeus*; = *minutus*

amyntor Klug 1855: 655; Kenya, Mozambique, RSA, Zimbabwe.

–*amyntor* Harold 1869a: 61; = *harrisi*

–*anaglypticus* Say 1823: 204; = *fricator fricator*
anceus (Olivier 1789: 116), as *Scarabaeus*; RSA (Cape).

andrewesi (Waterhouse); see **Paracopris**

**angolensis* Ferreira 1962b: 144; ssp. of *cassius*

angusticornis Arrow 1933: 427; China (Fujian, Hubei, Sichuan, Yunnan), Thailand, Vietnam.

**angusticornis* Nguyen-Phung and Cambefort; ssp. of *laius*

angustus Nguyen-phung and Cambefort 1986: 407; Benin, Ivory Coast, Mali, Senegal.

anomiopseoides (Boucomont); see **Paracopris**

antares Ferreira 1958a: 5; RSA (Free State).

apicepunctatus Balthasar; see **Microcopris**

arcturus Gillet 1907: 179; DRC, Gabon.

ares Zelenka 1993: 242; RSA.

arimotoi Ochi and Araya 1992: 83; Indonesia (Sumatra).

arizonensis Schaeffer 1906: 254, 256; Mexico (Chihuahua), USA (Arizona, New Mexico, Texas).

armatus Harold 1869c: 498; Mexico (DF, Guerrero, Hidalgo, Jalisco, México, Michoacán).

armeniacus Faldermann 1835: 238; Armenia, Azerbaijan, Georgia, Iran, Turkey. [sp. inquirenda in Ziani 2017]

armiger Gillet 1910: 1; Burundi, DRC, Kenya, Mozambique, RSA (Transvaal), Tanzania, Zambia, Zimbabwe.

arrowi Felsche 1910: 350; “South China”, Thailand.

aspericollis Gillet 1910: 3; Costa Rica, El Salvador, Guatemala, Mexico (Chiapas).

atropolitus Gillet 1910: 7; DRC, Kenya, Tanzania.

–*baileyi* Blackburn; see **Coptodactyla**

barclayi Ochi, Kon and Bai; see **Sinocopris**

bartolozzii (Ochi, Kon and Pham); see **Paracopris**

basilewskyi Ferreira 1962a: 101; DRC.

basipunctatus (Balthasar); see **Sinocopris**

–*belisama* (Schrank 1798: 394), as *Pilularius*; = *lunaris*

bellator Chevrolat in Guérin-Méneville 1844: 81; Indonesia (Java), Malaysia.

bengalensis Gillet 1911a: 289; China (Guizhou, Xizang, Yunnan), Myanmar, Thailand.

bidens Kolbe 1893: 200; Cameroon.

–*bifidus* (Poda von Neuhaus 1761: 18), as *Scarabaeus*; = *lunaris*

- bihamatus* Balthasar 1965: 20, as *Paracopris*; = *fidius*
bootes Klug 1855: 655; Botswana, Kenya, Mozambique, RSA (Transvaal), Tanzania.
- **borneensis* Ochi and Kon; ssp. of *gibbulus*
- bornemisszai* Ferreira 1972: 167, 783; = *bootes*
boucardi Harold 1869c: 497; El Salvador, Guatemala, Mexico (Guerrero, Oaxaca).
bovinus Gillet 1908a: 68; Angola, DRC.
brachypterus brachypterus Nomura 1964: 50; Japan (Okinawa: Amami-Ōshima).
brachypterus toguchii Ochi and Kawahara 2012: i; Japan (Tokunoshima).
brittoni Ferreira 1962a: 103; DRC, Tanzania.
brooksi Matthews; see ***Coptodactyla***
caelatus Fabricius 1794: 435; Lesotho, Mozambique, RSA.
- **caffer* Gillet; ssp. of *orion*
caliginosus Kohlmann, Cano and Delgado 2003: 2; Guatemala.
- calvus* Sharp 1875: 46; = *saundersi*
cambeforti Nguyen-Phung 1988c: 12; RSA (Transvaal).
cambodiensis Ochi, Kon and Kawahara 2008: 243; Cambodia.
camerunus Felsche 1904: 402; Cameroon.
capensis Waterhouse 1891a: 513; Lesotho, RSA (Cape).
cariniceps (Felsche); see ***Paracopris***
carinicus Gillet 1910: 8; China (Yunnan), India (Assam), Laos, Myanmar, Thailand.
carmelita Fabricius 1801: 39; Benin, Burkina Faso, DRC, Gambia, Guinea, Sierra Leone, Senegal, Uganda.
- **cartwrighti* Robinson 1941: 131; = ssp. of *fricator*
cassius Péringuey 1901: 344, 351; Angola, Botswana, Mozambique, RSA (Cape), Zimbabwe.
- castaneus* Mulsant 1842: 73, as var. of *C. lunaris*; = *lunaris*
- **cavolini* (Petagna); ssp. of *hispanus* [Prevailing usage of the subsequent spelling *cavolinii* has not been officially demonstrated; S. Ziani and T. Branco, pers. comm.]
celebensis Lansberge 1886: 9; Indonesia (Sulawesi).
- **centralis* Gillet; ssp. of *orion*
cheni (Ochi, Kon and Bai); see ***Sinocopris***
chinmontanus (Ochi, Kon and Kawahara); see ***Paracopris***
- **chuduraziensis* Ochi, Kon and Kawahara; ssp. of *pseudochus*; see ***Sinocopris***
- cipriani* Balthasar 1939a: 3, as *Paracopris*; = *coriarius*
–*claudius* (Harold 1877a: 48), as *Catharsius*; = *repertus*
–*clavicornis* Matthews and Halffter 1959: 191; = *moechus*
colmanti Gillet 1908b: 56; Cameroon, DRC, Gabon.
complexus Nguyen-Phung 1989: 206; Burundi, Cameroon, DRC, Kenya, Malawi, Rwanda, Tanzania, Uganda.
compressipennis (Gillet); see ***Paracopris***
confucius Harold 1877a: 48; Cambodia, China (Fujian, Guangdong, Guizhou, Hongkong, Sichuan, Yunnan), Laos, Malaysia, Myanmar, Taiwan, Thailand, Vietnam.
- confusus* Boheman 1857: 240; = *amyntor*
- consobrinus* (Lansberge); see ***Microcopris***
- **continentalis* Ochi and Kon; ssp. of *pecuarius*; see ***Sinocopris***
- contractus* Boheman 1857: 236; = *caelatus*
–*contractus* Péringuey 1901: 344, 352; = *obesus*
convexiusculus Shipp 1897: 450; Somaliland.
coriarius Gillet 1907: 178; DRC, Eritrea, Ethiopia, Guinea, Ivory Coast, Malawi, Nigeria, RSA, Tanzania, Uganda, Zimbabwe [var. of *mesacanthus* in Ferreira 1961: 156].
- corniculatus* Mulsant 1842: 73, as ab. of *lunaris*; = *lunaris*
cornifrons Boheman 1860: 110; Botswana, Mozambique, RSA (Cape).
corniger Sahlberg 1823: 6; Ethiopia, Kenya, Lesotho, RSA.
–*corniger* Harold 1869c: 1014; = *bellator*

