



Coleoptera Associated with Vertebrate Necromass and Dung

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Chapter 3

Coleoptera associated with vertebrate necromass and dung

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and Teruo Ochi

Summary

Coleoptera (primarily the families Silphidae, Leiodidae, Geotrupidae, and Scarabaeidae), were sampled from vertebrate carrion and dung at three sites in Ganzi Prefecture, Sichuan Province, China between 21 August and 9 September 2005. The sites sampled were: (1) Danba County, road S of Donggu town (2-17 km S) along Kui Yong creek valley (2) Kangding County, Pengta Town, Tongling village road up Zhong Gu Lou gou Valley, and (3) Yajiang County, Valley S of Decha village. Identifications to genus or species rank were accomplished for 672 beetle specimens that represent 42-43 species, of which 10-11 are undescribed (24%). These were distributed among the following families: Silphidae (13-14 species, 1-2 new), Leiodidae (9 species, 7 new), Geotrupidae (6 species, 1 new), Scarabaeidae (14 species, 1 new).

Fourteen of the 32 described species (44%) are known only from records in China and are, therefore, possibly endemic to China – five of which are known only from Sichuan Province (16%). Two described geotrupid species known previously only from Yunnan Province are reported from Sichuan Province for the first time (*Enoplotrupes yunnanus* and *Odontotrupes meymintang*). Including the undescribed / newly discovered species, Site 1 had 8 species known only from China, 3 of which were known only from Sichuan Province; Site 2 had 12 species known only from China, 4 of which were known only from Sichuan Province, and Site 3 had 15 species known only from China, 8 of which were known only from Sichuan Province. Site 3 therefore had the greatest counts of species known only from China and Sichuan Province.

Introduction

Carrion and dung associated insect assemblages constitute rich and ecologically important components of terrestrial ecosystems (Puman 1978, 1983; Hanski and Camberfort 1991; Sikes 1994; DeVault et al. 2003). These species remove carrion and dung as food for their offspring and thus increase nutrient cycling (Bornemissza and Williams 1970) while reducing total vertebrate parasite and pathogen transmission (Bryan 1976, Berdela et al. 1994). In addition, they benefit some plant communities by dispersing and burying seeds in dung (Janzen 1982). These insects are relatively easy to sample using baits of their food sources which makes them ideal targets for rapid ecological assessment. Although many insect species can survive in small patches of habitat, dung and carrion feeders are dependent on the continual health of the vertebrates which produce their food – and these larger organisms typically need fairly large and undisturbed patches of habitat. Samples of carrion and dung associated insects therefore provide information on both habitat health, in general, and terrestrial vertebrate community health in particular. Klein (1989) demonstrated that clear differences in the dung and carrion beetle fauna could be detected between plots of forest of different fragment sizes in the Amazon. Forest fragments had fewer species, sparser populations, and smaller beetles than intact forests (Klein 1989).

For this RAP survey we chose to sample carrion beetles of two families: Silphidae and Leiodidae. Dung beetles were sampled from two families: Geotrupidae and Scarabaeidae (although some carrion associated species sometimes visit dung and vice versa).

The beetle family Silphidae contains two subfamilies: the Silphinae which breed using large (>300 g) vertebrate carcasses as resources and the Nicrophorinae which breed using small (<300 g, typically <100g) vertebrate carcasses. These beetles are therefore indicator species of different components of vertebrate communities. They are also, unlike many insects, better represented in the temperate

zones than the tropics. When they do occur in the tropics they are found at high elevations in cool, moist forests.

The subfamily Nicrophorinae is hypothesized to have originated in Asia in or near current Sichuan Province (Peck and Anderson 1985, Sikes 2003). The evidence for this is based on the preliminary phylogeny of the group which suggests that all the basal lineages (3 genera and 1 subgenus) of the subfamily occur near or in this region (Sikes 2003). At least 12 species of nicrophorines are known from Sichuan Province, which is a sizeable number for this taxon – representing 18% of the species in the subfamily, 31% of the Palearctic fauna (39 species) and more than the entire nicrophorine fauna of Japan (10 species). It is safe to say that Sichuan Province is not only the most probable region for the evolutionary origin of these carrion beetles but is also a hotspot of species diversity. Based on prior study of museum specimens we anticipated finding an additional 1-2 undescribed nicrophorine species.