- coronatus* (Harold 1877b: 98), as *Catharsius*; = *signatus*
corpulentus Gillet 1910: 13; China (Fujian, Sichuan, Yunnan), India (Arunachal Pradesh), Laos, Myanmar, Thailand, Vietnam.
costaricensis costaricensis Gahan 1894: 116; Costa Rica, Mexico (Chiapas), Panama.
costaricensis dolichocerus Matthews 1961: 97; Guatemala, Mexico (Chiapas).
cribratus (Gillet); see **Paracopris**
cribricollis Gillet 1910: 6; Tanzania.
- curvicornis* Boheman 1860: 110; = *cornifrons* ♀
- davidis* (Deyrolle 1878: 95), as *Catharsius*; = *Catharsius molossus* (syn. Cheung et al. 2018)
davisi Nguyen-Phung and Cambefort 1986b: 104; Angola.
davisoni (Waterhouse); see **Paracopris**
decellei Cambefort 1992a: 29; DRC, Guinea, Rwanda, Uganda.
- deletus* Mulsant 1842: 73, as var. of *lunaris*; = *lunaris*
delicatus Arrow 1931: 117; China (Yunnan), India (Arunachal Pradesh, Assam, Sikkim).
denticulatus Nguyen-Phung 1988b: 216; Mozambique, RSA, Zimbabwe.
depressa Paulian; see **Coptodactyla**
- **dicyrtus* Matthews and Halffter; ssp. of *remotus*
diversus Waterhouse 1891a: 518; Kenya, Somalia, Sudan, Tanzania, Madagascar; introduced into Australia (Queensland, NT, WA).
- **dolichocerus* Matthews; ssp. of *costaricensis*
doriae (Harold); see **Microcopris**
draco Arrow 1906: 127; Angola.
dracunculus Ferreira 1959: 13; DRC.
ducalis Blackburn; see **Coptodactyla**
dudleyi Cambefort 1992a: 30; Malawi.
eburneus Cambefort 1992a: 28; Ivory Coast.
elpheneroides Felsche 1910: 345; Tanzania.
elphenor Klug 1855: 655; Angola, Burkina Faso, Botswana, Cameroon, DRC, Ethiopia, Kenya, Mozambique, Namibia, RSA, Tanzania, Zimbabwe; introduced into Australia (Queensland).
- emarginatus* (Olivier 1789: 115), as *Scarabaeus*; = *lunaris*
erratus erratus Lansberge 1886: 13; Sulawesi.
erratus masayukii Ochi and Kon 2004a: 28; Indonesia (Sulawesi: Peleng I).
evanidus Klug 1855: 655; Botswana, Ethiopia, Kenya, Mozambique, RSA, Tanzania, Uganda, Zimbabwe.
- excavatus* Klug 1855: 655; = *bootes*
excisus (Waterhouse); see **Paracopris**
fallaciosus Gillet 1907: 180; Botswana, Ethiopia, Kenya, Mozambique, Namibia, RSA, Somalia, Uganda, Zimbabwe; introduced into Australia (Queensland).
fallax Felsche 1910: 349; Namibia.
felschei Reitter 1892: 216 [= 1893: 95]; Armenia, Azerbaijan, Georgia, Iran, e. Turkey.
- ferreirae* Frey 1974: 273; = *megaceratoides*
fidius (Olivier 1789: 184), as *Scarabaeus*; DRC, Mozambique, Namibia, RSA.
- **formosanus* Gillet; ssp. of *punctatus*
- frankenbergeri* Balthasar 1934: 149; = *acutidens*
frankenbergerianus Balthasar 1958: 477; China (Sichuan).
freyi Ferreira 1961a: 138; Gabon.
fricator fricator (Fabricius 1787: 15), as *Scarabaeus*; India, Sri Lanka; introduced into much of e.+c. USA and se. Canada (Ontario).
fricator cartwrighti Robinson 1941: 131, as sp.; USA (South Carolina).
- fricator* Harold 1877a: 46; = *erratus*
fujiokai fujiokai Ochi and Kon; see **Microcopris**
fujiokai poringensis Ochi and Kon; see **Microcopris**
fukiensis Balthasar 1953: 225; China (Fujian, Zhejiang), Taiwan.
furciceps (Felsche); see **Paracopris**