Fourteen species of the silphid subfamily Silphinae have been recorded from Sichuan Province (Růžička and Schneider 2004). This number is also relatively large – the Palearctic region has a total of 77 species, therefore Sichuan province holds representatives of 18% of this total.

Certain species of the subfamily Cholevinae (family Leiodidae), often called “small carrion beetles” because they range in size from 3-6 mm, frequently co-occur with larger carrion beetles (family Silphidae) on carcasses. A number of undescribed species in the cholevine genus *Catops* were expected or known to occur in Sichuan Province.

The coprophagous, or dung-associated, beetles we targeted included species in the family Geotrupidae and two subfamilies of the family Scarabaeidae: the Scarabaeinae and the Aphodiinae. Numerous species endemic to China are known in these taxa and undescribed species were expected as well.

Methods

We sampled for carrion and dung associated Coleoptera using standard baited traps either sunk into the ground (pitfall) or hung from trees. Baits were typically ca. 200 g rotten fish carcass or human dung. Traps were placed ca. 300 m from each other at each site across an elevational gradient, usually covering about 1000 m in elevation. Effort was made to sample multiple habitat types (grassland, forest, disturbed and virgin, etc.). Each trap line consisted of 20 hanging traps and 10 ground traps. Ground traps are more often disturbed by vertebrate scavengers such as dogs so these were used less often. Hanging traps work very well for silphids and leiodids but less well for dung associated species. These were targeted specifically using ground traps. Rain roofs were placed over the opening of the traps to prevent drowning of beetles. No preservative was used in the traps – the beetles were caught and kept alive so they could be placed alive into 99% ethanol for later DNA extraction. Traps were checked daily, often one hour after sundown because silphids typically fly at sundown. Specimens were collected into 99% ethanol-filled 15 ml vials – one specimen per vial for the silphids (which are large bodied insects) and multiple specimens per vial for small insects such as leiodids and flies. After a required 5-8 specimens for DNA work had been obtained all extra specimens were stored in large groups in 70% ethanol in whirlpak bags. A complete data label was placed in each vial or bag.

Results

Listed below are species of carrion-associated and coprophilous Coleoptera from the three surveyed sites in Sichuan Province, China. Specimens of the family Silphidae were identified by D. S. Sikes using keys in Sikes (2003) and Portevin (1926), those of the family Leiodidae by J. Růžička using Szymczakowski (1964) and Perreau (2000), and those of Geotrupidae and Scarabaeidae by M. Kon and T. Ochi. The literature used to identify these last two families include Boucomont (1902, 1905, 1906, 1911, 1912), Paulian (1945), Balthasar (1963, 1964), Dellacasa (1986, 1988), Dellacasa et al. (2001), and Kral et al. (2001). Specimens are stored in the collections of the determiners although type specimens of new species will be deposited in the Chinese Academy of Sciences, Institute of Zoology, Beijing, China. Counts of specimens are provided although they are, at best, only approximately representative of the abundance or rarity of each species at each site. We also provide what is known of each species' distributions within the Palearctic geographic realm (we provide little information for extra-palaearctic distributional information, thus these listings should not be considered complete for widespread species). Two new province records for Sichuan are indicated. The term n. sp. indicates that the species is new to science. In cases where multiple new species in the same genus were present, as in the genus *Catops*, a numbering system was used (i.e., “n. sp1”). The numbering is consistent for a given taxon throughout this report. The term “sp. undet.” indicates that the species has not yet been definitively identified, and may possibly be undescribed, or simply unidentifiable given the current taxonomic literature.

Included in this list are identifications to genus or species for 672 beetle specimens which represent 42-43 species, of which 10-11 are undescribed (24%). These were distributed among the following families: Silphidae (13-14 species, 1-2 new), Leiodidae (9 species, 7 new), Geotrupidae (6 species, 1 new), Scarabaeidae (14 species, 1 new). Fourteen of the 32 described species (44%) are known only from records in China and are, therefore, possibly endemic to China – five of which are known only from Sichuan Province (16%). Two described species are reported from Sichuan Province for the first time (*Enoplotrupes yunnanus* and *Odontotrupes meyomintang*).

Site (1) Danba County, road S of Donggu town (2-17 km S) along Kui Yong creek valley, 2843-3514 m 30°29'-30°35'N 101°45'-101°47'E. SITE 1 TOTAL: 15-16 species (3-4 undescribed), 339 specimens.

SILPHIDAE: 5-6 species (one potential undescribed species), 262 specimens

NICROPHORINAE:

Nicrophorus n. sp. near *investigator* – 19 (4 in alcohol for DNA work); China: Gansu, Qinghai, Sichuan, and Yunnan Provinces (all unpublished records).

Nicrophorus smefarka Háva, Schneider & Růžička – 12 (9 in alcohol for DNA work); China: Hubei, Shaanxi, and Sichuan Provinces.

Nicrophorus investigator Zetterstedt – 1 in alcohol for DNA work; Holarctic: Europe, n India, (Kashmir), northern and western (mountainous) North America, Korea, Japan, Mongolia, China, Russia: Siberia, Sakhalin, Kuriles, Ussuri reg., Turkey, Uzbekistan, Tajikistan, Kazakhstan, Pakistan, Kyrgyzstan, Afghanistan, Iran, Turkmenistan, Transcaucasia.

SILPHINAE:

Necrodes littoralis (L.) – 21 (5 in alcohol for DNA work); Palaearctic: Europe and Asia (incl. Sichuan)

Oiceoptoma hypocrita (Portevin) – 118 (5 in alcohol for DNA work); Palaearctic: Bhutan, India (Himachal Pradesh, Sikkim, Uttaranchal, Uttar Pradesh), Nepal, China: Shaanxi, Sichuan, Tibet, Yunnan; Oriental region.

Oiceoptoma picescens (Fairmaire) – 78 (5 in alcohol for DNA work); China: Sichuan, Yunnan Provinces.

LEIODIDAE: 4 species (3 undescribed), 59 specimens

CHOLEVINAE:

Catops gr. hilleri n. sp.1 – 7 (undescribed species)

Catops gr. longulus n. sp.1 – 44 (undescribed species)

Catops gr. longulus n. sp.2 – 2 (undescribed species)

Catopodes emeicola Perreau, 1990 – 6; described from Emei Shan mts, unpublished records from further 10 localities in China: Hubei, Shaanxi, Sichuan and Yunnan provinces [J. Růžička, unpubl.].

SCARABAEIDAE: 6 species, 18 specimens

APHODIINAE:

Aphodius (Acrossus) sp. undet.1 – 6 [not yet identified to species]

Aphodius (Acrossus) sp. undet.3 – 1 [not yet identified to species]

Aphodius (Acrossus) sp. undet.4 – 1 [not yet identified to species]

Aphodius (Aphodius) calichromus Balthasar, 1932 – 1; China: Sichuan, Fujian (Fukien)

Aphodius (Colobopterus) erraticus (Linne, 1758) – 1; China, Russia, Whole Europe, Afghanistan, North Africa, North America.

Aphodius (Aphodius) elegans Allibert, 1847 – 8; China, North Vietnam, Korea, Japan

Site (2) Kangding County, Pengta Town, Tongling village road up Zhong Gu Lou gou Valley 2392 - 2915 m, 30°28.518'N-30°29.755'N, 102°17.709'E-102°19.178'E. SITE 2 TOTAL: 19-20 species (2-4 undescribed), 134 specimens.

SILPHIDAE: 8-9 species (1-2 undescribed), 96 specimens

NICROPHORINAE:

Nicrophorus nepalensis Hope – 62 (4 in alcohol for DNA work); Oriental: nPakistan, Himalayas, Indonesia: Java, Flores, China, Laos, Burma, Malaysia, Japan: Ryukyu; Philippines, Taiwan, Thailand, Vietnam

Nicrophorus schawalleri Sikes and Madge (Sikes at al. 2006) – 22 (5 in alcohol for DNA work); Oriental: China: Sichuan, Gansu, Shaanxi Provinces.

Nicrophorus concolor Kraatz – 1 adult in alcohol for DNA work; Palearctic: Japan; Korea; China: Hunan, Sichuan, Yunnan, Guizhou, Zhejiang, Heilongjiang Provinces; Taiwan; nIndia; Nepal; Bhutan; Russia: Ussuri reg.

Nicrophorus n. sp. near *investigator* – 2 in alcohol for DNA work; China: Gansu, Qinghai, Sichuan, and Yunnan Provinces (all unpublished records).