- furcillatus* Felsche 1910: 345; = *costaricensis*
- **gabonicus* Cambefort; ssp. of *phungae*
- garambae* Cambefort 1992a: 27; DRC
- gazellarum* Gillet 1918: 148; Burkina Faso, DRC, Sudan, Uganda.
- **genopunctatus* Nguyen-Phung; ssp. of *vankhaii*
- gibbulus gibbulus* Lansberge 1886: 17; Malaysia, Borneo, Java, Sumatra.
- gibbulus borneensis* Ochi and Kon 2005: 71; Malaysia (Sabah).
- gilleti* Kolbe 1907: 25; Tanzania.
- gistelianus* Gistel 1857: 587; = *lunaris*
- glabriceps* Felsche 1910: 346; = *acutidens*
- glabricollis* (Hope); see ***Coptodactyla***
- gladiator* Arrow 1933: 425; Myanmar.
- globulipennis* Waterhouse 1891a: 512; = *sexdentatus* Thunberg
- gopheri* Hubbard 1894: 310; USA (Florida).
- gracilis* Waterhouse 1891a: 518; Namibia.
- **grandis* Nguyen-Phung and Cambefort; ssp. of *inhalatus*
- graueri* Kolbe 1914: 312; Tanzania.
- grossa* (Thomson); see ***Pseudopedaria***
- halffteri* Matthews 1959: 133; Mexico (Guerrero, Morelos, Puebla, San Luis Potosí).
- haroldi* Lansberge 1886: 15; = *spinator*
- harrisi* Waterhouse 1891a: 515; Benin, CAR, DRC, Eritrea, Ethiopia, Kenya, Sierra Leone, Somalia, Sudan, Tanzania, Uganda, Zimbabwe.
- hartli* Frey 1975: 294; Tanzania.
- hatayamai* Ochi and Araya 1992: 79; Malaysia.
- hidakai* Ochi and Kon; see ***Microcopris***
- hintoni* Saylor 1933: 238; = *klugi*
- hispanicus* (Poiret 1789: 297), as *Scarabaeus*; = *hispanus hispanus*
- hispanus hispanus* (Linnaeus 1764: 12), as *Scarabaeus*; western ssp.: s. France incl. Corsica, Sardinia (Italy), Iberian peninsula, Morocco, Tunisia; introduced into Australia (WA).
- hispanus cavolini* (Petagna 1792: 140), as sp. of *Scarabaeus*; eastern ssp.: continental Italy + Sicily, Balkans, Turkey, Israel, n. Iran, c. Asia. [For *C. hispanus* and *C. cavolini* as separate species see Falahee and Angus 2010.]
- hispanus persianus* Mikšić 1958: 1; = *hispanus cavolini*
- hosakai* Ochi and Kon; see ***Microcopris***
- howdeni* Matthews and Halffter 1959: 200; USA (Florida, Georgia?, South Carolina).
- humilis* Gillet 1908a: 71; Tanzania.
- hybridus* Gillet 1910: 11; Tanzania.
- igualensis* Warner 1990: 236; Mexico (Guerrero).
- illotus* Balthasar 1942b: 189; China (Fujian).
- imitans* (Felsche); see ***Paracopris***
- imitatrix* Balthasar; see ***Coptodactyla***
- inaequabilis* Zhang 1997: 758; China (Hubei).
- incertus* Say 1835: 175; Colombia, Ecuador, Mexico (Hidalgo, Puebla, San Luis Potosí, Tamaulipas, Yucatán), Panama; introduced into Hawaii, New Zealand, Vanuatu.
- indicus* Gillet 1910: 5; = *fricator fricator*
- inemarginatus* Blatchley 1918: 54; USA (Florida).
- inhalatus inhalatus* Quedenfeldt 1884: 272; Angola, DRC, Mozambique, Namibia, RSA (Cape), Zimbabwe.
- inhalatus grandis* Nguyen-Phung and Cambefort 1986b: 102; Zimbabwe.
- inhalatus perturbator* Péringuey 1901: 352, as sp.; Botswana, Namibia, RSA, Zimbabwe.
- inhalatus sanctaeluciae* Nguyen-Phung and Cambefort 1986b: 102; RSA (Natal).
- insidiosus* Péringuey 1901: 346, 366; Burundi, DRC, Rwanda, Tanzania, Uganda, Zimbabwe.
- integer* Reiche 1850: 312; Burkina Faso, Burundi, DRC, Ethiopia, Kenya, Rwanda, Tanzania, Zimbabwe.

- integer* Harold 1869a: 61; = *fallaciosus*
interioris Kolbe 1897: 143; Burundi, Cameroon, DRC, Gambia, Guinea, Nigeria, Senegal, Uganda, Tanzania.
iris Sharp 1875: 45; Laos, Malaysia, Myanmar, Thailand, Vietnam.
**isthmiensis* Matthews; ssp. of *lecontei*
jacchoides Nguyen-Phung and Cambefort 1987: 70; Lesotho, RSA.
jacchus (Fabricius 1775: 20), as *Scarabaeus*; Lesotho, Namibia, RSA, Zimbabwe.
jahi Nguyen-Phung and Cambefort 1986a: 413; Cameroon.
javanensis (Bui, Ziegler and Bonkowski); see **Paracopris**
–*jenisonianus* Gistel 1857: 586; = *lunaris*
jucundus Gillet 1933: 326; Cameroon, Guinea.
kachinensis Ochi, Kon and Kawahara 2008: 245; Myanmar.
kasagii (Ochi and Kon); see **Paracopris**
katangae Cambefort and Nguyen-Phung 1996: 286; DRC.
keralensis Gill 1986: 632; India (Kerala).
kershawi Blackburn; see **Thyregis**
kiuchii (Masumoto); see **Sinocopris**
klapperichi Balthasar 1942a: 116; China (Fujian).
klugi klugi Harold 1869c: 498; Mexico (most states), Central America.
klugi sierrensis Matthews 1961: 72; Mexico.
kusakabei (Ochi, Kon and Kawahara); see **Sinocopris**
laeviceps Harold 1869c: 498; Belize, Colombia, Costa Rica, Guatemala, Honduras, Mexico (Chiapas, DF, Oaxaca, Veracruz).
–*laevicollis* Mulsant 1842: 69, as var. of *hispanus*; = *hispanus hispanus*
laevigatus (Gillet); see **Sinocopris**
laiiformis Nguyen-Phung and Cambefort 1987: 72; Zimbabwe.
laioides Boucomont 1932: 46; DRC, Namibia, Zambia, Zimbabwe.
laius laius Harold 1868a: 81; Burkina Faso, DRC, Gambia, Guinea Bissau, Senegal, Sudan.
laius angusticornis Nguyen-phung and Cambefort 1987: 73; Cameroon, Chad, Sudan, Uganda.
lannathai Hanboonsong, Masumoto and Ochi 2003: 108; Thailand.
–*lar* (Fabricius 1787: 13), as *Scarabaeus*; = *minutus*
–*laticornis* Boheman 1857: 226; = *elphenor*
–*laticornis* Wallengren 1881: 20; = *jacchus*
–*laticornis* Péringuey 1901: 343, 347; = *corniger*, *fallaciosus*
lecontei lecontei Matthews 1961: 98; USA (Arizona, New Mexico), Mexico (Chihuahua, Colima, Guerrero, Jalisco, Nayarit, Oaxaca, Sinaloa, Sonora).
lecontei isthmiensis Matthews 1961: 102; Mexico.
lesnei Paulian; see **Coptodactyla**
–*lineatus* Wiedemann 1823: 9; = *sexdentatus*
lugubris Boheman 1858: 42; Belize, Costa Rica, El Salvador, Guatemala, Honduras, Mexico (most states), Nicaragua, Panama.
–*lunarioides* Waterhouse 1891a: 513; = *corniger*
lunaris (Linnaeus 1758: 346), as *Scarabaeus*; UK, s. Sweden, c.+s.+e. Europe, w. China, w. Siberia, Turkey, Syria, Iran, c. Asia, Kazakhstan; introduced to Australia.
lunaticeps (Gillet); see **Pseudocopris**
–*lunus* (Schrank 1798: 393), as *Pilularius*; = *lunaris*
macacus Lansberge 1886: 14; Indonesia (Sulawesi).
macclevei Warner 1990: 232; Mexico (Sonora), USA (Arizona).
macer Péringuey 1901: 343, 346; Angola, Mozambique, Namibia, RSA (Transvaal), Swaziland, Tanzania, Zimbabwe.
maesi Ratcliffe 1998: 93; Nicaragua.
magicus Harold 1881: 88; China (Guizhou, Hubei, Hunan, Sichuan, Xinjiang, Yunnan), India (Sikkim), Laos, Myanmar, Thailand, Vietnam.

- manni* (Ochi, Kon and Bai); see ***Sinocopris***
- marcoberrai* Ochi, Kon and Pham 2019: 435; c. Vietnam (Quang Nam).
- marcus* (Gillet); see ***Microcopris***
- marianus* (Petiver 1764: 27), as *Scarabaeus*; = *hispanus hispanus*
- martinae* Nguyen-Phung 1988a: 257; Tanzania.
- martinezi* Matthews and Halffter 1968: 154; Mexico (Durango).
- **masayukii* Ochi and Kon; ssp. of *erratus*
- matthewsi* Reid; see ***Coptodactyla***
- matthewsi matthewsi* Delgado and Kohlmann 2001: 344; Guatemala, Mexico (Chiapas).
- matthewsi pacificus* Delgado and Kohlmann 2001: 348; El Salvador, Guatemala, Mexico.
- medogensis* Zhang 1988: 228; China (Xizang).
- megaceratoides* Waterhouse 1891a: 511; DRC, Gambia, Guinea, Nigeria, Senegal.
- megasoma* Matthews and Halffter 1959: 194; Mexico (Durango, Michoacán).
- merdeka* Reid; see ***Coptodactyla***
- meridionalis* Matthews; see ***Coptodactyla***
- mesacanthus mesacanthus* Harold 1878: 45; Angola, DRC, Malawi, Mozambique, Namibia, RSA, Zambia, Zimbabwe.
- mesacanthus transvaalensis* Nguyen-Phung 1988c: 10; RSA.
- mexicanus* Matthews and Halffter 1959: 194; Mexico (Michoacán).
- minator* Harold 1880: 152; = *anceus* [valid in Gillet 1910]
- mindorensis* (Ochi); see ***Microcopris***
- minutissimus* (Kryzhanovskii and Medvedev); see ***Microcopris***
- minutus* (Drury 1770: 78), as *Scarabaeus*; e.+c. USA.
- misellus* Péringuey 1901: 344, 349; Botswana, DRC, Mozambique, Namibia, RSA, Zambia, Zimbabwe.
- modestus* Boheman 1857: 242; = *evanidus*
- moechus* LeConte 1854: 222; Mexico (Chihuahua, Durango), USA (Texas).
- moffartsi* Gillet 1907: 177; Burundi, Cameroon, DRC, Kenya, Rwanda, Uganda.
- mongkhoni* Hanboonsong, Masumoto and Ochi 2003: 114; Thailand.
- monstrosa* Felsche; see ***Coptodactyla***
- monteithi* Matthews; see ***Thyregis***
- **montivagus* Gillet 1908a: 80, as var. of *harrisi* [valid sp. in Gillet 1910, var. of *harrisi* in Ferreira 1961: 209].
- montreuili* (Ochi, Kon and Pham); see ***Paracopris***
- morgani* Waterhouse 1891a: 514; = *carmelita*
- morphaeus* Gillet 1932: 325; Kenya.
- mourgliai* Zelenka 1993: 239; Somalia.
- muelleri* Balthasar 1939b: 42; = *acutidens*
- muticus* (Boheman); see ***Litocopris***
- muticus* (Péringuey); see ***Litocopris***
- neglectus* Moxey 1963: 25; India (Tamil Nadu).
- nepos* Gillet 1908a: 76; Burundi, DRC, Kenya, Rwanda, Tanzania, Uganda, Zimbabwe.
- nepticulus* Kolbe 1897: 144; = *diversus*
- neptis* Reiche 1850: 314; = *orphanus* Guérin-Ménéville
- nevinsoni* Waterhouse 1891a: 519; Cambodia, Laos, Malaysia, Thailand, Vietnam.
- nitida* Paulian; see ***Coptodactyla***
- novaki* Zelenka 1992: 167; Malaysia.
- nubilosus* Kohlmann, Cano and Delgado 2003: 4; Guatemala, Honduras.
- numa* Lansberge 1886: 19; India (Assam), Indonesia (Borneo, Sumatra), Malaysia, Myanmar.
- obenbergeri* (Balthasar); see ***Sinocopris***
- obesus* Boheman 1857: 237; Lesotho, Mozambique, RSA, Tanzania, Zimbabwe.
- obliteratus* Mulsant 1842: 73, as var. of *lunaris*; = *lunaris*
- ochus* (Motschulsky); see ***Sinocopris***
- oedipus* (Fabricius 1775: 20), as *Scarabaeus*; = *jacchus*