Nicrophorus smefarka Háva, Schneider & Růžička – 2; China: Hubei, Shaanxi, and Sichuan Provinces.

SILPHINAE:

Necrodes littoralis (L.) – 2; Palaearctic: Europe and Asia (incl. Sichuan)

Oiceoptoma hypocrita (Portevin) – 2; Palaearctic: Bhutan, India (Himachal Pradesh, Sikkim, Uttaranchal, Uttar Pradesh), Nepal, China: Shaanxi, Sichuan, Tibet, Yunnan; Oriental region.

Oiceoptoma picescens (Fairmaire) – 2; China: Sichuan, Yunnan Provinces.

Necrophila (Calosilpha) brunnicollis (Kraatz) – 1 adult in alcohol for DNA work; Palaearctic: Bhutan, Russia Far East, Japan, North and South Korea, India (Sikkim), China: Beijing, Fujian, Gansu, Guandong, Guizhou, Guanxi, Hainan, Hubei, Hunan, Jiangxi, Sichuan, Shaanxi, Shanxi, Taiwan, Yunnan, Zhejiang.

GEOTRUPIDAE: 2 species (1 probably undescribed), 3 specimens

Geotrupes corinthius Fairmaire – 1; China: Yunnan, Sichuan Provinces.

Sinogeotrupes n. sp. (probably undescribed) – 2

SCARABAEIDAE: SCARABAEINAE: 9 species (1 undescribed), 35 specimens

ONTICELLINAE:

Liatongus denticornis (Fairmaire) – 2; China: Sichuan, Yunnan Provinces.

ONTHOPHAGINAE:

Caccobius gonoderus (Fairmaire) – 1; China: Sichuan, Yunnan, Guizhou Provinces.

Caccobius boucomonti Balthasar – 1; China: Sichuan Province.

Onthophagus (Strandius) n. sp. (undescribed) – 8

Onthophagus (Strandius) procurvus Balthasar, 1935 – 1; China: Sichuan Province.

APHODIINAE:

Aphodius (Colobopterus) propraetor Balthasar – 1; China, Korea, Far Eastern Russia, Japan.

Aphodius (Acrossus) sp. undet.2 – 3 [not yet identified to species]

Aphodius (Aphodius) elegans Allibert – 15; China, North Vietnam, Korea, Japan.

Aphodius (Aphodius) calichromus Balthasar – 3; China: Sichuan, Fujian (Fukien) Provinces.

Site (3) Yajiang, Valley S of Decha village, 3624-4000m
29.66°N 100.76-100.78°E. SITE 3 TOTAL: 19-20 species (4-5
undescribed, 1 possible new subspecies), 212 specimens.

SILPHIDAE: 7-8 species (1 possibly undescribed), 95 specimens

NICROPHORINAE:

Nicrophorus n. sp. near *investigator* – 23; China: Gansu,
Qinghai, Sichuan, and Yunnan Provinces (all
unpublished records).

Nicrophorus smefarka Háva, Schneider & Růžička – 3; China:
Hubei, Shaanxi, and Sichuan Provinces.

Nicrophorus oberthuri Portevin – 2 in alcohol for DNA work;
Palearctic: China: Yunnan, Shaanxi, Qinghai, Sichuan
Provinces; nBurma.

SILPHINAE:

Oiceoptoma hypocrita (Portevin) – 1; Palearctic: Bhutan,
India (Himachal Pradesh, Sikkim, Uttarakhand, Uttar
Pradesh), Nepal, China: Shaanxi, Sichuan, Tibet,
Yunnan; Oriental region.

Oiceoptoma picescens (Fairmaire) – 13; China: Sichuan,
Yunnan Provinces.

Thanatophilus dentiger (Semenov-Tian-Shanskij) – 50 (5 in
alcohol for DNA work); Palearctic: India (Himachal
Pradesh, Kashmir, Uttarakhand), Nepal, Pakistan,
Tajikistan, China: Qinghai, Sichuan, Tibet, Yunnan.

Thanatophilus rugosus (L.) – 1 in alcohol for DNA work;
Palearctic: Europe and Asia, (incl Sichuan).

Necrophila (Eusilpha) cyaneocincta (Fairmaire) – 2 in alcohol
for DNA work; China: Sichuan Province.