- olivieri* (Ochi, Kon and Kawahara); see ***Paracopris***
onitoides Gillet; see ***Coptodactyla***
 –*orientalis* Fabricius 1792: 52; = *repertus*
orion orion Klug 1835: 34; Angola, Burkina Faso, Burundi, Cameroon, DRC, Gambia, Kenya, Mozambique, Namibia, RSA, Rwanda, Senegal, Tanzania.
orion caffer Gillet 1908a: 70, as var.; RSA.
orion centralis Gillet 1908a: 70, as var.; DRC.
orion overlaeti (Balthasar 1961: 98), as sp.; DRC, Gabon, Rwanda(?).
orphanus Guérin-Ménéville 1847: 308; Angola, Burundi, DRC, Ethiopia, Guinea, Kenya, Rwanda, Tanzania, Uganda.
 –*orphanus* Péringuey 1901: 344, 350; = *evanidus*
 –*orphanus* Ferreira 1958b: 501; = *gracilis*
 –*oryctes* (Herbst); see ***Microcopris***
 **overlaeti* (Balthasar); ssp. of *orion*
 **pacificus* Delgado and Kohlmann; ssp. of *matthewsi*
 –*paniscus* (Fabricius 1775: 123), as *Scarabaeus*; = *hispanus hispanus papua* Lansberge; see ***Coptodactyla***
parapecuarius (Ochi, Kon and Kawahara); see ***Sinocopris***
parasonensis Ochi, Kon and Pham 2019: 437; Laos (Hua Phan).
pauliani Nguyen-Phung and Cambefort 1986a: 413; Cameroon.
 –*pauliani* (Frey); see ***Thyregis***
pecuarius pecuarius (Lewis); see ***Sinocopris***
pecuarius continentalis Ochi and Kon; see ***Sinocopris***
pedarioides (Lansberge); see ***Paracopris***
 –*persianus* Mikšić 1958:1; = *hispanus cavolini*
 –*persimilis* Felsche 1908: 273; = *fallaciosus*
 **perturbator* Péringuey; ssp. of *inhalatus*
phungae phungae Cambefort 1992b: 181; Gabon, Ivory Coast.
phungae gabonicus Cambefort 1992b: 182; Gabon.
phylax Gillet 1908b: 59; Cameroon, DRC, Ivory Coast.
 –*pluridens* Gillet 1908a: 70; = *interioris*
 –*plutus* (Fabricius 1794: 436), as *Scarabaeus*; = *fidius*
poggii Ochi and Kon 2005: 69; Malaysia (Sabah).
 –*pompilius* Waterhouse 1875: 75; = *sarpedon*
popaensis (Ochi, Kon and Kawahara); see ***Paracopris***
 poringensis* Ochi and Kon; ssp. of *fujiokai*; see *Microcopris***
potanini Semenov 1891: 310; China (Gansu).
 –*procidius* Say 1835: 176; = *incertus* [var. of *incertus* in Gillet 1910]
 –*pronus* Gerstaecker 1884: 50; = *integer*
propinquus (Felsche); see ***Microcopris***
 –*pseudobootes* Ferreira 1962a: 104; = *typhoeus*
pseudochus pseudochus (Ochi and Kon); see ***Sinocopris***
pseudochus chuduraziensis Ochi, Kon and Kawahara; see ***Sinocopris***
 –*pseudolunaris* Ferreira 1969: 3; = *hispanus hispanus*
pseudosinicus Balthasar 1958: 475; “China”.
pueli Mollandin de Boissy 1905: 110; Algeria, Tunisia, Armenia?, Iran?, Turkey?
pumiliaris Wallengren 1881: 20; RSA (Transvaal).
punctatus punctatus Gillet 1910: 4; China (Fujian, Sichuan), Myanmar, Thailand.
punctatus formosanus Gillet 1921: 126; Taiwan.
puncticollis Boheman 1857: 243; Mozambique, Zimbabwe.
punctipennis Boucomont 1914: 333, 335; Indonesia (Sumatra).
punctiventris Waterhouse; see ***Litocopris***
punctulatus punctulatus (Wiedemann); see ***Paracopris***

- punctulatus septentrionalis* (Ochi, Kon and Pham); see ***Paracopris***
- punjabensis* (Gillet); see ***Paracopris***
- quadridentatus* (DeGeer 1778: 638), as *Scarabaeus*; = *lunaris*
- quasilaevigatus* (Ochi, Kon and Bai); see ***Sinocopris***
- ramosiceps* (Gillet); see ***Paracopris***
- rebouchei* Harold 1869c: 497; Mexico (Guerrero, Jalisco, México, Michoacán, Morelos, Nuevo León, Puebla, Veracruz).
- reflexus* (Fabricius); see ***Microcopris***
- reflexus* (Panzer 1794: 7), as *Scarabaeus*; = *minutus*
- relictus* Matthews; see ***Thyregis***
- remotus remotus* LeConte 1866: 381; Mexico (Coahuila, Nuevo León, Tamaulipas), USA (Oklahoma, Texas).
- remotus dicyrthus* Matthews and Halffter 1959: 198; Mexico.
- renwarti* Nguyen-Phung and Cambefort 1986a: 407; Ivory Coast.
- repterus* Walker 1858: 208; China (Xizang, Yunnan), India (Himachal Pradesh, Sikkim, Uttar Pradesh), Nepal, Sri Lanka, Thailand.
- retusus* Mulsant 1842: 68, as var. of *C. paniscus*; = *hispanus hispanus*
- ribbei* Lansberge 1886a: 12; Indonesia (Sulawesi).
- riekoei* Ochi and Kon 2003: 51; Laos.
- ritsemae* Harold 1875: 137; Lesotho, RSA.
- ruandanus* (Balthasar); see ***Litocopris***
- rugosus* Gillet 1908a: 77; Uganda.
- ruvicola* Balthasar 1933: 266; China (Sichuan).
- sabinus* (Gillet); see ***Sinocopris***
- sacontala* (Kollar and Redtenbacher) [in Redtenbacher]; see ***Sinocopris***
- sallei* Harold 1869c: 496; Mexico (Veracruz to Chiapas).
- **sanctaeluciae* Nguyen-Phung and Cambefort; ssp. of *inhalatus*
- sarpedon* Harold 1869b: 104 [replacement name for *sexdentatus* Kollar and Redtenbacher]; India (Himachal Pradesh, Uttar Pradesh), Nepal, Thailand, Vietnam–Laos (Annam).
- saundersi* Harold 1868b: 99; Sulawesi.
- schoolmeestersi* Ochi and Kon 2010: 127; Nepal.
- schoutedeni* Boucomont 1928: 419; = *wiesei*
- scorpio* Zelenka 1993: 241; Tanzania.
- senegalensis* Gillet 1910: 15; Senegal.
- **septentrionalis* (Ochi, Kon and Pham); ssp. of *punctulatus*; see ***Paracopris***
- serius* Nguyen-Phung 1987: 271; Tanzania.
- servius* Harold 1877a: 46; = *agnus*
- sexdentatus* Thunberg 1818: 404; RSA (Cape), Zimbabwe.
- sexdentatus* Kollar and Redtenbacher 1844: 520 [in Redtenbacher]; = *sarpedon*
- siamensis* Gillet 1910: 12; Thailand.
- siangensis* Biswas 1979: 339; India (Arunachal Pradesh).
- **sierrensis* Matthews; ssp. of *klugi*
- signatus* (Walker); see ***Paracopris***
- silenus* (Fabricius 1775: 21), as *Scarabaeus*; = *minutus*
- similis* Balthasar 1939a: 4, as *Paracopris*; = *mesacanthus*
- simillimus* Felsche 1910: 346 [erroneously as from “Sierra Leone”]; = *minutus*
- simonettai* Cambefort 1992b: 179; Somalia.
- simplex* (Harold); see ***Litocopris***
- simulator* Nguyen-Phung and Cambefort 1986a: 409; Chad.
- singularis* Nguyen-Phung and Cambefort 1986a: 406; Ethiopia.
- sinicus* Hope 1842a: 60; China (Fujian, Hubei, Jiangxi, Sichuan, Shanghai, Yunnan), Cambodia, Indonesia (Java), Malaysia, Thailand, Vietnam–Laos (Annam).
- sinon* (Olivier 1789: 123), as *Scarabaeus*; Gambia, Mauritania, Senegal.