LEIODIDAE: 5 species (4 undescribed), 42 specimens

CHOLEVINAE:

Catops gr. alpinus n. sp1 – 26 (undescribed species)

Catops gr. alpinus n. sp2 – 3 (undescribed species)

Catops gr. hilleri n. sp1 – 11 (undescribed species)

Catops gr. longulus n. sp3 – 1 (undescribed species)

Catops curvipes Perreau – 1 (described from Emei Shan mts,
unpublished records from further three localities in
Sichuan and Yunnan provinces [J. Růžička, unpubl.]

GEOTRUPIDAE: 5 species, (one possible new subspecies), 40
specimens

Geotrupes corinthius Fairmaire – 9; China: Yunnan and
Sichuan Provinces.

Odontotrypes szetshwanus (Nikolajev) – 15; China: Sichuan
Province.

Odontotrypes n. subsp. (possibly a Sichuan subspecies of
O. meyomintang Kral, Maly, Schneider, known from
Yunnan Province; New Record for Sichuan Province) – 3

Phelotrupes (Phelotrupes) davidis (Deyrolle in Deyrolle et
Fairmaire) – 10; China: Sichuan Province.

Enoplotrupes yunnanus Fairmaire – 3; China: Yunnan
Province (New Record for Sichuan Province).

SCARABAEIDAE: SCARABAEINAE: 2 species, 35 specimens

ONTHOPHAGINIAE:

Onthophagus (Onthophagus) inelegans Balthasar – 32; China:
Sichuan Province.

APHODIINAE:

Aphodius (Colobopterus) erraticus (Linne) – 3; China, Russia,
Whole Europe, Afghanistan, North Africa, North
America.

Discussion

General impressions of each site / habitat

The following impressions are limited to those relating to the
sampling of carrion and dung associated insects. The first site,
Danba County, road S of Donggu town (2-17 km S) along Kui
Yong creek valley (2843-3514 m), was high in elevation. This
resulted in the collection of numerous high-elevation leiodids,
and a holarctically distributed species of *Nicrophorus* (Silphidae)
that is typically associated with montane habitats (*N. investigator*).
The habitat diversity was not great and some areas were clearly
disturbed due to logging. More time spent at the lower portion
of the drainage, near Donggu town, below 3000 m would have
probably yielded additional insect species for this site. During our
survey of the first site it rained over 14 hours a day which also
must have depressed the insect activity. Overall, this was the least
productive site (in part due to rain).

The second site, Kangding County, Pengta Town, Tongling
village road up Zhong Gu Lou gou Valley (2392 - 2915 m), was
considerably lower in elevation and was thus warmer. This site
had heavily disturbed habitats – most due to grazing of livestock.
Nonetheless, due no doubt to the lower elevation, this site had
a greater insect diversity. Two of the very widespread species of
Nicrophorus were collected at this site, one in great numbers.
Overall this was a productive site but with more common, lower
elevation species. Surprisingly, no leiodids were found at this site.

The third site, Yajiang County, Valley S of Decha village,
3624-4000m 29.66°N 100.76-100.78°E, was the highest in
elevation of the three sites. A greater variety of habitats were
accessible at this site than the first and there was little to no rain.
This site produced a number of species not found at either of the
first two sites, including some grassland associated species. This
site had what appeared to be virgin forests with lush litter layers.
Overall, this site had the greatest number of rare, higher elevation
species.

Notable species

Of 13 species in two genera of microphorine beetles known from
Sichuan Province, 6-7 species in one genus (*Nicrophorus*) were
found. Three of these species are endemic to China (*N. n. sp.?*,
N. schawalleri Sikes & Madge, *N. smefarka*), two of which are
undescribed (ms in prep and Sikes et al. 2006, respectively).
A fourth species is known only from China and Bhutan (*N.*
oberthuri). The remaining three species are relatively widespread
throughout Asia.

The species *N. smefarka* was an exciting find – it had been
only recently discovered and described in 1999. Preliminary
phylogenetic work indicates it is a basal lineage to the large
radiation of *Nicrophorus* species. Only eight specimens were
known prior to this survey. Over 20 additional specimens were

collected during the RAP survey. This is one of the rarest and most poorly known species of the subfamily.