- sinuatus* Mulsant 1842: 68, as var. of *C. paniscus*; = *hispanus cavolini*
sodalis Walker 1858: 208; Sri Lanka.
sorex Balthasar 1942a: 117; China (Fujian).
sphaeropterus Harold 1877b: 98; RSA (Cape), Zimbabwe.
spinator Harold 1881: 89; India (Nicobar Is.), Indonesia (Borneo, Sumatra), Malaysia.
stereocera Gillet; see ***Coptodactyla***
storeyi Reid; see ***Coptodactyla***
subaenea Harold; see ***Coptodactyla***
subdolosus Balthasar 1958: 476; China (Fujian).
subpunctatus Gillet 1910: 3; Costa Rica, Panama.
subsidents Péringuey 1901: 344, 355; Botswana, Namibia.
–*sulcicollis* Lansberge 1886: 10; = *sinicus* [valid in Gillet 1910]
sumatrensis Gillet 1921: 123; Sumatra.
surdus (Arrow); see ***Paracopris***
szechouanicus Balthasar 1958: 479; China (Fujian, Guizhou, Hunan, Sichuan, Zhejiang).
–*taprobanus* Gillet 1910: 9; = *sodalis*
tarsatus (Paulian); see ***Thyregis***
tetraodon Gillet 1910: 11; Philippines.
–*tiberius* Schaufuss 1885: 188; = *saundersi*
**toguchii* Ochi and Kawahara; ssp. of *brachypterus*
torresica Matthews; see ***Coptodactyla***
**transvaalensis* Nguyen-Phung; ssp. of *mesacanthus*
tridens Felsche 1901: 150; Cameroon, DRC.
–*tridens* Mulsant 1842: 68, as var. of *paniscus*; = *hispanus cavolini*
tridentatus Solís and Kohlmann 2003: 2; Costa Rica.
tripartitus Waterhouse 1875: 74; China (Fujian, Sichuan, Yunnan), Taiwan, Japan, Korean peninsula.
–*trogodytarum* Roth 1851: 124; = *integer*
truncatus Felsche 1901: 150; Ivory Coast.
tsukamotoi (Ochi, Kon and Kawahara); see ***Sinocopris***
tuberculata Gillet; see ***Coptodactyla***
tubericollis (Felsche); see ***Pseudocopris***
–*tullius* (Olivier 1789: 118), as *Scarabaeus*; = *fricator fricator*
–*tullius* Harold 1877a: 45; = *spinator*
typhoeus Gerstaecker 1884: 50; Kenya.
uenoi (Hanboonsong, Masumoto and Ochi); see ***Sinocopris***
umbilicatus Abeille de Perrin 1901: 68; Albania, Bulgaria, Croatia, France (incl. Corsica), Greece, Hungary, Italy, Romania, Slovakia, Turkey.
urus Boheman 1857: 229; Mozambique, RSA, Swaziland.
usambaricus Gillet 1908a: 80; Kenya, Tanzania.
vankhahii vankhahii Nguyen-Phung 1988c: 12; Ethiopia, Somalia.
vankhahii genopunctatus Nguyen-Phung 1988c: 15; Kenya, Tanzania.
victorini Boheman 1857: 234; RSA (Cape, Natal).
–*victorini* Péringuey 1901: 344, 354; = *ritsemae*
vietnamicus Kabakov 1994: 300; Vietnam.
vilhenai Ferreira 1962b: 154; Angola.
villiersi Walter; see ***Pseudopedaria***
vitalisi (Gillet); see ***Microcopris***
vrydaghi Ferreira 1962a: 105; DRC, RSA (Natal).
warneri McCleve and Kohlmann 2005: 18; Mexico (Chihuahua, Sonora).
wiesei Kolbe 1914: 310; Burundi, DRC, RSA (Cape), Rwanda, Tanzania, Uganda.
–*yamamotoi* (Tesař); see ***Sinocopris***
yangi (Ochi, Kon and Bai); see ***Sinocopris***
yokoae Ochi, Kusui and Pham; see ***Microcopris***

youngai Balthasar 1967: 49, 50; PRC (Brazzaville).
zhangii (Ochi, Kon and Bai); see *Sinocopris*

***Coptodactyla* Burmeister**

Burmeister 1846: 90; type sp. *Copris glabricollis* Hope, 1842b.

–*Boucomontia* Paulian 1933: 67, as sg.; no type sp., invalid name (Matthews 1976: 28).

Species-group taxa

–*acuticeps* Felsche 1909: 754; = *ducalis*
 –*baileyi* Blackburn 1889: 1251; = *glabricollis*
brooksi Matthews 1976: 43; Australia (n. Queensland).
depressa Paulian 1933: 70; Australia (n. Queensland).
ducalis Blackburn 1903: 263; Australia (n. Queensland).
glabricollis (Hope 1842b: 424), as *Copris*; Australia (NT, n. Queensland).
 –*imitatrix* Balthasar 1965: 21; = *depressa*
lesnei Paulian 1933: 72; Australia (NT).
matthewsi Reid 2000: 236; Australia (n. Queensland).
merdeka Reid 2000: 240; WNG.
meridionalis Matthews 1976: 34; Australia (s. Queensland).
monstrosa Felsche 1909: 754; Australia (n. Queensland).
nitida Paulian 1933: 70; Australia (n. Queensland).
onitoides Gillet 1925: 6; Australia (c.+n. Queensland).
papua Lansberge 1885: 393; w. PNG.
stereocera Gillet 1911a: 288; Australia (NT).
storeyi Reid 2000: 244; Australia (n. Queensland).
subaenea Harold 1877a: 40; Australia (n. Queensland).
torresica Matthews 1976: 49; Australia (n. Queensland).
tuberculata Gillet 1925: 5; “Nouvelle-Guinée”.

***Litocopris* Waterhouse**

Waterhouse 1891b: 53; type sp. *Litocopris punctiventris* Waterhouse, 1891.

Species-group taxa

muticus (Boheman 1857: 238), as *Copris mutica*; Burundi, DRC, RSA (Cape), Rwanda, Uganda.
 –*muticus* (Péringuey 1901: 346, 367), as *Copris*; = *simplex*
punctiventris Waterhouse 1891b: 54; Burundi, DRC, Cameroon, Rwanda, Senegal, Tanzania, Togo, Uganda.
ruandanus (Balthasar 1961: 99), as sg. of *Copris*; Rwanda.
simplex (Harold 1868a: 81), as *Copris*; RSA (Cape).

***Microcopris* Balthasar**

Balthasar 1958: 474; type sp. *Scarabaeus reflexus* Fabricius, 1787.

Species-group taxa

apicepunctatus Balthasar 1942b: 190; China (Fujian).
 –*consobrinus* (Lansberge 1886: 22), as *Copris*; = *doriae* [valid in Gillet 1910]
doriae (Harold 1877a: 49), as *Copris*; Indonesia (Borneo, Sumatra), Malaysia (Malacca), Myanmar (Tenasserim).
fujiokai fujiokai Ochi and Kon 1996: 20; Borneo (w. Kalimantan).
fujiokai poringensis Ochi and Kon 2005: 73; Malaysia (Sabah).
hidakai Ochi and Kon 1996: 22; Malaysia (Sabah).

- hosakai* Ochi and Kon 2014: 86; Malay peninsula.
 –*marcus* (Gillet 1921: 123), as *Copris*; Cambodia, Malaysia. [syn. of *nevinsoni* (*Copris*) in Balthasar 1963: 345]
mindorensis (Ochi 1992: 13), as sg. of *Copris*; Philippines (Mindoro I.).
 –*minutissimus* (Kryzhanovskii and Medvedev 1966: 392), as *Copris*; = *propinquus*
 –*oryctes* (Herbst 1789: 215), as *Scarabaeus*; = *reflexus* Fabricius [valid in Gillet 1910]
 **poringensis* Ochi and Kon; ssp. of *fujiokai*
propinquus (Felsche 1910: 347), as *Copris*; China (Fujian, Sichuan, Yunnan), Taiwan, se. Asia.
reflexus (Fabricius 1787: 16), as *Scarabaeus*; China (Fujian, Hainan, Hubei, Sichuan, Yunnan).
vitalisi (Gillet 1921: 124), as *Copris*; Cambodia, China (Yunnan), India (Assam), Laos, Myanmar, Thailand, Vietnam.
yokoae Ochi, Kusui and Pham 2019: 44; Vietnam.

Paracopris Balthasar

Balthasar 1939a: 2; type sp. *Copris punctulatus* Wiedemann, 1823.