The two undescribed species, *N. schawalleri* and *N. n. sp.* had been known to be undescribed species based on museum specimens for many years. Both, however, were known only from dried specimens and no DNA material had been obtained to confirm their unique status and phylogenetic relationship to other species of the genus. During this RAP survey enough specimens of both species were obtained to provide ample genetic material for analysis. *Nicrophorus schawalleri* was described in 2006. The species *N. n. sp.* is awaiting additional genetic analysis. Preliminary phylogenetic analyses are indicating it may not be sufficiently distinct from two sister species: *N. encaustus* and *N. investigator* to warrant species status. If not a species, this population might be described as a subspecies.

Early and mid-season species, including two rare “living fossil” species of high priority, were not found (*Ptomascopus zhangla* and *Nicrophorus przewalskii*). Despite the late season of the survey, (late August and early September) a good number of silphids were found. To put these results in perspective, in most regions of the world there are five or fewer species of silphids available for collection at any given time of the year.

Conservation Recommendations

The third site appeared to contain the greatest amount of undisturbed habitat in addition to being the most easily accessible for survey work. The sites yielded the following species counts: Site 1 (Danba), 15-16 with 3-4 new; Site 2 (Kangding), 19-20 with 2-4 new; and Site 3 (Yajiang), 19-20 with 4-5 new. Although the second site was lower in elevation and thus rich in insects it also had fewer rare species and more common species than the other, higher elevation, sites. This is seen in there being fewer new species at Site 2 (which also lacked any species of the family Leiodidae during this survey). In sum, and including the undescribed / newly discovered species, Site 1 had eight species known only from China, three of which were known only from Sichuan Province; Site 2 had 12 species known only from China, four of which were known only from Sichuan Province, and Site 3 had 15 species known only from China, eight of which were known only from Sichuan Province. Site 3 therefore had the greatest counts of species known only from China and Sichuan Province.

At Site 3 a good trap line was set near a grassland south of camp. This grassland appeared to be in the process of being planted for conversion to a conifer plantation / forest. The grassland seemed mature and had a great diversity of flower and insect species in addition to some small mammals. Traps and dung near this grassland produced the majority of the new and/or rare species for this site. We suggest that such habitat not be converted to a monoculture of conifers. Preservation of the virgin forests and mature grasslands at Site 3, given the apparent rarity of such undisturbed habitats in Sites 1 and 2, seems a high priority for maintenance of these insect populations and the vertebrates on which they depend.

Sites 1 and 2 were both more disturbed than Site 3, although the second more than the first. Site 1 seemed more suitable as a protected area than Site 2, given the immediate proximity of the human population at Site 2, but Site 3 seemed the best choice for a conservation focus. However, additional surveys should be done

to replicate these efforts in different seasons (especially during spring and summer).

Necrophilous and coprophilous beetles are excellent indicator species that can be rapidly surveyed to assess both general habitat quality and specifically the health of the vertebrate community (which supplies the carrion and dung for these beetles). The results from this survey indicate that all three sites have a similar and high species richness in these groups but that, in general, the beetle fauna of these regions of Sichuan Province is poorly known (almost one-quarter of sampled species were undescribed). The high endemicity of these beetles at Site 3 corroborated the first author's general impressions that this site was the most biologically rich and interesting of the three.