Species-group taxa

- andrewesi* (Waterhouse 1891a: 521), as *Copris*; India (Karnataka, Madhya Pradesh, Maharashtra, Orissa, Rajasthan, West Bengal), Nepal.
anomiopseoides (Boucomont 1924: 210), as *Copris*; Laos, Myanmar, Vietnam.
bartolozzii (Ochi, Kon and Pham 2019: 439); as sg. of *Copris*; Vietnam (Bac Kan).
cariniceps (Felsche 1910: 348), as *Copris*; China (Fujian, Hongkong, Jiangsu, Jiangxi, Nanjing, Shanghai, Yunnan, Zhejiang), Taiwan (Kaohsiung, Kenting, Lanyu I.), Vietnam.
chinmontanus (Ochi, Kon and Kawahara 2019: 476), as sg. of *Copris*; Myanmar (Chin).
compressipennis (Gillet 1910: 14), as *Copris*; India (Assam, Manipur, Sikkim, West Bengal).
cribratus (Gillet 1927: 253), as *Copris*; India (Arunachal Pradesh, Gujarat, Karnataka, Kerala, Meghalaya, Rajasthan, Tamil Nadu, Uttar Pradesh).
davisoni (Waterhouse 1891a: 520), as *Copris*; c.+s. India (Madhya Pradesh, Karnataka, Kerala, Tamil Nadu).
excisus (Waterhouse 1891a: 521), as *Copris*; India (Himachal Pradesh, Punjab, Uttarakhand), Pakistan (Azad Kashmir).
furciceps (Felsche 1910: 348), as *Copris*; India (Arunachal Pradesh, Gujarat, Meghalaya, Rajasthan, Sikkim, Uttar Pradesh, West Bengal), Laos, Myanmar, Thailand, China.
imitans (Felsche 1910: 347), as *Copris*; India (Chhattisgarh, Goa, Gujarat, Karnataka, Madhya Pradesh, Maharashtra, Rajasthan), Nepal.
javanensis (Bui, Ziegler and Bonkowski 2019: 53), as sg. of *Copris*; Indonesia (Java).
kasagii (Ochi and Kon 1996: 25), as sg. of *Copris*; Indonesia (Sumatra).
montreuili (Ochi, Kon and Pham 2019: 442), as sg. of *Copris*; Vietnam (Quang Nam).
olivieri (Ochi, Kon and Kawahara 2019: 470), as sg. of *Copris*; Myanmar (Kachin).
pedarioides (Lansberge 1886: 23), as *Copris*; India (Madhya Pradesh), Indonesia (Java), Malaysia.
popaensis (Ochi, Kon and Kawahara 2019: 474), as sg. of *Copris*; Myanmar (Mandalai region).
punctulatus punctulatus (Wiedemann 1823: 11), as *Copris*; Cambodia, China (Anhui, Yunnan), India (Arunachal Pradesh, Assam, Rajasthan), Indonesia (Java, Sulawesi), Laos, Malaysia, Myanmar, Thailand, Vietnam (Son La, Dien Bien, Quang Binh).
punctulatus septentrionalis (Ochi, Kon and Pham 2019: 444), as sg. of *Copris*; Vietnam (Phu Tho).
punjabensis (Gillet 1921: 126), as *Copris*; India (Haryana, Himachal Pradesh, Punjab, Uttarakhand), Nepal, Pakistan.
ramosiceps (Gillet 1921: 126), as *Copris*; Borneo, s. China, India, Malaysia, Myanmar.
 **septentrionalis* (Ochi, Kon and Pham); ssp. of *punctulatus*
signatus (Walker 1858: 208), as *Copris*; India (Himachal Pradesh, Karnataka, Kerala, Madhya Pradesh, Maharashtra, Puducherry, Rajasthan, Tamil Nadu), Laos.
surdus (Arrow 1931: 132), as *Copris*; India (Madhya Pradesh, Rajasthan, Uttarakhand).

***Pseudocopris* Ferreira**

Ferreira 1960: 4; type sp. *Copris lunaticeps* Gillet, 1910.

Species-group taxa

lunaticeps (Gillet 1910: 16), as *Copris*; Angola (type loc. Zambeze), Zambia.
tubericollis (Felsche 1910: 349), as *Copris*; DRC, Kenya, Tanzania, Zambia.

***Pseudopedaria* Felsche**

Felsche 1904: 400; type sp. *Pedaria grossa* Thomson, 1858.

Species-group taxa

grossa (Thomson 1858: 49), as *Pedaria*; Cameroon, DRC.
villiersi Walter 1984: 90; Gabon.

***Sinocopris* Ochi, Kon and Bai**

Ochi, Kon and Bai 2009: 207; type sp. *Copris uenoi* Hanboonsong, Masumoto and Ochi, 2003.

Species-group taxa

- barclayi* Ochi, Kon and Bai 2009: 209; China (Yunnan).
basipunctatus (Balthasar 1942a: 115), as *Copris*; China (Fujian).
cheni (Ochi, Kon and Bai 2007: 137), as *Copris*; China (Xizang).
 **chuduraziensis* Ochi, Kon and Kawahara; ssp. of *pseudochus*
 **continentalis* Ochi and Kon; ssp. of *pecuarius*
kiuchii (Masumoto 1989: 87), as *Copris*; Thailand.
kusakabei (Ochi, Kon and Kawahara 2005: 275), as *Copris*; Myanmar (Kachin).
laevigatus (Gillet 1927: 252), as *Copris*; China (Sichuan), India (Assam), Thailand.
manni (Ochi, Kon and Bai 2009: 211), as *Copris*; China (Sichuan, Shanxi, Guanxi).
obenbergeri (Balthasar 1933: 263), as *Copris*; China (Henan, Sichuan, Yunnan), Thailand.
ochus (Motschulsky 1861: 13), as *Catharsius*; China (Fujian, Guangdong, Henan, Nei Mongol, Zhejiang),
 Japan, Korean peninsula, Mongolia(?), Russia (se. Siberia).
parapecuarius (Ochi, Kon and Kawahara 2008: 251), as *Copris*; Myanmar.
pecuarius pecuarius (Lewis 1884: 17), as *Copris*; Japan, Korean peninsula, Russia (e. Siberia).
pecuarius continentalis Ochi and Kon 2010: 130; North Korea.
pseudochus pseudochus (Ochi and Kon 2004b: 343), as *Copris*; China (Guizhou).
pseudochus chuduraziensis Ochi, Kon and Kawahara 2019: 469; Myanmar (Kachin).
quasilaevigatus (Ochi, Kon and Bai 2007: 142), as *Copris*; China (Sichuan, Xizang).
sabinus (Gillet 1910: 17), as *Copris*; India (Himachal Pradesh, Uttar Pradesh), Nepal.
sacotala (Kollar and Redtenbacher 1844: 519) [in Redtenbacher], as *Copris*; China (Xizang), India
 (Himachal Pradesh, Sikkim, Uttar Pradesh), Nepal.
tsukamotoi (Ochi, Kon and Kawahara 2008: 248), as *Copris*; Myanmar.
uenoi (Hanboonsong, Masumoto and Ochi 2003: 106), as *Copris*; Thailand.
 –*yamamotoi* (Tesař 1937: 101), as *Copris*; = *pecuarius pecuarius*
yangi (Ochi, Kon and Bai 2007: 140), as *Copris*; China (Sichuan).
zhangii (Ochi, Kon and Bai 2009: 214), as *Copris*; China (Quinhai, Guizhou, Sichuan).

***Thyregis* Blackburn**

Blackburn 1904: 145; type sp. *T. kershawi* Blackburn, 1904.

–*Arrowianella* Paulian 1933: 68; type sp. *A. tarsata* Paulian, 1933.

Species-group taxa

kershawi Blackburn 1904: 145; Australia (e. NSW, Victoria).

- monteithi* Matthews 1976: 26; Australia (s. Queensland).
–*pauliani* (Frey 1970: 153), as *Arrowianella*; = *kershawi*
relictus Matthews 1976: 25; Australia (NSW).
tarsatus (Paulian 1933: 68), as *Arrowianella*; Australia (NSW, WA).

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