References

- Balthasar, V. 1963. Monographie der Scarabaeidae und Aphodiidae der palaearktischen und orientalische Region, Praha, 2:628 pp.
- Balthasar, V. 1964. Monographie der Scarabaeidae und Aphodiidae der palaearktischen und orientalischen Region. Praha, 3: 652 pp.
- Berdela G., Lustigman B. & P. Shubeck 1994: List of bacterial flora residing in the mid and hindgut regions of six species of carrion beetles (Coleoptera: Silphidae). Entomological News 105(1): 47-58.
- Bornemissza, G. F. and C. H. Williams. 1970. An effect of dung beetle activity on plant yield. Pedobiologia 10:1-7.
- Boucomont A. 1902. Coleoptera Lamellicornia, fam. Geotrupidae. In Wytsman P. (ed.): Genera Insectum, 7. P. Wytsman, Bruxelles, 20pp.
- Boucomont A. 1905. Etudes sur les Enoplotrupes et Geotrupes d'Asie. Rev. Entomol., 23: 209-252.
- Boucomont, A. 1906. Catalogue Provisoire des Geotrupidae. Cosne, Imprimerie A. Bureau, 44pp.
- Boucomont A. 1911. Contribution a la classification des Geotrupidae. Ann. Soc. Entomol. fr., 79(1910): 333-350.
- Boucomont A. 1912. Scarabaeidae:Taurocerastinae, Geotrupinae. In Junk W. & S. (eds): Coleopterprum Catalogus pars 46: 47pp. W. Junk, Berlin.
- Bryan, R. P. 1976. The effect of the dung beetle, *Onthophagus gazella*, on the ecology of the infective larvae of gastrointestinal nematodes of cattle. Australian Journal of Agricultural Research 27: 567-574.
- Dellacasa, G. 1986. A world-wide revision of *Aphodius* sharing large scutellum (Coleoptera, Scarabaeidae, Aphodiinae). Frustula. Entomologica (N.S.), 7/8: 173-282.
- Dellacasa, M. 1988. Contribution to a world-wide catalogue of Aegialiidae, Aphodiidae, Aulonocnemidae, Termitotrogidae, (Coleoptera, Scarabaeoidea). Mem. Soc. ent. ital., 66: 1-456.
- Dellacasa, G., Bordat, P., and M. Deallacasa. 2001. A revisional essay of world genus-group taxa of Aphodiinae (Coleoptera, Aphodiidae). Mem. Soc. entomol. ital., 79: 1-482.
- DeVault, T.L., O.E. Rhodes, Jr. and J.A. Shivik. 2003. Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. Oikos 102: 225-234.
- Hanski, I. and Y. Cambefort (eds). 1991. Dung Beetle Ecology. Princeton University Press, New Jersey. xiii + 481 pp.

- Janzen, D. H. 1982. Seasonal change in abundance of large nocturnal dung beetles (Scarabaeidae) in Costa Rican deciduous forest and adjacent horse pasture. *Oikos* 41: 274-283.
- Klein, B. C. 1989. Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia. *Ecology*, 70:1715-1725
- Kral D., Maly V., & J. Schneider 2001. Revision of the genera *Odontotrypes* and *Phelotrupes* (Coleoptera: Geotrupidae). *Folia Heyrovskyana*, Suppl., 8: 1-178.
- Paulian R., 1945. Coleopteres Scarabaeides de l'Indochine - Fn. Emp. fr., 3: 1-225. Larose, Paris.
- Peck, S. B. and R. S. Anderson. 1985. Taxonomy, phylogeny and biogeography of the carrion beetles of Latin America (Coleoptera: Silphidae). *Quaestiones Entomologicae* 21: 247-317.
- Perreau, M. 2000. Catalogue des Coleopteres Leiodidae Cholevinae et Platypyllinae. *Mém. Soc. Entomol. Fr.* 4: 1-460.
- Portevin, G. 1926. Les Grands Nécrophages du Globe. Silphini - Necrodini - Necrophorini. *Encyclopédie Entomologique (A)*, Vol. 6, Lechevalier, Paris. 270 pp.
- Putman, R. J. 1978. The role of carrion-frequenting arthropods in the decay process. *Ecological Entomology*, 3:133-139.
- Putman, R. J. 1983. *Carrion and Dung: The Decomposition of Animal Wastes*. Edward Arnold, London.
- Růžička, J. and Schneider, J. 2004. Silphidae pp. 229-237. In Löbl, I. and Smetana, A. (eds.), *Catalogue of Palaearctic Coleoptera vol. 2: Hydrophiloidea - Histeroidea - Staphylinoidea*, pp. 942.
- Sikes, D. S. 1994. Influences of ungulate carcasses on coleopteran communities in Yellowstone National Park. MSc thesis - Montana State University: x + 179.
- Sikes, D. S. 2003. Systematic revision of the subfamily Nicrophorinae (Coleoptera: Silphidae). PhD Dissertation, University of Connecticut.: xxiv + 938 pp.
- Sikes, D. S., R. B. Madge and S. T. Trumbo. 2006. Revision of *Nicrophorus* in part: New species and inferred phylogeny of the *nepalensis* group based on evidence from morphology and mitochondrial DNA (Coleoptera: Silphidae: Nicrophorinae). *Invertebrate Systematics*. 20: 305-365.
- Szymczakowski, W. 1964. Analyse systematique et zoogeographie des Catopidae (Coleoptera) de la region orientale. *Acta Zool. Cracov.* 9: 55-283.